

PHENOLOGY OF EELGRASS, *ZOSTERA MARINA* L., ALONG LATITUDINAL GRADIENTS IN NORTH AMERICA

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ABSTRACT

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Eelgrass, *Zostera marina* L., was collected monthly from 1976 to 1979 and its phenology compared in the distributional range on both coastlines of North America. Each of three reproductive phenophases (initial appearance of macroscopically visible flower buds, initial anthesis, initial appearance of visible fruits) differed significantly among the sites in their dates of occurrence. Among the sites, flowering at the same latitude was later in the Atlantic than in the Pacific and flowering along a latitudinal gradient occurred increasingly later at more northern latitudes in the Atlantic than in the Pacific. Although the reproductive periodicity probably is controlled primarily by water temperature at the different sites, the variation in timing at the same latitude among Pacific and Atlantic sites indicates that *Z. marina* may include genotypes with different temperature requirements that are selectively adapted to different habitats along the latitudinal gradients.

INTRODUCTION

The reproductive periodicity of eelgrass, *Zostera marina* L., has been studied by a series of investigators. Setchell (1929) examined collections on both coasts of North America between 1921 and 1924 and concluded that anthesis and seed production occurred only between 15–20°C. Several subsequent investigations, including those of Tutin in England (1938), McRoy in Alaska (1970), Felger and McRoy in the Sea of Cortez, Mexico (1975) and Churchill and Riner in New York (1978), supported the conclusions of Setchell and reported anthesis and seed production at or above 15°C. Several other investigators, however, reported that flowering occurred at temperatures below those listed by Setchell. Phillips (1972) reported that anthesis in Puget

Sound, Washington, occurred with water temperature at 7–9°C and that seeds matured at 11–14°C. Harrison and Mann (1975) indicated flowering under conditions of 8–9°C in Nova Scotia, and Jacobs and Pierson (1981) reported flowering at water temperatures of 10–15°C at Roscoff, France. The differences in the reported temperatures and the phenology patterns have raised questions concerning the role of other environmental conditions, such as photoperiod, and the possible role of genetic variation among the diverse populations of *Z. marina*.

To further assess reproductive periodicity in *Z. marina*, a phenological study was initiated in 1976 that involved monthly collections on both coastlines of North America. Three collecting stations were selected to represent distributional and environmental gradients on each coast. The inclusion of Puget Sound on the west coast and Nova Scotia on the east coast permitted further studies at sites where flowering had been reported at temperatures below those indicated above by Setchell. The continuous sampling from 1976 to 1979 allowed an evaluation of the annual variation in reproductive periodicity.

MATERIALS AND METHODS

Collections of short shoots were made monthly at each of six major stations (Fig. 1). The range of collection dates varied slightly among the sites: Atlantic: Halifax, Nova Scotia, Canada, lat. 45°N, 1 January 1976–13 May 1979; Charlestown and Quonchontaug Ponds, RI, Lat. 41°N, 21 February 1976–10 June 1979; Beaufort, NC, lat. 35°N, 25 February 1976–24 February 1979. Pacific: Izembek Lagoon, AK, lat. 56°N, 4 May 1976–27 April 1979; Puget Sound, WA, lat. 48°N, 10 February 1976–15 May 1979; Aqua Hedionda Lagoon, San Diego, CA, lat. 33°N, 22 July 1976–24 May 1978. At the last site on the Pacific, San Diego, two earlier collections were available, 9 February and 6 April 1974. In Alaska, samples also were taken at Sitka, lat. 57°N, in 1978 and at Auke Bay, lat. 58°N, in 1978 and 1979. At each site, the monthly collections included 50 short shoots, along with water temperature and salinity readings, from a shallow seagrass meadow that was not affected by thermal stress, sewage or other human activities. In Puget Sound, subtidal populations were sampled also. The collections of short shoots were shipped to Seattle in 10% formalin (in seawater) for an evaluation of phenology. Voucher specimens of the short shoots were deposited in the Seattle Pacific University Herbarium.

Of 14 phenophases that were analyzed (Phillips, 1976), three were pertinent to the study of reproductive periodicity. The dates of these three phenophases (initial appearance of macroscopically visible floral buds, initial appearance of anthesis, initial appearance of macroscopically visible fruits), along with site, latitude, water temperature and salinity, were evaluated with a series of computer programs at the University of Texas and the University of Hawaii. Latitude, ocean (Pacific and Atlantic) and site were designated as predictors and the phenophase date, temperature and salinity as criteria (variables to be predicted).

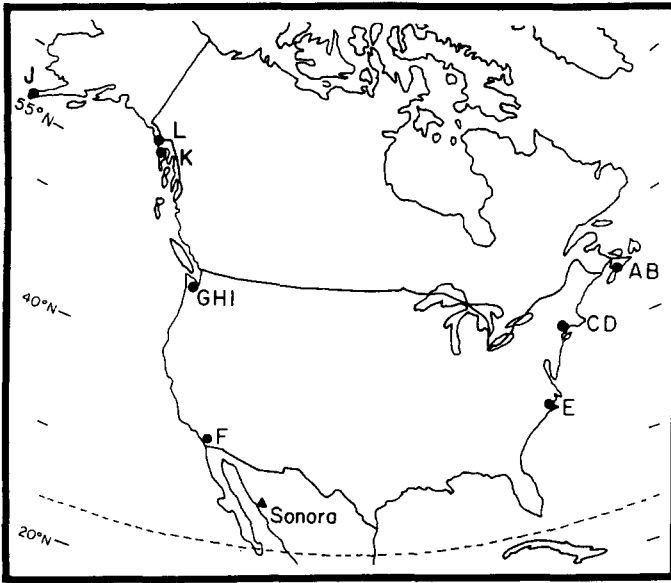


Fig. 1. Map of North America showing phenology sites: Conrad Beach (A) and Peggy's Cove (B), Halifax, Nova Scotia, Canada; Charlestown Pond (C) and Quonchontaug Pond (D), Rhode Island; Beaufort (E), North Carolina; San Diego (F), California; Puget Sound, subtidal, Edmonds (G) and Anderson Beach (H), and intertidal, Young's Beach (I), Washington; Izembek Lagoon (J), Sitka (K) and Auke Bay (L), Alaska. The southernmost distribution of *Zostera marina* on the Atlantic Coast is at the Beaufort site, but on the Pacific Coast is south of the San Diego site on the Sonora, Mexico, coast of the Sea of Cortez (▲).

A series of linear predictive models were constructed from descriptive and inferential analyses. The descriptive analyses were used to determine the characteristics of each of the sites and the average characteristics of any given site. Inferential analyses were used to determine site differences in criteria and general criterial relationships involving latitude and ocean. Both analyses of variance (ANOVA) for site differences and linear regressions for differences due to latitude or ocean were included, but linear regressions were performed only if ANOVA results indicated significant site variation at less than $P = 0.1$ for the dependent variable (date, temperature or salinity at phenophase occurrence).

Three linear predictive models were used to determine the dissimilarity between Atlantic and Pacific sites:

$$Y = c_1A + c_2P + c_3AL + c_4PL$$

$$Y = c_1A + c_2P + c_3L$$

$$Y = c_1 + c_2L$$

where Y is the criterion (date, temperature or salinity at phenophase occurrence), A is a location variable (Atlantic site); P is a location variable (Pacific site), L is the latitude of the site and c_1 , c_2 , c_3 and c_4 are constants. In each of the models, the Julian date for a phenophase occurrence was used as a criterion.

TABLE I

Variation in dates of three reproductive phenophases and accompanying water temperatures at each of six phenological sites^a

Site	Year	Date of initial appearance of visible floral buds	Temperature (°C)	Date of initial anthesis	Temperature (°C)	Date of first visible fruit	Temperature (°C)
Atlantic							
Halifax, Nova Scotia, Canada ^b	1976	1 May	15	26 May	10	23 June	23
	1977	29 June	20	9 July	19	14 August	20
	1978	17 May	10	24 June	20	30 July	18
	1979	13 May	15	*	*	*	*
Rhode Island,							
Charlestown Pond	1976	19 April	9	19 April	9	—	—
	1977	—	—	23 June	21	—	—
	1978	—	—	—	—	19 June	20
	1979	10 May	21	—	—	10 June	23
Quonochontaug Pond	1976	19 April	8	19 April	8	15 June	20
	1977	27 April	11	23 June	19	—	—
	1978	30 March	6	—	—	19 June	21
	1979	10 May	21	—	—	10 June	23
Beaufort,							
North Carolina	1976	—	—	—	—	—	—
	1977	19 March	17	—	—	16 May	25
	1978	27 February	5	14 April	18	28 May	25
	1979	24 February	7	*	*	*	*
Pacific							
Izembek Lagoon, Alaska ^c	1976	23 June	19	7 July	16	5 August	17
	1977	5 June	11	8 July	13	28 July	14
	1978	5 June	8	26 June	10	17 July	16
	1979	13 April	10	*	*	*	*
Puget Sound, Washington ^d	1976	29 April	8	9 June	11	22 July	18
	1977	5 April	10	30 April	10	20 June	13
	1978	15 March	9	1 April	10	1 May	16
	1979	23 April	9	—	—	*	*

Table I (continued)

San Diego, California	1974	9 February	14	—	—	6 April	15
	1976	February ^e	—	—	—	—	—
	1977	—	—	—	—	19 July	18
	1978	—	—	*	*	*	*

^a The collection dates differed slightly among the six phenological sites; therefore, the variation in data within a month reflect collection dates rather than actual phenological variation. Phenological collections were terminated on different dates: 13 May 1979, Nova Scotia; 10 June 1979, Rhode Island; 24 February 1979, North Carolina; 27 April 1979, Alaska; 15 May 1979, Washington and 24 May 1978, San Diego. The phenophases and temperatures that would have occurred after the last dates of collection are indicated by (*).

^b Phenology data were collected at both Conrad Beach and at Peggy's Cove in Halifax. The earliest dates each year for the reproductive phenophases are those for Conrad Beach. Dates for both sites are included in Figs. 2, 3, and 4.

^c Two additional sites in Alaska were studied: Sitka, lat. 57°N, in 1978, and Auke Bay, lat. 58°N, in 1978 and 1979. Data for reproductive phenophases at these two sites are included in Figs. 2 and 4; dates for initial anthesis were not recorded and were not available for comparison in Fig. 3.

^d Phenology data were recorded in subtidal and intertidal sites in Puget Sound. Subtidal populations were studied from 1976 to 1979 and intertidal populations were studied from 1977 to 1979. The earliest dates for the reproductive phenology are shown above; dates for both subtidal and intertidal phenology are included in Figs. 2, 3, and 4.

^e The February date for the initial appearance of visible floral buds was not recorded by the collector at San Diego.

RESULTS

Site variation

The water temperatures that were recorded with the monthly phenological samples showed a wider range for the Atlantic sites. At Halifax, Nova Scotia, the temperatures ranged from 0.2 to 29°C, at the Rhode Island sites from 2 to 29°C and at Beaufort, NC, from 5–30°C. Among the Pacific sites, the least annual variation was found at San Diego, 14–18°C. The Puget Sound site had temperatures that ranged from 6–19°C and the Izembek Lagoon site from -2–19°C. The temperature progressions among the sites following winter minima showed that higher water temperatures occurred earlier in the Pacific than in the Atlantic and that the north–south differences in water temperature were smaller in the Pacific than in the Atlantic.

Salinities varied in the shallow seagrass beds as a consequence of intermittent precipitation and did not show seasonal progressions that related to temperature. The range of salinities at the Pacific sites was 18–30‰ at Puget Sound and 11–30‰ at Izembek Lagoon (no salinity data were recorded at San Diego). The range at the Atlantic sites included 30–36‰ at Beaufort, 24–32‰ at the Rhode Island ponds and 5–35‰ at Halifax.

Variation in reproductive phenophases

The dates of occurrence of each of the three reproductive phenophases showed wide within-site variation during the years of observation (Table I). Some of this may reflect the varying dates of collection. For example, both the initial appearance of visible floral buds and the initial anthesis were detected in the Rhode Island sampling of 19 April 1976. Because the records were made monthly, the floral buds in the Rhode Island plants probably had appeared between the March and April collections. The sampling at Puget Sound in 1978 included the earliest dates for two phenophases, the initial appearance of visible floral buds and the initial anthesis, recorded at that site during the four-year comparison and the separation of the dates of the two phenophases at Puget Sound was facilitated by sampling at less than a month's interval. Because of the variation in the records of the three reproductive phenophases, the occurrence of a phenophase in the data base ranged from one to four for a collection site.

Both intertidal and subtidal seagrass beds were studied in Puget Sound. For the two intertidal sites, reproductive phenophases were recorded at Young's Beach, but only vegetative phenophases were collected at Anderson Beach. Reproductive phenophases were recorded at both subtidal sites, Anderson Beach and Edmonds. Although the data were insufficient for comparisons of each year, the dates for the three reproductive phenophases during 1978 at the subtidal Anderson Beach site occurred approximately one month earlier than at the intertidal Young's Beach site.

Relationship of site, latitude, temperature and salinity to phenophase

Reproductive phenophases occurred earlier in the year at the southernmost sites on both coasts and occurred progressively later in the year toward the north (Table I; Figs. 2, 3, 4). Initial visible floral buds were recorded at the southernmost sites, San Diego, CA, and Beaufort, NC, in February and March and at the northernmost sites, Halifax, Nova Scotia, and Izembek Lagoon, AK, in April, May and June. At the latitudinally-intermediate sites, visible floral buds were initially recorded in March, April and May.

The latitudinal progression along both coasts showed wide year-to-year variation in reproductive periodicity (Table I). In 1977, the dates of the initial appearance of visible floral buds were clearly separated for the north and central sites on either coast but, in 1979, the dates for this phenophase were similar; May on the east coast and April on the west coast. The southern sites were significantly different in the early timing of the initial appearance of visible floral buds from the other two sites on either coast.

The analyses of variance (ANOVA) summary in Table II shows the relationship of site differences and the Julian date of occurrence for five phenophases. The sites had significantly different dates ($P < 0.10$) for initial appearance of macroscopic floral buds, initial anthesis, initial appearance of fruits and maximum biomass, but the sites were not significantly different for the dates for minimum biomass. The values for the standard error of the estimate (SEE) that correspond to the average standard deviation within sites increased in orderly fashion for the three reproductive phenophases with the lowest value,

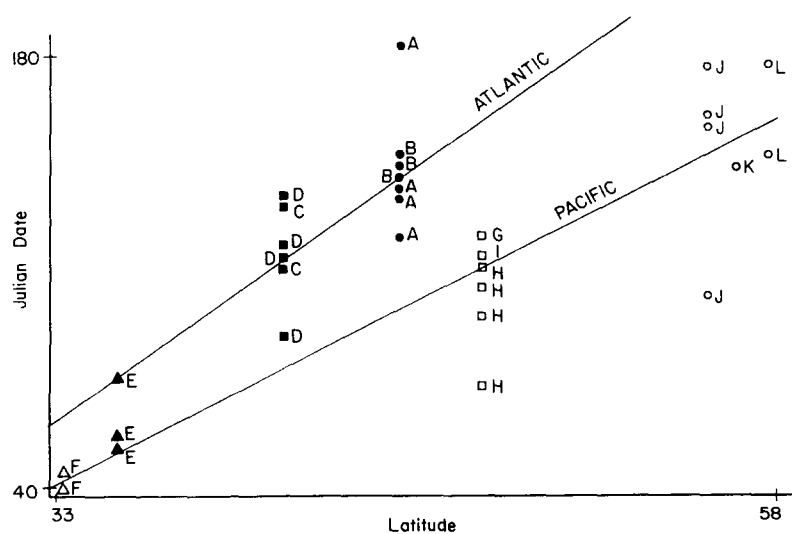


Fig. 2. Relationship of latitude and the Julian date for initial appearance of macroscopically visible floral buds. See Fig. 1 for site codes and Table III for the best prediction model.

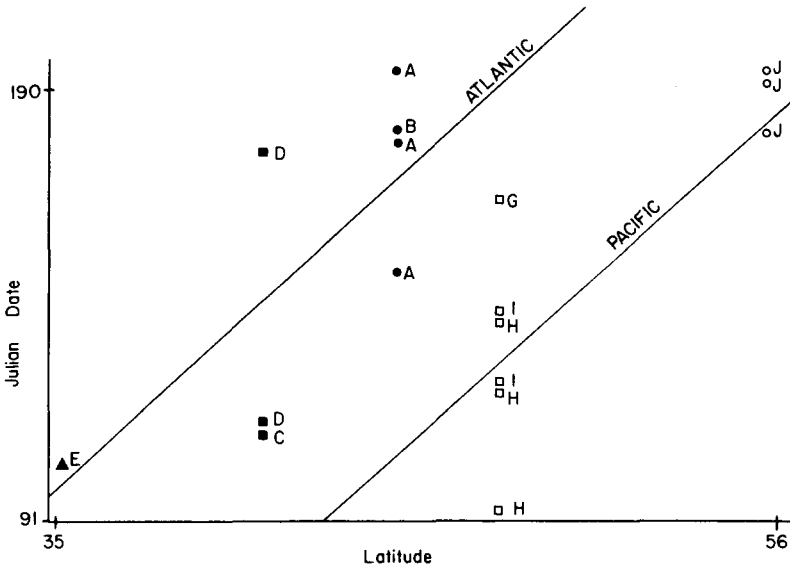


Fig. 3. Relationship of latitude and the Julian date for initial anthesis. See Fig. 1 for the site codes and Table III for the best prediction model.

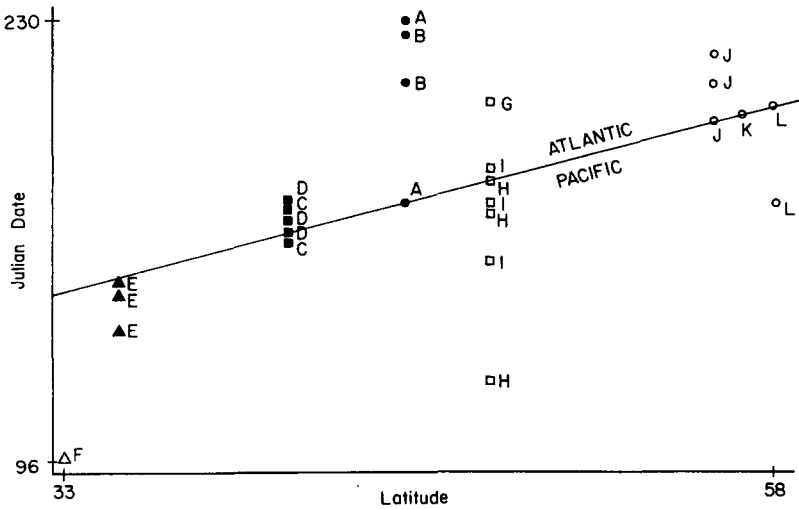


Fig. 4. Relationship of latitude and the Julian date for initial appearance of macroscopically visible fruits. See Fig. 1 for site codes and Table III for the best prediction model. Filled symbols are Atlantic sites and open symbols are Pacific sites.

19.86 days, for initial floral bud appearance and the highest value, 25.86 days, for initial fruit appearance. The variability for maximum biomass (SEE = 30.74) was greater than that for the reproductive phases and that for minimum biomass (SEE = 72.61) was very large. The 95% confidence interval (calculated by multiplying the SEE by 1.96) implied that an observed value for

TABLE II

ANOVA summary for site differences and Julian date of phenophase occurrence

Phenophase	Chance probability (<i>P</i>)	SEE ^a	95% CI of estimate ^b	Range of CI ^c
Initial appearance of macroscopic floral buds	0.001	19.86 days	± 38.92 days	77.84 days
Initial anthesis	0.053	22.90 days	± 44.88 days	89.76 days
Initial appearance of fruits	0.080	25.68 days	± 50.33 days	100.66 days
Maximum biomass	0.005	30.74 days	± 60.25 days	120.50 days
Minimum biomass	0.10	72.61 days	± 142.32 days	284.64 days

^a Standard error of the estimate.^b The 95% confidence interval of the estimate.^c The range of the confidence interval.

TABLE III

Regression summary for Julian date of phenophase occurrence

Phenophase	Best prediction model	Model characteristics ^a		
		<i>P</i>	<i>R</i> ²	SEE
Initial appearance of macroscopic floral buds	$Y = -208.8A - 116.4P + 7.8AL + 4.7PL$	0.000	0.795	17.81
Initial anthesis	$Y = -160.1A - 223.5P + 7.3L$	0.001	0.629	22.03
Initial appearance of fruits	$Y = 78.0 + 2.2L$	0.004	0.285	27.13
Maximum biomass	None found	—	—	—
Minimum biomass	Not analyzed ^b	—	—	—

^a Model characteristics are *P* (significance level), *R*² (proportion of variance actually predicted) and SEE (standard error of the estimate and represents the average prediction error for the model).^b ANOVA was not significant at the 0.10 level and therefore regression analyses were not performed.

initial flowering should be within 38.96 days of the site mean during 95% of the time. The range of the confidence interval for initial appearance of floral buds indicated that the observed values should fall within a range of 77.84 days during 95% of the time. The results of the ANOVA evaluation indicated that the three reproductive phenophases and one vegetative phenophase, the maximum biomass, differed significantly among the sites and should be studied with predictive models.

Regression analyses were performed for the four phenophases with significant ANOVA results (Table III). Valid prediction models were found for the

three reproductive phenophases, the most complex model being for initial appearance of floral buds, the next most complex one for initial anthesis and the simplest for the initial fruit appearance. The graphical representations of the three valid prediction models are shown in Table III and the detailed scattergrams for these models are given in Figs. 2, 3 and 4. The influence of latitude is strongest for initial visible appearance of flower buds ($R^2 = 0.795$ and $SEE = 17.81$), weaker for initial anthesis ($R^2 = 0.629$ and $SEE = 22.03$) and weakest for initial fruiting ($R^2 = 0.285$ and $SEE = 27.13$). These results are consistent with a hypothesis that date of flowering is controlled by a single or small set of latitude-related factors and that additional factors come into play with regard to the dates of anthesis and initial fruiting.

Temperature and salinity as criteria for prediction of the dates of the three reproductive phenophases were also evaluated with ANOVA. The analyses showed that neither the water temperature nor salinity recorded at the time of a phenophase was significantly different for the three phenophases. Because of the lack of significance, no models were constructed for these criteria.

Phenophases that related to vegetative growth did not show differences that were correlated with site or season. New vegetative growth of leaves, rhizomes and roots appeared at each of the six major sites during the entire year. Although there were periods of greater and lesser vegetative activity, these phenophases showed no correlation at any site with water temperature, salinity or date of occurrence. There was no sustained dormancy period detected at any of the latitudinally-diverse sites.

DISCUSSION

The reproductive periodicity in *Z. marina* was shown to be related to factors associated with latitude (Figs. 2, 3, 4). Of the three reproductive phenophases, the initial appearance of macroscopically visible floral buds probably is controlled by a single factor or a small set of factors. The other two reproductive phenophases, initial anthesis and initial appearance of visible fruits, probably are controlled by a larger set of factors.

If a single latitude-related factor is involved in the timing of the initial appearance of floral buds, that factor could be day length or water temperature. The data preclude day length because the prediction line (Fig. 2) for the Atlantic sites is always above that for the Pacific sites. This later flowering at the same latitude on the Atlantic coast than on the Pacific is complicated by the slope of the prediction line (Fig. 2) being steeper for the Atlantic than for the Pacific. This difference in the steepness of the slope of the prediction line signifies that flowering along a latitudinal gradient occurs increasingly later at more northern latitudes in the Atlantic than in the Pacific. Because the sequence of photoperiods is the same at the same latitude along both the Atlantic and Pacific gradients, day length is rejected as the primary latitude-related factor that controls the timing of the appearance of macroscopically visible floral buds.

Of the latitude-related factors, water temperature could be the sole controlling factor for the earliest date of macroscopically visible flowers at a site. The data base shows that higher water temperatures occur earlier in the Pacific than in the Atlantic and that north-to-south differences in water temperature are smaller in the Pacific than in the Atlantic. Setchell (1929) regarded water temperature as the primary factor in the reproduction of eelgrass, but his studies were confined to a comparison of only one site on the Pacific coast (Paradise Cove in the San Francisco Bay, CA) with a series of sites on the Atlantic (Beaufort, NC to New Brunswick, Canada). The inclusion of other sites on the Pacific has established that other factors, along with water temperature, are probably involved in eelgrass phenology.

Genotypic variation among eelgrass populations could play a role in the differences in phenology. Plants in the Pacific could respond differently to temperature than do plants in the Atlantic. These adaptive differences could contribute to the differences in phenology that were observed between Atlantic and Pacific populations. To fully assess this possibility, however, studies under controlled conditions would be essential.

The effects on flowering of water temperature and genotypic differentiation, as well as day length, have been studied in other seagrass species. The studies of *Thalassia testudinum* Banks ex König by Phillips et al. (1981), that combined investigations of phenology in natural seagrass beds and under controlled conditions, indicated that temperature responses for Caribbean plants were probably genotypically different from those of plants from Florida and Texas. The studies also showed that experimental cultures of *Thalassia* that were kept continuously under 24-h light conditions flowered in response to changes in temperature. Other studies have indicated that flowers of *Syringodium*, *Halophila*, *Cymodocea*, *Halodule* and *Zostera capricorni* Aschers. are produced under continuous light at the proper inductive temperature (McMillan, 1976, 1981, 1982; McMillan et al., 1981). Future studies could probably identify the temperature requirements for floral induction in *Z. marina* and the possible range of genotypic responses to temperature. The present investigation dealt with water temperatures that occurred at the time of the initial appearance of macroscopically visible floral buds.

The timing of microscopically visible floral buds would occur earlier and possibly at lower water temperatures at most sites. Churchill and Riner (1978) reported that collections of eelgrass in Great South Bay, New York, had microscopically visible floral buds with a water temperature of 0.5–3°C in January. If floral induction also occurs in January at other sites, it would be expected to be associated with a range of temperatures. For example, water temperatures at the southernmost collection site on the Pacific, San Diego, CA, ranges from 14–16°C in January 1977–79. The studies of the timing of floral induction along both the Atlantic and the Pacific coasts and under controlled conditions will be needed to determine the relationship of flowering to water temperature and the role of genotypic differentiation in the flowering patterns on the Atlantic and Pacific coasts of North America.

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