

A novel three-dimensional analysis of functional architecture that describes the properties of macroalgae as a refuge

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ABSTRACT: Foundation species like macroalgae provide habitat for large numbers of animals. The spatial structure between branches or thalli can act as a refuge from larger predators and can affect the number and distribution of inhabitant species. Most metrics for habitat architecture are based on 2-dimensional measurements, but habitats are 3-dimensional. We report a new method, spherical space analysis, for characterizing the 3-dimensional volume distribution by size of interstitial spaces for 3 species of macroalgae (seaweed) with distinct architectures. This analysis gives the distribution of volumes within a foundation species that are inaccessible by an idealized spherical organism—an 'inaccessible volume curve'. A second product is an 'inaccessible surface area curve'. We incorporated abundances and size ranges of meso-invertebrates into spherical space analysis to predict predator–prey interactions as a function of the relationship between inaccessible volume and area and the size of predators and prey. The results show that filamentous forms of macroalgae have more smaller interstitial volume and area than branched or blade forms of macroalgae that support a larger number of smaller meso-invertebrates. The model suggests that the spatial structure of macroalgae affects predator–prey interactions with a greater number of smaller spaces providing more refuge. This was particularly apparent for kelp. Spherical space analysis provides a mechanism for understanding how the spatial architecture of a macroalgal environment mediates the network of feeding interactions occurring within it. This can have implications for restoration efforts, as the morphology and density of foundation species are integral in the maintenance of communities.

KEY WORDS: Habitat architecture · Foundation species · Kelp · Invasive species · Macroalgae · Predator–prey dynamics · Macrophyte architecture · Spatial structure · Benthic habitat.

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1. INTRODUCTION

Functional traits provide a mechanistic basis for linking specific traits to competitive interactions (Bertness et al. 2006), predator–prey relationships (Warfe & Barmuta 2004) and other population- or community-level processes (Lazzari & Stone 2006, Angelini et al. 2011). As such, they are known to be key drivers of ecosystem services (Hooper et al. 2005,

Díaz et al. 2007). Previous studies suggest that the variety of functional traits, and not just the diversity of species, are important to the maintenance of ecosystem health and resilience to disturbance (e.g. Cadotte et al. 2011, de la Riva et al. 2017). Structural traits in foundation species (e.g. branch length, width and other factors) are particularly important to discern as they affect abundance and diversity of associated species such as crustaceans, gastropods and

insects (e.g. Warfe & Barmuta 2004, Wonham et al. 2005, Severns & Warren 2008). They can also mediate the network of feeding interactions through the number and sizes of available spaces to determine the level of concealment and accessibility of those spaces by larger predators (e.g. Warfe & Barmuta 2004). Understanding the underlying functional traits that contribute to ecological processes can offer fundamental insights into choosing the best functional form to support ecosystem services (e.g. provide food, shelter and habitat). This is particularly important as structure-forming foundation species are rapidly changing (Asner et al. 2008, Wernberg et al. 2016, Dijkstra et al. 2017).

Many of the metrics used to describe the morphology of foundation species are 1- or 2-dimensional. These include branch length, height, weight, morphological complexity and total volume. Examples include biomass per unit area (Cyr & Downing 1988, Heck & Crowder 1991), which can be taken as a proxy for surface area (Attrill et al. 2000), cover (Carlisle & Hawkins 1998, Bartholomew et al. 2000), number of seagrass blades per square meter (James & Heck 1994), surface area to volume ratio (Coull & Wells 1983) and fractal dimension of samples (Bradbury & Reihelt 1983, Dibble & Thomaz 2009). Three-dimensional (3D) models have been developed that describe plant canopies for remote sensing applications (Phattaralerphong & Sinoquet 2005). They have also been used to model different structural stages of plant growth (Fournier & Andrieu 1998, Dornbusch et al. 2007). In recent years, commercial software algorithms that compute 3D shapes using structure from motion or make use of multiple-view stereo imagery have enabled reconstruction of sparse canopy height with relative ease. However, models and metrics describing refuge as a function of plant architecture are lacking. Having a metric that describes and predicts how shifts in the morphology of foundation species will affect community-level processes is important for predicting ecosystem-level changes.

The volume of free space is one such metric in which associated species use the volume provided by the morphology of foundation species (i.e. architecture) for refuge or foraging (e.g. Angelini et al. 2011). For example, the size distribution of interstitial spaces (defined as the space between 2 objects; e.g. between branches or oysters) directly mediates the interactions between predators and prey, and can determine recruitment potential of recipient species (Grabowski 2004, Toscano & Griffen 2013). Past studies of newly settled invertebrates and fishes have

determined that small, shelter-providing habitats create demographically important refuge from predators (Wahle & Steneck 1992, Carr 1994). Other ecological variables, such as number of individuals and size of associated species, may also depend on the size of the interstitial volume and surface area of the species (Steneck et al. 2013). As such, the development of 3D metrics of volume will aid in predicting the ecological consequences of the replacement of one morphological foundational form with another.

Previous studies specifically related to macroalgae have focused on the volume occupied by the plant thallus and the total available interstitial volume created by its branches (Hacker & Steneck 1990, Warfe et al. 2008, Steneck et al. 2013). In particular, Hacker & Steneck (1990) proposed a metric of interstitial volume based on a minimum bounding box containing a sample. The interstitial volume was calculated by subtracting the thallus volume from the bounding box volume. They also proposed a metric they called the interstitial space area, defined as the 'area between branches that have the same point of bifurcation'. However, they did not consider the shape and arrangement of interstitial spaces. Consequently, their interstitial volume metric does not take into account the fineness of the interstitial spaces. A finely branched individual might have the same volume as a coarsely branched individual but will have much smaller interstitial spaces. Moreover, spaces are also determined by branches not having the same point of bifurcation. In a similar vein, in intertidal macroalgae, Bartholomew et al. (2000) proposed the ratio Sp/Pr , where Sp is the average linear interstructural space distance, and Pr is the predator's size. They argued that, for a particular combination of predator and habitat architecture, this metric should predict prey survivorship. In freshwater macrophytes, Warfe et al. (2008) measured interstitial spaces by means of a photographic method using depth of focus to isolate a plane through the macrophyte sample suspended in water, and obtained Bartholomew's Sp/Pr metric. The morphological forms of foundation species provide a range of interstitial spaces available for habitats. It is possible to conceive of 2 species with similar average gaps, where one of them provides a significant volume of small interstitial spaces combined with a few large spaces and the other provides only spaces near the mean.

In the present study, we characterized the spatial structure (interstitial volume and surface area) for a more complete description of foundation species using macroalgae as an example. We first applied a

novel method (spherical space analysis) to examine predator–prey relationships by calculating the volume accessible by meso-invertebrates of a particular size or smaller but not accessible by larger invertebrates or fish. The products of spherical space analysis are (1) an inaccessible volume function: the volume within a structure that is inaccessible to an idealized spherical organism of a particular diameter or larger; and (2) an inaccessible surface area function: the surface area of a structure that is inaccessible to an organism of a particular diameter or larger. We built models of 3 common forms of macroalgae in the Gulf of Maine: *Saccharina latissima*, *Codium fragile* spp. *fragile* and *Dasysiphonia japonica*.

2. METHODS

Spherical space analysis has 2 stages that are independent of one another. The first stage (illustrated in Fig. 1) is the construction of a computer graphics model of a given macrophyte sample. This model is based on detailed measurements (e.g. branch length[s], width[s], height etc.) of the whole individual. The second stage is the development of the spherical space analysis to generate inaccessible interstitial volume and surface area curves for an individual macrophyte.

2.1. Stage 1: constructing the 3D macrophyte models

Our spherical space analysis method requires 3D computer graphics models of macroalgae based on samples from the field. We took advantage of prior methods for models of plants developed both for the computer graphics animation industry and for morphogenesis with applications in agriculture (Room et al. 1996, Fourcaud et al. 2008). Early approaches used Lindemayer systems (L-systems), simple recur-

sive grammars capable of producing branching structures (Prusinkiewicz et al. 1988). Stochastic L-systems have also been used to add variation to what would otherwise be rigidly symmetrical structures, and context-sensitive grammars are capable of creating more elaborate and varied structures where the size and shape of the branches changes with distance from the root (Allen et al. 2005).

The species we chose to model represent a wide variety of macroalgae morphologies. They are common members of macroalgal assemblages in the Gulf of Maine, and have at one time in the last 30+ yr dominated the macroalgal assemblage (Dijkstra et al. 2017). *Codium fragile* spp. *fragile* and *Dasysiphonia japonica* are introduced species, while *Saccharina latissima* is native. *C. f.* spp. *fragile* has a fleshy branching structure; *D. japonica* is also branching, but with a much finer filamentous parts; *S. latissima* has broad blades with a single blade for each hold-fast. *S. latissima* dominated the Gulf of Maine prior to the early 1980s (Dijkstra et al. 2017).

Modeling was based on a variety of measurements, some of which were carried out based on photographs taken *in situ*, while others were carried out in the laboratory in small tanks. Fine structure measurements of *D. japonica* were done using dissecting microscopes.

Based on these measurements, models of *C. f.* spp. *fragile* and *D. japonica* were developed to mimic the field samples (Fig. 2) using a recursive algorithm to reproduce the branching structure. For *S. latissima*, quadrats were photographed *in situ*. Following this, the *S. latissima* blades running through the quadrat were removed and measured in the lab. The 9 blades were modeled with a triangular mesh and adjusted using a finite element physics package that ensured no intersections between blades. Adjustments made to spring parameters within each blade resulted in the wavy edge pattern characteristic of this species. Supplement 1 in the supplementary material at

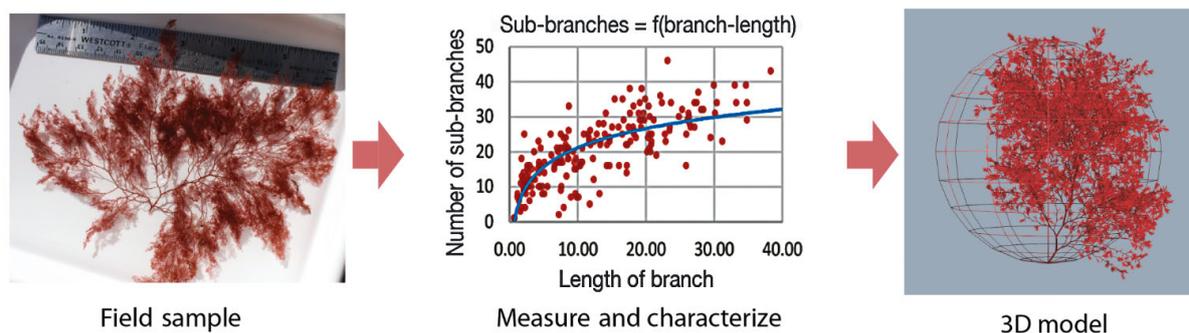


Fig. 1. Our method involved collecting samples, measuring the thallus, characterizing the architecture, and building 3D models based on the measured properties of the samples

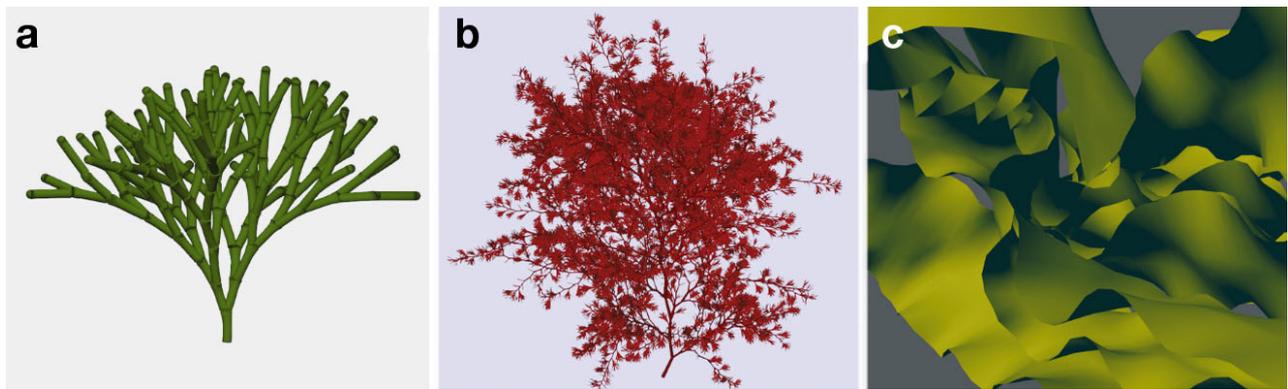


Fig. 2. Models of (a) the non-native macroalgae *Codium fragile* spp. *fragile*, that was a dominant member of Gulf of Maine subtidal communities in the 1990s and early 2000s, (b) non-native *Dasysiphonia japonica* that over the past few years has come to dominate large areas of the near-shore eastern seaboard of New England, and (c) *Saccharina latissima*, a broad-bladed kelp that was once dominant in the Gulf of Maine

www.int-res.com/articles/suppl/m608p093_supp.pdf details the methods used to construct each of the 3 models.

2.2. Stage 2: spherical space analysis (surface area and interstitial volume)

The motivation for the inaccessible volume and inaccessible surface area metrics is that the interstitial volume is the space used to seek refuge or inhabit, and within this volume, interstitial surface area describes the available surface to which the organisms can attach. In particular, it is the volume (or area) that is available to a prey organism, but not to a predator, which matters. The concepts of accessibility and inaccessibility are illustrated in Figs. 3 & 4. Given a predator radius and a prey radius, the volume of refuge available to the prey is the difference between the volume inaccessible by the predator and the volume inaccessible by the prey:

$$\text{Volume_of_Refuge} = \text{inaccessibleVolume}(\text{Predator_radius}) - \text{inaccessibleVolume}(\text{Prey_radius}) \quad (1)$$

Consider the arbitrary case of a predator with a diameter of 0.6 cm ($r = 0.3$ cm)—this value might represent the head width of a small fish, and a prey diameter of 0.1 cm ($r = 0.05$ cm)—a typical meso-invertebrate. The area of refuge calculation is the same only it uses the inaccessible area function in place of the inaccessible volume function:

$$\text{Area_of_Refuge} = \text{inaccessibleArea}(\text{Predator_radius}) - \text{inaccessibleArea}(\text{Prey_radius}) \quad (2)$$

The methods we describe in the following sections are all based on a voxel-based representation of the

macrophyte model and the space surrounding it. A voxel representation is simply a 3D grid where each cell (called a voxel) contains either macrophyte tissue or water. The working volume is defined and dis-

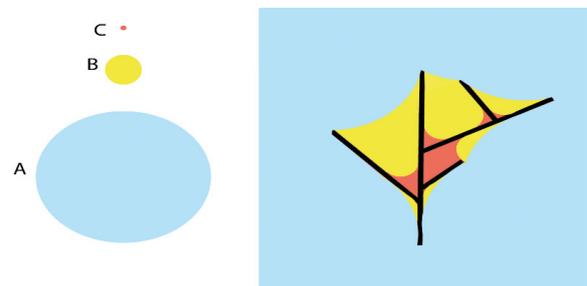


Fig. 3. Two-dimensional illustration of the accessibility concept. The yellow area is the region where organism B can reach, while not being accessible to the largest organism, A. The combined red and yellow areas represent the region where organism C can reach while being inaccessible by organism A

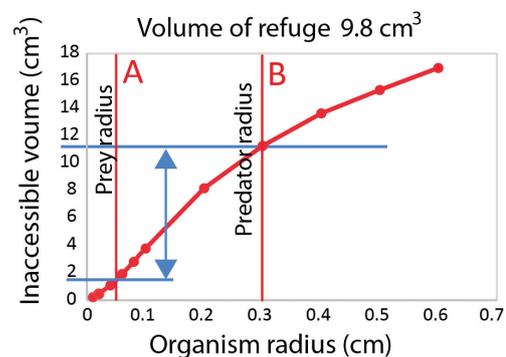


Fig. 4. Example of an inaccessible volume curve for a *Dasysiphonia japonica* model. Given a predator organism B and a prey organism A, the safe volume for A can be read off from the curve as the range indicated by the blue double-ended arrow

cretized in voxels, which are labeled as follows for an idealized spherical organism having radius r : macrophyte, inaccessible water, and accessible water.

In its simplest conceptual form, the spherical space analysis algorithm is as follows. First, voxelize the macrophyte model so that every voxel inside the model is labeled differently from every voxel outside the model. Second, for every water voxel in the modeled volume, determine if any of the voxels within radius r are labeled plant voxels; if not, then label every voxel within radius r as accessible. All voxels not labeled as plant and not labeled accessible will become inaccessible volume for that radius. Unfortunately, a simple brute force implementation of this method would be prohibitively slow, with compute time proportional to $D^3 \times R^3$, where D is the size of the voxelized volume and R is the radius of the idealized organism. Supplement 2 describes the algorithmic methods we developed to speed up the process and make it computationally tractable.

Figs. 5 & 6 illustrate the application of spherical space analysis to models of *C. f. spp. fragile* and *D. japonica*, showing how the inaccessible volume increases with radius.

For the purposes of habitat analysis, it is necessary to know the volume of refuge on a per-square-meter basis. To illustrate a comparison between different macroalgal species in terms of their spatial distributions, we considered the simplified case of 1 m² of seafloor densely packed with a single species. For

example, there could be 400 *D. japonica* (5.0 cm size) in 1 m². Similarly, there could be 156 *C. f. spp. fragile* (8.0 cm) in 1 m². We treated *S. latissima* somewhat differently, since our model consisted not of single individuals, but of a set of individuals passing through a 50 × 50 cm quadrat. In this case we simply multiplied the volume and area curves by 4. Admittedly, this is a simplification compared with the case where there is a distribution of many different macroalgal species, but still useful as a method for comparing how different species structure the seafloor on a per-meter basis. Also, in some cases, *D. japonica*, *C. f. spp. fragile* and *S. latissima* have each been observed to form dense, unbroken carpets of many square meters (Harris & Tyrrell 2001, Ramsay-Newton et al. 2017).

Results from re-processed meso-invertebrate abundance (Dijkstra et al. 2017) and size ranges of meso-invertebrates (collected from 10 individuals of each macroalgal species during the summer months in 2016 and 2017) were incorporated into the spherical space analysis to predict inaccessible volume as a function of organism size, inaccessible refuge as a function of prey and predator size per macroalgal species and then scaled up to habitat (1 m²). Macroalgae were collected from several sites by placing a plastic bag over individual specimens and gently ripping the holdfast from the substrate. *C. f. spp. fragile* was collected at 5 sites off the coast of New Hampshire (York, ME, Star, White [2 sites], and Lunging

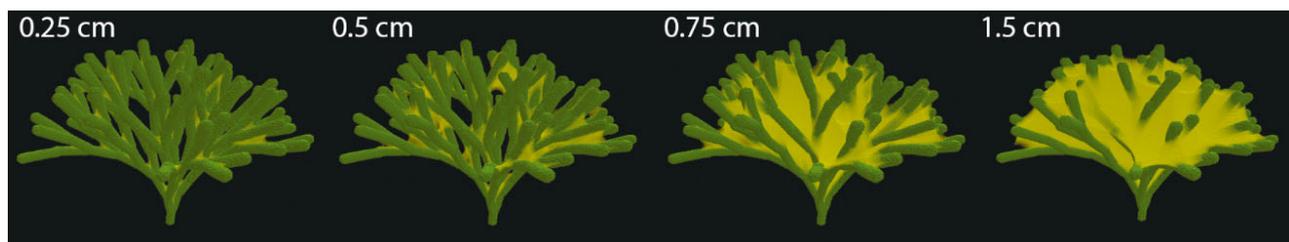


Fig. 5. Spherical space analysis applied to the *Codium fragile* spp. *fragile* model. Yellow regions: volumes which are inaccessible by an idealized spherical organism of a particular size

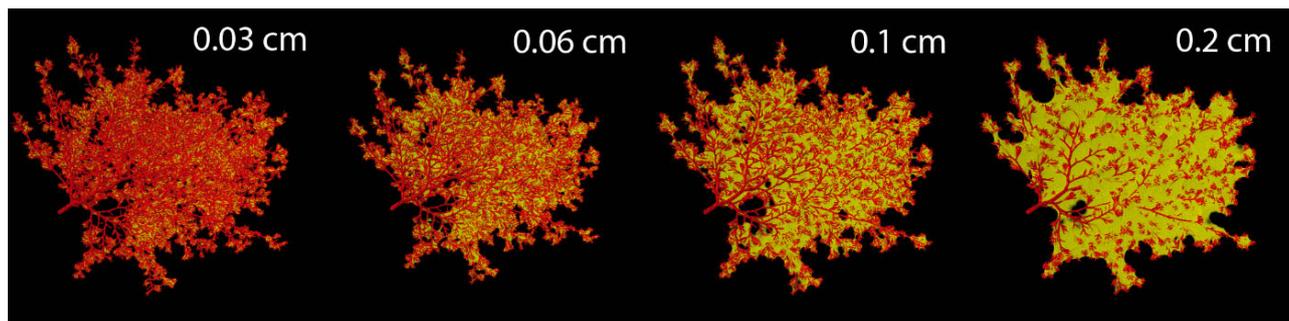


Fig. 6. Spherical space analysis applied to the *Dasysiphonia japonica* model

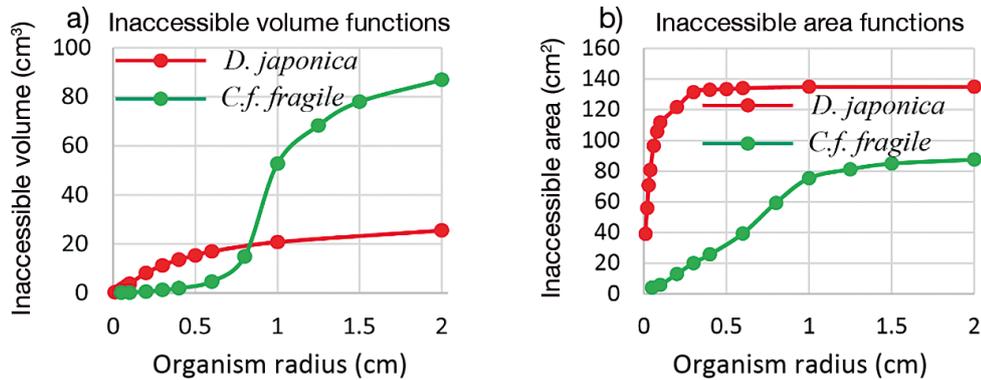


Fig. 7. Computed inaccessible (a) volume and (b) area functions for samples of *Dasysiphonia japonica* and *Codium fragile* spp. *fragile*

Islands, a cluster of islands 7 miles offshore)). *D. japonica* was collected at 5 sites (York, ME, Appledore [2 sites], White and Star Islands), and *S. latissima* was collected at 6 sites (York, ME, Appledore [2 sites], Lunging and White Islands [2 sites]). Meso-invertebrates were removed from the macroalgae by placing each alga in a freshwater bath for ~2 min as per Holmlund et al. (1990); all remaining individuals were picked off using tweezers under a dissecting scope. The water was then sieved using a 0.0125 cm sieve, and all meso-invertebrates were placed in a tube filled with ethanol and labeled. Sizes of *Mytilus edulis* and aggregated amphipods and caprellids associated to macroalgal individuals were determined. Sizes were weighted with respect to abundance of *M. edulis*, amphipods, and caprellids observed within each size class on macroalgal species.

3. RESULTS

Fig. 7 shows inaccessible volume and area functions for individual modeled specimens of *Codium fragile* spp. *fragile* and *Dasysiphonia japonica*, computed using the methods described. Fig. 8 shows inaccessible volume and area functions for *S. latissima*

sima, plotted on different axes because of the large difference in scale between this species and the other 2. As can be seen, the 3 species each have radically different distributions of inaccessible space according to size. In particular, *D. japonica* has significantly greater interstitial volume and area below a radius of 0.75 cm.

Weighted size class ranges of the 3 invertebrate taxa ranged from 0.33–0.39 cm for the macroalga size class range of 0–0.05 cm, 0.62–0.68 cm for the size class range of 0.05–1.0 cm, and 1.27–1.58 for the size class range >1.0 cm (Table 1). Percent abundance of each size class varied with macroalga species; 19.2, 20.5 and 60.3% of meso-invertebrates associated with *S. latissima* were found in 0–0.05, 0.05–1.0 and >1.0 cm classes respectively. Further, 51.8, 31.9 and 16.3% of meso-invertebrates associated with *C. f.* spp. *fragile* were found from the smallest to the largest size classes, and 60.7, 23.2 and 16.1% of meso-invertebrates associated with *D. japonica* were found from the smallest to the largest size classes.

But these comparisons are for single individuals of each species. Applying the methods described above to obtain results on a per-square-meter basis gives the results shown in Fig. 9 for inaccessible volume and inaccessible surface area. Simple inspection of these

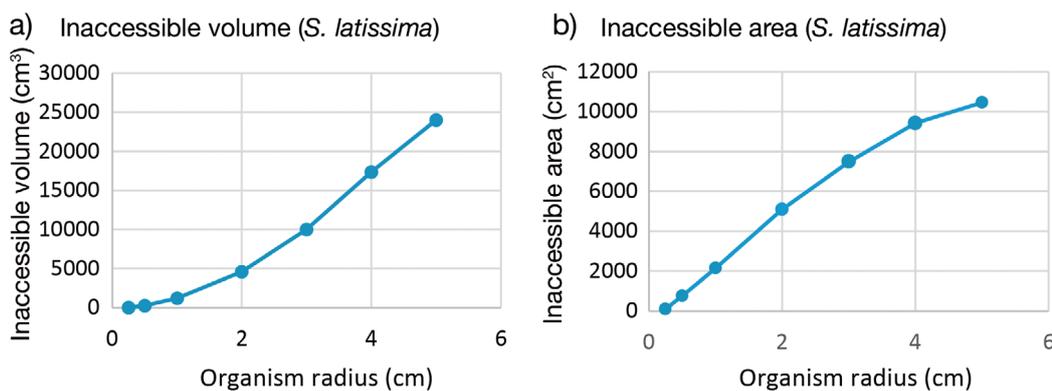


Fig. 8. Computed inaccessible (a) volume and (b) area function for a 50 cm³ quadrat of *Saccharina latissima*

Table 1. Weighted mean meso-invertebrate sizes and abundances estimated on a per-square-meter basis for the 3 macroalgal species

Species	Macroalga size class range					
	0.0–0.05 cm		0.05–0.1 cm		>0.1 cm	
	Mean size	Estimated abundance m ⁻²	Mean size	Estimated abundance m ⁻²	Mean size	Estimated abundance m ⁻²
<i>Dasysiphonia japonica</i>	0.033	45929.4	0.063	17566.0	0.126	12141.72
<i>Codium fragile</i> spp. <i>fragile</i>	0.039	4291.8	0.063	2641.8	0.135	1352.9
<i>Saccharina latissima</i>	0.034	98.4	0.068	105.44	0.158	309.60

functions shows *D. japonica* is striking in that it has far greater areas and volumes for organisms having a radius of 0.75 cm and less. There are also interesting crossover points in terms of inaccessible volume that may predict preferences for organisms of particular sizes.

There is also an obvious limitation to the fact that we only modeled a single individual of each macroalgal species. To somewhat mitigate this, we generated variants on each using what we felt to be reasonable parameter changes. In the case of *C. f. spp. fragile*, we increased the branching depth from 7 to 8, which, because it is a binary branching structure, roughly doubles the number of limbs. In the case of *D. japonica*, we constructed a sparser version by randomly dropping 40% of the limbs at each branch point, reducing the branching depth and increasing the limb length. This produced a plausible scrawny alternative. In the case of *S. latissima*, we increased the number of blades in the quadrat from 8 to 13. The alternative curves that were generated in this way are shown as dashed lines in Fig. 9.

To obtain an estimated abundance of meso-invertebrates per square meter for the 3 macroalgae modeled here, we also re-analyzed meso-invertebrate abundance per individual of each species of macroalga from Dijkstra et al. (2017) and similarly scaled these values to achieve counts on a per-square-meter basis. We did this for 3 size ranges and the results are

given in Table 1. This shows the weighed mean sizes and estimated abundances per square meter for the 3 macroalgal species. As can be seen there were orders of magnitude in difference in abundance between the 3 species for the smaller size ranges. Note that even though we excluded the holdfasts (because we did not model them), the large differences in meso-invertebrate abundance would remain even if we had included them.

We calculated refuge habitat volume and areas for the mean prey sizes in each size category assuming a predator (head) sizes of 1.0 and 0.5 cm diameter, representing small fish, and a prey sizes of 0.1 and 0.05 cm (note that body width or diameter is more relevant than length in terms of how well a predator can access a prey individual). Using these values in the calculation (Eqs. 1 & 2) for both of the 2 models of each macroalgal species results in 8 estimates of refuge volume and area for each species.

The results showing the relationship between invertebrate counts and both volume and area of refuge are shown in Fig. 10. This shows that *D. japonica* harbors much greater abundance, consistent with the greater volume of small inaccessible spaces and areas. The comparison between *C. f. spp. fragile* and *S. latissima* is more nuanced. There is considerable overlap between the volume of refuge for the sizes we tested, but *C. f. spp. fragile* may provide a greater area of refuge.

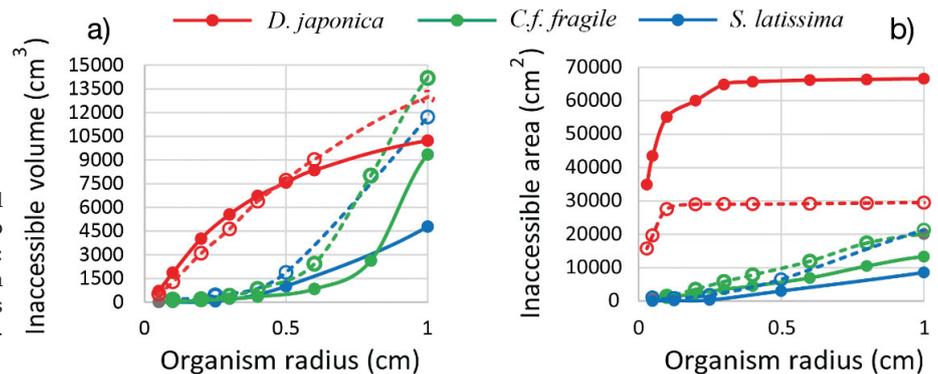


Fig. 9. Inaccessible (a) volume and (b) area functions generalized to 1 m² of seafloor. Colored curves: derived from models based on field measurements. Grey curves of similar shapes are based on constructed variants

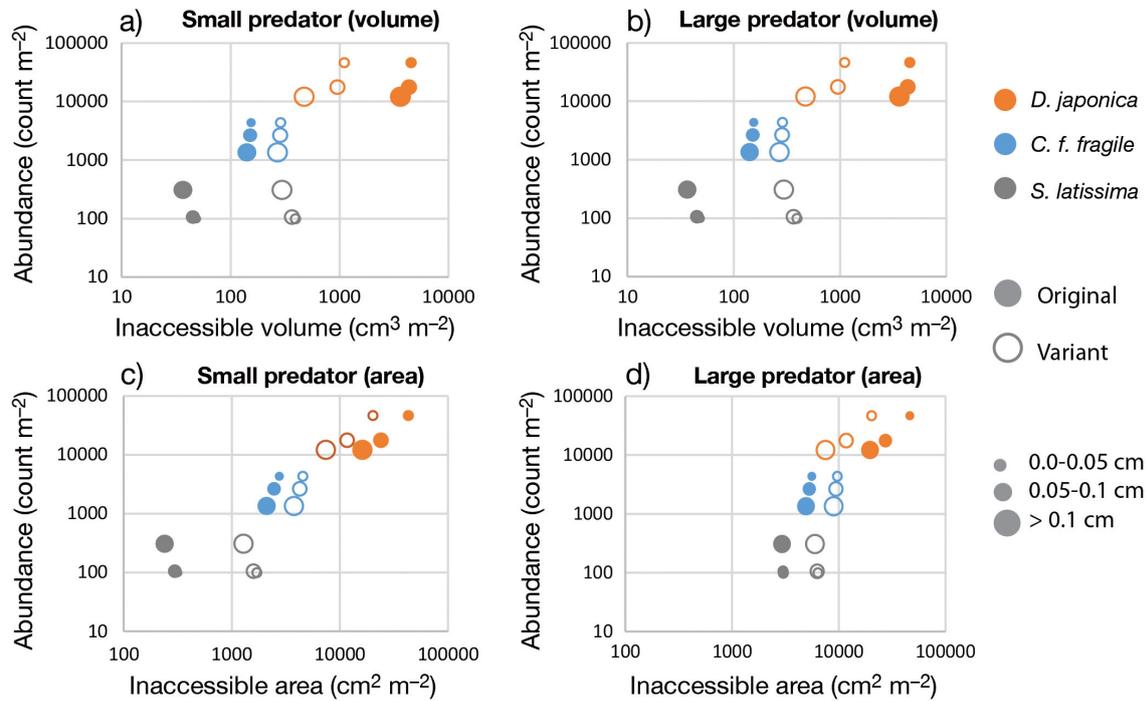


Fig. 10. Estimated abundance in terms of meso-invertebrates per square meter related to the estimated (a,b) refuge volume and (c,d) refuge area for 1 m² of seafloor covered by each of the 3 macroalgal species. Two predator and 3 prey sizes were used to generate the points. Open circles are based on modeled macroalgal variants

4. DISCUSSION

Temperate reef systems around the globe are experiencing dramatic shifts in species composition in which kelp beds are receding, and short filamentous and tufted forms of macroalgae are rising (Connell & Irving 2008, Dijkstra et al. 2017, Rindi et al. 2017). This study provides a novel concept to evaluate how this shift may affect ecosystem function. Spherical space analysis describes 2 ecologically important functional traits, inaccessible volume and area, at the individual and habitat level. It provides a way of describing the 'habitable spaces' in 3D for small organisms such as meso-invertebrates, and can be used to predict predator–prey interactions in the face of shifting foundation species.

Our model of varying sizes and branch lengths of macroalgae indicate that filamentous forms of macroalgae have more volume and area of refuge for meso-invertebrates than forms with larger thicker branches, or blades. The differences are most pronounced for organism sizes of less than 1.0 cm in diameter, where *Dasysiphonia japonica* has many times the inaccessible volume compared to *Codium fragile* spp. *fragile* and *Saccharina latissima*. The habitable volume and inaccessible volume of *S. latissima* continues to increase well above 4 cm, sug-

gesting that this species can provide a better refuge for small fishes (<2.0 cm body diameter) from larger fishes. This difference appears to be robust in that it is equally pronounced in the model variants we constructed as well as the original models that were based on direct measurements of macroalgae. Spherical space analysis shows that for larger organisms (~1 cm body diameter) the differences in inaccessible volume and area between the 3 species is much less. It is likely that this relationship will hold true for many filamentous forms, particularly the tufted forms (Connell et al. 2014, Benedetti-Cecchi et al. 2015) of macroalgae, as volumes of smaller spaces between thallus branches increase faster with distance from the holdfast than the volume of larger spaces. For example, if the length of thalli decreases and the pattern of the branching structure becomes more intricate, then there is a larger volume of smaller spaces and a smaller volume of larger spaces. The filamentous forms of macroalgae have a larger volume of smaller spaces that appear to harbor greater numbers of individuals that are smaller in size than those associated with blade forms, as shown in this study.

Spherical space analysis is motivated by the concept of ecological affordances (Gibson 1979), in this case the affordances offered in the form of refuge

from predators. By definition, a refuge necessarily involves both an organism and a potential predator. It is the difference between the volume that is accessible by one organism, but inaccessible by another, that is a critical component of predator–prey interactions. Our model suggests that a kelp bed has an enormous accessible volume for meso-invertebrates, but it is also mostly accessible by various sized fishes, whereas a bed of *D. japonica* has a much smaller accessible volume for meso-invertebrates, but is even more limited in terms of accessibility by small fish.

Predation of small fishes on meso-invertebrates will be less frequent in a habitat dominated by filamentous and turf-forming macroalgae than in branched (e.g. *C. f. spp. fragile* or *Fucus spp.*) or blade forms (e.g. *S. latissima*). This is particularly true for species such as gastropods, bivalves and some amphipods, whose mobility is limited (O'Brien et al. 2018). While morphological variations among heterospecific macroalgae will likely outweigh morphological variations within conspecifics (Dijkstra et al. 2017), our model suggests the density of thalli in filamentous and branched forms will moderately affect the volume of refuge and predator–prey interactions. In contrast, the density of blades in kelp beds will greatly increase the volume of refuge, as our model predicted a positive relationship between refuge volume/area and blade number. This is particularly true for sizes >1 cm, suggesting that greater density of kelp not only provides more refuge for species that occur at the base of the food web, but also for upper trophic-level species such as juvenile fishes.

The central simplifying assumptions of spherical space analysis are that organisms are spherical and that the plants are rigid. Clearly the rigidity assumption is violated for macroalgae. Nevertheless, spaces within macroalgae become substantially less accessible when the passageways between their thalli become smaller than an organism attempting to prey on meso-invertebrates contained within. The analysis in terms of spherical organisms also clearly does not match reality. Nevertheless, in most cases a small fish, amphipod or worm will likely be able to inhabit approximately the same volume, equating body radius to sphere radius. Spherical space analysis, despite its assumptions, is a metric that is 3D at the outset, a property missing from most previous measures. One metric that is similar (Bartholomew et al. 2000) considers only the average interstitial distance, not the distribution of spaces. Further, our model has been primarily concerned with the spatial architec-

ture of particular species of macroalga, each considered in isolation. But any particular region of benthic habitat will contain a diversity of macrophyte species. Given appropriate sampling methods and a set of parameterized macroalga models, it will be possible to estimate spherical space functions on a square meter basis for any distribution of macroalgae.

The methods we developed to carry out spherical space analysis involve developing 3D models of individual macroalgae and subjecting them to a computationally expensive process to construct inaccessible volume and area functions. However, spherical space analysis does not depend on the particular methods and algorithms described in this paper, nor does it depend on the use of computer graphic models. With a method for directly measuring the 3D structures of macroalgae in water, the results could be used as input to spherical space analysis. For example, a sample might be frozen, microtomed and imaged to generate a 3D voxel set. Alternatively, it should be possible to create functions which produce inaccessible volume and area curves directly from sampled properties of macroalgae. Such functions could be validated by the methods we have developed, and thereafter it would be only necessary to sample macroalgae to determine statistical branching properties (number of sub-branches for each branch, branching depth), branch lengths and diameters, and from these properties estimate inaccessible volume and area functions.

In recent years, kelp forests have declined and been replaced with turf or filamentous forms of macroalgae (e.g. Connell & Irving 2008, Dijkstra et al. 2017). As various kelp forests provide ecosystem services and goods valued >\$2M km⁻¹ yr⁻¹ (Vasquez et al. 2014, Bennett et al. 2016, Blamey & Bolton 2018), it is important to disentangle and identify differences in ecological processes in kelp and other morphological forms of macroalgae. This is particularly critical for restoration efforts, as it will elucidate which morphological form and density of forms would preserve ecological functions that maintain the integrity of the community. Spherical space analysis can help to explicate this process, as it provides a mechanistic basis for the relationship between various forms of macroalgae, abundance and size of species that exist at the base of the food web, and predator–prey interactions. Though more research is needed for an evaluation of the power of inaccessible space to account for variation in epifauna at the community level, this tool can help to predict the retention or release of ecosystem services caused by a change in foundation species.

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LITERATURE CITED

- Allen MT, Pruisinkiewicz P, DeJong TM (2005) Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-Peach model. *New Phytol* 166:869–880
- Angelini C, Altieri A, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience* 61:782–789
- Asner GP, Hughes RF, Vitousek PM, Knapp DE and others (2008) Invasive plants transform the three-dimensional structure of rain forests. *Proc Natl Acad Sci USA* 105:4519–4523
- Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23:114–121
- Bartholomew A, Diaz RJ, Cicchetti G (2000) New dimensionless indices of structure habitat complexity: predicted and actual effects on a predator's foraging success. *Mar Ecol Prog Ser* 206:45–58
- Benedetti-Cecchi L, Tamburello L, Maggi E, Bulleri F (2015) Experimental perturbations modify the performance of early warning indicators of regime shift. *Curr Biol* 25:1867–1872
- Bennett S, Wernberg T, Connell S, Hobday A, Johnson C, Poloczanska E (2016) The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. *Mar Freshw Res* 67:47–56
- Bertness MD, Crain CM, Silliman BR, Bazterrica MC, Reyna VM, Hildago F, Farina JK (2006) The community structure of western Atlantic Patagonian rocky shores. *Ecol Monogr* 76:439–460
- Blamey L, Bolton J (2018) The economic value of South African kelp forests and temperate reefs: past, present and future. *J Mar Syst* 188:172–181
- Bradbury RH, Reihelt RE (1983) Fractal dimension of a coral reef at ecological scales. *Mar Ecol Prog Ser* 10:169–171
- Cadotte M, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087
- Carlisle DM, Hawkins CP (1998) Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. *J N Am Benthol Soc* 17:286–300
- Carr MH (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320–1333
- Connell SD, Irving AD (2008) Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *J Biogeogr* 35:1608–1621
- Connell SD, Foster MS, Airoidi L (2014) What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser* 495:299–307
- Coull BC, Wells JBJ (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* 64:1599–1609
- Cyr H, Downing JA (1988) Empirical relationships of phyto-macrofaunal abundance to plant biomass and macrophyte bed characteristics. *Can J Fish Aquat Sci* 45:976–984
- de la Riva E, Lloret F, Perez-Ramos I, Maranon T, Saura-Mas S, Diaz-Delgado R, Villar R (2017) The importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events. *J Plant Ecol* 10:281–293
- Diaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci USA* 104:20684–20689
- Dibble ED, Thomaz SM (2009) Use of fractal dimension to assess habitat complexity and its influence on dominant invertebrates inhabiting tropical and temperate macrophytes. *J Freshwat Ecol* 24:93–102
- Dijkstra JA, Harris LG, Mello K, Litterer A, Wells C, Ware C (2017) Invasive seaweeds transform habitat structure and increase biodiversity of associated species. *J Ecol* 105:1668–1678
- Dornbusch T, Werneck P, Diepenbrock W (2007) A method to extract morphological traits of plant organs from 3D point clouds as a database for an architectural plant model. *Ecol Modell* 200:119–129
- Fourcaud T, Zhang X, Stokes A, Lambers H, Körner C (2008) Plant growth modelling and applications: the increasing importance of plant architecture in growth models. *Ann Bot* 101:1053–1063
- Fournier C, Andrieu B (1998) A 3D architectural and process-based model of maize development. *Ann Bot* 81:233–250
- Gibson J (1979) *The ecological approach to visual perception*. Houghton Mifflin, Boston, MA
- Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004
- Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71:2269–2285
- Harris LG, Tyrrell MC (2001) Changing community states in the Gulf of Maine: synergisms between invaders, overfishing and climate change. *Biol Invasions* 3:9–21
- Heck KL Jr, Crowder LB (1991) Habitat structure and predator-prey interactions in vegetated aquatic ecosystems. In: Bell SS, McCoy ED, Mushinsky ER (eds) *Habitat structure of objects in space*. Chapman & Hall, London, p 281–299
- Holmlund MB, Peterson CH, Hay ME (1990) Does algal morphology affect amphipod susceptibility to fish predation? *J Exp Mar Biol Ecol* 139:65–83
- Hooper DU, Chapin FSI, Ewel JJ, Hector A and others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- James PL, Heck KL Jr (1994) The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *J Exp Mar Biol Ecol* 176:187–200
- Lazzari MA, Stone BZ (2006) Use of submerged aquatic vegetation as habitat by young-of-the-year epibenthic fishes in shallow Maine nearshore waters. *Estuar Coast Shelf Sci* 69:591–606
- O'Brien BS, Mello K, Litterer A, Dijkstra JA (2018) Seaweed structure shapes trophic interactions: a case study using a mid-trophic level fish species. *J Exp Mar Biol Ecol* 506:1–8

- Phattaralerphong J, Sinoquet H (2005) A method for 3D reconstruction of tree crown volume from photographs: assessment with 3D-digitized plants. *Tree Physiol* 25: 1229–1242
- Prusinkiewicz PA, Lindemayer A, Hanan J (1988) Development models of herbaceous plants for computer imagery purposes. *ACM SIGGRAPH Comput Graph* 22: 141–150
- Ramsay-Newton C, Drouin A, Hughes AR, Bracken MES (2017) Species, community, and ecosystem-level responses following invasion of the red alga, *Dasysiphonia japonica*, to the western North Atlantic Ocean. *Biol Invasions* 19:537–547
- Rindi L, Dal Bello M, Dai L, Gore J, Benedetti-Cecchi L (2017) Direct observation of increasing recovery length before collapse of a marine benthic ecosystem. *Nat Ecol Evol* 1:0153
- Room P, Hanan J, Prusinkiewicz P (1996) Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. *Trends Plant Sci* 1:33–38
- Severns PM, Warren AD (2008) Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. *Anim Conserv* 11:476–483
- Steneck RS, Leland A, McNaught DC, Vavrinc J (2013) Ecosystem flips and feedbacks: the lasting effects of fisheries on Maine's kelp forest ecosystem. *Bull Mar Sci* 89: 31–55
- Toscano BJ, Griffen BD (2013) Predator size interacts with habitat structure to determine the allometric scaling of the functional response. *Oikos* 122:454–462
- Vasquez J, Zuniga S, Tala F, Piaget N, Rodriguez D, Vega J (2014) Economic value of kelp forests in northern Chile: values of goods and services of the ecosystem. *J Appl Phycol* 26:1081–1088
- Warfe DM, Barmuta LA (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171–178
- Warfe DM, Barmuta LA, Wotherspoon S (2008) Quantifying habitat structure: surface convolution and living space for species in complex environments. *Oikos* 117:1764–1773
- Wernberg T, Bennett S, Babcock RC, De Bettignies T and others (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353:169–172
- Wahle RA, Steneck RS (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *J Exp Mar Biol Ecol* 157:91–114
- Wonham MJ, O'Connor M, Harley CDG (2005) Positive effects of a dominant invader on introduced and native mudflat species. *Mar Ecol Prog Ser* 289:109–116

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