Effects of simulated overfishing on the succession of benthic algae and invertebrates in an upwelling-influenced coral reef of Pacific Costa Rica

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ABSTRACT

Overfishing and nutrient enrichment are among the major local stressors to coral reefs worldwide, as they can alter the benthic reef community by promoting fast growing algae and bioeroders. The Northern coast of Pacific Costa Rica is strongly influenced by seasonal upwelling events that naturally increase nutrient concentrations between December and March. This study therefore investigated the combined effects of simulated overfishing and naturally increased nutrients on benthic community composition and succession on settlement tiles over a period of 24 weeks (October 2013 until March 2014) using exclusion cages deployed in a coral reef in the Gulf of Papagayo. Tile cover of functional groups and development of organic C and N on light-exposed and –shaded tile sites were assessed. Results revealed that the exclusion of fish significantly increased the development of organic C and N and decreased the C/N ratio on light-exposed tiles. Large filamentous algae (>2 mm), fleshy macroalgae and the colonial ascidian *Didemnum* sp. (Savigny 1816) (up to 80% tile coverage) were dominant on both tile sites. A significant peak of filamentous algae growth and associated organic matter C/N ratio occurred on light-exposed tiles throughout all treatments in February when nutrient concentrations were elevated. These results suggest that both herbivore exclusion and natural eutrophication have a strong influence on the benthic reef community composition and its early succession patterns. The presence of *Didemnum* sp. and turf algae could represent good early warning bioindicators for local overfishing and eutrophication and may therefore be included in management and monitoring strategies.

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1. Introduction

Many coral reefs around the world suffer from combined effects of elevated nutrient concentrations and depleted fish stocks, which may result in pronounced changes in the benthic community composition (Burke et al., 2011). Recent studies have shown that not only filamentous turf- and fleshy macroalgae are major competitors to corals (Hughes, 1994), but also sponges, colonial ascidians and other sessile invertebrates successfully compete for space (reviewed in Chadwick and Morrow, 2011; Glynn and Enochs, 2011).

Herbivorous fish play a crucial role in preconditioning coral reefs to allow for a successful coral recruitment and recovery (Bellwood et al., 2004). Their grazing activities limit turf- and macroalgae growth and therefore not only decrease coral-algae interactions but also opens space for crustose coralline algae (CCA) (Mumby, 2009). The latter can facilitate the settlement of coral larvae by chemical cues (Harrington et al., 2004; Heyward and Negri, 1999; Ritson-Williams et al., 2010). Additionally, a loss of herbivores attributable to fishing activities may result in increased growth of fleshy algae and therefore a loss of hard coral cover due to competition (e.g. Burkepile and Hay, 2009; McCook et al., 2001; Smith et al., 2010). Subsequently, coral reefs may face a reduction of habitat with a structural complexity (reviewed in McCook et al., 2001), which provides refuge also for invertebrate predators such as Balistidae, Labridae and Haemulidae (McClanahan et al., 1999). Bioeroders like sponges and ascidians generally comprise only a minor part of the benthic reef community (Glynn and Enochs, 2011); nevertheless, they can compete successfully with scleractinian corals due to their fast growth and high reproduction rates, or the use of allelochemicals (Bak et al., 1981; Loh et al., 2015; López-Victoria et al., 2006; Sawada et al., 2001). The proliferation of benthic invertebrates or bioeroders is often triggered by changes in environmental conditions (e.g. decreased predation pressure or increased food availability) (Chadwick and Morrow, 2011).

A second local stressor is the over-enrichment with nutrients in coastal waters. Scleractinian corals are adapted to oligotrophic coastal

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waters (Muscatine and Porter, 1977). Some of the direct negative effects of high nutrient concentrations include a reduction in calcification rates (Ferrier-Pages et al., 2000), combined with limited coral growth (Fabricius et al., 2013) and a decrease in the reproduction activity (Loya et al., 2004). Eutrophication may also be tightly linked to the deleterious effects of coral bleaching (Wiedenmann et al., 2012) and an increased susceptibility to coral diseases (Vega Thurber et al., 2014). Furthermore, elevated levels of nitrate and phosphate may promote the growth of benthic as well as planktonic algae (McClanahan et al., 2007). As a source of food, the increased availability of organic matter in the water column can additionally favor filter feeders, which are not physiologically inhibited by higher concentrations of nutrients (Bak et al., 1996; Ward-Paige et al., 2005).

Coral reefs at the northern coast of Pacific Costa Rica are exposed to highly dynamic environmental conditions. Seasonally elevated nutrient concentrations due to coastal upwelling (Clarke, 1988; Stumpf and Legeckis, 1977) and a highly developed fishing industry challenge the present reefs (Mathiesen, 2012). Strong wind jets channeled through a mountain gap in the Central American cordillera between December and April (McCreary et al., 1989; Romero-Centeno et al., 2007) displace surface water masses away from the coast, which are then replaced by colder and denser water from the depth (Bakun, 1990). Primary productivity is high during upwelling season when nutrient rich water masses are welled up to the surface (Small and Menzies, 1981). Furthermore, marine ecosystems in this area have to cope with strong impacts by local fisheries. Almost 80% of the landings derive from artisanal fisheries, which target for reef and coastal fish species (Wehrtmann and Nielsen-Muñoz, 2009) to meet the high demand of fish products for the tourism sector (Salas et al., 2011).

Even though studies have analyzed the combined effects of human induced eutrophication and overfishing on benthic algae growth, these investigations have almost exclusively been carried out in the Caribbean and the Red Sea (e.g. Burkepile et al., 2013; Jessen et al., 2013; Rasher et al., 2012; Smith et al., 2010). Additionally, most studies have only considered the impacts on the algal community, but little is known about the influences on invertebrate recruitment in this context (e.g. Abelson et al., 2005; Jessen et al., 2014). Furthermore, there are no studies available, how natural enhanced nutrient concentrations due to coastal upwelling may influence the benthic community composition and succession on tropical coral reefs. However, in order to sustain coral reef systems worldwide and to implement protecting management strategies, it is necessary to get a detailed understanding of the respective ecosystem (Daily et al., 2009; Hoegh-Guldberg et al., 2007). This study thus for the first time investigated the combined effects of simulated overfishing and natural seasonal eutrophication on the composition and succession of benthic algae and sessile invertebrate communities in a Pacific coral reef along the American continent. Fish exclusion cages with settlement tiles and the natural effects of coastal upwelling were used to: (1) assess the impact of simulated overfishing on *in-situ* succession of benthic algae and invertebrates and (2) determine the effects of changing nutrient concentrations due to coastal upwelling on settling succession and composition of benthic algae along with invertebrates on a temporal scale.

2. Material and methods

2.1. Study site

The study was carried out from October 2013 until March 2014 (duration = 24 weeks) in a patch reef located in the Gulf of Papagayo at the Northern Pacific coast of Costa Rica (N10°32′18.6″ , W85°45′ 54.4″) (Fig. 1). Matapalo Reef is located southwest of the well-studied bay Bahía Culebra (reviews by Cortés, 2012a,b). The reef is situated in close distance to the shore (approximately 20–30 m), in water depth of 5–7 m, depending on the tide. It is dominated by the branching hard coral *Pocillopora* sp.. The Gulf of Papagayo experiences seasonal

coastal upwelling that usually takes place between December and March (Jiménez, 2001).

2.2. Nutrient concentration measurements

Water samples were taken in triplicates directly from above the reef over the total study period of 24 weeks in a biweekly resolution. Concentrations of ammonium (NH_4^+), nitrate (NO_3^-) and phosphate (PO_4^{3-}) were determined. Samples were filtered through syringe pre-filters and analyzed directly for concentrations of NH_4^+ and PO_4^{3-} using a Trilogy® Laboratory Fluorometer (Turner Designs) for fluorometric analysis of ammonia and spectrophotometric determination of phosphate according to Murphy and Riley (1962). A part of the samples was frozen for determination of nitrite and nitrate using a method with the reduction of nitrate by vanadium(III) and a Photometer *Thermo Scientific UV Evolution 201®*. Chlorophyll a (Chl a) concentrations were measured by filtering 3 L of seawater on pre-combusted filters (particle retention 1.6 μm), which were then incubated in 10 mL 90% Acetone for 24 h at 4 °C before analyzed with a spectrophotometer.

2.3. Enumeration of fishes

Visual surveys of fish were carried out using underwater fish census methods described by Green et al. (2009) Five transects with a length of 10 m each (n = 3 long-swims/replicates) were observed monthly from November 2013 to March 2014 investigating abundance, biomass and size classes of the fish community. The surveys were conducted between 9 am and 12 pm, 2.5 m left and right of the transect lines, surveying a total area of 250 m². All individuals ≥ 5 cm were counted and grouped in one of 6 size classes (5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm, 25–30 cm and 30–40 cm). Cryptic species were not included in the surveys. Biomass estimations were calculated using known length-weight relationships (LWR) for fishes: The weight in grams (W) of a fish can be predicted by its fork length in cm (L) by using the formulae $W = aL^b$ (Froese et al., 2014). Parameters a and b are compiled at FishBase (Froese and Pauly, 2009) for most species. If parameters were not available for single species, a higher taxonomic rank (e.g. family) was chosen. The mid value of each size category was used for the biomass estimation (e.g. 17.5 cm for size category 15–20 cm). Fish diversity was calculated for each sampling using the Shannon-Wiener index (Shannon, 2001). Fishes were categorized as carnivore or herbivore, according to their ability to remove benthic algae (information taken from Froese and Pauly, 2009). Due to their potential positive effect on algae growth through gardening and / or their territorial behavior (Hoey and Bellwood, 2010), damselfish were not classified as herbivores in this study.

2.4. Experimental cage set-up

Twelve anodized aluminum frames (50 x 50 cm) were deployed in the reef with at least 1.5 m distance to each other. Three different treatments were applied to the frames (each with n = 4 replicates): (1) open cage / control (only the frame structure); (2) closed cage (frame structure surrounded with plastic net with a mesh size of 2 cm to exclude larger fishes and invertebrate grazers like sea urchins); (3) semi-closed cage (frame with closed sides but open top to only exclude large invertebrate grazers like sea urchins, but not fishes). Previous experiments have shown that exclusion nets have no significant effects on response parameters on settlement tiles (Miller et al., 1999; Smith et al., 2001). Each frame was equipped with 24 terracotta tiles, each with an average surface area of 168.8 ± 0.8 cm². Rough terracotta tiles were used, as their heterogeneous surface simulates coral rock and enhances species richness and biomass compared to other artificial substrates (Brock, 1979; Fitzhardinge and Bailey-Brock, 1989). Tiles were arranged pairwise on top of each other with plastic
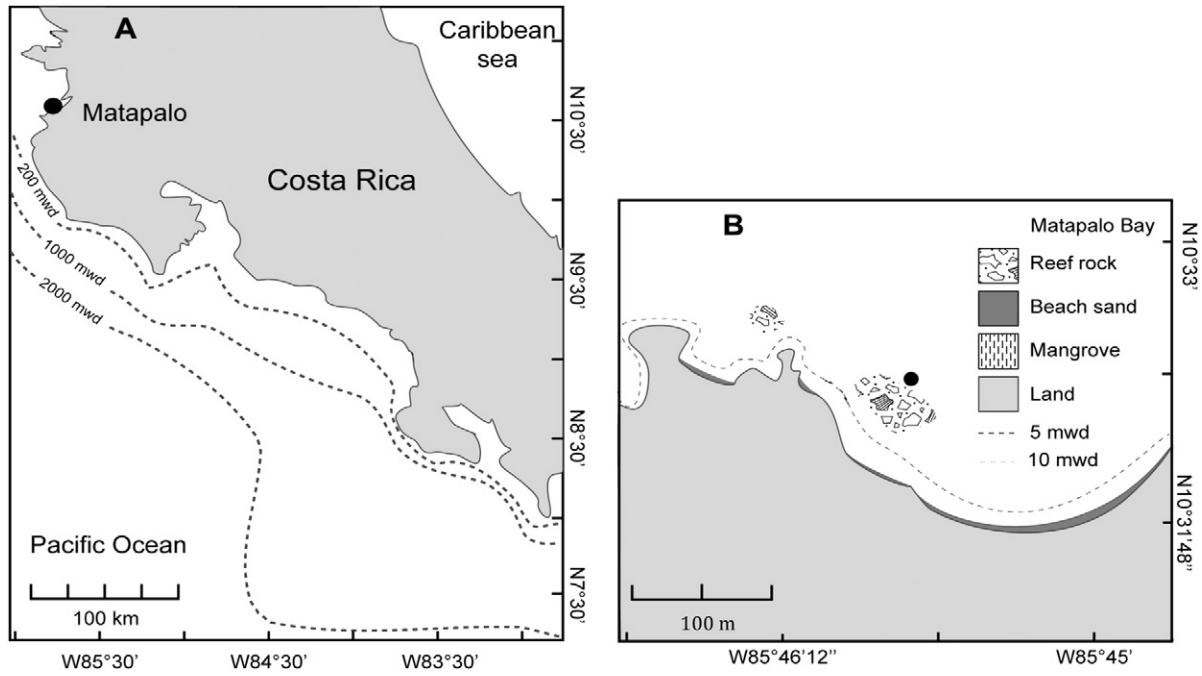
Fig. 1. Maps of the Pacific coast of Costa Rica (A) and the study site Matapalo Reef (B). Map (A) indicates the location of the study site Matapalo Reef at the Northwestern Pacific coast of Costa Rica. Map (B) shows the location of the experimental set-ups (maps adapted from C. Reymond).

bolts and nuts, resulting in 12 upper (light-exposed) and 12 lower (shaded) tiles. Lost surface area due to drill holes and nuts was considered in calculations. To reduce sedimentation, tiles were installed in a 45 degree angle relative to the substrate / bottom on a tough plastic net fixed between the vertical poles. Every two weeks, a random pair of tiles (light-exposed and shaded) was collected from each cage by SCUBA diving. Removed tiles were replaced by a new pair of tiles that then only stayed in the reef for the following two weeks. This procedure resulted in two data sets: (1) Long-term succession, where the development of organisms on tiles could be observed over the total study period of 24 weeks in a biweekly resolution; (2) Short-term succession, where the development of organisms within two weeks could be observed with changing start dates over the whole study period.

2.5. Response variables on settlement tiles

After removing the tiles from the frames, they were immediately photographed under water for later compositional analyses. Afterwards, they were put in separate Ziploc bags for transportation to the laboratory. Later, all the tiles were rinsed with freshwater to remove mobile invertebrates, sediments and salt. All sessile organisms (including algae, invertebrates etc.) were scraped off with razor blades and collected in pre-combusted, pre-weighted tinfoil. Tinfoil packages with content were dried at 40 °C for 24 h and kept dry until analysis. Dry mass was determined with a precision balance (G&G; accuracy 0.001 g).

Quantitative differences in succession and species composition were determined using photo documentation of tiles. Pictures were analyzed with the software Coral Point Count with Excel extension (CPCe) 4.1 (Kohler and Gill, 2006) using 100 randomly overlaid points which were then assigned to the following functional groups and subgroups: (1) Non biotic cover / bare terracotta; (2) Filamentous algae: Large filamentous algae (>2 mm); Small filamentous algae (<2 mm); (3) Fleshy macroalgae: brown macroalgae; green macroalgae; red macroalgae; (4) Coral (5) Sessile invertebrates other than corals: barnacles; bryozoans; polychaetes; tunicates; (6) Cyanobacteria; (7) Crustose

Coralline Algae (CCA); (8) Crustose algae other than CCA (9) Sponges. Thereby proportional cover for each functional group on settlement tiles could be determined.

Samples from light-exposed tiles were homogenized using mortar and pestle for Elemental analysis of total carbon (C), nitrogen (N) and organic carbon (C_{org}) contents. Ground powdered samples were weighted to 1 mg and put into 10 x 10 mm silver (C_{org}) and tin (C/N) cups. For analysis of C_{org} content, 200 μL 1 N HCl was added to sample to remove $CaCO_3$ before dried again at 40 °C for 24 h. Elemental analysis was carried out with an *Eurovector Euro EA 3000* elemental analyzer with a precision of ±0.18% for C and ±0.13% for N (calculated with Apfelblatt SRM 1515 standard).
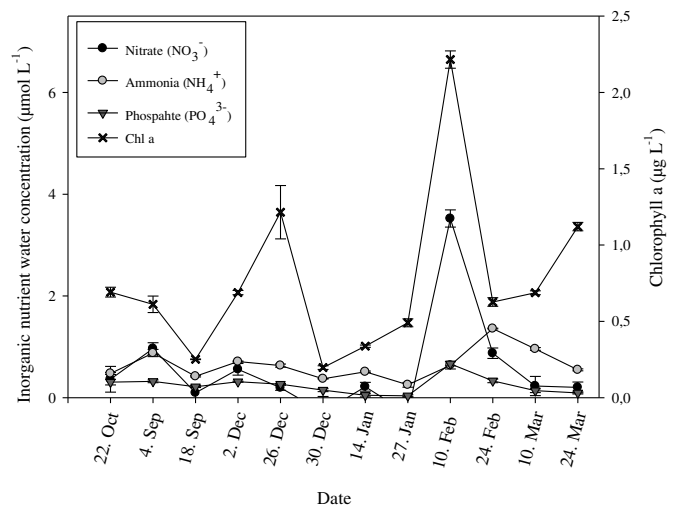

Fig. 2. Concentrations of nitrate (NO_3^-), ammonia (NH_4^+), phosphate (PO_4^{3-}) and chlorophyll a in seawater. Water samples from above the reef. Values presented as mean ± SE.

Table 1

Results of the two-factorial ANOVA comparing effects of treatments on functional groups on light-exposed settlement tiles (long-term succession). Response variables are shown in the first row, the two independent factors (C = caging; T = time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by the asterisks.

	Bare substratum			Sessile invertebrates			Crustose coralline algae			Tunicates		
	df	F	p	df	F	p	df	F	p	df	F	p
C	2	10.76	<0.001*	2	38.73	<0.001*	2	24.98	<0.001*	2	201.24	<0.001*
T	11	17.74	<0.001*	11	1.50	0.203	11	4.87	<0.001*	11	9.37	0.526
Open vs. closed			0.001 *			<0.001*			<0.001*			<0.001*
Semi-closed vs. closed			0.002 *			<0.001*			<0.001*			<0.001*
Open vs. semi-closed			0.795			0.495			0.142			0.789

2.6. Statistical data analysis

Statistical analyses were performed using SigmaPlot 12.5 and IBM - SPSS Statistics software. Data were tested for Gaussian distribution with normal probability plots (Q-Q-plot) and / or Shapiro-Wilk-Test prior to analysis. Data for Chl a and nutrient analysis were grouped into upwelling (Oct.–Jan.) and non-upwelling (Feb.–Mar.) periods and tested for differences with a t-test. Differences in cover of functional groups as well as dry mass, organic C, N content and C_{org}/N ratio were analyzed using 2-factorial analysis of variance (ANOVA) with caging (open, semi-closed, closed) and time (12 sampling times) as fixed factors. Holm-Sidak Tests were used for post-hoc pairwise comparisons. To meet assumptions of normal distribution, data for nitrogen and organic carbon (long-term succession tiles) and dry mass (short-term succession) were log(x + 1) transformed prior to analysis. Correlation of the proportional cover of filamentous algae and sessile invertebrates with nitrate concentrations was tested with linear regression analysis. Additionally, the benthic community composition on settlement tiles (proportional cover) was explored with Principal Coordinate Ordinations (PCO) and statistically tested by Permutation Multivariate Analyses of Variance (PERMANOVA) in PRIMER-e v6 with PERMANOVA+ add-on (Clarke and Gorley, 2006). Fixed factors for analysis were (1) Time, (2) Caging and (3) Nutrient availability. Prior to analysis, the resemblance matrix of the benthic community was calculated using Bray Curtis similarity.

3. Results

3.1. Coastal upwelling and naturally increased nutrient concentrations

Chl a along with NH_4^+, NO_3^-, and PO_4^{3-} water concentrations were significantly higher during upwelling compared to non-upwelling times (p = 0.003, <0.001, 0.038 and 0.017 respectively; t-test). Additionally, Chl a levels peaked between week 8 and 10 (2-fold increase compared to the mean over time) and increased after week 16 (2.5-fold). NH_4^+, NO_3^- and PO_4^{3-} increased after week 16 (4-fold, 8-fold and 4-fold respectively; compared to mean over time) (Fig. 2).

3.2. Fish surveys

During five fish surveys, a total number of n = 3235 fish was counted, belonging to 29 different species (thereof 12 herbivores). A total fish abundance of 0.86 ± 0.24 ind. m^{-2} and a total fish biomass of 51.32 ± 13.12 g m^{-2} were observed. Herbivorous fish accounted for 40% (0.34 ± 0.07 ind. m^{-2}) in terms of abundance and 41% in terms of fish biomass (21.19 ± 5.55 g m^{-2}). Parrotfish (Scaridae) were the most abundant family in the reef (32%), followed by Damselfish (Pomacentridae) (30%), Triggerfish (Balistidae) (10%) and Wrasses (Labridae) (10%). Parrotfish were also considered as the main roving herbivores at the study site. The only occurring species, Scarus ghobban, accounted for 87% of all herbivorous fish. Surgeonfish were sometimes observed on the reef, but hardly counted during surveys. Other herbivores such as some Acanthuridae (1%), Chaetodontidae (7%) or Pomacanthidae (4%) occurred in low numbers. The average fish diversity, expressed by the Shannon-Wiener Index, was 1.91 ± 0.08.

Observations on cage set-ups showed that significantly more fishes were entering open (21.0 ± 5.0 ind. fish min^{-1}) or semi-closed treatments (18.5 ± 2.5 ind. fishes min^{-1}) in comparison to closed cage structures (3.0 ± 1.0 ind. fish min^{-1}) (p = 0.006, t-test). The same was observed for the number of bites per minute on settlement tiles, both on light-exposed and shaded sites. On average, light-exposed tiles in open cages experienced 9.5 ± 1.0 bites min^{-1}, whereas tiles in closed cages experienced bite rates of 1.1 ± 0.8 bites min^{-1} (p = <0.001, t-test).

3.3. Effects of simulated overfishing

The exclusion of larger invertebrate grazers like sea urchins with semi-closed cages had no significant effect on the community composition, dry mass and organic C and N content developing on tiles compared to the controls, and thereby resembled open plots in all measured response parameters (Holm-Sidak post-hoc analysis in Tables 1, 2, 3 and 4).

Simulated overfishing with closed cages resulted in significant changes in the benthic community composition: dominant functional

Table 2

Results of the two-factorial ANOVA comparing effects of treatments on functional groups on shaded settlement tiles (long-term succession). Response variables are shown in the first row, the two independent factors (C = caging; T = time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by the asterisks.

	Bare substratum			Macroalgae			Filamentous algae			Tunicates		
	df	F	p	df	F	p	df	F	p	df	F	p
C	2	26.32	<0.001*	2	20.03	<0.001*	2	6.97	0.039*	2	3.97	0.034 *
T	11	8.18	<0.001*	11	1.01	0.470	11	4.06	0.011*	11	3.06	0.012 *
Open vs. closed			<0.001*			<0.001*			0.031*			<0.001*
Semi-closed vs. closed			<0.001*			<0.001*			0.016*			<0.001*
Open vs. semi-closed			0.091			0.962			0.288			0.987

Table 3

Results of the two-factorial ANOVA of response parameters on light exposed tiles (long-term succession). Response variables are shown in the first row, the two independent factors (C = caging; T = time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by the asterisks.

	Dry mass			Nitrogen			Organic carbon			C_{org} / N ratio		
	df	F	p	df	F	p	df	F	p	df	F	p
C	2	24.51	<0.001*	2	16.39	<0.001*	2	24.36	<0.001*	2	46.40	<0.001*
T	10	2.71	0.022 *	10	2.24	0.049 *	10	14763	<0.001*	10	7.16	<0.001*
Open vs. closed			<0.001*			<0.001*			<0.001*			<0.001*
Semi-closed vs. closed			<0.001*			<0.001*			<0.001*			<0.001*
Open vs. semi-closed			0.777			0.882			0.741			0.054

groups on light-exposed tiles in closed cages were filamentous turf algae (50% mean cover over time), tunicates (28%) and fleshy macroalgae (8%), whereas prevailing functional groups in open treatments were filamentous algae (60%), bare substratum (24%) and crustose algae other than CCA (9%). No fleshy macroalgae or tunicates were observed in open cages (Fig. 3, Table 1). On shaded tiles, the exclusion of fish caused a 5-fold reduction of sessile invertebrates and a 8-fold reduction of CCAs and, as on light-exposed tiles, promoted the establishment of tunicates (71% coverage) (Fig. 4, Table 2).

Most variation in the community composition on light-exposed tiles is explained by multivariate analyses along PCO1 (66.7%), which correlates ($r = - 0.74$) with the factor "caging". Analysis revealed two clusters: a) caged and b) open and semi-caged settlement tiles. The community composition on caged settlement tiles was therefore significantly different from the other two treatments (Pseudo-$F = 32.669$, $p(\text{perm}) = 0.001$, perms = 997; PERMANOVA). Further variation in the data is explained along PCO2 (25%) which correlates ($r = 0.77$) with time, indicating a succession in community composition in all treatments over the study period (Pseudo-$F = 3.9339$, $p(\text{perm}) = 0.001$, perms = 997; PERMANOVA) (Fig. 5).

Simulated overfishing furthermore resulted in a significant increase in dry mass (11-fold), and organic C (8-fold) and N (16-fold) contents on tiles compared to controls and decreased the organic C/N ratio by 30% (Fig. 6, Table 3).

In the short-term succession experiments, simulated overfishing did not have a significant influence on the benthic community composition or development of organic C and N within two-week periods.

3.4. Effects of naturally increased nutrient concentrations caused by upwelling

Established communities on long-term succession tiles did not experience pronounced changes during the study period related to naturally increased nutrient water concentrations caused by coastal upwelling. Bare terracotta tiles of the short-term succession experiments however showed a two-fold increase of filamentous turf algae in response to enhanced nutrient availability ($r^2 = 0.83$; $p < 0.001$; linear regression analysis; Fig. 8), and a peak of sessile invertebrate settlement could be observed with a two week delay ($r^2 = 0.81$; $p < 0.001$; linear regression analysis; Fig. 8) relative to increased nutrient concentrations

in week 16 (Fig. 7). Dry mass along with organic carbon and nitrogen values on light exposed tiles doubled within these two weeks (wk 16 - wk 18) and stayed high until the end of the experiment in March. The C_{org}/N ratio significantly decreased in all treatments ($p < 0.001$, two-factorial ANOVA) during that period. Whereas the ratio returned to former values in open treatments within 4 weeks, it stayed low in closed cages until the end of the experiments (Fig. 9).

4. Discussion

Concordant to several other studies (McClanahan et al. 2003, Burkepile and Hay, 2009; Rasher et al., 2012; Jessen et al., 2013; Stuhldreier et al., 2015), herbivorous fish seemed to exert major control over the benthic community structure of the investigated reef. Additionally, we could show the importance of invertebrate feeding fish, as they control for bioeroding and highly competitive organisms such as ascidians or sponges. Furthermore, the current study also highlights that nutrients may influence the early development of a benthic community, if present in high concentrations. In this case, upwelling derived nutrients enhanced filamentous algae growth.

4.1. Reef parameters

The nutrient analysis in seawater confirmed that the studied reef was seasonally exposed to coastal upwelling during the study period. Concentrations of ammonia and nitrate at the study site significantly increased during upwelling season between February and April compared to non-upwelling season. This corresponds with findings of climatological studies of Wyrtki (1964) and Fiedler (2002), who analyzed the structure and seasonal evolution of the Costa Rica upwelling dome. Along with inorganic nutrient concentrations, the chlorophyll a concentration doubled within the given time frame, indicating high phytoplankton activity. Since bioavailable nitrogen is the limiting nutrient in most tropical waters where iron is available in sufficient amounts (Barber and Chavez, 1991), these findings corroborate that natural eutrophication took place between February and April. Results also indicate that upwelling in the northern part of Pacific Costa Rica is not a constant event, but compromises several upwelling peaks with non-upwelling conditions in between; as previously described for Bahía Culebra (Alfaro and Cortés, 2012; Jiménez, 2001). This phenomenon is

Table 4

Results of the two-factorial ANOVA of response parameters on light exposed tiles (short-term succession). Response variables are shown in the first row, the two independent factors (C = caging; T = time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by the asterisks.

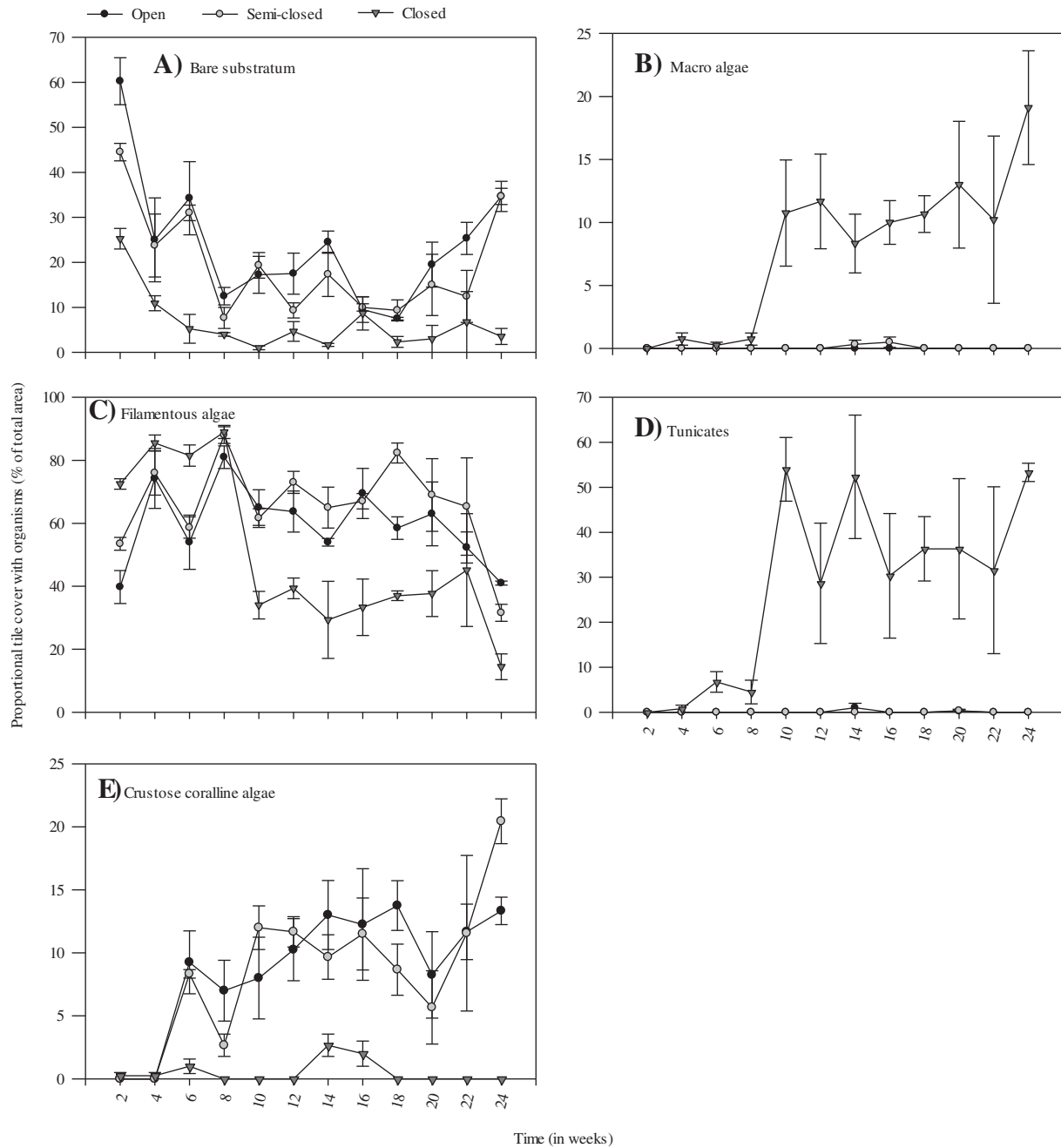|	Dry mass			Nitrogen			Organic carbon			C_{org} / N ratio		
	df	F	p	df	F	p	df	F	p	df	F	p
C	2	8.29	0.002*	2	9.76	0.538	2	2.55	0.103	2	4.47	0.025*
T	10	8.99	<0.001*	10	31.94	<0.001*	10	19.30	<0.001*	10	7.16	0.001*
Open vs. closed			0.002*			-			-			0.024*
Semi-closed vs. closed			0.022*			-			-			0.120
Open vs. semi-closed			0.261			-			-			0.351

Fig. 3. Cover of organisms on light-exposed settlement tiles (long-term experiment). Shown is the proportional cover of different functional groups (A: Bare substratum, B: Macroalgae, C: Filamentous algae, D: Tunicates and E: Crustose coralline algae) over the study period of 24 weeks in the three treatments (open, semi-closed and closed cages). Values presented as mean ± SE.

typical for upwelling systems around the world (Small and Menzies, 1981) and related to altering wind jets (Huntsman and Barber, 1977) but also highlights that the benthic community has to be highly adapted to the pronounced seasonal changes in water parameters.

A meta study of Mesoamerican Reefs showed a lower average herbivorous biomass of 14.5 g m^{-2} (Wilkinson and Souter, 2008) compared to our findings (21.2 g m^{-2}), indicating that Matapalo Reef corresponds to relatively unfished reefs in Central America. However, the comparison of such data is questionable since regional differences in species composition and richness due to their evolutionary history and oceanographic condition might exist. No comparable data on herbivorous biomass of Pacific Costa Rica is published.

4.2. Effects of simulated overfishing

Sea urchins (e.g. *Diadema mexicanum*) and other large invertebrate herbivores were never observed in experimental plots, although they were abundant in the surrounding reef (5.31 ± 0.36 ind. m^{-2}; Stuhldreier, unpublished data). Likewise to experiments by Jessen et al., 2013 with similar cage constructions, the experimental cage set-up seems to disable sea urchins to reach the settlement tiles deployed within cage structures. Their influence on the experimental results is therefore negligible, even though sea urchins may play a major consumer role as herbivores in coral ecosystems (Roff and Mumby, 2012).
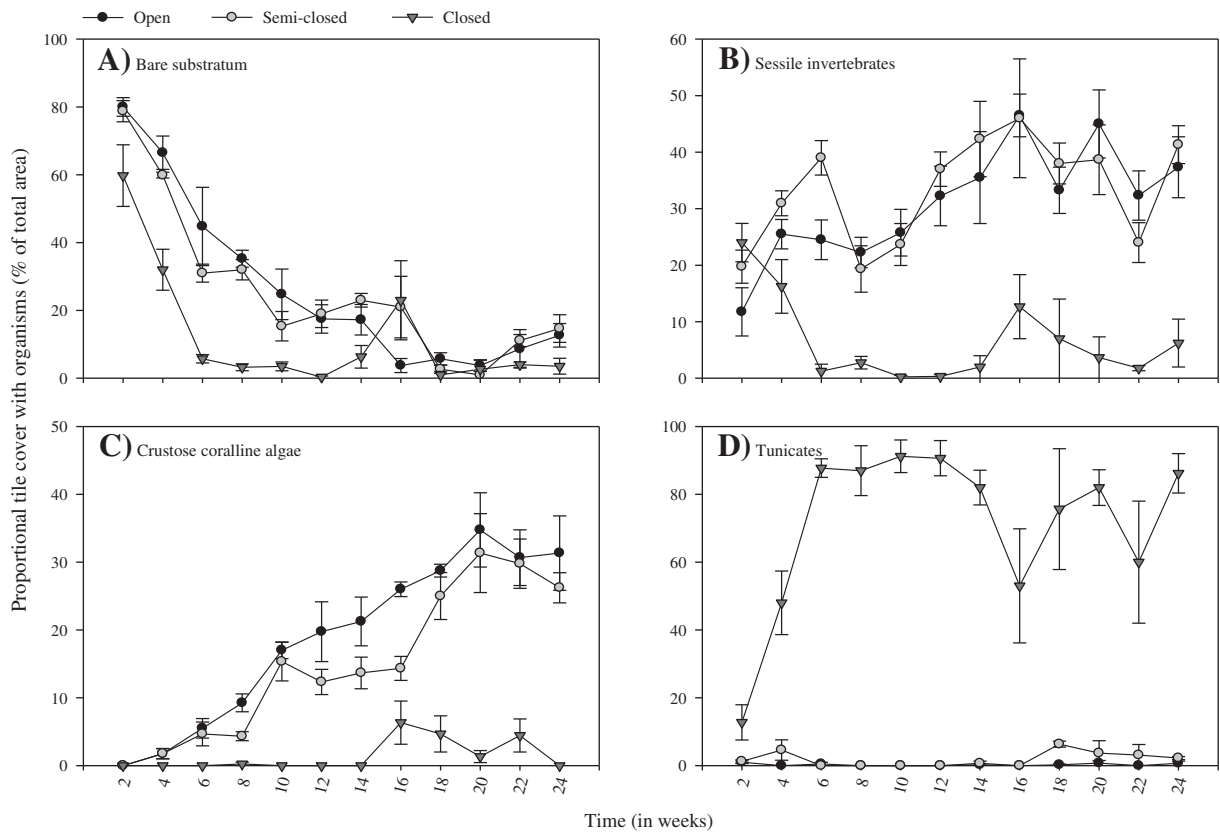
Fig. 4. Cover of organisms on shaded settlement tiles (long-term experiment). Shown is the proportional cover of different functional groups (A: Bare substratum, B: Sessile invertebrates, C: Crustose coralline algae and D: Tunicates) over the study period of 24 weeks in the three treatments (open, semi-closed and closed cages). Values presented as mean ± SE.

Herbivorous fish were efficient in the removal of fleshy brown macroalgae of the genus *Dictyota* sp., which were only present in closed cages. This result is concordant with other studies, where fleshy brown algae were found on experimental tiles after a few weeks (Burkepile and Hay, 2009; Smith et al., 2010). Frondose macroalgae are particularly attractive to herbivores (Hay, 1984; Littler and Littler, 1984) and become abundant only when grazing pressure is reduced, suggesting that they can serve as indicators for overfishing in coral reefs (Cooper et al., 2009). Similar to studies by Burkepile and Hay, 2009; Smith et al., 2010 and Chadwick and Morrow, 2011, the exclusion of fish in the present study reduced the recruitment of sessile invertebrates such as barnacles and polychaetes and completely inhibited the settlement of crustose coralline algae. Instead, the colonial ascidian *Didemnum* sp. rapidly dominated cover on shaded and light-exposed tiles in caged treatments. Even though ascidians typically constitute a small component of the benthic community on coral reefs (Chadwick and Morrow, 2011), studies have shown a strong potential of dispersal, spreading and even overgrowth if predators are lacking or nutrients are increased (Lambert, 2002; Shenkar et al., 2008; Stuhldreier et al., 2015). The low dispersal range of *Didemnum* sp. with only 10 m distance (Bak et al., 1996) suggests that colonies must have been already present in the studied reef. Benthic surveys in the immediate vicinity of the experimental plots did not show any colonies of *Didemnum* sp. (Sánchez, unpublished data). Thereof, one has to consider that the artificial substrate might facilitate *Didemnum* sp. settlement. However, by scanning the reef with a close look between branching corals, the ascidian was found at the base of many *Pocillopora* colonies. This implies that *Didemnum* sp. is able to grow where predator fish have limited access, regardless of the substratum. The successful establishment of *Didemnum* sp. in Eastern Pacific coastal waters of Central America is a newly observed phenomenon and outbreaks on the west coast of North America have only been reported within the last decade

(e.g. Lambert & Lambert, 2003, Bullard et al., 2007). Ascidians closely related with the genus *Didemnum* have simultaneously undergone rapid population expansions worldwide. Bak et al. (1996) reported a 9-fold increase in the density of *TriDidemnum solidum* over a period of 15 years in a Caribbean reef and Witman and Smith (2003) showed a 3-fold increase of ascidian biomass in a reef of Galapagos within one year, underlining the strong competitive potential of colonial ascidians which may further benefit under anthropogenic stressors (e.g. invasion of species, reduced predation pressure and high nutrient concentrations).

Dry mass along with organic carbon and nitrogen contents on settlement tiles showed a significant increase when fishes were excluded from experimental plots. This confirms previous experiments (Hughes et al., 2007; Jessen et al., 2013; McCook et al., 2001; Smith et al., 2001, 2010; Tamai and Sakai, 2013), suggesting the efficient reduction of algae-derived organic matter by herbivorous fish. Results of the present study support the findings of Jessen et al. (2013), where herbivores efficiently removed algal N content on settlement tiles (27-fold decrease compared to controls). The lower C_{org}/N ratio in closed cages compared to controls implies that herbivores particularly fed on nitrogen rich algae in open treatments, likely to maximize their foraging efficiency (Goecker et al., 2005; Mattson, 1980; Minkenberg and Ottenheim, 1990).

4.3. Effects of naturally increased nutrient concentrations caused by upwelling

Coastal upwelling between February and April did not result in visible effects on the established benthic community on long-term succession tiles, however significantly increased the relative proportional cover of filamentous algae on the two-week succession tiles. In this case, filamentous algae were able to outcompete other algal groups
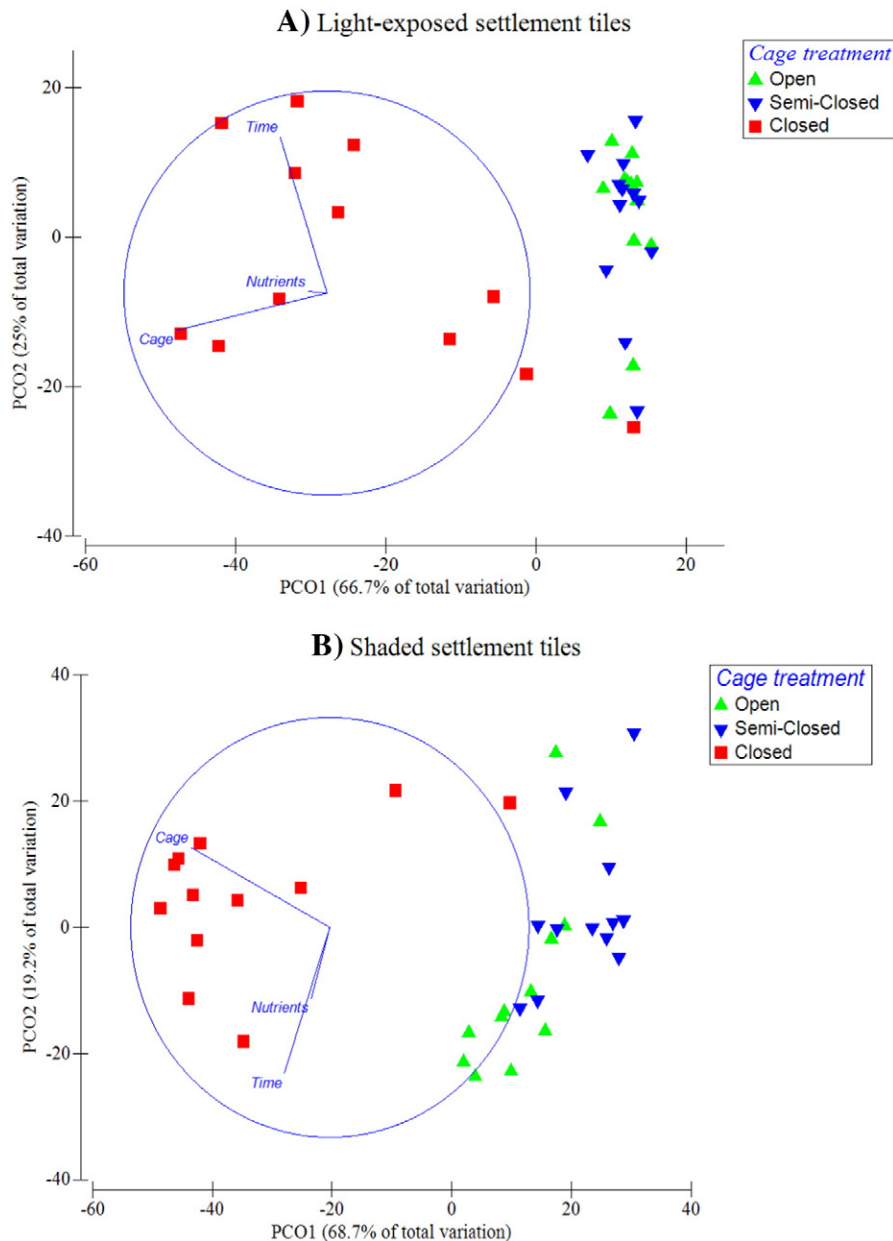
Fig. 5. Shifts in benthic community structure on (a) light-exposed and (b) shaded settlement tiles. The distance between data points reflects their similarity in benthic community composition (close = similar) and the shift along axes can be assigned to changes in variables. On light-exposed tiles, PCO1 correlates negatively to the treatment of caging (r = − 0.74) and PCO2 correlates positively to the factor time (r = 0.77). On shaded settlement tiles, PCO1 correlates negatively to the treatment of caging (r = − 0.69) and PCO2 correlates positively to the factor time (r = 0.70).

and organisms by their fast colonization of light-exposed substratum (Borowitzka et al., 1978; Kendrick, 1991). This demonstrates that nutrient enrichment can influence coral reef community composition without requiring experimentally reduced herbivory, which is concordant to a recent study by Muthukrishnan and Fong, 2014. The decreased C_{org}/N ratio during weeks 16 to 12 on light-exposed tiles indicates an effective uptake of available nutrients resulting in algal growth (Atkinson and Smith, 1983). Similar results have been reported before (Lapointe et al., 2004; Littler et al., 2006; Smith et al., 2001; Vermeij et al., 2010), where a significant increase of filamentous turf algae in response to elevated nutrient concentrations was shown. As primary producers, filamentous algae are likely to take advantage from high nutrient conditions (Carpenter, 1990) and may therefore represent a good indicator for high ambient nutrient concentrations. Linear regression analysis also indicated that barnacles indirectly benefited from elevated nutrient levels in seawater. Nutrients provided by coastal

upwelling can lead to an increase of phytoplankton biomass and the production of particulate organic carbon (Small and Menzies, 1981). Filter-feeding organisms can therefore benefit from higher food availability (Hallock, 2001), which makes them strong competitors for space under more eutrophic conditions (Birkeland, 1977). The increased occurrence of barnacles followed increased nutrient concentrations with a delay of two weeks. This period may represent the time the trophic cascade needs to transform nutrients to available food particles for filter-feeding organisms (Croll et al., 2005).

5. Concluding remarks

Concordant to studies from all over the world, these results support the importance of a healthy and abundant fish community in coral reefs (e.g. Burkepile and Hay, 2006; Hughes et al., 2007; Muthukrishnan and Fong, 2014; Rasher et al., 2012; Stuhldreier, 2015). Their lack can lead to
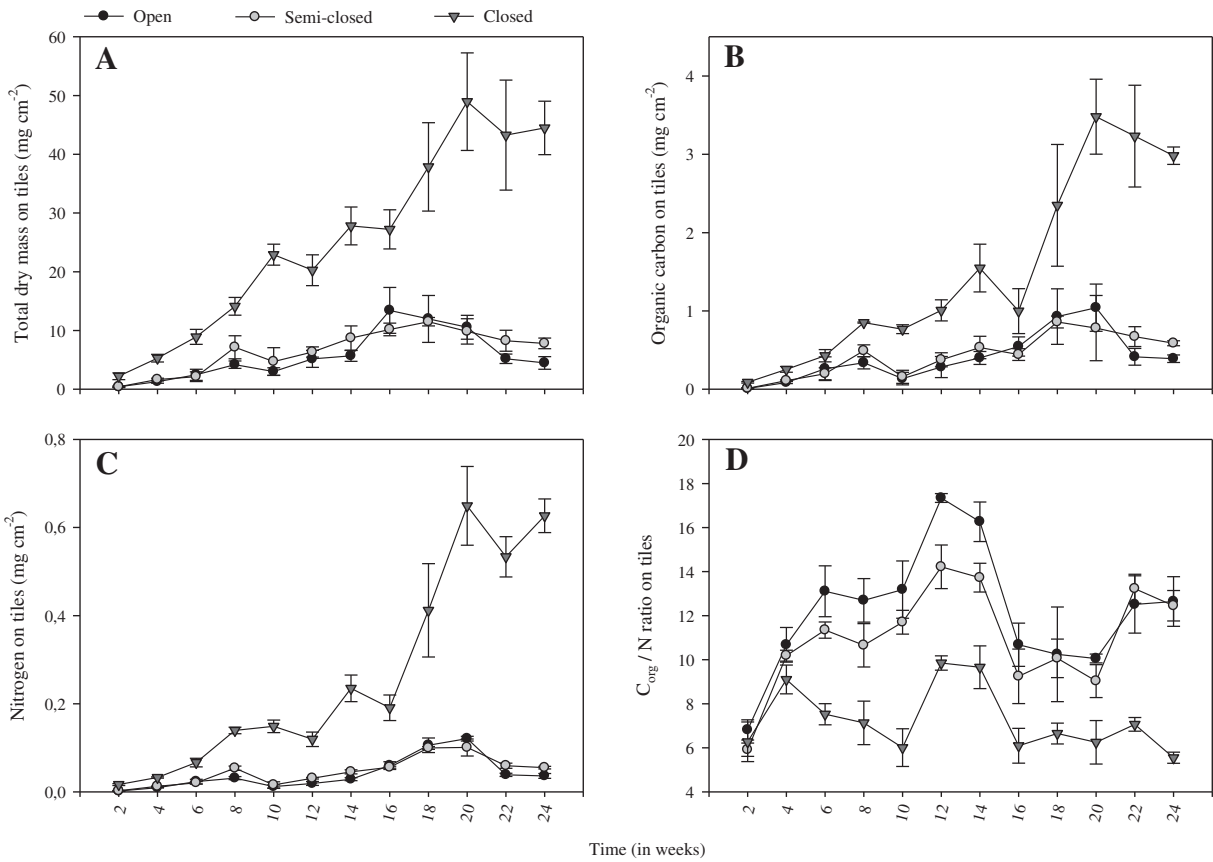
Fig. 6. Development of total dry mass (A), organic carbon content (B), nitrogen content (C) and organic C/N ratio (D) on light exposed settlement tiles (long-term experiments). Values given as means ± SE over the study period of 24 weeks.

pronounced changes in the benthic community with shifts to algal dominated states. This accompanies with a reduced coral recruitment and survivorship, strong sedimentation and unconsolidated substratum. Herbivores thus play a crucial role in coral reef resilience by limiting the development and growth of algal communities that impede coral establishment. However, our study from the Eastern Tropical Pacific has shown an additional successful and strong competitor for space if

predatory fish are missing. The colonial ascidian *Didemnum* sp. has the potential to cause great ecological and economic damage due to its rapid proliferation and strong competitive abilities when predation pressure is lowered. Considering that large coastal areas of Pacific Costa Rica are already impacted by the overexploitation of fish (Wehrtmann and Nielsen-Muñoz, 2009), remaining coral reefs, such as Matapalo, are threatened if not protected and managed
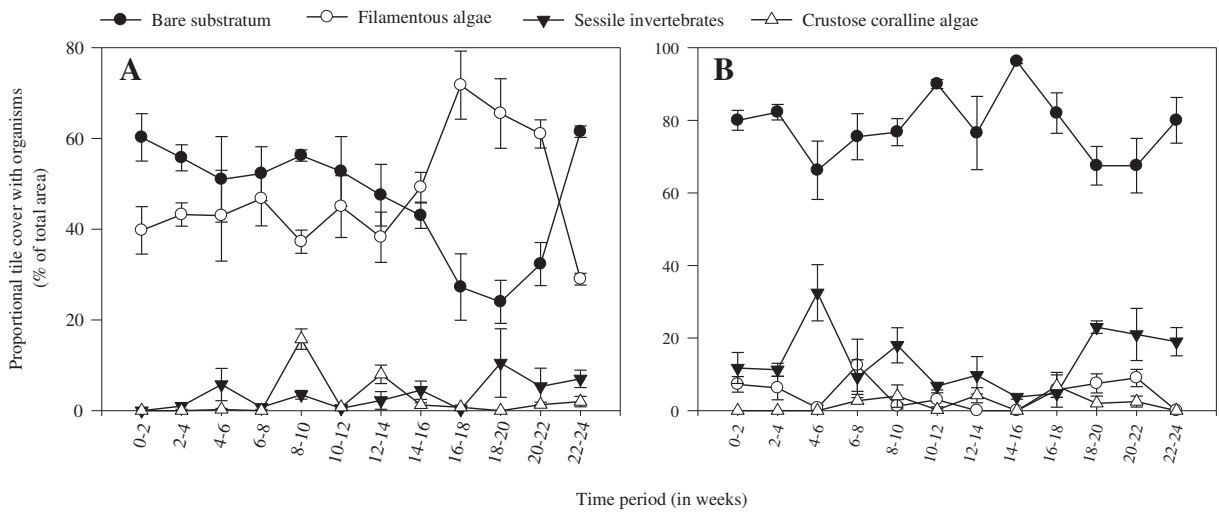

Fig. 7. Cover of organisms on light-exposed (A) and shaded (B) settlement tiles in open cages (short-term experiment). Shown is the proportional cover of functional groups developing in the two-week periods over the whole study time. Values presented as mean ± SE. Graphs show data of open cages only, as there was no significant difference to other treatments, because no significant differences could be found to closed and semi-closed treatments (2-facotrial ANOVA and Holm-Sidak post-hoc test).
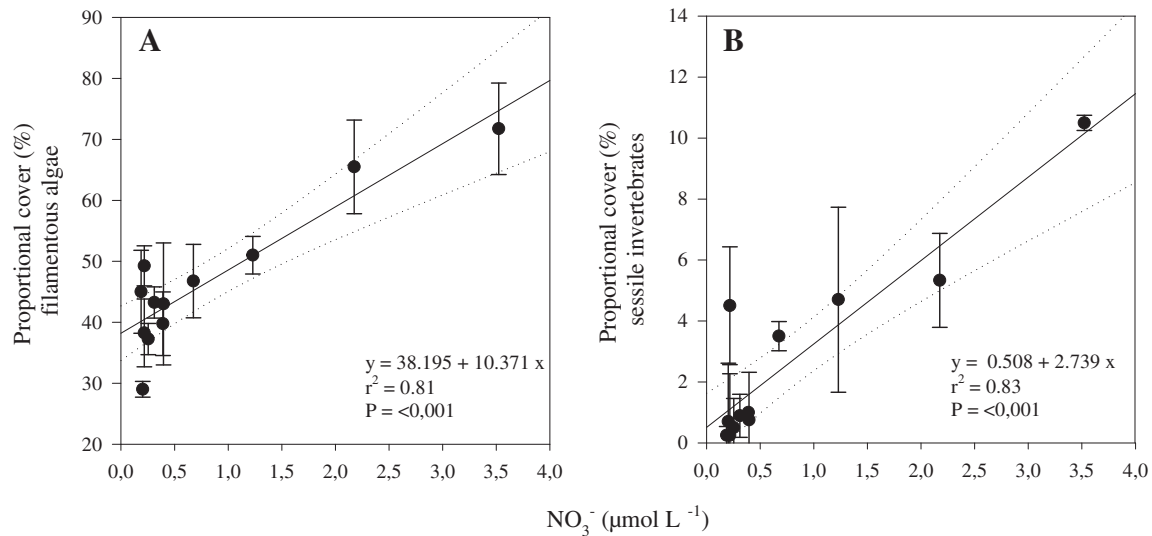
A

$y = 38.195 + 10.371\ x$
$r^2 = 0.81$
$P = <0,001$

B

$y = 0.508 + 2.739\ x$
$r^2 = 0.83$
$P = <0,001$

NO_3^- ($\mu mol\ L^{-1}$)

Fig. 8. Proportional cover of filamentous algae (A) and proportional cover of sessile invertebrates (B) on light-exposed tiles in correlation to nitrate concentration. Regression analysis using nitrate concentration as independent variable. Proportional cover of sessile invertebrates is plotted with a two-week delay. Solid lines represent the regression line. Dotted lines indicate the confidence interval (95%). Normality Test (Shapiro-Wilk) and Constant Variance Test passed in both cases.

appropriately. The ability of fleshy macroalgae and the colonial ascidian *Didemnum* sp. to dominate reefs should therefore be considered and their presence used as indicators of overfishing. Supplementary, coral reefs in the studied area are influenced by seasonally elevated nutrient concentrations due to coastal upwelling. While there is no direct impact visible on an established benthic community, bare substratum (e.g. after disturbances such as storms) is dominantly colonized by fast growing turf algae, intensifying the problems related to overfishing. This indicates that nutrient enrichment can influence coral reef community development and composition even without requiring experimentally reduced herbivory. Integrated management strategies to improve coral reef health in the northern part of Costa Rica should therefore prioritize on such local key drivers of resilience and further monitor the coral reef health status under the above stated aspects.
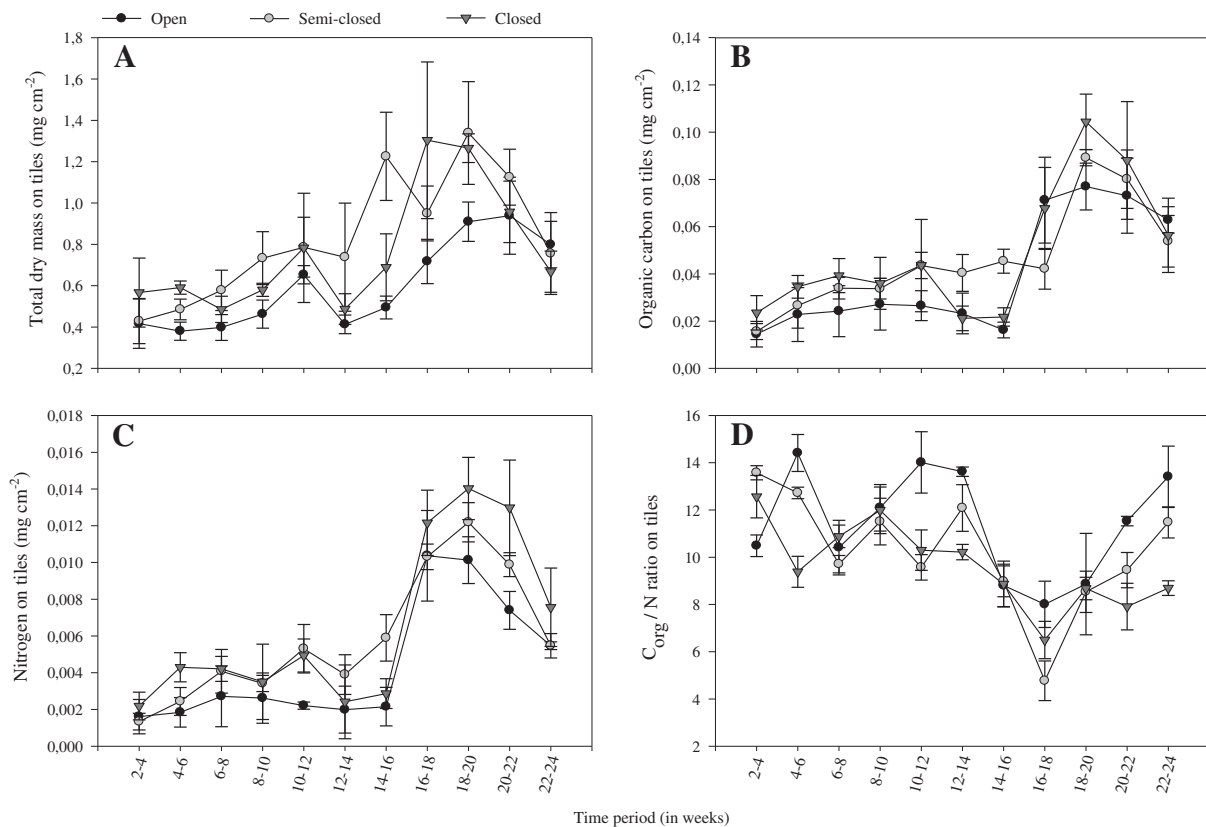

Fig. 9. Total dry mass (A), organic carbon content (B), nitrogen content (C) and organic C/N ratio (D) on light exposed settlement tiles (short-term experiments). Values given as means ± SE for each two-week time period.

Acknowledgements

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