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ZONATION AND PHENOLOGY OF THREE SPECIES OF SARGASSUM IN
THE INTERTIDAL ZONE OF THE NORTHERN GULF OF CALIFORNIA

The University of Arizona

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ZONATION AND PHENOLOGY OF THREE SPECIES OF
SARGASSUM IN THE INTERTIDAL ZONE OF
THE NORTHERN GULF OF CALIFORNIA

by

Richard Matthew McCourt

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
In the Graduate College
THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by Richard Matthew McCourt

entitled Zonation and Phenology of Three Species of *Sargassum* in the
Intertidal Zone of the Northern Gulf of California

and recommend that it be accepted as fulfilling the dissertation requirement
for the Degree of Doctor of Philosophy.

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Final approval and acceptance of this dissertation is contingent upon the
candidate's submission of the final copy of the dissertation to the Graduate
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SIGNED: Richard Matthew McCombs

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ABSTRACT

Three species of Sargassum are the most abundant intertidal macroalgae at Puerto Peñasco, Sonora, Mexico. Sargassum johnstonii Setchell & Gardner, S. herporhizum Setchell & Gardner, and S. sinicola Setchell & Gardner var. camouii (Dawson) Norris & Yensen are zoned on emergent reef in low intertidal areas. Sargassum johnstonii occurs in a zone above dense stands of S. herporhizum, and scattered patches of S. sinicola occur on the lowest emergent reef. Sargassum sinicola, the most abundant species, predominates in pools throughout the intertidal zone. In mid-intertidal pools the species show the same zonation with respect to water depth that they do on emergent reef. Ecological separation is clear, the species occurring in different vertical zones or different habitats (pools or emergent reef) . At some sites where S. herporhizum is rare or absent, the upper limit of emergent S. sinicola plants shifts upward probably because of a combination of physical and biological factors.

The three species in this highly seasonal region reach maximum size and canopy cover in early spring. All produce fertile receptacles in the spring and shed their branches and die back in summer. Surviving S. sinicola persist through the summer at larger sizes, recommence growth and produce a second crop of receptacles in the fall; the other two species grow but are not fertile until the following spring.

The species differ in allocation of biomass to vegetative and sexual reproductive structures. Sargassum herporhizum invests a high

proportion of its wet and dry biomass into extensively branched, rhizoidal holdfasts. The holdfasts of the other two species are smaller relative to their upper branches, and are not rhizoidal. Experimental clearings showed that S. herporhizum was the most effective at recovering continuous space after disturbance and also after normal summer dieback.

Sargassum johnstonii and S. sinicola produce large volumes of sexual receptacles on buoyant branches, which have the potential for wide dispersal, whereas S. herporhizum produces a relatively small volume. A trade-off between short-range vegetative encroachment abilities and potential for long-range dispersal of sexual propagules may have occurred in the evolution of reproductive strategies of these Sargassum species.

CHAPTER 1

INTRODUCTION

This dissertation reports on the distributional ecology of three species of Sargassum, S. johnstonii Setchell & Gardner, S. herporhizum Setchell & Gardner, and S. sinicola Setchell & Gardner var. camouii (Dawson) Norris & Yensen, from the perspective of resource partitioning and strategies for seasonal growth and reproduction. The species make up most of the canopy of large overstory algae in the intertidal zone on rocky shores in the northern Gulf of California at Puerto Peñasco, Sonora, Mexico. They constitute a set of closely related, structurally similar species occurring on an environmental gradient. Comparisons of patterns of growth, distribution, and reproduction among coexisting species often reveal differences that suggest how species deal with their environment and with each other. In practice, differences are most noticeable against a background of similarity, in the case of Sargassum, similar morphology and reproduction.

The investigations reported here were an attempt to define key components of the niches of the species, which included spatial components (distribution on several spatial scales) and functional morphological components (growth and reproductive morphology). Definition of niche components and how they change in response to different conditions are important in understanding the interactions (or lack thereof) of these species and the factors that determine their distributions.

The focus of this work was at a level intermediate between that of autecological studies of a single species and that of community-level studies on a wide and diverse group of species. The former approach suffers from a lack of generality, whereas the latter tends to be so complex that factors of interest are usually confounded and resistant to detailed analysis. Although study of a smaller subset of species from a community provides no complete escape from either of these limitations, it does allow for a more realistic inclusion of potential interactions between species as factors affecting the niches of the species.

The results of this work provide an interesting comparison to previous work on Sargassum and on marine algal communities in other regions. The environment at Puerto Peñasco, the study site in the northern Gulf of California, is highly seasonal compared to those where Sargassum occurs in either temperate or tropical areas. The flora and fauna of this region are more tropical than those of the less seasonal Pacific Coast of North America, where many studies of intertidal ecology have been done (see reviews by Connell, 1972, 1974). The existence of a subtropical community in a highly seasonal environment makes a unique ecological situation.

Aside from the primarily taxonomic work of Dawson (see references in Abbott, 1966) and Norris and his associates (Fenical and Norris, 1975; Norris, 1975; Norris and Bucher, 1976, 1977), very little is known of the marine algae in the Gulf of California. The above investigators commented on the general habitats and seasonal abundances of many species, but only a few papers have touched on specific ecological themes such as seasonality (Wynne and Norris, 1976; Norris

and Yensen, n.d.), or grazing (Montgomery, 1980; Montgomery, Gerrodette and Marshall, 1980).

The literature on tropical algal ecology and phenology is sparse, although it is beginning to expand (De Wreede, 1976; Prince and O'Neal, 1979; Dawes, 1981; Vadas and Norton, 1982). Because Sargassum is the most common large brown alga in tropical areas (Stephenson and Stephenson, 1972), data on the species in the northern Gulf of California are valuable for comparison with other species worldwide. This is particularly true because of the extreme tidal and annual temperature ranges at Puerto Peñasco, which are greater than those at nearly all other localities where Sargassum has been studied (De Wreede, 1976; Prince and O'Neal, 1979).

The three major parts of this study are dealt with in separate chapters, each with its own literature review, materials and methods, results, and discussion sections. A final summary chapter draws together the general results of the study. Details of the study area and descriptions of the species studied are included in the materials and methods section in Chapter 2.

CHAPTER 2

INTERTIDAL DISTRIBUTION AND HABITATS OF THE SARGASSUM SPECIES

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), but very little is known of the local distribution or habitat requirements of Sargassum in the intertidal zone, let alone the functional role of particular species in their communities.

In this chapter are documented zonation and habitat distributions of three Sargassum species at four intertidal areas near Puerto Peñasco, Sonora, Mexico. These will be compared to zonation and habitat features occurring on a small scale within tide pools. The resulting patterns yield insight into the factors that may control Sargassum distributions in this area.

In a recent detailed review of the literature on Sargassum ecology De Wreede (1973) was forced to rely primarily on studies of other brown algae (Phaeophyta) because studies of Sargassum were so rare. Since then the literature has expanded, in part because of numerous studies on S. muticum (Yendo) Fensholt, an invasive species that has spread to the temperate shorelines of western North America (Abbott and Hollenberg, 1976; Norton, 1977a, 1977b; De Wreede, 1978; Deysher and Norton, 1982) and Great Britain (Farnham, Fletcher, and Irvine, 1973; Fletcher and Fletcher, 1975a, 1975b; Jephson and Gray,

1977; Critchley, 1980). Recent literature has dealt mainly with seasonality of abundance and phenology of species in Hawaii (De Wreede, 1976), Guam (Tsuda, 1972, 1974), Florida (Prince and O'Neal, 1979; Prince and Daly, 1981), and India (Misra, 1966; Rao, 1969; Raju and Venugopal, 1971; Chauhan and Krishnamurthy, 1972). A number of studies have also concentrated on growth of embryos and portions of adult plants under various culture conditions (Chauhan, 1972; Fletcher and Fletcher, 1975a, 1975b; Chamberlain et al., 1979; Kane and Chamberlain, 1979; Norton, 1977a, 1977b, 1980). Schiel and Choat (1980) have reported on the effects of Sargassum plant density on growth rate.

Relatively few studies have dealt with the ecology of Sargassum in terms of habitat differences or interactions with other species. Zonation of species of Sargassum in the intertidal zone has been described for only a few tropical coral reef species (Tsuda, 1972; De Wreede, 1973) and a temperate species introduced into western North America (Norton, 1977b; De Wreede, 1978). In addition, only two studies have compared habitat requirements of Sargassum species occurring in the same intertidal zone or lagoon (Tsuda, 1972; De Wreede, 1973).

There is a conspicuous absence in the Gulf of California of kelps (Laminariales) and furoid algae (Fucales) other than Sargassum, which is the dominant brown alga of intertidal and subtidal areas (Dawson, 1944, 1960, 1966). At Puerto Peñasco, it may play a particularly important role in the intertidal zone because it constitutes of the overstory of large fleshy algae in this sizable intertidal zone. Sargassum species provide shelter for many small invertebrates

(mollusks, crustaceans, bryozoans) that live in and among its blades or sometimes grow encrusted on the plants themselves (Brusca, 1980). Sargassum is also a major source of cover and foraging sites for fishes in this region, including primary resident fishes of tide pools (Thomson and Lehner, 1976; Thomson Findley, and Kerstitch, 1979).

It is particularly interesting that at Puerto Peñasco the over-story consists mostly of three congeneric algae of relatively similar form. Similar species are likely to share some habitat requirements, but they are often found to differ in others; i.e., they partition resources to reduce interspecific competition (Ricklefs, 1973; Schoener, 1974). This partitioning of resources may, but need not always, involve the competitive exclusion of species from limiting resources or habitats (Colwell and Fuentes, 1975). Intertidal zonation among related species may be viewed as the vertical partitioning of space on the shoreline. This chapter describes intertidal zonation in terms of habitat partitioning of the three Sargassum species.

Mackie and Boyer (1977) described the zonation of macroinvertebrates at Station Beach, one of the sites investigated in my study. They found that zones were more diffuse than those typical of many shorelines (Lewis, 1964; Ricketts, Calvin, and Hedgpeth, 1968; Stephenson and Stephenson, 1972). Mackie and Boyer (1977) postulated that the less distinct zonation at Station Beach was due to the greater variety of habitats afforded by the soft coquina reef and the gentle slope of the reef that results in a correspondingly gentler exposure gradient.

Brusca (1980) presented a generalized zonation scheme for the Gulf of California that is quite similar to the scheme of Ricketts et al. (1968) for the west coast of North America. Nevertheless, Brusca (1980) suggested that invertebrate intertidal communities in the gulf are so much more complex than their temperate counterparts that one may find very few of the discrete zones typical of California coastlines. Data presented here show that this is not generally true for Sargassum zonation.

Material and Methods

Study Sites

The four 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), who characterized it as one of extremes in temperature and tidal range.

As a virtual inland sea in the midst of the Sonoran Desert, the Gulf of California is more affected by temperature fluctuations of the adjacent land mass than typical western North American coastal areas. Monthly sea surface temperatures average near 14°C in winter and 30°C in summer (Fig. 2). 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 22 ft (7 m) (Thomson, 1981) and is among the largest in Pacific North America.

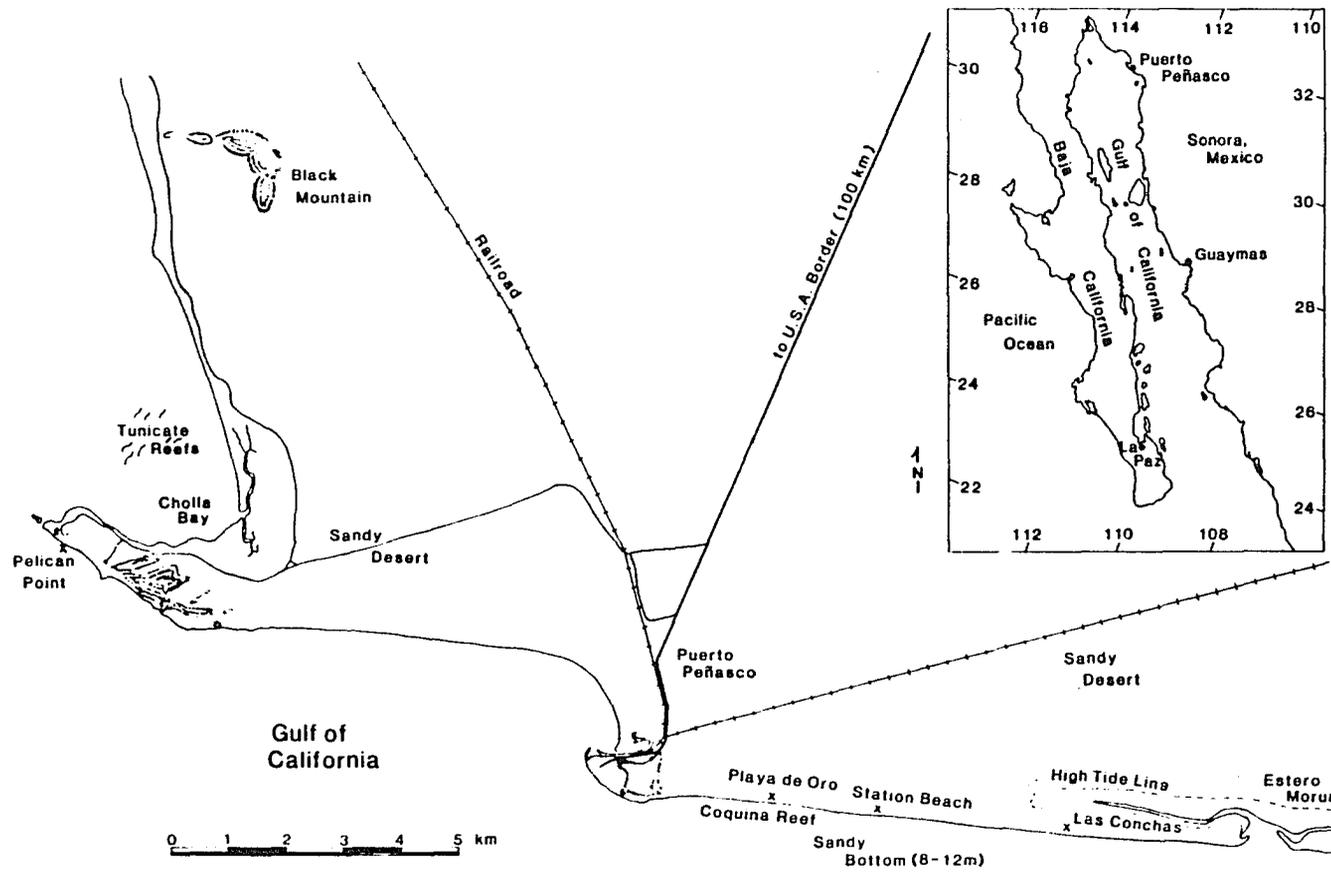


Figure 1. Location of study sites at Puerto Peñasco and vicinity, Sonora, Mexico

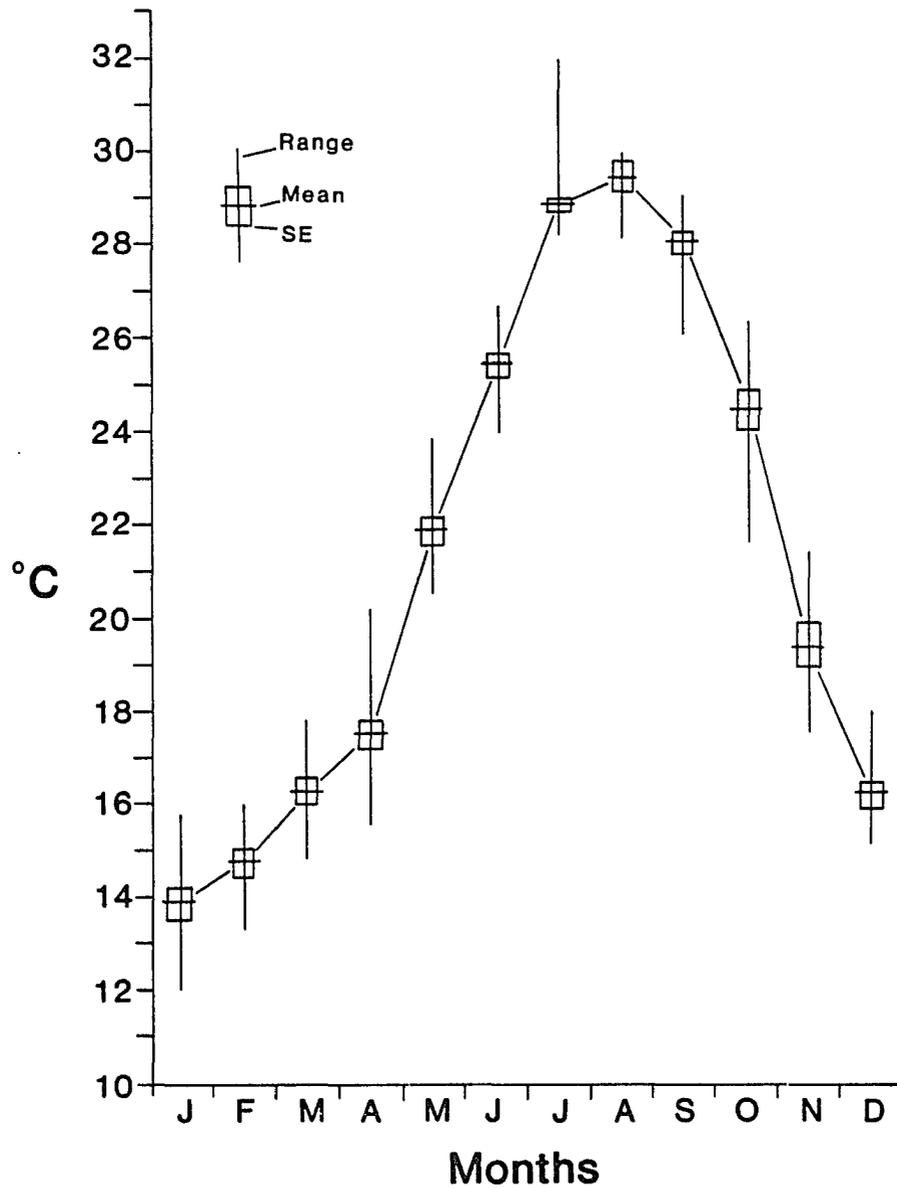


Figure 2. Annual sea-surface temperature regime at Puerto Peñasco, Sonora, Mexico. -- Means, ranges, and standard errors of monthly sea-surface temperatures from 1964 to 1978. Modified from Thomson and Gilligan (n.d.).

Hereafter, tide levels will be expressed in feet in relation to mean low water at 0 ft for ease of reference to Thomson's (1981) work.

Three of the four study sites were Playa de Oro, Station Beach, and Las Conchas (Fig. 1). All were located on a unbroken stretch of south-facing coastline that extends from Punta Peñasco to the mouth of a negative estuary, 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 two major topographic areas by a fault in the reef at about the 60-m mark on the transects at which point the reef drops abruptly from the +1-ft to the -1-ft level. Below the fault the reef slope is steeper than in the area near Station Pool.

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. Wave action is normally lighter than in nearby areas outside the Gulf of California (Thomson and Lehner, 1976), but the wave action is sufficient to move sand in and out of the tide pools. Storms move large amounts of sand and sometimes bury large areas of reef to a depth of many centimeters. Over a period of days these areas are uncovered by normal wave action.

The fourth 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 the other sites. The substrate is mostly granitic outcrops and boulders, with an expanse of coquina only in the very low, intertidal (below -4 ft). Although wave action is light (wave height rarely greater than 0.75 m), tidal currents around the point expose this site to greater water motion than that found at the other sites. Despite its proximity to the Cholla Bay mud flats, sand accumulation appears comparable to that at Station Beach.

Sargassum Species at Puerto Peñasco

According to recent studies by Norris and Yensen (n.d.) on the taxonomy of Sargassum in the northern Gulf of California, there are three species in this area: S. johnstonii Setchell & Gardner, S. herporhizum Setchell & Gardner, and S. sinicola Setcje;; et Gardner. Norris and Yensen (n.d.) also differentiated a separate form (f. macdougalii within S. johnstonii and two distinct varieties of S. sinicola (var. sinicola and var. camouii). This is a significant reduction of the number of species originally reported by Setchell and Gardner (1924, 1925) and later revised by Dawson (1944, 1966). The reductions were due primarily to the synonomizing of species described from fragmentary drift material from the upper branch systems of plants, which may be quite variable in form within a single species.

The investigations reported here centered on S. johnstonii (Fig. 3), S. herporhizum (Fig. 4), and S. sinicola var. camouii (Fig. 5). Their distinguishing features and geographical distributions are

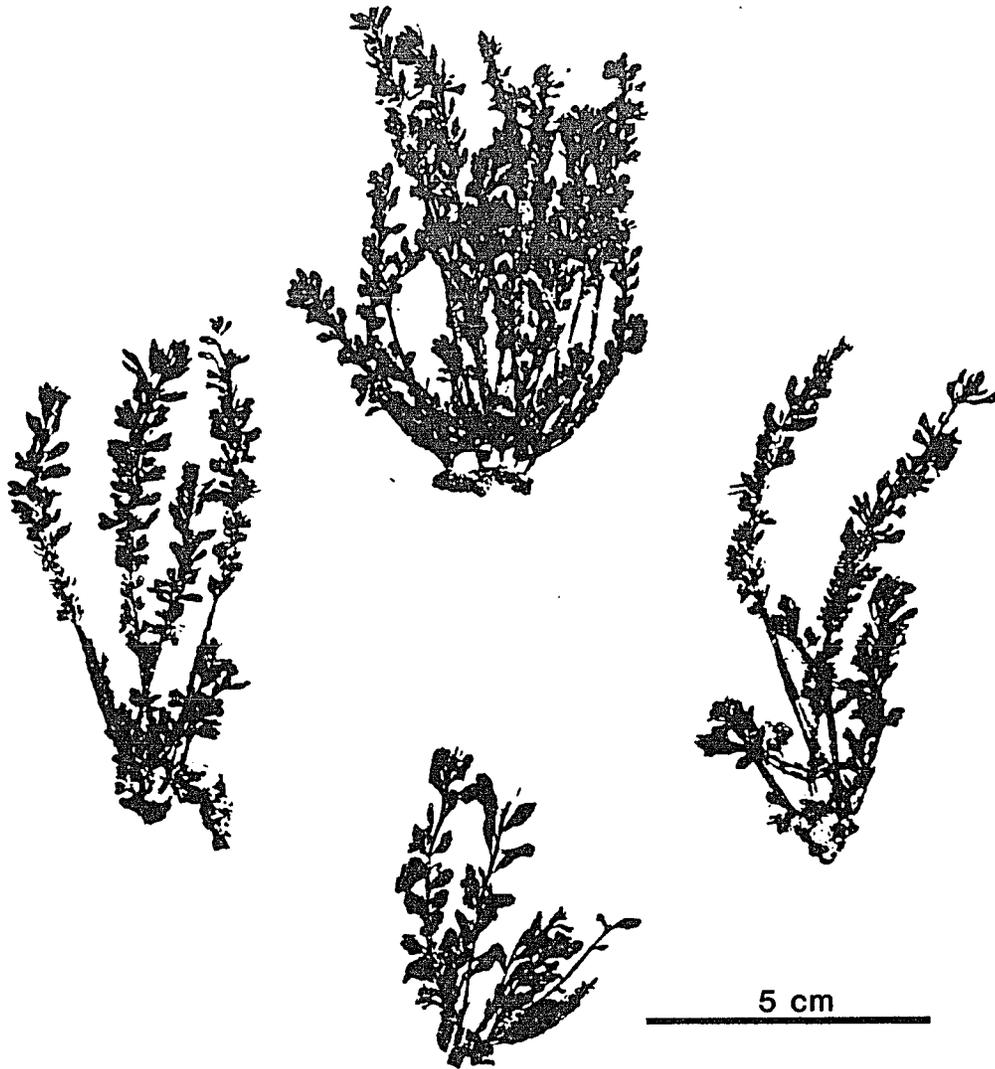


Figure 3. Sargassum johnstonii Setchell & Gardner

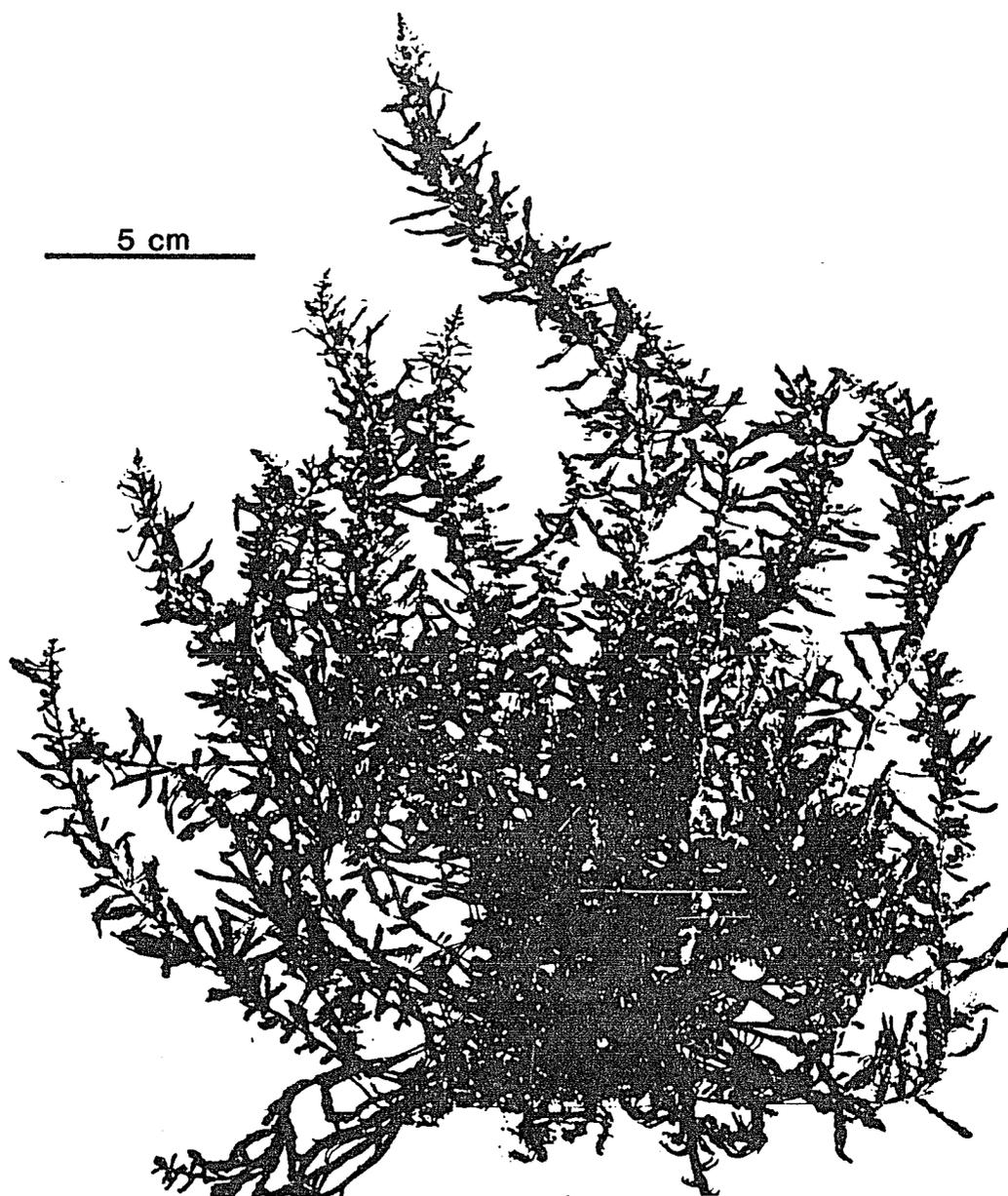


Figure 4. Sargassum herporhizum Setchell & Gardner

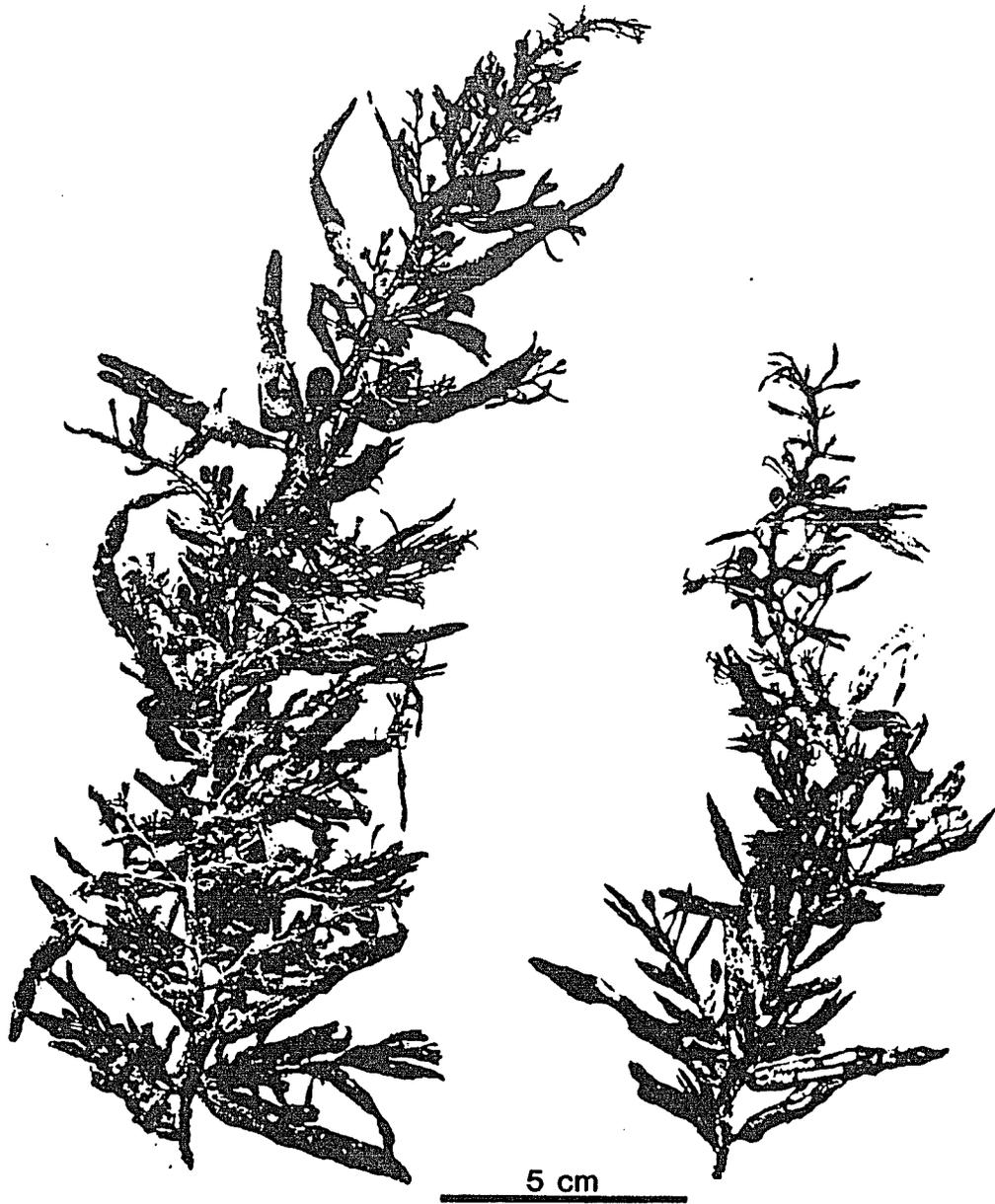


Figure 5. *Sargassum sinicola* Setchell & Gardner var. *camouii*
(Dawson) Norris & Yensen

summarized in Table 1. During the study S. johnstonii f. macdougalii was not differentiated from S. johnstonii. Sargassum sinicola var. sinicola occurs on subtidal patch reefs and rarely in the intertidal zone. Throughout this dissertation, S. sinicola refers only to the variety camouii unless otherwise noted. Voucher specimens have been deposited with the University of Arizona Herbarium.

Intertidal Transects

The basic pattern of intertidal zonation was documented on Station Beach in the area near a large tide pool known as Station Pool (Thomson and Lehner, 1976). Five transects, extending perpendicular to the shoreline from the upper limit of the coquina reef (~ +6 ft) to the lowest spring-tide level (~ -6 ft), were laid out to survey the patchy distribution of Sargassum at this site (Fig. 6). The five replicate transects were spaced 10 m apart. Transect length ranged from 90 to 110 m; some transects were shorter than others due to submergence of the lowest segments during the census. 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 pools or on emergent reef. Percent occurrence for each species in 5-m intervals was calculated as the number of points where a species occurred divided by the total number of points sampled multiplied by 100. This was taken to be an estimate of the percentage of the substratum covered by the canopy of Sargassum plants.

Table 1. Summary of distinguishing morphological features of intertidal Sargassum species at Puerto Peñasco. Based on data from Norris and Yensen (n.d.), and personal observations

	<u>Sargassum</u> Species		
	<u>S. johnstonii</u>	<u>S. herporhizum</u>	<u>S. sinicola</u> var. <u>camouii</u>
Holdfast	crust, disc-shaped, up to several cm across; several to many stipes	extensively branched rhizoidal system; stipes numerous; separate plants in a patch indistinguishable	conical, several cm across, with one to several primary stipes
Stipes	lax; terete, smooth; many secondary branches of short primary stipes; lateral branches bearing blades, bladders, and receptacles	thin and springy, terete, smooth; secondary branches short if present, with many lateral branches	coarse and semi-rigid, muricate; many large secondary branches, numerous smaller lateral branches
Blades	lacking midrib; variable in shape, long and terete to short and broad, fleshy, margins serrate or entire; cryptostomata present	leaflike with midrib; margins serrate to dentate; cryptostomata sparse	leaflike with midrib; margins dentate; many cryptostomata
Air bladders	spherical to elongate, apiculate	spherical to ovoid	spherical
Geographical range	Puerto Peñasco to La Paz	Puerto Peñasco to Isla San Pedro Nolasco and Bahía Concepción	Puerto Peñasco to Isla San Esteban; Bahía Vizcaino on outer coast of Baja California

Gulf of California

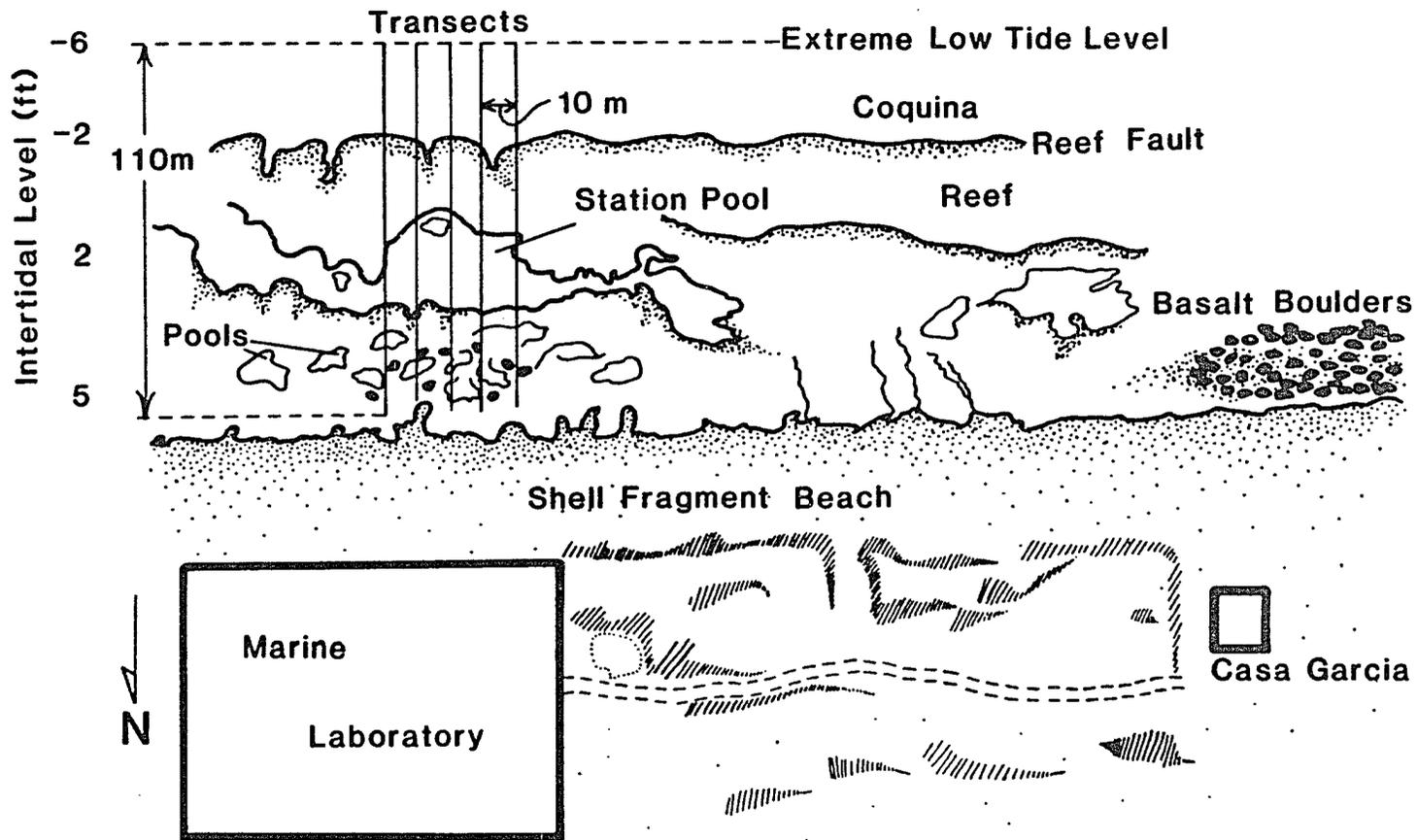


Figure 6. Layout of seasonal intertidal transects in Station Pool area of Station Beach

Intertidal distributions along the sand gradient from Punta Peñasco to Las Conchas were documented with transects at Playa de Oro and Las Conchas (Fig. 1). In February 1981 two transects were surveyed at each site. Percent occurrence and habitat were recorded as on Station Beach transects. An additional five transects were conducted at Station Beach in February 1981, and in April 1981 five transects were conducted at Pelican Point to assess Sargassum distributions at this relatively exposed site.

Topographic profiles were mapped for transect stations at Station Beach, Las Conchas, and Pelican Point, using the Emory line method (Dawes, 1981). Playa de Oro is less than 1 km from Station Beach and has essentially the same profile. On the Las Conchas profile continuous patches of sand greater than 5 m in diameter were recorded. (Sand patches of this size did not occur at the other sites.)

Pool Transects and Habitat Measurements

Transects were conducted across tide pools of various sizes in the mid-intertidal ($\sim +2$ ft) interval at Station Beach to determine the distribution, habitats, and sizes of Sargassum within tide pools. Data were collected in the spring of 1977. A transect line that intercepted one or more patches of Sargassum was laid out across each pool. Data recorded at 10-cm intervals along the line were: species of Sargassum, if present; maximum length of plant; and water and sand depth at the plant's holdfast. Linear measurements were made to the nearest 0.5 cm. A total of 425 points (42.5 m of transects) were sampled in 14 pools.

Habitat measurements for the three species were also made at Playa de Oro and Las Conchas in the spring of 1980. Short transects were laid out across Sargassum patches to randomly sample the Sargassum in these areas. Data recorded for each plant were the same as on the pool transects.

At Playa de Oro 25 plants of each of the three species were sampled at the same tide level as that of the Station Beach pools (+2 ft). At Las Conchas no S. herporhizum was found, so only S. johnstonii and S. sinicola could be sampled. Twenty-five plants of each species were sampled at two locations (n = 50 per species). One location was in a pool with an intertidal level comparable to that (+2 ft) of the sampling sites at Station Beach and Playa de Oro; the other location was in a lower area (-2 ft) with more sand. These two areas, Las Conchas +2-ft and Las Conchas -2-ft, reflect the range of reef habitats found at Las Conchas.

Drying Experiments

The water-retaining abilities of the species were determined by drying experiments. On 2 days in spring 1977 five plants of each species were collected with their holdfasts intact and taken to an indoor laboratory. Each plant was blotted dry with paper towels, weighed to the nearest 0.01 g, placed on a tared paper plate, and set out to dry at ambient room temperature (24°C). Plants were weighed at set intervals over a 24-hour period.

Transplants

Several attempts were made to transplant intact plants of one species to the habitat of another. One plant of each species was attached in random order on each of a series of metal strips (plumber's tape) with a sea-going epoxy. Four strips were nailed down in existing stands of each species in mid-intertidal pools and monitored after 2 weeks and again after 1 month.

Three plants of each species were pulled up intact from a tide pool and moved to the area in the low intertidal where S. johnstonii occurs on emergent reef. They were attached with plastic cable ties to nails hammered into the coquina. The plants were observed at low tide on the next 2 days.

Results

The distribution of Sargassum will be described on three spatial scales. Zonation of the three species at Station Beach will be described. The basic zonation scheme will then be compared to zonation patterns at several nearby areas that differ in sand abundance and their exposure to currents. Differences between species on a smaller spatial scale are documented with data on habitats and plant size.

Intertidal Transects

Canopy cover on the Station Beach transects in autumn 1977, estimated from total percent occurrence for all three Sargassum species, was nearly 29% of the reef area. The canopy cover of S. sinicola was slightly over 17%, about three times that of S. herporhizum (6.3%) and S. johnstonii (5.2%). Most of the remaining 71% of the reef area was

covered by emergent algal turf, coralline algae in tide pools, and various algae and sessile animals. Patches of sand occurred in tide pools, and a small amount of bare reef was found at the upper border between the coquina and the shell-fragment beach.

Two distinct zones of Sargassum distribution were identified: an upper zone above +1 ft and a lower zone below -1 ft. These zones were separated by the reef fault at the 60-m mark on the transects (Fig. 7). The abundance of S. sinicola was similar in both upper and lower zones. Sargassum johnstonii and S. herporhizum were less common in the upper zone but were markedly more abundant in the lower zone.

The species showed distinct differences in their occurrence in emergent or pool habitats on these transects. Most (93.3%) S. sinicola occurred in pools throughout both zones (Fig. 7). Its habitats were for the most part permanently submerged. In contrast, the habitats of S. herporhizum and S. johnstonii were mostly emergent (77.4% and 90.8%, respectively).

Above the reef fault all Sargassum species were restricted to pools. The hiatus in Sargassum occurrence between approximately +1 ft and -1 ft coincided with the absence of pools there. Below -1 ft, pools were common as evidenced by the frequent occurrence of S. sinicola in submerged habitats.

In the lower zone, S. johnstonii and S. herporhizum occurred primarily on emergent coquina and were vertically zoned (Fig. 7). Sargassum johnstonii dropped out entirely below -5 ft. Below this point S. herporhizum was the most abundant Sargassum on emergent coquina,

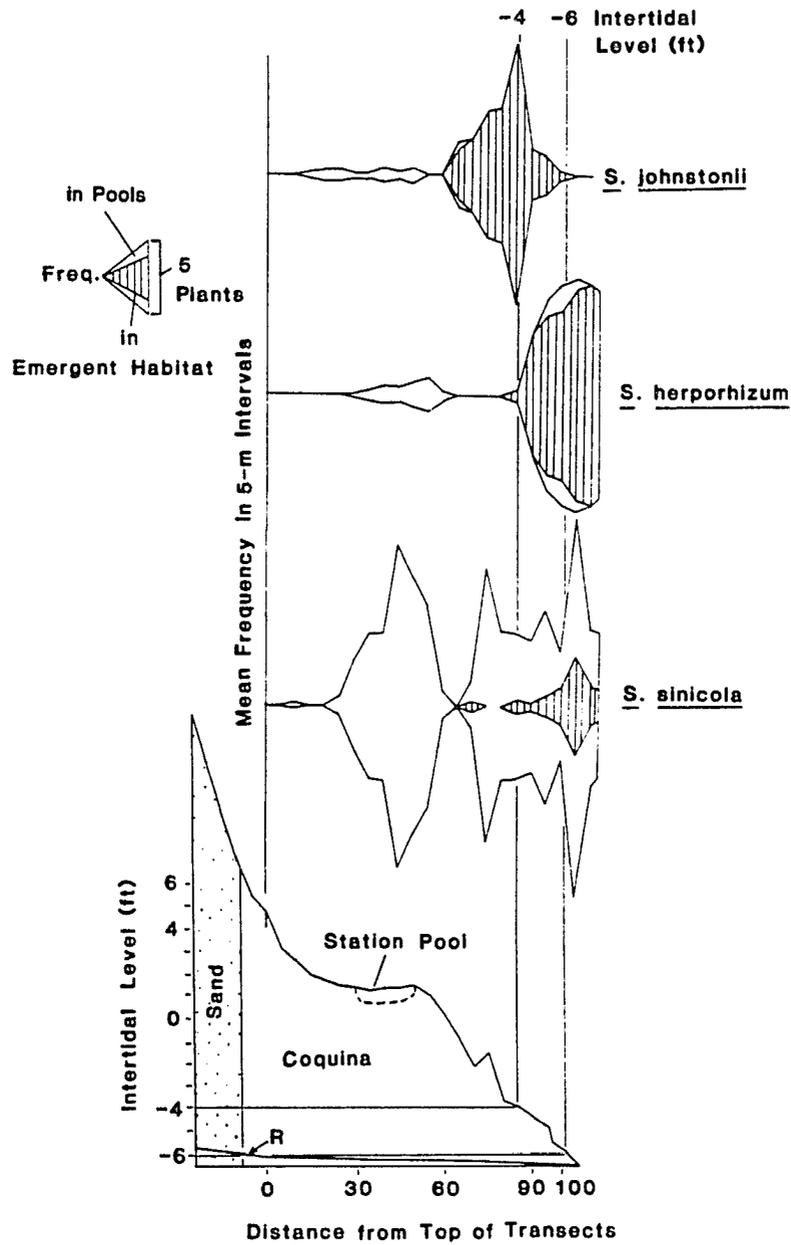


Figure 7. Intertidal distribution of *Sargassum* species at Station Beach, fall 1977. -- R = profile with both axes at same scale.

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.

The distributions of S. sinicola and S. herporhizum in Figure 7 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, and S. sinicola. var. sinicola is found on subtidal patch reefs (Norris and Yensen, n.d.).

Sargassum zonation at Station Beach (Fig. 8) and Playa de Oro (Fig. 9) in 1981 were basically similar to the pattern found at Station Beach in 1977 (Fig. 7). Sargassum herporhizum drops out of the zonation pattern between Station Beach and Las Conchas. There was almost no S. herporhizum on the reef at Las Conchas (Fig. 10). 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 shallower slope than the other sites (Fig. 10). Despite a larger intertidal zone there is less coquina substrate here because much of the intertidal zone is covered by sand (Fig. 10).

In contrast to its abundance in the lower zone at Station Beach, S. herporhizum was relatively scarce at Pelican Point, where Sargassum plants were restricted largely to the lower intertidal zone on the emergent coquina shelf (Fig. 11). Pools were infrequent on the shelf. Sargassum herporhizum was occasionally found in tide pools in the

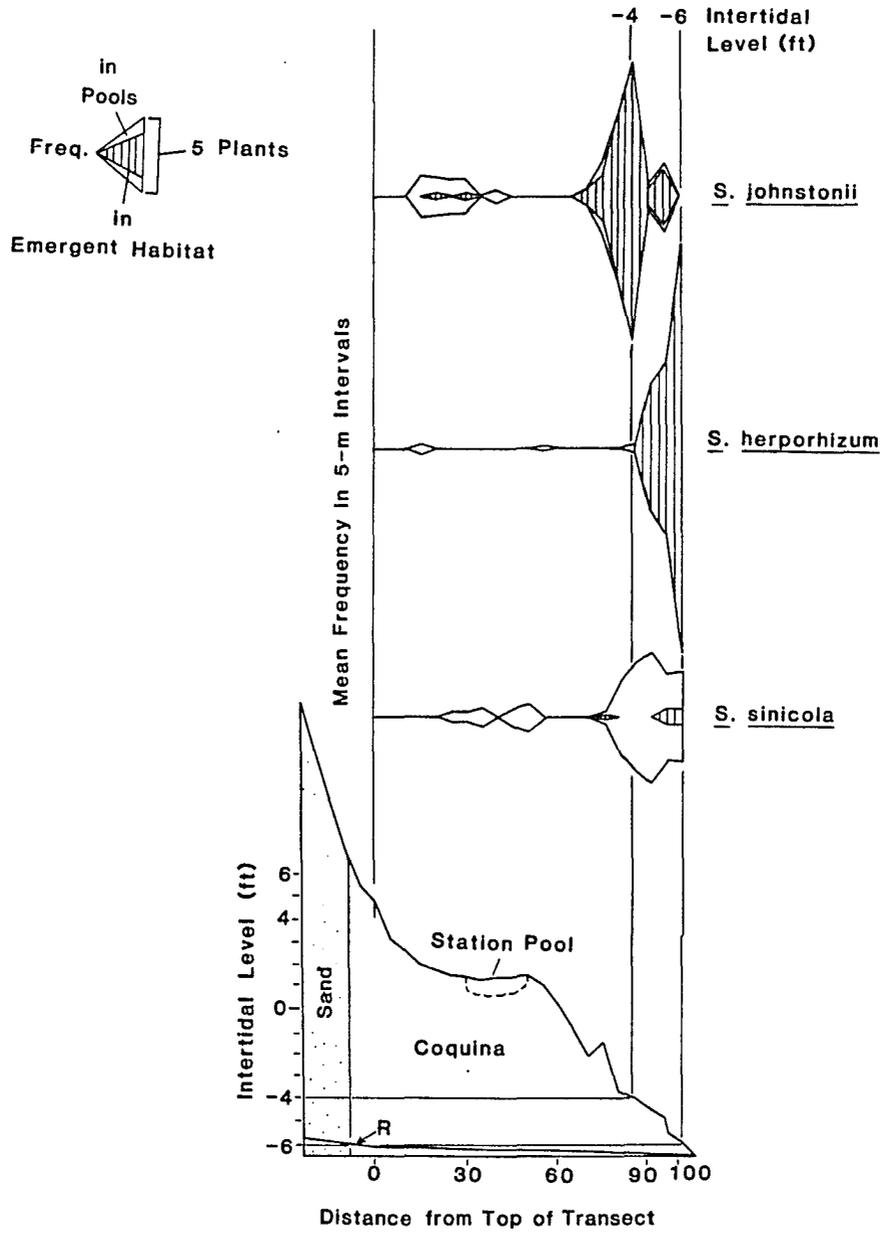


Figure 8. Intertidal distribution of *Sargassum* species at Station Beach, spring 1981. -- R = profile with both axes at same scale.

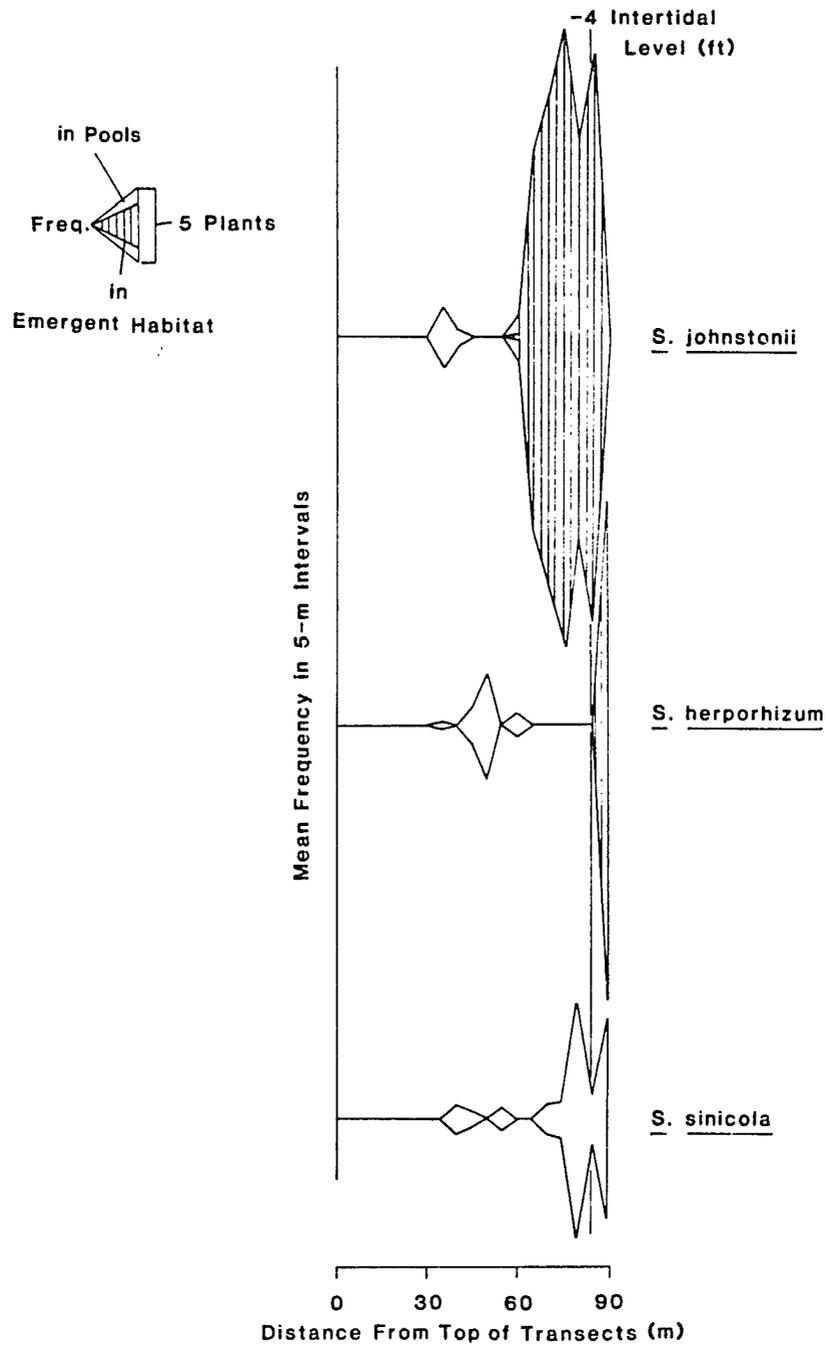


Figure 9. Intertidal distribution of *Sargassum* species at Playa de Oro, spring 1981

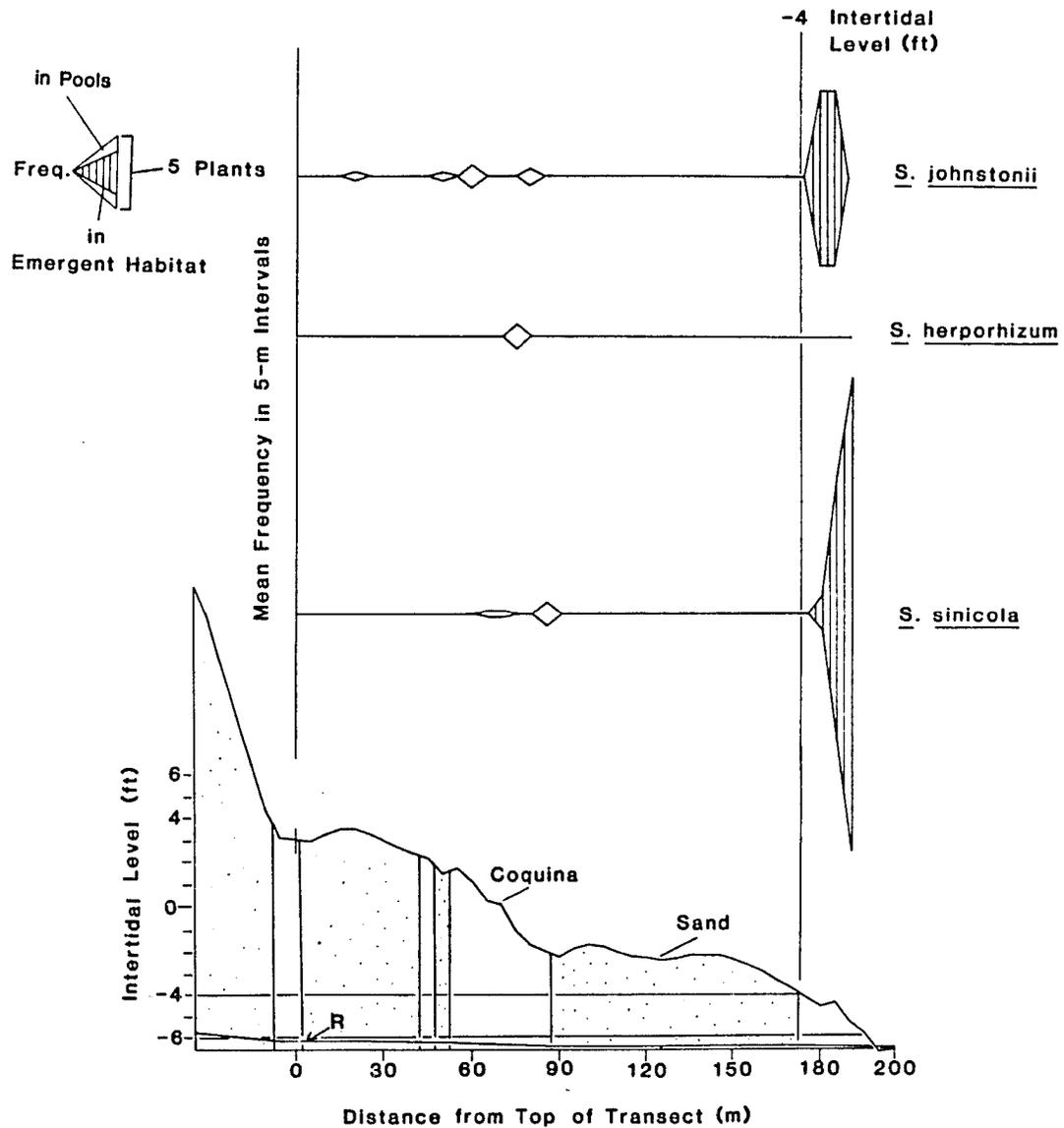


Figure 10. Intertidal distribution of *Sargassum* species at Las Conchas, spring 1981. -- R = profile with both axes at same scale.

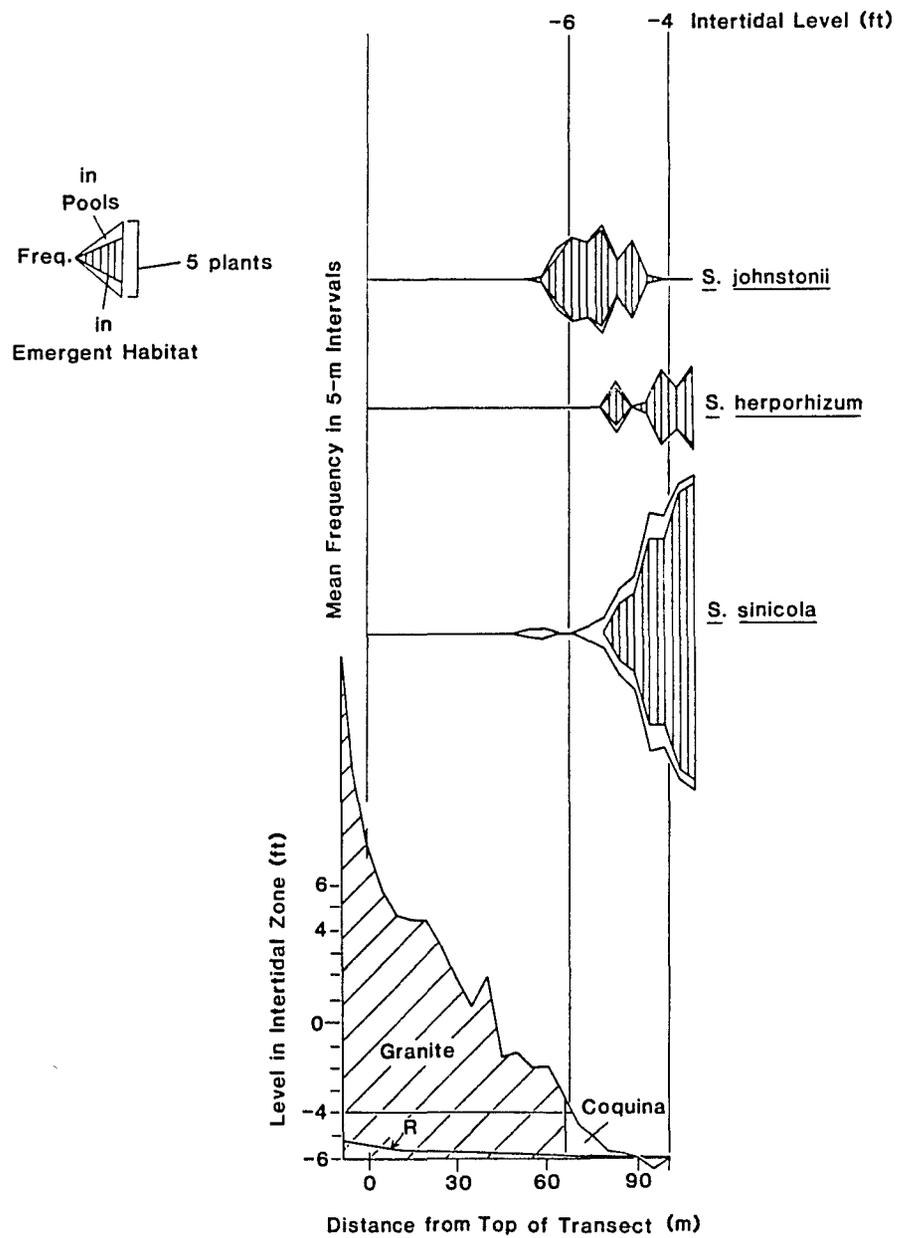


Figure 11. Intertidal distribution of Sargassum species at Pelican Point, spring 1981. -- R = profile with both axes at same scale.

granitic outcrops higher in the intertidal zone, although no pools occurred on the transects.

At sites where S. herporhizum was scarce (Pelican Point) or absent (Las Conchas), many emergent plants of S. sinicola occurred slightly higher in the intertidal zone, i.e., -4 ft compared to -5 or -6 ft at Station Beach (Figs. 10 and 11). Furthermore, the habitat distribution of S. sinicola at these sites was the reverse of that at Station Beach: most plants occurred on emergent coquina instead of in pools (Fig. 12). The latter finding may be due, in part, to the low frequency of pools in the coquina shelf at Pelican Point. Sargassum johnstonii and S. herporhizum occurred primarily on emergent substrate at all sites (Fig. 12).

Pool Transects and Habitat Measurements

Data from the 14 pools sampled at Station Beach were combined for presentation. If 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 where appropriate.

Mean water depths for the three species (Fig. 13) were significantly different ($p < .01$, Welch's ANOVA, pairwise t' test; see Dixon and Brown, 1979). This depth zonation in pools was similar to the intertidal pattern on emergent coquina (Fig. 7). 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.

L : Las Conchas
 P : Pelican Point
 SITES O : Playa de Oro
 S1: Station Beach, 1981
 S2: Station Beach, 1977

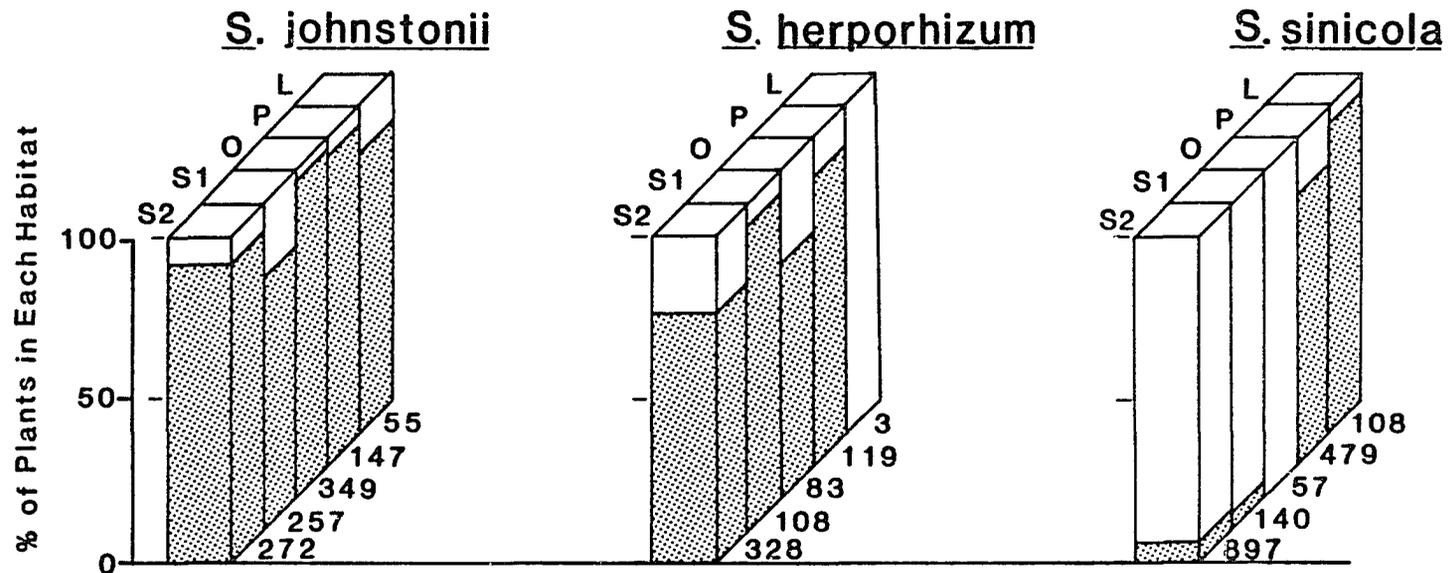
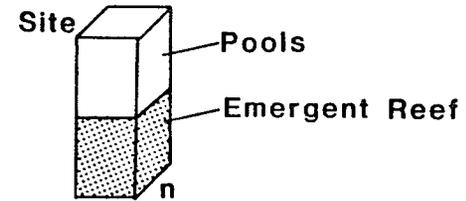


Figure 12. Percentage of plants of each Sargassum species in pool or emergent habitats at four sites in the vicinity of Puerto Peñasco

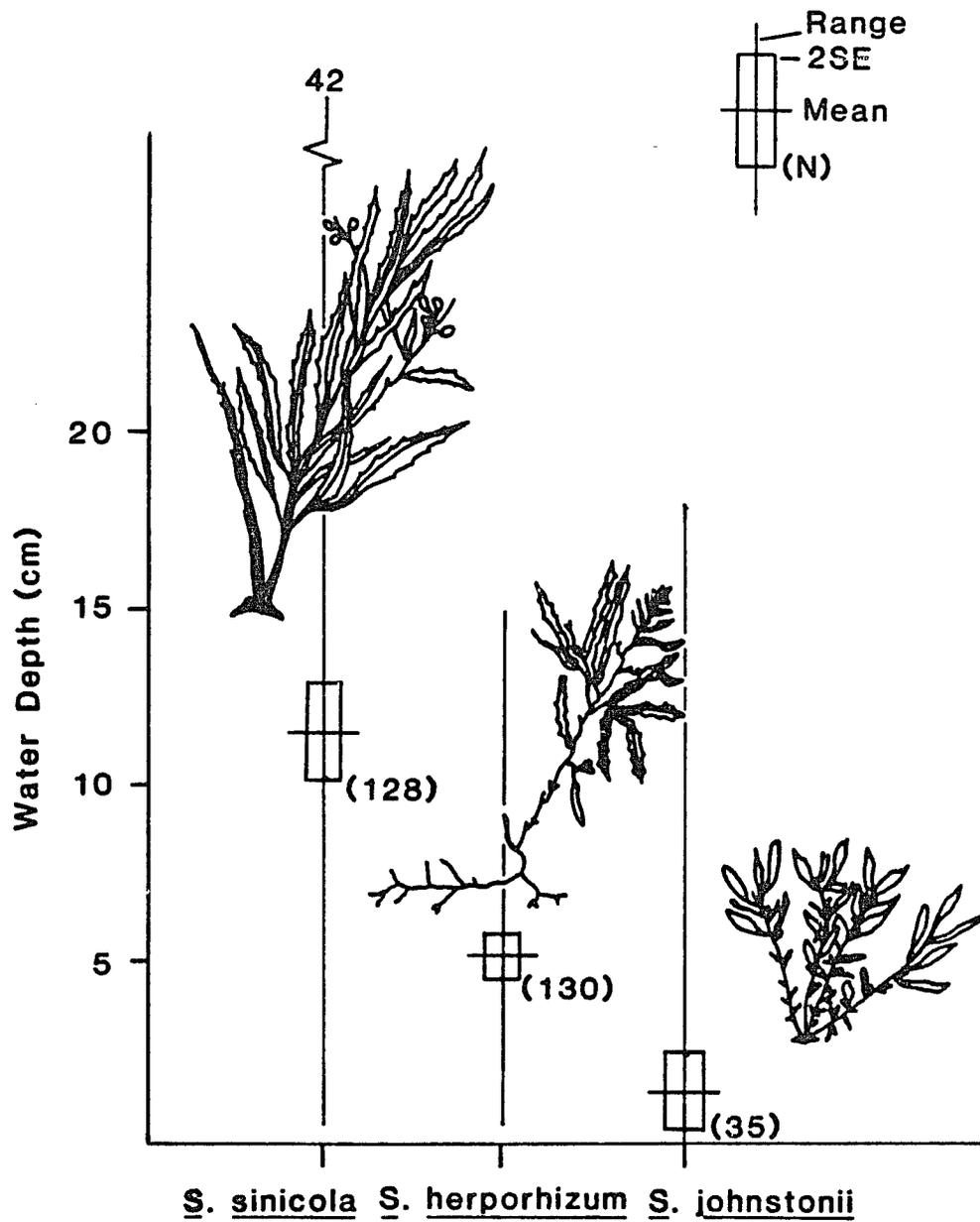


Figure 13. Mean water depths of the *Sargassum* species in Station Beach tide pools

Regardless of the maximum depth of the pool, the three species maintained the same position relative to average water depths (Fig. 14). Average depth for S. sinicola correlated with maximum depth of the pool (Fig. 14). Average depth of S. herporhizum less closely correlated 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.

Average sand depths for the three species paralleled average water depths (Fig. 15), which is to be expected because sand accumulates in the deeper parts of pools. Saragassum johnstonii had the shallowest mean sand depth, significantly different from depths for the other species ($p < .05$, 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. Compared to water depth in a pool, sand levels are more dynamic and a plant must deal with a range of sand depths rather than with one discrete level. Population variance of sand depth provides an additional indication of the sand conditions a single plant must 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.

The lengths of S. herporhizum and S. sinicola plants positively correlated with the water depth at which they were found, whereas the length of S. johnstonii at the edges of pools did not (Fig. 16). The

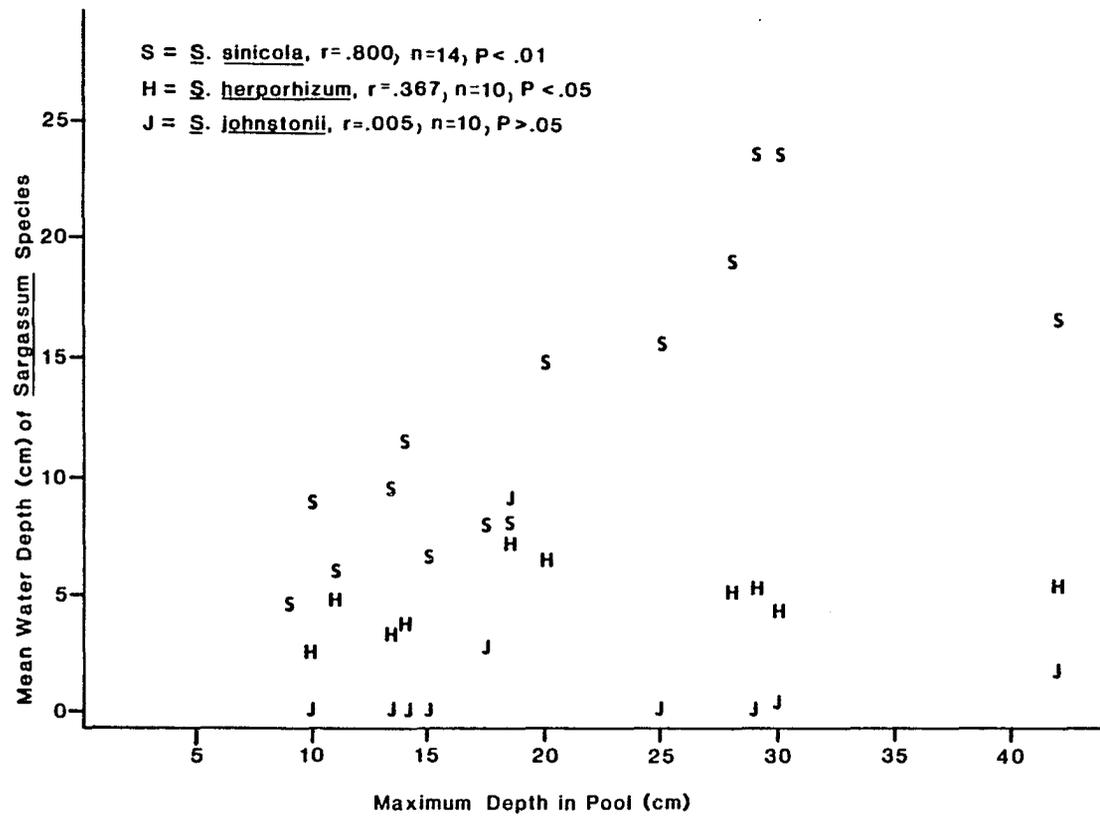


Figure 14. Mean water depth of the *Sargassum* species in individual pools at Station Beach as a function of maximum water depth in each pool

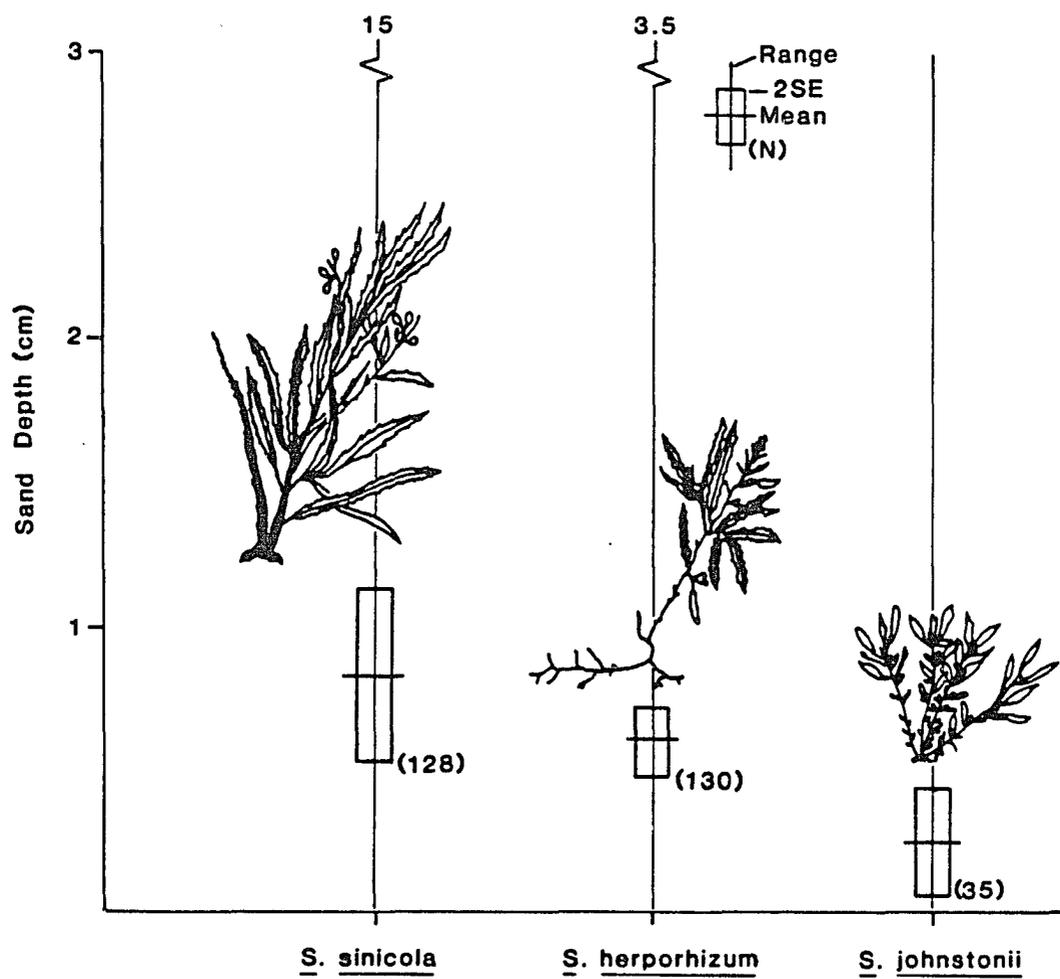


Figure 15. Mean sand depth of the Sargassum species in Station Beach tide pools

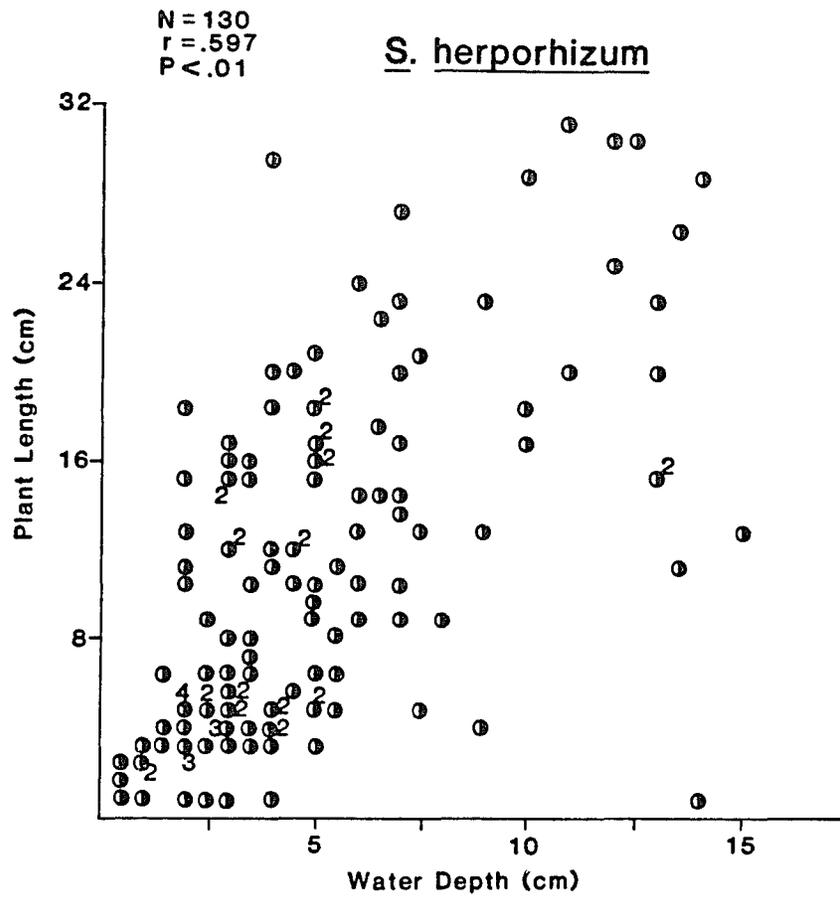


Figure 16. Length of Sargassum plants as a function of water depth in Station Beach tide pools. -- Number = number of points plotted as one point.

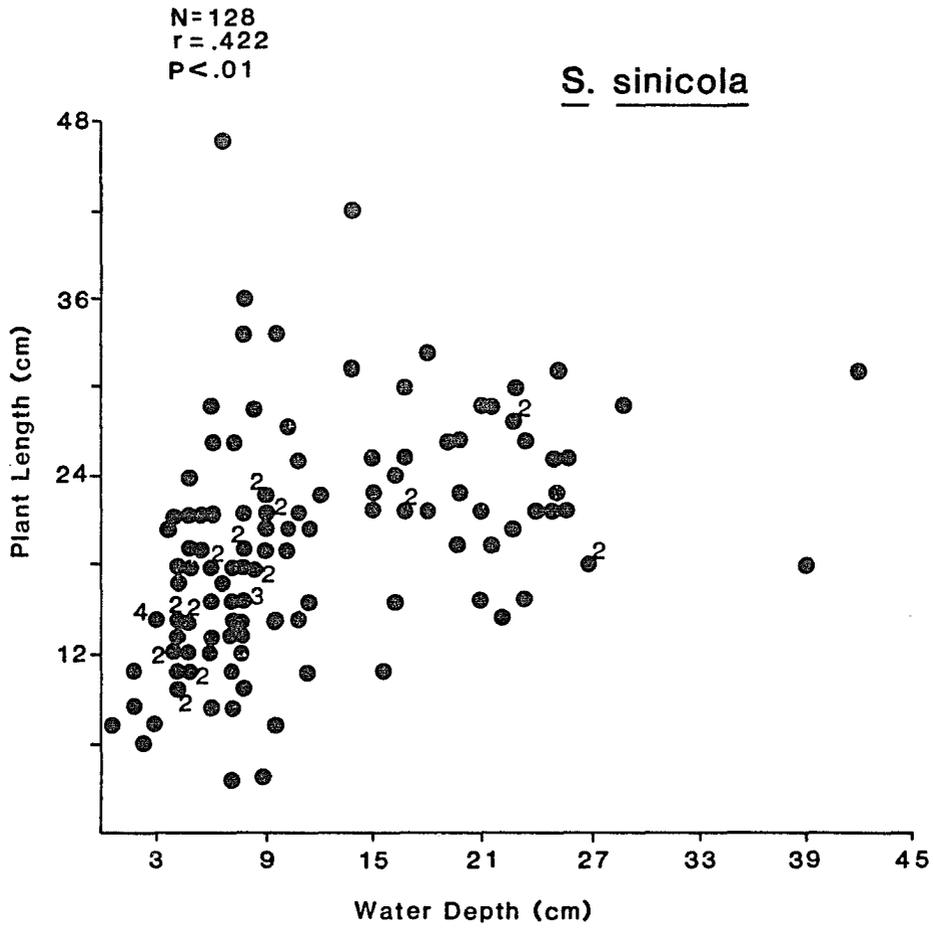
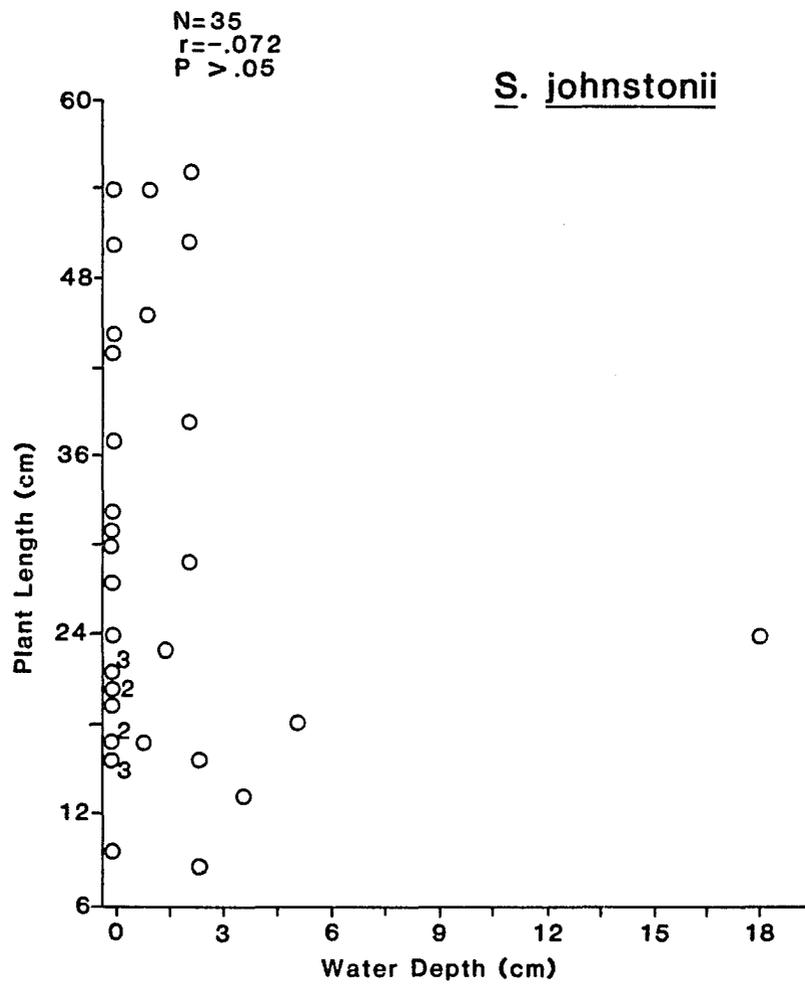


Figure 16. Length of Sargassum--Continued



curve for S. sinicola began to level off for depths greater than 15 cm of water, coincidentally the maximum depth recorded for S. herporhizum on the pool transects.

The three species show significant differences in average length ($p < .05$, Welch's ANOVA and pairwise t' tests) (Fig. 17). This may be an indication of the constraints on length imposed by water depth, which differed significantly for these two species (Fig. 13). Sargassum johnstonii, whose length was independent of water depth, attained the greatest length (Fig. 17).

Habitat and length measurements show consistent patterns across species and sites (Table 2). At all sites plant lengths and water depths within species were comparable and maintained the same relative values among species.

Sand depth varied the most (Table 2). In this area Sargassum plants were usually in pools. Plants at the Las Conchas -2-ft site occurred in depressions filled with water-saturated sand, and sand depths for S. sinicola and S. johnstonii were significantly greater than at other sites ($p < .05$, pairwise t' tests). At the Las Conchas +2-ft site, sand depth was greater than at other sites for S. sinicola but not for S. johnstonii.

Drying Experiments

Data on water loss during the first 12 hours of drying were analyzed separately for each of the 2 days. Proportion weight lost in each interval was arc-sine transformed and the data subjected to a repeated measures ANOVA, with initial weight as a covariate (Dixon and

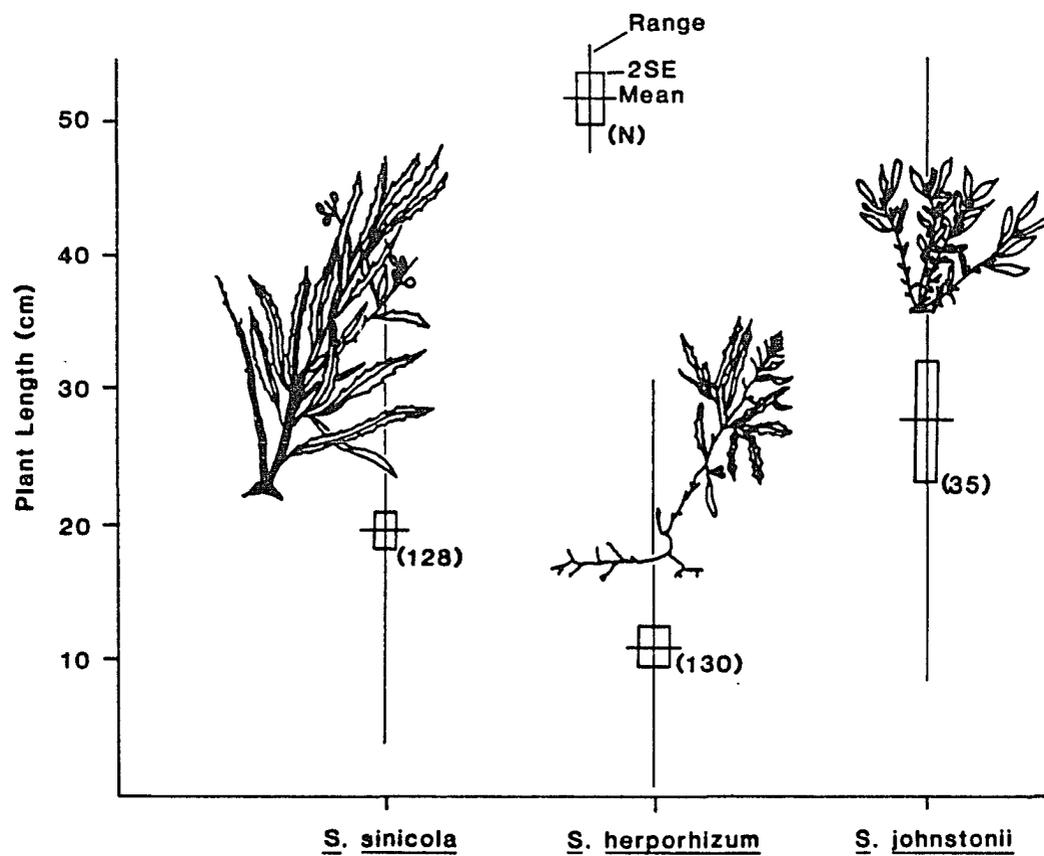


Figure 17. Mean length of Sargassum plants in Station Beach tide pools.

Table 2. Habitat measurements and plant length for three Sargassum species in mid-intertidal pools at several sites in the Puerto Peñasco area

Site	Mean (SE)		
	<u>S. johnstonii</u>	<u>S. herporhizum</u>	<u>S. sinicola</u>
<u>Water Depth (cm)</u>			
Playa de Oro	0.94 (0.40)	6.94 (0.34)	14.78 (0.72)
Station Beach	1.26 (0.53)	5.14 (0.30)	11.55 (0.72)
Las Conchas +2 ft	0.18 (0.10)	--	10.04(0.81)
Las Conchas -2 ft	1.83 (0.22)	--	7.44(0.58)
<u>Sand Depth (cm)</u>			
Playa de Oro	0.12 (0.05)	0.96 (0.34)	0.40 (0.11)
Station Beach	0.27 (0.10)	0.61 (0.06)	0.84 (0.16)
Las Conchas +2 ft	0.06 (0.04)	--	1.58 (0.40)
Las Conchas -2 ft	1.79 (0.23)	--	6.42 (0.52)
<u>Plant Length (cm)</u>			
Playa de Oro	26.36 (1.98)	8.70 (0.74)	21.22 (0.99)
Station Beach	28.10 (2.34)	11.14 (0.69)	19.35 (0.66)
Las Conchas +2 ft	22.98 (1.05)	--	20.58 (1.47)
Las Conchas -2 ft	24.65 (1.17)	--	18.24 (1.15)
<u>Sample Size (N)</u>			
Playa de Oro	25	25	25
Station Beach	35	130	128
Las Conchas +2 ft	25	--	25
Las Conchas -2 ft	25	--	25

Brown, 1979). On both days, the amount of water lost differed significantly between species ($p < .05$); water loss was slowest in S. johnstonii, intermediate in S. sinicola, and fastest in S. herporhizum. Smaller plants lost water significantly faster than larger plants ($p < .05$). The effect of size was most pronounced in S. herporhizum.

Transplants

Transplants in tide pools were generally unsuccessful because the epoxy caused a rotting of the stipe and the plants often broke loose. If plants did remain attached to the strips, they showed few obvious signs of damage, although S. sinicola and S. herporhizum placed in stands of S. johnstonii displayed some blackening of distal blades and stipes, presumably from desiccation at the pool surface.

Sargassum sinicola and S. herporhizum plants transplanted to the emergent S. johnstonii area (fastened with plastic ties instead of epoxy) showed signs of severe desiccation (blackened blades and stipes) after only one low-tide period. Transplanted S. johnstonii showed no such damage.

Discussion

The distributions of S. johnstonii, S. herporhizum, and S. sinicola show definite patterns of vertical zonation and habitat separation. Their zonation is more discrete than Brusca (1980) suggested is the case for invertebrate communities in northern Gulf of California and more discrete than the invertebrate zonation at Station Beach reported by Mackie and Boyer (1977). This may be because the present study focused in detail on three congeneric species. Closely related

species generally show more clearly defined niche differences (Colwell and Fuentes, 1975).

At Station Beach, intertidal Sargassum occurred in two distinctly separate zones: in mid-intertidal pools above the reef fault and in pools and on emergent coquina below the fault (Fig. 7). 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), who also found Sargassum plants in two spatially separated areas in upper and lower intertidal zones. At Station Beach the separation is probably due to the restriction of Sargassum to pools in the mid-intertidal zone combined with a general absence of these pools from +1 to -1 ft. Below this level the three species are apparently better able to withstand the exposure during low tides and can survive outside the pools.

In both areas the species achieve clear spatial separation. In the lower zone at Station Beach the three species occupied different vertical zones or different habitats. Sargassum sinicola dominated pools, whereas S. johnstonii and S. herporhizum grew primarily on emergent coquina; the latter two species were vertically zoned, with S. johnstonii higher on the shore. Within pools in the upper zone there was an even more distinct zonation of the three species with respect to water depth (Fig. 13). The zonation pattern in pools was similar to that found in the lower zone. Sargassum sinicola occurred in the deepest water, S. johnstonii in the shallowest, and S. herporhizum at intermediate depths.

Zonation studies of more than one Sargassum species in the same intertidal area are uncommon. Tsuda (1972) reported a clear spatial separation of two species in a lagoon environment in Guam. The two species were exposed to different regimes of desiccation in areas many meters apart. De Wreede (1973) reported Sargassum zonation on Hawaiian reefs, although the three species he studied overlapped extensively in their zonation on some reefs. Tsuda and De Wreede found some evidence of habitat differences between species.

Many low intertidal species also grow in intertidal pools (Lewis, 1964; Ricketts et al., 1968), but at Puerto Peñasco the similar zonation of three overstory (canopy) species in both locations is unique. Dayton (1975) found no such parallel pattern among small kelps (Laminariales) in Pacific Northwest tide pools. Moreover, he showed experimentally that patterns of succession in tide pools were slow and inconclusive compared to those involving the same species in exposed intertidal areas, perhaps because the pools were suboptimal habitats for the canopy species (Dayton, 1975). In light of the similar zonation patterns in the two situations at Puerto Peñasco, it seems likely that the same factors may be at work controlling the zonation of Sargassum in pools and in the lower zone at Station Beach.

The physical factors of desiccation in summer and frosting in winter have been shown to affect the upper intertidal limit of S. muticum in the San Juan Islands (Norton, 1977a). Desiccation may be important at Puerto Peñasco. Drying experiments showed that S. johnstonii, the uppermost species in all zonation patterns at Puerto Peñasco, lost water more slowly than the other two species. In

addition, S. herporhizum and S. sinicola transplanted to the zone of emergent S. johnstonii showed signs of severe desiccation after only one low tide period. Desiccation at low tide probably sets the upper limit of emergent Sargassum.

In coral reef areas freshwater runoff (Tsuda, 1972) and water turbulence (De Wreede, 1973) have been suggested as important physical factors in Sargassum zonation. The Puerto Peñasco intertidal zone is in the midst of the Sonoran Desert and Sargassum plants experience little freshwater stress. Salinity is actually slightly higher in this region than in the open Pacific Ocean (Brusca, 1980), but its effect on Sargassum is unknown. Water turbulence at Puerto Peñasco is more homogeneous across the intertidal than in the coral reef lagoon systems studied by Tsuda (1972) and De Wreede (1973).

Water depths in pools may have a limiting influence on length of S. sinicola and S. herporhizum. The positive correlation between plant length and pool depth reported here 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, Sargassum branches with their air bladders float up toward the surface, and they may branch rather than keep elongating when they reach the surface of pools. Longer plants, or at least their distal parts, may be more easily dislodged by water motion in the shallow

parts of pools as the tide comes in. 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).

Sargassum johnstonii, which occurs in pools in such shallow water that the plants often lie on emergent substrate adjacent to pools at low tide, shows 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, which would increase its reproductive output. Larger plants produce more sexual reproductive structures and therefore the ability of S. johnstonii to grow large independent of water depth increases its reproductive output.

Sand burial or scour may affect Sargassum distributions in the deeper parts of pools and at the more sandy Las Conchas end of the sand gradient from Station Beach to the mouth of Estero Morua (Fig. 1). In the deeper parts of pools where sand levels are greatest and most variable only S. sinicola with its coarse sand-resistant stipe may be able to withstand partial burial and scour. In addition, data presented in Chapter 4 suggest that this species, by producing copious amounts of sexual propagules, may be the best able among the three to colonize the small safe sites (Werner, 1979) of coquina exposed on an irregular basis by changing sand levels.

Sand burial and scour have been shown to affect the availability of substrate and survival of adults and newly settled marine algal propagules (Markham, 1973a, 1973b; Markham and Newroth, 1972; Daly and Mathieson, 1977). Based on other studies of large brown algae in

sandy areas, the prediction would be that S. herporhizum would be the most sand-adapted Sargassum at Puerto Peñasco. Yet this species is virtually absent from the sandy Las Conchas reef.

Markham (1972, 1973a, 1973b) studied the sand-adapted brown alga Laminaria sinclairii (Harvey) Farlow, Anderson & Eaton. This species reproduces primarily through vegetative spread of haptera, which is also a major means of reproduction in S. herporhizum, but L. sinclairii actually thrives in areas of sand scour, whereas S. herporhizum does not (Markham 1972, 1973a, 1973b). Markham (1973a) reasoned that any microscopic gametophytes produced by L. sinclairii are likely to be scoured off the rocks by sand, leaving vegetative proliferation as the only effective means of reproduction (Markham, 1973a). Daly and Mathieson (1977) also listed regeneration of upper thalli from basal parts as a reproductive adaptation of psammophytic (sand-loving) algae in general.

Although Sargassum does not produce microscopic gametophytes like Laminaria, it does begin growth as a small germling that would be susceptible to sand scour, making vegetative proliferation by established plants advantageous in sand-scoured areas. Apparently factors other than simple sand scour are at work affecting Sargassum herporhizum at Las Conchas.

Regrowth from a prostrate mat of haptera is probably adaptive in recolonizing an area after any kind of disturbance that does not kill a plant entirely. Laminaria longipes Bory, an Alaskan species with a rhizoidal holdfast, recovers very quickly after removal of its upper thalli and maintains space more effectively than other Laminaria species

in the face of experimental removal (Dayton, 1974). Similar results were obtained in experimental removals of the three species in pools at Puerto Peñasco (Chapter 4). Sargassum herporhizum was the quickest to recover, even if the holdfast was removed to leave only tiny pieces of holdfast embedded in the coquina substrate. At Las Conchas, long-term sand burial may frequently kill entire plants rather than remove only the upper portions. In Chapter 4, the suggestion is made that the distribution of this species has been limited by its dispersal abilities; it may not be able to maintain long-lived patches in the habitat at Las Conchas due to chance elimination of propagules by sand burial.

Two physical factors may limit distributions of the species at each end of the gradient of water depth within tide pools. In shallow water only the desiccation-resistant S. johnstonii is able to establish itself. Although habitat characteristics of species were distinct and species were not observed to occur in mixed stands, the evidence suggests that competition may play a role in Sargassum distributions. Sargassum johnstonii in tide pools occurs in shallow habitats more prone to desiccation and S. sinicola in deeper habitats subject to greater and unpredictable cover by sand. But sand cover and chance of desiccation are both decreased on sloping substrates at intermediate depths. Sargassum herporhizum, with its rhizoidal holdfast and ability to rapidly and effectively grow over the substrate, may be a competitive dominant for space in this habitat. Removal of plants from small single-species patches was always followed by regrowth of only the original resident species (Chapter 4). Moreover, S. herporhizum regrew faster and more

completely than the other two species. These results are consistent with two different mechanisms for habitat distributions: habitat specialization by all three species and competitive dominance at intermediate depths by S. herporhizum, which can recover quickly following any nonlethal disturbance. The mechanisms are not necessarily mutually exclusive. Only further removal experiments and knowledge of juvenile recruitment success will show if either or both mechanism is operating.

At intermediate depths in tide pools a coralline algal turf occupies large areas of submerged coquina not covered by sand. Sargassum herporhizum with its laterally encroaching holdfast is well adapted to take advantage of any colonization event. By spreading out from a small initially colonized space in the turf, it can then expand its canopy and holdfast coverage by shading and outcompeting the smaller coralline algae. Successful settlement by other Sargassum species within dense stands of S. herporhizum will also be prevented by canopy shading. A rhizoidal holdfast is unsuitable for dispersal across the sand-covered substrate in the deeper parts of the pools.

Comparison of the different sites (Figs. 7-11) revealed shifts in the upper limit and in the habitat of S. sinicola in the intertidal zone. These shifts may be due to a combination of differences in desiccation severity and presence or absence of the competitively dominant S. herporhizum at the sites. At Las Conchas and Pelican Point the zones of emergent S. johnstonii and S. sinicola were contiguous, with emergent S. sinicola occurring higher in the low intertidal zone. There was also a shift in the predominant habitat of S. sinicola in the lower

intertidal zone at these sites; it was found mainly on emergent substrate instead of in pools as at Station Beach and Playa de Oro.

Although S. johnstonii occurs highest in the zonation pattern at Las Conchas and Pelican Point, its upper limit at these sites is lower than at Station Beach and Playa de Oro. Its upper limit coincides with the abrupt change from coquina substrate to sand at Las Conchas and to granite at Pelican Point. Deep sand is an unstable support for Sargassum plants. Although Sargassum does grow on granite in the lower intertidal zones at Pelican Point (S. herporhizum is the most abundant of the three on this substrate), at higher levels nonporous granite may heat up more than coquina, which would dry out any germ-lings that settle on it.

The upward extension of the limit of emergent S. sinicola plants at Las Conchas and Pelican Point may be related to the absence or rarity of S. herporhizum at these sites. The dense stands of the latter species that are common in the lower intertidal zone at Station Beach are probably very effective at monopolizing space and preventing settlement of S. sinicola. As suggested above, sand burial may prevent S. herporhizum from occurring at Las Conchas. Its absence from Pelican Point may be due to greater desiccation stress. As the drying experiments showed, S. herporhizum is the least desiccation resistant of the three species. The lower intertidal coquina shelf at Pelican Point, without a beach berm and large tide pools at higher levels, is subject to less continuous drainage, and there are few pools in the coquina. During the several days of extreme tides in spring when the transects were conducted at Pelican Point there occurred extensive blackening of

S. herporhizum plants that were not next to tide pools. The absence of dense stands of this species may allow S. sinicola with its greater desiccation resistance to occupy more space on emergent coquina at this site.

CHAPTER 3

SEASONAL PATTERNS

Occurrence of seasonal cycles of abundance in intertidal algal assemblages is nearly universal, even in thermally uniform tropical regions (Conover, 1964; Tsuda, 1972, 1974; Mathieson and Dawes, 1974). Sargassum is often the predominant algal species in tropical and subtropical coastal waters in terms of biomass and canopy cover (Fritsch, 1945; De Wreede, 1973, 1976; Prince and O'Neal, 1979). It usually exhibits a consistent pattern of seasonal fluctuations in abundance wherever it occurs, although this has not been quantitatively shown in most reports (see review in De Wreede, 1976). These cycles of vegetative growth and attrition are closely related to cycles of sexual reproduction (Tsuda, 1972; De Wreede, 1976; Prince and O'Neal, 1979) and therefore influence a species' ability to disperse, colonize, and persist in a locally patchy environment. This chapter reports on seasonal variations in abundance, size, habitat, and distribution of the three species of Sargassum in the intertidal zone at Puerto Peñasco. It also documents patterns of spatial patchiness and long-term changes in abundance from 1977 to 1981.

These patterns are interpreted as growth strategies of the three species at Puerto Peñasco. The growth strategy of a plant is taken here to be the temporal pattern of growth and reproductive periods in a plant population. These patterns are strategies in that

they are to some degree facultative in response to local conditions, and certain patterns will be more successful than others under a given set of conditions.

Reproductive Cycle in Sargassum

The thallus of a typical Sargassum plant consists of a basal holdfast and one or more upright main axes each with a lateral branch system of leaflike blades and hollow air bladders (Fritsch, 1945; Bold and Wynne, 1978; Lee, 1980). During fertile periods sexual receptacles are produced on short branches in the axils of blades (Fritsch, 1945). These receptacles are cylindrical, sometimes branched structures, approximately 0.5 to 2 mm wide and up to 25 mm long in the species at Puerto Peñasco (Norris and Yensen, n.d.). They contain gametes in flask-shaped cavities called conceptacles (Fritsch, 1945). The holdfast and sometimes part of the main axis are perennial (Bold and Wynne, 1978), although ages of plants in natural populations are not generally known (Yoshida, cited in Russell, 1973). Most of the upright branch system is shed each year just after the development of fertile receptacles (Fritsch, 1945; De Wreede, 1976; Prince and O'Neal, 1979). Branched portions of various sizes detach from the parent plant and float away, buoyed up by the air bladders. These portions are alive and capable of growth as shown by their ability to be readily cultured in the laboratory (Fletcher and Fletcher, 1975b; Kane and Chamberlain, 1979; Deysher and Norton, 1982). In fact, pelagic Sargassum species are assumed to be derived from detached benthic forms (Parr, 1939; Ryther, 1956). Floating vegetative portions derived from benthic plants

play an important role in dispersal of sexual propagules, because they may become fertile during their pelagic existence and establish new populations at great distances from the parent plant (Deysher and Norton, 1982). Large quantities of fertile branches in drift material at Puerto Peñasco were observed during the reproductive season.

Because the seasonal cycle of growth is usually followed by the shedding of fertile branches, it is an important feature in the life history of Sargassum. De Wreede (1976) has shown that in Hawaii fertile branches are shed at a time when water temperatures are optimal for embryo growth. He also found differences in the timing of receptacle production in three Hawaiian species and theorized that this allowed for staggered periods of settlement by germlings of the three species at times when cover of their respective adult populations would be low. This hypothesis implies temporal separation in reproduction that would contribute to ecological separation between adult plants. His suggestion is intriguing with respect to the present study because of the clear differences found at Puerto Peñasco in distribution and habitats of the three species in the intertidal zone.

Seasonal patterns of abundance and phenology of tropical and subtropical brown algae in general are poorly known (Russell, 1973). De Wreede (1976) has reviewed the literature on seasonality in tropical Sargassum species and found that peak abundance generally occurs during the colder months of the year. Sargassum muticum occurs in temperate regions, often as an invasive introduced species (Farnham, Fletcher, and Irvine, 1973; Norton, 1977a, 1977b; Abbott and Hollenberg, 1976; De Wreede, 1978). In the cold waters of the British Isles

this species reaches peak size in summer (Fletcher and Fletcher, 1975a; Jephson and Gray, 1977; Kane and Chamberlain, 1979). In British Columbia the same species achieves peak biomass and size in April (De Wreede, 1978). Thus, for species studied so far, the time of peak abundance is in warmer months in temperate regions and in colder months in tropical and subtropical regions. The exception to this pattern is S. duplicatum (= cristaefolium, De Wreede, 1976) in Guam, which peaks in size and abundance in June (Tsuda, 1972). In this tropical area, however, summer sea surface temperatures are only about 2°C higher than in winter (Tsuda, 1972).

In view of the generally contrary patterns of seasonal abundance in temperate and tropical areas, it was not entirely clear what seasonal patterns the Puerto Peñasco species would show in the highly seasonal northern Gulf of California (Thomson and Lehner, 1976). Either season's extreme temperatures (Fig. 2) may have a detrimental effect on standing crops.

Several investigators have remarked on the obvious seasonality of the algal flora in the northern Gulf of California (Dawson, 1944; Norris, 1975), but quantitative studies are few. Norris (1978, pers. commun.) surveyed an intertidal transect at Station Beach at intervals of 2 months for 1 year. Some published results from this transect (Wynne and Norris, 1976) show that three species of Colpomenia occur as winter annuals. There were also indications that the three Sargassum species display a maximum canopy cover in mid-winter and a minimum in summer (Norris and Yensen, n.d.). These findings would conform with the general pattern for the tropical and subtropical

Sargassum as noted above. The observations reported in this chapter expand on the latter studies and represent the first detailed report on algal seasonality in the northern Gulf of California.

Populations of species may undergo long-term changes in local abundance that are superimposed on cyclic seasonal fluctuations. Such changes are difficult to predict, but their documentation is an important first step in understanding the underlying causes and possible consequences of such fluctuations. Evidence of such changes in abundances of Sargassum species emerged during the course of seasonal studies and is reported here. These changes will be discussed in light of recent climatic anomalies (Duggins, 1981)) and the dramatic decline of the asteroid Heliaster kubiniji, an important predator in this area (Dungan, Miller, and Thomson, 1982).

Materials and Methods

The occurrence of the Sargassum species in the intertidal zone at Station Beach is very patchy and no single measurement can adequately portray their distribution and seasonality. Abundances and growth cycles were therefore measured by several means on two spatial scales.

Seasonal and Long-term Changes in Abundance and Intertidal Distribution of Sargassum

The large-scale intertidal distribution was surveyed on the transects in the area of Station Pool (Fig. 6), a large tide pool 40 m long, 20 m wide, and up to 0.6 m deep. Thomson and Lehner (1976) provided a diagram and further details on its physical characteristics.

Five replicate transects were set up in the area, spaced 10 m apart and extending from the upper border of the reef to the lowest part uncovered by spring tides. One of the replicate transects covered the same area as that of Norris (Wynne and Norris, 1976; Norris and Yensen, n.d.). At each 10-cm mark along the transect, the presence or absence of a Sargassum species was noted. Each plant's habitat was recorded as "pool" or "emergent," according to whether its holdfast at low tide was submerged or exposed to air, respectively. Abundance was calculated as percent occurrence (= number of points where a species occurred divided by the number of points sampled). This estimated the percentage of the reef covered by the Sargassum canopy.

A baseline census of these transects was conducted in the autumn (October-November) of 1977 (Fig. 7). This was followed by transect series in the following winter (February 1978) and later summer (July- September, 1978). Three years later, starting in April 1980, the transects were conducted at intervals of several months for over a year through July 1981. The lowermost segments of the transects varied in length, depending on the low-tide level on the census date. Most transects were at least 90 m long. Due to insufficiently low tides, data were collected for only the upper 60 m in late summer (September) 1980 and upper 80 m in summer (July) 1981.

Graphs of the intertidal zonation of the three species on the transects were compiled for each sampling date to assess seasonal changes (if any) in relative vertical positioning of the three species on the shoreline.

Transect data were also used to determine seasonal changes in habitats of the three species. The species showed clear differences in their frequency of occurrence in pools or on emergent substrate. Each set of transects on a particular date was divided into upper and lower segments as noted above. The data for each date from the upper segments of the five transects were pooled and frequency of occurrence of each species in pools and on emergent substrates was calculated; frequency of occurrence of species in each habitat type on the lower segments were calculated in the same manner. This procedure yielded a four-way classification scheme (date, species, location in intertidal zone, habitat). Based on these frequencies, the "habitat proportion" of a species on a given date was calculated as the percentage of plants occurring in each habitat.

Seasonal Changes in Tide-pool Canopy Cover of Sargassum

Canopy cover in four small patches of each species in a tide pool were monitored for a 1-year period to assess seasonal changes in Sargassum canopy cover on a small spatial scale. The patches were located in a large tide pool at Playa de Oro, about 600 m west of Station Pool (Fig. 1). Four square patches in a pure stand of each Sargassum species were marked out with nails. The patches for S. johnstonii and S. herporhizum were 10 cm on a side; the patches for S. sinicola, which has a larger canopy cover by one plant, were 20 cm on a side. All patches were photographed periodically from April 1980 to March 1981. The resulting color slides were displayed on a checker-board-type grid of 100 points. At each point the presence or absence

of a Sargassum plant was noted. The sum of points for each species on a slide was used as an estimate of the species' percent canopy cover on a given date.

Seasonal Variation in Size and Fertility of Sargassum

The seasonal growth cycles of the three species were monitored by two means that parallel the measurements of canopy cover for large and small spatial scales.

Stipes of the three species were collected at approximately 1-month intervals from fall 1979 to spring 1981 (plus two collection in the spring of 1979) in the area between Station Pool and Playa de Oro. Only one stipe was collected from each plant to avoid destructive removal of the entire plant. In each collection, 25 stipes of each species chosen at random were measured from base to apex. Stipes from these three collections were scored for the presence or absence of sexual receptacles. This procedure provided an estimate of the time of onset of fertility and proportion of fertile stipes in populations of the three species.

Stipe length was also measured in smaller, permanently marked patches in tide pools. Two patches of each species were marked in an area just east of Station Pool. Patches ranged from 1 to 3 m in diameter. At intervals of about one month from fall 1979 to fall 1980, lengths were recorded for 25 plants selected at random in each patch ($n = 50$ per species). Length was measured as the distance from the holdfast to apex of the longest branch.

Settlement Blocks

Attempts were made to recruit Sargassum germlings onto settlement blocks of natural substrate. Each block consisted of two slabs of clean sun-dried coquina, 10-20 cm in diameter, cemented to a concrete block 9 cm by 39.5 cm. Blocks were anchored to the substrate by placing a strip of plumber's tape across the center between the coquina slabs and nailing the strip to the reef on either side of the block. Nine blocks (three per species) were placed near existing stands of Sargassum in Station Beach tide pools in spring 1980 and nine more were placed nearby in fall 1980. These were photographed or observed approximately monthly until November 1981.

Results

Because of variation in transect length, percent occurrence rather than frequency was used in analysis of data. It should be noted that if lower segments were less than 30 m long, they did not adequately sample the populations of S. herporhizum in the zone below the fault. This was taken into account in the conclusions that follow.

Seasonal and Long-term Changes in Abundance

The transect data from 1980-81 showed a cyclic change in seasonal abundance of the three species (Fig. 18). They declined in canopy cover from April 1980 to a minimum in late summer, then increased to a maximum cover in later winter and spring (February-April). Cover again decline to a minimum in July. Transect lengths were less than 90 m on dates when the minima occurred (September

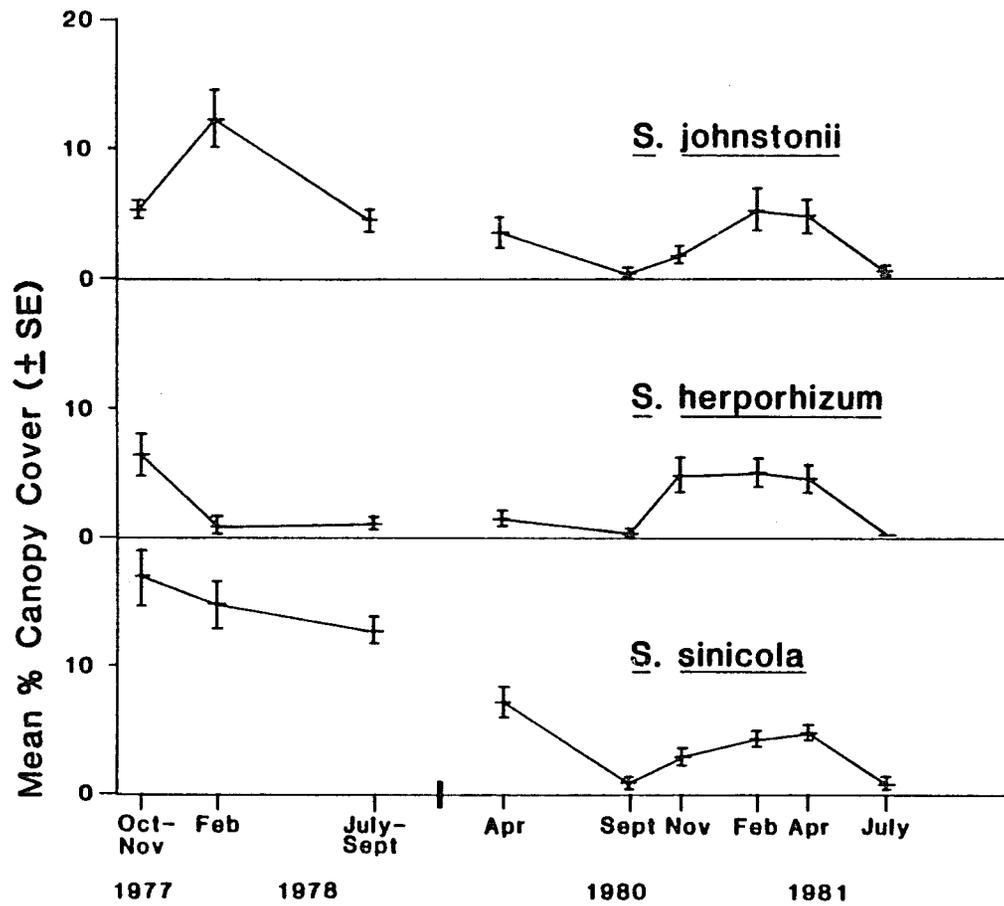


Figure 18. Seasonal variation in canopy cover for *Sargassum* species on Station Beach transects

1980, July 1981), which may have been responsible for part of the decreases in these species' abundances, but this does not explain their virtual absence in 1980 and 1981 in areas in the mid-intertidal zone where they had been abundant. The summer minima for S. herporhizum were probably entirely due to the shortness of the lower segments of the transects, which failed to sample the main part of the distribution of this species below the reef fault.

Canopy cover of species in 1977-78 and 1980-81 were compared using Wilcoxon's signed rank test by matching upper or lower segments of the transects (i.e., above and below the reef fault) with their counterparts in the same month in different years. Sargassum johnstonii and S. sinicola were significantly less abundant in 1980-81 than in 1977-78; S. herporhizum displayed little or no change over the same time interval (Table 3). Again, however, data for the last species did not cover the bulk of its occurrence below the reef fault.

Canopy cover of the three species did not show the same clearly cyclic pattern in 1977-78 (Fig. 18). Sargassum johnstonii did achieve a peak in winter, but the other two species did not. Cover of S. herporhizum dropped markedly after the initial census in fall 1977 and remained low from winter to late summer. Canopy cover of S. sinicola also declined but less markedly than that of S. herporhizum.

The decline in Sargassum cover on the transects was most obvious in Station Pool, which was almost devoid of Sargassum in September 1980 and July 1981. It is obvious that the Sargassum abundances have decreased in the past 3 years in this sampling area of approximately 4,000 m².

Table 3. Long-term changes in abundance of Sargassum species on Station Beach transects. Abundances compared between dates using Wilcoxon signed ranks test (Dixon and Brown, 1979) in the same month in different years

Species	Mean Percent Occurrence (Cover) (SE)					
	November		February		July	
	1977	1980	1978	1981	1978 ^a	1981
<u>S. johnstonii</u>	5.22(0.58)	1.82(0.65)*	12.00(2.04)	5.14(1.73)*	4.36(0.76)	0.34(0.15)*
<u>S. herporhizum</u>	6.34(1.49)	4.64(1.31)	0.87(0.47)	4.82(1.31)	1.00(0.40)	0.0 (0.0)*
<u>S. sinicola</u>	16.93(2.11)	2.78(0.46)**	14.67(1.99)	2.78(0.46)*	12.67(1.02)	0.80(0.43)**

a. Collection period July to September.

* $p < .05$.

** $p < .01$.

Seasonal Changes in Zonation

No distinct seasonal changes in zonation of the three Sargassum species were observed. The species maintained the same relative vertical positions on the shore despite marked changes in abundance.

Seasonal Variation in Occurrence of Sargassum in Habitats

Differences in habitat proportions between the three species have been discussed in Chapter 2. The same patterns were evident in the present series of transects. Differences across seasons in the species' habitat proportions in the upper and lower intertidal zones were compared using the G test (Sokal and Rohlf, 1969). Significant seasonal differences were found in some cases, but in general the habitat proportions of each species were the same in all seasons; no cyclic patterns were observed (Fig. 19). Sargassum johnstonii is the most desiccation-resistant species (see Chapter 2) and showed significant variation across seasons in the proportion of plants occurring outside pools in the upper intertidal zone ($p < .05$) but not in the lower intertidal zone ($p < .2$) (Fig. 19). Sargassum sinicola and S. herporhizum are less desiccation resistant (see Chapter 2). Their habitat proportions varied significantly ($p < .005$) across seasons only in the lower intertidal zone, i.e., the proportion of plants occurring on emergent substrate varied, although the general pattern for each species held (Fig. 19). Habitat proportions of these two species did not vary significantly ($p < .9$) in the upper intertidal zone where both were almost entirely restricted to tide pools.

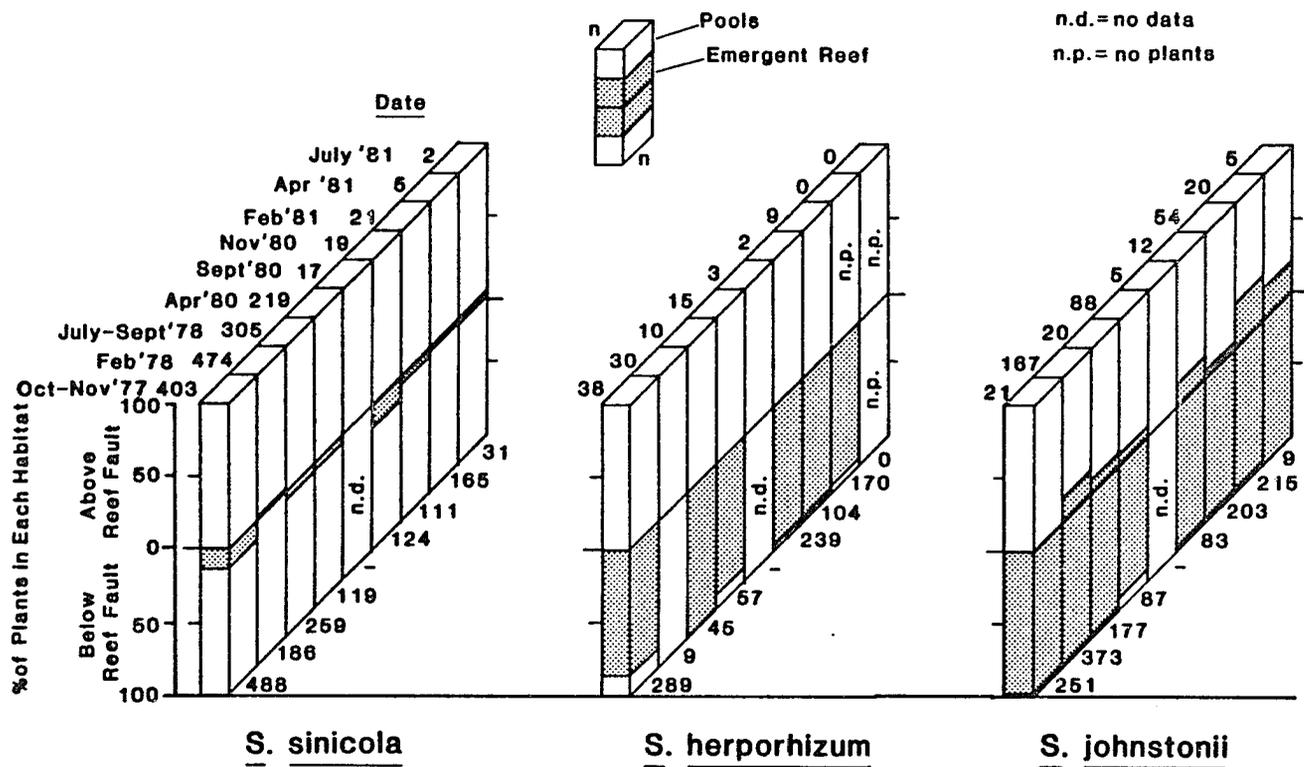


Figure 19. Seasonal variation in habitat type for *Sargassum* species on Station Beach transects

Seasonal Changes in Canopy Cover in Tide Pools

On a small spatial scale the canopy cover in single-species patches showed a common pattern for all three species (Fig. 20). Mean percent cover in selected patches decreased from 100% in April to a minimum in late summer (September 1980). Canopy cover of S. sinicola and S. johnstonii dropped to less than 20% mean canopy cover in the summer, whereas S. herporhizum maintained an average 35% cover.

Regrowth of canopy cover in spring 1981 did not reach the 100% level of the previous year for any species, demonstrating that canopy cover in a small patch changes from year to year. Mean canopy regrowth by spring 1981 was greatest in patches of S. herporhizum; S. johnstonii and S. sinicola patches recovered to a lesser extent and showed greater statistical variance than those of S. herporhizum (Fig. 20). Two S. johnstonii patches and two S. sinicola patches recovered to less than 5% cover by the spring of 1981. None of the patches of these two species recovered to more than 60% by March 1981. In contrast, the minimum recovery of S. herporhizum by March 1981 was 26% and the maximum was 90%. Recovery for all three species was probably through regrowth from perennating holdfast and stipes, because no new patches of Sargassum, indicative of newly settled plants, were observed in the immediate vicinity.

Seasonal Changes in Stipe Length in the Station Beach Collections

Stipes of all three species reached a peak length in the spring, although in 1980 the S. sinicola stipes attained maximum size slightly

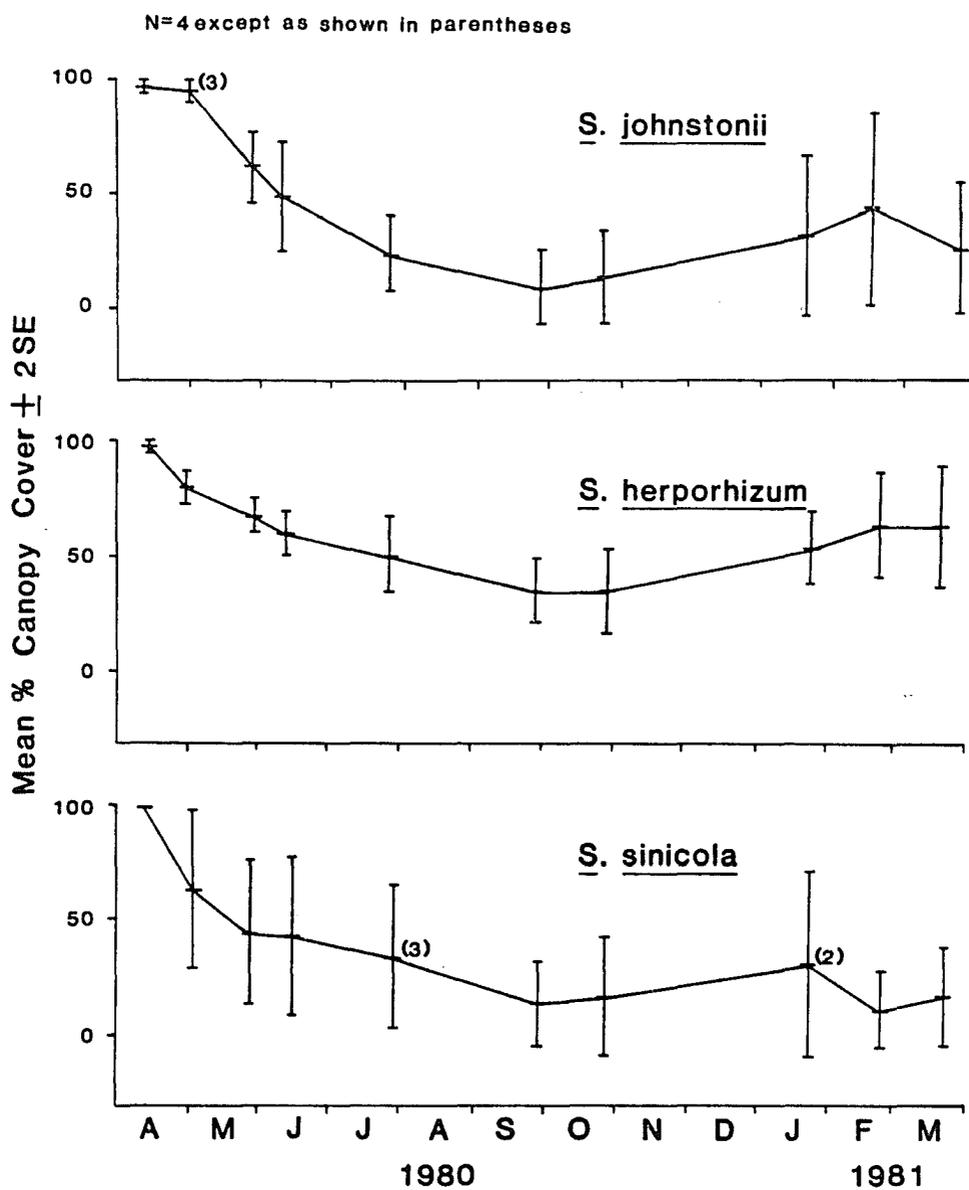


Figure 20. Seasonal variation in canopy cover in selected patches of Sargassum in a tide pool at Playa de Oro

later than did those of the other two species (Fig. 21). Sargassum sinicola stipes also showed a second peak in size in the fall 1979 and 1980 (Fig. 21). Stipes of all three species were shortest in summer. In September 1980, S. johnstonii in the collection area were either absent or too small to be identifiable, and no stipes were collected. Sargassum sinicola maintained a greater average length throughout the year than the other two species.

Seasonal Changes in Stipe Length in Selected Patches

Stipe length in permanently marked patches followed the same seasonal pattern found in stipe collections from Station Beach. Length differences between patches of a species were minor and data were therefore pooled for analysis. Stipes of all three species attained minimum size in summer and maximum size in spring. Stipes of S. sinicola declined initially from what was another peak in size in the fall (Fig. 22).

The pattern of stipe length variation showed the ephemeral nature of some patches. In July 1980, S. johnstonii died back so much in one patch that no plants were found to measure (note that $n=25$ in Fig. 22). In the following month, August, only two plants with stipes longer than 0.5 cm were found in the remaining patch (note that $n=2$ in Fig. 22). A similar situation occurred with S. herporhizum as indicated by samples sizes less than 50 in July, August, and September, 1980 (Fig. 22). One patch of each of these two species died out to the extent that plants from two nearby patches were measured in October

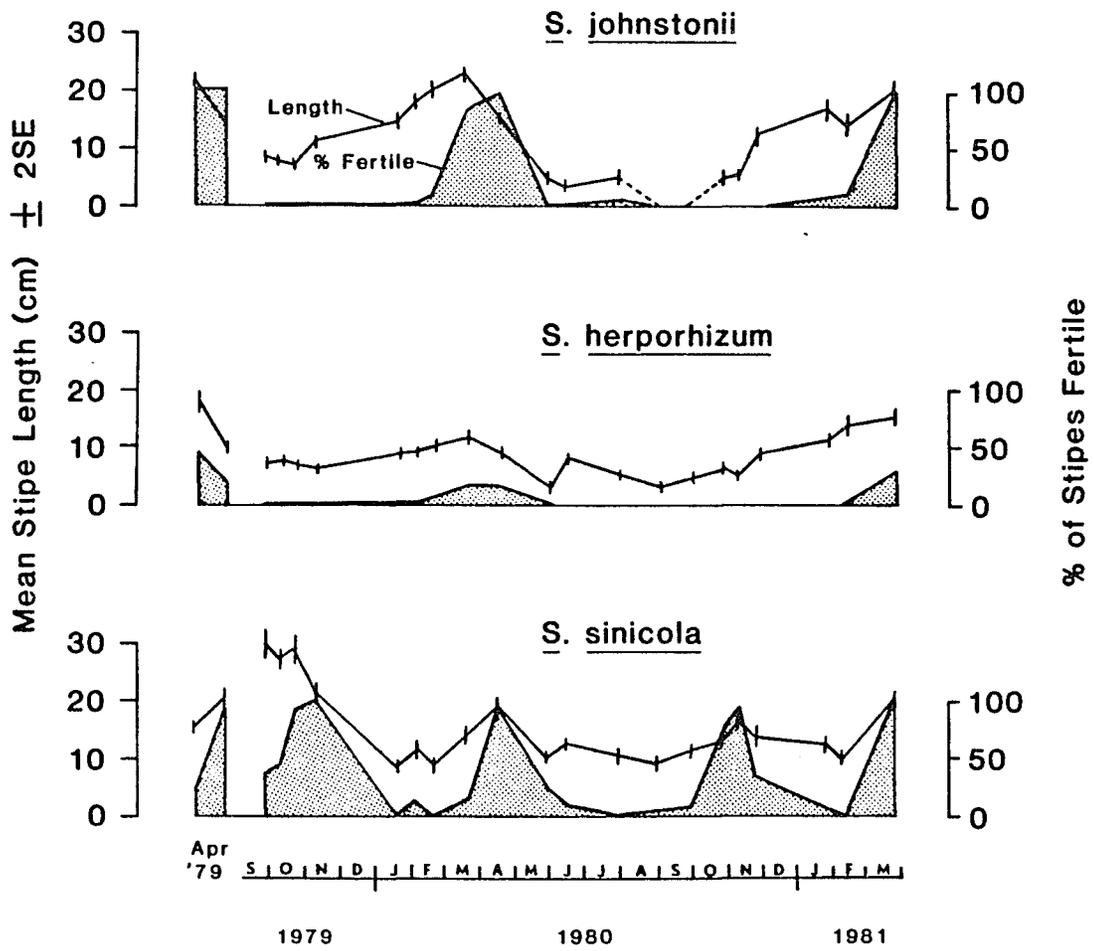


Figure 21. Seasonal variation in stipe length and percentage of fertile stipes in *Sargassum* collections from Station Beach

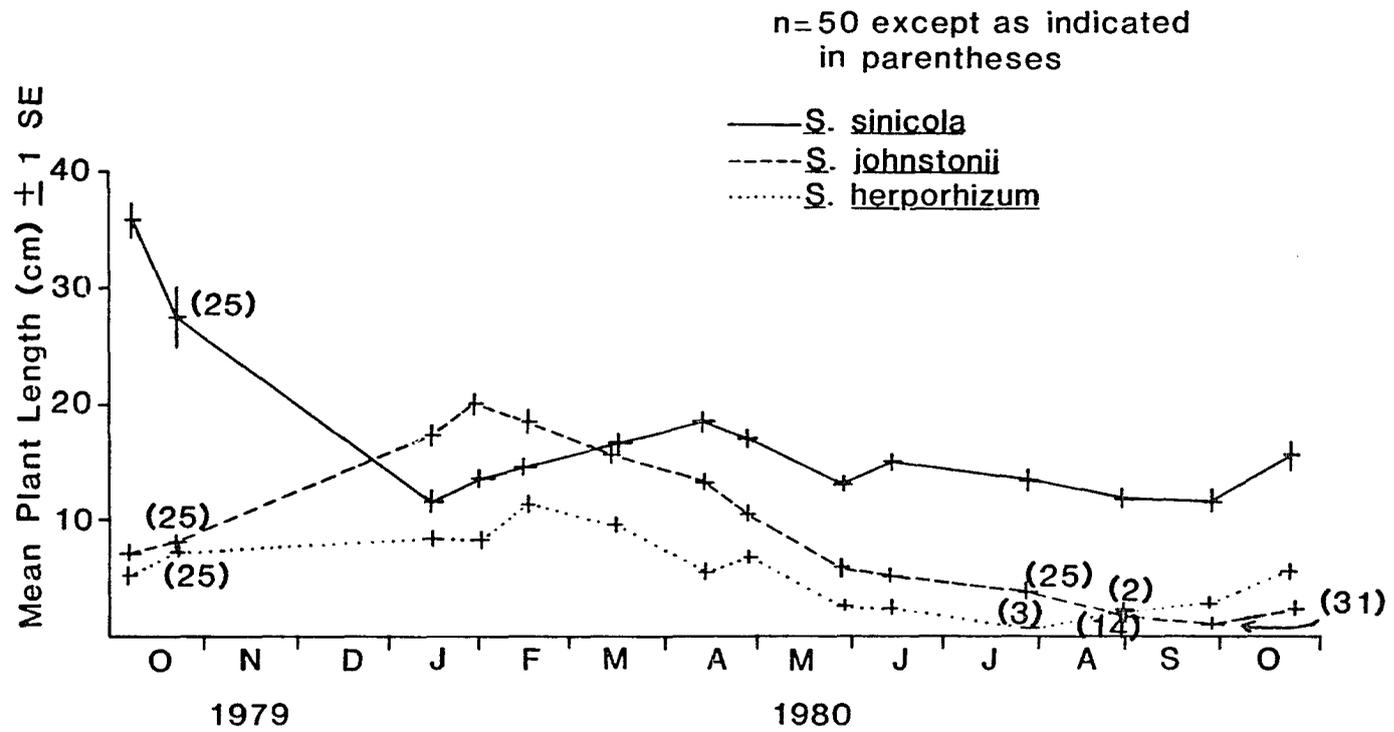


Figure 22. Seasonal variation in mean plant length for Sargassum in selected patches in Station Beach tide pools

1980 to bring the sample sizes up to 50. During this period plants in nearby patches appeared healthy and were growing.

Sargassum sinicola did not die back as far as the other two species (Fig. 22). Plants of this species retained more of their main axes through the summer, even though they were often heavily covered by epiphytes (e.g., Jania, Dictyota). Although S. sinicola did become more scarce within the two selected patches over the summer and never quite recovered its original canopy cover, surviving plants maintained a greater mean stipe length than the other species.

Sargassum sinicola stipes displayed a large decrease in length after fall 1979 in both stipe collections (Fig. 21) and patches (Fig. 22). Neither species regained the mean length first measured in October 1977. Because neither of the other two species showed a permanent decline in length, this may have been an artifact of sampling of S. sinicola or it may instead represent a decrease in length corresponding to the general decrease in abundance observed on the larger intertidal transects at Station Beach from 1978 to 1980 (Fig. 18).

Reproductive Phenology in Stipe Collections

The three Sargassum species became fertile just after or concurrent with maximum stipe length in the spring (Fig. 21). Stipes of S. sinicola developed mature receptacles slightly later than the other species. All three species shed their branches after the receptacles were developed, which would account for the decrease in size in late spring. The second annual peak in size attained by stipes of S.

sinicola in the falls of 1979 and 1980 was accompanied by another crop of receptacles and a subsequent decrease in length.

The proportion of stipes in the population that became fertile varied between species (Fig. 21). Virtually every stipe of S. johnstonii and S. sinicola was fertile in the spring. The same was true for S. sinicola in the fall. In contrast, less than half of the S. herporhizum stipes were found to be fertile (44% in April 1979; 16% in March and April, 1980; 28% in March 1981).

Settlement Blocks

At no time were any Sargassum plants observed on any of the settlement blocks. Most space was covered by crustose and branched coralline algae after 4 to 5 months. Occasionally, a Padina or Dictyota was found on the coquina. Colpomenia tuberculata settled abundantly on several of the blocks in fall 1980. After 6 months the coquina slabs set out in both seasons supported roughly the same turf communities observed on nearby natural substrates in the tide pools.

Discussion

Seasonal Patterns in Abundance of Sargassum at Puerto Peñasco

Sargassum species from tropical and subtropical areas are usually most abundant in the cooler part of the year, some time between November and March (De Wreede, 1976; Prince and O'Neal, 1979). The three species at Puerto Peñasco attained maximum size (Figs. 21 and 22) and canopy cover (Figs. 18 and 20) between February and April as temperatures began to rise. Sargassum sinicola also showed a second

peak in size in the fall. The three species shed their branches after the reproductive period in the spring and are therefore smallest and least abundant in the summer. Sargassum sinicola also sheds its branches after the fertile period in autumn.

Prince and O'Neal (1979) have argued that for maximum plant size to be attained in winter, growth rates must be highest in the preceding warmer months, perhaps even in the hottest months of the year. This was not found for the Puerto Peñasco species, whose growth period extends from October to March, the coldest part of the year. Sargassum sinicola does reach a second peak in size in the fall, implying that it grows substantially in August and September at temperatures up to 15°C higher than in February and March (Fig. 2). It also reaches maximum size in the spring at a slightly later and warmer time than the other two species.

New germlings of the three species produced in the spring must survive and perhaps even grow throughout the hot summer months at Puerto Peñasco. De Wreede (1976) found that water temperatures in Hawaii during the period just after Sargassum gametes were shed were optimal (24°C) for embryonic development. Whether high temperatures enhance survival and growth of Puerto Peñasco species or are simply tolerated must be determined by future culture studies of embryos.

Mathieson and Dawes (1974) reported that among the several genera of red algae they studied in Florida the more southern species grew fastest in winter, whereas more northern species did so in summer. Despite different seasons of highest growth rates, temperature optima of the two groups of algae remained the same, i.e.,

northern and southern species grew fastest at similar temperatures, but these temperatures were reached in different seasons at different latitudes. From their study of S. pteropleuron in Florida, Prince and O'Neal (1979) disputed the idea of opposite seasons of maximum growth in cold and warm regions. If, however, one considers peak abundance rather than maximum growth rate, the pattern proposed by Mathieson and Dawes (1974) is generally true for Sargassum. Tropical and subtropical species, including S. pteropleuron (Prince and O'Neal, 1979), tend to reach peak abundance in cooler months, and temperate species tend to do so in warmer months (Fletcher and Fletcher, 1975a; De Wreede, 1976, 1978; Jephson and Gray, 1977). This parallels the pattern found by Mathieson and Dawes (1974), because temperatures during peak Sargassum seasons are roughly comparable, but they occur at different times of the year at different latitudes.

At Puerto Peñasco, with its tropical summer and temperate winter temperatures, the three species attain maximum size in spring in between times of extreme temperatures. The second size maximum and fertile period of S. sinicola in autumn also falls between seasonal temperature extremes.

Peak abundance usually coincides with peak fertility. The different abundance peaks in temperate and tropical areas may represent adaptive shifts in the timing of gamete development and release and early embryonic development. In warmer tropical waters Sargassum is usually fertile in cooler months; in colder temperate areas plants are fertile in warmer months. Sargassum apparently avoids reproducing during the season of the most extreme temperatures. In the northern

Gulf of California seasonal extremes are comparable to those in temperate winters and tropical summers (Fig. 2). By having fertile seasons in the spring or fall, the Sargassum species avoid reproducing during either season of temperature extremes. Thus the seasonal fertility patterns of Sargassum at Puerto Peñasco provides an examples of a compromise in adaptive timing of reproduction compared to patterns in tropical and temperate climates.

Seasonal Constancy of Sargassum Habitat Types and Distributions in the Intertidal Zone

Some seasonal differences in habitat distribution were observed within the three Sargassum species, but the basic patterns remained the same throughout the year. Habitat data from the seasonal transects showed that the three species differed significantly in their occurrence in pools and on emergent reef (Fig. 19). In addition, each species differed in its habitat preference in the upper and lower intertidal zones; all species occurred proportionately more often on emergent reef in the lower intertidal zone.

Despite seasonal changes in abundance the basic patterns of distribution in the intertidal zone remained the same throughout the year. There were no changes in relative vertical positioning of the three species in the intertidal zone. No evidence for seasonal replacement of one Sargassum species by another was observed.

Reproductive Phenology and Growth Strategy

The differing growth strategies of the three species may explain the existence of two fertile periods in S. sinicola compared to a single

season in the other two species. Temperature and photoperiod are the most likely physical cues for the development of receptacles (De Wreede, 1976; Prince and O'Neal, 1979). At Puerto Peñasco receptacles reach full development in spring and fall in between periods of extreme heat or cold. In addition, a critical size may be necessary before a plant becomes fertile. Becoming fertile after maximum size is reached would maximize the reproductive output in a growing season because larger plants bear more receptacle tissue. In fact, for the three species reported on here, larger plants are the first to develop receptacles (Chapter 4). Although there is a general attrition of all Sargassum during the summer, surviving S. sinicola plants maintain a greater average length than plants of the other two species (Figs. 21 and 22). This may be because most of its population at Station Beach is found in tide pools (Fig. 12), making it less susceptible to damage from summer heat. By maintaining a larger size through the summer it is able to reach the size necessary for receptacle development after only a few months of growth in the fall. Meanwhile, the other two species are still growing and will not reach the critical size until the following spring.

The spring fertile period of S. herporhizum coincides with that of S. johnstonii and both are slightly earlier than that of S. sinicola (Fig. 21). This pattern is similar to the staggered reproductive periods De Wreede (1976) found for three Hawaiian species of Sargassum; however, he reported offset fertile periods for all three of his species. This staggered reproductive pattern may serve, as De Wreede implied, to separate the settlement time of one species of

Sargassum from another and reduce interspecific competition for settlement sites. At Puerto Peñasco, however, the temporal separation is not as clear as in Hawaii, and in light of the zonation and habitat differences between the three species, reduction of competition through separation of settlement time would seem superfluous. The staggered reproductive periods may allow these species to take advantage of temporal differences in habitat availability.

De Wreede (1976) pointed out that Sargassum germlings settle and grow during the season of low adult abundance, following the annual dieback. At Puerto Peñasco the period of reduced shading from canopy cover and increased availability of primary space to settle in summer may facilitate germling survival. By reproducing in the fall as well as the spring, S. sinicola may also gain access to space newly opened during the late summer, the time of minimum Sargassum cover.

Persistence of Sargassum in Tide Pools

Annual growth patterns of the Puerto Peñasco species showed a consistent seasonal cycle, but the persistence of the species in discrete patches in tide pools and even in large areas such as Station Pool was less consistent (Figs. 18, 20, and 22). Long-term persistence in an area appears to consist of an annually changing mosaic of patches. Although Sargassum species are the predominant overstory algae in this area, individual patches of Sargassum plants may be more ephemeral than patches of articulated coralline algae that cover considerable space in the tide pools. This ephemerality is probably more characteristic of the mid-intertidal populations of Sargassum in

tide pools than of the lower intertidal populations, which displayed less seasonal fluctuations in abundance.

Canopy cover of S. herporhizum in the selected patches recovered more completely after the summer dieback than that of the other two species (Fig. 20). This may be due to its capacity for regrowth from its extensive rhizoidal holdfast. The non-rhizoidal holdfasts of S. johnstonii and S. sinicola are less effective in lateral spreading to enlarge or maintain a patch. Both of the latter species invest relatively more resources than does S. herporhizum to sexual structures and may be more effective in dispersing the species to a new site (Chapter 4).

Long-term Changes in Sargassum Abundance at Puerto Peñasco

A general decline in abundance of populations of S. johnstonii and S. sinicola from 1978 to 1980 was observed in the Station Pool area (Fig. 18 and Table 3). While collecting stipes at Station Beach in summer 1980 I noticed that S. johnstonii plants were extremely rare, which may have been due to low frequency of successful settlement by germlings. No Sargassum settled on the two sets of settlement blocks placed in tide pools in the spring and fall of 1980. As of late 1981 these plates appeared identical to nearby areas that were covered with articulated coralline algae. The bare coquina may have been unsuitable for Sargassum, although Deysher and Norton (1982) found that S. muticum settled much more densely on unoccupied substrates than on substrates already colonized by other algae. Raju and Venugopal (1971) observed a lag time of 9 to 10 months in India before Sargassum settled on concrete blocks, but they set out their blocks in January,

which is near the end of the fertile season. The settlement blocks placed in the intertidal zone at Puerto Peñasco were set out in April during the peak fertile period in the spring of 1980, in some places directly beneath fruiting plants. Nevertheless Sargassum failed to settle on the plates.

Recent anomalous water temperatures observed in the Gulf of California may have affected several species of intertidal organisms. Dungan et al. (1982) have described the near extinction of the asteroid Heliaster kubiniji Xantus from Puerto Peñasco and other areas in the Gulf of California in 1978. The cause of mortality was not definitely established, but the presence of a concurrent bacterial infection, which may have been the primary cause of death, was demonstrated. During 1978 anomalously warm temperatures were recorded in the Gulf of California (Dungan et al., 1982) and along much of the Pacific Coast of North America (Duggins, 1981). Dungan et al. (1982) suggested that this period of slightly but significantly warmer temperatures from September 1977 to August 1978 may have increased the abundance of the bacteria or increased the susceptibility of the asteroid to the bacteria, or may have done both.

Summer is the normal season of attrition for Sargassum, and this period of record warm temperatures may have accentuated the annual Sargassum decline, resulting in the death of a larger portion of the population than normally. Shallow areas would be subject to the greatest increases in water temperature, and Dungan et al. noted that shallow-water Heliaster were more affected during the dieoff than those in deeper water. My data also showed that Sargassum populations in

mid-intertidal pools such as Station Pool decreased more than those in the lower intertidal zone from 1977 to 1981.

The possibility exists that Sargassum may have been responding indirectly rather than directly to the removal of Heliaster from the food web (Paine, 1966). Removal of Heliaster may have resulted in an increase in the number of herbivorous snails that are normally eaten by Heliaster. Boyer and Yensen (n.d.) have documented marked increases in several species of herbivorous snails (Columbella fuscata Sowerby, Nerita funiculata Menke, Tegula spp., Turbo fluctuosus Wood, for examples) at Station Beach since the decline of Heliaster. Some of these species (Columbella, Turbo) were observed swarming over the settlement blocks, laying eggs, and presumably grazing. Adult Sargassum are rarely eaten due to their chemical and structural defenses (Conover and Sieburth, 1964, 1966; Montgomery et al., 1980), and therefore increased grazing would probably be concentrated on juveniles. The effect of this process would probably not be apparent in the adult Sargassum population for 1 or 2 years.

Duggins (1981) has documented a possibly analogous indirect effect of temperature change on kelp populations in Alaska. In 1978 salps and diatoms increased in inshore areas due to anomalous current patterns and increased temperatures in the eastern Pacific Ocean. Urchins deflected their normal feeding behavior from juvenile kelps to the abundant diatoms and salps, allowing more kelp juveniles to reach a size large enough to be impervious to urchin grazing. The scenario hypothesized for Sargassum is one in which the the herbivorous snail populations may have increased locally at Station

Beach, resulting in a decline in juvenile Sargassum populations. Any decline in Sargassum would be self-reinforcing for a period of time, because reproductive output is directly proportional to amount of canopy of cover, which has been generally low since 1980 (Fig. 18).

Heliaster is still very rare in the Puerto Peñasco (Dungan et al., 1982). Further studies on Heliaster, herbivorous snails, and Sargassum may provide evidence for a possible interrelationship in their population dynamics.

CHAPTER 4

BIOMASS ALLOCATION PATTERNS

Despite diverse life histories and morphologies marine algae have rarely been the subjects of studies on resource allocation and reproductive strategies. In contrast the literature on terrestrial plant population biology is replete with studies of how biomass or nutrients are allocated to various structures (petals, flowers, seeds, stems) and the adaptiveness of different allocation patterns in different habitats (Harper and Ogden, 1970; Harper, 1977; Hickman, 1977; Lovett Doust, 1980a, 1980b; Thompson and Stewart, 1981). The basic assumption is that biomass represents the amount of finite resources devoted to one structure at the expense of other structures that could be produced (Cody, 1966; MacArthur and Wilson, 1967; Harper and Ogden, 1970). Allocation patterns have been used to explain the coexistence of closely related species in the same area or their distributions along an environmental gradient (Hickman, 1977; Werner, 1979; Lovett Doust, 1980a, 1980b). In this chapter, biomass allocation patterns of the three Sargassum species are examined in relation to their distributions and habitats on the intertidal gradient.

Biomass Allocation in Marine Algae

The relationship of reproductive phenology to environment is less well understood in marine algae than in higher plants (Anthophyta). For example, there is no comparable body of knowledge

regarding marine algae that can match the literature on seed size, shape, and numbers in relation to life history strategies of higher plants (Harper, Lovell, and Moore, 1970; Harper and Ogden, 1970; Harper, 1977). Much is known of the physiological tolerances of germlings and adult plants to growth conditions in culture and, to a lesser extent, in the field (see review in Vadas and Norton, 1982). The adaptiveness of these features and their effects on dispersal and survival strategies are not well known, although studies by Neuschul and associates (Neuschul and Dahl, 1967; Neuschul, 1972; Okuda and Neuschul, 1981) suggest that algal spore morphology and dormancy may represent adaptive responses to environmental conditions.

Thompson and Stewart (1981) have recently criticized studies of biomass allocation in higher plants as being inherently flawed because reproductive parts are capable of enough photosynthetic production to provide partly or entirely for their own energy needs. This violates the basic assumption that a finite pool of biomass is being allocated (Cody, 1966; MacArthur and Wilson, 1967). The criticism also applies to marine algae whose reproductive parts are usually pigmented and capable of photosynthesis. One would expect less translocation of materials throughout the plant than occurs in higher plants because the vascular systems of marine algae are generally less complex (Bold and Wynne, 1978; Bold, Alexopoulos, and Delevoryas, 1980). Thompson and Stewart (1981) asserted that allocation studies of mineral nutrients rather than biomass are valid for terrestrial plants because these nutrients are often a limited resource in soils. This may apply as well to marine algae, although they are bathed in their nutrient medium and

use rootlike structures (holdfasts) primarily for anchorage rather than nutrient absorption (Bold and Wynne, 1978).

The question then arises: Is biomass allocation a valuable concept in the study of marine algal phenology? Clearly the special characteristics of algal structure and reproduction must be taken into account.

In Macrocystis pyrifera the amount of photoassimilate translocated from blades to holdfast and reproductive structures may be substantial (Parker, 1965). The occurrence of primary pit fields in medullary cells (Fagerberg and Dawes, 1977; Prince and Daly, 1981) and studies by Titlyanov and Peshekhodko cited in Prince and Daly, 1981) suggest that translocation does occur in Sargassum. Moreover Buggeln (1981) has shown that in blades of Alaria esculenta (L.) Grev. the amount of photoassimilate translocated from a distal to a more proximal portion can be altered by experimentally removing parts of the blade or basal sporophylls. In other words, the movement of fixed carbon in the plant depends on the pattern of supply and demand throughout the plant. By extrapolation one may conclude that adaptive change in biomass is possible in marine algae by loss or reduction of some plant parts through natural selection rather than experimental surgery.

Allocation patterns in brown algae may affect not only the translocation of photoassimilate from blades. Allocation to upper parts in algae with large canopies such as the kelps may inhibit self-sustained growth in shaded holdfasts. Light limitation in kelp forests affects other understory species (Neuschul and Dahl, 1967; Foster, 1975a, 1975b) and probably affects kelp holdfast growth as well.

The form and function of a structure are interrelated (Littler and Littler, 1980) and therefore are affected by allocation patterns. An alga's competitive and dispersal abilities are affected by its growth strategy. For example, a plant producing a small amount of predator-resistant tissue such as coralline crusts may have a very different mode of growth and dispersal than an upright deciduous fleshy alga that produces many zoospores for dispersal. Given a finite amount of space in a plant's canopy, the production of a receptacle instead of a blade will have different consequences on growth rate of branches in Sargassum (Norton, 1977a). In this sense, studies of the relation between allocation strategies and environment are valid and important regardless of the constraints on translocation.

Only one study was found that addressed the issue of biomass allocation in species of marine algae in terms of life history strategy. Russell (1979) suggested that the "heavy receptacles" of Fucus vesiculosus L. are an adaptation of plants to disturbed habitats. He argued that production of more receptacle tissue results in more propagules, which are better able to colonize newly opened space in habitats subject to heavy surf. In protected areas where less space is opened up by disturbance, less receptacle tissue is produced. Instead, relatively more tissue is devoted to vegetative fronds, which enable a plant to compete better against other algae in less physically disturbed habitats.

Sargassum species may allocate biomass differentially to different modes of reproduction. Norton (1977a) showed that vegetative branches grow five times faster than branches bearing sexual

structures (receptacles). The complete lack of sexual reproduction by Sargassum in the Sargasso Sea (Parr, 1939; Ryther, 1956; Bold and Wynne, 1978) implies that there is a trade-off involved between sexual reproduction and vegetative propagation. The pelagic environment selects against the production of propagules that need to settle on hard substrates. Nevertheless, sexual reproduction might have been retained in some modified way, say, with in situ development of embryos on parent receptacles, which commonly occurs on benthic forms (Fritsch, 1945; Fletcher, 1980; Norton, 1981; Deysher and Norton, 1982). Instead, sexual reproduction is absent, and it is logical to assume that its loss was not only adaptive in avoiding the waste of propagules but also in allowing the increased allocation of resources to vegetative structures (blades, bladders, and stipes), which would enhance a plant's competitive ability in the surface waters of the ocean.

The occurrence of three Sargassum species on the same intertidal gradient at Puerto Peñasco provides an excellent opportunity for a comparative study of reproductive phenology in relation to interspecific competition and niche separation. Werner (1979) has reviewed the literature on competition and coexistence of similar terrestrial plant species. She delineated two types of competition: interactive competition where the activities of an established plant adversely affect another and preemptive competition in which a plant arrives at a safe site first and excludes later arrivals. She pointed out that the latter may be interpreted not as competition but rather as escape from it and is a tactic practiced by fugitive or colonizing species

that disperse widely. The following comment by Werner (1979, p. 292) is pertinent to the present study of three congeneric marine algae:

In order to study, in an empirical manner, plant adaptations which reduce either type of competition and which permit co-existence, a researcher must have a group of closely related plants living in the same area. Ideally, the plants should be congeners, or genotypic races, that remain genetically isolated when growing in the same habitat. In actuality, such situations are not often found: The more taxonomically related the plants, the less likely they are to be found in the same habitat.

The Sargassum species at Puerto Peñasco satisfy these conditions. In addition, they are of a reasonable size and display an adequate complexity of reproductive structures for studies on biomass allocation.

Attached intertidal Sargassum plants may invest in two basic modes of reproduction: vegetative proliferation of the holdfast and production of germlings from gametes in sexual receptacles on the upper parts of the thallus. Although mature Sargassum plants shed the upper branches each year, at least part of the remaining holdfast probably survives for several years (Yoshida, cited in Russell, 1973). Holdfasts of most species are solid and nonspreading, but a few are extensive crusts or systems of rhizoidal haptera (De Wreede, 1973). For such plants the basal holdfast represents vegetative reproduction, or short-distance dispersal through lateral encroachment.

Vernet and Harper (1980) have discussed the costs of sex in Fucalean algae other than Sargassum. They correctly argued that the amount of biomass allocated to gametes is negligible. Nevertheless, the amount allocated to receptacle tissue was significant and this was the feature they found to be most closely correlated with plant fecundity.

Deysher and Norton (1982) studied dispersal in S. muticum in California. Most germlings shed from the receptacles settle within 2 to 3 m of the parent plant but have the potential to disperse much farther. Flotation of buoyant fragments, which are either fertile or become fertile while pelagic, disperses sexual propagules to other sites, which may be many kilometers away. The fragments themselves are incapable of reattaching to the substrate.

Materials and Methods

Relative reproductive effort was estimated by measuring various morphological features of the three species associated with the two modes of reproduction. Biomass devoted to sexual (receptacle) and vegetative (holdfast) reproductive tissue and the relationship of plant size to fertility were determined. The functional significance of vegetative investment to holdfast tissue was tested with field experiments.

Allocation of Biomass to Holdfast and Branch Systems

Individuals of S. johnstonii and S. herporhizum are very difficult to distinguish between in the field due to the lack of discrete visible holdfast boundaries. Therefore the allocation of biomass to holdfasts and upper branch system was measured in all three species by using material collected from small equal-sized patches in the midst of pure stands of each species. All plant material was collected from the patches by scraping the substrate with a putty knife. This removed holdfasts and attached branches nearly intact. Samples from each patch

were collected from tide-pool populations of each species in February 1978 (five patches per species), April 1980 (four patches per species), and February 1981 (four patches per species). These months were times of near-peak canopy cover for the three species; April 1980 was also a time of peak reproduction (Fig. 21). The area of each patch was 0.01 m², except for patches of S. sinicola measured in April 1980, which were 0.04 m². The measurements for the latter collections were adjusted to values for 0.01 m² for statistical analysis.

The holdfasts and attached branches collected from each patch were preserved in 3% formalin-sea water. Samples were rinsed in fresh water in the laboratory and dissected into holdfast and upper branch subsamples, which were blotted dry, cleaned of bits of attached coquina, and weighed to the nearest 0.01 g.

Dry mass was calculated for 1980 and 1981 samples. Holdfast subsamples were dried for 2 days at 104°C, then reweighed. Proportion dry mass (dry mass/wet mass) in the holdfast subsample was calculated.

Branch subsamples were divided into two parts. One part was returned to the 3% formalin-sea water solution and saved for measurements of receptacle size and number. The other part was weighed for wet mass, then placed in the drying oven for 2 days at 104°C. The dried material was weighed and proportion dry mass calculated. The proportion dry mass of this part of the subsample was used to estimate the total dry mass of the original branch subsample (proportion dry mass × wet mass of branch subsample).

The data on proportion dry mass in the holdfasts and branches of each species were also used to compare the amount of photoassimilate devoted to a given amount of wet plant tissue. This amount is assumed to be proportional to the caloric-value cost of producing the tissue (Hickman and Pitelka, 1975). A two-way ANOVA was used to test for variation between species and years in proportion dry mass (= cost) of each structure (holdfast or branch). Within a species, the difference between proportion dry mass for holdfast and branches in a single-species patch was tested for significance by a paired t test (Dixon and Brown, 1979). All proportions were arc-sine transformed (Sokal and Rohlf, 1969).

Plant Size and Fertility

The basic pattern of reproductive seasonality in the three species has been described in Chapter 3 (Fig. 21). Size distribution histograms for plants with and without receptacles were constructed for each sample using the same stipe collections. The relationship between plant size and fertility within each species was examined by comparing the sizes of fertile and nonfertile stipes pooled across all collections and in single collections where both types occurred.

Receptacle Production

The fecundities of the species were compared, using estimates of the volume of receptacles produced per unit mass of fertile branch (volume density). Vernet and Harper (1980) found that mass of

receptacle tissue correlated with plant fecundity. Volume densities were estimated as follows.

Number of receptacles per gram of fertile portion of the plant (receptacle density) was estimated using material from the April 1980 patch removals. This was the time of peak reproduction in that spring (Fig. 21). Thalli from each patch were sorted into fertile and nonfertile portions, blotted dry, and weighed. The nonfertile portions included branches without receptacles and the lower part of some fertile branches. These provided an estimate of the relative amounts of fertile and nonfertile tissue in the patches.

From the subsample of fertile branches in each patch, 10 sections of stipe were cut off at random, blotted dry, and weighed. Each section comprised a short length (1 to 2 cm) of stipe with attached blades, bladders, and receptacles. The number of receptacles was counted, and receptacle density calculated for each section. Some receptacles were branched: Branches greater than 2 mm long were counted as separate receptacles.

Receptacle production in March 1981 was estimated from the Station Beach stipe collections for that month. The 25 stipes in each species' collection were treated as a "patch" and 10 stipe sections were sampled at random from fertile branches. Receptacles were counted and density determined for each stipe section. Receptacle density for S. sinicola stipe collections from the autumn fertile periods (October 1979 and November 1980) was calculated in the same manner.

The length (L) and width (W) of 100 randomly selected receptacles per species were measured. Twenty-five receptacles of S.

johnstonii and S. sinicola were measured from each fertile patch in 1980; 100 receptacles from the sole fertile patch of S. herporhizum were measured. Volume (V) was calculated for each receptacle based on an assumed cylindrical shape:

$$V = \pi(W/2)^2L$$

The mean receptacle volume density for each patch can be estimated from calculations of receptacle density and volume:

$$\begin{aligned} & \text{mean volume (mm}^3\text{) of receptacles/g fertile branch} \\ & = (\text{mean number receptacles/g fertile branch}) \\ & \quad \times (\text{mean volume (mm}^3\text{) a receptacle}) \end{aligned}$$

In two S. herporhizum patches no fertile branches were present, so values of zero were used for receptacle volume density. A value of zero was also used for a patch with one fertile branch tip in over 50 stipes. Four estimates of volume density were obtained for each species (one per patch).

The total volume of receptacles produced in each patch was also estimated:

$$\begin{aligned} & \text{Total receptacle volume (mm}^3\text{)/patch} \\ & = (\text{mean receptacle volume (mm}^3\text{)/g fertile branch}) \\ & \quad \times (\text{total g fertile branches in patch}) \end{aligned}$$

Sargassum gametes are produced on receptacles in small cavities called conceptacles, which open to the outside via pores called ostioles (Fritsch, 1945). To ascertain the relationship between receptacle size

and number of conceptacles, 30 receptacles from each species were measured for length, width, and number of ostioles visible on one side. Linear regressions of ostiole number on receptacle size were calculated for each species. Ostiole density (number ostioles/mm³ receptacle tissue) was also calculated for each receptacle. Gametes per conceptacle were not counted, but several receptacles from each species were sectioned and examined under the microscope to verify that receptacles were producing gametes.

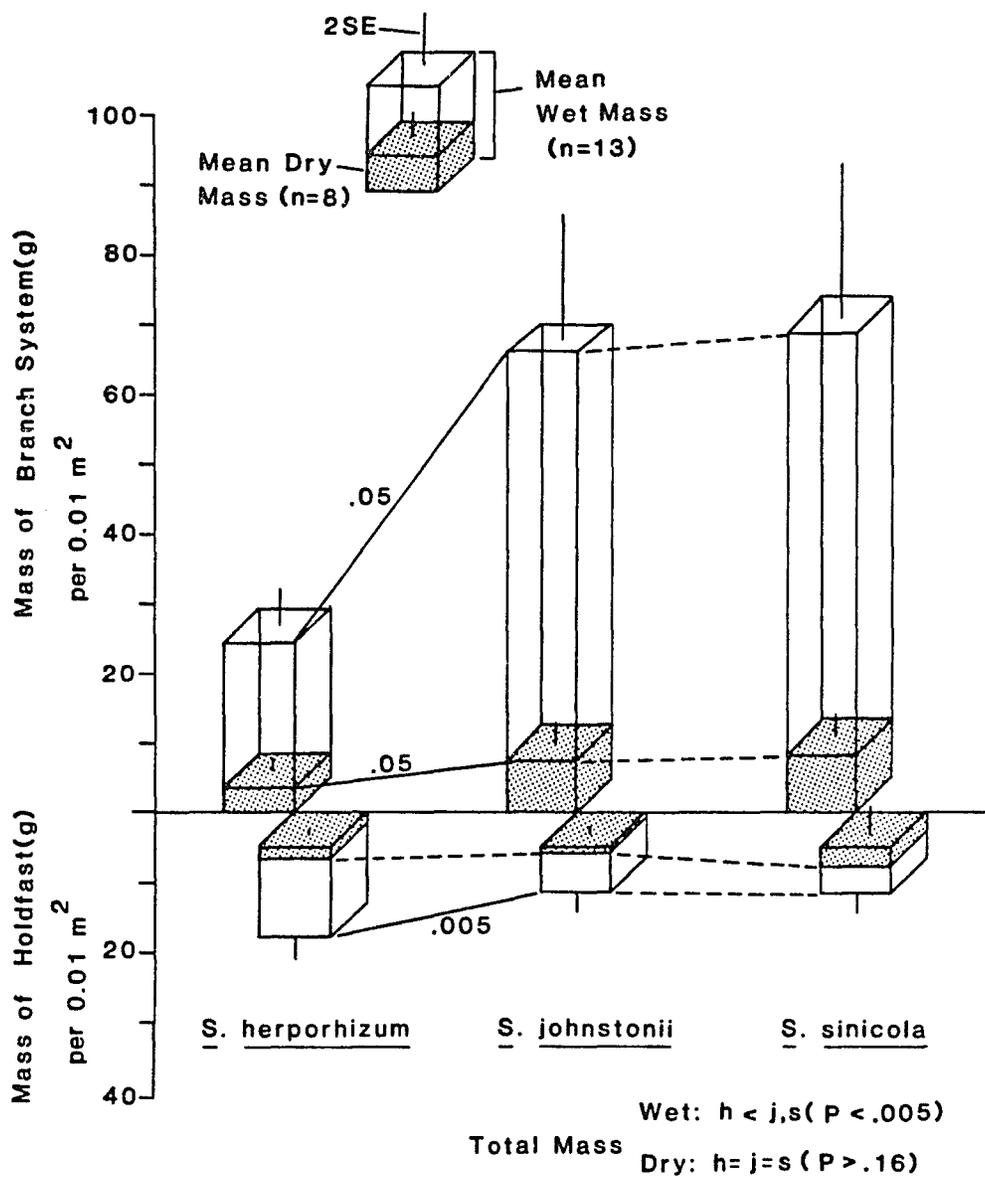
Canopy Regrowth in Experimentally Cleared Sargassum Patches in Tide Pools

The four patches per species collected in April 1980 were monitored for 1 year following removal of thalli. From color slides, percent cover of Sargassum canopy and common understory species in each patch was calculated at approximately monthly intervals, using the grid technique described in Chapter 2. Nearby undisturbed control patches (four per species) were monitored over the same period. The results indicate the ability of a species to recover from both short-term experimental removal and long-term seasonal decrease in cover.

Results

Allocation of Biomass to Holdfast and Branch Systems

In terms of wet mass S. herporhizum produced less vegetative branch tissue and more holdfast tissue per unit area in pure stands than the other two species (Fig. 23). The same patterns held for measurements of dry mass, except that holdfast dry mass was equal



Solid line: difference significant at $p <$ values shown.
 Dotted line: difference not significant.
 h = S. herporhizum; j = S. johnstonii; s = S. sinicola.

Figure 23. Mass of holdfasts and branches for Sargassum species in patches in Station Beach tide pools

across species (Fig. 23; two-way ANOVAs, species \times year, on log-transformed measurements of mass).

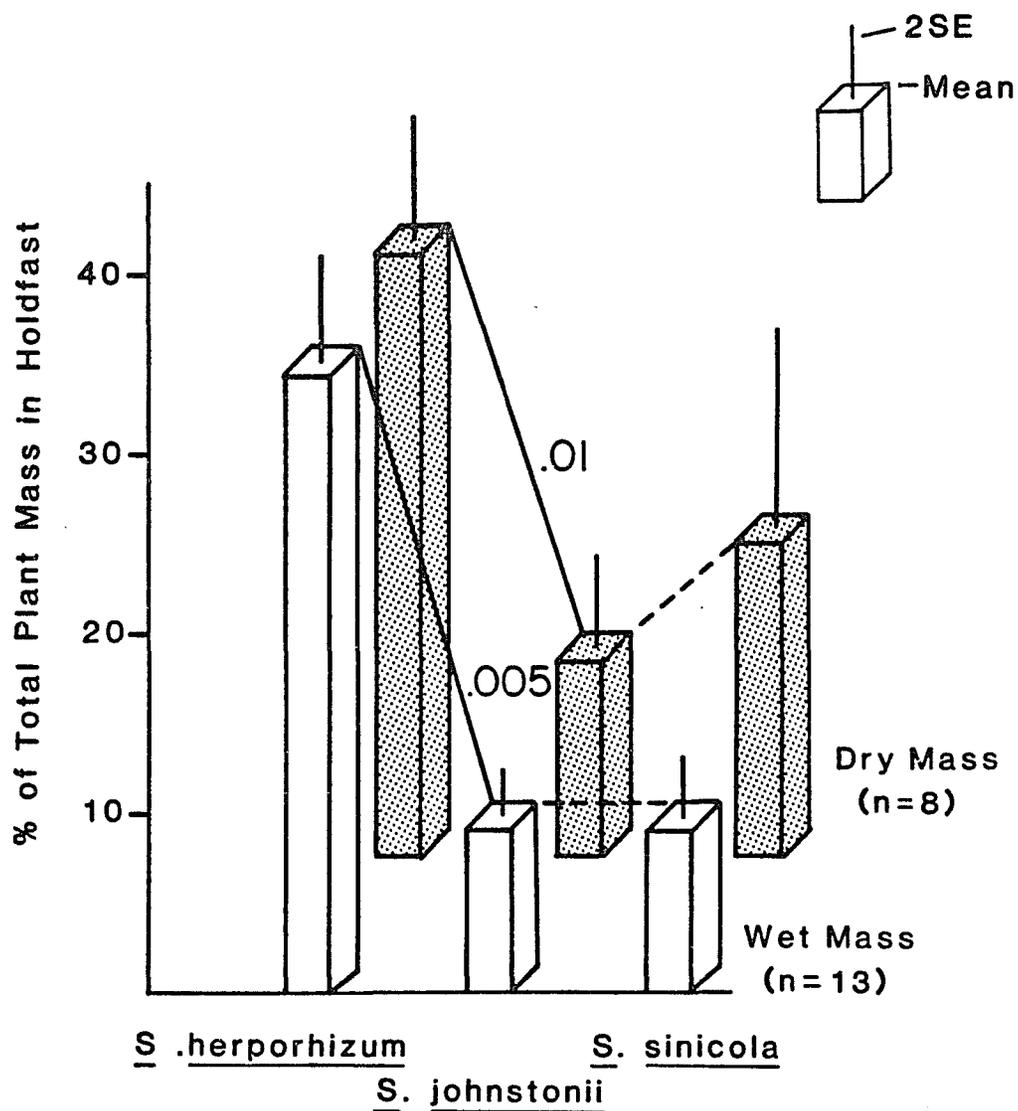
Sargassum herporhizum devoted a significantly greater amount of its total mass to holdfast tissue. The proportion of total wet and dry mass devoted to holdfast was significantly higher in S. herporhizum than in the other two species (Fig. 24; two-way ANOVAs, species \times years, on arc sine-transformed proportions).

Thus species produced roughly similar amounts of dry mass per unit area but apportioned it in different ways to holdfasts and vegetative branches. Species showed no significant differences in total plant dry mass per unit area (Fig. 23). The mean for S. herporhizum was slightly less than for the other species, and perhaps a larger sample size would reveal a clear difference.

The cost of producing branches was uniform across species (Fig. 25; two-way ANOVA, species \times year, on arcsin-transformed data). Vegetative material of the three species averaged nearly 15% dry matter (or 85% water).

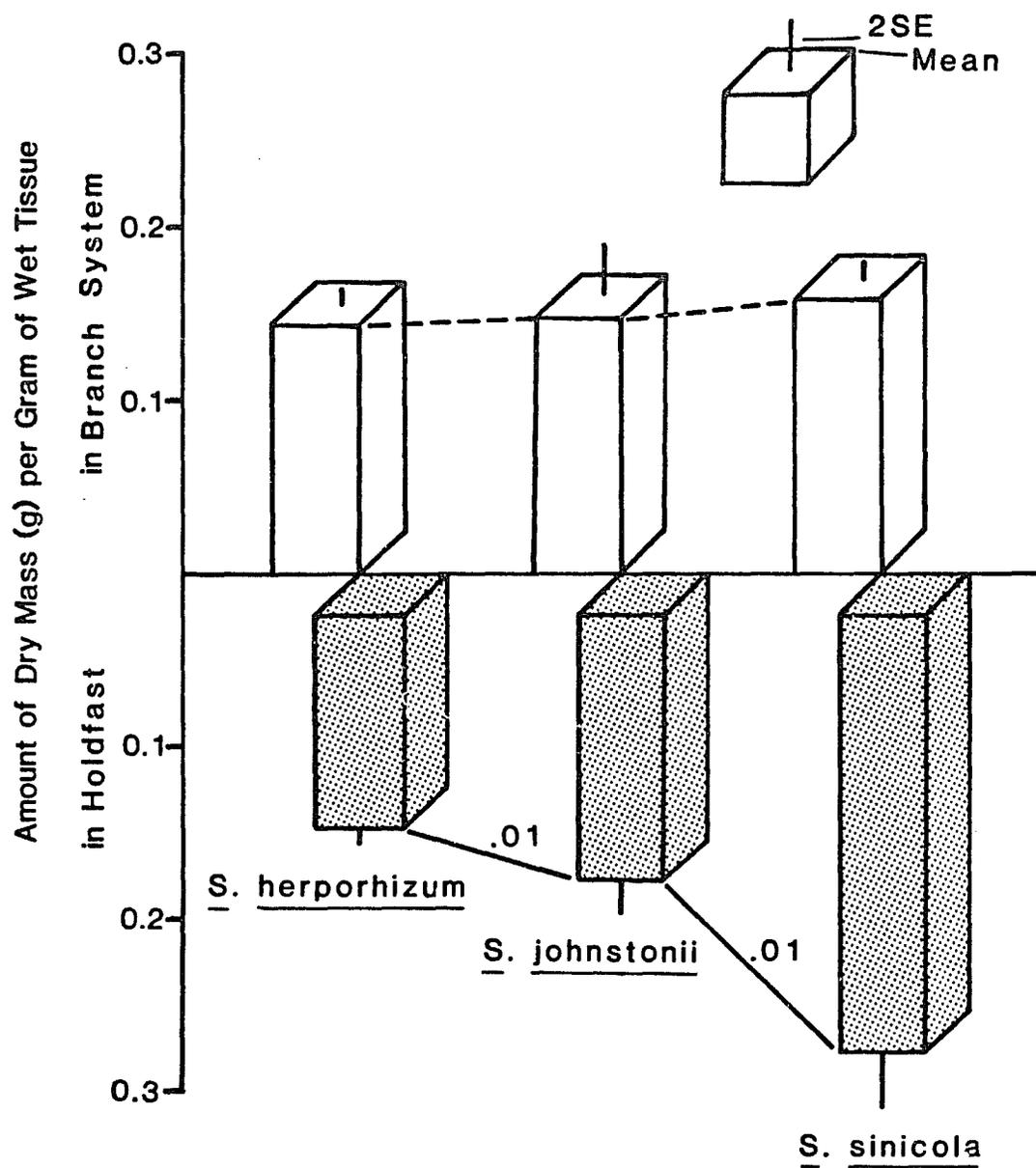
The species differed significantly in cost of producing their holdfasts (Fig. 25; two-way ANOVA, species \times year, on arc sine-transformed data). Sargassum sinicola holdfasts averaged 25.3% dry matter, whereas those of S. johnstonii and S. herporhizum averaged 17.8% and 12.4%, respectively (Fig. 25).

One may also compare within species the relative costs (dry matter per unit wet weight) of producing holdfast and branch tissue. Sargassum johnstonii holdfasts and vegetative branches contained the same percentage of dry matter despite very different morphologies



Solid line: difference significant at $p <$ values shown
 Dotted line: differences not significant.

Figure 24. Percentage of total plant mass devoted to holdfast tissue in patches of the three Sargassum species



Solid line: difference significant at $p <$ values shown
 Dotted line: differences not significant.

Figure 25. Relative costs to plant of producing holdfast and branch tissue in the three Sargassum species. -- Cost expressed as grams of dry mass in one gram of wet tissue mass.

(Fig. 25; $p < .05$, paired t test on arc sine-transformed proportion dry matter in holdfast and branch in patch). In contrast, S. sinicola was found to have a higher percentage of dry matter in its holdfast (25.8%) than in its upper vegetative branches (15.9%) (Fig. 25; $p < .05$, paired t test). Sargassum herporhizum holdfast tissue was made up of a significantly smaller percentage of dry matter than branch tissue (Fig. 25; $p < .05$, paired t test). Thus the haptera of S. herporhizum cost less to produce per gram of tissue than do the stipes and branches.

Plant Size and Fertility

Size distributions of fertile and non-fertile plants (Fig. 26) reiterate the point that fertility is associated with the peak in size attained by plants of the three species in spring and for S. sinicola with a second peak in size in the fall. Pooled across all collections, fertile stipes of each species were longer than nonfertile stipes ($p < .001$, Mann-Whitney test). In individual collections of each species with mixtures of fertile and nonfertile stipes, fertile stipes were generally longer than non-fertile stipes (Fig. 26). In other words, the largest plants were the first to become fertile during the reproductive season. This pattern is not statistically evident in single collections of S. johnstonii because within any one collection stipes tended to be either all fertile or all nonfertile. In no collections of any of the three species was the mean length of nonfertile plants significantly greater than that of fertile plants.

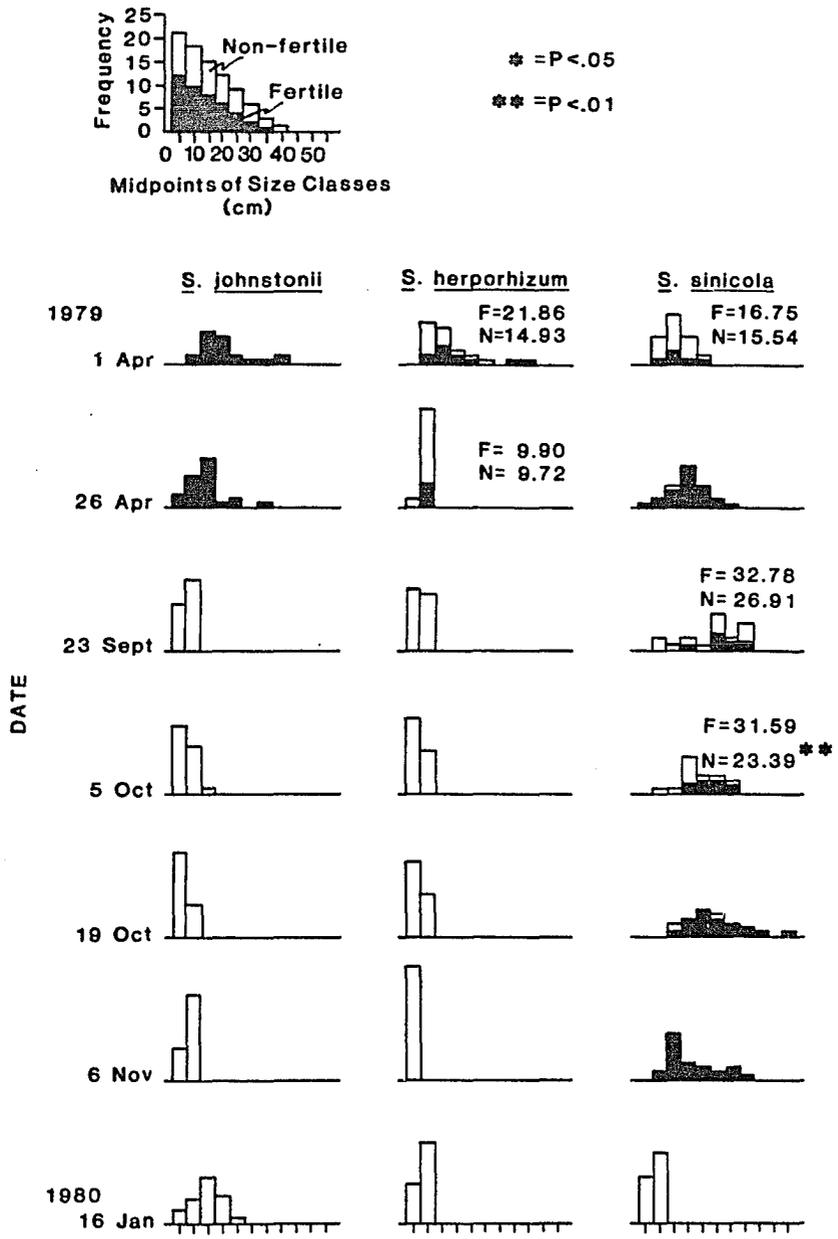


Figure 26. Seasonal changes in length and fertility in stipe collections of *Sargassum* species at Station Beach. -- Mean lengths of fertile (F) and nonfertile (N) stipes tested with Mann-Whitney test.

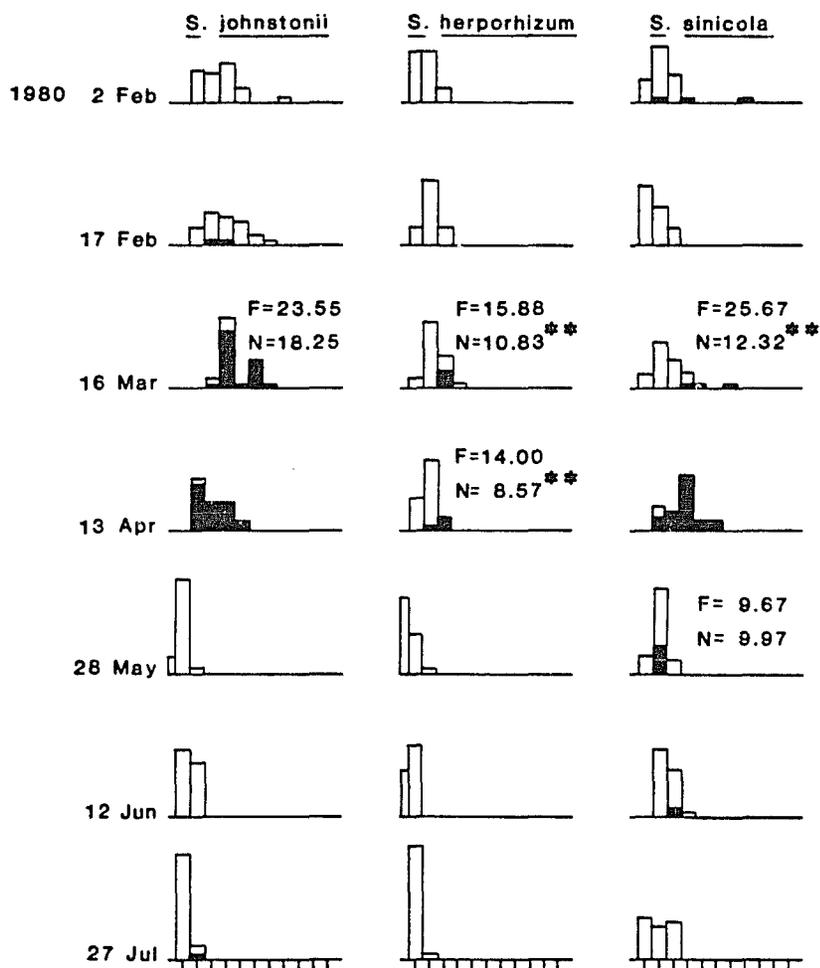


Figure 26. Seasonal changes--Continued

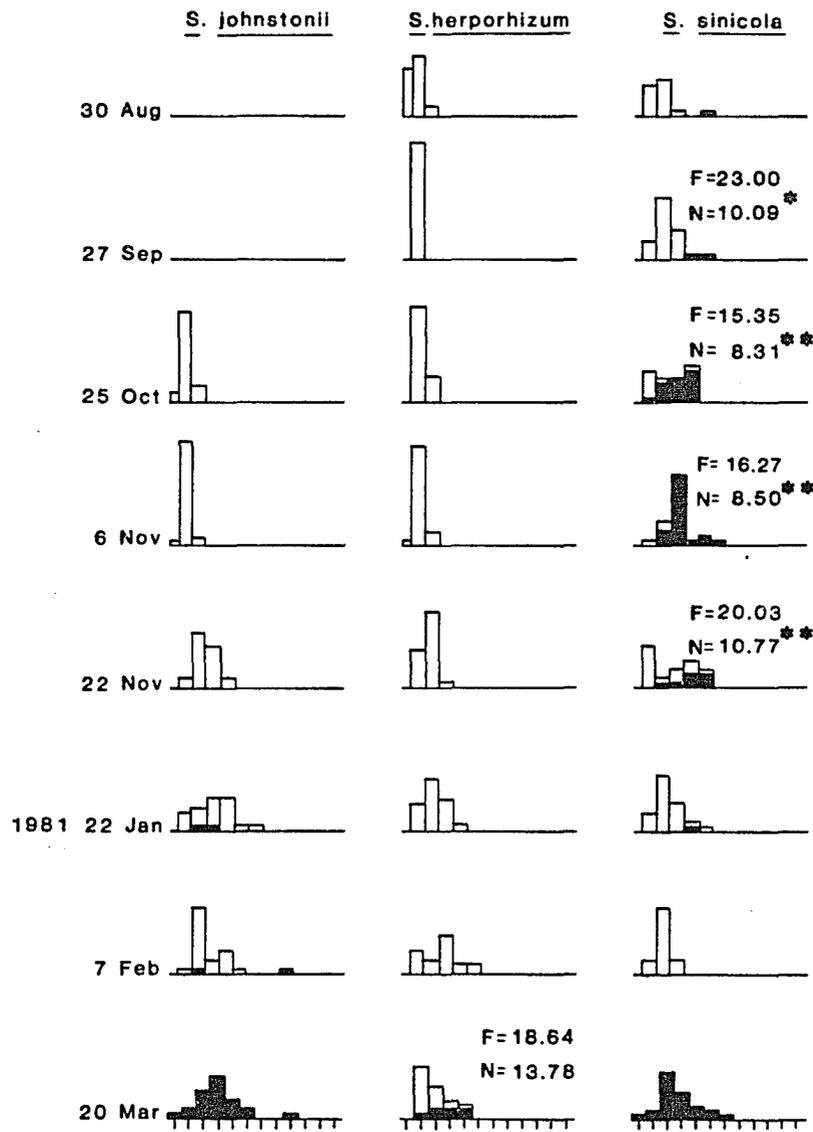


Figure 26. Seasonal changes--Continued

Receptacle Production

Statistical analysis of receptacle production in patches was complicated by the near absence of fertile tissue in three of the four patches of S. herporhizum (Table 4). This in itself was evidence of reduced sexual biomass production by this species. For this reason receptacle densities were first compared for S. johnstonii and S. sinicola only (two-level nested ANOVA, patches within species). There was significant variation among patches ($p < .001$), and S. johnstonii produced a much higher receptacle density than S. sinicola ($p < .001$) (Fig. 27).

Because three of the four S. herporhizum patches contained virtually no receptacles in April 1980, they are not directly comparable with the patches of the other two species in a nested ANOVA. However, the mean receptacle density of the one fertile patch of S. herporhizum was nearly as great as the mean density of S. johnstonii (Fig. 27). The difference between the two was not significant ($p < .19$, t' test, Sokal and Rohlf, 1969). The mean receptacle density for S. herporhizum was significantly greater than that for S. sinicola in this season ($p < .001$, t' test) (Fig. 27).

Within species, S. johnstonii and S. sinicola showed no difference in receptacle density between April 1980 and March 1981 ($p < .4$, t' test) Sargassum herporhizum showed a lower receptacle density in March 1981 than in April 1980 ($p < .05$, t' test), but in both years the values were intermediate in size between the densities of S. johnstonii and S. sinicola. Sargassum sinicola receptacle densities

Table 4. Wet mass of fertile and sterile branch tissue in subsamples from four patches of each Sargassum species, April 1980

	Wet Mass			
	Fertile		Sterile	
	g	% Total Mass	g	% Total Mass
<u>S. herporhizum</u>	1.07	26.68	2.94	73.32
	0.00	0.00	28.97	100.00
	0.00	0.00	17.60	100.00
	<u>0.08^a</u>	<u>0.80</u>	<u>9.96</u>	<u>99.20</u>
Mean	0.29	6.87	14.82	93.13
<u>S. johnstonii</u>	6.45	73.38	2.34	26.62
	5.06	68.56	2.32	31.44
	5.50	74.12	1.92	25.88
	<u>4.02</u>	<u>44.18</u>	<u>5.08</u>	<u>55.82</u>
Mean	5.26	65.06	2.92	34.94
<u>S. sinicola</u>	13.24	91.75	1.19	8.25
	31.00	66.28	15.77	33.72
	37.41	79.19	9.83	20.81
	<u>9.52</u>	<u>59.39</u>	<u>6.51</u>	<u>40.61</u>
Mean	22.79	74.16	8.33	25.84

a. One fertile tip from over 50 stipes.

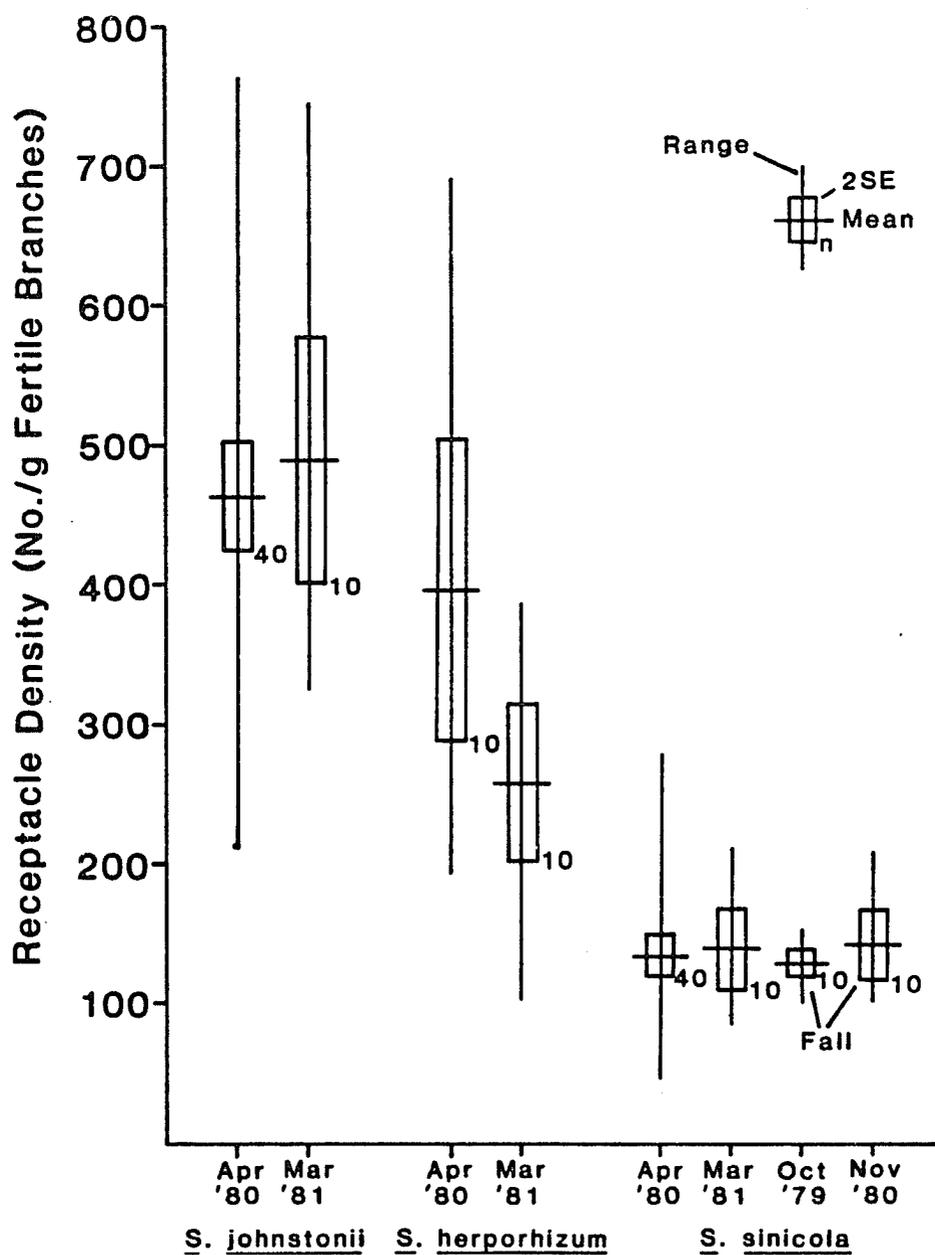


Figure 27. Receptacle density of the three Sargassum species in spring fertile periods and of *S. sinicola* in fall fertile periods

across all spring and autumn fertile periods were not significantly different (Fig. 27; $p < .9$, one-way ANOVA).

Sargassum sinicola receptacles were by far the largest for the three species, S. johnstonii receptacles were intermediate in size, and S. herporhizum produced the smallest receptacles (Fig. 28). Sargassum johnstonii and S. sinicola receptacle volumes varied significantly ($p < .01$) across patches nested within species and S. sinicola receptacles were significantly larger than those of S. johnstonii (Fig. 28; $p < .01$, two-level nested ANOVA). Receptacles of S. herporhizum came from the single fertile patch and could not be compared with those of the other species in a two-level nested ANOVA. Analysis using a pairwise t' test showed that the three species differed significantly in average receptacle volume ($p < .001$).

Estimates of the total volume of receptacle tissue produced per gram of fertile branch tissue (volume density) showed that what S. sinicola lacks in number it makes up for in size (Table 5). Sargassum sinicola and S. johnstonii produced a significantly higher receptacle volume per fertile gram of branch tissue and per patch than S. herporhizum (Table 5). Although S. johnstonii and S. sinicola both produced large volumes of receptacles, they did so in different ways. Sargassum sinicola produced a few large receptacles per gram of fertile vegetative material, whereas S. johnstonii produced many of intermediate size. Sargassum herporhizum produced many small receptacles and had a much lower volume density than did the other two species (Table 5).

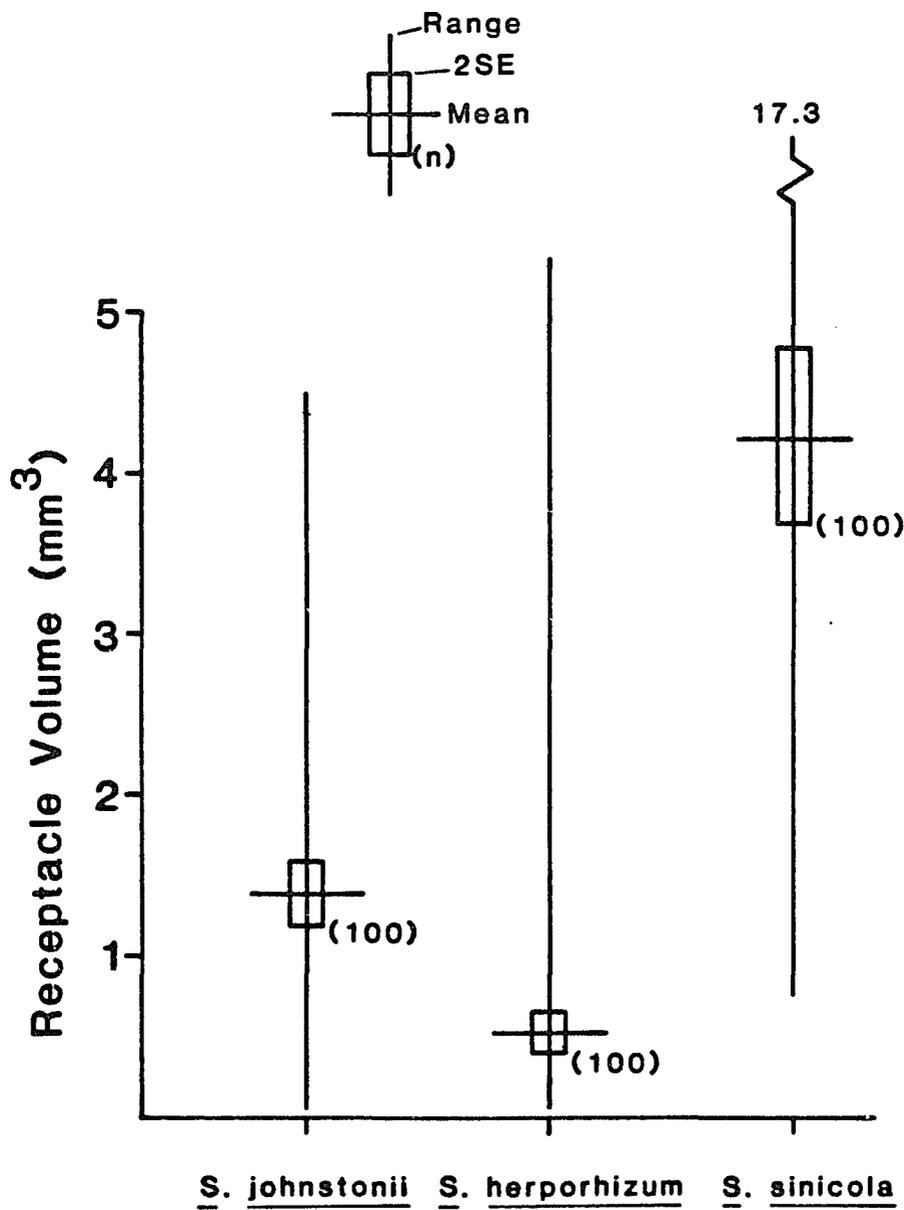


Figure 28. Volume of receptacles for the three Sargassum species

Table 5. Mean volume density and mean total volume of receptacle tissue produced per patch for each Sargassum species, April 1980

	Mean		
	<u>S. herporhizum</u>	<u>S. johnstonii</u>	<u>S. sinicola</u>
Mean receptacle volume density	<u>64.66</u>	<u>658.25</u>	<u>538.62^a</u>
Total receptacle volume/patch	<u>463.21</u>	<u>24,812.07</u>	<u>26,201.99</u>

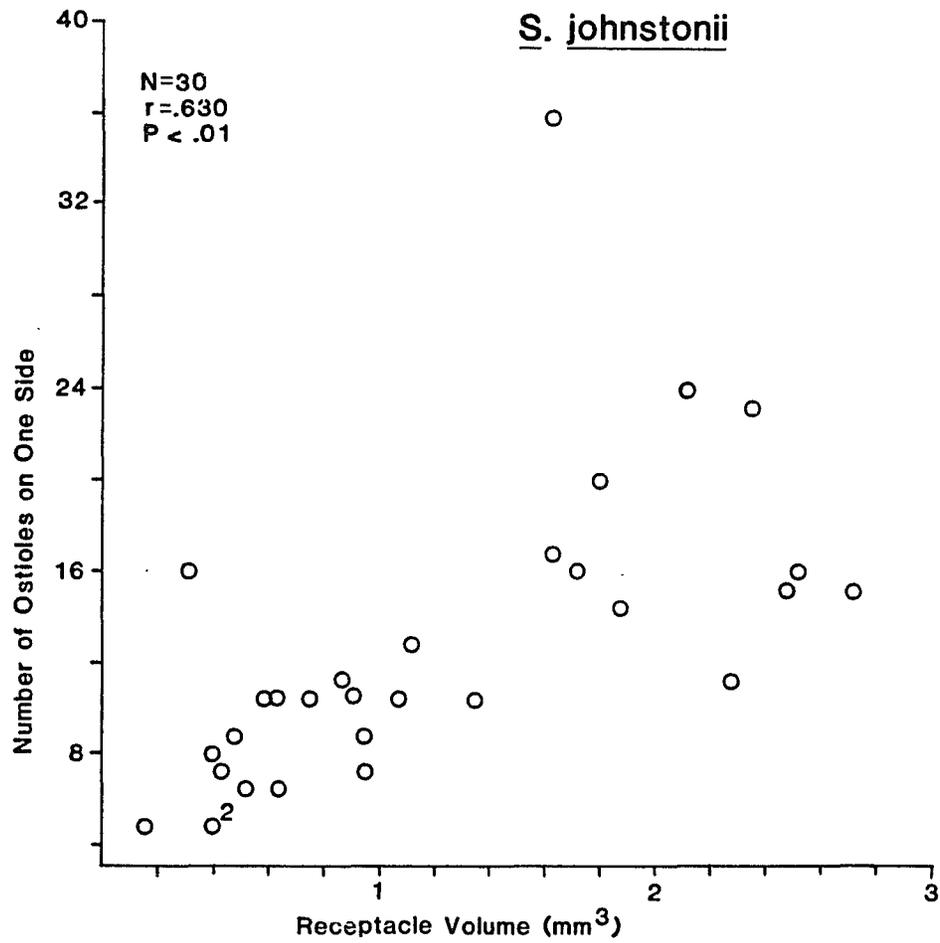
a. Means not joined by common underlining are significantly different ($p < .01$, ANOVA and LSD tests).

The number of ostioles increased with receptacle volume in all three species (Fig. 29). Ostiole density (number/mm³) in S. sinicola was significantly less than that of the other two species (Fig. 30). In other words, S. sinicola devoted much more receptacle tissue to one conceptacle than did the other species. This may have an effect on number or size of gametes produced, but this was not investigated in the present study. Ostiole density decreased exponentially with increasing receptacle size in all three species (Fig. 31). This may indicate that ostioles and conceptacles are formed early during receptacle development and thereafter their numbers remain unchanged, whereas their densities (number per mm³ of receptacle) decrease as the receptacles enlarge.

Cross sections of the receptacles of the three species showed that they produce gametes in the spring, although percentage of conceptacles that become fertile in each species could not be determined from preserved collections. In addition, mature eggs were seen extruded from receptacles produced in the fall by S. sinicola. Smaller receptacles tended to be nonfertile and were probably immature.

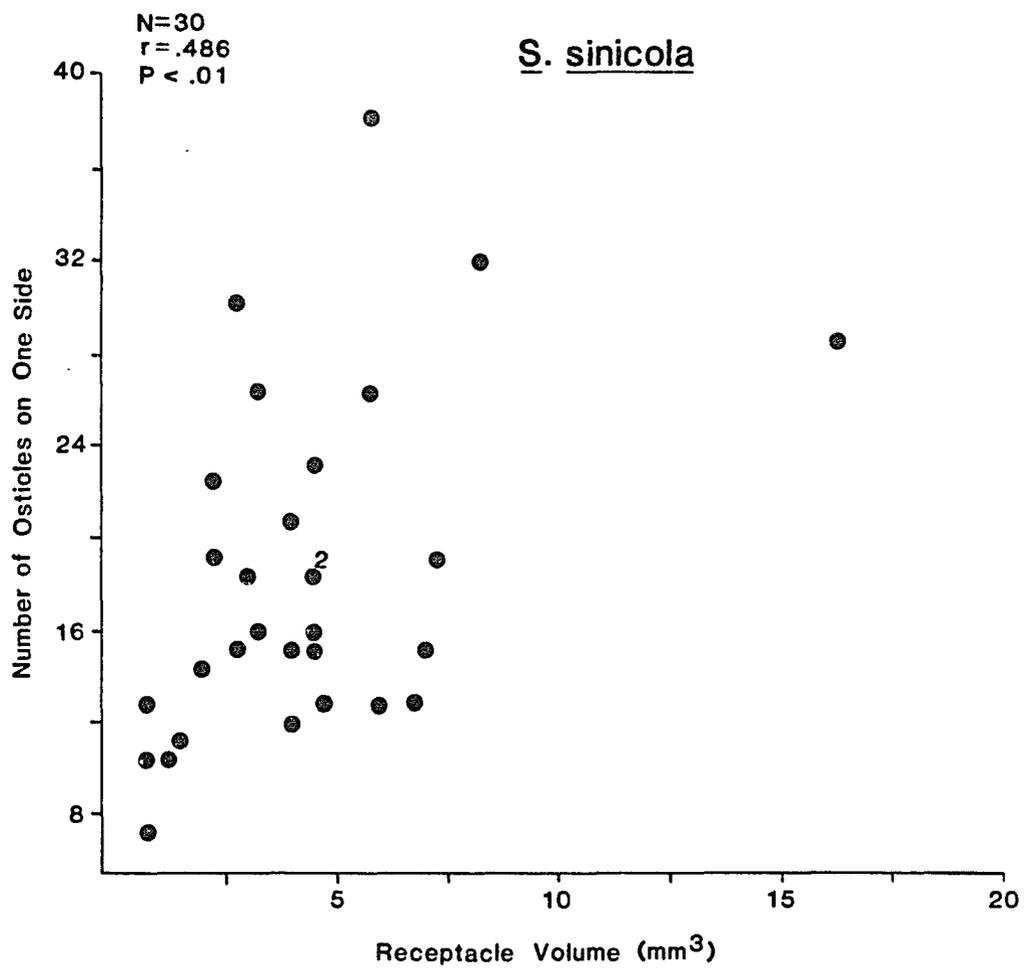
Canopy Regrowth in Experimentally Cleared Sargassum Patches in Tide Pools

The canopy of S. herporhizum recovered more rapidly and completely than that of the other two species (Fig. 32). After less than 1 month (in early May) S. herporhizum canopy cover was significantly greater than that of other two species (Fig. 32). Moreover, mean canopy cover in S. herporhizum patches was significantly greater than in patches of the other two species on every date sampled ($p < .05$,



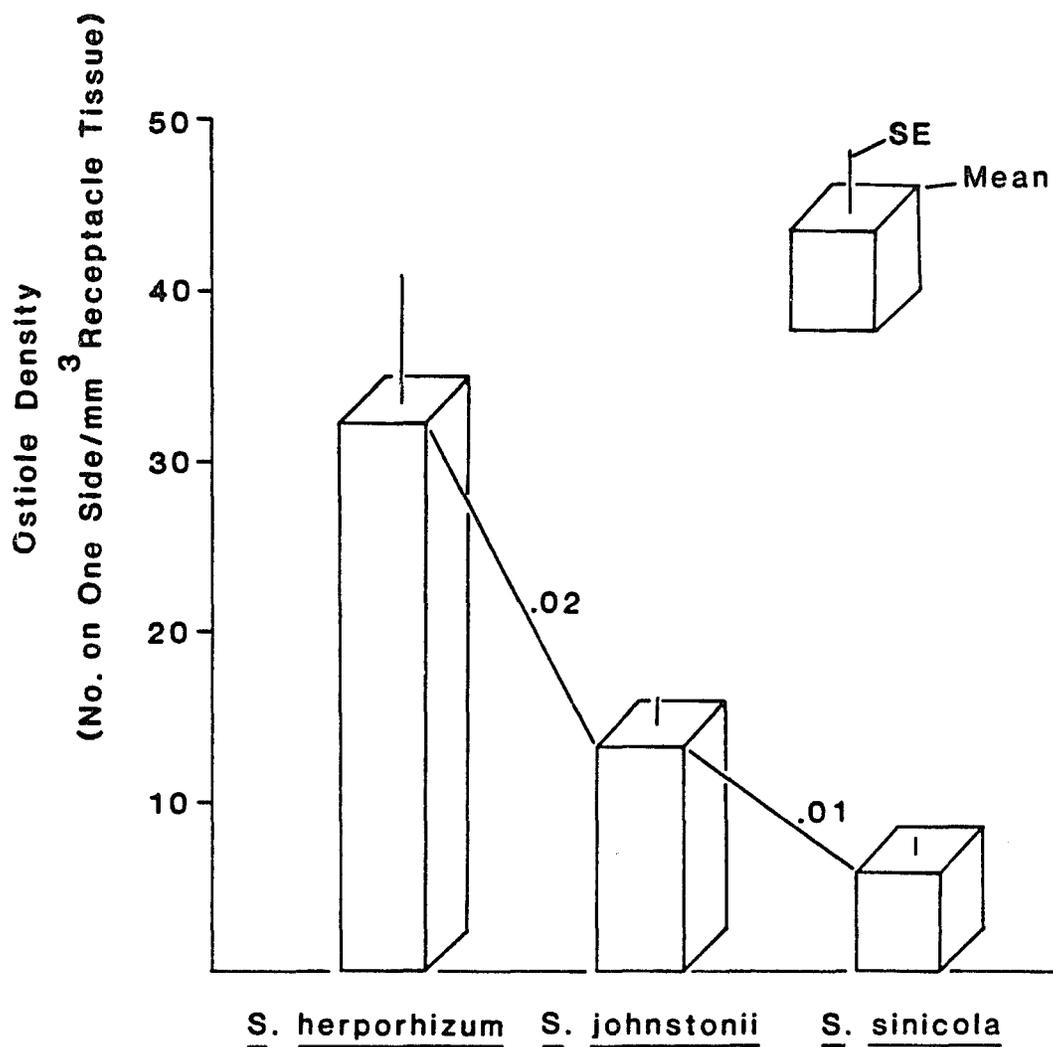
Number = number of points plotted as one

Figure 29. Ostiole number as a function of receptacle volume for the three Sargassum species



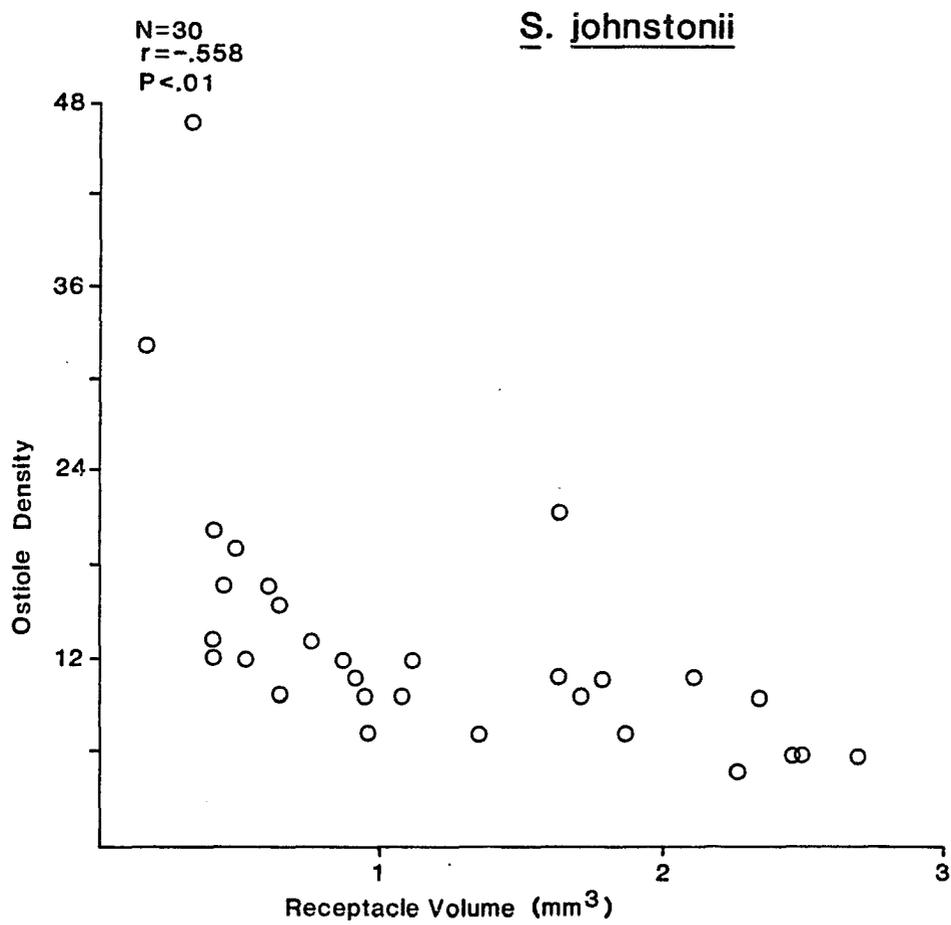
Number = number of points plotted as one

Figure 29. Ostiole number--Continued



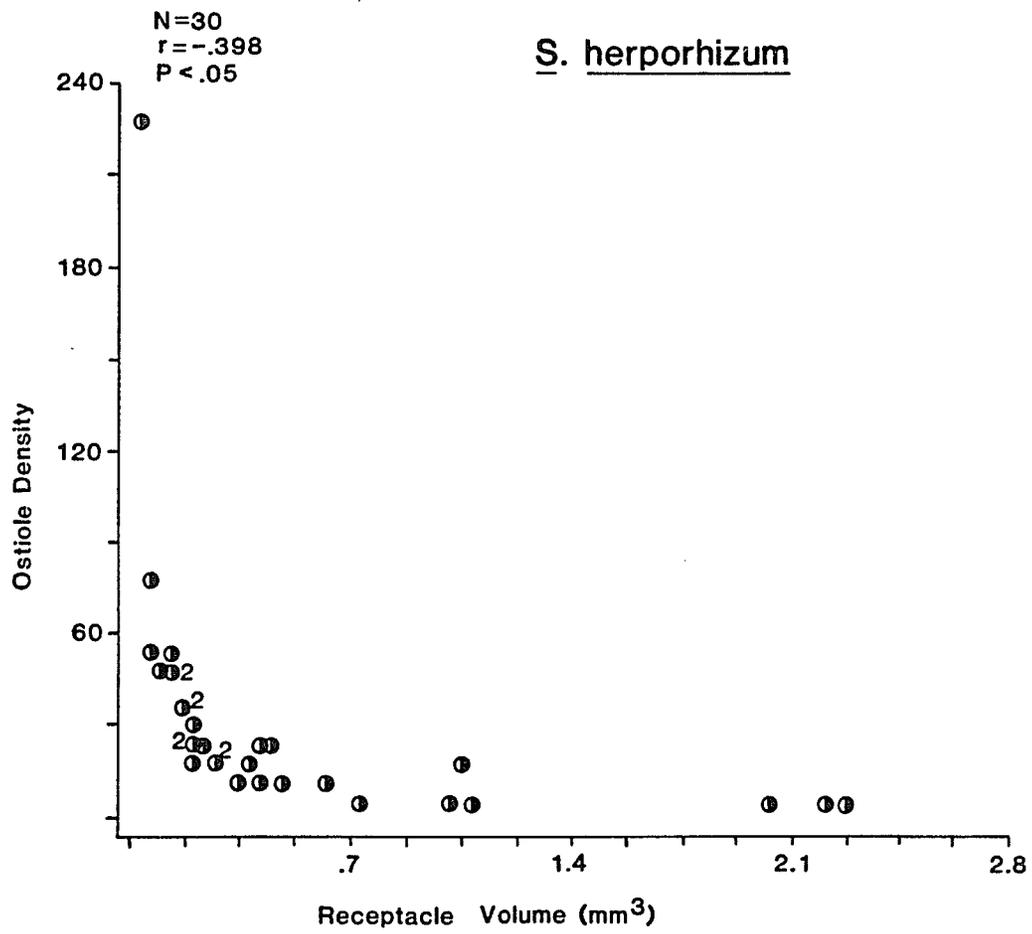
Solid line: difference significant at $p <$ value shown

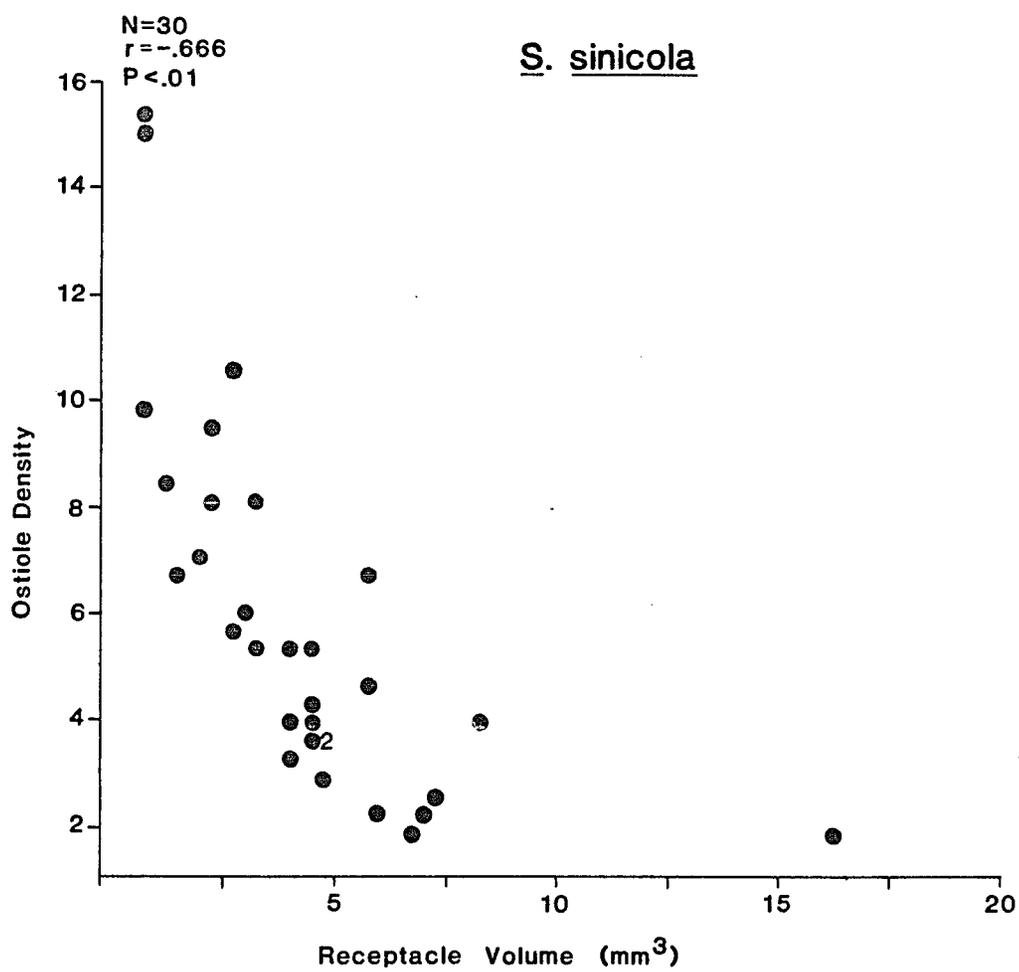
Figure 30. Ostiole density on receptacles for the three Sargassum species



Number = number of points plotted as one

Figure 31. Ostiole density as a function of receptacle volume for the three Sargassum species

Figure 31. Ostiole density--Continued

Figure 31. Ostiole density--Continued

ANOVA on arc sine-transformed data for each date, LSD test). Sargassum herporhizum recovered to nearly 50% mean canopy cover after 1.5 months of regrowth. Recovery included regrowth of haptera as well as upper vegetative branches. Encroachment by holdfasts of plants adjacent to the removals occurred in addition to regeneration from tiny pieces of holdfast in the coquina substrate that were unremovable without extensive destruction of the substrate. By June, after 2 months, S. johnstonii recovered to a little over 20% mean canopy cover. Cover in S. sinicola removals was lowest at this time. Differences between removals of all three species on this date were highly significant ($p < .01$, ANOVA on arc sine-transformed data, LSD test). Poorest regrowth was shown by S. sinicola, which recovered to less than 20% after 3 months. For S. johnstonii and S. sinicola, regrowth appeared to be from unremovable remnants of holdfast in the coquina. Neither encroachment by nearby plants nor settlement of new plants in experimental plots on nearby areas was observed.

The levels of canopy cover in the removals of all three species converged with those in their respective control patches during the course of the summer dieback (Fig. 32; t test, arc sine-transformed data). Canopy cover in S. sinicola and S. johnstonii removals was lower than that of their respective controls in the subsequent spring, whereas S. herporhizum removals actually surpassed the controls in canopy cover a year after removal. Nevertheless none of these differences was significant (Fig. 32).

There were no marked changes in the most common understory species (Dictyota spp., Amphiroa spp.) in removals compared to

controls for any species of Sargassum (Fig. 33). There was an indication that these two species peak in percent cover in the summer, perhaps taking advantage of the reduced shading effects from Sargassum canopy in both removals and controls.

Sand cover was greatest and most variable in the S. sinicola patches but showed no consistent difference between removal and control patches (Fig. 33).

Discussion

The data on the three Sargassum species suggest the existence of two different modes of biomass allocation to reproductive structures. Sargassum herporhizum ranks relatively high in several measurements of vegetative allocation and low in sexual reproductive effort, whereas in the other two species this pattern is reversed (Table 6).

Sargassum herporhizum devotes a larger proportion of its wet and dry biomass to its holdfast than the other two species, which are very similar in this respect. Although the three species produce approximately the same dry mass of holdfast tissue, S. herporhizum, by incorporating a larger amount of water per unit mass, produces more holdfast tissue for the same dry mass investment. The result is a more effective cover of the substrate in the form of rhizoidal haptera, which are essentially bladeless, horizontal stipes. Sargassum johnstonii holdfasts are made up of significantly less water per unit mass than S. herporhizum, and S. sinicola holdfasts have the lowest water content of the three. The moderately spreading, crustose holdfast of S. johnstonii and the conical, tough holdfast of S. sinicola cover relatively small areas

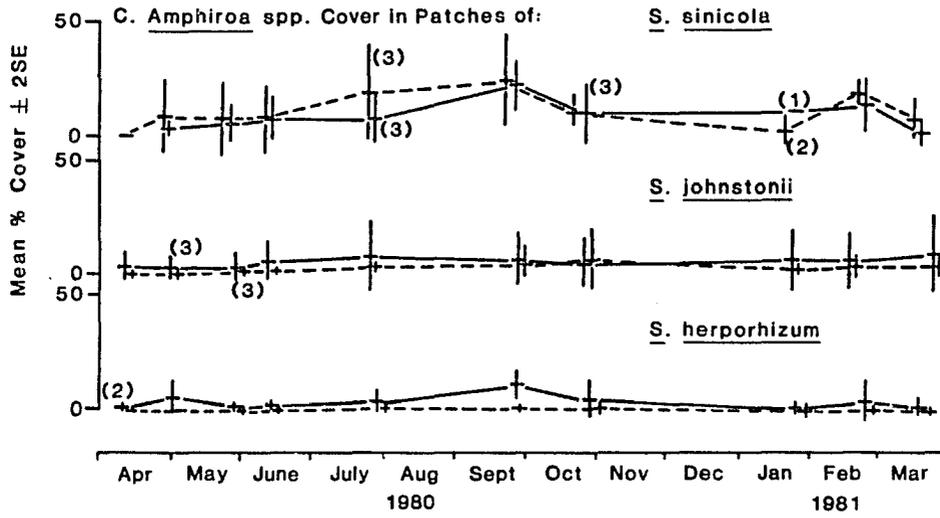


Figure 33. Changes in canopy cover--Continued

Table 6. Comparison of reproductive features of the three Sargassum species at Puerto Peñasco

	<u>S. herporhizum</u>	<u>S. johnstonii</u>	<u>S. sinicola</u>
<u>Vegetative Reproduction</u>			
Proportion of plant mass devoted to holdfast	high	low	low
Cost of producing holdfast tissue	low	moderate	high
Rate of regrowth of canopy following removal or seasonal decline	high	moderate	low
<u>Sexual Reproduction</u>			
Receptacle production (volume/(g fertile branches))	low	high	high
Fertile seasons per year	1	1	2
Percentage of fertile stipes during peak of season(s)	16-45	90-100	90-100

of substrate and reflect the respective proportions of dry matter invested.

The differences in holdfast morphology resulted in a more complete and higher rate of canopy recovery by S. herporhizum in the 3 to 4 months following its experimental removal from small patches (Fig. 32). This species also showed greater long-term (one-year) resilience to experimental and seasonal changes in canopy cover than did S. johnstonii or S. sinicola. One may conclude that the short-term disturbance represented by these removals in pure stands had little effect when compared to the natural seasonal fluctuations in canopy cover. This seems especially true if one considers that removal involved vigorous scraping of the substrate, which may account for the slightly lower values for S. johnstonii and S. sinicola in the spring of 1981. In S. herporhizum patches such scraping, if anything, only served to enhance later recovery of this species' canopy (Fig. 32).

The pattern of investment is generally reversed if several aspects of sexual reproductive investments by the three species are compared (Table 6). Vernet and Harper (1980) found that the number of receptacles produced by a Fucus plant is the morphological trait that correlates best with fecundity. Sargassum johnstonii and S. sinicola produced approximately the same high volume of receptacle tissue per gram of fertile branches; S. herporhizum produced far less (Table 5). Compounded with the much smaller proportion of S. herporhizum stipes that became fertile (Fig. 21), generally shorter stipe length (Fig. 22), and a smaller proportion of fertile tissue in a patch (Table 4),

production of sexual propagules per plant was much lower in this species than in the other two.

Sargassum sinicola experiences two periods of sexual reproduction each year, compared to a single season for the other species. In spring and autumn nearly all stipes of S. sinicola are fertile and of comparable average size (Figs. 21 and 26) and equal receptacle densities are produced (Fig. 27). Sargassum johnstonii is similar to S. sinicola in its high proportion of fertile stipes and receptacle volume per gram of fertile branches (Table 5), but it is fertile only once in the spring.

Sargassum sinicola is the most common of the three species in this area, especially in tide pools and on subtidal patch reefs, and in light of the above measurements of sexual reproduction, is probably producing the highest numbers of sexual propagules on an annual basis. Perhaps more importantly, it is producing germlings in the autumn, which can colonize suitable habitats that have opened up during the summer attrition of all three species. Sargassum sinicola may be able to preempt some space during the winter and prevent colonization by the other species, which are fertile only in the spring.

The Sargassum species may be categorized according to two models of reproduction outlined by Williams (1975). Sargassum herporrhizum exhibits a combination of sexual and vegetative reproduction that fits the strawberry-coral model of "sessile organisms that multiply vegetatively in continuous habitats . . . [whose] widely dispersed propagules are sexually produced" (Williams, 1975, p. 26). Sargassum sinicola, and to a lesser extent S. johnstonii, fits the elm-oyster model

of "organisms that have no clonal proliferation at all." Every physiologically distinct individual is genetically unique and cannot be duplicated. It can grow but there are real if flexible limits on attainable size" (Williams, 1975, p. 35). This situation begs the interesting question of why such divergent modes of reproduction occur in three closely related species that form the bulk of the canopy on the same intertidal gradient.

There are parallels in the literature on higher plants involving the coexistence of sets of closely related species and their reproductive strategies. Sarukhán (1976) studied three species of Ranunculus in the coastal grasslands of Wales and found that they invested approximately the same amount of biomass to reproductive structures, but not necessarily to the same kinds of structures. One of the three species produced few flowers, fruits (achenes), and ancillary structures (flowering stems) but instead produced an equivalent mass of vegetative structures (stolons and stolon leaves). Sarukhán suggested that vegetative reproduction by stolons and stolon leaves is purchased at the expense of fewer seeds being produced. A similar kind of tradeoff between sexual and vegetative reproduction has been reported within a single species of goldenrod (Solidago canadensis) by Werner (1979). She found that more biomass was invested in new rhizomes by plants occurring in newly disturbed (early successional) habitats. Rhizomes permit clonal expansion in these uncrowded habitats. Hickman (1977) has also interpreted differences in reproductive output of a group of Polygonum species as strategies for coexistence in terms of habitat features and competitive interactions. Some aspects of the life history

theory may be used to interpret the biomass allocation patterns in Sargassum.

Sargassum sinicola with its biannual high level of propagule production and persistence of a greater part of the plant over the summer dieback is the elm or oak tree of the tide pools in the northern Gulf of California. This species occurred consistently the deeper parts of pools where sand accumulates and where sand levels tend to be greater and more variable than in habitats preferred by the other two species (Figs. 15 and 33). Such small islands of coquina substrate are available for settlement on a temporally and spatially irregular basis. A strategy of copious propagule production would be most effective in reaching these transitory islands of substrate.

Of the three species, S. johnstonii most resembles a fugitive species (Hutchinson, 1951). It produces a high volume of receptacles per unit mass of branch tissue (Table 5) and experiences the most severe dieback in tide pools during the summer (Figs. 21 and 22). Its habitat at the edges of pools is probably as patchy as that of S. sinicola in the sandy bottoms of tide pools. Fluctuations in tide-pool depth due to irregular drainage patterns do occur in the tide pools of Station Beach. The resulting erratic regimes of desiccation would affect the suitability of this habitat for germling settlement and survival. Again a large number of propagules would most effectively assure some survival of propagules colonizing this type of habitat.

An interesting difference in packaging gametes was noted between S. sinicola and S. johnstonii. The receptacles of S. johnstonii were smaller but had higher densities of conceptacles than those of S.

sinicola. In effect, S. sinicola devoted more receptacle tissue than did S. johnstonii to production of a single conceptacle. Thin sections of receptacles of both species revealed some rudimentary vascular tissue extending from the stipes into the receptacles. It is conceivable that receptacle tissue somehow nourishes the gametes in the conceptacles during development and therefore the gametes of S. sinicola receive relatively more parental sustenance than do those of S. johnstonii. Even after fertilization germlings often remain attached to the receptacle (Fritsch, 1945; Fletcher and Fletcher, 1975a; Norton, 1981) and may continue to receive some nourishment before dropping off at a more advanced stage of development to attach to the substrate. In higher plants the tradeoff between greater dispersability of small seeds and the higher germination success and competitive abilities of large seeds is well known (Werner, 1979). This tradeoff has not been reported in propagules of any marine alga, but the data presented here suggest that differences in size and parental sustenance may well occur in Sargassum. Vernet and Harper (1980) have shown large differences between egg sizes in other species of intertidal Furoid algae.

There are additional aspects of the packaging of Sargassum receptacles that warrant further study. Dispersal of sexual propagules will be affected by the patterns of fragmentation of stipes as they are shed. A greater number of smaller fragments would more effectively reach a more patchy, unpredictable distribution of safe sites. A smaller number of large fragments would carry more receptacles that could better exploit large patches of open substrate by settling more germlings. Dispersal abilities (flotation time and distance) will also be

affected by the number of air bladders and their distribution on a given fragment. Again, wider dispersal would be achieved by production of more air bladders and their apportionment into a large number of branch fragments. Analysis of naturally occurring drift Sargassum would perhaps yield some very interesting differences between species. Drift Sargassum collected in spring 1980 on the berm at Station Beach were made up mostly of fertile S. sinicola branches, with a smaller amount of S. johnstonii, and very few S. herporhizum fragments.

With its extensive hapteral system and regenerative powers, S. herporhizum is a grasslike species of Sargassum in Station Beach tide pools. Its habitat is the most stable of the three species, being removed from extremes of desiccation in shallow water and sand coverage in the bottoms of pools. Encroachment by its rhizomelike holdfast and a dense canopy probably make it the competitive dominant at intermediate depths in tide pools where it is able to establish. It is probably limited in this habitat by its relatively low output of sexual propagules, which makes successful establishment uncommon in the coralline turf that is abundant in tide pools. The inhibiting effects of coralline algae on settlement by new germlings of many species is well known. Nevertheless, once established, it is very successful at maintaining space after removal by disturbance or seasonal dieback (Fig. 32).

Sargassum herporhizum is absent from the Las Conchas reef, which is subjected to more sand inundation than Station Beach. The reef at Las Conchas may be buried for considerable lengths of time on

an unpredictable basis. The relatively low propagule output of S. herporhizum may restrict its ability to consistently recolonize and maintain long-lived patches in this area. The contrast of this Sargassum species with Laminaria species that have rhizoidal holdfasts is illuminating. Laminaria sinclairii and S. herporhizum both have extensive hapteral systems but are apparently very different in their tolerance to sand-stressed habitats. Whereas L. sinclairii thrives in sand-scoured habitats (Markham, 1972, 1973a, 1973b), S. herporhizum is absent from the sandiest areas around Puerto Peñasco. This may be due to the difference in the nature of the disturbance caused by the sand. In L. sinclairii's habitat, the sand scour is severe and frequent and burial of plants for several months may occur in the summer (Markham, 1972, 1973b). At Las Conchas, actual scour of S. herporhizum is probably moderate, but burial is not as seasonally predictable as it is in California and may last for a considerable time. I have seen parts of the coquina substrate that were free of sand for months suddenly become inundated by sand for several succeeding months. Haptera are only adaptive in disturbed habitats if the disturbance does not entirely kill the plant. Sand stress at Las Conchas may be severe enough to scour the limited numbers of S. herporhizum propagules that arrive or to bury occasional patches that manage to establish. The other two Sargassum species may, through force of numbers, be able to preempt most of the suitable habitat.

Another sand-stressed coquina reef occurs in the very low intertidal on the Cholla Bay mud flats (Fig. 1). The movement of silt and sand in this area makes it a very disturbed habitat. The reef is

dominated by a variety of tunicates, but attached Sargassum plants are found here. I have collected only S. sinicola at this site, as one might expect on the basis of its dispersal abilities.

These hypothetical relationships of dispersal tactics and habitat type do not explain why the two dispersal-oriented species do not invade one another's habitat. In none of the canopy regrowth experiments (Fig. 32) did one species colonize the habitat of another following removal from patches in pure stands even though all three were fertile at the time of removal. This suggests that the species may be habitat specialists and do not compete for primary substrate during germling establishment. This issue may be illuminated by future studies of juvenile survival in various habitats.

The present investigations have been limited to Station Beach tide pool populations. Significant intraspecific variation in biomass allocation is possible given the phenotypic plasticity of Sargassum, especially with respect to receptacle morphology (De Wreede, 1973). Collections of S. herporhizum from sites subject to varying degrees of disturbance may reveal considerable variation in sexual reproductive effort because this species has the greatest potential for variation in both vegetative (holdfast) and sexual (receptacle) development. Indeed, in collections made in spring 1982, plants at Station Beach appeared to have generally higher receptacle production than that found in the same area in 1980 and 1981.

Closely related species of marine algae are often found in the same general intertidal or subtidal areas (Lewis, 1964; Ricketts et al., 1968; Stephenson and Stephenson, 1972) and thus satisfy Werner's

(1979) conditions for the study of dispersal abilities and competition. Nonetheless, such studies are rare (Russell, 1979). It is likely that further research will reveal tradeoffs between asexual and sexual reproduction, and perhaps between propagule size and dispersability, similar to the patterns found in flowering plants (Werner, 1979). Considering the important role that studies of marine algae have played in the understanding of competition and predation in relation to community structure (see Lubchenco and Gaines, 1981, and Vadas and Norton, 1982, for reviews), further study of dispersal strategies of marine algae should prove equally valuable. Conversely, life history theory can offer insights into the evolution and ecology of the baffling array of life cycles and life histories of marine algae.

CHAPTER 5

SUMMARY

This research is most notable for its delineation of intriguing differences between the three species of Sargassum at Puerto Peñasco, Sargassum sinicola, S. johnstonii, and S. herporhizum. It is among closely related species such as these that the importance and meaning of ecological differences become more apparent. The species differ in intertidal distribution, habitats, and reproductive phenology.

Distribution and Habitats of Sargassum

The three species of Sargassum are distinctly different in their distributions; they do not occur in mixed stands and show a clear separation on both large (intertidal zone) and small tide pool scales. These differences in intertidal zonation translate into differences in exposure to desiccation. On a finer scale within tide pools there are differences in water and sand depths. Overall the three species exhibit similar patterns of vertical zonation on emergent coquina substrate in the lower intertidal zone and from the edges to the bottoms of tide pools in the mid-intertidal zone.

At several study sites in the Puerto Peñasco vicinity the three species showed shifts in their habitat distributions. At Las Conchas and Pelican Point, S. sinicola occurred slightly higher on emergent coquina than at Station Beach. It was suggested that this was due to a

decreased abundance of the potential competitive dominant, S. herporhizum, at these sites. A decrease in drainage and tide pools at Pelican Point may result in more desiccation and a decrease in abundance of S. herporhizum. Sand may prevent S. herporhizum from establishing at Las Conchas. In the very low intertidal zone at Station Beach, this species occurs in broad, dense stands, which may exclude S. sinicola. The absence of S. herporhizum would also allow an upward shift in the zonation of S. sinicola at the two other sites.

It is surprising that S. herporhizum, the species with the rhizoidal holdfast, is absent from the most sandy area (Las Conchas). Based on the literature for Laminaria species with rhizoidal holdfasts (Markham, 1972, 1973a, 1973b), the prediction could be made that such holdfasts are adaptive for holding space in sandy disturbed habitats. I suggest that S. herporhizum is absent at Las Conchas because of the patchy distribution and irregular availability of sand-free coquina substrate, coupled with this species' low output of sexual propagules. Together these features may make successful colonization of new sites by this species a rare occurrence.

Seasonality

The three Sargassum species are similar in their seasonal patterns of growth and attrition. A maximum in canopy cover and size in early spring coincides with the production of sexually fertile branches that bear receptacles. Following this, the three species, like all others studied (De Wreede, 1976; Prince and O'Neal, 1979), shed their fertile branches and partly or completely die back with only pieces of stipe

and sometimes holdfast remaining. Growth recommences in late summer. Unlike S. herporhizum and S. johnstonii, S. sinicola experiences a second period of reproduction and branch-shedding in the fall.

Despite large changes in abundance, no seasonal changes in habitat proportions (pools or emergent coquina) or intertidal zonation were observed.

In their seasonal abundance patterns, the three Puerto Peñasco species are similar to most other tropical and subtropical Sargassum species (De Wreede, 1976; Prince and O'Neal, 1979): they are most abundant in the cooler months and die back in the summer. These results do, however, contrast with the seasonal pattern of S. pteropleuron in Florida (Prince and O'Neal, 1979). The former species is fertile in the fall, showing maximum growth rates in the warmest months. At Puerto Peñasco I did not measure growth rates of individual plants, but because maximum height and fertility were reached in late winter-early spring, growth had occurred primarily in the coolest months of the year (September to March).

The existence of two fertile periods in S. sinicola is an important feature of its phenology. Biannual production of receptacles is rare in Sargassum (De Wreede, 1976). Its value in the life history of S. sinicola reinforces the suggestion that this species is like an elm tree in its reproductive strategy, being an iteroparous producer of large numbers of propagules (Williams, 1975). The ability of S. sinicola to reproduce sexually twice a year may be related to the persistence of a larger portion of its thallus through the summer season of attrition, which in turn may be due to its occurrence mostly in protected habitats

(i.e., in pools). I suggest that in addition to a critical temperature cue for sexual reproduction, Sargassum plants must also reach a minimum critical size during the growth cycle, which is achieved by S. sinicola in fall and spring. The other two species experience a severe dieback (S. johnstonii) or produce generally less in the way of sexual structures (S. herporhizum) such that they grow only vegetatively in the fall.

At Station Beach a decrease in Sargassum canopy cover was recorded from 1977 to 1980, especially in the area of Station Pool (Figs. 19). As of the winter of 1981-82 Sargassum abundance was still low in this area. In the interim, between 1977 and 1980, a period of elevated sea surface temperatures occurred in this part of the Pacific Ocean, which had important effects on the abundances of shallow-water marine organisms (Duggins, 1981; Dungan et al., 1982). This warming climatic trend may have accentuated the annual dieback of Sargassum in the warmer months, or it may have affected the plants indirectly by causing a decline in the starfish Heliaster and a subsequent increase in herbivore densities.

Biomass Allocation Patterns

Sargassum plants possess a more or less perennial holdfast, which produces a deciduous upper vegetative portion each year. Primary substrate is occupied by the holdfast, which is usually restricted in size; spreading rhizoidal holdfasts are uncommon (De Wreede, 1973). At Puerto Peñasco, however, one of the species, S. herporhizum, does have a rhizoidal holdfast that makes up a much

larger proportion of its wet and dry biomass than in the other two species (Fig. 24). Holdfast tissue in S. herporhizum is made of a higher percentage of water than the other two species; i.e., it takes less photoassimilate to make a given amount of holdfast tissue. The result is a more effective cover of the substrate and a larger absolute mass of holdfast produced per unit area of substrate (Fig. 23). These attributes suggest that S. herporhizum should be effective at encroaching into newly cleared contiguous space and at regrowth following disturbance or seasonal dieback. Experimental clearings showed that this did occur.

If there are constraints such as sunlight or nutrients on a plant's capacity to produce tissue, one might expect the production of a large holdfast to preclude the production of tissue in the upper thallus. Furthermore, because sexual receptacles are borne on the upper thallus, the amount of upper thallus tissue produced by a plant will affect its sexual output.

It turns out that the species with the smaller holdfasts (S. johnstonii and S. sinicola) did produce more upper thallus tissue, both proportionately and absolutely (Fig. 23). They also produced a much greater volume of receptacles per gram of fertile branch tissue than did S. herporhizum (Table 5). The net result was, in the area studied at Playa de Oro, an order of magnitude difference in sexual tissue production between these two species and S. herporhizum.

Attempts to test for differences in recruitment of new plants among the three species were unsuccessful. Although in other regions recruitment of Sargassum plants on experimental substrate has been

easily achieved (Raju and Venugopal, 1971; Deysher and Norton, 1982), no Sargassum settled on clean the clean coquina substrate I placed in Station Beach tide pools in the spring and fall of 1980. That year may have been a poor one for Sargassum recruitment due to the same reasons discussed regarding a long-term decline of Sargassum in this area.

Experimental evaluation of the abilities of the several species to recover space after removal was more successful. Sargassum herporhizum was markedly better able to regrow its canopy following experimental clearing and after the summer dieback (Fig. 32). In this respect, S. herporhizum is similar to Laminaria longipes in Alaska (Dayton, 1974). Estimates of the relative sexual biomass investment in Laminaria species are not available; they may show the same tradeoff described here for Sargassum.

The biomass allocation patterns in the three species at Puerto Peñasco suggest that there is a tradeoff between short- and long-distance dispersal. Deysher and Norton (1982) demonstrated the potential for long-distance dispersal by S. muticum through the shedding of fragments that are either fertile or may become so while free floating. My observations showed the effectiveness of a rhizoidal holdfast at dispersing into adjacent free space and documented the low output of sexual propagules by S. herporhizum. There are constraints on the capacity of Sargassum species to produce different tissues and as a result dispersal abilities differ. The species occupy different habitats, and their ability to successfully colonize and maintain space in these habitats is certainly affected by their dispersal abilities.

The data on biomass allocation presented here are the first to deal with a set of closely related species of marine algae in the same intertidal area. Examination of algal morphology from this perspective has been extremely rare (Russell, 1979). The prediction is made that the tradeoff observed in the study area will prove to be a general pattern in Sargassum and perhaps in other marine algae. Further study of reproductive strategies in marine algae should prove valuable in understanding intertidal community structure.

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