

THE EFFECTS OF MYSID GRAZING ON KELP ZOOSPORE SURVIVAL AND SETTLEMENT¹

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Recent studies have indicated that long-distance dispersal by kelp zoospores may play an important role in the colonization of newly exposed rocky habitats and in the recovery of recently disturbed kelp forests. This may be facilitated by the vertical transport of zoospores into the shallower portions of the water column where they are exposed to greater alongshore currents that increase their dispersal potential. However, this vertical transport can also expose them to elevated irradiances and enhanced grazing by zooplankton, both of which negatively impact zoospore survival and settlement. In this study, we used plankton tows to show that zooplankton (mysids) were at least seven times more abundant in the surface waters than near the benthos along the edge of a large kelp forest at the time of our spring sampling. We then used feeding experiments and epifluorescence microscopy to verify that these mysids grazed on kelp zoospores. Finally, we conducted laboratory experiments to show that grazing by these mysids over a 12 h period reduced kelp zoospore settlement by at least 50% relative to treatments without grazing. Together with previous studies that have revealed the impacts of high irradiance on zoospore survival and settlement, our study indicates that the vertical transport of kelp zoospores into the shallower portions of the water can also expose them to significantly increased mortality from mysid grazing. Thus, if these patterns are consistent over broader temporal and geographic scales, vertical transport may not be a viable method for sustained long-distance zoospore dispersal.

Key index words: grazing; kelp; long-distance dispersal; *Macrocystis*; mysid; zooplankton; zoospore

The persistence of biological populations is often dependent on local adult reproduction and/or dispersal of propagules from distant habitats (Underwood and Fairweather 1989, Caley et al. 1996, Mora and Sale 2002). This may be especially important in marine ecosystems where the adult life stages of many species are sessile and benthic while their reproductive propagules (i.e., larvae, spores) are

motile and dispersive (Caley et al. 1996). As a result, patterns of species distribution and abundance in marine populations have been linked to processes that control the survival and dispersal of their propagules (Thorson 1946, 1950, Grosberg and Levitan 1992, Hughes et al. 2000, Graham 2002, Corell et al. 2012). Simply, processes that enhance propagule survival can allow them to remain in the water column longer and thereby increase their dispersal potential, whereas processes that reduce propagule survival can reduce their dispersal potential. Once in the water column, ocean currents, turbulent mixing, and water column stratification all play determining roles in how far they will disperse and thus the larvae of some species respond to depth-specific differences in these factors by altering their position in the water column (Morgan 1990, Corell et al. 2012). However, this can also result in exposure to higher levels of predation, irradiance and UV radiation, which can significantly reduce propagule survival and postsettlement competency (Morgan and Christy 1995, 1996, Cie and Edwards 2008). Therefore, discerning the processes that regulate propagule survival in the water column can prove fundamental to understanding how far they can disperse, and ultimately patterns of adult distribution and abundance.

Kelps, large brown algae in the order Laminariales, dominate the coastal marine environments of temperate to polar waters (reviewed in Foster and Schiel 1985). These algae exhibit heteromorphic life histories in which large diploid sporophytes alternate with microscopic haploid gametophytes and planktonic zoospores (reviewed in Schiel and Foster 2006). Following their release from the parental sporophytes, the zoospores are passively dispersed along the benthos via advective and/or diffusive processes, with dispersal generally limited to within a few meters (Reed et al. 1992, Gaylord et al. 2002, Graham 2003). However, dispersal in the giant kelp, *Macrocystis pyrifera* (L.) C. Agardh, has been observed to occur over several kilometers (Reed et al. 1988) and is believed important for the colonization of isolated habitats such as newly established artificial reefs (Reed and Schroeter 2004). Such long-distance dispersal may be a result of drifting sporogenic material (Hobday 2000, Macaya 2005, Hernandez-Carmona et al. 2006) or by the vertical transport of zoospores into the water

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column where they are exposed to greater along-shore current flows (Reed et al. 1992, Gaylord et al. 2002, Stevens et al. 2003). For example, Cie and Edwards (2011) used settling plates positioned throughout the water column to show that *M. pyrifera* zoospores are transported vertically into the water column, presumably due to the vertical movement of water that is associated with the vertical components of the wave orbitals and how they interact with bottom topography, but that their density decreases exponentially with increasing distance from the benthos. Furthermore, although overall zoospore density varies seasonally (see also Graham 2003), Cie and Edwards (2011) observed this transport occurs year-round and is generalizable throughout the large kelp forest (i.e., Point Loma, CA) within which it was studied. However, if this vertical transport occurs during the day, it can also result in exposure to greater irradiances that can negatively impact zoospore survival and postsettlement competency (Cie and Edwards 2008). In fact, exposure to irradiances of $\sim 275 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (levels expected just a few meters below the surface) for as little as 4 h can result in high zoospore mortality and a near 100% reduction in postsettlement reproductive competency (Cie and Edwards 2008). In contrast, if the zoospores are transported to the surface waters during the night and are able to return to the benthos before the following day, they may avoid these negative irradiance impacts. However, such rapid return to the benthos is unlikely given their slow swimming speeds ($0.0012 \text{ mm} \cdot \text{s}^{-1}$) which prevent the zoospores from effectively moving significant distances through the water column except when they occur in the boundary layer (Stevens et al. 2003), and the complex physical forces required to transport them to the benthos (Gaylord et al. 2002, Cie and Edwards 2011).

In addition to higher irradiances near the surface, many zooplankton also exhibit heterogeneous distributions throughout the water column, often in response to food availability (Clutter 1966). For example, while many species of mysids (Crustacea, Mysida) exhibit diel vertical migration in response to light and food (Beeton and Bowers 1982, Rudstam et al. 1989), some species in coastal environments are generally more abundant near the benthos, whereas others are more abundant in the upper portions of the water column where they can be strongly associated with kelp canopies (Coyer 1984, Turpen et al. 1994). These filter-feeding, shrimp-like crustaceans are primarily omnivorous, using their legs to filter detritus, phytoplankton, and smaller zooplankton from the water column (Fulton 1982, Fockede and Mees 1999, Viherluoto et al. 2000). Furthermore, although mysids are unusual among marine invertebrate planktivores in that they have imaging-forming compound eyes that enable them to selectively capture food in the light (Mauchline 1970, Mauchline 1980, Siegfried and Kopache 1980), some

species feed more heavily at night with feeding rates independent on prey density, whereas others feed during the day with feeding rates dependent on prey density (Fulton 1982). In southern California, several species of mysids are strongly associated with *M. pyrifera* canopies where they can be important planktivores (Coyer 1984, Turpen et al. 1994), although it remains unclear whether these mysids feed on kelp zoospores and thereby reduce their survival in the water column. If so, this can be especially important if grazing is similar between the day and night and thus the time of spore release does not significantly impact zoospore survival as seen for irradiance. In this study, we address the simple questions of (i) are mysids more abundant in the surface waters near the edge of a large kelp forest than near the benthos, (ii) do mysids graze on *M. pyrifera* zoospores, (iii) does this grazing result in reduced survival and settlement of *M. pyrifera* zoospores, and (iv) do these interactions differ between daytime and nighttime conditions?

METHODS

This study was done in the Point Loma kelp forest, near San Diego, CA during spring 2012. First, to examine differences in the relative abundance of mysids between surface waters and near the benthos, six 50 m long plankton tows were taken on a single day between 1,100 and 1,300 h near the southern edge of the forest by dragging a 120 μm mesh plankton net with a 10 cm diameter opening behind our research vessel at a speed of $\sim 2\text{--}3$ knots. This resulted in sampling $\sim 1.57 \text{ m}^3$ (1,579 L) of the water during each tow. Three of these tows were taken near the surface (<1 m depth) and three tows were taken near the benthos (~ 10 m depth) by adding lead weights to the towline. Following each tow, all organisms collected in the net were transferred to glass jars filled with 70% ETOH and stored for later sorting. Samples were then transferred to the laboratory where they were examined under a dissecting microscope, sorted to the lowest taxonomic level possible, and enumerated. This revealed that the majority ($>90\%$) of all organisms collected were mysids, and we consequently focus the remainder of our study on this group. Differences in mysid abundance between surface waters and those near the benthos were then assessed using a two-sample *t*-test.

To test our hypothesis that mysids graze on kelp zoospores and thereby are able to reduce their survival and settlement, an additional plankton tow was done and all the collected mysids were transferred to a 1 L glass jar filled with seawater pumped directly from the site. This jar was placed in a cooler and taken to the laboratory where the mysids were starved for 24 h to ensure their guts were empty. In addition, ~ 20 *M. pyrifera* sporophylls with reproductive sori were collected from the site on SCUBA, transported to the laboratory, and desiccated overnight in the dark at 4°C . The following day, 20 glass culture dishes were filled with 200 mL of filtered seawater and a single microscope slide was placed on the bottom of each dish. Five mysids were then placed into each of 10 of these dishes while leaving the remaining 10 dishes without mysids. At this time, the sporophylls were immersed in a separate container filled with filtered seawater, which caused them to release their zoospores (see also Carney and Edwards 2010). Zoospore density in this solution was estimated using a hemocytometer and found to be $\sim 1.3 \times 10^6$ zoospores $\cdot \text{mL}^{-1}$.

Following this, 15 mL aliquots of this solution (each containing $\sim 2 \times 10^7$ zoospores) were added to the 20 glass culture dishes so that each dish had a swimming zoospore density of $\sim 1 \times 10^5$ zoospores \cdot mL $^{-1}$. Ten of these dishes, five containing kelp zoospores plus mysids and five containing only kelp zoospores were then placed into each of two Percival E-6L culture chambers, one of which had its internal lights turned on (hereafter "light" treatment) to simulate the daytime and the other had its lights turned off (hereafter "dark" treatment) to simulate the night. Following this, 10 additional culture dishes were filled with filtered seawater but were not inoculated with zoospores. Five mysids were then added to each of these dishes and half of them were placed in the light and half in the dark as described above. Both culture chambers were set to 12°C and the mysids were allowed to graze for 12 h. The following day the mysids were removed from all the culture dishes and examined under UV light using epifluorescence microscopy. This caused the chlorophyll within the zoospores to fluoresce red, which was visible through the mysid carapaces and allowed us to identify chlorophyll in the mysid guts to verify grazing.

After removing the mysids, all of the glass culture dishes in which zoospores were added were transferred to the dark and the remaining zoospores were allowed to settle overnight. The next day, the dishes were transferred to the light and incubated for 2 d. After 2 d, the density of settled zoospores on the microscope slides in each dish was estimated by counting the number of settled zoospores that had subsequently germinated into gametophytes, per three fields of view (FOV) under 400 \times magnification (FOV sample area = 0.0875 mm 2). While we recognize that each light/dark treatment was established within a single incubator due to chamber availability, we point out that these incubators hold light and temperature conditions constant and thus should reduce exogenous sources of environmental variation. Consequently, while the five replicate culture dishes in each chamber represent replicates for the chambers themselves, we believe that they adequately estimated treatment effects and consider them as such, although we alert the reader to this issue (see Hurlbert 1984). Differences in settlement density among treatments were assessed using a two-way model I ANOVA, with mysid presence versus absence, and light versus dark conditions as factors. Prior to analysis, all data were examined for homoscedasticity and normality, and were found to meet the assumptions of parametric statistics.

RESULTS

Mysid density near the southern edge of the Point Loma kelp forest was nearly seven times greater at the surface than near the benthos on the day we conducted the plankton tows (t -test: $t_4 = 5.079$, $P < 0.05$; Fig. 1). Furthermore, of the mysids that were taken to the laboratory and starved for 24 h, those that were then allowed to graze on kelp zoospores for 12 h exhibited red fluorescence in their guts when examined under UV light, verifying the presence of chlorophyll (K. VanMeter, M.S. Edwards, personal observation). In contrast, the mysids that were not allowed to graze on kelp zoospores did not exhibit red fluorescence when examined under UV light, indicating they did not have chlorophyll in their guts (personal observation). This supported our hypothesis that the mysids did in fact graze on the kelp zoospores and suggested the possibility that they may have a negative impact on zoospore survival.

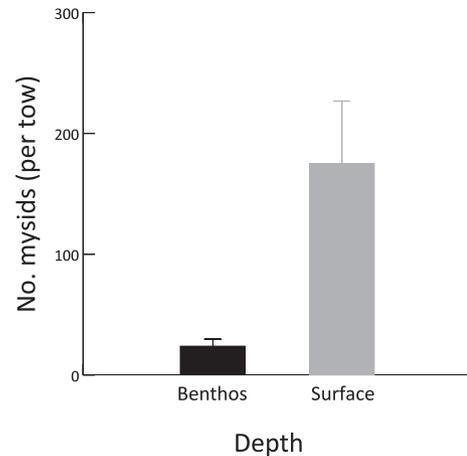


FIG. 1. Mean mysid density (+SE) per 50 m plankton tow (1,579 L) near the benthos (10 m depth) and at the surface (<1 m depth) along the southern edge of the Point Loma kelp forest ($n = 3$).

Macrocyctis pyrifera zoospore settlement within the culture dishes varied significantly between dishes with mysids and without mysids (ANOVA: $F_{1,16} = 16.69$, $P < 0.001$), but not between the light and dark conditions ($F_{1,16} = 1.89$, $P = 0.187$; Fig. 2; Table 1). Furthermore, the two factors did not interact ($F_{1,16} = 0.44$, $P = 0.516$), indicating that the mysids exerted similar grazing pressures during the day and the night. Specifically, zoospore settlement decreased by approximately one-half within the dishes with mysids relative to the dishes without mysids, indicating the mysid grazing significantly reduced kelp zoospore survival and settlement.

DISCUSSION

Long-distance dispersal by kelp zoospores may be enhanced by the vertical transport of zoospores from

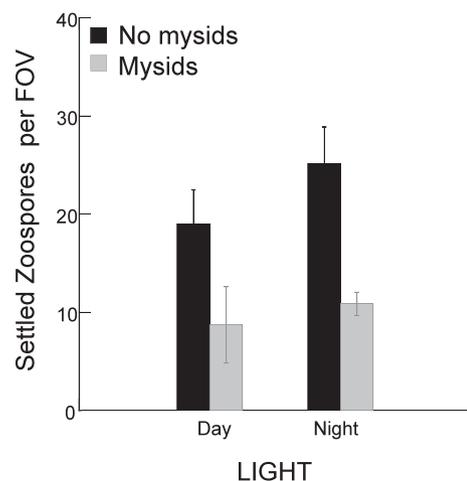


FIG. 2. Mean zoospore settlement (+SE) per field of view (FOV) under 400 \times magnification (FOV area = 0.0875 mm 2) in culture dishes after exposure to mysid grazing for 12 h in the light and the dark ($n = 5$).

TABLE 1. Results of two-way Model I ANOVA testing differences in *Macrocystis pyrifera* zoospore settlement in the presence versus absence of mysid grazing, and in the light versus the dark ($n = 5$).

Source	Type III SS	df	Mean squares	F-ratio	P-value
Light	83.90	1	83.90	1.89	0.187
Grazers	737.66	1	737.66	16.69	0.001
Light*Grazers	19.48	1	19.48	0.44	0.516
Error	706.80	16	44.17		

their site of release near the benthos into the shallower portions of the water column where they are exposed to greater alongshore currents (Reed et al. 1992, Cie and Edwards 2011). However, this also exposes them to increased irradiances that can negatively impact their survival and postsettlement competency (Graham 1996, Cie and Edwards 2008). Given that zoospores will likely encounter high irradiances for at least several hours when transported to near the surface during the day, this suggests that these zoospores may not play an important role in successful prolonged long-distance dispersal. In contrast, if the zoospores are transported to the shallower portions of the water column during the night, they may avoid negative irradiance impacts if they are able to return to the benthos before the following day (Cie and Edwards 2008). However, given the slow zoospore swimming speeds ($\sim 0.0012 \text{ mm} \cdot \text{s}^{-1}$), which prevent them from actively moving significant distances in the water column, and the complex physical processes needed to return the zoospores to the benthos (Gaylord et al. 2002, Cie and Edwards 2011), this seems an unlikely.

In addition to increased irradiances, the transport of zoospores into shallower water can expose them to enhanced grazing pressures from zooplankton, which can further reduce their survival in the water column. This may be especially important along the down-current edge of kelp forests where the zoospores are presumably dispersing away from the forests (Graham 2002). The most abundant zooplankton at our study site along the south edge of the Point Loma kelp forest during the spring sampling were mysids, which are filter-feeding, shrimp-like crustaceans that are known to be strongly associated with the surface canopies of *M. pyrifera* in southern California (Coyer 1984). Together, our data indicate that during our spring sampling, (i) mysids were at least seven times more abundant in the surface waters than near the benthos along the down-current edge of the kelp forest, (ii) mysids graze on kelp zoospores, (iii) mysid grazing can reduce zoospore settlement by at least 50%, and (iv) this impact does not differ between the light (daytime) and dark (nighttime) conditions. The lack of any differences in grazing impacts between the daytime and nighttime conditions is not surprising given that although mysids possess image-forming compound eyes which result in differences in

prey capture rates between the day and night (Fulton 1982), they primarily use their legs to filter food particles from the water and thus do not require light to find and capture food particles (Mauchline and Fisher 1969, Mauchline 1980, Focke and Mees 1999). Consequently, unlike irradiance impacts, zoospores may not be able to avoid grazing pressure by being released from their parental sporophytes during the night. This may be especially important given many species of mysids exhibit diel vertical migration in which they move into shallower water during periods of low light and thus may be even more abundant in the surface waters at night (Beeton and Bowers 1982, Rudstam et al. 1989). However, because we did not sample during the night or in other seasons, or along the edge of other kelp forests, we cannot determine if mysids were more abundant in the surface at night, or assess how spatially and temporally generalizable these patterns are. This is important given that *M. pyrifera* reproduction and the vertical transport of its zoospores occur both throughout the day and year-round, and that this appears consistent across the entire Point Loma kelp forest (Graham 2003, Cie and Edwards 2011). Thus, we present these patterns as a proof of concept that mysids do, in fact, graze on kelp zoospores and this can potentially reduce their survival in the water column, but that any seasonal or geographic differences in zooplankton distribution and/or abundance or in their grazing activities may act to reduce the generality of these findings.

Although we did not directly measure zoospore dispersal in this study, when combined with those of Cie and Edwards (2008), our results indicate that zoospores that are transported from the benthos into shallower water can potentially experience significantly higher mortality from both increased irradiances and elevated grazing. Consequently, while this may allow some zoospores to disperse over large distances, it may not be an important mechanism of sustained effective long-distance dispersal if these grazing impacts significantly reduce zoospore densities in the water column. In our study, the zoospore and mysid densities used were greater than those observed in nature and thus while the potential for mysid grazing to impact zoospore survival is clear, the full ecological significance of this remains to be addressed. However, it is important to note that while individual kelps can produce billions of zoospores per year (reviewed in Schiel and Foster 2006), they can also synchronize release of their zoospores with nearby kelps to enhance zoospore density in the water column and effectively increase their dispersal potential and reducing per capita grazing impacts, especially during episodic events such as storms (Reed et al. 1997, Reed et al. 1998). When integrated across the entire forest, this can result in substantial numbers of zoospores being transported into the surface waters at any time (Cie and

Edwards 2011). For example, Graham (2003) found that zoospore density in bottom waters of the Point Loma kelp forest range from ~250 to more than 50,000 zoospores · L⁻¹, of which a small number are expected to be transported vertically to the surface (Cie and Edwards 2011). Even if only a small fraction of these are then able to survive the high irradiances, they still may not play a significant role in long-distance dispersal due to mysid grazing. Given that successful reproduction among the resulting gametophytes requires at least one male and one female to settle in close proximity (usually within 1 mm) to each other (Reed 1990), it seems unlikely that sufficient zoospore densities will be maintained in the water column at significant distances from the kelp forests to facilitate such settlement. Consequently, we believe that unlike drifting sporogenic thalli (Hobday 2000, Macaya 2005, Hernandez-Carmona et al. 2006), vertical transport into the shallower portions of the water column may enhance the dispersal potential of some zoospores and facilitate episodic recruitment on distant substrates (e.g., Reed et al. 1988, Reed and Schroeter 2004), but it is unlikely that this is a viable mechanism for sustained long-distance dispersal.

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