

Effects of drought on fish across axes of space, time and ecological complexity

WILLIAM J. MATTHEWS AND EDIE MARSH-MATTHEWS

Department of Zoology, and Biological Station, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK, U.S.A.

SUMMARY

1. We evaluate the position of 50 previously published studies of fish and drought with respect to spatial scale of study (individual stream pools to subcontinents), length of the dry period (weeks to centuries), and level of system complexity (individual fish to ecosystems). Most papers address short (months to a year) droughts or dry periods, in local reaches of streams, and impacts on populations or local assemblages. In these 50 papers, the most frequently demonstrated effects of drought were population declines, loss of habitat, changes in the community, negative effects from changes in water quality, movement within catchments, and crowding of fish in reduced microhabitats. Thirteen other less frequent effects also were identified.
2. Gaps in knowledge exist on effects of long-term droughts (decades to centuries), influence of drought on fish effects in ecosystems, and at the spatial scale of river basins to subcontinents. However, some of these gaps have recently been addressed, particularly additive effects of repeated drying episodes and whole-lake or basin-wide effects of drought, and in using molecular techniques to seek signals of drought at wide geographic scales because of events in the deep past. Gaps in knowledge remain for effects of very short dry periods, on drought effects on higher levels of complexity, and on the manner in which droughts at the scale of decades affect fish.
3. Data from streams in Oklahoma and elsewhere in the south-western U.S.A. suggest that most droughts may leave little persistent signal in the existing fish fauna, i.e. that recovery from drought by fish populations or assemblages in the region can be rapid. However, species that are vulnerable to drought or water loss in streams may have disappeared from some basins in the region before the mid-1900s, and recent evidence also suggests that extreme droughts do sometimes alter fish assemblages.
4. Little is known about mechanisms by which droughts have direct or indirect effects on fish, the roles of droughts in the evolution of fish species, and the ways droughts alter effects of fish in ecosystems. Global climate changes may have serious consequences for future local or regional fish faunas, but ongoing studies of fish experiencing drought may aid in future conservation of what will become species at risk under climate-change scenarios.

Keywords: community change, drought, fish evolution, freshwater fish, Oklahoma, scale

Introduction

Do droughts hurt fish? Yes. Drought, as an immediate, proximate stressor, clearly affects local populations by outright destruction of individuals as pools dry or water quality erodes. However, a better

Correspondence: William J. Matthews, Department of Zoology, and Biological Station, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK 73019, U.S.A. E-mail: wmatthews@ou.edu

question may be how drought influences fishes on scales of space, time and organizational complexity. This broader view suggests that drought can influence evolution of species, local communities, ecosystems or fish faunas at a continental scale. Considering drought as a selective pressure, evaluating present-day droughts in the context of natural versus anthropogenic causes, and asking how droughts of different lengths (short 'dry spells' to centuries) affect fish, helps forge conceptual links between drought and the present or future fishes in aquatic ecosystems.

Many effects of drought are considered to affect fishes at different levels of organization (Table 1). Ichthyologists and ecologists have documented immediate or short-term changes in populations or assemblages of fishes resulting from drying, loss of habitat, or changes in water quality under drought conditions (Magoulick & Kobza, 2003). Less has been reported about specific mechanisms underlying population declines, such as tolerance for stress under actual field conditions, changes in life history or reproductive factors like egg size, fecundity or size of larvae, or changes in competitive and predatory interactions during drought. Drought is difficult to study, because as an event it is largely unpredictable (although seasonal dry periods can be anticipated in many systems). It is also difficult to sample adequately to test effects of drought, because some effects may become obvious only after a lag of a year or more, systems may have a high level of background noise in population sizes even under normal non-drought conditions, or effects could be mediated through changes in invertebrate food availability or other indirect mechanisms. Numerous studies of fish experiencing drought conditions have been opportunistic, following effects of short-term episodes on local species or assemblages. Only a few (Grossman *et al.*, 1998; Grossman & Ratajczak, 1998) have provided details on changes in fish distribution or microhabitat use before, during and after drought in studies spanning multiple years.

Empirical studies of drought have been summarized by Matthews (1998), who postulates stages of drought and its effect on fish. James (1934); Wickliff (1945) and Hubbs & Hettler (1958) chronicle effects on stream fishes of severe North American droughts in the 1930s and early 1950s. Starrett (1950), Starrett (1951), Paloumpis (1957, 1958; Larimore, Childers &

Heckrotte (1959) and Deacon (1961) document local effects of dry periods on fishes of specific systems with respect to survival, recolonization or population changes. More recent studies by Griswold, Edwards & Woods (1982); Canton *et al.* (1984); Cross, Moss & Collins (1985); Ross, Matthews & Echelle (1985); Schlosser (1985); Matthews (1987); Capone & Kushlan (1991); Bayley & Osborne (1993); Closs & Lake (1996) and Grossman & Ratajczak (1998) address drought-related survivorship, recovery of populations, changes in species distributions, microhabitats or competitive interactions, or changes in assemblage composition. Bailey (1955); Tramer (1977); Matthews, Surat & Hill (1982) and Mundahl (1990) quantified direct death or differential survival of fish in drying habitats. Physiological and behavioral traits of fishes that promote survival in drought are described by John (1964); Lewis (1970); Minckley & Barber (1971); Matthews & Hill (1979); Matthews (1987) and Smale & Rabeni (1995). Welcomme (1986) and Lae (1995) describe drought effect on fisheries of river basins.

Instead of annotating individual studies, we took an overview of 50 previous studies that addressed effects of drought or drying of aquatic ecosystems in one form or another, on fishes, along three axes of study, to identify what has not been carried out as much as what has. There is no single, accepted operational definition of drought. We included studies in which the original authors identified the conditions in their study as drought, as well as papers on topics like survival of fish in drying pools, or effects of dry spells, dry seasons, low flow periods, or dewatering of streams on fishes. In fact, only half of these papers included the word drought in the title, abstract, or introductory paragraph, with the rest using terms like dry spell to indicate the conditions under study. Some of the included studies only documented drought-like effects within a study of life history or natural history of a species. All of the papers we included have information on the ways fish are affected by drought or similar phenomena, but in some it is necessary to read carefully to find it.

We scored the 50 published papers on three axes of study, including (1) space: from individual pools or small ponds to large river basins or sub-continents; (2) length of drought or dry period: from days or weeks to centuries or longer; and (3) level of organization studied: from individuals to basin-level fish

Individuals

Survivorship and mortality as a result of desiccation, lack of physiological tolerances
 Energetic balance, reflected in reduced condition, growth, reproductive output
 Reduced lifespan
 Local movements and emigration
 Microhabitat changes, with changes in food use or predator pressure

Local populations

Local extinction
 Genetic bottlenecks
 Hybridization
 Intraspecific competition and density effects
 Change in population size
 Cohort failure
 Population fragmentation
 Changes in total biomass

Local assemblages

Changed assemblage composition
 Changed emergent properties such as diversity, richness, evenness
 Increased interspecific competition, crowding
 Intensified predation
 Changes in assemblage biomass

Metapopulations

Increased extinction rates, lowered rescue rates
 Changed gene frequencies for 'rescuers'

Basin or regional faunas

Geographic distributions
 Basin-regional extinction

Effects of fish in ecosystems

Altered primary productivity and structure of algal communities
 Changes in invertebrate assemblages or biomass
 Changes in fish-mediated processing or transport of nutrients and particulate organic matter
 Bioengineering including disturbance of substrata
 Altered rates of other ecosystem processes

Evolutionary effects

Changes in gene frequencies
 Isolation and vicariance
 Speciation and diversification
 Physiological adaptations
 Evolution of higher taxa
 Faunal regionalization and continental faunal patterns

Table 1 Phenomena related to fishes reported or predicted to be affected by drought, across increasing scales of organizational complexity

faunas. We determined where on the three axes studies were lacking or information was scant, and where on those axes additional recent, mostly unpublished data sets would fit. Finally, we used original field data from streams in Oklahoma (U.S.A.) to explore whether short-term drought leaves a persistent signal of fish community change in the long-term. We offer one caveat: because these field studies were carried out in streams where drought or dry periods are common, they may provide a view different than that emerging from analyses of drought effects on fish in more mesic regions.

Methods

Literature review

Fifty papers available in English were scored on axes of spatial scale, length of drought and organizational level studied. We included most papers on drought from Matthews (1998), and other recent studies located by searching two databases for combinations of 'fish' and 'drought' since 1990. These 50 papers do not include all pertinent literature, but should be representative of the kinds of studies published since about 1930. Appendix summarizes scoring of the 50

papers on each axis, as indicated by the original authors, or by our reading of the paper. There was subjectivity in our scoring. For example, the report by Bailey (1955) on mortality of fishes on a hot day could have been scored as an 'assemblage' study if we took in aggregate his comments about individual species. However, we tried to reflect in our scoring the emphasis of the original author in the study. The studies were placed on combinations of two and of all three axes, to determine regions either having or lacking coverage in these published studies. Then, from submitted abstracts (Appendix) we similarly scored 11 studies on drought effects on fish presented at the Symposium on the Role of Drought in Aquatic Ecosystems (Albury, Australia) in 2001, to ask if they filled existing gaps in knowledge.

We also tallied the effects of drought on fish, as reported by the authors of the original 50 papers, but in some cases made judgments about their conclusions. Unfortunately, in most papers original data were not provided such that we could statistically test results given by the authors, but we made a point in accepting original author statements only if they appeared to be clearly supported by data or observation. For example, in some papers authors had speculated about effects, e.g. that competition was a factor when fish were crowded in shrinking pools, without testing for those effects. We scored such assumptions as 'speculative' in the Appendix, and did not include them in total number of studies finding a particular effect. For each paper, we also indicated in Appendix if an effect was tested for but not found. However, in many of the papers the authors had not specifically tried to identify any particular effect or suite of effects, but merely reported observations of fish during drought or drying conditions. We also tallied the results of the 50 studies with respect to recovery time from drought, if specified, while recognizing that many of the short-term studies were not sufficiently long to allow recovery from an event.

Field studies

From field sampling by us or colleagues, we analysed multi-year data sets (described in detail below) that had potential for signals of persistent change in fish assemblages as a result of drought or dry periods. For each data set, we used appropriate

indices or multivariate techniques to compare samples taken during or immediately after drought with those made at other times. To compare any two samples we used a Percent Similarity Index (PSI; also known as Schoener's or Renkonen's Index), which has been used frequently in fish community ecology (Matthews, Cashner & Gelwick, 1988). For multiple-sample comparisons we used correspondence analysis (CA) or detrended correspondence analysis (DCA; Gauch, 1982). In addition to whole-assemblage assessments, we examined graphically long-term trends in abundance of individual common species to look for evidence of drought-related changes. As part of a long-term study in Oklahoma (U.S.A.) streams, the late Mr Jimmie Pigg (Oklahoma Department of Environmental Quality), sampled fish by seining in June or July, yearly, from the mid-1970s to 1995 at a total of four sites on the North Fork Red, South Canadian, North Canadian and Washita rivers. The study sites were on medium-sized river mainstems (fourth or fifth order; by Horton-Strahler classification), spanning Oklahoma from south to north. His samples for the 1990s, and all of his field notes, are archived in the Sam Noble Oklahoma Museum of Natural History. Detrended correspondence analysis was carried out separately for each site on the basis of abundance of fish species. DCA allows similar scaling in terms of species turnover on axes for comparability among sites. Locations of samples in two-dimensional DCA space was examined relative to general drought occurrence in Oklahoma to ask if drought-year fish assemblages differ from assemblages in other years. On the basis of monthly averages of statewide Palmer Drought Index values for the 12 months before and including each summer sample we identified the years of severest drought in Oklahoma.

We collected additional detailed data on composition of the fish assemblage by snorkeling surveys in a 1-km reach of Brier Creek, a small, prairie-margin stream in Marshall County (OK, U.S.A.) (Power, Matthews & Stewart (1985); Matthews, Harvey & Power, 1994). In this reach, 14 pools (see Power & Matthews (1983), for map, and see Matthews *et al.* (1994), for description of pools and survey techniques) in limestone-sandstone-gravel substratum and usually with clear water, are connected at base flow by shallow riffles. In dry summers, surface flow sometimes ceases across riffles, but in most years at

least some surface flow persists. Snorkel surveys to count fish in all pools were made at approximately monthly intervals from autumn 1982 to autumn 1983 (except in cold winter weather), and on 10 dates from 1995 to 2001. The surveys in 1999 and 2001 were in the years following the two most severe drought years on record in Brier Creek, with no surface flow for much of late summer and autumn, long reaches of streambed dewatered and remaining pools much reduced in size. Brier Creek is not gauged, but the nearest Red River tributary of similar size that is gauged (Mud Creek, Jefferson County) had approximately 60 days without flow in summer–autumn 1998, which was the longest no-flow episode for Mud Creek in the decade. Although the drought of 1998 was severe in south Oklahoma, it was followed in summer–autumn 2000 by even worse dry conditions, with the least rainfall on record for the month of August in Oklahoma. At worst drought conditions (October 2000), our study reach in Brier Creek consisted of even fewer, smaller pools than in the 1998 drought. Thus, we again surveyed the pools in Brier Creek in June 2001 to assess impacts of extreme dryness on this system on fishes in the following year. We compared all surveys, with data combined among pools, using CA, and also examined graphically trends (not shown) in abundance of common species.

Results

Literature review and papers in this symposium

Fig. 1 shows placement of the 50 previously published studies and 11 recent studies, most of them unpublished to date (Appendix) in three-dimensional space defined by space, drought length and organizational complexity. Many of the published studies were of dry periods of a year or less, with fewer of multi-year droughts. The spatial scales considered in those studies tended to be small, with many focusing on discrete stream reaches or shrinking pools, although several were at the scale of whole catchments or river basins, and one was of a sub-continent. The organizational complexity studied was mostly of populations or local assemblages, or both. Relatively few published studies assessed impacts of drought on individual fish (except in laboratory studies) and none explicitly addressed

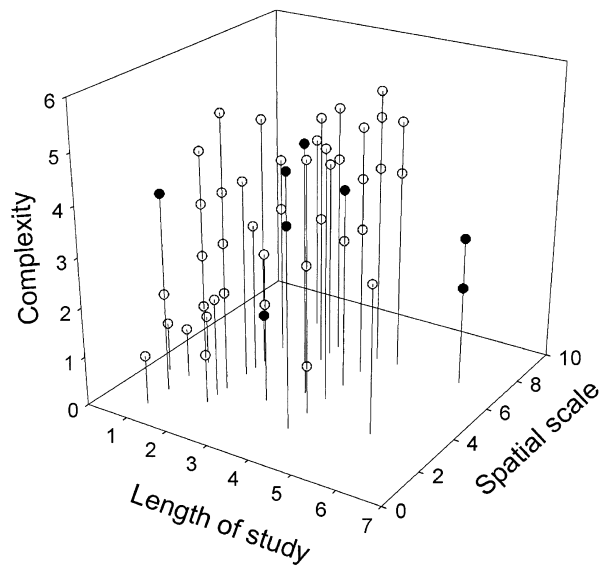


Fig. 1 Distribution of 50 previously published studies (open symbols) and 11 recent studies (solid symbols, three hidden) on axes of spatial scale, length of drought, and ecological complexity, with axis scales as defined in Appendix.

the interaction of drought with effects of fish in ecosystems.

Two-dimensional combinations of these axes (not shown) revealed more detail about the kinds of studies that have or have not been carried out. Some regions of space \times study length combined axes lack studies for obvious reasons. For example, it is impossible to study a centuries-long drought at the spatial scale of a single pool; studies of very long droughts seem possible only with zoogeographic or evolutionary information. However, studies of long-term droughts could focus on spatial scales like whole river basins, but such studies seem lacking. Another possible scale of time–space study could be effects of short-term drought (e.g. within a season) on fishes of whole river basins, but we did not find any such study.

On combined axes (not shown) of spatial scale and organizational complexity, some kinds of studies were not found in the literature. Certain kinds of studies clearly are impossible, e.g. studies of an individual across catchments or larger spatial units. However, studies of populations of a species across whole river basins or larger scale as a result of drought were also lacking, although such studies should be possible. This finding suggests minimal attention to effects of drought on metapopulation dynamics for fishes.

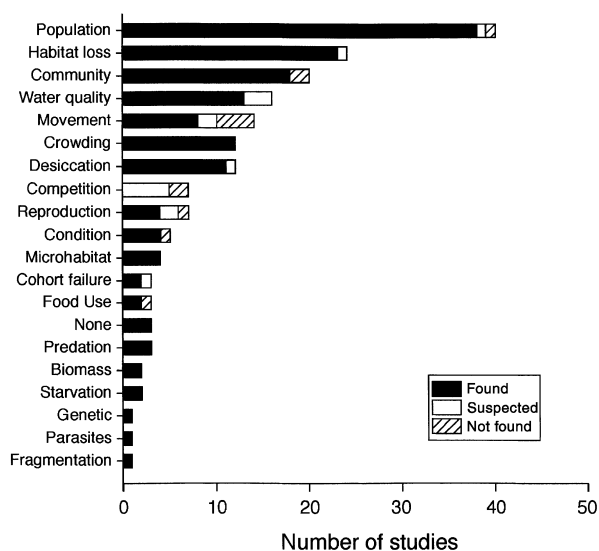


Fig. 2 Numbers of studies showing specified effects of drought on fishes, summarized from 50 previously published papers listed in Appendix. Solid bar, effect found by original authors or accepted by us as valid; open bar, speculative or unconfirmed; hatched bar, effect tested for but did not found significant by original authors.

Combined axes of study length and ecological complexity showed a lack of published studies of local fish assemblages in droughts lasting decades, which seem possible. None of the studies carried out at the scale of short-term drying (e.g. weeks) were scored as being focused on whole assemblages.

For effects reported in the 50 studies previously published, the greatest number were scored as showing 'population declines' (Fig. 2), which was a broad category that included everything from reports of mass mortality of species to long-term declines in population densities during extended drought. Several studies (Deacon, 1961; Grossman *et al.*, 1998) showed declines of some populations during drought but concomitant increases of other species. Other prevalent findings (Fig. 2) were loss of habitat (complete drying of stream beds or decreases in water volume); death as a result of eroded water quality (particularly oxygen concentration or temperature, although some detected species tolerant of hypoxia or hyperthermia); changes in whole communities or assemblages; death because of complete desiccation of habitat; movement or redistribution within catchments; general crowding and decreased reproduction. Fewer studies provided data on mechanisms causing effects like starvation, cohort failures,

changes in food or microhabitat use (but see Grossman & Ratajczak, 1998), increases in predation, or population fragmentation. A few studies suggested no negative effects of droughts on fishes. One study (Rutledge, Zimmerman & Beiting, 1990) documented changes in gene frequency because of a 'bottleneck' effect of drought, and one study assessed changes in parasite loads as a result of drought (Janovy, Snyder & Clopton, 1997), mediated through changes in abundance of intermediate hosts (snails). In five papers, the original authors indicated or suggested that competition was a factor during drought, but none provided testable data, so we scored all of these as speculative and omitted them from Fig. 2.

Fig. 1 also shows locations of 11 recent data sets, most of them unpublished, on the axes of space, study length and complexity. A few of these studies concern individuals to populations, but most addressed scales ranging from one or several populations to whole assemblages. None of these recent studies focused on the ways drought changes effects of fish in ecosystems, so this gap in knowledge remains. Eight of the papers focused on dry periods of a season or less, or seasonally across several years. Two studies were of drought at a geologic time scale, using molecular approaches to assess drought-influenced genetic changes in fishes across a large river basin, a scale not previously addressed by published studies. Two of the recent studies were of individuals or populations at a spatial scale of whole lake to river basin, helping fill a gap in knowledge. Overall, Fig. 1 suggests a remaining gap in knowledge at the scales of the effects of very short drying periods (weeks) on higher levels of complexity (assemblages, ecosystem), and another obvious gap in knowledge is the ways droughts impact fishes at the scale of decades, which have occurred in recent history (Soule, 1993; Tarboton, 1995).

Field studies

To test for long-term drought effects on fish communities at J. Pigg's river sites in Oklahoma, we identified 4 years (1977, 1978, 1981 and 1991) when statewide drought conditions were most severe. In each of these years, Palmer Drought Indices were below a value of -1.0 (mild drought, or worse) for at least 5 months, and remained negative in the sampling month. In Fig. 3, drought years (only 2 years

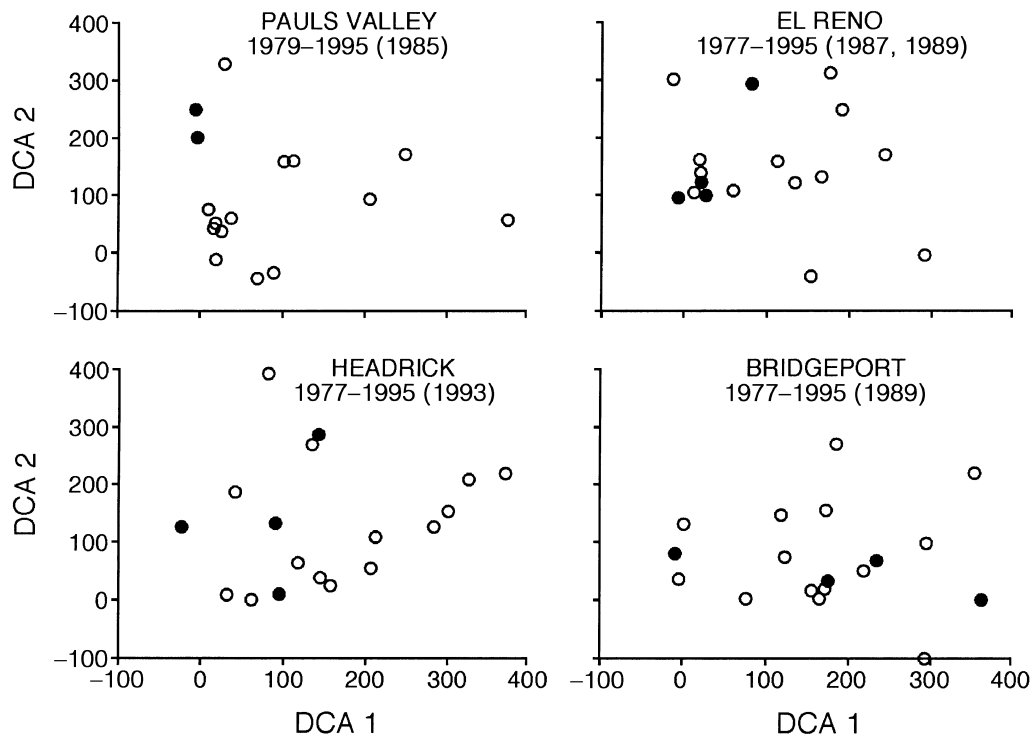


Fig. 3 Position of annual fish samples collected by J. Pigg from four Oklahoma rivers on axis 1 \times axis 2 space from detrended correspondence analysis based on species abundances. Axes are scaled so that 100 = one standard deviation on that axis. Solid circles represent dry years as defined in text.

sampled at Pauls Valley – Washita River; all 4 years included at others) lie within the DCA 1 versus 2 space occupied by both drought and non-drought years. At three of the sites (Pauls Valley, El Reno – North Canadian River, Headrick – North Fork Red River), the drought year samples lie in roughly the left-hand half of axis 1, but they do not appear different from other non-drought year samples, which also are to the left on that axis.

Ordination methods provide overall summaries of assemblages, but might overlook changes relating to individual species. Consequently, we screened the long-term data for any detectable changes in abundance of individual species in or following drought years. For the 10–12 most abundant species at each of the four sites, we graphically examined abundances across all sample years, and found none that on average appeared different in abundance in drought versus non-drought years. However, for several species there were trends of potential interest (Fig. 5). For example, red shiner, *Cyprinella lutrensis* (Baird and Girard), which is the most common species in much of

the midwestern U.S.A. (Marsh-Matthews & Matthews, 2000), reached its greatest abundance at all four river sites in Palmer drought years. However, Fig. 5a also shows that in some dry years red shiners are not markedly abundant. In addition to red shiner, western mosquitofish, *Gambusia affinis* (Baird and Girard) and bullhead minnow, *Pimephales vigilax* (Baird and Girard), were most abundant at three of the four sites during drought years (Fig. 5b,c), but in other drought years they were only moderately abundant. Thus, dry years may promote abundance of these or other species, but there must be other factors that influence abundance of these fishes, such as density effects, timing of reproduction relative to drying, and other interactions between innate traits of the species and vagaries of the environment.

Other species that were common across at least three of the study sites showed no strong abundance differences in drought years (Fig. 5d–f), although the plains minnow, *Hybognathus placitus* Girard, showed a tendency for lower abundances in dry years. Three species [sand shiner, *Notropis stramineus* (Cope),

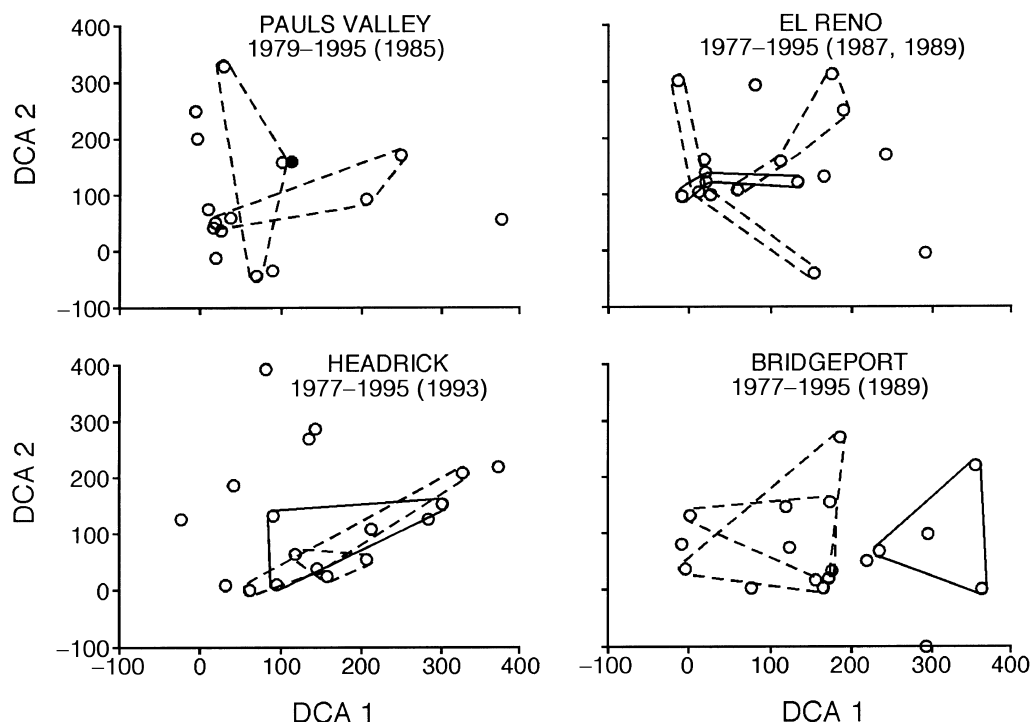


Fig. 4 Position of annual fish samples collected by J. Pigg from four Oklahoma rivers on axis 1 \times axis 2 space from detrended correspondence analysis based on species abundances. Solid lines encompass consecutive dry series of years and dashed lines encompass wet series of years, as defined in text. For Pauls Valley, only 1 year in the series of dry years was available as shown by a solid circle.

plains killifish, *Fundulus zebrinus* Jordan and Gilbert, river carpsucker, *Carpionodes carpio* (Rafinesque)], which were common at two or more of the sites, showed both very high and very low abundances in dry years. Six species [fathead minnow, *Pimephales promelas* Rafinesque, emerald shiner, *Notropis atherinoides* Rafinesque, suckermouth minnow, *Phenacobius mirabilis* (Girard), channel catfish, *Ictalurus punctatus* (Rafinesque), orangespotted sunfish, *Lepomis humilis* (Girard), green sunfish *Lepomis cyanellus* Rafinesque], which were abundant at two or more sites, exhibited only low to moderate abundance during dry years, but none of these appeared different in drought versus non-drought years. Instead, all six showed one or more strong peaks in abundance, but none in drought years. Thus in long-term data, which is inherently 'noisy' and incorporates many factors, we found no strong signal of drought effects either in ordinations of whole assemblages or long-term abundances of individual species at these four sites. This is not to say that dry years have no effect on species of these rivers, but merely that fish assemblages in

drought years do not appear markedly different from those in wetter years.

Effects of drought in one year could be more evident in the next, after a lag allowing delayed (e.g. reproductive) effects to appear in populations, so we also examined Fig. 5 for evidence of unusual population sizes in the years immediately after the Palmer Index dry years. Three species (red shiner, bullhead minnow and western mosquitofish) had a tendency (not shown) for low abundances in the year following a dry year as defined by the Palmer Index, and of these three, only red shiners showed a single peak in abundance in a year following drought. Thus, while all three species showed increased abundance in dry years, the signal was largely lost in the year following the drought, i.e. the drought years lacked discernable longer impacts on the populations. None of the other three species (sand shiner, plains minnow and plains killifish) showed noteworthy abundance patterns in the year following a drought, with both very high and low abundances at some sites in the postdrought year.

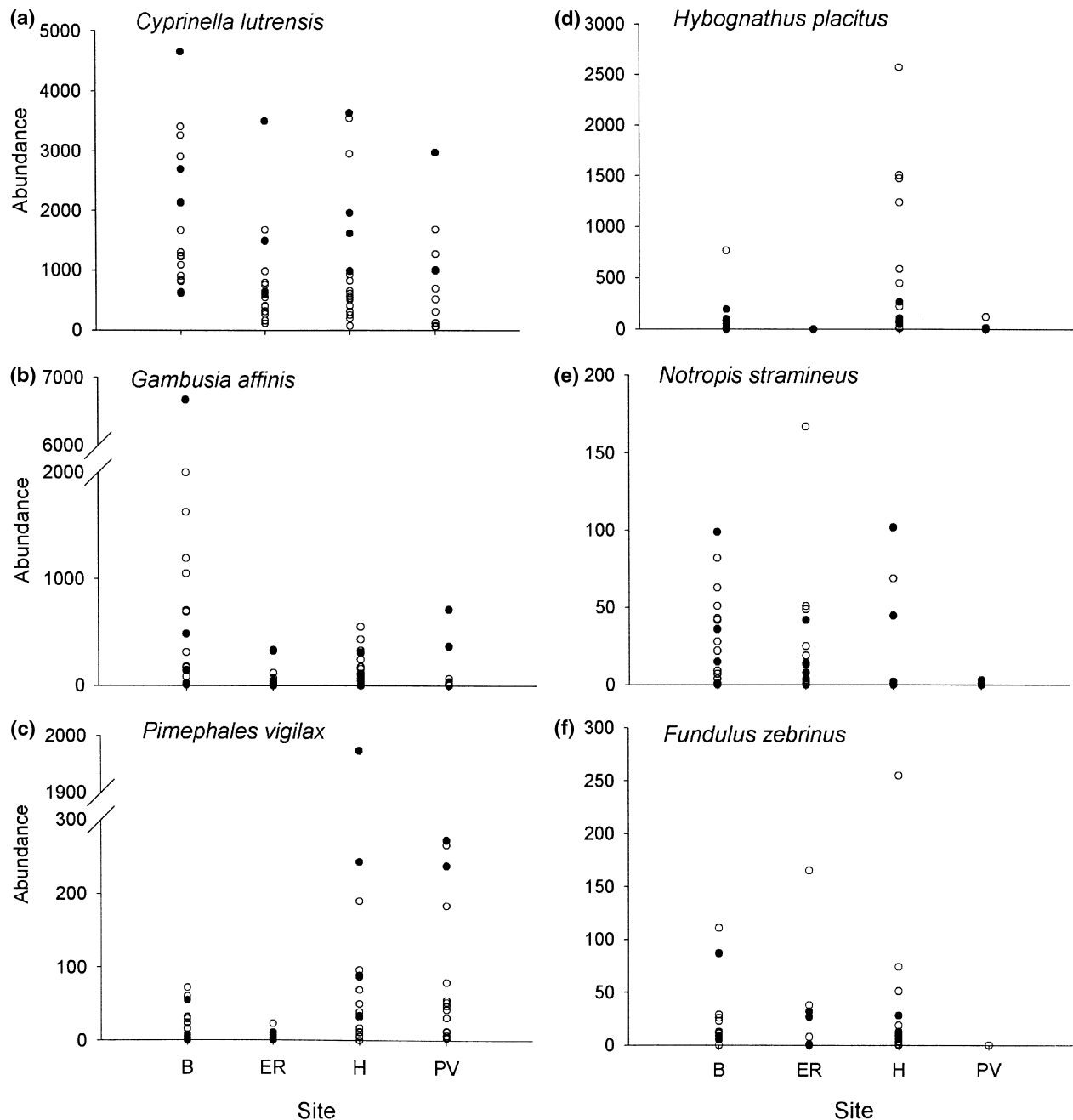


Fig. 5 Abundance (numbers of individuals collected by J. Pigg) of species at four sites on rivers in Oklahoma [Bridgeport (B), on South Canadian River; ElReno (ER), on North Canadian River; Headrick (H), on North Fork Red River; Pauls Valley (PV), on Washita River]. For each species (a–f) at each site, the solid circle = abundance in a dry year as indicated by statewide Palmer Drought Index, and open circle = abundance in all other years from the 1970s to 1995.

Finally, we asked if multi-year periods of continuous wet versus dry conditions included in these sample years resulted in detectable differences in fish assemblages. The years 1977–79 were all very dry by Oklahoma monthly average Palmer indices, and two

spans of years (1985–88 and 1992–95) were wet to very wet. For three of the four sites (Fig. 4), the wet-years and dry-years series of samples did not segregate in DCA space. At the El Reno (North Canadian River) and Headrick (North Fork Red River) sites, the series

of wet and dry years overlapped strongly in DCA space, and at the Pauls Valley site (Washita River), only one of the years in the dry series had been sampled, but that sample was within the two-dimensional space surrounded by the wet-year series. Only at the Bridgeport site (South Canadian River) were dry years separated from the two series of wet years, but over the two decades of study one of the formerly most abundant (Matthews & Hill, 1980) species in the river, Arkansas River shiner, *Notropis girardi* Hubbs and Ortenburger, declined in relative abundance throughout its range (Pigg, 1991). Regardless of any separation of dry and wet series samples at Bridgeport, three of the four Oklahoma river sites would show no long-term segregation of samples from wet and dry year series. All three levels of analysis of J. Pigg's data (single drought year; single year post-drought; multi-year dry-wet) thus suggest that although drought can have effects on some individual species, drought alone is not an overriding or simplifying explanation for much of the long-term variation that is evident in the extant fish assemblages of Midwest rivers in the U.S.A.

Our snorkeling surveys in Brier Creek provided two different views of effects of extreme drought in fish of small streams. The fish assemblage surveyed in the 1-km reach in July 1999 was not unique in CA space (Fig. 6) in comparison with the assemblages observed during other surveys in 1995–97. There was

substantial variation in the fish assemblage during 1995–99, and the 1990s samples differed markedly from those in the 1980s, but the July 1999 sample actually represented movement of the assemblage in multivariate space back towards an average position for the 1990s, after a somewhat extreme assemblage structure in the previous survey (July 1996). Thus, the drought of 1998 left little persistent signal in the following year. However, a more extreme drought in 2000 did apparently result in noteworthy changes in the fish assemblage in this reach that lasted into the following summer (June 2001), as indicated by the unique position of this survey, separate from all others (Fig. 6). The unique position of the 2001 assemblage in multivariate space was not the result of any one species, as shown by the consistently unique position of the 2001 survey when we repeated the analysis leaving out various species one at a time. More details of these surveys will be published elsewhere, but, in summary, several species showed marked changes in abundance in the year after the 2000 drought. Some common Brier Creek species were markedly lower in abundance, including bigeye shiner, *Notropis boops* Gilbert and blackstripe topminnow, *Fundulus notatus* (Rafinesque). Adult largemouth bass, *Micropterus salmoides* (Lacepede) and spotted bass *M. punctulatus* (Rafinesque) were very scarce relative to their usual higher abundance in the reach, although young-of-year of these species were abundant. Young redhorse suckers of the genus *Moxostoma* were far more abundant than in any other surveys. Central stoneroller minnows, *Campestris anomalum* (Rafinesque) and orangethroat darters, *Etheostoma spectabile* (Agassiz) had an apparently explosive reproduction in the spring following the 2000 drought, and small young-of-year of these species were of literally uncountable abundance here and throughout much of Brier Creek (W.J. Matthews, pers. observ.). Several species (red shiner, bullhead minnow and orangespotted sunfish) that had been absent from this reach for several years appeared in the June 2001 survey. It is not possible to determine from our visual surveys the mechanisms that may have favoured or negatively impacted various species during the severe drought of 2000, or to determine why previous droughts (e.g. 1998) left no signal. Therefore, we are now inducing experimental droughts in large outdoor artificial streams to address these questions.

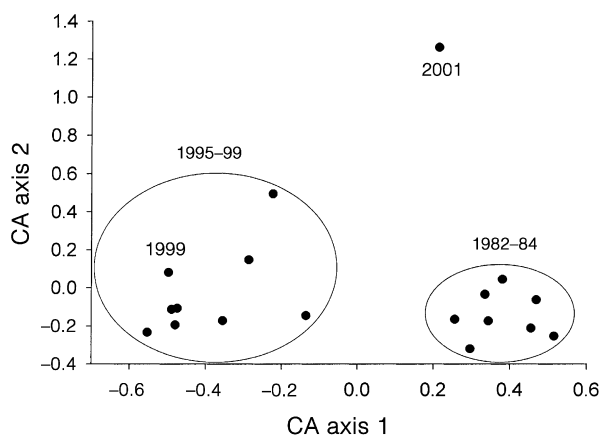


Fig. 6 Position of fish assemblages detected in snorkel surveys in 14 pools of Brier Creek, Oklahoma, on a total of eighteen dates between 1982 and 2001, in the two-dimensional space from axes 1 and 2 of a correspondence analysis. The years 1999 and 2001, each followed a previous year of severe drought. Ellipses surround all samples in the 1980s and 1990s, respectively.

Samples from the Smoky Hill River in central Kansas (U.S.A.), also lack evidence of persistent effects of recent drought on the fish assemblage. In June 1995 we sampled in the Smoky Hill River south of Russell (Kansas), seining in the same way that this site had been sampled in June 1978 (Matthews, 1985). There is substantial evidence from nearby stream flow gauges of the U.S. Geological Survey (USGS) of episodes of low flow or dewatering of reaches of the central Smoky Hill River in the 17 years between our samples. In spite of these episodes of very low or no flow in the central Smoky Hill River, our samples taken 17 years apart showed a percent similarity of 0.90, the highest PSI that we found for any of more than 60 sites in the southern Great Plains and Gulf Coastal drainages that we sampled in both years. The same two species of minnows (red shiner and sand shiner) dominated the assemblage in 1978 and 1995.

Similar evidence exists in a study of fish distributions in tributaries and the mainstem of the upper Red River in western Oklahoma (Hargrave, 2000). Hargrave sampled monthly for a year at nine sites in the Red River basin, at the same locations sampled monthly by Taylor, Winston & Matthews (1996) a decade earlier. Immediately before Hargrave began sampling in October 1998, western Oklahoma had one of the most severe droughts in many years, as noted above, for Brier Creek. At the beginning of Hargrave's (2000) sampling, at least one upstream site remained completely dry. Over the next year, fish assemblages at these sites exhibited seasonal dynamics similar to those found by Taylor *et al.* (1996) a decade earlier in a relatively wet year. Fish assemblages at most sites sampled in 1998–99 were rather similar in composition to those at the same sites a decade earlier (Hargrave, 2000) in spite of the 1998 drought. Additionally, the same species were community dominants in both decades, with the exception of the plains minnow, which was much greater in abundance in Hargrave's samples.

Discussion

Existing studies of drought effects on fish

Drought has reported effects across levels of organization from individual fish in small systems to the fauna of large geographic areas, and from brief to

very long dry periods. The results from our survey of published and unpublished data suggest that few studies take 'long' or 'large' views, and most focus on local events as they occur. Most studies of fish and drought are in reaction to a developing event or are embedded in long-term studies undertaken for other reasons, although some take advantage of predictable seasonal drying. Quantification is needed on effects at broader scales, like those of droughts across evolutionary time or at the scale of river basins. However, some recent studies (Appendix) began to fill gaps in knowledge about drought effects on fishes. For example, some recent studies place their work in a more theoretical context (e.g. source-sink dynamics in streams; Magoulick & Kobza, 2003), viewing management implications of droughts, providing detailed and wide-scale assessment of low-flow and drying events on whole assemblages of species, and testing drought effects in unique habitats (solution holes in karst wetlands) or in mesocosm experiments. One new approach is the interpretation of molecular signals of drought of geologic proportions (Douglas, Brunner & Douglas, 2003). Still, much remains to be learned about effects of drought on fish, such as context-specific effects as influenced by the environmental template, direct or indirect mechanisms of effects on fishes, evolutionary effects, effects on movements of fishes or metapopulation dynamics, ways drought influences fish effects in ecosystems, and the potential for future drought impacts on fishes related to climate change.

Drought effects on fish in harsh versus benign habitats

Many streams in the western interior of North America and elsewhere are characterized by harsh physical conditions (Hefley (1937); (Matthews & Hill, 1979, 1980); Matthews & Zimmerman, 1990). Their assemblages may be relatively independent of, or recover quickly from, drought events. Detectable drought effects in the contemporaneous fish assemblages of these streams may be lacking because the fish species present are tolerant of environmental stress (Matthews, 1987), having passed through environmental or physiological evolutionary filters (Smith & Powell, 1971). As a result, fish in such streams may inherently show less impact of dry years than do species in regions where flow is more stable. A

testable hypothesis would be that drought has worse effects on fish in perennial systems, but the existing data (e.g. the studies in our review) cannot adequately address the issue, because most studies on effects of drought on fish have been in arid-land streams. Less is known about effects of droughts in historically perennial streams, because it is difficult to plan observational studies of drought in streams where it rarely occurs. For example, the Kiamichi River, in mesic southeast Oklahoma, which normally has sustained flow, experienced unusually severe drought with extensive dewatering in 1998 and in 2000 (C. Vaughn, pers. comm), but we were unable logistically to assess the consequences to the fishes. Best opportunities to test drought effects in perennial systems seem to be in planned long-term studies of a decade or more (Grossman *et al.*, 1998), by rapid response to a developing drought situation (e.g. Larimore *et al.*, 1959), or by experimental approaches.

We do know that prolonged or permanent loss of flow has altered fish communities in arid regions of the American Southwest (Cross & Moss, 1987). Cross & Moss (1987) showed that at least eight minnow (Cyprinidae) and one sucker (Catostomidae) species disappeared from rivers of west Kansas before 1961, most by the 1930s. Thus, to conclude from contemporary studies of a relatively drought-resistant fish fauna that now remains that drought does not hurt fish may be misleading, if the species with less tolerance for stress disappeared before detailed studies of these systems were made. One might ask in a comparative study, using populations from elsewhere, if the species that were eliminated from those rivers are less physiologically tolerant than the species that remain, but this has not been carried out.

Natural droughts in harsh habitats may have only transient effects on fish assemblages. Little is known about the effect of droughts if they are extended or aggravated by anthropogenic influences. Severe droughts in the 1930s and 1950s in the western U.S.A., with effects in streams exacerbated by poor land use practices, were devastating to fishes (James, 1934; Wickliff, 1945), but there is now little evidence of permanent changes in fish faunas as a result of those particular events (although the ichthyological record in the region is imperfect). Overall, there may be more changes in the fish fauna in western North America from widespread dam building in the mid 1900s, or

from introductions of exotic fishes, than from any of the great historical droughts.

Mechanisms by which fish survive or are affected by drought

Mechanisms by which droughts have immediate effects on fish are poorly known. For example, how does outright physiological tolerance of fishes influence the ways they respond to stress during drought? How different in vulnerability are populations of a species? Fish species (Matthews, 1987) or local populations (Feminella & Matthews, 1984) in harsh streams may be relatively resistant to thermal or oxygen stress. Feminella & Matthews (1984) showed that the local population of orangethroat darters in the highly fluctuating Brier Creek habitat had greater thermal tolerance than conspecifics in streams with more stable temperatures. In contrast, Matthews (1986) showed that red shiner populations across a north-south span of 1200 km in the south-western U.S.A. did not differ in mean tolerance of thermal stress. Species that are most successful in drought-prone environments may have wider physiological tolerances (Matthews & Maness, 1979; Matthews, 1987; Smale & Rabeni, 1995) than those from less fluctuating systems, but little is known about the applicability of the results of laboratory tolerance studies to fish in the field under sustained drought conditions.

Where human activities have permanently altered stream flows and caused chronic aggravation of drought effects, some species suffer disproportionately because of their life history traits. Hardest-hit may be species that require high flows for reproduction such as plains minnow or Arkansas River shiner (Cross *et al.*, 1985). What other factors cause reproductive declines during or after drought? Is the mechanism as simple as drought = crowding and lowered productivity = increased competition = loss of condition = poor fecundity = fewer offspring, or is the mechanism more complicated, involving, for example, physiological responses by which maternal investment in embryos of the livebearer *Gambusia* changes under different stress conditions (as now under study by E. Marsh-Matthews)? When, under drought conditions, do female *Gambusia* give up reproductive investment and change to responses enhancing their own survival? Also poorly known is the future reproductive value of fish that survive

drought. Numerous studies of fish in drying pools, including an experiment we carried out in summer 2000 (E. Marsh-Matthews and W.J. Matthews, unpublished data), show that individuals may survive drought in diminished pools (Capone & Kushlan, 1991), but the future reproductive value of these individuals or the degree to which they move to repopulate a catchment is not known. Will they produce smaller or fewer eggs, spawn fewer times, be less able to move to spawning sites, build and protect nests, and so on? We are presently testing some of these questions in large experimental streams. If they do reproduce, have they been through a genetic bottleneck that changes gene frequencies in the populations, as shown by Rutledge *et al.* (1990) for fish in small, harsh streams?

What are other indirect mechanisms by which drought changes fish assemblages? Are there strong indirect effects, perhaps with lag time, such as loss of periphyton or invertebrates because of drying, resulting in less food for adult or larval fishes, hence population declines? Are there stress factors that show up not in the survivors of drought, but in their offspring? Do drought effects in the riparian zone (e.g. loss of trees or other vegetation, increased soil erosion?) alter ecosystem functioning (primary productivity, allochthonous and autochthonous organic matter turnover) in ways that eventually cause change in populations of fishes at various trophic levels? Was Starrett (1951) right in assuming that events that removed older adults might enhance opportunities for juveniles? Are some species in most systems actually favoured by drought? Most studies of drought and fish have not considered lag, indirect effects, or other such consequences in detail, making possible answers to these questions highly speculative at present.

Evolutionary effects of drought

Stressful conditions like drought can be 'extremely effective in shifting the mean of a trait by imposing directional selection' (Hoffman & Hercus, 2000). Droughts at the scale of centuries to millennia may have been important in fish evolution. Cichlids of the Great Lakes of Africa have apparently speciated extremely rapidly after drying fragmented populations (Meyer, 1993), and intermediate haplotypes shown by a recent phylogeographic analysis to be

missing among Lake Victoria cichlids may be the result of mass extinctions from desiccation about 15 000 years ago (Verheyen *et al.*, 2003). McCune, Thomson & Olsen (1984) showed rapid evolution of semionotid fishes, with great diversity of body forms, in prehistoric lakes in the north-east U.S.A. because of repeated episodes of drying. Within some clades of fishes, like *Cyprinella* in the south-western U.S.A. and Mexico (Taylor & Gotelli, 1994), increasing aridity has affected speciation and range sizes. The pupfishes (*Cyprinodon*) of western North America show rapid speciation as a result of isolation of populations by drying of previously large inland lakes (Hubbs, Miller & Hubbs, 1974). Overall, the modern distribution of fish species richness in North America (McAllister *et al.*, 1986) is strongly influenced by recent and prehistoric patterns of aridity, stream drying, and drought in the Midwest and Southwest. Thus, many large-scale zoogeographic studies suggest the powerful evolutionary influence of drought, but only now are such problems being addressed in a relatively direct way at the scale of evolutionary time, such as research on molecular evolution of Colorado River Basin fishes (Douglas *et al.*, 2003). Finally, how do quasi-predictable events affect evolution of fish species? Mol *et al.* (2000) showed a loss of reproduction in fishes of South American streams during an El Niño-related drought. However, in that El Niño events are cyclic, and hence broadly predictable, how will such repeated stressors influence evolution of these species life history traits?

Movements

Drought ultimately limits fish movement in a stream, but onset of drought can stimulate movement of fishes, possibly increasing gene flow within typically sedentary species. Hill & Grossman (1987) and Scalet (1973) showed that some fish spent their lives within a short stream reach (e.g. in one pool 37 m long) or in one riffle. However, Grossman *et al.* (1998) found some fish species moving upstream or downstream into their study reach during dry years, and F. P. Gelwick (pers. comm.) showed that typically sedentary orangebelly darter, *Etheostoma radiosum* (Hubbs and Black), the subject of Scalet (1973), moved downstream in one small Oklahoma stream during seasonal desiccation. Ross *et al.* (1985) found typical

headwater species further downstream in Brier Creek, Oklahoma, after a drought. Gowan & Fausch (1996) found more movement of brook trout in two Colorado (U.S.A.) streams in a dry than a wet year as individuals apparently abandoned drying reaches of streams. Thus, there is substantial empirical evidence that drought can initially increase, rather than decrease, movements of fishes in a stream; hence drought might actually cause an increase in mixing of a species gene pool in a catchment.

Movement of fish across riffles at onset of drought may be species-specific. Schaefer (2001) showed differences in propensity of three minnow species to cross shallow riffles. Manmade structures may worsen effects of drought by interfering with normal movements of fishes. Winston, Taylor & Pigg (1991); Wilde & Ostrand (1999) and Lienesch, Lutterschmidt & Schaefer (2000) suggested that small fishes in streams upstream from artificial reservoirs may be in increased danger of local extirpation during drought. Drying may force small stream fishes into an unnatural lentic reservoir environment where they become prey to larger piscivores. After upstream reaches are rewatered, reinvansion from downstream is barred by the dam itself or by a lack of the species in the reservoir. At a smaller scale, manmade road crossings that constrict stream flow in culverts or other narrowed passages (Warren & Pardew, 1998) may become inaccessible barriers to fish movement during low-flow conditions. Population fragmentation during breeding season could thus result for such small-bodied stream fishes. Finally, rescue effects in metapopulation models (Hanski, 1999) require movement of individuals among localized populations. How well fishes are represented by metapopulation models is not yet clear (in spite of tests of models or movement by Fausch & Young (1995); Schlosser & Angermeier (1995); Gotelli & Taylor, 1999), but to the extent that drought prevents movement of individuals, it might change over a long-term the capacity of a species to act as a metapopulation in a system.

Roles of fish in ecosystems, as affected by drought

Fish play important roles in ecosystem dynamics in lentic and lotic habitats (Matthews, 1998). In temperate (Power & Matthews (1983); Power *et al.* (1985); Grimm (1988); Gelwick & Matthews (1992); Gido & Matthews, 2000) and tropical streams (Power, 1984;

(Flecker, 1996, 1997); (Pringle & Hamazaki, 1997, 1998)), fish alter primary productivity, nutrient dynamics, algal and invertebrate composition, particulate organic matter dynamics, and other important ecosystem-level processes and properties. Few studies of fish effects in ecosystems have allowed testing for drought effects. However, Wootton, Parker & Power (1996) and Power, Parker & Wootton (1995) suggested that roles of fish in stream food webs are altered in drought years, and Gelwick, Stock & Matthews (1997) detected differences in benthic fish effects during normal and lowered flow conditions.

Influence of drought on the effects of fish in ecosystems may relate to movement of the fish or of materials. The algivorous central stoneroller minnow in Brier Creek, Oklahoma (e.g. Power *et al.* (1985); Gelwick & Matthews, 1992) has more noticeable impact during low flow conditions. Not only is their consumption of algae intensified in local patches under low-flow, crowded conditions, but important byproducts of the fish (faeces, nutrients and fragmented particulate organic matter) tend to remain in the pool, whereas at higher flows such materials are likely to be flushed downstream and distributed more evenly in the system. Effects of fishes (or other fauna, such as invertebrates) on ecosystem properties may be more localized or patchy during drought, as individuals are isolated in individual pools or move less among pools as riffle thalwegs shrink, but field experiments to test this postulate are lacking. Drought should be included as one of many context-specific factors that influence the ways fish or other organisms affect stream ecosystems.

Global climate change

Finally, if anticipated levels of global warming become reality, massive changes in fish faunas will follow. Fish confined to discrete aquatic systems are particularly vulnerable, not just in lakes, but in many stream networks as well (Matthews & Zimmerman, 1990). For example, in southwestern North America, most river basins flow west to east, and there is no route by which fish could migrate substantially northward to escape future loss of stream habitats or increased temperatures. Fish in many of these rivers, which are some of the hottest on Earth, are already living near the threshold of temperature tolerance (Matthews & Zimmerman, 1990). These species cannot tolerate a

4–6 °C increase in average temperatures. Eaton & Scheller (1996) predict that some of the greatest losses of fish in North America from global warming will be in the central U.S.A. The best estimates suggest that, although some of the species like red shiners are genetically malleable, they cannot adapt at a sufficient rate to escape extinction (Matthews & Zimmerman, 1990) if local temperature increases match those predicted by many current models. As global warming increases, we will probably see widespread extirpations of fish species in many regions, although uncertainty about warmer–drier versus warmer–wetter scenarios make any predictions about streams and lakes habitats tenuous. However, studies of drought carried out now may help managers deal with fish in altered future environments.

Predictions and future studies

Facing the uncertain future of global climate change, drought appears likely to exacerbate in many parts of the world in the next century. Fishes in many parts of the world have already been subjected to increasing droughts. Governments, through scientifically-driven compacts, may be able to ameliorate climate change, but biologists working with fish and attempting to predict global-change effects would be prudent to consider worst-case scenarios. We suggest use of the following approaches to study effects of drought on fish.

(i) Experimental low flows (Schlosser, 1998) in small streams, e.g. by water diversions, to the extent that they are legal and ethical, coordinated for studies of all biota and processes including fishes.

(ii) Controlled tests of indirect effects of drought on fishes, allowing lag time for postdrought changes in invertebrate densities, food quality and other phenomena to have indirect effects on fish populations.

(iii) Tests of cumulative effects of repeated droughts on fish populations, using existing large data bases, or future monitoring in streams. Such studies could be incorporated into widespread monitoring of fish populations in regions with varying likelihood for drought.

(iv) Studies of drought effects in systems that are normally perennial (e.g. Grossman *et al.*, 1998), with the hypothesis that effects on fish will be greatest where drought is rarely experienced.

(v) Planned basin-wide studies of drought-year effects on fish, as well as general aquatic ecosys-

tem structure and functioning, taking advantage of improved long-range weather forecasting.

(vi) Controlled mesocosm experiments to compare effects of dry periods on individual species condition, recovery from drought, future reproduction and similar biological responses.

(vii) Studies of fish effects in ecosystems, under drought versus average flow conditions. Integrate fish as components of studies of drought in lentic and lotic systems and assess effects of changes in fish distributions or population abundance on distributions of invertebrates, ecological processes and related phenomena.

(viii) Comparisons of laboratory stress or survival tests with short and long-term responses of fish in the real world to drought conditions.

(ix) Fit of fish movement and distribution to metapopulation models, determining effects of droughts/dry periods on rescue of locally extirpated populations.

(x) Operational thresholds at which drought alters biology of fishes. For example, should drought be based on number of 'no flow' days below average in a particular system? On area or volume of remaining pools within a particular reach of stream? On percent reduction of habitat during dry periods to some level that negatively affects fish?

(xi) Levels of drying at which interchanges between fish and the terrestrial environment are interrupted, such as loss of flood-pulse effects on fishes, or change in transfer of nutrients in and out of systems?

(xii) Innovative comparisons of large-scale, long-term effects, using geologic, zoogeographic, and molecular information with assess evolutionary effects of drought periods in prehistory.

We end with a request for funding not just for studies of fish and droughts, but for studies on effects of drought in aquatic ecosystems in general. The major impediment to studies of drought remains their unpredictability coupled with current funding schemes. Few universities, governments or agencies, worldwide, can allocate funds to anticipate drought by beginning studies under normal, non-drought conditions, thus most drought studies remain local and reactive. The lack of baseline information in normal times, on both population dynamics and the ways whole ecosystems work, remains the most significant hurdle for scientists trying to understand drought effects in aquatic ecosystems. Keeping personnel alert and equipment just to study droughts is prohibitively

expensive, but if the badly-needed general studies of aquatic ecosystems were better funded, investigators would have both the background information and the resources to make meaningful measurements when droughts occur. Such information would be immeasurably useful as growing world populations increasingly require water and protein, and turn to existing aquatic ecosystems for both.

Acknowledgments

We thank Keith Gido for help with production of figures, Donna Cobb for help searching websites, Becky Marsh and Andrew Marsh for field assistance, and the late Jimmie Pigg for his samples of fish. We also thank the many friends and colleagues who have assisted with other sampling or discussions of the problem of drought effects on fishes. This paper was originally presented in the Symposium on the Role of Drought in Aquatic Ecosystems (12–14 February 2001 in Albury, NSW, Australia). We thank the organizers of this symposium, Paul Humphries and Darren Baldwin, for their many kindnesses, and acknowledge with particular appreciation the organizational skills of Rhonda Sinclair. Suggestions by Gary Grossman and an anonymous reviewer substantially improved the paper. Support for our field studies has been from the National Science Foundation and Environmental Protection Agency of the United States, and a Raney Fund Award from the American Society of Ichthyologists and Herpetologists to WJM.

References

- Bailey R.M. (1955) Differential mortality from high temperature in a mixed population of fishes in southern Michigan. *Ecology*, **36**, 526–528.
- Bayley P.B. & Osborne L.L. (1993) Natural rehabilitation of stream fish populations in an Illinois catchment. *Freshwater Biology*, **29**, 295–300.
- Burr B.M. & Warren M.L. Jr. (1993) Fishes of the Big Muddy River Drainage with emphasis on historical changes. *Biological Report*, **19**, 186–209.
- Canton S.P., Cline L.D., Short R.A. & Ward J.V. (1984) The macroinvertebrates and fish of a Colorado stream during a period of fluctuation discharge. *Freshwater Biology*, **14**, 311–316.
- Capone T.A. & Kushlan J.A. (1991) Fish community structure in dry-season stream pools. *Ecology*, **72**, 983–992.
- Chapman L.J. & Kramer D.L. (1991) The consequences of flooding for the dispersal and fate of poeciliid fish in an intermittent tropical stream. *Oecologia*, **87**, 299–306.
- Closs G.P. & Lake P.S. (1996) Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes*, **47**, 17–26.
- Cowx I.G., Young W.O. & Hellowell J.M. (1984) The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology*, **14**, 165–177.
- Cross F.B. & Moss R.E. (1987) Historic changes in fish communities and aquatic habitats in plains streams of Kansas. In: *Community and Evolutionary Ecology of North American Stream Fishes* (Eds W.J. Matthews & D.C. Heins), pp. 155–165, University of Oklahoma Press, Norman, OK.
- Cross F.B., Moss R.E. & Collins J.T. (1985) Assessment of dewatering impacts on stream fisheries in the Arkansas and Cimarron Rivers. *Final Report of Nongame Wildlife Contract No. 46, Kansas Fish and Game Commission and The University of Kansas (KU 5400–0705)*.
- Deacon J.E. (1961) Fish populations, following a drought, in the Neosho and Marais des Cygnes Rivers of Kansas. *University of Kansas Publications Museum of Natural History*, **13**, 359–427.
- Douglas, M.R., Brunner, P.C. & Douglas, M.E. (2003) Drought in an evolutionary context: molecular variability in the Flannelmouth Sucker (*Catostomus latipinnis*) from the Colorado River Basin of western North America. *Freshwater Biology*, **48**, 1256–1275.
- Eaton J.G. & Scheller R.M. (1996) Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography*, **41**, 1109–1115.
- Eberle M.E., Ernsting G.W., Tomelleri J.R. & Wells S.L. (1993) Assessment of restored streamflow on fish communities in the Arkansas River of southwestern Kansas. *Transactions of the Kansas Academy of Science*, **96**, 114–130.
- Edwards R.J. & Contreras-Balderas S. (1991) Historical changes in the ichthyofauna of the lower Rio Grande (Rio Bravo del Norte), Texas and Mexico. *The Southwestern Naturalist*, **36**, 201–212.
- Fausch K.D. & Bramblett R.G. (1991) Disturbance and fish communities in intermittent tributaries of a Western Great Plains river. *Copeia*, **1991**, 659–674.
- Fausch K.D. & Young M.K. (1995) Evolutionary significant units and movement of resident stream fishes: a cautionary tale. In: *Proceedings of the Symposium on Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation* (Eds J.L. Nielsen & D.A.

- Powers), pp. 360–370, American Fisheries Society, Bethesda, MD.
- Feminella J.W. & Matthews W.J. (1984) Intraspecific differences in thermal tolerance of *Etheostoma spectabile* (Agassiz) in constant versus fluctuating environments. *Journal of Fish Biology*, **25**, 455–461.
- Flecker A.S. (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology*, **77**, 1845–1854.
- Flecker A.S. (1997) Habitat modification by tropical fishes: environmental heterogeneity and variability of interaction strength. *Journal of the North American Benthological Society*, **16**, 286–295.
- Gauch H.G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Gelwick F.P. & Matthews W.J. (1992) Effects of an algivorous minnow on temperate stream ecosystem properties. *Ecology*, **73**, 1630–1645.
- Gelwick F.P., Stock M.S. & Matthews W.J. (1997) Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river system. *Oikos*, **80**, 382–389.
- Gido K.B. & Matthews W.J. (2000) Ecosystem effects of water column minnows in experimental streams. *Oecologia*, **126**, 247–253.
- Gotelli N.J. & Taylor C.M. (1999) Testing metapopulation models with stream-fish assemblages. *Evolutionary Ecology Research*, **1**, 835–845.
- Gowan C. & Fausch K.D. (1996) Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1370–1381.
- Grimm N.B. (1988) Feeding dynamics, nitrogen budgets, and ecosystem role of a desert stream omnivore, *Agosia chrysogaster* (Pisces: Cyprinidae). *Environmental Biology of Fishes*, **21**, 143–152.
- Griswold B.L., Edwards C.J. & Woods L.C. I (1982) Recolonization of macroinvertebrates and fish in a channelized stream after a drought. *Ohio Journal of Science*, **82**, 96–102.
- Grossman G.D. & Ratajczak R.E. Jr. (1998) Long-term patterns of microhabitat use by fish in a southern Appalachian stream from 1983 to 1992: effects of hydrologic period, season and fish length. *Ecology of Freshwater Fish*, **7**, 108–131.
- Grossman G.D., Ratajczak R.E. Jr., Crawford M. & Freeman M.C. (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs*, **68**, 395–420.
- Hanski I. (1999) *Metapopulation Ecology*. Oxford University Press, New York.
- Hargrave C.W. (2000) A Decade of Stability in Fish Assemblages of a Harsh, Prairie River System. Unpublished MS thesis, Department of Zoology, University of Oklahoma, Norman, OK.
- Hefley H.M. (1937) Ecological studies on the Canadian River floodplain in Cleveland County, Oklahoma. *Ecological Monographs*, **7**, 345–402.
- Hill J.A. & Grossman G.D. (1987) Home range estimators for three North American stream fishes. *Copeia*, **1987**, 376–380.
- Hoffman A.A. & Hercus M. J. (2000) Environmental stress as an evolutionary force. *BioScience*, **50**, 217–226.
- Hubbs C. (1990) Declining fishes of the Chihuahuan Desert. In: *Papers from the Third Symposium on Resources of the Chihuahuan Desert Basin, United States and Mexico* (Eds A.M. Powell, R.R. Hollander, J.C. Barlow, W.B. McGillivray & D.J. Schmidly), pp. 89–96, Chihuahuan Desert Research Institute, Alpine, Texas.
- Hubbs, C. (2001) Environmental correlates to the abundance of spring-adapted versus stream-adapted fishes. *Texas Journal of Science*, **53**, 299–326.
- Hubbs C. & Hettler W.F. (1958) Fluctuations of some central Texas fish populations. *The Southwestern Naturalist*, **3**, 13–16.
- Hubbs C.L., Miller R.R. & Hubbs L.C. (1974) Hydrographic history and relict fishes of the north-central Great Basin. *Memoirs of the California Academy of Science*, **7**, 1–259.
- James M.C. (1934) Effect of 1934 drought on fish life. *Transactions of the American Fisheries Society*, **64**, 57–62.
- Janovy J. Jr., Snyder S.D. & Clopton R.E. (1997) Evolutionary constraints on population structure: the parasites of *Fundulus zebrinus* (Pisces: Cyprinodontidae) in the South Platte River of Nebraska. *Journal of Parasitology*, **83**, 584–592.
- John K.R. (1964) Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. *Ecology*, **45**, 112–119.
- Kelsch S.W. (1994) Lotic fish-community structure following transition from severe drought to high discharge. *Journal of Freshwater Ecology*, **9**, 331–341.
- Lae R. (1995) Climatic and anthropogenic effects on fish diversity and fish yields in the Central Delta of the Niger River. *Aquatic Living Resources*, **8**, 43–58.
- Larimore R.W., Childers W.F. & Heckrotte C. (1959) Destruction and re-establishment of stream fish and invertebrates affected by drought. *Transactions of the American Fisheries Society*, **88**, 261–285.
- Lewis W.M. (1970) Morphological adaptations of cyprinodontids for inhabiting oxygen deficient water. *Copeia*, **1970**, 319–326.
- Lienesch P.W., Lutterschmidt W.I. & Schaefer J.F. (2000) Seasonal and long-term changes in the fish assemblage

- of a small stream isolated by a reservoir. *The Southwestern Naturalist*, **45**, 274–288.
- McAllister D.E., Platania S.P., Schueler F.W., Baldwin M.E. & Lee D.S. (1986) Ichthyofaunal patterns on a geographic grid. In: *The Zoogeography of North American Freshwater Fishes* (Eds C.H. Hocutt & E.O. Wiley), pp. 17–51, John Wiley and Sons, New York.
- McCune A.R., Thomson K.S. & Olsen P.E. (1984) Semionotid fishes from the Mesozoic great lakes of North America. In: *Evolution of Fish Species Flocks* (Eds A.A. Echelle & I. Kornfield), pp. 27–44, University of Maine Press, Orono, ME.
- Magoulick, D.D. & Kobza, R.M. (2003) The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology*, **48**, 1186–1198.
- Marsh-Matthews, E. & Matthews, W.J. (2000) Spatial variation in relative abundance of a widespread, numerically dominant fish species and its effect on fish assemblage structure. *Oecologia*, **125**, 283–292.
- Marshall B.E. (1988) Seasonal and annual variations in the abundance of pelagic sardines in Lake Kariba, with special reference to the effects of drought. *Archiv für Hydrobiologie*, **112**, 399–409.
- Matthews W.J. (1985) Distribution of Midwestern fishes on multivariate environmental gradients, with emphasis upon *Notropis lutrensis*. *American Midland Naturalist*, **113**, 225–237.
- Matthews W.J. (1986) Geographic variation in thermal tolerance of a widespread minnow (*Notropis lutrensis*) of the North American midwest. *Journal of Fish Biology*, **27**, 407–417.
- Matthews W.J. (1987) Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. In: *Community and Evolutionary Ecology of North American Stream Fishes* (Eds W.J. Matthews & D.C. Heins), pp. 111–120, University of Oklahoma Press, Norman, OK.
- Matthews W.J. (1998) *Patterns in Freshwater Fish Ecology*. Chapter 7. Chapman and Hall, New York.
- Matthews W.J. & Hill L.G. (1979) Influence of physicochemical factors on habitat selection by red shiners, *Notropis lutrensis* (Pisces: Cyprinidae). *Copeia*, **1979**, 70–81.
- Matthews W.J. & Hill L.G. (1980) Habitat partitioning in the fish community of a southwestern river. *The Southwestern Naturalist*, **25**, 51–66.
- Matthews W.J. & Maness J.D. (1979) Critical thermal maxima, oxygen tolerances and success of cyprinid fishes in a southwestern river. *The American Midland Naturalist*, **102**, 374–377.
- Matthews W.J. & Zimmerman E.G. (1990) Potential effects of global warming on native fishes of the southern Great Plains and the Southwest. *Fisheries*, **15**, 26–32.
- Matthews W.J., Cashner R.C. & Gelwick F.P. (1988) Stability and persistence of fish faunas and assemblages in three midwestern streams. *Copeia*, **1988**, 945–955.
- Matthews W.J., Surat E. & Hill L.G. (1982) Heat death of the orangethroat darter, *Etheostoma spectabile* (Percidae) in a natural environment. *The Southwestern Naturalist*, **27**, 216–217.
- Matthews W.J., Harvey B.C. & Power M.E. (1994) Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (USA). *Environmental Biology of Fishes*, **39**, 381–397.
- Meyer A. (1993) Phylogenetic relationships and evolutionary processes in East African cichlid fishes. *Trends in Ecology and Evolution*, **8**, 279–284.
- Minckley W.L. & Barber W.E. (1971) Some aspects of biology of the longfin dace, a cyprinid fish characteristic of streams in the Sonoran Desert. *The Southwestern Naturalist*, **15**, 459–464.
- Mol, J.H., Resida D., Ramlal J.S. & Becker C.R. (2000) Effects of El Nino-related drought on freshwater and brackish-water in Suriname, South America. *Environmental Biology of Fishes*, **59**, 429–440.
- Mundahl N.D. (1990) Heat death of fish in shrinking stream pools. *The American Midland Naturalist*, **123**, 40–46.
- Ostrand K.G. & Marks D.E. (2000) Mortality of prairie stream fishes confined in an isolated pool. *Texas Journal of Science*, **52**, 255–258.
- Paloumpis A.A. (1957) The effects of drought conditions on the fish and bottom organisms of two small oxbow ponds. *Transactions of the Illinois State Academy of Science*, **50**, 60–64.
- Paloumpis A.A. (1958) Responses of some minnows to flood and drought conditions in an intermittent stream. *Iowa State College Journal of Science*, **32**, 547–561.
- Piet G.J. (1998) Impact of environmental perturbation on a tropical fish community. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1842–1853.
- Pigg J. (1991) Decreasing distribution and current status of the Arkansas River Shiner, *Notropis girardi*, in the rivers of Oklahoma and Kansas. *Proceedings of the Oklahoma Academy of Science*, **71**, 5–15.
- Power M.E. (1984) The importance of sediment in the grazing ecology and size class interactions of an armored catfish, *Ancistrus spinosus*. *Environmental Biology of Fishes*, **10**, 173–181.
- Power M.E. & Matthews W.J. (1983) Algae-grazing minnows (*Camptostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached

- algae in a small prairie-margin stream. *Oecologia*, **60**, 328–332.
- Power M.E., Matthews W.J. & Stewart A.J. (1985) Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. *Ecology*, **66**, 1448–1456.
- Power M.E., Parker M.S. & Wootton J.T. (1995) Disturbance and food chain length in rivers. In: *Food Webs* (Eds G.A. Polis & K.O. Winemiller), pp. 286–297, Chapman and Hall, New York.
- Pringle C.M. & Hamazaki T. (1997) Effects of fishes on algal response to storms in a tropical stream. *Ecology*, **78**, 2432–2442.
- Pringle C.M. & Hamazaki T. (1998) The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology*, **79**, 269–280.
- Ross S.T., Matthews W.J. & Echelle A.A. (1985) Persistence of stream fish assemblages: Effects of environmental change. *American Naturalist*, **126**, 24–40.
- Rutledge C.J., Zimmerman E.G. & Beiting T.L. (1990) Population genetic responses of two minnow species (Cyprinidae) to seasonal stream intermittency. *Genetica*, **80**, 209–219.
- Scalet C.G. (1973) Stream movements and population density of the orangebelly darter, *Etheostoma radiosum cyanorum* (Osteichthyes: Percidae). *The Southwestern Naturalist*, **17**, 381–387.
- Schaefer J. (2001) Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Camptostoma anomalum*, and *Cyprinella venusta*). *Freshwater Biology*, **46**, 379–388.
- Schlosser I.J. (1985) Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology*, **66**, 1484–1490.
- Schlosser I.J. (1998) Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia*, **113**, 260–268.
- Schlosser I.J. & Angermeier P.L. (1995) Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. In: *Proceedings of the Symposium on Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation* (Eds J.L. Nielsen & D.A. Powers), pp. 392–401, American Fisheries Society, Bethesda, MD.
- Schwartz F.J. (1988) Pre- and post-drought fish surveys of selected freshwater ponds located in Nags Head Woods, Nags Head, North Carolina. *Association of Southeastern Biologists Bulletin*, **35**, 189–198.
- Shirvell C.S. (1994) Effect of changes in streamflow on the microhabitat use and movements of sympatric juvenile coho salmon (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) in a natural stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1644–1652.
- Smale M.A. & Rabeni C.F. (1995) Influences of hypoxia and hyperthermia on fish species composition in headwater streams. *Transactions of the American Fisheries Society*, **124**, 711–725.
- Smith C.L. & Powell C.R. (1971) The summer fish communities of Brier Creek, Marshall County, Oklahoma. *American Museum Novitates*, **2458**, 1–30.
- Snodgrass J.W., A. L. Bryan J., Lide R.F. & Smith G.M. (1996) Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 443–454.
- Soule P.T. (1993) Hydrologic drought in the contiguous United States, 1900–1989: Spatial patterns and multiple comparison of means. *Geophysical Research Letters*, **20**, 2367–2370.
- Spranza J.J. & Stanley E.H. (2000) Condition, growth, and reproductive styles of fishes exposed to different environmental regimes in a prairie drainage. *Environmental Biology of Fishes*, **59**, 99–109.
- Starrett W.C. (1950) Distribution of the fishes of Boone County, Iowa, with special reference to the minnows and darters. *The American Midland Naturalist*, **43**, 112–127.
- Starrett W.C. (1951) Some factors affecting the abundance of minnows in the Des Moines River, Iowa. *Ecology*, **32**, 13–24.
- Swales S., Storey A.W., Roderick I.D. & Figa B.S. (1999) Fishes of floodplain habitats of the Fly River system, Papua New Guinea, and changes associated with El Niño droughts and algal blooms. *Environmental Biology of Fishes*, **54**, 389–404.
- Tarboton D.G. (1995) Hydrologic scenarios for severe sustained drought in the southwestern United States. *Water Research Bulletin*, **31**, 417–424.
- Taylor C.M. & Gotelli N.J. (1994) The macroecology of *Cyprinella*: correlates of phylogeny, body size, and geographical range. *American Naturalist*, **144**, 549–569.
- Taylor C.M., Winston M.R. & Matthews W.J. (1996) Temporal variation in tributary and mainstream fish assemblages in a Great Plains stream system. *Copeia*, **1996**, 280–289.
- Titus R.G. & Mosegaard H. (1992) Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. *Journal of Fish Biology*, **41**, 239–255.
- Tramer E.J. (1977) Catastrophic mortality of stream fishes trapped in shrinking pools. *The American Midland Naturalist*, **97**, 469–478.
- Verheyen E., Salzburger W., Snoeks J. & Meyer A. (2003) Origin of the superstock of cichlid fishes from Lake Victoria, East Africa. *Science*, **300**, 325–329.

- Warren M.L. & Pardew M.G. (1998) Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society*, **127**, 637–644.
- Welcomme R.L. (1986) The effects of the Sahelian drought in the fishery of the central delta of the Niger River. *Aquaculture and Fisheries Management*, **17**, 147–154.
- Wickliff E.L. (1945) Some effects of droughts and floods on stream fish. *Ohio State University Engineering Experiment Station News*, **17**, 23–31.
- Wilde G.R. & Ostrand K.G. (1999) Changes in the fish assemblage of an intermittent prairie stream upstream from a Texas impoundment. *Texas Journal of Science*, **51**, 203–210.
- Williams L.R., Echelle A.A., Toepfer C.S., Williams M.G. & Fisher W.L. (1999) Simulation modeling of population viability for the leopard darter (Percidae: *Percina pantherina*). *The Southwestern Naturalist*, **44**, 471–478.
- Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, **60**, 331–367.
- Winston M.R., Taylor C.M. & Pigg J. (1991) Upstream extirpation of four minnow species due to damming of a prairie stream. *Transactions of the American Fisheries Society*, **120**, 98–105.
- Wootton J.T., Parker M.S. & Power M.E. (1996) Effects of disturbance on river food webs. *Science*, **273**, 1558–1561.
- Zaret T.M. & Rand, A.S. (1971) Competition in tropical stream fishes: Support for the competitive exclusion principle. *Ecology*, **52**, 336–342.

(Manuscript accepted 28 December 2002)

Appendix Scoring of 50 papers on fish and drought, on axes of spatial scale of study (Space), length of drought under study (Length), and level of ecological complexity under study (Complexity), scored quantitatively as indicated below, and effects of drought on fish as indicated by original authors

Reference	Space*	Length†	Complexity‡	Time to recovery§	Effects documented§	Effects suspected§	Effects examined but not found§
James (1934)	8	2	4	Not studied	2, 7, 10, 11, 16, 20		
Wickliff (1945)	6	4	5	Not studied	10, 11, 12, 16		4
Starrett (1951)	3	2	2	Year	2, 10, 16	8	
Bailey (1955)	4	1	1	Weeks	2, 5, 11, 12		
Paloumpis (1957)	4	2	4	None detected	2, 10, 11, 12, 16		
Paloumpis (1958)	6	4	3	Not studied	2, 8, 12, 16		
Hubbs & Hettler (1958)	6	4	3	None detected	2		
Larimore <i>et al.</i> (1959)	6	4	4	Year	2, 5, 10, 11, 12, 16, 20		4
Deacon (1961)	7	4	4	Years	2, 4, 5, 8, 12, 16		
John (1964)	2.5	2	2	Not studied	2, 3, 7, 8, 10, 11, 12, 16		
Minckley & Barber (1971)	3	4	1	Not studied	2, 10		
Zaret & Rand (1971)	2	2	5	Months	17, 18	6	
Tramer (1977)	2	2	4	Years	2, 11, 12, 16	6	
Matthews & Maness (1979)	3	2	3	Year	2, 8		
Matthews <i>et al.</i> (1982)	1	1	1	Months	2, 11		
Griswold <i>et al.</i> (1982)	6	2	4	None detected	2, 5, 12, 16		
Cowx, Young & Hellawell (1984)	3	3	3	Year	5, 9, 11	8	6, 18
Canton <i>et al.</i> (1984)	3	2	3	Year	2, 3, 12	4	
Schlosser (1985)	3	2	4	Not studied	2, 5		
Cross <i>et al.</i> (1985)	7	4.5	4	None detected	2, 5, 12		
Welcomme (1986)	7	4	4	Year	2, 5, 19		
Schwartz (1988)	4	4	5	None detected	2, 5, 12		
Marshall (1988)	5	4	3	Year	2		
Hubbs (1990)	3	5.5	3	None detected	2	10	
Rutledge <i>et al.</i> (1990)	2	2	2	None detected	14		
Mundahl (1990)	2	1	2	Weeks	2, 4, 11, 12, 17	6	
Winemiller (1990)	3	2	5.5	Not studied	4, 12, 16, 18, 20		
Chapman & Kramer (1991)	2	1	2	Months	2, 4, 10	6	
Edwards & Contreras-Balderas (1991)	7	4.5	5	None detected	5		
Capone & Kushlan (1991)	2	2	5	Not studied	5, 10, 12		
Fausch & Bramblett (1991)	2	2	3	Not studied	1	11	2, 4, 5
Winston <i>et al.</i> (1991)	6	2	3	None detected		2, 4, 9, 12	
Titus & Mosegaard (1992)	3	3	2	Not studied	2, 4, 9, 10		8
Bayley & Osborne (1993)	6	3	5	Year	2, 12, 19		4, 5
Eberle <i>et al.</i> (1993)	7	3	4	Years	1**, 2, 5		
Burr & Warren (1993)	6.5	3	4	None detected	2, 5, 11, 12		
Kelsch (1994)	6	4	4	Years	2, 5		
Shirvell (1994)	3	0.5	1	Not studied	4, 17		
Smale & Rabeni (1995)	7	4	5	Not studied	2, 12		
Lae (1995)	7	4	5.5	None detected	2, 5, 12, 13, 16		
Closs & Lake (1996)	6	3	3	Years	2, 4	11	
Snodgrass <i>et al.</i> (1996)	4.5	2	3	Not studied	2, 10		6
Janovy <i>et al.</i> (1997)	3	4	1	Years	2, 15		
Piet (1998)	5	2	5	None detected	2, 3, 5, 7, 11, 12	6	
Grossman <i>et al.</i> (1998)	3	4	5	Year	1, 4, 5, 12, 17		6
Swales <i>et al.</i> (1999)	7	3	5	Years	2, 12		3
Williams <i>et al.</i> (1999)	3	3	3	Not studied	2		
Spranza & Stanley (2000)	3	1	1	Weeks	3		
Ostrand & Marks (2000)	2	2	1	Not studied	2, 11		
Hubbs (2001)	3	4	3	Not studied	2, 5, 12	11	

Appendix (Continued)

Reference	Space*	Length†	Complexity‡	Time to recovery§	Effects documented§	Effects suspected§	Effects examined but not found§
Recent studies							
Kobza & Trexler (pers. comm.)¶	4	3.5	5				
Marsh-Matthews & Matthews (pers. comm.)	2	2	4				
Douglas & Douglas (pers. comm.)	7	6	3				
Douglas <i>et al.</i> (2003)	7	6	2				
Kennard <i>et al.</i> (pers. comm.)	2	4	5				
Baker & Jennings (pers. comm.)	5	2	1				
Magoulick (pers. comm.)	2	4	4				
Wilde <i>et al.</i> (pers. comm.)	2	4	4				
Moffatt (pers. comm.)	6	4	5				
Ilhéu <i>et al.</i> (pers. comm.)	2	1	4				
Cashner <i>et al.</i> (pers. comm.)	5	4	4				

*1 = single pool or riffle, 2 = pools, 3 = stream reach, 4 = ponds, 5 = lake, 6 = catchment, 7 = river basin or lake district, 8 = subcontinent.

†1 = weeks, 2 = season, 3 = one year, 4 = years, 5 = decades, 6 = centuries or longer.

‡1 = individuals, 2 = individuals and population, 3 = population, 4 = population and whole assemblage, 5 = whole assemblage/regional fauna, 6 = ecosystem processes.

§1 = no effect, 2 = population decline, 3 = low condition, 4 = movement, 5 = community change, 6 = increased competition, 7 = starvation, 8 = reproductive decline, 9 = cohort failure, 10 = death by desiccation, 11 = death by lowered water quality, 12 = habitat loss, 13 = population fragmentation, 14 = genetic bottleneck, 15 = parasites, 16 = crowding, 17 = microhabitat shift, 18 = food use shift, 19 = biomass, 20 = predation.

¶Based on abstract of paper presented at the Symposium on the Role of Drought in Aquatic Ecosystems (Albury, Australia) in 2001.

**Effects differed among species.