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Abstract

Seventy-four specimens from four genera of native gastropods were cooled from 2.0°C to — 3.3°C over a 3 hour period under laboratory conditions. The taxa examined included two terrestrial pulmonates {Anguispira alternata and Mesodon inflecta), a pulmonale known to occupy both permanent and ephemeral aquatic habitats {Physella mtegra), and an aquatic prosobranch {Pleurocera canaliculatum) . There was no mortality in the pulmonates, but 39% mortality occurred in the prosobranch Pleurocera. Additionally, a sample of 43 zebra mussels {Dreissena polymorpha), a non-native but recently introduced species, were aerially exposed to the same temperature cycle. Of the 43 mussels, 20 had been acclimated to 2°C, and 23 acclimated to 15°C. Mortality occurred in both treatments (35% mortality in the 15°C acclimated and 25% in the 2°C acclimated) and did not differ significantly between the two groups. No mortality occurred among controls.

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Comparative Survivorship of Sympatric Native North American Gastropods (*Anguispira*, *Mesodon*, *Physella*, *Pleurocera*) and an Introduced Bivalve (*Dreissena*) Exposed to Freezing Temperatures

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Abstract. Seventy-four specimens from four genera of native gastropods were cooled from 2.0°C to −3.3°C over a 3 hour period under laboratory conditions. The taxa examined included two terrestrial pulmonates (*Anguispira alternata* and *Mesodon inflecta*), a pulmonate known to occupy both permanent and ephemeral aquatic habitats (*Physella integra*), and an aquatic prosobranch (*Pleurocera canaliculatum*). There was no mortality in the pulmonates, but 39% mortality occurred in the prosobranch *Pleurocera*. Additionally, a sample of 43 zebra mussels (*Dreissena polymorpha*), a non-native but recently introduced species, were aerially exposed to the same temperature cycle. Of the 43 mussels, 20 had been acclimated to 2°C, and 23 acclimated to 15°C. Mortality occurred in both treatments (35% mortality in the 15°C acclimated and 25% in the 2°C acclimated) and did not differ significantly between the two groups. No mortality occurred among controls.

INTRODUCTION

The most common ways in which organisms survive in a subfreezing environment are avoidance (including supercooling) and/or freeze tolerance. Supercooling, the extension of the liquid phase below the equilibrium freezing point of tissue fluids, has been documented in a diversity of animal groups including various mollusks and intertidal invertebrates, terrestrial arthropods, and both terrestrial and aquatic vertebrates (Storey & Storey, 1988). Freeze tolerance, although less common, has also been reported for such animals as some marine invertebrates and some vertebrates (Storey & Storey, 1988).

Illinois gastropods occur in a wide variety of habitats and include terrestrial, aquatic, and semi-aquatic species. These forms may all be periodically exposed to subfreezing temperatures, particularly during the spring and fall months when ambient temperatures can vary widely within a 24 hour period. However, there is little information available on how these species tolerate periodic and short-term exposure to subfreezing temperatures. The purposes of this study were twofold: (1) to examine the effects of a temperature cycle that would expose four species of native mollusks to freezing temperatures, and (2) to determine whether an introduced mollusk is more or less able to withstand exposure to subfreezing temperatures compared to the native mollusks we studied. Our study was not intended to determine mortality curves or to investigate the efficacy of freezing as a control method for the zebra mussel *Dreissena polymorpha*.

We selected a prosobranch, *Pleurocera canaliculatum* (Say, 1821), which is strictly aquatic and occupies large rivers (Burch, 1982). We also included three pulmonates. One, *Physella integra* (Haldeman, 1841), Family Physidae, is a basommatophoran pulmonate that occupies both permanent and ephemeral aquatic habitats (Te, 1978). Additionally, two terrestrial stylomatophoran species, *Anguispira alternata* (Say, 1816), Family Endodontidae, and *Mesodon inflecta* (Say, 1821), Family Polygyridae, were included. The two terrestrial species are active during spring and fall months and are readily obtained during these seasons. As such, individuals are likely to encounter subfreezing temperatures under natural conditions.

We also included specimens of an introduced bivalve, the zebra mussel *Dreissena polymorpha* (Pallas, 1771), in this study. Zebra mussels attach themselves with a byssus to firm substrates. Included among these substrates are the shells of various species of native unionid bivalves (Nalepa & Schloesser, 1993; Tucker et al., 1993) and species of native gastropods including *P. canaliculatum* (Tucker, 1994).

MATERIALS AND METHODS

Gastropods were collected in October and November 1993 in Madison County, Illinois at the following locations: *P. integra* were collected on 1 November from bullrush stems exposed to air and in water (13°C) of a ditch near the junction of Old Poag Road and Wanda Road, SW¼ Sec. 12, T. 4 N, R. 9 W, 0.3 km W of Poag; *P. canaliculatum* were collected on 3 November crawling on or partially buried in silt-clay substrate in 2 to 8 cm of water (11°C) along the main stem of the Mississippi River at Clifton Terrace Road, NW¼ Sec. 32, T. 6 N, R. 10 W, 0.6 km S of Clifton Terrace; *M. inflecta* and *A. alternata* were collected on 1 November from under debris near Old Poag Road, SW¼ Sec. 12, T. 4 N, R. 9 W, 0.3 km W of Poag; additional specimens of *M. inflecta* were collected on 22 October from the base of bluffs along Illinois Route 100, SE¼ Sec. 4, T. 5 N, R. 10 W, 0.6 km W of Alton. *D. polymorpha* were collected on 8 November from 2 to 20 cm of water (12°C) in clumps or druzes at the boat ramp at Grafton, Jersey County, Illinois. Voucher specimens of all species used in this experiment are deposited in the collections of the Illinois Natural History Survey.

Gastropods were refrigerated at 4°C until 8 November and then kept at 15°C until 20 November. The bivalves were placed in aerated river water and maintained at 15°C until 20 November. On 20 November, 20 of the bivalves were transferred in fresh river water from the collection site to an environmental chamber and gradually cooled to 2°C.

On 20 November, animals were placed in dry, 13 × 18 cm plastic containers, with each species being maintained in a separate container. All animals were gently tamped dry before being placed into the containers. Containers were covered and allowed to equilibrate at 2°C in the environmental chamber for 48 hours. Chamber temperature and the temperature within one of the experimental containers were recorded at 15 minute intervals. Chamber temperature was reduced 1°C after 30 minute intervals until temperatures in the container and the chamber reached −3.1° to −3.3°C. Animals were maintained at this temperature for 30 minutes, gradually warmed to 2°C over a 30 minute interval, and then were transferred to 15°C. *D. polymorpha*, *P. canaliculatum*, and *P. integra* were covered with fresh river water. An additional sample of 20 *P. canaliculatum* were aerially exposed at 5°C for 12 and 24 hours to examine the potential effects of aerial exposure versus the cooling cycle on survivorship. Control samples ($n = 20$) of *D. polymorpha* and *P. integra* were also exposed aerially for periods of at least 24 hours at 5°C. All controls were handled in the same manner as experimental animals excepting exposure to the experimental cooling cycle.

Mortality of mollusks was assessed approximately 12 hours after transfer to 15°C. We believed 12 hr to be adequate time to permit mollusks either to recover from or succumb to the effects of the treatment. Bivalves were considered dead if they continued to gape even after being touched. Gastropods were considered dead if they did not crawl or failed to retract the operculum when it was touched.

Mortality data were analyzed with two-way G tests (Sokal & Rohlf, 1981). Similar to the chi-square test, the G test evaluates the goodness of fit of the observed data relative to expected results. For the experiment we conducted, the G test is the most appropriate statistical test to apply to mortality data (Sokal & Rohlf, 1981) which has but two outcomes (i.e., lived or died). Values for P reported herein were obtained by substituting the G values into a computer chi-square function program (SAS Institute, 1988). All statistically significant P values were sufficient to exclude type I errors at the 0.05 level for these multiple G tests (Rice, 1989).

RESULTS

Ninety-seven of the 117 animals survived the cooling cycle (Table 1). Among gastropods, only *P. canaliculatum* suffered mortality, and this decreased survivorship was significantly different from the other gastropods ($G = 22.273$,

$P < 0.001$, df = 4). Mortality also occurred among *D. polymorpha*, but did not differ significantly between individuals acclimated at 2°C or 15°C ($G = 0.489$, $P > 0.40$, df = 1). The mortality that we observed for *P. canaliculatum* was not significantly different from *D. polymorpha* acclimated at 2° and 15°C ($G = 0.425$, $P. > 0.50$, df = 1). Control samples of *D. polymorpha*, *P. integra*, and *P. canaliculatum* showed no mortality when aerially exposed at 5°C for 24 hours.

At the time that the gastropods were transferred to 15°C, following the cooling cycle, and after being gradually warmed to 2 C, it was noted that almost all of the *M. inflecta* were actively crawling in the experimental containers. Within several minutes after being transferred to 15°C, at least some individuals of *A. alternata* and *P. integra* were also actively crawling in the containers.

Table 1

Survivorship of four species of native gastropods and an introduced bivalve to exposure to subfreezing temperatures. Animals were cooled from +2.0° to −3.1°C to −3.3°C over a period of 3 hours.

	Dead	Alive	Total
Gastropoda			
Anguispira alternata	0	21	21
Mesodon inflecta	0	18	18
Physella integra	0	17	17
Pleurocera canaliculatum	7	11	18
Bivalvia			
Dreissena polymorpha 2°C Acclimated	8	15	23
Dreissena polymorpha 15°C Acclimated	5	15	20
Controls			
Physella integra	0	20	20
Pleurocera canaliculatum	0	20	20
Dreissena polymorpha	0	20	20

DISCUSSION

Our results suggest that both the terrestrial and aquatic species of pulmonates that we studied are much better able to withstand exposure to subfreezing temperatures for short durations than are either the prosobranch or the bivalve that we studied. However, we hesitate to generalize these results to all pulmonates and prosobranchs making up Illinois' diverse molluscan fauna (i.e., Cummings, 1991). Since the former are much more likely to experience such conditions in nature than are the latter, which occupy more predictable aquatic habitats, our results are consistent with the natural histories of these species. There is some evidence, however, that these aquatic species may also occasionally encounter subfreezing temperatures in nature (*Pleurocera*—Dazo, 1965; *Physella*—Cheatum, 1934). *Dreissena polymorpha* may also be exposed to subfreezing temperatures due to fluctuations in water levels during winter months. We observed living individuals of *D. polymorpha* and *P. canaliculatum* exposed during winter drawdowns at the collecting sites in Pool 26 of the Mississippi River, clearly indicating that exposure to subfreezing temperatures occurs in nature.

Because our study was not designed to determine the maximum duration of exposure to subfreezing temperatures that could be tolerated, we do not know if the three pulmonates we studied vary in this trait. However, all three species appeared to recover completely from the cooling cycle once warmed. Therefore, *M. inflecta*, a species near the northern limit of its range in Illinois, was able to tolerate short exposure to subfreezing temperatures as well as the widely distributed *A. alternata*. Likewise, the aquatic pulmonate, *P. integra*, withstood these conditions as well as the two terrestrial pulmonate species. *P. gyrina*, a species closely related to *P. integra*, is known to be active in winter months and has been observed crawling on the underside of the ice in frozen lakes in Illinois (Zetek, 1918).

Although our experiments were not designed to determine freezing kill curves or LT_{50} for differing temperature regimens (e.g., Clarke et al., 1993), our results are remarkably consistent with the LT_{50} at −3°C of 3.2 h determined by Clarke et al. (1993) for *D. polymorpha*. Our cooling cycle exposed this bivalve to subfreezing temperatures averaging −1.7°C for 2.5 h. Not surprisingly, the mortality we observed (35%) was slightly lower than the mortality for the cooling cycle used by Clarke et al. (1993) to arrive at the LT_{50} for −3°C.

Our results suggest that the exotic species, *D. polymorpha*, is able to withstand short-term exposure to subfreezing temperatures as well as the native prosobranch *P. canaliculatum*. Therefore, exposure of *D. polymorpha* to freezing temperatures through river drawdowns, as is practiced in early spring along navigable rivers (Sparks, 1992), will probably not result in greater mortality rates in *D. polymorpha* than in *P. canaliculatum* and provides no relative advantage to either species. Dewatering during the winter months has been suggested as a method to control *D. polymorpha* populations (Claudi & Mackie, 1994). Our results indicate that this technique would likely result in similar levels of mortality in native aquatic gastropods such as *P. canaliculatum*.

The possible effects of aerial exposure may complicate the interpretation of the results of our study for the mollusks that are normally aquatic. Since these animals are usually submerged in water, the mortality we observed may be due to aerial exposure rather than to freezing temperatures. However, *P. canaliculatum* controls that were aerially exposed for 12 and 24 hours at 5°C showed no mortality in this study. Additionally, in other experiments designed to determine effects of aerial exposure on *D. polymorpha* and *P. integra*, we found no mortality among individuals of either species exposed at 5°C for 60 hours (Paukstis et al., unpublished observations; Tucker et al., in press). Thus, we believe that the mortality we observed in this study was due to low temperatures and not to desiccation.

The ability of *M. inflecta*, *A. alternata*, and *P. integra* to tolerate exposure to subfreezing temperatures and to become active at low temperatures following exposure to subfreezing temperatures may be of considerable advantage to these species in areas such as central Illinois where passages of spring and fall cold fronts can result in widely varing ambient temperatures. For *M. inflecta* and *A. alternata*, this may allow active feeding late into the fall and early in the spring, resulting in faster growth and ability to put additional resources into reproductive tissue.

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