



Nutrient enrichment stimulates herbivory and alters epibiont assemblages at the edge but not inside subtidal macroalgal forests

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Abstract

Nutrient enrichment is a major threat to subtidal macroalgal forests. Several studies have shown that nutrient inputs can enhance the ability of opportunistic algal species to acquire space freed by disturbance, at the expense of architecturally complex species that form forests. However, competition between canopy- and turf-forming macroalgae is not limited to the aftermath of disturbance. Canopy-forming macroalgae can provide suitable substratum for diverse epibiont assemblages, including both algae (epiphytes) and sessile invertebrates (epizoans). Despite evidence of enhanced epiphyte loading under eutrophic conditions, few experimental studies have assessed how nutrient enrichment influences the structure of epibiont assemblages on canopy-forming macroalgae at the edge versus inside forests. In oligotrophic waters of the NW Mediterranean, we experimentally tested the hypothesis that nutrient-driven proliferation of opportunistic epiphytic algae would affect the performance of the furoid, *Carpodesmia brachycarpa*, and reduce the richness and abundance of the epizoan species they support. We predicted negative effects of nutrient enrichment to be greater at the edge than inside forests and on thalli that had recovered in cleared areas than on those within undisturbed canopy stands. Nutrient enrichment did not affect the photosynthetic efficiency and reproductive output of *C. brachycarpa*. By contrast, it enhanced herbivore consumption and decreased the cover and diversity of epizoans at forest edges, likely by stimulating the foraging activity of *Arbacia lixula*, the most abundant sea urchin in adjacent encrusting coralline barrens. Fertilization of areas inside forests had no effect on either *C. brachycarpa* or epibiont assemblages. Finally, nutrient enrichment effects did not vary between cleared and undisturbed areas. Our results show that moderate nutrient enrichment of oligotrophic waters does not necessarily cause the proliferation of epiphytes and, hence, a strengthening of their competitive effects on canopy-forming macroalgae. Nevertheless, enhanced herbivory damage to fertilized thalli at forest edges suggests that fragmentation could reduce the resilience of macroalgal forests and associated epibiont assemblages to nutrient enrichment.

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Introduction

Coastal environments are under siege from human stressors (Halpern et al. 2008; Hoegh-Guldberg and Bruno 2010). Loss of foundation species (i.e. species that form or modify habitat) is of particular concern due to their key role in sustaining biodiversity and ecosystem functioning (Angelini et al. 2011; O'Leary et al. 2017; Gribben et al. 2019). Along temperate coasts worldwide, brown canopy-forming macroalgae, either Furoids or Laminariales, are being progressively replaced by less complex, turf-forming species, impairing the functioning of shallow rocky reefs (Kautsky et al. 1986; Vogt and Schramm 1991; Bulleri and Benedetti-Cecchi 2006; Airoldi and Beck 2007; Gorman et al. 2009; Crowe et al. 2013; Strain et al. 2014; Krumhansl et al. 2016; Filbee-Dexter and Wernberg 2018).

Although there is substantial consensus over this state transition to be the result of cumulative effects of regional and global stressors (Estes and Palmisano 1974; Benedetti-Cecchi et al. 2001; Gorgula and Connell 2004; Airoidi and Beck 2007; Gorman et al. 2009; Smale and Wernberg 2013; Verges et al. 2014; Alestra and Schiel 2015; Ling et al. 2015; Wernberg et al. 2016; Bulleri et al. 2017), enhanced nutrient loading has been long identified among the primary drivers of macroalgal forest loss (Ballesteros et al. 1998; Benedetti-Cecchi et al. 2001; Gorgula and Connell 2004; Mangialajo et al. 2008; Gorman et al. 2009). Nonetheless, most of the evidence for nutrient-driven decline of macroalgal forests has been generated from eutrophic basins (e.g. the Skagerrak: Moy and Christie 2012; the Baltic Sea: Kautsky et al. 1986; Vogt and Schramm 1991; Havelange et al. 1997; Bergström et al. 2003; da Gama et al. 2008; the Adriatic Sea: Iveša et al. 2016; Strain et al. 2015), agricultural or urban catchments (Coleman et al. 2008; Mangialajo et al. 2008; Gorman et al. 2009) and, hence, it is not representative of temperate coasts characterized by lower nutrient status (Menge et al. 1999; Bulleri et al. 2012; Clausing et al. 2020).

In non-eutrophic basins, there is limited evidence for direct negative effects of moderate nutrient enrichment on canopy-forming macroalgae (Creed et al. 1997; Bokn et al. 2003; Steen and Ruess 2004; Steen and Scrosati 2004; Alestra and Schiel 2015; Chu et al. 2019; Tamburello et al.

2019). Brown macroalgae can, in fact, face seasonal nutrient limitation and benefit from nutrient inputs, especially when occurring as pulses (Schaffelke and Klumpp 1998) (Fig. 1). Increased nutritional value of plant tissue (i.e. lower C/N ratio) under elevated nutrient levels can stimulate canopy consumption by herbivores (Fig. 1) and, indeed, alter their behavior and foster their growth and reproduction (Hemmi and Jormalainen 2002, 2004; Kraufvelin et al. 2006; Valentine and Duffy 2006; Balata et al. 2010; Ghedini et al. 2015; Tuya et al. 2015; Ravaglioli et al. 2018). On the other hand, use of internal N stores, along with efficient external uptake, can provide a competitive advantage to complex macroalgae, such as Laminariales and Fucales, over ephemeral algal species (Pedersen and Borum 1997; Falkenberg et al. 2013; Kriegisch et al. 2019; Tamburello et al. 2019).

Several experimental studies have assessed the effects of nutrient enrichment on the ability of canopy-forming versus opportunistic species (either turfs or non-natives) to acquire space in the aftermath of disturbance (Gorgula and Connell 2004; Kraufvelin et al. 2010; Bulleri et al. 2012; Alestra and Schiel 2014; Carnell and Keough 2014; Piazzini and Ceccherelli 2017; Tamburello et al. 2019). By contrast, few studies (Russell et al. 2005; Werner et al. 2016) have experimentally investigated the effects of elevated nutrient levels on the interaction between canopy-formers and epibionts and these have exclusively focused on established

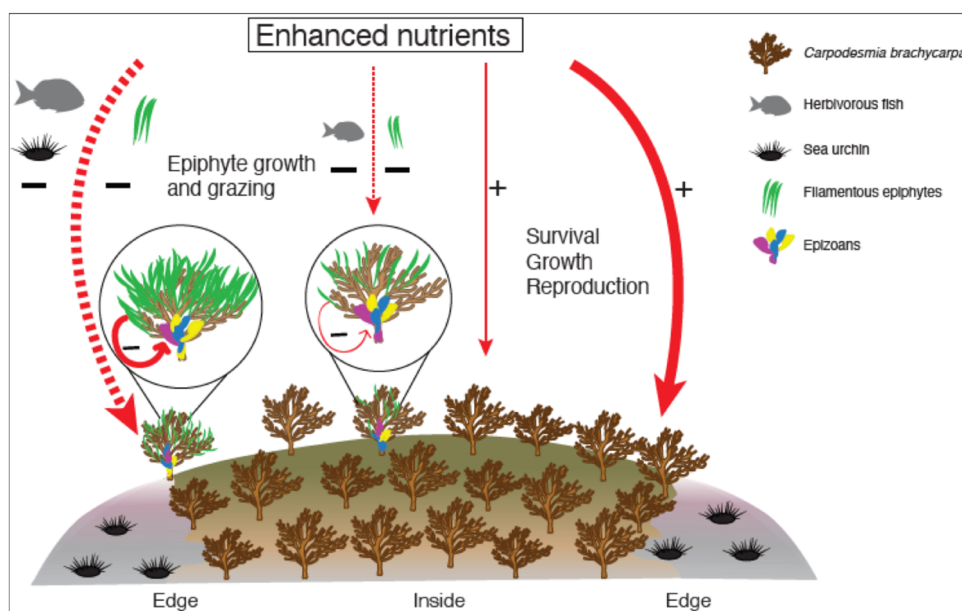


Fig. 1 Schematic representation of main direct (solid lines) and indirect (dashed lines) effects of enhanced nutrient levels on subtidal macroalgal forests formed by *Carpodesmia brachycarpa*. In oligotrophic waters, moderate inputs of nutrients can directly enhance the survival, growth and reproduction of brown seaweeds by alleviating resource limitation. Increased nutritional value of macroalgal tissues under nutrient enrichment can negatively influence canopy-forming

macroalgae by stimulating herbivore consumption by fish and, at the edge with barrens, by sea urchins. Nutrients can also promote epiphyte proliferation, increasing their competitive pressure on both *C. brachycarpa* and epizoans. Since greater water motion could foster nutrient uptake, direct and indirect effects of enrichment are expected to be greater at the edge than inside macroalgal forests. The size of lines represents the intensity of the effects

canopy stands made of adult thalli. Thus, we know little of the structure of epibiont assemblages on canopy-forming macroalgae that have recruited and grown in disturbed areas, under enriched conditions.

In addition, most studies have focused on epiphytes, despite macroalgal canopies provide suitable substrata also for diverse assemblages of sessile invertebrates (Thorner et al. 2016; Teagle et al. 2017). As shown for epiphytes (D'Antonio 1985; Buschmann and Gómez 1993; Saier and Chapman 2004; Wahl 2008; Thorner et al. 2016), some epizoans, such as encrusting bryozoans, tunicates and sponges, can damage their macroalgal host by reducing light harvesting, nutrient uptake and reproductive output or promoting blade breakage from hydrodynamic forces (Dixon et al. 1981; Wong and Vercaemer 2012; Andersen et al. 2019). However, the effects of epibionts can be also positive. For instance, both epiphytes and epizoans can reduce host consumption by herbivores (Karez et al. 2000; Löffler et al. 2015). Sessile and mobile invertebrates can further sustain host growth through the provision of N-rich catabolites (Hepburn and Hurd 2005; Bracken et al. 2007; Hepburn et al. 2012; Peters et al. 2019). Thus, the net outcome of epibiosis is likely the result of a trade-off between negative and positive interactions (Thorner et al. 2016). Nutrient enrichment can alter such trade-offs by fostering the proliferation of opportunistic algae (e.g. the filamentous), at the expense of more complex algal forms (i.e. the foliose and corticated) and epizoans (Fig. 1).

Finally, the effects of nutrient enrichment on canopy-former epibionts can also vary according to the spatial configuration of canopy stands and, more specifically, among individuals at the edge versus inside forests (Fig. 1). Key features of both habitat-forming macrophytes (i.e. biomass, density, growth) and associated assemblages (diversity and relative abundances) can differ between forest edge and interior. In addition, thalli and epibiont assemblages at forest edges are exposed to different biotic (e.g. recruitment, grazing, predation) and abiotic (e.g. light, water flow, sedimentation, physical disturbance) conditions in comparison to those at the interior (Boström et al. 2006; Gaylord et al. 2007; Stewart et al. 2009; Arkema and Samhuri 2019).

In oligotrophic waters of the NW Mediterranean, we assessed how nutrient enrichment affects the photosynthetic efficiency, the reproductive output and herbivore damage in the furoid, *Carpodesmia brachycarpa*, and the structure of the epibiont assemblage it supports. In particular, we tested the hypothesis that nutrient enrichment would facilitate the proliferation of opportunistic epiphytic algae at the expense of more complex algal forms and epizoans. We expected changes induced by nutrient enrichment to be greater at the edge than inside forests, since greater water motion can facilitate nutrient uptake (Ballesteros et al. 1998; Hurd 2000; Gaylord et al. 2007; Stewart et al. 2009). Since

early life stages are generally more responsive to alterations in environmental conditions and resource availability, we predicted that nutrient-driven changes in the physiology of *C. brachycarpa* and associated epibiont assemblages would be greater for individuals that recruited in cleared areas and grew under enriched conditions than for adult specimens that were exposed to elevated nutrient levels when already fully developed.

Materials and methods

This study was carried out along the south-eastern coast of Capraia Island, in the Tuscan Archipelago (43.05° N, 9.85° E), between June 2014 and July 2016, within the framework of a broader project aimed to assess the mechanisms underlying shifts among alternative stable states on temperate rocky reefs. At depths between 2 and 8 m, the furoid, *Carpodesmia brachycarpa* (J. Agardh) Orellana and Sansón (previously *Cystoseira brachycarpa*), forms lush canopy stands that alternate with patches dominated by either encrusting corallines or algal mats made of foliose (*Dictyota* spp., *Padina pavonica*), filamentous (Sphacelariales), siphonous algae (*Acetabularia acetabulum*, *Caulerpa cylindracea*) and corticated Rhodophyta (e.g. *Laurencia obtusa*, *Gastroclonium* sp.) (Bulleri et al. 2017; Tamburello et al. 2019). Patches of habitat alternatives to macroalgal forests are produced by intensive grazing by sea urchins or disturbance due to hydrodynamic forces (Bulleri et al. 2018).

At 4–6 m depths, we randomly selected 8 boulders completely covered by *C. brachycarpa* canopies (hereafter referred to as forest habitat: FH) and 8 boulders over which urchins had formed barren patches (2–3 m²) within canopies (hereafter referred to as edge habitat: EH). All boulders were about ~15 m² in surface area. *Arbacia lixula* was the dominant sea urchin in barren patches (mean density·m⁻² ± SE = 3.344 ± 0.168), while *Paracentrotus lividus* densities were remarkably low (mean density·m⁻² ± SE = 0.136 ± 0.024) (Tamburello et al. 2019). On each boulder, a 1.5 × 0.5 m area was marked, using epoxy putty, either inside the forest on FH boulders (> 1 m from the edge of the boulders) or at the edges between the forest and the barren on EH boulders. To assess how nutrient enrichment influences the physiology of newly established thalli and the structure of the epibiont assemblage they support, canopies were totally removed from marked areas in four FH and four EH, randomly chosen, boulders. Thus, there were 4 boulders for each combination of habitat (FH versus EH) and canopy treatment (Control versus Cleared).

Nutrients were elevated in 2 randomly identified boulders for each combination of habitat and canopy treatment, using slow-release fertilizer pellets (Osmocote, 6 months, 17:11:10 N:P:K) contained in plastic mesh bags (1 mm),

a common method for elevating nutrient levels in seawater (Worm et al. 2000; Russell et al. 2005; Balata et al. 2010; Bulleri et al. 2012; Tuya et al. 2015; Ravaglioli et al. 2018). To achieve nutrient levels found in nearby urban areas, 8 bags, each containing 100 g of fertilizer, were fixed with plastic cables ties to steel hooks inserted in the rock within each area. Bags within an area were at least 30 cm apart and were replaced every 3 months to guarantee continuous nutrient release. At each of two times (June and November 2015), two seawater samples were taken ~3 cm above each fertilized area, using a 60 ml syringe ($n = 16$). Background nutrient levels in the area were assessed taking two water samples from each of six randomly chosen areas maintained at ambient nutrients, using the same method. These included also partial canopy removal areas that were generated within the framework of the broader project and not useful for the test of the hypotheses in this study (i.e. 30% and 70% canopy removal; see Tamburello et al. 2019 for details). Samples were immediately filtered (0.45 μm) and frozen prior to transport to the laboratory, where concentrations of nitrites (NO_2), nitrates (NO_3) and phosphates (PO_4) were assessed by means of a continuous-flow AA3 Auto-Analyzer (Bran-Luebbe), following standard methods (Grasshoff et al. 1999). Although moderate, there was an increase in the concentration of NO_3 and PO_4 at both times of sampling and in that of NO_2 at Time 1 (See Electronic Supplementary Material, ESM Fig. S1).

Measurements of nutrient levels from water samples collected nearby the releasing devices are generally highly variable in time and do not provide accurate estimates of mean concentrations achieved throughout the duration of an experiment (Russell et al. 2005; Bulleri et al. 2012). Thus, the weight of nutrient pellets in each bag was measured before deployment with a precision scale and, following retrieval from the field, after residual pellets were kept in a muffle oven for 28 h at 60 °C. The difference between the initial and final weight provides a more reliable estimate of daily rates of nutrient release (Carnell and Keough 2014). Across the duration of the experiment, the average daily release of N and P within each area was consistent among treatments (mean $\text{g day}^{-1} \pm \text{SE}$; FH: canopy control, $N = 0.392 \pm 0.040$, $P = 0.254 \pm 0.024$; canopy removal, $N = 0.421 \pm 0.040$, $P = 0.272 \pm 0.027$; EH: canopy control, $N = 0.38 \pm 0.031$, $P = 0.247 \pm 0.020$; canopy removal, $N = 0.400 \pm 0.038$, $P = 0.259 \pm 0.024$).

Two years after the start of the experiment, *C. brachycarpa* had recovered in experimentally cleared areas, although to a greater extent under nutrient enrichment (Tamburello et al. 2019). Thus, five *C. brachycarpa* thalli were randomly identified in each of the areas assigned to a combination of habitat (FH versus EH), canopy (Control versus Cleared) and nutrient (Ambient versus Enhanced) treatments, for a total of 80 thalli. The length of thalli ranged

between 8 and 24 cm, but the average length did not differ among experimental treatments (See Electronic Supplementary Material, ESM Table S1). Selected thalli were about 30 cm apart one from another and, in nutrient enriched areas, 20–30 cm apart from the nearest nutrient bag. For each thallus, in vivo chlorophyll fluorescence was measured on 3 randomly chosen branches with a pulse-amplitude-modulated (PAM) fluorometer (Diving-PAM, Walz). Effective quantum yield, an estimate of the photosynthetic efficiency of photosystem II (PSII) in light-adapted thalli, was measured in situ, between 11:00 a.m. and 14:00, by means of the saturating-light method on branches under ambient conditions. These thalli were then collected, sealed in transparent plastic bags and brought to the lab in an ice cooler, where they were preserved at -20°C until further analyses.

The main consumers of *C. brachycarpa* in the Mediterranean are the sea urchins, *P. lividus*, and *A. lixula*, and the sparid fish, *Sarpa salpa* (Vergés et al. 2009; Agnetta et al. 2015). At our study site, urchins were absent inside *C. brachycarpa* stands and their grazing was, thus, limited to the boundary with barren areas. Thalli inside and at the edge of forests were exposed to herbivory by *S. salpa* (Vergés et al. 2009). To assess the effects of nutrient enrichment on herbivore consumption, we quantified the percentage of primary branches damaged in each thallus. In addition, since previous studies have shown that seawater nutrient levels influence the fecundity of brown seaweeds (Wahl 2008; O'Brien et al. 2013), the number of receptacles was counted on 5 randomly chosen primary fronds for each of four experimental thalli, under a dissecting microscope. The number of receptacles was standardized per frond surface area (i.e. expressed as density).

For each of the five experimental thalli, the abundance of algae and sessile animals was assessed on 5 randomly chosen primary branches. Species abundance was quantified as the surface occupied by the vertical projection of individuals of each species and expressed as a percent cover (Boudouresque 1971). Species were identified to the lowest taxonomic level possible, generally the genus or the species, except for encrusting corallines, Serpulidae, Foraminifera and Porifera.

Analysis of data

Replicate measures taken within thalli (3 for quantum yield and 5 for receptacle number and relative abundances of epibiont species) were averaged for analysis. The percentage of damaged fronds, effective quantum yield and number of receptacles were analyzed by means of ANOVAs, including the factors Habitat (fixed), Canopy treatment (fixed and crossed with Habitat), Nutrients (fixed and crossed with Habitat and Canopy treatment) and Boulder (random and nested within the other three factors).

The same four-factor design was used for multivariate and univariate analyses of epibionts. A four-factor PERMANOVA (Anderson 2001) on Bray–Curtis dissimilarities calculated on square-root transformed data was used to assess the response of the whole epibiont assemblage to the experimental conditions. Multivariate patterns were visualized using non-metric multidimensional scaling (nMDS). Multivariate analyses were performed using Primer 6 and PERMANOVA + (PRIMER-E 2008). Variations in total epibiont, epiphyte and epizoan cover and species richness, as well as variations in the relative abundance of the most abundant taxa, were analyzed by means of ANOVA. Pooling procedures were also used as recommended by Underwood (1997) to enhance the power of the statistical tests. More specifically, in the analyses of receptacle density and bryozoan abundance, the factor Boulder (Habitat \times Canopy treatment \times Nutrients) was not significant at $P=0.25$ and was removed from the analyses, allowing the F tests for fixed factors and higher-order interactions to be carried out using the Residual term as the denominator. In all ANOVAs, homogeneity of variances was checked with Cochran's C test and, when necessary, data were log-transformed. Student–Neuman–Keuls (SNK) tests were used for the ranking of the means.

Results

Nutrient enrichment did not influence the effective quantum yield or receptacle density in *C. brachycarpa*, while it increased the percentage of branches damaged by herbivores in thalli at forest edges (Fig. 2A–C, Table 1A–C). Receptacle density was significantly greater in thalli from cleared than canopy control areas (Fig. 2B, Table 1B).

C. brachycarpa supported a total of 102 epibiont taxa (Table S2). The structure of the epibiont assemblage differed between the edge and the inside of forests and between ambient and enriched nutrient levels (Fig. 3; Table 2). In the nMDS, symbols representing thalli exposed to nutrient enrichment are segregated from those maintained at ambient nutrient levels, while differences between habitats are not evident (Fig. 3). The high value of stress indicates considerable distortion in the two-dimensional representation of data.

The total cover of epibionts on *C. brachycarpa* was greater at the edge than inside the forest and decreased under nutrient enrichment, consistently between canopy treatments (Table 3, Fig. 4A). Nutrient enrichment significantly decreased the cover of epizoans on thalli at forest edges, but not on those inside the forest (Fig. 4C). By contrast, there was no effect of nutrient enrichment on epiphyte cover (Fig. 4B). Likewise, epizoan species richness decreased under nutrient enrichment, while there was no change in both total and epiphyte species richness (Table 3,

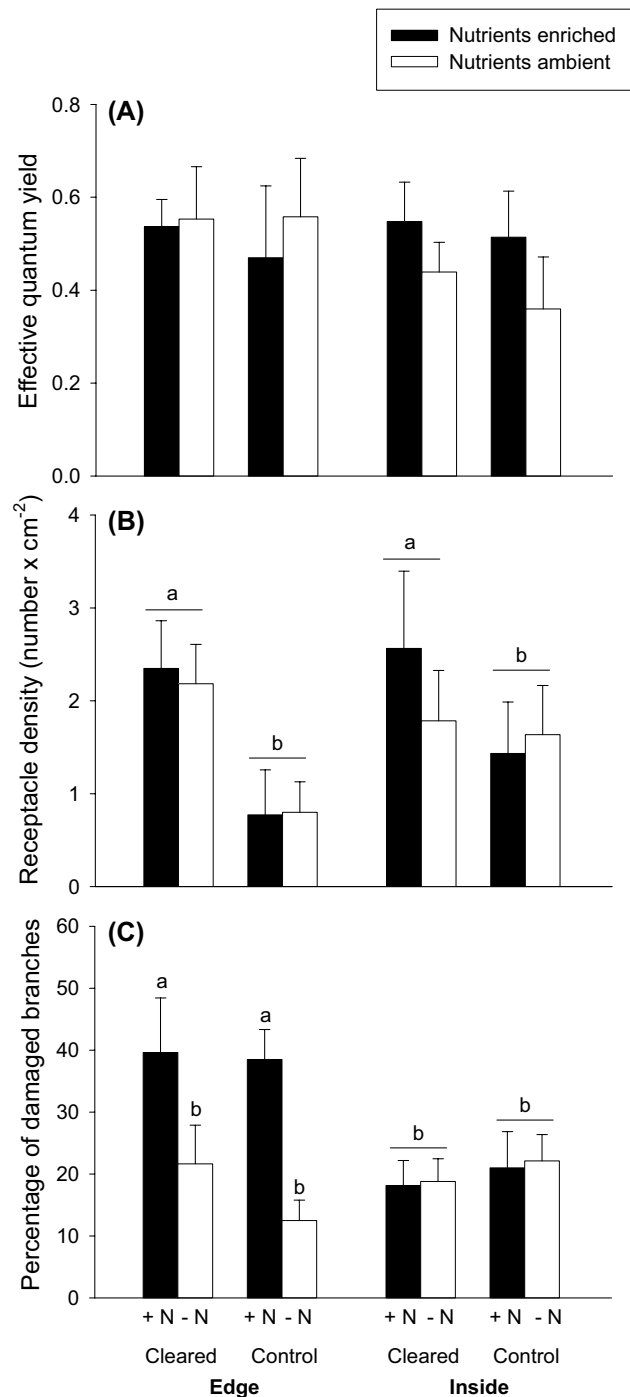


Fig. 2 Effective quantum yield (A), receptacle density (B) and herbivore frond damage (C) in thalli of *C. brachycarpa* at the edge or inside forests, exposed to different levels of nutrients (enriched versus ambient) and canopy treatments (cleared versus control). Data are means \pm SE; $n=10$ for (A) and (B); $n=8$ for (C). Different letters above bars indicate significant differences from SNK tests

Fig. 4D–F). Epizoan species richness was also greater on thalli in cleared than in control areas and inside the forest than at the edge of the forest (Fig. 4F).

Table 1 ANOVA on the effects of Habitat (forest edge versus forest inside), Canopy treatment (cleared versus control), Nutrients (ambient versus enhanced) and Boulder on (A) effective quantum yield, (B) receptacle density and (C) percentage of herbivore-damaged branches

Source of variation	df	(A)		(B)		(C)	
		MS	F	MS	F	MS	F
Habitat = H	1	0.086	2.02	1.939	1.05	1297.90	3.40
Canopy treat. = C	1	0.041	0.97	8.212	4.46*	20.81	0.05
Nutrients = N	1	0.028	0.67	1.138	0.62	2229.57	5.85*
H × C	1	0.004	0.10	0.622	0.34	338.06	0.89
H × N	1	0.163	3.81	0.470	0.26	2615.33	6.86*
C × N	1	0.001	0.03	0.019	0.01	71.148	0.19
H × C × N	1	0.015	0.35	0.037	0.002	89.91	0.24
Boulder (H × C × N)	8	0.043	5.97***	1.964	Eliminated	381.38	0.89
Residual	64 (48)	0.007		1.841		280.08	
Transformation		None		None		None	
Cochran's test			$P > 0.05$		$P > 0.05$		$P > 0.05$

Residual degrees of freedom for (C) are reported in brackets. In (B), the factor Boulder (H × C × N) was eliminated and the effects of Habitat, Canopy treatment, Nutrients and their interactions are tested against the Residual term

* $P < 0.05$; *** $P < 0.001$

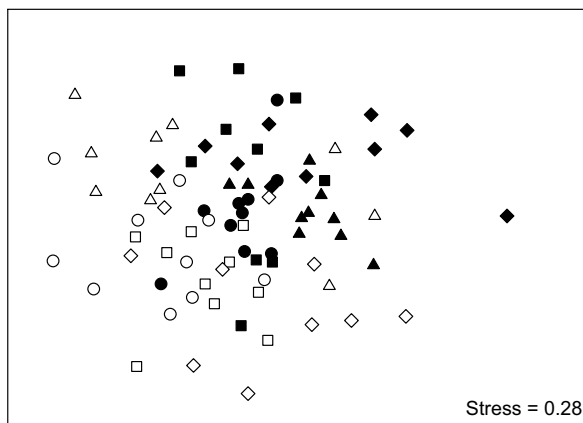
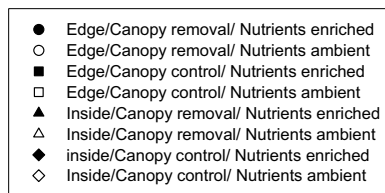


Fig. 3 nMDS ordination plots comparing epibiont assemblages among thalli at the edge and inside forests, exposed to different levels of nutrients (enriched versus ambient) and canopy treatments (cleared versus control). Each symbol represents one thallus. Filled and empty symbols represent enriched and non-enriched thalli, respectively

None of the macroalgal groups, except for articulated coral-lines, responded to seawater fertilization (Table 4). This group decreased under enhanced nutrient levels, but cover values were generally very low, making these changes unlikely to be biologically meaningful (Fig. 5A). By contrast, nutrient enrichment decreased the cover of bryozoans on thalli at

Table 2 PERMANOVA on the effects of Habitat (forest edge versus forest inside), Canopy treatment (cleared versus control), Nutrients (ambient versus enriched) and Boulder on epibiont assemblages on *C. brachycarpa*

Source of variation	df	MS	Pseudo-F	P (perm)
Habitat = H	1	5350.0	2.409	0.029
Canopy treat. = C	1	4451.5	2.005	0.054
Nutrients = N	1	7294.8	3.285	0.012
H × C	1	1162.0	0.523	0.841
H × N	1	2240.5	1.009	0.453
C × N	1	2821.8	1.271	0.263
H × C × N	1	2122.7	0.956	0.464
Boulder (H × C × N)	8	2220.7	1.963	0.001
Residual	64			

Analysis on Bray–Curtis dissimilarities calculated from square-root transformed data

forest edges and that of hydrozoans on thalli from both habitats (Fig. 5B, C; Table 4). The analysis also indicated a significant effect of the interaction Habitat × Canopy treatment on the cover of hydrozoans, but the SNK tests did not show differences between means for any of the level comparisons. There was no effect of nutrient enrichment on sponges and serpulids, which covers on *C. brachycarpa* varied neither between cleared and control areas nor between the edge and inside of forests (Table 4).

Table 3 ANOVA on the effects of Habitat (forest edge versus forest inside), Canopy treatment (cleared versus control) Nutrients (ambient versus enhanced) and Boulder on (A) total epibiont cover, (B) epi-

phyte cover, (C) epizoan cover, (D) total species richness, (E) epiphyte species richness and (F) epizoan species richness

Cover		(A) Total		(B) Epiphytes		(C) Epizoans	
Source of variation	<i>df</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Habitat = H	1	6257.2	10.55*	693.67	1.28	2784.4	17.32**
Canopy treat. = C	1	1595.6	2.96	123.38	0.23	831.8	5.17
Nutrients = N	1	4568.9	7.70*	2.27	0.00	4774.1	29.69***
H × C	1	385.3	0.65	13.16	0.02	540.9	3.36
H × N	1	512.4	0.86	176.69	0.33	1290.4	8.03*
C × N	1	951.1	1.60	970.29	1.79	0.0	0.00
H × C × N	1	428.5	0.72	39.83	0.07	207.0	1.29
Boulder (H × C × N)	8	593.1	1.56	543.57	2.78*	160.8	1.05
Residual	64	379.3		234.29		153.7	
Transformation		None		None		None	
Cochran's test		<i>P</i> > 0.05		<i>P</i> > 0.05		<i>P</i> > 0.05	
Species richness		(D) Total		(E) Epiphytes		(F) Epizoans	
Source of variation	<i>df</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Habitat = H	1	57.80	0.97	0.80	0.00	27.61	10.27*
Canopy treat. = C	1	39.20	0.66	2.45	0.05	35.51	12.10**
Nutrients = N	1	211.25	3.54	80.00	1.78	25.31	9.42*
H × C	1	54.45	0.91	72.20	1.61	1.01	0.38
H × N	1	64.80	1.09	42.05	0.94	3.61	1.34
C × N	1	217.80	3.65	156.80	3.50	5.51	2.05
H × C × N	1	48.05	0.81	22.05	0.49	2.11	0.79
Boulder (H × C × N)	8	59.67	2.44*	44.85	4.56***	2.69	0.33
Residual	64	24.44		9.82		8.12	
Transformation		None		None		None	
Cochran's test		<i>P</i> > 0.05		<i>P</i> > 0.05		<i>P</i> > 0.05	

P* < 0.05; *P* < 0.01; ****P* < 0.001

Discussion

Nutrient enrichment had weak effects on the photosynthetic efficiency and reproductive output of the canopy-forming macroalga, *C. brachycarpa*. By contrast, it increased frond damage by herbivores at forest edges. Grazing by sea urchins is often intense at boundaries between barren patches and algal forests (Andrew 1994; Gagnon et al. 2004; Bulleri 2013). Greater water motion and light availability at forest edges may have facilitated nutrient uptake by macroalgae (Ballesteros et al. 1998; Hurd 2000; Stewart et al. 2009), enhancing their nutritional value and, hence, consumer pressure (Valentine and Duffy 2006; Balata et al. 2010; Prado et al. 2010b; Ghedini et al. 2015). *P. lividus*, a species actively feeding on *Cystoseira*, had very low densities in barrens on experimental boulders (i.e. 1.4 individuals · 10 m⁻²) and was unlikely to cause significant frond damage. Fertilization may have attracted *A. lixula* towards thalli at forest edges. This species has a limited ability to handle

and consume intact *Cystoseira* and feeds mostly on encrusting algae and sessile invertebrates (Wangensteen et al. 2011; Agnetta et al. 2013, 2015).

Isotopic analyses have indeed shown that *A. lixula* occupies a higher trophic level than *P. lividus* and that it has, in some cases, a diet similar to that of a strict carnivore (Wangensteen et al. 2011). *A. lixula* attracted at forest edges, may have targeted epizoan preys on *C. brachycarpa*, halving their total cover and reducing their species richness. The decline of epizoans cannot be due to increased competition from epiphytes since their abundance, in contrast with our predictions, was not enhanced by nutrient enrichment.

This hypothesis would be supported by several lines of evidence: first, *A. lixula* was absent underneath intact canopies, explaining the lower damage of thalli inside the forest. Second, the abundance of sessile invertebrates, an important component of the diet of *A. lixula*, was very low in barren areas (i.e. total cover < 4%). Filter-feeders can benefit from nutrient enrichment via increased availability

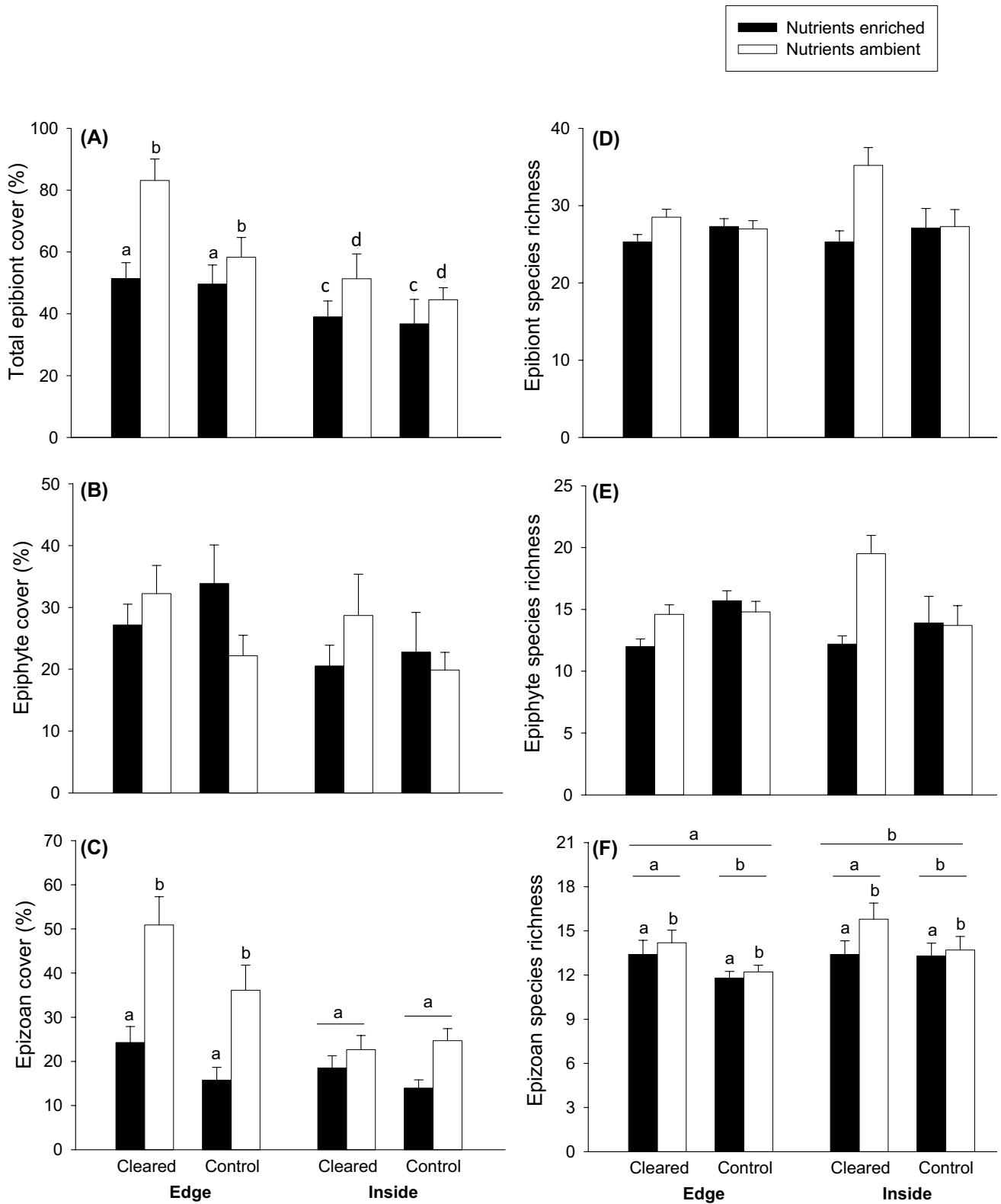


Fig. 4 Total percentage cover of epibionts (A), epiphytes (B), and epizoans (C) and total species richness of epibionts (D), epiphytes (E) and epizoan (F) on thalli of *C. brachycarpa* at the edge and inside forests, exposed to different levels of nutrients (enriched ver-

sus ambient) and canopy treatment (cleared versus control). Data are means \pm SE; $n=10$. Different letters above bars indicate significant differences from SNK tests

Table 4 ANOVA on the effects of Habitat (forest edge versus forest inside), Canopy treatment (cleared versus control) Nutrients (ambient versus enhanced) and Boulder on epiphyte taxa: (A) articulated coral-

line algae, (B) corticated-terete algae, (C) encrusting algae, (D) filamentous algae, (E) sheet-like algae and epizoan taxa: (F) Bryozoans, (G) Hydrozoans, (H) Serpulids and (I) sponges

Epiphytes		(A)		(B)		(C)		(D)		(E)	
Source of variation	df	MS	F	MS	F	MS	F	MS	F	MS	F
Habitat = H	1	4.511	1.31	1.363	0.17	0.056	0.03	32.06	0.14	3.334	0.97
Canopy treat. = C	1	3.856	1.12	1.400	0.17	1.200	0.70	865.51	3.67	2.738	0.79
Nutrients = N	1	22.593	6.55*	0.041	0.01	1.018	0.59	30.57	0.13	2.764	0.80
H × C	1	0.245	0.07	3.087	0.87	0.711	0.41	8.62	0.04	2.472	0.72
H × N	1	0.001	0.00	1.317	0.16	1.141	0.67	32.81	0.14	3.843	0.32
C × N	1	3.267	0.95	0.677	0.08	1.488	0.87	236.73	1.00	3.912	1.13
H × C × N	1	0.000	0.00	0.102	0.01	1.356	0.79	143.27	0.61	5.739	1.66
Boulder (H × C × N)	8	3.448	2.01	8.129	4.35***	1.716	1.87	236.03	4.38***	3.454	3.10**
Residual	64	1.715		1.871		0.917		53.90		1.116	
Transformation		Ln (x+0.1)		Ln (x+0.1)		Ln (x+0.1)		None		Ln (x+0.1)	
Cochran's test		P>0.05		P>0.05		P>0.05		P>0.05		P>0.05	

Epizoans		(F)		(G)		(H)		(I)	
Source of variation	df	MS	F	MS	F	MS	F	MS	F
Habitat = H	1	5.980	16.37***	0.024	0.02	6.143	2.79	0.019	0.01
Canopy treat. = C	1	1.887	5.14*	0.555	0.43	3.668	1.67	0.004	0.00
Nutrients = N	1	3.343	9.15**	40.190	31.06***	5.313	2.41	0.913	0.58
H × C	1	0.080	0.22	7.924	6.12*	5.146	2.34	0.301	0.19
H × N	1	1.601	4.38*	2.179	1.68	0.179	0.08	0.006	0.00
C × N	1	0.900	2.47	0.326	0.25	0.001	0.00	2.690	1.70
H × C × N	1	0.300	0.82	2.793	2.16	0.018	0.01	0.244	0.15
Boulder (H × C × N)	8	0.485	Eliminated	1.294	1.22	2.201	1.03	1.584	0.79
Residual	64	0.365		1.058		2.140		1.995	
Transformation		Ln (x+0.1)		Ln (x+0.1)		None		None	
Cochran's test		P>0.05		P>0.05		P>0.05		P>0.05	

In (F), the factor Boulder (H × C × N) was eliminated and the effects of Habitat, Canopy treatment, Nutrients and their interactions are tested against the Residual term

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

of plankton and organic particles. Such effects are common at sites exposed to sustained nutrient inputs (Gili and Coma 1998; Prado et al. 2010a; Rorig et al. 2017). Nutrients may have also enhanced the quality of epizoans as food. Stoichiometric theory assumes fixed elemental composition (i.e. homeostasis), but intraspecific variation in P content has been documented in some invertebrates and explained by dietary availability (Small and Pringle 2010). Although mostly limited to freshwater environments, there is evidence that the effects of nutrient enrichment on elemental compositions can propagate across trophic levels (Singer and Battin 2007; Small and Pringle 2010). Since foraging in invertebrate predators can be nutrient-specific (Mayntz et al. 2005), enhanced nutritional value (i.e. higher N and/or P content) of epizoans exposed to enrichment might have sustained predation by *A. lixula*.

Finally, as also documented in *Cystoseira tamariscifolia* (Otero Schmitt and Perez Cirera 1996), epizoans represented the dominant component of epibiont assemblages in the shaded, lower part of *C. brachycarpa*, while they were scant in the well-lit upper part, likely due to strong competition from macroalgae (Authors' personal observation). Although *A. lixula* has a limited ability to bend down thalli and feed on apical fronds (Agnetta et al. 2015), it might be able to prey upon sessile invertebrates colonizing the cauloid and fronds closer to the bottom. Under these circumstances, frond damage would be a coincidental aspect of urchin foraging on epizoans, a phenomenon also termed as shared-doom (Dixon et al. 1981; Wahl and Hay 1995; da Gama et al. 2008).

Increased herbivore attraction to fertilized thalli at forest edges might also be the consequence of direct negative effects on epizoans. At ambient nutrient levels, thalli

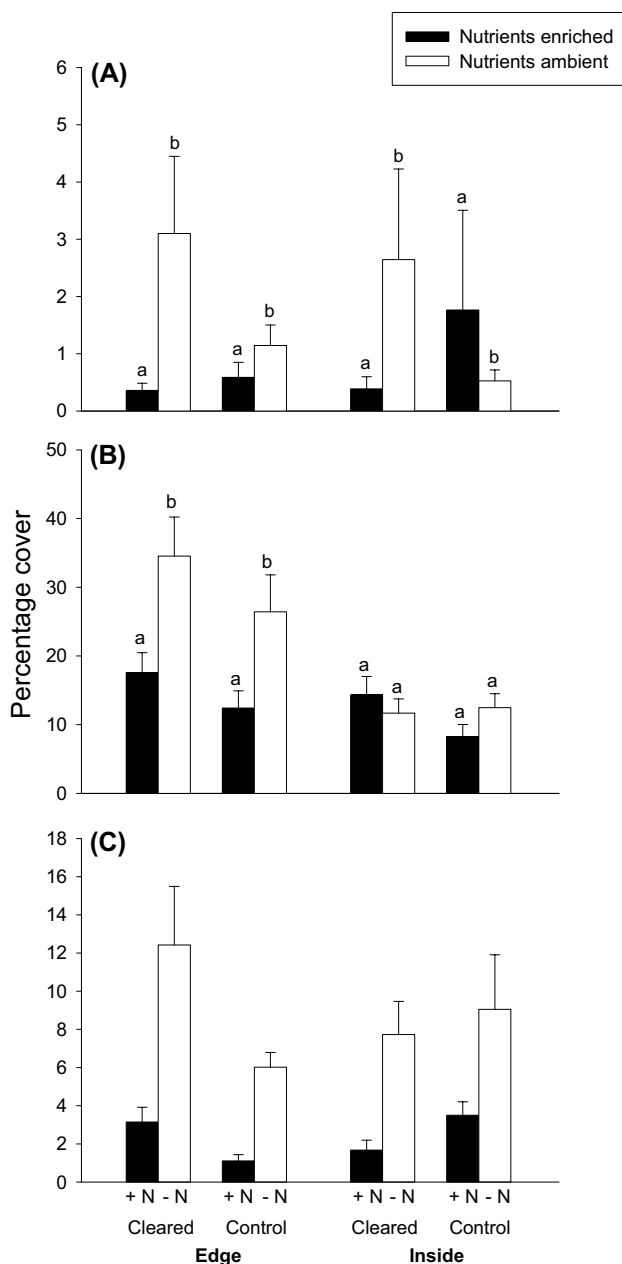


Fig. 5 Total percentage cover of articulated corallines (A), bryozoans (B), and hydrozoans (C) on thalli of *C. brachycarpa* at the edge and inside forests, exposed to different levels of nutrients (enriched versus ambient) and canopy treatments (cleared versus control). Data are means \pm SE; $n=10$. Different letters above bars indicate significant differences from SNK tests

at forests edges supported a greater cover and diversity of epizoans than thalli inside forests. There are examples of epizoans deterring herbivory: the bryozoans, *Lichenopora novae-zelandiae* and *Membranipora membranacea*, reduced consumption of their host, respectively, *Agarum fimbriatum* and *Saccharina latissimi*, from herbivorous gastropods (Durante and Chia 1991; O'Brien et al. 2013). Likewise,

along the coasts of Chile, consumption by the snail *Tegula tridentata* on the kelp, *Lessonia trabeculata*, colonized by hydroids was 3–4 times lower than on kelps without hydroids (González-Duarte et al. 2020). A decline of epizoans is very unlikely to have stimulated grazing by *A. lixula* on *C. brachycarpa*, but may have stimulated that by the fish, *Sarpa salpa*. This is a true herbivore (Havelange et al. 1997; Prado et al. 2010a) and may have preferentially browsed on fertilized thalli characterized by higher nutritional value (higher P and N content) and lower epizoan loading. Heavy consumption of *Posidonia oceanica* plants within fertilized patches inside seagrass beds and preferential feeding on *Cystoseira* branches bearing reproductive structures, suggests active selection of more nutritional plant tissues by *S. salpa* (Gianni et al. 2017; Ravaglioli et al. 2018). In addition, fertilized thalli may have lower levels of defensive compounds, such as phenolics (Ilvessalo and Tuomi 1989; Yates and Peckol 1993; Pavia and Toth 2000; Ravaglioli et al. 2018). Nonetheless, we did not observe more intense grazing on thalli in cleared areas, despite they supported higher numbers of receptacles. In addition, *S. salpa* is highly mobile and should have caused comparable damage to fertilized thalli both at the edge and inside forests.

Rapid recovery of canopies in areas cleared within forests (i.e. not subjected to urchin grazing) and exposed to nutrient addition (Tamburello et al. 2019), further suggests a weak grazing pressure by *S. salpa*. Thus, the hypothesis of enhanced frond damage at forest edges due to increased herbivory from *S. salpa* does not seem to be supported by our data. For the same reason, enhanced consumption by fish is unlikely to explain the weak response of epiphytes to fertilization both inside and at the edge of forests. This does not exclude trophic compensation of nutrient effects by meso-grazers (e.g. gastropods and amphipods) living within *C. brachycarpa* canopies (Piazzi et al. 2018). For example, the gastropod herbivore, *Turbo undulatus*, could absorb positive effects of nutrient enrichment, maintaining algal turf growth under check (Ghedini et al. 2015). Alternatively, greater nutrient uptake efficiency of *C. brachycarpa* may have limited the proliferation of weedy species either composing turfs (Tamburello et al. 2019) or growing as epiphytes (this study). In oligotrophic waters, low or moderate nutrient inputs can advantage complex, slow-growing macroalgae, such as Fucales, over ephemeral species (Pedersen and Borum 1997).

Ammonium excretion by sessile invertebrates can represent an important source of nitrogen for macroalgae during shortage periods (e.g. in summer) (Hurd et al. 1994; Hepburn and Hurd 2005; Bracken et al. 2007; Hepburn et al. 2012). Independently from the underpinning mechanisms, nutrient enrichment caused a decrease in the cover of sessile invertebrates on the lower part of thalli of *C. brachycarpa*. Such a decline did not influence the photosynthetic

activity or the development of reproductive structures, as *Carpodesmia* can efficiently take up N in the form of nitrates (Epiardlahaye 1988). In general, brown seaweeds can use ammonium and nitrates simultaneously and the uptake of one form does not influence the uptake of the other (Haines and Wheeler 1978). Thus, decreased abundance of the animal component of the epibiont assemblages during events of nutrient release should not limit the productivity of brown seaweed stands.

There were no differences in the response to nutrient enrichment between *C. brachycarpa* within established stands and those that recolonized cleared areas during the study (i.e. 2 years). Elevation of nutrient levels has been found to reduce invertebrate settlement, likely through the alteration of biofilm chemical cues (Lawes et al. 2018). Our data indicate that nutrients did not influence the recruitment of sessile invertebrates on *C. brachycarpa* or that the alterations caused at the earlier stages of epibiont colonization were not long-lasting. Under these circumstances, the effects of nutrient enrichment on the structure of the epibiont assemblage supported by *C. brachycarpa* would not change when fertilization occurs simultaneously with acute events of mechanical disturbance. Interestingly, thalli in cleared areas had more receptacles, suggesting that reduced competition for light could foster the reproduction (Dayton et al. 1992; Viejo and Åberg 2001). Increased reproductive output might be key for the recovery of *C. brachycarpa* stands after disturbances and this process appears not to be altered by nutrient enrichment.

Our results suggest that fragmentation of macroalgal forests, increasing the perimeter to area ratio, could exacerbate nutrient effects on *C. brachycarpa* and its epibionts by increasing herbivore damage. Such indirect effects of nutrient enrichment are likely dependent upon the composition of the herbivore assemblage. The extent of the damage suffered by *C. brachycarpa* could be expected to be greater when macroalgal forests are adjacent to barren areas supporting higher densities of *P. lividus*. Indeed, at high densities, this species is able to completely eliminate erect macroalgae, forming barren grounds (Agnetta et al. 2015). Sparse densities of this species on shallow rocky reefs around the island, can be explained by a strengthening of predatory control in response to the establishment of partially or fully protected areas (Bulleri et al. 2018). Similarly, reduced densities and/or foraging efficiency of *S. salpa* due to predation may explain why there was not an increase in consumption rates on *C. brachycarpa* and its epiphytes in fertilized areas. Re-establishment of lost predatory control through fishery management is recognized as a valid strategy for mitigating the effects of nutrient inputs on habitat-forming macrophytes (Östman et al. 2016). Our study suggests that reducing the intensity and frequency of mechanical disturbances fragmenting

macroalgal forests could further enhance their resistance and resilience to nutrient loading. Controlling disturbances linked with climate change, such as sea storms, requires a transnational and long-term effort. By contrast, targeting localized disturbances, such as those due to boat anchoring and fishing gear, might be a more viable strategy in the short-term. In particular, it may sustain the persistence of macroalgal forest in the face of nutrient enrichment in systems characterized by weak top-down control (e.g. outside MPAs).

In summary, our experiment shows that moderate nutrient enrichment of oligotrophic waters does not necessarily cause the proliferation of opportunistic epiphytes and, hence, a strengthening of their competitive effects on canopy-forming macroalgae. In particular, thalli inside forests appear little susceptible to either direct or indirect effects of nutrient enrichment. Our results reinforce the findings of previous experimental studies suggesting that nutrient enrichment can reduce the resilience of Mediterranean macroalgal forests to other disturbances, but it is unlikely, per se, to cause a shift towards a less productive state dominated by algal turfs (Piazzi and Ceccherelli 2017; Tamburello et al. 2019; Kraufvelin et al. 2020). It is worth noting that the net effects of seawater enrichment on canopy-forming macroalgae can vary according to the intensity and temporal regime (i.e. chronic versus acute) of nutrient inputs, their natural concentration in the receiving water body and composition of the herbivore assemblage (Russell et al. 2005; Bulleri et al. 2012; Tuya et al. 2015; Östman et al. 2016; Ravaglioli et al. 2018). This brings two main caveats: (i) caution should be used in generalizing the results of single-site studies—such as ours—to broader areas; (ii) strategies for mitigating the impact of nutrient enrichment on marine macrophytes should be tailored regionally, on biotic and abiotic features of targeted ecosystems.

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Availability of data and material The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

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

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