Research Brief

Responses of epiphytic aquatic macroinvertebrates to hypoxia

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Abstract

Different species of aquatic macrophytes have strongly contrasting effects on the oxygen dynamics of the waters they inhabit. We conducted laboratory experiments to test the hypothesis that macroinvertebrates inhabiting stands of the floating-leaved water-chestnut (*Trapa natans*), which causes severe hypoxia, are more resistant to low oxygen concentrations (0.5–1 mg L^{-1}) than those that inhabit submerged aquatic vegetation (*Vallisneria americana* and *Myriophyllum spicatum*), which do not cause hypoxia. Chironomids and amphipods associated with *T. natans* were more resistant to hypoxia than those associated with submerged plants, in support of our hypothesis. Gastropods showed the opposite pattern. Survival was significantly related to exposure time as well in these 3 groups. Ostracods from the 2 habitats were equally resistant to hypoxia, with high survival regardless of exposure time. Almost all zygopterans died when exposed to hypoxia. Different kinds of macroinvertebrates have distinct responses to hypoxia, so different kinds of hypoxic macrophyte beds may support distinct assemblages of macroinvertebrates. Specifically, the spatial and temporal extent of hypoxia will be critical, and shifts in macrophyte species composition caused by species invasions or other reasons may have differential effects on macroinvertebrates by causing different oxygen regimes.

Key words: dissolved oxygen, invasive species, macrophyte-dwelling fauna, submerged vegetation, *Trapa natans*

Introduction

Many organisms rely on the habitats that aquatic macrophytes create in lakes and rivers. These plants not only provide physical structure that can be used for attachment, sheltering, feeding, and refuge by organisms (Taniguchi et al. 2003, Dibble and Pelicice 2010), but they also control chemical and physical aspects of water and sediments (Kleeberg et al. 2010, Tall et al. 2011), and thus are ecosystem engineers (Bouma et al. 2005, Caraco et al. 2006). Among the many features that aquatic macrophytes can control, dissolved oxygen is one of the most crucial in determining the suitability of macrophyte-created habitats for animals.

Daily variation of dissolved oxygen is expected within dense macrophyte beds, with high concentrations during the day, when light is most available to photosynthesis, and lower concentrations at night, when respiration dominates (Jones et al. 1996, Miranda et al. 2000, Thomaz et al. 2001, Colon-Gaud et al. 2004). This dynamic is influenced by the architecture of plants and the size and density of stands, as well, because they affect water circulation and atmosphere exchange, and thus oxygen movement (Jones et al. 1996, Miranda and Hodges 2000, Bunch et al. 2010).

Specifically, oxygen dynamics in emergent and floating-leaved macrophyte beds are expected to differ from those in submerged plants. Emergent and floating-leaved macrophytes release photosynthesis-produced oxygen to the atmosphere while consuming it from the water during respiration, increasing the occurrence of hypoxia (Caraco et al. 2006, Bunch et al. 2010). Thus, different macrophyte communities will have different impacts on dissolved oxygen dynamics and therefore will demand different adaptations of their faunas.

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Different kinds of macrophytes often support different kinds of macroinvertebrates (Strayer et al. 2003, Phiri et al. 2011, Walker et al. 2013). We asked whether differing adaptations to hypoxia or lack of such adaptations might underlie observed differences in macroinvertebrates across different macrophytes. Specifically, we tested the hypothesis that the macroinvertebrates inhabiting water-chestnut (*Trapa natans*) beds, a floating-leaved plant that produces severe hypoxia, are more resistant to hypoxia than those inhabiting submerged vegetation, where hypoxia does not occur, and discuss what adaptations could lead to differences in resistance to hypoxia.

Study area

North and South Tivoli Bays encompass 290 ha of freshwater tidal marshes, subtidal shallows, and intertidal mudflats along 3 km of the eastern shore of the Hudson River. The marshes are dominated by narrow-leaved cattail (*Typha angustifolia*), the subtidal shallows by the submerged species *Vallisneria americana* and *Myriophyllum spicatum*, and the South Bay mudflats are now dominated by the nonnative *T. natans* (Yozzo et al. 2005). All these macrophytes support dense and diverse macroinvertebrate communities, although species composition is not the same among the different macrophytes (Strayer et al. 2003, Kornijów et al. 2010, Yozzo and Osgood 2013).

Dissolved oxygen dynamics in these habitats were described by Caraco and Cole (2002), who showed that *T. natans*-dominated sites are frequently severely hypoxic (dissolved oxygen <2.5 mg L^{-1}), but normoxia is restored every 6 hours when they are flooded with well-oxygenated water. They also showed that sites dominated by submerged aquatic vegetation are rarely hypoxic.

Materials and methods

Experimental design

To determine if macroinvertebrates from *T. natans* (TNA) and submerged aquatic vegetation (SAV) differed in their resistance to hypoxia, we experimentally subjected members of higher taxa that occur in both TNA and SAV habitats to hypoxic conditions and compared their survival. We used paired hypoxic treatments and normoxic controls, repeated in blocks of 3–5 replicates according to the availability of organisms. This setting (Fig. 1) was repeated independently for organisms of different origins, TNA, and SAV, within each of 5 taxonomic groups: Amphipoda, Chironomidae, Gastropoda, Ostracoda, and Zygoptera. We used 2 incubation periods: 6 h to simulate the hypoxia that occurs in tidal habitats; and 18 h to simulate longer-term hypoxia.

Collecting the macroinvertebrates

Organisms were collected from TNA beds in South Tivoli Bay and from SAV beds in North Tivoli Bay 1 day before each trial from mid-August until late September 2013, a period that usually encompasses both TNA and SAV peak biomasses (Caraco and Cole 2002). The water used in the trials was collected from the same sites as the organisms. We used a bucket to wash the invertebrates off macrophytes and a plankton net (118µm mesh size) to concentrate them. Organisms were kept in jars on ice while transported. In the laboratory, animals were sorted under a microscope and kept in jars until trials were run the next day (amphipods were kept in aerated water and fed live chironomids up to 5 days prior to one of the trials due to difficulties in finding enough organisms).

Experimental setting

We sparged half of the water with nitrogen gas until the dissolved oxygen (DO) concentration was 0.5–1 mg L^{-1}. The remaining water was oxygenated when needed until DO concentrations were 8.5–9 mg L^{-1}. Water was distributed into 300 mL biological oxygen demand bottles that served as experimental units. We then measured DO and temperature (YSI ProODO meter) in each bottle, added 10 (ostracods) or 5 (all other groups) specimens from either SAV or TNA, and sealed the bottles. Each bottle contained 1–5 species of each group (Amphipoda, Chironomidae, Gastropoda, Ostracoda, and Zygoptera), and no substrate was used.

After 6 or 18 h, we opened the bottles, measured DO and temperature, and counted live and dead organisms. We considered animals dead if they did not move spontaneously or respond to touch within 5 minutes of observation. The total number of organisms recovered, which differed for some groups from the initial number probably due to predation and/or difficulties in handling, was used to calculate the survival percentage. All organisms were kept in 70% alcohol for later taxonomic identification (Supplementary Table S1).

Data analysis

From the number of live and dead organisms, we calculated a survival rate for treatments and controls by dividing the number of live animals by the number of total animals in each bottle. We then divided the survival rate in the hypoxic treatments by the survival rate in the normoxic controls to account for mortality due to reasons other than hypoxia. This final value, which we call survival, was used as the response variable in our statistical analysis.

We applied PERMANOVAs to test for differences between the survival of organisms from different origins

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(TNA vs. SAV) for different periods of hypoxia (6 and 18 h). The analysis was made considering all groups together, as well as for individual taxonomic groups (Amphipoda, Chironomidae, Gastropoda, Ostracoda, Zygoptera). A PERMANOVA tests the null hypothesis that the group (treatments) centroids in a Euclidian space (if the Euclidian distance was used) are equivalent for all groups, meaning there is no effect of the factors being tested (Anderson and Walsh 2013). Significance of differences among treatments is tested via permutation, so the analysis is robust to heterogeneity in data variances for balanced designs (Anderson and Walsh 2013). Tests were performed with R (R Core Team 2013).

Results

Initial and final concentrations of DO in hypoxic treatments averaged (mean ± SD) 0.69 ± 0.2 and 0.25 ± 0.3 mg L^{-1}, respectively, while normoxic concentrations averaged 8.65 ± 0.3 mg L^{-1} at the beginning of experiments and 7.29 ± 1.5 mg L^{-1} at the end. Most (97 ± 9%, SAV and TNA, 6 and 18 h, n = 98) animals survived in the normoxic controls, which indicates that handling and experimental conditions alone did not kill many animals.

When we combined data for all taxa, we found no significant differences between TNA- and SAV-dwelling organisms (Fig. 2; Table 1). There was a significant effect of time, however; we observed that increasing exposure time from 6 to 18 h reduced average survival.

When we analyzed data of each group separately, we observed distinct responses of taxa to hypoxia (Fig. 2; Table 1). Amphipod survival was affected by the interaction of origin and time. The organisms from TNA were more resistant than those from SAV for the 6 h trial, but they were equally highly sensitive (0% survival) to 18 h hypoxia. Chironomids were affected both by exposure time and marginally by origin. Contrary to our hypothesis, gastropod survival was higher for animals from SAV in both the 6 and 18 h trials, and the effects of time and origin were statistically significant. Few zygopterans survived any of the hypoxic treatments. Ostracods were resistant to hypoxia regardless of origin and exposure time.

Discussion

Our results provided little support for our hypothesis that macroinvertebrates from TNA are more resistant to hypoxia than those from SAV. Only results for amphipods supported our hypothesis. Chironomids were affected chiefly by exposure time but tended to be more resistant when collected in TNA than SAV. The results for gastropods were the opposite of our prediction; survival was higher for organisms collected in SAV than for those from TNA. The other groups showed no effects of origin and time, with high mortality of zygopterans and high survival of ostracods. Thus, our results indicate that the differences in macroinvertebrate community composition found by Strayer et al. (2003) between TNA and SAV cannot be attributed to differential resistance to hypoxia.

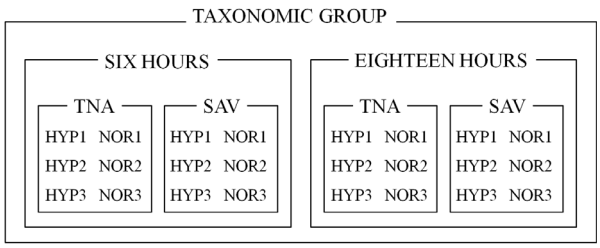

Fig. 1. Experimental design. Taxonomic groups: amphipods, chironomids, gastropods, ostracods, and zygopterans; TNA = *Trapa natans* stands; SAV = submerged aquatic vegetation stands; HYP = hypoxia; NOR = normoxia. Numbers denote replicates, which varied among taxa from 3 to 5.

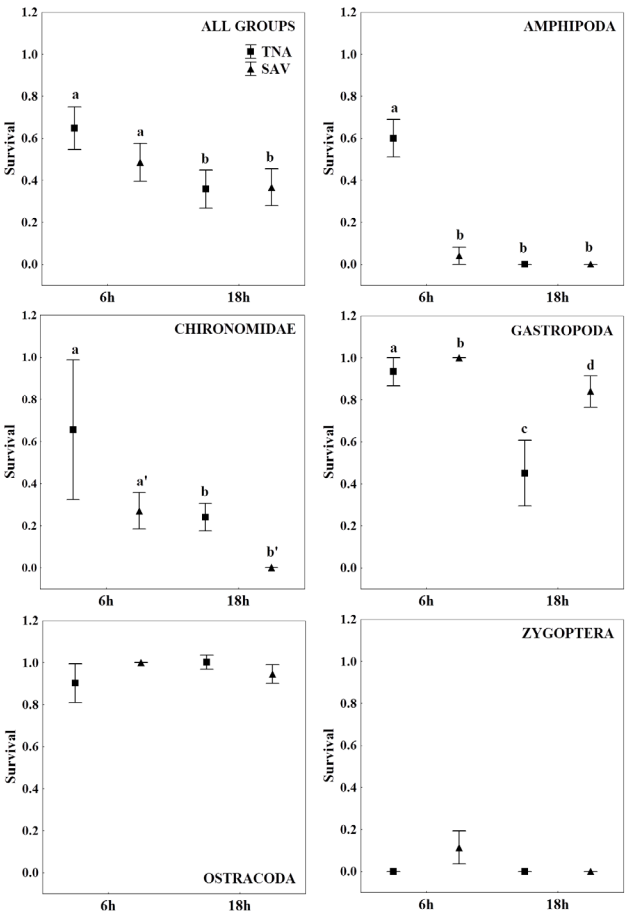

Fig. 2. Survival under hypoxia (mean ± standard error) of organisms associated with *T. natans* (TNA) and submerged aquatic vegetation (SAV) in 6 and 18 h exposures. Different letters indicate significant difference ($p < 0.05$), and the apostrophes indicate near significant difference ($p < 0.06$).

Table 1. PERMANOVA results for the effects of origin (TNA or SAV) and time (6 or 18 h) on survival of invertebrates under hypoxia.

	Factor	Pseudo-F	p
All groups	Origin	0.749	0.382
	Time	4.601	**0.034**
	Origin*time	0.667	0.422
Amphipoda	Origin	32.667	**0.000**
	Time	42.667	**0.000**
	Origin*time	32.667	**0.000**
Chironomidae	Origin	3.195	**0.054**
	Time	3.838	**0.029**
	Origin*time	0.172	0.801
Gastropoda	Origin	8.252	**0.011**
	Time	8.685	**0.010**
	Origin*time	2.494	0.134
Ostracoda	Origin	0.144	0.715
	Time	0.176	0.675
	Origin*time	2.033	0.172
Zygoptera	Origin	1.170	0.290
	Time	1.949	0.217
	Origin*time	1.170	0.475

Our results also allow us to infer to a certain extent the mechanisms that each group of macroinvertebrates may use to survive in hypoxic TNA beds. The chironomids and amphipods from TNA and SAV had different tolerances to hypoxia. Some members of each of these groups have hemoglobin or hemocyanin (Sutcliffe 1984, Spicer 1993, Panis et al. 1996), and it is possible that interspecific or intraspecific variation in concentrations of such respiratory pigments account for these differences. Among the chironomids, differences in structures such as thoracic horns or fringed anal lobes (Marziali et al. 2006), ventilatory movements (Panis et al. 1996), or the ability to perform long-term anaerobic metabolism (Frank 1983, Hamburger et al. 1995, 2000) could help the species living in TNA survive hypoxia. Because their composition varied between TNA and SAV, differences in all these traits could possibly account for the differences in survival. Amphipods, however, belonged to only one genus, possibly one species, so there is the interesting possibility of populations from TNA and SAV being differentially adapted to hypoxia. Also worth noting is that the mechanism used by amphipods (whether respiratory pigments or some other mechanism) was effective for 6 h exposure, but not for 18 h, highlighting the importance of hypoxia duration.

Higher survival of gastropods associated with SAV in comparison with those associated with TNA is probably related to the different species found in those habitats and used in the trials. *Amnicola limosa*, which was much more abundant in TNA than in SAV, is the only species we used that does not have lungs, and therefore, is the only test organism independent of atmospheric oxygen. Results show, however, that even the species with lungs were able to resist hypoxia. Among additional possible mechanisms for gastropods is the presence of respiratory pigments (Von Brand et al. 1948, Alyakrinskaya 2004) and the ability of oxy-regulation (Hanley and Ultsch 1999).

Ostracods were highly resistant to hypoxia, regardless of habitat of origin, even in 18 h trials. Previous studies have also shown that some ostracods tolerate low DO (Hagerman 1969, Rossi et al. 2002), although some species may be sensitive to it (Rosseti et al. 2004, Ruiz et al. 2013). The presence of respiratory pigments in ostracods (Fox 1957) is the most probable mechanism allowing them to survive hypoxia because they are not capable of regulating DO consumption (Corbari et al. 2004, 2005) or changing to an anaerobic metabolism (Rossi et al. 2002).

Zygopterans had high mortality in all hypoxia treatments, regardless of the length of the trial or the origin of the animals, yet they are abundant in nature in TNA beds (Strayer et al. 2003, Kornijów et al. 2010). This finding suggests that some mechanism not tested in our trials allows these animals to survive in natural TNA beds. For example, zygopterans migrate toward the water surface to find higher DO concentrations (Robinson et al. 1991, Apodaca and Chapman 2004, Sesterhenn et al. 2013), which might be an important mechanism in Hudson River habitats; Strayer et al. (2003) found them to occur on plants but not sediments, and Kornijów et al. (2010) collected them from TNA leaves but not from other parts of the plants.

Macroinvertebrates inhabiting hypoxic macrophyte beds such as TNA beds in the Hudson therefore have 2 alternatives to cope with the hypoxic habitat within the beds: they can escape to more oxygenated micro-habitats, or they possess adaptations to survive through hypoxia. The first alternative was not available for the animals in our experiment, so with the exception of Zygoptera, which must survive hypoxia by escaping to oxygen-rich zones, all other groups tested must have adaptations to survive hypoxia in place. Ostracoda displayed the same ability to survive hypoxia whether their habitat requires them to do so (TNA beds) or not (SAV). In comparison, Chironomidae and Amphipoda inhabiting TNA beds have better resistance to hypoxia than their relatives in SAV, while SAV-associated Gastropoda were more able to cope with hypoxia than those associated with TNA.

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DO is not the only variable that differs between TNA and SAV beds. Plant structure itself influences macroinvertebrate composition through many mechanisms, such as food availability and refuge efficacy against predation (Cremona et al. 2008, Fisher et al. 2012). Many other physical and chemical characteristics, some of which can also be regulated by macrophytes, can influence the fauna and interact with DO dynamics in determining community composition (Strayer and Malcom 2007 and references therein). Because DO is a basic need for all animals, however, it represents a strong link between macrophytes and associated organisms.

Because of their engineering activities on DO, macrophyte beds can pose challenges as well as benefits for the macroinvertebrates that live there. Whether through their regular dark respiration and daylight photosynthesis or growth form-related DO fluctuations, large macrophyte beds create peculiar habitats with abiotic filters that may require specific adaptations of organisms. Our results show that these challenges can be met in several ways by macroinvertebrates: probable movement to nearby oxygenated habitats by zygopterans; short-term (6–18 h) tolerance of hypoxia by amphipods and chironomids; and long-term (>18 h) tolerance of hypoxia by gastropods and ostracods. Because different invertebrates meet the challenge of hypoxia in different ways, different kinds of hypoxic macrophyte beds may support different assemblages of macroinvertebrates. Specifically, the spatial and temporal extent of hypoxia will be critical, such as whether well-oxygenated refuges are nearby, or whether the hypoxia is brief (overnight or during a tidal cycle) or long-term. Likewise, shifts in macrophyte species composition caused by species invasions or other reasons may have differential effects on macroinvertebrates that are caused by different oxygen regimes.

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References

Alyakrinskaya IO. 2004. Tissue hemoglobins of Gastropoda (Mollusca). Biol Bull. 31:519–531.

Anderson MJ, Walsh DC. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr. 83:557–574.

Apodaca CK, Chapman LJ. 2004. Larval damselflies in extreme environments: behavioral and physiological response to hypoxic stress. J Insect Physiol. 50:767–775.

Bouma TJ, de Vries MB, Low E, Peralta G, Tánczos IC, van de Koppel J, Herman PMJ. 2005. Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. Ecology. 86:2187–2199.

Bunch AJ, Allen MS, Gwinn DC. 2010. Spatial and temporal hypoxia dynamics in dense emergent macrophytes in a Florida lake. Wetlands. 30:429–435.

Caraco NF, Cole JJ. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in large river. Ecol Appl. 12:1496–1509.

Caraco NF, Cole JJ, Findlay S, Wigand C. 2006. Vascular plants as engineers of oxygen in aquatic systems. BioScience. 56:219–225.

Colon-Gaud J, Kelso WE, Rutherford DA. 2004. Spatial distribution of macroinvertebrates inhabiting hydrilla and coontail beds in the Atchafalaya Basin, Louisiana. J Aquat Plant Manage. 42:85–91.

Corbari L, Carbonel P, Massabuau J. 2004. How a low tissue O_2 strategy could be conserved in early crustaceans: the example of the podocopid ostracods. J Exp Biol. 207:4415–4425.

Corbari L, Carbonel P, Massabuau J. 2005. The early life history of tissue oxygenation in crustaceans: the strategy of the myodocopid ostracod *Cylindroleberis mariae*. J Exp Biol. 208:661–670.

Cremona F, Planas D, Lucotte M. 2008. Biomass and composition of macroinvertebrate communities associated with different types of macrophyte architectures and habitats in a large fluvial lake. Fund Appl Limnol. 171:119–130.

Dibble ED, Pelicice FM. 2010. Influence of aquatic plant-specific habitat on an assemblage of small neotropical floodplain fishes. Ecol Freshw Fish. 19:381–389.

Fisher JC, Kelso WE, Rutherford DA. 2012. Macrophyte mediated predation on hydrilla-dwelling macroinvertebrates. Fund Appl Limnol. 181:25–38.

Fox HM. 1957. Haemoglobin in the Crustacea. Nature. 164:59.

Frank C. 1983. Ecology, production and anaerobic metabolism of *Chironomus plumosus* L. larvae in a shallow lake. II Anaerobic metabolism. Arch Hydrobiol. 96:354–362.

Hagerman L. 1969. Respiration, anaerobic survival and diel locomotory periodicity in *Hirschmannia viridis* Müller (Ostracoda). Oikos. 20:384–391.

Hamburger K, Dall PC, Lindegaard C. 1995. Effects of oxygen deficiency on survival and glycogen content of *Chironomus anthracinus* (Diptera, Chironomidae) under laboratory and field conditions. Hydrobiologia. 297:187–200.

Hamburger K, Dall PC, Lindegaard C, Nilson IB. 2000. Survival and energy metabolism in an oxygen deficient environment: field and laboratory studies on the bottom fauna from the profundal zone of Lake Esrom, Denmark. Hydrobiologia. 432:173–188.

Hanley RW, Ultsch GR. 1999. Ambient oxygen tension, metabolic rate, and habitat selection in freshwater snails. Arch Hydrobiol. 144:195–214.

Jones JI, Hardwick K, Eaton JW. 1996. Diurnal carbon restriction on the photosynthesis of dense stands of *Elodea nuttallii* (Planch) St. John. Hydrobiologia. 340:11–16.

Kleeberg A, Köhler J, Sukhodolova T, Sukhodolov A. 2010. Effects of aquatic macrophytes on organic matter deposition, resuspension and phosphorus entrainment in a lowland river. Freshwater Biol. 55:326–345.

Kornijów R, Strayer DL, Caraco NF. 2010. Macroinvertebrate communities of hypoxic habitats created by an invasive plant *Trapa natans* in the freshwater tidal Hudson River. Fund Appl Limnol. 176:199–207.

Marziali L, Lencione V, Rossaro B. 2006. Adaptations of pupae of Chironomidae (Insecta: Diptera) to oxygen-poor habitats. Pol J Ecol. 54:687–693.

Miranda LE, Driscoll MP, Allen MS. 2000. Transient physicochemical microhabitats facilitate fish survival in inhospitable aquatic plant stands. Freshwater Biol. 44:617–628.

Miranda LE, Hodges KB. 2000. Role of aquatic vegetation coverage on hypoxia and sunfish abundance in bays of a eutrophic reservoir. Hydrobiologia. 427:51–57.

Panis LI, Goddeeris B, Verheyen R. 1996. On the relationship between vertical microdistribution and adaptations to oxygen stress in littoral Chironomidae (Diptera). Hydrobiologia. 318:61–67.

Phiri C, Chakona A, Day JA. 2011. Aquatic insects associated with two morphologically different submerged macrophytes, *Lagarosiphon ilicifolius* and *Vallisneria aethiopica*, in small fishless ponds. Aquat Ecol. 45:405–416.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing; [cited October 31, 2013]. Available from http://www.R-project.org

Robinson JV, Shaffer LR, Hagemier DD, Smatresk NJ. 1991. The ecological role of caudal lamellae loss in the larval damselfly, *Ischnura posita* (Hagen) (Odonata: Zygoptera). Oecologia. 87:1–7.

Rosseti G, Bartoli M, Martens K. 2004. Limnological characteristics and recent ostracods (Crustacea, Ostracoda) of freshwater wetlands in the Parco Oglio Sud (Northern Italy). Ann Limnol. 40:329–341.

Rossi V, Todeschi EBA, Gandolfi A, Invidia M, Menozzi P. 2002. Hypoxia and starvation tolerance in individuals from a riverine and a lacustrine population of *Darwinula stevensoni* (Crustacea: Ostracoda). Arch Hydrobiol. 154:151–171.

Ruiz F, Abad M, Bodergat AM, Carbonel P, Rodríguez-Lázaro J, Gonzalez-Regalado ML, Toscano A, Garcia EX, Prenda J. 2013. Freshwater ostracods as environmental tracers. Int J Environ Sci Tec. 10:1115–1128.

Sesterhenn TM, Reardon EE, Chapman LJ. 2013. Hypoxia and lost gills: respiratory ecology of a temperate larval damselfly. J Insect Physiol. 59:19–25.

Spicer J. 1993. Oxygen binding by amphipod (Crustacea) haemocyanins. Mar Behav Physiol. 24:123–136.

Strayer DL, Lutz C, Malcom HM, Munger K, Shaw WH. 2003. Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. Freshwater Biol. 48:1938–1949.

Strayer DL, Malcom HM. 2007. Submersed vegetation as habitat for invertebrates in the Hudson River estuary. Estuar Coast. 30:253–264.

Stucliffe DW. 1984. Quantitative aspects of oxygen uptake by *Gammarus* (Crustacea, Amphipoda): a critical review. Freshwater Biol. 14:443–489.

Tall L, Caraco N, Maranger R. 2011. Denitrification hot spots: dominant role of invasive macrophyte *Trapa natans* in removing nitrogen from a tidal river. Ecol Appl. 21:3104–3114.

Taniguchi H, Nakano S, Tokeshi M. 2003. Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. Freshwater Biol. 48:718–728.

Thomaz SM, Enrich-Prast A, Gonçalves JF Jr, dos Santos AM, Esteves FA. 2001. Metabolism and gaseous exchanges in two coastal lagoons from Rio de Janeiro with distinct limnological characteristics. Braz Arch Biol Techn. 44:433–438.

Von Brand T, Nolan MO, Mann ER. 1948. Observations on the respiration of *Australorbis glabratus* and some other aquatic snails. Biol Bull. 95:199–213.

Walker PD, Wijnhoven S, van der Velde G. 2013. Macrophyte presence and growth form influence macroinvertebrate community structure. Aquat Bot. 104:80–87.

Yozzo DJ, Andersen JL, Cianciola MM, Nieder WC, Miller DE, Ciparis S, McAvoy J. 2005. Ecological profile of the Hudson River National Estuarine Research Reserve. Albany (NY): New York Department of Environmental Conservation.

Yozzo DJ, Osgood DT. 2013. Invertebrate communities of low-salinity wetlands: overview and comparison between *Phragmites* and *Typha* marshes within the Hudson River estuary. Estuar Coasts. 36:575–584.

Supplementary Material

Supplementary Material is available for download via the Inland Waters website, https://www.fba.org.uk/journals/index.php/IW:

Supplementary table S1.

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