Niche differences between sympatric Sargassum species in the northern Gulf of California

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ABSTRACT: Sargassum johnstonii Setchell & Gardner, S. herporhizum Setchell & Gardner, and S. sinicola Setchell & Gardner var. camouii (Dawson) Norris & Yensen display spatial separation in large- and small-scale zonation patterns and habitat differences at low tide on an intertidal coquina limestone reef in the northern Gulf of California, Mexico. On a small scale within mid-intertidal pools, S. johnstonii occurs in the shallowest depths, followed by S. herporhizum and S. sinicola var. camouii at successively greater depths in the pools. On a large scale in the lower intertidal zone on emergent coquina S. johnstonii again occurs in the uppermost position in zonation, with S. herporhizum below. In this lower area the distribution of S. sinicola var. camouii overlaps with that of emergent S. herporhizum but most plants of the former species occur in pools. Thus, in the same low-tide habitat (pools or emergent coquina) the species occupy the different vertical zones, whereas when they do occupy the same vertical zone they occupy different habitats. At some sites where S. herporhizum and tide pools are rare or absent, S. sinicola var. camouii in the intertidal zone shifts its habitat from tide pools to mostly emergent habitats.

INTRODUCTION

Species of Sargassum frequently constitute the most abundant overstory algae on tropical and subtropical shorelines (Fritsch, 1945; Stephenson and Stephenson, 1972; De Wreede, 1976; Prince and O'Neal, 1979). Studies of intertidal zonation of Sargassum have demonstrated that the genus is generally found in low intertidal areas and tide pools (Stephenson and Stephenson, 1972; De Wreede, 1973, 1978). Few studies have documented zonation and habitat differences of several Sargassum species occurring in the same intertidal area (Tsuda, 1972; De Wreede, 1973). Differences between species are most apparent against a background of similarity, and for congeneric species, differences in the spatial dimensions of their niches indicate some of the underlying mechanisms determining distributions. These differences are more significant when, as in the present situation, the species involved are the predominant, large components of the vegetation canopy.

This paper documents differences in intertidal zonation and habitat between Sargassum johnstonii Setchell & Gardner, S. herporhizum Setchell & Gardner, and S. sinicola Setchell & Gardner var. camouii (Dawson) Norris & Yensen near Puerto Peñasco, Sonora, Mexico. These large-scale patterns will be compared to zonation and habitat features occurring on a small scale within tide pools.

Species of Sargassum are the only algae in the Gulf of California that approach the size of kelps (Laminariales), which are virtually absent from the region (Dawson, 1944; Norris, 1975). Sargassum plants form a large habitat for a diverse assemblage of invertebrates (Brusca, 1980), fishes (Thomson and Lehner, 1976), and epiphytic and understory algae (Dawson, 1966). Niche differences between Sargassum species will affect and be affected by these assemblages.

Intertidal zonation of algae in the northern Gulf of California has been the subject of few reports. Littler and Littler (1981) studied intertidal zonation of algae at Pelican Point, near one of the study sites of the investigations reported here. They, however, were primarily interested in aspects of productivity and morphology of smaller, higher intertidal species rather than the delineation of zonation and habitat differences. Moreover, their study did not include the extensive stands of Sargassum in the low intertidal zone at Pelican Point. Recent studies of seasonal patterns of
abundance of algae in this region include those of Wynne and Norris (1979), Norris and Yensen (in press), and McCourt (1983, 1984).

Mackie and Boyer (1977) described the zonation of macroinvertebrates at Station Beach in the northern Gulf of California, one of the sites investigated in my study. They found that zones were more diffuse than those typical of many shorelines (Lewis, 1964; Ricketts et al., 1968; Stephenson and Stephenson, 1972). Mackie and Boyer (1977) postulated that the less distinct zonation at Station Beach is due to the greater variety of habitats afforded by the soft coquina limestone reef and the gentle slope of the reef that results in a correspondingly gentler exposure gradient. Brusca (1980) presented a generalized zonation scheme for intertidal communities throughout the Gulf of California and concluded that invertebrate intertidal communities display very few of the discrete zones typical of California coastlines. The present study examined the discreteness of intertidal zonation of a closely related set of algae that are important vegetational components of such communities.

MATERIAL AND METHODS

Study sites

The 3 study sites were in the vicinity of Puerto Peñasco, Sonora, Mexico, in the northern Gulf of California (Fig. 1). The physical environment has been described in detail by Thomson and Lehner (1976). Monthly onshore sea surface temperatures average near 14 °C in winter and 30 °C in summer. Exposed tide pools in intertidal areas are subject to slightly greater extremes in temperature in both winter and summer (Thomson and Lehner, 1976). Spring tide range at Puerto Peñasco exceeds 7 m (Thomson, 1981) and is among the largest in Pacific North America. Hereafter, tide levels will be expressed in meters in relation to mean low water, which serves as zero-tide level on the annual tide calendars for the northern Gulf of California (Thomson, 1981).

Two of the 3 study sites, Station Beach and Las Conchas (Fig. 1), were located on an unbroken stretch of south-facing coastline that extends from Puerto Peñasco to the mouth of a negative estuary, or estero, Estero Morua. Low tides expose a reef made of coquina limestone, an erodible substrate easily penetrated by the holdfasts of many algae. Extensive erosion has produced tide pools and depressions ranging from centimeters to tens of meters in diameter. The intertidal coquina reef is divided into 2 major topographic areas by a fault in the reef at about the zero-tide level, below which the reef slope becomes steeper.

Throughout its length the reef is bordered above by a shell-fragment beach and below by a sandy-bottom subtidal area. Sand and shell fragments collect in the bottoms of the pools and in patches on the reef. Sand is progressively more abundant eastward on the shoreline until the reef is nearly covered by sand at the mouth of Estero Morua. In addition, the slope of the reef becomes more shallow toward the estero.

The third site surveyed was Pelican Point, 10 km northwest of Puerto Peñasco (Fig. 1). The section of shoreline studied faces southwest and has a steeper slope than those of the other sites. The substrate is mostly granitic outcrops and boulders, with an expanse

Fig. 1. Location of study sites at Puerto Peñasco and vicinity, Sonora, Mexico
of coquina only in the lowest region of the intertidal zone. Despite its proximity to the Cholla Bay mud flats and a sandy-bottom subtidal area, sand accumulation appears comparable to that at Station Beach.

Species studied

Three *Sargassum* species occur in the northern Gulf of California (Norris and Yensen, in press): *S. johnstonii*, *S. herporhizum*, and *S. sinicola*. Two varieties of *S. sinicola* occur at Puerto Peñasco: var. *sinicola* and var. *camouii*. The investigations reported here centered on *S. johnstonii*, *S. herporhizum*, and *S. sinicola* var. *camouii*. *S. sinicola* var. *sinicola* occurs on subtidal patch reefs and rarely in the intertidal zone. Throughout this paper, *S. sinicola* refers only to the variety *camouii* unless otherwise noted. Further discussions of the taxonomy and morphology of the species have been provided by Norris and Yensen (in press) and McCourt (1983).

Intertidal transects

Norris and Yensen (in press) and McCourt (1984) have described seasonal patterns of abundance of the 3 *Sargassum* species in the study area. All species are most abundant in late winter and in spring. McCourt (1984) reported that, despite seasonal differences in abundance, the species maintained differences in habitat and relative position in the zonation pattern throughout the year.

The basic pattern of intertidal zonation on Station Beach was documented in fall 1977 in the area near a large tide pool (70 x 20 m) known as Station Pool. Five transects, spaced 10 m apart, were established, extending perpendicular to the shoreline from the upper limit of the coquina reef (1.8 m) to the lowest spring-tide level (1.8 m). Transect length ranged from 90 to 110 m; some transects were shorter than others due to submergence of the lowest segments during census and to differences in reef slope between transects. At 10-cm intervals along the transect line, presence of a species of *Sargassum* was recorded if a portion of the plant lay beneath that point on the line. Plants were traced to their holdfasts, which were noted as either in tide pools or on emergent reef. The terms 'emergent' and 'tide pool' refer to a plant's habitat at low tide. Percent occurrence for each species in 5-m intervals was calculated as the number of points at which a species occurred divided by the total number of points sampled and multiplied by 100. This was taken to be an estimate of the percentage of the substratum covered by the canopy of *Sargassum* plants.

Intertidal distributions at the other study sites were surveyed in late winter and spring. One site, Las Conchas, provided an example of *Sargassum* zonation in a very sandy area. Two transects were surveyed at this site in February 1981. The other site, Pelican Point, provided 2 different types of solid substrate, coquina and granite, with the former restricted to the lowest part of the intertidal zone. Five transects were surveyed at Pelican Point in April 1981. Data collected in spring 1981 from 5 Station Beach transects are also presented for comparison with that from transects at these other sites.

Topographic profiles were mapped for transect stations, using the Emory line method (Dawes, 1981). Elevations relative to the zero-tide level and substrate type were recorded at 5-m intervals.

Pool transects and habitat measurements

Transects were conducted across 14 tide pools of various sizes and depths in the lower mid-intertidal (+ 0.6 m) interval at Station Beach in spring 1977 to determine the distribution, habitats, and sizes of *Sargassum* on a small scale within tide pools. Transects were established across the centers of *Sargassum* patches in the pools. Data recorded at 10-cm intervals along the line were: species of *Sargassum*, if present; maximum length of plant; and water and sand depths at the plant's holdfast. Linear measurements were made to the nearest 0.5 cm. Combined length of all transects totaled 42.5 m, and 293 *Sargassum* plants were sampled.

RESULTS

The distribution of *Sargassum* will be described on 3 spatial scales. First, zonation of the three species in the intertidal zone at Station Beach will be described. The basic zonation scheme will then be compared to zonation patterns at the other sites. Finally, differences between species on a smaller spatial scale will be documented with data on zonation, habitats, and plant size within tide pools.

Intertidal transects

Canopy cover on the Station Beach transects in autumn 1977, estimated from total percent occurrence for all 3 *Sargassum* species, was 28% of the reef area. The canopy cover of *S. sinicola* was 17%, about 3 times that of *S. herporhizum* (6%) and *S. johnstonii* (5%). Most of the remaining 72% of the reef area was covered by emergent algal turf such as that described
for this area by Stewart (1982), sand in tide pools, and various sessile animals.

Two distinct zones of *Sargassum* distribution were identified: an upper zone above +0.3 m and a lower zone below −0.3 m (Fig. 2). These zones were separated by the reef fault at the zero-tide level, 60 m from the top of the transects (Fig. 2). The abundance of *S. sinicola* was similar in both upper and lower zones. *S. johnstonii* and *S. herporhizum* were markedly more abundant in the lower than in the upper zone.

The *Sargassum* species showed distinct differences in their occurrence in emergent or pool habitats on these transects. Most (93%) *S. sinicola* occurred in pools throughout both zones (Fig. 2). In contrast, the habitats of *S. herporhizum* and *S. johnstonii* were mostly emergent (77 and 91%, respectively), particularly in the lower zone.

Above the reef fault all *Sargassum* species were restricted to the pools. The hiatus in *Sargassum* occurrence between approximately +0.3 m and −0.3 m coincided with the absence of pools across the reef fault. Pools were common below −0.3 m, although usually only *S. sinicola* occurred in pools in the lower zone.

In the lower zone outside the pools, *Sargassum johnstonii* and *S. herporhizum* occurred primarily on emergent coquina and were vertically zoned (Fig. 2). *S. johnstonii* was almost entirely absent below −1.5 m. Below this point *S. herporhizum* was the most abundant *Sargassum* on emergent coquina, growing in large monospecific stands. A few patches of *S. sinicola* were found on emergent coquina at this very low tide level, but most plants of this species were found in pools.

In Fig. 2 the distributions of *Sargassum sinicola* and *S. herporhizum* appear truncated only because the transects were terminated at the water's edge. Both species occur subtidally, but *S. sinicola* extends farther seaward than *S. herporhizum* on coquina patch reefs on the sandy bottom. *Sargassum* zonation patterns at Station Beach (Fig. 3) in 1981 were similar to the pattern found at Station Beach in 1977 (Fig. 2) despite changes in abundance (McCourt, 1984). *S. herporhizum* dropped out of the zonation pattern between Station Beach and Las Conchas; there were almost no *S. herporhizum* on the reef at Las Conchas (Fig. 4). On the transects themselves only one small patch of *S. herporhizum* occurred in a pool. A search of the reef for 50 m in either direction failed to turn up more plants of...
this species. Nor were any found in a search of the reef up to 2 km westward of the transects. The Las Conchas shoreline has a much more gradual slope than the other sites (Fig. 4). Despite a larger intertidal zone there is less coquina substrate here because much of the intertidal zone is covered by sand.

In contrast to its abundance in the lower zone at Station Beach, *Sargassum herporhizum* was relatively scarce at Pelican Point, where *Sargassum* plants were largely restricted to the lower intertidal zone on the emergent parts of the coquina shelf (Fig. 5). Pools were infrequent on the shelf and no large tide pools comparable to Station Pool occurred at Pelican Point. *S. herporhizum* was occasionally found in tide pools in the granitic outcrops higher in the intertidal zone, although no pools occurred on the transects.

At sites where *Sargassum herporhizum* was scarce (Pelican Point) or absent (Las Conchas), a larger proportion of plants of *S. sinicola* occurred in emergent habitats. The relative frequencies of *S. sinicola* plants occurring in emergent or pool habitats at these sites were the reverse of those at Station Beach: most plants occurred on emergent coquina instead of in pools (Fig. 6). *S. johnstonii* and *S. herporhizum* occurred primarily on emergent substrate at all sites (Fig. 6) (the 3 *S. herporhizum* plants at Las Conchas were in 1 tide pool).

Data from the 14 pools sampled at Station Beach were combined for presentation. When data from individual pools were analyzed separately, the same trends were evident, but sample sizes were sometimes too small to achieve statistical significance. Within-pool deviations from trends in the combined data are noted.

Mean water depths for the 3 species (Fig. 7) were significantly different (*p* < .01, Welch’s ANOVA as described by Dixon and Brown, 1979; and pairwise *t*-test). This depth zonation in pools was similar to the zonation pattern on emergent coquina at Station Beach (Fig. 2). *Sargassum johnstonii* occurred in shallow water near the edges of pools, whereas *S. herporhizum* and *S. sinicola* occurred in successively deeper parts of the pools.

Average depth for *Sargassum sinicola* in a pool correlated with maximum depth in the 14 pools (*r* = .800, *p* < .01), i.e. this species always tended to occur in the deeper parts of pools regardless of the pool depth. Average depth of *S. herporhizum* correlated less closely (*r* = .367, *p* > .05) with maximum depth in the pool because even in the deepest pools, plants still occurred at only intermediate depths. Average depth of *S. johnstonii* plants at the edges of pools was independent of maximum pool depth (*r* = .005, *p* > .05).
Thus, regardless of the maximum depth of the pool, the 3 species maintained the same positions relative to their average water depths.

The lengths of Sargassum herporhizum and S. sinicola plants correlated positively with the water depths at which they were found, \( r = .597, n = 130, p < .01 \) and \( r = .422, n = 128, p < .01 \), respectively. The length of S. johnstonii did not correlate with water depth of the plant \( r = -.072, n = 35, p > .05 \). The 3 species also showed significant differences in average length (Fig. 8) \( p < .01 \), Welch's ANOVA, and pairwise t-tests). Sargassum johnstonii, whose length was independent of water depth, attained the greatest length (Fig. 8).

Average sand depths for the 3 species (Fig. 9) showed a pattern similar to that for average water depths, which would be expected because sand accumulates in the deeper parts of pools. Sargassum johnstonii had the shallowest mean sand depth, significantly different from depths for the other species \( p < .03 \), Welch's ANOVA, and pairwise t-tests). Mean sand depth for S. herporhizum was less than that for S. sinicola, but the difference was not statistically significant. Sand levels are dynamic and a plant must deal with a wider range of sand depths than water depths. Although water in a tide pool may partially drain out during low tide, sand cover can change rapidly between tides when wave action either deposits or removes sand. Variation of sand depth in the pools provides an additional indication of the sand conditions a single plant may endure. The sand depth variance of S. sinicola was significantly greater than the variances for S. herporhizum and S. johnstonii \( p < .05 \), Levene's test, Dixon and Brown, 1979), reflecting the more variable sand level in the habitat of S. sinicola in the deeper parts of pools.

**DISCUSSION**

The distributions of Sargassum johnstonii, S. herporhizum, and S. sinicola show distinct differences in vertical zonation and habitat. Intertidal Sargassum plants at Station Beach occurred in 2 distinctly sepa-
Fig. 8. Mean length of *Sargassum* species in Station Beach tide pools

Fig. 9. Mean sand depth of *Sargassum* species in Station Beach tide pools
rate zones: in mid-intertidal pools above the reef fault (above zero-tide level) and in pools and on emergent coquina below the fault (below zero-tide level) (Fig. 2).

This distribution pattern is similar to that of an introduced species, *S. muticum*, in the Strait of Georgia, British Columbia, as reported by De Wreede (1978, 1984), who also found *Sargassum* plants in 2 separate areas, one in the upper and one in the lower intertidal zone. These results do not necessarily contradict the conclusions of Brusca (1980) and Mackie and Boyer (1977) on the discreteness of intertidal invertebrate communities in the Gulf of California. They described a lack of discreteness in the zonation of communities in this region, whereas this study reveals clear differences between a set of closely related species. The existence of a 3-species zonation pattern within the setting of a more diffuse pattern of community zonation indicates that the *Sargassum* species, though abundant as canopy organisms, do not exert a dominating, pattern-inducing effect on zonation.

In the lower zone at Station Beach *Sargassum sinicola* dominated pools, whereas *S. johnstonii* and *S. herporhizum* grew primarily on emergent coquina (Fig. 2). Although the latter 2 species shared the same emergent habitat type, they were vertically zoned, with *S. johnstonii* higher on the shore (Fig. 2). Within pools in the upper vertical zonation of the 3 species with respect to water depth was observed (Fig. 7). The zonation pattern in pools was similar to that found on emergent substrates in the lower zone: *S. sinicola* occurred in the deepest water, *S. herporhizum* in intermediate depths, and *S. johnstonii* in the shallowest. In summary, when 2 or 3 species occupy the same habitat type at low tide (pool or emergent coquina) they occur in different vertical zones, whereas when they occupy the same vertical zone they occur in different habitat types.

Physical factors usually set the upper limits to a species' intertidal distribution (Connell, 1972, 1974). The physical factors most likely affecting zonation of the 3 *Sargassum* species in pools and in the intertidal zone as a whole are exposure to air and sand stress in the form of scour or burial. Norton (1977) showed that desiccation in summer and frothing in winter affected the upper intertidal limit of *S. muticum* in the San Juan Islands. Drying experiments on Puerto Penasco species (McCourt, 1963) showed that *S. johnstonii*, the uppermost species in all zonation patterns, lost water more slowly than the other 2 species. Different rates of desiccation at low tide probably set the different upper limits of the three *Sargassum* species on emergent coquina habitats.

At Pelican Point and Las Conchas the upper limits of *Sargassum johnstonii* in the intertidal zone coincide with changes in substrate. The deep sand at Las Conchas is obviously unsuitable for juvenile settlement. *Sargassum* plants do grow on granite in some tide pools at Pelican Point, however, and the reason for their absence from this substrate is unclear. Coquina is porous and retains some water at low tide, making it a cooler surface to grow on. Higher temperatures on nonporous granite surfaces in the mid-intertidal zone may preclude settlement and survival of even the desiccation-resistant *S. johnstonii*.

Exposure to air may also affect the small-scale zonation of plants in tide pools in the mid-intertidal zone. Although these habitats are by and large continuously submerged, plants at the edges of pools will be subject to greater probability of desiccation due to minor changes in pool water depth (gradual draining during low tide) or random positioning of plants. *Sargassum johnstonii*, the species with the slowest rate of water loss, is found at pool edges in the shallowest water. Plants of this species are commonly found at low tide with holdfasts anchored in only a few centimeters of water, whereas most branches lie on adjacent emergent reef. Certainly the greater desiccation resistance of this species is important in allowing it to occur here.

*Sargassum johnstonii* in tide pools show no correlation of plant height with water depth. Its greater resistance to desiccation may free it from the need to be completely submerged in the mid-intertidal zone and thereby also allow it to reach a larger size in this habitat and increase the amount of reproductive structures produced.

The positive correlation between plant length and pool depth reported here for *Sargassum sinicola* and *S. herporhizum* was also reported by De Wreede (1978) for *S. muticum* in pools in the Strait of Georgia. This correlation is interesting because plants spend most of their time submerged by several meters of water at high tide. A plant's length may depend more on the character of its habitat when the tide is out than when the tide is in. De Wreede (1978) found that intertidal *S. muticum* plants were more highly branched than lower intertidal forms. When under water the lateral *Sargassum* branches with their air bladders float upward, and they may branch rather than keep elongating when they reach the surface of pools. If distal segments are removed or damaged by desiccation at the surface of a pool, increased branching or development of blades may be induced (Fagerberg and Dawes, 1977).

The absence of *Sargassum herporhizum* from the very sandy Las Conchas site suggests that sand burial or scour may have an adverse effect on this species. The absence of this species with a rhizoidal holdfast from a sandy habitat is anomalous compared to some kelp species with rhizoidal holdfasts that occur in sites subject to severe sand scour. Markham (1972, 1973a, b) found that *Laminaria sinclairii* (Harvey) Farlow,
Anderson & Eaton in sand-scoured habitats reproduces primarily through the spread of its rhizoidal holdfast. Markham (1973a) reasoned that microscopic gametophytes were scoured off surfaces by sand, whereas adults could survive and spread vegetatively once established. By analogy, S. herporhizum adults should also thrive in sandy areas where juvenile recruitment is low but they do not. McCourt et. al. (1984) reported evidence of unpredictable long-term burial of portions of the coquina reef at Las Conchas that killed nearly all attached plants and animals. Nevertheless, it is not clear why S. herporhizum should be more susceptible to damage from sand than the other two Sargassum species.

Several researchers (Ebert and Dexter, 1975; Thomson and Lehner, 1976; Littler and Littler, 1981) have suggested that communities in the northern Gulf of California are more influenced by physical factors (temperature fluctuations, desiccation) than by biological factors (competition, predation). Littler and Littler (1981) claimed that the seasonally disturbed environment of the northern gulf has selected for structurally simple, opportunistic algal species with high individual net productivity. They cited the species composition and productivity of intertidal communities at Pelican Point in support of this hypothesis. But their study site, though near that of the present work, sampled algae from higher intertidal areas on granite and failed to include the extensive stands of Sargassum on coquina in the lower intertidal area. The 3 Sargassum species, occurring in the more constant environment of the lower intertidal zone, are better described by Littler and Littler's generalizations regarding intertidal algal communities at comparable latitudes outside the Gulf of California: long-lived, large, complex thalli, with low individual net productivity. Littler and Littler stated that these features enable species to better cope with biological interactions (competition, predation).

Little is known of the effects of herbivores on Sargassum distributions, although adult plants are generally not preferred by herbivorous fish (Montgomery and Gerking, 1980; Montgomery et al., 1980). Differences in spatial distribution such as those reported here for the Sargassum species are sometimes interpreted as evidence of present or past competition between species (Schoener, 1982). That competition between the species may be occurring in some places now is suggested by the habitat shift from mostly tide pools to mostly emergent coquina by S. sinicola at sites where pools are less abundant and S. herporhizum is rare or absent (Las Conchas, Pelican Point) (Fig. 6). This shows that S. sinicola can survive in large numbers on emergent substrate at this intertidal level (-1.8 m) in the intertidal zone. That it occurs mostly in tide pools at Station Beach suggests that it may be excluded from the emergent habitat by large stands of S. herporhizum. Nevertheless, clearing of single-species stands of Sargassum during the spring period of sexual reproduction and dispersal resulted in the regrowth of the original resident, regardless of species cleared (McCourt, 1983). In addition, the differences in distribution, though distinct, do not often result in contiguous stands of different species of Sargassum, which would be the precint of the most intense competition. This indicates that competition, if it does occur, is probably infrequent and sporadic.

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