THE EFFECTS OF IRRADIANCE IN DETERMINING THE VERTICAL DISTRIBUTION OF ELK KELP *PELAGOPHYCUS PORRA*

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DEDICATION

This thesis is dedicated to my family and friends who have encouraged and supported me through the trials and challenges that accompany such an undertaking. A special thanks to Colby Smith who believed in me even when I didn't believe in myself.

“Whatever you are be a good one”

-Abraham Lincoln

ABSTRACT OF THE THESIS

The Effects of Irradiance in Determining the Vertical Distribution
of Elk Kelp, *Pelagophycus porra*
by
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Elk Kelp, *Pelagophycus porra*, is commonly observed in deep (20-30 m) water along the outer edge of Giant Kelp, *Macrocystis pyrifera*, beds in southern California, USA and northern Baja California, MEX, but rarely occurs in shallower water or within beds of *M. pyrifera*. Due to the nature of *P. porra's* heteromorphic life history that alternates between a macroscopic diploid sporophyte and a microscopic haploid gametophyte, investigations of both life history stages were needed to understand *P. porra*' apparent inability to encroach into *Macrocystis* beds along the southern California coast.

Juvenile P. porra sporophytes were transplanted (1)within the *Pelagophycus* zone along the offshore edge of the *M. pyrifera* bed at 20 m, (2) within the center of the *M. pyrifera* bed at 15 m and (3) along the inshore edge of the *M. pyrifera* bed at 8 m. Transplanted *P. porra* exhibited similar growth across all depths, but the onset of reproductive maturity was observed only at shallower depths. Stipe length at the onset of maturity differed between depths, increasing significantly from inshore and within the center of *M. pyrifera* beds to offshore within naturally occurring *P. porra* beds. Photosynthetic measurements of *P. porra* blades using PAM fluorometry indicated that although *P. porra* initially exhibits characteristics of a low-light adapted species (20m depth), individuals are able to photoacclimate to increasing light levels showing traits of high-light adapted species in the midwater zone and at the surface.

When the presence of *P. porra* propagules was increased, *P. porra* was unable to recruit within *M. pyrifera* beds. No *P. porra* recruits were observed near sori bags placed within *M. pyrifera* beds while heavy recruitment (6.5 ± 0.604 SE and 2.5 $\pm$ 0.394S E for 1m and 2m away from sori bag respectively) was observed near the sori bags within the *P. porra* bed. These seeding experiments indicated that a factor other than spore dispersal is limiting *P. porra* distribution to deeper depths.

Culture experiments were carried out in the laboratory using microscopic gametophytes and embryonic sporophytes of *P. porra* to investigate the effects of the higher light levels found within *M. pyrifera* beds. Cultures were grown under low light (2 µmol photons m^{-2} s^{-1}) conditions and then moved to high light conditions (16 µmol photons m^{-2} s^{-1}) at which time both embryonic sporophytes and gametophytes experienced 100% mortality. When grown under constantly higher (18 µmol photons m^{-2} s^{1}) light conditions, the ability of *P. porra* to photoacclimate decreased. The vunerability of *P. porra* microscopic stages to higher irradiances appears to be the major limiting factor inhibiting *P. porra* from becoming established within *Macrocystis* beds and stresses the importance of a multiple life-history approach when investigating species distributions.

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INTRODUCTION

Patterns of biological zonation along vertical gradients are ubiquitous in both terrestrial and marine environments (Connell 1989; Hemp 2006; Menge and Sutherland 1976) and have been widely investigated in order to understand local to regional patterns of the distribution and abundance of organisms (Denny 2006; Hutchins 1947; Kang et al. 2005; Konar et al. in press). Such patterns are particularly evident in the marine environment in which early work by Connell (1961) revealed that biotic interactions such as herbivore grazing and interspecific competition are important in setting the lower limits of species distributions in the rocky intertidal zone, whereas a species upper limits are often determined by abiotic factors such temperature, emersion time, humidity and salinity (see also Chapman 1995). Furthermore, physical stress in the intertidal zone has been associated with a decrease in growth, reproduction, and survival in some invertebrate (e.g. mussel) species (Petes et al. 2007). Similarly, vertical attenuation of light in the subtidal environment is important in regulating zonation patterns of many algal species along depth gradients (e.g. Shaughnessy and DeWreede et al. 1996; Vernon 2000). This irradiance gradient is linked to spectral changes in light quality and often compounded by the level of structural complexity of the habitat (Frade and De Jongh et al. 2008). For example, shading created by kelp canopies have the ability to reduce light to < 1% of surface irradiance, inhibiting the development of other species (Clark and Edwards et al. 2004; Dayton and Currie et al. 1984; Kennelly 1987; Reed and Foster 1984) and therefore heavily influencing the species diversity found beneath the canopy.

The depth limits of subtidal algae is determined, assuming adequate substratum availability, by minimum levels of irradiance needed for growth (e.g. Foster and Schiel 1985, Spalding et al. 2003), whereas the upper limit may be set by excess irradiance and/or wave action (Graham 1997) that can have negative consequences for their growth, fecundity and ultimately, survival (Deysher and Dean 1986a, Graham 1996, Luning and Neushul 1978), though degree to which algal species are affected maybe dependent on the life-history stage in question (e.g. Matson and Edwards 2007). Kelps, large brown algae of the order Laminariales, exhibit a heteromorphic life history, alternating between a microscopic haploid

gametophyte and a macroscopic diploid sporophyte. At maturity, kelps release zoospores that disperse and settle to the rocky substratum below. If the habitat is suitable, the zoospores then undergo gametogenesis to form gametophytes, which undergo sexual reproduction and produce the next generation's sporophytes. Some kelp species (e.g., the Giant Kelp *Macrocystis pyrifera*; hereafter *Macrocystis*) have sporophytes that can grow to more than 30 m in length extending from the benthos, where irradiance can be very low (< 1% surface irradiance) to the surface where irradiance can be extremely high (up to 1200 µmol photons $m^{-2}s^{-1}$; light levels from Edwards and Kim in review). Several studies have shown that although low irradiance can inhibit kelp recruitment (Deysher and Dean 1986b; Reed and Foster 1984), high irradiance can negatively affect survival of both their microscopic (Graham 1996), or macroscopic (Altamirano and Murakami et al. 2004; Copertino and Cheshire et al. 2006; Hanelt and Wiencke et al. 1997; Karsten and Bischof et al. 2001; Nielson and Blanchette et al. 2006) life-history stages. High irradiance can cause photoinhibiton and photodamage, thereby resulting in decreased photosynthetic capacity (Copertino and Cheshire et al. 2006), resulting in mortality. Photoacclimation and tolerance to changing irradiance can be species-specific, categorizing those species that are adapted to high-light and low-light areas which provides insight into local patterns of algal distribution and abundance (e.g. Clark and Edwards et al. 2004; Karsten and Bischof et al. 2001). Environments that experience high irradiance, such as shallow habitats or areas where kelp canopies have been removed tend to favor recruitment and growth of high-light adapted species due to their ability to respond and recover more rapidly to irradiance exposure than low-light adapted species (Hader and Lebert et al 1998; Hanelt and Li et al. 1994; Jimenez and Figueroa et al. 1998). Although the surface canopy can greatly reduce light to lower levels that are potentially tolerable to low-light adapted species, canopy cover is highly variable throughout the year and therefore may not provide consistently suitable habitat needed for low-light adapted species. In contrast, deeper habitats where irradiances remain low year round tend to favor the recruitment and survival of low-light adapted species. Therefore, the upper limit of deep-water algal species could potentially be set by irradiance levels that are relatively tolerable to shallower species (Hader and Lebert et al. 1998).

The deep-water kelp *Pelagophycus porra* (hereafter *Pelagophycus*) exhibits a single unbranched stipe (reaching 27 m in length) that terminates in a single spherical pneumatocyst

that can be up to 20 cm in diameter (Fig. 1). Arising from the large pneumatocyst are two branches with numerous sympodially branched branchlets from which blades grow up to 20 m long and 1 m wide (Abbot and Hollenberg 1976, Stewart 1991). *Pelagophycus* grows at depths of 20-50 m from Point Conception, California, USA to Isla San Benito, Baja California, MEX (Abbot and Hollenberg 1976; Miller and Olsen et al. 2000; Stewart 1991). Near San Diego, California, the *Pelagophycus* population in the Point Loma kelp forest is perennial, with individuals reaching maturity at 2-3 years of age and recruiting in monthly pulses throughout the year. Other southern California populations (e.g., at Santa Catalina Island) are known to be annuals with recruitment occurring in the early summer months (Miller and Olsen et al. 2000).

Figure 1. Adult sporophyte of *Pelagophycus porra*.

Pelagophycus grows from the substratum to the surface, and the juvenile stages experience lower light levels (~5 µmol photons $m^{-2}s^{-1}$) relative to mature adults occurring at the surface (up to 1000-1200 µmol photons $m^{-2}s^{-1}$; Edwards and Kim in review). Near Point Loma, the cross-shore distribution of *Pelagophycus* is limited to areas offshore from beds of *Macrocystis*. The morphology of *Pelagophycus* is well-suited for drifting and thus may serve

as a source of kelp spores for subsequent establishment in other areas. Individuals of *Pelagophycus* can occur as shallow as 15 m, however, are extremely rare in the Point Loma kelp beds (personal observation), and these individuals occur singly and not in dense stands. Although other pneumatocyst-bearing species (e.g., the bull kelp, *Nereocystis luetkeana),* have been observed well outside of their established ranges (Miller and Estes 1989), *Pelagophycus* appears to be unable to invade areas within adjacent *Macrocystis* beds.

Determining the factors that limit the distribution of *Pelagophycus* at shallower depths may help to explain why this species does not encroach into the more abundant *Macrocystis* beds along the southern California coast, which will ultimately provide insight into local-scale patterns of species distribution along a depth gradient. Compared to other canopy-forming kelps, little is known about the ecology of *Pelagophycus*, and there are no studies that have evaluated its physiological and ecological performance at different depths or for multiple life history stages. This thesis investigates these subjects through both field-based monitoring, manipulative experiments, physiological assessments via the use of PAM (pulse amplitude modulated) fluorometry and laboratory-based controlled culturing of the microscopic stages.

MATERIALS AND METHODS

This section includes a description of the study site, methods for the macroscopic and microscopic life history stage experiments and statistical analysis.

STUDY SITE

Field experiments were carried out within the Point Loma kelp beds in San Diego, California, USA (32º4'N, 117º7'W) from October 2006 through January 2008 (Fig. 2). The Point Loma kelp forest spans a linear distance of 8-10 km and is 1 km wide situated on a mudstone-sandstone shelf (Tegner et al. 1995). The shallow edge of the forest occurs in 6-8 m depth with patchy beds of *Egresia menziesii* occurring inshore. The deeper edge of the *Macrocystis* bed occurs at approximately 20 m depth with *Pelagophycus* stands occurring offshore (to 50 m depth). A 1-km long transect was established perpendicular to shore, beginning in the offshore *Pelagophycus* zone and running inshore through the *Macrocystis* bed. Along the transect, three permanent sites were selected; a deep site within the *Pelagophycus* zone (20 m), a middle site within the *Macrocystis* bed (15 m), and a shallow site just inshore of the *Macrocystis* bed (8 m). Three additional sites were established within the *Macrocystis* bed to observe the effects of shading on recruitment of *Pelagophycus.*

MACROSCOPIC STAGES: SURVIVAL, GROWTH, MATURITY AND PHOTOSYNTHETIC ACTIVITY

To evaluate demographic characters such as density, size (stipe length), and reproductive condition (presence of reproductive patches called sori) in naturally occurring sporphytes of *Pelagophycus*, 40 haphazardly selected adult *Pelagophycus* were collected just offshore of the Point Loma *Macrocysitis* forest in October 2007 and January 2008. The density of *Pelagophycus* was estimated within the *Pelagophycus* zone, within *Macrocystis* beds, and just inshore of *Macrocystis* beds by counting all individuals > 1 m height in 20 randomly placed 1 m^2 quadrats at each location.

Chlorophyll fluorescence was assessed in February through April, June through July, and in October 2007 to investigate photoacclimation in *Pelagophycus* sporophytes as they grow from the benthos towards the surface using a diving pulse amplitude modulated (PAM)

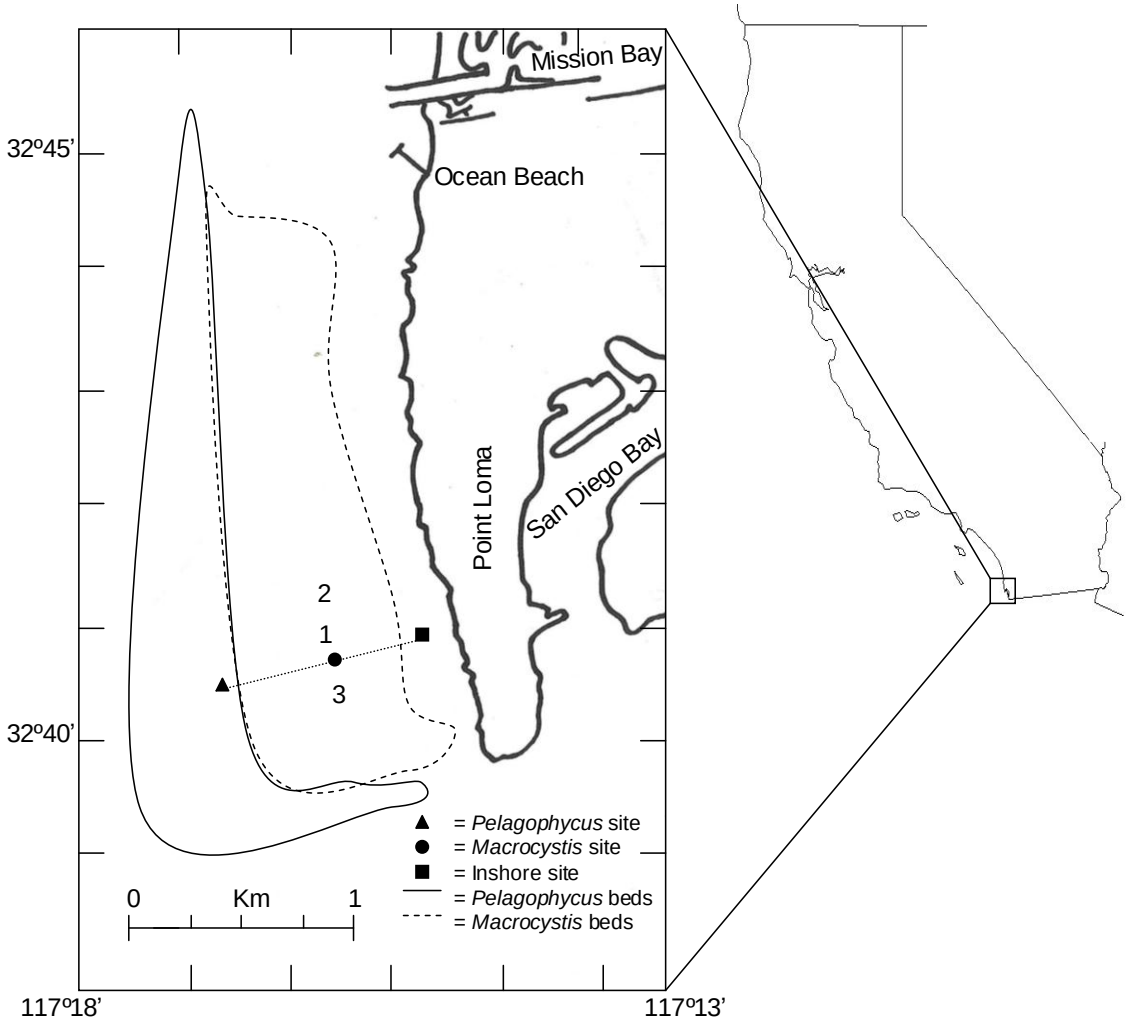

Figure 2. Map of Point Loma, California showing transplant sites in the *Pelagophycus* zone, within and just inshore of the *Macrocystis* bed. Clearing and seeding experiments were carried out within the *Macrocystis* bed at sites 1, 2, and 3.

fluorometer (Walz GmbH, Effeltrich, Germany). Two blade portions, the apex (near the pneumatocyst) and terminus (deepest portion without sori or discoloration), were collected from each of five naturally occurring individuals within the *Pelagophycus* zone at three depths: from juveniles near the benthos (20 m), from sub-adults that have grown to the middle of the water column (10-12 m) and from adults that have reached the surface (Fig 3). Measurements were taken in an on-board measuring chamber supplied with running seawater pumped from the site. Leaf clips (Diving-LC, Walz) were clipped to blades to dark adapt blades and photon flux density (PFD) increased during 90 seconds in eight consecutive steps (plus initial darkness measurement) separated by 10 seconds. At each PFD, a saturating light pulse was applied to determine rapid light curves (RLCs), relative electron transport rate (rETR) plotted against PFD. The rETR was calculated as the product of the quantum efficiency of PSII (Φ_{PSII}) and the absorbed photon flux density (PFD); rETR = Φ_{PSII} x PPFD x 0.5 x 0.84, where PPFD is photosynthetic photon flux density of photosynthetically active radiation (PAR 400-700 nm). This equation assumes that PSII absorbs half (0.5) the quanta of available light (Schreiber 1994) and that an average photosynthetic unit absorbs about 84% of incident PAR (Björkman and Demmig 1987). The quantum efficiency for photosynthetic electron transport in the light calculated followed Genty and Briantais et al. (1989) as $\Phi_{PSII} = \Delta F/F'_m = (F'_m - F)/F'_m$, in which F'_m is the maximum fluorescence yield when a light-acclimated thallus is exposed to a pulse of saturating light, and F is the steady-state fluorescence yield of a light-acclimated thallus. To determine photosynthetic parameters (α = photosynthetic efficiency, E_k = saturation irradiance, $rETR_{max}$ = maximum relative electron transport maximum), RLCs must be fitted to a curve. These curves were measured using a pre-installed software routine, in which the actinic illumination is incremented in eight steps. Empirical data were mathematically fitted to a double exponential decay function (Platt & Gallegos et al. 1980). PAM was also used to determine the photosynthetic efficiency from the maximum (F_m) and minimum fluorescence (F_o) after dark acclimation; the intrinsic potential quantum efficiency or maximum quantum yield of Photosystem II [$F_v/ F_m = (F_m - F_o)/F_m$) as well as maximum quantum yield (F_v/ F_m).

To examine the potential mechanisms responsible for *Pelagophycus'* ability to photoacclimate as it grows through the water column, chlorophyll *a* concentration was assessed for the months of February through July, and during October 2007. After

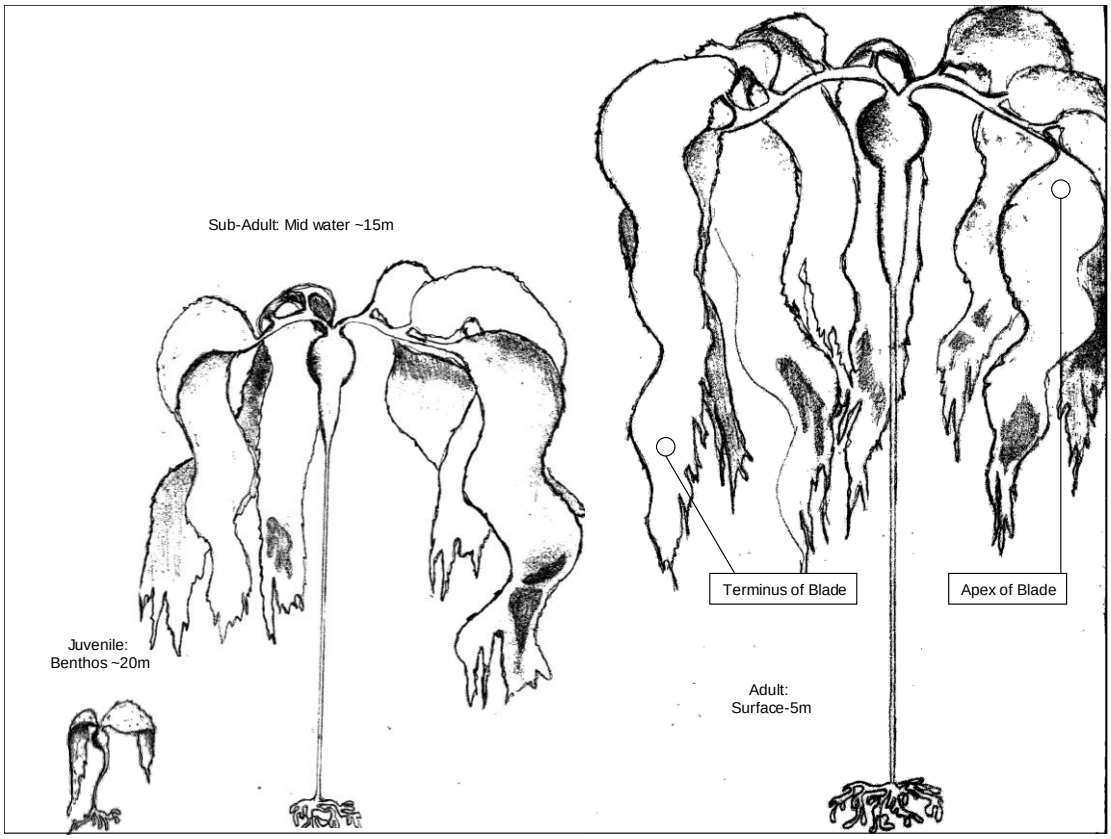

Figure 3. Macroscopic sporophyte of *Pelagophycus porra* at different life stages. Juveniles exhibit a slightly different morphology than other life stages and occur near the benthos (20 m depth). Sub-adults occur in midwater (~ 10 m depth) while adults are found near or at the surface (< 5 m depth). Apex and terminus portions of blades were collected from all three stages for PAM measurements and analysis of chlorophyll *a* content.

chlorophyll florescence was measured, a 1.8-cm diameter disc was cut from the dark adapted tissues covered by the leaf clip in the apex and the terminus blade portions. Blade portions were immediately added to 5-ml N, N-dimethyl-formamide (DMF) to extract chlorophyll *a* from the blade sample. Chlorophyll *a* extracts were stored at 4ºC for up to 1 wk from the collection date (Henley and Dunton 1995). Absorption was analyzed in a 1-cm cuvette using a Beckman Spectrophotometer at wavelengths of 480, 510, 630, 645, 647, 664 and 750 nm. Absorption at 750 nm was subtracted from all other absorbance values to correct for turbidity (Parsons and Strickland 1963). The amount of Chlorophyll *a* was converted to molar amounts and normalized to a one-sided surface area.

To examine if the inability of *Pelagophycus* to establish populations in the *Macrocystis* bed was due to reduced growth and survival of macroscopic life stages, juvenile individuals were transplanted from the *Pelagophycus* zone to inshore and within the *Macrocystis* bed and also back to the *Pelagophycus* zone (procedural control) on three occasions. Three separate transplant experiments were preformed, each initiated on July 24, 2006, October 12, 2006 and April 28, 2007 and conducted for 3 mo, 6 mo, and 6 mo, respectively. For each experiment, 30 *Pelagophycus* juveniles (ranging from 0.1 to 2.31 m in height) were collected from the *Pelagophycus* zone using SCUBA, brought to the surface, and maintained in a seawater bath while their holdfasts were inserted through the braid of individual 25-cm length pieces of 1.9 cm polypropylene rope. Each rope segment was returned to the benthos and nailed to the substrate in groups of 10 at the three different depths that represented the *Pelagophycus* zone and within and inshore of the *Macrocystis* beds, with the exception that only four individuals were placed at each depth for the experiment initiated on July 24. Stipe length (distance from the top of the holdfast to the base of the pneumatocyst) and mortality was measured each month. Mortality was noted as (1) complete loss (transplant rope and transplant missing), assumed to be caused by substrate failure or (2) stipe failure (transplant rope and holdfast remain intact, but pneumatocyst and blades missing), assumed to be caused by herbivory or stipe breakage due to wave force. In addition, for transplant experiments initiated in October 2006 and April 2007, each individual was assessed for the presence of reproductive sori by noting the presence of reproductive sori patches on blades and stipe length at the onset of maturity.

MICROSCOPIC STAGES: RECRUITMENT AND LIGHT SENSITIVITY

To investigate the survival and photosynthetic performance of *Pelagophycus* microscopic stages (gametophytes and embryonic sporophytes) and to determine if the high light conditions associated with shallower depths inhibits the ability of *Pelagophycus* to recruit within the *Macrocystis* bed, three sites were established in the Point Loma *Macrocystis* bed in March 2007 and in August 2007. In addition, a site within the *Pelagophycus* zone was identified as a methodological control in August 2007. Canopy presence/removal and natural/artificial seeding was established in a block design within the *Macrocystis* bed. Each site within the *Macrocystis* bed was divided into four 20 m x 20 m plots. To manipulate light levels within the *Macrocystis* bed, the canopy was cleared from half of each plot by cutting the stipe just below the primary dichotomy with hedge clippers. *Pelagophycus* recruitment was assessed in non-seeded (natural) and artificially seeded (addition of *Pelagophycus* propagules) plots to determine if the inability of *Pelagophycus* to recruit inside the *Macrocystis* bed was due to limited dispersal of zoospores. Artificial seeding was attempted with the use of sori-bags (mesh bags filled with sporogenic material to facilitate propagule presence). Sori were collected from 10 mature individual *Pelagophycus*, placed into mesh bags, returned to the benthos and nailed to the substrate haphazardly throughout artificially seeded plots and within the methodological control. At the site within the *Pelagophycus* zone, the density of natural recruits was compared to the density of recruits immediately adjacent to the sori bags using randomly placed 1 m^2 quadrats. Both sites within the *Macrocystis* bed and sites within the *Pelagophycus* zone were sampled monthly using SCUBA surveys for visual estimates of *Pelagophycus* recruitment.

To examine whether the higher irradiance levels found within shallower waters inhibited the survival and reproduction of *Pelagophycus* microscopic stages, a series of laboratory experiments were conducted using cultured gametophytes and embryonic sporophytes. Blades containing sori were collected from mature adults of *Pelagophycus* in naturally occurring beds on 28 Jun 2007. Blades were placed in a dry cooler and transported to the laboratory where they were then held in the dark at 12˚C for 1 h. After 1 h, the sori were removed and blotted dry. A small portion (approximate 2 cm^2) was cut from each sori patch and placed in 12˚C filtered seawater for 1 h to hydrostatically release zoospores (Reed

1990). The zoospore solution was held at 12˚C for 1 h until a zoospore concentration of 8 x 10^5 spores ml^{-1} was attained. Zoospore concentration was estimated using a hemocytometer and then diluted to a desired concentration of approximately 1 x 10^4 zoospores ml^{-1} (Reed et al. 1991).

Twenty Petri dishes (60 mm x 15 mm), each containing 15 ml Provosoli's solution (Provasoli 1968), were inoculated with zoospore solution to reach a desired concentration of 1 x 10^4 zoospores ml^{-1}. Microscopic stages were cultured at low irradiance levels (~2 µmol photons m^{-2} s^{-1}; similar to levels measured in the *Pelagophycus* zone) with a 14:10 L:D photoperiod at 12˚C in a Percival 6EL growth chamber. Provasoli's solution was changed every 2 wk and the density of gametophytes and embryonic sporophytes was quantified weekly by using an inverted Leica microscope. Densities of gametophytes and embryonic sporophytes were estimated in each dish within three haphazardly selected fields of view under 10X power. Gametophytes and embryonic sporophytes were grown under low light and transferred to high light (16 µmol photons m^{-2} s^{-1}, similar to levels measured in the *Macrocystis* bed using the diving PAM's light sensor) at 98, 106, 113 and 120 d in culture (with five replicates of each). One week after moving the dishes to higher light levels, densities of eggs and embryonic sporophytes were quantified for that age treatment and then the next age treatment was moved to higher light levels (~16 µmol photons m^{-2} s^{-1}). Once dishes were moved to higher light levels they remained there for the duration of the experiment.

To compare potential differences in photoacclimation and tolerance to irradiance levels found with the *Macrocystis* bed, the microscopic stages of *Pelagophycus* and M*acrocystis* were cultured side-by-side under 18 µmol photons m^{-2} s^{-1}. Photosynthetic activity was assessed using the PAM in order to create RLCs. Following a 15-min dark adaptation, the photosynthetic parameters α, E_k, and $rETR_{max}$ and (F_v/ F_m).were evaluated. Photosynthetic parameters were used to quantitatively compare *Macrocystis* and *Pelagophycus* cultures continually grown at higher light levels likely to be experienced within the *Macrocystis* beds (18 µmol photons m^{-2} s^{-1}).

STATISTICAL ANALYSIS

All data were analyzed using SYSTAT (ver. 12). Prior to analysis, data were examined for normality by graphical interpretation of residuals, and for homoscedacity with a Cochran's C test. Those cases that did not meet the assumptions were transformed in order to correct the problem (transformation type discussed on case-by-case basis).Variation in $rETR_{max}$, Ek, α and Chlorophyll *a* content were evaluated among depths and blade types using separate mixed-factor two-way ANOVAs, with blade portion as a fixed factor and depth as a random factor. Fisher's LSD pairwise comparisons were used to determine differences among levels of significant factors.

Initial stipe length was analyzed using a two-way ANOVA between depth and date for all transplant experiments to reveal a significant difference between dates (see results). Separate one-way ANOVAs then were performed to evaluate differences between depths for each transplant experiment. When evaluating variation in stipe growth rates (final stipe length – initial stipe length) / months after transplant) among depths, data were not homoscedastic and therefore log-transformed, which then met the assumption of homscedasticity. The data for stipe length at first observation of maturity also were not homoscedastic and thus square-root transformed to correct the problem. Variation in stipe length among depths was then analyzed using a one-way ANOVA followed by a Fisher's LSD pairwise comparison.

Data for recruitment of Pelagophycus within the Macrocystis bed and at the control site within the Pelagophycus zone were heteroscedastic and a square-root transformation was use which corrected the problem. A one-way ANOVA was used to evaluate significant differences in recruitment 1 m and 2 m distance from sori bags as well as natural recruitment within the control site. Densities of Pelagophycus recruits within the Macrocystis bed was compared to the densities of recruits within the Pelagophycus zone. Photosynthetic parameters and maximum quantum yield of Pelagophycus cultures moved from low to high light were not homoscedastic and therefore SIN- transformed to correct the problem. A one-way ANOVA was used to assess whether there were significant differences in photosynthetic parameters for cultures in which Pelagophycus was moved from low to high light levels as

well as when comparing *Pelagophycus* and *Macrocystis* microscopic stages continually grown at high light.

RESULTS

This section describes the results for field and laboratory experiments with macroscopic and microscopic life history stages of *Pelagophycus porra*.

MACROSCOPIC STAGES: SURVIVAL, GROWTH, MATURITY AND PHOTOSYNTHETIC ACTIVITY

The distribution of *Pelagophycus* extended the length of the Point Loma *Macrocystis* bed (8-10 km) first appearing at depths of 20 m. Adult *Pelagophycus* were found buoyed (still attached to the benthos) with pneumatocyst at the surface most of the year with the exception of early fall (September and October). *Pelagophycus* density within the study sites reached 2.6 m^{-2} $\pm$ 0.34 SE within the *Pelagophycus* zone, but no *Pelagophycus* were observed in the inshore or within the *Macrocystis* study sites. Although the rare (1 in every 3km of coastline) naturally occurring *Pelagophycus* individual was found within the *Macrocystis* beds throughout Point Loma. Average stipe length of naturally occurring individuals sampled October 2007 and January 2008 was 4.48 m ($\pm$ 0.72 SE) with 22.5% being reproductively mature (noted by the presence of sori patches). Mature individuals can be easily found throughout the year though recruitment of *Pelagophycus* occurs in monthly pulses, with the strongest recruitment occurring in the spring (April and May). Of the individuals that were sampled and found to be reproductively mature the average stipe length was more than twice as long (8.88 m $\pm$ 1.46 SE) as those that were not mature (3.21 m $\pm$ 0.67 SE) (Fig 4).

Within and inshore of the *Macrocystis* beds, transplanted *Pelagophycus* juveniles exhibited differences in both the time it takes to reach reproductive maturity and the stipe length at the onset of maturity. Initial stipe length was compared among depths and date of each transplant experiment and was significantly different between dates ($p < 0.001$)(Fig. 5). Differences between depths for each transplant experiment were not significantly different ($p = 0.189$, $p = 0.432$, $p = 0.234$ for transplant experiments initiated on July 24, 2006, October 12, 2006 and April 28, 2007 respectively) (Fig. 5). Mean stipe length at the onset of reproductive maturity for the transplanted *Pelagophycus* varied significantly among depths

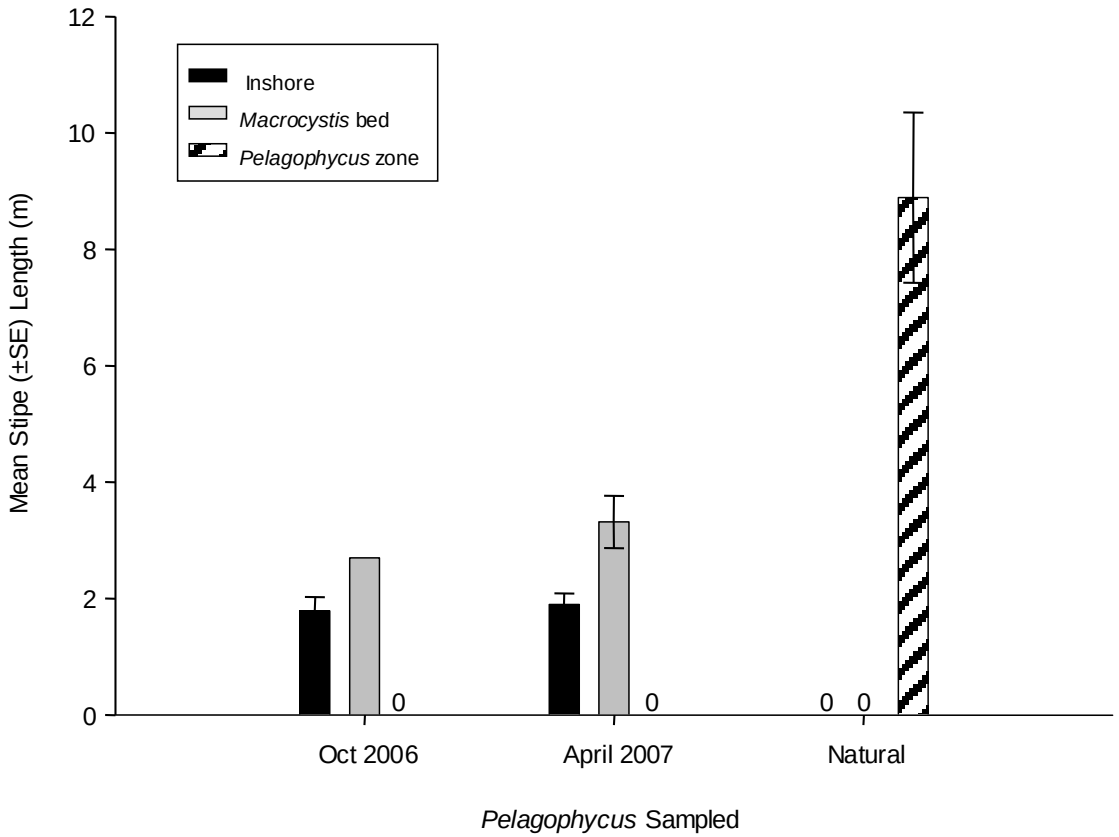

Figure 4. Mean (± SE) stipe length of reproductively mature *Pelagophycus* individuals for both transplant experiments initiated October 2006 and April 2007 as well naturally occurring individuals.

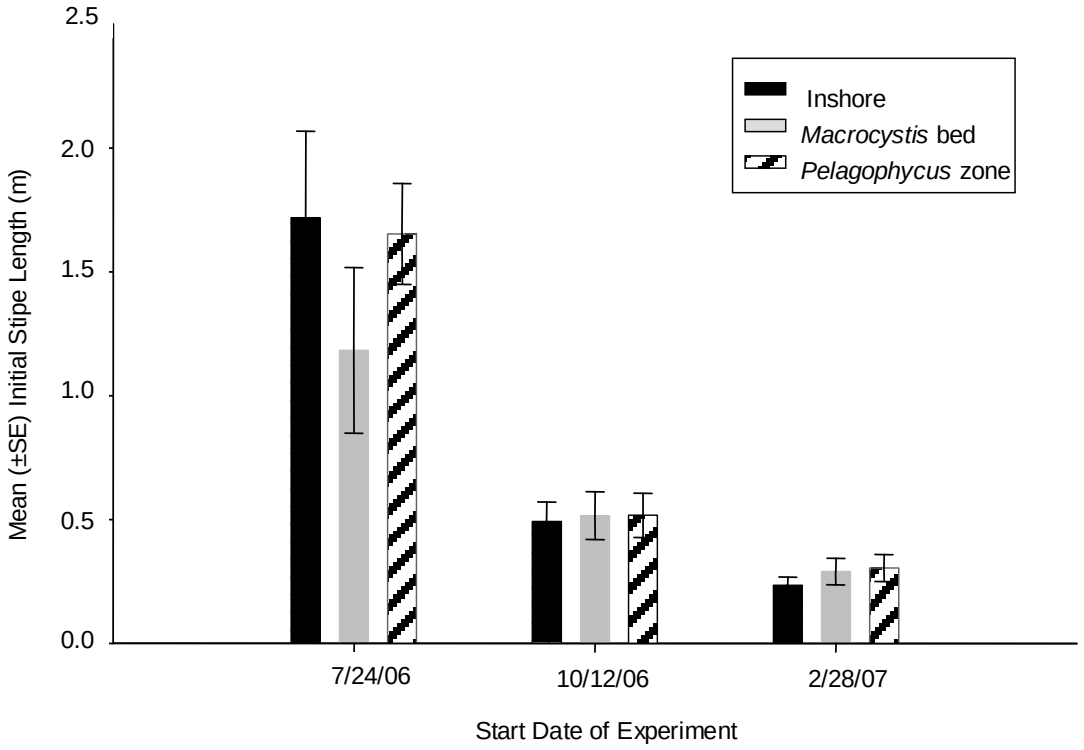

Figure 5. Mean (± SE) initial stipe length for juvenile *Pelagophycus* transplants for experiments initiated July 24, 2006, October 12, 2006 and April 28, 2007. Initial stipe length was measured before they were transplanted (either in the *Pelagophycus* zone, within or inshore of the *Macrocystis* bed).

($p < 0.001$) and between naturally occurring individuals ($p < 0.001$);(Fig 4, p. 15). During the transplant experiment initiated April 27, 2007 maturity for the *Pelagophycus* transplanted to the inshore shallow site was observed earlier (within four months) and in smaller individuals (1.90m $\pm$ 0.189 SE) than those transplanted to the middle of the *Macrocystis* beds (six months; 3.31m $\pm$ 0.448SE respectively) (Fig 6). None of the *Pelagophycus* transplanted to the *Pelagophycus* zone reached maturity during the six month experiment.

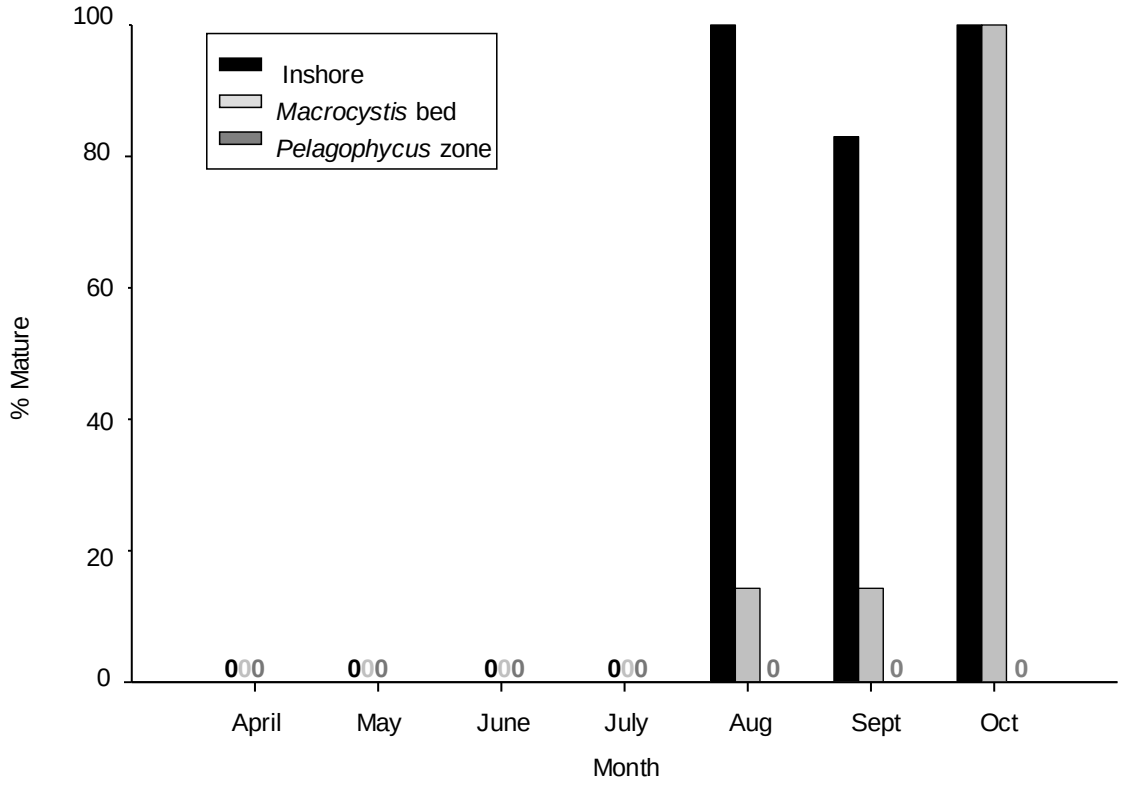

Figure 6. Percent of *Pelagophycus* transplants that became reproductively mature over the course of the experiment initiated on April 27, 2007.

Significant variation in RLC parameters were observed among depths, but not in blade portions (Table 1d, e, and f). Specifically, $rETR_{max}$ varied significantly among depths in March, April and October while E_k was significant for all months except July (Table 1a and b). Estimates of α varied significantly among depths for February, June, and October (Table 1 c). The results of pairwise comparisons showed $rETR_{max}$ and E_k (Table 2a and b)was significantly different across all depths in March and April. While α was not significantly different among all depths in any one month, but showed significant difference between two depths in February, June and October (Table 2 c). None of the RLC parameters

Table 1. Results of Mixed-Factor 2-Way ANOVA for Photosynthetic Parameters Among Depth a) rETRmax, b) Ek, and c) α and Blade Type d) rETRmax, e) Ek, and f) α for Naturally Occurring Individuals as they Grow from Benthos to Surface. Only Bold Values Indicate a Significant Difference ($p < 0.05$) (1 of 2).

a)

$rETR_{max}$					
Month	SS	df	Mean Squares	F-ratio	p-value
February	110.987	2	55.493	2.188	0.143
March	1688.411	2	844.206	29.027	**<0.001**
April	1432.471	2	716.236	66.573	**<0.001**
June	272.85	2	136.425	2.455	0.109
July	193.237	2	96.619	2.208	0.135
October	532. 436	2	266.218	11.784	**0.001**

b)

E_k					
Month	SS	df	Mean Squares	F-ratio	p-value
February	1325.228	2	662.614	4.648	0.025
March	8019.62	2	4009.81	31.71	**<0.001**
April	9028.089	2	4514.044	30.934	**<0.001**
June	38048.78	2	19024.39	14.758	**<0.001**
July	1377.76	2	688.88	1.247	0.308
October	4904.083	2	2452.041	7.939	**0.005**

c)

A					
Month	SS	df	Mean Squares	F-ratio	p-value
February	0.015	2	0.007	17.013	**<0.001**
March	0.003	2	0.002	1.987	0.174
April	0.001	2	0.001	1.193	0.322
June	0.083	2	0.042	33.877	**<0.001**
July	0.020	2	0.010	2.885	0.078
October	0.028	2	0.014	6.422	**0.01**

Table 2. Results of Mixed-Factor 2-Way ANOVA for Photosynthetic Parameters Among Depth a) rETRmax, b) Ek, and c) α and Blade Type d) rETRmax, e) Ek, and f) α for Naturally Occurring Individuals as they Grow from Benthos to Surface. Only Bold Values Indicate a Significant Difference ($p < 0.05$) (2 of 2).

d)

$rETR_{max}$					
Month	SS	df	Mean Squares	F-ratio	p-value
February	54.554	1	54.554	2.860	0.233
March	201.569	1	201.569	3.074	0.222
April	54.388	1	54.388	4.346	0.172
June	64.341	1	64.341	1.196	0.388
July	3.020	1	3.020	0.208	0.693
October	2.250	1	2.250	.693	0.264

e)

E_k					
Month	SS	df	Mean Squares	F-ratio	p-value
February	65.965	1	662.614	0.729	0.483
March	1846.742	1	1846.742	3.046	0.223
April	508.585	1	508.585	1.449	0.352
June	1144.521	1	1144.521	5.404	0.146
July	104.016	1	104.016	0.160	0.728
October	0.088	1	0.088	0.012	0.922

f)

A					
Month	SS	df	Mean Squares	F-ratio	p-value
February	0.004	1	0.004	3.773	0.192
March	0.003	1	0.003	0.318	0.582
April	0.002	1	0.002	0.144	0.741
June	0.003	1	0.003	0.431	0.579
July	0.002	1	0.002	0.010	0.931
October	0.002	1	0.002	0.128	0.728

Table 2. Results of Fisher's LSD Pair Wise Comparisons for Differences Between Depths Following a Mixed-Factor 2-WayANOVA for Photosynthetic Parameters a) $rETR_{max}$, b) E_k, and c) α as Naturally Occurring Individuals Grow Through the Water Column. Only Bold Values Indicate a Significant Difference ($p < 0.05$).

a)

$rETR_{max}$							
Depth	Depth	February	March	April	June	July	October
Benthos	Mid	**0.052**	**0.002**	**<0.001**	0.18	0.094	0.067
Benthos	Surface	0.316	**<0.001**	**<0.001<**	**0.041**	0.814	**0.006**
Mid	Surface	0.287	**0.003**	**<0.001**	0.381	0.083	**<0.001**

b)

E_k							
Depth	Depth	February	March	April	June	July	October
Benthos	Mid	**0.034**	**0.002**	**0.002**	0.581	0.369	**0.006**
Benthos	Surface	**0.009**	**<0.001**	**<0.001**	**<0.001**	0.133	0.470
Mid	Surface	0.526	**0.002**	**0.001**	**<0.001**	0.472	**0.003**

c)

α							
Depth	Depth	February	March	April	June	July	October
Benthos	Mid	0.850	0.277	0.163	0.292	0.367	**0.027**
Benthos	Surface	**<0.001**	0.068	0.259	**<0.001**	0.133	**0.004**
Mid	Surface	**<0.001**	0.0541	0.716	**<0.001**	**0.026**	0.273

varied significantly between blade portions.

Chlorophyll *a* content in naturally occurring individuals varied significantly among depths in all months; February ($p = 0.034$), March ($p < 0.001$), May ($p = 0.011$), July ($p < 0.001$) and October ($p < 0.001$). Post hoc tests revealed significant differences between the benthos and surface ($p = 0.007$ and $p < 0.005$) as well as mid-water and surface ($p = 0.01$ and $p = 0.017$) for February and May respectively. Significant differences in Chlorophyll *a* content were found between the benthos and mid-water ($p < 0.001$ and $p < 0.001$) as well as benthos and surface ($p < 0.001$ and $p < 0.001$) for March and July respectively. Differences in Chlorophyll *a* content between blade portions were only significant in May ($p = 0.014$). For the month of October, only the benthos and mid-water were compared due to loss of replicates.

MICROSCOPIC STAGES: RECRUITMENT AND LIGHT SENSITIVITY

Macrocystis removals and the addition of *Pelagophycus* propagules within the *Macrocystis* beds did not yield any *Pelagophycus* recruits in either experiment (March 2007 and August 2007). However, the addition of a control within the *Pelagophyc*us zone (in August 2007) produced *Pelagophycus* recruits within four months. Density of *Pelagophycus* recruits near to the sori-bags (6.5 ± 0.604 SE and 2.5 ± 0.394SE for 1m and 2m away from sori bag respectively) significantly differed from natural recruitment (1.125 ± 0.398 SE) haphazardly sampled throughout the site($p < 0.001$) (Fig. 7).

Photosynthetic performance of laboratory-reared gametophytes and embryonic sporophytes was significantly impacted by the higher irradiances levels found within the *Macrocystis* beds. Specifically, gametophytes grown under irradiances similar to those observed in the naturally occurring deeper *Pelagophycus* zone exhibited greater maximum quantum yield ($F_v/F_m = 0.563 \pm .013$ SE) than those grown under higher irradiances similar to those observed in the shallower *Macrocystis* bed ($F_v/F_m = 0.474 \pm 0.024$ SE) ($p < 0.001$). However, when the microscopic stages were moved from low light levels to the higher light levels, densities of both gametophytes and embryonic sporophytes decreased to zero, indicating total mortality (Fig. 8a and 8b). RLCs comparing cultures grown at low light (Fig 9a) and then moved to high light(Fig 9b) show a decrease in the slope of rETR (although not significantly different) at higher levels of irradiance, indicating a decrease in the ability to

photoacclimate, when moved to higher light levels. Furthermore, photosynthetic parameters for cultures of the microscopic stages grown continuously at low light yielded significantly higher alpha α ($p = 0.001$) and F_v/F_m ($p < 0.001$) than cultures moved to higher light. Similarly, RLCs comparing *Pelagophycus* (Fig 10a) and *Macrocystis* (Fig 10b) cultures continually grown under high light revealed that *Macrocystis* has a much steeper change in the slope of rETR at higher levels of irradiance indicating that *Macrocystis* is acclimating more efficiently at these higher irradiance levels than *Pelagophycus*. The photosynthetic parameters α ($p = 0.006$) and F_v/ F_m ($p = 0.006$) were significantly different when comparing the photosynthetic parameters of *Macrocystis* and *Pelagophycus* continually grown under high light.

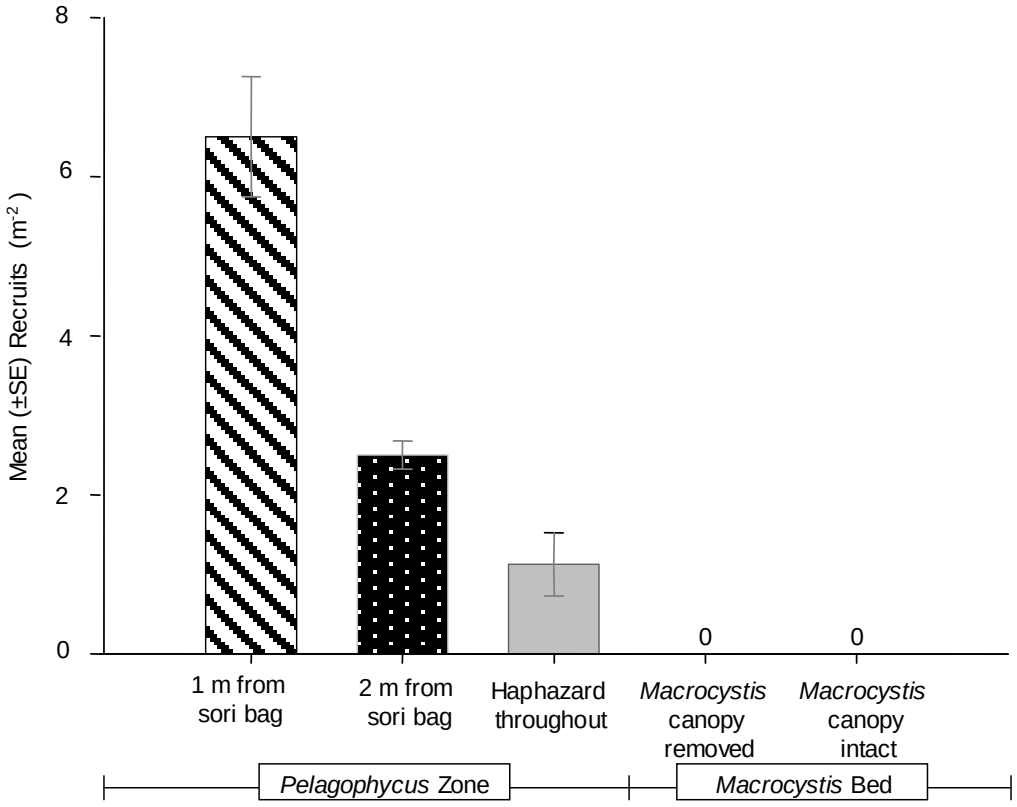

Figure 7. Mean (± SE) density of *Pelagophycus* recruits in plots that were artificially seeded (through the use of sori bags) within the *Pelagophycus* zone and the *Macrocystis* bed. Recruitment in *Pelagophycus* zone was observed within 1 m and2 m from the sori bag as well as haphazardly throughout the site. Within the *Macrocystis* bed recruitment was observed within areas where *Macrocystis* canopy was removed or left intact.

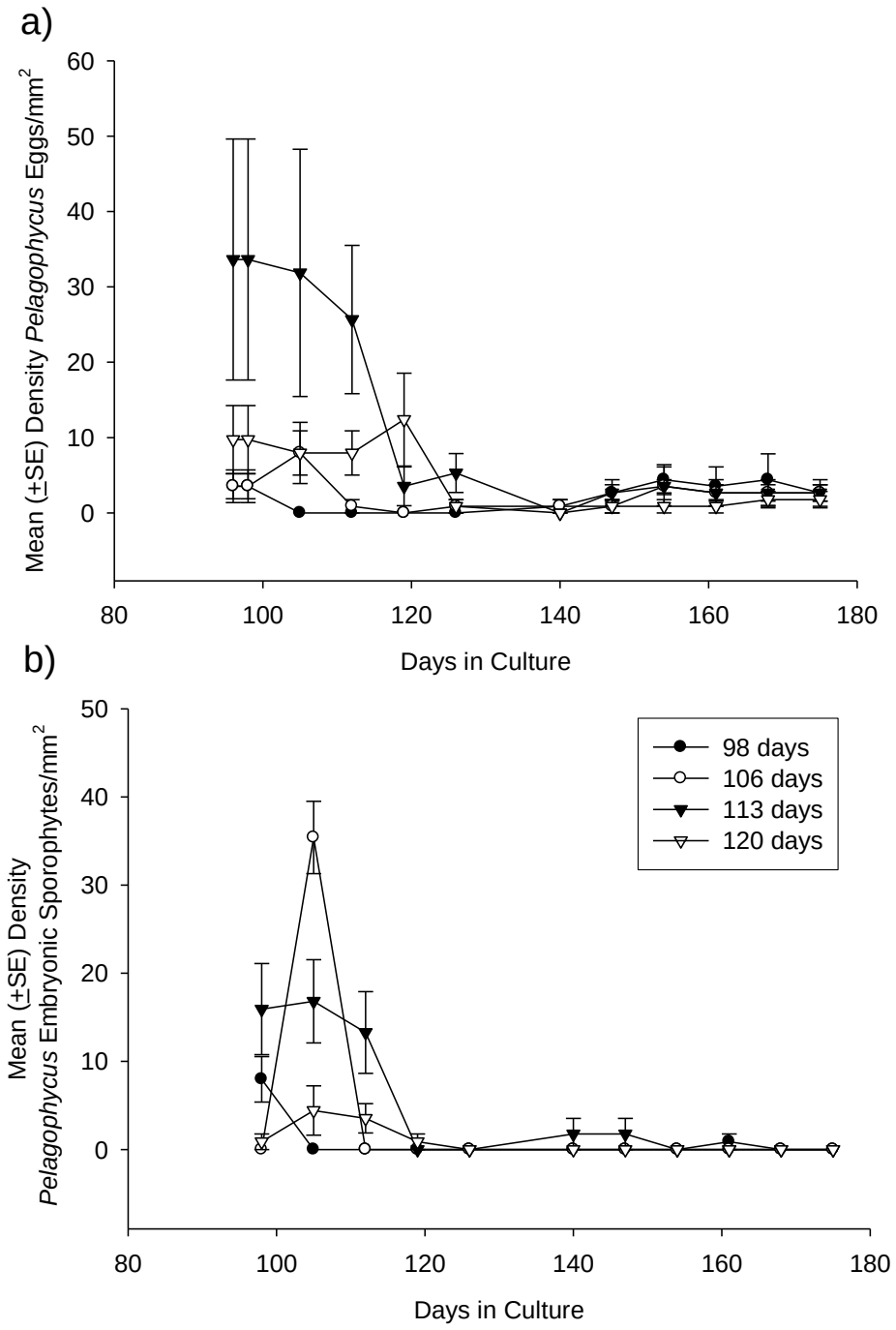

Figure 8. Mean (± SE) density of *Pelagophycus* a)eggs and b) embryonic sporophytes grown at low light levels and then moved to higher light levels at 98, 106, 113, and 120 days.

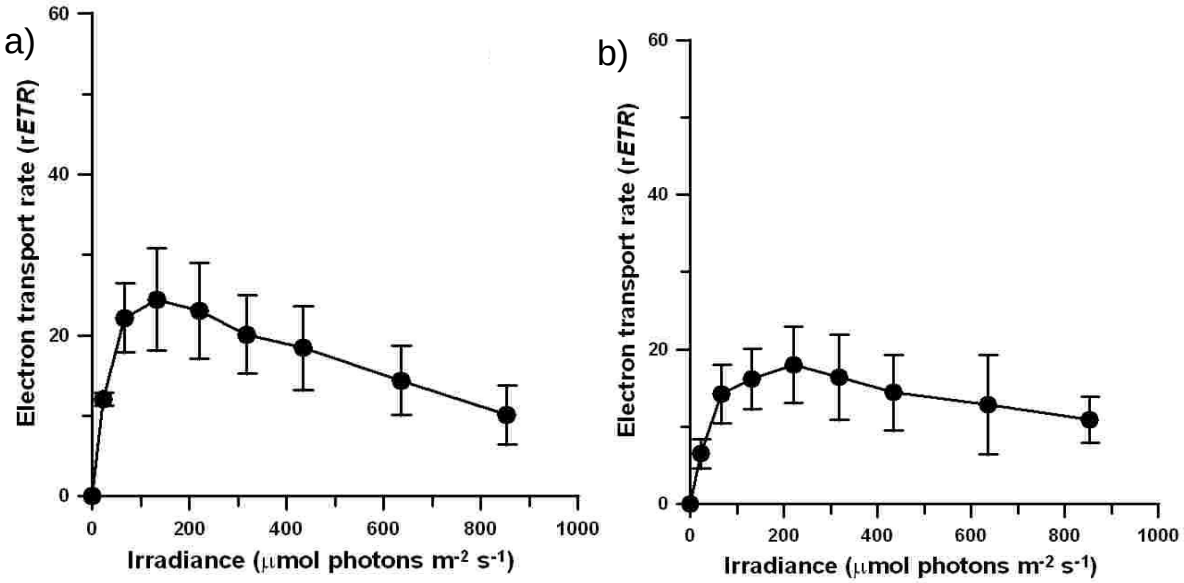

Figure 9. Rapid Light Curves, mean (± SE) electron transport rate (rETR) vs. irradiance for *Pelagophycus* gametophytes and embryonic sporophytes cultured under a) low light conditions similar to the those observed in the *Pelagophycus* zone and then b) moved to higher light conditions similar to those within the *Macrocystis* beds.

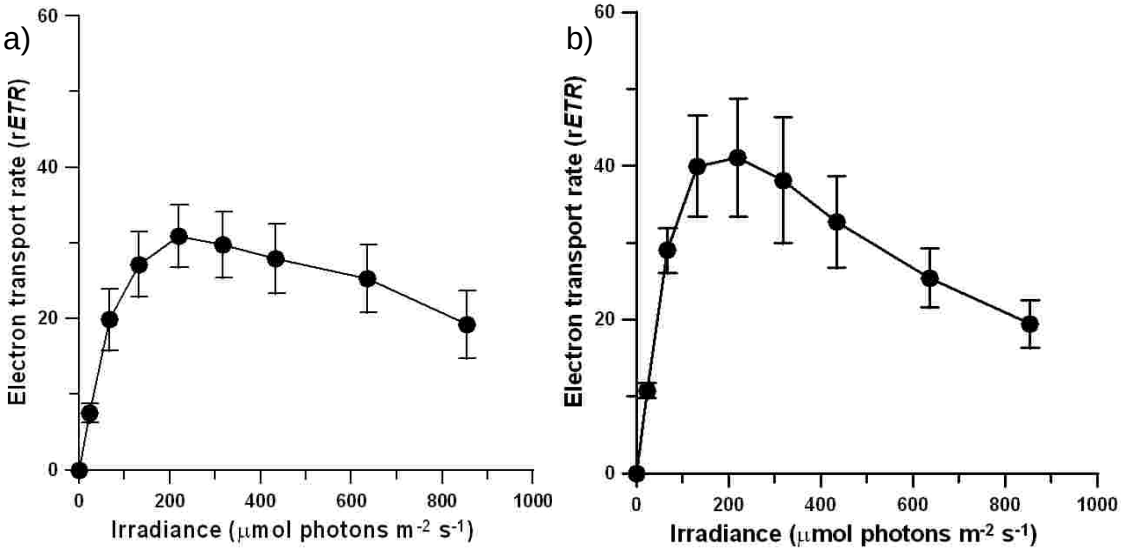

Figure 10. Rapid Light Curves, mean (± SE) electron transport rate (rETR) vs. increasing irradiance comparing a) *Pelagophycus* gametophytes and embryonic sporophytes and b) *Macrocystis* gametophytes and embryonic sporophytes cultured under high light conditions equivalent to levels found within the *Macrocystis* beds.

DISCUSSION

Zonation patterns are a result of changing factors along a gradient that results in species replacement because species are only specialized for a particular portion of that gradient (Connell 1961). Zonation along vertical gradients can be found in both terrestrial and marine environments (Menge and Sutherland 1976). Patterns of zonation along gradients are particularly evident in the marine environment where species distribution may be determined by one or more abiotic, biotic or a combination of factors (Graham 1997; Lubchenco 1980). In addition to the diverse factors that can influence an organism distribution, different life history stages maybe affected by that same factor differently with particular sensitivity in earlier life history stages (Graham 1996, Zacherl et al. 2003). *Pelagophycus'* latitudinal distribution extends hundreds of kilometers along the coast of southern California, encompassing the entire length of the Point Loma *Macrocystis* bed (8-10km), but its vertical distribution in Point Loma is limited offshore of the dense *Macrocystis* bed. In order to identify the factors responsible for limiting *Pelagophycus* distribution to deeper depths within the Point Loma kelp bed this study utilized a multiple life history stage approach and employed a combination field-based monitoring, manipulative experiments as well as laboratory-based controlled culturing.

The effects of depth were evaluated for the juvenile, sub-adult and adult macroscopic portions of Pelagophycus life history by assessing the ability of naturally occurring individuals to photoacclimate as they grow through the water column. Saturation irradiance (Ek) was the major statistically different factor between depths. This is important because Ek occurs at the irradiance at which photosynthesis switches from photon absorption and photochemical conversion to activating photoprotective mechanisms and therefore Ek can be used as an indicator of photoacclimation (Ralph and Gademann 2005, Sakshaug and Bricaud et al. 1997). Pelagophycus utilizes multiple adaptation techniques; behaving as a low light adapted species as a juvenile near the benthos (with higher Ek) and then shifting to high light adapted strategies (with lower Ek) as it grows toward the surface during sub-adult and adult life history stages. This is supported by Chlorophyll a analysis revealing a general trend of higher levels occurring in juveniles near the benthos and lower levels in adults near the surface. Pelagophycus ability to photoacclimate as it naturally grows through the water

column suggests that the macroscopic stages of Pelagophycus are well adapted to acclimate to increasing irradiance levels it experiences throughout its macroscopic life history stages.

The use of common garden transplant experiments provided a better understanding of the effects of different environmental conditions on the growth and survival of *Pelagophycus* sporophytes. *Pelagophycus* juveniles transplanted inshore, among and offshore of the *Macrocystis* beds displayed no difference in stipe growth or survival among depths, but time to maturity decreased at shallower depths. Mortality of transplants was only caused by failure of the experimental attachment site and was not dependent on depth. Individuals that were transplanted to the *Pelagophycus* zone never reached reproductive maturity during the 2 year study. This supports previous work done by Miller et al. (2000) that revealed *Pelagophycus* requires two to three years to reach reproductive maturity in Point Loma. However, *Pelagophycus* transplanted inshore of their natural range (into shallower water) reached maturity in only 4 month. It is possible that the earlier onset of reproductive maturity in shallow transplants maybe initiated by the distance from the surface and therefore coupled with light intensity or quality of light.

The two major factors affecting irradiance at depth are canopy shading and attenuation of light throughout the water column (Shaughnessy et al 1996, Frade et al 2008). While the later is dependent on turbidity and depth, canopy structure is dependent on the species that form the canopies. *Macrocystis* forms a much denser surface canopy than *Pelagophycus* (personal observation) with a subsurface canopy composed of *Laminaria farlowii* and *Pterygophora californica* found under both canopy types. Sub-surface canopies where not manipulated in this study and therefore these combination canopy areas could potentially act as a low light refuge where *Pelagophycus* may recruit. Even when propagule presence was insured through seeding or from the shallow transplants that reached reproductive maturity (proved to be fertile producing gametophytes and sporophytes when cultured in lab) no *Pelagophycus* recruits were ever observed within the *Macrocystis* beds. It is uncertain why *Pelagophycus* does not recruit to these combination canopy areas within the *Macrocystis* beds, but competition, is likely to deter recruitment of *Pelagophycus* even if spores were able to survive. Further exploration of competition between *Macrocystis* and other potential competitors may provide a better understanding of this microscopic battle that *Pelagophycus* must undertake to establish within these shallower environments.

Levels of irradiance that were easily tolerated by the macroscopic portion of *Pelagophycus* life history were shown to be intolerable to the microscopic stages and therefore play an important role in determining its distribution. Gametophytes and embryonic sporophytes of *Pelagophycus* proved to be sensitive to the small increase (as little as 14 µmol photons m^{-2} s^{-1}) in irradiance found between the *Macrocystis* and *Pelagophycus* beds, producing negative affects in both the embryonic sporophytes and gametophytes. *Pelagophycus* microscopic stages experienced 100% mortality when moved from low light levels found within the *Pelagophycus* zone to higher light levels found within the *Macrocystis* bed. Additionally, *Macrocystis* microscopic stages are able to acclimate more effectively than *Pelagophycus* under higher irradiances potentially providing *Macrocystis* with a competitive advantage in shallower waters. While it is possible to produce *Pelagophycus* sporophytes under high light conditions, I stress the rarity of this event in nature because only rare individuals (one every 3 km) are observed within the *Macrocystis* beds.

Due to the nature of kelps' biphasic life history, a multiple life history approach proved necessary to investigate the apparent inability of *Pelagophycus* to invade and permanently establish within the *Macrocystis* beds thereby adding support to the growing body of literature that emphasizes a multiple life history approach (Kinlan and Gaines 2003; Matson and Edwards 2007; Zacheral et al. 2003).

This study highlights the effects of irradiance on the microscopic life history stages of *Pelagophycus* by demonstrating how seemingly subtle differences in a single abiotic factor can determine the distribution of species. This study showed (1) naturally occurring individuals are able to photoacclimate as they grow towards the surface (2) *Pelagophycus* survival and growth of macroscopic stages is not effected by depth, but onset of reproductive maturity occurs sooner at shallower depths (3) microscopic stages are highly vulnerable to shallower light conditions. Insight on the varying sensitivity of different life history stages to changing environmental gradients may provide better ability to manage commercially important species that use different habitats and exposed to changing abiotic factors throughout their life cycles. Additionally, a better understanding of species like *Pelagophycus* that creates structure and thereby essential habitat in an environment that is

otherwise completely lacking structure can help to maintain high levels of diversity within the marine ecosystem.

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ABSTRACT OF THE THESIS

The Effects of Irradiance in Determining the Vertical Distribution of
Elk Kelp, *Pelagophycus porra*

by
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Elk Kelp, *Pelagophycus porra*, is commonly observed in deep (20-30 m) water along the outer edge of Giant Kelp, *Macrocystis pyrifera*, beds in southern California, USA and northern Baja California, MEX, but rarely occurs in shallower water or within beds of *M. pyrifera*. Due to the nature of *P. porra's* heteromorphic life history that alternates between a macroscopic diploid sporophyte and a microscopic haploid gametophyte, investigations of both life history stages were needed to understand *P. porra*' apparent inability to encroach into *Macrocystis* beds along the southern California coast.

Juvenile P. porra sporophytes were transplanted (1)within the *Pelagophycus* zone along the offshore edge of the *M. pyrifera* bed at 20 m, (2) within the center of the *M. pyrifera* bed at 15 m and (3) along the inshore edge of the *M. pyrifera* bed at 8 m. Transplanted *P. porra* exhibited similar growth across all depths, but the onset of reproductive maturity was observed only at shallower depths. Stipe length at the onset of maturity differed between depths, increasing significantly from inshore and within the center of *M. pyrifera* beds to offshore within naturally occurring *P. porra* beds. Photosynthetic measurements of *P. porra* blades using PAM fluorometry indicated that although *P. porra* initially exhibits characteristics of a low-light adapted species (20m depth), individuals are able to photoacclimate to increasing light levels showing traits of high-light adapted species in the midwater zone and at the surface.

When the presence of *P. porra* propagules was increased, *P. porra* was unable to recruit within *M. pyrifera* beds. No *P. porra* recruits were observed near sori bags placed within *M. pyrifera* beds while heavy recruitment (6.5 ± 0.604 SE and 2.5 $\pm$ 0.394S E for 1m and 2m away from sori bag respectively) was observed near the sori bags within the *P. porra* bed. These seeding experiments indicated that a factor other than spore dispersal is limiting *P. porra* distribution to deeper depths.

Culture experiments were carried out in the laboratory using microscopic gametophytes and embryonic sporophytes of *P. porra* to investigate the effects of the higher light levels found within *M. pyrifera* beds. Cultures were grown under low light (2 µmol photons m^{-2} s^{-1}) conditions and then moved to high light conditions (16 µmol photons m^{-2} s^{-1}) at which time both embryonic sporophytes and gametophytes experienced 100% mortality. When grown under constantly higher (18 µmol photons m^{-2} s^{1}) light conditions, the ability of *P. porra* to photoacclimate decreased. The vunerability of *P. porra* microscopic stages to higher irradiances appears to be the major limiting factor inhibiting *P. porra* from becoming established within *Macrocystis* beds and stresses the importance of a multiple life-history approach when investigating species distributions.