

Fish predation and local prey diversity

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Synopsis

Local species richness and evenness of a prey assemblage can change in a variety of patterns as the intensity of predation by fishes increases. Documenting this pattern requires measurements of prey diversity at a minimum of three widely spaced predation intensities. The particular pattern that occurs depends largely upon: (1) the processes structuring the prey assemblage in the absence of fish predation (recruitment limitation, physical disturbances, non-fish predators, mutualisms, competitive networks, or competitive hierarchies); (2) the pattern of prey population reduction by fish predation (equivalent, disproportionate on competitive dominants, or disproportionate on competitive subordinates); and (3) the processes governing local extinctions and immigrations in the prey assemblage (prey refuges, recruitment patterns, and local versus global species richness). A literature review of the impact of fish predation on other fishes, plankton, and benthos in a variety of freshwater and marine systems indicated that local effects on prey diversity are seldom documented adequately. Only seven experiments documented both prey diversity as a function of at least three predation intensities, as well as the probable mechanisms underlying the prey diversity response. Of these, two studies of freshwater benthos detected virtually no effects on prey diversity, apparently due to rapid prey recolonization or predator inefficiency. Two studies of freshwater zooplankton and three studies of coral-reef algae detected keystone-predator induced hump-shaped patterns characteristic of the intermediate-disturbance hypothesis. Two additional studies of coral-reef benthos detected negative effects on prey diversity over a range of at least three predation intensities, but the underlying mechanisms were unclear. Spatial prey refuges, particularly those provided by aquatic plants on soft bottoms and crevices on hard bottoms, have been shown to minimize the effects of fish predation on the diversity of benthic assemblages in both freshwater and marine systems. The concepts summarized in this paper suggest improvements for future studies of the impact of fishes on prey community structure.

Introduction

Species diversity is one of the major parameters characterizing ecological communities (Pielou 1975). The fact that predators can influence the local or within-habitat diversity of their prey has been known at least since the time of Darwin, and

the general importance of predators in structuring prey communities is well documented (review by Connell 1975). However, only recently have the effects of predation by fishes on prey diversity been studied explicitly. (Here I include both carnivory and herbivory as forms of predation [Lubchenco 1979].) Early field manipulations in freshwater sys-

tems showed that fish predation can influence the local abundance of plants (Anderson 1950, Threinen & Helm 1954) and invertebrates (Ball & Hayne 1952, Hayne & Ball 1956), but effects on prey diversity per se were not reported. Not until the 1960's, with the surge of interest in community ecology, did researchers design studies to determine how fishes influence the local species richness and relative abundances of their prey.

The goals of this review are threefold. First, I will synthesize the general concepts on how predators may affect local prey diversity. This synthesis indicates the kinds of information needed for determining both the patterns by which prey diversity responds to increasing predation intensity, as well as the mechanisms underlying those patterns. Second, I will review field studies of the effects of fish predation on prey diversity in various freshwater and marine systems in an effort to document the extent of our knowledge on this subject. This survey includes papers appearing in major English-language journals and books published through 1984. Third, I will suggest approaches for future research. My ultimate intent is to provide a general conceptual framework for further studies.

Definitions

The pattern by which predation affects prey diversity is determined by examining the 'local species diversity' of the prey assemblage as a function of 'predation intensity', that is, by examining what I will call the prey 'diversity-response' curve (see Fig. 1 for examples). Before proceeding, these key variables must be defined. 'Species diversity' consists of two components (Pielou 1975): species number (richness) and equitability of relative abundances among species (evenness). Popular indices of diversity (such as the Shannon-Wiener H') combine these components into a single composite measure (reviews by Peet 1974, Pielou 1975). I will call such measures 'composite diversity' to distinguish them from measures of richness and evenness. Because richness and evenness can vary independently and because different composite measures differ in their sensitivity to changes in these components, it is necessary to consider richness

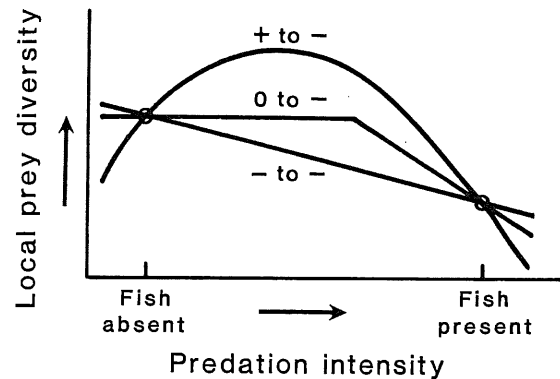


Fig. 1. Fish removal or exclosure experiments provide data on only two levels of predation intensity (fish present and fish absent), which are insufficient to determine the overall shape of the prey diversity-response curve. In this example, the same two points could lie on any one of three different curves: a hump-shaped response (+ to -), no response shifting to a negative response (0 to -), and a purely negative response (- to -).

and evenness separately if the mechanisms underlying prey diversity responses are to be elucidated.

'Local' species diversity is a more problematical and subjective concept. Although 'local' generally means 'within-habitat', the spatial scale of the local system can be either the entire habitat or a subsection of any size, determined entirely by the area or volume of the habitat that a researcher studies. Thus, for two examples, 'local' can refer to the entire plankton community in a small pond or to the benthic assemblage occupying a single settling plate on a large coral reef. This fact renders comparisons between different systems difficult, if not impossible. In any case, this paper deals with local or within-habitat (as opposed to global or between-habitat) species diversity.

Because the prey diversity response includes changes in evenness, the definition of predation intensity must include the effects of predators on the sizes of prey populations. Therefore, 'predation intensity' is defined here as a measure of the extent to which the combined abundances of the affected prey species are reduced by predation relative to their combined abundances in the absence of predation. The term 'affected' is important because some prey populations may not be reduced significantly by predators. Thus, if a prey population responds to increased predation pressure by compensatory increases in reproduction and/or re-

cruitment, such that the population size is unaffected, then the effective predation intensity is zero as far as any change in prey diversity is concerned. Similarly, if spatial refuges or prey defenses prevent predators from affecting prey population sizes, then the effective predation intensity is also zero. Because of these factors, the most common measure of predation intensity – the population density of predators – may be inaccurate in some cases and is best replaced by direct measures of prey population reductions.

General concepts on predation and prey diversity

Our knowledge of the patterns and mechanisms by which predators affect the diversity of their prey has come from a large number of empirical studies (reviews by Harper 1969, Connell 1975, Murdoch & Oaten 1975, Lubchenco & Gaines 1981, Sousa 1984). Particular progress in this area has been made in studies of rocky intertidal systems (Paine 1966, Paine & Vadas 1969, Menge & Sutherland 1976, Lubchenco 1978, reviews by Paine 1977, Hughes 1980). Close behind the fieldworkers have been the theoreticians, who have modelled various scenarios concerning the effects of different kinds of predation on the diversity of different kinds of prey assemblages (MacArthur 1972, Smith 1972, Emlen 1973, Van Valen 1974, Holt 1977, Caswell 1978, Hastings 1978, Yodzis 1978, Crowley 1979, Huston 1979). These empirical and theoretical studies have produced a set of concepts that cannot be attributed to any single investigator; the following synthesis reflects and extends the work of many individuals.

As with any conceptual generalization, many complicating factors of real systems are excluded from this review. Two such complexities are perhaps most relevant to the present analysis. The first is the role of ontogenetic shifts in species interactions, such as cases where one species may prey upon the young of another species, yet be competitively dominated by the surviving adults of that same species (review by Werner & Gilliam 1984). Thus, the boundary between predation and competition is not always as obvious as the general con-

cepts would lead us to believe. The second complexity is the temporal scale of the prey diversity response. Such responses do not occur instantly. If predation intensity changes suddenly, as in the case of all predator manipulation experiments, a certain (often unknown) period of time will pass before prey diversity stabilizes. Although few field studies have determined whether a documented prey diversity response is transient or equilibrial, long-term studies should be regarded as more appropriate than short-term studies in evaluating the concepts discussed below. This is because these concepts are generally based on the assumption that prey diversity reaches some equilibrium value at each successive level of predation intensity.

To determine how fish may affect the local diversity of their prey, the structure of the prey assemblage in the absence of fish predation must first be known. With fish absent, the prey assemblage at any given time will be structured predominantly by one of five categories of factors: (1) pre-settlement factors (recruitment limitation, e.g., Keough 1983) or post-settlement events (physical disturbances, e.g., Sousa 1979) which limit population abundances to levels where substantial interactions among the prey species are precluded; (2) predation (or parasitism) by animals other than fishes; (3) mutualisms among the prey species; (4) non-transitive competitive networks (Buss & Jackson 1979); or (5) linear competitive hierarchies. Note that, while one of these factors should predominate at any one time, any given prey assemblage is probably structured by a cyclical or noncyclical sequence of several factors over the course of ecological time. Thus, considering these factors separately is a further (albeit necessary) conceptual simplification. In any case, once the determinants of the richness and evenness of the prey assemblage in the absence of fish predation are known, the effects and underlying mechanisms of the addition of fishes can be inferred by comparison.

Little information is available on the effects of adding fish predators to prey systems structured by recruitment limitation, physical disturbances, or non-fish predation, and virtually none is available for systems structured by mutualisms or competitive networks. The following discussion hypothes-

izes the prey diversity responses that would occur in prey assemblages structured by each of these categories of factors, as summarized in Table 1.

In the first category (Table 1A), limited recruitment and/or physical disturbances prevent the prey populations from reaching densities where they interact, so the local population size of any one prey species is unaffected by that of any other prey species. Therefore, the addition of fish to the system may or may not increase prey evenness, depending upon which prey populations are reduced. At high predation intensities, prey richness will decline as some species become locally extinct. Due to the lack of interactions between the prey populations, the extinction of one prey species cannot allow the immigration of any new prey species, so predation should not increase prey richness in such systems (Lubchenco & Gaines 1981).

In the second category (Table 1B), the prey assemblage in the absence of fish predation is structured by non-fish predators. Here, the effects of adding fish depend to a large extent on whether or not the fish consume the non-fish predators as well as the original prey. If they do not (e.g., if the non-fish predators are larger than the fish), then the fish may intensify the effects of the non-fish predators, be they positive or negative, only if the diets of the fish and non-fish predators are similar. Otherwise, the combined impact of all predators must be known to determine the prey diversity response and its underlying mechanisms. If the fish do consume the non-fish predators, then the effects on prey diversity are still unpredictable without extensive knowledge of the system. For example, if the

non-fish predators enhance prey diversity in the absence of fish, then disproportionate consumption of these predators by fish may indirectly cause a decrease in overall prey diversity. On the other hand, if non-fish predators reduce prey diversity, then consumption of these predators by fish may enhance overall prey diversity indirectly by freeing the lowest trophic levels from predation by intermediate levels. This latter outcome, involving three trophic levels, has been suggested as an alternative to the 'size-efficiency hypothesis' discussed below for freshwater zooplankton.

In the third category, mutualisms (Table 1C), the population size of each prey species is positively affected by those of the others. Therefore, the addition of predators to the system will probably not affect prey evenness; as one mutualist is reduced in abundance, the others will decline proportionately. However, if predation intensity reaches a level where a prey species becomes locally extinct, so may one or more mutualist species, causing a decrease in prey richness. Because mutualisms are often coevolved (Thompson 1982), any immigration of new species into the system facilitated by predation removing the mutualists would possibly change the character of the system to one of the other categories. Note that our knowledge of the role of mutualisms in most communities is virtually nonexistent (Addicott 1984).

In the fourth category, competitive networks (Table 1D), a kind of competitive balance is maintained among prey species. For example, species A outcompetes species B, species B outcompetes species C, but species C outcompetes species A

Table 1. Changes in the local prey diversity of systems not structured by competitive hierarchies following increases in fish predation intensity.

Process structuring prey assemblage in the absence of fishes	Response ¹ of prey diversity to increased fish predation intensity		
	Richness	Evenness	Composite
A. Recruitment limitation or physical disturbance	0 to -	? to ?	? to ?
B. Non-fish predation	? to ?	? to ?	? to ?
C. Mutualism	0 to -	0 to 0	0 to -
D. Competitive network	0 to -	? to -	? to -

¹ 0: none, -: decrease, ?: unpredictable without additional information (see text). The format 'a to b' indicates response 'a' at low predation intensities shifting to response 'b' at high intensities (see Fig. 1 for examples).

(Buss & Jackson 1979). Unless the intensity of predation is exactly equivalent on all prey species (Lubchenco & Gaines 1981), the addition of predators to the system can only break this competitive balance, eventually reducing both prey richness and evenness at high predation intensities. If predation facilitated the immigration of new species into the system, then the character of the system would likely change to that of a competitive hierarchy.

In summary, adding fish to prey systems structured by recruitment limitation, physical disturbances, non-fish predators, mutualisms, or nontransitive competitive networks may or may not affect prey evenness, but should usually cause a decrease in prey richness at high predation intensities (Table 1).

The effects of adding predators to prey assemblages structured predominantly by linear competitive hierarchies has received the most attention in the literature. In the absence of predation, the superior competitors among the prey should come to numerically dominate such a system (Paine 1984). Competitively subordinate prey species may persist in the system due to some low level of physical disturbance, with fugitive strategies or priority effects (*sensu* Paine 1977) perhaps allowing established subordinates to hold space against dominants. In any case, the prey system in the absence of predators should be dominated by the superior competitors, with subordinate competitors being rare or even locally excluded. If predators are added to the system and proceed to effectively reduce the population size of one or more prey species, then the effect on prey diversity depends largely upon two factors: first, which prey species are reduced with respect to the competitive hierarchy of the prey (Lubchenco 1978); and second, the pattern by which predation and other factors effect the local extinction of species in the prey assemblage and/or the immigration of new prey species.

First, consider the pattern of prey reduction by predation. Predators may: (1) reduce all prey by the same proportion (called 'equivalent predation' by Van Valen 1974); (2) disproportionately reduce one or more competitively dominant prey species;

or (3) disproportionately reduce one or more competitively subordinate species. Obviously, an equivalent predator is a trophic generalist. However, the other two kinds of predators may be either generalists or specialists. All that matters in terms of the diversity responses of the prey assemblage is that either competitively dominant or subordinate species are differentially reduced in abundance relative to the other prey species.

Now, consider the pattern of local extinction and immigration of prey species. If predation reduces the total abundance of prey under any of the above patterns, then the possibility exists that species will become locally extinct and/or new species will invade the system. Four general patterns are possible (Table 2): (I) no extinctions or immigrations; (II) extinctions with no immigrations; (III) no extinctions with immigrations of new species; and (IV) both extinctions of established species and immigrations of new species. Local extinctions are likely when prey refuges are locally scarce and recruitment of members of the original prey assemblage is limited. Immigrations of new species are likely when the local species pool is smaller than the regional species pool and barriers to dispersal and establishment are few. Thus, scenarios (I) and (II), lacking immigration, are most likely to occur in isolated systems, such as small ponds where the local system is the entire pond, or in larger systems where the availability of immigrants of new species is limited.

Scenario (IV) in Table 2 is the most complex situation, but as far as responses in prey diversity are concerned, all that is important is the net change in the number of prey species after each successive increase in predation intensity. Thus, if the number of extinctions of original prey species is exactly balanced by immigrations of new species, then the net outcome is identical to that of scenario (I). Similarly, if the numbers of extinctions and immigrations are not equal, then the net outcome can be identical to either scenario (II) or (III). Of greater interest is an outcome where immigrations exceed extinctions at moderate predation intensities, and vice versa at high intensities. In such a case, as predation intensity increases from zero, prey richness initially will be unaffected, then in-

Table 2. Local extinction and immigration scenarios in prey assemblages subjected to predation, each listed with contributing causative factors.

Immigration of new prey species?	Extinction of established prey species?	
	No:	Yes:
No:	I: many refuges; local = regional species pool	II: few refuges; local = regional species pool
Yes:	III: many refuges; local < regional species pool	IV: few refuges; local < regional species pool

crease, and ultimately decrease. I will consider this outcome in detail.

Considering all combinations of the three patterns of prey population reduction and the four patterns of prey extinction and immigration presented above, 12 general patterns of prey diversity responses to increasing predation intensity result (Table 3). The apparent complexity of Table 3 disappears if each column is examined separately. Entries in the column labelled 'richness' are set by the definitions of the extinction/immigration scenarios (see Table 2). Presumably, prey richness is not affected at low predation intensities, indicated by '0' entries. Each entry in the column labelled 'composite' combines the adjacent listings in the richness and evenness columns. In cases where a

positive response ('+') in one column is combined with a negative response ('-') in the other (e.g., Case A.II), the composite outcome is unpredictable ('?'). Most entries in the column labelled 'evenness' have not been considered in previous publications, so an explanation for each follows:

Case A.I: By definition, equivalent predation decreases all prey populations by the same proportion. If richness does not change, then evenness will be unaffected (Van Valen 1974).

Case A.II: If predation intensity reaches a level where rare species in the system go extinct, then evenness will increase with each extinction because the remaining species will exhibit more equitable relative abundances.

Case A.III: If new species invade the system, the

Table 3. Predator induced changes in local prey diversity of systems structured by competitive hierarchies.

Pattern of prey reduction by predation	Extinction/immigration scenario (Table 2)	Response ¹ of prey diversity to increased predation intensity		
		Richness	Evenness	Composite
A. Equivalent	I	0 to 0	0 to 0	0 to 0
	II	0 to -	0 to +	0 to ?
	III	0 to +	0 to ?	0 to ?
	IV	0 to + to -	0 to ? to +	0 to ? to ?
B. Disproportionate on competitively dominant species	I	0 to 0	+ to -	+ to -
	II	0 to -	+ to -	+ to -
	III	0 to +	+ to ?	+ to ?
	IV	0 to + to -	+ to ? to -	+ to ? to -
C. Disproportionate on competitively subordinate species	I	0 to 0	- to -	- to -
	II	0 to -	- to -	- to -
	III	0 to +	- to ?	- to ?
	IV	0 to + to -	- to ? to -	- to ? to -

¹ 0: none, +: increase, -: decrease, ?: unpredictable (see text). The format 'a to b' indicates response 'a' at low predation intensities shifting to response 'b' at high intensities. The format 'a to b to c' indicates responses at low ('a'), moderate ('b'), and high ('c') predation intensities. Thus, '+ to -' and '+ to ? to -' both indicate hump-shaped responses (see Fig. 1).

effect on evenness depends upon the number and relative abundances of the immigrants relative to the original assemblage. The pattern of immigration cannot be predicted a priori.

Case A.IV: This situation is a combination of Case A.I at low predation intensities, Case A.III at moderate intensities, and Case A.II at high intensities.

Case B.I: Disproportionate predation on the competitively and numerically dominant species increases evenness at low intensities. This outcome occurs whether or not the subordinate prey increase in abundance due to competitive release because the abundances of the dominants are reduced toward those of the subordinates, thus increasing the equitability of relative abundances. This outcome is the basis of Paine's (1969) 'key-stone species' concept. However, at greater predation intensities the competitive dominants will be reduced to the point of becoming relatively rare, and evenness will subsequently decline.

Case B.II: This situation will be identical to the previous case, except that as each dominant species becomes extinct, evenness may increase slightly (as in Case A.II) before continuing to decline as predation intensity progressively increases and reduces the next most dominant species.

Case B.III: As the abundances of the dominant species are reduced toward those of the subordinates at low predation intensities, evenness will increase (as in Case B.I). However, once new species immigrate, the effect on evenness becomes unpredictable (as in Case A.III).

Case B.IV: This situation is a combination of Case B.I at low predation intensities, Case B.III at moderate intensities, and Case B.II at high intensities.

Case C.I: Disproportionate predation on the relatively rare, competitively subordinate species can only decrease evenness because the rare species in the system become even rarer.

Case C.II: This situation is similar to the previous case in the same way Case B.II resembles Case B.I (see above).

Case C.III: As the relatively rare subordinate species become even rarer at low predation intensities, evenness will decrease (as in Case C.I).

However, once new species immigrate, the effect on evenness becomes unpredictable (as in Case A.III).

Case C.IV: This situation is a combination of Case C.I at low predation intensities, Case C.III at moderate intensities, and Case C.II at high intensities.

An overview of Table 3 provides two major conclusions. First, only half of the 12 prey diversity-response patterns listed produce outcomes that are unequivocal for all three diversity measures: case A.I, where equivalent predation has no effect on prey diversity (Van Valen 1974); cases B.I, B.II, and B.IV, where disproportionate predation on competitively dominant species causes hump-shaped (+ to -) responses in prey evenness and composite diversity, characteristic of the 'intermediate-disturbance hypothesis' (Connell 1978); and cases C.I and C.II, where disproportionate predation on competitively subordinate species decreases prey evenness and composite diversity (Lubchenco 1978). No case unequivocally produces a positive response over a full range of predation intensities, although such responses are possible (e.g. case B.III).

Second, the shape of the curve describing prey evenness or composite diversity as a function of predation intensity can, at least theoretically, assume any shape in situations where new species immigrate to the affected system (scenarios III and IV in Tables 2 and 3). Therefore, if new species become established in the system, the shape of the prey diversity-response curve cannot be predicted a priori.

Of what use are these ideas and patterns in understanding the effects of fish predation on prey diversity? Although derived from non-fish systems, these concepts indicate that, first, predicting the shape of the prey diversity-response curve is often impossible, and second, understanding the mechanisms causing observed patterns requires considerable knowledge of both the prey assemblage and the fishes. Of particular practical importance is the fact that at least three widely spaced levels of predation intensively must be investigated to adequately determine the shape of the prey diversity-response curve. As illustrated in Figure 1,

the common experimental design in which fish are simply removed from a system or locally excluded by cages, providing only two levels of predation intensity, is inadequate. As will become clear below, this presence/absence problem appears repeatedly in the literature.

I will now review the literature on the effects of fish predation on prey diversity in an effort to extract any general patterns, and to determine which studies have adequately determined both the shape of the prey diversity-response curve and the underlying mechanisms. I will not list the particular design flaws of each individual study. For such critiques, the reader is referred to Allan (1983, 1984) for freshwater systems and Choat (1982) for marine systems. The review is divided into two major sections: freshwater systems and marine systems (including estuaries). Within each section, I will consider three general prey categories (other fishes, plankton, and benthos).

Freshwater systems

General reviews of predator-prey interactions involving freshwater fishes are provided by Macan (1977), Clepper (1979), and Healey (1984). Most published studies have not considered the effects of fish predation on prey diversity.

Piscine prey

Despite a number of experimental studies showing that predatory fishes can affect the standing stocks of prey fishes (Foerster & Ricker 1941, Garman & Nielsen 1982), few studies have investigated the effects of native predatory fishes on the local diversity of native prey fishes. Perhaps the most relevant study is that of Clady & Nielsen (1978), who sampled the fish fauna of Oneida Lake, New York, over a 13-year period. They found that the species richness and composite diversity of prey fishes other than yellow perch was positively correlated with the abundance of young-of-the-year yellow perch, *Perca flavescens*. The walleye, *Stizostedion vitreum*, which was the dominant piscivore in this system, apparently preferred the young yellow

perch as prey, so predation intensity on other fishes was reduced when yellow perch were abundant (Forney 1974). Clady & Nielsen thus suggested that their pattern was interpretable as a negative relationship between the evenness of prey species other than yellow perch and the intensity of walleye predation on those species, with apparent changes in prey richness due to some species becoming so rare that they were not sampled. They proposed that the mechanisms causing this pattern were those described for a negative response in prey diversity in a system where few competitive interactions occur among the prey (Table 1A). However, as the authors noted, no data were gathered on either the food habits of walleye during this period or the interactions between the prey fishes, so the proposed pattern and mechanisms were entirely speculative.

The most compelling evidence of predatory fishes affecting the local diversity of prey fishes comes from studies of introduced piscivores (see Courtenay & Stauffer 1984, Moyle 1985 for reviews). Because introduced predators and native prey usually have not coevolved, the prey often lack refuges from these new sources of mortality. In such circumstances, the impact of novel predators on prey assemblages can be extreme. For example, the introduction of brown trout, *Salmo trutta*, to the continental United States has resulted in the local decline of a variety of native prey fishes in a variety of systems (review by Taylor et al. 1984). Similarly, Christie (1974) among others reviewed the general decline and extirpation of native fishes following the introduction of the sea lamprey, *Petromyzon marinus*, to the Great Lakes (see also Smith 1980 and included papers). Crowder (1980) has hypothesized that exotic planktivorous fishes have contributed to this decline by consuming the pelagic eggs and larvae of native fishes. In one of the most dramatic documented impacts of an exotic predatory fish, the cichlid *Cichla ocellaris* caused the local extinction of six native fish species in man-made Gatun Lake, Panama (Zaret & Paine 1973). While such examples are definite cases of predators decreasing prey richness, the mechanisms causing these patterns have not been documented.

Once clear pattern that has emerged from studies of predator-prey interactions among freshwater fishes is the importance of spatial refuges in moderating the effects of piscivores. In the Gatun Lake study, a turbid river flowing into the lake provided a refuge for native species; apparently *Cichla* was an ineffective predator in murky water (Zaret 1979). Other observations (Jackson 1961), recently bolstered by experimental studies (Fraser & Cerri 1982, Savino & Stein 1982, Werner et al. 1983, Mittelbach 1984), have demonstrated that aquatic vegetation provides an effective refuge for prey fishes. However, I could find no studies documenting prey fish diversity as a function of predation intensity over a range of refuge availabilities.

Planktonic prey

Interactions between planktivorous fishes and freshwater zooplankton have been studied more intensively than any other predator-prey relationship involving fishes (see Nilsson 1978, Kerfoot 1980, Zaret 1980 for reviews). A well-documented pattern is that zooplankton species composition shifts toward smaller forms when planktivorous fishes are abundant (Hrbaček et al. 1961, Hrbaček 1962, Brooks & Dodson 1965, Reif & Tappa 1966, Galbraith 1967, Hall et al. 1970, Wells 1970, Hutchinson 1971, Nilsson 1972, Sprules 1972, Stenson 1972, Warshaw 1972, Nilsson & Pejler 1973, Andersson et al. 1978, Stenson et al. 1978, Lynch 1979, Stenson 1982, Hamrin 1983, Spencer & King 1984, but see Drenner et al. 1982). Recently, this pattern has also been documented in phytoplankton systems (Drenner et al. 1984). However, very few of these studies reported explicit changes in measures of the diversity of the plankton community at different intensities of fish predation.

Of the few studies that did report responses in plankton diversity, most investigated only two levels of fish predation (fish present and fish absent). This fact makes it impossible to know the overall shape of the prey diversity-response curve (Fig. 1). In any case, most studies comparing zooplankton communities in lakes with and without planktivorous fishes, or before and after planktivorous fishes were introduced, reported a decrease in the

species richness of the zooplankters investigated (Brooks & Dodson 1965, Galbraith 1967, Pope et al. 1973, Carter & Kwik 1977, Northcote et al. 1978, Stenson 1978, Von Ende 1979, Doroshev in Li & Moyle 1981, Hurlbert & Mulla 1981). In contrast, planktivory by fishes enhanced all components of zooplankton diversity in an extensive experimental study of small pond systems (Hall et al. 1970).

Several correlative studies provided numerous between- or within-system comparisons of zooplankton diversity, possibly caused by a range of (i.e. more than two) predation intensities. For example, Nilsson & Pejler (1973) made comparisons between twenty-eight Swedish lakes. Zaret (1980) interpreted their data as demonstrating that zooplankton species richness increased monotonically with increasing fish predation intensity. Within Swedish lakes, Hamrin (1983) correlated seasonal changes in zooplankton diversity with seasonal changes in the abundance of an obligate planktivore, the vendace or ciscoe, *Coregonus albula*. Zooplankton species richness decreased monotonically as vendace populations increased. Of course, such studies share the problem of all 'natural experiments': lack of controls (Connell 1975).

The general conclusion that emerges from such studies is that predation has a definite impact on local plankton diversity, but the nature of that impact is usually unknown (or at least unreported). However, the behavioral components of fish planktivory have been well-documented: particulate-feeding fishes select large and/or highly visible zooplankters lacking morphological defenses (review by O'Brien 1979). (This generalization may not apply to filter-feeding fishes [Drenner et al. 1982, see also Janssen 1980].) To understand the mechanisms by which such size-selective predation affects zooplankton diversity, the processes structuring the plankton community in the absence of fishes must be known. Brooks & Dodson (1965) suggested that large zooplankters dominate smaller species in competition for food. Thus, as fishes reduce the abundance of large species, the smaller species would increase in abundance due to competitive release (review by Hall et al. 1976). The resulting effects on zooplankton diversity would be the same as those listed in Table 3B, often

assuming a hump-shaped response over a full range of predation intensities.

This idea, known as the 'size-efficiency hypothesis', has been challenged by the alternative hypothesis that fishes may reduce not only large zooplankters but also the invertebrate predators of small zooplankters. Therefore, small species may increase in abundance due to release from predation rather than competition (Dodson 1974). Moreover, both Neill (1975) and Lynch (1978, 1979) determined experimentally that the moderate-sized cladoceran *Ceriodaphnia* competitively dominates larger zooplankters in some systems. These two studies are the only I found that not only documented the processes structuring the prey assemblage, but also investigated more than two intensities of fish predation.

Neill's (1975) laboratory experiments were conducted in replicate two-liter microcosms originally stocked with twelve species of crustacean zooplankton, four of which were at detectable abundances at the beginning of the predation tests (Table 4). The microcosms were subjected to predation by zero, one, or two mosquitofish, which preyed disproportionately on the competitively dominant zooplankters. Explicit diversity indices were not reported. However, the equilibrium zooplankton richnesses after 13 weeks were four species with no fish, seven species with one fish, and six species with two fish (Neill's Table 3). Thus, the response of prey richness (and probably composite diversity) to increasing predation intensity was hump-shaped. Although these systems were unrealistic, given the artificial composition of the initial prey assemblages, this experiment documented a hump-shaped response similar to case B.IV (Table 3).

Lynch's (1979) field experiments were conducted in approximately cubic-meter enclosures containing natural pond-water zooplankton assemblages subjected to predation by bluegill sunfish (Table 4). There were basically three intensities of predation: no fish, one or two fish, and four or five fish. Fish preyed disproportionately on the competitively dominant zooplankters, as well as on the planktonic predator *Chaoborus*. Again, explicit diversity indices were not reported. Nonetheless, by

the end of the experiment, the enclosures with no fish contained a total of nine zooplankton species, those with moderate fish predation contained twelve species, and those with the greatest fish predation contained eleven species (Lynch's Fig. 3 and 4). Similar to Neill's study, these results suggest that the response of prey richness (and perhaps composite diversity) to increasing predation intensity was hump-shaped. However, the mechanisms causing this response were probably a combination of those described for both case B.IV (Table 3), since Lynch's enclosures appeared to be open to immigration, as well as a release from invertebrate predation (Table 1B), since the fish removed *Chaoborus*.

Benthic prey

Most studies of the effects of fish predation on benthic plant and animal communities in freshwater reported a negative impact on the abundance of benthos, but no explicit data on benthic species diversity (Anderson 1950, Ball & Hayne 1952, Threinen & Helm 1954, Hayne & Ball 1956, Straškraba 1965, Kajak et al. 1972, Andersson et al. 1978, Stenson et al. 1978, Crowder & Cooper 1982, Power & Matthews 1983, Hemphill & Cooper 1984, Post & Cucin 1984, Power et al. 1985, reviews by Prejs 1984 for herbivorous fishes and Taylor et al. 1984 for introduced fishes). An apparently common pattern is that the abundances of large invertebrates are reduced more extensively than those of smaller species (Hall et al. 1970, Crowder & Cooper 1982, Hemphill & Cooper 1984, Morin 1984a, Post & Cucin 1984), similar to the effect of size-selective predation by planktivores (see above).

Most experimental studies that did report diversity information investigated only two levels of fish predation (fish present and fish absent), so the overall shape of the prey diversity-response curve was unknown (Fig. 1). No differences in the species richness and minor differences in the evenness of benthic invertebrates between the two treatments were reported in most experiments, which included fish density manipulations in ponds (Hall et al. 1970) and streams (Zelinka 1974, Allan 1982), as

Table 4. Field and microcosm experiments investigating the effects of at least three levels of fish predation intensity upon local prey diversity.

Source & System	Predator ¹	Prey	Predation intensity ²		Prey diversity response ³			Apparent mechanism
			Manipulation	Duration	Richness	Evenness	Composite	
FIELD EXPERIMENTS:								
Lynch 1978, 1979 freshwater pond (Minnesota)	sunfish ^a	zoo- plankton	enclosures: L: 0 fish, M: 1-2 fish, H: 4-5 fish	40 days	+ to -	nr	nr	Table 3, Case B.IV; & Table 1B
Flecker 1984 freshwater stream (W. Virginia)	sculpins ^b	aquatic insects	enclosures: L: 0 fish, M: 3-6 fish, H: 12 fish & open	2 weeks	0 to 0	nr	nr	rapid prey recolonization
Gilinsky 1984 freshwater pond (N. Carolina)	sunfish ^a	benthic inverts.	enclosures: L: 0 fish, M: 20 fish, H: 60 fish	1 year	0 to 0	nr	nr	predator inefficiency
Lassuy 1980 marine coral reef (Yap Island)	damsel- fish ^c , other fishes	benthic algae	L: caged, M: exposed to other fish, H: weeded by damsel fish	2 months	nr	- to -	- to -	predator weeding behavior
Lassuy 1980 marine coral reef (Guam)	damsel- fish ^d , other fishes	benthic algae	L: caged, M: defended by d-fish, H: exposed to other fish	2 months	nr	+ to -	+ to -	Table 3, Case B.IV
Hixon & Brostoff 1981, 1982, 1983 marine coral reef (Hawaii)	damsel- fish ^e , parrot- fishes, surgeon- fishes	benthic algae	L: caged, M: defended by d-fish, H: exposed to p-fishes & s-fishes ⁴	1 year	+ to -	+ to -	+ to -	Table 3, Case B.IV
Sammarco 1983 marine coral reef (Australia)	damsel- fish ^c , other fishes	benthic algae	L: caged, M: defended by d-fish H: exposed to other fish	11 months	+ to -	+ to -	+ to -	Table 3, Case B.IV
MICROCOSM EXPERIMENTS:								
Neill 1975 freshwater (Texas)	mosquito- fish ^f	zoo- plankton	bowls: L: 0 fish, M: 1 fish, H: 2 fish	13 weeks	+ to -	nr	nr	Table 3, Case B.IV
Brock 1979 marine (Hawaii)	parrotfish ^g	reef benthos	tanks: L: 0-2 fish, M: 3-5 fish, H: 6-8 fish	36 days	- to -	nr	- to -	Table 3, Case A.II?

¹ Predator species: a: *Lepomis macrochirus*, b: *Cottus bairdi* and *C. girardi*, c: *Hemiglyphidodon plagiometopon*, d: *Eupomacentrus* (now *Stegastes*) *lividus*, e: *Stegastes fasciolatus*, f: *Gambusia affinis*, g: *Scarus taeniurus*.

² Relative predation intensities: L: low, M: moderate, H: high. See text for enclosure sizes.

³ Prey diversity response: see Tables 1 & 3 for explanation and Fig. 1 for examples (nr: not reported).

⁴ Predation intensity measured directly.

well as caging experiments in ponds (Thorp & Bergey 1981) and streams (Reice 1983, Flecker & Allan 1984).

Only two studies investigated three levels of fish predation intensity, thus allowing a determination of the shape of the prey diversity-response curve. Flecker (1984) placed $97 \times 38 \times 45$ cm enclosures containing 0, 3, 6, or 12 sculpins (including open controls) in a West Virginia stream (Table 4). After two weeks, the numbers of aquatic insect taxa were statistically indistinguishable among the replicated treatments. Species evenness and composite diversity values were not reported, although the populations of some taxa (especially Chironomidae) were reduced more than others. Flecker suggested that prey diversity was largely unaffected because of rapid recolonization of the enclosures by drifting insects.

In a similar experiment, Gilinsky (1984) placed $2 \times 3 \times 1.5$ m enclosures containing 0, 20, or 60 bluegill sunfish in a North Carolina pond (Table 4). Additionally, each fish treatment compared enclosures stocked with artificial (rope) 'macrophytes' (high heterogeneity) with bare enclosures (low heterogeneity). After one year, the numbers of benthic invertebrate species were virtually identical among the replicated fish treatments within each heterogeneity treatment. That is, all the high-heterogeneity enclosures yielded about the same species richness regardless of fish density, as did all the low-heterogeneity enclosures. Species evenness and composite diversity values were not reported. Gilinsky (1984) suggested that prey diversity was largely unaffected because fish alone were not sufficiently efficient predators. Overall, the high-heterogeneity enclosures supported more benthic species than the low-heterogeneity enclosures, indicating that the 'macrophytes' enhanced diversity by supplying additional microhabitats rather than prey refuges per se.

Reviewing experimental studies in stream systems, Allan (1983) concluded that benthic communities are seldom structured by predation. He suggested that fish may not interact strongly with the benthos due to either the abundance of spatial refuges available to bottom-living organisms or the evolution of anti-predatory adaptations by the

prey. The importance of aquatic vegetation as a spatial refuge preventing the local extinction of the benthic prey of freshwater fishes has been suggested in a variety of field observations (Hemphill & Cooper 1984), laboratory experiments (Ware 1973, Brusven & Rose 1981, Cook & Streams 1984), and field manipulations (Macan 1966, 1977, Hall et al. 1970, Cooper & Crowder 1979, Crowder & Cooper 1982, but see Flecker & Allan 1984, Gilinsky 1984).

I found only three experiments, all in lake systems, which documented changes in benthic species richness, all indicating a decrease in the number of species investigated in the presence of fish (Macan 1966, 1977, Henrikson & Oscarson 1978, Morin 1984a, b). By far, the most detailed of these studies was that of Morin (1984a, b), who compared the diversity of dragonfly larvae metamorphosing from pens accessible and closed to predation mostly by bluegill sunfish, *Lepomis macrochirus*. Four species metamorphosed from closed pens, three abundantly, while a very low number of only two species metamorphosed from the pens accessible to fishes. In the absence of fish predation, the species composition of dragonfly larvae was governed by priority effects, suggesting that early breeding species competitively inhibited the establishment of late breeding species. However, fish predation was so intense that it lowered the abundance of all species, indicating that no species were able to increase in abundance due to competitive release. Thus, while this system may be structured by a competitive hierarchy of sorts in the absence of predation, the lack of data on intermediate predation intensities precludes a determination of either the entire prey diversity-response pattern (Fig. 1) or the underlying mechanisms (Table 3).

Marine systems

Relatively few studies have been published on the effects of marine fishes on prey diversity. Virtually all studies investigated benthic prey assemblages.

Piscine prey

I found no studies reporting an impact of predatory marine fishes on the diversity of other fishes. Although predatory fishes apparently influence the behavior of other reef fishes (Hobson 1972, Ebeling & Bray 1976, Ebeling & Laur 1985, Schmitt & Holbrook 1985), attempts to investigate experimentally the impact of such piscivores upon reef-fish communities have not yielded clear results (Bohnsack 1982, J. Stimson, personal communication). The logistic constraints of such experiments are obvious. Nonetheless, because some reef fishes have been shown to compete interspecifically (Hixon 1980, Larson 1980), and such fishes are prey of both teleost and elasmobranch predators (Bray & Hixon 1978), local predation effects on prey diversity by the mechanisms in Table 3 seem possible.

Planktonic prey

I also found no studies reporting an effect of planktivorous marine fishes on the diversity of their prey. Although local effects of particulate-feeding fishes on the abundance of marine zooplankton assemblages follow the general pattern of size-selective predation documented in freshwater systems (Hobson & Chess 1976, 1978, Bray 1981), no diversity responses have yet been demonstrated.

Benthic prey

Unlike freshwater studies, which have been restricted largely to temperate systems, analyses of interactions between marine fishes and benthic communities have been conducted in a wide variety of geographical settings. Because fundamental differences between geographic regions are evident, I will review polar, temperate, and tropical studies separately.

Polar systems

I found only one study of the effect of polar fishes on the diversity of their prey. Comparing intertidal pools in Antarctica, Duarte & Moreno (1981) docu-

mented a positive correlation between the population density of the amphipod-specialist nototheniid, *Harpagifer bispinis*, and the species richness, evenness, and composite diversity of amphipods. They hypothesized that the mechanisms creating this pattern were those of a case B.III prey diversity response (Table 3).

Temperate systems

The effect of marine fishes on benthic prey in temperate waters appears to depend on the substrate of the habitat. Virnstein (1978) and Peterson (1979) reviewed experimental caging studies in coastal soft-bottom habitats. The general effect of excluding fishes and other large predators from unvegetated areas appears to be an increase in infaunal species richness, with no tendency for any competitively dominant species excluding others in the absence of predation (Naqvi 1968, Reise 1977, Virnstein 1977). This pattern suggests that the infaunal communities of estuaries may be structured by two of the processes described above for Table 1A and B: physical disturbance and/or non-fish predation. In the latter case, large predators like fishes may consume mostly predatory infauna, so that when large predators are excluded, the predatory infauna increase in abundance and reduce the diversity of prey infauna (Ambrose 1984, Summerson & Peterson 1984).

Infaunal diversity generally is greater in vegetated than exposed areas of estuaries (Orth 1977, Reise 1977, Virnstein 1977, Summerson & Peterson 1984). This pattern may be due to vegetation providing refuges from predation by fishes and other large predators, increased microhabitat complexity providing opportunities for additional prey species, and/or increased substrate density, with increases in diversity being a simple artifact of increases in the overall density of organisms (Summerson & Peterson 1984). In any case, caging experiments in vegetated areas generally fail to detect an effect on prey diversity (e.g., Young et al. 1976, Orth 1977, Reise 1977, Virnstein 1978, Young & Young 1978, Summerson & Peterson 1984). These and other results from salt-marsh and seagrass systems (review by Cooper & Crowder 1979, more recently Nelson 1979, Stoner 1979, Heck & Tho-

man 1981, Kneib & Stiven 1982, Minello & Zimmerman 1983) indicate that spatial prey refuges provided by vegetation prevent fishes or any other large predators from significantly affecting species diversity in soft-bottom benthic communities.

Regardless of the true mechanisms operating in soft-bottom predator-prey interactions, most studies in estuaries do not allow a clear demonstration of the impact of fishes. First, the cages in such studies usually exclude birds and large invertebrate predators as well as fishes. Quammen (1984) separated the impact of fishes from other large predators experimentally and detected no effects of fishes on invertebrate diversity in two different California estuaries. Second, even with adequate controls, cages present the familiar fish-present versus fish-absent problem: investigating only two levels of predation intensity cannot determine the shape of the prey diversity-response curve (Fig. 1). It appears that any general effects of fishes on the diversity of soft-bottom infauna are yet to be documented.

Choat (1982) reviewed studies of the effects of fish predation on temperate hard-bottom communities. He concluded that 'the potential for temperate fishes to have general and unequivocally recognizable effects on the distribution and abundance of their benthic prey is not apparently realized' (p. 441). For example, although seasonal changes in the abundance of amphipods and polychaetes on rock reefs off New Zealand varied inversely with those of the sparid *Chrysophrys auratus*, caging experiments detected little evidence for a fish predation effect upon either the magnitude or seasonality of invertebrate abundance (Choat & Kingett 1982). In the same general study area, Ayling (1981) determined experimentally that intense grazing by the monacanthid *Parika scaber* may decrease the abundance of sponges and ascidians, but found that grazing by urchins was the most influential factor affecting benthic communities. Off Australia, Keough (1984) found that monacanthids inhibited the successful establishment of tunicates on bivalve shells. Although the tunicates were the potential competitive dominants among the epifauna, they were usually recruitment limited, so that the fish simply eliminated already rare species

by the mechanisms described above for Table 1A.

The local diversity of temperate algae also appears to be seldom influenced by fishes. For example, caging experiments by Foster (1975) and Kennelly (1983) revealed no consistent relationship between fish grazing intensity and algal diversity in Californian and Australian kelp beds, respectively (see also Wheeler 1980).

Nonetheless, significant fish predation effects have been documented in other temperate systems, especially on relatively simple substrates. For example, Russ (1980) found that settling plates protected from fish grazing off Australia became covered by ascidians, the apparent competitive dominants. At the same time, plates exposed to fishes exhibited a greater composite diversity of epifauna, suggesting a prey diversity response similar to case B.III (Table 3). The opposite response was documented by Bernstein & Jung (1979), who found that predation by the labrid *Oxyjulis californica* decreased the diversity of epifauna on blades of kelp off California. This fish differentially reduced the abundance of organisms such as barnacles, which were inferior competitors for space on kelp blades relative to bryozoans. Thus, this system may illustrate a prey diversity response similar to case C.II (Table 3). However, the overall shape of the diversity-response curves in both these studies are unknown, since only two levels of fish predation (fish present and fish absent) were investigated (Fig. 1).

In summary, available evidence suggests that temperate marine fishes may have negligible effects on the diversity of benthic prey inhabiting both soft and hard bottoms. For soft-bottom systems, this pattern may be due to the prey communities being structured mostly by physical disturbances or invertebrate predation. For hard-bottom systems, this pattern may be a result of the complexity of natural substrates (both primary and secondary space) providing ample prey refuges, since studies of relatively homogeneous surfaces have demonstrated significant effects of fish predation. Clearly, more data are needed to substantiate or refute these tentative generalizations.

Tropical systems

Fishes appear to have more pronounced effects on the benthic diversity of coral-reef systems, with the greatest impact made by herbivorous fishes on macroalgal assemblages (reviews by Ogden & Lobel 1978, Borowitzka 1981, Lubchenco & Gaines 1981, Gaines & Lubchenco 1982, Hixon 1983). Unlike temperate regions, tropical reefs support a great diversity of herbivorous fishes, especially parrotfishes (Scaridae) and surgeonfishes (Acanthuridae). (Gaines & Lubchenco [1982] have reviewed the hypotheses proposed to account for this striking zoogeographic pattern.) Field experiments have shown that such fishes are intense grazers, greatly affecting the local abundance (Stephenson & Searles 1960, Randall 1961, Hatcher 1981, Hatcher & Larkum 1983) and between-habitat distribution of macroalgae (John & Pople 1973, Hay 1981, Hay et al. 1983). Within-habitat caging experiments have demonstrated that algal diversity is greater on substrates protected from parrotfish and surgeonfish grazing (John & Pople 1973, Day 1977, Lassuy 1980, Hixon & Brostoff 1982, 1983), with grazer-resistant crustose forms dominating exposed substrates (Vine 1974, Wanders 1977, Hixon & Brostoff 1981, 1985).

Three similar experiments – in Guam (Lassuy 1980), Hawaii (Hixon & Brostoff 1981, 1982, 1983), and Australia (Sammarco 1983) – investigated three levels of fish grazing intensity, permitting determinations of the overall shape of the prey diversity-response curve (Table 4). Each study examined the algal assemblages which developed on substrates exposed to each of three treatments: (1) protected within cages (low intensity); (2) inside the defended territories of individual herbivorous damselfishes (moderate intensity); and (3) exposed outside territories to herbivorous parrotfishes, surgeonfishes, and others (high intensity). All these fishes have similar diets, yet parrotfishes and surgeonfishes are more destructive grazers and typically occur at greater densities than damselfishes. Only Hixon & Brostoff (1982, 1983) quantified grazing intensity by counting the 'standing crop' of fish bite marks on experimental surfaces. Destructive grazing was more than an order of magnitude greater on surfaces exposed outside territories

(about 270 bites per 50 cm²) than on those protected by damselfish aggression inside territories (about 15 bites per 50 cm²), and no bite marks were found on surfaces within the cages. Moreover, urchins and other large invertebrate grazers were rare in the Hawaiian system, so the cages manipulated only fishes. Cage controls indicated no secondary effects on algal diversity.

The result of all three experiments was that all components of algal diversity were greatest inside damselfish territories. Thus, the general prey diversity response appeared to be hump-shaped, despite the fact that the experiments involved different reef systems and species. In the Hawaiian study, the caged surfaces became dominated by a few coarsely branched erect algal species, while intensely grazed exposed surfaces became covered by a few crustose and prostrate forms. Similar patterns occurred in the studies off Guam and Australia. There appears to be a general evolutionary trade-off among macroalgae between competitive ability, characteristic of many erect species, and resistance to grazing, characteristic of mostly crustose and prostrate species (Hay 1981, Lubchenco & Gaines 1981, Littler et al. 1983). To the extent that this generalization is true, the results of Lassuy (1980), Hixon & Brostoff (1982, 1983) and Sammarco (1983) illustrate the mechanisms of a case B.IV hump-shaped prey diversity response (Table 3).

However, territorial damselfishes do not always cause hump-shaped patterns. In some systems, predation intensity can be greater inside territories than outside. For example, damselfish off Yap Island actively 'weeded' certain algal species from their algal mats (Lassuy 1980, see also Irvine 1982). Using the same experimental design as the Guam, Hawaii, and Australia studies discussed above, Lassuy (1980) found that algal diversity decreased as predation intensity (grazing plus weeding) apparently increased from cages to outside territories to inside territories. Thus, the overall prey diversity response appeared to be negative (Table 4). Similarly, Montgomery (1980) found in the Gulf of California that intensive grazing by the damselfish *Microspathodon dorsalis* maintained a near monoculture of a single alga within its territory. Finally,

note that the overall intensity of grazing occurring within damselfish territories is a function of two factors: the grazing by the damselfish itself and the extent to which the damselfish is successful in excluding other grazers. In situations where parrotfishes and surgeonfishes form large schools, they can successfully invade and perhaps overgraze territories (Barlow 1974, Robertson et al. 1976), although some damselfish can effectively exclude grazing sea urchins from their territories (Williams 1981). Thus, despite the fact that damselfish territories generally exhibit a greater biomass of algae than surrounding areas (Vine 1974, Brawley & Adey 1977, Lassuy 1980, Montgomery 1980, Hixon & Brostoff 1981, 1982, Sammarco 1983), algal diversity within territories may or may not be greater than in surrounding areas.

The few studies demonstrating fish predation effects on corals and other tropical invertebrate assemblages (Neudecker 1979, Wellington 1982, Fitz et al. 1983, Wolf et al. 1983) usually have not reported explicit impacts on prey diversity (review by Hixon 1983). Day (1977) compared the epifauna which grew on caged and uncaged settling plates placed in a subtidal cave on the Great Barrier Reef. He found that species richness was greater on the uncaged plates, which were exposed to grazing by pomacanthid and balistid fishes. Day concluded that the mechanisms causing the pattern were basically those described for case B.III (Table 3), but no data on the mechanisms were provided. In Hawaii, Brock (1979) compared the benthic assemblages which developed after 36 days in $117 \times 117 \times 40$ cm outdoor microcosms containing a range of 0 to 8 parrotfish (Table 4). He found that the species richness and composite diversity of benthic flora and fauna on exposed surfaces declined with increasing parrotfish density. Because Brock investigated a wide range of fish densities, his data demonstrate a definite negative response in prey diversity, although the mechanisms causing this pattern were not documented. However, given that parrotfish are highly destructive grazers (Hixon & Brostoff 1982, 1983), it seems likely that predation was equivalent on the bare tank surfaces, suggesting a pattern similar to case A.II (Table 3). Finally, recent experimental studies of Panama-

nian rocky intertidal systems demonstrated that fishes and invertebrate predators together caused a hump-shaped response in benthic prey diversity (Menge et al. 1985), but the role of fishes alone was not investigated over a range of predation intensities.

In summary, herbivorous fishes strongly affect the local diversity of tropical algae, with several experimental studies documenting hump-shaped prey diversity responses. Relatively few studies of the diversity responses of corals and other tropical invertebrates have been reported, with available evidence indicating definite impacts by fishes. However, the overall patterns of these impacts and their underlying mechanisms are largely unknown. Given the major effects of fishes on reef benthos documented in some systems, spatial prey refuges could be expected to enhance benthic diversity in areas where fishes are abundant. In fact, experimental studies have shown that benthic diversity is greater in crevices than on exposed surfaces when grazing intensity is high, but not when grazing intensity is low (Brock 1979, Hixon & Brostoff 1985).

Discussion

The preceding review provides four major conclusions. First, most studies investigating the impact of fishes on prey systems did not report explicit diversity measures. Second, most studies that did provide diversity data either relied on comparisons of different systems or experimentally investigated only two levels of predation intensity (fish present and fish absent). Third, most studies found no or few fish effects on prey diversity, often because of an abundance of spatial refuges in the habitat. Refuges, particularly those provided by aquatic plants on soft bottoms and crevices in hard bottoms, have been found to be important in preventing the local extinction of prey species in a variety of freshwater and marine systems where fishes are the dominant predators.

Fourth, I found only nine experiments (summarized in Table 4) which investigated at least three levels of fish predation intensity, three levels being the minimum necessary to determine the

overall shape of the prey diversity-response curve (Fig. 1). Of these, two studies of freshwater benthic systems detected virtually no fish effects on prey diversity (Flecker 1984, Gilinsky 1984). Two studies of coral-reef benthos (Brock 1979, Lassuy 1980 [off Yap]) detected negative effects of fish on prey diversity, but the exact mechanisms causing this pattern were not documented. Finally, two studies of temperate freshwater zooplankton (Neill 1975, Lynch 1978, 1979) and three studies of coral-reef benthic algae (Lassuy 1980 [off Guam], Hixon & Brostoff 1981, 1982, 1983, Sammarco 1983) detected hump-shaped responses characteristic of the intermediate-disturbance hypothesis (*sensu* Connell 1978). These last five studies also demonstrated keystone-species effects (*sensu* Paine 1969) caused by the predators disproportionately reducing the abundance of the competitively dominant prey species (Table 3, case B.IV).

Of the nine experiments, two took place in microcosms (Neill 1975, Brock 1979), so the results were of unknown applicability to natural systems. Four of the studies were of short duration (two months or less; Lynch 1978, 1979, Brock 1979, Lassuy 1980, Flecker 1984), so whether the results represented stabilized prey diversity responses was unknown. Finally, only Hixon & Brostoff (1982, 1983) included direct measurements of fish grazing intensity.

I will now discuss the ramifications of these conclusions in suggesting approaches for future research. A striking pattern from surveying the literature was that studies of benthic systems reported species diversity indices much more often than studies of planktonic systems. This pattern occurred despite the fact that plankton studies usually provided data on the relative abundances of species. Composite diversity indices certainly have their drawbacks (reviews by Peet 1974, Pielou 1975), but explicit richness and evenness measures are required if the precise impacts of fishes on local prey diversity are to be documented.

One of the greatest logistic challenges for future studies will be to determine adequately the overall shape of the prey diversity-response curve. This will require the analysis of a full range of fish predation intensities, the endpoints being, at one

extreme, the absence of fish, and at the other extreme, the highest predation intensity encountered at natural fish densities. (Note that, if fish predation intensity is limited by factors other than the abundance of prey, then the highest naturally occurring predation intensities may not be greater than the 'low' levels listed in Tables 1 and 3. The possible result of such a situation could be the documentation of only the ascending part of an otherwise hump-shaped prey diversity response.) In any event, comparisons of natural systems with different fish population densities can provide only correlations. Simple fish-present versus fish-absent data (as pointed-out repeatedly above) can determine only whether or not there is a fish predation effect, not the general nature of that effect. Experimental subdivisions of natural lakes (*cf.* Henrikson & Oscarson 1978) or replicate experimental ponds (*cf.* Hall et al. 1970) containing different fish densities may be the most effective manipulations in small freshwater systems. Large replicate enclosures with different fish densities may be the best approach in marine and large freshwater systems. Investigating one fish species at a time is advisable. Under any circumstances, the smaller the enclosures used and the less extensive the experimental controls employed, the greater the probability of unrealistic artifacts. In any case, the mechanisms by which fish affect the local diversity of their prey cannot be elucidated unless the overall pattern of that effect is first documented.

Given the documented importance of spatial refuges in a variety of predator-prey systems involving fishes, especially benthic systems, the role of refuges in altering prey diversity responses should be a fruitful area of future research. In general, adding refuges should act to lower the probabilities of local prey extinctions, shifting the extinction/immigration patterns in Table 2 from scenarios II and IV to scenarios I and III. Computer simulations suggest that, as the proportion of the habitat providing spatial refuges increases, the shape of the prey diversity-response curve changes in predictable ways (Hixon unpublished). Experimental studies will require factorial designs in which the effects of a range of predation intensities are analyzed over a range of refuge availabilities (Brock 1979,

Gilinsky 1984, Hixon & Brostoff 1985).

Finally, focusing not only on the fishes as the predators (determining patterns of selectivity and prey population reduction), but also on the prey assemblage itself will be essential for elucidating the mechanisms by which prey diversity responds to varying predation intensity. In particular, the processes structuring prey assemblages in the absence of fish predation must be known, as well as the factors contributing to local patterns of extinction and immigration. Such studies will undoubtedly require collaboration between fish ecologists and experts on the prey species.

The bottom line of this review is that, considering the effects of predation by fishes on local prey diversity, we know a fair amount about several systems and very little or nothing about most. A substantial body of concepts and theory stands largely untested for fish predator-prey systems. Not simply more data are needed, but more studies designed to test explicit mechanistic hypotheses.

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