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Introduction

Klaus Rohde

It is obvious that nature is undergoing rapid changes as a result of human activities such as industry, agriculture, travel, fisheries, urbanization, etc. What effects do these activities have? Are they disturbing equilibria in ecological populations and communities, i.e., are they upsetting the balance of nature, or are they enhancing naturally occurring disequilibria, perhaps with even worse consequences? This book examines these questions, first by providing evidence for equilibrium and nonequilibrium (= disequilibrium) conditions in natural systems, and second by examining human-induced effects, among them those due to climate change, habitat destruction and introduction of alien species. One often hears the argument, not only from non-scientists but also from some scientists, that large-scale fluctuations in climate, sea levels etc. have occurred over and over again in the geological past, long before human activities could possibly have had any impact, that human effects are very small compared to those naturally occurring anyway, and that they cannot significantly affect the environment. Is this indeed so? Or is it possible that naturally occurring fluctuations are being dangerously enhanced by humans?

(1) The concept of ecological equilibrium is used differently by different authors. A detailed historical discussion of the meaning of the concept with many examples was given in Rohde (2005). According to the most widely accepted usage, those ecological systems are in equilibrium which fluctuate around some stable point, i.e., return to it after disturbance due to "self-correcting mechanisms" (Hutchinson, 1948). Competition is usually considered to be the most important of these mechanisms. How common are equilibrium and nonequilibrium states in ecological systems, under what conditions are populations, communities and ecosystems likely to be in or approaching equilibrium? In particular, how important are they in evolution? Richard Dawkins (1976) has claimed that the development of the concept of evolutionarily stable strategies (ESSs) may be the most important contribution to evolutionary theory since Darwin. The concept of ESS relies on equilibrium assumptions, and so does that of evolutionarily stable states (a concept closely related to ESS). Maynard Smith defines an evolutionarily stable state of a population as a genetic composition that is restored by selection after a disturbance, provided the disturbance is not too large (see Maynard Smith & Price, 1973, and Maynard Smith, 1982). However, large disturbances are frequent in many ecosystems and for many

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populations, and establishment of evolutionarily stable states will therefore often be difficult or impossible. Communities – as shown in theoretical and experimental studies (e.g., of plankton dynamics) – may never reach equilibrium even in homogeneous and relatively constant environments, because multi-species interactions may lead to oscillations and chaos. The fate of ecological systems, because of such factors, is often unpredictable, and interspecific competition, often thought to be the major factor in "regulating" community structure, may in fact bring about the opposite: disequilibrium. In view of this, we can re-phrase the major aim of this book as an evaluation of how common evolutionarily stable strategies (or states) in populations and establishment of equilibria in communities due to competition are.

(2) Almost all of the world's ecosystems have now been modified by human activity, through habitat loss, fragmentation and degradation, as well as by pollution and invasive species. Furthermore, they are now being subjected to climate change, largely the result of human activity. A second major aim of the book is to examine the extent to which equilibrium in ecological communities (where it existed) has been upset by human-induced changes, and to what extent disequilibria have been enhanced. There is abundant evidence that species' distributions and population sizes are changing, in many cases detrimentally. Communities are losing species and gaining new ones, so that interspecific interactions, such as competition, predation and mutualism, are being reframed.

The book examines the various topics, beginning with a discussion of examples of nonequilibrium and equilibrium in populations and metapopulations, in communities, and in ecosystems at geographical scales. Latitudinal gradients in biodiversity, i.e., the most pervasive and best-documented trends in the geographical distribution of animals and plants, are discussed, as well as some important hypotheses explaining them, including the hypothesis of effective evolutionary time, which does not rely on equilibrium assumptions, and molecular evidence for it.

The part on human-induced effects includes discussions of invading species and climate change. An environmental physicist discusses the physics of climate change; other chapters deal with current and predicted effects on changes in species diversity and species ranges due to climate change, species invasions and habitat losses of amphibians, reptiles, birds and insects, as well as discussions of the expected fates of the most diverse marine ecosystems on Earth, i.e., coral reefs. This part also contains a chapter by a mathematician on the features of invading species that determine successful invasions, using an equation-based model, and another chapter on the effects of invasions in evolutionary history and what a study of such effects can teach us about present events. Also discussed is the potential for the development of new infectious diseases due to changing climatic conditions.

Emphasis is laid on the importance of autecological studies, that is of the importance of long-term studies of single species. There is an account of such long-term studies of some flatworms which suggests that not competitive interactions between species but evolutionary and ecological contingencies are largely responsible for ecological adaptations and niche selection. It also shows that at least some species have such intricate

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morphological and ecological adaptations that they cannot easily be replaced if habitats are destroyed, and that each species will react differently to environmental disturbance and climate change.

In the final part, "An overall view", some important conclusions based on the book chapters and literature accounts, and some important consequences of climate change and ecological disturbance, are discussed. We return to the questions asked in the first paragraph: how common are evolutionarily stable states in populations and how important is interspecific competition for determining community structure, and what are some of the consequences of the enhanced environmental fluctuations in a changing world? The conclusion is: evolutionarily stable states are not as common and interspecific competition is not as important as assumed by many, and consequences of climate change are often unpredictable in detail, but overall may be catastrophic. Patterns of disease transmission will be changed, and the enhanced disequilibrium poses important challenges for managing biodiversity and conservation. In a joint section, several authors who have contributed chapters to the book examine the question on what steps should be taken to secure future biodiversity.

This book is aimed at scientists, students and interested lay people. Many scientists at the forefront of research contributed chapters, which provide a review of what is known in their fields and stimulate ideas for future research. The book can be used as a source for university courses, and it is hoped to provide useful information to lay people who wish to inform themselves on current topics of ecological research, particularly that related to human impact on the environment, including climate change. Examples have been selected from a large range of animal and plant groups on the basis of how well they have been examined with regard to equilibrium and nonequilibrium strategies and states, or the extent to which human impact on them has been documented. The book provides a basis for public discussions of human impact on the environment and what to do about it, with easy access to a large body of (mainly recent) literature and discussions of aspects insufficiently discussed in standard texts on ecology.

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Part I

Nonequilibrium and Equilibrium in Populations and Metapopulations

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1 Reef fishes: density dependence and equilibrium in populations?

Graham E. Forrester and Mark A. Steele

Summary

Small colorful coral reef fishes have been excellent subjects for ecological field experiments (Sale, 2002). They have provided substantial insight about the strength of density-dependent interactions and their underlying biological causes. In this chapter we first summarize what we know about the biological mechanisms of density-dependent regulation in coral reef fishes, highlighting one pervasive mechanism – competition for structural refuges used to avoid predators. We then summarize the evidence for ongoing coral declines and the progressive loss of architectural complexity on reefs. We argue that as reefs become architecturally simpler they provide fewer refuges from predation, and so the carrying capacity for many fish populations is declining. As a result of ongoing competition for gradually diminishing supply of refuges, we hypothesize that some species of reef fishes will continue to experience density-dependent mortality even as their populations decline globally. This hypothesis contradicts conventional views on the regulation of marine populations, which hold that density-dependent interactions should diminish in importance as populations decline (Figures 1.1 and 1.2).

Background: the development of ideas about density dependence in reef fishes

A long-standing controversy in ecology has revolved around the relative effects of density-dependent and density-independent processes on population dynamics (Murdoch, 1994; Cappuccino & Price, 1995). Although it is necessary for long-term persistence, recognizing that density dependence need not have a strong effect at all times on the dynamics of a population was a key step in resolving a major historical controversy over density dependence and density independence as mutually exclusive alternatives (Andrewartha & Birch, 1954; Nicholson, 1957). In fact, both sorts of processes affect most populations (Turchin *et al.*, 1995). Ideas about populations of reef fishes and other marine species have followed a similar path, following early controversy over which processes control dynamics (Doherty, 1991; Jones, 1991).

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Figure 1.1. The bridled goby (*Coryphopterus glaucofraenum*) suffers density-dependent mortality when crevices used to hide from predators are limited. See plate section for color version.

Figure 1.2. Most coral reef fishes depend upon shelter provided by the physical structure of living corals. As coral reefs continue to degrade, shelter may become more limited and even if fish populations decline in density they may still experience density-dependent mortality. See plate section for color version.

Like many marine organisms, coral reef fishes produce pelagic larvae that can disperse over wide areas. Density dependence could be occurring during the pelagic larval phase (Sandin & Pacala, 2005), but because of the difficulty of estimating mortality of pelagic individuals there is no empirical evidence for or against this possibility. Instead, early

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debates revolved around whether the dynamics of benthic populations are controlled by the influx of pelagic larvae (called settlement) or by density-dependent interactions among juveniles and adults in the benthic habitat. These explanations for population dynamics were initially presented as dichotomous alternatives. The hypothesis that abundance was limited by the rate of larval input (called recruitment limitation) predicts that mortality rates in the benthic habitat are density-independent, so that benthic populations fluctuate in correspondence with the rate of replenishment via larval influx. This hypothesis was presented as an alternative to the hypothesis that abundance was limited by density-dependent interactions (competition and predation) affecting individuals within the benthic habitat (Doherty, 1983; Victor, 1983; Connell, 1985).

The recruit-adult hypothesis

It has been acknowledged more recently that processes influencing both the rate of input to populations via settlement and output via mortality will influence the dynamics of most benthic marine populations (Gaines & Roughgarden, 1985; Menge & Sutherland, 1987; Caley *et al.*, 1996). Considerable progress has been made in developing models that can evaluate the relative effects of density-dependent and density-independent processes. A simple idea that captures the essence of most models is the "recruit-adult hypothesis" (Menge, 2000). This hypothesis was developed for marine invertebrates that occupy primary space on the substratum. These benthic populations are ultimately resource limited because of the obvious limit to two-dimensional space for species that require attachment sites on the substratum. The recruit-adult hypothesis posits that variation in oceanographic processes controls the influx of larvae to populations and determines the extent to which populations in different locations reach their carrying capacity: sites with high settlement are chronically space limited, whereas sites with low settlement rarely reach their carrying capacity and adult densities are sensitive to larval influx (Connolly & Roughgarden, 1998; Menge, 2000; Connolly *et al.*, 2001; Muko *et al.*, 2001) (Figure 1.3).

The recruit-adult hypothesis is also applicable when density-dependent mortality arises from causes other than limitation of two-dimensional space, and analyses of reef fish populations have confirmed two key predictions of this hypothesis. Firstly, the sensitivity of adult densities to larval input is greater where settlement is low (Schmitt *et al.*, 1999). Second, mortality after settlement was shown to be consistently density-dependent in dozens of manipulations in small patches of habitat, as long as experimental densities encompassed the high end of the natural range (Osenberg *et al.*, 2002).

Competition for refuges is a widespread cause of density dependence

Moving beyond simple manipulations of population density, several researchers studying reef fishes have manipulated both local density and putative causes of density dependence (food, predators, shelter) in cross-factored experiments (Forrester, 1990; Hixon & Jones, 2005). For animals like reef fishes, for whom causes of death are difficult to

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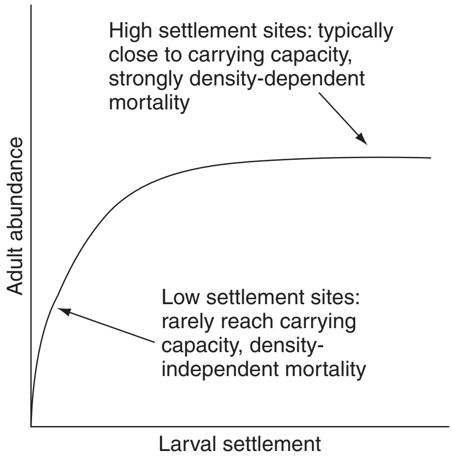

Figure 1.3. The recruit-adult hypothesis: a simple conceptual model for benthic marine populations. Oceanographic processes controlling larval influx determine whether populations are typically recruitment-limited or resource-limited.

establish by observation, this is a powerful method to identify the biological interactions responsible for density-dependent mortality.

Our experiments with two small reef fishes, the bridled goby (*Coryphopterus glaucofraenum*) and the goldspot goby (*Gnatholepis thompsoni*), provide a good example of this approach, and yielded results that appear to be representative of many species (White *et al.*, 2010). Establishing a gradient of goby density in the presence and absence of larger predatory fishes showed that predation was the agent of most mortality, and the proximate cause of density dependence (Forrester & Steele, 2000). Like many reef fishes, gobies use structural habitat features as refuges from predation. By manipulating both goby density and the abundance of refuges within small plots, we showed that the ultimate cause of density dependence was competition for a limited supply of refuges (Forrester & Steele, 2004). Gobies rapidly retreat to shared unguarded refuges when a predator approaches or attacks, and only when refuges are relatively abundant do all prey individuals actually escape. Competition for refuges thus resembles the childhood game of musical chairs, and this process is well described by simple mortality functions in which the per capita prey mortality rate depends on the ratio of prey (gobies) to refuges (Samhouri *et al.*, 2009). These manipulations, like most ecological experiments, were performed at a small spatial scale (using replicate reef patches a few meters in extent). Interactions between density-dependent processes and local heterogeneity in density and environmental factors often cause population dynamics at large scales to differ from predictions based on small-scale measurements (Rastetter *et al.*, 1992; Gardner *et al.*, 2001). In some cases, the so-called "scale transition" is strong enough to make extrapolating from small-scale experiments wildly inaccurate (Chesson, 1998). Gobies, however, displayed similar relationships between density and mortality on both small and large reefs (Steele & Forrester, 2005; Forrester *et al.*, 2008a) and a simulation model tailored to bridled goby demography suggests that the scale-transition should be modest (Vance *et al.*, 2010).