THERMAL RESPONSES IN THE EVOLUTIONARY ECOLOGY OF AQUATIC INSECTS

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PERSPECTIVES AND OVERVIEW

Temperature has been ascribed a major role in the ecology and evolution of aquatic insects (22, 34, 82, 83, 92, 124, 131, 151). Aquatic insects respond to the entire thermal regime, which is a composite of patterns of absolute temperatures, diel and seasonal amplitudes, and rates of change, all superimposed upon phase relationships with other environmental components such as photoperiod. The thermal history to which an organism has been exposed shapes responses operative at the organismic, population, and community levels of organization, which are manifest on both ecological and evolutionary time scales.

The majority of investigations dealing with ecological and evolutionary responses of aquatic insects to temperature have been conducted rather recently. There are, of course, notable exceptions (86, 166), and there is a relatively rich early literature on the thermal biology of mosquitoes (see 4). Several major works dealing specifically with thermal biology (145, 148,

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193) include some data on aquatic insects, primarily at the organismic and suborganismic levels. Other volumes (54, 59, 101) and an annual literature review (171) deal broadly with effects of thermal pollution. Bursell (24) and Clarke (29) reviewed aspects of temperature as it affects insects from physiological, and largely terrestrial, perspectives.

No attempt is made in this chapter to review the total literature on thermal responses of aquatic insects, as length restrictions preclude such an analysis. The major thrust of this review is to consider the sublethal responses that have major ecological and evolutionary ramifications. No special meaning is ascribed to the term "evolutionary ecology"; its use in this paper is meant to convey the interrelatedness of ecological and evolutionary responses to temperature. Data on tolerance levels and physiological aspects will be referred to cursorily and selectively. Likewise, the vast literature on thermal pollution is drawn upon primarily where such data provide insight into the responses of insects residing in waters to which waste heat has not been added. Consideration is given to both lentic (inland standing waters) and lotic (running waters) habitats.

This review begins by describing the thermal heterogeneity that has shaped temperature response patterns of aquatic insects and that is subject to anthropogenic alteration. This is followed by an analysis of the influence of temperature on distribution patterns, life cycle phenomena, behavioral responses, and trophic relationships. The final section relates patterns of temperature to biotic diversity and suggests that analysis of man-induced temperature gradients provides opportunities for insight into the evolutionary ecology of aquatic insects.

THERMAL DIVERSITY OF AQUATIC HABITATS

The thermal diversity to which aquatic insects are exposed varies spatially and temporally and is subject to anthropogenic alteration. In addition to latitude and altitude, hydrological, topographical, and meteorological factors are responsible for thermal patterns in lotic systems (163); morphometry and continentality are additional major determinants of thermal regimes in lentic waters (81).

Temperatures of streams, ponds, and the littoral zones of lakes may be highly responsive to air temperatures (19, 125, 128, 163, 172) and solar radiation (21, 39, 48, 121, 178). In early spring, thermal conditions near the substrate of shallow areas may be much more favorable for aquatic insects than open water temperatures would indicate (19, 39).

An idealized annual temperature pattern is shown in Figure 1 to illustrate the major components that may influence aquatic insects. For many aquatic habitats of temperate and high latitudes, the annual minimum temperature

(T_{min}) is 0°C and its duration (t_1) represents the period of ice cover. The period of time (t_2) above the developmental threshold (DT) is the growing season. DT is developmental zero in degree day calculations. There may be a higher threshold, referred to here as the maturation threshold (MT), which must be exceeded (sometimes for a specified time, t_3) to complete larval development. Some species require a yet higher temperature as an emergence cue. Habitat temperature may exceed an upper level, not shown in Figure 1, beyond which growth or development ceases, and a lower level may be required to break diapause. The time of year (t_{max}) at which the maximum temperature (T_{max}) is attained varies between water bodies, between years, and is responsive to man-induced change. Rates of vernal temperature rise (S_v) and autumnal decline (S_a) are additional considerations. Ideally, a single diel cycle may be conceptualized in the same manner.

Rarely have more than one or two of these variables been considered, especially in laboratory studies which often analyze effects of several constant temperatures on a species. Only in special aquatic habitats are constant temperatures indicative of natural conditions in surface waters.

Maximum summer temperatures of lakes and streams at higher latitudes rarely exceed 25°C (81, 162). Tropical lakes and rivers rarely exceed 32°C (9, 81), although smaller water bodies may attain higher temperatures.

The absolute value and duration of the minimum temperature to which aquatic insects are exposed is significant (14, 109, 183, 188). Although liquid water does not drop much below 0°C, aquatic insects of high latitudes or altitudes may be exposed to much lower temperatures (40, 147), and anchor ice has direct and indirect effects on stream species (126).
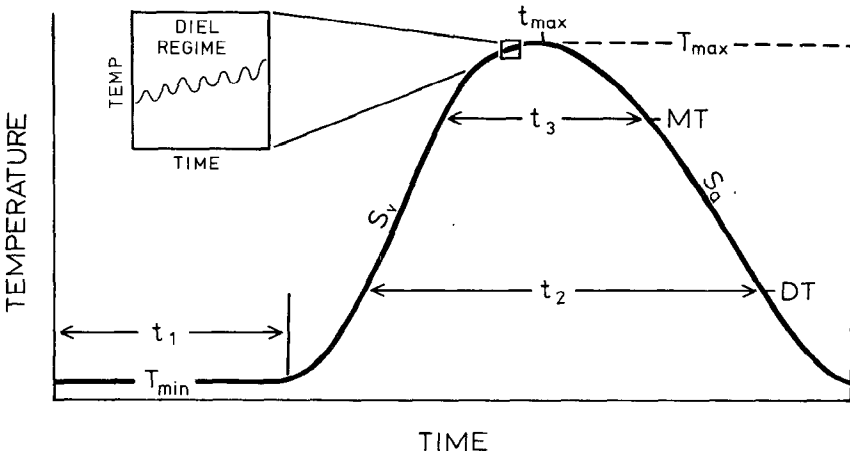

Figure 1 Major components of an idealized annual temperature pattern. Inset shows the diel regime over a seven-day period. See text for further explanation.

Several authors have emphasized the importance of diel temperature regimes for aquatic insects (20, 44, 92, 169, 170, 184, 188). The amplitude of diel fluctuations varies spatially as a function of position along the stream profile (180), depth (26), and distance from the bank (60, 92, 140); and temporally according to season and meteorological conditions (121, 128). Hyporheic waters in the gravel of stream beds exhibit more constant thermal conditions than surface waters (157, 196) and provide a refuge for cold stenothermal insects (157), as well as protection from adverse conditions (82).

Few studies have considered rates of vernal rise or autumnal decline in temperature, despite their importance for some aquatic insects (11, 32, 33, 43, 66, 109, 118, 119, 123, 158, 164). A few more data are available for diel cycles. Small, exposed streams have rates of change up to 3.3°C per hour, thus exhibiting greater variations in one hour than the daily fluctuations in rivers (21). Even tropical waters may exhibit high rates of short-term temperature change (199).

By moving very short distances, aquatic insects may encounter a wide range of thermal conditions, especially in smaller water bodies (53, 128). In a 24-hr period, small bodies of water may mimic the annual stratification pattern of temperate lakes (53).

Aquatic insects respond to the summation of thermal units (i.e. degree days) as well as absolute temperatures [see (5) for a review of the degree day concept].

Annual degree days may be similar in waters having quite different annual ranges in temperatures. Only a few investigators have considered the ecological and evolutionary significance of the seasonal distribution of thermal units (30, 38, 100).

Man-induced changes that may most severely modify components of the natural temperature regime (Figure 1) include thermal pollution (101, 105, 199), artificial destratification (103), pumped storage operations (90), impoundment (6), stream regulation (188), logging (25), and grazing (28).

In this section we have emphasized the thermal diversity to which an aquatic organism may be exposed. It is our contention that an understanding of the evolutionary ecology of aquatic insects is predicated upon an appreciation of the spatiotemporal patterns and gradients of temperature.

TEMPERATURE AND DISTRIBUTION

There is evidence that cool headwaters represent the ancestral habitat of many major groups of aquatic insects (22, 34, 82, 83, 150, 151, 194) and that colonization of lower reaches of rivers and lentic waters partly involved evolutionary adaptation to the different thermal conditions (22, 150, 180,

195). For example, only after the major larval types evolved in cool, lotic waters (early Cretaceous) did the great habitat diversification of caddisflies take place (151). Likewise, the presence of chironomids in virtually all lentic and lotic habitats, and in the sea, is attributed to secondary adaptive radiation from cool running waters, the ancestral home of the family (22). Most aquatic insects of temporary pools are considered later derivatives of ancestral lines that originated in cool, lotic waters and adapted (thermally and otherwise) to lentic habitats (195). There is evidence that thermophilic insects were derived from those which first adapted to the extreme temperatures along wet margins of ponds and streams (hygropetric or madicolous habitat), which preadapted them to hot springs (131). The ability of many aquatic insects to grow at or near 0°C (19, 31, 82, 83, 104, 178) and possession of mechanisms to avoid or withstand high summer temperatures (43, 82–85, 95–97, 143) provide additional evidence for an evolutionary history associated with cool habitats.

Latitudinal Gradients

According to the thermal equilibrium hypothesis (181), it is near the center of a species' latitudinal range, where the thermal regime is optimal, that adult body size, fecundity, and abundance will be maximized. Conversely, populations living under suboptimal thermal conditions will be smaller and will have lower fecundity and abundances, with a correspondingly reduced competitive position within the community. Such populations will be vulnerable to elimination (or enhancement) because of climatic change or anthropogenic alterations of the thermal regime. Since insects generally lack well-developed temperature compensation (or acclimation) mechanisms (23, 147, 169), a species' response to thermal regimes that mimic more northern or southern locations may provide useful information. For example, a mayfly species, apparently living near the southern limits of its range, more than doubled in adult size when reared in a cooler experimental temperature regime (181). Plecoptera may exhibit reduced wing size to body size ratios, thereby reducing gene flow, at the northern or southern limits of their range (115).

The anomalous occurrence of *Dinocras cephalotes* (Plecoptera), generally of a more southern distribution, at higher (but not lower) elevations in Swedish Lapland is due to the higher summer temperatures in exposed streams above treeline (178). Comprehensive analyses of life cycles along latitudinal gradients have been made for Ephemeroptera (31; see Brittain, this volume) and Odonata (33, 35).

Continentality, not latitude, may in some cases play the major role. Lillehammer (112) reported a progressive increase in species diversity of

Plecoptera from coastal to inland regions of Norway, in habitats selected to vary only in respect to temperature.

Altitudinal and Longitudinal Gradients

Temperature has been ascribed a major role in determining diversity, distribution, and abundance patterns of aquatic insects over altitudinal gradients and downstream along watercourses (15, 20, 44, 45, 86, 89, 92, 99, 166, 185, 186), although competitive displacement may truncate the range of temperature that a species could occupy (62, 82, 136).

Later emergence at higher elevations has been attributed to lower temperatures (13, 19, 113, 142, 198). Exceptions to the altitudinal pattern of emergence in special thermal habitats (113, 134) support the role of temperature as the major controlling factor.

Many Plecoptera exhibit a decrease in wing length with increasing elevation (13, 82), although this effect is influenced by position within the geographical range of a species (115).

Several authors have reported a downstream serial succession of closely related species (8, 74, 142, 200), which apparently reflects direct and indirect effects of the temperature regime acting in concert with interspecific competition (82). A well-documented example involves spatial segregation of hydropsychid caddisflies by temperature-metabolic responses (74). There was no evidence that spatial partitioning was related to food type or availability. In the case of congeneric damselflies (200), the competitive outcome apparently related to the temperature-oxygen relationships.

Temperature as an Isolating Mechanism

Climatic changes incurred since the last glacial epoch have thermally isolated three kinds of relicts in Danish springs (136). Arctic relicts, such as the caddisfly *Apatania muliebris,* maintain an Arctic life cycle not fully exploitive of the constant temperature habitat, except in a spring where two parthenogenetic subspecies occur. Oceanic relicts extended their range northward during a period of postglacial warming (Atlantic Period) and are now restricted to Danish springs because of the winter warm conditions. Continental relicts, which require high summer temperatures, entered Denmark during the Subboreal Period of more continental climate and are now restricted to shallow waters exposed to solar radiation (136).

During warm periods, mountain waters are refuges for cool-adapted forms (150). In the Mesozoic, most of southern Africa was in the South Temperate Zone (70). As the continent moved toward the equator, the temperate aquatic fauna became restricted to mountain waters. The remains of this cold stenothermal fauna have "Gondwanaland" affinities with ancient forms on other southern continents.

In Europe, stoneflies have speciated in upper stream reaches to which they were restricted as the climate warmed (88). The tendency of brachyptery at high altitudes enhances the isolation of stoneflies (115).

Thermal conditions in Lake Baikal have precluded invasion of the ancient endemic fauna by Siberian species (100).

There is a remarkable worldwide similarity of the insect fauna in hot springs (197). Tropical and subtropical relicts have been reported from thermal waters in Iceland (177) and Siberia (100). A dense population of *Helicopsyche,* a caddisfly normally restricted to low elevations (185), was located in a warm spring at 3109 m in the Rocky Mountains (Ward, unpublished data). Electrophoretic analyses of *Argia vivida* (Odonata) distributed along a steep thermal gradient show adaptations involving both an isozyme response and higher enzyme production at higher temperatures (155).

LIFE CYCLE RESPONSES

Eggs and Fecundity

Effects of temperature on fecundity, and responses of eggs to the thermal regime, influence distribution patterns and the competitive position of a species at a given location. Temperature may influence the egg incubation period, hatching success, duration of hatching, and the induction and termination of diapause. See Brittain (this volume) for a detailed account of the influence of temperature on mayfly eggs.

The relationship of temperature to incubation period, within the range of egg viability, generally follows a hyperbolic (51) or power law function (80). Hatching success may be optimal at a lower temperature than that which produces most rapid egg development (7).

Under diel cycles of temperature, eggs may hatch sooner than under constant thermal conditions [(78); but see (50)]. The greater the amplitude of the diel cycle, the fewer degree hours required for eclosion of corixid eggs (170). Thermal heterogeneity may be especially important for species with embryonic diapause (154).

Eggs of some species exhibit flexibility in response to temperatures of different habitats, which may represent ecotypic adaptation (80, 97). Interspecific differences in responses of eggs to temperature may serve as temporal isolation mechanisms for sympatric congeners (80).

Duration of hatching is highly variable within and between species (82, 122, 172), and may be correlated with temperature (7, 10, 50, 51, 58). Extended hatching has obvious adaptive value, especially in unpredictable habitats.

Fecundity in aquatic insects is directly related to adult female body size (14, 172, 181). Because the temperature regime to which an individual or species has been exposed may dramatically influence body size (49, 168, 181), both ecological and evolutionary implications are apparent. The pitcher plant mosquito, *Wyeomyia smithii*, exhibited a sevenfold greater fecundity when exposed to fluctuating, as opposed to constant, temperatures (12).

Dormancy

Quiescence has been reported for all life cycle stages of aquatic insects (195). The caddisfly *Rhyacophila evoluta*, because it can enter diapause at any stage, has attained a life cycle flexibility enabling colonization of waters with a wide variety of thermal conditions (44).

Diapause, as a response to avoid warm periods, is especially common among stream insects (46, 68, 96, 144; Brittain, this volume) and preadapts them to survive drought or to colonize temporary waters (68, 83). Stream populations of the stonefly *Diura bicaudata* produced only diapausing eggs, whereas lake populations laid mainly nondiapausing eggs (97).

Although rising temperatures tend to terminate diapause, and falling temperatures to induce it in terrestrial insects (75), the opposite may be true of aquatic species (10, 95, 137, 154). A drop in temperature may (by stimulating diapause development) shorten the time to eclosion following return to a higher temperature, compared to continuous exposure to the higher temperature (154).

In addition to serving as a resistant stage, diapause may function to synchronize life cycles (33, 120, 124), temporally segregate closely related species (27), and provide the flexibility needed for survival in unpredictable habitats (164). Photoperiod and temperature may operate independently or in concert (12, 35, 153).

Increased water temperatures caused by a power plant effluent eliminated the quiescent larval stage of *Hydropsyche pellucidula* and advanced emergence by three to four months (56). Warm temperatures may also retard emergence by delaying the drop in temperature necessary to stimulate hatching (198).

Growth and Maturation

Temperature plays a major role in regulating seasonal changes in growth rates of aquatic insects and operates, at least to some extent, independently of nutritional factors (18, 130, 181) or photoperiod (18, 120). Some species exhibit precise temperature thresholds for growth (107, 173), thus supporting the "Entwicklungsnullspunkt" theory (87); others respond to thermal summation (36, 98, 149). For an aquatic hemipteran, the length of time and

degree hours required to reach adulthood decreased with increasing temperature (170). However, temperatures optimal for high growth rates may be suboptimal for growth efficiency, emergence success, or adult longevity (73).

Species of both lentic (14, 19, 116) and lotic habitats (31, 71, 82, 178) grow and remain active at or near 0°C. A subalpine lake population of *Diura bicaudata* completed two thirds of nymphal growth under ice at 0–1°C (116).

Differential temperature-growth responses have been ascribed a temporal niche segregation role (86, 181). Coexistence of univoltine mayflies in a subalpine lake was attributed to the portion of nymphal growth occurring during ice cover, which ranged from 0 to 96% along a species continuum (19). Other authors attribute coexistence to species-specific temperature thresholds for growth (86), or to temporally segregated periods of maximum growth (86, 104, 181).

Huffaker (76) found that fluctuating temperatures stimulated growth of mosquito larvae. Although Sweeney (169) reported increased development rates of eggs and immature aquatic insects as diel amplitudes increased, minimum temperatures of each regime were similar, making comparison difficult. Some species in constant temperature springs maintain distinct seasonal cycles (136, 175), whereas other grow almost continuously (64, 93, 175). *Baetis rhodani* grows at the same rate in isothermic and normal streams despite many fewer degree days in the former habitat (55). Although the pitcher plant mosquito *Wyeomyia smithii* develops more slowly under fluctuating than constant temperatures, thermal heterogeneity results in a sevenfold increase in fecundity and a 50% greater capacity for increase (12).

Lutz (120) found photoperiodic effects on larval development under constant thermal regimes, but immatures maintained under natural temperatures responded similarly to long, short, and natural day lengths. However, Corbet (35) emphasizes the important interaction of temperature and photoperiod in regulating growth.

Adaptations in special habitats include continuous growth at extremely high rates (200–350 degree days per generation) in desert streams (65), and the high thermal coefficients of temporary pond insects (195). A trichopteran that occurs in temporary waters in England is restricted to permanent waters in Iceland because there is not sufficient time to complete development in temporary habitats at the prevailing lower temperatures (61).

Voltinism

Flexibility in the number of generations per year may be a response to thermal differences between habitats at different latitudes or altitudes (31,

35, 44, 63, 67, 79, 85, 143, 144, 174), although nutrition may also play a role (106, 114, 127). *Ischnura elegans* is trivoltine at 43°N, univoltine at 53°N, and semivoltine at 57°N (35). *Rhyacophila evoluta* has a one-, two-, or three-year life cycle, depending on habitat temperature (44). The winter warm conditions of springbrooks may increase the number of generations (135, 175). The mayfly *Cloeon dipterum* produces an extra generation during especially warm summers (125), and the thermal characteristics of lake outfalls (178) or streams below dams (127) may allow some species to complete an extra generation each year. Stoneflies adapted to intermittent streams in hot climates exhibit extreme flexibility in patterns of voltinism (164), as do the temperate stoneflies in southeastern Australia (85) where climatic conditions are likewise highly unpredictable. Hynes & Hynes (85) cautiously present evidence suggesting that *Spaniocerca tillyardi* switches from univoltinism to bivoltinism in habits where temperatures are *below* 10°C.

Emergence

The timing and duration of emergence in aquatic insects involves responses to temperature (16, 42, 69, 77, 113, 119), often interacting with photoperiod (52, 82, 134, 141).

Emergence normally occurs earlier at lower latitudes and elevations (13, 16, 17, 84, 134, 142, 172, 198) and in warmer years (14, 19, 42, 69, 110, 113, 141, 166), and the length of the emergence period may be correspondingly increased or decreased depending on the species (14, 82, 86, 124, 172, 198). Emergence occurs earlier in shallow water bodies and from shallower depths of deeper lentic habitats (42, 57). Emergence occurs earlier, and the emergence period is often extended, in winter warm habitats (13, 134, 156, 175) and streams below deep-release dams (188). Artificial elevation of winter temperatures also results in earlier emergence [(17, 114, 152); but see (3, 105)], with accelerated emergences of greater than three months reported (56, 133).

Precise temperature thresholds for ecdysis have been reported for some aquatic insects (42, 110, 125, 141, 176). Migration of mature larvae to shorelines where spring and summer temperatures are higher and more sensitive to terrestrial conditions has been reported for lentic and lotic species (17, 167).

Differential responses to temperature may temporally segregate closely related species within a habitat, resulting in a successional pattern of emergence (19, 69, 82, 86, 110, 144, 166, 181). Although year-to-year changes in temperature alter the emergence times, the order in which species emerge does not change (19, 84). Corbet (32) devised a model to explain emergence

synchrony in Odonata, based upon an ascending series of lower temperature thresholds (LTT's) for progressively later instars. Accordingly, rising vernal temperatures would stimulate growth of early instars (with lower LTT's) before the LTT of later instars is attained. This theory, which has since received empirical support (118), provides an explanation for synchrony in species that emerge in the spring. A single threshold temperature for emergence, if high enough, would give the same result (42). Vannote & Sweeney (181) suggest that adult tissue maturation, at the expense of larval growth, is initiated over a wide range of larval sizes when temperature exceeds a critical threshold.

The diel patterns of emergence of some chironomid species closely tracked diel water temperature fluctuations; in contrast, light provided the major diel emergence cue for other species, with water temperature determining the intensity of emergence (191). In the high Arctic, where light is not a reliable measure of air temperature, diel emergence patterns are cued to water temperature and emergence is restricted to midday during the warmest period of the year (41). At lower latitudes, chironomids emerge during midday in the spring, but mainly at dusk during summer (102), thus avoiding cold vernal air temperatures and reducing desiccation and predation during summer.

Longevity of the adult stage of aquatic insects is determined in part by water temperatures to which the immatures were exposed (124, 132) and by air temperatures encountered after emergence (77). At higher water temperatures, there was a greater temporal separation in the emergence of males and females (133). Several authors have reported intraspecific decreases in adult size from the beginning to the end of the emergence period (85, 95, 172, 181); in a series of congeneric species, the first to emerge in spring tends to be the largest, with later species being progressively smaller (86, 181). Summer generations of multivoltine species generally emerge at a much lesser size than other generations (36, 49, 143, 172, 181), which does not appear to relate to quality or quantity of food (181). These differences in adult size are believed to be primarily a function of water temperatures to which the immatures were exposed [(124, 143, 172, 181); but see (55)]. Since fecundity is positively correlated with adult size, deviations from optimal thermal conditions influence the competitive potential of a population.

BEHAVIORAL RESPONSES

Thermoregulatory behavior of adult Odonata is an important adaptation at higher latitudes but is less developed in tropical species (35). Spring populations of overwintered adult *Gerris* spp. exhibit "underwater basking" (165).

By submerging during portions of the diel cycle when water is warmer than air, accumulation of degree days is enhanced and gonadal maturation is advanced. Preemergent nymphs of *Anax junius* that do not encounter air temperatures above the threshold for ecdysis (12.6°C) return to the water to emerge the following day (176).

Investigators have reported critical temperature thresholds for mating and oviposition behavior (170). Stonefly drumming requires a threshold air temperature that may not be reached if emergence is advanced by warm winter water temperatures (152). Major modifications in feeding and mating behavior in Arctic black flies, compared with temperate species, are attributed to evolutionary responses to low air temperatures (47).

Although only rarely has temperature been implicated as the entraining agent (Zeitgeber) in the diel pattern of behavioral drift of aquatic insects, high temperatures may increase drift amplitude in some species (192), and abrupt changes may induce catastrophic drift (56). Upstream migrations of immature insects into tributary waters during spring may (138) or may not (72; H. F. Clifford, personal communication) represent a temperature response.

Thermoperiods with higher temperatures during the scotophase or dark period (the normal situation during diel vertical migration) caused faster development and inhibited induction of dormancy in *Chaoborus crystallinus*, compared to constant temperatures or thermoperiods with lower temperatures during scotophase (146). Cranefly larvae in a horizontal temperature gradient selected maximum temperatures (16–18°C) during scotophase and minimum temperatures (12–14°C) during photophase; under constant light, temperature selection continued as a free-running circadian rhythm of behavioral thermoregulation (94).

Other behavioral adaptations or responses include the influence of temperature on attack coefficients of Odonata (173), filtering and net-spinning behavior of Trichoptera (36, 182), and cocoon construction of chironomidae (40).

TROPHIC RELATIONSHIPS

Temperature influences trophic dynamics directly through its effects on phenomena such as feeding rates and indirectly primarily through the food base available to aquatic insects. Processing of terrestrial leaf litter, a major energy source for aquatic insects of woodland streams, is greater at higher temperatures (2, 160). However, as Cummins (37) points out, processing per unit of temperature is higher in the cooler headwaters where the community best adapted to utilize this energy source evolved. This is supported by the extremely rapid processing of leaf detritus in a mountain headwater stream, despite water temperatures at or near 0°C (159).

Growth in some aquatic insects is regulated by the interaction of temperature and food quality (1). Seasonal changes in food quality, partly a function of temperature, may determine the effect of a given temperature on growth (64, 91).

Feeding rates, assimilation efficiency, and egestion are often a function of temperature (63, 73, 132, 161, 182). A marked downstream succession of closely related caddisflies was attributed to sequential differences in temperatures which corresponded with species-specific differences in assimilation efficiencies (74).

Anthropogenic alterations, such as stream regulation, may alter the food base of aquatic systems (117). Such changes in trophic conditions, partly engendered by the modified thermal regime, may dramatically alter insect communities (188).

SPECIES DIVERSITY AND THERMAL HETEROGENEITY

Having begun this chapter by emphasizing the spatial and temporal thermal heterogeneity of aquatic habitats, in this final section we attempt to relate patterns of temperature to biotic diversity. We are somewhat handicapped in this task by the paucity of data on aquatic insect ecology in tropical waters and therefore direct primary discussion toward temperate habitats. It is also necessary to point out that conditions enhancing the development of species diversity along an evolutionary time frame may have opposite effects on an ecological scale.

The highly variable, but relatively predictable (on an evolutionary scale) natural temperature regime has allowed development of a diverse insect community through niche segregation mechanisms that have evolved in response to thermal diversity (19, 69, 74, 82, 86, 104, 110, 144, 166, 179, 181). Unpredictability, within limits, may enhance species diversity on an ecological time scale by reducing competitive exclusion (139, 184, 188, 189). Thus, superimposed upon the evolutionarily derived species packing resulting from a variable, but generally predictable environment, there is an added diversity engendered by species overlap under short-term (ecological time scale) nonequilibrium conditions.

A wide annual temperature range enhances species diversity in several ways. Conditions are suitable for warm and cold stenotherms, as well as eurytherms. Species may temporally segregate by differential thermal responses along the ascending vernal slope or the descending autumnal slope of the annual cycle (27, 32, 158, 179). Low winter temperatures and high summer temperatures have enabled the evolution of dormancy mechanisms at both extremes (10, 14, 68, 96, 144), which remove species from active

competition during part of the year. Species-specific thermal responses for induction and termination of dormancy, coupled with temporal separation of major periods of resource use and emergence times, provide additional niche segregation (27, 86, 166, 180). It has been suggested (180, 184, 188) that a wider daily variation in temperature increases species packing by providing a wider range of thermal optima, even though suboptimal conditions occur over a portion of the diel cycle for each species. Vannote et al (180) hypothesize that curves of biotic diversity closely track the pattern of diel thermal maxima along the longitudinal stream profile.

The concept of resource variability itself behaving as an abstract resource (111) appears applicable to thermal heterogeneity in aquatic habitats. The reduced diversity of aquatic insects in headwater reaches (86, 180), spring-brooks (129, 186), and certain anthropogenetically altered aquatic systems (183, 184, 188) is, in some cases, largely attributable to environmental constancy.

A highly restricted insect fauna characterizes regulated streams below dams, even where conditions other than temperature are favorable (108, 140, 183, 184, 187, 188). The thermal regime below deep-release dams differs in several ways from that of natural streams: diel and seasonal ranges are depressed, winter warm and summer cool conditions prevail, and the seasonal maximum is retarded (184, 188). A theoretical model was developed to conceptualize the interrelated factors that result in the reduction of species (on an ecological time scale) under such altered thermal conditions (184, 188).

Regulated streams below deep-release dams may be viewed as large-scale experiments on temperature modification (190). Since the thermal regime recovers rapidly downstream from the dam, a gentle gradient of thermal conditions occurs over a relatively short distance. An elucidation of the ecological interactions prevailing in a variety of such manipulated aquatic systems provides exceptional opportunities for insight into the evolutionary ecology of aquatic insects.

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