A Benthic Habitat Template for Pacific Canada's Continental Shelf

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2016

Canadian Technical Report of Hydrography and Ocean Sciences 312

Canadian Technical Report of Hydrography and Ocean Sciences

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A BENTHIC HABITAT TEMPLATE FOR PACIFIC CANADA'S CONTINENTAL SHELF

by

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Cat. No. Fs97-18/312E	ISBN 978-0-660-05719-4	ISSN 0711-6764 (paper)
Cat. No. Fs97-18/312E-PDF	ISBN 978-0-660-05720-0	ISSN 1488-5417 (pdf)

Correct Citation for this publication:

Gregr, E.J., Gryba, R., Li, M.Z., Alidina, H., Kostylev, V., and Hannah, C.G. 2016. A benthic habitat template for Pacific Canada's continental shelf. Can. Tech. Rep. Hydrogr. Ocean Sci. 312: vii + 37 p.

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ABSTRACT

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Classifications of the marine environment are essential to inform marine spatial planning strategies such as protected area designation, and can support assessments of the cumulative impacts of human activities and the development of species-habitat associations. The benthic habitat template developed here for the shelf waters (30 - 500 m) of Canada's Pacific coast is one such classification. The template differs from more common correlation-based approaches in that it uses hypotheses grounded in functional ecology to integrate physical data into a functional description of the benthic environment. We adapted methods originally used on Canada's Atlantic coast to the available data and unique characteristics of Canada's Pacific coast. We found the habitat template correlated better with benthic diversity than linear geographic distance, corroborating earlier findings from Atlantic Canada. The habitat template, particularly the Disturbance axis, was negatively correlated with the Shannon-Weiner biodiversity index, showing that high disturbance habitats are less diverse. These results demonstrate that the template, by considering the influence of physical drivers on functional adaptation in the classification process, represents an ecologically relevant classification of the marine environment. As such, it has the potential to contribute to Canada's Marine Protected Area strategy by identifying areas of rarity, high diversity, and representativity, important determinants of Ecologically or Biologically Significant Areas (EBSAs). Also, the ability to correlate species diversity with distance provides a way to quantitatively identify ecologically significant regional boundaries, something that is critical to understanding the ecology on the coast, and a potentially important refinement to questions of representativity. We expect both the habitat template and the associated sediment grain size model to serve key roles for marine spatial planning on Canada's Pacific Coast.

RÉSUMÉ

Gregr, E.J., Gryba, R., Li, M.Z., Alidina, H., Kostylev, V., et Hannah, C.G. 2016. A benthic habitat template for Pacific Canada's continental shelf. Rapp. tech. can. hydrogr. sci. océan. 312 : vii + 37 p.

Les classifications du milieu marin sont essentielles pour éclairer les stratégies de planification spatiale marine telles que la désignation des aires protégées, et peuvent appuyer les évaluations des effets cumulatifs des activités humaines et l'établissement des associations espèces-habitat. Le modèle d'habitat benthique élaboré ici pour les eaux du plateau (30-500 m) de la côte canadienne du Pacifique est un exemple de classification. Le modèle diffère des approches plus fréquentes basées sur la corrélation dans la mesure où il utilise des hypothèses fondées sur l'écologie fonctionnelle pour intégrer des données physiques à une description fonctionnelle de l'environnement benthique. Nous avons adapté les méthodes utilisées au départ sur la côte Atlantique du Canada aux données disponibles et aux caractéristiques uniques de la côte du Pacifique du Canada. Nous avons constaté que le modèle d'habitat montrait une meilleure corrélation avec la diversité benthique que la distance géographique linéaire, corroborant les conclusions antérieures concernant le Canada atlantique. Le modèle d'habitat, en particulier l'axe de perturbation, présentait une corrélation négative avec l'indice de biodiversité de Shannon-Weiner, indiquant que les habitats à fortes perturbations sont moins diversifiés. Ces résultats démontrent que le modèle, en tenant compte de l'influence des facteurs physiques sur l'adaptation fonctionnelle dans le processus de classification, représente une classification du milieu marin pertinente sur le plan écologique. Par conséquent, le modèle pourrait contribuer à la Stratégie fédérale sur les aires marines protégées du Canada en désignant les zones de rareté, les zones de grande diversité, et la représentativité, qui sont d'importants déterminants des zones d'importance écologique ou biologique (ZIEB). De plus, la capacité à établir une corrélation, entre la diversité des espèces et la distance, est un moyen de définir quantitativement les limites régionales d'importance écologique, ce qui est essentiel à la compréhension de l'écologie sur la côte, et représente une amélioration potentiellement importante des questions de représentativité. Nous nous attendons à ce que le modèle d'habitat et le modèle de granulométrie des sédiments jouent un rôle essentiel dans la planification spatiale marine sur la côte canadienne du Pacifique.

INTRODUCTION

Sustainable management of the marine environment depends in part on a comprehensive characterisation of space suitable for defining benthic biological units. Classifications based on physical or biological characteristics are commonly used to support identification of Marine Protected Areas (Roff et al. 2003), analyses of cumulative impacts of human activity, and the development of species-habitat associations. Ideally, any such classification would capture both ecologically and biologically important areas, providing a basis for protecting biodiversity and maintaining the sustainability of marine systems.

Navigating the many ways physiographic and zoological data can be combined into classified maps, and the interpretation of these maps to extract ecological information relevant to management, is a complex and challenging task. These challenges have lead to classification methods that generally fall into two somewhat disciplinary categories: physiographic and zoogeographic.

Physiographic approaches rely on clustering methods that group areas with similar physical characteristics, while zoogeographic methods rely on knowledge of species distributions (Gregr et al. 2012). Physiographic approaches can be further divided into quantitative and qualitative approaches using different types of analysis. For example, statistical clustering (e.g., Devred et al. 2007, Gregr and Bodtker 2007) is a common quantitative approach, while qualitative analysis typically uses spatial intersections to classified environmental variables (e.g., Roff et al. 2003).

However, because physiographic classifications by definition lack biota, best practices require a demonstration of the ecological or biological significance of the classes - something that is not often done (Gregr et al. 2012). Where such validation has been applied to classifications of strictly physical data (e.g., from acoustic survey multibeam reflectance data), species assemblages are generally poorly correlated (McGonigle et al. 2009).

This challenge of successfully associating species' distributions with physiographic classes enhances the appeal of zoogeographical methods, which in contrast are explicitly biological. However, biological classifications tend to be done either at spatial extents that match local data availability, making them difficult to generalize, or at global scales, where poorly resolved data limit the classifications to what are effectively potential range maps (e.g., Kaschner et al. 2006, Spalding et al. 2007).

An alternative, more integrative approach is to define a mechanistic classification using hypotheses to relate physical processes to observed or proposed biological distributions. Such an approach, based on the theory of niche adaptation (Southwood (1977, 1988), has been developed for benthic habitat mapping (Kostylev et al 2005; Kostylev and Hannah 2007). The underlying theory predicts that species evolve functional adaptations to different combinations of disturbance and adversity (Disturbance is defined as the likelihood of natural habitat alteration and Adversity relates to the natural factors limiting growth and reproduction). This ecological, process-based approach to characterising habitat differs from traditional physiographic or zoogeographic methods where classification is based on correlation, and ecological function is then hypothesised based on the observed correlations.

The idea of functional niche, which assumes that species' traits reflect evolutionary adaptations to their environment, underlies considerable research in community ecology. Current work focuses largely on species traits (Díaz et al. 2016) and how the functional adaptation of these traits relates to abiotic constraints and ecological interactions (McGill et al. 2006). While there are some examples of functional ecology applied to aquatic systems (Neumann et al. 2016, Winemiller and Rose 1992), much of the theoretical and empirical work has been on plants. This terrestrial focus has led to many studies of how species' influence their environment (Funk et al. 2016), but the influence of environment on species' traits appears to have received less empirical treatment in community ecology.

Southwood (1988) considered how environment may shape functional traits, and provided a habitat template hypothesising the guiding role of habitat in functional ecology. He proposed that the duration of substrate stability (Disturbance) and the severity of environmental conditions (here termed Adversity) are strong, independent, drivers of species' life history traits, describing how adaptations of traits related to defence, migration, fecundity, longevity, and resilience could be influenced by these two environmental gradients (Table 1). The template is intended to characterise areas with similar driving forces that lead to particular life history characteristics or survival strategies without imposing uniformity on the traits or adaptations that underlie those strategies. The importance of Disturbance and Adversity (variously termed Scope for Growth, Nutrients, Growth Rate, and Resource Constraints) as drivers of species' traits is generally recognised (Greenslade 1983, Huston 1979, Huston 1994, Roff et al. 2003, Winemiller and Rose 1992).

A corollary of this theory is that communities should be comprised of organisms functionally adapted to different ecological conditions. The template should therefore provide a basis to classify expressions of biodiversity, a critical aspect of MPA design, as well as aspects of uniqueness or rarity, a second important consideration for marine planning generally (Gregr et al. 2012) and Ecologically or Biologically Significant Areas (EBSAs) specifically (Dunn et al. 2014, Fisheries and Oceans Canada 2013).

The marine habitat template was developed on Canada's Atlantic coast (Kostylev and Hannah 2007, Kostylev et al. 2005), and has been applied in the eastern English Channel (Foveau and Vaz 2010), the Bay of Biscay, northern Spain (Galparsoro et al. 2013) and in reduced form to all of Canada's oceans (Kostylev et al. 2015) as a tool to support ocean planning and management (Fisheries and Oceans Canada 2005). On the Scotian Shelf, the habitat template served as a better predictor of species similarity than geographic distance (Kostylev and Hannah 2007), and explained the spatial distribution of fish species diversity (Fisher et al. 2011). Kostylev et al. (2005) also demonstrated the relevance of the habitat template at a more local scale, showing that megabenthos assemblages followed gradients in Disturbance and Scope for Growth in the Gulf of Maine.

The work described here adapts the functional hypotheses proposed by Kostylev to the Pacific Canadian shelf. Adaptation was necessary because no outputs from either a sediment transport model or an ocean circulation model were available for the Pacific region. A high resolution circulation model (Masson and Fine 2012) is under continued development, but outputs were not available at the time of this study. The absence of circulation model output (and thus the associated ocean chemistry parameters such as nutrients, dissolved O_2) required the Disturbance and Adversity hypotheses to be simplified to accommodate these data gaps. The absence of a sediment transport (or bottom type) model was the second major limitation. We addressed this gap by developing a sediment grain size model (described herein), allowing the habitat template to be defined for the entire Pacific Canadian Shelf.

METHODS

Available, relevant data were collected, and processed to reflect their hypothesised role in structuring the benthic marine ecosystem. We used equations (described below) revised from Kostylev and Hannah (2007) to combine available oceanographic data into representations of benthic marine Disturbance and Adversity. While Kostylev and Hannah (2007) used the inverse term Scope for Growth, we retain Adversity as it reduced jargon and also scales in the same direction as Disturbance.

We first introduce and describe the constituent data layers (Table 2) and the development of a sediment grain size model (an essential aspect of Disturbance), before describing how the Disturbance and Adversity equations were adapted for the Pacific Canadian shelf.

DATA LAYERS

Bathymetry

We used a bathymetric raster with a spatial resolution of 100 m x 100 m developed by Gregr (2012) to address gaps both along the shore and around the western edges of the EEZ evident in earlier bathymetries of the region. This raster was foundational to the classification as it was used to calculate two continuous measures of rugosity based on the Benthic Positioning Index (BPI - Wright et al. 2012) to support the sediment modelling component. We calculated a fine-scale BPI using a five cell (500 m) radius to capture higher resolution features on the shelf such as individual reefs and the variability around the edges of prominent features. We defined a broad-scale BPI using a 50 cell (5,000 m) buffer to capture larger features such as seamounts, troughs, and reef complexes in their entirety. We preferred the continuous BPI value as a measure of bottom complexity over its derived categorical representation (i.e., features) for this analysis.

Temperature, salinity and density

We obtained long-term averaged summer and winter bottom temperature and salinity measurements from (Foreman et al. 2008). We also derived a summer stratification index (S_d) to use as a proxy for mixed layer depth by subtracting the summer density at 30 m from that at the surface.

Hydrodynamic energy

We derived an energy surface by combining tides, ocean currents, and wind waves. These different types of water motion contribute energy differentially throughout the study area, making the inclusion of all three important.

We combined modelled maximum spring bottom tidal speed (Foreman et al. 2008) with long-term average, winter and summer bottom ocean currents extracted from the Hybrid Coordinate Ocean Model (HYCOM; http://hycom.org/). We interpolated a 5 x 5 km^2 maximum bottom ocean current raster for the study area from the native HYCOM 1/12° resolution using the ArcGIS Natural Neighbour function. The method interpolates within a convex polygon, thereby avoiding extrapolation of the ocean currents to sheltered areas (e.g., the Strait of Georgia). To avoid having NoData values bias the Disturbance calculation in these sheltered waters, we created a zero raster with the extents of the base bathymetric layer and the native resolution of the HYCOM data. We then mosaiced this with each of the winter and summer HYCOM grids before interpolation to replace the NoData values in sheltered waters with zeros - a reasonable assumption. The source data (available on request from the lead author) include additional details in the metadata.

We included wind waves from a hindcast (2002-2005) model created by NCEP (National Centers for Environmental Prediction, National Oceanic and Atmospheric Administration) downloaded and compiled by the Geological Survey of Canada (M. Li, unpublished data). We used the maximum significant wave heights and the associated peak wave periods to represent maximum potential disturbance.

Nutrient input

We derived chlorophyll-a (Chla) concentration values (mg/m^3) for the Pacific Canadian shelf from the algal_1 band of the Medium Resolution Imaging Spectrometer (MERIS), from the European Space Agency ENVIronmental SATellite (ENVISAT) platform. We downloaded daily swath Chla data from the ESA MERIS website (ftp://eoa-up.eo.esa.int) for 2007-2011 for a spring bloom period (March 18 to June 21) based on timing observed in the study region (Pan et al. 1988, Peña et al. 1999, Stockner et al. 1979), with a week added on either side to allow for temporal variation. We mosaiced the daily swaths together and calculated monthly means using mission-specific software (BEAM 4.9 - the ESA Envisat Project, Brockmann Consultants, 2011). We exported the result as netcdf files and imported them into ArcGIS 9.3 where we clipped the gridded point data to 3° beyond the Pacific Canadian EEZ. We removed the cloud cover remaining from the monthly means by interpolating across the gaps using the Natural Neighbour algorithm (ArcGIS 9.3) to a resolution of 0.015 degrees (the native ENVISAT resolution). We then scaled the data to convert from numerical to true geophysical values (see the ENVISAT metatdata).

We calculated monthly bloom frequency by selecting regions where [Chla] ≥ 2.0 mg/m^3. This is the average of two thresholds reported for the study area (> 1 mg/m^3, Gower 2004, and > 3 mg/m^3, Mackas et al. 2007). For each month, every grid cell was classified as either blooming or not. We then added the 20 monthly layers together to get a final layer of bloom frequency. Values of 20 represent regions where monthly Chla concentrations exceeded the bloom threshold during all months, for all 5 years, with decreasing values representing a linear decrease in bloom frequency. We projected the final raster into BC Albers projection, and re-sampled the layer to our study area resolution (100 x 100 m^2).

SEDIMENT MODELLING

We created a comprehensive map of benthic sediment grain size for the Pacific Canadian Shelf using a statistical model to correlate grain size data from the Natural Resources Canada (NRCan) Expedition database (Natural Resources Canada 2016) with a suite of independent physical data.

Variable selection

We used the surficial grain size data from the grabs and vertical cores available in the Expedition database as the dependent data in this analysis (n=5,185; Table 2). While we considered other potential sources of bottom type data (e.g., Fisheries and Oceans grab samples; the ShoreZone coastline data), the integration of these categorical data in the analysis would have necessitated a loss of detail in the NRCan data (which record grain size).

The independent variables, most described above, also included slope, and maximum bottom current (obtained by summing the tidal and ocean current velocities – Table 2). We also explored the utility of a categorical variable to divide the coast into regions of potentially different geomorphic origin, as recent surveys suggest that the West coast of Vancouver Island was not glaciated during the Quaternary period, and thus has limited glacially deposited soft sediments (K. Conway, Geological Survey of Canada, NRCan, personal communication). Additionally, Queen Charlotte Sound and the West coast of Vancouver Island are more exposed to ocean currents than other areas of the shelf, justifying the delineation of four regions with different sediment characterisations: Strait of Georgia, Queen Charlotte Sound, West Coast Vancouver Island, and North Coast.

Model development

We limited the analysis to shelf waters (< 1,000 m depth) for three reasons. First, this is where the majority of the sediment sampling occurred. Second, the dynamics of bottom type are expected to be very different beyond the shelf break and at abyssal depths thereby reducing the accuracy on the shelf. Third, it is where management challenges are most significant. We also recognised the nearshore (i.e., waters shallower than shoaling depth) as a unique region of the shelf, with different dynamics, that would require a separate analysis with additional data, especially given the under-sampling closer to shore. We therefore defined the 30 m depth contour as the landward limit of this analysis. A mask with the extents of the sediment model (30 - 1,000 m) is included in the geodatabase (Table 2).

We hypothesised that grain size is related to a small set of reasonably well described physical characteristics (independent variables). We used ArcGIS 9.3 to prepare the raw grain size data, and R version 2.11.1 for the statistical analysis. We used the MGET package (Marine Geospatial Ecology Tools version 0.8z40, Roberts et al. 2010) to generate the predicted spatial grain size raster in ArcGIS.

We chose generalised additive models (GAMs; R package 'gam') as the statistical framework for this analysis because the non-parametric smoothing used by GAMs had the best potential to fit the highly skewed data. We identified the best model structure using forward/backward stepwise variable selection applied to the complete set of dependent data, with AIC as the stopping criteria. The scope for the independent variables included both linear and smoothed terms. We used the default settings for GAM smoothing (df = 4) and error distribution (Gaussian). The four sediment regions were included as a categorical variable.

We evaluated model performance using a cross-validation analysis. We divided the Expedition data into training (70%) and testing (30%) subsets. We then fit the GAMs to the training data, predicted the testing data, and calculated the correlation between the predicted and observed (testing) values. We repeated this 10,000 times to create a distribution of correlation values.

DISTURBANCE-ADVERSITY MODELLING

The habitat template was created for the Canadian Pacific shelf from 30 - 500 m depth. The landward limit was constrained by the sediment model (above), while deeper waters were excluded because they contain the top of the continental slope, a region with significant differences in oceanography (e.g., steepness, the dominance of ocean currents and upwellings). These differences would introduce a significant bias into the analysis, leading to a very different characterisation of the shelf benthic ecosystem.

Disturbance

Disturbance (***D***) is the potential for physical disturbance of the benthos due to the mobilisation of sediment by water flow. It was defined by Kostylev and Hannah (2007) as the ratio of bottom shear velocity ($\boldsymbol{u_*}$) and the critical shear velocity ($\boldsymbol{u_{*cr}}$ - the shear velocity required to mobilise bottom sediments). The ratio is logged (base 10) to improve normality:

$$D = \log\left(\frac{u_*}{u_{*cr}}\right) \qquad \text{Equation 1}$$

$\boldsymbol{u_*}$ is calculated as the sum of tidal (τ_t), ocean current (τ_o), and wave (τ_w) shear stresses. Tidal and ocean current shear stresses were calculated according to Li and Amos (1995):

$$\tau = 0.5\,\rho\,f_c\,V^2 = 0.003075\,V^2 \qquad \text{Equation 2}$$

where ρ = 1.025 is the fluid density (g/cm^3), f_c = 0.006 is the steady current friction factor, and V represents either the bottom tidal or ocean current velocity, in cm/s. Maximum ocean current velocities were extracted from the HYCOM ocean circulation model (Consortium for Data Assimilative Modelling 2012). Maximum tidal currents were based on the root mean square of spring tides, modelled by Foreman et al. (2008).

Calculating wave shear stress (Eq. 9) was more involved, because the wave orbital velocity (u_w, m/s) does not behave like a steady current. We calculated maximum wave-induced bottom current velocities using linear wave theory equations (Denny 1995) described by Collyer (2006):

$$u_w = \left(\frac{\pi h_0}{t}\right)\left(\frac{1}{\sinh(kd)}\right) \qquad \text{Equation 3}$$

where k is the wave number defined by:

$$k = \frac{2\pi}{l_w}$$ Equation 4

With the wave length (l_w) given by

$$l_w = (\frac{gT^2}{2\pi}) * \sqrt{\tanh(\frac{4\pi^2 d}{T^2 g})}$$ Equation 5

The parameters (and units) in Eqns. 3 through 5 and below include: standard gravity (g = 9.81 m/s^2); T = wave period (s); d = water depth (m); and h_0 = shoaled wave height (m).

For T and h_0 we used the maximum significant wave height and the associated peak wave period from the 3-year wave hindcast (M. Li, unpublished data). From wave orbital velocity u_w and wave period T we calculated wave orbital excursion amplitude A_b as:

$$A_b = u_w / (2\pi/T)$$ Equation 6

and then calculated the wave friction factor (f_w) using u_w , A_b, and the bottom roughness height (K_b) according to Li and Amos (1995):

$$K_b = 2.5 * c$$ Equation 7

if $A_b/K_b <= 1.7$: $f_w = 0.28$
else ($A_b/K_b > 1.7$): $f_w = \exp(5.213(K_b/A_b)^{0.194} - 5.977)$ Equation 8

where c is the sediment grain size (m).

Finally, wave shear stress was calculated as:

$$\tau_w = 0.5\, \rho f_w u_w^2$$ Equation 9

Assuming coincident direction of currents and waves, the cumulative bottom shear stress is:

$$\tau = \tau_t + \tau_o + \tau_w$$ Equation 10

The total seabed shear velocity $\boldsymbol{u_*}$ was then obtained from the quadratic stress law:

$$\tau = \rho\, u_*^2$$ Equation 11

Areas with breaking waves were excluded from the study because this higher-energy region cannot be modelled using the above equations. We therefore excluded areas shallower than the shoaling depth (d_s), calculated assuming a 10 second wave period (Collyer 2006):

$$d_s <= \frac{l_w}{25}$$ Equation 12

Critical shear velocity (u_{*cr}) was based on the widely used Yalin method (Miller et al. 1997) as described by Li and Amos (1995). It is calculated from critical shear stress (τ_{cr}) and ρ:

$$u_{*cr} = \sqrt{\frac{\tau_{cr}}{\rho}}$$ Equation 13

Critical shear stress τ_{cr} was calculated from Shield's parameter (θ_t), grain density (ρ_s - g/cm^3), ρ, standard gravity (g), and the sediment grain size (c):

$$\tau_{cr} = \theta_t(\rho_s - \rho)\, gc \qquad \text{Equation 14}$$

Shield's parameter is defined piece-wise:

if Y <= 100: $\log(\theta_t) = 0.041(\log(Y))^2 - 0.356(\log(Y) - 0.977$

if Y >100 and Y <=3000: $\log(\theta_t) = 0.132(\log(Y) - 1.804$

else (Y > 3000): $(\theta_t) = 0.045$ Equation 15

where Yalin's parameter (Y) was defined as:

$$Y = \sqrt{\frac{(\rho_z - \rho)gc^3}{\rho v^2}} \qquad \text{Equation 16}$$

requiring an additional fluid viscosity parameter (ν = 0.013 cm^2/s).

Adversity

Adversity (***A***) is defined as the severity of the environment, and represents how difficult it is for organisms to meet their bioenergetic needs for growth and reproduction. Key components include food availability and temperature. In a temperate marine ecosystem, annual temperature extremes and mean temperature during the growth and reproduction phase are likely key contributors to ***A***. We represented food availability ($\boldsymbol{F_a}$) by scaling primary production (as measured by Chla) with depth and stratification to represent vertical mixing and thus estimate the relative transport of surface nutrients to benthic habitats.

Kostylev and Hannah (2007) defined Scope for Growth (1 − ***A***) using a linear combination of normalised indices representing average dissolved oxygen (O), food availability (F_a), annual mean bottom temperature (T_m), seasonal temperature variability (T_e), and inter-annual temperature variability (T_i):

$$G = \log\left(\frac{O + F_a + T_m - T_e - T_i}{5}\right) \qquad \text{Equation 17}$$

There are insufficient data to calculate inter-annual temperature variation in our study area, and the limited O_2 data do not have sufficient spatial distribution to reasonably estimate a comprehensive spatial coverage. We addressed these data gaps by redefining ***A*** for Pacific Canada as directly related to temperature range (as species must adapt to more dynamic conditions), and inversely related to both F_a and mean summer temperatures (Equation 18):

$$A = \frac{T_r - T_a - F_a}{3}) \qquad \text{Equation 18}$$

Where T_r is defined as the annual range in bottom temperature (calculated as the absolute difference between mean summer and winter bottom temperatures), and T_a is the average summer bottom temperature. Numerators in Equation 18 were transformed into indices on the range [0, 1] before calculating ***A*** (we calculated indices by shifting the data to have a minimum of zero and then dividing by the resulting maximum giving a value on the range [0, 1]).

We retained F_a as defined by Kostylev and Hannah (2007):

$$F_a = \log(\frac{Chla}{d}) - S_d \qquad \text{Equation 19}$$

F_a is a combination of spring bloom frequency (*Chla*), a summer stratification index (S_d), and depth (d). The ratio of *Chla* to d represents the decreasing utility of phytoplankton production with increasing depth, while S_d can be considered a measure of how well mixed the photic zone is (i.e., a proxy for mixed layer depth). We converted S_d and $\log(\frac{Chla}{d})$ to indices before calculating the difference and then scaling F_a onto the range [0, 1].

Ecological validation

As a proposed classification of the functional niche of benthic species, it is reasonable to expect the habitat template to correlate with ecological indicators. For example, Kostylev and Hannah (2007) showed that the template was a better predictor benthic community similarity across samples than linear distance. We conducted a similar evaluation here, examining the correlation between the habitat template and measures of community diversity.

From a complimentary analysis by DFO (Rubidge et al. 2016), we obtained the Shannon-Wiener diversity index (SWDI) and the Bray-Curtis dissimilarity index (BCDI) calculated for 4451 bottom trawl research survey stations collected across large parts of the study area between 2003 and 2013. Trawl positions were calculated as midpoint of each trawl, and both indices were calculated from catch-per-unit-effort values, combining both finfish and benthic invertebrates (Rubidge et al. 2016). Retaining those stations that occurred within the habitat template gave a working sample of 4098 stations.

We assessed how well the template predicted community diversity by comparing the SWDI directly to the ***D*** and ***A*** axes of our habitat template, and to an integrated habitat (IH) distance measure (Eq. 20) using Spearman's ranked correlation.

$$\text{IH distance} = \sqrt{(D1 - D2)^2 + (A1 - A2)^2} \qquad \text{Equation 20}$$

Where (D1, A1) and (D2, A2) represent the disturbance and adversity at two compared sites. Further, recognising that the Pacific Canadian shelf contains a number of very different bioregions, we tested for a regional effect by examining six regional samples (Fig. 10) for differences.

Comparing the BCDI to the habitat template was more complicated, as the BCDI is a paired index which measures the distance between two points (Eq. 21):

$$BCDI_{ij} = 1 - \frac{2C_{ij}}{S_i - S_j} \qquad \text{Equation 21}$$

where C_{ij} is the sum of the values for only those species in common between both sites, and S_i and S_j are the total number of specimens counted at the two sites.

Following Kostylev and Hannah (2007), we compared the BCDI with both IH distance and geographic distance (calculated for pairs of geographic coordinates following Equation 20). However, because these statistics are calculated between points, the resulting sample for the entire trawl data set yields over 9 million (4098 x 4098) values, creating computational difficulties. Even when partitioned into the six test regions, the number of pair-wise samples was still potentially quite large since all regions (except the Strait of Georgia) had more than 500 samples (Table 4). We therefore drew a random sample of 200 points from each of the test regions for BCDI analysis (we used all the Strait of Georgia data). In addition to overcoming the computational problem, this use of a balanced design for regional comparisons is preferred.

To account for Kostylev and Hannah's (2007) finding that the correlation with BCDI weakened with distance, we pooled the regional samples into 20 distance bins, using distances from 10 to 200 km, at 10 km intervals and examined how the mean Spearman's rank correlation changes with distance (Fig. 11). We calculated the three indices (BCDI, geographic distance, and IH distance) across all points within the specified distance. While the gave sample sizes that increased with distance, non-parametric correlation coefficients have been described as relatively insensitive to sample size (Goodwin and Leech 2006).

RESULTS AND DISCUSSION

SEDIMENT MODELLING

We evaluated the performance of various sediment models according to how well they reduced the deviance between the sediment data and model predictions. We used reduction in deviance (*Dev = 1 – residual deviance/null deviance) because it is a better estimate of variance explained (i.e., r^2) when errors are non-normal (R Core Team 2015), as they are assumed to be in GAM models. We use *Dev instead of AIC (Akaike Information Criterion) because AIC is intended for model selection, thus ranking the relative complexity of models but not providing an absolute measure of fit. Here we were more concerned with how well the models explained the data. Specifically, regional differences in explanatory power were more important than relative differences due to parameterization, making *Dev a better choice.

The model with the best *Dev across the full study area (i.e., coast-wide) included all independent variables (depth, slope, maximum bottom current, and coarse-scale BPI) except fine-scale BPI (Table 3). However, artefacts due to the Slope predictor (see Limitations, below) were evident in the prediction. When we examined coast-wide models with and without the slope variable, we found its contribution to *Dev to be minimal (Table 3). Since Slope is likely superseded in the model by the fine-scale BPI, we dropped it from the analysis.

The inclusion of Region as an independent variable contributed considerably to reducing *Dev (Table 3) in the coast-wide model. Recognising that this regional effect is likely manifest by different relationships with the oceanographic variables, we wanted to include Region as an interaction term. However the standard R gam package does not support categorical interactions with smoothed variables. We tried including Region as an interaction term in Generalised Linear Models (GLMs), with polynomial terms in place of the non-parametric smoothes used by the GAMs, but the *Dev (0.357) was low compared to the region-specific models. We also tried using the R library that supports interactions (mgcv), but the *Dev was also notably lower (0.251) than that achieved with our initial GAM containing Region as a linear term. We therefore chose to fit GAMs to each sediment region independently, as this provided the most flexibility in terms of fitting the regional effect.

The step-wise variable selection led to unique (though similar) model structures for each region. We refined these models by 1) removing the Slope predictor from the NCoast region because of visible artefacts in the prediction; and 2) using smoothed instead of linear bathymetry in the QCS region because it made it more comparable with the NCoast region while also giving a notable improvement in *Dev. The predictions from these region-specific models were more comparable across regions than a single coast-wide model (Table 3, row 1), which generated apparent artefacts at the extremes of the oceanographic variable ranges, further supporting our decision to analyse the data by sediment region.

We created a coast-wide sediment surface (mean grain size in phi; Fig. 1) from a mosaic of the regional predictions. We first generated regional predictions for the entire study area. We then clipped these predictions to the region boundaries, buffered to 1000 m, before using the ArcGIS mosaicing tool to combine the predictions and blend the boundaries to create the final comprehensive sediment surface. The 1000 m buffer ensured any artefacts at the boundaries were removed. For the QCS Sound region, boundaries were refined by aligning them with areas of lowest prediction discrepancy (i.e., the absolute difference) with adjacent regions. The final sediment region boundaries are included in the project geodatabase (Table 2).

Evaluation

Mean correlations (r) between the training and the testing data used for the sediment model ranged from 0.51 (Strait of Georgia) to 0.67 for the west coast of Vancouver Island (Fig. 2) showing that the models explain a sizeable portion of the variability in the data. Scatter plots showing examples of observed vs. predicted grain size (Fig. 3) suggest that model predictions are biased towards smaller particle sizes. Nevertheless, the predicted values of grain size are likely accurate in a relative sense, and provide an index of representativity in different areas of the shelf. These results suggest that the models are a reasonable starting point for creating a coastal sediment surface. The predicted particle size distribution will likely be improved with additional data and analysis.

In relation to the habitat template, we note that the maximum particle size on the Scotian Shelf (32 mm $=2r^{-(-5)}$, where phi = -5 is the largest particle from Kostylev and Hannah's Figure 4H and $2r^{-phi}$ is the conversion equation from phi to mm) was over 2.5 times the maximum (12.1 mm) on the Pacific shelf. This broader distribution of particle sizes undoubtedly contributed to the greater texture evident in the Scotian shelf habitat template.

The relative merits of predictive sediment grain size modelling vs. regional interpolation (*sensu* Kostylev and Hannah 2007) have not been evaluated. However, our experience suggests that interpolation methods are much more robust in areas with a more regular shape and without complex barriers. While a common approach for creating terrain maps from point data, interpolation can be severely compromised by the abundance of land barriers in coastal marine systems like the northeastern Pacific. Even when guided by estimates of spatial autocorrelation (i.e., kriging), locally variable energy dynamics violate the stationarity assumption essential to effective kriging. The crenulated coastline also complicates interpolation. We therefore chose a predictive modelling approach assuming it would be more robust for Pacific Canada's relatively narrow shelf and complex coastline.

The Habitat Template

The resulting ***D*** surface had a long negative tail (Fig. 4a), for which visual inspection showed that values < 0.25 were restricted to a few mainland fjords. We therefore removed these data to broaden the distribution, making values in other regions more distinct (Fig 4b). The final ***D*** surface (Fig. 5) shows the resulting index on the range [0.25, 1]. Areas of lowest ***D*** are the Strait of Georgia, and in mainland inlets and fjords. Highest ***D*** is along the west coast of Vancouver Island, on the shallower banks in Hecate Strait, and on the north side of Haida Gwaii in Dixon Entrance.

The ***A*** surface, after being clipped to the depth range, had long tails in both the positive and negative directions (Fig. 4c). Visual inspection showed that high values (> 0.85) were associated with the shelf edge, while low values (< 0.2) were again limited to a few mainland fjords. We removed these extreme values to improve the distribution of the data (Fig. 4d). The final ***A*** surface (Fig. 6) shows the resulting index on the range [0.2, 0.85]. The Strait of Georgia had by far the lowest ***A*** on the Pacific Shelf, followed by the west coast of Vancouver Island, nearshore waters along the mainland Coast, and the shallower banks in Hecate Strait (Fig. 6). Highest ***A*** values were associated with the shelf edge around Haida Gwaii, and deeper waters on the shelf and in mainland fjords.

Examining the temperature and stratification components of ***A***, we found summer bottom temperature ranged from 1.5 to 18.7 C, with the coldest locations also being the deepest. The warmest waters were in the sheltered waters of Haida Gwaii, and the southern and Northern Gulf Islands. The calculated temperature range (the difference between summer and winter bottom temperature layers) gave values on the range [0, 11.36], with the highest values again in the sheltered waters of Haida Gwaii but also in many nearshore areas throughout the coast. Areas with low temperature range occurred throughout the coast, notably in the body of the Strait of Georgia, and many mainland inlets. The most highly stratified waters (based on the stratification index, S_d) also occurred in the Strait of Georgia, and in the excluded fjords, while the greatest mixing (lowest stratification) was off the west coast of Vancouver Island and in Dixon Entrance.

We combined the final ***D*** and ***A*** surfaces into a single composite image (Fig. 7) to create the habitat template. Such multispectral displays of data typically provide more information than examining the bands individually (ESRI 2008).

Interpretation

We examined how well the predictions are distributed across the ***D***-***A*** space, and identified in what part of this space various geographic features occurred (Fig. 8). For example, the Strait of Georgia, effectively an inland sea, is characterised as having low ***A***, with ***D*** varying with depth (e.g., Fig. 5). Inlets and fjords are also characterised as low ***D***, but here it is ***A*** that varies in response to depth. In fact, the most adverse areas (shelf edge, Dixon Entrance, and on-shelf canyons) are highly correlated with depth.

A closer look at the role of depth in the habitat template shows its influence on both components of the habitat template (Fig. 9). ***A*** is generally well dispersed across depth despite the explicit correlation between depth and both T_a and T_r, as well as the Chla component of the F_a calculation. Outside the Strait of Georgia, the correlation between ***A*** and depth is likely due to the depth-temperature relationship (Figs. 8, 9).

This depth-temperature correlation is less evident in Kostylev and Hannah's (2007) Scotian Shelf template (compare Kostylev and Hannah's (2007) Fig 4A (depth) with our 4E (T_a) and 4F (T_r)). The offshore waters of the Scotian shelf also appear to be more homogeneous, reducing the range-wide variability of key variables such as Chla and T_r.

The relationship between ***D*** and depth shows high disturbance occurring only in the shallower (i.e., < 100 m) parts of the study area (Fig. 9). This is likely due to the explicit role of depth in the estimation of wind wave energy (Eqs. 3, 5), though the role of depth in predicting bottom particle size could also have an effect.

Ecological evaluation

In our regional analysis of the correlation between diversity indices, ***D***, ***A***, and the IH distance (Eq. 21), we found that SWDI was significantly correlated with ***D*** and IH when considered over the entire shelf (Table 4), but the relationship was weak (R < 0.1). Regionally, correlations were significant (at p=0.05) for all test areas except the WCVI and Barkley Sound, and in some cases quite strong (Table 4). Where the correlation was significant, species diversity was inversely correlated with ***D***, except in the Strait of Georgia, where we found a strong positive correlation. Correlations between species diversity and ***A*** were positive in Hecate Strait and Queen Charlotte Sound, but negative in Dixon Entrance and the Strait of Georgia. On the whole, the correlation between species diversity and ***D*** was somewhat stronger than with ***A***. This suggests that ***D*** can influence the diversity of species, and that at least in some cases, the effect of ***A*** is synergistic, such as in Dixon Entrance, where the correlation between diversity and the IH index was almost 0.40.

Looking at the relationship with BCDI, IH distance was more strongly correlated with BCDI than geographic distance in all six of the test regions (Table 5). This supports the findings of Kostylev and Hannah (2007) that the habitat template is a better predictor of community similarity than geographic distance.

The variability among regions (with correlations ranging from 0.44 to 0.65) suggests that the hypothesised role(s) of the physical processes in the template are regionally variable. That is, their net effect is not the same in each region. This process variability also appears to have a distance component, which can be seen in how well the habitat template (IH) correlates with diversity (BCDI) as a function of separation distance (Fig. 11). A higher correlation indicates better prediction of biodiversity by the template. Four regions (Hecate, WCVI, QCS and Barkley) show an increasingly positive correlation with distance, reaching a steady value around 50 km. One interpretation is that the processes hypothesised in the habitat template are not stationary at distances < 50 km (assuming the BCDI is insensitive to distance). This would suggest these processes are more stable in some regions (e.g., Strait of Georgia) and unstable in others (e.g., Hecate Strait). It could also be an indication of how ecologically homogeneous the different regions are. The spatial resolution of the underlying physical data are also relevant, as the features that can be resolved are a function of the resolution of the source data.

The correlation between the habitat template and the indicators of benthic diversity strongly suggest the template can help identify areas with relatively high or low benthic biodiversity, as well as other aspects of function diversity such as assemblage groups and other expressions of biodiversity such as sensitivity (Kostylev and Hannah 2007), and rare or unique habitats that may qualify as EBSAs. The exploration of correlation over different extents, while preliminary, suggests the habitat template may provide a way to quantitatively identify bioregional boundaries, something that is critical to understanding the coastal ecology of Pacific Canada, and to questions of representativity in MPA design.

LIMITATIONS

In this analysis, artefacts were evident in a number of the source data layers. For example, the slope predictor generated from the bathymetry showed unrealistic string-like features indicative of the chart contours from which it was derived. Such artefacts suggest the interpolation of those data used a neighbourhood that was too small, producing the 'platforms' evident in the result. Slope was therefore dropped as a predictor to prevent these artefacts from entering the predictions. While we expect the BPI to be somewhat less sensitive to this interpolation error, an updated bathymetry would allow slope to be included, and likely improve the predictive power of the other depth derivatives.

The bottom temperature and density values obtained from Foreman et al. (2008) also show a number of artefacts. The irregular finite element grid that underpins these data likely contributed to interpolation errors. Similarly, the ocean currents, while useful, are, at 1/12°, relatively coarse for this analysis. The same is true of the wave data. The contribution of these two features would likely be improved if they were sourced from well calibrated, high resolution circulation models. We note that we expect the disturbance surface (Fig. 5) to represent a characteristically high disturbance value because 1) maximum waves and bottom currents were used to calculate the seabed shear velocity, and 2) currents are assumed to be in parallel. However, it is not necessarily the maximum possible, since other dynamics (e.g., eddies, density driven flows, small scale interactions between currents and topography) were omitted.

The Chla data were much better resolved, but the algorithms used to translate reflectance to Chla concentrations can result in biased classification along shore. This suggests that cells containing land are best ignored, which fortunately corresponds well with the depth restriction imposed by the shoaling depth in the sediment layer. However, we found some variability amongst the swath data in the land classification along complex regions of the coastline, raising additional concerns about the precision of compiled remote sensing data, particularly in narrow channels, inlets and fjords.

We followed Kostylev et al. (2005) and used spring Chla concentrations as a proxy for the nutrient input to the benthic environment. Using surface estimates of primary production for what is fundamentally the input of detritus to the seabed requires strong assumptions about the fate of phytoplankton. It also ignores the significant contribution of macrophytes to detritus. Nevertheless, as one of the few comprehensive estimates of production available, its use is unavoidable. However, because of the importance of food availability to the template, it is critical that the uncertainty introduced by the necessary assumptions be considered.

While primary production can be transported long distances, the absence of a circulation model required the use assumptions to describe how Chla contributes to benthic communities. Using the average from a time series (e.g., summer) creates a diffuse picture, and assumes a symmetry of process that is likely unrealistic in some locations. We therefore chose to use Chla bloom frequency rather than concentration means or maxima because we believe this better reflects local productivity, which in turn is arguably closer to the intended use as a proxy for benthic nutrient input. Inter-annual and seasonal variability are captured and contribute to the diffusion of the prediction, although unevenly across the study area. In the Adversity calculation, in recognition of the movement of primary production, this potential nutrient input is scaled using depth and a stratification index, assuming deeper, more stratified waters receive less input. This illustrates how complex the uncertainty in many modelling assumptions can be, and the need to at least recognise and consider their possible impacts (see Limitations).

Finally, the sediment surface, while representing a good first step on integrating the available data, could be improved though increased sampling, and the refinement of the independent data layers mentioned above (e.g., bathymetry and its derivatives). It must also be recognised that sediment grab data are biased towards soft sediments in deeper waters, as failed grabs on hard bottom are generally not recorded. This explains in part why the maximum predicted grain size in Pacific Canada was much lower than on the Scotian shelf. An additional factor is that NRCan samples are typically collected some distance from shore (Fig. 10). This adds the additional bias of ignoring shallower, often harder substrates from the analysis.

The near shore portion of the shelf is unrepresented because of the 30 - 500 m depth restriction. Some additional areas are also unrepresented because the sediment predictions were not extrapolated outside the spatial extents of the observed independent data (Fig. 12). These areas could be interpolated if surrounded by valid predictions, but areas along the edge of the study area could not. Of course, additional sampling would help this situation, as would the development of a near shore sediment model.

UNCERTAINTIES

The sources of uncertainty in this analysis, as in most modelling exercises, are myriad. They range from observational error in the various environmental layers, to structural uncertainties like missing variables (e.g., dissolved O_2), and the formulation of the Disturbance and Adversity hypotheses. This is in addition to the epistemic uncertainty in the habitat template theory itself, including assumptions like the environmental forcing being independent of species interactions.

While some uncertainties (like the confidence in the abiotic predictors) could be estimated empirically from the available data, most of the uncertainty inherent to this and other classification models lies in the model assumptions and is thus difficult to quantify. Such assumptions permeate every variable and interaction represented in the ***D*** and ***A*** functions. In such a dependent chain of operations, the cascade of uncertainties can be significant, but is numerically intractable because of the unknown uncertainty in necessary but often erroneous assumptions (e.g., nutrient input).

There is currently no way of knowing how assumption uncertainties influence the precision and accuracy of the final results, except through comparison with observations. That is why evaluations of such models rely on estimates of their overall performance, typically based on how well the final predictions correlate with observations and, increasingly, with other models.

This begs the question of how good a classification needs to be, and this is entirely dependent on the intended use of the model, where the distinction between models for understanding and models for management is critical (Gregr 2016). Understanding and formalising model objectives can provide important insights into the sufficiency of model complexity (Canessa et al. 2015, McDaniels et al. 2006). In contrast, developing models to advance understanding (e.g., by reducing uncertainty), while a perfectly valid undertaking, lacks a clear endpoint, and can thus be a never-ending effort.

Since it is generally accepted that the full suite of uncertainties in a complex ecological system can never be fully characterised, model performance will continue to rely on inferences from comparisons with independent data. Determining when a model is suitable (i.e., has sufficient certainty) for use in a particular management activity (e.g., marine spatial planning) thus depends on its robustness to changes in input data and design assumptions, and how well it predicts various independent data sets.

FUTURE EFFORTS

The preliminary evaluation of the ecological relevance of the habitat template is encouraging, though more comprehensive assessments of model assumptions and performance are recommended. Straightforward assessments include examining how individual species are distributed across the template, and a closer look at the effect of distance on the both the individual indicators and their correlations, perhaps using autocorrelation methods such as Mantel tests. Understanding regional differences across the Pacific Canadian shelf is critical to effective marine spatial planning.

How individual benthic species respond to the habitat template will depend on their life history. Thus pooling them by life history strategies (e.g., invertebrates, finfish), guided by clear ecological principles (Kindsvater et al. 2016), would likely emphasise their shared functional ecology and bring the relationship between biology and the habitat template into better focus.

A second potential avenue for advancing the utility of the template is to explore its potential for informing habitat suitability. As an integrated, process-based predictor, it could provide both theoretical and practical advances in understanding species distribution and managing species at risk. Important initial questions are whether the integrated template provides more information than the individual predictors. This is again something that could be addressed by comparing different models.

Methodologically, the habitat template itself would benefit most from the output from a regional ocean circulation model capable of producing seasonal temperature, salinity and current climatologies (e.g., Masson and Fine 2012). Improvements to the bathymetry, would also be valuable, particularly if artefacts were removed allowing depth derivatives to be more accurately calculated.

The biological relevance of the habitat template is well grounded in the theory of functional ecology, and our quantitative assessment using empirically-based diversity indices is encouraging. However, the high correlation of the various data sets with depth suggests it may be fruitful to explore alternative formulations, where the physiographic layers are less correlated and have more even leverage on the results. Such investigations would be facilitated if developed in conjunction with more comprehensive observational data, with some attention to functional ecology of the species. For example, separating finfish from invertebrates in the observational data may yield further insights. This would refine the ecological hypotheses, resulting in a more defensible classification of Canada's Pacific shelf.

Additionally, as articulated by Kostylev and Hannah (2007), while maximum biodiversity is hypothesised to occur near the centre of the habitat template, this depends on the ***D*** and ***A*** values spanning the global range of values. Understanding how well the global ***D*** and ***A*** extremes are captured would contribute significantly to the predictive value of the template with respect to biodiversity.

The sediment grain size model also shows promise, but given the limitations described above, we expect it would be significantly improved by using a more comprehensive data set. Multi-model comparisons would also be useful, and could lead to model integration if the strengths and weaknesses of the available methods are understood. We suggest a complementary analysis, generating a type of modified (categorical) Folk classification to provide an indicator of hard bottom, would be useful in this regard. Such an analysis could use the proportional data available in the NRCan grab samples, as well as integrating grab sample data from Fisheries and Oceans Canada, and opportunistically collected local ecological knowledge primarily from fishers, which is likely to provide a good indication of hard bottom. A more detailed investigation of interactions and error distributions is also warranted. While it is not clear that this would produce a significantly better prediction, these analytical considerations are included in anticipation of an update to this very important data layer in the near future.

CONCLUSIONS

Of the many ways a marine classification can be assembled from physiographic data, the habitat template is the only one that uses a priori hypotheses to characterise potential ecological niches. We have shown that an abiotic classification guided with hypotheses about how the physical environment may influence the functional evolution of marine species yields a meaningful classification that correlates with biodiversity. In doing so, it provides a habitat template that describes the study area's relative representativity and species diversity, and can provide an indication of species composition. As an integrative, process-based, ecologically defensible approach to marine classification, the template thus has enormous potential for informing the sensitivity, rarity, representativity, and diversity criteria of Canada's marine protected area strategy.

Our results corroborate findings in other regions (Fisher et al. 2011, Galparsoro et al. 2013, Kostylev and Hannah 2007, Kostylev et al. 2005) where the template has been found to correlate well with local species composition, suggesting the approach may be relatively robust to both study area and the quantitative expression of the disturbance and adversity hypotheses. The explicit articulation of these hypotheses will allow them to be tested and refined, furthering both our understanding the important ecological linkages and the utility of this information for marine spatial management.

Our results also provide evidence for the existence of distinct bioregions on the Pacific Canadian Shelf. While such regions have been variously described for the coast (Robinson and McBlane 2013, Zacharias et al. 1998), examining how the template correlates with species distribution across distance has the potential to empirically identify and define these boundaries. This is critical for the application of any ecosystem analysis of the coast, as it can no longer be assumed that the underlying ecological processes are the same across the entire shelf.

The grain size analysis conducted to support the habitat template is an example of the value of cross-disciplinary analyses. By bringing statistical techniques more often applied in ecology to bear on the problem of interpolating a sediment surface, we have derived a data layer that, in addition to being a key component of the habitat template, is also likely to be an important layer in its own right for studies of the Pacific Canadian shelf. In addition to supporting analyses of marine classification, we envision this critical piece of spatial data informing other analyses such as acoustic propagation, and cumulative benthic effects.

All things considered, the sediment layer and the habitat template produced through this work provide an important contribution to coastal studies in Pacific Canada. Upgrades to the oceanographic data and a more comprehensive ecological validation would significantly improve the utility of these data products to marine spatial planning in Canada.

ACKNOWLEDGEMENTS

Kim Conway, Mike Foreman, Cliff Robinson, and Alan Sinclair provided a review of the early template results. Katie Gale and Emily Rubidge provided support with the groundfish data for validation. We thank Peter Neelands, Barbara Szlavko, Kim Conway, Vaughn Barrie and their co-op students (GSC) for facilitating the delivery of the updated GSC sediment data. Detailed, thoughtful reviews of the final draft by Cliff Robinson and Emily Rubidge greatly improved both the clarity and relevance of this report. EJG was supported in this work by DFO and NRCan in various forms over many years. The sediment model and the latest version of the template were supported by Tides Canada via WWF Canada. We especially recognise the contribution of Dr. Glen Jamieson (DFO, Emeritus) for initiating the work in Pacific Canada and championing the habitat template for many years.

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Table 1: Qualitative values of 5 tactics in the four quadrants of the Disturbance-Adversity benthic habitat template (adapted from Southwood 1988).

Scope for Growth(A) **Disturbance (*D*)**	**Low**		**High**	
Stable (low)	Defense	high	Defense	medium
	Migration	low	Migration	low
	Offspring	few / large	Offspring	medium / small
	Longevity	high	Longevity	medium
	Tolerance	high	Tolerance	low
Disturbed (high)	Defense	high	Defense	low
	Migration	high	Migration	high
	Offspring	medium / large	Offspring	many / small
	Longevity	medium	Longevity	low
	Tolerance	high	Tolerance	low

Table 2: Raster data derived and documented for the creation of the Disturbance-Adversity surface for the Pacific Canadian continental shelf.

Layer name	Description	Source/Notes
BC_SourceData.gdb - All layers at 100 x 100 m^2 resolution unless noted		
bathymetry	Bathymetry (m)	Source data: Living Oceans Society (75m); NOAA (250 m)
bpi_brd50sd	Broad-scale BPI	Derived from bathymetry
bpi_fine5sd	Fine-scale BPI	Derived from bathymetry
max_tidal	Bottom tidal velocity (cm/s)	Foreman et al. (2008). Modelled values for maximum spring tidal flow; variable grid
temp_summer	Summer bottom temperature (°C)	Foreman et al. (2008). Long-term average.
temp_winter	Winter bottom temperature (°C)	Foreman et al. (2008) Long-term average.
sigma_diff	Summer stratification (sigma-t)	Derived from Foreman et al. (2008).
hycom_maxsum	Summer bottom ocean currents (cm/s) at 5 km x 5 km	HYCOM; source = 1/12°; Summer months, 2004-2008
hycom_maxwin	Winter bottom ocean currents (cm/s) at 5 km x 5 km	HYCOM ; source = 1/12°; Winter months, 2004-2008
chla_bloom	Spring chlorophyll-a bloom frequency	MERIS; source = 1.2 x 1.2 km^2; Monthly bloom frequency based on monthly averages (March-June), 2007-2011
BC_Sediments.gdb - All layers at 100 x 100 m^2 resolution		
depth_mask	Defines the study area for the sediment prediction surface	30 to < 1000 m
NRCAN_Expedition_ Data _2011	Available surficial sediment samples for the Canadian Pacific shelf	Includes mean phi, and proportions of gravel, sand, silt, and clay. (soft biased)
grain_size	mean bottom particle size (phi) phi = $-\log_2$(grain diameter, in mm)	Predicted particle size based on Generalised Additive Model
marine_bioregions	Divides study area into regions of potentially different geomorphic origin & ocean current exposure	4 levels: North Coast; Queen Charlotte Sound; West Coast Vancouver Island; East Coast Vancouver Island
BC_HabitatTemplate.gdb - All layers at 100 x 100 m^2 resolution		
max_velocity	Characteristic water velocity at the sea floor (m/s)	Combined tidal, wind-wave, and ocean current maxima
disturbed_idx	Disturbance index	Potential for substrate disturbance
adverse_idx	Adversity index	Measure of ecological Adversity
dist_adv	The Habitat Template	2-band composite of Disturbance & Adversity

Each layer includes metadata in compliance with Federal Geographic Data Committee standards (FGDC 1998). FGDC compliance was evaluated using the MP tool contained in the TKME package (Schweitzer et al. 2010) available from the USGS.

Table 3: Structure of coast-wide and regional GAM models used to predict grain size on the Pacific Canadian shelf. Coast-wide models (first 3 rows) show how model performance (ΔDev) responded to Slope and Region. Regional models (North Coast, Queen Charlotte Sound, West Coast Vancouver Island, and Strait of Georgia) show structures used for regional predictions. Predictor variables are shown as absent (--), linear (L) or smoothed (S). Deviance reduced (ΔDev) is (1 - residual deviance/null deviance), an accepted proxy for variance explained.

Extents	N	Bathy	Slope	Energy	CoarseBPI	FineBPI	Region	*Dev
Coast-wide	3757	S	S	S	S	--	L	0.418
Coast-wide	3757	S	--	S	S	--	L	0.416
Coast-wide	3757	S	S	S	S	--	--	0.364
N Coast	1371	S	--	S	S	S	--	0.358
QC Sound	368	S	--	S	S	--	--	0.436
WCVI	1024	S	--	S	S	--	--	0.459
SoG	994	S	S	S	S	--	--	0.308

Table 4: Correlation (Spearman's r) between Shannon-Wiener Diversity Index (SWDI) and Adversity (SWDI-Adv), Disturbance (SWDI-Dist) and the integrated habitat distance (SWDI-IH) for all values on the shelf, and for each of the regions considered. N is sample size. Shaded values were not significant at the 0.05 level.

	Entire Shelf	Hecate	WCVI	Dixon	QCS	SOG	Barkley
N	4098	2569	822	676	906	53	495
SWDI - Adv	0.030	0.135	0.003	-0.151	0.138	-0.031	0.024
SWDI - Dist	-0.067	-0.192	0.017	-0.116	-0.140	0.241	-0.006
SWDI- IH	-0.116	-0.206	0.019	-0.380	-0.110	0.246	-0.010

Table 5: Correlation (Spearman's r) between the Brey-Curtis Dissimilarity Index (BCDI) of the bottom trawl survey data, the integrated habitat distance (IH) and geographic distance (Geo) for each test region (Fig. 10). All correlations were significant due to the large sample size.

Test region	BCDI-IH	BCDI-Geo	IH-Geo
Hecate	0.534	0.255	0.259
WCVI	0.648	0.142	0.153
Dixon	0.442	0.440	0.500
QCS	0.580	0.116	0.104
SoG	0.539	0.099	0.032
Barkley	0.543	0.140	0.160

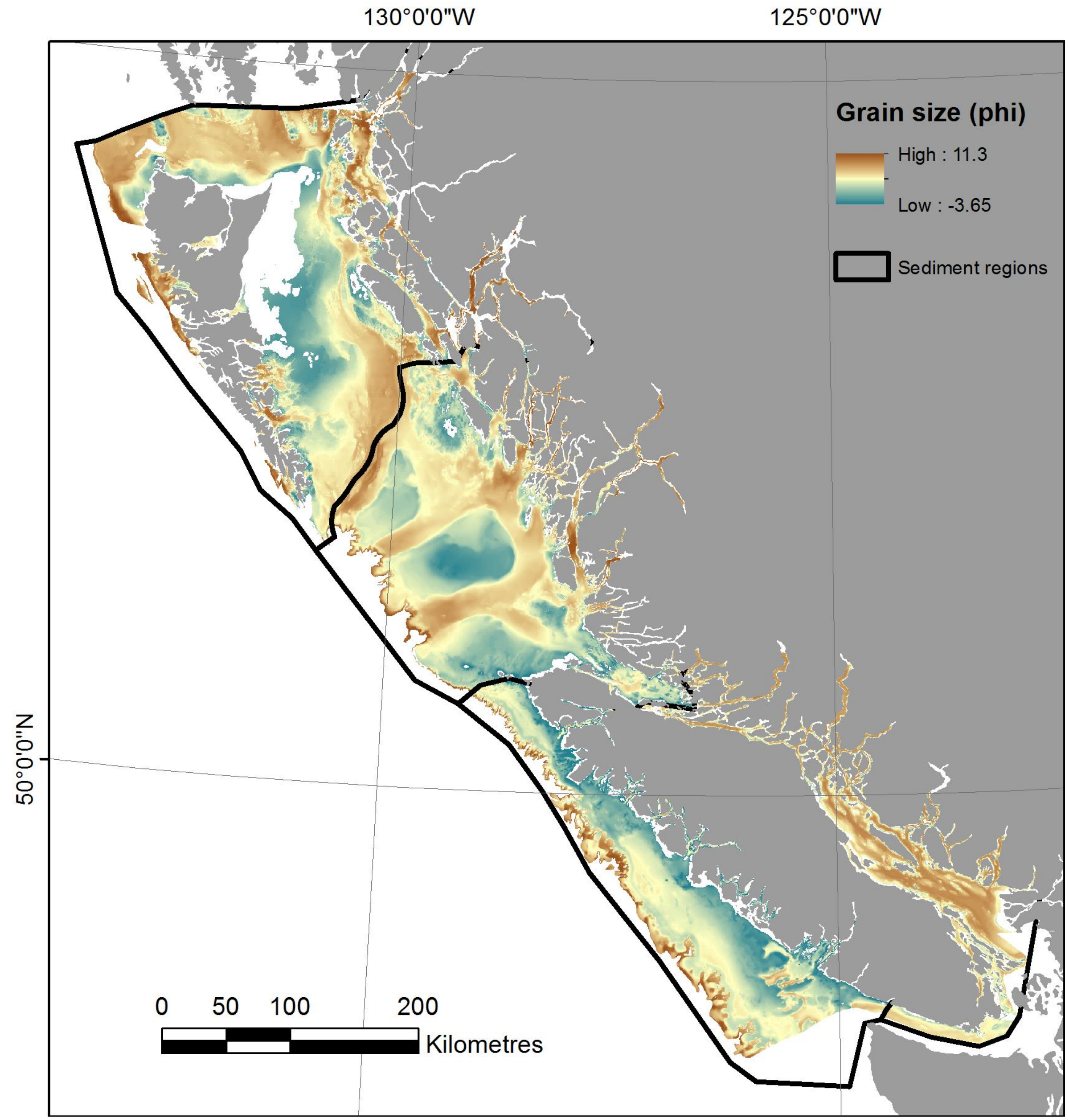

Figure 1: Predicted grain size (Phi units: -log2(grain size in mm)) for Canada's Pacific shelf. Blue indicates larger particles and brown finer particles. White areas contain NoData either because they were oustide the modelled depth range or the recorded range of an independent variable. Models were developed for each sediment region and a mosaic was used to create the comprehensive sediment map.

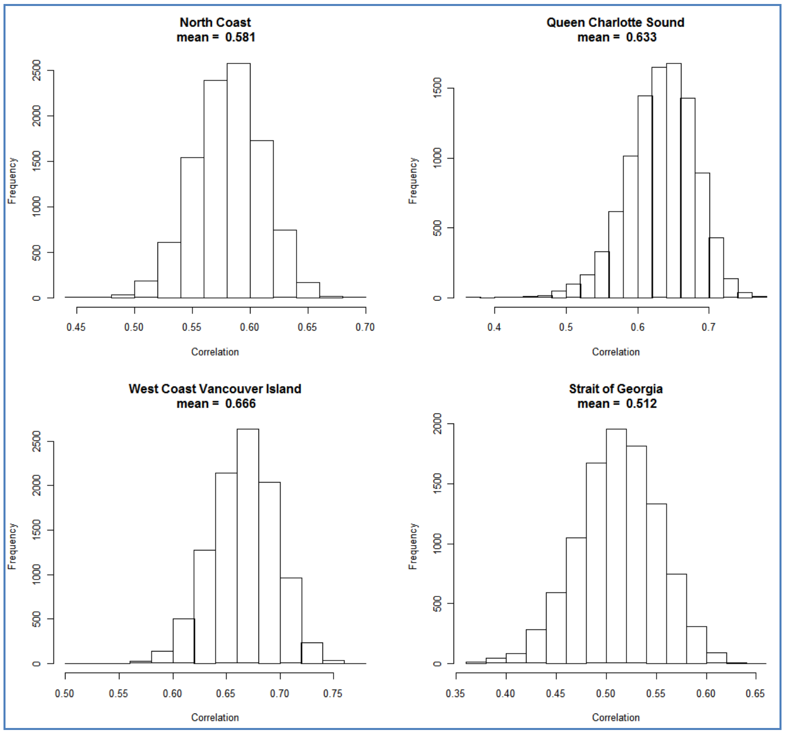

Figure 2: Histograms of cross-validation of regional models. 10,000 partitions of training (70%) and testing (30%) data.

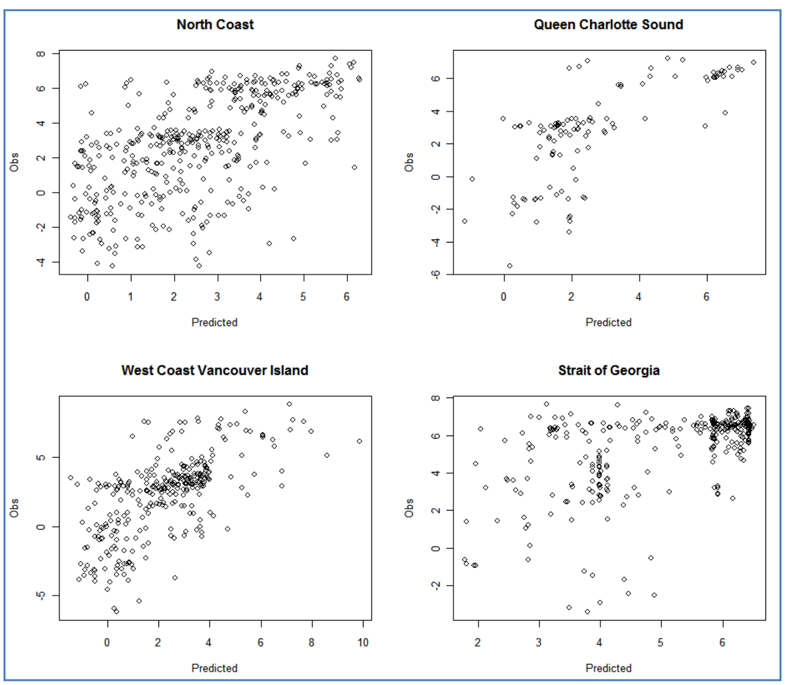

Figure 3: Scatter plot of predicted vs. observed values (in phi) by region for one set of training and testing data.

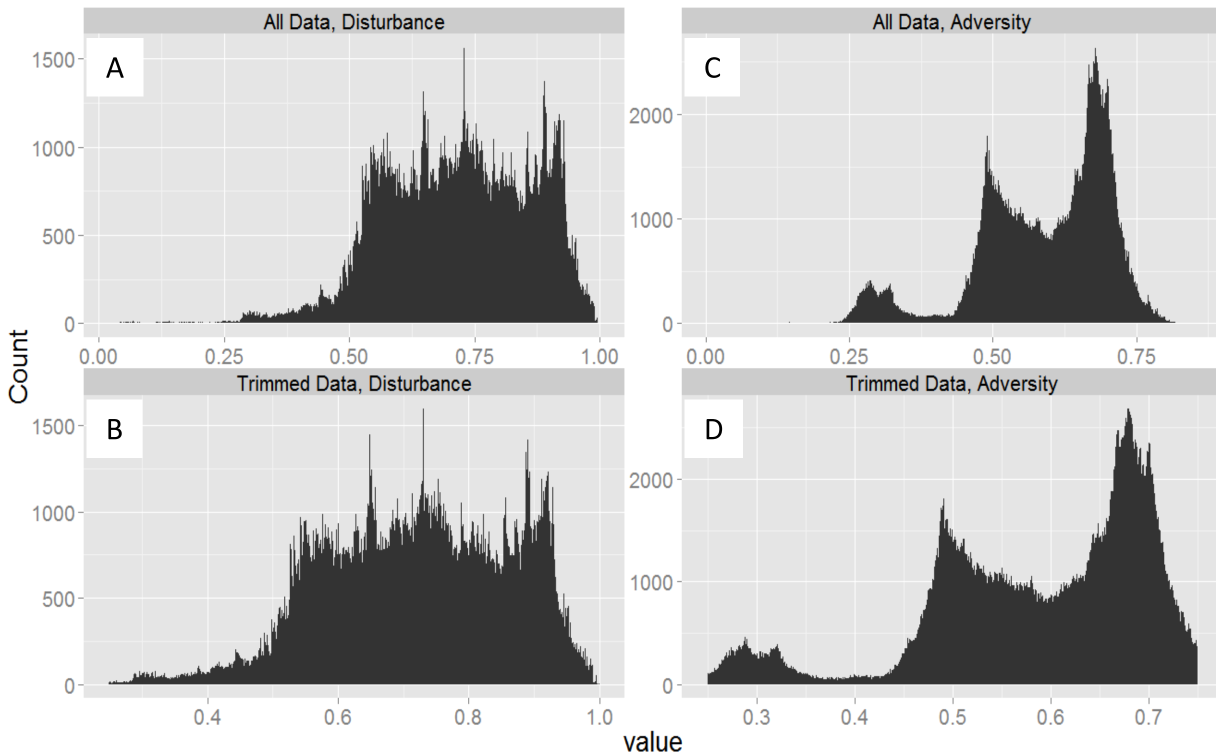

Figure 4: Distribution of a 500 k sample of Disturbance and Adversity values across the study area showing the full range (A, C), and the trimmed distribution after removing extreme values in the tails (B, D). We standardized the trimmed ranges (Disturbance: [0.25, 1.0]; Adversity: [0.25, 0.85]) for the final habitat template.

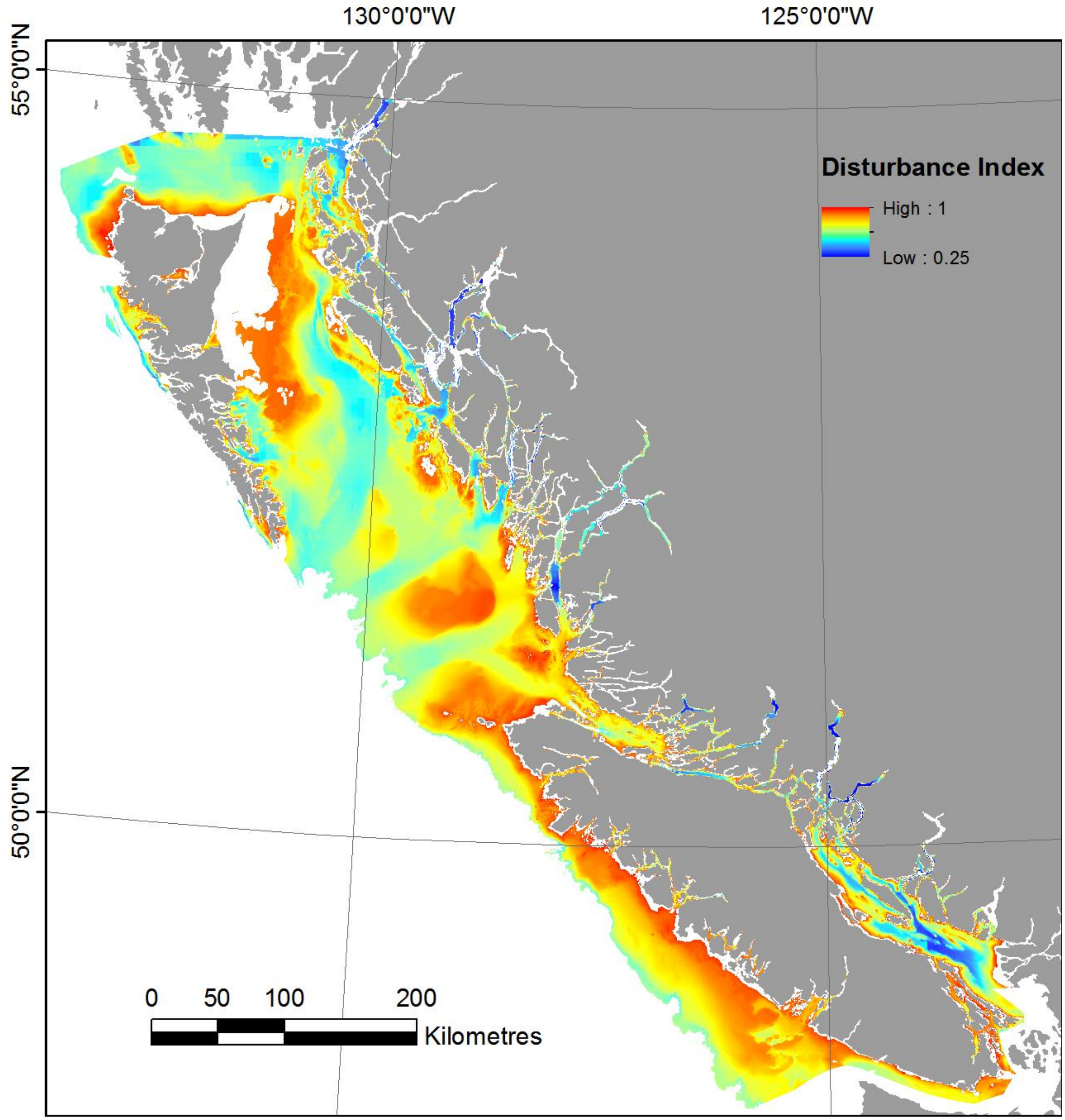

Figure 5: Indexed Disturbance surface for Pacific Canadian shelf shown with colour ramp restricted to [0.25 to 1] to increase contrast. White areas contain NoData due to depth restriction or missing sediment prediction. See text for details.

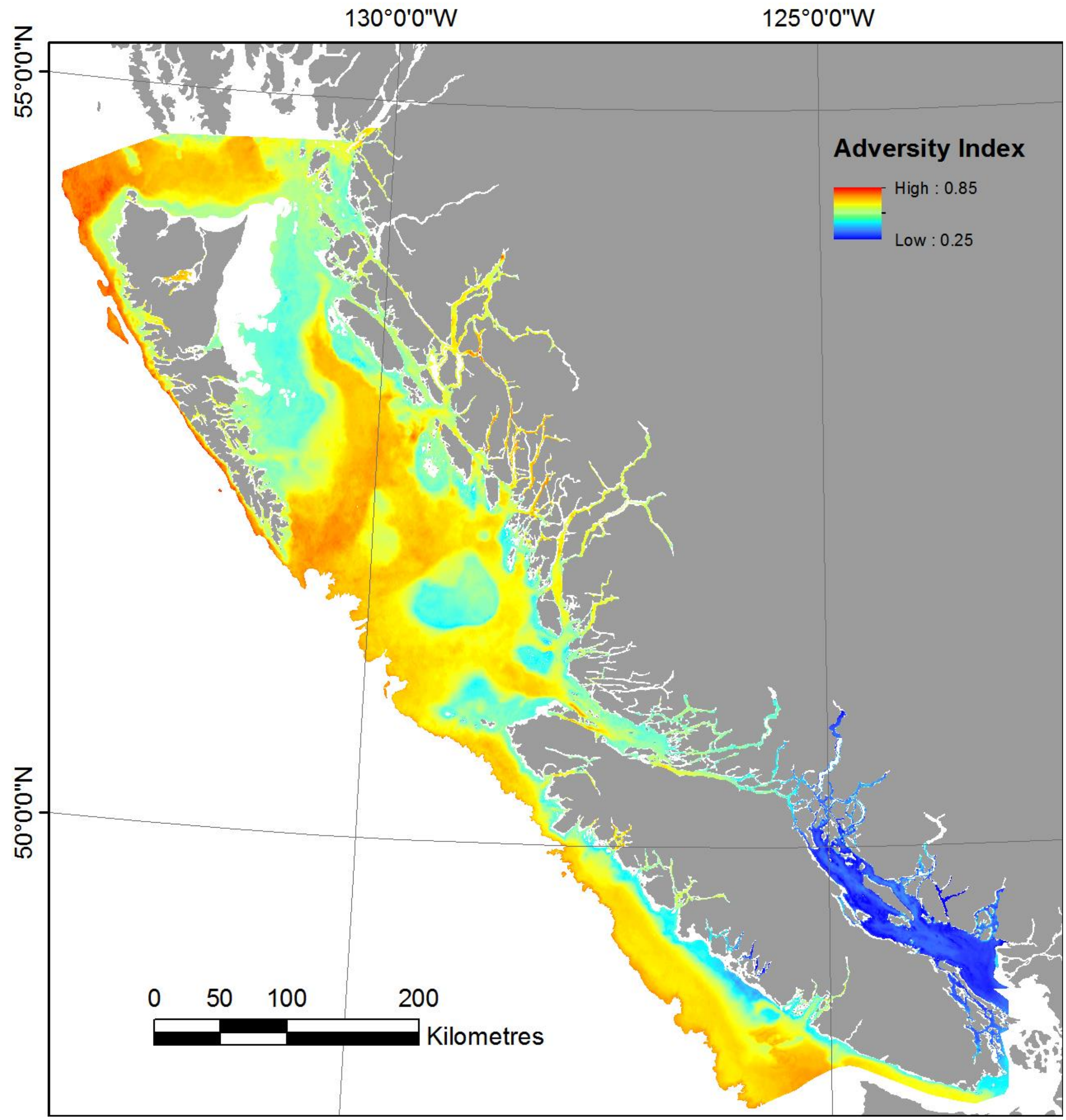

Figure 6: Indexed Adversitysurface for the Pacific Canadian shelf shown with colour ramp restricted to [0.25 to 0.85]. White strip near shore and depths > 500 m contain NoData due to depth restriction. See text for details.

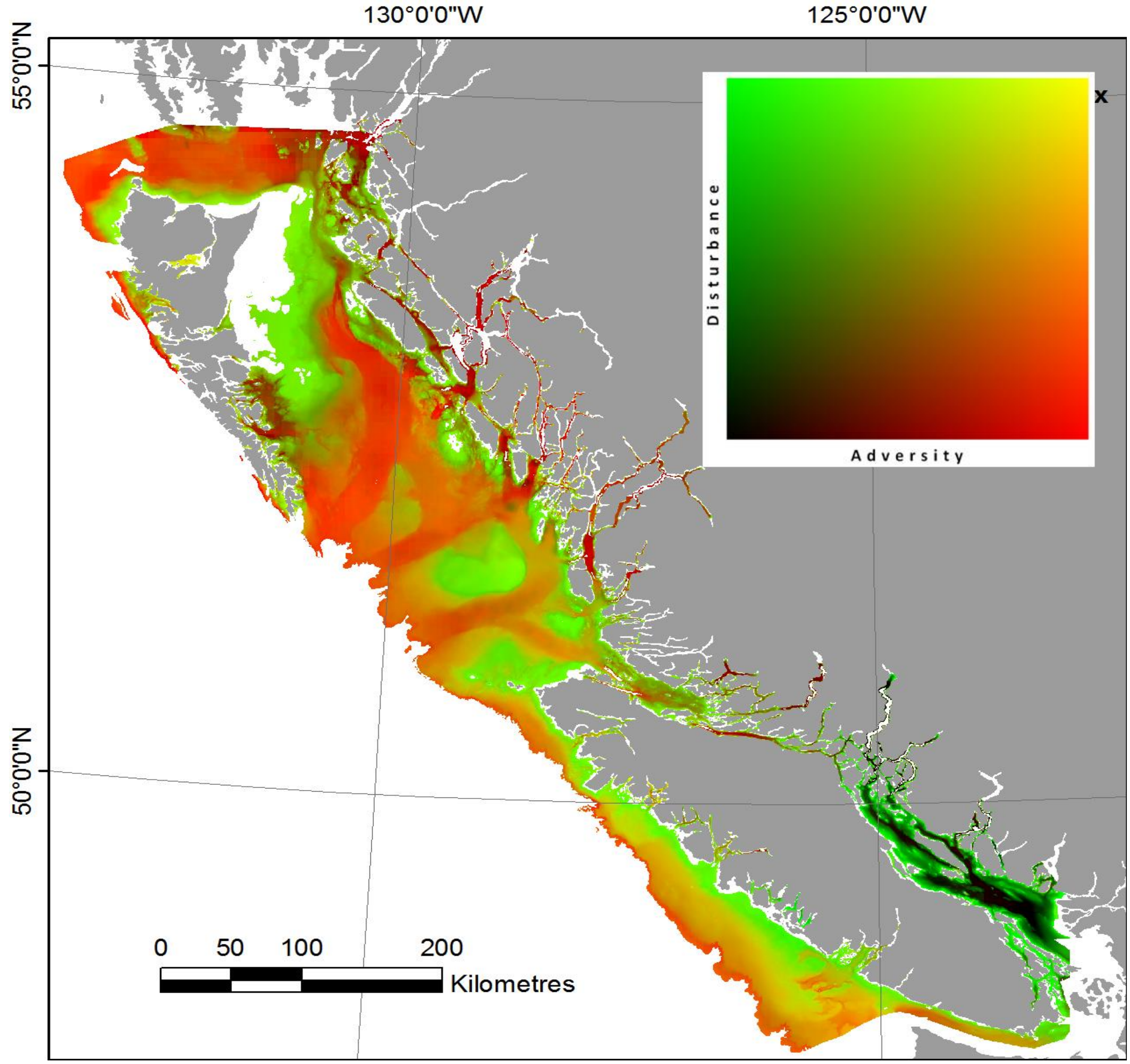

Figure 7: Disturbance-Adversity surface for the Pacific Canadian shelf shown as a two-band image. Disturbance is shown increasing in the green spectrum and Adversity increases in the red spectrum. Darker areas are low on both axes, while brighter yellow and orange areas are both highly Disturbed and Adverse.

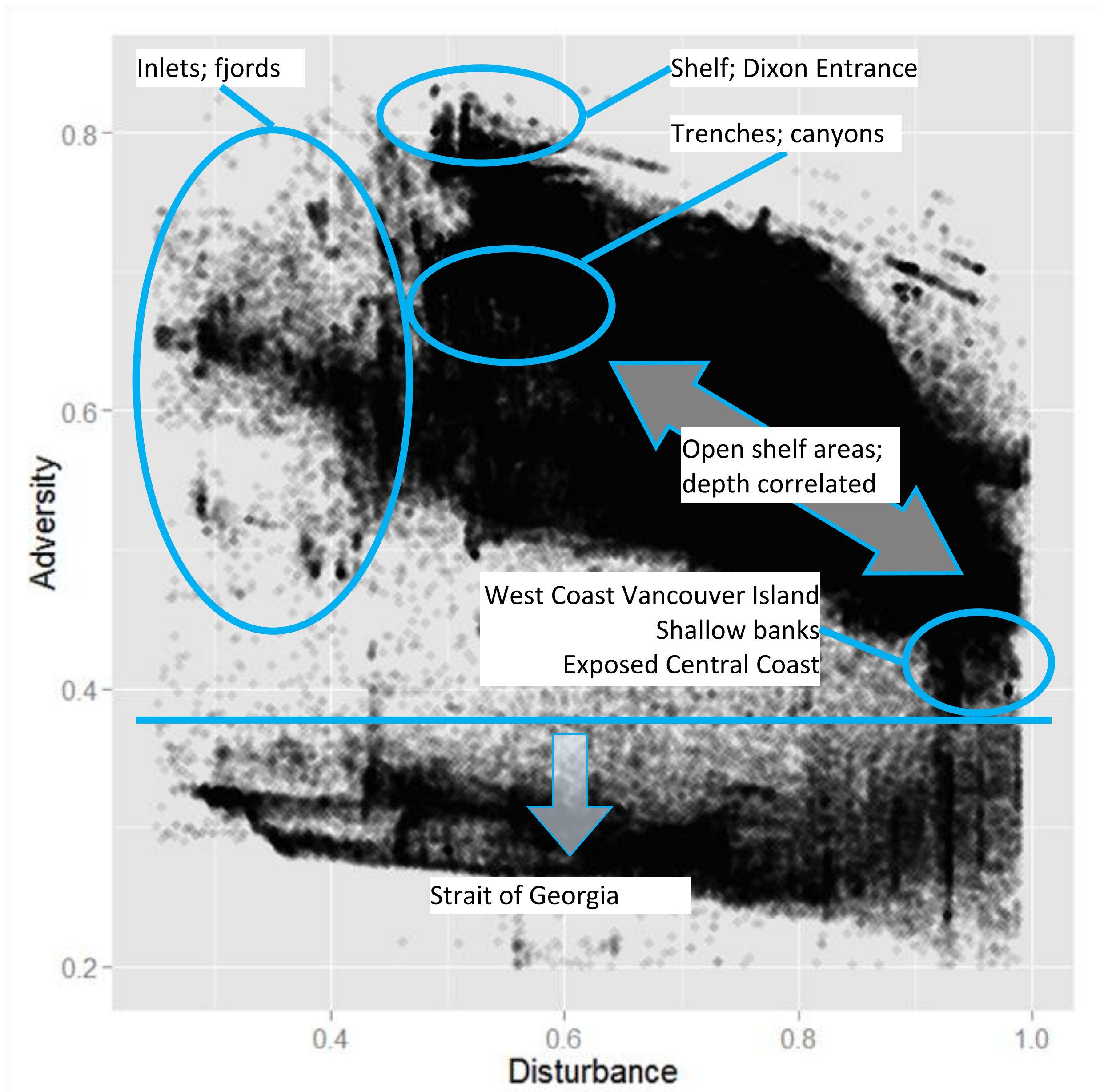

Figure 8: Disturbance-Adversity space for the Pacific Canadian shelf from 30 to 500 m depth. Each point represents a 100 x 100 m^2 grid cell.

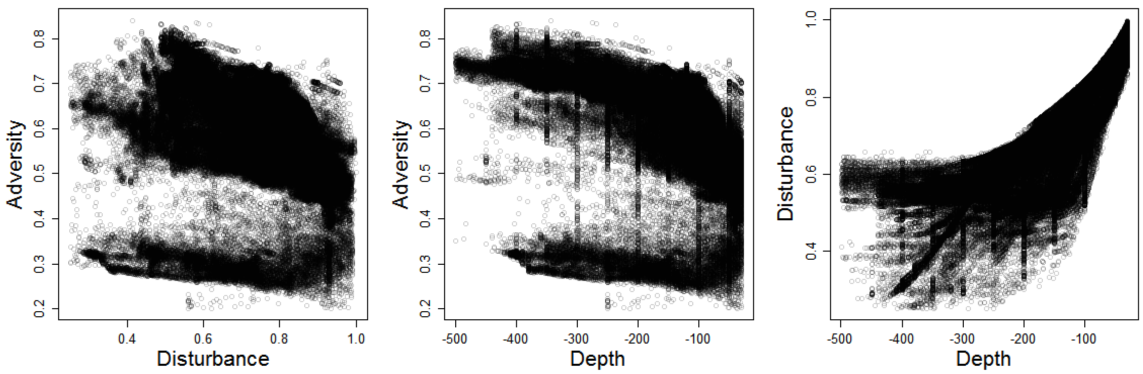

Figure 9: The relationship between Disturbance and Adversity, and the corresponding influence of depth on these components of the habitat template.

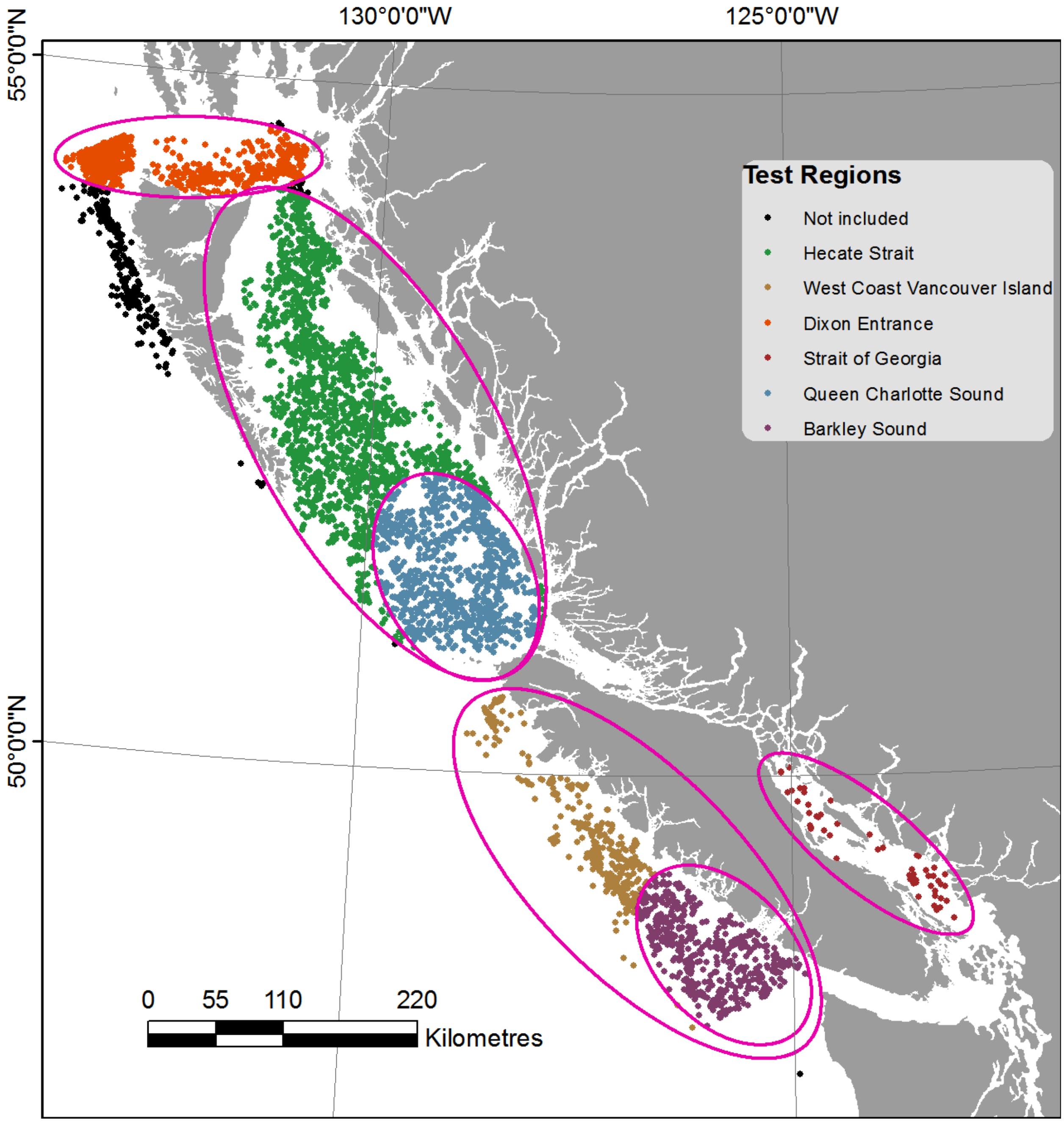

Figure 10: The distribution of the groundfish sampling data and the sample regions used to test for regional differences in the correlation between species associations, the habitat template, and geographic distance.

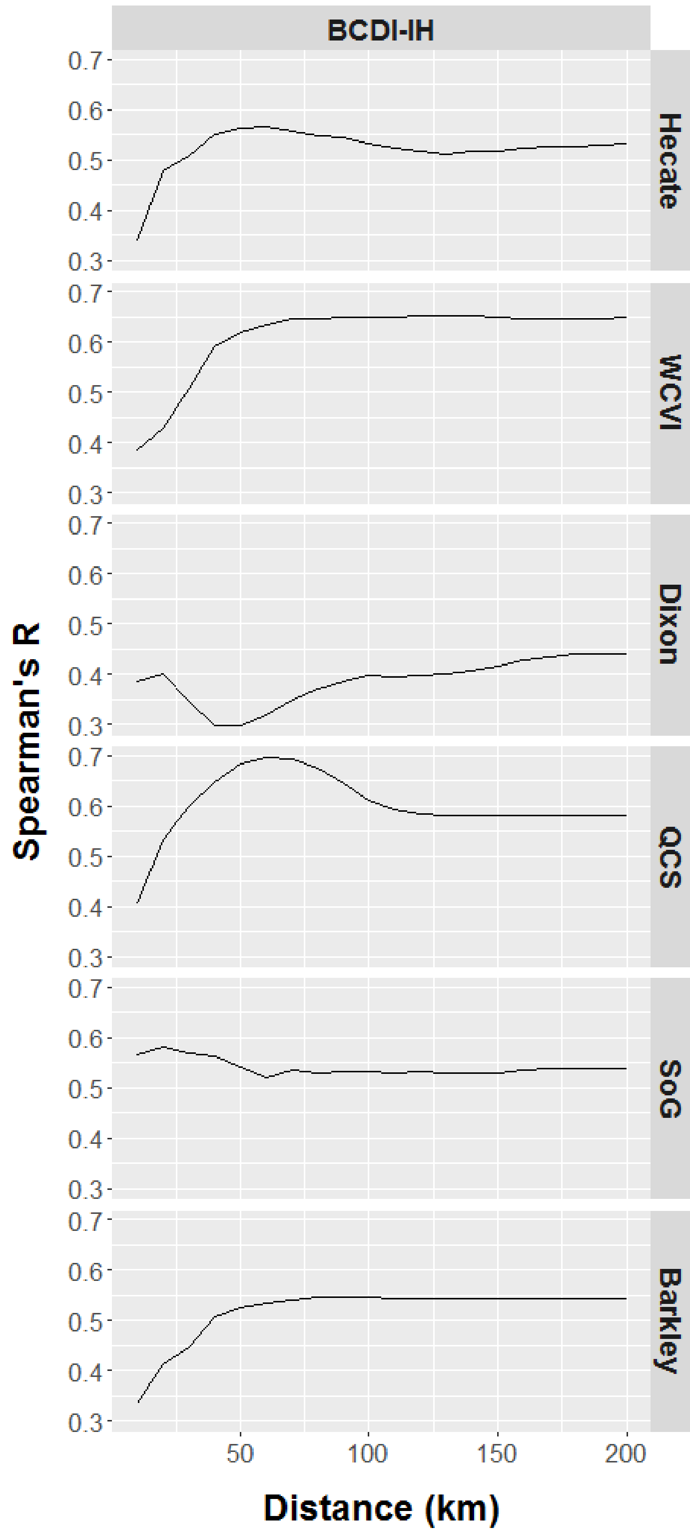

Figure 11: Correlation (Spearman's R) between the Brey-Curtis dissimilarity index (BCDI) and the integrated habitat distance (IH) at 20 equally spaced distances (10 to 200 km) for each of the 6 test regions (Fig. 10). Correlations were significant ($p < 0.001$) for all distances. See text for details.

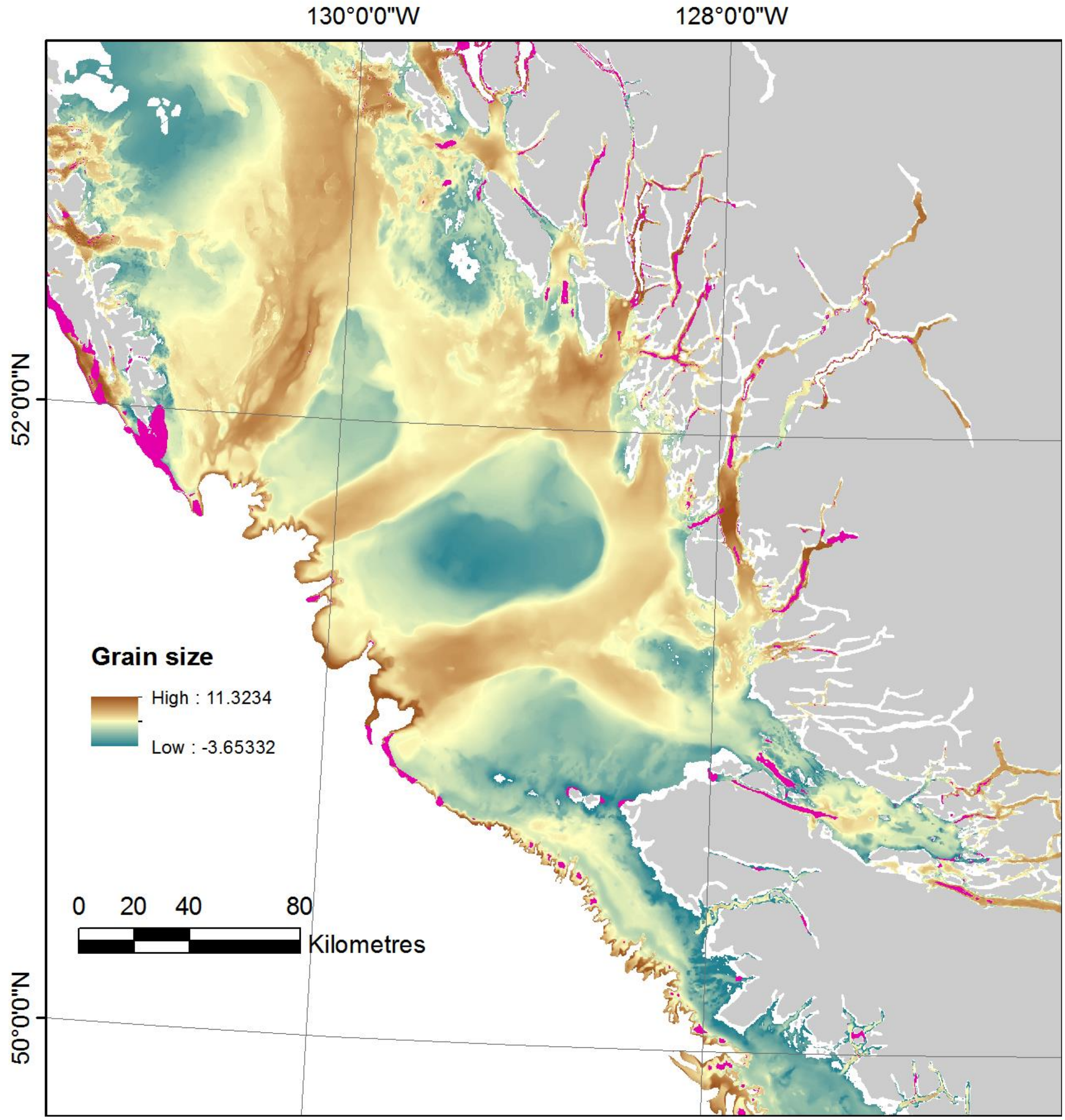

Figure 12: Central portion of the study area showing grain size (as phi) and emphasising the unrepresented regions on the shelf. These include the white strip (0 to 30 m depth) surrounding land (grey), and the areas (shown in purple) where predictor values where outside the range of the grain size model.