

Epibiont load causes sinking of viable kelp rafts: seasonal variation in floating persistence of giant kelp *Macrocystis pyrifera*

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Abstract Floating seaweeds serve as dispersal agents for various organisms, but their survival at the sea surface may be compromised by physiological stress and epibiont overgrowth. Most previous experiments have been conducted in laboratory mesocosms where epibiont colonization is limited, but in their natural environment floating seaweeds are frequently overgrown by epibionts, which might negatively affect seaweeds or even cause their sinking. To test this hypothesis, we conducted field experiments in northern-central Chile (30°S) with floating giant kelps *Macrocystis pyrifera* to determine the time until sinking, epibiotic bryozoan load, and their physiological status across different seasons. Floating sporophytes persisted for at least 4 weeks at the sea surface and sank in all seasons after bryozoan loads exceeded 40 % of the raft biomass. At the time of sinking, the kelp rafts were physiologically viable and biomass losses were relatively minor. In autumn, kelp rafts

stayed afloat for an average of 41 days (maximum: 52 days) during moderate environmental conditions (cool water temperature and moderate solar radiation) and slow growth of epibionts. However, higher water temperatures in summer seemed to enhance the growth of epibiotic bryozoans but not the growth of *M. pyrifera*, causing earlier sinking. The results indicate that the high growth rates of encrusting bryozoans provoke sinking of the kelp rafts, representing the first demonstrated case of epibiont-induced sinking of otherwise healthy floating seaweeds. Increasing global temperatures may enhance epibiont growth and thereby suppress the dispersal potential of floating seaweeds, even of species known for their high acclimation potential to the conditions at the sea surface.

Introduction

Floating seaweeds are found in most oceans, where they can serve as dispersal agents for a wide diversity of associated organisms and for the seaweeds themselves (Vandriessche et al. 2006; Fraser et al. 2011; Clarkin et al. 2012; Rothäusler et al. 2012; Gutow et al. 2015). Large kelps with buoyant structures have a particularly high floating potential (Smith 2002), and after detachment, they continue to grow vigorously when environmental conditions (water temperature, solar irradiation) are favorable (Rothäusler et al. 2009, 2011a).

In order to evaluate whether floating seaweeds may contribute to population connectivity in a particular geographic region, it is important to understand and identify the factors that drive their abundance and temporal distribution. Several studies have described seasonal variations in the abundances of floating seaweeds in particular areas (Kingsford 1992, 1995; Hobday 2000a; Hirata et al. 2001; Hinojosa

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et al. 2010, 2011; Tala et al. 2013), which have been attributed to differential supply from benthic sources or to variable persistence times of seaweed rafts. During rafting journeys, herbivory, epibiont load, solar radiation, and water temperature are important factors that affect the persistence of seaweed rafts (Edgar 1987; Hobday 2000b; Thiel and Gutow 2005a; Vandendriessche et al. 2007a; Rothäusler et al. 2009, 2011a, b, Graiff et al. 2013; Gutow et al. 2015).

Mobile mesograzers influence raft persistence by removing tissue and thereby compromising photosynthesis and growth (Hinojosa et al. 2007; Rothäusler et al. 2011b, c), which finally results in decay and sinking of the seaweeds. Also, floating seaweeds are substratum for many sessile epibionts, including encrusting bryozoans. These epibiotic associations create complex interactions of benefit and costs between epibionts and basibionts (Hepburn and Hurd 2005; Liuzzi and López Gappa 2008; Saunders and Metaxas 2008). In fact, epifauna generate benefits to host seaweeds, e.g., by providing carbon dioxide from their respiration (Mercado et al. 1998) and nitrogen from excretion of ammonium (Hurd et al. 2000; Hepburn and Hurd 2005; Hepburn et al. 2006). However, dense colonization of encrusting bryozoans also enhances the susceptibility of fronds to breakage (Dixon et al. 1981), and by covering photosynthetic tissues suppress the amount of incoming solar irradiation (Hurd et al. 2000). Furthermore, the additional weight of the epibionts may cause a reduction in buoyancy of the floating seaweeds. In general, it can be assumed that negative effects of grazing pressure and epibiont load increase over time, provoking deterioration and ultimately sinking of rafts (Rothäusler et al. 2011b).

At present, our understanding of growth, physiology, epibiont load, herbivory, and persistence of floating seaweeds comes mainly from laboratory mesocosm experiments (Rothäusler et al. 2009, 2011b, d; Vandendriessche et al. 2007a), where epibiont colonization is low or absent (most epibiont propagules are eliminated by seawater filters). These studies provide initial insights about the influence of the important abiotic and biotic factors on floating kelps, but their contribution to our understanding about the floating time of kelps is limited, because they only partly reflect natural floating conditions. In particular, the effects of seasonally variable conditions on the persistence and epibiont overgrowth of floating seaweeds have not been examined.

Along the Chilean Pacific coast, giant kelps *Macrocystis pyrifera* form extensive populations in intertidal and subtidal habitats between 18°S and 60°S (Dayton 1985; Westermeier and Möller 1990; Macaya et al. 2005). The gas-filled pneumatocysts allow them to float freely at the sea surface after detachment (Hobday 2000c; Rothäusler et al. 2012), and indeed, giant kelp rafts are commonly found floating in Chilean coastal waters (Macaya et al. 2005; Hinojosa et al. 2010, 2011; Wichmann et al. 2012).

Rafting kelps are exposed to seasonally highly variable environmental conditions at the sea surface which influence their floating persistence (Rothäusler et al. 2011d; Graiff et al. 2013). In summer, high solar radiation, UV, and water temperatures negatively affect temperate floating seaweeds resulting in disintegration, high biomass losses, and sinking, whereas persistence of rafts at the sea surface is favored under moderate environmental conditions (Rothäusler et al. 2009; Graiff et al. 2013; Tala et al. 2013).

In order to determine the seasonal variation in floating persistence and the factors contributing to the demise of floating *M. pyrifera*, we conducted field experiments during different seasons. We hypothesized that floating persistence at the sea surface depends on the growth of epibiotic bryozoans and seasonally variable environmental conditions. To test our hypothesis, we conducted experiments in the four seasons to determine the time until sinking and how variable environmental conditions affect growth, photophysiology, and epibiont load of floating sporophytes of *M. pyrifera* tethered in their natural coastal environment.

Materials and methods

Seasonal sampling of kelps

Kelps for the tethering experiments were collected during each austral season (spring: November 7, 2011; summer: January 26, 2012; autumn: May 7, 2012; winter: August 1, 2012) during low tide from the shore of Mineral de Talca, Province of Limarí, Chile (30°51'S, 71°42'W). Each season, 30–33 complete sporophytes of *M. pyrifera* (i.e., individuals including their holdfasts) were carefully detached from their natural habitat. After sampling, the kelps were immediately transported in coolers with seawater (protected from light and desiccation) to the marine laboratory at Universidad Católica del Norte, Coquimbo, Chile (29°57'S, 71°20'W). Kelps were kept overnight in flow-through seawater tanks (2000 L) before being measured and tethered in the field. Kelps collected in winter were shorter than those collected in the other seasons (ANOVA with *post hoc* Tukey's test; total length: $F = 10.4$, $df = 3$, $p < 0.001$, Supplement table 2), but they were only lighter compared to autumn (ANOVA with *post hoc* Tukey's test; wet mass: $F = 7.7$, $df = 3$, $p < 0.001$, Supplement table 3). Regardless of these differences, there was a broad length and mass overlap among the seasons (Supplement table 1), and all sporophytes had reached adult sizes.

Environmental conditions

During each experimental season, the incident ultraviolet B (UV B; 290–340 nm) and ultraviolet A (UV A;

Table 1 Environmental conditions during the seasonal experiments: average, minimum and maximum seawater temperatures (°C), and range of maximum values, average, and daily dose of PAR (400–700 nm), UV A (340–400 nm), and UV B (290–340 nm) radiation

	Spring November 8–December 13, 2011	Summer January 27–February 24, 2012	Autumn May 8–June 30, 2012	Winter August 2–September 7, 2012
Sea surface temperature				
Mean \pm SD (°C)	16.2 \pm 0.9	18.3 \pm 1.0	14.2 \pm 0.6	13.6 \pm 0.4
Min (°C)	14.2	15.7	13.0	12.9
Max (°C)	19.3	21.3	16.2	15.7
PAR				
Maximum range ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1024.5–2879.6	2392.0–2942.2	356.6–1364.4	337.0–1955.4
Mean \pm SD ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	1012.4 \pm 260.3	1255.8 \pm 168.8	445.7 \pm 152.6	514.2 \pm 206.4
Daily dose (kJ m^{-2})	9837.1 \pm 2465.8	11,524.6 \pm 2280.1	3893.3 \pm 1321.6	1615.5 \pm 657.7
UV A				
Maximum range (W m^{-2})	8.5–23.7	16.1–21.8	2.0–10.1	1.9–16.3
Mean \pm SD (W m^{-2})	7.8 \pm 2.1	9.2 \pm 1.5	3.0 \pm 1.1	3.9 \pm 1.7
Daily dose (kJ m^{-2})	353.8 \pm 90.3	396.5 \pm 63.3	121.9 \pm 44.6	56.2 \pm 24.4
UV B				
Maximum range (W m^{-2})	3.2–10.0	6.2–8.4	2.0–7.9	2.1–5.2
Mean \pm SD (W m^{-2})	2.8 \pm 1.0	3.4 \pm 0.6	1.3 \pm 0.1	1.5 \pm 0.3
Daily dose (kJ m^{-2})	126.5 \pm 29.7	144.4 \pm 22.9	50.9 \pm 5.0	22.1 \pm 5.2

PAR photosynthetically active radiation, UV A ultraviolet A, UV B ultraviolet B

340–400 nm) radiations were measured using the UV3pB and UV3pA sensors (Delta-T Devices Ltd, Cambridge, UK) connected to a Li-Cor-1400 data logger (Li-Cor Bioscience, Lincoln, NE, USA). While the UV B sensor slightly overestimated the defined UV B waveband [290–315 nm according to the International Commission on Illumination (CIE) definition], the UV A sensor produced a corresponding underestimation (315–400 nm). Additionally, photosynthetically active radiation (PAR, 400–700 nm) data were obtained with a Li-190SA quantum sensor (Li-Cor Bioscience) also connected to the data logger. Radiometers were placed free of physical interference, and ultraviolet and photosynthetically active irradiances were measured every 5 or 15 min throughout the day from 07:00 to 19:00. This information was used to calculate the daily doses of ultraviolet radiation and PAR by integrating instantaneous data. Water temperature was monitored every 3 min with a data logger installed 50 cm below the sea surface (HOBO® TidbiT v2 data logger, Onset computer corporation, Bourne, MA, USA) (Table 1).

Experimental design

Individual sporophytes of *M. pyrifera* (spring: $n = 31$; summer: $n = 30$; autumn: $n = 33$; winter: $n = 31$) were tethered in the relatively enclosed Bahía La Herradura, Coquimbo, Chile, at the sea surface in the university aquaculture area

(Supplement figure 1). The experimental rafts were tied to a line of buoys in random order at about 1–2 m distance from each other. During the seasonal experiments, some sporophytes were lost due to breakage of the tether, but the majority of the experimental rafts were maintained until sinking (spring: $n = 21$; summer: $n = 27$; autumn: $n = 32$; winter: $n = 22$).

Each kelp raft received an identification tag attached to its holdfast and tied with a plastic cord (1 m length) to a single buoy. To tether the sporophyte to the buoy, a cable tie surrounded by bicycle inner tubing (to reduce the risk of physical damage) was put around the holdfast of the sporophyte and pulled through a loop made from the plastic cord. The plastic cord had a loop also at its other end, which was fixed to the buoy using a cable tie. This setup allowed the sporophytes to freely sway and float in the water. After the first week of floating, the kelps were checked daily to determine their exact days of sinking. The kelps were considered as having sunk when they were completely submerged and no part remained at the sea surface.

Throughout the course of the experiments, occasionally sea gulls (*Larus dominicanus*) were observed pecking at the floating sporophytes of *M. pyrifera*. Most likely, these birds consume organisms associated with patches of floating seaweeds (Vandendriessche et al. 2007b). This may have caused damage to the blades, stipes, and/or pneumatocysts, as fouled blades are more fragile and break off easily

(Dixon et al. 1981). Additionally, this is enhancing the process of degradation and may lead to the sudden loss of large thallus pieces.

Bryozoan coverage and biomass

Floating kelps are frequently colonized and overgrown by bryozoans *Membranipora isabelleana*, especially in coastal waters (Rothäusler et al. 2011d). In order to monitor the abundance of bryozoans during the experiments, their cover on the sporophytes was determined every 7 days until the day of sinking. Three blades from the middle part of each alga were photographed in situ using a floating board with a tape rule as reference. Bryozoan cover was measured using Image-Pro® plus 6.0 from the photographs and expressed as percent total bryozoans cover. To estimate the area covered by bryozoans, the widest part of each blade was photographed (surface area: $23.42 \pm 5.01 \text{ cm}^2$, mean \pm SD), because the distal parts of the blades sometimes degraded during the experiments.

In order to determine the total biomass of bryozoans at the moment of sinking, an indirect method of measurements was necessary, because at this stage we could only weigh the combined mass of kelps and bryozoans as they were intricately and inseparably joint on the sporophytes. Proportional bryozoan biomass at the day of sinking was calculated from the photographed percent total bryozoan cover, using the following equation:

$$\text{BrM} = 4.5516 \times \text{BrC}^{0.524}$$

where BrM is the bryozoan proportional mass (%) and BrC is the bryozoan cover (%) (Supplement 2 and Supplement figure 2). Using this procedure was necessary to separate bryozoan mass from kelp mass at the day of sinking.

Measurement of morphological parameters

The experimental *M. pyrifera* sporophytes were measured for morphological parameters (length and total wet mass) on day 0 and on their individual day of sinking. Maximum length was measured as length of the longest stipe to the centimeter using a tape rule. Daily length change was calculated using a linear formula for length:

$$\text{length change } (\%d^{-1}) = 100 \frac{x_t - x_0}{x_0 \times t}$$

where x_0 represents length (cm) at day 0 and x_t the length (cm) after t days (d) at the individual day of sinking.

Additionally, the wet mass of each *Macrocystis* individual was measured. The complete sporophytes were weighed for total wet mass at day 0. On day 0, there were only scattered small or no bryozoan colonies visible on the sporophytes. However, at the day of sinking, kelps were

completely overgrown by bryozoans and kelp biomass could not be measured directly. Therefore, we subtracted the absolute bryozoan biomass from the kelp biomass. The absolute biomass of bryozoans (Bryo) at the day of sinking was calculated using the following equation:

$$\text{Bryo (g)} = \frac{(\text{BCBM} + \text{BCSTM}) \times \text{BrM}}{100 \%}$$

where BCBM is bryozoan-covered mass of blades (g), BCSTM is the bryozoan-covered mass of stipes (g), and BrM is the calculated proportional bryozoan mass (%) for the respective kelp. For the calculation of the bryozoan biomass, we used the wet mass of blades and stipes only, because the biomass of the holdfast is not affected by bryozoan colonization due to the small surface available for settling of bryozoans. Therefore, the kelps were dissected on their day of sinking into holdfasts and blades + stipes, and wet masses of holdfasts were determined separately. Finally, in order to determine the bryozoan-free kelp wet mass (BFKM) on the day of sinking, the following equation was used:

$$\text{BFKM (g)} = \text{HM} + \text{BCBM} + \text{BCSTM} - \text{Bryo}$$

where HM is the mass of the holdfast (g), BCBM is the bryozoan-covered mass of blades (g), BCSTM is the bryozoan-covered mass of stipes (g), and Bryo is the calculated absolute bryozoan biomass (g). The application of this correction procedure allowed calculating the kelp wet mass (without the bryozoan mass) at the day of sinking for each single *M. pyrifera* sporophyte.

After calculating the bryozoan-free kelp wet mass (BFKM) on the day of sinking, the relative daily biomass change in each sporophyte was calculated using the following equation for wet mass:

$$\text{biomass change } (\%d^{-1}) = 100 \frac{\text{BFKM}_t - \text{BFKM}_0}{\text{BFKM}_0 \times t}$$

where BFKM_0 is the bryozoan-free kelp wet mass (g) at day 0 and BFKM_t is the bryozoan-free kelp wet mass (g) at the day of sinking, i.e., after t days (d) of floating.

Measurement of photophysiological parameters

The physiological performance of initial *M. pyrifera* individuals and on the individual day of sinking was determined using the chlorophyll *a* fluorescence of photosystem II (PSII). Considering the complex morphology of *M. pyrifera* with heterogeneous photosynthetic performance along the thallus and within the blades, vegetative blades from the upper part of the sporophyte were used (see, e.g., Rothäusler et al. 2011b, c). In order to standardize the floating kelp status, all measurements were taken on intact tissue in the middle blade zone. Previous studies had shown

that small pieces of photosynthetically active tissues are suitable to determine physiological changes to environmental conditions (e.g., Bischof et al. 1998a; Gómez et al. 2004; Colombo-Pallotta et al. 2006; Gómez and Huovinen 2011; Koch et al. 2016). In order to minimize the extraction of sporophytes from natural kelp beds, the initial physiological performance of eight sporophytes from their native habitat was only determined in the two seasons with the most extreme environmental conditions, summer (January 10, 2012) and winter (August 2, 2012).

For the *in vivo* chlorophyll *a* fluorescence measurements, a portable pulse-amplitude-modulated fluorometer (PAM 2500; Walz, Effeltrich, Germany) was used. Three samples were cut from a blade of the main stipe of the initial *M. pyrifera* individuals (summer and winter) and on the day of sinking for each kelp. The samples were cleaned of epibionts with a soft sponge and seawater. They were incubated for 20 min in darkness and measured six times for maximum quantum yield (F_v/F_m). The potential maximum quantum yield represents a sensitive indicator of photosynthetic performance and, hence, of viability of algae, which is affected by stress exposure.

Subsequently, kelp samples were exposed to increasing photon flux densities (PFD) of actinic red light (0–1299 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) provided by a light-emitting diode lamp of the PAM device for the estimation of the relative PSII electron transport rate, as described in Schreiber et al. (1994). For each PAR range, the absorbance of light and the effective quantum yield (F_v'/F_m') of the samples were determined. The electron transport rate (ETR) parameters, such as ETR_{max} and saturation irradiance (I_k), were estimated by using the effective quantum yield, the PFD, and the absorbance of the individual sample (Hanelt et al. 1997a, b; Bischof et al. 1998a, b; Gómez et al. 2004). Photosynthesis versus irradiance curves (PI curves) with ETR as a function of PFD were fitted after Walsby (1997) due to the presence of slight photoinhibition. In addition, the non-photochemical quenching (NPQ) capacity was calculated according to Govindjee (1995) for each kelp sample.

Statistical analyses

Floating persistence was analyzed using Kaplan–Meier survival analysis. The different Kaplan–Meier survival curves were compared with the Peto–Wilcoxon test. Logistic curves were fitted to the floating (0) or sinking (1) probability of sporophytes depending on bryozoan biomass. For each season, the inflection points of the curves were calculated when sinking probability is 50 %.

Seasonal differences in algal wet mass and length at day 0 were analyzed with one-way ANOVAs. Similarly, we used ANOVAs to compare seasonal differences in floating

persistence and the chlorophyll *a* fluorescence parameters (ETR_{max} , I_k , NPQ, F_v/F_m) at the day of sinking. Biomass at day 0, I_k , and NPQ data were ln-transformed before analyses to achieve homogeneity of variances (Underwood 1997). Chlorophyll *a* fluorescence parameters (ETR_{max} , I_k , NPQ, F_v/F_m) of initial kelps were compared to day of sinking in summer and winter using Student's *t* test.

The comparisons between wet mass and kelp length at day 0 and the day of sinking (spring: $n = 21$; summer: $n = 27$; autumn: $n = 32$; winter: $n = 22$) were done with a two-way ANOVA. The two factors were season (spring, summer, autumn, and winter) and type of kelp (kelps on day 0, sunken kelp). Before analyzing with the two-way ANOVA, the wet mass data were ln-transformed to achieve homogeneity of variances (Underwood 1997). The daily biomass and length changes while floating were analyzed with a one-way ANOVA for seasonal differences. Correlation of total kelp biomass and kelp length at day 0 with floating persistence was analyzed with a Pearson's correlation test for each season. Data were tested for normality with the Shapiro–Wilk test and for homogeneity with the Levene's test and transformed, if necessary, to comply with requirements. When the ANOVAs revealed significant differences, *post hoc* Tukey's honest significant difference tests were applied. Data were analyzed using the R software (R Development Core Team 2014) and SPSS Statistics 22 (IBM, Armonk, NY, USA).

Results

Floating persistence

Kelp rafts persisted for at least 4 weeks at the sea surface in all seasons. In autumn, 100 % of *M. pyrifera* sporophytes stayed afloat for at least 28 days at the sea surface. In the other seasons, kelps sank faster: In winter only 50 % and in spring 29 % persisted until day 28, while in summer no kelp sporophyte stayed afloat until day 28 and the first sporophyte already sank at day 10 (Fig. 1). Consequently, the floating persistence of *Macrocystis* sporophytes differed significantly between seasons (Peto–Wilcoxon test $\chi^2 = 85.5$, $df = 3$, $p < 0.001$). The survival curve of *Macrocystis* in autumn compared to the curves of the other seasons, and the summer curve in comparison with the winter curve, showed significant differences (Peto–Wilcoxon test, Supplement table 4). The floating longevity of sporophytes in autumn (41 ± 6 days; mean \pm SD), with moderate water temperature and solar radiation (Table 2), was significantly higher compared to the other seasons (summer: 25 ± 4 days, spring: 27 ± 5 days, winter: 29 ± 5 days, mean \pm SD) (one-way ANOVA with *post hoc* Tukey's test, $F = 63.7$, $df = 3$, $p < 0.001$; Supplement table 5).

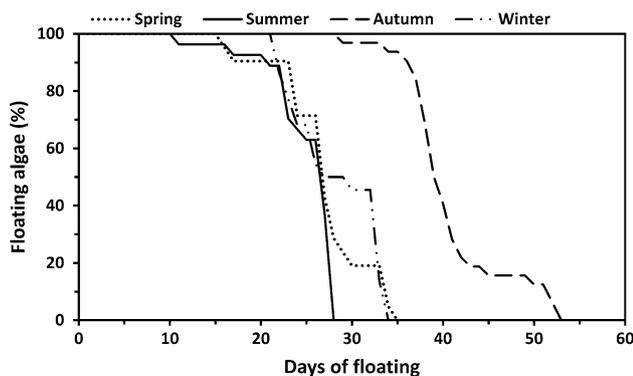


Fig. 1 *Macrocyctis pyrifera*: floating persistence (days) of sporophytes during the different seasons (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September)

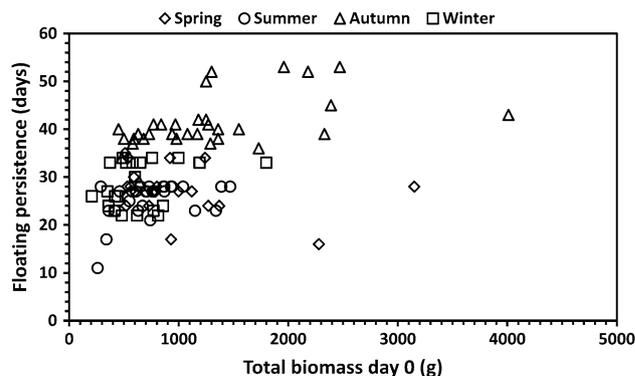


Fig. 2 *Macrocyctis pyrifera*: relation between total wet mass of experimental individuals on day 0 and floating persistence (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September)

There was no relationship between kelp biomass at day 0 and floating persistence in spring and winter (Pearson correlation: spring: $r = -0.303$, $n = 21$, $p = 0.182$; winter: $r = 0.363$, $n = 22$, $p = 0.097$). However, there were slightly positive correlations in summer and autumn for biomass of sporophytes at day 0 and floating persistence (Pearson correlation: summer: $r = 0.425$, $n = 27$, $p = 0.027$; autumn: $r = 0.495$, $n = 32$, $p = 0.004$; Fig. 2).

Epibiont cover and biomass

Within 1 week of floating at the study site, bryozoans (*Membranipora isabelleana*) started to colonize the experimental sporophytes of *M. pyrifera*. In all seasons, the bryozoan cover on day 7 ranged from 0.1 to 4.5 %, indicating a similar initial colonization process throughout the seasons (spring: 1.0 ± 0.9 %, summer: 1.1 ± 0.8 %, autumn: 0.7 ± 0.6 %, winter: 0.6 ± 0.3 %; mean \pm SD). However, after 14 days of floating, the cover increased up to 20–25 % in the warmer seasons (spring and summer) and 10–15 % in autumn and winter (Fig. 3). Consequently, the time periods required to reach a maximum bryozoan cover of 100 % on the floating *M. pyrifera* differed between seasons (Fig. 3).

During autumn and winter, the maximum proportional bryozoan biomass (winter: 42 %, and autumn: 51 %) of the

total *Macrocyctis* raft biomass (sporophyte + bryozoans) was reached after 30 or 40 days, respectively. In the warmer seasons, the maximum proportional bryozoan biomass (spring and summer: ~50 %) was reached after 25–26 days (Supplement figure 3). The mean proportional bryozoan biomass at the day of sinking was similar between the seasons (Table 2). Therefore, sinking of *Macrocyctis* was linked to a bryozoan biomass surpassing ~40 % of total *M. pyrifera* biomass in every season (spring = 44.6 %, summer = 40.0 %, autumn = 44.5 %, winter = 33.7 %), which was revealed by calculating the inflection points of the fitted logistic regressions (Fig. 4).

Growth and photophysiological characteristics

In all seasons, the total length of *Macrocyctis* did not substantially decrease during the floating experiments (Fig. 5). Between day 0 and the day of sinking, total length decreased by only 4 % in spring compared to the other seasons with slightly higher total length losses (14–23 %) (two-way ANOVA, season: $F = 24.08$, $df = 3$, $p < 0.001$; Supplement table 6). Daily length loss was higher in winter compared to the other seasons, but this tendency was not significant (one-way ANOVA with *post hoc* Tukey’s test, $F = 2.51$, $df = 3$, $p = 0.063$; Supplement figure 4).

Table 2 Mean proportional biomass (%) of bryozoans of the total *Macrocyctis* raft biomass (sporophyte + bryozoans) and final absolute biomass (g) of bryozoans per sporophyte \pm SD at the day of

sinking (spring: November/December; summer: January/February; autumn: May/June; winter: August/September) calculated according to the described procedure (see Supplement 1)

	<i>n</i>	Proportional biomass (%)	Min (%)	Max (%)	Biomass (g)	Min (g)	Max (g)	Mean floating persistence (days)
Spring	21	46.5 \pm 5.5	26.0	50.7	572.7 \pm 483.2	35.0	1960.9	27 \pm 5
Summer	27	44.8 \pm 8.3	12.1	50.8	400.7 \pm 362.9	28.3	1451.1	25 \pm 4
Autumn	32	46.9 \pm 3.6	39.3	50.8	694.1 \pm 430.5	161.0	1936.7	41 \pm 6
Winter	22	35.4 \pm 11.1	13.4	50.5	178.5 \pm 173.6	16.8	623.3	29 \pm 5

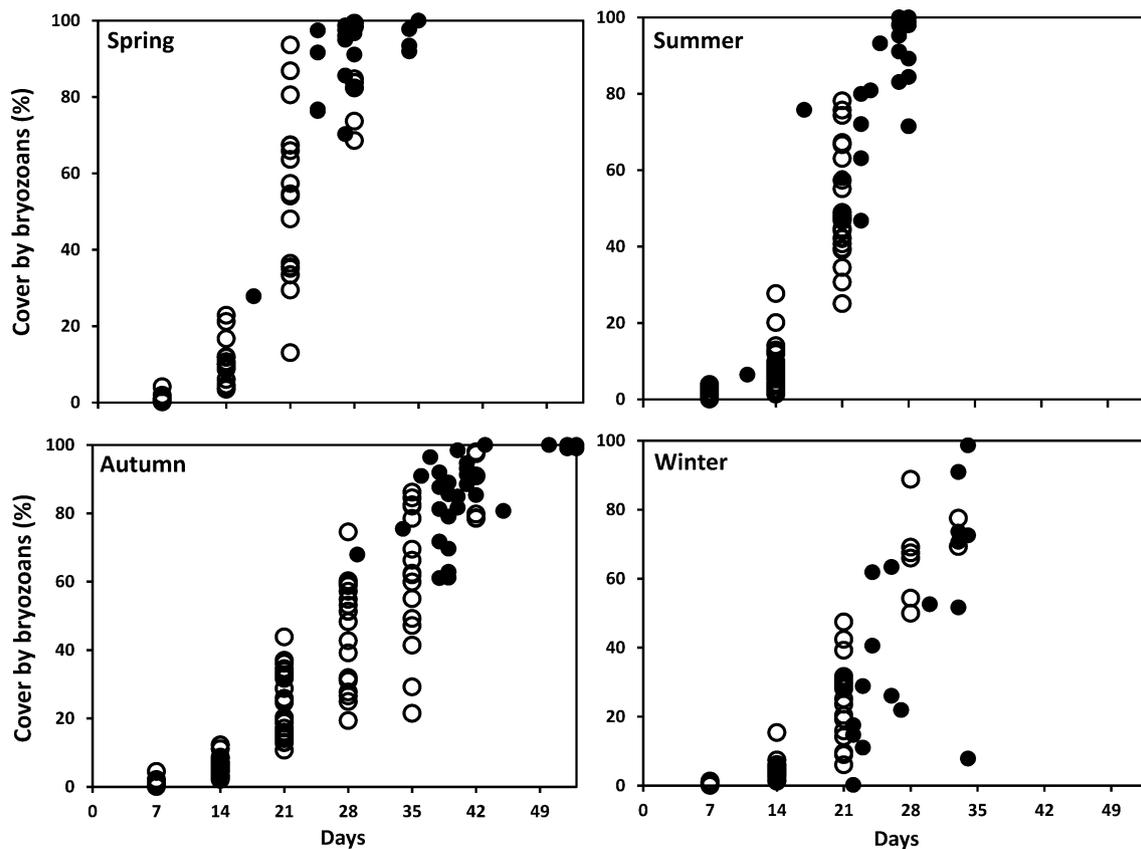


Fig. 3 *Macrocyctis pyrifera*: relationship between experimental duration (days) and cover by bryozoans (%) of experimental individuals. Open dots were measured every 7 days and black dots on the day of

sinking (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September)

In summer and winter, kelps lost 17 or 29 % of their total biomass, respectively, during the floating experiment, whereas in spring an increase in total biomass (by 12 %) was observed (Fig. 5; two-way ANOVA, season: $F = 23.25$, $df = 3$, $p < 0.001$; Supplement table 6). The daily biomass losses were ca. 1 % in summer and winter, but in spring sporophytes significantly gained in biomass during the experiment (one-way ANOVA with *post hoc* Tukey's test, $F = 4.73$, $df = 3$, $p = 0.004$). In autumn, the daily biomass change in floating *Macrocyctis* was very low (Supplement figure 4).

Initial kelps in summer had higher maximal electron transport rates (ETR_{max}) than on the day of sinking, but this was not the case in winter (*t* test; summer: $t = 2.3$, $df = 31$, $p < 0.05$; winter: $t = 0.9$, $df = 27$, $p = 0.401$). The initial *Macrocyctis* sporophytes as well as the experimental kelps on the day of sinking from the winter had the highest ETR_{max} . Light-saturated photosynthesis (ETR_{max}) of kelps on the day of sinking varied significantly between seasons (one-way ANOVA with *post hoc* Tukey's test, $F = 25.9$, $df = 3$, $p < 0.001$; Table 3). The comparison of

ETR_{max} between seasons on the day of sinking revealed that the electron transport rate in spring and summer was reduced (by almost 50 %) compared to autumn and winter (Table 3 and Supplement figure 5). Light saturation points (I_k) varied between the seasons from 104 to 149 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for the initial kelps (summer and winter) and from 113 to 170 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for the experimental kelps on their days of sinking (Table 3). The values of I_k on the day of sinking were significantly lower in spring compared to autumn and winter (one-way ANOVA with *post hoc* Tukey's test, $F = 7.1$, $df = 3$, $p < 0.001$). The initial kelps in summer had higher values of non-photochemical quenching (NPQ) than kelps on their day of sinking, but not in winter (*t* test; summer: $t = 9.3$, $df = 31$, $p < 0.001$; winter: $t = -1.0$, $df = 27$, $p = 0.322$). This photoprotective mechanism via heat dissipation was lower on the day of sinking in summer compared to spring and autumn (one-way ANOVA with *post hoc* Tukey's test, $F = 10.7$, $df = 3$, $p < 0.001$; Table 3). Values of the maximum quantum yield (F_v/F_m) were not reduced on the day of sinking in comparison with the initial status of

Fig. 4 *Macrocystis pyrifera*: floating (0) or sinking (1) probability of sporophytes depending on proportional bryozoan biomass (%) of the total *Macrocystis* raft biomass (sporophyte + bryozoans) in the different seasons (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September). Curves were fitted by logistic regression analysis

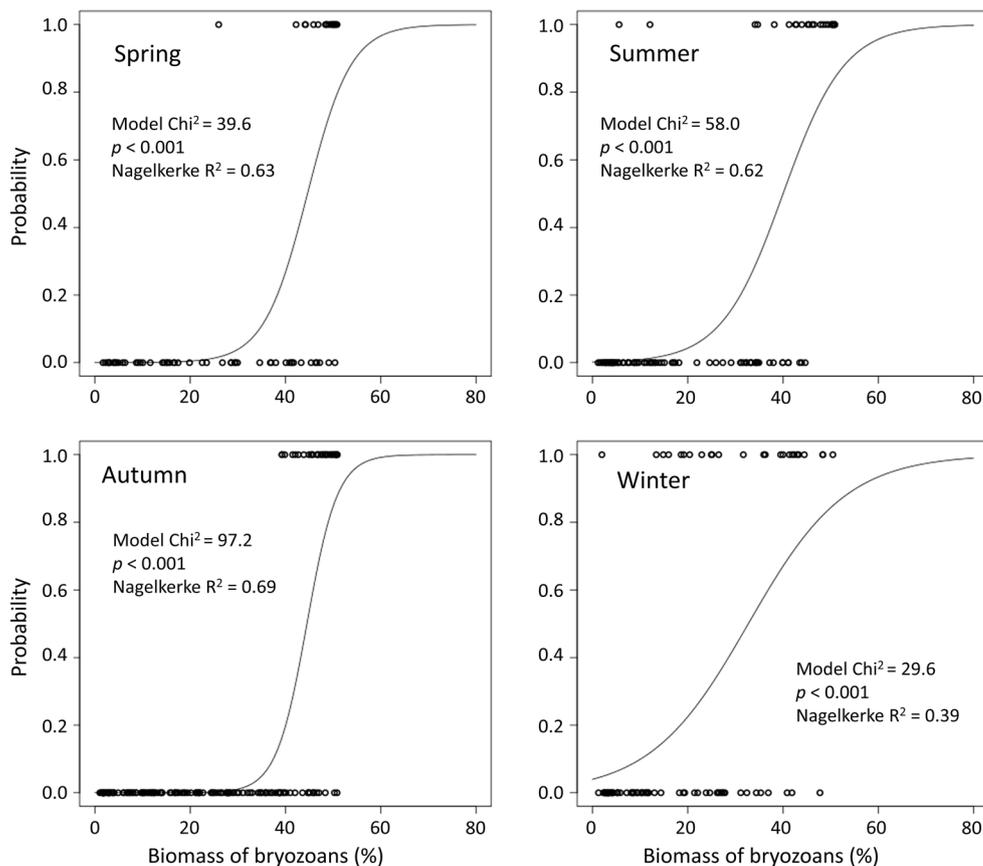


Table 3 *Macrocystis pyrifera*: physiological responses of initial individuals (initial; $n = 8$) and those at the day of sinking (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September)

	Photosynthesis–irradiance curve parameters		Non-photochemical quenching
	ETR _{max} (μmol e ⁻ m ⁻² s ⁻¹)	I _k (μmol photons m ⁻² s ⁻¹)	
Spring			
Sinking	26.8 ± 8.5a	112.6 ± 26.1a	4.0 ± 2.4a
Summer			
Initial	42.8 ± 7.1	95.8 ± 17.7	5.0 ± 1.4
Sinking	32.5 ± 11.9a	121.9 ± 20.3ac	1.7 ± 0.9b
Autumn			
Sinking	50.9 ± 14.2b	152.4 ± 43.3b	4.5 ± 3.6a
Winter			
Initial	59.8 ± 12.0	150.2 ± 26.6	2.1 ± 1.2
Sinking	54.9 ± 14.2b	138.8 ± 30.2bc	2.7 ± 1.7ab

Values are mean ± SD. Different lowercase (comparison of values at the day of sinking between the seasons) letters indicate significantly different means ($p < 0.05$; one-way ANOVA with *post hoc* Tukey's test)

the algae in summer and winter (t test; summer: $t = 0.68$, $df = 33$, $p = 0.50$; winter: $t = 0.4$, $df = 27$, $p = 0.69$). Maximum quantum yield was high on the day of sinking in all seasons, but F_v/F_m was significantly higher in autumn compared to the other seasons (one-way ANOVA with *post hoc* Tukey's test, $F = 18.5$, $df = 3$, $p < 0.001$; Fig. 6).

Discussion

Floating *Macrocystis* sporophytes stayed afloat for more than 1 month during moderate environmental conditions (cool water temperature and moderate solar radiation) and slow growth of epibionts in autumn. Higher water temperatures in summer seemed to enhance the growth of epibionts, but not

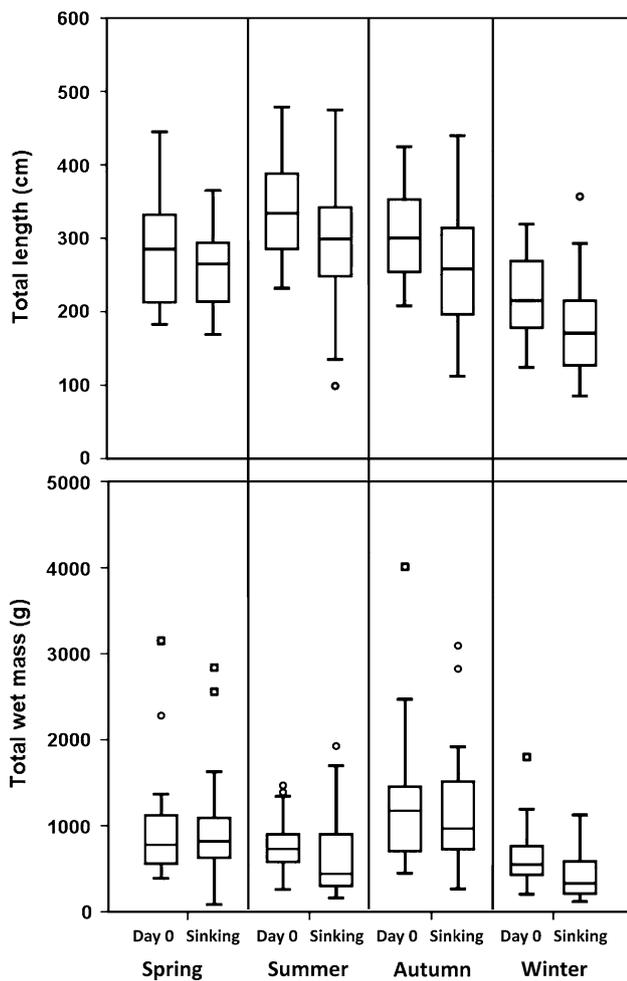


Fig. 5 *Macrocystis pyrifera*: total lengths and wet masses of experimental algae on day 0 and on the day of sinking (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September). Sporophyte wet masses at the day of sinking were corrected for bryozoan wet mass according to the described correction procedure. Horizontal lines represent the median; boxes the interquartile range; whiskers $1.5 \times$ interquartile range; circles the outliers; and squares extreme values

the growth of *M. pyrifera*, which resulted in earlier sinking compared to autumn. Growth and photophysiological parameters of *Macrocystis* showed only minor seasonal variation, confirming the high acclimation potential of giant kelp to rafting conditions. The results of this study document for the first time that kelps remained physiologically active and viable until the day of sinking, but that the large load of the rapidly growing bryozoan epibionts caused sinking of the kelp rafts.

Longevity at the sea surface

Rafts of *Macrocystis* sporophytes stayed afloat for at least 10 days and up to 53 days depending on the season. Natural

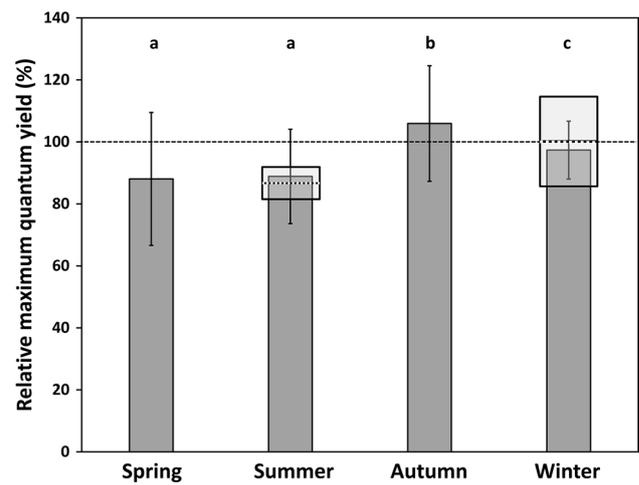


Fig. 6 *Macrocystis pyrifera*: relative maximum quantum yields of the initial kelp individuals ($n = 8$ in summer and winter) and of the experimental thalli on the days of sinking (spring: $n = 21$, November/December; summer: $n = 27$, January/February; autumn: $n = 32$, May/June; winter: $n = 22$, August/September) in the different experimental seasons. The means and SDs of the measured values of winter individuals ($F_v/F_m = 0.70$) were normalized to 100 %. Boxes indicate the values of initial kelp (summer and winter) with the broken line showing the mean and the upper and lower edges of the box the SD. Different lowercase letters indicate significantly different means ($p < 0.001$; one-way ANOVA with *post hoc* Tukey's test)

rafts of giant kelp had been found floating for 14 days and more than 100 days depending on the season and the particular geographic region (Helmuth et al. 1994; Hobday 2000c; Hernández-Carmona et al. 2006; Rothäusler et al. 2011d). Other temperate floating seaweed species (*Ascophyllum nodosum* and *Fucus vesiculosus*) remained floating for at least 15–20 days in microcosm studies as well under natural conditions (Ingólfsson 1995; Vandendriessche et al. 2007a). For natural rafts of *D. antarctica*, floating periods of 65 days have been estimated (Fraser et al. 2011). During these occasionally extensive time periods, floating seaweeds can be transported by winds and currents over long distances, thereby connecting populations of seaweeds themselves and of associated organisms (Thiel and Gutow 2005a, b; Thiel and Haye 2006; Muhlin et al. 2008; Fraser et al. 2009).

In the present study, *M. pyrifera* sporophytes stayed floating at the sea surface on average for 41 days in autumn and for 25–29 days in the other seasons (spring, summer, and winter). In contrast, at the same site, Graiff et al. (2013) showed for the bull kelp *D. antarctica* that during the moderate and cold seasons (winter, spring, and autumn), the floating persistence was higher (>37 days) than during the summer season (22 days). *Durvillaea antarctica* floats longer under benign environmental conditions (low temperature and moderate solar radiation), which does not seem to be the case for *Macrocystis* in winter and spring.

These differences may also be reflected in their biogeography as *D. antarctica* is better adapted to colder temperatures and distributed in the subantarctic region (Fraser et al. 2010), whereas *M. pyrifera* is also found along temperate and warmer coasts of the Pacific ocean and adjacent seas in both hemispheres (Graham et al. 2007). Therefore, the seasonal differences in floating persistence between the two kelp species might be due to other factors such as their different susceptibility to epibiont load and species-specific physiological traits (see also Tala et al. 2016).

Epibionts cause sinking

During our experiments, the floating *Macrocystis* sporophytes were rapidly overgrown by the bryozoan *Membranipora isabelleana*. This bryozoan also dominated the epibiont community on freely floating kelp rafts from the Coastal System of Coquimbo (Rothäusler et al. 2011d) and is found frequently in coastal waters (Pacheco et al. 2011). After 14 days, a maximum bryozoan cover of 10–25 % on floating *Macrocystis* was observed, which is comparable to the bryozoan cover found by Rothäusler et al. (2011d). In our experiments, the bryozoan colonies continued to grow actively, which led to a cover of up to 90 % after 21 days, but no colonization by stalked barnacles (*Lepas* spp.) was observed which is probably due to the fact that settlement of stalked barnacles is very limited in coastal waters. In contrast, epibiont cover (bryozoans and barnacles) found on freely floating kelps by Rothäusler et al. (2011d) rarely exceeded 20 %. Naturally floating seaweeds are often fouled by abundant stalked barnacles and/or bivalves which may significantly accelerate sinking in the open ocean due to the additional mass of these calcifying epibionts (Helmuth et al. 1994; Ingólfsson 1998; Hobday 2000b; Macaya et al. 2005; Rothäusler et al. 2011d). The fact that most experimental kelps sank after the bryozoan biomass had reached consistent values of 40–50 % of the kelp biomass (regardless of the time until sinking) is the indication that these epibionts indeed were responsible for the sinking of the kelp rafts.

The time until a maximum bryozoan cover of 100 % on the floating *M. pyrifera* was reached depended on the season. During autumn, the maximum bryozoan cover was reached after ~40 days, but in summer and spring, only 26–28 days were needed until bryozoan colonies had covered the entire kelp thallus. In the study by Rothäusler et al. (2011d), the total epibiont cover increased in northward direction which coincides with warmer surface water conditions. This suggested that increased ambient water temperatures accelerated the growth rate of bryozoans in spring and summer, whereas bryozoan growth seems to be slowed down at lower water temperatures prevailing in autumn and winter as the initial colonization process was

similar throughout the seasons. Supporting this suggestion, increasing temperatures enhanced the growth rates of North Sea as well as Atlantic bryozoans in laboratory and field studies (Menon 1972; Amui-Vedel et al. 2007; Saunders and Metaxas 2009). In the study from summer 2009, Rothäusler et al. (2011d) also found very high growth rates of *M. isabelleana* colonies on giant kelp blades, underscoring the fact that bryozoan growth consistently reaches high values during the summer months.

Epibionts might also generate benefits through the provision of carbon dioxide and ammonium released directly onto the kelp tissues (Muñoz et al. 1991; Hurd et al. 1994; Mercado et al. 1998; Hepburn and Hurd 2005). Especially during the initial phases of bryozoan colonization, the still uncalcified epibiont colonies may protect algal tissues against strong UV radiation. Similarly, a photoprotective function by blocking UV radiation was shown for sediment coating, thereby enhancing the photosynthetic performance of *Saccharina latissima* sporophytes (Roleda et al. 2008; Roleda and Dethleff 2011). Finally, the cover of bryozoans reached up to 100 % on the floating *Macrocystis* sporophytes, which may have protected kelp tissues from strong solar irradiances and UV radiation at the sea surface, supporting the high physiological performance of the rafts. Despite these positive impacts, calcified encrusting epibionts may reduce algal photosynthetic performance as they attenuate as much as 45–55 % of available light (Cancino et al. 1987; Muñoz et al. 1991). Therefore, the physiological relationship between floating *M. pyrifera* and bryozoans may depend on the degree of bryozoan cover and the physiological status of the kelps while floating. Dense accumulations of epibionts, sometimes in double layers as seen once bryozoan cover approached 100 %, may cause a loss of buoyancy of floating kelps due to the weight of their calcareous structures (Thiel and Gutow 2005b). Dixon et al. (1981) also showed that blade loss of benthic *M. pyrifera* depends on the intensity of bryozoan colonization. Thus, when kelps are fully covered by encrusting bryozoans, it is likely that the negative aspects outweigh any initial potential benefits.

Growth and physiological health at sinking

Once kelps float at the sea surface, they become exposed to strong variations in sea surface temperatures and irradiance, which may increase the risk of physiological stress (Macaya et al. 2005; Rothäusler et al. 2011c). High water temperatures (>24 °C) contribute to rapid degradation (within 1 week) and reduced floating persistence of *M. pyrifera* (Rothäusler et al. 2011c). However, not only thermal limits but also sublethal conditions may cause stress and reduced physiological performance (Weidner and Ziemens 1975; Davison and Pearson 1996). Indeed, growth

of benthic *M. pyrifera* populations in southern Chile was reduced at temperatures above 17–18 °C (Buschmann et al. 2014), and in a mesocosm experiment, growth of *Macrocystis* declined at temperatures exceeding 20 °C (Rothäusler et al. 2009). During our summer experiment, water temperatures rose above 18 °C, which may be suppressing floating persistence of *M. pyrifera* compared to the colder seasons as a thermal threshold was surpassed. For other temperate floating seaweeds, a high persistence after detachment has been reported at low water temperatures (Ingólfsson 1998; Salovius and Bonsdorff 2004; Vandendriessche et al. 2007a; Graiff et al. 2013; Tala et al. 2013). During autumn with moderate environmental conditions, the floating persistence of *M. pyrifera* was significantly higher (41 days), which suggests a high dispersal potential in this season.

The seasonal growth and reproduction pattern of *M. pyrifera* might also influence its floating potential at the sea surface. In winter, elongation rates of *M. pyrifera* are low due to seasonal growth and reproductive patterns (Buschmann et al. 2004; Graham et al. 2007; Buschmann et al. 2014). Accordingly, *Macrocystis* lost biomass during winter, suggesting that energy investment in growth was reduced. These intrinsic differences due to seasonally adjusted investment in growth or reproduction might result in seasonally different responses of the kelps despite similar environmental conditions. The gas-filled pneumatocysts which provide buoyancy for giant kelp stayed intact during sinking (A. Graiff et al., personal observations). In all seasons, there was no relationship between number of intact pneumatocysts at sinking and floating persistence (Supplement figure 6), and consequently sinking of *M. pyrifera* rafts most likely is due to the increasing weight of encrusting epibionts.

Our data on variable chlorophyll *a* fluorescence of photosystem II (PSII) reflect the high physiological acclimation potential of *M. pyrifera* emphasized by other studies (e.g., Colombo-Pallotta et al. 2006; Gómez and Huovinen 2011; Rothäusler et al. 2011a, c; Koch et al. 2016). Initially (summer and winter) and at the day of sinking, sporophytes had high maximum quantum yield (F_v/F_m) values in all seasons which was also shown by other studies at the same latitude (Rothäusler et al. 2011a, c, d), indicating physiological adjustment to the highly variable conditions of solar radiation and temperature observed in their benthic habitats (Gerard 1984, 1986). In summer, sporophytes showed decreased non-photochemical quenching (NPQ) and maximal electron transport rates (ETR_{max}) compared to initial kelps, which can be explained by the presence of temperature-sensitive enzymes and thermal susceptibility of PSII (Allakhverdiev et al. 2008). While during most seasons (spring, autumn, and winter) at the time of sinking the kelps were physiologically in good conditions (as indicated

by high ETR_{max} and F_v/F_m), in summer environmental stress due to high temperatures and solar radiation might have caused *M. pyrifera* rafts to be in suboptimal physiological conditions at the moment of sinking. However, even in summer (under extreme abiotic conditions), the tissue of the floating sporophytes stayed intact. This is in strong contrast to *D. antarctica* where in all seasons the tissue of the fronds decayed over time, which was accompanied by a dramatic reduction in the physiological performance on the day of sinking compared to the initial status (Graiff et al. 2013). Nevertheless, physiological performance of floating kelps *M. pyrifera* was favored under optimal conditions (moderate water temperatures and solar radiation) prevailing in autumn at this latitude when all sporophytes stayed afloat for almost 1 month.

Our results confirm that giant kelp is capable of acclimating to abiotic conditions at the sea surface at this latitude, but biotic interactions, either with grazers (e.g., Rothäusler et al. 2009) or with epibionts (Rothäusler et al. 2011d, this study) frequently have negative impacts on their floating persistence at intermediate latitudes (~30°S). At higher latitudes, *Macrocystis* is performing even better (Tala et al. 2016), probably facilitated by that fact that grazing effects are weak (Rothäusler et al. 2009) and epibiont colonization is low (Tala et al., unpublished data).

Conclusions and outlook

Macrocystis pyrifera is an important eco-engineer in coastal habitats (e.g., Graham et al. 2007) and one of the most common floating seaweeds along the coast of Chile (Macaya et al. 2005; Hinojosa et al. 2010, 2011; Wichmann et al. 2012). In the present study, which was conducted in northern-central Chile under coastal conditions, most floating *Macrocystis* sporophytes stayed physiologically healthy and viable for 1 month or more at the sea surface in all seasons before they finally sunk, pulled down by the mass of encrusting bryozoans. Consequently, under more favorable environmental conditions and slower growth rates of bryozoans (as in southern Chile), detached *Macrocystis* sporophytes might stay afloat for substantially longer periods. This might also contribute to the high abundances and biomasses of floating *Macrocystis* found in southern Chile (Wichmann et al. 2012).

Sea surface temperatures have increased over the past decades in many areas of the world's ocean and are predicted to continue rising (Lima and Wethey 2012; IPCC 2013). Negative effects of ocean warming on the physiological performance and fitness of seaweed populations (Bartsch et al. 2013) result in retractions and poleward shifts of distributional ranges (Wernberg et al. 2011a, b; Bartsch et al. 2012; Wernberg et al. 2013). Concurrently, epibionts seem to benefit from ocean warming, resulting in higher growth

rates and range expansions at the expense of seaweeds, as heavy encrustations of bryozoans have already precipitated declines in kelp populations (Amui-Vedel et al. 2007; Saier and Chapman 2004; Saunders and Metaxas 2008; Scheibling and Gagnon 2009; Saunders et al. 2010; Filbee-Dexter et al. 2016). Since floating seaweeds are likely to interconnect even distant habitats (Macaya and Zuccarello 2010), their longevity at the sea surface is crucial. Raft persistence strongly depends on favorable seawater conditions which makes these macrophyte rafts highly susceptible to global climate change (MacReadie et al. 2011). Our study documented for the first time a case of epibiont-induced sinking of otherwise healthy floating seaweeds. Increasing temperatures in the global oceans may enhance epibiont growth and thereby suppress the dispersal potential of floating seaweeds, even of species well known to rapidly acclimate to stressful conditions at the sea surface.

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Human and animals rights This article does not contain any studies with human participants or animals performed by any of the authors.

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