Regulation of structured populations: an example

It has been noted in Ch6.4.3 (p.114) that the individuals of many taxa – insects, amphibians, and fish – may change their habitat, diet or predator during their life. This phenomenon is called the “ontogenetic niche shift”, whose consequence is that the survival probabilities or the fecundities of the individuals of different sizes or developmental stages may be sensitive to different regulating variables, and these regulating variables may be differentially impacted by the individuals at different stages. Thus, determining the niche of such populations requires considering their structures (Ch10.2.4, p.212). Primarily based on the work of Gary G. Mittelbach and his colleagues this section presents empirical results on the population regulation of sunfish species whose individuals become competitors due to their common predators. These studies are also examples of species niches being dependent on the actual niche space (Tbox 10.1, p.205): niches are affected by the presence or absence of the predator as well as by that of the competitor. We will show an example of modelling regulation in such a structured population in OLM 9.6.

The largemouth bass (*Micropterus salmoides*) is an ontogenetic diet shifting fish species of Michigan lakes (Figure 10.10, p.213). Adult largemouth bass individuals are piscivorous; the indirect, non-consumptive effect of their presence is that they force juvenile sunfish to feed on vegetation-dwelling invertebrates in the fully protected coastal zone of small lakes and ponds (Mittelbach and Chesson 1987). The presence of largemouth bass induces competition for food between juvenile individuals of two closely related, very similar and often co-occurring sunfish species, the abundant bluegill sunfish (*Lepomis gibbosus*) and the pumpkinseed sunfish (*L. macrochirus*), while the adults of these species do not compete. It was shown experimentally (by target-neighbor experiments) that increasing the density of juvenile bluegills decreases the growth of juvenile pumpkinseeds (Mittelbach 1988). Adult bluegills consume the high-density zooplankton (*Daphnia*) in the water body, whereas adult pumpkinseeds are specialized in consuming aquatic snails in the littoral zone. Correspondingly, the functional morphology of the two species differ, and laboratory experiments showed that bluegills are more efficient at feeding on zooplankton while pumpkinseeds are better at consuming stronger-shelled snails (Mittelbach 1984). Growing to the adult stage means protection from predation (refuge size, TBE p. 271) and relief from interspecific competition at the same time for both species (Figure 6.4.1).
The two stages and their corresponding food sources in two closely related, very similar and co-occurring sunfish species. The arrows denote the chain of effects of increased bluegill adult density on the adult survival of pumpkinseeds (top: Mittelbach and Chesson 1987, bottom: after Osenberg et al. 1992).

The straightforward consequence of this type of regulation is that, when an increase in the abundance of zooplankton increases the adult survival and fecundity of bluegills, the density of pumpkinseed adults decreases due to the rise in the density of bluegill larvae, which amplifies juvenile competition. Thus, the equilibrium stage-structure of the sympatric sunfish populations is under the effect of this joint regulatory mechanism (Mittelbach and Chesson 1987). This mechanism of population regulation may also affect the relative growth rates ($RGR$, TBE p. 45) of the coexisting individuals (Arendt and Wilson 1997). The growth curves within the $F_1$ generation of pumpkinseeds originating from six lakes in Ontario, Canada, have been determined in a common garden experiment. In lakes with bluegills the relative growth rate of the pumpkinseeds is higher than in those without bluegills (Figure 6.4.2). This is the expected result if the variants with rapid growth have higher chance to enter the adult stage representing a refuge from competition.
The effect of bluegills on the population regulation, growth rate, and functional morphology of pumpkinseeds is supported by a case study as well. Osenberg et al. (1992) have studied the feeding of pumpkinseeds in three small lakes in Michigan. A winter kill event at the end of the seventies had extinguished bluegill sunfish from one of the lakes. A decade later it was detected that the density of snails had decreased to the extreme both in this lake and in the diet of pumpkinseeds, along with their growth slowing down (Figure 6.4.3). The ontogenetic niche-shift disappeared, pumpkinseeds fed on soft-bodied invertebrates in the littoral zone throughout their life cycle; moreover, their morphology changed, and their consumption of hard-shelled snails proved to be less efficient compared to the specimen from another lake with bluegill present. The most plausible explanation to these changes is that with the extinction of bluegills the pumpkinseed population had increased to high density, driving snails close to extinction, consequently losing advantage of their specific morphological features evolved for efficient snail handling.

Figure 6.4.3 A comparative study in three lakes

The diets (a) and the growth rates (b) of the pumpkinseed sunfish in three small lakes of Michigan. In Wintergreen Lake, from which bluegills were absent, the ontogenetic diet shift had ceased to occur while the growth of the fish had become slower (Osenberg et al. 1992). Reprinted by permission of John Wiley & Sons.
This case has interesting implications for niche theory and speciation as well. The regulating factors, thus the niche space and the niche of the pumpkinseed sunfish, highly depend on the presence of its predator as well as on its abundant competitor. Perhaps the specialization of pumpkinseeds on snails is the direct result of competition with a zooplankton specialist or generalist species. However, this evolutionary hypothesis has not been investigated to our best knowledge.

References


