Ann. Zool. Fennici 27:165–182
Helsinki 26 September 1990

ISSN 0003-455X
© 1990 Finnish Zoological Publishing Board

Mechanistic individual-based approaches in the population/community ecology of fish

Lennart Persson & Sebastian Diehl

Department of Animal Ecology, University of Umeå, S-901 87 Umeå, Sweden

Received 6 December 1989, revised 26 February 1990

During the last decade, mechanistic approaches to understanding population/community processes have formed a significant trend in fish ecology and in ecology in general. Unlike more traditional models, mechanistic models are characterized by a high degree of lower level derivability. This means that population/community properties are derived from behavioural, physiological and/or morphological properties of individual organisms. Mechanistic approaches will introduce explicit constraints on the foraging and metabolic capacities of organisms. In taxa of size-structured populations, such as fish, additional constraints are set by ontogenetic covariance between different size stages. Theoretical studies show that one mechanistic element, the inclusion of active predator choice with respect to diet and patch use, has a stabilizing effect on predator-prey dynamics. However, the qualitative discrepancies in predictions are small between predator-prey models with optimally foraging predators, and the more traditional predator-prey models with switching and predator aggregation. Experimental studies on fish show that active predator choice is generally present, but deviations from predictions of the basic diet model are frequently observed. Both theoretical and experimental studies suggest that the restriction of classical foraging models to the predator's diet and habitat choice, and the assumption of behaviourally inflexible encounter rates are major limitations. Flexible predator foraging mode and flexible prey avoidance behaviour have substantial effects on predator-prey dynamics. In many cases, prey behaviour may be more important in determining the predator's diet than the predator's decision after encounter. Inclusion of mechanistic details of foraging and antipredator behaviour in population/community models tends to make models less general and more system-specific. We also suggest that the hierarchy community-population-individual is incomplete in many respects, necessitating an integrated mechanistic research strategy including studies at different levels. Although a mechanistic research program is expected to form a productive trend in ecology in the future, there will still be a need for less mechanistic but more general theories.

1. Introduction

Classical models of population and community ecology usually assume that within a species, individuals are identical and behave in a random way. More recently, it has been recognized that individual variation and behavioural interactions among individuals fundamentally affect the dynamics and stability of ecological communities. For example, a considerable degree of intrapopulation variability is present in most taxa, including fish, in the form of size structure. Experimental and theoretical work demonstrates that the presence of size structure in populations has far-reaching consequences for both behavioural and population/community processes (Werner & Gilliam 1984, Ebenmann & Persson 1988). Furthermore, population models incorporating intrapopulational variation (Lomnicki 1980, 1988) or flexible behaviour (Abrams 1982, 1984, 1987) predict profound effects of these factors on population dynamics.

Many experimental studies on the implications of size structure for the dynamics of fish populations have used a mechanistic approach (Werner & Hall 1977, 1979, 1988, Mittelbach 1981, 1983, 1984, 1988, Werner et al. 1983a, b, Gilliam 1982, Hamrin & Persson 1986, Persson 1987a, 1988, Persson & Greenberg 1990a, b). In a paper advocating a more mechanistic approach to community ecology, Schoener (1986) attempted to show that community ecology, population ecology and individual ecology form a perfect hierarchy of reducible disciplines, and that individual ecology itself can be divided into physiological, functional-morphological and behavioural ecology. In that framework, a mechanistic approach would, in principle, allow qualitative and quantitative predictions about community dynamics to be made from behavioural, morphological and physiological considerations (Schoener 1986). Some optimistic behavioural ecologists have expressed the belief that future theories of community organization will be based upon the behavioural characteristics of constituent species (Dill 1987). In contrast, Hassell & May (1985) argued that the level of behavioural information required in population ecology should be restricted to accurate knowledge of the end product of a behaviour, an example of such an end product being the negative binomial distribution of individuals often found in nature. Given the different views expressed by different authors, we might ask to what extent behavioural ecology, ecomorphology and ecophysiology have contributed, and may in future contribute, to population/community ecology?

In this paper we review theoretical, experimental and field studies that investigate population/community dynamics from the perspective of the individual organism, with an emphasis on the role of species- and size-specific capacities, constraints and behavioural flexibility. First, we give a background summary of mechanistic approaches, and show how these have been applied to the study of fish populations and communities. We discuss size-specific metabolic, morphological, and ontogenetic constraints that are present in organisms in general, and specifically in size-structured populations such as fish populations. Secondly, on the basis of theoretical and experimental evidence, we try to evaluate the degree to which classical foraging models have contributed to an increased understanding of population and community processes. Next, we discuss the importance of flexible predator and prey behaviour to population dynamics. Finally, we make suggestions for future studies of behavioural mechanisms potentially important to population/community ecology and try to give a perspective for the further integration of behavioural and population/community ecology. Although our examples are derived from fish, the arguments developed and conclusions drawn should be valid for organisms in general.

2. Mechanistic approaches in population/community ecology

2.1. General background

A mechanistic approach is defined as the use of individual ecological concepts — from behavioural ecology, ecomorphology and physiological ecology — as the basis for the development of a conceptual framework for understanding patterns and processes at the population and community levels (Schoener 1986). In comparison with more traditional "descriptive" models, mechanistic models are characterized by a high degree of lower-level derivability, i.e. terms in population/community models are derivable from individual properties. It is important to recognize that what is meant by a mechanistic model differs between population/community ecologists and ethologists. While an optimal foraging model, in which individual properties are included in the values of handling time and encounter rate, may be regarded as a mechanistic model by a community ecologist, this is certainly not the case for an ethologist. Mechanistic models are usually less general, and more system-specific than traditional descriptive models. An extreme example is physiologically based population models of stage(size)-structured populations (Metz & Diekmann 1986, Metz et al. 1988).

Mechanistic approaches to the understanding of population and community processes can roughly be divided into those based on behavioural concepts and those based on physiological variables (Schoener 1986). Since foraging models often include physiological variables, these two approaches are nonexclusive. Typically, studies based on behavioural concepts explicitly include a decision variable that allows different options to the forager, but lack explicit population variables such as birth and death rates (Schoener 1986, for examples see Mittelbach 1981, Werner et al. 1983a, Osenberg & Mittelbach 1989, Persson & Greenberg 1990b). In contrast, ecophysiological approaches generally involve explicit population parameters, but lack explicit options for the forager (for examples of the latter see references in Schoener 1986). Taken together, the above studies suggest that inclusion of complete population parameters occurs at the cost of mechanistic details of forager behaviour, and vice versa.

Mechanistic and descriptive approaches should not be viewed as exclusive alternatives, but rather as end-points of a continuous gradient (Schoener 1986). For example, the formula for the competition coefficient (alpha) derived by MacArthur & Levins (1967) for the Lotka-Volterra equations (cited as an example of a descriptive model by Schoener 1986) may be interpreted in behavioural and physiological terms to some extent, whereas the formula derived by Schoener (1974) himself includes non-mechanistic elements. However, the MacArthur & Levins formula rests on several precarious assumptions, such as the utilization functions being normal and constant, the areas under these functions being equal, and the alphas being density-independent constants (Roughgarden 1974, Abrams 1975, 1983, Schoener 1986). A mechanistic approach makes no a priori assumptions about utilization functions, but rather looks at resource consumption at the individual level, in relation to metabolic and behavioural considerations (Schoener 1986). Instead of assuming utilizations to be constant, a behaviourally based mechanistic approach focuses on the probability that an individual consumes a particular resource and how this probability is affected by competing species (see Werner & Hall 1977, 1979 for examples).

2.2. Size-specific foraging capacities and metabolic demands

In classical Lotka-Volterra competition theory, the outcome of the interactions between species relates to the competition coefficients (alphas) and the carrying capacities (*K*:s) of the interacting species. The meaning of alpha in its classical form is rather obtuse: it is generally defined as a ratio relating interspecific competition to intraspecific competition (Schoener 1974, Abrams 1980b, Persson 1985). Constraints on the value of alpha for a species in relation to its carrying capacity, were recognized by Levins (1968) and MacArthur (1972) in the "principle of allocation" and the concept that "a jack of all trades is a master of none". While alpha and *K* in the Lotka-Volterra equations are independent and can take any values, a more mechanistic view of competition will recognize possible constraints on the values of alpha and *K*. For example, the foraging capacity (related to alpha) of an animal is positively related to body size (Schoener 1969, Wilson 1975, Sebens 1988, Werner 1988), and the same is the case for the animal's metabolic requirements (related to *K*) (Wilson 1975, Case 1979, Persson 1985). Hence alpha and *K* of an organism will be so interrelated that a larger animal will have a foraging (alpha) advantage, while a smaller animal will have a metabolic (*K*) advantage (Wilson 1975, Persson 1985, Werner 1988). This interaction between foraging and metabolic advantages was

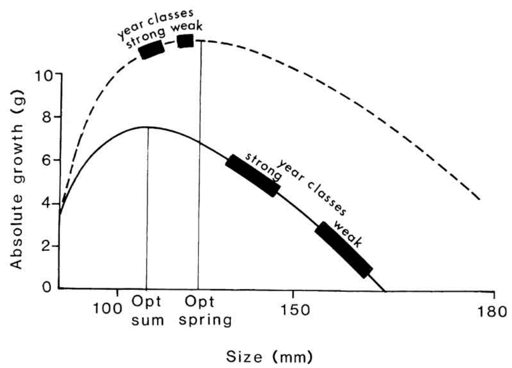

Fig. 1. The relation between size and absolute growth in vendace for the periods May – July (dashed line) and July – October (solid line). Thick solid bars indicate the size ranges of strong and weak year-classes of 1+ vendace. The curves were obtained from regression lines of mean instantaneous growth rates on vendace size. From Hamrin & Persson (1986).

suggested to explain the 2-year population cycle in a planktivorous fish species, the vendace (*Coregonus albula*) (Hamrin and Persson 1986). In the system studied, two environmental variables vary predictably from spring to summer: temperature increases, increasing metabolic demands, and the availability of resources (pelagic zooplankton) decreases (due to vendace predation), diminishing foraging gains. As both these circumstances adversely affect larger size classes compared to smaller ones, the optimum body size with respect to growth was expected to decrease from spring to summer, an expectation in agreement with growth data (Fig. 1).

The mechanism behind the observed two-year oscillation in the vendace population was suggested to be as follows. When a strong year-class was recruited, density-dependent growth resulted in 1) relatively small size of 0+ individuals after their first summer, and 2) poor gonad development in 1+ vendace (which amounted to 90% of the spawning population). As a result, there was poor reproductive output during autumn spawning. Compared to a weak year-class, the growth of a strong year-class was lower during its second spring (as body size was below the optimal size at that time), but was relatively higher during summer (Fig. 1). The latter could be related to 1) a small body size being closer to the summer optimum, and 2) low inter-age class competition (only a few 0+ vendace were present). The high growth rate during summer resulted in a high reproductive output during autumn, after which the population entered the next cycle.

2.3. Morphological constraints on foraging capacities

The above example shows that the traditional assumption of constant competition coefficients and carrying capacities can obscure the picture of the actual intensity and direction of competitive asymmetries. Similarly, the use of field data on diet overlap can yield misleading conclusions regarding the intensity of competitive interactions (Werner & Hall 1979, Abrams 1980c). Diet overlap between species or size classes may be much smaller in sympatry than in allopatry, reflecting relative foraging capacities with respect to resource size distribution and density, and to habitat type. An organism's foraging capacity is, in turn, partly determined by species- and size-specific functional morphology. Morphological constraints on foraging capacity are most apparent in the locomotory and feeding apparatus of animals (O'Brien 1987, Wainwright 1988). For example, increasing body size will enable an animal to capture larger prey as a result of greater locomotory capacity, as well as larger mouth and gut size. However, there may be a decrease in capacity to catch smaller prey due to decreased manoeuvrability and ability to handle smaller prey (Mittelbach 1981, Persson 1988). Similarly, species-specific body shape and positioning of locomotory organs set morphological constraints on foraging efficiency in different habitats (Werner 1977).

Morphological constraints of body size were suggested to partly explain the habitat use of interacting size classes of European perch (*Perca fluviatilis*) (Persson 1987a). In the laboratory, 1+ perch had higher absolute feeding rates on small prey items (zooplankton) than 2+ perch, and the relationship was the opposite for larger benthic prey (Persson 1987a). In an enclosure experiment in a lake with low benthic prey abundance, both size classes of perch utilized similar resources in allopatry (mixed zooplankton/macroinvertebrate diet in early summer, exclusive zooplankton diet at the extremely low densities of benthic invertebrates in late summer). In sympatry, however, 1+ perch ate zooplankton, and 2+ perch benthic prey throughout the experiment. Together with growth data, this result suggested a reverse in intensity and direction of the mutual alpha impacts of the size classes upon each other, as resource availability in the littoral and pelagic zones changed. The habitat segregation between smaller and larger perch observed in the lake in late summer could thus be attributed to a habitat shift by the smaller perch due to higher profitability of the pelagic habitat.

Morphological constraints were also suggested to explain the habitat distribution pattern of three co-occurring North American sunfishes, which differ in body plan and functional morphology of the feeding apparatus: the bluegill (*Lepomis macrochirus*), the green (*L. cyanellus*) and the pumpkinseed sunfishes (*L. gibbosus*) (Werner & Hall 1977, 1979). Introduced in alloptary into ponds, all species preferred the vegetation over other habitats. However, differences in habitat-specific foraging efficiencies between the species were found, the green sunfish being the superior forager in vegetated habitats and the pumpkinseed being the most efficient benthivorous species in open habitats. When introduced together into a pond with initially high return rates from the vegetation, all three species foraged (in agreement with predictions) initially in the vegetation, and, as the relative profitability of the vegetation declined, first the pumpkinseed, and later the bluegill, shifted to foraging on sediment prey (Werner & Hall 1979). The distribution pattern of the three species in central North American lakes is generally consistent with the predictions from the experiments, as far as the larger stages are concerned (Werner et al. 1976). However, habitat use by the juveniles is additionally affected by the need to avoid predators (see also section 4 and Werner et al. 1983b).

2.4. Size-specific constraints on foraging — implications in size-structured populations

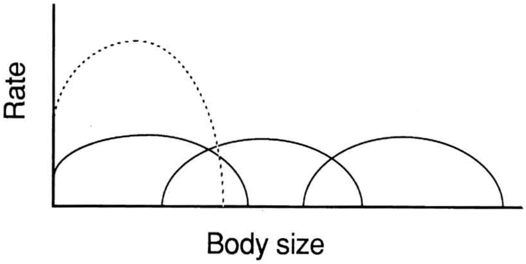

Fig. 2. Resource utilization rate efficiencies in relation to body size and ontogenetic niche shifts. The dashed line represents a species with small adult body size utilizing the same resource with a high efficiency during its entire lifetime. Solid lines represent a species with large adult body size utilizing the same resource as the previous species when young, but undergoing two discrete resource niche shifts with increasing body size. For this second species, the maximum efficiency is expected to be lower.

Size- and species-specific morphological and metabolic constraintst on resource use are found in organisms in general. Additionally, individuals of size-structured populations, such as fish, are constrained by their ontogeny. Most fish species have the potential to increase in size during their whole life, which often necessitates a series of ontogenetic niche shifts towards larger prey sizes. In fish, the change in body morphology with age is largely a change in body size with the same basic body plane, resulting in a high degree of genetic covariance between different stages (Ebenman & Persson 1988, Kirkpatrick 1988, Werner 1988). An ontogenetic trade-off situation is thus present, resulting in small and planktivorous stages of an adult piscivorous species being burdened with a body morphology preadapted for piscivorous feeding (Werner & Hall 1979, Werner 1986, Persson 1988). It has been suggested that a species undergoing substantial niche shifts will be less efficient in utilizing resources when small (young) than a species utilizing a narrow range of resources over its entire life time (Werner & Hall 1979, Werner 1986, Persson 1988) (Fig. 2). The latter species may thus compete severely with the young stages of the former species (Persson 1988). Even if the larger individuals of the larger species are resource-limited to only a small extent, resource limitation at young stages may affect the recruitment of larger individuals, resulting in a competitive juvenile bottleneck (Neill 1975, Werner 1986, Persson 1988, Persson & Greenberg 1990a).

Our research has focused on the competitive interactions between perch, a potentially piscivorous species, and roach (*Rutilus rutilus*), a superior zooplankton feeder. Roach at high densities cause the young stages of perch to shift from feeding on zooplankton to feeding on benthic (littoral) prey earlier than at low roach densities (Persson 1986, 1987b, 1988, Persson & Greenberg 1990a). This advanced shift in diet transforms into reduced growth rates, which increase the time before perch enter the piscivorous stage and decrease the numbers entering this stage. The competitive superiority of roach may be related to the fact that perch undergo more substantial niche shifts than roach with respect to prey size. The perch-roach interaction is further complicated by the fact that, if perch become large enough, they may start to prey on roach. The interaction between these species is thus dependent on a delicate balance between competitive and predatory forces (Persson 1988). A similar situation has been suggested for the largemouth bass (*Micropterus salmoides*) – bluegill sunfish interaction (Werner & Hall 1979, Gilliam 1982).

3. Mechanistic approaches and classical foraging models

So far, we have discussed how constraints set on the organism affect the efficiency with which it can utilize different resources. In terms of the predation cycle, these factors relate to the probability that a predator will encounter a specific prey type, and the probability that an attacked prey will be successfully captured (Fig. 3). In the interaction between behavioural ecology and population/community ecology, one key variable is a predator's choice between attacking and not attacking an encountered prey, a topic which is explicitly treated by classical foraging theory (Stephens & Krebs 1986). In this section, we discuss the theoretical consequences of optimal foraging in predators for predator-prey population dynamics and compare these with predictions from more traditional approaches. We then critically evaluate the relevance of classical foraging models to population and community processes, as deduced from experimental field tests.

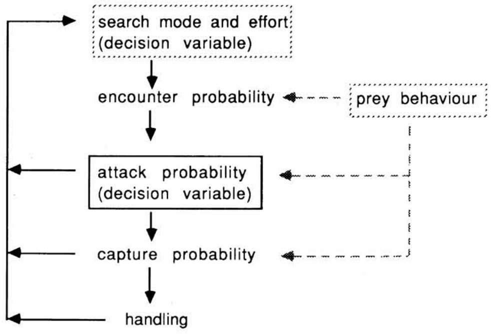

Fig. 3. Cycle of events in the predation process. Solid arrows indicate the predation cycle as experienced by the predator. Classical foraging models focus mainly on the predator's decision whether or not to attack an encountered prey (solid box). Strippled boxes and arrows indicate behaviourally flexible determinants of the predator diet that are potentially important to population/community ecology, but have received less attention from foraging theoreticians.

3.1. Theoretical aspects

The classical diet model assumes that search and handling are mutually exclusive predator activities and that potential prey differ substantially in profitability (Stephens & Krebs 1986). The encounter rate with highly profitable prey then determines which prey items are to be included in the diet, in order to maximize long-term net energy intake. In traditional predator-prey population models, a decision variable does not occur, and the probabilities of encounter, attack and capture for a predator are lumped together into one parameter, the attack coefficient (a). To our knowledge, the only attempt to include optimal prey choice, based on the diet model, in a population model, stems from Gleeson and Wilson (1986). They considered a predator preying upon two competing prey species and assumed a type II functional response of the predator which, if both prey are included in the diet, gives Holling's

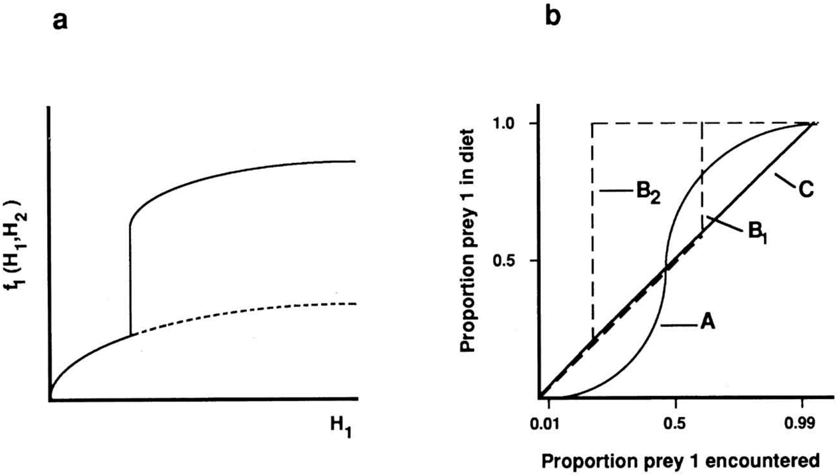

Fig. 4. Absolute and relative functional responses of a predator feeding on two alternative types of prey either according to the diet model, indiscriminately or with positive density-dependence. — Left. Functional response to the density (H_1) of the more profitable prey 1, if prey 2 is dropped from the diet above some threshold density of prey 1 (solid line), and if prey 1 and 2 are consumed as encountered at all densities (dashed line). The predator is assumed to have a type II functional response. — Right. Relative consumption of prey 1, if the predator feeds with positive density-dependence (switching) on both prey (A), and if the predator feeds according to the diet model (B_1, B_2). In case A, attack coefficients for both prey are assumed to be equal. In case B_1, the relative profitability of prey 1 is low (but still higher than that of prey 2), whereas in B_2 it is higher. Line C represents the case with indiscriminate predation. Both figures assume a constant density of prey 2.

(1959) disc equation for two alternative prey species (Fig. 4a) (Murdoch 1973, Abrams 1987):

$$f_i(H_1,H_2) = a_iH_i \,/\, (1+a_1H_1h_1+a_2H_2h_2), \qquad (1)$$

where H_1 and H_2 are the densities of prey 1 and 2, i refers to either prey 1 or 2, a_i is the attack coefficient for prey i while the predator is searching, and h_i is the handling time for each prey i. An optimal forager will maximize the net energy intake (E^*) according to the formula (Stephens & Krebs 1986):

$$E^* = \frac{\sum_{i=1}^{n} \lambda_i e_i}{1 + \sum_{i=1}^{n} \lambda_i h_i}, \qquad (2)$$

where the encounter rate $\lambda_i = a_iH_i$ and e_i is the net energy return from prey i (including the saved energetic cost of not searching when handling). According to the diet model, a given prey type is either always attacked on encounter or always neglected, depending on the encounter rate with higher ranked prey types. Gleeson & Wilson assumed that prey 1 is both the superior competitor and the more profitable prey, which leads to an interesting case of three-species coexistence not found in the absence of optimal prey choice by the predator: If the predator-prey 1 interaction is intrinsically unstable, optimal prey choice by the predator will produce a sort of switching, which, under certain assumptions, will lead to cyclic coexistence: when H_1 drops below some threshold density, it is profitable to include prey 2 in the predator diet, which implies that $f_1(H_1,H_2)$ decreases from $a_1H_1/(1+a_1H_1h_1)$ to eqn. (1) and $f_2(H_1,H_2)$ increases from zero to eqn. (1) (Fig. 4a). With prey 2 in the diet, predator numbers will not drop to values low enough to allow prey 1 to increase so much as to competitively exclude prey 2. Optimal prey choice by the predator thus tends to dampen oscillations in intrinsically unstable predator-prey systems, and broadens the conditions for coexistence, as compared to models assuming a type I or type II functional response of the predator. In the latter case, three-species coexistence requires a delicate balance of parameters

(Cramer & May 1972, Comins & Hassell 1976, Vance 1978, Noy-Meir 1981).

Gleeson & Wilson's analysis is based on a type II functional response, and compares an optimally foraging predator with a predator consuming prey as encountered. However, as optimal foraging introduces a selection option, a comparison with the predictions of traditional models including frequency-dependent selection (switching behaviour) in the predator would be more relevant. One example of a switching response of the predator is given by Vance (1978):

$$f_i(H_1,H_2) = c_i[H_i/(H_1+H_2)]^n. \qquad (3)$$

Here c_i is the capture rate constant for prey i and increasing values of the positive constant n indicate increasing preference for the more common prey (note that n has no explicit mechanistic interpretation). Predator switching substantially broadens the conditions for coexistence, and three-species coexistence may become possible even under the assumption of totally identical prey species (Murdoch & Oaten 1975, Vance 1978). In traditional switching models, the predator shows partial prey preference at all prey densities, depending on the *relative* encounter frequencies only. In contrast, the predator's choice in the diet model is based on the *absolute* encounter frequency with the more profitable prey, yielding indiscriminate predation below and 100% preference above the threshold value (Fig. 4b). Compared to the diet model, traditional switching models predict a suboptimal diet at virtually all prey densities (Fig. 4b). Although traditional non-mechanistic switching models were criticized by Holt (1983) as portraying suboptimal predators, they could be justified by explicit specification of constraints on optimal foraging within a mechanistic model (Holt 1983). Examples of possibly widespread constraints are the inability to recognize poor quality prey without handling it, and prey species requiring very different search tactics. The true prey choice behaviour of a predator might therefore be characterized by a traditional smooth sigmoid curve, the switching point being determined by the relative profitability of the more profitable prey (Fig. 4b).

While the diet model focuses on diet selection, the patch model focuses on how long to stay and forage in an encountered food patch. According to the patch model, patch residence time of the predator is positively related to the expected food intake rate from that patch, the least profitable patches being left immediately on encounter. Consequently, individual foragers will concentrate their foraging efforts on highly profitable patches, which will lead to an aggregative predator response. Irrespective of whether or not the predator aggregation strategy is fixed (i.e. not based on any mechanism, Hassell & May 1973), based on encounter frequency-dependent patch residence time (Hassell & May 1974), or based on optimal patch choice according to the patch model (Comins & Hassell 1979), essentially the same population consequences arise: an aggregative predator response will always contribute to stability, and stability is enhanced by increasing variance in the host abundance. In the case of two prey species, predator aggregation in patches of high total prey density produces a switching effect, if the prey species do not covary too much in their distribution pattern. This spatially mediated switching tends to promote coexistence of unequal competitors, even if the predator feeds on them in constant proportion (i.e. the predator chooses habitat but not prey within a habitat, Comins & Hassell 1987).

It may be concluded that, compared to models in which the predator is simply assumed to show a linear or decelerating functional response, coexistence of a predator and two competing prey may become more likely if the predator forages according to the classical diet model. Generally, the predictions of the diet model are in agreement with predictions of models including switching behaviour in the predator (note, however, that the predictions based on the diet model depend on absolute prey densities, whereas the predictions of switching models depend on relative prey densities). Similarly, the population consequences of patch choice based on the patch model do not deviate substantially from the predictions of more traditional models including predator aggregation: in both cases stability is increased.

3.2. Experimental studies

From the population and community ecologist's point of view, field tests of optimal foraging models are essential and necessary to evaluate the usefulness of optimal foraging models to studies of population and community processes. Although the development of an economic theory of diet and habitat use by animals was a major aim of MacArthur (MacArthur & Pianka 1966, MacArthur 1972), to our knowledge, only 4 quantitative field studies have been made with animals feeding on natural prey, and with independent estimates of encounter rates and handling times (which are essential to test the classical foraging models) (Mittelbach 1981, Werner et al. 1983a, Osenberg & Mittelbach 1989, Persson & Greenberg 1990b). All of these studies have used fish as foragers, and have also used essentially the same foraging model as is presented in Mittelbach (1981). In principle this model is the classical diet model (Stephens & Krebs 1986, see eqn 2). The assumptions of the classical diet model have been questioned on both theoretical and empirical grounds, particularly with respect to sequential encounter, complete information and constancy of encounter rates and handling times for a specific prey and its density (Stephens & Krebs 1986). During recent years more complex models have been developed in which dynamic optimization has played an important role (Gilliam 1982, Mangel & Clark 1986, McNamara & Houston 1986, Godin 1990). Still it can be argued that to be tractable in population models, simplifications regarding behavioural aspects of animal foraging have to be made (Persson 1990). When testing the usefulness of optimal foraging models in the study of population and community processes, the four above-mentioned studies have focused on 3 different aspects: 1) predictions of diet breadth within a habitat, 2) predictions of habitat shifts related to profitabilities of different habitats, and 3) individual growth performances based on predicted net energy intakes (Mittelbach 1981, 1988, Werner et al. 1983a, Osenberg & Mittelbach 1989, Persson & Greenberg 1990b, Persson 1990) (Table 1). The predictions were based on estimates of encounter rates and handling times obtained in laboratory experiments combined with measured resource levels in the environment.

In the first study, Mittelbach (1981) studied the seasonal shifts in habitat use of different size (age) classes of bluegills in a lake. He found an agreement between predicted and observed habitat use although a certain time delay was present. The delay in the smallest size class was hypothesized to be the result of a higher predation risk in the more profitable habitat. This hypothesis, which was later corroborated (Werner et al. 1983b), shows an advantage of using quantitative foraging models: a quantitative deviation from predicted patterns (not detectable by qualitative models) can be used to advance other potential mechanisms of importance. With respect to diet, Mittelbach found that bluegills captured prey with a mean size larger than that encountered in the environment. However, inclusion of non-profitable prey size classes was frequently observed (Table 1). In the second study, Werner et al. (1983a) stocked a pond with bluegills of different size classes. The bluegills' choice of pelagic prey (but not benthic prey) and habitat shifts over time were largely in accordance with that predicted from eqn. (2). Bluegills consumed pelagic prey larger than that encountered, but again non-profitable prey were commonly observed in the diet (Table 1). In the third study, Osenberg & Mittelbach (1989) predicted the prey choice of pump-

Table 1. Accuracy of the diet model in predicting diet and habitat use of different fish species in field experiments and studies.

	Species	System	Diet use:		Habitat use:
			mean prey size	least profitable prey	habitat shift
Mittelbach 1981	Bluegill	Lake	Eaten>Encountered	Eaten<Pred	Time delay
Werner et al. 1983a	Bluegill	Pond	Eaten>Encountered	Eaten<Pred	Precise
Osenberg & Mittelbach 1989	Pumpkinseed	Lake	Eaten>Encountered	Eaten<Pred*	–
Persson & Greenberg 1990b	Perch	Pond	Eaten>Encountered	Eaten=Pred**	Time delay

* different models tested, encountered ≈ optimal but size refuges important

** partial preferences within optimal diet kinseed sunfish foraging on gastropods in a range of lakes using 3 different models. One model was based on size-specific encounter only, another was based on encounter and prey size refuges, and finally one was based on optimal foraging theory (eqn. (2) plus the assumption that the probability of successfully capturing an encountered prey could deviate from one). For most field situations, the model incorporating only size-specific encounters explained a large part of the variation in diet. However, in cases with significant prey size refuges, the encounter model with prey size refuges gave better predictions. Although predictions based on the optimal foraging model sometimes resulted in a smaller residual variance, the model based on only size-specific encounter did as well in most cases (Table 1). The pumpkinseed did not consume prey as encountered, but ignored prey of low profitability and became more selective as the quality of the environment increased.

Finally, Persson & Greenberg (1990b) manipulated resource levels of pelagic prey by stocking different enclosures in a pond with varying densities of a forager (roach) mainly affecting pelagic prey, and studied the resource use of juvenile perch. In agreement with predictions, perch shifted from feeding on pelagic prey to feeding on benthic prey, first in high roach density enclosures, and later also in medium roach density enclosures. The smallest pelagic prey size included in the diet was accurately predicted from eqn (2). However, partial preferences (attack probabilities <1) within the predicted optimal diet size range were present. The observed habitat shift from pelagic to benthic feeding was qualitatively in accordance with that predicted, but occurred with a considerable time lag and partial habitat use was also observed (Table 1). This study, like several others, has shown a positive relationship between individual growth rates and predicted net return rates, suggesting that foraging theory can be a powerful tool in predicting individual performance (Mittelbach 1988, Mittelbach et al. 1988, Persson & Greenberg 1990b). However, analyses based on the data in Persson & Greenberg (1990b), showed that calculations based on encounter rates only generated almost as good predictions of growth rates as those based on net return rates predicted by the diet model (Persson 1990, see also Osenberg & Mittelbach 1989 for diet selection).

The inclusion of species-specific and prey type-specific encounter rates is a qualitative step forward in understanding population and community patterns compared to traditional population and community approaches. This advance concerns especially the prediction of population and community statics (Mittelbach 1984, Persson 1987a, b, Werner & Hall 1988, Persson 1990, see also section 2.3). Improvements made by the additional inclusion of optimal foraging predators, as treated in this section, are more ambiguous. The studies suggest that prey use by foragers deviates significantly from the prey distribution encountered, i.e. active selection is present. However, deviations from the predictions of the basic diet model, with respect to both diet use within habitats and habitat shifts, are frequently observed. Quantitative deviations from the predictions of the diet model have been frequently documented in the ecological literature, and this is mainly believed to result from learning phenomena and sampling programs, by which animals obtain information about resource levels in alternative habitats (Goss-Custard 1977, Hughes 1979, McNair 1980, Werner et al. 1981, Krebs & McCleery 1984, Pyke 1984). On the basis of swimming speed observations, Persson & Greenberg (1990b) proposed that habitat- and prey-dependent optimal search rates were one explanation for partial preferences. The presence of prey type- and prey density-dependent search rates in predators points to one limitation in the experimental studies discussed above: the assumption that encounter rate is determined only by the size and type of predator and prey at a given prey density, and not by flexible behaviour. As will become apparent in the next section, explicit consideration of adaptive and flexible behaviours by both predators and prey, has substantial effects on the population dynamics.

4. Adaptive and flexible predator and prey behaviour

The probabilities of encounter, attack and capture depend on the total characteristics of both predator and prey (Fig. 3). A predator can behaviourally alter these probabilities by active choice of which habitat to forage in and by choice of activity level and search mode within a habitat. The presence of flexible search rates in predators has been demonstrated in both theoretical models and empirical studies and has been related to both the metabolic costs and gains of different search modes, as well as prey crypticity-dependent search rates (Norberg 1977, Andersson 1980, Jaeger & Barnard 1981, Gendron & Staddon 1983, Sih 1984, Ehlinger 1989, Persson & Greenberg 1990b). Flexible predator behaviour may have profound effects on predator-prey dynamics. Prey density-dependent predator search activity, for example, may lead to a type III functional response in the predator (Hassell 1978).

Only recently has it been acknowledged in population models that also prey organisms may show adaptive behaviour. The risk of predation may cause potential prey to decrease their own foraging effort, enhance crypsis, stay in refuge, or invest in morphological defences (Sih 1984, 1987a, Abrams 1984, 1987). All these behaviours tend to reduce encounter rate and attack success by a predator and thus might be considered as refuge use (Sih 1987b). Prey refuge use has been shown to have strongly stabilizing effects on predator-prey dynamics, but the models usually assume a constant number or proportion of prey in refuge, and/or equal prey growth rates inside and outside the refuge (Maynard Smith 1974, Tanner 1975, Stenseth 1980, McNair 1986). Adaptive prey, however, should increase their use of refuges as predation intensity increases, and should pay a cost of reduced growth in the refuge, both factors affecting stability in opposite ways (Sih 1987b). In intrinsically stable one predator-one prey models, adaptive antipredator behaviour will slow down growth rates and dampen oscillatory tendencies, since behavioural responses of the prey to changes in predator density are much more rapid than numerical responses (Ives & Dobson 1987) (Fig. 5).

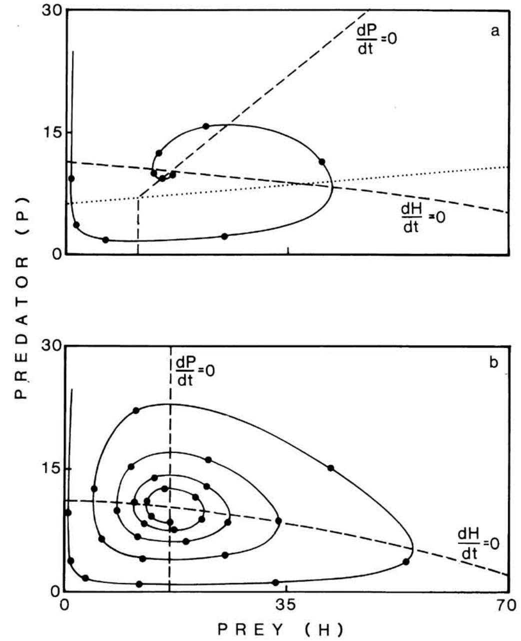

Fig. 5. Predator-prey dynamics with and without adaptive flexible antipredator behaviour in the prey. In both figures, predator and prey densities remain positive and bounded, and in the case with flexible antipredator investment, prey growth rate decreases linearly with increased investment in antipredator behaviour. — a. Example of a trajectory of population densities with prey assumed to optimally adapt its antipredator investment to actual predator density. — b. Same as (a), but prey uses fixed antipredator investment. The dots on the trajectories are placed at equal time intervals. The dotted line is the boundary above which optimal investment in antipredator behaviour > 0. Dashed lines are predator and prey isoclines. From Ives & Dobson (1987).

The above conclusions may change if the prey's resources are included in the model. Ecologists working with fish have repeatedly demonstrated that behavioural decisions in animals which are simultaneously predator and prey, have to be based on a trade-off between foraging gains and predation risk (Milinski & Heller 1978, Werner et al. 1983b, Cerri & Fraser 1983, Power 1984, Gilliam & Fraser 1987, Godin & Smith 1988). Adaptive animals change behaviour in response to both predation risk and resource levels, which makes the inclusion of mortality risk an essential step in the development of foraging theory. Werner & Gilliam (1984) presented a theoretical framework for predicting habitat choice, given a growth rate/mortality rate trade-off associated with each habitat. They advocated the decision rule "minimize mortality risk per unit growth increment", as a simple alternative to the rule "maximize energy intake per unit time" traditionally used in foraging theory. Within this framework, habitat (and hence dietary) overlap or segregation between species (or size classes) can be predicted from the resource levels and predation risks associated with each habitat (Gilliam & Fraser 1988).

Abrams (1982, 1984, 1987) analyzed population dynamics resulting from risk-sensitive foraging under the assumption of a trade-off between resource consumption and predator avoidance. He showed that an adaptive consumer could have an overall functional response to resource density with several accelerating and decelerating sections (Abrams 1982). In three trophic level models, indirect effects (i.e. interactions between the resource and top consumer populations or between the top consumers intraspecifically) arising from foraging effort optimization in the intermediate consumer could be of the same order of magnitude as the effects between the directly linked populations (Abrams 1984). Finally, if a second intermediate consumer is introduced into the model, both apparent competition and mutual enhancement between the two intermediate consumers may occur, and their risk-sensitive foraging behaviour may lead to increases or decreases in equilibrium densities of all populations involved, when compared to a behaviourally static situation (Abrams 1987).

From the above discussion, it becomes clear that the assumption of adaptive behaviour in organisms fundamentally changes the nature of the equations used in modelling population dynamics. In many situations, population models have to become more mechanistic in order to account for important indirect effects. For example, adaptive behaviour in competitors and their resources may require the inclusion of resource dynamics in the competition models. Consequently, competition can no longer be modelled by equations using standard competition coefficients. Instead, competitors should be treated as predators preying upon one or more common resources (Abrams 1980d). Similarly, predator-prey models, which traditionally consider only the numerical effects of predator and prey, must take into account how behavioural responses to changes in population densities affect the predation rate. Finally, models of competition under predation have to consider that both the numerical and the behavioural effects of the predator may change the intensity of the competitive interactions (see Kotler & Holt 1989 for a more detailed discussion). To account for the possibility of predator-induced behavioural effects on competitive interactions, the per capita growth rates of competing prey species (g) traditionally represented as in eqn. (4a) (e.g. Vance 1978, Gleeson & Wilson 1986) will also have to be made functions of predator density as in eqn. (4b) (Kotler & Holt 1989):

$$dH_i/dt = H_i g_i(H_i, H_j) - Pf_i(H_i,H_j) \qquad (4a)$$

$$dH_i/dt = H_i g_i(H_i, H_j, P) - Pf_i(H_i,H_j). \qquad (4b)$$

Kotler & Holt (1989) suggest that models (4a) and (4b) are appropriate for different kinds of communities and that mobile organisms competing for food in heterogeneous environments (for example most fish species) may best be characterized by model (4b). An example of behaviourally mediated interspecific competition has been theoretically investigated by Mittelbach & Chesson (1987). They modelled the interaction between the bluegill and the pumpkinseed sunfish (Fig. 6). In the absence of predators, interspecific competition between bluegills and juvenile pumpkinseeds is rather weak, and intraspecific size-class competition is present only in the bluegill (Werner & Hall 1979, Werner et al. 1983a, Mittelbach & Chesson 1987). Presence of predators restricts juvenile bluegills to the vegetation, where they compete intensely with juvenile pumpkinseeds (Mittelbach & Chesson 1987, Mittelbach 1988). Although direct competition between the adults is absent in the model, indirect competition between the adults arises because adult fecundity translates into density-dependent survival of the juveniles.

5. The integration of behavioural and population/community ecology in a mechanistic perspective

It is evident that population/community ecologists in many cases need to consider the implications of flexible behaviour by predators and their prey. It is equally true that behavioural ecologists

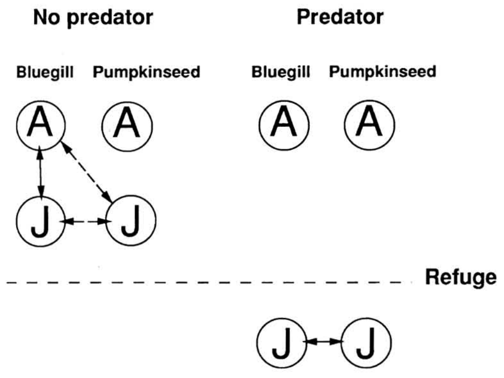

Fig. 6. Competitive interactions between juveniles (J) and adults (A) of the bluegill and pumpkinseed sunfishes. In the absence of a predator, both juvenile and adult bluegills compete for zooplankton in the open water (solid arrows) (Werner et al. 1983b). Juvenile pumpkinseeds, which feed with higher efficiency on benthic prey than juvenile bluegills (Werner & Hall 1979), probably compete rather weakly with both size classes of bluegill (hatched arrows). Adult pumpkinseeds specialize on an exclusive resource (snails). In the presence of a gape-limited predator (e.g. largemouth bass), juveniles of both sunfish species are restricted to a common refuge (littoral vegetation), where they have similar foraging capacities, resulting in intense juvenile competition (Mittelbach 1984, 1988, Mittelbach & Chesson 1987). The adults of both species are not affected by the presence of the predator.

should not neglect population/community aspects. Consideration of these subjects is especially important because of the present trend towards behavioural ecology being split up into a purely behaviour oriented current, and a more population oriented current (compare for example Krebs & Davies 1977 with Krebs & Davies 1984, Hughes 1990). At its simplest, effects of population numbers on the behaviour of an individual can be monitored through effects on resource levels. In other behavioural scenarios, such as theories based on the ideal free distribution (Sutherland & Parker 1984) and theories based on group dynamics (Pulliam & Caraco 1984), population aspects are introduced as the number of individuals. On a short time scale (relative to population processes), population numbers can be approximated to a constant, and it may be sufficient simply to include population density in models as an input variable like other environmental variables (Schoener 1986). However, on a longer time scale, it may be necessary to explicitly introduce population dynamics, because population numbers will have feedback on individual strategies and how to predict them (Schoener 1986). Consider, for example, the arms-race analogy in predator-prey dynamics. According to this analogy, an (antipredator) adaptive change in the prey species will cause a counteradaptation in the predator species to overcome prey defences, which will, at least partly, offset the prey antipredator adaptation (Dawkins & Krebs 1979). This analogy was developed without considering population dynamics, but an analysis by Abrams (1986) using explicit population models suggests that the arms race analogy will fail under many circumstances. One reason for this (among others), is that an increased investment in prey defence will cause an increase in prey population numbers, which in turn results in resource availability (as sensed by the predator) remaining unchanged.

At present, there exist mechanistic models and experimental tests of population regulation for several specific ecological systems (e.g. Abrams 1980a, 1981a, b, Tilman 1982, 1988, Belovsky 1984a, b, 1986). These studies have successfully incorporated ecophysiological parameters into population models. Behavioural concepts, especially those of foraging theory, have so far only been included either in a rather general way in purely theoretical population models (Abrams 1982, 1984, 1987, Sih 1984, Holt 1983, 1984), or in more detailed mechanistic models that have been experimentally tested, but lack explicit population parameters (Mittelbach 1981, Werner et al. 1983a, Osenberg & Mittelbach 1989, Persson & Greenberg 1990b). Schoener (1986) tried to show that there is no formal impediment to extending the domain of mechanistic population models to include behaviourally flexible organisms, size-structured populations or many-species food webs, but expressed the reservation that the resulting complexity of the models could be a major practical impediment. This trade-off suggests that the cost of incorporating additional mechanistic details of predator or prey behaviour into population/community models has to be carefully balanced against the resulting increase in understanding of community organization. An overly mechanistic approach might in some cases obscure insight into general patterns, and be a rather unproductive research strategy. On the level of science theory, the difference between formal and practical impediment reflects the questions whether ontological or epistemological reduction is possible, and whether methodological reduction is desirable (ontological reductionism relates to whether behavioural entities and processes underlie population processes, epistemological reductionism to whether population models may be built on behavioural ecological concepts and variables, whereas methodological reductionism relates to whether or not the most productive way to study population/community processes is always to study the underlying behavioural processes, see Persson 1990).

In Schoener's (1986) view, community, population and individual form a perfect hierarchy. This may be true at the ontological level, as all community processes result from the births, deaths and movements of individuals. However, it is less certain that all processes at the population and community levels may be deduced from individual properties, and this is crucial to our interpretation of the mechanistic approach to population/community ecology as being a "basis for constructing a theoretical framework with which to interpret the phenomena of community ecology" (Schoener 1986). In our view, the hierarchy community-population-individual is incomplete not only at the methodological level but also at the epistemological level. For example, it is likely that temporal and spatial scale-dependent processes (see Carpenter 1988) may set explicit constraints on what can be deduced from individual properties. Considering this, we suggest that in approaching processes with temporal and spatial scale-dependent complexity, we need a research strategy including studies on different scales, from laboratory experiments to whole system studies, studies at different levels being interpreted in relation to other levels (Table 2). Table 2 also explicitly shows the advantages of an integrative mechanistic approach compared to a more traditional approach (i.e. Diamond 1986) with respect to questions raised on different spatial scales. In an integrative mechanistic approach, laboratory studies could, for example, be directed towards the foraging rate of a predator on different prey types to provide a mechanistic understanding of population processes and possibly also to predict population and community statics (see sections 2.3, 3.2 above and Persson 1990). In contrast, studies of explicit population and community dynamics will be referred to larger scales (Table 2),

Table 2. Comparison between an integrative mechanistic approach and a more traditional approach with respect to examples of questions raised in experiments on different spatial scales.

Type of experiment	Scale time/space	Replication	Integrative mechanistic approach Questions	Generality	Realism	Traditional approach Questions	Generality	Realism
Laboratory experiment	shortest/ smallest	easy	Foraging rate* vs. prey density food conversion	high	moderate	Diet, growth fecundity popul. dynam.	low	lowest
Field experiment (enclosure)	short/ small	feasible	Foraging search* behaviour diet, growth fecundity	high	high	Diet, growth fecundity popul. dynam.	moderate	low
Field experiment (whole system)	long/ large	difficult	Diet, growth fecundity popul. dynam.	high	high	Diet, growth fecundity popul. dynam.	high	high
Field study (comparative)	longest/ largest	feasible	Diet, growth fecundity popul. dynam.	high	high	Diet, growth fecundity popul. dynam.	high	highest

* provides mechanistic understanding of processes on larger scales

the interpretation of phenomena observed being related to laboratory experiments. In contrast to traditional approaches, the questions raised will thus be scale-dependent, which in turn has the result that the generality and realism of the studies will largely be scale-independent (see Table 2).

It is still premature to say which aspects of behaviour are of such importance that they cannot be ignored in population models. Researchers dealing with foraging theory have, up to now, focused mainly on predator behaviour, emphasizing the role of the predator's habitat and diet choice in species interactions (see Pulliam 1989 for a recent example). In contrast, the fact that encounter probabilities are not simple functions of predator type, prey type and prey density, but are partly under behavioural control has received less attention. Both the theoretical and the experimental studies reviewed here suggest that:

1) predator decisions that alter the probability of encounter with prey may have a greater impact on individual performance and population dynamics than predator decisions whether or not to attack a prey encountered, and
2) flexible predator-avoidance behaviour in the prey may have far-reaching population consequences.

Furthermore, a recent review suggests that in many cases, prey behaviour may be more important in determining predator diets than predator choice (Sih 1990). From the above, it may be concluded that the encounter, attack and capture probabilities (which combined make up to the attack coefficient *a* of population models) all have behaviourally flexible components that have the potential to affect population dynamics. We suggest that predator and prey behaviours affecting encounter rates are especially important in this context, and deserve more attention in the future.

It is obvious that a theory taking into account all the above-listed aspects of predator and prey behaviour must be rather specific. Schoener (1986) speculates in his "mechanistic ecologist's utopia" that future community ecology might develop a pluralistic, organism- and system-specific theory, where models will have to be mechanistically justifiable, de-emphasizing macroparameters of community ecology and the mere description of structure and interactions. However, ecologists have always attempted to discover universal patterns and tried to explain them by theories that have the virtue of generality. Theories relating community organization to such factors as productivity, disturbance or spatial structure (Hairston et al. 1960, Oksanen et al. 1981, Menge & Sutherland 1987) will undoubtedly lose their claim to general validity if too many mechanistic details are incorporated. Thus, although a mechanistic research program may be a major trend at present, ecology will still need less mechanistic, but more general theories.

Acknowledgements. We thank Paul Haemig, Heikki Hirvonen and Andy Turner for comments on a previous draft of this paper. We also thank Kai Lindström and Esa Ranta for inviting us to attend the symposium on "Behaviour of Fishes — Ecological Consequences" and making our stay at Tvärminne field station such a pleasant one. Support for the research on which parts of this paper are based was given by the Swedish Natural Science Research Council to Lennart Persson. Sebastian Diehl was supported by a grant from the Swedish Council for Forestry and Agricultural Research to Lennart Persson.

References

Abrams, P. A. 1975: Limiting similarity and the form of the competition coefficient. — Theor. Pop. Biol. 8:356–375.

— 1980a: Resource partitioning and interspecific competition in a tropical hermit crab community. — Oecologia (Berl.) 46:365–379.

— 1980b: Are competition coefficients constant? Inductive versus deductive approaches. — Amer. Nat. 116:730–735.

— 1980c: Some comments on niche overlap. — Ecology 61:44–49.

— 1980d: Consumer functional response and competition in consumer-resource systems. — Theor. Pop. Biol. 17:80–102.

— 1981a: Alternative methods of measuring competition applied to Australian hermit crabs. — Oecologia (Berl.) 51:233–239.

— 1981b: Competition in the Indo-Pacific hermit crab community. — Oecologia (Berl.) 53:240–249.

— 1982: Functional responses of optimal foragers. — Amer. Nat. 120:382–390.

— 1983: The theory of limiting similarity. — Ann. Rev. Ecol. Syst. 14:359–376.

— 1984: Foraging time optimization and interactions in food webs. — Amer. Nat. 124:80–96.

— 1986: Adaptive responses of predators to prey and prey to predators: The failure of the arms-race analogy. — Evolution 40:1229–1247.

— 1987: Indirect interactions between species that share a predator: varieties of indirect effects. — In: Kerfoot, W. C. & Sih, A. (eds.), Predation: direct and indirect impacts on aquatic communities: 38–54. New England University Press, Hanover.

Andersson, M. 1980: On optimal predator search. — Theor. Pop. Biol. 19:58–86.

Belovsky 1984a: Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. — Oecologia (Berl.) 61:150–159.

— 1984b: Snowshoe hare optimal foraging and its implications for population dynamics. — Theor. Pop. Biol. 25:235–264.

— 1986: Optimal foraging and community structure: Implications for a guild of generalist grassland herbivores. — Oecologia (Berl.) 70:35–52.

Carpenter, S. R. 1988: Transmission of variance through lake food webs. — In: Carpenter, S. R. (ed.), Complex Interactions in Lake Communities: 119–135. Springer Verlag, New York.

Case, T. J. 1979: Optimal size and an animal's diet. — Acta Biotheoretica 28:54–69.

Cerri, R. D. & Fraser, D. F. 1983: Predation and risk in foraging minnows: Balancing conflicting demands. — Amer. Nat. 121:552–561.

Comins, H. N. & Hassell, M. P. 1976: Predation in multiprey communities. — J. Theor. Biol. 62:93–114.

— 1979: The dynamics of optimally foraging predators and parasitoids. — J. Anim. Ecol. 48:335–351.

— 1987: The dynamics of predation and competition in patchy environments. — Theor. Pop. Biol. 31:393–421.

Cramer, N. F. & May, R. M. 1972: Interspecific competition, predation, and species diversity: a comment. — J. Theor. Biol. 34:289–293.

Dawkins, R. & Krebs, J. R. 1979: Arms race between and within species. — Proc. Royal Soc. Lond. B 205:489–511.

Diamond, J. 1986: Overview: laboratory experiments, field experiments, and natural experiments. — In: Diamond, J. M. & Case, T. J. (eds.), Community ecology: 3–22. Harper & Row, New York.

Dill, L. M. 1987: Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. — Can. J. Zool. 65:803–811.

Ebenman, B. & Persson, L. 1988: Dynamics of size-structured populations — an overview. — In: Ebenman, B. & Persson, L. (eds.), Size-structured populations: ecology and evolution: 3–9. Springer, Berlin.

Ehlinger, T. 1989: Learning and individual foraging in bluegill sunfish: habitat specific techniques. — Animal Behav. 38:643–658.

Gendron, R. P. & Staddon, J. E. R. 1983: Searching for cryptic prey: the effect of search rate. — Amer. Nat. 121:172–186.

Gilliam, J. F. 1982: Habitat use and competitive bottlenecks in size-structured populations. — Ph. D. thesis, Michigan State University.

Gilliam, J. F. & Fraser, D. F. 1987: Habitat selection under predation hazard: test of a model with foraging minnows. — Ecology 68:1856–1862.

— 1988: Resource depletion and habitat segregation by competitors under predation hazard. — In: Ebenman, B. & Persson, L. (eds.), Size-structured populations: ecology and evolution: 173–184. Springer, Berlin.

Gleeson, S. K. & Wilson, D. S. 1986: Equilibrium diet: optimal foraging and prey coexistence. — Oikos 46:139–144.

Godin, J.-G. J. 1990: Diet selection under the risk of predation. — In: Hughes, R. N. (ed.), Behavioural mechanisms of food selection. NATO ASI Series, Subseries G: Ecological Sciences: 739–770. Springer, Heidelberg.

Godin, J.-G. J. & Smith, S. A. 1988: A fitness cost of foraging in the guppy. — Nature 333:69–71.

Goss-Custard, J. D. 1977: Optimal foraging and the size selection of worms by redshank, Tringia totanus (L.), and a preferred prey, Corophium volutator (Pallus). — J. Animal Ecol. 46:21–35.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960: Community structure, population control and competition. — Amer. Nat. 94:421–425.

Hamrin, S. F. & Persson, L. 1986: Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. — Oikos 47:223–232.

Hassell, M. P. 1978: The dynamics of arthropod predator-prey systems. — Princeton University Press, Princeton.

Hassell, M. P. & May, R. M. 1973: Stability in insect host-parasite models. — J. Animal Ecol. 42:693–726.

— 1974: Aggregation in predators and insect parasites and its effect on stability. — J. Animal Ecol. 43:567–594.

— 1985: Individual behaviour and population dynamics. — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural ecology: Ecological consequences of adaptive behaviour: 3–32. Blackwell's, Oxford.

Holling, C. S. 1959: Some characteristics of simple types of predation and parasitism. — Can. Entomol. 91:385–398.

Holt, R. D. 1983: Optimal foraging and the form of the predator isocline. — Amer. Nat. 122:521–541.

— 1984: Spatial heterogeneity, indirect interactions, and the coexistence of prey species. — Amer. Nat. 124:377–406.

Hughes, R. N. 1979: Optimal diets under the energy maximization premise: the effects of recognition time and learning. — Amer. Nat. 113:209–221.

— (ed.) 1990: Behavioural mechanisms of food selection. — NATO ASI Series, Subseries G: Ecological Sciences. Springer, Heidelberg.

Ives, A. R. & Dobson, A. P. 1987: Antipredator behaviour and the population dynamics of simple predator-prey systems. — Amer. Nat. 130:431–447.

Jaeger, R. G. & Barnard, D. E. 1981: Foraging tactics of a terrestrial salamander: choice of diet in structurally simple environments. — Amer. Nat. 117:639–664.

Kirkpatrick, M. 1988: The evolution of size in size-structured populations. — In: Ebenman, B. & Persson, L. (eds.), Size-structured populations: ecology and evolution: 13–28. Springer, Berlin.

Kotler, B. P. & Holt, R. D. 1989: Predation and competition: the interaction of two types of species interactions. — Oikos 54: 256–260.

Krebs, J. R. & Davies, N. B. (eds.) 1977: Behavioural ecology: An evolutionary approach. First ed. — Blackwell Scientific Publications, Oxford.

— 1984: Behavioural ecology: An evolutionary approach. Second Edition. Blackwell Scientific Publications, Oxford.

Krebs, J. R. & McCleery, R. H. 1984: Optimization in behavioural ecology. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: An evolutionary approach: 91–121. Blackwell Scientific Publications, Oxford.

Levins, R. 1968: Evolution in changing environments. — Princeton University Press, Princeton, New Jersey.

Lomnicki, A. 1980: Regulation of population density due to individual differences and patchy environment. — Oikos 35:185–193.

— 1988: Population ecology of individuals. — Princeton University Press, Princeton, New Jersey.

MacArthur, R. H. 1972: Geographical ecology: Patterns and distributions of species. — Harper & Row, Publishers, Inc., New York.

MacArthur, R. H. & Levins, R. 1967: The limiting similarity, convergence and divergence of coexisting species. — Amer. Nat. 101:377–385.

MacArthur, R. H. & Pianka, E. R. 1966: On optimal use of a patchy environment. — Amer. Nat. 100:603–609.

Mangel, M. & Clark, C. W. 1986: Towards a unified foraging theory. — Ecology 67:1127–1138.

Maynard Smith, J. 1974: Models in ecology. — Cambridge Univ. Press, Cambridge.

McNair, J. N. 1980: A stochastic foraging model with predator training effects: I. Functional response, switching, and run lengths. — Theor. Popul. Biol. 17:141–166.

— 1986: The effects of refuges on predator-prey interactions: a reconsideration. — Theor. Pop. Biol. 29:38–63.

McNamara, J. M. & Houston, A. I. 1986: The common currency for behavioral decisions. — Amer. Nat. 127:358–378.

Menge, B. & Sutherland, J. P. 1987: Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. — Amer. Nat. 130: 730–757.

Metz, J. A. J. & Diekmann, O. 1986: The dynamics of physiologically structured populations. — Springer, Berlin.

Metz, J. A. J., De Roos, A. M. & van den Bosch, F. 1988: Population models incorporating physiological structure: A quick survey of the basic concepts and an application to size-structured population dynamics in waterfleas. — In: Ebenman, B. & Persson, L. (eds.), Size-structured populations: ecology and evolution: 106–126. Springer, Berlin.

Milinski, M. & Heller, R. 1978: Influence of a predator on the optimal foraging behaviour of sticklebacks (Gasterosteus aculeatus L.). — Nature 275:642–644.

Mittelbach, G. G. 1981: Foraging efficiency and body size: a study of optimal diet and habitat use by bluegill sunfish. — Ecology 62:1370–1386.

— 1983: Optimal foraging and growth in bluegills. — Oecologia 59:157–162.

— 1984: Predation and resource partitioning in two sunfishes (Centrarchidae). — Ecology 65:499–513.

— 1988: Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. — Ecology 69:614–623.

Mittelbach, G. G. & Chesson, P. L. 1987: Predation risk: indirect effects on fish populations. — In: Kerfoot, W. C. & Sih, A. (eds.), Predation: direct and indirect impacts on aquatic communities: 315–332. New England University Press, Hanover.

Mittelbach, G. G., Osenberg, C. W. & Leibold, M. A. 1988: Trophic relations and ontogenetic niche shifts in aquatic ecosystems. — In: Ebenman, B. & Persson, L. (eds.), Size-structured populations: ecology and evolution: 315–332. Springer, Berlin.

Murdoch, W. W. 1969: Switching in general predators: experiments on predator specifity and stability of prey populations. — Ecol. Monogr. 39:335–354.

— 1973: The functional response of predators. — J. Appl. Ecol. 10:335–341.

Murdoch, W. W. & Oaten, A. 1975: Predation and population stability. — Adv. Ecol. Res. 9:1–131.

Neill, W. E. 1975: Experimental studies of microcrustacean competition, community composition and resource utilization. — Ecology 56:809–826.

Norberg, R. Å. 1977: An ecological theory on foraging time and energetics and choice of optimal food-searching method. — J. Animal Ecol. 46:511–529.

Noy-Meir, I. 1981: Theoretical dynamics of competitors under predation. — Oecologia (Berlin) 50:277–284.

O'Brien, W. J. 1987: Planktivory by freshwater fish: thrust and parry in the pelagia. — In: Kerfoot, W. C. & Sih, A. (eds.), Predation: direct and indirect impacts on aquatic communities: 3–16. New England University Press, Hanover.

Oksanen, L. Fretwell, S. D., Arruda, J. & Niemelä, P. 1981: Exploitation ecosystems in gradients of primary productivity. — Amer. Nat. 118:240–261.

Osenberg, C. W. & Mittelbach, G. G. 1989: The effects of body size on predator-prey interaction between pumpkinseed sunfish and gastropods. — Ecol. Monogr. 59:405–432.

Persson, L. 1985: Asymmetrical competition — are larger animals competitively superior? — Amer. Nat. 26:261–266.

— 1986: Effects of reduced interspecific competition on resource utilization of perch (Perca fluviatilis). — Ecology 67:355–364.

— 1987a: The effects of resource availability and distribution on size class interactions in perch (Perca fluviatilis). — Oikos 48:148–160.

— 1987b: Effects of habitat and season on competitive interactions between roach (Rutilus rutilus) and perch (Perca fluviatilis). — Oecologia (Berl.) 73:170–177.

— 1988: Asymmetries in predatory and competitive interactions in fish populations. — In: Ebenman, B. & Persson, L. (eds.), Size-structured populations: ecology and evolution: 203–218. Springer, Berlin.

— 1990: Predicting ontogenetic niche shifts in the field: What can be gained by foraging theory? — In: Hughes, R. N. (ed.), Behavioural mechanisms of food selection. NATO ASI Series, Subseries G: Ecological Sciences: 303–321. Springer, Heidelberg.

Persson, L. & Greenberg, L. A. 1990a: Juvenile competitive bottlenecks: the perch (Perca fluviatilis)-roach (Rutilus rutilus) interaction. — Ecology 71:44–56.

— 1990b: Optimal foraging and habitat shifts of perch (Perca fluviatilis) in an experimentally-induced resource gradient. — Ecology 71 (in press).

Power, M. E. 1984: Depth distributions of armored catfish: predator-induced resource avoidance? — Ecology 65:523–528.

Pulliam, H. R. 1989: Individual behaviour and the procurement of essential resources. — In: Roughgarden, J., May, R. M. & Levin, S. A. (eds.), Perspectives in ecological theory: 25–38. Princeton University Press, Princeton.

Pulliam, H. R. & Caraco,T. 1984: Living in groups: Is there an optimal group size? — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: An evolutionary approach: 122–147. Blackwell Scientific Publications, Oxford.

Pyke, G. H. 1984: Optimal foraging theory: a critical review. — Ann. Rev. Ecol. Syst. 15:523–575.

Roughgarden, J. 1974: Species packing and the competition function with illustrations from coral reef fish. — Theor. Pop. Biol. 5:163–186.

Schoener, T. W. 1969: Models of optimal body size for solitary predators. — Amer. Nat. 103:227–313.

— 1974: Some methods for calculating competition coefficients from resource-utilization spectra. — Amer. Nat. 108:332–340.

— 1986: Mechanistic approaches to community ecology: a new reductionism? — Amer. Zool. 26:81–106.

Sebens, K. P. 1988: The ecology of indeterminate growth. — Ann. Rev. Ecol. Syst. 18:371–407.

Sih, A. 1984: Optimal behavior and density-dependent predation. — Amer. Nat. 123:314–326.

— 1987a: Predators and prey lifestyles: an evolutionary and ecological overview. — In: Kerfoot, W. C. & Sih, A. (eds.), Predation: direct and indirect impacts on aquatic communities: 203–224. New England University Press, Hanover.

— 1987b: Prey refuges and predator-prey stability. — Theor. Pop. Biol. 31:1–12.

— 1990: Interacting effects of predator and prey behaviour in determining diets. — In: Hughes, R. N. (ed.), Behavioural mechanisms of food selection. NATO ASI Series, Subseries G: Ecological Sciences: 771–796. Springer, Heidelberg.

Stenseth, N. C. 1980: Spatial heterogeneity and population stability: some evolutionary consequences. — Oikos 35:165–184.

Stephens, D. W. & Krebs, J. R. 1986: Foraging theory. — Princeton University Press. Princeton, New Jersey.

Sutherland, W. J. & Parker, G. A. 1984. Distribution of unequal competitors. — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural ecology: Ecological consequences of adaptive behaviour: 255–273. Blackwell's, Oxford.

Tanner, J. T. 1975: The stability and the intrinsic growth rates of prey and predator populations. — Ecology 56:855–867.

Tilman, D. 1982: Resource competition and community structure. — Princeton University Press, Princeton, New Jersey.

— 1988: Dynamics and structure of plant communities. — Princeton University Press, Princeton, New Jersey.

Vance, R. R. 1978: Predation and resource partitioning in one predator-two prey model communities. — Amer. Nat. 112:797–813.

Wainwright, P.C. 1988: Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. — Ecology 69:635–645.

Werner, E. E. 1977: Species packing and niche complementarity in three sunfishes. — Amer. Nat. 111:553–578.

— 1986: Species interactions in freshwater fish communities. — In: Diamond, J. M. & Case, T. J. (eds.), Community ecology: 344–358. Harper & Row, New York.

— 1988: Size, scaling and the evolution of life cycles. — In: Ebenman, B. & Persson, L. (eds.), Size structured populations: 60–81. Springer Verlag, Berlin.

Werner, E. E. & Gilliam, J. F. 1984: The ontogenetic niche and species interactions in size-structured populations. — Ann. Rev. Ecol. Syst. 15:393–425.

Werner, E. E. & Hall, D. J. 1977: Competition and habitat shift in two sunfishes (Centrarchidae). — Ecology 58:869–876.

— 1979: Foraging efficiency and habitat switching in competing sunfishes. — Ecology 60:256–264.

— 1988: Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. — Ecology 69:1352–1366.

Werner, E. E., Hall, D. J., Laughlin, D. R., Wagner, D. J., Wilsman, L. A. & Funk, F. C. 1976: Habitat partitioning in a freshwater fish community. — J. Fish. Res. Board Can. 34:360–370.

Werner, E. E., Mittelbach, G. G. & Hall, D. J. 1981: The role of foraging profitability and experience in habitat use by the bluegill sunfish. — Ecology 62:116–125.

Werner, E. E., Mittelbach, G. G., Hall, D. J. & Gilliam, J. F. 1983a: Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. — Ecology 64:1525–1539.

Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. 1983b: An experimental test of the effects of predation risk on habitat use in fish. — Ecology 64:1540–1548.

Wilson, D. S. 1975: The adequacy of body size as a niche difference. — Amer. Nat. 109:769–784.