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Exploring spatial distributions of larval yellow perch *Perca flavescens*, bluegill *Lepomis macrochirus* and their prey in relation to wind

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The objectives of the present study were to determine if spatial differences existed between zooplankton, larval yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus* (<13 mm total length, L_T) in Pelican Lake (332 ha), NE, U.S.A. It was hypothesized that wind could act as a transport mechanism for larval fishes in this shallow lake, because strong winds are common at this geographic location. Potential spatial differences were explored, relating to zooplankton densities, size structure and densities of larval *P. flavescens* and *L. macrochirus*. Density differences (east *v.* west side of the lake) were detected for small- (two occasions), medium- (two occasions) and large-sized (one occasion) *L. macrochirus* larvae. No density differences were detected for small *P. flavescens* larvae; however, densities of medium- and large-sized *P. flavescens* were each higher on the west side of the lake on two occasions. There was no evidence that larval *P. flavescens* and *L. macrochirus* distributions were related to wind because they were not associated with large wind events. Likewise, large wind event days did not result in any detectable spatial differences of larval *P. flavescens* and *L. macrochirus* densities. There appeared to be no spatial mismatch between larval densities and associated prey in the years examined. Thus, wind was not apparently an influential mechanism for zooplankton and larval *P. flavescens* and *L. macrochirus* transport within Pelican Lake, and spatial differences in density may instead be related to vegetation and habitat complexities or spawning locations within this shallow lake.

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Key words: habitat; larval fishes; larval transport; match–mismatch; zooplankton.

INTRODUCTION

The recruitment process in fishes is often complex and arguably one of the least understood dynamic rate functions (*i.e.* recruitment, growth and mortality) in fisheries science. Factors thought to influence recruitment of fishes operate on several spatial and temporal scales and include prey availability (Welker *et al.*, 1994), predation (Miller *et al.*, 1988; Santucci & Wahl, 2003), environmental conditions such as wind, temperature and precipitation (Pope *et al.*, 1996; Ward *et al.*, 2004) and the timing of reproduction (Beard, 1982; Cargnelli & Gross, 1996; Garvey *et al.*, 2002), among

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others. Isolating which factors are most important remains difficult, because many of these variables probably interact and affect recruitment differentially, depending on species, habitat and developmental stage (*e.g.* egg, larva and juvenile).

Wind direction and velocity, among the environmental variables used to explain recruitment variability, have been negatively related to the survival of fish eggs and larvae (Clady & Hutchinson, 1975; Clady, 1976; Kallemeyn, 1987; Ward *et al.*, 2004). High winds causing wind-induced waves and currents directly dislodge and destroy fish eggs by physical destruction on hard substrata (Clady & Hutchinson, 1975; Roseman *et al.*, 2001). In addition, high winds can affect temperature regimes experienced by eggs and pro-larvae before the fishes become limnetic and negatively influence survival in the early stages of development (Clady, 1976). While previous studies speculated that wind may act as a transport mechanism for fish eggs, few studies have attempted to examine spatial differences in larval fishes and relate them to wind direction and velocities.

Wind has been negatively related to larval abundances in several species of fishes in the mid-west of the U.S.A., most probably because high sustained winds are common and little protection from these wind events is provided in this geographic region. Winds in this region may induce strong waves and currents that potentially dislodge eggs or cause transportation of larvae to unfavourable temperature regimes (Mitzner, 1991; Ward *et al.*, 2004; Phelps *et al.*, 2008). Recruitment for some species may be established during the early stages of egg and larval development in this region (Anderson *et al.*, 1998; Isermann & Willis, 2008). Although wind has been negatively related to larval abundances and adult year class strength and is considered an important factor that may regulate recruitment for some fishes in the mid-west (Mitzner, 1991; Ward *et al.*, 2004; Phelps *et al.*, 2008), the mechanism involved in this process has not been identified. Therefore, further examination in exploring relationships between wind and early life stages of fishes is warranted.

Most larval fishes are dependent on zooplankton as a food source during the early stages of life. Zooplankton densities may vary spatially and temporally, and at low prey densities growth and mortality of larval fishes can be negatively affected (Puvanendran & Brown, 1999; Seljeset *et al.*, 2010). Several authors suggested that at low zooplankton densities, larval fish survival is suppressed due to starvation (Werner & Blaxter, 1980; Eldridge *et al.*, 1981; Li & Mathias, 1982; Dettmers *et al.*, 2003); this prey density threshold is, however, based on a minimum of 10% larval survival in the laboratory (Saksena & Houde, 1972). Tsai (1991) argued, however, that the density threshold is arbitrarily assigned and that some fishes within a population may require higher or lower densities than 100 organisms l^{-1} . As a result, it remains difficult to determine the lower threshold required for the recruitment of larval fishes in relation to prey availability, but in general, survival is positively related to prey availability (Tsai, 1991; Welker *et al.*, 1994).

For larval fishes to successfully recruit to the next life stage, it is critical that adequate prey is available and that both predator and prey overlap spatially and temporally. Much research focused on the temporal overlap of these resources (*e.g.* match–mismatch hypothesis; Cushing, 1975, 1990). More recent work has incorporated the dimension of space into the match–mismatch framework (Chick & Van Den Avyle, 1999; Romare *et al.*, 2003; Beauchamp *et al.*, 2004) in which both space and time are realized as important variables while relating zooplankton availability to larval fish growth and survival to better understand the recruitment process in fishes.

Both yellow perch *Perca flavescens* (Mitchill 1814) and bluegill *Lepomis macrochirus* (Rafinesque 1819) exhibit similar ontogenetic habitat shifts, where eggs are deposited within the littoral zone and upon hatching the larvae distribute across the limnetic zone (Werner, 1967; Whiteside *et al.*, 1985). While in the limnetic zone, both species depend on zooplankton to grow and ultimately survive to the next life stage (Welker *et al.*, 1994; Graeb *et al.*, 2004). Therefore, it is important to more fully understand the spatial distribution of both *P. flavescens* and *L. macrochirus* larvae and their associated prey as a potential spatial mismatch may result in lower survivorship at the larval stage.

Jolley *et al.* (2010) explored temporal match–mismatch with prey for larval *P. flavescens* and *L. macrochirus* in Pelican Lake. These authors did not, however, examine spatial overlap with prey. Therefore, the objectives were to determine if spatial differences existed in density, size and prey of larval *P. flavescens* and *L. macrochirus* in Pelican Lake, NE, U.S.A. from 2004 to 2008. If differences in spatial larval density existed, then those differences were related to wind effects under the assumption that wind could act as a transport mechanism in this shallow, windswept lake. If wind does act as a transport mechanism, it may cause larval fish densities to be higher in areas with lower densities of prey, resulting in slower growth and ultimately starvation. Larval fishes may be transported similarly to their prey; a complete spatial overlap would, however, assume that the point of origin prior to a wind event for both fishes and zooplankton is the same. Differences in spatial larval fish sizes were examined to potentially elucidate if smaller larvae are more likely to be transported by wind-induced waves.

MATERIALS AND METHODS

Pelican Lake is a 332 ha, shallow (mean depth = 1.3 m) natural lake in the Sandhills region of north central Nebraska, U.S.A., within the Valentine National Wildlife Refuge (Fig. 1). Total vegetation coverage during peak foliage (emergent and submergent combined) ranged from 40 to 52% during midsummer in 2004 and 2005 (Jolley, 2009). Emergent vegetation is mainly concentrated along the shoreline extending upward of 30–40 m into the lake, with several isolated patches in the main basin of the lake. Submergent vegetation primarily exists on the northern portion of the main basin due to a shallow depth contour and in most cases does not reach the water surface. This region also experiences high sustained wind velocities (some daily means >26.3 km h⁻¹, with prevailing winds from the north-west) throughout much of the year, but especially during the spring (Dewey, 1977; Wilhite & Hubbard, 1989). Pelican Lake has a north-west to south-east orientation, deviating c. 25° from a straight east to west position (Fig. 1).

Larval fishes were collected every 10 days from late April to late August or early September at Pelican Lake from 2004 to 2008. Recently hatched larval *P. flavescens* and *L. macrochirus* (total length, $L_T \leq 13$ mm) were sampled and indexed using a surface trawl with a 0.76 m diameter opening and 1000 µm mesh (bar measure) towed in large ellipses. Trawl duration was c. 3–5 min at an estimated speed of 1.75 m s⁻¹. The lake was divided into 16 quadrats (each c. 20.75 ha; eight east and eight west) and 10 of those quadrats were randomly chosen and trawled on each occasion. The amount of water volume trawled was calculated using a flowmeter (Ocean Test Equipment, Inc.; www.oceantestequip.com) in the mouth of the trawl. All larval samples were preserved in 70% ethanol and returned to the laboratory for identification and further analysis. All field data collection occurred during daylight hours.

Larval fishes were identified to genus using identification keys (Auer, 1982; Holland-Bartels *et al.*, 1990). All larvae were enumerated and up to 200 randomly chosen fish per sample for each species were measured (L_T) from each quadrat sampled. Larvae of $L_T \leq 13$ mm were

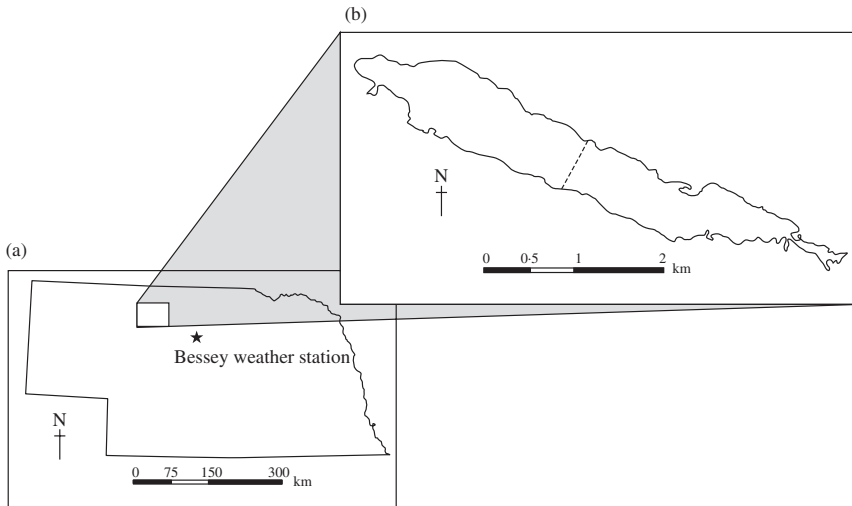


FIG. 1. Nebraska, U.S.A., and location of (a) the Bessey weather station (★) and (b) Pelican Lake (-----, dividing line between the east and west basins of the lake).

used to calculate larval abundances; fishes of $L_T > 13$ mm were considered juveniles. Garvey *et al.* (2002) characterized *L. macrochirus* larvae as those < 15 mm L_T . *Lepomis macrochirus* generally begin a migration to littoral habitats between 12 and 20 mm L_T (Werner & Hall, 1988; Garvey *et al.*, 1998; Santucci & Wahl, 2003) and *P. flavescens* begin migrating between 8 and 40 mm L_T (Urho, 1996).

Zooplankton were collected at the time of each trawl sample in Pelican Lake using a 2 m long tube sampler (Rabeni, 1996). Two zooplankton samples were taken at each quadrat and filtered through a 65 μ m mesh net, stored in 90% ethanol and then processed separately. Zooplankton were enumerated and identified to family for cladocerans (*i.e.* Bosminidae, Chydoridae and Daphnidae), and as cyclopoid or calanoid copepods and copepod nauplii. Each sample was diluted with water to a measured volume of 30 ml. Three sub-samples were taken with a 5 ml Hensen-Stempel pipette and placed in a Ward counting wheel (www.wildco.com). Zooplankton were enumerated within each sub-sample and the total number of zooplankton of each taxon in a sample was calculated by dividing the number of organisms counted by the proportion of the sample volume processed. Density was calculated by multiplying the number of zooplankton of each taxon by the volume of the water filtered with the tube sampler.

The lake was bisected into two basins in a west to east fashion, yielding the longest fetch, so spatial differences of larval densities attributed to wind effects were more likely to be detected. Wind direction and intensity were obtained from the nearest remote automated weather station (Bessey recreation complex, Nebraska 84 km south-east of the lake; Fig. 1) that contained the most consistent data throughout the duration of the study (National Oceanic and Atmospheric Administration; www.raws.dri.edu). A closer weather station (Miller Field, Valentine, Nebraska), within 40 km of the lake, provided an incomplete weather database; wind direction was, however, similar and wind speeds over the course of the study (2004–2008) at both weather stations were highly correlated ($r = 0.88$). A wind index (I_W) modified from George & Edwards (1976) was used to characterize and incorporate information on wind intensity, direction and changes in direction, which assumes winds more immediate to the sampling event have more influence on the distribution of larval fishes. As such, wind speeds closer to the sampling event were more heavily weighted: $I_W = (V_1 + 1 \times 2^{-1} V_2 + 1 \times 4^{-1} V_3 + 1 \times 8^{-1} V_4 + 1 \times 16^{-1} V_5 + 1 \times 32^{-1} V_6) (D_1 + 1 \times 2^{-1} D_2 + 1 \times 4^{-1} D_3 + 1 \times 8^{-1} D_4 + 1 \times 16^{-1} D_5 + 1 \times 32^{-1} D_6)$, where V_i is the wind velocity means for two consecutive hours with V_1 being the 2 h immediately prior to the sampling event and V_2 relates to the two consecutive hours prior to V_1 time set, *etc.* This allowed a quantitative estimate of wind

events occurring over a 12 h period (*i.e.* six time sets \times 2 h blocks = 12 h time period prior to sampling). In addition to examining wind events in a 12 h period prior to sampling, an I_W for 4, 6 and 8 h blocks was calculated, resulting in 24, 36 and 48 h time periods prior to sampling. Four different time periods were estimated because of the uncertainty at which time wind would no longer affect the movement of larval fishes. Wind direction (D) was incorporated into I_D which assumes winds not within 50 cardinal degrees of the maximum fetch (290° , 110°) of the lake would probably not influence the movement of larval fishes between the east and west sides of the lake. A value of -1 was assigned to directions corresponding to those within 50 cardinal degrees of the east side of the lake's maximum fetch (*i.e.* 85 – 135°) and a value of $+1$ was assigned similarly to those within 50° of the west side of the lake's maximum fetch (*i.e.* 265 – 315° ; George & Edwards, 1976). Larger negative values would correspond to high wind velocities from the south-east and large positive values, higher wind velocities from the north-west. All other directions were assigned a value of zero. Therefore, D_i is the mean wind direction value for those same hour periods as described for the wind velocity estimates.

An ANOVA was used to detect differences in larval densities (number 100 m^{-3}) and zooplankton densities according to the taxa Cladocera and Copepoda (number l^{-1}) between east and west sides of the lake. Larval *P. flavescens* and *L. macrochirus* densities were analysed according to three size classes: small (<7 mm, L_T), medium (≥ 7 and <10 mm, L_T) and large (≥ 10 and <13 mm, L_T). Size classes were chosen at a level that would maximize the precision in detail within the data set and minimize information lost due to inadequate sample sizes. Significant differences were assessed by adjusting alpha by the number of sampling dates (*i.e.* a sampling occasion where at least one larval fish was captured) each year for each species to account for the lack of independence among samples (*i.e.* 0.05 per number of sampling dates each year for each species; Allen & DeVries, 1993). Due to the non-constant variability in the dependent variables, a mixed model was used (PROC MIXED; SAS Institute Inc.; www.sas.com). The maximum likelihood method was used because it allowed for unbalanced designs (*e.g.* more quadrants sampled on one side of the lake; Littell *et al.*, 1996). The proportion of larval *P. flavescens* and *L. macrochirus* size classes, based on 1 mm L_T groups, captured on the east and west side of the lake, was evaluated for each year sampled. Data were analysed using a graphical approach and were limited to years when >300 larvae were sampled and size bins contained a total sample size of >9 (D. F. Markle, unpubl. data). This approach potentially allows determination of the area of the lake in which most spawning occurs. For example, if one side of the lake contains a significant portion of smaller larvae than the other, it may suggest more spawning occurred there resulting in a higher accumulation of smaller sized larvae. Zooplankton data were analysed according to crustacean group (*i.e.* Cladocera and Copepoda) as these groups are most important during the early life stages of both *L. macrochirus* and *P. flavescens* (Welker *et al.*, 1994; Graeb *et al.*, 2004). Larval *L. macrochirus*, *P. flavescens* and zooplankton densities were $\log_{10}(x + 1)$ transformed to better approximate normality.

To further evaluate the role of wind influencing the spatial distribution of larvae and zooplankton prey in Pelican Lake, a binary response code was given to each sampling date representing the side of the lake with a larger point estimate of larval fishes according to size class and zooplankton taxa Cladocera and Copepoda. A larger point estimate of larval fishes or prey on the east side of the lake was given a value of one and conversely a value of zero represented a larger point estimate on the west side of the lake. Logistic regression (PROC LOGISTIC; SAS Institute Inc.) was then used to determine if I_W values (*i.e.* independent variable) could predict the probability of more larval fishes being distributed on the east or west sides of the lake. Separate models were evaluated for each larval size class for each species and different time periods prior to sampling (*i.e.* 12, 24, 36 and 48 h). An alpha of 0.05 was used to determine significant differences.

RESULTS

During the 2004–2008 sampling seasons, 48 h prior to sampling larval fishes, primary wind direction was predominantly from the south (11/51 sampling events),

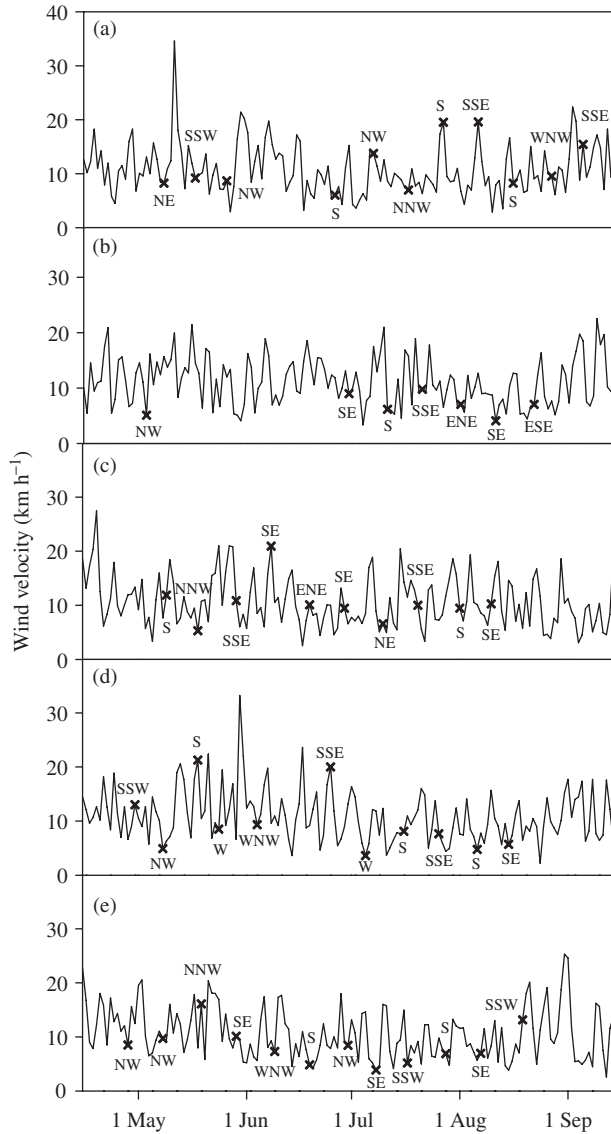


FIG. 2. Mean daily wind velocities recorded at the Bessey weather station in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008 (x, sampling dates). Letters correspond to dominant cardinal wind direction 48 h prior to sampling event.

followed by the south-east (9/51 sampling events; Fig. 2). Daily sustained wind velocities ranged from 2.2 to 34.6 km h⁻¹ (Fig. 2). Mean daily wind velocities over the duration of the sampling season ranged between 9.9 and 10.9 km h⁻¹.

The highest observed mean density of all size classes combined for larval *P. flavescens* recorded on the east side of the lake was 1307 m⁻³ on 29 May 2008, and the highest density observed on the west side of the lake was 1107 m⁻³ on 9 June 2008, in the years examined. There was no significant difference (ANOVA,

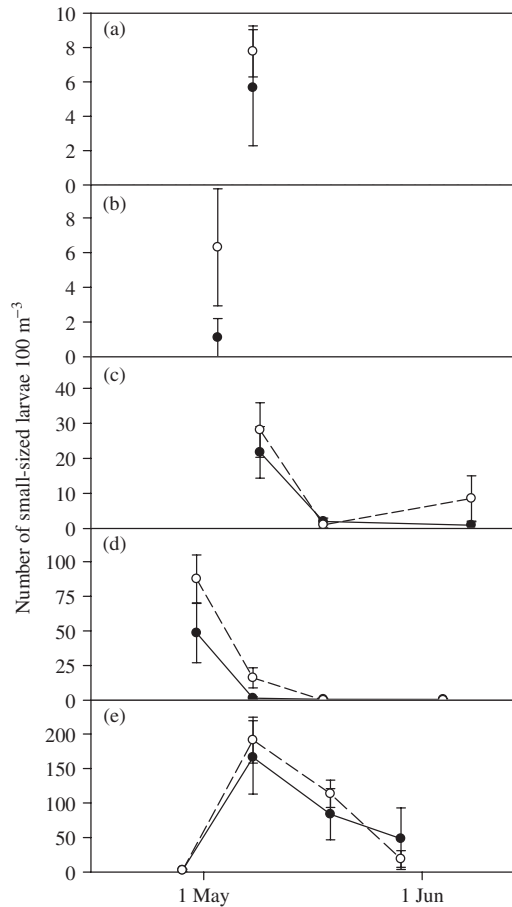


FIG. 3. Mean \pm S.E. density of small-sized (<7 mm total length, L_T) larval *Perca flavescens* on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008.

$n = 13$ sampling dates, $P > 0.05$) in spatial densities of small-sized *P. flavescens* larvae during 2004–2008 (Fig. 3). Medium-sized *P. flavescens* larval density was significantly higher on the west side of Pelican Lake on 18 May 2006 (ANOVA, d.f. = 1,8, $P < 0.01$) and on 8 May 2008 (ANOVA, d.f. = 1,7, $P < 0.01$) compared to the east side of the lake (Fig. 4). Densities of large-sized *P. flavescens* larvae were greatest on the west side of the lake on 18 May 2006 (ANOVA, d.f. = 1,8, $P < 0.01$) and on 9 June 2008 (ANOVA, d.f. = 1,8, $P < 0.01$) compared to the east side of the lake (Fig. 5). Significant larval *P. flavescens* spatial density differences were not detected on any other sampling dates for medium- and large-sized larvae (ANOVA, $n = 11$ sampling dates each, $P > 0.05$; Figs 4 and 5).

Total larval *L. macrochirus* densities (*i.e.* all size classes combined) were highest on the east side of the lake on 20 July 2006 at 2055 m^{-3} and highest on the west side at 3290 m^{-3} on 17 July 2008 from 2004 to 2008. A higher density of small-sized larval *L. macrochirus* was observed on the west side of the lake on 8 August 2004 (ANOVA, d.f. = 1,8, $P < 0.01$) and 16 July 2007 (ANOVA, d.f. = 1,8, $P < 0.01$)

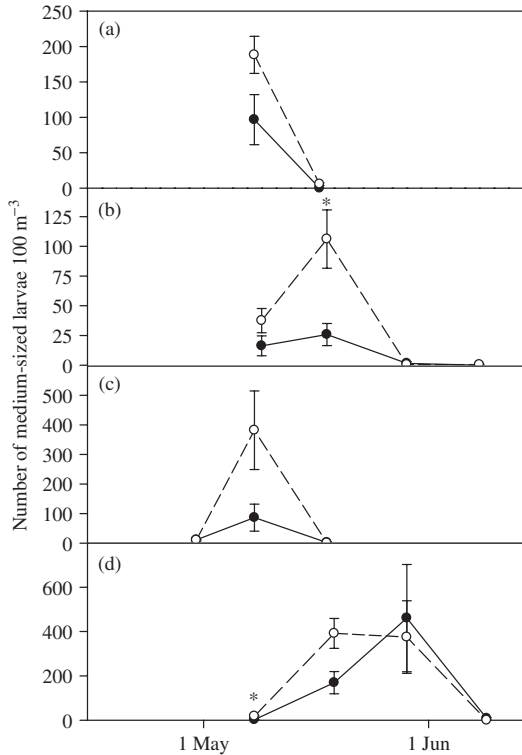


FIG. 4. Mean \pm s.e. density of medium-sized (≥ 7 and < 10 mm total length, L_T) larval *Perca flavescens* on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2006, (c) 2007 and (d) 2008. *, dates on which significant differences ($P < 0.05$) were observed between east and west sides of the lake.

in comparison with the east side of the lake (Fig. 6). The west side of the lake compared to the east side contained a significantly higher density of medium-sized *L. macrochirus* on 16 August 2004 (ANOVA, d.f. = 1,8, $P < 0.01$) and 1 August 2006 (ANOVA, d.f. = 1,8, $P < 0.001$; Fig. 7). Large-sized *L. macrochirus* larvae were significantly higher in abundance on the west side of the lake on 11 August 2005 (ANOVA, d.f. = 1,8, $P < 0.01$) compared to the east side of the lake (Fig. 8). Significant larval *L. macrochirus* spatial density differences were not detected (ANOVA, $P > 0.05$) on any other sampling dates for small- ($n = 25$), medium- ($n = 30$) and large-sized larvae ($n = 30$; Figs 6 to 8).

A higher proportion ($> 68\%$) of small (< 7 mm L_T) *P. flavescens* larvae was located on the west side of Pelican Lake compared to the east side of the lake in 2007. In addition, the west side of the lake compared to the east side contained a higher proportion of larger *P. flavescens* (> 10 mm L_T) in 2004 ($> 71\%$) and 2006 ($> 85\%$; Fig. 9). Due to an inadequate sample size, spatial differences in the proportion of *P. flavescens* larvae lengths could not be evaluated for 2005. *Lepomis macrochirus* larvae did not exhibit any distinct relationships between the proportion of larvae and the associated lengths distributed between east and west sides of Pelican Lake from 2004 to 2008 (Fig. 10). Copepod density ranged from 6 to 237 l^{-1} on the east side and 5 to 283 l^{-1} on the west side of the lake. Copepod density was highest

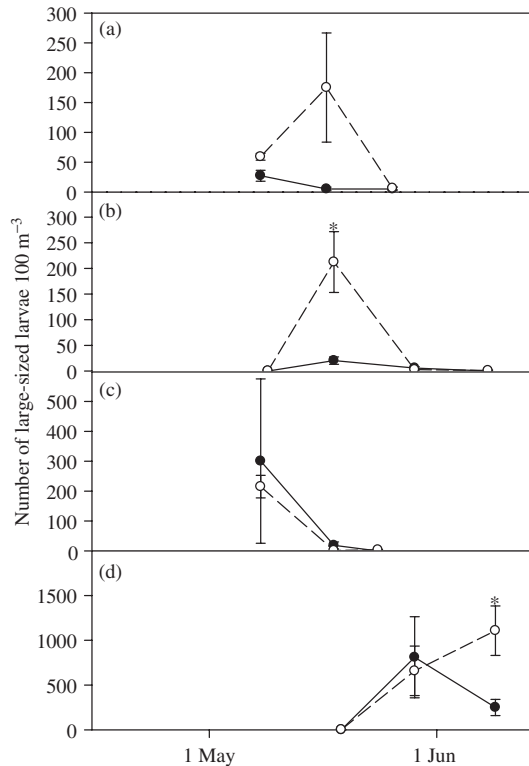


FIG. 5. Mean \pm S.E. density of large-sized (≥ 10 and < 13 mm total length, L_T) larval *Perca flavescens* on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2006, (c) 2007 and (d) 2008. *, dates on which significant differences ($P < 0.05$) were observed between east and west sides of the lake.

on the west side of the lake on 27 August 2004 (ANOVA, d.f. = 1,8, $P < 0.01$) and 20 July 2006 (ANOVA, d.f. = 1,8, $P < 0.01$), but higher on the east side of the lake on 11 August 2005 (ANOVA, d.f. = 1,8, $P < 0.01$; Fig. 11). Copepod density did not differ between the east and west sides of the lake on any other sampling date (ANOVA, $n = 70$, $P > 0.05$). Cladoceran densities were 3–3837 l^{-1} on the east side of the lake and 3–3511 l^{-1} on the west side of the lake. There were no significant spatial differences in cladoceran densities during 2004–2008 in Pelican Lake (ANOVA, $n = 73$, $P > 0.05$; Fig. 12).

There were no significant relationships ($P > 0.1$) between wind index values at 12, 24, 36 or 48 h before sampling and small-, medium- and large-sized larval *P. flavescens* and *L. macrochirus* densities. Similarly, no relationship existed ($P > 0.1$) between I_W values and copepod and cladoceran densities during the 12, 24, 36 or 48 h period prior to sampling.

DISCUSSION

Spatial distribution patterns of larval fishes and their zooplankton prey in this small, vegetated, shallow lake were not associated with wind velocity or direction.

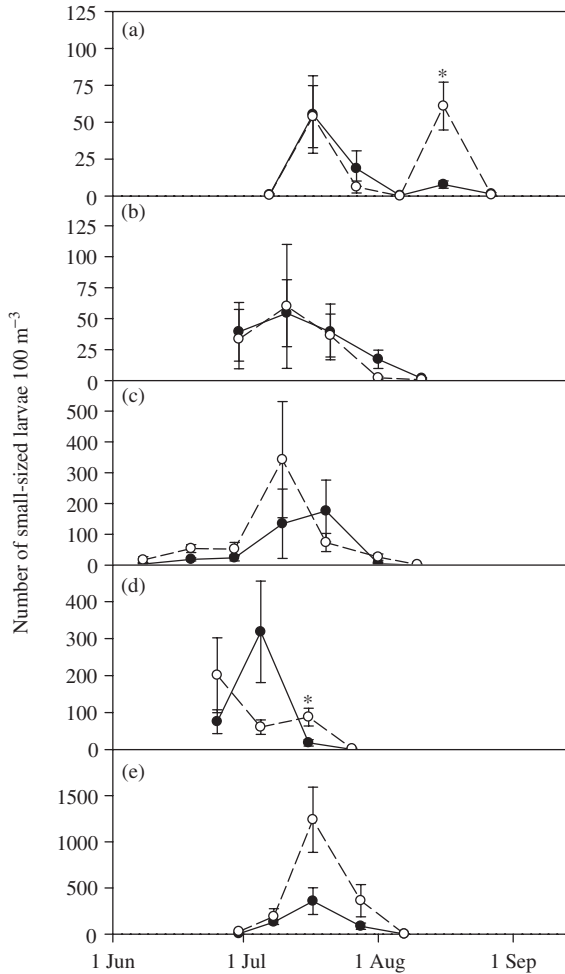


FIG. 6. Mean \pm s.e. density of small-sized (<7 mm total length, L_T) larval *Lepomis macrochirus* on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008. *, dates on which significant differences ($P < 0.05$) were observed between east and west sides of the lake.

Other studies that have documented larval fish transportation in relation to wind and current advectations were in systems much larger than Pelican Lake (Dettmers *et al.*, 2005; Auer & Oyadomari, 2008; McKenna *et al.*, 2008), with undoubtedly more complex wind-induced currents compared to the system in the present study. Most studies documenting the influence of wind as a transport mechanism in small lakes (<500 ha) have focused on phytoplankton (George & Edwards, 1976; George & Heaney, 1978) and few studies have exclusively focused on larval fishes (Coles, 1981). It was assumed that larval fishes would drift downwind in Pelican Lake, especially as wind velocities increased, because newly hatched larval *P. flavescens* cannot swim against water currents (Houde, 1969). George & Edwards (1976) employed wind drogues in a small reservoir and found that the drogues drifted downwind at depths of 0.5 and 1.0 m (*i.e.* typically where larval fishes are distributed).

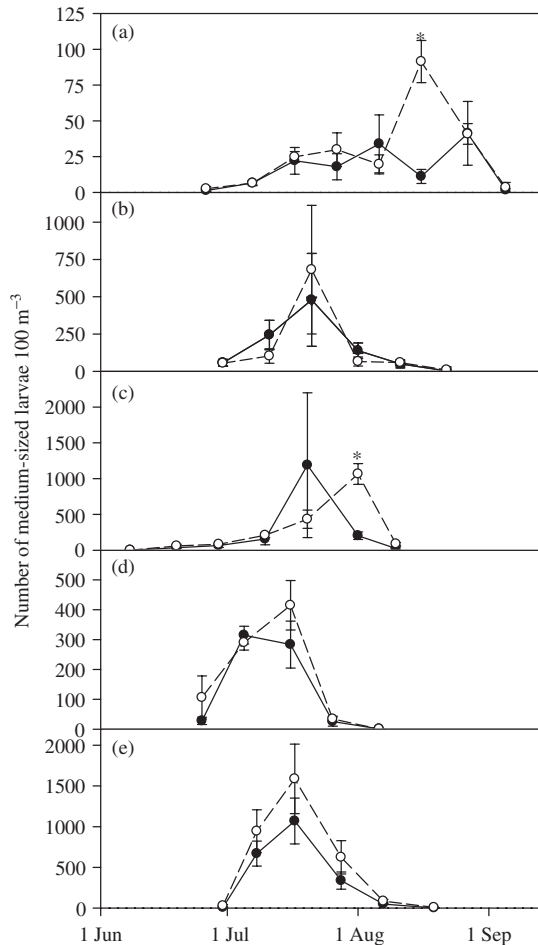


FIG. 7. Mean \pm S.E. density of medium-sized (≥ 7 and < 10 mm total length, L_T) larval *Lepomis macrochirus* on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008. *, dates on which significant differences ($P < 0.05$) were observed between east and west sides of the lake.

One potential reason for the lack of a relationship between wind and the spatial distribution of larval fishes in Pelican Lake could be related to the multiple emergent vegetation patches (mainly *Scirpus* spp.) interspersed across the main basin of the lake (Paukert & Willis, 2002). Markle *et al.* (2009) speculated that larval suckers [shortnose sucker *Chasmistes brevirostris* Cope 1879 and Lost River sucker *Deltistes luxatus* (Cope 1879)] accumulated in emergent vegetation and thus were less subject to predation. They further suggested that the retention of larval fishes may be related to habitat variables such as vegetation, among others, in a large Oregon lake. If emergent vegetation acts as a buffer, inhibiting larval fish movement, spatial differences of larval fishes would not be detected in relation to wind in Pelican Lake, as these differences could be compromised by vegetation. Spatial distributions of larval fishes could potentially still be related to wind in shallow lakes where the

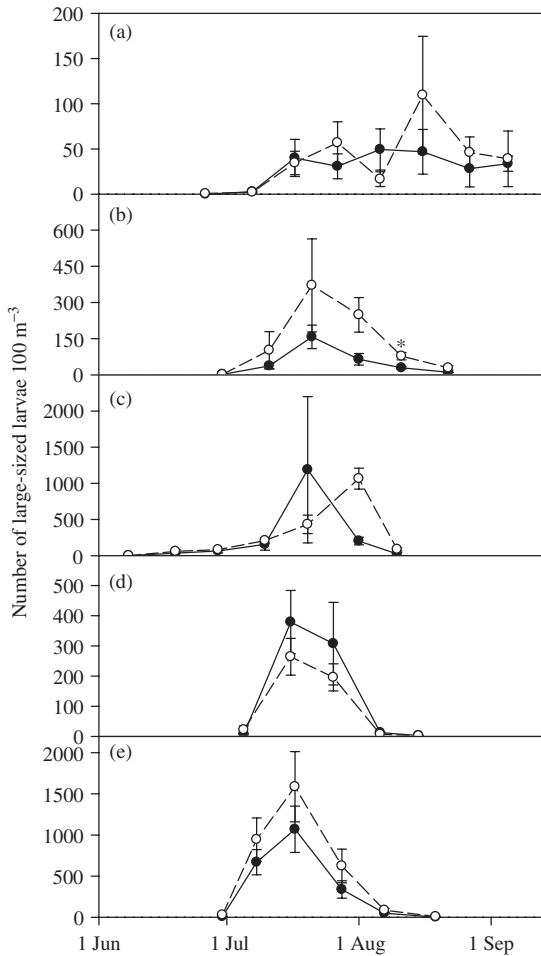


FIG. 8. Mean \pm s.e. density of large-sized (≥ 10 and < 13 mm total length, L_T) larval *Lepomis macrochirus* on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008. *, dates on which significant differences ($P < 0.05$) were observed between east and west sides of the lake.

main lake basin is void of vegetation. Future research should focus on the effects of vegetation in small lakes and its ability to retain larval fishes or restrict wind-induced currents.

Wind-generated currents in Pelican Lake could be more complex than initially thought, which would lead to difficulties detecting any spatial patterns in larval fish densities. Livingstone (1954) proposed that wind currents in an isothermal lake, such as Pelican Lake, generate currents in the main lake basin in the direction of the wind but are balanced by an opposite feedback current along the nearshore areas of the lake. This type of wind-induced water current pattern was also found by Verhagen (1994); the longshore gradient return direction was, however, found to be opposite from that reported by Livingstone (1954) and was attributed in part to the shoreline gradient. The shoreline gradient of Pelican Lake is best described as a gentle slope

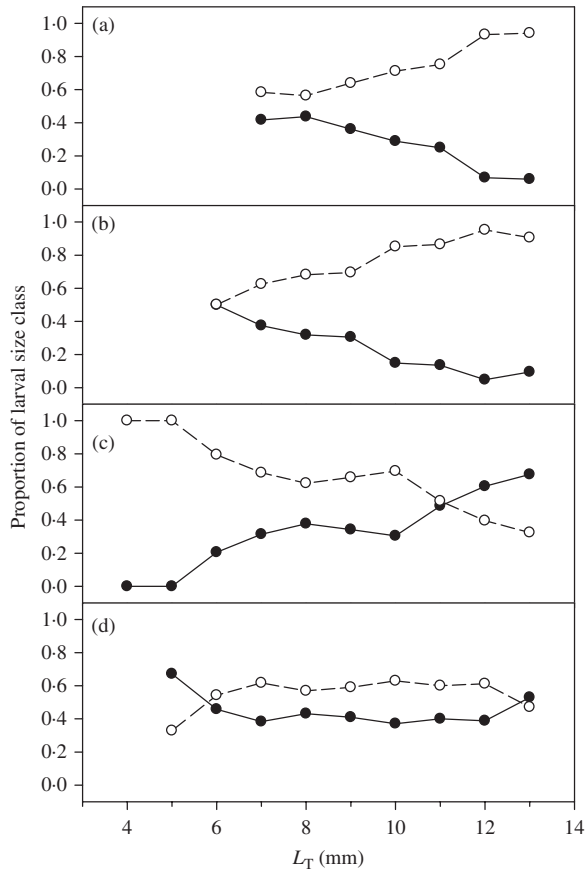


FIG. 9. Proportion of larval *Perca flavescens* size classes (per 1 mm total length, L_T) captured on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2006, (c) 2007 and (d) 2008 (no data in 2005 due to low sample sizes).

and highly vegetated with emergents (in most cases out to 30 m; unpubl. data), in which an opposite feedback may be modified and less pronounced than in other shallow lakes because vegetation can influence water currents (Leonard & Luther, 1995; Nepf *et al.*, 1997).

Although spatial larval densities could not be related to wind effects, these differences could be attributed to spawning sites for adult *P. flavescens*. Higher densities of adults spawning in the west side of the lake could produce more larvae, thus increasing the chance of detecting more larval fishes on this side of the lake. For *P. flavescens* in 2007, a higher proportion of smaller larvae was found on the west side of the lake, potentially corresponding to increased spawning activity in this area; this relationship was not, however, supported in other years examined. Higher catches of adult *P. flavescens* have been observed on the west side of Pelican Lake (J. C. Jolley & M. A. Kaemingk, unpubl. data), concomitant with the observed spatial density differences. Alternatively, *L. macrochirus* appear to be utilizing the entire lake for spawning, as indicated by the lack of disproportionate abundances of each

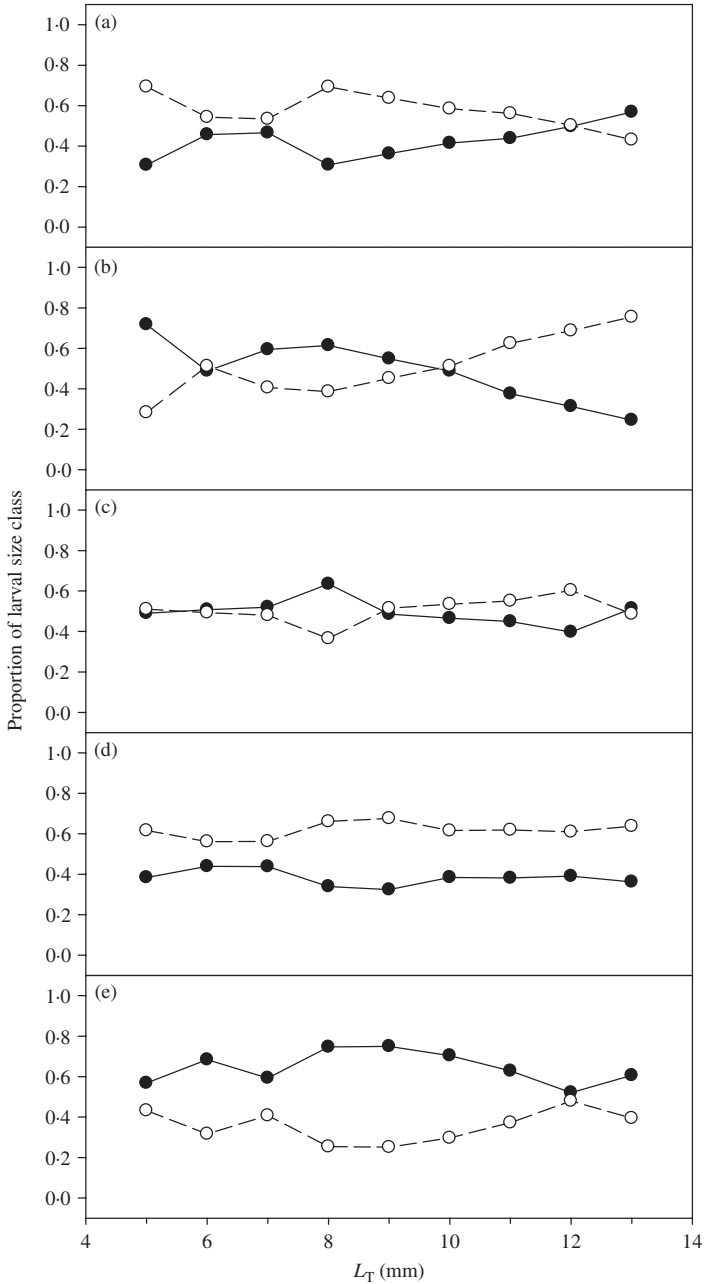


FIG. 10. Proportion of larval *Lepomis macrochirus* size classes (per 1 mm total length, L_T) captured on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008.

size class of larvae captured on the east and west side of the lake. This further suggests that spatial density differences of larval *L. macrochirus* are a result of something other than spawning location, such as wind effects, and are mediated by vegetation

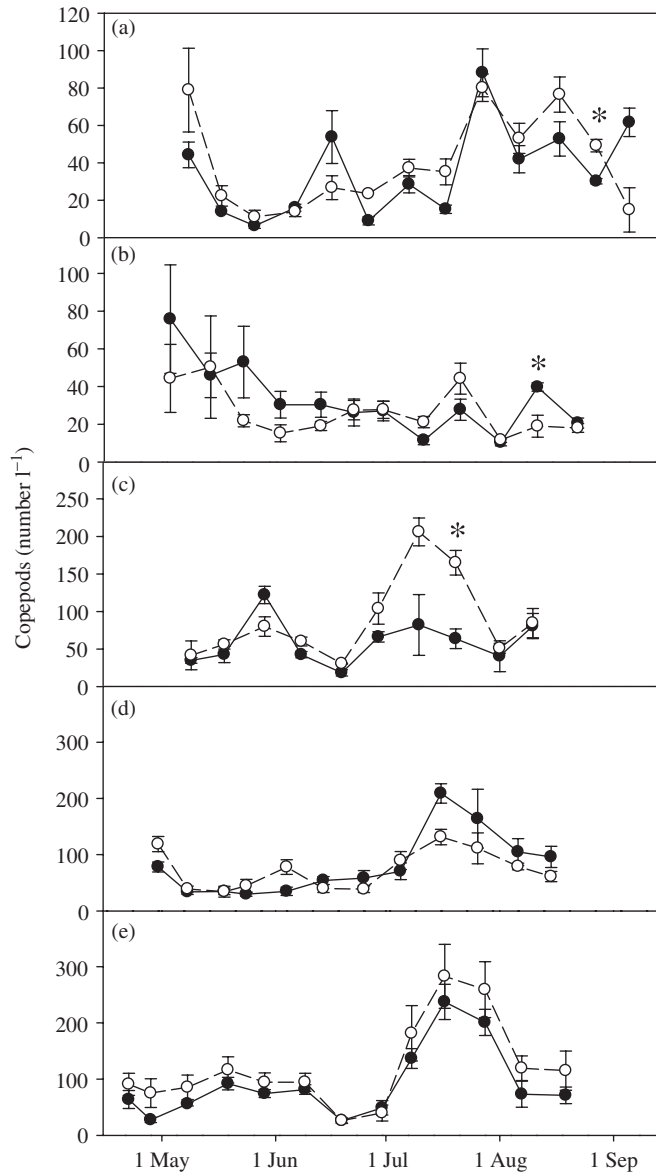


FIG. 11. Mean \pm s.e. copepod densities on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008. *, dates on which significant differences ($P < 0.05$) were observed between east and west sides of the lake.

interspersed throughout the lake. Perch *Perca fluviatilis* L. 1758 in Llyn Tegid Lake, north Wales also spawned in the upwind side of the lake (Coles, 1981), similar to Pelican Lake where prevailing winds are from the north-west. The north-west end of Pelican Lake is also more likely to experience warmer water temperatures because it is more protected, thus having the potential to attract higher densities of spawning *P. fluviatilis*. Other studies have found larval *P. fluviatilis* spatial density

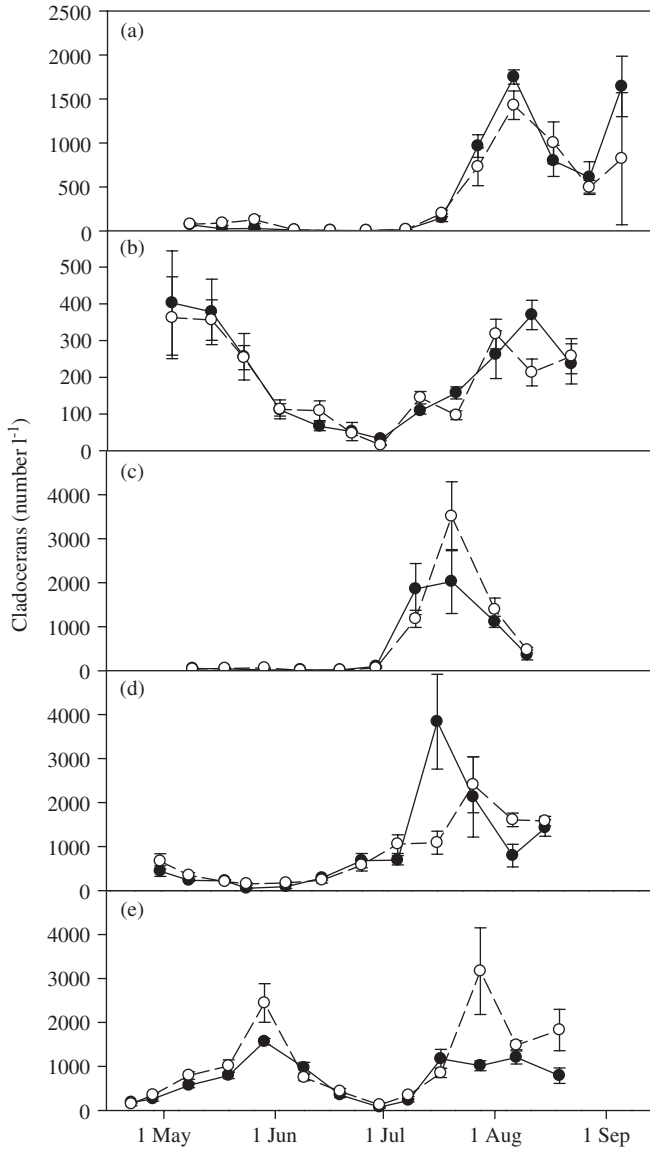


FIG. 12. Mean \pm S.E. cladocean densities on east (●) and west (○) sides of Pelican Lake in (a) 2004, (b) 2005, (c) 2006, (d) 2007 and (e) 2008. No significant differences were observed on any sampling dates.

relationships to spawning ground locations (Coles *et al.*, 1977; Coles, 1981) and have attributed their subsequent distribution to wind-induced effects (Coles, 1981).

There was much variability in *P. flavescens* recruitment and some degree of variability in *L. macrochirus* recruitment in Pelican Lake during 2004–2008 (Jolley, 2009). This variability in recruitment does not appear to be a result of a spatial mismatch between *P. flavescens* and *L. macrochirus* larvae and associated zooplankton prey (*i.e.* higher densities of prey on opposite sides of the lake where higher

densities of larvae were observed). Recruitment variability may, however, be a result of low copepod densities during the early larval stages, with most sampling dates (53/60 east side, 48/60 west side) exhibiting mean densities of copepods $<100\text{ l}^{-1}$. Zooplankton densities <100 organisms l^{-1} are below the suggested threshold that results in reduced larval fish growth and increased mortality (Werner & Blaxter, 1980; Eldridge *et al.*, 1981; Li & Mathias, 1982; Dettmers *et al.*, 2003). In addition, half of the sampling dates fell below 50 copepods l^{-1} . Conversely, fewer sampling dates (19/60 east side, 15/60) yielded cladoceran densities below this threshold, and a majority far exceeded this density.

Perca flavescens larvae in Pelican Lake during 2004 initially selected copepods, whereas *L. macrochirus* larvae selected *Bosmina* sp. and copepods during 2004 and 2005 (Jolley *et al.*, 2010). Because of the importance of copepods during the first feeding of larval *L. macrochirus* and *P. flavescens* in Pelican Lake and the lower density estimates of this zooplankton taxon, it is possible that growth could be compromised and ultimately result in higher mortality rates. Zooplankton biomass has been related to early growth of larval black crappie *Pomoxis nigromaculatus* (Lesueur 1829) (Bunnell *et al.*, 2003); however, Garvey *et al.* (2002) failed to find any relationship between zooplankton abundance and larval *L. macrochirus* survival. If copepod densities are adequate and do not inhibit initial larval growth, there does not appear to be any spatial or temporal mismatch between these larval fishes and prey in Pelican Lake, as peak *P. flavescens* and *L. macrochirus* larval abundances commonly matched peak abundances of copepods and *Bosmina* sp. (*L. macrochirus*) on a temporal scale (Jolley *et al.*, 2010) during 2004–2008.

Despite low copepod densities observed on several sampling dates, larval fishes may encounter localized (*i.e.* on a metre scale) patches of dense zooplankton and density estimates recorded on the spatial scale used in this study may not ultimately reflect absolute densities encountered by larval fishes in this study (Young *et al.*, 2009). Spatial differences in zooplankton densities were more pronounced when comparing samples collected between the east and west sides of the lake in contrast to those taken within the east or west sides of the lake, suggesting more large-scale than small-scale variability (unpubl. data). Furthermore, only on three sampling dates over 5 years was there any evidence of spatial differences in copepod densities and no sampling dates differed with respect to cladoceran densities. The topic of spatial and temporal overlap of predators and prey on a fine spatial scale (*i.e.* 1 m) warrants further investigation.

This study represents one of the few studies to examine wind effects on larval fishes and their distribution in a small, shallow lake and the findings indicate spatial differences are evident, but are not at all related to wind events. The spatial overlap between predators and prey in this system appears to be congruent and thus a spatial mismatch is not likely; prey densities over this spatial scale appear, however, to be in the range of other reported studies where larval growth was negatively affected. Future studies should aim to explain spatial differences in the light of other variables (*i.e.* vegetation and spawning location) and how these interact with food availability over a smaller spatial scale.

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