

A PREDATOR-PREY SYSTEM WITH SEASONAL REPRODUCTION:
THEORETICAL AND STATISTICAL DEVELOPMENTS

A Dissertation

by

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ABSTRACT

Predator-prey interaction (PPI) is important in both ecological theory and application. Various theoretical and empirical approaches have been proposed to develop mathematical and statistical tools for studying PPI. The aim of this dissertation is to expand our understanding along these two lines.

Using mathematical models, I compare the dynamics of predator-prey models with one specific type of interaction, where both predator and prey exhibit seasonal reproduction and predation is continuous. I show that the use of a continuous-time predator-prey model with an instantaneous approximation of seasonal reproduction can produce unstable dynamics, whereas the use of a discrete-time model, which incorporates seasonal reproduction, always produces locally stable equilibria. Finally, with stage-structured predator-prey models, I demonstrate how demographic parameters affect asymptotic dynamics.

I then explore statistical methods to infer the type of PPI from non-stationary time series. Traditional approaches assume that each population in a community is itself regulated, i.e., each time series is stationary. However, complex community structure and a lack of regulation in an individual population alone can result in inappropriate inferences based on traditional approaches. I introduce a statistical framework to analyze non-stationary time series that could be collectively regulated. I also demonstrate the method with time series of selected shrimp and fish populations in the Gulf of Mexico.

Finally, I compare the performance of four methods to determine the type of PPI from short and noisy time series. The data-generating model includes nonlinear predation, compensatory density-dependence, and both process and observation errors. To represent our uncertainty about the true form of species interaction, none of the statistical models incorporate all these factors. I show that three methods that account for autocorrelation have better performance in terms of type-I error rates. Among these three methods, only one method produces consistent type-I error rates at all three commonly used significant levels, but it has low power. This method provides a conservative approach to identify PPI.

In conclusion, my research identified challenging aspects for research aimed at understanding the dynamical significance of PPI, and explored the potential for mathematical modeling integrated with analysis of empirical time series data to advance knowledge.

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TABLE OF CONTENTS

	Page
ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS	v
LIST OF FIGURES.....	vii
LIST OF TABLES	ix
CHAPTER I INTRODUCTION AND LITERATURE REVIEW	1
Predator-prey dynamics models	4
Statistical methods.....	5
CHAPTER II DYNAMICS OF A PREDATOR-PREY INTERACTION WITH SEASONAL REPRODUCTION AND CONTINUOUS PREDATION	8
Introduction	8
Methods.....	13
Models	13
Analysis	19
Results	20
Unstructured model	20
Migration	26
Stage structured predator and prey	28
Discussion and conclusion	39
CHAPTER III FINDING REGULATION AMONG SEEMINGLY UNREGULATED POPULATIONS.....	45
Introduction	45
Materials and methods	50
Overview of the proposed method	50
A multi-species linear population model.....	53
Significance of a focal population in the long-run component of the assemblage dynamics.....	56
Significance of bottom-up and top-down effects in the long-run component.....	57

Data	58
CPUE standardization of shrimp and fish populations in the Gulf of Mexico from SEAMAP shrimp/ground fish program	59
Results	61
Discussion	64
 CHAPTER IV A COMPARISON OF STATISTICAL METHODS FOR DETECTING SPECIES INTERACTIONS FROM SHORT, NOISY TIME SERIES DATA	 68
Introduction	68
Methods	70
Data generating model	70
Simple linear regression (SLR) procedure	72
Correlation coefficient (CC) procedure	74
Multivariate autoregressive (MAR) procedure	75
Integration-cointegration robust (ICR) procedure	76
Performance measures	77
A case study from the Gulf of Mexico	78
Results and discussion	79
Type-I error rate	79
Type-II error rate (power analysis)	81
Application to real data	82
Conclusions	85
 CHAPTER V CONCLUSION	 87
 REFERENCES	 88
 APPENDIX A	 104
 APPENDIX B	 109
 APPENDIX C	 112
 APPENDIX D	 120

LIST OF FIGURES

	Page
Figure 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 through E).....	11
Figure 2 Life cycle graph of the unstructured discrete-time predator-prey system.	12
Figure 3 Isocline of the bottom-up case of the unstructured predator-prey model.	21
Figure 4 Isocline of the top-down case of the unstructured predator-prey model.	22
Figure 5 Isocline configurations for unstructured predator-prey model with migration..	27
Figure 6 Predator and prey life cycle graphs and their interactions.....	31
Figure 7 Predator and prey life cycle graphs and their interactions.....	32
Figure 8 Bottom-up, top-down and non-persistence zones based on prey life history parameters from Eq. 2.19 with low prey adult background survival.....	34
Figure 9 Bottom-up, top-down and non-persistence zone based on prey life history parameters from Eq. 2.19 with medium prey adult background survival.	35
Figure 10 Bottom-up, top-down and non-persistence zone based on prey life history parameters from Eq. 2.19 with high prey adult background survival.	36
Figure 11 Asymptotic abundances of a predator-prey system, where adult predator's adult prey is explicitly modeled from Eq. 2.19.	38
Figure 12 Diagram showing an example of three-species interactions.....	49
Figure 13 Steps in analyzing multivariate time series data.	52
Figure 14 Standardized CPUE time series of brown shrimp (a), Atlantic croaker (b), silver seatrout (c) and sand seatrout (d) from statistical zone 15 in the Gulf of Mexico from 1986 to 2011	60
Figure 15 Simulated time series of a bottom-up controlled predator-prey model.	73
Figure 16 Brown shrimp and largehead hairtail CPUE (logarithmic scale) time series. .	84

Figure 17 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the MAR method on the data with the lowest noise level.....	125
Figure 18 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the ICR method on the data with the lowest noise level.....	126
Figure 19 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the MAR method on the data with the lowest noise level	127
Figure 20 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the ICR method on the data with the lowest noise level...	128
Figure 21 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the MAR method on the data with the lowest noise level.....	129
Figure 22 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the ICR method on the data with the lowest noise level.....	130
Figure 23 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the MAR method on the data with the medium noise level.....	131
Figure 24 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the ICR method on the data with the medium noise level	132
Figure 25 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the MAR method on the data with the medium noise level.....	133
Figure 26 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the ICR method on the data with the medium noise level.....	134
Figure 27 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the MAR method on the data with the medium noise level.....	135
Figure 28 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the ICR method on the data with the medium noise level.....	136

LIST OF TABLES

	Page
Table 1 Results for augmented Dickey-Fuller tests on variables from statistical zone 15	62
Table 2 Johansen cointegration test of the rank of matrix B from the intercept restricted model from statistical zone 15 with critical values at the 5% and the 1% level	62
Table 3 Maximum likelihood estimates of α and β in Model $H_1^*(2)$ of statistical zone 15	62
Table 4 Number of Equilibrium relationships (E.R.s) and p -values of the test of the significance of brown shrimp in community assemblage dynamics	63
Table 5 Tests of bottom-up and top-down effects in zones 16 to 18	63
Table 6 Estimated percentages of correctly accepting the null hypothesis of no interaction using the four different methods at a nominal 5% significance level and the associated signal to noise levels (SNR).....	80
Table 7 Estimated percentages of correctly accepting the alternative hypothesis of interaction using the four different methods at a nominal 5% significance level and the associated signal to noise levels (SNR).....	82
Table 8 Results of non-stationary and stationary tests on population densities in level and first differenced time series.....	84
Table 9 Small sample properties of the tests based on simulations of a predator-prey model	115
Table 10 Estimated percentages of correctly accepting the null hypothesis of no interaction using the four different methods at a nominal 10% significance level and the associated signal to noise levels (SNR).....	123
Table 11 Estimated percentages of correctly accepting the alternative hypothesis of interaction using the four different methods at a nominal 10% significance level and the associated signal to noise levels (SNR).....	123
Table 12 Estimated percentages of correctly accepting the null hypothesis of no interaction using the four different methods at a nominal 1% significance level and the associated signal to noise levels (SNR).....	124

Table 13 Estimated percentages of correctly accepting the alternative hypothesis of interaction using the four different methods at a nominal 1% significance level and the associated signal to noise levels (SNR).....124

CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Predator-prey interactions, e.g. top-down and bottom-up processes (later abbreviated as TD and BU, respectively), are important in both ecological theory and application (Hairston et al. 1960, Paine 1980, Strong 1986, Hunter and Price 1992, Mutshinda et al. 2009). The modern interpretation of bottom-up control dates back to the concepts of biomass pyramids in ecology (Elton 1927) and the limitation of primary production on the food chain length (Lindeman 1942). It was thought to be the primary means of regulation in community dynamics, until Hairston et al. (1960)'s famous “green world” hypothesis, which proposed that ecosystems are maintained in a green state dominated by living plant biomass through the top-down control of herbivores by their predators. By the late 20th century, ecologists reached a consensus that both TD and BU processes play important roles in the regulation of community dynamics (Rosenzweig 1973, Oksanen et al. 1981). On the practical side, knowing how natural populations are regulated through trophic interactions could provide us effective means in the biological control of pests and management of fisheries (Hawkins et al. 1999, Müller and Brodeur 2002, Worm and Myers 2003, Christensen and Walters 2004, Frederiksen et al. 2007, Mcowen et al. 2014). Various approaches have been proposed to study TD and BU processes in community dynamics. Some approaches have gained wide popularity among ecologists despite having some widely recognized problems. The aim of this dissertation is to improve mathematical and statistical methods for studying TD and BU processes. In

this chapter, I review some of the approaches currently used in ecology to studying TD and BU processes.

The idea of TD and BU processes refers to the influence of one trophic level to food web structure and dynamics (Moore et al. 1970). This general definition does not come with any associated mathematical or statistical method to identify these processes. As a result, researchers often invoke TD and BU processes to explain particular patterns in comparative and experimental data. These definitions can be categorized into two main types, those based upon population rates, e.g. birth and death rates, and those based upon population abundances. When population rates are affected by either a resource or consumer population, then they are said to be under bottom-up control or top-down control (Rosemond et al. 1993, Gotelli 1995, Sinclair and Krebs 2002). Some studies focus on specific parts of the life cycle when examining how population rates and population growth are affected by other populations. Unfortunately, such data are not available for most natural populations. Instead, we often have large amounts of time series data for population abundance or density. Consequently, many researchers have been motivated to apply methods based on population abundance time series data, with correlative methods being the most common approach (Pyper and Peterman 1998, Worm and Myers 2003, Mcowen et al. 2014). This method owes its continuing popularity to its minimum data requirement and ease of implementation despite some major drawbacks pointed out in recent publications (Sugihara et al. 2012, Zhou et al. 2013). A number of new methods are available that improve upon the correlation coefficient approach. These include the Granger causality based spectral method (Granger 1969, Detto et al. 2012), the

convergent-cross-mapping method (Sugihara et al. 2012), the multivariate autoregressive method (Hampton et al. 2013) and the cointegration method (Johansen and Juselius 1990a). Each of these methods has specific assumptions about underlying dynamics. For example, the cross-mapping method assumes complex nonlinear dynamics and the cointegration method assumes non-stationarity. Accordingly, these methods are process specific, and their applicability often depends on the nature of the underlying processes.

Parallel to the above mentioned statistical research, there is another direction that takes a mathematical modeling approach to the community regulation problem. In this line of research, different types of predator-prey models and community models are built to investigate potential dynamics that arise from putative processes (Wang and Chen 1997, Gourley and Kuang 2004, Kar and Jana 2012). The interaction between predator and prey populations is usually interactive, which means that the prey population is influenced by the predator population and *vice versa*. For example, in the Lotka-Volterra predator-prey model, the predator population reduces the survival rate of the prey through the Hollings type-I functional response, and the prey population increases the reproductive and survival rate of the predator through the numerical response of the same type. This tight link, the presence of both functional response and numerical response, often produces interesting dynamics. With the absence of either response, the model becomes a top-down or bottom-up sub-model. The former sub-model is a predator-prey model stripped of the numerical response, and the latter sub-model is a predator-prey model stripped of the functional response. In addition, life history differences are not emphasized enough in theoretical predator-prey models.

The empiricists' statistical analysis approach and the theoreticians' mathematical modeling approach are complementary to each other. They both try to provide insights into the same ecological phenomenon. Empirical studies tend to focus on specific life history processes because it gives better resolution of where and how population regulation works (Murdoch 1994), and this information is ecologically interesting and also useful in natural resource management. Theoreticians, in contrast, tend to focus on the general properties of the system. The objectives of this dissertation are to improve predator-prey modelling by incorporating life history differences and to develop statistical methods to infer top-down and bottom-up interactions from multivariate population time series. In the following sections, I provide a brief overview of existing mathematical and statistical predator-prey models.

Predator-prey dynamics models

The distinguishing feature of a predator-prey model from other population dynamic models, e.g. competition and logistic growth model, is the functional response term, which defines predator foraging efficiency as a function of prey and/or predator population abundance. Earlier models with the mass-action type functional response make counterintuitive predictions; e.g. the paradox of enrichment (Hairston et al. 1960), whereby, with an increase of the prey carrying capacity, only the predator abundance increases and the prey abundance holds constant; and the paradox of biological control (Luck 1990, Arditi and Berryman 1991), whereby the prey abundance cannot be maintained at a low level without large scale fluctuations. Many field observations contradict these model predictions (Hagen and Franz 1973, DeBach and Rosen 1991).

Later developments introduce prey saturation, prey switching (Real 1977, Akre and Johnson 1979) and ratio-dependence (Arditi and Ginzburg 1989) into the form of functional response, and these models do not yield the aforementioned paradoxes.

Among all types of functional responses, two particular types, namely the prey-dependent functional response and ratio-dependent functional response, generated the most debate and controversy (Abrams 1994, Akçakaya et al. 1995, Abrams and Ginzburg 2000). Examples of prey-dependent functional response are the previously mentioned Hollings type-I through III (Holling 1965) and Rosenzweig and MacArthur (1963) models. In a ratio-dependent functional response, the predatory mortality depends on the predator-prey ratio instead. The first ratio-dependent functional response originated from work on a coastal system (Arditi and Ginzburg 1989). It provides a simple representation of the fast (behavioral) time scale predation process on a slow (population dynamical) time scale (Arditi and Ginzburg 1989, Berryman 1992). View points of either model remain divergent (Arditi and Ginzburg 2012, Abrams 2014). In Chapter 2, I use a ratio-dependent functional response to link the dynamics on two different time scales, and analyze the population dynamic effects of life history properties.

Statistical methods

Attempts to elucidate TD and BU controls commonly employ the correlation analysis. A lag-zero cross-correlation between two time series data (e.g. count of individuals, catch-per-unit-effort and density estimates) is used to identify two types of controls. A positive correlation between predator and prey time series suggests bottom-up control, while a negative correlation between those two time series suggests top-down

control. This method only works for communities with simple dynamics, such as a mesocosm community with a simple structure. Furthermore, the biological mechanisms behind such associations often cannot be identified and chaotic dynamics or non-stationarity may introduce spurious correlation that prevents correctly identifying the processes (Sugihara et al. 2012).

Most ecological time series data may be non-stationary (Niwa 2007). Adjustment for autocorrelation is often recommended, but it is not clear whether such an adjustment is sufficient on short time series. In Chapter 3, I show that non-trophic interactions may also weaken and even reverse the correlation relationship between two populations, and I present an alternative method to identify species interactions from non-stationary time series data.

For stochastic processes, the concepts of TD and BU processes can be interpreted based on Granger causality (Detto et al. 2012). Both processes are unidirectional with respect to cause and effect. In Granger's sense, if one ecological variable is causing the changes in the other variable, the inclusion of that variable will improve the prediction of the other variable. This concept is applicable to both linear and nonlinear stochastic dynamics. The concept of Granger causality can be incorporated into existing statistical models, e.g. multivariate autoregressive models (Hampton et al. 2013) and spectral domain models (Detto et al. 2012). The statistical methods proposed in this dissertation are based on this concept.

When we have complex community dynamics, e.g. chaos, the attractor cannot be reasonably approximated by a simple geometric structure, e.g. lines and planes, and in

such cases the method of convergent-cross-mapping (Sugihara et al. 2012) can be used. This method reconstructs the attractor manifold of a dynamic system from a single observation variable of the system based on Takens' embedding theorem (Takens 1981). The interaction between two populations can then be inferred from the predictability of the time series based on the reconstructed attractor manifolds. This method has been used to demonstrate the association between sardines and anchovies landings in California is due to shared climate forcing and not species interactions (Sugihara et al. 2012). However, strong nonlinear dynamics, such as chaos, may be rare in natural systems according to Mueller and Joshi (2000), and I focus my attention to non-chaotic systems.

One of the problems with these methods is that they apply to a specific set of dynamic systems, and the degree of correspondence of natural systems to these dynamic systems usually is unclear. For example, both the correlation coefficient and multivariate autoregressive methods require the dynamic system to be stationary, while the cointegration method requires some of the time series to be non-stationary. Although stationary and non-stationary time series have different long-term behaviors and many statistical tests are available for testing non-stationary data, it is still difficult to arrive at a definite conclusion based on data collected over short time intervals. Moreover, assumptions of density-dependence usually are untested. In Chapter 4, I generate data using the predator-prey model developed in Chapter 2, compare the performance of these statistical methods on short and noisy time series data, and give recommendations about the uses for these methods.

CHAPTER II

DYNAMICS OF A PREDATOR-PREY INTERACTION WITH SEASONAL REPRODUCTION AND CONTINUOUS PREDATION¹

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, Haderler 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 “impulse differential equations,” also exists. These models use differential equations to describe

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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 advantage of the rich analytical tools available for ODE or difference equation models.

In this chapter, I investigate the effect of population structures on predator-prey dynamics. More specifically, I 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 et al. 2009), and the piscivorous fish system in coral reefs (Connell 1997, 1998). Recent studies have emphasized the importance of 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 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 (Frederiksen et al. 2007, Graham et al. 2007). The dynamics of those stage-structured populations are often studied

within the framework of matrix population models (Lima and Paez 1997, Jarry et al. 1998, Fujiwara and Caswell 2001, Wilson 2003, Zabel et al. 2006, Crozier et al. 2008, Perry 2010). 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 the predator-prey systems (Figure 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 Figure 1). Note that natural populations are almost always structured. I compared 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

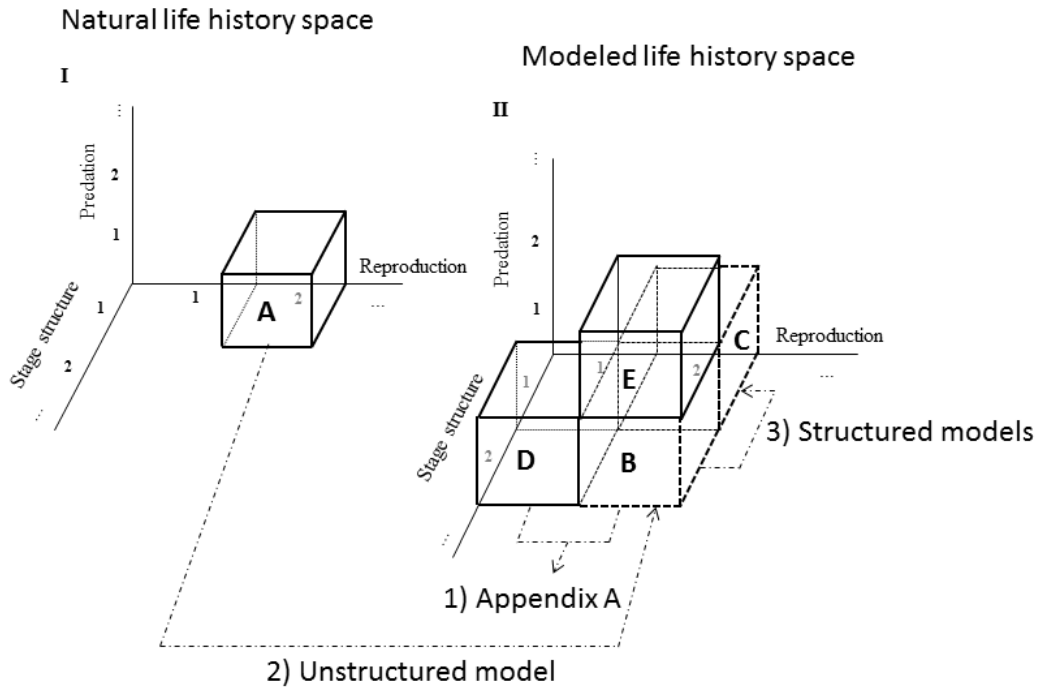


Figure 1 Alternative methods of mapping the life history state space of a predator-prey system in which both predator and prey exhibit seasonal reproduction and predation is continuous (sector A) into modeled life history state space (sectors B through E). Here, state space is defined by three categorical variables: reproduction (1 = continuous, 2 = discrete), predation (1 = continuous, 2 = discrete), and population stage structure (1= structured, 2 = non-structured). See *Introduction* for details.

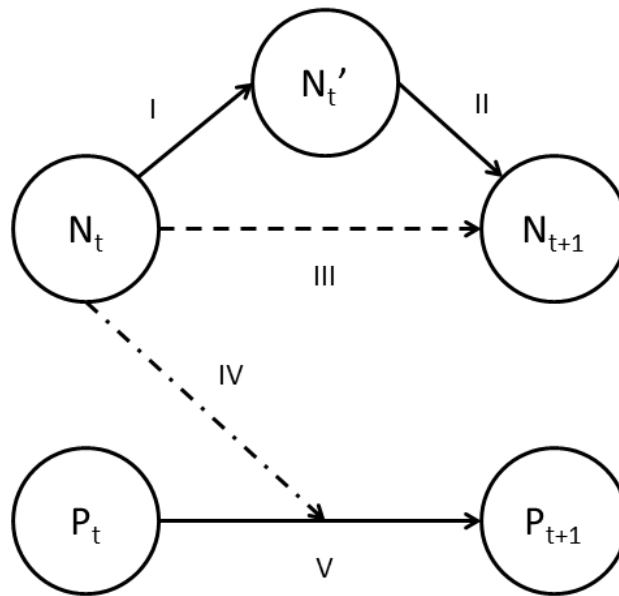


Figure 2 Life cycle graph of the unstructured discrete-time predator-prey system. Circles represent populations, N for prey and P for predator, at the time denoted by the subscript. Arrows represent ecological processes that affect the size of the population between steps: I, survival from predation and other natural causes; II, recruitment of prey to the next generation; III, the overall effect of survival and recruitment of prey population from time t to $t+1$; IV, trophic interaction between prey and predator population; V, the turnover rate of predators over one time step.

process in Appendix A. This is to highlight the potential problems associated with the timescale approximation process. Then, I develop an unstructured model (B) from a natural predator-prey system (A) (Getz, 1984). Later, I incorporate stage structure (C) into the previous unstructured model and compare their dynamics. Another modeling sector

(E) (Neubert and Kot 1992, Jing and Yang 2006, Liu and Xiao 2007), which are known to be able to exhibit complex dynamics, is of mathematical interest, but it 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 *Discussion*.

Methods

Models

I develop three models beginning with one in which both predator and prey populations are unstructured (sector B in Figure 1). Next, I introduce spatial structure to the predator population. In this model, a predator can move from one location to the other unidirectionally. I envision that this type of system can be useful in investigating the possibility of biological control of pests using their predators. Finally, I 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), I describe the development of unstructured and structured predator-prey models.

Unstructured model

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

$$N_{t+1} = F[G(N_t, P_t)]N_t, \quad (2.1)$$

$$P_{t+1} = H(N_t, P_t)P_t, \quad (2.2)$$

where N_t is prey abundance at time t , P_t is predator abundance at time t , $G(\cdot)$ is the annual rate of survival of prey from predation and other causes, $F(\cdot)$ is the annual rate of recruitment of prey into the next generation, and $H(\cdot)$ is the annual rate of recruitment of predators into the next generation. Both populations are transitioned over a one-year interval from immediately before the hunting season to the end of the recruitment events (Figure 2). Eq. (2.1 - 2.2) can be conveniently written as

$$\mathbf{Y}_{t+1} = \mathbf{A}_t \mathbf{Y}_t, \quad (2.3)$$

where the transition matrix \mathbf{A}_t is

$$\mathbf{A}_t = \begin{bmatrix} F[G(N_t, P_t)] & 0 \\ 0 & H(N_t, P_t) \end{bmatrix},$$

and vector \mathbf{Y}_t has two components, N_t and P_t .

I used a Holling type-II ratio-dependent functional response (Getz 1984, Arditi and Ginzburg 1989) to represent the mortality rate of prey from predation. For organisms with discrete reproduction and continuous predation, reproductive rate and predation rate can be considered separately (Abrams 1994), and population dynamics between two consecutive recruitment events are similar to controlled predator-prey experiments with no prey replenishment, e.g. killed prey individuals are not replaced with new prey individuals during the course of the experiment. Under this “no-prey-replenishment” condition, the Holling type-II ratio-dependent functional response approximates the number of prey killed at the end of a hunting season (Royama 1971). Under the same

condition, Okuyama and Ruyle (2011) also analytically derived functions to be used for the functional response. But those functions are generally complicated in form, and it is not practical to use them for further analysis. On the other hand, Holling type-II ratio-dependent functional response is qualitatively similar to and simpler in form than the derived functions.

The original Hollings type-II ratio-dependent functional response (Arditi and Ginzburg 1989) is given by

$$W = \frac{\alpha NP}{\beta P + N}, \quad (2.4)$$

where W is the number of prey consumed by predators during the hunting season, β describes how fast the predation curve reaches the asymptote as the ratio of prey to predator increases, and $\frac{\alpha}{\beta}$ determines the location of the asymptote, which is the maximum proportion of the prey population consumable by predators in one foraging season. From Eq. (2.4), the per capita rate of prey mortality (z) due to predation during the hunting season is

$$z = \frac{W}{N} = \frac{\alpha P}{\beta P + N}. \quad (2.5)$$

As the ratio of prey and predator density approaches 0, z tends to $\frac{\alpha}{\beta}$, which I denote by

r (i.e., $r = \frac{\alpha}{\beta}$). It is the maximum annual exploitation rate of prey by predators.

In addition to mortality due to predation, there are also background mortalities from other sources, such as diseases, starvation, and predation by other predators. By taking into account these other sources of mortality, the annual survival rate for prey (s_1) is

$$s_1 = s_0(1 - z), \quad (2.6)$$

where s_0 is the background survival rate of prey.

The predators' reproductive rate (f_2) is defined as

$$f_2 = \frac{c\alpha N}{\beta P + N}, \quad (2.7)$$

where the product of c and α is the maximum biological reproductive output for the predator population, and c measures the efficiency of adult predators to convert consumed prey into new predators. In other words, the predator's reproductive rate is assumed to be proportional to the total number of prey consumed in the same season up to the reproductive event, which occurs at the end of the season. This reproductive rate (f_2) can be viewed as the Beverton-Holt density-dependent process with a maximum reproductive output ($c\alpha$) and a carrying capacity for the predator population ($\frac{c\alpha - 1}{\beta} N$) when N is constant. Therefore, the carrying capacity is proportional to prey abundance and adjusted by predator's reproductive rate and the exploitation rate of prey.

Prey population, from Eq. (2.5 - 2.6), abundance (N_{t+}) immediately after all mortalities, but before the recruitment of the following generation of prey, is

$$N_{t+} = s_o \left(1 - \frac{\alpha P_t}{\beta P_t + N_t}\right) N_t . \quad (2.8)$$

Compensatory density-dependence was then added to the recruitment process to create a finite carrying capacity for the prey population. The recruitment process of prey is given as

$$N_{t+1} = \frac{a}{1 + bN_{t+}} N_{t+} , \quad (2.9)$$

where a represents the maximum per capita recruitment rate, and the asymptotic level of recruitment for prey is determined through relationship $b = (a - 1) / K_0$, where K_0 is the environmental carrying capacity for the recruitment. With no predators, this model becomes a single population, Verhulst logistic model for the prey population.

It should be noted that the discrete-time model considered here, Eq. (2.8 - 2.9), is different from the model analyzed, Eq. (A.1-2) in Appendix A. Although both include the same ratio-dependent function, the equations here are used in discrete-time model, and the equations in Appendix A are used in a continuous-time model. The ratio-dependent function in the model was derived from modeling the life cycle processes of a natural system, whereas the model in Appendix A was derived by erroneously incorporating a discrete-time function into a continuous-time model.

For the predator population, from Eq. (2.7), predator abundance at time $t+1$ is given as

$$P_{t+1} = \frac{c\alpha N_t}{\beta P_t + N_t} P_t . \quad (2.10)$$

Stage-structured model

In this section, juvenile-adult stage structure is added to both predator and prey in the model. The transition matrix in Eq. (2.3) is now

$$\mathbf{A} = \begin{bmatrix} \mathbf{M}_1 & 0 \\ 0 & \mathbf{M}_2 \end{bmatrix}, \quad (2.11)$$

where each block diagonal matrix is

$$\mathbf{M}_i = \begin{bmatrix} s_i(1-m_i) & f_i \\ s_i m_i & p_i \end{bmatrix}, \quad (2.12)$$

where s_i is the annual survival rate for juveniles, m_i is the maturation rate, f_i is the per capita fertility rate for adults, which is the number of offspring per adult surviving at least one time step, and p_i is the survival rate for adults. Subscript i denotes population with 1 for prey and 2 for predators. In particular, s_1 and f_2 are defined in Eq. (2.6 - 2.7) when adult predators feed on juvenile prey. Matrix 2.11 is termed a community matrix herein, and it transitions a state vector

$$\mathbf{Y}_t = \begin{bmatrix} N_{J,t} & N_{A,t} & P_{J,t} & P_{A,t} \end{bmatrix}^T \quad (2.13)$$

where subscript J denotes juvenile stage and A adult stage. The community matrix can accommodate a vast range of life history strategies of both prey and predator by changing the four life history parameters defined in Eq. (2.12) (Neubert and Caswell 2000). For example, as m_i approaches unity from zero, individuals tend to mature earlier. Similarly, as p_i approaches unity, individuals reproduce repeatedly (iteroparity), but as p_i

approaches zero, individuals reproduce only a few times or only once (semelparity). Furthermore, one can change the distribution of survivorship from birth to reproduction by changing m_i and s_i , and also can alter the life expectancies by changing f_i , s_i , and p_i (Fujiwara et al. 2011).

It is assumed that adult predators can prey upon either juvenile prey or the adult prey in the structured model. When adult predators feed on adult prey, p_1 is the function of predator density. It is assumed that the maturation of prey changes susceptibility to predation. Many organisms change their behavior or spatial distribution dramatically upon sexual maturation, which could change their susceptibility to predators. For others, in which changes in predation risks do not correspond with sexual maturation, the model can be further generalized by dividing the prey population into more stages (e.g. pre-juvenile, post-juvenile, pre-adult and post-adult stages).

Analysis

Equilibrium points are determined by the isocline method for discrete-time systems (Fujiwara et al. 2011). When one of the populations reaches its equilibrium, its state variable (e.g. prey abundance) at time t and time $t + 1$ remains the same. Substituting the equilibrium value into the difference equation, I obtain the isocline for that population (e.g. prey isocline), which is also called the zero-growth curve where the rate of change for prey is zero. I also obtain the isocline for the other population (e.g. the predator isocline) and plot it on the same graph with the previous isocline. The intersections of these two isoclines are the equilibrium points for the two-population model.

Local stability of the equilibria is determined by the dominant eigenvalue of the linearized model at those equilibria (Caswell 2000). Unfortunately, although it is simple to find the linearized population matrix, it is not trivial to obtain an analytical expression of its dominant eigenvalue unless one or both of the populations are at zero. Here, dominant eigenvalues are calculated numerically. First, demographic parameters were randomly generated within biological limits, then the equilibrium point was numerically obtained by solving the model iteratively from an arbitrary positive initial condition until the difference between two consecutive solutions were smaller than a preset threshold ($\Delta \leq 10^{-20}$), and then the dominant eigenvalue of the matrix linearized around the equilibrium point was calculated. The magnitude of the dominant eigenvalue determines whether the equilibrium point is locally stable (less than one) or not (larger than one); and the imaginary part determines if solutions approach monotonically (when the imaginary part is zero) or in a spiral (when the imaginary part is nonzero). This procedure was repeated for 10^4 times to cover a wide parameter space.

Results

Unstructured model

With a ratio-dependent type-II functional response and a Beverton-Holt stock recruitment relationship for the prey population (Fig. 2), the predator isocline was derived from Eq. (2.10):

$$P^* = \frac{c\alpha - 1}{\beta} N^* , \tag{2.14}$$

and the prey isocline was derived from Eq. (2.8-2.10):

$$P^* = \frac{N^*(-bs_oN^* + as_o - 1)}{bs_o(\beta - \alpha)N^* + \beta - as_o(\beta - \alpha)} \quad (2.15)$$

The prey isocline (Figure 3-4) intercepts the horizontal axis at $N = 0$ and $N = K$,

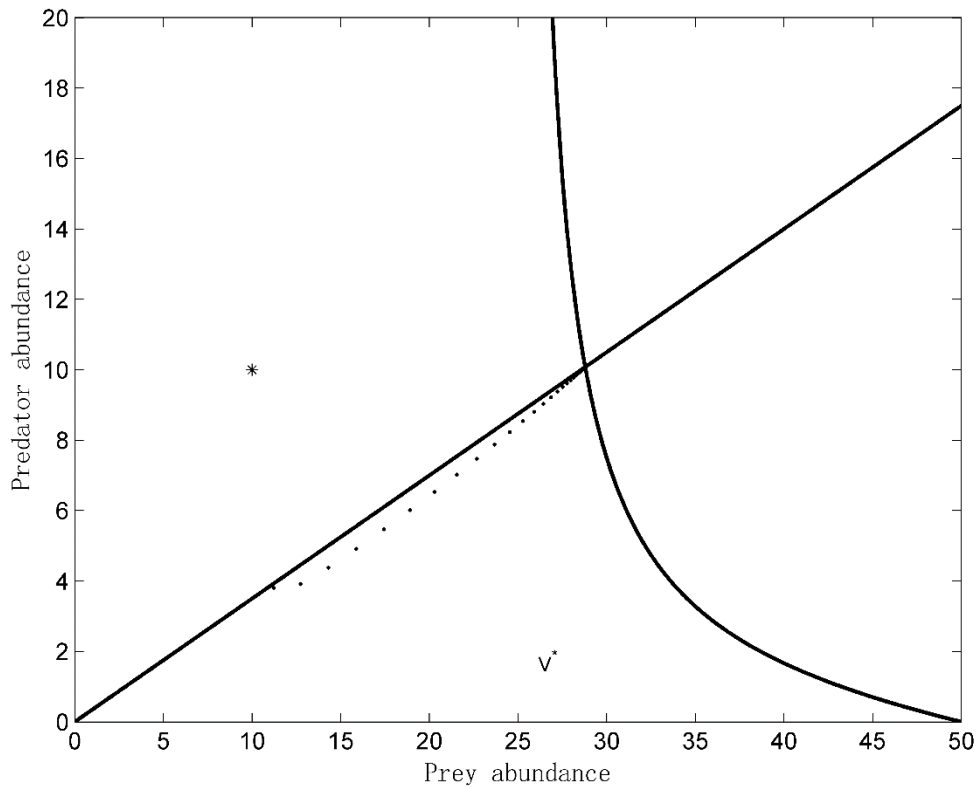


Figure 3 Isocline of the bottom-up case of the unstructured predator-prey model. The predator isocline is a slanted line. The predator-prey dynamics falls within this case when the predator’s annual rate of utilization “ r ” is smaller than the threshold set by the demographic parameters of prey population. A typical trajectory is represented; asterisk represents the initial point and dots the trajectory.

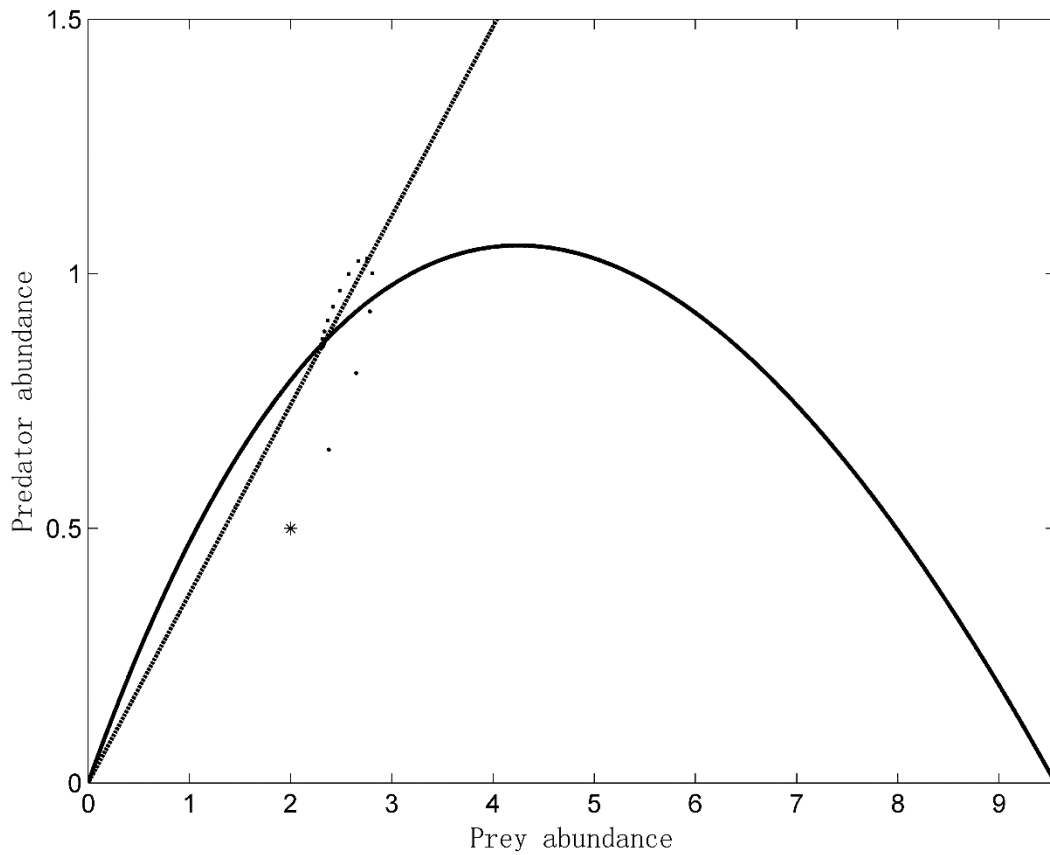


Figure 4 Isocline of the top-down case of the unstructured predator-prey model. The predator isocline is a slanted line, and the prey isocline is humped. The predator-prey dynamics falls within this case when the predator’s annual rate of utilization “ r ” is larger than the threshold set by the demographic parameters of prey population. A typical trajectory is plotted; asterisk represents the initial point and dots the trajectory.

where

$$K = \frac{s_0 a - 1}{s_0 (a - 1)} K_0, \quad (2.16)$$

and it has a pole at $N = x$, where

$$x = \frac{s_0 a - \beta / (\beta - \alpha)}{s_0 (a - 1)} K_0.$$

The location of the pole x is to the left of the intercept K , because $\frac{\alpha}{\beta}$ is less than one (Eq. 2.5, $r = \frac{\alpha}{\beta}$). Based on the dominant eigenvalues of the linearized matrices around equilibrium points, calculated over a wide range of parameters, interior equilibria were determined to be always stable. Therefore, the existence of the interior equilibrium implies the system is locally attracted to this equilibrium.

Prey density at K (Eq. 2.16) is the environmental carrying capacity for prey without the presence of predators. It is a function of the population parameters of prey, and can be seen as a fraction of the asymptotic level of prey recruitment, K_0 , with post-recruitment mortality. It can be shown that the sign of x determines the shape of the prey isocline. When the predator's maximum exploitation rate r is smaller than $\frac{s_0 a - 1}{s_0 a}$, which is a function of the prey parameters, x is positive, and the prey isocline is L-shaped (Figure 3). Under this condition, the predator has a limited ability to suppress the prey population. Hereafter, I call this case a “bottom-up” process [i.e., “limited predation” by

Arditi and Ginzburg (1989)]. When r is greater than the threshold value, x is negative and the prey isocline is humped shaped (Figure 4). I call this case a “top-down” process. In addition, when K is non-positive, the prey population cannot persist by itself, and I call this case “non-persistence”.

The shape of the prey isocline determines the location of the equilibrium point. Because an interior equilibrium point is always stable, the shape also determines the types of asymptotic states of the system. Generally, for closed predator-prey systems, there are three possible asymptotic states: 1) coexistence state: survival of both prey and predator; 2) no predator state: extinction of predator and survival of prey; 3) double-extinction state: extinction of both prey and predator. In the top-down case, the system is capable of showing all three of these asymptotic states, whereas in the bottom-up case the system cannot show the double-extinction state because of the limited ability of the predator to suppress prey population.

The coexistence state in the top-down case can be found by analyzing the slope of both predator and prey isoclines. The maximum slope of the prey isocline,

$$P' \Big|_{N=0} = \frac{as_o - 1}{\beta - as_o(\beta - \alpha)} \quad (\text{Eq. 2.15}),$$

occurs at the origin. It is obtained by taking the first derivative of the prey isocline with respect to prey density evaluated at $N = 0$. If I further assume that the prey population is capable of sustaining itself without the presence of the predator, the environmental carrying capacity for the prey is to the right hand side of the origin. At the same time, the predator isocline, Eq. (2.14), is a line through the origin with a constant slope. Therefore, if the slope of the predator isocline is smaller than the

maximum slope of the prey isocline and still positive, two isoclines would intersect at positive value, and thus the existence of the two populations at a nontrivial equilibrium.

Therefore, the coexistence state exists when

$$0 < \frac{c\alpha - 1}{\beta} < \frac{as_o - 1}{\beta - as_o(\beta - \alpha)} .$$

A relatively low conversion rate c , i.e., low reproductive output for predators, has a positive effect to promote the coexistence. Similarly, a relatively high recruitment rate for the prey population also contributes positively to the coexistence.

The condition for the coexistence state in the bottom-up case is $c\alpha - 1 > 0$. Since, in the bottom-up case, predators cannot deplete the prey population, the coexistence state is automatically achieved when the maximum reproductive output of the predator population is greater than one.

Under the no-predator equilibrium state, predators are so inefficient in turning consumed prey into new predators that the predator population will eventually go extinct and the prey population will grow to its carrying capacity. In both top-down and bottom-up cases, this happens when $c\alpha - 1 \leq 0$.

Under the double-extinction state, the slope of the predator isocline is greater than or equal to $P'|_{N=0}$, and the origin is the only intersection in the first quadrant. Therefore,

the condition for the double extinction is $\frac{c\alpha - 1}{\beta} \geq \frac{as_o - 1}{\beta - as_o(\beta - \alpha)}$.

Here, the predator population over-exploits the prey population, and a positive equilibrium point does not exist. In this case, predators would deplete the prey population first, and then the predators would go extinct.

Migration

Here, I expand the previous single patch closed-population model by introducing a unidirectional transport of predators in a two-patch system. This expansion can be used to model biological control scenarios by introducing predators. Suppose the predator population in patch one (upstream patch) has already reached an equilibrium state and is exporting a constant percentage of its total abundance to patch two (downstream patch). Then the dynamics of the population in the upstream patch can still be described in the form of Eq. (2.9 - 2.10) because the emigration rate is proportional to the size of the population. The emigration can be seen as a deduction in birth rate and included into the conversion rate. Therefore, the isocline configuration for the upstream patch is the same as the single patch system with an adjusted conversion rate (Figure 5). However, the dynamics of the populations in the downstream patch will not remain the same because, in the model, the rate of immigration is assumed to be proportional to the density in the upstream patch not the downstream patch. When the predator population in the upstream patch is at equilibrium, the input of predators from the upstream population would be constant (denoted by I). The size of the predator population in the downstream patch is given by

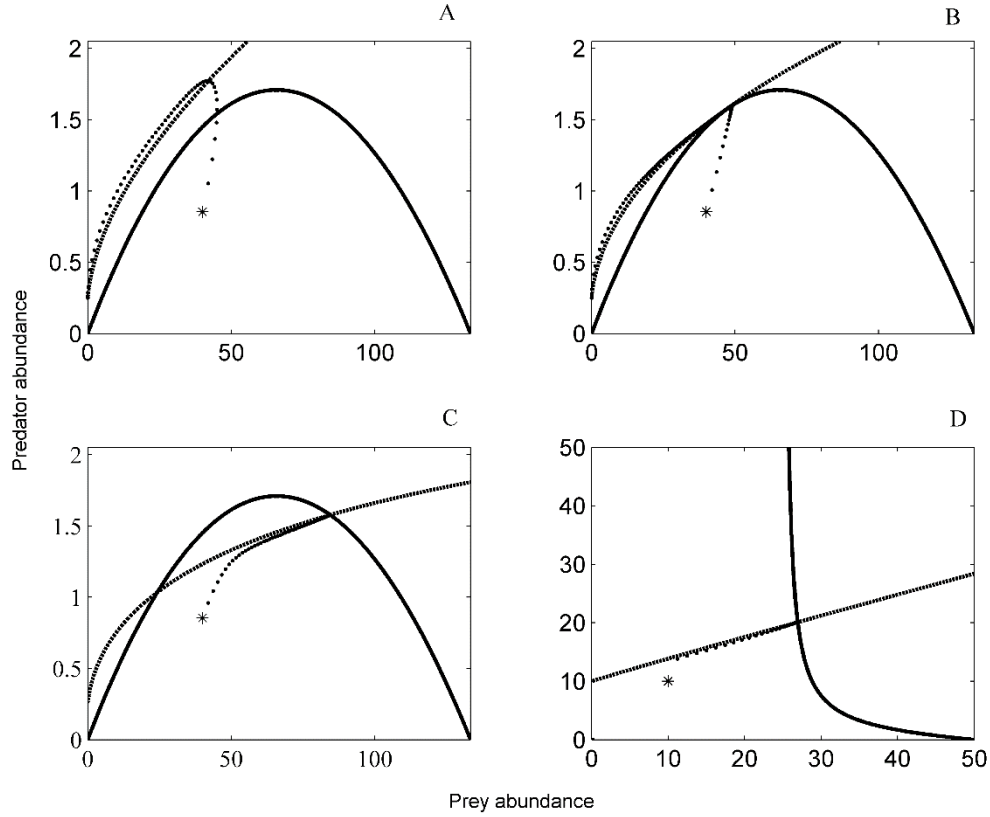


Figure 5 Isocline configurations for unstructured predator-prey model with migration. Predator isocline (dashed line) can have 0 (Panel A), 1 (Panel B), or 2 (Panel C) intersections with humped shaped prey isocline (solid line), and 1 (Panel D) intersection with L shaped prey isocline. One trajectory (dots) for each configuration is plotted together with the initial conditions (*), and a small perturbation is incorporated into numerical solutions to show the local stability.

$$P_{t+1} = \frac{c\alpha N_t}{\beta P_t + N_t} P_t + I, \quad (2.17)$$

The predator isocline of the system is

$$N^* = \frac{\beta P^* (P^* - I)}{(c\alpha - 1)P^* + I}. \quad (2.18)$$

The prey isocline is the same as that of a single patch system, Eq. (2.15), because no migration of prey is included in the model.

Next, I provide a graphical explanation of the dynamic behavior of the downstream patch. In the downstream patch, the predator isocline (Figure 5) intercepts the vertical axis at the origin and a point $(0, I)$. In the bottom-up scenario, the dynamics are the same as in the single patch system: the predator isocline always intersects prey isocline once and this equilibrium point is always stable (Figure 5D). In the top-down scenario, the predator isocline could have 0, 1 or 2 intersections with the prey isocline, and the asymptotic behavior is as follows: when two lines do not intersect (Figure 5A), the prey population will go extinct and the predator population will stay at size I ; when predator isocline is tangent to the prey isocline (Figure 5B), that point of interception is not stable and predators will deplete their prey source and then stay at density I ; when the predator isocline intersects the prey isocline twice (Figure 5C), the equilibrium point with higher prey abundance is stable and the other equilibrium point is unstable. In the third case, an Allee effect is produced by excessive predation from the introduced predators when the initial prey population is low.

Stage-structured predator and prey

In this section, an adult-juvenile stage structure is added to the unstructured model to explore the effect of stage structure and life history strategy on system behavior. For the two-stage models, I model the interaction between adult predators and either juvenile or adult prey. First, the model with adult predator interacting with adult prey is developed. The prey population has a Beverton-Holt stock-recruitment relationship, and mortality is

assumed to precede maturation for both predator and prey populations. From Eq. (2.5, 2.12), the transition matrix for this system is given as

$$A = \begin{bmatrix} M_1 & 0 \\ 0 & M_2 \end{bmatrix} = \begin{bmatrix} s_1(1-m_1) & \frac{a}{1 + \frac{a-1}{k} N_A} & & 0 \\ s_1 m_1 & p_1 \left(1 - \frac{\alpha P_A}{\beta P_A + N_A}\right) & & \\ & 0 & s_2(1-m_2) & \frac{c\alpha N_A}{\beta P_A + N_A} \\ & & s_2 m_2 & p_2 \end{bmatrix}, \quad (2.19)$$

where k is the asymptotic level of recruitment in the Beverton-Holt density-dependent process. The isoclines for adult prey (Eq. 2.20) and adult predator (Eq. 2.21) are obtained as

$$P_A^* = \frac{N_A^* (\varphi_1 N_A^* + \varphi_2)}{\varphi_3 N_A^* + \varphi_4}, \quad (2.20)$$

$$P_A^* = \varphi_5 N_A^*, \quad (2.21)$$

where φ_j s ($j=1$ to 5) are functions of predator and prey life history parameters (see Appendix B for parameter expressions and derivation of both isoclines). For the stage-structured models, interior equilibria were also locally stable according to the dominant eigenvalues of the linearized matrices under the models with simulated parameters.

The prey isocline intercepts with the horizontal axis at $(0,0)$ and $(K_2, 0)$, where $K_2 = -\varphi_2/\varphi_1$, and there is a pole at $N = x_2$, where $x_2 = -\varphi_4/\varphi_3$. The condition for a

positive K_2 is the same as the condition for the prey population to have a positive equilibrium point without the presence of the predator being modeled, which is

$$a > \frac{(1-s_o)(m_1s_1 - s_1 + 1)}{m_1s_1}, \quad (2.22)$$

and I determined that x_2 is always smaller than K_2 through numerically testing randomly-generated population parameters. Similar to the unstructured model, the prey isocline in the stage-structured model also shows both top-down and bottom-up cases, with the bifurcation point being a function of population parameters of the prey and the annual maximum rate of exploitation of the predators.

For the second stage-structured model, adult predators and their juvenile prey are modeled (Figure 6-7). Using the same method, I obtained the transition matrix

$$A = \begin{bmatrix} M_1 & 0 \\ 0 & M_2 \end{bmatrix} = \begin{bmatrix} s_1(1 - \frac{\alpha P_A}{\beta P_A + N_J})(1 - m_1) & \frac{a}{1 + \frac{a-1}{k} N_A} & & 0 \\ s_1(1 - \frac{\alpha P_A}{\beta P_A + N_J})m_1 & p_1 & & \\ & & s_2(1 - m_2) & \frac{c\alpha N_J}{\beta P_A + N_J} \\ & & s_2m_2 & p_2 \end{bmatrix}, \quad (2.23)$$

and the associated prey and predator isoclines

$$P_A^* = \frac{N_J^*(\varphi_6 N_A^* + \varphi_7)}{(\varphi_8 N_A^* + \varphi_9)}, \quad (2.24)$$

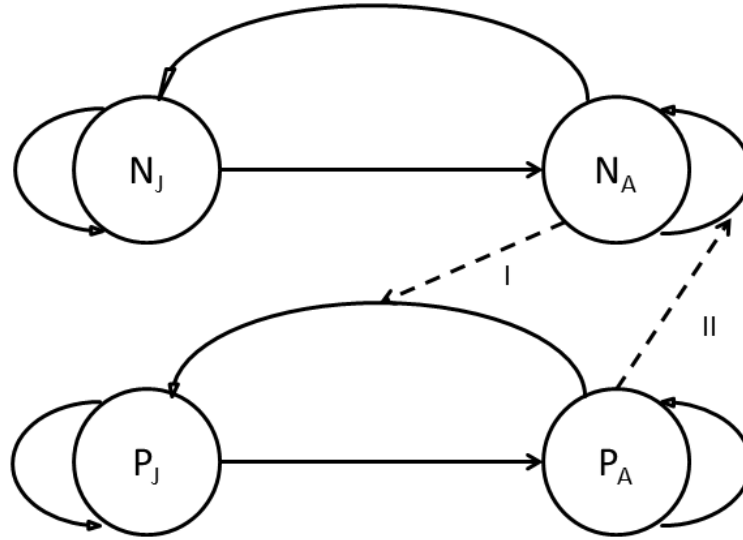


Figure 6 Predator and prey life cycle graphs and their interactions. Both predator and prey population have juvenile and adult stages. Solid arrows represent transitions of individuals from one time step to the next. Dashed arrows represent predator-prey interaction: I denotes the positive effect of adult prey (N_A) on predator's fertility; II denotes the negative effect of adult predator (P_A) on the adult survival rate.

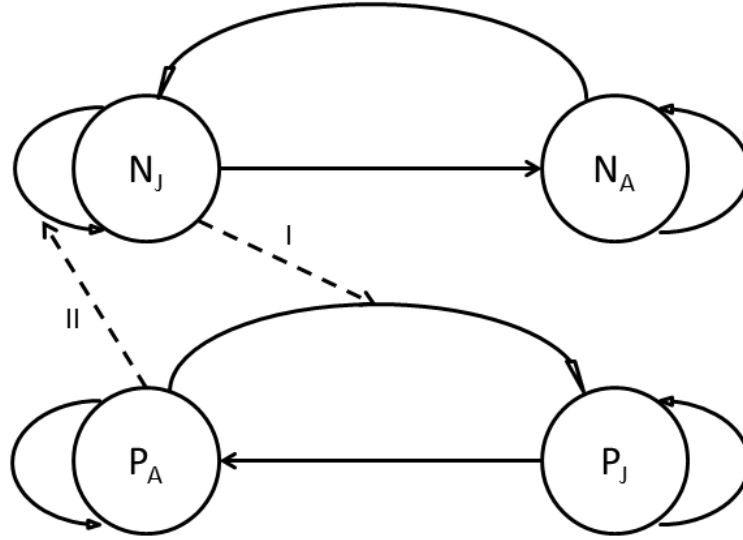


Figure 7 Predator and prey life cycle graphs and their interactions. Both predator and prey populations have juvenile and adult stages. Solid arrows represent transitions of individuals from one time step to the next. Dashed arrows represent predator-prey interaction: I denotes the positive effect of juvenile prey (N_J) on predator's fertility; II denotes the negative effect of adult predator (P_A) on the juvenile survival rate.

$$P_A^* = \varphi_{10} N_J^*, \quad (2.25)$$

where φ_k ($k=6$ to 10) are functions of life history parameters from predator, prey and predation terms (see Appendix B for more detail). The prey isocline intercepts the horizontal axis at $(0,0)$ and $(K_3,0)$, where $K_3 = -\varphi_7/\varphi_6$, and there is a pole at $N = x_3$, where $x_3 = -\varphi_9/\varphi_8$. These isoclines also produce two cases of predator-prey relationships depending on the sign of x_3 . The interior equilibria are also stable for this model based on the numerical analysis. The condition for the prey population to be able to asymptotically sustain itself without predation is the same as in the previous structured model.

Similar to the previous unstructured model, prey parameters play an important role in determining system behavior in stage-structured models. As an example, I analyze the stage-structured model, Eq. (2.19), where the adult predator's adult prey is modeled (Figure 10). For prey parameters, three levels of recruitment strengths (a), three levels of adult background survival rates (p_1), and the full range (from zero to one) of juvenile survival rates (s_1) and maturation rates (m_1) were used, and the asymptotic level of recruitment (k) was fixed to unity; for the predator-prey interaction terms, three levels of annual maximum exploitation rates (r) were used to generate the result.

The systems are categorized into bottom-up, top-down, and non-persistence, and these categories are shown in Figure 8-10 in different shades: the bottom-up zone (black), top-down zone (grey), and non-persistence zone (white). The bottom-up zone is always at the upper right corner, the non-persistence zone is at the lower left corner, and

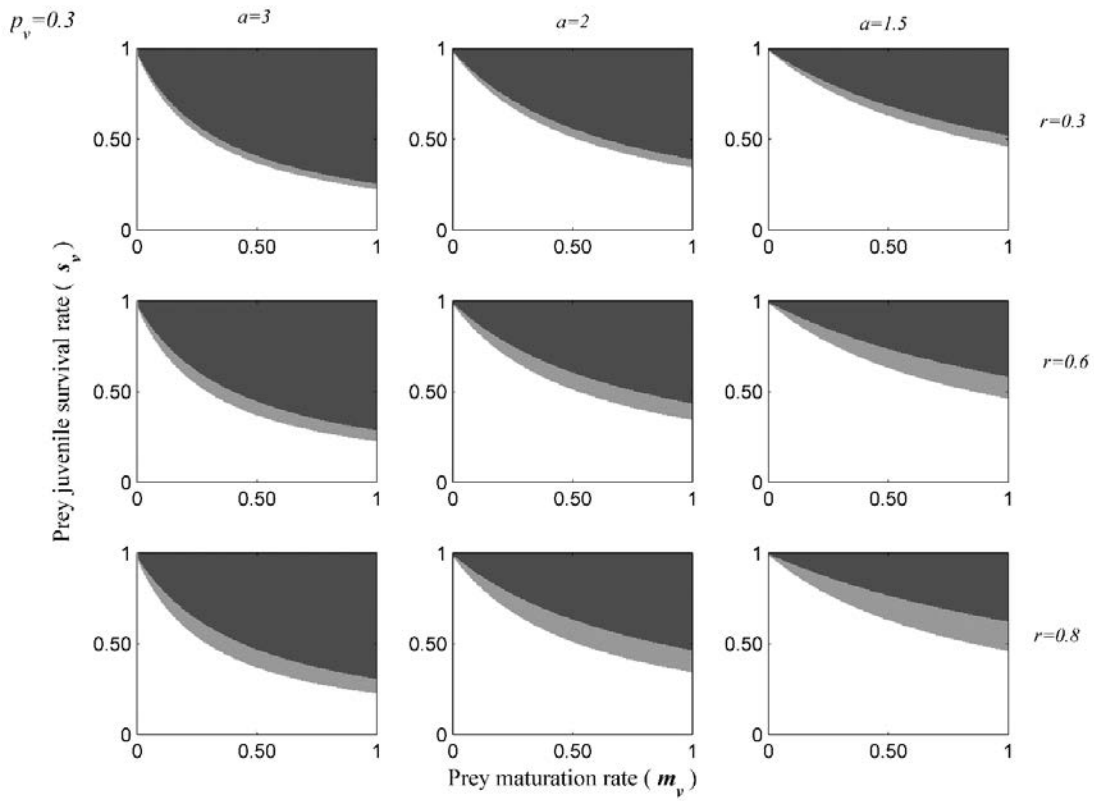


Figure 8 Bottom-up, top-down and non-persistence zones based on prey life history parameters from Eq. 2.19 with low prey adult background survival. The prey population had three levels of recruitment strengths (a), and a full range (from zero to one) of juvenile survival rates (s_1) and maturation rates (m_1) was used; for predator-prey interaction terms, three levels of annual maximum exploitation rates (r) was used to generate the plot. Black area of each panel is the bottom-up zone where prey isocline is L shaped with a positive pole, grey area is the top-down zone where prey isocline is humped shaped, and blank area is the zone of non-persistence where prey population cannot persist on its own.

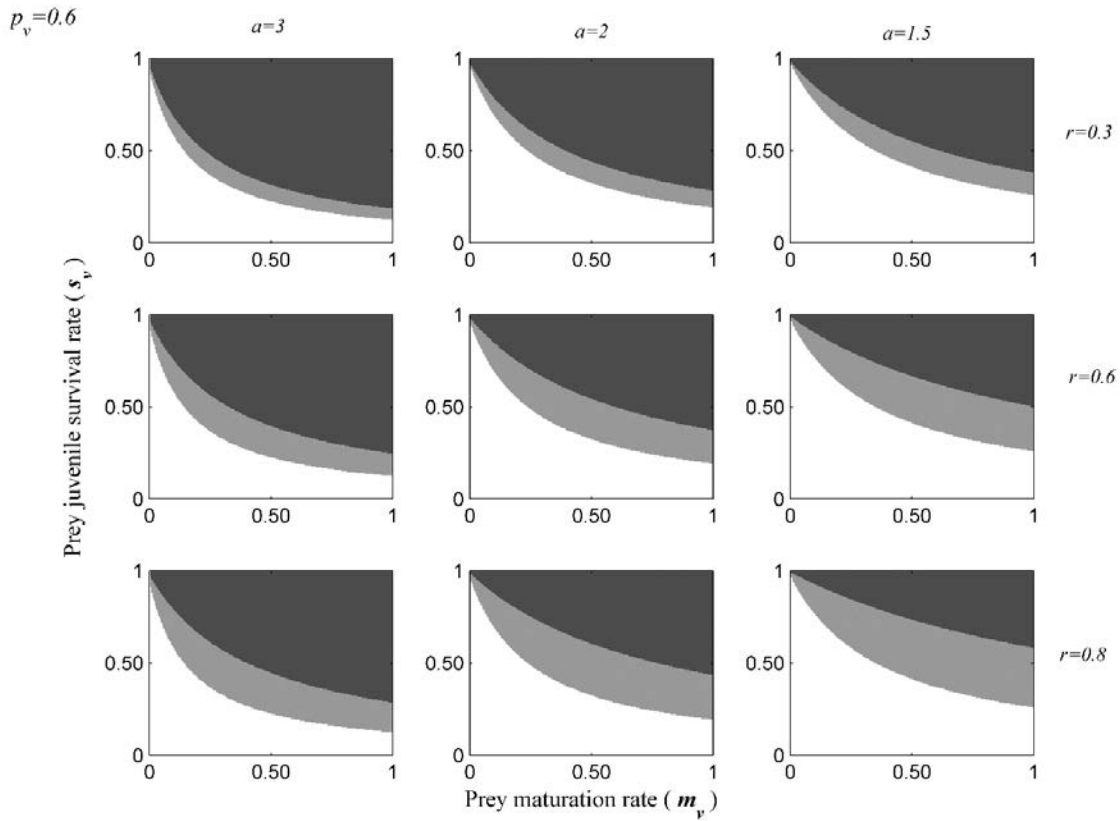


Figure 9 Bottom-up, top-down and non-persistence zone based on prey life history parameters from Eq. 2.19 with medium prey adult background survival. In addition, prey population has three levels of recruitment strength (a), and a full range (from zero to one) of juvenile survival rate (s_1) and maturation rate (m_1) are used; for predator-prey interaction terms, three levels of annual maximum exploitation rate (r) was used to generate the plot. Black area of each panel is the bottom-up zone where prey isocline is L shaped with a positive pole, grey area is the top-down zone where prey isocline is humped shaped, and blank area is the zone of non-persistence where prey population cannot persist on its own.

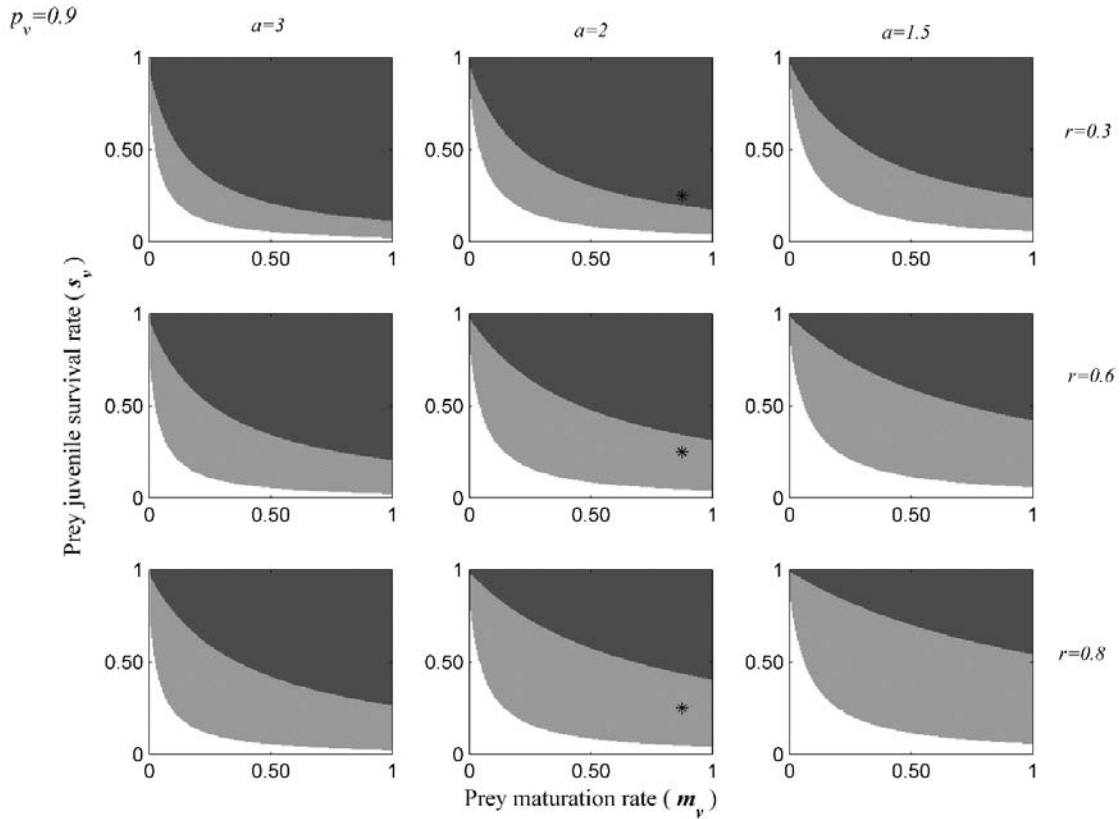


Figure 10 Bottom-up, top-down and non-persistence zone based on prey life history parameters from Eq. 2.19 with high prey adult background survival. In addition, prey population has three levels of recruitment strength (a), three levels of adult background survival rate (p_1), and the full range (from zero to one) of juvenile survival rate (s_1) and maturation rate (m_1) are used; for predator-prey interaction terms, three levels of annual maximum exploitation rate (r) was used to generate the plots. Black area of each panel is the bottom-up zone where prey isocline is L shaped with a positive pole, grey area is the top-down zone where prey isocline is humped shaped, and blank area is the zone of non-persistence where prey population cannot persist on its own. One unique prey population was marked (*) to illustrate the change from a bottom-up to a top-down process with an increase in predator's annual maximum exploitation rate.

the top-down zone is located between two other zones. Predator-prey coexistence is promoted if the bottom-up zone increases in size because the predator population will persist without overexploiting the prey population. Both the bottom-up and top-down zones expand in size as recruitment strength (a) or background adult survival (p_1) increases, and an increase in maturation rate (m_1) also promotes coexistence.

For biological control purposes, the top-down zone is the only area where it is possible to eliminate the prey population by introducing predators. Increasing r , by introducing less efficient predators, shifts the boundary between the top-down zone and the bottom-up zone upwards, while having no effect on the non-persistence zone. In effect, more parameter space will be included into the top-down zone, and hence, the system will be more controllable. In general, a combination of prey with a high growth potential and a fast life cycle, and efficient predators has a better chance of coexistence.

In Figure 10, every dot in each panel represents a pair with a unique prey population and a type of predator population with a specified interaction term. To determine the outcomes of population pairs' interaction, additional life history parameters of predator population are needed within the top-down zone; while for species pairs in the other two zones, no further information is needed. According to the three asymptotic states established in the analysis of unstructured models, the whole parameter space can be partitioned into three regions: region I, coexistence of predator and prey; region II, only the survival of the prey, and region III, dual-extinction. The asymptotic predator abundance has distinct boundaries between these regions, whereas prey abundance is continuous between region I and II. A two dimensional section of the whole parameter

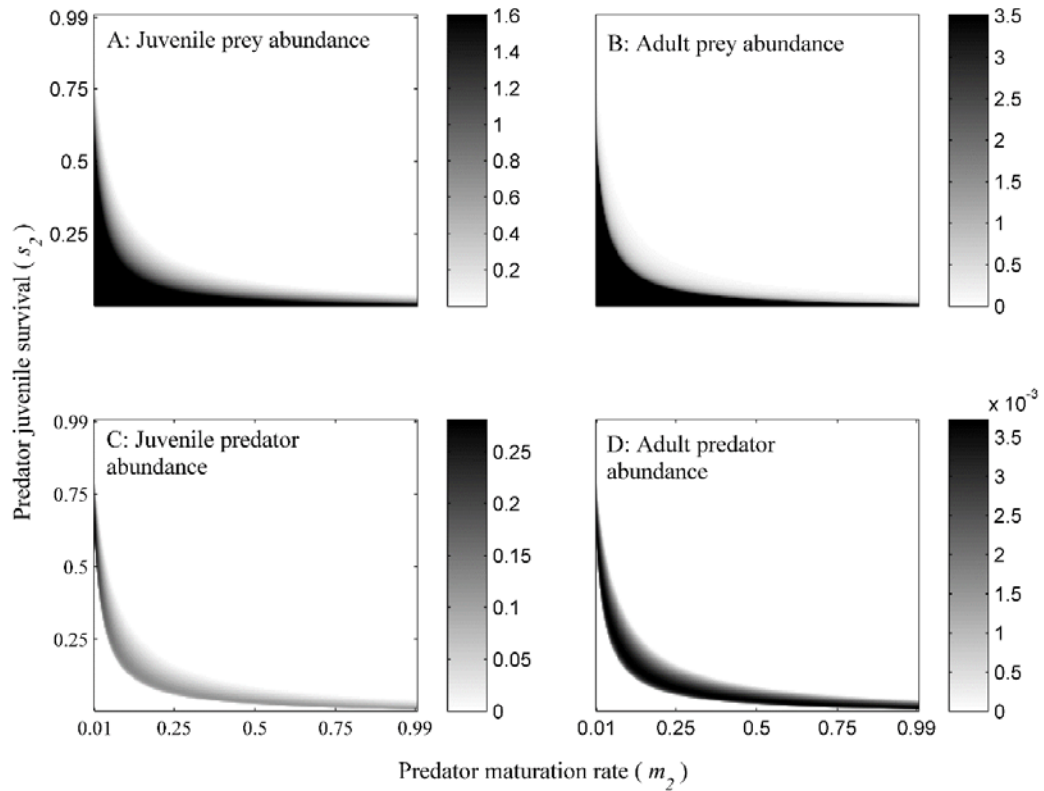


Figure 11 Asymptotic abundances of a predator-prey system, where adult predator's adult prey is explicitly modeled from Eq. 2.19. In this example, one particular prey population was chosen (the asterisked prey population in Figure 10) to illustrate the effects of predator life history on system dynamics in a top-down system, with prey parameters $p_1 = 0.9$, $m_1 = 0.875$, $s_1 = 0.25$, $a = 2$, $k = 1$, predator parameters $c = 0.8$, $\alpha = 35$, $p_2 = 0.8$, and the interaction term $r = 0.6$. Shaded area shows the region of life history parameter combinations that permit positive asymptotic abundance. At the lower left corner, this type of prey is not a viable food source for those predator populations, with asymptotic prey abundances staying at the environmental carrying capacity. As predator maturation rate and or juvenile survival increase, predator can maintain a stable equilibrium with this prey population. Note the curvilinear compensation relationship of maturation rate and juvenile survival. As these two predator parameters further increase, predators will over-exploit this prey population, and over time both populations will go extinct.

space of a predator-prey system based on model 2.19 is shown (Figure 11). In the region of coexistence, if the predator's juvenile stage survival rate is constrained at a relatively low level, then a higher maturation rate is preferred for the long-term persistence of the predator population; but if the juvenile survival is relatively high, then a minimum maturation rate is more beneficial for the predator population.

Discussion and conclusion

Although the same biological processes are used in continuous- and discrete-time models, differences in modeled system behavior can arise from the way empirical data are interpreted. My model and the model by Getz (1984) are different in how life history events are modeled, i.e., seasonal reproduction and continuous predation in my model. Also, the stability properties of the asymptotic states are not shared between these two models. But both models exhibit bottom-up scenarios with an L-shaped prey isocline as well as top-down scenarios with a classic hump shaped prey isocline. This study shows the dynamic behaviors of predator-prey models with the same kind of ecological processes with a discrete-time interpretation of the ecological system as the continuous-time interpretation by Getz (1984), and the results can be compared between these models.

Results show that a discrete-time model exhibits more stability than a continuous-time model. In the continuous-time model, limit cycles can arise, but in my discrete-time models interior equilibria are always stable. Here, a system is considered stable in the sense that, after small perturbations, all state variables of the system will return to a fixed level determined by the current state of the system. It should be noted that the word "stability" is often used in an imprecise manner in ecology with different meanings

assumed by different people (Murdoch 1970, Pimm 1991). According to my definition, model results imply that discrete reproduction (i.e., seasonal reproduction) might be playing a stabilizing role in predator-prey interactions.

The reason that dynamics of my discrete-time model do not conform exactly to those of the continuous-time model developed by Getz (1984) is that the timing of population events is different, as mentioned above. In the continuous-time model, the process of predation (ratio-dependent functional response) and reproduction are concurrent, while in my discrete-time model these two processes are sequential, in the same way as they occur in the predator-prey system being modeled. Both theoretical and field studies have shown that sequential density-dependence generates markedly different population responses compared to simultaneous density-dependent processes (Ratikainen 2007). Predation is an inter-specific density-dependent process, and its sequential relationship with the intra-specific density-dependence in the recruitment process generates the difference between Getz's model and my model. The arrangement of those processes in the model is crucial, and should reflect the basic ecology of the populations in order to avoid introducing mathematical artifacts into modeling.

For the predation function, the choice between prey dependent and predator-prey ratio-dependent functional responses was heatedly debated in the 1990's (Abrams and Ginzburg 2000), and one of the major differences lies in the timescale interpretation of the predation process, as the former describes an instantaneous hunting process and the latter an integrated hunting process (Akçakaya et al. 1995, Abrams and Ginzburg 2000). For the functional response, I used a ratio-dependent trophic function in my discrete-time model.

Arditi and Ginzburg (1989) had looked at timescale difference between fast behavioral phenomenon and slow population level responses, and used this difference to justify the ratio-dependent trophic function. Although the justification has been debated (Oksanen et al. 1992, Abrams 1994, Akçakaya et al. 1995), I consider their ratio-dependent trophic function appropriate for modeling snails *Urosalpinx cinerea* and barnacles *Semibalanus balanoides*, which they considered in their study, because both predator and prey have discrete annual reproductive interval and their trophic function should be representative of the end result of the predation of an entire season. However, although their ratio-dependent trophic function was derived from discrete-time observation, it was incorporated into a continuous-time model. This could introduce a mathematical artifact into their model (Appendix A). For populations with between-year discrete processes, ratio-dependent functional responses modeled through difference equations serve well as a surrogate to nonlinear differential equations to describe the between-year dynamics in a “semi-discrete” model. Some mathematical intricacy is sacrificed for the fully analytically solvable model. The numerical response function is assumed to be proportional to the functional response, and there is a linkage between my discrete-time ratio-dependent numerical response (Eq. 2.7) and the Beverton-Holt stock recruitment process. Both functions have discrete-time interpretation, and they share the same mathematical form. The Beverton-Holt stock recruitment process in a predator population would arise from a discrete-time type-II ratio-dependent type predation. Alternative mechanistic interpretations of the Beverton-Holt stock recruitment process can be obtained from single population models, e.g. the logistic model (Yodzis 1989), distribution of cannibalism

(Thieme 2003), intra-specific aggression (Eskola and Geritz 2007), and from resource-consumer models with type-I predation processes (Geritz 2004).

Our theoretical understanding about the relationship between size- or stage-dependent population dynamics and community processes is still limited (De Roos et al. 2003). Matrix models have been used extensively to model dynamics of structured populations (Caswell 2000), and my work constitutes one of the first efforts to extend single-population matrix models to two-population models with interspecies interaction. In my structured models, population parameters of predator and prey populations explicitly determine the dynamic behavior of the system. For example, in a stage-structured predator-prey model, where adult predator reproduction is affected by adult prey abundance (Figure 11), when both predator juvenile survival and maturation rate are constrained at a low level, the predator population will not have enough adult predators to replenish the population through reproduction and recruitment. Thus, the primary constraint for population growth is the predator's population rates. However, if the predator population enjoys both high juvenile survival and maturation rate, and therefore has a high proportion of adult predator in the population, the primary constraint for growth would be over-exploitation of the prey (since I am considering the trophic interaction between the adult predator and their adult prey). For the predator population, a lower maturation rate could compensate the effect of a high level of juvenile predator survival in maintaining a positive stable equilibrium, and *vice versa*. I also found that potential dynamics of the stage-structured models are the same as the unstructured models, which is also true for the unstructured and structured competition models considered by Fujiwara

et al. (2011). This justifies the use of unstructured models (Faria et al. 2011) for the initial exploration of complex systems. The conservation of potential dynamics is due to the linear update rule between juvenile and adult stages, and this conservation would be violated with further addition of nonlinear density-dependence between stages. Furthermore, the inclusion of stage structure enables us to explain system dynamics based on population parameters.

It is crucial to match the timescale of observations with the analysis of the model, since transients will appear if predator and prey dynamics operate on different timescales (Hastings 2004). Only the asymptotic behavior of the system is analyzed here, because, in my model, the same timescale for both predator and prey populations is required. Many predator-prey systems fit into this category, e.g. wolf and moose system on Isle Royale (Vucetich et al. 2009), and trophic interactions among fishes of coral reefs (Connell 1997, 1998). For others, the periodic matrix population method (Caswell 2000) may be used, and these situations merit further study.

In conclusion, this study extends matrix population methods to predator-prey modeling for populations with discrete reproduction and continuous predation. Discrete-time interpretation of data and modeling methods could generate qualitatively different dynamics than the commonly used continuous-time approach. Care should be taken in data interpretation and modeling process so as not to introduce bias. From my results, although incorporating complex life history did not alter the dynamics of a simpler, lumped-parameter model, the incorporation of stage- and spatial-structure allowed for a more detailed understanding of the modeled systems. Discrete-time modeling has the

potential for bridging the gap between theoretical modeling and empirical observations. The timescale that is inherent in the sampling frequency associated with empirical observations makes discrete-time modeling a suitable option.

CHAPTER III

FINDING REGULATION AMONG SEEMINGLY UNREGULATED POPULATIONS

Introduction

The identification of forces that regulate the dynamics of ecological communities has important implications in both theory (Hairston et al. 1960, Paine 1980, Oksanen et al. 1981, Strong 1986, Hunter and Price 1992, Mutshinda et al. 2009) and management (Rabalais et al. 2002, Smith et al. 2010). These forces include environmental stochasticity, demographic stochasticity and density-dependent regulation (Lande et al. 2003, Wilson and Lundberg 2006). In this chapter, I restrict my attention to density-dependent regulation among “seemingly” unregulated populations. I use the word “seemingly” because although populations may be regulated in the long-run, they do not appear to be regulated statistically when time series are short. From such data, I try to identify two types of population interactions, top-down and bottom-up control. Top-down control is herein defined as one where the predator population abundance regulates the abundance of its prey population, and bottom-up control is defined as one where the abundance of the prey population regulates that of its predator. Therefore, the interaction between two populations may include both trophic and non-trophic effects.

Empirical approaches to identify bottom-up and top-down processes in multi-species communities commonly involve correlation analyses of time series data on abundance indices, e.g. biomass, or catch-per-unit-effort (CPUE) (Shiomoto et al. 1997, Worm and Myers 2003, Frank et al. 2005, Laundre et al. 2014). This method associates

top-down effect with a negative correlation between time series of consumer and resource, and bottom-up effect with a positive correlation between the two. However, both the non-stationarity in the time series of community dynamics and the inability to observe all the interacting species pose serious problems in making appropriate inferences regarding community dynamics as described below.

The prevalence of non-stationarity in ecological and fisheries data is one problem inherent in the analysis of population time series (Steele 1985, Pimm and Redfearn 1988, Inchausti and Halley 2001, Stergiou 2002, Halley and Stergiou 2005, Wilberg and Bence 2006, Niwa 2007, Rouyer et al. 2008, Knappe and De Valpine 2012). Non-stationarity often violates model assumptions and produces spurious results. The correlations among non-stationary time series data are spurious in the sense that the estimated coefficients are statistically significant when there are no real relationships among variables (inflated type-I error rate). For example, in the analysis of fisheries time series data, spurious results are often produced by correlating cumulative-sum (CUSUM)-transformed variables, because the CUSUM transformation generates non-stationary time series from stationary time series (Cloern et al. 2012).

One approach for dealing with non-stationary time series is to model them as unit-root processes (Enders 2008). A time series is considered to have a unit-root when it can be made stationary by taking a first difference. The most common unit-root processes in the ecology and fisheries literature are random walks. The time series produced by first differencing a random walking time series is white noise, which is stationary (note that the first difference of a unit-root time series is not necessarily a white noise sequence). A

random walk process has a variance that increases with time, and it has a power spectrum that approaches infinity with decreasing frequency (spectral reddening). Increasing variance and spectral reddening are features commonly observed in fisheries and other population time series (Steele 1985, Pimm and Redfearn 1988, Inchausti and Halley 2001, Stergiou 2002, Halley and Stergiou 2005, Niwa 2007). This suggests that it may be appropriate to model each univariate non-stationary population time series as a unit-root process.

Persistent natural populations should show evidence of regulation in the long-term historic trends of population abundances, whether they are regulated towards an equilibrium point or an equilibrium zone (Strong 1986, Krebs et al. 1994, Murdoch 1994). In this case, population time series are expected to be stationary in the long term. However, the regulation may not be obvious in short time series, especially with univariate time series. For example, the existence of an equilibrium point or equilibrium zone was questioned by Strong (1986) in the dynamics of some populations, and the phenomenon of a lack of density-dependence in persistent populations was coined “vague” density-dependence. However, it is generally acknowledged that density-dependence is necessary for population regulation (Murdoch 1994). Many factors have been considered as potential causes of the density “vagueness” phenomenon, which include the lack of statistical power of statistical tests and the short length of time series data. Here, I explore the situation when there exists an equilibrium zone within which the population abundance is weakly regulated. A relatively short observation of the dynamics would reveal no or insufficient information on population regulation to conclude density-dependence. Therefore, when I

have non-stationary time series, instead of assuming each individual population is individually regulated, I test for stationarity with two or more non-stationary time series together. When such a relation is identified, it is included in the further analysis to investigate population interactions.

The other problem in identifying bottom-up and top-down effects is that, invariably, analyses are performed on a subset of the trophic web and inferences must be made based on our knowledge of a partially-observed system (Stenseth et al. 1997). Furthermore, trophic “cross-links” (Paine 1980) can act as indirect pathways to produce unexpected indirect effects in ecological communities (Wootton 1994). Problems resulting from the inability to observe potentially important species interactions can be illustrated by a hypothetical ecological community with two consumers and one common resource denoted by P_1 , P_2 and V (Figure 12). In this example, consumer and resource abundances in a bottom-up forced community could be either positively correlated, negatively correlated or uncorrelated. P_1 and P_2 compete, with P_1 being competitively superior to P_2 , and both P_1 and P_2 affected by changes in V (bottom-up). If P_2 can be observed, but not P_1 , and the positive impact of the bottom-up effect is weaker than the negative impact from competition with P_1 , then fluctuations in V and P_2 will be correlated negatively, leading to the spurious inference of top-down effect. An example of three-species indirect facilitation, in which there is a positive indirect relation between a keystone predator and a consumer population, has been reported in a freshwater benthic community by (Holomuzki et al. 2010). Thus, identification of bottom-up versus top-down control of a food web based on the sign of correlation coefficients is difficult,

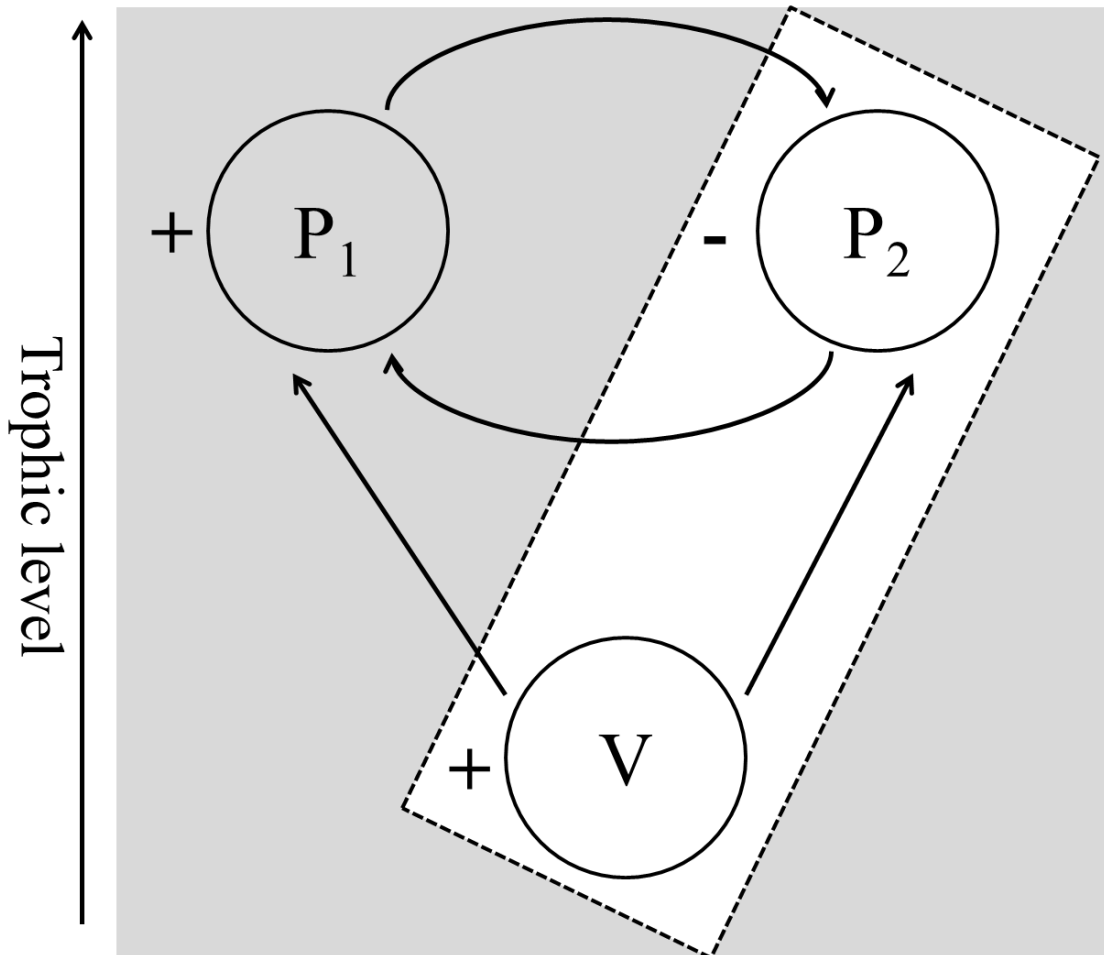


Figure 12 Diagram showing an example of three-species interactions. This bottom-up driven community has two trophic levels. Each circle represents a population, and arrows represent population interactions and the direction of that interaction, e.g. the arrow running from population V to population P_1 denotes a positive numerical response from the resource to the consumer population, and this interaction is unilateral. The two consumer populations at the higher trophic level are competitors for available resources. The sign at the left hand side of each circle represents one scenario where a spurious inference could arise from the correlation method. The gray area denotes the population not observed, or excluded from the model formulation, and the white area denotes available data.

if not impossible. However, the direction of the effect of species interaction is invariant under indirect species interactions, e.g. in the above example, a change in the resource population drives a change in the consumer population, whether positive or negative. This example illustrates the importance of using a Granger causality based method (Granger 1969, Detto et al. 2012), rather than the direct correlation approach.

In the sections that follow, I describe a new practical approach to identify bottom-up and top-down control, which overcomes the statistical difficulties associated with the non-stationarity of ecological time series data and also reduces the difficulties resulting from the inability to observe potentially important ecological interactions. I first provide an overview of the approach to the analysis of multivariate time series of CPUE data, which are potentially non-stationary. I then describe a quantitative framework for a linear, multi-species community model. Then, I demonstrate an application of the approach by analyzing CPUE time series data from the shrimp/ground fish fishery in the Gulf of Mexico. Finally, I discuss some implications of the results.

Materials and methods

Overview of the proposed method

An overview of the steps involved in the approach to identifying bottom-up and top-down control by analyzing multivariate time series data is presented in Figure 13. First, non-stationarity in the time series is checked visually based on time series plots. Then, to confirm the observation, univariate unit-root tests, e.g. the KPSS test (Kwiatkowski et al. 1992) and the Dickey-Fuller tests (Dickey and Fuller 1979, Said and Dickey 1984), can be applied. The unit-root tests indicate whether the time series is stationary or a unit-root

exists. I note that there are other processes generating non-stationarity in the data (Engle 1982, Stenseth et al. 2004), but they are beyond the scope of this chapter. If the time series is produced by a unit-root process, it is not stationary, but its first difference is stationary. For this reason, a unit-root process is also considered integrated of order one, denoted as $I(1)$; the first difference of a unit-root process is considered integrated of order zero, denoted by $I(0)$, because the difference is stationary without further differencing.

Next, linear models are built. If every time series is stationary, vector autoregressive (VAR) or multivariate autoregressive (MAR) models (Ives et al. 2003, Hampton et al. 2013) can be applied directly. If some or all of the time series are integrated of order one, multivariate unit-root tests (Johansen and Juselius 1990b) are used to test if a non-trivial linear combination of $I(1)$ processes is integrated of order zero. If such a linear relationship exists, the linear combination is considered to be the co-integration relation. Because non-stationarity is common among population time series, the approach will expand the applicability of the analysis by incorporating the non-stationarity into a VAR or MAR model. Based on the presence or the lack of co-integration relation(s) among the non-stationary time series, VAR models that incorporate various ecological hypotheses related to community structures are built. This is described in the next section.

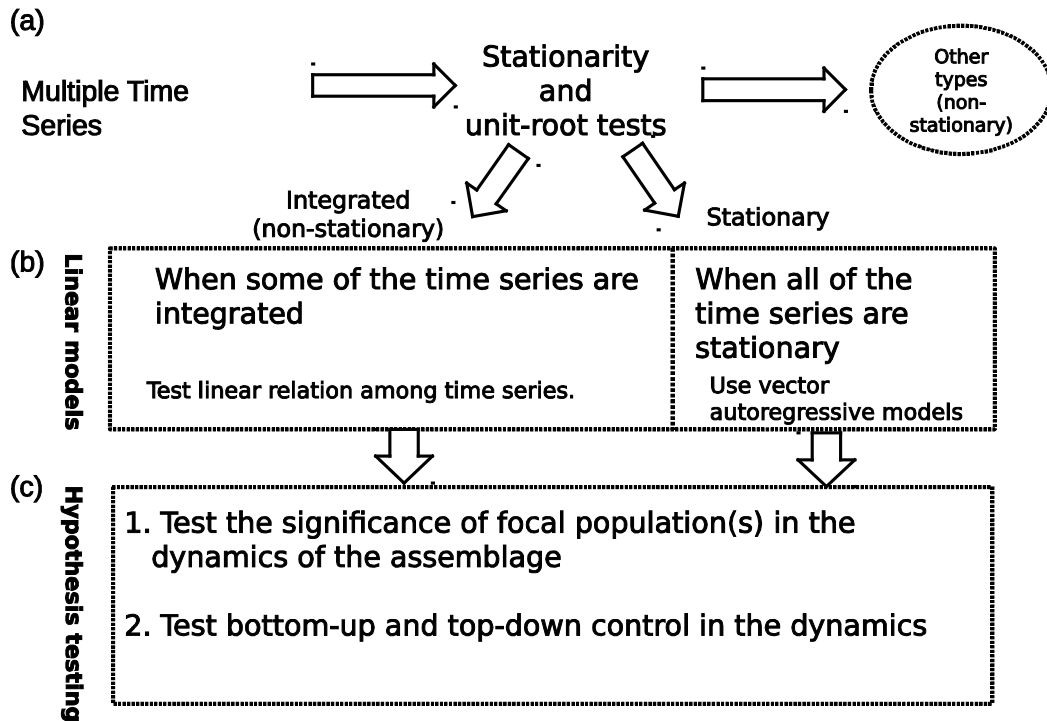


Figure 13 Steps in analyzing multivariate time series data. a: After plotting each individual time series, I first check visually for non-stationary behavior. Then, various stationarity and unit-root tests, e.g. KPSS test and Dickey-Fuller test, can be conducted to confirm the stationarity or the existence of a unit-root in the time series. A time series having a unit-root in its characteristic equation is not stationary. There are other types of non-stationarity as mentioned in the introduction, but I do not discuss them here. b: Next, linear models are built. When some (≥ 2) of the time series are integrated, I use multivariate unit-root tests to determine the long-run relationship between time series. c: Given the long-run relationship, ecological hypotheses can be tested. If test results indicated that only one time series x_t is non-stationary, other time series should be linearly independent of x_t because a non-trivial linear combination of a non-stationary time series and stationary time series cannot be stationary. When all the individual time series are stationary, vector autoregressive models can be used, and all the hypothesis tests outlined above can be conducted in a similar fashion.

A multi-species linear population model

Vector autoregressive (VAR) models are routinely used to model population time series data (Hampton et al. 2013). Due to the presence of non-stationary time series, here, the VAR model is written in a vector error correction model (VECM) form (Engle and Granger 1987). A p th order VAR model for s populations has a VECM representation

$$\Delta \mathbf{N}(t) = \mathbf{B}\mathbf{N}(t-1) + \sum_{i=1}^{p-1} \Theta_i \Delta \mathbf{N}(t-i) + \mathbf{C} + \mathbf{W}(t), \quad (3.1)$$

where $\mathbf{B}(t)$ is an $s \times 1$ vector of log-transformed population abundances at time t , $\Delta \mathbf{N}(t) = \mathbf{N}(t) - \mathbf{N}(t-1)$, \mathbf{B} and Θ_i 's are $s \times s$ matrices for the coefficient matrices of the VAR(p) model, vector \mathbf{C} is an intercept term, and vector $\mathbf{W}(t)$ is a stochastic term. Matrix \mathbf{B} ($s \times s$ with rank r) can be written as a matrix product $\alpha\beta^T$ with α and β each with dimension $s \times r$, and \mathbf{T} denotes the transpose of a vector. Each column of β contains coefficients for the co-integration relation, and each column of α contains what are called adjustment coefficients. On the left hand side of Eq. (3.1) is the change of the s -dimensional state vector at time t . This change is decomposed into four components on the right hand side of the equation. From left to right, I interpret these terms as the long-run relationship, short-run relationship, intercept term and stochastic term, respectively. Each individual time series in vector $\mathbf{B}(t)$ can be either integrated of order one or zero.

In the main text, I focus on inferences on the long-run component of the model, and defer the results on the short-run component to the Appendix C. Inferences on the short-run component of the model are well known and covered elsewhere (Lutkepohl 2007, Hampton et al. 2013). I expect that when regulation is not strong at the individual

population level, i.e., the non-stationarity of some univariate population time series cannot be rejected, the long-run component of the model plays the major role in community dynamics.

Whether the long-run component of the model contributes significantly to community dynamics is determined by the rank of \mathbf{B} . The equilibrium states of the system defined by Eq. (3.1) can be found by setting stochastic terms to zero, substituting \mathbf{N}^* into $\mathbf{N}(t)$ and $\mathbf{N}(t-1)$, and solving for \mathbf{N}^* . The equilibrium states are in the null space of matrix \mathbf{B} , and their dimension depends on the number of differences that need to be taken before the time series becomes stationary and the linear dependency of the time series. When all the components of vector \mathbf{N} are stationary, matrix \mathbf{B} is of full rank (i.e., $r=s$), and the equilibrium state is a point in the s -dimensional space. If this equilibrium point is stable, it attracts community trajectories in the long run. On the other hand, in cases where some of the components of vector \mathbf{N} are not stationary, matrix \mathbf{B} is of reduced rank, and the long-run component plays a large part in community dynamics. If some of these time series co-integrate (Engle and Granger 1987), i.e., there is a non-trivial linear combination of $I(1)$ time series that produces a stationary time series, the community dynamics are regulated. If all the time series are integrated of order one and do not co-integrate, the rank is zero (Johansen 1995) and the community dynamics are not regulated. In addition, I consider an equilibrium relationship exists among all the species considered if the disequilibrium errors, i.e., each component of \mathbf{BN} , follow a stationary process (Banerjee et al. 1993).

The number of linear equilibrium relationships among potentially non-stationary time series, i.e., the rank of matrix \mathbf{B} , can be estimated by Johansen's test of co-integration, which has been verified with simulated data sets and extensively used in econometrics (Johansen and Juselius 1990b, Johansen 1995). First, VAR models were fitted to the data, and order p was chosen based on BIC (Tsay and others 1984). Then, likelihood ratio tests were used to determine the rank of matrix \mathbf{B} . The test statistic (trace statistics) was calculated successively to determine the rank of matrix \mathbf{B} starting from the null hypothesis of no equilibrium relationship ($r=0$) against at least one equilibrium relationship ($r \geq 1$) and adding the number of equilibrium relationships at each step. With the rank of matrix \mathbf{B} set to r , different hypotheses based on α and β were formed and tested using likelihood ratio tests (Johansen 1995).

When every component of matrix \mathbf{N} is stationary, a VAR model can be applied directly to the population data. The test of bottom-up effect becomes the test of the significance of the coefficients of the resource population terms in the consumer equations, and the test of top-down effect becomes the test of the significance of the coefficients of the consumer population terms in the resource equations. Likelihood ratio tests can then be constructed to test the significance of each hypothesis (Lutkepohl 2007).

When not all the components of vector \mathbf{N} are stationary, and some of those non-stationary components co-integrate, matrix \mathbf{B} is singular, and estimation becomes an eigenvalue problem. The coefficients that make the linear combinations of components of \mathbf{N} stationary are in the rows of β . These linear combinations become factors, into which the equilibrium relationship for each component population is partitioned. The factor

scores are found in the columns of α . By testing constraints (restrictions) on β , I can determine which species have an equilibrium relationship. Similarly, by testing restrictions on α , I can determine the direction of species interactions.

Finally, when all the time series are non-stationary and linearly independent, the rank of matrix \mathbf{B} is zero. In this case, there is no simple equilibrium relationship among these time series, and bottom-up and top-down hypotheses cannot be tested in this framework.

\mathbf{N} may also have a drifting trend. This trend is incorporated into \mathbf{C} , and its significance can then be tested (Johansen and Juselius 1990b). When the population dynamics do not have a drift term, the intercept term (\mathbf{C}) in Eq. (3.1) can be moved inside the matrix product \mathbf{BN} , and it will be stacked at the first row of β with \mathbf{N} augmented by a constant. Such a model is called a restricted intercept model.

Significance of a focal population in the long-run component of the assemblage dynamics

When the community assemblage has one or more equilibrium relationships identified through testing the rank of \mathbf{B} , the significance of a focal population in the equilibrium relationship(s) can be tested. The testing procedure is as follows. The null hypothesis assumes that the focal population does not have any equilibrium relationship with the rest. This hypothesis can be constructed by restricting the coefficient(s) corresponding to resource population(s) in each equilibrium relationship to zero (coefficients in the columns of β for the co-integration relation). The likelihood ratio test is used to test the significance of the focal population in the equilibrium relationship.

Significance of bottom-up and top-down effects in the long-run component

If the resource population is found to contribute significantly to the dynamics, I then test the significance of bottom-up and top-down effects in the dynamics. These hypotheses are formed by restricting elements of α .

The top-down hypothesis assumes that only the resource population is responding to deviations from the equilibrium relationship(s), and other populations are not. This hypothesis can be constructed by restricting the adjustment coefficients for the consumer populations to zero, while allowing the coefficient for the resource population to vary freely. When we have only one resource population, the restriction on α forces $r \leq 1$. When there is more than one equilibrium relationship, this identified equilibrium relationship is a linear combination of all the equilibrium relationships. The likelihood ratio test can be constructed, and the test statistic has an asymptotic χ^2 distribution. Deviations from the null hypothesis indicates bottom-up control.

Meanwhile, the bottom-up hypothesis assumes that only the consumer group was responding to deviations from the equilibrium relationship(s). Similar to the top-down hypothesis, for this null hypothesis the adjustment coefficients for the resource group are set to zero, and those of the consumer populations are allowed to vary freely. Deviations from the null hypothesis indicate top-down control.

To test density-dependence in the short-term component of the model, see Appendix C. Moreover, in Appendix C, a nonlinear predator-prey model was used to

explore small sample properties of the co-integration method and bottom-up and top-down tests, and these tests showed reasonable performance even with short time series.

Data

The analysis testing ecological hypotheses is illustrated using monitoring data collected for fisheries management. Data were collected by the United States National Marine Fisheries Service (NMFS) Southeast Area Monitoring and Assessment Program (Stuntz 1983). The analysis used the semi-annual shrimp/ground fish surveys conducted from 1986 to 2011 in the northern Gulf of Mexico between Mobile Bay, Alabama and Brownsville, Texas. In each year, approximately 300 to 400 bottom trawl samples were collected. Although the SEAMAP shrimp/ground fish program started in 1982, the data from 1982 to 1985 were omitted from the analysis due to inconsistent coverage and changes in sampling methods. Surveys were conducted once during the summer (May-July) and once during the fall (October-November). The northern part of the Gulf of Mexico is divided into 21 statistical zones for fisheries surveys. The analysis used data from 10 statistical zones in the west, zones 11 through 21, excluding zone 12. The location of bottom trawl stations was randomly selected at each sampling occasion within each zone. At each sampling station, time and environment variables, e.g. water temperature, salinity and depth, were recorded at the time of sampling.

Penaeid shrimps found in the northern Gulf of Mexico include brown shrimp, *Farfantepenaeus Aztecs*, white shrimp, *Litopenaeus setiferus*, and pink shrimp, *Farfantepenaeus duorarum* (Perez-Farfante and Kensley 1997). The commercial shrimp fishery targets all of these species. In 2009, landings were estimated at 118 million kg and

valued at 340 million U.S. dollars (National Marine Fisheries Service 2010). Brown shrimp was the most abundant among the three species.

Three finfish species, Atlantic croaker, *Micropogonias undulatus*, silver seatrout, *Cynoscion nothus*, and sand seatrout, *Cynoscion arenarius*, were included in the analysis. Their distribution patterns, ecological roles, and status in bottom fisheries, with an emphasis on their relation with penaeid shrimps, are outlined in the Appendix C. These fish species were chosen because they ranked high in catches in the surveys as well as bycatch in the shrimp fishery (Diamond 2004). The fact that these fish species coexist in large numbers with brown shrimp suggests the potential for ecological interactions between these fish species and brown shrimp.

*CPUE standardization of shrimp and fish populations in the Gulf of Mexico from
SEAMAP shrimp/ground fish program*

Data were standardized applying a mixture generalized linear model (Fletcher et al. 2005) to each species in each statistical zone to extract annual abundance indices. This procedure was needed because sampling locations were chosen randomly within each statistical zone, and the species distributions were expected to be heterogeneous over space. Also this method accounted for changes in observations that were unrelated to actual changes in abundance (see the Appendix C for details). All the following analyses were conducted on the natural logarithms of the standardized CPUE data in the time series.

The existence of a unit root was tested using the augmented Dickey-Fuller (ADF) test (Said and Dickey 1984). The null hypothesis was that the tested time series was a unit root process. I used Bayesian Information Criterion (BIC) for model selection from a set

of models (Schwert 2002), which had different time lags. All the statistical analyses were performed using R statistical software (R Development Core Team 2015), and the scripts used in this chapter can be found in the supplementary material.

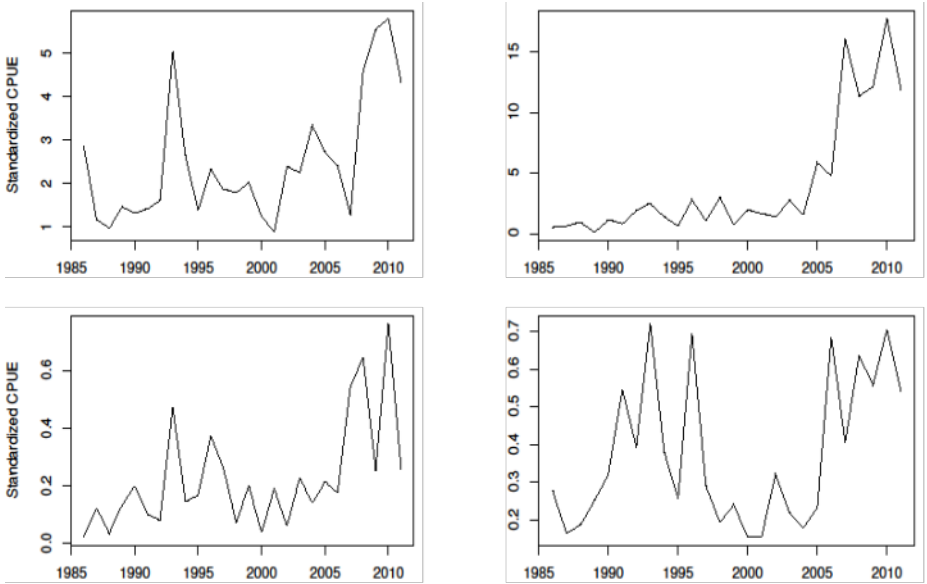


Figure 14 Standardized CPUE time series of brown shrimp (a), Atlantic croaker (b), silver seatrout (c) and sand seatrout (d) from statistical zone 15 in the Gulf of Mexico from 1986 to 2011

Results

The CPUE time series of brown shrimp and three fish species in zone 15 from 1986 to 2011 are shown in Figure 14. Time series of other zones can be found in the supplementary material. The zone-specific results that follow are for zone 15 unless specifically noted otherwise. Brown shrimp showed an intermediate level of fluctuations among all the species considered over the 26-year period, with CPUEs peaking in 1993 and 2010. Atlantic croaker was the most abundant among all the species, and its CPUE abruptly increased from 2006 to 2007. Silver seatrout and sand seatrout showed patterns similar to brown shrimp, with peaks around 1995 and 2009, but their time series appeared to exhibit a higher frequency of fluctuations.

ADF tests showed that the existence of a unit-root could not be rejected, and the tests on first differenced data all rejected the existence of a unit-root at the 1% level (Table 1). This suggested that the original log-transformed time series were non-stationary, and were integrated of order one. Unit-root tests on the data from other zones also showed the prevalence of unit-root non-stationarity in the CPUE time series (see supplementary material).

The likelihood ratio test statistic of a restricted intercept model against the unrestricted model was 0.68 ($p=0.88$). The tests from other zones all supported the model with a restriction on the intercept. The Johansen rank test showed that, under the restricted model, the null hypothesis of no equilibrium relationships was rejected at the 5% level, and the null of less than or equal to one equilibrium relationship could not be rejected (Table 2). For this case, I accepted that there was one equilibrium relationship in the

community assemblage dynamics. Estimates of α and β from the intercept-restricted model with $r=1$ were then obtained (Table 3).

Table 1 Results for augmented Dickey-Fuller tests on variables from statistical zone 15

Variables	P.A.	M.U.	C.N.	C.A.	Δ P.A.	Δ M.U.	Δ C.N.	Δ C.A.
Statistics	-0.43	0.52	-1.51	-1.34	-4.67**	-4.33**	-5.73**	-4.90**
Lags	1	1	1	1	1	1	1	1

P.A.: brown shrimp, M.U.: Atlantic croaker, C.N: Silver seatrout, C.A.: sand seatrout. The critical values for a Dickey-Fuller distribution without drift with sample size $N=25$ at 1%, 5% and 10% levels are -2.66, -1.60 and -1.95 respectively (Banerjee et al. 1993).

* Significant at the 5% level; ** Significant at 1% level.

Table 2 Johansen co-integration test of the rank of matrix **B** from the intercept restricted model from statistical zone 15 with critical values at the 5% and the 1% level

H_0	H_a	Statistics	5%	1%
$r=0$	$r \geq 1$	53.58*	53.42	60.42
$r \leq 1$	$r \geq 2$	26.08	34.8	40.84
$r \leq 2$	$r \geq 3$	9.18	19.99	24.74
$r \leq 3$	$r \geq 4$	2	9.13	12.73

Table 3 Maximum likelihood estimates of α and β in Model $H_1^*(2)$ of statistical zone 15

Variable	Intercept	P.A.	M.U.	C.N.	C.A.
β	6.97	-1.76	-1.12	4.48	-2.55
α		-0.015	0.16	-0.41	-0.021

Table 4 Number of equilibrium relationships (E.R.s) and p -values of the test of the significance of brown shrimp in community assemblage dynamics

Zone	No. of E.R.s	Significance of P.A.
11	1	0.79
13	1	0.53
14	0	-
15	1	0.35
16	2	<0.001
17	2	<0.001
18	1	0.0059
19	0	-
20	1	0.097
21	1	0.087

Table 5 Tests of bottom-up and top-down effects in zones 16 to 18

Zone		Bottom-up effect	Top-down effect
16	Statistics	11.2	4.17
	p -value	0.011	0.12
17	Statistics	2.18	4.03
	p -value	0.54	0.13
18	Statistics	18.8	1.87
	p -value	<0.001	0.17

The hypotheses testing showed that the species interaction pattern was location-dependent in the Gulf of Mexico. Community assemblages in zones 14 and 19 did not show any equilibrium relationship, those in zones 16 and 17 showed two equilibrium relationships, and the rest of the locations showed one significant relationship (Table 4). The test of significance of the brown shrimp population in the equilibrium relationship(s)

showed positive results in zones 16, 17 and 18, indicating a significant contribution of brown shrimp. The tests of bottom-up and top-down control then were conducted on these three zones. The contribution of the brown shrimp population to the equilibrium relationship was not significant in zones 11, 13, 15, 20 and 21, where the recognized equilibrium relationship was among the fish species.

Significant bottom-up effect was identified in two out of those three assemblages, where the brown shrimp population had significant contributions to the long-run component in the community dynamics (Table 5). Top-down effect was not significant in those three assemblages. In zone 17, neither the bottom-up nor the top-down effect was identified.

Discussion

In this chapter, I demonstrated a new practical approach for testing bottom-up and top-down processes in a multi-species community with short time series that appear to be non-stationary. This approach explicitly tests for and incorporates non-stationary dynamics in multivariate time series, which are common in ecological and fisheries data. Compared with the traditional correlation approach, results of this method are robust against complex and/or partially observable community structure. The method demonstrated here is a type of restricted VAR model, and it explicitly incorporates non-stationary dynamics in the model formulation and estimation. For systems exhibiting high-frequency fluctuation due to strong nonlinearity, e.g. chaotic dynamics, a method based on nonlinear state-space reconstruction can be used (Sugihara et al. 2012).

The method presented in this chapter is related to MAR models in fisheries (Hampton et al. 2013). The new method here adds to traditional MAR modeling by using the non-stationarity feature of the data to highlight long-term relationships within the community. The utility of the method presented in this chapter is not necessarily the addition of non-stationarity into the statistical model, but the ecological questions we can ask based on this data-oriented modeling framework. The approach could be applied to a large number of existing data sets to test hypotheses of species interaction patterns in community dynamics.

The analysis of reduced rank VECM as presented in this chapter is also closely related to dynamic factor analysis (DFA) (Zuur et al. 2003) in the fisheries literature. The motivations for both methods are similar in analyzing non-stationary dynamics in time series, but the difference lies in their representations of the process. DFA characterizes time series in terms of a linear combination of unobserved random walks or common trends, and the co-integration method constructs time series using the disequilibrium error from equilibrium relationships. These two approaches are in fact complementary (Engle and Granger 1987, Johansen 1995). The dynamic factor analysis focuses on the extraction of common trends, which do not attach any immediate ecological meaning other than the fact that these common trends are shared across multiple time series. The method presented here finds linear combinations of the original time series that cancel out the shared common trends in order to extract a more stable time series. Finally, this method is built upon a multi-species model and various ecological hypotheses can be readily constructed, e.g. top-down and bottom-up controls.

Can unit-root processes represent the non-stationary dynamics exhibited by natural populations? The Lewontin-Cohen model (Lewontin and Cohen 1969) is an example of unit-root model representing a population under a stochastic environment (Niwa 2007, Cohen 2013). As in the Lewontin-Cohen model, unit-root processes are statistical approximations to the dynamics; therefore, they should not be taken as representing the true underlying mechanism. For example, according to this model, individual population abundances can grow arbitrarily large given enough time, but for natural populations, there is always some upper bound imposed on population growth, e.g. by food shortage or lack of suitable habitat. On a longer time scale, this behavior of natural populations contradicts the model. However, when the observation period is relatively short for ecological studies, e.g. 26 years in this study and 31 to 60 years in (Niwa 2007), unit-root models can provide reasonable approximations to the underlying processes and can be used to gain insights into the population and community dynamics.

When top-down processes exist, they are often referred to as trophic cascades, which implies that top-down forces mainly occur in communities with chain-like trophic structures, or trophic ladders (Strong 1986). The simplistic view of top-down process was the assumption behind the correlation analysis. Top-down processes, as defined in the introduction of this chapter, on the other hand, can incorporate more species interactions.

In marine ecosystems, bottom-up processes are considered more prevalent (Cushing 1975, Aebischer et al. 1990, Verity and Smetacek 1996, Chavez et al. 2003) and sometimes are treated as the “normal state” (Strong 1986, Frank et al. 2006), whereas top-down processes are considered to be limited to near-shore and inter-tidal communities

with simple trophic structures (Chapin et al. 1997, Pinnegar et al. 2000). Results for the Gulf of Mexico marine communities indicate a diversity of species interaction may be involved in dynamics. Brown shrimp did not have an equilibrium relationship with the three fish species investigated in either the west or north sides of the study area. In the central zones of the study area, brown shrimp contributed significantly to the community assemblage dynamics. A significant bottom-up effect was identified in two of those three central zones. In this study, fish species were selected based on their high population density, and this might have resulted in an inability to detect top-down effect. Further research should also investigate how environmental covariates, including anthropological factors, impact observed community dynamics.

CHAPTER IV

A COMPARISON OF STATISTICAL METHODS FOR TESTING SPECIES INTERACTIONS FROM SHORT, NOISY TIME SERIES DATA

Introduction

Species interactions are critically important in ecological research and population management. For example, recent models of species invasion (Cronin et al. 2014, Henriksson et al. 2014, LeBrun et al. 2014), species distribution (Clark et al. 2014, Yackulic et al. 2014), infectious disease (Bauer and Hoyer 2014, Selakovic et al. 2014, Wood et al. 2014) and fisheries management (Link et al. 2011, Möllmann et al. 2014, Plagányi et al. 2014) incorporate biotic interactions among species to address deficiencies in single species models. However, one of the difficulties in incorporating species interactions is determination of the functional form and associated parameters related to species interactions. In this chapter, I compare four different methods to detect species interactions from time series data, and evaluate their performance on short and noisy data, a common situation in ecology.

There are two major ways to study the dynamic patterns of species interaction: one based on manipulative experiments (Lubchenco and Menge 1978, Paine 1980) and the other based on analysis of time series data from surveys (Stenseth et al. 1997, Turchin et al. 2000, Berryman and Turchin 2001). These different approaches offer complementary views on community dynamics. Manipulative experiments can focus on specific aspects of species interactions and offer high resolution regarding the functional form of the

interaction (Holling 1966, Arditi and Ginzburg 1989, Jost et al. 2005a). However, an efficient implementation of manipulative experiments is not always feasible. Furthermore, the spatial scale of the ecological community can be too large to be manipulated in experiments, and as the number of species in a community grows, the number of potentially interacting species can become overwhelmingly large. On the other hand, the inference of species interactions based on time series data analysis focuses on the long-term integrated response of both inter- and intra-specific interactions because of the coarser temporal resolution of the data, often consisting of annual observations. This type of analysis can be used to explore species interactions based on available databases that include time series data on multiple populations from the same location (Stuntz 1983, Inchausti and Halley 2001). In this chapter, I focus on the latter type of study.

Different statistical approaches have been used to detect species interactions from population time series data. The most common method is the correlation coefficient (CC) method. It is the easiest to apply among the four to be compared in this study and widely used in spite of known problems (Sugihara et al. 2012). The second approach, simple linear regression (SLR), often is used to incorporate a time lag in ecological responses by regressing the response variable on a time lagged predictor variable. The third approach, multivariate autoregressive (MAR) models, is the currently recommended approach to study biotic and abiotic interactions (Hampton et al. 2013). As a generalization of the lagged SLR method, this method incorporates more than just one time lag. In MAR models, the underlying process is presumed to be stationary (Ives et al. 2003). When some time series are non-stationary, the approach proposed by Zhou and Fujiwara (2015) can

be used, but it is not always easy to distinguish between stationarity and non-stationarity based on observed population time series, especially when time series are short and noisy. In this study, I propose a fourth method, integration-cointegration robust (ICR) models, to detect species interaction when there is uncertainty about the stationarity of the data.

In this chapter, I first compare the performance of the four different statistical methods (CC, SLR, MAR, ICR) by applying them to short and noisy time series data generated by hypothetical predator-prey models representing three types of predator-prey relationships (interactive, bottom-up, top-down) at each of three levels of observational noise (low, medium, high). Then I apply the methods to population time series of a predator-prey pair from the Gulf of Mexico to demonstrate their use.

Methods

Data generating model

Here, I used a predator-prey model to generate the data; however, other species interaction models also could be used. The data-generating model was configured to mimic natural population dynamics. The long-term dynamics of the system were stationary, but the short-term dynamics might exhibit apparent non-stationary fluctuations similar to a random walk. I chose this type of dynamics for the simulation model because of the commonly observed non-stationary fluctuations in a previous study (Zhou and Fujiwara 2015). To ensure long-term coexistence, I restricted the long-term dynamics to be stationary, such that neither of the populations would go extinct nor become arbitrarily large in the long-run. In addition, the interaction between prey and predator in the

simulation model included nonlinearity. However, to represent our uncertainty about the true form of species interaction, none of the testing models incorporated this nonlinearity.

To generate population time series, I used a predator-prey model with a ratio-dependent predation and Beverton-Holt density-dependent the prey survival (Zhou et al. 2013). In this study, both predator and prey populations were unstructured. Three types of interaction between predator and prey populations were explored. The first type was the interactive case, where I retained both the effect of prey on predator abundance and the effect of predator on prey abundance. The second type was the bottom-up case, where only the effect of prey on predator abundance was retained. For the third type, the top-down case, only the effect of predator on prey abundance was retained. Data sets generated with these models were used to obtain the false acceptance rates (type-II statistical error) of the statistical methods.

In order to obtain the false rejection rate (Type-I statistical error), I ran two separate sets of simulations, with each set containing each type of predator-prey model (bottom-up, top-down, interactive). I then combined the prey time series from each model in the first set with the predator time series from the corresponding model in the second set (e.g. I combined the prey time series from the bottom-up model in the first set of simulations with the predator time series from the bottom-up model in the second set of simulations).

When simulating the data as described above, process error was incorporated by allowing a demographic parameter of either the prey or predator population to fluctuate. I chose to let the prey background survival and predator conversion rates fluctuate in this study. The fluctuation in population density resulting from the process error was

stationary, but it often exhibited apparent non-stationarity because of the short observation period (Nicolau 2002). One simulation of a bottom-up controlled system is plotted in Figure 15. The simulated prey abundance fluctuated around the population mean abundance in the long-run (Figure 15 a). However, when the observation period was short, the dynamics appeared to be non-stationary (Figure 15 b).

A zero-mean Gaussian observation error (noise) was also added to all of the simulated time series data. The level of observation error was measured by signal-to-noise ratio (SNR). It was calculated as the ratio of the variance of the simulated data without noise to the variance of the added noise. I used three levels of observation noise: low (10:0.5), medium (10:2, 10:1) and high (10:4).

For each scenario, a time series of 230 data points were simulated with the final 30 data points retained for testing. See supplied code for model specifications.

Simple linear regression (SLR) procedure

Under a simple linear regression procedure, the predator (P_t) and prey (V_t) populations were modeled as

$$P_t = bV_{t-1} + c_1 + \varepsilon_t,$$

$$V_t = dP_{t-1} + c_2 + v_t,$$

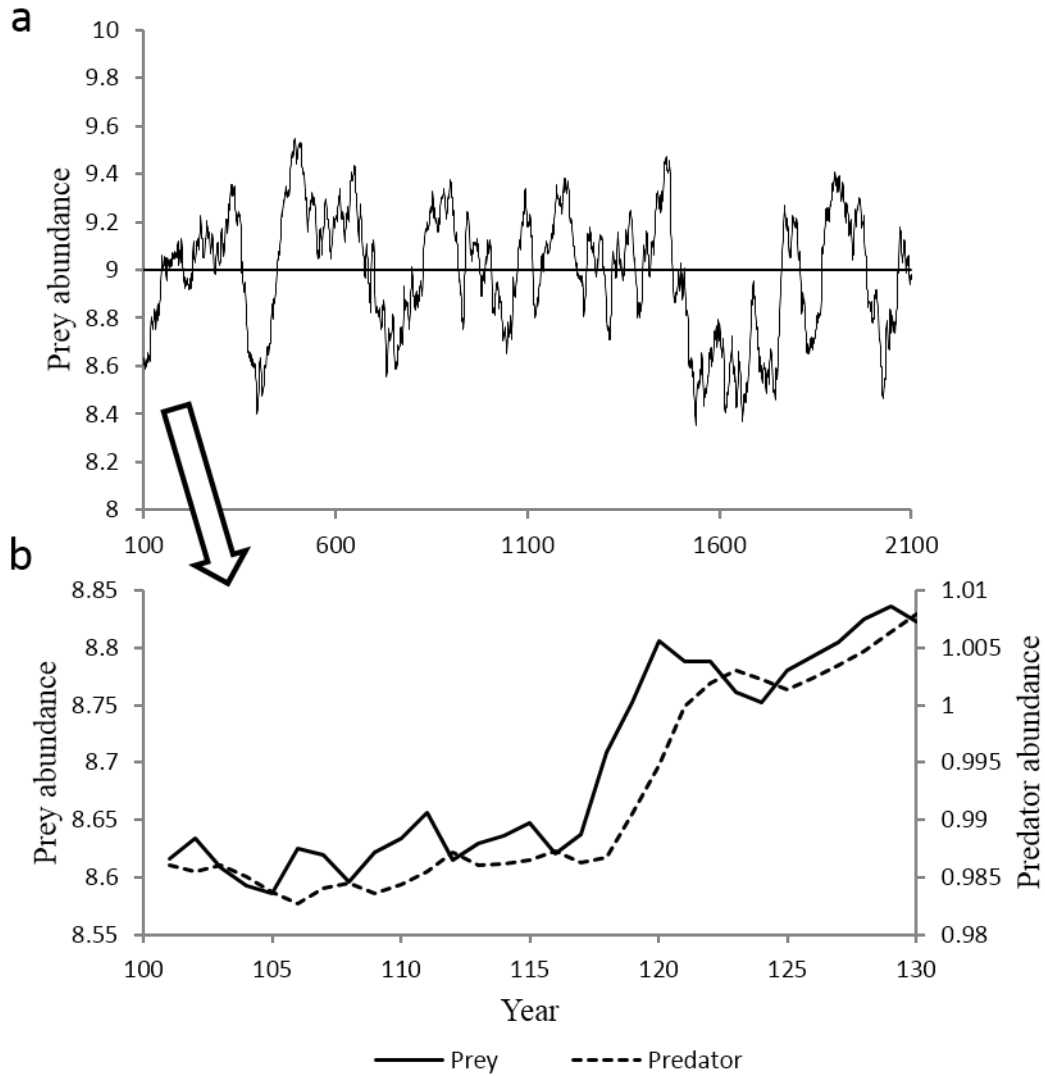


Figure 15 Simulated time series of a bottom-up controlled predator-prey model. The prey population (a) had a stationary fluctuation around its theoretical population mean (the horizontal line in panel a). The predator abundance followed the prey abundance with a time lag over the 30-year period (b). The model was simulated for 2100 years, and the first 100 years of data were discarded.

where b and d measured the interspecific effects, c_1 and c_2 were intercepts, and ε_t and v_t were stochastic terms for predator and prey, respectively. The SLR method classified the system into all four categories: bottom-up, top-down, interactive, and no interaction. The system was bottom-up when the $d = 0$ and $b \neq 0$; the system was top-down when $d \neq 0$ and $b = 0$; the system was interactive when both interspecific effects were not zero; and finally, there was no interaction when both coefficients were zero. Significance was determined through a nonparametric bootstrap. First, a model was fitted to the data to obtain the residuals. A random sample was drawn with replacement from the residuals. Then, the model was refitted to a new data set formed by combining the fitted values with the random sample. This was repeated 499 times.

Correlation coefficient (CC) procedure

Using the correlation coefficient of predator and prey time series data, the interaction was classified into: 1) bottom-up, 2) top-down and 3) indeterminate. These categories corresponded to a significant positive, significant negative and insignificant correlation coefficient, respectively. Note that this method did not allow the identification of an interactive case. Pearson's product moment correlation coefficient (r) was calculated as an initial estimate. Then, r was adjusted for autocorrelation with a modified Shelton method (Pyper and Peterman 1998). Because of the time lag in the data generation model, the bottom-up hypothesis was tested based on the adjusted correlation coefficient of prey abundance at time t (V_t) and predator abundance at time $t-1$ (P_{t-1}), and the top-down hypothesis was based on the adjusted correlation coefficient of predator abundance

at time t (P_t) and prey abundance at time $t-1$ (V_{t-1}). This assumed I knew the appropriate time lag *a priori*.

Multivariate autoregressive (MAR) procedure

Under the MAR procedure, the vector of predator and prey populations, $X_t = (P_t, V_t)^T$, was modelled as

$$X_t = \mu + \sum_{i=1}^k \Phi_i X_{t-i} + \varepsilon_t ,$$

where μ was a vector of intercepts, k was the number of lags to be included in the model, Φ_i was a matrix of coefficients for lagged variable X_{t-i} and ε_t was a vector of stochastic terms. Ordinary least square estimates were used for estimating parameters, and the maximum lag order k was chosen based on BIC (Schwarz 1978).

Likelihood ratio tests were used to test hypotheses about interaction types. To test for a bottom-up effect, the null hypothesis of no prey effect on the predator dynamics was constructed as zero-restrictions on the coefficients corresponding to lagged prey variables in the predator equation, i.e., every (1,2) element of matrix Φ_i was set to zero. To test for a top-down effect, the null hypothesis of no predator effect on prey dynamics was constructed as zero-restrictions on the coefficients corresponding to lagged predator variables in the prey equation, i.e., every (2,1) element of matrix Φ_i was set to zero. Finally, to test for an interactive effect, the null hypothesis of no interaction between predator and prey was constructed by placing both types of restrictions, as in the tests of bottom-up and top-down effects. For stationary time series, the likelihood ratio test

statistic had an asymptotic χ^2 distribution, but for short time series, the approximation based on large sample theory was poor. Therefore, the test statistics were compared to a distribution estimated by a nonparametric bootstrap. First, a model was fitted to the data to obtain a T by n residual matrix, where T was the length of the time series and n was the number of species, e.g. in this study 30 by 2. Then, in each bootstrap step, a random sample was drawn from the residual matrix with replacement to create a new set of residuals. To maintain the covariance structure of errors for different species, the residuals were sampled as a set in each row from the same time point. Finally, the model was fitted to the new data set formed by combining the fitted values with the random sample. For the estimation of type-I and type-II error rates, each bootstrap procedure had 499 replicates, and for the case study, the number of replicates was set to 1999.

Integration-cointegration robust (ICR) procedure

When the stationarity assumption of time series is not met, the likelihood ratio test statistics in the MAR procedure have a nonstandard asymptotic distribution (Sims et al. 1990, Toda and Phillips 1993). In such cases, the estimation can be done in the error correction form of the MAR model by finding linear combinations of time series to form stationary time series (Johansen and Juselius 1990a). However, this procedure requires additional pretesting of the time series (i.e., testing for the existence of any cointegration relationship), and the interpretation of the final test statistics is not straightforward because their distribution is a mixture of nonstandard distributions. Here, I used a method proposed by Toda and Yamamoto (1995) to overcome these issues. To my knowledge, it is the first time this method is applied to ecological data.

Toda and Yamamoto's method can be implemented into the MAR procedure with relative ease. Instead of estimating a MAR model with the selected order k , a $MAR(k+d)$ model was estimated, where d denotes the hypothesized minimum number of repeated first differencing to make the original time series stationary. For ecological time series, d is often thought to be 1 (Niwa 2007), and it was set to 1 in this study. First, lag length k was selected based on BIC, and then a $MAR(k+d)$ model was fitted to the data. In constructing the likelihood ratio tests, the estimates of the last d coefficient matrices were ignored, and only the estimates of the first k coefficient matrices were used. The likelihood ratio test statistics calculated from this procedure had the standard asymptotic distribution, and they were bootstrapped as in the MAR procedure. Furthermore, this procedure is applicable to multivariate time series that may be stationary or with any order of required differencing (by increasing d).

Performance measures

To measure the performance of each statistical method, I applied each procedure to the simulated dataset, and recorded the results. The process was repeated 5,000 times for the combination of each interaction type and each noise level. I chose the length 30 years because this length is becoming common in ecological data, e.g. Niwa (2007), Stuntz (1983), Yao et al. (2000), but from a statistical point of view, it is still short.

Both the type-I and type-II error rates were assessed at nominal significance levels of 1%, 5% and 10%. The results of the nominal 5% significance level are presented in the main text, and the results on the other two significance levels can be found in Appendix D. The nominal significance level, denoted as α , is the level of type-I error rate chosen by

researchers before conducting the study. However, the real type-I error rate of the method may differ from the nominal level when, for example, the distribution of the test statistic is based on large sample theory and the sample size is small, or the method is not robust against violations of some assumptions not met by the data. In this study, with the interaction type for each data set known *a priori*, I calculated the real type-I error rate of each method based on simulated data and then compare the real type-I error rate with the nominal significance level. This would provide insight about the performance of each method with field data where the actual mechanism is unknown. All of the analyses were done with R (R Development Core Team 2015).

A case study from the Gulf of Mexico

Time series of catch per unit effort (CPUE) data of brown shrimp (*Farfantepenaeus aztecus*) and largehead hairtail (*Trichiurus lepturus*) were used in this study. Brown shrimp is the most abundant among the penaeid shrimps found in the northern Gulf of Mexico (Farfante and Kensley 1997), and largehead hairtail is a predatory fish that primarily feeds on small fish, shrimp and squid (Bittar et al. 2012). Data were collected annually by the United States National Marine Fisheries Service through the Southeast Area Monitoring and Assessment program (Stuntz 1983). I first tested the non-stationarity of the time series using both unit-root and stationarity tests (See the Appendix D for details). Then, I applied all of the four statistical procedures to analyze the type of population interaction.

Results and discussion

Type-I error rate

A summary of the type-I error rates is shown in Table 6 for the four procedures described above. The error rates for the SLR, CC and MAR procedure were consistently higher than 5% when α was set at 5%. This bias was expected because they failed to account for potential non-stationarity in the data. The ICR method, which accounts for potential non-stationarity, exhibited improved performance in controlling the type-I error rates.

The modified Shelton method adjustment under CC had consistently higher error rates than the 5% nominal value at all the noise levels and all the interaction types. However, the pattern of the error rates varied at other α values (for $\alpha=0.01$, this method was conservative, and for $\alpha=0.10$, the error rate exceeded the 10% value by a large margin, Appendix D). A test is conservative if, when constructed for a given nominal significance level, the true probability of incorrectly rejecting the null hypothesis is smaller or equal to the nominal level. The uneven distribution of the p values from this method under the null hypothesis revealed that adjusting the sample alone, as in the modified Shelton method under CC, was not sufficient to account for autocorrelation in the underlying processes that generated the data.

Results for the MAR procedure showed that the error rates were consistently higher than the α value, and they depended on the type of predator-prey interaction (Appendix D). With the interactive model, this procedure had higher error rates than those from a bottom-up or top-down controlled model at the same noise level. With increasing

noise level, the error rate also increased within the same interaction category. This trend came from the reduced information on species interaction due to the elevated noise level in the data set.

Table 6 Estimated percentages of correctly accepting the null hypothesis of no interaction using the four different methods at a nominal 5% significance level and the associated signal to noise levels (SNR)

SNR	Type of interaction	ICR	MAR	CC	SLR
10:0.5	Interactive	95.98	90.14	-	89.50
	Bottom-up	96.28	93.04	93.22	93.24
	Top-down	96.24	92.50	93.70	92.40
10:1	Interactive	95.58	90.28	-	89.66
	Bottom-up	96.58	92.72	93.46	93.26
	Top-down	95.62	91.92	93.26	92.12
10:2	Interactive	94.44	87.54	-	88.48
	Bottom-up	95.30	91.54	92.94	92.42
	Top-down	95.02	91.16	92.56	91.12
10:4	Interactive	93.96	87.96	-	87.44
	Bottom-up	94.84	91.20	93.12	92.32
	Top-down	94.32	89.98	92.92	91.00

Finally, the ICR procedure was conservative at the low noise level, and the error rates were consistent at different α values (Appendix D). At the low noise level, the error rates were smaller than the α values, i.e., the test procedure became an α level test. The distribution of the p values from the null hypothesis further showed that, for the low noise level, the distribution was skewed to the right, and for medium and high noise levels, the

distributions were approximately uniform (Appendix D Figure 17-28). Therefore, the results from the ICR procedure were approximately valid at the specified α level.

These results suggest that the common procedures (modified Shelton and MAR methods) to correct for autocorrelation in time series data may not be sufficient. Such methods may confer false confidence about identified interactions when the time series has apparent non-stationarity. On the other hand, the ICR method had the best control over the type-I error rate, and it was conservative when the noise level was low.

Type-II error rate (power analysis)

A summary of the empirical power of four different testing procedures is shown in Table 7. Results showed that both the level of observation noise and the type of interaction strongly affected the ability of the procedures to identify the correct effect. With an increasing level of observation noise, the ability to determine the interaction type declined under all testing procedures. Among the four procedures, the CC procedure had the highest percentage of correctly identifying bottom-up and top-down controls.

Among the other three approaches, the SLR and MAR methods showed similar statistical power in detecting the type of species interactions, and the ICR method showed lower statistical power than the SLR and MAR methods. In addition, I adjusted the p value of each test to 5% based on the simulated distribution of the test statistics under the null hypothesis, and found that the ICR method still had lower power than the CC and MAR methods.

Table 7 Estimated percentages of correctly accepting the alternative hypothesis of interaction using the four different methods at a nominal 5% significance level and the associated signal to noise levels (SNR)

SNR	Type of interaction	ICR	MAR	CC	LR
10:0.5	Interactive	13.44	38.28	-	36.84
	Bottom-up	17.36	50.70	56.70	52.90
	Top-down	15.40	40.98	56.72	41.92
10:1	Interactive	13.38	35.36	-	34.30
	Bottom-up	14.40	37.74	45.90	44.26
	Top-down	12.44	31.88	47.70	30.22
10:2	Interactive	11.62	32.62	-	34.62
	Bottom-up	14.00	32.78	43.14	29.82
	Top-down	10.26	25.48	30.68	27.42
10:4	Interactive	11.28	27.82	-	29.44
	Bottom-up	11.82	23.40	22.44	24.98
	Top-down	10.00	21.46	20.14	22.40

Compared with the CC and MAR methods, results suggested that using the robust method (ICR) incurs a loss in the power to detect an interaction. Therefore, I recommend using the use of all three methods with the ICR method as a baseline result, whenever non-stationarity is a concern.

Application to real data

To show how different identification procedures work with empirical data, I used a bivariate time series of brown shrimp and largehead hairtail catch per unit effort (CPUE) data from the Gulf of Mexico (Figure 16). Based on unit-root test results, the non-stationarity could not be rejected for both population time series at the 10% level, and the non-stationarity of the first differenced time series were all rejected at the 1% level (Table 8). This result suggested that the original time series was non-stationary, but became

stationary after first differencing. This was further corroborated by the result from the stationary test.

I applied SLR, CC, MAR, and ICR methods to this pair of population time series. The SLR method identified both bottom-up ($p=0.0215$) and top-down ($p=0.02$) effects, but the interactive interaction was not significant ($p=0.2155$). The CC method failed to identify any effect with a one-year time lag (bottom-up: $p=0.078$, top-down: $p=0.13$). Both the MAR and ICR methods identified a significant bottom-up effect (MAR: $p=0.0175$, ICR: $p=0.0205$).

Based on these results, I conclude that there is a significant bottom-up effect of brown shrimp on the dynamics of largehead hairtail. Both population time series were tested to be non-stationary, whereby violated the stationary assumption of the SLR, CC and MAR methods. Thus, the significance of the test could be overestimated based on those methods. With the ICR method, the bottom-up effect was still significant after correction for non-stationarity. Finally, the modified Shelton adjustment probably over-corrected the p value because the CC method displayed a non-uniform distortion of the p values based on the simulated data sets.

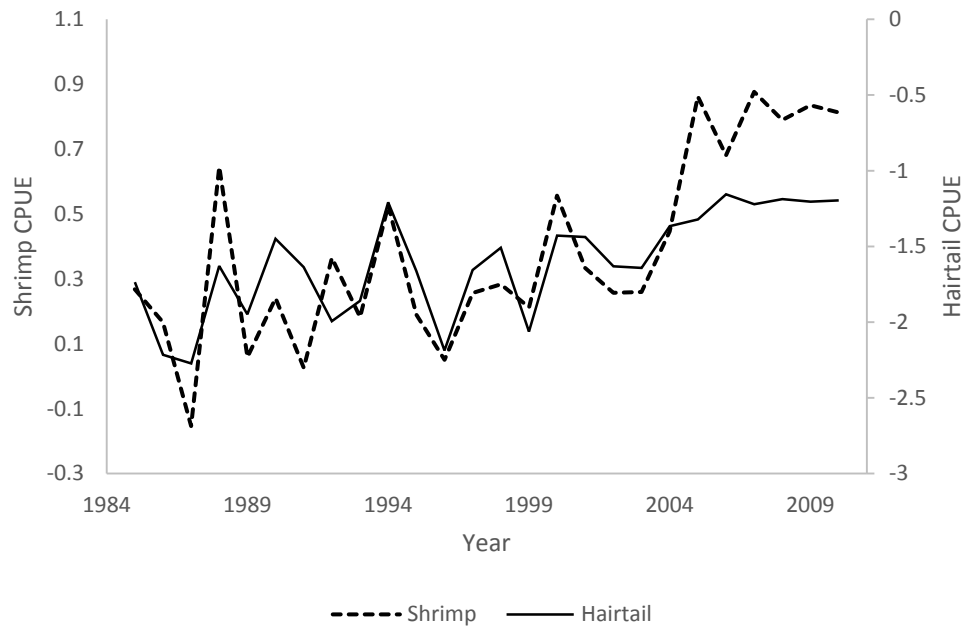


Figure 16 Brown shrimp and largehead hairtail CPUE (logarithmic scale) time series. Data are from the Southeast Area Monitoring and Assessment program of the National Marine Fisheries Service (Stuntz 1983).

Table 8 Results of non-stationary and stationary tests on population densities in level and first differenced time series

		Unit root tests			Stationary test
		ADF	ERS	PP	KPSS
Shrimp	Original	0.45	11.95	-2.51	0.71*
	First-differenced	-3.67**	0.44**	-11.28**	0.093
Hairtail	Original	-1.46	14.92	-2.7	0.76**
	First-differenced	-9.21**	0.2**	-9.65**	0.1

The null hypothesis of unit root tests (ADF, ERS and PP) are that there is a unit root, i.e., non-stationary, while the null hypothesis of the stationarity test (KPSS) is that the process is stationary. See Appendix C for details.

Significance levels: ** 0.01, * 0.05.

Conclusions

In this chapter, I compared four different procedures to detect species interaction types from short and noisy time series data. Although this chapter revealed difficulties in detecting species interactions, we can still make some inferences about species interactions from such data. Among the four methods compared, CC, MAR, and ICR accounted for autocorrelation in time series data, but only ICR accounted for non-stationarity. I suspect these differences led to the differences in the performance of the methods.

As expected, SLR, CC and MAR methods had very high type-I error rate. This suggests we should avoid using these methods for testing species interactions. The ICR method had the best control over the type-I error rate; however, the power of the method was weak. On the other hand, the SLR, CC and the MAR modelling approaches had higher power, but could not adequately control the type-I error rate. As a result, I recommend different methods for different purposes: the ICR method is preferred for hypothesis testing with short and noisy time series data because it had the best control over type I error rate; the SLR, CC and MAR methods are preferred for classification problems, but the p -value produced by these methods should not be trusted.

Non-stationary fluctuation in abundance has been documented in many marine populations (Niwa 2007), but there also are much data exhibiting stationary fluctuations (Beisner et al. 2003). This difference in observed dynamics may stem from how each population is regulated (Strong 1986). Such information, i.e., the form of density-dependence, is expected to be specific to each population and difficult to identify. Under

such uncertainty, the ICR method is probably best suited to explore species interactions with a controlled α , i.e., when the ICR method detects an effect, for which there is confidence regarding its effect at the chosen significance level. However, it is also important to keep in mind that the power of the ICR method is weak and the ICR method may fail to detect an existing effect. In sum, the ICR method is robust in testing species interactions with short and noisy time series, and researchers should carefully consider the rigor of alternative statistical methods, their assumptions about underlying processes and the aim of the study when choosing the method to use.

CHAPTER V

CONCLUSION

In this dissertation, I have demonstrated theoretical and practical difficulties in studying species interactions, specifically, predator-prey interactions, but many of those difficulties can be dealt with through careful modeling and data analysis. Dynamics of the predator-prey models are strongly affected by the life history properties of the populations. This underscores the importance of including life history information into mathematical models. Concerning analysis of empirical data, it is important to evaluate the validity of the assumptions behind the methods and to choose appropriate methods to avoid spurious results. When some of the time series are non-stationary, the co-integration method proposed in Chapter III appears to be most suitable. The ICR method proposed in Chapter IV should be used when the stationarity of the system is uncertain and the priority is in controlling type-I error; however this method had low statistical power. In practice, I recommend using the ICR method along with other methods to balance statistical robustness of statistical methods with assumptions about underlying population dynamic processes. At the same time, other approaches, such as experimentation and life table analysis, also can provide important insights into species interactions.

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APPENDIX A

In this section, I describe a general predator-prey model using ODEs and the stability analyses to show that bias will be introduced when a continuous-time model is used to approximate a discrete system without care. A general predator-prey model can be written as

$$\frac{dN}{dt} = f(N)N - g(N, P)P, \quad (\text{A.1})$$

$$\frac{dP}{dt} = h(N, P)P - \mu P, \quad (\text{A.2})$$

where $f(\cdot)$ is the per capita rate of growth of prey in the absence of predator, $g(\cdot)$ is the per capita kill rate of predator on prey, $h(\cdot)$ is the per capita growth rate of predator, and μ is the per capita mortality rate of predator in the absence of prey. The production of predators [$h(\cdot)$] can be approximated by a linear function of the per capita kill rate of predator [$g(\cdot)$].

The mathematical forms of the right hand sides of Eq. (A.1-2) will be determined by empirical evidence from manipulative experiments or surveys, and all the empirical evidence directly obtained from experiments is discrete in nature. For example, attack functions derived from these empirical methods are recognized by Royama (1971) and Berryman (1995) as “overall” hunting equations that measures the number of prey killed during time τ , which is the duration of the experiment. Going back to the general model, we can see that now the right hand side of Eq. (A.1- 2) is a discrete-time process that

shows the change in abundance over a finite period of time, at least τ the duration of the experiment, and the left hand side is an instantaneous process that shows the rate of change in abundance when τ approaches zero. This disparity in time, if not treated properly, could introduce artifacts into the final model. At the same time, I agree with the idea that if time τ is sufficiently small in the experiments, or the loss of prey during the experiment period is negligible compared with other errors in data (Jost et al. 2005b), then the discrete-time process could be a good approximation of the instantaneous process for practical purposes. Yet, for the predator-prey systems exhibiting seasonal reproduction and continuous predation, the final model needs the number of prey killed during the entire period in between two adjacent recruitment events, and this requirement makes τ ecologically different from an instantaneous time. Therefore, the inherent time step should not be omitted in the overall model of the form Eq. (A.1 - 2), regardless of the length of the experiment. Next I show one way to properly treat this time step issue in differential equations.

Suppose the inherent time step of empirical experiments to be τ , which is the duration of one hunting season for reasons stated above, and then I obtain the rate of change of prey abundance as

$$\frac{\Delta N}{\Delta t} = \frac{N(t + \tau) - N(t)}{(t + \tau) - t} = \hat{y}, \quad (\text{A.3})$$

where $N(t)$ is prey abundance at the start of one season, $N(t + \tau)$ is prey abundance at the start of the next season and reflects predatory mortality and recruitment, and \hat{y} is the specific function obtained from empirical experiments, which is usually an implicit

function of time. Next, suppose function $N(t)$ is infinitely differentiable in the neighborhood of t , then I expand $N(t + \tau)$ around t in Eq. (A.3),

$$\frac{\Delta N}{\Delta t} = \frac{dN}{dt} + \frac{\tau}{2!} \frac{d^2 N}{dt^2} + \frac{\tau^2}{3!} \frac{d^3 N}{dt^3} + \dots, \quad (\text{A.4})$$

From Eq. (A.3-4), I obtain

$$\frac{dN}{dt} = \hat{y} - X_n(\tau \ddot{N}), \quad (\text{A.5})$$

where $X_n(\cdot)$ is a polynomial of second and higher order derivatives of N with respect to time. The same argument could be made for the predator population

$$\frac{dP}{dt} = \hat{z} - X_p(\tau \ddot{P}), \quad (\text{A.6})$$

where \hat{z} is obtained from empirical experiments, and $X_p(\cdot)$ is another polynomial of second and higher order derivatives of P with respect to time. This final model (Eq. A.5 - 5) written in differential equations is the ‘underlying model’ for the data, and $X_n(\cdot)$ and $X_p(\cdot)$ are the terms omitted in models constructed by directly using empirical data without treatment, which I call the ‘instantaneous approximation model’.

Here, I do a side-by-side comparison of the dynamics of an underlying model and an approximated model:

Equilibria: Two models have the same equilibria, because at the equilibrium the first derivative of predator and prey abundance and all the higher derivatives all equal zero,

both $X_p(\cdot)$ and $X_n(\cdot)$ are eliminated. Thus, two models have the same sets of equilibria and isoclines.

Stability of these equilibria: Two models predict different dynamics around equilibria. The stability of a nonlinear system is assessed using Jacobian matrix, which is a linear approximation of the nonlinear model around equilibria. The Jacobian of the approximated model is

$$J_1 = \begin{bmatrix} \left. \frac{\partial}{\partial N} \hat{y} \right|_{N^* P^*} & \left. \frac{\partial}{\partial P} \hat{y} \right|_{N^* P^*} \\ \left. \frac{\partial}{\partial N} \hat{z} \right|_{N^* P^*} & \left. \frac{\partial}{\partial P} \hat{z} \right|_{N^* P^*} \end{bmatrix},$$

and the Jacobian of the underlying model is

$$J_2 = J_1 - \begin{bmatrix} \left. \frac{\partial}{\partial N} X_n(\tau \ddot{N}) \right|_{N^* P^*} & \left. \frac{\partial}{\partial P} X_n(\tau \ddot{N}) \right|_{N^* P^*} \\ \left. \frac{\partial}{\partial N} X_p(\tau \ddot{P}) \right|_{N^* P^*} & \left. \frac{\partial}{\partial P} X_p(\tau \ddot{P}) \right|_{N^* P^*} \end{bmatrix}. \quad (\text{A.7})$$

The extra term in Eq. A.7 cannot eliminate itself, and accounts for bias of the approximated model from the modeling process. Generally speaking, the dynamic behavior of the approximated model predicts different dynamics from the underlying model.

There are at least two ways to treat the original model to conform to the underlying model. One way is to exhaustively calculate all the higher order terms in continuous-time models, and it can be accomplished by carefully choosing the algebraic form of the trophic

function derived from empirical data. Much simpler and more natural way to our understanding is to use difference equations.

APPENDIX B

In this section, I present an analytical treatment of a predator-prey system exhibiting seasonal reproduction and continuous predation with difference equations. Similar to finding isoclines of ODE systems, isoclines of a discrete system are found when the rate of change of stage density is zero. It means that the dominant eigenvalue of the system is one. The eigenvalues of a $n \times n$ matrix \mathbf{A} are precisely those values of λ that satisfies $\det(\mathbf{A} - \lambda\mathbf{I}) = 0$. For the prey population in the community matrix (19), by setting λ to 1, I have

$$\det \begin{bmatrix} s_1(1-m_1)-1 & \frac{a}{1+\frac{a-1}{k}N_A} \\ s_1m_1 & p_1\left(1-\frac{\alpha P_A}{\beta P_A+N_A}\right)-1 \end{bmatrix} = 0. \quad (\text{B.1})$$

Let $\delta_1 = \frac{a-1}{k}$. Eq. (B.1) is calculated as

$$\left[s_1(1-m_1)-1 \right] \cdot \left[p_1\left(1-\frac{\alpha P_A}{\beta P_A+N_A}\right)-1 \right] - s_1m_1 \cdot \frac{a}{1+\delta_1N_A} = 0. \quad (\text{B.2})$$

I further denote $\delta_2 = s_1(1-m_1)-1$, $\delta_3 = s_1m_1a$. Thus, Eq. (B.2) is

$$\delta_2 p_1 \left(1 - \frac{\alpha P_A}{\beta P_A + N_A} \right) - \delta_2 - \frac{\delta_3}{1 + \delta_1 N_A} = 0. \quad (\text{B.3})$$

Further, let $\delta_4 = -\delta_2 p_1 \alpha$, $\delta_5 = \delta_2(1-p_1) + \frac{\delta_3}{1+\delta_1 N_A}$. From Eq. (B.3), the prey isocline is

$$P_A = \frac{N_A \delta_5}{\delta_4 - \beta \delta_5}. \quad (\text{B.4})$$

After back substitution, I can get expressions of φ_1 to φ_4 in Eq. 2.20.

The calculation of the predator isocline follows the same procedure. First, set λ to 1, and then the determinant can be calculated as

$$[s_2(1-m_2)-1](p_2-1) - s_2 m_2 \frac{c\alpha N_A}{\beta P_A + N_A} = 0. \quad (\text{B.5})$$

Let $\delta_6 = [s_2(1-m_2)-1](p_2-1)$, $\delta_7 = s_2 m_2 c\alpha$. From Eq.(B.5), the predator isocline is

$$P_A = \frac{\delta_7 - \delta_6}{\beta \delta_6} N_A,$$

and φ_5 in Eq. 2.21 is $\frac{\delta_7 - \delta_6}{\beta \delta_6}$.

Isoclines for the matrix 2.23 are calculated in the same way as shown above. For the prey isocline, by setting λ to 1, I have

$$\det \left(\begin{array}{cc} s_1 \left(1 - \frac{\alpha P_A}{\beta P_A + N_J} \right) (1 - m_1) - 1 & \frac{a}{1 + \frac{a-1}{k} N_A} \\ s_1 \left(1 - \frac{\alpha P_A}{\beta P_A + N_J} \right) m_1 & p_1 - 1 \end{array} \right) = 0,$$

which is calculated as

$$\left[s_1 \left(1 - \frac{\alpha P_A}{\beta P_A + N_J} \right) (1 - m_1) - 1 \right] (p_1 - 1) - s_1 m_1 \left(1 - \frac{\alpha P_A}{\beta P_A + N_J} \right) \frac{a}{1 + \frac{a-1}{k} N_A} = 0 \quad .$$

(B.6)

Then, substitute $\delta_1 = \frac{a-1}{k}$. After rearrangement, Eq. (B.6) becomes

$$\left(1 - \frac{\alpha P_A}{\beta P_A + N_J} \right) \left[s_1 (P_A - 1) (1 - m_1) - s_1 m_1 \frac{a}{1 + \delta_1 N_A} \right] - p_1 + 1 = 0 \quad (B.7)$$

Substituting $\delta_8 = s_1 (P_A - 1) (1 - m_1) - s_1 m_1 \frac{a}{1 + \delta_1 N_A}$, $\delta_9 = p_1 - 1$ into Eq. (B.7), I have

$$\frac{\alpha P_A}{\beta P_A + N_J} = 1 - \frac{\delta_9}{\delta_8} \quad (B.8)$$

Further substitute $\delta_{10} = 1 - \frac{\delta_9}{\delta_8}$, I have the prey isocline

$$P_A = \frac{V_J \delta_{10}}{\alpha - \beta \delta_{10}}.$$

Expressions for φ_6 to φ_9 can be found by back substitution.

Since the structure of the predator sub-matrix M_2 in matrix 2.23 remains unchanged compared to the one in matrix 2.19, I get the predator isocline in the same way as before

$$P_A = \frac{\delta_7 - \delta_6}{\beta \delta_6} N_J,$$

with φ_5 in Eq. 2.25 as $\frac{\delta_7 - \delta_6}{\beta \delta_6}$.

APPENDIX C

In this section, I describe how the hypotheses of bottom-up control and top-down control were tested for the Gulf of Mexico example in Chapter III. Four populations were divided into two groups according to trophic level, the brown shrimp population and the fish group. For the top-down scenario, only the shrimp population was responding to the deviations from the equilibrium relationship, while the fish group was not. The null hypothesis was constructed as forming restrictions on α . The indirect parameterization of the restrictions was

$$\mathbf{B}_t^T \alpha = \mathbf{0}_{3,1}$$

where $\mathbf{B}_t = [\mathbf{0}_{3,1} \ \mathbf{I}_3]^T$. Note that from the second to the fourth entries of α were restricted to zero, and thus, there were overall 3 restrictions. In addition, the direct parameterization was

$$\alpha = \mathbf{A}_t \varphi_t$$

where $\mathbf{A}_t = [1 \ \mathbf{0}_{1,3}]^T$ was a vector of length 4, and φ_t was a scalar. The form of the top-down restriction on α implied $r \leq 1$, because matrix \mathbf{A}_t had a rank of 1. When there was more than one equilibrium relationship, this identified equilibrium relationship was a linear combination of all the equilibrium relationships. The indirect parameterization picked out parameters that needed to be restricted, while direct parameterization directly specified free-varying parameters to be estimated and fixed restricted parameters to zero.

For the bottom-up scenario, only the fish group was responding to changes in the equilibrium relationship. This hypothesis was constructed by restricting the adjustment coefficient for the brown shrimp to zero, and those coefficients for the fish group were allowed to vary freely. The indirect parameterization of the restriction was

$$\mathbf{B}_b^T \alpha = \mathbf{0}_{r,1}$$

where each row of \mathbf{B} was $[1 \mathbf{0}_{1,3}]$, and the direct parameterization was

$$\alpha = \mathbf{A}_b \boldsymbol{\varphi}_b$$

where $\mathbf{A}_b = [\mathbf{0}_{3,1} \mathbf{I}_3]^T$, and $\boldsymbol{\varphi}_b$ was a $3 \times r$ matrix of coefficients. The form of bottom-up restrictions (\mathbf{A}_b) implied $r \leq 4$, because matrix \mathbf{A}_b had a rank of 4. Thus, this hypothesis placed no restriction on the rank of matrix \mathbf{B} . The parameter estimation procedure of both tests follows (Johansen 1995).

Small sample properties of the method with simulated data

To explore the statistical properties of the method presented in the main text, a modified discrete-time predator-prey model with ratio-dependent predation (Zhou et al. 2013) was used. The data-generating process is a bottom-up controlled community. The prey population, \mathbf{V} , follows an independent random walk, and the predator population, \mathbf{P} , depends on the prey population through a numerical response,

$$V_t = V_{t-1} + \epsilon_t,$$

$$P_t = c\alpha V_{t-1} P_{t-1} / (\beta P_{t-1} + V_{t-1}) + \nu_t,$$

where, ϵ_t and ν_t are independent normal random variables, α and β are the coefficients in the numerical response, and c is the conversion rate of consumed prey by the predator. Parameters used are $a=3.5$, $b=0.25$, $c=0.6$, $\alpha=6$, $\beta=7$, $\sigma(\epsilon) = 0.1$, $\sigma(\nu) = 0.01$ and the initial population densities are $\mathbf{V}_0=2$, $\mathbf{P}_0=0.5$.

First, predator-prey time series data of a short (25-year), medium (50-year) and long (100-year) length were simulated. Second, the co-integration test was applied to the simulated dataset to identify the number of species interactions. Then, assuming there was an interaction between this population pair, the tests of bottom-up and top-down effects were conducted. Both of these test statistics follow an asymptotic χ^2 distribution with 1 degree of freedom. I repeated this process 1000 times for each time series length (short, medium and long) to calculate the error rates of the tests for the 3 different lengths.

The results are as follows (Table 9): The power of the first step of the co-integration test was low for the short time series, but it improved monotonically with increasing length. The type-I error rate of the second step of the co-integration test corresponded reasonably to its asymptotic level across all lengths. The type-I error rate of the bottom-up test exceeded its asymptotic level for all lengths, and there was a gradual drop with increasing length. The power of the top-down test was good even for the short time series.

Table 9 Small sample properties of the tests based on simulations of a predator-prey model

Tests	Length	Type-I error rate	Type-II error rate
Cointegration: step 1 (asymptotic 1%)	25	-	0.762
	50	-	0.29
	100	-	0.0028
Cointegration: step 2 (asymptotic 1%)	25	0.008	-
	50	0.009	-
	100	0.005	-
Cointegration: step 1 (asymptotic 5%)	25	-	0.487
	50	-	0.139
	100	-	0.003
Cointegration: step 2 (asymptotic 5%)	25	0.058	-
	50	0.052	-
	100	0.052	-
Bottom-up and top-down tests (asymptotic 5%)	25	0.141	0.153
	50	0.071	0.024
	100	0.059	0

A couple of things can be learned from this simulation exercise. First, the small sample properties of the tests also depend on the form of density-dependence between two populations, i.e., if a different numerical response was used to generate data, results would be different (I tried different sets of parameters for the numerical response). Second, it should be noted that for the data generation I used an arbitrary nonlinear numerical response, and for testing I used a linear approximation, which sacrifices performance, but those tests still performed reasonably well on the medium-length time series. In addition, the lack of power in the co-integration test for short time series suggests that some species interactions may not be adequately picked up for the Gulf of Mexico example shown in

the text, which has a time series length of 26 and potentially more complicated forms of species interactions.

Trophic interactions in the stationary component of the model

After the non-stationary component of the model has been determined (matrix β), the remaining coefficients of the VECM can be estimated through ordinary least squares regression. The bottom-up and top-down tests presented in the text examined the significance of trophic interactions in the long-run component. The significance of trophic interactions in the short-run component can be examined through the significance of the elements of matrix Θ_i in Eq. 1 of the main text. I ran multiple linear models on data from all the zones, and found in the short-run component 1) significant bottom-up effect from zones 13, 16, 18, 20 and 21, and 2) significant top-down effect only from zone 18 (all at the nominal 5% level).

Biological characteristics for Atlantic croaker, silver seatrout and sand seatrout

Atlantic croaker, *M. undulatus*, was found to be the most common finfish species caught by shrimp trawls both by weight and by number (Bryan et al. 1982). During the development of *M. undulatus*, dietary shifts occur during three active feeding stages (Darnell 1961). The diet of individuals 125-325mm in total length consists of macro-invertebrates, including commercially important penaeid shrimps (Darnell 1961). A study in Chesapeake Bay found benthic organisms comprised 4.3% of the diet of *M. undulatus* (Nye 2008).

Silver seatrout, *Cynoscion nothus*, are abundant in the nearshore waters of the northern Gulf of Mexico (Hildebrand and Schroeder 1928, Moore et al. 1970), and they

are among the most common species caught in industrial bottom fisheries and as bycatch in shrimp fisheries (Roithmayr 1965, Warren 1981). In sampling, larger silver seatrout appear more susceptible to trawling during the day (DeVries and Chittenden 1982). Adult silver seatrout show seasonal distribution patterns in nearshore and offshore waters in the Gulf of Mexico (Gunter 1938, Miller 1965, DeVries and Chittenden 1982). Fish and shrimp are found to be the primary foods for silver seatrout in the northern Gulf (Rogers 1977, Overstreet and Heard 1982, Sheridan et al. 1984). Also, there is a shift in the diet composition of silver seatrout with body length (Rogers 1977).

Sand seatrout, *Cynoscion arenarius*, are sometimes difficult to distinguish from silver seatrout. The sand seatrout is one of the most abundant fishes in the estuarine and nearshore waters of the Gulf (Gunter 1945, Christmas and Waller 1973), and it is also a major component of the bottom fisheries and as bycatch in the shrimp fisheries (Roithmayr 1965, Sheridan et al. 1984). In sampling, sand seatrout are more susceptible at night than in daytime during May and June in Mississippi Sound (Warren 1981). Silver seatrout were found to be more common in shallower waters, while sand seatrout were more abundant farther offshore (Ginsburg 1931), and (Miller 1965) suggested that the distribution of sand seatrout and silver seatrout overlapped at water depths of 5 to 16 m. In the dietary analysis of sand seatrout from the Gulf of Mexico, fish components predominate (Reid 1954, Reid 1955, Reid et al. 1956, Springer and Woodburn 1960, Sheridan 1979, Sheridan and Livingston 1979). Crustaceans are also regularly eaten by sand seatrout (Moffett et al. 1979, Overstreet and Heard 1982, Sheridan et al. 1984).

Mixture generalized linear models

Because each sampling location was randomly selected within each statistical zone and the distribution of each species was generally not uniform, there is a high chance of sampling outside of the natural aggregations of a particular species and getting zero catches compared to sampling within carefully selected locations for any particular species. To incorporate the heterogeneity of species distributions, I adopted a mixture generalized linear model to extract annual abundance indices from the raw CPUE data. This model is also called a Delta model in some literature. Here, the sampling procedure was modeled as a two-step process: first, the event that a sampling location fell within a species' range of distribution followed a binomial distribution (later referred to as the occurrence model); second, given that the sampling location was outside of the distribution range, I had a zero catch with probability one, and given that the sampling station was within the distribution range, the log-transformed CPUE was normally distributed (later referred to as the abundance model). The assumption of this method is that the sampling procedure is efficient, which means that within the range, samples always yield positive catches. This is a valid assumption for the bottom trawl sampling method used in this study. The occurrence model with a logit link function was

$$\text{logit}\pi_i = \mathbf{x}_i^T \boldsymbol{\beta}$$

where π_i was the probability that the i th sampling location fell within the distribution range, \mathbf{x}_i was a vector of covariates, and $\boldsymbol{\beta}$ was a vector of parameters to estimate. The

abundance model was a mixture of two distributions: given sampling within range, the CPUE was modeled as

$$\ln(CPUE | \textit{within range}) = \mathbf{z}_i^T \boldsymbol{\gamma}$$

where, for the i th sampling station, \mathbf{z}_i was a vector of covariates, and $\boldsymbol{\gamma}$ was a vector of parameters to estimate, and for out of range samplings, $Pr(CPUE = 0 | \textit{out of range}) = 1$.

The raw CPUE data were organized as follows: each row represented an individual survey sample, and in the columns were species-specific log-transformed CPUE (number of individuals caught/min) and covariates, including sampling year, statistical zone, season (summer and fall), depth, time of the day (day and night), water temperature, dissolved oxygen, salinity, number of minutes fished and the designation of the survey ship (NMFS, TX and AL). Two data sets were generated from the raw CPUE dataset, one showing the presence or the absence of those four species at all the sampling stations (data for the occurrence model), and the other one showing the log-transformed CPUEs from stations with positive catches (data for the abundance model). I then modeled the occurrence data and the abundance data separately. For both models, covariates for selection included year, season (summer and fall), depth, time of the day (day and night), water temperature, dissolved oxygen, salinity and the designation of the survey ship (NMFS, TX and AL). In addition, the number of minutes fished was also included for selection in occurrence models. A stepwise backward selection procedure was used for model selection. The selected models for both occurrence and abundance data were used to estimate yearly abundance indices for each statistical zone for each of the 26 years.

APPENDIX D

In this section, I present additional methods and results for Chapter IV.

Methods

Unit root and stationarity tests

These tests are for testing stationarity/non-stationarity of time series. Unit root process is a type of non-stationary time series. The variance of a unit root process approaches infinity with time. The major difference between unit root tests and stationarity tests is that they have different null hypotheses. The null hypothesis of the unit root tests is that there is a unit root, while the null of the stationarity tests is that there is no unit root. Because the power of the unit root tests can be low with short time series, these test could not distinguish a near unit root process with a unit root process. It is safe to perform stationarity tests along with the unit root tests to confirm the results.

Augmented Dickey Fuller (ADF) test

The ADF test is a modified version of the Dickey-Fuller unit root test (Dickey and Fuller 1979). It address the issue of higher order auto-regression in the data by introducing lagged Δy_t as regressors in the regression equation (Said and Dickey 1984). The ADF model used in this study was

$$\Delta y_t = \gamma y_{t-1} + \sum_{i=1}^{p-1} \delta_i \Delta y_{t-i} + \varepsilon_t,$$

where y_t is a univariate time series, Δ is a difference operator, p is the lag order of y_t and γ and δ_i are the coefficients to be estimated from data. The lag order p was chosen

based on Bayesian information criterion (BIC). The t statistic for γ is calculated and compared to the Dickey-Fuller table for the significant level. The null hypothesis is that there is a unit root without drift.

Elliott, Rothenberg & Stock (ERS) test

The ERS test performs a modified version of the ADF test. Studies have shown that this test has significantly greater power than the previous versions of ADF tests (Elliott et al. 1996).

Phillips & Perron (PP) test

The PP test is a modified version of the Dickey-Fuller test. It differs from ADF test in how to address the issue of higher order auto-regression in the data. Instead of using lagged Δy_t in the test equation, the PP test uses a non-parametric correction to the test statistic. This test is robust with respect to the autocorrelation and heteroscedasticity in the stochastic term (Phillips and Perron 1988). It has been shown that the PP test performs worse than the ADF test in finite samples (Davidson and MacKinnon 2004).

Kwiatkowski, Phillips, Schmidt & Shin (KPSS) test

The KPSS test uses a null hypothesis that the time series is stationary around a deterministic trend (Kwiatkowski et al. 1992). As such, this test compliments the unit root tests derived from the Dickey-Fuller test mentioned above. The KPSS test is taken alongside with the unit root tests to corroborate the conclusion reached by unit root tests. The lag order is set to 2 to obtain the results in Table 3 of the main text, and changing the lag order does not change the conclusion of the result.

Results

In addition to the results on type-I and type-II error rates at a 5% value shown in the main text, results of the ICR, MAR and CC methods at 10% and 1% values were summarized in Table 10-13.

The p -value can be interpreted as the probability of obtaining more extreme results when the null hypothesis is true. Thus, the distribution of the p -value under the null hypothesis is uniformly distributed. If the distribution shifts to the right regarding the uniform distribution, the test is conservative, and if there is a left shift, the nominal significant level does not hold for the test result, and we are likely to obtain spurious results. The distribution of p value of the likelihood ratio test statistic using the MAR and ICR methods on data with the low noise (SNR=10:0.5) and medium (SNR=10:2) noise level were shown in Figure 17-27. Results for the high noise level (SNR=10:4) were similar to those for the medium noise level, and they are not shown here. Results show that the CC and MAR method could produce spurious results, and the ICR method adequately controlled the type-I error rate.

Table 10 Estimated percentages of correctly accepting the null hypothesis of no interaction using the four different methods at a nominal 10% significance level and the associated signal to noise levels (SNR)

SNR	Type of interaction	ICR	MAR	CC	SLR
10:0.5	Interactive	91.56	82.24	-	82.34
	Bottom-up	92.40	87.86	76.92	87.00
	Top-down	92.24	86.00	75.20	86.42
10:1	Interactive	91.66	82.30	-	81.74
	Bottom-up	92.54	87.24	80.80	87.28
	Top-down	91.14	84.58	77.58	85.46
10:2	Interactive	89.54	79.62	-	80.10
	Bottom-up	91.08	84.92	78.52	85.30
	Top-down	90.44	84.00	78.52	84.42
10:4	Interactive	88.84	79.68	-	79.36
	Bottom-up	89.88	84.10	83.46	85.26
	Top-down	89	83.18	83.20	84.14

Table 11 Estimated percentages of correctly accepting the alternative hypothesis of interaction using the four different methods at a nominal 10% significance level and the associated signal to noise levels (SNR)

SNR	Type of interaction	ICR	MAR	CC	SLR
10:0.5	Interactive	20.80	53.98	-	53.78
	Bottom-up	27.10	67.16	89.96	68.54
	Top-down	23.92	57.92	93.22	59.18
10:1	Interactive	20.66	52.46	-	51.40
	Bottom-up	22.66	53.36	77.90	59.82
	Top-down	21.04	47.10	81.21	45.48
10:2	Interactive	19.28	48.04	-	50.04
	Bottom-up	22	47.78	75.32	43.28
	Top-down	17.78	40.02	56.76	41.48
10:4	Interactive	18.64	40.00	-	42.34
	Bottom-up	19.28	36.00	44.74	38.12
	Top-down	17	32.90	39.72	34.66

Table 12 Estimated percentages of correctly accepting the null hypothesis of no interaction using the four different methods at a nominal 1% significance level and the associated signal to noise levels (SNR)

SNR	Type of interaction	ICR	MAR	CC	SLR
10:0.5	Interactive	99.26	97.44	-	96.88
	Bottom-up	99.06	98.02	99.68	98.44
	Top-down	99.28	98.06	99.70	98.00
10:1	Interactive	98.98	97.22	-	97.52
	Bottom-up	99.24	98.00	99.28	98.44
	Top-down	98.96	97.84	99.60	98.02
10:2	Interactive	98.92	96.50	-	96.72
	Bottom-up	98.98	97.74	99.60	98.24
	Top-down	98.90	98	99.60	97.62
10:4	Interactive	98.64	96.94	-	96.06
	Bottom-up	98.80	97.82	99.18	97.90
	Top-down	99	97.10	99.18	97.78

Table 13 Estimated percentages of correctly accepting the alternative hypothesis of interaction using the four different methods at a nominal 1% significance level and the associated signal to noise levels (SNR)

SNR	Type of interaction	ICR	MAR	CC	SLR
10:0.5	Interactive	3.80	16.20	-	14.16
	Bottom-up	6.14	20.74	6.78	20.20
	Top-down	5.36	15.38	6.32	14.62
10:1	Interactive	3.76	13.12	-	11.34
	Bottom-up	5.24	13.14	4.70	16.74
	Top-down	3.60	10.30	4.74	9.44
10:2	Interactive	1.08	3.50	-	11.80
	Bottom-up	4.00	10.96	3.80	10.42
	Top-down	3.16	7.80	3.44	8.24
10:4	Interactive	2.70	9.92	-	11.10
	Bottom-up	3.12	7.62	2.80	8.18
	Top-down	3.00	6.90	2.46	7.58

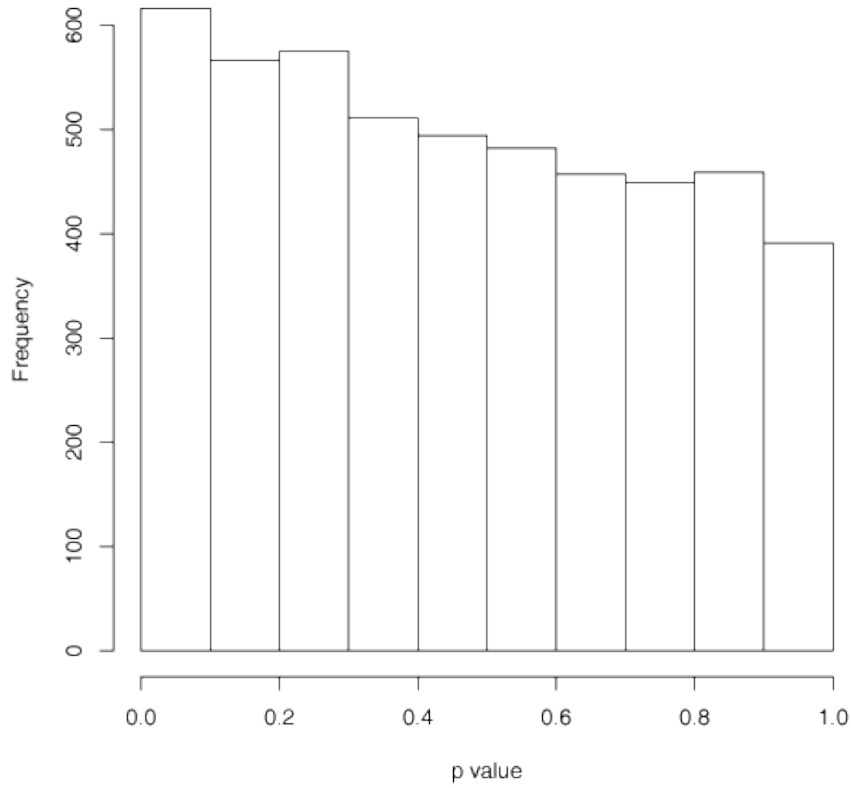


Figure 17 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the MAR method on the data with the lowest noise level

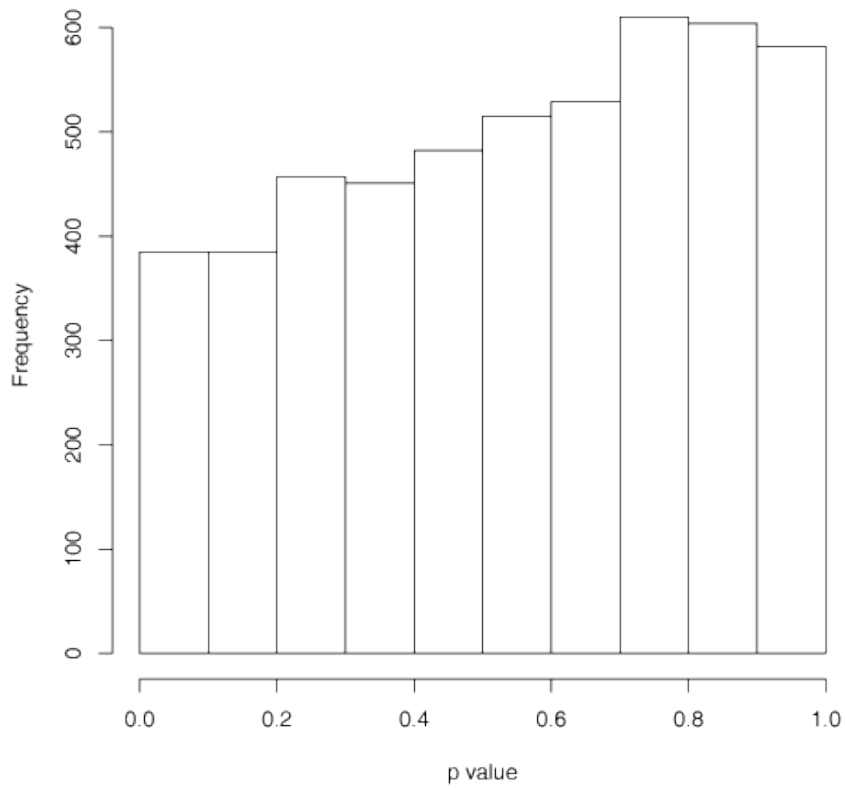


Figure 18 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the ICR method on the data with the lowest noise level

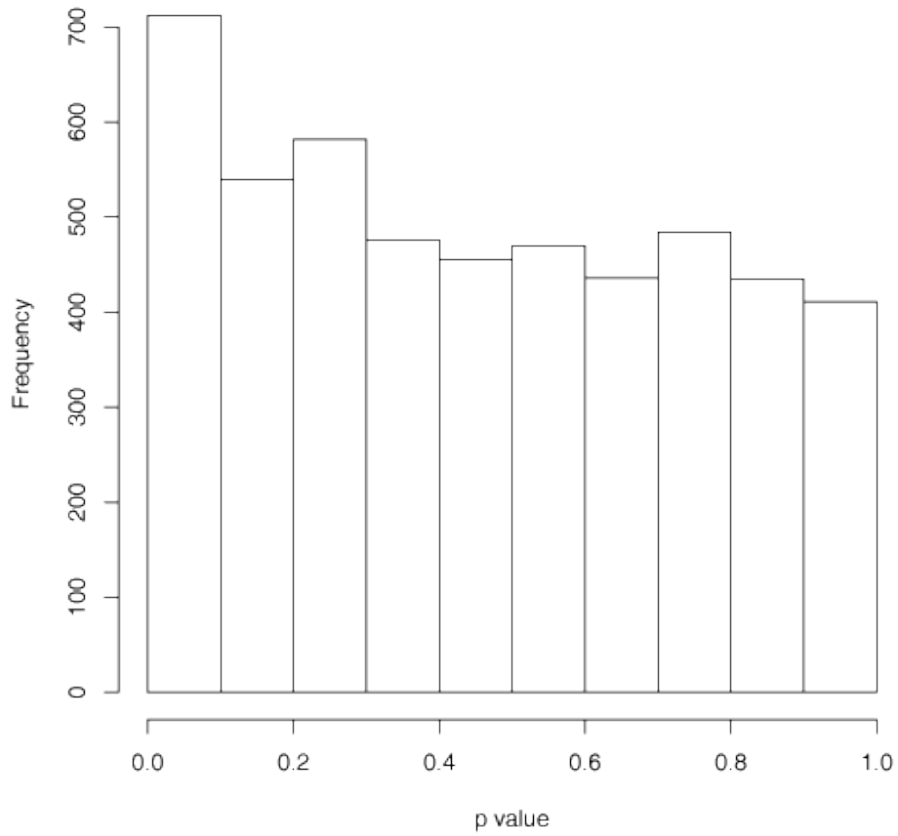


Figure 19 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the MAR method on the data with the lowest noise level

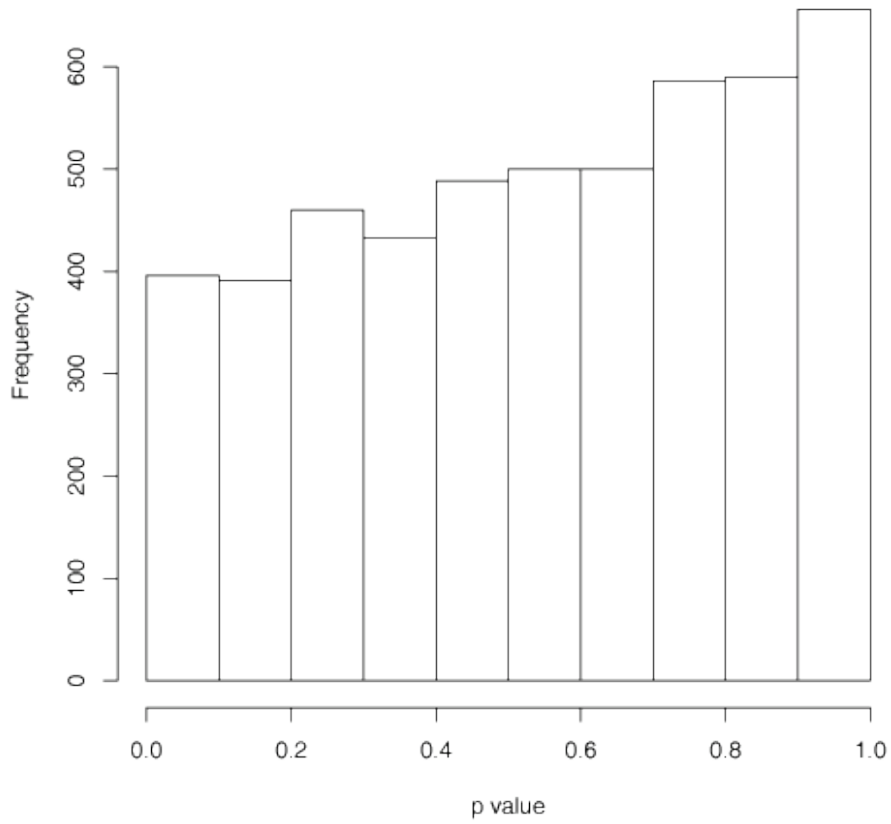


Figure 20 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the ICR method on the data with the lowest noise level

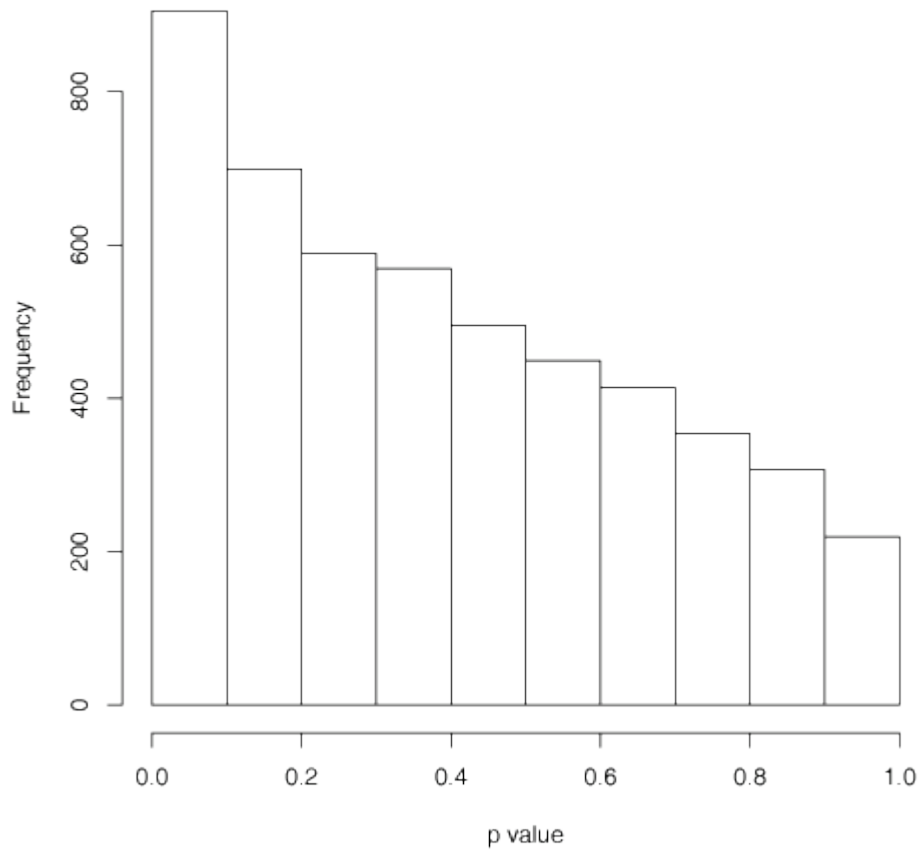


Figure 21 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the MAR method on the data with the lowest noise level

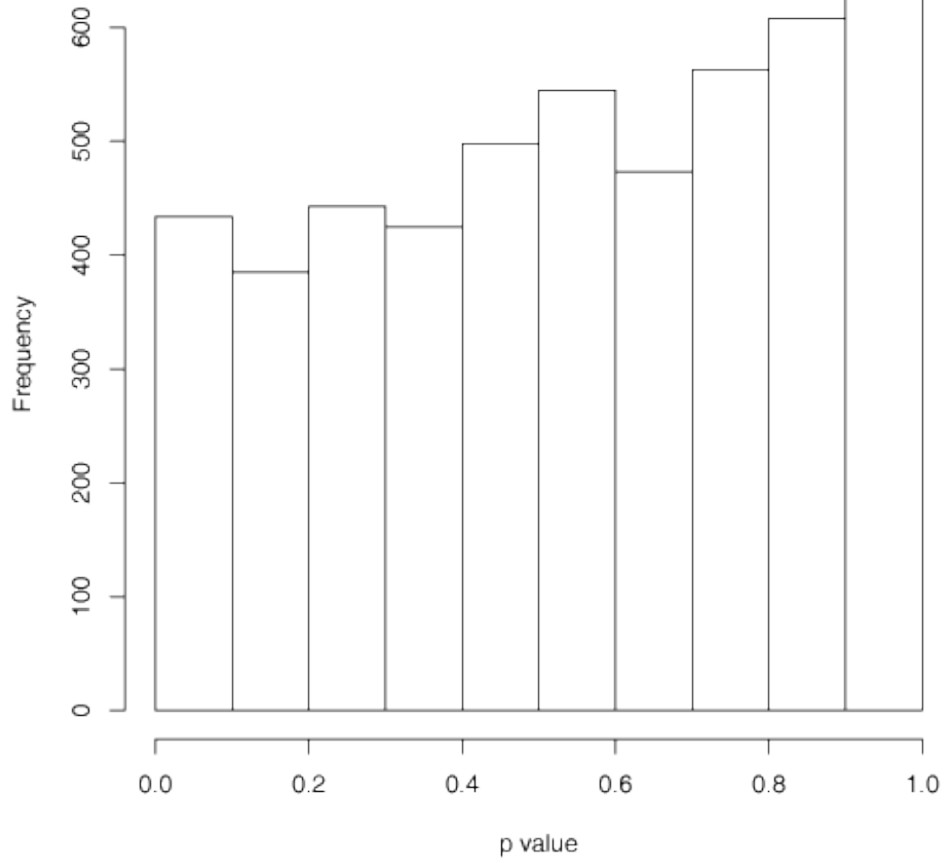


Figure 22 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the ICR method on the data with the lowest noise level

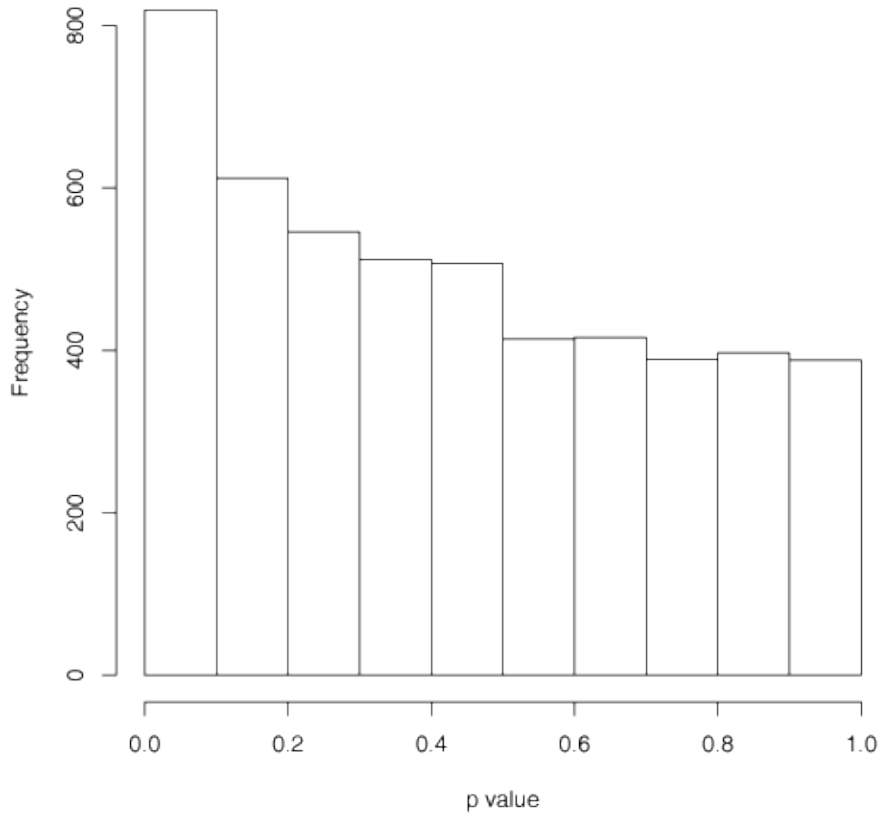


Figure 23 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the MAR method on the data with the medium noise level

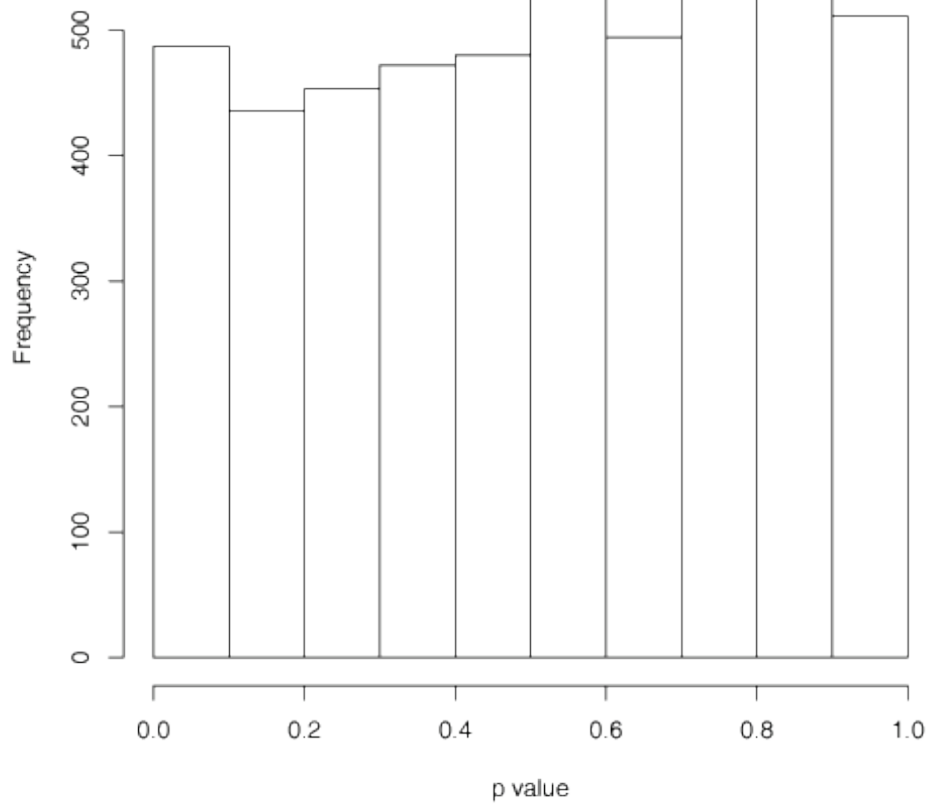


Figure 24 Distribution of p -value of the likelihood ratio test statistics testing for a top-down effect using the ICR method on the data with the medium noise level

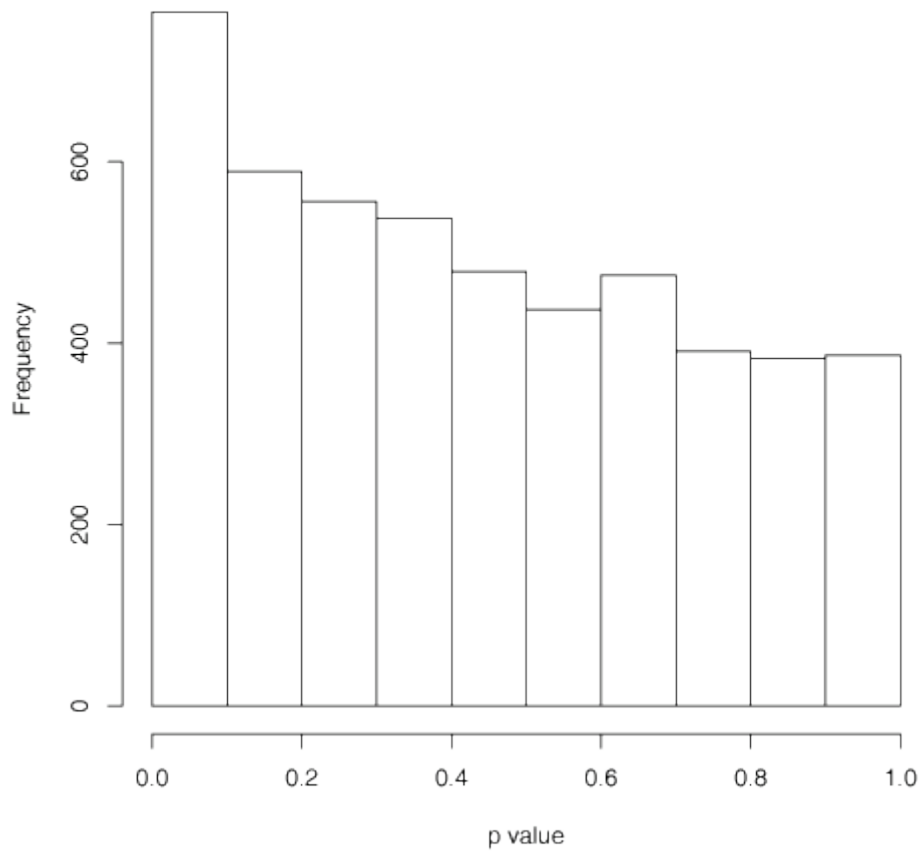


Figure 25 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the MAR method on the data with the medium noise level

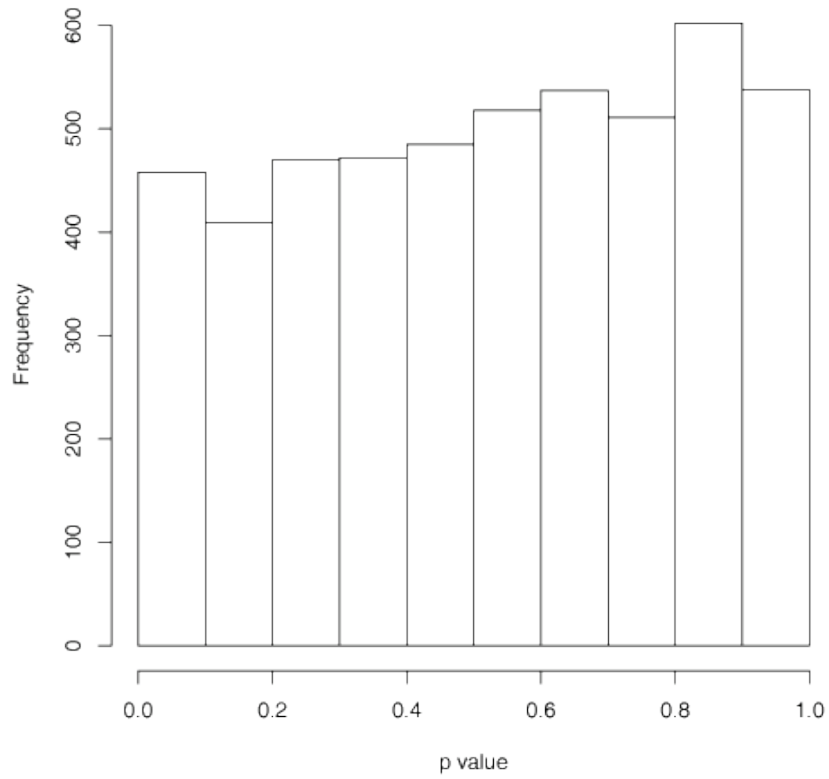


Figure 26 Distribution of p -value of the likelihood ratio test statistics testing for a bottom-up effect using the ICR method on the data with the medium noise level

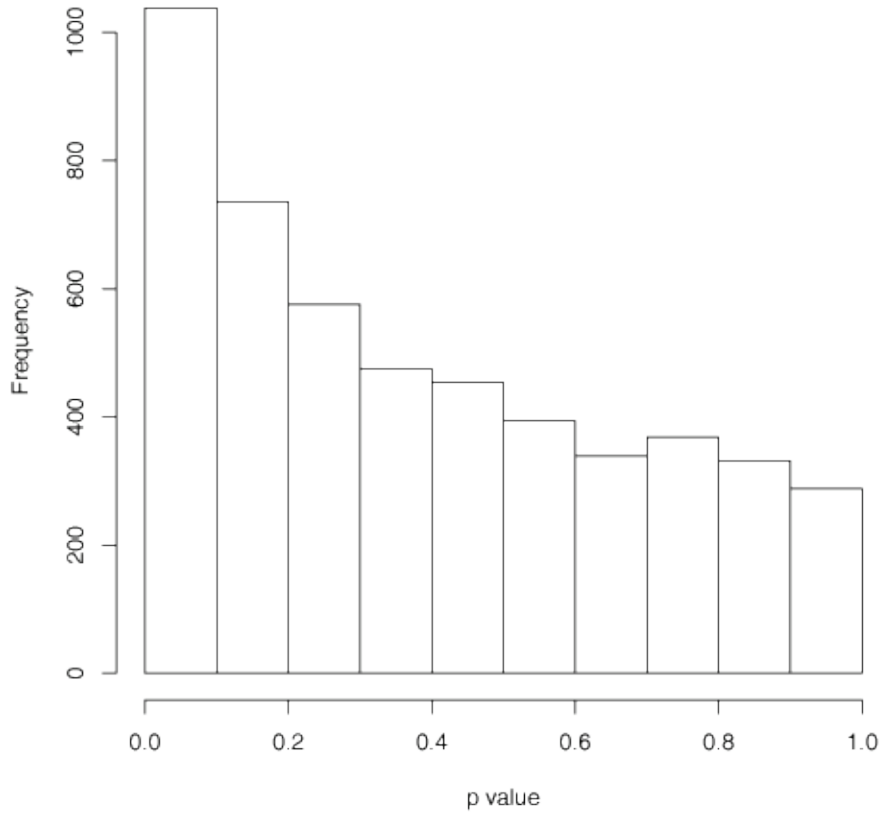


Figure 27 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the MAR method on the data with the medium noise level

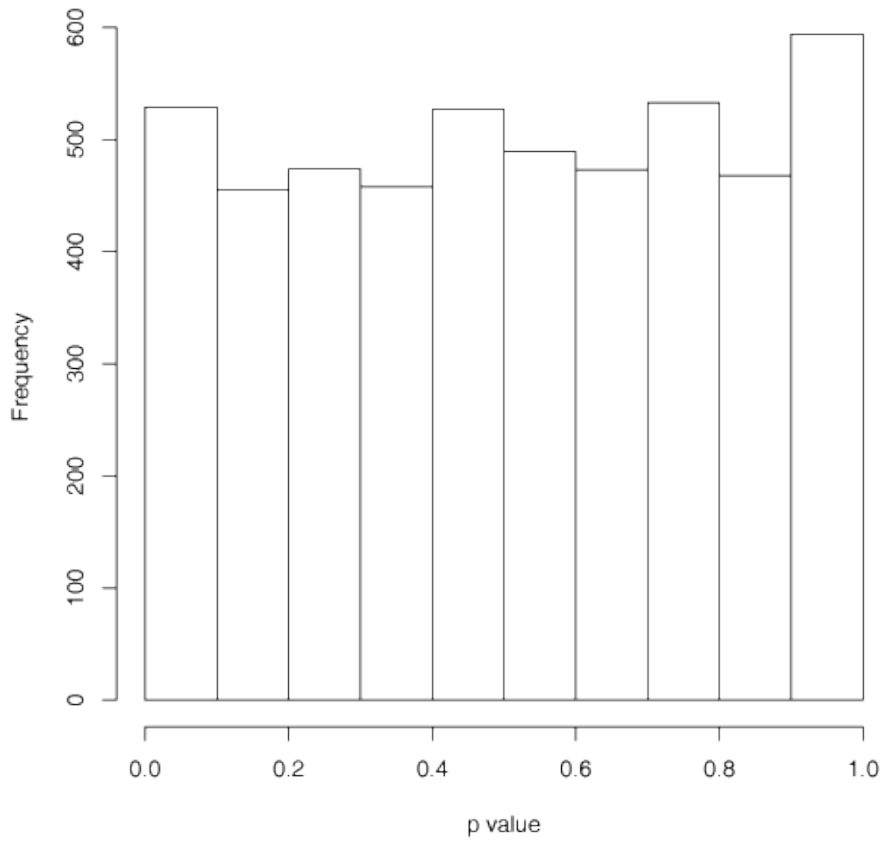


Figure 28 Distribution of p -value of the likelihood ratio test statistics testing for an interactive effect using the ICR method on the data with the medium noise level