TEMPERATURE, ORGANIC MATTER AND THE SUSTAINABILITY OF AQUATIC SYSTEMS

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Introduction

Temperature has many effects on aquatic systems and this essay will, inevitably, make a broad sweep rather than take an "in depth" approach. The focus is on *aquatic* systems (i.e. all those where water is the medium) because many of the direct, and indirect, effects of temperature are similar both in marine and fresh waters. The article thus provides another opportunity to combine the two branches of aquatic science. Primary literature sources are deliberately omitted. Readers interested in the topics covered will find full bibliographies in the books cited.

Before proceeding we require a definition of sustainability. The Concise Oxford Dictionary carries eight definitions of the verb "to sustain". The one which is most appropriate to the ideas presented in this article is "to keep going continuously". Changes in sustainability of aquatic ecosystems are likely to be brought by the global warming that has been widely predicted. Before making consideration of these changes we need to review the effects of temperature on water-bodies, some of which will be well-known, others less well-known, to readers of *Freshwater Forum.*

Temperature, water density and stratification

Water is most dense at 4°C, so warm water floats on colder water. Similarly, water that is colder than 4°C also tends to float, continued cooling resulting in ice formation at the water surface. Ice forms on the surface of rivers at high latitude but, for the most part, the depth, and the discharge, of water in rivers ensures that density-induced stratification is uncommon. In contrast, lakes often stratify during summer and again during winter, the two periods being separated by turnovers in spring and autumn when water in the lake becomes thoroughly mixed. In lakes that are stratified during summer the downward flux of particulate organic matter causes the removal of nutrients from surface waters. This can provide limiting conditions for growth of algae in the euphotic zone and the downward export can result in low oxygen tensions in the deeper waters of productive lakes where aerobic heterotrophs are abundant. Nutrients, mineralised from dead organic matter by heterotrophs, are returned to the surface waters when the lake "turns over" and are again available to support plant and animal growth. There are several patterns of lake stratification, with lakes being mixed once, twice, often, rarely, or not at all. There is a general relationship between the pattern of mixis, altitude and latitude (Wetzel 1977) but there are many exceptions to the general rule. For example, shallow lakes and ponds may be consistently warm (or cold).

Tropical oceans are permanently stratified with a thermocline marking the transition between the warm surface waters and the rest of the water mass (Nybakken 1988). As a general rule, temperate oceans are thermally stratified during the summer months but these waters are relatively turbid and the thermocline is closer to the surface than at lower latitudes; polar oceans do not stratify thermally as there is insufficient light penetration during the summer and there is low solar Vadiation in winter. Apart from a zone at the surface, all oceans are completely dark and also cold, although there are pockets of hot water, and high productivity, around hydrothermal vents. Oceans are also well-oxygenated, oxygen minima being found close to the thermocline where aerobic heterotrophic breakdown of descending particles is at its greatest. Oxygen levels at depth are therefore similar to those in oligotrophic lakes.

Organic matter that descends through the water column of tropical oceans is lost to the euphotic zone and there are no regular periods of mixing to ensure that nutrients are returned to surface waters from depth. This explains why these water-bodies have low productivity when other factors, e.g. good light and high water temperatures, are favourable for primary production. Mechanisms that retain organic matter in the euphotic zone are thus important in the nutrient-poor tropical oceans (Wotton 1994), though centres of high productivity at the surface are found in coral reefs and also where there are upwellings of nutrient-rich water. Upwellings result from large-scale lateral water movements in the oceans whereas turnover in lakes - the analogous ecosystem process - results from increasing homogeneity of water temperature throughout the basin and wind-driven mixing through the water column.

Temperature, water movements and turbulence in lakes and oceans

The littoral fringes of marine habitats are under tidal influence, with plants and animals of the intertidal being exposed in a semi-diel cycle which is not an effect of temperature. However, there are other forms of large-scale water movements than tides in oceanic water-bodies, where temperature does play a part.

Oceanic surface water movements are well-known, the Gulf Stream and North Atlantic drift being among the most familiar. Less well-known are deep currents that have a quite different distribution (Nybakken 1988) but it is these large movements deep within the water-body that carry nutrients from polar oceans to upwellings in tropical oceans. One of these upwellings off the west coast of South America is the source of nutrients that previously sustained the Peruvian anchoveta *(Engraulis)* fishery. A combination of overfishing and climatic episodes that prevent the upwelling reaching the surface waters (warm El Nino water currents that occlude the upwellings) have been responsible for the collapse of this fishery.

There are also surface and deeper movements of water in lakes. A constant wind causes water to be blown to one end of a lake and this returns, and oscillates, across the lake basin in a surface seiche. Where the lake is thermally stratified, the lighter warm water above the thermocline has the highest displacement and here the seiche is also internal, with the oscillation being mainly of warm water tipping the thermocline first in one direction and then the opposite. With persistent wind action, water can be blown across the surface of the lake and return, in a cyclical pattern, over the density boundary marked by the thermocline in stratified lakes. It is important to note that these water movements, strongly influenced by temperature effects, cause large-scale turbulence and shear in the surface waters.

Shear creates conditions where organic matter can flocculate. Langmuir circulation causes surface-film organic matter to accumulate in rows of floe and similar processes promote the aggregation of organic matter within the water column. For example, shear, resulting from changes in kinematic viscosity, causes the accumulation of organic matter just above the thermocline where there is a noticeable change in viscosity. Shear, resulting from turbulence and changes in viscosity, also operates on a small scale and it then results in particle formation from colloids and other "dissolved" organic matter. We are only just beginning to appreciate the importance of these small-scale processes in aquatic systems.

Temperature in flowing waters

Streams and rivers have small surface areas relative to the area they drain, and air and ground temperatures within the catchment have a strong influence on the water temperature. Upland streams are characteristically cooler than streams of similar size at low altitude and high latitude streams are similarly cooler than those at low latitude. The smaller discharge of low-order streams provides a lower thermal inertia and these can show pronounced diel variations in temperature as a result. The strongest diel variation is found where there is high insolation and warm air temperatures, when a daily range of more than 10°C can occur. Rivers of higher order will be less prone to diel fluctuations, as will small streams during rainfall and spate.

As a general rule, oxygen is not limiting in flowing waters as mixing of the water column is common. However, some lowland rivers can have reduced oxygen tensions at depth, especially if there is a rich deposition of organic matter over their bed. There is a seasonality in organic matter flux in river systems in temperate and high latitude regions. Most lotic habitats receive their organic inputs from allochthonous (i.e. external) sources, although streams of mid order have higher levels of autochthonous (i.e. internal) production. The input of organic matter coincides with seasonal leaf fall and die-back of rooted and riparian vegetation.

Where lakes are formed by impounding streams two patterns of temperature can be identified in the outlet, depending on the point of discharge within the reservoir. Water draining from the surface is constantly warm during summer stratification and is also rich in particulate organic matter. In contrast, releases from deep within the lake are cooler in the summer and richer in plant nutrients, but low in living and dead particles. The consequences for the fauna and flora are thus different for the two classes of outlet and the extent of the downstream influence is positively related to discharge.

Biota and temperature in aquatic systems

Almost all aquatic organisms require exogenous heat before they metabolise efficiently. An organism that is adapted to warm temperature will have a higher rate of metabolism and this increases feeding rate. In addition, an increase in temperature raises the metabolism of food organisms, so food quality can also be altered. This combination of factors causes a shortening of the life cycle and results in a higher ratio of production : mean biomass. This is another way of saying that a unit of habitat is used more efficiently since biomass is turned over more rapidly. Shortening of life cycles is also of evolutionary significance in that it promotes a higher rate of genetic selection.

Aquatic organisms range from "psychrophiles", developing at the very low temperatures found under permanent ice sheets, and in ocean depths, to the organisms that exploit boiling mud pools. Although most habitats are not this extreme, the temperatures found will affect the distribution of the biota. Some plants and animals only tolerate a narrow temperature range while others are much more tolerant. They also have different optimum temperatures. For example, the photosynthetic efficiency of phytoplankton varies from species to species (Wetzel 1977) and there are similar effects on the digestive metabolism of autotrophs. Such reactions to temperature will influence whether organisms can survive in a particular aquatic habitat and their life cycles will be adapted to both seasonal and diel changes in temperature as appropriate.

Organisms living in the marine littoral, or in small streams, are particularly exposed to short-term changes in temperature. As air temperature is mostly warmer than sea temperature, the intertidal biota must have the capacity to withstand warming and also drying. The extent to which they are tolerant determines their place on the shoreline and some taxa are able to survive with only occasional wetting from high spring tides. Low spring tides, in contrast, expose animals and plants only briefly; at other times they remain submerged. The biota of small streams face diel temperature fluctuations and also seasonal ones.

Where populations have a different tolerance to temperature the result is habitat partitioning. For example, animals requiring a low thermal sum for hatching have a "head start" in development and can utilise different resources from those used by later-hatching taxa that could be competitors. Differing thermal regimes in geographical regions also promote the diverse distribution of the biota. This is a continuing process and varies with climatic changes; "glacial relicts", for example, had quite a different geographical range during the last period of glaciation from that found today. Climatic changes over shorter time-scales can also have an effect on taxa. "Warm summers" and "cold summers" cause changes in the composition of communities in streams at mid to high latitudes and this effect of temperature change is a point we will return to later in this article.

In addition to the direct effects of temperature, there are indirect effects and four examples can be given here: the seasonal decay of plants in autumn supports many of the biota of temperate streams during the winter months, when cool temperatures mean slow growth; the cycling of organic matter in lakes, with release of mineralised organic matter from deep water, can only occur when thermal stratification has broken down; lowered water density, resulting from warming, will bring less buoyancy so that animals and plants that are dependent on passive flotation will need to adjust when temperature rises; altered water viscosity may also affect feeding in animals that generate currents as warm water, with lower viscosity, requires lower energy expenditure for the movement of particulate food (Vanderploeg 1994).

Temperature and surface films

All water-bodies have a surface film and associated surface microlayers of organic matter. The microlayers are enriched with lipids, proteins, polypeptides and other organic compounds that have an hydrophobic component in their structure (Maki & Hermansson 1994). Some of these compounds, the dry surfactants, are not miscible with water and they accumulate at the air water interface, other surfactants forming layers or a gel-like accumulation just under the surface. Whether discrete layers form at the surface, or whether the materials accumulate in a gel, is not known as surface film cannot be sectioned.

There is a high enrichment of heterotrophic bacteria here and characteristic neustonic animals and plants are also found, many of which have mechanisms that allow them to anchor to the surface film from below, or above (Guthrie 1989). The extent of development of the surface microlayers will vary with the trophic status of the water-body, eutrophic waters having a relatively thicker surface film structure than that found in oligotrophic waters. What is clear is that the microlayers of all water-bodies are very thin, just fractions of a millimetre deep, but they cover most of the World's surface. Put crudely, all the blue areas on a globe are surface film and it is this part of aquatic systems that is most affected by solar radiation. It is the site of gas exchange, the region of highest temperature within many water-bodies (except for hydrothermal sources), volatile organic matter evaporates from the surface, and high ultraviolet light intensity promotes the photolytic breakdown of organic complexes. Recently, considerable attention has focused on the role played by benthic biofilms but rather less attention has been paid to the study of surface biofilms. This is being redressed as we understand more of the significance of surface materials in the functioning of aquatic ecosystems. This interface is certainly likely to be affected by any large-scale changes in global temperature regime.

Temperature, drying and the threat of desiccation

One effect of prolonged high temperature is that it causes water to evaporate readily. In the marine littoral this is not an important problem as tides will replenish water in pools, except on the highest parts of the shore. Animals and plants of the exposed marine littoral show adaptations to the short-term drying that is characteristic of shores, and the consequent change in temperature mentioned earlier. Several of the mechanisms used by rocky-shore organisms can be listed: tolerance of drying, e.g. chitons and some seaweeds; provision of a shell or calcareous covering, e.g. mussels and barnacles; seeking shelter from exposure e.g. crabs and amphipod crustaceans. Organisms of sandy and muddy shores survive by burrowing into the substratum.

In hot climates, lakes that contain high levels of dissolved salts will show striking changes in salinity as they dry (Beadle 1974). Here, bodies of ostensibly fresh water, filled during the rainy season, can evaporate to produce saline pools that are devoid of animals and plants except for some cyanobacteria. These waters are, of course, very much more saline than marine habitats.

Small rain pools are found in many tropical countries during the rainy season and these become completely dried at intervals. The biota of such pools must have resistant stages within the life cycle that enable them to cope with periods of drying. Many organisms have a resistant spore or egg stage which sediments out during drying and hatches when rains refill pools in the next wet season. Other organisms are able to cope with drying during the adult phase, e.g. lungfish and some anurans, which cocoon themselves in an impervious mucous coating. These animals can breathe air and this is a necessity for their survival. Adult insects are air-breathing and many aquatic insects have a completely terrestrial life stage during the drying phase. However, larvae of one insect, the chironomid midge *Polypedilum vanderplanki,* and small animals such as some tardigrades, rotifers and nematodes, survive periods of drying by means of anhydrobiosis (Williams 1987). In this state, free water is replaced by binding chemicals such as inositol and dipicolinic acid and the organisms can then remain in suspended animation. By entering the anhydrobiotic state they are able to survive and complete their life cycle during the wet season, despite periods when the pools in which they live become dry. Tardigrades and nematodes also undergo morphological changes during drying, the former compressing into "tuns" and the latter becoming tightly coiled. Both mechanisms reduce surface area and thus the potential danger of abrasion, or evaporation of volatile organic matter.

Small streams can dry in summer in temperate latitudes and even large rivers dry in tropical zones. A suite of mechanisms have evolved that allow the survival of lotic animals. Just as in lentic waters, a principle mechanism is to have a life cycle synchronised with the dry phase. As we have seen, this is a characteristic of insects. Another mechanism is for displacement downstream by drifting, by migration deep into the bed (the hyporheic zone), or by movement into pools formed within the drying stream (Williams 1987). The biota displaced downstream in the drift need a compensatory upstream colonisation and many aquatic insects displaced in this way are known to be effective colonisers as adults. Other animals move upstream when flow returns and there will also be a migration from pools and from deep within the hyporheic where humidity is high and where the presence of free water allows survival through a drying phase.

Sustainability and the effects of global warming

There is general agreement among experts that we are entering a climatic phase that is likely to promote global warming. This will have many consequences for aquatic systems and for their sustainability. Some important ones are summarised below.

(1) Parts of existing coastlines will be altered as increasing sea level causes swamping of terrestrial habitat, introducing mineral particles and potentially rich organic matter to coastal systems. There will be changes in salinity near melting ice caps but this is unlikely to have far-reaching effects and the majority of the increase in sea-level will be caused by expansion of the water in existing oceans, with some contribution from melting glaciers.

There will be little change in the pattern of stratification in oceans but there may be changes in stratified lakes, e.g. some dimictic lakes may become monomictic, etc. Global warming will also have effects on currents, and on the pattern of upwellings, but these are not easy to predict. Perhaps we will face other losses of productivity like that of the anchoveta fishery off the west coast of South America.

(2) If global warming is accompanied by reductions in rainfall, some land masses will see the development of more deserts. A consequence of desertification will be the need for more water to supply predicted increases in the human population. Impoundments are one solution and their construction, and effect on rivers, will continue to promote controversy. They will also require regular replacement if they fill rapidly with sediment.

Higher temperatures are likely to increase the incidence of temporary streams and pools and the biota of these water-bodies will change accordingly. All the mechanisms described in the earlier section on drying remind us of the ways in which aquatic organisms have evolved to cope with the threat of desiccation. Such adaptations will clearly be an advantage if drying events become more common.

There will be changes in the composition of the flora and fauna at existing locations as populations alter their range. Such changes in community structure are likely to apply widely, although the biota living in the bulk water of oceans will be little changed in distribution as these waters will remain uniformly cold.

(3) Increased water temperature will promote higher turnover of biomass and this could be useful if the increased productivity can be harvested to produce a sustainable crop of protein. However, higher productivity also has a negative aspect as it results in an increased rate of organic matter accumulation and conditions may be good for blooming, or excessive population growth, of algae.

(4) The effects of warming on the surface microlayers, especially if coupled with increased insolation and ultraviolet radiation, may adversely affect the processing of organic matter at this important interface.

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