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ARTICLE

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Tiger reefs: Self-organized regular patterns in deep-sea cold-water coral reefs

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Abstract

Complexity theory predicts that self-organized, regularly patterned ecosystems store more biomass and are more resilient than spatially uniform systems. Self-organized ecosystems are well-known from the terrestrial realm, with "tiger bushes" being the archetypical example and mussel beds and tropical coral reefs the marine examples. We here identify regular spatial patterns in cold-water coral reefs (nicknamed "tiger reefs") from video transects and argue that these are likely the result of self-organization. We used variograms and Lomb–Scargle analysis of seven annotated video transects to analyze spatial patterns in live coral and dead coral (i.e., skeletal remains) cover at the Logachev coral mound province (NE Atlantic Ocean) and found regular spatial patterns with length scales between 62 and 523 m in live and dead coral distribution along these transects that point to self-organization of cold-water coral reefs. Self-organization theory shows that self-organized ecosystems can withstand large environmental changes by adjusting their spatial configuration. We found indications that cold-water corals can similarly adjust their spatial configuration, possibly providing resilience in the face of climate change. Dead coral framework remains in the environment for extended periods of time, providing a template for spatial patterns that facilitates live coral recovery. The notion of regular spatial patterns in cold-water coral reefs is interesting for cold-water coral restoration, as transplantation will be more successful when it follows the patterns that are naturally present. This finding also underlines that anthropogenic effects such as ocean acidification and bottom trawling that destroy the dead coral template undermine cold-water coral resilience. Differences in the pattern periodicities of live and dead coral cover further present an interesting new angle to investigate past and present environmental conditions in cold-water coral reefs.

KEYWORDS
cold-water coral reefs, deep sea, ecosystem engineering, feedbacks, self-organization, spatial ecology

INTRODUCTION

Framework-forming cold-water corals are ecosystem engineers (Jones et al., 1997) that increase their own food supply by affecting local currents (de Froe et al., 2022; Soetaert et al., 2016). With their dendritic skeletons, corals attenuate and slow down the currents around, within, and behind a coral patch, thus promoting turbulence in their lee (Bartzke et al., 2021; Hennige et al., 2021; Mienis et al., 2019). These flow modifications increase the rate at which coral polyps can filter food particles from the water column (Corbera et al., 2022; Hennige et al., 2021) and increase sediment deposition within the patch, stabilizing the coral framework and stimulating coral reef formation (Bartzke et al., 2021; Douarin et al., 2014; Wang et al., 2021). Downstream of a coral reef, the water is depleted of food particles (Corbera et al., 2022; Wagner et al., 2011), and around a coral reef, erosive scouring can negatively affect reef formation (Huvenne et al., 2009; Lim et al., 2018).

These ecosystem engineering mechanisms act on different spatial scales. The positive effects on coral growth as described above are effective on a small spatial scale, that is, at or within the coral framework, while negative effects act at a larger spatial scale (Corbera et al., 2022; van der Kaaden et al., 2020). When an organism affects its own growth differently at distinct spatial scales by the so-called "scale-dependent feedbacks," this can give rise to regular spatial patterns in the distribution of the organism, that is, "spatial self-organization" (Rietkerk & van de Koppel, 2008).

Suggestions of spatial pattern formation in cold-water coral reefs exist (Correa et al., 2012; van der Kaaden et al., 2020) but have not yet been formally demonstrated because of the challenges of obtaining spatial data in the deep sea. The deep sea, defined as the ocean below 200-m depth, is void of light, has a low temperature, high pressures, and strongly reduced food availability (Ramirez-Llodra et al., 2010). Nonetheless, framework-forming cold-water corals somehow acquire enough resources to build extensive reefs on the seafloor that are important biodiversity hotspots in the deep sea (Buhl-Mortensen et al., 2010; Henry & Roberts, 2007).

Ecosystem-wide patterns in natural systems may arise due to local-scale interactions between organisms and their environment, a process referred to as "self-organization" (Camazine et al., 2001). The formation of regular patterns allows an organism to grow at resource conditions that are insufficient to sustain a full cover of the organism. Pattern formation further provides an organism with a means to adjust gradually to changing environmental conditions (Bastiaansen et al., 2020; Rietkerk et al., 2021). However, regular spatial patterns can also signal the existence of an alternative, degraded stable state where the organism is absent, and recolonization is nearly impossible (Rietkerk et al., 2004). The ecosystem can tip between such patterned and bare uniform states after a large enough disturbance to its biomass and/or because of environmental conditions changing relatively fast (Rietkerk et al., 2004; Siteur et al., 2016). Such tipping events, to a state where cold-water coral reef formation is not possible, are known from geological history (e.g., Douarin et al., 2014; Hebbeln et al., 2019).

Currently, the oceans are changing at unprecedented rates, and the cold-water coral reef habitat is predicted to be reduced by 30%–79% by 2100 (Morato et al., 2020), which begs the question whether tipping points will occur in cold-water coral reef systems. Cold-water coral reefs, however, currently cope with highly variable environmental conditions (Findlay et al., 2013; Maier et al., 2019, 2020) and seem to be able to adapt to adverse local environmental conditions (Hebbeln et al., 2019; Kurman et al., 2017; Morrison et al., 2011). Predicting how these important ecosystems will respond to global change (e.g., ocean warming and acidification) and other anthropogenic stressors (e.g., bottom trawling) is vital. Investigating the cold-water coral ecosystem from the perspective of self-organization theory can increase our understanding of their expected response to global change and shed light on cold-water coral food supply and resource use.

The archetypical example of an ecological self-organized system is "tiger bushes," that is, vegetation-forming bands in arid conditions. Other examples from the terrestrial realm include peatlands (Eppinga et al., 2008) and dunes (Nield & Baas, 2009) and examples from the marine environment include mussel beds (van de Koppel et al., 2005), tropical coral reefs (Schlager & Purkis, 2015), and benthic diatoms (van de Vijsel et al., 2020). Self-organization is a ubiquitous, well-developed theory that, when applicable to a certain system, sheds light on many complex properties of that system. We here investigate regular pattern formation in cold-water coral reefs and interpret this system in light of self-organization theory.

We use video-transect observations and (geo-)statistical tools to investigate regular pattern formation in cold-water coral reefs. The videos were recorded along seven transects in the Logachev coral mound province, North-East Atlantic (De Clippele et al., 2021; Maier et al., 2021b). We analyzed whether reef cover shows regular spatial patterns that are indicative of self-organization by creating variograms at different spatial scales and using spectral analysis via Lomb–Scargle periodograms.

METHODS

Site description

The Logachev coral mound province is located on the southeast Rockall Bank margin, west of Ireland, and consists of cold-water coral mound clusters situated between 600- and 1100-m water depth. For this study, annotated video frames were used from seven transects on various mounds (Figure 1): transects 1–6 from De Clippele et al. (2021) and transect 7 from Maier et al. (2021a, 2021b).

Video-transect observation data

Video transects 1–6 were recorded between 600- and 850-m with the remotely operated vehicle "Holland-I" during the Changing Oceans Expedition 2012 cruise 073 (Roberts & Shipboard Party, 2013). From the high-definition videos, 1196 video frames were manually annotated for live coral, dead coral (i.e., the skeletal remains), coral rubble, sediment, rocks, and other substrates (see De Clippele et al., 2021 for more details). Transect 7 was taken between 600- and 700-m water depth with the Hopper camera frame deployed from the *RV Pelagia* cruise 64PE360 in October 2012, from which 192 video frames were annotated for the cover of live coral, dead coral (less degraded and more degraded framework), coral rubble, sediment, rocks, sponges, and other substrates (see Maier et al., 2021a, 2021b for more details). From the images, we used the benthic cover (in percentage [%]) of live reef-forming corals ("live coral") and dead coral framework ("dead coral") for our analyses. See Figure 2 for an example of three consecutive annotated images.

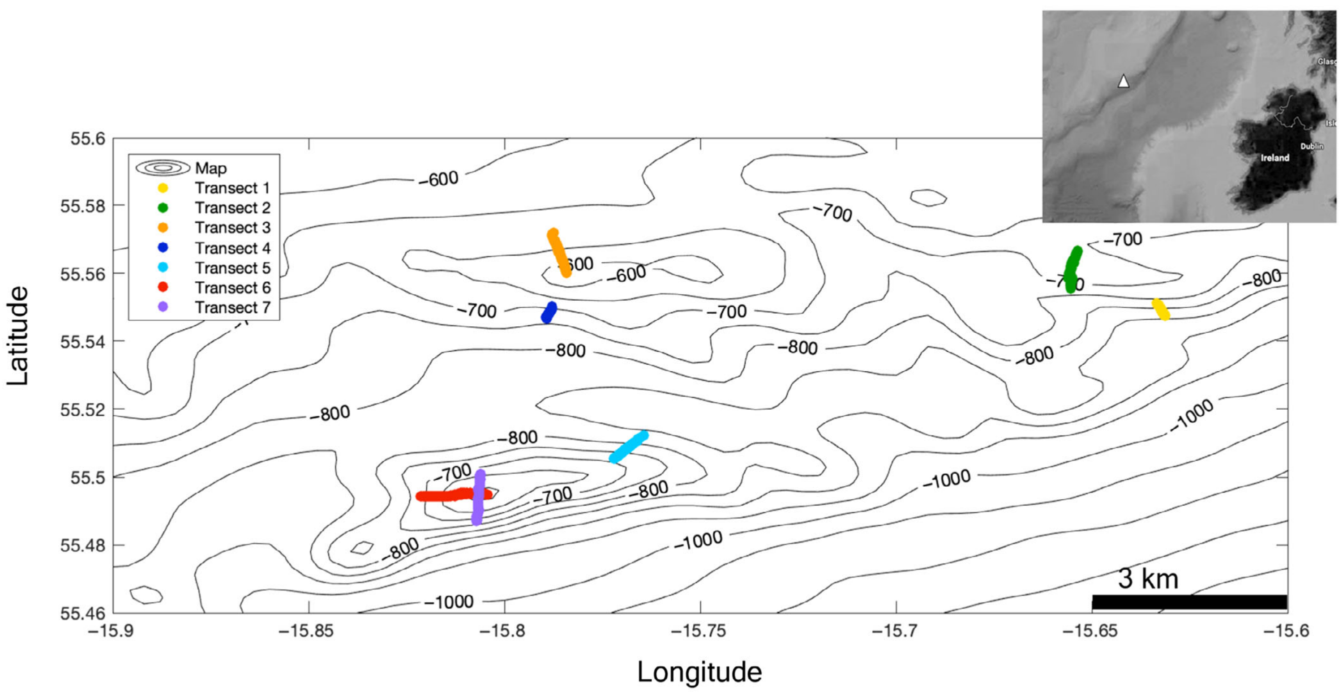

FIGURE 1 Map of part of the Logachev cold-water coral mound province with the seven transects. The inset in the top right shows the location of the Logachev coral mound province (white triangle).

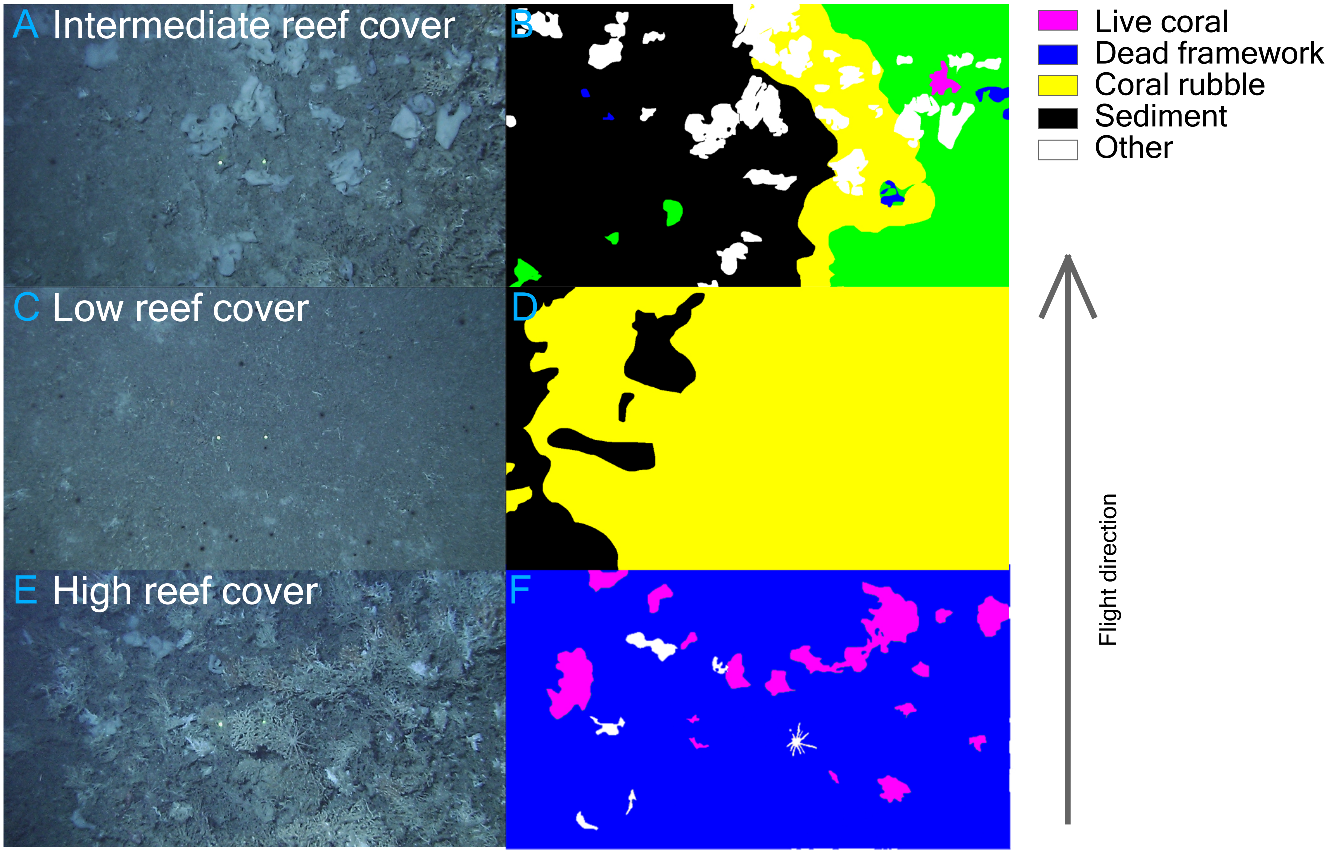

FIGURE 2 Three examples of consecutive images (<8 m apart) from transect 7 with (A, B) high reef cover (98.8%), (C, D) low reef cover (0.0%), and (E, F) intermediate reef cover (24.4%) with the annotated images (on the right), based on Maier et al. (2021a, 2021b). The laser dots in the images are 30 cm apart. The images were taken from the *RV Pelagia* cruise 64PE360 in October 2012. ©2012 Furu Mienis, The Royal Dutch Institute for Sea Research (NIOZ).

Geo-statistical analyses

We investigated whether regular spatial patterns exist in the placement of live and dead cold-water coral framework and live + dead framework ("reef") as well as in the topography (as recorded by the ship) along the transects using variograms and Lomb–Scargle periodograms (Radeloff et al., 2000; Rietkerk et al., 2000). Variograms depict the variance of data points at certain lag distance intervals. Since data points close to one another typically share more characteristics than data points separated by greater distance, variograms typically increase with increasing lag distance interval. A dip in the variogram at a certain lag distance interval indicates that the environment becomes more similar again after that distance from most data points. Any dip in a variogram therefore indicates that data points become more similar again after a typical distance, that is, the length scale. Since a variogram shows the variance at a certain distance from all data points along the transect, a dip in variance suggests a regular pattern. Variograms were produced for the entire transect length (from transects 1 to 7: 568, 1565, 3215, 1223, 1022, 1682, 1564 m) and for transect sections (see next).

The transects ran perpendicular to the bathymetry contour lines, that is, between mound foot and summit, crossing different depths (Figure 1), so patterns in reef cover might change along a cold-water coral mound due to, for example, water depth. To investigate whether regular patterns change along a transect, we also divided the transects into partly overlapping sections of about 600 m (568–606 m). From transects 1–7, the transects were divided into 1, 3, 7, 3, 2, 3, and 3 sections, respectively (Figure 3).

The regularity of the patterns was further investigated using Lomb–Scargle periodograms. Lomb–Scargle periodograms are similar in concept to Fourier transforms, which have been used in comparable studies to identify regularity in coral reef patterns (Davis & Chojnacki, 2017; Purkis et al., 2015; Sous et al., 2020), and have the advantage that they can be used on irregularly spaced data points. Fast Fourier transforms, by contrast, demand regularly spaced data points. The Lomb–Scargle periodogram fits sine functions to the

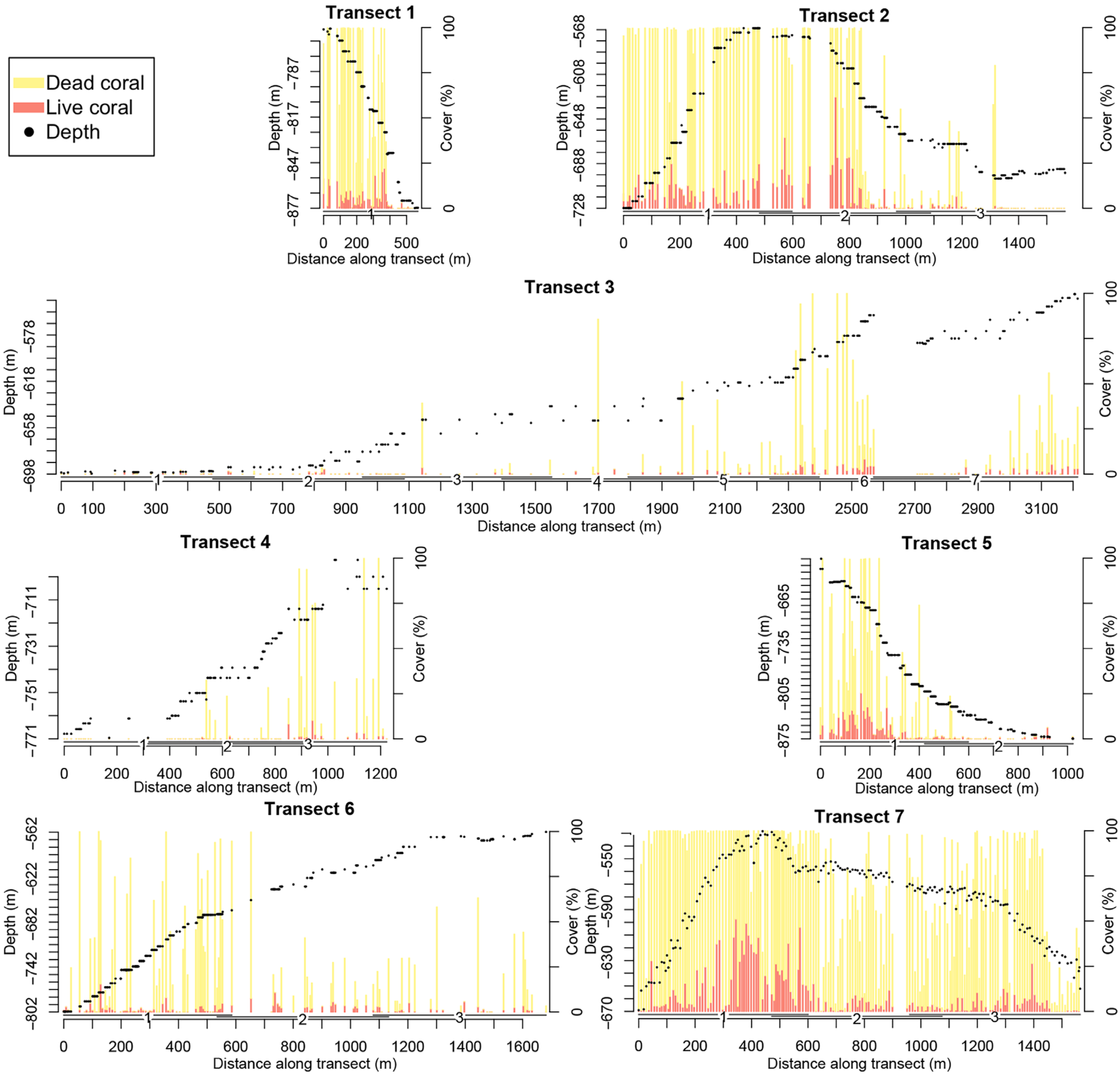

FIGURE 3 Stacked barplots show dead and live coral cover (in percent of the annotated image) of the seven transects. Each bar represents one annotated video frame. Note that for visibility, only frames at >5.5 m distance apart are shown. Black dots show the transect depth (left *y*-axis). Sections are indicated below the bars, on the *x*-axis.

data and extracts the frequencies that are significantly present in the data (VanderPlas, 2018). Significance ($p < 0.05$) levels of frequency peaks were calculated using the Lomb package in R from 1000 randomized transect(-section)s. We fitted sine waves of a maximum length scale of 2000 m, since frequencies that can be linked to regular pattern formation will be well below 2000 m (see next section). Lomb–Scargle analysis might thus identify length scales that are longer than the transect length.

Lomb–Scargle periodograms typically use a single dimension, often "time." Transects are positioned with latitudinal and longitudinal coordinates and are thus two-dimensional. For the individual data points, we therefore used the distance between the data points as "time"-dimension into the Lomb–Scargle analysis (i.e., the *x*-axis of Figure 3). For the variograms, we used the lag distance interval (i.e., the *x*-axis of Figure 4) as "time"-dimension into the Lomb–Scargle analyses. We detrended the variograms prior to the Lomb–Scargle

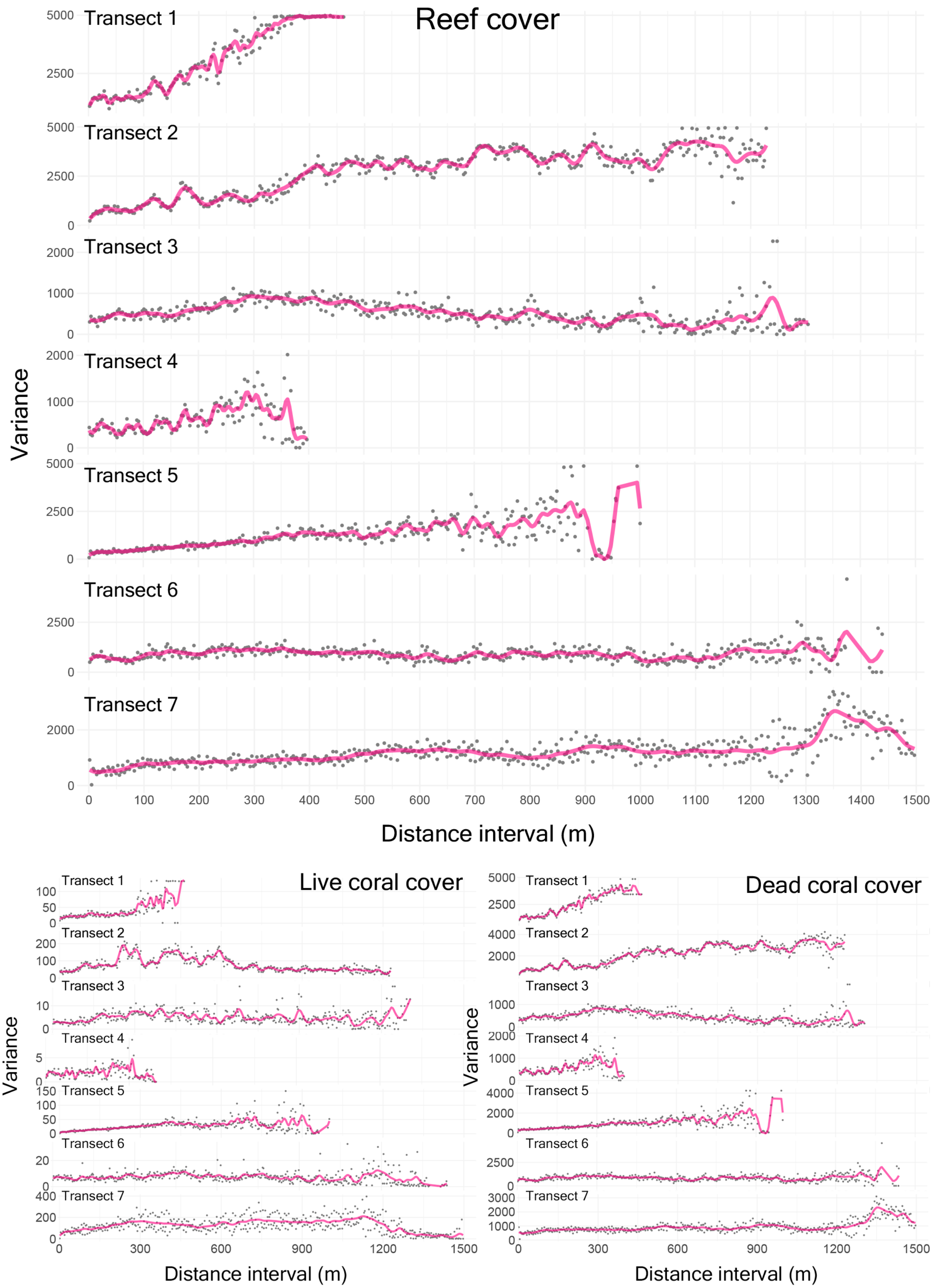

FIGURE 4 Variograms depict the variance in coral reef (live + dead coral) cover between data points at an increasing distance interval for the seven transects (from top to bottom). Variograms for live and dead coral cover on the seven transects are also shown. Note that the maximum distance between two data points, that is, the maximum value on the *x*-axis, is not necessarily the same as the transect distance in Figure 3. The red line depicts a fitted polynomial to highlight the general trend.

analysis to remove the increasing trend that is typical of variograms. Detrending the data before producing the variogram gave only few minor differences in significant frequencies.

Interpreting regular patterns in deep-sea coral reefs

We will now discuss how we determine which of the results can be confidently linked to regular patterns in the reefs, considering the advantages and drawbacks of various analyses. We investigate whether regular patterns are present in the cover of live and dead cold-water corals on the seafloor. In addition, we analyze the living and dead coral cover together ("reef" cover) since a layer of dead framework is often present beneath the living corals (Hennige et al., 2021; Maier et al., 2021a, 2021b), and image annotations for "live" coral therefore likely also incorporate "dead" coral. We will thus interpret periodicities in dead coral cover but not live coral cover as a pattern in the dead coral framework and not in the living corals. A periodicity in live coral cover, however, does not exclude that there is a similar periodicity in dead coral cover.

We further analyze the depth as recorded by the ship, since any regular patterns in cold-water coral reefs should similarly be found in the topography. Ship depth measurements, however, will not have been in exactly the same location as the video recordings and might be influenced by ship movements. A periodicity in seafloor topography can thus serve as an additional argument for regular pattern formation, but we will only interpret a periodicity in the seafloor topography as a regular pattern in the reef if we find similar periodicities in coral cover.

Periodicities found in the Lomb–Scargle analysis at wavelengths shorter than 10 m can indicate a regular pattern at that length scale but might also correspond to the spacing chosen in the variograms or to the distance between annotated video frames (VanderPlas, 2018). Significant periodicities at half or more of the length of a transect cannot be interpreted as a regular pattern with confidence as they do not cover a recurring pattern and more likely reflect that (live) reef cover is generally higher toward mound summits (Freiwald, 2002; Lim et al., 2017; Roberts et al., 2005). We therefore ignore periodicities at length scales shorter than 10 m and longer than half the transect length, as we cannot confidently link those patterns to real regular patterns in reef cover.

Regular patterns can more easily be picked up on longer transects (Davis & Chojnacki, 2017), but pattern periodicities might change with depth, so we complemented the analysis of entire transects with the analysis of transect sections. Lomb–Scargle analyses on the raw data will probably provide the best evidence for a regular pattern in reef cover, but only work well when the transect is relatively straight. We thus interpret periodicities in the raw data as a regular pattern, provided that the transect was relatively straight, which can easily be seen by the difference between the raw transect length and variogram length (Table 1). Since regular patterns might be missed on a straight transect when they are regular in another direction than the transect, we complement the analysis of the raw data with the variograms.

Variograms provide a measure for regularity in all directions and do not require a straight transect, but results from variograms should be interpreted as a regular pattern with care (Radeloff et al., 2000). In the variograms, we interpret periodicities as a regular pattern when the length scale is larger than 10 m and shorter than half of the transect length. For the transect sections, we interpret some periodicities above half of the section length as a regular pattern when similar periodicities were found on the entire transect or on other sections.

RESULTS

Dead and live coral reef cover were found to vary together: dead coral cover is typically high when live coral cover is high and low when live coral cover is low (Spearman correlation coefficient $r_S = 0.66$, $p < 1 \times 10^{-15}$; Figure 3). Live corals with dead coral framework can together be seen as the "reef" (see Figure 2 for an example of three consecutive video frames with high, low, and intermediate reef cover). A typical trend in reef cover is not evident in the raw data, but reef cover does seem to fluctuate along the transect.

Variograms show that these fluctuations are regular patterns in reef cover (Figure 4), as the variance between data points oscillates on all transects. The variance in reef cover also typically increases as the distance between data points increases, except for transects 3 and 6. On transect 3, variance increases in the first 300 m, and then decreases, and on transect 6, variance is more constant. Variograms for dead coral cover are very similar to the variograms for reef cover. The variograms for live coral cover are different from the variograms for reef cover but also show fluctuations on all transects. Variograms for live coral cover do not show a general increase with increasing distance interval, except for transect 1.

Lomb–Scargle analysis identified regular patterns in topography, reef cover, and dead and live coral cover for

TABLE 1 Peaks identified by Lomb–Scargle analyses of the raw transect data (raw) and variograms (vgm) for the seafloor topography (depth), reef cover (live + dead coral cover), dead coral cover, and live coral cover.

Transect or section	Data type	Length (m)	Peaks identified by Lomb–Scargle analysis			
			Depth	Reef cover	Dead coral	Live coral
Transect 1	raw	568	568	568	568	
	vgm	463	222, 444	444		444
Transect 2	raw	1565	782, 1565	1565	1565	1565
	vgm	1228	1224	**175**, **306**, 1224	**175**, **306**, 1224	**153**, **175**, 612, 1224
2.1	raw	597	597	**75**, **199**	**75**, **199**	**100**
	vgm	461	**154**, 230, 461	**77**	**77**, 230	461
2.2	raw	606	606	606	606	606
	vgm	481	**79**, **159**, 476	476		476
2.3	raw	597	**149**, 597			
	vgm	425	**208**, 416			
Transect 3	raw	3215	201, 643, 1607	643, 804	643	643, 804
	vgm	1305	321, **429**, 643, 1286	**429**, 643, 1286	**429**, 643, 1286	1286
3.1	raw	610				
	vgm	396	**77**, 387	**65**, **77**		
3.2	raw	605	605			
	vgm	181	45	179		179
3.3	raw	598				
	vgm	146	**71**			
3.4	raw	604	101			
	vgm	119	115			
3.5	raw	604	302, 604			
	vgm	255	251			
3.6	raw	597	299, 597	597	597	597
	vgm	429	**211**, **422**	**211**, **422**	**211**, **422**	**422**
3.7	raw	645	323, 645	645	645	
	vgm	375	**185**, 370	**185**, 370	**185**, 370	370
Transect 4	raw	1223	1223			
	vgm	397	388	388	388	388
4.1	raw	598	299			
	vgm	191	187			
4.2	raw	602	602			
	vgm	310	101, 302			
4.3	raw	595	595			
	vgm	225	219	219	219	
Transect 5	raw	1022	511, 1022	511, 1022	1022	511, 1022
	vgm	1001	223, 297, 892			892
5.1	raw	598	598	598	598	598
	vgm	585	**262**, 523	**262**	**262**	**262**, 523
5.2	raw	601	127, 300, 601			
	vgm	574	102, 169, **254**			

TABLE 1 (Continued)

Transect or section	Data type	Length (m)	Peaks identified by Lomb–Scargle analysis			
			Depth	Reef cover	Dead coral	Live coral
Transect 6	raw	1682	561, 841, 1682			
	vgm	1438	**523**, 1046	**349**	**349**	**523**
6.1	raw	586	586	586	586	
	vgm	681	**493**			**62**
6.2	raw	598	37, 75, 85, 100, 149, 199, 598			
	vgm	385	144, **287**	**287**	**287**	
6.3	raw	602	301, 602			
	vgm	495	179, **358**		**358**	
Transect 7	raw	1564	782, 1564	**391**, 1564	**391**, 1564	782, 1564
	vgm	1537	769, 1538	220, **256**, **308**, **385**, **513**, 769	5, **256**, **385**, **513**, 769, 1538	5, 9, 769, 1538
7.1	raw	600	600		600	600
	vgm	585	8, 9, 581			5, 9
7.2	raw	603	201			**302**
	vgm	600	**300**, 600	7, 600	7	5, 9
7.3	raw	604	9, 604			
	vgm	594	593	593	593	593

Note: Peaks are in terms of length scales (in meters). Peaks that can be associated with confidence to regular patterns appear in boldface. Blank cells indicate that no regular patterns were found for this type of data in the analyses.

all transects, with length scales of 5–1607 m (Table 1 and Figure 5). When analyzing 600-m long, partly overlapping transect sections, Lomb–Scargle analysis identified regular patterns in all transects. Given the restrictions of the various analyses (as outlined in the *Methods*), we found periodicities that can be interpreted as a regular pattern in coral reefs on transects 2, 3, 5, 6, and 7 at length scales between 62 and 523 m (Table 1 and Figure 6). Typical length scales are around 70 m (transects 2, 3, and 6), 160 m (transect 2), 200 m (transects 2 and 3), 280 m (transects 2, 5, 6, and 7), 390 m (transects 3 and 7), and 510 m (transects 6 and 7). So, similar length scales are found at different transects, and different length scales are found on the same transects. In some instances, the periodicity of the dead framework is double that of the living corals (transect 2 and transect section 2.1) or the periodicity of the living corals is double that of the dead framework (transect section 3.6 and transect 6). Hence, both the variograms and Lomb–Scargle analysis support the notion of regular spatial patterns in reef cover at multiple wavelengths.

In addition to the transects, we analyzed regular pattern formation in 168 images from transect 7 with a maximum diameter of 4.5 m. We downscaled the image resolution by a quarter and created variograms from 0 to 4.5 m at intervals of 0.05 m for live and dead coral cover, and reef (live + dead) coral cover. Following the same protocol as outlined for the transects, we identified regular patterns at length scales between 0.69 and 1.12 m in 11 images (Appendix S1: Figure S1). Regular patterns at these scales might be related to coral morphology, which is beyond the scope of the present paper (but see e.g., De Clippele, Huvenne, et al., 2017; Hennige et al., 2021; Monismith, 2007). We did not extend the analysis to include more images since only few images displayed convincing regular patterns (based on our interpretation as outlined in *Methods*), and the patterns are likely formed through different mechanisms than the reefs.

DISCUSSION

Regular patterns in cold-water coral reefs

We show that reef cover on several transects (2, 3, 5, 6, and 7) on cold-water coral mounds display regular spatial patterns at length scales between 62 and 523 m (Table 1 and Figure 6). Transects 1 and 4 either do not have regular patterns or were too short for the identification of such patterns. The length scales found in this study compare

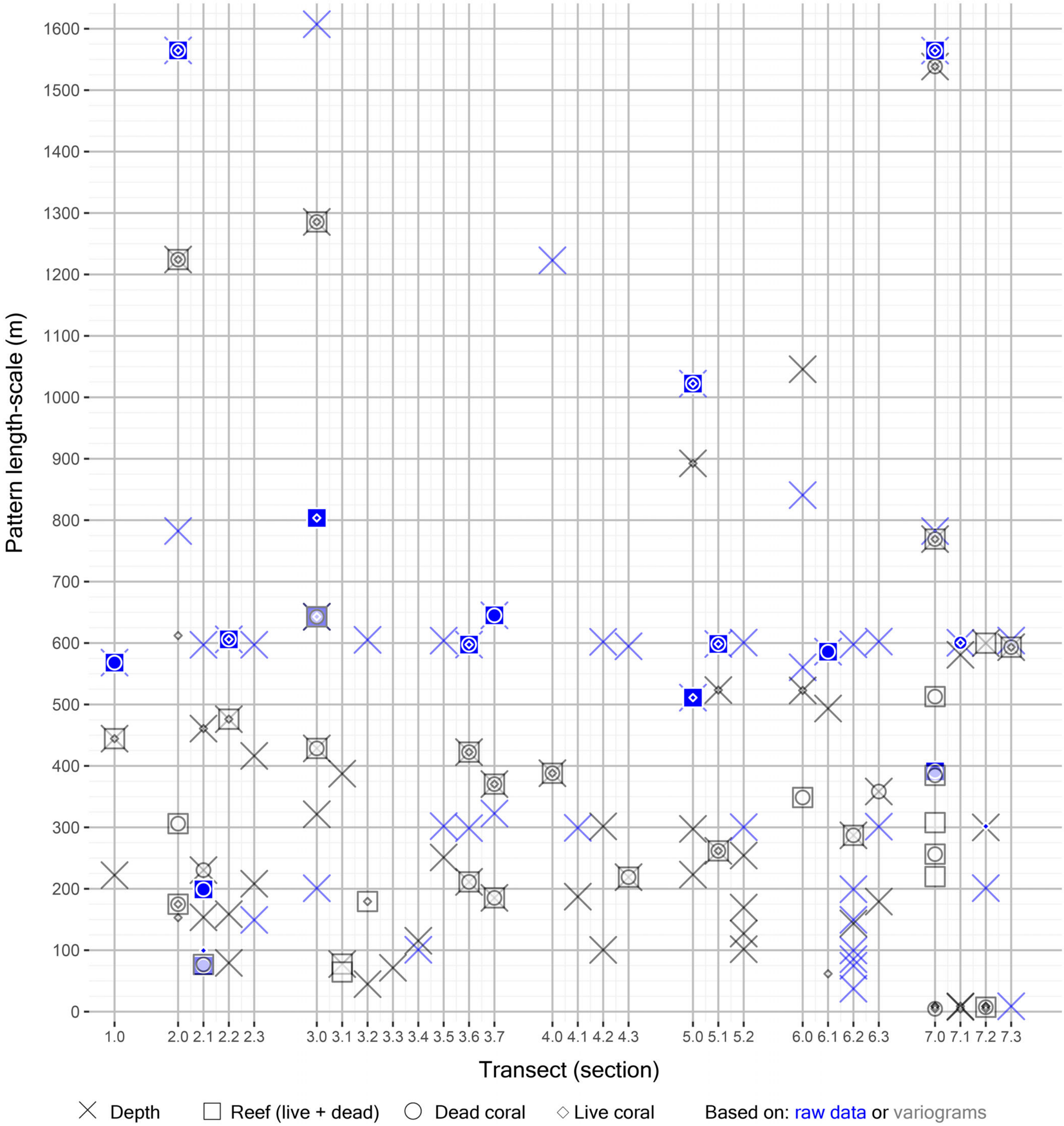

FIGURE 5 All peaks as identified by Lomb–Scargle analysis of the raw data or variograms of the seafloor topography (depth), coral reef cover (live + dead corals), dead coral cover, and live coral cover. The peaks are organized by entire transects (1–7) and transect sections (2.1, 2.2, 2.3, 3.1, etc.) on the *x*-axis. The *y*-axis shows the peak length scale.

well with reports from other studies. For example, Correa et al. (2012) identified regular cold-water coral ridges at length scales between 50 and 200 m, which is similar to regular cold-water coral ridges reported by Matos et al. (2017). De Clippele, Gafeira, et al. (2017) found that cold-water corals cluster into mini mounds of 13–108 m in size. Cold-water coral reefs presented in Bøe et al. (2016) form ridges that are spaced apart about 400 m, and Cathalot et al. (2015) present aligned cold-water coral reefs of 120 m in width that grow into the prevailing current, similarly to bands of arid vegetation. We thus hypothesize that the cold-water coral reefs on the coral mounds at Logachev cold-water coral mound province form regular bands or (aligned) clusters (as in Bøe et al., 2016; Cathalot

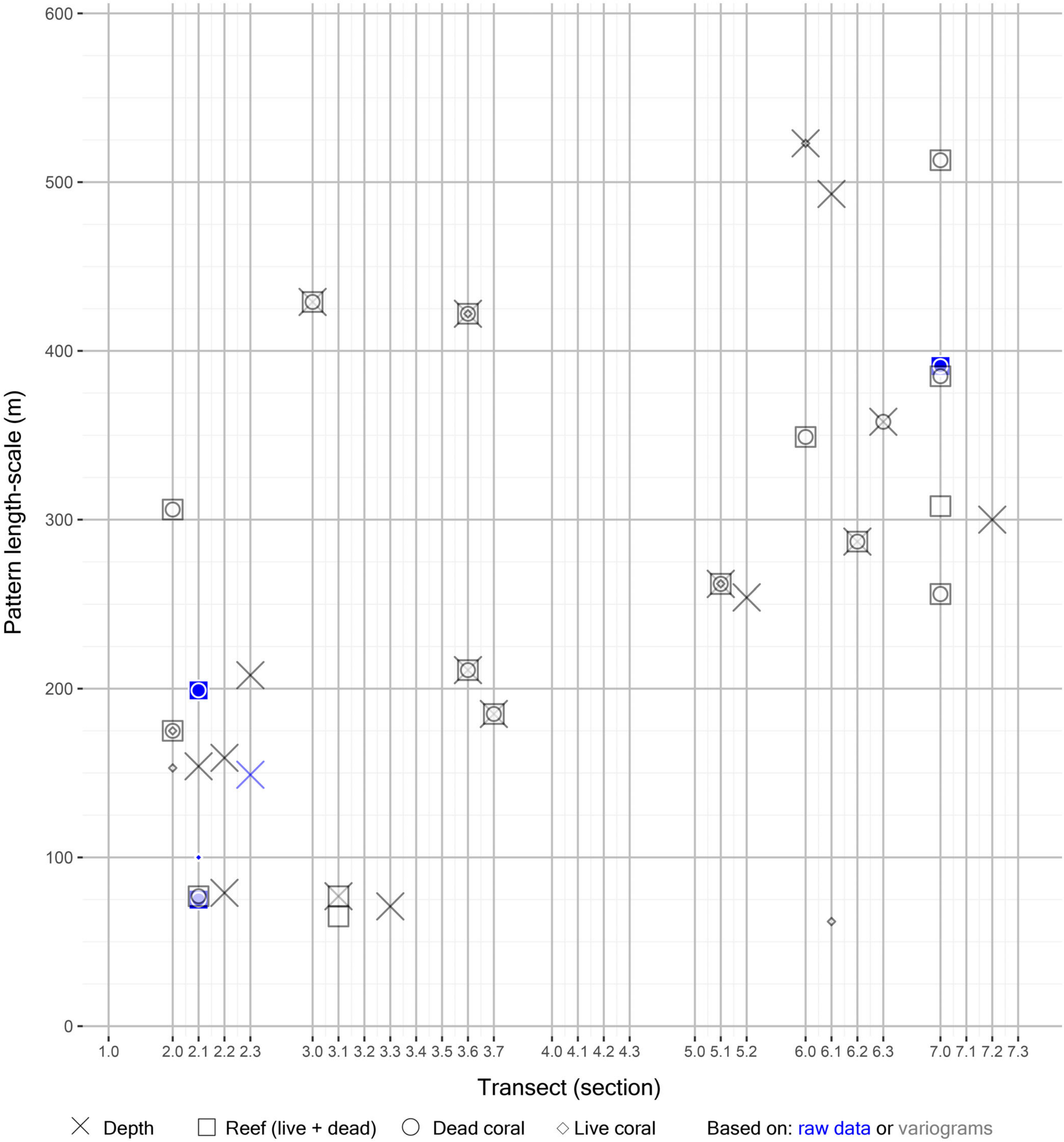

FIGURE 6 Similar to Figure 5, but this figure displays only the peaks identified by the Lomb–Scargle analysis of the raw data or variograms that can be associated with regular patterns in the seafloor topography, coral reef cover (live + dead corals), dead coral cover, and live coral cover.

et al., 2015; Correa et al., 2012; Matos et al., 2017), although patterns may also be as patches (as in De Clippele, Gafeira, et al., 2017).

In agreement with ecosystem engineering and self-organization theory, the regularity in the configuration of cold-water coral reefs on the seafloor provides observational affirmation that cold-water corals are ecosystem engineers that organize themselves by modifying their local environment. An alternative hypothesis for the explanation of regular patterns in cold-water coral reefs is that the corals simply follow specified, non-engineered environmental conditions. One such condition could be antecedent topography with regular patterns, such as karst or sand waves. Antecedent karst can be ruled out because the coral mounds in this study area are biogenic (Mienis et al., 2006; van der Land et al., 2014), and regular patterns in karst are not easily detected by analyses such as ours (Davis & Chojnacki, 2017). The colonization of sand waves is also unlikely as cold-water corals need a hard substrate to settle. The colonization would also likely change the morphology of the sand wave by fixing the sand, as is the case for vegetation on dunes (Tsoar & Blumberg, 2002), so self-organization processes would take over after initial settlement.

Known environmental conditions that restrict the occurrence of reef-forming cold-water corals are aragonite saturation, temperature, and oxygen (Barbosa et al., 2020; da Costa Portilho-Ramos et al., 2022; Davies et al., 2008; Davies & Guinotte, 2011). Aragonite saturation, temperature, and oxygen will, however, not vary regularly on length scales at which regular patterns are found in this study, so these environmental factors are unlikely explanations for the observed patterns. Currents and organic matter availability are important for cold-water coral occurrence (da Costa Portilho-Ramos et al., 2022; De Clippele et al., 2021) but are also modified by coral reef presence, as demonstrated by observational, experimental, and modeling studies (e.g., Bartzke et al., 2021; Corbera et al., 2022; Davies et al., 2009; Soetaert et al., 2016; Wagner et al., 2011). We suggest that the regular patterns found in the cold-water coral reefs at the Logachev cold-water coral mound province are the result of self-organization. In analogy with the archetypical example of self-organized tiger bushes in the terrestrial realm, we refer to the regular reef patterns as "tiger reefs." Next, we will discuss how these regular patterns in cold-water coral reefs at Logachev cold-water coral mound province link to self-organization theory.

Mechanisms for self-organization in deep-sea corals

Interestingly, variance in reef cover on transects 2, 5, and 7 oscillates but also steadily increases with increasing distance interval. This suggests that reef cover displays regular patterns on those transects, while overall reef cover changes steadily. Cold-water corals largely depend on the capture of sinking organic matter produced in the sunlit upper ocean (de Froe et al., 2022; Duineveld et al., 2007), meaning that their main food source is generally limited in the deep sea (Cathalot et al., 2015; Hennige et al., 2021; Soetaert et al., 2016). Several explanations already exist for the conundrum of highly productive reefs under seemingly food-limited conditions (Cathalot et al., 2015; van Oevelen et al., 2009). For example, cold-water corals typically occur at locations of increased export production (da Costa Portilho-Ramos et al., 2022; Maier et al., 2023; Wienberg & Titschack, 2017). Self-organization in cold-water coral reefs can be an additional explanation for how cold-water coral reefs can maintain a high productivity with many associated fauna in the deep sea, or simply an emergent characteristic of cold-water coral ecosystems.

Regular patterns in ecosystems typically arise when resource inputs are too low to sustain a homogenous cover of, for example, vegetation, mussels, or corals (Rietkerk & van de Koppel, 2008). By engineering their environment, ecosystem engineers can extract resources from a broader area to improve their conditions only locally, giving rise to regular patterns in their spatial configuration (Bastiaansen et al., 2020; Rietkerk & van de Koppel, 2008). In this patterned state, ecosystem engineers, such as corals, can be present under environmental conditions that would not otherwise sustain their growth. Resource depletion through filter feeding by the inhabitants of cold-water coral reefs (van Oevelen et al., 2009; Wagner et al., 2011) is thus a likely mechanism for self-organization in cold-water coral reefs. Other mechanisms than resource depletion that provide a negative feedback at some distance of the reefs can also be responsible for regular pattern formation in cold-water coral reefs (Rietkerk & van de Koppel, 2008). Such mechanisms most likely would be related to hydrodynamic processes, as cold-water coral reefs are known to affect the hydrodynamics and vice versa (Corbera et al., 2022).

The length scale of the regular reef pattern might be coupled to the scale at which the negative feedbacks act, as theory shows that the length scale of a self-organized pattern adjusts as environmental conditions worsen (Rietkerk et al., 2004; Rietkerk & van de Koppel, 2008). Recent advances in self-organization theory, however, show that many different pattern configurations can exist for similar environmental conditions and similar pattern configurations can exist under different environmental conditions (Bastiaansen et al., 2018; Rietkerk et al., 2021; Siteur et al., 2014). Next, we will discuss how the length scales that we found in the cold-water coral reefs at Logachev cold-water coral mound province might relate to the different concepts known from self-organization theory.

Self-organized ecosystems can evade tipping points

In terrestrial arid ecosystems, vegetation forms bands ("tiger bushes") as it captures water that runs over sloping ground, depleting the soil behind the band and leaving it unsuitable for vegetation growth. Depending on ground slope (i.e., resource input), the vegetation bands can be further apart and wider, or closer together and smaller (i.e., have different periodicities; Bastiaansen et al., 2018; Siteur et al., 2014). Live and dead coral framework often occur together (Figure 3), and on transect 2, section 3.6, and section 5.1, the living corals indeed displayed the same pattern configuration as the dead coral framework. On transect 2 and in section 2.1, however, the periodicity of the dead framework was double that of the living corals, which can happen when living corals die in the center of a reef patch or band (as described by Wilson, 1979 and observed on mini-mounds by De Clippele, Gafeira, et al., 2017; Lim et al., 2017). This suggests that the configuration of living cold-water corals can be smaller or wider, perhaps in response to environmental changes or disturbances, as theory predicts for self-organized ecosystems (Bastiaansen et al., 2018; Rietkerk et al., 2021; Siteur et al., 2014).

Historically, self-organized regular patterns in arid vegetation were thought to indicate that the ecosystem could suddenly change from a vegetated to a bare state (Rietkerk et al., 2004). However, recent work shows that tiger bushes can withstand large long-term environmental changes and recover after short-term disturbances through gradual adjustments to their pattern configuration (Bastiaansen et al., 2020; Rietkerk et al., 2021). Cold-water coral reefs might similarly be able to adjust gradually to environmental changes, so we hypothesize that they would respond as follows to changing environmental conditions: When resource input decreases or stress increases, the center of a living reef band would die off, allowing two thinner reef bands to survive and causing a change in the periodicity of the spatial pattern. As environmental conditions improve, resource inputs can sustain broader reef bands, allowing the living reef to expand again, causing another change in the periodicity of the spatial pattern.

System history: A template for patterns

Self-organized systems can be very difficult to restore after a large disturbance to the organism's biomass, because the system functioning depends on the history of the formed interactions (so-called "hysteresis"; Dizon & Yap, 2006; Rietkerk et al., 2004). However, when a template for regular spatial patterns exists, restoration of self-organized systems after a disturbance can be more successful (Berghuis et al., 2020; Colden et al., 2016; De Paoli et al., 2017). The live corals likely actively form reefs through self-organization, while the corals beneath the living reef die, creating a habitat of dead coral framework (Cathalot et al., 2015; De Clippele, Gafeira, et al., 2017; Hennige et al., 2021; Maier et al., 2021b) that has the same pattern configuration. The dead framework further provides hard substrate for settlement and propagation of living corals (Lim et al., 2018; Vertino et al., 2010), thus acting as a template for regular spatial patterns. The spatial configuration maintained by the dead coral framework can thus provide resilience to cold-water coral reefs by increasing the chance of successful recovery and recolonization of living corals after disturbances.

Unfortunately, ocean acidification dissolves the dead coral framework (Hennige et al., 2020) and anthropogenic activities such as bottom trawling (Huvenne et al., 2016) can destroy the template patterns. Since regular patterns can only return through self-organization of the living corals, destroying the existing pattern template possibly causes irreversible damage to the cold-water coral ecosystem. Furthermore, despite high cost and complex logistics, cold-water coral reef restoration in the form of transplantation of cold-water corals is being increasingly considered as a method of conservation intervention (Danovaro et al., 2021; Montseny et al., 2020). We suggest that the efficacy of such restoration efforts is more likely to be successful when reefs are transplanted (on artificial structures) following the regular patterns that are naturally present (Berghuis et al., 2020; Colden et al., 2016; De Paoli et al., 2017; Silliman et al., 2015).

Evaluating the impact of climate change on cold-water coral reefs using regular patterns

The engineering ability of self-organizing ecosystem engineers allows them to adjust gradually to environmental conditions, providing resilience in the face of environmental change (Rietkerk et al., 2021). But to adjust gradually to changing environmental conditions, organisms must be able to propagate "freely," which, in the case of cold-water corals, could be hampered by the dead coral framework that is essentially immobile. This immobility, or "system history," causes the self-organized patterns to persist under changing environmental conditions until a critical point. At this critical point the current configuration of the living system cannot be sustained, and it suddenly switches to another configuration (Bastiaansen et al., 2020; Siteur et al., 2014). This new configuration typically has double the periodicity of the old configuration (so-called "period doubling"). For cold-water corals, this would imply that the periodicity of the living reef is expected to double while the periodicity of the dead coral framework remains unaltered.

On transect section 3.6 and transect 6, the periodicity of the pattern of the living reef was double that of the pattern of the dead coral framework, which could be an indication of period doubling. In systems where the underlying environmental conditions are spatially heterogenous, as would be expected on a cold-water coral mound with significant depth-differences, self-organized systems also typically react to environmental changes by sudden large adjustments to their pattern periodicity (Bastiaansen et al., 2022). Differences in the pattern periodicity of living cold-water corals as compared with the dead coral framework, especially when the periodicity is (almost) double that of the dead framework, can thus be a sign that the ecosystem is currently experiencing worse environmental conditions than in the past. Analyzing the regular patterns in live and dead cold-water coral cover can therefore provide an interesting angle when investigating the impact of environmental changes on a cold-water coral ecosystem.

CONCLUSION AND OUTLOOK

In this paper, we present evidence for the existence of regular (periodic) spatial patterns in cold-water coral reefs that are likely the result of self-organization through scale-dependent feedbacks between cold-water coral reefs and their environment. Food depletion downstream and around cold-water coral reefs is a likely mechanism for self-organization. Characteristics of self-organized systems, well-established for terrestrial and shallow-water examples, likely also apply to cold-water coral ecosystems: Regular pattern formation might provide a means by which the cold-water corals can adjust gradually to environmental change.

Self-organized systems can adjust to environmental change by reorganizing their spatial configuration. We found indications that cold-water corals might similarly adjust their spatial configuration to the environmental conditions. The immobile dead framework underneath the living corals further acts as a template for pattern formation, which increases the chance of recovery of live corals after disturbances. However, ocean acidification and anthropogenic activities such as bottom trawling that remove the reminiscent spatial reef patterns are detrimental for cold-water coral resilience and undermine the chances for cold-water coral recovery. Differences in the pattern periodicities of live and dead coral cover also present an interesting new angle to investigate past and present environmental conditions at cold-water coral reefs.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from Maier et al. (2021a, 2021b) are available from Zenodo: https://zenodo.org/record/4076147. Data from De Clippele et al. (2021, 2023) are available from Pangaea: https://doi.pangaea.de/10.1594/PANGAEA.959612.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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