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HABITAT PERSISTENCE UNDERLIES INTRASPECIFIC VARIATION IN THE DISPERSAL STRATEGIES OF PLANTHOPPERS[1]

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Abstract. Dispersal is considered a vital life history characteristic for insects exploiting temporary habitats, and life history theorists have often hypothesized an inverse relationship between dispersal capability and habitat persistence. Most often, this hypothesis has been tested using interspecific comparisons of dispersal capability and qualitative estimates of habitat persistence. Consequently, most assessments have failed to control for possible phylogenetic nonindependence and they also lack quantitative rigor.

We capitalized on existing intraspecific variation in the dispersal capability of *Prokelisia* planthoppers to examine the relationship between habitat persistence and dispersal, thereby minimizing possible phylogenetic effects. Two congeneric species (*Prokelisia marginata* and *P. dolus*) occur in the intertidal marshes of North America, where they feed exclusively on cordgrasses (*Spartina*). Because these planthoppers exhibit wing dimorphism, flight-capable adults (macropters with fully developed wings) are easily differentiated from flight-less adults (brachypters with reduced wings). Thus, dispersal capability can be readily estimated by the percentage of macropters in a population.

At a regional spatial scale, we found a highly significant negative relationship between dispersal capability (percent macroptery) and habitat persistence. In this system, habitat persistence is influenced by a combination of marsh elevation, winter severity, and tidal range, which interact to determine the ability of planthoppers to endure through winter in their primary habitat for development. *P. marginata* develops primarily in low-marsh habitats during summer, habitats that can be subjected to pronounced winter disturbance due to ice scouring and/or extensive tidal inundation. Levels of winter disturbance of the low marsh are extreme along the Atlantic coast, intermediate along the Pacific, and low along the Gulf. Both the failure of *P. marginata* populations to remain through winter in this habitat, and the dispersal ability of these populations (92%, 29%, and 17% macroptery, respectively), are correlated with levels of disturbance. Thus, in regions where winter disturbance is high, levels of dispersal are correspondingly high to allow for recolonization of extirpated habitats from overwintering sites on the high marsh. Unlike *P. marginata*, *P. dolus* develops primarily in high-marsh habitats, which are much less disturbed on all coasts during winter. Consequently, this species remains year-round in its primary habitat for development, and most populations exhibit relatively low levels of macroptery (<10%).

When raised under common garden conditions, many more macropters of both species were produced from Atlantic compared to Gulf populations. Thus the proportion of macropters produced from the populations used in this experiment paralleled the incidence of macroptery measured in the field, providing evidence that the geographic variation in dispersal capability in both species has in part a genetic basis. The results of this study provide strong intraspecific evidence for an inverse relationship between the dispersal capability of insects and the persistence of their habitats.

Key words: dispersal, habitat disturbance and persistence, life history strategy, planthopper, Prokelisia marginata, Prokelisia dolus, salt marsh, Spartina, wing polymorphism.

INTRODUCTION

Historically, dispersal by flight has been considered essential for the success of insect species exploiting temporary habitats (Southwood 1962, 1977). In contrast, dispersal in persistent habitats is not nearly as important (Southwood 1962). Thus, in persistent habitats, the evolution of dispersal may be greatly influenced by trade-offs with other life history demands (Roff 1986*a*, 1994, Denno et al. 1989). For example, in a wide variety of insect species there is a cost to dispersal that results in delayed reproduction and/or reduced fecundity (Roff 1984, 1986*a*, Zera 1984, Dixon 1985, Denno et al. 1989). Because of these reproductive costs, insects should exhibit reduced dispersal

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in persistent compared to temporary habitats (Roff 1990, Denno et al. 1991). Despite the abundance of theory that predicts elevated levels of dispersal in ephemeral, patchy habitats (Reddingius and den Boer 1970, Roff 1974a, b, 1986a, 1990, Denno 1983, Fahrig 1990), there have been few rigorous empirical studies documenting an inverse relationship between habitat persistence and the incidence of dispersal (see Roff 1990, Denno et al. 1991).

Several factors have hindered investigations of the relationship between habitat persistence and dispersal. First, determining the fraction of potential dispersers in a population is problematic because many insect species are monomorphic for wing length and potential dispersers are not easily differentiated from nondispersers (Denno 1994b). Second, quantifying habitat persistence is not easy because it requires a knowledge of the length of both the time a habitat remains suitable for development and the generation time of the organism in question (Southwood 1962, Southwood et al. 1974, Roff 1990, Denno et al. 1991). Third, variation in dispersal capability is often greater among related species (e.g., the flightless and volant species of grasshoppers, crickets, water striders, planthoppers, and ground beetles) than it is among populations of the same species (Vepsäläinen 1978, den Boer et al. 1980, Roff 1990, Denno et al. 1991, Denno 1994b). As a consequence of these difficulties, most insect studies assessing the relationship between habitat persistence and the incidence of dispersal have been qualitative in nature, have relied on interspecific comparisons (reviewed in Roff 1990), and are possibly confounded by phylogenetic nonindependence (Wagner and Liebherr 1992, but see Denno et al. 1991).

A less confounded approach is to study intraspecific variation in the incidence of dispersal among populations and the underlying cause of this variation. Planthoppers in the genus *Prokelisia* (Homoptera: Delphacidae) exhibit intraspecific geographic variation in dispersal tendency (Denno et al. 1991, Denno 1994b), and thereby provide a unique opportunity to explore the effect of habitat persistence on the incidence of flight capability. Furthermore, *Prokelisia* planthoppers are wing dimorphic, facilitating the identification of potential dispersers in different populations (Denno et al. 1987, Denno and Roderick 1990, 1992).

Two congeners, *Prokelisia marginata* and *P. dolus,* are native residents of the intertidal marshes along the Atlantic, Gulf, and Pacific coasts of North America where they feed and develop exclusively on cordgrass (*Spartina*) (Denno et al. 1987, Denno 1994a, b). *Spartina* occupies a variety of saltmarsh habitats at both north temperate and subtropical latitudes, and is exposed to significant geographic variation in winter disturbance and tidal inundation (Blum 1968, Kirby and Gosselink 1976, Turner 1976, Denno and Grissell 1979, Zedler et al. 1992). Such variation in disturbance may influence the persistence of *Spartina* habitats for plant-

hopper exploitation. Thus, this system offers a novel opportunity for testing the hypothesis that intraspecific variation in dispersal capability parallels variation in habitat persistence. In this report, we first establish the primary habitat for development of each *Prokelisia* species over a broad geographic scale and assess the ability of each to remain in that habitat year-round. Second, we detail intraspecific variation in the dispersal capability of *Prokelisia* planthoppers within and among regions. Third, we correlate variation in dispersal capability with variation in habitat persistence, as measured by the ability of planthoppers to remain throughout the year in their primary developmental habitat. Last, we provide evidence that geographic variation in the dispersal capability of each *Prokelisia* species is genetically based, and thereby reflects underlying variation in life history strategies.

NATURAL HISTORY OF PLANTHOPPERS AND THEIR HOST PLANTS

Geographic distribution of cordgrass host plants and saltmarsh planthoppers

Two species of closely related perennial cordgrass, *Spartina alterniflora* Lois. and *Spartina foliosa* Trin., serve as the only recorded host plants for the planthoppers *Prokelisia marginata* and *Prokelisia dolus* (Denno et al. 1987). Both cordgrass species are limited to intertidal salt marshes and are native to only the New World (Mobberley 1956). *S. alterniflora* is broadly distributed along the Atlantic and Gulf coasts of North and Central America and the Atlantic coast of South America (Mobberley 1956). In addition, *S. alterniflora* has been introduced along the Pacific coast of North America where it now occurs from northern California to Washington (Mobberley 1956, Aberle 1990, Callaway and Josselyn 1992, Daehler and Strong 1994, Stiller and Denton 1995).

S. foliosa has a more restricted native distribution, occurring only along the Pacific coast of North America in California and Mexico (Mobberley 1956). This grass occurs in the San Francisco Bay area, is absent south along a 500-km stretch of coast, and appears again in southern California and Baja California where it occurs as isolated patches in secluded estuaries (Mobberley 1956, Neuenschwander et al. 1979, Zedler 1982, 1993, Roberts 1989, Zedler et al. 1992).

Prokelisia marginata and *P. dolus* occur sympatrically along much of the Atlantic and Gulf coasts of North America where they feed and develop exclusively on *Spartina alterniflora* (Denno et al. 1987). Along the Pacific coast, the two planthoppers are allopatric; *P. marginata* occurs in northern California on both *S. foliosa* (Roderick 1987) and on the introduced populations of *S. alterniflora* (Daehler and Strong 1994), whereas *P. dolus* feeds and reproduces on *S. foliosa* in the marshes of southern and Baja California (Wilson 1982, Denno et al. 1987).

Habitats and growth forms of cordgrass

S. alterniflora dominates the vegetation of many Atlantic, Gulf, and Pacific intertidal marshes, often occurring in extensive, pure stands (Adams 1963, Redfield 1972, Duncan 1974, Turner and Gosselink 1975, Kirby and Gosselink 1976, Aberle 1990). S. alterniflora is restricted to the intertidal zone ranging from ≈ Mean High Water level (MHW) to elevations as much as ·2 m below MHW (Blum 1968, Redfield 1972). Along this elevational gradient, this grass characteristically occurs in two growth forms (Miller and Egler 1950, Teal 1962, Adams 1963, Redfield 1972, Hatcher and Mann 1975, Turner 1976, Denno and Grissell 1979, Ornes and Kaplan 1989). Tall-form plants (1–2 m in height) grow in low-marsh habitats along the depressed banks of tidal creeks, along bay edges, and occasionally as isolated stands on low tidal flats (Redfield 1972). Further inland near MHW (hereafter the high marsh), short-form S. alterniflora grows as a dense bed of short rosettes in vast meadows, attaining heights of only 10–40 cm (Blum 1968, Redfield 1972). Many of the intertidal marshes along the Atlantic, Gulf, and Pacific coasts are characterized by expanses of short-form S. alterniflora on the high marsh, which abruptly intergrade into a fringe of tall-form plants bordering tidal creeks and bay edges (Adams 1963, Duncan 1974, Turner and Gosselink 1975, Kirby and Gosselink 1976, Turner 1976, Denno and Grissell 1979, Mendelsshon et al. 1981, Stout 1984, Daehler and Strong 1994).

There is an extensive literature concerning the genetic and environmental factors influencing the growth form of S. alterniflora (reviewed in Anderson and Treshow 1980). Nitrogen availability, salinity, sulfide level, and soil drainage are among the most commonly espoused environmental causes of growth-form variation (reviewed in Gallagher et al. 1988, Ornes and Kaplan 1989). Although genetic factors play some role (Gallagher et al. 1988), most evidence indicates that environmental factors are largely responsible for differences in growth form (Ornes and Kaplan 1989).

At most Pacific coast locations the structure of the Spartina foliosa marsh is not comparable to S. alterniflora marshes in that growth forms are not clearly distinguished (Zedler 1982, 1993, Zedler et al. 1992). Although S. foliosa occupies an elevational range from MHW to as much as 0.5 m below MHW (Ustin et al. 1982, Zedler 1982), it is typically limited to a narrow band of intertidal vegetation or isolated patches along the seaward edge of the marsh (Ustin et al. 1982, Zedler 1982, 1993, Zedler et al. 1992).

Geographic variation in the disturbance and destruction of cordgrass habitats

Regional differences in tidal range, tidal frequency, and winter severity influence the level of disturbance of Spartina habitats (Denno and Grissell 1979, Denno 1983). Several lines of evidence support the contention that regional variation in disturbance is greater for tall-form than short-form Spartina.

Throughout much of the Atlantic coast, new shoots of both growth forms appear in spring, maximum live biomass is attained during summer or early fall, and plants begin to senesce in late fall (Blum 1968, Squiers and Good 1974, Denno and Grissell 1979). On the high marsh, the dead rosettes of short-form Spartina remain in place over winter and then decay during the course of the next season (Squiers and Good 1974). In stark contrast, the action of winter tidewaters, winds and shifting ice shear off the culms of tall-form plants leaving exposed creek banks often free of litter (Denno and Grissell 1979; Fig. 1A and B). The selective winter destruction of the tall-form Spartina habitat has been documented from Massachusetts to Georgia (Teal 1962, Blum 1968, Squiers and Good 1974, Denno and Grissell 1979, Niering and Warren 1980). Above 37° N latitude (north of North Carolina), no living aboveground biomass of Spartina overwinters in either the streamside or high-marsh habitats (Turner 1976).

In addition to differences in winter destruction, tidal inundation also varies markedly between the major Spartina habitats along the Atlantic coast. For example, short-form plants in Massachusetts are flooded only 6% of the time compared to 55% for tall-form plants (Redfield 1972). Furthermore, streamside plants on the Atlantic coast do not grow tall enough to escape significant tidal inundation until spring or early summer, at which time they become available for exploitation by herbivorous insects (Denno and Grissell 1979).

The growth dynamics and winter disturbance of Spartina on the Gulf coast contrasts with that along the Atlantic coast (Kurz and Wagner 1957, Turner 1976, Denno and Grissell 1979, Stout 1984). The mild climate allows living shoots of both tall-form and short-form plants to persist throughout winter and promotes year-round growth (Kirby and Gosselink 1976, Turner 1976). Maximum live biomass occurs in early fall, after which aboveground portions of plants begin to senesce, but the understory of new shoots continues to grow (Kirby and Gosselink 1976). Destruction of low-marsh habitats along the Gulf coast is minimal due to reduced tidal range (Tide Tables 1992), an absence of ice, and reduced frequency of tidal submergence during winter (Kirby and Gosselink 1976, Denno and Grissell 1979; Fig. 1C and D). The large amounts of litter or standing dead vegetation on Gulf marshes during winter provide further evidence for reduced tidal disturbance along the Gulf (Kirby and Gosselink 1976, Denno and Grissell 1979). Nevertheless, even along the Gulf coast during winter and early spring when regrowth is short, vegetation in the lowest portion of the tidal range can incur significant inundation (Antolin and Strong 1987, Throckmorton 1989).

Although less extreme than along the Atlantic coast, there is evidence for an elevational gradient in the disturbance of Spartina foliosa occupying the Pacific

FIG. 1. Comparative seasonal destruction of tall-form *Spartina alterniflora* growing on stream banks in Atlantic and Gulf coast intertidal marshes. (A) Robust, tall-form plants (>1 m in height) during summer at Tuckerton, New Jersey, senesce during late fall and are destroyed during winter by storms and shifting ice leaving, (B) bare creekbanks unsuitable as overwintering habitats for planthoppers. (C) During summer, plants also grow tall along the tidal creeks in the low marsh at Cedar Key, on the Gulf coast of Florida. (D) In contrast to Atlantic locations, senescing culms remain standing through winter along the Gulf, have associated with them an understory of regrowth, incur no ice scouring, and provide a habitat in which planthoppers can persist through winter.

marshes of the San Francisco Bay area. In these marshes where mean tidal range is moderate (Tide Tables 1993), living shoots are not evident during winter in many low-marsh habitats, but do persist throughout the year on the high marsh (Ustin et al. 1982, Roderick 1987). In contrast, on southern California and Baja California marshes, mean tidal range is comparatively less (Tide Tables 1993), frost is rare, and the mediterranean-like climate promotes year-round growth of *S. foliosa* (Neuenschwander et al. 1979, Zedler 1982, 1993, Zedler et al. 1992).

Life history of saltmarsh planthoppers

Both nymphs (five instars) and adults of *P. marginata* and *P. dolus* feed on the phloem sap of their hosts from the upper surface of the leaves (Denno et al. 1987, Cook and Denno 1994). Along the central Atlantic coast both planthoppers are trivoltine and adults are absent from the marsh from November through March (Denno et al. 1987). On the Gulf coast, both species are multivoltine and reproduction occurs year-round (Denno and Grissell 1979, Denno 1983, Strong and

Stiling 1983; Denno et al. 1987). *P. marginata* is trivoltine in the San Francisco Bay area marshes with adults absent from December through February (Roderick 1987). In southern California and Mexico, adults of *P. dolus* are present throughout the year and the species breeds continuously (Johnson 1991; R. F. Denno, *personal observation*).

In New Jersey, both species overwinter on the high marsh as active nymphs nestled in litter (Denno et al. 1987), as does *P. marginata* on northern California marshes (Roderick 1987). Experimental evidence indicates that litter is critical for winter survival on the high marsh (Tallamy and Denno 1979). In contrast, nymphs do not survive the winter in low-marsh habitats in either New Jersey or northern California populations (Denno and Grissell 1979, Roderick 1987). Because females of both species insert their eggs exclusively in living leaf blades (Denno et al. 1987, Denno 1994b), eggs are unable to persist in habitats free of living culms. All stages of *Prokelisia* planthoppers, including adults, are able to withstand short-term tidal inundation

(Vince et al. 1981, Roderick 1987, Throckmorton 1989).

Wing dimorphism, dispersal capability, and planthopper habitats

Adults of both *Prokelisia* species are wing dimorphic; both fully-winged individuals (macropters) and adults with reduced wings (brachypters) occur in most populations (Wilson 1982, Denno et al. 1985, 1987, Denno 1994*b*). Macropters are capable of long-distance flight (>30 km) (Denno and Grissell 1979, Denno 1983, Sparks et al. 1986, Antolin and Strong 1987, Roderick 1987), whereas brachypters move only short distances of several metres by walking or jumping (Denno and Grissell 1979, Denno et al. 1985, Denno 1994*b*). Brachypters reproduce at a significantly earlier age and are more fecund than macropters (Denno et al. 1989, Denno 1994*b*).

Wing form in *Prokelisia* planthoppers is determined by a developmental switch that responds to environmental cues (Denno et al. 1985, 1991, Roderick 1987, Denno and Roderick 1992). The sensitivity of the switch is heritable and under polygenic control (Roderick 1987, Denno and Roderick 1990, Denno 1994*b*). Of the environmental factors known to affect wing form in *Prokelisia* planthoppers, population density is by far the most significant (Denno et al. 1985). The production of macropters is positively density dependent in both species (Denno et al. 1985, Denno and Roderick 1992).

Data from one New Jersey population suggest that the primary habitat for development differs between *P. marginata* and *P. dolus*. For *P. marginata,* density-dependent dispersal results in interhabitat movements between overwintering habitats on the high marsh (short-form meadows of *Spartina*) and summer sites for development in the low marsh (stands of tall-form *Spartina*) (Denno and Grissell 1979, Denno et al. 1985). By contrast, *P. dolus* is a much more sedentary species, which appears to both overwinter and develop on the high marsh (Denno et al. 1987). However, it has not been established whether this difference in habitat selection between the two species is consistent throughout their range in North America.

Geographic variation in the dispersal capability of *Prokelisia* planthoppers has been suggested on the basis of studies at a few locations on the Atlantic and Gulf coasts (Denno and Grissell 1979, McCoy and Rey 1981, Wilson 1982, Strong and Stiling 1983). For example, the incidence of macroptery in one New Jersey population of *P. marginata* is much higher (>80%) than that reported for two neighboring Florida populations on the Gulf (<10%) (Denno and Grissell 1979, Strong and Stiling 1983, Denno et al. 1987). However, broad-scale variation in wing-form composition and its underlying cause has not been thoroughly documented for either species.

Hypotheses Concerning Habitat Persistence and Dispersal

For *Prokelisia* planthoppers, habitat persistence is probably determined in large part by three interacting factors: winter severity, tidal disturbance, and marsh elevation. Due to enormous regional differences in the selective destruction and disturbance of the low-marsh habitat during winter (Teal 1962, Blum 1968, Squiers and Good 1974, Kirby and Gosselink 1976, Turner 1976, Niering and Warren 1980, Stout 1984), low-marsh inhabitants should face much greater geographic variability in habitat persistence than high-marsh occupants. In particular, in regions where low-marsh habitats are destroyed or disturbed during winter (Atlantic and Pacific coasts), exploitation of these habitats must depend on annual recolonization events. Such recolonization is probably much less critical for the exploitation of either low-marsh habitats in regions with minimal winter disturbance (Gulf coast), or high-marsh habitats, which incur little disturbance in any region.

We hypothesize that in regions where planthoppers fail to remain through winter in their primary developmental habitat, high levels of dispersal capability (% macroptery) will be evident. Conversely, we predict low levels of macroptery in association with high levels of endurance through winter in the habitat where most development occurs. Limited data suggest that *P. marginata* is a low-marsh inhabitant, whereas *P. dolus* resides mostly on the high marsh (Denno and Grissell 1979, Denno et al. 1987). Thus, we predict that *P. marginata* will exhibit regional variation in levels of dispersal that parallels regional variation in low-marsh disturbance. We also predict that *P. dolus* will exhibit minimal variation in levels of dispersal due to the low levels of disturbance of the high marsh across all regions. We test these predictions concerning habitat persistence and dispersal by: (1) examining regional patterns of low-marsh and high-marsh occupancy by the *Prokelisia* species and assessing their ability to remain in their primary habitat for development year-round, (2) detailing intraspecific variation in dispersal capability (percent macroptery) within and among regions, and (3) correlating variation in dispersal capability with variation in habitat persistence, as measured by the ability of planthoppers to remain throughout the year in their primary developmental habitat.

In addition, we hypothesize that regional differences in dispersal capability are genetically based. We test this hypothesis by determining the wing-form response of Atlantic and Gulf coast populations of both *Prokelisia* species across a range of representative densities. Population differences in the frequency of macropter production at a common high density would be consistent with our hypothesis regarding genetic differences among populations.

Primary developmental habitats of planthoppers and their suitability for year-round occupancy

To determine the primary habitat for development of both *Prokelisia* species and to assess how well each species endures throughout the year in that habitat, we examined in detail the year-round patterns of high-marsh and low-marsh exploitation by the two *Prokelisia* species at one Atlantic coast location (Tuckerton, Ocean County, New Jersey). To examine these issues at a regional scale, we compared warm-season and cold-season patterns of low-marsh and high-marsh occupancy by populations on the Atlantic coast (a region experiencing extensive winter disturbance of the low marsh) and the Gulf coast (a region incurring much less winter disturbance).

Patterns of habitat occupation at Tuckerton, New Jersey were determined by sampling *Prokelisia* planthoppers in both low-marsh (tall-form) and high-marsh (short-form) habitats on six dates throughout the year (9 May, 23 May, 6 June, 17 July, 28 August, and 25 September, 1986). Eight pairs of plots (100 m²) were established with one plot of the pair in each habitat type. Planthoppers were sampled using a D-Vac suction sampler with a 0.093-m² sampling head. All plots were sampled once on each date, and each sample consisted of 16 30-s placements of the sampling head over the *Spartina* vegetation (see Denno et al. 1980 for details). For each *Prokelisia* species the proportion of the population occupying the low-marsh habitat (no. conspecifics in low-marsh *Spartina*/no. conspecifics in low-marsh + high-marsh *Spartina*) was determined from each plot pair. The effect of species (*P. marginata* and *P. dolus*), date, and their interaction on the angular-transformed proportion of adult planthoppers in the low-marsh habitat was assessed with repeated-measures ANOVA (SAS 1990). Failure to remain in one habitat year-round would be suggested by a significant effect of date and/or a significant date by species interaction, whereby one or both species shifts its distribution from one habitat to the other.

We also determined at a regional scale the primary habitat for development of both *Prokelisia* species, and the ability of each species to endure throughout the year in that habitat. To do so, we compared warm-season and cold-season patterns of low-marsh (tall-form) vs. high-marsh (short-form) occupancy between populations on the Atlantic coast and the Gulf coast. For each geographic location, the proportion of both *P. marginata* and *P. dolus* occupying the low-marsh habitat was determined from the pooled totals of adults from three sweep-net samples (one sample = 25 sweeps with a 36 cm diameter net) (see Appendix for locations and sample sizes). To determine seasonal differences in habitat occupation between regions, samples were divided into: (1) warm-season samples (late spring, summer, and fall), and (2) cold-season samples (winter or immediately after winter). These temporal categories were explicitly established in order to assess habitat occupation during the cold season when low-marsh disturbance is maximal and planthoppers have not yet undergone spring migration, as well as during the warm season after such migrations to the low marsh have occurred (see Denno 1983, Denno et al. 1985, 1986, Antolin and Strong 1987). The effect of region (Atlantic and Gulf), season (warm and cold), species (*P. marginata* and *P. dolus*), and their interaction on the angular-transformed proportion of adult planthoppers in the low-marsh habitat was assessed using ANOVA and specific means were compared using Sidak's adjustment for multiple comparisons (SAS 1990). A regional difference in planthopper endurance in the low marsh would be indicated by a significant region by season interaction in which the proportion of the population in the low marsh declines more during the cold season in one region than the other. The Pacific coast region was excluded from this analysis because we were unable to obtain a sufficient number of cold-season samples (northern California), and because the distinction between high-marsh and low-marsh habitats is often ambiguous on southern California marshes due to the small patch size of *Spartina* and its rather homogeneous growth form.

Geographic variation in the dispersal capability of planthoppers

To detail geographic variation in the dispersal capability of both *P. marginata* and *P. dolus,* we sampled planthoppers from 112 locations along the Atlantic, Gulf, and Pacific coasts (see Appendix for locations and sample dates). At each location, three sweep-net samples were taken in both low-marsh (tall-form *Spartina*) and high-marsh habitats (short-form *Spartina*). Sweep samples of planthoppers were placed in ethyl alcohol (95%) and returned to the lab for censusing. Subsequently, all planthoppers in each sample were sorted by species and wing form and counted.

The dispersal capability of the *Prokelisia* species at each geographic location was estimated by determining the percentage of macropters (no. macropters/[no. macropters + brachypters]) in pooled samples of all conspecific adults from all habitats. The effects of region (Atlantic, Gulf, and Pacific), *Prokelisia* species, and their interaction on macroptery (angular-transformed percentage) were determined using ANOVA and means were compared using Sidak's adjustment for multiple comparisons (SAS 1990). For each species, a site was included in this analysis only if 25 or more adults of that species were obtained from the pooled samples. For *P. marginata*, 13, 20, and 28 sites were included, and for *P. dolus,* 8, 23, and 53 sites were available from the Pacific, Gulf, and Atlantic coasts, respectively (see Appendix).

Relationship between habitat persistence and dispersal capability

To test the hypothesis that levels of dispersal increase with decreasing habitat persistence, we determined the relationship between the dispersal capability (percent macroptery) of *Prokelisia* planthoppers and their ability to endure through winter in their primary habitat for development. We reasoned that in regions where planthoppers fail to endure through winter in their primary habitat for development, high levels of dispersal capability (percent macroptery) should be evident in order to facilitate the recolonization of this habitat from overwintering sites. As an index of habitat persistence for each species, we determined the proportion of that species' population occupying the primary habitat for development (low marsh for *P. marginata* and high marsh for *P. dolus*) during or just following winter. For example, a small proportion of a *P. marginata* population in the low marsh (relative to the high marsh) just after winter, would be indicative of poor persistence of the low marsh habitat. As above, this mean proportion was calculated from the pooled sum of three sweep samples taken in both low-marsh and high-marsh habitats at each location. This proportion was then regressed against the level of macroptery (percent) observed in the field during the growing season (late spring through fall) for *P. marginata* and for the two *Prokelisia* species combined. In all, data from 17 locations were available for analysis, 9 for *P. marginata* (5 Atlantic, 3 Gulf, and 1 Pacific) and 8 for *P. dolus* (5 Atlantic and 3 Gulf) (see Appendix). Data for the one Pacific coast population of *P. marginata* were taken from Roderick (1987).

Evidence that regional differences in dispersal capability are genetically based

To investigate a possible genetic basis for the regional differences in dispersal capability (percent macroptery) observed in field populations of both *Prokelisia* species, we raised individuals from one Atlantic and one Gulf coast population across the same range of densities in the laboratory and compared their density–wing form responses. The density–wing form response was compared between *P. marginata* populations from Tuckerton, New Jersey and Cedar Key, Florida, and between *P. dolus* populations from Tuckerton, New Jersey and East Tampa, Florida.

Plants containing eggs from East Tampa (*P. dolus*), Cedar Key (*P. marginata*) and Tuckerton (both species) were transplanted into pots on 20 May, 31 May, and 20 July 1987, respectively. First-instar nymphs hatching from these eggs were used to establish three conspecific density treatments (3, 11, and 40 nymphs/tube cage) on *Spartina* seedlings, representing the naturally occurring range of densities in the field (Denno and Roderick 1992) (see Denno et al. 1985 for details on *Spartina* culture). The density treatments of 3, 11, and
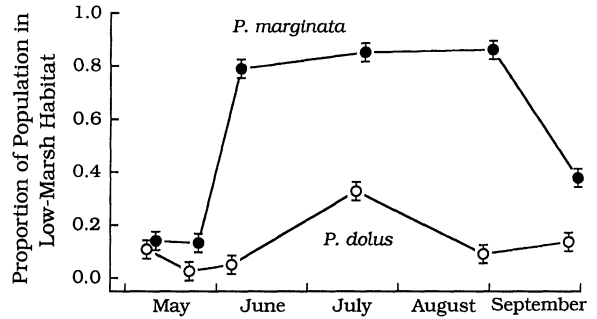

FIG. 2. Seasonal patterns of low-marsh occupation (proportion of population in low marsh compared to high marsh) by *Prokelisia marginata* and *P. dolus* at Tuckerton, New Jersey (1986), a site where destruction of the low-marsh habitat occurs annually during winter (Fig. 1B). Note the shift in the population of *P. marginata* from the high marsh (overwintering habitat) to the low marsh (primary habitat for development) in May, and then back to the high marsh in fall. The population shift results from interhabitat dispersal. In contrast, *P. dolus* overwinters on the high marsh and remains there throughout the year. Means ±1 SE are shown.

40, were replicated 25, 20, and 15 times, respectively. Caged seedlings from all experiments were maintained in incubators at 24 ± 2°C in a 14:10 light-dark cycle. As adults emerged, their wing form was determined. The effects of population (Gulf and Atlantic), rearing density (3, 11, and 40), and their interaction on macroptery (percent) were determined using ANOVA, and means were compared using Sidak's adjustment for multiple comparisons (SAS 1990).

Because the eggs used in this experiment were taken from a largely macropterous population in New Jersey and a primarily brachypterous population in Florida, it could be argued that maternal effects might contribute to any observed differences in wing form between populations. However, for several planthopper species, including *P. marginata,* there is no clear relationship between the wing form of parents and offspring (Kisimoto 1965, Raatikainen 1967, Roderick 1987), suggesting that such maternal effects are minimal or nonexistent.

RESULTS

Primary developmental habitats of planthoppers and their suitability for year-round occupancy

Seasonal patterns of low-marsh and high-marsh occupation by the two *Prokelisia* species were assessed in detail at Tuckerton, New Jersey, where destruction of the low-marsh habitat occurs annually during winter (Fig. 1B). Following winter in early May, most of the population of both species (≈90%) occurred on the high marsh (Fig. 2). The small fraction of adults sampled in the low marsh at this time (10% of the population) was probably an overestimate, due to the difficulty of timing the sample after nymphs begin molting to adults yet before those adults engage in spring migration (see Denno et al. 1987). Despite their co-oc-

currence on the marsh during winter and early spring, the two species exhibited very different patterns of habitat exploitation during summer and fall. During this time, >80% of the *P. marginata* population occurred in the low-marsh habitat, whereas a mere 20% of the *P. dolus* population occupied the low marsh. The shift in the distribution of the *P. marginata* population from the high to the low marsh in June corresponds with the period of spring–summer migration for this species (Denno et al. 1985, 1986, Denno 1994b). During fall, the decline in the proportion of the *P. marginata* population in the low-marsh habitat is associated with the emigration of macropterous adults from tall-form *Spartina* and their colonization of high-marsh habitats prior to the onset of winter (Denno 1983). Thus, *P. marginata* selectively exploits the low-marsh habitat for development during the summer and fall, and *P. dolus* remains mostly on the high marsh, its primary habitat for development, throughout the year. These differences in habitat occupancy are supported by a significant species effect ($F_{1,14} = 171.4$; $P < 0.001$), date effect ($F_{5,70} = 56.4$; $P < 0.001$), and species by date interaction ($F_{5,70} = 27.1$; $P < 0.001$) on the proportion of the adult population inhabiting the low-marsh habitat.

Habitat exploitation in the two *Prokelisia* species was also determined at a much larger geographic scale by comparing warm and cold season patterns of low-marsh and high-marsh occupancy between the Atlantic coast and the Gulf coast (Fig. 3). Regardless of region, the proportion of the *P. marginata* population inhabiting the low marsh was significantly higher than that for *P. dolus* ($F^{Species}_{1,87} = 36.92$, $P < 0.001$; $F^{Species \times Region}_{1,87} = 2.26$, $P = 0.14$). This pattern corroborates that the difference between the species in their primary habitat for development, which we detailed in New Jersey, also occurs over a broad geographic scale.

For *P. marginata,* the proportion of the population in the low marsh during the warm season was high in both Atlantic (64%) and Gulf coast regions (72%) (Fig. 3). During the cold season, however, the proportion of the population remaining in the low marsh plummeted to 7% on Atlantic marshes, but only dropped to 40% in Gulf coast marshes. These data demonstrate that *P. marginata* is better able to endure winter conditions on the low marsh along the Gulf compared to the Atlantic coast. In contrast, *P. dolus* showed only a slight shift of the population from the high marsh to the low marsh during the warm season along the Atlantic, but exhibited no such shift along the Gulf coast (Fig. 3). However, along both coasts, only a small proportion of *P. dolus* populations (<20%; Fig. 3) occurred on the low marsh during either season. The difference between the two species in their warm-season and cold-season occupancy of the low-marsh habitat was statistically significant ($F^{Season}_{1,87} = 35.03$, $P < 0.001$; $F^{Species \times Season}_{1,87} = 8.98$, $P = 0.004$). Moreover, the seasonal disparity in the occupancy of the low marsh was significantly
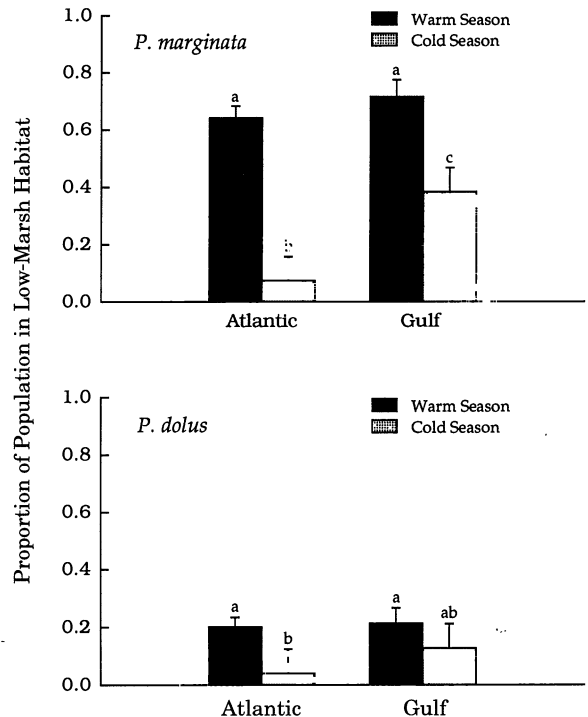

FIG. 3. Warm and cold seasonal patterns of low-marsh occupancy (proportion of population in low marsh compared to high marsh) by *Prokelisia marginata* and *P. dolus* at sites along the Atlantic where low-marsh habitats are destroyed during winter, and at locations along the Gulf coast where low-marsh habitats are less disturbed during winter (see Appendix for specific locations). Note that for *P. marginata* (top), the proportion of the population remaining through the cold season in the low marsh is much lower for Atlantic than Gulf coast locations, yet during the warm season most individuals occupy the low marsh on both coasts. In contrast, the proportion of the *P. dolus* population in the low marsh (bottom) remains low during both seasons. Means with different letters are significantly different ($P < 0.05$, ANOVA followed by Sidak's adjustment for multiple comparisons).

greater along the Atlantic than the Gulf coast ($F^{Region}_{1,87} = 7.64$, $P = 0.007$; $F^{Region \times Season}_{1,87} = 6.07$, $P = 0.047$).

Geographic variation in the dispersal capability of planthoppers

Our survey revealed significant geographic variation in dispersal capability (percent macroptery) of both *P. marginata* and *P. dolus,* but the effect of region on macroptery differed between the two species ($F^{Region}_{2, 140} = 101.7$, $P < 0.001$; $F^{Species}_{1, 140} = 231.6$, $P < 0.001$; $F^{Region \times Species}_{2, 140} = 76.3$, $P < 0.001$; Figs. 4–6). Populations of *P. marginata* with the greatest capacity for dispersal occurred along the Atlantic coast (92 ± 2% macroptery, mean ±1 SE), followed by Pacific populations (29 ± 4%), and then Gulf populations (17 ± 5%) (all means differ, $P < 0.01$; Figs. 4 and 6). Overall, the dispersal capability of *P. dolus* was much less than that for *P. marginata,* with levels of macroptery significantly higher in both Atlantic (8
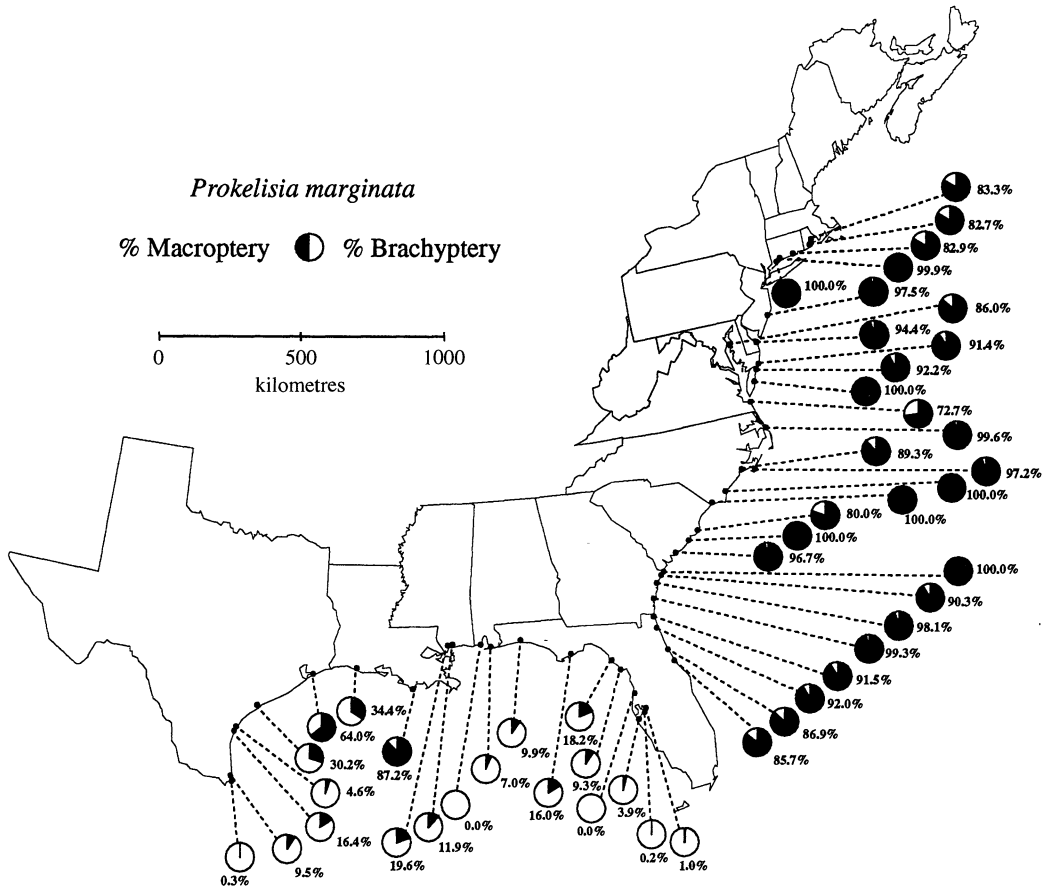
FIG. 4. Geographic variation in the dispersal capability (percentage macroptery) of Atlantic and Gulf coast populations of *Prokelisia marginata* (see Appendix for specific locations). Atlantic populations are much more macropterous than Gulf coast populations.

± 2%) and Gulf coast populations (6 ± 2%) than in Pacific coast populations (0.2 ± 0.1%; $P < 0.03$; Figs. 5 and 6).

Within regions, levels of macroptery remained rather constant (Figs. 4–6). There were a few notable exceptions to intra-regional constancy in macroptery. Higher-than-average levels of macroptery were observed in a few Texas and Louisiana populations of *P. marginata* and *P. dolus* (Figs. 4 and 5) as well as in a few mid-Atlantic populations of *P. dolus* (Fig. 5). In two of these cases (64% macroptery in an eastern Texas population of *P. marginata*, and 84% in a Maryland population of *P. dolus*), we observed the aerial dispersal of macropters under population outbreak conditions.

Relationship between habitat persistence and dispersal capability

The level of macroptery (percent) was inversely related to habitat persistence (indexed as the proportion of each species' population able to endure through winter in the primary habitat for development), when only populations of *P. marginata* were considered in the analysis ($Y^{Macroptery} = 99.7 - 148.7X$, $R^2 = 0.76$, $P =$

0.001), and when populations of both species were pooled for analysis ($Y^{Macroptery} = 89.8 - 90.8X$, $R^2 = 0.75$, $P = 0.001$) (Fig. 7). At Atlantic and Pacific locations, the proportion of the *P. marginata* population remaining through winter in the primary habitat for development (low marsh) was low (<20%), and associated levels of macroptery during the growing season were high (>75%). In contrast, the proportion of the *P. marginata* population remaining through winter in the low marsh on the Gulf was high (30–70%), and associated levels of macroptery were low (<15%). The proportion of *P. dolus* populations remaining through winter in their primary habitat for development (high marsh) was high (>70%) at all locations along the Atlantic coast and levels of macroptery were low (<35%). These results suggest that along the Atlantic and Pacific coasts, large-scale dispersal is necessary for *P. marginata* to recolonize the low marsh, a habitat that is unsuitable for winter survival in these regions. In contrast, the low levels of macroptery in most Gulf coast populations of *P. marginata* apparently reflect the ability of this species to remain on the low marsh year-round in this equitable region.
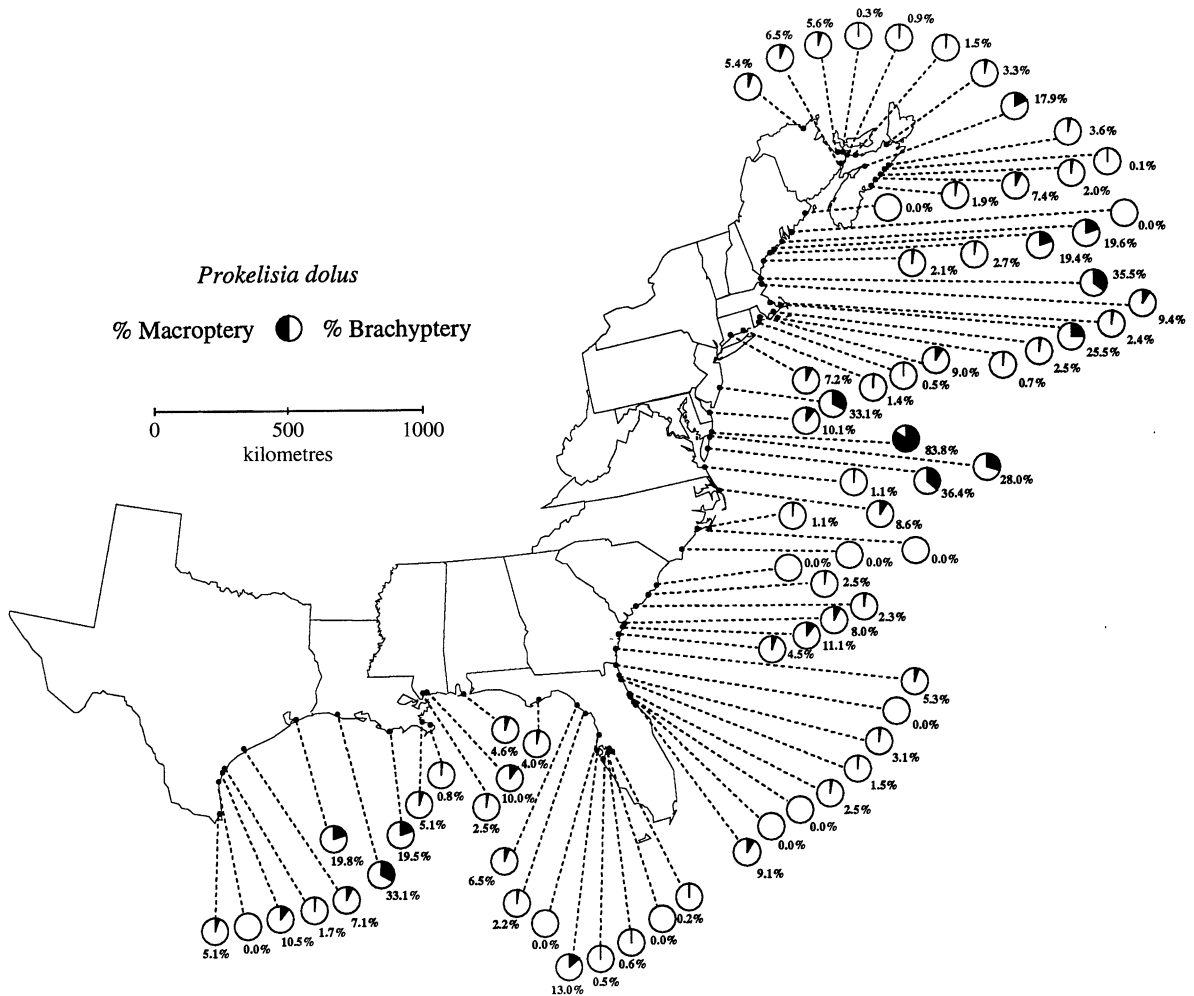
Fig. 5. Geographic variation in the dispersal capability (percentage macroptery) of Atlantic and Gulf coast populations of *Prokelisia dolus* (see Appendix for specific locations). Levels of macroptery are similarly low in both Atlantic and Gulf coast populations.

Low levels of dispersal occur in all populations of *P. dolus,* a species that remains throughout the year in its primary habitat for development on the less-disturbed high marsh.

Evidence that regional differences in dispersal capability are genetically based

New Jersey and Florida (Gulf) populations of both *Prokelisia* species differed dramatically in their tendency to produce macropters (Fig. 8). For the two populations of *P. marginata,* more adults molted into macropters as rearing density increased, but the overall level of macroptery (percent) was much higher in the New Jersey population across all rearing densities ($F^{\text{Density}}_{2, 103} = 38.96$, $P < 0.001$; $F^{\text{Population}}_{1, 103} = 76.51$, $P < 0.001$; $F^{\text{Density} \times \text{Population}}_{2, 103} = 2.40$, $P = 0.09$). Similarly, macroptery (percent) increased with crowding in both populations of *P. dolus,* but this response was significantly higher in the New Jersey population

than the Florida population (Fig. 8; $F^{\text{Density}}_{2,93} = 12.60$, $P < 0.001$; $F^{\text{Population}}_{1,93} = 85.04$, $P < 0.001$; $F^{\text{Density} \times \text{Population}}_{2,93} = 0.76$, $P = 0.47$).

These data suggest that selection for dispersal capability has acted differentially in these Atlantic and Gulf coast populations, resulting in a greater production of macropters at a given density in the New Jersey populations of both *Prokelisia* species. Not surprisingly, these density–wing form responses paralleled the incidence of macroptery observed in the field. For *P. marginata,* field levels of macroptery were 98% for the New Jersey population and 9% for the Florida population. Similarly, for *P. dolus,* field levels of macroptery were 33% and 0.6% for the New Jersey and Florida populations, respectively. Thus, interregional variation in macroptery observed in field populations of the *Prokelisia* planthoppers (Figs. 4–6) apparently reflects genetically based differences in dispersal capability.
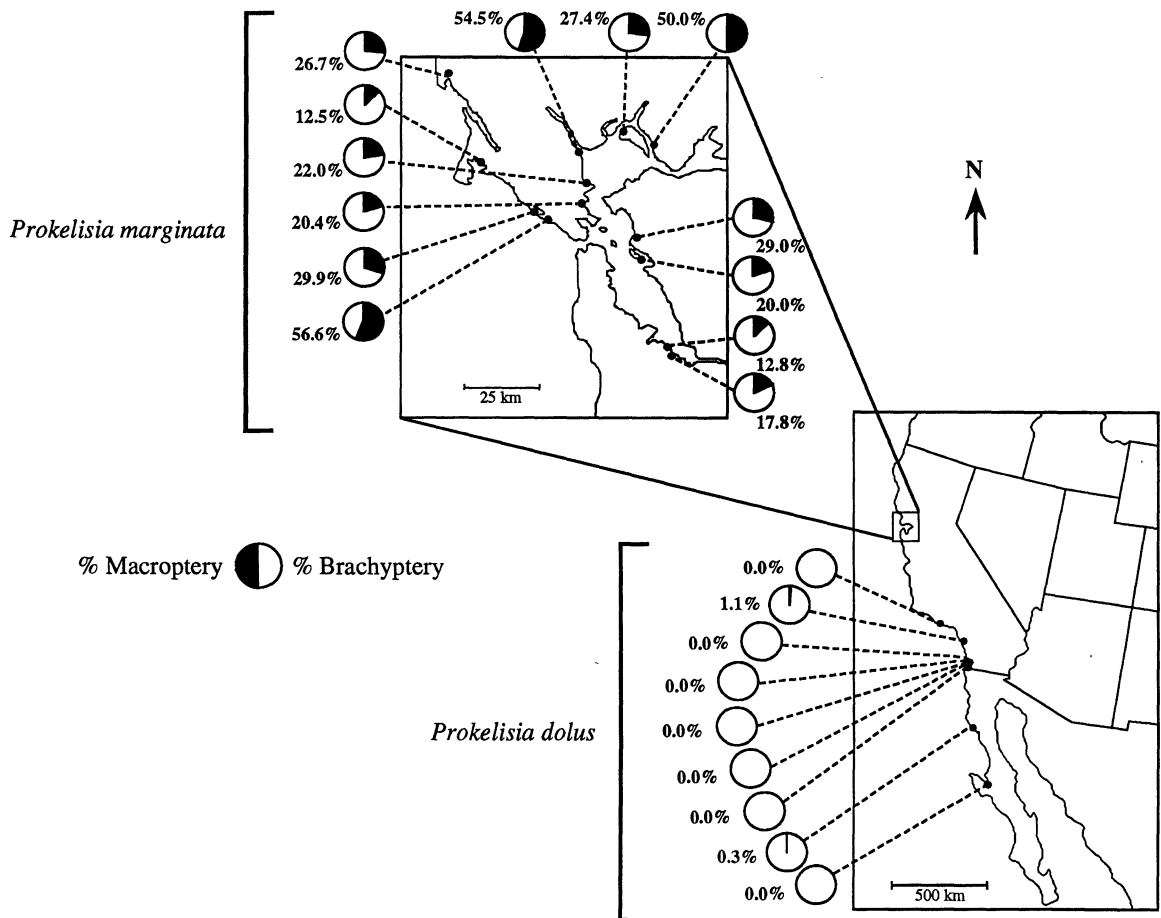
FIG. 6. Geographic variation in the dispersal capability (percentage macroptery) of Pacific coast populations of *Prokelisia marginata* in the San Francisco Bay area of California, and *P. dolus* in southern and Baja California (see Appendix for specific locations).

DISCUSSION

Dispersal can be a vitally important life history trait for organisms that exploit spatially-variable habitats (Dingle 1985, Roff 1986b, 1990, Taylor and Karban 1986, Denno et al. 1991, Roff and Fairbairn 1991). Also, dispersal can stabilize population dynamics (Reddingius and den Boer 1970, Vance 1980, den Boer 1981, Hastings 1982, Roff 1986a, Denno and Peterson 1995), determine the nature of linkages within metapopulations (Ebenhard 1991, Hansson 1991, Harrison 1991), influence species interactions (Crowley 1981, Denno and Roderick 1992), and determine the genetic structure of populations (Slatkin 1985, Roderick 1996, Peterson and Denno, *in press*). Consequently, understanding those factors that influence the evolution and maintenance of dispersal is central to most of population biology.

Of those ecological factors influencing dispersal, habitat persistence is considered to be pivotal (Southwood 1962, 1977, Southwood et al. 1974, Harrison 1980, Brown 1986, Roff 1990). Although dispersal characters may be retained at low frequencies in per-

sistent habitats if adults compete for limited resources (Hamilton and May 1977), or if winged individuals rarely fly (Fairbairn 1986, 1988, Roff 1986a), dispersal is essential for the tracking of changing resources in temporally and spatially heterogeneous environments (Roff 1974a, b, 1986a, Solbreck 1978, Leigh 1981). However, there is widespread evidence that dispersal entails significant costs, due both to the failure to find suitable habitats (Roff 1986a, Edwards and Sugg 1993) and to reduced reproduction resulting from energetic trade-offs with flight capability (reviewed in Roff 1986a, Denno et al. 1989, Roff and Fairbairn 1991). As a consequence of such phenotypic trade-offs, selection should act against dispersal in persistent habitats, and there should be an inverse relationship between habitat persistence and levels of dispersal (Roff 1990, Denno et al. 1991).

Rigorous tests of the habitat persistence–dispersal hypothesis, however, have been few and these are restricted for the most part to interspecific comparisons (see Roff 1990, Denno et al. 1991). To control for possible phylogenetic nonindependence, a preferred test
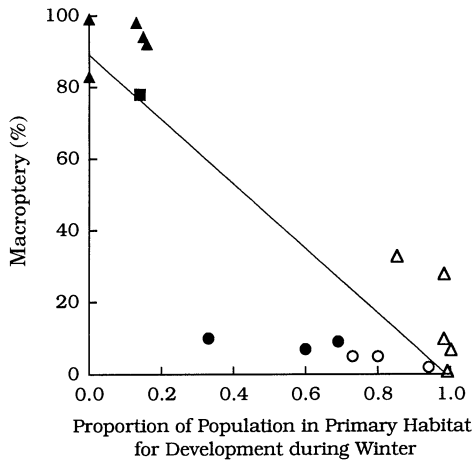
FIG. 7. Relationship between the level of macroptery (percentage) observed in field populations of *Prokelisia* plant-hoppers and the proportion of each species' population enduring through winter in the primary habitat for development ($Y^{Macroptery} = 89.8 - 90.8X$, $R^2 = 0.75$, $P < 0.001$). Populations that endure poorly through winter in their primary habitat exhibit high levels of dispersal capability. *P. marginata* populations: Atlantic coast (▲), Gulf coast (●), and Pacific coast (■). *P. dolus* populations: Atlantic coast (△) and Gulf coast (○). See Appendix for specific locations.
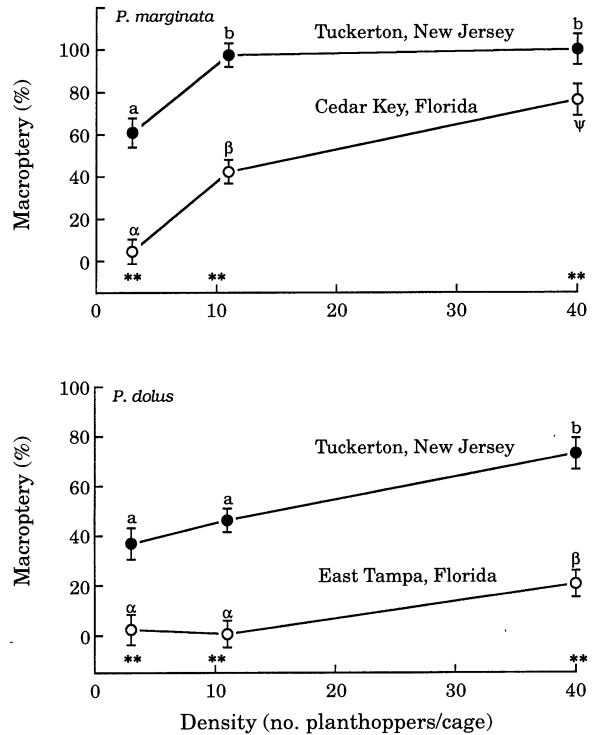

FIG. 8. Effect of rearing density on the production of macropters (percentage) in Atlantic and Gulf coast populations of *Prokelisia marginata* (top: Tuckerton, New Jersey and Cedar Key, Florida) and *P. dolus* (bottom: Tuckerton, New Jersey and East Tampa, Florida). Means (±1 SE) with different letters (Greek for Florida and Roman for New Jersey) are significantly different ($P < 0.05$). Significant differences between populations (within-density comparisons) are indicated along the abscissa (** = $P < 0.01$; ANOVA followed by Sidak's adjustment for multiple comparisons). Selection for dispersal capability has apparently acted differentially in these Atlantic and Gulf coast populations, resulting in greater production of macropters across all densities in the New Jersey populations of both *Prokelisia* species.

of the hypothesis would be to assess the relationship between habitat persistence and dispersal among populations of the same species. Although population-level variation in dispersal capability has been documented for a number of insect species including planthoppers (Masaki 1973, Dingle 1978, Vepsäläinen 1978, Iwanaga et al. 1987, Roff 1990, Denno 1994b), such variation has never been directly linked to explicit measures of habitat persistence.

In this study, we detailed geographic variation in the dispersal capability (percent macroptery) of *Prokelisia* planthoppers throughout most of their geographic range. Several lines of evidence suggest that this variation in macroptery reflects variation in actual dispersal. First, macropters of *Prokelisia* are capable of long-distance flight (>30 km) (Denno and Grissell 1979, Sparks et al. 1986, Antolin and Strong 1987), whereas brachypters can walk or jump only a few metres (Denno and Grissell 1979, Denno et al. 1985, Denno 1994b). Second, macropters of *Prokelisia* are the only wing form to effectively colonize distant habitats (Antolin and Strong 1987, Denno and Roderick 1990, Denno 1994b). Furthermore, for other wing-dimorphic insects, both the flight threshold and the extent of wing muscle histolysis are negatively associated with the proportion of macropters in the population (Fairbairn 1986, Fairbairn and Desranleau 1987, Roff and Fairbairn 1991). Thus, the dispersal capability of macropters should be reduced for populations or species in which the proportion of macroptery is low. Whether this is the case for *Prokelisia* is not known. Nonetheless, the clear association between macroptery and dis-

persal in *Prokelisia* planthoppers allowed us to use macroptery as a reliable index of dispersal for assessing the relationship between habitat persistence and dispersal.

The results of this study provide strong intraspecific support for the hypothesis that geographic variation in dispersal capability is inversely related to habitat persistence (Fig. 7). High levels of dispersal capability (92% macroptery) in Atlantic coast populations of *P. marginata* are associated with this species' inability to remain through winter in the low marsh, its primary habitat for development. Conversely, low levels of dispersal (17% macroptery) are affiliated with high endurance through winter in low-marsh habitats along the Gulf. There is widespread evidence in the literature that low-marsh habitats are severely disturbed by storms, tides, and shifting ice during winter along much of the Atlantic coast (Teal 1962, Blum 1968, Squiers and Good 1974, Denno and Grissell 1979, Niering and Warren 1980), providing an explanation for the failure of

P. marginata to remain year-round in the low-marsh habitat in this region (Denno and Grissell 1979, Denno 1983, 1988). A similar pattern prevails in northern California where intermediate levels of dispersal (29% macroptery) occur in populations of *P. marginata* (Fig. 6). In this region, low-marsh habitats are perturbed to some degree during winter, low-marsh populations of planthoppers are reduced in this season, and interhabitat dispersal between high-marsh and low-marsh habitats occurs annually (Roderick 1987).

One might ask why there is so little variation in macroptery in populations of *P. marginata* along the entire Atlantic coast (Fig. 4), when the effects of ice scouring and the subsequent destruction of tall-form *Spartina* are much more severe to the north (Blum 1968, Squiers and Good 1974, Niering and Warren 1980). The answer lies in the multitude of factors that contribute to the ephemeral nature of the low-marsh habitat throughout this region. First, living culms of *Spartina* do not persist during winter in this habitat north of 37° N latitude (Turner 1976), leaving the low-marsh habitat devoid of food and oviposition sites. Second, litter is selectively removed by tidewaters from this habitat during winter (Denno and Grissell 1979), and protective litter is needed for the successful overwintering of *Prokelisia* planthoppers (Tallamy and Denno 1979). Third, the tidal range is high along most of the Atlantic coast including locations far to the south in Florida and Georgia (Tide Tables 1992). Thus, even though living culms persist during winter along the Atlantic coast of the southern United States, they incur long periods of inundation, and do not grow tall enough for exploitation until later in spring (Denno and Grissell 1979). Consequently, although the window of opportunity for low-marsh occupancy is wider along the Atlantic coast from Florida to North Carolina, it nonetheless does close during winter and dispersal becomes a necessary strategy for the exploitation of this marsh habitat. Because high-marsh and low-marsh habitats are typically separated by distances greater than the ambit of brachypters (Denno et al. 1980, Denno 1994*b*), only macropters can colonize the low-marsh habitat in spring and escape it in fall before the onset of winter (Denno and Grissell 1979, Denno et al. 1980, Antolin and Strong 1987). Indeed, large accumulations of exclusively macropterous adults can be seen annually in spring as they colonize previously unoccupied patches of tall-form *Spartina* (Denno 1983, 1988).

Low-marsh habitats are far more persistent along the Gulf coast (Kurz and Wagner 1957, Turner 1976, Denno and Grissell 1979, Stout 1984), and *P. marginata* is much less prone to disperse in this region (Figs. 4 and 7). The equitable climate, lack of ice formation, year-round growth of *Spartina,* presence of litter, and reduced range and diurnal frequency of tides (Kirby and Gosselink 1976, Turner 1976, Denno and Grissell 1979) all undoubtedly contribute to the increased ability of *P. marginata* to remain through winter in low-

marsh habitats. Yet, dispersal capability in *P. marginata* is not lost altogether in this region (Fig. 4). We do not argue that low-marsh habitats are altogether persistent along the Gulf, only that they are much more stable here than along the Atlantic coast. Indeed, populations of this species fail to survive during winter on the smallest of *Spartina* islets located in the lowest portion of the tidal range (Antolin and Strong 1987). However, we show that on average, 40% of *P. marginata* populations occur in the mainland strand of tall-form *Spartina* habitats during winter (Fig. 3), and Antolin and Strong (1987) report successful overwintering on large *Spartina* islands as well. We contend that much lower levels of dispersal are required along the Gulf coast for *P. marginata* to exploit its primary, low-marsh habitat. Nonetheless, spring bouts of dispersal by macropters do occur along the Gulf, resulting in the colonization of extirpated habitats in the lowest portion of the *Spartina* marsh (Antolin and Strong 1987).

Because *P. dolus* both develops and successfully overwinters primarily in the same habitat on the high marsh along the Atlantic and Gulf coasts (Figs. 2 and 3), dispersal by flight is not essential for most individuals to locate suitable host plants (Fig. 5). As a consequence of high habitat persistence, average levels of dispersal are similarly low in both the Atlantic (8% macroptery) and Gulf coast regions (6% macroptery). Nevertheless, dispersal is not lost completely in these regions. Under conditions of high population density, planthoppers induce nutritional changes in plants, causing them to deteriorate (Cagampang et al. 1974, Cook and Denno 1994). For *P. dolus,* heavy infestations alter the suitability of *Spartina* such that development rate is significantly prolonged in individuals subsequently raised on the same plants (R. F. Denno and J. Cheng, *unpublished data*). For planthoppers in general, the production of macropterous adults is intensified on deteriorating host plants (Kisimoto 1965, Denno et al. 1985, 1994). Thus, conditions favoring the retention of dispersal capability may occasionally occur during population outbreaks on the high marsh. Indeed, one instance of mass aerial dispersal by *P. dolus* was observed at George Island Landing, Maryland during May 1988, in which an unusually high level of ambient macroptery (84%) was coincident with an outbreak density (R. F. Denno, *unpublished data*). In the case of *P. dolus,* such population eruptions and accompanying large-scale dispersal events are very rare. During 19 yr of study at Tuckerton, New Jersey, we never observed a large-scale aerial dispersal of *P. dolus,* yet aerial dispersal is seen annually in *P. marginata* (Denno 1988, Denno et al. 1994). Nevertheless, these rare bouts of aerial dispersal by *P. dolus* may explain why dispersal ability is not sacrificed altogether, even though its habitats are for the most part persistent along the Atlantic and Gulf coasts.

Extremely low levels of dispersal (0.2% macroptery) are characteristic of *P. dolus* populations on the Pacific

coast (Fig. 6). The frost-free climate, year-round growth of *Spartina,* and low tidal energy in southern and Baja California (Neuenschwander et al. 1979, Zedler 1982, 1993, Zedler et al. 1992) suggest that planthopper habitats there are persistent. The occurrence of high densities of *P. dolus* during "midwinter" in the only patches of *Spartina* present is consistent with the notion that habitats are persistent in this region (Appendix). However, it is difficult to argue that planthopper habitats are more persistent in this region than along the Gulf coast, where winters are no more harsh and tidal ranges are slightly less (Pearce and Smith 1990, Tide Tables 1992, 1993).

We suggest that the extremely low levels of dispersal seen in California populations of *P. dolus* result from selective pressures associated with habitat persistence as well as isolation. In a patchy environment over time, the constant loss of winged dispersers from isolated patches results in a rapid increase in the proportion of nondispersers to dispersers (Roff 1986*b,* 1990). The configuration of planthopper habitats in southern California conforms to such a situation in which most dispersal would be disadvantageous. There, *Spartina* marshes are nestled in isolated bays and are widely separated by uninhabitable coast (Zedler 1982, 1993, Zedler et al. 1992). For instance, the marsh at Point Mugu occurs nearly 100 km north of the next nearest *Spartina* marsh complex in the Anaheim–Newport area, which occurs 130 km north of the next nearest *Spartina* marshes in Mission Bay (Zedler 1982). Similarly, most of the *Spartina* marshes in Baja California are separated by distances of 100 km or more (Roberts 1989). Furthermore, within most of these isolated marshes, *Spartina* grows as a fragmented archipelago of very small, isolated patches (Zedler 1993), a situation which differs from the extensive expanses of *Spartina* that occur along most of the Atlantic and Gulf coasts (Adams 1963, Duncan 1974, Turner and Gosselink 1975, Turner 1976, Stout 1984).

That habitat isolation influences dispersal capability can be seen in the density–wing form responses of New Jersey and East Tampa populations of *P. dolus* (Fig. 8). High-marsh habitats are persistent at both locations, but *Spartina* is very patchy at its southern limit in East Tampa (Duncan 1974, Turner 1976). Although relatively low levels of macropters are produced under crowded conditions for both populations, significantly fewer macropters are produced in the East Tampa population. Overall, however, it appears that selection imposed by habitat persistence, coupled with high levels of gene flow, has had a stronger influence on the evolution of dispersal strategies in local *Prokelisia* populations than has selection imposed by habitat isolation.

Our argument for the role of selection in determining the dispersal strategies of *Prokelisia* planthoppers is strengthened by data that suggest that intraspecific variation in the dispersal capability of both *Prokelisia* species has a genetic basis. The evidence for this assertion stems from our common-garden experiment in which the production of macropters in Atlantic and Gulf coast populations of both *Prokelisia* species paralleled field levels of macroptery observed in the source populations (Fig. 8). Although our experiment was potentially confounded by maternal effects, which have been shown to influence wing form in some insects (Dixon 1985, Messina 1987, 1993, Dingle 1991), previous studies on planthoppers including *P. marginata* have indicated that maternal effects on wing form are nonexistent or weak at best (reviewed in Denno et al. 1991). Thus, the most plausible explanation for the geographic variation in wing form in both *Prokelisia* species is that it reflects genetically based differences in dispersal strategies. The selective differences operating to maintain the striking contrast in the dispersal strategies of Atlantic and Gulf coast populations of *P. marginata* must be great, since the populations differ despite high levels of gene flow across peninsular Florida (M. A. Peterson and R. F. Denno, *unpublished data*).

To date, the vast majority of evidence supporting the habitat persistence–dispersal hypothesis is qualitative and based on crude estimates of habitat variability (see Southwood 1962 and Roff 1990 for a discussion). Many of these assessments have shown a tentative link between habitat persistence and interspecific variation in dispersal (Southwood 1962, Vepsäläinen 1978, den Boer et al. 1980, Brown 1986, Roff 1990). However, most studies are compromised by the failure to control for possible phylogenetic nonindependence (but see Denno et al. 1991). Herein, we capitalized on intraspecific variation in dispersal capability (percent macroptery) to examine the relationship between habitat persistence and dispersal, thereby minimizing possible phylogenetic effects. To establish this relationship, we employed a rigorous assay of habitat persistence based on the ability of *Prokelisia* planthoppers to endure winter in their primary habitat for development. The results of this study provide the strongest evidence to date that intraspecific variation in the dispersal capability of insects is inversely related to the persistence of their habitats.

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APPENDIX

Locations of specific North American intertidal marshes from which *Prokelisia* planthoppers were sampled. For each location, the growth form of *Spartina* present (tall-form and/or short-form) and sampled for planthoppers is shown. Also listed are the sampling date(s) and sample sizes of both *P. marginata* and *P. dolus*. Data are sorted into four geographic regions: Atlantic coast (both *Prokelisia* species), Gulf coast (both *Prokelisia* species), Pacific coast in northern California (only *P. marginata*), and Pacific coast in southern and Baja California (only *P. dolus*).

Site no.	Location	*Spartina* growth form sampled	Sample date	*P. marginata* (sample size)	*P. dolus* (sample size)
Atlantic coast					
1	La Pocatiere, Kamouraska County, Quebec	Tall, short	August 1989	0	0
2	Riviere-du-Loup, Riviere-du-Loup County, Quebec	Tall, short	August 1989	0	0
3	Rimouski, Rimouski County, Quebec	Tall, short	August 1989	0	0
4	Campbellton, Restigouche County, New Brunswick	Tall	August 1989	0	0
5	Bathurst, Gloucester County, New Brunswick†	Tall, short	August 1989	0	3799
6	Cocagne, Kent County, New Brunswick	Short	August 1989	0	24
7	Shediac, Westmorland County, New Brunswick†	Tall, short	August 1989	0	891
8	Shemogue, Westmorland County, New Brunswick	Short	August 1989	0	288
9	Baie Verte, Westmorland County, New Brunswick	Tall	August 1989	0	220
10	Pugwash, Cumberland County, Nova Scotia	Tall	August 1989	0	1066
11	Antigonish, Antigonish County, Nova Scotia	Tall	August 1989	0	30
12	Ecum Secum, Guysborough County, Nova Scotia†	Tall, short	August 1989	0	3211
13	Beaver Harbour, Halifax County, Nova Scotia	Tall	August 1989	0	1492
14	Sheet Harbour, Halifax County, Nova Scotia	Tall	August 1989	0	16
15	Petpeswick, Halifax County, Nova Scotia	Tall	August 1989	0	50
16	Seaforth, Halifax County, Nova Scotia†	Tall, short	August 1989	0	176
17	Halifax, Halifax County, Nova Scotia	Short	August 1989	0	259
18	Old Barns, Colchester County, Nova Scotia	Tall	August 1989	0	169
19	Amherst, Cumberland County, Nova Scotia†	Tall, short	August 1989	0	843
20	Machias, Washington County, Maine	Tall	August 1994	0	129
21	Bass Harbor, Hancock County, Maine†	Tall, short	August 1989	0	566
22	Warren, Knox County, Maine	Tall	August 1994	0	266
23	Wiscasset, Lincoln County, Maine	Tall	August 1989	0	31
24	Bath, Sagadahoc County, Maine	Tall	August 1989	2	113
25	Scarborough, Cumberland County, Maine†	Tall, short	August 1989	1	3351
26	Seabrook, Rockingham County, New Hampshire†	Tall, short	August 1989, August 1994	0	5357
27	Newbury, Essex County, Massachusetts†	Tall, short	August 1989	0	2712
28	South Duxbury, Plymouth County, Massachusetts	Short	August 1994	0	41
29	Barnstable, Barnstable County, Massachusetts†	Tall, short	August 1989	7	3802
30	Martha's Vineyard, Dukes County, Massachusetts†	Tall, short	August 1989	3	284
31	Sippewissett, Barnstable County, Massachusetts†	Tall, short	August 1989	7	402
32	Barrington, Bristol County, Rhode Island§,†	Tall, short	August 1989	54	1585
33	Jerusalem, Washington County, Rhode Island§,‖,†,‡	Tall, short	August 1989, August 1994, May 1995	191	737
34	Old Saybrook, Middlesex County, Connecticut	Short	August 1989	5	220
35	Fenwick, Middlesex County, Connecticut	Tall	August 1989	41	0
36	Westport, Fairfield County, Connecticut	Tall	August 1989	6808	4
37	Greens Farms, Fairfield County, Connecticut§,‖,†,‡	Tall, short	August 1989, August 1994, May 1995	1784	278
38	Saugatuck, Fairfield County, Connecticut	Tall	August 1994	12	12
39	Tuckerton, Ocean County, New Jersey§,‖,†,‡	Tall, short	July 1985, April 1986, July 1986	9627	3324
40	Slaughter Beach, Sussex County, Delaware§,‖,†,‡	Tall, short	August 1988, April 1995	4406	2611
41	Kent Island, Queen Annes County, Maryland	Short	September 1988	57	22
42	George Island, Worcester County, Maryland§,†	Tall, short	May 1988	406	1005
43	Chincoteague, Acomack County, Virginia§,‖,†,‡	Tall, short	April 1995, July 1995	294	550
44	Wachapreague, Acomack County, Virginia§,†	Tall, short	May 1988	896	33
45	Virginia Beach, Chesapeake County, Virginia§,†	Tall, short	September 1994	538	188
46	Wanchese, Dare County, North Carolina	Tall, short	May 1994	232	1855
47	Beaufort, Carteret County, North Carolina§,†	Tall, short	May 1988	644	67
48	Swansboro, Onslow County, North Carolina§,†	Tall, short	May 1994	383	94
49	Wrightsville Beach, New Hanover County, North Carolina§,†	Tall, short	May 1988	55	165
50	Sunset Beach, Brunswick County, North Carolina§,†	Tall, short	May 1994	34	21
51	Pawleys Island, Georgetown County, South Carolina§,†	Tall, short	May 1988	40	506

APPENDIX. Continued.

Site no.	Location	Spartina growth form sampled	Sample date	P. marginata (sample size)	P. dolus (sample size)
52	Whitehall Terrace, Berkeley County, South Carolina	Tall, short	May 1994	62	122
53	Edisto Island, Colleton County, South Carolina§,†	Tall, short	May 1988	398	133
54	Tybee Island, Effingham County, Georgia	Tall, short	May 1994	230	25
55	Savannah, Effingham County, Georgia	Tall, short	May 1994	31	25
56	Harris Neck, McIntosh County, Georgia§,†	Tall, short	May 1988	52	63
57	Jekyll Island, Glynn County, Georgia§,†	Tall, short	May 1988	302	264
58	Fernandina Beach, Nassau County, Florida§,†	Tall, short	May 1988	47	139
59	Mayport, Duval County, Florida§,†	Tall, short	May 1988	113	159
60	Ponte Vedra Beach, St. Johns County, Florida	Tall, short	May 1994	4	68
61	Crescent Beach, St. Johns County, Florida§,†	Tall, short	May 1988	198	201
62	Marineland, Flagler County, Florida	Tall	October 1976	0	86
63	Port Orange, Volusia County, Florida†	Tall, short	May 1994	63	614
64	Oak Hill, Volusia County, Florida	Tall	May 1994	0	109

Gulf coast

Site no.	Location	Spartina growth form sampled	Sample date	P. marginata (sample size)	P. dolus (sample size)
65	Anton Lizardo, Veracruz, Mexico	Tall	December 1987	0	228
66	S. Padre Island, Cameron County, Texas‖	Tall, short	December 1989, May 1994	1085	0
67	Port Isabel, Cameron County, Texas‖,‡	Tall, short	December 1989, May 1994	4398	79
68	Corpus Christi, Nueces County, Texas‡	Tall, short	December 1989	14	244
69	Port Aransas, Nueces County, Texas§,†	Tall, short	May 1994	55	67
70	Rockport, Aransas County, Texas	Tall, short	December 1989	1117	842
71	Matagorda, Matagorda County, Texas§,†	Tall, short	May 1994	139	438
72	Gilchrist, Chambers County, Texas§,†	Tall, short	May 1994	1204	2839
73	Oak Grove, Cameron Parish, Louisiana§,†	Tall, short	May 1994	32	118
74	Cocodrie, Terrebonne Parish, Louisiana§,†	Tall, short	May 1994	39	87
75	Port Sulphur, Plaquemines Parish, Louisiana	Tall, short	December 1990	0	177
76	Buras, Plaquemines Parish, Louisiana	Tall, short	December 1990	0	129
77	Waveland, Hancock County, Mississippi‖,‡	Tall, short	December 1990	138	161
78	Pass Christian, Harrison County, Mississippi§,†	Tall, short	May 1994	247	30
79	Dauphin Island, Mobile County, Alabama	Tall, short	December 1990	86	18
80	Fort Morgan, Baldwin County, Alabama	Tall, short	May 1994	597	304
81	Destin, Okaloosa County, Florida	Tall	May 1994	71	23
82	Eastpoint, Franklin County, Florida†	Tall, short	May 1994	964	700
83	Dekle Beach, Taylor County, Florida§,†	Tall, short	June 1987	2035	31
84	Cedar Key, Levy County, Florida§,‖,†,‡	Tall, short	May 1987, May 1988, February 1995	1477	231
85	Pine Island, Hernando County, Florida§,†	Tall	June 1987	106	50
86	Anclote, Pasco County, Florida	Short	June 1987	3	115
87	Riverview, Hillsborough County, Florida§,†	Tall, short	May 1988	1555	639
88	Gibsonton, Hillsborough County, Florida	Tall, short	June 1987	15	148
89	East Tampa, Hillsborough County, Florida†	Tall, short	May 1994	103	509
90	Archie Creek, Hillsborough County, Florida	Tall, short	June 1987	78	416

Pacific coast
(northern California)

Site no.	Location	Spartina growth form sampled	Sample date	P. marginata (sample size)	P. dolus (sample size)
91	Bodega Bay, Sonoma County, California	Tall, short	August 1988	30	0
92	Drakes Estero, Marin County, California	Tall	August 1988	72	0
93	Bolinas, Marin County, California§,‖	Tall, short	August 1988	1352	0
94	Stinson Beach, Marin County, California	Tall, short	August 1988	823	0
95	Corte Madera, Marin County, California	Tall, short	August 1988	475	0
96	China Camp, Marin County, California	Tall, short	August 1988	618	0
97	Petaluma River, Marin County, California	Tall, short	August 1988	615	0
98	Skaggs Island, Napa County, California	Tall	August 1988	412	0
99	Vallejo, Solano County, California	Tall	August 1988	1227	0
100	Emeryville, Alameda County, California	Tall, short	August 1988	821	0
101	Alameda, Alameda County, California	Tall, short	August 1988	845	0
102	East Palo Alto, San Mateo County, California	Tall, short	August 1988	551	0
103	Palo Alto, Santa Clara County, California	Tall, short	August 1988	615	0

(southern and Baja California)

Site no.	Location	Spartina growth form sampled	Sample date	P. marginata (sample size)	P. dolus (sample size)
104	Point Mugu, Ventura County, California	Tall	June 1986, February 1989	0	525
105	Newport Beach, Orange County, California	Tall	December 1978, June 1986	0	184
106	Mission Bay, San Diego County, California	Tall	February 1989	0	51
107	Seaworld, San Diego County, California	Tall	February 1989	0	79

APPENDIX. Continued.

Site no.	Location	*Spartina* growth form sampled	Sample date	*P. marginata* (sample size)	*P. dolus* (sample size)
108	Coronado, San Diego County, California	Tall	February 1989	0	41
109	Chula Vista, San Diego County, California	Tall	February 1989	0	242
110	Tijuana Estuary, San Diego County, California	Tall	June 1986	0	25
111	San Quintin, Baja California Norte, Mexico	Tall, short	February 1990	0	660
112	Guerrero Negro, Baja California Sur, Mexico	Tall	February 1990	0	889

Notes: Locations used for analysis of the proportional abundance of *P. dolus* in tall- and short-form habitats during the warm season (†) and during the cold season (‡). The table also indicates the locations used for analysis of the proportional abundance of *P. marginata* in tall- and short-form habitats during the warm season (§) and during the cold season (‖).