



Recovery of algal turfs following removal

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ABSTRACT

As a consequence of the increasing human footprint on the environment, marine ecosystems are rapidly transforming into new configurations dominated by early-successional and weedy life forms. Algal turfs, in particular, are emerging as a common and widespread configuration of shallow temperate and tropical reefs, and are predicted to transform reef dynamics and ecosystem services. Restoration is an increasingly used approach to mitigate these transformations, with turf removal being proposed as a tool to shift back the competitive balance and facilitate the recovery of initial species, such as forest-forming seaweeds. Yet, our practical understanding of turf recovery trajectories following removal is limited, and removal success may be hindered by strong feedback mechanisms that reinforce turf dominance once turfs are established. Here we investigate the recovery of algal turfs and their properties (mean height, turf biomass and sediment load) to experimental clearance across six turf-dominated reefs at ca. 9 m in subtropical western Australia. Turf cover, mean height, and sediment loads exhibited a rapid recovery following experimental clearing, with all experimental sites reaching pre-clearing turf conditions between 28 and 46 days. This response was mostly driven by the growth of filamentous turf species, whose cover exhibited a positive relationship with sediment load, and are well-known to rapidly recover after disturbance. Turf abundance and turf properties remained relatively constant for the remaining experimental period. Our results suggest that clearing turfs creates only a small time window for recovery of seaweed forests, which limits the effectiveness of turf clearing as a restoration tool. System-specific quantitative evidence on the recovery capacity of turfs may thus be necessary to guide restoration initiatives and develop decision support systems that account for the risks, feasibility, and costs and benefits of restoring turf-dominated systems to previous configurations.

1. Introduction

Earth has entered the Anthropocene, an era where human-driven disturbances to ecosystems exceed or rival those arising from natural processes (Williams et al., 2016). While disturbances have long been recognized as integral to ecosystem dynamics (Cooper, 1913; Grime, 1977), humans are increasingly altering disturbance regimes in unprecedented ways (Turner, 2010). In the marine realm, increasingly frequent disturbance regimes are driving dramatic reconfigurations of shallow reefs across all climate zones (e.g., Hughes et al., 2018; Wernberg, 2021). These reconfigurations usually involve the decline of long-lived 3-dimensional foundation species ('K-strategists') such as stony corals, forest-forming seaweeds, seagrasses and bivalves (Wernberg et al., 2023), and the increase of weedy, opportunistic or

ruderal-like taxa ('r-strategists') (Doubleday and Connell, 2018; Filbee-Dexter and Wernberg, 2018). Algal turfs – carpet-like aggregations of low-lying macroalgae – are emerging as one of the most prevalent replacement states for transformed reef seascapes across the globe (Airoldi et al., 1996; Dijkstra et al., 2017; Gorgula and Connell, 2004; Pessarrodona et al., 2021a; Tebbett et al., 2023).

Forest-forming seaweeds and stony corals typically competitively dominate over turfs under low-disturbance low-stress regimes *sensu* Grime (1977) (Irving and Connell, 2006; McCook and Jompa, 2001), as their traits allow them to displace turfs through several mechanisms (reviewed in McCook and Jompa, 2001; O'Brien and Scheibling, 2018). For example, corals inhibit algal turfs through shading, stinging, and a range of allelopathic effects (McCook and Jompa, 2001), while forest-forming seaweeds cause declines in turf cover through physical

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abrasion, reductions of light, and sedimentation (Connell, 2003; Wernberg et al., 2005). Natural disturbances such as warming anomalies or storms cause coral and seaweed mortality, and facilitate the proliferation of turfs in open gaps (Irving et al., 2004; Russell, 2005), which are otherwise infrequent and restricted in space (Connell and Irving, 2008). A range of anthropogenic disturbances and stressors such as warming, heatwaves, eutrophication, sedimentation or ocean acidification however compound natural disturbance regimes and modify the competitive balance between forest-forming seaweeds, corals and algal turfs (Falkenberg et al., 2013; O'Brien and Scheibling, 2018; Thomsen and South, 2019), facilitating regime shifts where turfs become the dominant habitat occupiers. Once established, turfs maintain their competitive dominance through a series of reinforcing feedbacks (Filbee-Dexter and Wernberg, 2018; O'Brien and Scheibling, 2018). For example, dense turfs often accumulate sediments, resulting in an environment prone to oscillations between anoxia and hyperoxia that can inhibit the recruitment of forest-forming seaweeds and corals (Birrell et al., 2005; Layton et al., 2019a, 2019b; Speare et al., 2019).

Turf resilience is strongly tied to sedimentation regimes (Airoldi and Virgilio, 1998; Gorgula and Connell, 2004), as the nature and competitiveness of algal turfs is substantially influenced by the quantity and quality of sediments they trap (Irving and Connell, 2002; Tebbett and Bellwood, 2019). Turfs are generally able to withstand sedimentation better than other algae (Airoldi, 1998), as turfs have extremely rapid growth and their densely-packed matrices and mucilaginous nature facilitate sediment deposition and retention (Carpenter and Williams, 1993). Indeed, sediment loads in turfs are often several times higher than those encountered in nearby areas (Latrille et al., 2019). Sediment loads can also influence the type of turfs, with increased sedimentation increasing the dominance of longer, lower biomass and more unproductive turfs in some coral reef systems (Tebbett and Bellwood, 2019). Characterizing turf sediments is thus crucial to understand how they modulate turf function and the wider system's sediment dynamics.

The accelerating decline of seaweed forests and coral reefs in the last few decades has been followed by a global surge in restoration efforts (Duarte et al., 2020; Saunders et al., 2020). One of the proposed ways to enhance the restoration success is to remove turfs via clearing the substrate (Gorman and Connell, 2009), thereby relaxing some of the competitive effects (e.g. sediment accumulation, variable O₂ concentrations) that advantage turfs over the recruits of foundation species. Whilst these mechanisms are well established (Filbee-Dexter and Wernberg, 2018; Gorgula and Connell, 2004; Kennelly, 1987; Layton et al., 2019a; O'Brien and Scheibling, 2018), our quantitative understanding of the trajectories turfs take after removal is limited, and these trajectories may vary substantially across space (Airoldi and Virgilio, 1998). Yet, understanding turf recovery trajectories and the feedbacks acting within them is crucial to determine their stability and to develop decision support systems that account for the risks, feasibility, costs, and benefits of restoration. Here, we investigate the recovery of algal turf cover and several other turf properties (mean height, sediment load, biomass) following experimental clearing in a system that has recently transitioned from a seaweed forest to a turf-dominated state.

2. Material and methods

2.1. Study area and experimental design

The study was conducted at Port Gregory (28.2° S, 114.2° E) in Western Australia (Fig. S1), where coastal reefs sit in a temperate-tropical transition zone. Kelp forests of *Ecklonia radiata* and *Sargassum* spp. dominated (>60% cover) much of the benthos of Port Gregory reefs until 2011, when an extreme marine heatwave and a concurrent increase in tropical herbivores caused the loss of kelp and proliferation of algal turfs (Bennett et al., 2015; Wernberg, 2021). Turfs on these reefs form low-lying (1–2 cm) multispecies assemblages (20–30 species per 100 cm²) dominated by filamentous algae (Pessarrodona et al., 2021a).

Turfs presently dominate (~60% cover; Bosch et al., 2022a) the benthic cover on all of these reefs, which are also interspersed with patches of warm-affinity *Sargassum* spp. (~25% cover; Bosch et al., 2022a); kelp plants remain only in four of the sites (PG2-PG5) at low densities (0.01–1 plants · 0.25 m⁻², Pessarrodona unpub. data). Despite a decline in abundance of herbivorous fishes and intensity of herbivory over the past 10 years since the marine heatwave, the kelp forests have not recovered to pre-heatwave conditions and remain dominated by algal turfs (Bosch et al., 2022a; Wernberg, 2021).

To investigate turf responses to artificial disturbance, we established three 7.07 m² (1.5 m radius) plots for each experimental treatment (clearing or control) at 6–9 m depth at six sites. Sites were separated by at least 1 km, distributed across ca. 20 km coastline (total of 36 plots). Plots were marked by an eyebolt drilled into the bottom. Control plots were left undisturbed, while clearing plots had as much erect algae as possible (i.e. turfs and other algae) removed by divers using paint scrapers and metal wire brushes. Our experiment began during austral spring (October–November) 2019 and plots were revisited in November (20–28 days after clearing), December (45–57 days), February (106–108 days) and June (234 days).

2.2. Recovery measurements

The cover of algal turfs and their properties (mean height, biomass and sediment load) was measured throughout the experiment within 1 m radius (3.14 m²) of the eye bolts, leaving the outer 0.5 m of the plot to minimize edge effects. Benthic cover was quantified by photographing three randomly-placed 0.25 m² quadrats within each experimental plot. The cover of turfs in the quadrat was then estimated with the aid of a reticulum of 25 cells (5 × 5) superimposed over the photograph in Adobe Photoshop CC (Adobe Systems Inc.). Mean turf height (hereafter “turf height”) was measured by randomly sticking the depth probe of a caliper in the turf matrix at 5 different points, and then taking the average. Turf biomass and sediment load was measured with a 400 cm² quadrat (n = 3 per subplot) by suction-sampling all non-encrusting macroalgae and sediments within the quadrat using an airlift or venturi suction sampler and collected in 125 µm mesh bags attached to the end of the sampler (therefore collecting fine to coarse sands, ISO 14688-1:2017) (Pessarrodona et al., 2021a). All the non-encrusting algae were gently scraped off the rock using a putty knife and suctioned. Algal material was frozen and transported to the laboratory where it was thawed, identified and weighed separately in the following morpho-functional classifications following (Steneck and Dethier, 1994): filamentous (e.g. *Ceramium*, *Polysiphonia*), foliose (e.g. *Porphyra*), corticated (e.g. *Dictyota*), leathery (e.g. *Ecklonia*, *Sargassum*) and articulated calcareous (e.g. *Amphiroa*, *Corallina*). We assumed that the destructive subsamples of our plot had negligible effects to subsequent data collections as they constituted a minor fraction (1.3%) of the overall plot area, and were taken in different sections of the larger plot.

2.3. Statistical analyses

To examine the response of turfs to disturbance, we used a linear mixed-effect model (LMM) using the package lme4 (Bates et al., 2015) testing for the effects on the benthic cover (%) of turfs from clearing treatment (2 levels, fixed factor), months (5 levels, fixed factor), sites (6 levels, random) and plots (3 levels, nested within sites). Interactions between all factors were included in the analysis. We inspected homoscedasticity and normality of the residuals using quantile-quantile and residuals versus fitted plots. Pairwise comparisons of interest (i.e. between months and treatments) were conducted contrasting the estimated mean effects separately, holding one factor fixed at each level as recommended (Lenth, 2023).

Differences in mean height (cm), biomass (g DW 100 cm⁻²), and sediment load (g DW 100 cm⁻²) between months (5 levels, fixed factor), sites (6 levels, random) and plots (3 levels, nested within sites) were

examined with permutational ANOVA, which is more robust to the non-normal structuring of residuals and heterogeneity of variances detected in the preliminary analysis. Our overall design was unbalanced due to diving restrictions and conditions at remote locations limiting sampling time, with only 3 sites being sampled in the month of November and 4 sites in June. Between 1 and 3 samples were additionally lost during some sampling events, not making the theoretical 54 samples per sampling event ($n = 53$ total samples for pre-clearing, $n = 22$ in November, $n = 52$ in December, $n = 51$ in February and $n = 42$ in June). For each response variable, we generated a similarity matrix based on Euclidian distances with untransformed data using PRIMER software with the PERMANOVA add-on (Anderson et al., 2008; Clarke and Gorley, 2015). The main effects were tested with 9999 unrestricted permutations of the raw data, and PERMDISP tests were conducted to examine heterogeneity of dispersions.

3. Results and discussion

3.1. Turf cover

There were no differences in benthic composition or turf cover between treatments across sites before clearing (PERMANOVA, $p = 0.16$; LMM treatment pairwise comparison, $p = 0.21$; Fig. 1, Fig. S2). Clearing reduced average turf cover by ca. 85%, from a global average of $55.4\% \pm 4.16$ – $9.0\% \pm 1.5$ (pre-post clearing pairwise comparison, $p < 0.001$), as some filamentous algae proved extremely difficult to remove completely, which also is likely to be the same during natural disturbances or any management removal intervention (Gorman, 2009).

Turf cover in the cleared plots recovered rapidly after clearing, often surpassing the pre-clearing cover (Fig. 1a). Indeed, turf cover in the cleared plots was significantly higher than before the start of the experiment during November ($72.8\% \pm 3.6$; 20–28 days after clearing), December ($69.3\% \pm 2.2$; 45–57 days) and February ($74.0\% \pm 2.2$; 106–108 days) (pairwise comparison between months, $p = 0.001$, $p = 0.001$, $p < 0.001$ respectively) until June (234 days), when turf covers were no longer higher than prior to clearing ($p = 0.88$). At this point turf cover in clearings was also no longer different from control plots (treatment pairwise comparison, $p = 0.78$). This observation is consistent with other coastlines with limited nutrient input, where algal turfs contract seasonally during winter (Gorman, 2009), when storms typically reduce their thickness and sediments on the bottom (Airoldi et al., 1995; Airoldi and Virgilio, 1998). In contrast, turf covers in the control plots did not vary significantly over time ($p = 0.82$ – 1.00 for any given

month pairwise comparison), indicating that ‘old’ established turfs may be relatively stable.

3.2. Turf properties

Turf height and sediment load (weight of sediments retained within the turf) also exhibited rapid recovery after clearing (Fig. 2A and B). The three sites that could be sampled in November (PG2, PG3, PG5; 20–28 days after clearing) showed no significant differences compared to pre-clearing conditions, nor did all of the sites when more favourable conditions allowed complete sampling in December (45–47 days). Sediment load in the cleared plots remained mostly unchanged throughout the rest of the experiment, while mean turf height showed a moderate decrease towards June, when mean height was significantly lower than pre-clearing conditions (Fig. 2A). This again probably reflected seasonal variation in turf cover in sediment loads, being lower during winter when increased activity naturally clears turf patches. Turf biomass, on the other hand, showed a slower recovery (Fig. 2C). Mean biomass across all sites in November (0.2 ± 0.02 g DW 100 cm^{-2} ; mean \pm standard error) was only 15% pre-clearing values (1.16 ± 0.13 g DW 100 cm^{-2}) and progressively increased until February, before exhibiting a moderate decrease towards winter (June).

There was significant heterogeneity of dispersions (PERMDISP, $p < 0.05$) between months for turf sediment load and biomass analyses, but not for mean turf height (PERMDISP, $p = 0.09$). This was partly due to the nature of our unbalanced design, as randomly removing samples to balance it resulted in dispersion homogeneity between factors in the sediment load analysis (but not for the turf biomass analysis). Consequently, differences among means in these treatments should be interpreted with caution.

Interestingly, the amount of sediment in the cleared plots remained more or less constant throughout the experiment, with the exception of immediately after the clearing when divers had purposefully removed all sediment as part of the turf clearing process. This suggests either that on-reef sediment load was unaffected by turfs (e.g., driven by local sediment transport processes), or that turfs were able to rapidly regrow and recover their trapping function. The amount of sediment on the benthos is determined by the complex interplay of sediment delivery to the water column, sediment deposition, resuspension, and retention by algal turfs (Gorgula and Connell, 2004; Schlaefer et al., 2021). Algal turfs with similar heights and biomasses at our sites (e.g. 4, PG6) contained different sediment loads, suggesting that local sedimentary conditions are an important determinant of on-reef sediment load. Still, the

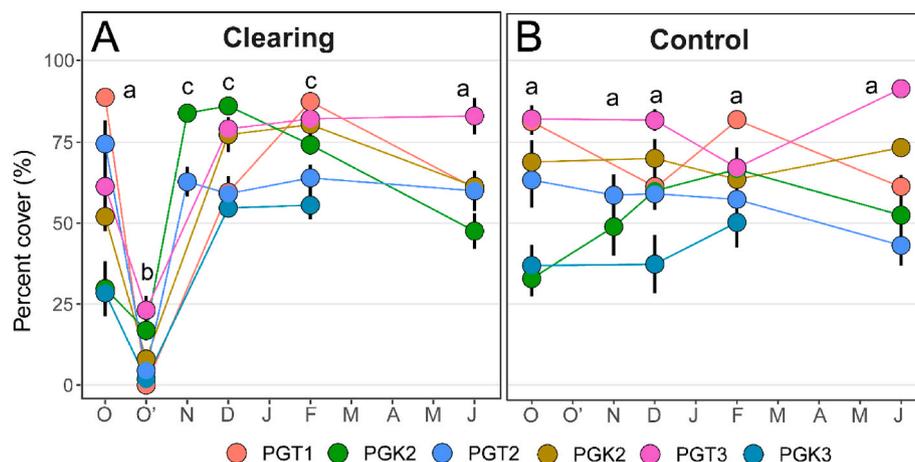


Fig. 1. Turf cover within cleared (A) and control (B) plots at our six sampling sites. Dots and error bars depict means \pm standard error. Letters denote significant differences between months within each treatment at $\alpha = 0.05$. Turf covers were significantly different between treatments after clearing, in November and February, but these contrasts are not shown. Months are indicated by their capital letter and listed in chronological order. N = 53, 55, 19, 54, 54 and 45 for October (pre-sampling), October (post-sampling), November, December, February and June respectively.

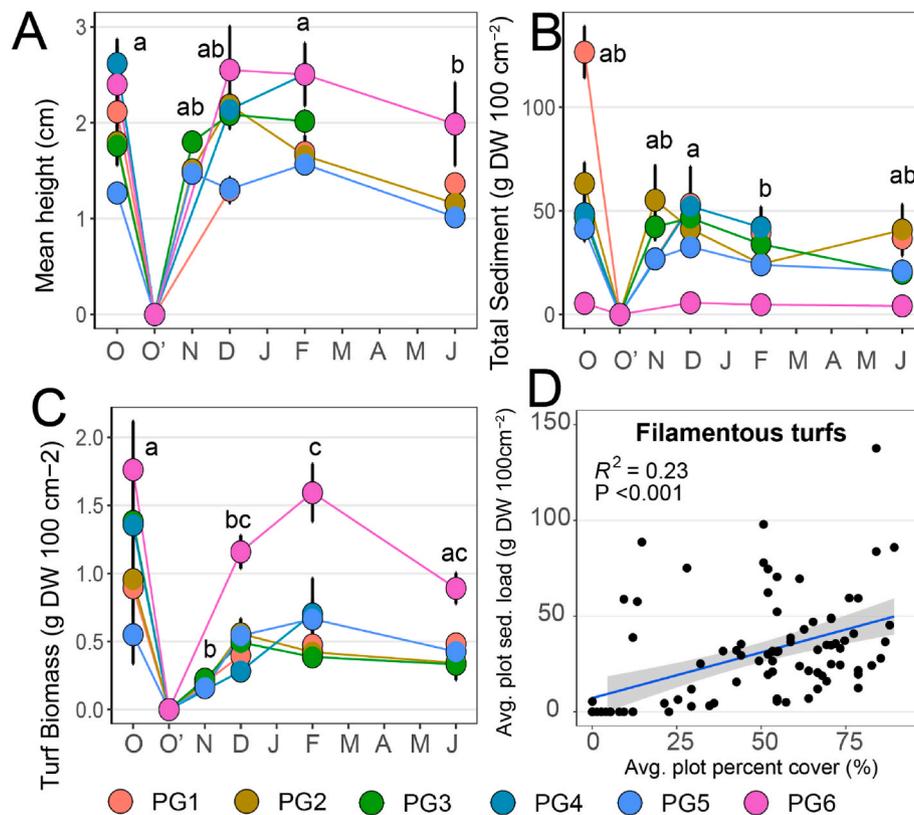


Fig. 2. Response of turf properties to experimental clearing. Turf mean height (A), sediment load (B) and biomass (C) within cleared plots across all sites. Dots and error bars depict means \pm standard error. Panel D depicts the relationship between plot-level average filamentous turf cover and sediment load throughout the duration of the experiment (234 days). Months are indicated by their capital letter and listed in chronological order. N = 53, 53, 22, 54, 54 and 45 for October (pre-sampling), October (post-sampling), November, December, February and June respectively.

turf matrix has a well-demonstrated ability to trap and retain sediment (Tebbett and Bellwood, 2019), often surpassing man-made sediment traps (Latrille et al., 2019; Schlaefer et al., 2022). Indeed, under the right conditions, ‘emptied’ turfs may have the capacity to regain initial sediment loads in ~ 14 days (Latrille et al., 2019; Schlaefer et al., 2022), which aligns with the experimental timeframe here. In our cleared plots, sediment retention was linked to the cover of filamentous turfs, which exhibited a significant positive relationship (linear regression, $R^2 = 0.23$, $p < 0.0001$) with plot-level average sediment load (Fig. 2D). Filamentous turfs are capable of completely regrowing after 4 days of being cropped by grazers (Bonaldo and Bellwood, 2011), and could therefore start accumulating sediment shortly after being cleared. Indeed, we also observed a rapid recovery of turf height and filamentous cover. In contrast, the cover of foliose algae, corallines or forest-forming algae showed no relationship (linear regression, $p = 0.25\text{--}0.84$) with the average plot sediment load, while corticated turfs (e.g. short *Dictyota*) exhibited a significant, but weaker negative relationship (linear regression, $R^2 = 0.11$, $p = 0.002$). These findings align with previous studies documenting density-dependent effects of erect seaweeds on sediment cover, with negligible effects at low densities (Wernberg et al., 2005) such as the ones present in the study area.

The experimental removal of algal turfs can lead to increases in the density of forest-forming seaweeds (e.g., (Chapman, 1984; Dayton et al., 1984; Gorman and Connell, 2009), but not always (Kennelly, 1987). This context-specificity suggests that any forest restoration activities should thoroughly assess the drivers of forest decline and turf expansion before implementation. Obtaining experimental evidence on the recovery capacity of turfs in each system will be crucial to support decisions on whether ecosystems should be restored to previous configurations. The density of forest-forming plants plays a key role in determining propagule pressure and the inhibitory effects of forests on

turfs (Layton et al., 2019b; Wernberg et al., 2005), and so it is likely that restoration efforts may be more successful in forested areas with turf patches (Gorman and Connell, 2009), rather than turf-dominated reefs like the ones studied here. Additionally, it is important to note that the loss of certain canopy species may not always lead to a turf-dominated endpoint, with alternative foundation species becoming dominant (Wernberg et al., 2020; Thomsen and South, 2019). This prompts a better understanding of the ecology of alternative ecosystem states before attempting restoration.

It is clear that algal turfs are expanding in many of the world’s shallow reefs as a consequence of escalating human pressures on the marine environment, including climate change (Doubleday and Connell, 2018; Filbee-Dexter and Wernberg, 2018; Pessarrodona et al., 2021a; Tebbett et al., 2023). Urgent action is needed to address some of the drivers leading to turf shifts (e.g. nutrient pollution, habitat destruction), and fortify ecosystems against future disturbances (Wood et al., 2019). Indeed, ecosystems can return to their historical states if drivers facilitating turf expansion are suppressed (Christie et al., 2019; Duarte et al., 2020; Kraufvelin et al., 2006). Yet, the rapid recovery of turfs observed here and the inevitability and irreversibility of some of drivers of shifts to turf-dominance also warrants consideration of the role they can play in sustaining biological functions (Hobbs et al., 2009; Vergés et al., 2019). Recent work shows that turfs can negatively affect ecosystem properties such as habitat structure and primary productivity (Pessarrodona et al., 2021a, 2022), but also lead to potential gains in others (e.g. epifaunal and herbivorous fish production (Bosch et al., 2022b; Kramer et al., 2013; Pessarrodona et al., 2021b). Adapting to these novel conditions as we further move into the Anthropocene will necessitate recalibrating ecosystem management and governance approaches (Bellwood et al., 2019; Hobbs et al., 2009), as well as recalibrating our own understanding of ecosystem ‘value’.

CRediT authorship contribution statement

Albert Pessarrodona: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Karen Filbee-Dexter:** Investigation, Supervision, Writing – review & editing. **Thomas Wernberg:** Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.106185>.

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