Comparing methodologies in marine habitat monitoring research: An assessment of species-habitat relationships as revealed by baited and unbaited remote underwater video systems

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ABSTRACT

Remote underwater video systems (RUVS) are increasingly used in scientific studies to monitor marine ecosystems. RUVS can be deployed baited (BRUVS) or unbaited (UBRUVS) and allow for an estimation of the MaxN metric, a relative measure of species abundance. Recording species MaxN in a variety of marine habitats provides associations between species abundance and habitat type, known as 'species-habitat relationships'. However, the introduction of bait in BRUVS could obscure such relationships by inadvertently attracting fish from neighbouring habitats. Here, we investigate the species-habitat relationships of seven temperate marine species: Atlantic cod (*Gadus morhua*), right-eyed flatfish (*Pleuronectinae spp.*), Atlantic herring (*Clupea harengus*), whiting (*Merlangius merlangus*), goldsinny wrasse (*Ctenolabrus rupestris*), two-spotted goby (*Gobiusculus flavescens*) and shore crab (*Carcinus maenas*) as revealed by BRUVS and UBRUVS. Video systems were deployed in coastal areas in the Western Baltic, with a cobble coverage ranging from 0% to 100%. Results show that all focal species responded to changes in cobble coverage, highlighting the importance of benthic habitat for a range of animals including benthopelagic species. Specifically, mean abundances of goldsinny wrasse and two-spotted goby were positively associated with cobble coverage, whilst right-eyed flatfish, herring, whiting and shore crab showed a negative association. Atlantic cod was found to be most abundant at intermediate cobble coverage between 65 and 70%, showing a unimodal trend with the mean abundance decreasing again at higher coverage. The relationships suggest that anthropogenic activities modifying benthic habitats, including extraction of material from the seabed and bottom trawling, likely change abundances of a range of marine species. Our comparative analysis suggests that both BRUVS and UBRUVS can identify previously documented species-habitat relationships. However, BRUVS demonstrated some superiority by confirming documented relationships for Atlantic cod and whiting, whilst UBRUVS failed to record any patterns for those species. Our data highlight the ability of BRUVS to identify changes in abundance across different habitats for a variety of species. Although the bait plume serves to attract organisms to the field of view, current results suggest that the use of BRUVS does not obscure species-habitat relationships in patchy coastal habitats. Therefore, future studies examining the importance of different marine areas may benefit from using BRUVS to quantify relationships between habitat variables and species abundance. Developing a better understanding of such relationships will be crucial in ensuring adequate management and protection of ecologically important marine habitats.

1. Introduction

Anthropogenic pressures on marine ecosystems have been recorded globally; highly impacted areas range from the North Sea and coastal areas of the Baltic Sea, to eastern Caribbean and Japanese waters (Halpern et al., 2008; Korpinen et al., 2012). Impacts can be due to

direct exploitation of coastal resources, including overfishing and land reclamation of shallow-water habitats, but also indirect effects of rapid population growth on urbanisation and industry (Brown et al., 2018; Halpern et al., 2008; Korpinen et al., 2012; Lin and Yu, 2018; Pihl et al., 2006; Vasconcelos et al., 2007). Globally, directives have been put in place to protect marine habitats (European Parliament and Council of the European Union, 2008; Feng et al., 2016; Fernandes et al., 2005; UK Parliament, 2009). In the European Union, protection includes the establishment of 'Natura 2000' areas. The Natura 2000 legislation covers one of the largest protected areas in the world (Kristensen et al., 2017). Management of Natura 2000 areas varies from minor interventions such as reducing disruptive activities during breeding seasons, to major restoration works of degraded marine habitats in order to protect threatened species (Kristensen et al., 2017; Nature Agency, 2016). Surveys of these habitats allow for the assessment of changing habitat variables and associated marine community responses. These surveys generate important information including abundance data, commonly used to investigate the impacts of anthropogenic pressures (Bellwood et al., 2012; Hillebrand et al., 2018; Stallings, 2009), as well as the influence of natural habitat components, such as vegetation (Alós et al., 2018) and habitat complexity (Bell et al., 1987; Watson et al., 2005) on fish populations. Specifically, in terms of habitat restoration and management, long-term monitoring is required to examine the ecological responses to management measures and assess the efficacy of the restoration efforts. Ultimately, this helps inform future restoration strategies and marine spatial planning (Lester et al., 2018; McHenry et al., 2017; Pınarbaşı et al., 2017).

Habitat complexity encompasses size, shape and texture of seafloor features (Connell and Jones, 1991; Gee and Warwick, 1994). For example, rocky seafloors have a higher habitat complexity than sandy bottoms (Kristensen et al., 2017). Past findings have indicated that marine environments with high habitat complexity often support greater abundance of individual species than less complex environments (Campbell et al., 2018; Connell and Jones, 1991; Green et al., 2013; Jenkins and Wheatley, 1998). However, there are examples of limited (Almany, 2004) or no influence (Roberts and Ormond, 1987) of habitat complexity on species abundance indicating that some species do not exhibit this preference for high complexity. Importantly, it is still unclear to what extent different methodologies used to investigate fish abundance produce comparable results (Cappo et al., 2004; Cappo et al., 2003; Cundy et al., 2017; Willis and Babcock, 2000).

The umbrella term RUVS (remote underwater video systems) is used to describe underwater recording techniques, including Baited RUVS (BRUVS) and Unbaited RUVS (UBRUVS). RUVS can be limited by poor water visibility and can make the observation of cryptic fish species challenging, particularly in complex habitats (Hannah and Blume, 2012; Watson et al., 2005). However, RUVS have a significant advantage because they are non-extractive and less damaging to complex seafloors, compared to many netting and trawling methods (Ebner and Morgan, 2013; Morrison and Carbines, 2006; Willis and Babcock, 2000). This is crucial for sampling in protected sites such as Natura 2000 areas, where reefs are listed as an important habitat type for conservation (Nature Agency, 2016). Because of the minimised impact on benthic habitats, BRUVS have been used regularly to investigate the effectiveness of designated marine reserves such as 'no take' areas (Coleman et al., 2015; McLaren et al., 2015), as well as the spatial distribution of species across a variety of marine habitats (Espinoza et al., 2014; Langlois et al., 2012; White et al., 2013). BRUVS are considered an effective way to study species abundance because the bait attracts fish to the field of view (FOV), thus allowing for accurate counts and identification (Hardinge et al., 2013; Watson et al., 2005). BRUVS document not only species attracted to the bait itself, but also those that pass the FOV by chance or are attracted to the general activity surrounding the bait (Harvey et al., 2007). The overall attraction means BRUVS generally sample more fish, which reduces the variance of species abundance per habitat, and increases statistical power

(Harvey et al., 2007).

Although many studies have used BRUVS, there are some concerns surrounding bias in the fish attracted to BRUVS (Whitmarsh et al., 2017). Firstly, BRUVS may attract a disproportionate number of carnivorous fish species compared to herbivores (Bernard and Götz, 2012; Colton and Swearer, 2010; Watson et al., 2005; Wraith et al., 2013). Secondly, BRUVS may yield an overrepresentation of larger specimens because they forage further, or demonstrate dominance and predatory behaviour towards smaller fish (Hardinge et al., 2013; White et al., 2013). Finally, fish attracted to the bait may originate from a neighbouring habitat (Hannah and Blume, 2012). Overall, these biases imply there is a risk that the relationship between a habitat variable and a certain species' abundance (henceforth termed 'species-habitat relationships') may be obscured by BRUVS.

UBRUVS offer an alternative underwater video method which may produce more robust species-habitat relationships and provide more accurate representations of the fish population because there is no bait plume (Colton and Swearer, 2010; Hannah and Blume, 2012; Harvey et al., 2007). However, fewer studies use UBRUVS, mainly because they rely solely on fish passing the FOV by chance. Consequently, species abundances recorded by UBRUVS have been consistently lower than those sampled by BRUVS (Cappo et al., 2006; Hardinge et al., 2013; Watson et al., 2005). Therefore, a larger number of UBRUVS site replicates are needed to ensure adequate statistical power (Watson et al., 2005). Increased deployments inevitably increase the costs associated with fieldwork, as well as the time required to complete data collection and video analysis.

We investigated species-habitat relationships for seven temperate marine species in the Western Baltic Sea and compared the direction of these relationships as recorded by BRUVS and UBRUVS. Specifically, the hypotheses tested were that: 1) abundances of all focal species vary with respect to benthic cobble coverage, ranging from 0 to 100% cobble; 2) the directions of the species-habitat relationships are comparable between the two sampling methods and 3) UBRUVS record more robust species-habitat relationships than BRUVS due to the obscuring effects of BRUVS.

2. Materials and methods

2.1. Study area

Sampling was carried out between April and May 2017 in the Sønderborg Bay area of the Flensborg Fjord (Fig. 1), situated in the Western Baltic, between Denmark and Germany. A total of six sites were sampled: two cobble reef habitats (Vesterhage and Spar Es) and four sand habitats (Vemmingbund, Kegnæs Ende, Sønderskov and Dybbøl Mølle). In each of the six sites, sampling took place within a 200 m wide and 500 m long rectangular area along the coastline to ensure standardisation of both sampling area and water depth. All sampling was carried out at depths ranging between 6 and 7 m.

2.2. RUVS setup and deployment

GoPro cameras (Hero 3, 3+ and 4; www.gopro.com) were used for both BRUVS and UBRUVS. All cameras were set with identical video settings including 720p video resolution and 30 frames per second (NTSC). Cameras used for UBRUVS were equipped with intervalometers (model: Time Lapse Intervalometer or BlinkX, CamDo Solutions; www.cam-do.com). All intervalometers and BlinkX's were programmed such that every hour the UBRUVS would turn on, record for 2 min, and then turn off. Due to the current study being part of a larger monitoring program with various aims, this setting was applied to ensure that all UBRUVS recorded for > 24 h and data would cover the entire diel cycle. In contrast, BRUVS started recording immediately after deployment and ran continuously. BRUVS were therefore equipped with an extra battery (BacPac; www.gopro.com) to ensure adequate recording
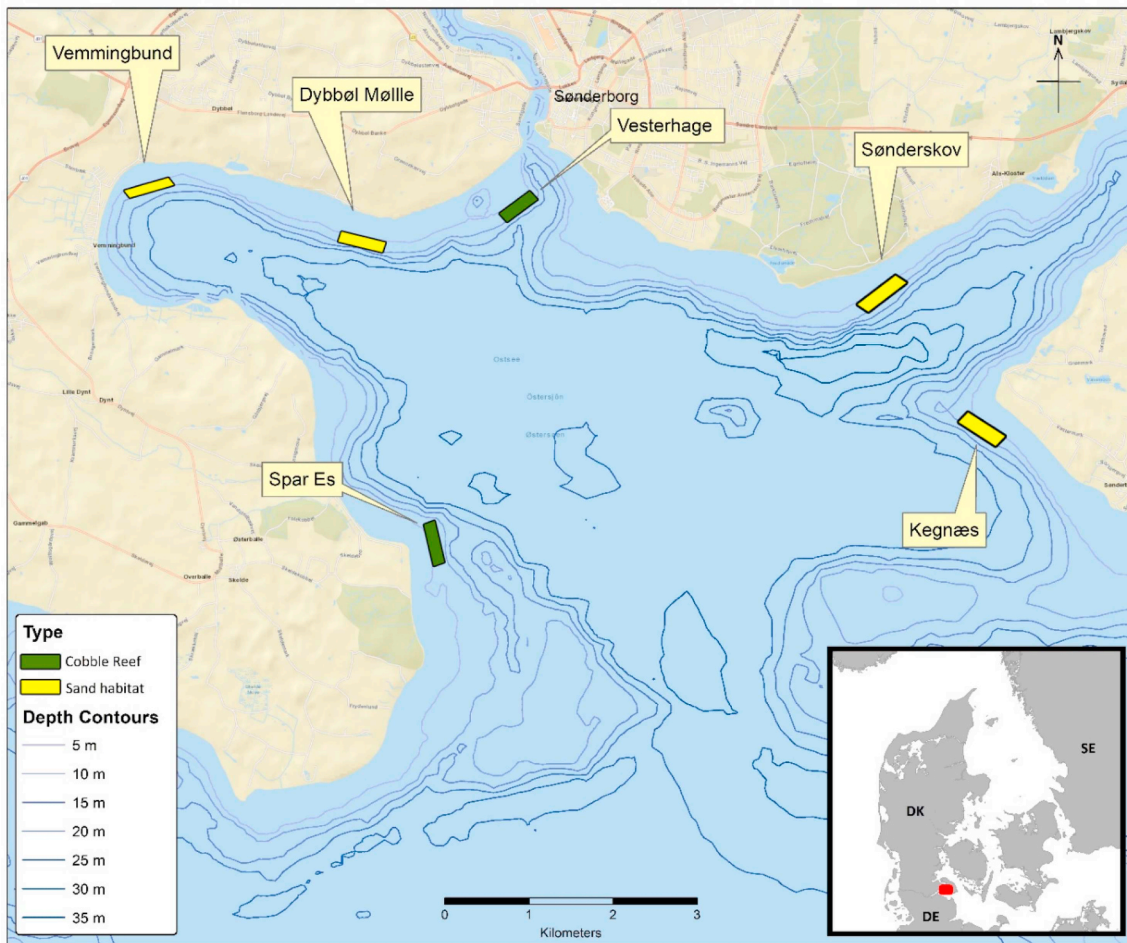
Fig. 1. Sønderborg Bay in southern Denmark where the six study sites are indicated. Underwater video systems were deployed within rectangular areas along the coast to ensure a water depth between 6 and 7 m. The bay is dominated by either cobble reef (green rectangles) or sand bottom habitats (yellow rectangles), however, scattered cobble reef occurs intermittently in the sand habitat and vice versa, reflecting the mosaic nature of the seabed in Sønderborg Bay. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

time to capture the bait plume effect (Harasti et al., 2015). Accordingly, BRUVS recorded for a minimum of 40 min and up until 2 h, whilst UBRUVS recordings exceeded 24 h and typically ran for 40 h (recording 2 min per hour). Standard GoPro waterproof housing held the cameras in position.

The RUVS setup consisted of a metal pole (3 cm diameter; 100 cm high) fixed to a concrete base (45 × 45 × 5 cm; length × width × height). The camera was secured horizontally to the pole at a height of 20 cm above the seafloor. Below the cameras used for BRUVS, an 80 cm long bait arm was attached to hold a mesh bait bag containing 500 g of fresh Atlantic herring (*Clupea harengus*) bait chopped into 1–2 cm chunks. Each 10 cm increment along the bait arm was marked with tape for visibility estimates (Fig. 2a; Cappo et al., 2003). UBRUVS setup resembled that of BRUVS, but instead of a bait arm, a rope was attached to the concrete base and extended horizontally in the camera's FOV. The rope lay flat along the seafloor, kept taut by an anchor at the end. Metre markers were attached to the rope and used for visibility estimates (Fig. 2b).

Deployment procedure resembled previous studies (for detailed account see Langlois et al., 2018). Similar to Gilby et al. (2017), there was a maximum of two temporally overlapping deployments (either two BRUVS or two UBRUVS) at each of the six sites (Fig. 1). BRUVS and UBRUVS could run concurrently if they were at separate sites, but they were never run at the same time within a single site. Seafloors with either mainly sand (Fig. 2b) or cobble (Fig. 2c) were identified within each site using a side scanner (Lowrance Elite-7 Ti; www.lowrance.

com). The side scanner was used to confirm there was at least 25 m diameter of the desired habitat (sand or cobble or a mix) for each camera deployment. In those cases where two BRUVS or two UBRUVS were running simultaneously within a site, the distance between the two systems depended on the available habitat and ranged between 50 and 450 m (comparable to e.g. Hesse et al., 2016; Wakefield et al., 2013). Notably, all deployments were conducted during daylight hours and BRUVS were deployed at least 2 h before sunset to ensure adequate light levels for the continuous recordings. Video samples in complete darkness, i.e. produced by UBRUVS that had continued recording into the night, were discarded. Day lengths varied between 13 and 17 h during the study period. Accordingly, a total of 293 deployments were identified as successful based on these criteria, consisting of 141 BRUVS and 152 UBRUVS deployments. The UBRUVS deployments in turn produced 2621 video samples between all locations (Table 1), each with a recording time of two minutes.

2.3. Video analyses

Recordings were analysed using the VLC Media Player (VideoLan; www.videolan.org). Video analysis revealed the species present and the maximum number of each species in a frame at one time, the MaxN metric (Cappo et al., 2004; Ellis and DeMartini, 1995; Priede and Merrett, 1996). The use of MaxN eliminates the risk of repeated counts of the same individuals re-entering the FOV and provides a conservative estimate of species abundance (Campbell et al., 2018; Colton and

Fig. 2. Multi-pane overview of the RUVS used for monitoring in this study. A) BRUVS setup with a bait arm extended within the FOV, marked with tape at 10 cm increments used for visibility estimates, B) Sand site with low cobble coverage recorded by a BRUVS, C) Reef site with high cobble coverage, recorded by an UBRUVS with a sponge attached to a rope at 1 m distance from the camera for visibility estimates and D) a school of Atlantic cod (*Gadus morhua*) passing the FOV, recorded at intermediate cobble coverage by a BRUVS at one of the reef sites.

Table 1
Successful BRUVS and UBRUVS replicate deployments and individual sampling units with respect to the field sites (see Fig. 1).

Location	Habitat type	BRUVS	UBRUVS	
		Deployments	Deployments	2-minute samples
Dybbøl Mølle	Sand	25	27	469
Kegnæs	Sand	25	24	262
Spar Es	Reef	24	24	636
Sønderskov	Sand	22	27	337
Vemmingbund	Sand	21	28	492
Vesterhage	Reef	24	22	425

Swearer, 2010; Harvey et al., 2007; Watson et al., 2005). Individuals were ideally classified to species level using compiled reference images, as well as by consulting colleagues with expertise in specific fish families. Following Cundy et al. (2017) and Hardinge et al. (2013), where species identification was not possible, individuals were assembled in groups by using the lowest common taxonomic level possible. Most notably for this study, flounder (*Platichthys flesus*), dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) were grouped under the common sub-family of right-eyed flatfish, *Pleuronectinae*. There were only few sightings for certain species, so it was decided to focus the analysis on species for which there were a sufficient number of observations (Campbell et al., 2018; Unsworth et al., 2015). Accordingly, we analysed the abundances of Atlantic cod ("cod"; Fig. 2d; *Gadus morhua*), right-eyed flatfish ("flatfish"; *Pleuronectinae spp.*), Atlantic herring ("herring"; *Clupea harengus*), whiting (*Merlangius merlangus*), goldsinny wrasse (*Ctenolabrus rupestris*), two-spotted goby (*Gobiusculus flavescens*) and shore crab (*Carcinus maenus*).

Ultimately, for each sampling unit, data were collected on the species present (or lowest taxonomic level), MaxN, cobble coverage

(%), functional visibility (m) and FOV obstruction (%; abbreviated FOV Ob). Functional visibility was defined as the furthest distance in which a fish would still be identifiable; this varied with water turbidity and was estimated using the bait arm (BRUVS) or rope markers (UBRUVS). Obstruction of the FOV was estimated using the percentage of seabed structures or macroalgae rising above the seafloor, and obstructing the view, within the distance of the functional visibility. Cobble coverage (%) was assessed using the video footage by estimating the percentage of the visible seafloor which was made up of cobble. Cobble is defined as 'a heterogeneous mixture of pebbles, cobbles, and boulders' (Shepard, 1963; Wahle and Steneck, 1992). Specifically, the size range for cobble is classed as rocks between 6 and 26 cm diameter (Greene et al., 1999; Hannah and Blume, 2012; Wahle and Steneck, 1992). Occasionally, a boulder (diameter > 26 cm) was present in the FOV and included in the cobble coverage. Cobble coverage was then used as an explanatory variable in the analysis to model the species-habitat relationships.

2.4. Statistical analysis

We used generalised linear mixed models (GLMMs) to analyse the effect of cobble coverage (CC) on the abundance (MaxN) of the seven focal species of this study. To investigate whether any of the focal species showed a unimodal relationship with cobble coverage, we also included a quadratic term of this predictor (CC^2) in all initial models. Following from the sampling design, a nested error structure was included in the UBRUVS models, with deployment ID (a unique ID assigned to each deployment) being nested in site ID. This allowed the models to incorporate potential correlations between sampling units from the same deployment, as well as between deployments coming from the same field site. For BRUVS models, we instead used the single random effect of site ID since sampling units consisted of whole

deployments. In addition, we defined the soak time (i.e. total recording time) of BRUVS as an exposure term, by adding the logarithm of soak time as a predictor in the model (Zuur and Ieno, 2016) to account for differences in recording time. Functional visibility and FOV obstruction were included as additional covariates for both sampling methods, since these two variables potentially indirectly influenced results by altering the area size in the FOV. Model selection was performed using a backward elimination routine based on Akaike Information Criterion (AIC) values. This involved comparing the full model (i.e. the polynomial regression model) with nested models containing a relevant subset of predictors. In the case of ΔAIC-values < 2, implying substantial empirical support for either model (Burnham and Anderson, 2002), we selected the most parsimonious model (i.e. the linear regression model) whilst retaining the effects of differences in exposure (soak time, BRUVS only) and FOV. Models were fitted using a log-link function with the response variable following either a Poisson or negative binomial distribution. Since none of the models showed signs of overdispersion, the choice of the distribution was instead based on comparison of the AIC values.

As highlighted by Colton and Swearer (2010), comparison between methodologies is often confounded by differences in the data collection process. In this study, sampling units for BRUVS and UBRUVS differed in recording time, due to the data collection process being conducted as part of multiple monitoring studies with various aims. Since this precludes a direct comparison between species abundances as sampled by the two methods, we used separate GLMMs for BRUVS and UBRUVS instead of including sampling method as a predictor in a pooled model.

Data were analysed in R version 3.4.4 (R Development Core Team, 2014) using package glmmTMB version 0.2.1.0 (Brooks et al., 2017).

3. Results

3.1. Species-habitat relationships

The effect of cobble coverage on cod (*Gadus morhua*) abundance was found to be dependent on the sampling method. Specifically, BRUVS identified a unimodal relationship between cod abundance and cobble coverage (Fig. 3a; quadratic term in Table 2, $p < .05$), with the number of cod increasing until a tipping point between 65 and 70% coverage and slightly decreasing again at higher coverage. In contrast, UBRUVS did not record any significant cobble effect on mean cod abundance across the interval from 0% to 100% cobble coverage (Fig. 4a; Table 2; $p > .1$). For the subfamily of right-eyed flatfish (*Pleuronectinae spp.*), both sampling methods documented a similar species-habitat relationship (Table 2). Results show that increasing cobble coverage led to a significant reduction in mean flatfish abundance as recorded by BRUVS (Fig. 3b; $p < .05$) and UBRUVS (Fig. 4b; $p < .01$). This negative trend was found across the entire cobble coverage range without any evidence for unimodality recorded by the two sampling methods (Table 2).

The effect of cobble coverage on the abundance of Atlantic herring (*Clupea harengus*) was less pronounced. BRUVS revealed a decreasing trend of herring abundance with increasing cobble coverage (Fig. 3c), yet this relationship was not found to be statistically significant at the 95% level (Table 2; $p < .1$). In addition, no significant effects of cobble were recorded by UBRUVS despite a slightly decreasing trend in predicted herring abundance across cobble coverage (Fig. 4c). For whiting (*Merlangius merlangus*), BRUVS documented a negative association with cobble coverage (Fig. 3d; Table 2; $p < .001$). This relationship was found to be linear, with no evidence of a tipping point at higher ranges of cobble coverage. In contrast, UBRUVS recorded a weakly defined relationship for whiting with no significant effect in the linear and quadratic terms of cobble coverage (Table 2). This lack of a clear habitat association for whiting was likely due to no individuals being recorded by UBRUVS at an intermediate cobble coverage, which was also apparent from the widening confidence band across these

intermediate values (Fig. 4d).

The goldsinny wrasse (*Ctenolabrus rupestris*) showed a positive association with cobble, as evidenced by recordings from both sampling methods (Table 2; $p < .001$ for both methods). BRUVS documented a unimodal relationship with wrasse abundance peaking at 85–90% cobble coverage (Fig. 3e), whilst UBRUVS showed a linear increase in wrasse abundance across the range of cobble coverage (Fig. 4e; $p < .001$). Similarly, two-spotted goby (*Gobiusculus flavescens*) clearly increased in abundance from sand to reef habitat. Results from the BRUVS model showed a significant effect for the quadratic term of cobble coverage (Table 2; $p < .05$) with an increase in goby abundance up until 85% coverage after which goby numbers plateaued (Fig. 3f). This trend was absent in UBRUVS, which instead showed a linear increase across the range of cobble coverage (Fig. 4f; $p < .001$).

Finally, both sampling methods documented a negative unimodal relationship between shore crab (*Carcinus maenas*) abundance and cobble coverage (quadratic term in Table 2; $p < .05$ for both methods). Shore crabs were most abundant on sandy bottoms low in cobble coverage, decreasing steadily in abundance at the lower-intermediate range before slightly increasing again at higher coverages (Fig. 3g). However, similar to the results for whiting, UBRUVS recorded few shore crabs at an intermediate cobble coverage, causing increased uncertainty in the model predictions across these intermediate values (Fig. 4g).

3.2. Visibility and FOV obstruction

A number of effects were observed when accounting for visibility, which varied between species and sampling method. For flatfish and two-spotted goby there was a significant positive effect of visibility on the mean abundance documented by both methods, whilst an effect was only found in UBRUVS for herring and shore crab (Table 2). No significant influence of visibility was found in the models for whiting and goldsinny wrasse ($p > .1$). The FOV obstruction appeared to have little effect on the output of the models. Apart from a positive effect on the number of goldsinny wrasse recorded by BRUVS (Table 2; $p < .05$) and a negative (but not statistically significant) effect on the abundance of cod ($p < .1$), the FOV obstruction did not influence the results for the focal species in this study.

4. Discussion

Using two different underwater video methods, BRUVS and UBRUVS, this study examined changes in the abundance of seven temperate marine species in habitats with varying cobble coverages. For all species, the mean abundance changed with cobble coverage, revealing the importance of benthic habitats for a variety of organisms including benthopelagic species. The identified relationships indicate that changes in cobble coverage, whether caused by human activity or natural events, could lead to a shift in the abundance of a range of marine species. Notably, we examined whether the use of bait in underwater video monitoring could bias associations between species abundance and habitat type, by potentially attracting individuals from greater distances and different habitats (Hannah and Blume, 2012). Our results reveal that BRUVS and UBRUVS were equally capable of identifying directions of species-habitat relationships for four out of the seven focal species in this study (flatfish, wrasse, goby and shore crab; Table 2). BRUVS recorded a significant relationship for an additional two species, cod and whiting, whilst UBRUVS failed to capture a significant habitat association for these species. This suggests that BRUVS did not obscure species-habitat relationships, but may in fact reveal more robust relationships compared to UBRUVS.

Following the concept of an inherent trade-off between environmental heterogeneity and the amount of habitat available to individual species (Allouche et al., 2012), we tested for unimodality within the species-habitat relationships. The abundance of a particular species
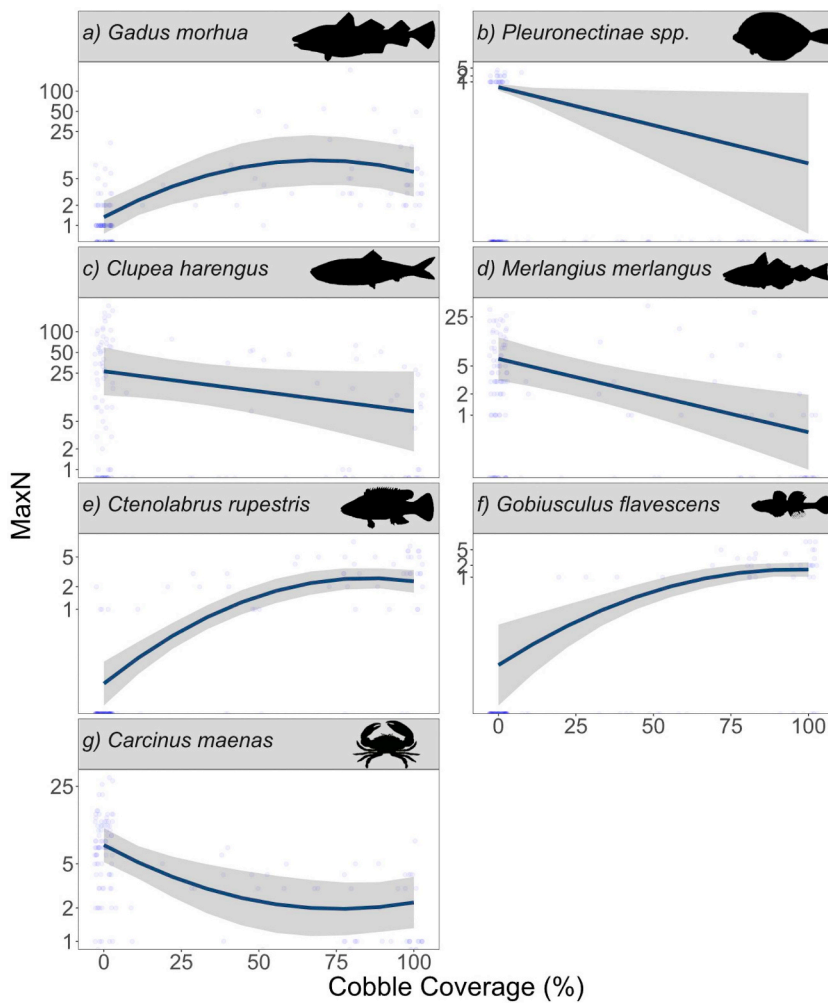
Fig. 3. Observed and predicted abundances (MaxN) recorded by BRUVS across varying cobble coverage. Distances between MaxN values on the y-axis were log-transformed for improved visualisation of the relationships. Solid lines show the mean GLMM predictions and the shaded areas represent the 95% confidence intervals. The blue dots show the original observations, which were jittered to improve visual representation. Results are shown for each of the focal species: (a) Atlantic cod (*Gadus morhua*); (b) Flatfish (*Pleuronectinae spp.*); (c) Atlantic herring (*Clupea harengus*); (d) Whiting (*Merlangius merlangus*); (e) Goldsinny wrasse (*Ctenolabrus rupestris*); (f) Two-spotted goby (*Gobiusculus flavescens*) and (g) Shore crab (*Carcinus maenas*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

may potentially be maximised or minimised at an intermediate cobble coverage, instead of increasing or decreasing continuously with coverage. Accordingly, a quadratic term for cobble coverage (CC^2) was included in all initial models and assessed for its significance (Table 2). The importance of considering unimodal patterns between fish community metrics and habitat complexity was recently highlighted for natural and artificial temperate reefs (Paxton et al., 2017). The authors reported that fish abundance was maximised at intermediate reef complexity, rather than increasing across the entire interval from low to high complexity. This pattern was observed both for artificial and

Table 2

GLMM parameter estimates for each of the seven focal species using either a Poisson or negative binomial (NB) distribution. Separate models were used for the two different sampling methods (BRUVS and UBRUVS). Significant effects ($p < .05$) of cobble coverage (CC) and the quadratic term (CC^2) are highlighted in bold, with the latter denoting a unimodal relationship between species abundance and cobble coverage. Visibility and FOV Obstruction (FOV Ob) were included as additional covariates. [excl. = excluded (based on AIC), N.A. = not applicable, (*) = $p < .1$; * = $p < .05$; ** = $p < .01$, *** = $p < .001$.]

| Species	Common name	Sampling method	Distribution	Intercept	CC	CC^2	Visibility	FOV Ob	log Soak
Gadus morhua	Atlantic cod	BRUVS	NB	−1.57	**5.67****	−4.12*	1.10(*)	1.57	0.98
		UBRUVS	NB	−2.50	0.56	excl.	0.41(*)	−3.48(*)	N.A.
Pleuronectinae spp.	Right-eyed flatfish	BRUVS	NB	−4.14	**−8.84***	excl.	2.93*	excl.	0.77
		UBRUVS	Poisson	−4.14	**−4.20****	excl.	0.67*	−1.14	N.A.
Clupea harengus	Atlantic herring	BRUVS	NB	2.74	−1.34(*)	excl.	excl.	excl.	0.94
		UBRUVS	NB	−5.10	−1.94	excl.	2.93***	−7.70	N.A.
Merlangius merlangus	Whiting	BRUVS	NB	0.77	**−2.40*****	excl.	0.61	excl.	0.76
		UBRUVS	NB	−2.89	−28.83	26.92	−0.69	−13.98	N.A.
Ctenolabrus rupestris	Goldsinny wrasse	BRUVS	Poisson	−3.16	**7.62*****	−4.47***	0.69	1.38*	0.10
		UBRUVS	Poisson	−8.02	**3.39*****	excl.	excl.	excl.	N.A.
Gobiusculus flavescens	Two-spotted goby	BRUVS	NB	−8.12	**11.72*****	−6.10*	2.07**	excl.	1.33
		UBRUVS	NB	−10.19	**5.19*****	excl.	1.51***	2.61	N.A.
Carcinus maenas	Shore crab	BRUVS	NB	1.92	**−3.49****	2.30*	−0.45	excl.	0.96***
		UBRUVS	Poisson	−3.91	**−14.06***	11.93*	0.74**	−4.22	N.A.
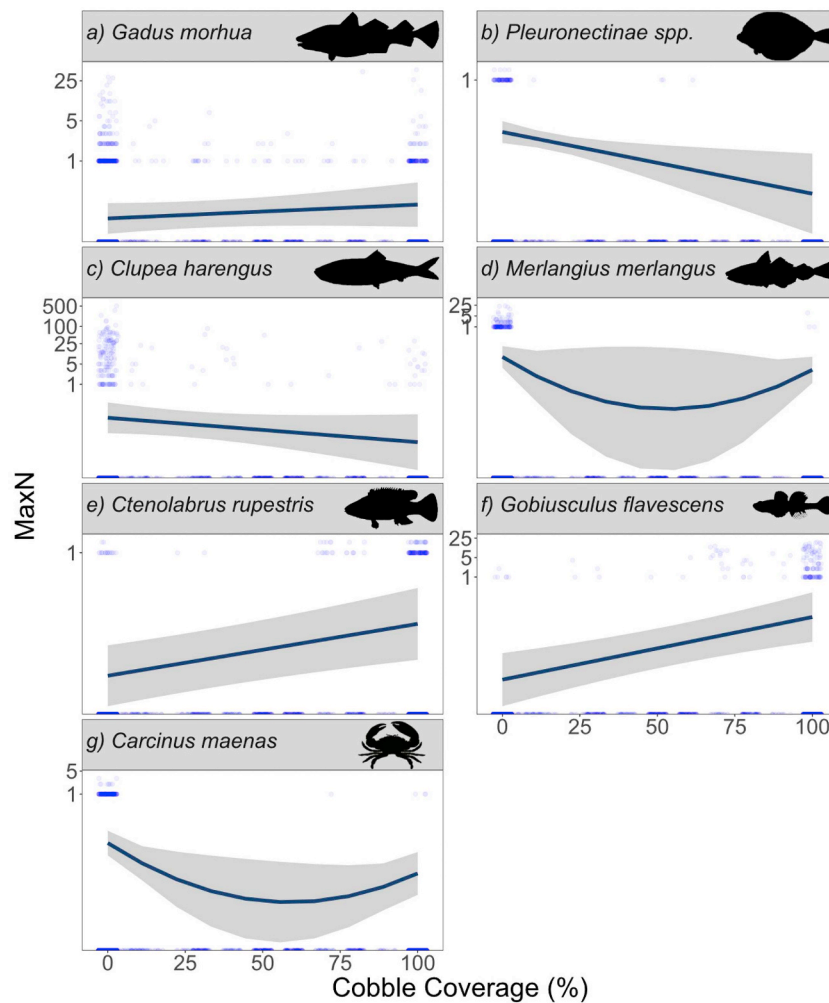
Fig. 4. Observed and predicted abundances (MaxN) recorded by UBRUVS across varying cobble coverage. See caption of Fig. 3 for explanation of the plots. Results are shown for each of the focal species: (a) Atlantic cod (*Gadus morhua*); (b) Flatfish (*Pleuronectinae* spp.); (c) Atlantic herring (*Clupea harengus*); (d) Whiting (*Merlangius merlangus*); (e) Goldsinny wrasse (*Ctenolabrus rupestris*); (f) Two-spotted goby (*Gobiusculus flavescens*) and (g) Shore crab (*Carcinus maenas*).

natural temperate reefs. In the current study, the abundance of shore crab was found to be minimised at intermediate cobble coverage, whilst the abundance of cod peaked across this intermediate range. Shore crabs appear to be highly adaptable, able to populate diverse habitats including sand, mud and rocks (Cohen et al., 1995; Grosholz and Ruiz, 1995), which was also reflected by their presence at both sand and rocky sites in our study. Cod increased in abundance up to 65–70% of cobble coverage and slightly decreased again at higher coverage. This pattern suggests that cod abundance peaked in habitats of intermediate composition, e.g. reef edges or mosaics of hard and soft bottoms. Such habitats may offer elevated prey resources for cod by allowing the fish to include sand bottoms for foraging, whilst remaining in close proximity to reef structures for refuge against predation (Posey and Ambrose, 1994; Rosemond et al., 2018). In fact, since young cod largely prey on crustaceans (Pihl, 1982) and individuals recorded in our study typically were of subadult size, we cannot rule out the possibility that the low number of crabs recorded at intermediate cobble coverage is a direct consequence of maximised cod abundance at intermediate cobble coverage. Notably, unimodality was only recorded by BRUVS whilst UBRUVS failed to demonstrate any significant habitat association for cod. We propose that UBRUVS did not capture individuals hidden within the cobble reefs, whereas hiding individuals were likely attracted to the FOV by the bait and thereby contributed to a stronger species-habitat relationship documented by BRUVS. Previous studies have investigated the demersal habits of juvenile cod; identifying a

migratory pattern into shallow soft bottom areas (1–2 m) during the night to feed (Pihl, 1982) and a preference for cobble or rocky habitats in the presence of predators in laboratory studies (Fraser et al., 1996; Gotceitas et al., 1995). However, there are fewer studies on adult cod demersal behaviour (Table 3; Kristensen et al., 2017). When comparing younger with older juvenile cod, Gregory and Anderson (1997) found older cod associated more with rocky habitats compared to younger cod, which were more abundant near habitats of finer particle size (e.g. gravel). This could imply that as cod age, they associate more with rocky habitats, perhaps because older cod require larger interstitial spaces to accommodate the larger body size. However, the age of the cod recorded in the present study is unknown and future efforts to elucidate their demersal habitat preferences across different life stages are warranted.

Generally, the abundance of two-spotted goby and goldsinny wrasse increased with cobble coverage, although BRUVS revealed a slight decrease in wrasse abundance and a plateauing mean abundance of gobies at high cobble coverage. Previous studies investigating two-spotted goby (Perry et al., 2018; Wilkins and Myers, 1992) and goldsinny wrasse (Pihl and Wennhage, 2002; Stål et al., 2007) have also identified a preference for rocky compared to soft bottom habitats (Table 3). Two-spotted goby males are territorial nest holders, typically adopting hard substrates as nesting sites from where they attract females (Utne-Palm et al., 2015). Wrasses play an important role in structuring rocky reef ecosystems by preying on small algae-eating amphipods (Olsen et al.,

Table 3
Overview of previously documented relationships between species abundance and increasing cobble coverage for the seven focal species of this study.

Species	Common name	Association with increasing cobble coverage	Methodology used	References
Gadus morhua	Atlantic cod	Positive	Stereo BRUVS; Free diving submersible with external video cameras; Tagging individual fish (telemetry)	Elliott et al., 2017; Gregory and Anderson, 1997; Kristensen et al., 2017
Pleuronectinae spp.	Right-eyed flatfish	Negative	Seine nets; Dive transects and netting methods (incl. Mono-filament, fyke and gill)	Jenkins and Wheatley, 1998; Pihl and Wennhage, 2002
Clupea harengus	Atlantic herring	Negative	Mono-filament nets and stomach analysis; Personal observation	Stål et al., 2007; Stevenson and Scott, 2005
Merlangius merlangus	Whiting	Negative	Laboratory study (incl. habitat choice trials); Stereo BRUVS	Atkinson et al., 2004; Elliott et al., 2017
Ctenolabrus rupestris	Goldsinny wrasse	Positive	Dive transects and netting methods (incl. mono-filament, fyke and gill); Mono-filament nets and stomach analysis	Pihl and Wennhage, 2002; Stål et al., 2007
Gobiusculus flavescens	Two-spotted goby	Positive	Stereo UBRUVS; Dive transects	Perry et al., 2018; Wilkins and Myers, 1992
Carcinus maenas	Shore crab	Negative	Personal observation	Cohen et al., 1995; Grosholz and Ruiz, 1995

2019), while serving as prey species for larger marine predators, such as Atlantic cod (Enoksen and Reiss, 2018). Both RUVS methods used in this study confirmed the importance of hard substrate for wrasse and goby. The use of bait did not seem to affect the capability of BRUVS to capture habitat associations for wrasse and goby, as the relationships for both species were clearly defined with significant first and second order terms of cobble coverage in the BRUVS models (Table 2). Small individuals often appeared attracted to the overall activity surrounding the bait, even in the presence of larger predators such as cod, suggesting that a potential bias in BRUVS towards sampling dominant large-sized predators may be minimal.

In contrast, abundances of flatfish, whiting and herring decreased as cobble coverage increased. Flatfish often exhibit preference for featureless sand habitats (Table 3; Jenkins and Wheatley, 1998; Pihl and Wennhage, 2002), corroborated by the current study. However, there is less literature available on the association between benthic habitat and species abundances of herring and whiting. Herring is a pelagic fish, typically only utilising hard bottom substrate or macrophytes when spawning (Stevenson and Scott, 2005). Therefore, herring spend less time near the seafloor, suggesting they do not possess a strong preference for a particular benthic habitat. This potential lack of habitat preference was confirmed by the two sampling methods in the current study. UBRUVS failed to record any effects of cobble coverage on herring abundance, whilst BRUVS identified a negative association which was not statistically significant (Table 2; $p < .1$). Overall, herring can be found in a diverse range of habitats, although Stål et al. (2007) found herring to be most common on soft bottoms (Table 3), comparable to the trends observed in the present study. Notably, herring appeared unaffected by the presence of bait, with sporadic encounters consisting of large schools passing the FOV high up in the water column. Although there are reports of cannibalism of adult herring towards larvae (Corten, 2013; Gröger et al., 2010), the use of herring as the bait type in our study may provide an additional explanation for BRUVS recording a relatively weak habitat association for herring compared to the other focal species. Whiting are similar, being found in a range of habitats, with some evidence of a preference for sand over more complex habitats (Table 3; Atkinson et al., 2004; Elliott et al., 2017). The present study supports this association of whiting with soft bottom habitats, although UBRUVS recorded very few individuals of whiting and did not document any significant effect of cobble coverage.

Abundance estimates from underwater videos can be affected by the FOV of a camera at a particular site. For example, reduced visibility or rocks obstructing the view may lower species counts obtained from videos. To address these concerns, we included functional visibility and FOV obstruction as covariates in our models. Our data suggest that including measures of visibility could benefit future RUVS studies. Specifically, there was a significant effect of visibility on four out of the seven species abundances (flatfish, herring, two-spotted goby and shore crab), indicating that including visibility in the models for these species helped to explain some of the variation in the data. Identifying the importance of including functional visibility in our models suggests that an extension on the current study would be to use a more rigorous approach to obtain accurate functional visibility measurements. Stereo-RUVS use two cameras which can be calibrated to determine functional visibility with high precision, along with the additional advantage of recording more accurate fish length measurements (Cundy et al., 2017; Perry et al., 2018; Whitmarsh et al., 2017). Using the coarser visibility estimates in the current study was sufficient to evaluate any relative variations in visibility between samples. However, the number of significant visibility effects demonstrate the need to include functional visibility in RUVS studies and therefore highlights the importance of using higher accuracy measurements produced by systems such as stereo-RUVS. These improved measurements would also enhance comparability both within and between studies where visibility varies drastically (Espinoza et al., 2014; Whitmarsh et al., 2017).

In conjunction with our results, BRUVS have been used previously

to successfully identify species-habitat relationships (Espinoza et al., 2014). Information on how species abundance changes in relation to habitat variables, such as cobble coverage, helps determine the significance of different habitats for individual species. This is important when designing appropriate management strategies, especially those that involve altering the benthic environment or protecting certain areas. Presently, Natura 2000 legislation involves the protection and active restoration of geogenic (i.e. rocky) reefs (Nature Agency, 2016). For example, Støttrup et al. (2017) reported a reef restoration study where 100,000 t of rocks were deposited in the Kattegat Sea to restore previously extracted boulder reefs. Ultimately, it is vital to know what effects such targeted management strategies have on each species, especially in relation to nearby fisheries (both recreational and commercial).

Results from the current study suggest that BRUVS and UBRUVS are both capable of detecting changes in species abundance, but BRUVS may reveal more robust species-habitat relationships by recording a higher number of individuals that are attracted by the bait. However, it remains particularly challenging to quantify the area sampled by BRUVS. Predicting the maximum distance at which species are attracted to bait requires accurate bait plume models, which thus far have only been developed for deep-sea conditions (Sainte-Marie and Hargrave, 1987). In coastal areas, such as in the present study (6–7 m), water turbulence and temperature are more variable compared to deep sea environments; there is also a greater number of species, each with different foraging strategies and odour detection thresholds (Colton and Swearer, 2010; Hardinge et al., 2013; Priede and Merrett, 1996). Without a suitable model that takes these variables into account, abundance data from BRUVS cannot be converted into absolute density estimates, which could be compared between studies (Harvey et al., 2007; Willis and Babcock, 2000). Still, even though the size of the bait plume was unknown in the present study, the plume did not appear to attract fish from surrounding habitats as we did not observe major deviations from previously documented habitat associations (Table 3). It is possible that the use of bait in the BRUVS deployments could have inflated rather than obscured species-habitat relationships, yet the underpinning mechanisms for such a pattern remain unknown and should be examined in future studies.

In conclusion, this study revealed that different RUVS are able to identify previously documented habitat associations for temperate marine species in a patchy coastal area. Thus, this non-extractive technique with minimal benthic impact represents a promising tool for fisheries management. BRUVS documented more robust species-habitat relationships for three out of seven focal species compared to UBRUVS, and identified similar habitat associations for the remaining species. Ultimately, this indicates that equipping RUVS with bait does not obscure relationships between habitat variables and species abundances. BRUVS clearly identified changes in abundance for each species across habitats and provided the additional advantage of higher statistical power over UBRUVS (Bernard and Götz, 2012; Watson et al., 2005). Collectively, these findings support the use of BRUVS as a monitoring tool to address important knowledge gaps in marine ecology.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Acknowledgements

Contributors

J.C.S., J.G.S. and B.M.K. conceived the study design; G.R., H.F., B.M.K. and J.C.S. carried out the fieldwork; N.R., J.L.B. and G.R. analysed the video footage; N.R., T.W. and H.B. performed the statistical analysis; N.R. and T.W. led the writing of the manuscript. All authors discussed the results and contributed critically to the final draft of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151315.

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