Chapter 4

Modeling of Semelparous/Iteroparous Coexistence

As discussed in Chapter 2, the semelparous and iteroparous morphs of *Botryllus schlosseri* coexist. An interesting question is whether this coexistence, mediated by *Botrylloides leachi*, is stable (i.e. is in some form of equilibrium) or not. Although the two morphs are actually part of the same species, their population densities fluctuate in such a manner that there is little inter-morph breeding (Grosberg 1982). Also, since most of the young from any inter-breeding are one morph or the other (Grosberg 1982), for the purposes of modeling, the two morphs can be treated as separate species.

The next section will discuss some earlier models that looked at two or more species sharing a resource to see how they can be applied to the *Botryllus schlosseri* coexistence.

4.1 Previous Modeling

4.1.1 Lotka-Volterra Equations

In the absence of any restraining influence, the rate of growth of a single population, $N$, would be proportional to its existing population, i.e.

$$\frac{dN}{dt} = rN$$

resulting in an exponential (Malthusian) law of population growth at rate $r$ (Lotka 1932). Of course, for most real populations, although (4.47) might apply to populations at low density levels, as the population grows, the rate of increase, $r$, would decrease as the population approaches its carrying capacity. In the simplest case, $r$ would be a linear
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function of \( N \) so (4.47) would become

\[
\frac{dN}{dt} = r_0 N (1 - phN)
\]  

(4.48)

which is the Verhulst-Pearl law of population growth that has been found to very acceptably fit a number of observed examples of population growth (Lotka 1932).

The extension of (4.48) to two populations competing for a common food supply is

\[
\frac{dN_1}{dt} = r_1 N_1 [1 - p_1 (hN_1 + kN_2)]
\]  

(4.49)

\[
\frac{dN_2}{dt} = r_2 N_2 [1 - p_2 (hN_1 + kN_2)]
\]  

(4.50)

(Volterra 1926,1931 (cited in Lotka 1932)). The same constants \( h, k \) appearing in both equations mean that both species consume a single food or, if mixed, then the proportion of each food is the same for both species (Lotka 1932). Thus, the two species share each resource identically. This system of equations is analyzed by Lotka (1932) who shows that there are three possible equilibria - an unstable origin, one stable, and one other one unstable. However, all of these equilibria involve one or both species dying out. This implies that two species that are resource limited cannot coexist on one resource.

4.1.2 Gause(-Volterra) Principle

This result was substantiated experimentally by Gause's experiments on competition between Paramecium auxatum and P. aurelia (Gause 1934 (cited in Levin 1970)). Later theoretical work by MacArthur and Levins (1964 (cited in Levin 1970)) extended this concept (called the Gause(-Volterra) Principle) to show that, in general, there cannot be more species than resources to support them.

However, there are many examples in real life, such as that of Botryllus schlosseri, that apparently contradicts the Gause Principle. Some apparent contradictions, on closer
examination, have proven to not be so. For example, MacArthur (1958 (cited in Levin 1970)) studied five congeneric species of warbler that at first appeared to have overly similar ecological preferences. However, he showed that their feeding habits were distinct enough for them to be actually occupying distinct ecological niches. This shows that competition can result in adaptive changes among the species rather than the elimination of one species. However, this does not appear to be a factor in the *Botryllus schlosseri* coexistence.

A fundamental reason why *Botryllus schlosseri* does not obey the Gause Principle is that the underlying model given by (4.49) is too simplistic. The model can be enhanced to make it more realistic in basically two ways: (a) add different types of competition and (b) make the parameters depend on space and/or time. Equations (4.49) involve only exploitation competition, whereby each consumer affects the other by reducing resource abundance. However, interference competition, whereby one species directly interferes with the other species ability to exploit the resources, is also possible. This definitely happens when *Botrylloides leachi* overgrows a semelparous *Botryllus schlosseri* colony, or even possibly when two colonies come in contact and stop growing along the line of contact.

### 4.1.3 Interference Competition

Interference competition is less well understood than exploitation competition primarily because it has not been clear how to describe it mathematically (Waltman et al. 1980 (cited in Vance 1984)), although it can still be analyzed qualitatively. The influence of *Botrylloides leachi* makes the system more of a three-species Lotka-Volterra system. Usually, the system will be transitive in that the most efficient competitor will completely exclude the other two. However, interference competition permits nontransitive relationships since each inter-species interference interaction may be unique (Gilpin 1975), thus
possibly permitting stable coexistence.

Next, the following paragraphs describe the effect of spatial and/or temporal variation in the model parameters.

4.1.4 Spatial Heterogeneity

Tilman (1980, 1982 (cited in Vance 1984)) and others have suggested that coexistence is possible given the existence of sufficient spatial variability in resource abundance. Chesson and Warner (1981 (cited in Chesson 1985)) state that, with pure spatial variation, species can coexist purely from variation in adult death rates. Of course, the semelparous and iteroparous morphs have different adult death rates.

4.1.5 Temporal Variation

Seasonal (or daily or other periodic) influences make most of the temporal variation in an environment cyclic or periodic in nature. Species survival can depend on this periodicity; namely, two competing species, one of which would be doomed to extinction in a constant environment, can under certain circumstances coexist in a periodic environment in a limit cycle sense. The idea is that at low population densities with plentiful resources for both species, the competition will be low and consequently both species increase (roughly exponentially) as they would in isolation. Usually, this will continue until increased competition causes a decline in the density of the inferior species. However, if some event causes a significant loss in density so that both species return to the same previously low levels, then the cycle is renewed. If this cycle repeats itself periodically, the inferior species might coexist in a periodically fluctuating (limit cycle) fashion (Cushing 1980). This is roughly what happens with Botryllus schlosseri when Botrylloides leachi overgrows the semelparous morph during the summer. However, this seasonal “kill” only affects one of
the “species”, and also the overwinter mortality/reduction in size has a large influence as shown in the previous chapter.

Another important factor is migration into the pond (Grosberg 1982). Chesson (1985) showed that variation in the ratios of migration rates will favor coexistence of species.

The effect of *Botrylloides leachi* can be looked at as a physical disturbance that causes disproportionately greater mortality of the superior species (semelparous *Botryllus schlosseri*). This can prevent the lower ranked species (iteroparous *Botryllus schlosseri*) from being competitively excluded locally (Paine 1966).

The above models suggest, qualitatively, the possibility of stable iteroparous / semelparous coexistence mediated by *Botrylloides leachi*. However, none of them individually is precise enough to show, with any degree of confidence, that the two morphs are actually stably coexisting. Another important consideration, even more important than in the modeling of the last chapter, is the clonality effect. The following aspects will have a direct bearing on possible coexistence:

1. Clonal organisms are often phenotypically plastic so that the differences in genotypes may be masked by responses to habitat characteristics. This would also likely delay competitive exclusion.

2. Genotypic differences allow the potential for slight niche differentiation between conspecific clones.

3. Seasonal phenomena may provide “balancing selection” whereby two or more genotypes are favored sequentially. Even though the balance may not be exact, it could at least prolong clonal coexistence.

(Sebens 1985). Finally, another important consideration is that for sessile organisms the arrangement of neighbours becomes important as individuals cannot move except via
dispersal of young (Grosberg 1982). The only modeling technique that I know of that can potentially model the Botryllus schlosseri situation accurately enough is that used in the previous chapter, dynamic programming.

4.2 Dynamic Programming

Dynamic programming, as explained in the previous chapter, assumes that the organism acts in a manner that optimizes its discounted expected future reproduction. In the model of the previous chapter, only the time, size, and age of the colony influenced its behaviour. However, when dealing with the coexistence of species, this decision also depends on the actions of the other members of the same morph and that of the competing morph. The resulting strategy is assumed to result in an equilibrium stable under environmental fluctuations. This strategy is called an environmentally stable strategy (ESS).

4.2.1 Environmentally Stable Strategies (ESS)

Unlike the model in the previous chapter, stochasticity and random effects cannot be ignored in an ESS since coexistence depends critically on how the colonies are spatially distributed. A standard ESS predicts a particular strategy to be superior. However, in a stochastic setting, no individual strategy will necessarily always win out over all others for several reasons. Any strategy, no matter how inferior it is on average, could be favoured during a chance run of years (Levin 1984). Also, a strategy’s endurance might depend on its density, with certain types of strategies favoured only when they are sufficiently abundant in the population. Although it might have difficulty becoming established among an established morph, it could nonetheless do so sporadically. However, the original morph could also reinvade sporadically, especially among local populations of interbreeding organisms (Yoshimura and Clark 1991).
A more basic problem than the potentially complex solutions is the fact that stochastic dynamic programming models are extremely difficult to solve. Even almost trivial problems can involve a lot of work to solve them (Mangel and Clark 1988).

A yet more basic problem is that the model requires, among many other things, knowledge of the spatial distribution of the morphs and their progeny and the dependence of the state variables on the population density of all possible phenotypes. Since I do not have this information, I have not tried creating a dynamic programming model to analyze the situation.
Chapter 5

Discussion

The dynamic programming model in Chapter 3 is able to quite accurately predict the average age of first sexual reproduction in *Botryllus schlosseri*, especially for the iteroparous morph. This indicates that the life-history characteristics of the two morphs of *Botryllus schlosseri*, individually, are at least near equilibrium. It also suggests that the colonies can tell the time of the year since the after winter growth rate change causes fluctuations in the age of first sexual reproduction throughout the year. Finally, iteroparous colonies continue to reproduce sexually once they begin because it is optimal rather than due to some energetic or physical constraint. However, the full variation in the age of first sexual reproduction cannot be predicted by the model, probably due to spatial heterogeneity not being incorporated.

The most interesting question about *B. schlosseri* at Eel Pond is whether the two morphs and *Botrylloides leachi* are in stable co-existence. Chapter 4 discusses several models that, applied to the system, suggest co-existence is possible. However, none of the models appears to encompass the important factors accurately enough to state, with any confidence, that this system is actually in equilibrium. Although dynamic programming appears to be the best technique to model this system, it unfortunately requires a more intimate knowledge of the trade-offs inherent in the biology of the organisms than is currently available. Since any convincing model of this co-existence would require at least some knowledge of the inherent trade-offs, understanding the stability of the co-existence will have to wait for more experimental data.

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Bibliography


