

Kelp rafts in the Humboldt Current: Interplay of abiotic and biotic factors limit their floating persistence and dispersal potential

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Abstract

During summer 2009, we conducted a field experiment and a field survey at 30°S in the coastal Humboldt Current to determine how floating time affects the physiological performance of kelp rafts. For the field experiment kelp rafts were tethered in coastal waters and the field survey was specifically designed to collect free-floating *Macrocystis pyrifera* across a latitudinal temperature gradient that reflects natural floating time. Experimental kelps were kept under photosynthetic active radiation (PAR) and PAR + ultraviolet (UV; PAR + UV) using filter foils, and tethered at the sea surface in their natural habitat. Ultraviolet radiation (UVR) did not affect kelp physiology, but caused a decrease in kelp biomass. The field survey confirmed that sea-surface temperature increased with distance from upstream source populations of *M. pyrifera*. Rafts sampled at increasing distance from sources showed high epibiont cover and reduced blade lengths. Physiological performance declined with increasing size of algal epibionts, which are indicators of floating time. Rafts that were farthest from the southern source populations had lost their sporophylls, suggesting that dispersal potential decreases with increasing floating time. The combined effects of abiotic (UVR and temperature) and biotic factors accelerate degradation of *M. pyrifera* and, thus, can impede successful dispersal in the Humboldt Current at 30°S. This suggests that floating macroalgae can be important dispersal vectors in areas with moderate environmental stress (i.e., in temperate oceans).

Dispersal is one of the key processes for species expansion and connectivity in marine systems. Many invertebrates have autonomous dispersal stages, namely planktonic larvae that move in the water column to position themselves in currents favorable for dispersal. In contrast, species without planktonic larvae rely on other mechanisms to reach new habitats. Rafting on floating algae has been suggested as an important dispersal mechanism for these invertebrates (Nikula et al. 2010). Here dispersal depends not only on the organisms themselves but also on the floating substratum and its persistence at the sea surface.

Floating macroalgae can be found in all major oceans but they are more abundant in coastal waters where their abundances decrease with distance from source populations (Thiel and Gutow 2005a). Persistence of algae at the sea surface can be influenced by winds and currents, causing algae to be held back in retention zones (Hinojosa et al. 2010) or to be accumulated on local beaches (Harrold and Lisin 1989). Furthermore, upon detachment, all parts of the algae are transferred to surface conditions, which might negatively influence their potential to serve as long-distance dispersal vectors. For instance, Helmuth et al. (1994) showed that kelp rafts farther away from their

potential source regions in Tierra del Fuego had more epibionts and signs of degradation. A similar trend was observed by Safran and Omori (1990) for algal rafts in Japanese waters. Possibly, the combination of biotic and abiotic factors that kelp rafts experience at the sea surface accelerates degradation.

During their rafting journeys, performance of floating algae can be compromised by (1) grazing, (2) photodamage, (3) high temperature, and (4) increasing epibiont load. Mobile mesograzers suppress raft persistence by removing key metabolically active tissues, resulting in diminished photosynthesis. Furthermore, sessile epifauna such as bryozoans are likely to influence the physiology and growth of benthic macroalgae by covering photosynthetic tissues (Hurd et al. 2000; Hepburn et al. 2006). Dense colonization with bryozoans can also increase the susceptibility to tissue loss as a result of wave or current action (Dixon et al. 1981). In general, the abundance and species composition of organisms associated with floating algae can be highly variable in time and space and it is suggested that successional changes are related to floating time and distance from the shore (Thiel and Gutow 2005b). Overall, continuous grazing pressure and increasing epibiont load over extending floating time might negatively affect the physiological potential of floating algae and provoke deterioration and ultimately sinking of these rafts.

High solar radiation at the sea surface can also negatively affect floating algae. Transplanting benthic (nonfloating) *Laminaria solidungula* from deep to shallow

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waters resulted in a strong decrease in photosynthetic performance (Karsten et al. 2001). Similar responses can be expected for detached benthic algae that suddenly float to the sea surface and are exposed to continuously high irradiance levels. Another important factor that can affect the floating persistence of algae in their natural habitat is seawater temperature (Hobday 2000). Although cold Icelandic waters favor the floating persistence of *Ascophyllum nodosum* (Ingólfsson 1998), recent laboratory studies showed for *A. nodosum* and *Fucus vesiculosus* a reduced persistence at water temperatures $> 15^{\circ}\text{C}$ (Vandendriessche et al. 2007). Similar results were obtained for floating individuals of *Macrocystis pyrifera* maintained in outdoor tanks, which lost biomass at water temperatures $> 20^{\circ}\text{C}$, and rapid disintegration and sinking of algae was observed at 24°C (Rothäusler et al. 2009). These results strongly suggest that thermal stress (e.g., during summer months) has negative effects on floating algae. Elevated water temperatures during El Niño events are also known to affect benthic populations of *M. pyrifera* in both hemispheres (Tegner and Dayton 1987; Vega et al. 2005), and likely will negatively affect floating kelps in similar ways. These thermal anomalies have influenced the southern hemisphere since at least the Holocene (Ortlieb et al. 2000) and, thus, may have played a role in the dispersal of algal populations since that time.

At present, our knowledge of growth and physiology of floating algae comes mainly from mesocosm experiments with artificial light (when done indoors; Vandendriessche et al. 2007), or limited flow-and-wave motion in outdoor tanks (Rothäusler et al. 2009). Even though these laboratory studies provide initial insights about the influence of the most important abiotic and biotic factors on floating algae, their usefulness is limited because they only partially mimic natural floating conditions. The hydrodynamic environment in laboratory mesocosms is often restricted to moderate or no water movements, while at sea, algae might frequently be turned over by waves or winds. Similarly, many epibionts are filtered out by water intake systems and, thus, the development of epibiont communities on algal tissue is restricted. Possibly, on algal rafts floating in the natural environment, epibionts that cover photosynthetic tissues may initially serve as ultraviolet radiation (UVR) screens, but at later stages of succession epibiont effects may become negative. Wave and wind action will move algal rafts in the field, ensuring that not always the same algal tissues are exposed to high irradiance conditions, which can positively influence raft physiology and growth and, thus, their persistence at the sea surface. Therefore, we aim to investigate for the first time UVR effects on physiology and growth of floating algae in a field-based study.

Abundant populations of *M. pyrifera* are found along temperate coasts worldwide (Graham et al. 2007). They can reach sizes up to 40 m and, thus, benthic sporophytes experience vertical gradients of important abiotic factors, namely nutrients, irradiance, and temperature. Based on the above considerations, we hypothesized that UVR at the sea surface suppresses photosynthesis and pigment contents of floating *M. pyrifera*, with negative consequences for kelp

physiology and growth. Furthermore, epibiont colonization will increase with extended floating time, thereby curtailing overall kelp physiology (even though effects might initially be positive) and floating persistence. Herein, we tested these hypotheses by studying *M. pyrifera* under natural floating conditions. We surveyed natural kelp rafts at different distances from source populations and at the same time we manipulated incident irradiances of algae tethered in a field experiment. This was done to examine how UVR and epibionts affect the persistence of *M. pyrifera* in their pelagic environment, and whether the physiological performance and epibiont colonization of freely floating *M. pyrifera* changes with distance from source populations and, hence, over time. Kelp responses were studied through growth, chlorophyll fluorescence, pigments, and enzyme activity.

Methods

Study area—Algae were sampled in the Coastal System of Coquimbo (CSC) on the northern-central coast of Chile (Fig. 1). The CSC extends from Punta Lengua de Vaca ($30^{\circ}17'\text{S}$, $71^{\circ}36'\text{W}$) in the south up to Punta de Choros ($29^{\circ}14'\text{S}$, $71^{\circ}28'\text{W}$) in the north. Extensive benthic source populations of *M. pyrifera* occur only south and north of the CSC, which are separated by > 130 km from each other. A similar gap in the distribution of *M. pyrifera* is present further north between 26°S and 23°S . Within the CSC, *M. pyrifera* can often be found floating and rafts generally pass the system in a northward direction, driven by the predominant winds from the southwest (Moraga and Olivares 1993). Furthermore, this region is under the influence of the coastal branch of the Humboldt Current System, with surface waters generally moving toward the north and northwest (Marín and Delgado 2007). Consequently, connectivity across the gap between southern and northern populations can be expected in a south–north direction. Two upwelling zones close to Punta Lengua de Vaca and Punta de Choros are identified within this bay system (Rutllant and Montecino 2002).

During the experimental period, incident ultraviolet B (280–320-nm) radiation data were monitored by a national meteorological agency (<http://www.meteochile.cl>), and values ranged between 1.0 Wm^{-2} and 3.4 Wm^{-2} . The photosynthetic active radiation (PAR) data (400–700-nm) were obtained from the meteorological station of CEAZA (<http://www.ceaza.cl>), which registered values between $330 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and $2149 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ during the experimental period. Sea-surface temperature measured in situ showed a latitudinal variation within the CSC, with temperatures increasing from $\sim 14.0^{\circ}\text{C}$ in the southern part to $\sim 18.0^{\circ}\text{C}$ in the northern part (Fig. 1).

Influence of UV-radiation on algal floating potential—Collection of sporophytes and experimental set-up: In order to estimate the importance of UVR on *M. pyrifera* floating in their natural habitat, we conducted a field experiment in the vicinity of the marine laboratory at Universidad Católica del Norte, Coquimbo, Chile (Fig. 1)

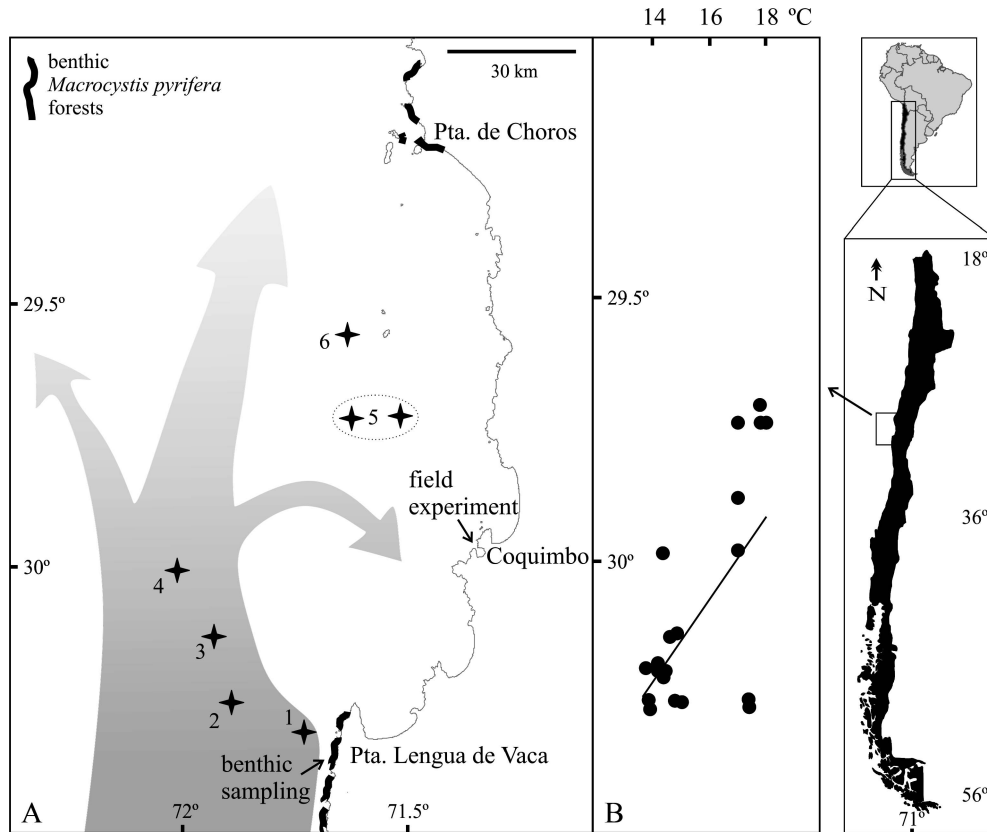


Fig. 1. (A) Study area at mid-latitudes and sampling stations (1–6) of floating and benthic sporophytes of *Macrocystis pyrifera*, as well as source populations of kelp forests. Light grey arrows represent the main current direction. There are two upwelling centers in the Coastal System of Coquimbo (CSC), a very persistent one at Punta (Pta.) Lengua de Vaca and another one at Pta. de Choros. (B) Latitudinal variation of sea-surface temperature measured in austral summer 2009.

in austral summer 2009 (14–21 Jan 2009). Thirty-eight sporophytes, including their holdfasts, were detached via snorkeling at low tide from a nearby shallow subtidal kelp bed (2–4-m depth) at Punta Lengua de Vaca (30°17'S, 71°36'W; Fig. 1). Sporophytes were transported to the laboratory, where they were kept overnight in a large outdoor flow-through tank (1000 liters). Before experimentation, sporophytes were thoroughly rinsed to remove associated fauna and epiphytes.

Incident solar radiation was manipulated by standardized UV-filter foils clamped to a frame of polyvinyl chloride (PVC) tubes (dimensions = 80 cm × 55 cm), which was individually fixed ~ 25 cm above a small PVC float (dimensions = 100 cm × 80 cm). The complete structure (hereafter, termed filter float) obtained its floatability by four styrofoam buoys, which were fixed to each of the four sides of the frame. The following solar radiation treatments were realized: exposure to complete radiation (PAR + UV) by using Ultraphan foils (295-nm Ultraphan 0.3-mm transparent foil; Digefra) that blocked wavelengths < 295 nm; exposure to PAR alone by using Ultraphan cut-off foils (URUV farblos 0.12-mm; Digefra) blocking wavelengths < 395 nm. In addition, sporophytes were kept without filter foils under natural solar radiation (NATSR), allowing to test for potential filter artifacts in

comparison with the PAR + UV treatment. No filter artifacts were detected for all comparisons of the dependent variables, except for blade elongation rate (BER) where the NATSR treatment differed from the filter foils that let the entire light spectrum (PAR + UV) pass. Consequently, where no filter artifact was detected, the NATSR data were considered redundant and excluded from the analyses, but the analysis for BER included the NATSR treatment.

Sporophytes with an initial wet weight of 193.1 ± 31.1 g were randomly distributed over the experimental filter floats and carefully entangled to the base of the PVC structure, so that they could freely sway in the water and were simultaneously covered by their respective filter foils. Each treatment combination was replicated 10 times (i.e., we had 10 filter floats each for PAR and PAR + UV, respectively), which were complemented by the set of sporophytes ($n = 10$) that was kept without filter floats under NATSR. Experimental filter floats and NATSR sporophytes were individually tethered to a main line, which was ~ 1 m below the sea surface. The experiment lasted 15 d and sporophytes were monitored in 5-d intervals. This sampling time was chosen because previous mesocosm experiments conducted in Coquimbo confirmed that sporophytes of *M. pyrifera* already showed a reduced physiological performance after being afloat for 10 d

(Rothäusler et al. 2009, 2011a). Thus, the kelp responses measured herein provide insights about the physiological changes of *M. pyrifera* after detachment.

As physiological response variables we measured the activity of total carbonic anhydrase (CA) and maximal quantum yield of chlorophyll fluorescence ($F_v:F_m$; see below) at each of the 3 sampling days (5 d, 10 d, and 15 d after start). Photosynthesis vs. light curve (P-I curve) parameters, pigments (chlorophyll *a*, *c* [Chl *a*, *c*], carotenoids), and nitrogen content were measured only at day 15. Growth responses such as biomass change, blade elongation rate, and loss of distal blade tissue were measured at each sampling day, while the within-sporophyte biomass distribution and reproductive status were determined at the end of the experiment. We also determined the epibiont cover (day 15) as well as the growth rate of the bryozoan colonies at days 10 and 15 of experimentation.

Field survey of floating kelp rafts along a south–north gradient—In order to determine the physiological status and epibiont cover of freely floating rafts of *M. pyrifera* in the field, we sampled algal rafts in their natural environment at different distances from the southern source populations (Fig. 1). For this survey we exploited the fact that algae detached near Punta Lengua de Vaca generally move in a northward direction within the CSC. Rafts were collected at six different stations within a south–north gradient (Fig. 1), during ship cruises from 14 until 21 January 2009 (the research vessel returned to port every night). When algal aggregations were encountered in convergence zones, sporophytes ($n = 8$) of *M. pyrifera* were randomly taken from different rafts and their position was recorded with a hand-held global positioning system. Rafts were sampled with a boat hook and immediately placed in a large tank filled with seawater (500 liters) and covered with a dark mesh, so that all floating structures were always moistened with seawater.

Generally, rafts floating in their natural habitat are continuously colonized by epibionts, especially by bryozoans and stalked barnacles, which are found almost exclusively on floating items (Thiel and Gutow 2005b). Assuming that these epibionts colonize floating algae shortly after they become detached, their growth rates serve as good approximations of minimum algal floating duration (Macaya et al. 2005). Thus, the approximate growth rate of bryozoans and stalked barnacles was used to evaluate whether the distance from source populations is related to floating time.

Back in the laboratory, rafts were kept overnight in a large outdoor flow-through tank (2000 liters) to be processed on the following day. In total, eight sporophytes from each station were used to determine physiological variables such as maximal quantum yield of chlorophyll fluorescence ($F_v:F_m$), P-I curve parameters (maximal electron transport rate [ETR], initial slope α , and saturating irradiance), pigments (Chl *a*, *c*; carotenoids), CA, and nitrogen tissue status. We also determined the within-sporophyte biomass distribution of floating algal rafts, their blade length, reproductive output, and epibiont cover.

Measurements of kelp response variables—General measuring procedure: All physiological variables were measured for algae from the field survey (floating sporophytes) and for UVR-treated algae (experimental sporophytes). In addition, physiological responses were also measured for eight initial algae (benthic sporophytes) that were detached together with the experimental sporophytes. These samples were taken to determine the physiological status of *M. pyrifera* in their benthic habitat and served as control values for floating and experimental sporophytes. Sporophyte sampling started at 08:00 h (local time), when one vegetative blade from the upper region of each sporophyte was cut off and further processed such as described in Rothäusler et al. (2011a).

Tissue nitrogen status, pigments and CA-activity: To determine the nitrogen status of floating and experimental sporophytes, kelp tissue was dried at 60°C until constant weight. Dried material was ground and total nitrogen was determined separately for each sample using an elemental analyzer (Elementar Vario EL III). Results for floating and experimental sporophytes showed nitrogen concentrations above 1.5% and 1.3%, respectively, suggesting that *M. pyrifera* had sufficient nitrogen available while afloat (Gerard 1982).

*Pigments (Chl *a*, *c* and total carotenoids)* were determined from blade samples that were stored in liquid nitrogen. Three disks (each with a wet weight [wet wt] of ~12 mg) were excised and used individually for pigment determination. Measured pigment contents of these three sample disks represented the mean value for one sporophyte. The determination of pigments was based on an extraction with N,N-dimethylformamide for 24 h at 4°C in darkness. The extinctions of the extract and the determination of Chl *a*, Chl *c*, and total carotenoids (mg g^{-1} wet wt) were calculated such as described in Rothäusler et al. (2011a).

The activity of the enzyme CA was measured according to Haglund et al. (1992) with some modifications (Huovinen et al. 2007). From blade samples (previously stored in liquid nitrogen), three disks, each with a wet wt of 10–20 mg were excised, and individually ground in a mortar and dissolved in 3-mL buffer (50 mol L⁻¹ Tris, 25 mol L⁻¹ ascorbic acid, 5 mL ethylenediaminetetraacetic acid, pH 9.0). The reaction of CA activity was measured for each sample disk as described in Rothäusler et al. (2011a) and expressed as relative enzymatic activity (REA) g⁻¹ wet wt. The CA activity of the three sample disks represented the mean value for one sporophyte.

*Chl *a* fluorescence measurements*: In vivo Chl *a* fluorescence of PSII was measured with a portable pulse modulation fluorometer (PAM 2000; Walz), by incubating one blade section of each sporophyte for 20 min in the dark and measuring it six times for maximal quantum yield of fluorescence ($F_v:F_m$). Mean values of the six measurements represented the average $F_v:F_m$ response of one sporophyte. For estimation of ETR, three small disks were excised from one blade section of each sporophyte. Each sample disk was put in a stainless-steel chamber and irradiated individually with increasing intensities of PAR

(up to 500 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) provided by a light-emitting diode lamp of the PAM device (Schreiber et al. 1994). The ETR parameters, ETR_{max} , initial slope of the P–I curve (α), and saturation irradiance (E_k) were estimated by using the effective quantum yield (Genty parameter; Φ_{PSII}), the intensity of the radiation, and the sporophyte absorptance as described in Gómez et al. (2004).

Growth measurements: Growth responses of experimental sporophytes were measured as within-sporophyte biomass distribution, biomass change (BC), blade elongation rate (BER), and loss of distal blade tissue rate (LBR). The within-sporophyte biomass distribution was determined by destructive sampling. Benthic, floating, and experimental sporophytes were separated into holdfast, vegetative blade, stipe, pneumatocyst, reproductive blade, and sporophyll using a scalpel. The wet wt (g) from each kelp tissue was determined and afterward transformed to percent kelp tissue on the basis of total sporophyte wet wt in order to determine percent within-sporophyte biomass distribution. In addition, we measured the blade length (BL, mm) from six randomly selected vegetative blades of all sporophytes. Benthic and floating sporophytes were sampled at one single point in time; therefore, we only could determine within-sporophyte biomass distribution (but not growth) for them.

For the experimental sporophytes, we also measured growth (BC, BER, and LBR). Percent BC ($\text{BC}, \% \text{ d}^{-1}$) was estimated with the equation: $\text{BC} = (\text{FW} - \text{IW}) \times 100 \times (\text{T} \times \text{IW})^{-1}$, where FW and IW are the final and initial wet wt of the sporophytes at the respective sampling days and T the time in days between the subsequent sampling dates. BER (mm d^{-1}) of apical blades of *M. pyrifera* was determined by using the punch-hole method (Parke 1948) and the equation $\text{BER} = (\text{HF} - \text{HI}) \times \text{T}^{-1}$, where HF and HI are the final and initial hole position of the blade and T the time between the sampling dates. LBR (mm d^{-1}) was determined for each sampling day using the equation $\text{LBR} = (\text{LI} + (\text{HF} - \text{HI}) - \text{LF}) \times \text{T}^{-1}$, where LI and LF are the initial and the final blade lengths and T the time between the sampling dates (Rothäusler et al. 2009).

Reproductive status: Benthic, floating and experimental sporophytes were checked for the presence of sporophylls. From each sporophyte, three sporophylls (if present) were brought to the laboratory. Photos were taken to determine the percent reproductive area allocation with Image-Pro plus 4.5 such as described in Rothäusler et al. (2011b). Sporulation assays confirmed that spores were motile and, hence, viable.

Epibiont cover and bryozoan growth: All sporophytes were examined for the presence of epibionts. From the middle part of each sporophyte different tissues were sampled, namely vegetative blade, node, pneumatocyst, and stipe. These were photographed and their total area, as well as the area of epibiont cover, was measured using Image-Pro plus 4.5 and expressed as percent total epibiont cover. For each algal tissue three subsamples were taken, while the stipe was cut into three sections.

Simultaneously, the daily colony growth rate of epiphytic bryozoans (DCG) from experimental sporophytes was determined from photos taken at days 10 and 15 of the field experiment. From each of the 10 sporophytes, three photos from vegetative blades were taken to determine the diameter (mm) of encrusting bryozoan colonies (BCD), using Image-Pro plus 4.5. The mean from the three largest colonies of each sporophyte was used to estimate the DCG (mm d^{-1}) via the equation: $\text{DCG} = \text{BCD} \times \text{D}^{-1}$, where BCD is the bryozoan colony diameter and D the number of days after which the experiment had been started.

For the floating sporophytes from the field survey, we also measured the BCD. However, in order to avoid potential interference of colony growth by neighboring bryozoans, only the diameter of circular and solitary bryozoans was measured, except for Sta. 2, where vegetative blade samples showed strong ruggedness and bryozoan colonies were, therefore, not perfectly circular. In this case, we measured the length and the width of the colonies and its mean values represented the average bryozoan diameter. Within all stations, we used the three largest colonies to estimate the approximate floating time (FT) of algal rafts along a downstream gradient. We calculated FT by using the DCG for the following equation: $\text{FT} = \text{BCD} \times \text{DCG}^{-1}$.

Additionally, when floating sporophytes were colonized by stalked barnacles, these were removed and counted, and the length of the capitulum was measured. The body size of stalked barnacles (*Lepas* spp.) serves as a good proxy of minimum floating time because they are common on floating substrata but do not grow on attached algae (Thiel and Gutow 2005b). According to Thiel and Gutow (2005b), the capitulum of *Lepas anatifera* has a daily growth rate of 0.44 mm d^{-1} and *L. pectinata* has a daily growth rate of 0.37 mm d^{-1} . Based on this, we estimated the approximate FT of algal rafts separately for both species with the equation: $\text{FT} = \text{CL} \times \text{DGRL}^{-1}$, where CL is the capitulum length and DGRL the daily growth rate of the stalked barnacles.

Statistical analyses

To evaluate the effect of different solar radiation regimes (PAR, PAR + UV) on experimental sporophytes, kelp responses (including $F_v:F_m$, CA-activity, BER, LBR, and BC) were analyzed with repeated-measures ANOVA, with the within-subject factor Time (days 5, 10, and 15), and the between-subject factor Filter radiation treatment (PAR, PAR + UV). If the assumption of sphericity (Mauchly-Test), required for repeated-measures ANOVA, was not met, the univariate approach with Greenhouse–Geisser-adjusted degrees of freedom of the *F*-test was applied (Von Ende 1993). One-way ANOVA was used to test for the effect of solar radiation (PAR, PAR + UV) on pigments (Chl *a*, Chl *c*, and carotenoids), PI-curve parameters (α , ETR_{max} , and E_k) and epibiont cover at the end of the experiment (day 15).

The relationship between bryozoan colonies and physiological variables such as $F_v:F_m$, PI-curve parameters, and pigment content of floating kelp rafts were tested using the Spearman rank procedure, because the assumptions did

Table 1. Physiological responses of benthic *Macrocystis pyrifera* sporophytes at the beginning of the experiment and of experimental sporophytes kept under two solar radiation treatments (PAR, PAR + UV) after 15 d of floating.

Physiological responses†		Benthic sporophytes	PAR	PAR+UV
(A) Maximal quantum yield	$F_v:F_m$	0.66±0.01	0.63±0.01	0.62±0.01
(B) P–I curve parameters*	ETR_{max} ($\mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1}$)	76.32±20.75	41.30±3.13	46.02±3.58
	α [$(\mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1})/(\mu\text{mol m}^{-2} \text{s}^{-1})$] ⁻¹	0.45±0.03	0.40±0.02	0.41±0.03
	E_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	171.72±55.3	104.42±12.07	114.23±16.04
(C) Pigments	Chl <i>a</i> (mg g ⁻¹ wet weight)	0.61±0.06	0.30±0.03	0.31±0.05
	Chl <i>c</i>	0.11±0.04	0.05±0.01	0.05±0.01
	Total carotenoids	0.27±0.04	0.16±0.02	0.15±0.03

* Photosynthesis vs. light curve.

† $F_v:F_m$ = maximal quantum yield of chlorophyll fluorescence; ETR_{max} = maximal electron transport rate; α = initial slope of the P–I curve; E_k = saturation irradiance; Chl *a*, *c* = chlorophyll *a* and chlorophyll *c*.

not fulfill the requirements for a parametric correlation. The same procedure was used to examine whether BL, bryozoan cover, and BCD are correlated with different latitudes.

In all cases, homogeneity of variances was assessed with a Levene test. Square-root transformation was applied to achieve homogeneity of variances in the case of CA-activity. Percentage data (biomass change and epibiont cover) were arcsin-transformed prior to analysis. Transformations did not lead to homogeneity of variances for Chl *a*, BER, LBR, BCD, and total epibiont cover. We, therefore, decided to lower the α level to 0.01 and proceeded with the parametric analysis (Underwood 1997).

Permutational multivariate analyses of variance (PERMANOVA; McArdle and Anderson 2001; Anderson 2001, 2005) were used to examine whether within-sporophyte biomass distribution varied significantly across sampling sites (field survey) or UVR treatments (field experiment) by using Euclidean distance. The Monte–Carlo and permutational *p*-value were calculated by using 9999 permutations (Anderson 2005).

Results

Influence of UV-radiation on algal floating potential—Physiological responses: The physiological potential of all experimental sporophytes remained high during the experiment, regardless of the treatment. UVR did not affect the

effective quantum yield of fluorescence ($F_v:F_m$) and experimental sporophytes after 15 d showed similarly high values as benthic sporophytes at the start of the experiment (Table 1A). Overall, experimental sporophytes responded with high photosynthetic efficiency and showed only a very slight decrease in their photosynthetic performance (2–5%) at day 15 (Table 2A); these values were significantly different from those measured at days 5 ($p < 0.001$) and 10 ($p = 0.006$). Similarly, photosynthetic parameters estimated using P–I curves (ETR_{max} , α , and E_k) were not affected by UVR. Experimental sporophytes showed similar values in the PAR and PAR + UV treatment after 15 d of floating (Table 1B and Table 3A).

The two solar radiation treatments (PAR and PAR + UV) also did not affect algal pigment content (Chl *a*, Chl *c*, and carotenoids) of the sporophytes after 15 d (Table 1C and 3B). However, experimental sporophytes had lower pigment contents compared to benthic sporophytes, indicating that floating kelps adjust pigment concentrations to the prevalent light climate, thereby achieving high physiological performance of tethered kelp rafts.

CA-activity was not affected by the two solar radiation treatments but changed over time (Table 2B). PAR + UV-treated sporophytes showed highest CA activities at day 5, which decreased at days 10 and 15 ($p < 0.001$ for both comparisons). Sporophytes kept without UVR showed overall moderate CA activities, with decreasing values at day 15 (Fig. 2). These opposing patterns provoked an

Table 2. Results from the statistical analysis of maximal quantum yield ($F_v:F_m$) and carbonic anhydrase (CA) activity in *Macrocystis pyrifera*, using repeated-measures ANOVA, with the within-subject factor time (day 5, 10, and 15) and the between-subject factor solar radiation (PAR, PAR + UV). *p*-values in bold highlight significant differences at $p < 0.05$.

	(A) $F_v:F_m$			(B) CA-activity		
	df	<i>F</i> -ratio	<i>p</i> -value	df	<i>F</i> -ratio	<i>p</i> -value
Within subjects						
Time	2	13.482	<0.001	2	328.530	<0.001
Time×irradiance	2	0.268	0.767	2	339.936	<0.001
Error	36	—	—	36	—	—
Between subjects						
Irradiance	1	2.394	0.139	1	2.829	0.110
Error	18	—	—	18	—	—

Table 3. Results from the statistical analysis of P-I curve parameters (ETR_{max} , E_k , and α) and pigment content (Chl *a*, Chl *c*, and carotenoids) in *Macrocystis pyrifera* at the two solar radiation treatments (PAR, PAR + UV), using one-way ANOVA.

	(A) P-I curve parameters*									(B) Pigments†								
	ETR_{max}			E_k			α			Chl <i>a</i>			Chl <i>c</i>			Carotenoids		
	df	F	p-value	df	F	p-value	df	F	p-value	df	F	p-value	df	F	p-value	df	F	p-value
Irradiance	1	0.043	0.839	1	0.057	0.814	1	0.016	0.902	1	0.535	0.474	1	0.004	0.950	1	0.904	0.763
Error	18	—	—	18	—	—	18	—	—	18	—	—	18	—	—	18	—	—

* P-I = photosynthesis vs. light curve; ETR_{max} = maximal electron transport rate; E_k = saturation irradiance; α = initial slope of the P-I curve.

† Chl *a*, *c* = chlorophyll *a* and chlorophyll *c*.

interaction effect between time and solar radiation treatments (Table 2B), showing that UVR slightly stressed kelps at day 5 but not toward the end of the experiment.

Growth responses: Overall, growth responses such as BER, LBR, and within-sporophyte biomass distribution were not affected by UVR but sporophytes lost biomass in the presence of UVR (Fig. 3; Table 4A). While PAR-treated sporophytes showed biomass gains until the end of the experiment, sporophytes in the presence of UVR lost biomass with floating time, provoking significant differences between day 5 and day 10 ($p > 0.001$), and between day 5 and day 15 ($p < 0.001$) of the experiment. Although within-sporophyte biomass distribution was not affected by UVR, the loss of biomass is reflected in the decline of their vegetative blade portion. Sporophylls persisted in both PAR and PAR + UV-treated kelps during the 15 d of the experiment (Fig. 4), but reproductive area allocation in PAR ($8.6\% \pm 2.4\%$) and PAR + UV ($6.7\% \pm 1.4\%$) treated kelps decreased during the experiment compared to the initial values of benthic sporophytes ($17.5\% \pm 3.2\%$).

Generally, BER decreased with floating time (Table 4B) while blade losses increased (Table 4C). Blades continuously grew until day 5 and a decline was detected toward the end ($p > 0.001$), when marked blades already become

older and were replaced by new blades below the apical meristem.

Epibionts: After 15 d floating at the sea surface, experimental sporophytes were only colonized by the bryozoan *Membranipora isabelleana*. The two different solar radiation treatments did not affect bryozoan cover. Total epibiont cover of the analyzed area for sporophytes kept under PAR + UV was $4.4\% \pm 3.8\%$ and for sporophytes with only PAR it was $8.6\% \pm 5.6\%$. The mean colony diameter of bryozoans measured on days 10 and 15 were 16.6 ± 2.4 mm and 22.9 ± 9.1 mm, respectively. Accordingly, the approximate growth rates of these bryozoans were 1.66 mm d^{-1} on day 10 and 1.53 mm d^{-1} on day 15.

Field survey of *Macrocystis pyrifera* rafts along a south-north gradient—Physiology of kelp rafts: Physiological responses, measured as the activity of CA, declined with distance from benthic source populations. Overall, CA-activity in floating *M. pyrifera* ranged from 47 REA g^{-1} wet wt to 67 REA g^{-1} wet wt, provoking significant differences between latitudes ($F_{(5,47)} = 16.190$, $p < 0.001$). Highest values were observed in benthic algae from $30.45^\circ S$

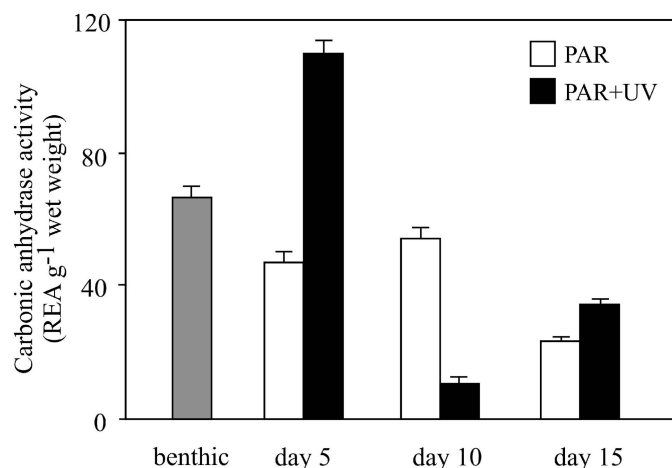


Fig. 2. Relative enzymatic activity (REA g^{-1} wet wt) of carbonic anhydrase (CA) from benthic (mean \pm SD, $n = 8$) and experimental *Macrocystis pyrifera* sporophytes (mean \pm SD, $n = 10$) at days 5, 10, and 15, kept under two solar radiation treatments (PAR, PAR + UV).

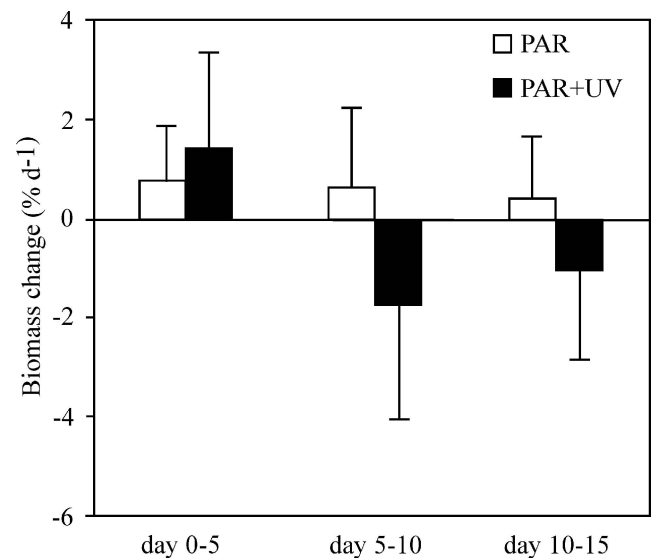


Fig. 3. Percent biomass change d^{-1} of experimental *Macrocystis pyrifera* sporophytes (mean \pm SD, $n = 10$) at the two solar radiation treatments (PAR, PAR + UV).

Table 4. Results from the statistical analysis of (A) biomass change, (B) blade elongation, and (C) distal blade tissue loss in *Macrocystis pyrifera*, using repeated-measures ANOVA, with the within-subject factor time (day 5, 10, and 15), and the between-subject factors solar radiation treatments (PAR, PAR + UV, and NATSR in the case of blade elongation rate). *p*-values in bold highlight significant differences at *p* < 0.05.

	(A) Biomass change			(B) Elongation rate			(C) Tissue loss		
	df	<i>F</i>	<i>p</i> -value	df*	<i>F</i>	<i>p</i> -value	df*	<i>F</i>	<i>p</i> -value
Within subjects									
Time	2	5.034	0.012	1.166 _{GG}	84.160	<0.001 †	1.142 _{GG}	11.148	0.003 †
Time×irradiance	2	3.791	0.032	2.331 _{GG}	2.378	0.105	1.142 _{GG}	0.025	0.903
Error	36	—	—	26.809 _{GG}	—	—	17.132 _{GG}	—	—
Between subjects									
Irradiance	1	4.451	0.049	2	3.228	0.058	1	0.167	0.689
Error	18	—	—	23	—	—	15	—	—

*_{GG} denotes that all values were adjusted following the Greenhouse–Geisser *F*-test, if sphericity requirement was not met.

† Significant differences at level 0.01.

and in floating algae collected at 30.08°S, while lowest CA activities were detected at 29.99°S and 29.72°S (Fig. 5).

Morphological responses and changes in reproductive status of floating rafts: The BL of floating sporophytes sampled at different latitudes within a south–north gradient, showed a negative relationship with latitude, with BL decreasing toward the north (Fig. 6A). Overall, these BL suggested that algal rafts were older (indicated by shorter blades) at increasing distances from Punta Lengua de Vaca.

The within-sporophyte biomass distribution did not differ between the sporophytes sampled at different latitudes and the benthic control sporophytes (*p*[perm]-

value = 0.1159; Fig. 7). However, there was a tendency that sporophytes sampled in the northern area of the CSC lost vegetative blade tissues and the stipe represented the tissue with the highest percentage of total kelp biomass.

Interestingly, *M. pyrifera* rafts from the two northernmost sampling sites with highest estimated floating time had lost all their sporophylls. Also, rafts sampled at latitude 30.08°S did not present sporophylls. Overall, the highest reproductive potential was detected for sporophytes found close to the putative source populations (Fig. 7).

Epibionts of floating rafts: Algal rafts that were sampled at different latitudes within the CSC showed varying epibiont cover. The bryozoan species *Membranipora isabelleana* dominated the epibiont community on floating algae, while diatoms and cyanobacteria were scarce. Benthic control sporophytes were not colonized by epibionts. Total epibiont cover increased in northward direction, showing a negative relationship between total epibiont cover and latitude (Fig. 6B).

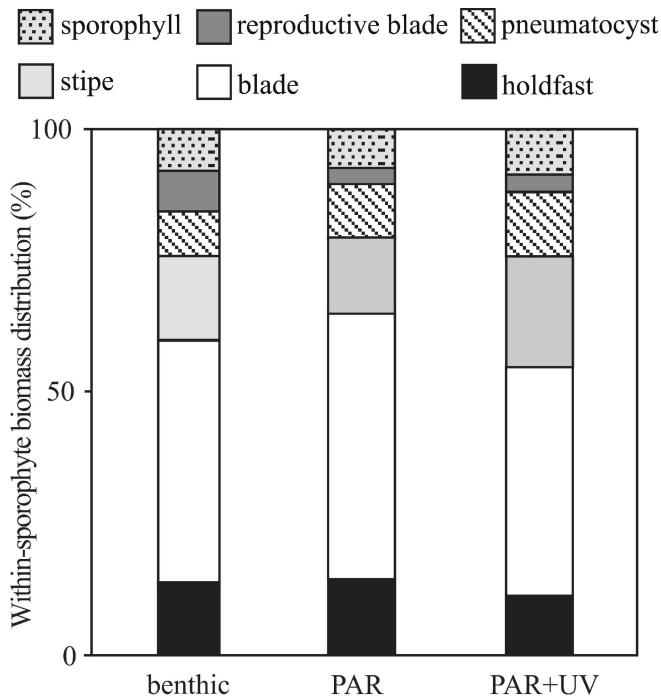


Fig. 4. Within-sporophyte biomass distribution of benthic sporophytes (mean ± SD, *n* = 8) and experimental sporophytes of *Macrocystis pyrifera* (mean ± SD, *n* = 10) at the two solar radiation treatments (PAR, PAR + UV).

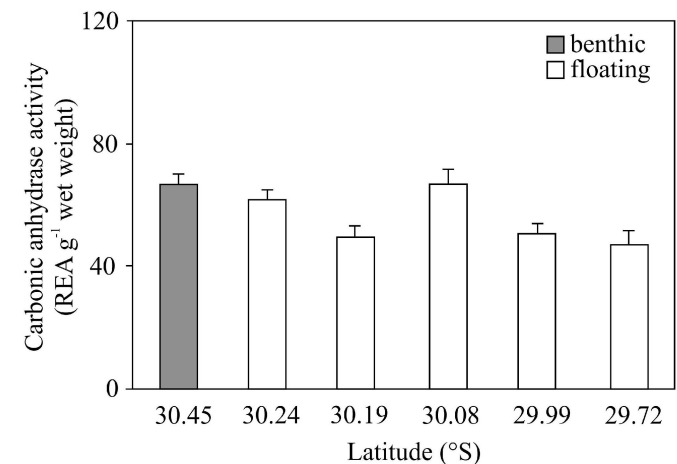


Fig. 5. Relative enzymatic activity (REA g⁻¹ wet wt) of carbonic anhydrase (CA) from benthic (mean ± SD, *n* = 8) and field-surveyed *Macrocystis pyrifera* sporophytes (mean ± SD, *n* = 8) at different latitudes. Values from algae sampled at the northernmost latitude (29.56°S) are missing due to loss of replicates.

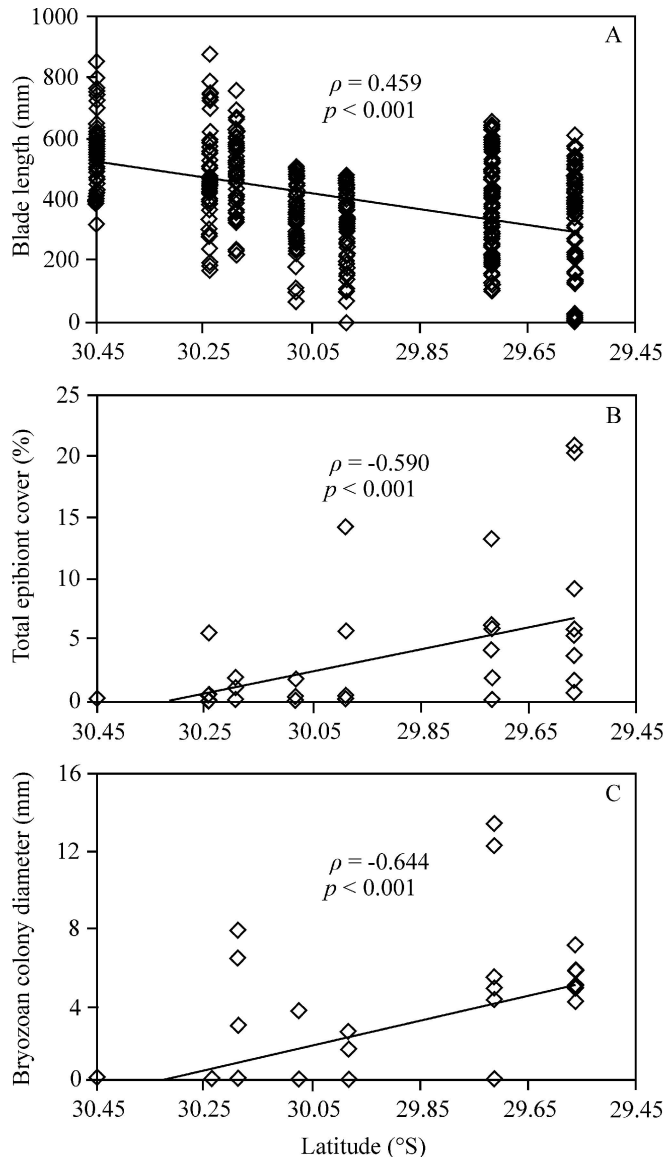


Fig. 6. (A) Blade length (cm; $n = 48$), (B) total epibiont cover (% of analyzed area; $n = 8$), and (C) bryozoan colony diameter (cm; $n = 8$) of *Macrocyctis pyrifera* at the different sampling sites in a south–north gradient.

The same was true for the correlation between size of bryozoan colonies and latitude. *M. pyrifera* rafts sampled in the north had larger colonies of encrusting bryozoans than algae that were sampled closer to their potential benthic source populations in the south (Fig. 6C). Calculating the approximate floating time of these rafts via the bryozoan colony diameter, it was confirmed that sporophytes sampled at the two northernmost latitudes were afloat between 4.5 d and 8.5 d, respectively, while samples from the south showed an approximate floating time between 2 d and 4 d (Table 5).

The stalked barnacles *Lepas anatifera* and *L. pectinata* appeared in some of the samples from the northern study area, but *L. pectinata* was absent in samples from the northernmost site. The capitulum size of the stalked

barnacles increased with latitude and, thus, algae from the northernmost sites were estimated to have been afloat between 6.8 d and 17.6 d (Table 5). At latitude 30.08°S, only one individual with a capitulum length of 2 mm was detected, which corresponds to 4.5 d afloat. The sizes of epibionts confirmed our general assumption that rafts sampled in the north had been floating for longer time periods.

Interactive responses: The combined effects of biotic and abiotic factors determined via the correlation between bryozoan colony diameter and kelp physiological responses were significantly negative for $F_v:F_m$ (Spearman $\rho = -0.553$, $p < 0.001$), the initial slope α (Spearman $\rho = -0.322$, $p = 0.026$), the maximal electron transport rate (ETR_{max} ; Spearman $\rho = -0.519$, $p < 0.001$), and the saturation irradiance (E_k ; Spearman $\rho = -0.472$, $p = 0.001$), demonstrating that these physiological responses decline with increasing floating time (estimated via the size of bryozoan colonies). No relationship was observed between bryozoan colony diameter and pigment contents (Chl *a*, Chl *c*, and carotenoids).

Discussion

Our study confirmed that sporophytes of *M. pyrifera* floating in a south–north gradient of the CSC had higher estimated floating times with increasing distance from southern source populations. Accordingly, physiological performance, blade lengths, and reproductive output decreased toward the north. UVR provoked a loss in biomass in the field experiment but did not affect the physiological performance of kelps. Our results suggest that the simultaneous exposure to a set of environmental stress factors such as increasing water temperature, high solar irradiance, and epibiont overgrowth can accelerate algal degradation within the CSC. Detached *M. pyrifera* from southern source populations are thought to travel mainly in a northward direction where the next downstream populations of *M. pyrifera* are found at a distance of ~ 130 km. Results indicate that successful dispersal of *M. pyrifera* across this gap strongly depends on the synergistic effects of abiotic and biotic factors experienced by floating kelps.

UVR at mid-latitudes and its effect on the floating persistence of kelp rafts—UVR is known to impair the photosynthesis of benthic macroalgae, but sporophytes of *M. pyrifera* tethered in their natural habitat showed high photoacclimation potential to the prevailing summer irradiance at 30°S. The changing light climate at the sea surface provoked a decline in pigment contents of tethered kelp rafts after 15 d afloat compared to benthic conspecifics. This confirms that algae can acclimate to different light environments by an adjustment of their pigment contents (Falkowski and LaRoche 1991; Rothäusler et al. 2011a). Accordingly, tethered kelps responded with high photosynthetic plasticity to the irradiance climate at mid-latitudes, evidenced by high fluorescence values. A similar acclimation potential had been observed for the pelagic brown alga *Sargassum natans* floating in the Gulf of Mexico (Schofield et al. 1998).

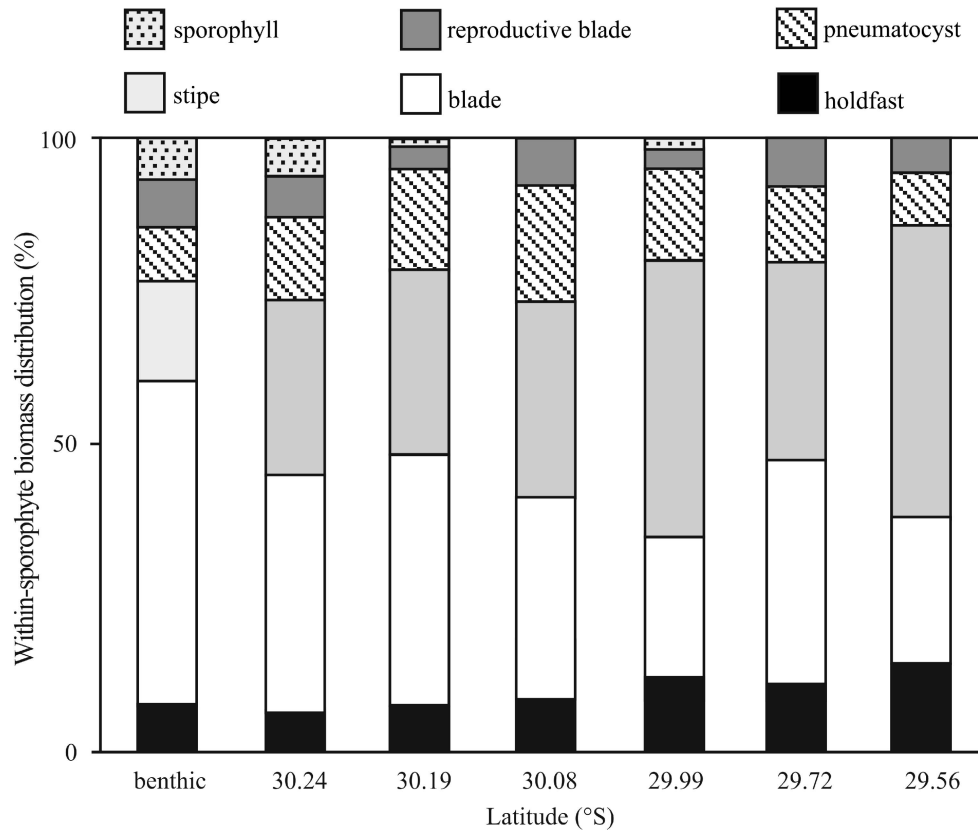


Fig. 7. Percent within-sporophyte biomass distribution of benthic sporophytes (mean \pm SD, $n = 8$) and floating sporophytes of *Macrocyctis pyrifera* (mean \pm SD, $n = 8$).

The enzymatic activity of carbonic anhydrase, which delivers inorganic carbon to the algal cells, increased at day 5 in *M. pyrifera* sporophytes exposed to UVR. This could be due to an enhanced carbon fixation in the Calvin–Benson cycle, which was indirectly evidenced by high electron transport rates (ETR_{max}), or due to a high demand for carbon skeletons of these recently detached algae, possibly for the production of secondary metabolites such as phlorotannins. Other studies had shown that these compounds, which are polymerized in the cell wall

(Schoenwaelder 2002), can act as UV-induced sunscreens (Swanson and Druehl 2002; Gómez and Huovinen 2010).

Overall, the observed photoacclimation to changing abiotic conditions enables algae with positive buoyancy to persist at the sea surface, but these responses can be costly. The UVR-treated sporophytes lost biomass between days 5 and 15, which can be explained by a higher energy demand for repair mechanisms and/or synthesis of UV-sunscreens at the expense of growth. The fact that growth of *M. pyrifera* decreased while its photosynthetic efficiency

Table 5. Results of bryozoan colony diameter (mm) and capitulum size (mm) of stalked barnacles at different latitudes and its respective approximate (approx.) floating time (d). NO = no organisms (stalked barnacles or bryozoans) were found at these latitudes.

	Latitude (south–north gradient)						
	30.0°	30.24°	30.19°	30.08°	29.99°	29.72°	29.56°
<i>Membranipora isabelleana</i>							
Diameter (mm)	NO	NO	6.4 \pm 0.3	3.9 \pm 0.8	3.0 \pm 0.1	13.5 \pm 0.5	7.3 \pm 0.9
Approx. floating time in days	—	—	4.0	2.4	1.9	8.5	4.5
<i>Lepas pectinata</i>							
Capitulum (mm)	NO	NO	NO	1.9 \pm 0.2	1.7 \pm 0.2	2.5 \pm 0.2	NO
Approx. floating time in days	—	—	—	5.2	4.5	6.8	—
<i>Lepas anatifera</i>							
Capitulum (mm)	NO	NO	NO	2.0	1.8 \pm 0.4	7.8 \pm 0.0	6.6 \pm 1.1
Approx. floating time in days	—	—	—	4.5	4.2	17.6	15.0

was maintained parallels observations made by Rothäusler et al. (2011b) for floating *M. pyrifera* sporophytes that had been exposed to natural irradiance conditions.

Not only vegetative blades, but also reproductive blades may be sensitive to the conditions at the sea surface. Herein, exposure of tethered algae for 15 d to different light treatments did not lead to the disappearance of sporophylls, but caused a substantial decrease in their reproductive area allocation. Zoospore release was low in these algae, suggesting that temperature and irradiance conditions at the sea surface were stressful for their reproductive activity, similar to that observed for *M. pyrifera* kept in outdoor tanks (Rothäusler et al. 2009).

The results of the present study indicate that during initial phases of bryozoan colonization, the still uncalcified epibiont colonies may protect algal tissues against strong UVR. However, calcified bryozoans can reduce the amount of light reaching the seaweed surface between 45% and 55% (Cancino et al. 1987; Muñoz et al. 1991). Large colonies of encrusting bryozoans that spread over the sporophytes with increasing floating time may not only reduce the amount of light reaching the kelp tissue, but also inhibit uptake of nutrients and exchange of gases (Hurd et al. 1994, 2000). Consequently, increasing bryozoan cover may finally lead to a reduction in the energy available for C fixation and, thus, can negatively affect overall kelp physiology and persistence at the sea surface.

Performance of kelp rafts at different distances from source populations—Upon detachment abiotic and biotic factors can synergistically affect algal growth and photosynthesis, similar to that reported for benthic algae (Gómez et al. 2001; Rautenberger and Bischof 2006). A natural temperature gradient is found in the CSC, with increasing values toward the north and, thus, during their northward journey, rafts move into regions of higher water temperatures and risk of physiological stress. Simultaneously, floating algae are rapidly colonized by larvae of common fouling organisms such as bryozoans and lepadid barnacles (Thiel and Gutow 2005b). Based on growth estimates of *Membranipora isabelleana* and *Lepas anatifera*, kelp rafts sampled in the northern region of the CSC had been afloat at least between 9 d and 18 d, respectively. These algae probably originated from benthic source populations south of the bay system from where they moved northward, driven by the equatorward surface circulations and southwesterly winds in the coastal branch of the Humboldt Current (Marín and Delgado 2007). Considering a mean raft velocity of 0.17–1.28 km h⁻¹ for floating kelps (M. Thiel, unpubl.), rafts travelled ~ 37–276 km (based on bryozoa) or 74–553 km (based on stalked barnacles) within the CSC. Rafts can become trapped in the CSC due to local convergence zones, similar to that shown for *M. pyrifera* in coastal waters of California (Kingsford 1995) and/or they might travel in circular movements such as described for surface buoys (Marín and Delgado 2007).

Degradation rates are expected to be more pronounced in floating algae already stressed by epibionts, temperature, and irradiance. Blade lengths of rafts collected within the natural temperature gradient of the CSC declined toward the

north, where temperature was highest. Also, these algal rafts from northern sites showed highest epibiont cover, confirming their extended floating time within the CSC. Similarly, the study by Helmuth et al. (1994) in the West Wind Drift east of Tierra del Fuego showed reduced blade lengths of *M. pyrifera* with distance from the shore, indicating high deterioration of these rafts. Hobday (2000) reported that reduced blade length of *M. pyrifera* can be related to the aging of blades over time and Dixon et al. (1981) demonstrated that blade loss of benthic *Fucus serratus* depends on the intensity of bryozoan colonization. A similar defoliation effect might occur in floating kelps sampled in the northernmost region of the CSC, which probably lost some vegetative blade tissues due to increased epibiont growth and high water temperature. A recent outdoor laboratory experiment confirmed that at water temperatures > 20°C, floating kelps lost biomass (Rothäusler et al. 2009). Thus, it can be suggested that a combination of enhanced epibiont cover, UVR, and high temperature is responsible for the observed loss of vegetative kelp tissue. Possibly, the same is true for the sensitive sporophyll tissue, which had been lost in kelps collected at the northernmost sites, indicating that the dispersal of zoospores and, thus, the connectivity between populations within the CSC is limited by synergistic effects of abiotic and biotic factors.

Floating algae are commonly inhabited by mesograzers (e.g., amphipods and isopods), which at high densities can contribute to a significant loss of vegetative blades, thereby affecting the overall growth and physiology of floating algae (Rothäusler et al. 2009, 2011a). At the same time, bryozoan colonies successively cover their floating substratum, which is suggested to suppress algal photosynthesis (Oswald et al. 1984). In the present study, physiological parameters declined with increasing bryozoan size and, thus, floating time. However, pigment contents of vegetative blades did not increase with increasing bryozoan cover, indicating that the light reaching the photosynthetic tissues is still sufficient to maintain physiological functioning, which is in line with the moderate carbonic anhydrase activity detected. Overall, low epibiont cover such as shown herein for kelps close to their benthic source populations does not harm floating algae, because algal tissue free from bryozoan colonization can compensate for any negative effects of the colonization of other sections of the sporophyte, such as previously suggested by Hepburn and Hurd (2005) for benthic *M. pyrifera*. In contrast, dense accumulations of epibionts (bryozoans and lepadid barnacles), such as observed in algae sampled toward the north, lead to a reduction in algal physiological performance and may even cause a loss of buoyancy due to their calcareous structures (Thiel and Gutow 2005b).

Floating kelps in the CSC and population connectivity—The fate of floating *M. pyrifera* in the CSC strongly depends on the synergistic effect of abiotic and biotic factors, which can act as a dispersal barrier for floating kelps. Single abiotic and biotic factors were not stressful for algae as shown herein in our UVR field experiment, where floating conditions were mimicked. Previous studies conducted with *M. pyrifera* in outdoor tank experiments

had confirmed that the negative effect of single abiotic and biotic factors (temperature, irradiance, and herbivory) on the floating potential of kelps depends on the intensity of these stressors (Rothäusler et al. 2009, 2011b). Especially UVR and herbivory only had a strong negative effect on floating kelps at high water temperatures, underlining the importance of synergistic effects.

Within the study area, southern source populations of benthic *M. pyrifera* are separated from northern populations by the CSC. Depending on their floating velocity and residence times in the CSC, kelp rafts might be able to successfully connect to local northern populations. Long-distance dispersal of *M. pyrifera* has been observed in other studies (Hobday 2000; Hernández-Carmona et al. 2006); therefore, transport of sporophytes of *M. pyrifera* across the ~ 130-km-wide distributional gap may be frequent. Indeed, prevalent current patterns and a continuous supply of floating kelps from southern sources suggest a frequent transport of kelps across the CSC. However, increased epibiont growth, strong solar irradiance, and high water temperature during austral summer result in enhanced degradation of kelp rafts and loss of reproductive potential, which is essential for successful colonization.

During El Niño events, when the study area is under the influence of warm equatorial waters, it is unlikely that sporophytes cross the distances within the CSC and between similar distributional gaps along the northern coast. Since the Holocene, El Niño events have had a major influence on the Chilean coast (Ortlieb et al. 2000) and, thus, possibly restricted the dispersal of northern kelp populations. Based on our results, we suggest that in the past, present, and future, low water temperatures and moderate irradiance conditions, together with reduced epibiont growth, as observed from late summer to early spring and during La Niña conditions, are favorable for the dispersal of *M. pyrifera* across the CSC and between other disjunct populations in the Humboldt Current System.

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