Causes and consequences of recent freshwater invasions by saltwater animals

Carol Eunmi Lee and Michael A. Bell

Transitions from marine to freshwater habitats constitute dramatic shifts between ‘adaptive zones’ that have initiated the radiation of many taxa. As recently as 10 000 years ago, deglaciation resulted in marine fauna being trapped in freshwater lakes. In modern times, human activity has caused the acceleration of freshwater invasions from marine or brackish habitats, leading to serious environmental problems. The rapid pace of these invasions provides ideal opportunities for examining initial responses to environmental change and mechanisms involved in habitat transitions. Despite conservation and evolutionary applications, recent transitions to fresh water remain inadequately explored.

Information on pathways and mechanisms of freshwater invasion is gaining importance because recent immigrants from salt water are becoming environmental hazards. In most cases, saltwater sources and timing of invasion have been inferred from distributional data but have not been rigorously tested. Application of molecular tools can now provide insight into pathways, timing, sources and direction of invasions.

Biogeography of freshwater invasions

The interface between marine and freshwater habitats poses a formidable barrier that few species have been able to penetrate. Dispersal between habitats is prevented most conspicuously by gradients in osmotic pressure and ionic concentration that marine or brackish organisms must overcome to penetrate. Dispersal between habitats is prevented most conspicuously by gradients in osmotic pressure and ionic concentration that marine or brackish organisms must overcome to penetrate.

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Glacial relics arose through the entrapment of marine fauna in postglacial lakes during deglaciation. Since the height of the last glacial period (18 000 years BP), sea level has risen about 120 m as a result of glacial melting. New lakes formed where seawater and ice. New lakes formed where seawater was isolated in basins and became fresh over time from precipitation. The recency of these uplifted lakes led to the belief that the freshwater residents were of recent marine origin and independently derived from the sea. For many diadromous fishes, recent and repeated postglacial landlocking is supported with genetic evidence. However, molecular (allozymes) and morphological studies demonstrate that for textbook examples of glacial relics, the mysid *Mysis relicta* and the amphipod *Pontoporeia affinis* have independent marine origins of crustacean species once considered to be classic examples of ‘glacial relics’. For many diadromous fishes, recent and repeated postglacial landlocking is supported with genetic evidence. However, molecular (allozymes) and morphological studies demonstrate that for textbook examples of glacial relics, the mysid *Mysis relicta* and the amphipod *Pontoporeia affinis* have independent marine origins of crustacean species once considered to be classic examples of ‘glacial relics’.

An estimate of when invasions from salt water occurred is important for understanding mechanisms of habitat transition and determining rates of adaptation. Inference of timing based solely on observation or on geological history can be misleading. For instance, recent studies refute hypotheses of recent and independent marine origins of crustacean species once considered to be classic examples of ‘glacial relics’.

Reconstructing timing, pathways and sources of invasion

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Freshwater relugia apparently persisted during recent glaciations, permitting re-colonization of previously ice-covered habitats by older freshwater populations of these two species23.

Some freshwater subterranean and cave species, such as hadzioid amphipods, might have been derived directly from marine ancestors following marine regressions and postglacial uplift. The genus Bahadzia, in particular, might have been derived from marine ancestors during the late Pleistocene16 (within the past 200,000 years). A two-step process has been hypothesized, involving first the invasion of cave and subsurface habitats by marine animals that migrate between marine and fresh water at regular and predictable phases of diadromy. Such a taxonomic group would have members that occupy a broad diversity of habitats. However, invasion pathways and timing are uncertain18.

An important question is whether modern invasions are indeed recently derived from salt water, as suggested by direct observations. With few exceptions these observations have not yet been confirmed using genetic data. Recent impoundments appear to have resulted in new freshwater populations (Table 1).

Table 1. Examples of historical freshwater invasions by marine or brackish species, exclusive of fishes (200 years up to the present)a

<table>
<thead>
<tr>
<th>Taxa Location</th>
<th>Marine and/or brackish species</th>
<th>Approximate invasion date</th>
<th>Hypothesized cause</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arthropoda (Crustacea)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphipoda</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corophiidae</td>
<td>Poland, UK</td>
<td>Ponto-Caspian sea</td>
<td>1930c</td>
<td>Shipping traffic</td>
</tr>
<tr>
<td>Corophium speciosum</td>
<td>Lake Merced, USA</td>
<td>Merced Lagoon, USA</td>
<td>1869–1894</td>
<td>Lagoon impoundment</td>
</tr>
<tr>
<td>Corophium sarsi</td>
<td>Poland</td>
<td>Ponto-Caspian sea</td>
<td>1930c</td>
<td>Shipping traffic</td>
</tr>
<tr>
<td>Gammarus tigrinus</td>
<td>Eastern USA coast</td>
<td>1931</td>
<td>Ballast water?</td>
<td>3</td>
</tr>
<tr>
<td>Gammarus duebeni</td>
<td>Zuiderzee, The Netherlands</td>
<td>1932</td>
<td>Lagoon impoundment</td>
<td>48</td>
</tr>
<tr>
<td>Oxeodeamia crassus</td>
<td>Kaunas estuar, Lithuania</td>
<td>Ponto-Caspian sea</td>
<td>1931</td>
<td>Transplanted</td>
</tr>
<tr>
<td>Anthoxiella cristata</td>
<td>Droopovskoe reservoirs</td>
<td>Ponto-Caspian sea</td>
<td>1937</td>
<td>Transplanted</td>
</tr>
<tr>
<td>Omeina pubiloba</td>
<td>Droope-Kirov R. canal</td>
<td>Ponto-Caspian sea</td>
<td>1937</td>
<td>Transplanted</td>
</tr>
<tr>
<td>Coxeidae</td>
<td>Gulf of Mexico (estuaries)</td>
<td>1930s–1980s</td>
<td>Brackish lakes, Japan</td>
<td>32</td>
</tr>
<tr>
<td>Exochorephorus arenacrisis</td>
<td>Lake Ohnuma, Japan</td>
<td>1931</td>
<td>Fish transport</td>
<td>32</td>
</tr>
<tr>
<td>Isopoda</td>
<td>Eastern Scheldt estuary, The Netherlands</td>
<td>1987</td>
<td>River impoundment</td>
<td>50</td>
</tr>
<tr>
<td>Eurythemia sericea</td>
<td>Eastern Scheldt estuary, Baltic or Ponto-Caspian sea</td>
<td>Early 20th century</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Branchiopoda</td>
<td>Gulf of Mexico (estuaries)</td>
<td>1930s–1980s</td>
<td>Brackish lakes, Japan</td>
<td>32</td>
</tr>
<tr>
<td>Brachionus plicatilis</td>
<td>Lake Ohnuma, Japan</td>
<td>1931</td>
<td>Fish transport</td>
<td>32</td>
</tr>
</tbody>
</table>
| Diadromous: animals that migrate between marine and fresh water at regular and predictable phases of their life cycle.
| Catadromous: animals that are born in the sea, migrate to and spend most of their lives in fresh water, and then return to the sea as adults to spawn (e.g. salmonids, sturionids, sticklebacks and osmerids). | 18 |
| Anadromous: animals that are born in fresh water, migrate to and spend most of their lives in the sea, and then return to fresh water as adults to spawn (e.g. salmonids, sturgeonids, sticklebackids and osmerids). | 18 |
| Euryhaline: tolerant of wide ranges in salinity, its usage varies between disciplines. | 18 |
| Biogeography: species with broad habitat distributions, without examining tolerances of particular populations. | 18 |
| Physiological: individuals with broad tolerances, without reference to variation at the intra- or inter-population level. | 18 |
| Evolution: a taxonomic group that has the evolutionary propensity (genetic, physiological) to invade new salinities. Such a taxonomic group would have members that occupy a broad diversity of habitats. | 18 |
| Freshwater invasive populations that gain the ability to complete their entire life cycle in fresh water. | 18 |
| Salinity ranges: freshwater, 0–0.5 PSU (parts per thousand); brackish water, 0.5–30 PSU; marine, >30 PSU (Ref. 6). | 18 |
and Aral (Ponto-Caspian) seas through canals into inland waterways of Europe and Asia\(^2\) (Table 1). Ship traffic traversing these canals was probably the main transport vector. Consequently, organisms once restricted to the Ponto-Caspian region have become widespread. Examples include the amphipod Corophium curvispinum, which has become the most numerous macroinvertebrate in the Rhine River\(^19\), and the threespine stickleback\(^21\) in inland waters\(^5\). Freshwater populations of the copepod Eurytemora affinis\(^2\) (Table 1) and the mussel Dreissena polymorpha, which eventually reached the USA in 1986 and is rapidly extending its freshwater range\(^2\). Many Ponto-Caspian species, particularly crustaceans such as mysids and amphipods, were deliberately transplanted into freshwater habitats in Russia and Europe to replace native species that had gone extinct\(^2\). Freshwater kokanee (Oncorhynchus nerka) and the threespine stickleback (Gasterosteus aculeatus), which are native to the southeastern USA\(^3\), failed to occur in 12 phyla (e.g. Echinodermata, Ctenophora and Brachiopoda)\(^2\), and many major clades within the remaining phyla\(^2\). However, once this innovation arose in a clade, freshwater invasion appears to occur repeatedly, giving rise to recent invaders. For instance, the copepod genus Eurytemora consists of species from diverse habitats, such as fresh, brackish, and marine and hypersaline waters\(^5\), but is far more common in anadromous than catadromous species (Box 1), which suggests that the ability to reproduce or spend early life stages in fresh water is critical for invading fresh water.

### Physiological traits and habitat of origin

Populations within species might vary in their propensity to invade fresh water because of differences in physiological traits among populations\(^5\). This variation might result from variation in acclimation or selection regime among habitats\(^5\). Freshwater invaders might originate more readily from habitats that have wide temporal or spatial ranges in salinity, where broad salinity tolerances can form. The timescale of salinity fluctuations (diel or seasonal) in a habitat could be an important factor because such timescales can affect rates of acclimation response.

### Temperature

Temperature is another environmental factor that might pose a barrier to freshwater invasion\(^5\). Freshwater habitats tend to have lower temperatures than do brackish or marine habitats. Given that temperature fluctuates more at higher latitudes, it has been proposed that the propensity to invade should increase at lower latitudes\(^5\). However, salinity and temperature interact in their effects on tolerance\(^2,3\), with temperature affecting metabolic rate, ion uptake rate and membrane permeability. At higher temperatures, some species, such as zebra and quagga mussels (Dreissena bugensis), have greater difficulty osmoregulating\(^2\), whereas others gain broader salinity tolerances\(^5\). Effect of temperature on salinity tolerance has not been examined extensively and might influence where freshwater invasions can take place.

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Fig. 1. Alternative hypotheses for the colonisation of freshwater habitats, represented by phylogenetic trees. (a) Independent colonisation of freshwater habitats. (b) A single colonisation of a freshwater habitat followed by dispersal. Key: FW = freshwater population; SW = saltwater population; shaded crossbars represent habitat transitions.

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### Habitat availability

Catastrophic events, such as glaciation, drought and disruption by humans, have left freshwater habitats depauperate and prone to colonization without competition from indigenous fauna\(^3\). Such depauperate conditions apparently allowed the entry of migratory fishes into post-glacial lakes\(^12,27\) and numerous species into newly constructed reservoirs\(^3,4\) and polluted waters\(^2\) (Table 1). Depauperate habitats could provide safe havens for freshwater acclimation and adaptation, allowing further range expansion into natural communities.

### Artificial habitats

Artificial habitats, such as reservoirs, appear to have facilitated entry into inland waters\(^3\). Freshwater populations of the copepod Eurytemora affinis is typically found in artificial ponds and reservoirs in Europe\(^5\), whereas those of E. affinis occur predominantly in reservoirs in the southeastern USA\(^3\). Similarly, many brackish species have colonized fresh waters of Europe that were left depauperate from industrial, agricultural and domestic sewage\(^12,24\). The North American anadromous Gammarus tigrinus was introduced to the Werra River, Germany, to replace freshwater Gammarus species that had gone extinct\(^2\). Likewise, species from the Ponto-Caspian region, such as amphipods Corophium curvispinum and G. tigrinus and the mussel Dreissena polymorpha, are dominant in the polluted Rhine River in Germany\(^2\). It is unclear why brackish invaders outperform native fauna in polluted fresh waters.

### Traits that facilitate transitions to fresh water

Phylogenetic bias of recent invaders might allow the ability to invade fresh water to requires evolutionary innovation that has failed to occur in 12 phyla (e.g. Echinodermata, Ctenophora and Brachiopoda)\(^2\) and many major clades within the remaining phyla\(^2\). However, once this innovation arose in a clade, freshwater invasion appears to occur repeatedly, giving rise to recent invaders. For instance, the copepod genus Eurytemora consists of species from diverse habitats, such as fresh, brackish, and marine and hypersaline waters\(^5\), but is far more common in anadromous than catadromous species (Box 1), which suggests that the ability to reproduce or spend early life stages in fresh water is critical for invading fresh water.

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**Box 1** Evolution of tolerance to fresh water

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Life-history traits

Particular life-history traits might preclude certain invasive species to persist in lakes, by countering problems such as drought and fluctuations in temperature and food availability. For instance, the copepods *E. affinis* and *E. velox* can produce desiccation-resistant resting eggs under seasonal stress. Likewise, regulator relative to native sphaeriid *Corophium*, zebra mussels drive to extinction. These species might be successful while they are expanding their ranges but it is unclear whether they will persist in fresh water over geological timescales.

Traits that evolve as a consequence of freshwater invasion

Salinity adaptation

Populations that have invaded fresh water within the past 200 years appear to be less efficient than ancient fresh water species at osmoregulation in fresh water. The zebra mussel is a poor hyperosmotic stance, the copepods *E. affinis* and *E. velox* requires more energy to regulate sodium in fresh water than do freshwater amphipods. Some populations that have invaded fresh water have appeared to have lost their high salinity tolerance – a pattern found in more ancient freshwater habitats. The zebra mussel is a poor hyperosmotic regulator relative to native sphaeriid and unionid bivalves. Likewise, *Corophium* requires more energy to regulate sodium in fresh water than do freshwater amphipods. Some populations that have invaded fresh water have appeared to have lost their high salinity tolerance – a pattern found in more ancient freshwater habitats.

Morphological divergence reflecting diverse ecological differences between marine and freshwater habitats might occur after freshwater invasion in anadromous fish, but has not been observed in recently invading invertebrates. Such divergence reflects demands that predation regime and food availability place on feeding, locomotory and sensory performance. For example, evolution of reduced armor in freshwater threespine stickleback relative to marine and anadromous ancestors probably results from a reduction in gape-limited predators. In addition, heritable morphological divergence occurs within lake habitats between plankton-feeding and bottom-feeding forms. Such patterns of morphological divergence emerge repeatedly during independent invasions into fresh water, and to different degrees. A population of three-spine stickleback impounded in 1960 in a freshwater pond demonstrates a striking example of initial stages of morphological divergence. Morphological divergence from the anadromous form was observed over a ten-year period, during which traits of older (-1000-year-old) freshwater populations began to appear, such as reduction in armor and changes in body shape. From the rate of change found in this study, a complete change in frequency in the population from a full to low-armored phenotype is predicted to occur in 130 years.

References


Evolutionary applications and implications for conservation

Water invasions to freshwater habitats have been of great interest to evolutionary biologists and paleontologists because they constitute major evolutionary transitions. For instance, freshwater habitats might have provided stepping stones for the invasion of land for many taxa, because adaptation to low oxygen levels in fresh water might have led to the evolution of air-breathing in terrestrial vertebrates. Recent freshwater invasions can offer insights into evolutionary adaptation in progress. Information on the timing of invasion allows calibration of evolutionary rates of change. Adaptations following freshwater invasion can occur within a few years, making it possible to examine initial responses to freshwater conditions. Freshwater invasions often occur by multiple isolates (e.g. postglacial colonization), with each following an independent evolutionary trajectory. This pattern allows inference of whether independent invasions are governed by similar evolutionary processes, and whether the same sequence of trait gain and loss occurs during independent invasions. Additionally, because these invasions were recent, comparisons between saltwater ancestors and freshwater derivatives are at the intraspecific level. Such intraspecific comparisons minimize the confounding effect of phylogenetic distance on the evolutionary response of different populations to similar selection regimes. The full potential of theoretical and practical applications of these systems is far from realized. Understanding evolutionary and physiological mechanisms of recent freshwater invasions has become critical given imminent threats to inland waters posed by accelerated rates of invasion from saltwater habitats.

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