Distribution and abundance of the alkali fly (*Ephydra hians*) Say at Mono Lake, California (USA) in relation to physical habitat

David B. Herbst
Sierra Nevada Aquatic Research Laboratory, University of California, Star Route 1, Box 198, Mammoth Lakes, CA 93546, USA

Abstract

The distribution and abundance of larval, pupal, and adult stages of the alkali fly *Ephydra hians* Say were examined in relation to location, benthic substrate type, and shoreline features at Mono Lake. Generation time was calculated as a degree-day model for development time at different temperatures, and compared to the thermal environment of the lake at different depths.

Larvae and pupae have a contagious distribution and occur in greatest abundance in benthic habitats containing tufa (a porous limestone deposit), and in least abundance on sand or sand/mud substrates. Numbers increase with increasing area of tufa present in a sample, but not on other rocky substrates (alluvial gravel/cobble or cemented sand). Standing stock densities are greatest at locations around the lake containing a mixture of tufa deposits, detrital mud sediments, and submerged vegetation. Shoreline adult abundance is also greatest in areas adjacent to tufa. The shore fly (ephydrid) community varies in composition among different shoreline habitats and shows a zonation with distance from shore.

The duration of pupation (from pupa formation to adult eclosion) becomes shorter as temperature increases. The temperature dependence of pupa development time is not linear and results in prolonged time requirements to complete development at temperatures below 20 °C. About 700 to 1000 degree-days are required to complete a generation. Degree-days of time available in nature declines by 10 to 50% at depths of 5 and 10 metres relative to surface waters (depending on the extent of mixing), resulting in fewer possible generations. Essentially no growth would be expected at 15 m, where temperature seldom exceeds the developmental minimum. It is concluded that reduced substrate availability and low temperatures may limit productivity of the alkali fly at increasing depths in Mono Lake.

Introduction

Ephydrids are common in saline aquatic habitats throughout the world, and are often the most abundant inhabitants of the benthic and shoreline portions of these ecosystems. Ephydrids display a remarkable capacity for physiological adap-tation to extreme physicochemical conditions (Nemenz, 1960; Wirth & Mathis, 1979; Barnby, 1987; Herbst *et al.*, 1988). In addition to living in inland salt lakes and ponds varying from perma-nent to seasonally ephemeral, ephydrids inhabit alkaline and acidic thermal springs, mud flats and playa seeps, tidal splash pools, and coastal salt

marshes. As consumers of benthic algae and detritus, and in turn being a major food resource to a variety of migratory water birds, these flies occupy a key trophic position in transforming these harsh environments into important wildlife habitats. Despite the abundance, varied habitats, and potential ecological role of halobiont ephydrids, we know little about how the physical environment may influence their distribution and abundance.

Ephydra Fallen is the main genus of brine flies found in saline waters of both the New World (Wirth, 1971), and Old World (Wirth, 1975). The genus is absent only in Australia, where it is apparently replaced by the endemic *Ephydrella* Tonnoir and Malloch.

The account of Aldrich (1912) on the distribution and biology of the alkali fly, *Ephydra hians* Say, has essentially been the sole source of information on this insect. Most of the lakes where *E. hians* has been found are alkaline, thus the common name. The alkali fly was the first North American species of *Ephydra* described (Say, 1830). Wirth (1971) provided distribution records from museum specimens, and an excellent review of the natural history of the genus. Simpson (1976) described larvae and pupae of *E. hians* and *E. cinerea* Jones. Studies by Herbst *et al.* (1988) have shown that *E. hians* survives longer and osmoregulates more effectively in natural alkaline carbonate waters than in sea water, indicating that this species is alkali-adapted.

In studies of *E. cinerea* from Great Salt Lake (Utah), Collins (1980a) found that larvae tend to emigrate from sand substrates, and occur in greatest densities on bioherm reef-rock or shallow water mud substrates. Both this species and *E. hians* have clawed larval prolegs used in crawling over and clinging to bottom substrates, and pupae that attach to submerged objects. At Mono Lake, where sand, mud, and rock substrates occur, larval and pupal densities were expected to be greatest on the rocky substrates used for pupal attachment, and least on sand.

The objective of this paper is to describe the distribution of the alkali fly in relation to benthic habitat and substrate associations, and the influence of temperature on development and generation time. These studies are based on field sampling of the population from Mono Lake (California, USA).

Life cycle of the alkali fly and ecological setting

All life stages except eggs have been collected throughout the year at Mono Lake. This suggests, as Collins (1980a) reported for *E. cinerea* from Great Salt Lake (Utah), that there is no developmental diapause stage for this species. Low temperatures slow the development of all life stages, and prolong the lifespan. Adults apparently do not oviposit during winter months, and show no vitellogenic activity, indicating possible reproductive diapause during this time (Herbst, 1988). In contrast to *E. cinerea*, which deposits its eggs on the water surface, where they may settle into unfavourable habitat, *E. hians* may choose oviposition sites. Adult females are able to go underwater by walking down partially submerged objects into the water. An air bubble forms around the bodies of the flies due to presence of a dense covering of hairs and bristles, and acts as a physical gill. Flies may then search over the lake bottom, using their long tarsal claws to hold on. Females often place their eggs in mats of algae, substrate presumably favorable to larval development. Some oviposition may occur on the water surface, and has been observed on floating algal mats. Although most submerged flies are found to be females, males too are sometimes observed, suggesting that this behavior may not be exclusively related to egg laying. Close observation reveals that adults spend much time feeding, rasping the film of algae off rock surfaces. Food quality is critical to reproductive success in *E. hians* (Herbst, 1986) and benthic epilithic algae and algal mats probably represent a superior food source to that onshore (except possibly on detrital mud flats). Submergence may thus have evolved originally as an adult feeding habit. This is consistent with the fact that oviposition may occur without feeding (autogenously) in *E. cinerea* (Collins, 1980b), whereas feeding is essential for

E. hians. Eggs hatch in 1–2 days and develop through 3 larval instars. Larvae also feed on epilithic and sediment surface algal mats, composed mainly of diatoms, filamentous green, and blue-green algae, and the microbial-detrital component of the sediments (benthic algal species are listed in Herbst, 1988). Prolonged recruitment by oviposition over much of the year, and variable larval development rates result in overlapping generations, without clearly distinguishable cohorts.

Morphology and behavior of larvae and pupae appear to provide safeguards from mortality caused by storm-related dislodgement from lake bottom habitats. Clawed prolegs permit the clinging larvae to retain their hold in the wave-swept rocky littoral shallows along the open, windy shores of desert lakes. Larvae have a caudal respiratory siphon, as do related ephydrids, but they respire primarily by diffusion of dissolved gases across the cuticle and seldom rise to the surface to breathe. The siphon probably serves as a tracheal gill in this insect. In addition, mature larvae usually select the protected undersides of rocks to pupate, and the coarctate pupae remain attached by means of the clamp-like terminal prolegs. Larvae cast adrift are subject to resettling in unfavorable regions (such as profundal sediments or sandy deposits), and dislodged pupae will invariably float to the surface and be cast on the shore in windrows where they are subject to desiccation, parasitism, and predation. Pupae may be subject to attack by the pteromalid parasitoid *Urolepis rufipes* (Ashm.) (Essig, 1926), with those cast ashore in windrows being especially vulnerable (Herbst, unpubl. data).

Mono Lake is located on the eastern side of the Sierra Nevada mountains in east-central California, at an elevation of almost 1950 meters. Mono Lakes becomes thermally stratified during the summer at a depth usually between 10 and 15 meters. Below the thermocline, the profundal lake bottom consists primarily of fine detrital sediments of autochthonous origin (anaerobic much of the year), and fine alluvium. Localized around sublacustrine springs and seeps (found mostly along the western, NW and SW lake margins), are extensive formations of the main hard substrate of the littoral region, porous limestone deposits known as tufa (Dunn, 1953). On the south and southeast lakeshore, the bottom is covered by windblown volcanic sands. East and northeast shores are composed mainly of soft detrital muds, with some areas having a surface veneer of sand.

Material and methods

Benthic sampling

The densities of larvae and pupae at different sites around Mono Lake, and on different substrate types, were estimated from samples taken with a 15 cm (0.018 m^{-2}) diameter coring tube (Wilding or stovepipe sampler type, Merritt & Cummins, 1984). Samples were taken in spring, summer, and autumn of 1986 at 15 sites in locations representing each of the major geologic substrata of the shallow littoral region (Fig. 1). These are deposits of tufa, sand, alluvial gravel and mud. In addition, combinations of these substrates with detritus deposits, submerged terrestrial vegetation, pumice, cemented sands, and algal mats produce varied habitat around the lake.

Samples were collected at depths between 20 and 50 cm by working the core sampler into the substrate and removing the stirred contents at the base of the tube using a bilge pump and/or fine mesh hand net. Five samples at each site were taken both in early July and late October (corresponding to early and late in peak seasonal abundance, Herbst, 1988). Each sample was selected at random along a 100 m transect parallel to shore at a marked location. Any rock material larger than a centimeter was removed for processing and measuring of surface area. Samples were taken to the laboratory for processing within 12–24 hours after collection (refridgerated). Samples were put into a large volume of saturated sodium chloride to float out all insect life stages in the sample. These were filtered off and the remaining debris examined microscopically for any remaining larvae or pupae. These samples were preserved for counting. Surface area of rock substrate in
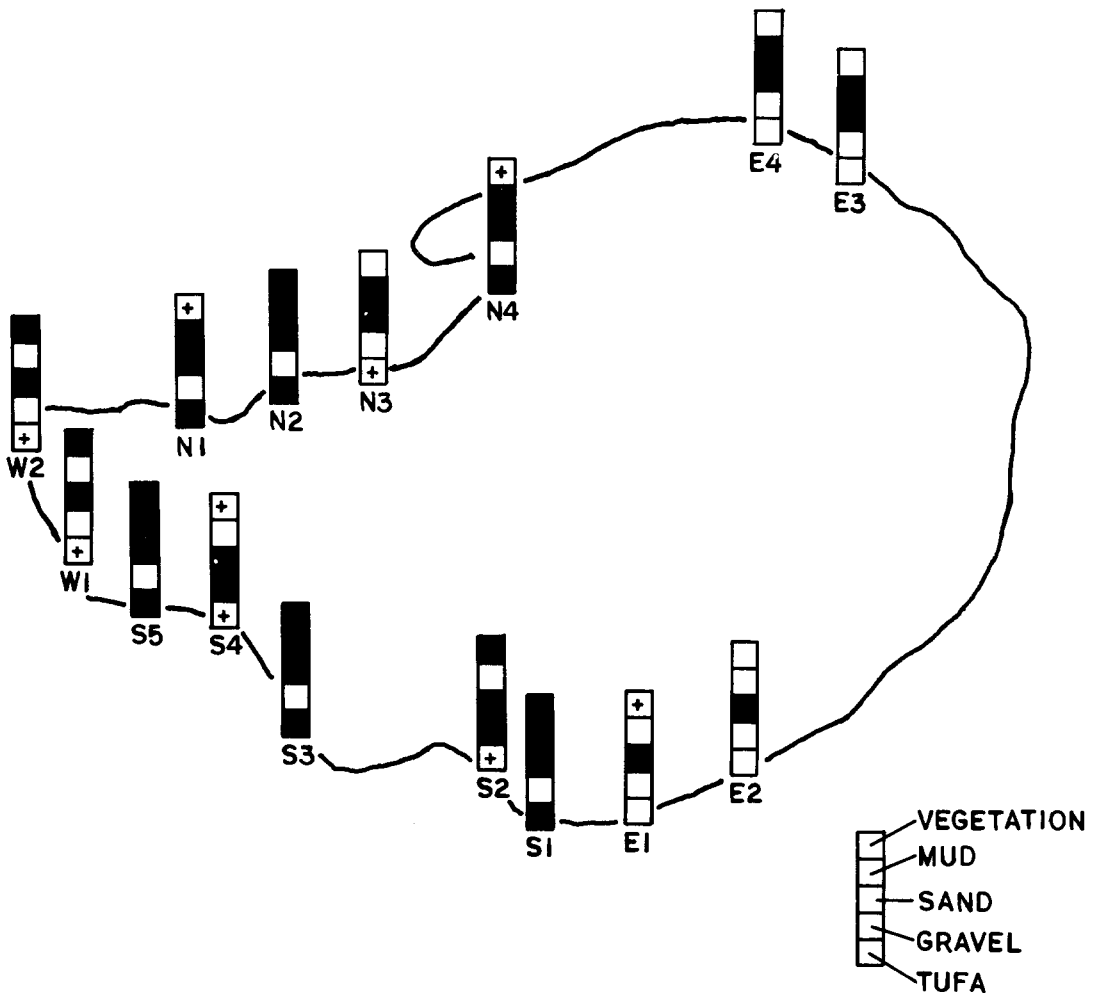
Fig. 1. Substrate composition of benthic samples sites at Mono Lake. Site prefix refers to compass sector of location. Boxes are filled if half or more of the samples taken contained that substrate type. Boxes with a plus (+) show a substrate was present but in less than half the samples.

samples was estimated by outlining their contours on graph paper and measuring the area on the grid (2-dimensional area). Salinity was measured from surface to bottom along the transect as specific gravity (using a hydrometer and translucent cylinder). Temperature was recorded at the same time using a standard mercury thermometer. Substrate type in each sample was scored as presence or absence of each of the five categories listed in Fig. 1.

First, second, and third larval instars and pupae were counted in each sample and the frequency distributions of larval and pupal abundance examined for conformity to a contagious or clumped distribution. This was done by a chi-square test of the dispersion coefficient (k) to a negative binomial distribution (Elliott, 1977). The value of k was obtained using the maximum-likelihood equation and this was used to determine sample size requirements.

Substrate preference was examined by plotting the frequency distribution of densities for samples containing (1) tufa (2) gravel alluvium (3) consolidated or cemented sand (4) unconsolidated sand or sand/mud mixture and (5) submerged vegetation present on sand or sand/mud mixtures.

The relationship of hard substrate area available in a sample to density of larvae and pupae was plotted to compare suitability of different hard substrates (categories 1, 2 and 3 above).

The relative abundance of adult *Ephydra hians* at different locations and on different shore substrates around the lake shoreline was evaluated by coating 25 × 75 mm slides with sticky-trap (trademark), and setting them out for 15 minute intervals. Zonation away from the shoreline, and species composition of the shore insect community was observed from these samples.

Temperature Effects on Development

Temperature effects on development were measured using the duration of the pupal stage as an indicator. Field-collected 3rd instar larvae from Mono Lake were held in the laboratory in the lake water at 20 °C, and within several hours after pupariation (puparium formation), were transferred to incubation chambers at 5, 10, 15, 20, and 25 °C, on a L : D 14 : 10 photoperiod. Eclosions were recorded daily. Larval development time at 25 °C was also determined, with laboratory cultured algae (mainly diatoms and filamentous blue-green algae) provided regularly as food, at a salinity of 100 g l^{-1} (near present lake salinity). Larval development at other temperatures was assumed to change in proportion to that observed for the effect of temperature on pupation time. Pupation time is independent of environmental factors such as food and salinity (Herbst, 1986) and is used here as a standardizing factor that reduces natural variability in larval development not due solely to temperature. Total degree-days from egg to adult was estimated from these data at each experimental temperature. Degree-days in the field (above a developmental temperature minimum) were calculated from data on temperature at the water surface, 5 m, 10 m and 15 m depth (using data from pelagic monitoring stations, courtesy G. Dana & R. Jellison). These were compared to the laboratory data on development times to estimate potential generations completed during the growing season within the epilimnion (the thermocline usually forms between 10 and 15 meters depth).

Results

Habitat associations and Ephydra hians distribution at Mono Lake

The map of dominant substrate types present in samples from study sites (Fig. 1) show some general patterns:
(1) East shore sites are composed almost exclusively of sand substrate except in the north, where some detrital mud deposition occurs. In addition, consolidated or cemented sand provides a hard substrate in some locations, and patches of submerged vegetation and a few scattered tufa formations also occur.
(2) West shore sites (sites with W, S or N prefixes) are a heterogenous mix of substrates composed of tufa, sand, mud, detritus, alluvial gravel, and submerged vegetation, each of which may be locally dominant.

Shallow tufa shoals in certain areas (N1, N2, S1, S5) also promote stabilization and protection of detrital mud deposits, permitting the development of a benthic algal-microbial mat in these locations. Submerged vegetation has its origin in the growth of salt grass (*Distichlis spicata*) onto lakeshore exposed by dropping lake level that has since become re-submerged by rising water. The submerged salt grass is a dead rhizomatous mat, and is an erodable, impermanent substrate feature. This root mass has an important stabilizing effect on sand/mud substrates, and extends around much of the lake as a band parallel to the lakeshore (Burch *et al.*, 1977).

A preliminary set of 50 benthic samples were taken in May 1986 from the mixed substrates of the west bay area (S5-W1-W2) to determine the spatial dispersion of larvae and pupae, and the sampling intensity required to estimate mean density with a 20% SE. Maximum-likelihood values calculated for the index of dispersion k (Elliot, 1977) showed significant conformity to a negative binomial distribution by a chi-squared goodness-

of-fit test. Smaller values of k for pupae relative to larvae indicated pupae had an even more clumped distribution than larvae. A sample size of 29 was calculated to obtain 40% precision in estimation of the 95% CI for the mean density. Since aggregated distributions of benthos are often due to substrate preferences (behavior and morphology of *E. hians* larvae and pupae clearly suggest this), sampling was expanded to incorporate other locations and substrate types (sample $n = 75$).

The distribution map of larval and pupal abundance (Fig. 2) shows large variations among sample sites, but that densities within sites are similar between summer and autumn samples. The most densely occupied locations around the lake are associated with areas of mixed tufa deposition, detrital mud sediments, and submerged vegetation. Sand was poorly inhabited unless tufa and/or vegetation was also present. Substrate preferences are examined in the frequency distribution of densities for different substrate categories (Fig. 3). Densities are highest on tufa (mean = $14050\ m^{-2}$) and vegetated
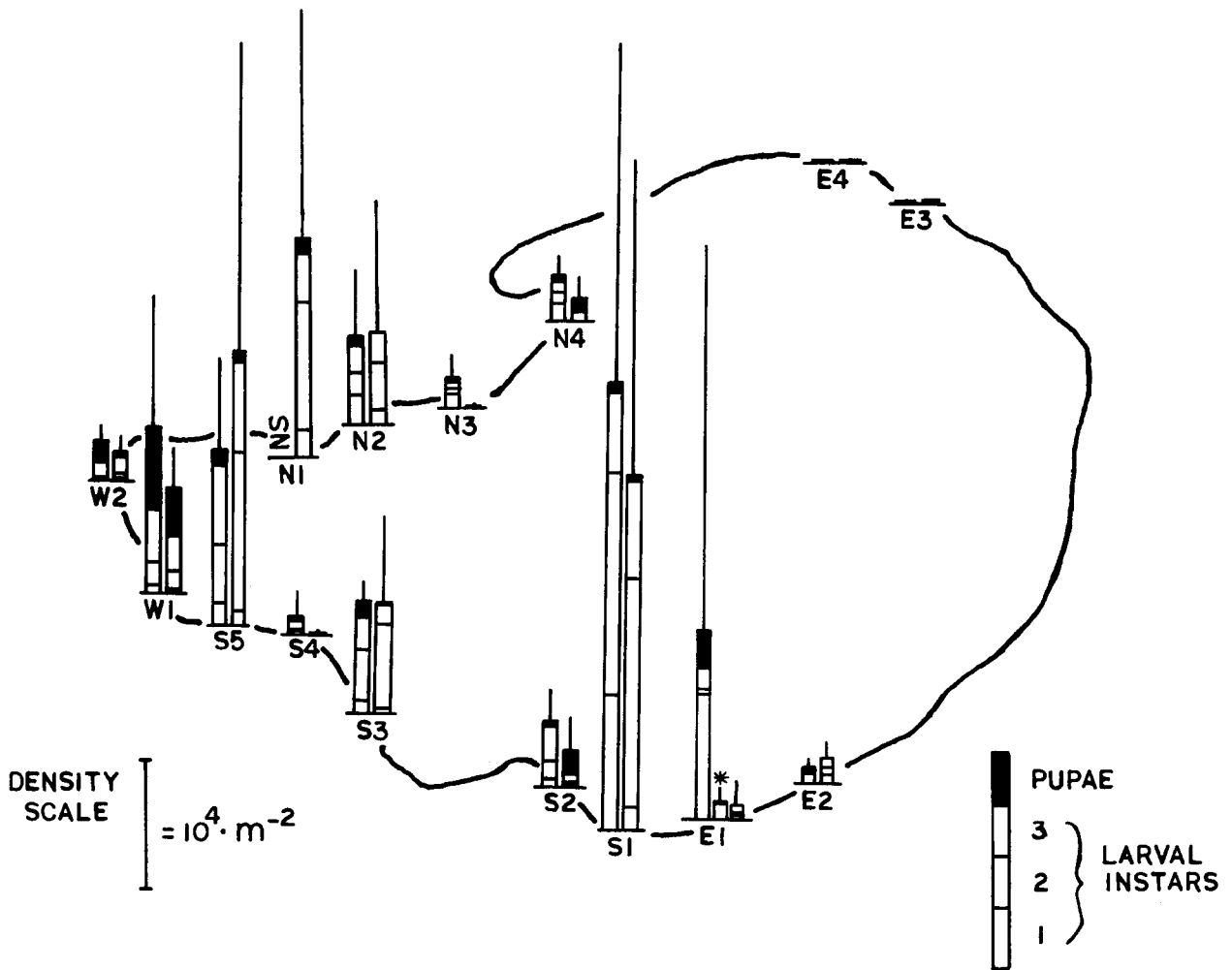

Fig. 2. Density of larval instars and pupae at sample sites in summer (left bar at each site, 1–9 July) and autumn (second bar at each site, 20–30 October) of 1986. N = 5 samples each, SD shown as line at top of each bar. Note that N1 was not sampled (NS) in summer, and middle bar (*) of E1 is the summer collection with 1 sample removed that contained a branch of drifted vegetation covered with attached larvae and pupae.
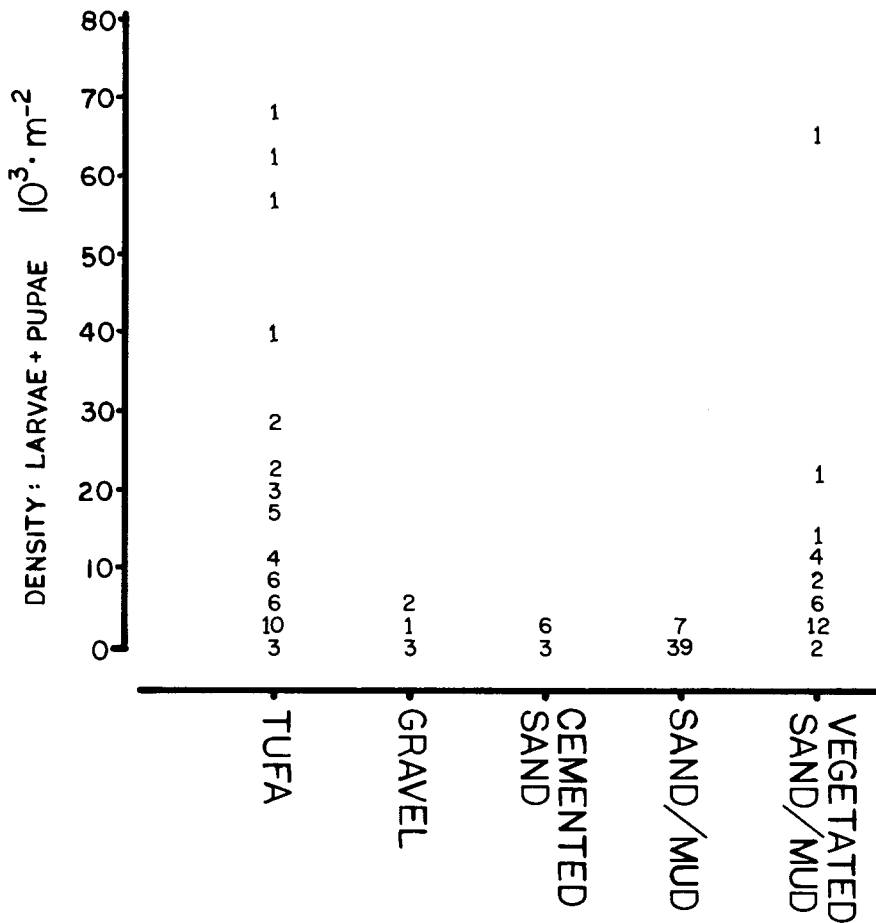
Fig. 3. Frequency distribution of abundance (larvae + pupae m^{-2}) on different substrate types for summer and autumn samples pooled. Number on graph is the frequency of samples in each density class, drawn from a total of 145 benthic collections. Tufa, gravel and cemented sand (hard substrates) were samples in which only one of these substrates was present, but sand, mud, or vegetation could also be present. Sand/mud was samples consisting exclusively of sand or sand/mud mixtures; or vegetated sand/mud if submerged vegetation was present.

sand/mud (8100 m^{-2}), intermediate on gravel (2400^{-2}) and cemented sand (1850 m^{-2}), and lowest on sand or sand/mud deposits (550 m^{-2}). Over the 0–150 cm^{-2} size range of hard substrates sampled, the abundance of larvae and pupae increases significantly with the area of tufa present, but not on gravel or consolidated sand substrate (Fig. 4).

To examine changes in population age structure from summer into autumn, changes in the proportion of each life stage were compared as matched-pairs within sites (to control for location and substrate effects) using Wilcoxon's signed-

ranks test (Fig. 5). This showed significantly fewer first instars and more second instars in autumn.

Adult abundance along Mono Lake shores is greatest adjacent to littoral zones where tufa substrate is present (Table 1). Adult density also decreases rapidly with distance from shore, and most flies are usually found in a band less than a meter wide along the shoreline. Other ephydrid species occur back from the shoreline (1–3 meters), out of the zone where *E. hians* is most abundant. In addition, although the alkali fly is abundant at a nearby saline pond, *Mosillus bidentatus* and *Paracoenia bisetosa* are also com-
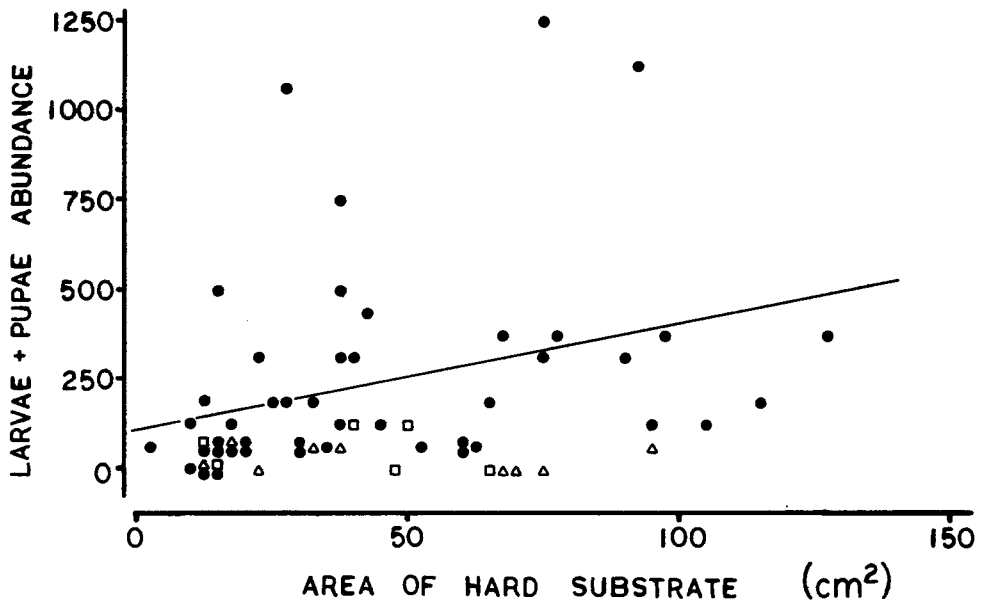
Fig. 4. Abundance of larvae and pupae on different hard substrate types in relation to substrate area (for areas up to 150 cm^2). Filled circles = tufa; open squares = gravel, open triangles = cemented sand. Regression least squares line for tufa only: r = 0.32 (p = 0.03).
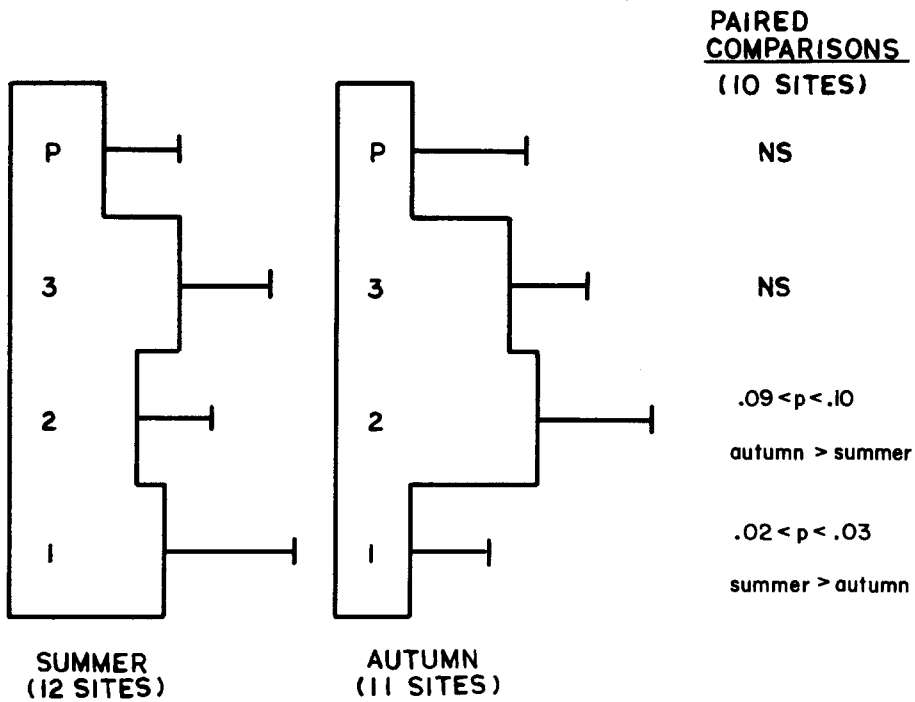

Fig. 5. Population age structure: overall average proportions of larval instar and pupa stages in summer and autumn samples. Compared within sites using Wilcoxon's matched-pair signed-ranks test (2-tailed), for differences between summer and autumn sample periods. Mean for sites calculated using only samples with n > 20 larvae + pupae (n = 10 paired sites). Error bars are SD of proportions.

Table 1. Lakeshore habitat and adult shore fly distribution at Mono Lake and nearby ponds in July/August 1980.

Substrate and habitat type	N	Distance from shore	Ephydrid (species)				
			Eh	Mb	Pb	Lc	Po
Detrital mud							
Tufa present	7	0 m	***********	0	0	0	+
	7	1 m	*	0	0	0	+
	4	3 m	0	0	0	+	+
Tufa absent	3	0 m	*	0	0	0	0
	3	1 m	+	+	0	0	0
	3	3 m	+	+	0	0	*
Sand							
Tufa present	4	0 m	********	0	0	0	0
	4	1 m	*	0	0	+	+
Tufa absent	6	0 m	+	0	0	0	0
	6	1 m	0	0	0	*	+
Saline pond (2 km from ML)							
Mud	3	0 m	********	+	+	0	0
	3	3 m	*******	*****	***	0	0
	3	15 m	0	0	0	0	**
Sand	3	0 m	0	***	0	0	*
	3	2 m	0	0	0	0	**
Freshwater seep pool (20 m from ML)							
Mud	7	0 m	0	+	*	0	0

Key: N = sample size, each * represents an average of 10 flies per sample, each + indicates a species is present, but fewer than 10 flies in a collection. Coefficient of variation = 30–50% for most samples. Tufa presence or absence refers to submerged nearshore tufa habitat. Species abbreviations: Eh = *Ephydra hians* Say, Mb = *Mosillus bidentatus* (Cresson), Pb = *Paracoenia bisetosa* (Coquillett), Lc = *Lamproscatella cephalotes* Cresson, Po = *Ptilomyia occidentalis* Sturtevant and Wheeler. Other species commonly encountered onshore:
Hydrophorus plumbeus Aldrich (Dolichopodidae)
Saldula arenicola (Scholz) (Saldidae)
Lispe sp. (Anthomyiidae)
Cicindela fulgida Say (Cicindelidae)

mon, and these species are the only ones found in samples at a freshwater seep adjacent to the lake.

Temperature and generation time

Pupa development time for *E. hians* is temperature-dependent (Fig. 6), and is more rapid in comparison to *E. cinerea* from Great Salt Lake (Collins, 1980a). This is a useful indication of seasonal effects on growth rate, independent of food and salinity, because pupae are non-feeding, and sequestered from the aquatic environment (Herbst, 1986). The most rapid change in development rate occurs between 10–20 °C for both species. This corresponds to the temperature range found in spring and autumn, coincident with periods of population growth and decline.
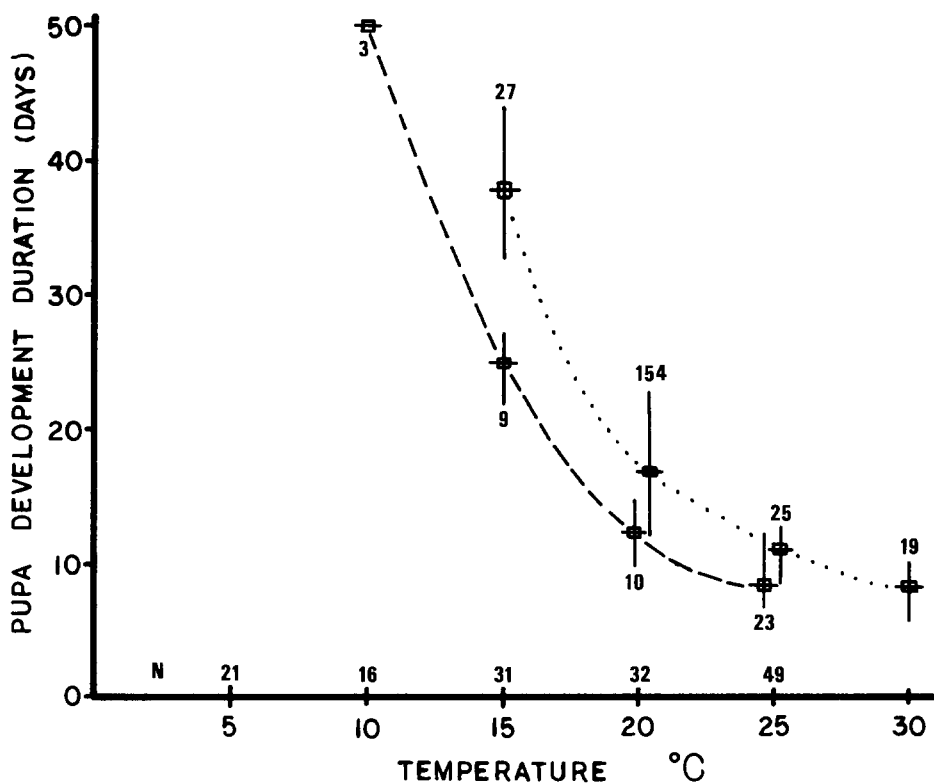
202

Fig. 6. Influence of temperature on pupa development time in *Ephydra hians* (dashed curve) compared to *E. cinerea* (dotted curve; data taken from Collins, 1980a). Vertical bars are the SE of the mean (horizontal lines), and vertical lines are the range. N above X axis refers to the total number of *E. hians* pupae exposed to that temperature.

The relation of temperature to development is non-linear and has a Q-10 of 2.1 over 20–25 °C, but is 4.1 over the 10 to 20 °C range.

The minimum temperature for development is estimated as 10 °C since no adults emerged from pupae exposed to 5 °C, but a few emerged at 10 °C. Based on laboratory experiments of larval development at 25 °C, egg hatching to pupa formation requires 40 to 60 days.

Combining pupation times with the ranges estimated for larval development times at each temperature provides a measure of egg to adult generation time in degree-days (Table 2). Using 10 °C as the developmental minimum, the estimates agree at all temperatures that 700–1000 degree-days are required to complete a generation (excluding adult reproduction time).

Degree-days of development time available in nature vary with depth and location (Fig. 7). In surface waters, between 1200 and 1400 degree-days are accumulated above the 10 °C minimum temperature. In a warm year (e.g. 1984), when the epilimnion was well-mixed, degree-day time was reduced by only 10 to 20% at 5 and 10 meters depth, respectively (relative to the surface). in colder years (1982 and 1983), degree-days were reduced by 20 to over 50% at the same depths. Greater variability at the surface between east and west sides of the lake (separated by a large island) suggests that in any year, the thermal environment is more constant in deep water. The relative thermal inertia of deep water is likely to be even more pronounced in the benthic littoral region due to solar radiation inputs to substrate in shallow water. Herbst (1988) observed large variations in shallow benthic temperatures within and between locations studied in 1983 and 1984. In 1984, mean degree-days accumulated above 10 °C was 1650,

Table 2. Degree-days generation time at different temperatures, using pupation time as a standard.

Temperature °C	Puration Time (d)	Larval Development Time (d)*	Estimated Sum** Degree-Days Required for Egg to Adult Generation Time
25	9	40–60	735–1035
20	13	60–85	730– 980
15	25	110–170	675– 975
10	50 +	200–300	–

* Larval development time at 20, 15, and 10 °C calculated from the range found at 25 °C, proportional to the increase in pupation time.

** Degree-days calculated as degrees above 10 °C times total days of larval + pupal development time.
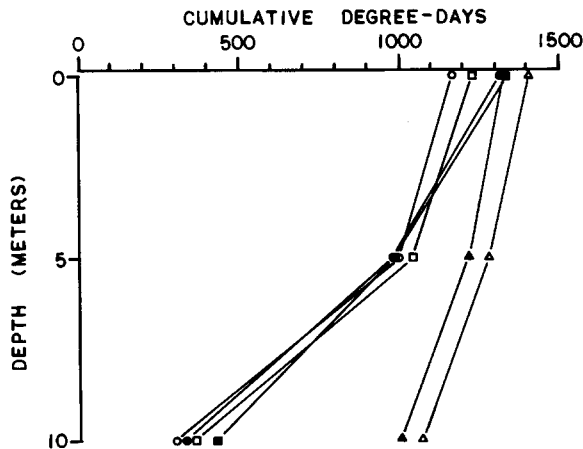

Fig. 7. Cumulative degree-days of development time available at different epilimnion depths for 1982 (circles), 1983 (squares) and 1984 (triangles). Calculated from pelagic temperature profiles using 10 °C as the minimum developmental temperature of *Ephydra hians.* Filled symbols from profiles taken on west side of lake, open symbols from east side of lake.

and the maximum annual sum (at site N1) was 3150. Using the minimum generation time, between 2.4 and 4.5 generations per year would be possible under these conditions. Applied to the degree-day data of Fig. 7, between 1.7 to 2.0 generations could be completed in shallow surface waters, 1.4 to 1.8 at 5 m, and from less than 1 to 1.5 at 10 m. Only in 1984 did temperatures at 15 m reach 10 °C or above, and only 80–120 degree-days were accumulated.

Discussion

Tufa is apparently the most suitable substrate for aggregation and persistence of the immature stages of the alkali fly, unless soft or unconsolidated substrates are otherwise stabilized and protected from wave action (Figs. 2, 3 and 4). Collins (1980a) also showed that abundance of *E. cinerea* was greater on the rocky, reef-like bioherms of Great Salt Lake than in sandy areas. At Abert Lake (Oregon), another western Great Basin lake where *E. hians* is common, larvae and pupae occur mainly among the rocky fragments of porous basalt on the eastern shore (Herbst, 1988). Tufa provides an attachment site for pupae, and is actively grazed by larvae since it serves as an epilithic growth site for diatoms. The association of adults with shorelines adjacent to offshore tufa (Table 1), and the observation of adult feeding and oviposition on partially submerged tufa, is also consistent with the importance of this rocky substrate in the distribution of the alkali fly at Mono Lake. The other hard substrates that occurred in samples (alluvial gravel/cobble, and cemented sands) did hold higher densities than unconsolidated sand or sand/mud, but apparently the surface of these substrates was not as useful for attachment, because area was not correlated with larval and pupal abundance (Fig. 4). Submerged vegetation also serves as an attachment site, but the value of the habitat it occurs in

for larval development probably depends more on food availability and quality.

Declining lake levels at Mono Lake, resulting from the diversion of inflowing streams, has become a major conservation concern in California (National Academy of Sciences, 1987). Among the potential problems are that exposed lakebed will result in the elimination of submerged tufa habitat. Geomorphic studies of the benthic topography of Mono Lake indicate that the distribution of tufa is restricted mainly to shallow water (Stine, 1988). Approximately 60% of presently submerged tufa would be exposed by a 3 meter decline in lake elevation (5–10 years from present, at the current diversion rate). The results of the present study show that tufa is preferred substrate of alkali fly larvae and pupae, suggesting that lower lake levels will restrict habitat availability, and thus limit the distribution and abundance of this benthic insect.

Although densities within sites remain consistent between early and late season samples, there is a significant decline in the proportion of first instars present, and increase in second instars (Fig. 5). This change in age structure matches the autumn decline in adult reproductive condition and ovipositional activity previously noted by Herbst (1988). Fewer eggs were observed in autumn collections as well, indicating that little or no new recruitment is occurring at this time, and that slow growth into later instars and pupae should characterize the overwintering, non-diapausing population.

Temperature effects on growth are a useful way of modeling and comparing the population dynamics of aquatic insects (Sweeney, 1984). The more rapid development rates for E. hians than for E. cinerea (Fig. 6) are indicative of an intrinsic difference that should permit earlier seasonal activity and greater potential productivity (growing season) for the alkali fly, under comparable ecological conditions. Collins (1980a) reports that probably no more than 1 to 2 generations of E. cinerea occur annually at Great Salt Lake. In contrast, Mono Lake E. hians can probably complete 2 to 3 or more generations in shallow habitat, depending on local heating conditions. In deeper

littoral waters there may be much less potential for growth because of lower temperatures (Fig. 7). However, in warm years, with deeper mixing, there may be only a slight reduction in development time available (see 1984 in Fig. 7). Although there are certainly other factors influencing development (e.g. food and salinity: Herbst 1986), further studies of seasonal and local variations in the thermal environment would be useful in understanding annual trends in population growth and life history traits. In addition, surveys of the depth distribution of larvae and pupae in Mono Lake should be conducted to substantiate the conclusion that productivity will be limited in deep water by decreased substrate habitat availability and less degree-day time available for development.

References

Aldrich, J. M., 1912. The biology of some western species of the dipterous genus Ephydra. J. N.Y. Ent. Soc. 20: 77–99.

Barnby, M. A., 1987. Osmotic and ionic regulation of two brine fly species (Diptera: Ephydridae) from a saline hot spring. Physiol. Zool. 60: 327–338.

Burch, J. B., J. Robbins & T. Wainwright, 1977. Botany. In D. W. Winkler (ed.), An ecological study of Mono Lake, California. University of California at Davis, Institute of Ecology, Publ. no. 12: 114–142.

Collins, N. C., 1980a. Population ecology of Ephydra cinerea Jones (Diptera: Ephydridae), the only benthic metazoan of the Great Salt Lake, USA, Hydrobiologia 68: 99–112.

Collins, N. C., 1980b. Developmental responses to food limitation as indicators of environmental conditions for Ephydra cinerea Jones (Diptera). Ecology 61: 650–661.

Dunn, R. C., 1953. The origin of the deposits of tufa at Mono Lake. J. Sed. Petrol. 23: 18–23.

Elliot, J. M., 1977. Some methods for the statistical analysis of samples of benthic invertebrates. 2ne edition. Freshwater Biological Association Scientific Publication No. 25, Ambleside, England. 160 pp.

Essig, E. O., 1926. Insects of western North America. The Macmillan Co. New York, 1050 pp.

Herbst, D. B., 1986. Comparative studies of the population ecology and life history patterns of an alkaline salt lake insect: *Ephydra (Hydropyrus) hians* (Diptera: Ephydridae). PhD thesis, Oregon State University, Corvallis. 206 pp.

Herbst, D. B., 1988. Comparative population ecology of *Ephydra hians* Say (Diptera: Ephydridae) at Mono Lake (California) and Abert Lake (Oregon). Hydrobiologia 158: 145–166.

Herbst, D. B., F. P. Conte & V. J. Brookes, 1988. Osmoregulation in an alkaline salt lake insect, *Ephydra (Hydropyrus) hians* Say (Diptera: Ephydridae), in relation to water chemistry. J. Insect Physiol. 34: 903–909.

Merritt, R. W. & K. W. Cummins (eds), 1984. An introduction to the aquatic insects of North America. 2nd edition. Kendall/Hunt Publishing Co., Dubuque, IA. 722 pp.

National Academy of Sciences, 1987. The Mono Basin ecosystem: effects of changing lake level. National Academy press, Washington, D.C.: 272 pp.

Nemenz, H., 1960. On the osmotic regulation of the larvae of *Ephydra cinerea*. J. Insect Physiol. 4: 38–44.

Say, T., 1830. Descriptions of North American dipterous insects. J. Acad. Nat. Sci. Philadelphia. 6: 183–188.

Simpson, K. W., 1976. The mature larvae and puparia of *Ephydra (Halephydra) cinerea* Jones and *Ephydra (Hydropyrus) hians* Say (Diptera: Ephydridae). Proc. Ent. Soc. Wash. 78: 263–269.

Stine, S., 1988. Geomorphic and geohydrographic aspects of the Mono Lake controversy. In D. B. Botkin *et al.* (eds), The future of Mono Lake. University of California Water Resources Center, Riverside. Report No. 68. Appendix D: 1–135.

Sweeney, B. W., 1984. Factors influencing life history patterns of aquatic insects. In Resh, V. H. & D. M. Rosenberg (eds), The ecology of aquatic insects. Praeger Publishers, N.Y.: 56–100.

Wirth, W. W., 1971. The brine flies of the genus *Ephydra* in North America (Diptera: Ephydridae). Ann. ent. Soc. Am. 64: 357–377.

Wirth, W. W., 1975. A revision of the brine flies of the genus *Ephydra* of the Old World (Diptera: Ephydridae). Ent. Scand. 6: 11–44.

Wirth, W. W. & W. N. Mathis, 1979. A review of the Ephydridae (Diptera) living in thermal springs. In D. L. Doenier (ed.), First symposium on the systematics and ecology of Ephydridae (Diptera). North American Benthological Society publ. Lawrence (KS): 21–45.