

Recruitment limitation: A theoretical perspective

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Abstract A theoretical analysis of the concept of recruitment limitation leads to the conclusion that most populations should be regarded as jointly limited by recruitment and interactions between individuals after recruitment. The open nature of local marine systems does not permit avoidance of density-dependent interactions; it simply may make them more difficult to detect. Local populations consisting of settled organisms may not experience density-dependent interactions under some circumstances, but the entire species population consisting of the collection of local populations and their planktonic larvae must have density-dependent dynamics. Any local population of settled individuals can escape density dependence if sufficient density dependence occurs among planktonic larvae or within other local populations. Common conceptions of density dependence are too narrow, leading too often to the conclusion that it is absent from a system. It is equally wrong to expect that density-dependent interactions after settlement determine local population densities independently of recruitment. Special circumstances allowing density dependence to act strongly and quickly are needed before density dependence can neutralize the effects of recruitment. Recruitment limitation and density-dependent interactions therefore should not be regarded as alternatives but as jointly acting to determine the densities of marine benthic populations. Moreover, the interaction between fluctuating recruitment and density dependence is potentially the most interesting feature of recruitment limitation. For example, this interaction may be an important diversity-maintaining mechanism for marine systems.

Key words: density dependence, equilibrium, larval supply, recruitment fluctuations.

INTRODUCTION

Are populations of marine benthic organisms limited more by recruitment than by interactions between individuals after recruitment? This question has been prominent in the minds of many marine ecologists during the past decade and a half (Keough 1988; Jones 1991; Doherty & Fowler 1994; Caley *et al.* 1996). After early enthusiasm for the study of interactions between settled organisms, some studies concluded that recruitment rates may often be too low for interactions after settlement to be important (Doherty 1983). Given also that recruitment rates may be highly variable in space and time, it appeared that recruitment may exert a dominant influence on abundance patterns. Evidence for important roles for interactions after recruitment, however, has been found for some systems (Jones 1987,

1991; Hixon 1991). It should also be appreciated that the complexity and variability of ecological systems mean that, despite various heroic efforts in data collection and experimentation, the key question asked here has not been answered with confidence for any marine system.

The complexity and variability of ecological systems also pose serious theoretical challenges. Many ecologists have rejected the deterministic, equilibrium-centred approaches to ecological theory that were popular two decades ago (Underwood & Denley 1984; Roughgarden 1989). However, modern theory has moved far beyond this framework to deal with systems varying in time and space on multiple scales (Chesson & Huntly 1993). It is no longer necessary theoretically to hope that the variability of real systems does not affect theoretical conclusions, because such variability can be taken into account in the theory. It is the aim of this article to use modern theory to clarify the question of recruitment limitation, with the hope that it will also help focus empirical studies on the most promising avenues of investigation.

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RECRUITMENT LIMITATION

Recruitment limitation refers fundamentally to the idea that the local density may be limited by the rate at which larvae arrive at a site with the potential of settling and maturing to adulthood (Doherty 1983; Victor 1986; Doherty & Fowler 1994). I use the term 'larva' for an individual that has not settled and 'juvenile' for an individual that has settled but has not yet matured as an adult. Although ideally it would be best to measure the rate of arrival of larvae, it is easier in empirical studies to count juveniles after they have had a chance to grow. Thus, an implicit operational definition in some studies replaces rate of arrival of larvae with the rate of recruitment into a juvenile stage or even the adult stage. However, such older individuals may already reflect interactions with others in the settling and growth processes (Bertness *et al.* 1992; Kaufman *et al.* 1992); for example, if there is competition for resources necessary for settling and maturation. Indeed, limitation by the numbers recruiting into any juvenile or adult stage may not be cleanly separated from interactions at a locality. Fundamentally, the notion 'recruitment limitation' is limitation by the supply of larvae to a site, and not limitation by the rate of recruitment to any settled stage. Operationally, one may be forced to consider a broader concept, but in doing so it is important to keep in mind that critical interactions at a site may have already occurred.

As recruitment limitation is held in opposition to local interactions at a site, two contrasting positions can be recognized: (i) local abundance is determined solely by the input of recruits (or larvae); and (ii) local abundance is determined solely by interactions after recruitment (or after arrival of larvae). Interactions between the individuals at a locality are expected to lead to density-dependent population dynamics, and it has been argued that confirmation of (i) means that the dynamics of a population are density independent (Doherty & Fowler 1994). By considering a range of possible scenarios below, I argue that these two positions are extreme, and neither is likely to apply in nature to many populations. Moreover, I show that even if position (i) is true for a particular local population, its dynamics are not likely to be independent of its density unless it is a sink population (i.e. has a reproductive rate below replacement for the locality; Roughgarden & Iwasa 1986), and is therefore dependent on a net surplus of larvae arriving from other localities for persistence. Related arguments are presented by Hixon (1998).

LIMITATION OF LOCAL ABUNDANCE BY RECRUITMENT ALONE

If local abundance is limited by recruitment alone, survival of individuals after recruitment must be completely independent of local density (Doherty & Fowler

1994) and, following the idea of recruitment limitation strictly, settlement must simply be proportional to larval abundance. Many local populations studied by marine ecologists are open in the sense that many recruits are the offspring of individuals in other local populations. However, closed populations can occur on isolated reefs or in a gulf or bay where juveniles recruit into the population of their birth (e.g. Leis 1994). Although the species may have planktonic larvae, current circulation or isolation by distance limits immigration of larvae from other populations to minor levels. Consideration of such closed populations first is the simplest route to understanding the critical arguments of this section.

Closed populations

Although post-settlement mortality may be density independent, important density dependence may occur in the planktonic stage of the life cycle. Moreover, interactions between settled individuals may lead to density-dependent fecundity even if they do not lead to density-dependent mortality. The alternative to all these possibilities is the complete absence of density dependence at all stages in the life cycle. Such a scenario is theoretically highly implausible. A completely density-independent system would exhibit exponential growth in the long run, even though it may fluctuate on shorter timescales (Chesson 1996).

Positive exponential growth clearly cannot be sustained for long. Negative exponential growth means that the population becomes extinct. The final alternative is exponential growth at a zero average rate. Even if theoretical mean per capita growth rates are zero, actual population growth will still fail to be zero because stochastic environmental fluctuations and demographic stochasticity will ensure that it must either drift to extinction or drift to arbitrarily high population densities. Even if drift to high densities were possible, the laws of probability insist that such a population must drift back to extinction again (Feller 1971). It has been pointed out that such drift to extinction may take a long time (Hubbell 1979), but this argument relies on drift due to demographic stochasticity alone, and omits the much stronger effects that stochastic environmental fluctuations can have (Lande 1993; Chesson & Huntly 1997). A more important question, however, is not how long it would take for such a population to become extinct, but whether such populations are likely to arise and retain their defining property of zero mean per capita growth in the absence of density dependence. No mechanism has ever been proposed by which a density-independent population achieves a zero mean per capita growth rate, and although such a population might arise occasionally by chance, additive genetic variation in average fitness would move the mean per capita growth rate above zero, leading to an expand-

ing population (Chesson 1996). Thus, the case of density-independent growth at a zero mean rate, which has preoccupied thinking in this area, seems likely to arise rarely and to persist fleetingly.

Density dependence is necessary for a population to have an abundance in a range definable by the properties of the system of which it is a part. It is sometimes argued that a harsh environment leads to low recruitment rates, which in turn leads to weak and therefore unimportant density-dependence. However, Chesson and Huntly (1997) show that in such circumstances density dependence remains important, even though weak, because low rates of recruitment mean that a small additional impact from density dependence can lead to negative population growth rates, population decline and extinction.

A model of recruitment limitation in barnacles (Roughgarden & Iwasa 1986), as applied to a closed population ($w = 1$), is instructive. Local abundance is proportional to the recruitment rate divided by the mortality rate of settled adults, which may give the impression that local abundance has density-independent dynamics. However, the recruitment rate involves an interaction between settled adults and settling larvae. Thus, recruitment is density dependent and proportional to the space not already taken by adults. The parameter expressing the degree of density dependence is the area that an individual barnacle occupies to the exclusion of others. Vary this area and the equilibrium abundance changes; indeed, in the closed-population version of the model, the equilibrium abundance is inversely proportional to the area occupied by a barnacle. This is so even if density dependence is very weak due to very low rates of larval supply, revealing that even weak density dependence can have major effects. Note that the density dependence in this model comes from space pre-emption. Mortality of settled individuals, which is so prominent in discussions of recruitment limitation, is not density dependent. Density dependence can be complex and indirect acting through a resource (competition) or predator (density-dependent predation or 'apparent competition'), and therefore may operate with a time lag (Chesson 1996). Too narrow a conception of how density dependence arises may lead to its false rejection.

The arguments above imply that a closed persisting population must have density dependence somewhere in the life cycle. If it is not in settlement or subsequent survival, it may be in reproduction or survival at the larval stage. When there is density-dependent limitation at the larval stage it is theoretically possible that recruitment could be low enough that there is negligible density dependence at or after settlement. One could then regard densities of settled organisms as set entirely by larval supply. Note, however, that potentially complex interactions between settled organisms have been replaced in this scenario by interactions at the

larval level. If species have similar niches, then co-existence between the species must depend on interactions at the larval stage (cf. lake fishes: Mittelbach & Chesson 1987).

Populations that are open on the local scale

Andrewartha and Birch (1954) suggested that populations that are locally open may persist essentially indefinitely without density dependence. Their argument is that spatial and temporal heterogeneity in survival and reproduction prevent local populations from becoming extinct simultaneously so that any unoccupied locality can be recolonized from other places. More recently, metapopulation models have been cited as evidence for this view (Caswell 1978). However, such models invariably contain hidden but strong density dependence (Chesson 1996). It is the interaction between spatial and temporal heterogeneity and density dependence that leads to the remarkable conclusions of metapopulation models, not spatial and temporal heterogeneity alone (Chesson 1996). Indeed, it can be shown quite generally that subdivision of a population into local populations, even with much spatial and temporal variation, does not remove the essential requirement of density dependence in persisting populations because in the absence of density dependence, such populations continue to show long-term exponential growth, just like populations without spatial structure (Chesson 1996).

We must conclude that if density dependence does not occur at the larval stage, it must occur at least in some local populations, some of the time. We must entertain the proposition that it occurs in most places much of the time but may be weak and hard to detect in the presence of high variation in a system (e.g. Hassell 1987; Ray & Hastings 1996). Some localities may also be sink locations (Roughgarden & Iwasa 1986; Pulliam 1988), if not all of the time then potentially in some years. In such locations, no density dependence need be present and only survival rates after settlement need affect local densities. It is quite reasonable for such populations to persist indefinitely without density dependence, provided that density dependence at other localities or among larvae holds down recruitment to levels too low for density-dependent interactions at the sink locality. Being a sink population, however, does not automatically eliminate density-dependent interactions after settlement. Indeed, in theory, a sink locality could occur because recruitment rates are much higher than the local resources can support, or because of high rates of predation or disease (Hixon 1991; Bailey 1994), either of which may be density dependent.

Warner and Hughes (1988) and Hughes (1990) have developed models that might be viewed as showing that density dependence is unnecessary for persistence at a

locality. However, because recruitment is entirely from external sources unaffected by the population in question, they are in fact best viewed as models in which density dependence takes place externally to the local population being modelled. Density dependence in the plankton is the only candidate for the general absence of density dependence between settled or settling organisms in all local populations. We may well say then that local populations are limited by recruitment alone, but we can only say this because recruitment itself is limited by density-dependent interactions in the larval stage of the life cycle. Unless recruitment limitation occurs by strong intraspecific density-dependent processes in the plankton, interactions at or after settlement will still play important roles in population densities (Shulman & Ogden 1987).

LOCAL LIMITATION INDEPENDENT OF RECRUITMENT

Is it plausible that local abundances could be determined independently of the recruitment or larval supply rates at a site (Doherty & Fowler 1994)? As local populations are replenished by recruitment, is there some process that could eliminate the effect of the numbers of recruits or larvae on local population densities?

The equilibrium approach to population dynamics and species interactions has emphasized convergence of a population or community to an equilibrium independent of initial conditions and dependent only on species interactions. Is this relevant to local communities replenished by recruitment? Could recruitment be regarded as an initial condition whose value is irrelevant to a later equilibrium achieved at the site? In general, the answer is no, because there is an enormous difference between the two situations. In the standard equilibrium scenario, for example, as represented by the logistic equation or the two-species Lotka–Volterra competition equations with a stable equilibrium, the equilibrium is approached over many generations. A local community replenished by recruitment normally has less than a generation between recruitment events. Moreover, the local population of recruits represents just part of the life cycle of the species and therefore just part of the dynamics of the system. It is instructive in this regard to note that in deterministic models like the logistic and Lotka–Volterra models, a different equilibrium would be achieved if a constant immigration term were added to the equations, and this equilibrium would depend on the value of the immigration term. Thus, the equilibrium approach to ecology gives no reason to expect that local communities could be independent of recruitment or larval supply rates. Indeed, the message is the opposite: local communities should depend on such rates.

Could there be special circumstances under which

local communities are independent of recruitment rates? Is it conceivable, for example in space-limited organisms, that the local population density is independent of the rate of arrival of larvae provided only that larval supply rates are high? In the space-limited case, it is sufficient that enough recruits arrive to fill up the available space. Such a process requires space limitation within species and not between species. Fish species with interspecific territoriality, for instance, would not satisfy this requirement unless there was very strict temporal partitioning between species in the arrival of larvae. There is also a requirement that territories do not become smaller with crowding or that territoriality does not break down as it does in some fishes with increasing density (Doherty 1982).

Processes other than space limitation conceivably might also remove the dependence of local densities on recruitment rates. For example, density-dependent intraspecific resource limitation and density-dependent intraspecific predation could operate in this way if they were very strong and acted on a very short timescale so that a local equilibrium was established quickly. Otherwise, the system would not be at an equilibrium set by predators or resources at a site, but would deviate from such an equilibrium by an amount dependent on the recruitment rate. Varying density-independent environmental factors affecting mortality at a site would increase the variance about the relationship between larval supply rate and local density, but would not eliminate the relationship.

The requirements above for independence of local densities on recruitment rates are very strict and unlikely to apply in anything but species-poor systems. The most likely situation in nature is that local abundances are determined by both local recruitment rates and by local interactions. Thus, in essence, all populations are recruitment limited in the sense that larval supply rates and recruitment rates into any settled stage affect abundances at later stages. The magnitude of the effect of recruitment limitation compared with that of other processes is an issue, but it seems most appropriate to expect that recruitment will interact with other processes to determine local abundances.

EMPIRICAL PATTERNS

How can these theoretical conclusions be reconciled with the empirical results of Doherty and Fowler (1994) implying that recruitment can explain essentially all the spatial variation in abundance of a particular tropical damselfish?

Two hypotheses seem worth entertaining. First, given the evidence of high rates of mortality in early life, density dependence may occur before recruitment (i.e. before the April censuses of newly settled fish). Thus, precensus mortality may be density dependent, or

settlement or larval supply rate may be density dependent. The data, however, are also consistent with density-dependent processes after recruitment. The preservation of the pattern of recruitment fluctuations in the age structure of the population is not evidence against density dependence but against unlikely strong action of density dependence on age classes individually.

The second hypothesis that I think should be considered is that there is, at most, weak density dependence in the populations considered, and that a substantial fraction of the recruits to these reefs are spawned from populations further north, and follow the currents as planktonic larvae to the group of reefs in the study. Recruitment on individual reefs could then primarily be a reflection of physical factors; for example, water temperatures and current patterns applying during particular larval movements. The reefs in the study might be sinks, in which case no density dependence would be necessary, or most reefs comprising the species population might simply have weak density dependence without violating the logic of the arguments here, as indicated previously. In these circumstances, density dependence might most easily be detected by artificially augmenting local populations to increase the magnitude of density-dependent effects. Individual growth as well as survival rates might be measured to give a more sensitive test of the effects of density on the well-being of individuals.

Some species show strong, easily detected density dependence (Forrester 1995). Recruitment may be dependent on the density of resident fishes at the locality, implying an asymmetrical interaction between larvae and residents (Stimson 1990). However, Jones (1991) argued that juvenile-adult interactions are more likely than larval-adult interactions. Strong density dependence of adult survival is unusual but does occur (Forrester 1995). Jones (1991) pointed out that intraspecific competition can often be detected in growth, maturation and reproduction even though it may not have strong effects on survival. Whichever of these variables is measured, the ultimate result is the same: lower per capita reproductive output at higher population densities. Such density dependence would regulate the size of the regional larval pool, and if reproduction were the only source of density dependence, it would have a major effect on regional abundance even though it need not have major effects on distribution patterns if larvae disperse widely.

DISCUSSION

The life of an organism is a cycle, with every stage connected by development or descent to every other stage. Surely this means that the abundance of any stage is affected by events at all other stages, as implied by Jones

(1991)? We have seen here that strong intraspecific density-dependent interactions are necessary within a stage before the abundance of that stage can be fixed independently of other stages. In this light, attempts to explain marine benthic populations on the basis of interactions between settled organisms alone seems doomed to fail. Concepts of recruitment limitation that treat larval supply as an independent variable not related to events taking place after settlement are no less deficient. Such independence of larval supply would require strong intraspecific density-dependent limitation to occur among planktonic larvae.

Marine benthic systems are not only connected in time through the life cycle but also connected in space through larval movements. The fact that any locality may receive larval inputs from a variety of other localities weakens the relationship between benthic densities and larval supply at any locality, tempting the view that larval supply can be treated as an independent input. However, settled organisms collectively, perhaps over many localities, yield the larval supply, and although interactions between larvae and with environmental processes may have major effects on larval supply, they are unlikely to eliminate the effects of settled stages. The fact that many marine benthic populations are open on the local population scale on which sampling occurs is not an escape from the connectedness of the life cycle. Marine ecology has been ill-served by a narrow concept of recruitment limitation which proposes it as a strict alternative to density-dependent interactions among settled individuals.

I have emphasized that density dependence is essentially unavoidable, but density dependence need not operate uniformly in time or in space to have important effects (Hassell 1987), and may often operate indirectly through other organisms and with time lags (Chesson 1996). Although harsh environmental conditions may weaken density dependence, such conditions also make a population less tolerant of negative density-dependent effects, and therefore need not lessen the importance of density-dependent interactions (Chesson & Huntly 1997). Marine benthic ecology has been ill-served by a narrow concept of density dependence focusing on mortality of settled individuals when growth, fecundity and offspring quality are far more likely to be density dependent (Jones 1991). Moreover, little consideration has been given to the potential for density dependence among planktonic larvae.

The dichotomy between recruitment limitation and density-dependent interactions is often seen as a dichotomy between density-independent fluctuations and equilibrium. Strong (1986) suggested that density dependence and density-independent fluctuations are both features of the dynamics of most populations, but that density dependence may be more important at the extremes of density while at other densities, density-

independent fluctuations may be dominant. A different perspective comes from theoretical models (Caswell 1978; Hastings 1980; Chesson 1985; Hassell 1987; Chesson & Huntly 1993), which imply that density-independent fluctuations average out on a larger temporal or spatial scale unless they interact with density-dependent processes (Chesson 1998; Chesson & Huntly 1997). Without such critical interactions, density-independent fluctuations merely add temporary or local detail to population dynamics and have no real significance to the ecology of the organism.

The storage effect hypothesis for species coexistence (Chesson 1985; Warner & Chesson 1985) provides a good example of a potentially important interaction between density-independent fluctuations and density-dependent processes. According to this hypothesis, temporally or spatially variable larval supply rates (Underwood & Denley 1983; Doherty & Williams 1988; Jones 1991), partially asynchronous for different species, combined with multispecies density limitation of settled individuals, enable long-term species coexistence. Essential to this hypothesis is the fact that per capita population growth rates involve an interaction between fluctuating larval supply (which is assumed to reflect fluctuating density-independent factors) and competition for settling sites. Life-history traits such as high survival of settled individuals (Chesson 1994) or long-distance dispersal of larvae (Chesson 1985) buffer the impact of unfavourable conditions for recruitment. Consequently, the combined effect of low larval supply and high competition, or high larval supply and low competition, results in higher per capita population growth than the separate effects of larval supply and competition would suggest. These properties characterize a subadditive interaction (Chesson 1994) between larval supply and competition, and they lead to net population increase when conditions fluctuate between equally favourable and unfavourable states, a property that is essential to the long-term maintenance of diversity under the storage-effect hypothesis.

The storage effect provides one example of how interactions between density dependence and fluctuations in environmental factors or population density may arise very simply in an ecological population or community. The intermediate disturbance hypothesis (Connell 1978; Hastings 1980) is another example (Chesson & Huntly 1997). Marine ecologists have often been impressed by fluctuating phenomena such as recruitment (Sale 1977; Connell 1978). Understanding their true significance means understanding their interactions with density dependence through empirical studies and the development of theoretical concepts. Existing theoretical models (Caswell 1978; Hastings 1980; Chesson 1985, 1998; Roughgarden & Iwasa 1986; Warner & Hughes 1988; Chesson & Huntly 1993, 1997) provide a conceptual beginning.

Empirical studies with a broad view of density dependence and explicit consideration of the interaction between density dependence and other factors provide an empirical beginning, but a close interplay between theory and empiricism would be most helpful.

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