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Technical Progress Report

Microbiology of Thermally Polluted Environments

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Introduction

This report provides details of research carried out on this contract during part of the fifth and sixth years of its existence. Several papers concerning work supported in part or fully by this contract have been published, and reprints are attached. Other work in press or in manuscript form will be supplied at a later date.

The main portion of the following project report constitutes a review paper entitled: Predicting the Consequences of Thermal Pollution from Observations on Geothermal Environments. This paper is an attempt to synthesize the work by the Principal Investigator over the past five and one-half years under A.E.C. support which bears on the whole question of environmental impact of thermal pollution. The reader will find that the various publications contributed under A.E.C. auspices, plus relevant work supported by other funds, have been integrated into a major review of the field. In addition to a set of general conclusions placed at the end of the paper, the reader will also find a set of recommendations of a more practical sort, related primarily to the question of power plant siting. It is hoped that these recommendations may prove of some use in providing a scientific base for the decision on where nuclear power plants should be located.

The Principal Investigator spent about 10% of his time on this project. Other personnel involved in these studies were Dr. William Doemel, Dr. Ben Bohlool, Research Associates James Hoffman and Charlene Knaack, and Student Assistants Donald Weller, Sandra Peterson, Cynthia Cirillo, and John Connor. Several other individuals from this laboratory made contributions to this project although they were supported by funds from other sources. These include Dr. Jerry Mosser (Senior Research Associate), and John Bauld, David Ward, and Michael Madigan (graduate students).

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Predicting the Ecological Consequences of Thermal Pollution from Observations on Geothermal Habitats

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Predicting the Ecological Consequences of Thermal Pollution from Observations on Geothermal Habitats

The potential ecological impact on natural habitats by discharge of heated waters from power plants has been well described (Krenkel and Parker, 1969). Unfortunately, most of the data upon which predictions can be made have been obtained from laboratory studies on the effect of increased temperatures on organisms. There have been few studies in which the effect of heating has been studied directly on natural ecosystems. For many purposes, it is desirable to be able to predict the future consequences of increased heating of a habitat. Although this can to some extent be done by analogy to other similar habitats which are already receiving thermal inputs, in many cases a similar habitat may not be available. Ideally, what is needed is a set of general principles on the responses of various organisms in ecosystems to increased habitat temperature. From the application of these principles, the consequences of thermal input in a new habitat may then be predicted, at least in a general way.

How can such general principles be derived? At least one way is through ecological studies on habitats receiving thermal inputs from natural sources, such as geothermal activity (Brock, 1970). By examining habitats which are being heated from hot springs, geysers, and other thermal sources, the temperature tolerances and responses of organisms in these habitats can be determined. There are several advantages of such studies on naturally heated systems. Such systems are usually well defined, with stable thermal histories and predictable thermal loadings. Thus one is not faced with interpreting responses of organisms in a thermal regime which may be varying widely and unpredictably. Second, in natural thermal habitats, thermal gradients are often set up, giving one a whole range of thermal habitats within a small, well-defined area, so that the development of a series of ecosystems at various temperatures can be studied under conditions in which temperature is the sole or chief variable. Third, geothermal ecosystems are often easy to sample and to modify, and ecological studies of an experimental nature can thus be performed simply and cheaply. Fourth, geothermal habitats usually have long-term stability, frequently remaining relatively constant over many months or years. This long-term stability provides the means for studying the ability of organisms to adapt and evolve to changing thermal regimes, offering the possibility of predicting the long-term consequences of thermal pollution. Fifth, observations on natural geothermal habitats may suggest to the investigator the kinds of observations which would be of most relevance to make on thermally polluted environments. Finally, because of the stability and well-defined nature of the systems, the observations made should have considerable generality, and thus be applicable to a variety of practical situations.

Response of organisms to changes in temperature. Temperature can affect living organisms in either of two opposing ways. As temperature rises, chemical and enzymatic reactions in the cell proceed at more rapid rates and growth may become faster. On the other hand, proteins, nucleic acids, and other cellular components are sensitive to high temperatures and may be irreversibly inactivated. Usually, therefore, as the temperature is increased within a given range, growth and metabolic function increase up to a point where inactivation reactions set in. Above this point cell functions fall sharply to zero. Thus we find that for every organism there is a minimum temperature below which growth no longer occurs, an optimum temperature at which at which growth is most rapid, and a maximum temperature above which growth is not possible (Figure 1). The optimum temperature is always nearer the maximum than the minimum. These three temperatures, called the cardinal temperatures, are generally characteristic for each organism, although minor variations may be induced by other environmental factors, such as pH, nutrition, and hydrostatic pressure. The cardinal temperatures of different organisms differ widely; some organisms have temperature optima as low as 5° to 10°C and some as high as 75° to 80°C. The temperature range throughout which growth occurs is even wider than this, from below freezing (-12°C) up to boiling (100°C). No single organism will grow over this whole temperature range, however; the usual range for a given organism is about 30 to 40 degrees, although some have a much broader temperature range than others. Those organisms with narrow temperature ranges are called stenothermal, and are generally found in habitats of relatively constant temperature. Eurythermal organisms have a wider temperature range and are usually found in environments where the temperature varies considerably.

The cardinal temperatures are genetically fixed properties of an organism and do not readily change even as a result of mutation. Thus, when habitat temperature changes, Figure 1 shows that growth will slow if the change is to either below or above the optimum. However, when the temperature of an organism is reduced from its optimum, growth merely gradually slows, whereas if it is raised above the optimum, growth sharply decreases to zero. Indeed, usually at a few degrees above the maximum growth temperature, thermal death begins, and the organism is rapidly killed. Since the optimum temperature is always nearer the maximum than the minimum, this means that only slight increases in temperature above the optimum can lead to death. Because of this, most organisms do not live in nature at their optimum temperatures, but usually at temperatures somewhat below their optima. Because of this, moderate increases in temperature of the habitat will result in increased growth, since temperature will then be closer to the optimum.

In general, small changes in habitat temperature do not affect the existing population structure, but large changes will. If temperature increases by 10°C, it is likely that the existing organisms will be pushed over their temperature optima, and growth will drop sharply to zero. Then new organisms can move in and colonize the habitat left vacant. Thus, ecosystems respond to large temperature variations by changes in population structure, rather than by changes in existing organisms. However, as will become evident later, in temperate habitats, where seasonal temperature changes as great as 30°C exist, the situation is more complicated, since at the cold temperatures prevailing throughout most of the year, organisms are generally living at temperatures far below their optima and warming rarely pushes the temperature over the optimum. This difference is important for predicting the consequences of thermal pollution in temperate environments.

Thermal Pollution

Sources of man-made thermal water. The most extensive production of thermal water by man probably occurs in steam-operated electrical power plants, fired either by the burning of fossil fuels or by the release of nuclear energy. Power plants use a convenient natural water as a cooling source, heat the water, and (usually) discharge this heated water back into the natural environment. It is with this source of heat that this article will be mainly concerned. However, there are many other ways in which thermal water is generated by man, and some of these might be noted here since in some environmental situations it may be necessary to sort out the contributions of these sources from those of power plants.

Probably the most widespread production of thermal water occurs in domestic, commercial, and industrial hot water heaters, hot water being produced because of its superior solvent properties in cleaning. Hot water heaters operate continuously for long periods of time at constant temperature, the temperature of individual heaters ranging from 55-80°C. Very little of this hot water gets directly into the environment, but much of it gets into sewage, and sewage water is warmer than that of the local water bodies. Vast amounts of this slightly warm water are thus returned to the environment through sewage treatment systems.

Another major source of hot water is condensed steam. In situations where a number of separate buildings are heated from a central steam plant, there are numerous opportunities for heated water to enter the environment. Relief valves may liberate steam at reasonably high temperature, usually at ground level. Within the heating system itself, after the steam has released its heat, it condenses, and the condensate water is still at fairly high temperatures. This condensate is returned to the plant by a series of buried pipes, and many opportunities for leakage of these pipes occur. Because the steam condensate is at the low pressure end of the system, the leaks may not be detected by the steam plant operators and may continue for long periods of time. We once observed a leak such as this which for over a year poured a fast flow of 48-56°C water into a small stream on the campus of Indiana University (Brock and Yoder, 1971).

Another source of warm water is the condensation from air conditioning systems. Especially in warm humid climates, the operation of air conditioners creates large quantities of warm water, and if large buildings are cooled by central air conditioning systems, this warm water is generated at a single source. In many cases, this warm water is discharged directly into a convenient water body. We observed a discharge of this sort at Indiana University, Bloomington, where a single air conditioning unit discharged a large stream of water at 36°C (Brock and Yoder, 1971). This discharge ran constantly through the summer, at a time when thermal input to the receiving stream would be expected to be of greatest harm.

A variety of industrial operations produce steam or hot water for manufacturing purposes, and may discharge some heated water into the environment. Examples are: pulp and paper mills, sugar refineries, textile mills, petroleum refineries, steel mills, smelters, chemical plants, and foundries.

Virtually all of the above-mentioned sources release water which is at considerably higher temperatures than is the water from electric power plants. However, in terms of quantity of heat released, power plants far exceed all other sources, since the amounts of water which they use and release are so vast. An important distinction between power plants and other sources is that power plants release large amounts of barely warm water, whereas other industrial sources release much smaller amounts of water which may be quite warm. This latter water will probably have only localized effects on aquatic ecosystems, but in the region of release quite drastic effects may occur which are readily measureable. Release of warm water from power plants will rarely have drastic effects, and quite sensitive means may be necessary to detect the specific effects which this warm water may have on aquatic ecosystems.

Thermal consequences of thermal pollution. Power plants can have quite variable effects on the temperatures of the aquatic habitats into which they discharge (Parker and Krenkel, 1969). First, the temperature of the water used for cooling can vary considerably seasonally, and may even vary diurnally to some extent. The temperature increase which the cooling water experiences during passage through the plant can vary with the efficiency of the plant, the size of the plant, and the power output (which may vary from one time to another). If water is taken from a lake, the location within the lake from which the water is taken can influence its temperature markedly, as hypolimnetic water will be cooler than epilimnetic water in summer. Power plant heating effects are usually expressed as the difference between intake and outlet temperatures (ΔT) and values of 8-10°C are not uncommon. Nuclear plants are less efficient than fossil-fuel-fired plants, and have consequently somewhat increased temperature differentials. According to Harleman and Stolzenbach (1972), typical values for 1000 MW power plants would be 9°C for a fossil-fuel-fired plant and 13°C for a nuclear plant. Our measurements of a fossil-fuel-fired plant on Lake Monona, Wisconsin, revealed an average temperature increase over an annual cycle of 8°C, although at certain times the increase was considerably higher (Brock and Hoffman, 1974).

How this heated water will affect the temperature of the receiving water will depend on the manner in which the water is discharged, on meteorological conditions, on the volume or flow rate of the receiving water, and on other factors. In most cases there is a mixing zone, within which the heated water mixes with the receiving water, and the size and shape of this mixing zone will depend on how the water is discharged (surface or subsurface discharge, diffused or layered discharge), meteorological conditions, the volume and flow rate of the receiving water, salinity, and other factors. It is within mixing zones that the highest temperatures are reached, and in most cases the only area of real ecological concern will be the mixing zone.

However, in the case of rivers, significant effects may occur outside the mixing zone. Certain rivers exhibit wide variation in flow volume, and at certain seasons of the year the natural river flow may be so low that a power plant could use a significant percentage of the river water and, on discharging it, markedly increase the temperature of the river. Since only a few days or weeks of unusual heating may be enough to modify an ecosystem permanently, such seasonal heating effects may be of considerable importance. Such effects are much less likely to occur in lakes, and are not at all likely in the oceans.

Mixing zones are frequently difficult to study ecologically, because of the wide fluctuation in temperature. In this respect, rivers are simpler than lakes, since in lakes the manner in which the heated water will mix will depend greatly on wind, waves, and currents, whereas in rivers mixing is simpler and more predictable. However, volume of flow in rivers may change drastically throughout the year, greatly affecting the temperature rise within the mixing zone, whereas lake levels and volumes fluctuate much less drastically. All of these considerations emphasize the difficulty of predicting thermal effects by studies on existing power plants, since it is difficult to separate effects due to local conditions from those of a more general nature.

Thermal effects on water quality. In sorting out the effect of temperature on organisms and ecosystems, it is important to keep in mind that temperature has indirect effect on water quality. Temperature markedly effects many physical and chemical properties of water in itself (e.g. density, viscosity, ionization) and any of these effects could theoretically lead to biological consequences. However, probably the most significant effect biologically is the decrease in oxygen solubility with increase in temperature. For instance, the solubility of oxygen from air into water is 16% lower at 30°C than at 20°C, and is 29% lower at 40°C than at 20°C. Although this decrease in oxygen solubility is not great (indeed, altitude effects may be greater), if it were coupled with an increase in oxygen utilization by living organisms, the net result could be a markedly decreased oxygen content of the receiving water. However, most of the effects of temperature to be discussed below are probably direct thermal effects rather than effects arising indirectly through influence on oxygen solubility.

Natural Habitats Receiving Thermal Additions

Geothermal habitats. The temperatures in active volcanoes are much too hot for living organisms (molten lava can have a temperature of 1000°C or over), but hot springs associated with volcanic activity often have temperatures within a more reasonable range and are usually richly colonized with living organisms. Temperatures of hot springs range from the 30s up to boiling (90-100°C depending on altitute) (Waring, 1965). Fumaroles which consist of only steam vapor can have temperatures considerably higher than 100°C, but such high-temperature sources seem to be devoid of living organisms, probably because of the absence of liquid water. The water of hot springs varies greatly in chemical nature. The pH of hot springs varies, and springs are known with values lower than 1.0 and greater than 10.0; a single spring, however, often has a remarkably constant pH. Many, but by no means all, hot springs have significant amounts of hydrogen sulfide, and the concentrations of many other elements such as fluoride, boron, arsenic, ammonia, and chloride, can vary markedly. Many springs are moderately radioactive, whereas others have no more radioactivity than normal ground waters. Some springs precipitate silica, others deposit calcium carbonate, and still others form elemental sulfur. When one considers the chemical, hydrologic, thermal, and geographical variation, it is clear that every hot spring can be considered as an individual, differing in minor or major ways from other springs. Within a single geothermal area, such as Yellowstone Park, virtually every type of hot spring seen throughout the world can be found. However, many springs are more similar than different. For instance, in Yellowstone Park, virtually all of the geysers and boiling or superheated silica-depositing springs contain mildly alkaline waters in which the predominant elements are sodium and chloride. Some springs have been remarkably constant in properties for many years, and it is this constancy or steady-state condition which makes them especially suitable for ecological study, since it eliminates many of the complications which interfere with a sophisticated analysis of ecological relationships. Further, many springs form relatively well-defined outflow channels, and, as the water cools along these channels, relatively stable thermal gradients are created. In the thermal gradient of a single spring, under appropriate conditions, the only significant variable may be temperature (Brock and Brock, 1966; Brock, 1967). We thus have what is essentially an experiment in nature, and we can ask questions about the ecology and evolutionary relationships of organisms at different temperatures along these thermal gradients.

Geothermal modification of normal aquatic ecosystems. In addition to a study of geothermal habitats themselves, it is also possible to study normal aquatic ecosystems in the neighborhood of geothermal areas and observe how they are modified by geothermal activity. Most geothermal areas have lakes, rivers, or marine habitats which receive input of water from geothermal sources and are locally modified in their thermal characteristics. The most extensively studied system is the Firehold River in Yellowstone National Park, which begins as a cold mountain stream but becomes markedly heated as it flows through the main geyser basins of the Park. The Firehole River itself has an approximate flow of 135 ft^3/sec and receives about 55 ft^3/sec of thermal water (Allen and Day, 1935), so that about 40% of its water comes from thermal sources, of various temperatures. This results in an increase in the temperature of the whole Firehole River (excluding mixing zones) of about 14°C (Boylen and Brock, 1973), and this temperature differential exists throughout most of the year, although the temperature curve of course shifts with the season. A whole series of thermal habitats are created along the course of the river, depending upon how much thermal water it has received, and these thermal habitats provide an excellent study area for the observation of adaptation of a river ecosystem to heating. Further, once the river leaves the geyser basins, it receives no more thermal water, and gradually cools, thus providing a recovery zone as a further habitat for study. The valuable thing about a study area such as the Firehole River is that it is stable, predictable, and has been around for a long time, so that the end results of adaptation to thermal loading can be studied. Of additional interest is that the Firehole River is considered an excellent trout stream, even in the sections experiencing the greatest increase in temperature.

Ecological Observations on Geothermal Habitats

The above material shows that a variety of geothermal habitats are available for study, and suggests that ecological observations should be of relevance to the prediction of the consequences of thermal pollution. What kind of information has been obtained from ecological studies of geothermal habitats, and how may it be applied?

Upper temperature limits for various taxonomic groups. One of the most far-reaching conclusions from ecological observations on geothermal habitats is that there are distinct upper temperature limits for whole taxonomic groups, such as the vascular plants, vertebrates, invertebrates, etc. Temperature acts as an evolutionary barrier which has been insurmountable by any member of certain groups, whereas other groups have readily passed this barrier, only to be blocked by another one at a higher temperature. The elimination of whole groups of organisms above certain temperature limits, without elimination of other groups, leads to dramatic changes in the structure and function of ecosystems.

The upper temperature limits for various taxonomic groups have been determined both by comparative observations of the biota of springs of different temperatures, and by the examination of the biota at different temperatures along the thermal gradients created by the effluents of single springs. Although both kinds of observations have given approximately the same results, studies of the latter type are perhaps more meaningful since one is comparing habitats subjected to the same light conditions and chemical composition. It is of course essential to know that the spring has been flowing and available for colonization long enough for equilibrium to have been reached. At least in Yellowstone Park, the development of a hot spring community in a new spring is quite rapid, and communities which appear to be complete have been observed to be established in less than 6 months (Brock and Brock, 1969).

The approximate upper temperature limits for various taxonomic groups are given in Table 1. Note that here we are considering not the ability of an organism to survive or endure a given high temperature, but its ability to carry out its complete life cycle. For instance, many animals and plants will survive temperatures greater than 50°C, but will not grow. Also, the limits given are not for all members of a group, but only for certain members. Usually it is found that the members able to grow near the upper temperature limit for that group are not optimally adapted to temperatures at the upper limit, but may be optimally adapted to temperatures slightly below this. Therefore, for most purposes temperatures about 5°C below the upper limit are probably the cutoff point for any significant ecological development of an organism.

In addition to the effect of high temperature on development of whole taxonomic groups, temperature profoundly affects the species diversity within a group. Table 2 presents data on the relationship between temperature and species diversity for water beetles and blue-green algae, and shows how simplified the population structure of each group becomes at temperatures near the upper limit. The temperature range is shifted about 20 degrees higher for the blue-green algae than the water beetles. Such relationships probably also exist for other groups, although they have not been quantified.

Temperature and fish. I do not propose to go into the vast literature on the effect of temperature on fish (Raney and Menzel, 1969). In most cases, the studies were done by removing fish from their natural habitat and subjecting them to higher temperatures in the laboratory or in simulated streams. Such studies are of course of considerable importance in interpreting the immediate consequences of new additions of thermal water to a receiving water body, but do not relate to the question of long-term effects on the total ecosystem.

As seen in Table 1, there is an upper temperature limit for fish at about 38°C, and no fish should ever be able to maintain a population in an ecosystem heated above this temperature barrier. Even if the habitat temperature exceeds this barrier for only a few days or weeks, this should be enough to eliminate the fish population. Such temperatures could easily be reached in thermally altered habitats in warmer parts of the world.

The kinds of fish which are able to maintain populations at temperatures near the upper limit are quite limited. All are members of the family Cyprinidae, which includes the carp, minnows, suckers, and goldfish. Also included are a group of species commonly called pupfish which are found in desert pools. The Cyprinidae evolved first in the warm waters of southeast Asia and have become distributed throughout the world; some species are found in warm springs. Those species found in springs are always small. Different genera are found in different parts of the world: <u>Cyprinodon</u> or <u>Crenichthus</u> in the western United States, <u>Mollienesia</u> in New Zealand, and <u>Barbus</u> in North Africa. Depending on the vagaries of dispersal, some thermal areas may lack these fish completely. Thus cyprinids are not present even at the appropriate temperatures in Yellowstone hot springs, presumably because there has not been sufficient time for colonization since the end of the Pleistocene glaciation.

The work of Mason (1939) on the cyprinid <u>Barbus callensis</u> (common name "barbel") of the Algerian hot springs at Hammam Meskoutine is of interest in relation to the ability of fish to adapt to high temperatures. At these springs, a series of pools of various temperatures is formed in the travertine deposits, and it was thus possible to relate the distribution of fish to the thermal habitat. Barbels were found at temperatures of 37°C, and they made occasional excursions into water of 38°C but were never found at higher temperatures. They were also present in large numbers in various streams at temperatures below 37°C. Mason studied the thermal death of the same species of fish collected from habitats of different temperatures: "cold" (8-20°C), "medium" (8-30°C), and "hot" (30-36°C). The results of this study showed clearly that there are at least two and possibly three populations with distinct temperature limits. The warm water population could withstand 37°C but not 38°C. Since a population did evolve capable of withstanding 37°C, and since there were no fish found at temperatures above this, it may be suggested that this is truly the upper temperature limit beyond which further evolutionary changes are not possible.

There is some evidence that trout in the Firehole River may adapt to higher temperatures than they normally tolerate, and that the time required for adaptation is not too long. Trout populations occur in the portions of the Firehole River which are considerably warmed by thermal water from the Yellowstone geyser basins. The warmest section of this river has an average mid-summer temperature of 26°C and reaches even higher temperatures occasionally. Note that this is not the temperature within a mixing zone near hot water input, but is the average temperature of the whole river after receiving the maximum thermal input. Visual observations have shown significant populations of trout in the warmest section of the river at temperatures of 27°C, whereas the highest temperature that trout are normally considered to tolerate is 25°C (Wilber, 1969). Interestingly, trout were absent from this section of the Firehole River before 1889, due to the migration barrier of the Firehole falls, and were introduced by man (Benson et al. 1959). Thus, if adaptation to the warmer water has occurred, it has been within a time period of less than 100 years. Detailed studies of the temperature acclimation of the Firehole River trout would be of considerable interest in helping to predict the long-term consequences of thermal pollution for this important fish family.

Ecological consequences of species restriction by temperature. The data in Table 1, and the effects upon species diversity illustrated in Table 2, have profound consequences for any considerations of the ecological consequences of thermal pollution. We can see that at temperatures greater than 40°C, the population structure of ecosystems can become greatly simplified. At these temperatures, fish and other vertebrates are completely absent, insects and other invertebrate groups are greatly reduced, and higher plants are absent or greatly reduced. Temperature thus converts the ecosystem into one which is virtually exclusively microbial. In the absence of animal grazers and predators, nutrient cycling may be inhibited, and large populations of microbes may build up. This is precisely what has been observed in hot spring thermal gradients; at temperatures above 45-50°C massive algal-bacterial mats develop, (Brock, 1967), whereas at lower temperatures these mats are less extensive, even though the productivity of the lower temperature systems is considerably higher. Almost certainly, one reason why algae develop so extensively in man-made thermally polluted waters is because of the elimination of some or all of the animals which feed on them (Castenholz, 1969).

Two general types of effects of animal grazers on aquatic communities can be envisaged: 1. biological and biochemical effects of the animals on the communities by way of feeding and excretion processes, 2. mechanical effects such as fragmentation and comminution of the plant material. Mechanical effects are readily observed in the hot springs. At temperatures above 50°C, where animals are absent, the algal-bacterial mats are even, compact, and clearly stratified into layers (Brock, 1970); gas and nutrient exchange are probably low. At temperatures below 40°C, where animals are plentiful, the mats are rough and corrugated, and much less compact; gases and nutrients probably exchange well (M.L. Brock et al. 1969). The animals may also affect the species distribution and growth form of hot spring algae. There is some evidence that the lowest temperature at which Oscillatoria terebriformis is found is controlled by the grazing activities of an ostracod (Wickstrom and Castenholz, 1973); when the ostracod is absent the alga can grow in nature at lower temperatures (Castenholz, 1969). It has also been shown that the ostracod modifies the growth form of blue-green algal mats; where the ostracod is present, the mats are nodular, presumably because the nodular form is resistant to ostracod feeding (Castenholz, 1969).

Although temperatures greater than 60°C should never develop in even the most grossly man-polluted habitat, it is of interest that at these temperatures the population structure of communities becomes even more restricted. Eucaryotic microorganisms have upper temperature limits at about 60°C, so that at higher temperatures fungi and eucaryotic algae will be absent, and only procaryotes will be present. At temperatures greater than 70-73°C, all photosynthetic life is absent, and the ecosystems (if they can still be called that) are composed exclusively of bacteria. It may be of some interest that hot water heaters and steam condensate lines in industrial, commercial, and domestic establishments often have temperatures of 70°C or greater, and that the same kinds of bacteria found in hot springs at these temperatures are also found in hot water heaters (Brock and Boylen, 1973), presumably growing attached to the walls of the pipes and heaters. These bacteria are carried from hot water heaters or steam lines into the environment, and can even be used as indicators of the addition to natural waters of heated water (Brock and Yoder, 1971).

Fluctuating temperatures. One of the common characteristics of power plant effluents is that constant temperatures are not maintained; changes in power requirements, outages due to equipment malfunction, or other factors may result in a marked change in the temperature of the effluent. It is thus of interest to see how ecosystems respond to such changes in temperature of the habitat. The clear impression one obtains from observing geothermal habitats is that if the temperature fluctuates markedly in a random fashion, biological development is poor to virtually absent. Technical difficulties of measuring temperature variations in randomly fluctuating habitats have prevented any detailed observations, but some studies have been done (Mosser and Brock, 1971) on an algal population colonizing the effluent channel of a periodic geyser, Bead Geyser, in Yellowstone National Park. This geyser is notable for its highly predictable eruptions; on the numerous occasions when it was observed over a five year period, it erupted every 23-25 minutes for 2.5 minutes (Figure 2). Between eruptions the water drains from the effluent channel and rapidly cools.

At one selected location in the channel, a habitat was found which varied from 65°C to less than 30°C during the 25-30 minute period; the average temperature of this habitat was 36°C. An algal mat existed in the effluent channel at this location, but the mat was very poorly developed in comparison to mats in similar springs developing at constant temperatures. The comparison between mats was carried out using quantitative measurements of chlorophyll and cell number. It did not matter whether the comparison of the Bead Geyser mat was made with mats from constant temperatures developing at 36°C, the average temperature of the Bead Geyser mat, or at 65°C, the upper temperature of the mat, or even at 25°C, the lowest temperature of the mat. By any comparison, the Bead Geyser mat was very poorly developed, suggesting that the algae were experiencing difficulty in colonizing a habitat of widely fluctuating, albeit predictable, temperatures. This difficulty was readily explained when the temperature optimum of the Bead Geyser alga was studied. The optimum was 45-50°C, a temperature which the alga actually experienced for only about 10% of the time. For maximum growth, a temperature optimum of less than 40°C would be expected, since the habitat was at temperatures below 40°C for about 70% of an eruption cycle. However, it is likely that an alga with an optimum below 40°C would be heat sensitive and would be killed by the periodic heating to temperatures as high as 65°C. It thus appears that it is essential for the alga to have a higher temperature optimum in order to tolerate the periodic heating, but in the process of acquiring this higher temperature optimum it has had to forego the opportunity of growing well at the temperatures which the environment experiences most frequently. Experiments showed that this alga was able to tolerate temperatures of 65°C for as long as five minutes, whereas algae with similar temperature optima (45-50°C) from a constant temperature habitat were killed within two minutes at 65°C. Thus the Bead Geyser alga is considerably more eurythermal than a similar alga from a constant temperature environment.

However, it might be noted that the way in which temperature is allowed to fluctuate can have a significant effect on how the ecosystem develops. Another spring studied by Mosser and Brock (1971) fluctuated in such a manner that it flowed 90% of the time, then ceased to flow. In spite of the fact that the algae in the outflow channel experienced a variation in temperature of 45°C, they exhibited a temperature optimum close to the computed mean environmental temperature, quite in contrast to the Bead Geyser algae. The mat developed was virtually normal in biomass. Here the temperature conditions appeared not to differ sufficiently from those of a constant environment, whereas in Bead Geyser, with its rapid wide fluctuation in temperature, conditions were much less favorable for algal growth.

The significance of these observations for thermal pollution seems clear. Fluctuating temperatures inhibit growth and will depress algal growth even more than constant high temperatures. This seems to remain true even if the constant temperatures are higher than the average temperature of a fluctuating habitat. Thus, if a constant high temperature is maintained in a power plant outfall, organisms will develop well at appropriate temperatures along the thermal gradient generated, and stable ecosystems should arise. If the outfall temperature varies especially rapidly or over a wide range, ecosystem development will be depressed.

General Ecological Consequences of Thermal Pollution

Important differences between thermal effects on cold and warm water habitats. One of the most important observations that has been made on temperature responses of organisms is that true thermophilic organisms exist and are widespread whereas organisms adapted to temperatures below 25°C are either rare or absent in environments outside high altitudes, the Antaractic, and the high Arctic (Brock, Passman and Yoder, 1973; Boylen and Brock, 1973). Thus, in temperate habitats (of most concern here, since it is in such habitats that human habitation is most extensive, at least in relation to thermal pollution), when temperature decreases seasonally to less than 25°C, organisms adapted to these lowered temperatures do not usually develop. Ecosystem activity slows down when water temperatures cool; however the organisms usually continue to persist with low population densities occurring. Then, when temperature increases again seasonally, the organisms can quickly develop to their previous extent. Of significance from the point of view of thermal pollution is that heated waters from power plants will warm the habitat locally during the winter, so that extensive ecosystem development can occur even during the time of year that it would normally be impossible. However, in this case, the same organisms will probably exist in both the heated and unheated water, temperature thus having no significant effect on the species composition of the ecosystem, but only on the amount of growth. In temperate habitats, thermal pollution will probably be beneficial in winter, but may be harmful in summer (see Table 3).

In warm water habitats, on the other hand, seasonal temperature fluctuations are usually not as great, and rarely would water temperatures greater than 30-35°C be reached, even in summer, except in very shallow areas. However, temperatures of 35°C are close to the upper limit for animals, higher plants, and many eucaryotic microorganisms. If power plant heating results in a temperature increase above 40°C, the ecosystem will be drastically affected; all existing species will probably disappear and a population of thermophilic algae and bacteria will develop. In Arctic systems, thermal pollution will probably always be beneficial. Thus, one cannot generalize from studies in one ecosystem to that of others; the seasonal thermal regime of each ecosystem must be considered individually in relation to the consequences of thermal pollution.

Adaptation to the thermal environment. Although there is some evidence that organisms can modify their temperature optima and maxima, in most cases the temperature limits of individual organisms seem fixed (Brock, 1967a). The temperature limits of an organism are genetically determined and can probably only be altered by changes in a large number of genes. Thus, in any case in which the temperature of a habitat is changed, the population structure probably changes primarily by migration and growth of new species rather than through physiological or genetic changes in the species already present. Thus after heating, as existing organisms are killed or inhibited from growth, we must think in terms of migration into the ecosystem of preadapted organisms. The rate of community adaptation will probably depend on the distance the source of inoculum is from the habitat, and how readily the organisms in question can disperse (see the discussion of dispersal later in this paper). It is likely that microorganisms will disperse more readily than higher organisms, and because of their inherently more rapid growth rates, the new communities which develop after a temperature change may be exclusively microbial for some time, until animals become established.

A number of studies have been done by our group to relate the temperature optima of organisms to the temperatures of their habitats. Some of the studies were done using hot spring thermal gradients and examining the temperature optima of natural populations, using radioisotope techniques. These studies showed that both algae (Brock, 1967) and bacteria (Brock and Brock, 1968) living at different temperatures along these gradients had temperature optima similar to their habitat temperatures. To extend these studies to more normal temperature regimes, studies were also done on bacteria (Zeikus and Brock, 1972) and algae (Boylen and Brock, 1973) living at different temperatures in the thermally heated Firehole River. In the Firehole River, there was a direct correspondence between the temperature of the habitat and the temperature optimum of the resident population, showing that temperature does select the microbial population. However, it should be noted that in both cases the temperature optimum is a few degrees higher than the average habitat temperature. There is a theoretical explanation for this lack of precise correspondence between habitat and optimum temperature. As is well known, the optimum temperature of most organisms is nearer the maximum than the minimum, so that the curve relating temperature to life processes is skewed (Figure 1). If organisms had optima precisely at their habitat temperatures, then transient increases in temperature of a few degrees, such as almost certainly could occur naturally under certain climatic conditions, would cause growth to stop and might even lead to death. By growing most of its life at temperatures somewhat below its optimum, an organism is able to survive (even grow) when the temperature of the habitat undergoes a sudden increase. In fact, it is likely that it is precisely such transient increases in habitat temperature which select the populations which are present. Thus we have in the temperature optimum of the resident population a history of the temperature regime of the habitat. In temperate climates, natural seasonal changes in temperature may be as great as the temperature increases to be expected as a result of thermal pollution. There is good evidence in the case of algae (Boylen and Brock, 1973; Brock and Hoffman, 1974) that throughout an annual cycle of temperature change there is no change in the temperature optimum of the algae. The algae are adapted to the highest temperature which the habitat reaches in mid-summer and retain this optimum throughout the winter. This surprising discovery is not easily explained; conceivably algal growth is too slow for changes in population structure to occur within a single season.

Effect of temperature on growth rate. It is well established that organisms living in warm or hot environments grow faster than organisms in colder environments. However, the quantitative relationships have not been studied except with bacteria. The bacterial studies are rather interesting because of their applicability to the interpretation of the Arrhenius equation.

The Arrhenius equation takes the following form:

$$\ln k = \frac{E}{RT} + \text{constant}$$

where k is the reaction rate, R is the gas constant, T is the absolute temperature, and E is an energy term usually called the activation energy (Glasstone, 1940). If ln k is plotted against 1/T a straight line should result, and the slope of the line is proportional to the activation energy. The slope of the line indicates how rapidly an organism or process responds to temperature changes.

Living systems usually show a greater response to increased temperature than nonliving systems, up to an optimum temperature. However, in contrast to nonliving systems, living systems show a distinct temperature optimum, and at temperatures above the optimum the rate drops sharply to zero. Nonliving systems do not show this optimum, and the rate of the process usually continues to increase as temperature is raised to even higher values. Studies with the Arrhenius equation on organisms have usually been performed by taking single species and measuring the effect on them of temperature, using a range of temperatures below the optimum. In this way, a curve such as that shown for Escherichia coli in Figure 3 is obtained, with a rather steep slope. Such a curve is valid when a single species is studied in the laboratory, but in nature we are dealing with mixed species, and as explained above, when temperature is changed, the likely result is that the already established species will be replaced by species which are more closely adapted to the new temperature. Thus, when we apply the Arrhenius equation to ecosystems, we must study the rates of performance of organisms optimally adapted to each temperature. Only with bacteria do we have sufficient data over a sufficiently wide range so that such a comparison is possible (Brock, 1967a). The results obtained are summarized in the composite curve in Figure 3. All of the points for the composite curve fall on a line which generally trends upward, but is much less steep in slope than the curve for a single organism. If a similar type of relationship exists for other organisms in ecosystems, an important consequence is that rate of ecosystem function will not increase nearly as fast as would be predicted from the usual Arrhenius equation. The activation energy for the composite reaction is about one-half that for the single organism. Put another way, for a 10°C rise in temperature, the growth rate of the single organism increases about four-fold, whereas the growth rate of the composite increases about one and one-half to two-fold. Assuming that this relationship holds over the whole temperature range of interest in thermal pollution studies (and for all of the organisms of the affected ecosystem), this would suggest that increased ecosystem activity would not be nearly as great as might be anticipated.

What will be the consequence for microbial growth of a sudden increase in the temperature of a water body as a result of thermal input? Although it might initially be thought that an increase in temperature would lead to an immediate increase in microbial growth rate, this is not necessarily the case. Much depends upon the range over which the water temperature is fluctuating. When considering the temperature range from about 20-25°C upward to 40°C or higher, an increase in water temperature might actually lead to an initial decrease in microbial activity, followed later by a recovery to the original or a higher rate of activity. The reason for this is that in the temperature range above 20-25°C, organism optimally adapted to various temperatures exist in nature and a population optimally adapted to the base temperature of the water already is present in the ecosystem. Thus, if a water body warms, the existing organisms, already at their optimum, should slow in growth rate, and if the temperature increase is sufficient they will probably be killed. Thus an increase in water temperature should eliminate the resident population and microbial development should be hindered. However, if the new temperature is maintained for a long enough period of time, a new population should develop, optimally adapted to the new temperature, and as suggested by Figure 3, the rate of microbial activity will be somewhat higher than it was previously, although not as high as might be predicted by the Arrhenius plot of a single organism.

However, if we are considering a temperature range from 0-25°C, a quite different situation will probably occur. As we have shown (Boylen and Brock, 1973a; Brock, Passman and Yoder, 1973), organisms optimally adapted to this temperature range do not occur in temperate habitats, and organisms with optima around 25°C predominate. Thus, over the range 0-25°C, microbial growth is definitely limited by temperature. If temperature is increased, the resident microbial population should immediately begin at a faster rate, and increased microbial development should occur. The effect of temperature on growth will probably follow the Arrhenius equation, as in fact has been found for microbial populations in sewage treatment systems when temperatures are in the 0-25°C range (Phelps, 1944; Wuhrmann, 1956; Zanoni, 1967).

There is some suggestion that if habitats in colder parts of the world are studied, where temperatures never rise above 10-15°C, that populations optimally adapted to low temperatures might occur (Morita and Burton, 1970). If so, in such areas, increase in water temperature would not immediately lead to an increase in microbial activity, since the resident population should be killed, and time would be required for colonization of the habitat by a population adapted to the new temperature. These considerations emphasize the dangers of generalizing about the effects of thermal pollution without taking into consideration the normal temperature range and the temperature optima of the resident populations.

As is noted above in the section on fluctuating temperatures, the most effective means of keeping microbial development low is to create a habitat in which temperature fluctuates widely and randomly. Thus, one way to prevent excessive microbial development as a result of thermal pollution would be to vary the temperature of the outfall habitat considerably. The easiest way to do this would be to establish two or more separate outfalls, and to alternate their use on a random basis.

<u>Temperature and water quality</u>. Temperature has direct effects on water quality, such as the reduction in solubility of oxygen. Additionally, for many domestic and industrial purposes, warm water is less desirable than cool water, so that thermal pollution leads to a direct degradation of water quality. Temperature also has indirect effects on water quality through effects on biological processes, and it is this aspect which is

under discussion here. As we have noted in an earlier section, there is an increase in rate of biological processes accompanying an increase in temperature, and increased reaction rate, accompanied by a decrease in oxygen solubility at the higher temperatures, should lead to an even more rapid decrease in oxygen concentration, as the oxygen-utilizing bacteria present consume the remaining oxygen. Thus, thermal pollution can in two ways lead to the conversion of a water body to anaerobic conditions, and development of anaerobic conditions can have a number of serious consequences for an ecosystem. However, oxygen-consuming bacteria will only be able to act if there is organic matter or other oxidizable materials in the water, so that it does not necessarily follow that thermal pollution will lead to a direct biological reduction in oxygen content. Many aquatic ecosystems are so low in oxidizable materials that increased oxygen utilization will not occur; much depends on the water quality. Thus, one way to avoid problems of increased biological oxygen depletion is to site power plants in areas of pristine water. In such areas slight oxygen depletion will occur due to the increased temperature, but biological oxygen depletion will not occur, since oxidizable organic matter is not present. Thus, clean water should more readily tolerate thermal inputs than dirty water.

One of the presumed consequences of thermal pollution is an increase in growth of blue-green algae (Patrick et al. 1969), and since blue-green algae products toxins, bad odors, and flavors in fresh water, such increased growth could lead to degradation of water quality. However, observations in several areas suggest that rarely are temperatures increased sufficiently so that blue-green algae develop preferentially. As we have noted, it is only at temperatures over 40°C that blue-green algae will completely replace eucaryotic algae, and such temperatures will only develop as a result of thermal pollution in natural waters in warmer parts of the world. Observations in Yellowstone (Boylen and Brock, 1973) and in Wisconsin (Brock and Hoffman, 1974) where temperature increases of 10-15°C still do not push the water temperature above 40°C, have shown that warming of natural waters does not lead to extensive blue-green algal development. In their study of the Firehole River, Boylen and Brock (1973) found blue-green algae at some of their stations, but blue-green algal development could not be correlated with water temperature. Indeed, at the locations where water was the warmest, green algae of the genera Spirogyra, Oedogonium, Cladophora, and Stigeoclonium dominated.

Observations made in the warm outfall of a power plant at Lake Monona, Wisconsin did not show that blue-green algal development predominated (Brock and Hoffman, 1974). Even in the middle of the summer, when the power plant outfall had temperatures of 30°C or over, one of the dominant forms was the green alga Stigeoclonium. However, Patrick et al. (1969) have shown using an experimental stream installation that experimentally increasing water temperature from an average of 20°C, where diatoms were dominant, to an average of 38°C, resulted in an increase in blue-green and filamentous green algae. Although no quantitative data were given, in some cases blue-green algae were the dominant forms. However, these studies must be interpreted carefully because observations of the algal flora were made on microscope slides immersed in the streams, and such habitats are almost certainly selective for smaller species such as the diatoms and blue-green algae. In the work of Boylen and Brock (1973) observations were made on algae living on large stones occurring naturally in the river, and these stones provided suitable habitats for the larger species of algae. It seems likely, on the basis of our work (Boylen and

Brock, 1973; Brock and Hoffman, 1974; Brock and Brock, 1966; Brock, 1967) in most cases blue-green algae will become dominant only when water temperatures are increased above 40°C.

Temperatures of 35-40°C, often reached in power plant effluents, are close to the temperature of the human body, and since human pathogens usually have temperature optima around 37°C, some concern might be raised that thermal pollution could lead to replication of human pathogens in the water, with possible increased spread of infection. However, there is no evidence that increased temperature will lead to increased growth of pathogens in natural waters. Studies with Wabash River water have shown (Silver and Brock, unpublished) that *Escherichia coli* actually dies faster in water at 35°C than in cooler water, presumably due to the effect of the warmer temperature on starvation processes. Conceivably, water rich in organic matter might serve as a nutrient for growth of pathogens, thus leading to increased pathogen replication in thermally polluted water. Habitats with water containing sufficient organic matter to promote pathogen growth should probably not be used for power plant sites.

The conclusion from the above considerations is that thermal pollution may lead to a degradation of water quality, but that this is unlikely to be dramatic unless the water is already grossly polluted with organic matter.

Dispersal. It is of great interest in considering the rate at which ecosystems adapt to changing temperatures to consider how effectively organisms are dispersed to new habitats created by man. A thermally-heated aquatic habitat is analogous to an island, a localized area of warm water surrounded by cooler water. There are a number of observations on the dispersal of hot spring organisms which are relevant to the whole question of rate and efficiency of dispersal.

As might be expected, microorganisms have little difficulty becoming dispersed to new locations. The same species of algae and bacteria are found in hot springs throughout the world, provided the springs compared are of similar chemical and thermal characteristics. The eucaryotic alga Cyanidium caldarium, a unique alga of acid thermal environments, has been found in such diverse locations as Western United States, El Salvador, Dominica (Caribbean), Iceland, Italy, Japan, Indonesia, and New Zealand. Interestingly, this alga is rather sensitive to drying (Smith and Brock, 1973), yet this has not prevented its spread to a series of remote and rather restricted environments. The blue-green alga Mastigocladus laminosus is also of world-wide distribution, having been reported from thermal springs on virtually every continent (Castenholz, 1969). Among the bacteria, the organism Sulfolobus acidocaldarius, which lives only at high temperature and low pH, has been found at a variety of suitable locations in North and Central America, the Caribbean, Iceland, and Europe (Italy). There are exceptions to this general rule of world-wide dispersal (Castenholz, 1969a), but in general it can be concluded that hot spring algae and bacteria (and by inference, most algae and aquatic bacteria) disperse quite successfully.

Another indication of the efficient dispersal of organisms adapted to high temperatures is the study of Brock and Boylen (1973) on the thermophilic bacteria (primarily Thermus aquaticus) living in hot water heaters. These bacteria are able to live only at high temperatures (55-80°C), and hence are unable to maintain populations in normal aquatic habitats. Of the hot water heaters examined in Madison, Wisconsin, about one-third had detectable populations of organisms related to Thermus aquaticus. Since the same organism was not found in the local cold water, it was concluded that the organism was living within the hot water heater itself. Since few of the hot water heaters studied had been in existence for longer than 10 years, it seems clear that colonization of these highly localized thermal sources is rapid and efficient. The initial sources of the colonizing populations are almost certainly natural thermal habitats such as hot springs, but it is likely that the immediate sources are other hot water heaters nearby. Man has maintained hot water heaters during the past 50-75 years. It is likely that organisms originally colonized hot water heaters from natural thermal sources and then have continued to spread from one heater to another.

Higher organisms have greater problems of dispersal than do microorganisms, and it can be anticipated that the kinds of observations presented above on microorganisms might not apply. When examining the species of animals and plants present in hot springs (once temperature has reduced sufficiently so that these organisms are able to grow) one is struck by the fact that the colonizing species are not the same from spring to spring throughout the world, as they are for microorganisms, but seem to be related to the local flora and fauna. This is especially noteworthy with respect to higher plants, since comparisons of vegetation around hot springs in Yellowstone, New Zealand, and Iceland reveal that not only are the species different, but that they are not even in related families (Brock, unpublished). In the case of insects, there seems to be some pattern of similarity, since hot springs around the world all have insects from the family Ephydridae (the shore flies), even though each thermal area has its own characteristic group of genera. Shore flies live along the warm margins of ponds, lakes, and ocean shores, and it seems reasonable that the provenance of the hot spring species has been such widespread water margin habitats (Mitchell, 1960). If this is the case, we cannot look upon hot springs as reservoirs for animals able to colonize warm habitats, but merely localized manifestations of a type of habitat already existing. Of course, such warm margins of lakes and oceans will also provide habitats for microorganisms as well, and these microbes should also be able to colonize the lower temperature habitats of hot spring systems.

It seems reasonable to conclude from these studies that provided the habitat created by a power plant outfall is reasonably stable, it will be quickly colonized by organisms adapted to this new environment. The first coloniers might come from natural thermal habitats, either geothermal (in the case of microorganisms), or shallow water margins of lakes and oceans (in the case of both microbes and higher organisms), but once a series of power plant habitats has been created in a region, these could themselves provide the source of inoculum for newer power plants.

We can also anticipate that some evolutionary events will occur within the power plant habitat itself, so that ultimately species will be present which are better adapted to the man-made habitat than they were to the original natural habitat. The natural habitat, however, remains as a continuously available reservoir of organisms which can serve as an inoculum for any new man-made thermal habitat which might be created.

Bacterial indicators of thermal pollution. Because of the difficulty of continuously monitoring thermal inputs to natural ecosystems, the identification of species indicative of thermal pollution would be quite desirable. In the same way that the presence of intestinal bacteria such as *Escherichia coli* the used to monitor sewage pollution, the presence of bacteria adapted to higher temperatures might be useful for monitoring thermal pollution. A brief consideration, however, will show that bacterial indicator species will not be useful for monitoring thermal pollution from power plants, although they might be useful for monitoring higher temperature inputs from the other kinds of industrial and domestic heat sources discussed at the beginning of this paper.

In power plants, the rise in temperature is rarely greater than 10°C above ambient, and except when warm tropical waters are being used, the effluent temperature will not be so high that specific thermophilic types would be selected out. Even more important, the transit time of cooling water through a power plant is only a few minutes, insufficient time for any organisms to grow. The only differential effects on bacterial species which we could anticipate within the plant itself would be the selective destruction of the most heat sensitive forms from the mixed population of aquatic bacteria entering the plant. However, it seems unlikely that any differential count of bacteria affected by the (at most) 10°C rise in temperature would be sufficiently sensitive to detect thermal effects away from the region of the immediate power plant outfall. Of course, one does not need any complicated biological indicators to detect input of thermal water at the outfall itself, simple observation being sufficient.

Bacterial indicators might be useful in detecting inputs of thermal water from the high temperature sources mentioned at the beginning of this article: hot water heaters, steam condensate lines, pulp, textile, and steel mills, etc. As we have shown (Brock and Boylen, 1973) such habitats may provide for the selective growth of bacteria specifically adapted to high temperatures. An organism like _Thermus aquaticus_, which grows well in hot water heaters, is not present in the natural environment except in the quite localized areas of geothermal habitats, so that its detection in a natural water is a good indication (given the absence of geothermal activity) that some input of hot water has occurred. _Thermus_ aquaticus is detected by incubating inoculated media at 75°C, a temperature at which thermophilic bacteria derived from soil and other relatively low temperature environments will not grow. Water samples can be passed through membrane filters to increase the sensitivity of the isolation method. The only technical tricks are that an increased concentration (3%) of agar must be used so that the plates remain gelled at the incubation temperature, and the plates must be wrapped in water-impermeable plastic or incubated in a moist chamber to prevent drying during the two to three day incubation period. Details of culturing T. aquaticus can be found in Brock and Freeze (1969).

Brock and Yoder (1971) were able to show that Thermus aquaticus was present in the Jordan River on the Indiana University campus in a region where a warm water input from a leaking steam condensate line occurred, but that the same organism was absent from areas of the river that were not receiving thermal inputs. Brock and Boylen (1973) showed that Thermus aquaticus-like organisms were liberated with the hot water from many water heaters; if this hot water were discharged into the environment the bacteria might still be found. The ability to specifically select T. aquaticus by culturing at 75°C makes it easy to design a procedure for using this organism as an indicator of this type of thermal pollution.

Zeikus and Brock (1972) did a study to determine the fate of Thermus aquaticus after it was released into normal river water. For this work, the Firehole River in Yellowstone Park was used. In the large number of hot springs bordering this river, T. aquaticus grows extensively and is released in large numbers into the river. No T. aquaticus was detectable in the portion of the river which had not received thermal input, and the numbers of bacteria rose sharply as the river flowed through the geyser basins. The bacterial counts decreased again after the river flowed away from the area of thermal input, but some bacteria were still detectable several kilometers below the last sources of thermal input. Presumably in the river the bacteria did not grow and disappeared either by death, settling, or ingestion by bottom fauna.

These results show that bacterial indicators of high temperature thermal pollution exist, but that indicators of low temperature thermal pollution by power plants can probably not be developed. It may be of some advantage, in areas where power plants and other industrial plants both occur, to use these indicator bacteria to look for thermal inputs from industrial sources, since these sources are likely to release water much hotter than that released by power plants. Since small flows of hot water might not be detectable visually, or even by remote sensing, indicator bacteria may serve a useful purpose. It seems likely that with some further work, the technique for detecting <u>T. aquaticus</u> could be made more sensitive and readily applicable to routine work.

Conclusions

1. The following conclusions concern only those aspects of power plant impact related to temperature effects in mixing zones. Nonthermal aspects of power plant impact, such as chlorination, entrainment, current effects (scouring, induction of migration patterns) etc. are not considered. The conclusions relate primarily to temperate habitats, where there is marked winter cooling and summer warming of the natural aquatic habitats. In some important respects, constantly cold and constantly warm habitats respond differently to thermal pollution (Table 3).

2. Heating effects when habitat temperature ranges around 25°C (summer maximum). Microorganisms exist with temperature optima for growth at many temperatures above 25°C and thus a whole spectrum of organisms with different temperature optima exists in the world. Because of this, when a habitat is warmed above 25°C, the resident population should be inhibited from growth and be replaced by a new population optimally adapted to the new temperature. Thus, warming should lead to a transient reduction in microbial population density, followed by an increase to the same or a higher level as a population with a temperature optimum at the new temperature develops.

3. Heating effects when habitat temperature is below 25°C (winter, spring and fall). Below 25°C, microorganisms with temperature optima matching those of the environment are rare or do not exist (except possibly in constantly cold environments not being considered here). The microorganisms present in environments below 25°C have optima of 25°C or even higher, thus warming of a habitat from a low temperature does not lead to changes in population structure, as described in No. 2, but should cause an increase in the growth rate of the preexisting organisms. Thus, thermal pollution

should cause an immediate increase in the population density (given the reasonable assumption that population density is related to growth rate).

4. Algae in temperate habitats do not change their temperature optima seasonally, but retain their mid-summer optima (around 30°C) throughout the year. Thus, algae are temperature limited for growth during most of the year. They are consequently preadapted to warm temperatures, and thermal pollution should lead to an increase in algal growth during most of the year. Thermal pollution in mid-summer may raise the temperature of the habitat above the preadapted optimum, leading to a decrease in algal growth.

5. Above 25°C, where optimally adapted organisms should be present, temperature does not increase growth rate as fast as predicted by the Arrhenius equation with the usual value for activation energy. Thus, if optimally adapted populations are compared at the different temperatures, increase in growth rate with a 10°C rise in temperature will only be about 1.5-fold, rather than the 2- to 4-fold increase usually predicted by the Arrhenius equation.

6. At temperatures below 25°C, where optimally adapted organisms are not present, temperature should increase growth rate in the manner predicted by the Arrhenius equation with the usual value for activation energy.

7. All of the above conclusions relate to the fundamental point that thermal pollution affects habitats with temperatures below 25°C differently than it does those of higher temperature.

8. There are distinct upper temperature limits for different taxonomic groups of organisms. Fish (and probably other aquatic vertebrates) have upper temperature limits at about 37°C, higher plants have upper limits around 45°C, invertebrates have upper limits at about 48°C, protozoa at 50°C, eucaryotic algae at 56°C, fungi at 60°C, and blue-green algae at

70-73°C. No upper temperature limit for bacteria has been found, certain bacteria thriving at temperatures of 99-100°C. It should be emphasized that for each taxonomic group, only a few species are able to grow at temperatures near the upper temperature limit, and over the whole temperature range that a group can grow, only some species will be able to grow optimally at any particular temperature. Organisms may be characterized as stenothermal (narrow temperature range for growth) or eurythermal (wide temperature range for growth), but even the most eurythermal organisms will only grow over temperature spans of 30-40 degrees centrigrade.

9. The critical 40°C point. In most situations, eucaryotic algae will not be present in significant numbers about 40°C, even though certain eucaryotes can grow at temperatures up to 56°C. This is because certain blue-green algae are able to grow so much better than eucaryotic algae at temperatures above 40°C that they usually are the winners in any competition. Only when the habitat is unfavorable for blue-green algae, as for instance, when the pH is less than 4-5, will eucaryotic algae colonize habitats at temperatures above 40°C successfully. Thus, at temperatures above 40°C blue-green algae should be the predominant photosynthetic organisms in most aquatic ecosystems. Since 40°C eliminates all vertebrates, and most invertebrates, this temperature can be considered a critical one, and increases above this level resulting from thermal pollution should be avoided.

10. In part following from the considerations in No's. 8 and 9, it can be seen that temperature will greatly affect species diversity of ecosystems. Especially near the upper temperature limits for particular groups, the species diversity can be greatly decreased, and even at 5-10°C below this upper limit the species diversity may be quite restricted. This restriction may markedly influence ecosystem stability.

11. Thermal pollution can have a small direct effect on concentration of dissolved oxygen in an aquatic habitat, due to the effect of temperature on the solubility of oxygen in water. Temperature can have a much more serious effect on dissolved oxygen concentration if it leads to increased growth of oxygen-consuming bacteria, as will almost certainly occur when temperatures are increased over the range 0-25°C. However, oxygen-consuming bacteria will only be able to act if there is oxidizable organic matter in the water. Thus, oxygen depletion should be much less in waters which are relatively pristine, such as highly oligotrophic waters and waters low in phytoplankton. Waters receiving organic inputs from domestic sewage or other sources are likely to be unusually susceptible to the oxygen-depleting influence of thermal pollution.

12. Although there is an upper temperature limit for fish as a group, beyond which evolutionary processes are probably incapable of acting, certain fish can adapt to changes in temperature, extending their range to higher temperatures. There is a little evidence that even trout may adapt to temperatures higher than they are normally able to live, given enough time.

13. Fluctuating temperatures are especially detrimental to ecosystem development. If temperature fluctuates widely enough (probably over a span of 15-20°C) and randomly, no biological colonization may occur and the ecosystem may remain uncolonized. High constant temperatures should be more favorable for ecosystem development than low widely fluctuating temperatures.

14. The sources of organisms for the colonization of new power plant-created habitats are diverse. Geothermal habitats are the ultimate reservoir of organisms adapted to temperatures greater than 35-40°C, but in most cases local shallow margins of lakes and oceans, heated by the

sun, should provide habitats which can serve as reservoirs of organisms adapted to warm waters. Existing power plants can also serve as reservoirs for inoculum for new power plant habitats. In general, microorganisms seem to have no problem becoming dispersed to new habitats, and should become established in periods less than 6 months. Higher organisms may be less readily dispersed, so that in the early stages of the colonization of a power plant-created habitat, a simplified population structure may occur.

15. Thermophilic bacteria have been considered as biological indicators of thermal pollution. It is concluded that thermophilic bacteria cannot serve as indicators of thermal pollution from power plants, but might serve as indicators of the high temperature thermal pollution arising from industrial activities (hot water heaters, pulp, textile, and steel mills, etc.).

Recommendations

Disclaimer. These recommendations must not be considered absolute, but only tentative recommendations based on the limited knowledge currently available. Also, they consider only temperature effects in mixing zones. They do not consider nonthermal effects of power plants, such as effects of chlorination, scouring by outfall effluents, entrainment, or atmospheric effects.

1. Avoid siting power plants on rivers unless they are quite large and do not show significant seasonal changes in volume or flow rate.

2. Avoid siting power plants on warm water habitats (over 30°C).

3. To avoid O_2 depletion, site power plants on the cleanest, most oligotrophic waters available.

4. It may be worth large increases in transmission costs to site a power plant on a large, cold, clean body of water.

5. Consider carefully the thermal regime of the receiving body in establishing the site of a power plant and in deciding how the effluent is to be handled. Waters which rise in temperature seasonally above 30-35°C, even for only a few weeks, should be avoided if at all possible.

6. Avoid using hypolimnetic water or other nutrient-enriched water for cooling.

7. Thermal effects on organisms entrained with the cooling water and carried into the plant are probably minimal, given the usual temperature increases, and are unlikely to be significant ecologically.

8. It should be possible to avoid extensive algal development in power plant outfalls by creating habitats of widely fluctuating temperature. This might best be done by establishing two or more outfalls, at well

separated locations, and using these alternately on a random schedule, with no more than a two week interval used for a single outfall.

9. Arbitrary standards for allowable temperatures of power plant effluents should not be established. Standards used should have some reference to the conditions of each particular plant.

10. Outside of mixing zones, it is unlikely that power plants sited on large bodies of water will have any significant effects on aquatic ecosystems. Power plants on rivers, however, especially those which show seasonal minima in flow or volume, may have significant effects on aquatic ecosystems, even outside of mixing zones.

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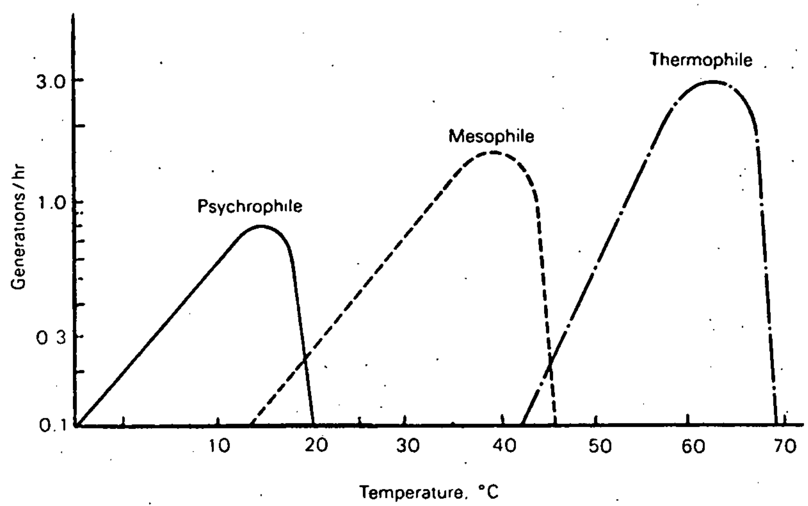

Figure 1. Relation of temperature to growth rate for psychrophilic, mesophilic, and thermophilic microorganisms.

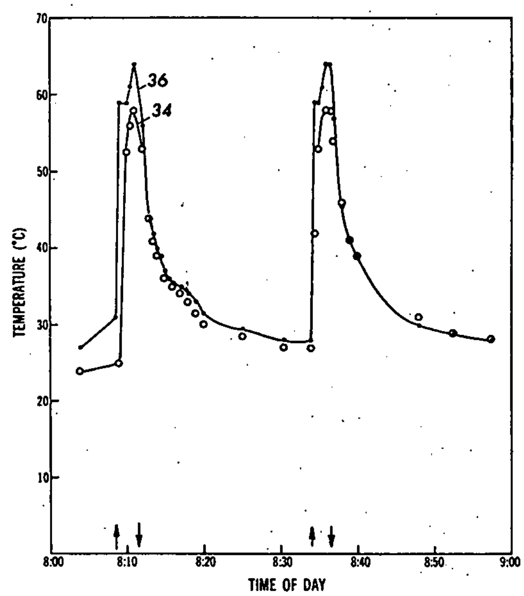

Figure 2. Temperature variation in the Bead Geyser effluent channel. Solid circles-station 1; open circles-station 2. The numerical labels are the mean temperatures, computed by averaging the temperatures at each 1-minute interval. Upward arrows indicate the beginning of eruption; downward arrows, the end. From Mosser and Brock, 1971.

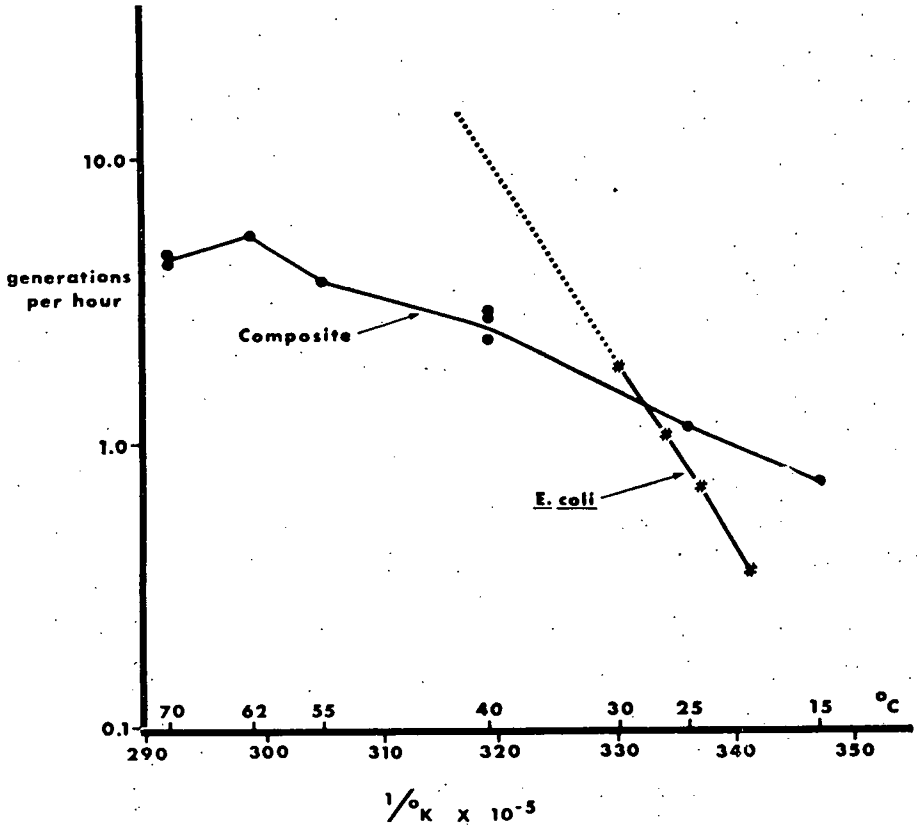

Figure 3. Arrhenius plots of the relationship between growth rate and temperature for bacteria. The composite curve represents the growth rates of a series of bacteria, each measured at its optimum temperature under optimum growth conditions. The other curve represents the effect of temperature on growth rate of <u>Escherichia coli</u>, an organism with a temperature optimum for growth of about 40 C. From Brock, 1967a.

Table 1. Upper temperature limits for different groups of organisms.

Group	Temperature
Animals	
Fish and other aquatic vertebrates	38°C
Insects	45-50°C
Ostracods (crustaceans)	49-50°C
Protozoa	50°C
Plants	
Vascular plants	45°C
Mosses	50°C
Eucaryotic algae	56°C
Fungi	60°C
Procaryotic microorganisms	
Blue-green algae	70-73°C
Photosynthetic bacteria	70-73°C
Nonphotosynthetic bacteria	>99°C

Data from Brock, 1967a, 1970; Castenholz, 1969. Values are only approximate limits.

Table 2. Number of species of water beetles and blue-green algae collected in hot springs at different temperatures.

Water beetles		Blue-green algae	
Temperature	Number of species	Temperature	Number of species
30	60	10-15	42
31	58	15-20	54
32	55	20-25	76
33	52	25-30	86
34	47	30-35	90
35	46	35-40	86
36	45	40-45	76
37	35	45-50	60
38	33	50-55	25
39	33	55-60	24
40	22	60-65	2
41	15	65-70	1
42	10	70-75	1
43	6		
44	4		
45	2		

Data for water beetles from Brues, 1932. Data for blue-green algae from Copeland (1936) but modified at temperatures above 45-50°C based on more recent data. (Note also that the validity of some of the data described by Copeland at lower temperatures may also be subject to question.)

Table 3. Consequences of thermal pollution in summer and winter, in temperate, tropical, and arctic habitats.

Habitat	Thermal regime	Unpolluted	Polluted (ΔT 10°C)	Overall effect of thermal pollution
Temperate				
Summer	25°C	Normal algal growth	Some increase in algal growth, population structure possibly shifting towards blue-green algae	Probably Harmful
Winter	$\leq$ 0°C	Greatly depressed algal growth (ice)	Marked increase in algal growth, not favoring blue-green algae (ice-free)	Beneficial
Tropical				
Summer	30-35°C	Normal algal growth	Marked inhibition of normal algae; replacement by exclusive blue-green algal community	Harmful
Winter	30-35°C	same as summer	same as summer	Harmful
Arctic (also alpine)				
Summer	10-15°C	Normal algal growth	Some increase in algal growth, but probably no selection towards blue-green algae	Beneficial
Winter	$\leq$0°C	Greatly depressed algal growth (ice)	Some increase in algal growth, not favoring blue-green algae (ice-free)	Beneficial

Temperature regimes are only approximate, and it should be recognized that local shallow water may be warmer.

The evaluations of Harmful and Beneficial are based on the premise that blue-green algae are always bad, but that some increase in algal growth from a low base-line will be valuable, since it will provide for increased food for higher tropic levels.