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Resource Partitioning in Fish Assemblages: A Review of Field Studies

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In this study I review the literature on resource partitioning in fish assemblages from 1940–83. Studies are grouped into seven global habitats: tropical reefs, temperate reefs, coastal marine, the Antarctic, mesopelagic/slope environments and freshwater streams and lakes. Freshwater systems first attracted the interest of resource ecologists; however, the number of studies of assemblages in all global habitats has risen sharply in the last decade.

Studies treating single fish families show that resource partitioning occurs along more resource axes in more diverse assemblages. Unlike terrestrial systems, trophic separation is more important than habitat separation in fish assemblages. Based on 37 studies which concurrently examined habitat, food and temporal axes, 32% showed primary separation by habitat, 57% showed the greatest separation by food and 11% showed temporal separation to be most important. Global habitat differences in the importance of major resource axes are difficult to determine because of sampling bias; however, fish assemblages in most habitats show approximately equal importance of separation along spatial and trophic dimensions. The exceptions are marine systems, especially temperate marine reef assemblages which show greater importance of trophic separation. Global habitat differences in the amount of resource partitioning are not apparent, given the level of resolution of this study. Assemblages from all habitats show rather high separation of coexisting species along at least one resource dimension.

The degree of taxonomic relatedness varies significantly over assemblages from the seven major global habitats. Investigation of tropical reef fish assemblages and also stream fish assemblages, has focused on more closely related faunas than studies of assemblages from other habitats. The degree of relatedness has a significant effect on ecological separation for both congeneric-confamilial and confamilial-conordinal species pairs, with less related pairs showing greater differences in resource use. Comparisons of niche overlap between assemblages of different taxonomic structure will thus be biased by historical effects. Unlike habitat or trophic partitioning, temporal partitioning was significantly more important in less related species pairs so that temporal partitioning, at least to a major degree, may reflect historical effects, rather than coevolution within a particular community. Few studies have attempted to deal with most or all life history stages of species in an assemblage so that our knowledge of resource partitioning is biased toward late juvenile to adult stages. The inclusion of more life history stages, the control (or awareness) of biases due to historical effects or sampling design and a more experimental approach will be important components of future studies of resource partitioning.

THE use of resources by organisms has a major influence on population and community interactions, on the dynamics of resource availability and on the fate of resources in the ecosystem. As such, studies of species resource requirements have been used in attempts to understand factors controlling the distribution and abundance of organisms. The term "resource partitioning," meaning how species differ in resource use, was introduced in the 1960's (Toft, 1985). The primary goal of resource partitioning studies is to describe the limits that interspecific competition places on the number of species that may stably coexist (MacArthur, 1965; Schoener, 1974a; Roughgarden, 1976). Schoener (1974a) provided a synthesis of the literature on resource partitioning among metazoans. However, information on aquatic organisms, especially fishes was limited. Sale (1979), Werner (1979) and Fishelson (1980) have since treated aspects of resource partitioning in fishes.

Herein I review the literature on resource partitioning in fish assemblages from 1940–83, to seek general patterns and test specific hypotheses concerning the relation of resource partitioning to community structure. I also consider the interplay between approaches used in the studies and the nature of the results. The papers I have included are primarily based on descriptive field studies. Relatively few include controlled field experiments (sensu Schoener, 1983) and most have not dealt in depth with mechanisms responsible for the patterns.

In this paper I consider resource partitioning to be any substantial difference in resource use between coexisting species, realizing that differences may be due to many factors, only one of which is competition. Multicausation of differential resource use is undoubtedly the rule, rather than the exception. The understanding of factors responsible for patterns in resource use and the role of resource partitioning in community structure have been hampered by emphasis on single factors (Hilborn and Stearns, 1982).

Fishes are challenging subjects for studies of resource partitioning. Unlike most vertebrates, fishes exhibit indeterminate growth resulting in a complex size structure of many populations (Nilsson, 1955; Werner, 1977; Werner and Gilliam, 1984). Also, many fish assemblages, especially coastal ones, are temporally structured, using a given habitat for only part of the year or period of the life cycle. The nature of the aquatic habitat obviously also provides greater challenges for study than many terrestrial systems.

APPROACH

To assess changes in the degree or type of resource partitioning across different global habitats I grouped the literature into seven broad categories: 1) lakes (including reservoirs); 2) streams; 3) coastal marine (including soft substratum systems such as marshes, grass beds, estuaries and shallow continental shelf areas); 4) temperate reefs (including the intertidal and kelp forests); 5) tropical reefs; 6) the deep sea (including mesopelagic to slope habitats); and 7) a regional category of the Antarctic. The latter was chosen because of the very high endemism of the area (Targett, 1981). These groupings are of necessity a compromise between boundaries which are restrictive enough so that different environmental and biological mechanisms may be operative and broad enough so that sample sizes are not unreasonably small.

To objectively compare studies and rank the importance of resource dimensions I constructed matrices of pairwise resource separation from each appropriate publication. I then tallied the number of separations and expressed these as the percent of species pairs segregating by a particular resource dimension (following Pianka, 1969, the three general dimensions along which species may segregate are food, habitat and time). This approach is essentially that used by Schoener (1974a) and Toft (1985). I scored each species pair on the basis of whether or not "substantial" differences occurred in resource use in the majority of habitats sampled, following the author's decisions in assessing the difference in resource use between species and the importance of overlap values (if calculated). If no criteria were given as to the meaning of the overlap values I considered species resource use to substantially differ if overlap values (on a scale of 0–1.0) were <.40. In many instances studies provided data sets on resource use of species without comparative analysis. If the data were appropriate, I computed an index of proportional overlap (Schoener, 1968) for each resource dimension.

This approach of ranking resource dimensions has disadvantages, but allows objective comparison of diverse studies. Possible shortcomings are: 1) only papers treating three or more species may be used; 2) the dynamics of ontogenetic, seasonal or spatial changes in resource use may be masked. If overlaps showed strong spatial or temporal patterns, I based decisions on minimum overlap values since these showed how species differ when resources might be limiting. Major ontogenetic shifts in feeding occur for many fishes (Ross, 1978; Livingston, 1982). Where such shifts were judged by the author to be significant I treated each trophic unit individually in constructing the overlap matrix. Other problems which apply to resource partitioning studies in general are: 1) the difficulty of knowing whether individual resource states are orthogonal—because of this difficulty I included each resource dimension along which a species pair differed. 2) The wide differential in duration (the total time span, in months, covered by the study). The median duration was 12 months, ranging from 1–239 (Table 1). The actual number of months in which

TABLE 1. STUDIES OF FISH ASSEMBLAGES USED IN THE COMPARATIVE ANALYSIS OF RESOURCE PARTITIONING, ARRANGED BY HABITAT CATEGORIES. Only studies treating two or more major resource dimensions are shown.[1] The number in parentheses is the percent of species pairs separated by a particular dimension. Numbers to the left of the parentheses are ranks and are given only to the major categories. T/L = separation on the basis of foraging technique or microlocation due to foraging technique; F:G:S = number of families, genera and species included in the pairwise comparisons. Duration indicates the number of months spanned by the study; the actual number of months in which field work was done is shown in parentheses if different from the duration. Taxa are listed by genus if N < 7. Abbreviations for non-food descriptions are: act. = temporal activity; elev. = elevation in the intertidal; feed. = temporal feeding activity; hab. = temporal habitat use; horiz. = horizontal separation; long. = longitudinal separation; rep. = timing of reproduction; size = size of water body; sub. = substratum; temp. = temperature; veg. = vegetation; vert. = vertical separation in the water column. Abbreviations for food items are: AL = algae; AMP = amphipods; BIN = benthic invertebrates; BRY = bryozoans; COP = copepods; CRST = crustaceans; DEC = decapod crustaceans; DET = detritus; DI = diatoms; ECH = echinoderms; EUP = euphausids; FI = fishes; IN = insects; ISO = isopods; MYS = mysids; MOL = molluscs; OLI = oligochaetes; OST= ostracods; PHY = phytoplankton; PLA = plant material; POL = polychaetes; TUN = tunicates; ZPL = zooplankton.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
Tropical reefs														
W. Atlantic: Fla. Keys	*Abudefduf* *Chromis* *Eupomacentrus* *Microspathodon*	1:4:12	2 (53)	(21)	(39)	1 (56)	(17) CRST TUN AL	—	(44)	3 (0)	(0)	—	?	Emery, 1973
Caribbean: U.S. Virgin Is.	Apoginidae Emmelichthyidae Gobiidae Holocentridae Labridae Pomacentridae Pomadasyidae Tetraodontidae	2:8:22	1 (78)	—	(78) horiz., vert.	—	—	—	—	2 (52)	(52) feed.	—	2	Smith & Tyler, 1972
Caribbean: Curacao	Apogonidae Gobiidae Holocentridae Labridae Pomacentridae Priacanthidae	6:9:15	1 (54)	—	(54) vert., depth	3 (25)	(25) ZPL CRST	—	—	2 (51)	(51)	—	6	Luckhurst & Luckhurst, 1978a

TABLE 1. CONTINUED.

Region	Taxa	F:G:S	Partitioning										Dur.	Reference
			Habitat			Food				Time				
			Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.		
Caribbean: Curacao	Apogonidae Chaetodontidae Cirrhitidae Clinidae Gobiidae Grammidae Holocentridae Pomacentridae Priacanthidae Sciaenidae Serranidae Syngnathidae	12:19:25	1 (87)	—	(87) sub., depth, horiz.	2 (62)	(62) ZPL CRST AL	—	—	3 (45)	(45) feed.	—	18	Luckhurst & Luckhurst, 1978b
Caribbean: St. Croix	*Adioryx* *Flammeo* *Holocentrus* *Plectrypops*	1:4:7	2 (67)	(52)	(29) sub.	1 (71)	(57) shrimp crabs	(14)	—	—	—	—	2	Gladfelter & Johnson, 1983
Indian Ocean: Aldabra Atoll	*Acanthurus* *Naso* *Zebrasoma*	1:3:9	2 (50)	(22)	(28) horiz.	1 (69)	(69) AL	—	—	—	—	—	7	Robertson et al., 1979
Indian Ocean: Tulear	*Holocentrus* *Myripristis*	1:2:3	1 (100)	(100)	(67) vert.	2 (67)	(67) BIN, ZPL	—	—	3 (33)	(33)	—	?	Vivien & Peyrot-Clausade, 1974
C. Pacific: Hawaii	*Acanthurus* *Ctenochatus* *Naso* *Zebrasoma*	1:4:20	1 (83)	(83)	—	2 (71)	(57) AL DI ZPL	—	(14)	—	—	—	?	Jones, 1968
C. Pacific: Johnston Is.	*Acanthurus* *Ctenochatus* *Naso* *Zebrasoma*	1:4:13	2 (55)	(55)	—	1 (64)	(46) AL DI	—	(18)	—	—	—	?	Jones, 1968

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
C. Pacific: Enewetak Atoll	*Amblyglyphidodon* *Apogon* *Chromis* *Dascyllus* *Myripristis* *Pomacentrus*	3:6:12	—	—	—	1 (53)	(53) ZPL AL	—	—	2 (48)	(48)	—	1	Hobson & Chess, 1978
Temperate Reefs														
E. N. Atlantic: W. Scotland	Cottidae Gasterosteidae Gobiidae Labridae Pholidae Syngnathidae Zoarcidae	7:8:8	2 (54)	—	(54) vert.	1 (61)	(61) CRST	—	—	—	—	—	13	Kislalioglu & Gibson, 1977
E. N. Atlantic: Great Britain; English Channel	*Blennius* *Coryphoblennius* *Parablennius*	1:3:3	2.5 (67)	—	(67) horiz. vert.	1 (100)	(67) BIN AL	(67)	—	2.5 (67)	—	(67) rep.	36	Milton, 1983
E. N. Atlantic: France: English Channel	Anguillidae Blenniidae Cottidae Gadidae Gobiesocidae Gobiidae Labridae Liparidae Syngnathidae	9:12:13	2 (24)	(13)	(19) elev.	1 (41)	(41) BIN AL	—	—	—	—	—	2	Gibson, 1972
W. Mediterranean France &	*Blennius* *Cristiceps* *Gaidropsaurus*	6:6:12	1 (62)	(62)	—	2 (58)	(58) BIN AL	—	—	—	—	—	2	Gibson, 1698

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
Spain	*Gobius* *Lepadogaster* *Tripterygion*													
Indian Ocean: South Africa; Eastern Cape	*Sarpa* *Diplodus*	1:2:3	—	—	—	1 (100)	(100) BIN, AL DI	—	(33)	2 (33)	—	(33) rep.	11	Christensen, 1978
E. Pacific: Calif.; San Mateo	*Artedius* *Clinocottus* *Oligocottus*	1:3:3	2 (40)	(40)	—	1 (100)	(60) BIN FI, AL	(40)	—	—	—	—	35 (13)	Yoshiyama, 1980
E. Pacific: Calif.; San Luis Obispo	*Anoplarchus* *Cebidichthys* *Xererpes* *Xiphister*	2:4:5	2 (30)	(30) elev.	—	1 (100)	(100) AL CRST	—	—	—	—	—	9 habitat 3 food	Barton, 1982
E. Pacific: Calif.; Santa Barbara	*Brachyistius* *Oxyjulus* *Phanerodon*	2:3:3	2 (33)	—	(33) vert.	1 (100)	(67) CRST, BRY MOL	—	(33)	3 (0)	(0) feed.	—	24	Bray & Ebeling, 1975
E. Pacific: Calif.; Santa Barbara	*Embiotoca* *Rhacochilus*	1:2:4	2 (50)	—	(50) subst. vert.	1 (67)	—	—	(67)	3 (50)	(50) feed.	—	16	Alevizon, 1975
E. Pacific: Calif.; Santa Barbara	Cottidae Embiotocidae Gobiidae Hexagrammidae Kyphosidae Labridae Pomacentridae Scorpaenidae Serranidae	9:18:25	1 (33)	—	(33) vert.	—	—	—	—	2 (9)	(9) hab.	—	18	Ebeling & Bray, 1976
E. Pacific: Calif.; Santa Barbara	*Paralabrax* *Sebastes*	2:2:3	2 (33)	—	(33) vert.	1 (100)	(100) FI, BIN ZPL	—	—	—	—	—	16 (8) food	Love & Ebeling, 1978

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
E. Pacific: Calif.; Santa Barbara	*Damalichthys* *Embiotoca* *Hypsurus* *Rhacochilus*	1:4:5	2 (40)	—	(40) subst.	1 (80)	(60) CRST MOL	—	(50)	3 (40)	(40) feed.	—	5	Laur & Ebeling, 1983
E. Pacific: Calif.; Catalina Is.	Embiotocidae Labridae Pomacentridae Pomadasyidae Sciaenidae Scorpaenidae	6:7:8	—	—	—	1 (69)	(69) CRST ZPL	—	—	2 (53)	(53) feed.	—	9	Hobson & Chess, 1976
E. Pacific: Calif.; Newport	*Hypsoblennius*	1:1:3	1 (100)	(67)	(100) subst.	2 (100)	(33) MOL, AL CRST, ZPL	—	(100)	3 (33)	—	(33) rep.	31+ (?)	Stephens et al., 1970
E. Pacific: S. Calif.	*Embiotoca* *Hypsurus* *Micrometrus* *Phanerodon* *Rhacochilus*	1:5:5	2 (80)	—	(80) depth	1 (80)	(80) AMPP MOL	—	—	3 (20)	(20) feed.	(0) hab.	12	Ellison et al., 1979; Terry & Stephens, 1976
Coastal marine														
W. N. Atlantic: Gulf of St. Lawrence	*Apeltes* *Gasterosteus* *Pungitius*	1:3:4	2 (50)	(50)	—	3 (0)	(0)	—	—	1 (83)	(0) act.	(83) hab. rep.	24 (8) 1	Worgan & FitzGerald, 1981a, b
W. N. Atlantic: New Brunswick; Passamaquoddy Bay	Cottidae Gadidae Pleuronectidae Rajidae Zoarcidae	5:11:13	—	—	—	1 (46)	(46) POL MOL CRST FI	—	—	2 (15)	—	(15) hab.	16	Tyler, 1971; 1972
W. N. Atlantic: Maine; Johns Bay	Bothidae Cottidae Gadidae Pleuronectidae Rajidae Zoarcidae	6:8:8	—	—	—	1 (61)	(54) CRST MOL FI	(20)	(25)	2 (43)	—	(43) hab.	13	Hacunda, 1981

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
W. N. Atlantic: Cape Hatteras-Gulf of Maine	*Raja*	1:1:4	2 (33)	(33)	—	1 (67)	(67) CRST POL, ZPL	—	—	3 (0)	(0) feed.	—	14 (8)	McEachran et al., 1976
W. N. Atlantic: Maryland	*Fundulus*	1:1:3	3 (0)	(0)	—	2 (33)	(33) CRST, POL PLA	(0)	—	1 (33)	(0) feed.	(33) hab.	15 (8)	Baker-Dittus, 1978
W. N. Atlantic: Chesapeake Bay; Virginia	Sciaenidae	1:6:6	3 (33)	(33)	—	1 (73)	(20) ZPL, FI BIN, POL	—	(60)	2 (67)	—	(67) hab.	36	Chao & Musick, 1977
W. N. Atlantic: Georgia	*Ancylopsetta* *Citharichthys* *Etropus* *Scopthalmus*	1:4:4	—	—	—	1 (50)	(50) POL CRST FI	(50)	—	2 (33)	—	(33) hab.	12?	Stickney et al., 1974
W. N. Atlantic: Florida; Indian R.	Centropomidae Cyprinodontidae Elopidae Mugilidae Poeciliidae Sparidae	6:10:11	—	—	—	1 (80)	(80) PLA IN ZPL FI	—	—	2 (55)	—	(55) hab.	2	Harrington & Harrington, 1961
N. Gulf of Mexico	*Brevoortia*[2] *Leiostomus*[2] *Micropogonias*[2]	2:3:3	2 (100)	—	(100) cooccurrence	1 (100)	(100) PHY ZPL	(0)	—	3 (0)	(0) feed.	—	15 (9)	Govoni et al., 1983
N. Gulf of Mexico: Miss.; Horn Is.	*Anchoa* *Harengula* *Menticirrhus* *Trachinotus*	4:4:5	2 (60)	—	(60) horiz., vert.	1 (60)	(60) ZPL MOL POL	(10)	—	3 (50)	(50) feed.	(0)	7 (6)	Modde & Ross, 1983
N. E. Gulf of Mexico: Fla.; Apalachicola Bay	*Cynoscion* *Leiostomus* *Micropogonias*	1:3:3	—	—	—	1 (100)	(100) POL, MOL CRST, FI	(67)	(67)	2 (33)	—	(33) hab.	11	Sheridan, 1979

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
N. E. Gulf of Mexico: Fla.	*Bellator* *Prionotus*	1:2:5	1 (50)	(50) depth	—	2 (40)	(40) CRST, FI	—	—	—	—	—	28 (14)	Lewis & Yerger, 1976
E. Gulf of Mexico: Fla.	*Bellator* *Prionotus*	1:7:8	1 (86)	(86) depth	—	2 (86)	(71) CRST, POL FI	(54)	—	3 (0)	(0) feed.	(0) hab.	28	Ross, 1977; 1983
Caribbean: Costa Rica	*Dormitator* *Eleotris* *Gobiomorus* *Leptophilypnus*	1:4:5	1 (80)	(20) salin. horiz.	(60) vert	2 (50)	(50) CRST IN FI, PLA	—	—	—	—	—	>12 (2?)	Nordlie, 1979, 1981
North Sea: Skagerrak; Sweden	Anguillidae Gasterosteidae Gobiidae Pleuronectidae	4:8:8	3 (14)	(14)	—	1 (39)	(32) CRST IN	—	(25)	2 (18)	—	(18) hab.	5 (4)	Thorman, 1982
Bothnian Sea: Sweden	Cyprinidae Gasterosteidae Gobiidae	3:5:6	—	—	—	1 (20)	(20) CRST IN	—	—	2 (13)	—	(13) hab.	7	Thorman & Wiederholm, 1983
E. N. Atlantic: W. Scotland	Agonidae Gobiidae Pleuronectidae	3:4:5	1 (80)	(60) depth	(40) horiz.	2 (70)	(70) CRST POL	—	—	—	—	—	13 food 32 (12?) hab.	Gibson, 1973 Kislalioglu & Gibson, 1977
E. N. Atlantic: W. Scotland	Atherinidae Ammodytidae Gadidae Gasterosteidae	4:5:5	2 (60)	—	(60) vert.	1 (70)	(70) CRST ZPL	—	—	—	—	—	13	Kislalioglu & Gibson, 1977
E. N. Atlantic: Irish Sea; Isle of Man	*Gadus* *Trisopterus*	1:2:3	2 (0)	(0)	—	1 (100)	—	(100)	—	—	—	—	12	Armstrong, 1982

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
E. N. Atlantic: North Sea, English Channel	Gadidae[2] Merlucciidae[2] Pleuronectidae[2] Soleidae[2]	4:7:7	—	—	—	1 (71)	(71) ZPL PHY	—	—	2 (29)	(0)	(29) hab.	6	Last, 1978a, b
Indian Ocean: S. Africa: Natal	*Gerres*	1:1:5	3 (20)	(20)	—	2 (50)	(50) POL IN	—	—	1 (60)	—	(60) hab.	25 (7)	Cyrus & Blaber, 1983
Indian Ocean: S. Africa: Natal	*Gilchristella* *Hilsa* *Thryssa*	2:3:3	—	—	—	2 (67)	(67) COP, FI DI	(67)	—	1 (67)	(0)	(67) hab.	24	Blaber, 1979
Mesopelagic & Slope														
W. N. Atlantic: Norfolk Can.; demersal	Bathysauridae Chimaeridae Gadidae Halosauridae Macrouridae Moridae Simenchelyidae Synaphobranchidae Zoarcidae	9:10:11	2 (42)	(42) depth	—	1 (78)	(78) BIN ZPL FI DET	—	(53)	—	—	—	30 (8)	Sedberry & Musick, 1978
E. N. Atlantic: Canary Basin; mesopelagic	Chauliodontidae Gonostomatidae Myctophidae Sternoptychidae	4:6:7	3 (29)	—	(29) vert.	1 (67)	(67) COP OST AMP, FI	—	—	2 (52)	(52)	—	1	Merrett & Roe, 1974

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
W. Mediterranean: Cont. Slope; demersal	*Coelorhynchus* *Hymenocephalus* *Nezumia* *Trachyrhynchus*	1:4:4	2 (83)	(33) depth	(50) vert.	1 (100)	(50) CRST POL	(67)	(33)	3 (0)	—	(0) hab. food	25	Macpherson, 1979
W. Mediterranean: Cont. Slope; demersal	Apogonidae Bothidae Caproidae Chimaeridae Congridae Cynoglossidae Gadidae Hexanchidae Lophiidae Macrouridae Notacanthidae Scorpaenidae Scyliorhynidae Squalidae Trichuridae Triglidae	16:26:26	2 (6)	(6) depth	—	1 (92)	(85) CRST POL FI MOL	(62)	(52)	—	—	—	25	Macpherson, 1981
E. N. Pacific: Cascadia & Tuft Abyssal Plains; demersal	*Coryphaenoides*	1:1:5	2 (60)	(60) depth	—	1 (67)	(67) CRST MOL, POL ECH	—	—	—	—	—	132 (?)	Pearcy & Ambler, 1974
E. N. Pacific: Oregon; mesopelagic	*Diaphus* *Stenobrachius* *Tarletonbeania*	1:3:3	1 (67)	—	(67) vert.	2.5 (0)	(0) EUP COP	—	—	2.5 (0)	(0)	—	>12 (?)	Tyler & Pearcy, 1975

TABLE 1. CONTINUED.

Region	Taxa	F:G:S	Partitioning										Dur.	Reference
			Habitat			Food				Time				
			Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.		
Antarctic region														
S. Atlantic: Scotia Sea; S. Orkney Is.	*Chaenocephalus* *Champsocephalus* *Notothenia* *Parachaenichthys* *Trematomus*	3:5:8	—	—	—	1 (71)	(71) POL AMP ISO COP	—	—	2 (0)	(0) feed.	—	1	Targett, 1981
Drake Passage: Palmer Penin.	Bathydraconidae Harpagiferidae Nototheniidae	3:8:14	2 (51)	—	(51) vert.	1 (66)	(66) AMP, POL ISO	—	—	—	—	—	12	Daniels, 1982
Drake Passage: Palmer Penin.	Bathydraconidae Channichthyidae Harpagiferidae Nototheniidae	4:6:10	1 (80)	(33) depth	(78) subst. vert.	—	—	—	—	2 (7)	—	(7) hab.	12	Daniels & Lipps, 1982
S. Atlantic: Scotia Sea; S. Georgia Is.	Channichthyidae Muraenolepidae Nototheniidae Rajidae	4:7:10	2 (31)	—	(31) vert.	1 (75)	(75) EUP, MYS DEC, FI POL	—	—	—	—	—	60 (6)	Permitin & Tarverdiyeva, 1972
S. Atlantic: Scotia Sea; S. Georgia Is.	Bathydraconidae Channichthyidae Harpagiferidae Muraenolepidae Nototheniidae	5:7:9	—	—	—	1 (75)	(75) EUP MYS POL	—	—	2 (0)	(0) feed.	—	1	Targett, 1981

Table 1. Continued.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
S. Atlantic: Scotia Sea; S. Georgia Is.	Bathydraconidae Channichthyidae Harpagiferidae Muraenolepidae Nototheniidae	5:6:11	—	—	—	1 (64)	(64) MYS EUP AMP POL	—	—	2 (0)	(0) feed.	—	1	Targett, 1981
S. Indian Ocean: Prince Edward Is.	*Harpagifer* *Notothenia*	2:2:3	1.5 (100)	—	(100) depth	1.5 (100)	(100) MOL, CRST POL, AL	(100)	—	—	—	—	12	Blankley, 1982
S. Pacific: Wilkes Land; Adelie Coast	*Notothenia* *Trematomus*	1:2:3	2.5 (0)	(0)	(0) vert.	1 (67)	(67) POL, MOL AL	—	—	2.5 (0)	(0) feed.	—	52 (16)	Arnaud & Hureau, 1966
Streams														
Iowa (summer)	Cyprinidae	1:7:13	—	—	—	1 (79)	(79) IN, DET PLA	—	—	2 (0)	(0) feed.	—	4	Starrett, 1950
Wisconsin	*Notropis*	1:1:4	1 (83)	(0)	(83) vert. horiz.	3 (50)	(50) IN, OLI CRST	—	—	2 (53)	(33) act.	(24) hab.	60	Mendelson, 1975
Illinois	Centrarchidae Cyprinidae Ictaluridae	3:7:9	—	—	—	2 (0)	(0) BIN IN	(0)	—	1 (58)	—	(58) food	13 (10)	Angermeier, 1982
Mississippi	*Ericymba* *Notropis*	1:2:8	1 (93)	(29)	(93) vert. veg.	—	—	—	—	2 (25)	(25) feed.	(0) hab.	17	Baker & Ross, 1981
Canada: Ontario	Catostomidae Centrarchidae	7:11:11	2 (18)	(18)	—	1 (88)	(77) IN	—	(50)	3 (0)	—	(0) hab.	48 (24)	Keast, 1966

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
	Cyprinidae Esocidae Gasterosteidae Ictaluridae Umbridae						DET AL							
Canada: Ontario	*Etheostoma*	1:1:4	2 (67)	(67)	—	1 (100)	(100) IN	—	—	—	—	—	12 (4)	Paine et al., 1982
Ohio	*Etheostoma*	1:1:3	1 (33)	—	(33) horiz.	2 (0)	(0) IN	—	—	—	—	—	8 (3)	Hlohowskyj & White, 1983
Ohio	*Etheostoma*	1:1:3	2 (100)	—	(100)	1 (100)	(0) IN	(100)	—	3 (67)	—	(67) rep.	12 (11)	Wynes & Wissing, 1982
Ohio	*Etheostoma*	1:1:3	—	—	—	1 (67)	(67) IN	—		2 (0)	(0) feed.	—	13 (5?)	Adamson & Wissing, 1977
Virginia	*Etheostoma* *Percina*	1:2:3	1 (67)	(67) long.	(33) current	2.5 (0)	(0) IN	(0)	—	2.5 (0)	(0) feed.	—	12	Matthews et al., 1982
Virginia	*Notropis*	1:1:3	1 (100)	(0) long.	(100) weak vert.	2 (67)	(67) IN	—	—	3 (0)	(0) feed.	(0) hab.	12	Surat et al., 1982
Central America: Panama	Characidae Cichlidae Eleotridae Pimelotidae Poeciliidae Synbranchidae	6:10:10	2 (73)	—	(73) vert. horiz.	1 (84)	(84) IN CRST FI PLA	—	—	3 (36)	(36) feed.	—	6 (2)	Zaret & Rand, 1971
Scotland	*Salmo* *Nemachilus* *Phoxinus*	2:3:4	1 (33)	(0) long.	(33) current depth	2 (0)	(0) IN, CRST OLI, AL	—	—	—	—	—	12	Maitland, 1965
Czechoslovakia	*Cottus* *Phoxinus* *Salmo*	3:3:3	2 (33)	(33) long.	—	1 (100)	(100) IN, AL	—	—	—	—	—	1	Straskraba et al., 1966

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
Sri Lanka	*Puntius*	1:1:3	1 (100)	—	(100) horiz. vert.	2 (33)	(33) AL, DI DET	—	—	—	—	—	3	De Silva & Kortmulder, 1977
Sri Lanka	*Danio* *Puntius* *Rasbora*	1:3:4	2 (0)	(0)	(0) current	1 (67)	(67) AL, IN CRST	—	(67)	—	—	—	12	De Silva et al., 1980
New Zealand	*Anguilla* *Galaxias* *Gobiomorus* *Salmo*[3]	4:4:5	3 (40)	(0)	(40) vert. current	2 (50)	(50) IN FI	(40)	—	1 (70)	(70) feed.	(10) rep.	10 (3)	Cadwallader, 1975
Lakes														
Minnesota	*Notropis* *Pimephales*	1:2:3	1 (100)	(0)	(100) vert. depth	3 (33)	(33) IN, AL DET	—	(33)	2 (100)	(0) feed.	(100) rep.	27 (12)	Moyle, 1973
Lake Michigan	*Alosa*[3] *Notropis* *Osmerus*[3] *Perca* *Percopsis*	5:5:5	2 (60)	—	(60) temp.	1 (93)	(93) CRST IN	—	—	3 (0)	(0) feed. hab.	—	1	Brandt et al., 1980; Crowder et al., 1981
Michigan:	*Lepomis* *Micropterus* *Notropis* *Perca* *Pomoxis*	3:5:9	1 (77)	(53) depth	(60) veg. vert.	3 (3)	—	(3)	—	2 (7)	(7) feed.	—	2	Werner et al., 1977
Michigan:	Catostomidae Centrarchidae Cyprinidae Percidae	4:7:12	1 (58)	(49) depth	(10) vert.	3 (2)	—	(2)	—	2 (7)	(7) feed.	—	2	Werner et al., 1977
Canada: Ontario	Atherinidae Clupeidae[3] Centrarchidae Cyprinidae	9:15:17	3 (68)	(44)	(67) vert.	1 (82)	(82) DET AL CRST	—	—	2 (69)	(53) feed. hab.	(64) rep.	240	Amundrud et al., 1974; Keast, 1978;

TABLE 1. CONTINUED.

			Partitioning											
			Habitat			Food				Time				
Region	Taxa	F:G:S	Total	Macro	Micro	Total	Kind	Size	T/L	Total	Diel	Seas.	Dur.	Reference
	Cyprinodontidae Esocidae Ictaluridae Percidae Umbridae						IN FI							Keast & Harker, 1977; Keast et al., 1978; Keast & Webb, 1966; Keast & Welsh, 1968
Canada: Quebec	*Etheostoma* *Hybognathus* *Notemigonus* *Notropis* *Pimephales*	2:5:5	2 (10)	—	(10) veg.	1 (80))	(80) DET IN CRST	—	—	—	—	—	18	Gascon & Leggett, 1977
Vermont	Cyprinidae Cyprinodontidae Percidae	3:6:6	2.5 (0)	—	(0)	1 (27)	(27) DET, IN CRST	—	—	2.5 (0)	(0) feed.	—	18	Gascon & Leggett, 1977
Florida	*Fundulus* *Labidesthes* *Lepomis* *Micropterus* *Notemigonus*	4:5:6	2 (53)	(0)	(53) vert.	1 (60)	(40) CRST IN	(27)	—	—	—	—	1	Werner et al., 1978
Nicaragua	*Cichlasoma* *Neetroplus*	1:2:9	1 (72)	(11)	(67) spawning subst.	—	—	—	—	2 (64)	—	(64) rep.	25 (11?)	McKaye, 1977
Sweden	*Coregonus*	1:1:3	2 (67)	—	(67) vert.	1 (67)	(67) ZPL, IN FI	—	—	—	—	—	?	Nilsson, 1960
W. Africa: Ghana	*Barilus* *Cyanothrissa* *Pellonula* *Physailia* *Siluranodon*	3:5:5	2 (30)	—	(30) vert.	1 (80)	(70) AL IN ZPL FI	—	(80)	3 (20)	(20) feed.	—	32	Reynolds, 1970

TABLE 1. CONTINUED.

Region	Taxa	F:G:S	Partitioning: Habitat Total	Habitat Macro	Habitat Micro	Food Total	Food Kind	Food Size	T/L	Time Total	Time Diel	Time Seas.	Dur.	Reference
E. Africa: Uganda	*Haplochromis* *Sarotherodon*	1:2:7	1 (81)	(81)	—	2 (71)	(71) DET, PHY IN, FI	—	—	—	—	—	43	Dunn, 1975

[1] Studies which treated only one resource dimension which are included in the analyses are: Bell et al., 1978; Desselle et al., 1978; DeVries & Eastman, 1981; Finger, 1982; Hartley, 1948; Itzkowitz, 1977; Kravitz et al., 1976; Laroche, 1982; Matthews & Hill, 1980; Molles, 1978; Moreno et al., 1977; Munro, 1967; Nagabushanam, 1965; Nursall, 1981; Robertson & Lassig, 1980; Sadzikowski & Wallace, 1976; Sale, 1974a; Sale, 1975, Targett, 1981 (S. Orkney & S. Sandwich Is.); Thomas, 1962; Tribble & Nishikawa, 1982; Waldner & Robertson, 1980; Werner et al., 1978 (Florida Lake); Yoshiyama, 1981.

[2] Larval forms.

[3] Exotic species.

field work occurred ranged from 1–60, with a median of nine. These differences in the period of study may affect the degree of apparent resource partitioning because there was a low correlation of the percent of species pairs showing substantial ecological differences with the number of months of field work (Spearman rank correlation, $r_s = .17$; $P < .05$). 3) The unequal treatment of resource dimensions. Most studies focus on only several of potentially many resource states so that comparisons of the importance of various dimensions may be biased. 4) The effect of scale in characterizing resource use. For example, Greenfield and Greenfield (1982) showed fine-scale habitat partitioning of two Caribbean chaenopsids which co-occur on the same coral heads. A study which considered entire coral heads as the basic habitat unit would have missed this difference.

I have necessarily made subjective decisions about papers appropriate for inclusion. Resource partitioning studies generally deal with assemblages of closely related species or assemblages united by some common resource requirement. Studies of taxonomically or ecologically diverse assemblages become less germane to understanding the role of resource partitioning in shaping community structure as other interactions, such as predator-prey, may increase in importance. In this review I have been guided primarily by the author's stated purpose and have included studies which quantitatively evaluated differential resource use with the stated or implied goal of using the information to understand something of community structure. Papers were generally not included if resource-use data were given in inventory fashion without quantitative comparative analysis, or if they lacked a meaningful biological basis for selecting the species to be included (e.g., guild membership, taxonomic relationship, numerical dominance in the assemblage).

From 233 studies treating resource ecology of three or more fish species, 128 publications describing 116 fish assemblages were appropriate for determination of pairwise ranking of resource separation (Table 1). Studies are arranged by major habitat and placed geographically in approximately a N–S then E–W progression. Trends in data presented in Table 1 (or in studies cited therein) were analyzed by non-parametric statistics following Siegel (1956), using the Statistical Package for the Social Sciences, Release 7.05 (Nie et al., 1975; Hull and Nie, 1981). The Spearman rank correlation was corrected for ties following Siegel (1956) and

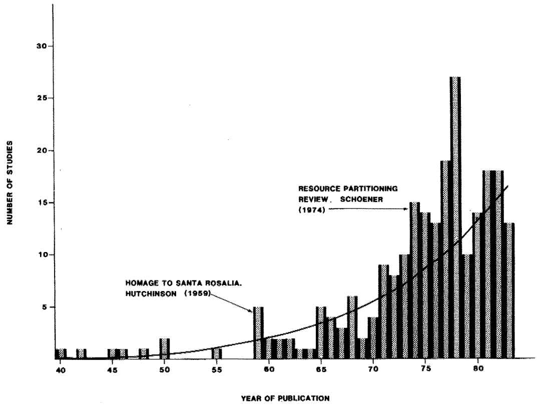

Fig. 1. The number of published papers presenting original data on comparative resource ecology of fish assemblages comprised of three or more species, 1940–1983 (N = 233).

significance was determined by Siegel's large sample method using a two-tailed test (ns = $P > .05$).

Chronology

Interest in resource ecology of fishes has risen sharply in the last decade, as evidenced by the ichthyological literature from 1940–83 (Fig. 1). Data are for studies of three or more species which related directly or indirectly to resource partitioning. While this selection of papers (N = 233) does not include all possible published studies, it does represent the result of extensive bibliographic research in which I examined over 400 papers on resource ecology of fishes. Thus, while the absolute number of papers per year may be underestimated (especially for 1983), the pattern is no doubt real. For example, only 25% of the papers appeared before 1973, the cut-off date for studies included in Schoener (1974a). The number of studies has increased exponentially (slope = .07/yr; $r^2 = .77$); however, the rate of increase has lagged behind that for studies of resource partitioning in general. Schoener (1974a) reported a rate of increase of .25/yr for 1959–72 (all metazoans). The differential still exists when the rate of increase of fish studies is based on papers from 1959–82 (slope = .10). Studies on fish resource ecology have consequently increased at a rate much closer to the rate of increase for scientific papers overall (.05–.07/yr); de Solla Price (1963, cited in Schoener, 1974a).

Different chronologies exist for the seven broad habitat categories (Fig. 2). Studies of resource ecology of freshwater fishes generally preceded marine studies, as shown by early synecological papers by Swynnerton and Worthington (1940); Burton and Odum (1945); Frost (1946); Hartley (1948); Northcote (1954); Campbell (1955); and Nilsson (1955). However, tropical reefs and coastal marine habitats were first to show the major increase in number of studies characteristic of the 1970's and 1980's. Several areas, e.g., the deep sea and Antarctica, have only recently attracted major interest. All systems, however, show a sharp increase in the number of studies over the last 8–12 yr.

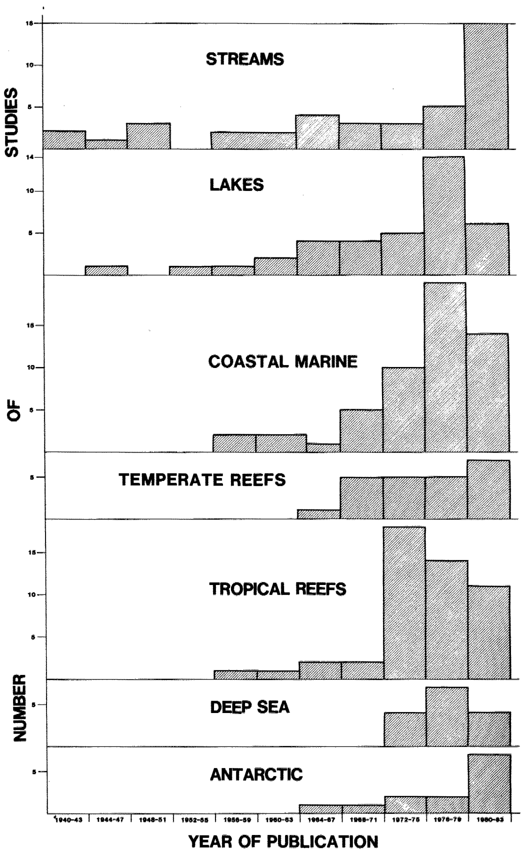

Fig. 2. A chronology of resource partitioning studies (as selected in Fig. 1) for seven major habitats (1940–1983).

Assemblage richness and the number of important dimensions

If resource partitioning is important in the organization of species assemblages, then species must ultimately segregate along more resource dimensions and/or show decreases in niche breadth, to maintain a minimum level of niche separation as the number of species in an assemblage increases (Schoener, 1974a). If the null hypothesis of no change in the number of resource dimensions (or no decrease in niche breadth) as species numbers increase holds true, then the utility of resource partitioning in affecting community structure would seem limited. Unfortunately, it is difficult to test this hypothesis with the available data since most studies examine relatively few resource dimensions (range = 1–8). In addition, the number of species studied may be chosen in various ways, such as by taxonomic group, by guild or by species occupying a particular habitat, so that the number of species studied may be unrelated to actual assemblage or guild diversity. Thus, a first step is to test the relationship of the number of species studied to the number of species in the assemblage. I estimated the total number of fish species in a community from those studies which listed the total number of species collected in the community. I chose not to obtain estimates of assemblage diversity from regional faunal studies since these would likely overestimate diversity of a particular assemblage.

The number of species studied is not correlated ($r_s = .26$; n.s.; N = 53) with the total number of species in the fish assemblage. Consequently, the use of all resource partitioning studies to test the above hypothesis would be invalid. Also, bias would occur if the number of studied dimensions increased with regional diversity, or the number of species studied (i.e., if ecologists anticipated more separation in diverse systems and thus looked at more resource axes). This, however, is not true, as there is no relationship between the number of resources studied and either the number of species studied ($r_s = -.08$; n.s.; N = 116), or assemblage diversity ($r_s = .17$; n.s.; N = 51).

Family level studies, however, may be more appropriate for examining the relationship between species number and the number of resource axes along which separation occurs. There is a significant correlation between the number of species studied and the total number of confamilial species in the assemblage ($r_s = .65$; $P < .001$; N = 31). Such assemblages may also provide greater potential for biotic interaction than taxonomically less related ones.

I tested the hypothesis of a positive relationship between the number of important resource dimensions and the number of species in an assemblage in two ways, using only studies of single families. I considered a resource dimension to be important if there was a non-zero value for percent separation. In the more general approach I used all confamilial studies (N = 56) without controlling for possible bias resulting from the obvious influence of the number of studied resource dimensions affecting the number of dimensions that appear important. Not surprisingly, this approach failed to indicate a significant relationship ($r_s = .16$; n.s.; one-tailed test). When this bias is partially controlled by limiting the analysis only to papers in which at least one more dimension was studied than was found to be important (N = 22) there is a positive relationship between the number of important resource dimensions and the number of species ($r_s = .41$; $P < .01$; one-tailed test). While the generality of this result may be limited due to the reduced data set, because of a number of ties in the correlation analysis and the rather broad categories of resource axes, the test is likely conservative. The results support the view that resource partitioning occurs along more axes in diverse assemblages and that it may be important in the structuring of fish assemblages.

HIERARCHY OF RESOURCE DIMENSIONS

Schoener (1974a) found for metazoans that habitat separation was more common than dietary separation, which was more common than temporal separation; a pattern also predicted on a short term basis by the compression hypothesis (MacArthur and Pianka, 1966; MacArthur and Wilson, 1967; Schoener, 1974b). Numerous authors have since compared their findings with Schoener's (1974a) hierarchy. Schoener (1974a) used both the percent of groups where the most important dimension fell into one of the three categories, as well as the percent of groups where each kind of dimension is known to have some importance in separating species. Using the first approach, his values for metazoans overall were 55% habitat, 40% food and 5% time. Fish assemblages, however, differ from this pattern. Using only studies (Table 1; N = 37) in which all three major resource axes were examined, food is by far the most common resource axis along which separation occurs, followed by spatial and temporal dimensions (Table 2A). Because so few studies provided data on all three major dimensions I also examined the hierarchy of resource axes by considering studies that looked at 2–3 of the major axes (N = 90). In this approach the number of assemblages separating primarily by one of the three dimensions was divided by the number of studies in which that resource dimension was examined; tied categories were both counted. The percent separation for each resource axis was then scaled so that all three summed to 100% (Table 2B). The greater importance of trophic separation is again demontrated, as well as a possible trend of increased importance of temporal separation compared to Schoener's (1974a) results.

I also evaluated the relative importance of spatial and trophic dimensions by determining for each assemblage the difference in the percent of species pairs separated by habitat and food dimensions. Data are from studies (Table 1) which concurrently evaluated both dimensions (N = 68). The null hypothesis of no difference in percent separation of species along spatial or trophic dimensions was tested with Wilcoxon's signed-rank test using a two-tailed test. The average percent of species pairs separated by spatial dimensions is 54%, compared to 64% for trophic dimensions (Table 3). Significantly greater separation occurred along trophic compared to spatial dimensions, further supporting the tentative suggestion by Schoener (1974a) of the greater importance of trophic than habitat partitioning in aquatic communities. The data used in the above comparison also indicate the independence of separation along habitat and food dimensions for the 68 studies ($r_s = .07$; n.s.).

Schoener (1974a) suggested that the apparent difference in the importance of trophic partitioning between terrestrial and aquatic systems may result from lower habitat heterogeneity, less climatic variation and greater resource mobility in aquatic systems. While these factors may be important, many aquatic habitats, e.g., kelp forests, coral reefs and lakes and streams with submerged or emergent vegetation, offer considerable habitat diversity. Such heterogeneity may be reduced in large lakes and in the open ocean, although the importance of temperature in providing "structure" in large water bodies has recently been demonstrated for lakes (Brandt et al., 1980) and various physical factors such as light and temperature are likely important environmental cues for open ocean fishes (Willis and Pearcy, 1982). Increased resource mobility may be especially important since this mobility, for instance by drift in streams, or ocean or lake currents, may allow aquatic predators to efficiently partition food resources while remaining in the same general habitat. Morphological specialization of trophic mechanisms in fishes is often pronounced (Keast and Webb, 1966; Emery, 1973; Liem, 1973; McKaye and Marsh, 1983) so that partitioning of prey through different capture or handling techniques may be greater than for many terrestrial organisms. In addition, habitats may be of limited duration, especially in many freshwater (Larkin, 1956) or coastal marine systems (Perkins, 1974), limiting the potential for high levels of habitat specialization. Crowder et al. (1981) also observed that native fishes in the Great Lakes tended to segregate more along food dimensions, while exotic species differed more by habitat, leading them to suggest that trophic morphology and feeding behavior may be less flexible than habitat choice. Other possibilities for the increased importance of trophic partitioning in fish assemblages include various biases in the studies, such as greater subdivision of food than habitat dimensions, a fact which can have a major influence on overlap values (Colwell and Futuyma, 1971) and the scale over which resources are studied. Werner (1977) argued that one effect of size structuring of fish assemblages would be to reduce the potential for separation, at least on the food size axis and thus increase the importance of habitat separation. That this prediction is not borne out by the available literature may be, in part, due to many studies not addressing the full age/size range of species in an assemblage.

Diel and seasonal temporal dimensions seem to be less important than trophic or spatial dimensions; being the primary mode of separa-

TABLE 2. RANKING OF MAJOR RESOURCE AXES BASED ON THE PERCENT OF STUDIES IN WHICH A PARTICULAR DIMENSION WAS LISTED AS MOST IMPORTANT. A = ranking based on the 37 studies which examined all three major resource dimensions; B = ranking based on the 90 studies which examined 2–3 major resource axes. The number of times a dimension was most important is shown over the number of times it was studied. The lower percent is scaled to sum to 100%.

	Habitat		Food		Time	
	N	(%)	N	(%)	N	(%)
A.	12	(32.4)	21	(56.8)	4	(10.8)
B.	27/74	(36.5)	58/85	(68.2)	6/59	(10.2)
		(31.8)		(59.4)		(8.9)

TABLE 3. HABITAT DIFFERENCES IN THE RELATIVE IMPORTANCE OF SPATIAL AND TROPHIC DIMENSIONS. * Indicates a significant difference.

Habitat group	N	No. of studies with habitat > food separation	$\bar{x}$ % species separated by habitat	No. of studies with food > habitat separation	$\bar{x}$ % species separated by food	Z	P
All assemblages	68	20	(54)	40	(64)	−2.19	<.05*
Marine	44	10	(52)	28	(69)	−2.94	<.01*
Freshwater	24	10	(56)	12	(56)	−.032	.97
Tropical reefs	8	4	(69)	4	(61)	−.98	.33
Temperate reefs	12	1	(51)	9	(82)	−2.70	<.01*
Coastal marine	14	4	(48)	7	(60)	−1.20	.23
Streams	13	6	(58)	6	(57)	0	1.00
Lakes	11	4	(55)	6	(54)	−.05	.96

tion in only 9% of the fish assemblages. The limited number of ways in which temporal use of resources may be subdivided, the rate of replenishment of resources and the balance of no benefit from a resource if it is not used for a time interval, vs at least some benefit if it is used, give theoretical support (Schoener 1974a, b) for the lesser importance of temporal dimensions (Jaksić, 1982). Temporal separation may, however, be somewhat more important in aquatic than terrestrial systems (5% in primarily terrestrial metazoans vs 9% in fishes) because of the increased potential for resource renewal and the possible greater potential for temporal spacing of reproduction afforded by many aquatic environments, compared to terrestrial systems. This effect may be due to the decreased threat of dessiccation and the moderated thermal regime of aquatic habitats. Temporal spacing of the occurrence of larval fishes is well known (Amundrud et al., 1974; Floyd et al., 1984) possibly as a mechanism to reduce potential trophic competition in the critical period (May, 1974) following yolk sac absorption. Toft (1985) also found that temporal separation was extremely important for amphibian larvae.

GLOBAL HABITAT DIFFERENCES IN THE IMPORTANCE OF MAJOR RESOURCE AXES

Studies of fish assemblages suggest that generalized differences may exist among the major aquatic habitats of the world with respect to the resource axes along which species segregate. For instance, Mendelson (1975) and Baker and Ross (1981) suggested that habitat separation may be the major means of resource partitioning in freshwater fishes. Horn (1974) also argued that, due to the striking difference in the amount of space available for marine vs freshwater fishes, there is greater habitat partitioning among freshwater than marine fishes. There is strong support in the literature (Sale, 1974a, 1978a; Smith and Tyler, 1973; Bohnsack and Talbot, 1980; Robertson and Lassig, 1980) that habitat separation is more important than food separation in coral reef areas, although Sale (1977) in a review of the tropical reef fish literature found it surprising that reef fishes did not show greater habitat than trophic partitioning, especially because of the evidence that they were more likely to compete for space. Ross (1977) found that habitat separation was most important for a group of demersal marine fishes. In contrast, Gascon and Leggett (1977) have argued that trophic separation is more important than habitat separation in freshwater fishes.

Sampling bias presents a major problem in comparing the importance of the principal resource dimensions in different habitats. For instance, almost all studies of tropical reef fish assemblages have examined habitat segregation (including both macro- and micro-habitats) and have found habitat segregation to be important (Fig. 3). Approximately half of the tropical reef studies have examined trophic resource dimensions and, of these, all have found food partitioning to be important. This would indicate that trophic separation may be more important in tropical reef fish assemblages than is currently thought, or that fewer studies found food separation important and negative results were not reported. Fewer studies of tropical reefs have looked at temporal dimensions (diel time only) and most of these have shown diel time to be an important axis along which separation occurs. Thus it is difficult to argue that one particular resource dimension is most important, since the distribution of important dimensions is virtually a mirror image of the frequen-

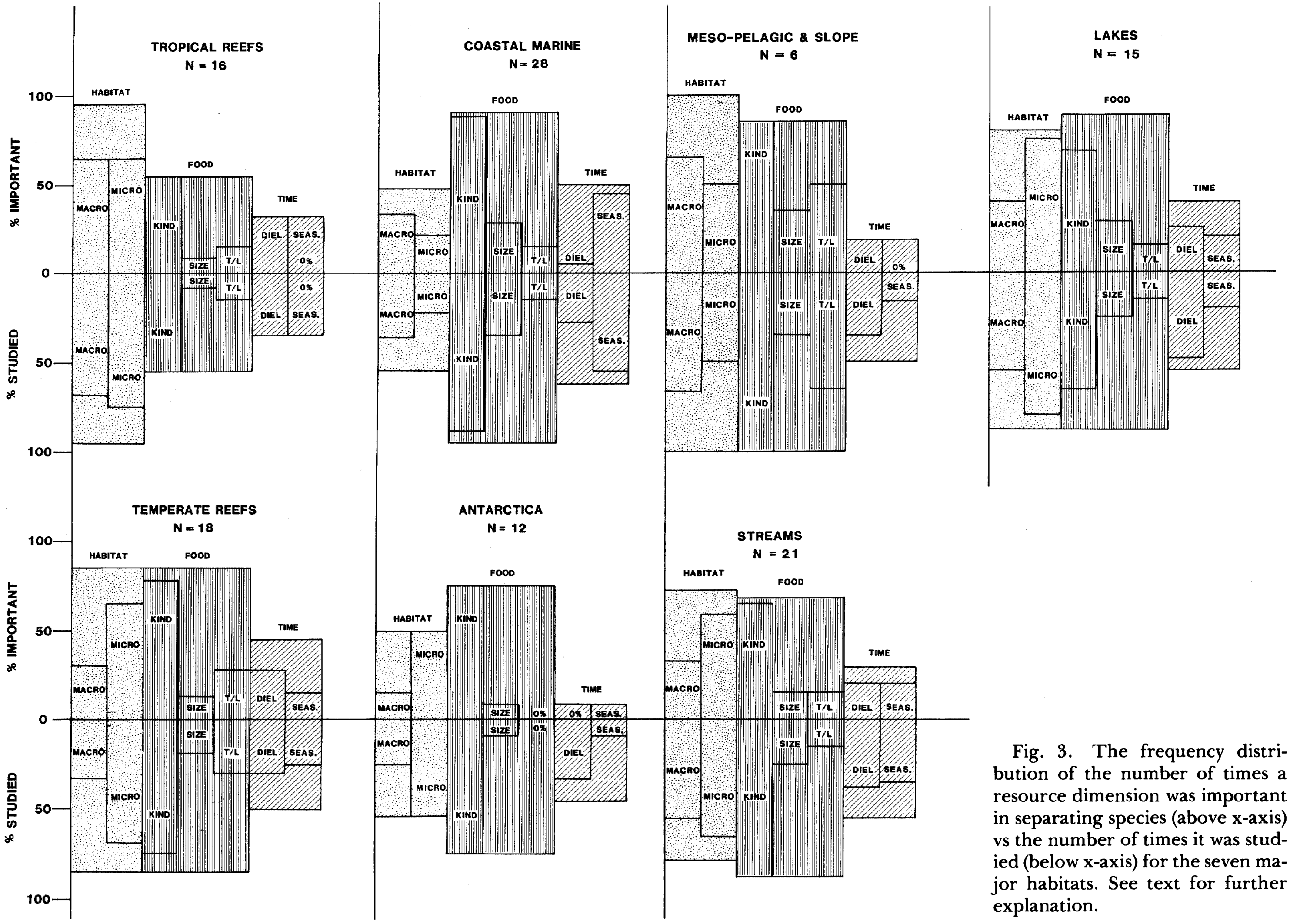

Fig. 3. The frequency distribution of the number of times a resource dimension was important in separating species (above x-axis) vs the number of times it was studied (below x-axis) for the seven major habitats. See text for further explanation.

TABLE 4. THE DISTRIBUTION OF SAMPLING TECHNIQUES BY HABITAT CATEGORY FOR STUDIES FROM TABLE 1. All methods used in a study are listed.

	Habitat category													
	Tropical reef		Temperate reef		Coastal marine		Mesopelagic/slope		Antarctic		Streams		Lakes	
Sampling method	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
Seines, gill nets, & other netting devices	—		5	(28)	11	(39)			2	(17)	18	(86)	9	(60)
Trawls, dredges, plankton nets	—		1	(6)	19	(68)	6	(100)	10	(83)	—		1	(7)
Trapping	—		—		2	(7)			2	(17)	3	(14)	—	
Ichthyocides & explosives	2	(13)	7	(39)	3	(11)			—		1	(5)	—	
Spearing	4	(25)	6	(33)	—				—		1	(5)	—	
Hook & line	—		1	(6)	1	(4)			2	(17)	2	(10)	1	(7)
Electrofishing	—		—		—				—		4	(19)	1	(7)
Visual observations	16	(100)	11	(61)	1	(4)			3	(25)	2	(10)	7	(47)
Number of studies	16		18		28		6		12		21		15	

cy distribution of those studied. In contrast to coral reef systems, temperate reefs, the mesopelagic and slope region and freshwater systems all show much greater evenness in study emphasis on habitat and food dimensions. These regions also show rather similar importance in the major resource dimensions. Trophic dimensions in coastal marine and Antarctic assemblages have been studied most often and again show frequency distributions of important dimensions which are virtually mirror images of the frequency distribution of the dimensions studied. Time is less often studied than other major dimensions. However, in Antarctic, mesopelagic/slope and freshwater fish assemblages considerably more studies examined temporal dimensions than found them to be important, suggesting that temporal separation may be less common in these habitats.

Temporal separation appears to vary in different environments. Seasonal separation is well studied in coastal marine areas and is generally important, especially as temporal spacing of reproduction. Although less often studied in temperate reefs and lakes, it was important in all works which examined it. A difference in the timing of reproduction was the major means of seasonal separation. Such differences may reflect separation on food and/or habitat parameters. Diel separation, primarily in time of feeding, seems especially important in reef habitats and to a lesser extent in freshwater systems, occurring in approximately half of the freshwater studies which examined it. This pattern may be more common in habitats supporting structure-oriented fishes which tend to forage in restricted areas, primarily on zooplankton or small nekton. Such food resources may show rapid renewal due to transport by water currents, making diel separation in food use a viable approach to resource partitioning. Both marine zooplankton (Hobson and Chess, 1976; Robertson and Howard, 1978) and invertebrate drift in streams (Waters, 1962; Hynes, 1970) often show strong diel changes in composition and abundance in the water column. Consequently, selective zooplankton predators experience periods of very low foraging profitability during the less active (or benthic) periods of their prey. The impact of predation in causing diel changes in feeding activity of both fishes and zooplankton may also be especially important in these environments (Hobson, 1975; Robertson and Howard, 1978) so that any benefits that might accrue from feeding over broader time periods are outweighed by increased predation risks.

The difference in studied resource dimensions between major habitats is to a large degree dictated by the sampling methodology appropriate for the various habitats. Visual observations predominate in tropical reef studies, and to a lesser extent in temperate reefs and in lakes (Table 4). Vessel powered nets (trawls, dredges, plankton nets) are the only sampling devices used in mesopelagic/slope studies and predominate in Antarctic and coastal marine studies. Seines or gill nets predominate in stream and lake systems. Comparing sampling methods (Table 4) with the frequency distribution of studied resource dimensions (Fig. 3), it is obvious that where visual observations predominate, spatial resource parameters are emphasized relative to other dimensions. Regions where information comes primarily from the physical collection of fishes (coastal marine, mesopelagic/slope, Antarctic and streams) are characterized by increased emphasis on food dimensions, or approximately equal emphasis on spatial and trophic dimensions. These studies often place greater emphasis on macrohabitat rather than on microhabitat parameters. Studies of lakes and temperate reefs are more evenly balanced between observational and collecting approaches, and show more even emphasis on trophic and spatial dimensions, with greater attention to microhabitat, rather than macrohabitat parameters.

As an initial test for differences in the importance of major resource axes among habitats, I limited the analysis to assemblages represented by eight or more studies, which provided concurrent data on both habitat and food (Table 3). I tested the null hypothesis of no difference in the percent of species pairs separated by spatial or trophic dimensions by the Wilcoxon signed-rank test (two-tailed comparison). Studies of marine assemblages overall indicate significantly greater importance of trophic than habitat separation, especially temperate reef systems (Table 3). Other assemblages, including tropical reefs, coastal marine, streams and lakes do not show a significant difference in the importance of trophic and spatial dimensions.

Differences in major resource axes by global habitat types are thus strongly controlled by sampling methodology as dictated by the nature of the environment. Such bias makes generalizations drawn from the literature essentially meaningless if not controlled. Fish assemblages in most habitats show approximately equal importance of separation along spatial and trophic dimensions, with the exception of temperate reefs which show greater importance of trophic separation.

DIFFERENCES IN THE MAGNITUDE OF RESOURCE SEPARATION BY GLOBAL HABITAT

Currently there is debate among ecologists concerning mechanisms of community control and the prevalence of equilibrial (deterministic) vs non-equilibrial (stochastic) processes (Sale, 1977, 1978b; Connell, 1978; Smith, 1978; Anderson et al., 1981; Grossman et al., 1982; Schlosser and Toth, 1984). In communities showing strong equilibrial control the degree of niche specialization may be greater with concomitantly greater resource partitioning than if species populations are influenced primarily by chance processes. The degree of overlap is influenced also by the shape of the resource utilization function (Roughgarden, 1974) and the distribution and abundance of resources (Colwell and Futuyma, 1971).

The wide range of habitats occupied by fish assemblages suggests a potential for different mechanisms of community control to be operative, so that different degrees of resource partitioning, irrespective of the resource type, may characterize fish assemblages of these habitats. For instance, there are an estimated 21,723 species of fishes of which approximately 39% occur primarily in freshwater (Cohen, 1970; Nelson, 1984). Horn (1972) determined that there is about 7500 times more habitat available to marine than freshwater species and, considering only the marine shore and shelf species, there is still a twenty-fold difference. The volume of water per individual is estimated to be 10–10,000 times less for freshwater fishes. The disparity suggests that resource partitioning may be of greater importance in freshwater systems (i.e., resource limitation may have a greater probability of occurrence). Sale (1977) and Sale and Williams (1982) argued that many reef fishes do not show fine resource partitioning, in contrast to other types of communities (Anderson et al., 1981). Also, there may be varied mechanisms of community control within similar marine habitats of different areas. Helfman (1978) suggested that the controversy over mechanisms of community control in tropical reef habitats might, in part, be caused by Caribbean reef fish assemblages being more deterministically controlled than Indo-Pacific fish assemblages. This idea has recently been supported by Thresher (1982) who found that western Atlantic fish communities may be more nearly saturated with individuals and thus more prone to competitive interactions than fish communities of western Pacific reefs, although experiments of Bohnsack and Talbot (1980) do not support this view.

As a crude initial approach to evaluating the null hypothesis of no difference in the magnitude of resource partitioning among the seven major global habitats, I used the percent of species pairs from each study that showed a minimum of one substantial difference on any resource axis. This underestimates the degree of resource partitioning since studies looking at more resource dimensions have the potential for finding greater separation. Given the limitation of this approach, the studies listed in Table 1 offer no basis for arguing that major differences in resource partitioning occur between habitats (Kruskal-Wallis test; $\chi^2 = 3.34$; n.s.). Mean values for percent of species pairs separated ranged from a low of 73% for coastal marine habitats, 77% for the Antarctic, 79% for streams, 80% for temperate reefs, 82% for tropical reefs and lakes, to 87% for mesopelagic/slope habitats. Thus, at the level of resolution afforded by this comparison, assemblages of all habitats show rather high separation of coexisting species along at least one resource dimension.

It is perhaps unreasonable to expect habitat-wide differences in resource partitioning to exist when the habitat categories used are broad and intra-habitat variation in resource partitioning is high. For instance, the tropical reef category includes both Caribbean and Indo-Pacific studies and possible differences may exist in the control of these systems (Helfman, 1978). The temperate reef category includes both subtidal as well as intertidal regions. Grossman (1982) presented evidence that fishes of rocky intertidal areas showed deterministic traits and Yoshiyama (1980, 1981) demonstrated fine scale resource partitioning and niche complementarity in habitat and food use for intertidal fishes. Thompson and Lehner (1976) also found high resilience and low faunal variability in rocky intertidal fishes. In contrast, Stephens and Zerba (1981) have argued that in a subtidal fish assemblage off California niche specialization has not contributed significantly to species packing and that the system shows considerable change over time. In yet other subtidal, temperate reef studies Ebeling et al. (1980) found that persistence of major species was high over time and that levels of annual variability (Wolda, 1978) were comparable with diverse communities in stable environments and Larson (1980) and Hixon (1980) demonstrated the importance of competition in causing resource partitioning of pairs of subtidal reef fishes. Thorman (1982) found that competition was apparently important in structuring the fish community of one Swedish estuary, but in another system with harsher environmental conditions and lower productivity, there was no evidence that food competition was important in structuring the assemblage.

Matthews and Hill (1980) found little evidence of resource partitioning in the physically variable South Canadian River in Oklahoma and Ross et al. have shown that the fish assemblage of Brier Creek, Oklahoma, has changed significantly over approximately one decade, while a more physically benign stream in the Arkansas Ozarks did not show significant faunal change over the same period. Grossman et al. (1982) generalized that most stream fish assemblages were stochastically controlled and Schlosser and Toth (1984) suggested that interspecific competition may be relatively unimportant in structuring communities of temporally variable environments.

This sampling of studies shows the difficulty of formulating broad generalizations of community control. One pattern, however, which often appears is a decrease in importance of biotic interactions in structuring fish assemblages in harsher environments. Until more comparable data are available other generalizations concerning global habitat differences will remain tenuous at best. The interpretation of resource partitioning studies is further confounded by effects of taxonomic structure and by increased complexity due to intraspecific changes in resource use during ontogeny.

TAXONOMIC STRUCTURE

The influence of taxonomic structure is generally overlooked in the interpretation of resource partitioning data, although some authors, including Mendelson (1975), Clarke (1977), Keast (1978) and Schlosser and Toth (1984) have variously considered it. Fish assemblages of the seven global habitat groups vary significantly in both the number of species per genus and number of genera per family (Table 5). Tropical reefs and streams show the greatest number of congeneric species, while temperate reef assemblages show the fewest. Studies of tropical reefs also show the greatest number of genera per family. Thus, investigations of tropical reef fish assemblages and to a lesser extent stream fish assemblages, have focused on more closely related faunas, both at the specific and generic levels (for tropical reefs), compared to studies of temperate reefs, the Antarctic or freshwater lakes.

If historical effects, as evidenced in this case by taxonomic structure, do not influence resource partitioning, then an appropriate null hypothesis would be that there are no differences in resource separation between species pairs of different levels of relatedness. To test this hypothesis I selected studies which treated three or more species pairs in adjacent taxonomic ranks (e.g., congeneric, confamilial, conordinal) and determined the percent of species pairs of each taxonomic rank which showed a substantial difference on at least one resource dimension and on habitat, food and temporal dimensions (Table 6). Species pairs were categorized by the lowest shared taxonomic category. From these 52 studies I tested various pairwise comparisons relative to the null hypothesis of no difference in resource separation, or axis partitioned, as a function of taxonomic relatedness (Table 7).

The degree of relatedness of species pairs has a significant effect on ecological separation for both congeneric-confamilial and confamilial-conordinal comparisons, with less related pairs showing greater percent separation (Table 7). Relatedness has no effect on ecological separation for comparisons between species pairs related at the ordinal-supraordinal (or higher) levels and is strongest for the comparison between congeneric and confamilial species. The data consequently indicate that comparisons of niche overlap between assemblages of different taxonomic structure will reflect, to an unknown degree, the level of relatedness of the component species. While coadaptation resulting in reduced niche overlap may be important, such comparisons may equally reflect the historical events of speciation and processes of assembly of communities. For example, the random assembly of a community from a species pool with a low species/genus ratio would produce more apparent partitioning than the random assembly from a species pool with a high species/genus ratio. The critical question then is whether resource partitioning is instrumental in the recruitment of species to the community and in the maintenance of the community, or if it is simply a non-essential by-product of the taxonomic structure.

The type of resource along which species pairs differ does not appear to be influenced by the relatedness of the species pair, with the striking exception of temporal separation (Tables 6 and 7). Temporal separation was important in the segregation of congeneric species pairs in only 3 of 18 studies. Confamilial species pairs showed significantly greater temporal separation than congeneric pairs and conordinal pairs showed significantly greater temporal separation than confamilial pairs. Again there was no difference between conordinal-supraordinal (or higher) species pairs. Differences in the timing of feeding, particularly diurnal-nocturnal differences, or secondarily, major differences in the timing of reproduction or habitat use, may require greater morphological, physiological or ethological differentiation than normally occurs at the generic level. Various authors (Hobson, 1972, 1975; Ebeling and Bray, 1976; Hobson et al., 1981) have shown that differences in day-night activity of fishes often, but not always, break along family or ordinal lines, showing a strong ancestral effect. As a consequence, temporal partitioning, at least to a major degree, may reflect historical effects, rather than coevolution within a particular community. This is not to say, however, that such differences may be unimportant to community assembly and maintenance.

TABLE 5. HABITAT DIFFERENCES IN MEANS OF THE RATIO OF SPECIES TO GENUS (S/G) AND GENERA TO FAMILIES (G/F) OF STUDIES LISTED IN TABLE 1.

	S/G	G/F
Tropical reefs	2.3	3.0
Temperate reefs	1.5	2.1
Coastal marine	1.7	2.2
Mesopelagic/Slope	1.7	2.0
Antarctic	1.7	1.7
Streams	2.1	1.7
Lakes	1.8	1.6
Kruskal-Wallis Anova	$\chi^2 = 14.3$ $P < .05$	$\chi^2 = 17.2$ $P < .01$

ONTOGENETIC CHANGES

Fish assemblages are often strongly size structured so that a variety of interactions, including competition and predation, may potentially occur between different life history stages of species. The impact of body size on resource use of fishes has been well documented (Carr and Adams, 1973; Hobson and Chess, 1976; Ross, 1978; Grossman, 1980; Livingston, 1982) and Werner and Gilliam (1984) have reviewed the effect of age/size differences on community interactions of primarily lower vertebrates and invertebrates. Relatively few resource partitioning studies of fish assemblages, however, have atempted to incorporate age/size differences over more than the late juvenile to adult stages and virtually no studies have included all life history stages of the fish assemblage under consideration. An exception is Markle et al. (1982) who studied ontogenetic spatial and temporal

TABLE 6. THE INFLUENCE OF TAXONOMIC RELATEDNESS ON RESOURCE SEPARATION BASED ON STUDIES FROM TABLE 1. Only studies with three or more species pairs in adjacent taxonomic categories are included. The super-ordinal category includes all species pairs related at the super-ordinal level or above (classification follows Nelson, 1984). N = number of species pairs; To = percent of species pairs differing in use of at least one resource; H = percent of species pairs separated by habitat, F = percent of species pairs separated by food; Ti = percent of species pairs separated by temporal dimensions.

Congeneric					Confamilial					Conordinal					Super-ordinal					
N	To	H	F	Ti	N	To	H	F	Ti	N	To	H	F	Ti	N	To	H	F	Ti	Source
3	0	—	—	0	10	40	—	—	40	—	—	—	—	—	23	70	—	—	70	Angermeier, 1982
21	95	95	—	0	7	86	86	—	100	—	—	—	—	—	—	—	—	—	—	Baker & Ross, 1981
—	—	—	—	—	5	60	40	60	—	4	100	25	100	—	—	—	—	—	—	Barton, 1982
13	62	31	62	—	20	59	53	59	—	32	74	56	67	—	—	—	—	—	—	Daniels, 1982
6	83	83	—	—	15	93	93	—	—	24	75	75	—	—	—	—	—	—	—	Daniels & Lipps, 1982
21	81	81	—	—	34	91	91	—	—	23	74	74	—	—	—	—	—	—	—	DeVries & Eastman, 1981
11	82	82	64	—	10	100	80	80	—	—	—	—	—	—	—	—	—	—	—	Dunn, 1975
22	41	41	—	0	25	4	0	—	4	104	43	20	—	14	150	46	46	—	8	Ebeling & Bray, 1976
20	50	35	25	—	46	87	63	63	—	—	—	—	—	—	—	—	—	—	—	Emery, 1973
—	—	—	—	—	7	0	0	—	—	8	25	25	—	—	12	17	17	—	—	Finger, 1982
10	50	50	30	—	—	—	—	—	—	27	81	44	74	—	29	93	55	48	—	Gibson, 1968
—	—	—	—	—	3	0	0	0	—	9	56	11	44	—	66	58	27	39	—	Gibson, 1972
4	100	50	75	—	17	94	82	65	—	—	—	—	—	—	—	—	—	—	—	Gladfelter & Johnson, 1983
—	—	—	—	—	6	33	—	33	—	11	64	—	64	—	—	—	—	—	—	Harrington & Harrington, 1961
—	—	—	—	—	5	0	—	0	—	5	20	—	20	—	44	30	—	30	—	Hartley, 1948
8	25	—	25	25	17	47	—	47	0	21	81	—	62	67	20	85	—	60	80	Hobson & Chess, 1978
8	67	67	—	—	24	79	79	—	—	—	—	—	—	—	—	—	—	—	—	Itzkowitz, 1977
73	74	73	58	—	117	92	65	77	—	—	—	—	—	—	—	—	—	—	—	Jones, 1968
24	67	67	42	—	54	87	48	74	—	—	—	—	—	—	—	—	—	—	—	Jones, 1968
20	95	25	95	—	8	88	13	88	—	48	88	27	83	—	—	—	—	—	—	Keast, 1966
—	—	—	—	—	17	76	47	65	41	13	100	38	62	69	104	96	72	77	13	Keast, 1978[1]
—	—	—	—	—	—	—	—	—	—	7	86	71	71	—	20	75	45	55	—	Kislalioglu & Gibson, 1977
—	—	—	—	—	6	83	—	83	—	4	100	—	100	—	—	—	—	—	—	Kravitz et al., 1976
3	67	—	67	—	7	100	—	100	—	—	—	—	—	—	—	—	—	—	—	Laroche, 1982
—	—	—	—	—	4	75	—	75	25	5	60	—	60	40	12	75	—	75	25	Last, 1978a, b
6	83	50	50	—	4	50	25	25	—	—	—	—	—	—	—	—	—	—	—	Lewis & Yerger, 1976
12	58	58	—	—	4	100	100	0	0	53	92	64	4	64	35	100	34	66	54	Luckhurst & Luckhurst, 1978a
9	78	67	11	0	11	91	91	45	0	194	95	89	70	41	87	94	83	56	64	Luckhurst & Luckhurst, 1978c
—	—	—	—	—	21	90	5	86	—	29	97	14	93	—	275	93	5	92	—	MacPherson, 1981
28	79	68	—	50	8	100	75	—	50	—	—	—	—	—	—	—	—	—	—	McKaye, 1977
3	67	67	67	0	5	100	0	80	40	12	100	33	67	75	—	—	—	—	—	Merrett & Roe, 1974
3	100	33	33	33	6	100	100	100	33	—	—	—	—	—	—	—	—	—	—	Modde & Ross, 1983

TABLE 6. CONTINUED.

	Congeneric					Confamilial					Conordinal					Super-ordinal					
	N	To	H	F	Ti	N	To	H	F	Ti	N	To	H	F	Ti	N	To	H	F	Ti	Source
	8	38	38	—	—	58	57	57	—	—	—	—	—	—	—	—	—	—	—	—	Molles, 1978
	7	86	86	—	—	14	71	71	—	—	15	53	53	—	—	—	—	—	—	—	Moreno et al., 1977
	6	50	50	50	—	7	71	0	71	—	15	87	27	87	—	17	76	41	71	—	Permitin & Tarverdiyeva, 1972
	4	75	75	—	—	11	73	73	—	—	—	—	—	—	—	—	—	—	—	—	Robertson & Lassig, 1980
	10	90	70	30	—	26	100	42	85	—	—	—	—	—	—	—	—	—	—	—	Robertson et al., 1979
	21	100	95	95	0	7	85	57	57	0	—	—	—	—	—	—	—	—	—	—	Ross, 1977, 1983
	12	42	42	—	—	24	79	79	—	—	—	—	—	—	—	—	—	—	—	—	Sale, 1974a
	—	—	—	—	—	3	67	0	67	—	5	100	60	60	—	47	91	45	83	—	Sedberry & Musick, 1978
	13	46	46	—	0	15	60	60	—	0	140	90	80	—	64	63	76	73	—	56	Smith & Tyer, 1972
	12	75	—	75	0	66	79	—	79	0	—	—	—	—	—	—	—	—	—	—	Starrett, 1950
	3	67	—	71	0	7	71	—	71	0	18	72	—	72	0	—	—	—	—	—	Targett, 1981
	3	67	—	67	—	5	80	—	80	—	20	95	—	95	—	8	100	—	100	—	Targett, 1981
	3	67	—	67	0	3	67	—	67	0	30	77	—	77	0	—	—	—	—	—	Targett, 1981
	11	27	—	27	0	5	80	—	80	0	39	72	—	72	0	—	—	—	—	—	Targett, 1981
	3	33	—	33	0	11	64	—	45	18	5	60	—	40	20	59	59	—	44	14	Tyler 1971, 1972
	15	100	100	—	—	6	100	100	—	—	—	—	—	—	—	—	—	—	—	—	Waldner & Robertson, 1980
	7	86	86	0	0	9	100	67	11	22	6	67	67	0	0	8	100	100	0	0	Werner et al., 1977
	9	78	78	0	0	12	100	58	8	33	9	89	89	0	0	35	46	46	0	0	Werner et al., 1977
	—	—	—	—	—	—	—	—	—	—	4	100	100	—	—	16	94	94	—	—	Werner et al., 1978
	5	40	40	—	—	26	50	50	—	—	29	52	52	—	—	60	53	53	—	—	Yoshiyama, 1981
Median		67	67	50	1		79	58	67	4		81	53	67	21		76	46	56	25	
Mode		67	50	67	0		100	0	80	0		100	25	0	0		100	45	0	0	

[1] Other authors as listed in Table 1.

TABLE 7. ANALYSIS OF PAIRWISE COMPARISONS OF RESOURCE SEPARATION USING WILCOXON'S SIGNED RANK TEST. * Indicates a significant difference.

Comparison		Number pairs	A > B	B > A	Z	P
A versus	B					
I. Total separation						
Congeneric	Confamilial	39	9	27	−3.39	.001*
Confamilial	Conordinal	30	9	19	−2.18	.03*
Conordinal	Super-ordinal	21	11	10	−.24	.81
II. Congeneric, Habitat	Food	18	10	3	−1.54	.12
III. Confamilial, Habitat	Food	22	5	11	−1.14	.26
IV. Conordinal, Habitat	Food	15	4	9	−.91	.36
V. Super-ordinal, Habitat	Food	11	4	7	−.53	.59
VI. Temporal separation						
Congeneric	Confamilial	18	1	7	−1.96	.05*
Confamilial	Conordinal	14	2	9	−2.05	.04*
Conordinal	Super-ordinal	10	6	2	−.84	.40

partitioning in *Urophycis chuss* and *U. tenuis* on the Scotian Shelf.

Ecological studies of larval fishes generally indicate that interspecific resource overlap is greatest at the earlier stages and declines with growth (Nagabhushanam, 1965; Pearcy and Ambler, 1974; Itzkowitz, 1977; Christensen, 1978). However, Last (1978a, b), Laroche (1982) and Govoni et al. (1983) all presented evidence of marked resource partitioning among larval forms. Markle et al. (1982) showed progressively greater temporal and spatial overlap in two *Urophycis* species, but did not identify larvae under 18mm to species. Kane (1984) has shown that cod and haddock larvae initially partitioned food resources during the period immediately following yolk sac absorption. The amount of overlap increased, however, by the time the larvae reached 6 mm. Crecco and Blake (1983) also found that first-feeding American shad and blueback herring larvae had lower food overlap than later larval stages. Density dependent mechanisms may be important among recently hatched larvae when population sizes are largest (Cushing, 1974). This, along with the lowered feeding success of first-feeding larvae, may select for greater resource separation among early-stage larvae of co-occurring species (Crecco and Blake, 1983). As the population of an age class declines with time, density dependent interactions may decline as well (Cushing, 1974), so that there is perhaps less of a fitness penalty for resource overlap of older larvae and juveniles. Resource segregation may again increase in importance as fishes attempt to meet evergy demands of maturity.

Helfman (1978) suggested that competitive or anti-predator mechanisms may be more common in larvae of lake and continental shoreline species, where suitable larval habitats are more continuous (than in reef habitats). The above studies showing larval resource partitioning are consistent with this idea, if resource partitioning is viewed as evidence of competition. Sale and Dybdahl (1975) have shown high spatial overlap of newly settled pomacentrids in a tropical reef environment. Sale (1974a, 1975) found that essentially all suitable juvenile and adult habitats were occupied at Heron Island, in the Great Barrier Reef and that any vacant space was rapidly re-occupied. However, the lottery hypothesis (Sale, 1977, 1978a, b) requires that newly settled juveniles be able to hold an area once they have recruited to it. Thus, while resource overlap is high, interference competition for space may be important. Larson (1980) found that newly settled rockfish (*Sebastes carnatus* and *S. chrysomelas*) showed habitat segregation similar to adults, in apparent contradiction to Helfman's suggestion. However, adult rockfish do not exclude newly settled juveniles from their territories, while tropical reef dwelling pomacentrids (Sale, 1974a, 1976; Sale et al., 1980) show aggressive behavior toward juveniles, especially juvenile conspecifics. (The extent to which adults effectively exclude juveniles may vary as Doherty [1982] found that resident *Pomacentrus wardi* were unable to prevent other pomacentrid larvae from colonizing their territories, perhaps because of recruits being able to occupy small spatial refuges.) The effect may be much greater habitat availability for young rockfish, compared to pomacentrids, allowing habitat selection by young fish to be a viable tactic in community organization of temperate reefs.

CONCLUSIONS

Differential resource use has been widely documented in diverse fish assemblages, with generally high levels of ecological separation between the majority of species. Such differences may be due to varying tolerances to physical-chemical variables, environmental change and uncertainty, local spatio-temporal resource availability, predation risks and competition. Causation for differences in resource use has generally not been determined, especially for assemblages of three or more species.

Inference of underlying mechanisms is obfuscated in descriptive studies of resource partitioning, in part through problems of interpreting overlap values (Colwell and Futuyma, 1971; Sale, 1974b). Descriptive studies of resource partitioning come closest to demonstrating competition when documenting niche shifts under varying resource levels. For instance, Zaret and Rand (1971) and Greenfield et al. (1983) showed reduced niche overlap of Central American stream fishes during the dry season, when food was presumed limiting; Gascon and Leggett (1977) demonstrated reduced niche overlap in less productive than in more productive areas of a lake with a strong nutrient gradient; Nilsson (1955) showed less niche overlap between trout and char during periods of low food abuundance; Harrington and Harrington (1961) presented data which showed high overlap of salt marsh fishes during high food abundance and segregation by diet during periods of lower food abundance; and Thorman (1982) showed increased dietary segregation of estuarine fishes during a period of declining food abundance. The occurrence of strong niche complementarity also can suggest the importance of competition. Ross (1977) showed that searobins with high habitat overlap tended to differ in prey size; Yoshiyama (1980) showed strong complementarity in habitat and food use for two of three intertidal cottids and argued that the complementarity and resource partitioning suggested the importance of competition in shaping the pattern of resource use. Baker and Ross (1981) showed that stream fishes with high spatial overlap differed in time of feeding.

The general consensus of most recent studies is that the best approach to understanding resource partitioning and its importance to community structure lies in manipulative field experiments (Colwell and Fuentes, 1975; Connell, 1975; Werner, 1979; Sale, 1979; Williams, 1980; Crowder et al., 1981; Yoshiyama, 1981). Studies incorporating both descriptive field observations and field and laboratory work on fishes are becoming increasingly common (Sale and Dybdahl, 1975; Werner and Hall, 1976, 1977; Molles, 1978; Bohnsack and Talbot, 1980; Hixon, 1980; Larson, 1980; Edlund and Magnhagen, 1981; Baltz et al., 1982; Magnhagen and Wiederholm, 1982; Schlosser and Toth, 1984). Many of these studies indicate that biotic interactions, such as competition (often interference competition), are important in causing the observed patterns, but are by no means the only causative factors. For instance, Baltz et al. (1982) showed that sculpin (*Cottus gulosus*) were able to exclude speckled dace (*Rhinichthys osculus*) from preferred microhabitats, but that dace could tolerate warmer temperatures than sculpin, thus obtaining a refugium from competition in warmer stream sections. Hixon (1980), demonstrated that surfperch congeners (*Embiotoca*) actively compete in sympatry, with *E. lateralis* excluding *E. jacksoni* from productive, shallow reef zones. *E. jacksoni* finds a competitive refugium in deeper, less productive reef areas. The extension of *E. lateralis* into other reef areas occupied by *E. jacksoni* is apparently limited by higher water temperature, so that the superior competitor is limited more by unfavorable physical factors than by competitive interactions. These studies, as well as Larson (1980) support the observation by Colwell and Fuentes (1975) that when interference competition occurred between a generalist and a specialist, it was the specialist that successfully interfered with the generalist. Larson (1980) points out, however, that the interaction may not be totally one-sided.

Resource partitioning has provided a useful conceptual framework for collecting and assessing data on fish assemblages. Some important roles of resource partitioning studies are to: 1) provide an understanding of species interactions in a community; 2) identify major resource dimensions along which species segregate; 3) provide the requisite background for generating testable hypotheses concerning the roles of equilibrium or non-equilibrium factors in community control. Resource partitioning studies serve an important practical need in providing information on habitat requirements of fishes. Should additional studies of resource partitioning be encouraged? I feel the answer is a definite yes, with the qualification that such studies attempt to deal with problems of sampling bias, effects of taxonomic structure (e.g., historical effects), temporal and spatial variability and a more complete representation of life history stages. Importantly, documentation of patterns of resource partitioning in a community should only be the initial step, albeit a major one, in the study of the structure and function of fish assemblages. The subsequent challenge is to address the mechanisms responsible for the patterns through carefully designed and executed field and laboratory experiments.

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Fish Faunal Structure in an Ozark Stream: Stability, Persistence and a Catastrophic Flood

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In December 1982, widespread, physically catastrophic flooding occurred in the Ozark Mountains of northern Arkansas. In the Piney Creek watershed (Izard County), flooding resulted in an immediate change in rank order abundance of numerically dominant fishes and moderate alteration in composition of the entire fauna. At badly scoured locations, local assemblages of fishes were markedly altered. These changes in the fish fauna of Piney Creek exceeded seasonal changes in the fishes that were found in an earlier, non-flood year. The Piney Creek fish fauna showed rapid recovery from the flood, however, and by August 1983, eight months later, the total fish fauna and the local fish assemblages closely resembled those of August 1982, before the flood. Comprehensive sampling of the watershed in 1972, 1973, 1981 (in part), 1982 and 1983 suggests that the fish fauna was stable (via elasticity) and persistent across years, seasons and a drastic flood.

FLOODS pique our curiosity: they seem likely to affect fishes and fish assemblages but opportunities to quantify effects with pre- and post-flood data are infrequent. Erosive floods can alter fish populations (Hoopes, 1975; Rinne, 1975; Collins et al., 1981) or community structure (Harrell, 1978; Grossman et al., 1982 and references therein; Power et al., 1985). How-