# EFFECT OF TEMPERATURE AND GRAZING ON GROWTH AND REPRODUCTION OF FLOATING *MACROCYSTIS* SPP. (PHAEOPHYCEAE) ALONG A LATITUDINAL GRADIENT<sup>1</sup>

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Macroalgal rafts frequently occur floating in coastal waters of temperate regions of the world's oceans. These rafts are considered important dispersal vehicles for associated organisms with direct development. However, environmental factors may limit the floating potential of kelp and thereby the dispersal of associated organisms. To examine the effect of water temperature and grazing on growth, reproductive output, and survival of floating Macrocystis spp., experiments were conducted in outdoor tanks during austral summer 2006/2007 at three sites along the Chilean Pacific coast (20° S, 30° S, 40° S). At each site, Macrocystis spp. was maintained individually at three different water temperatures (ambient, ambient - 4°C, ambient + 4°C) and in the presence or absence of the amphipod grazer Peramphithoe femorata for 14 d. High water temperatures (>20°C) provoked rapid degradation of Macrocystis spp. rafts. At moderate temperatures (15°C-20°C), algal survival depended on the presence of associated grazers. In the absence of grazers, algal rafts gained in biomass while grazing caused considerable losses of algal biomass. Algal survival was the highest under cooler conditions (<15°C), where raft degradation was slow and grazer-induced biomass losses were compensated by continuing algal growth. Our results indicate that floating kelp rafts can survive for long time periods at the sea surface, but survival depends on the interaction between temperature and grazing. We suggest that these processes limiting the survival of kelp rafts in warmer temperatures may act as a dispersal barrier for kelp and its associated passengers.

*Key index words:* Chile; detachment; floating; grazing; growth; macroalgae; *Macrocystis*; rafting; reproduction; temperature

Rafting on floating macroalgae is common in nature, and it is considered an important dispersal mechanism for many organisms with limited autonomous dispersal capacity (Edgar 1987, Helmuth et al. 1994, Ingólfsson 1998, Ó Foighil et al. 1999, Hobday 2000a, Thiel 2003). Successful dispersal via algal rafting depends on the availability of floating algae and on their longevity at the sea surface (Smith 2002, Thiel and Gutow 2005a). At present, little information is available on algal biology and survival after detachment, even though it is recognized that the potential of the algae to persist at the sea surface is fundamental to ensure long-distance dispersal (Helmuth et al. 1994, Hobday 2000b, Thiel and Gutow 2005a). To evaluate algal persistence after detachment, it is particularly important to know whether algae continue to

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grow and to which degree associated grazers contribute to the demise of floating algae.

Most large kelps grow attached to the bottom by a holdfast, and in many species, the large fronds are maintained in the water column by gas-filled pneumatocysts or gas-containing cells (Dromgoole 1982, Norton and Mathieson 1983, Hay 1994). When fragments, branches, or entire individuals become detached, these float to the sea surface. A variety of factors contribute to detachment, including grazerinduced weakening of stipes or holdfasts, wave action, or entanglement with subsequent wear and tear (Dayton and Tegner 1984, Tegner et al. 1995, Graham et al. 2007). While afloat, detached macroalgae continue growing and may even produce and release viable zoospores (Macaya et al. 2005a, Hernández-Carmona et al. 2006).

Floating algae often harbor a diverse fauna of boring and grazing organisms (Edgar 1987, Bushing 1994, Helmuth et al. 1994, Ingólfsson 1995, 1998, Hobday 2000a, Thiel and Gutow 2005b). The composition of the rafting community and the abundance of individual species can be highly variable in time and space, and successional changes are probably related to travel time and distance from the shore (Safran and Omori 1990, Ingólfsson 1995, Vandendriessche et al. 2006). Previous estimates of the survival periods of floating algae are inconsistent and range from a few days to several months (Harrold and Lisin 1989, Helmuth et al. 1994, Ingólfsson 1998, Hobday 2000b). This high variability in survival times may be primarily due to the fact that most of these estimates are based on indirect measurements, such as associated sessile species (e.g., body size of stalked barnacles), or on morphometric characteristics of algae, such as blade deterioration (Helmuth et al. 1994, Hobday 2000a, Macaya et al. 2005a). The uncertainties associated with indirect measures of survival times at the sea surface make it difficult to accurately estimate the potential dispersal distances of the algae and their associated fauna.

It is generally believed that the survival of freely floating kelps depends on several biotic and abiotic factors that differ from those in benthic conditions. The main factors regulating the survival of floating algae are herbivory (Thiel and Gutow 2005a) and different temperature regimes (Hobday 2000a, Vandendriessche et al. 2007). Edgar (1987) also suggested that nutrient availability can play an important role. In addition, the extreme solar insolation at the sea surface (Jokiel 1980) and low salinities in estuarine waters may affect algal growth and thus floatability.

Along the Pacific coast of Chile, kelp forests composed of *Macrocystis integrifolia* Bory and *M. pyrifera* (L.) C. Agardh occur abundantly in subtidal waters between  $18^{\circ}$  S and  $60^{\circ}$  S (Westermeier and Möller 1990, Vega et al. 2005), and these kelps are commonly found floating in coastal waters. Following detachment, kelps are caught in particular water masses, and depending on environmental conditions (temperature, herbivory, nutrients), algal degradation may proceed more or less rapidly. Moreover, in the eastern Pacific, benthic populations of giant kelp are occasionally impacted by poleward incursions of warm and nutrient-poor ocean waters during El Niño events (Camus 1994, Edwards 2004). Floating algae might also be exposed to these environmental shifts. Seawater temperature may not only affect growth of floating algae but also the grazing activity of associated herbivores (Bulnheim 1974, Gutow 2003, Vandendriessche et al. 2007). The dominant consumers of floating macroalgae are amphipods and isopods (Kingsford 1992, Geertz-Hansen et al. 1993, Ingólfsson 2000, Vandendriessche et al. 2006), and there is evidence that increasing temperatures can enhance algal consumption by associated mesograzers (Vandendriessche et al. 2007).

Ocean temperatures generally tend to increase with decreasing latitude, and grazing pressure by herbivores is thought to be strongly related to seasurface temperature (Broitman et al. 2001). Surface waters along the Chilean coast exhibit a strong latitudinal temperature gradient (from <14°C in southern Chile to >20°C in northern Chile). Previous studies suggested that latitudinal environmental differences in ocean temperatures and herbivore pressure can affect benthic algal populations (e.g., Broitman et al. 2001, Rinde and Sjotun 2005, Matson and Edwards 2007). In addition, there are regional temperature and herbivore variations, which fluctuate depending on the magnitude of upwelling and mixing of the water column (Vega et al. 2005). Temporal variations in herbivore pressure can have a strong impact on kelp populations (Vásquez et al. 2006). Given the latitudinal temperature gradients and the highly variable herbivore pressure in time, benthic and floating populations of Macrocystis spp. in northern Chile are expected to experience different conditions than those in southern Chile. Thus, it can be hypothesized that individuals of Macrocystis spp. floating in northern Chile have different survival times and dispersal distances than their counterparts from the south. Measuring the longevity of *Macrocystis* spp. rafts along a latitudinal temperature gradient is an important step in estimating the effective distance over which dispersal of associated organisms can be successful. The purpose of the present study was to examine whether the floating potential of Macrocystis spp. depends on temperature and grazing. An outdoor-tank experiment was conducted at three sites along the Chilean coast (northern, central, and southern Chile), simulating three different temperature regimes in the absence and presence of herbivores in order to test whether kelp biomass, blade growth, and loss of distal blade tissue decreases with increasing water temperatures and in the presence of grazers. The effect of water temperature on algal

reproductive output was examined to gain insights into the importance of floating algae in spore dispersal.

### MATERIALS AND METHODS

Field sampling of sporophytes and amphipods. Identical outdoor-tank experiments were carried out during austral summer 2006/2007 at three locations: Iquique  $(20^{\circ}14' \text{ S}, 70^{\circ}08' \text{ W})$ , Coquimbo  $(29^{\circ}58' \text{ S}, 71^{\circ}21' \text{ W})$ , and Calfuco  $(39^{\circ}45' \text{ S}, 73^{\circ}23' \text{ W})$ , encompassing the natural temperature ranges to which floating rafts are exposed along the coast of the SE Pacific (Fig. 1). At each experimental location, a total of 32 young fertile *Macrocystis* spp. sporophytes (sizes ranged between ~1 and 1.5 m) were detached from nearby kelp beds via snorkeling. Complete sporophytes including their holdfasts were carefully removed from the substratum using dive knives. All collecting sites are semiexposed to waves, and algae were collected during low tide in the shallow subtidal at 0.5–2.5 m depth.

Traditionally, along the Chilean coast, two species of *Macrocystis* have been distinguished based on morphological characters, namely, *M. integrifolia* (northern-central Chile; with a rhizomatous holdfast and narrow blades) and *M. pyrifera* (southern Chile; with a conical holdfast and wide blades) (Santelices 1989, Graham et al. 2007). Sporophytes collected in the present study were morphologically representative of both species. Algae from northern and central Chile had *M. integrifolia* characteristics, while algae from the south were more similar to *M. pyrifera*. However, in a molecular study, Coyer et al. (2001) suggested that *Macrocystis* is a monospecific genus, and Graham et al. (2007) noted that depending on the habitat, the genus *Macrocystis* shows a high morphological plasticity. Sporophytes corresponding to the *integrifolia* or *pyrifera* morphological plasticity.

phology are also known to hybridize successfully (Westermeier et al. 2007). Since the taxonomic situation of the genus Macrocystis is not yet fully resolved, and specimens from northern and southern Chile show few molecular differences using mitochondrial markers (E. Macaya, personal comm.) the algae used in the present study were treated as Macrocystis spp. The herbivorous amphipod P. femorata, which lives in close association with Macrocystis spp., was collected from subtidal habitats of the same locations, except for Calfuco, where amphipods were collected on the island of Chiloé (41°52' S, 73°50' W). This amphipod (kelp curler) is known to curl the blades, forming open-ended "nests" that are inhabited by one or more individuals, which intensively graze on the blades from within the nest. P. femorata was selected because these amphipods are common on Macrocystis spp. (on both attached and floating sporophytes), cling efficiently to the substratum (nest builder), and rarely switch between floating algae. Furthermore, their offspring can directly recruit within the parental raft, thereby allowing the persistence of the species during prolonged journeys. Nests with their amphipods were handcollected by semiautonomous divers. After collection, sporophytes and amphipods were kept in a cooler at their ambient temperature and immediately transferred to seawater tanks with running seawater. Adult amphipods used in the experiments had a body length of  $13.8 \pm 3.1$  mm.

General experimental set-up for each location. Experimental design: Floating sporophytes were cultured for 14 d in 90 L containers with flowing unfiltered seawater. At each location, the algae were maintained at three different water temperatures (Table 1): ambient (incoming ambient seawater temperature), warm (ambient temperature + 4°C), and cool (ambient temperature - 4°C). The eight containers from each temperature treatment were subdivided into two groups, one that received amphipod grazers and one without grazers.



FIG. 1. Map of Chile with the locations of the experimental sites and the natural sea-surface temperature gradient. (SST modified after Hinojosa et al. 2006).

TABLE 1. Average seawater tank temperatures (cool, ambient, warm) at the three locations, measured with a handheld thermometer during the 14 d of experiments; temperature measurements were taken every day at 9, 12, 15, and 18 h in all experimental tanks; data represent means  $\pm$  SD for the entire experimental duration (14 d).

°C	Cool	Ambient	Warm		
Iquique Coquimbo Calfuco	$16.9 \pm 0.7$ $13.6 \pm 0.8$ $12.3 \pm 1.2$	$\begin{array}{c} 19.9 \pm 1.2 \\ 17.6 \pm 1.6 \\ 15.5 \pm 1.8 \end{array}$	$\begin{array}{c} 24.7 \pm 0.1 \\ 20.6 \pm 0.6 \\ 18.9 \pm 1.1 \end{array}$		

Selection of algae and grazers for experiments: Sporophytes were carefully rinsed with seawater in order to remove associated grazers and epiphytes. A total of 24 algae were randomly distributed among the experimental units. The mean wet weight of initial sporophytes was: Iquique  $145.2 \pm 55.9$  g, Coquimbo  $168.2 \pm 25.4$  g, and Calfuco  $170.1 \pm 30.6$  g. At each experimental site, young fertile sporophytes that were similar in size and weight were collected in order to diminish size/age effects on growth responses. While sporophytes in Iquique were slightly smaller than at the other two sites, most individuals were reproductive, indicating that they were well developed.

P. femorata was added randomly to four containers of each temperature treatment while the other four were kept grazerfree as control treatments. Amphipods were added at a proportion of one adult amphipod per 3 g wet sporophyte biomass (estimated after considering unpublished data from E. Rothäusler and M. Thiel). To examine whether consumption rates of the amphipod P. femorata were temperature dependent, small assays were run at each location. Consumption (C) of the amphipod was calculated using the formula as described in Cronin and Hay (1996):  $C = (W_i^* C_{f'})$  $C_i$ )- $W_f$ , where  $W_i$  is the initial weight of algal tissue in the presence of grazers;  $C_{\rm f}$ , the final weight of the growth control;  $C_{\rm t}$ , the initial weight of the growth control; and  $W_{\rm f}$ , the final weight of algal tissue in the presence of grazers. Amphipods showed no temperature-dependent consumption rate. One amphipod consumed an average of 37.1 ± 15.8 mg kelp tissue  $d^{-1}$  (*n* = 4 replicates per temperature and location).

Treatment of seawater for experiments: Seawater was continuously pumped into three large head tanks (1,800 L). Two of these tanks were equipped with a chiller or alternatively with a heater to regulate the cool and the warm water temperatures, respectively. The third tank, which did not receive any temperature modification, was used to maintain the incoming ambient water temperature. From the large tanks, the seawater was then redistributed via gravity into the 90 L containers. Each temperature (cool, ambient, and warm) was represented with eight experimental units. The flow rate for each container was  $\sim$ 3 L · min<sup>-1</sup>. Containers were additionally maintained with air bubbling to ensure continuous movement of algae. During the experimental period, the water temperature in the containers was monitored at 9:00, 12:00, 15:00, and 18:00 h (local time). This was performed to check if the temperatures in the experimental units were in the correct experimental range. Containers were occasionally cleaned from diatoms using a kitchen sponge.

Measurements of algal responses. Within-sporophyte biomass distribution: At the start and end of the experiments, we took destructive samples and dissected sporophytes to obtain the biomass distribution of different tissue components within single sporophytes. Eight initial sporophytes were measured to estimate the natural within-kelp biomass distribution in the field. At day 14, all sporophytes from the experimental units were analyzed to determine the within-sporophyte biomass distribution in the absence or presence of grazers and at the three different experimental temperatures. Each sporophyte was separated into holdfast, stipe, vegetative blades, pneumatocysts (gas-filled bladders), reproductive blades, and sporophylls using a scalpel. In this study, we refer to basal blades that bear sori as "sporophylls," while basal blades without mature sori are called "reproductive blades" (sporophylls were also analyzed for reproductive activity—see below). All algal parts were weighed (g), and the values were transformed afterward to percentage kelp tissue on the basis of the total wet weight.

Measurement of algal growth: Growth rates of algae were measured as (1) change in total biomass, (2) blade elongation, and (3) the loss of distal blade tissue. Sporophytes were sampled at days 0, 5, 10, and 14 of the experiment. To estimate biomass changes at different temperature and grazing regimes, all algae were weighed at each of these sampling days. Biomass change (BC) was calculated with the equation BC = (FW-IW)/T, where FW and IW are the final and initial wet weight of the sporophytes at the respective sampling days; and T, the time period between each sampling day. Changes in algal biomass were expressed afterward as percentage biomass change per day.

The elongation of blades was quantified using the punchhole technique of Parke (1948). At day 0, a 3 mm diameter hole was punched in the central part of the blade at a distance of 9 cm  $(H_i, cm)$  from the pneumatocyst/lamina transition region (meristem) using a cork borer. At each sampling date, the displacement of this hole was recorded ( $H_{\rm f}$ , cm; Fig. 2). The first free blades after the apical meristem were chosen because of their active growth. In total, three apical blades from each sporophyte were perforated, and hole displacement was calculated using the mean values for these three blades. Growth was expressed as daily elongation rate (cm · d-Fig. 2). In cases where the holes had displaced toward the distal-most blade parts, blades were marked again. In addition, if marked blades could not be recovered due to grazing or disintegration, new blades were selected and marked for the determination of the elongation rate during the subsequent growth interval.

The expected lengths ( $L_e$ , without loss of distal blade) of the marked blades were determined according to Tala and Edding (2005) by summing the initial length ( $L_i$ , cm) and the displacement of the hole ( $H_f$ - $H_i$ ) (Fig. 2). To estimate the rate of loss of distal blade tissue in cm  $\cdot$  d<sup>-1</sup>, at each sampling day, the observed final length was subtracted from the expected length (Fig. 2).

Algal reproductive output: The reproductive output of *Macrocystis* spp. was evaluated at the start and end of each experiment. The eight initial sporophytes were used to represent the reproductive status of the algae in the field, and at the end of the experiments, all sporophytes were analyzed to test for the effects of temperature and herbivory on reproductive output. If present, three sporophylls from each sporophyte were brought to the laboratory to determine the reproductive area represented by the percentage area of the sori. Each sporophyll was photographed, and its total area as well as the area of its sorus was calculated with Image-Pro, version 4.0 (Media Cybernetics Inc., Bethesda, MD, USA).

Spore release was determined on 2 mm diameter disks of sori obtained from each sporophyll using a perforator. Tissue samples were induced to sporulate by immersion for 60 min in 0.2 mL of 0.45  $\mu$ m filter-sterilized seawater. Spore numbers were determined separately for each tissue sample using a hemacytometer chamber (Thoma<sup>®</sup>, Kayagiki Corp., Tokyo, Japan; 1/10 mm depth and 1/400 mm<sup>2</sup> area).

*Statistics.* Growth responses including biomass change, blade elongation rate, and the loss of distal blade tissue were analyzed with repeated-measures analysis of variance (ANOVA)



FIG. 2. Biomass allocation and the measurements used for the determination of blade elongation rate and loss of distal blade tissue rate of *Macrocystis* spp. sporophytes.

separately for each locality, with the within-subject factor Time, and the between-subject factors Grazing (with and without grazers) and Temperature (cool, ambient, warm). 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 for the *F*test was applied (Von Ende 1993). Data were tested for homogeneity with Levene's test and transformed if necessary, to comply with requirements. When the ANOVA revealed significant differences, a post hoc Tukey's HSD was applied. Since algae from the warm water treatment in Iquique sank already at day 5 of the experiment, biomass change for this day was analyzed with a two-factorial ANOVA with the factors Temperature (fixed factor) and Grazing (with or without grazers, fixed factor).

For each location, differences in within-sporophyte biomass distribution between the three temperature and the two grazing regimes were examined using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001, 2005, McArdle and Anderson 2001). PERMANOVA tested the response of six algal tissues (holdfast, stipe, vegetative blade, pneumatocyst, reproductive blade, and sporophyll) to the factors Grazing and Temperature in an ANOVA experimental design on the basis of Euclidean distance measure, using permutations.

#### RESULTS

Algal survival during the experiments. All sporophytes of *Macrocystis* spp. survived at water temperatures between 12°C and 20°C during the 14 d of the experiments. At water temperatures above 20°C, algal survival was dramatically reduced. At the northernmost location (Iquique), algae kept in the warm water treatment showed positive buoyancy only until day 5, irrespective of the presence of grazers. In moderate water temperatures (Coquimbo), algal growth and hence survival depended on the presence of grazers. The highest kelp persistence was detected under cool conditions (Calfuco), where biomass losses were compensated by continuing blade elongation (Table 2).

Algal status at the beginning and end of the experiment. Within-sporophyte biomass distribution: At all three locations, there was no significant interaction between the factors temperature and grazing on within-sporophyte biomass distribution (Fig. 3, Table 3). Biomass distribution of *Macrocystis* spp. at the northernmost location (Iquique) significantly depended on temperature (Monte Carlo *P*-value = 0.0258). Within-sporophyte biomass distribution of the cool and the ambient temperature treatment significantly differed from the biomass distribution in the warm water treatment (Monte Carlo P-value = 0.0394 for both comparisons). At ambient (presence of grazers) and warm water temperatures, the proportion of vegetative blades decreased and the holdfast represented the tissue with the highest percentage of total kelp biomass. In Coquimbo (central Chile), within-sporophyte biomass distribution in the presence of grazers was significantly different from that of algae kept without grazers (Monte Carlo P-value = 0.0085). At all temperatures tested, sporophytes exposed to amphipod grazers lost vegetative blade tissue, with the consequent relative increase of the other thallus parts, in particular the stipes. No significant differences between the biomass distributions of algae kept in different grazing and temperature regimes were observed for the southernmost location (Calfuco). Here, almost 50% of the biomass was represented by vegetative blades (Fig. 3). The sporophylls, which accounted for 10%-15% of the biomass in

TABLE 2. Sporophyte survival (%) and net blade elongation rates (cm  $\cdot$ d<sup>-1</sup>) of *Macrocystis* spp. after 14 d of floating at different water temperatures and experimental sites. Data are expressed as mean values ± SD (*n* = 4). For Coquimbo, no SD could be calculated for the ambient treatment because many replicates were lost due to high grazing activity.

	Cool		Ambient		Warm		
	control	grazing	control	grazing	control	grazing	
Iauiaue	100%		100%		0% (day 5)		Survival
1 1	$1.0 \pm 0.7$	$0.7 \pm 0.1$	$1.2 \pm 0.6$	_ <sup>a</sup>	_ <sup>b</sup>	́_ <sup>6</sup>	Net elongation rate
Coquimbo	0 100%		100%		100%		Survival
1	$1.8 \pm 0.7$	$1.3 \pm 0.4$	$2.0 \pm 0.2$	0.8	$1.6 \pm 0.8$	_ <sup>a</sup>	Net elongation rate
Calfuco	100%		100%		100%		Survival
	$2.3\pm0.6$	$2.0\pm0.8$	$1.8\pm0.8$	$1.5 \pm 0.6$	$1.9\pm0.3$	$1.3 \pm 0.6$	Net elongation rate

<sup>a</sup>Blades disintegrated; <sup>b</sup>Sporophytes sank at day 5.



FIG. 3. Within-sporophyte biomass distribution of *Macrocystis* spp. sporophytes at the start (natural; n = 8) and the end of the experiments (n = 4), for each location and treatment combination (cool, ambient, warm and grazing vs. control). Note that sporophytes kept in the warm temperature in Iquique already sank at day 5. Data represent mean percent values.

the natural condition decreased considerably at all three sites and in all treatment combinations.

Algal reproductive output: In Iquique and Calfuco, six of the eight initial sporophytes had fertile sporophylls, while in Coquimbo, all initial sporophytes presented fertile sporophylls. The highest reproductive area allocation was detected in thalli from

Iquique, and the lowest in Coquimbo (Fig. 4). Sporulation assays confirmed for each location that all sporophylls released motile zoospores. During the 14 d experiment, sporophytes from northern and central Chile lost sporophylls at temperatures >20°C, and their percentage area allocation decreased in all other treatments. For both sites, at temperatures around 17°C, only one sporophyte bore sporophylls in the absence of amphipods. In addition, in Coquimbo, sporophylls were also present in the cool control treatment. Only in Calfuco, at the coolest experimental site, where temperatures never rose above 20°C, sporophylls were represented at all temperatures tested (Fig. 4). Even though at this site many floating sporophytes lost fertile sporophylls, those that persisted throughout the 14 d period showed high reproductive output.

Growth status of algae in time. Biomass change: The patterns of algal biomass change were considerably different between the three locations (Fig. 5, Table 4a). At the northernmost location (Iquique), biomass losses of algae kept at ambient and cool water temperatures significantly increased in time with differences between day 5 and day 10 (P = 0.049), and between day 5 and day 14 of the experiment (P = 0.008). In addition, at this site, when comparing only algae from day 5 of the experiment, biomass losses significantly depended on water temperature (two-factorial ANOVA, df = 2, F = 19.601, P < 0.001). Algae kept at the warmest water temperature ( $\sim$ 24.7°C; Fig. 5) showed higher biomass losses than algae kept at ambient and cool water temperatures (P = 0.001 and P < 0.001, respectively), which caused the fragmentation and sinking of these sporophytes within 5 d of the experiment. Biomass change was negative for all treatment combinations throughout the experimental period, with the single exception of the cool control treatment at day 5 of the experiment. In Coquimbo, floating sporophytes survived in the absence of grazers but lost biomass in the presence of grazers (Table 4a). We also found a significant effect for the time × temperature interaction on kelp biomass change. At our southernmost location (Calfuco), kelp biomass continued to increase at all temperatures and independent of the grazing

TABLE 3. Results from the statistical analysis of within-sporophyte biomass distribution for each experimental site using permutational multivariate analysis of variance (PERMANOVA). *P*-value (MC), Monte Carlo; Temp, temperature; C, Control; and G, Grazing.

Within biomass change	Iquique			Coquimbo			Calfuco		
	df	Fratio	P-value (MC)	df	<i>F</i> -ratio	P-value (MC)	df	<i>F</i> -ratio	P-value (MC)
Temp	2	3.536	0.026	2	0.848	0.505	2	0.0472	0.9697
CG	1	0.266	0.734	1	5.636	0.008	1	0.2435	0.6367
$Temp \times CG$	2	0.088	0.986	2	1.023	0.412	2	0.0725	0.9428



FIG. 4. Reproductive output of *Macrocystis* spp. at the start (natural) and the end of the experiments, for each location and treatment combination, expressed as percentage reproductive area allocation. N = number of sporophytes with sporophylls/number of replicates; if present from each sporophyte, n = 3 sporophylls were measured, and if >2 measurements were obtained, we calculated the mean for each replicate; figure shows grand mean ± SD.

treatment (grazed vs. ungrazed) until day 10. At day 14, a decrease in biomass was observed in the sporophytes from the warm grazing treatment, with a significant grazing  $\times$  time interaction (Table 4a). Biomass change differed between day 5 and day 14, and between day 10 and day 14 of the experiment, which is mainly due to grazing effects at ambient (decreasing biomass gain) and high temperatures (biomass loss; Fig. 5). In addition, an interaction effect between time and temperature on biomass change was detected (Table 4a).

Blade elongation rate: Water temperatures between 12°C and 20°C had only minor effects on blade elongation rates of *Macrocystis* spp. (Fig. 6, Table 4b). Sporophytes continuously grew at moderate and low temperatures, but water temperatures >20°C strongly influenced blade elongation rates. At all experimental sites, Iquique, Coquimbo, and Calfuco, blade elongation rate significantly decreased over time (Table 4b), with the lowest elongation



FIG. 5. Percent biomass change  $\cdot d^{-1}$  of *Macrocystis* spp. (mean  $\pm$  SD, n = 4) at the three temperature treatments (cool, ambient, warm) and in the absence (control) and presence (grazing) of the amphipod grazer *Peramphithoe femorata*; symbols indicate that algae had died before the sampling and were not available for measurements.

rates at day 14. In Iquique, differences in blade elongation rate were measured between day 5 and day 14 (P = 0.003), between day 10 and day 14 (P = 0.002), and between day 5 and day 10 (P = 0.042) of the experiment. A time effect in central-Chile (Coquimbo) was detected between elongation rates of day 5 and day 14 (P = 0.002), and between day 10 and day 14 (P < 0.001). The blade elongation rate at Calfuco was different between days 5 and 14, and between days 10 and 14 of the experiment (P < 0.001 for both comparisons). Furthermore, there was a significant effect of the interaction time × temperature (Table 4b).

Loss of distal blade tissue: This parameter strongly varied among the three locations (Fig. 7, Table 4c).

TABLE 4. Results from the statistical analysis of (a) biomass change, (b) blade elongation rate, and (c) distal blade tissue loss, for each experimental site using repeated-measures analysis of variance (ANOVA), with the within-subject factor time, and the between-subject factors temperature (=temp: cool, ambient, warm) and Control (=C) and Grazing (=G). For Iquique, the warm temperature treatment was excluded from the analysis because algae died on day 5.

P-value
< 0.001
0.050
0.019
0.232
0.336
0.106
0.288
< 0.001
< 0.001
0.975
0.950
0.213
0.150
0.948
0.738
0.315
0.072
0.141
0.579
0.023
0.693

 $df_{GG}$  denotes that degrees of freedom were adjusted following the Greenhouse-Geisser *F*-test, if sphericity requirement were not met.

In Iquique, no significant differences were detected between temperature and grazing effects on the loss of distal blade tissue. In central Chile, a time effect on distal blade loss was detected (Table 4c), with differences between day 5 and day 14 of the experiment (P = 0.044). At this site, the losses were high in the three temperature treatments (maximal values close to 3 cm  $\cdot$  d<sup>-1</sup>). The lowest tissue losses occurred in Calfuco, where they were significantly dependent on the presence of grazers (Table 4c).

#### DISCUSSION

Our results indicate that floating kelp sporophytes can continue to grow at moderate and low seawater temperatures. High water temperatures prevailing in northern Chile caused significant biomass losses and rapid raft destruction. At moderate temperatures in central Chile, raft survival strongly depended on the presence of grazers; without grazers the algae increased their biomass, whereas in the presence of grazers algae substantially lost biomass. Algal floating potential was the highest under the cool conditions in southern Chile, where raft degradation was very low and biomass losses were compensated by algal growth. These results have important implications for the understanding of dispersal on floating macroalgae.

Survival and performance of floating Macrocystis along a natural temperature gradient. The utility of floating macroalgae as dispersal vehicles for associated fauna depends on their food value and in particular on their capacity to grow and resist sinking during rafting. Different growth responses of floating Macrocystis spp. due to changing seawater temperatures along a latitudinal gradient were clearly demonstrated in our study. At the northernmost location (Iquique), at temperatures exceeding 20°C, weight loss was accelerated and experimental algae survived only 5 d at the sea surface. Similar observations had been reported by North (1971) for benthic populations of Macrocystis pyrifera in southern California. This kelp grew poorly at temperatures above 20°C, and symptoms of temperature damage appeared



FIG. 6. Elongation rate  $(\text{cm} \cdot \text{d}^{-1})$  of apical blades of *Macrocystis* spp. at the three temperature treatments (cool, ambient, warm) and in the absence (control) and presence (grazing) of the amphipod grazer *Peramphithoe femorata*; symbols indicate that algae had died before the sampling and were not available for measurements. For each treatment combination (n = 4), three blades were marked to ensure that at least one marked blade was available at the survey day, and if >2 measurements were available, we calculated the mean for each replicate; figure shows grand mean  $\pm$  SD.

within less than a week once temperatures exceeded 24°C. In a transplant experiment by Hernández-Carmona et al. (2001), survival of juvenile sporophytes of *Macrocystis pyrifera* was poor at temperatures  $\sim 23^{\circ}$ C. Benthic sporophytes of *Macrocystis* normally start to die when frond deterioration exceeds frond growth and the biomass necessary to sustain meristems is lost (Graham et al. 2007). However, when biomass losses are low and without impact on basal blade portions, benthic individuals can sprout new fronds when temperatures become cooler (Hay 1990). Possibly, the same is true for floating algae when traveling from warmer into cooler water masses. In northern Chile, detached algae that are carried away from coastal kelp forests near upwelling sites probably suffer high temperatures when floating at the sea surface (e.g., Kaplan et al. 2003). Thus, in northern Chile, kelp forests can thrive at some nearshore sites, but survival of floating kelp rafts in open coastal waters with higher water temperatures is very limited.

High water temperatures provoked the highest biomass loss in Iquique. Similarly, results from preliminary experiments had shown that meristematic blades of *M. integrifolia* from central Chile kept at temperatures >20°C suffered high biomass losses (E. Rothäusler and M. Thiel, unpublished data), suggesting that algae from different latitudes may show similar responses to high water temperatures. In our experiments, algae from the three locations were not cultivated under identical temperature regimes, and thus we cannot be entirely sure how algae from



FIG. 7. Loss of distal blade tissue rate  $(\text{cm} \cdot \text{d}^{-1})$  of apical blades of *Macrocystis* spp. at the three temperature treatments (cool, ambient, warm) and in the absence (control) and presence (grazing) of the amphipod grazer *Peramphithoe femorata*; symbols indicate that algae had died before the sampling and were not available for measurements. For each treatment combination (n = 4), three blades were marked to ensure that at least one marked blade was available at the survey day, and if >2 measurements were available, we calculated the mean for each replicate; figure shows grand mean  $\pm$  SD.

southern Chile would have reacted to the high temperatures to which algae were exposed in northern Chile. However, if we assume that algae in southern Chile were adapted to relatively low water temperatures, it is highly likely that at high temperatures (>20°C) they would have responded similarly as or even degraded more rapidly than algae from northern Chile. We therefore consider that we can generalize algal responses across the overall temperature regimes studied herein.

At moderate (16°C–19°C) and low (12°C–15°C) water temperatures (central and southern Chile, respectively), the experimental algae continuously grew and survived until the end of the experiments. However, kelp growth was low at  $\sim 20^{\circ}$ C. Hobday (2000b) estimated that algal decomposition increases dramatically at temperatures >20°C. At all locations, the observed decrease in elongation rate with increasing detachment time might be attributed to thermal stress and possibly deleterious effects of higher irradiance at the sea surface as well as nutrient depletion in the surrounding water body (Jokiel 1980, Edgar 1987). However, during our experiments, nutrients were sufficiently available for algal growth, and thus we suggest that other factors, such as light and temperature, are responsible for the observed temporal decrease in algal growth.

Hay (1990) proposed *M. pyrifera* as a reliable biological indicator of sea-surface temperatures in

coastal waters of New Zealand, with populations being restricted to areas where the warmest monthly temperatures do not exceed 18°C. For other temperate algae, similar results about the negative influence of high water temperatures on algal growth and performance have been reported by several authors (Bolton and Lüning 1982, Breeman 1988, Lüning and Freshwater 1988, Matson and Edwards 2007), and others emphasized high survival of detached algae at low water temperatures (Ingólfsson 1998, Salovius and Bonsdorff 2004).

Impact of grazing. The effect of grazing from associated rafters on the survival of Macrocystis was site-specific, and in some cases, a strong interaction with temperature was detected. In the north, algal survival was not affected by the grazing activity of the amphipod P. femorata. Here the warm water temperatures were responsible for high biomass losses and subsequently for the disintegration and sinking of the experimental algae (at  $\sim 24^{\circ}$ C). Contrarily, in central Chile, at water temperatures between 13°C and 20°C, biomass of experimental algae decreased in the presence of amphipods, suggesting that sporophytes from this location are unable to survive such grazing attacks when experienced over a longer period. Other gammaridean amphipods, primarily Peramphithoe humeralis, have been described to cause considerable damage to large areas of benthic Macrocystis forests off San Diego, following a period of elevated sea-surface temperatures (Tegner and Dayton 1987). In coastal and oceanic waters, floating rafts provide important habitat for fish that might keep the local grazer stocks low (Dempster and Kingsford 2004). Herein, this effect (suppression of grazer populations by fish predators) was not considered, but probably can enhance raft survival at intermediate water temperatures.

At our coolest experimental location in southern Chile, the factor grazing had only minor impacts on kelp survival throughout the tested temperature range ( $12^{\circ}C-19^{\circ}C$ ); algae grew and survived well. Nevertheless, amphipod grazing at this site affected the distal blade tissue losses. Although *P. femorata* grazed the blades, biomass losses were very low and not harmful to the kelp. With rapid growth rates, benthic *Macrocystis* can escape and tolerate grazing by many of the smaller herbivores (Dayton 1985). Our results from the southern location indicated that floating *Macrocystis* spp. can compensate grazing by *P. femorata* through its high growth capacity.

Overall, at all experimental sites, holdfasts and stipes were not consumed by the amphipods probably due to their resistance to penetration (tissue toughness) (Littler et al. 1983). Similar results were detected by Macaya et al. (2005b), where authors revealed that stipes of *M. integrifolia* were structurally defended. Vegetative blades of *M. integrifolia* also showed low defensive responses against amphipod grazers (Rothäusler and Thiel 2006, Pansch et al. 2008) and thus were probably preferentially con-

sumed by *P. femorata* in the northern and central location. Sporophytes in Calfuco probably are able to compensate grazer-induced blade tissue losses due to high growth rates. In Iquique and Coquimbo, loss of reproductive blades, which are the precursors for sporophylls, was particularly pronounced in the grazing treatments. Stress due to high temperatures or changing light regimes might have led to a decrease in defense, which is high in reproductive blades of attached sporophytes (Pansch et al. 2008). No evidence was detected that sporophylls were preferentially consumed by the amphipods.

Rafting and reproductive capacity. After detachment from their primary substratum, sporophytes of Macrocystis spp. are able to maintain their reproductive structures and even release viable zoospores while floating (Macaya et al. 2005a, Hernández-Carmona et al. 2006). In the present study, Macrocystis spp. was able to maintain at least some sporophylls with viable spores during the 14 d period of the experiments at temperatures <20°C. However, in northern and central Chile, the experimental algae lost their sporophylls due to high water temperatures. These findings are in accord with Macaya et al. (2005a) who reported that floating Macrocystis rafts from northern Chile had no or few sporophylls. While sporophylls in algal rafts might be close to the sea surface, in attached sporophytes, the sporophylls are situated just above the holdfast apex, normally facing cooler temperatures and lower light conditions than vegetative blades at the surface (North 1994). In our experiments, we noticed that sporophylls were more delicate than other tissues and disintegrated first in response to thermal shock (personal observations). Therefore, high temperatures and light levels at the sea surface might be the main reason for sporophylls disappearing at water temperatures >20°C. This effect is probably more pronounced in sporophylls from deeper growing algae (>5 m) because they are even more acclimated to lower subsurface temperatures and light conditions.

In contrast to what was observed for the northern and central location, floating kelp rafts from the southernmost location maintained sporophylls at all temperatures tested. Nevertheless, presence of sporophylls decreased toward the end of the experiment. Sporophylls that persisted throughout the experimental period, however, were able to increase their percentage reproductive area allocation in comparison to the benthic natural sporophytes. In the south, water temperatures never exceeded the 20°C temperature limit, and it is known from benthic populations of M. pyrifera from southern Chile that reproductive performance is high at temperatures between 15°C and 18°C (Buschmann et al. 2004). Probably, for this reason, floating sporophytes were able to maintain some of their heat-sensitive sporophylls and could even increase their reproductive area.

In summary, the delicate sporophylls appear to suffer from high water temperatures and high solar irradiance, which was lethal to these tissues in northern and central Chile. Consequently, the dispersal of zoospores via floating rafts seems to be limited at low latitudes but is very likely at high latitudes (see also Macaya et al. 2005a).

Survival of algal rafts in temperature gradients and global implications. The observed latitudinal persistence of floating Macrocystis spp. along the Chilean coast strengthens the hypothesis that brown macroalgae traveling in cooler waters (mid- and high latitudes) have longer survival times and dispersal distances than macroalgae traveling in warmer waters (low latitudes) (Thiel and Gutow 2005a). At water temperatures >20°C (northern Chile), Macrocystis kelp rafts disintegrated at faster rates than algae kept at moderate and cool water temperatures (in central and southern Chile, respectively). Hobday (2000b) demonstrated for M. pyrifera floating in coastal waters of Southern California that loss of biomass increased dramatically when temperatures exceed 20°C. Conversely, he found that at water temperatures <20°C, rafts survived between 63 and 109 d.

Similarly, a study by Vandendriessche et al. (2007) revealed for two fucoid kelp species (*Ascophyllum nodosum* and *Fucus vesiculosus*), which frequently occur floating in the North Atlantic (Ingólfsson 1995, Muhlin et al. 2008), that raft survival is temperature and grazer dependent. At constant water temperatures ~18°C, both species sank within 100 d compared to algae kept at 5°C, which floated 211 d until the experiment was stopped (Vandendriessche et al. 2007). Survival of both *Macrocystis* spp. and *Ascophyllum/Fucus* rafts is significantly suppressed by the presence of amphipods and isopods, which consume the algae during their voyage.

Overall, temperate kelp species that float after detachment seem to be equipped for long distance dispersal, but their upper temperature thresholds for growth, and thus survival, appear to be in the range of  $15^{\circ}$ C– $20^{\circ}$ C. Temperate kelp rafts traveling at water temperatures > $20^{\circ}$ C dramatically lose biomass and consequently sink rapidly. Disintegration of floating algae at these temperatures is further accelerated by the presence of grazers, implying that these unfavorable conditions act as a barrier for kelp rafting. When traveling in waters < $15^{\circ}$ C, temperate kelp species have high survival times, indicating that at these temperatures passive dispersal of organisms rafting on floating kelps is more important than in warmer waters.

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