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CHARACTER RELEASE AND DISPLACEMENT IN FISHES: A NEGLECTED LITERATURE

BEREN W. ROBINSON* AND DAVID SLOAN WILSON

Department of Biological Sciences, State University of New York at Binghamton, Binghamton, New York 13902-6000

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Abstract.—Biologists concerned with the evolutionary consequences of competition seem unaware of a large literature on freshwater fishes that bears directly on the debates over ecological character displacement, character release, and the concept of "empty niches." Only five potential instances of character displacement in teleosts are cited in the conceptually oriented literature, whereas data exist for 97 species comprising 52 genera and 17 families. We review these studies, focusing on lacustrine species, and draw the following conclusions. First, competition is frequently a diversifying force that creates differences between species (character displacement) and differences within species (character release) when other closely related species are absent. Second, differentiation in lakes occurs along predictable pathways and almost always includes pelagic and benthic forms. The lake environment can therefore be viewed as a set of non-Hutchinsonian or "environmental" niches that exist apart from the species that occupy them. Third, a traditional criterion for demonstrating character displacement has been that phenotypic differences between populations in sympatry and allopatry should have a genetic basis. Although this criterion is frequently met in freshwater fish, it is not necessary because phenotypic plasticity can itself be an evolutionary consequence of competition. Finally, in the conceptually oriented literature, the evolutionary consequences of predation are well accepted, but the evolutionary consequences of competition are regarded more skeptically. This skepticism is unwarranted for freshwater fish, whose evolution is clearly influenced by both predators and competitors.

Although competition is readily observable at the ecological level, its evolutionary consequences continue to be debated (Grant 1972, 1975; Wiens 1977; Conner and Simberloff 1979; Connell 1980, 1983; Arthur 1982; Schoener 1983, 1985; Walter et al. 1984; Abrams 1990; Liem 1990). Traditional approaches to the study of ecological character displacement and character release take the form of analyzing trait differences between sites of sympatry and allopatry in species with partially overlapping geographical ranges (see, e.g., Fenchel 1975; Schluter et al. 1985). The distinction between character displacement and release is based on the historical relationship between the sympatric and allopatric populations. Character displacement is expected when two geographically isolated species form a zone of sympatry (Brown and Wilson 1956), while character release is expected when species (sympatric elsewhere) are occasionally found in isolation, as on islands (Lack 1947; Van Valen 1965). Both processes promote adaptive differentiation of characters involved in resource use, although at distinct taxonomic levels. Character displacement results in differentiation between coexisting

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* To whom correspondence should be addressed. E-mail: vy0896@BINGVAXA.BITNET.

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species, while character release produces differentiation within species found in allopatry. Both hypotheses assume that competition is a diversifying force that occurs interspecifically when more than one species is present and intraspecifically otherwise (a theoretical literature on character convergence also exists but remains largely untested: MacArthur and Levins 1967; MacArthur and Wilson 1967; Grant 1972; Slatkin 1980; Abrams 1986, 1987*a*, 1987*b;* Vadas 1990).

Attempts to test the character displacement or character release hypotheses have been troubled by a variety of problems (see critiques in Grant 1975; Arthur 1982; Strong et al. 1984; Taper and Case 1985, 1992; Case and Taper 1986; Abrams 1990), which has led to an increasingly stringent list of requirements (described below) that must now be met in any empirical study (see, e.g., Connell 1980; Diamond 1987; Diamond et al. 1989; Losos 1990; Schluter and McPhail 1992). Not surprisingly, only a handful of studies have even come close to meeting all of these criteria (see, e.g., Fjeldsa 1983 and reviewed in Diamond 1987; Schluter and McPhail 1992), which has led many biologists to become skeptical about the importance of inter- and intraspecific competition as an evolutionary force (Grant 1972, 1975; Roughgarden 1976; Wiens 1977; Connell 1980, 1983; Arthur 1982; Schoener 1983, 1985; Walter et al. 1984; Abrams 1990; but see reviews in Schoener 1984, 1988). A search for character displacement among larger sets of species (as opposed to species pairs) has also had mixed success (see, e.g., Strong et al. 1979; Grant and Schluter 1984; Schluter 1988; Dayan et al. 1989, 1990).

In the conceptually oriented literature on character displacement and character release, we can find only five references to teleost fish (see italicized references in table 1). Nevertheless, a large literature exists for fish that bears directly on these issues (see also Nursall 1974; Schluter and McPhail 1993). In this review we attempt to integrate the two literatures and evaluate the evolutionary consequences of competition, both for freshwater fish and in general.

Before proceeding, it is important to understand why the fish literature has been neglected. Much of this research is conducted by biologists studying fisheries and applied management questions and is published in journals that are not regularly read by conceptually oriented biologists. Some of it, however, is conducted by biologists with a more conceptual orientation and is published in journals such as *Evolution* but nevertheless is not related to the specific issues of character displacement and character release. For example, some of the most spectacular adaptive radiations have occurred in fish and have received a great deal of attention from evolutionary biologists (Fryer and Iles 1972; Echelle and Kornfield 1984; Liem and Kaufman 1984; McKaye et al. 1984; Meyer 1990*a*). Many of these authors tend to discount competition as an important cause of adaptive radiations (but see Humphries 1984; Smith and Todd 1984), focusing instead on other factors such as morphological innovations (Liem 1974, 1980; Stiassny and Jensen 1987), sexual selection (Kosswig 1947; Dominey 1984; McElroy and Kornfield 1990), and parental care (Dobzhansky 1951), even though the differentiation is often trophic in nature (Nursall 1974; Greenwood 1984) or correlated with habitat variables (McElroy et al. 1991). One of the most distinguished fish functional morphologists (Liem 1990, p. 215) has even claimed that competition is not a force promoting morphological diversification in the feeding apparatus of teleost fishes

TABLE 1

Fish Taxa for Which Trophic Polymorphisms, Shifted, or Expanded Phenotypic Variation Exists

Taxon, Genus, Species	Eco-/Phenotype	Environment	Mechanism	Citation	Table 2
Catostomidae (suckers):					
Catostomus:					
3 species	Gill-raker morphs	R		*Dunham et al. 1979*	1
Centrachidae (sunfishes):					
Lepomis:					
gibbosus	Littoral/pelagic	L		Robinson et al. 1993	2
	Littoral/pelagic	L	G, E	B. Robinson and D. Wilson, unpublished	3
	Hard/soft prey	L	E	Wainwright et al. 1991*b*	4
	Hard/soft prey	L	E	Mittelbach et al. 1992	
macrochirrus	Littoral/pelagic	L		Ehlinger and Wilson 1988	5
	Littoral/pelagic	L		Layzer and Clady 1987	
Micropterus:					
coosae		L		*Brown and Wilson 1956*	6
punctulatus		L		*Brown and Wilson 1956*	
Acipenseridae (Chondrostei):					
Acipenser:					
baeri	Sterlet form	R		Mina 1991, p. 176	
Cichlidae (cichlids), New World:					
Geophagus:					
brasiliensis	Sucker/biter	L	E	Wimberger 1991, 1992	
steindachneri	Sucker/biter	L	E	Wimberger 1991, 1992	
Heros = Cichlasoma:					
citrinellum	Molar-/papilliform	L		Barlow and Munsey 1976	7
	Color	L	G?	McKaye and Barlow 1976	8
	Benthic/limnetic	L	E	Meyer 1987	
	Benthic/limnetic	L	E, G?	Meyer 1989	9
	Benthic/limnetic	L		Meyer 1990*a*	10
	Benthic/limnetic	L	E	Meyer 1990*b*	11
haitensis	Molar-/papilliform	L		Meyer, in press	12
labiatum	Molar-/papilliform	L		Barlow and Munsey 1976	
	Molar-/papilliform	L	E	Meyer, in press	
managuense	Molar-/papilliform	L	E	Meyer 1987	
minckleyi	Molar-/papilliform	L	G?	LaBounty 1974	13
	Molar-/papilliform	L	E	Kornfield and Koehn 1975	
	Benthic/limnetic	L, R	E	Sage and Selander 1975	14
	Benthic/limnetic	L	E	Kornfield et al. 1982	15
	Benthic/limnetic	L		Kornfield and Taylor 1983	16
	Benthic/limnetic	L		Liem and Kaufman 1984	17

Cichlidae (cichlids), Old World:					
Astatoreochromis:					
alluaudi	Molar-/papilliform	L		Greenwood 1959	18
		L	E, G?	Greenwood 1965	19
	Molar-/papilliform	L	E	Hoogerhoud 1986*a*, 1994	20
Gaurochromis:					
hiatus	Molar-/papilliform	L		Hoogerhoud 1984, 1986*b*	21
iris	Molar-/papilliform	L		Hoogerhoud 1984, 1986*b*	21
Haplochromis:					
ishmaeli	Molar-/papilliform	L		Greenwood 1959	
malacophagus	Molar-/papilliform	L		Greenwood 1959	
obtusidens	Molar-/papilliform	L		Greenwood 1959	
pharyngomylus	Molar-/papilliform	L		Greenwood 1959	
squamipinnis	Sucker/biter	L	E	Witte 1984	22
Hemichromis:					
letourneauxi	Molar-/papilliform	L		Loiselle 1979	
Labeochromis:					
ptistes	Molar-/papilliform	L		Hoogerhoud 1984, 1986*b*	
Labidochromis:					
caeruleus	Molar-/papilliform	L		Lewis 1982	
Lethrinops:					
mylodon	Molar-/papilliform	L		Lewis 1982	
Oreochromis:					
aureus	Molar-/papilliform	L	G?	Kornfield 1991	23
Pseudotropheus:					
zebra	Color	L	G	McKaye et al. 1984	24
Coregonidae (whitefishes):					
Coregonus:					
albula	Benthic/limnetic	L		Behnke 1972, p. 663	25
clupeaformis	Benthic/limnetic	L	G	Fenderson 1964	26
	Benthic/limnetic	L		Lindsey 1963	27
	Benthic/limnetic	L		McPhail and Lindsey 1970	
	Benthic/limnetic	L		Kliewer 1970	28
	Benthic/limnetic	L		Lindsey et al. 1970	29
	Benthic/limnetic	L		Bodaly 1979	30
	Benthic/limnetic	L	G	Bodaly et al. 1988	31
	Benthic/limnetic	L	G	Kirkpatrick and Selander 1979	32
	Benthic/limnetic	L	G, E	Bernatchez and Dodson 1990	33
	Dwarf/normal	L		Kennedy 1943	
hoyi	Benthic/pelagic	L		Crowder 1984, 1986	34

TABLE 1 (*Continued*)

Taxon, Genus, Species	Eco-/Phenotype	Environment	Mechanism	Citation	Table 2
lavaretus	Benthic/limnetic	L	G, E	Svardson 1957	
	Benthic/limnetic	L	E	Svardson 1970	
	Benthic/limnetic	L	G, E	Svardson 1979	35
macrophthalmus		L		Berg 1970	36
peled	Benthic/pelagic	L		Crowder 1984, 1986	34
Various	Benthic/limnetic	L		Behnke 1972, pp. 659–665	25
	Benthic/limnetic	L	G, E	Lindsey 1981	37
	Benthic/limnetic	L	E	Todd et al. 1981	
Leucichthys:					
Various	Benthic/limnetic	L	G, E	Lindsey 1981	37
	Benthic/limnetic	L	G, E	Todd et al. 1981	38
Prosopium:					
coulteri	Benthic/limnetic	L		McCart 1970	39
Various	Benthic/limnetic	L		Behnke 1972, p. 657	25
Cottidae (sculpins):					
Cottus:					
poecilopus	Current morphs	R, L		Andreasson 1969, 1972	40
gobio	Current morphs	R, L		Andreasson 1969, 1972	40
Myoxocephalus:					
quadricornis	Egg color	L		Svardson 1961	
	Trophic morphs	R, L		Nyman and Westin 1968	
Cyprinidae (minnows):					
Notropis:					
volucellus	Current morphs	R		Trautman 1931	
Rutilus:					
rutilus	Dental morphs	M		Mina 1991, p. 133	
Siphateles:					
obesus	Benthic/limnetic	L		Hubbs 1961, p. 13	
11 genera:					
27 species	Dental formula	R, L		Eastman and Underhill 1973	
Embiotocidae (surfperch):					
Embiotoca:					
jacksoni	Winnower	M		*Hixon 1980*	
lateralis	Picker & browser	M		Schmitt and Holbrook 1986	
	Picker & browser	M		Laur and Ebeling 1983	

Gadidae (codfish):					
Arctogadus:					
borisovi	"Gadus ogac" type	M		Boulva 1972	41
Gadus:					
morhua		M		Mina 1991, pp. 129–130	
Gasterosteidae (stickleback):					
Gasterosteus:					
aculeatus	Benthic/limnetic	L	G	Larson 1976	42
	Benthic/limnetic	L	G	*Schluter and McPhail 1992*	43
	Benthic/limnetic	L		Bentzen and McPhail 1984	44
	Benthic/limnetic	L	G	McPhail 1984	45
	Benthic/limnetic	L	G	McPhail 1992	46
	Benthic/limnetic	L	G	Ridgway and McPhail 1984	47
	Benthic/limnetic	L		Bentzen et al. 1984	48
		L		Lavin and McPhail 1985, 1986	49
		L	G	Lavin and McPhail 1987	50
	Benthic/limnetic	L	G	MacLean 1980	
	Lateral-plate morphs	R	G	Bell 1981	51
	Lateral-plate morphs	L		Hagen and Gilbertson 1972	52
	Lateral-plate morphs	L	G	Hagen 1973	53
	Lateral-plate morphs	L	G	Mina 1991, pp. 95–96	54
Goodeidae (goodeids):					
Goodea:					
atripinnis	Mouth morphs	R	G	White and Turner 1984	55
Ilyodon:					
furcidens	Broad/narrow mouth	R	G	Turner and Grosse 1980	56
	Broad/narrow mouth	R	E	Turner et al. 1983	57
	Broad/narrow mouth	R	G, E	Grudzien and Turner 1984*a*, 1984*b*	58
Osmeridae (smelt):					
Osmerus:					
eperlanus	Dwarf/normal	L		Svardson 1961, p. 500	
	Dwarf/normal	L	G	Legault and Delisle 1968	59
	Dwarf/normal	L	G	Taylor and Bentzen 1993	60
Paradontidae (characins):					
Saccodon:					
dariensis	Jaw & dental morphs	R		Roberts 1974	61
wagneri	Jaw & dental morphs	R		Roberts 1974	61
Percidae (perches):					
Etheostoma:					
nigrum	Littoral/pelagic	L		Hubbs 1961, p. 15	
	Littoral/pelagic	R, L	G	Lagler and Bailey 1947	62
Perca:					
flavescens	Littoral/pelagic	L		Hubbs 1961, p. 20	

TABLE 1 (*Continued*)

Taxon, Genus, Species	Eco-/Phenotype	Environment	Mechanism	Citation	Table 2
Poecilidae (poecilids):					
Mollienisia:					
mexicana	Littoral/pelagic	L		Hubbs 1961, p. 16	
Poeciliopsis:					
monacha	Current phenotypes	R	G	Vrijenhoek et al. 1987	63
lucida	Current phenotypes	R	G	Vrijenhoek et al. 1987	63
Xiphophorus:					
variatus	Color morphs	R	G	Borowsky 1990	64
Rajidae (skates):					
Raja:					
ocellata	Epi-/infaunal	M	G	*McEachran and Martin 1977*	65
Salmonidae (salmonids):					
Brachymystax:					
lenok	Blunt/sharp snout	L, R	G	Mina 1991, pp. 47–52, 115–122	66
Oncorhynchus:					
kisutch	Lake/stream	L, R	G?	Swain and Holtby 1989	67
nerka	Benthic/limnetic	L	G	Kurenkov 1978	68
	Benthic/limnetic	L	E	McCart and Andersen 1967	
Salmo:					
carpio	Multiple forms	L		Mina 1991, pp. 113–114	
ischchan	Multiple forms	L		Mina 1991, pp. 113–114	
letnica	Multiple forms	L		Mina 1991, pp. 113–114	
trutta	Deep/lacustrine	L		Behnke 1972, p. 651	25
	Benthic/pelagic	L	G	Ferguson and Mason 1981	69
	Benthic/pelagic	L	G	Ferguson 1986	70
	Dwarf/normal	L	G	Ryman et al. 1979	71
		L		Behnke 1972, p. 651	

Salvelinus:					
alpinus	Benthic/limnetic	L		Savvaitova 1973	
	Benthic/limnetic	L		Balon 1980*a*	
	Benthic/limnetic	L		Johnson 1980	
	Benthic/limnetic	L	E	Hindar and Jonsson 1982	72
	Benthic/limnetic	L	E	Nordeng 1983	
	Benthic/limnetic	L	G	Hammar 1984	73
	Benthic/limnetic	L	E, G?	Hindar et al. 1986	74
	Benthic/limnetic	L	E	Riget et al. 1986	
	Benthic/limnetic	L	G, E	Magnusson and Ferguson 1987	75
	Benthic/limnetic	L		Sandlund et al. 1987	76
	Benthic/limnetic	L		Sandlund et al. 1988	77
	Benthic/limnetic	L	G, E	Jonsson et al. 1988	78
	Benthic/limnetic	L		Frandsen et al. 1989	79
	Benthic/limnetic	L	G	Skulason et al. 1989*a*	80
	Benthic/limnetic	L		Skulason et al. 1989*b*	81
	Benthic/limnetic	L		Bernatchez and Dodson 1990	
	Benthic/limnetic	L	G	Snorrason et al. 1989	82
	Benthic/limnetic	L		Behnke 1972, pp. 641–649	25
	Benthic/limnetic	L		Vrijenhoek et al. 1987	
	Benthic/limnetic	L		Danzmann et al. 1991	
	Benthic/limnetic	L		Malmquist et al. 1992	83
	Benthic/limnetic	L		Malmquist 1992	84
	Benthic/limnetic	L	G	Skulason et al. 1993	85
fontinalis		L		Magnan 1988	86
		L		Magnan and Stevens 1993	
willughbii	Dwarf/normal	L		Frost 1965	87
	Dwarf/normal	L		Frost and Kipling 1980	88
		L	G	Child 1984	89

NOTE.—The "Eco-/Phenotype" column refers to the type of morphological, feeding behavior, or habitat differentiation described in each citation. The "Environment" column refers to differentiation in lacustrine (L), riverine (R), and marine (M) environments. The "Mechanism" column indicates whether genetic (G) or environmental (E) mechanisms are known to contribute to the differentiation. Specific numbered citations referred to in the right-hand column correspond to the numerical entries in table 2. Well-recognized studies of character displacement in fish are given in italic (e.g., Dunham et al. 1979).

because of their intrinsic versatility. As evidence, he asserts that "not a single well-documented example of character displacement in the feeding apparatus of aquatic vertebrates has been reported." Similarly, Crowder (1986, p. 150), in his description of an example of character shift in whitefish responding to an introduced competitor, comments that he is "unaware of any examples from fishes for which even the minimum rate of character displacement can be estimated or for which the morphological shift can be related directly to a shift in resource use." One of the purposes of our review is to correct this impression that exists even among evolutionary biologists concerned with fishes.

THE EVIDENCE

Table 1 lists 97 teleost species comprising 52 genera in 17 families that display trophically related shifts in morphological and/or behavioral characters in lake, stream, or marine environments. At least 48 of these species (25 genera) exist in lacustrine environments (differentiation in many species of minnows is not classified to lake or stream although many of these species are found in lakes; see, e.g., Eastman and Underhill 1973). We focus on lacustrine species because they provide unparalleled replication, in the form of repeated natural experiments, at two levels. First, single species often exist in thousands of widely separated lakes (even on different continents), largely genetically isolated from each other, and the lakes vary in the presence and absence of competing species. Comparisons of local populations within a single species can therefore be conducted on a very large scale. Second, trends can be compared across taxa because the examples in table 1 include groups as diverse as the Centrarchidae (sunfish), the New and Old World Cichlidae (cichlids), Coregonidae (whitefishes), Cottidae (sculpins), Gasterosteidae (sticklebacks), Osmeridae (smelt), Percidae (perches), and Salmonidae (trouts and salmons).

Two interesting features emerge from table 1. First, trophic and morphological diversification predominates in species-poor communities such as the Nearctic, which suggests that the absence of competitors allows species to expand their niche (possible exceptions to this rule include sunfish and Old World cichlids). Second, for 37 of the 48 species, diversification includes coexisting benthic and pelagic forms, which suggests that most lakes offer a similar array of habitats and resources that can be regarded as "niches" that exist apart from the species that inhabit them. Schluter and McPhail (1993) reach the same conclusion in their recent review of a subset of this literature.

Empirical studies of character displacement and release are measured against at least six criteria (Schluter and McPhail 1992; see also Connell 1980; Diamond 1987; Diamond et al. 1989; Losos 1990): the relationship between phenotypic differences and resource use must be clearly demonstrated; phenotypic differences between populations in sympatry and allopatry must have a genetic basis; sympatric and allopatric sites must be ecologically similar, such that the major difference is the presence and absence of the competing species; independent evidence of resource competition between similar phenotypes is required; chance should be ruled out as an explanation of the pattern; and enhanced differences between sympatric species should result from evolutionary shifts. Table 2 evaluates the references in table 1 with respect to these criteria. There is abundant evidence for all six criteria for lacustrine fish in general, although gaps of information exist for some taxa. Although some authors (e.g., Connell 1980; Schluter and McPhail 1992) expect all criteria to be satisfied on a case-by-case basis, we employ an alternative strategy of evaluating the data that exist for some taxa, and we separately appraise whether it can reasonably be applied to other taxa for which information is lacking. The relative merits of these two strategies are discussed after the data have been evaluated.

In our discussion of each criterion below, we treat ecological character release and character displacement simultaneously. This is because both hypotheses invoke the importance of adaptive differentiation via competition (between and within species respectively) and are distinguished primarily by a historical sequence of events (i.e., from allopatry to sympatry or vice versa).

Phenotypic Differences Should Reflect Differences in Resource Use Such That Diet, Habitat Use, Morphology, and Its Functional Significance Must Be Clearly Demonstrated

Frequently, empirical tests of character displacement and character release proceed in the absence of detailed ecological information and require simplifying assumptions. For example, in many taxa there is the assumption that diversification will take the form of differences in body size or the size of trophic structures, when the functional relationship between a trait such as body size and specific prey resources can be insubstantial (see, e.g., Dunham et al. 1979; Allendorf et al. 1987; Dayan et al. 1989, 1990). These assumptions constitute a weak link in the chain of reasoning, which contributes to the skepticism that surrounds character displacement and release (Grant 1972, 1975; Strong et al. 1984). In contrast, the relationship between morphology and resource use in fish is well understood, at least in broad outline. Pelagic fish of virtually all taxa converge on a fusiform body shape that is hydrodynamically efficient for swimming through open water (Webb 1982, 1984). The retention of small particles such as zooplankton is accomplished by a large number of closely spaced gill rakers that act either as a sievelike mechanism of water exiting the gills (McCart and Andersen 1967; Kliewer 1970; Magnuson and Heitz 1971; Lindsey 1981; Lavin and McPhail 1985, 1986; Schluter and McPhail 1993) or by controlling the fluid dynamics in the buccal cavity (Sanderson et al. 1991; but see Robinson et al. 1993). Fish that eat hard-bodied prey such as snails have obvious crushing mechanisms such as pharyngeal mills with molariform teeth (Liem 1974; Werner and Hall 1979; Meyer 1989; Wainwright et al. 1991*a*, 1991*b*) and enlarged musculature. Mouths are usually oriented downward in benthic feeders, terminally in pelagic feeders and upturned in surface feeders (Keast and Webb 1966; Lindsey 1981). These morphological differences are so repeatable across taxa and so obviously related to function, because of their close correlation with dietary patterns, that when they occur within a species they are easily interpreted. The fact that diversification so often consists of a benthic and a pelagic form contributes to the ease of interpretation.

It is interesting that body size, one of the standard indexes of character dis-

TABLE 2

STUDIES OF CHARACTER RELEASE AND DISPLACEMENT IN FISHES

	CENTRARCHIDAE	CICHLIDAE	COREGONIDAE	GASTEROSTEIDAE	SALMONIDAE	
CRITERIA	Sunfish	Cichlids	Whitefish	Sticklebacks	Salmonids	VARIOUS
Functional significance	2, 4, 5	9, 10, 11, 12, 14, 15, 16, 17, 18, 19, 20, 21, 22	26, 27, 28, 30, 31, 32, 35, 36, 37, 39	42, 43, 44, 45, 48, 49	67, 68, 69, 72, 76, 78, 80, 82, 83, 84, 87, 88, 89	1, 41, 56, 64, 65
Genetic differentiation	3	13, 23, 24	26, 27, 31, 32, 33, 35, 37, 38	43, 45, 46, 47, 50, 51, 52, 53, 54	66, 68, 69, 70, 71, 73, 74, 78, 80, 81, 85, 88, 89	55, 56, 57, 58, 59, 60, 62, 63, 64
Site similarity	2, 4, 6	11, 14	28, 29, 30, 31, 33, 34, 35, 36, 37, 39	43, 51	25, 73, 74, 86	1, 7, 13, 41, 55, 57, 58, 59, 61, 63, 64, 65
Resource competition	2	8, 9, 11, 17	30, 34, 36, 37, 39	42	69, 72, 73, 76, 77, 79, 82, 83	1, 40, 61, 63
Rule out chance and biases	2, 5, 6	9, 10, 11, 12, 14, 15, 17, 19, 22, 24	29, 30, 31, 33, 34, 35, 36, 37	42, 43, 45, 52	25, 69, 73, 74, 75, 80, 83, 86	1, 40, 41, 55, 56, 58, 59, 60, 61, 63, 64, 65

NOTE.—The numbers under each taxon refer to specific studies identified in the right-hand column of table 1. Within families, these references are collected together with respect to the criteria required of any empirical study of character displacement and release as described in the text.

placement in terrestrial species, is not a very good indicator of resource use in fish. Although resources are often correlated with body size over ontogeny, diversification can also involve a "normal" and a "dwarf" form of adult fish (in which body size and gape width are often correlated). In these cases, mouth size is often poorly related to prey size, and no simple rule exists for predicting which form is associated with a given habitat or resource, even for a single species inhabiting lakes within a local region (see, e.g., Lindsey 1981; Bernatchez and Dodson 1990; for marine examples, see Schmitt and Coyer 1982; Laur and Ebeling 1983). We therefore ignore body size per se in tables 1 and 2 and restrict ourselves to morphological structures that are known to be directly involved with resource use (for evolutionary discussions of dwarf and normal forms, see Balon 1980*b,* 1984; Taylor and Bentzen 1993).

Table 2 lists 50 citations spanning five families of freshwater fish that specifically relate phenotype to resource use. References included under this criterion (table 2) required at the least a clear demonstration of a correlation between phenotype and either diet or lake habitat. Other references demonstrate the effectiveness of phenotypes based on foraging studies and habitat use. Space permits only a few of these examples to be discussed. McPhail (1994) and Schluter and McPhail (1992, 1993) have shown that sticklebacks (*Gasterosteus aculeatus*) occurring alone in small lakes of coastal British Columbia have an intermediate number of gill rakers and use both the pelagic and benthic habitats. A few lakes contain two species (Schluter and McPhail 1992, 1993; McPhail 1994) that inhabit the pelagic and benthic zones, display large and small numbers of gill rakers, and are planktivorous and littoral foragers, respectively. They propose that the two-species lakes were formed by the double invasion of a marine ancestor in the space of 1,500 yr, which prompted character displacement in gill rakers and correlated body morphology over the last 11,000 yr.

Arctic char (*Salvelinus alpinus*) have been a long-standing problem to taxonomists because of their morphological diversity (see, e.g., Behnke 1972; Nordeng 1983; Klemetsen 1984; Noakes et al. 1989). In the Icelandic lake Thingvallavatn, for example, at least four different morphs of this char species coexist: small benthic, large benthic, small limnetic, and large limnetic, along with two other species of fish (brown trout, *Salmo trutta,* and sticklebacks, *Gasterosteus aculeatus*). Benthic types display a robust body form, subterminal mouth, broad, rounded snout, large pectoral fins, and relatively few gill rakers, while the limnetic types have a more fusiform body shape, short pectoral fins, a terminal mouth with a long pointed snout, and relatively many gill rakers (Snorrason et al. 1989). Malmquist et al. (1992) show that, while all of the char morphs use the benthos to a depth of 20 m, the limnetics almost exclusively feed in the open water, while the benthic morphs feed by picking food items from the bottom substrate. Benthic morphs forage better on the zoobenthos, especially on mollusks, while the small and large limnetics feed extensively and more efficiently in the open water on zooplankton and fish (sticklebacks and juvenile char), respectively (Malmquist 1992). There is little overlap in the specific diets of benthics and limnetics in fish older than 1 yr, except in the spring when all morphs converge on a superabundant flush of insect pupae. Small benthic char can eat larger snails relative to those eaten by similarly sized large benthic char, apparently because of a larger head and a downward-oriented mouth that displays a larger gape. In contrast, the large limnetics appear to be an older and larger version of the small limnetics, which develop through an ontogenetic shift at a size of 22 cm. Each morph also show distinct infection patterns by parasites that agree well with dietary and habitat partitioning (Frandsen et al. 1989). The arctic char morphs present in Thingvallavatn appear to have evolved in sympatry within the last 5,000–10,000 yr (Skulason et al. 1989*b*). Although some questions remain at a detailed level, the clear correlations between ecology and morphology along predicted lines suggest that the char phenotypes are adapted to the benthic and pelagic niches available in Thingvallavatn (Malmquist et al. 1992).

Our final example involves whitefish (Coregonidae), which Lindsey (1981) describes as "chameleons" that alter their form depending on other species of fish with which they coexist. Two genera, *Prosopium* and *Coregonus* (divided into subgenera: *Leucichthys* and *Coregonus*), consistently display character convergence and divergence. On the average, *Prosopium* have low gill-raker counts (ranging from 13 to 23), *Coregonus* (whitefish) is typically a benthivore with medium gill-raker counts (from 20 to 40), and *Leucichthys* (ciscoes) have high gill-raker counts (from 40 to 45) and appear adapted to planktonic feeding. Lake Superior, for example, has at least seven sympatric coregonid species including all three taxonomic groups, which collectively span a range of 15–50 gill rakers (fig. 1 in Lindsey 1981). Throughout their distribution in the Northern Hemisphere, hundreds of lakes have every possible combination of one, two, and three of these genera. In Sweden's Hornavan Lake, five species of only *Coregonus* are present with raker counts ranging from 18 to 45, filling the vacant *Prosopium* and *Leucichthys* niches. In Bear Lake (Utah), four species of *Prosopium* are present with gill-raker counts ranging from 20 to 41 with one species exploiting the planktonic prey normally consumed by the missing *Leucichthys*. Many of these character shifts appear to have occurred within the last 10,000 yr (Svardson 1961; Behnke 1972; Lindsey 1981). Some of the shifts in gill-raker numbers do not simply converge on the phenotype of the missing genera but can even exceed its typical value. In Sweden, the most extreme planktivorous form of whitefish exceeds in mean number of gill rakers all Swedish populations of ciscoes. In the one lake in which this extreme whitefish exists in sympatry with a ciscoe, the ciscoe is a dwarf form that occupies the benthos, whereas the whitefish is large and displays 11 more gill rakers than the ciscoe. In this lake, a whitefish has displaced ciscoes from the planktivore niche (Lindsey 1981)!

To summarize, the relationship between phenotypic differences and differences in resource use is well established in freshwater fish, both in general and for the specific studies cited in tables 1 and 2, which satisfies the first criterion.

Phenotypic Differences Should Have a Genetic Basis

Evidence for genetic differentiation is less extensive but nevertheless exists for 19 of the 48 lacustrine species (table 1). References included in table 2 under this criterion include studies that have attempted to measure the heritability of trophically related traits, studies demonstrating differences in spawning location or timing, and "common garden" type experiments in which either wild-caught samples or lab-raised offspring of different phenotypes are reared in the same environment to test for behavioral or morphological differentiation. We also include allozyme studies that indicate genetic differentiation within species because they suggest further segregation of phenotypes, although such studies are rarely able to link genetic differentiation directly to resource-related phenotypic traits. The fact that evidence exists for only 19 lacustrine species does not imply that genetic differences are absent in the other species but only that they have not been demonstrated.

One well-studied example of genetic differentiation involves the sticklebacks described above (Schluter and McPhail 1992). Phenotypic differences between the benthic and pelagic forms persist even when they are reared in the lab and fed the same diet (McPhail 1984, 1994; Lavin and McPhail 1987). Within-population variation in phenotype has been shown to have a strong heritable component in sticklebacks (Hagen 1973; Lavin and McPhail 1987), and Schluter and McPhail (1992) report an estimate of heritability for size-adjusted gill raker length of $h^2 = 0.45$ based on phenotypic comparisons of wild limnetic parents with their offspring reared in the lab. Therefore, a genetic component to the trophic differentiation exists in sticklebacks that can rapidly respond to natural selection. Svardson (reported in Nursall 1974) performed an interesting experiment using as parents individuals at the extremes of the gill-raker distribution of a single whitefish population. He found that it was possible to rapidly derive high and low selected offspring (mean = 38.3 and 33.9 gill rakers, respectively) of an order of difference equivalent to many sympatric species pairs. This result demonstrates that sufficient genetic variation does exist in natural whitefish populations to account for the differentiation of trophically related traits such as gill rakers given adequate selective pressures.

Although genetic differentiation is relatively well documented, evidence for phenotypic plasticity also exists for 14 of the 48 lake species, including spectacular examples that are well known to evolutionary biologists (Lindsey 1981; Nordeng 1983; Meyer 1990*b;* Wainwright et al. 1991*b*). According to the second criterion, these examples of phenotypic differentiation do not provide evidence for character displacement and release because they do not have a genetic basis (Arthur 1987). We suggest that this criterion is too restrictive because patterns of phenotypic plasticity themselves have a genetic basis that could evolve in response to competition. We elaborate on this theme in our discussion and conclude here that the phenotypic differences frequently have a genetic basis in freshwater fish, which satisfies the second criterion.

Sympatric and Allopatric Sites Should Be Ecologically Similar So That the Cause of the Character Change in Sympatry Results from the Presence of the Competitor and Not Some Other Factor

A basic assumption underlying comparative studies of species pairs in sympatry and allopatry is that the only significant difference between these sites is the presence/absence of one of the species and not other ecological factors. This assumption is one of the most difficult to verify because natural habitats are never truly identical, and the only way to demonstrate rigorously the absence of hidden factors is with species introductions, which are seldom possible (Connell 1980; Colwell 1992). Thirty-three references in tables 1 and 2 specifically comment on site similarity, although these tend to be clustered in the whitefish category, and quantitative data are often not provided. Table 2 includes references under this criterion in which character changes have occurred in a single population in response to an introduced competitor, reports that demonstrate some degree of ecological similarity based on prey taxa availability and fish community data, or within which references are cited supporting the notion of ecological similarity among the lakes under study.

Circumstantial evidence also suggests that this criterion is frequently met in lake environments. Certainly, all lakes by their nature contain open water and benthic habitats, albeit in different proportions (Smith and Todd 1984). Since differentiation so often consists of open water and benthic forms, ecological similarity at this coarse level is uncontroversial. In addition, sympatric and allopatric fish populations do not always occur along gradients running north-south (which makes the effects of competition difficult to distinguish from other factors that vary with latitude, such as temperature). Populations are distributed equally frequently longitudinally, and on a smaller scale as a mosaic among lakes of a given region. Finally, it is unlikely that hidden factors correlate with the presence/absence of competing species when the patterns are repeated across many lakes. In Sweden for example, it is estimated that there are over 800 lakes with two or more coexisting whitefish morphs (Svardson 1979). The arctic char provides another example in which polymorphic populations are widely distributed throughout the Nearctic, including England (Frost and Kipling 1980; Child 1984), Sweden (Hammar 1984), Norway (Hindar and Jonsson 1982; Hindar et al. 1986), Greenland (Riget et al. 1986), and North America (Lindsey 1981; Balon 1984; see also reviews in Behnke 1972; Johnson 1980; Lindsey 1981). Even if all of these polymorphic populations are not independent natural "experiments," it seems unlikely that many of the widely spaced cases of benthic-limnetic differentiation (both within and among taxa) can be explained by chance or hidden ecological factors.

In a few cases it is possible to perform species introductions or reconstruct the effects of past introductions to demonstrate rigorously the similarity of sympatric and allopatric sites. For example, the planktivorous bluegill sunfish (*Lepomis macrochirus*) and the molluscivorous pumpkinseed sunfish (*Lepomis gibbosus*) frequently occur in a ratio of 6:1 to 10:1 in lakes where they coexist. Bluegill are absent from many drainage basins of the northeastern United States, and pumpkinseeds are trophically polymorphic in at least some of these lakes, including a planktivorous form (Robinson et al. 1993). Both a genetic and phenotypically plastic component underlie this trophic differentiation (B. W. Robinson and D. S. Wilson, unpublished data). Although bluegill are historically absent from these drainage basins, they have been introduced into many specific lakes, including three in the Adirondack region of New York that we are studying (B. W. Robinson and D. S. Wilson, unpublished data). In all cases bluegill are numerically dominant, and the planktivorous pumpkinseed form is absent (although a larger survey of bluegill-free lakes is required to demonstrate the causal effects of interspecific competition and the absence of other relevant ecological factors). The human passion for altering fish biogeography has created many natural experiments of this sort, which can be analyzed with respect to evolutionary effects of competition (see, e.g., Berg 1970; Lindsey 1981; Crowder 1984, 1986; Magnan 1988; Magnan and Stevens 1993).

We do not mean to imply that all lakes are identical. Indeed, it appears that phenotypic differentiation can reflect the number of niches that are "available" in some lakes. For example, Nordeng (1983) demonstrated a heritable component to the development of char progeny into two morphs in a lake with greater habitat segregation because of its two basins (one littoral and the other limnetic) and only one morph in a shallow lake 8 km upstream, which indicates that char polymorphisms are locally adaptable. Thingvallavatn in Iceland is sufficiently complex and productive to support four discrete trophic morphs (two each in the benthic and pelagic habitats; Malmquist et al. 1992). These examples and others suggest that polymorphisms in lacustrine fish are also dependent on quantitative aspects of lakes such as size, morphometry, and productivity (Hindar and Jonsson 1982). Differences in abiotic factors such as lake chemistry also exist that can have important effects on biotic interactions (see, e.g., Bell et al. 1993). Nevertheless, most lakes are similar at the coarsest level of containing benthic and pelagic habitats (Smith and Todd 1984). The many examples of trophic divergence by fishes into these niches are far more likely to be explained by the presence and absence of competing species than by unspecified hidden factors.

Independent Evidence of Resource Competition between Similar Phenotypes Is Required

Early studies of character displacement and release sometimes used patterns of phenotypic differentiation to infer a past history of competition. More recently, direct evidence for competition has become a criterion for demonstrating character displacement and release (see, e.g., Connell 1980). As with the site-similarity criterion, this issue can be addressed for the specific studies listed in tables 1 and 2 and for fish communities in general. Twenty-three of the studies in table 2 provide evidence of competition among similar phenotypes. We include studies that show that the diet segregation between species or morphs breaks down during periods of high food abundance and is reasserted as food becomes rare during ecological bottlenecks, which implies a role for competition. Studies of foraging and dietary patterns before and after the introduction of a putative competitor are included, as are instances of a greater degree of dietary specialization among sibling species in sympatric compared with allopatric conditions and, finally, examples of active interference competition and dietary overlap between coexisting species.

More generally, competitive effects of one fish species on another via the suppression of resources have been amply demonstrated in aquatic ecosystems (Nilsson 1963; Werner and Hall 1976, 1977, 1979; Keast 1977, 1978; Werner 1977, 1986; Hixon 1980; Schmitt and Holbrook 1986; Osenberg et al. 1992). In general, there is overwhelming evidence that lacustrine fish have large effects on the abundance and species composition of their prey that percolate throughout the entire ecosystem. The presence and absence of fish is perhaps the single most important factor governing the community structure of zooplankton (see, e.g., O'Brien 1979, 1987; Adams and DeAngelis 1987; Kitchell and Carpenter 1987; Magnan 1988; Hall and Ehlinger 1989), the littoral zone (Mittelbach 1988) and benthic invertebrates (Osenberg et al. 1992). Fish quickly remove the largest and most active species among their prey, leaving a subset that is small, cryptic, evasive, or otherwise inaccessible to fish predation (see, e.g., Magnan 1988). The current interest in "top-down" processes among aquatic ecologists reflects the dominating effects of fish on lake ecosystems (Mills et al. 1987; Vanni 1987; Person et al. 1988; Vanni et al. 1990; but see Persson et al. 1992). The proposition that a species of planktivorous fish, when faced with a more efficient competitor that quickly depleted a lake's zooplankton, would encounter abundant benthic and littoral zone resources that favored a niche shift would be regarded as uncontroversial by many aquatic ecologists. Indeed, an example of this scenario has been well documented by Crowder (1984, 1986; Crowder and Crawford 1984). Resource use patterns, diet, and gill-raker morphology of *Coregonus hoyi* (a native ciscoe) were compared before and 20 yr after the alewife (*Alosa pseudoharengus*), an efficient pelagic planktivore, was introduced into Lake Michigan. Ciscoe displayed significantly fewer and shorter gill rakers following the alewife's introduction. Over the same period, resource use patterns of the ciscoes shifted from pelagic zooplanktivory to a benthic diet at least 2 yr earlier in their life history than they did before alewives became abundant. To summarize, both the specific studies cited here and the general literature on lacustrine communities show that this criterion (evidence of competition between similar phenotypes) is satisfied, even when it is not addressed on a case-by-case basis.

Chance Should Be Ruled Out as an Explanation of the Pattern

Numerous opportunities exist for chance to create enhanced differences between sympatric species that do not require coevolution in response to competition. Apparent differences between sympatric species can arise through the action of founder effects, random population fluctuations, or a variable environment in which sympatric species diverge by a random walk (genetic drift). Note that none of these mechanisms are applicable to studies of character release since the differentiation arises within a single local population. In any case, the patterns of trophic divergence in fish are usually so highly repeated, both within and among taxa, that chance can reasonably be ruled out as an explanation (see references under *Sympatric and Allopatric Sites* above).

Enhanced Differences in Sympatry Should Result from Evolutionary Shifts and Not Some Other Process

This criterion is intended primarily for studies that attempt to infer competition from patterns of differences between species on islands or island-like habitats or other isolated communities such as watersheds (see, e.g., Gatz 1979). Differences in sympatric species can arise through the biased colonization or extinction of similar species through competitive exclusion or introgression. Sympatric species could then display patterns of phenotypic divergence in comparison to allopatric populations. Existing distributions are supposed to be compared to a "null" distribution that would obtain if the species were allowed to colonize the islands at random (Strong et al. 1979; Harvey et al. 1983; Greene 1987). As for the criterion requiring that chance be ruled out as an explanation of the pattern, the comparison of sympatric species distributions across many (sometimes hundreds) of widely spaced and similar lakes may be examined for cases of unusual species composition in a way analogous to statistical resampling procedures. We combine the references for the last two criteria (those requiring that chance be ruled out as an explanation of the pattern and that differences in sympatry result from evolutionary shifts) in table 2, including all cases of character release, because chance and biased colonization or extinction events cannot play a significant role in the expanded phenotypic variation within local populations and cases of similar character divergence repeated across multiple isolated populations within species.

DISCUSSION

In our opinion, there is no doubt that competition acts as a diversifying evolutionary force in freshwater fish communities, intraspecifically when other species are absent and interspecifically when they are present. The common claim that little evidence exists for character displacement and release is simply untenable in light of this fish literature (see, e.g., Crowder 1986). Similarly, Liem's (1990) conjecture that competition is unimportant in fish because of their trophic versatility can also be authoritatively rejected.

Some authors (see, e.g., Schluter and McPhail 1992) have suggested that single studies must meet all six criteria to qualify as evidence for character displacement and release. The effort required to satisfy all six criteria is usually so great, however, that even species that have been intensively studied for a decade or more, and for which all the evidence that does exist is positive, still fall short of this ultimate standard (e.g., morphs of Thingvallavatn char, character shifts in whitefish in Lake Michigan, and the sticklebacks of British Columbia). We have therefore adopted a different approach by evaluating the six criteria for a larger body of data that includes many fish species and many populations within species. For example, heritability of trophic differences has been demonstrated in 19 lacustrine fish species. To our knowledge, no study that has looked for the heritability of trophically related characters has failed to find it in fishes. The absence of information about heritability for 29 additional lacustrine fish species merely reflects our ignorance and does not constitute evidence against heritability, despite Arthur's (1987, p. 101) claim that the "lack of information on heritability is the biggest single failing in most claims that have been made for character displacement." Empirical studies in evolutionary ecology routinely assume the heritability of traits without proving it on a case-by-case basis. Why should studies of character displacement and release be subject to different standards? More generally, our review of the fish literature shows compelling evidence for all six criteria under similar lacustrine conditions, even when they have not been demonstrated on a case-by-case basis.

We have focused almost exclusively on the action of interspecific and intraspecific competition in fish assemblages on the ecological and evolutionary timescales. Our neglect of other important ecological relationships, including predation and parasitism, should not be construed to mean that these interactions are unimportant in fish communities. Not only are they important in their own right, but they might also interact with competition to produce unexpected results. For example, effective predators in the open water of lakes might prevent the evolution of a limnetic form from a benthic form, even in the absence of competing limnetic species. The existing literature does not allow us to detect these subtleties, however, which must be the subject of future studies. Our goal here is to provide as exhaustive a review of the effects of competition on morphological and ecological diversification in fish assemblages as we are able. In the remainder of our discussion we will focus on three more specific topics.

Phenotypic Plasticity as an Evolutionary Consequence of Competition

Genetic differences between sympatric and allopatric populations, or between sympatric populations when the character divergence occurs in situ, is often regarded as a criterion for demonstrating character displacement and release. For example, Arthur (1982, p. 147) also states, "If the heritability of a character is low or unknown then not only is there a serious gap in the argument for character displacement, but there is indeed a possible non-evolutionary explanation for frequent divergence in characters between two species in sympatry."

Although the heritability of resource-related traits is frequently demonstrated in fish, we feel that it is an overly restrictive criterion for demonstrating character displacement and release. Consider a species that experiences two environmental states, E_A and E_B, which require adaptive phenotypes P_A and P_B, respectively. Are the two phenotypes produced by separate genotypes or a single phenotypically plastic genotype? The usual answer to this question depends on the timescale of environmental change. When the environmental state remains constant for many generations, adaptation is likely to be genetic and relatively inflexible because of the expected costs of plasticity, including incorrectly responding to environmental cues and the cost of maintaining an unused plastic phenotype (reviewed in Newman 1992). Fluctuating environments favor the evolution of a single genotype that can develop into P_A or P_B, depending on current conditions, because the phenotype can be better matched to the environment in comparison to a fixed genotype (reviewed in Stearns 1989; Thompson 1991). This general conclusion applies to any two environmental states, including the presence and absence of a competitor. The distinction between genetic polymorphism versus phenotypic plasticity says nothing about selective forces per se but only about the timescale on which selective forces change. It follows that character displacement and release can be accomplished entirely by mechanisms of phenotypic plasticity if the presence and absence of competitors is experienced on the appropriate temporal scale. The question of genetic differences versus phenotypic plasticity is therefore independent of the question of competition versus other factors (see also Vrijenhoek et al. 1987).

The environments of many lacustrine fish species are unpredictable over a variety of timescales. For example, temperate lakes are widely distributed but also ephemeral because of rapidly changing watersheds through isostatic rebound, further glacial activity, erosion, and watershed capture (see, e.g., Svardson 1961; Behnke 1972; Ferguson and Mason 1981; Danzmann et al. 1991; Mina 1991). The immigration routes that fish species can take will open, close, and shift in such a landscape, which easily will lead to a diversity of fish communities among lakes of a region. Consider two competing fish species that randomly colonize such a region, which creates a mosaic of one- and two-species lakes. It is possible that developmentally plastic genotypes would be favored over fixed genotypes; nevertheless, competition would still be the diversifying evolutionary force. Alternatively, the relative abundance of two fish species might fluctuate within a single lake, which would create fluctuations in the relative importance of intra- versus interspecific competition that could be tracked only by developmental plasticity. Once again, competition would be the diversifying force that manifests itself as an adaptive pattern of phenotypic plasticity rather than as a genetic polymorphism.

We now outline a plausible example of how phenotypic diversity might be caused by genetic differences in one fish taxon and developmental plasticity in another. Most freshwater sticklebacks (*Gasterosteus aculeatus*) are derived from a globally distributed and very old marine form that repeatedly colonizes rivers and lakes that form from geological activity (Bell 1988; McPhail 1992). Although the freshwater populations are morphologically diverse, which reflects adaptation to local selection pressures, the marine form itself is relatively uniform throughout its geographical range, which presumably reflects the stability of the marine environment. We therefore predict that developmental plasticity in trophic characters has been selected against in the ancestral marine form and that phenotypic diversity in the relatively ephemeral freshwater species is accomplished primarily through genetic differentiation. Phenotypic plasticity has not been studied in sticklebacks, although some experiments are in progress (D. Schluter, personal communication).

In contrast, the ancestral environment of whitefish (Corogonidae) is an ever-changing mosaic of lakes subject to the abiotic and biotic variation described above. These dynamic conditions would have resulted in a checkerboard pattern of lakes in which whitefish existed in allopatry and sympatry for unpredictable periods before being shuffled into new patterns of isolation and coexistence. We therefore predict that developmental plasticity plays a larger role in the phenotypic diversity of whitefish (and perhaps char) populations in comparison to the sticklebacks discussed above. Lindsey's (1981) belief, that the relative influence of genotype and environment differs for almost every character examined in whitefish and among drainages, is consistent with this prediction. One method to test this prediction would be to compare the reaction norms of two taxa that have evolved under regimes of differing ecological variability by rearing them under benthic and pelagic conditions (allowing for a comparison of relative plasticity).

Niches as a Property of the Environment

Niche is one of the most difficult ecological terms to define and also one of the most difficult to refrain from using (reviewed in Arthur 1987; Schoener 1989;

Colwell 1992). Grinnell (1917, 1924) and Elton (1927) envisioned niches as aspects of the environment that exist even when unoccupied by species. Hutchinson (1957) redefined the niche to be a property of species, which rendered the concept of "empty niches" meaningless (see also Fry, reviewed in Kerr 1980). Although both usages persist, the environmental niche is often regarded as erroneous (see, e.g., Connell and Orias 1964; Herbold and Moyle 1986) or almost impossible to demonstrate (Colwell 1992).

The repeated evolution of benthic and pelagic forms, both within and between taxa, makes it difficult to avoid thinking of niches as properties of the environment that are "filled" by fish species, by either colonization or evolution in situ. We also do not see why this usage should be controversial. Lakes by their nature contain qualitatively different physical habitats that broadly govern the properties of all species that occupy them (Hindar and Jonsson 1982; Smith and Todd 1984; Lavin and McPhail 1986; Noakes et al. 1989). Schluter and McPhail (1993) make the same point for not only fish but also lizards on Caribbean islands, which predictably fill niches offered by their arboreal environment. Each niche (e.g., foraging on twigs) requires a suite of morphological adaptations regardless of what island they occur on or the particular lizard species that exists on the island. Niches are not entirely properties of the environment, but surely there is an environmental component, perhaps more important in some physical environments than others, that must be included in the niche concept. Although the problems of demonstrating the environmental component of niches may be "daunting" (Colwell 1992), they are partially overcome by the very high sample size afforded by lacustrine fish studies.

The Importance of Competition as an Evolutionary Force

Resource competition was once regarded as the primary ecological and evolutionary force governing community structure but then came under sustained attack during the 1970s and 1980s (see, e.g., Grant 1975; Wiens 1977; Arthur 1982; Strong et al. 1984; Walter et al. 1984; Abrams 1990). Some of the criticisms were justified and had a number of beneficial effects. Community ecology became more pluralistic, for example, by including the effects of predation and mutualism (see, e.g., Diamond and Case 1986; Schoener 1988, 1989), and standards of excellence for empirical studies were increased. At the same time, however, competition was surrounded by a cloud of skepticism from which it has not yet emerged. For example, the conceptually oriented literature on fish gives the distinct impression that the evolutionary effects of predation are well documented while the evolutionary effects of competition are problematical (see, e.g., Hagen and Gilbertson 1972; Moodie 1972; Endler 1980; Reznick and Endler 1982; Mittelbach and Chesson 1987; Tulley and Huntingford 1987*a*, 1987*b*; Godin and Smith 1988; Werner and Hall 1988; Magurran 1990; Magurran and Seghers 1990; Reznick et al. 1990; Bronmark and Miner 1992; Reimchen 1994). Evolutionary biologists who study adaptive radiations in fish often seem to avoid explicitly invoking competition whenever possible (see, e.g., Greenwood 1984; Liem and Kaufman 1984; but see Nursal 1974; Humphries 1984; Smith and Todd 1984). The literature on salmonid differentiation is full of double-invasion scenarios leading to genetically based trophic divergence with almost no consideration of the role competition may have played (see, e.g., Kurenkov 1978; Ferguson and Mason 1981; Klemetsen 1984; but see Hammar 1984). Liem's (1990) claim that competition is unimportant in fish communities is perhaps the culmination of this trend, and, since he seems to have intended his article as a lightning rod, we trust that he will not be offended when we vigorously strike it.

We wish we could say that the fish literature has been neglected because it was simply buried in fisheries journals, but the real reasons are more complicated and interesting. There seems to be a dynamic in which a process (e.g., competition) seems so plausible that it is uncritically accepted; the process comes under intense critical scrutiny; criteria for demonstrating the process are made so stringent that they are seldom met, if only for logistic reasons; the small number of studies that meet the criteria are used as evidence that the process is unimportant in nature; and scientists avoid invoking the process, even when it operates in their system, for fear of attracting undue criticism. In statistical terms, this is like trading an unacceptably large Type II error (that the hypothesis will be erroneously accepted) for an unacceptably large Type I error (that the hypothesis will be erroneously rejected).

We hope that this review will help dispel the cloud of skepticism that surrounds the study of competition, which would result in a more balanced pluralism (see also Crowder 1986; Schoener 1988). Competition is not the only evolutionary force structuring freshwater fish communities, but it is a major force that frequently results in ecological character displacement and character release. It is not an onerous concept, and its role in adaptive radiations and functional morphology should be reexamined.

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