The Fresh-water Invertebrate Fauna: Problems and Solutions for Evolutionary Success

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SYNOPSIS. The volume of salt waters of the world is more than 10,000 times the highly fragmented volume of inhabitable fresh waters, yet the latter has come to support a rich and euryokous fauna. In making the salt-brackish-fresh transition, the fresh-water (carbonate) fauna has developed clusters of new adaptations. The vast majority of marine species are restricted to a narrow and monotonous chemical environment, but most fresh-water species thrive in habitats exhibiting a wide (e.g., 10-fold) range of dissolved salts, featuring high carbonates, low sodium chloride, and low potassium.

In comparison with their ancestral marine forms, the temperate fresh-water fauna is generally characterized by: (1) much more efficient osmoregulatory systems, (2) smaller body size, (3) lower reproductive potential, (4) loss of specialized larval stages, (5) a wide variety of anabiotic devices and strategies, (6) well developed low temperature tolerances, (7) aestivation stages in adults, (8) a remarkable facility for overland geographical migration and ecesis by disseminules, (9) facility and adaptations for withstanding prolonged habitat silting, (10) adaptations to swift unidirectional currents by many lotic species, and (11) a more general ability to live anaerobically.

Certain characters of the marine biota have usually been lost during transition and ecesis in the fresh-water environment, such as bioluminescence, bright body coloration, and distinctive bright color patterns. Morphological embellishments in the marine biota are common, including cirri, palps, setation, protuberances, and respiratory devices, but such structures are uncommon among fresh-water species. It is suggested that respiratory stratagems have been developed to an excessive and "unnecessary" degree among many marine forms, as well as in a few fresh-water insects and most Eubranchiopoda.

INTRODUCTION

It is a shortcoming of the fresh-water invertebrate literature that information bearing on the fundamental mechanisms for colonization and ecesis in the rigorous fresh-water environment is generally fragmentary, scattered, ignored, or mentioned incidentally (Pennak, 1978; Macan, 1961). I should like, therefore, to integrate such information under one title. Unfortunately, space limitations forbid a detailed discussion, and I must be satisfied with briefly presenting a series of topics, and only minimal documentation and analysis. I have no new generalizations, but I hope to present some of them in a different light. I am also taking the liberty of making certain germane speculations. Bear in mind that each generalization may have notable exceptions. Thus, this contribution is written in the form of an essay.

I shall not recite long lists of taxa inhabiting fresh waters, comparing them with those found in salt waters, but remember that only aquatic spiders, mites, insects, pulmonate gastropods, and perhaps the rotifers, cladocerans, and eubranchiopods, are not derived directly from the sea. Rather I am interested in considering the morphological and physiological adaptations that have appeared on a grand scale within the fresh-water kingdom. In other words, what are the major evolutionary problems that have been solved as prerequisites to an existence within the rigorous fresh-water environment, and how do they operate? Some of these items are obvious; others are more subtle and obscure.

Further, I am restricting my remarks to the "true" fresh-water invertebrate fauna on the one hand and the "true" marine invertebrate fauna on the other hand, even though the brackish environment is the site where fresh-water adaptations begin and where salt-water adaptations may be lost. A discussion of these comparative and complicated marine-brackish-fresh-water adaptations is reserved for another occasion.
Table 1. Waters of the world.

<table>
<thead>
<tr>
<th>Water item</th>
<th>Volume, cubic km</th>
<th>Percentage of the world's total water</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lakes, ponds, and reservoirs</td>
<td>125,000</td>
<td>0.009</td>
</tr>
<tr>
<td>Average instantaneous volume of rivers</td>
<td>1,250</td>
<td>0.0001</td>
</tr>
<tr>
<td>Saline inland waters</td>
<td>104,000</td>
<td>0.008</td>
</tr>
<tr>
<td>Soil moisture and vadose water</td>
<td>67,000</td>
<td>0.005</td>
</tr>
<tr>
<td>Ground water</td>
<td>8,350,000</td>
<td>0.61</td>
</tr>
<tr>
<td>Icecaps and glaciers</td>
<td>29,200,000</td>
<td>2.14</td>
</tr>
<tr>
<td>Atmosphere</td>
<td>13,000</td>
<td>0.001</td>
</tr>
<tr>
<td>World oceans</td>
<td>1,320,000,000</td>
<td>97.3</td>
</tr>
</tbody>
</table>

Nevertheless, this small fraction of Earth's water has been thoroughly colonized by fresh-water invertebrates.

This brings us to another point. Excluding the atmosphere, salt waters constitute our finest example of a physically continuous environment. That is, any (small) part of the seas is theoretically accessible to any other part. There are no formidable dry land barriers—only ecological barriers, temperature, distance, food conditions, substrate, and competition, which, I submit, can often be at least temporarily tolerated.

The fresh waters of the world, on the other hand, are hopelessly fragmented into an enormous array of isolated habitats. To be sure, a large river system or a large lake is a considerable habitat-mass, though not without internal ecological barriers, but consider the millions of reservoirs, small lakes, and ponds of the world, ranging down to such restricted habitats as a stock tank completely isolated on our short grass plains, 10 km from its nearest neighboring stock tank or water hole, and dependent upon a windmill and well for its source of water. This, of course, is an extreme example of the environmental situation to which a segment of the fresh-water fauna must be adapted. The small pond as an isolated microcosm is a neglected concept that was first emphasized very long ago in a classical paper by Forbes (1887).

The chemical divergence

The most obvious marine–fresh-water distinction lies, of course, in the salt content of these two regimes. The great bulk of marine habitat mass ranges between only 3.30 and 3.70 percent salt, of which 80% consists of sodium chloride. The vast majority of “true” marine species therefore are restricted to a chemically monotonous environment (Fig. 1), and they may be said to constitute the "chloride fauna."

Most fresh-water species, on the other hand, tolerate and occur naturally over a surprising range of total dissolved solids (TDS). From a chemical standpoint, and unlike the oceans, there is no such thing as an “average” fresh-water habitat. Each lotic or lentic situation has its own chem-
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Marine Fauna

Freshwater Fauna

Brackish

Fig. 1. Salt content and environmental preferences of the aquatic faunas. This figure shows only natural occurrence of the faunas; it does not show limits of tolerance.

Istury, but customarily the higher the altitude and the nearer a body of water is to the headwaters of its flowage system, the lower the TDS. Nevertheless, the dominant and most distinctive ions are the carbonate-bicarbonate complex, which usually accounts for more than 55% of the TDS. We may thus refer to fresh waters generally and collectively as “carbonate” waters, and to the fauna as the “carbonate fauna.” It must be acknowledged, however, that a significant minority of fresh waters are dominated by sulfates, rather than by the carbonate complex. Sodium chloride is present only in small quantities in most fresh waters, seldom exceeding 5% of the TDS.

Aside from the carbonate and sodium chloride situation, I have long felt that another major ionic and biological distinction between the two types of aquatic environments is centered around potassium as a key element. The average potassium content of seawater is about 380 mg per liter, while fresh waters usually contain less than 10 mg per liter, and often only traces. Large quantities of potassium salts in fresh waters are known to be toxic to many invertebrates, and consequently marine groups making the evolutionary passage into fresh waters must have made an extreme physiological potassium adjustment.

The fresh-water fauna is clearly distinguished by its occurrence in waters that, while dilute, have a wide range of dissolved salts, and thus it is, relatively speaking, an euryhaline fauna (Fig. 1). The true marine fauna, on the other hand, cannot reproduce and complete life cycles over wide ranges of salinity (Dorgelo, 1976).

In general, we may arbitrarily set 1,000 mg per liter as the usual upper limit of TDS for the fresh-water fauna and 10 mg per liter as the lower limit. Within this wide range are permanent populations of many common species that tolerate, for example, a 10-fold range of 50 to 500 mg per liter. Running waters are especially notable for
their annual variations in dissolved materials, depending on the local geochemistry and seasonal changes in discharge. Generally, an annual variation of ±50% in dissolved load is typical (Pennak, 1977), and in exceptional cases ±80%. Most stream invertebrates endure such variations without difficulty.

Seawater seldom exceeds a range of pH 7.8 to pH 8.3 in surface samples, but the "normal" biological range for most fresh waters is about pH 4.4 to pH 8.6. A single habitat, during the course of a year, may vary as much as two full pH units, depending on the vagaries of photosynthesis, light, current, respiratory processes, biota, circulation, etc. The very large literature on this subject shows that many common species adjust to such variations with no difficulty.

The osmotic problem

To cope with such a wide range in habitat chemistry, the carbonate fauna utilizes remarkably efficient mechanisms for osmotic control and adjustment, including protonephridial systems, integument, contractile vacuoles, nephridia, blood gills, and a wide variety of other specialized glandular devices. The same or similar mechanisms are usually present in marine forms, but they operate at a much lower level of efficiency (Krogh, 1939; Beadle, 1957; Fox and Simmons, 1933), owing to the fact that the body fluids of marine forms are generally isotonic or slightly hypertonic to seawater. In contrast, fresh-water body fluids are weakly to strongly hypertonic, depending on the particular habitat. In relation to this situation, it has been observed many times that fresh-water malacostracans have proportionately larger osmoregulatory devices than their marine relatives.

One of the most striking osmotic conditions may be found among invertebrates in our high mountain tarns, where there are usually populations of cladocerans, copepods, protozoans, rotifers, nematodes, oligochaetes, many immature insects, and even seed clams (Sphaeriidae). Here the total dissolved solids may be only 10 mg per liter, distributed as follows:

<table>
<thead>
<tr>
<th>Component</th>
<th>Concentration</th>
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<tbody>
<tr>
<td>dissolved organics</td>
<td>3 mg per liter</td>
</tr>
<tr>
<td>carbonate-bicarbonate complex</td>
<td>4</td>
</tr>
<tr>
<td>silicon complex</td>
<td>2</td>
</tr>
<tr>
<td>all other salts</td>
<td>1</td>
</tr>
</tbody>
</table>

Such water is more dilute than what passes for the usual "distilled water" in our laboratories. Within 1 mg of "all other salts" are the chlorides, sulfates, nitrates, phosphates, magnesium, and iron, plus a host of other essential ions—all present in trace quantities in such dilute mountain waters. Evolutionary perfection of osmotic systems and integuments gives these animals the ability (1) to absorb from such water, in various ways, all (essential) ions on a basis that is seemingly atom-by-atom, and (2) to retain these absorbed internal ions as well as those obtained through ingested food. Indeed, this is illustrated by the fact that many fresh-water arthropods will live in distilled water for weeks at a time.

Other things being equal, fresh-water invertebrates use more oxygen than their close marine relatives, presumably because of the greater energy needs to maintain the proper internal osmotic pressure.

A few marine species are specialized for absorbing and concentrating such exotic elements as zinc, vanadium, copper, and iodine (Galtsoff, 1934; Vinogradov, 1953), but I know of no comparable examples of American fresh-water invertebrates which selectively concentrate any unusual ions. Instead, inhabitants of exceptionally soft waters must take up essentially all ions against an unfavorable osmotic gradient.

Macan (1963) points out that the fauna of the most dilute fresh waters tends to be ultimately of terrestrial origin. This has not been my experience, as shown for extremely soft high altitude waters.

Body Size

In my own mind, I cannot rationalize the fundamental difference in size (body weight) of marine as compared with fresh-water invertebrates. In general, the temperate marine macrofauna consists of taxa whose average size is larger than that of their close fresh-water relatives. It would seem, however, to be reasonable to expect
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this situation. Fresh-water forms would have a metabolic and osmotic disadvantage in being larger since area (body surface) increases as the square, while body volume increases as the cube, thereby conferring a theoretical osmoregulatory disadvantage upon (large) fresh-water forms in the dilute milieu. We suspect, however, that the answer might lie in the fact that food in fresh waters is less available and less abundant than in salt waters, and that this limiting factor has taken precedence over osmoregulatory and other physiological problems. At any rate, the evolutionary processes have appeared to screen out those large species having the potential of making the transition into fresh waters. In this respect, Brandt (1897) showed that the size of Baltic Sea mollusks is correlated directly with salinity. In fresh waters there are only two taxa having bodies of any size—mussels and crayfish.

REPRODUCTIVE POTENTIAL

No one seems to have collected extensive data to show conclusively whether there is a broad difference between fecundity in marine invertebrates and their fresh-water counterparts, but most of us are familiar with a few examples. Thus, in a few fresh-water hydroids such as *Hydra*, reproduction is restricted to one or a few fertilized eggs at a time. Its relative *Cordylophora* produces twice or more as many embryos in brackish as in fresh waters. Making allowances for the size difference, lobsters in berry carry proportionately more eggs than fresh-water crayfish. Fresh-water flatworms produce few eggs, and the same is often true, comparatively, for fresh-water Mysidacea, Amphipoda, and Gastropoda. Needham (1930) and Barrington (1967) point out that the common oyster releases 1,800,000 eggs at once and that oviparous oysters may produce 100,000,000 eggs per spawning. The fresh-water *Anodonta cygnea*, however, produces only 15,000 to 20,000 (rarely) eggs. As a whole, fresh-water mussels produce several thousand to 3,000,000 embryos, depending on the size of the species. The marine gastropod *Buccinum* may deposit 12,000 eggs and *Nucella* about 245 capsules containing 400 to 600 eggs each, while fresh-water snails lay only a trivial 10 to hundreds at a time.

There has been some speculation about this fundamental difference in reproductive potential between the chloride fauna and the carbonate fauna. One such speculation argues that trace element nutrients are more difficult to accumulate in necessary quantities in fresh-water invertebrates, and as compensation their eggs must be larger (to store such materials for early growth), and hence the total number of eggs is much smaller. I consider this a weak explanation, especially in view of the ability of fresh-water forms to live and reproduce in extremely dilute waters. Furthermore, most fresh-water microcrustaceans are notable exceptions in having small eggs. And Thorson (1946) presents abundant evidence to show that eggs of marine invertebrates range widely in their yolk content, and in their small to large size. Careful experimental work on euryokous species might be revealing.

Egg-carrying habits may be related to this problem. In fresh-water species the eggs are often carried by the parent until hatching and release of the young. This situation occurs notably in certain rotifers and most cladocerans, mussels, copepods, and malacostracans, as well as in other taxa. The egg-carrying habit is also true for some marine species, but it is by no means as common as it is in fresh waters. If eggs must be carried until the hatchling is sufficiently grown to assume an independent existence, we may reason that there is less room on the female body for the clutch of eggs. Hence the small number of (larger) eggs.

Another explanation for fewer (larger) eggs is that the fresh-water organism must eclose with fully developed osmoregulatory capabilities, i.e., must be at a more advanced stage to cope with the highly dilute surroundings.

In marine forms the production of (lightweight) planktonic eggs is common, while fresh-water eggs are heavy and remain or sink to the bottom.

DISTINCTIVE LARVAL STAGES

Unlike most of their marine relatives, fresh-water invertebrates produce special
larval stages in only a few major taxa, as shown in Table 2. To this Table could be added the Eubranchiopoda exception; this taxon is restricted to fresh waters and inland saline waters and does have nauplius stages.

Barrington (1967) states that "The disadvantage of fresh-water larval stages are so clear," but does not actually discuss the problem. I believe that there is probably a variety of evolutionary reasons, operating through a very long geological time frame, to explain the paucity of special larval stages in fresh-water invertebrates. It is, however, truly unusual that the fresh-water Copepoda, an eminently successful group, have retained the basic nauplius stages in the life history. It is, furthermore, a remarkably euryokous group, very closely tied to its salt-water relatives. Fresh-water copepods of modern aspect are known to have existed by Miocene times (Palmer, 1960).

Nine major taxa are well represented in both fresh and salt waters, but special larval stages are present in neither environment, the young being hatched in an advanced stage of development; these are: Gastrotricha, Rotifera, Nematoda, Tardigrada, Oligochaeta, Hirudinea, Mysidacea, Isopoda, and Amphipoda.

Anabiotic Strategies

It is in the production of anabiotic devices that fresh-water invertebrates excel, and we are here using the term "anabiosis" (Gr. "recovery of life") in the broad sense to include all special resistant eggs, cysts, and other small resting stages that are produced to tide the animal over periods of desiccation, extreme cold, heat, anaerobic situations, lack of food, and other adverse conditions (Figs. 2 and 3). It seems logical to suppose that such fresh-water mechanisms have arisen in response to variable and unpredictable environmental situations usually not found in the more stable and predictable marine surroundings. The fact that such devices are not present in marine species but are present in fresh-water species in the same ancient taxon is indicative of the probable early appearance of these devices in the transitory primordial fresh-water environment. Table 3 is an attempt to summarize the anabiotic devices for taxa that occur in both the chloride and carbonate environments.

If difficult to find accurate information as to the supposed existence of resistant devices among marine invertebrates, and the data in the middle column of Table 3 therefore are subject to minor modifications. Recently, I resorted to asking a group of five experienced protozoologists about the relative frequency of resistant cyst stages in fresh waters as compared with salt water. They were surprisingly in agreement that: (1) cysts are known to occur (or "probably occur") in more than 90 percent of fresh-water protozoans, but (2) are essentially unknown or rare in "true" stenohaline marine protozoans (as opposed to brackish forms).

In general, the third column in Table 3 shows the striking tendency for evolution-
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ary development of thick-walled anabiotic stages, even though the associated instigating environmental conditions may be quite different from one time or one taxon to another. Indeed, this is a classical display of parallel adaptive evolution on a massive scale. Note the sharp break between ostracods and isopods in Table 3. It clearly sep-

### Table 3. Relative occurrence of anabiotic stages in marine and fresh-water invertebrates. Only those taxa occurring commonly in both environments are listed.

<table>
<thead>
<tr>
<th>Fresh-water and marine taxon</th>
<th>Anabiotic devices in marine species</th>
<th>Anabiotic devices in at least some fresh-water species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protozoa</td>
<td>Resistant stages rare</td>
<td>Many kinds of resistant cyst stages</td>
</tr>
<tr>
<td>Porifera</td>
<td>&quot;Gemmule-like&quot; structures rare</td>
<td>Gemmules, &quot;reduction bodies&quot;</td>
</tr>
<tr>
<td>Coelenterata</td>
<td></td>
<td>&quot;Thecated embryos&quot;</td>
</tr>
<tr>
<td>Turbellaria</td>
<td></td>
<td>Cocoons, fragmentation cysts, &quot;winter&quot; eggs</td>
</tr>
<tr>
<td>gastrotricha</td>
<td></td>
<td>Opsiiblastic eggs</td>
</tr>
<tr>
<td>Rotifera</td>
<td></td>
<td>Resting eggs, winter eggs, anabiotic stage of adult</td>
</tr>
<tr>
<td>Nematomida</td>
<td></td>
<td>Resting eggs, desiccated individuals</td>
</tr>
<tr>
<td>Tardigrada</td>
<td></td>
<td>Various stages described as: tun, cyst stage, anabiotic stage, cryptobiotic stage</td>
</tr>
<tr>
<td>Nematoda</td>
<td></td>
<td>Cysts</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td></td>
<td>Statoblasts (at least six types), hibernacula</td>
</tr>
<tr>
<td>Ostracoda</td>
<td></td>
<td>Hibernacula</td>
</tr>
<tr>
<td>Amphipoda</td>
<td></td>
<td>&quot;Resting eggs&quot; in a few spp., diapause cocoon stage</td>
</tr>
<tr>
<td>Decapoda</td>
<td></td>
<td>Resting eggs, advanced instars able to withstand cold and drying in diapause</td>
</tr>
<tr>
<td>Mysidacea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pelecypoda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastropoda</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

arates the microscopic anabiotic groups from the macroscopic non-anabiotic groups. In addition to the material in this Table, there are a few taxa essentially restricted to fresh waters (and originating in fresh waters?) that have also developed special anabiotic devices, including the highly resistant resting eggs of the Eubranchiopoda and the ephippial eggs of Cladocera (ignoring the very few marine Cladocera). Many Eubranchiopoda are macroscopic, and in this respect they are an exception to the size vs. anabiotic stage principle just mentioned. Most, however, are restricted to astatic waters. And many aquatic insects, being largely restricted to fresh waters, have a diapause or diapause-like period in the larval, pupal, or nymphal stages which are resistant to unfavorable environmental conditions (see Mansingh, 1971). Anabiotic stages of many fresh-water taxa actually require a period of cold, freezing, drying, or anaerobiosis before they will hatch.

Many years ago I acquired a quantity of dried mud that had just been collected from the bottom of a small pond in the Galápagos Islands. Annually thereafter for ten years I put some of the mud in filtered pond water and periodically examined this microcosm for active invertebrates. Within a few days to weeks I always found active excysted protozoans, rotifers, tardigrades, nematodes, and microcrustaceans. Any student may duplicate these observations with dried pond mud. Dried intertidal marine mud, however, produces no such comparable populations when given similar treatment.

Also, I have many unpublished obser-
vations on the anabiotic effectiveness of pond invertebrates at high altitudes where the entire water mass and as much as 0.5 m of the substrate are annually frozen solid for six months or more. Each summer, beginning with ice melt, the normal population of pond invertebrates is restored.

In the laboratory, the fantastic tolerances of cyst stages for drying, anaerobiosis, and temperature conditions far exceeding normal ranges are legendary (von Brand, 1946; Ashwood-Smith and Farrant, 1980). Rotifer, protozoan, crustacean, and tardigrade anabiotic stages are especially resistant, and a surprising fraction of anabiotic stages recover and become active after such drastic treatment.

Low Temperature Tolerances
Aside from the resistant inactive anabiotic stages, the active stages of many freshwater invertebrates also withstand and recover from freezing and thawing of the substrates of lake shores and stream sides, as well as in the substrate of ponds that freeze solidly for several weeks to as much as nine months (Neldner and Pennak, 1955; Olsson, 1981; Kenk, 1949; Dougherty and Harris, 1963; Scholander et al., 1953; Ser nnov, 1927). In reality, ice and frozen substrates typically contain anabiotic stages in addition to immature and adult stages, depending on the particular species.

In marine habitats, on the other hand, subtidal species are unable to recover from freezing, although some intertidal forms, especially mollusks, can withstand being frozen in ice for days or weeks (Kanwisher, 1955).

Aestivation
Aestivation is a phenomenon closely associated with the production of anabiotic stages, but usually involves an inactive state of the whole mature animal, rather than an inactive state of an anabiotic device produced by that animal. We also prefer to think of aestivation as applying only to the desiccation conditions of heat and dryness. In marine habitats temporary aestivation is restricted to a relatively few species inhabiting rocky shores near the high tide line, such as barnacles and mollusks.

Fresh-water aestivation is most clearly shown for populations of temporary pools and ponds; see especially the extensive study by Wiggins et al. (1980). These authors designate aestivation forms as "overwintering residents," including juveniles and adults of such taxa as oligochaetes and leeches that secrete a protective coat of mucus, snails that secrete a mucoid epiphragm, a few copepods in the diapause stage, and a few immature and adult insects. These are species that actually survive true dry conditions, brought on before cold weather begins. In addition, there is always a large population of species that overwinter in crevices, in the water of crayfish burrows, in damp vegetable debris, and in damp pondside soil. These are not true examples of aestivation, however, in the sense that we are using the term here.

Overland Transport
In addition to withstanding unfavorable conditions, resistant stages have the further function of making overland transport and geographical dissemination possible. For without such a function, colonization of new fresh-water areas would be slow and extremely difficult in the discontinuum of fresh waters. Even the most isolated puddles, ponds, and streams have thriving communities of invertebrates. It has been a constant source of interest for me to come upon newly created mountain ponds or prairie waterholes that are completely isolated from the nearest supply of invertebrates by as much as five or more km, only to find a complex and thriving community of gastropods, aquatic insects, microcrustaceans, water mites, microoligochaetes, tardigrades, nematodes, rotifers, microturbellarians, and protozoans. This ease of colonization vastly surpasses any such mechanisms among their marine relatives. Small ponds commonly contain a faunal list all out of proportion to their size. Williams (1983), for example, reported 98 metazoan taxa from a temporary pond in Ontario.

Ecologists are generally agreed that the constant spread and reclamation of freshwater bodies is a process facilitated by anabiotic transport on the bodies or via the
digestive tracts of vagile (adult) aquatic insects and aquatic birds, and by wind which blows resistant stages about as dust. Indeed, every new and isolated body of fresh water may be thought of as an island in a wide area of dry land that is colonized with amazing rapidity. One of the most unusual examples of such colonizations is the occurrence of protozoan and micrometazoan communities in miniature kryokonite depressions on the surface of the Greenland icecap.

The literature of anabiotic transport by wind and vagile animals consists chiefly of fragmentary and widely scattered papers; a few of the more significant are: Niethammer, 1953; Lansbury, 1955; Löfler, 1963; Maguire, 1963; Malone, 1965; Proctor and Malone, 1965; Dundee et al., 1967; Stewart et al., 1970; Carroll and Viglierchio, 1981; Fernando, 1958.

It is not easy to explain the faunal composition of small springbrooks on the basis of anabiotic structures and overland transport. Such habitats are abundant and widely scattered over the United States, but are effectively isolated from each other by a matter of a few to many km. The community make-up is readily predictable. A dense growth of water cress (*Nasturtium officinale*) is almost invariably present, the substrate is usually gravel, temperature is constant and cool, and the whole community, extending from the emergence point of water from the ground to the mouth of the brook, or to the point where water cress is no longer present, usually ranges from 10 to 200 m in length. The macrofauna is composed of planarians, isopods, amphipods, small snails (*Physa*), leeches, and a few insects, mostly dipteran and beetle larvae, and mayfly nymphs. Few of these species have anabiotic stages that would facilitate geographic distribution. Adult springbrook insects can, of course, easily migrate from one site to another, but most of the other springbrook species are presumably transported on the bodies of flying insects, water birds, and shore birds. Since springbrooks are first-order streams, it would be difficult for the various species to migrate actively and extensively downstream and upstream throughout large flowages, and through unfavorable habitats in so doing. We have seen many small springbrooks on steep, rocky canyon walls; active migrations into such sites would be impossible, except for adult insects.

It is tempting to theorize that springbrooks are stable habitats, and that their corresponding faunal community therefore is composed largely of species that do not produce anabiotic or diapause stages.

While it is now convenient to explain the colonization of aquatic areas by disseminules distributed especially by insects and birds, I wonder about the zoogeographic spread of fresh-water invertebrates in the long-time sense. How, for example, was it brought about before the evolutionary appearance of insects, birds, and other terrestrial vertebrates in Earth's history? Surely a fresh-water fauna existed before birds and insects. Were winds, flooding, and changing drainage patterns then the chief means of distributing disseminules?

THE SILT AND CURRENT PROBLEM

Most running waters (except for springbrooks) exhibit periodic silting. Heavy loads of suspended silt may be present for only a few hours after a heavy shower, or they may be present continuously for two or three months during spring and summer runoff. Suspended loads commonly reach levels of 1.0 g per liter or more, and the water transparency approaches zero. Fine organic and inorganic particles have both abrasive and suffocative action, and while spates always have some decimating effects on lotic faunas, the stream bottom metazoans, especially insects, have remarkable powers of survival and resistance, so that "normal" population levels may soon be restored (Pennak, 1977; Hynes, 1970). Indeed, fresh-water pelecypods are dependent upon the continuous (but moderate) existence of a load of silt as a food source. Continuously clear streams seldom have an appreciable population of clams.

Stream species exhibit another cluster of adaptations that are minimally developed in marine invertebrates found in intertidal habitats. Bottom insects, for example, are often greatly flattened and can thus hide in narrow rubble crevices. They also remain
sufficiently active to dislodge silt that accumulates on the body. Special devices to combat silting and swift currents include streamlining, suckers, friction pads, hooks, sticky secretions, and protective ballast cases (Hynes, 1970). To be sure, the intertidal zone may be temporarily silted by waves, tides, and storms, but, except for major storms and hurricanes, silt periods are brief and have not generally brought about major evolutionary adaptations. Morphological adaptation to turbulence in marine habitats seems to be mostly in the nature of crustose or flattened growth forms, e.g., a few sponges, tunicates, bryozoans, limpets, and sea anemones. Of additional importance, however, is the relatively small size of stream invertebrates as compared with marine invertebrates of the intertidal zone, and this may be a protective adaptation.

Another important distinction is the fact that the current in a swift stream microhabitat is constant and relatively unidirectional in the force exerted upon a metazoan, while intertidal turbulence is intermittent and multidirectional (Denny, 1983). Possibly this distinction is responsible for the wide divergence in adaptations in streams as compared with tidal zone turbulence.

**Anaerobiosis**

There seems to be no pervasive and consistent distinction between fresh-water invertebrates and their marine relatives with respect to an ability to withstand anaerobic conditions. In both environments there are many related and unrelated taxa that have developed the ability to live for a few hours to a few months in the absence of oxygen, or where oxygen is present in concentrations below ten percent saturation. It is probable, nevertheless, that the fresh-water fauna has more frequently developed the physiological mechanisms for withstanding anaerobic conditions for long periods than is the case for marine invertebrates. Examples include the fauna of sewage treatment waters and the benthic and plankton faunas of eutrophic lakes and ponds whose bottom waters are anaerobic or near-anaerobic for months in both summer and winter. Both marine and fresh-water environments, however, are commonly and continuously anaerobic or near-anaerobic below the surface of organic bottom muds. Perhaps our best marine example involves the subtidal thio-biotic microfauna.

**Evolutionary Shortcomings in Fresh Waters**

Thus far we have been concerned chiefly with adaptations that have come about as the result of migrations of marine taxa ancestors into fresh waters, where the new adaptations have permitted the incipient fauna to become established. In so doing, however, it appears that some features of the marine ancestors have become lost, and, for the most part, are not to be found in fresh waters. Three of these features are briefly discussed in the following paragraphs.

**Bioluminescence**

We need give only passing mention of the sharp separation of fresh and salt-water faunas with respect to bioluminescence. It occurs commonly in many marine taxa, and a wide variety of functions has been ascribed to the phenomenon (Harvey, 1952). In striking contrast, it is extremely rare in fresh-water invertebrates. The proper combinations of anatomical adaptations, physiological mechanisms, bacteria, and essential enzyme systems have been lost in the environmental transition, or have not yet evolved in the shallower carbonate waters.

**Morphological embellishments**

Many marine species are notable for an abundance of external growths on the body surface, such as excessive setation, spines, palps, fleshy protuberances, and respiratory devices (Fig. 4). Such embellishments occur generally but are most common among Crustacea, Polychaeta, and Mollusca. Some devices are presumed to retard sinking in plankton species; others are sensory; a few are feeding devices; and perhaps most frequently they are assumed to be respiratory. It seems to me, however,
that excessive respiratory surfaces, such as a rich array of palps and antennae in polychaetes, are an unnecessary waste of energy, and that most marine forms should be able to get along quite well with more modest respiratory surface areas, even where the species is a burrower. There seems to be no correlation between the total expanded
body surface and the usual oxygen content of the habitat of marine invertebrates.

In making the evolutionary adjustments to become established in fresh waters, the great majority of fresh-water invertebrates have either lost or never had an imposing array of external protuberances. Exceptions (Figs. 5 and 6) include: a few species of fresh-water gastrotrichs which have excessive spination; an oligochaete *Branchiura sowerbyi* with excessive "gills"; and several species of polychaetes that breed in fresh waters, which are probably recent invaders, and which have retained their excess parapodia, palps, and cirri. In the United States these polychaetes include one species each of *Lycastoides*, *Namanereis*, *Nereis*, and *Manayunkia*. Entoprocts and ectoprocts in both environments have equally developed tentacular crowns but these are chiefly food-gathering devices.

The only other fresh-water taxa having significant morphological embellishments are (1) some insect larvae and nymphs with spines or abundant gills, and (2) the Eubranchiopoda (fairy shrimps, tadpole shrimps, and clam shrimps), all of which possess 10 to 71 pairs of complicated flat respiratory appendages on the segments. Insects are of terrestrial origin, and the Eubranchiopoda are presumed to have originated in fresh waters, so neither group has immediate marine relatives, and the modifications are fresh-water acquisitions.

We are therefore left with the great majority of fresh-water invertebrates, none of which appear to have wasted significant growth energetics on overgrowths or external structures that have no obvious or critical functions. Indeed, it is remarkable that fresh-water invertebrates have not developed a whole series of special respiratory embellishments, especially since so many species are exposed to anaerobic or near-anaerobic conditions at some time during the life cycle. A modest complement of gills and other respiratory structures seems to be adequate.

Let me cite an anomalous example occurring in swift streams. Often the bottom fauna contains several species of stone-fly nymphs occupying similar spatial niches. Here it is common to find, in the same sample, nymphs with no external gills (*e.g.*, *Isoperla*), as well as nymphs with a great abundance of finger-like gills (*e.g.*, *Pteronarcy*s). Such streams are always at or close to 100 percent saturation with oxygen, yet there is a pronounced adaptive difference. Similar parallel examples may be found among the Trichoptera and Ephemeroptera, and, for that matter, similar parallel examples are abundant in marine taxa.

The whole problem of "minimal," "adequate," and "excessive" respiratory surfaces for both marine and fresh-water faunas needs investigation.
Coloration and color patterns

One of the most pervasive differences between marine and fresh-water invertebrates is the general lack of bright colors and contrasting patterns among the latter. Only a few exceptions can be cited: Freshwater sponges are often bright green owing to their intracellular algal populations. Some high-altitude copepods are bright scarlet or bluish. A few gammarids have an orange coloration. Some water mites are bright red, blue, yellow, or green. And some dipteran larvae are red or greenish. These colors serve a variety of functions. Red copepods are said to be protected against short-wave radiation (Hairston, 1976); red water mites are said to be aposematic (first noted by Elton, 1922); and the red in some chironomid larvae is produced by hemoglobin. In addition, most small and translucent metazoans may have transient colors produced by food in the gut (e.g., eubranchiopods). Some crayfish are purple, reddish, or orange, but hues are drab and seldom can be called “bright” colors.

Distinct and contrasting patterns in coloration are similarly lacking in nearly all fresh-water forms. Some leeches and planarians have a finely dotted coloration pattern, and many water mites have elaborate patterns produced by pigments in the body wall and by the varied contents of the visceral organs. Otherwise most distinctive patterns are to be found among immature aquatic insects, and especially in Ephemeroptera and Plecoptera, where there are yellow, brown, and tan pigment deposits in the integument. Personally, I think it is...
regrettable that in view of the enormous diversity of fresh-water insects that the evolutionary processes have not been more generous in distributing brightly patterned coloration among the aquatic stages in the life history.

Marine invertebrates, on the other hand, are often brilliantly colored and patterned. One need look no further than the abundance of color plates in identification manuals, natural history magazines, and decorative "coffee-table" volumes.

Variable, or chromatophore, coloration is almost restricted to marine forms where it sometimes reaches astounding levels, especially in certain mollusks and crustaceans. I know of very few American fresh-water species that can make (rapid) changes in coloration. One example is *Palaemonetes* where chromatophores can color-adapt to the background in less than 24 hr, but this is a far cry from what we see in so many marine species.

No one has suggested the fundamental evolutionary reasons for the notable coloration disparity between marine and fresh-water species. It must stem from the differing results of an evolutionary complex of taxon age, genetics, behavior, food, excretory mechanisms, etc. Indeed, the whole matter of colors and color patterns among aquatic forms is a fundamental problem that has scarcely been touched.

**Comment**

By way of brief summary, we must accept the proposition that incipient colonizers of fresh waters must have first acquired, in varying degrees, whole clusters of special devices and mechanisms in order to establish successful and permanent populations in the harsh and variable fresh-water environment. At the same time, certain specializations for the marine existence must have been lost. Our understanding of evolutionary and genetic processes does not permit the *de novo* establishment of fresh-water taxa. Rather we think of these groups as only very rarely and precariously being successful in the new environment. We visualize the age of fresh-water taxa as being quite different from each other. Some are probably "new"; others are "ancient." But, in my own estimation, and regardless of age, the presiding requisite for life in fresh waters is that of euryoky.

At the beginning of this essay, I mentioned the fact that there are exceptions to many of my generalizations. A few of the most striking of these are as follows: Encystment by a marine copepod (Coull and Grant, 1981) and by a marine tardi-grade (Schulz, 1935); polychaetes living in fresh waters (Foster, 1972); bioluminescence of fresh-water oligochaetes (Bogatov *et al.*, 1980); limpets, shrimp, and flies (Harvey, 1952); a veliger stage known for one (European) fresh-water mussel, *Dreissena polymorpha*, a recent invader of marine ancestry.

A number of fresh-water invertebrate rarities and ecological curiosities in the United States are associated in various ways with the topics we have enumerated. Some involve "escapes," that is, certain uncommon fresh-water invertebrates with close marine ancestry that have made the marine–(brackish?)–fresh-water transition accidentally, and contrary to the situation among their closest relatives. Space does not permit discussion or extended reference lists, but some of the more intriguing items may be listed as follows: hot spring faunas, hyporheic faunas, Acoela, ice worms, cave species, Nemertea, Archinannelida, glacial marine relicts, Thermosbaenacea, Bathynellacea, *Cordylophora*, *Urnatella*, intertidal and shoreline insects. Investigations of these topics and taxa may be instrumental in answering some of the questions posed in the foregoing paragraphs.

Undoubtedly many who read this essay will disagree with some of my generalizations and suggestions. If so, I shall be pleased in knowing that I have been responsible for such attention being accorded to the fresh-water invertebrate biota. I hope such controversy will generate significant field and laboratory research.

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REFERENCES


Lansbury, I. 1955. Some notes on invertebrates other than insects found attached to water-bugs *(Hemiptera-Heteroptera)*. *Entomologist* 88:159–140.


