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Natural History of Mainland and Island Populations of the Deep Water Elk Kelp *Pelagophycus* (Laminariales, Phaeophyta): How Many Species?

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Abstract. The elk kelp, *Pelagophycus porra* (Leman) Setchell (Phaeophyta, Laminariales) is endemic to the coastal waters of southern California and northwestern Baja California, Mexico. This species grows at a depth of 20–50 m depth, often along the seaward margins of *Macrocystis pyrifera* beds. Suites of morphological characters (stipe and holdfast dimensions, number and texture of blades) are consistently correlated with habitat: exposed, rocky substrate on the mainland vs sheltered, soft substrate on the leeside of the Channel Islands. These morphs have been recognized as separate species in the past, but are currently considered to be ecological variants of a single, phenotypically plastic species. Studies to date have focused exclusively on the biology of the "sheltered" morph at Santa Catalina Island. Our studies of the distribution of *Pelagophycus* document extensive beds of the "exposed" morph off the mainland and identify for the first time populations of this morph in the California Channel Islands. Our data on growth rates, phenology and longevity of the "exposed" morph off Point Loma reveal substantial differences when compared to those on the "sheltered" morph reported in the literature. While the latter have been shown to be annuals, we find that the Point Loma population is composed of perennial plants. We report inconclusive results from a reciprocal transplant experiment and discuss the question: Are the "sheltered" and "exposed" forms expressions of habitat-specific phenotypic variation in a single species, or do they represent separate species?

Keywords: California Channel Islands; *Pelagophycus*; Laminariales; Phaeophyta; systematics; kelp; demography; biogeography; growth; morphology; phenotypic variation.

Introduction

The elk kelp, *Pelagophycus porra*, is a giant brown kelp found forming dense groves in deep water or cast ashore on the coasts of southern California and Baja California, Mexico, and Santa Catalina, San Clemente and Santa Cruz islands in the California Channel Islands (Dawson 1962; Parker and Dawson 1964; Parker and Bleck 1965). Despite its great size, abundance and unusual habitat, *P. porra* is poorly understood. After reviewing the systematic and nomenclatural history of the genus and records of its geographical distribution, we present the results of the first demographic study of a mainland population at Point Loma, California, and a reciprocal transplant experiment between island and mainland populations; we also report new information on the distribution of *Pelagophycus* in coastal waters of the Channel Islands and of the mainland in the southern part of its range.

We offer an account of the natural history of this genus as a context for further studies to re-evaluate the question: Should populations of *Pelagophycus* that are distinct on the basis of morphology, demography and ecology be recognized as separate species? We propose 2 alternative hypotheses: (1) that *Pelagophycus* is represented by a single, phenotypically plastic species with a wide range of morphological responses to, and broad tolerances of, distinctly different habitats; and (2) that *Pelagophycus* comprises 2 species that can be described as distinct on the basis of morphological, demographic and ecological differences.

Nomenclatural History of *Pelagophycus*

Pelagophycus was recognized by early mariners as an aid to navigation long before it was described by botanists. Because of the buoyancy conferred by their large pneumatocysts, plants dislodged by storms from mainland populations typically floated out to sea. Anson's expedition in the early 1740s reported:

> . . . and when she has run into the longitude of 96° from Cape Espiritu Santo, she generally meets with a plant floating on the sea, which being called "Porra" by the Spaniards, is, I presume, a species of sea-leek. On the sight of this plant they esteem themselves sufficiently near the California shore, and immediately stand to the southward; and so much do they rely on this circumstance that on the first discovery of the plant the whole ship's company chaunt a solemn *Te Deum*, esteeming the difficulties and hazards of their passage to be now at an end; and they constantly correct their longitude thereby, without ever coming within sight of land (Setchell 1908).

LeGentil, during his 1768–1769 expedition to observe the transit of Venus, made the first illustration of Pelagophycus and recognized it as a plant hitherto unknown to European science; it is his report that is the basis of the first critical botanical diagnosis, in French by Leman, under the name *Laminaria porra*: "Very long stipe, ending in a fusiform swelling, bearing a large spherical bladder crowned with lanceolate blades, very elongate and deeply dentate. This species was observed in the southern sea by LeGentile. The Spanish sailors named it *porra*. Its length is remarkable, exceeding . . . 200 feet" (Leman 1822, in Setchell 1908; our translation).

Without knowledge of Leman's description, Areschoug redescribed the species, placing it in the genus *Nereocystis* as *Nereocystis gigantea*, based on a specimen collected near Santa Catalina Island by Dr. Gustav Eisen (Areschoug 1876). He subsequently created a new genus, *Pelagophycus*, to receive this species, making the new name *Pelagophycus giganteus* (Areschoug) Areschoug (Areschoug 1881). Setchell initially believed that the elk kelp had closer affinities to *Nereocystis* (Setchell 1896) but accepted Areschoug's genus *Pelagophycus*.

Recognizing the earlier specific epithet of Leman he published the name as *Pelagophycus porra* (Leman) Setchell (Setchell 1908). Although no specimen was preserved, the type locality for this species is LeGentil's "southern ocean" ("dans le mer du Sud"), not Santa Catalina Island as is reported in Abbott and Hollenberg (1976).

Pelagophycus porra was the accepted name for the species in this monotypic genus for 54 yr, until Dawson, Parker and Bleck, working in the Channel Islands, distinguished 2 new species: *Pelagophycus giganteus* (Areschoug) Areschoug (Dawson 1962) and *Pelagophycus intermedius* Parker and Bleck (Parker and Bleck 1965). *Pelagophycus giganteus* is based on the Eisen type specimen from Santa Catalina Island (housed in the Naturhistorska Rikmuseet, Stockholm, Sweden), which Dawson states is similar to his topotypes collected at Emerald Cove, near White's Point (Dawson 1962). Dawson differentiated *P. giganteus* from *P. porra* on the basis of differences in holdfast dimensions and development, stipe length, pneumatocyst shape, degree of flattening of the antlers, and number of blades (Dawson 1962). Additional specimens from Santa Catalina and San Clemente Islands and Point Loma necessitated a re-evaluation of the characteristics previously used to separate the species (Parker and Dawson 1964). They described variability in the morphology of the antlers and pneumatocysts and suggested that the holdfast and stipe dimensions were more stable criteria for separating the species. Parker and Fu (1965) summarized differences in internal anatomy between *P. porra* and *P. giganteus* (size and shape of cortical and medullary cells in the stipe, morphology of mucilage ducts), and presented presumptive evidence for polyploidy between the 2 species, based on the volume of interphase meristoderm nuclei (51 cu. µ in *P. giganteus* vs 28 cu. µ in *P. porra*). Parker and Bleck (1966) concurred that polyploidy was a possible mode of speciation when they reported that zoospores of *P. giganteus* had twice the volume of those of *P. porra*. These anatomical and cytological studies have not been re-examined or extended since their publication.

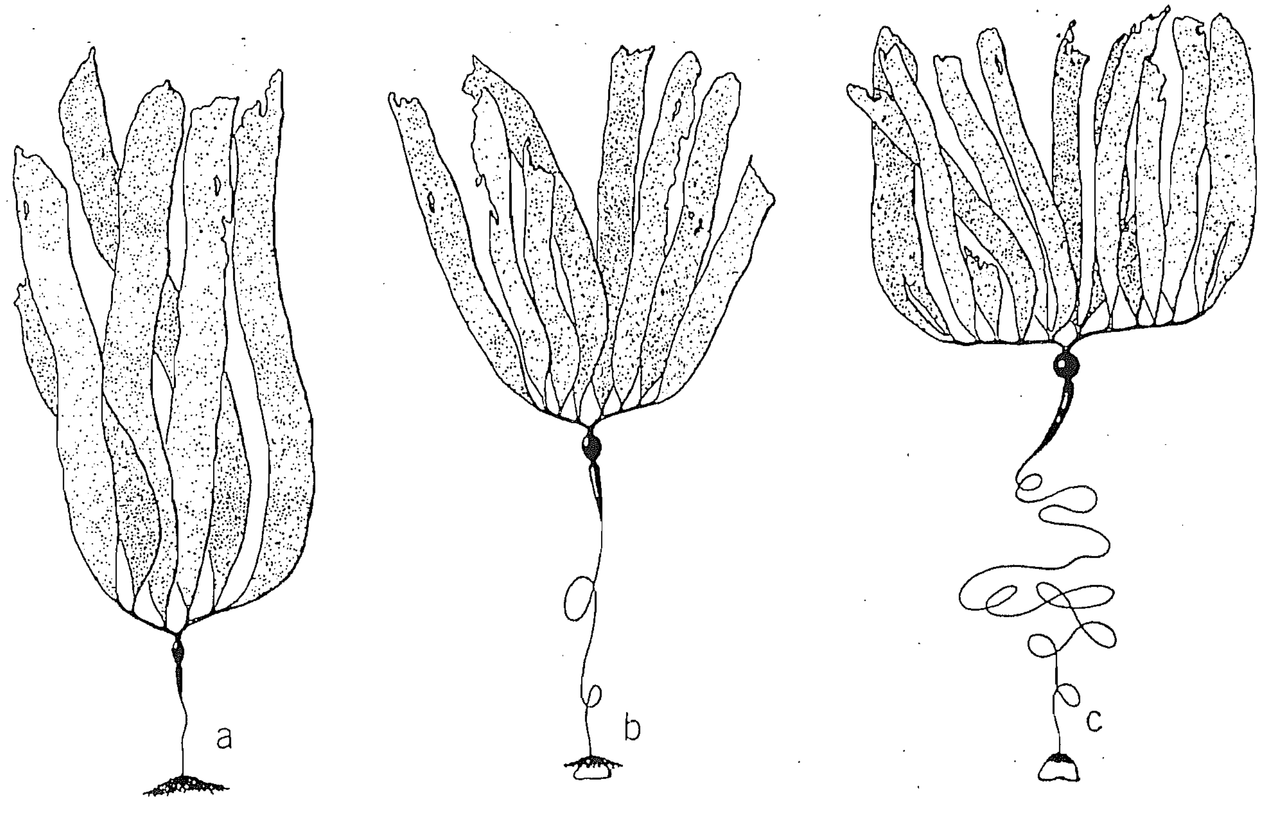

Figure 1. The 3 species of *Pelagophycus* (magnification X 0.01). **1A.** *P. giganteus* (Areschoug) Areschoug; **1B.** *P. intermedius* Parker and Bleck; **1C.** *P. porra* (Leman) Setchell. From Parker and Bleck (1965).

Parker and Bleck (1965) described *Pelagophycus intermedius* from Santa Cruz Island, reporting a gross morphology in this new species intermediate in characteristics between the other 2 species (Parker and Bleck 1965; Fig.1). They proposed that *P. intermedius* is an autoallopolyploid derived from hybridization of *P. porra* and *P. giganteus* that might have come about when the now extinct population at San Pedro flourished within 15 mi of those at Santa Catalina Island. This species has not, to our knowledge, been collected or mentioned in the literature since its description, and will not be treated here.

The most recent nomenclatural chapter in the saga of *Pelagophycus* was written 11 yr later, when Nicolson merged *P. giganteus* and *P. intermedius* into *P. porra* (Abbott and Hollenberg 1976). Her description of *P. porra* includes broad ranges for holdfast diameter (10–20 cm), stipe length (7–27 m), pneumatocyst diameter (10–20 cm) and blade length (6–20 m), with blade number ranging from 6 to 20. The taxonomic decision implicit in this merger is that the range of variation in these morphometric characters is encompassed by a single, phenotypically plastic species. Although she cited Santa Catalina Island as the type locality of *P. porra*, in error, she did not include the Channel Islands in the distributional range of the species.

Geographical Distribution

Mainland

In mainland coastal waters, the endpoints of the geographic distribution of *Pelagophycus* are reported to be Point Conception, California and Isla San Benito, Baja California, Mexico (Abbott and Hollenberg 1976). There is little recent information on the northern endpoint, but it seems certain that *Pelagophycus* occurs well south of Point Conception. The northernmost published report is San Pedro, California (Setchell 1896; Herbst and Johnstone 1937), but *Pelagophycus* hasn't been seen there since the disappearance of the *Macrocystis* canopy in the 1930s (Schott 1976). Clearly, the offshore communities in this part of the Southern California Bight have changed radically in the last 50 years.

After the 1982–1983 El Niño event, a population of *Pelagophycus* was observed growing in central California on a deep reef near Pecho Rock 5.8 km south of Diablo Cove (North et al. 1989). Warm water fish species were noted as well. This report did not include information about the persistence of this population beyond the time of its discovery.

Pelagophycus is abundant from La Jolla to Point Loma (Dawson 1962; Dayton et al. 1984). However, the Mexican distribution of *Pelagophycus* has been poorly documented in the literature. Dawson (1962) reported a population midway between Point Loma and Islas Coronados off Tijuana Slough, observed *in situ* by J. R. Stewart; a population off Punta San José observed *in situ* by M. Neushul; and populations from Punta San José to Isla San Martin observed by C. Martin from a ship. A collection was made by Wheeler North in 1964 at Punta Santo Tomás; some individuals had extremely long (27 m) stipes. In 1990, Ron McPeak used aerial surveys to map the distribution of *Pelagophycus* off Baja California, Mexico (Dorr 1991). These populations, some of which are huge, lie offshore, usually seaward of *Macrocystis* beds. They occur at 10 locations, the last of which, Sacramento Reef, represents the southern endpoint of the distribution of the species (Table 1).

Table 1. Distribution of *Pelagophycus* in Baja California, Mexico.

1. Islas Coronados.
2. Discontinuous beds from Punta Santo Tomás to Punta San José.
3. Punta San José and southward, covering several square miles.
4. Offshore of Key Patch, north of Cabo Colonet; some at Sandy Beach.
5. Punta San Telmo and offshore to Punta San Jacinto.
6. Punta San Jacinto south to Isla San Martin.
7. Long continuous bed from El Socorrito to rivermouth at El Rosario.
8. Patches 1–2 mi north of Punta Baja.
9. Extensive beds throughout Bahia San Rosario.
10. Just north of Sacramento Reef.

Channel Islands

Pelagophycus has been reported from Santa Catalina Island (Herbst and Johnstone 1937; Dawson 1962; Parker and Dawson 1964; Parker and Bleck 1965; Coyer and Zaugg-Hagland 1982), San Clemente Island (Dawson 1962; Parker and Dawson 1964; Parker and Bleck 1965), and Santa Cruz Island (Parker and Bleck 1965). We can now add Santa Barbara Island and, with less certainty, San Nicolas Island (J. Engle 1993, pers. comm.). The records of populations at Yellowbanks, Santa Cruz Island, mark the northern endpoint of the distribution of elk kelp.

The depth at which *Pelagophycus* populations occur in the Channel Islands varies from about 20 m to more than 50 m, usually well below the thermocline. The depth at which kelp populations occur can change from year to year, probably as a result of thermocline (and concurrent nutrient level) changes (Zimmerman and Robertson 1985). During warm years, and especially El Niño events, populations tend to occur at greater depths (J. Engle and J. Coyer 1993, pers. comm.)

Morphology and Distribution in the Channel Islands

The recognition of *Pelagophycus giganteus* as distinct from *Pelagophycus porra* was based on differences in external morphology (Dawson 1962; Parker and Dawson 1964; Parker and Bleck 1965). The size and shape of the holdfast (large and spreading in *P. giganteus*, small and compact in *P. porra*), the number of blades (6–9 vs 12–20, respectively), and the length of the stipe (considerably shorter in *P. giganteus*) were considered diagnostic characters. Respecting Nicholson's synonymy (Abbott and Hollenberg 1976), we will refer to these suites of morphological characters as morphs: "P. porra" and "P. giganteus."

In the past, these morphs have been tightly correlated with geographic distribution, with "P. porra" occurring off the mainland and "P. giganteus" off the islands. Previous observations and collections of *Pelagophycus* from Santa Catalina and San Clemente islands were made solely at sites on the lee (east) side of the islands. We report, for the first time, not only new *in situ* observations of *Pelagophycus* from the windward side of San Clemente Island, but also that these populations represent the "P. porra", or mainland, morph. In June 1993, we collected specimens from Cove Point and Moon Rock, at the southwest and northwest ends of San Clemente Island, and observed populations from China Point to Lost Point. Aerial surveys and reports from abalone and urchin divers support the occurrence of *Pelagophycus* along the west side of San Clemente Island from Lost Point to Castle Rock (Dorr 1991).

In October 1978, the "P. porra" morph was also collected on an anchor near Arch Point at Santa Barbara Island (J. Engle 1993, pers. comm.) and in September 1993 was observed *in situ* by Ron McPeak off Webster Point, Santa Barbara Island. Heretofore, it was assumed that the mainland was the source of drift plants referable to the "P. porra" morph that are frequently observed throughout the Channel Islands; we now know that populations of the "P. porra" morph occur at San Clemente and Santa Barbara Islands. The population at Santa Cruz Island needs to be re-examined.

Distinctive Habitats and Habits

At San Clemente Island, the habitats of the 2 morphs are distinctly different. The windward sides of the island are extremely exposed to heavy wave action and deep surge. The substrate consists of bedrock, boulders and rocks. The water can be extremely turbulent, even at great depth. In many respects, this environment is reminiscent of mainland sites, like Point Loma, having the same exposure to the open fetch of the ocean. *Pelagophycus* growing in these exposed habitats are huge, with stipes 15 to 20+ m in length, and proportionately small, compact holdfasts attached to rock. Their large pneumatocysts buoy them upright, and as many as 20 streaming blades (~5 m in length) form a patchy subsurface canopy where densities are high. Blades are leathery in texture.

In contrast, the leeward sides of San Clemente and Santa Catalina Islands are sheltered from wave action, although strong currents and storm-generated surge are common (Parker and Bleck 1966; Coyer and Zaugg-Hagland 1982). The substrate may be rocky in shallow water, but falls off, at depths where *Pelagophycus* occurs, to soft silt and sand. The spreading holdfasts of *Pelagophycus* are attached to pebbles and wormtubes and ramify over the soft substrate. Plants are relatively short, with stipes usually < 3 m, but their 4–6 blades are very long (~10+ m). Their relatively small pneumatocysts cannot support the weight of the blades, so the plants tend to arch down, with blades spread along the bottom in the manner of *Laminaria farlowii*. The texture of the blades is delicate and crisp.

Morphometrics and Notes on Development

In June 1993, we collected samples of plants from 3 San Clemente Island populations by cutting their holdfasts free from the bottom and letting them float to the surface, whereupon they were gathered and brought back to the ship. Plants grew at depths of 27–40+ m. Individuals from Cove Point (32°49'N, 118°23.42'W) and Moon Rock (33°3'N, 118°36'W) populations (from the very exposed southwest and northwest windward sides of the island, respectively) agree with the "P. porra" morph, while those from Mosquito Cove (32°52'N, 118°23'W), at the southeast leeward end of the island, represent the "P. giganteus" morph. We measured stipe length, holdfast diameter, pneumatocyst length and circumference, in addition to counting blades. We realize that our collections included a range of age classes (juveniles were present at all 3 sites), which reduces the power of our comparisons. Nevertheless, we can make the following observations, based on simple descriptive statistics (Figs. 2 and 3) and comparative statistical tests (Oneway ANOVA, followed by Tukey's Comparison Test or Kruskall-Wallis, followed by paired Mann-Whitney U tests, 95% confidence). Sample sizes are presented in figures 2 and 3. Statistics were performed using MINITAB.

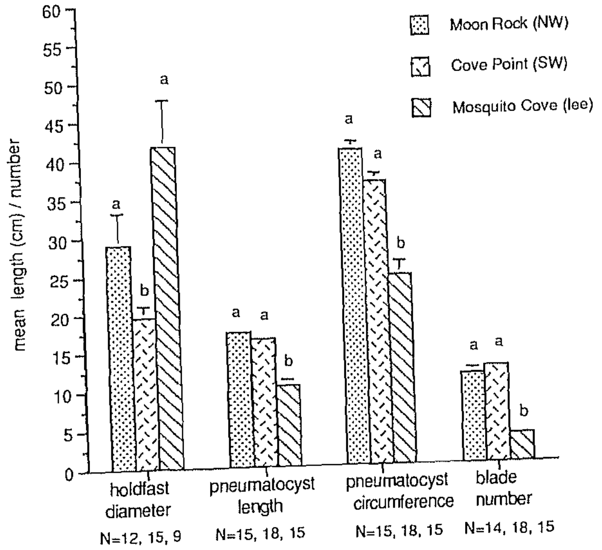

Figure 2. Mean values (cm) for measurements of holdfast diameter, pneumatocyst length and circumference, and blade number for *Pelagophycus* at 3 sites off San Clemente Island. Moon Rock and Cove Point are on the extremely exposed northwest and southwest ends of the island, respectively. Mosquito Cove is located on the southeastern lee side of the island. Bars represent positive standard error of the mean; letters above the histograms represent results of multiple comparison tests.

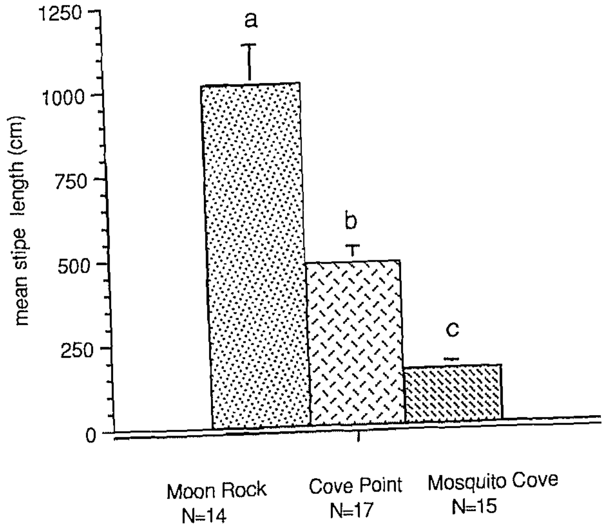

Figure 3. Mean values (cm) for measurements of stipe length for *Pelagophycus* at the sites described in Figure 2. Bars represent positive standard error of the mean; letters above the histograms represent results of multiple comparison tests.

For holdfast diameter, the means for the windward populations (29.0 and 19.6 cm) are smaller than for the lee population (41.7 cm) (Fig. 2), but the northwest and southwest populations differ significantly (Kruskall-Wallis: H = 33.99, p = 0.00; Mann-Whitney U test: W = 161, p = 0.01). The standard error of the mean is large for this measurement, indicating substantial variability within populations. For mean pneumatocyst length, the windward populations are statistically indistinguishable and significantly different from the leeward (ANOVA: p = 0.00; Tukey's Comparison) (Fig. 2). Blade number is clearly discrete between the two morphs, with the windward plants bearing 6–16 blades, and the leeward 2–6 (Fig. 2). Blade number between the windward populations is statistically indistinguishable (Mann-Whitney U test: W = 314, p = 0.48) but statistically different from the leeward (Kruskall-Wallis: H = 26.90, p = 0.00; Mann-Whitney U test: W = 315, 441; p = 0.00, 0.00). The mean stipe lengths for the windward populations (1,013.0 and 479.6 cm) are much greater than the leeward (161.2 cm) (Fig. 3), but all 3 are statistically different from one another (Kruskall-Wallis: H = 30.60, p = 0.00; Mann-Whitney U test: W = 311, 315, 402; p = 0.001, 0.00, 0.00). These dimensions and their range of variabilities conform with those described for *P. giganteus* and *P. porra* (Dawson 1962; Parker and Bleck 1965).

We noticed that the antlers were terete and the pneumatocysts were subspherical to spherical in both the windward ("P. porra") and leeward ("P. giganteus") populations. This agrees with the variability noted by Parker and Dawson (1964).

Dawson (1962) illustrated developmental differences between juveniles (single-bladed individuals) of *P. porra* and *P. giganteus*. Our observations confirm his. Juvenile "P. giganteus" tend to have short stipes, without pneumatocysts, and long, wide blades. Larger juveniles develop small, elliptical pneumatocysts concurrent with relatively little stipe elongation. At all stages of development, these juveniles lay on the bottom. By comparison, juvenile "P. porra" have longer stipes, spherical pneumatocysts, and shorter, narrow blades; juveniles are buoyed upright from a very early age and exhibit rapid stipe growth. Splitting of the blades and formation of antlers apparently occur early in "P. porra" morph juveniles.

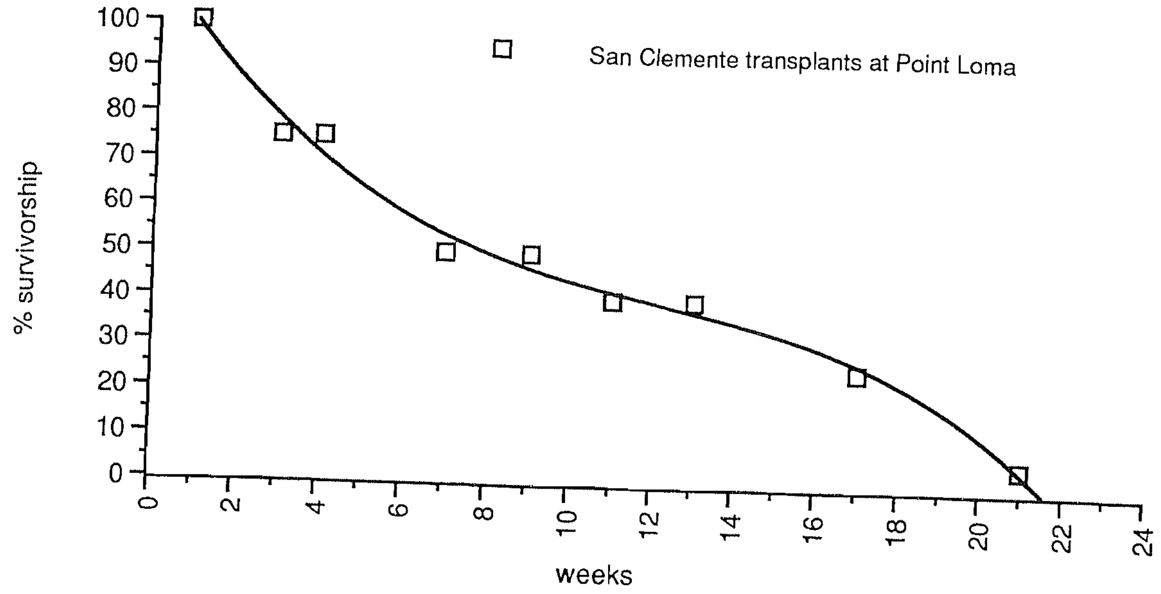

Figure 4. Percent survivorship of 20 San Clemente Island transplants at Point Loma. Mortality was due to mechanical damage by surge and herbivory by the bat star, *Asterina miniata*. The last plant disappeared after 22 weeks.

A Reciprocal Transplant Experiment

Parker and Bleck (1966) transplanted 105 juvenile *Pelagophycus* from La Jolla to Long Point, Santa Catalina Island. Within a day, 10 were lost and 20 suffered imploded pneumatocysts. Within a month, all but 2 individuals lacked blades and/or had imploded pneumatocysts; the survivors, the smallest of those transplanted, exhibited no growth during that month. Parker and Bleck concluded that *P. porra* could not develop in the habitats occupied by *P. giganteus*, and used this as evidence for considering the two to be separate species. We designed a reciprocal transplant experiment to test this hypothesis and to learn more about demography and growth of *Pelagophycus* at Point Loma, which have yet to be studied.

In April 1990, the second author transplanted 20 juveniles from a site located 2.25 km due west of Point Loma (32°44'N, 117°17'W) to concrete blocks at Mosquito Cove, on the southeastern lee side of San Clemente Island (32°57'N, 118°24'W). Twenty Mosquito Cove juveniles were also transplanted to concrete blocks at Point Loma (for detailed methods, see Dorr [1991]). Depths at each site were 21–24 m, but the habitats were, as described above, distinctly different. Survivorship was monitored and stipe elongation measured in the transplants, tagged native individuals, and controls (natives that had been collected and returned to their original site on concrete blocks).

The Point Loma individuals transplanted to San Clemente did not survive; however, imploded pneumatocysts were not observed. Fifteen out of 20 remained after 6 wk, during which mean stipe elongation was about 0.16 cm/dy, markedly less than the 0.3 cm/dy reported for Catalina Island juveniles of about the same size during the same season (Coyer and Zaugg-Hagland 1982). At 28 wk, only 1 damaged plant remained.

The San Clemente Island transplants at Point Loma survived only 21 wk (Fig. 4). The delicate blades and developing antlers of the transplants were damaged by surge in this very exposed habitat. In addition, the long, drooping blades typical of "P. giganteus" juveniles caused them to be vulnerable to herbivory by *Asterina miniata*, the bat star, a common scavenger and omnivore at Point Loma (Dayton et al. 1984). Bat stars were observed to feed upon drift native *Pelagophycus* blades as well as the transplants. In October 1990, densities of *Asterina* in the vicinity of the study site were 1.18 (± 1.74) individuals per m^2 (n = 17). The density of *Asterina* within a meter of the transplant blocks was 11.2 per m^2, suggesting that they were aggregating around the transplants. "P. porra" juveniles, with their early development of pneumatocysts and erect habit, were not as susceptible to herbivory as were the "P. giganteus" transplants. *Asterina* was not observed at the San Clemente Island site; this source of mortality for *Pelagophycus* juveniles appears to be unique to the Point Loma site.

At the San Clemente Island site, it was not possible to relocate the 7 natives marked and left undisturbed due to the dense development of surrounding understory algae. The stipe length of native controls on concrete blocks was measured at wk 6 and again at wk 28 (Fig. 5); between those times, they grew, on average, only 0.07 cm/dy—only 10% of the rate reported by Coyer and Zaugg-Hagland (1982) for Catalina Island plants during the same season. This rate is statistically indistinguishable from that of the San Clemente Island transplants at Point Loma (T test: t = 0.11, $p < 0.05$) (Fig. 5).

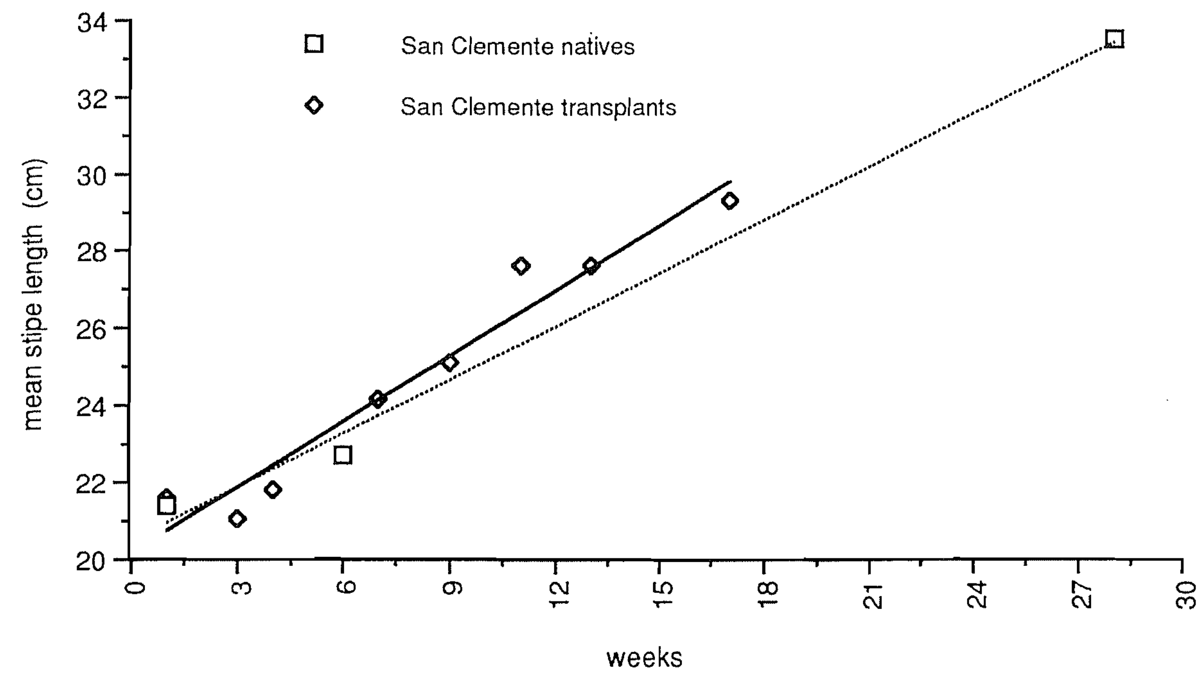

Figure 5. Mean stipe lengths (cm) of San Clemente Island natives at San Clemente Island and San Clemente Island transplants at Point Loma.

Demographic Studies of *Pelagophycus* at Point Loma

Studies of the demography of *Pelagophycus* populations ("P. giganteus" morph) at Santa Catalina Island have established that it is an annual plant, with most individuals surviving up to 12 mo, although a few thalli may persist to 25 mo (Coyer and Zaugg-Hagland 1982; Parker and Bleck 1966). Studies by the second author indicate that *Pelagophycus* at Point Loma is not an annual; we present demographic information for the Point Loma population to compare survivorship and growth rates of "P. porra" morph with those of "P. giganteus" (Dorr 1991).

Survivorship

In March 1990, 130 plants (0.14 individuals per m^2) were counted in a 900-m^2 plot at the Point Loma study site. Of these, 60 had stipe lengths greater than 2 m, 30 were 1–2 m in height, and 40 were juveniles (single blades, less than 1 m stipe length). Recruitment of juveniles was observed throughout the year, roughly in monthly flushes. This differed from populations at Santa Catalina Island where recruitment apparently occurs only in early summer (Coyer and Zaugg-Hagland 1982; Parker and Bleck 1966). Twenty-one juveniles (stipe length less than 20 cm) were tagged in April and May 1990. An additional 20 were transplanted to concrete blocks placed in the study plot. The percent survivorship of this cohort of 41 was monitored closely for 1 yr, and at infrequent intervals for 2 more yr (Dorr 1991).

Survivorship of the Point Loma cohort for the first year (Fig 6), is similar to that for the Santa Catalina Island population studied by Coyer and Zaugg-Hagland (1982). This Type III curve is typical of species with high juvenile mortality and low adult mortality (Deevey 1947). However, at Point Loma, at least 30% of the cohort lived more than 12 mo, with almost 10% surviving nearly 30 mo (Fig. 7). Although quantitative evidence is not presented here, storm damage (broken antlers and blade loss) and entanglement with conspecifics have been observed as the greatest sources of mortality in this population (Dorr 1991).

Because of the high rates of early mortality, it would be necessary to follow a larger cohort to demonstrate survivorship rates of plants more than 1 yr old. Nevertheless, this sample suggests that individuals in the Point Loma population are not annuals. This is corroborated by the fact that the first plant in the cohort to reach reproductive maturity was almost 2 yr of age. Furthermore, after more than 3 yr, the last survivor in the cohort (plant #73, which was healthy and non-reproductive at the last observation) was 8.5 m tall, while most of the surrounding, reproductively mature plants in the population had stipes more than 20 m in length. At the time of the final measurement,

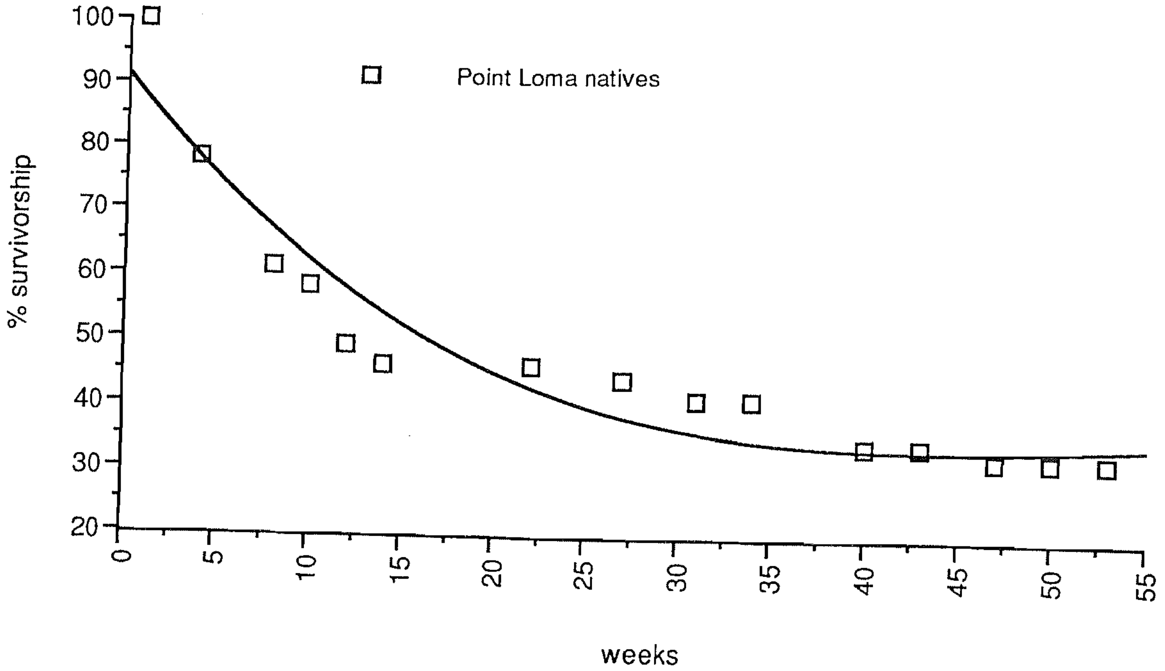

Figure 6. Percent survivorship of 41 Point Loma natives during 1 year. The curve indicates high juvenile mortality in the first 10 weeks after tagging and lower rates thereafter. Mortality was due to entanglement with conspecifics and storm damage.

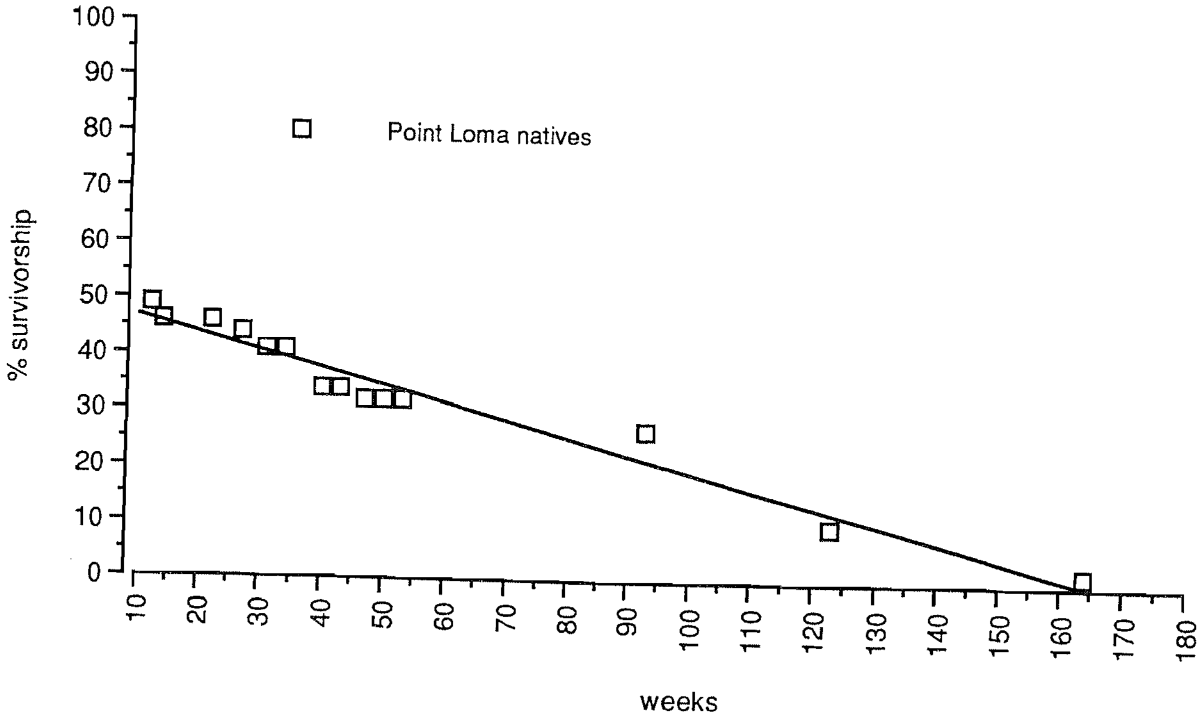

Figure 7. Percent survivorship of Point Loma natives surviving from week 10 to week 164 (3 years). The depletion curve is nearly linear, but 30% of the original cohort survived beyond 2 years.

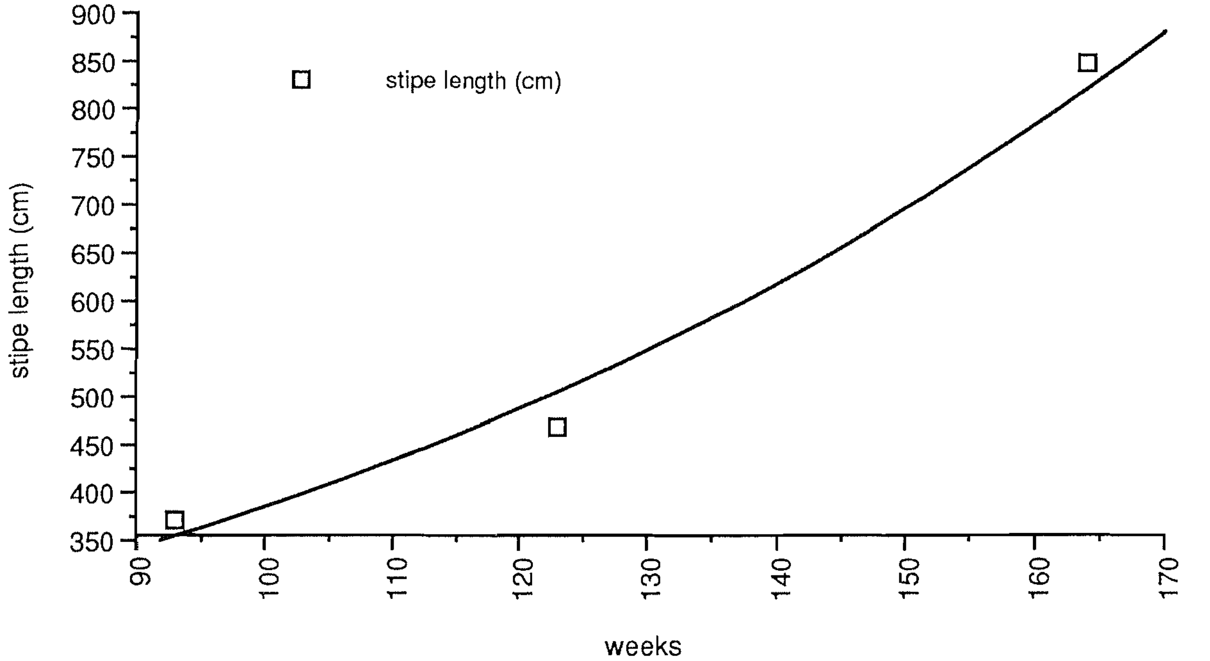

Figure 8. Stipe length (cm) for the oldest plant in the Point Loma native cohort from week 93 (about 2 yr of age) to week 164 (more than 3 yr of age). The curve describing stipe elongation rate is exponential, suggesting further future growth.

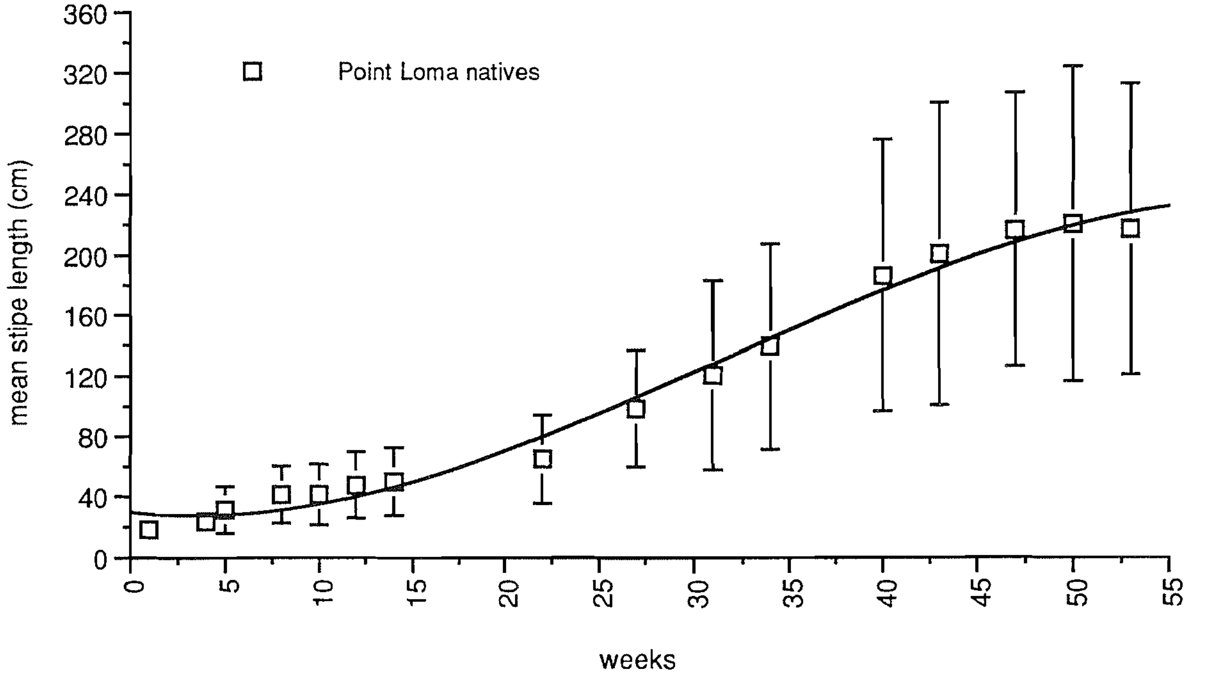

Figure 9. Mean stipe length (cm) for the cohort of 41 Point Loma natives over the first year. The rate of stipe elongation increases with time.

Table 2. Rates of stipe elongation for *Pelagophycus* on Point Loma and Santa Catalina, Channel Islands.

Coyer and Zaugg-Hagland (1982)		This study (Point Loma)	
May–June 1977	0.3 cm/day	April–June 1990	0.3 cm/day
July–November 1977	0.7 cm/day	July–November 1990	0.6 cm/day
December 1977–October 1979	0.2 cm/day	December 1990–January 1992	0.8 cm/day

the rate of stipe elongation in plant #73 was exponential, indicating a potential for attaining an even greater size (Dorr 1991) (Fig. 8).

Although we have not studied the "P. porra" populations on the windward side of San Clemente Island, these individuals resemble those at Point Loma in size and morphology. We hypothesize that demographic patterns may be similar at both sites.

Stipe elongation rates

Stipe length of the tagged plants at Point Loma was measured at 2- to 3-wk intervals, depending on weather and water conditions, for 53 wk (Fig. 9). Because growth rates of plants on native substrate and concrete blocks were indistinguishable, the data were pooled (data not shown). Survivors were measured again at wk 93, 123 and 164. The rate of stipe elongation in the Point Loma sample was far greater than that of the San Clemente Island natives and transplants (Dorr 1991) (compare Figs. 5 and 9). The high standard deviations in the Point Loma cohort are a result of increasingly small samples, as time went on, as well as intrinsic variability in stipe length within the population, similar to that observed by Coyer and Zaugg-Hagland (1982). Although the sigmoid curve appears to flatten out at about 200 cm at wk 50 (Fig. 9), a mean stipe length of 482 cm (±307) was measured for the 11 plants remaining at wk 93, with a range of 81 to 1,007 cm. The growth of the last plant (#73) remaining in the cohort is described above (Fig. 8).

The rates of stipe elongation during the first year are comparable to those reported for plants at Santa Catalina Island by Coyer and Zaugg-Hagland (1982), but the stipe growth in plants exceeding 1 yr of age is distinctly greater at Point Loma (Table 2).

The high elongation rates for older plants, though based on a small sample, again suggests the potential for greater longevity for *Pelagophycus* at Point Loma (and probably on the windward side of San Clemente Island) relative to populations at Santa Catalina Island. All growth rates measured in *Pelagophycus* are low when compared to other giant kelps such as *Nereocystis* (25 cm/dy) and *Macrocystis* (50 cm/dy) (Coyer and Zaugg-Hagland 1982). This is doubtless due to low ambient light levels at the great depths at which *Pelagophycus* grows.

Conclusions

Our surveys and demographic studies have shown that the morphs "P. porra" and "P. gigantea" are clearly distinguished on the basis of (1) habitat, including differences in wave exposure, substrate, predation pressure and possibly nutrient levels; (2) development of the juvenile sporophyte; (3) morphometric characters, especially stipe and pneumatocyst length and blade number; and (4) demography of the sporophyte, including periodicity of recruitment, patterns of stipe elongation, onset of reproductive maturity, and longevity. We now know that "P. porra" grows in extensive beds off Baja, California, Mexico, and that it is not limited to the mainland, but occurs on the windward side of San Clemente and Santa Barbara Islands, although these populations have yet to be studied in detail.

We find the differences in habit (stipe length and pneumatocyst length, blade number and buoyancy of the pneumatocyst) between the 2 morphs consistent and striking. We speculate that both are adaptations for light-gathering in very different environments. In its sheltered habitat, the "P. giganteus" morph allocates its biomass to relatively fragile blade surface area. The blades are draped along the bottom; light penetration through the clear, oligotrophic water is sufficient for growth, even at depth. For the "P. porra" morph, rough water conditions dictate an allocation to a long, tough stipe and subsequent elevation of the blades in a habitat where water clarity and light penetration are relatively limited.

The difference in longevity between Point Loma and Santa Catalina Island individuals is also remarkable. Clearly, the growth rates measured at Point Loma in this study are too low to permit full growth of the "P. porra" morph in a single year.

On the other hand, the holdfast dimensions may be plastic, dependent on substrate stability. We have observed similar variation in the dimensions of the holdfasts in the kelp *Nereocystis luetkeana* (Mert.) Post. and Rupr. in Puget Sound, Washington: holdfasts of plants growing on sand and cobble are broad and spreading, while those of plants attached to rock are small and compact. Similarly, texture of the blades (thin vs leathery) may be a phenotypic response to differing intensities of water motion (Gerard and Mann 1979).

Have our studies brought us closer to answering the questions: Does a single species in the genus *Pelagophycus* occupy both habitats and express its form and life history differently in each? Or have the distinct habitats selected for suites of characters that have become genetically fixed and can be recognized as ecotypes or even separate species? Unfortunately, they have not. Studies on other kelps have reported differences in morphology (reviewed in Mathieson et al. 1981), temperature tolerance (Gerard and DuBois 1988), light responses (Gerard 1988), and responses to nitrogen levels (Espinoza and Chapman 1983; Kopczak et al. 1991) that are the result of genetic differentiation among geographically isolated populations; other studies have demonstrated phenotypic variation, e.g., in nitrogen uptake (Druehl et al. 1989) and morphological responses to water motion (Gerard and Mann 1979). The answers to these questions must be determined experimentally.

Because of low survivorship, our reciprocal transplant experiment could not distinguish between the expression of genotypically fixed and phenotypically plastic morphological traits in the mainland and island populations. We could demonstrate that island plants grew, in the short term, at Point Loma while Point Loma plants did not survive at San Clemente Island. Parker and Bleck (1966) noted a similar response in their San Pedro transplants to Santa Catalina Island. Although the reasons remain unknown, it is possible that, even at depth, the lee island sites may be oligotrophic compared to the mainland, and that Point Loma *Pelagophycus* has physiologically adapted to higher nitrogen levels (cf. Kopczak et al. 1991).

We have evidence that the "P. porra" morph lives longer than the "P. giganteus," morph, and that older age classes of the "P. porra" morph grow substantially faster than those of the "P. giganteus" morph. We also observed intense herbivory on the island transplants at Point Loma that is absent at San Clemente and Santa Catalina Islands (Coyer and Zaugg-Hagland 1982), and from which native juveniles at Point Loma seem to have refuge.

Future Studies

Field studies are limited by time and access to the populations as well as plagued by the vagaries of nature that superimpose huge year-to-year variation and not infrequent disasters on the best laid plans. Crossing experiments in culture to discern reproductive isolation are not promising, due to the well-recognized propensity of kelps to hybridize (e.g., Lewis and Neushul 1994)—even across generic boundaries (Sanbonsuga and Neushul 1978; Coyer et al. 1992). We believe the next step in understanding the systematics of the genus *Pelagophycus* will require molecular tools to understand population genetics, the process by which these morphs have come about.

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The Influence of Topography on the Distribution of Giant Kelp (*Macrocystis pyrifera*) Beds around Santa Catalina Island Using a Geographic Information System

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Abstract. Geographic information systems (GIS) are becoming established tools for analyzing species distributions in relation to environmental factors at various ecological scales. This study utilizes GIS technology to investigate the influence of terrestrial and submarine topography on the distribution of giant kelp, *Macrocystis pyrifera*, (Laminariales, Lessoniaceae) around Santa Catalina Island. For this paper, a single kelp distribution map was chosen to test procedures that will eventually be applied to a series of temporally distinct maps covering a period of about 80 years. A digital elevation model (DEM) and digital bathymetric model (DBM) for the island were generated. Several additional layers were produced from the DEM and DBM including slope, aspect and hillshading images. Kelp distribution was then evaluated statistically relative to several factors influenced by topography including depth, submarine slope, submarine aspect (storm exposure), topographic relief and solar illumination (hillshading) patterns. Clear relationships between observed kelp bed distribution and environmental factors related to topography were apparent. However, it is difficult to isolate the effect of individual factors due to their synergistic nature, the fact that they are often closely linked, and the lack of comprehensive field sampling.

Keywords: Phaeophyta; Laminariales; Lessoniaceae; Channel Islands; sediment; solar irradiance.

Introduction

This study utilizes geographic information systems (GIS) technology to investigate island and submarine topography as factors influencing the distribution of giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island. A GIS is an effective tool for studying the environmental factors responsible for marine species distributions on landscape and other ecological or biogeographic scales (Welch and Remillard 1988; Meaille and Wald 1990). Santa Catalina Island offers an excellent opportunity for investigation due to its varied topography and geographic orientation. The windward and leeward coasts, combined with locally irregular coastlines, present a wide spectrum of submarine aspects, slopes and depths and corresponding exposures to storms, swell, light, and wind.

Macrocystis plays an important role in the marine environment of our offshore islands by providing food and habitat for a wide range of marine life. Physical factors affecting the distribution of kelp include exposure to storms and other water motion, irradiance and spectral distribution, bottom relief, substrate type, water temperature, nutrients and sediments (North 1971; Dean and Jacobsen 1983; Foster and Schiel 1985). Biological factors include grazing by invertebrates and fish, self shading, encrusting growth, competition from other algae and "black rot" (North 1971; Foster and Schiel 1985).

Macrocystis is found in depths ranging from the shallow subtidal to 120 ft or more, but most commonly in depths less than about 60 ft in turbid coastal waters (Mel 1977; Neushul Mariculture Inc. 1981; Foster and Schiel 1985). *Macrocystis* generally requires rocky substrate along more exposed coasts (North 1991), but may establish on soft substrate in quiet waters where burial by sediment is not a problem (North 1971).

Kelp forests are best developed in areas protected from heavy wave surge or storms (North 1968). Such conditions prevail on the gently sloping mainland continental shelf protected by the offshore islands. The steep submarine slopes off Santa Catalina may be less ideal even though the water is clearer and free from pollution.

North (1991) outlined a seasonal cycle in physical factors influencing kelp distribution such as storm regime, daylength, water temperature, wind, rainfall, and nutrient enrichment due to upwelling or terrestrial runoff. Such changes in the physical environment may affect juvenile and adult stages of *Macrocystis* differently.

The current study focuses on a general description and a multi-variate characterization of some physical factors affecting kelp bed distribution around Santa Catalina Island. The test hypothesis was to investigate the influence of differences due to topography on kelp distribution between the exposed windward and more protected lee-