Short-term Water Mass Movements in Lake Michigan: Implications for Larval Fish Transport

Tomas O. Höök[1,2,*], Michael J. McCormick[2], Edward S. Rutherford[3], Doran M. Mason[2], and Glenn S. Carter[3]

[1]*Cooperative Institute for Limnology and Ecosystems Research*
School of Natural Resources and Environment
University of Michigan
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105

[2]*Great Lakes Environmental Research Laboratory*
National Oceanic and Atmospheric Administration
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105

[3]*Institute for Fisheries Research*
School of Natural Resources and Environment
University of Michigan
1109 N. University
Ann Arbor, Michigan 48109

ABSTRACT. *Water mass movement within the Great Lakes may rapidly transport fish larvae from favorable nursery areas to less favorable habitats, thereby affecting recruitment success. During 2001 and 2002, we released satellite-tracked drifting buoys in eastern Lake Michigan to follow discrete water masses, and used ichthyoplankton nets to repeatedly sample larval fish within these water masses. Observed nearshore water currents were highly variable in both direction and velocity. Current velocities far exceeded potential larval fish swimming speeds, suggesting that currents can potentially rapidly advect fish larvae throughout the lake. Evidence suggests that while paired drifters released during 2002 were able to track relatively small alewife* (Alosa pseudoharengus) *and yellow perch* (Perca flavescens) *larvae within an alongshore coastal current, paired drifters released during 2001 failed to track larger alewife larvae when flow was more offshore and highly variable. These results are consistent with the decorrelation scales associated with alongshore and offshore transport.*

INDEX WORDS: *Drifting buoys, alewives, yellow perch, ichthyoplankton, transport, Lake Michigan.*

INTRODUCTION

Transport of marine fish larvae by water currents into, or out of favorable nursery habitats has long been recognized as an important factor influencing individual, cohort, and year-class recruitment success (Hjort 1914, Cowan and Shaw 2002). Given the large geographical extant and dynamic circulation patterns of the Great Lakes (e.g., Beletsky *et al.* 1999), it is likely that water currents also influ-

ence recruitment success of Great Lakes fishes (e.g., Heufelder *et al.* 1982, Dettmers *et al.* 2005).

Past studies imply that water currents may play an important role in transporting fish larvae in Lake Michigan over both short and long distances. Heufelder *et al.* (1982) suggested that during upwelling events, water currents can rapidly transport larval alewives (*Alosa pseudoharengus*) away from favorable nearshore areas, thereby affecting local recruitment success. Beletsky *et al.* (2004) studied transport processes of larval yellow perch (*Perca flavescens*) in Lake Michigan during 1998–2000

*Corresponding author. E-mail: thook@umich.edu

using coupled hydrodynamic and individual-based particle models. Their analyses suggest that water currents may rapidly advect larval yellow perch over great distances (Beletsky *et al.* 2004). Similarly, collections of larval yellow perch at multiple spatial scales indicate a potential net movement (perhaps attributable to transport by water currents) of larval yellow perch from nearshore areas in western Lake Michigan toward offshore habitats (Dettmers *et al.* 2005). Finally, Miller (2003) found that while yellow perch from various Lake Michigan locations were genetically similar, these same groups were genetically distinct from Green Bay yellow perch. He partially attributed these spatial patterns to the actions of water currents transporting yellow perch larvae throughout Lake Michigan proper, while isolating larval yellow perch in Green Bay (Miller 2003).

These studies assumed that water currents are an important vector transporting fish larvae throughout Lake Michigan, but did not directly measure water currents, or compare current velocities with potential larval fish swimming speeds and densities. Satellite-tracked drifting buoys (drifters) are useful tools for tracking flows and quantifying water currents, and have been used for such purposes in the Great Lakes (e.g., McCormick *et al.* 2002). In marine systems, drifting buoys have also been used to track groups of fish larvae over multiple days (e.g., Pepin and Helbig 1997, Okazaki *et al.* 2003). Here, we present results from three experimental releases of satellite-tracked drifters in eastern Lake Michigan in order to 1) quantify the spatio-temporal dynamics of nearshore water currents and 2) evaluate the potential role of water currents in transporting fish larvae throughout Lake Michigan.

METHODS

On three occasions (12:00 EST 10 July, 2001; 11:00 EST 24 July, 2001; and 11:00 EST 24 June, 2002), we released pairs of drifting buoys (Coastal Ocean Dynamics Experiment drifters manufactured by Clearwater Instruments Inc.) in eastern Lake Michigan (near Muskegon, Michigan, USA). The drifters have a center of effort ~1.0 m below the surface, and thus track near surface currents (see McCormick *et al.* 2002 for more details). The drifters used during 2001 and 2002 were identical with the exception that drifter positions were determined by only Argos (Service Argos Inc.; positions determined via Doppler shifting detected by a single satellite) during 2001, while both Argos and GPS (Global Positioning System; positions determined via multi-satellite triangulation) were used during 2002 (i.e., positions determined more precisely during 2002). Individual drifters transmitted every 90 s from their Argos PTT (platform transmitting terminal). When a NOAA Tiros satellite was in view of a PTT and able to receive a signal it computed the distance to the PTT via Doppler shifting, and after recovering several signals computed the location of the transmitter (satellite fixes average approximately 11 times daily). Argos assigns an accuracy score of 1 (accuracy estimate of 1 km), 2 (350 m), or 3 (150 m) based upon a statistical evaluation of the accuracy of position estimates. The vast majority of fixes used in these analyses received accuracy scores of 3. Argos drifter positions were edited and checked for excessive speeds and resulting data were temporally interpolated to hourly positions. During 2002, drifters also determined their GPS positions hourly and subsequently archived these data (storage capacity of 17 fixes). When a satellite was able to detect a drifter PTT, it received an encoded data stream with up to 17 of the previous positions calculated by GPS. Clearwater Instruments received data (both data message and Argos positions) directly from Argos, decoded these data, and electronically forwarded resulting GPS fixes, allowing us to obtain near real-time highly accurate estimates of drifter trajectories on an hourly basis. During drifter releases, we characterized thermal and light environments near drifters by measuring 1) surface water temperatures (0.5-m below surface), 2) thermal profile with a Seabird CTD (conductivity, temperature, and depth) profiler, and 3) Secchi disk depth (a measure of the light environment).

On 24 July, 2001, and 24 June, 2002, we released drifters at locations with observed relatively (compared to densities observed at other locations during the same time periods) high larval fish densities. These locations were identified during systematic larval fish collections conducted in conjunction with a study of larval alewife dynamics. We used ichthyoplankton nets to collect fish larvae near drifters at the time of release and during subsequent time periods. To collect fish larvae, we used a 60-cm diameter bongo sampler with 335 and 500-μm mesh nets. To catch larger larvae that would avoid the bongo sampler, we also used a 2-m^2 Tucker trawl sampler of 700-μm mesh. In keeping with the survey design of the larval alewife study, we towed all ichthyoplankton samplers obliquely at 1–2 kts. for 5 minutes. Volume of water filtered by ichthy-

TABLE 1.   *Characteristics of paired (A and B) drifters released in eastern Lake Michigan during 2001 and 2002.*

Drifter	Total distance traveled (km)	Net distance traveled (km)	Mean Velocity (m s^{-1}; ±SD)	Maximum Velocity (m s^{-1})
10 July, 2001 (48 hr release)				
A	29	13	0.17 ± 0.11	0.51
B	26	13	0.15 ± 0.10	0.45
24 July, 2001 (72 hr release)				
A	60	18	0.23 ± 0.16	0.82
B	56	14	0.21 ± 0.19	0.80
24 June, 2002 (24 hr release)				
A	28	28	0.33 ± 0.05	0.43
B	27	27	0.31 ± 0.05	0.37

oplankton nets was determined with flow meters placed inside the nets. Further, we noted the length and angle of line deployed, allowing us to subsequently estimate the portion of water column sampled by ichthyoplankton nets. During the 2001 experiment, we towed ichthyoplankton samplers on paths which passed approximately midway between the two drifters. During each sampling visit, we towed the bongo sampler on two occasions and the Tucker trawl only once, thereby collecting a total of five samples (two with 335-μm net; two with 500-μm net; and one with 700-μm net). We expanded our larval fish sampling during the 2002 experiment, and towed ichthyoplankton samplers on three defined paths; 1) approximately 250 m inshore of the inshore drifter, 2) approximately midway between the two drifters, and 3) approximately 250 m offshore of the offshore drifter. Thus, we collected a total of nine samples during each sampling visit (three with 335-μm net; three with 500-μm net; and three with 700-μm net).

In the field, ichthyoplankton samples were preserved in 90% ethanol. In the laboratory, larvae and juveniles were identified to lowest possible taxonomic level using keys by Auer (1982) and Wallus and Kay (1990), and total lengths (to 0.1 mm) were measured using a dissecting microscope and Optimus image capturing software.

RESULTS

The pair of drifters released 12:00 (EST) 10 July, 2001 traveled a total distance of ~28 km (net distance of ~13 km) in a southward direction during the 48 hour release with trajectories composed of inertial oscillations superimposed upon a mean flow (Table 1, Figure 1). CTD data obtained at the time of drifter release were lost, but a CTD cast taken near the release location on the previous day (9 July, 2001) revealed weak thermal stratification (Fig. 2).

The pair of drifters released 11:00 (EST) 24 July, 2001 primarily traveled offshore and traveled a total distance of ~58 km (net distance of < 18 km) during the 72 hour release (Table 1, Figs. 1 and 3). Again, strong inertial signals were apparent in the trajectories. However, unlike 2 weeks earlier the water column was characterized by sharp thermal stratification (Fig. 2). We used ichthyoplankton nets to sample waters in the vicinity of these drifters at the time of release, 24 hours after release (25 July) and at the time of retrieval (27 July). On all three occasions, we only caught alewife larvae (Table 2). The mean lengths (± SE) of individual alewives in the vicinity of these drifters decreased over time (24 July, 17.4 ± 0.5 mm; 25 July, 16.7 ± 2.0 mm; 27 July, 9.9 ± 0.3 mm; see Fig. 4).

The pair of drifters released 11:00 (EST) 24 June, 2002 traveled rapidly NNW along the shoreline, and traveled ~29 km during the 24 hour release (Table 1, Fig. 1). At the time of drifter release, thermal stratification was very weak. At this time, we collected alewife, yellow perch, rainbow smelt (*Osmerus mordax*), burbot (*Lota lota*), and bloater (*Coregonus hoyi*) larvae, but only collected three of these species (alewife, yellow perch, and rainbow smelt) at the time of drifter retrieval. Density estimates for the two most abundant species (alewife and yellow perch) increased from time of release to time of retrieval (Table 2). Further, although size distributions of larval alewives and yellow perch
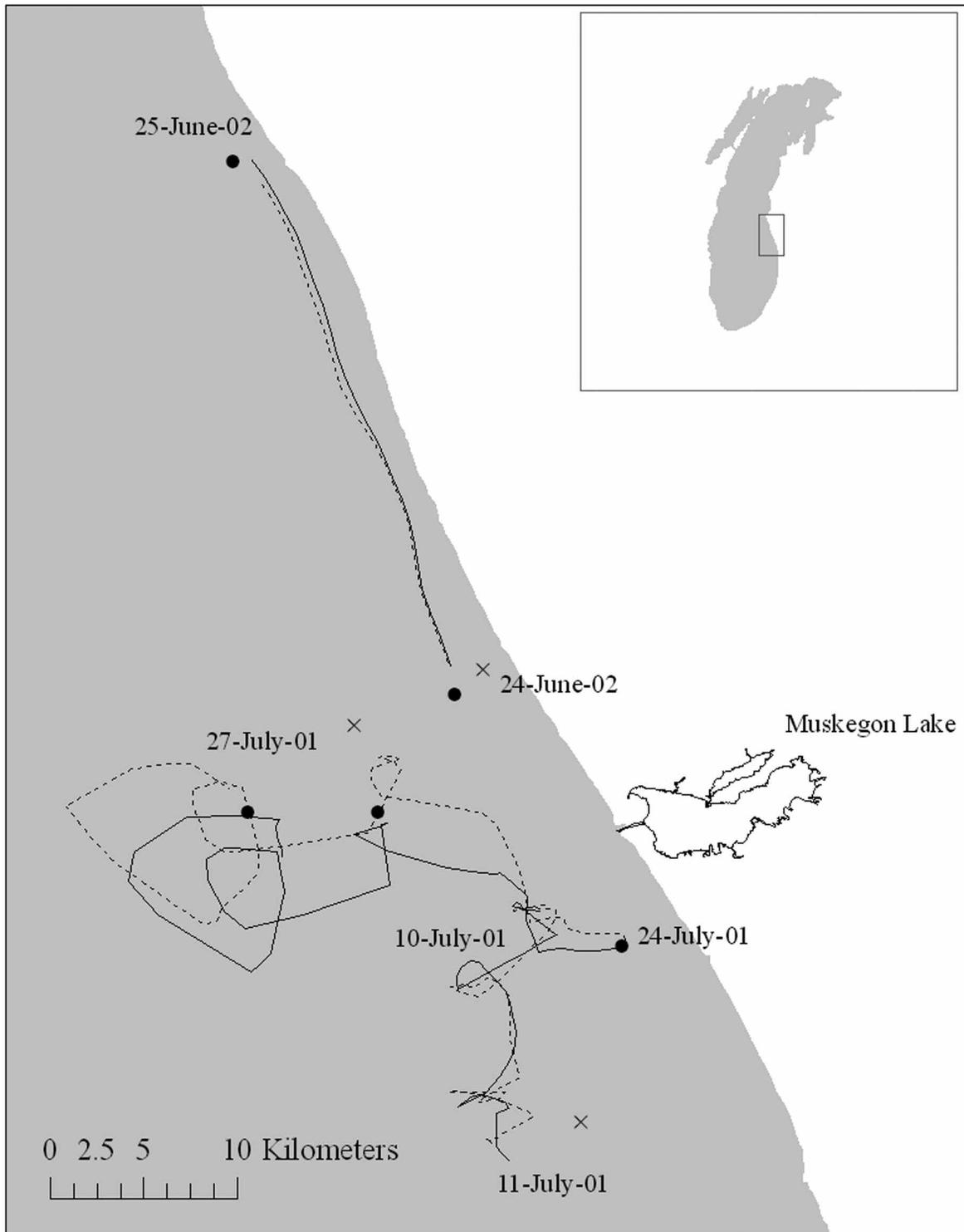
FIG. 1. Map showing the location (inset) and horizontal tracks (solid and dashed lines) of paired drifters released in Lake Michigan on 10 July, 2001, 24 July, 2001, and 24 June, 2002. Larval fish sampling locations (24, 25, and 27 July, 2001 and 24 and 25 June, 2002) are depicted by solid points. Additional stations sampled for larval fish on 24 June, 2002 are shown (× ; see text for details). The location of Muskegon Lake is included for reference.
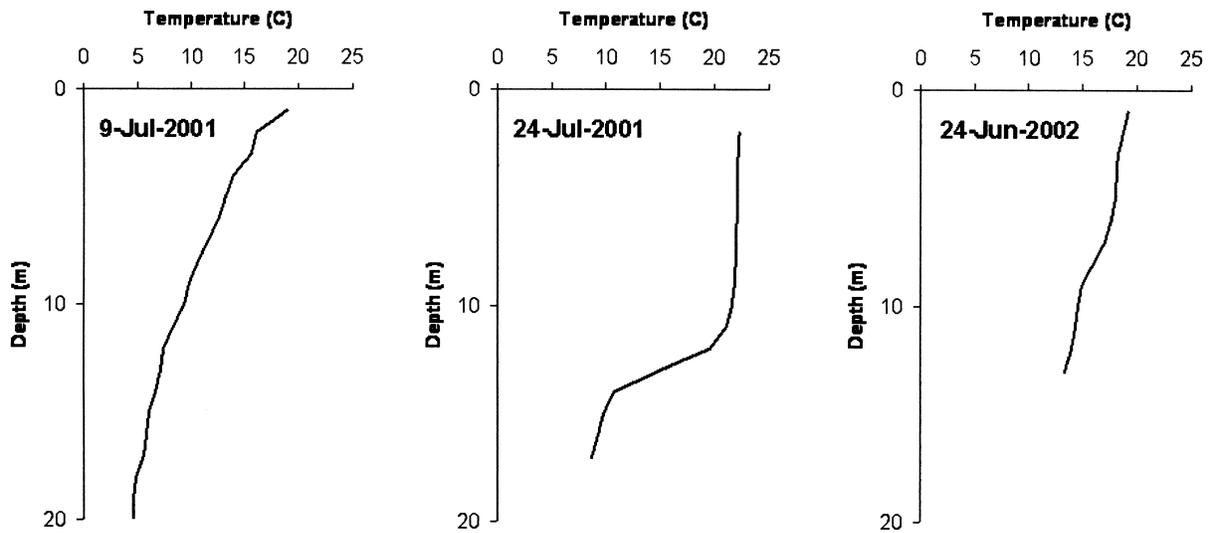
FIG. 2.   *Thermal profiles in our eastern Lake Michigan study area based on CTD casts.*
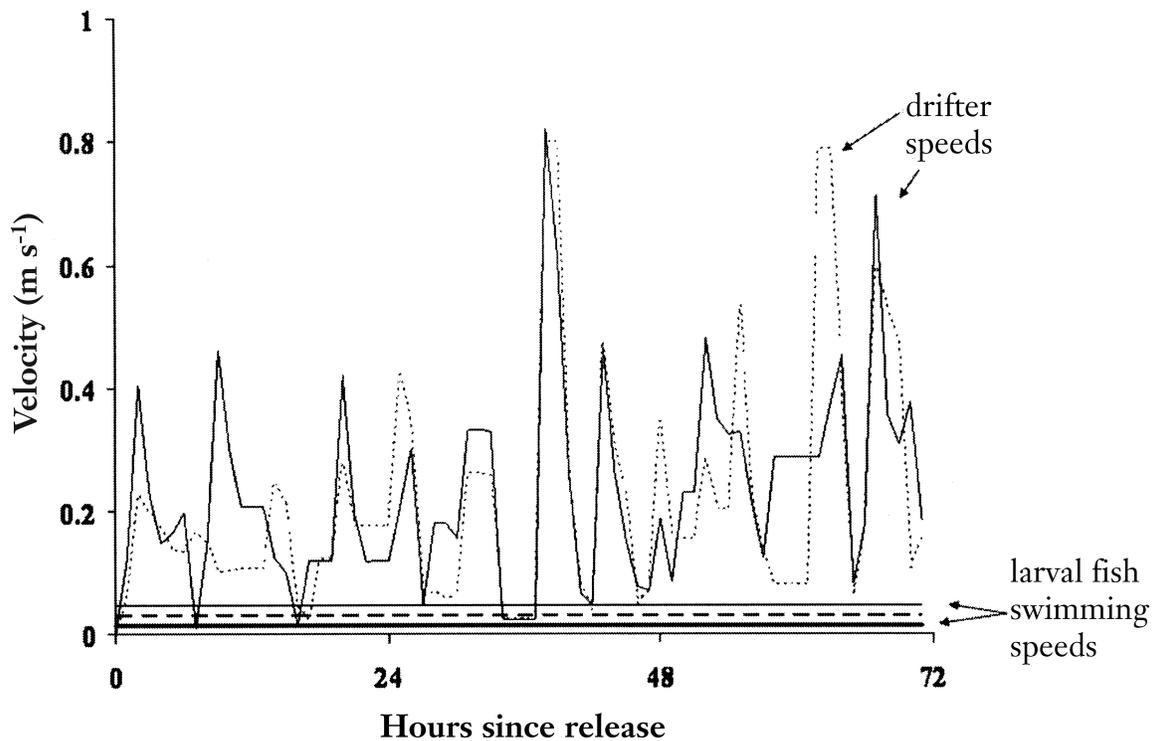
FIG. 3.   *Surface velocities (m s⁻¹) of paired drifters (solid and dashed lines) from 24 July, 2001 to 27 July, 2001. Surface velocities were calculated based on distances between locations transmitted hourly to satellite. Horizontal lines depict laboratory derived estimates of sustained swimming speeds of larval yellow perch and alewives (from Houde 1969 and Klumb et al. 2003, respectively); solid, bold line = 0.015 m s⁻¹, i.e., 10 mm alewives at 22°C; dashed line = 0.03 m s⁻¹, i.e., 20 mm alewives at 22°C and 10 mm yellow perch at 13°C; solid, thin line = 0.046 m s⁻¹, i.e., 13.5 mm yellow perch at 12°C.*

TABLE 2. *Mean densities of larval fish (larvae 100 m^{-3} ± SE) by species collected in the vicinity of drifters during 2001 and 2002. Maximum depths sampled were calculated as the cosine of line angle multiplied by line distance. The range (if > 1 tow for corresponding net type) of maximum depths sampled is shown.*

	NET (μm)	Maximum depth (m)	Alewife	Yellow perch	Rainbow smelt	Bloater	Burbot
2001							
24 July	335	13–15	0.47 ± 0.33	0	0	0	0
	500	13–15	0.46 ± 0.33	0	0	0	0
	700	7	0.42	0	0	0	0
25 July	335	26–26	0	0	0	0	0
	500	26–26	0.32 ± 0.23	0	0	0	0
	700	30	0.24	0	0	0	0
27 July	335	34–34	0	0	0	0	0
	500	34–34	0.64 ± 0.03	0	0	0	0
	700	42	0.17	0	0	0	0
2002							
24 June	335	6–12	8.76 ± 0.86	1.32 ± 0.66	0	0.34 ± 0.34	0.34 ± 0.34
	500	6–12	3.31 ± 1.25	1.17 ± 0.59	0.2 ± 0.2	0.21 ± 0.21	0.21 ± 0.21
	700	9–11	0.11 ± 0.06	0.42 ± 0.25	0	0.04 ± 0.04	0.08 ± 0.04
25 June	335	7–14	12.15 ± 2.83	2.47 ± 1.69	0	0	0
	500	7–14	7.13 ± 0.4	2.82 ± 1.41	0	0	0
	700	7–14	0.21 ± 0.05	0.13 ± 0.07	0.04 ± 0.04	0	0

collected in the vicinity of drifters at the time of release (24 June) and retrieval (25 June) largely overlapped (Fig. 4), the mean lengths (± SE) of both alewife and yellow perch larvae collected at the time of release (alewife, 5.5 ± 0.2 mm; yellow perch, 6.5 ± 0.3 mm) were greater than mean lengths at the time of retrieval (alewife, 5.0 ± 0.1 mm; yellow perch, 5.8 ± 0.1 mm).

DISCUSSION

Experimental drifter releases suggest that direction and speed of coastal water currents are highly dynamic in eastern Lake Michigan, and thus no simple procedure exists to predict particle transport. While surface currents in our study area generally flow along shore in a northerly direction (Beletsky *et al.* 1999), paired drifters released within this area on three occasions during 2001 and 2002 traveled along distinctly different horizontal paths (see Fig. 1). The 2001 trajectories show trochoidal motions due to inertial oscillations characteristic of offshore circulation, while the 2002 trajectories show longshore motion characteristic of coastal circulation.

During summer stratification inertial oscillations are frequently the dominant feature of currents and thus larval fish transport in regions more than 5–10 km from shore (Mortimer 2004). The drifter trajectories during the 2001 experiments show a strong signal near the inertial period (approximately 17 h). These oscillations are clockwise (in the northern hemisphere) in direction and were evident throughout the 2001 deployments. The radii of pure inertial motions depend solely upon the latitude and current speed. The overall mean drifter speed for 2001 (Table 1) was 0.19 m s^{-1} which corresponds to a radius of inertial oscillation of approximately 2 km at 42° latitude. When a mean flow is combined with inertial currents it results in a trajectory that is more trochoidal in appearance. Both types of motion, indicating mean flow plus inertial flow and nearly pure inertial flow, are evident in the 2001 trajectories.

In contrast, the drifter trajectories from 2002 were dominated by a coastal jet (with no alongshore flow reversals). Near the coast, relatively strong currents may exist in response to both local wind stress and basin-scale circulation. Thus, coastal currents will vary primarily in speed, while direction may change due to alongshore flow reversals. Although observed drifter speeds during 2002 were
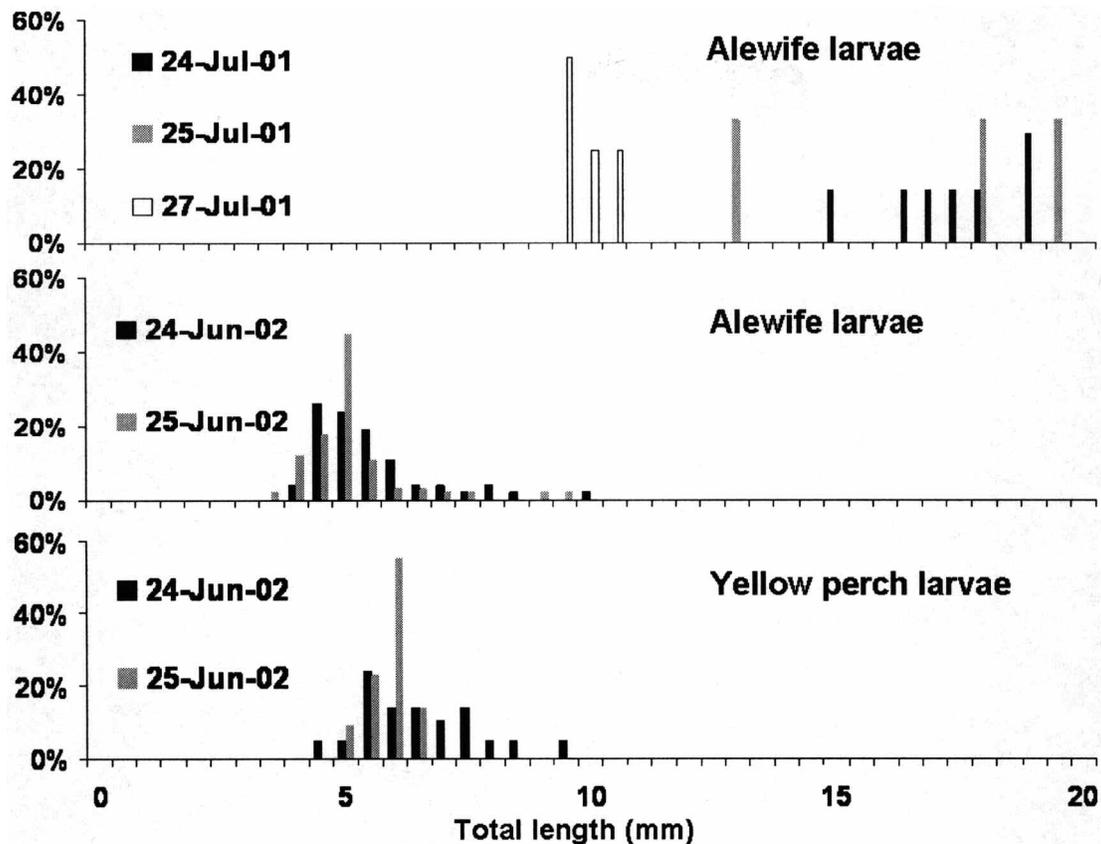
FIG. 4. *Length distributions of larval alewives and yellow perch (grouped by 0.5 mm total length categories) caught in the vicinity of drifters during 2001 and 2002.*

higher than during 2001 (Table 1), the coefficient of variation was lower in 2002 reflecting the contribution and importance of basin-scale motions to coastal currents.

Several past studies imply that larval fish in Lake Michigan may be passively transported by water currents (e.g., Heufelder *et al.* 1982, Beletsky *et al.* 2004, Miller 2003, Dettmers *et al.* 2005). Our observed current velocities far exceeded potential larval fish swimming speeds (Fig. 3). Therefore, our results are consistent with Miller's (2003) hypothesis that water currents can play an important role in connecting spatially-distinct groups of Lake Michigan fish populations, and with Dettmers *et al.*'s (2005) assertion that larval perch may be passively advected offshore.

Collections of fish larvae in the vicinity of drifters should be considered in the context of additional ichthyoplankton sampling within this region of Lake Michigan during 2001 and 2002. Such sampling documented that larval fish were highly patchy in space and time (see Höök 2005 for de-

tails). For instance, out of 61 oblique, 5 minute tows with the 335-μm ichthyoplankton net during June–July 2001 and 2002, 61% of tows captured no larval alewives, and only 11% of tows captured > 5 alewife larvae per 100 m³ of water sampled. On 24 June, 2002 we also sampled ichthyoplankton (with 335-μm, 500-μm, and 700-μm mesh nets) at three additional locations (one inshore location, 11-m depth and two offshore locations, 40 and 50-m depths) within our nearshore Lake Michigan study region (see Fig. 1 for exact locations). The additional inshore site was located only 1.4 km from the point of drifter release and contained similar fish larvae (i.e., small larval alewives and yellow perch) as the drifter release site. At two offshore sites, however, we only captured deepwater sculpin (*Myoxocephalus thompsoni*) larvae. Finally, in order to index spatial distributions of larval yellow perch Dettmers *et al.* (2005) sampled ichthyoplankton (30-min. tows) near our study area on 26–28 June, 2002, and in so doing collected no yellow perch larvae. In short, small larval alewives and yellow

perch were clearly not ubiquitous and their densities were highly variable throughout our study area.

Our sampling of fish larvae, however, led to equivocal conclusions regarding the ability of drifters to track patches of fish larvae as they are transported by water currents. We did not mark larval fish when we released drifters, and therefore can not be certain that fish larvae collected on days subsequent to drifter release were also present in the vicinity of drifters at the time of release. If a cohort of fish larvae remains within a water mass indefinitely, then over time, the mean individual size would likely increase (due to growth) and cohort abundance would likely decrease (due to mortality). Such trends may, however, not be apparent when sampling fish larvae over time because of, 1) microscale patchiness within the water mass leading to variation in number and size of larvae caught and 2) size-selective sampling gear.

All three ichthyoplankton samplers (335-μm, 500-μm, and 700-μm mesh nets) used in this study are highly size-selective (Höök 2005). While growth rates of larval alewives and yellow perch in Lake Michigan are variable, average observed growth rates of both species (alewives, 0.74 mm d^{-1}, based on otolith microstructure analysis of field-caught larvae, Höök 2005; yellow perch, ~0.4 mm d^{-1}, based on laboratory-reared larvae, Graeb *et al.* 2004) could dramatically alter the susceptibility of individual fish to the three ichthyoplankton samplers over a single day. Therefore, over a range of larval fish sizes, we actually would expect an increase in catches over time as fish grow and become progressively more vulnerable to sampling gear. As an example, although larval alewives emerge at lengths from 3.5 to 4.0 mm they do not become fully vulnerable to the finest mesh (335-μm) ichthyoplankton sampler until they grow to ~5.0 mm (likely due to extrusion of very small larvae through the net; Höök 2005). The most abundant size category of larval alewives captured on 25 June, 2002 was the 5.0 mm length category (i.e., from 4.75 mm to 5.24 mm), while the most abundant size category of larval alewives captured on 24 June, 2002 was the 4.5 mm length category (i.e., individuals likely to grow into the 5.0 mm length category during a single day). However, density estimates for the 4.5 mm length category on 24 June, 2002 were much lower than for the 5.0 mm length category on 25 June, 2002, perhaps due to an increase in gear vulnerability with size (Fig. 4).

Because of such confounding effects, we qualitatively compared densities and size distributions over time. Based on these comparisons and other evidence (see below), we argue that while drifters likely did not track an assemblage of fish larvae during the 24 July, 2001 release, it is very probable (but not unequivocal) that we successfully tracked an assemblage of fish larvae during the 24 June, 2002 release. While we estimated similar larval alewife densities from 24 to 27 July, 2001, the mean size of larval alewives in the vicinity of drifters decreased over this time period (Fig. 4). This alone suggests a failure to track a spatio-temporal distinct cohort. In contrast, during 2002 at a time when fish larvae were clearly not ubiquitous in our study area (see above) we collected similar species, densities, and sizes of fish larvae when we released and retrieved drifters, suggesting that we successfully tracked an ichthyoplankton assemblage.

This differential ability of drifters to track fish larvae is likely related to multiple factors. 1) Mean sizes of larval fish captured at the time of drifter release were relatively large on 24 July, 2001 (alewives, 17.4 ± 0.5 mm) and relatively small on 24 June, 2002 (alewives, 5.5 ± 0.2 mm; yellow perch, 6.5 ± 0.3 mm). Swimming abilities of fish larvae tend to increase with size (e.g., Houde 1969, Miller *et al.* 1988, Klumb *et al.* 2003), and thus larger fish larvae are more likely to overcome the advective forces of water currents (i.e., not remain in the vicinity of the drifters). 2) Natural dispersion is inherent in all turbulent flows. For example, lagrangian studies in Lake Michigan estimated the integral length scales for alongshore flow to vary from 3–18 km while in the offshore direction it was 2–6 km (McCormick *et al.* 2002). Similarly, recent modeling studies (Cowen *et al.* 2006) suggest larval dispersal distances of 10–100 km in the Caribbean region. The longer coherence scales observed in alongshore transport during 2002 suggest that fish larvae could be tracked over a relatively long time. Conversely, the opposite was likely during 2001 deployments when significant offshore transport occurred with its correspondingly shorter coherence scales in both time and space. 3) While drifters had a center of effort ~1 m below surface, we used oblique tows (from some maximum depth to surface; see Table 2) to collect fish larvae. Past studies demonstrate that larval alewives in the Great Lakes primarily occupy surface waters (O'Gorman 1983, Nash and Geffen 1991). Thus, while we probably collected the majority of alewife larvae near surface (i.e., the vertical portion of the water column tracked by drifters), Great Lakes fish larvae (e.g.,

yellow perch; Hamley *et al.* 1983, Perrone *et al.* 1983, Nash and Geffen 1991) are not confined to surface waters. Thus, it is possible that some larvae in the horizontal vicinity of drifters were collected well below surface. However, the potential bias introduced by this vertical mismatch is likely minimal when horizontal currents 1 m below surface are indicative of horizontal currents throughout the water column (or at least from surface to maximum depth sampled). Such a criterion is most likely to hold for nearshore currents during weak thermal stratification (particularly for currents traveling alongshore; Beletsky *et al.* 2003), i.e., during the 2002 drifter deployment, but not during the 2001 deployments (see Figs. 1 and 2).

In summary, successful sampling of fish larvae over time in the vicinity of surface drifters is dependent on an appreciation of both larval fish attributes and governing physics. Small, poor swimming larvae entrained in water currents of consistent speeds are most readily tracked. In the coastal environments of the Great Lakes the potential contribution of the basin-scale circulation will, in general, be concentrated in the longshore flow whereby the decorrelation time and length scales will often be significantly larger than that for the offshore component. Our results for the 2001 and 2002 experiments are consistent with this physical interpretation and suggest that larval dispersal may be strongly influenced by time and spatial scales that are intrinsic to the system under study.

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