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COUPLING PROPAGULE OUTPUT TO SUPPLY AT THE EDGE AND INTERIOR OF A GIANT KELP FOREST

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ABSTRACT

Propagule dispersal is fundamental in regulating the strength of demographic and genetic interactions between individuals both within and among populations. I studied spatiotemporal variability in propagule (zoospore) supply of a continuously reproducing seaweed, giant kelp *Macrocystis pyrifera*, to examine: (1) the extent to which local zoospore production is coupled to (correlated with) temporal variability in zoospore supply; and (2) spatial variability in the strength of such coupling. *Macrocystis pyrifera* planktonic zoospores were quantified from seawater samples pumped on numerous dates in 1999 from just above the substratum at various sites in the Point Loma kelp forest, southern California, USA. Zoospore collections were made at a site in the forest interior approximately three times per month from late February through mid November. Sample collection overlapped with complete demographic surveys of the local population (100 m^2) to determine local reproductive output. Temporal variability in zoospore supply was strongly correlated with relative changes in the density and size structure of local reproductive adult sporophytes; 76% of variability in zoospore supply was explained by local reproductive output. This tight coupling between zoospore supply and local reproduction appeared to be driven by low displacement, oscillating currents in the forest interior due to the cumulative drag of adult sporophytes, keeping zoospores close to their release site. High coupling between zoospore supply and local reproduction was validated at two additional interior sites separated by 1 km; 78% of variability in zoospore supply was explained by local reproductive output at these sites. Due to lower sporophyte densities, however, the forest edges experienced rapid, uni-directional currents that appeared to transport zoospores far from their release site, effectively de-coupling zoospore supply from local reproduction; only 38% of variability in zoospore supply was explained by local reproductive output at these sites. The results suggest that the size of and location within kelp populations is an important determinant of the importance of local reproduction to zoospore supply due to the effects of flow-modification by kelp canopies on zoospore dispersal.

Key words: kelp canopies, flow modification, propagule supply, giant kelp zoospores, *Macrocystis pyrifera*, population dynamics, reproductive coupling, scale-dependent dispersal

Key phrases: local versus remote zoospore production, coupling between zoospore supply and local reproduction, spatiotemporal variability in zoospore supply, kelp canopies modify dispersal

INTRODUCTION

The extent to which species display demographic and genetic structure ultimately depends upon the strength of demographic and genetic linkages (dispersal and gene flow) among constituent populations, individuals, and even life history stages. It has recently been shown that marine species exist along a continuum of population subdivision, with most structured at regional, and sometimes even local, spatial scales (Palumbi 1995, Burton 1998, Bohonak 1999, Grosberg and Cunningham 2000). For organisms that alternate between distinct benthic and planktonic life history stages (e.g. seaweeds and many invertebrates and fishes), recent population dynamics studies have focused on physical/biological interactions that link the two stages. Such “supply-side” studies (*sensu* Lewin 1986) have addressed the importance of the production and supply of planktonic propagules in regulating recruitment, colonization, and connectivity among populations, with most studies focusing on benthic marine invertebrates and fishes (see reviews by Underwood and Fairweather 1989, Gaines and Lafferty 1995, Caley et al. 1996, Underwood and Keough 2001, Hixon et al. 2002). Since the larvae of most non-brooding marine invertebrates and fish are not competent for settlement until some time after release, many remain in the plankton by swimming or buoyancy regulation for weeks to months prior to settlement (e.g. Victor 1991, Young 1995).

For such taxa, the supply of larvae competent for settlement can be de-coupled from local demographic and reproductive processes because the larvae are advected far from the adults that produced them (Roughgarden et al. 1988, Victor 1991, Shanks 1995, Downes and Keough 1998, Wing et al. 1998, Shanks et al. 2000). For other taxa, however, larval behavior and/or physical transport processes (e.g. currents, eddies, or fronts) retain larvae near the site of release, coupling larval supply to local reproduction (Jones et al. 1999, Swearer et al. 1999). As such, marine invertebrate and fish populations are generally considered to be either “open”, with recruitment determined primarily by the supply of larvae from remote locations, or “closed”, with a stronger link to local larval sources (Sale 1991, Gaines and Lafferty 1995, Caley et al. 1996, Cowen et al. 2000, Hughes et al. 2000, Hixon et al. 2002).

The dynamics of kelp populations (brown algae of the order Laminariales) offer an interesting contrast to supply-side models developed for invertebrates and fish. Unlike most larvae, kelp propagules (zoospores) can settle immediately upon release from the adults, with most settlement likely occurring within minutes to days of release (Reed et al. 1992). Kelp zoospore planktonic duration, therefore, depends primarily on the time it takes to reach suitable settlement substrate. Kelp zoospores are small (~3 x 7 μm), with slow swimming speeds (~0.0012 mm/s; Gaylord et al. 2002), and consequently are considered passive planktonic particles. As such, dispersal is thought to be dependent upon the advective and diffusive transport of zoospores to the sea floor, which models predict is regulated primarily by hydrodynamic processes in the water column (Gaylord et al. 2002).

Because they tend to form large aggregations, kelps can modify many physical and biological characteristics of their local environment. Although research at the scale of kelp forests has focused primarily on the effect of canopy shading on algal recruitment and population structure (Dayton 1975, Reed and Foster 1984, Kennelly 1989, Graham et al. 1997, Edwards 1998, Dayton et al. 1999) and the production of particulate and dissolved organic matter (Duggins et al. 1989, Duggins and Eckman 1997), ecologists have long been aware, at least qualitatively, that large kelp forests can also affect ocean currents (Jackson and Winant 1983, Jackson 1997). Large and sessile kelp thalli impose drag on the water and result in the dampening of both along- and across-shore flows within forests, as well as the diversion of currents around forests (Jackson and Winant 1983). In particular, Jackson (1997) found that along-shore currents on the edge of the largest continuous giant kelp (*Macrocystis pyrifera*) forest in southern California (at Point Loma in San Diego County, ~ 1 km wide by 8 km long) were uni-directional and an order of magnitude greater (2.1 ± 9.9 cm/s) than the bi-directional, oscillatory currents in the interior (0.2 ± 2.0 cm/s); across-shore currents were similarly dampened. Although such flow-modification by kelp forests is likely important to kelp population dynamics, previous studies have been limited to the effects of kelp forests on sediment transport and beach nourishment (Elwany and Flick 1996), flow-mediated nutrient transport (Jackson 1997), and sea urchin recruitment (Schroeter et al. 1996).

This study examines whether flow-dampening by giant kelp canopies modifies the coupling/de-coupling of giant kelp zoospore supply to local reproduction, and has implications for current theories of “open” and “closed” marine population dynamics. Given the large minimum size of kelp populations necessary to dampen currents (~100 m diameter; Jackson and Winant 1983), kelp canopy removals across scales broad enough to alter flow were not feasible. Instead, I chose to study canopy effects on giant kelp reproductive coupling by developing simultaneous time series of zoospore production and supply in the Point Loma kelp forest over various temporal and spatial scales. The study design builds upon Jackson’s (1997) thorough quantification of the differences in along- and across-shore currents between the forest interior and its edges. The primary goals were to: (1) estimate the extent to which local giant kelp zoospore production is correlated with temporal variability in zoospore supply in the forest interior; and (2) test the generality of the strength of this relationship between propagule production and supply both within the forest and along its edges.

NATURAL HISTORY OF THE STUDY SYSTEM

Giant kelp exhibits a biphasic life history where adult diploid sporophytes release planktonic flagellated haploid zoospores that ultimately settle upon rocky substrates and germinate into microscopic male or female haploid gametophytes (generally < 100 microns length). Given adequate light and nutrient conditions, gametogenesis and fertilization occur, and a new microscopic sporophyte generation grows to macroscopic size from the female gametophyte. Sporophytes are anchored by perennial holdfasts (often > 5 years duration) that can be up to a meter in diameter and from which many short-lived vegetative fronds (< 6 months duration) grow to the surface (North 1994). In addition to having high productivity (Towle and Pearse 1973), giant kelp fronds can form extensive surface canopies over broad rocky subtidal reefs approximately 6 to 25 meters depth (Foster and Schiel 1985), and in exceptional years the Point Loma giant kelp canopy can have 100% coverage (~8 km^2; Dayton et al. 1992). Experimental studies have demonstrated giant kelp's competitive dominance due to shading by its canopies, and have quantified its underlying role in regulating kelp assemblage structure (Reed and Foster 1984, Dayton et al. 1999). Furthermore, giant kelp population dynamics in southern California are driven primarily by pulses of strong recruitment following physical disturbance (e.g. storms; Dayton et al. 1992) and subsequent self-thinning that ultimately determines giant kelp sporophyte size and density (Dayton et al. 1992, Graham et al. 1997, Tegner et al. 1997). Multiple overlapping cohorts at different stages of self-thinning generally results in high variability in sporophyte size and density at scales less than 10 m (Graham 2002), except during episodic forest-wide disturbances such as ENSO, when broad-scale giant kelp mortality is uniformly high (Edwards 2001).

Aside from the occasional drifting adult sporophyte, zoospores represent the primary giant kelp dispersal stage. Zoospores are released from sporogenous tissue (sori) located on specialized blades (sporophylls) just above the holdfast (~0.5 m off the substrate). Reproductive giant kelp sporophytes can generally be found throughout the year in southern California, except during the height of severe ENSO events, and giant kelp populations in this region can therefore be considered as continuously reproductive (Neushul 1963, McPeak 1981, Graham 1999). Individuals, however, cycle between fertility (sori present) and sterility (sori absent) due to fluctuations in sporophyte biomass (Graham 2002); Reed (1987) demonstrated that biomass of sporophylls was also related to total plant biomass. This vulnerability to biomass loss is apparently due to the low nutrient storage capacity of giant kelp sporophytes (Gerard 1982, North 1994). Therefore, spatial variability in giant kelp reproductive output ultimately reflects the high small-scale variability in sporophyte size and density (Graham 2002).

METHODS

Study sites

The research was done within the central portion of the Point Loma kelp forest located offshore of San Diego, California, USA (Figure 1). This large kelp forest has been extensively studied since the early 1950's (reviewed in North 1971) and has been the site of continuous ecological study since 1971 (Dayton et al. 1984, 1992, 1999, Dayton and Tegner 1984, Tegner et al. 1996, 1997). The kelp forest grows on a submerged rocky terrace that is flat and gradually sloping with isolated regions of high vertical relief (rocks, pinnacles, and ledges), and is bound by sand in deep water (~30 m) and to the north and south by the mouths of Mission Bay and San Diego Bay, respectively. Giant kelp, a sub-canopy kelp (*Pterygophora californica*), and a prostrate kelp (*Laminaria farlowii*) were abundant at each site. The percent cover of various red, green, and brown turf algae varied according to depth, with > 50% cover at the inside edge, 15-30% cover in the interior, and < 5% cover at the outside edge. An along- and across-shore array of five study sites was created (Figure 1): the three sites of the along-shore leg ran along the 15 m isobath (North, Central, and South) and represent "forest interior" sites; the across-shore leg added additional sites at 12 m (East) and 18 m (West) that represented "forest edge" sites. Most studies were done at Central, which was at the junction of the two legs. Each site was separated from its neighbor by 300-500 m and marked with a permanent 100-m^2 circular leadline grid (11.3 m diameter); all interior sites were > 500 m from the nearest forest edge. Buoy lines were mounted to stainless steel eyebolts on steel plates at the center of each site. All sites had low vertical relief.

Demography and reproduction

All identifiable giant kelp sporophytes were mapped within the 100-m^2 circular grid at each site. Sporophytes greater than 10 cm length were marked with plastic tags attached using small cable ties. This tagging method has a low tag loss rate and does not affect mortalities (Graham et al. 1997). Tags were replaced as they were over-grown. For a given site, all sporophytes were censused on each sampling date to determine giant kelp density, size-structure, and reproductive condition. Sporophyte size was quantified by hand as the number of fronds greater than 2 m length (Dayton et al. 1992, Graham 2002). Sporophyte fertility was based on soral presence and quality: sori were scored as 1) absent, 2) present and non-sloughing, or 3) present and sloughing. Sloughing is a condition in which sori are vigorously releasing zoospores and can easily be distinguished from non-sloughing sori based on the presence of white tattered sporophylls (Neushul 1963, Graham 2002). At Point Loma, sporophylls can occur in densities of up to 200 per sporophyte, although most sporophytes have 30-50 sporophylls. Since sporophylls are bundled in a single location on each sporophyte, bundle size was quantified for each sporophyte as simply small or large, with small sporophyll bundles having < 20 individual sporophyll blades (Graham 2002).

Zoospore sampling

In situ plankton samples were collected using a subtidal pumping system described in Graham (1999). Briefly, the system consisted of a 25 m long hose (1.5 cm diameter) connected to a diaphragm pump that was operated from a small boat using a marine battery. The submerged end of the hose was fitted with a right-angle nozzle, which allowed the horizontal intake of water. The nozzle was rigged with a detachable clip that could be secured to permanent hardware at the base of the buoy lines ensuring that the nozzle opening was always located ~3 cm above the substrate. Pumped water was passed through 1 mm mesh, fixed immediately using 0.5% buffered formaldehyde, and stored in 2-L 99.9%-opaque high-density polyethylene containers. It took approximately 40 s to collect a 2-L sample from depths of less than 20 m. Sample containers were transported to the laboratory on ice and processed within six hours of returning to the laboratory.

Plankton samples were pre-filtered through 333 µm, 90 µm, and 10 µm nested sieves and then concentrated using a tangential-flow filtration unit fitted with a 1 µm cassette (see Graham 1999). Filtration retained greater than 99.99% of particles larger than 1 µm diameter and resulted in 40-60 ml concentrated samples. Concentrated samples were vacuum-filtered onto 47 mm diameter transparent membrane filters (1 µm pore diameter), preserved with ~5 ml of 2.0% buffered glutaraldehyde, and mounted onto glass microscope slides using immersion oil (Graham and Mitchell 1999). Each mounted filter contained all particles between 1-10 µm diameters from a single 2-L sample. Mounted filters were stored in the dark at ≤ -10˚C for up to 2 days before analysis (Graham and Mitchell 1999). Number of giant kelp zoospores per L was estimated microscopically for each sample (see Graham 1999 for detailed methods). Giant kelp zoospores were distinguished from those of *Pterygophora californica*, *Laminaria farlowii*, and *Eisenia arborea* based on species-specific absorption spectra of plastids within the zoospores, obtained by microphotometry (Graham 1999, Graham and Mitchell 1999). This method has a minimum detectable zoospore density of 11 zoospores/L and a validated accuracy for giant kelp zoospores of greater than 98% (Graham 1999).

Zoospore supply

Zoospore supply vs. local reproduction - Along- and across-shore currents in the center of the Point Loma kelp forest have very low net displacement (Jackson 1997), yet they can oscillate at relatively high instantaneous horizontal and vertical velocities (> 20 cm/s). In this hydrodynamic setting, advection-diffusion models emphasize diffusive zoospore dispersal and predict relatively symmetrical zoospore dispersal curves with highest zoospore concentrations around the adult sporophytes that released them (Graham unpublished data). In contrast, under conditions of uni-directional currents with high net displacement, advection-diffusion models emphasize advective zoospore dispersal and predict asymmetrical zoospore dispersal curves as zoospores are transported downstream (Gaylord et al. 2002). Low zoospore transport due to low-displacement flows in the forest interior therefore would be expected to couple among-day temporal variability in zoospore supply to local reproduction, whereas high zoospore transport would de-couple zoospore supply from local reproduction. Among-day sampling of zoospore supply and local reproductive output was designed to test the null hypothesis that *zoospore supply at Central is independent of (or de-coupled from) zoospore production*.

An among-day zoospore supply time series was collected at Central by determining average daily zoospore supply on 26 dates in 1999 spanning a period of 262 days (February 28, 1999 to November 16, 1999). Three replicate plankton samples were taken on each sampling date; the individual samples were collected 15 minutes apart with the first sample taken between 10-11 am. These samples were collected simultaneously with demographic surveys at Central that estimated giant kelp sporophyte size, density, and reproductive output (see below). Various within-day time series of zoospore supply were also collected at Central in 1999 to assess whether among-day patterns in zoospore supply were biased by smaller-scale patterns (e.g. a diel cycle in zoospore release). Two within-day time series were sampled every minute for 20 minutes (June 16 & September 1); one was sampled every 10 minutes for 200 minutes (July 15); and one was sampled every 100 minutes for 1600 minutes (November 16). For each of the 4 within-day sampling bouts, zoospore supply did not vary significantly as a function of time (linear/curvilinear regression: all $P > 0.25$, minimum detectable $r^2 = 0.37$ for 1 and 10 minute samples and 0.42 for 100 minute samples [$\alpha = 0.05$, $\beta = 0.05$; G-power 2.1.2, Buchner et al. 1997]), nor did sample estimates differ significantly from those predicted by random (Poisson) distributions (Kolmogorov-Smirnov goodness-of-fit and Runs tests: all $P > 0.4$). None of the within-day time series were auto-correlated ($P > 0.2$ at all time lags). These observations suggest that 15-minute sample spacing was appropriate for estimating average daily zoospore supply in the among-day time series. Furthermore, the among-day time series was also not found to be auto-correlated at any time lag ($P > 0.2$) indicating that the replicate among-day plankton samples taken at Central in 1999 were temporally independent of each other.

Preliminary analyses of zoospore supply vs. local reproduction showed that the density of sloughing sporophytes with large sporophyll bundles alone exhibited the strongest relationship with zoospore supply (Graham 2000), and therefore only these plants were considered (referred to simply as sloughing sporophytes). Preliminary graphical analyses also suggested that size-structure of sloughing sporophytes explained additional among-day variability in zoospore supply (Graham 2000) likely due to size-specific giant kelp mortality rates (Dayton et al. 1992, Graham et al. 1997), and therefore size specific decreases in the denisity of sloughing sporophytes. Density of sloughing sporophytes therefore was partitioned into 5 size classes: ≤ 8 stipes, 9-15 stipes, 16-20 stipes, 21-25 stipes, and ≥ 26 stipes. The relationship between zoospore supply and the density of sloughing sporophytes in these 5 size-classes was tested using a forward-stepping sequential regression. The explanatory variables were collinear (Table 1), in which case, sequential regression provides more accurate model parameterization and less ambiguous model creation than ordinary multiple regression (Tabachnick and Fidell 1996, Graham in review). The order (priority) in which individual variables entered the model was fixed prior to the sequential regression analysis and determined by the strength of the partial regression coefficients for each explanatory variable estimated when all other variables were included in a preliminary model (priorities in decreasing order: ≤ 8 stipes, 9-15 stipes, 21-25 stipes, 16-20 stipes, ≥ 26 stipes). By setting a fixed entrance order and recording parameter values, marginal statistics, and P values only when each variable first entered the model, the significance of individual variables did not vary as other collinear variables were added (Graham in review). This is because the marginal statistics for a given explanatory variable represent variability in the response explained by that variable *minus* variability shared with *all* explanatory variables of higher priority (Tabachnick and Fidell 1996, Graham in review). Only significant explanatory variables ($P \leq 0.15$) were retained in the final model; the higher than normal P value for entrance into the model ensured that even marginally significant, yet potentially useful, explanatory variables were accounted for (Tabachnick and Fidell 1996).

Spatial variability in reproductive coupling - If reproductive coupling in giant kelp is strongest under conditions of low current displacement, and giant kelp canopies modify such displacement, then the strength of reproductive coupling should vary among interior and edge sites at Point Loma. Additional among-day sampling of zoospore supply and local reproductive output at Point Loma was designed to test the null hypothesis that *the strength of the zoospore production/supply relationship (coupling) is independent of study site location (i.e. forest interior [North and South] versus forest edges [East and West]).*

Plankton samples and demographic surveys were collected in 1999 at both the interior (North and South, collected together on 7 dates) and edge sites (East and West, collected together on 8 dates). Each interior or edge sampling bout occurred on a date when Central was also sampled. As with Central, three replicate samples were taken every 15 minutes, although the timing of sampling differed: South and West were sampled approximately 1 hour before, and North and East were sampled approximately 1 hour after, sampling at Central. Spatial variability in the strength of reproductive coupling was studied by comparing the deviation of average daily zoospore supply sampled at the interior and edge sites from average daily zoospore supply estimated for each site after entering the site's demographic data into the final parameterized sequential regression model (see *Zoospore supply vs. local reproduction*). Coupling strength was studied by comparing the magnitude of deviations (statistical fit) using adjusted R^2. Differences in statistical fit between interior and edge sites would reject the null hypothesis that the strength of reproductive coupling is independent of location within the Point Loma kelp forest. That the spatial sampling design actually tests this null hypothesis assumes that the general sequential regression model developed for Central was actually indicative of interior sites; differences in statistical fit between interior sites and Central would indicate a violation of this assumption.

The notion that a statistical relationship between zoospore supply and the density of sloughing sporophytes reflects tight reproductive coupling can be confounded by synchronous reproductive output. Specifically, if many different local populations have similar densities of sloughing sporophytes, release zoospores synchronously (e.g. during periods of high water motion; Reed et al. 1997), and the zoospores are dispersed long distances (as suggested by Reed et al. 1988 and Gaylord et al. 2002), then each population can exhibit among-day variability in zoospore abundance that is correlated with local reproduction despite the fact that zoospores are coming primarily from remote sources. Additional analyses were therefore done to test for among-site differences in the density of sloughing sporophytes, among-site differences in zoospore supply, and the contribution of local vs. remote zoospore production. Log-linear models were used to test for independence between Date and Site effects on the density of sloughing sporophytes at the 5 study sites; that is, whether Date effects (temporal variability) were general across all sites. Analyses were done on the density of sloughing sporophytes in each size class (counts per 100 m^2) included in the final sequential regression model (see *Zoospore supply vs. local reproduction*), as well as the sum of sporophytes among these size classes; the analyses assumed a Poisson error distribution. Type II analysis of variance (ANOVA) was used to test for main effects and interactions of Date and Site on zoospore supply at the 5 study sites, with the 3 individual plankton samples taken per site per date serving as replicates. Since all sites were randomly chosen to represent either interior or edge populations, and sampling dates were dictated by weather, both Date and Site were treated as random factors. Variance components and magnitude of effects (% variance explained) were estimated for main effects and interactions (Graham and Edwards 2001). Because all five sites were not sampled on the same dates, two log-linear models and two ANOVAs were needed to compare interior and edge sites to Central: along-shore (i.e. among interior sites North, Central, and South), and across-shore (i.e. among edge sites East, Central, and West). For ANOVA analyses, significant Date effects indicated synchrony among sites, whereas significant Site effects and Date * Site interactions indicated time-independent and time-dependent site-specificity, respectively. Finally, if zoospores were primarily dispersed short distances then the density of sloughing sporophytes at each site should explain most of the temporal and spatial variability in zoospore supply at each site. To test this hypothesis, the final sequential regression model established for

Central was used to predict daily zoospore supply at each of the 5 sampling sites using the demographic data from each site. These predicted values were then subtracted from each replicate daily zoospore supply sample to give estimates of zoospore supply not explained by local reproduction ("adjusted" zoospore supply). Additional ANOVAs were done using these adjusted zoospore supply values as response variables, and changes in variance components and magnitude of effects were analyzed to determine whether significant levels of temporal and spatial variability in daily zoospore supply remained unexplained.

Statistical analyses

Zoospore density estimates were square root transformed prior to sequential regression and ANOVA analyses. Linearity, independence, normality, and equality of error terms were confirmed by analysis of residuals. Simple linear, curvilinear, and sequential regressions, ANOVAs, and log-linear analyses were done using SPSS 10.0.

RESULTS

Zoospore supply versus local reproduction

Average daily zoospore supply varied more than 2 orders-of-magnitude from as little as ~250 zoospores/L to over 54,000 zoospores/L (Figure 2). Zoospore supply was initially high during March and early April 1999 before falling to less than 1,500 zoospores/L in mid-late April. Zoospore supply rebounded during spring/summer and then remained relatively low from July to the end of the study in November. Within-day variability in the among-day time series (variance among the 3 replicate daily samples) was generally low, and high within-day variability was observed only during periods of high average daily zoospore supply.

Sequential regression analyses identified a significant positive relationship between average daily zoospore supply and the density of sloughing sporophytes in the ≤ 8, 9-15, and 21-25 stipe size classes (Figure 2, Table 2). Among-day variability in zoospore supply was best predicted by changes in the number of small sloughing sporophytes (≤ 8 stipes). Increasingly larger size classes explained decreasing amounts of variability in zoospore supply not already explained by the smallest size class. A functional relationship between size class structure and zoospore supply, however, was not inferred since the density and size of local reproductive sporophytes was not manipulated. That is, the fact that the ≤ 8 stipe size class was the most significant explanatory variable does not indicate that these small sporophytes contributed more propagules per capita than larger sporophytes, but simply that temporal variability in the density of smaller sporophytes was a better predictor of average daily zoospore supply. In fact, since the ≤ 8 stipe size class had the highest priority its regression coefficient represented both its unique contribution to variance in zoospore supply as well as the contribution shared among all other size classes. The regression coefficient for the 9-15 stipe size class, however, represented its unique variance contribution and the contribution shared among all other size classes except ≤ 8 stipes. As such, the observed statistical relationship simply represents the best predictive model. In the end, local reproduction explained 76% of the total among-day variability in zoospore supply (Figure 3A, Table 2). Significant relationships were not detected between average daily zoospore supply and additional oceanographic variables (e.g. wave height, sea temperature, and tides; Graham 2000).

Spatial variability in reproductive coupling

The strength of reproductive coupling varied within the Point Loma kelp forest. Cross-validation of the final sequential regression model with data from North and South supported the hypothesis that the strong relationship between zoospore supply and local reproduction observed at

Central was general among interior sites (Figure 3B, $R^2 = 0.78$). Moreover, the statistical fit of the Central model to data from the other interior sites was almost identical to the fit of the Central model to Central data. This was despite the fact that these sites were broadly distributed along the 15 m isobath (North and South were separated by ~1 km), with a correspondingly broad range of among-site variability in sporophyte density and reproductive condition (described below). Data from the edge sites (East and West), however, exhibited a much poorer fit to the Central model (Figure 3B, $R^2 = 0.38$), despite having a slightly higher sample size ($n = 8$) than for the interior sites ($n = 7$). Statistical fit of the regression model from Central to data from North, South, East, and West was as good or better than models parameterized individually for these sites.

Temporal and spatial patterns in the density of sloughing sporophytes both along- and across-shore indicated that reproductive output did not vary in concert among the study sites (Figure 4, Table 3). There was clear temporal variability in the density of the ≤ 8, 9-15, and 21-25 stipe size classes, as well as the summed density of the 3 size classes. Log-linear analyses, however, indicated that the temporal variability was strongly dependent on site for the summed density and most of the individual size classes, signifying general site-specificity in the density of sloughing sporophytes; the 2 non-significant likelihood ratios corresponded with the size classes with the lowest replication and thus the lowest statistical power. Along- and across-shore patterns in zoospore supply, however, were more complex (Figure 5AB). The main effects of Date and Site were significant in both the along- (Table 4A) and across-shore analyses (Table 5A). However Date effects explained 77% of the total variability in zoospore supply in the along-shore analyses (Table 4A) and 52% of the total variability in zoospore supply in the across-shore analyses (Table 5A). Date * Site interactions were also significant in both analyses, although the interactions explained less variability in zoospore supply than the combined main effects. Main effects and interactions together explained 94% of along-shore variability in zoospore supply and 89% of across-shore variability. Total along-shore variance (2513.7; Table 4A) was less than total across-shore variance (3114.5; Table 5A).

After adjusting zoospore supply for the predicted effects of local reproduction, total variability in zoospore supply was greatly reduced (Figure 5CD). Total along-shore variance decreased by 82% (2513.7 to 448.7; Table 4) and across-shore variance decreased by 54% (3114.5 to 1417.0; Table 5). Error variance was unchanged since the same predicted average daily zoospore supply was subtracted from each of the within-day samples at a given site. The reduction in total variability in zoospore supply was due primarily to large decreases in the main effects of Date and Site. For the along-shore analyses, among-date variance decreased by 98% (1934 to 30; Table 4) and among-site variance decreased by 74% (207.3 to 54.1; Table 4), both shifting from highly significant to highly non-significant. For the across-shore analyses, among-date variance decreased by 62% (1632.2 to 618.3; Table 5) and remained significant, however, among-site variance decreased by 100% (361.9 to 0; Table 5). In contrast, interaction terms decreased only 3-41% and remained significant for both analyses (Table 4 & 5).

DISCUSSION

Aggregations of organisms often exhibit group properties beyond those observed at the scale of individuals, as exemplified by the enhanced foraging success, increased protection, and improved hydrodynamic efficiency afforded to schooling fishes and flocking birds (Moyle and Cech 1988, Dickman 1992, Helfman et al. 1997). Such emergent properties of aggregations can have important population, community, and ecosystem consequences, especially in systems where most energy and habitat structure is provided primarily by a few foundation species (*sensu* Dayton 1972). For instance, organisms living within large terrestrial forests clearly experience different physical and biological environments than those living near isolated trees. Forest canopies modify the quantity and quality of light that regulates the growth of understory plants, organism color patterns, and the visibility of both predators and prey (Lowman and Nardkarni 1995, Leigh et al. 1996). Canopies also dampen winds that drive propagule dispersal and the transportation and accumulation of detritus and organic matter, and alter local climate (Kittredge 1948, Windsor 1990, Mabberley 1992). This study has shown that large kelp forests can also exhibit group properties through the effects of canopy flow-modification on kelp dispersal, with potentially important consequences to kelp population dynamics, and thus the provision of habitat and energy to their associated communities.

The low current displacement (Jackson 1997) and random pattern of within-day zoospore supply (this study) observed within the Point Loma kelp forest suggests that giant kelp zoospores simply slosh back and forth around their site of release. The subsequent prediction that among-day zoospore supply would be coupled to local reproduction at sites in the forest interior was strongly supported by the high statistical fit of the regression model parameterized using data from Central, and was validated using equivalent data from North and South. Still, a little over 20% of among-day variability in zoospore supply at the interior sites remained unexplained by local reproduction, suggesting that remote zoospore production may have partially contributed to variability in zoospore supply at these sites. The turbulent nature of the water column can keep some zoospores in the plankton long enough to be transported away from the adults that produced them (Gaylord et al. 2002). Drifting reproductive sporophytes or sporogenous tissue may also provide a remotely produced zoospore source (Dayton et al. 1984, Dayton 1985). Furthermore, although their planktonic duration is limited to a few days (Reed et al. 1988), it is likely that zoospores can briefly accumulate in the plankton to provide a background abundance onto which newly released zoospores are continuously added. The intercept of the sequential regression analysis estimated this background zoospore abundance at Central to be ~717 zoospores/L (Table 2). Although generally weak relative to the tight local reproductive coupling previously described, this potential link between long-distance dispersal and zoospore supply might be important in regulating kelp recruitment during periods of localized disappearance of reproductive giant kelp sporophytes (e.g. during episodic grazing events; Graham 2002).

Ultimately, the along- and across-shore studies of zoospore supply at Point Loma supported the hypothesis that current dampening by giant kelp canopies results in spatially-variable coupling between zoospore supply and local reproduction. The Central, North, and South study sites were all greater than 0.5 km from the nearest forest edge, exceeding the minimum forest size estimated to significantly dampen both along- and across-shore currents (~100 m; Jackson and Winant 1983). The East and West sites, however, were located along the inner and outer edges of the forest, respectively, where both along- and across-shore currents have been shown to be more than an order-of-magnitude greater currents than in the interior (Jackson and Winant 1983, Jackson 1997). It was subsequently predicted that reproductive coupling at the edge sites would be less than at the interior sites, due to the advection of zoospores away from their parents. This hypothesis was strongly supported by the 50% decrease in the amount of variability in zoospore supply explained by local reproduction at edge sites relative to interior sites.

That zoospore supply at the interior sites was coupled to local reproduction, however, did not in itself demonstrate that zoospores were coming primarily from local propagules sources. As previously suggested, reproductive synchrony (Reed et al. 1997) in combination with long-distance dispersal (Reed et al. 1988) may also result in coupling between zoospore supply and local reproduction. Two lines of evidence, however, suggested that zoospore supply at the interior sites did come primarily from local reproduction. First, although significant and strong main effects of Date were detected during along- and across-shore sampling of zoospore supply, suggesting some level of synchrony among sites, 62 to 98% of this variability was accounted for by local reproduction. And second, since there was little similarity in the temporal variability of sloughing sporophyte densities among the 5 study sites, the observed reproductive coupling was due to the individual contribution of each site's local reproductive population. The most probable explanation for the observed synchrony (i.e. strong Date effects) is therefore an external constraint on local reproduction. That is, a general pattern of increased zoospore supply as oceanographic conditions conducive to good kelp growth and reproduction become established throughout the Point Loma kelp forest, and decreased zoospore supply as conditions deteriorate or broad-scale grazing occurs (Graham 2002); such externally-driven reproductive synchrony can exist independently of synchronized changes in sporophyte density.

Whether giant kelp populations are "open" or "closed", the answer is not simple. Although adult sporophytes of similar reproductive condition likely produce similar amounts of zoospores, zoospore dispersal is strongly dependent on temporal and spatial variability in hydrodynamics. Additionally, variability in hydrodynamics will reflect variability in adult size, distribution, and abundance; for example, small kelp forests will not have the capacity to dampen flows to the same extent that larger forests can (Jackson and Winant 1983). As such, giant kelp has a unique and potentially important role in determining the fate of its propagules and in regulating demographic and genetic exchanges within and among populations. Furthermore, the high temporal and spatial variability in coastal flows within and between giant kelp forests supports a continuous rather than dichotomous view of population connectivity (see also Hixon et al. 2002). In highly connected open systems, propagule retention will be low with most propagules transported away from the site of production, whereas in poorly connected closed systems, propagule retention will be high. But these two levels of population connectivity are simply upper and lower bounds of a continuum. In fact, the two different strengths of reproductive coupling observed during this study (78% within the Point Loma kelp forest and 38% along the edges) highlight the fact that natural populations may lie *within* the continuum rather than at one extreme of connectivity or the other. More interesting than the question of “open” versus “closed” systems, therefore, is where populations, species, or functional taxonomic groupings are positioned along this connectivity continuum, and what processes regulate whether these positions are constant or variable in space and time. For example, a shift along the continuum of population connectivity from open to closed populations may be observed as the local population of interest shifts to the forest interior, or the kelp forest grows in size.

This potential pattern of increased reproductive coupling with increasing kelp forest size helps to explain the apparent controversy of whether kelp dispersal occurs over primarily short or long distances. Dayton et al. (1984) described a rapid decrease in the density of giant kelp recruits with increasing distance from adult sporophytes in a clearing in the Point Loma kelp forest, suggesting that most zoospore dispersal (or at least survival following dispersal, settlement, and fertilization) was limited to within 10 m of the nearest adult giant kelp sporophytes. This pattern was strongly supported by the tight reproductive coupling observed within the Point Loma kelp forest during this study. In contrast, Reed et al. (1988) observed settlement of *Pterygophora californica* zoospores over 4 km from the nearest known zoospore source. Their study, however, was conducted in Santa Barbara, California, in a region with small kelp populations, sustained uni-directional currents (often greater than 5 cm/s), and high net current displacement (Washburn et al. 1999). In this setting, the probability of long-distance zoospore transport is predicted to be much greater than within the Point Loma kelp forest (Gaylord et al. 2002). Thus, although zoospore dispersal distances may be short in the center of large kelp forests, zoospores produced by sporophytes along forest perimeters, or in small forests, may be physically transported long distances.

The interaction between kelp forest size, net current displacement, and reproductive coupling may also have significant consequences for kelp colonization. Following an initial colonization event, a kelp assemblage will be too small to significantly dampen currents and modify net current displacement. Subsequently, the contribution of local reproduction to zoospore supply will be small due to the advection of zoospores away from the assemblage, limiting the potential for the kelp population to seed itself, yet increasing the percentage of zoospores capable of colonizing distant habitat. Recruitment will likely be limited to the close vicinity of the initial colonists (Anderson and North 1966), and as the density of adult kelp sporophytes gradually increases, so does the effect of the kelp assemblage on net current displacement, increasing the retention of zoospores and the contribution of local reproduction. As such, there may exist a threshold in kelp assemblage size above which more zoospores are retained locally than transported away. Assuming that zoospore settlement reflects patterns in zoospore supply (Santelices et al. 1995), subsequent fertilization, recruitment success, and self-seeding may be facilitated; Reed et al. (1991) clearly demonstrated that a threshold in zoospore settlement existed below which kelp recruitment was not possible. If true, the population dynamics of large kelp forests may be more stable than small ones; that is, there will be less chance of recruitment failure in large kelp forests. This hypothesis was tested using North et al.’s (1993) published time series of population sizes for numerous giant kelp forests in southern California. A plot of standardized temporal variability in population size versus the maximum size of each population confirmed that larger giant kelp forests are, in fact, more temporally stable than smaller forests (Figure 6).

This relationship between kelp forest size and reproductive coupling immediately spawns two new questions for investigation: (1) what is the spatial scale or threshold for flow modification by giant kelp sporophytes?; and (2) how can patterns of spatial variability in reproductive coupling be used to study the genetic consequences of demographic exchanges within and among giant kelp populations? The first question requires extensive empirical studies of along- and across-shore flows throughout kelp forests of different sizes. It is important to understand quantitatively the extent to which individual sporophytes interact to modify flows over broad spatial scales, and how such flow-modification varies as sporophytes are aggregated into forests. Furthermore, we need to understand how this modification varies temporally as currents fluctuate, stratification of the water column changes, and sporophytes gain and lose biomass. The second question cannot be addressed without a better understanding of these aspects of flow modification. Even then, however, the modeling of demographic exchanges will be challenging. Tight reproductive coupling observed in the center of the Point Loma kelp forest suggests that recruits will not be displaced far from their parents. Consequently, these juveniles will have a high probability of experiencing the same selective pressures as the adults, suggesting a potential for adaptation of kelp populations to local environmental conditions. Tight reproductive coupling and short-distance dispersal will also likely increase rates of self-fertilization and may lead to small-scale genetic structure within kelp forests.

The realization that coupling between giant kelp zoospore production and supply is dependent on physical properties of the populations themselves, broadens our view of giant kelp as a foundation species in nearshore marine communities. This species not only provides the structure and energy for one of the most productive marine ecosystems in the world (Barnes and Hughes 1988), but as it now appears may also contribute to the regulation of its own distribution and abundance through feedback mechanisms involved in dispersal. The flow-mediated coupling that was identified in this study will also likely affect the dispersal capabilities of other kelp forest seaweeds and animals with relatively short planktonic durations. Giant kelp essentially creates areas of low net current displacement in coastal regions that are generally characterized by swift uni-directional currents, and therefore may significantly alter the dynamics of entire assemblages of nearshore marine organisms.

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Table 1. VIF-Correlation matrix of density of sloughing sporophytes in 5 size classes. Data along diagonal are variance-inflation-factors (VIF = $1/(1-R_i^{2*})$, where R_i^{2*} is the coefficient of determination when variable *i* is regressed against all other variables; Tabachnick and Fidell 1996). Off-diagonal data are Pearson product-moment correlations (*r*) between pairs of variables. VIF values ≥ 2 and *r* values ≥ |0.3| represented high collinearity among the size classes which served as explanatory variables in subsequent sequential regression analyses (Table 2; Graham in review).

	≤ 8 stipes	9-15 stipes	16-20 stipes	21-25 stipes	≥ 26 stipes
≤ 8 stipes	**1.49**	-	-	-	-
9-15 stipes	0.41	**2.74**	-	-	-
16-20 stipes	0.05	0.66	**2.03**	-	-
21-25 stipes	0.44	0.49	0.26	**1.50**	-
≥ 26 stipes	-0.05	0.32	0.35	0.05	**1.24**

Table 2. Sequential regression analysis of the effects of local reproduction on daily zoospore supply. Explanatory variables were the density of sloughing sporophytes in 5 size classes (same as in Table 1). *t* tests H_o: $b = 0$.

Variable	*b*	*SE*	*t*	*P*	r^2
Constant	32.71	8.20	3.99	0.0006	-
≤ 8 stipe size class	59.38	10.05	5.91	< 0.0001	0.592
9-15 stipe size class	4.19	1.28	3.26	0.0034	0.129
21-25 stipe size class	12.32	6.37	1.94	0.0685	0.041

Analysis of Variance

Source	*SS*	*df*	*MS*	*F*	*P*	R^2
Regression	43251.4	3	14417.1	23.47	< 0.0001	0.762
Error	13516.3	22	614.4			

Table 3. Log-linear analyses testing independence of Date and Site effects on the density of sloughing sporophytes in the ≤ 8, 9-15, and 21-25 stipe size classes, and the summed density among these size classes. (A) Along-shore sites (North, Central, and South) (B) across-shore sites (East, Central, and West). Across-shore analyses could not be done for the 21-25 stipe size class since sporophytes in this size class were only present at 1 site (Central, see Figure 5).

	Size class	*Likelihood ratio*	*df*	*P*
A)	≤ 8	14.192	8	0.077
	9-15	26.470	12	0.009
	21-25	3.527	5	0.219
	Total (≤8, 9-15, 21-25)	38.53	12	0.0001
B)	≤ 8	21.317	12	0.046
	9-15	36.284	14	0.001
	21-25	NA	NA	NA
	Total (≤8, 9-15, 21-25)	53.79	14	<0.0001

Table 4. Model II ANOVAs testing the effects of Date, Site, and Date * Site on (A) daily zoospore supply and (B) adjusted daily zoospore supply sampled along-shore. Adjusted daily zoospore supply estimates are the result of statistically removing the effects of local reproduction using the final parameterized sequential regression model (Table 2). *F*-ratios for the main effects of Date and Site utilized the interaction *MS* in the denominator, whereas the *F*-ratio for the interaction utilized the Error *MS* in the denominator. VC equals the variance contribution (variance component) of individual main effects, interactions, or error to the response. In A, % equals percent variance contribution relative to total variance. In B, % equals percent variance contribution relative to unadjusted total variance given in A. N = 63.

	Source	*SS*	*df*	*MS*	*F*	*P*	VC	%
A)	Date	109742.0	6	18290.4	21.79	< 0.0001	1934.0	76.9
	Site	10384.1	2	5192.0	6.18	0.0143	207.3	8.3
	Date * Site	10073.6	12	839.5	6.05	< 0.0001	233.6	9.3
	Error	5831.3	42	138.8	-	-	138.8	5.5
	Total						2513.7	100.0
B)	Date	6516.1	6	1086.1	1.33	0.3167	30.0	1.2
	Site	3906.2	2	1953.1	2.39	0.1338	54.1	2.2
	Date * Site	9793.0	12	816.1	5.88	< 0.0001	225.8	9.0
	Error	5831.6	42	138.8	-	-	138.8	5.5
	Total						448.7	17.9

Table 5. Model II ANOVAs testing the effects of Date, Site, and Date * Site on (A) daily zoospore supply and (B) adjusted daily zoospore supply sampled across-shore. Format is the same as Table 4. N = 72. The negative VC for Site effects in B was remedied using the “pool-the-minimum-violator” technique (Graham and Edwards 2001).

Source	*SS*	*df*	*MS*	*F*	*P*	VC	%
A) Date	121708.0	7	17386.9	6.45	0.0016	1632.2	52.4
Site	22760.2	2	11380.1	4.22	0.0368	361.9	11.6
Date * Site	37754.2	14	2696.7	8.12	< 0.0001	788.1	25.3
Error	15948.6	48	332.3	-	-	332.3	10.7
Total						3114.5	100.0
B) Date	51074.0	7	7296.3	4.02	0.0129	618.3	19.9
Site	2299.9	2	1149.9	0.63	0.5451	0	0
Date * Site	25402.1	14	1814.4	5.46	< 0.0001	466.4	15.0
Error	15949.4	48	332.3	-	-	332.3	10.7
Total						1417.0	45.6

FIGURE LEGENDS

Figure 1. Study sites at Point Loma with map of giant kelp canopy (gray) on August 12, 1996.

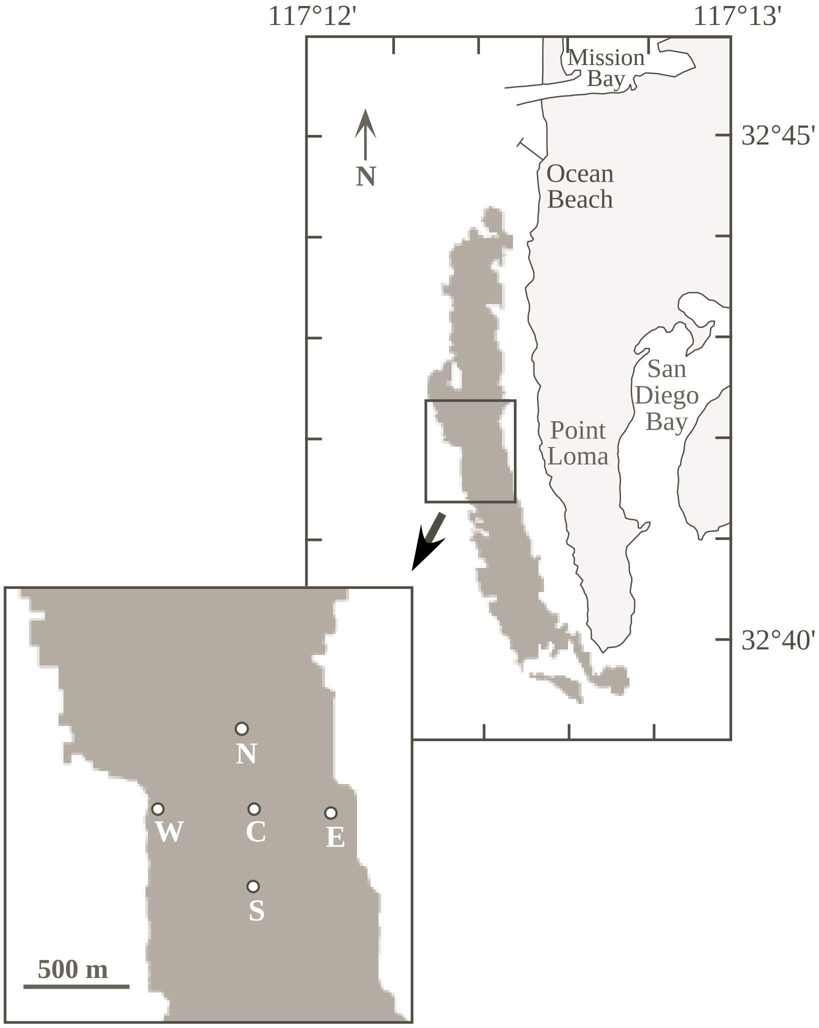
Figure 2. Among-day patterns of temporal variability in average daily zoospore supply (±SE), and the density of sloughing sporophytes in the ≤ 8, 9-15, and 21-25 stipe size classes. Collinearity of sloughing sporophyte densities among the 3 size classes has been removed using residual regression (Graham in review) according to priorities used in the sequential regression analyses.

Figure 3. Relationship between average daily zoospore supply (square-root-transformed) and daily zoospore supply predicted by the sequential regression model (square-root-transformed) at (A) Central and (B) North, South, East, and West. Lines represent 1:1 fit of sampled versus predicted zoospore supply. In B, the triangle is the average of all zoospore supply samples taken on dates when sloughing sporophyte density was zero in all size classes, as these are essentially replicates of the y-intercept.

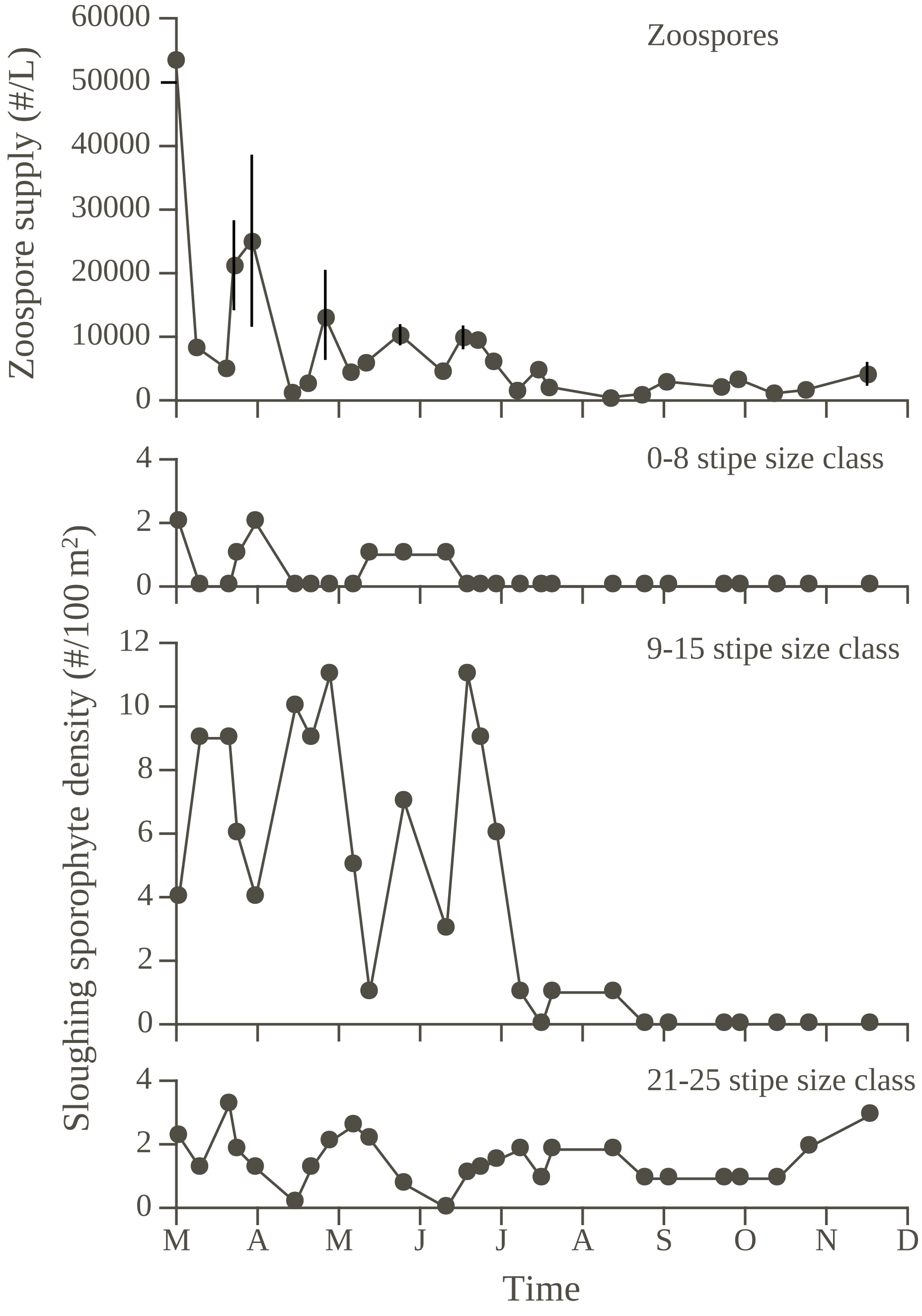
Figure 4. Along- (left panels) and across-shore (right panels) patterns of among-date and -site variability in the density of sloughing sporophytes in the ≤ 8, 9-15, and 21-25 stipe size classes.

Figure 5. Among-date and -site variability in daily zoospore supply (A & B), adjusted daily zoospore supply (i.e. after effects of local reproduction were removed; C & D), and total density of sloughing sporophytes (E & F) both along-shore (left panels) and across-shore (right panels). Error bars are standard errors.

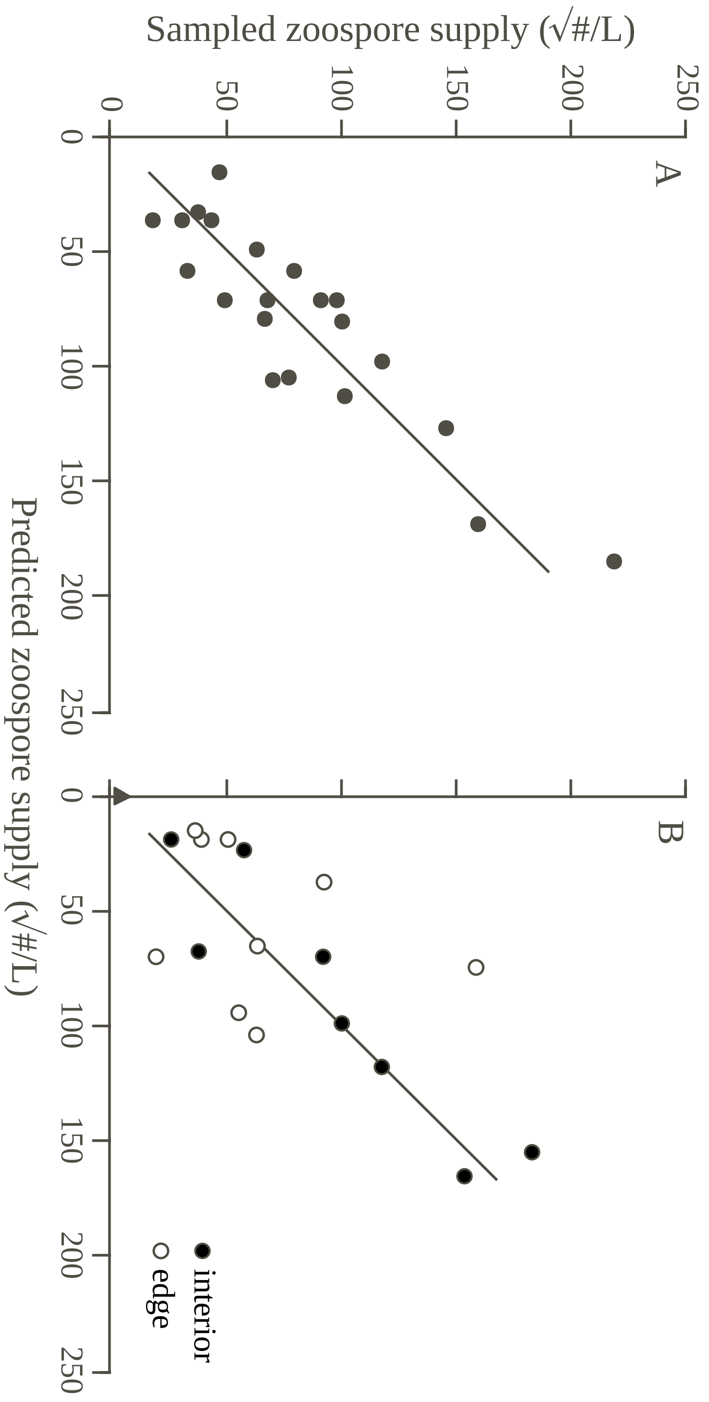
Figure 6. Standardized temporal variability in giant kelp forest canopy cover (coefficients of variation) versus maximum annual canopy cover (km^2). Each replicate is 1 of 20 individual kelp forests from southern California. Temporal variability estimates are calculated over 25 years of quarterly aerial surveys for each site from 1967 to 1991. Statistical fit of regression line: $r^2 = 0.41$, $F_{1,18} = 7.53$, $P = 0.013$. CV data are $\log_{10}$ transformed. Original canopy cover data are from North et al. (1993).



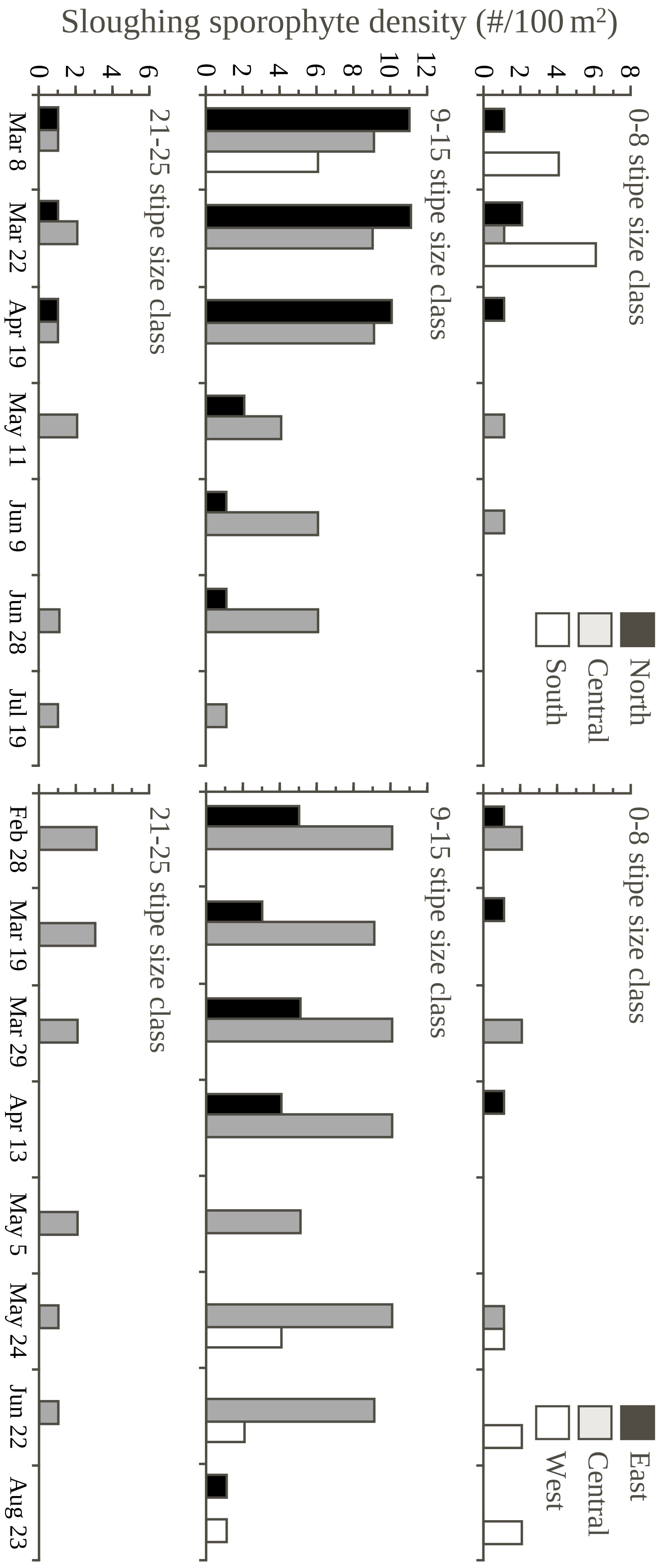
Graham Figure 1



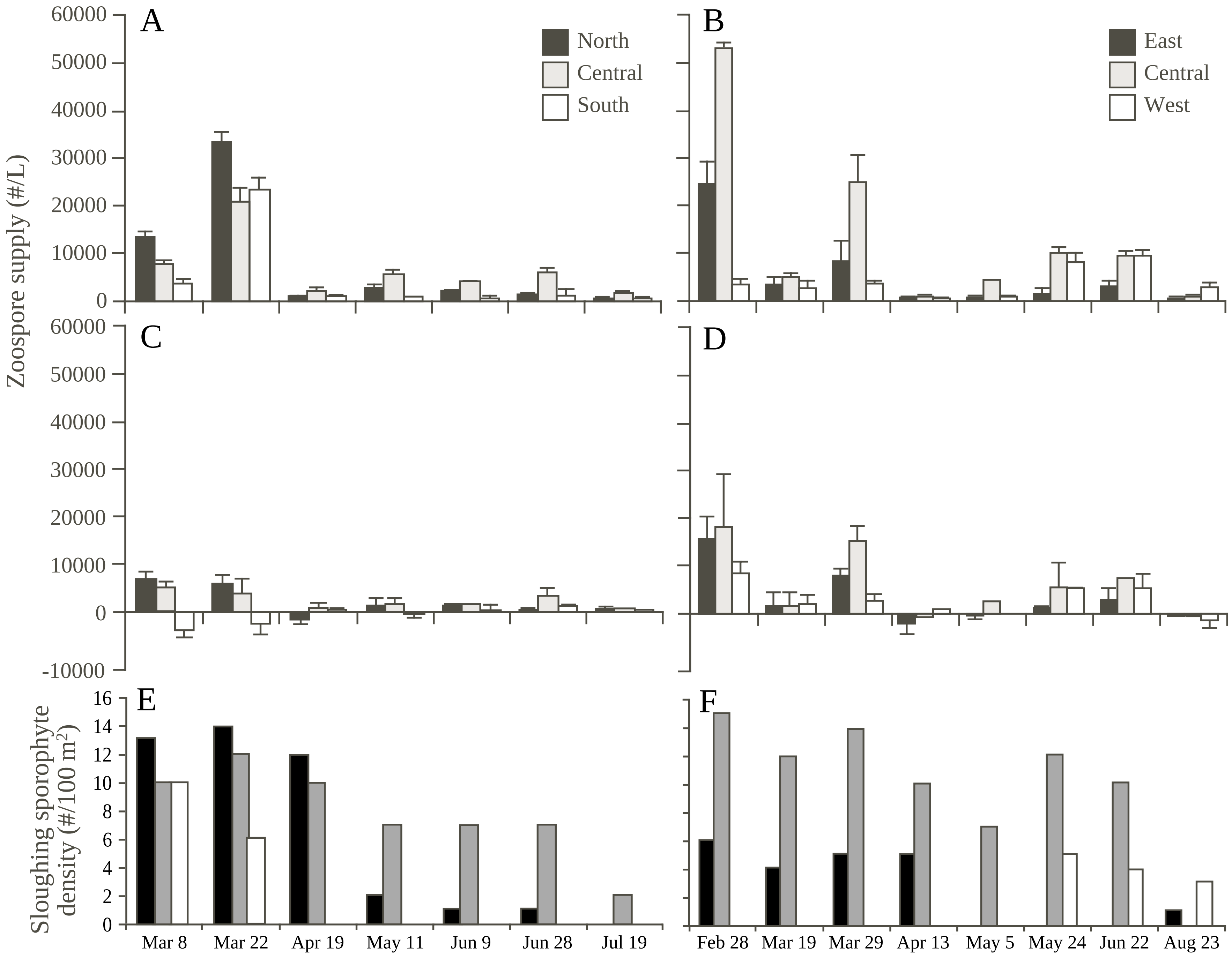
Graham Figure 2



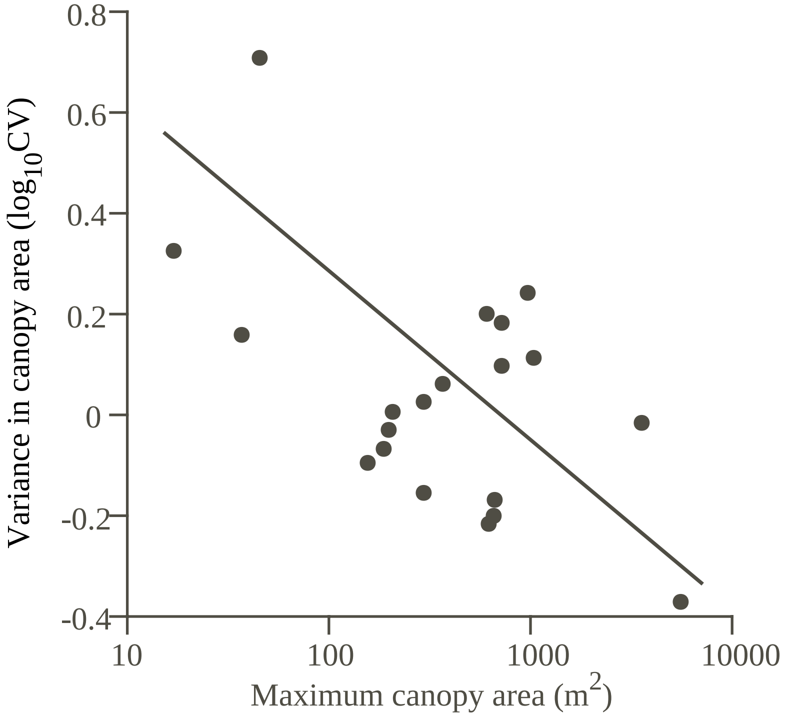
Graham Figure 3


Sloughing sporophyte density (#/100 m²)
0-8 stipe size class
9-15 stipe size class
21-25 stipe size class
North
Central
South
East
Central
West
0
2
4
6
8
10
12
Mar 8
Mar 22
Apr 19
May 11
Jun 9
Jun 28
Jul 19
Feb 28
Mar 19
Mar 29
Apr 13
May 5
May 24
Jun 22
Aug 23

Graham Fig 4



Graham Figure 5



0.8
0.6
0.4
0.2
0
-0.2
-0.4
10
100
1000
10000
Variance in canopy area ($\log_{10}$CV)
Maximum canopy area (m^2)

Graham Fig 6