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Consequences of postsettlement mortality at the community level: a theoretical perspective

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Post-recruitment mortality may reduce the fitness of a species relative to other species

Mortality may reduce fitness of a species and may lead to a decline in absolute and relative abundance. Such an effect is likely regardless of whether species interact, but in the presence of mutually negative interactions (for example, competition or shared predators ['apparent competition', Holt 1977, Holt and Lawton 1994, Menge 1995]) such changes in relative fitness could result in exclusion or prevent an otherwise superior competitor (more generally, 'interactor') from dominating the system (the 'keystone predator effect', Paine 1966, Menge 1995).

Levels of mortality that alter relative fitnesses depend on the intrinsic rates of increase of the species in question, which may in turn depend on individual growth rates (Lubchenco 1978, Chesson and Huntly ms). Slow growing species are less tolerant of increases in mortality rates, and therefore suffer more than other species from the same levels of mortality.

I emphasise changes in relative fitness because an important way in which keystone predation may work is by creating a tradeoff between competitive ability and reduction in fitness due to mortality (Connell et al 1984, Huntly 1991). Such mortality should not be thought of as a coexistence mechanism, but a coexistence-mechanism helper. I define a coexistence mechanism as the means by which a species' long-term population growth rate increases when its density is reduced to low values (see arguments in Chesson 1991 and 1994). Mortality can alter the values of the long-term low-density growth rates but cannot act as a coexistence mechanism unless it acts in a frequency-dependent way by providing a specific advantage to a species at low density. Traditional niche differences are one example of a coexistence mechanism, as they do lead to increases in a species' long-term growth rate if it falls to low density. However, for species to coexist, any individual species' growth rate must not only increase as its density falls, but must increase to a positive value. Sufficient differences in relative fitness between species can mean that some species have negative long-term low-density growth rates, i.e. the increase at low density caused by the niche differences is not sufficient for these growth rates to become positive. A keystone predator, by adjusting the relative fitnesses of species, can create the situation where the increases in long-term growth rates coming from a coexistence mechanism (such

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as niche differences) are sufficient to make all species have positive long-term low-density growth rates, allowing them to coexist (Chesson and Huntly ms).

As nature is spatially variable, it may be that death rates are spatially variable with the potential of altering relative fitnesses by different amounts in different spatial locations. There are major theoretical consequences of such a possibility. If different species have different spatial patterns of death rate variation, then species in effect have separate spatial niches. Adult breeding populations of a species can build up in abundance relative to other species in places where they are favoured by relatively higher survival. Theoretical evidence suggests that this can have a strong coexistence promoting effect (Chesson 1985). Note that such effects do not preclude broad overlap in distributions (Williams 1983), as coexistence that results from variation in population parameters operates on the residual variation left after common patterns of variation have been removed (Chesson 1994).

On the other hand, spatially correlated fluctuating relative mortality may promote competitive exclusion of space competitors, as it disadvantages a species at low abundance (Chesson 1982).

Post recruitment mortality as opening up space or other resources

For species that occupy space, post recruitment mortality has the effect of freeing space and making it available for the community at large. This can be important at the community level even if mortality falls equally on all species (Connell 1978). The reason is the potential for a successional sequence to take place at the vacated site. Succession (Connell and Slatyer 1977) need not be deterministic but can have highly stochastic components. Moreover, although the nature of succession may depend on the size of an area vacated, there is no reason to deny the potential for a successional sequence to operate on very small areas down to the space that can be occupied by just a single individual. Of most importance is the requirement of an inverse relationship across species between ability to persist at a site and rapidity of colonisation after the site has been vacated. In the traditional scenario modelled by Caswell (1978) and Hastings (1980), early arriving species are eliminated by competition from later arriving species. Although such competition is not necessary to drive a successional sequence (Connell and Slatyer 1977), it or something like it may be necessary for diversity maintenance by this mechanism. I say this because simple calculations show that Hastings' (1980) model altered to have a priority effect for holding a site, rather than a linear competitive hierarchy, leads to dominance of the system by the species with the highest ratio of colonisation rate to extinction rate.

The outcome of succession of the right type (for example one involving a tradeoff between competitive and colonising abilities) coupled with mortality that opens space and initiates succession, is a landscape in a mosaic of successional states of high species diversity. An intermediate level of mortality, resulting from an intermediate level of disturbance, is believed to maximise diversity (Connell 1978). An alternative

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model of intermediate disturbance (Huston 1979) does not lead to succession but possibly slow competitive displacement under rather special conditions (Chesson and Huntly, ms).

Mortality as shortening life times and reducing temporal scales

Longevity of individuals sets an important temporal scale for the dynamics of the species in a system. Death rates after recruitment therefore determine this temporal scale. The temporal scale of adult survival relative to the temporal scale recruitment fluctuations has a major effect on fluctuations in local population density. For example, in simple models using a time-scale on which recruitment fluctuations appear uncorrelated from one time unit to the next, the variance of local population fluctuations is approximately proportional to the adult death rate (Chesson 1982). However, there is a more profound community significance of individual longevity if individuals compete as juveniles, and recruitment fluctuates. Under these circumstances persistence of adults leads to diversity maintenance by the storage effect, viz periods of good recruitment for a species have long lasting effects and permit a species to build up its population in good periods when it competitors are doing less well (Chesson 1994). The strength of this effect is proportional to the adult survival rate. However, this effect will be of most significance when recruitment fluctuations are correlated over broad areas, for in other circumstances dispersal of offspring in space can substitute for persistence at a given locality (Comins and Noble 1985, Chesson 1985) leading to coexistence in a manner suggested by Sale's (1977) lottery hypothesis.

Mortality as a predator-mediated indirect interaction

Shared predators or pathogens can lead to indirect interactions between species such as 'apparent competition' (Holt 1977, Holt and Lawton 1994). Acting in an analogous way to competition, 'apparent competition' may lead to exclusion of species. Holt, Grover and Tilman (1994) showed that in the absence of ameliorating factors, a shared predator leads to domination of a system by the species able to tolerate (i.e. not experience negative population growth) the highest predator density. This is exactly analogous to Tilman's (1992) rule that the species able to tolerate the lowest density of a limiting resource will dominate a system without other ameliorating factors. A shared predator creates an indirect interaction between species. An increase in one species favours predator increase, which then leads to higher predation on all species sharing the predator, just as an increase in one species favours resource decrease and lower resource availabilities for all species that depend on the resource.

Ameliorating factors, which counteract the tendency for exclusion resulting from shared predators or shared resources, are many and varied and are the general subject of diversity maintenance mechanisms. Just as differential dependence on multiple resources can lead to coexistence of competitors, differential susceptibility to multiple predators could similarly lead to species coexistence (MacArthur 1970). Alternatively, a mixture of differential susceptibility to predation and differential dependence on

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resources could favour species coexistence (Levin 1970). Moreover, as a predator may exhibit frequency-dependent foraging behaviour (Murdoch and Bence 1987), a predator may counteract the tendency for apparent competitive exclusion by reducing predation on a species as its density declines.

Piscivorous fishes on reefs may be much more wide ranging than their prey, and thus the effect they have could be on a much larger spatial scale than competitive interactions, which may be relatively local for sedentary fish species. The complexity of the density-dependent interactions created by apparent competition can be very great when predator behaviour in a patchy environment is accounted for (Holt 1984, Abrams 1987a), and at the present time the ability to make unambiguous predictions is limited. Nevertheless, there is evidence that apparent competition occurs in reef systems (Schmitt 1987, Menge 1995), and it is an interaction that should be taken seriously.

Mortality as a factor that reduces densities below levels at which significant mutually negative interactions (e.g. competition) occur

Lower densities of organisms presumably mean less intense interactions between organisms. Higher mortality rates are one means of lowering the densities of organisms. Species may compete less at lower density (Huston 1979), but Abrams (1987) and Chesson and Huntly (ms) argue that this does not necessarily reduce the effect of competition. The reason is that higher mortality rates reduce the fitness of a species, and unless the reduction in competition leads to a disproportionate increase in fitness, the overall change in fitness of a species with an increase in mortality may in fact be negative, meaning that competitive exclusion can still occur. In the absence of other density-dependent factors, a species will normally fluctuate in a range where competition, even if weak, just presents further increase. If mortalities are so high that the population can never increase to the point where it feels competition, then it must have negative fitness and be on its way to extinction in any case (Chesson and Huntly ms).

Mortality may eliminate competition however, if mortality is density-dependent. Competition is then replaced by apparent competition, as discussed above. Additionally, it is possible that interspecific competition could be eliminated by mortality if species are limited separately intraspecifically. The way this occurs is that the mortality agent increases the sensitivity of a species to its unique intraspecific density limitation agent, and then densities may never get high enough that interspecific density limitation agents become active (Hutson 1979).

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