Salinity Tolerance and Osmoregulation of the Arctic Marine Amphipods *Onisimus litoralis* (Krøyer) and *Anonyx nugax* (Phipps)

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Salt tolerance and Osmoregulation in Arctic Marine Gammarid Amphipods

Abstract

The gammarid amphipod Onisimus litoralis, which inhabits the Arctic and Subarctic intertidal zone and under-ice environment, is a euryhaline hyperosmotic regulator. It survives 10 d exposures to salinities from 5 to 55°/oo. It exhibits strong hyperregulation of its hemolymph osmotic pressure during 3 h exposures to dilutions of normal seawater and remains hyperosmotic to these media for at least 2 w. It becomes almost isosmotic to higher than normal salinity seawater up to 1600 mOs (≃50°/oo) after exposures of 3 h. After 12 h exposures to any salinity above normal seawater, it is isosmotic to the media. Anonyx nugax, a gammarid inhabiting the Arctic and Subarctic subtidal zone, is a more stenohaline osmoconformer. It tolerates a salinity range from 23 to 45°/oo without significant mortality. Its hemolymph becomes isosmotic to all dilute salinities within its tolerance range after 12 h and osmoconforms to concentrated media after 3 h. The salinity tolerance and osmoregulatory abilities of the 2 species relate to the animals' observed distributions.

Résumé

L'Amphipode gammaridien Onisimus litoralis, qui colonise l'intertidal et la surface inférieure de la glace des zones arctiques et subarctiques, est un régulateur hyperosmotique euryhalin. Il survit à une incubation de 10 jours dans des salinités de 5 à 55°/oo. Il démontre une hyperrégulation forte de sa pression osmotique d'hémolymphe pendant 3 heures dans des salinités diluées et reste hyperosmotique dans ces salinités pendant au moins 2 semaines. Il devient presqu'isosmotique aux salinités élevées jusqu'à 1600 mOs (≃50°/oo) après une incubation de 3 heures. Après 12 heures d'incubation aux salinités plus élevées que la normale il est au moins isosmotique au milieu. Anonyx nugax, un gammaridien de l' infralittoral des zones arctiques et subarctiques, est un conformeur osmotique plus sténohalin. Il tolére des salinités de 23 à 45°/oo sans mortalité significative. Après 12 heures, son hémolymphe devient isosmotique aux salinités diluées et dans les milieux concentrés elle se conforme après 3 heures. Les capacités osmorégulatrices des 2 espèces sont appropriées à leurs aires de distribution respectives.

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Preface

Concerning thesis format

This thesis has been prepared as a paper which has been submitted to the journal "Marine Ecology-Progress Series".

Statement of contribution to co-authorship

Dr. Jonathan A. Percy, the candidate's Research Supervisor at the Arctic Biological Station, appears as second author on the manuscript. His contribution to this work was equivalent to the normal supervision and advice given by a thesis director.

Statement of Contribution to Original Knowledge

To my knowledge and that of my thesis committee the work presented here is the only study of the osmoregulatory capacities of the gammarid amphipods Onisimus litoralis and Anonyx nugax. It is the only study of arctic amphipods which used a wide range of salinities including both dilutions and concentrations of normal seawater and a large number of replicates in each salinity. It is also the most extensive salinity tolerance study of the 2 species. Schneider's (1980) (see Literature Cited) unpublished salinity tolerance study of these and other invertebrates was conducted over a shorter 96 h duration using less salinities and no replicates. He did not study the osmoregulatory abilities of his subjects.

Acknowledgments

Throughout my academic career I have been fortunate enough to be exposed to many quality people. I would like to thank Dr. Henry Reiswig for first introducing me to the invertebrates as an undergraduate and for recently stepping in to help with administrative matters. To Dr. Max Dunbar I extend thanks for introducing me to Arctic Oceanography. I would like to especially thank Dr. Brian Marcotte for both piquing my interest in the crustacea during my senior year and supervising my Graduate work at McGill.

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Running head: Shea & Percy: Osmoregulation in Arctic Amphipods.

Abstract

The gammarid amphipod Onisimus litoralis, which inhabits the Arctic and Subarctic intertidal zone and under-ice environment, is a euryhaline hyperosmotic regulator. It survives 10 d exposures to salinities from 5 to 55°/oo. It exhibits strong hyperregulation of its hemolymph osmotic pressure during 3 h exposures to dilutions of normal seawater and remains hyperosmotic to these media for at least 2 w. It becomes almost isosmotic to higher than normal salinity seawater up to 1600 mOs (≃50°/oo) after exposures of 3 h. After 12 h exposures to any salinity above normal seawater, it is isosmotic to the media. Anonyx nugax, a gammarid inhabiting the Arctic and Subarctic subtidal zone, is a more stenohaline osmoconformer. It tolerates a salinity range from 23 to 45°/oo without significant mortality. Its hemolymph becomes isosmotic to all dilute salinities within its tolerance range after 12 h and osmoconforms to concentrated media after 3 h. The salinity tolerance and osmoregulatory abilities of the 2 species relate to the animals' observed distributions.

Introduction

The osmoregulatory abilities of aquatic animals are the subject of a large body of literature. Krogh (1939) reviewed early studies in this field. Several other authors, including, Potts and Parry (1963), Kinne (1971), Gilles (1975), and Rankin & Davenport (1981) have reviewed much of the modern work. Lockwood (1962, 1977), Kinne (1964), Schoffeniels & Gilles (1970), Kirschner (1979), Gilles (1982), and Mantel & Farmer (1983), among others, have reviewed the work on crustacea. In spite of this interest, salinity tolerance and/or osmoregulation studies of Arctic or Subarctic (sensu Dunbar 1968) Amphipoda are rare (eg. Busdosh and Atlas 1975, Percy 1975, Davenport 1979, Schneider 1980, Aarset and Aunaas 1987).

Although salinity in most of the Arctic and Subarctic is relatively stable (Dunbar 1951, Treshnikov 1977), there are important habitats, such as that of the intertidal zone and also those within or immediately beneath the sea ice, that are characterized by widely fluctuating salinity (Davenport 1979, Schell 1974).

In most regions, intertidal zones are particularly stressful environments (Bruce 1928, Stephenson 1953, Meadows & Campbell 1972, Vernberg and Vernberg 1972). Intertidal zone salinities can fluctuate dramatically. Rain, terrestrial run-off and seepage from the sub-soil can cause surface interstitial salinities on sandy beaches to fall sharply (Reid 1932, Emery & Foster 1948, Smith 1955). Evaporation of the interstitial water of exposed areas can raise surface salinity far above

normal (Emery & Foster 1948).

The salinity of intertidal pools also fluctuates (Rankin & Davenport 1981), however, the lower strata of deeper pools generally have stable salinities (Pyefinch 1943, Davenport et al. 1980). In the Arctic and Subarctic this stability is often lost when the release of salts, during the formation of grease and surface ice in pools, increases the salinity of underlying water (Ganning 1971, Davenport 1979).

The sub-ice habitat is unique to polar and sub-polar latitudes and offers its inhabitants fluctuating environmental salinities. The formation and melting of sea ice causes swings in salinity in the under-ice environment. During initial freeze up, brine is expelled from the ice matrix raising the salinity near the under-ice surface (Bennington 1963, Cox & Weeks 1974). Continued growth of the ice and convective overturn in the brine channels results in a constant release of brine (Lake & Lewis 1970, Niedrauer & Martin 1979). Schell (1974), for example, reported under-ice salinities of up to 65.9°/oo in shallow near-shore areas near Barrow, Alaska. In the spring, melt water from snow forces itself into the brine channel system and flushes out most of the remaining salt (Cox & Weeks 1974). The spill of melt-water into leads and holes in the ice can cause fresh water pools to form under the ice (Hanson 1965).

While both habitats are stressful, an abundance of food makes them attractive to robust species. There is a large input of food into most intertidal zones (Dahl 1953) and the under-ice has a rich, highly

concentrated flora (Apollonio 1961, 1965, Horner & Alexander 1972) that supports a complex food web (Grainger & Hsiao 1982).

To take advantage of either habitat, organisms must avoid, tolerate or regulate against the short and long period fluctuations in salinity that they encounter. However, little is known about the physiological adaptations permitting arctic animals to live in these two habitats. One way to study the adaptations necessary is to carry out comparative studies on similar species that do and do not use these particular habitats. Two such species are the gammarid amphipods Onisimus litoralis and Anonyx nugax.

Onisimus litoralis is a species that makes extensive use of both habitats. It has a circumpolar distribution (Holmquist 1965) and is one of the most abundant intertidal amphipods in the Arctic and Subarctic (Dunbar 1954, Shoemaker 1955, Thomson et al. 1986). During the open water season it can be found in large numbers buried in sand and mud on the intertidal, in tide pools, or in shallow water close to shore (Dunbar 1954, Shoemaker 1955, Steele 1961, Thomson et al. 1986, Shea & Marcotte in prep.). During the ice covered seasons it is associated with the under-ice surface in near-shore areas (L.G.L. Ltd. 1982, Cross & Martin 1983, Shea & Marcotte in prep.).

Anonyx nugax, on the other hand, is a common Arctic and Subarctic species that makes little, if any, use of the intertidal or sub-ice habitats. It has a circumpolar distribution and penetrates into the boreal regions of the North Pacific, Skagerak, North Atlantic, and North Sea (Stephensen 1923). In Northern Canada it is a nearshore benthic

species inhabiting depths ranging from 10 to 120 m (Dunbar 1954, Steele 1961). It has also been taken from depths of 1469 m just north of the Faeroes (Stephensen 1923). It has been taken in small numbers at the under-ice surface (Thomson et al. 1975, Cross & Martin 1983, Shea & Marcotte in prep.) and rarely, and possibly under special circumstances, on beaches (Shoemaker 1955).

Both species are abundant in Upper Frobisher Bay, providing an opportunity for comparative ecophysiological studies. In this study their salinity tolerance and osmoregulatory abilities are compared.

Materials and Methods

Animal Collection

Amphipods were collected from Upper Frobisher Bay, N.W.T., Canada (63° 44'N, 68° 31'W). Onisimus litoralis was collected with a dip net at the water line during a rising tide. Anonyx nugax was collected in modified minnow traps baited with Arctic charr heads wrapped in fine mesh screen. The traps were set on the bottom at depths of 45 m to 55 m.

Animals were transported to the local laboratory in seawater in insulated boxes. The largest size class (14.2 mm ± 1.0 mm S.D. N=67 for Onisimus litoralis and 38 mm ± 3 mm S.D. N=50 for Anonyx nugax) of each species was sorted into holding trays and held without food for 24 h at 0° C before experimentation or further shipping was undertaken.

Live material for the osmoregulation experiment was flown to the Arctic Biological Station (ABS) at Ste. Anne-de-Bellevue, Quebec in

polyethylene bags of seawater in insulated containers. Total transit took less than 7 h and no mortality occurred.

At ABS the animals were held at 1° C ± 1° C and 33°/oo ± 0.5°/oo in a high-capacity refrigerated synthetic seawater (Instant Ocean™) re-circulation system. They were held for at least 72 h before experimentation began. Animals were fed frozen Arctic charr periodically. The light regime followed that of Frobisher Bay. Environmental conditions in the system were favorable since some unused animals became gravid 2 months after the study was completed and many animals survived for more than a year.

Media Preparation

Dilutions of 33°/oo artificial and natural seawater were made using deionized water. A concentrated Instant Ocean™ brine was aged, filtered and diluted with seawater or re-circulation system water to produce high salinity media. The 0°/oo medium was aerated deionized-distilled water. Final values of the various salinities were measured with an Autosal™ 8400A salinometer.

Salinity Tolerance

Effects of acute exposure to extremes in salinity were investigated for each species. Groups of 10 animals per species were incubated in salinities ranging from 0°/oo to 93.5°/oo for Onisimus litoralis and from 10°/oo to 65°/oo for Anonyx nugax. Groups were transferred directly from normal seawater to the test medium. They were held without food in

compartmentalized trays containing 400 ml of medium. Compartments were checked for dead individuals at short intervals for the first 10 h and then every 12 h for the duration of the experiment. Animals were considered dead when no appendage movement occurred after gentle prodding. The water was changed after 2 d. Duplicate runs were performed and the results were averaged.

After examining the short term tolerance data, we investigated the long term salinity tolerance of Onisimus litoralis by exposing them to a range of salinities from 0°/oo to 65°/oo in 5°/oo steps and of Anonyx nugax from 17°/oo to 52°/oo in 2 to 3°/oo steps. At hourly intervals animals were transferred stepwise in groups of 10 to their final test salinity. Animals were checked every few hours for the first 24 h and then daily for a total of 10 d. Water was changed every 2 d. The same criterion for death was employed and the results were treated in the same way as above.

Osmoregulation

Changes in hemolymph osmotic pressure (milliosmoles (mOs)) of Onisimus litoralis were measured during acute exposures to salinities ranging from 0°/oo to 65°/oo in approximately 5°/oo increments. Duplicate or triplicate hemolymph samples were taken from each of 6 animals following 1, 3, 12, 72 h and up to 2 w exposures to each test salinity. Anonyx nugax was treated in the same way except that salinities ranged from 17°/oo to 52°/oo in increments of 2 or 3°/oo. The osmotic pressure of each incubation medium was also determined. Animals

were held without food in compartmentalized trays containing 400 ml of medium. Water was changed every 2 d during the long incubations. Some of the animals died during the 72 h and 2 w exposures to extreme salinities. This resulted in fewer replicates or no values for some incubations.

Osmotic pressure was measured with a Biological Cryostat/Nanoliter Osmometer (Clifton Technical Physics). Animals were rinsed with deionized-distilled water and blotted on dry tissue. An incision was made dorsally into the pericardial cavity and clear hemolymph was collected in an alkali-free capillary pipette pulled to a fine point. The sample was transferred immediately to the osmometer platform for measurement. Measurements followed the method outlined in the osmometer manual.

Experiments were completed within 6 w of collecting the animals.

Results

Salinity Tolerance

Onisimus litoralis tolerated a much wider range of salinities than Anonyx nugax (Fig. 1). All O. litoralis survived for 3 d over a range from 2°/oo to 55°/oo, while 85% survived at 0°/oo and 10% survived at 63°/oo (Fig. 1A). 100% continued to survive 6 d exposures to 2°/oo, but 10% survived at 0°/oo and 63°/oo (Fig. 1B). After 10 d all survived between 5 and 55°/oo, but none survived 0°/oo. No data are available for 2°/oo (Fig. 1C).

Figure 1. Salinity tolerance of Anonyx nugax (open squares) and Onisimus litoralis (closed squares) incubated in various salinities for (A) 3 d (B) 6 d and (C) 10 d.

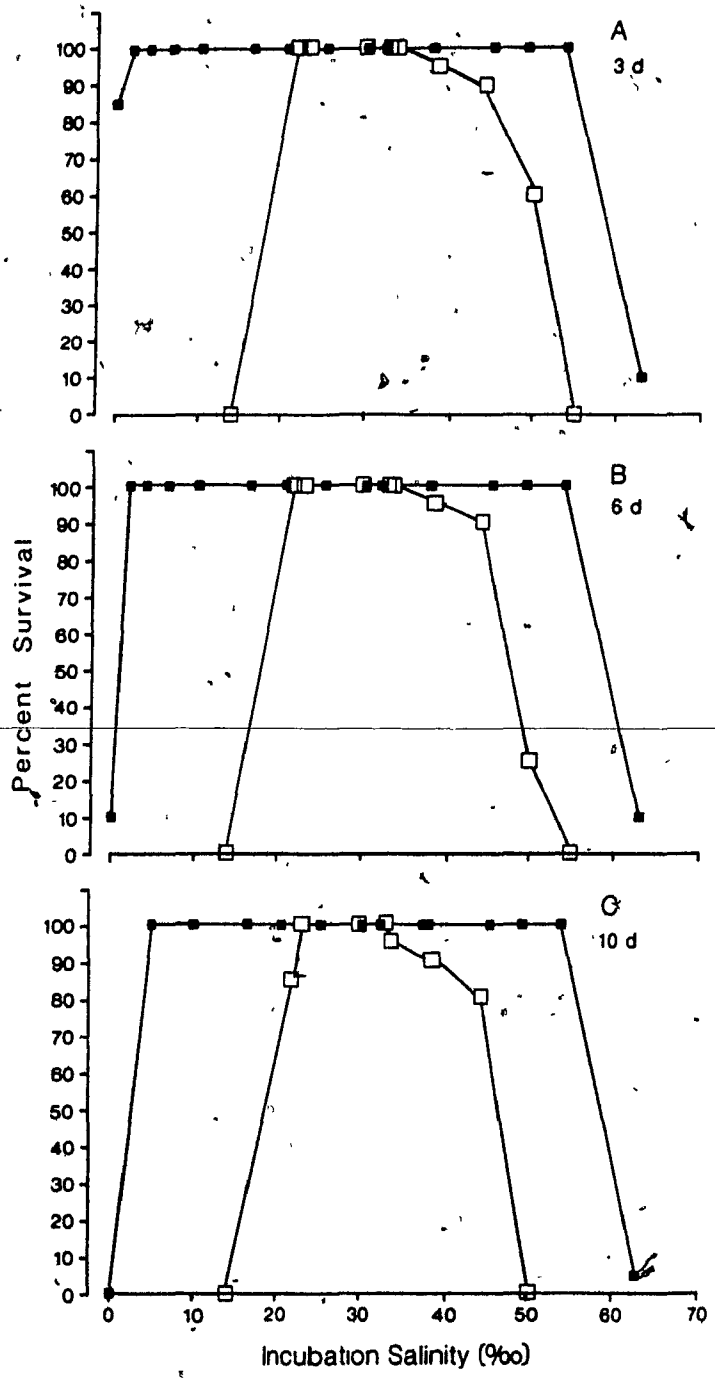
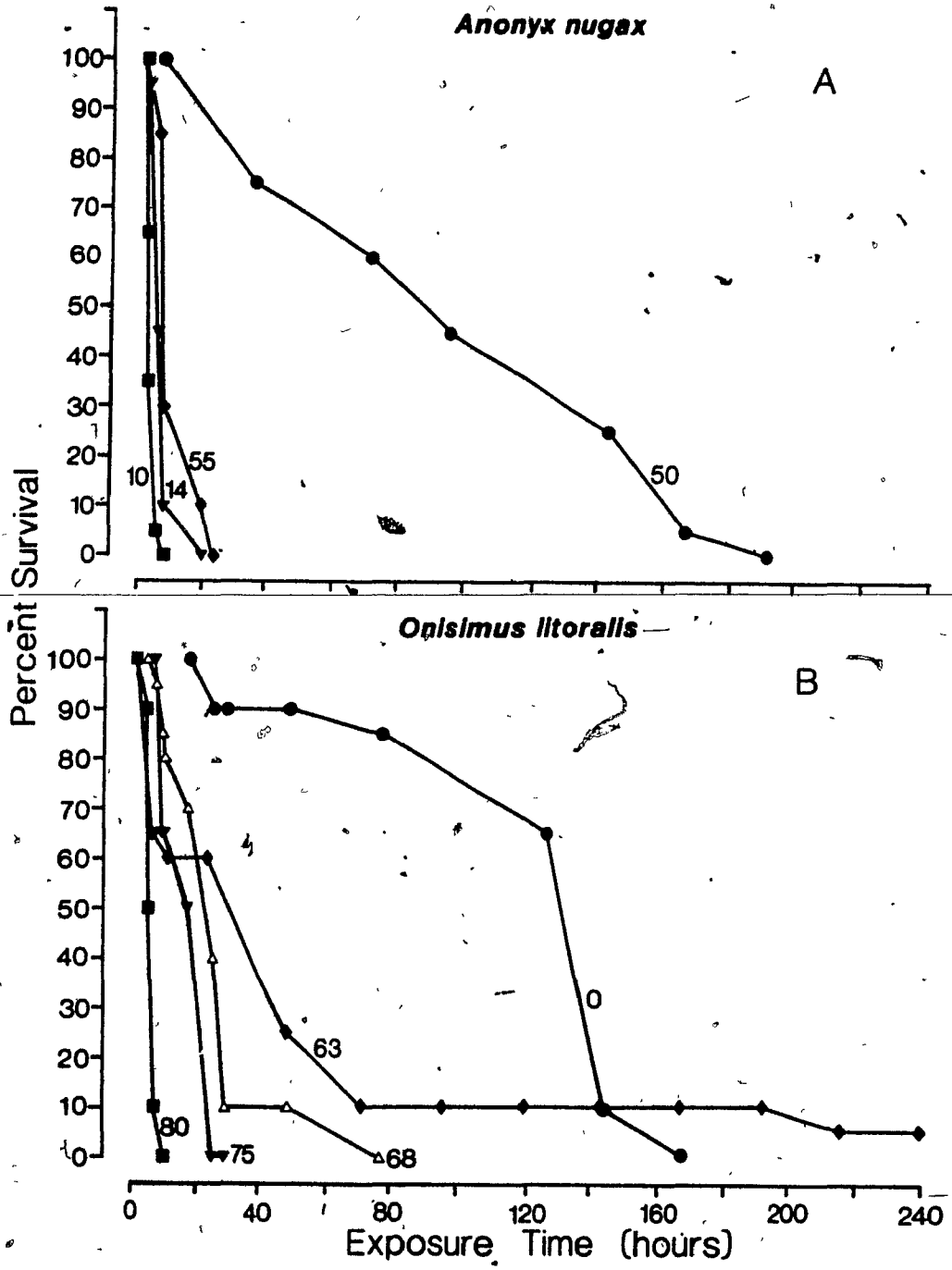

A
3 d
B
6 d
C
10 d
Percent Survival
Incubation Salinity (‰)
0
10
20
30
40
50
60
70
80
90
100

Figure 2. Time course of mortality at salinity extremes for (A) Anonyx nugax (B) Onisimus litoralis. Exposure salinity (°/oo) indicated adjacent to curves.


Anonyx nugax
A
Percent Survival
100
90
80
70
60
50
40
30
20
10
0
10
14
55
50
Onisimus litoralis
B
0
63
80
75
68
0
40
80
120
160
200
240
Exposure Time (hours)

Anonyx nugax had a much narrower salinity tolerance range (Fig. 1). All survived 3 d in salinities between 22°/oo and 34°/oo, 95% survived at 38°/oo and 90% at 44°/oo. All animals died at 14°/oo or below and above 55°/oo, but 60% were alive in 50°/oo seawater (Fig. 1A). After 6 d the same survival as 3 d occurred except for 25% survival at 50°/oo (Fig. 1B). All survived for 10 d in salinities ranging from 22°/oo to 33°/oo, 95% survived at 34°/oo, 90% at 38°/oo and 80% at 45°/oo . No animals survived at 50°/oo (Fig. 1C).

Time course mortalities show that Anonyx nugax can tolerate 14°/oo for 6 h and 55°/oo for 12 h without large mortalities (Fig. 2A). In a similar way, Onisimus litoralis survived 3 d in deionized-distilled water (0°/oo) and in 68°/oo seawater for 6 h (Fig. 2B).

Osmoregulation

The osmotic pressure of normal 32 to 33°/oo Frobisher Bay seawater is approximately 1000 mOs. The hemolymph of Anonyx nugax was hyperosmotic to dilutions of normal seawater during the 1 and 3 h incubations (Fig. 3A & C). After 12 h its hemolymph was isosmotic to the dilute media (Fig. 3E) and remained so for up to 2 w (Fig. 4A & C). In concentrated seawater A. nugax did not osmoregulate. After 3 h the hemolymph became and remained isosmotic or hyperosmotic to all media (Figs. 3C & E, Fig. 4A & C).

Onisimus litoralis regulated its hemolymph osmotic pressure strongly during the 1 and 3 h incubations in dilute seawater. For example, it maintained its hemolymph more than 600 mOs higher than 288

Figure 3. Osmoregulation of Anonyx nugax (A), (C), (E) and Onisimus litoralis (B), (D), (F) for 1, 3 and 12 h incubations, respectively. Standard deviation for each value is within the point except where plotted as a vertical bar. Each point is the mean of 6 individuals except where indicated.

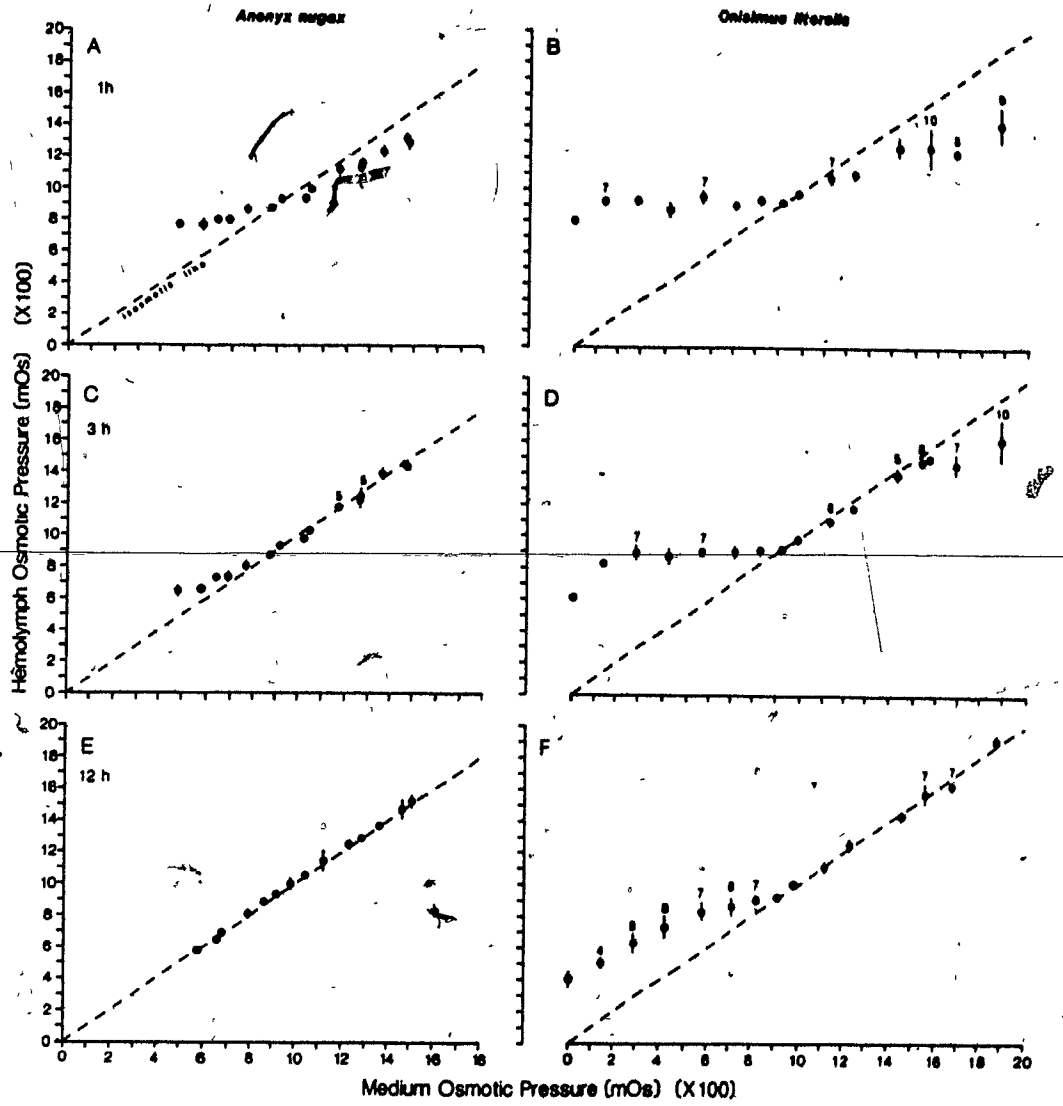
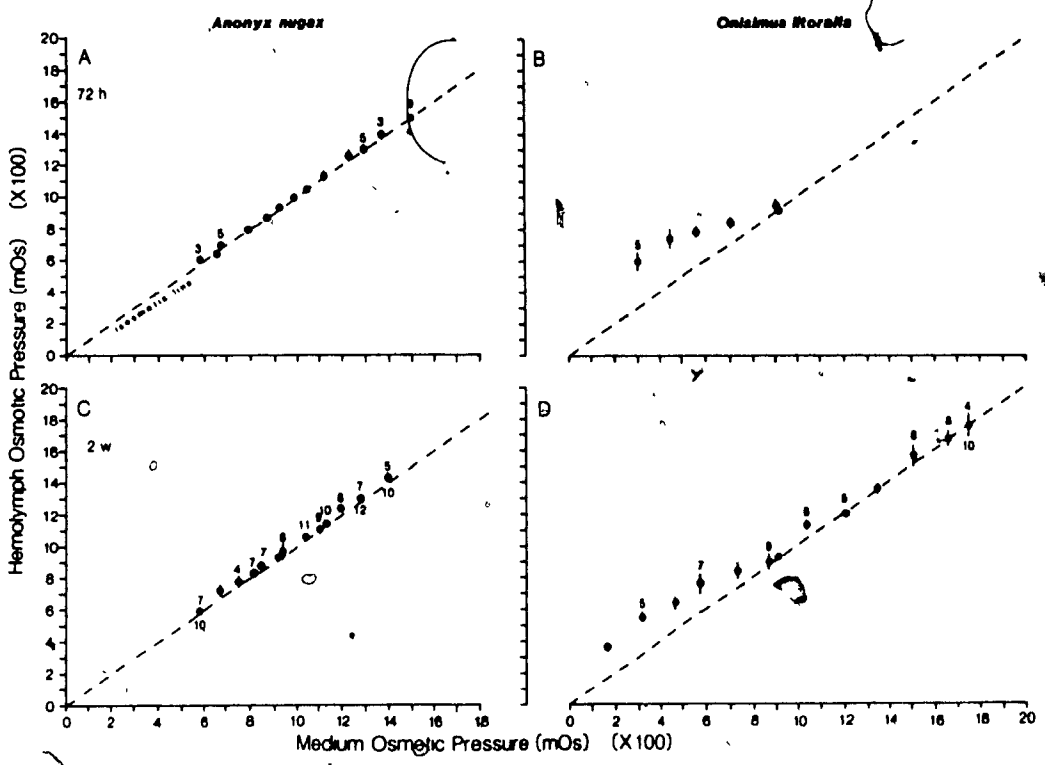

Anonyx nugax
Onisimus litoralis
A
1h
B
C
3 h
D
E
12 h
F
Hémolymph Osmotic Pressure (mOs) (X100)
Medium Osmotic Pressure (mOs) (X100)

Figure 4. Osmoregulation of Anonyx nugax (A) and (C) and Onisimus litoralis (B) and (D) for 72 h and 2 w incubations, respectively. Standard deviation for each value is within the point except where plotted as a vertical bar. Each point is the mean of 6 individuals except where indicated above the point. Labels below the point indicate the exposure time in days.

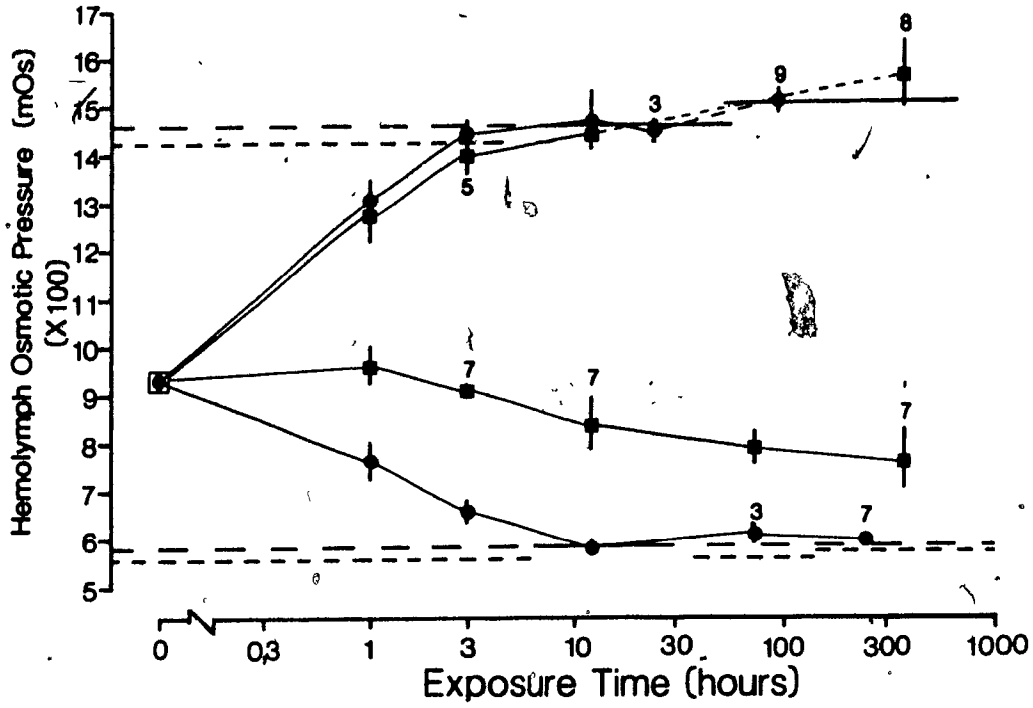

Anonyx nugax
Onisimus litoralis
A
72 h
B
C
2 w
D
Hemolymph Osmotic Pressure (mOs) (X100)
Medium Osmotic Pressure (mOs) (X100)

mOs (≃9°/oo) seawater (Fig. 3B & D). After 12 h in 288 mOs seawater it hyperregulated moderately, the hemolymph osmotic pressure was more than 300 mOs higher than the medium. After 72 h and 2 w it remained more than 200 mOs higher (Fig. 4B & D). In fresh water the species lost osmotic pressure faster than in other low salinity media (Fig. 3B & D).

In high salinity seawater below 1600 mOs (≃50°/oo) the hemolymph osmotic pressure of Onisimus litoralis became almost isosmotic to the media after 3 h (Fig. 3D). Above 1600 mOs it became isosmotic to the media after 12 h (Fig. 3F), and remained isosmotic or hyperosmotic to the media for at least 2 w (Fig. 4D).

The time course of changes in hemolymph osmotic pressure of Anonyx nugax and Onisimus litoralis incubated at low and high salinities is shown in figure 5. The hemolymph osmotic pressure of A. nugax dropped dramatically during 1 and 3 h incubations in low salinities in contrast to that of O. litoralis. A. nugax hemolymph osmotic pressure declined by 150 mOs after 1 h and 250 mOs over 3 h in a 578 mOs (≃19°/oo) medium. After 12 h its hemolymph was isosmotic with the medium. In comparison, the hemolymph osmotic pressure of O. litoralis decreased slightly after 3 h and by only 100 mOs after a 12 h incubation in 570 mOs medium. After 12 h it remained unchanged for up to 2 w. In concentrated media, both species gained osmotic pressure at a similar rate and became isosmotic to the medium. A. nugax became isosmotic to the concentrated medium faster than the dilute medium even though the magnitude of difference between the exposure salinity and normal salinity was larger for the higher salinity.

Figure 5. Time course of changes in hemolymph osmotic pressure for Anonyx nugax (closed circles) and Onisimus litoralis (closed squares) incubated in high and low salinities. Medium osmotic pressures for incubations of O. litoralis (– – –) and A. nugax (— —) or both (————) are plotted. Standard deviation for each value is within the point except where plotted as a vertical bar. Each point is the mean of 6 individuals except where indicated.


Hemolymph Osmotic Pressure (mOs) (X100)
17
16
15
14
13
12
11
10
9
8
7
6
5
8
9
3
5
7
7
7
3
7
0
0,3
1
3
10
30
100
300
1000
Exposure Time (hours)

Discussion

Onisimus litoralis and Anonyx nugax have markedly different salinity tolerances. O. litoralis is a euryhaline species. It survives with no mortality in 5 to 55°/oo over 10 d incubations. In contrast, A. nugax is a more stenohaline species which survives 10 d exposures to a range from 23 to 45°/oo without large mortality.

The salinity tolerances of Onisimus litoralis and Anonyx nugax from Barrow, Alaska (Schneider 1980) are similar to the results presented here. In the Alaskan study O. litoralis survived well in salinities of 5°/oo or 10°/oo to 65°/oo and A. nugax from 20°/oo to 50°/oo during a shorter, 96 h incubation. Schneider (1980) did not conduct a study of osmoregulatory ability.

Crustacea respond physiologically to changes in environmental salinities in 3 basic ways (Lockwood 1962). Osmoconformers do not regulate their hemolymph osmotic pressure, it remains isosmotic to the medium over the tolerated salinity range. Hyperosmotic regulators maintain their blood osmotic pressure higher than dilute media and at least isosmotic to high salinities. Hypo-hyperosmotic regulators, which are the most advanced forms, maintain hemolymph hyperosmotic to dilute media and hypo-osmotic to concentrated salinities.

Onisimus litoralis hyperregulates strongly over 3 h and maintains moderate hyperosmotic regulation over 2 w incubations in dilute seawater. In concentrated seawater below 1600 mOs (~50°/oo) it becomes almost isosmotic within 3 h. After 12 h it is isosmotic to all

concentrated media. In contrast, Anonyx nugax hyperregulates weakly over 1 and 3 h incubations in dilute seawater and osmoconforms to concentrated media. It is isosmotic to concentrated seawater within 3 h. It becomes isosmotic to dilute media after 12 h and remains as such for 2 w.

The physiological mechanisms involved in hemolymph osmoregulation involve specialized functions and adaptations of gills, gut and excretory organs (Mantel and Farmer 1983, for review). Onisimus litoralis, and to a lesser extent Anonyx nugax, in dilute media must undergo physiological change. To osmoregulate they may reduce their permeabilities to the osmotic inflow of water and loss of inorganic ions, and increase urine production and active transport uptake of salts.

Some crustacea also depend on food as a source of ions for osmoregulation and starvation may result in a fall in blood osmoconcentration (Krogh 1939, Lockwood 1962). Onisimus litoralis will follow the water line scavenging for anything that has died or is able to be caught (MacGinitie 1955, Holmquist 1965, pers. obs.) obtaining an almost constant supply of food. However, it cannot store food in its gut for extended periods of time (Sainte-Marie & Shea in prep.). The animals were not fed during the incubations and therefore starvation may have lowered their ability to osmoregulate. On the other hand, Anonyx nugax has the ability to store food and use it at a slower rate. It stores and digests food for up to 15 d or more (Sainte-Marie & Percy submitted) and could use this food as a long term source of ions. However, food

deprived A. nugax do not osmoregulate better than the starving O. litoralis over any incubation length tested.

As shown here, euryhaline invertebrates, whether regulators or not, can withstand large swings in hemolymph osmotic pressure. In such cases the tolerance range of the animal is dictated by the ability of the tissue to adjust or tolerate tissue water volume (Gilles 1979 for review). The tissues of Anonyx nugax and Onisimus litoralis are able to withstand or regulate against at least 750 mOs and 1300 mOs swings, respectively, in their hemolymph osmotic pressure for extended periods.

Aarset and Aunaas (1987) showed that the under-ice amphipod Onisimus glacialis, a species very closely related to O. litoralis, is a "highly efficient osmoregulator". It maintains hemolymph osmotic pressure constant over a range of seawater dilutions. After 24 h in approximately $6^{0}/oo$ seawater it maintained its hemolymph more than 700 mOs hyperosmotic to the medium. In comparison, O. litoralis in approximately $5^{0}/oo$ seawater could maintain only a 300 mOs difference from the medium after half as long an incubation.

Our unpublished salinity tolerance data for Onisimus glacialis show that this species can tolerate the same wide salinity range as Onisimus litoralis. Since these species have the same salinity tolerances but hyperregulate with different efficiencies, it is likely that tissue water volume regulation and/or tolerance is very different in each of them. This requires further investigation which may also provide useful information to taxonomists concerning physiological differences between the Onisimus species.

Behavioral responses are important to survival in environments with fluctuating salinity (Davenport 1985). Both Anonyx nugax and Onisimus litoralis survive brief exposures to salinities that will eventually kill them. In the wild they may be able to escape abrupt changes in salinity by moving to less osmotically stressful areas or by burrowing into environmentally stable substrate.

The burrowing behavior observed in both species (Sainte-Marie & Shea in prep.) could be useful in regulating hemolymph osmotic pressure during salinity fluctuations. Interstitial water salinities of exposed intertidal flats or estuaries usually change slowly even when the overlying water is fresh (Reid 1930, 1932, Kinne 1971, Shea & Marcotte in prep.). During osmotically stressful periods either species could ensure a more stable hemolymph osmotic pressure by burrowing into the substrate to take advantage of the less variable salinity.

The distribution of each species reflects its physiological abilities to respond to salinity fluctuations. The ability of Onisimus litoralis to hyperregulate strongly for up to 3 h relates well to its distribution in the intertidal zone of Upper Frobisher Bay. It follows the ebb tide to the lower areas of the intertidal zone and then may dig into the sand or mud, remain in tidal pools or stay in the shallow subtidal zone until the tide starts to come back in (Shea & Marcotte in prep.). Its use of the mid and lower intertidal zone ensures that it will only be exposed to fluctuations in salinity for short periods whether buried or free swimming. O. litoralis can tolerate high and low salinities for extended periods of up to at least 10 d. This ability may

be critical when the species is stranded in tidal pools or during freeze up and melt periods.

The ability of Onisimus litoralis to increase its osmotic pressure and remain isosmotic or slightly hyperosmotic to concentrated seawater reflects its ability to survive in intertidal pools when they freeze over (Shea & Marcotte in prep.). The formation of ice in tide pools is linked with decreasing temperature and increasing salinity. Therefore, the physiological mechanism observed ensures that trapped individuals will not freeze since the freezing point depression of hemolymph will always be at least as great as that of the environment.

In Upper Frobisher Bay, Anonyx nugax lives subtidally (Shea & Marcotte in prep.) in stable salinities of 32°/oo to 34°/oo (Lovrity 1984). Its narrower salinity tolerance spectrum and weak osmoregulatory ability relate well to its observed distribution. It could however, withstand some of the fluctuations that it would encounter in its sporadic occurrences on beaches and under the ice. However, these would have to be mild and brief salinity shifts. Otherwise, the species' physiological limitations should exclude it from these environments. The sudden and drastic changes in salinity which can occur in the Upper Frobisher Bay intertidal zone seem to account for the total lack of A. nugax in that habitat (Shea & Marcotte in prep.).

Some mobile intertidal organisms which can withstand fluctuations in salinity can take advantage of the under-ice environment. From distributional studies (L.G.L. Ltd. 1982, Cross & Martin 1983, Shea & Marcotte in prep.) we expect Onisimus litoralis to be well adapted to

life under the ice. The data presented here confirm that it is physiologically capable of withstanding most of the osmotic stresses of that environment. Anonyx nugax however, does not appear under the ice in Upper Frobisher Bay in large numbers (Shea & Marcotte in prep.) or in other locations (Thomson et al. 1975, Cross & Martin 1983). This could be a result of factors other than osmotic stress since it can tolerate the moderate swings in salinity which would occur during slow ice growth. One explanation may be that its food is not available. Although A. nugax specimens taken from the under-ice had diatoms in their guts (Thomson et al. 1975), the carrion and polychaetes upon which it usually feeds (Sainte-Marie & Lamarche 1985) are not present. Alternatively, it may not negotiate the 20 m or so from the sea floor to the under-ice surface, whereas Onisimus litoralis readily spreads out on to the under-ice surface from the littoral zone. However, in any case, during freeze-up and periods of quick ice growth or melt, A. nugax must be excluded from the under-ice environment by its inability to tolerate salinity extremes.

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