

## **Recruitment limitation: a theoretical perspective**

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### **Simultaneous limitation by more than one thing**

There has been a tendency in ecology to speak as if only one thing can limit a population at any time and place. This is perhaps influenced by Liebig's law of the minimum where growth of crop plants seemed to be limited by the resource in shortest supply (Barbour et al 1980). Such a situation corresponds to population growth according to Tilman's (1982) essential resource criterion. However, we can normally expect population growth rates to depend simultaneously on several things, for even seemingly essential resources are partially substitutable. Moreover, there is every reason to believe that a combination of resources and physical factors will limit a population's growth. For example, temperature and food availability must surely be factors that simultaneously contribute to individual fish growth and survival; and therefore they must also contribute to population growth and ultimately abundance of the population.

### **Recruitment limitation**

Recruitment limitation refers fundamentally to the idea that the local density may be limited by the number of juvenile individuals arriving at a site with the potential of settling there and recruiting to the adult population (Doherty 1983, Doherty and Fowler 1994, Victor 1986). This view is often held in opposition to interactions between individuals within and between species at a locality (Jones 1987, Holbrook 1995). Empirically, it is easier to measure individuals after they have recruited, but recruitment may already reflect interactions between individuals in the settling process (Bertness et al 1992, Kaufman et al 1992), for example, if there is competition for resources necessary for settling and maturation. Thus, limitation by the numbers recruiting cannot be cleanly separated from interactions at a locality. Therefore I suggest the term 'prerecruit', for an individual arriving at a site and competent to settle, regardless of whether it actually does settle. Prerecruitment limitation refers to dependence of local abundance on numbers of such prerecruits. Although more difficult to deal with empirically, it appears to be an intellectually clearer notion. For simplicity of discussion, however, we shall not distinguish between the two ideas for much of the presentation, but will be careful to make the distinction where it becomes critical.

With recruitment limitation held in opposition to local interactions at a site, two extreme positions can be recognised: (1) Local abundance is determined solely by the input of recruits, or (2) Local abundance is determined solely by interactions after

recruitment. There are strong theoretical grounds for rejecting these extreme positions as follows.

### **Limitation of local abundance by recruitment alone**

(A) A closed population: First consider the situation of a closed population such as that found on an isolated reef or in a gulf or bay where juveniles recruit into the population of their birth (see e.g. Leis 1994). The idea that local density is determined by interactions after settlement is a strongly density-dependent perspective. The opposite position is that there are no interactions on or after settlement contributing density dependence, perhaps because the densities of prerecruits are too low (Doherty 1983, Mapstone and Fowler 1988). Is this a reasonable position? Two possibilities arise:

#### ***(1) There is no density-dependent limitation at the planktonic larval stage***

This situation is implausible. The system will exhibit exponential growth, potentially fluctuating with various factors, but a long-term exponential growth trend (Chesson 1996). Positive exponential growth clearly cannot be sustained for long, and so this possibility is not plausible. Negative exponential growth means that the population becomes extinct, and therefore does not apply to a persisting closed population. The final alternative is exponential growth at a zero average rate. Even if theoretical mean per capita growth rates are zero (and it is hard to see how this could arise very often in the absence of density dependence, Chesson 1996) actual population growth will still fail to be zero as 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). In fact one can say that without density dependence, abundance cannot be limited at all, although growth rates can be. Therefore, we must reject this proposition.

An intermediate alternative is Strong's density vague notion (Strong 1986) where there may not be much density dependence a lot of the time. Nevertheless, density dependence is critical for a population to actually have an abundance in any reasonably definable range. For example, Chesson and Huntly (ms) have shown that making environmental conditions harsh so that recruitment is low makes a population more sensitive to competition. Although competition may be weak, it remains important because the low rates of recruitment mean that a small additional impact from competition can make population growth rates negative, leading to population decline and extinction.

A model of recruitment limitation in barnacles (Roughgarden and Iwasa 1986) 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, recruitment rate involves an interaction between settled adults and prerecruits. 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 and the equilibrium abundance changes; indeed in the closed population version of the model, the equilibrium abundance is inversely proportional to the area excluded by a barnacle. This is so even if density dependence is very weak due to very low rates of prerecruitment, which reveals that even weak density dependence can have major effects.

*(2) There is density-dependent limitation at the planktonic larval stage*

If there is density-dependent limitation of the pelagic larvae it is certainly theoretically possible that recruitment could be low enough that there is negligible density dependence at or after settlement. One then could regard densities of settled organisms as set entirely by prerecruitment. Note, however, that potentially complex interactions between settled organisms have been replaced in this scenario by interactions at the planktonic level. If species have similar niches, then coexistence between the species must depend on interactions at the planktonic stage (cf. lake fishes: Mittelbach and Chesson 1987). Also, density-independent processes after settlement will still affect densities in two ways. First, variation in survivorship rates of settled organisms will lead to variation in densities: long-lived organisms will have higher densities than short-lived organisms with the same recruitment rates. Moreover, except in the unlikely event of very tight intraspecific regulation in the plankton, such that the final numbers surviving the planktonic stage are independent of the numbers entering the stage (e.g. the saturation model of Levin et al 1984) density-independent survival and reproductive processes for adult fishes will alter the recruitment rate by leading to higher absolute reproduction, and a larger initial larval pool. Both absolute and relative numbers of recruits will be affected. Strong joint limitation in the plankton of species in the same guild is insufficient as factors affecting the relative reproductive outputs of different species will still affect relative numbers of recruits, although not the combined number of recruits. As a consequence, recruitment becomes partly determined by postrecruitment processes.

(B) Recruitment limitation perhaps has the greatest application to local populations that are open to inputs from other local populations. For example Sale (1977) drew attention to the fact that recruitment to a local population is often very weakly related to the local stock. One explanation for this is that most of the recruits come from elsewhere. However, 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 (Chesson 1996). Thus, if density dependence does not occur at the larval stage it must occur at least in some patches 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 the variation in a system (see e.g. Hassell 1987).

Some localities may also be sink locations (Pulliam 1988), if not all of the time, potentially in some years. In such locations, no density dependence need be present and only survival rates after settlement need affect local densities. Locally, populations could still be density-dependent, however, depending on the behaviour of predators and diseases (Bailey 1994, Chesson 1996).

Thus, we must come to the conclusion that unless recruitment limitation occurs by strong intra-specific density-dependent processes in the plankton, factors at and after settlement will still play an important roles in population densities (Shulman and Ogden 1987). We should not be misled by models in which recruitment is treated entirely as an external input to the system (Warner and Hughes 1988, Hughes 1990), for although such models create the appearance of equilibrium or stability, their properties depend on assumptions such as constancy or stability of the mean and variance of external inputs, which remain unexplained.

### **Local limitation independent of recruitment**

Is it plausible that local abundances could be determined independently of the recruitment or prerecruitment rates to a site (Doherty and Fowler 1994)? Since local populations are replenished by recruitment, is there some process that could eliminate the effect of the numbers of recruits or prerecruits?

The equilibrium approach to population dynamics and species interactions has emphasised 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 lifecycle 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 prerecruitment 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? Provided potential recruitment is large, it is conceivable, for example in space limited organisms, that the local population density is independent

of the rate of arrival of prerecruits. 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 were very strict temporal partitioning between species in arrival of prerecruits.

Processes other than space limitation conceivably 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 time-scale 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.

These requirements 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. 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 have occurred before recruitment, i.e. before the April censuses of newly settled fish. Recruitment may be density-dependent or the prerecruitment 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. Indeed, the data are consistent with each reef being a closed system, locally regulated at an equilibrium that varies from reef to reef. Under this scenario, high recruitment could be looked upon as a reflection of high standing density in especially favourable habitat because high standing density would lead to high total reproduction and thus high recruitment.

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 emigrants from populations further north, which have

followed the currents to the group of reefs in the study. Recruitments on individual reefs could then primarily be a reflection physical factors.

Some species show strong easily detected density dependence (Forrester 1995). Most commonly, recruitment is dependent on the density of resident fishes at the locality, and thus an asymmetrical interaction between prerecruits and residents (Stimson 1990). In such a situation it is theoretically possible that recruitment rates are independent of prerecruitment rates, i.e. density-dependent interactions do not occur among prerecruits. Forrester (1995) also found the usual pattern of strong density dependence in adult survival.

### **Theoretical consequences of recruitment limitation**

#### *Differences in recruitment between systems:*

*What general predictions can be made for systems that differ in their overall level of recruitment?*

A system with low recruitment may have less intense local interactions, but the importance of these interactions to species persistence and coexistence is not diminished unless the larval stage is density dependent. Without density-dependent arrival, tolerance of competition or other mutually negative direct or indirect local interactions, is lower and its effects on community structure and species persistence can be just as strong as a situation with higher recruitment (Chesson and Huntly ms). The reason is largely the fact that a density-independent larval stage means that numbers of prerecruits (those leaving the larval stage) are proportional to numbers entering the larval stage. Therefore, events in the larval stage cannot counteract events occurring at other stages in the life cycle. This result does not mean that variation between systems cannot have effects, but it says simply that we do not yet know in much detail what these effects are. Our best indications come from studies of how dispersal rates affect overall dynamics: viz low dispersal rates often permit the development of local uniqueness, and therefore more spatial heterogeneity, which can have the effect of stabilising a system on the larger spatial scale (Reeve 1988). The intermediate disturbance mechanism in the form that depends on successional processes (Connell 1978) is also relevant, as higher recruitment rates may allow earlier establishment of late successional species diminishing opportunities for diversity maintenance.

Density-dependent prerecruitment, however, means that lower recruitment diminishes the importance of local interactions. The reason is that a density-dependent larval stage can compensate for events taking place at other stages. Thus, fluctuations in the numbers entering the larval stage can be diminished by larval density dependence. Density-dependent predation is a prime candidate for such density dependence in the larval stage (Bailey 1994).

*What general predictions can we make about the consequences of recruitment variation within systems?*

Recruitment varies spatially, temporally, and with a space by time interaction. These components are commonly separated empirically by analysis of variance. This empirical method of partitioning variation is useful theoretically. For example in a study of the role of recruitment variation in diversity maintenance, Chesson (1985) found that these three different components of recruitment variation contributed approximately additively to an overall diversity promoting effect.

**A. Fixed spatial variation:** Theoretically, there can be major consequences for diversity maintenance. Differences between species in the spatial pattern of arrival of potential recruits can be a major promoter of species diversity permitting different spatial locations to act as spatial niches. This sort of effect is seen in a wide variety of models including those that are designed specifically for marine systems (Chesson 1985, Iwasa and Roughgarden 1986), and those originally directed at other systems (Atkinson and Shorrocks 1981, Ives 1988). Additionally, it can promote diversity by enhancing the storage effect (Chesson 1994), which relies on temporal variation. It can do this if some places have lower variation in recruitment and lower variation in competition after settlement than other places. These may be places with lower average recruitment also. Such places may buffer temporal variation in the system as a whole permitting riskier strategies to be adopted elsewhere (Chesson 1990).

**B. Spatio-temporal variation:** Theoretical competition systems suggest that spatio-temporal variation in recruitment acts very similarly to fixed spatial variation in recruitment in the promotion of species diversity (Chesson 1985, Comins and Noble 1985). If adults are persistent at localities, however, less spatial variation in species distributions will arise from spatio-temporal variation in recruitment than fixed spatial variation. Such spatio-temporal variation coupled with the potential for local competition for settling sites seems to fit well Sale's (1977) lottery hypothesis for the maintenance of species diversity (Chesson 1985, Comins and Noble 1985). While Pacala and Crawley (1992) and Bailey (1994) have studied the way predation may create variation in actual recruitment at a site, Bailey (1994) has emphasised how predation may diminish recruitment fluctuations. Depending on how predators respond to the various species, this could reduce the diversity promoting effect of variation, but at the same time may add a frequency dependent component that would help maintain species diversity locally in space as well as in the system as a whole.

I am not aware of studies of how recruitment variation translates into effects on higher trophic levels or on the stability of predator-prey interactions. However, related work is suggestive. For example, host-parasitoid models in which variation in the risk of parasitism is a major promoter of the stability of the interaction suggest that variation in recruitment rate of the parasitoid (which is really a special kind of predator) into prey patches should promote persistence of the interaction (Hassell et al

1991). Variation in host recruitment could also have this effect in the likely event that it affected the rate of parasitism. There seem to be abundant opportunities to study these effects in more complex trophic interactions too, but to my knowledge this has not been done.

**C. Temporal variation.** Temporal variation in recruitment can also be a strong promoter of diversity independently of spatial fluctuations in recruitment. This works by the mechanism called the storage effect and relies on species having different temporal patterns of recruitment, combined with a mechanism for survival of populations over periods when recruitment is poor (Chesson 1994). Originally, this was thought to require overlapping generations, but seasonal differences in the recruitment patterns of annual species can also be effective (Chesson and Huntly 1993). In addition, as remarked above, spatial variation, independently of whether spatial patterns differ between species, can enhance coexistence by the storage effect. The role of temporal variation as a factor modifying the outcomes of species interactions has not been studied more generally in community ecology, and so the way in which interactions other than competition will be affected is not clear, although given the analogy between spatial and temporal variation, some important effects of temporal variation on predator-prey relationships and more general food web interactions can be expected.

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