RESEARCH ARTICLE

A seascape approach for guiding effective habitat enhancement: Spatially explicit modeling of kelp—grazer interactions

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Kelp habitats are threatened across the globe, and because of their ecological importance, active conservation and restoration solutions are needed. The use of man-made structures as artificial reefs is one way to enhance kelp habitat by providing suitable substrata, but in the past the ecology of artificial structures has been investigated mainly in contrast to natural coastal habitats, not as elements integrated into the seascape. Indeed, it is now emerging that structuring processes, including ecological interactions (e.g., herbivory), can depend on properties of the surrounding seascape. In Eastern Canada, grazing by the green sea urchin can jeopardize the success of artificial reefs for kelp enhancement. Urchin activity is, however, likely to be influenced by the bottom composition, and thus a seascape approach is needed to integrate urchin behavior and habitat heterogeneity. Adopting a spatially explicit framework, we investigated whether the seascape creates areas of differential grazing risk for kelp by affecting urchin habitat use. Specifically, we transplanted kelp onto modules of artificial substrata distributed on a heterogeneous area that we mapped for bottom type and algal cover. After following kelp survival and urchin distribution over time, we modeled kelp survival as function of urchin metrics and coupled it to urchin use of the habitat models to map grazing risk in the area. Kelp survival was a function of the frequency of the urchins presence. Urchins avoided sandy patches, while bottom composition and algal cover modulated the within-patch urchin use of the habitat, creating heterogeneity in grazing risk. Discrete seascape features (boulders) also increased the grazing risk locally. The heterogeneity of coastal seafloor can thus play a major role in determining the ecological outcomes on artificial structures. Incorporating this information when planning artificial reefs could minimize the detrimental grazing risk, thereby increasing the success of artificial reefs for kelp habitat enhancement.

Introduction

In temperate to polar coastal environments, large brown macroalgae, commonly known as "kelp", are highly valued as important primary producers and formers of structurally complex habitats for invertebrates and fish (Steneck et al., 2002; Krumhansl and Scheibling, 2012; Bertocci et al., 2015). However, kelp habitats are being lost in over one-third of their global distribution, threatened by a suit of interacting natural and anthropogenic drivers (Krumhansl et al., 2016; Kriegisch, Reeves, Johnson, and Ling, 2019). Globally, increasing water temperatures are exceeding the physiological thresholds of kelp, often allowing turf algae to replace them (e.g., Filbee-Dexter and Wernberg, 2018; Dijkstra et al., 2019). More locally, a major threat to kelp habitats is overgrazing by urchins (Ling et al., 2015), which

can lock the system into a less diverse and productive "barren" state dominated by coralline algae (Steneck et al., 2013).

To counter kelp habitat loss, several restoration approaches have been proposed, including urchin removal (e.g., Sanderson et al., 2016), clearing turf from substrata (e.g., Perkol-Finkel and Airoldi, 2010), and transplanting kelp onto artificial structures (e.g., Terawaki et al., 2001; Perkol-Finkel et al., 2012), including artificial reefs, which are commonly used for habitat restoration in general (Fabi et al., 2011; Feary et al., 2011). More recently, the use of a modular design for artificial reefs allows separate units to be distributed across the seascape (Dyson and Yocom, 2015; Tessier et al., 2015).

In Eastern Canadian coastal ecosystems and in particular the Gulf of Saint Lawrence (GSL), modular reefs have been used to comply with regulations requiring offsets for damage to marine habitats caused by coastal development (Fisheries Act, 2019). This approach makes the GSL an ideal situation for the use of artificial reefs to enhance kelp habitats in a region where they are typically restricted

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in their distribution due to winter ice scouring in shallow areas and urchin overgrazing in deeper areas (Tamigneaux and Johnson, 2016). Indeed, due the lack of biological controls, exceptionally high densities of the green sea urchin, *Strongylocentrotus droebachiensis* (up to 500 ind. m^{-2}; Gagnon et al., 2004) occur in the GSL, making it an extreme case of a state of urchin barrens (Ling et al. 2015; Johnson et al., 2019).

In this context, if artificial reefs can be colonized by urchins, overgrazing poses a serious threat to kelp enhancement projects (Terawaki et al., 2003). However, since urchins are mainly associated with rocky bottoms (Christian et al., 2010), heterogeneous habitats with less favorable substrata (e.g., sand) interspersed among patches of preferred substrata (e.g., cobbles, boulders) could affect the activity of these consumers, thus offering refugia from herbivory for kelp growing on artificial reefs.

Despite significant research advances on the ecological functioning and quality of artificial structures as novel habitats for benthic assemblages (Dyson and Yocom, 2015; Bishop et al., 2017; Mayer-Pinto et al., 2017; Perkol-Finkel et al., 2018), experimental investigations have generally compared contrasting alternative categories (e.g., artificial–natural, vegetated–unvegetated, hard–soft bottoms) over the more heterogeneous situations typical of most bottoms. While such binary contrasts can be informative, they often represent the end points of environmental gradients or are mainly applied at larger spatial scales. Moreover, they may not adequately account for ecological interactions (e.g., herbivory, predation), especially those involving mobile consumers operating at smaller scales. For example, on coastal defense structures, the fate of algal transplants was largely determined by grazers (Ferrario et al., 2016).

In contrast, landscape ecology—a well-established discipline in terrestrial studies—recognizes the role of the spatial configuration of the surrounding landscape in influencing how species use their habitats and interact locally. For instance, large herbivores adapt their movement and grazing activity to the types of land cover (e.g., refuge-offering forest stands) in their proximity and their exposure to predation risk (Fortin et al., 2005; Mason and Fortin, 2017), whereas forest heterogeneity determines paths of differential movement resistance affecting the outbreaks and spread of pests (Powell et al., 2018). However, in spite of difficulties in both mapping the bottom and tracking animals in marine systems, ecologists have increasingly considered the spatial configuration of seascapes (i.e., heterogeneous areas of the coastal sea floor; Boström et al., 2011) to better identify the mechanisms underlying the ecological patterns. A pioneering study showed that areas of seagrass acted as corridors for predatory crabs from salt marshes to distant oyster reefs (Micheli and Peterson, 1999). Similarly, predation risk for a Mediterranean urchin has been found to be a function of the arrangement of seagrass patches (Farina et al., 2016), and aerial imagery and seascape mapping demonstrated that grazing pressure on macroalgae decreases with the distance from the coral reefs that provide shelter to herbivorous fishes (Madin et al., 2011; Gil et al., 2017).

Seascape approaches and species distribution models that study the distribution of kelp beds and urchin barrens have been so far conducted at large scales and using only abiotic environmental parameters as predictors (e.g., Rinde et al., 2014; Parnell, 2015). While such large-scale studies highlight general trends, they may offer an over-simplified representation of the seascape, ignoring any effect of local habitat patchiness and heterogeneity on ecological interactions at smaller scales. Their utility may thus be limited for the design and deployment of artificial reefs. Indeed, understanding the effects of the seascape on local ecological interactions appears essential to assess the achievability of the ecological goals of artificial reefs, and this knowledge will assist managers and conservationists in minimizing the risk of failure of habitat enhancement projects.

In this work, we investigated whether seascape heterogeneity creates areas of lower grazing risk (i.e., refugia) for kelp transplanted onto modules of artificial substrata and characterized the properties that define this risk. We focused our attention on the effect of 3 seascape properties: bottom substratum (e.g., boulders, gravel, sand), algal cover, and spatial configuration (i.e., position of various elements relative to one another). Specifically, our research questions were (1) does kelp survival decrease in areas with higher rocky substrata due to a greater abundance by urchins there? (2) does the abundance of other algae impact urchin distributions thus potentially influencing kelp survival? and (3) is the distribution of urchins affected by the spatial arrangement of the modules, either promoting movement as "stepping stones" or reducing movement by acting as local "sinks", that is, features that retain urchins at one location?

Methods
Study area

The study was conducted in the late summer 2015 at Baie du petit Métis, a small bay on the south shore of the St. Lawrence maritime estuary (48°40′37.30″ N, 68° 0′41.24″ W; Québec, Canada; **Figure 1**). The bay is separated on the northwest side from the St. Lawrence River by a narrow peninsula characterized by rocky shores, while sandy beaches become gradually predominant moving eastward. A wide intertidal mudflat with sparse rocky outcrops is followed subtidally by unconsolidated gravel, cobble and boulders heterogeneously arranged among large patches of sand. Fucoid seaweeds (i.e., *Ascophyllum* and *Fucus* spp.) are the most abundant vegetation in the rocky intertidal zone. Kelp in the bay are spatially confined to rocky intertidal pools and the shallow subtidal (approximately 1 m), primarily represented by perennial species *Alaria esculenta*, *Saccharina latissima*, and *Agarum clathratum* (Bégin et al., 2004; Krause-Jensen et al., 2012). No subtidal patches of kelp were present at the time of the study. Red foliose algae *Ptilota serrata* and *Phycodrys rubens* (Himmelman, 1991) are common in the GSL, and although we did not identify foliose algae taxonomically, these species were likely representing the majority of the seaweeds in the study area based on observations while diving.
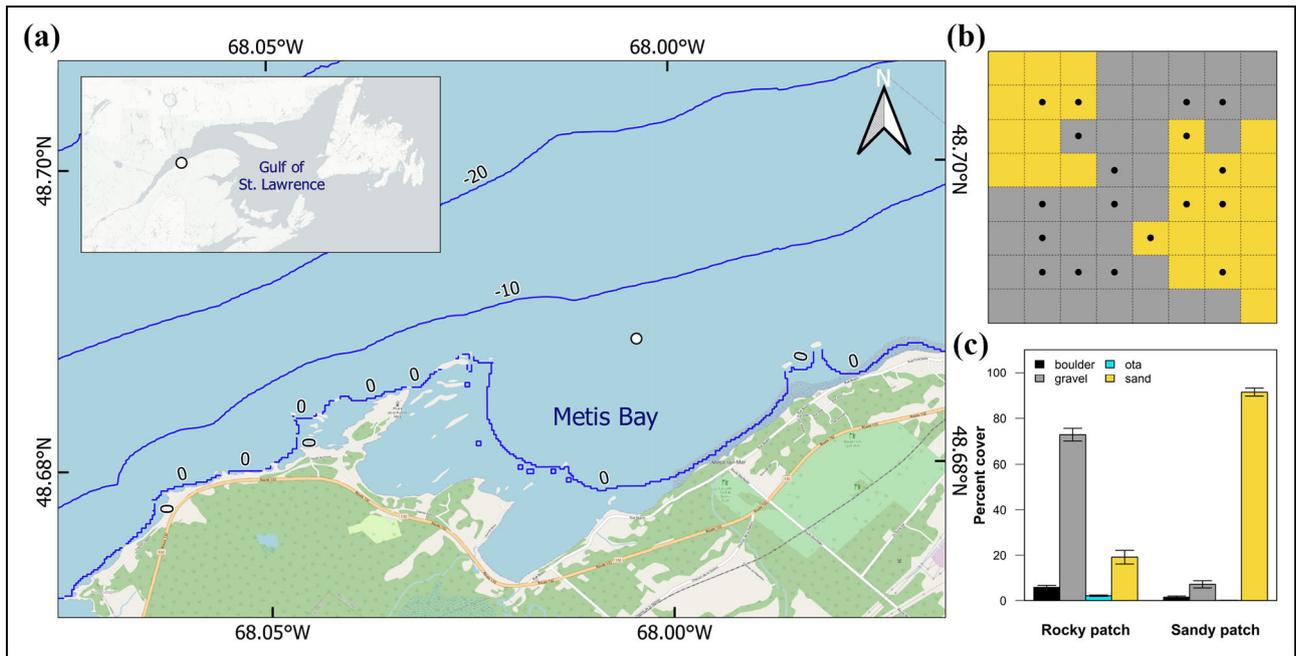
Figure 1. Map of the Baie du petit Métis, spatial configuration, and bottom composition and of the study site. (a) Location of the study site in the bay (open circle) and regional context (inset). Isobaths represented as blue lines at 10-m depth intervals. Base map acquired from OpenStreetMap. (b) The study site included 2 sandy patches (yellow cells) and 1 rocky patch (gray cells). Black dots represent the arrangement of blocks with kelp transplants at the beginning of the experiment. Dashed lines depict cell borders. (c) Average percent cover of boulders, gravel, sand, and foliose algae (ota) of cells within rocky and sandy patch (mean $\pm$ standard error). DOI: https://doi.org/10.1525/elementa.2021.00013.f1

The only sea urchin in the area is the green sea urchin *S. droebachiensis*, an omnivore that preferentially feeds on perennial kelp such as *A. esculenta* but includes other algae (including red algae) as well as animal tissues in its diet (Himmelman and Steele, 1971). Preliminary surveys indicated that urchins in the bay had a variable density of 8 ± 10 ind. m^{-2} (average $\pm$ *SD*, $n = 94$).

Experimental design and modeling approach

To evaluate how the seascape might influence survival of subtidal kelp, we selected a site of 256 m^2 featuring a heterogeneous bottom (i.e., a mix of sandy and rocky patches) at an 8-m depth within the bay (**Figure 1b**). The area of the site was chosen as a trade-off between the need of capturing bottom heterogeneity, the required workload in SCUBA, and the mobility of green sea urchins (up to 5 m d^{-1}; Dumont et al., 2006). The site depth was chosen to be representative of the subtidal bottom usually overgrazed by urchin in the GSL and well within the depth range typically occupied by kelp. Initial surveys mapped relevant seascape variables (see *Bottom mapping*) after which the survival of transplanted kelp was monitored (see *Kelp survival and urchin distribution*). We adopted a two-step modeling approach to describe first the survival of kelp as a function of different urchin metrics (e.g., presence/absence, density), and second the habitat use by urchins as a function of seascape properties. By coupling the 2 models, we mapped the grazing risk in the area.

Bottom mapping

We mapped the study site utilizing a photographic sampling method via SCUBA over a permanent 16×16-m grid divided into 64 2×2-m cells (Figure S1). Each cell was subdivided into 4 parcels and photographed using a GoPro Hero3$^+$ camera mounted on a frame (Figure S2). We defined the areal extent a priori to optimize the workload.

Photographs were analyzed to quantify percent cover of substratum type and selected algal categories. Substratum type included 3 categories: "boulders" (>25 cm), "cobble and gravel" (0.2–25 cm, grouped to facilitate the analysis), and "sand" (<0.2 cm; sensu Wentworth, 1922). Algal categories included foliose algae (mainly red algae), turf-sediment, and crustose coralline algae. Algal cover was estimated at all sampling times to monitor changes, while bottom type classification was conducted only on photographs taken at the beginning of the experiments and then assumed to remain constant. Refer to Supplemental Material for further details.

Kelp survival and urchin distribution

We transplanted one reproductive individual of *A. esculenta* on each of 18 modules that each consisted of one concrete masonry unit (aka cinder block, but henceforth "block") measuring $15 \times 40 \times 20$ cm, W $\times$ L $\times$ H; Figure S3a) on August 5, 2015 ($T_{days} = 0$). Each block was placed on its side (thus with openings to hollow interior accessible directly from the bottom) and positioned in the center of cells randomly chosen from among the 36 cells of the

inner grid (i.e., excluding cells located along the edge of the grid to allow calculation of neighboring statistics). The number of blocks used was chosen to occupy only half the available cells to have the variation in between-block distances. Random assignment of blocks resulted in 10 deployed in rocky cells, 8 in sandy cells (**Figure 1**). Kelp survival was assessed every 10–20 days until October 13 ($T_{days} = 69$) by confirming its primary meristem was still present (Mann, 1973).

We counted the number of visible urchins in each photograph using the Cell Counter plug-in for ImageJ 1.47, considering only individuals with a diameter greater than 20 mm (smaller urchins are generally cryptic). Urchins found inside the cavities of the artificial blocks (hereafter "hiding urchins") were also counted.

Verification of transplant technique and suitable kelp growing conditions

Grazing was not the only possible cause for kelp loss, particularly with transplant experiments. Poor growing conditions, transplant stress, and dislodgment were other possible mortality vectors. To evaluate our transplant technique and test the suitability of the physical environment, we also transplanted kelp onto a frame suspended off the bottom (i.e., 3 ropes arranged in a pyramidal structure; Supplemental Material). This frame served as an effective herbivore deterrent while exposing them to similar hydrodynamic conditions as those transplanted onto blocks. We deployed the kelp frame in July 2015 with kelp plants spaced 30 cm apart along the lines (Figure S4). In October, we recovered all kelp transplants, recording for each (i) its position (depth) on the frame, (ii) whether it had "survived" (described above), (iii) whether transplants developed reproductive sporophylls, and, if so, (iv) sporophyll length.

Statistical analyses
Kelp survival model
We modeled kelp survival as a function of different sea urchin metrics using survival analysis. This approach models the "time until an event occurs"—that is, survival time—and accommodates censoring by retaining individuals with unknown survival time in the data set (Kleinbaum and Klein, 2005). We defined the survival time as the number of days from the start of the experiment ($T_{days} = 0$) to the midpoint between the sampling date when the loss of an individual kelp was first observed and preceding sampling date (e.g., for a kelp observed at $T_{days} = 20$ but not observed at $T_{days} = 30$, survival time $= 25$). We considered 6 predictor variables: "urchin frequency," defined as the number of times that urchins were present in a cell with a block; "urchin density" as the median of the average urchin density recorded at each sampling time in a cell with a block; median urchin frequency in neighboring cells (i.e., the 8 cells surrounding the focal one); median of the urchin density in neighboring cells; "frequency of hiding urchins" as the number of times when urchins were found in cavities of the block; and finally the median of the number of urchins hiding in the block.

We fitted semiparametric Cox Proportional Hazards (CoxPH), Weibull, and exponential parametric survival models for each predictor and a null model (i.e., no effect of predictors) for a total of 21 candidate models and compared them via second-order Akaike information criterion for small sample sizes, AICc (Mazerolle, 2006). Because of the limited sample size ($n = 18$), we did not specified models with more than one predictor. We checked the assumption requirements (Kleinbaum and Klein, 2005) and hereafter report only the CoxPH models since they outcompeted their parametric alternatives.

Urchin habitat use
We modeled sea urchin presence/absence as a function of 4 major seascape properties: bottom composition, algal cover, spatial configuration of patches and discrete natural features, and spatial arrangement of the artificial reef (i.e., reef setup). In addition to the variables described in the bottom mapping section, predictors included the median values of the cover of cobble and gravel, foliose algae, coralline algae, and turf-sediment in neighboring parcels. We assigned each parcel to either a sandy or a rocky patch and calculated spatial configuration predictors as the shortest distance of a parcel to a sandy patch, to a rocky patch, and to the closest parcel containing a boulder. Finally, we considered the reef setup calculating the distance from the closest parcel of a cell containing a block. All distances were in relative units (i.e., between parcels distance).

We checked all potential predictors for collinearity and retained those deemed more relevant. We modeled urchin presence in each parcel and sampling time using Binomial Generalized Linear Mixed Models with a logit link and "parcel" as a random effect following Zuur et al. (2009); percent cover predictors were arcsin transformed. We built a set of 17 candidate models that included selected combinations of seascape properties (see model set in **Table 2**) and compared them using AIC.

Model selection and averaging
For both analyses of kelp survival and urchin habitat use, we considered models to have substantial support when they had a ΔAICc or ΔAIC < 2 (Mazerolle, 2006). Whereas only one model for kelp survival met this criterion and was thus selected as the "best" model, 3 models for urchin habitat use showed comparable support and were thus averaged to decrease the selection bias (Mazerolle, 2006).

All statistical analyses were performed using R 3.3.2 (R Core Team, 2016). We used packages "*raster*" for spatial analysis, "*survival*" and "*lme4*" for model fitting, and "*MuMIn*" for model averaging. All estimates of variance listed hereafter are standard error (*SE*). See Supplemental Material for more details on analyses.

Mapping grazing risk
Models describing the urchin distribution and kelp survival were coupled to create a map representing the risk for a kelp of being grazed in different areas throughout the site. Using the "urchin habitat use" model, we first mapped urchin frequency, assigning to each cell the

maximum value between the maxima of predicted urchin presence probabilities in its parcels at different times. We then used this map as the input for the kelp survival model. The output of a CoxPH model is the log-hazard ratio, log(HR), here representing the risk for a kelp to be grazed and expressed relative to a cell with urchin frequency equal to 0. When the log(HR) equals 0 then two cells have the same risk.

Results

Site description

The spatial configuration of our study site was characterized by 2 sandy patches divided by 1 continuous patch of rocky bottom (**Figure 1b** and **c**); however, the 2 bottom types were almost equally represented (27:37, sandy: rocky cells). Rocky patches were mainly composed of cobbles and gravel with boulders covering only $5.73 \pm 0.1\%$ (mean $\pm$ *SE*), while sand accounted for $19.1 \pm 3.0\%$. Sandy patch composition was more homogeneous with sand covering $91.3 \pm 1.7\%$ of the bottom with a sparse presence of cobble and gravel, and boulders ($7.0 \pm 1.6\%$ and $1.5 \pm 0.5\%$, respectively). Throughout the experiment the density of visible sea urchins in the rocky patch was 0.92 ± 0.08 ind. m^{-2} (mean $\pm$ *SE*, $n = 740$) and of 0.13 ± 0.02 ind. m^{-2} ($n = 540$) in the sandy patches.

Herbivory exclusion and transplant mortality

In the absence of herbivory from sea urchins (i.e., on the kelp frames), 83% of kelp transplants survived and all developed reproductive sporophylls (sporophyll length $= 26.1 \pm 0.1$ cm, Figure S5), indicating that very little mortality was due to the transplant technique and that the physical environment was suitable for kelp growth. There was no statistical effect of depth on the number of lost transplants ($p = 0.17$, Generalized Linear Model with a Poisson distribution) or on sporophyll length ($p = 0.4$, Figure S5).

Kelp survival

40% of initially transplanted kelp survived until the end of the study (**Figure 2**). We observed a sharp decrease in survival (40% decrease) in the first 25 days followed by a constant decrease. Kelp survival was significantly related to the local urchin frequency, log(HR) $\pm$ 0.95 confidence interval (CI) $= 5.8 \pm 2.9$; Likelihood Ratio: $\chi^2 = 21.1$, 1 *df*, $P < .001$; **Table 1**. The risk exposure decreased (i.e., hazard ratio < 1) as urchin frequency decreased from the average value toward zero, whereas it greatly increased (hazard ratio > 1) as urchin were more frequently present in a cell (**Figure 3**).

Urchin use of the habitat

Three models resulted as good candidates between the ones tested and were therefore averaged (ΔAIC < 2; **Table 2**). The averaged model retained the variables boulders, cobble and gravel, foliose algae, coralline algae, neighboring foliose algae, and distance to block. All variables, except distance to block, were positively correlated with urchin frequency, although only boulders and cobble and gravel were significant, while coralline algae were almost
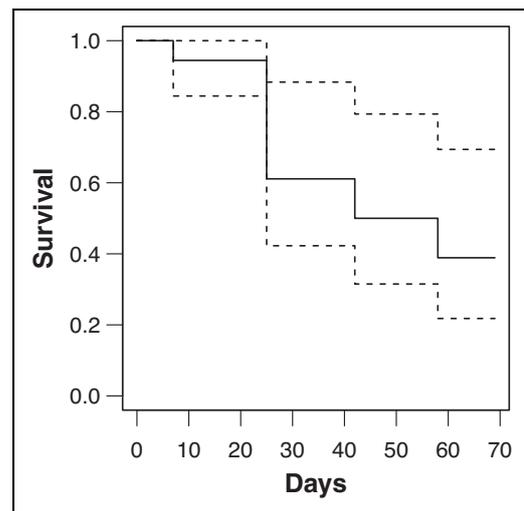

Figure 2. Kaplan–Maier survival curve for kelp. Vertical segments represent changes in survival at sampling times (*x*-axis, days from transplanting). Solid line represents the kelp survival, while dashed lines represent the 95% confidence intervals. DOI: https://doi.org/10.1525/elementa.2021.00013.f2

significant (**Table 3**). The percentage cover of boulders in a parcel had the greater effect size, meaning that an increase in boulder cover contributes the most in the frequency of urchin presence (**Figure 4**). The averaged model showed a good calibration (i.e., a good agreement between observed and fitted values) for fitted values below 0.4, otherwise the model seemed to slightly underestimate the observed values (Figure S6). Model discrimination (i.e., the ability of model-predicted values to discriminate between those with and without the outcome), assessed by the area under the receiver curve, was satisfactory (Area Under the receiver operating characteristic Curve [AUC] $\pm$ .95 CI $= 0.95 \pm 0.01$; perfect discrimination when AUC is equal to 1).

Map of grazing risk

The grazing risk was concentrated on but not limited to the rocky patch where it was generally higher than on the sandy part of the bottom (**Figure 5**). The distribution of risk intensity also differed in the 2 patch types: risk intensity in rocky cells ranged between 0.6 and 5.2 and presented an overall uniform distribution, while log hazard ratio on sand ranged between 0 and 4.0, but 55% of the cells were associated with the lowest risk (Figure S7).

A visual analysis of the map of grazing risk revealed the existence of hotspots of risk in both rocky and sandy regions (i.e., darker cells in **Figure 5**): Cells associated with the highest risk were distributed at different positions in the grid and separated from each other by lower risk cells. The position of the risk hotspots seemed to be driven primarily by the distribution of boulders in the grid. Indeed, **Figure 4** showed that an increase in the percent cover of boulders in a given cell determined a more direct increase of urchin frequency compared to the amount of cobbles and gravel, the other significant variable in the

Table 1. Kelp survival model selection. DOI: https://doi.org/10.1525/elementa.2021.00013.t1

Cox Models

Survival ~ ….	AICc	ΔAICc[a]	Akaike Weights[b]	Rank
Null (i.e., ~ 1)	55.7	18.89	0.000	7
Urchin density	39.9	3.07	0.176	2
Neighboring urchin density	51.3	14.46	0.001	5
Urchin frequency	**36.9**	**0.00**	**0.821**	**1**
Neighboring urchin frequency	51.0	14.17	0.001	4
Number of urchins hiding	50.1	13.29	0.001	3
Frequency of urchins hiding	53.9	17.01	0.000	6

Model selected is in bold (ΔAICc < 2). AICc = Akaike information criterion for small sample sizes.

[a]Difference between AICc of a given model and the AICc of the best model.

[b]Ratio of the ΔAICc of a given model relative to the whole set of candidate models. Higher scores indicate the probability that the model is the best among the whole set of candidate models (Mazerolle, 2006).

model (**Table 3**). Interestingly, kelp surviving to the end of the experiment in 2015 were still alive at the beginning of the next summer (**Figure 5**).

Discussion

For kelp-urchin dynamics (e.g., Steneck et al., 2002; Scheibling et al., 2011; Ling et al., 2015) and the design and functioning of artificial reefs (Bulleri and Chapman, 2010; Fabi et al., 2011; Feary et al., 2011; Lima et al., 2019, and references therein), the binary contrast of alternative habitats (i.e., kelp bed vs. barren ground or artificial vs. natural reefs) examines the end points of what is actually a continuum. By specifically examining small-scale seascape heterogeneity, we provide a novel spatially explicit framework that incorporates ecological processes and is more relevant for the scale for the design of artificial reefs relative to more commonly used species distribution models. Using this framework, we investigated for the first time the role of the local seascape heterogeneity in modulating the interaction between urchins and kelp. We showed that grazing risk intensity is modulated by the seascape properties, including biological characteristics and discrete seascape features, to locally alter microhabitat use by this herbivore, even within the same patch. Importantly, we showed that we can quantify grazing risk, that is, kelp refugia, at small spatial scales based on local seascape heterogeneity.

Levels of seascape heterogeneity
Seascape heterogeneity often results from multiple concurrent organizational levels (Didham, 2010). Here, we examined heterogeneity over 3 levels: bottom patchiness,
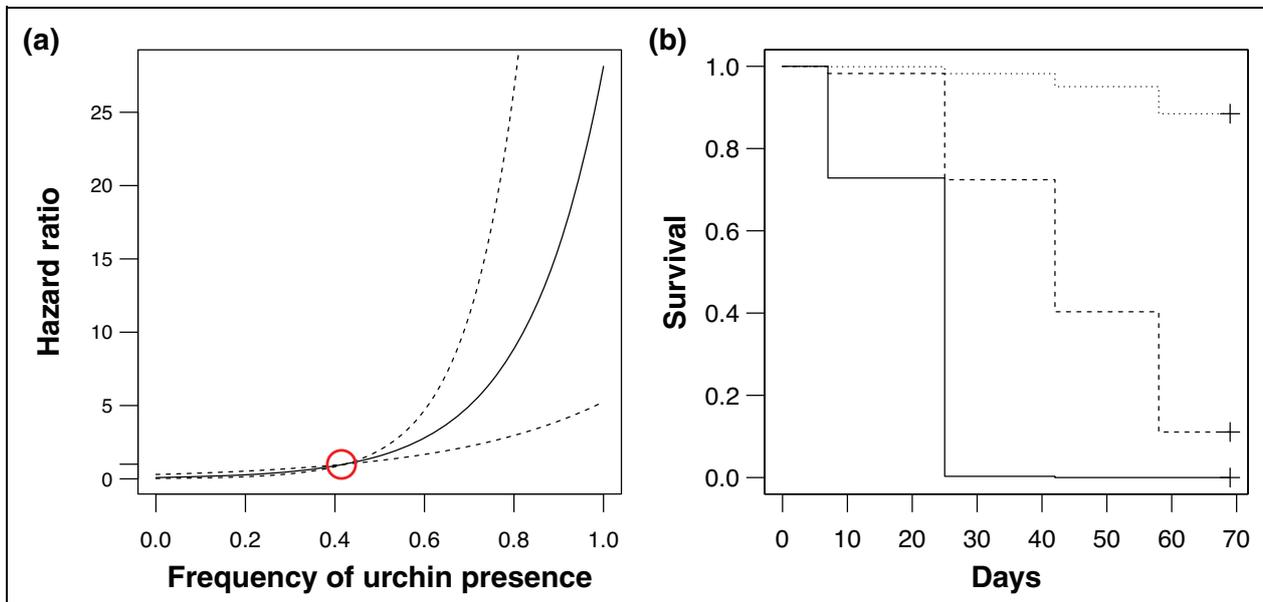
Figure 3. Fitted Cox Proportional Hazard model for kelp survival. (a) Hazard ratio as function of urchin frequency (i.e., presence of urchin in a cell through time). The hazard ratio is calculated relative to the average urchin frequency, that is, 0.42 (red circle). Dashed lines show the 0.95 confidence interval, (b) fitted survival curves for 3 levels of urchin frequency (0: dotted line, 0.5: dashed line, 1: solid line). DOI: https://doi.org/10.1525/elementa.2021.00013.f3

Table 2. Urchin use of the habitat model selection and averaging. DOI: https://doi.org/10.1525/elementa.2021.00013.t2

Model	Predictors Bottom Type (% Cover)		Algal Cover (% Cover)			Spatial Configuration		Reef Setup	ΔAIC[a]	Akaike Weights[b]	Rank
Bottom + Spatial + Setup											
SG1	BLD	CAG	-	-	-	dSND	dBLD	dBLOCK	4.56	0.033	7
M1	BLD	CAG	-	-	-	dSND	dBLD		3.92	0.045	5
M2	BLD	CAG	-	-	-	-	-	dBLOCK	4.35	0.036	6
M3	BLD	CAG	-	-	-	-	-		3.04	0.070	4
Bottom + Biological + Setup											
SG2	**BLD**	**CAG**	**Algae**	**AlgaeNeib**	**CCA**	-	-	**dBLOCK**	**0.98**	**0.195**	**3**
M4	**BLD**	**CAG**	**Algae**	**AlgaeNeib**	**CCA**	-	-		**0.10**	**0.303**	**2**
M5	-	-	Algae	AlgaeNeib	CCA	-	-	dBLOCK	43.00	0.000	14
M6	-	-	Algae	AlgaeNeib	CCA	-	-		41.64	0.000	13
M7	-	-	Algae	-	CCA	-	-		46.82	0.000	15
M8	**BLD**	**CAG**	**Algae**	-	**CCA**	-	-		**0.00**	**0.318**	**1**
M9	-	-	Algae	-	CCA	-	-	dBLOCK	48.43	0.000	16
Biological + Spatial + Setup											
SG3	-	-	Algae	AlgaeNeib	CCA	dSND	dBLD	dBLOCK	16.09	0.000	10
M10	-	-	Algae	AlgaeNeib	CCA	dSND	dBLD	-	16.03	0.000	9
M11	-	-	-	-	-	dSND	dBLD	dBLOCK	33.04	0.000	12
M12	-	-	-	-	-	dSND	dBLD	-	32.51	0.000	11
M13	-	-	Algae	-	CCA	dSND	dBLD	-	15.05	0.000	8
M14	-	-	-	-	-	-	-	dBLOCK	104.79	0.000	17

Models selected for averaging are in bold (ΔAIC < 2). Subglobal models are named "SG." AIC = Akaike information criterion; BLD = boulder; CAG = cobble and gravel; AlgaeNeib = neighboring foliose algae; CCA = crustose coralline algae; dSND, dBLD, dBLOCK = distance to sand, boulder, block, respectively.

[a]Difference between AIC of a given model and the AIC of the best model.

[b]Ratio of the ΔAIC of a given model relative to the whole set of candidate models. Higher scores indicate the probability that the model is the best among the whole set of candidate models (Mazerolle, 2006).

within-patch variability, and spatial configuration. The patchiness of bottom composition played a major role in determining kelp refugia. Sandy patches were overall safer for kelp compared to rocky patches, an expected outcome as urchins prefer hard substrata. This result confirms the utility of coarse bottom classification into binary categories for preliminary identification of kelp refugia in the seascape when planning the deployment of artificial reefs modules.

Next, we resolved patch heterogeneity at a finer scale using our two-step experimental approach to couple kelp survival with urchin habitat use. By identifying the factors affecting kelp survival, we could translate within-patch heterogeneity into variability of grazing risk, which did not follow an all-or-nothing pattern corresponding to the binary bottom classification. Boulders emerged as a key seascape feature, creating hotspots of grazing risk within both rocky and sandy patches. This source of heterogeneity drove the urchin distribution at our study site by locally enhancing the structural complexity of the bottom. Elsewhere, urchins greatly favor boulders over cobble beds, apparently for reducing predation risk (Scheibling and Hamm, 1991). Similarly, urchins prefer microhabitats that minimize dislodgment risk (Frey and Gagnon, 2016). The cover of foliose algae, both in focal and neighboring cells, also contributed to this within-patch heterogeneity and had a predictive value for urchin presence and therefore for grazing risk in the area. As a potential food source, their presence could either attract and/or retain urchins or simply interfere with movements. Urchins often move randomly (Lauzon-Guay et al., 2006) and thus in an area dominated by foliose algae would more frequently encounter algal patches increasing the chances of remaining in the area. Similarly, the percent cover of coralline algae was a predictor of urchin presence, but

Table 3. Averaged model summary. DOI: https://doi.org/10.1525/elementa.2021.00013.t3

Model Parameter	Estimate[a]	Adjusted *SE*	*z* Value	*P* Value
Intercept	−5.406	0.604	8.96	< .001
BLD	4.681	0.973	4.81	< .001
CAG	2.191	0.502	4.36	< .001
Algae	0.882	0.886	1.00	.32
CCA	2.178	1.090	2.00	.05
AlgaeNeib	1.562	1.097	1.42	.15
dBLOCK	−0.205	0.195	1.05	.29

SE = standard error; BLD = boulder; CAG = cobble and gravel; AlgaeNeib = neighboring foliose algae; CCA = crustose coralline algae; dBLOCK = distance to block.

[a]Coefficients are shrinked estimates resulting from the "full" average (i.e., considering a parameter equal to zero when not present in a given model). Values are in the scale of individual linear predictor.

more likely as the result of past grazing activity (e.g., either exposing coralline algae after the removal of erect algae or freeing the substratum for coralline expansion) rather than acting as a resource.

Finally, the heterogeneity resulting from the spatial configuration of the landscape can affect species interactions (Didham, 2010). For example, meadow proximity influences the trajectory of free-ranging bison moving in a patchy forest landscape (Dancose et al., 2011), corridors of vegetation ease the spread of mountain pine beetles (Powell et al., 2018), and the spatial arrangement of seagrass affects predation on urchins (Farina et al., 2016). Our models included variables describing the spatial configuration of both the seascape and arrangement of the modules (**Table 2**). However, the limited spatial extent of our study or the abundance of cells containing boulders (**Figure 4**) possibly hindered our ability to capture an effect of seascape configuration. Nonetheless, the slightly negative effect of the distance from a block on urchin frequency suggests that blocks could have possibly acted as urchin attractors. Indeed, we commonly observed urchins occupying the block cavities (Figure S8), a behavior consistent with their preference for sheltered microhabitats (Scheibling and Hamm, 1991).

Grazing risk as an emergent property related to heterogeneity and urchin movement

Grazing risk for kelp is thus an emergent property resulting from the interaction between urchins and local habitat heterogeneity. The survival of kelp was negatively correlated to the frequency of urchin presence in a given cell. Since urchins are mobile and capable of moving among cells within a day (Dumont et al., 2006), their movement behavior ultimately underlies their local distribution including their density, which was the second-best explanatory variable for our predictions of risk. Unfortunately, we

were not able to determine whether higher urchin frequency or densities were due to an accumulation of urchins in particular cells or to a more dynamic reshuffling of individuals between samplings (tracking the movement of individuals would have been necessary to distinguish these two possibilities but is logistically complex). Our results confirmed that urchins are associated with particular characteristics or hard bottom features of the seascape but not exclusively. Indeed, recent studies (MacGregor, 2020) have shown that sand is not a barrier to urchin movement, but it affects urchins in that they will cross patches of sand but not remain on them. This behavior would help explain the higher risk associated with certain landscape features within sandy patches (i.e., isolated boulders) as well as the colonization by urchins of our blocks placed there. The propensity of urchins to move onto soft substrata is still poorly known, but it likely underlies the low grazing risk for kelp in such habitats. If individuals are less likely to venture onto soft substrata, then the probability of encountering small rocks or isolated boulders would be reduced. Moreover, once on a sandy bottom, *S. droebachiensis* appears to move further across the bottom (possibly either more quickly or more directly) than on rocky bottoms (Dumont et al., 2006), which would also reduce the encounter probability. Finally, once on an isolated hard substratum, an urchin might be more likely to leave due to the limited suitable habitat.

A seascape approach to enhance artificial reefs success and their ecological benefits

Seascape ecology offers a conceptual framework to identify areas with differential intensity of species interaction, and while of fundamental interest, it also informs ecosystem management. Our modeling approach offers a method to inform stakeholders with both predictions of risk at the site scale and an indication of which predictor variables need to be measured. In our specific case, we assessed grazing risk at the small scale at which artificial reefs are used in restoration and habitat enhancement projects. This predictive capability could allow the successful development of artificial reefs in locations that are more relevant, namely the heterogeneous bottoms that are more typical of shallow coastal waters. In particular, the ability to deploy reef modules closer to natural rocky bottoms reduces some drawbacks of past approaches while promoting connectivity between artificial and natural habitats (Dethier et al., 2003; Bishop et al., 2017). For example, to minimize grazing impacts, reefs are usually deployed in areas of extensive sandy bottoms or built to greater heights (Terawaki et al., 2001; Terawaki et al., 2003; Reed et al., 2006) where greater exposure to wave action reduces urchin foraging (Blain and Gagnon, 2014). These measures likely increase costs (e.g., more construction material, further distances) and result in the isolation of kelp beds. Moreover, the introduction of hard substrata into soft-sediment habitats alters their ecology (e.g., hydrodynamics, sedimentation, organic matter inputs; Bishop et al., 2017; Heery et al., 2017), yet grazers can still colonize through recruitment, removing macroalgae and
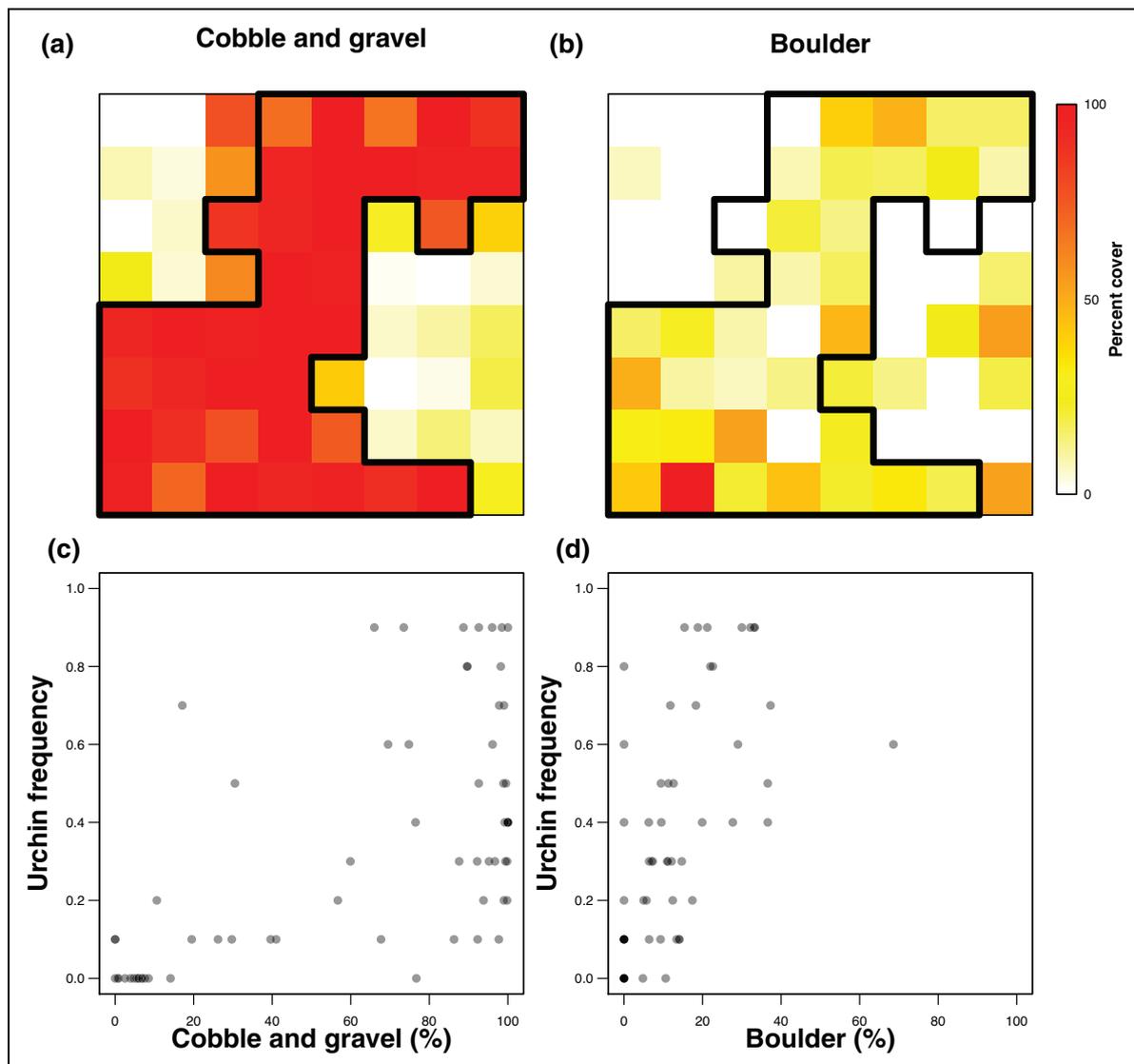
Figure 4. Distribution of categories of substratum and their effects on urchin frequency. Heatmaps: (a) cobble and gravel and (b) boulders percent cover and relationship with the observed urchin frequency per cell in scatterplots, (c) and (d), respectively. The black outline delimits the border of the rocky patch. DOI: https://doi.org/10.1525/elementa.2021.00013.f4

possibly creating opportunities for invasive species (Dafforn et al., 2012). In contrast, deploying reefs modules in proximity of existing rocky bottoms but within areas of reduced grazing risk could promote positive feedback on natural habitats. In particular, kelp refugia within such seascapes would enhance recruitment (kelp are generally poor dispersers; Gaylord et al., 2004) and productivity. Indeed, the addition of locally derived kelp detritus could enhance food resources for urchins, enhancing their commercial value (Claisse et al., 2013; Cresson et al., 2014) and reducing destructive grazing perhaps to the point that the ecosystem switches to the alternative stable state of a kelp forest (Kriegisch, Reeves, Flukes, et al., 2019).

Long-term outlook of kelp enhancement performance

Ultimately the performance of kelp-enhancing artificial reefs must be sustainable through time, ideally without active maintenance. Although our work was not designed to look at seasonality and long-term performance, some speculation can be advanced. Grazing risk may decrease overwinter primarily because urchins tend to migrate in deeper areas or to seek refuge in crevices to escape increased wave disturbance during winter storms (Konar and Estes, 2003; Adey and Hayek, 2011). Additionally, food intake in *S. droebachiensis* reaches minima during winter (Siikavuopio et al., 2007) indicating that seasonality seems to affect feeding rates more than temperature (Suskiewicz and Johnson, 2017). From a kelp perspective, winter represents a relatively inactive season because of reduced light availability. However, winter irradiance levels might become less limiting if the current trend in climate change induced sea-ice cover reduction persists (Krause-Jensen et al., 2012; Galbraith et al., 2019). We witnessed the overwintering of kelp when we opportunistically revisited our study site at the beginning of the next
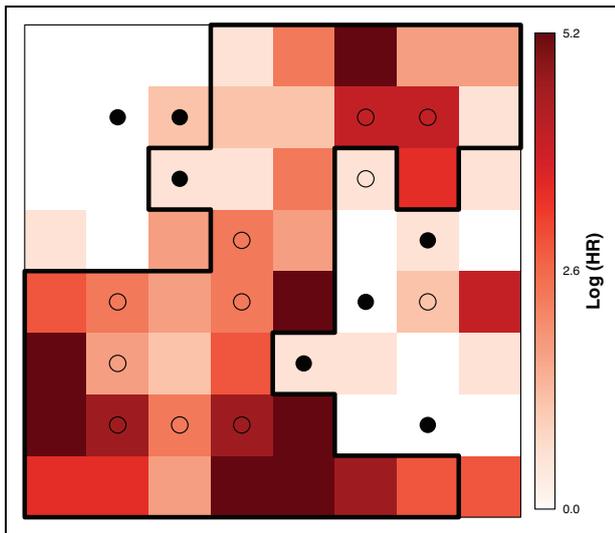
Figure 5. Grazing risk map. Risk is expressed as log hazard ratio (log(HR)) relative to cells with urchin frequency equal to zero. The darker the color, the higher the risk of a kelp of being grazed; white cells have log(HR) equal to zero and represent the reference level. The black outline delimits the border of the rocky patch. Black dots depict the position of surviving kelp both at the end of the experiment and 1 year after; open circles represent lost kelp. DOI: https://doi.org/10.1525/elementa.2021.00013.f5

summer season (**Figure 5**). Despite having just an anecdotal connotation, this observation is encouraging, and we cautiously suggest that seasonality might not negatively affect the kelp-urchin dynamic described here. Finally, having observed that artificial reefs on isolated sandy areas in the GSL can successfully maintain kelp population for several years (Johnson and Ferrario, personal observations, August 2018), we are confident that long-term performance of artificial reefs will not be an issue provided that the number of sea urchins reaching the reef can be limited.

Moving forward
Since restoration projects are necessarily implemented at the local scale, our seascape approach to assess the intensity of species interactions can act as a guide. Several factors, however, need to be considered when applied more widely. First, the mobility (e.g., range, behavior) of relevant species needs to be clearly assessed as it determines the spatial scale and resolution at which seascape data need to be acquired. Unfortunately, this information is often largely absent. Second, accurate mapping of the bottom of coastal habitats, with a particular attention to biological data (e.g., vegetation, benthic invertebrates) is needed. Finally, artificial reef projects should be carefully monitored to identify factors leading to failure, but relevant information is often not collected or is not publicly available (Tessier et al., 2015).

Our work demonstrates that with such information, we can understand how the intensity of species interactions is modulated by the surrounding seascape and can be readily incorporated in the planning phase of restoration projects to increase their rate of success and ensuring lasting results.

Data accessibility statement

Supplemental files
The supplemental files for this article can be found as follows:

Text S1. Figures S1–S8.Docx.

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Author contributions
Contributed to conception and design of the study: FF, LEJ.

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Contributed to analysis and interpretation of data: FF.

Contributed to leading the writing of the article: FF.

Contributed to critical revision and approval of the article: FF, LEJ, TS.

References
Adey, WH, Hayek, L-AC. 2011. Elucidating marine biogeography with macrophytes: Quantitative analysis of the North Atlantic supports the thermogeographic model and demonstrates a distinct subarctic region in the Northwestern Atlantic. *Northeastern Naturalist* **18**(Monograph 8): 1–128. DOI: http://dx.doi.org/10.1656/045.018.m801.

Bégin, C, Johnson, LE, Himmelman, JH. 2004. Macroalgal canopies: Distribution and diversity of associated invertebrates and effects on the recruitment

and growth of mussels. *Marine Ecology Progress Series* **271**: 121–132.

Bertocci, I, Araújo, R, Oliveira, P, Sousa-Pinto, I. 2015. Potential effects of kelp species on local fisheries. *Journal of Applied Ecology* **52**(5): 1216–1226. DOI: http://dx.doi.org/10.1111/1365-2664.12483.

Bishop, MJ, Mayer-Pinto, M, Airoldi, L, Firth, LB, Morris, RL, Loke, LHL, Hawkins, SJ, Naylor, LA, Coleman, RA, Chee, SY, Dafforn, KA. 2017. Effects of ocean sprawl on ecological connectivity: Impacts and solutions. *Journal of Experimental Marine Biology and Ecology* **492**: 7–30. DOI: http://dx.doi.org/10.1016/j.jembe.2017.01.021.

Blain, C, Gagnon, P. 2014. Canopy-forming seaweeds in urchin-dominated systems in Eastern Canada: Structuring forces or simple prey for keystone grazers? *PLoS One* **9**(5): e98204. DOI: http://dx.doi.org/10.1371/journal.pone.0098204.

Boström, C, Pittman, SJ, Simenstad, C, Kneib, RT. 2011. Seascape ecology of coastal biogenic habitats: Advances, gaps, and challenges. *Marine Ecology Progress Series* **427**: 191–217. DOI: http://dx.doi.org/10.3354/meps09051.

Bulleri, F, Chapman, MG. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology* **47**(1): 26–35. DOI: http://dx.doi.org/10.1111/j.1365-2664.2009.01751.x.

Christian, JR, Grant, CGJ, Meade, JD, Noble, LD. 2010. Habitat requirements and life history characteristics of selected marine invertebrate species occurring in the Newfoundland and Labrador region. Canadian Manuscript Report of Fisheries and Aquatic Science, 2925, pp. 1–226. St. Jhon's, Newfoundland and Labrador. Available at http://www.dfo-mpo.gc.ca/Library/340301.pdf. Accessed February 27 2018.

Claisse, JT, Williams, JP, Ford, T, Pondella, DJ, Meux, B, Protopapadakis, L. 2013. Kelp forest habitat restoration has the potential to increase sea urchin gonad biomass. *Ecosphere* **4**(3): 38. DOI: http://dx.doi.org/10.1890/ES12-00408.1.

Cresson, P, Ruitton, S, Harmelin-Vivien, M. 2014. Artificial reefs do increase secondary biomass production: Mechanisms evidenced by stable isotopes. *Marine Ecology Progress Series* **509**: 15–26. DOI: http://dx.doi.org/10.3354/meps10866.

Dafforn, KA, Glasby, TM, Johnston, EL. 2012. Comparing the invasibility of experimental "reefs" with field observations of natural reefs and artificial structures. *PLoS One* **7**(5): e38124. DOI: http://dx.doi.org/10.1371/journal.pone.0038124.

Dancose, K, Fortin, D, Xulin, GUO. 2011. Mechanisms of functional connectivity: The case of free-ranging bison in a forest landscape. *Ecological Applications* **21**(5): 1871–1885. DOI: http://dx.doi.org/10.1890/10-0779.1.

Dethier, MN, McDonald, K, Strathmann, RR. 2003. Colonization and connectivity of habitat patches for coastal marine species distant from source populations. *Conservation Biology* **17**(4): 1024–1035. DOI: http://dx.doi.org/10.1046/j.1523-1739.2003.01606.x.

Didham, RK. 2010. Ecological consequences of habitat fragmentation, in *Encyclopedia of life sciences*. Chichester, UK: John Wiley. DOI: http://dx.doi.org/10.1002/9780470015902.a0021904.

Dijkstra, JA, Litterer, A, Mello, K, O'Brien, BS, Rzhanov, Y. 2019. Temperature, phenology, and turf macroalgae drive seascape change: Connections to mid-trophic level species. *Ecosphere* **10**(11). DOI: http://dx.doi.org/10.1002/ecs2.2923.

Dumont, CP, Himmelman, JH, Russell, MP. 2006. Daily movement of the sea urchin *Strongylocentrotus droebachiensis* in different subtidal habitats in eastern Canada. *Marine Ecology Progress Series* **317**: 87–99. DOI: http://dx.doi.org/10.3354/meps317087.

Dyson, K, Yocom, K. 2015. Ecological design for urban waterfronts. *Urban Ecosystems* **18**(1): 189–208. DOI: http://dx.doi.org/10.1007/s11252-014-0385-9.

Fabi, G, Spagnolo, A, Bellan-Santini, D, Charbonnel, E, Çiçek, BA, García, JJG, Jensen, AC, Kallianiotis, A, Santos, MN dos. 2011. Overview on artificial reefs in Europe. *Brazilian Journal of Oceanography* **59**(spe1): 155–166. DOI: http://dx.doi.org/10.1590/s1679-87592011000300017.

Farina, S, Guala, I, Oliva, S, Piazzi, L, Pires da Silva, R, Ceccherelli, G. 2016. The seagrass effect turned upside down changes the prospective of sea urchin survival and landscape implications. *PLoS One* **11**(10): e0164294. DOI: http://dx.doi.org/10.1371/journal.pone.0164294.

Feary, DA, Burt, JA, Bartholomew, A. 2011. Artificial marine habitats in the Arabian Gulf: Review of current use, benefits and management implications. *Ocean and Coastal Management* **54**(10): 742–749. DOI: http://dx.doi.org/10.1016/j.ocecoaman.2011.07.008.

Ferrario, F, Iveša, L, Jaklin, A, Perkol-Finkel, S, Airoldi, L. 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. *Journal of Applied Ecology* **53**(1): 16–24. DOI: http://dx.doi.org/10.1111/1365-2664.12533.

Filbee-Dexter, K, Wernberg, T. 2018. Rise of turfs: A new battlefront for globally declining kelp forests. *BioScience* **68**(2): 64–76. DOI: http://dx.doi.org/10.1093/biosci/bix147.

Fisheries Act. 2019. Government of Canada. Available at https://laws-lois.justice.gc.ca/eng/acts/f-14/.

Fortin, D, Beyer, HL, Boyce, MS, Smith, DW, Duchesne, T, Mao, JS. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**(5): 1320–1330. DOI: http://dx.doi.org/10.1890/04-0953.

Frey, DL, Gagnon, P. 2016. Spatial dynamics of the green sea urchin *Strongylocentrotus droebachiensis* in food-depleted habitats. *Marine Ecology Progress Series* **552**: 223–240. DOI: http://dx.doi.org/10.3354/meps11787.

Gagnon, P, Himmelman, JH, Johnson, LE. 2004. Temporal variation in community interfaces: Kelp-bed boundary dynamics adjacent to persistent urchin barrens. *Marine Biology* **144**(6): 1191–1203. DOI: http://dx.doi.org/10.1007/s00227-003-1270-x.

Galbraith, PS, Chassé, J, Caverhill, C, Nicot, P, Gilbert, D, Lefaivre, D, Lafleur, C. 2019. Physical oceanographic conditions in the Gulf of St. Lawrence during 2018. *DFO Canadian Science Advisory Secretariat* **49**: 82.

Gaylord, B, Reed, DC, Washburn, L, Raimondi, PT. 2004. Physical-biological coupling in spore dispersal of kelp forest macroalgae. *Journal of Marine Systems* **49**(1–4): 19–39. DOI: http://dx.doi.org/10.1016/j.jmarsys.2003.05.003.

Gil, MA, Zill, J, Ponciano, JM. 2017. Context-dependent landscape of fear: Algal density elicits risky herbivory in a coral reef. *Ecology* **98**(2): 534–544. DOI: http://dx.doi.org/10.1002/ecy.1668.

Heery, EC, Bishop, MJ, Critchley, LP, Bugnot, AB, Airoldi, L, Mayer-Pinto, M, Sheehan, EV, Colem, RA, Lok, LHL, Johnsto, EL, Komyakova, V, Morris, R, Strain, EMA, Naylor, LA, Dafforn, KA. 2017. Identifying the consequences of ocean sprawl for sedimentary habitats. *Journal of Experimental Marine Biology and Ecology* **492**: 31–48. DOI: http://dx.doi.org/10.1016/j.jembe.2017.01.020.

Himmelman, JH. 1991. Diving observation of subtidal communities in the northern Gulf of Saint Lawrence. *Canadian Special Publication of Fisheries and Aquatic Sciences* **113**(113): 319–332.

Himmelman, JH, Steele, DH. 1971. Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. *Marine Biology* **9**(4): 315–322. DOI: http://dx.doi.org/10.1007/BF00372825.

Johnson, LE, MacGregor, KA, Narvaez, CA, Suskiewicz, TS. 2019. Subtidal rocky shores of the north-west Atlantic Ocean, in Hawkins, SJ, Bohn, K, Firth, LB, Williams, GA eds., *Interactions in the Marine Benthos: Global patterns and processes.* Cambridge University Press: 90–127. DOI: http://dx.doi.org/10.1017/9781108235792.006.

Kleinbaum, DG, Klein, M. 2005. *Survival analysis—A self-learning text.* New York, NY: Springer.

Konar, B, Estes, JA. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* **84**(1): 174–185. DOI: http://dx.doi.org/http://www.jstor.org/stable/3108007.

Krause-Jensen, D, Marbà, N, Olesen, B, Sejr, MK, Christensen, PB, Rodrigues, J, Renaud, PE, Balsby, TJS, Rysgaard, S. 2012. Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Global Change Biology* **18**(10): 2981–2994. DOI: http://dx.doi.org/10.1111/j.1365-2486.2012.02765.x.

Kriegisch, N, Reeves, SE, Flukes, EB, Johnson, CR, Ling, SD. 2019. Drift-kelp suppresses foraging movement of overgrazing sea urchins. *Oecologia* **190**(3): 665–677. DOI: http://dx.doi.org/10.1007/s00442-019-04445-6.

Kriegisch, N, Reeves, SE, Johnson, CR, Ling, SD. 2019. Top-down sea urchin overgrazing overwhelms bottom-up stimulation of kelp beds despite sediment enhancement. *Journal of Experimental Marine Biology and Ecology* **514−515**: 48–58. DOI: http://dx.doi.org/10.1016/j.jembe.2019.03.012.

Krumhansl, KA, Okamoto, DK, Rassweiler, A, Novak, M, Bolton, JJ, Cavanaugh, KC, Connell, SD, Johnson, CR, Konar, B, Ling, SD, Micheli, F. 2016. Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences* **113**(48): 13785–13790. DOI: http://dx.doi.org/10.1073/pnas.1606102113.

Krumhansl, KA, Scheibling, RE. 2012. Production and fate of kelp detritus. *Marine Ecology Progress Series* **467**: 281–302. DOI: http://dx.doi.org/10.3354/meps09940.

Lauzon-Guay, JS, Scheibling, RE, Barbeau, MA. 2006. Movement patterns in the green sea urchin *Strongylocentrotus droebachiensis. Journal of the Marine Biological Association of the United Kingdom* **86**(1): 167−174. DOI: http://dx.doi.org/10.1017/S0025315406012999.

Lima, JS, Zalmon, IR, Love, M. 2019. Overview and trends of ecological and socioeconomic research on artificial reefs. *Marine Environmental Research* **145**: 81–96. DOI: http://dx.doi.org/10.1016/j.marenvres.2019.01.010.

Ling, SD, Scheibling, RE, Rassweiler, A, Johnson, CR, Shears, N, Connell, SD, Salomon, AK, Norderhaug, KM, Pérez-Matus, A, Hernández, JC, Clemente, S. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**(1659): 1–10. DOI: http://dx.doi.org/10.1098/rstb.2013.0269.

MacGregor, KA. 2020. Individual and population level response to the environment: Environmental modification of movement behaviour in the green sea urchin, Strongylocentrotus droebachiensis. Québec, Canada: Université Laval.

Madin, EMP, Madin, JS, Booth, DJ. 2011. Landscape of fear visible from space. *Scientific Reports* **1**: 4. DOI: http://dx.doi.org/1410.1038/srep00014.

Mann, KH. 1973. Seaweeds: Their productivity and strategy for growth. *Science* **182**(4116): 975–981. DOI: http://dx.doi.org/10.1126/science.182.4116.975.

Mason, THE, Fortin, D. 2017. Functional responses in animal movement explain spatial heterogeneity in animal-habitat relationships. *Journal of Animal Ecology* **86**(4): 960–971. DOI: http://dx.doi.org/10.1111/1365-2656.12682.

Mayer-Pinto, M, Johnston, EL, Bugnot, AB, Glasby, TM, Airoldi, L, Mitchell, A, Dafforn, KA. 2017. Building "blue": An eco-engineering framework for foreshore developments. *Journal of Environmental Management* **189**: 109–114. DOI: http://dx.doi.org/10.1016/j.jenvman.2016.12.039.

Mazerolle, MJ. 2006. Improving data analysis in herpetology: Using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia* **27**(2): 169–180. DOI: http://dx.doi.org/10.1163/156853806777239922.

Micheli, F, Peterson, CH. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology* **13**(4): 869–881. DOI: http://dx.doi.org/10.1046/j.1523-1739.1999.98233.x.

Parnell, PE. 2015. The effects of seascape pattern on algal patch structure, sea urchin barrens, and ecological processes. *Journal of Experimental Marine Biology and Ecology* **465**: 64–76. DOI: http://dx.doi.org/10.1016/j.jembe.2015.01.010.

Perkol-Finkel, S, Airoldi, L. 2010. Loss and recovery potential of marine habitats: An experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. *PLoS One* **5**(5): e10791. DOI: http://dx.doi.org/10.1371%2Fjournal.pone.0010791.

Perkol-Finkel, S, Ferrario, F, Nicotera, V, Airoldi, L. 2012. Conservation challenges in urban seascapes: Promoting the growth of threatened species on coastal infrastructures. *Journal of Applied Ecology* **49**(6): 1457–1466. DOI: http://dx.doi.org/10.1111/j.1365-2664.2012.02204.x.

Perkol-Finkel, S, Hadary, T, Rella, A, Shirazi, R, Sella, I. 2018. Seascape architecture—Incorporating ecological considerations in design of coastal and marine infrastructure. *Ecological Engineering* **120**: 645–654. DOI: http://dx.doi.org/10.1016/j.ecoleng.2017.06.051.

Powell, JA, Garlick, MJ, Bentz, BJ, Friedenberg, N. 2018. Differential dispersal and the Allee effect create power-law behaviour: Distribution of spot infestations during mountain pine beetle outbreaks. *Journal of Animal Ecology* **87**(1): 73–86. DOI: http://dx.doi.org/10.1111/1365-2656.12700.

R Core Team. 2016. R: *A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. Available at http://www.r-project.org.

Reed, DC, Schroeter, SC, Huang, D, Anderson, TW, Ambrose, RF. 2006. Quantitative assessment of different artificial reef designs in mitigating losses to kelp forest fishes. *Bulletin of Marine Science* **78**(1): 133–150.

Rinde, E, Christie, H, Fagerli, CW, Bekkby, T, Gundersen, H, Norderhaug, KM, Hjermann, D. 2014. The influence of physical factors on kelp and sea urchin distribution in previously and still grazed areas in the NE Atlantic. *PLoS One* **9**(6): e100222. DOI: http://dx.doi.org/10.1371/journal.pone.0100222.

Sanderson, JC, Ling, SD, Dominguez, JG, Johnson, CR. 2016. Limited effectiveness of divers to mitigate "barrens" formation by culling sea urchins while fishing for abalone. *Marine and Freshwater Research* **67**(1): 84–95. DOI: http://dx.doi.org/10.1071/MF14255.

Scheibling, RE, Hamm, J. 1991. Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. *Marine Biology* **110**(1): 105–116. DOI: http://dx.doi.org/10.1007/BF01313097.

Scheibling, RE, Hennigar, AW, Balch, T. 2011. Destructive grazing, epiphytism, and disease: The dynamics of sea urchin–kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **56**(12): 2300–2314. DOI: http://dx.doi.org/10.1139/f99-163.

Siikavuopio, SI, Christiansen, JS, Sæther, BS, Dale, T. 2007. Seasonal variation in feed intake under constant temperature and natural photoperiod in the green sea urchin (*Strongylocentrotus droebachiensis*). *Aquaculture* **272**(1–4): 328–334. DOI: http://dx.doi.org/10.1016/j.aquaculture.2007.09.003.

Steneck, RS, Graham, MH, Bourque, BJ, Corbett, D, Erlandson, JM, Estes, JA, Tegner, MJ. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation* **29**(4): 436–459. DOI: http://dx.doi.org/10.1017/S0376892902000322.

Steneck, RS, Leland, A, McNaught, DC, Vavrinec, J. 2013. Ecosystem flips, locks, and feedbacks: The lasting effects of fisheries on Maine's kelp forest ecosystem. *Bulletin of Marine Science* **89**(1): 31–55. DOI: http://dx.doi.org/10.5343/bms.2011.1148.

Suskiewicz, TS, Johnson, LE. 2017. Consumption rates of a key marine herbivore: A review of the extrinsic and intrinsic control of feeding in the green sea urchin. *Marine Biology* **164**(6): 131. DOI: http://dx.doi.org/10.1007/s00227-017-3159-0.

Tamigneaux, É, Johnson, LE. 2016. Les macroalgues du Saint-Laurent: Une composante essentielle d'un écosystème marin unique et une ressource naturelle précieuse dans un contexte de changement global. *Le Naturaliste Canadien* **140**(2): 62. DOI: http://dx.doi.org/10.7202/1036505ar.

Terawaki, T, Hasegawa, H, Arai, S, Ohno, M. 2001. Management-free techniques for restoration of *Eisenia* and *Ecklonia* beds along the central Pacific coast of Japan. *Journal of Applied Phycology* **13**(1): 13–17. DOI: http://dx.doi.org/10.1023/A:1008135515037.

Terawaki, T, Yoshikawa, K, Yoshida, G, Uchimura, M, Iseki, K. 2003. Ecology and restoration techniques for *Sargassum* beds in the Seto Inland Sea, Japan. *Marine Pollution Bulletin* **47**(1–6): 198–201. DOI: http://dx.doi.org/10.1016/S0025-326X(03)00054-7.

Tessier, A, Francour, P, Charbonnel, E, Dalias, N, Bodilis, P, Seaman, W, Lenfant, P. 2015. Assessment of French artificial reefs: Due to limitations of research, trends may be misleading. *Hydrobiologia* **753**(1): 1–29. DOI: http://dx.doi.org/10.1007/s10750-015-2213-5.

Wentworth, CK. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* **30**(5): 377–392.

Zuur, AF, Ieno, EN, Walker, NJ, Saveliev, AA, Smith, GM. 2009. Mixed effects models and extensions in ecology with R, in Gail, M, Krickeberg, K, Samet, JM, Tsiatis, A, Wong, W eds., *Statistics for biology and health.* Springer New York. DOI: http://dx.doi.org/10.1007/978-0-387-87458-6_1.

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