

## 21. Predation Risk: Indirect Effects on Fish Populations

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Predators exert a strong influence on the diets and habitat use of their prey and consequently may indirectly affect resource competition within and between prey species. In this chapter, we explore several examples of how predator-mediated habitat use may affect species and size-class interactions in fish. At the intraspecific level, size-specific risk can lead to habitat segregation between size classes and a reduction in competition between large and small fish. This nonlethal effect of predators appears to play a major role in regulating population size structure in fishes such as the bluegill (*Lepomis macrochirus*) and perch (*Perca* spp.). At the inter-specific level, predators often concentrate vulner-

able size classes (usually small fish) from a number of species into a common protective habitat. As a result, competition may be intensified at certain stages in the life history of a species. We discuss a potential example of this effect in two sunfishes. We then develop a model, based on stock-recruitment relations, that illustrates how predator-induced competition among juveniles can lead to complex interactions between prey species. One particularly interesting feature of the model is the transmission of competitive effects between adults of two prey species, even when they use different resources.

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Fish live highly flexible lives. Their diets, habitat use, and growth rates often change dramatically with ontogeny and also may vary between environments. For example, as lake trout (*Salvelinus namaycush*) in Lake Opeongo, Ontario, increase in size, they shift from feeding on zooplankton to insect larvae to fish. In nearby Cradle Lake, lake trout feed on zooplankton their entire life (Martin 1966, 1970). Such differences in diet may be due to size-specific foraging abilities and prey abundances and can have significant consequences for species interactions (Werner and Gilliam 1984). Recent work has shown that these same types of ontogenetic changes in diet or habitat also may be mediated by predation risk. In experimental studies, fish have been shown to respond to predators by moving to protective habitats (Cerri and Fraser 1983; Werner et al. 1983a; Power et al. 1985), reducing foraging distances (Dill and Fraser 1984), and/or limiting feeding time and intake (Milinski and Heller 1978; Power et al. 1985; Schmitt and Holbrook 1985). Because vulnerability varies with body size, these responses are often highly

size-specific. Abundant field observations of habitat segregation by fish of different sizes also provide evidence of the importance of predation risk in determining size-specific resource use (e.g., Jackson 1961; Hobson and Chess 1976; Hall and Werner 1977; Helfman 1978; Hall et al. 1979; Laughlin and Werner 1980; Bray 1981; Mittelbach 1981; Haraldstad and Jonsson 1983; Power 1984; Jones 1984; Sandheinrich and Hubert 1984; Ebeling and Laur 1985). In each of these examples, fish of the most vulnerable sizes are found in the most protected habitats.

The studies cited above clearly document behavioral responses of fish to their predators, and much theoretical and empirical work is directed toward determining how well individuals can balance predation risks and foraging gains. However, little consideration has been given to how these predator-mediated changes in diet and habitat may affect competing species or size classes. For example, if two prey species move to separate habitats or refuges in the presence of the predator, competition between them is diminished; if they move to the same

refuge, however, competition may be increased. We here term these effects on prey diets and habitat use as indirect or nonlethal effects of predation, in contrast to the direct effect of predators killing their prey. Note that this type of indirect effect is distinct from those considered by Levine (1976), Holt (1977, 1984) and others; in their examples, indirect effects involve prey deaths and numerical responses by predators and prey.

In this paper, we explore several examples of how predator-mediated habitat use may affect interactions between species and size classes of fish. We first deal with intraspecific consequences of size-class segregation. Bluegills (*Lepomis macrochirus*) and perch (*Perca* spp.) are considered as specific examples of fishes in which predation risk appears to play a major role in regulating population size structure. We then consider indirect effects of predation on interspecific competition. In this section, we discuss a specific example involving the interaction between two species of sunfish. Finally, we present a model illustrating some of the population consequences of predator-mediated habitat use in these and other fishes.

## INTRASPECIFIC COMPETITION

Experimental studies by H. S. Swingle and his associates provide some of the clearest evidence for the importance of predation in mediating intraspecific competition in fish. In a series of studies begun in the late 1930s, Swingle experimentally stocked various combinations of predator and prey species in small Alabama ponds and lakes. The two species most frequently studied were the bluegill and its predator, the largemouth bass (*Micropterus salmoides*). Swingle and Smith (1940) found that when bluegills were stocked in the absence of predators, the stocked fish grew rapidly at first (gaining >10 times their weight in 3 months). However, after the bluegill population reproduced and large numbers of small fish were present, growth of the original bluegills ceased. The investigators repeated this experiment many times with the same result; bluegills stocked in the absence of predators inevitably developed populations dominated by small, slow-growing fish, commonly referred to as "stunted" in the fisheries' literature.

The causes for bluegill stunting in the absence of predators are now clear. First, bluegills

have relatively small mouths and are unable to shift to feeding on larger prey as they grow (Werner 1974). Thus, after bluegills reach a length of approximately 50 mm they are in direct competition with all larger conspecifics. Cannibalism is essentially absent because the bluegill is unable to feed effectively on larval fish (Werner 1977). Second, when prey resources are severely limited, small bluegills are at a competitive advantage over larger fish (Mittelbach 1981, 1983) because the higher metabolic costs of large bluegills significantly outweigh their small advantage in prey handling times and prey encounter rates (Mittelbach 1983). Thus, as bluegill numbers in a pond or lake increase, and prey become depressed, only small bluegills are able to maintain positive energy budgets. A related example of asymmetrical competition between size classes has recently been observed by Hamrin and Persson (personal communication) for Vendace (*Coregonus albula*). Finally, bluegills are able to reach sexual maturity at small sizes. Thus, in the absence of larger individuals, these small fish are capable of successfully spawning and maintaining the population.

When largemouth bass are stocked with bluegills, the pattern of stunting noted above may be altered. Studies by H. S. Swingle and others (review in Dillard and Novinger 1975) show that the presence of bass often results in more "balanced" bluegill populations, where a number of bluegill size classes coexist and large fish are able to maintain positive growth rates. Traditionally, the interaction between bluegills and largemouth bass has been viewed as a simple predator-prey system, with balanced populations occurring when bass predation rates effectively control bluegill numbers and reduce intraspecific competition. However, recent work has shown that bass have additional effects on bluegill populations beyond the simple removal of individuals and that these behavioral effects may be equally important in reducing intraspecific competition.

In the presence of largemouth bass, small bluegills show restricted habitat use, feeding only in or near protective vegetation (Mittelbach 1981; Werner et al. 1983a). When predators are removed, however, small bluegills shift to feeding in the open water on zooplankton (*Daphnia*) or from the bare sediments on infauna, if these habitats offer the highest foraging return (Werner et al. 1983b). Thus, small

bluegills have the behavioral flexibility to use open habitats but do not do so in the presence of predators. Mittelbach (1981) estimated that small bluegills in a natural lake could increase their net energy gain up to 50% by feeding in the open water on zooplankton instead of feeding in the vegetation. Large bluegills, on the other hand, are relatively invulnerable to predators and feed in either vegetated or open habitats depending on relative foraging gain. Predation risk thus establishes habitat segregation between bluegill size classes, open habitats becoming exclusive resources for larger fish. Largemouth bass therefore have two major effects on bluegill populations: (1) the direct effect of predation on small fish and (2) the indirect effect of modifying bluegill behavior and causing large and small bluegills to partition resources. Both factors potentially reduce competition between size classes.

Recent studies on both European perch (*Perca fluviatilis*) and yellow perch (*P. flavescens*) provide a situation analogous to that in the bluegill. Perch, like bluegills, are prone to producing stunted populations in small lakes. Stunting is reported to be especially common in shallow lakes with relatively homogeneous habitat structure (Eschmeyer 1937; Alm 1946; Persson 1983). In lakes with little habitat diversity, diet overlap between large and small perch is high, and intraspecific competition is intense (Eschmeyer 1937; Persson 1983). However, in lakes containing both vegetated and open habitats, perch segregate by size classes, with small perch occupying the vegetation and adults feeding in the open water or in the more open bottom habitats (Keast 1977; Sandheinrich and Hubert 1984). In these lakes, adult perch grow well, and the populations are not stunted. Although there is no direct experimental evidence that size-class segregation in perch is due to predation risk, it is reasonable to assume that the smallest perch are most vulnerable and that vegetation provides them with significant protection from predators (Glass 1971; Savino and Stein 1982).

Keast (1977) suggested that the ability of perch to shift to feeding on continually larger prey as they grow is the major factor preventing the development of stunting. However, Sandheinrich and Hubert (1984) showed that even when large perch are feeding predominantly on zooplankton, they can grow at average or above average rates. In the population

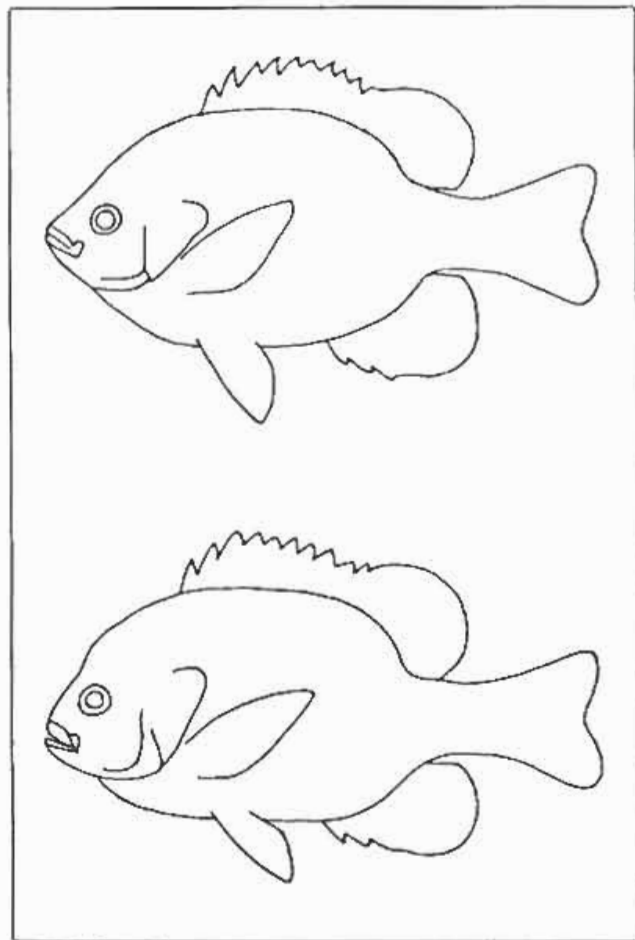
studied by Sandheinrich and Hubert, habitat segregation by different size classes of perch appeared to be the most important factor reducing intraspecific competition.

The studies with perch and bluegills illustrate the potential importance of predator-induced habitat partitioning in regulating competition between size classes. Additional examples of size-class segregation in fish populations abound (see citations in the opening section), and the restriction of vulnerable individuals to protective habitats appears to be a general phenomenon in fish and other size-structured taxa. Other environmental factors besides physical structure also act as prey refuges, e.g., differences in water depth, turbidity, and temperature. These factors also must be considered when one evaluates the importance of predators in promoting size-class segregation. It will be important in future research to disentangle the indirect effects of predators in maintaining resource partitioning from the direct effects of predators killing prey. Both kinds of effects tend to reduce intraspecific competition between size classes of prey.

## INTERSPECIFIC COMPETITION

Although a behavioral response to predators may segregate size classes within a species, it is also likely to concentrate vulnerable size classes of different species into a common refuge. For example, as many as five to six species of sunfish co-occur in the vegetation of small lakes during their first 2 to 3 years of life (Werner et al. 1977; Keast 1978a; Laughlin 1979; Mittelbach 1984). While occupying the vegetation, these small fish feed on similar prey, and their diets overlap considerably (Keast 1978b; Laughlin 1979; Mittelbach 1984). Thus, a similar response to predation risk may increase interspecific competition early in a species' life history. McCabe et al. (1983) discuss an interesting case where juvenile chinook salmon (*Oncorhynchus kisutch*) pass through the Columbia River estuary before moving out to sea. While the salmon are in the estuary, their diets overlap broadly with the diets of other (nonsalmonid) species. McCabe et al. hypothesize that the estuary represents a refuge from many oceanic predators. If so, juvenile salmon may experience a period of interspecific competition in the estuary due to the antipredator responses of a number of fish spe-





**Figure 21.1.** Outline drawings of adult bluegill (top) and pumpkinseed sunfish (bottom).

cies. Many other co-occurring species of fish occupy a common protective habitat during vulnerable stages in their life history (Power 1984; Werner 1986; and others). If resources are limited in the refuge, interspecific competition may be intensified by the presence of predators. This effect runs counter to the traditional view that predation reduces interspecific competition only by removing individuals (but see also Holt 1984).

Below we present a specific example illustrating how predation risk may affect the interaction between two species of sunfish, the bluegill and its congener, the pumpkinseed (*L. gibbosus*). First we review the evidence for predator-mediated resource use in these species. Much of this work is drawn from Mittelbach (1984). We then discuss the evidence for resource limitation among juveniles during the time they are restricted to a refuge. Finally, we present a model illustrating how predator-mediated interactions among juveniles may affect species abundances and lead to the transmission of

competitive effects between adults, even though the adults of the two species feed on different prey.

### The Bluegill-Pumpkinseed Interaction

Bluegill and pumpkinseed are native to the northeastern United States and southern Canada and commonly co-occur in a variety of small lakes and ponds. The species are quite similar in appearance (fig. 21.1) but differ significantly in their functional morphology and feeding efficiency (Keast 1978b; Mittelbach 1984). These differences in turn cause large bluegills and pumpkinseeds (>75 mm standard length) to feed on different prey types found in separate habitats. In a study of three Michigan lakes, large bluegills foraged primarily on open-water zooplankton (*Daphnia*), and large pumpkinseeds specialized on snails (table 21.1; see also Seaburg and Moyle 1964, Keast 1978b). This separation in diet is directly related to differences in the morphology and foraging ability of the two species. In laboratory experiments, pumpkinseeds feed on larger and stronger-shelled snails than do the bluegill, and take less time to handle the same-size snail. The bluegill, on the other hand, is more efficient at feeding on zooplankton (Mittelbach 1984).

In contrast to the differing diets and habitat use of large bluegills and pumpkinseeds, those of small fish ( $\leq 75$  mm) are very similar (table 21.1). Small fish of both species feed predominantly in the vegetation, and 80 to 90% of their average seasonal diet is composed of vegetation-dwelling invertebrates (excluding snails). Calculated diet overlaps (Schoener 1970) average about 50% for small bluegills and pumpkinseeds but only 2 to 8% for large fish in lakes with true limnetic zones (Mittelbach 1984). Laughlin (1979) also measured diet overlaps between juvenile pumpkinseeds and juvenile northern longear sunfish (*L. megalotis peltastes*). He found that fish <75 mm total length shared about 50% of their prey in common, whereas diet overlaps among larger fish were <20%. Like young bluegills and pumpkinseeds, juvenile northern longear sunfish are concentrated in the vegetation refuge, whereas adults feed in areas of bare sediments.

The high overlap in diet among small bluegills and pumpkinseeds is due to two factors: (1) piscivorous fish restrict small sunfish to the

**Table 21.1.** Average seasonal diets classified by habitat (prey) type for bluegills and pumpkinseeds in three Michigan lakes; sample sizes range from 21 to 44 fish per species per lake; average N = 32

	Average diet composition (% dry mass, $\bar{x} \pm SE$ )					
	Lawrence Lake		Three Lakes II		Three Lakes III	
	Bluegill	Pumpkinseed	Bluegill	Pumpkinseed	Bluegill	Pumpkinseed
<b>SMALL FISH (<math>\leq 75</math> mm SL)</b>						
Vegetation-dwelling prey (nongastropods)	86 $\pm$ 4	79 $\pm$ 5	78 $\pm$ 5	76 $\pm$ 5	91 $\pm$ 4	84 $\pm$ 7
Gastropods	<1	19 $\pm$ 5	<1	22 $\pm$ 5	0	16 $\pm$ 7
Zooplankton	6 $\pm$ 3	0	3 $\pm$ 1	1 $\pm$ 1	5 $\pm$ 2	0
<b>LARGE FISH (<math>&gt; 75</math> mm SL)</b>						
Vegetation-dwelling prey (nongastropods)	36 $\pm$ 6	25 $\pm$ 6	46 $\pm$ 9	36 $\pm$ 8	67 $\pm$ 7	33 $\pm$ 7
Gastropods	<1	73 $\pm$ 6	0	63 $\pm$ 8	<1	67 $\pm$ 6
Zooplankton	54 $\pm$ 7	0	46 $\pm$ 10	0	24 $\pm$ 6	<1

Some percents do not sum to 100 because not all prey could be classified among the three habitat types. Three Lakes III is very shallow and contains few large zooplankton.

Adapted from Mittelbach (1984).

vegetation, where they are less vulnerable, and (2) small pumpkinseeds are unable to crush effectively any but the tiniest snails and therefore cannot use the adult resource in the vegetation. Size-specific predation risks and foraging efficiencies therefore create what may be viewed as a two-stage life history for these species. Small fish are confined to a common habitat and share a common prey resource, whereas larger, less vulnerable bluegills and pumpkinseeds shift to feeding on different prey and have reduced diet overlaps. Whether the concentration of juveniles in response to predators influences interspecific competition will depend, in part, on whether juveniles are competing for limited resources in the refuge. For bluegills and pumpkinseeds, the available evidence indicates that resources are limiting in natural lakes.

Growth in fish is very sensitive to prey availability (Werner 1986). When we compared growth rates of young (age 1) bluegills and pumpkinseeds from a series of experimental ponds and natural lakes in southwest Michigan, we found that juvenile growth rates were three to eight times higher in the experimental ponds than in nearby natural lakes (Mittelbach 1986). In both environments, fish were feeding in the vegetation, and water temperatures were similar. However, no competitors were present in the ponds prior to the intro-

duction of bluegills or pumpkinseeds, and invertebrate prey were extremely abundant. Cage experiments conducted in the littoral zone of a natural lake also showed that growth rates of juvenile bluegills were density-dependent over the natural range of bluegill densities found in the lake (Mittelbach 1986). These studies therefore suggest that young bluegills and pumpkinseeds are competing for limited prey resources while they are restricted to the vegetation.

Interestingly, we have failed to detect any major difference in the juvenile competitive abilities of these species. In laboratory feeding experiments, small bluegills and pumpkinseeds harvested natural prey (amphipods) at identical rates from a habitat of *Chara* vegetation (Mittelbach 1984). Studies of growth rates in the field also show no difference in the foraging abilities of these small fish. While occupying the vegetation, both species grew at the same rate within a pond or lake (three natural lakes and two experimental ponds), although growth rates differed significantly between lakes or ponds (Werner and Hall 1979; Mittelbach 1984; 1986). Thus, juvenile bluegills and pumpkinseeds appear to have similar abilities to forage from the vegetation and grow through this stage of their life history at equal rates. The two species also show similar mortality

rates when exposed to predation by largemouth bass (Mittelbach, unpublished data). We would therefore expect juvenile competition between these species to be equal and symmetrical. This does not mean, however, that predator-induced juvenile interactions have no effect on the population dynamics or abundance of these species.

Survivorship and growth rate are positively correlated in many fish (for reviews see Backiel and LeCren 1978; Ware 1975; Werner 1986), and density-dependent growth has long been postulated as the principal factor regulating juvenile mortality in fishes (Ricker and Foerster 1948). Put simply, fish that grow quickly are vulnerable to predators for a shorter time and have higher survival. Gilliam (1982) has further shown mathematically that for stages of the life history where survivorship is already low (i.e., among juvenile fish), a small reduction in growth can cause a very large reduction in survivorship (see also Werner et al. 1983a). Thus, any density-dependent effects on growth that result from behavioral responses of juvenile fish to their predators are likely to have important consequences for survival, recruitment, and overall population density.

In the following section, we develop a model illustrating how predator-induced juvenile competition can lead to interesting and complex interactions between prey species. The model is essentially a two-species stock-recruitment model, and the single species components share much in common with Ware's (1980) bioenergetic approach to stock and recruitment. An important conclusion from the model is that strong competition in the juvenile stage can result in the transmission of negative effects between adults, even though the adults of two species use different resources.

## A POPULATION MODEL

Above we have argued that the presence of predators may often cause juvenile fish to compete within a refuge, while having little impact on adult behaviors. To begin to explore the population consequences of this effect, we consider a simple model in which each species has two life stages, juveniles and adults. Juveniles are assumed to occupy the same habitat and compete for the same resources, whereas adults feed on different prey and do not compete directly. This is the essence of the bluegill-

pumpkinseed interaction. The two main components of the model are density-dependent adult fecundity and density-dependent juvenile survival. By density-dependent, we mean that per capita fecundity declines with an increase in adult density, whereas the probability of surviving through the juvenile stage decreases as juvenile density increases. Thus, the per capita fecundity will be represented as a function  $F(X)$  of the adult density  $X$ , and the juvenile survival will be a function  $\ell(L)$  of juvenile density  $L$ . These functions are shown as monotonically decreasing in figure 21.2a.

The general phenomenon of density-dependent fecundity is well documented in fishes (for reviews, see Nikol'skii 1962; Schopka and Hempel 1973; McFadden 1977; Bagenal 1978; Ware 1980; for examples with bluegills and pumpkinseeds, Parker 1958; Cooper et al. 1971), although the exact shape of the fecundity curve is poorly known for any species. Survival of juveniles is by no means always density-dependent in fishes, but it is to be expected whenever competition for resources affects juvenile growth rates. Any factor that slows individual growth prolongs the time spent in vulnerable size classes and therefore increases the overall probability of death (Beverton 1962; Ricker 1979; Sheperd and Cushing 1980; Lasker 1981; Werner 1986). An added potential effect of reduced juvenile growth is an increase in time to maturity. For simplicity of presentation, the model given here does not allow for this effect. However, in Appendix C, we consider a more general model that includes the possibility that competition delays maturity. There it is shown that the results from the simple model given here carry over in essential details to the more general case. Yield data on density-dependent juvenile survival can be found in LeCren (1962, 1965), Egglishaw and Shackley (1977), Elliott (1984), and Beyerle and Williams (1972) for bluegills.

Per capita survival and fecundity are naturally expected to be monotonically decreasing functions, but total fecundity and survival, which are obtained by multiplying these per capita rates by density, need not be monotonic. There are two possibilities. These total rates may be monotonically increasing, or they may increase at first and then decrease to give a humped form (fig. 21.2b). The monotone case is simply the situation where increasing the number of individuals entering a life stage re-



sults in more output from that life stage. The outputs are reproduction or survival and maturation depending on whether the stage is adult or juvenile. The humped situation occurs when density dependence becomes so extreme at high densities that increased input eventually yields less output. Field evidence for the existence of monotonic and humped curves can be found in Burd and Parnell (1973), Lett et al. (1975), Lett (1980), and Ware (1980).

Putting together the juvenile survival and fecundity for a single species leads us to postulate the following dynamical equations:

$$L(t) = X(t)F(X(t)), \quad (21.1a)$$

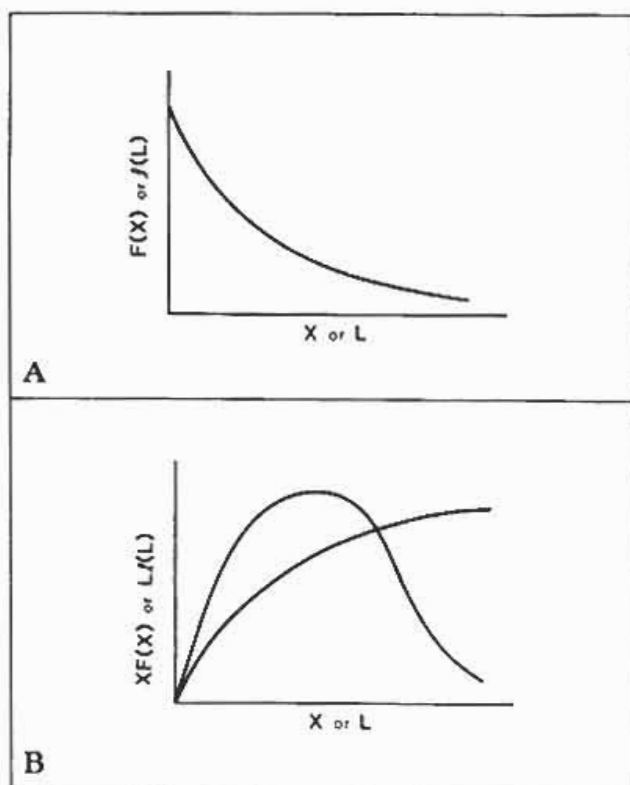
$$X(t + 1) = L(t)\ell(L(t)), \quad (21.1b)$$

where  $L(t)$  is the number of juveniles at time  $t$ ,  $X$  equals the number of adults,  $F$  is the fecundity per individual and  $\ell$  is the probability of surviving through the juvenile stage. These equations can be written as one difference equation describing the change in adult numbers from one time to the next:

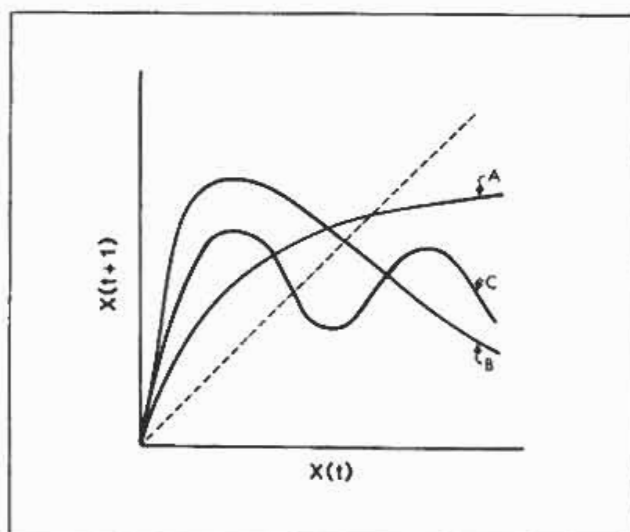
$$X(t + 1) = X(t)F(X(t))\ell(X(t)F(X(t))). \quad (21.2)$$

The dynamics of the system can be understood by considering a graph of  $X(t + 1)$  against  $X(t)$ , as in figure 21.3. There are three different possible forms of this relationship (A, B, C). The monotonic form A arises when the curves for total juvenile survival and total reproduction are both monotone. This form also can arise when larval survival is humped but peaks for an initial juvenile density higher than the possible total reproduction for the system. The form B, with just a single hump, occurs when either total reproduction or total survival is humped, and it also can occur in some cases where both are humped. The double-hump curve can occur only when both curves are humped but does not arise when the maximum reproduction occurs on an increasing part of the curve for total juvenile survival. Thus, if the humps of these component curves are broad and flat, a double hump is unlikely (see May and Oster 1976 for further discussion or iterated humped curves).

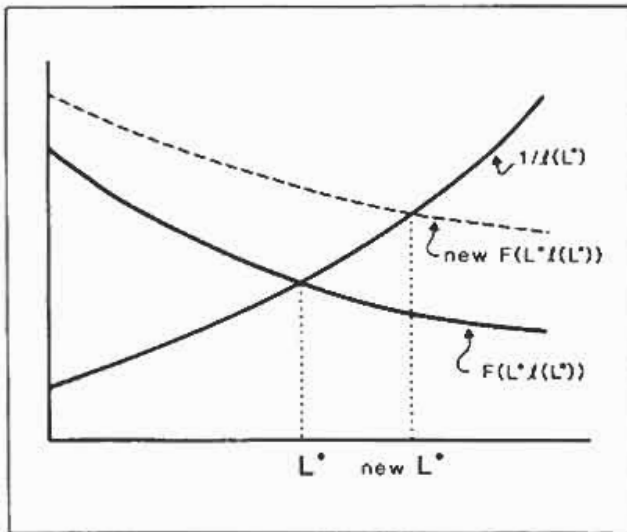
Equilibrium points are determined by the intersection of the curves in figure 21.3 with the 45-degree line, i.e., the line  $X(t + 1) = X(t)$ . There is at least one equilibrium point when-



**Figure 21.2.** a: Per individual fecundity,  $F(X)$ , or juvenile survivorship  $\ell(L)$ , as a function of adult density,  $X$  or juvenile density,  $L$ , respectively. b: Two possible relationships between total fecundity,  $X F(X)$ , and adult density,  $X$ , or between total juvenile survival [i.e., recruitment,  $L \ell(L)$ ] and juvenile density,  $L$ . Conditions leading to humped-shaped versus monotonic curves are described in the text.



**Figure 21.3.** Three possible forms (A,B,C) of the dynamical relationship between  $X(t)$  and  $X(t + 1)$ . The intersection(s) of each curve with the dashed 45-degree line describes the condition where  $X(t + 1) = X(t)$  and the population is at equilibrium. The stability of the various equilibria are discussed in the text.



**Figure 21.4.** An illustration of how the equilibrium number of juveniles of a single species changes with an increase in per capita fecundity.  $F(L)l(L)$  describes per individual fecundity as a function of juvenile density,  $L$ , while  $1/l(L)$  describes the average number of juveniles needed to replace one adult. The intersection of the  $F(L)l(L)$  and  $1/l(L)$  curves defines the point where per individual fecundity equals juvenile mortality and the population is at equilibrium. Increasing per individual fecundity (new  $F(L)l(L)$ ) moves the intersection point to the right and increases the equilibrium juvenile density from  $L^*$  to new  $L^*$ . Since  $Ll(L)$  is assumed to be monotonic in  $L$ , an increase in juvenile density implies an increase in adult density at equilibrium.

ever  $l(0)F(0) > 1$ , i.e., whenever the species can have positive growth at low density. If there is only one equilibrium and it occurs on a rising part of the curve, that equilibrium is locally stable. Intersections that occur on falling parts of the curve will be locally stable if the slope is no steeper than  $-1$ . Extreme density dependence at equilibrium can lead to a slope steeper than  $-1$ , and thus to instability. Cyclic or chaotic population dynamics are then likely (May and Oster 1976). Three equilibria will occur in case C if the 45-degree line cuts both humps. The middle equilibrium is necessarily unstable, but the other equilibria will be locally stable if they satisfy the criteria listed above for single equilibria. See May and Oster (1976), Fisher and Goh (1977), Rosenkranz (1983) for further information on stability of equations of this sort.

We now ask how the equilibrium density is changed when parameters of the model are changed. We assume that we are in a situation where stability occurs, which essentially

amounts to a constraint on the severity of density dependence. If  $X^*$  and  $L^*$  represent respectively the adult and juvenile densities at equilibrium, the following equation must hold:

$$l(L^*)F(X^*) = 1 \quad (21.3)$$

i.e., the product of per capita juvenile survival and per capita reproduction must equal 1. This means that a single adult gives rise on average to exactly one adult in the next generation. From equation (21.1b) we see that

$$X^* = L^*l(L^*), \quad (21.4)$$

and substituting in equation 21.3 we see that

$$F(L^*l(L^*)) = 1/l(L^*). \quad (21.5)$$

Figure 21.4 plots  $F(L)l(L)$  and  $1/l(L)$  as functions of  $L$ , and by equation 21.4 their intersection determines the equilibrium juvenile density. The diagram depends on the assumption that  $Ll(L)$  is monotone in  $L$ , for otherwise  $F(L)l(L)$  would not be monotonic. This diagram can now be used to determine what would happen to the equilibrium if per capita reproduction,  $F(X)$ , were increased. This is the sort of situation to expect if more resources were made available to adults. The dotted curve in figure 21.4 illustrates this case, and it is clear that the equilibrium number of juveniles must increase, as might naturally be expected. Also, the monotonicity of total juvenile survival implies that the equilibrium adult density obtained from equation 21.4 will also increase as resources for adults increase. These conclusions must be modified if the total juvenile survival function is not monotonic. Although the equilibrium juvenile densities can still be seen to increase if the reproduction curve is increased, it does not follow that the adult equilibria (there now can be more than one) will increase, because an adult equilibrium may correspond to a declining part of the total juvenile survival curve. In this case, an increase in adult resources will cause the adult equilibrium to decline.

Now consider a system of two interacting species, where juveniles compete interspecifically but adults do not. In this case, we leave the total reproduction functions the same as in the single-species model, except for the addition of a subscript to indicate the species and



to allow the possibility that these functions differ between species. Thus we have:

$$L_i(t) = X_i(t)F_i(X_i(t)), \quad (21.6a)$$

$i = 1, 2$ . The juvenile survival equations become

$$X_i(t + 1) = L_i \ell(L(t)) \quad (21.6b)$$

where now  $L(t) = L_1(t) + L_2(t)$  is the total number of juveniles in the system. Here per capita survival of juveniles of species  $i$  declines as a function of total juvenile density, not just the density of juveniles of species  $i$ .

These equations demonstrate immediately how the adults of one species may affect adults of the other indirectly through juvenile competition. For example, an increase in the adult density of species 1 may increase juvenile output of that species and thereby increase competition among juveniles of both species. The outcome of this will be a reduction of juvenile survival of both species, but in particular the resulting adult density of species 2 will be less.

Simple analyses like the one above are useful in sorting out the effects of temporary perturbations to the system; however, they are of little use for looking at long-term effects, for instance, the effects of a permanent increase in the resources for the adults of one species. To begin to get an idea of the ramifications of permanent changes to a system, or alternatively, the effects of permanent differences between systems, we shall examine the behavior of the equilibrium densities of the two-species system. Throughout we continue to make the assumption that  $L\ell(L)$  is monotonic.

Since the juvenile survival rate is the same for both species in this system, the equilibrium must satisfy

$$F_1(X_1^*) = F_2(X_2^*) = 1/\ell(L^*). \quad (21.7)$$

Thus, the two species also must have equal per capita fecundities at equilibrium. Equilibrium per capita fecundities of the two species need not be equal when the species are present alone, i.e., in a single-species systems. Away from equilibrium the per capita fecundities will, of course, generally be different. In particular, the per capita fecundities at low adult densities,  $F_1(0)$  and  $F_2(0)$  may be different. The difference between  $F_1(0)$  and  $F_2(0)$  has impor-

tant consequences for the existence of the two-species equilibrium.

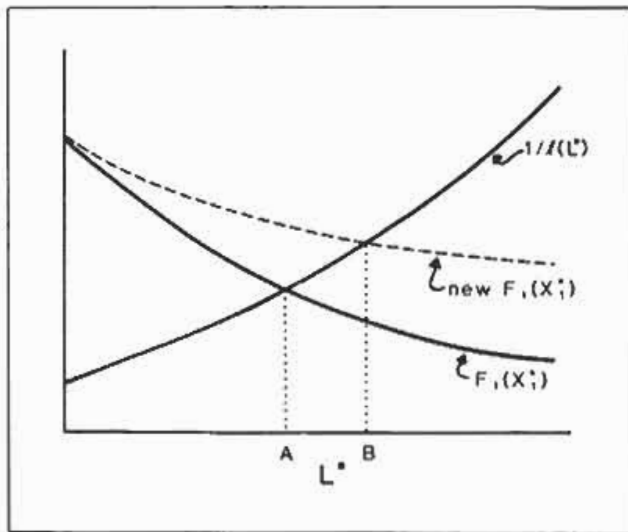
For the sake of argument, suppose  $F_1(0) \leq F_2(0)$ , so that species 1 has a lower per capita fecundity than species 2 at low density. There will be some minimum value  $X_{2min}$  of  $X_2$  so that  $F_1(0) = F_2(X_{2min})$ . The equilibrium value of  $X_2$  in the two-species system must be greater than  $X_{2min}$ . The equilibrium total juvenile density must be greater than  $L_{min}$ , where  $L_{min}\ell(L_{min}) = X_{2min}$ ; i.e.,  $L_{min}$  is the number of juveniles of species 2 needed to produce  $X_{2min}$  adults of species 2. The sole condition for the existence of a two-species equilibrium then turns out to be

$$F_1(0)\ell(L_{min}) > 1, F_2(0)\ell(L_{min}) > 1, \quad (21.8)$$

i.e., each species must be able to increase from low density when the number of juveniles in the system is at the infimum ("minimum") of possible equilibrium juvenile densities. If  $F_2(0) < F_1(0)$ , this condition continues to hold, but  $L_{min}$  is defined in terms of  $X_{1min}$ , where  $F_1(X_{1min}) = F_2(0)$ . This result can be understood from the discussion below on the behavior of the equilibrium. Naturally enough, condition 21.8 also can be shown to be equivalent to the requirement that each species can invade a system in which the other species is at its single-species equilibrium.

Local stability of the equilibrium is investigated in Appendix A, where it is shown that in the absence of severe density dependence the equilibrium is always locally stable. This result reflects the fact that intraspecific competition is always stronger than interspecific competition among adults, whereas intra- and interspecific competition are equal among juveniles. Local stability has been investigated in a number of other discrete-time competition models involving age structure (e.g., Hassell and Comins 1976; Travis et al. 1980). Fisher and Goh (1977) show how results on local stability for discrete time competition models may be extended to global stability.

To examine changes in the equilibrium that result from changes in the parameters of the model, we note that equation 21.7 establishes a relationship between  $X_1^*$  and  $X_2^*$ , and consequently the equilibrium adult density for species 2 can be written as a function of the equilibrium adult density for species 1. We can in fact go further than this: total adult equilibrium density can be written in terms of total ju-



**Figure 21.5.** A similar case to fig. 21.4 except that we now consider two interacting species with total juvenile density,  $L = L_1 + L_2$ . Illustrated here are the population consequences of increasing the per individual fecundity of species 2. By the arguments given in the text, increasing  $F_2(X_2)$  results in an increase in  $F_1(X_1^*)$  as a function of  $L^*$  and an increase in the total equilibrium juvenile density,  $L^*$  from A to B. As a result of the increase in  $F_2(X_2)$  and  $L^*$ , the equilibrium number of adults of species 1,  $X_1^*$ , declines.

venile equilibrium density according to the relationship

$$L^* \ell(L^*) = X_1^* + X_2^* \quad (21.9)$$

This equation, together with the relationship between  $X_1^*$  and  $X_2^*$  allows us to write  $X_1^*$  as a function of  $L^* \ell(L^*)$ , i.e.,

$$X_1^* = f(L^* \ell(L^*)) \quad (21.10)$$

where  $f$  is some function. The precise details of how  $f$  is obtained are given in Appendix B. In figure 21.5 we use this equation (21.10) to plot  $F_1(X_1^*)$  and  $1/\ell(L^*)$  as functions of  $L^*$ . The intersection of these two curves then gives us the equilibrium total juvenile density, as in the single-species case.

We can now ask what happens to the equilibrium when the reproduction curve of one species is increased. This is not a simple procedure because the reproduction curve is used several times in the definition of the function  $f$  relating  $X_1^*$  and  $L^*$ . However, if  $F_2$  is increased, the effect is to decrease the function  $f(L^* \ell(L^*))$  for fixed  $L^*$  (see Appendix B). It follows that  $F_1(f(L^* \ell(L^*)))$  must be increased. Thus, the dotted line in figure 21.5 gives the curve  $F_1(X_1^*)$

that applies with an increased value of  $F_2(X_2)$ . Figure 21.5 thus implies that increasing  $F_2$  will shift  $L^*$  from the point A to the point B, i.e., the total equilibrium juvenile density increases from A to B. A number of other changes can be deduced:

- Average juvenile survival of both species,  $\ell(L^*)$  must decrease, because increased numbers of juveniles result in a lower per capita juvenile survival. But if equilibrium is to be maintained this means, by equation 21.7, that
- Equilibrium per capita reproduction of species 1 and 2,  $F_1(X_1^*)$  and  $F_2(X_2^*)$ , must increase. Because the reproduction curve of species 1 has not changed, an increase in per capita fecundity in species 1 can occur only if the equilibrium density of adults declines; therefore,
- $X_1^*$  must decrease. This is not true of species 2, however, because its reproduction curve has increased. Indeed, the fact that  $L^*$  increases means that  $L^* \ell(L^*)$ , which equals  $X_1^* + X_2^*$ , must increase. Together with (c) this means that
- $X_2^*$  must increase.

Thus, we have a complete solution to the changes in adult densities. Do the juvenile densities change in the same way? The answer for species 1 depends on whether the equilibrium adult density occurs on an increasing or decreasing part of the reproduction curve. If increasing,  $L_1^*$  will decrease, but if the reproduction curve is decreasing at equilibrium,  $L_1^*$  must increase. For species 2, however, these considerations do not apply. It is clear from (b) and (d) that both  $F_2(X_2^*)$  and  $X_2^*$  must increase; therefore,  $X_2^* F_2(X_2^*) = L_2^*$  must increase also.

In summary, a rise in the reproduction curve of species 2 increases the adult density of species 2 and its juvenile density, decreases the adult density of species 1, and decreases or increases the juvenile density of species 1. The equilibrium total juvenile density must, however, be increased.

Consequence (b) above is perhaps counterintuitive, for at first sight it does not seem reasonable that increasing the per capita reproduction of one species should increase the per capita reproduction of its juvenile-stage competitor. However, this is an important consequence of the indirect interaction that occurs

between adult densities mediated by the juvenile stage. Total reproduction for species 2 is increased, which means that species 2 increases competition at the juvenile stage. This leads to a reduction in juvenile survival for both species, but in particular the number of adults of species 1 is reduced. Since resources for adults of species 1 remain the same, there is less competition at the adult stage and consequently a greater per capita reproductive output.

Our explanation of the behavior of equilibrium densities, though general in not specifying the particular functions involved, nevertheless deals with a qualitatively narrow range of situations. Fortunately, the conclusions are robust to changes in these specific features, as shown in Appendix C. It also would be useful to look at this sort of model in a stochastic setting because variation is a striking feature of reproduction and juvenile survival in many natural fish communities. However, experience with stochastic models suggests that the present analysis is adequate for small to moderate levels of stochastic variation.

## DISCUSSION

The majority of taxa have populations containing numerous size classes (e.g., fish, amphibians, reptiles, most invertebrates, and plants). In many of these organisms, vulnerability to predators is strongly size-dependent (e.g., Dayton 1971; Ware 1975; Paine 1977; Peterson and Wroblewski 1984), the smallest individuals often being the most vulnerable (zooplankton show the reverse trend; see Brooks and Dodson 1965; Hall et al. 1976). Given that foraging in different habitats or on different prey types often carries with it differences in predation risk, we expect predators to routinely exert a strong size-specific influence on the diet and habitat use of a species. We have here considered some of the consequences of these predator-mediated behaviors to exploitative competition in fish. We have limited our discussion to fish in part because they provide some of the clearest examples available. However, recent studies on insects (Sih 1980, 1982), lizards (Stamps 1983), and snails (Schmitt 1982) indicate that many of the processes discussed here apply in broad fashion to other size-structured taxa as well. The chapters by Sih and Abrams in this volume also provide evidence for the importance of pred-

tors in modifying species interactions through changes in prey foraging behaviors and lifestyles.

We expect the behaviors of juveniles or larvae to be most commonly affected by predation risk, since prey vulnerability is inversely related to increasing body size in many species. When behavioral responses to predators lead to size-specific interactions, competition between species can become complex (Werner and Gilliam 1984). One interesting feature of predator-induced competition among juveniles is the potential transmission of competitive effects between adults, even when the adults of two species utilize separate resources. This result points out the danger in judging the strength of interspecific competition from studies in which only one stage in a species life history is examined. For example, many studies of fish food habits have examined only the diets of adult fish because large fish are often more easily caught or are available from commercial landings. These studies of adults then become the basis for inferences about the likelihood of interspecific competition. However, as the two-species stock-recruitment model demonstrates, adults may show strong negative effects even when there is no overlap in their resource use. Thus, studies of resource partitioning in which only a portion of a species life history is considered may be very misleading with regard to the potential for exploitative competition. This same caution of course applies to size-distributed taxa other than fish (e.g., lizards, snails, etc.).

In the specific case of the bluegill and pumpkinseed, it appears that juveniles of the two species have similar foraging abilities and growth rates while they feed in the vegetation refuge. It is interesting to consider the potential causes and consequences of this juvenile equivalence. Hubbell and Foster (1986) suggested that a common juvenile environment has selected for the extreme similarity observed among young tropical trees. By restricting species to a common protective habitat, predators also may indirectly lead to evolutionary convergence in phenotype and foraging behavior among their prey. This convergence may be a factor in the apparent equivalence of juvenile bluegills and pumpkinseeds. In addition, selection for divergence in resource use among juveniles may be constrained by factors that operate on adults. Without a radical metamorphosis, morphologi-



cal features present in juveniles are carried directly into the adult stage (potentially modified by allometric growth). Thus, selection for differences in morphology and resource use at the juvenile stage may be opposed by selection for resource partitioning among adults.

When adults do exhibit pronounced resource partitioning (as in the bluegill and pumpkinseed), their differences in resource use actually may favor convergence at the juvenile stage. The reason is that compensation at the adult stage can at least partly make up for differences in feeding efficiencies of the two species as juveniles. This compensation lessens the disadvantage experienced by the less efficient species when the juveniles converge on the same resources. It must be kept in mind, however, that within any group of related species the earliest stages of ontogeny are most similar and development tends to proceed from the general to the special (Von Baer's law, Gould 1977). Thus, similarities among juveniles may represent developmental constraints as well as selection for convergence.

Whatever the ultimate causes, if species have similar competitive abilities as juveniles and use separate resources as adults, we might expect their local abundances to be determined largely by adult resource supply. In small lakes and ponds, the bluegill is generally dominant in numbers and biomass (Werner et al. 1977). Dominance by the bluegill may reflect the fact that it is an efficient planktivore and that the total production of zooplankton is generally much greater than the production of littoral prey (due to the relative volumes of the two habitats). Thus, the plankton resource may be able to support the greater biomass of adult fish. Numerous studies of salmonid species in Scandinavian and North American lakes also document a general pattern where the most planktivorous fish species is also the most abundant (Svardson 1976; Nilsson 1963; Andrusak and Northcote 1971; Nilsson and Northcote 1981; review in Werner 1986), although the exact nature of the competitive interactions between species is unclear. When species are not equal competitors as juveniles, bottlenecks to recruitment may result. Neill's (1975) laboratory study of competing cladocera demonstrates how strong, asymmetrical juvenile competition may lead to the elimination of a species from the community, even when adults of that species have abundant and ex-

clusive resources. Although no cases of asymmetrical juvenile competition and recruitment bottlenecks have been documented for fish, their existence seems likely.

Behavioral responses to predators affect not only the interactions within and between fish species but also the dynamics of the fishes' food resource. For example, by concentrating small fish in the vegetation, predation risk indirectly results in increased foraging intensity on littoral cladocera and decreased foraging on limnetic zooplankton. Kerfoot (1975) and Fulton (1985) showed that these differences in foraging intensity between habitats can strongly affect natural zooplankton communities. Werner et al. (1983a) manipulated predation risk on small bluegills and also found a significant indirect effect of a planktivore's predator on zooplankton populations. In their experiment, a small pond was divided in half, and bluegills and piscivorous largemouth bass were stocked on one side of the pond and only bluegills on the other. The bluegills quickly (<10 days) eliminated *Daphnia pulex* from the side of the pond without bass. However, in the presence of the bass, the daphnids were able to coexist with bluegills for 20 days. These results are especially striking, considering the proximity of open water and vegetation habitats in this small pond and the fact that small bluegills could feed on *Daphnia* within a few meters from the vegetation. It is not inconceivable that in natural lakes, where habitats are more clearly separated, the impact of piscivores on the distribution of planktivores may be a major factor determining zooplankton species composition and abundance. In a series of recent studies, Power (1984 and this volume; Power and Matthews 1983; Power et al. 1985) has also shown that predator avoidance by grazing fishes can dramatically affect the distribution of algae in streams.

The only theoretical treatment of the effects of predator-mediated foraging behavior on food web dynamics is that of Abrams (1984). Abrams considered the situation in which a forager must expose itself to greater risk while foraging, and adjusts its foraging time adaptively to maximize fitness. He found that under this situation the adjustment of foraging time to predation risk can result in (1) interactions between the forager's predator and the forager's food, (2) predator self-limitation, and (3) potential interactions between food species.

From the above discussion it is clear that many of these same results can occur if foragers modify habitat use rather than foraging time in the presence of predators. Abrams was also able to show that these indirect effects can often be equal to or larger than the direct effects between trophic levels.

Although it can be shown that predators affect species' diets and habitat use, few general predictions can be made concerning what will happen to interactions if predators are removed. For example, in the absence of a size- or habitat-specific predator, prey may shift their resource use and no longer face the same suites of competitors. However, it is difficult in any reasonably complex community to predict the eventual competitive interactions that result because the response of each species will depend in part on the responses of other species and on changes in resource dynamics due to the shift in foraging pressure. In addition, the direct effect of the predator on prey mortality will be changed. Clearly, one way to begin to sort out these effects of predators on community structure is through field manipulations. Ecologists working in the intertidal zone have long employed predator removal-and-addition experiments, and their studies reveal a complex array of direct and indirect effects in many communities (e.g., Connell 1961; Paine 1966; Dayton 1971; Menge 1976; Lubchenco and Menge 1978; Garrity and Levings 1981). However, these studies have not generally measured the relative importance of these two factors. A major challenge in designing future experiments will be to separate out the direct and indirect effects of predators and to quantify their relative impact. If the impact of predators on prey foraging behaviors and habitat use turns out to be significant in regulating populations, ecologists will have to reevaluate many traditional views of how predation and competition act in structuring communities.

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## APPENDIX A

The equations for the two-species model can be written as

$$\mathbf{X}(t + 1) = \mathbf{G}(\mathbf{H}(\mathbf{X}(t))), \quad (21.A1)$$

where  $\mathbf{X}(t) = (X_1(t), X_2(t))'$ , and  $\mathbf{G}$  and  $\mathbf{H}$  are vector-valued functions with  $G_i(\mathbf{L}) = L_i \ell(L)$ ,  $H_i(\mathbf{X}) = X_i F_i(X_i)$ . The local stability of the system is determined by the matrix  $\mathbf{A}$  with  $i - j$ th element equal to  $\partial X_i(t + 1) / \partial X_j(t)$ ,

evaluated at equilibrium. Application of the chain rule to (A1) shows that

$$\mathbf{A} = \mathbf{BC}, \quad (21.A2)$$

where  $\ell(\mathbf{L}^*)\mathbf{B} = (\partial G_i / \partial L_j)$  and  $F_i(X_i^*)\mathbf{C} = (\partial H_i / \partial X_j)$ , evaluated at equilibrium. We make use here of the equilibrium equation  $\ell(\mathbf{L}^*)F_i(X_i^*) = 1$ .

Defining  $\beta = -d \log \ell(\mathbf{L}) / d\mathbf{L} |_{\mathbf{L}=\mathbf{L}^*}$  and

$\gamma_i = -d \log F_i(X_i)/dX_i|_{X_i=X_i^*}$ , then  $\beta$  and  $\gamma_i$  represent the magnitude of density dependence in the juvenile and adult populations respectively. The matrices  $\mathbf{B}$  and  $\mathbf{C}$  can be now written as follows:

$$\mathbf{B} = \begin{bmatrix} 1 - L_1^* \beta & -L_1^* \beta \\ -L_2^* \beta & 1 - L_2^* \beta \end{bmatrix}; \quad (21.A3)$$

$$\mathbf{C} = \begin{bmatrix} 1 - X_1^* \gamma_1 & 0 \\ 0 & 1 - X_2^* \gamma_2 \end{bmatrix}.$$

The equilibrium will be locally stable if the eigenvalues of  $\mathbf{A}$  are less than 1 in absolute

value. Using the fact the  $(L_1^* + L_2^*)\beta < 1$ , because  $L\ell(L)$  is monotone, the Schur-Cohn criterion (May 1974, p. 220) is easily applied to  $\mathbf{A}$  to show that the equilibrium will be locally stable whenever  $|1 - X_i^* \gamma_i| < 1$ ,  $i = 1, 2$ . Since  $\gamma_i > 0$ , this can be rewritten as

$$X_i^* \gamma_i < 2, i = 1, 2. \quad (21.A4)$$

Condition 21.A4 is a sufficient condition for local stability, not a necessary condition. However, it becomes both necessary and sufficient whenever  $X_1^* \gamma_1 = X_2^* \gamma_2$ .

## APPENDIX B

Equation 21.7 in the text allows us to write

$$X_2^* = g(X_1^*) \quad (21.B1)$$

where  $g(X_1^*) = F_2^{-1}(F_1(X_1^*))$ . Because both  $F_1$  and  $F_2$  are decreasing functions,  $g$  is an increasing function. Also, if  $F_2$  is increased as a function, then the function  $g$  must also increase. Combining equations 21.B1 and 21.9 in the text we get

$$L^* \ell(L^*) = X_1^* + g(X_1^*). \quad (21.B2)$$

Since the RHS of (B2) is an increasing function, we can write  $X_1^*$  in terms of  $L^* \ell(L^*)$ ,

$$X_1^* = f(L^* \ell(L^*)) \quad (21.B3)$$

where  $f$  is the inverse function of  $X + g(X)$ . Note that  $f$  is necessarily an increasing function, and also that increasing the function  $g$  must necessarily decrease the function  $f$ , which means that the function  $F_1(f(L^* \ell(L^*)))$  must be increased. It follows that increasing the function  $F_2$  necessarily increases  $F_1(f(L^* \ell(L^*)))$  as a function of  $L^*$ .

## APPENDIX C

### Generalizations of the Model

In the text, we presented a simplified model to illustrate the effects of juvenile competition and adult fecundity on species' abundances. Here we show that conclusions concerning changes in equilibrium abundances, derived from the simple model, also apply when we allow for overlapping generations and a delay in maturity due to juvenile competition.

We use the symbol  $L_{ij}(t)$  to refer to the number of juveniles of species  $i$  and age  $j$ ,  $j = 0, 1, 2, \dots$ . We assume that the total amount of competition that juveniles experience is determined by a weighted sum,  $L(t)$ , of the juveniles densities:

$$L(t) = \sum_j c_j (L_{1j}(t) + L_{2j}(t)), \quad (21.C1)$$

where the  $c_j$  are constants allowing different age classes to contribute differently to competitive pressure.

The number of adults of species  $i$  is determined by the number of juveniles that mature, and the number of adults surviving from the previous time period:

$$X_i(t+1) = \sum_j L_{ij}(t) a_j(L(t)) + (1 - d_i) X_i(t), \quad (21.C2)$$

where  $d_i$  is the adult death rate of species  $i$  and  $a_j(L(t))$  is the density-dependent fraction of larvae of age  $j$  that mature before age  $j + 1$ .

Juvenile dynamics are described as follows:

$$L_{i0}(t) = X_i(t) F_i(X_i(t)), \quad (21.C3)$$



$$L_{j+1}(t+1) = L_j(t)p_j(L(t)), \quad (21.C4)$$

where  $p_j(L(t))$  is the density-dependent fraction of juveniles of age class  $j$  surviving, but not maturing, from time  $t$  to time  $t+1$ .

At equilibrium, equation 21.C4 implies

$$L_j^* = L_{i0}^* \prod_{v=0}^{j-1} p_v(L^*) = L_{i0}^* \ell_j(L^*) \quad (21.C5)$$

Thus,

$$\begin{aligned} L^* &= (L_{10}^* + L_{20}^*) \sum c_j \ell_j(L^*) \\ &= L_{00}^* s(L^*), \end{aligned} \quad (21.C6)$$

where  $L_{00}^*$  is the sum of age 0 juveniles and  $s(L^*)$  is the weighted sum of the  $\ell_j(L^*)$ .

Expression 21.C2 implies

$$\begin{aligned} d_i X_i^* &= \sum_j L_{ij}^* a_j(L^*) \\ &= L_{i0}^* \sum_j \ell_j(L^*) a_j(L^*), \\ &= L_{i0}^* \theta(L^*), \text{ say,} \end{aligned} \quad (21.C7)$$

and therefore that

$$\begin{aligned} d_1 X_1^* + d_2 X_2^* &= L_{00}^* \theta(L^*) \\ &= L^* \lambda(L^*), \end{aligned} \quad (21.C8)$$

where  $\lambda(L^*) = \theta(L^*)/s(L^*)$ . Equation 21.C8 is a generalization of equation 21.9 in the text.

To obtain a generalization of equation 21.7, we note from equation 21.C3 that

$$L_{i0}^* = X_i^* F_i(X_i^*). \quad (21.C9)$$

Combining this with equation 21.C7 we get

$$F_1(X_1^*)/d_1 = F_2(X_2^*)/d_2 = 1/\theta(L^*), \quad (21.C10)$$

which is the sought generalization of equation 21.7.

To obtain generalizations of the results in the text, we must assume that  $L\lambda(L)$  is an increasing function of  $L$  and that  $\theta(L)$  is a decreasing function of  $L$ . When these conditions hold, all of the conclusions in the text concerning changes in  $L^*$ ,  $X_i^*$  and  $F_i^*(X_i^*)$ ,  $i=1,2$ , continue to apply. The conclusions in the text about the  $L_i^*$  become conclusions about the  $L_{i0}^*$  here.

To interpret the above assumptions, note that  $\theta(L)$  will be a decreasing function of  $L$  if the total fraction of any cohort that survives to maturity decreases as a function of the competition it experiences, when the amount of competition is constant over time. This decrease in the fraction maturing is consistent with decreased age-specific survival rates, delayed maturity with no change in age-specific survival, or both of these in combination. The assumption that  $L\lambda(L)$  increases with  $L$  merely requires that the competition be not too extreme.

We have not determined the conditions under which the equilibrium of this more complex model will be stable. It is likely, however, that density dependence must be milder for stability of this model as a result of the time lags introduced by allowing maturity over a number of ages.