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Seagrass growth, reproductive, and morphological plasticity across environmental gradients over a large spatial scale

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ABSTRACT

Phenotypic variability is a valuable adaptive mechanism for seagrass species that exist in a dynamic environment and can lead to significant intraspecific regional distinctions in life history. Research is lacking in studies examining the significance of within-species phenotypic variation in relation to gradients in environmental condition at a large spatial scale. These studies are essential to better understanding the potential for acclimatization and tolerance capabilities of seagrasses in declining coastal environments. *Thalassia testudinum* (turtlegrass) is a ubiquitous keystone seagrass species across the Caribbean and Gulf of Mexico (GoM) that populates both environmentally dynamic estuaries and stable coastal environments. In order to elucidate environmentally driven distinctions in spatially separated populations, we examined characteristics of shoots exposed to widely separated distinct coastal environments with varying degrees of environmental stability and suitability. In our comparison, three sampling locations vary considerably in ambient water temperature, salinity, and water column clarity along a gradient from oscillating, higher stress conditions to stable, more favorable conditions. Shoots tended to have larger leaves with more biomass in the stable environment and also exhibited an older shoot age structure and higher horizontal expansion rate. However, shoots in the more variable, higher stress environment exhibited greater evidence of flowering and first flowered at an earlier age. The results elucidate large spatially distinct and environmentally relevant differences in morphology, growth, and life history highlighting the need for more studies regarding phenotypic variability of seagrass populations across environmental gradients.

1. Introduction

Seagrasses are subject to many inherent environmental stressors in their submerged marine habitats. For instance, fluctuating conditions of light, temperature, and salinity can have large effects on seagrass morphology, growth, and function (Short et al., 1996). Seagrasses are capable of acclimating to varying environmental conditions by utilizing the innate plasticity of individual seagrass modules provided by phenotypic variation (Hemminga and Duarte, 2000). Phenotypic variation is a well-documented adaptive mechanism that can drive morphological, demographic, reproductive, and physiological changes for environmental acclimation in seagrasses (Cabaço et al., 2009; Kim et al., 2014). Accordingly, past studies have found intraspecies differences in morphological and functional attributes across environmental gradients of light, temperature, and salinity (Kaldy et al., 2000; Enriquez et al., 2002; Kendrick et al., 2008). Nevertheless, studies documenting species-specific phenotypic variation at large spatial scales, and how such variation may be related to parallel environmental gradients, are scarce. Here we contribute to filling this gap by examining seagrass phenotypic plasticity in morphological, growth and functional attributes across a large swath of the Gulf of Mexico (GoM).

We studied turtlegrass (*Thalassia testudinum*), a subtropical/tropical seagrass widely distributed throughout the Caribbean and GoM, with a large literature representation that provides a plethora of information regarding this species' optimum envi-

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Table 1
Environmental characteristics of sampling areas with means of variables with coefficient of variation [CV] and lowest/highest observations. We were primarily interested in capturing the period 2002–2010 (i.e., the previous eight years to collection) since this corresponded on average to the maximum age of the shoots collected. However, data from this period was limited for EF, therefore we searched for additional data for this area and found collections from 1990 to 1995. Overall the limited data for 2002–2010 are consistent with the more abundant data from 1990 to 1995 at this site, which offers reassurance to our comparison and differences inferred among sites based on the 2002–2010 data sets.

	Site depth (m)	Salinity (ppt)	SST (°C)	Regional annual rainfall[a] (cm)	Light extinction (K_d, m^{-1})	Estimated annual PAR at depth[b] ($mJ\,m^{-3}$)
		mean [CV] (range)	mean [CV] (range)	30 year normals (1980–2010)	mean [CV] (range)	mean
BL[c,f] 2002–2010	0.7	21.4 [0.22] (7.5–31.6)	23.2 [0.28] (7.6–33.5)	155	1.6 [0.53] (0.44–3.32)	930.08
EF[d,f] 1990–1995	0.7	29.5 [0.12] (20.6–35.2)	21.9 [0.28] (10.1–32.6)	80.8	1.1 [0.64] (0.19–2.43)	1202.49[g]
2002–2010		30.4 [0.17] (14.5–39.0)	23.4 [0.26] (10.1–32.7)		1.4 [0.27] (0.86–1.80)	
LKSP[e,f] 2002–2010	2.3	36.5 [0.02] (34.1–37.8)	27.2 [0.14] (12.7–33.4)	116.8	0.4 [0.81] (0.01–1.11)	1422.51

[a] Data provided by climate normal tables from NOAA National Center for Environmental Information: ncdc.noaa.gov.
[b] Calculated using mean K_d and annual insolation from summation of monthly mean daily broadband insolation at Mobile (BL), Corpus Christi (EF), and Key West (LKSP) airports. PAR = 0.45 × broadband (Jacovides et al., 2003).
[c] Christiaen et al., DISL, unpublished data; data collection periods: 2002–2010 (salinity); 2003–2010 (light and SST).
[d] Dr. Paul Montagna at Texas A&M, Corpus Christi; Dunton, 1994; Herzka and Dunton, 1997; Kopecky and Dunton, 2006; data collection periods: 1990–1995 and 2002–2010 (light); 1991–1995 and 2003–2010 (salinity); 1993–1995 and 2003–2010 (SST).
[e] FKNMS Seagrass Status and Trends Monitoring Data, Site 241 (http://serc.fiu.edu/seagrass/!cdreport/datahome.htm); data collection periods: 2002–2010 (light); 2002–2008 (salinity); 2003–2010 (SST).
[f] Supplemental metadata provided by TCOON and/or NOAA NDBC.
[g] Calculated using Kd for both timeframes 1990–1995 and 2002–2010.

ronmental preferences. Previous studies have determined the optimal temperature for *T. testudinum* ranges between 27 and 30 °C, optimum salinity between 24 and 35‰, and the minimum light requirement is approximately 18% surface irradiance (Phillips, 1960; Lee et al., 2007; Garrote-Moreno et al., 2014). For sub-optimal conditions, previous work indicates this species may have substantial phenotypic variation in multiple morphological and functional traits (Manuel et al., 2013; Garrote-Moreno et al., 2014). For instance, turtlegrass may acclimate to reduced light availability by reducing leaf surface area, increasing leaf chlorophyll content, and increasing the chlorophyll *b* to chlorophyll a ratio (Major and Dunton, 2002; Lambers et al., 2008). Turtlegrass, like other seagrass species, may also modify its reproductive output to cope with sub-optimal conditions of light, temperature, and salinity (Obeso, 2002; Reusch et al., 2005). The extent to which these environmentally linked life history variations coincide is largely unknown since large-scale phenotypic comparisons for this species has not been thoroughly examined.

Substantial phenotypic variation for turtlegrass may exist across the GoM due to the occurrence of marked environmental gradients. The northern coastline has a warm-temperate to subtropical climate. It has relatively turbid waters due to inputs from large watersheds along the coastline (USGS, 2004), although annual rainfall varies widely across this region from a maximum of 178 cm east of the Mississippi River to 18 cm on the South Texas coastline (Bailey, 1995). In contrast, the coastline surrounding the Florida Keys has overall higher temperatures due to its tropical climate and much clearer waters with typical annual rainfall levels approximately 100 cm (Bailey, 1995). Therefore, environmental conditions of light, temperature and salinity produce an environmental variability and, as a result, a seagrass suitability gradient across the Gulf of Mexico coastline.

In this paper, we examine the extent of phenotypic variability in a broad suite of morphological, growth, and functional features of turtlegrass populations from three widely separated habitats. These habitats range in abiotic influence and represent the distinct environments often encountered across extensive coastlines, such as the Gulf of Mexico. We examine the range of environmental variation in light availability, temperature, and salinity conditions of each environment to better understand the degree of phenotypic variation encountered, as well as suggesting some potential mechanisms partially responsible for this variation. This comparison provides a measure of phenotypic variation for a vital habitat forming species across a gradient of environmental variability to provide greater insight into the factors driving intraspecific growth, life history, and morphological differences among widely separated populations.

2. Materials and methods

2.1. Study areas

The *T. testudinum* populations studied are located in the Gulf Islands National Seashore in Big Lagoon (BL), Florida (30.18°N, 87.25°W); East Flats (EF) in Corpus Christi Bay, Texas (27.49°N, 97.07°W); and near Long Key State Park (LKSP) in the Florida Keys National Marine Sanctuary (24.48°N, 80.49°W) (Fig. S1). BL is a shallow body of water that connects lower Perdido and Pensacola Bays to the northcentral Gulf of Mexico. Turtlegrass is the dominant seagrass species and the population appears to be stable with an areal coverage of 2.2 km^2 (Moss, 2011). This area has moderate to low light availability and highly variable salinities (Fig. S2, Table 1) due to inputs from the Perdido and Pensacola estuaries (Schwenning and Bruce Handley, 2007).