Trophic Relations and Ontogenetic Niche Shifts in Aquatic Ecosystems

G. G. MITTELBACH, C. W. OSENBERG and M. A. LEIBOLD

1 Introduction

One of the most pronounced and consistent patterns in freshwater lakes is that the biomasses of producers and consumers increase along a gradient of increased nutrient (phosphorous) loading. For example, phytoplankton biomass is positively correlated with total phosphorus concentration (Stockner and Shortreed 1985 and references therein), as is the biomass of zooplankton (Hanson and Peters 1984; Pace 1984), and fish (Hanson and Leggett 1982). Given that the biomass of aquatic producers, herbivores, and carnivores each positively covaries with phosphorus loading, the abundances of adjacent trophic levels should also be positively correlated across productivity gradients. Indeed, such positive correlations between consumers and their resources are common; i.e., zooplankton biomass is positively correlated with phytoplankton biomass (references in McQueen et al. 1986), plantivore density is positively related to zooplankton biomass (Mills and Shiavone 1982), and fish density positively covaries with macrobenthos biomass (Hanson and Leggett 1982; Nakashima and Leggett 1975).

Aquatic ecologists are well aware of the above patterns, indeed, they are often cited as support for the view that aquatic communities are regulated from the “bottom-up” by nutrient input (see McQueen et al. 1986 for discussion). In this paper, we suggest that most models of exploitative trophic-level interactions in fact do not predict the above patterns. We than discuss some ways in which simple equilibrium models may be modified to account for these patterns. In particular, we discuss how the inclusion of population size (or age) structure and a separation in resource use between size (or age) classes, provides a simple mechanism to generate positive correlations between consumer and resource densities across a productivity gradient. We illustrate this result using a simple population model containing two life stages. In addition, we provide data for two species of sunfishes (Centrarchidae) in a series of Michigan lakes, supporting predictions of the model.

2 A Theoretical Perspective

The equilibrium abundance of organisms at each trophic level represents a balance between mortality rates (in part, a function of predator densities) and

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Fig. 1. Relationships between equilibrium biomass (standing stock) at various trophic levels (e.g., phytoplankton, zooplankton, planktivores, piscivores) and potential primary productivity ($G$), e.g., phosphorus loading. Relationships are based on the model in Oksanen et al. (1981), which assumes that increases in potential primary productivity permit the addition of higher trophic levels (denoted by $TL$ in the figure). Potential discontinuities and instabilities in the transition regions between trophic states along the productivity axis are ignored in this simplified presentation (see Oksanen et al. 1981 for details). Two potential responses are shown for phytoplankton, depending on the functional response of the planktivores (see text for details).

Birth rates (in part, a function of resource densities). Determining how birth and mortality rates equilibrate to set the abundances of organisms at various trophic levels, therefore, requires a theory of biological exploitation among a number of trophic levels. There have been a few notable attempts to build such a theory (Rosenzweig and MacArthur 1963; Smith 1969; Rosenzweig 1973, 1977; Wollkind 1976; Wiegert 1977; Oksanen et al. 1981), although many of these studies have concentrated on the question of system stability rather than species abundance. The model of Oksanen et al. (1981) provides the most thorough look at how the equilibrium biomasses of several different trophic levels should change across a gradient in potential primary productivity (i.e., nutrient loading). One interesting result of Oksanen et al.'s model is that it predicts no correlation between the equilibrium biomasses of consumers and resources within a given trophic structure.

In Fig. 1, we have drawn the predicted relationships between equilibrium biomass (standing stock) at various trophic levels (e.g., phytoplankton, zooplankton, planktivores, and piscivores) and potential primary productivity ($G$), e.g., phosphorus loading. The relationships are based on the model in Oksanen et al. (1981), which assumes that increases in potential primary productivity permit the addition of higher trophic levels. In their model, mortality on the highest existing trophic level is assumed constant and density-independent. For a one-trophic level system (containing only phytoplankton), any increase in $G$ results in an increase in phytoplankton biomass. In a two-trophic level system (containing only phytoplankton and zooplankton), increases in $G$ translate into increases in zooplankton biomass and no change in phytoplankton biomass. This constancy in phytoplankton biomass is due to the fact that per-capita mortality on zooplankton (the top trophic level in this case) is assumed constant and density-independent. A con-
stant per-capita mortality rate implies a constant per-capita birth rate at equilibrium. Thus, the biomass of the zooplankton’s resource (phytoplankton) should remain constant across the productivity gradient in a two-trophic level system (see Oksanen et al. 1981 for details). By the same argument, for three trophic levels (phytoplankton, zooplankton, and planktivores), increases in potential productivity (G) lead to an increase in the biomass of planktivores and phytoplankton, but no change in zooplankton biomass. Finally, in a four-trophic level system (containing phytoplankton, zooplankton, planktivores and piscivores), increases in G result in an increase in the biomass of piscivores and zooplankton, no change in planktivore biomass, and no change or a decrease in the biomass of phytoplankton. A decrease in phytoplankton biomass in the four-trophic level system is expected if the planktivore has a Holling type II functional response (as in Oksanen et al. 1981); i.e., for a given density of planktivores the per-capita mortality rate of the zooplankton decreases as the density of zooplankton increases. In this case, although planktivore density is constant, the increase in zooplankton abundance leads to a decreasing per-capita mortality rate of the zooplankton; therefore, the abundance of phytoplankton should decrease. If a type I functional response is assumed (per capita mortality is independent of prey density), then the phytoplankton density remains constant.

From Fig. 1, we see that within a given trophic structure (i.e., holding the number of trophic levels constant), there should be no correlation between the biomass of a consumer and its resource. However, the nearly ubiquitous pattern in aquatic systems is that the biomasses of consumers and resources positively covary across a gradient in nutrient input. Therefore, we are left with something of a paradox. An inspection of Fig. 1 suggests one simple resolution to this problem. If lake surveys documenting a positive correlation between trophic level biomass and nutrient loading include lakes with different numbers of trophic levels, then we would expect to see a general increase in the biomass at each trophic level with an increase in nutrient loading. However, in the one study reporting the number of trophic levels contained in each lake surveyed (Mills and Schiavone 1982), positive correlations between consumers and resources were observed across lakes that each contained four trophic levels. Furthermore, empirical analyses of food webs by Pimm (1982) and by Briand and Cohen (1987) show no relationship between productivity and the number of trophic levels in either terrestrial or aquatic ecosystems. Thus, we are skeptical that the general pattern of increased trophic level biomass with increased nutrient loading is simply a consequence of surveying a series of lakes with varying numbers of trophic levels.

Using conventional predator-prey isocline analyses (Rosenzweig and MacArthur 1963; Rosenzweig 1971), we can examine the general conditions necessary for a positive correlation between consumer and resource densities over productivity gradients, when the number of trophic levels remains constant. In standard consumer-resource models, the consumer isocline is perpendicular to the resource axis (Fig. 2a). As resource productivity increases (which elevates the resource isocline but does not affect the consumer isocline), the equilibrium abundance of the consumer increases (C* to C*), but the equilibrium abundance of the resource remains constant (R* = R*). In order to produce a positive response of both trophic levels to the increased productivity, the consumer isocline must bend
away from the consumer axis as consumer density increases (Fig. 2b). A bent consumer isocline occurs when there is density dependence in the mortality or the energetic requirements of the consumers. These density-dependent effects are absent in Oksanen et al.’s model and their model does not predict positive correlations between consumers and resources. Furthermore, while Fig. 2 shows only two trophic levels, the density-dependence experienced by the consumer population in Fig. 2 cascades down the food web. If all predators exhibit type I functional responses (i.e., per-capita prey mortality is independent of prey density), then the equilibrium abundances of all trophic levels will be positively correlated. If, however, the functional responses are nonlinear (e.g., type II), then the signs of the resulting correlations at lower trophic levels will depend on the relative effects of the predator’s numerical and functional responses on the prey’s per-capita mortality rates.

We can now ask: what are some of the mechanisms that can cause density-dependent increases in consumer mortality or energetic requirements? One factor that can increase consumer mortality is an increase in the equilibrium density of the consumer’s predator. However, postulating an increase in the equilibrium density of a consumer’s predator with an increase in the equilibrium density of the consumer simply shifts the problem up a trophic level without really resolving it. Again, we have to ask what allows the densities of the consumer and its predator to positively covary with increased productivity. Another factor that can produce density-dependent consumer mortality or energetic requirements is direct interference among the consumers (Wollkind 1976). Thus, in aquatic systems, direct interference among piscivores could explain the general pattern of positive covariance of biomass at all trophic levels with increasing productivity. Below, we
show how an alternate mechanism involving population structure and associated ontogenetic niche shifts can also produce positive correlations between the density of fish and their resources.

3 Population Size Structure and Ontogenetic Niche Shifts

Most aquatic organisms grow substantially in size from birth to death, resulting in pronounced size structure within populations. Associated with this change in body size, there is often an abrupt shift in diet or habitat use with ontogeny (Werner and Gilliam 1984). These ontogenetic niche shifts can be a consequence of changes in an organism's foraging ability, such that it feeds more efficiently on different sizes or types of prey, or in different habitats, as it grows. Size-dependent changes in predation risk can also cause organisms to shift from feeding in protected habitats when vulnerable to feeding in more open areas at relatively invulnerable sizes (examples in Werner and Gilliam 1984; Mittelbach and Chesson 1987; see also Werner this Vol.).

Shifts in an organism's diet or habitat use during ontogeny can have important consequences for the expected patterns between consumer and resource abundance. Ontogenetic niche shifts act to partially decouple the various life stages. Thus, density-dependent performance (e.g., survival or fecundity) at one life stage can result in the other life stage exhibiting a positive correlation between its equilibrium density and the equilibrium density of its resource. Below we use a very simple two life-stage model to illustrate this effect.

A Two Life-Stage Model

The model presented below was developed by Mittelbach and Chesson (1987) and is similar in form to the model of Tschumy (1982). Here we consider a single species consisting of two life stages (juveniles and adults). Juveniles and adults are assumed to occupy separate habitats and/or feed on separate resources. That is, there is a complete niche shift during ontogeny. We also assume that density dependence occurs at each life stage. At the adult stage, per-capita birth rate declines with an increase in adult density; at the juvenile stage, per-capita juvenile survival declines with an increase in juvenile density. Density-dependent fecundity and juvenile survivorship have been demonstrated in many groups of organisms and are likely to be common phenomena in size-structured species. The densities of juveniles and adults in the population can be expressed as:

\[ J(t) = A(t)F(A(t)) \]  
\[ A(t+1) = J(t) / (J(t)) \]  

where \( J(t) \) is the number of juveniles at time \( t \), \( A \) equals the number of adults, \( F \) is the per-capita fecundity and \( / \) is the probability of surviving through the juvenile stage. These equations can be written as a single difference equation describing the change in adult numbers from one time to the next:
Fig. 3a, b. Production curves for adults and juveniles. In a, curve \( m \) describes the number of juveniles produced at a given adult density and is the product of per capita adult fecundity \( F(A) \) and adult density \( A \); curve \( n \) describes the number of adults produced from a given density of juveniles and is the product of per capita juvenile survival \( r(J) \) and juvenile density \( J \). The intersection of the adult and juvenile production curves defines the equilibrium densities of the two life stages and is the point where \( F(A^*)/J^* = 1 \). b shows the effects of increasing per capita fecundity \( f(A) \) on the equilibrium densities of adults and juveniles. Dashed lines represent increased fecundities. Equilibrium densities determined as in a.

\[
A(t+1) = A(t)F[A(t)]/ [A(t)F[A(t)]]
\]

(3)

In this simple model, we assume no overlap in generations. Mittelbach and Chesson (1987) show how the above model may be generalized (without affecting the major conclusions) to allow for overlapping generations, and for juvenile density to affect time to maturity as well as survival.

We can examine the behavior of the model and determine the equilibrium densities of juveniles and adults by constructing juvenile and adult production curves as shown in Fig. 3a. Curve \( m \) describes the number of juveniles produced at a given adult density and it is the product of per-capita adult fecundity \( F(A) \) and adult density \( A \); curve \( n \) describes the number of adults produced from a given density of juveniles and is the product of per-capita juvenile survival \( r(J) \) and juvenile density \( J \). The intersection of the adult and juvenile production curves defines the equilibrium densities of the two life stages and is the point where \( F(A^*)/J^* = 1 \). In Fig. 3a, the production of juveniles is shown as a monotonically increasing function of adult density and recruitment into the adult class is shown as a monotonically increasing function of juvenile density. Humped-shaped production curves are possible if density dependence at a life stage is sufficiently strong (Tschumy 1982; Mittelbach and Chesson 1987; Wilbur this Vol.). However, in the following analysis, we limit consideration to those cases where both the juvenile and adult production curves increase monotonically; this simply requires that density dependence at either life stage be not too severe.

We can now ask what happens to the equilibrium densities of juveniles and adults when resource productivity for a life stage changes. For example, an increase in adult resources should result in an increase in per-capita fecundity at a given adult density. Figure 3b illustrates how such in change in the fecundity curve affects the equilibrium densities of adults and juveniles in the system, as well as the per-capita performances of adults and juveniles (i.e., fecundity and sur-
vival respectively). From Fig. 3b we see that an increase in adult resource productivity leads to:

1. an increase in the equilibrium density of adults,
2. an increase in the equilibrium density of juveniles,
3. an increase in per-capita fecundity (the ratio of juveniles/adult at equilibrium), and
4. a decrease in per-capita juvenile survival probability (the ratio of adults/juvenile at equilibrium).

Changes in juvenile resources, given that they affect juvenile survival, can be similarly modeled. An increase in juvenile resources and a corresponding increase in the juvenile survival curve will also generate predictions (1) and (2) above, however, predictions (3) and (4) will be changed, namely, per-capita fecundity will decrease and per-capita juvenile survival will increase.

Therefore, the above model predicts a positive covariance between equilibrium consumer density and the equilibrium density of the resource whose productivity was altered. This positive covariance occurs because density dependence at one life stage prevents the other stage from responding completely to a change in its own resource productivity. Thus, the response between consumers and resources in this simple stage-structured model is quite different from that shown by the models of Oksanen et al. (1981) and others. In aquatic systems, the vast majority of taxa are size-structured and many species exhibit distinct shifts in diet and/or habitat between life stages. Therefore, we suggest that the recognition of these ontogenetic niche shifts and the fact that life stages often show density-dependent responses to different resources, provides a likely mechanism whereby the densities of consumers and their resources will positively covaary within a life stage. In the following section, we present field data for the bluegill sunfish (*Lepomis macrochirus*) illustrating how a species exhibiting a distinct ontogenetic niche shift may respond to variation in its resources in a manner consistent with the model presented above.

## 4 Ontogenetic Niche Shifts in the Bluegill

In small, Michigan lakes the bluegill shows a pronounced habitat shift with ontogeny; small bluegills (≤75 mm standard length) feed on benthic invertebrates in or near littoral-zone vegetation, whereas larger bluegills shift to feeding on open-water zooplankton (*Daphnia* sp.) (Mittelbach 1981, 1984; Werner and Hall 1988). We have shown that the use of vegetation by small bluegills is primarily a response to high predation risk in the open-water and that when predators (i.e., largemouth bass, *Micropterus salmoides*) are removed, small bluegills will feed on zooplankton (Werner et al. 1983). Bluegills >75 mm are relatively immune to predation by bass and consequently can feed in the open water under little risk. Thus, in these lakes the bluegill exhibits essentially a two-stage life history with regard to resource use; juvenile bluegills occupy the littoral zone and feed on benthic invertebrates while adult bluegills feed extensively on open-water zooplankton. For simplicity, we ignore a brief (2–3 wks) early life history period, when
bluegill fry feed in large schools in the limnetic zone (Werner and Hall 1988). The life history to the bluegill therefore roughly corresponds to the simple stage-structured model presented above. While we do not know the degree of which juvenile and adult bluegill exhibit density-dependent survival and fecundity, we have shown that juvenile bluegill growth (and thus perhaps survival) is density-dependent in our study lakes (Osenberg et al. 1988, Mittelbach 1988) and Beyerle and Williams (1972) have observed density dependence in bluegill fecundities. Adult bluegill growth is also food-limited in our lakes (Osenberg et al. 1988). Thus, the bluegill life history fits the model reasonably well, although we cannot as yet make quantitative tests of the model's predictions. We can, however, use a large data set on bluegill growth rates and densities from seven Michigan lakes to compare a number of important qualitative predictions from the model regarding how variation in adult and juvenile resource productivity should affect the performances and densities of the two life stages.

In the model, adult and juvenile performances are measured in terms of per-capita fecundity and per-capita survival, respectively. Both of these parameters are extremely difficult to measure accurately for natural fish populations. Fortunately, we can use the rate of individual body growth as a reasonable surrogate for both parameters. Body size (the result of growth history) and fecundity are highly correlated in bluegills and other fishes (Carlander 1977; Bagenal 1978). Further, if some fraction of the net energy gained by a foraging adult is allocated to growth and reproduction, then growth and fecundity will be positively correlated. Therefore, we expect adult growth rates to be positively correlated with fecundities. Juvenile survival to adulthood should also positively covary with juvenile growth rates because, in part, vulnerability to predators generally decreases with size in juvenile fishes (Ware 1975; Craig 1982; Werner 1986). Larger individuals are also less susceptible to starvation and physicochemical factors (Oliver et al. 1979). Thus, an increase in juvenile growth should decrease the time spent in vulnerable size classes and therefore decrease the overall probability of death. In the following analyses, we measure adult and juvenile performances in terms of individual growth rates, and assume that increases in growth rate reflect increases in fecundity or juvenile survivorship. Furthermore, our field data for bluegills demonstrate that adult bluegill growth rates within a lake are positively correlated with predicted energetic returns available from the zooplankton (Fig. 4). Thus, adult bluegill growth rates increase with an increase in their resource availability, and we can use increased growth rates of adults as an index of increased adult resources as well as increased fecundity. Similarly, juvenile growth is positively correlated with predicted energetic returns from the littoral habitat (Mittelbach 1988), so we can also use increased growth of juveniles as an index of increased juvenile resources.

Table 1 presents the correlations between bluegill growth rates and densities from seven Michigan lakes. These correlations can be compared with the predicted correlations based upon variation in either adult resources or juvenile resources. There are three significant (p < 0.05) correlations in Table 1, and each of these is consistent with what the model would predict if the lakes varied primarily in adult (zooplankton) resources (Fig. 3b). First, adult bluegill density is positively correlated with adult growth rates. That is, adult bluegill density is
Fig. 4. Relationship between predicted net energy gain averaged over the growth season (Joules/second foraging time) and average annual growth rates of large bluegills in four Michigan lakes (two lakes represented by 2 years of data). Energy gains were calculated using the optimal foraging model in Mittelbach (1981) and are the average energy gains derived from the size-density distributions of zooplankton sampled in each lake (6 dates/summer/lake). (See Osenberg et al. 1988 for calculation of bluegill growth rates)

Table 1. Correlations among bluegill growth rates and densities from seven Michigan Lakes. Small bluegills are ≤75 mm SL by mid-summer; large bluegill > 75 mm SL. (Data from Osenberg et al. (1988) and Osenberg et al. unpubl.)

<table>
<thead>
<tr>
<th></th>
<th>Small Bg growth</th>
<th>Large Bg growth</th>
<th>Small Bg density</th>
<th>Large Bg density</th>
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<tr>
<td>Small Bg growth</td>
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* p < 0.05

greater in lakes with greater adult resource densities. (A significant positive relationship between adult bluegill density and foraging return from the zooplankton (E/T) is also found in the four lakes for which we have zooplankton data (Osenberg et al. 1988); r = 0.96, p < 0.05.) Second, adult bluegill density is positively correlated with small bluegill density. Third, small bluegill growth is negatively correlated with small bluegill density. The above correlations agree with the model’s predictions regarding the effects of changes in adult resources on adult and juvenile densities and performances. In addition, the other three correlations in the matrix (while not significant at p < 0.05), are all in the direction predicted by variation in adult resources.

Thus, variation in adult resources correctly predicts all six of the observed correlations for the bluegill. In particular, note that the key model prediction of a positive correlation between adult performance and adult density, in conjunction with a negative correlation between juvenile performance and juvenile density, is supported. Model predictions based upon variation in juvenile resources across lakes are consistent with only one of the three significant correlations and only two of the six total correlations (Table 1). Thus, the bluegill data provide an example where adult consumer and resource densities positively covary across a series
of lakes with the same trophic structure, and the entire entire data set is consistent with predictions of the two life-stage model presented in the text.

5 Ontogenetic Niche Shifts and Species Interactions

The above analyses have concentrated on how the inclusion of size (age) structure can affect the relations between consumers and resources within a single species. However, it is clear that a given trophic level rarely contains a single species and that consumer species will often interact with each other as well as with their resources. In the case of species undergoing ontogenetic niche shifts, it is common for species to share habitats or food resources at some life stages, but not others (Werner and Gilliam 1984). When competition occurs for these shared resources, the population dynamics of the species become linked due to interactions at specific life stages. This linkage of populations can greatly modify the predicted patterns of covariation in density, growth and resources derived from the single-species model presented earlier. Below we examine the particular case where consumer species compete as juveniles but not as adults. We expect this to be a common interaction among-size structured species where small (young) individuals often share a common protective habitat (refuge) due to their vulnerability to size-limited predators (Mittelbach 1986; Mittelbach and Chesson 1987). First, we show how the two life-stage model for a single species can be modified to include a second species that is a juvenile stage competitor. We then look at model predictions for how juvenile and adult performances and densities for two species should vary as resource production for juveniles and adults of each species vary. Then, we return to the field data for sunfish growth and density and examine the patterns of covariation in density and growth for the bluegill and its congener, the pumpkinseed (L. gibbosus), in light of model predictions.

A Two Life-Stage Model for Competing Species

We now consider a system of two interacting species, where juveniles compete interspecifically but adults do not. An empirical example of this situation is illustrated by the interaction between the bluegill and pumpkinseed sunfish in small Michigan lakes. Small bluegills and pumpkinseeds (ca. <75 mm) commonly co-occur in the vegetated littoral zone, where they compete for invertebrate resources (Mittelbach 1984, 1988). At large sizes, each species shifts to feeding on a separate resource, with the bluegill concentrating on zooplankton and the pumpkinseed feeding extensively on snails (Mittelbach 1984). Thus, each species undergoes an ontogenetic niche shift, with the juvenile stages occupying the same habitat and competing for resources, while the adults show little direct interspecific interactions.

We can examine this type of interaction using a two species, two life-stage model developed in Mittelbach and Chesson (1987). In this model, we leave the total reproduction functions the same as in the single species model [Eq. (1)], 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:
\[ J_i(t) = A_i(t)F_i[A_i(t)] , \]
\[ i = 1, 2. \] The juvenile survival equations become:
\[ A_i(t+1) = J_i/\mu[J(t)] , \]
where \( J(t) = J_1(t) + J_2(t) \) is now 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 species \( i \). For simplicity, we assume that juvenile survival probabilities for both species are equal. For the bluegill and pumpkinseed this appears to be a reasonable approximation (Mittelbach 1986). Mittelbach and Chesson (1987) show how Eqs. (4) and (5) can be used to specify the equilibrium densities of juveniles and adults of both species. Further, these equilibrium densities will be locally stable under the conditions previously specified for the single-species case (see Appendix A in Mittelbach and Chesson 1987).

As in the single-species case, the two-species, two-life stage model makes a series of predictions concerning how variation in adult and juvenile resource productivities will affect the densities and performances of juveniles and adults of each species. These predictions can then be compared to the observed patterns of variation in bluegill and pumpkinseed performances across lakes. For example, if the productivity of the bluegill’s adult resource (i.e., zooplankton) varies across lakes, the model predicts that an increase in zooplankton productivity will result in:

1. an increase in the equilibrium density of juvenile and adult bluegills,
2. an increase in adult bluegill and adult pumpkinseed performance (fecundity or growth),
3. a decrease in juvenile bluegill and juvenile pumpkinseed performance (survival or growth),
4. a decrease in the equilibrium density of juvenile and adult pumpkinseeds,
5. an increase in the total density of juveniles (bluegills and pumpkinseeds combined).

These increases and decreases predict a particular set of correlations among the growth and density responses of the two species. Different sets of predictions will be generated if there is variation in adult pumpkinseed resources (snails) or juvenile sunfish resources (littoral invertebrates). These predictions can then be compared to the observed patterns of growth and density variation exhibited by the two species (Osenberg et al. 1988).

Table 2 presents the correlations among growth rates and fish densities of bluegills and pumpkinseeds from seven Michigan lakes. Five of the 21 correlations listed in this matrix are significant at \( p < 0.05 \), with a sixth correlation being marginally significant at \( p < 0.07 \). We compare the signs of these six correlations with the predicted signs of the correlations based upon the two-species, two-life stage model, assuming variation between lakes occurs primarily in bluegill adult resources (zooplankton), pumpkinseed adult resources (snails), or juvenile resources (littoral-zone invertebrates). Table 3 shows that variation in productivity of adult bluegill resources correctly predicts the sign of all six correlations, while variation in the productivities of snails or littoral-zone invertebrates predicts only
Table 2. Correlations among growth rates and fish densities from seven Michigan Lakes. Large and small fish defined as in Table 1. Correlations > 0.75 or < -0.75 are significant at p < 0.05. (Data from Osenberg et al. 1988, Table 4)

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Table 3. Comparisons between model predictions and observed correlations in Table 2. Signs of the six strongest correlations in Table 2 are compared to their predicted signs if variation between lakes is primarily in bluegill adult resources (zooplankton), pumpkinseed adult resources (snails), or juvenile resources (littoral-zone invertebrates). Listed at the bottom of the prediction columns are the number of observed correlations whose sign is correctly predicted by variation in each of the three resources. Also listed are the number of cases where variation in each of the three resources correctly predicts the sign of the 21 total correlations presented in Table 2.

<table>
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<th>Observed correlations</th>
<th>Predicted correlations</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>zooplankton</td>
<td>snails</td>
<td>Juv. resources</td>
<td></td>
</tr>
<tr>
<td>Small Bg growth versus small Ps growth</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Small Ps growth versus small fish density</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Small Bg growth versus small fish density</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Large Bg density versus large Bg growth</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Large Bg density versus small Ps growth</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Large Bg density versus small fish density</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>6</td>
<td>no. correct</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>All correlations</td>
<td>21</td>
<td>20</td>
<td>12</td>
<td>10</td>
<td></td>
</tr>
</tbody>
</table>

About half of the correlations. We can also ask how well variation in the productivity of zooplankton, snails, or juvenile resources predicts the sign of all 21 of the correlations presented in Table 2, irrespective of the magnitude of the individual correlation. In this case, variation in zooplankton correctly predicts over
95% (20/21) of the correlations, while variation in the other two resources predicts only about 50% of the observed correlations correctly.

While comparisons between the model predictions and the field data for the bluegill and pumpkinseed are not as direct as we would like (e.g., they measure individual performance in different units), the correspondence between predictions based upon variation in adult bluegill resources and the observed data is compelling. The overall response by bluegills and pumpkinseeds suggests that variability in zooplankton production between lakes, in conjunction with juvenile competition linking that dynamics of two species, may be a primary factor determining the species growth and abundance patterns we observe in the fish community.

6 Discussion

Size structure is nearly ubiquitous among aquatic animals and often leads to dramatic niche shifts during ontogeny. We have shown that these niche shifts, which lead to segregation among members of the same population, can lead to positive correlations among consumer and resource abundances (for one stage of the life history) when measured along a gradient in resource productivity. This positive correlation arises despite competition among consumers. These results are quite different than those predicted by standard intraspecific competition models, and are consistent with the patterns we see for the adult bluegill and pumpkinseed. Of course, if we were to measure the resource abundances for the juvenile stages, they would be negatively correlated with consumer densities. Often, however, resources for the entire life history are not assessed, and in general it is the adult stage of the population and its resources that are monitored. Resolution of the compete relationship between consumer and resource abundances can only be made by recognizing the effect of ontogeny of the consumer's ecology.

Although niche shifts can produce positive correlations among consumers and resources, niche shifts can in some cases obscure these patterns. For example, during the early stages of their ontogenies, many piscivorous fish feed on zooplankton (Werner 1986). Therefore, these piscivores, which are predators of planktivorous fish species, may also compete with their prey early in their life histories. Bottlenecks in the recruitment of piscivores can arise through these competitive interactions (Werner and Gilliam 1984; Persson, this Vol.), and these bottlenecks can prevent piscivore biomass from increasing with increased production of its prey, therefore leading to diminished (or even negative) correlations among the abundances of the piscivore species and their prey (Persson et al. 1988). These types of mixed interactions where a population occupies two (or more) trophic levels seem to be more common at higher levels in the food chain (e.g., piscivorous fish often feed on zooplankton, planktivores, and juvenile piscivores, and can be thought of as occupying up to four trophic levels). This mixing (or blurring) of trophic relationships at higher trophic levels may be partially responsible for the reduction in the correlation between the abundances of consumers and resources as the focal trophic level is increased (a pattern suggested by McQueen et al. 1986).
As discussed in the introduction, the positive correlation between the biomass of consumers and their resources requires a bend in the consumer isocline. The niche shift explanation we have developed in this paper (in which resources refer only to those for one of the life history stages) causes the consumer isocline to bend due to the increased mortality experienced by the other life stage. This buffering of the consumer population’s response to resources requires that, as consumer densities increase, more resources be present to offset the loss of individuals (or energy) incurred during the other life history stage. Interference among consumers can also produce positive correlations between consumer and resource abundances (e.g., Wollkind 1976; Wiegert 1977). In this case, an increased consumer density requires a greater resource density due to increased energy losses and/or decreased time available for foraging.

Differential edibility among components of the resource category can also lead to positive correlations between consumer and “resource” abundance. It has commonly been observed that increased consumer densities lead to shifts in the resource community toward less desirable resource types (e.g., McCauley and Briand 1979; Zaret 1980). Increased consumer densities should favor lower quality resources; therefore, in reference to the general relationship shown in Fig. 2b, higher total resource densities would be needed to maintain the consumer population (thus bending the consumer isocline). Walters et al. (1987) have recently suggested differential edibility as a possible cause of the positive correlation between zooplankton and phytoplankton abundances, though their discussion of the process is not consistent with the earlier work of Phillips (1974). Leibold (1988), in a general synthesis of the models of Oksanen et al. (1981) and Phillips (1974), demonstrates more clearly the conditions under which differential edibility can affect consumer and resource abundances across gradients in resource productivity and consumer mortality. He shows that the equilibrium resource availabilities, measured across productivity gradients, can be positively correlated with consumer densities, but that the positive correlation arises primarily through changes in the densities of the relatively inedible components of the resources: the total abundance of resources, when weighted by their contribution to the consumer's birth rate (e.g., a measure of their edibilities), does not change across the productivity gradient (unless the death rate also changes).

The distinction between edible and relatively inedible resources raises a general point with regard to measuring resources. Clearly, not all resources contribute equally to the population growth of the consumer. Further, measures of resource density in the environment are not necessarily good estimates of resource availability. In our studies, we have been able to resolve this problem by using foraging models that incorporate differences in prey availability and value (Mittelbach 1981; Osenberg 1988). These models provide good descriptions of foraging rates and growth rates (Fig. 3; Mittelbach 1981, 1983, 1988; Osenberg 1988; Osenberg et al. 1988), and can therefore be used to estimate resource availability based on the abundances and size distributions of potential prey organisms in the environment. Discrepancies between resource abundance (e.g., biomass/m²) and resource availabilities (e.g., measured as a feeding rate) can be large if the resources change much in terms of their relative abundances and/or size structure. For example, estimates of the foraging returns for bluegills feeding on zooplank-
ton are not correlated with zooplankton biomasses from these same samples (n = 38 for the data summarized in Fig. 3, r = 0.05, p > 0.75). Obviously, the patterns that we have documented using foraging return and growth rates would not have emerged if we had used a less accurate estimator of resource availability (e.g., biomass of all "prey").

In addressing what factors create and maintain positive correlations between consumers and resources along productivity gradients, we kept the analysis simple. For example, we assumed that increased resources would lead to increased performance (e.g., birth and growth rates) of a consumer. In the real world, where trophic levels are not clearly defined and many species comprise a trophic level, this might not be the case, as the previous discussion demonstrates. In these cases a thorough understanding of the processes that control resource and consumer abundances must include information about the way consumers utilize resources (and therefore influence the resources' mortality rates). Foraging theory is a powerful tool that can be used to approach this problem. This study illustrates one useful application of these mechanistic models to the study of ecosystem patterns.

Finally, the distinction between resource quality and quantity helps focus our attention on the beneficial effects of the environment to individuals (e.g., as reflected in birth rates or growth rates), and allows us to explore how these effects are balanced by detrimental effects of the environment (e.g., as reflected in mortality rates or energetic losses). Ultimately, population densities are the outcome of the summation of many rate functions that measure the gain and loss to a specified population. If population densities remain constant or fluctuate within defined limits, average gains and losses (defined over an appropriate time scale) must balance: e.g., birth rates equal mortality rates. However, ecologists too often tend to dichotomize the processes that regulate populations, which is evident in the recurring debates over whether communities are structured by competition versus predation, or top-down versus bottom-up processes. Indeed, control is mediated in the ways population densities and the environment interact to equilibrate gain and loss rates; neither top-down nor bottom-up processes control population densities, instead densities are set by the equilibration to both. Advances in our understanding of the structure and function of communities and ecosystems must advance through the recognition of the important interrelation of these processes.

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