Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient

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ABSTRACT: Sporophyte recruitment, holdfast growth, and mortality of giant kelp *Macrocystis pyrifera* were measured seasonally on permanent transects at 3 sites (protected, intermediate, and exposed) along a wave exposure gradient on the Monterey Peninsula, central California (USA) between 1988 and 1991 The constant presence of cold, nutrient-rich water and the relative absence of other kelps and large grazers allowed the dynamics of *M. pyrifera* populations to be examined under conditions in which wave exposure was highly variable and influences of other abiotic and biotic factors were minimized. Recovery of *M. pyrifera* populations from decreased adult density (presumably due to storm-induced mortality; adult density was negatively correlated with storm activity) was a 2-stage process requiring the establishment of juvenile populations and conditions suitable for juvenile growth to adult size. Sporophyte recruitment was negatively correlated with *M. pyrifera* canopy cover, and thus appeared to be related to irradiance. Recruitment was low and continuous under a temporally stable *M. pyrifera* canopy at the protected site. At the intermediate and exposed sites, canopy cover was more variable, canopy loss was greater, and durations of low canopy cover were longer than at the protected site, resulting in episodic sporophyte recruitment. These distinct patterns in sporophyte recruitment resulted in continuous juvenile populations at the protected site and intermittent juvenile populations at the intermediate and exposed sites. Growth of juveniles to adult size required additional irradiance probably due to greater light requirements for juvenile growth than for sporophyte recruitment. We observed that juveniles grew to adult size when canopy cover was low and adults were below a threshold density estimated at ~10 plants 100 m^{-2}, but juveniles also occasionally grew to adult size following periods of low canopy cover only. Episodic sporophyte recruitment at the intermediate and exposed sites resulted in decreased coincidence of the 2 recovery stages; adult densities were often decreased below threshold prior to the establishment of juvenile populations. Recovery time, that required by populations to return to densities above threshold, was equal to the time lag between occurrence of the 2 recovery stages and was therefore greatest at the more exposed sites. Comparisons between central and southern California *M. pyrifera* populations suggest that by altering recovery time, variable frequency and magnitude of storm disturbance may result in different periodicities of adult population cycles.

KEY WORDS: Giant kelp · *Macrocystis pyrifera* · Wave exposure · Demography · Recruitment · Recovery

INTRODUCTION

Recent investigations of the population dynamics of giant kelp *Macrocystis pyrifera* (hereafter *Macrocystis*) have addressed the effects of various abiotic (e.g.

water motion, temperature, nutrients, and light) and biotic (e.g. competition, grazing, and self-shading) factors on the different life history stages of the species (Foster 1982, Dayton et al. 1984, 1992, Foster & Schiel 1985, Dean & Jacobsen 1986, Deysher & Dean 1986, Dean et al. 1989, Reed 1990). Most of these studies, however, have been done in regions where several limiting factors naturally co-vary. For example, temperature and nutrient levels co-vary in southern California (Jackson 1977, Zimmerman & Robertson 1985),

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and their effects on *Macrocystis* during episodic El Niño events often are confounded by increased frequency and magnitude of storm disturbance (Tegner & Dayton 1987). Under such circumstances, it may be impossible to isolate the effects of individual factors or their interactions on *Macrocystis* populations.

Although many studies have addressed the effect of wave exposure on macroalgal populations, most have done so with qualitative estimates of wave exposure. Quantitative estimates may provide both an unbiased assessment of among-site differences in wave exposure, as well as an accurate temporal record of wave activity (i.e. storms). Seymour et al. (1989) were the first to quantify wave exposure for estimating mortality of *Macrocystis* due to waves. They observed that increased horizontal orbital velocities corresponded with increased mortality of *Macrocystis* in southern California. Along the Monterey Peninsula, where a gradient in storm disturbance is thought to have a strong role in regulating macroalgal community structure (Foster 1982, Kimura & Foster 1984, Reed & Foster 1984, Harrold et al. 1988), quantification of temporal and spatial variability in wave activity may provide a good correlative test of the effect of wave exposure on *Macrocystis* populations.

The nearshore environment of the Monterey Peninsula offers a unique setting to study the effects of water motion on population dynamics of *Macrocystis*. Large magnitude storm disturbance occurs frequently in central California; some regions experience high orbital velocities (large, high frequency waves) during much of the year. This is in sharp contrast to the large magnitude but low frequency storm disturbances described for southern California (Seymour et al. 1989). Furthermore, strong upwelling and tidal flushing from nearshore submarine canyons result in the presence of cold, nutrient-rich water throughout the year (Traganza et al. 1981, Breaker & Broenkow 1994). Temperatures along the Monterey Peninsula rarely exceed those in southern California which were observed to be detrimental to *Macrocystis* reproduction (Deysher & Dean 1986), juvenile growth (Kopczak et al. 1991), or adult growth (Zimmerman & Robertson 1985). Also, since the re-establishment of sea otter populations along this coast in the late 1960s, the effect of sea urchin grazing on *Macrocystis* populations along the Monterey Peninsula has been minimal and isolated, the last documented episode occurring in 1986 (Watanabe & Harrold 1991). Finally, Harrold et al. (1988) observed that the understory stipitate kelp *Pterygophora californica*, a common competitor with *Macrocystis* for light and space (Dayton et al. 1984, 1992, Reed & Foster 1984), was sparsely distributed along the north coast of the Monterey Peninsula. In this context, only intra-specific competition and storm distur-

bance remain as the primary factors regulating *Macrocystis* populations in this region (Kimura & Foster 1984, Harrold et al. 1988).

Our objectives were (1) to examine the relationship between wave exposure and population dynamics of *Macrocystis* by comparing recruitment, holdfast growth, and mortality of its macroscopic life history stages at 3 sites along a wave exposure gradient on the Monterey Peninsula, central California, and (2) to study the response (i.e. recovery) of *Macrocystis* populations to decreased adult density. Lastly, we compared our results to previous work on *Macrocystis* in southern California and offer a potential explanation for the divergent patterns in population dynamics observed among central and southern California *Macrocystis* populations.

METHODS

Study sites. Three study sites were chosen along a putative wave exposure gradient on the Monterey Peninsula (Harrold et al. 1988) (Fig. 1): Site A (most protected), Site B (intermediate), and Site C (most exposed). All 3 sites occurred along 8.5 km of coastline from the protected, southern shore of Monterey Bay to the exposed outer coast of the Monterey Peninsula. Study sites were selected to be as similar as possible in all aspects except exposure to waves. However, each site was distinctive in its physical attributes (Fig. 1). The substratum at all sites consisted of granodioritic outcrops surrounded by medium- to coarse-grained sand and shell rubble; sand cover was low (10 to 15%)
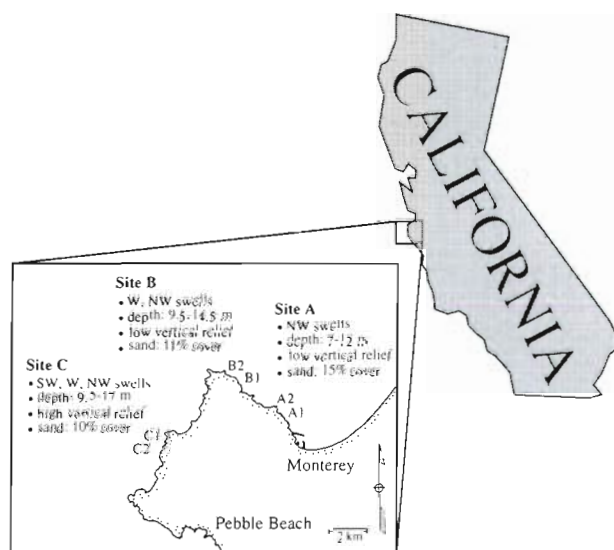

Fig. 1. Locations and physical attributes of study sites. X1, X2 indicate stations within sites

at all sites (Harrold et al. 1988). The biological communities characterizing each site were described in detail in Harrold et al. (1988). Briefly, *Macrocystis* was found at all 3 sites. Bull kelp (*Nereocystis luetkeana*) and understory kelps (*Laminaria setchellii* and *Pterygophora californica*) were found in low densities and only at Site C (maximum densities between 1988 and 1991; 0.01 *N. luetkeana* m^{-2}, 0.25 *L. setchellii* m^{-2}, 1.10 *P. californica* m^{-2}). Fleshy red algae were more abundant at Sites A and B than at Site C (approx. 45, 30, and 10% cover, respectively), whereas geniculate coralline algae were less abundant at Sites A and B than at Site C (approx. 15, 20, and 30% cover, respectively).

Two sampling stations, placed between 100 m and 300 m apart, were established at each site (Stn A1, A2, etc.; Fig. 1). Each station consisted of a 2 × 50 m swath placed parallel to shore and marked with permanent stainless steel eyebolts embedded in the rock substratum with Splash-Zone® underwater epoxy. The swaths were defined by marked lead lines attached to the eyebolts. Lead lines were removed between sampling periods.

Wave exposure and bottom temperature. Significant wave height (average height of 1/3 largest waves) and dominant wave period were obtained from a permanent pressure transducer (i.e. continuous record) anchored at Site A (Stn A1; 10 m depth) and portable pressure transducers anchored at Sites B and C (Stns B1 and C1; 15 m depth). Significant wave height was calculated as 4 × standard deviation of the pressure record (Bowden 1983) after correcting for the effect of high frequency attenuation (W. Broenkow pers. comm.) and a non-static water column (Denny 1988). Significant wave height was measured 4 times daily at Site A and 3 times daily at Sites B and C, and averaged to estimate mean daily significant wave height at each site. Instrument failure and short battery life resulted in discontinuous data records from the portable pressure transducers at Sites B and C. Regression relationships between these records and the continuous record from the permanent pressure transducer at Site A were obtained for mean daily significant wave height estimates (see 'Results'); missing data at Sites B and C were interpolated from the continuous Site A data using the regression equations. Horizontal orbital velocity (m s^{-1}) at the surface was estimated from mean daily significant wave height and dominant wave period using linear wave theory (Denny 1988: p. 51). Weekly maximum horizontal orbital velocities were determined for all 3 sites. An additional portable pressure transducer was placed next to the permanent pressure transducer at Site A for 33 d to calibrate the 2 sensors. Bottom temperature was recorded simultaneously with wave data and averaged daily at each site.

Analysis of covariance (ANCOVA) was used to test for significant among-site differences in wave exposure. ANCOVA compared the slopes of regressions between significant wave heights measured by the permanent sensor at Site A and each of the portable sensors at Sites A, B, and C (dependent variable, significant wave height measured by portable sensors; independent factor, site; covariate, significant wave height measured by the permanent sensor at Site A). Among-site differences in significant wave height were tested using Bonferroni-corrected contrasts of the site × covariate interaction term (SYSTAT 1992). Among-site differences in ANCOVA residuals were not significant using analysis of variance, indicating that the assumption of homogeneity of variances was met.

Canopy cover. To estimate the extent of self-shading by adult *Macrocystis*, infrared aerial photography was used to determine canopy cover over each station (EcoScan, Watsonville, CA). Photographs were taken using infrared film (Ektachrome, Kodak) from an altitude of 2500 m during periods of similar tidal, sea and weather conditions. Surveys were conducted monthly in 1988 and 1989, bimonthly in 1990, and quarterly in 1991. Canopy maps were created by projecting transparencies onto 1:28000 scale baseline maps. Video images of the maps were digitized and percentage canopy cover was determined within 1 ha (100 × 100 m) plots placed directly over the location of each station. We were unable to differentiate between *Macrocystis*, *Nereocystis luetkeana*, and *Cystoseira osmundacea* canopies using this technique. However, field surveys indicated that the density of *N. luetkeana* was nearly zero at all sites, and *C. osmundacea* reproductive fronds only reached the surface during summer at Site A.

Demography. We defined sporophyte recruitment as the appearance of sporophytes large enough to tag (approx. 10 cm tall). Sporophytes were considered recruits only during the sampling period that they were first tagged. Generally, recruits were assumed to be the result of spore settlement within 3 mo of tagging (Deysher & Dean 1986); slow-growing recruits, however, may have resulted from spore settlement >3 mo prior to tagging. The growth of young sporophytes to adult size (>14 cm holdfast diameter, see 'Results') was defined as 'adult recruitment', and these individuals were referred to as 'new adults'. Young sporophytes that were observed on more than 1 sampling period (i.e. non-recruits) but had not reached adult size (i.e. had holdfast diameters ≤14 cm) were considered juveniles.

All swaths were sampled quarterly during each season for 3 yr from fall 1988 to fall 1991. All *Macrocystis* sporophytes were counted within the swaths and tagged to

determine recruitment, holdfast growth, and mortality. Tags consisted of small plastic cable ties with numbered plastic labels fitted loosely below the stipe dichotomy. When sporophytes began forming haptera and could support larger tags, the smaller ones were replaced; experiments indicated that tag loss was rare. Tags were also replaced as they became overgrown with haptera, and each sporophyte was tracked until its death (loss of all fronds and decomposition of holdfast) or disappearance from the swath. Sporophyll condition (with or without developed sori) was determined for all tagged sporophytes present from winter 1990/91 to fall 1991, and was used to estimate the size when sporophytes reached adulthood (i.e. became reproductive). Spearman's rank correlation (r_s) was used to test for linear relationships among orbital velocity, canopy cover, and various demographic variables, as the assumption of bivariate normality was rarely met; p-values were adjusted for the total number of correlation tests using Bonferroni corrections.

Holdfast growth. Since holdfast basal diameter is probably a good estimate of the strength of sporophyte attachment to the substrate, we evaluated holdfast growth rates. Basal diameters were measured using small plastic calipers for holdfasts ≤10 cm diameter and large (1 m long) aluminum calipers for holdfasts >10 cm. Holdfast diameters of all tagged sporophytes were measured during each sampling period. Holdfast growth rates [(final diameter – initial diameter)/age at death] were determined for all sporophytes that recruited to the swaths during the study. Each sporophyte was treated as an independent replicate of station, and individual growth rates were compared among sites with nested ANOVA (station nested within site) and Bonferroni-corrected contrasts. When $\log(x + 0.1)$ transformed, holdfast growth rates met assumptions of normality and homoscedasticity (Cochran's test).

RESULTS

Wave exposure and bottom temperature

The 3 sites differed significantly in wave exposure. The relationships between mean daily significant wave height estimated by the portable pressure transducers placed at each site (dependent variables) and the permanent pressure transducer at Site A (independent variable) were highly linear (Fig. 2; Table 1). The y-intercepts were near zero, suggesting that among-site differences in the relationship between the dependent and independent variables were due primarily to the slopes. Slopes of the relationships increased significantly from Site A to Site C (ANCOVA comparison of slopes, Site A < Site B < Site C; Table 1). Mean daily significant wave height was 3.0 times higher at Site C than at Site A, and 1.7 times higher at Site B than at Site A, the regression equations explaining 85 and 92% of the variation in wave height, respectively. The lower r^2 value for the Site C relative to Site A comparison was due to the inability to isolate incident swell direction in the analysis, as only Site C was exposed to SW swells. A highly significant linear relationship with an $r^2 = 0.959$ and a slope near unity was observed when both sensors were simultaneously placed at Site A, indicating that the permanent and portable pressure transducers measured wave height similarly.

Time series of horizontal orbital velocity were nearly identical at all 3 sites, differing only in magnitude

Table 1. Regression and ANCOVA analyses of among-site differences in wave exposure. Regressions were used to predict significant wave height measured by portable sensors placed at Sites A, B, and C from significant wave height measured by the permanent sensor placed at Site A. Notice the near 1:1 relationship when both sensors were placed at Site A, indicating that the 2 sensors were estimating significant wave height similarly. ANCOVA tested for among-site differences in regression slopes using Bonferroni-corrected contrasts of the interaction term (SYSTAT 1992); different slopes indicated different wave exposures. For example, on a given day significant wave height was 3 times greater at Site C than at Site A. Residual analysis indicated the assumption of homogeneity of variances was met

Regressions Location of portable sensor	Intercept (±SE)	Slope (±SE)	r^2	n	p
Site A	−0.02 (0.02)	0.97 (0.04)	0.959	33	≤0.0001
Site B	−0.03 (0.01)	1.76 (0.03)	0.924	355	≤0.0001
Site C	0.08 (0.02)	3.01 (0.04)	0.854	1075	≤0.0001

ANCOVA (H_0: regression slopes are equal) Source	df	MS	F	p
Site	2	0.216	4.653	0.01
Covariate (wave height)	1	27.589	593.481	≤0.0001
Site × Covariate	2	9.843	211.735	≤0.0001
Error	1457	0.046		

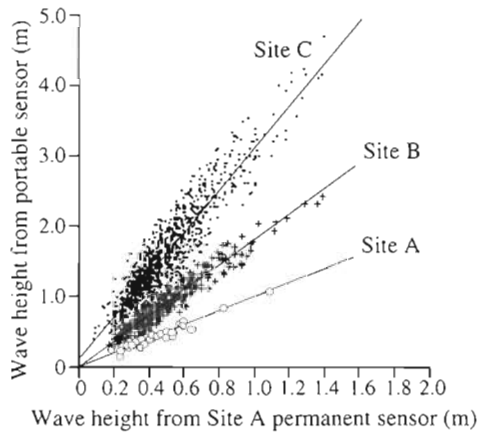| Between-site contrasts of Site × Covariate interaction Source	df	MS	F	p
Site A vs Site B	1	1.598	34.739	≤0.0001
Site B vs Site C	1	66.733	1450.72	≤0.0001
Error	1457	0.046		

Fig. 2. Linear relationship between significant wave height measured by a permanent sensor (continuous record) at Site A and portable sensors (discontinuous records) at Sites A, B, and C. Parameters of linear regressions are given in Table 1

Fig. 3. Weekly maximum horizontal orbital speed measured at Sites A, B, and C

(Fig. 3). Orbital velocities peaked during winter/spring indicating high storm activity, and were lowest during summer months. Highest weekly maximum values for each site occurred during winter 1989/90 (Site A, 1.34 m s^{-1}; Site B, 1.86 m s^{-1}; Site C, 2.84 m s^{-1}), and lowest weekly maximum values occurred during summer 1991 (Site A, 0.36 m s^{-1}; Site B, 0.56 m s^{-1}; Site C, 1.07 m s^{-1}). Although storm activity was highest during winter/spring, periods of increased orbital velocity (i.e. storms) were observed throughout the study. Mean daily bottom temperatures varied among sites, but temperatures were rarely above 15°C at any site during the study and never exceeded 16°C.

Canopy cover

Between-station differences in canopy cover were evident within Site C (i.e. Stns C1 vs C2), but not within Sites A and B (Fig. 4). Canopy cover was negatively correlated with orbital velocity ($r_s = -0.435$, n = 78, p ≪ 0.001; data were average values between sampling periods), though yearly minima in canopy cover at all sites coincided with the first storms after summer (Fig. 3), rather than the most severe storms. Canopy cover was more variable, canopy loss was greater, and the duration of low canopy cover was longer at the more exposed sites than at the protected site. Temporal variability (standard deviation among sampling periods) in canopy cover increased from Stns A1 (16.0%) and A2 (15.1%) to Stns B1 (26.0%) and B2 (25.0%) to Stn C2 (28.3%), but was lowest at Stn C1 (9.1%). Sites B and C typically had lower canopy cover in winter and higher canopy cover in spring and summer than Site A, except for Stn C1 which had low canopy cover throughout the study. Moreover, canopies at Site A, though often very low, persisted
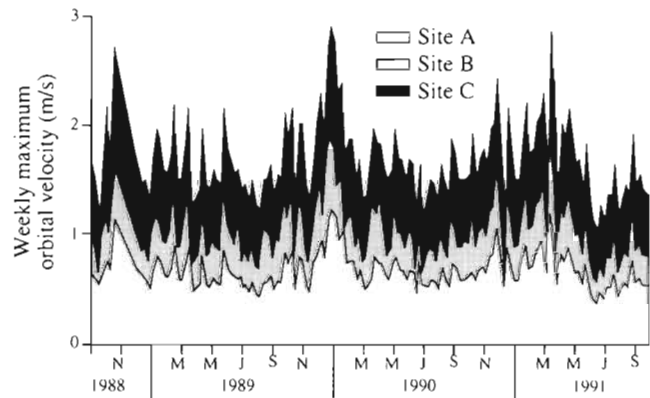
throughout the study whereas canopies at Sites B and C were often absent (e.g. canopy cover was zero at Stn C2 for more than 3 mo in 1990).

Reproduction

The onset of reproductive maturity was used to identify adult *Macrocystis* sporophytes. The first sori appeared over a wide range of holdfast diameters and sporophyte ages (Fig. 5). The analysis was limited to sporophytes that recruited during the study (i.e. of known age) and first developed fertile sori between
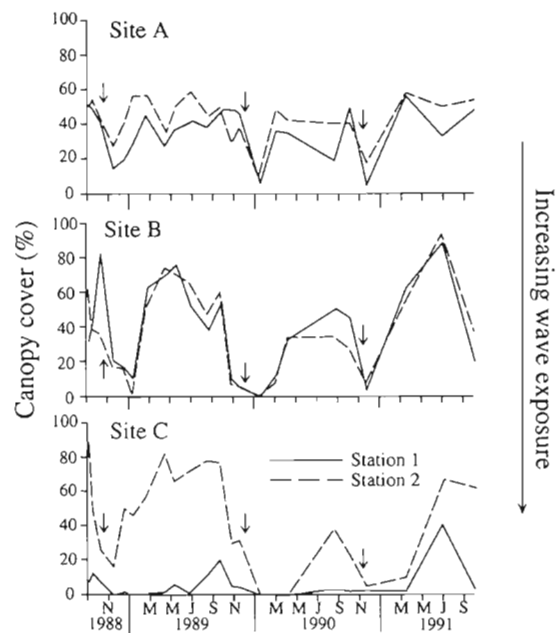

Fig. 4. *Macrocystis* canopy cover (%) within each site. Arrows indicate the occurrence of the first storms after summer. Sites are arranged from top to bottom in order of increasing wave exposure
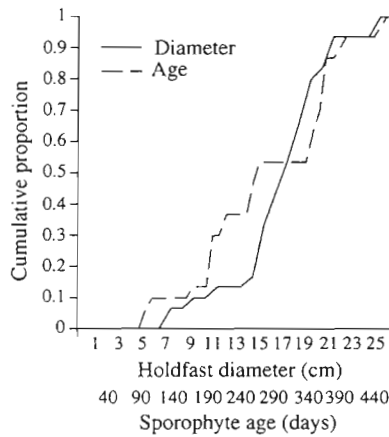
Fig. 5. Cumulative proportion of *Macrocystis* with developed sori as a function of holdfast diameter and sporophyte age, n = 30

winter 1990/91 and fall 1991. Adults were defined as sporophytes with holdfast diameters ≥14 cm due to the sharp increase in reproductive sporophytes with holdfasts larger than this size (only 15% of the sporophytes sampled for sori became reproductive at diameters <14 cm, n = 30). It was not possible to predict reproductive maturity as a function of sporophyte age since there was no obvious increase in the frequency of reproductive sporophytes at any particular age.
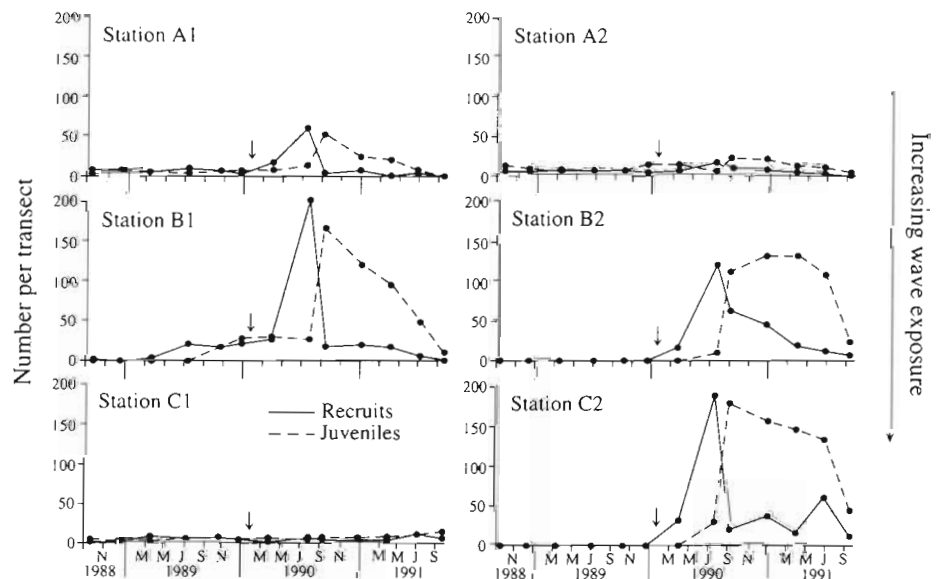
Sporophyte recruitment

Sporophyte recruitment was negatively correlated with canopy cover (r_s = –0.413, n = 72, p ≪ 0.001; canopy cover data were average values between sampling periods); in order to account for the apparent lag between canopy cover loss and subsequent sporophyte recruitment (Figs. 4 & 6), sporophyte recruitment data from a given sampling period were paired with canopy cover data from the previous sampling period. Although the lag between canopy cover loss and subsequent sporophyte recruitment was generally 1 sampling period, it is unknown how often slow-growing recruits resulting from canopy loss during a given sampling period (but too small to tag) contributed to sporophyte recruitment during subsequent sampling periods.

Sporophyte recruitment at Site A was low and continuous during the study (Fig. 6). Low sporophyte recruitment at this site corresponded with a persistent canopy throughout most of the study; canopy cover was less than 20% only briefly, during winter 1989/90, but was never greater than 60% (Fig. 4). Although not continuous, sporophyte recruitment was observed at Stn B1 from spring 1989 until summer 1991, peaking in summer 1990 following massive canopy loss in winter/spring 1990. In contrast, sporophyte recruitment at Stns B2 and C2 was episodic, being zero under dense canopies between the winters of 1988/89 and 1989/90, and also peaking in summer 1990. Sporophyte recruitment at Stns B1, B2, and C2 remained relatively high until fall 1991 corresponding with an extended period of low canopy cover (less than 60% cover at Stn B1 and less than 40% cover at Stns B2 and C2; Fig. 4). Sporophyte recruitment was consistently very low at Stn C1. This station, however, had a minimal surface canopy throughout the study (Fig. 4), suggesting that light limitation by surface canopy was not regulating the magnitude of recruitment at this station.

Fig. 6. Number of *Macrocystis* recruits and juveniles per transect for each station. Recruits were all sporophytes that received their first tag during a given sampling period; juveniles were all sporophytes (excluding recruits) with holdfast diameters <14 cm. Arrows indicate the period of lowest canopy cover at each station. Stations are arranged from top to bottom in order of increasing wave exposure

Juvenile density

As expected, fluctuations in juvenile *Macrocystis* density were similar to the patterns described for sporophyte recruitment (Fig. 6). Juveniles were observed throughout the study at Site A but did not appear at Stn B1 until fall 1989 and Stns B2 and C2 until summer 1990. Thus, continuous sporophyte recruitment resulted in continuous juvenile populations at Stns A1 and A2, whereas episodic sporophyte recruitment resulted in intermittent juvenile populations at Stns B1, B2, and C2. Juvenile densities peaked in fall 1990 at Stns A1, A2, B1, and C2, and in winter 1990/1991 and spring 1991 at Stn B2. As with sporophyte recruitment, juvenile densities were consistently very low at Stn C1 during the study.

Adult density

Among all stations, adult *Macrocystis* density was negatively correlated with orbital velocity (r_s = −0.480, n = 78, p ≪ 0.001; orbital velocity data were average values between sampling periods), and adult mortalities were observed throughout the study (Fig. 7). Further, the appearence of new adults (adult recruitment) during a given sampling period was positively correlated with the density of juveniles from the previous sampling period (r_s = 0.439, n = 72, p ≪ 0.001). Adult *Macrocystis* densities at Stns A1 and A2 ranged from 8 to 25 sporophytes 100 m^{-2} (Fig. 7). In the presence of a continuous juvenile population, decreases in adult densities to less than ~10 sporophytes 100 m^{-2} were followed by adult recruitment (Fig. 7; notice that new adults appeared 1 sampling period after decreases in

adult density). Adult recruitment was also observed at Stn A1 during fall 1990 when adult densities were greater than 10 sporophytes 100 m^{-2} but canopy cover was less than 20%. Adult densities at Stns B1 and B2 ranged from 7 to 34 sporophytes 100 m^{-2}. Again, when juveniles were present, new adults were observed after adult densities decreased to less than ~10 sporophytes 100 m^{-2} (e.g. summer 1990 at Stn B1 and winter 1990/91 at Stn B2) or when canopy cover was low (e.g. winter 1990/1991 at Stn B1). New adults, however, were not observed at Stn B2 when adult density decreased below 10 sporophytes 100 m^{-2} and juveniles were not present (e.g. spring/summer 1990). The adult population at Stn C2 had constant attrition in the absence of a juvenile population, from 15 to 18 sporophytes 100 m^{-2} in fall 1988 to 4 sporophytes 100 m^{-2} in spring 1990. Although adult densities had been below 10 sporophytes 100 m^{-2} since summer 1989, new adults were only observed at C2 when adult densities less than 10 sporophytes 100 m^{-2} coincided with the presence of a juvenile population. High adult recruitment during summer 1991 increased adult density to levels comparable to those observed at the beginning of the study. The adult population at Stn C1 was not as dynamic as at the other stations. Adult density decreased from 10 sporophytes 100 m^{-2} to 0 sporophytes 100 m^{-2} between spring 1989 and spring 1991 during which only 2 new adults were observed.

Holdfast growth

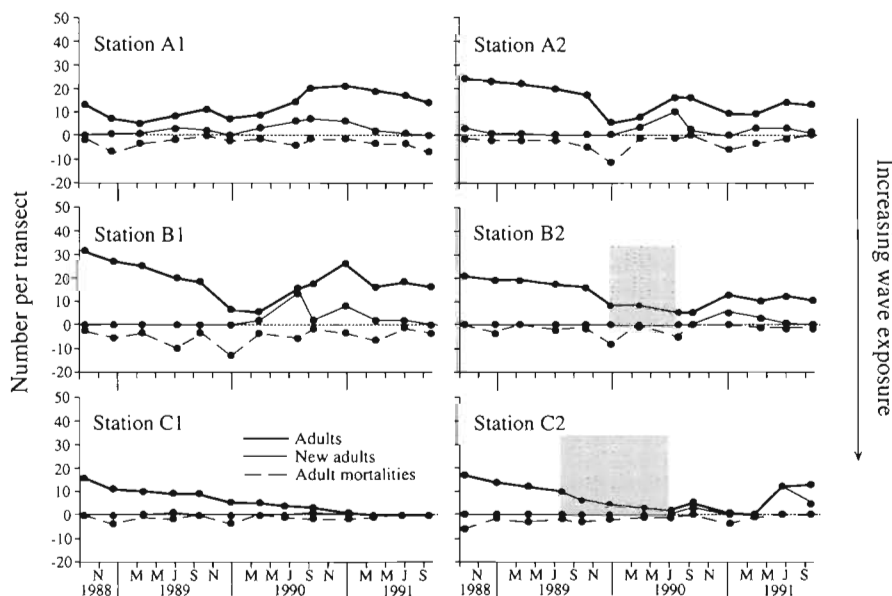Holdfast growth rates decreased with increasing wave exposure. The nested factor (stations within

Fig. 7. Number of *Macrocystis* adults, new adults, and adult mortalities, per transect for each station. New adults were sporophytes that first attained holdfast diameters ≥14 cm during each sampling period; adult mortalities were sporophytes whose absences (i.e. deaths) were recorded during each sampling period. Shaded regions at Stns B2 and C2 indicate the time period between a decrease in adult density to below 10 plants 100 m^{-2} and the establishment of a juvenile population, and represent the minimum lag time for recovery of adult populations; Stns A1, A2, B1, and C1 had established juvenile populations by the time adult densities had decreased to below 10 plants 100 m^{-2}. Stations are arranged from top to bottom in order of increasing wave exposure

sites) was insignificant [Station(Site); F = 0.15; df = 3,387; p = 0.927] so the sums-of-squares and degrees of freedom for the nested factor and error term were pooled (Site; F = 29.01; df = 2,390; p < 0.0001). Mean growth rates (± SE) at Site A (0.47 ± 0.05 mm/day; n = 106) were significantly higher than at Site B (0.21 ± 0.03 mm d^{-1}; n = 165) (Bonferroni-corrected p < 0.0001), but the difference in growth rate between Site B and Site C (0.17 ± 0.02 mm d^{-1}; n = 144) was not significant (Bonferroni-corrected p > 0.3).

DISCUSSION

Dynamics of *Macrocystis* populations

Deysher & Dean (1986) observed that sporophyte recruitment in southern California occurred only at temperatures below 16.3°C and irradiances above 0.4 mol photons m^{-2} d^{-1}. Due to extensive seasonal upwelling and close proximity to offshore canyons, however, the Monterey Peninsula rarely experiences temperatures higher than 15°C (Traganza et al. 1981, Breaker & Broenkow 1994, this study). At our sites, sporophyte recruitment was negatively correlated with canopy cover, and thus irradiance was probably the main factor limiting recruitment during our study. Further, canopy cover was negatively correlated with orbital velocity. At the protected site (which experienced relatively low orbital velocities throughout the study), stable canopies with maximum cover less than 60% probably stimulated the low continuous sporophyte recruitment observed; irradiance may never have been low enough to inhibit sporophyte recruitment nor canopy cover decreased long enough to produce high recruit densities. As wave exposure increased (i.e. from Site A to Site C), surface canopy cover became more variable and sporophyte recruitment became episodic. Long periods of decreased canopy cover (e.g. winter/spring 1990) were followed by massive sporophyte recruitment at Stns B1, B2, and C2. These distinct patterns in sporophyte recruitment resulted in continuous juvenile populations at the protected site and intermittent juvenile populations at the intermediate and exposed sites (except Stn C1).

Additional irradiance was apparently required for growth of juveniles to adult size. Dean & Jacobsen (1986) demonstrated that the compensation point for juvenile growth of *Macrocystis* in southern California was ~0.7 mol photons m^{-2} d^{-1}. Therefore, increased irradiance levels due to decreased canopy cover, although stimulating sporophyte recruitment, may not have been sufficient for juvenile growth to adult size. Adult recruitment at our sites generally occurred when canopy cover was low and adult densities were below ~10 sporo-

phytes 100 m^{-2}; adult recruitment occasionally occurred when canopy cover was low and adult densities were above ~10 sporophytes 100 m^{-2}. Therefore, we propose the idea of a 'threshold density', below which irradiance becomes available for adult recruitment. Interestingly, our estimated threshold density of ~10 sporophytes 100 m^{-2} was the same as that predicted in a model by Burgman & Gerard (1990) and similar to carrying capacities measured by Dayton et al. (1992) for the Pt. Loma kelp bed (~8 to 15 sporophytes 100 m^{-2}). Additional studies utilizing experimental manipulations will help clarify the relationship between adult density, canopy cover, and adult recruitment.

Variability in population recovery rate was observed among our study sites. The protected site had relatively stable canopies, and continuous sporophyte recruitment resulting in continuous juvenile populations throughout the study. Decreases in adult density below threshold in conjunction with canopy loss appeared to stimulate immediate growth of juveniles to the adult size class, resulting in rapid recovery (within the 3 mo between sampling periods). Recovery of adult populations at the intermediate and exposed sites was slower. Increased magnitude of winter storms at the intermediate and exposed sites apparently caused greater subsequent canopy loss (extent and duration) than at the protected site. Also, greater increases in canopy cover were observed at the intermediate and exposed sites during periods of decreased wave exposure. J. Watanabe & R. Phillips (unpubl. data) observed that frond growth rates at Stn C1 were low during winter and increased rapidly by spring, often to levels greater than those at Stn A2. Thus, higher frond growth rates may have caused the more extensive spring canopies observed at the intermediate and exposed sites than at the protected site. This would result in more severe extremes and seasonal variability in irradiance as wave exposure increased. The episodic sporophyte recruitment observed at the intermediate and exposed sites was probably a response to these irregular light conditions and resulted in intermittent juvenile populations. The absence of juvenile populations following periods of low canopy cover and decreased adult density below threshold resulted in a lag between the occurrence of conditions suitable for juvenile growth and adult recruitment, delaying recovery (i.e. increasing recovery time) at the intermediate and exposed sites (Fig. 7; note Stn C1 did not recover during the study).

The significant decrease in holdfast growth rates with increasing wave exposure could have potentially intensified the positive relationship between recovery time and wave exposure. McCleneghan & Houk (1985) observed significant decreases in hapteral division with the experimental removal of surface canopy. They

suggested that translocation of photosynthates was diverted to production of new fronds rather than hold-fast growth. This may explain the low holdfast growth rates at our more exposed sites where canopy loss was massive. However, although decreased holdfast growth probably weakened substrate attachments at the intermediate and exposed sites, high adult mortalities at the protected site do not support a relationship between holdfast growth rates and recovery time.

The dynamics of the *Macrocystis* population at Stn C1 were different than those described above for the other stations. In the presence of low canopy cover, a small but continuous juvenile population, and constant decreases in adult density, recovery of the adult population was not observed. Although we are unable to account for this discrepancy, it may be that the conditions at Stn C1 during this study were simply unsuitable for growth of juveniles to adult size. We suspect that Stn C1 may be the most exposed of the 6 stations, and that the lack of adult recruitment events at this station was caused by a higher turnover rate of juveniles due to extreme water motion. Stn C1 had a total of 51 juveniles with the potential to grow to adult size during the entire study, compared to 647 juveniles at Stn C2. Consequently, adult recruitment at Stn C1 may not just require periods of increased irradiance (the putative mechanism for stimulating growth of juveniles to adult size at the other stations), but also periods of decreased water motion. Additional work is needed to determine what factors limit adult recruitment at Stn C1

We suggest that the dynamics of *Macrocystis* populations at our study sites in central California are best represented by a 2-stage recovery process: successful recovery requires the coincidence of a juvenile population with conditions suitable for growth of juveniles to adult size. We originally hypothesized that adult mortality (i.e. disturbance) due to wave exposure would be the dominant factor regulating the population dynamics of *Macrocystis* along the Monterey Peninsula. It is now apparent, however, that the *Macrocystis* populations at our study sites are fluctuating more due to sporophyte recruitment events than adult mortalities. Furthermore, we propose that the actual role of storm disturbance in the dynamics of *Macrocystis* populations may be in altering the coincidence of juvenile populations and suitable juvenile growth conditions.

Comparisons with southern California *Macrocystis* populations

The utility of examining recovery of *Macrocystis* as a 2-stage process is also evident from studies of the Del Mar, Pt. Loma, and San Onofre kelp forests in southern California. Dayton et al. (1992) found that 'every release in *Macrocystis* canopy cover was followed by a strong recruitment event'. Large magnitude storms are infrequent in southern California (Seymour et al. 1989) resulting in episodic recruitment events occurring on a cycle of 2 to 5 yr (approximate frequency of storm disturbance), longer than the 2 to 3 yr necessary for self-thinning to decrease adult populations to carrying capacity (i.e. threshold density) (Rosenthal et al. 1974, Dean et al. 1989, Dayton et al. 1992, Southern California Edison Company 1993). Thus, in addition to stimulating sporophyte recruitment (via decreased canopy cover), these storms probably simultaneously increased irradiance required for growth of juveniles to adult size (via decreased adult density). In the presence of few adult sporophytes, irradiance levels would be high long enough for adult recruitment to increase adult density beyond threshold, resulting in rapid recovery. When sporophyte recruitment was stimulated by canopy removal during periods of high adult density, however, adult recruitment was unsuccessful (e.g. following 1983 winter storms; Dayton et al. 1992).

Though the recovery process appeared similar, recovery time differed between these southern and central California *Macrocystis* populations. Recovery time at all sites appeared equal to the time between the establishment of juvenile populations and subsequent growth of juveniles to the adult size class. Large magnitude, low frequency storm disturbances in southern California resulted in rapid recovery, as previously described. Small magnitude, high frequency storm disturbance at our protected site on the Monterey Peninsula allowed for continuous sporophyte recruitment and a continuous juvenile population. Subsequent adult mortalities that decreased adult density below threshold also caused rapid recovery. As wave exposure increased, the magnitude of seasonal storm disturbance increased causing extreme maxima and minima in canopy cover and episodic recruitment similar to southern California. Decreases in adult density below threshold prior to sporophyte recruitment events, however, resulted in less frequent coincidence of juvenile populations and sufficient juvenile growth conditions, and caused recovery to be delayed.

Nisbet & Bence (1989) modeled density fluctuations in adult *Macrocystis* in southern California based on the regulation of sporophyte recruitment by irradiance, temperature, and unknown stochastic factors. Their results suggest that differences in dynamics between southern and central California *Macrocystis* populations were due to annual recruitment bursts caused by 'high mortality and strong seasonal forcing' in central California. Our research, however, suggests that large magnitude, high frequency storm distur-
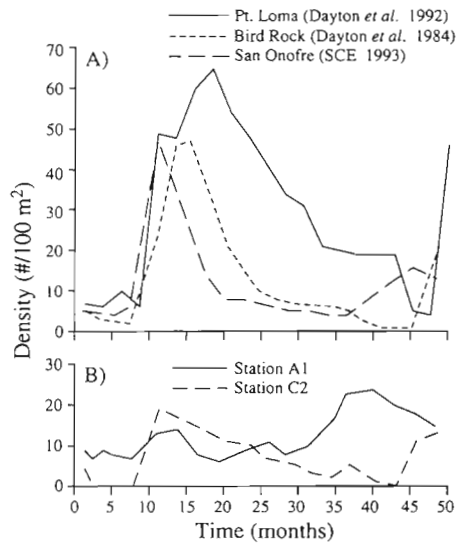
Fig. 8. Adult *Macrocystis* density (no. sporophytes 100 m^{-2}) at (A) 3 sites in southern California and (B) Stns A1 and C2. Populations at the southern California sites and Stn C2 fluctuated on cycles of 2 to 5 yr, while the population at Stn A1 fluctuated on a more frequent cycle (SCE: Southern California Edison Company)

bance along the Monterey Peninsula actually produced episodic (i.e. less frequent than annual) sporophyte recruitment similar to that observed in the large magnitude, low frequency storm-disturbed *Macrocystis* populations of southern California. Episodic recruitment at Del Mar (Rosenthal et al. 1974), Pt. Loma (Dayton et al. 1984), San Onofre (Dean et al. 1989, Southern California Edison Company 1993), Catalina Island (Dayton et al. 1992), and the exposed site in this study, all resulted in long-period adult population cycles on the order of 2 to 5 yr (Fig. 8). Specifically, in southern California, where there appears to be no lag between the occurrence of the 2 recovery stages, periodicity of population cycles was determined by the frequency of large magnitude storm disturbances; in central California, where many large magnitude storm disturbances occur each year, periodicity of population cycles was determined by the lag between the occurrence of the 2 recovery stages. In contrast, continuous recruitment at the protected site in this study produced a continuous juvenile population and the resulting adult population fluctuated near the threshold density (Fig. 8B; as far as we know, this is the only example of *Macrocystis* fluctuating on a short-period cycle, although computer simulations by Burgman & Gerard (1990) predicted this for southern California populations). Consequently, frequency of sporophyte recruitment does appear to regulate adult density fluctuations in California *Macrocystis* populations, by maintaining juvenile populations. The effects of magnitude and frequency of storm disturbance on the coincidence of juvenile populations and conditions suitable for growth of juveniles to adult size, however, appears to vary between southern and central California *Macrocystis* populations.

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