

Resource Depletion and Habitat Segregation by Competitors Under Predation Hazard

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1 Introduction *Evolution*, Springer-Verlag.

Individuals of different sizes in size-structured populations often differ greatly in the use of resources and/or space. Spectacular examples include shifts, within a lifetime, from carnivory to herbivory (e.g., some turtles; Clark and Gibbons 1969), or from herbivory to carnivory (e.g., some copepods; Neill and Peacock 1980), or from aquatic to terrestrial habitats (e.g., many amphibians). Many other species show large shifts in prey size or habitat use as they grow, but yet other species show little difference across sizes (Fraser 1976; Polis 1984; Werner and Gilliam 1984; Persson this Vol.). Thus, patterns of resource and habitat use within a species vary from complete segregation between two given size classes, to partial overlap, to complete overlap. The presence or absence of such diet or habitat segregation between different size classes can greatly affect population structure and dynamics. For example, the degree of overlap between different size classes influences population stability, and the intensity of competition between classes influences, in interesting ways, whether increases in the density of a given class increases or decreases the density of other classes (Tschumy 1982; Mittelbach and Chesson 1987; Ebenman this Vol.).

Some of the shifts in diet or habitat use might be rather inflexible in the ontogeny of a given individual. However, a large literature demonstrates that many mobile animals show rapid behavioral changes in diet or use of space as resources change across time or space (Stephens and Krebs 1986). Further, several recent experimental studies show that alteration of predation hazard alters habitat selection or feeding behavior by mobile animals (e.g., reviews by Helfman 1986; Milinski 1986; Dill 1987; and Sih 1987 for aquatic systems). Flexible behavior by individuals greatly enriches the range of population structures and dynamics that we might expect to observe in nature, because behavioral shifts in habitat use can rapidly alter the degree of size class (or species) overlap, and may also suddenly alter size-specific mortality and growth rates.

A hypothetical example is illustrated in Fig. 1. Mortality rate is usually taken to be an increasing function of predator density, but this need not be true if individuals can shift habitats in response to the hazard of predation (e.g., Iwasa 1982; Werner and Gilliam 1984). In Fig. 1, the mortality rate of a given size class is assumed to increase as a function of predator density over some interval, but

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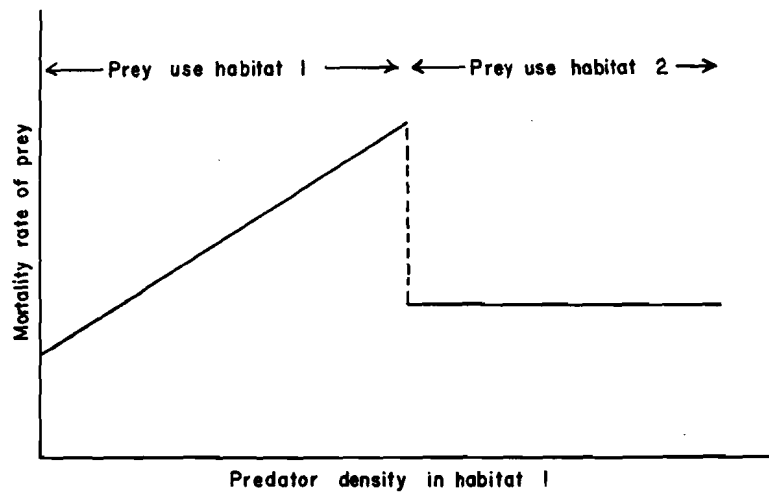


Fig. 1. One reason to consider individual behavior in models of population dynamics. Hypothetical mortality rate of a prey size class or species showing active habitat selection

to show a saltatory drop to a lower level as the predator density reaches a level which induces a discrete shift to a safer habitat (examples of such shifts, and ways of predicting them, are treated below). A corresponding step function in individual growth rate could also be expected, if the habitats differ in resource levels or energetic costs. A discrete habitat shift is depicted, but in some cases the shift away from a hazardous site might be more gradual.

Similarly, appreciation of active, flexible habitat choice can also alter the way we would view genetic responses to biotic or abiotic environmental changes. Natural selection might produce animals adapted to their environment, but by habitat selection animals can choose environments to which they are adapted. For example, the abscissa in Fig. 1 could be relabeled "selection gradient" to indicate the strength of selection on some morphological trait which confers protection from the predator. As the predator increases in density, selection for the trait might increase, but above some threshold the evolution of the trait becomes insensitive to changes in predator density, because the prey just leaves. Such a cusp for a given trait might be accompanied by cusps in other traits which become subject to stronger or weaker selection in the "new" habitat. A question of this nature was addressed, in a preliminary way, by Werner and Gilliam (1984), in the context of morphological response to species introductions.

Below, we first outline experimental studies which demonstrate how the introduction of a predator can cause habitat shifts which increase or decrease segregation between different size classes in fish populations. We then develop a model which addresses two problems. First, if a single size class depletes resources in two sites which differ in the risk of death, how will the difference in predation hazard indirectly affect relative resource levels in those sites? Second, if two or more size classes (or species) have different vulnerabilities to a predator, how will resources be depleted simultaneously by the consumers, and what is the resultant habitat use by each size class?

2 Experimental Studies of Predator-Induced Alterations of Size-Class Overlap

2.1 Predator-Induced Segregation

Experimental work with bluegill sunfish, *Lepomis macrochirus*, has demonstrated how the presence of a predator can cause size-class segregation (Werner et al. 1983a, b). In the absence of predators in an experimental pond, all bluegill size classes chose the most energetically profitable areas, which were nonvegetated areas. However, in the presence a predator (largemouth bass, *Micropterus salmoides*), small, vulnerable sizes showed a shift to the energetically poorer vegetated areas, but larger sizes showed no such shift. The shift by the smaller bluegills corresponded to a reduced individual growth rate in the presence of the predator, presumably reflecting the poorer foraging rate among vegetation, or possibly increased vigilance in the presence of the predator. Simultaneously, larger bluegills showed higher growth rates than in the absence of predators, apparently reflecting lessened competition from smaller conspecifics. Thus, the effect of the predator was not just to remove individuals; rather, it was to restructure competitive relations among individuals of different sizes. Mittelbach et al. (this Vol.) and Werner and Hall (1988) further discuss this interaction.

Recent experimental work by Schlosser (1987) has shown that predator intimidation can also increase size-class segregation in stream fish, and distributional patterns of size classes often suggest such an effect in fish and other taxa (e.g. Sih 1980; Polis 1981; Stamps 1983; Power 1987; Kneib 1987; Polis and McCormick 1987).

2.2 Predator-Induced Overlap

While the above work shows how behavioral responses to a predator causes size-class segregation, we might also expect to find cases in which the introduction of a predator decreases segregation. Indeed, Power et al. (1985) found this effect in studies of a herbivorous minnow, *Campostoma anomalum*. In the absence of piscine predators in a stream pool, young-of-year minnows (2–3 cm standard length) occupied shallow edge areas, and larger conspecifics (4–8 cm) mainly used deeper areas. However, the introduction of piscivorous largemouth bass (18–23 cm) into the pool resulted in extensive overlap, as the large minnows shifted to shallow areas (Power et al. 1985; Power 1987). Unlike the above bass-bluegill experiment, all size classes of *Campostoma* were vulnerable to the introduced bass.

We have identified a second case in which experimental manipulation of a predator can result in reduction of size-class segregation. In the Northern Range mountains in Trinidad, West Indies, populations of the guppy (*Poecilia reticulata*) in the larger rivers are subject to predation from several effective piscine predators, including the pike cichlid (*Crenicichla alta*) and the guabine (*Hoplias malabaricus*). However, above barrier falls, a weaker predator, Hart's rivulus (*Rivulus hartii*), is often the only piscine predator. Several studies have investigated how upstream and downstream guppy populations differ in behavior,

life history, and morphology (e.g., Haskins et al. 1961; Liley and Seghers 1975; Endler 1980; Reznick 1982; Breden and Stoner 1987; Fraser and Gilliam 1987; Houde 1988).

While many sites in the Trinidadian streams fall cleanly into "downstream (strong predation)" or "upstream (weak predation)" categories, others do not. We have been studying such a site, a first- and second-order headwater stream which is a tributary of the Arima River near the William Beebe Tropical Research Station (Simla). The Arima River contains a full complement of predators, including the pike cichlid and the guabine. However, neither the pike cichlid nor the guabine was observed in the tributary during three surveys prior to a survey in August 1987, when guabine appeared in some of the pools. Guabine apparently appear intermittently in the stream, and we asked whether the appearance of guabine might restructure use of space by guppies.

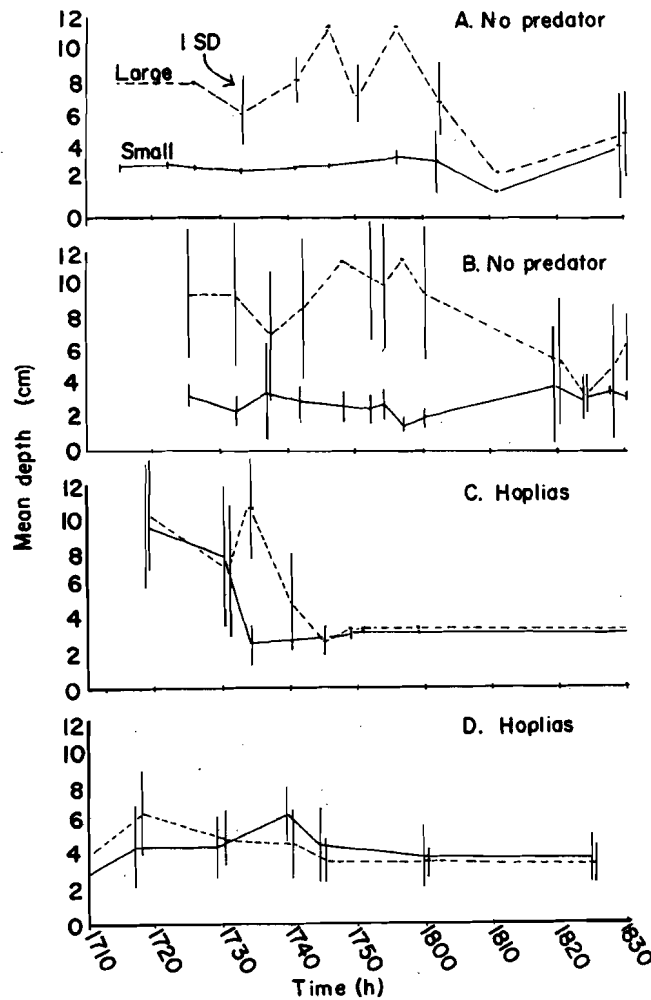


Fig. 2. The effect of a predator, *Hoplias malabaricus*, on the depth distributions of two guppy size classes in a headwater pool

To determine whether the use of space by the guppy population can be altered during periods in which guabine are present, we selected an upstream pool, 2 m wide \times 3 m long, averaging 0.16 m deep, and screened the up- and downstream ends with seines. After removing all fish from the pool, we restocked 15 adult (25–30 mm TL) and 15 juvenile (15–20 mm TL) guppies, approximating natural densities. We then observed the spatial distributions of the two size classes in the late afternoon and through dusk for 2 days, and then introduced one guabine, 120 mm TL, for the following 2 days. Prior to the introduction of the guabine, the two size classes of guppies were spatially separated by depth (Fig. 2, panels A and B). This segregation broke down after sunset (1800 h) when adult guppies shifted to shallow water (Fig. 2A and B). However, following the addition of the predator, the guppies no longer showed segregation (Fig. 2C and D). The guabine spent most of the time in the deeper part of the pool, but it occasionally made forays into shallow areas.

This initial experiment shows that the appearance of guabine can eliminate extensive size-class segregation, at least near dusk (the effect might be quite different in mid-day periods, when guabine are much less active). However, it is not immediately clear whether segregation among the guppies, or the minnows studied by Power et al., might be reestablished over the longer term, as resources are depleted in shallow areas. Below, we explore how resource depletion might result in complete segregation, complete overlap, or some intermediate pattern as resources are depleted.

3 Predicting Spatial Distributions of Size Classes (or Species) Differing in Vulnerability

3.1 Choices with Resources and Predation Hazard Held Constant

It is clear from experimental studies that habitat use is strongly influenced by resources and predation hazard in alternative sites. However, the creation of a practical theoretical basis for predicting such decisions by animals is a difficult endeavor still in its infancy. The difficulty is not only in integrating the different units of energetic gain and mortality hazard into a decision rule, but also in formulating the problem in measurable parameters amenable to field experimentation.

For size-structured populations, one way of reducing the problem to measurable parameters was offered by Werner and Gilliam (1984), who suggested a "minimize mortality rate to growth rate (minimize u/g)" hypothesis. The hypothesis is based on the observation that a juvenile in a purely size-structured population (all properties, including maturation, dependent only on body size) would maximize expected lifetime reproduction by maximizing survival to each size, including size at maturation. This is done by accumulating each bit of mass at the lowest mortality cost; i.e., minimizing u/g at each size, regardless of the relationship between size and mortality. The hypothesis applies in a constant environment, in a constant population with continuous reproduction, but is an approximation otherwise.

We (Gilliam and Fraser 1987) developed an experimental system to test the "minimize u/g " hypothesis. However, in the process of developing a way of manipulating growth rates in alternative sites, we realized that we could further simplify the problem. Rather than measuring mortality and growth rates in alternative sites to predict choice, we found that an alternative formulation of the problem would allow predictions of choice on the basis of mortality rates and, more simply, gross foraging rates in alternative sites. The hypothesis we actually tested was a "minimize u/f " hypothesis: the model predicted that foraging fish, when venturing out of a foodless refuge, would prefer the site with the lowest ratio of mortality rate (u) to gross foraging rate (f). The "minimize u/f " hypothesis assumes that: (1) metabolic rates are similar in each site; (2) some time is spent not feeding; and (3) when not feeding, the mortality rate is zero, such as in an absolute refuge. Alteration of these assumptions alters the u/f hypothesis (Gilliam and Fraser 1987).

We tested the utility of the hypothesis in a series of choice experiments by juvenile creek chubs, *Semotilus atromaculatus*, in an experimental field stream. The juvenile chubs could allocate time among a foodless refuge and two foraging areas, in which mortality hazard (density of adult creek chubs) and resource levels (tubificid worms) were manipulated. The experiments established the following (Gilliam and Fraser 1987). First, a higher risk of death in an area does not preclude its use; a sufficiently high energetic return in the more hazardous site can induce a shift to that site. Second, the foragers could assess different levels of hazard (1, 2, or 3 predators) in different sites, as well as different levels of energetic gain; the ability to assess hazard extends beyond detection of presence or absence of predators. Third, choices corresponded closely to those predicted by the "minimize u/f " hypothesis, given independent prior estimates of mortality hazard and intake rate in alternative sites. In particular, it was possible to predict the level of resource enrichment necessary to induce a shift to a more hazardous site.

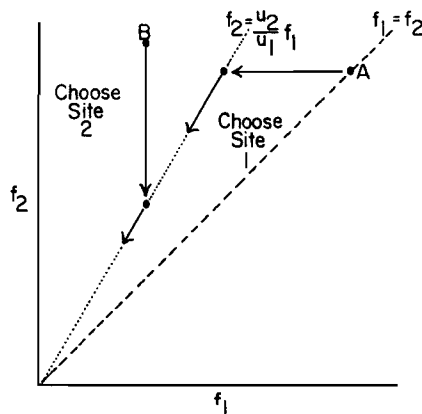
The above experiments involved resources which were not substantially depleted over the course of the experiment, and a single size class of foragers. Below, we use the "minimize u/f " hypothesis to develop a model which predicts how depletable resources will be structured by a single size class using two sites differing in predation hazard. The model is then extended to multiple size classes.

Throughout, we assume that an individual will choose to forage in a site which minimizes the ratio of mortality to foraging rate (u/f), so the above three assumptions also apply.

3.2 Depletable Resources: Use of Two Sites by a Single Size Class

If feeding animals prefer safer areas, resources should be impacted more severely in such areas. Power (1987) reviews experimental demonstrations of such effects across three trophic levels, in which predators on herbivorous minnows indirectly structure algal communities in streams, by altering use of space by the minnows. The effects on the algae were caused by behavioral shifts by the minnows, rather than numerical reduction of the total minnow population. We also know that the

Fig. 3. Predicted trajectories of resource depletion in two sites differing in mortality hazard. Site 2 is more hazardous than Site 1. f foraging rate; u mortality rate in a site



stream benthic invertebrate community is altered if the local density of juvenile creek chubs is experimentally altered (Gilliam et al. 1989), so the chubs' responses to predation hazard should also tend to structure the invertebrate community. Other processes, such as physical disturbance, could counteract the effect of predation hazard.

The "minimize u/f " hypothesis provides a way to predict the pattern of resource depletion among sites differing in mortality hazard (Fig. 3). Site 1 is safer than Site 2 ($u_1 < u_2$), and the axes the foraging rates in each site, reflecting resource levels. Given initially equal foraging rates in each of two sites (Point A), a forager is predicted to choose the safer site (Site 1) when feeding, because $u_1/f_1 < u_2/f_2$. In the idealized case of perfect choice, resource depletion is depicted by a horizontal vector pointing to the left (in practice, Site 2 will also receive some use, as in Gilliam and Fraser 1987). The foraging rate in Site 1 will be decreased (via resource depletion) until the point representing foraging rates touches the "switching curve" with slope u_2/u_1 ; along the switching curve, $u_1/f_1 = u_2/f_2$, or $f_2 = (u_2/u_1)f_1$. Then a hypothetical forager would allocate time to each habitat so as to cause the foraging rate in each to decline along the indicated path. Identical arguments apply to depletable resources started at Point B, except initial use of Site 2 is predicted because $u_2/f_2 < u_1/f_1$ at Point B.

Along the switching curve, $f_2/f_1 = u_2/u_1$. That is, the hypothetical consumer structures resource levels such that the relative foraging rates equal the relative mortality rates in each site. Identical arguments apply to multiple sites, or to continuous gradients such as distance from shore or cover.

3.3 Simultaneous Depletion by Two or More Consumer Classes

Now consider two size classes (or two species) consuming identical resources in the two sites. One size class is vulnerable to predators, and the other is invulnerable. For convenience, these classes will be called "Small" and "Large," respectively, although in many cases larger individuals need not be less vulnerable.

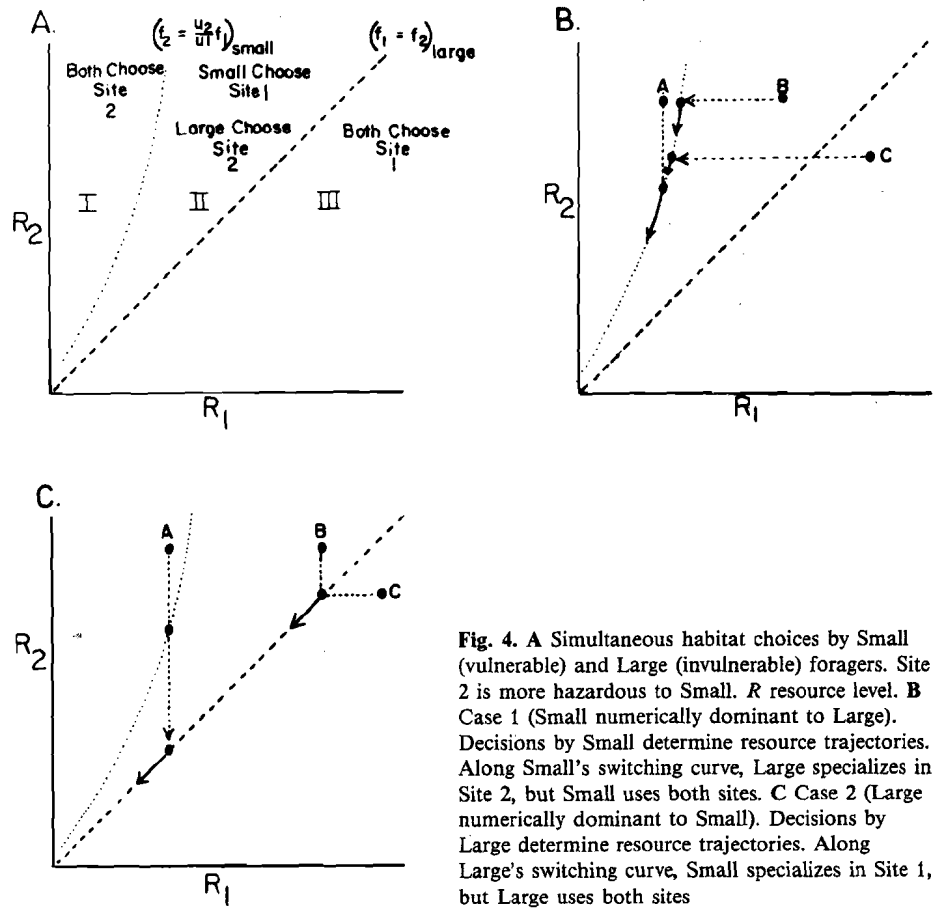


Fig. 4. A Simultaneous habitat choices by Small (vulnerable) and Large (invulnerable) foragers. Site 2 is more hazardous to Small. R resource level. B Case 1 (Small numerically dominant to Large). Decisions by Small determine resource trajectories. Along Small's switching curve, Large specializes in Site 2, but Small uses both sites. C Case 2 (Large numerically dominant to Small). Decisions by Large determine resource trajectories. Along Large's switching curve, Small specializes in Site 1, but Large uses both sites

Exploitative competition occurs in two sites which differ in mortality hazard. If Small tends to produce unequal resource levels in the two sites (as above), but Large tends to equalize resource levels, how does all this settle out? The following approach uses some elements from ideal free models of habitat selection (e.g., Rosenzweig 1981; Parker and Sutherland 1986; Fagan 1987), but also explicitly includes differing mortality hazard in alternative sites.

Hypothetical habitat selection for given resource levels are shown in Fig. 4A. Small is vulnerable with mortality rates u_1 and u_2 in the safer and more hazardous sites, respectively. Large is invulnerable to predators and is assumed to use the site with the greater resource level. The hypothesized choices by each competitor fall into three regions. In Region I, resources in Site 2 are much higher than in Site 1, and both Small and Large are predicted to choose Site 2. In Region II, Small and Large segregate; Large are hypothesized to still choose Site 2 (there is more food there), but Small chooses Site 1 (because u/f is lower there). In Region III, both Small and Large choose Site 1; it has the highest resources, and is also

safer for Small. Along the boundaries (the "switching curves" of Small and Large) of the Regions, each site is equally attractive. The switching curve of Small is nonlinear because foraging rate is taken to be a nonlinear function of resource level; the curve in Fig. 4A was calculated from data for juvenile creek chubs (Fig. 5 in Gilliam and Fraser 1987). The model assumes purely exploitative competition.

Given initial resource levels, the patterns of habitat shifts and the asymptotic distributions will depend upon the resource trajectories, and hence the densities and relative frequency of Large and Small. Consider two limiting cases: Case 1, in which Small is much more abundant than Large, and Case 2, in which Small is much less abundant than Large.

The trajectories for Case 1 (Fig. 4B) are determined by the decisions of the numerically dominant Small. In the ideal case (perfect omniscient decisions by Small, and negligible effects of Large), the resource trajectories are as indicated. Given initial resource levels indicated by Point A in Fig. 4B, the shifts are as follows. Initially Small and Large both specialize in Site 2, but resources are depleted to a level at which Small generalizes across Site 2 and Site 1, so as to drive the resource level along Small's switching curve; Large remains specialized in Site 2. If resources were started at Point C, the prediction is that initial specialization in Site 1 by both Small and Large will be followed by a period of habitat segregation (Small still in Site 1, but Large in Site 2), and then, as above, generalization by Small but specialization by Large.

Trajectories for Case 2 are shown in Fig. 4C. Here, Large is numerically dominant to Small, and Large tends to equalize resources in the two sites. As before, complete habitat segregation or complete overlap can occur for certain combinations of resource levels. However, the asymptotic distribution, as resources are depleted, is that Small specializes in the safer site (Site 1), and Large allocates time between sites so as to maintain equality of resource levels.

In this example, Large is invulnerable, but different mortality rates for Large in the two sites would just be represented by a different switching curve.

The main predictions for two competing classes are: (1) habitat segregation or complete overlap can result from different, but specifiable, resource levels; (2) if resource levels are "driven" by the consumers, the asymptotic distribution will be characterized by specialization by one competitor class, and generalization (relatively) by the other; and (3) the specializing class will be the one without a dominant demand on resources. Finally, if resource levels are determined by factors other than consumption by Small and Large (e.g. by other consumers in the system, or by changing abiotic conditions), then the resource levels are unlikely to lie on a switching curve at any instant. In that case, segregation (Region II) or congruence (Regions I or III) is predicted at a given time.

4 Conclusion

Our main aim has been to extend the "minimize u/f " hypothesis to begin to predict how competing size classes or species would structure resources when sites differ in mortality hazard, and how patterns of habitat use would result. For il-

illustrative purposes, we have done this by considering just two competitor classes. By introducing a switching curve for each size class or species, the approach is readily extended to multiple consumer classes, or a continuous distribution of sizes. If the switching curves are distinct for each size class (or species), the model predicts specialization by all size classes except possibly one; for a given size class, there is one best place to be, unless the resource levels lie exactly on the switching curve. Parker and Sutherland (1986) make a similar point when considering unequal competitive abilities of different sizes (mortality hazard was not considered). If one size class consumes food x times as fast as another in each of two sites, there are many stable configurations of size classes among the sites (e.g., Fig. 14.3 in Sutherland and Parker 1985). However, if one size class consumes food x times as fast as the other size class in Site 1, but y times as fast in Site 2 ($x \neq y$), then one size class is predicted to specialize in one site, and the other is expected to distribute itself so as to equalize its intake rate in each site. Thus, asymmetries in competitive ability (Parker and Sutherland 1986) or mortality hazard (this chapter) tend to produce specialization, if the asymmetry between consumer classes differs across sites.

The processes hypothesized in Figs. 3 and 4 follow from the "minimize u/f " hypothesis, to which certain assumptions are attached. Notably, the original formulation of the hypothesis (Gilliam and Fraser 1987) assumes use of a foodless refuge when not foraging. This assumption might be met approximately even if no physical refuge is used, if periods of inactivity and extreme vigilance, creating refuge-like conditions temporally, are interspersed with periods of active foraging. However, we have not solved, to our satisfaction, the related problem of ideal free distribution of a single size class between two foraging sites with no refuge or opportunities for safe periods, given that increased food translates into a benefit of faster growth. Abrahams and Dill (1989) offer an empirical approach, which asks the foragers to reveal how they convert energy and death into fitness.

It is clear that foraging fish readily respond to both resource levels and mortality hazard in choosing foraging sites, and some progress has been made in combining theory and field experiments to construct a predictive basis for such shifts. It is also clear that such shifts are important in population dynamics (Ebenman this Vol.; Mittelbach et al. this Vol.). However, a satisfactory link between flexible decisions and population dynamics has not yet been made for size-structured populations. Models of populations without age- or size-structure show how predator-prey dynamics are altered if the model includes flexible behavior of prey responding to predation hazard (Abrams 1984; Sih 1987; Ives and Dobson 1987). In these models, flexible prey behavior often appears to be stabilizing, because responses of prey to high predator density lowers the efficiency of predators in finding prey; the result is analogous to increased interference among predators as predator density increases. Investigations of such questions in size-structured populations is likely to lead to rich dynamical behavior, as different size classes respond differently to hazard, and the effects of behavioral decisions by small individuals linger as the cohort ages. The development of behavioral theory applicable to field experiments is difficult and still in its infancy, but the central roles of resource and habitat use to ecological and evolutionary processes warrants continued attention to flexible behavior in ecological settings.

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