Causes and consequences of recent freshwater invasions by saltwater animals

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Transitions from marine to freshwater habitats constitute dramatic shifts between 'adaptive zones' that have initiated the radiation and speciation 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 implications and evolutionary applications, recent transitions to fresh water remain inadequately explored.

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George Gaylord Simpson argued that shifts between 'adaptive zones' should cause rapid evolutionary radiations[1]. A striking example of such a shift is the invasion of fresh water from saline or brackish habitats. On macroevolutionary timescales, the transition from marine to fresh water occurred more frequently than the transition from aquatic to terrestrial habitats. Among the approximately 30 animal phyla, all of which evolved in the sea, 16 have colonized fresh water, whereas only seven have made the transition to land[2].

However, transitions to freshwater have occurred not only on macroevolutionary scales, but also recently, continuing to the present day. Recent deglaciation events during the past several millennia have resulted in isolated populations in inland lakes and caves. More recently, human activity has facilitated freshwater introductions during the past 200 years (Table 1). The fact that many highly invasive and disruptive species in fresh water are recent immigrants from saline habitats[3,4] is not often emphasized in the literature.

Both these 'postglacial' and 'modern' freshwater invasions provide invaluable resources for studying the tempo and mode of evolutionary, ecological and physiological changes that accompany dramatic habitat shifts. Examining recent freshwater invasions can yield insight into the osmoregulatory systems that enabled the invasion of freshwater habitats. Literature on recent freshwater invasions is scarce and, in particular, modern invasions have not been discussed in relevance to evolutionary questions.

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[3,4]. 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[5]. Dispersal between habitats is prevented most conspicuously by gradients in osmotic pressure and ionic concentration[6]. Whereas salt water tends to be closer to body fluids in ionic composition, fresh water has very low concentrations of ions. These low levels force freshwater organisms to expend typically more energy regulating osmotic pressure and ionic concentration than is required for marine or brackish organisms[7]. A few exceptionally euryhaline species (Box 1), such as the killifish *Fundulus heteroclitus*[8], can move instantaneously between salt and freshwater habitats and reproduce in either habitat. Such species have specialized gills and other adaptations that allow rapid regulation of ion exchange when moving between habitats[8,9].

Many diadromous (Box 1) fish populations have become landlocked in freshwater lakes in postglacial and modern times. However, because diadromous species already live in both fresh and saltwater habitats at different stages of their life cycle (Box 1), becoming trapped in fresh water does not represent a complete transformation from salt to freshwater existence. Nevertheless, diadromous species are included in this review because interesting adaptations are associated with their invasion of fresh water.

Of particular interest is the marked increase, in historical times, of freshwater invaders (Box 1) not previously known to occur in fresh water, and without obvious mechanisms for tolerating freshwater conditions (Table 1). Most of these species are not vagile and require a transport vector to invade new habitats. Opportunities provided by humans have probably facilitated these recent invasions, through the creation of transport vectors and depauperate habitats. It remains to be seen whether these recent invasions will occur through a pattern of extinction and recolonization or persist over time.

Reconstructing timing, pathways and sources of invasion

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 relicts'[10].

Glacial relicts 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. Nevertheless, local isostatic uplift caused by the unburdening of land from the weight of ice resulted in postglacial uplift of boreal terrain previously covered by seawater and ice. New lakes formed where marine water was isolated in basins and then 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[10]. For many diadromous fishes, recent and repeated postglacial landlocking is supported with genetic evidence[11–13].

However, molecular (allozymes) and morphological studies demonstrate that for textbook examples of glacial relicts, the mysid *Mysis relicta* and the amphipod *Pontoporeia affinis*, freshwater populations each share a common ancestry distinct from saltwater forms. Moreover, these freshwater lineages diverged from saltwater forms several million years ago, long before the last glaciation[14,15].

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

Taxa	Location	Marine and/or brackish source	Approximate invasion date	Hypothesized cause	Refs[b]
Cnidaria					
Anthomedusae					
Cordylophora lacustris	UK and Belgian rivers	Ponto-Caspian sea	1854	Unknown	47
Cordylophora caspia	IJsselmeer, The Netherlands	Zuiderzee	1932	Bay impoundment	18
Annelida					
Polychaeta					
Neanthes limnicola	Lake Merced, USA	Merced Lagoon, USA	1869–1894	Lagoon impoundment	48
Mollusca					
Dreissenidae					
Dreissena polymorpha	Volga river	Ponto-Caspian sea	1824	Shipping traffic	49
Arthropoda (Crustacea)					
Amphipoda					
Corophium curvispinum	Poland, UK	Ponto-Caspian sea	1930s	Shipping traffic	3
Corophium spinicorne	Lake Merced, USA	Merced Lagoon, USA	1869–1894	Lagoon impoundment	48
Echinogammarus ischnus	Poland	Ponto-Caspian sea		Shipping traffic	3
Gammarus tigrinus	UK	Eastern USA coast	1931	Ballast water?	3
Gammarus duebeni	IJsselmeer, The Netherlands	Zuiderzee	1932	Bay impoundment	18
Obesogammarus crassus	Kaunasskor Res., Lithuania	Ponto-Caspian sea	1961	Transplanted	3
Amathillina cristata	Dneprovskoe reservoirs	Ponto-Caspian sea	1957	Transplanted	3
Gmelina pusilla	Dnieper-Krivoj Rog canal	Ponto-Caspian sea	1975		3
Copepoda					
Eurytemora affinis	Mississippi river reservoirs, USA	Gulf of Mexico (estuaries)	1930s–1980s	Shipping traffic	22
(=*E. hirundoides*)	Lake Ohnuma, Japan	Brackish lakes, Japan	1981	Fish transport	32
	IJsselmeer, The Netherlands	Zuiderzee	1932	Bay impoundment	18
	Volkerak-Zoommeer, The Netherlands	Eastern Scheldt estuary	1987	River impoundment	50
Eurytemora velox	European reservoirs	Baltic or Ponto-Caspian seas	Early 20th century		5
Isopoda					
Exosphaeroma oregonensis	Lake Merced, USA	Merced Lagoon, USA	1869–1894	Lagoon impoundment	48
Sphaereoma hookeri	IJsselmeer, The Netherlands	Zuiderzee	1932	Bay impoundment	18
Mysidacea					
Neomysis mercedis	Lake Merced, USA	Merced Lagoon, USA	1869–1894	Lagoon impoundment	48
Neomysis integer	IJsselmeer, The Netherlands	Zuiderzee	1932	Bay impoundment	18

[a] See Refs 12 and 23 for examples of recent landlocking in diadromous fishes.

[b] Some secondary sources were cited to minimize number of references.

Freshwater refugia apparently persisted during recent glaciations, permitting recolonization of previously ice-covered habitats by older freshwater populations of these two species[15].

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 Pleistocene[16] (within the past 200 000 years). A two-step process has been hypothesized, involving first the invasion of cave and subsurface habitats by marine populations, followed by uplift and freshening of these habitats. However, invasion pathways and timing are uncertain[17].

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). A well documented example is the decline and ultimate extinction of marine and brackish species during the six-year transformation of the saline Zuiderzee Bay, The Netherlands, into the freshwater IJssel Lake (IJsselmeer), starting in 1932. Very few of the hundreds of animal species monitored during this period survived: only four crustaceans, one hydrozoan and seven diadromous fishes[18] (Table 1).

A dramatic example of human-mediated dispersal is the transport of many brackish species from the Black, Caspian

Box 1. Glossary

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, sturgeons, sticklebacks and osmerids).

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. anguillid eels, some clupeids, some percichthyids, some cottids and mugilids, and one galaxiid).

Diadromous: animals that migrate between marine and fresh water at regular and predictable phases of their life cycle.

Euryhaline: tolerant of wide ranges in salinity. Its usage varies between disciplines.

- Biogeography: species with broad habitat distributions, without examining tolerances of particular populations.
- Physiology: individuals with broad tolerances, without reference to variation at the intra- or inter-population level.
- Evolution: a taxonomic group that has the evolutionary propensity (genetic, physiological) to invade new salinities[5]. Such a taxonomic group would have members that occupy a broad diversity of habitats.

Freshwater invader: populations that gain the ability to complete their entire life cycle in fresh water. Populations were included even if reversals and reinvasions of fresh water have occurred in the lineage. To be included in this perspective, a study had to have evidence for timing and direction of invasions such as: (1) robust molecular genetic data supporting the evolutionary history of freshwater invasion, (2) information on timing of freshwater invasion, such as accurate geological history (timing of deglaciation and formation of postglacial lakes) or date of impoundment, or (3) introduction history, such as historical records documenting timing and sources (as in the case of transplantation).

Salinity ranges: freshwater, 0–0.5 PSU (parts per thousand); brackish water, 0.5–30 PSU; marine, >30 PSU (Ref. 6).

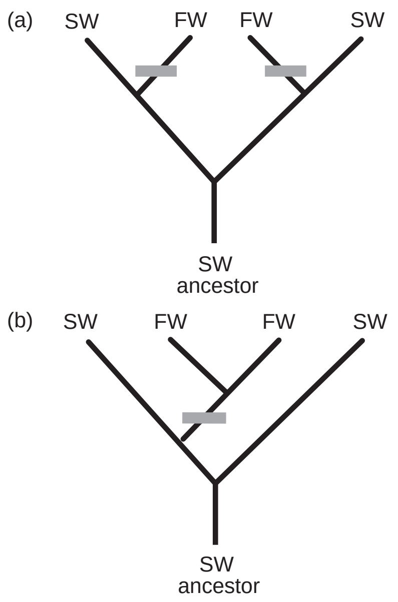

Fig. 1. Alternative hypotheses for the colonization of freshwater habitats, represented by phylogenetic trees. (a) Independent colonizations of freshwater habitats. (b) A single colonization of a freshwater habitat followed by dispersal. Key: FW = freshwater population; SW = saltwater population; shaded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

and Aral (Ponto-Caspian) seas through canals into inland waterways of Europe and Asia[3] (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 zebra mussel *Dreissena polymorpha*, which eventually reached the USA in 1986 and is rapidly extending its fresh-water range[20]. 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 and to promote fisheries in artificial lakes[3,19].

In terms of invasion pathways, freshwater populations might have arisen independently from distinct sources (Fig. 1a) or from a single source with subsequent spread (Fig. 1b), or through a combination of both processes. For many diadromous fishes, such as the salmonid *Oncorhynchus nerka*[21] and the threespine stickleback (*Gasterosteus aculeatus*), multiple independent invasions of postglacial lakes (Fig. 1a) are supported with genetic evidence. For the copepod *Eurytemora affinis*, mitochondrial DNA sequences indicate independent freshwater invasions from genetically distinct estuarine populations in each river drainage (Fig. 1a), but dispersal among freshwater populations within a drainage (Fig. 1b)[22]. Although genetic evidence is not yet available, species endemic to the Ponto-Caspian seas appear to have radiated from this single source (Fig. 1b) into inland fresh waters of Europe and Asia (Table 1).

Phenotypic data alone are often unreliable for testing hypotheses of invasions because such characters can be subject to convergent adaptive evolution during the marine-to-freshwater transition. For instance, morphological traits would incorrectly place populations of freshwater kokanee (*Oncorhynchus nerka*)[21] and threespine stickleback[11] in separate clades from the marine populations from which they were derived. Thus, molecular genetic data are crucial for determining invasion history of freshwater isolates.

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[3,5]. Such depauperate conditions apparently allowed the entry of migratory fishes into postglacial lakes[12,23] and numerous species into newly constructed reservoirs[3,4] and polluted waters[19,24] (Table 1). Depauperate habitats could provide safe havens for freshwater acclimation and adaptation, allowing further range expansion into natural communities.

Artificial habitats, such as reservoirs, appear to have facilitated entry into inland waters[5]. Freshwater populations of the copepod *Eurytemora velox* is typically found in artificial ponds and reservoirs in Europe[5], whereas those of *E. affinis* occur predominantly in reservoirs in the southeastern USA[4]. Similarly, many brackish species have colonized fresh waters of Europe that were left depauperate from industrial, agricultural and domestic sewage[3,19,24]. The North American amphipod *Gammarus tigrinus* was introduced to the Werra River, Germany, to replace freshwater *Gammarus* species that had gone extinct[25]. 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[19]. 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

The ability to invade fresh water 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[25]. However, once this innovation arises 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, marine and hypersaline waters[5,26]. The molluscan subclass Heterodonta, which includes zebra mussels, contains a disproportionately large number of brackish and freshwater species[27]. Thus, habitat diversity and range within a taxonomic group might indicate the propensity to invade fresh water[5].

Among invertebrates, crustaceans are reported most frequently as recent freshwater invaders (Table 1), possibly because of the morphological and physiological traits of this group, such as the ability to reduce membrane permeability[7]. Among fishes, landlocking occurs in several unrelated groups of diadromous fishes[12,23], 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[5,28]. This variation might result from variation in acclimation or selection regime among habitats[28]. 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 is another environmental factor that might pose a barrier to freshwater invasion[5]. Freshwater habitats tend to experience greater fluctuations in temperature 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[29,30], 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[30], whereas others gain broader salinity tolerances[31]. Effect of temperature on salinity tolerance has not been examined extensively and might influence where freshwater invasions can take place.

Life-history traits

Particular life-history traits might predispose certain invading 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 as a means of escaping stressful conditions[5,32]. In contrast, many historical invaders have traits that favor colonization rather than persistence in fresh water. Invaders from salt water with high fecundity and population growth rates have frequently replaced indigenous freshwater species. For instance, the amphipod *C. curvispinum* reaches densities as high as 750 000 per m^2 on hard substrata in the Rhine river, and has a shorter generation time and relatively larger clutch size than other *Corophium* species[19]. Zebra mussels are free spawners with earlier maturity, more rapid growth and higher fecundity than the unionid mussels they are driving to extinction[20]. 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 regulator relative to native sphaeriid and unionid bivalves[33]. Likewise, *C. curvispinum* requires more energy to regulate sodium in fresh water than do freshwater amphipods[34].

Some populations that have invaded fresh water appear to have lost their high salinity tolerance – a pattern found in more ancient freshwater inhabitants[27]. This pattern suggests tradeoffs in osmoregulatory capability. Direct comparisons between landlocked and anadromous populations of juvenile arctic char, *Salvelinus alpinus*, reared under identical conditions, showed that freshwater populations have much lower seawater tolerances than the anadromous populations[35]. In their native Ponto-Caspian region, zebra mussels live at salinities of 6–10 PSU (parts per thousand), whereas freshwater populations in North America cannot tolerate salinities above 4 PSU (Ref. 20). However, North American zebra mussels appear to be reinvading brackish habitats, and extending their ranges into the Hudson River estuary[36].

Life-history evolution

Ancient freshwater residents have evolved life-history strategies for persisting in freshwater habitats. These habitats are smaller, more fragmented, more ephemeral and have a less consistent food supply than the sea. Such strategies might include investing in fewer and more expensive offspring (e.g. larger egg size), loss (or abbreviation) of larval stages, nonfeeding larvae and production of resting stages[37–39]. Some recent invaders have acquired some of these traits subsequent to invasion. The pattern of larger and fewer offspring seen in ancient freshwater species often occurs in recent freshwater populations, such as the larger and fewer eggs observed in many populations of diadromous fishes landlocked in postglacial lakes[12,13,40]. In some cases, life-history changes take place to accommodate more highly seasonal lake conditions. For instance, a population of *Galaxias truttaceus* in a 3000–7000-year old lake spawns in the spring, avoiding cold and food-poor winter conditions, whereas the ancestral catadromous population spawns in autumn, in less seasonally variable marine waters[13].

Morphological radiation

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[23]. 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[11]. In addition, heritable[41] morphological divergence occurs within lake habitats between plankton-feeding and bottom-feeding forms[41,42]. Such patterns of morphological divergence emerge repeatedly during independent invasions into fresh water, and to different degrees. A population of threespine stickleback impounded in 1960 in a freshwater pond demonstrates a striking example of initial stages of morphological divergence[43]. 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.

Evolutionary applications and implications for conservation

Freshwater invasions have been of great interest to evolutionary biologists and paleontologists because they constitute major evolutionary transitions[25,44]. 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[2]. Recent freshwater invasions can offer excellent systems for observing 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[43], 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[45], 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[46]. 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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