Do Tides Affect Coastal Insect Communities?

GUY N. CAMERON
Program in Population Biology, Department of Biology, University of Houston, Houston, Texas 77004

ABSTRACT: Clip-quadrat samples taken prior to, during and after inundating tides in *Salicornia* and *Spartina* salt marshes during 1 year revealed that periodic tidal inundation had little effect upon the number of adult species or their vertical stratification within the marsh vegetation. Possible explanations for the insects' remaining in the marsh during inundation are considered. Sorensen's Quotient of Similarity demonstrated little alteration in species composition, and a trophic analysis showed no change in the relative proportion of herbivores, saprovores or predators as a result of inundation. The possibility that salt-marsh insects remaining in place on the vegetation during inundating tides may be a result of early morning sampling is considered. These findings support previous conclusions that salt-marsh insect populations are regulated primarily by biological rather than physical factors.

INTRODUCTION

Periodic inundation is a characteristic of intertidal—as well as other—ecosystems, which necessarily influences growth, distribution and activity of resident organisms (Doty, 1946; Harrington and Harrington, 1961; Sheppe and Osborne, 1971; Evans, 1972; Sheppe, 1972; Sudd, 1972). Intertidal air-breathing animals must retreat to higher ground, climb above the high-water mark, remain afloat, swim or endure submersion to survive inundating tides. Birds and small mammals have been reported to take refuge on floating debris and emergent vegetation or to migrate to higher ground during high tides (Harris, 1953; Johnston, 1955, 1957; Sibley, 1955; Fisler, 1961; Shure, 1971; Hadaway and Newman, 1971). The effects of high tides upon the many species of air-breathing insects that live in salt marshes are not clear. Davis and Gray (1966) and Teal and Teal (1969) suggest that salt-marsh insects escape inundation by vertical migration to plant tops or by moving out of the marsh until the tidal waters recede, but earlier workers reported that some insects remain underwater in totally inundated marshes (Arndt, 1914; Metcalf and Osborn, 1920; Saunders, 1928; Brown, 1948). I tested the hypothesis that adult insects are unable to survive inundation and respond by moving up the vegetation to dry refuges ahead of the rising tide or by leaving the marsh area if the vegetation is totally inundated.

METHODS

The study area was located on the bayside of agricultural levee systems on the western side of Tolay Creek, Sonoma Co., California; this area is on the northern shore of San Pablo Bay, the northern arm of San Francisco Bay. The marsh was composed of two fairly homogeneous plant communities distinguished by their respective dominants, *Salicornia pacifica* Standley (Chenopodiaceae), a dense, woody perennial reaching 30 cm in height, and *Spartina foliosa* Trin. (Gramineae), a reedlike plant lacking perennial aboveground parts and reaching 120 cm in height. The *Salicornia* community was located between the levee system and the *Spartina* community which bordered directly on the bay waters. The sharp transition between communities in this marsh, as in other marshes, is maintained by regular schedules of tidal submergence and exposure (Chapman, 1939, 1940; Miller and Egler, 1950; Hinde, 1954; Redfield, 1972; Nixon and Oviatt, 1973). Standing water in these communities resulted when tides exceeded 6 ft (1.8 m), which occurred 195 days during the study year. When tides exceeded 7 ft (2.1 m), water completely submerged the *Salicornia* plants (water depth > 45 cm), but only covered the lower half of the *Spartina* plants (water depth > 60 cm). Such tides occurred 27 days during the study year and are henceforth referred to as inundating tides.

The annual tidal cycle for the study area consists of seasonal high tides during summer (May to July) and winter (November to February), with the lowest tides during autumn (August to October) and spring (March to April). The tidal range during the study year was 9.45 ft (2.9 m); the highest (+ 7.45 ft (2.3 m)) and lowest (— 2.00 ft (— 0.61 m)) tides occurred in late December and late June. Maximum submergence time of the *Salicornia* community during the highest tides was approximately 5 hr. *Spartina* was never totally submerged, but the lower portion was underwater for a similar duration.

Five random 0.25 m^2 clip-quadrat samples were taken weekly from a 0.71-ha area in each marsh community from July 1968 through June 1969. Vegetation within the sampling frame was clipped from four arbitrarily determined vertical strata (ground, 1-10, 11-20 and 21-30 cm in the *Salicornia* community; and ground, 1-40, 41-80 and 81-120 cm in the *Spartina* community), placed in separate plastic bags with a minimum of disturbance to the vegetation, and returned to the laboratory. When all vegetation had been removed, the litter was scraped from the ground stratum. No belowground samples were taken. This sampling regime continued as described even though six of the sampling periods coincided with inundating tides (dates of these samples were 22 November 1968, 20 December 1968, 17 January 1969, 14 February 1969, 28 May 1969 and 26 June 1969). Samples taken while the vegetation was underwater during these periods were compared with weekly samples taken during noninundated periods. Further details of the sampling procedure are in Cameron (1972).

Insects were extracted from the vegetation in the laboratory by Berlese-Tullgren funnels. Plant samples were placed loosely in the funnels and left for 10-12 hr to maximum yield. Extraction efficiency, checked against a flotation method (Southwood, 1966), was greater than 90%. The Berlese-Tullgren method of extraction is based upon behavioral responses of animals in the sample. This is important because nearly all the specimens collected from samples taken underwater must have been alive when the samples were obtained. Only adult insects were considered in this study to simplify taxonomic determinations. Adult insects from each stratum were sorted, identified to species, and the number of individuals per species recorded.

RESULTS

All insect species collected underwater, except collembolans, were flying forms which could conceivably leave the marsh during inundation. To detect whether or not species left during inundation, the numbers of insect species present in all strata in *Salicornia* and *Spartina* during periods of tidal inundation were compared with the number of species present during previous weeks of no tidal inundation, by a *t*-test for paired comparisons (Sokal and Rohlf, 1969). This test uses the average difference in the number of species ($\bar{D}$) between the six paired inundated vs. noninundated weeks to assess the effect of tide. The formula

$$t = \frac{\bar{D} - (\mu_1 - \mu_2)}{s_{\bar{D}}}$$

is used, where $\bar{D}$ = the mean difference between the paired observations, $s_{\bar{D}}$ = the standard error of D, and $(\mu_1 - \mu_2)$, the true difference between the mean of the two groups, is assumed to equal zero. Values of $\bar{D}$ and $s_{\bar{D}}$ are used to compute *t*-values for the total community and for the separated strata. For this and all following comparisons, the six samples taken during inundation were pooled and compared with six similarly pooled noninundated samples taken during the preceding week. All the *t*-values are below the critical value for this comparison (Table 1), indicating no significant difference in the number of species present during inundated or noninundated weeks and, hence, no significant effect of tide ($t_{critical} = 2.57$; $p > 0.05$).

The possibility of residual (time-lag) effects of tidal inundation upon adult insects was tested by comparing species composition between the week preceding and the week following inundating tides (Table 1). There was no significant difference in the number of species, indicating no short-term time-lag response due to tides ($t_{critical} = 2.57$; $p > 0.05$). This does not suggest, however, that abundance or emergence of some of the species may not be cued by the tidal cycle, as shown experimentally for some insects (Pfluger and Neumann, 1971).

Upward movement of the insects in response to rising tide would not be detected by the preceding analysis because individual strata were not analyzed separately. Interstrata comparisons within each marsh community can test for such escape movement. Vertical movement should be most evident in *Spartina,* because only half the vegetation is covered at maximum inundation and the remaining half could serve as a temporary refuge. A *t*-test for paired comparisons showed no significant difference ($t_{critical} = 2.57$; $p > 0.05$) in the number of species between the week previous to the inundating tide and the week of the inundating tide for any strata in either community (Table 1) suggesting that insects do not move up the marsh plants ahead of advancing tides, but instead remain within the vegetation stratum during inundation.

Inundating tides could affect insect species composition without altering the number of species present by selecting for or against certain species. Gross taxonomic structure (at the ordinal level), however, was not altered in either community by inundation (Table 2); there was no significant change in the taxonomic apportionment in either community as a result of inundation (*Salicornia*, $\chi^2 = 1.33$, $p > 0.1$; *Spartina*, $\chi^2 = 0.35$, $p > .05$). At the species level, Sorensen's Quotient of Similarity (Southwood, 1966) was computed for each pair of samples taken during inundated and previous noninundated weeks to detect changes in species composition attributable to inundation. A mean species overlap value was then computed from these individual week pairs for the total *Salicornia* and *Spartina* communities as well as for each vertical stratum (Table 3, QS Tide). Lower similarity values at ground level result from loss of species when detritus floats out of the marsh during tidal flux (Cameron, 1972). High similarities in species composition for the total community and the partitioned strata between inundated and noninundated samples indicate that a similar insect fauna was sampled and that the species composition was not affected

TABLE 1.—Comparison of the number of species present in *Salicornia* and *Spartina* marshes during (1) the week before and the week of the inundating tide, and (2) the week before and the week after the inundating tide by a *t*-test for paired comparisons. Comparisons based upon the average difference in the number of species present between week pairs ($\bar{D}$) are made for the total unstratified community and for the community divided into vertical strata

	Comparison					
	Week before vs. week of tide			Week before vs. week after tide		
Salicornia	$\bar{D}$[1]	$s_{\bar{D}}$	t[2]	$\bar{D}$[1]	$s_{\bar{D}}$	t[2]
Total community	1.00	2.09	0.48	–1.00	1.16	0.87
ground	–0.50	0.43	1.12	0.67	0.33	2.03
0-10 cm	1.67	1.31	1.27	–1.17	0.47	2.48
11-20 cm	0.17	0.87	0.19	–0.50	0.62	0.81
21-30 cm	–0.33	1.38	0.24	–1.00	0.80	0.26
Spartina						
Total community	–1.50	1.54	0.98	–2.67	1.30	2.05
ground	–2.33	1.52	1.53	–1.67	1.54	1.08
0-40 cm	–0.67	0.72	0.94	–0.33	0.64	0.51
41-80 cm	0.17	0.54	0.31	–1.00	0.73	1.37
81-120 cm	0.83	0.83	1.00	–1.00	1.17	0.85

[1] Negative value denotes previous week contained greater number of species
[2] $t_{critical} = 2.57$

by the tide. To verify these findings, six pairs of successive noninundated weeks from all seasons were chosen and a QS computed to compare with the inundated weeks (Table 3, QS No Tide). These values are similar to the values obtained when using the inundated weeks, indicating a high degree of interweek similarity in species composition regardless of water level and reinforcing previous conclusions that inundation has little effect upon species composition.

Finally, the possibility of trophic rearrangement in response to inundation was considered. Insect species were grouped into three trophic categories (herbivore, saprovore or predator) and the number of species in each category compared during inundated and noninundated weeks (Table 4). There were no significant trophic differences during inundation in either community, again suggesting little effect of inundation upon salt-marsh insect community structure [$\chi^2 = 1.38$ (herbivores), 0.09 (predators) and 2.13 (saprovores) for *Salicornia* and $\chi^2 = 0.20$ (herbivores), 0.00 (predators) and 0.22 (saprovores) for *Spartina*; $p > 0.1$].

DISCUSSION

Exposure of marsh communities to periodic tidal inundation causes temporary turnover in some vertebrate species, but, as shown by this study, has little effect upon the insect component. Inundation does not alter the number of species represented by adults, vertical stratification within the vegetative matrix, taxonomic composition of the community or the trophic structure of the community. High similarity (QS) between weeks of inundation and noninundation is comparable to the similarity between consecutive weeks of noninundation, reflecting a low species turnover between weeks. Insects did not move up the vegetation ahead of the advancing tide in either community but remained

TABLE 2.—Taxonomic composition of insect fauna in *Salicornia* and *Spartina* marshes, comparing inundated and noninundated samples. The noninundated period used for this comparison was the sample week immediately preceding the inundation

Order	*Salicornia* Non-inundated no. of species	*Salicornia* Inundated no. of species	*Spartina* Non-inundated no. of species	*Spartina* Inundated no. of species
Diptera	12	13	6	8
Coleoptera	6	9	4	6
Thysanoptera	2	3	3	3
Hymenoptera	2	3	3	3
Hemiptera	0	0	2	2
Homoptera	1	2	0	0
Psocoptera	1	2	1	1
Lepidoptera	1	1	1	1
Collembola	1	1	1	1
Neuroptera	0	1	0	0
TOTAL	26	35	21	25

in place on the vegetation during inundation; dry *Spartina* tops did not serve as a refuge during inundation. These findings prompt rejection of the hypothesis that adult insects are unable to withstand inundation and reinforce previous conclusions (Cameron, 1972) that salt-marsh insect populations are predominately controlled by biological, especially productional, factors rather than physical factors.

Why should insects remain during inundation? Since many marsh insect species are seasonal, remaining as adults in the marsh for only a few weeks during the year, partitioning periodic movement out of the marsh into strict time budgets while maximizing developmental, reproductive and dispersal functions would be difficult. Timing of these ecological events is critical since summer's inundating tides occur during peak primary and secondary production (relevant to herbivores and their predators), and winter inundating tides occur during peak litter accumulation (important to saprovores and their predators) (Cameron, 1972). Alternatively, insects may remain during inundation because sedentary insects are less conspicuous to predators than are actively moving ones, and periodic movements out of the marsh may expose the insects to avian predation. Another possibility, that insects may be submerged when inactive and have no recourse but to remain firmly attached to avoid being swept away by the tide, is considered.

Adult aquatic insects employ numerous behavioral and morphological mechanisms to secure oxygen underwater (Roeder, 1953; Wigglesworth, 1965). Field and laboratory observations during this study of adult Diptera, Coleoptera and Hymenoptera clinging to submerged marsh vegetation detected a covering of air bubbles. With this or some similar mechanism, short periods of submergence during routine tidal cycles do not represent insurmountable obstacles to the survival of air-breathing marsh insects nor do they affect vertical dispersion patterns

TABLE 3.—Mean species overlap computed with Sorensen's Quotient of Similarity (QS) for the total unstratified community and for the community divided into vertical strata. Comparison between (1) weeks of inundation and the prior weeks of noninundation (QS Tide) and (2) successive weeks of noninundation (QS No Tide) are given

	Salicornia	
Strata	QS Tide	QS No Tide
ground	0.42	0.46
0-10 cm	0.61	0.65
11-20 cm	0.75	0.73
21-30 cm	0.61	0.63
Total community	0.58	0.62

	Spartina	
Strata	QS Tide	QS No Tide
ground	0.53	0.49
0-40 cm	0.73	0.66
41-80 cm	0.71	0.68
81-120 cm	0.73	0.80
Total community	0.63	0.66

within marsh vegetation.

These findings agree with earlier observations (Arndt, 1914; Metcalf and Osborn, 1920; Saunders, 1928; Brown, 1948), but differ from laboratory findings of Davis and Gray (1966). One explanation may be that Davis and Gray's experiments were conducted at 22-25 C, while my sampling was during early morning hours when temperatures in the marsh were much lower than 20 C, except during June 1969 (Cameron, 1972). Seemingly, Davis and Gray and I sampled during different environmental conditions, and both observations of the insect's response to inundation may be correct. I sampled when the insects were inactive (early cool morning) because of low body temperature and darkness (most salt-marsh insects are diurnal). Low temperatures suppress the insect's metabolic rate and increase the chance of survival during inundation on the limited amount of oxygen available in surface bubbles. Davis and Gray (1966), on the other hand, performed their experiments with active insects whose response was to avoid inundation. It may be possible that if I sampled during late afternoon tides when the temperature was higher and the insects active that I would have obtained results similar to Davis and Gray (L. Davis, pers. comm.). In short, Davis and Gray and I sampled both ends of a response spectrum: when insects are inactive, their response to tidal inundation is to cling to vegetation to avoid being swept away, but when they are active, their response is to seek a dry refuge to avoid submergence.

Most collection techniques select particular types of insects (*e.g.*, flying forms, ground forms) or are most useful in particular plant growth forms (*e.g.*, grasses). Clip-quadrat efficiency was increased by sampling during the cool, foggy early morning hours when dew was present on the vegetation. Insects are rarely active before late morning and thus the chance of losing active insects while taking samples was markedly lessened. The suitability of the clip-quadrat as an entomological sampling procedure was determined by comparing the samples with another insect study in a marsh at the S end of San

TABLE 4.—Trophic composition of insect fauna in *Salicornia* and *Spartina* marshes, comparing inundated and noninundated samples. The noninundated period used for this comparison was the sample week immediately preceding the inundation

	Salicornia		*Spartina*	
Trophic level	Noninundated no. of species	Inundated no. of species	Noninundated no. of species	Inundated no. of species
Herbivore	10	16	9	11
Saprovore	8	15	8	10
Predator	5	6	5	5
TOTAL[1]	23	37	22	26

[1] Species totals are inaccurate with respect to the total number of species collected since some species are represented in several trophic levels. Correct totals in Table 2

Francisco Bay, which utilized a variety of sampling methods, including sweet nets, aerial traps, blacklight traps and soil cores (Lane, 1969). Clip-quadrats sampled groups which were either not sampled by Lane or were sampled in lower proportions (*i.e.*, ground-dwelling Coleoptera, flightless Thysanura and litter-dwelling Psocoptera). In addition, Sorensen's Quotient of Similarity computed for species composition revealed a high overlap between these studies, supporting the reliability of the clip-quadrat (QS = 0.62 at family level and QS = 0.51 at species level). Lower similarities at the species level may be the result of differences in environmental factors and habitats between the two areas. The S end of the Bay is more saline, has a smaller tidal amplitude, and is much warmer than the N end. In addition, much of the original marsh flora and fauna is being replaced by species adapted to disturbance by reclamation and the establishment of salt-evaporating ponds, while marshes at the N end of the Bay are relatively undisturbed.

Acknowledgments.—I thank L. R. Lawlor, University of Texas, and R. L. Rudd, G. W. Salt and K. E. F. Watt, University of California, Davis, for helpful suggestions, and E. H. Bryant, N. Fotheringham and D. L. Jameson, University of Houston, for critically reading the manuscript and suggesting improvements. The University of Houston Computer Center provided computer time for statistical analyses.

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SUBMITTED 5 AUGUST 1974 ACCEPTED 26 SEPTEMBER 1974