

REPRODUCTIVE LONGEVITY OF DRIFTING KELP *MACROCYSTIS PYRIFERA* (PHAEOPHYCEAE) IN MONTEREY BAY, USA¹

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Drifting *Macrocystis pyrifera* (L.) C. Agardh sporophytes have long been viewed as the primary long-distance dispersal vector; yet, few data exist that support the ability of reproductive viable sporophytes to actually travel the presumed hundreds to thousands of kilometers. This study addressed the reproductive longevity of experimental and naturally occurring *M. pyrifera* drifters. Temporal variability in sporophyte size and reproduction was estimated for experimental drifting sporophytes that were tethered to surface buoys and compared with attached plants (controls). Reproductive viability was also studied for beach-cast drifters (BCD), and naturally drifting sporophytes observed during field surveys in Monterey Bay. Detached drifting sporophytes were tracked with radio transmitters to follow drifter trajectories and to measure drifting speed. Experimental drifters (ED) experienced a 74% reduction in frond length after 35 days, a 76% reduction in average frond number after 70 days, and a reduction in average sorus area by 83% after 28 days. Although zoospore production was reduced following detachment, sporophytes remained fertile with high zoospore germination success as long as sori were present (125 days). Zoospore production and germination success for natural and BCD was similar to ED. The average displacement of radio-tagged drifters was $7.12 \text{ km} \cdot \text{day}^{-1}$, suggesting that a sporophyte adrift for 125 days disperses viable propagules (zoospores) over 890 km (± 363). Dispersal of propagules is important for population restoration, distribution, and genetic diversity. Such dispersal distances are long enough to connect potentially all Northern Hemisphere *Macrocystis* populations across a generational timescale and may facilitate inter-hemispheric gene flow.

Key index words: dispersal; drifting; germination; kelp; longevity; *Macrocystis*; Monterey Bay; rafts; reproduction

Dispersal determines the largest scale at which species interact with their environment, respond to perturbations, and evolve (Palumbi 1994, Johst and Brandl 1997, Holmes and Wilson 1998). Although the fluid nature of the ocean may enhance the long-distance dispersal potential for many marine organisms, the spatial scale over which such dispersal effectively occurs has been difficult to characterize, especially for seaweeds (Norton 1992, Eckman 1996, Kinlan and Gaines 2003, Reed et al. 2006). The giant kelp *Macrocystis pyrifera* is the most widely distributed kelp genus in the world, with an amphitropical distribution that spans the west coasts of North and South America and also includes Argentina, South Africa, Australia, New Zealand, and most of the sub-Antarctic islands (Neushul 1971). With a likely origin in the North Pacific (Coyer et al. 2001), it has been suggested that *Macrocystis*'s amphitropical distribution resulted from long-distance transport of drifting, reproductively viable sporophytes across the eastern equatorial Pacific, and subsequently among isolated Southern Hemisphere populations (North 1971, Nicholson 1978, Estes and Steinberg 1988, Lindberg 1991). Coyer et al. (2001) further suggested that gene flow between Northern and Southern Hemisphere *Macrocystis* populations may have occurred as recently as 10,000 years ago. Such dispersal distances range from hundreds to thousands of kilometers, whereas regional dispersal (<10s of kilometers) may be facilitated by direct dispersal of planktonic spores that connect available habitat (Reed et al. 2004), especially during episodic storm events (Reed et al. 1988).

Despite the apparent acceptance of drifting sporophytes as the primary long-distance dispersal vector for *Macrocystis* (Lüning 1990), few data exist that support the ability of reproductively viable *Macrocystis* sporophytes to actually travel hundreds to thousands of kilometers. Drifting *Macrocystis* sporophytes (kelp rafts) are created following sporophyte detachment from benthic substrata, which, in California, occurs primarily during the winter months (November–February; ZoBell 1971, Hobday 2000a). Buoyed to the surface by numerous pneumatocysts, *Macrocystis* sporophytes have been estimated to remain alive and adrift for up

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to 109 days (Hobday 2000b); assuming they are not deposited on nearby beaches, *Macrocystis* drifters may travel over 1000 km before mortality (Harrold and Lisin 1989, Helmuth et al. 1994, Hobday 2000a, Smith 2002). To date, however, only two studies have discussed whether *Macrocystis* sporophytes can remain reproductive while drifting (van den Hoek 1987, Macaya et al. 2005). Most recently, Macaya et al. (2005) measured the body size of stalked barnacles (*Lepas* spp.) attached to drifting kelp to estimate drifter age (using size–age correlation), and assigned that value (in days) as minimum drift kelp floating time. They determined that 26% of drifting *Macrocystis* sporophytes along the coast of Chile possessed sporophylls with sori containing sporangia, and they estimated that drifter fertility could be maintained for at least 21 days. These data were the first direct evidence that *Macrocystis* drifters may remain reproductively viable while adrift.

Macaya et al.'s (2005) drifter fertility data, however, are only the first step in determining the potential for *Macrocystis* drifters to serve as effective long-distance (>100s km) dispersal vectors. First, without tracking individual drifters, Macaya et al. (2005) resorted to an indirect measure of drifter life span; their 21-day life span results in a predicted dispersal distance of only 150–180 km (Harrold and Lisin 1989, Hobday 2000a). Second, establishment of a new population following long-distance dispersal requires completion of *Macrocystis*'s heteromorphic alternation of generations life history. Fertile sori release flagellated haploid zoospores that settle and germinate into dioecious haploid gametophytes, and upon successful gametogenesis and fertilization, diploid sporophytes are produced that grow from microscopic to macroscopic size (Sauvageau 1915). The simple presence of sori and sporangia (as measured by Macaya et al. 2005), however, does not represent full reproductive viability, as many kelp taxa only release viable zoospores toward the end of sorus development (Graham 1999, McConnico and Foster 2005), and subsequent zoospore germination success can be highly variable (0%–100%), especially in *Macrocystis* (Reed et al. 1996, Buschmann et al. 2004). Thus, direct measurement of the longevity of *Macrocystis* drifters capable of producing zoospores with high germination success is an important next step in estimating the effective distance over which *Macrocystis* drifters may transport spores.

The goal of this study was to estimate directly the reproductive longevity of drifting *M. pyrifera* in Monterey Bay, CA, USA. We considered *Macrocystis* drifters to be reproductively viable if they produced zoospores with nontrivial germination success (>10%). This percentage represents a settlement density greater than 10 spores · mm⁻², which is ecologically realistic (Reed et al. 1988, 1997). In this paper, we provide the first direct evidence that *Macrocystis* drifters have the potential to serve as effective long-distance (>100s km) dispersal vectors.

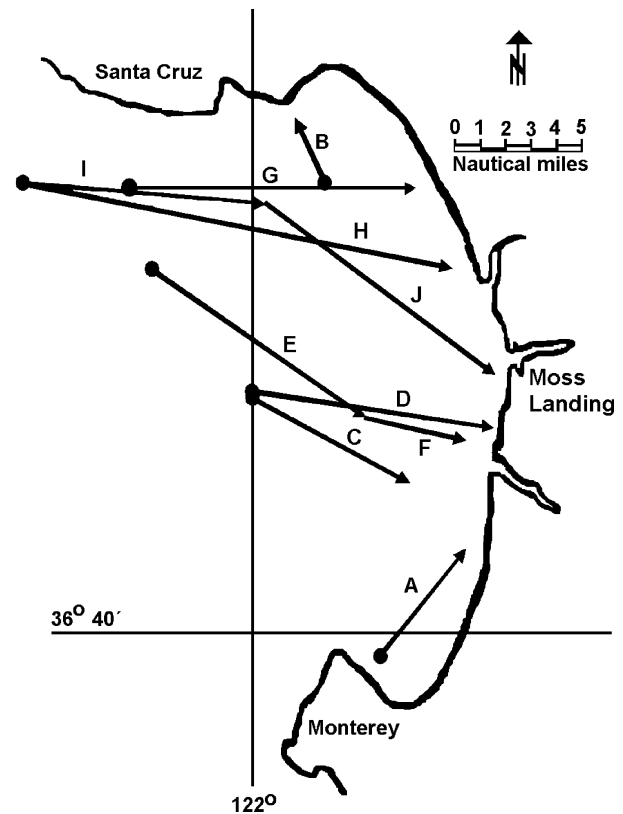


FIG. 1. Monterey Bay. Arrows represent the drifting trajectories obtained from radio tracking.

MATERIALS AND METHODS

Our studies combined observation on five "types" of *M. pyrifera* sporophytes: (a) plants attached to the substratum in a control bed or control kelp (CK); (b) plants experimentally attached to buoys or surface-attached drifter (SAD); (c) plants that were naturally detached and were found drifting in the ocean, or natural drifters (ND); (d) plants that were detached from the bottom, radio tagged, and put adrift, or experimental drifters (ED) and (e) plants that were collected on the beach and which we assumed were adrift for some time, or beach-cast drifters (BCD).

Reproductive longevity of surface-attached sporophytes (SAD). Seven *Macrocystis* sporophytes, ranging from 10 to 16 m long (mean = 12.7 m) and with 19–53 fronds/sporophyte (mean = 33), were detached from the bottom near Monterey Peninsula, CA, USA (Fig. 1), at 10–15 m depth using SCUBA in January 2004. Divers removed the holdfast from the rock, and the sporophytes were transported by boat to Moss Landing, CA (Fig. 1). During transport, the sporophytes were moistened with seawater to avoid desiccation. To mimic drifting conditions, the sporophyte holdfasts were attached at the water surface to independent buoys, using a nylon rope covered with neoprene to avoid damage to the stipes. From time zero, and then every 5–16 days (mean = 8 days) for the duration of the experiment, the number of fronds per sporophyte were counted, and the total length was measured to estimate the reduction in frond number and maximum frond length over time. The number of sporophylls per frond was estimated from five to 10 haphazardly selected fronds per sporophyte. In order to avoid an overestimation of reproductive output, we did not multiply these data by the total number of fronds, because the number of

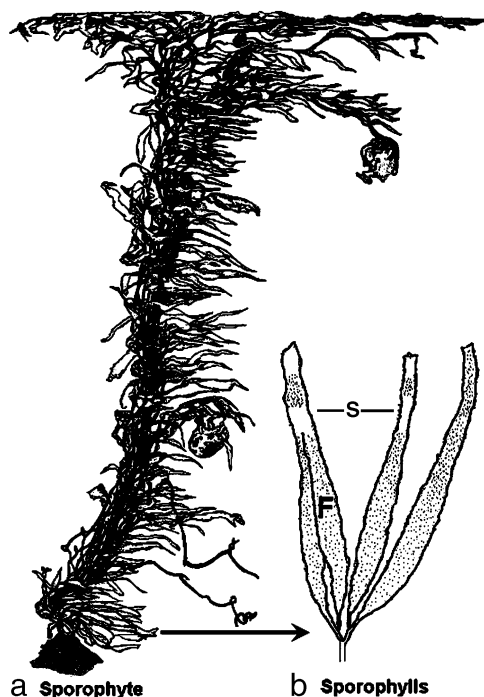


FIG. 2. (a) *Macrocyctis pyrifera* sporophyte with sporophylls growing near the base. (b) Sporophylls showing sterile areas (S) and fertile areas (F) or sorus. (Redrawn from Neushul 1963 and Reed 1990)

sporophylls per frond was highly variable. Ten sporophylls were collected from different fronds per sporophyte and transported to the laboratory to measure total sporophyll area and percentage of fertile area (sorus) from the total sporophyll area (Fig. 2). Measurements were made by inscribing rectangles and triangles, of the sporophyll and then the sorus, measuring their dimensions, calculating the areas, and summing per sporophyll. Detailed destructive measurements of sporophyll and sorus areas ($n = 20$) demonstrated <5% error for the non-destructive methods. At the beginning of the experiment, the number of sporophylls sampled was insignificant with respect to the total (about 400 per sporophytes). After 100 days, the sample size was reduced to five to leave as many sporophylls as possible on the sporophytes. Reproductive viability was assessed by inducing zoospore release and measuring zoospore production per gram of sporophyll per hour and the percent zoospore germination.

Estimation of reproductive viability. To measure reproductive viability, 10 sporophylls were collected haphazardly from each surface-attached sporophyte. Sporophylls were transported on ice between wet towels inside a dark cooler and zoospore suspensions were obtained using the methods of Reed et al. (1991), with minor modifications. The 10 sporophylls per sporophyte were desiccated for 30 min, and exactly 40 g of sporophyll tissue was used to obtain each zoospore suspensions. Zoospore release was induced by reimmersing the sporophylls in 500 mL of 0.2 μ m filtered seawater at 15–16°C for one h under ambient light. Zoospore suspensions were sampled microscopically to determine the density using four replicate grids of a hemocytometer (volume = 1×10^{-4} mL). Zoospore production per gram of sporophyll was estimated by dividing zoospore density by the exact weight of sporophyll tissue. After determining zoospore production, filtered seawater was added to the suspensions to bring zoospore density to 1×10^4 zoospores \cdot mL $^{-1}$ in 500 mL

(Anderson and Hunt 1988, Reed 1990). The 500 mL zoospore suspensions were then added to Petri dishes containing three glass slides and incubated in a water bath for 12 h at 15°C under 50 μ mol photons \cdot m $^{-2}$ \cdot s $^{-1}$ (Anderson and Hunt 1988, Reed et al. 1991). The density of settled zoospores was then estimated by counting five random fields of view on each of the three slides, using an inverted microscope at 64X. The Petri dishes were returned to the water bath, and after 24 h (11:13 light:dark) of culturing, the number of zoospores forming germ tubes was counted in five random fields of view for each of the three slides. Percentage germination was calculated by dividing the average number of germlings by the average number of initially settled zoospores, multiplied by 100. The average zoospore germination success per sporophyte was considered a replicate, and the average germination success for each sampling date was obtained by averaging the germination success for all sporophytes at the experimental buoys (the number of sporophytes decreased from seven on day 1 to one on day 91). *M. pyrifera* is very sensitive to changes in nutrients, especially during warm-water periods as occur during El Niño events (Hernández-Carmona et al. 2001). As our experimental plants were floating at the surface, there was little chance of nutrient replenishment from below the thermocline. In order to examine whether the loss of subsurface nutrients was a cause of drifter senescence, we measured changes in tissue nitrogen. Sporophylls from weekly samples from January–April 2004 were dried, milled, and analyzed for tissue N content using an autoanalyzer (CE Instruments NCS-2500 Elemental Analyzer, Rodano, Italy). Data were grouped by month and compared among sample dates using a one-way analysis of variance (ANOVA). No samples were dried for May and June because of the risk of a possible interference due to the epiphytes on the blades.

Reproductive viability of naturally attached sporophytes (control; CK). The reproductive viability of naturally attached sporophytes was estimated to control for the effect of sporophyte detachment (SAD) on reproduction. Frond length and number/sporophyte were estimated (as described above) every 28–34 days (mean = 30 days) from two naturally attached plants at two different sites of the Monterey Peninsula. For reproductive viability, 10 sporophylls were collected from at least three different sporophytes at each site ($n = 6$ plants), and the same parameters as the surface-attached sporophytes were measured, as described above.

Reproductive viability of naturally drifting (ND) and beach-cast sporophytes (BCD). We used small boats to search Monterey Bay for ND in order to compare sporophyll condition and reproductive viability with experimental and control plants. The search method consisted of (1) plotting a direct heading from Moss Landing harbor to the Monterey Peninsula, and (2) sampling all ND found along both sides of the heading, within sight of the boat. Sampling occurred every month during which control sporophylls were also collected from attached sporophytes at Monterey Peninsula. Some ND were also found during transit from Moss Landing harbor to our experimental drifter outplant site. The ND were observed on a total of 12 cruises. The reproductive viability of the ND was sampled as described above.

Independent of searching for ND, we visited Monterey Bay beaches (1 day per month from January–June 2004), traveling by car from the Monterey Peninsula to Moss Landing. BCD were found on seven such excursions. Sporophyll condition and reproductive viability were estimated (as described above) for one to seven moist BCD per day, using a total of 20–30 sporophylls for comparison with experimental and control plants. When multiple sporophytes were collected in one day, data were pooled to estimate average zoospore production and percentage germination for the sporophytes.

Tracking movement and reproductive viability of experimentally detached drifters (ED). Four sporophytes were experimentally detached off the Monterey Peninsula in October 2003 ($n = 1$) and January 2004 ($n = 3$) to create drifting rafts and calculate their displacement speed. The sporophytes were tagged at the surface using a radio-tracking transmitter with a bandwidth of 162–167 MHz. The radio transmitter was housed in a PVC pipe (60 cm long \times 10 cm diameter) filled with 150 cm³ of lead ballast at the bottom and foam for flotation. The top cap was drilled to extend an antenna out of the buoy (Harrold and Lisin 1989). After analyzing real-time CODAR current speeds and directions in Monterey Bay (<http://newark.cms.udel.edu/~brucel/realtime maps/>), the plants were transported to a deploying point from which we could likely recover the radio-tagged drifters after 2 days, before they were theoretically able to exit Monterey Bay or cast to the beach. The transmitter signal was located at sea every other day, using an Advanced Telemetry Systems (ATS™, Isanti, MN, USA) radio receiver. The receiver was connected to a four-element directional antenna with a coaxial cable. Once the kelp was located and recovered, the position was recorded, and the sporophyll condition and reproductive viability were estimated, as described above. Sporophytes were transported again to an appropriate point and rereleased to better estimate natural drifter speed within the bay. The new redeployed point was chosen based on the CODAR data using the same criteria explained above; the same tagged kelp was used because it is a less destructive method.

M. pyrifera is sensitive to water temperature, with sporophytes showing better development during cold years (La Niña) and poorer development during hot years (El Niño) (Edwards 2004), likely due to the tight negative correlation between nutrient concentration and sea surface temperature (SST; Zimmerman and Robertson 1985). In order to determine whether our experiment was carried out under normal temperature conditions (average from several years), we collected SST data for comparison with previous years. Historical SST data from 1987 to 2003 were obtained from NOAA Buoy Station 46042-MONTEREY, located at 27 nautical miles to the west of Monterey Bay, CA. Hourly temperatures were averaged over each month to give the average monthly SST ($n = 169$), and data gaps ($n = 35$) were filled using the long-term temperature record from Hopkins Marine Station on the Monterey Peninsula. The average monthly and interannual temperatures were also computed for the last 17 years (1987–2003) and compared with the monthly and annual average temperatures of 2004.

Statistics. Biological parameters were normally distributed and homoscedastic, and no data transformation was required. One-way ANOVA was used to compare the mean values of control sporophytes (CK) and surface-attached drifters (SAD) over time. The effects of time and sporophyte type (control kelp vs. surface attached kelp) on length, number of fronds, number of sporophylls per frond, sporophyll area (cm²), percentage of sorus area, zoospore production, and percentage of zoospore germination were analyzed as two-way ANOVAs with time as a random factor and *M. pyrifera* type fixed. Unequal N honest significant difference (HSD) *post hoc* test was used to detect the starting time when values were significantly different (Statistica 6.1). Data from natural and BCD were not compared statistically with CK, SAD, and ND because of the low number of replicates. However, basic statistics were computed (n , average, SD, \pm 1SD)

RESULTS

The average SST in Monterey Bay during 1987–2003 ranged from 12.2° C (January) to 14.9° C (September). The interannual average for that period was

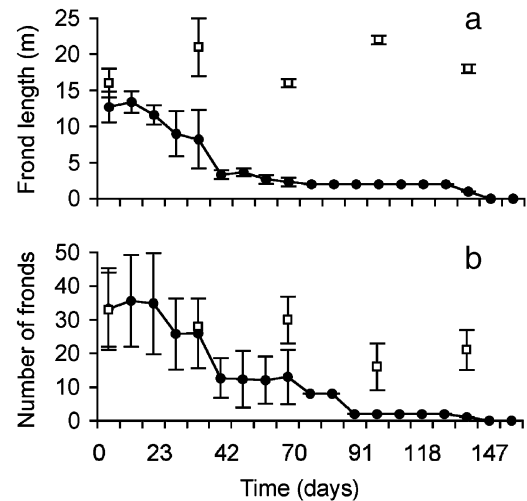


FIG. 3. Average frond length (a) and the average number of fronds (b) of the surface attached sporophytes at Moss Landing (●), and control sporophytes attached to the bottom at Monterey Peninsula (□) (\pm 1 SD).

13.2° C. During the experimental period (January–June 2004), SST ranged from 11.8° C (February) to 12.1° C (June), with an average of 12.2° C, and the annual average for 2004 was 13.3° C.

The average frond lengths of SAD were significantly reduced after 35 days ($P < 0.05$; Fig. 3a), decreasing from an average of 12.7–3.3 m (a 74% reduction). Upon reaching an average length of 2 meters (day 70), fronds did not significantly decrease in length ($P > 0.05$) until after day 118. All fronds were < 1 m long after 139 days. Frond lengths of CK ranged from 16 to 22 m and did not change significantly throughout the study ($P > 0.05$). The average number of fronds/sporophyte for SAD decreased significantly ($P < 0.05$) from 33 at the time of detachment to eight after 70 days (Table 1). The average number of fronds/sporophyte for CK ranged from 16 to 33 (Fig. 3b) and did not vary significantly with time ($P > 0.05$; Table 1).

The average number of sporophylls per frond for SAD decreased significantly ($P < 0.05$) from 14 at the beginning to 0 at the end of the experiment (Fig. 4a). The average sporophyll number for CK ranged from seven to 24 and did not vary significantly over time ($P > 0.05$). Sporophyll number for SAD was significantly lower than CK by day 28 (Table 1). Sporophyll number for ND was highly variable and ranged from four to 31. Although statistical analysis was not possible, the average sporophyll number tended to be higher for ND than CK. Sporophyll number for BCD ranged from six to 20 and tended to be lower than CK (Table 2).

The average sporophyll area for SAD ranged from 0 to 125 cm², whereas sporophyll area for CK ranged from 82 to 270 cm². The average sporophyll area for SAD was significantly lower than CK after day 62 ($P < 0.05$; Fig. 4b, Table 1). The average sporophyll area was similar between ND (86 cm²) and BCD

TABLE 1. Effects of time and sporophyte type (control kelp vs. surface attached kelp) on length, number of fronds, number of sporophylls per frond, sporophyll area (cm²), percentage of sorus area, zoospore production, and percentage of zoospore germination for *Macrocystis pyrifera* in Monterey Bay.

Source	df	Mean square	F value	P	Unequal N HSD <i>post hoc</i> test
a. Kelp length (m)					
Time (days)	4	19.3388	4.6322	0.0049	
Time × kelp type	4	28.33157	6.7862	0.0005	35 days, <i>P</i> = 0.0009
Error	30	4.1748			
b. Number of fronds					
Time (days)	4	215.3704	1.8385	0.1474	
Time × kelp type	4	46.4707	0.3867	0.8093	
Error	30				
c. Number of sporophylls per frond					
Time (days)	8	64.3200	2.7470	0.0013	
Time × kelp type	8	38.5529	1.6465	0.1366	28 days, <i>P</i> = 0.0237
Error	48	23.4138			
d. Sporophylls area (cm ²)					
Time (days)	9	4839.947	3.4278	0.0023	
Time × kelp type	9	4973.623	3.5225	0.0019	62 days, <i>P</i> = 0.0003
Error	50	1411.939			
e. Sorus area (%)					
Time (days)	8	893.9576	4.2186	0.0006	
Time × kelp type	8	604.3147	2.8518	0.0108	28 days, <i>P</i> = 0.0003
Error	50	211.904			
f. Zoospore production (g · h ⁻¹)					
Time (days)	8	47201940	3.0477	0.0074	
Time × kelp type	8	50916118	3.2875	0.0045	14 days, <i>P</i> = 0.0353
Error	48	15487520			
g. Zoospore germination (%)					
Time (days)	8	633.0724	2.7837	0.0129	
Time × kelp type	8	590.2055	2.5953	0.0192	154 days, <i>P</i> = 0.0078
Error	48	227.4132			

Data were analyzed as two-way ANOVAs with time as a random factor and *M. pyrifera* type fixed. Unequal N honest significant difference (HSD) post hoc test was used to detect the starting time when values were significantly different. See Figs. 3–5 for data.

(104 cm²; Table 2), but generally lower than CK. Sporophyll tissue N in SAD decreased significantly over time, from 2.0% (1.83–2.17% range) in January to 1.77% (1.6–1.94% range) in April, at which time sporophyll tissue N in SAD was significantly lower than in CK (2.0%, *P* < 0.05).

The average sorus area on SAD started at 73% and declined to 0% after 147 days, decreasing significantly only at day 22 (*P* < 0.05; Fig. 4c). Sorus area on CK did not change significantly (*P* > 0.05) during the study period (57%–92% range). Sorus area was significantly lower on SAD relative to CK after 28 days (*P* < 0.05, Table 1) and yet remained at these low levels without significant variation (*P* > 0.05) until the end of the experiment (147 days), at which time sorus was absent from the ED (last fertile day = 125). The average sorus area on ND was 53% (with only a single instance of 0%), whereas the sorus area on BCD (32%) was similar to the ED (22%).

Maximum zoospore production per gram of sporophyll tissue per hour from SAD was 14.168×10^3 at the beginning of the experiment (day 6), later decreasing to 4.427×10^3 . The average zoospore production did not vary significantly during the study (*P* > 0.05), likely due to high variability, but did decline to 0 after 147 days with the disappearance of sorus. Zoospore production from the CK ranged from 7.25×10^3 to 25.15×10^3 and showed a significantly lower value

(*P* < 0.05) only at day 42, maintaining high spore production throughout the experimental period (Fig. 5a). Zoospore production from SAD was significantly lower than CK after 14 days (*P* < 0.05; Table 1). Of the 21 ND observed, 16 produced zoospores (76%), with zoospore production ranging from 0.5×10^3 to 24.92×10^3 ; five ND (24%) were sterile. All 16 BCD were fertile, with zoospore production ranging from 2.08×10^3 to 8.38×10^3 . Again, a statistical comparison was not possible because of the lack of replicates BCD per date, but the data suggested that zoospore production of BCD (4.48×10^3) was less than CK (15.19×10^3) but similar to the SAD (4.43×10^3 ; Table 2).

The average zoospore germination success for SAD decreased from 95% to 33% by day 147. The average germination success for CK did not vary significantly, ranging from 60% to 90% (*P* > 0.05; Fig. 5b). Germination success for SAD was significantly lower than CK only on day 154 (Table 1). The average germination success was 76% for the 16 fertile ND, whereas germination success ranged from 16% to 70% for the BCD.

The average drifting distance was calculated for 10 radio-tracks from the four experimentally detached drifters and estimated to be 7.12 km/day (4.2–10.2 range; Fig. 1, Table 3). Given that the maximum time for reproductive longevity of ED was 125 days,

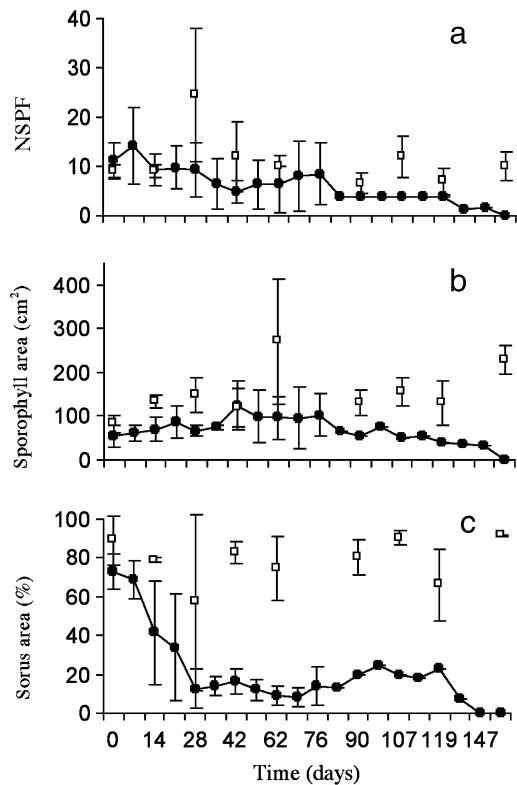


FIG. 4. Average number of sporophylls per frond (NSPF) (a), average total sporophyll area (cm^2) (b) average sorus area (%) (c). Control sporophytes (\square), experimental sporophytes (\bullet) (± 1 SD).

the radio-tracking data suggest an average effective dispersal distance of ~ 890 km (527–1254 range).

DISCUSSION

Drifting giant kelp *M. pyrifera* sporophytes are considered an important mechanism for long-distance dispersal, but the paucity of research on this topic reflects typical methodological problems encountered when attempting to estimate long-range dispersal in seaweeds (van den Hoek 1987). Although desirable, it is too costly to follow drifting kelp sporophytes for hundreds of days to determine their reproductive potential. Not only is it difficult to relocate drifters, but each

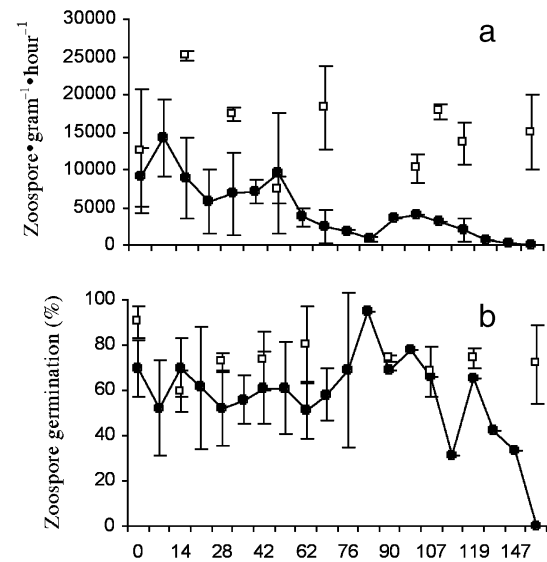


FIG. 5. Average number of zoospore $\cdot \text{g}^{-1} \cdot \text{h}^{-1}$ (a) and percentage of germination after 48 h in culture (b). Control sporophytes (\square), experimental sporophytes (\bullet) (± 1 SD).

day, drifters potentially move into regions of different water temperature and potential for physiological stress. As in many studies representing such logistic difficulties, a reasonable alternative is to mimic natural drifting conditions to give at least some approximation of the potential reproductive longevity of kelp drifters. Our study was conducted in Monterey Bay during a period when average SST varied little during the experimental year ($\pm 0.9^\circ \text{C}$) and was similar to previous years. During the experiment (January–June 2004), the temperature was almost constant; therefore, we assumed that temperature variation during the experiment did not influence the results.

The reduction in the length and number of fronds in the surface-attached kelps could be due to the effect of whiplash or tensile force, when the plants were attached to the buoys. The kelps were subjected to the strong force of local swell. Although they were not exposed to the same physical conditions as natural drifting kelp, after 35 days, this effect was reduced because the fronds were shorter, the tensile force was reduced, and the kelps maintained a fairly constant size (3.3 m) and residual biomass. Despite the loss of

TABLE 2. Reproductive potential of drifting *Macrocystis pyrifera* in Monterey Bay, USA.

Time (days)	NSPF		SpA		SA		ZGSH		G	
	ND	BCD	ND	BCD	ND	BCD	ND	BCD	ND	BCD
<i>N</i>	11	7	12	7	12	7	12	7	13	7
Average	19	13	86	104	53	32	8555	4484	44	46
SD	8	4	59	73	29	17	7871	1968	26	17
Minimum	11	9	27	31	23	15	684	2516	18	29
Maximum	27	17	145	178	82	48	16426	6452	70	63

ND, natural drifters; BCD, beach-cast drifters; NSPF, number of sporophylls per frond; SpA, sporophyll area (cm^2); SA, sorus area (%); ZGSH, zoospores per gram of sporophyll per h; G, percentage of germination.

TABLE 3. Trajectories of experimental drifting kelp *Macrocystis pyrifera*.

Route code	Dates	Deploying point	Recovering point	Drifting distance (miles · day ⁻¹)	Drifting distance (km · day ⁻¹)	Potential drifting distance (km) in 125 days
A	October 21–23, 2003	36°38.28'N 121°52.75'W	36°41.82'N 121°49.26'W	2.30	4.25	532
B	May 7–8, 2004	36°55.07'N 121°56.00'W	36°56.40'N 121°57.07'W	1.70	3.15	394
C	May 14–15, 2004	36°49.69'N 121°57.52'W	36°46.56'N 121°53.16'W	4.68	8.66	1082
D	May 15–17, 2004	36°49.69'N 121°57.52'W	36°46.36'N 121°48.17'W	4.19	7.76	970
E	May 18–19, 2004	36°52.64'N 122°00.78'W	36°49.11'N 121°56.26'W	4.65	8.61	1076
F	May 19–20, 2004	36°46.11'N 121°56.26'W	36°46.90'N 121°50.36'W	5.19	9.61	1201
G	May 20–22, 2004	36°54.91'N 121°02.68'W	36°54.78'N 121°53.63'W	3.64	6.73	842
H	May 22–25, 2004	36°55.00'N 121°05.00'W	36°52.01'N 121°50.57'W	4.00	7.41	926
I	May 25–27, 2004	36°55.00'N 122°05.00'W	36°54.66'N 121°09.50'W	1.64	3.03	379
J	May 27–29, 2004	36°55.00'N 122°09.50'W	36°47.10'N 121°48.00'W	6.49	12.01	1502
Average				3.85	7.12	890
SD				1.57	2.91	363
Minimum				2.28	4.22	527
Maximum				5.42	10.03	1254

Each trajectory corresponds to each release and recapture event.

biomass, the surface-attached kelp's reproductive potential was not significantly reduced during the first 5 months, in contrast with previous studies that showed a size-dependent reproductive collapse when canopy biomass was reduced (Reed 1987, Graham 2002). This finding is similar to the results of Buschmann et al. (2004) for annual *Macrocystis* populations in Chile, where short growing periods result in small sporophyte size and low soral surface area, yet high zoospore production and germination success. Thus, it appears that *Macrocystis* sporophytes may adapt reproductive output to the level of sporophyte biomass, in order to preserve high reproductive viability.

Previous studies have measured zoospore production in *M. pyrifera* as zoospores produced per hour per sporophyll (Anderson and North 1966). The size of a sporophyll or its biomass are, however, highly variable. Therefore, we scaled zoospore production rates to sporophyll biomass. Preliminary measurement on sporophylls from control plants ($n = 50$) showed that the average biomass of one mature sporophyll was 40 g (± 5 g). Therefore, the zoospore production rates obtained during this study would be on the order of 6×10^5 zoospores · g⁻¹ sporophyll, which is similar to previous reports (Anderson and North 1966, Graham 2002).

SAD also underwent a slow reduction of the number of sporophylls, along with a reduction of sporophyll area. These changes were associated with the loss of the longer fronds, together with sporophyll bundles, resulting in smaller fronds with small sporophylls. The sorus area was also reduced; however, after 28 days ~20% of the total sporophyll area with sorus was maintained for the remainder of the experiment. Tissue nitrogen content in the sporophylls was constantly reduced ($P < 0.05$) during the first four months from 2.0% to 1.77% and may have contributed to drifter senescence. The number of zoospores per gram of sporophyll tissue was constantly reduced, but any reproductive blade containing sorus produced viable

zoospores at relatively high production rates. This suggests that SAD remain fertile as long as sori are present, which, in Monterey Bay, may be as long as 125 days. Additional evidence of the fertility of the SAD was the numerous recruits found attached to their holdfasts. A maximum of 56 recruits were found on one sporophyte, ranging from 2.5 to 285 cm in length at the end of the experiment, suggesting that the high germination success observed in the laboratory was also occurring in the field. Finally, the observed fertility time of natural and surface-attached *Macrocystis* drifters was two to three times higher in Monterey Bay than along the coast of Chile (Macaya et al. 2005). One radio-tracked drifter trajectory was obtained during autumn (October), whereas the other nine trajectories were all followed in spring. Harrold and Lysin (1989) described typical springtime conditions in Monterey Bay as northwesterly winds increasing from the late morning to afternoon and then changing to a southerly direction in the evening. This pattern explains why drifters moved to the east and southeast, and why all drifting kelps were recovered near the coast or on the beach after 2–3 days. The dominant surface current was in accordance with drifter movement, and it was relatively easy to predict the trajectories from current direction. The mean displacement speed of $7.15 \text{ km} \cdot \text{day}^{-1}$ is equivalent to $8.2 \text{ cm} \cdot \text{s}^{-1}$. This value is higher than that obtained by Harrold and Lysin (1989) for springtime ($5.7 \text{ cm} \cdot \text{s}^{-1}$) and close to that obtained by Hobday (2000a), $8.5 \text{ km} \cdot \text{day}^{-1}$ or $9.84 \text{ cm} \cdot \text{s}^{-1}$. These data confirm the high velocity that drifters can reach. Although in our experiment most of the drifters were directed to the beach, eventually some kelp could change direction and travel out of the bay. At least one of the ND that we found in the Bay had large barnacles (*Lepas anatifera*; average 5.2 mm) on the blades. According to Skerman (1958), this size corresponds to organisms adrift for 15 days. This suggests that these kelps were floating for at least 15 days, probably traveling in circles inside the bay or

coming from outside of the bay. Similar results were observed in Chile, where *Lepas* spp. data were used to estimate that kelp can drift for at least three weeks (Macaya et al. 2005). Hobday (2000a) studied the abundance and dispersal of drifting kelp *M. pyrifera* rafts in the Southern California Bight and observed that loss of attached adults was higher in winter and lowest in fall. Raft density ranged from 0.78 to 6.96 plants · km⁻², and the instantaneous abundance ranged from 39,000 to 348,000 drifting rafts. Southward dispersal away from the coast was observed in all months of the year. Dispersal north was more frequent in summer and winter, while dispersal south was more frequent in late winter and early spring. He defined a “successful connection” event as a drifter starting less than 10 km and ending less than 5 km from the coast. Under this definition, 45% of all drifters released in his study were successful. The maximum drifting kelp displacement recorded by other researchers is 1092 km (Hobday 2000a). This suggests that drifting kelp has the potential to travel and disperse viable zoospores over long distances, enough to connect all kelp beds in the Northern Hemisphere over generational time-scales. Considering the instantaneous abundance of drifting kelp, the potential to seed the coast with zoospores is high.

Some biases may arise from the method used to tether the sporophytes to the surface, compared with ND (Hobday 2000b). The floating period may be extended as new water and nutrients move past the sporophyte, and thus, the potential drifting time may be overestimated. ND are estimated to float a maximum of 109 days (Hobday 2000b). In that case, the potential spore dispersal would be reduced to 779 km, which is a more conservative value than our estimates, but still four times the values predicted by Macaya et al. (2005).

We conclude that the reproductive longevity of drifting *Macrocystis* sporophytes is long enough to support long-distance dispersal of over 1000 km. Despite significant reduction in drifter size over time, drifter reproductive viability is maintained at relatively high levels as long as enough biomass is present to promote the production of sori. Furthermore, the determination that drifting *Macrocystis* sporophytes can maintain high levels of zoospore germination rates beyond four months of being adrift indicates that *Macrocystis* drifters are truly viable long-distance dispersal vectors. Future studies that examine drifter reproductive output as a function of oceanographic conditions (e.g. movement into oligotrophic tropical waters) will be a valuable contribution to the study of long-distance dispersal by drifting kelp.

Drifting kelp is not only important for its dispersal potential, but kelp forest fauna that remain on kelp rafts have the potential to be dispersed among isolated kelp forests (Helmuth et al. 1994, Hobday 2000c); more than 200 species of fish and invertebrates have been identified on *Macrocystis* rafts (Bushing 1994). Pelagic species with larval dispersal, such as *Lepas* spp. may complete a cycle of larval settlement, growth, and

reproduction before kelp rafts sink or arrive to the coast (Hobday 2000c). Hobday (2000c) further suggests that most of the common attached *M. pyrifera* fauna are unaffected by rafting and may persist for the entire duration that rafts are adrift.

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