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THE EFFECTS OF HIGH IRRADIANCE ON THE SETTLEMENT COMPETENCY AND VIABILITY OF KELP ZOOSPORES[1]

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Elevated irradiance has a profound effect on the successful dispersal and establishment of kelp zoospores, affecting their physiology and viability. The research to date, however, has been on zoospores localized near the benthos, with little attention on the importance of vertical transportation and subsequent exposure to increased irradiance. Therefore, we wanted to investigate the effects of exposure to high irradiance on the reproductive planktonic life-history stages of kelps *Macrocystis pyrifera* (L.) C. Agardh and *Pterygophora californica* Rupr. Zoospores of both species were exposed to different irradiances (75, 275, 575, 1,025 μmol photons · m^{-2} · s^{-1}) over varying durations (1, 2, 4, 8, 12 h) and subsequently monitored for settlement competency, gametophyte development, and reproductive viability. Settlement success for *M. pyrifera* was uniform throughout all irradiance × time treatments, while settlement for *P. californica* decreased with increasing exposure time but not irradiance, although settlement was generally reduced at the highest irradiance level. Following zoospore settlement, germ tube development was visible in the gametophytes of both species within 1 week, although a significant decline of germ tube density in *P. californica* was observed with increasing irradiance. Similarly, a decrease in germ tube development with increasing exposure was observed across all irradiance levels for *M. pyrifera*, but irradiance itself was not significant. Further development into embryonic sporophytes was remarkably similar to gametophyte development, suggesting that the effect of exposure of kelp zoospores to high irradiance on subsequent sporophyte production is mediated through gametophyte development as well as zoospore survival.

Key index words: **depth; gametophyte; irradiance; kelp; *Macrocystis; Pterygophora;* sporophyte; zoospore**

Abbreviations: **FOV, field of view; PES, Provasoli enriched seawater**

Long-distance dispersal by kelp zoospores may play an important role in the recovery of disturbed habitats following widespread kelp loss. Given that most kelp zoospores (e.g., those of *M. pyrifera* and *P. californica*) tend to settle within a few meters of the sporophytes that released them (Reed et al. 1992), processes that increase their dispersal potential may be integral to regional-scale patterns of kelp resilience. For example, *M. pyrifera* zoospores can disperse up to 4 km (Reed et al. 1988), remain swimming for up to 120 h after release (Reed et al. 1992), and facilitate recruitment on newly exposed isolated habitats (Reed and Schroeter 2004). While these zoospores produce energy via photosynthesis and retain lipid reserves, both of which can be used for swimming (Amsler 1988, Reed et al. 1992, 1999), their small size (~3–7 μm) and slow swimming speeds (~0.0012 mm · s^{-1}; Gaylord et al. 2002) suggest that swimming may be effective once the zoospores enter the boundary layer near the substrate (Stevens et al. 2003) and may therefore not play an active role in long-distance dispersal. However, zoospores can also be transported vertically from near the benthos into the water column by hydrodynamic forces, thus exposing them to a greater unidirectional flow and increasing their dispersal potential (D. K. Cie and M. S. Edwards, unpublished). Unfortunately, this phenomenon may also expose these zoospores to increased levels of harmful conditions, such as high irradiance, resulting in reduced survival and/or viability. This may be further exacerbated with increasing exposure to these irradiances. Even though these zoospores may represent only a small fraction of the total number in the water column at any one time (D. K. Cie and M. S. Edwards, unpublished), they may contribute disproportionately to the population's ability to disperse long distances and colonize remote habitats. Therefore, understanding how these zoospores are affected by exposure to elevated irradiances over varying durations may prove integral to understanding their overall importance to long-term kelp stability over local to regional scales.

In the coastal zone, irradiance decreases rapidly with depth according to Beer-Lambert's law: $I_z = I_0 e^{-z(E_w + E_p)}$, where z = depth, I_0 = surface irradiance, I_z = irradiance at depth z, E_w = the extinction coefficient of the water and its suspended particles, and E_p = biomass per unit volume (Duarte and Kalff

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1987). Given that high irradiance (i.e., PAR, 400–700 nm; UV radiation, 280–400 nm) generally has a negative impact on the microscopic life stages of kelp (Lüning and Neushul 1978, Fain and Murray 1982, Deysher and Dean 1984, 1986a,b, Gerard 1984, Wing et al. 1993, Graham 1996, Altamirano et al. 2004, Fairhead and Cheshire 2004), exposure of kelp zoospores to increased irradiance in shallower water may result in reduced development and viability. For example, Wiencke et al. (2004) observed that zoospores of *Laminaria digitata, L. saccharina*, and *Alaria esculenta* all became photoinhibited and exhibited a reduced viability under prolonged exposure to high irradiances characteristic of shallower water, but that the magnitude of these impacts varied depending on the depth at which the parent sporophytes resided. Similarly, Swanson and Druehl (2000) observed that zoospores of *M. integrifolia* were negatively impacted by exposure to elevated UV light, although their sensitivity varied with zoospore size. Likewise, when exposed to irradiances exceeding 900 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a period of 1–4 min, benthic gametophytes of *M. pyrifera* and the stipitate kelp, *P. californica*, ceased being viable (Lüning and Neushul 1978), supporting Graham's (1996) observation that recruitment of *M. pyrifera* to shallow water was inhibited by photodamage to its benthic microscopic gametophytes and embryonic sporophytes. Given this finding, it is likely that exposure of *M. pyrifera* and *P. californica* zoospores to high irradiances will result in reduced settlement competency, postsettlement development, and viability. Here, we examine how exposure to different levels of irradiances over varying time periods impacts settlement competency of *M. pyrifera* and *P. californica* zoospores and their postsettlement germination and sexual reproduction.

MATERIALS AND METHODS

To examine the effects of exposure to high irradiance (PAR) on kelp zoospore settlement, development, and viability, reproductive sporophylls (blades containing fertile sori) were collected from five randomly selected mature *M. pyrifera* and *P. californica* occurring at 12 m depth within the Point Loma kelp forest (study site: 32′41.965° N, 117′16.034° W), San Diego, California, USA. The blades were immediately placed in a dark cooler and transported back to the laboratory where they were rinsed with sterilized seawater and placed in the dark in a 4°C incubator for a period of 24 h. Zoospores were then obtained by cutting ~10 g of sorus material from each of the sporophylls and immersing the excised sori into a 400 mL Pyrex beaker filled with 300 mL of nutrient-enriched filtered seawater (Provasoli enriched seawater [PES], Provasoli 1968). Zoospores from all five sori were pooled in the same beaker, and their density estimated using a hemacytometer every few minutes until it exceeded 2.0×10^7 zoospores $\cdot$ mL^{-1}. At this time, the sorus material was removed from the beaker, and the spore solution diluted to produce a concentration of 5.0×10^6 zoospores $\cdot$ mL^{-1}. A 2 mL aliquot of this solution ($\sim 1.0 \times 10^7$ zoospores) was then added to each of 40 petri dishes (bottom surface area = 5,675 mm^2) containing 25 mL of PES to facilitate a target settlement density of

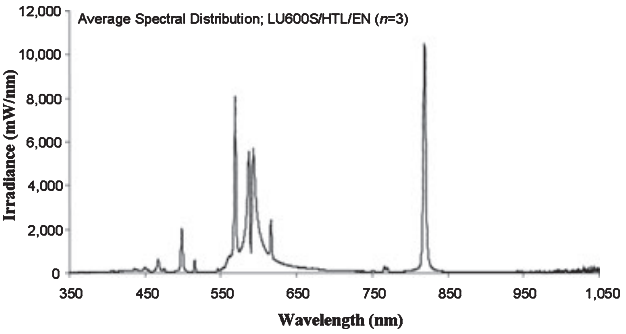

FIG. 1. Spectral data for the Hortilux Super HPS EN high-pressure sodium lamp (LU 600S/HTL/EN) used to irradiate zoospores. Graph courtesy of EYE Lighting International of North America.

$\sim 1.8 \times 10^3$ zoospores $\cdot$ mm^{-2}. All 40 dishes were then placed into a recirculating water bath 0.5 cm deep at 16°C (±0.5°C) under varying levels of irradiance and exposure periods. Illumination was supplied by a full-spectrum (27% relative energy at 500 nm) Hortilux Super HPS EN high-pressure sodium lamp (model LU 600S/HTL/EN; EYE Lighting International of North America Inc., Mentor, OH, USA). Average spectral distribution is provided in Figure 1. The light was unfiltered, allowing for full spectral transmittance to the zoospores. Four irradiance levels were established by positioning the dishes at different proximities to the light source, and irradiances verified using a LI-COR LI 250A light meter and LI 190SA quantum sensor (LI-COR Biosciences, Lincoln, NE, USA). Irradiance levels (75, 275, 575, 1,025 μmol photons $\cdot$ $m^{-2} \cdot s^{-1}$) were selected to represent potential levels that zoospores may experience at the surface and in the upper few meters of the water column during the day (Paulson and Simpson 1977; M. S. Edwards and K. Y. Kim, unpublished data). Five exposure times were established for each irradiance level by collecting dishes at predetermined intervals (1, 2, 4, 8, and 12 h). Exposure times were chosen to encompass a range of potential durations at elevated irradiances that zoospores may experience during a day, and each irradiance × exposure time treatment was replicated twice. Immediately following termination of each exposure treatment, dishes were transferred to a 12°C Percival E-36L incubator (Percival Scientific Inc., Perry, IA, USA) and cultured in PES under 60 μmol photons $\cdot$ $m^{-2} \cdot s^{-1}$ (Philips F17T8/TL741 fluorescent bulbs [Philips Electronics North America Corp., New York, NY, USA]; 0.04% relative energy at 500 nm) and 14:10 light:dark (L:D) conditions.

After the initial 48 h in the incubator, zoospore settlement within each dish was estimated within five haphazardly selected fields of view (FOV) under ×400 magnification using a Leitz Wetzlar DIAVERT inverted microscope (Leica Microsystems Inc., Bannockburn, IL, USA) equipped with a Leica DC-480 digital camera. Only those zoospores that settled and attached to the bottom were counted. Immediately after examination, the dishes were returned to the incubator. To reduce handling effects, dishes were not exposed to irradiances >60 μmol photons $\cdot$ $m^{-2} \cdot s^{-1}$ while outside of the incubator. Growth media in the dishes was exchanged every 2 weeks, and the dishes reexamined each week for 8 weeks and monitored for gametophyte development (i.e., germ tube production) and reproductive competency (i.e., embryonic sporophyte production). We used separate two-way random factor analysis of variance (ANOVA) to test the effects of irradiance and exposure time on zoospore settlement, development, and competency for each species. Following each analysis, the magnitudes of effect (percent contribution of each factor to overall total model

variance) were calculated using variance component analyses according to Graham and Edwards (2001). Prior to testing, data were examined for homogeneity of variances using Cochran's C test and for normality by graphical interpretation of residual plots.

RESULTS

P. californica zoospore settlement decreased significantly with increasing exposure times ($P \leq 0.001$) but not irradiance levels ($P \leq 0.098$, Table 1A). There was, however, a significant interaction between exposure time and irradiance level (Irradiance × exposure time interaction, $P \leq 0.035$), highlighting a clear trend in which settlement was reduced at higher irradiances, especially in the longest (12 h) exposure time (Fig. 2A). Settlement was observed in all dishes where zoospores were exposed to the lowest irradiances (75 and 275 μmol · $m^{-2} \cdot s^{-1}$), regardless of exposure time, although the zoospores exposed to 275 μmol · $m^{-2} \cdot s^{-1}$ for 12 h exhibited far lower settlement than did zoospores exposed to 75 μmol · $m^{-2} \cdot s^{-1}$ for the same duration. At intermediate exposure times (2, 4, and 8 h), zoospore settlement was similar among all irradiance levels (Fig. 2A). In contrast, settlement was not observed in any dishes when zoospores were exposed to irradiances of 575 and 1,025 μmol · $m^{-2} \cdot s^{-1}$ for 12 h (Fig. 2A). In contrast, *M. pyrifera* zoospore settlement was relatively high in all treatment combinations but did not vary among either irradiances ($P \leq 0.346$) or exposure times ($P \leq 0.415$), nor did these two factors interact with one another ($P \leq 0.552$, Table 2A; Fig. 3A). Interestingly, *P. californica* zoospore settlement was lower than *M. pyrifera* settlement in all treatment combinations except the lowest irradiance (75 μmol · $m^{-2} \cdot s^{-1}$) and shortest duration (1 h) when settlement was similar between the two species (Fig. 2A vs. 3A).

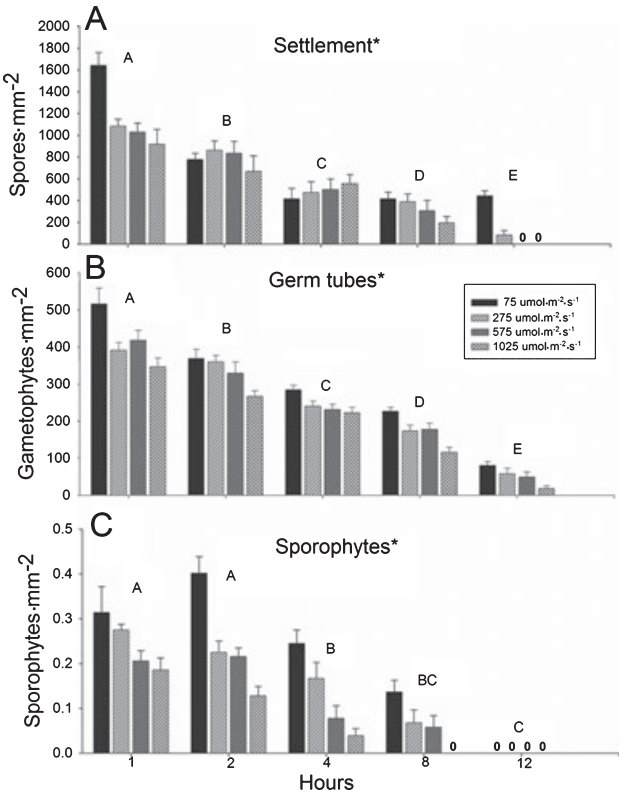

FIG. 2. Density of *Pteryogophora californica* (±SE) zoospores (A), gametophytes (B), and embryonic sporophytes (C) following four irradiance treatments. Data are representative of two independent trials. Asterisks indicate statistical significance.

Following zoospore settlement, germ tube development was visible in both *M. pyrifera* and *P. californica* gametophytes within 1 week. However, a significant decline in the density of *P. californica* gametophytes producing germ tubes was observed with both increasing exposure time ($P \leq 0.001$) and irradiance level ($P \leq 0.001$), and without any

TABLE 1. Results of separate two-way random effects ANOVAs testing the effects of irradiance level and exposure time on *Pterygophora californica* zoospore settlement (A), gametophyte development (germ tube production) (B), and reproductive competency (sporophyte production) (C).

Source	Sums of squares	df	MS	*F*-ratio	*P*	ω^2
A—Zoospore settlement						
Irradiance	403,345.196	3	134,448.399	2.621	0.098	0.005
Exposure time	5,288,234.984	4	1,322,058.746	25.769	**0.001**	0.975
Irradiance × Exposure time	615,644.344	12	51,303.695	2.486	**0.035**	0.010
Error	412,696.560	20	20,634.828			0.012
B—Germ tube development						
Irradiance	51,734.413	3	17,244.804	16.024	**0.001**	0.009
Exposure time	645,170.645	4	161,292.661	149.878	**0.001**	0.900
Irradiance × Exposure time	12,913.845	12	1,076.154	1.692	0.144	0.087
Error	12,724.168	20	636.208			0.004
C—Sporophyte production						
Irradiance	0.120	3	0.040	10.000	**0.001**	0.191
Exposure time	0.375	4	0.094	23.500	**0.001**	0.596
Irradiance × Exposure time	0.051	12	0.004	0.977	0.500	0.001
Error	0.087	20	0.004			0.212

ω^2 denotes the percent contribution of each factor to total model variance and was calculated according to Graham and Edwards (2001). Bold numbers indicate statistical significance ($P \leq 0.05$). ANOVA, analysis of variance.

TABLE 2. Results of separate two-way random effects ANOVAs testing the effects of irradiance level and exposure time on *Macrocystis pyrifera* zoospore settlement (A), gametophyte development (germ tube production) (B), and reproductive competency (sporophyte production) (C).

Source	Sums of squares	df	MS	*F*-ratio	*P*-value	ω^2
A—Zoospore settlement						
Irradiance	55,953.616	3	18,651.205	1.214	0.346	0.020
Exposure time	65,382.264	4	16,345.566	1.064	0.415	0.007
Irradiance × exposure time	184,399.624	12	15,366.635	0.912	0.552	0.000
Error	336,958.240	20	16,847.912			0.973
B—Germ tube development						
Irradiance	11,160.305	3	3,720.102	1.529	0.257	0.007
Exposure time	542,000.026	4	135,500.006	55.698	**0.001**	0.883
Irradiance × exposure time	29,192.910	12	2,432.742	1.390	0.249	0.018
Error	35,002.350	20	1,750.118			0.092
C—Sporophyte production						
Irradiance	0.022	3	0.007	0.411	0.748	0.000
Exposure time	0.665	4	0.166	9.765	**0.001**	0.871
Irradiance × exposure time	0.208	12	0.017	1.450	0.223	0.022
Error	0.240	20	0.012			0.107

ω^2 denotes the percent contribution of each factor to total model variance and was calculated according to Graham and Edwards (2001). Bold numbers indicate statistical significance ($P \leq 0.05$). ANOVA, analysis of variance.

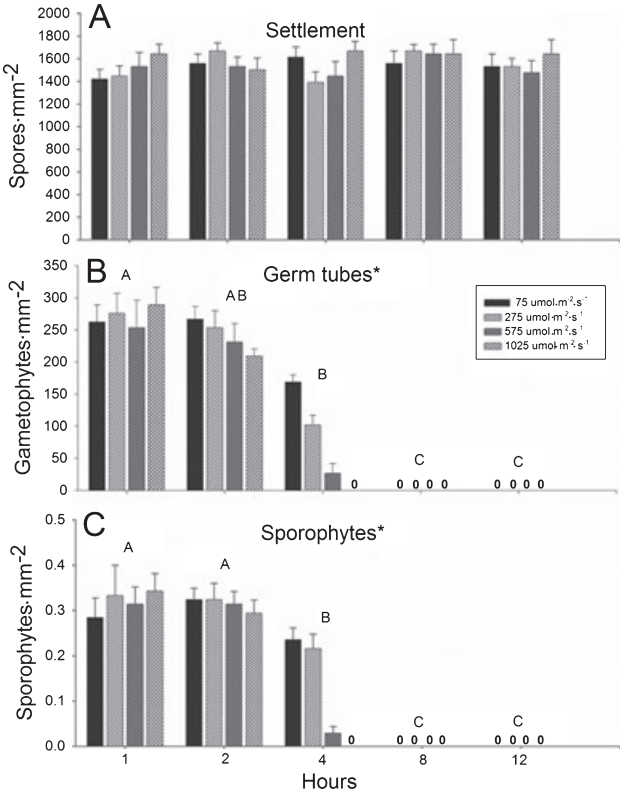

FIG. 3. Density of *Macrocystis pyrifera* (±SE) zoospores (A), gametophytes (B), and embryonic sporophytes (C) following four irradiance treatments. Data are representative of two independent trials. Asterisks show statistical significance.

interactions between these two factors ($P \leq 0.144$, Table 1B; Fig. 2B). Similarly, a significant decrease in the density of *M. pyrifera* gametophytes producing germ tubes was observed with increasing exposure times ($P \leq 0.001$), although not with increasing irradiance level ($P \leq 0.257$). In fact, no *M. pyrifera* gametophytes produced germ tubes in any treatment combinations beyond the 8 h exposure time, regardless of irradiance level (Fig. 3B).

Much as for gametophyte development, embryonic sporophyte production (used here as a proxy for reproductive viability) was greatly affected by exposure to high irradiances in both species. Specifically, *P. californica* sporophyte production declined significantly with increasing irradiance level ($P \leq 0.001$) and exposure time ($P \leq 0.001$, Table 1C; Fig. 2C), while *M. pyrifera* sporophyte production declined significantly with increasing exposure time ($P \leq 0.001$) but not irradiance levels ($P \leq 0.748$, Table 2C; Fig. 3C). Interestingly, these results followed very similar patterns observed for gametophyte germ tube production in both species (Fig. 2C vs. 3C) and, therefore, may have been a result of effects imposed on gametophyte development prior to sexual reproduction.

DISCUSSION

Recent studies have indicated that long-distance dispersal by kelp zoospores may play an important role in their colonization of newly exposed habitats (Reed and Schroeter 2004) and in the recovery of recently disturbed habitats (Graham 2003). Given that most kelp zoospores, especially those of *M. pyrifera* and *P. californica*, tend to settle within a few meters of the parental sporophytes (Reed et al. 1992), processes that increase dispersal potential may be integral to long-term regional-scale patterns of kelp persistence. Further, given that limited dispersal may result in propagules from the same individual settling in close proximity to each other and thus increasing rates of self-fertilization and subsequent reproductive viability (Raimondi et al. 2004), an increase in dispersal potential may play an important role in decreasing inbreeding depression,

and therefore increasing reproductive success by mixing propagules from distant sources. Unfortunately, processes that increase dispersal potential may also expose kelp zoospores to increased levels of harmful conditions, such as high irradiance (D. K. Cie and M. S. Edwards, unpublished), resulting in reduced viability. Most discussions on the matter, however, have focused on those zoospores in the water column near the benthos (Graham 2003, Gaylord et al. 2006) and have largely ignored the importance of zoospores that are transported from the benthos upward into the shallower portions of the water column where they may experience increased dispersal potential from greater unidirectional flow. Our results clearly show that exposure of *P. californica* and *M. pyrifera* zoospores to elevated irradiance (similar to levels that may be encountered in the upper portions of the water column during the day) over several hours has strong negative effects on their subsequent settlement, development (gametophyte germ tube development), and reproductive viability (embryonic sporophyte production). Also, similar to other studies that have observed significant variation among species with regard to zoospore sensitivity to high irradiance (Swanson and Druehl 2000, Wiencke et al. 2004), our results suggest that *P. californica* zoospores are more strongly affected by exposure to elevated irradiance than *M. pyrifera* zoospores. These effects were most pronounced in the later stages of gametophyte development and sexual reproduction, suggesting that the ultimate impacts of exposure to elevated irradiance may be delayed until several weeks after the exposure occurs. Given that zoospores may naturally encounter high irradiances over several hours when transported toward the surface suggests that these zoospores may not play an integral role in successful long-distance dispersal unless they are able to disperse during periods of low irradiance, such as at night or during cloudy or overcast days. This possibility, however, is yet to be tested in situ.

Following successful settlement, significant differences in germ tube development were noticeable among most of the treatment levels, with the exception of the shortest exposure times (1, 2, and 4 h) in *M. pyrifera*. Generally, however, gametophyte development decreased markedly with increasing exposure times and irradiance levels, with the greatest declines observed in the longest exposures to the highest irradiances. In fact, *M. pyrifera* gametophytes did not produce germ tubes in any irradiance once exposure time reached 8 h. This result was surprising given that naturally occurring zoospores can experience irradiance levels that approach this in areas where the kelp canopies have been removed and when the water is clear (Edwards 1998), but this effect may be limited only during the midday when irradiances are the greatest (M. S. Edwards and K. Y. Kim, unpublished). However, because germ tube development is directly dependent on zoospore settlement success, the observed reduction in postsettlement development could also be linked to density-dependent mortality and/or development of gametophytes (Reed 1990), or to the ''burn out'' phenomenon of irradiated zoospores that can lead to a reduction in photosynthetic pigments and decreased germ tube growth (Michler et al. 2002). Patterns of sporophyte production, in turn, were remarkably similar to those of gametophyte germ tube development in both kelp species. This finding suggested that the effects of zoospore exposure to high irradiance on subsequent sporophyte production were mediated through their effects on gametophyte development.

Our results indicate that, although kelps occur throughout the temperate regions of the world and inhabit various depths along the coastline, the microscopic stages of at least some species may be limited from certain habitats by exposure to high irradiance (Graham 1996). Much as with microscopic benthic stages, the differences in sensitivity to high irradiance between *M. pyrifera* and *P. californica* zoospores imply that within the Lamanariales, tolerance of zoospores to increased light levels may be species-specific (see also Swanson and Druehl 2000, Wiencke et al. 2004). Interestingly, these patterns seem to follow those that might be expected in the adult sporophyte stages; large portions of *M. pyrifera* thalli occur in shallower water or at the surface, while the thalli of *P. californica* primarily occur near the benthos (Foster 1975). This trend may have important implications given that Swanson and Druehl (2000) and Wiencke et al. (2004) observed that kelp zoospore sensitivity to high irradiance was dependent on the depth at which the parent sporophytes occur. However, we are currently unable to explain why zoospore settlement failed in all treatment combinations where exposure durations exceeded 8 h and in the highest irradiance for 4 h. While zoospores may not experience irradiances above 275 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in nature unless they are transported to near the surface, they probably do regularly experience irradiances of 75 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for at least several hours during the midday in areas where kelp canopies have been removed (Clark et al. 2004). It is unknown if these zoospores are able to fully develop and reproduce or if recruitment arises from zoospores that avoid these irradiances by being released during the night, on cloudy days, during periods of moderate to high turbidity (and thus low light attenuation in the water), or under existing kelp canopies. However, it is clear that exposing zoospores of either species to high irradiances for long durations reduces both development and viability. Therefore, while the transport of kelp zoospores from the benthos into the water column may increase their dispersal potential, if they are transported to depths where irradiances exceed their tolerances and remain there for extended periods, they may lose

their ability to successfully settle, develop, and produce sporophytes. Thus, hydrodynamic processes that transport these spores into shallower water must be balanced with forces that quickly return them to the benthos before they are damaged, or these processes must occur during periods of low irradiance in order for this to be a viable way of increasing dispersal potential.

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