

Modulation of different kelp life stages by herbivory: compensatory growth versus population decimation

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Abstract Partitioning the effects of herbivory on different life stages of primary producers is key to understanding the population-wide consequences of herbivory. We assessed the performance of microscopic (MiS <1 mm) juveniles, macroscopic (MaS) juveniles and adult kelp (*Laminaria ochroleuca*) under contrasting herbivory regimes through a herbivore exclusion field experiment. The abundance of MiS and the survival of MaS decreased by 67 and 63%, respectively, when herbivorous fishes and sea urchins were present. Blade growth (linear and area) of adult kelp displayed contrasting patterns under herbivore pressure: a 60% increase and a 46% decrease, respectively. These results indicate that while herbivory severely reduces juvenile survival, it

may also induce compensatory growth (measured as linear growth) in adult kelp. In summary, we here demonstrate how herbivory affects all sporophyte life stages of the kelp *L. ochroleuca*. This is likely to have important implications for situations where historical patterns of herbivore presence and herbivory are changing, such as is increasingly the case in many temperate regions due to warming around the world.

Introduction

Plant–herbivore interactions play a critical role in the dynamics of populations and assemblages across different habitats (Burkepile 2013) and productivity gradients (Proulx and Mazumder 1998). Green food webs, where herbivore–plant interactions play a significant role in energy transfer, are ubiquitous (e.g. Gaines and Lubchenco 1982; Duffy and Hay 2000; Moles et al. 2011) and the strength of such interactions shapes the patterns of distribution and abundance of many species involved (Maron and Crone

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2006). Consequently, changes in the direction, frequency and intensity of herbivory can ultimately lead to substantial shifts in the structure of whole ecosystems (Pace et al. 1999; Bruno and O'Connor 2005; Vergés et al. 2014; Hanley and La Pierre 2015). This is of particular concern since ongoing global pressures, including climate change and over-fishing, may impair biotic interactions through direct effects on both primary producers (e.g. reducing net productivity and/or diversity) and herbivores (e.g. changing abundance, behaviour and/or diversity).

In producer-based food webs, understanding plant–herbivore interactions is a challenging requirement for addressing a number of relevant questions, from predicting ecological dynamics to managing ecosystems under natural and anthropogenic pressures. In this context, it is important to understand the impact of herbivory over the full lifecycle of marine plants (Russell et al. 2012), which can be exposed to different levels of herbivory as they develop through different life stages. As a result, the impact of herbivores on plant resistance traits can vary with plant ontogeny, promoting changes in the amount and type of resistance traits during the development of the plant to minimize the impacts of herbivory (Boege and Marquis 2005). These changes can also be shaped by demographic priorities such as establishment, growth or reproduction of the individuals (Boege and Marquis 2005). Intraspecific variation in resistance to herbivory, including the different life stages of primary producers, should be tackled as an important element of plant–herbivore interactions. However, a vast majority of studies currently focus on effects on a single species and at a single ontogenetic stage; very few studies examine effects on multiple life stages of habitat-forming species, leading to population-level extrapolations that might be misleading or incomplete (Boege and Marquis 2005; Vergés et al. 2008).

Kelp are foundation species (Dayton 1972) in many near-shore temperate areas, where there is wide evidence that their patterns of abundance, distribution and functioning may be critically shaped by herbivores (Franco et al. 2015; Vergés et al. 2016; Zarco-Perello et al. 2017). Kelp possess natural defences against herbivores through a range of mechanisms, e.g. physiological adaptation, physical and associative traits, chemical defence and compensatory growth (Targett and Coen 1992; Gagnon et al. 2003; Cerda et al. 2009; Biskup et al. 2014). However, ‘extreme’ changes in herbivory levels may compromise the resilience of whole communities supported by these seaweeds (Steneck et al. 2002; Bennett et al. 2015; Vergés et al. 2016). Notable examples of this include the effects of sea-urchins which, through their intense grazing activity, may lead to the eradication of erect algae and their replacement with ‘barren’ areas (Ling et al. 2010; Filbee-Dexter and Scheibling 2014). Negative effects of herbivory on kelp are also reported for tropical fishes currently expanding into temperate regions (Vergés

et al. 2014, 2016; Bennett et al. 2015; Zarco-Perello et al. 2017).

Declines in abundance and induced herbivore- and/or temperature-driven phase shifts of kelp at regional or local scales have been extensively documented (Ling et al. 2014; Filbee-Dexter et al. 2016; Wernberg et al. 2016). In Europe, the causes for changes in kelp abundance are generally reported as being species-dependent and regionally variable (Araújo et al. 2016). For example, declines in northern and central Europe have mainly been attributed to human overharvesting of kelp and/or overgrazing by sea urchins (Sivertsen 2006; Raybaud et al. 2013). In southern Europe, increasing ocean temperature is a likely driver of declining kelp forests (Fernandez 2011; Voerman et al. 2013; Assis et al. 2016). In this context, Franco et al. (2015) recently reported that kelp from warmer, southern, locations along the Portuguese coast are exposed to more intense herbivory pressure than kelp from colder, northern, locations, suggesting indirect effects of temperature through herbivory could also play a key role in southern Europe.

The Portuguese coast spans more than 800 kilometres and is recognized as an important transitional zone between northeastern Atlantic warm-temperate and cold-temperate species, which makes this coast an area of great sensitivity to the effects of climate change (Tuya et al. 2012; Teixeira et al. 2014). A large number of cold- and warm-water species have their southern, or northern, distributional range edges along the west coast of the Iberian Peninsula. These include the cool-water kelp *Laminaria hyperborea* and *Saccharina latissima* (Lima et al. 2007). The number of records of fish and algal species with sub-tropical affinities extending northwards, relative to their usual distributional range, or increasing in abundance, have become more frequent in the past decade (Lima et al. 2007; Bañón and Mucientes 2009; Rodrigues et al. 2012; Piñeiro-Corbeira et al. 2016).

The present study aimed at examining the influence of herbivory on the ‘golden kelp’, *Laminaria ochroleuca*, in central Portugal. This warm-water species is currently expanding its distributional range northwards, locally competing with native *L. hyperborea* (Smale et al. 2015). We excluded macro-herbivores (fishes and sea urchins) from experimental plots and, subsequently, estimated the abundance, survival and growth of *L. ochroleuca* compared to control plots under herbivory. The responses of *L. ochroleuca* were examined for different development stages, including the abundance of microscopic (<1 mm) juveniles, the survival of macroscopic (between 3.5 and 4.5 cm, lamina length) juveniles and the growth of adult (>25 cm, lamina length) individuals. This allowed partitioning the effects of herbivory on three life stages of a kelp. Specifically, we have tested the hypothesis that herbivory would exert a negative impact on *L. ochroleuca* at different life stages, but that such an effect could be, at least in part, counteracted

by compensatory growth of adult individuals. Moreover, the experiment was replicated at each of two randomly selected sites (~6 km apart, at 5–7 m depth) representative of the region and characterized by similar rocky substrate and topography. This allowed to test whether the examined responses to experimental treatments were generalizable across the region, a relevant issue given the likely between-sites variation in uncontrolled potentially relevant factors such as the abundance of herbivores in the system (Franco et al. 2015).

Materials and methods

Study region and abiotic characterization

The study was carried out at Peniche, central Portugal (39.2°N, 9.2°W). This is considered a warm-temperate region along the Portuguese western coast (Tuya et al. 2012), with recent evidence of intense herbivore pressure on kelp (Franco et al. 2015). Macroalgal assemblages in the study region include perennial kelp species, which were once abundant and now show a sparse distribution, such as *L. ochroleuca*, or annual species, such as *Phyllariopsis* sp. (Assis et al. 2009; Tuya et al. 2012; Pinho et al. 2015). For abiotic characterization of the study area a set of data loggers was deployed throughout the course of the experiment to measure sea water temperature (°C) and illuminance (Lux) (HOBO data-loggers Pendant Temp-Light, Onset Computer Corporation), and water movement (m s^{-2}) using gravitational data loggers (HOBO Pendant G, Onset Computer Corporation), following (Figurski et al. 2011). The loggers were set to record the temperature and illuminance at 15 min intervals, and acceleration at 6 min intervals. For light, loggers were cleaned on a weekly basis to avoid fouling that would interfere with measurements. Mean levels of illuminance between 08:00 and 17:00 ($n = 1878$ measurements) were extracted. For water movement (WM), all values ($n = 26,160$ measurements) were extracted. Water samples were collected, at six occasions (two randomly dates within every 30 days), water samples ($n = 4$), approximately 1 m above the bottom, and immediately filtered and stored on ice until return to land. Samples were then frozen ($-20\text{ }^{\circ}\text{C}$) until chemical analysis for NO_3 and PO_4 , which was performed through a colorimetric auto-analyzer (Skalar® SAN Plus Segmented Flow Analyser).

Macro-herbivore abundance in the study region

Macro-herbivore abundances were visually assessed in July 2014 and July 2015 at five rocky reefs chosen at random within the study region. On each reef, all adult and sub-adult fishes were counted along five, randomly oriented, 25×4 m

belt transects (Tuya et al. 2012). Fishes were categorized according to their trophic affinities (according to Henriques et al. 2013; fishbase.org). Herbivorous fishes were considered as those able to consume algae, thus also including omnivorous species (Franco et al. 2015). The number of *Paracentrotus lividus*, the most common sea-urchin in continental Portugal (Jacinto et al. 2013), was counted along five 25×2 m transects.

Experimental design

A caging experiment was set up to assess the effect of the exclusion of macro-herbivores on the survival and growth of *L. ochroleuca* at two sites within the study region. At each site, steel cages ($50 \times 50 \times 50$ cm) were attached to the bottom through stainless steel eyebolts (Fig. S1). At each site, six cages were randomly allocated to each of three experimental conditions, for a total of 36 cages: exclusion of macro-herbivores (full cage: F), procedural control (partial cage with a roof and two half-sides, thus allowing access to herbivores: P), and unmanipulated control (50×50 cm plots just marked at corners with eyebolts: C). The cages (plots) were covered by polyethylene net (2 cm mesh size). Cages were randomly assigned to plots to ensure any small-scale effects of illuminance and water movement did not confound herbivore exclusion. Moreover, both illuminance (HOBO data-loggers Pendant Temp-Light, Onset Computer Corporation) and water movement (HOBO Pendant G, Onset Computer Corporation) were compared between a randomly chosen experimental replicate allocated to the F, P and C treatments. Measurements of illuminance and water movement across all treatments showed no cage artefacts (Fig. S2a, S2b, S3a, S3b, methodological details and data in supplementary).

Set-up and sampling of *L. ochroleuca* abundance, survival and growth

Three different life stages of *L. ochroleuca* were placed in each experimental plot ($n = 6$, Fig. S1): (a) two adult individuals (total length >25 cm), fastened by the holdfast to a 16×4 cm PVC tile using a rubber-protected cable tie that allowed the natural movement of each kelp; (b) four epoxy surface discs (total disk area = 2460 mm^2) screwed to a PVC tile with microscopic (<1 mm) sporophytes (MiS) (440 ± 50 , mean \pm SE, $n = 144$ discs); (c) 10 macroscopic (lamina length between 3.5 and 4.5 cm) juvenile sporophytes (MaS) distributed on a 15-cm long cotton rope attached to a PVC tile.

All adult individuals were collected at Mindelo (41.1°N, 8.74°W) and individually tagged with a numbered cable tie around the stipe. The blade area of each individual was measured, before the start of the experiment, by taking a

picture over a blank scaled surface where the blade was stretched by an acrylic transparent board. The same procedure was repeated at the end of the experiment. Using Image J (Muth 2012), the contrast analyses (before vs. after) of kelp laminae provided, for each individual, the growth during the course of the experiment. The linear growth of adult *L. ochroleuca* was estimated using the hole-punch method (Parke 1948). At the deployment day, two holes were punched in the centre of the lamina, at 2 and 4 cm above the main meristem at the junction between the stipe and the main blade. Thallus extension was assessed in situ every month after deployment (July, August and September 2014) by measuring the distance between the two holes and the meristem and subtracting the initial 4-cm distance. The total linear growth was calculated as the sum of all months.

Four weeks before the experiment started, gametophytes of *L. ochroleuca* from adults collected at Mindelo were cultivated in the laboratory (adapted from guidelines described in Pereira et al. 2011). The gametophyte solution resulting from the cultivation was then left in contact with sterile epoxy discs to allow them to become homogenized, fix to the disk and develop into MiS. The individuals growing on the seeded discs were counted in situ at the end of the experiment. It is worth noting that an observed reduction in the number of MiS between the beginning and the end of the experiment could have been due, in principle, by other (than herbivory) factors, including for instance environmental conditions, characterizing the experimental units. However, our experimental setting was such as the most obvious, potentially relevant uncontrolled factors (e.g. water movement, light) were likely to analogously affect all experimental units. Therefore, the relative effects of treatments ascribed to herbivory could be quantified in an unconfounded way. The same procedure was performed to obtain MaS, but cultivation started earlier to allow the growth until the desired size; a cotton rope was used instead of epoxy discs. The numbers of living individuals were counted in situ at the end of the experiment. All the biological material was kept in an aerated 500 L outdoor tank at 15 °C until deployment. The experiment ran from 14 June to 30 September 2014, including weekly visits for cleaning, maintaining and opening cages when needed for measurements.

Statistical analyses

The abundance of herbivorous fishes and the sea-urchin *P. lividus* was analysed by 2-way ANOVA, including year (2 levels, random) and Reef (5 levels, random and nested in years). The total linear growth, the total blade area growth, the abundance of MiS and the survival of MaS, at the end of the experiment, were analysed by 2-way ANOVA, including the crossed factors 'Site' (2 levels, random) and 'Herbivore exclusion' (3 levels: F, P and C, fixed). The same model was

used to analyse differences in the linear growth of *L. ochroleuca* separately for each of three sampling times. Before each ANOVA, the assumption of homogeneity of variances was checked with Cochran's *C* test. The percentage of survival of MaS was Arcsin transformed to achieve homogeneous variances. When relevant, post hoc comparisons of significant means were carried out with Student–Newman–Keuls (SNK) tests.

Results

Abiotic characterization and abundance of macro-herbivores

During the experiment (July to September 2014), the water temperature ranged between 14.4 and 21.5 °C (Fig. 1a), the mean illuminance at the bottom between 1296 and 13,395 Lux (Fig. 1b) and the water movement between 0.16 and 1.82 m s⁻² (Fig. 1c). The concentration of nitrate varied from 1.82 to 1.38 μmol L⁻¹, while that of phosphate between 1.69 and 1.80 μmol L⁻¹, respectively (Fig. 1d).

Abundance of herbivorous fishes was not different between reefs or among surveys (Table 1; Fig. 2a), while abundance of sea urchins varied significantly between reefs but not among surveys (Table 1; Fig. 2b). Macro-herbivores, including omnivorous species able to consume algae, were dominated by four fish species: *Sarpa salpa*, *Oblada melanura*, *Diplodus vulgaris* and *Diplodus sargus* (out of 13 recorded fish species; Table S1 in the supplementary material) and one sea urchin, *P. lividus* (Fig. 2b).

Abundance of MiS and survival of MaS

The abundance of MiS was, on average, 60 and 73% times greater within full cages compared to procedural and the unmanipulated controls (Table 1; Fig. 3a), respectively. The survival of MaS was, on average, 68 and 72% higher where herbivores were excluded relative to procedural and unmanipulated controls, respectively (Table 1; Fig. 3b).

Blade area and linear growth

Total blade area growth in the herbivory-excluded treatment was larger compared to both procedural and unmanipulated controls, with, respectively, an increase by 101.7 ± 26.2% and a decrease by 32.5 ± 9.3% and 58.5 ± 8.7% relative to the initial blade area (Table 1; Fig. 4). Conversely, the total linear growth, at the end of the experiment, was significantly reduced within full cages compared to procedural and unmanipulated controls (59.6 ± 1.2 and 60.7 ± 1.1%, respectively, Table 1; Fig. 4). The mean monthly linear growth was, across the three measured times, also significantly reduced

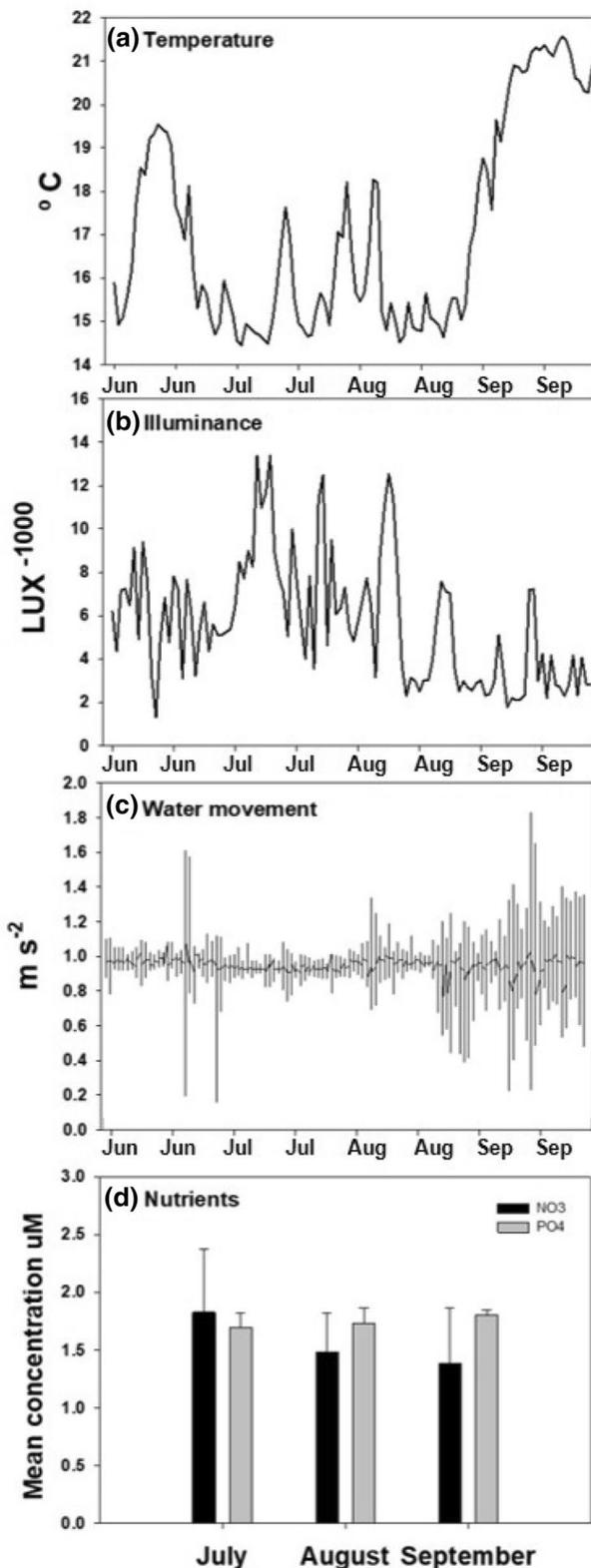


Fig. 1 Abiotic characterization of the study region. **a** Temperature daily mean values, **b** mean illuminance between 8:00 and 17:00 h, **c** water movement every 6 min, during the experimental period, and **d** mean nutrient concentration at three random times through the course of the experiment

within full cages compared to procedural and unmanipulated controls (60.3 ± 1.1 and $61.0 \pm 1.6\%$, respectively, Table 1; Fig. 5).

Discussion

Our findings indicate that the survival of both microscopic and macroscopic juveniles and the lamina extension of adult *L. ochroleuca* were considerably increased when released from grazing by sea urchins and fishes. This agrees, in general, with a previous study indicating that intense herbivory could contribute to limit kelp distribution and abundance in southern Europe (Franco et al. 2015).

Herbivory is often selective and its effects may vary depending on life-stages of both algae and grazers. Herbivores might change preference for specific life stages over the life cycle of the algae and a species representing a preferred food for juvenile herbivores is not necessarily a preferred food for adults. Differences between juvenile and adult algae in a number of physical and chemical properties, including texture, deterrent compounds and nitrogen concentration, are major causes affecting herbivore preference (Van Alstyne et al. 1999). Even though we were not able to quantify the variation of herbivory among different kelp life stages, our study indicated a considerable impact of herbivory on each of the studied life-stages of *L. ochroleuca*, as suggested by previous research involving other kelp species (e.g. Van Alstyne et al. 2001). Herbivorous sea urchins and fishes may reduce the population-level biomass of *L. ochroleuca* through both the consumption of blades of adult individuals and the elimination of small-sized sporophytes. Such biological disturbance is likely to compromise the future of this habitat-forming species which, once apparently abundant and widespread across Portugal, is already sparse in central and southern Portugal (Assis et al. 2009; Tuya et al. 2012; Pinho et al. 2015). It has been reported that damage induced by herbivorous fishes and sea urchins on adult kelp may lead to a critical reduction in their physiological performance and/or extent of reproductive tissue, which can ultimately cause death (Davenport and Anderson 2007). In extreme situations, overgrazing can provoke the collapse of entire kelp forests (Filbee-Dexter and Scheibling 2014; Ling et al. 2014; Vergés et al. 2016). At the same time, the consumption of kelp recruits can prevent the establishment of new adult populations (or recovery of old populations lost to other processes, (Bennett et al. 2015)), although such an adverse effect can be mitigated by the occurrence of natural refuges, e.g. crevices in the substratum, providing protection to juvenile kelp (Franco et al. 2015). Moreover, the effects of large herbivores can be further exacerbated by mesoherbivores, such as gastropods, amphipods and isopods, which were not examined in this study. In some cases, it

Table 1 Results of ANOVAs on the abundance of herbivorous fishes and sea urchins according to years (2014 vs. 2015) and reefs, and on effect of exclusion of herbivores at two reef sites on the abundance of microscopic sporophytes (MiS), the survival of macroscopic sporophytes (MaS), the total blade area growth, the total linear growth and the monthly linear growth of *Laminaria ochroleuca*

	Transformation	Cochran's test	df	MS	F	P
Abundance of grazing fishes	None	$C = 0.119$ (Ns)				
Year			1	69.62	0.55	0.479
Reef (year)			8	126.22	0.76	0.639
Residual			40	165.90		
Abundance of sea-urchin	$\ln(X + 1)$	$C = 0.291$ (Ns)				
Year			1	11.4317	0.85	0.3832
Reef (year)			8	13.4276	11.11	<0.001
Residual			40	1.2091		
Abundance of MiS	None	$C = 0.330$ (Ns)				
Site			1	2500.00	1.45	0.238
Cage treatment			2	56,319.44	38.62	0.025
Site \times cage treatment			2	1458.33	0.85	0.439
Residual			30	1722.22		
Survival of MaS	ArcSin %	$C = 0.302$ (Ns)				
Site			1	51.32	3.15	0.0861
Cage treatment			2	494.16	70.7	0.013
Site \times cage treatment			2	6.99	0.43	0.655
Residual			30	16.29		
Total blade area growth	None	$C = 0.413$ ($P < 0.01$)				
Site			1	7545.04	0.17	0.680
Cage treatment			2	1,540,214.40	112.28	0.009
Site \times cage treatment			2	13,717.62	0.31	0.733
Residual			66	43,957.98		
Total linear growth	None	$C = 0.2193$ (Ns)				
Site			1	690.68	2.11	0.152
Cage treatment			2	239,936.10	752.12	0.001
Site \times cage treatment			2	319.01	0.97	0.384
Residual			66	328.02		
July: linear growth	None	$C = 0.214$ (Ns)				
Site			1	2	0.01	0.9275
Cage treatment			2	68,065.71	83.34	0.011
Site \times cage treatment			2	816.69	3.41	0.0389
Residual			66	239.42		
August: linear growth	None	$C = 0.286$ (Ns)				
Site			1	288	3.93	0.5165
Cage treatment			2	51,411.88	455.2	0.002
Site \times cage treatment			2	112.94	1.54	0.2217
Residual			66	73.27		
September: linear growth	None	$C = 0.283$ (Ns)				
Site			1	34.72	0.73	0.3968
Cage treatment			2	43,874.06	12,523	<0.001
Site \times cage treatment			2	3.5	0.07	0.9293
Residual			66	47.73		

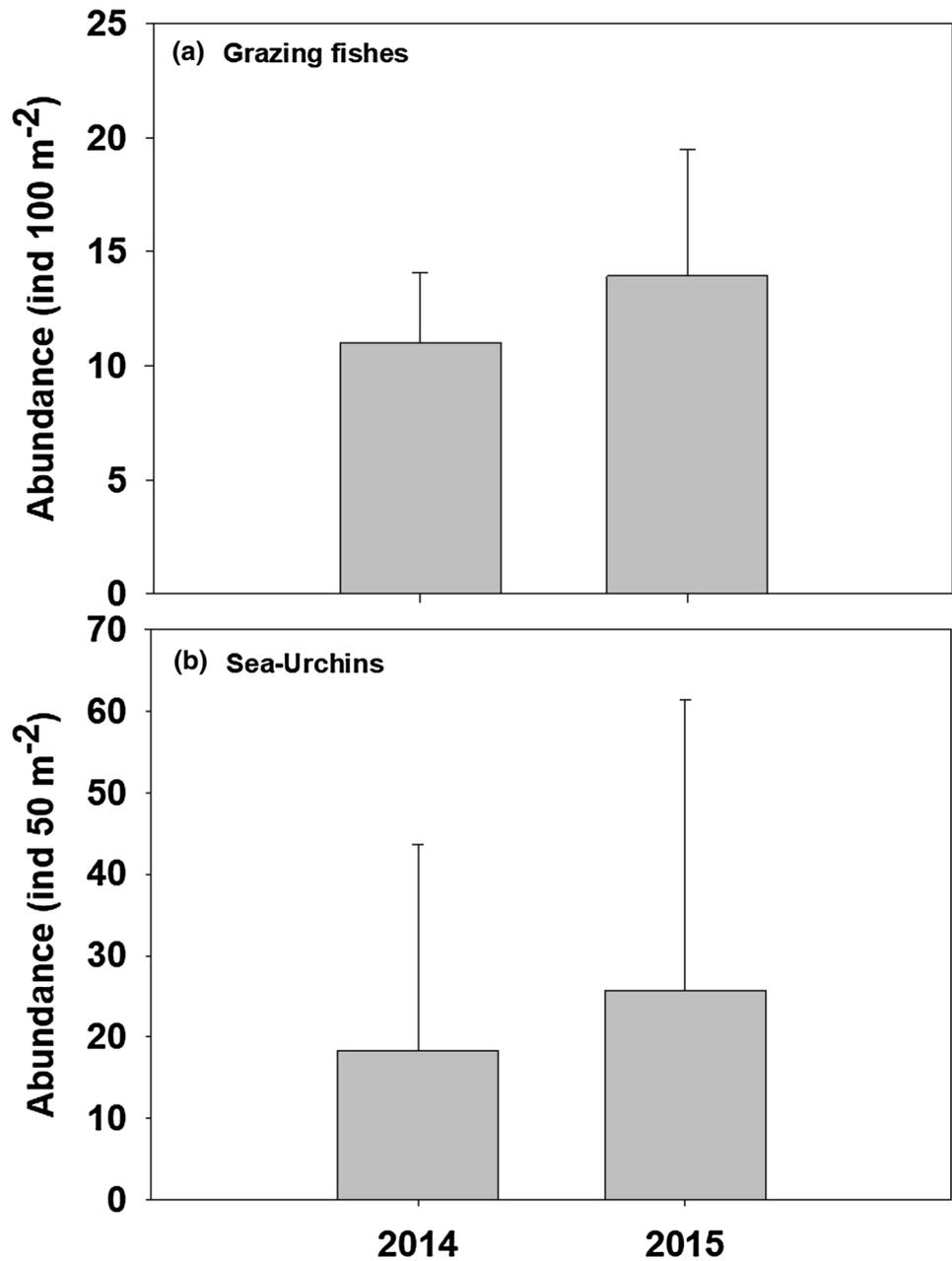
Bold values indicate $P < 0.05$

has been shown that mesoherbivores may disproportionately compromise the individual fitness and the structure of whole populations of kelp (Poore et al. 2014).

The evidence for strong kelp–herbivore interactions is especially relevant in transition zones such as the study

region in Portugal, where temperature increments can have profound implications for local marine communities (Lima et al. 2007), analogously to other geographic areas (Wernberg et al. 2016). Warming temperatures can strengthen plant–herbivore interactions (O'Connor 2009), particularly

Fig. 2 **a** Abundance of grazing fishes and **b** sea urchins in 2014 and 2015 (mean + SE, $n = 5$)



at the tropical-temperate boundary (Vergés et al. 2014; Zarco-Perello et al. 2017). For example, a complete shift from a temperate kelp forest to a system dominated by tropical and sub-tropical species was described in western Australia following a marine heat-wave (Wernberg et al. 2016). Sea-water temperature has recently been indicated as an important driver of changes in patterns of distribution and growth of *L. ochroleuca* (Franco et al. 2017). In addition, climate-driven range expansions of herbivorous fishes, and increasing abundance of already locally occurring herbivores, have been reported along the Portuguese coast (Franco et al. 2015)). However, since sea-water

temperature was within the optimal range (<20 °C, see Franco et al. 2017) throughout the experiment, present responses could be reasonably ascribed mainly to grazing effects, although potentially interacting with other biotic and abiotic processes.

Kelp have natural responses against herbivores, including physical and/or chemical defences (reviewed by Bartsch et al. 2008). Compensatory growth is considered an alternative strategy, which has been widely reported for terrestrial plants, but only in a few cases demonstrated for macroalgae (Hay et al. 2011), including kelp (Cerda et al. 2009; Gao et al. 2013). In this experiment, adult kelp exposed to herbivores

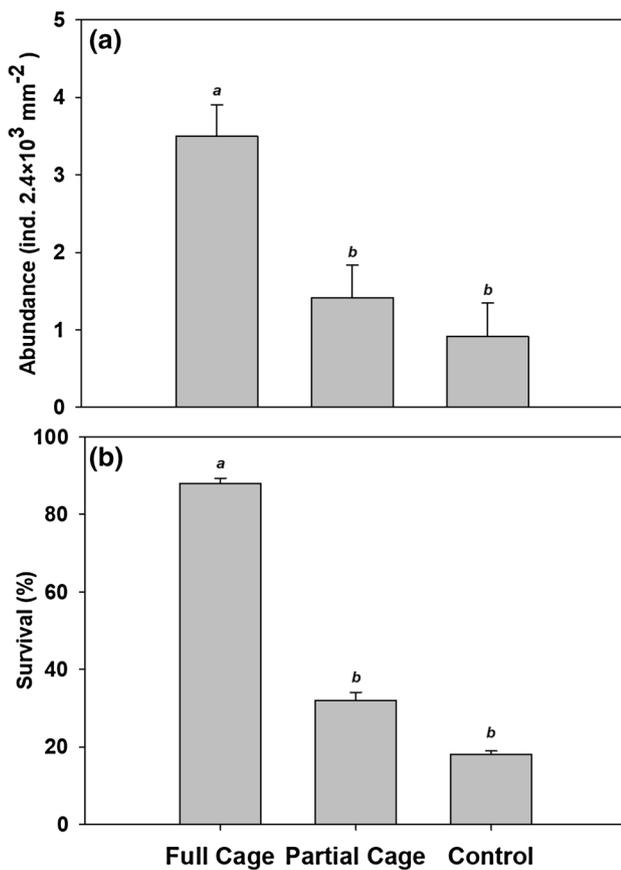


Fig. 3 **a** Abundance of microscopic sporophytes and **b** survival of macroscopic sporophytes (mean + SE, $n = 6$ and $n = 6$, respectively) for each experimental treatment at the end of the study. Different letters above bars indicate significantly different means according to SNK test

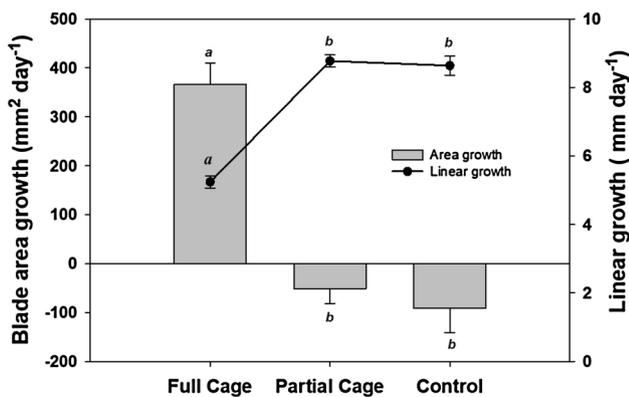


Fig. 4 Total blade area and linear growth of adult sporophytes (mean + SE, $n = 6$) for each experimental treatment at the end of the study. Different letters above/below bars and dots indicate significantly different means according to SNK test

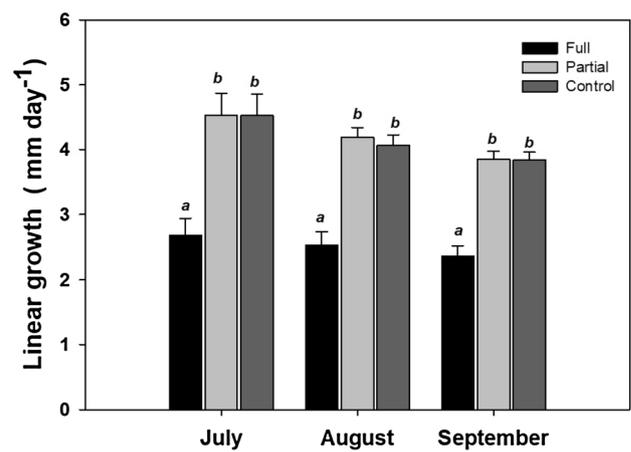


Fig. 5 Monthly linear growth of adult sporophytes (mean + SE, $n = 6$) for each experimental treatment. For each month, different letters above bars indicate significantly different means according to SNK test

displayed higher elongation rates of the meristematic tissue (i.e. linear growth). To our knowledge, this ability has never been shown for *L. ochroleuca* and, as far as we are aware, was previously described only for two other kelp species, *Macrocystis pyrifera* (Cerde et al. 2009) and *Undaria pinnatifida* (Gao et al. 2013). The development of reproductive structures (sori) in *L. ochroleuca* occurs through the transition from the vegetative to the reproductive stage (Bartsch et al. 2008) and this mechanism may allow to compensate the loss of blade tissue. The same was reported for *Lessonia nigrescens*, a kelp species with similar reproductive structures as *L. ochroleuca* (Pansch et al. 2008). However, the effectiveness of this compensation mechanism may vary through the year. Gao et al. (2013) demonstrated increased growth of *U. pinnatifida*, compensating artificial excision during the growing season, but not during the maturation season encompassed within the annual life cycle. In this experiment, *L. ochroleuca* showed a reduction of linear growth over the experimental period, which started in June and finished in September, corresponding to its growing and early maturation season, respectively. It is worth noting that our experimental procedures could only control for the exclusion of herbivory, but not for its intensity. Therefore, it cannot be excluded that, analogously to other Laminariales, *L. ochroleuca* is unable to compensate extreme losses of blade biomass at very high herbivory pressure (Cerde et al. 2009).

In conclusion, the present study showed compensatory growth of adult *L. ochroleuca* in response to herbivory. However, this ability was counterbalanced by negative effects on juvenile kelp, including their micro and macroscopic phases.

Negative effects of simultaneous herbivory pressure at different life stages are likely expected to be more evident in sparse kelp populations and/or in regions where patterns of herbivory are more prone to change (e.g. central Portugal). In conjunction with environmental perturbations, such as changes in seawater temperature, this herbivore pressure might contribute to the loss of these important habitat formers and, consequently, the loss of associated ecological and economic goods and services.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Ethical approval This article does not contain any studies with animals performed by any of the authors.

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