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contributed equally to this work.

Key Points:

- Video transects over tidal sand waves yielded detailed spatial information of both benthic organisms and small-scale seabed morphology
- Both epibenthos and endobenthos are more abundant in sand wave troughs compared to the crests
- Sand ripples are less abundant and more often irregularly shaped in the troughs, suggesting variations in seabed roughness over sand waves

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


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Video Transects Reveal That Tidal Sand Waves Affect the Spatial Distribution of Benthic Organisms and Sand Ripples

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Abstract The sandy seabed of shallow coastal shelf seas displays morphological patterns of various dimensions. The seabed also harbors a rich ecosystem. Increasing pressure from human-induced disturbances necessitates further study on drivers of benthic community distributions over morphological patterns. Moreover, a greater understanding of the sand ripple distribution over tidal sand waves may improve morphological model predictions. Here we analyzed the biotic abundance and ripple morphology in sand wave troughs and crests using video transects. We found that both the epibenthos and endobenthos are significantly more abundant in sand wave troughs, where ripples are less abundant and more irregularly shaped. Finally, we show that camera systems are relatively quick and effective tools to study biotic spatial patterns in relation to seabed morphology.

Plain Language Summary Coastal seabeds are important areas for human activities and constructions and are also inhabited by many organisms, collectively referred to as benthos. The interaction of tides, wind, sand and biology leads to the growth of large, rhythmic seabed patterns. They can grow up to several meters high, hundreds of meters long, and shift a few meters per year. Computer models can predict this behavior, but they lack understanding of biological processes and variations in sand ripple patterns. To increase the understanding of these effects, we present findings from two video transects, for which we lowered a video camera to the seabed and recorded both organisms and sand ripples for ~200 m. We show that, relative to crests, troughs have more benthic organisms, and sand ripples are often absent or less regularly shaped. Finally, we show that a camera is a quick and effective tool to study benthic spatial patterns.

1. Introduction

Worldwide, coastal seas are extensively used for numerous human activities. Fisheries, shipping, sand extraction, land reclamation, wind farms, oil and gas production, and recreation are putting an increasing pressure on the coastal environment (Eigaard et al., 2017; Halpern et al., 2008). Sustainable use of available resources requires information on the environmental impact of these activities. In this respect, knowledge concerning the distribution of benthic communities in these areas is crucial. It is well known that benthic community composition is related to various abiotic variables, such as sediment type, grain size, temperature, and chlorophyll- α content (Heip et al., 1992; Künitzer et al., 1992; Reiss et al., 2010). However, less is known about how macrobenthic species relate to both large and small-scale morphological bed patterns.

Bed patterns are common features in sandy coastal shelf seas and estuaries, shaped by the interplay of tides, currents, waves, and biology. Various types of offshore bed forms can be found, for instance, sand banks (Stride, 1982), long bed waves (Knaapen et al., 2001), tidal sand waves (van Veen, 1935), mega ripples (Stride, 1982), and sand ripples (Allen, 1984). Of all the described bed forms, sand waves are the most relevant to study as their dynamic behavior can pose a threat to offshore civil engineering constructions, such as pipelines (Németh et al., 2003) and cables to wind farms (Roetert et al., 2017). Sand wave crests are perpendicular

to the tidal current (Huntley et al., 1993), with heights up to 10 m, wavelengths of 100–1,000 m, and migration rates of several meters per year (Damen et al., 2018; van Dijk & Kleinhans, 2005). They are formed at time scales of 1–10 years (Knaapen & Hulscher, 2002). The smallest morphological bed patterns are mega ripples and sand ripples, which are usually superimposed on sand waves (van Santen et al., 2011). Their wavelengths are of the order of meters to centimeters, respectively, and they are highly mobile, migrating up to several meters per day (Idier et al., 2002). Both may serve as roughness indicators in morphological models (Idier et al., 2004). Sand waves commonly occur in many areas around the world but are primarily observed in coastal, semishallow areas (20 to 40 m water depth) with strong tidal currents (Fredsoe & Deigaard, 1992), for instance, in the Taiwan Strait (Boggs, 1974), the Bahia Blanca estuary (Aliotta & Perillo, 1987), the Bisaneto Sea (Katoh et al., 1998), and in the North Sea (McCave, 1971).

The coastal seabed is inhabited by rich benthic communities (Callaway et al., 2002). Benthic species may influence near-bed processes on a large spatial and temporal scale (Lohrer et al., 2005; Rabaut et al., 2007; Widdows & Brinsley, 2002). By their burrowing activity, sea urchins (*Echinocardium cordatum*) reduce seabed stability (Lohrer et al., 2005). Dense aggregations of the tube-building polychaete sand mason worm (*Lanice conchilega*), on the other hand, decrease near-bed flow velocities, and stabilize the seabed (Borsje et al., 2014; Eckman et al., 1981; Rabaut et al., 2007). Process-based modeling studies have shown that such activities can significantly influence sand wave dimensions (e.g., Borsje, de Vries, et al., 2009). Contrarily, coastal bed forms are reported to drive the spatial distribution of benthic communities. The crests of large-scale tidal sandbanks in the North Sea were shown to harbor a less dense and less diverse community, compared with the troughs (van Dijk et al., 2012). Baptist et al. (2006) studied sand wave effects on benthos spatial distribution. For two out of four seasons, they found different species compositions between the troughs and crests. However, they only studied endobenthos with a limited spatial resolution, due to their employed methodology (boxcores). Moreover, knowledge on benthos distribution in relation to small-scale morphology could not be acquired. No clear relationship has yet been delineated between seabed morphology and benthic communities of sand waves.

Both coastal engineering projects and ecological maintenance policies heavily rely on monitoring in order to assess the feasibility of engineering projects and the status quo of benthic communities, respectively. Morphological and ecological models complement these data as they allow for predicting the evolution of bed patterns and communities. Several existing models deal with sand wave evolution. Hulscher (1996) was the first to use a process-based model to study the initial growth phase, after which many additions were made (e.g., Campmans et al., 2017, and references therein). Also, more complex models are available which describe equilibrium amplitudes (Campmans et al., 2018; van Gerwen et al., 2018). Until now, these morphological models lack interaction with spatially varying small-scale biological processes. In order to construct and validate such models, more information is required about the spatial relationships among benthic habitats, (mega) ripples, and sand waves.

Studies on the distribution of benthic assemblages can be very time consuming and the spatial resolution is often limited. Common methods like grabs, boxcores and multicores are point measurements, which only give an indication of the endobenthic community in the area (Rees et al., 2007). Larger, mobile species living on and within the seabed are easily missed. In order to study the spatial distribution of such species, sledges and trawls are commonly used (Callaway et al., 2002; Witbaard et al., 2013). However, with these techniques, it remains difficult to capture the complex spatial structure of benthic communities: trawls and sledges provide species densities integrated over the total sampled area, losing information on variance within the track. Alternatively, camera systems can be used to increase the spatial resolution of species density information (Sheehan et al., 2010; Spencer et al., 2005). Using camera systems, observations on species composition and environmental characteristics can be done simultaneously. Another major advantage of a camera system is that it does not alter the bed structure and thus enables data collection of small-scale bed features such as ripples.

The main goal of this paper is (1) to investigate the spatial distribution of benthic assemblages over sand waves. Secondary objectives are (2) to relate sand wave patterns to the spatial distribution of small-scale morphology and (3) to present the use of a camera system as a method to simultaneously study benthic species abundance and small-scale morphology.

2. Materials and Methods

2.1. Study Site

Our study site is representative of sand waves occurring in the Dutch, Belgian, and English Continental Shelf in the North Sea. We selected an area of approximately 3.4 km², located 12 nautical miles (~22.2 km) off the coast of Texel, the Netherlands (N53°11.241'; E4°28.628'; Figure 1). It is characterized by sand waves, oriented in a northwest direction perpendicular to the coast. At an average depth of 30 m, the sand waves have an amplitude of around 3 m, a wavelength of around 200 m, and are covered by small sand ripples. The study site is located in a narrow stretch between two busy traffic lanes and therefore subjected to extremely low demersal fishing activity.

2.2. Bathymetric Data

A bathymetric survey was conducted in June 2017 using the RV Pelagia's hull-mounted Kongsberg EM302 Swath Multibeam Echosounder (MBES). MBES data were processed to a 1-m grid resolution. Two sand waves in the area were selected based on the accessibility of the area, and their crests and troughs were subsequently identified from the MBES data. This yielded four different study locations: the troughs (T1, T2), and crests (C1, C2) of sand waves 1 and 2, respectively (Figure 1).

2.3. Hopper Camera System

The NIOZ hopper camera that was used consisted of a custom-made drop frame with a downward facing HD video camera (Biber et al., 2014), an underwater light source (100 W), and two parallel green lasers (30 cm apart) for scaling. The camera system was lowered to 0.5 m above the seabed, tethered to the vessel by a Kevlar cable with glass fiber core allowing real-time video transfer. Positioning of the hopper camera above the seabed was manually controlled by adjusting the cable length from the winch, based on a live video feed. A sailing speed of ~0.3 knots (~0.56 km/hr) with respect to the stationary seabed was maintained.

2.4. Video Analysis

We performed two video transects within a 2-hr time frame from each other, around slack tide (after high water), and under relatively calm weather conditions. Both transects started on the sand wave crest and were oriented roughly perpendicular to the sand waves, crossing the adjacent trough and crest (Figure 1). The camera recorded the seabed continuously, and video stills were automatically created from this footage for every second (Figure 2). In addition, the exact location of the vessel was recorded every 30 seconds and subsequently linked to video stills by time matching. This enabled the plotting of video results in ArcGIS (ArcMAP 10.3, ESRI), although a small offset was probably present due to a mismatch between the exact positions of the camera and the vessel. This georeferenced information was used to select video stills to include in the analysis. Both the first and last video still in each study location (T1, T2, C1, and C2) were identified. The first and all subsequent video stills were selected with a fixed interval, until the registered time of the last video still within the study area was reached. To prevent overlap of consecutive video stills, a 10-s interval was used. If a selected video still comprised an invalid image (due to dust clouds or movement blur), the next video still was selected instead.

All selected video stills were visually analyzed with ImageJ 1.51n (Schneider et al., 2012) by two independently working observers. For each selected still, biotic abundance, sand ripple morphology and surface area were determined, using the laser dots as reference. If epibenthic organisms were present, they were identified to the lowest taxonomic level possible, sometimes with the additional use of the continuous footage. Moreover, the number of holes in the seabed was counted as a proxy for endobenthos abundance. All counts were transformed into surface densities (# m⁻²). For sand ripple morphology, both observers independently chose three random sand ripples and measured their crest-to-crest length (Figure 2). Additionally, a visual judgment of the sand ripple pattern regularity was made. Regularity was classified in four classes: no sand ripples (A), no regular sand ripple pattern (B), some regular sand ripple pattern (C), and a strong, regular sand ripple pattern (D).

2.5. Statistical Analysis

A total of 232 video stills, distributed unequally over the four study locations (T1: 37, T2: 61, C1: 91, and C2: 43) were analyzed, which were nested within the two video transects. Ripple length (cm), regularity class,

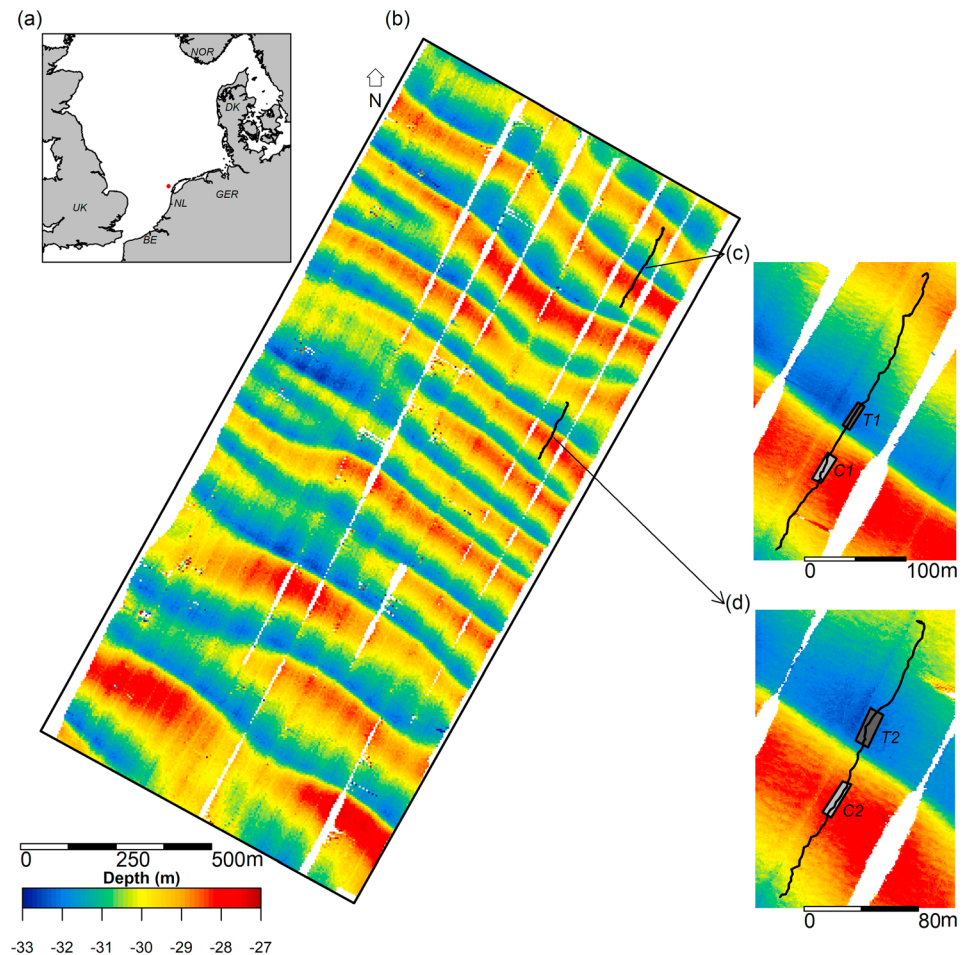


Figure 1. The study area. Its exact location in the North Sea, indicated with a red dot in (a). Detailed bathymetry of the complete area and the location of both video transects in (b). Enlarged versions of the video transects including the locations of the trough (T) and crest (C) in (c) and (d).

epibenthos abundance ($\# \text{ m}^{-2}$), and hole density ($\# \text{ m}^{-2}$) were available for each video still from both observers. The statistical analysis of this dataset was performed in R (R Core Team, 2018).

We used Linear Mixed Models (LMM) from the *nlme*-package (Pinheiro et al., 2018) to study the effects of location (trough versus crest) on epibenthos density, hole density, and average sand ripple length. Each model included location (trough/crest) as a fixed factor and transect and study location (T1, T2, C1, and C2) as random factors. The latter was included to minimize any spatial autocorrelation of observations within a trough or crest. Missing values were omitted. To elucidate potential observer-bias, we performed each LMM model three times, on different data sets. The first two models were performed for the two observers separately. Subsequently, the third model was fitted on the averaged values of the two observers. Next, likelihood Ratio Tests between the third model and a model without the explanatory variable (but with random factors included) were performed to assess the effect of the explanatory variable.

We analyzed the effects of the location on the regularity of the sand ripples using a Generalized Linear Mixed Model (GLMM) of the *binomial* family in the *lme4*-package (Bates et al., 2015). We needed a different model as using an LMM is limited to independent data. With more observations of a certain regularity class, the less observations of a different class could be made at that study location. To deal with this relation, we transformed the data into *successes* and *failures*, with successes being the observations and failures being all other observations in that study location. Next, the number of successes was modeled using the explanatory variables location (trough versus crest), interaction of location and regularity class (A, B, C, and D), and random effects of transect and study location (T1, T2, C1, and C2). The GLMM was performed on three distinct

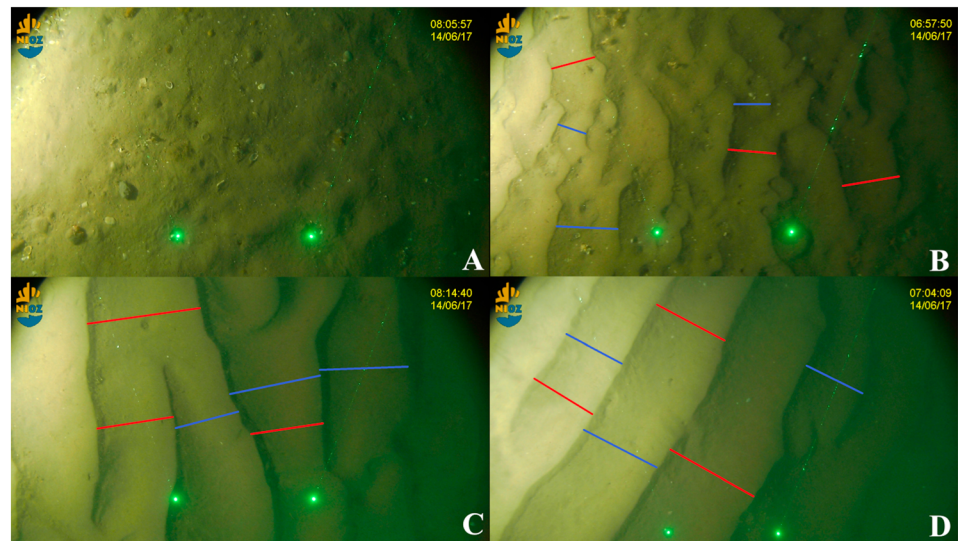


Figure 2. Video stills from the hopper camera for trough (a, b) and crest (c, d), classified for sand ripple regularity as classes A (no ripples), B (irregular ripples), C (some irregularity), and D (regular ripples). Red and blue lines represent the ripple length measurements of both observers; the green laser dots indicate a distance of 30 cm.

datasets: for both observers separately and one on the averaged values. Finally, a Likelihood Ratio Test between the averaged model and a similar model, but without the interaction of regularity class and location, was performed to assess the effect of regularity class per location.

3. Results

3.1. Bathymetric Data

Nearly complete coverage of the study area was achieved in the bathymetric survey, with a resolution of 1 m (Figures 1a and 1b). The study area comprised a total of 12 sand waves, having an average amplitude height difference of 3.0 m between trough and crest and an average wavelength of 207 m. The sand waves were asymmetrical in their cross section: the northeast facing slope being steeper than the southwest facing slope. The two selected sand waves for the video transects had their crests at -28.0 m and the troughs at -31.7 m depth with respect to mean sea level (Figures 1c and 1d).

3.2. Video Analysis: Biota

Hole density was on average 30 times higher in the troughs than on the crests (LMM; $\chi^2(1) = 7.18$, $p = 0.0074$), indicating that endobenthic species abundance was significantly higher in troughs than on the crests (Table 1 and Figure 3a). In line with this, we found four times more epibenthic organisms (LMM; $\chi^2(1) = 4.06$, $p = 0.044$) in the troughs than on the crests (Table 1 and Figure 3b). The two nonaveraged, observer-specific models for both hole density and epibenthos abundance yielded similar results (Table 1). Only a limited number of epibenthos species were observed in the video. The common star fish (*Asterias rubens*) was most frequently observed, followed by sand stars (*Ophiura* spp.), and the common hermit crab (*Pagurus bernhardus*). Tubes of the sand mason worm (*Lanice conchilega*) were frequently observed as well. However, it was impossible to determine from the video stills and footage whether the tubes were inhabited by live specimens. Other observations included anemones (*Sagartia* spp., but also *Metridium dianthus*), gobies (Gobiidae), brown crab (*Cancer pagurus*), bryozoans, and some flatfishes (Pleuronectidae).

3.3. Video Analysis: Sand Ripples

Sand ripple length was shorter in the sand wave troughs compared with the crests (LMM; $\chi^2(1) = 13.55$, $p = 0.00023$). In the troughs, sand ripple length was 11.2 cm on average, while on the crests, the ripples had an average length of 16.7 cm (Table 1 and Figure 3c). Observer-specific models yielded similar results as the final model based on the averaged data. In addition to the shorter sand ripple length, ripples were often absent in the sand wave troughs, or showed an irregularly shaped pattern. The relative proportions of classes A (no ripples) and B (irregular ripples) were much higher in the troughs than on the crests

Table 1

Results of the Linear Mixed Models for Hole Density (HD), Epibenthos Abundance (EBA), and Sand Ripple Length (SLR), As Well As the Results for the Generalized Linear Mixed Model for Sand Ripple Regularity Class (SRR)

Model		SD ϵ (transect)	SD ϵ (location)	SD residuals	Coefficient location
Hole density (HD)					
1	HD (obs1) \sim location + ϵ (transect) + ϵ (location)	2.79×10^{-6}	8.35	10.98	35.64
2	HD (obs2) \sim location + ϵ (transect) + ϵ (location)	0	5.54	11.10	29.48
3	HD (average) \sim location + ϵ (transect) + ϵ (location)	2.72×10^{-8}	6.98	10.50	32.57
4	HD (average) $\sim \epsilon$ (transect) + ϵ (location)	1.68×10^{-6}	17.79	10.50	—
Epibenthos abundance (EBA)					
1	EBA (obs1) \sim location + ϵ (transect) + ϵ (location)	2.35×10^{-7}	1.59	2.42	4.60
2	EBA (obs2) \sim location + ϵ (transect) + ϵ (location)	0	1.56	2.37	4.11
3	EBA (average) \sim location + ϵ (transect) + ϵ (location)	0	1.58	2.33	4.36
4	EBA (average) $\sim \epsilon$ (transect) + ϵ (location)	1.12×10^{-7}	2.70	2.33	—
Sand ripple length (SRL)					
1	SRL (obs1) \sim location + ϵ (transect) + ϵ (location)	0.00	2.19×10^{-3}	0.04	−0.055
2	SRL (obs2) \sim location + ϵ (transect) + ϵ (location)	0	0	0.03	−0.056
3	SRL (average) \sim location + ϵ (transect) + ϵ (location)	1.82×10^{-10}	8.844×10^{-11}	0.03	−0.056
4	SRL (average) $\sim \epsilon$ (transect) + ϵ (location)	0	0.02641	0.04	—

Model		Class A		Class B		Class C		Class D	
		Crest	Trough	Crest	Trough	Crest	Trough	Crest	Trough
Sand ripple regularity (SRR)									
1	SRR (obs1) \sim Location: class + location + ϵ (transect) + ϵ (location)	—	2.77	1.96	0.11	3.3	−0.24	2.89	−2.21
2	SRR (obs2) \sim Location: class + location + ϵ (transect) + ϵ (location)	—	2.15	1.01	0.21	2.60	−0.77	2.10	−2.33
3	SRR (average) \sim Location: class + Location + ϵ (transect) + ϵ (location)	—	2.40	1.43	0.16	2.87	−0.49	2.44	−2.27
4	SRR (average) \sim Location + ϵ (transect) + ϵ (location)	—	—	—	—	—	—	—	—

Note. Standard deviations (SD) of the random effects represent the variation explained by that factor. The coefficient of *location* shows the effect and direction of this fixed effect, with positive values representing positive effects for the troughs compared to the crests. The fourth models are only included to show the exact model formula for the model used in the likelihood ratio test. Observers are indicated by (obs1) and (obs2). The values displayed in classes A–D represent the slopes for that class in that location, in relation to the abundance of class A on the crest. Class A: no sand ripples; B: irregular ripples; C: some irregularity; D: regular ripples.

(Figure 3d). On the crests, sand ripples were classified more often as classes C (some regularity) and D (regular ripples). The GLMM supported that the location (trough versus crest) affected the chance of an observation in a certain class significantly (GLMM; $\chi^2(6) = 112.09$, $p = < 0.001$), with increased observations for classes C and D on the crests compared to observations of class A on the crests (Table 1).

4. Discussion

This study reveals for the first time that both epibenthos and endobenthos abundance is significantly higher in sand wave troughs compared to the crests. Our results are similar to patterns in larger-scale offshore bed forms, such as sand banks (van Dijk et al., 2012) and with observed differences in endobenthic community clusters over sand waves (Baptist et al., 2006). In addition, our results demonstrate that in sand wave troughs, sand ripples are generally less abundant than on sand wave crests, and if present, sand ripples have a less regularly shaped pattern. Finally, we have shown for the first time that using a camera system enables directly coupled observations of both small-scale seabed morphology and benthic community composition at high spatial resolution.

In this study, we used holes as an indicator for endobenthos abundance. This is based on the fact that, among others, sediment-inhabiting bivalve species use their siphon to access seawater for food and oxygen, resulting in a small hole at the seabed surface (Zwarts & Wanink, 1989). The majority of the encountered holes were small, with a diameter of several millimeters. It remains difficult, however, to pinpoint the exact species that produces these holes. Moreover, the abundance of species that do not produce surficial structures cannot be determined by merely using cameras. In order to provide this information, additional point measurements like boxcores could be used to establish a relationship between hole density and total endobenthos

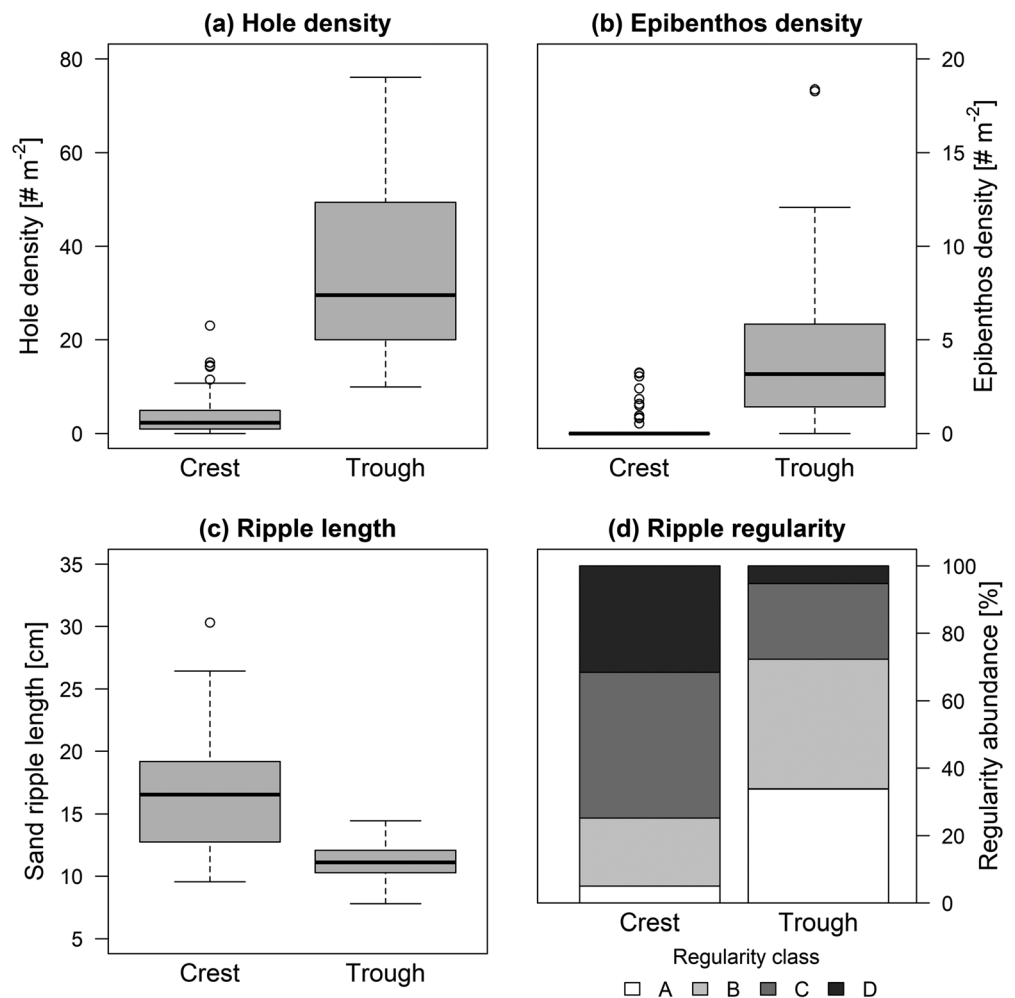


Figure 3. Hole density (a), epibenthos density (b), ripple length (c), and regularity class abundance (d) in the crests and on troughs of sand waves. Class A: no sand ripples, B: irregular ripples, C: some irregularity, and D: regular ripples.

abundance. Nevertheless, we feel confident that the number of holes can be used as an indicator for endobenthos density.

Higher epibenthos and endobenthos densities in the sand wave troughs could be explained by differences in abiotic conditions between the troughs and crests. Median grain size, for instance, is generally lower in the troughs of sand waves (Baptist et al., 2006; van Lancker & Jacobs, 2000), resulting from an interplay of both hydrodynamics and sediment dynamics (Roos et al., 2007; van Oyen et al., 2013). Whereas sand wave crests are more exposed to both strong tidal currents and surface gravity waves, sand wave troughs are somewhat sheltered, resulting in the sedimentation of smaller grains. Similarly, this process could also favor the deposition of dead organic matter in the troughs, which could serve as a food source for benthic species. Altogether, these processes likely lead to more favorable habitat conditions for benthic species in sand wave troughs.

We observed sand ripples less abundantly and less regularly shaped in the sand wave troughs. This is potentially caused by the result of the aforementioned interplay of hydrodynamics and sediment dynamics, with the sheltered conditions in the troughs resulting in irregular or absent ripples. Alternatively, as the presence and activity of biota may affect ripple formation (Featherstone & Risk, 1977; Friedrichs et al., 2009), the observed variations in ripple morphology could thus also be related to the spatial distribution of benthic organisms. Other complex processes (e.g., local turbulence) interact at the seabed-water interface as well, hindering quantification of the exact causality of the interaction between biota and small-scale morphology. Nevertheless, sand ripples are an important source of seabed roughness (Soulsby, 1983) and the observed

absence of sand ripples in the sand wave troughs clearly indicates that seabed roughness varies over sand waves.

Due to their migration rates, sand waves may pose risks to offshore human infrastructure on the seabed (Németh et al., 2003). Sand wave models provide information on various sand wave properties, such as migration rates and equilibrium heights, which is necessary for the planning of offshore engineering activities. Apart from some theoretical explorations (Borsje, de Vries, et al., 2009; Borsje, Hulscher, et al., 2009; Borsje et al., 2010), most sand wave models solely include hydrodynamics and sediment dynamics, without taking biotic effects into account. Moreover, they assume a uniform distribution of seabed roughness (e.g., Blondeaux & Vittori, 2016; van Gerwen et al., 2018). Here we demonstrated that both endobenthos and epibenthos are not evenly distributed over sand waves, with higher species densities in troughs. In addition, the troughs show irregularly shaped or a complete lack of sand ripples. By including this detailed spatial knowledge, the accuracy of biogeomorphological models, which predict both sand wave dynamics and benthic habitat distributions, is likely to improve. In turn, this may expedite licensing procedures and project realization for future offshore engineering activities (Damveld et al., 2016). Future monitoring of sand waves, along with model validation studies, should therefore aim to include phase-related spatial patterns of both benthic biota and small-scale seabed morphology.

Cameras are increasingly applied in marine habitat mapping (Guinan et al., 2009; Kendall et al., 2005; Stoner et al., 2007), and multiple guidelines exist for their onboard operation and subsequent footage analysis (Coggan et al., 2007; Hitchin et al., 2015; Sheehan et al., 2016; White et al., 2007). Video footage was analyzed by two independently working observers (Hitchin et al., 2015), and despite small absolute differences between observers, both observer-specific models and models based on the averaged data yielded similar results, showing that our methodology is robust. Due to the small offset between the GPS positions of the vessel and the camera system, we opted to be conservative in only distinguishing between sand wave crests and troughs (rather than studying a continuous elevation profile). In order to study both benthic organisms and small-scale morphology over sand waves in higher spatial detail, for instance on the slopes, future studies would benefit from including a more accurate positioning system. Nevertheless, we demonstrate that video transects may provide valuable insight into phase-related biological and morphological spatial patterns within sand waves, which combined with boxcores, could be a relatively fast and comprehensive method that yields high-resolution spatial information about benthic communities.

5. Conclusions

For two sand waves on the Dutch Continental Shelf, video transects were performed to count both visible epibenthic species and seabed holes, used as proxies for endobenthos abundance. Both show significantly higher abundance in the sand wave troughs compared to the crests. Thus, this study shows that sand waves affect the distribution of benthic communities.

The video transects also revealed that sand wave troughs are typified by a highly irregular ripple pattern with shorter wavelengths than those in sand wave crests. Finally, this study showed that video transects are an efficient method to collect data on both benthic communities and small-scale morphology with relevant spatial resolution.

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