

Damage to Cordgrass by Scale Insects in a Constructed Salt Marsh: Effects of Nitrogen Additions

KATHARYN E. BOYER¹
JOY B. ZEDLER
Pacific Estuarine Research Laboratory
San Diego State University
San Diego, California 92182-4614

ABSTRACT: Because tall cordgrass (*Spartina foliosa*) is needed for nesting by the endangered light-footed clapper rail, managers of constructed salt marshes in southern California are proposing large-scale nitrogen fertilization to improve cordgrass growth. How this might affect an existing infestation of scale insects (*Haliopsis spartina*) and the degree of damage these insects cause to their cordgrass hosts was unknown. We explored the effects of timing and duration of fertilization on *Haliopsis* damage to cordgrass, as well as the timing of *Haliopsis* dispersal, in a constructed marsh at Sweetwater Marsh National Wildlife Refuge in San Diego Bay, California. Fertilization did not result in increased *Haliopsis* abundance. After a large dispersal pulse in late May, *Haliopsis* establishment in the long-term fertilized plots was greater than in the controls; however, this trend reversed in August, when many more stems in the control plots were infested with large numbers of *Haliopsis*. Since adult *Haliopsis* cannot leave a feeding site, losses of individuals in the fertilized plots were apparently due to mortality, perhaps resulting from mechanical or chemical changes in the fertilized plants or increased predation. Late in the growing season, plots fertilized with 10 applications of urea over 20 wk had the lowest mean *Haliopsis* abundance. Plots fertilized only in March, April, June, or August did not differ from controls in mean *Haliopsis* abundance. *Haliopsis* was never abundant in the fertilized or control plots in the adjacent natural marsh. This study suggests that fertilization of constructed salt marshes in San Diego Bay may proceed without concern that further *Haliopsis* outbreaks will be facilitated.

Introduction

Loss of coastal wetland habitat in southern California has been extensive. In southern San Diego County there has been an 85% loss of salt marsh acreage in the last 100 yr (Macdonald 1990). While new wetlands can be constructed to mitigate losses, the constructed "Connector Marsh" at Sweetwater Marsh National Wildlife Refuge (SMNWR) in San Diego Bay was not functionally equivalent to an adjacent natural marsh, Paradise Creek, even 8 yr after construction (Zedler 1993). Cordgrass (*Spartina foliosa*) is significantly shorter in Connector Marsh than in Paradise Creek, and the lower canopy has been implicated in the failure of Connector Marsh to attract the federally-endangered light-footed clapper rail (*Rallus longirostris levipes*), as tall stems are used for nesting (Zedler 1993). Lower soil nitrogen in the constructed marsh may be partly responsible for poor cordgrass growth. In addition, outbreaks of the native scale insect, *Haliopsis spartina* (Homoptera: Diaspididae), have been seen only in constructed marshes of San Diego Bay (Williams 1990; Johnson 1991, personal

observation). In 1992, where the highest densities of *Haliopsis* occurred, cordgrass was shorter than in previous years and senesced unusually early in the season (Pacific Estuarine Research Laboratory, unpublished data).

Experiments in natural marshes have shown that *Spartina* spp. are nitrogen-limited, and that both foliar nitrogen concentrations and biomass increase following urea fertilization (Sullivan and Daiber 1974; Valiela and Teal 1974; Covin and Zedler 1988; Zedler et al. 1992). In the constructed marshes of San Diego Bay, the shorter cordgrass was hypothesized to relate to the lower soil nitrogen content compared to natural marshes (Langis et al. 1991). Consequently, large-scale fertilization of constructed marshes at SMNWR is being considered as a way to obtain tall vegetation and increase habitat suitability for nesting by light-footed clapper rails. However, such plans must also consider the potential effect on population growth of phytophagous insects, such as *Haliopsis spartina*, which might respond positively or negatively to fertilization of their host plants.

Other plant-herbivore systems suggest alternative outcomes of fertilization. It is well documented that nitrogen fertilization and increased foliar ni-

¹ Corresponding author.

trogen can increase phytophagous insect abundance (Pfeiffer and Wiegert 1981; McNeill and Southwood 1982; Bryant et al. 1987; Lightfoot and Whitford 1987; Strauss 1987). Our earlier observations agreed with these studies, as the highest scale abundances in 1992 were found in plots that had been fertilized in 1990 (Pacific Estuarine Research Laboratory unpublished data). Johnson (1991) also found higher abundance of scale insects after fertilizing another constructed marsh in San Diego Bay. Alternatively, others have found that environmentally-stressed plants are more susceptible to major damage by insects (Knerer and Atwood 1973; Mattson and Addy 1975; White 1976; Redak and Cates 1984; White 1984; Mattson and Haack 1987; Louda 1988; Larsson 1989). Low-nitrogen soils at the constructed marshes of SMNWR are likely to stress cordgrass, possibly allowing population growth of *Haliopsis*. Stressed plants may be more nutritious than nonstressed plants because of greater availability of soluble nitrogen and carbohydrates (White 1969, 1974, 1976; Rhoades 1979, 1983). Also, stressed plants, with limited energy and nutrient resources, may allocate less energy to defense (Rhoades 1983), both chemical and mechanical, allowing phytophagous insect populations to grow. Herbivore outbreaks on stressed plants may be due to an imbalance between proximate nutritional quality and defensive capability rather than to changes in proximate nutritional quality alone (Rhoades 1983).

Not knowing how *Haliopsis* might respond to fertilization in SMNWR, further study of nitrogen effects on existing populations of *Haliopsis* was needed. The present study assesses the effects of duration and timing of fertilization on *Haliopsis* abundance throughout the cordgrass growing season. We predicted that fertilization throughout the growing season would produce the greatest cordgrass growth response. However, based on our prior observations and those of Johnson (1991), we hypothesized that prolonged fertilization would stimulate an increase in scale insect populations, resulting in cordgrass damage. We use the terms "damage" and "abundance" interchangeably because more insects lead to more herbivory and more light interception on cordgrass leaves. We also hypothesized that short-term fertilization might increase cordgrass heights without significant growth in *Haliopsis* populations, but that this could depend on the timing of *Haliopsis* dispersal, of which very little was known. In 1993 we set up a field experiment to test these hypotheses, with 10 treatments and 7-fold replication. The treatments included four durations of fertilization, four times of application, and an additional factor:

clearing of dead cordgrass and associated *Haliopsis* eggs at the start of the experiment.

Study Location

Sweetwater Marsh National Wildlife Refuge is located in south San Diego Bay, between 24th Street in National City and E Street in Chula Vista (Fig. 1). The 128-ha complex is composed of both natural and constructed marshes. This study focused on the cordgrass-dominated low marsh of Connector Marsh, created as mitigation for damages during highway and flood control channel construction. Connector Marsh is a series of islands planted with marsh vegetation in 1985, 8 yr prior to this study. It is divided by a flood control channel into two units: 2.1 ha to the north and 2.8 ha to the south. Each of these units was intended to support one breeding pair of light-footed clapper rails (DeWald and Rieger 1982). Paradise Creek, a natural marsh remnant at the north end of the refuge, was used as a reference site because it previously supported clapper rails and has similar hydrology (Langis et al. 1991).

Methods

The experiment was set up on February 27, 1993, using a randomized complete block design in pure cordgrass stands at Connector Marsh. Blocks 1–5 were 40 m long, while blocks 6 and 7 consisted of two 20-m patches because there were not enough 40-m stands. Blocks were used to account for any gradient of effects relative to the flood control channel (e.g., inundation, nutrients, and deposition of water-borne toxic substances) or the natural marsh remnants (Sweetwater Marsh to the south and Paradise Creek to the north) where *Haliopsis* predators are present.

Each treatment plot was 2 m × 2 m, with 2-m buffers between plots. This size plot was large enough to allow sampling within the 0.10 m² central portion without concern for edge effects of fertilizer applications. Within each block, plots were randomly assigned to one of the 10 treatments shown in Fig. 2. The controls, "C" and "CC" (for "cleared control"), differed in the removal of dead cordgrass stems, which were a possible source of "founder" scales (eggs contained in adult tests on dead cordgrass are the source of the next year's starting population). The two 12-application fertilizer treatments ("12" and "C12") differed in the same way.

Urea fertilizer (46% N by weight, CO(NH₂)₂) was broadcast at a rate of 15 g N m⁻² every 2 wk, beginning in mid March. This application rate was above that of Valiela and Teal (1974) [5.2 g N m⁻² biweekly, also used by Covin and Zedler (1988) and Johnson (1991)] and Sullivan and Daiber

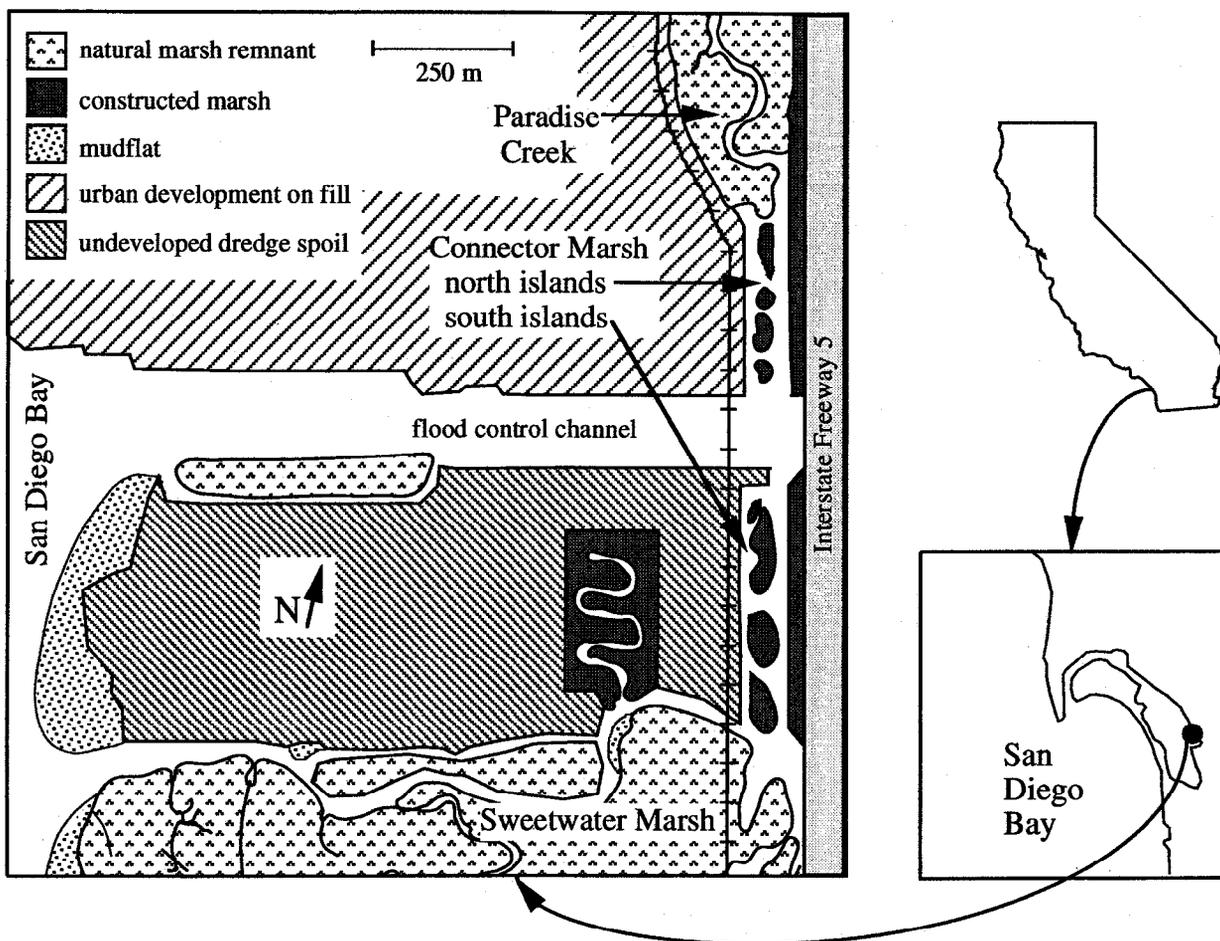


Fig. 1. Location of study at Sweetwater Marsh National Wildlife Refuge, San Diego Bay, San Diego, California (~32°N).

Treatment code	March	April	May	June	July	August
C	Control					
2Mr	2 appl.					
4	4 appl.					
8	8 appl.					
12	12 appl.					
2Ap	2 appl.					
2In	2 appl.					
2Ag	2 appl.					
CC	Control, previous year's dead cordgrass cleared					
C12	Previous year's dead cordgrass cleared 12 appl.					

Fig. 2. Fertilization treatment design. Bars represent duration of fertilization treatments. Urea fertilizer (15 g N m⁻²) was applied every 2 wk at low tide.

(1974, 10 g N m⁻² biweekly); it was chosen because of the high leaching rates of constructed marsh soils (Gibson et al. 1994).

As a natural marsh comparison site, four 6-m long blocks in Paradise Creek marsh were used, receiving only the control and the 12-application treatment. Fewer blocks and treatments were used in the natural marsh to avoid disturbing nesting by the endangered Belding's Savannah sparrow (*Paserculus sandwichensis beldingi*).

Once the first juveniles were observed on the leaves of new cordgrass shoots, biweekly estimates of *Haliopsis* densities began, using abundance classes to estimate numbers per stem: 0 = 0 *Haliopsis*, 1 = 1–9 *Haliopsis*, 2 = 10–99 *Haliopsis*, 3 = 100–999 *Haliopsis*, and 4 = 1,000 or more *Haliopsis*. Where numbers of individuals bordered between two abundance classes, exact counts were made. As total *Haliopsis* population size increased during the season, so did the total number of cordgrass stems. Because we were most interested in the degree of cordgrass damage, determining *Haliopsis* abun-

dance on a per stem basis allowed assessment of damage regardless of changes in total scale population numbers. Means of abundance classes were determined by averaging values for cordgrass stems within each 0.10-m² circular quadrat, then averaging the seven quadrats per treatment. The abundance estimates were continued until September 1993.

Measurements of cordgrass densities, foliar nitrogen, and stem heights were made from March until September. Stems were tallied in each 0.10-m² quadrat. To determine foliar nitrogen levels, four stems per 2 m × 2 m treatment plot were randomly selected. Two meter sticks were placed at right angles at the corner of a treatment plot to locate a random x- and y-coordinate, and the nearest stem was cut at ground level; this was done for all four corners of a plot using the same set of random coordinates in all plots on a sampling date. Stems were never removed from the center 0.10 m². These stems were returned to the laboratory, examined under a dissecting microscope (described below), washed, then dried to a constant mass and ground with a Wiley mill. Total Kjeldahl nitrogen was estimated using the methods described in American Public Health Association (1992). Once per month, we measured the stems in each quadrat from the base to the tip of the longest leaf. The height of the tallest stem per quadrat was used to calculate the average maximum height per treatment.

The stems collected once per month were examined under a dissecting microscope for the presence of eggs and/or juveniles within the adult *Haliaspis* tests, to look for trends we may have missed in the field, and to predict changes in abundance. When we saw abundant juveniles on stems in the laboratory, we expected an increase in adult abundance on the next field sampling date.

Two-way analysis of variance (ANOVA) was used to test for block and treatment effects on *Haliaspis* abundance, maximum stem height, stem density, and foliar nitrogen. Because of the varied timing and duration of fertilization, all 10 treatments were not complete until September (e.g., in July, the August treatment had not yet been applied and long-term treatments were incomplete). Prior to September, equivalent treatments were lumped for analysis (as controls or shorter term durations). Residuals were examined and Levene's tests were performed to insure that data met the assumptions of ANOVA; no transformations were performed. Only in the mean *Haliaspis* abundance data in April were variances heterogeneous; however, these data were not transformed (or tested non-parametrically) to be consistent with the other months analyzed.

If effects were significant in the ANOVAs, the Tukey-Kramer method was used to make multiple comparisons (Sokal and Rohlf 1981). This method is recommended when sample sizes are unequal (Day and Quinn 1989). Unequal sample size was common in this study because of the need to combine data into the same group for analysis when some treatments were still incomplete. Where sample sizes were equal (e.g., September), the Tukey method was used to make multiple comparisons (Tukey 1953).

Simple regression was used to examine the relationship between *Haliaspis* abundance and single predictor variables, such as stem density. The statistics programs, SYSTAT, version 5.2.1 (SYSTAT, Inc. 1992) and SuperANOVA (Abacus Concepts 1989–1990), were used for all analyses.

Results and Discussion

THE NATURAL MARSH

Haliaspis was never abundant in the natural marsh remnant, Paradise Creek. On three occasions, 1–3 newly-settled juveniles were seen on 1–5 cordgrass stems in the control plots in Paradise Creek (Boyer 1994). These individuals were not found during the next sampling session, though the cause of mortality was unclear. No *Haliaspis* were found in the fertilized plots on any sampling date. Nor did Johnson (1991) and Covin and Zedler (1988) find any *Haliaspis* in local natural marshes (Paradise Creek and Tijuana Estuary, respectively) before or after fertilization. Low *Haliaspis* abundance in natural marshes may be due to a variety of factors, including the degree of host-plant stress. Cordgrass with low stress may be unfavorable for *Haliaspis* population growth, possibly because of chemical or mechanical defenses or poor nutrition for the insects. Well-established predator populations are also expected to keep *Haliaspis* numbers low in natural marshes.

THE CONSTRUCTED MARSH

Seasonal Changes in Haliaspis Abundance

It was apparent early in 1993 that *Haliaspis* abundance would be much greater in Connector Marsh than in the natural marsh reference site. A large flood in January washed many of the previous year's dead cordgrass stems and their associated *Haliaspis* eggs out into San Diego Bay, yet in February, *Haliaspis* containing eggs were found throughout the marsh on remaining dead stems. On March 29, 1993, laboratory dissections of adult tests from the previous year's cordgrass revealed abundant eggs and juveniles. In the field, new cordgrass shoots grew rapidly and *Haliaspis* dispersal began. The first juveniles were found on

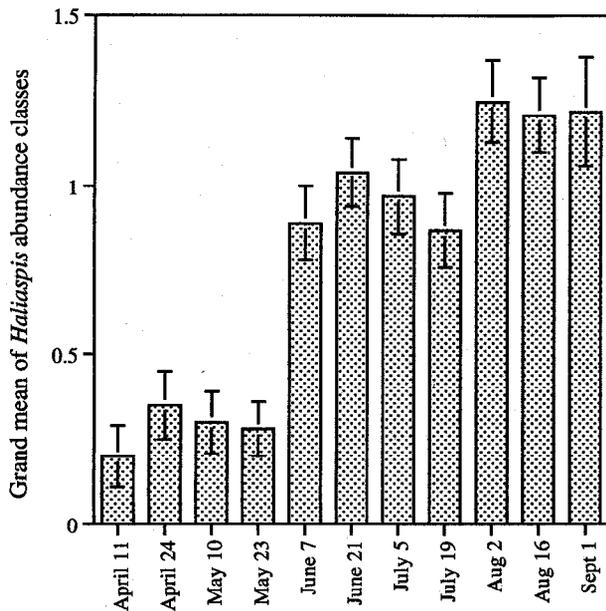


Fig. 3. Grand means of *Haliopsis* abundance classes on cordgrass stems in Connector Marsh, April to September 1993. Means include all fertilization treatments, in seventy 0.10-m² quadrats; error bars represent ± 1 SE

new cordgrass shoots throughout the marsh on April 11–13, 1993.

Mean *Haliopsis* abundance class increased 5-fold from April to September 1993 (Fig. 3). On April 11–13, the 1,639 stems collected from all 70 sample plots (including all treatment and control plots), had a mean abundance class of 0.20 (± 0.09 SE) per stem. Abundance classes ranged from 0 (no scales) to 3 (100–999 scales) per stem. Eleven percent of all stems had at least one scale present (Table 1). Mean *Haliopsis* abundance stayed relatively constant through May.

A marked increase in *Haliopsis* abundance occurred in early June when a large cohort of newly-settled juveniles was seen. Mean abundance class was 0.89 ± 0.11 for 2,092 stems sampled. A 3-fold increase in the number of infested stems had occurred; 60% of all stems sampled had become infested (Table 1), and nearly 30% had moderate levels of infestation (abundance classes 2 or 3). A conservative estimate of the total scale population in the 70 plots (7 m²) used the lowest number in the range of each abundance class (e.g., a stem with an abundance class of 2, which ranges from 10–99 scales, was counted as having 10 scales). Even this low estimate shows a dramatic increase in total scale numbers (Table 1). Stems collected on May 10–11 allowed for prediction of this increase in scale abundance, as 88% of the scale-infested stems returned to the laboratory had eggs present in at least one adult test (Table 2). A month later (June

TABLE 1. Stem densities and numbers of *Haliopsis*-infested stems in seventy 0.10-m² quadrats in Connector Marsh, April to September 1993.

Date	Total Stems in 7 m ²	Number of Infested Stems in 7 m ²	% Infested	Minimum Number of <i>Haliopsis</i> Talled in 7 m ²
April 11	1,639	186	11	1,626
May 10	1,665	398	24	956
June 7	2,092	1,249	60	9,772
July 5	2,419	1,668	69	10,011
August 2	2,322	1,802	78	26,732
September 1	3,022	2,456	81	20,780

7–9), only 13% of the scale-infested stems collected had eggs, indicating that a large dispersal of juveniles had occurred prior to this time. No pattern relative to either block or nitrogen treatment was apparent from the laboratory dissections, suggesting that juveniles had dispersed uniformly and relatively synchronously throughout the marsh.

In July, the number of new cordgrass shoots increased rapidly, as did the number of stems being infested (Table 1). These newly-infested stems had low scale abundance (class 1), causing a drop in the mean by the end of July (Fig. 3). However, a second major dispersal pulse was occurring, though it was not apparent in the field until early August. Our conservative estimate of the total number of scales present in the 70 sample plots increased from 10,011 individuals to 26,732 from July 5 to August 2 (Table 1). An increase in mean abundance class was also apparent (1.25 ± 0.12 for 2,322 stems), suggesting an increase in damage to cordgrass. For the first time in 1993, class 4 abundances were seen, with five plants having over 1,000 scales. Seventy-eight percent of all stems had *Haliopsis* present; 39% had moderate to high levels (abundance classes 2–4). The number of stems did not increase from the previous sampling period, but there were more stems in abundance classes 2 and 3 (and 4). As in June, this increase in scale abundance was predicted from stems brought to the laboratory on July 6–8: 62% of the scale-infested stems had eggs present in at least one adult test, a large increase from 13% a month earlier (Table

TABLE 2. Eggs present in adult *Haliopsis* tests on stems examined under dissecting microscope.

Date	Number Stems Collected	Number Stems with Scales and % of Total	Number Stems with Eggs and % Relative to Stems with Scales
May 10	224	97 (43%)	85 (88%)
June 7	128	108 (84%)	14 (13%)
July 5	140	125 (89%)	77 (62%)
August 2	135	114 (84%)	56 (49%)
September 1	84	68 (81%)	56 (82%)

2). By the August 2–4 stem collection, 49% of the scale-infested stems had eggs present in at least one adult test. This confirms that a second hatch and dispersal pulse occurred in July, in agreement with the increased population size seen in the field.

By September 1, 81% of the stems sampled were infested with *Haliaspis* (Table 1), with 40% moderately infested (abundance classes 2 or 3). These percentages and the mean abundance class value of 1.22 ± 0.16 were very similar to those for August 2. While the number of infested stems increased greatly (1,802 on August 2 to 2,456 on September 1), the number of stems overall increased at a similar rate (2,322 to 3,022), keeping the mean constant. By September, the percentage of infested stems with eggs present was high again, at 82% (Table 2). Broods of eggs diapause and overwinter within their mother's tests. The eggs present in September were likely to overwinter, as cordgrass was senescing.

In summary, establishment of *Haliaspis* on new cordgrass stems began around April 1, 1993, throughout Connector Marsh. These individuals matured and produced eggs; juveniles dispersed in late May in a large pulse that increased mean *Haliaspis* abundance dramatically. A second dispersal pulse occurred in late July, though it is unclear whether these juveniles emerged from the first or second generation of adults, or both. Dispersal was occurring at a lower rate throughout the season in addition to these two large pulses.

Fertilization Effects in the Constructed Marsh

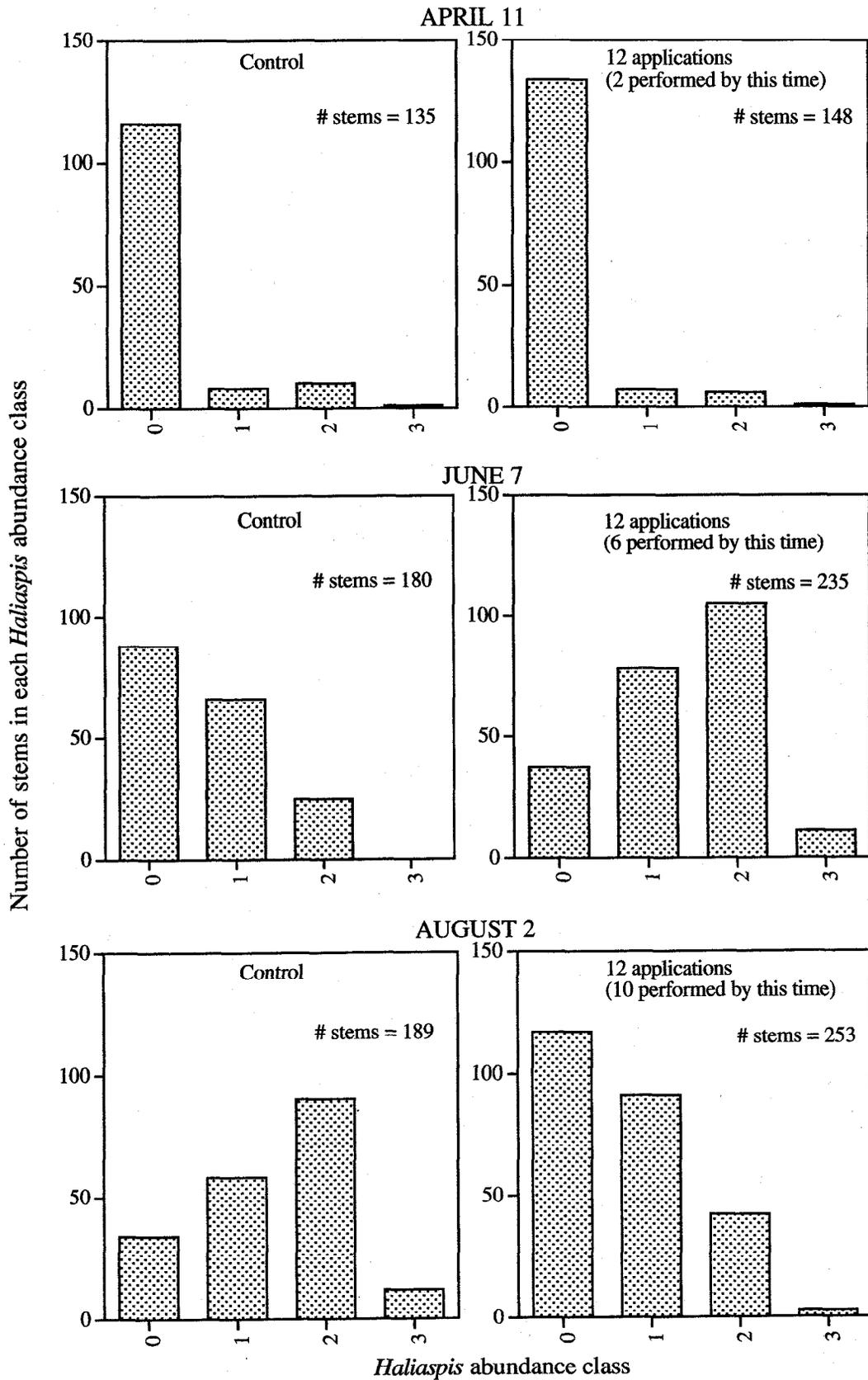
Although we predicted that the greatest increase in *Haliaspis* abundance would result from the longest application of nitrogen (12 applications), this was not what we found. The total number of stems in each *Haliaspis* abundance class for this treatment was compared to the control in April, June, and August (Fig. 4). In April, the plots were quite similar, with large numbers of stems having no scales and only a few plants having >100 scales. Nitrogen had been applied twice at that time. In June, after the first dispersal pulse had occurred and six of the 12 applications had been performed, the fertilized plots had many more infested stems than the control and more stems had >100 scales. This trend reversed in August: the control plots developed a larger number of infested stems and more stems had abundance classes

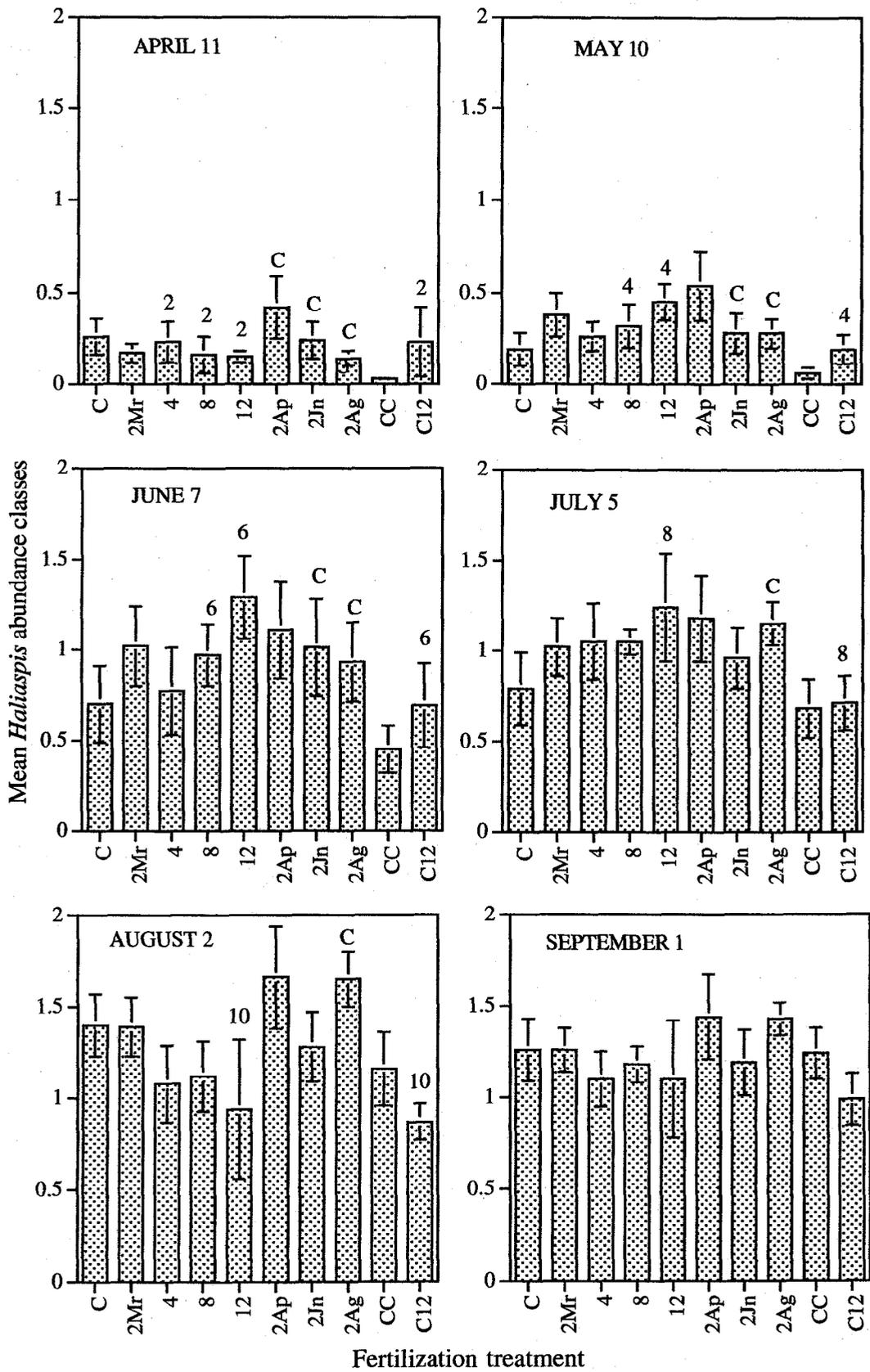
of 2 or 3; the long-term fertilized plots had fewer infested stems than in June and fewer stems in the higher abundance classes than before. These patterns found in August continued in September. Although *Haliaspis* establishment was greater with long-term fertilization in June, many of these individuals did not remain on the cordgrass. Once *Haliaspis* settles and begins feeding, it cannot leave. Thus, losses in the fertilized plots must have been due to mortality. Plants in the fertilized plots may have become more resistant or less nutritious, or predation may have been higher there.

The comparison of all timing and duration treatments was more complex (Fig. 5). Treatment plots fertilized only in the late season were equivalent to the control (no modification) before that time. These are noted with the letter "C" above the bars in Fig. 5. For the longer duration treatments, the actual number of applications completed at the time of sampling is noted in the figure. For example, on April 11, the 4-, 8-, and 12-application treatments had all only been fertilized twice.

We hypothesized that fertilization might stimulate *Haliaspis* population growth if it preceded *Haliaspis* dispersal. We also predicted that as nitrogen application continued, *Haliaspis* populations would increase. As seen in the histograms in Fig. 4, Fig. 5 shows initially higher population growth in the longer term fertilized plots relative to the controls, then a reverse in this trend by the later season. Two-way ANOVAs (with block and treatment as factors) performed for the first date each month through September yielded treatment effects on May 10 and August 2 ($p < 0.05$). Significant differences in May were largely due to the relatively high mean for the April treatment (2Ap), which was high before any fertilization occurred, and the very low mean in the cleared control plots (CC), discussed in a subsequent section. On August 2, while significant differences among treatments were detected by the ANOVA, the multiple comparison (Tukey-Kramer) did not detect differences. The Tukey-Kramer method is conservative (Hayter 1984); it increases the probability of Type II errors because the error rate per comparison is decreased to hold the experiment-wise error rate at or below the 5% level (Day and Quinn 1989). Examining the ranking of the treatments, the 12-application treatment (10 applications at that time) had the lowest mean *Haliaspis* abundance, followed by the 4- and 8-application treatments (Fig. 5). The controls (C and 2Ag, which had not

Fig. 4. Numbers of stems in each *Haliaspis* abundance class for the control and the 12-application treatment in April, June, and August 1993. Number of stems in seven 0.10-m² quadrats is shown in the upper right of each graph.





yet been fertilized) and single-month applications (2Mr, 2Ap, and 2Jn) had the highest mean *Haliaspis* abundances.

Contrary to our predictions, these data suggest that fertilization over a long period had a negative effect on *Haliaspis* population growth. No distinction can be made between effects of single-month applications, or between the single months and the control. There was no evidence of increased *Haliaspis* abundance in response to fertilization by the end of the season. This suggests that the large-scale fertilization proposed for increasing cordgrass heights and improving clapper rail habitat in Connector Marsh will not stimulate further outbreaks of *Haliaspis*.

Potential Causes

To help explain patterns of *Haliaspis* abundance, stem density, foliar nitrogen, and maximum stem height were examined. Root (1973) found areas of high plant density to be more likely to support folivorous insects, and that existing populations were more likely to stay where host plants were concentrated. However, other studies have not shown this trend (Bach 1980; McLain 1981; Solomon 1981). Stem density and *Haliaspis* abundance were not found to be related in any month (linear regressions, $p > 0.05$), though a delayed response to stem density may have occurred. In July, the plots fertilized most had the highest stem densities, and the controls had the lowest (Boyer and Zedler in preparation). In the following month, mean scale abundance was lowest where stem density was highest in July. This suggests that *Haliaspis* abundance per stem may have decreased in response to increased stem density, but not because of recruitment of new stems at a higher rate than *Haliaspis* populations grew. On the contrary, while stem density in the 12-application treatment plots in June was high relative to that of the control (235 stems and 180 stems, respectively; Fig. 4), few stems had >100 scales. The increase of only 18 stems in the fertilized plots from June to August indicates that mean *Haliaspis* abundance by August was not artificially reduced by recruitment of new, unfested stems in the fertilized plots. Although we do not know what reduced *Haliaspis* abundance in the fertilized plots, cordgrass there was quite rigid and leaves were very sharp-edged. The dense, robust stems may have abraded *Haliaspis*

individuals from the leaves (particularly juveniles, which seemed to be less firmly attached than adults).

Foliar nitrogen has been found to be a good measure of plant nutritional quality since nitrogen, or protein, can be limiting in the growth and reproduction of phytophagous insects (McNeill and Southwood 1978; Mattson 1980). However, late in the season (September), we found a significant negative relationship between mean *Haliaspis* abundance and mean leaf foliar nitrogen, though foliar nitrogen accounted for little variability in *Haliaspis* abundance (linear regression, $p = 0.01$, $r = -0.40$, $r^2 = 0.16$). As mean foliar nitrogen ranked according to the amount of nitrogen added (Boyer and Zedler in preparation), the positive effect of fertilization on foliar nitrogen may have led to a decline in mean *Haliaspis* abundance. As discussed previously, enrichment of low-nitrogen soils may relieve nitrogen-limitation stress, while decreasing susceptibility to insect herbivory.

Alternative or additional explanations for *Haliaspis* distribution pertain to predators. First, *Haliaspis* predators may have been attracted to denser patches of cordgrass because of the potential for a greater concentration of prey. If this occurred, then there apparently was a delayed response of the predators to increased stem density (as in Morris 1964), since mean scale abundance was lowest in August in the long-term fertilized plots, where stem density was highest in July. Second, taller cordgrass stems in the long-term fertilized plots may have attracted more predators of *Haliaspis*. Previous work by Williams (1990) suggests that a major predator of *Haliaspis*, a coccinellid beetle (*Coleomegilla fuscilabris*), requires tall plants as high-tide refuges. In August and September, average maximum stem height ranked according to the amount of nitrogen applied (Boyer and Zedler in preparation). *Haliaspis* abundance was lowest where stems were tallest; hence, stem height may have played a role in the reduction of *Haliaspis* in the fertilized plots, perhaps by providing high-tide refuges for the predatory beetle.

The results reported here are part of a larger study assessing patterns of *Haliaspis* infestation in marshes of different age, at sites with various degrees of inundation, and at sites at various proximities to a natural marsh supporting native predators (Boyer 1994). None of these variables seemed to be as strongly related to scale density as

Fig. 5. Means of mean *Haliaspis* abundance classes by treatment in Connector Marsh, April to September 1993. Means include seven 0.10-m² quadrats; error bars represent ± 1 SE. Incomplete treatments are indicated above bars with actual weeks fertilized. The letter C represents treatments not performed to date (equivalent to controls).

stem height, stem density, and foliar nitrogen levels.

*Effects of Clearing Cordgrass With Founder *Haliopsis**

It was hypothesized that if *Haliopsis* has limited dispersal abilities, the removal of a founder source might influence the results of nitrogen fertilization and reduce its abundance. However, while the cleared control (CC) had low scale abundance early in the season, this was short-lived (Fig. 5). No effect of clearing the plots was seen, as the control (C) was never significantly different in mean *Haliopsis* abundance from the cleared control (ANOVA, $p < 0.05$; Tukey-Kramer, $p > 0.05$), nor did the cleared and uncleared treatments receiving 12 applications differ in *Haliopsis* abundance. These results suggest that clearing dead stems with founder scales in small areas (2m \times 2m plots) does not deter scale population growth. Some dead plant material with founder scales may have been obscured by algae and left in the plots at the time of clearing. On the other hand, dispersal of eggs or juveniles on the surface of the water, by wind, or by crawling from stem to stem may be sufficient for widespread dispersal of *Haliopsis*.

Comparison of Constructed and Natural Marsh

As very few *Haliopsis* were found in Paradise Creek, cordgrass there may have had lower stress levels than Connector Marsh, possibly providing poorer nutrition or greater defense. Although we did not measure nitrogen-limitation stress directly, our data suggest that nitrogen-stress was lower in Paradise Creek. We found a smaller difference in foliar nitrogen between the fertilized and unfertilized plots in Paradise Creek than in Connector Marsh, and that the control quadrats had consistently higher foliar nitrogen than those in Connector Marsh (Boyer and Zedler in preparation). Fertilization did not significantly increase stem height or stem density in Paradise Creek (ANOVA, $p > 0.05$). These data suggest that cordgrass stands in the natural marsh were not highly nitrogen-limited. As other studies of natural cordgrass marshes have shown the contrary (Sullivan and Daiber 1974; Valiela and Teal 1974; Covin and Zedler 1988; Zedler et al. 1992), we suggest that nutrient contributions of the large flood in January 1993 may have decreased nitrogen-limitation throughout the marshes of SMNWR. Still, in years with presumably smaller nutrient inputs from flooding events, natural marsh soils have had higher nitrogen levels than constructed marshes (Langis et al. 1991). Higher soil nitrogen levels (and reduced cordgrass stress) may at least partly contribute to

poor *Haliopsis* establishment in the natural marsh. Clearly, other factors contribute to control of *Haliopsis* in the natural marsh, such as well-established predator populations.

Conclusions

In the constructed marshes of San Diego Bay, nitrogen fertilization is desirable to achieve tall cordgrass needed for nesting by the endangered light-footed clapper rail. The results of this study suggest that fertilization may proceed in the constructed marshes of San Diego Bay without fear of promoting growth of the existing scale insect population.

Contrary to our prediction, nitrogen fertilization did not exacerbate *Haliopsis* damage to cordgrass in the constructed Connector Marsh. In fact, long-term fertilization (10 applications over 20 wk) appeared to reduce *Haliopsis* densities relative to the controls by August. While early-season establishment of *Haliopsis* was greater in the 12-application treatment plots (six applications at that time) than in the controls, this trend in abundance reversed by August, when the control plots contained many more stems infested with large numbers of *Haliopsis* than the long-term fertilized plots. Mean abundance per stem also became lowest in the long-term fertilized plots.

Lower *Haliopsis* abundance per stem by the late season in the fertilized plots may have been due to one or more of the following: increased predation, facilitated by high tide refugia in tall plants; dislodging of *Haliopsis* (particularly juveniles) through abrasion of sharp-edged leaves; more difficult stylet penetration and prolonged attachment on hardened leaf tissue; or, relief from nitrogen-limitation stress, possibly leading to lower availability of soluble nitrogen, carbohydrates, and/or increased chemical defenses.

We documented temporal changes in *Haliopsis* abundance that were previously undescribed. In 1993, establishment of *Haliopsis* on new cordgrass shoots in Connector Marsh began around April 1; juveniles matured, produced eggs, and dispersed their young in two main pulses (late May and late July). Although we hypothesized that timing of *Haliopsis* dispersal might influence the end result of the fertilization experiment, it had no apparent effect.

ACKNOWLEDGMENTS

We thank Kevin Gibson for helping to set up the experiment, Boyd Collier for statistical advice, and Kathy Williams and Doug Stow for improving early versions of the manuscript. Donovan McIntire provided expertise on local insects and Raymond Gill at the California Department of Food and Agriculture confirmed insect identification. This project was funded in part by a grant from the National Sea Grant College Program, National

Oceanic and Atmospheric Administration, United States Department of Commerce, under grant numbers NA89AA-D-SG138 and NA36RG0537, project number R/NP-1-21E through the California Sea Grant College, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration or its sub-agencies. The United States Government is authorized to reproduce and distribute for governmental purposes. A grant from the County of San Diego Fish and Wildlife Advisory Commission also supported this work.

LITERATURE CITED

- AMERICAN PUBLIC HEALTH ASSOCIATION. 1992. Standard Methods for the Examination of Water and Wastewater, 18th edition. American Public Health Association, American Water Works Association, Water Pollution Control Federation, Washington, D.C.
- BACH, C. E. 1980. Effect of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata* (Fab.). *Ecology* 61:1515-30.
- BOYER, K. E. 1994. Scale insect damage in constructed salt marshes: Nitrogen and other factors. M.S. Thesis, San Diego State University, San Diego, California.
- BRYANT, J. P., T. P. CLAUSEN, P. B. REICHARDT, M. C. MCCARTHY, AND R. A. WERNER. 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortix (*Choristoneura conflictana* (Walker)). *Oecologia* 73: 513-517.
- COVIN, J. D. AND J. B. ZEDLER. 1988. Nitrogen effects on *Spartina foliosa* and *Salicornia virginica* in the salt marsh at Tijuana Estuary, California. *Wetlands* 8:51-65.
- DAY, R. W. AND G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59:433-463.
- DEWALD, J. M. AND J. RIEGER. 1982. Restoration of a degraded salt marsh: Objectives and techniques. California Department of Transportation, Environmental Analysis Branch. San Diego, California.
- GIBSON, K. D., J. B. ZEDLER, AND R. LANGIS. 1994. Limited response of cordgrass (*Spartina foliosa*) to soil amendments in a constructed marsh. *Ecological Applications* 4:757-767.
- HAYTER, A. J. 1984. A proof of the conjecture that the Tukey-Kramer multiple comparison procedure is conservative. *Annals of Statistics* 12:61-75.
- JOHNSON, K. M. 1991. The effects of host quality on a phytophagous insect (Homoptera: Delphacidae) and its predators in a California salt marsh. M.S. Thesis, San Diego State University, San Diego, California.
- KNERER, G. AND C. E. ATWOOD. 1973. Diprionid sawflies: Polymorphism and speciation. *Science* 179:1090-1099.
- LANGIS, R., M. ZALEJKO, AND J. B. ZEDLER. 1991. Nitrogen assessments in a constructed and a natural salt marsh of San Diego Bay, California. *Ecological Applications* 1:40-51.
- LARSSON, S. 1989. Stressful times for the plant stress-insect performance hypothesis. *Oikos* 56:277-283.
- LIGHTFOOT, D. C. AND W. G. WHITFORD. 1987. Variation in insect densities on desert creosotebush: Is nitrogen a factor? *Ecology* 68:547-557.
- LOUDA, S. M. 1988. Insect pests and plant stress as considerations for revegetation of disturbed ecosystems, p. 51-67. In J. Cairns (ed.), *Rehabilitating Damaged Ecosystems*. Vol II. CRC Press, Boca Raton, Florida.
- MCLAIN, D. K. 1981. Resource partitioning by three species of hemipteran herbivores on the basis of host plant density. *Oecologia* 48:414-7.
- MCNEILL, S. AND T. R. E. SOUTHWOOD. 1982. The role of nitrogen in the development of insect/plant relationships, p. 77-88. In J. B. Harborne (ed.), *Biochemical Aspects of Plant and Animal Coevolution*. Academic Press, London.
- MACDONALD, K. 1990. South San Diego Bay Enhancement Plan, Vol. 1 Resource Atlas, San Diego Unified Port District, San Diego, California.
- MATTSON, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119-161.
- MATTSON, W. J. AND N. D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515-522.
- MATTSON, W. J. AND R. A. HAACK. 1987. The role of drought stress in provoking outbreaks of phytophagous insects, p. 365-407. In P. Barbosa and J. C. Schultz (eds.), *Insect Outbreaks*. Academic Press, San Diego, California.
- MORRIS, R. F. 1964. The value of historical data in population research with particular reference to *Hyphantria ucineta* Drury. *Canadian Entomologist* 96:356-368.
- PFEIFFER, W. J. AND R. G. WIEGERT. 1981. Grazers on *Spartina* and their predators, p. 87-112. In L. R. Pomeroy and R. G. Wiegert (eds.), *The Ecology of a Salt Marsh*. Springer-Verlag, New York.
- REDAK, R. A. AND R. G. CATES. 1984. Douglas-fir (*Pseudotsuga menziesii*) -spruce budworm (*Choristoneura occidentalis*) interactions: The effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. *Oecologia* 62:61-67.
- RHOADES, D. F. 1979. Evolution of plant chemical defense against herbivores, p. 3-54. In G. A. Rosenthal and D. H. Janzen (eds.), *Herbivores: Their Interactions with Secondary Plant Metabolites*. Academic Press, London.
- RHOADES, D. F. 1983. Herbivore population dynamics and plant chemistry, p. 155-220. In R. F. Denno and M.S. McClure (eds.), *Variable Plants in Natural and Managed Systems*. Academic Press, New York.
- ROOT, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124.
- SOLOMON, B. P. 1981. Response of a host-specific herbivore to resource density, relative abundance and phenology. *Ecology* 62:1205-1214.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman and Company, New York.
- STRAUSS, S. 1987. Direct and indirect effects of host-plant fertilization on an insect community. *Ecology* 68:1670-1678.
- SULLIVAN, M. J. AND F. C. DAIBER. 1974. Response in production of cordgrass, *Spartina alterniflora*, to inorganic nitrogen and phosphorus fertilizer. *Chesapeake Science* 15:121-123.
- ABACUS CONCEPTS. 1989-90. Super ANOVA. Abacus Concepts. Berkeley, California.
- SYSTAT INC. 1992. SYSTAT, version 5.2.1. SYSTAT, Inc. Evanston, Illinois.
- TUKEY, J. W. 1953. Some selected quick and easy methods of statistical analysis. *Transactions of the New York Academy of Science*, Series 2, 16:88-97.
- VALIELA, I. AND J. M. TEAL. 1974. Nutrient limitation in salt marsh vegetation, p. 547-563. In R. J. Reimold and W. H. Queen (eds.), *Ecology of Halophytes*. Academic Press, New York.
- WHITE, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50:905-909.
- WHITE, T. C. R. 1974. A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia* 16:279-301.
- WHITE, T. C. R. 1976. Weather, food and plagues of locusts. *Oecologia* 22:119-134.
- WHITE, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63:90-105.

- WILLIAMS, K. 1990. Control of scale insect infestation at Chula Vista Wildlife Reserve. Project Report for Entrix and San Diego Unified Port District. San Diego, California.
- ZEDLER, J. B., C. S. NORDBY, AND B. E. KUS. 1992. The ecology of Tijuana Estuary: A national estuarine research reserve. National Oceanic and Atmospheric Administration Office of Coastal Resource Management, Sanctuaries and Reserves Division, Washington, D.C.

- ZEDLER, J. B. 1993. Canopy architecture of natural and planted cordgrass marshes: Selecting habitat evaluation criteria. *Ecological Applications* 3:123-138.

Received for consideration, August 29, 1994
Accepted for publication, April 25, 1995