MECHANISMS CREATING COMMUNITY STRUCTURE ACROSS A FRESHWATER HABITAT GRADIENT

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ABSTRACT

Lentic freshwater habitats in temperate regions exist along a gradient from small ephemeral ponds to large permanent lakes. This environmental continuum is a useful axis for understanding how attributes of individuals ultimately generate structure at the level of the community. Community structure across the gradient is determined by both (*a*) physical factors, such as pond drying and winter anoxia, that limit the potential breadth of species distributions, and (*b*) biotic effects mediated by ecological interactions, principally predation, that determine the realized success of species. Fitness tradeoffs associated with a few critical traits of individuals often form the basis for species turnover along the gradient. Among species that inhabit temporary ponds, distributions are often constrained because traits that enhance developmental rate and competitive ability also increase susceptibility to predators. In permanent ponds, changes in the composition of major predators over the gradient limit distributions of prey species because traits that reduce mortality risk in one region of the gradient cause increased risk in other regions of the gradient. Integrated across the gradient, these patterns in species success generate distinct patterns in community structure. Additionally, spatial heterogeneity among habitats along the gradient and the fitness tradeoffs created by this heterogeneity may hold important evolutionary implications for habitat specialization and lineage diversification in aquatic taxa.

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INTRODUCTION

Mechanistic approaches in ecology seek to functionally link traits of individuals to higher level processes such as the dynamics of populations and multispecies interactions, determinants of species distributions, and development and maintenance of community structure (175, 191). Studies conducted across environmental gradients can greatly enhance our understanding of the ways in which individual traits act to shape these higher level processes because they can reveal patterns of concordance in species traits and species assemblages across the changing ecological conditions of the gradients (24).

In this review we are concerned with a well-known gradient in lentic freshwater habitats (e.g. pools, marshes, ponds, and lakes) in temperate regions. These habitats can be placed on an axis ranging from small, highly ephemeral habitats to extremely large habitats that have been present for millennia (202). Ecologists have long recognized this environmental gradient as a critical axis along which aquatic communities are organized (17, 74, 196). Virtually every type of animal known to inhabit freshwater is also known to have a restricted distribution across this habitat gradient. Representatives from nearly every class of free-living freshwater animals sort among habitats according to their permanence or in relation to the distribution of predators whose own distributions are related to permanence (Table 1). With few exceptions, however, sorting occurs at the family level and below; most higher taxa (phyla, classes, orders) are not restricted to particular regions of the gradient. Among the groups in which these patterns have been quantified, species are often restricted to a subset of habitats, while the distribution of even a single genus can encompass a large portion of the entire range of available habitats (Figure 1). These patterns imply that overall body plan differences associated with higher order taxonomic classification do not usually represent constraints to use of different habitat types, but if constraints do exist, they occur among species, genera, and families.

The integration of restricted species distributions across the gradient leads to highly characteristic shifts in community structure (17, 23, 32, 67, 89, 149, 154, 195). Our thesis is that restricted species distributions and turnover in community composition along the gradient result largely from a relatively few important constraints on the life-styles of aquatic animals. As developed below, certain attributes of organisms such as body size, developmental rate, activity, and life history form axes for fitness tradeoffs across the habitat gradient. In each case, substantial evidence suggests that success at one point on the gradient entails having a phenotype that will hinder performance at other points along the gradient. We argue that changes in community structure along the gradient are best understood in terms of the critical fitness tradeoffs that determine a species' pattern of performance among habitats. Elucidating these mechanistic

Table 1 Free-living animals of lentic freshwater habitats whose distributions are known to vary with frequency of habitat drying or predator distribution. Representative references are given for each taxon.

Taxon	Common name	Permanence	Predators	Reference
Proifera	Sponges	x		200
Turbellaria	Flatworms	x		196
Nematoda	Roundworms	x		7
Rotifera	Rotifers	x		139
Bivalvia	Clams	x	x	90, 133
Gastropoda	Snails	x	x	181, 18, 19, 86
Hirudinea	Leeches	x	x	196, 94
Oligochaeta	Worms	x		196
Arachnida	Mites	x	x	196, 75
Anostraca	Fairy Shrimp	x	x	196, 89
Cladocera	Water Fleas	x	x	17, 196, 139, 89
Conchostraca	Clam Shrimp	x		9, 196, 139, 89
Notostraca	Tadpole Shrimp	x		51, 139
Copepoda	Copepods	x		22, 6, 89
Amphipoda	Amphipods	x	x	196, 188
Decapoda	Crayfish, Shrimp	x		196
Isopoda	Isopods	x		196
Ostracoda	Seed Shrimp	x		196
Anisoptera	Dragonflies	x	x	196, 95
Coleoptera	Beetles	x	x	80, 41
Diptera	True Flies	x	x	36, 91, 179, 182
Ephemeroptera	Mayflies	x		196
Hemiptera	True Bugs	x	x	27, 157
Megaloptera	Alderflies	x		200
Trichoptera	Caddisflies	x		114
Zygoptera	Damselflies	x	x	196, 95
Osteichthyes	Fishes	x		127
Anura	Frogs	x	x	23, 151
Caudata	Salamanders	x	x	23

links between individual- and community-level processes provides a fundamental understanding of how constituent species shape community structure and, conversely, how community structure may influence the distribution and evolution of species.

A Schematic Model

Changes in community structure along this freshwater habitat gradient are determined by the coupled effects of (*a*) physical environmental factors that limit the potential breadth of species distributions and (*b*) biotic interactions that determine the realized success of species. In Figure 2, we present a schematic

model of community structure across the gradient. The model depicts key nega-
tive effects, both biotic and abiotic, that underlie significant shifts in community
structure across the gradient. Bold arrows indicate strong effects and thinner
arrows represent weaker effects.

The physical environment forms the template along which communities de-
velop on the gradient. At the broadest scale, physical factors constrain the
potential pool of community members by eliminating species unable to cope
with the physical stress. In temporary pond habitats, the need to cope with pe-
riodic drying imposes severe constraints on a species' behavior, development,
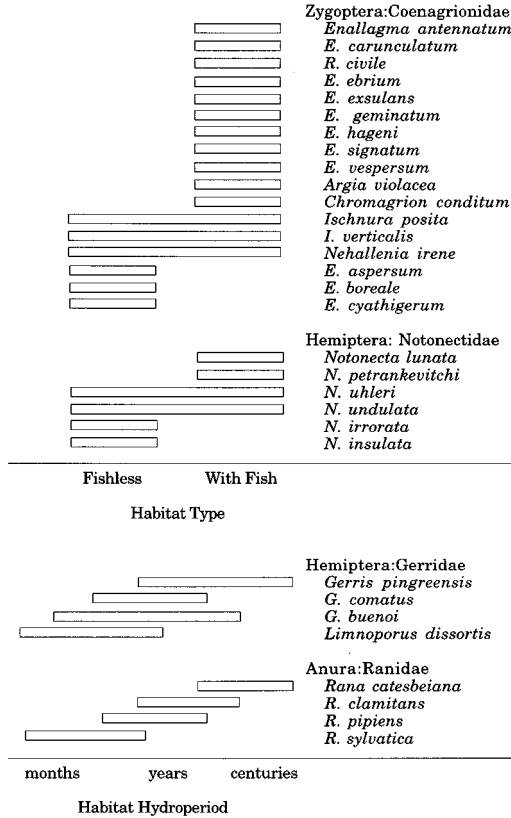and life history, and only those species able to deal with drying are successful

Figure 1 Distribution ranges of Zygoptera (95) and Notonecta (27) across habitats with and with-
out predatory fish, and Hemiptera (157) and Anura (23) across habitats that differ in hydroperiod.
Genera and families are distributed across a broad region of the gradient, but individual species are
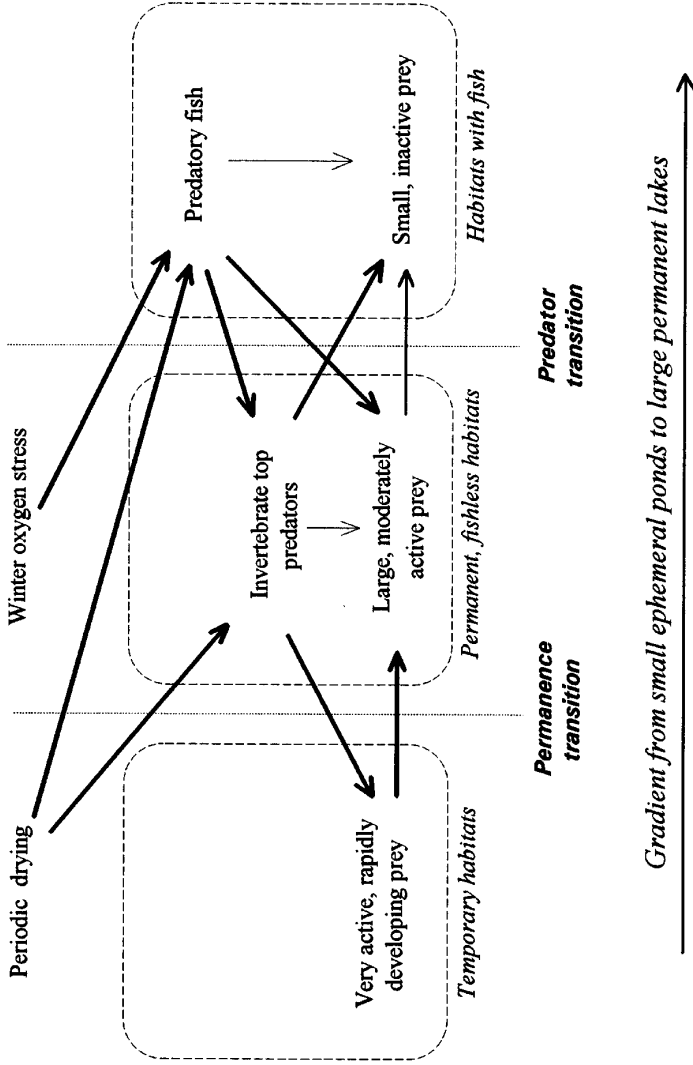often restricted to a narrow region.

Figure 2 A schematic model of mechanisms generating community structure along the freshwater habitat gradient. Arrows indicate direction of negative effects. Bold arrows indicate very strong effects that act to constrain the distribution of affected species. Thinner arrows indicate weaker trophic interactions that do not prevent coexistence of interacting species. Strong interactions resulting primarily from predation cause distinct transitions in community structure along the gradient. One major transition, the permanence transition, occurs between temporary habitats that contain few predators and permanent habitats that contain significant invertebrate predators. A second major transition in community structure on the gradient, the predator transition, occurs between permanent fishless and fish-containing habitats. Mechanisms causing differential interaction strengths and the critical phenotypic tradeoffs of individuals that mediate species and community transitions along the gradient are described in the text.

in these habitats (196). Importantly, this constraint prevents colonization by many key predators found elsewhere on the gradient because fish and important predatory invertebrates such as dragonfly larvae are highly susceptible to pond drying. Temporary pond habitats thus often contain fewer predators than do more permanent habitats (149, 208). In shallow permanent ponds, physical stresses such as low oxygen levels during periods of ice cover can impose heavy mortality on fish (28, 127, 177). Thus well-developed fish communities are often restricted to relatively deep permanent habitats (177).

While species-specific tolerances to physical factors determine the pool of species potentially able to exist in any habitat, biotic interactions determine the actual species composition of each community. Strong negative interactions, through either predation or competition, may prevent survival of affected populations, and thus restrict the distribution of these species to a narrow range of the gradient (10, 17, 95, 184). Weaker negative interactions may limit a population's density but do not cause the population to be eliminated (172, 189). It is the relative strengths of biotic interactions, under the backdrop of physical constraints, that shape community structure on the gradient.

This interplay of physical and biotic factors along the gradient tends to produce distinct, alternative community types (delineated by boxes in Figure 2), determined largely by hydroperiod and the key predators (if any) able to survive in the habitat. Temporary habitats are characterized by very active and rapidly developing species and few predators (149, 208). Permanent but fishless habitats have communities composed of large predatory invertebrates, such as larval dragonflies and pelagic Diptera, and large, moderately active prey species (95, 186, 212). In permanent habitats that contain fish, fish are often key predators, and animal species at lower trophic levels are small-bodied (186, 212) and inactive (96, 165). Between these community types are distinct transitions in community structure. We refer to the transition between temporary habitats and permanent fishless habitats as the permanence transition and the transition between permanent fishless habitats and habitats with fish as the predator transition. These transitions and the alternative community types they form arise on the gradient because strong interactions across transitions lead to selective elimination of species, while weaker interactions within community types do not.

To be sure, the model presents an idealized and highly simplified view of the habitat gradient, and numerous additional complexities and mitigating factors are certainly important. Nonetheless, we believe the model captures essential features of an important and prominent pattern among aquatic systems. This perspective on the structure of freshwater habitats is not new (145, 208, 212). Our goal here is to emphasize the insights gained by evaluating species

distributions and community structure in light of the effects of individual traits and key fitness tradeoffs expressed along the habitat gradient.

THE PERMANENCE GRADIENT

In this section we consider ponds that range from extremely temporary through those that may be permanent for years at a time, but which do not contain fish. Within these habitats, what factors determine the shape and limits of a species' distribution? We argue that both pond hydroperiod and predation are prevalent influences with important consequences for a species' distributional pattern that may be understood through a mechanistic analysis of key phenotypic traits.

Permanence and Developmental Rate

Temporary waters have often been considered distinct from permanent ponds (196, 200). Much of the early literature on temporary pond fauna was concerned with the question of survival in an ephemeral aquatic environment (7, 9, 51, 74, 138, 196). This focus on the adaptations to life in temporary ponds is understandable. The existence of a dry phase presents an obvious challenge to any "aquatic" animal. The persistence of these organisms requires that they survive the dry period in situ, migrate to other aquatic habitats, undergo a transition to a terrestrial phase, or recolonize following extinction. All of these strategies are found among temporary pond fauna (196, 200).

While there is a great variety of particular adaptations to ephemeral ponds, most resident species persist by reaching some critical developmental stage prior to pond drying (51, 200). Examples include holometabolous and hemimetabolous insects and amphibians that undergo metamorphosis into a terrestrial form. In addition, many invertebrates (e.g. cladocera, clam shrimp, copepods, fairy shrimp, mayflies, seed shrimp, tadpole shrimp) must reach adulthood and then produce encysted eggs that can endure the dry phase within the pond basin (200). For these groups, hydroperiod represents a maximum limit on development time. That this limit is frequently an active constraint on the performance and distribution of freshwater organisms is suggested by numerous reports of catastrophic mortality (34, 67, 108, 116, 131, 142, 170) and even local extinction (23, 67) associated with pond drying events. Experiments directed at the role of hydroperiod have been of two primary types. A number of artificial pond experiments have been conducted in which hydroperiod is imposed as a treatment (e.g. 136, 141, 197). In addition, several experiments have transplanted species among natural ponds that vary in permanence (92, 149, 153, 154). Together, these studies provide evidence that drying-associated mortality is often high and is correlated with developmental rate of the species.

In order to succeed in the most temporary aquatic environments, developmental rates must be phenomenal. A seed shrimp (Conchostroca) of the Saharan Desert is able to achieve maturity within just five days after pond filling (138). Spadefoot toads (*Scaphiopus couchii*) of the southwestern deserts of the United States can reach metamorphosis in just 10 days after hatching (176). In more permanent environments, the restriction on developmental rates is relaxed. North American frogs, for instance, have larval periods that range up to three years in length (209). Studies of tadpole distributions show that species with longer larval periods tend to be found in more permanent ponds (23, 32, 149, 154). As hydroperiod increases, so does the potential species pool. Correspondingly, a number of studies have noted correlations between permanence and species richness (36, 89, 111, 116, 211). While the total number of species might increase with permanence, there is also significant turnover in species composition. Most species that live in temporary ponds are absent from permanent ponds (23, 196). This pattern suggests that some factor, or suite of factors, can often prevent species from occupying habitats that are apparently suitable given developmental constraints.

Predation and Permanence

While there are many possible reasons why a species may be restricted from living in more permanent habitats than those it occupies (see caveats below), predation may be the most widespread. Predatory species are often entirely absent within the most temporary habitats (91, 139, 153) and are typically numerous and diverse within permanent fishless ponds (151). Along the intervening portion of the gradient, several studies have shown that the identity, density, and size distribution of predators changes with even small differences in permanence (41, 59, 67, 74, 80, 151, 153, 154, 208). For example, Woodward (208) reported an approximately fourfold increase in aquatic predator density in permanent versus temporary desert ponds in New Mexico. Similar trends have been found among Michigan ponds where predator density triples between annual temporary ponds and permanent ponds (149, 151). In these permanent ponds, average body lengths of predatory salamander, beetle larvae, and dragonfly larvae were longer by 100%, 36%, and 46%, respectively, than those of their counterparts in temporary ponds (151).

The association between permanence and predator distribution suggests that predation could be an important means by which prey distribution becomes limited in more permanent environments. Species may experience a refuge within more temporary ponds where they are relatively invulnerable to resident predators (68, 156). Indeed, many nonfish predators have strong effects on prey abundance (15, 44, 76, 199, 204). However, other studies from a range of habitats also suggest that aquatic predators can have little or no effect on prey

abundance (71, 166). Because the influence of a given predator is known to vary substantially among prey species (e.g. 198), evaluation of predator limitation requires comparing prey susceptibility to predation at multiple points along the permanence gradient. While these more directed analyses are relatively few, they uniformly suggest that predation has greater effects on prey survivorship in larger and more permanent habitats (115, 135, 149, 153, 154) and can lead to elimination of prey species (153).

Permanence, Predation, and Mechanistic Tradeoffs

Thus far we have argued that the negative effects of pond hydroperiod and predation are important and widespread. Because predator distributions are also limited by hydroperiod, these factors covary inversely. A generalist strategy would require mastering the very different situations imposed by predator-free temporary environments as well as permanent environments where numerous and diverse predators are found. The rarity of true generalists in these habitats (see below) suggests that restricted distributions may have some mechanistic basis.

Behavior may form the foundation of an important tradeoff for many aquatic taxa. Put simply, many animals must move to forage, but moving can also increase the likelihood of being detected by movement-oriented predators (82, 85, 145, 193, 208). Experiments substantiate that movement (or activity) is correlated with acquisition of food as well as both growth and developmental rates (147, 149, 152). Both interspecific comparisons and intraspecific manipulation of activity show that more active individuals are also at greater risk of predation (4, 21, 72, 148). Additionally, studies of diet preference show that activity is a strong predictor of relative risk of potential prey in aquatic environments (12, 84, 146).

If activity is a critical trait for assortment among aquatic habitats, then species from different regions of the habitat gradient should differ in activity. As expected, larval amphibians (82, 149, 154, 195, 208) and insects (27) from more temporary ponds tend to have higher activity levels than do their counterparts from permanent habitats. Where these comparisons have been coupled with field transplants across the permanence gradient, studies have demonstrated a strong association between phenotype and performance (149, 154).

Other Mechanisms and Some Caveats

Mechanistic approaches to the study of temporary pond communities are relatively new (154). More substantial evidence exists for the roles of activity and other traits in contributing to patterns of distribution in fish-containing versus fishless habitats (see below). In addition, information on temporary pond communities has a strong taxonomic bias. Most studies of distributional

mechanisms in temporary ponds have been conducted using larval amphibians. We know far less about the relationships among phenotype, performance, and distribution for the invertebrates in these habitats. Even if research on these other taxa also finds that activity is an important trait, there are other important mechanisms that can lead to restriction of a species distribution. Some species require drying or water level fluctuation as a physiological trigger for the initiation of embryonic development (51, 118). Many other species are sessile and not subject to activity tradeoffs. For these and other species for which movement is not related to risk, different traits may underlie patterns of distribution. For example, allocation of resources among morphological defense, development, and reproduction may provide critical axes for the sorting of groups such as snails among ponds that vary in permanence (19, 86). Specialization on food resources available in ponds of different permanence could be important for some taxa (1, 11).

Finally, interspecific competition has often been advanced to explain distributional patterns along the permanence gradient (e.g. 18, 37). There is strong evidence that interspecific competition can have severe effects, including competitive exclusion, in artificial pond experiments (e.g. 102, 104, 197, 198). While competition may have similar effects on distributional patterns in the field, relatively few experimental analyses have been conducted in natural environments. From these it appears that although competition can lead to species exclusion in some cases (91, 113, 205), it often has relatively small effects on survivorship, growth, and reproduction in other cases (86, 149, 150, 154, 195).

THE PREDATOR TRANSITION

That strong predator-prey interactions across the predator transition act as a sieve for community organization (Figure 2) is apparent when one compares studies that manipulate predator density within a single community type, where relatively weak interactions are expected, to studies that introduce a predator into a community type that does not normally contain that predator, a manipulation expected to produce pronounced changes in community composition (172, 190). When introduced into a previously fishless habitat, fish precipitate major changes in the community by substantially reducing the density of some prey species, sometimes to the point of local extinction (17, 30, 47, 57, 101, 124, 195). Similar conclusions are drawn from studies comparing the fauna of fishless and fish-containing habitats (27, 55, 95, 123, 163, 184). In contrast, manipulations of fish density in habitats normally containing fish often produce only minor changes in prey density (14, 43, 58, 173, 174, 190). Some studies of this sort have indicated more substantial effects of predatory fish (100, 103); however, only prey abundance, not species composition, is affected

in these studies. Similarly, when predatory invertebrates normally found only in fishless habitats are introduced into fish habitats (with fish excluded), these predators cause substantial reductions in prey density (95, 132, 179) and elimination of some taxa (179). Predatory invertebrates may have weaker effects, however, in their native fishless habitats (95).

To briefly illustrate the degree of change in community structure across the predator transition, we used published surveys to calculate average community similarity [using species relative abundance and an index of overlap (140)] between the two community types relative to the average similarity within community types. For Brooks & Dodson's (17) classic study of zooplankton in New England lakes with and without zooplanktivorous fish, community similarity of habitats across the predator transition was only 16% of that observed among habitats of the same lake type. Furthermore, 47% of the species sampled exhibited complete segregation by lake type. Similar patterns are seen in littoral communities. McPeek (95) sampled the larval odonate fauna of three fishless and three fish-containing lakes in Michigan. For *Enallagma* damselflies, a diverse group that constituted the majority of damselflies in the lakes, all seven species exhibited complete segregation by lake type (Figure 1). For larval dragonflies, community similarity of habitats across the predator transition was 57% of that observed among habitats of the same lake type. This comparatively high value is due to the presence of a single common species that is ubiquitous among lakes and does not reflect a general lack of habitat segregation among dragonflies in these lakes. In fact, of the eight species that occurred in more than one lake, four occurred in only one lake type.

The substantial changes in species composition that are observed across the predator transition arise because interactions between species from similar community types are weaker than those between species from different community types. For predator-prey interactions, interaction strengths are determined by the coupled effects of predator traits that determine foraging characteristics and prey traits that determine susceptibility. Thus, elucidation of mechanisms underlying changes in community structure across the transition requires an understanding of these predator and prey qualities.

Foraging Characteristics of Predators

Changes in community composition observed across the transition occur primarily because foraging characteristics of predatory fish and invertebrates are qualitatively different, and thus favorable prey defense attributes in one community type are generally unfavorable in another community type.

SIZE-BIASED PREDATION   Predatory fish and invertebrates often differ in the size of prey items consumed. Most fish disproportionately consume larger

individuals across the range of prey sizes that they are physically able to ingest (33, 49, 95, 99, 103, 107, 186, 212). In part, size selectivity may be a behavioral adaptation to maximize foraging gain (99, 194). Additionally, because fish are generally much larger than their invertebrate prey, only a few large prey species are able to grow to an invulnerable size (161). Thus the coupled effects of fish selectivity and their comparatively large size lead to the general trend of greatest predatory effect on larger prey species. In contrast to fish, predatory inverte-brates exhibit less size bias in prey consumption, generally consuming all prey within the range of prey sizes that they can capture and handle (2, 117, 126, 167, 171, 186). Predatory invertebrates typically have a disproportionate impact on small-bodied prey, however, because functional constraints often limit the abil-ity of these predators to consume larger prey. Additionally, because of the sim-ilarity in size to their invertebrate predators, many prey species may grow large enough to become invulnerable to invertebrate predation (178, 186, 203, 207).

MECHANISMS OF PREY DETECTION   Most fish species that have strong impacts in these habitats rely on vision for prey detection (54). Predatory invertebrates, in contrast, primarily use tactile cues to detect prey (117), although some may use a combination of visual and tactile cues (112). An important result of this difference in detection mechanisms is that fish can detect prey from a greater distance than can invertebrates (210, and see 95). Additionally, although both fish and invertebrates detect moving prey more easily than stationary prey (40, 54, 65, 125, 210), the acute vision of fish may enable them to detect less conspicuous prey motion than do predatory invertebrates.

SEARCH MODES   Predatory fish and invertebrates also tend to differ in search mode. Fish actively search for prey over a comparatively broad spatial area (39, 54, 65). Predatory invertebrates, in contrast, often employ a passive ambush, or "sit-and-wait," foraging mode in which they remain motionless and capture prey that come near them (117). The ambush foraging mode of predatory inver-tebrates greatly limits the area over which each predator forages and produces relatively low encounter rates with prey. Some predatory invertebrates do ac-tively stalk prey, but these are usually limited to slow movements along a plant stem or other substrate (96).

PURSUIT SPEED   While some predatory invertebrates are able to swim (e.g. dragonfly larvae and some beetle larvae), the pursuit speed of fish is greater than any typical predatory invertebrate. This disparity implies that while inver-tebrate prey may sometimes be able to escape from predatory invertebrates by swimming, the prey would have little chance of swimming away from a fish (96).

Traits of Prey that Influence Susceptibility to Predation

The contrasting foraging modes of predators imply that prey with traits that allow them to coexist with predators in one community type will fare poorly with predators in the alternative community type. Some key traits of prey that seem to underlie turnover on the gradient have been identified in several taxa.

BEHAVIOR   Prey activity may be the most important trait shaping changes in species composition across the predator transition. Higher activity levels increase encounter rates with predators and enhance a predator's ability to detect prey. Furthermore, because prey movement is usually for foraging, locating mates, or other essential activities, prey can not remain inactive, and thus are forced to strike an appropriate balance between the benefits and risks associated with activity (63, 144, 193). For most freshwater invertebrate species, the resolution of this tradeoff will involve lower activity levels in species that coexist with fish than in species coexisting with invertebrate top predators in fishless habitats (13, 26, 29, 70, 77, 96, 111, 165) because of the greater mortality risk associated with activity in the presence of fish (13, 26, 27, 56, 70, 77, 96).

The importance of the tradeoff between activity and risk in shaping the distribution of species across the predator transition seems especially strong for predatory invertebrates. For example, larvae of the dragonfly *Anax junius*, important top predators in many fishless habitats (95, 77, 132), are very active when foraging, a trait probably contributing to their success in fishless habitats (77). *Anax*, however, are thereby highly susceptible to fish predation (30, 77, 195), sufficiently so that they are excluded from habitats with predatory fish (30, 77, 95, 195). Similarly, the activity patterns of *Enallagma* damselfly larvae, intermediate level predators in freshwater communities, contribute substantially to their habitat distribution over the gradient (13, 96, 121). Species that coexist with fish are less active than those that face only predatory invertebrates (13, 96).

Besides general activity level, other behaviors contribute to changes in species composition over the predator transition. Both the encounter response (56, 96) and the use of protective microhabitats (8, 77, 120, 121, 137, 162, 189) are important in some taxa. For example, Pierce (120) examined microhabitat use and vulnerability to fish predation of larval dragonflies from fish-containing and fishless habitats. A species found commonly in fishless habitats often used exposed microhabitats, even in the presence of fish, while two related species that are abundant in habitats with fish overwhelmingly used habitats offering cover when fish were present. Accordingly, the species from the fishless habitat was more vulnerable to fish predation than the species native to the fish-containing habitat (120).

LIFE HISTORIES   Tradeoffs in prey life histories across the predator transition
may contribute to patterns of species turnover, especially for species that com-
plete their entire life cycle in the aquatic environment (46, 78, 88, 186, 206).
A fundamental life history trait that shapes species' success over the gradient
is the pattern of reproductive allocation over ontogeny (186, 188). For size-
structured populations, the optimal resolution of the tradeoff between allocation
of resources to growth versus reproduction over ontogeny will be strongly in-
fluenced by the ontogenetic pattern of mortality experienced by the population
(81, 186–188). Thus the differences between fish-containing and fishless habi-
tats in the form of size-biased predation may restrict prey species to habitats for
which their life histories are appropriate. For example, differences in reproduc-
tive allocation patterns between species of a littoral amphipod, *Hyalella,* appear
to be the primary determinant of species segregation between fish-containing
and fishless habitats (186). Predators in these two habitats impose qualitatively
different regimes of size-specific predation mortality on *Hyalella,* a difference
manifest in the overall mortality schedules of the amphipods in the two habi-
tats (186). Whereas mortality increases with body size in the fish-containing
habitat, it declines with size in the fishless habitat. *Hyalella* in lakes with fish
initiate reproduction at a smaller body size and have a greater size-specific re-
productive effort than do *Hyalella* from habitats with large dragonfly predators.
Thus, in the habitat where larger individuals are more susceptible to predators,
Hyalella shifts reproduction to smaller sizes, but in the habitat where smaller in-
dividuals are more susceptible, *Hyalella* shifts reproductive allocation to larger
size classes, thus allowing rapid growth through the most vulnerable size range
(186).

MORPHOLOGY   For many species, especially those occupying open water, the
most important morphological feature affecting their relative success across the
predator transition is body size (212), although other traits may also play a role
in some groups (52, 98). In habitats with fish, where larger individuals are most
vulnerable to predation, small-bodied prey species are most successful (64, 83,
122, 128, 160, 183, 186, 188). In fishless habitats, where smaller individuals
are disproportionately vulnerable to predation, large-bodied prey species are
most successful (50, 131, 183, 184, 186).

In summary, the contrasting modes of predation by major predators in fishless
and fish-containing habitats appear to be the primary cause underlying the de-
velopment of alternative community types across the predator transition. Prey
traits effective at mitigating risk of predation in one community type unavoid-
ably produce inimical effects in the alternative community type. Specifically,
the relatively large body size, high activity levels, and conspicuous microhabitat

use of prey that allow them to be successful in fishless habitats also make them highly conspicuous to predatory fish. Conversely, the relatively small body size, reduced activity, and cryptic behavior of those prey species that are successful in fish-containing habitats make them vulnerable to the invertebrate top predators found in fishless habitats.

Competition

Competitive effects may play some role in the segregation of species across the transition (105, 155, 180), but these effects are less important than predation (3, 95, 121, 179). Although early work in this system proposed that interspecific competition with larger-bodied zooplankton was the primary vehicle by which small-bodied zooplankton species were excluded from fishless habitats (17, 48), subsequent empirical studies demonstrated that predation by size-selective predatory invertebrates was often the principal cause of exclusion of these species (35, 179, 212). Although this dichotomous view of the effects of predation and competition is overly simplistic, since the two may work interactively to shape patterns of species success over the gradient (192), predation is clearly the major factor driving community changes over the predator transition.

SPECIALIZATION AND PHENOTYPIC PLASTICITY

Many aquatic species are habitat specialists, occurring in only one region of the gradient. That specialization is common on the gradient is perhaps to be expected since circumstances favoring the evolution of specialization (42, 60, 61) are common across much of the gradient. Specialization is especially likely to evolve (*a*) in spatially heterogeneous but temporally predictable environments, (*b*) when individuals face fitness tradeoffs associated with occupying different habitat types, and (*c*) when hard selection (e.g. strong mortality selection from predators and physical environmental factors) predominates. These qualities, common for permanent ponds and lakes, may foster the evolution of specialization in species occupying these habitats. Temporary ponds, however, often exhibit temporal changes in species composition caused by high variation in hydroperiod. Alternate wetter or drier years can alter species composition of habitats as "permanent pond taxa" spread out across the landscape during wet periods, only to "retreat" with the next dry period (67). Specialization is less likely to develop in species occupying these temporally heterogeneous habitats (60).

Holt (60, 61) has stressed the potential importance of habitat selection in the evolution of specialization. Habitat selection can limit the scope of natural selection on a population because only agents of selection operating within

the preferred habitat can guide evolutionary change in the population. This effect can lead to a self-reinforcing evolutionary process when individuals face fitness tradeoffs between habitat types (60). Habitat selection causes ever more precise adaptation to one habitat type (and consequently reduced performance in alternative habitat types), and this habitat specialization in turn favors ever greater proficiency for selecting the most appropriate habitat type. Many aquatic taxa have highly mobile terrestrial (amphibians) or aerial (insects) adult stages, and thus they have potential for selecting appropriate habitats along the gradient (73, 129, 130). Natal philopatry may also reinforce specialization, even in species unable to discriminate between habitats containing different community types (93).

Many freshwater species alter activity (26, 33, 53, 66, 69, 96, 143, 162, 201), microhabitat use (120, 121, 137, 163), morphology (52, 119), and life history (31, 62, 87, 109, 164, 168, 184, 185) in response to predators. For many aquatic prey species, such phenotypic plasticity appears to function as a mechanism for dealing with spatial or temporal variation in predator density within a single habitat type rather than as a mechanism allowing broader distribution across the habitat gradient. Thus, many species exhibiting plasticity in behavioral or other traits in response to predators are specialist species that occur in only one habitat type. For example, *Enallagma* damselfly species that occur only in fish-containing habitats and those species that occur only in fishless habitats respond to the predators with which they coexist by altering their behavior in ways that reduce predation risk (13, 96, 121). They do not respond appropriately, however, to predators with which they do not coexist (96). Thus, predator-mediated plasticity in *Enallagma* does not allow a broader distribution on the gradient.

Although phenotypic plasticity may often be of little importance in allowing species to maintain a broad distribution on the habitat gradient, it is probably of substantial importance in the success of species within a habitat type. Because the ability to deal with predation risk entails substantial fitness tradeoffs (193), species that facultatively alter their phenotype in response to changes in the immediate threat of predation can partially mitigate detrimental effects of these tradeoffs (145). Since this topic has been reviewed elsewhere (85, 145, 193), we will simply stress here that the prevalence of plasticity in response to predators among taxonomically diverse freshwater organisms underscores the considerable importance of these tradeoffs in this system.

For some species phenotypic plasticity does appear to facilitate a broader distribution on the gradient under some environmental conditions, but restricted breadth of reaction norms seems to limit the conditions under which a broader distribution might occur. For example, although their distributions may overlap, larval chorus frogs (*Pseudacris triseriata*) are most successful in more

temporary habitats with few predators, and larval spring peepers (*P. crucifer*) are most successful in more permanent habitats with predatory invertebrates; differential susceptibility to predation contributes importantly to this pattern (149). Both species facultatively respond to the presence of an invertebrate predator by reducing activity, but chorus frogs do not reduce activity to levels observed for spring peepers (149). This limit to the breadth of their reaction norm probably explains the low survival of chorus frogs in habitats with predatory invertebrates (149).

ADAPTATION AND SPECIATION ON THE HABITAT GRADIENT

The lentic freshwater habitat gradient presents a potentially potent template for evolutionary change and diversification in freshwater taxa (79, 97). Both the substantial heterogeneity among lentic habitats in critical selective agents and the inherent insularity of these habitats may drive adaptation and foster speciation. Relatively few studies, however, have explicitly examined evolutionary processes mediated by the key ecological agents shaping the habitat gradient, though many have interpreted species or population comparisons in adaptive terms.

Size-biased predation is one potentially important evolutionary agent that has been studied in some detail. Size-biased mortality will produce an evolutionary response in populations if heritable phenotypic variation in body size or associated life history traits exists in populations. At least moderate levels of heritability are common for a broad range of traits and taxa (134), and for morphological and life history traits of aquatic taxa specifically (169). These observations imply that an evolutionary response to size-biased predation may be common in aquatic prey populations, a conclusion supported by several studies. For example, natural (158) or simulated (38) size-biased predation on cladoceran zooplankton species cultured in the laboratory does produce adaptive change in body size and life history traits. Similarly, a natural population of *Daphnia galeata mendotae* (169) that experiences strong predation by fish displayed a genetically based reduction in mean body size and size at maturity over time, a response consistent with the form of size-biased predation experienced by the population.

For species distributed across major transitions on the habitat gradient, local adaptation may be an important source of differentiation among populations (20, 45). For example, Spitze (159) found genetic differentiation in body size among *Daphnia obtusa* populations. He suggested that variation among populations in predation regime is the likely cause of the divergence. Also, Neill (106) found

genetic differentiation in vertical migration patterns between two neighboring populations of a calanoid copepod, each of which appears to be locally adapted to deal with the form of size-specific predation it experiences.

Macroevolutionary diversification in aquatic taxa may occur in the context of the freshwater habitat gradient through the mechanism of evolutionary habitat shifts (98). This mechanism is a form of peripheral isolates speciation (16) in which a small founder population of a species normally found in one habitat type may sometimes disperse to an alternative habitat type. Rarely, these dispersing individuals might establish a population that persists long enough to adapt to local conditions. Speciation may be promoted by both the potential for rapid genetic change in small founder populations (5) and factors impeding backcrossing with ancestral populations, such as assortitive mating, natal habitat philopatry, and low dispersal rates due to the inherent insularity of ponds and lakes. Although historical evidence for this mechanism is sketchy, many closely related species do segregate on the gradient (Table 1, Figure 1), indicating that phylogenetic inertia need not constrain a lineage to one habitat type and that habitat shifts may occur across a wide range of freshwater taxa. The potential importance of evolutionary habitat shifts in fostering diversification can best be evaluated through phylogenetic techniques (16, 97, 98). Phylogenetic analysis of *Enallagma* damselflies suggests that coexistence with fish is the ancestral condition in the genus, and that species have independently invaded fishless habitats containing large dragonfly predators at least twice (97), indicating that habitat shifts have occurred in this group and may contribute to the high species diversity of the genus. More studies using phylogenetics are needed before we can draw general conclusions concerning the role of the habitat gradient in shaping lineage diversification.

Besides shedding light on historical patterns of diversification and speciation mechanisms, phylogenetic methods can also serve as a valuable tool for identifying causal ecological agents driving adaptive evolution and for identifying those phenotypic traits responsible for species success (16). Again, *Enallagma* damselflies are illustrative on this point. Through convergence, species invading fishless habitats have evolved robust abdomens and large caudal gills (97), characteristics that allow these species to evade predatory dragonflies (98).

CONCLUSION

As pointed out by Connell (25), if an assemblage of species is to be regarded as possessing organization or structure, it is the form and strengths of interactions among the species that must produce that structure. We would further suggest that it is the traits of individuals that determine the form and strengths of species interactions and thus ultimately produce structure at the level of the community.

Gradient studies greatly facilitate our ability to detect the ways in which individual traits give rise to community structure. On the freshwater habitat gradient, transitions in community structure are best understood in terms of critical fitness tradeoffs that limit species distributions along the gradient. This perspective would not emerge, however, if each habitat type were examined in isolation. For example, examining the influence of fish predation on littoral invertebrate communities of fish-containing lakes might lead to the conclusion that predation often has little effect on these communities. While this conclusion would often be correct within the context of this single habitat type, the broader perspective gained by the gradient approach would reveal the fundamental role of predation in organizing the community by limiting community membership to only a subset of potential species. Indeed, the permanent removal of fish from such habitats would likely result in wholesale changes in community structure (10). Moreover, evaluating the functional basis of differential species success across community types elucidates the mechanisms by which individual traits create community structure. Finally, these same ecological mechanisms may serve as important evolutionary agents of selection for aquatic taxa, driving adaptive evolution and forming a template for lineage diversification (97, 98).

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