Fisheries Management and Ecology, 2004, **11**, 107–116

Variation in larval fish communities: implications for management and sampling designs in reservoir systems

M. C. QUIST, K. R. PEMBER & C. S. GUY*

U.S. Geological Survey – Biological Resources Division, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan, KS, USA

J. L. STEPHEN

Kansas Department of Wildlife and Parks, Emporia, KS, USA

Abstract Understanding spatial and temporal patterns in larval fish distributions is important for investigating factors related to recruitment variability and for developing sampling methodologies. Variation in species diversity (Shannon index) and density (number 100 m^{-3}) of larval fishes from nearshore and pelagic habitats in Glen Elder Reservoir, KS, USA, was assessed during 1999 and 2000. Species diversity and densities of individual taxa were significantly higher ($P < 0.05$) in nearshore habitats than pelagic habitats during both years. Larval fish densities were generally higher in the year 1999 with higher spring water levels. Gizzard shad *Dorosoma cepedianum* (Lesueur) was the most abundant taxon in nearshore and pelagic habitats during both years. In addition, larval gizzard shad was sampled for the longest duration in the upper water column and overlapped with all taxa collected. High densities of gizzard shad in both habitats suggested that the potential for competitive interactions was high, especially given the lack of aquatic vegetation and habitat heterogeneity in littoral habitats. Most of the variation in larval fish diversity and density was because of temporal variation. If sampling effort must be limited and the purpose of sampling is to monitor larval diversity or density, attention should focus on sampling the same location over long time periods rather than across a variety of sampling locations.

KEYWORDS: diversity, Kansas, larval fish, reservoirs, spatial and temporal variation.

Introduction

The early life history of fish is often considered critical for recruitment to the adult population (Gulland 1982). Thus, understanding how larval fish populations vary through time and among habitats is important for answering questions related to both applied and theoretical ecology. For example, variability in larval fish distributions may provide insight on the factors influencing recruitment dynamics such as the location and suitability of spawning habitat (Parker & Franzin 1991; Donald 1997) or the effects of anthropogenic disturbances (e.g. elevated thermal regimes; Barwick 1978; Wilkonska 1994). Knowledge of larval fish distributions may also provide information on species interactions during early life history. Several studies suggest that larval niche partitioning has influenced the evolution (i.e. time of spawning, ontogenetic shifts in diet or habitat use) of sympatric species (Todd & Davis 1995; Chouinard & Bernatchez 1998). In addition to providing insight on factors influencing fish populations and communities, understanding spatial and temporal variation in larval fish distributions is extremely important for developing standardised sampling methodologies.

Most research on larval fishes has been conducted in marine systems (e.g. Miller, Crowder, Rice & Marschall 1988; Pepin, Dower & Davidson 2003;

Correspondence: Michael Quist, U.S. Geological Survey – Biological Resources Division, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071 3166, USA (e-mail: mcquist@uwyo.edu)

*Present address: U.S. Geological Survey – Biological Resources Division, Montana Cooperative Fishery Research Unit, Department of Ecology, 301 Lewis Hall, Montana State University, Bozeman, MT 59717, USA

Stratoudakis, Bernal, Borchers & Borges 2003). In freshwater, larval fish distributions have been studied in large rivers (Holland & Sylvester 1983; Copp 1993; Brown & Coon 1994), streams (Floyd, Hoyt & Timbrook 1984), and natural lakes (Amundrud, Faber & Keast 1974; Post & McQueen 1988; Economou, Daoulas, Psarras & Barbieri-Tseliki 1994; Wang & Eckmann 1994). Despite the abundance and importance of reservoirs, few studies have examined larval fish distributions in impounded systems, and of those, most have focused on a single species (Linlokken, Kleiven & Matzow 1991; Michaletz 1997; Chick & Van Den Avyle 1999) or family (Tisa, Ney & Whitehurst 1985; Sammons, Bettoli & Fiss 1998). The objective of this study was to examine spatial and temporal variation in larval fish communities in a large reservoir system, Glen Elder Reservoir, KS, USA. Because larval fish often have a patchy distribution (i.e. both spatially and temporally), the relative importance of spatial and temporal variation in larval fish diversity and densities to the design of sampling protocols was also examined.

Materials and methods

This study was conducted on Glen Elder Reservoir, a 5093 ha impoundment in north-central Kansas (39°29′ N; 98°18′ W). Glen Elder Reservoir is similar to other reservoirs in the Great Plains region of North America with regard to abiotic conditions and fish communities. In general, reservoirs in the region are turbid and warm (mean summer temperatures ≥ 30 °C), and rarely thermally stratify because of persistent wind action. Fish communities are diverse and all species spawn during the spring prior to or during high seasonal rainfall (i.e. April to June). Although many species are highly abundant and reproduce naturally [e.g. gizzard shad, *Dorosoma cepedianum* (Lesueur), channel catfish, *Ictalurus punctatus* (Rafinesque), white bass, *Morone chrysops* (Rafinesque)], other species are routinely stocked [e.g. walleye *Sander vitreus* (Mitchill), striped bass, *Morone saxatilis* (Walbaum)] to maintain or supplement populations that provide recreational angling opportunities. A detailed description of the abiotic conditions and fish communities in Glen Elder Reservoir and other Kansas reservoirs is provided in Quist (2002).

Larval fishes were sampled weekly from the last week in March until the end of June during 1999 and 2000 (Fig. 1). Although habitat (e.g. aquatic vegetation, woody debris) in Kansas reservoirs is rare or absent, that which does occur is located in shallow water habitats generally within 200 m of shore. In addition, management activities (e.g. habitat improvement) occur in nearshore areas indicating

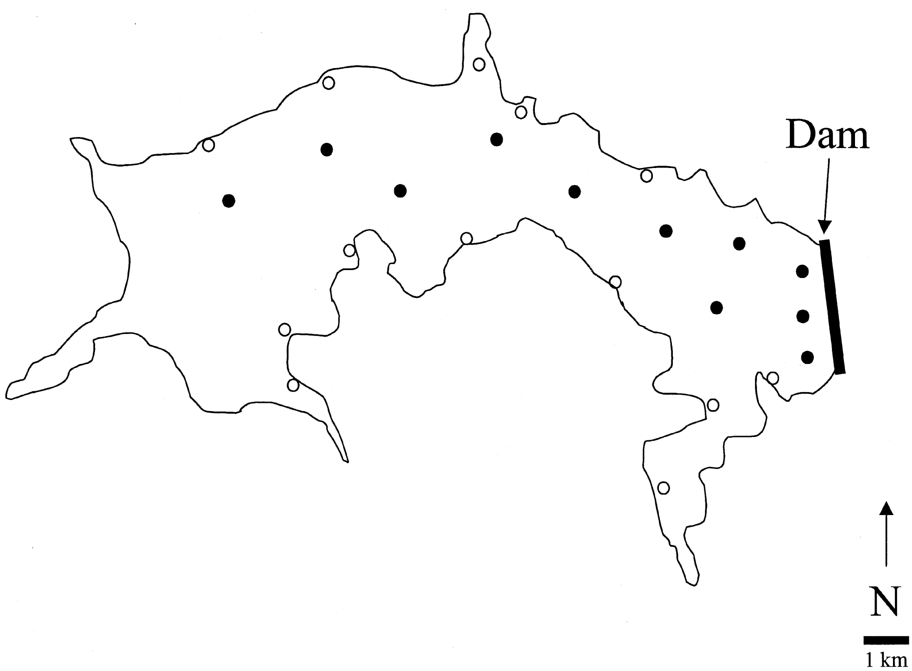

Figure 1. Location of ichthyoplankton sampling sites from nearshore (open symbols) and pelagic (solid symbols) habitats in Glen Elder Reservoir, Kansas (1999–2000).

the importance of areas within 200 m of shore for management purposes. A stratified-random sampling design was used to select sampling sites from nearshore and offshore habitat types. Nearshore habitats were defined as areas within 200 m from the shoreline and offshore habitats were those > 500 m from shore. Larval fish were sampled during the day at all sites using paired conical nets (bongo nets; 0.5 m diameter × 1.5 m long, 500 μm mesh) and a metered net (1.0 m diameter × 3.0 m long, 500 μm mesh). Bongo nets were pushed just below the surface of the water from the bow of the boat, and the metered net was towed behind the boat using an aluminium depressor to maintain the top of the net at a depth of 0.5 m from the surface. Nets were towed at a rate of 1.5 m s^{-1} for 15–20 min, although duration was occasionally reduced to prevent clogging the net with debris and algae. Flow meters (Model 2030R; General Oceanics, Inc., Miami, FL, USA) were fixed to the mouth of all nets and measured the distance travelled. Distance travelled was then multiplied with the surface area of the opening of the net to determine sample volume.

Ichthyoplankton samples were immediately preserved in 90% ethanol and transported back to the laboratory for identification. Larval fish were identified using keys provided by May & Gassaway (1967), Taber (1969) and Auer (1982). All larvae were identified to species where possible, but accurate identification of several taxa beyond the genus level is difficult or impossible without conducting molecular analyses (Rettig 1998). Therefore, *Lepomis* spp., *Pomoxis* spp., *Ictiobus* spp., and *Carpiodes* spp. were only identified to genus. Based on the relative abundance of adults in Glen Elder Reservoir, these taxa were probably dominated by green sunfish *Lepomis cyanellus* Rafinesque, bluegill *Lepomis macrochirus* Rafinesque, white crappie *Pomoxis annularis* Rafinesque, smallmouth buffalo *Ictiobus bubalus* (Rafinesque), and river carpsucker *Carpiodes carpio* (Rafinesque). Although larvae can exhibit difference in their spatial and temporal distribution depending on the ontogenetic status (e.g. Werner & Gilliam 1984), lack of basic ecological knowledge of species prevented identification of life stages. Once all larval fish were identified, species diversity at each site and sampling date was estimated using the Shannon index (Ney 1999). Repeated-measures analysis of variance (ANOVA; Milliken & Johnson 1992) was used to determine if species diversity and density (number 100 m^{-3}) differed over spatial and temporal scales during each year. When significant interactions occurred (i.e. habitat by sampling date), least-squared means were used to examine difference among habitats on individual sampling dates (Milliken & Johnson 1992). The importance of spatial and temporal variation was examined using methods first using repeated-measures ANOVA and then partial variance was estimated following the methods of Meador & Matthews (1992): $S^2_H = (MS_H - MS_I)/N_D$ and $S^2_D = (MS_D - MS_I)/N_H$, where, S^2 is the variance, MS the mean square from the ANOVA, N the sample size, H the habitat type, D the sampling date and I the interaction between habitat type and sampling date. The percentage of variation (model variation) was estimated from each component and partitioned into a ratio (i.e. $S^2_H : S^2_D$) to identify the relative importance of spatial and temporal variability on larval fish diversity and densities. All analyses were conducted using SAS (SAS Institute 1996) and $\alpha = 0.05$.

Results

A total of 41 168 larval fishes representing 14 different taxa were collected (Table 1). Larval walleye was the first species collected in 1999, followed by gizzard shad and white bass (Fig. 2). Most taxa were first collected during mid to late May, but *Ictiobus* spp. and *Carpiodes* spp. were first sampled during late May or early June. During 2000, gizzard shad was the first species collected, and similar to 1999, exhibited the most protracted temporal occupation of any species in the upper water column. Common carp *Cyprinus carpio* L., freshwater drum *Aplodinotus grunniens* Rafinesque, *Carpiodes* spp., and white suckers *Catostomus commersoni* (Lacépède) were only sampled during 1999. Although most taxa were sampled from both habitat types, logperch *Percina caprodes* (Rafinesque), *Pomoxis* spp., freshwater drum, and *Carpiodes* spp. were only sampled from nearshore habitats. No taxa were exclusively sampled from pelagic habitats during either year.

Diversity of larval fishes generally increased through time, but was highly variable among habitat types during both years (Fig. 3). Species diversity was low until the middle of May in 1999 and did not increase until the end of May in 2000, when water temperatures were 18–20 °C during both years. Species diversity was significantly higher ($P = 0.04$–0.0001) in nearshore than pelagic habitats on most sampling dates in both years (Fig. 3). Not only were nearshore habitats more diverse, but most taxa also had higher densities in nearshore habitats compared with pelagic habitats (Table 1). Although densities were generally low for most taxa, densities were usually higher in 1999 than 2000.

Gizzard shad, *Lepomis* spp., and white bass were the most abundant taxa during both years and comprised

Table 1. Summary of mean species diversity (Shannon index) and density (number 100 m^{-3}) of larval fishes sampled from nearshore and pelagic habitat types from Glen Elder Reservoir, Kansas, during 1999 and 2000. Numbers in parentheses represent 1 SE. Total density estimates represent densities of all larval fishes

	1999		2000	
Index or taxa	Nearshore	Pelagic	Nearshore	Pelagic
Diversity	0.17 (0.08)	0.04 (0.02)	0.16 (0.11)	0.11 (0.05)
Walleye	0.01 (0.01)	0.05 (0.04)	0 (0)	0.01 (0.01)
Gizzard shad	105.93 (53.59)	183.52 (135.82)	3.47 (1.74)	12.17 (7.17)
Common carp	0.02 (0.01)	0.02 (0.01)	0 (0)	0 (0)
White bass	0.12 (0.05)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)
Freshwater drum	0.05 (0.03)	0 (0)	0 (0)	0 (0)
Logperch	0.01 (0.01)	0 (0)	0 (0)	0.01 (0.01)
Lepomis spp.	1.31 (0.67)	0.29 (0.16)	0.04 (0.03)	0.02 (0.01)
Pomoxis spp.	0.06 (0.03)	0 (0)	0 (0)	0 (0)
Ictiobus spp.	0.09 (0.08)	0.03 (0.02)	0.01 (0.01)	0.01 (0.01)
Carpiodes spp.	0.01 (0.01)	0 (0)	0 (0)	0 (0)
Fathead minnow	0.02 (0.01)	0.03 (0.02)	0.01 (0.01)	0.01 (0.01)
Emerald shiner	0.01 (0.01)	0.01 (0.01)	0 (0)	0.01 (0.01)
Central stoneroller	0.01 (0.01)	0 (0)	0.01 (0.01)	0.01 (0.01)
White sucker	0.01 (0.01)	0.01 (0.01)	0 (0)	0 (0)
Total	107.65 (54.01)	183.99 (135.97)	3.47 (1.74)	12.23 (7.18)

over 96% (by number) of the larval fish collected. Therefore, spatial and temporal trends in abundance for these species were further examined (Fig. 4). During 1999, gizzard shad were generally more abundant in pelagic habitats ($P = 0.05$–0.0001) and peaked about a week later than in 2000. In 2000, gizzard shad densities were much lower than in 1999 and exhibited a bimodal distribution in pelagic habitats. Similar to 1999, gizzard shad were most abundant in pelagic habitats during 2000. White bass densities peaked about 1 week earlier and were higher ($P = 0.04$–0.0001) on individual sampling dates in nearshore than pelagic habitats in 1999. Although few white bass were sampled in 2000, most were sampled on one sampling date from pelagic sampling sites. *Lepomis* spp. densities were significantly higher ($P = 0.02$–0.0001) in nearshore habitats during both years. Similar to gizzard shad and white bass, *Lepomis* spp. densities were generally much higher in 1999 than 2000. Because gizzard shad were the most abundant species in both habitats and years, trends in total larval fish abundance were identical to the trends observed for gizzard shad.

Partial variance analysis indicated that most of the variation in species diversity and density of individual taxa was because of temporal variation rather than variation between habitat types (Table 2). Freshwater drum and *Pomoxis* spp. were the only taxa where spatial variation was higher than temporal variation.

Discussion

Distributions of larval fishes in lentic systems may reflect a response to predation (Johnston, Gaboury, Janusz & Janusz 1995), prey resources (Werner 1967), or drift because of wind-generated water currents (Noble 1972). Alternatively, the abundance and location of larvae may reflect the behaviour and spawning habitat requirements of adults (Storck, Dufford & Clement 1978; Wilkonska 1994; Pope & Willis 1998). Although the specific mechanisms responsible for the distribution patterns of larval fishes in Glen Elder Reservoir were not determined, the observed distributions likely reflect the spawning requirements of adults. For example, logperch, *Pomoxis* spp., *Lepomis* spp, and nearly all of the cyprinids collected in Glen Elder Reservoir spawn in shallow littoral areas (Cross & Collins 1995; Pflieger 1997). Consequently, diversity and densities were highest in nearshore habitats during both years. Although larval gizzard shad were ubiquitous during both years, densities were generally higher in pelagic habitats. Adult gizzard shad generally spawn in coves and other open-water habitats, which may explain their distribution in Glen Elder Reservoir. Similar distributions of gizzard shad have been reported for reservoirs in Illinois (Storck *et al.* 1978), Missouri (Michaletz 1997), Oklahoma (Matthews 1998), and Tennessee (Sammons & Bettoli 2002).

Densities were higher in 1999 than 2000 for nearly all taxa, likely reflecting differences in water level

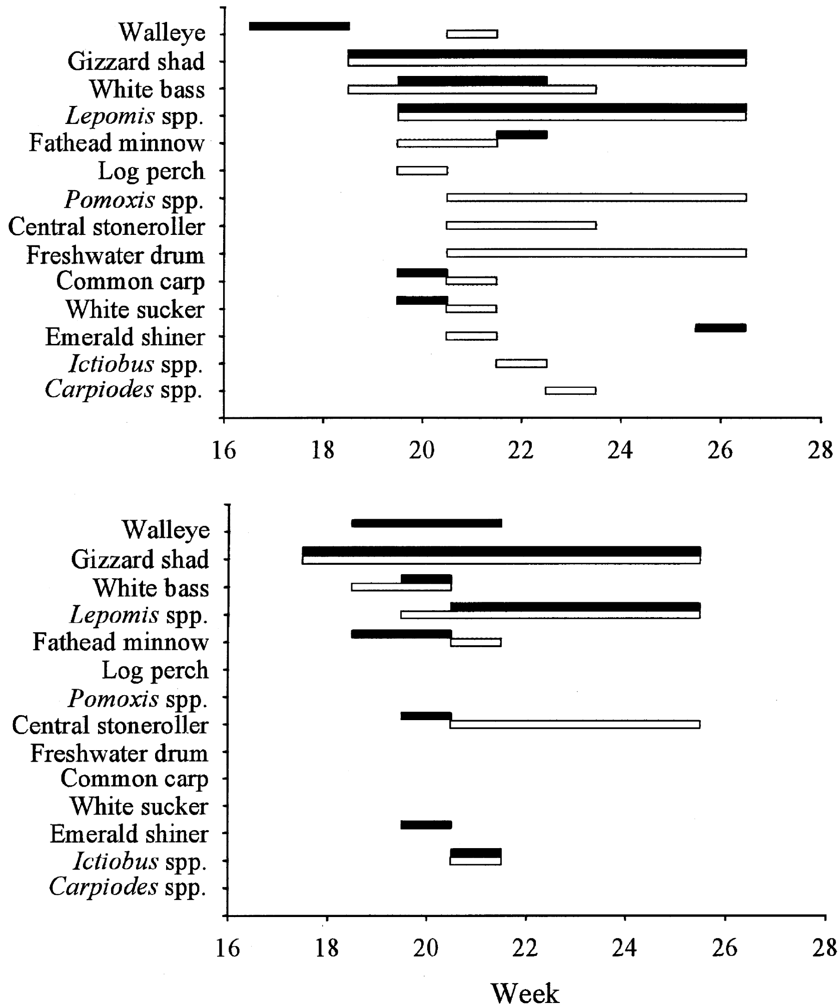

Figure 2. Chronology of larval fishes sampled from nearshore (open bars) and pelagic (solid bars) habitats by week of the year in Glen Elder Reservoir, Kansas, during 1999 and 2000. Although samples were collected during the end of March, the x-axis is truncated to the weeks when larval fishes were collected. Arrows represent the first day of each month.

characteristics. Many species, particularly those that spawn in littoral areas, depend on high water levels during the spring for spawning and production of prey resources for larvae (Martin, Mengel, Novotny & Walburg 1981). During 1999, water levels were 1–2 m higher than during 2000 (Quist 2002) and extensive flooding of terrestrial vegetation was observed. Therefore, spawning conditions and prey resources were probably better for most species in 1999 than during 2000. Michaletz (1997) found that high water levels resulted in extensive spawning activity and high densities of larval gizzard shad in two Missouri reservoirs. Similarly, Mitzner (1991) found that larval *Pomoxis* spp. densities were higher during years with elevated water levels in Rathbun Lake, Iowa.

Most studies on larval fish dynamics have been conducted in natural systems (e.g. Forney 1980; Economou *et al.* 1994; Todd & Davis 1995) and those conducted in reservoirs have generally focused on a single species (e.g. Michaletz 1997; Chick & Van Den Avyle 1999). Consequently, knowledge on interactions (i.e. competition, predation) during the early life history of fish in artificial systems is limited. Chouinard & Bernatchez (1998) stated that interactions among larval fishes have been largely ignored and that the greatest contributions to fitness in most fishes are likely maximised during the early life history. Nearly all larval fishes depend on zooplankton for adequate growth and survival (Miller *et al.* 1988) and the timing of spawning is closely associated to prey production in natural systems (Colby, McNicol & Ryder 1979; Werner & Gilliam 1984). In reservoirs, interactions among larval fishes are especially important because species have little evolutionary history of

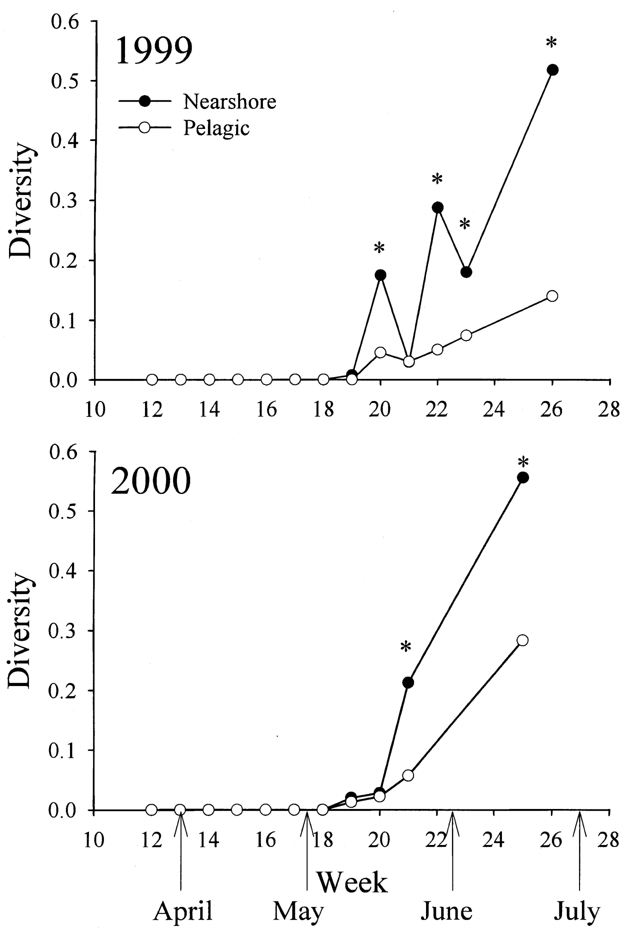

Figure 3. Mean species diversity (Shannon index) of larval fishes sampled from nearshore and pelagic habitats by week of the year in Glen Elder Reservoir, Kansas, during 1999 and 2000. Asterisks represent a significant difference ($P < 0.05$) between habitat types on a given sampling date. Arrows represent the first day of each month.

co-occurrence. Although the primary objective of this study was to describe distribution patterns, the results suggest that interactions among larvae may be high in Glen Elder Reservoir because spatial and temporal overlap was high for most larval taxa. Competitive interactions may be especially important when one species (e.g. gizzard shad) is highly abundant, has a larger body size, or displays aggressive behaviour (Davis & Todd 1992; Todd & Davis 1995; Chouinard & Bernatchez 1998).

Gizzard shad have been successful in reservoirs and may have important effects on other larval fishes. Not only are larval gizzard shad present at high density for extended time periods (Tisa *et al.* 1985; Michaletz 1997; Sammons & Bettoli 2002), but they also commonly reduce zooplankton abundance through top–down (direct predation on zooplankton) or bottom–up processes (grazing on phytoplankton; Stein, DeVries & Dettmers 1995). Garvey & Stein (1998) found that larval gizzard shad reduced survival of larval bluegills in Ohio reservoirs. Similar results were reported in Alabama (Kirk, Davies & Park 1986; Kim 1998), Texas (Guest, Drenner, Threlkeld, Martin & Smith 1990), and Oklahoma (Jenkins 1957). Mallin, Birchfield & Warren-Hicks (1985) found that diet overlap was high between larval gizzard shad and *Lepomis* spp. in a North Carolina reservoir and competitive interactions were most important for small larvae. The only habitat where larval gizzard shad were not collected in their study was extremely shallow littoral areas, suggesting that such areas may provide areas of refuge for species sensitive to the effects of gizzard shad. Thus, the general lack of habitat heterogeneity in nearshore areas of Glen Elder Reservoir, coupled with high larval fish densities and diversity suggests that management activities (e.g. habitat improvement) should focus on nearshore habitats.

Several caveats must be considered when interpreting the results of this study. First, sampling occurred only in the upper portion of the water column. However, over 70% of the fish collected were from the bongo nets (sampled 0–0.5 m from surface), suggesting that most fish were distributed near the surface. Sampling the entire water column requires specialised gears that are not readily available to management agencies. Therefore, the sampling gears used in this study are the gears most likely to be utilised by management personnel. The other potential bias with our data is that fish were collected during the day. A few ($n = 6$) samples were collected at night from sites also sampled during the day to help provide insight on this potential bias. However, larval densities and species composition of night-time samples were nearly identical to those collected during the day. Furthermore, management agency personnel are more likely to sample ichthyoplankton during the day, providing additional support for using a daytime sampling regime.

Predicting year-class strength and monitoring populations is important for successful management of sport and prey species. The objectives of this study did not address whether larval densities index recruitment; however, several studies have shown that larval densities provide an accurate prediction of year-class strength (Rijnsdorp, van Stralen & van der Veer 1985; Uphoff 1989; Sammons & Bettoli 1998). Regardless of whether larval densities index year-class strength, the results of this study provide important information for developing sampling methodologies

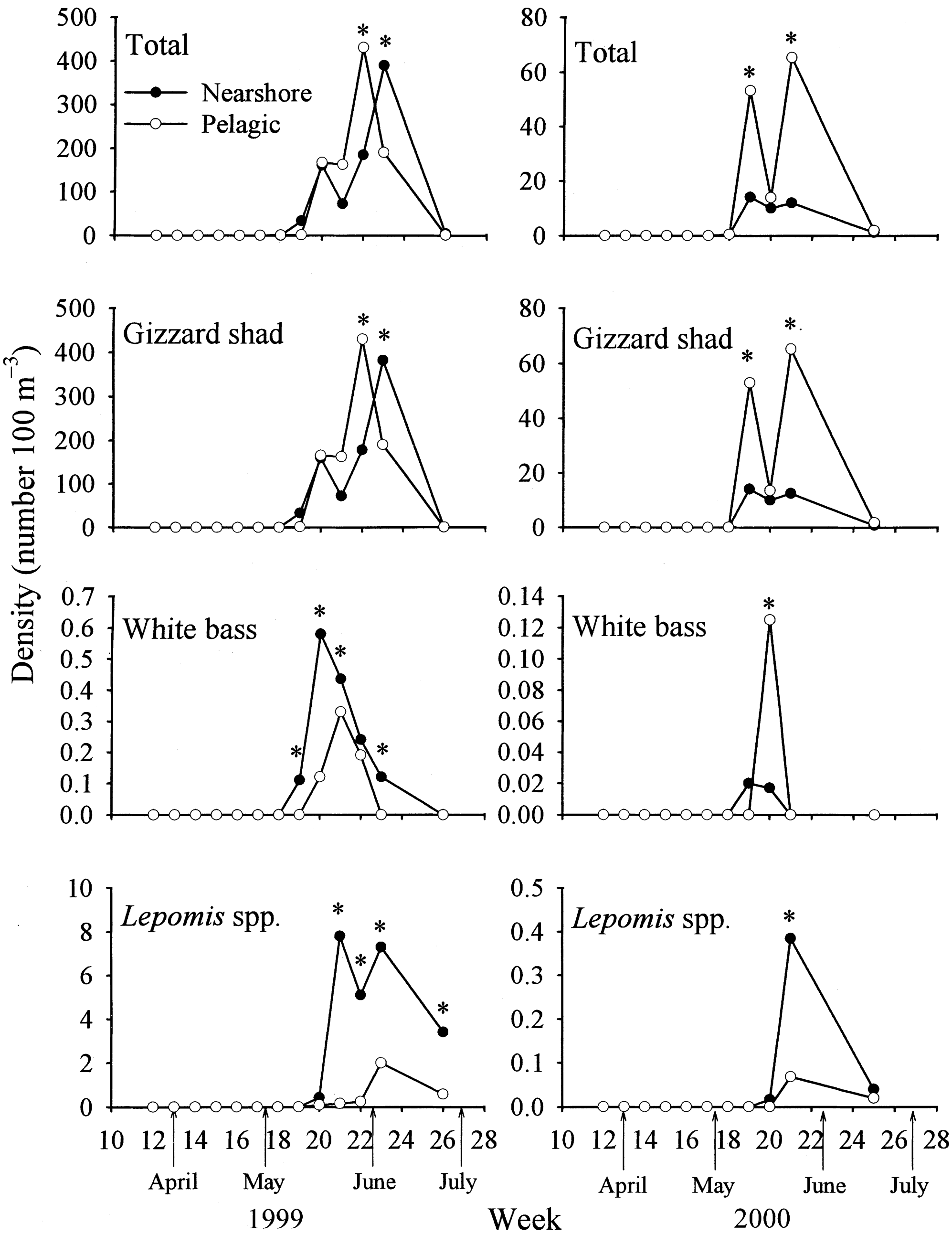

Figure 4. Mean density (number 100 m^{-3}) of larval gizzard shad, white bass, *Lepomis* spp., and all taxa sampled from nearshore and pelagic habitats by week of the year in Glen Elder Reservoir, Kansas, during 1999 and 2000. Asterisks represent a significant difference ($P < 0.05$) between habitat types on a given sampling date. Arrows represent the first day of each month.

related to monitoring and answering research or management questions. Although many studies have found high spatial and temporal variability in larval fish densities (e.g. Storck *et al.* 1978; Scott & Buchanan 1979; Sammons & Bettoli 2002), partial variance analysis indicated that temporal variation was higher than spatial variation for species diversity and densities of most taxa. Because sampling effort is often limited due to logistical constraints, studies designed to monitor larval fish densities and species composition should sample over a long time period. Whether these recommendations are applicable to other systems is unknown, but similar results are likely in reservoirs characteristic of those in the southern Great Plains.

Table 2. Ratio of spatial (sampling date) to temporal variation (habitat type) for species diversity (Shannon index) and densities of larval fishes sampled from Glen Elder Reservoir, Kansas, during 1999 and 2000

Index or taxa	1999	2000
Diversity	0.17	0.18
Walleye	0.09	0.03
Gizzard shad	0.05	0.10
Common carp	0.31	a
White bass	0.19	0.07
Freshwater drum	1.20	a
Logperch	0.12	0.45
Lepomis spp.	0.01	0.01
Pomoxis spp.	2.00	a
Ictiobus spp.	0.01	0.03
Carpiodes spp.	0.12	a
Fathead minnow	0.31	0.02
Emerald shiner	0.35	0.18
Central stoneroller	0.56	0.01
White sucker	0.19	a
Total	0.05	0.10

a, No fish were sampled from either habitat type.
Values above 1.0 indicate that spatial variation was higher than temporal variation, while values below 1.0 indicate that temporal variation was higher than spatial variation. See text for specific methods used to estimate variance components.

Acknowledgments

We thank S. Butler, J. Delp, J. Hart, and C. Schoeneback for assistance in the filed and laboratory. We also thank D. Snyder for confirming larval identifications. Helpful comments on an earlier draft of the manuscript were provided by R. Bernot and two anonymous reviewers. The Kansas Cooperative Fish and Wildlife Research Unit is jointly sponsored by Kansas State University, Division of Biology; Kansas Department of Wildlife and Parks; the U.S. Geological Survey–Biological Resources Division; and the Wildlife Management Institute. Funding was provided by the Kansas Department of Wildlife and Parks through Federal Aid in Sport Fish Restoration, project F-45-R2, and Kansas State University.

References

Amundrud J.R., Faber D.J. & Keast A. (1974) Seasonal succession of free-swimming perciform larvae in Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada* **31,** 1661–1665.

Auer N.A. (1982) *Identification of Larval Fishes of the Great Lakes Basin with Emphasis on the Lake Michigan Drainage*, Special Publication 82-3. Ann Arbor, MI: Great Lakes Fishery Commission, 744 pp.

Barwick D.H. (1978) Food of larval black crappies in relation to electrical power generation, Keowee Reservoir, South Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **32,** 485–489.

Brown D.J. & Coon T.G. (1994) Abundance and assemblage structure of fish larvae in the lower Missouri River and its tributaries. *Transactions of the American Fisheries Society* **123,** 718–732.

Chick J.H. & Van Den Avyle M.J. (1999) Zooplankton variability and larval striped bass foraging: evaluating potential match/mismatch regulation. *Ecological Applications* **9,** 320–334.

Chouinard A. & Bernatchez L. (1998) A study of trophic niche partitioning between larval populations of reproductively isolated whitefish (*Coregonus* sp.) ecotypes. *Journal of Fish Biology* **53,** 1231–1242.

Colby P.J., McNicol R.E. & Ryder R.A. (1979) *Synopsis of Biological Data on the Walleye* Stizostedion v. vitreum (Mitchell 1818). Fisheries Synopsis 119. Rome, Italy: Food and Agriculture Organization of the United Nations, 139 pp.

Copp G.H. (1993) Microhabitat use of fish larvae and 0+ juveniles in a small abandoned channel of the upper River Rhone, France. *Folia Zoologica* **42,** 63–74.

Cross F.B. & Collins J.T. (1995) *Fishes in Kansas*, 2nd edn revised. Lawrence, KS: University of Kansas Natural History Museum, 316 pp.

Davis B.M. & Todd T.N. (1992) Diet overlap in larval lake herring (*Coregonus artedi*) and bloaters (*Coregonus hoyi*). *Polskie Archiwum Hydrobiolgii* **39,** 279–287.

Donald D.B. (1997) Relationship between year-class strength for goldeyes and selected environmental variables during the first year of life. *Transactions of the American Fisheries Society* **126,** 361–368.

Economou A.N., Daoulas C., Psarras T. & Barbieri-Tseliki R. (1994) Freshwater larval fish from Lake Trichonis (Greece). *Journal of Fish Biology* **45,** 17–35.

Floyd K.B., Hoyt R.D. & Timbrook S. (1984) Chronology of appearance and habitat partitioning by stream larval fishes. *Transactions of the American Fisheries Society* **113,** 217–233.

Forney J.L. (1980) Evolution of a management strategy for the walleye in Oneida Lake, New York. *New York Fish and Game Journal* **27,** 105–141.

Garvey, J.E. & Stein R.A. (1998) Competition between larval fishes in reservoirs: the role of relative timing of appearance. *Transactions of the American Fisheries Society* **127,** 1021–1039.

Guest W.C., Drenner R.W., Threlkeld S.T., Martin F.D. & Smith J.D. (1990) Effects of gizzard shad and threadfin shad on zooplankton and young-of-year white crappie production. *Transactions of the American Fisheries Society* **119,** 529–536.

Gulland J.A. (1982) Why do fish numbers vary? *Journal of Theoretical Biology* **97,** 69–75.

Holland L.E. & Sylvester J.R. (1983) Distribution of larval fishes related to potential navigation impacts on the upper Mississippi River, Pool 7. *Transactions of the American Fisheries Society* **112,** 293–301.

Jenkins R.M. (1957) The effect of gizzard shad on the fish population of a small Oklahoma lake. *Transactions of the American Fisheries Society* **85,** 58–74.

Johnston T.A., Gaboury M.N., Janusz R.A. & Janusz L.R. (1995) Larval fish drift in the Valley River, Manitoba: influence of abiotic and biotic factors, and relationships with future year-class strengths. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 2423–2431.

Kim G.W. (1998) *Gizzard shad* Dorosoma cepedianum *Interactions with Age-0 Fishes: The Roles of Competition and Adult Fish Predation on Larval Fish*. M.S. thesis, Auburn, AL: Auburn University, 98 pp.

Kirk J.P., Davies W.D. & Park K. (1986) Response of some members of the fish community to gizzard shad removal from Chambers County public fishing lake, Alabama. *North American Journal of Fisheries Management* **6,** 252–255.

Linlokken A., Kleiven E. & Matzow D. (1991) Population structure, growth and fecundity of perch (*Perca fluviatilis* L.) in an acidified river system in southern Norway. *Hydrobiologia* **220,** 179–188.

Mallin M.A., Birchfield L.J. & Warren-Hicks W. (1985) Food habits and diet overlap of larval *Lepomis* spp. and gizzard shad in a Piedmont reservoir. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **39,** 146–155.

Martin D.D., Mengel L.J., Novotny J.F. & Walburg C.H. (1981) Spring and summer water levels in a Missouri River reservoir: effects on age-0 fish and zooplankton. *Transactions of the American Fisheries Society* **110,** 370–381.

Matthews W.J. (1998) *Patterns in Freshwater Fish Ecology*. New York, NY: Chapman & Hall, 756 pp.

May E.B. & Gassaway C.R. (1967) *A Preliminary Key to the Identification of Larval Fishes of Oklahoma, with Particular Reference to Canton Reservoir, Including a Selected Bibliography*. Oklahoma Fishery Research Laboratory Bulletin 5. Oklahoma City, OK: Oklahoma Department of Wildlife Conservation, 42 pp.

Meador M.R. & Matthews W.J. (1992) Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. *American Midland Naturalist* **127,** 106–114.

Michaletz P.H. (1997) Factors affecting abundance, growth, and survival of age-0 gizzard shad. *Transactions of the American Fisheries Society* **126,** 84–100.

Miller T.J., Crowder L.B., Rice J.A. & Marschall E.A. (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 1657–1670.

Milliken G.A. & Johnson D.E. (1992) *Analysis of Messy Data, Volume 1: Designed Experiments*. New York, NY: Chapman & Hall, 473 pp.

Mitzner L. (1991) Effect of environmental variables upon crappie young, year-class strength, and the sport fishery. *North American Journal of Fisheries Management* **11,** 534–542.

Ney J.J. (1999) Practical use of biological statistics. In: C.C. Kohler & W.A. Hubert (eds) *Inland Fisheries Management in North America*, 2nd edn. Bethesda, MD: American Fisheries Society, pp. 167–191.

Noble R.L. (1972) Mortality rates of walleye fry in a bay of Oneida Lake, New York. *Transactions of the American Fisheries Society* **102,** 720–723.

Parker B.R. & Franzin W.G. (1991) Reproductive biology of the quillback, *Carpiodes cyprinus*, in a small prairie river. *Canadian Journal of Zoology* **69,** 2133–2139.

Pepin P., Dower J.F. & Davidson F.J.M. (2003) A spatially-explicit study of prey–predator interactions in larval fish: assessing the influence of food and predator abundance on larval growth and survival. *Fisheries Oceanography* **12,** 19–33.

Pflieger W.L. (1997) *The Fishes of Missouri*, revised edition. Jefferson City, MO: Missouri Department of Conservation, 372 pp.

Pope K.L. & Willis D.W. (1998) Larval black crappie distribution: implications for sampling impoundments and natural lakes. *North American Journal of Fisheries Management* **18,** 470–474.

Post J.R. & McQueen D.J. (1988) Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predation? *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 1820–1826.

Quist M.C. (2002) *Abiotic Factors and Species Interactions that Influence Recruitment of Walleyes in Kansas Reservoirs*. PhD dissertation, Manhattan, KS: Kansas State University, 97 pp.

Rettig J.E. (1998) Variation in species composition of the larval assemblage in four southwest Michigan lakes: using allozyme analysis to identify larval sunfish. *Transactions of the American Fisheries Society* **127,** 661–668.

Rijnsdorp A.D., van Stralen M. & van der Veer H.W. (1985) Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. *Transactions of the American Fisheries Society* **114,** 461–470.

Sammons S.M. & Bettoli P.W. (1998) Larval sampling as a fisheries management tool: early detection of year-class strength. *North American Journal of Fisheries Management* **18,** 137–143.

Sammons S.M. & Bettoli P.W. (2002) Spatial and diel variation in distribution of limnetic larvae of fishes in a

Tennessee reservoir. *Journal of Freshwater Ecology* **17,** 45–53.

Sammons S.M., Bettoli P.W. & Fiss F.C. (1998) Effect of threadfin shad density on production of threadfin shad and gizzard shad larvae in a Tennessee reservoir. *Environmental Biology of Fishes* **53,** 65–73.

SAS Institute (1996) *SAS/STAT User's Guide for Personal Computers*, Version 6. Cary, NC: SAS Institute 1, 686 pp.

Scott E.M. Jr. & Buchanan J.P. (1979) Larval fish populations in Little Bear Creek Reservoir during the first three years of impoundment. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **33,** 660–672.

Stein R.A., DeVries D.R. & Dettmers J.M. (1995) Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 2518–2526.

Storck T.W., Dufford D.W. & Clement K.T. (1978) The distribution of limnetic fish larvae in a flood control reservoir in central Illinois. *Transactions of the American Fisheries Society* **107,** 419–424.

Stratoudakis Y., Bernal M., Borchers D.L. & Borges M.F. (2003) Changes in the distribution of sardine eggs and larvae off Portugal, 1985–2000. *Fisheries Oceanography* **12,** 49–60.

Taber C.A. (1969) *The Distribution and Identification of Larval Fishes in the Buncombe Creek Arm of Lake Texoma with Observations on Spawning Habits and Relative Abundance*. PhD dissertation, Norman, OK: University of Oklahoma, 120 pp.

Tisa M.S., Ney J.J. & Whitehurst D.K. (1985) Spatial and temporal distribution of larval alewives and gizzard shad in a Virginia reservoir. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* **39,** 65–73.

Todd T.N. & Davis B.M. (1995) Effects of fish density and relative abundance on competition between larval lake herring and lake whitefish for zooplankton. *Archivum für Hydrobiologie Special Issues in Advanced Limnology* **46,** 163–171.

Uphoff J.H. (1989) Environmental effects on survival of eggs, larvae, and juveniles of striped bass in the Choptank River, Maryland. *Transactions of the American Fisheries Society* **118,** 251–263.

Wang N. & Eckmann R. (1994) Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. *Hydrobiologia* **277,** 135–143.

Werner R.G. (1967) Intralacustrine movements of bluegill fry in Crane Lake, Indiana. *Transactions of the American Fisheries Society* **96,** 416–420.

Werner E.E. & Gilliam J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15,** 393–425.

Wilkonska H. (1994) Changes in the efficiency of natural reproduction and survival of fish larvae in heated Konin lakes. *Archives of Polish Fisheries* **2,** 285–299.