International Journal of Odonatology, 2016
Vol. 19, Nos. 1–2, 83–93, http://dx.doi.org/10.1080/13887890.2016.1183525

Taylor & Francis
Taylor & Francis Group

Pre-emergent movements and survival of F-0 larvae of *Ophiogomphus rupinsulensis* (Odonata: Gomphidae) in a northern Wisconsin river

Robert B. DuBois[a*] and William A. Smith[b]

[a]*Department of Natural Resources, Bureau of Natural Heritage Conservation, Superior, WI, USA*
[b]*Department of Natural Resources, Bureau of Natural Heritage Conservation, Madison, WI, USA*

(*Received 11 March 2016; final version received 25 April 2016*)

We marked and released 276 F-0 larvae of *Ophiogomphus rupinsulensis* in the fall of 2008 in a 99-m riffle (marking riffle) of a small, serially discontinuous, northern Wisconsin river (USA). We then recovered marked exuviae via exhaustive collecting on the banks of a 272-m sampling reach in which the marking riffle was located during spring of 2009. We collected 6054 exuviae of *O. rupinsulensis* along the sampling reach, including 3829 exuviae along the marking riffle (19.3 exuviae m^{-1}). Mark retention was complete and our ability to recover marked exuviae in the field was high (92%). We recovered 38 marked exuviae which provided a minimum estimate of survival (14%) for F-0 larvae from late September to the following June. The density of F-0 larvae in the marking riffle in late September was estimated at 22.6 larvae m^{-2}. Nearly all F-0 larvae made small downstream movements (97% moved < 60 m) at some time during the 36 weeks before emergence, but they did not make substantial longitudinal movements. These results affirmed the premise that locations of found exuviae of *O. rupinsulensis* along a small river are in close proximity to the habitats where the larvae developed.

Keywords: Odonata; dragonfly; Anisoptera; *Ophiogomphus*; larval movements; drift; emergence; exuviae

Introduction

Information is lacking about movements of larvae of *Ophiogomphus* Selys in rivers at any stage of their development. Pre-emergent movements of final stadium (F-0) larvae, especially substantial longitudinal movements, could have ecological implications worth noting. The presence of exuviae on the shore is widely regarded as the best indicator of the association of a species with a water body because they confirm that the site was used for breeding and demonstrate that the species was present at all stages of development (Aliberti Lubertazzi & Ginsberg, 2009; Corbet, 1999; Oertli, 2008; Raebel, Merckx, Riordan, MacDonald, 2010). However, if substantial longitudinal movements are undertaken by late-stadium larvae before emergence, then the locations of found exuviae could lead to erroneous conclusions about preferred river reaches and critical habitats for larvae.

Downstream drift of F-0 larvae could cause exuviae to be found in areas of lotic systems below the habitats where they developed. Larval forms of many aquatic insect taxa are known to drift

*Corresponding author. Email: robert.dubois@wisconsin.gov

in considerable numbers; thus drift is an integral part of their life history (reviewed by Brittain & Eikeland, 1988). Despite the clear ecosystem significance of aquatic insect drift, odonates are generally thought to have a low propensity to drift (Corbet, 1999, p. 15). However, results to date could be misleading because the densities of riverine species of odonates are often comparatively low. Being larger secondary and tertiary consumers, they would be expected to occur at lower densities than the many taxa of smaller aquatic insects on which they prey (the Pyramid of Numbers concept of Elton [1927]), and with which their drift rates could be compared. Further, the small drift nets typically used by aquatic entomologists to sample drift were not designed with larger drift targets like Anisoptera larvae in mind, and they might not be effective in capturing and retaining larger taxa (DuBois & Stoll, 1995). Therefore, drifting could be a non-trivial part of the life history of some riverine odonates, but one that goes largely undetected. For example, Arai (1993) reported that all stages of larvae of *Stylogomphus suzukii* (Matsumura) inhabit upper reaches of mountain streams in Japan, but that exuviae were found in lower reaches. He therefore noted that larvae appeared to move downstream.

To evaluate the propensity of *Ophiogomphus* larvae to move longitudinally prior to emergence, we marked F-0 larvae of *O. rupinsulensis* (Walsh) in late September 2008 in a riffle of a small, serially discontinuous river reach in northern Wisconsin (USA) and recaptured marked exuviae of this spring species the following June. *Ophiogomphus rupinsulensis* is a spring species in the northern USA that is known for a short, synchronous emergence period (Gibbs, Bradeen, & Boland, 2004). Last stadium larvae of Odonata, especially synchronous spring species, are thought to be ideal subjects for mark-recapture studies because exuviae are concentrated in time and space, and therefore marks can easily be recovered (Cordero-Rivera & Stoks, 2008). We also calculated a minimum estimate of survival between the times of marking and recapture, and estimated the densities of F-0 larvae of *O. rupinsulensis* in the riffle in late September.

Materials and methods

We selected a 900-m reach of the Eau Claire River in Bayfield County, Wisconsin (46.3033°, –091.5016°), for study because it was serially discontinuous between Upper Eau Claire and Middle Eau Claire lakes (Figure 1), which effectively formed ecological barriers that greatly reduced the chances of longitudinal movement of larvae of lotic species of Odonata into the reach from upstream or downstream. Additionally, the reach was known from prior larval sampling to contain a robust population of *O. rupinsulensis* (RBD unpublished data), one of the most common river gomphids in the region. Although the entire reach contained larvae of *O. rupinsulensis*, spot kicknetting throughout the reach indicated that a single 99-m sand, gravel, and cobble riffle (hereafter the marking riffle [MR]) contained higher densities of larvae than other sections of this predominantly sandy stream.

A 272-m section of the reach between Upper Eau Claire Lake and Outlet Bay Road was selected for intensive sampling (hereafter the sampling reach) and was divided into 19 stations for exuviae collections, which included the MR and areas both above and below it (Figure 1). The MR was divided into 13 stations, each 7.6 m long, that were flagged at each end on both banks. The mean width of the MR was 12.2 m as estimated from the average of distances between 11 pairs of streamside GPS waypoints overlain on a leaf-off aerial photograph layer. Four 30.5-m stations were established above the MR from its upstream edge to the base of a low-head dam at the downstream end of Upper Eau Claire Lake, and two stations, one 30.5 m long and one 20.4 m long, were marked downstream of the MR to Outlet Bay Road. Further downstream, a 244-m reach from Outlet Bay Road to State Highway (SH) 27 was not divided into sampling stations,

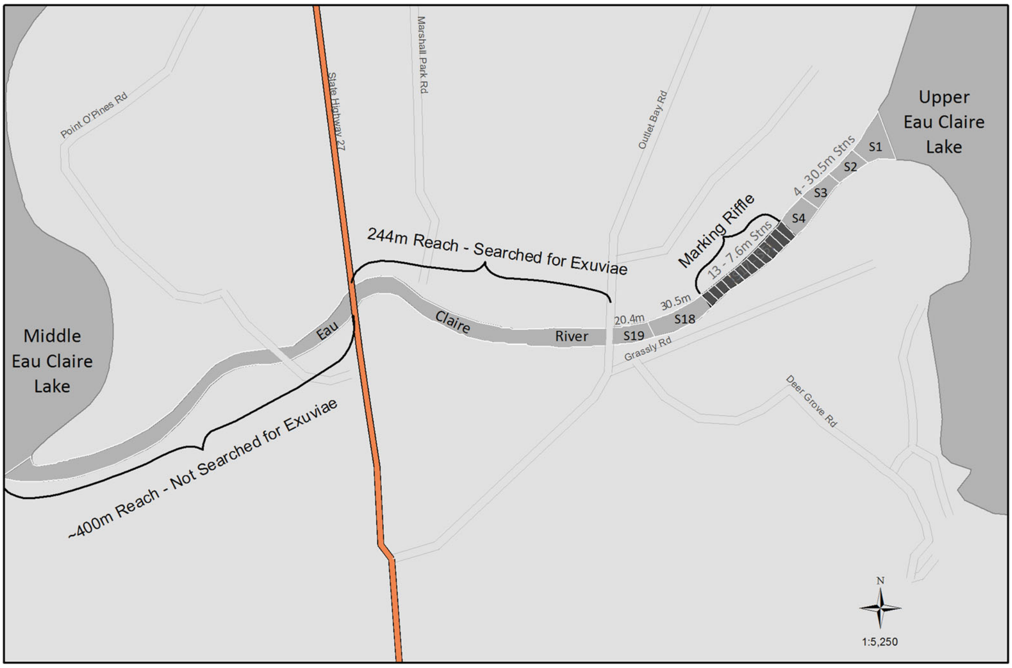

Figure 1. Eau Claire River, Bayfield County, Wisconsin, USA, where F-0 larvae of *O. rupinsulensis* were marked in September 2008 and were recovered as marked exuviae in June 2009. Shown are locations of 13 stations (Stns) in the marking riffle, six additional stations in the sampling reach between Outlet Bay Rd and Upper Eau Claire Lake, a reach between SH 27 and Outlet Bay Rd that was searched for marked exuviae, and a reach between SH 27 and Middle Eau Claire Lake that was not searched (river flow is from right to left).

but was search for marked exuviae as described below. An approximately 400-m reach between SH 27 and Middle Eau Claire Lake was not searched for marked exuviae.

On 24 September 2008, a crew of five workers used kick nets to collect 276 F-0 larvae of *O. rupinsulensis* from throughout the MR, then marked and released them. Younger stadia larvae that were caught were released unmarked. The dorsal surface of the abdomen of each F-0 larva was carefully patted dry with a hand towel, then a small dab of colored, fast-acting superglue (cyanoacrylate) was applied to one side of several mid- and rear-abdominal tergites onto which some glitter was also sprinkled (on average 4.5 tergites received the mark). The placement of the mark indicated both the capture location and release point (e.g. larvae caught on the right side of the thalweg, looking upstream, were marked on the right side of the abdomen). Larvae were then placed in a dry tub for several minutes while the glue set, after which they were released at the approximate midpoint of the MR (upper end of MR6, Table 1) in shallow, slow-moving water near shore on the same side of the thalweg from which they had been collected. We released 120 marked larvae on the south bank and 156 marked larvae on the north bank. An additional 14 marked larvae were reared in the lab to test the mark for any negative effect on the ability of larvae to emerge and for mark permanence. Because we sought to mark as many F-0 larvae as feasible, kick-netting continued throughout the MR for several hours during the marking day until it became difficult to collect more larvae.

The following spring we examined both banks of the sampling reach for evidence of emergence of *O. rupinsulensis*, which we first noted on 1 June 2009, and we began collecting exuviae exhaustively on 2 June. Collections were made on six days across a nine-day span (2, 3, 4, 5, 9, and 10 June; Table 2); between one and five experienced collectors worked each day. On 2, 3,

Table 1. Numbers and locations of marked exuviae (ME) of *O. rupinsulensis* recovered on bank stations of the Eau Claire River, Wisconsin (USA), during 2–10 June 2009. Marks on right (R) or left (L) abdominal tergites indicated the river side of capture and release (at upstream ends of MR6).

Station length (m)	Marking riffle (MR) station	North (left) bank station	Numbers of ME recovered along the north bank	South (right) bank station	Numbers of ME recovered along the south bank
30.5		N1		S1	
30.5		N2		S2	
30.5		N3		S3	
30.5		N4		S4	
7.6	MR1	N5		S5	
7.6	MR2	N6		S6	
7.6	MR3	N7		S7	
7.6	MR4	N8		S8	
7.6	MR5	N9		S9	L = 1
7.6	MR6	N10	L = 6	S10	R = 7; L = 1
7.6	MR7	N11	L = 2	S11	R = 1; L = 2
7.6	MR8	N12	R = 2; L = 1	S12	R = 3
7.6	MR9	N13	R = 1	S13	R = 3
7.6	MR10	N14		S14	R = 2
7.6	MR11	N15		S15	R = 2
7.6	MR12	N16	R = 1	S16	
7.6	MR13	N17	R = 2	S17	
30.5		N18		S18	R = 1
20.4		N19		S19	

Table 2. Numbers of *O. rupinsulensis* exuviae collected (marked and unmarked combined) according to reach station, MR station, MR collection trip number, date, and bank side during early June 2009 from the Eau Claire River, Wisconsin, USA (north bank/south bank; nc = no collection).

		1st trip			2nd trip	3rd trip
Reach station	MR station	2 June	3 June	4 June	5 June	9/10 June
N1/S1		124/122				123/nc
N2/S2		128/94				75/nc
N3/S3		108/107				50/nc
N4/S4		167/250				92/nc
N5/S5	MR1	80/40			21/15	14/ 9
N6/S6	MR2	nc/137	89/nc		22/41	16/ 5
N7/S7	MR3		43/142		14/27	14/ 21
N8/S8	MR4		134/166		25/125	15/ 41
N9/S9	MR5		175/137		26/68	27/ 42
N10/S10	MR6		163/158		51/69	14/ 15
N11/S11	MR7		93/101		57/37	25/ 16
N12/S12	MR8		114/111		13/44	30/ 10
N13/S13	MR9		nc/135	59/nc	6/36	8/13
N14/S14	MR10			45/153	4/18	6/16
N15/S15	MR11			29/52	4/18	10/ 6
N16/S16	MR12			63/66	16/20	7/5
N17/S17	MR13			98/47	16/7	8/6
N18/S18				86/249		83/nc
N19/S19				130/187		50/nc
Totals		607/750	811/950	510/754	275/525	667/205

and 4 June, collectors completed one collecting trip on both banks of all 19 stations of the sampling reach. On 5 June, two collectors completed a second collecting trip through all 13 stations of the MR on both banks. On 9 June, two collectors completed a third collecting trip through all 19 stations on the north bank. On 10 June, one collector completed a third collecting trip through

all 13 stations of the MR on the south bank. Thus, three complete collecting trips were made on both banks through all 13 stations of the MR during the nine-day collection period (Table 2). All found exuviae of *O. rupinsulensis* were retained during all of these collections. Exuviae of other species of Anisoptera were retained during some of the collections to inform about the community composition within the reach. On 4 June, three collectors searched for marked exuviae on both banks of the downstream reach from the Outlet Bay Road to SH 27. During this sampling trip the dorsal surfaces of all found exuviae of *O. rupinsulensis* were examined in hand for marks, but no exuviae were retained.

When searching for exuviae along a bank, collectors checked carefully from the water's edge to at least 1.5 m up the bank. Spot checks revealed that in some gradually sloping shoreline areas that lacked clearly defined banks, exuviae were occasionally found up to 3.5 m from the water's edge. Collectors were asked to search as far inland from the shoreline as necessary to find virtually all exuviae of *Ophiogomphus*. Collections were exhaustive, meaning collectors moved slowly while searching and they gently parted vegetation with their hands to improve sight angles (DuBois, 2015a). Equal sampling effort, which was controlled by the collectors, was maintained throughout all collecting trips.

Sampling rates were not measured in this study, but DuBois (2015a) reported a mean sampling rate of about 1 m min^{-1} when collecting exuviae exhaustively along 10 other river banks in northern Wisconsin. Sampling rates in this study were slower than that to an unknown extent because exuvial densities were relatively high, which would have increased the time required to pick exuviae and place them in jars, and the sampling area was wider on average in this study than on any of the study streams searched by DuBois (2015a). Found exuviae were placed in jars with date and location (station number) labels; marked and unmarked exuviae were placed in separate jars. All retained exuviae were examined under magnification in the lab to determine species and to examine jars of unmarked exuviae for erroneously placed marked exuviae that were not noticed in the field. Determinations to species were made using appropriate dichotomous larval keys and by comparison with reared exuviae. Many teneral and immature adults of *Ophiogomphus* were examined along the sampling reach during the course of this study and all were *O. rupinsulensis*.

Total precipitation during the collection period (2.84 cm spread across the last five days) was estimated post hoc by summing the daily totals recorded at the Hayward Municipal Airport (http://www.wunderground.com/history; accessed 27 October 2015), which was located about 35 km south of the study site.

We used the ratio of the number of marked exuviae that were recaptured along the MR in early June 2009 (k) to the number of larvae marked in late September 2008 (K) to calculate a minimum estimate of survival (S) of F-0 larvae of *O. rupinsulensis* during that time period ($S = k/K$). Using that estimate of survival, we calculated an estimate of population size (N) of F-0 larvae of *O. rupinsulensis* in the MR in September 2008 ($N = n/S$, where $n =$ the number of exuviae collected on the banks of the MR).

Results

Species composition, collection totals, and exuvial densities

We collected 8419 Anisoptera exuviae from the banks of the sampling reach during the six collection days, which included 6054 exuviae of *O. rupinsulensis*. Of these, 3829 exuviae of *O. rupinsulensis* were collected from the banks of the MR (average 19.3 exuviae m^{-1}). Numbers of *O. rupinsulensis* exuviae were greater on the south bank (22.0 exuviae m^{-1}) than on the north bank (16.7 exuviae m^{-1}). Four species made up 95% of the total number of exuviae

Table 3. Numbers of exuviae of *O. rupinsulensis* collected per collecting trip (% of line totals) during 2–10 June 2009, and numbers of marked larvae [ML] released and marked exuviae [ME] recovered, on the north and south banks of the MR on the Eau Claire River, Wisconsin, USA.

	Number of exuviae collected (trip)					
	1st trip	2nd trip	3rd trip	Total number of exuviae collected	Number of ML released	Number of ME recovered
North bank	1185 (72%)	275 (17%)	194 (12%)	1654	156	15
South bank	1445 (66%)	525 (24%)	205 (9%)	2175	120	23
Total	2630 (69%)	800 (21%)	399 (10%)	3829	276	38*

*One of these exuviae was found in S18 immediately downstream of the MR.

collected: *O. rupinsulensis* was most abundant (60%), followed by *Gomphus exilis* Selys (18%), *Epitheca cynosura* (Say) (12%), and *Gomphus lividus* Selys (5%). Smaller numbers of exuviae of *Basiaeschna janata* (Say), *Epitheca spinigera* (Selys), *Gomphus adelphus* Selys, *Hagenius brevistylus* Selys, *Ladona julia* (Uhler), and *Libellula quadrimaculata* Linnaeus were also collected along the sampling reach.

Recovery of marked exuviae, survival rate and density of F-0 larvae

We collected 35 marked exuviae on the banks of the sampling reach and found three additional marked exuviae when we examined jars containing collected exuviae from that reach that were thought to be unmarked. Thus, 92% of the marked exuviae collected were recognized in the field.

Overall mark recovery was 14% (38 recovered of 276 marked), which provided a minimum estimate of survival from late September to the following June. According to release and recovery locations, recoveries were 21% for larvae that were released near the south bank and 8% for those released near the north bank (Table 3). Based on 14% survival of F-0 larvae from late September 2008 to early June 2009, the population size in the MR in September 2008 was estimated at 27,350 F-0 larvae, for a mean in-stream density of 22.6 larvae m^{-2}.

Pre-emergent movements

All but one of the 38 recovered exuviae were collected from the MR bank stations; the single exception was found along the 30.5-m station (S18) immediately below the downstream-most MR station at a longitudinal distance of about 72 m from the release point (Table 1). Most of the recovered exuviae (60%) were found along MR bank stations downstream of the release station (MR6), while 37% were found on the banks of the release station. Because all marked larvae were released at the upstream end of MR6, any of those found along the banks of MR6 could have made slight movements downstream (up to 7.6 m) prior to emergence because only station numbers of found exuviae were recorded, not exact locations. Only one marked exuvia was found upstream of the release point in the station immediately above it (MR5). Nearly all recovered exuviae (97%) were found within 60 m of the release point and 79% had moved less than 30 m. Overall, 74% of marked exuviae were found on the same bank as their release point. More marked larvae were released along the north bank (156) than the south bank (120), yet more marked recoveries were found on the south bank (23) than the north bank (15; Table 1). Unmarked exuviae of *O. rupinsulensis* were also collected in greater numbers on the south bank (57%) than the north bank (43%; Table 3).

Discussion

Experimental and sampling designs

Although mark-recapture studies involving odonates have dealt almost exclusively with adults (Cordero-Rivera & Stoks, 2008), this study showed that F-0 larvae can be suitable subjects for some marking study applications if large numbers are marked and exuvial recovery efforts are extensive. Suhling (1994) similarly marked 224 F-0 larvae of *Onychogomphus uncatus* (Charpentier) in October, but recovered just two marked exuviae at the same location the following spring. The two studies differed in the species and systems studied and perhaps other factors, so the reason(s) for the difference in the proportions recovered are unknown.

Key assumptions of mark-recapture studies are that marking does not affect survival, emigration, or recapture rates of animals and that the population be closed to immigration (Cordero-Rivera & Stoks, 2008; Otis, Burnham, White, & Anderson, 1978). Additionally, our goals were that marks would not be lost during the period between the marking date and emergence, that they would not inhibit emergence, and that they would be large enough to be readily seen on exuviae in the field. The superglue and glitter mark we used met all of these goals. Mark retention was clearly complete throughout the study period because marks were easily recognizable 36 weeks after marking with no evidence that any marks were lost. All recoveries still had some glitter adhering to the superglue, but the superglue alone would have left a recognizable mark. We attempted to scrape the mark off larvae and exuviae in the lab with dissecting tools, but were unable to do so without destroying the chitin. Larvae held indoors into February and March 2009 showed readily identifiable marks throughout their time in captivity. Although marks were large, there was no evidence of deleterious effects of the marks on survival of larvae or on their ability to emerge. We note, however, that if marking affected survival, emigration or recapture rates in ways unknown to us, then the survival rate of unmarked larvae during the time frame would be underestimated and the late September population size would be overestimated to an unknown, but possibly substantial, extent. Because mortality of F-0 larvae of Anisoptera has been known to reach or exceed 80% (e.g. Benke & Benke, 1975; Suhling, 1994), the successful emergence of 50% of marked larvae that we reared in captivity argues against a substantial amount of handling-related trauma, and no larvae that appeared to be injured during the collection or marking process were released. Because the marks were large and conspicuous, we cannot rule out the possibility that marked larvae could have experienced higher predation rates by birds or insectivorous fishes than unmarked larvae. The field recognition of 92% of the marked exuviae that were collected on the banks of the sampling reach affirmed that marks were readily visible in the field in the great majority of cases and that few marked exuviae would have been missed along the banks of the river below Outlet Bay Road where exuviae were examined for marks, but were not collected. Further, no marked exuviae were found further than about 72 m from the release point. We therefore conclude that recoveries of marked larvae were affected by high natural mortality between the times of marking and emergence, not to losses of marks, low probability of marked larvae being recovered, or movement of marked larvae out of the study area.

We selected a serially discontinuous river reach for sampling in order to meet the assumption of population closure for mark-recapture studies. Because the reach was isolated by lakes above and below it, and habitat for larvae of *O. rupinsulensis* outside of the MR was evidently suboptimal, it is unlikely that large numbers of larvae populated the MR from elsewhere after the marking date. *Ophiogomphus rupinsulensis* overwinters in the F-0 stadium at the latitude of northern Wisconsin so that synchronous, early emergence in the spring is ensured. We selected a late September marking date because our experience indicated that F-1 larvae that would emerge the following spring would have molted to F-0 prior to the marking date. Gibbs et al. (2004) reported that many larvae of *O. rupinsulensis* and other species of *Ophiogomphus* in a Maine river were in the final stadium during their summer prior to emergence, in some cases as early as June, and that some larvae remained in the final stadium for almost a year prior to emergence. However, we note that no studies have followed individual cohorts of *O. rupinsulensis* throughout the seasons to document stadium frequency at various times. Therefore, while it seems unlikely that many F-1 larvae would have molted to F-0 after the marking date, we cannot make the point with certainty, so it is possible that the population was not fully closed at the time of marking.

The methodologies used in this study for sampling exuviae were similar to those used and discussed by DuBois (2015a) with the following exceptions: collecting trips were made over a nine-day period instead of four consecutive passes in one day, a wider sampling area was set (1.5–3.5 m in horizontal distance inland from the waters' edge versus 1.25 m used by DuBois [2015a]), and sampling efficiencies and detection probabilities were not calculated because the gaps of time between collecting trips violated the key assumption of population closure at the time of sampling. We made collecting trips during the emergence period instead of waiting until emergence had terminated to reduce losses of exuviae left early in the emergence period. We increased the distances searched inland from the water's edge because initial collecting efforts and spot checks revealed the presence of many exuviae further than 1.25 m from the water, particularly along low-gradient shoreline areas. We are not certain why some F-0 larvae moved greater distances from water before emerging in this study than they did at any of the 10 sites sampled by DuBois (2015a). The distances traveled to the supports chosen for ecdysis are known to be correlated with water temperature, air temperature, and moisture (Corbet, 1999), and it is also possible that larvae ascend high gradient, near-vertical banks more slowly than low gradient banks which could cause them to dry while closer to water. This topic would benefit from further research.

Our observations showed that the nine-day time frame of exuviae collections spanned the great majority of the emergence period of *O. rupinsulensis* in the Eau Claire River in 2009. Emergence likely began on 1 June, or at earliest a day or two before. When we arrived on the morning of 1 June, the numbers of F-0 larvae moving toward emergence supports, in the process of emerging, and the numbers of tenerals near their exuviae, all appeared large (though not tallied) relative to the number of unassociated exuviae. By the time of the third collecting trips on the Eau Claire River on 9 and 10 June, the numbers of found exuviae had increased only modestly since 5 June, tenerals were not seen near their exuviae and larvae were no longer found in the process of emerging. Therefore, emergence of *O. rupinsulensis* in 2009 appeared to be largely and perhaps virtually complete by 9 June. Further, *O. rupinsulensis* is known for a closely synchronized, early flight period in Wisconsin where emergence is heaviest early in the emergence period. For example, *O. rupinsulensis* completed 95% of its emergence on average within a nine-day period during three seasons (2002, 2004, and 2006) on the St. Croix River, Burnett County, Wisconsin (RBD unpublished data). Similarly, Suhling (1995) studied the emergence of *Onychogomphus uncatus* in a canal in Southern France where larvae also had overwintered in the final stadium and emergence was synchronous. Although he reported a 24-day emergence period from the canal, the EM_{50} was reached after just five days, and after seven days more than 80% of individuals had emerged, so the brunt of emergence of that species was also strongly front-loaded in the emergence period.

We were evidently inefficient when collecting larvae of *O. rupinsulensis* from a relatively small riffle that was easy to sample in late September, despite considerable sampling effort. While sampling we had gained the impression that a substantial portion of the F-0 larvae in the MR had been collected because collecting more larvae had become increasingly difficult toward the end of the marking day. However, if our 14% survival rate estimate for F-0 larvae from the time of marking to emergence is accurate, then we had actually collected less than 2% of the F-0 larvae present in the MR.

Densities and survival rates

Densities and survival rates have rarely been estimated for late-stadium larvae of *Ophiogomphus*. Gibbs et al. (2004) found that late-summer densities of F-0 larvae of *O. anomalus* Harvey and *O. mainensis* Packard in Walsh ranged from 0 to 35 m^{-2} among sites in the Aroostook River, Maine (USA). These results are similar to ours, although their study was done about a month earlier in the year. Kalniņš (2006) estimated total larval densities of *Gomphus vulgatissimus* (Linnaeus) (0.919 larvae m^{-2}) and *Onychogomphus forcipatus* (Linnaeus) (0.514 larvae m^{-2}) in a Latvian river, but densities of *Ophiogomphus cecilia* (Geoffroy in Fourcroy) there were too low to calculate a reliable value.

We did not identify the specific times or causes of mortality during the time frame of our study, and little is known about this topic for lotic species of Odonata. Suhling (1994) and Schutte, Schridde, and Suhling (1998) reported mortality of F-0 larvae of *Onychogomphus uncatus* in river reaches in southern France that reached or exceeded 90%. Among lentic species of odonates, larvae have usually exhibited most of their mortality in autumn and spring, with lower levels of mortality during winter (Banks & Thompson, 1987; Ubukata, 1981; Wissinger, 1988). However, Johnson (1986) reported substantial mortality of *Epitheca cynosura* (Say) in Tennessee (USA) during winter, and Wissinger (1988) reported heavy winter mortality of *Tramea lacerata* Hagen in Indiana (USA). The amount of mortality incurred by odonates during winter is likely dependent on food availability, crowding, predation pressure, and whether a population is located at latitude near the northern limit of its range (summarized by Corbet, 1999).

Although we cannot provide an estimate with confidence limits of the total number of *O. rupinsulensis* that emerged from the MR in early June of 2009, we suggest that our total collection numbers of exuviae were only slightly less than the number of larvae that emerged from the MR for the following reasons: (1) exhaustive collections spanned virtually the entire period of emergence; (2) banks were searched three times with short amounts of time between them; (3) rainfall, which is known to be a major cause of losses of exuviae (DuBois, 2015a), was relatively light (2.84 cm spread across the last five sampling days); (4) the numbers of exuviae missed after the third collecting trip would have been small; and (5) emergence-related losses of odonates are usually less than 10% (Byers, 1941; Deshefy, 1979; Jakob & Suhling, 2010; Trottier, 1966; Zebsa, Khelifa, Kahalerras, Djalal, & Houhamdi, 2014), although emergence-related mortality has been known to approach 30% (summarized by Corbet, 1999, p. 253).

Pre-emergent movements

The evidence strongly supports the interpretation that F-0 larvae of *O. rupinsulensis* made only slight downstream movements during the 36 weeks prior to their emergence. The exuviae of marked larvae were found on the banks of the MR with only one exception, and distances of marked exuviae downstream of the release point did not exceed 72 m. It is possible that some marked larvae emerged further downstream, below Outlet Bay Road, but their exuviae were not detected during our searches. If this occurred at all, the numbers of marked exuviae involved would have been small for three reasons: (1) two stations downstream of the MR were exhaustively searched, but only a single marked exuviae was found in the upper-most one of them; (2) by the time of the exhaustive searching below Outlet Bay Road on 4 June, emergence was likely past its peak; and (3) the numbers of unmarked exuviae of *O. rupinsulensis* declined dramatically downstream of the marking riffle as well, indicating that unmarked larvae also did not move substantially downstream. Since few if any of the larvae of *O. rupinsulensis* produced in the MR could have originated either in or above Upper Eau Claire Lake, we are confident that the great majority of larvae of all stadia developed within or immediately above the MR (a longitudinal distance of 122 m). Although it remains unclear as to whether or under what conditions some lotic species of Odonata might incorporate drift as a non-trivial part of their life history as do many other aquatic insects, our results concord with those of Gibbs et al. (2004) in showing no evidence of substantial downstream displacement of F-0 larvae of *O. rupinsulensis* via drifting.

The conclusion is therefore firm that F-0 larvae of *O. rupinsulensis* typically made small downstream movements at some time prior to emergence, but that they did not make substantial longitudinal movements either during winter or prior to emergence. This study therefore affirms an important concept that odonate researchers have largely taken for granted – that the locations of found exuviae are in close proximity to the key instream habitats where the larvae were produced. Because of the vital importance of exuviae collections in identifying habitats of larvae, we suggest that similar studies be replicated in other types of lotic habitats, especially in larger waters and in waters with unregulated hydraulic regimes.

Our results also provided some evidence of transverse instream movements of F-0 larvae of *O. rupinsulensis*, although we cannot be certain why recoveries of marked larvae were more than twice as high for those released on the south bank as for those released on the north bank. Indeed, more F-0 larvae were collected on the north side of the thalweg, and were marked, and released near the north shoreline than were collected, marked, and released near the south shoreline (57% versus 43%). Yet, more marked exuviae were collected on the south bank than the north bank (61% versus 39%). Further, greater numbers of unmarked exuviae were also collected on the south bank of the MR than on the north bank (57% versus 43%). Therefore, we tentatively suggest a tendency for larvae of *O. rupinsulensis* to have preferentially emerged on the south bank. In early June at the latitude of the study site, the morning sun rises considerably north of due east. Thus, the south bank is more quickly warmed by the early rays of morning sun than the north bank, which could be of some significance to the genus *Ophiogomphus*, other species of which emerge primarily in the morning (Gibbs et al. 2004; DuBois unpublished data). DuBois (2015b) also noted a case of higher densities of exuviae of several gomphid species on the west bank than the east bank of a northern Wisconsin river, and cited other examples of species of Anisoptera that appeared to prefer certain emergence areas based on sun exposure or shading.

Acknowledgments

We thank D. Johnson, P. McKearn, D. Pleski, J. Pleski, and G. Schuurman for assistance in the field and J. Bleser for creating the map. Funding for this research was provided by the Bureau of Natural Heritage Conservation of the Wisconsin Department of Natural Resources.

ORCID

Robert B. DuBois http://orcid.org/0000-0002-9202-4338

References

Aliberti Lubertazzi, M. A., & Ginsberg, H. S. (2009). Persistence of dragonfly exuviae on vegetation and rock substrates. *Northeastern Naturalist*, *16*, 141–147. Retrieved from http://www.eaglehill.us/NENAonline/articles/NENA-16-1/22-Aliberti.shtml

Arai, Y. (1993). Do larvae of a dragonfly, *Stylogomphus suzukii*, migrate downstream? Abstracts of papers read at the Twelfth International Symposium of Odonatology, Osaka.

Banks, M. J., & Thompson, D. J. (1987). Regulation of damselfly populations: the effects of larval density on larval survival, development rate and size in the field. *Freshwater Biology*, *17*, 357–365. doi:10.1111/j.1365-2427.1987.tb01055.x

Benke, A. C., & Benke, S. S. (1975). Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology*, *56*, 302–317. doi:10.2307/1934962

Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift – a review. *Hydrobiologia*, *166*, 77–93. doi:10.1007/BF00017485

Byers, C. F. (1941). Notes on the emergence and life history of the dragonfly *Pantala flavescens*. *Proceedings of the Florida Academy of Science*, *6*, 14–25.

Corbet, P. S. (1999). *Dragonflies: Behavior and ecology of Odonata*. Ithaca, NY: Cornell University Press.

Cordero-Rivera, A., & Stoks, R. (2008). Mark-recapture studies and demography (Chapter 2). In A. Cordoba-Aguilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (pp. 7–20). New York: Oxford University Press. doi:10.1093/acprof:oso/9780199230693.001.0001

Deshefy, G. S. (1979). Percent unsuccessful eclosion in dragonflies. *The Florida Entomologist*, *62*, 412. Retrieved from http://journals.fcla.edu/flaent/article/view/57431/55110

DuBois, R. B. (2015a). Detection probabilities and sampling rates for Anisoptera exuviae along river banks: influences of bank vegetation type, prior precipitation, and exuviae size. *International Journal of Odonatology*, *18*, 205–215. doi:10.1080/13887890.2015.1045560

DuBois, R. B. (2015b). Do pharate adults of lotic Anisoptera make in-stream movements to preferred emergence sites? *Argia 27*, 9–13. Retrieved from http://www.odonatacentral.org/index.php/IssueAction.get/issue_id/539/volume_id/190

DuBois, R. B., & Stoll, F. M. (1995). Downstream movement of leopard frogs in a Lake Superior tributary exemplifies the concept of a lotic macrodrift. *Journal of Freshwater Ecology*, *10*, 135–139. doi:10.1080/02705060.1995.9663428

Elton, C. (1927). The animal community (Chapter 5). In C. Elton (Ed.), *Animal ecology*. London: Sidgwick & Jackson. Retrieved from http://www.lancaster.ac.uk/users/philosophy/awaymave/onlineresources/animal%20community.pdf

Gibbs, K. E., Bradeen, B., & Boland, D. (2004). Spatial and temporal segregation among six species of coexisting *Ophiogomphus* (Odonata: Gomphidae) in the Aroostook River, Maine. *Northeastern Naturalist*, *11*, 295–312. Retrieved from http://www.jstor.org/stable/3858420

Jakob, C., & Suhling, F. (2010). Risky times? Mortality during emergence in two species of dragonflies (Odonata: Gomphidae, Libellulidae). *Aquatic Insects*, *21*, 1–10. doi:10.1076/aqin.21.1.1.4537.

Johnson, D. M. (1986). The life history of *Tetragoneuria cynosura* (Say) in Bays Mountain Lake, Tennessee, United States (Anisoptera: Corduliidae). *Odonatologica*, *15*, 81–90. Retrieved from http://natuurtijdschriften.nl/search?identifier = 591735;keyword = Odonatologica

Kalniņš, M. 2006. The distribution and occurrence frequency of Gomphidae (Odonata: Gomphidae) in river Gauja. *Acta Universitatis Latviensis*, *710*, 17–28. Retrieved from http://leb.daba.lv/047_Kalnins2006.pdf

Oertli, B. (2008). The use of dragonflies in the assessment and monitoring of aquatic habitats (Chapter 7). In A. Cordoba-Aguilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (pp. 79–95). New York: Oxford University Press. doi:10.1093/acprof:oso/9780199230693.001.0001

Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, *62*, 1–135. Retrieved from http://www.jstor.org/stable/3830650

Raebel, E. M., Merckx, T., Riordan, P., MacDonald, D. W., & Thompson, D. J. (2010). The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys. *Journal of Insect Conservation*, *14*, 523–533. doi:10.1007/s10841-010-9281-7

Schutte, C., Schridde, P., & Suhling, F. (1998). Life history patterns of *Onychogomphus uncatus* (Charpentier) (Anisoptera: Gomphidae). *Odonatologica*, *27*, 71–86. Retrieved from http://natuurtijdschriften.nl/search?identifier = 592227;keyword = Odonatologica

Suhling, F. (1994). Einnischungsmechanismen der Larven von *Onychogomphus uncatus* (Charpentier) (Odonata, Gomphidae). (Dissertation, Technische Universitat Braunsch-weig), Cuvillier-Verlag, Gottingen. (cited by Corbet, 1999)

Suhling, F. (1995). Temporal patterns of emergence of the riverine dragonfly *Onychogomphus uncatus* (Odonata: Gomphidae). *Hydrobiologia*, *302*, 113–118. doi:10.1007/BF00027036

Trottier, R. (1966). The emergence and sex ratio of *Anax junius* Drury (Odonata: Aeshnidae) in Canada. *The Canadian Entomologist*, *98*, 794–798. doi:10.4039/Ent98794-8

Ubukata, H. (1981). Survivorship curve and annual fluctuation in the size of emerging population of *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *Japanese Journal of Ecology*, *31*, 335–346. Retrieved from http://ci.nii.ac.jp/naid/110001881630/en

Wissinger, S. A. (1988). Spatial distribution, life history and estimates of survivorship in a fourteen-species assemblage of larval dragonflies (Odonata: Anisoptera). *Freshwater Biology*, *20*, 329–340. doi:10.1111/j.1365-2427.1988.tb00458.x

Zebsa, R., Khelifa, R., Kahalerras, A., Djalal, H., & Houhamdi, M. (2014). Emergence pattern, site selection, and seasonal regulation of *Onychogomphus costae* Selys, 1885 (Odonata: Gomphidae) in northeastern Algeria. *Aquatic Insects*, *36*, 257–265. doi:10.1080/1650424.2015.1087574