Chapter 8

Interspecific Competition

8.1 Introduction

The essence of interspecific competition is that individuals of one species suffer a reduction in fecundity, growth or survivorship as a result of resource exploitation or interference by individuals of another species. This competition is likely to affect the population dynamics of the competing species, and the dynamics, in their turn, can influence the species' distributions and their evolution. Of course, evolution, in *its* turn, can influence the species' distributions and dynamics. Here, we concentrate on the effects of competition on populations of species, whilst Chapter 19 examines the role of interspecific competition (along with predation and parasitism) in shaping the structure of ecological communities. There are several themes introduced in this chapter that are taken up and discussed more fully in Chapter 20. The two chapters should be read together for a full coverage of interspecific competition.

8.2 Some examples of interspecific competition

a diversity of examples of competition . . .

There have been many studies of interspecific competition between species of all kinds. We have chosen six initially, to illustrate a number of important ideas.

8.2.1 Competition between salmonid fishes

. . . between salmonid fishes, . . .

Salvelinus malma (Dolly Varden charr) and *S. leucomaenis* (white-spotted charr) are morphologically similar and closely related fishes in the family Salmonidae. The two species are found together in many streams on Hokkaido Island in Japan, but Dolly Varden are distributed at higher altitudes (further upstream) than white-spotted charr, with a zone of overlap at intermediate altitudes. In streams where one species happens to be absent, the other expands its range, indicating that the distributions may be maintained by competition (i.e. each species suffers, and is thus excluded from certain sites, in the presence of the other species). Water temperature, an abiotic factor with profound consequences for fish ecology (discussed already in Section 2.4.4), increases downstream.

By means of experiments in artificial streams, Taniguchi and Nakano (2000) showed that when either species was tested alone, higher temperatures led to increased aggression. But this effect was reversed for Dolly Varden when in the presence of white-spotted charr (Figure 8.1a). Reflecting this, at the higher temperature, Dolly Varden were suppressed from obtaining favorable foraging positions when white-spotted charr were present, and they suffered lower growth rates (Figure 8.1b, c) and a lower probability of survival.

Thus, the experiments lend support to the idea that Dolly Varden and white-spotted charr compete: one species, at least, suffers directly from the presence of the other. They coexist in the same river, but on a finer scale their distributions overlap very little. Specifically, the white-spotted charr appear to outcompete and exclude Dolly Varden from downstream locations in the latter's range. The reason for the upper boundary of white-spotted charr remains unknown as they did not suffer from the presence of Dolly Varden at the lower temperature.

8.2.2 Competition between barnacles

. . . between barnacles, . . .

The second study concerns two species of barnacle in Scotland: *Chthamalus stellatus* and *Balanus balanoides* (Figure 8.2) (Connell, 1961). These are frequently found together on the same Atlantic rocky shores of northwest

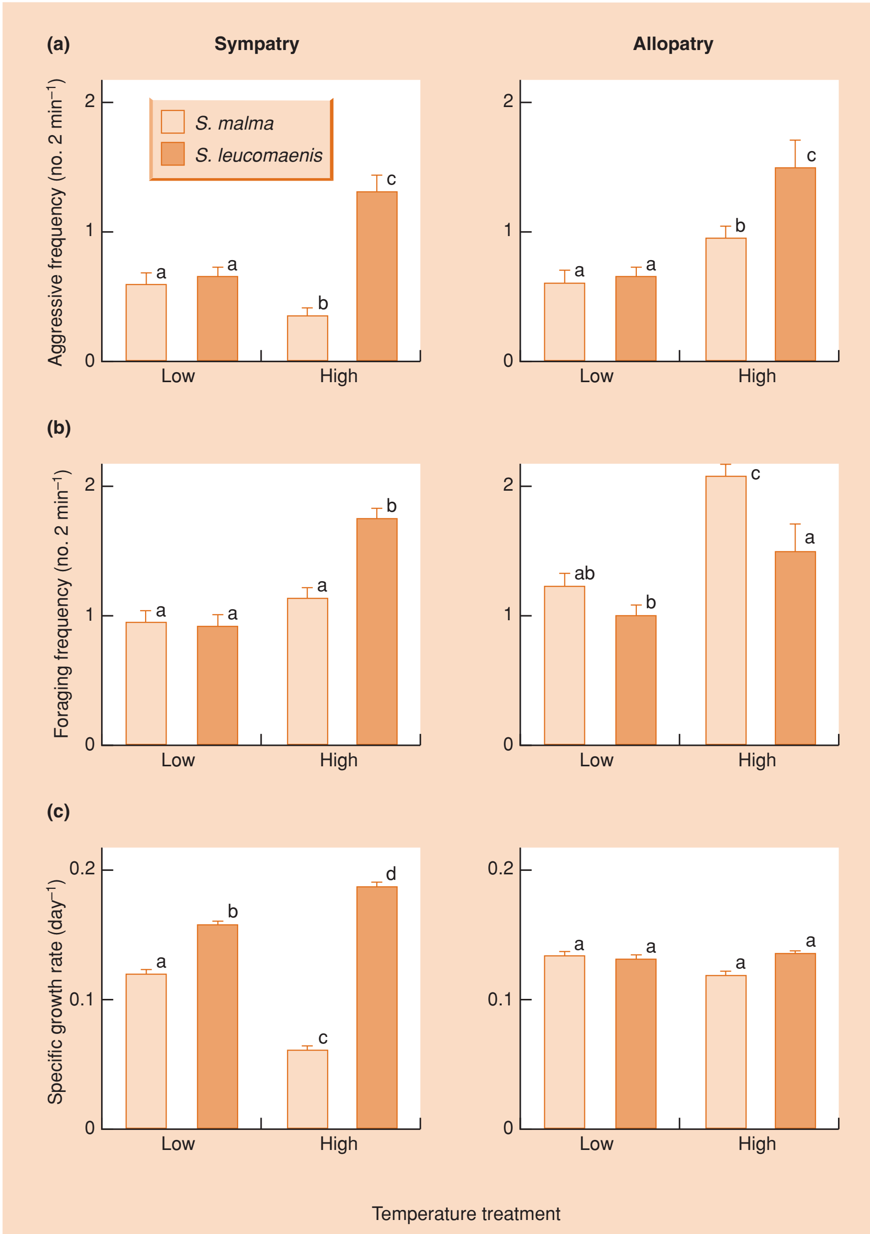

Figure 8.1 (a) Frequency of aggressive encounters initiated by individuals of each fish species during a 72-day experiment in artificial stream channels with two replicates each of 50 Dolly Varden (*Salvelinus malma*) or 50 white-spotted charr (*S. leucomaenis*) alone (allopatry) or 25 of each species together (sympatry). (b) Foraging frequency. (c) Specific growth rate in length. Different letters indicate that the means are significantly different from each other. (From Taniguchi & Nakano, 2000.)

Europe. However, adult *Chthamalus* generally occur in an intertidal zone that is higher up the shore than that of adult *Balanus*, even though young *Chthamalus* settle in considerable numbers in the *Balanus* zone. In an attempt to understand this zonation, Connell monitored the survival of young *Chthamalus* in the *Balanus* zone. He took successive censuses of mapped individuals over the period of 1 year and, most importantly, he ensured at some sites that young *Chthamalus* that settled in the *Balanus* zone were kept free from contact with *Balanus*. In contrast with the normal pattern, such individuals survived well, irrespective of the intertidal level. Thus, it seemed that the usual cause of mortality in young *Chthamalus* was not the increased submergence times of the lower zones, but competition from *Balanus* in those zones. Direct observation confirmed that *Balanus* smothered, undercut or crushed *Chthamalus*, and the greatest *Chthamalus* mortality occurred during the seasons of most rapid *Balanus* growth. Moreover, the few *Chthamalus* individuals that survived 1 year of *Balanus* crowding were much smaller than uncrowded ones, showing, since smaller barnacles produce fewer offspring, that interspecific competition was also reducing fecundity.

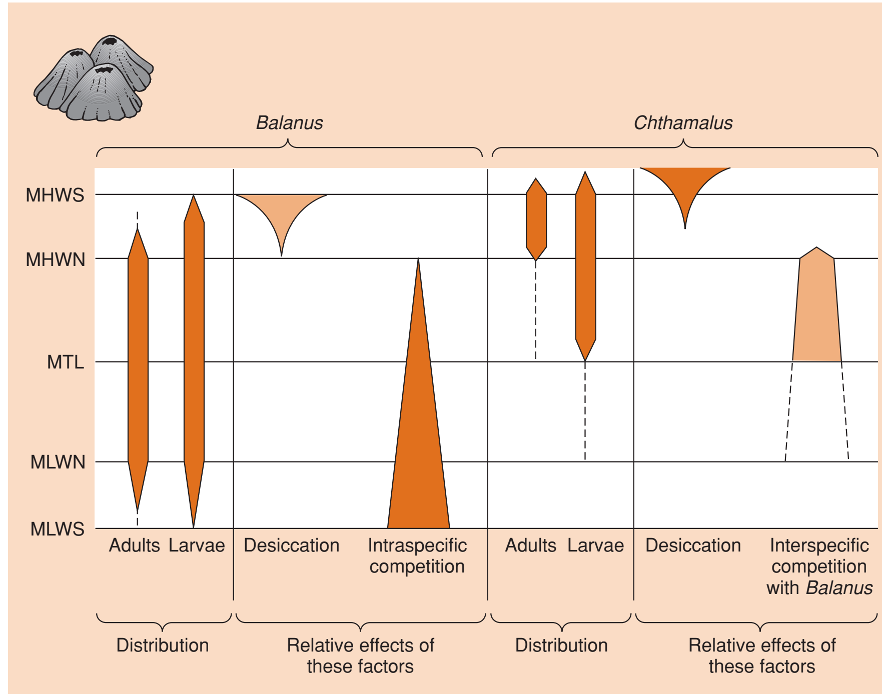

Figure 8.2 The intertidal distribution of adults and newly settled larvae of *Balanus balanoides* and *Chthamalus stellatus*, with a diagrammatic representation of the relative effects of desiccation and competition. Zones are indicated to the left: from MHWS (mean high water, spring) down to MLWS (mean low water, spring); MTL, mean tide level; N, neap. (After Connell, 1961.)

Thus, *Balanus* and *Chthamalus* compete. They coexist on the same shore but, like the fish in the previous section, on a finer scale their distributions overlap very little. *Balanus* outcompetes and excludes *Chthamalus* from the lower zones; but *Chthamalus* can survive in the upper zones where *Balanus*, because of its comparative sensitivity to desiccation, cannot.

8.2.3 Competition between bedstraws (*Galium* spp.)

. . . between bedstraws, . . .

A. G. Tansley, one of the greatest of the 'founding fathers' of plant ecology, studied competition between two species of bedstraw (Tansley, 1917). *Galium hercynicum* is a species which grows naturally in Great Britain at acidic sites, whilst *G. pumilum* is confined to more calcareous soils. Tansley found in experiments that as long as he grew them alone, both species would thrive on both the acidic soil from a *G. hercynicum* site and the calcareous soil from a *G. pumilum* site. Yet, if the species were grown together, only *G. hercynicum* grew successfully in the acidic soil and only *G. pumilum* grew successfully in the calcareous soil. It seems, therefore, that when they grow together the species compete, and that one species wins, whilst the other loses so badly that it is competitively excluded from the site. The outcome depends on the habitat in which the competition occurs.

8.2.4 Competition between *Paramecium* species

. . . between *Paramecium* species, . . .

The fourth example comes from the classic work of the great Russian ecologist G. F. Gause, who studied competition in laboratory experiments using three species of the protozoan *Paramecium* (Gause, 1934, 1935). All three species grew well alone, reaching stable carrying capacities in tubes of liquid medium. There, *Paramecium* consumed bacteria or yeast cells, which themselves lived on regularly replenished oatmeal (Figure 8.3a).

When Gause grew *P. aurelia* and *P. caudatum* together, *P. caudatum* always declined to the point of extinction, leaving *P. aurelia* as the victor (Figure 8.3b). *P. caudatum* would not normally have starved to death as quickly as it did, but Gause's experimental procedure involved the daily removal of 10% of the culture and animals. Thus, *P. aurelia* was successful in competition because near the point where its population size leveled off, it was still increasing by 10% per day (and able to counteract the enforced mortality), whilst *P. caudatum* was only increasing by 1.5% per day (Williamson, 1972).

By contrast, when *P. caudatum* and *P. bursaria* were grown together, neither species suffered a decline to the point of extinction – they coexisted. But, their stable densities were much lower than when grown alone (Figure 8.3c), indicating that they were in competition with one another (i.e. they 'suffered'). A closer

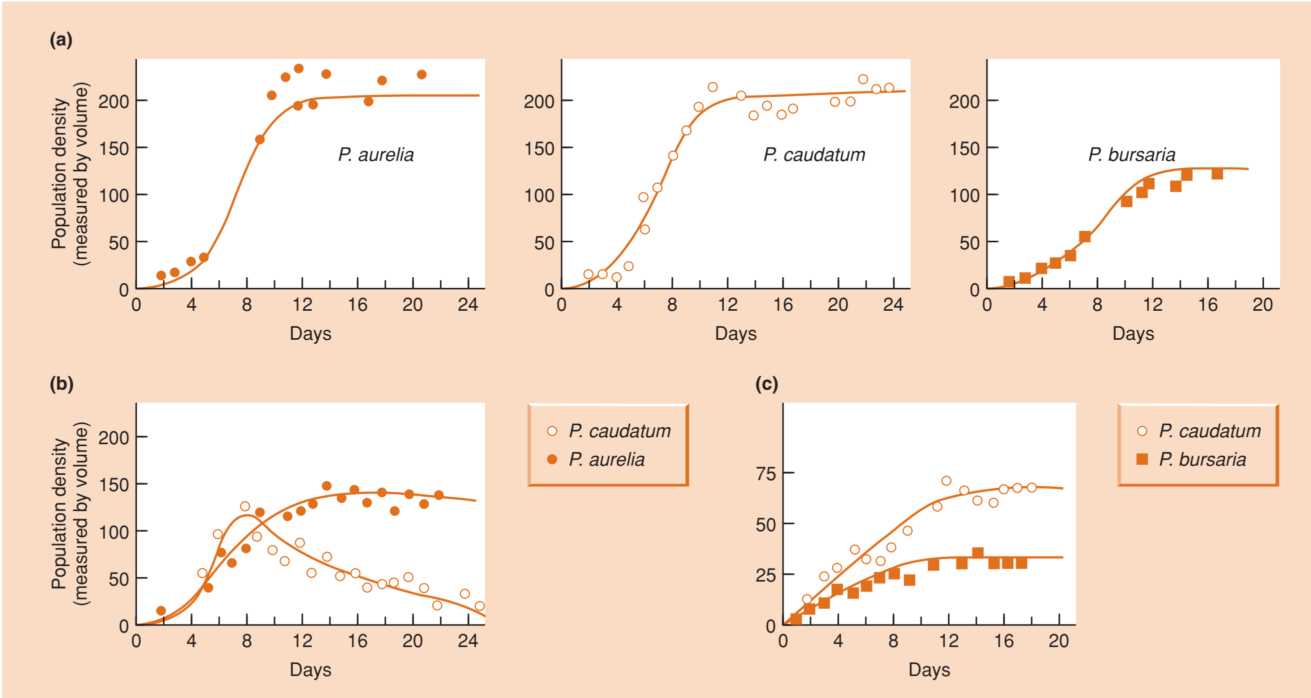

Figure 8.3 Competition in *Paramecium*. (a) *P. aurelia*, *P. caudatum* and *P. bursaria* all establish populations when grown alone in culture medium. (b) When grown together, *P. aurelia* drives *P. caudatum* towards extinction. (c) When grown together, *P. caudatum* and *P. bursaria* coexist, although at lower densities than when alone. (After Clapham, 1973; from Gause, 1934.)

look, however, revealed that although they lived together in the same tubes, they were, like Taniguchi and Nakano's fish and Connell's barnacles, spatially separated. *P. caudatum* tended to live and feed on the bacteria suspended in the medium, whilst *P. bursaria* was concentrated on the yeast cells at the bottom of the tubes.

8.2.5 Coexistence amongst birds

. . . among birds . . .

Ornithologists are well aware that closely related species of birds often coexist in the same habitat. For example, five *Parus* species occur together in English broad-leaved woodlands: the blue tit (*P. caeruleus*), the great tit (*P. major*), the marsh tit (*P. palustris*), the willow tit (*P. montanus*) and the coal tit (*P. ater*). All have short beaks and hunt for food chiefly on leaves and twigs, but at times on the ground; all eat insects throughout the year, and also seeds in winter; and all nest in holes, normally in trees. However, the closer we look at the details of the ecology of such coexisting species, the more likely we will find ecological differences – for example, in precisely where within the trees they feed, in the size of their insect prey and the hardness of the seeds they take. Despite their similarities, we may be tempted to conclude that the tit species compete but coexist by eating slightly different resources in slightly different ways. However, a scientifically rigorous approach to determine the current role of competition requires the removal of one or more of the competing species and monitoring the responses of those that remain. Martin and Martin (2001) did just this in a study of two very similar species: the orange-crowned warbler (*Vermivora celata*) and virginia's warbler (*V. virginiae*) whose breeding territories overlap in central Arizona. On plots where one of the two species had been removed, the remaining orange-crowned or virginia's warblers fledged between 78 and 129% more young per nest, respectively. The improved performance was due to improved access to preferred nest sites and consequent decreased losses of nestlings to predators. In the case of virginia's warblers, but not orange-crowned warblers, feeding rate also increased in plots from which the other species was removed (Figure 8.4).

8.2.6 Competition between diatoms

. . . and between diatoms

The final example is from a laboratory investigation of two species of freshwater diatom: *Asterionella formosa* and *Synedra ulna* (Tilman *et al.*, 1981). Both these algal species require silicate in the construction of their cell walls. The investigation was

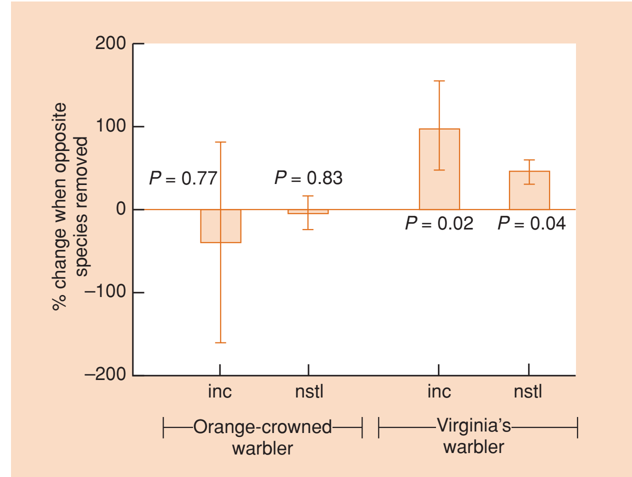

Figure 8.4 (*right*) Percentage difference in feeding rates (mean ± SE) at orange-crowned warbler and virginia's warbler nests on plots where the other species had been experimentally removed. Feeding rates (visits per hour to the nest with food) were measured during incubation (inc) (rates of male feeding of incubating females on the nest) and during the nestling period (nstl) (nestling feeding rates by both parents combined). *P* values are from *t*-tests of the hypothesis that each species fed at higher rates on plots from which the other had been removed. This hypothesis was supported for virginia's warblers but not orange-crowned warblers. (After Martin & Martin, 2001.)

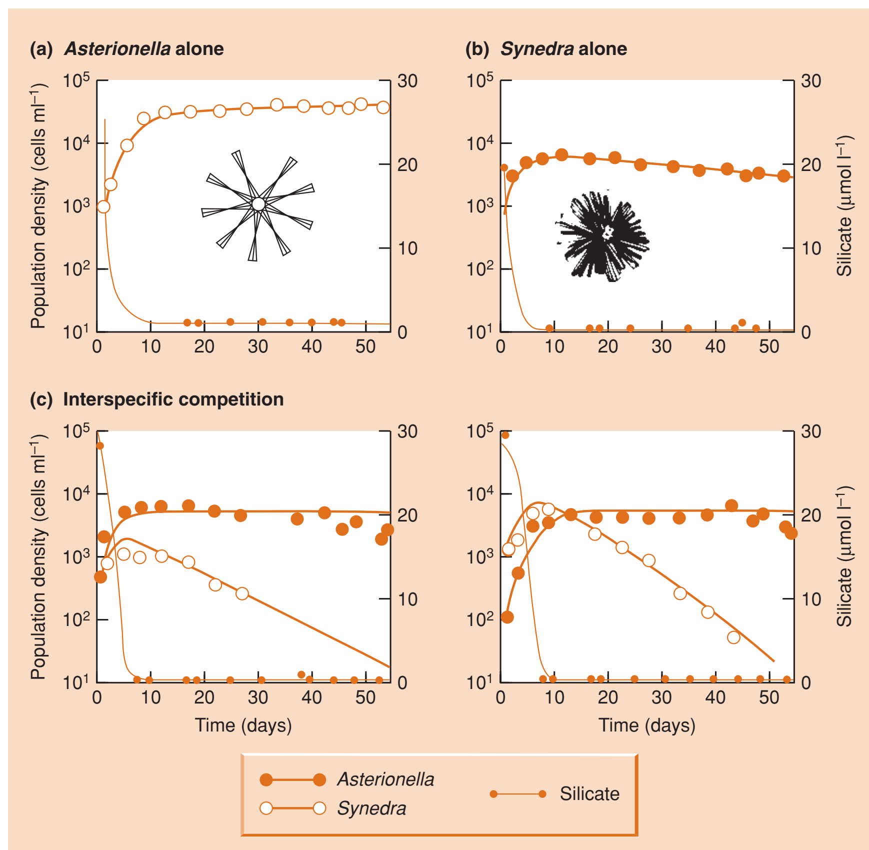

Figure 8.5 Competition between diatoms. (a) *Asterionella formosa*, when grown alone in a culture flask, establishes a stable population and maintains a resource, silicate, at a constant low level. (b) When *Synedra ulna* is grown alone it does the same, but maintains silicate at an even lower level. (c) When grown together, in two replicates, *Synedra* drives *Asterionella* to extinction. (After Tilman *et al.*, 1981.)

unusual because at the same time as population densities were being monitored, the impact of the species on their limiting resource (silicate) was being recorded. When either species was cultured alone in a liquid medium to which resources were continuously being added, it reached a stable carrying capacity whilst maintaining the silicate at a constant low concentration (Figure 8.5a, b). However, in exploiting this resource, *Synedra* reduced the silicate concentration to a lower level than did *Asterionella*. Hence, when the two species were grown together, *Synedra* maintained the concentration at a level that was too low for the survival and reproduction of *Asterionella*. *Synedra* therefore competitively excluded *Asterionella* from mixed cultures (Figure 8.5c).