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POPULATION REGULATION: HISTORICAL CONTEXT AND CONTEMPORARY CHALLENGES OF OPEN VS. CLOSED SYSTEMS

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Abstract. By definition, a population is regulated if it persists for many generations with fluctuations bounded above zero with high probability. Regulation thus requires density-dependent negative feedback whereby the population has a propensity to increase when small and decrease when large. Ultimately, extinction occurs due to regulating mechanisms becoming weaker than various disruptive events and stochastic variation. Population regulation is one of the foundational concepts of ecology, yet this paradigm has often been challenged, during the first half of the 20th century when the concept was not clearly defined, and more recently by some who study demographically open populations.

The history of ecology reveals that earlier manifestations of the concept focused mostly on competition as the mechanism of population regulation. Because competition is often not evident in nature, it was sometimes concluded that population regulation was therefore also absent. However, predation in the broadest sense can also cause density dependence. By the 1950s, the idea that demographic density dependence was essential (but not sufficient) for population regulation was well established, and since then, challenges to the general concept have been short lived. However, some now believe that metapopulations composed of demographically open local populations can persist without density dependence. In particular, some recent manifestations of the Recruitment Limitation Hypothesis all but preclude the possibility of regulation.

The theory of locally open populations indicates that persistence always relies on direct demographic density dependence at some spatial and temporal scale, even in models reportedly demonstrating the contrary. There is also increasing empirical evidence, especially in marine systems where competition for space is not self evident, that local density dependence is more pervasive than previously assumed and is often caused by predation. However, there are currently insufficient data to test unequivocally whether or not any persistent metapopulation is regulated. The challenge for more complete understanding of regulation of metapopulations lies in combined empirical and theoretical studies that bridge the gap between smaller scale field experiments and larger scale phenomena that can presently be explored solely by theory.

Key words: closed populations; density dependence; metapopulations; open populations; population regulation; recruitment limitation.

> *All Bodies have some Dependence upon one another.*
> —R. Bradley (1721)

INTRODUCTION

By definition, a population is regulated when it displays three closely related phenomena: (1) persistence, (2) boundedness, and (3) return tendency (Murdoch 1994, Turchin 1995). Persistence is the long-term survival of a population over many generations. Boundedness is the existence of constrained population fluctuations, the essential lower limit being above zero and the upper limit well below infinity in a regulated population. Return tendency is the propensity of a regulated population on average to increase in size when relatively small and decline when relatively large. Such phenomena necessarily involve negative feedback in response to changes in population size. Also, by definition, populations are unregulated as they inevitably decline to extinction.

Because of the stochastic nature of environmental influences on birth and death rates, all natural populations are subject to random fluctuations, and thus have a nonzero probability of extinction at all times. This fact makes precise mathematical definitions of population regulation problematic (e.g., Royama 1977, 1992, Turchin 2001). Nonetheless, in more mathematically explicit terms, boundedness refers to the probability that a population will remain between an upper and lower limit for a given period of time. Similarly, return tendency is an increased probability of population increase when a population is small and an increased probability of decrease when a population is large.

Population regulation is one of the foundational con-

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cepts of ecology (Egerton 1973, Kingsland 1985, McIntosh 1985, Cherrett 1989, Hanski et al. 1993, Cappuccino and Price 1995, Turchin 2001), and thus can be considered a paradigm in the Kuhnian sense (Kuhn 1962). However, the idea that populations are naturally regulated has been controversial since its inception, and has recently become both increasingly important and increasingly contentious. The recent importance of understanding population regulation stems from the worsening extinction crisis. Human activities drive other species toward extinction by degrading natural regulatory processes, so preserving those processes is crucial for conservation. Understanding regulatory processes is also essential for enlightened management of exploited populations and the communities to which they belong.

Recent controversy surrounding population regulation has two sources. First, old debates regarding the existence and nature of regulation in general have resurfaced (Wolda 1995), as exemplified by the recent exchange between Murray (1999) and Turchin (1999). Such exchanges indicate that history is repeating itself in the sense of fundamental misunderstanding of the regulation paradigm. Second, recent focus on demographically open populations, especially in the sea, have led some to question whether regulation is necessary for the persistence of such systems (e.g., Doherty and Fowler 1994, Sale and Tolimieri 2000). This question indicates an incomplete perspective of the spatial scale of regulation in open systems.

Clarifying these two issues are the dual themes of this paper. We first examine the issue of population regulation in general by briefly reviewing the historical development of the paradigm, summarizing past debates regarding the nature and mechanisms of regulation. We conclude that regulation due to demographic density dependence indeed exists and that recent controversy largely rehashes issues resolved some time ago. We then focus on theoretical and empirical challenges to understanding regulation in open local populations and the metapopulations that they form. Examples are drawn from both terrestrial and marine systems, with emphasis on the especially contentious field of coral-reef fish ecology. We conclude that lack of evidence for regulation in part of a metapopulation is insufficient grounds for concluding that the entire system is unregulated, although there is clearly much that is unknown about the ecology of metapopulations.

A Brief History of the Population Regulation Paradigm

Several major misconceptions about population regulation emerge repeatedly in the literature, the two most frequent being, first, that competition is the only source of regulation (so that if competition is not evident, then neither is regulation), and second, that regulation can occur in the absence of demographic density dependence. A review of the history of the regulation paradigm sheds light on the origin and fallacy of these misconceptions.

From exponential potential to regulated reality

The concept of population regulation predates ‘‘ecology’’ itself in that Verhulst (1838) published the simplest model of regulation, the logistic equation, nearly three decades before Haeckel (1866) defined the new science of *ökologie.* However, the foundations of the regulation concept stem from ancient Greece, and solidified during the Enlightenment. In the fifth century BC, Herodotos noted that ‘‘timid animals which are a prey to others are all made to produce young abundantly, that so the species may not be entirely eaten up and lost, while savage and noxious creatures are made very unfruitful,’’ thus clearly identifying a compensatory inverse relationship between mortality and fecundity (Egerton 1973). Giovanni Botero in 1588, Walter Raleigh in 1650, John Graunt in 1662, Matthew Hale in 1677, William Derham in 1713, Richard Bradley in 1721, Carl von Linné (Linnaeus) in 1742, Benjamin Franklin in 1751, and Louis de Buffon in 1756 all explored the capacity for populations to grow exponentially with the recognition that such growth must eventually be limited (Cole 1957, Egerton 1973, Hutchinson 1978). By the end of the 18th century, there was a well-developed notion of an economy or balance of nature, a description first used by Linnaeus (1749), inferring that populations are regulated (Cole 1957, Egerton 1973, Kingsland 1985). However, this ancestral concept included the major fallacy that population regulation was divinely mediated in such a way that species neither went extinct nor evolved (see Naeem 2002).

Early fallacies regarding population regulation were abandoned with the emergence of the theory of evolution. Malthus (1798) inspired Darwin’s (1859) ‘‘struggle for existence’’ in his graphic description of the human population dilemma:

> Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will show the immensity of the first power in comparison of the second. By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal. This implies a strong and constantly operating check on population from the difficulty of subsistence.

Thus, both Malthus and Darwin wed the notion of population regulation primarily with the process of competition, despite the fact that Darwin and many of his predecessors acknowledged the negative effects of predators (including disease, etc.) on prey populations. The mechanistic link between regulation and competition was implied by Verhulst’s (1838, 1845) publication of the logistic equation, which states mathematically that population size has a negative effect on its own growth rate, the simplest case of such a regulating feedback being intraspecific competition. The focus on competition provided an explanation that the loser populations or species in the struggle for existence go extinct, whereas the winners are regulated by limiting resources.

Debates regarding density dependence

These early ideas set the stage for major debates that developed early in the 20th century and reverberated to the present. While ecologists in general recognized that populations were limited below their exponential potential, the underlying mechanisms were less clear. On the theoretical side, Pearl and Reed (1920) rediscovered and publicized Verhulst's logistic model, which was soon modified by Volterra (1928) and Lotka (1932) to include interspecific competition. This focus, bolstered by Gause's (1934) classic laboratory studies of competition in protozoans (see Robles and Desharnais 2002), had two major effects. First, it reaffirmed the belief that the biotic process of competition was the source of regulation, especially given that the Lotka-Volterra predator–prey model was only neutrally stable and that Gause's predator–prey systems usually went extinct. Second, it formalized the notion that population regulation was caused by demographic density dependence. These seminal theoretical ideas provided the foundation of ecological modeling for the remainder of the century, both in basic ecology (Kingsland 1985, McIntosh 1985) and in applied ecology, such as fisheries (Smith 1994). Eventually, the logistic model was much maligned as overly simplistic, with a consequential tendency to throw out the ''baby'' concept of density dependence with this ''bathwater'' model (Kingsland 1982).

Demographic density dependence (hereafter simply density dependence) occurs when present or past population size affects the per capita population growth rate, which is comprised of input rates (natality and immigration) and loss rates (mortality and emigration). In particular, input rates are directly density dependent when they vary inversely with population size, whereas loss rates are density dependent when they vary directly with population size. (The opposite is true in the case of inverse density dependence, and the absence of substantial change in these vital or demographic rates in response to changes in population size is called density independence.) Importantly, there must be a causative link between changes in population size and changes in demographic rates for true demographic density dependence to occur. Royama (1977, 1992) explores the meaning of density dependence in detail.

Returning to history, in the face of theoretical assertions spurred by the logistic model, a rift emerged among empirical ecologists during the early 1900s regarding whether population dynamics were indeed controlled by biotic interactions (e.g., Howard and Fiske 1911) or instead by abiotic factors (e.g., Kropotkin 1902). Nicholson (1933) was a major advocate of population regulation via competition, with notable allies including Elton (Elton and Nicholson 1942, which represented substantial revision of Elton's earlier views [Elton 1930]) and Lack (1954). Debate expanded and peaked in the 1950s during heated exchanges between Nicholson (1954, 1957) and Andrewartha and Birch (1954; see also Andrewartha 1957, Birch 1957). In essence, Nicholson concurred with earlier notions that regulation could occur only via density dependence caused by competition (McIntosh 1985), although he sometimes included predation in this context (Kingsland 1996). Note that Nicholson used rather complex terminology instead of ''density dependence,'' a term that was actually coined by Smith (1935). In contrast to Nicholson's ideas, Andrewartha and Birch believed that competition was not pervasively evident in nature and that population dynamics could be explained entirely by variation in abiotic factors.

In fact, both sides were partially correct and partially incorrect. On one hand, Nicholson was correct that population regulation requires density dependence, but not that competition is the sole source of density dependence. Predation can also induce density dependence in prey populations (reviews by Murdoch and Oaten 1975, Taylor 1984, Sinclair and Pech 1996). On the other hand, Andrewartha and Birch were correct that competition is often precluded by predation, physical disturbance, and harsh abiotic conditions, as well as that abiotic factors both limit and cause fluctuations in population size, but not that abiotic factors alone can explain the long-term persistence of populations. Abiotic factors are not capable of responding directly to population fluctuations, and therefore cannot be the direct agents of population regulation.

The fact that regulation is essential for the indefinite persistence of a population, and that demographic density dependence is the only possible mechanism, was clarified by J. B. S. Haldane nearly half a century ago (Haldane 1953):

> Suppose P_n is the population in an area at a definite date in year n. . . . Let $P_{n+1} = R_n P_n$ where R_n is the net rate of increase or decrease in the population. R_n can be greater or less than 1. But, since $P_{n+2} = R_{n+1} R_n P_n$, and so on, the product of R_n over a number of years must be very close to 1. . . . How close they must lie is clear if we suppose that $R_n = 1.01$ over 1000 years. The population would increase by 21,000 times. Similarly, if R_n were 0.99 it would decrease to 0.000043 of its original number.

More explicitly, using the standard notation of N in place of P, t in place of n, and λ in place of R (to avoid confusion with our notation for recruitment), given that $N_{t+1} = N_t \lambda_t$ is true by definition, over many time periods we have the following:

$$N_t = N_0 \prod_{i=0}^{t-1} \lambda_i.$$

This equation is equivalent to the following:

$$N_t = N_0 \left[\left(\prod_{i=0}^{t-1} \lambda_i \right)^{1/t} \right]^t.$$

The quantity within the brackets is the long-term geometric mean of λ, or $\bar{\lambda}$. Therefore,

$$N_t = N_0 \bar{\lambda}^t.$$

Unless $\bar{\lambda}$ equals 1, any reasonably large value of t will cause the population either to crash (i.e., any value of $\bar{\lambda} < 1$, even 0.999999) or head toward infinity (i.e., any value of $\bar{\lambda} > 1$, even 1.000001). Only if the long-term geometric mean of λ is unity (i.e., $\bar{\lambda} = 1$) will the population persist, and there is no conceivable mechanism whereby $\bar{\lambda}$ could equal 1 besides density dependence. Indeed, models that reportedly demonstrate indefinite persistence without density dependence (e.g., den Boer and Reddingius 1996) actually have density dependence hidden within them (see Chesson 1981, 1996, Hanski 1990, Murdoch 1994, Walde 1995, Hanski and Gilpin 1997 for details).

Present state of the population regulation paradigm

Following a variety of subsidiary debates in the latter half of the 20th century, including whether populations were self regulating via group-selectionist mechanisms (e.g., Wynne-Edwards 1962, refuted by Williams 1966), a vast majority of ecologists now agree that populations that persist indefinitely do so because they are regulated according to the following major principles:

1) Population regulation is caused by demographic density dependence. Density dependence needs not be omnipresent to regulate a population (Wiens 1977), but is essential at some time and place for long-term persistence (Hassell 1986). Model populations subject only to density-independent variation eventually take random walks to extinction (Nisbet and Gurney 1982). However, under some relatively unlikely circumstances, model populations lacking density dependence can nonetheless persist for many generations (Nisbet and Gurney 1982). Moreover, the duration of a time series necessary to distinguish a stochastic but regulated population trajectory from an unregulated random walk is still uncertain (see Connell and Sousa 1983, Shenk et al. 1998). Some interpret this situation as a demonstration that regulation via density dependence is a nonfalsifiable tautology (e.g., Sale and Tolimieri 2000). The key problem has been the notorious difficulty of empirically detecting population regulation in nature (Sinclair 1989, Murdoch 1994). Analyses of population time series are especially problematic (Shenk et al. 1998), but fortunately, experimental field studies are on the rise, many of which have demonstrated density dependence (reviews by Harrison and Cappuccino 1995, Hixon and Webster 2002). Note that Krebs (1995) proposed a ‘‘mechanistic paradigm’’ for understanding population regulation in contrast to the prevailing ‘‘density-dependent paradigm.’’ Close examination reveals that both approaches involve density dependence, the former including mechanistic studies and the latter descriptive studies.

2) Density dependence is necessary but not sufficient for population regulation. Specifically, as reviewed by Turchin (1995), density dependence must be temporal (i.e., occur within each population rather than merely among populations). Moreover, if one demographic rate is inversely density dependent, another must be sufficiently density dependent to counteract it. Density dependence must also be sufficiently strong to counteract any disruptive effects of density-independent factors, yet the strength and time lag of density-dependent responses must not be so great as to cause destabilizing population cycles that rapidly drive the population extinct. Thus, density dependence does not always ensure persistence (e.g., Middleton et al. 1995). These criteria acknowledge that all populations eventually go extinct when density dependence becomes weaker than various disruptive events and stochastic variation.

3) Both competition and predation are possible sources of density dependence. On one hand, competition for actually or potentially limiting resources (bottom-up regulation) is always density dependent by definition, be it via interference (a direct interaction) or exploitation (an indirect interaction). The specific mechanisms can involve both the input rate (e.g., density-dependent fecundity) and the loss rate (e.g., density-dependent starvation). On the other hand, predation (broadly including disease, parasitism, parasitoids, and herbivory) is not always density dependent. For predators to cause top-down regulation via density-dependent prey mortality, they must have a regulating total response, which is the combination of a numerical response in predator population size, a functional response in the per capita consumption rate, and other behavioral and developmental responses to changes in prey abundance (reviews by Murdoch and Oaten 1975, Taylor 1984, Sinclair and Pech 1996). Regulating responses result in predators increasing the per capita mortality rate of prey as prey density increases. Thus, negative feedback causing regulation can be either intrinsic (e.g., intraspecific competition) or extrinsic (e.g., predation), as well as either rapid (e.g., interference competition) or delayed (e.g., a numerical response of predators). Note also that competition and predation can interact with each other to cause density dependence (review by Sih et al. 1985), and both interactions can involve abiotic factors. For example, competition for limiting spatial refuges from predation (review by Jeffries and Lawton 1984) can cause density-dependent mortality of prey. Additionally, both competition and predation can involve numerous spe-

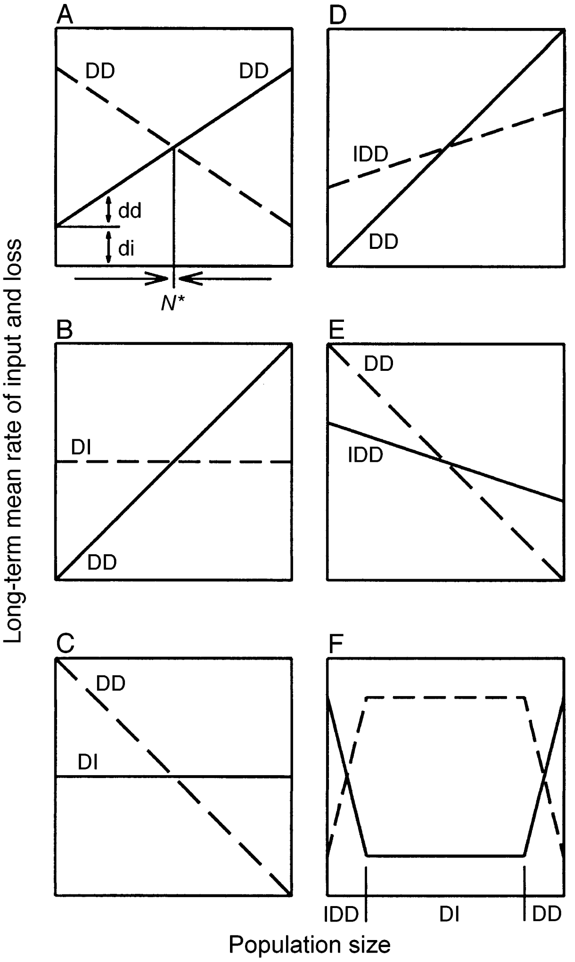


FIG. 1. (A–E) Long-term mean vital rates of input (birth and immigration, dashed lines) and loss (mortality and emigration, solid lines) that result in population regulation, the equilibrium point being where the curves cross (N^*). At least one rate is sufficiently density dependent (DD) in every case, even if the other rate is density independent (DI) or inversely density dependent (IDD), that input exceeds loss at sufficiently low population sizes and vice versa at high densities. Note that each density-dependent rate is composed of both a density-independent component (di, defined by the y-intercept) and a density-dependent component (dd, defined by the slope). (F) Murray's hypothesis, which includes the Allee effect (where both vital rates are inversely density dependent at low population sizes, thereby driving the population extinct once the loss rate exceeds the input rate), as well as a broad range of density independence at most population sizes. Besides incorporating the Allee effect, this scenario is basically the same as the pattern in (A).

cies, so that density dependence in any one species can be due to diffuse interspecific competition (sensu MacArthur 1972) as well as diffuse predation (sensu Hixon 1991). Thus, population regulation is truly a community-level phenomenon (Pimm 1991, see also Naeem 2002).

Based on these principles, the long-term mean input and loss rates over many generations must resemble one of the combinations in Fig. 1A–E for a population to persist indefinitely. (These patterns need not be linear as long as the curves intersect as shown.) In every case, at least one demographic rate is density dependent in such a way that input always exceeds loss at sufficiently low population sizes and vice versa at sufficiently high populations sizes. Thus, in these basic scenarios, population size heads toward a stable equilibrium point defined where the input and loss curves cross.

Of course, the patterns in Fig. 1A–E are far too simplistic to represent the span of variation and complexity found in nature. For example, Murray (1982, 1994, 1999) advocates the pattern in Fig. 1F as a common scenario. This pattern includes the Allee effect (Allee 1931) at low population sizes, density independence over a broad range of moderate abundance, and density dependence only at high population sizes. The Allee effect is inverse density dependence occurring in small populations, often due to a breakdown in the benefits of sociality (review by Courchamp et al. 1999). Thus, the Allee effect manifests an important threshold in conservation biology: the population size below which natural regulatory mechanisms collapse. Because all populations are eventually subject to extinction, it makes sense to include the Allee effect, which provides the basis for the concept of ''minimum viable population size'' (Soulé 1987). However, beyond the Allee effect, the pattern in Fig. 1F is simply a variation of the density-dependent pattern illustrated in Fig. 1A. Thus, the pattern in Fig. 1F is not, as reported by Murray (1999), an exception to density-dependent regulation (Turchin 1999).

An apparent problem with Fig. 1A–E is that each case has a single fixed equilibrium point (N^* in Fig. 1A), suggesting static population size, yet population fluctuations dominate in nature. It is important here to emphasize that the curves in Fig. 1 represent long-term means, and thus ignore the variance inherent in nature. In reality, the positions and slopes of the vital-rate curves vary through time as a function of demographic stochasticity (due to random births and deaths with discrete numbers of individuals), environmental stochasticity (caused by random exogenous events), and other sources of variation. Thus, for example, the long-term mean pattern in Fig. 1A can be illustrated as Fig. 2 when variance is included (see also Sinclair 1989). The net result of population regulation, then, is not a fixed equilibrium, but rather ''a long-term stationary probability distribution of population densities'' (Turchin 1995:22; see also Royama 1977, 1992). That is, the equilibrium point defined by the crossing of the input and loss curves is not a single point, but a ''cloud of points'' (sensu Wolda 1989, see also Nicholson 1954) often resulting in ''density-vague'' dynamics (sensu Strong 1986). The bottom line is that regulated populations can and do fluctuate substantially.

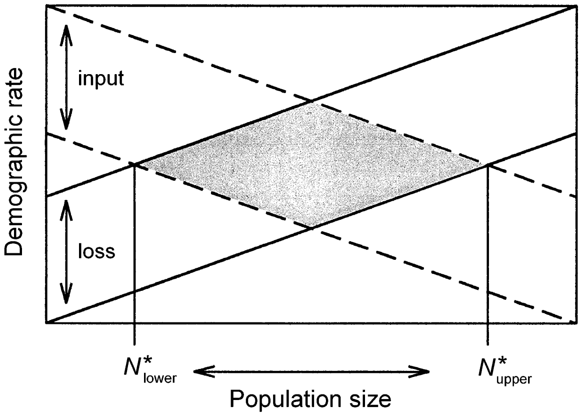


FIG. 2. Variation in both density-independent and density-dependent factors results in the positions and slopes of demographic rate curves shifting through time (cf. Fig. 1A). Thus, the equilibrial point at which the curves cross varies temporally within the filled region, such that population size fluctuates between N^*_{lower} and N^*_{upper} in a way that may appear stochastic. Despite these fluctuations, the population is still regulated by the three criteria of persistence, boundedness, and return tendency.

OPEN VS. CLOSED POPULATIONS

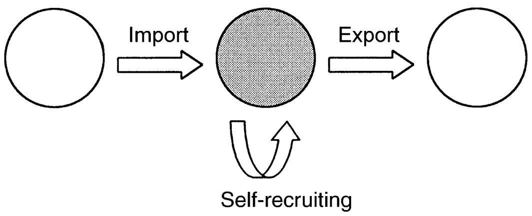
The concepts reviewed above regarding population regulation and density dependence were derived from the perspective of closed populations, where the only demographic rates are birth and death (i.e., immigration and emigration are negligible). Open populations, between which movement of individuals is demographically significant, occur when suitable habitat is patchy and the vagility of individuals is greater than gaps between those patches. When immigration and emigration of adults is substantial, it is easier to consider the situation as a closed population that is spatially patchy. The focus here is openness caused by dispersal of propagules between otherwise relatively isolated populations. Such vagility is common in species with bipartite life histories, such as plants with substantial seed dispersal, insects with aerial dispersal, and most marine organisms. In the sea, most movement between isolated local populations of benthic and demersal species (juveniles and adults living on and near the seafloor, respectively) occurs via pelagic dispersal of larvae, spores, and other propagules. The two-stage process of settlement of propagules from the water column to the seafloor and subsequent establishment in the local population as new juveniles is commonly called ''recruitment.''

Fig. 3 shows that there are five types of open populations, depending upon whether the local population successfully exports propagules to other populations (a ''source'' doing so, and a ''sink'' not; Pulliam 1988), as well as whether the local population is self recruiting (as in the case of an ''independent source'' or a ''facultative sink''). Of course, the relative level of propagule import, export, and self-recruitment can vary through time, so any particular local population can switch among the five types of openness as reproductive output, dispersal processes, and propagule survival fluctuate.

Open populations linked by such movements comprise a metapopulation, at least in the simplest sense of a ''population of populations'' (Levins 1969; we leave it to others to restrict the definition of metapopulation in ways that exclude some forms of patchy population structure [e.g., Harrison and Taylor 1997]). Because local populations can go extinct despite the persistence of the metapopulation as a whole, recent debate has centered on two questions: (1) Can metapopulations persist without density-dependent regulation, and if not, (2) how and at what spatial scales are metapopulations regulated (Murdoch 1994)? The remainder of this paper addresses controversy regarding regulation of open populations, especially in marine systems.

THEORETICAL CHALLENGES OF OPEN SYSTEMS

A common observation about the ecological modeling literature (e.g., Gaines and Lafferty 1995) is that we lack a well-developed theory of open populations relevant to marine systems (despite recent conspicuous exceptions, such as Roughgarden and Iwasa 1986, Possingham and Roughgarden 1990, Botsford et al. 1994, 1998, Roughgarden et al. 1994, Alexander and Roughgarden 1996). The idea that density dependence is essential to regulate open populations depends fundamentally on the fact that recruitment is always internal



Type	Import?	Self-recruiting?	Export?
Fully closed	No	Yes	No
Independent source	No	Yes	Yes
Dependent source	Yes	No	Yes
Obligatory sink	Yes	No	No
Facultative sink	Yes	Yes	No
Combination	Yes	Yes	Yes

FIG. 3. Comparison of fully closed population structure with five types of open populations. As illustrated for a single local population (filled circle), ''import'' is external recruitment by propagules from another population, ''self-recruiting'' is internal recruitment, and ''export'' is successful dispersal of propagules to another population.

at a sufficiently large spatial scale. It is because recruits come from within a metapopulation, not from some independent external basin, that population size would increase toward infinity or decrease to zero if there were no density dependence. Perhaps one reason that debates about density dependence have persisted longer in marine ecology than in other subdisciplines is that marine populations tend to be open at larger scales than terrestrial systems because of pelagic dispersal. What are the consequences of the relatively high degree of openness characterizing many marine populations? Does high openness somehow change the fundamental role of density dependence? Which mechanisms of population and community regulation are obviated by high openness and which are made more potent?

A population's degree of openness depends fundamentally on the spatial scale examined. An appropriate measure of openness is one minus the mean probability that an arriving recruit was born within the population boundaries in question. This openness measure is clearly equal to zero if the population encompasses the entire range of a species, but is close to one at spatial scales typical of field studies of benthic or demersal marine species. Moreover, the degree of openness in marine systems is typically close to one at scales that characterize the likely mechanisms of regulating density dependence. It is the difference between the scales of density dependence and the scales of propagule dispersal that has left marine ecologists debating the importance of population regulation far more intensely than many terrestrial ecologists. Here we focus on developments in the theoretical literature from the past two decades that shed some light on the problem of open systems.

We first discuss incomplete models, in which only the local population is considered, and recruits are taken from a black box outside the system (Fig. 4A). These models have the advantage that they are formulated at scales accessible to empirical studies, but the disadvantage that they fully address neither questions of metapopulation persistence, nor related issues of species coexistence and maintenance of species diversity. Obviously, extinction is impossible in the face of continual recruitment from outside the system. We then turn to complete models, in which a full range of scales is considered from the small scales at which the system is open to the large scales at which it is closed (Fig. 4B). In the simple complete models that dominate the theoretical literature, there are only two scales, with purely open dynamics at the small scale and purely closed dynamics at the large scale. Complete models of open systems are useful for two reasons. First, they permit one to investigate fundamental questions about regulation and stability that follow from global population closure, using the data on local dynamics accessible to field studies. Second, local interactions ultimately provide many of the mechanisms that regulate global dynamics. This perspective is clearly relevant to practical issues, such as the management of marine fisheries and the design of marine reserves.

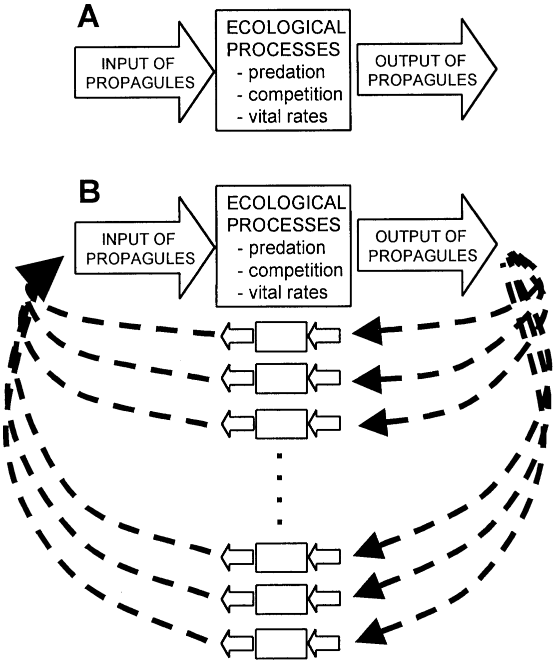


FIG. 4. Two ways demographically open populations have been modeled. (A) An incomplete model of metapopulation dynamics. The local population is essentially a filter, with an input of propagules being converted by various ecological processes into an output of offspring. These conversions may involve local population regulation (e.g., density-dependent mortality) or nonregulatory processes (e.g., density-independent vital rates). (B) A complete model of metapopulation dynamics in a purely open system. In this case, the offspring from the local population disperse to a well-mixed global pool of recruits. An infinite number of local populations disperse to a well-mixed global pool, and recruits to each local population are drawn from the pool.

Incomplete models of open systems

One approach to understanding the dynamics of open systems is to focus attention on the most tractable period of the organism's life cycle. For the purposes of this discussion, we will consider only organisms with a bipartite life history, beginning with a dispersive larval phase and ending in a sedentary reproductive phase. The majority of current theory treating incomplete life histories focuses on the dynamics of the sedentary adult population. The theory seeks an understanding of the effects of the local environment and adult interactions on the survivorship, growth, and reproduction of the sedentary population.

An example of an incomplete model of a locally open system is

$$N_{t+1} = f(t, N_t, R_t)N_t + s(t, N_t, R_t)R_t \qquad (1)$$

where N_t is the number of adults at time t, R_t is the number of new recruits (settling larvae) at time t, and $f(t, N_t, R_t)$ and $s(t, N_t, R_t)$ are the survivorship functions

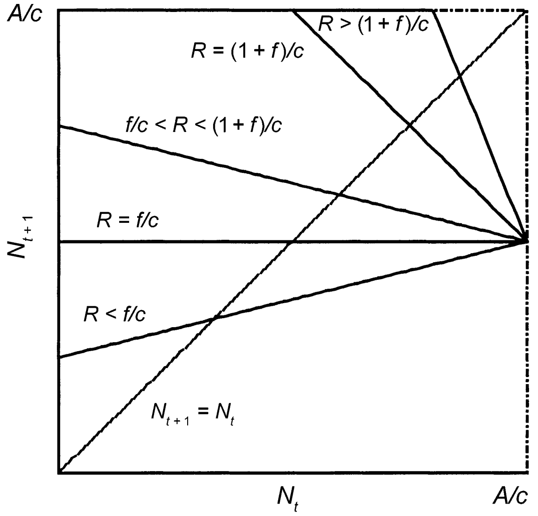


FIG. 5. Plots of difference equations (Eqs. 2a and 2b) for different levels of recruitment, R. When recruitment perfectly matches adult mortality ($R = f/c$), the population remains constant through time (parameters are described further in the text). The threshold for stability is when $R = (1 + f)/c$. At this point the slope of the line equals -1 at the equilibrium $N_t = N_{t+1}$. At values of R greater than this threshold, the population dynamics become unstable, as described in Levin and Paine (1974).

of adults and recruits, respectively. Notice that both recruit and adult survivorship can be functions of time, adult density, and recruit density. The element that distinguishes incomplete from complete models is that R_t is independent of local dynamics. Since we are considering the system to be open at the scale of this model, we have no information regarding feedback between number of adults one generation and the number of recruits in the next.

A broad range of dynamical behavior can emerge from Eq. 1. For example, suppose for simplicity that R_t is a constant R, that adult survivorship is a constant f, and that juvenile survivorship is proportional to the amount of free space, as in Roughgarden et al. (1985). Here, free space is the total amount of space A minus the fraction occupied cN_t, where c is the space occupied by an adult. With these assumptions, Eq. 1 becomes

$$N_{t+1} = fN_t + (A - cN_t)R \quad \text{if } N_{t+1} \leq A/c \qquad (2a)$$

$$N_{t+1} = A/c \quad \text{if } N_{t+1} > A/c. \qquad (2b)$$

The second equation is necessary because free space cannot become negative. If recruitment is large enough to eliminate free space, then Eq. 2b enforces a hard cap on population size.

Eq. 2a has an equilibrium at $N^* = RA/(1 - f + cR)$, which is stable if $R < (1 + f)/c$, as in Levin and Paine (1974), and unstable otherwise. The Ricker diagrams of Fig. 5 demonstrate that, as the recruitment rate increases, the first derivative of Eq. 2a at equilibrium decreases. The stability threshold for the model can be seen graphically when the slope reaches -1 at equilibrium, with unstable dynamics occurring beyond the threshold. The critical lesson (developed fully in Roughgarden et al. 1985, Bence and Nisbet 1989, Nisbet and Bence 1989, and Kuang and So 1995) is that recruitment and free-space-dependent survival strongly affect stability. With two sources of density dependence (in both f and s), regulation occurs primarily because of density dependence affecting recruit survival if R is low and density dependence affecting adult survival if R is high (Roughgarden et al. 1985).

Recruitment rates (R) larger than the critical threshold of $(1 + f)/c$ illustrate the important point that density dependence need not be stabilizing. If $R > (1 + f)/c$, then the population will approach a two-point limit cycle, alternating between years of complete occupancy (no free space) and years of abundance fA/c. This outcome occurs due to the time lag in the action of density dependence associated with discrete time generations in Eqs. 2a and 2b, and would not occur if recruitment and mortality were continuously readjusted.

The system described by Eqs. 2a and 2b also shows a complicated relationship between population regulation and density dependence. For example, t years after a small departure from an equilibrium of size n, the size of the departure will be $n(f - cR)^t$. This expression implies that the population's return tendency will vary inversely with the absolute magnitude of $f - cR$. Regulation is perfect when $R = f/c$, because perturbations are then eliminated in a single year (i.e., $n(f - cR)t = n(0)t = 0$, if $t > 0$). If R is either smaller or larger than f/c, then return times become larger and regulation becomes weaker. If $R > (1 + f)/c$, then the return time is infinite because perturbations grow in absolute magnitude as the population approaches the two-point limit cycle. This situation produces the unanticipated prediction that population regulation is greatest at intermediate recruitment rates.

Turning now to variable recruitment, an open system represented by Eq. 1 provides a particularly tractable means to determine how fluctuating recruitment interacts with local density dependence to produce fluctuating adult numbers (or biomass in an age- and size-structured version of Eq. 1). Holm (1990) showed in such models that density-dependent survivorship does not completely hide the history of past fluctuations in recruitment (see also Warner and Hughes 1988, Caley et al. 1996, Hixon 1998). Thus, we expect to see echoes of recruitment fluctuations in adult densities even with strong density dependence. More generally, let us consider the simple example of Eq. 2a with variable recruitment (R). We suppose that R_t fluctuates from year to year as a Gaussian random variable with mean $\bar{R}$ and variance σ_R^2. Using the methods in Roughgarden (1975), one can show that the corresponding variance in N will be

$$\sigma_N^2 = \{A^2[1 - c\bar{R}/(1 - f + c\bar{R})]^2/[1 - (c\bar{R} - f)^2]\}\sigma_R^2. \qquad (3)$$

To derive Eq. 3, we first linearize Eq. 2a around the equilibrium set by mean recruitment, $\bar{R}$. Stochastic fluctuations in recruitment are then converted to fluctuations in the population N as variation around the equilibrium $\bar{N}$. The right side of Eq. 3 is therefore an expression of the propagation of recruitment variance (σ_R^2) into variance of the adult population. This equation allows one to consider the extent to which demographic processes reduce or increase the variance driving the system, in this case stochastic recruitment in an open population. (For a thorough treatment of the mathematics behind variance estimates such as these, which use first-order autoregressive processes, see Cox and Miller 1972.)

Eq. 3 predicts that population variance will decrease as the mean recruitment rate $\bar{R}$ increases if $\bar{R}$ is sufficiently small, but will increase with the mean recruitment rate if $\bar{R}$ is sufficiently large. This behavior mirrors the return times to equilibrium of the simple system with constant recruitment. Population variance (σ_N^2) is relatively large when mean recruitment is either large or small because population regulation is then relatively weak. The variance increases to infinity as R approaches the stability threshold of the deterministic model (Eqs. 2a and 2b) simply because perturbations grow and oscillate deterministically if $\bar{R}$ exceeds $(1 + f)/c$. The fact that the variance approaches infinity rather than a finite limit is an artifact of the approximation leading to Eq. 3.

Complete models of open systems

The fundamental limitation of incomplete population models is that they cannot be used to study persistence of the entire metapopulation because recruitment occurs independently of local population dynamics (Gaines and Lafferty 1995). For this reason, several models have been developed of marine metapopulations with explicit assumptions about the way in which larvae disperse among a series of local populations (e.g., Roughgarden and Iwasa 1986, Possingham and Roughgarden 1990, Botsford et al. 1994, 1998, Roughgarden et al. 1994, Alexander and Roughgarden 1996). However, marine examples are few compared to the theory developed for terrestrial systems.

During the 1970s and 1980s, the push to develop a theory of population and community dynamics in spatially heterogeneous environments led to a class of ''patch'' models that, for reasons of mathematical convenience, assumed a habitat geometry conforming exactly to the simplest complete model that is purely open at small scale. In these models, an infinite number of local populations places dispersing propagules into a global pool and draws recruits from that pool at random, ensuring zero probability that an arriving recruit has been produced locally. Density dependence is typically assumed to occur only within each local population and vital rates are functions of local density, rather than some system-wide mean. Moreover, like in many marine systems, recruitment and subsequent dynamics are highly stochastic at the level of the individual patch. Most of the models include, at the local level, both demographic and environmental stochasticity.

There are many examples of such models that examine the dynamics of host–parasitoid interactions (Hassell and May 1973, Hassell 1978, Chesson and Murdoch 1986), animal competition (Atkinson and Shorrocks 1981, Ives and May 1985), plant populations and communities (Horn and MacArthur 1972, Pacala and Silander 1985, Tilman 1994), predator–prey systems (Murdoch and Oaten 1975, Murdoch and Stewart-Oaten 1989), and host–parasite interactions (Anderson and May 1992), as well as a comparatively few examples that address marine systems (e.g., Chesson and Warner 1981). In the past decade, the emphasis has been on relaxing the assumption that local populations are purely open, by allowing some (usually a small amount) of internal recruitment and recruitment from neighboring patches (Durrett and Levin 1994, Durrett and Neuhauser 1994, 1997, Rand et al. 1995, Levin and Durrett 1996, Pacala and Levin 1998, Bolker and Pacala 1999, Bolker et al. 2000, Dieckmann et al. 2000). Thus, theoretical ecologists interested in spatial problems have been working diligently to reduce the openness in models at the same time that marine ecologists have been calling for the development of a theory of openness.

At the risk of oversimplifying, one can identify four main developments in the patch/open-population modeling literature. It is instructive to review these in light of their possible relevance to marine systems.

1) *Heterogeneity and the regulation of predator–prey, host–parasitoid, and host–parasite systems.*—Consider a collection of patches, composed of, say, the individual host plants of an herbivorous insect species. We suppose that, at the beginning of each year, a global pool of insect recruits is distributed among these plants. Each plant receives a random (Poisson) number of recruits, perhaps modified into an even or clustered distribution by one or more deterministic factors (e.g., by how apparent plants are to herbivores or by the density of prior colonists). Further suppose that parasitoids or predators of the insects are now distributed in a similar fashion from a global pool, with the added possibility that the predators/parasitoids may preferentially colonize patches with many prey/hosts. After colonization, density-dependent dynamics within each patch produce offspring of both species, which are contributed to the global pools of recruits for the subsequent year.

This summary describes the structure of the many open-patch models developed to explain the persistence of host–parasitoid or predator–prey communities in nature despite their inherent instability observed in experiments and simple models (Nicholson and Bailey 1935, Huffaker 1958). The literature on patch models, especially combined with corresponding continuous-time models and models of parasitism, encompasses hundreds of papers. Entry points to the literature include Hassell (1978), Hassell et al. (1991*a, b*), and Anderson and May (1992). Perhaps the most important result is that heterogeneity, despite conspicuous exceptions (i.e., Murdoch and Stewart-Oaten 1989), often enhances stability (i.e., Hassell and May 1973, 1974, 1988, Hassell 1978, May 1978, Chesson and Murdoch 1986, Reeve 1988, Pacala et al. 1990, Hassell et al. 1991*a, b*). Although typically not stated in this way, this result is a direct consequence of the assumed openness of the local dynamics. Enhanced stability occurs because open recruitment disconnects prey/hosts from the local numerical response of their natural enemies, and continually creates mismatches between the abundances of natural enemies and their prey. The stabilizing effect of open recruitment typically increases with measures of its heterogeneity, such as the between-patch variance in recruit abundance (as in Hassell et al. 1991*b*).

These results are likely to be particularly relevant to reef-fish communities in light of recent experimental evidence demonstrating the importance of piscivory in causing density-dependent mortality (Beukers and Jones 1997, Hixon and Carr 1997, reviews by Hixon 1998, Hixon and Webster 2002). The modeling results imply that the open and erratic nature of recruitment might enhance stability at large scales because it causes large fluctuations on each local reef.

2) *Environmental niches and competition*.—The issue of coexistence of competing species living in metapopulations provides a community-level perspective of population persistence, and therefore insight on the broader concept of population regulation. In 1981, Chesson and Warner published a seminal paper on a patch model clarifying Sale's (1977) Competitive Lottery Hypothesis. In this model, the infinite number of patches each contained a single adult. Dynamics proceeded from one year to the next in three steps. The adults of each species first contributed offspring to a global pool of recruits. Adult deaths then opened a fraction of the sites to recolonization. Both fecundity and adult death rates were density independent and potentially species specific. Finally, a single recruit was randomly drawn to fill each vacant patch from the infinite pool of recruits in a (potentially biased) lottery. This lottery included a very strong form of density dependence because a single replacement is chosen for each dead adult, thereby keeping the population size of adults constant.

Chesson and Warner (1981) showed that purely random fluctuations in species-specific recruitment rates promote coexistence in such systems, unless the species' fluctuations are perfectly correlated. For example, suppose that species-specific survivorship rates in the plankton vary as statistically independent random variables. Chesson and Warner's results imply that these fluctuations alone will permit coexistence if they are large enough, even in the absence of any other coexistence mechanism.

Subsequent work has shown that lottery coexistence represents a mathematically subtle form of a more familiar mechanism, often referred to as the ''storage effect'' (Chesson 1983, 1984, 1985, 1986, 2000, Shmida and Ellner 1984, Comins and Noble 1985, Pacala and Tilman 1994). Suppose that each species in a community has a set of environmental conditions in which it is the best competitor—the species' environmental niche. Species can coexist by partitioning spatial and/or temporal environmental variation (e.g., Levin 1974, 1976). Persistence requires that a species be able to ''disperse'' across space and/or time, from one set of conditions in which it is the dominant competitor to another. Habitat partitioning of the kind commonly observed in benthic invertebrates (review by Connell 1972) and demersal fishes (review by Ebeling and Hixon 1991) is an example of purely spatial environmental niche partitioning, while the lottery mechanism is an example of purely temporal partitioning. Because species-specific survivorship fluctuates in the lottery model, the identity of the dominant competitor also fluctuates. Thus, the species in the lottery model partition unnamed environmental factors in the plankton that cause the fluctuations. Other examples of environmental niche partitioning from the open-patch literature include models of competition in both animals (Atkinson and Shorrocks 1981, Ives and May 1985, Ives 1991) and plants (Shmida and Ellner 1984, Pacala 1987, Pacala and Tilman 1994).

It is important to understand that spatial environmental partitioning represents a multispecies extension of source–sink dynamics in metapopulations (see Levin 1974, Hanski 1991, Hanski and Gilpin 1997). In a heterogeneous environment, some local populations (i.e., sinks, Fig. 3) may persist only because they consistently receive disproportionate amounts of recruitment from nearby sources (Pulliam 1988). In the extreme case in which one population is a source of propagules and all others are sinks, regulation of only one population is sufficient to control dynamics of the entire system. Source–sink dynamics highlight the importance of considering complete models of open systems (marine examples include Mumby 1999 and Tuck and Possingham 2000). Obviously, one could not deduce the pattern of regulation from empirical work conducted on sink populations alone. In models of spatial environmental niche partitioning, sinks occur both because of exogenous environmental factors and because of competition with species that are better adapted to the local environment.

The mechanism of environmental partitioning remains a dominant candidate to explain the diversity of benthic and demersal competitors. In addition to the documented cases of spatial habitat partitioning, observed fluctuations in recruitment should promote coexistence in the presence of density-dependent fecundity resulting from food limitation. The latter phenomenon is bound to occur in reef fishes because, first, fecundity increases with body size (review by Sadovy 1996), and second, growth is known to be density dependent (review by Jones 1991). Indeed, it is conceivable that a metapopulation could be regulated by density-dependent growth and size-specific fecundity alone, even if all local populations had density-independent postsettlement dynamics in the number of individuals. In such a case, postsettlement dynamics in local biomass would nonetheless still be density dependent.

The role of population openness in communities that partition environmental variation depends on the details of the partitioning. With purely spatial partitioning and static patches, openness works against coexistence because it continually brings together competitors that would occur only in separate patches if recruitment were locally closed. With spatiotemporal partitioning, openness is critical for each species' persistence because species must continually disperse to new sites as favorable sites become unfavorable. Indeed, there are models on the evolution of dispersal in such systems precisely because the degree of openness is so critical (Hamilton and May 1977, Cohen and Levin 1991, Ludwig and Levin 1991). Finally, with purely temporal partitioning, openness is largely irrelevant because persistence involves dispersal thorough time, not space.

Simple models of environmental niches depend on the assumption that dispersal occurs at a scale much larger than the scale of competition. When focusing on a few individuals, the system will appear completely open. Interesting and unexpected dynamics emerge when the scales of dispersal and competition begin to overlap.

3) *Spatial dynamics of succession*.—Open-patch models of ecological succession are relevant to the issue of persistence of metapopulations because they examine how early and late species coexist in a mosaic of habitat patches of different successional ages. In such models of successional dynamics, the local populations may be thought of as patches of vegetation dominated by a single successional stage, or as sites occupied by single individuals. When a local patch is cleared by disturbance, juveniles from a global pool compete to fill it. In models of the competition–colonization trade-off (Levins and Culver 1971, Horn and MacArthur 1972, Armstrong 1976, Hastings 1980, Shmida and Ellner 1984, Crawley and May 1987, Nee and May 1992, Tilman 1994), the species can be ordered in a perfect hierarchy, with competitive ability trading off against colonizing ability. Weak competitors have strong colonizing ability because they are disproportionately represented in the global pool of dispersers, as would be the case, for example, if weak competitors had high fecundity or high juvenile survivorship. A dispersing juvenile captures the local patch in which it lands if the site is either empty or contains a weaker competitor. The models show that the competition–colonization trade-off is capable of maintaining high levels of diversity. Succession occurs simply because early successional species arrive in recently disturbed habitats before late-successional species. The models also produce a number of nonobvious predictions, including the prediction that small amounts of habitat destruction could result in the delayed extinction of many late-successional species (Tilman et al. 1997).

In models of the successional niche, early successional species are assumed to be the dominant competitors under the resource-rich conditions typical of recently disturbed locations, rather than being weak competitors everywhere. Late-successional species displace the early species because they are the dominant competitors in the resource-poor conditions that subsequently develop. In both the competition–colonization and successional niche hypotheses, dynamics must be at least partially open because disturbance would otherwise drive every species to extinction. However, the addition of some local recruitment (a fraction of the arriving recruits drawn from the local site and the remaining fraction from the global pool) does not qualitatively change predictions, although it does slow the dynamics of succession.

Successional-patch models are likely to be relevant to some problems of competition in sessile invertebrates and seaweeds, where succession from fast- to slow-growing forms is observed (e.g., Farrell 1991, Hixon and Brostoff 1996). Examples of succession in reef-fish communities spring less readily to mind, perhaps because the rapid response of resources such as algae and incoming plankton to disturbance, together with the mobility of fish, reduce the effectiveness of early successional strategies. In any case, prior residency of particular reef-fish species, especially predators and territorial competitors, can influence subsequent patterns of colonization (e.g., Shulman et al. 1983, Sweatman 1985).

4) *Finite dispersal, neighborhood interactions, and effects of endogenous pattern formation*.—In the last five years, theoreticians have made rapid progress on an important class of problems relevant to population regulation that had been previously intractable. If interactions among individuals are spatially local and dispersal is finite, then spatial pattern may form spontaneously, with potentially large effects on dynamics. One may think of these explicitly spatial, individual-based models as variants of the patch models discussed above in which the spatial arrangement of the patches is specified and dispersal is partly closed at the local scale. Using new methods called moment or pair approximations, together with some direct approaches, the importance of endogenous pattern formation is beginning to be understood in systems of competitors (Durrett and Levin 1994, Pacala and Levin 1998, Bolker and Pacala 1999, Neuhauser and Pacala 1999, Bolker

et al. 2000, Dieckmann et al. 2000) as well as natural enemies and their victims (Hassell et al. 1991*b*, Rand et al. 1995, Levin and Durrett 1996, Keeling et al. 1997, Wilson and Hassell 1997, Wilson et al. 1998, Diekmann et al. 2000). These studies show that endogenous pattern formation may qualitatively change dynamics, for example, by eliminating founder control from models of competition. However, in most cases, effects of endogenous pattern formation are not large, unless both the dispersal distances and the distances over which individuals can interact (i.e., spatial scale of resource depletion, prey detection or disease transmission) are relatively small. Effects are typically large only if interaction and dispersal distances are small enough, on average, to encompass a neighborhood containing only a few individuals (usually $<$100).

Because scales of pelagic dispersal are so large, we suspect that the results to date on endogenous pattern formation in individual-based models will have limited relevance to many marine systems. However, in communities of sessile invertebrates, the results are likely to apply to situations in which most individuals are produced by budding, because most movements then involve the short distances associated with clonal growth.

Summary of the theory of open systems

Because of broad dispersal of propagules in most marine and some terrestrial systems, the modeling assumption of open recruitment at the local scale is likely to be a reasonable approximation in many cases. We thus believe that the theory of marine and similar terrestrial systems would benefit by incorporating ideas from existing models of open systems. Incomplete models ignore critical feedbacks at the scale of the entire metapopulation necessary to address most questions of regulation. Complete models, on the other hand, suffer from a lack of empirical support because of the difficulty in tracking widely dispersing species. New data on the magnitude of larval dispersal and large-scale dynamics (e.g., Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000) are critical to increase the coupling between open models and empirical studies. In any case, theory shows a variety of mechanisms whereby metapopulations can be regulated by density-dependent processes, including mechanisms which are not are not obvious at the scale of the local open population (Chesson 1998*a*).

EMPIRICAL CHALLENGES OF OPEN SYSTEMS

There are two major empirical issues for understanding the dynamics and regulation of metapopulations, particularly in the sea. The first issue is clarifying operational definitions and measurements associated with existing hypotheses regarding local open populations, especially the Recruitment Limitation Hypothesis. The second issue is identifying needs and future directions for measuring important parameters for which no data are presently available, particularly at larger spatial scales.

Operational definitions and measurements: the Recruitment Limitation Hypothesis

In marine ecology, the greatest challenge to the population regulation paradigm in recent years has been the Recruitment Limitation Hypothesis. Paradoxically, the original definition of recruitment limitation, which was subsequently adopted by other subdisciplines (such as terrestrial plant ecology), was entirely compatible with the notion of population regulation. The hypothesis was first formalized by Doherty (1981) with the forthright prediction that the supply of incoming propagules is so low (due to dilution and mortality during the dispersal phase) that local populations of juveniles and adults seldom reach levels where resources become limiting, thereby precluding competition. This original concept, popularized as ‘‘supply-side ecology’’ (Lewin 1986), was compatible with population regulation because density dependence could still conceivably occur during the dispersal phase, or predation could still cause density-dependent mortality of juveniles and adults. However, in subsequent manifestations regarding coral-reef fishes (Doherty and Williams 1988, Doherty and Fowler 1994, Doherty 1998), the Recruitment Limitation Hypothesis changed such that density dependence was de facto eliminated from the entire life cycle (Hixon 1998). This change was due to the operational definition of ‘‘limitation’’ becoming more restrictive at the same time that the operational definition of ‘‘recruitment’’ became less restrictive. Thus, it is worthwhile to explore both terms in detail.

‘‘Limitation’’ has special meaning to reef-fish ecologists that differs from general ecological usage. Sinclair (1989) provides a thorough discussion of the general definition, and contrasts limitation with regulation. As illustrated for the loss rate in Fig. 1A, each density-dependent demographic rate is comprised of both a density-independent component (defined by the y intercept) and a density-dependent component (defined by the slope). Changes in either component will cause a change in the equilibrial population size as the vital-rate curve shifts in position, which is the phenomenon of limitation. (Thus, complete knowledge of population dynamics requires investigations of both density-independent and density-dependent factors.) However, as reviewed above, only the density-dependent component can provide regulation. As generally defined, all populations always undergo limitation because the input rate can always conceivably be higher than it is, and the loss rate lower (Sinclair 1989).

In the context of the Recruitment Limitation Hypothesis, limitation originally meant limited to a population size below which competition would occur (Doherty 1981). In subsequent manifestations, this special definition was expanded to mean limited to a population size below which any form of postsettlement density dependence would occur, regardless of the mechanism (Doherty and Williams 1988, Doherty and Fowler 1994, Doherty 1998). This shift in meaning is important because, as far as is known, density dependence does not act during the pelagic larval stage in marine fishes (reviews by Houde 1987, Bailey and Houde 1989, Heath 1992). Therefore, unless density dependence does in fact occur during the larval stage, the latest version of the Recruitment Limitation Hypothesis implies that open marine populations have no source of density dependence.

What about the meaning of ''recruitment''? In the context of the Recruitment Limitation Hypothesis, recruitment is an estimation of settlement, which is the transition from the dispersive pelagic phase (larva) to the more sedentary benthic/demersal phase (juvenile and adult). Note that this definition differs from that commonly used in fisheries biology, where one estimates recruitment of larger fish to a fishery. It also differs from the general ecological definition, where recruitment is used with an explicit modifier to describe the transition between particular life history stages. In any case, as an estimate of the real biological phenomenon of settlement, measures of recruitment are subject to the vagaries of sampling design. Clearly, the more frequently one counts new recruits, the more accurate is one's estimate of settlement, and importantly, the less likely postsettlement mortality has altered patterns of settlement and thus larval supply (recall the original definition of recruitment limitation). The ramification of this issue is that recent evidence reportedly corroborating the Recruitment Limitation Hypothesis in reef fishes comes from studies where recruitment was measured long after settlement, up to several months in some cases (e.g., Doherty and Fowler 1994). In such studies, early postsettlement mortality, which is typically substantial (review by Hixon 1991) and often density dependent (Hixon and Webster 2002), was missed, possibly resulting in erroneous acceptance of the hypothesis.

Besides the prediction of no postsettlement density dependence, the Recruitment Limitation Hypothesis also predicts that variation in recruitment should be reflected in subsequent variation in local population size (Doherty and Williams 1988, Doherty and Fowler 1994, Doherty 1998). However, this pattern can also occur when mortality is density dependent (Warner and Hughes 1988, Holm 1990, Caley et al. 1996, Hixon 1998), so it fails to test the more recent version of the hypothesis. Nonetheless, there is still convincing evidence for recruitment limitation in several reef-fish systems (e.g., Victor 1986, Jones 1987, Tupper and Hunte 1994), even though a great majority of studies have revealed that postsettlement mortality is density dependent (review by Hixon and Webster 2002).

In summary, the evolving definition of recruitment limitation has resulted in at least two versions. The more general version simply asserts that an increase in the settlement rate causes an increase in local adult population size (e.g., the phenomenon of dominant cohorts or age classes). This version actually has little to do with density dependence per se because the predicted pattern can occur whether postsettlement mortality is density dependent (Fig. 6A) or density independent (Fig. 6B). Only intense or ''exactly compensating'' density dependence (sensu Sinclair and Pech 1996) can completely cancel a strong settlement pulse. The more restricted version of recruitment limitation asserts that postsettlement mortality is strictly density independent, in which case only Fig. 6B is predicted. These quite different definitions have caused unnecessary controversy that can be ameliorated simply by stating explicitly which version of recruitment limitation is being examined in any particular study (Hixon 1998). Armsworth (2002) examines these alternative definitions in detail from a theoretical perspective.

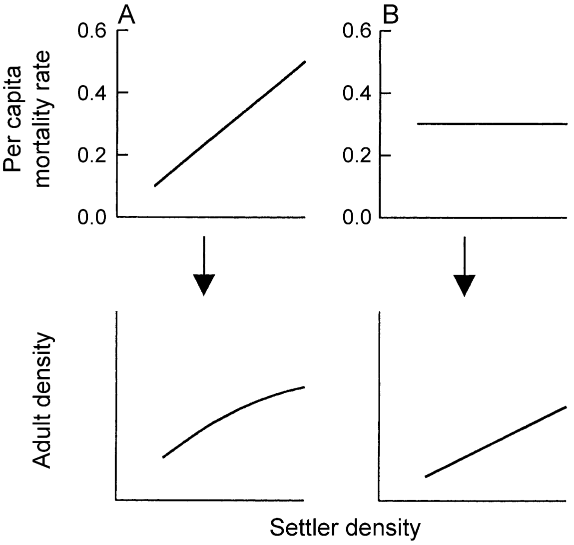


FIG. 6. Both density dependence and density independence can cause a positive relationship between the abundance of settlers and the subsequent abundance of adults from that settlement. (A) Post-settlement mortality that is linearly density dependent at low to moderate levels causes a curvilinear settler–adult function (that becomes unimodal at higher mortality rates). (B) Density-independent post-settlement mortality causes a linear settler–adult function (assuming that some settlers survive to maturity). If recruitment limitation is simply defined as a positive relationship between settler density and subsequent adult density, then the patterns in (A) and (B) are corroborative, and the issue of density dependence is irrelevent. Alternatively, if recruitment limitation is defined to predict only density-independent mortality, then only the pattern in (B) is corroborative.

Needs and future directions for empirical study of open systems

There are empirical needs for understanding the regulation of open systems at the scale of the local population as well as the entire metapopulation (Chesson

1998*b*, Sale 1998). At the scale of the local population, more research is needed to identify the existence (if any) and mechanisms of local density dependence. There are presently few data on whether the process of settlement is a density-dependent phenomenon, although there is evidence from reef fishes that prior recruits can have both positive and negative effects on local recruitment (e.g., Shulman et al. 1983, Sweatman 1985). There are ample data demonstrating postsettlement density-dependent mortality in seaweeds (review by Lobban and Harrison 1994), marine invertebrates (review by Bertness et al. 2001), and demersal fishes (review by Hixon and Webster 2002). However, data on the mechanisms causing this density dependence are relatively rare. Sessile organisms often appear to compete for space (including shading in seaweeds), and mobile organisms seem more frequently to suffer density-dependent mortality due to predation shortly after settlement. There is a glaring need for investigations of the mechanisms by which competitors, and especially predators, cause density-dependent mortality in these systems (see Abrams and Ginzburg 2000).

At the scale of the entire metapopulation, we know precious little. How any density dependence in fecundity translates into subsequent recruitment is virtually unknown, although it appears that mortality of pelagic fish larvae is largely density independent (reviews by Houde 1987, Bailey and Houde 1989, Heath 1992). It is also possible, but undocumented, that density-dependent growth combined with size-specific fecundity causes density dependence in local biomass, and thus regulates metapopulations even in the absence of local density dependence in numbers.

Sorely needed are means of tracking the fate of propagules at sea. One of the most crucial needs is a measure of the openness of local populations at nested spatial scales. Most models in the marine literature are either incomplete or assume unrealistic global dispersal simply because we lack empirical information about dispersive coupling. However, four recent developments suggest that this situation is about to change. Population genetics is offering insights in the scales of population isolation in various marine species (e.g., Weil 1993 and Benzie et al. 1995 on corals, Shulman 1998 on reef fishes, Barber et al. 2000 on stomatopods). Otoliths (calcium carbonate ear stones) of fish are providing means of estimating levels of self-recruitment, either via chemical tagging of the otoliths (Jones et al. 1999) or via microchemical signatures derived from ambient water masses (Milton et al. 1997, Thorrold et al. 1998*a, b*, Swearer et al. 1999). Oceanographic studies are providing information on currents and eddies that likely entrain pelagic larvae (e.g., Cowen and Castro 1994, Lee et al. 1994, Limouzy-Paris et al. 1997, Cowen et al. 2000). Finally, local effects of marine reserves are suggesting source–sink dynamics of marine populations at particular spatial scales (McClanahan and Kaunda-Arara 1996, Russ and Alcala 1996*a, b*, Bohnsack 1998).

CONCLUSIONS

Population regulation via demographic density dependence is real, and understanding how regulation operates is essential for managing and conserving populations and species. The ‘‘balance of nature’’ is not a divine force that prevents extinction, as historically envisioned, but rather the manifestation of density dependence that waxes and wanes in the context of environmental and demographic stochasticity, ensuring persistence only in a probabilistic sense.

The future of understanding regulation of open systems, especially in the sea, is by means of integrated, multiscale theory and fieldwork. This work will encompass both the reality of open dispersal at scales characterizing density dependence and the inevitability of closure at the large scales characterizing critical population-dynamic feedbacks. A three-scale approach could offer significant insights. At the smallest local scale, recruitment is open. Mechanisms of density dependence that affect vital rates during and after settlement operate at this scale. Because this is also the scale of most field studies, much information already exists about local-scale dynamics. The second scale may be thought of as the node of a metapopulation. Each node consists of a large number of local patches, and is itself large enough for considerable internal retention of propagules. One may think of islands—each containing many local reefs—that have been shown to maintain substantially internal self-recruitment of reef fishes (Cowen and Castro 1994, Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000). The final scale consists of a metapopulation of many nodes. Recruitment is fully closed at this scale. Internode dispersal is likely to be heterogeneous depending on spatial proximity and currents. In marine systems, the theory of reserve design has taken the first steps in the direction of multiscale study (e.g., Man et al. 1995, Hastings and Botsford 1999, Mangel 2000). Combined with previous related work (e.g., Roughgarden and Iwasa 1986, Possingham and Roughgarden 1990, Botsford et al. 1994, 1998, Roughgarden et al. 1994, Alexander and Roughgarden 1996) such studies offer promise for insights into the dynamics and regulation of open systems. In sum, we agree with Cappuccino (1995) that the important focus is not whether populations are regulated, but rather how they are regulated.

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