Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects

Katell Guizien, Marco Ghisalberti

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Katell GUIZIEN

Sorbonne Universités, CNRS, UPMC Univ Paris 06, Laboratoire d'Ecogéochimie des Environnements Benthiques (LECOB), Observatoire Océanologique, F-66650, Banyuls/Mer, France
e-mail : guizien@obs-banyuls.fr

Marco GHISALBERTI

Department of Infrastructure Engineering, University of Melbourne, Parkville, Melbourne, Victoria 3010, Australia

School of Civil, Environmental and Mining Engineering, University of Western Australia, Perth, WA 6009, Australia

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Abstract

Long-lived hard and soft coral species that are able to develop dense patches with a complex, three-dimensional structure form an animal forest canopy, similar to trees in terrestrial systems. Aside from the shelter provided by this canopy to other organisms, the animal forest can significantly modify the local physical and biogeochemical environment.

In the first part of this chapter, the modification of benthic boundary layer hydrodynamics in and above canopies is described, with a focus on the impacts of canopy density and flexibility. In the second part of this chapter, the structure of diffusive and advective mass transfer in canopies will be presented and discussed in relation to the biogeochemical transformations observed in animal forest canopies. Ongoing challenges in the conceptualisation of physical and biogeochemical processes in animal forest canopies are also exposed. In the third part of this chapter, we review the factors that form the basis of a mechanistic explanation of the development of micro-niches, which explain the large diversity hosted in animal forest canopies.

Keywords : Benthic boundary layer, flow instability, drag, micro-niche, spatial heterogeneity, gradients, filaments, biotic-abiotic interactions, ecosystem engineers

1. Introduction

The concept of the ‘marine animal forest’ was initially introduced based on aesthetic similarities between trees and large erect colonial animal communities (e.g. corals, Bruno and Bertness, 2001) that cover some marine substrates (see Figure 1, as well as Gutt et al. in this book). Similarly to terrestrial forests, marine animal forests form a sheltered habitat by reducing the foraging efficiency of consumers (Bartholomew 2000; Beukers and Jones 1997) and providing refuge for motile species like fishes or vagile invertebrates (Ross and Quattrini 2007). The similarities between marine and terrestrial forests extend beyond the provision of shelter, however, and include the manner in which these systems modify the local physical and biogeochemical environment. Despite differences in spatial scale and the properties (density, viscosity, heat capacity) of the fluid to which they are exposed, steady flows over atmospheric (O(10-100 m)) and aquatic canopies (O(0.1-1 m)) display a common characteristic flow structure, as detailed in Section 2. Because of such similarities, we use the terms ‘forest’ and ‘canopy’ interchangeably here.

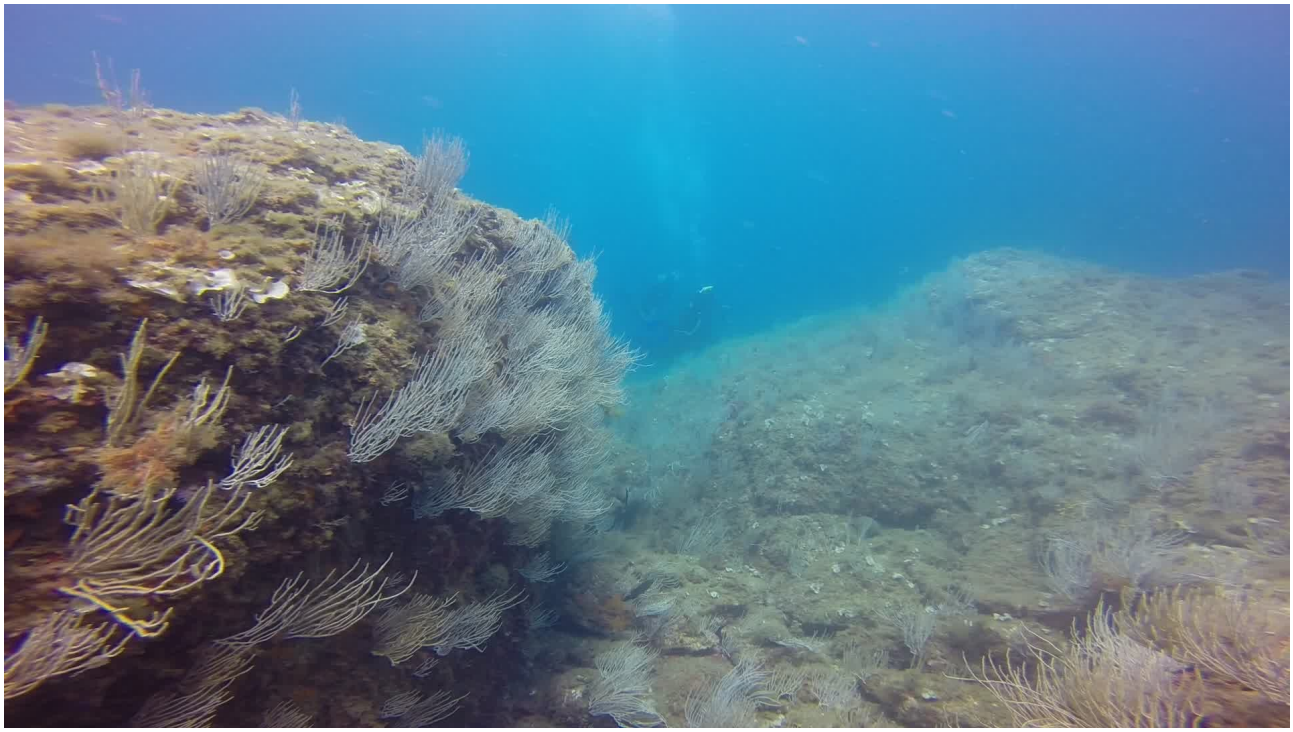


Figure 1: The white gorgonian, *Eunicella singularis*, covering a boulder at 15 meters depth in Cap L'Abeille (Réserve Naturelle Marine de Cerbère-Banyuls, NW Mediterranean sea, Photograph by Katell Guizien).

Organisms forming canopies are typically considered ‘ecosystem engineers’, a term which refers to organisms that, through causing changes in the local physical or biogeochemical conditions, directly or indirectly control the availability of resources (other than themselves) to other organisms and thus, modify, maintain or create habitats (Lawton, 1994). Autogenic engineers modify their environment through physical changes, while allogenic engineers do so through chemical transformations (Jones et al. 1997). Six factors have been identified by Jones et al. (1997) as defining the scale of impact of an ecosystem engineer: (1) the lifetime activity of individual organisms, (2) the population density and size, (3) the spatial distribution of the population, both at the local and regional level, (4) the length of time a population has been present at a site, (5) the durability of constructs, artifacts and impacts in the absence of the original engineer, and (6) the number and types of resource flows that are modulated by the constructs and artifacts, and the number of other species dependent upon these flows. On the basis of these factors, trees have

always been considered the paradigmatic example of ecosystem engineers in terrestrial habitats (Holling 1992).

Marine animal forests have been shown to act as autogenic ecosystem engineers in marine systems through the provision of habitat, colonization opportunities and increasing habitat complexity. For corals, these effects are well-established in shallow tropical environments, but also recognized in temperate (Scinto et al. 2009 ; Cerrano et al. 2010) and deep-water environments (Cordes et al. 2008; Freiwald and Roberts 2005). Animal forests also act as autogenic ecosystem engineers through modification of the mean and turbulent flow structure. The lower levels of turbulence inside the canopy increase sedimentation (Luckenbach 1986), causing the retention of propagules and enhancing larval settlement (Eckman 1985; Smith and Witman 1999; Bruno 2000). At the top of the canopy, the enhanced turbulence generated by the large canopy roughness augments the delivery of food and critical metabolites by reducing the thickness of the diffusive boundary layer on organism surfaces (Dennison and Barnes 1988; Thisle and Eckman 1990; Shashar et al. 1996). Flow modification by marine forests encompasses a wide range of processes on a range of spatial scales (reviewed for coral reefs by Monismith 2007) and it is now clear that the hydrodynamics of marine forests demonstrate strong similarities, regardless of whether the forest is comprised of plants (e.g. kelp forests or seagrass meadows, Eckman et al. 1989; Duarte 2000) or animals. This flow modification likely leads to the creation of highly dynamic micro-environments, which ultimately select those organisms able to feed, grow and reproduce within the marine forest.

Animal marine forests can also act as allogenic ecosystem engineers, although in the opposite manner to vegetation canopies. Indeed, marine forests of autotrophic primary producers are expected to be carbon sinks (like their terrestrial counterparts) through atmospheric carbon fixation by photosynthesis (Goreau 1992). In contrast, marine forests of heterotrophic consumers (except corals living in symbiosis with autotrophic algae) release inorganic carbon during organic matter assimilation in respiration. Nevertheless, the allogenic impact of the 'wall of mouths' of marine animal forests is expected to significantly alter the local biogeochemical conditions near the sea floor (Fabricius and Metzner 2004).

The objective of this chapter is to review the state-of-the-art understanding of the hydrodynamics and biogeochemistry of marine animal forests and their impact on living conditions inside the animal forest.

2. The hydrodynamics inside and above the marine animal forest

Marine animal forests can be found in both shallow and deep environments, exposing them to a range of hydrodynamic conditions in terms of the magnitude and steadiness of the flow. At the marine forest scale, steady flows include those generated by wind, buoyancy or tides, with surface waves (seas and swell) generating an unsteady flow. Flow in the oceanic bottom boundary layer is therefore often decomposed into a quasi-steady unidirectional component (the current) and a series of periodic components (waves). This decomposition is of utmost importance when considering the hydrodynamics inside and above the marine animal forest, as the bottom boundary layers associated with steady and unsteady flows differ greatly in their size and structure.

Structure of the turbulent boundary layer over flat beds in steady flows

The bottom boundary layer is the region where the flow velocity is impacted by the bed and where flows dissipate their energy into heat by viscous friction to reach a zero velocity at the bottom. Under unidirectional steady flows, the thickness (δ) of a turbulent boundary layer decreases with flow energy and is roughly given by $\delta \approx 6000\nu/u_*$ (Wilcox 1992) where ν is the kinematic viscosity and u_* the bottom friction velocity(defined as the square root of the bed shear stress divided by fluid density). This yields a typical value of $\delta \sim O$(m) for $u_* \sim O$(cm/s). The flow in a steady turbulent boundary layer exhibits a well-known vertical structure, with three distinct regions (Wilcox 1992): (1) the viscous sublayer nearest the bed, where the velocity is low and viscous forces dominate inertial forces, (2) the logarithmic (or inertial) layer, where viscous forces are progressively overwhelmed by inertial forces, and (3) the outer layer, where the flow velocities are greatest, and exceed the bottom friction velocity by at least an order of magnitude. (Figure 2A). The viscous sublayer and logarithmic layer form the inner part of the boundary layer, where the flow velocity scales on the bottom friction velocity. In the viscous sublayer, velocity increases linearly with distance from the bed up to $z_\nu \approx 30\ \nu/u_*$. In the logarithmic layer (of O(10 cm) in height for the typical flow considered above), the velocity increases logarithmically with distance from the bed according to the 'law of the wall' (Figure 2A). Over a rough bed, the viscous sublayer can vanish between roughness elements (Figure 2B). This is seen when $u_*k/\nu > 70$ (Sleath 1984), where k is the average height of the roughness elements ($k \approx 30\ z_0$, Nikuradse 1933) , and the law of the wall can be expressed as :

$$U(z) = u_*/\kappa \ln [z/z_0] \quad \text{for } k_N < z < z_{Log}=600\ \nu/u_* \qquad (1)$$

where $\kappa = 0.41$ is the von Karman constant.

In the outerlayer, velocity do not have as a simple formulation as in the viscous and Log layers.

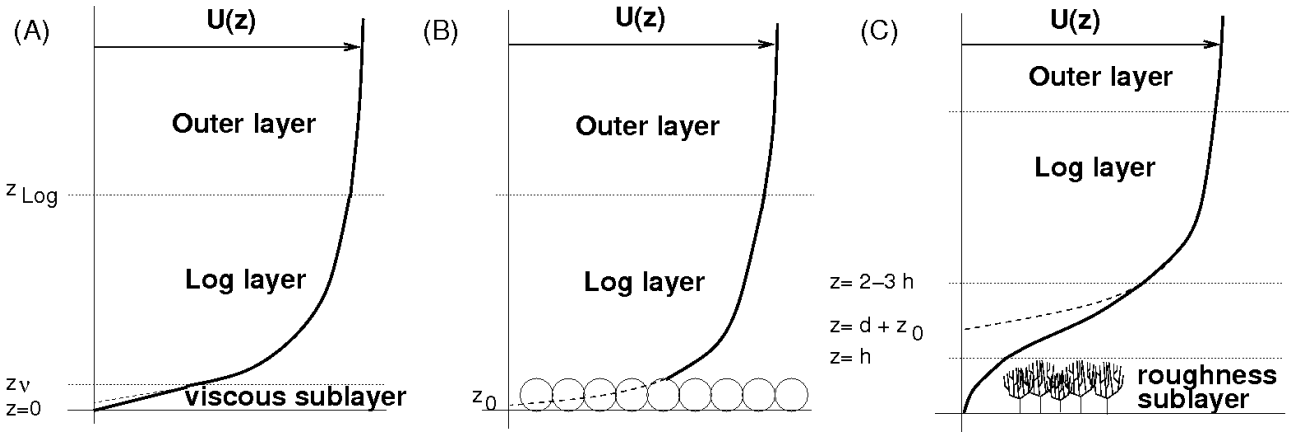


Figure 2: Schematic diagram of the vertical structure of the mean velocity in (A) a smooth-bottom boundary layer, (B) a rough-bottom boundary layer, and (C) a canopy boundary layer formed by obstacles of height *h*.

Structure of the turbulent boundary layer over large obstacles in steady flows: the canopy effect

When ocean beds are covered by large obstacles (i.e. a canopy) which extend into the theoretical logarithmic layer of the unobstructed flow, the classical boundary layer structure can be significantly modified when obstacles height is larger than 10 % of its drag length scale (see definition below, Nepf et al. 2007). This is typically the case in animal forests formed by erect organisms larger than a few centimeters. The wakes produced by these obstacles create strong spatial variations in the flow, over a region (embedded within the boundary layer) known as the roughness sublayer (RSL, Figure 2C). In an homogeneous canopy (of elements of height *h*), the RSL is estimated to extend to approximately 2-3*h* above the bed (MacDonald 2000). Above the RSL, where the flow is horizontally homogeneous, there is again a logarithmic dependence of velocity on height; the profile in (1) is shifted upwards by a displacement height, *d* (Raupach et al., 1980). Within the canopy (i.e. in the lower part of the roughness sublayer, below $z = h$), the vertical profile of horizontally-averaged flow velocity has been approximated by an exponential decay from its value at the top of the canopy (U_h) down to the bed (MacDonald 2000, Cheng and Castro 2002). The mean flow velocity, $U(z)$, inside and above animal forests is thus typically modelled as:

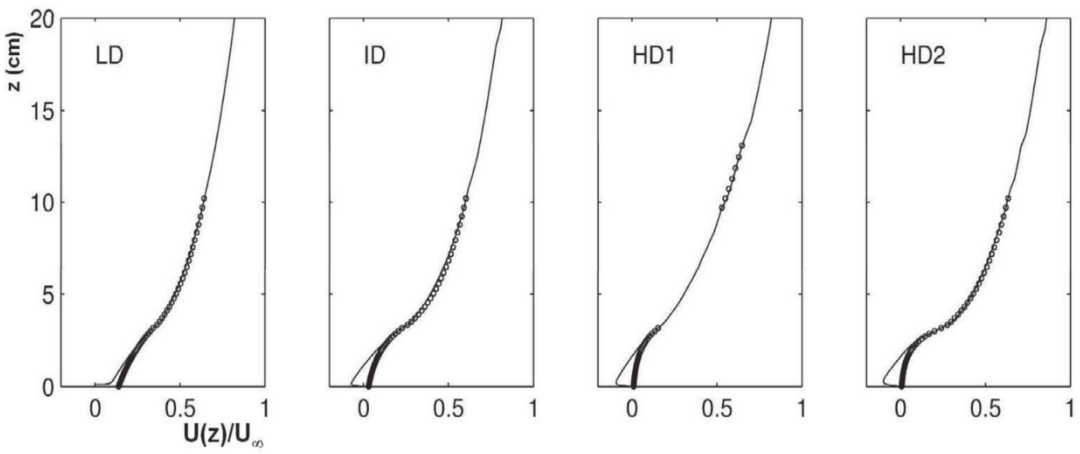
$$U(z) = u_*/\kappa \ln[(z-d)/z_0] \quad \text{for } z > 2\text{-}3h \quad (2)$$

$$= U_h \exp[\alpha(z/h - 1)] \quad \text{for } 0 < z < h \quad (3)$$

where z is the distance from the bottom, u_* is the friction velocity (which can be related to the flow velocity far above the canopy through a drag coefficient), α is the attenuation coefficient of velocity within the canopy (which increases with canopy density, MacDonald 2000) and z_0 is the canopy roughness length. Many attempts have been made to relate the displacement height and roughness length of vegetation canopies to the packing density of the obstacles as well as their arrangement & shape (e.g. Wooding et al. 1973). Similar studies are far less numerous for animal canopies, but similarly point out the difficulty in parameterizing drag and roughness in these systems (Rosman and Hench 2011). The mean velocity between the top of the canopy and the bottom of the logarithmic layer has not been fully described, but has been shown to contain characteristic features that engender strong similarities across the range of canopy flows (as discussed below).

The proposed exponential decay of horizontally-averaged velocity within the canopy (equation (3)) is in fact a crude approximation to the highly-spatially-variable flow that develops in dense canopies. Figure 3 displays the horizontally-averaged flow between two-dimensional fixed rippled topography and shows that a steady return flow appears near the bed as the spacing between ripples decreases. This renders an exponential fit inappropriate deep within the roughness. Moreover, simulations show that the flow inside the canopy depends not only on the roughness density but also on ripple (i.e. obstacle) shape.

A)



B)

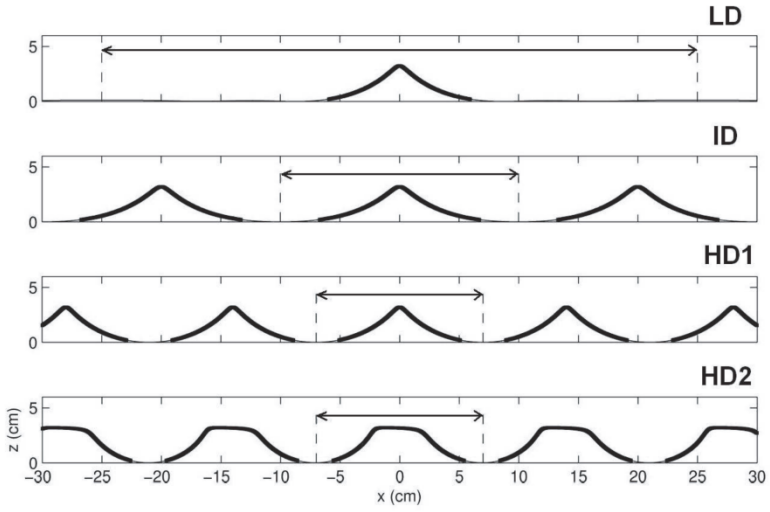


Figure 3: (A) Vertical profiles (solid lines) of the non-dimensional temporally- and horizontally-averaged longitudinal velocity ($U(z)/U_\infty$) for a steady flow of strength U_∞ above rippled beds with different densities. Fits for the logarithmic layer and for the exponential decay of velocity within the roughness are indicated by the circles; clearly, the exponential fit breaks down deep within the roughness (B) The varying densities and geometries of the rippled beds (LD = low density, ID = intermediate density, HD = high density, from Moulin et al., 2007, with kind permission of EDP Sciences).

Inherent similarities of canopy steady flows

A key feature of the mean velocity profile in canopy flows is the characteristic inflection point (i.e. a point of maximum velocity gradient) that is generated at the top of the canopy, the interface between the low speed in-canopy flow and high speed above-canopy flow. This inflection point yields the flow inherently unstable to Kelvin-Helmholtz-type vortices (Figure 4) that dominate the transport of mass and momentum across the top of the canopy (see, e.g., Ghisalberti and Nepf 2005, 2009).

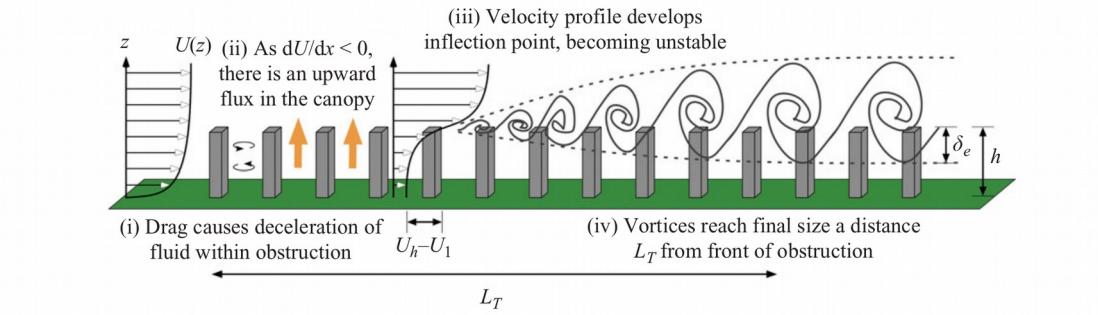


FIGURE 3. The evolution of flow along a submerged permeable medium. The distance required for full flow development L_T scales upon the drag length scale of the obstruction.

Figure 4: The streamwise evolution of steady canopy flow. The coherent vortices are a characteristic hydrodynamic feature of canopy flows (from Ghisalberti 2009, with kind permissions of Cambridge University Press).

Based on the dominance of these characteristic vortices, Ghisalberti (2009) demonstrated strong similarities across a range of canopy-type flows (termed 'obstructed shear flows'), including atmospheric flows over forest canopies and aquatic flows over coral reefs and seagrass meadows. These similarities exist across a range of canopy scales (from *O*(mm) – *O*(10 m)) and provide predictive capability for the structure of the mean and turbulent flow in animal forests. For example, the thickness (δ_e) of the region within the canopy where the vortices drive rapid transport (Figure 4) is shown to scale inversely with canopy density (given here as the canopy frontal area per unit volume, *a*), according to:

$$\delta_e = 1/3\ (C_D\ a)^{-1} \qquad (4)$$

where C_D is the drag coefficient of the obstacles in the canopy. $(C_D\ a)^{-1}$ is termed the canopy drag length scale. Similarly, the intensity of vertical turbulent fluctuations (w_{rms}) at the top of the canopy is directly related to the friction velocity:

$$w_{rms} = 1.1\ u_* \qquad (5)$$

Canopy drag coefficients (as employed in (3)) are not typically known with a high degree of accuracy. Drag coefficients for certain (isolated) geometric shapes are well known, and simplifications have been made using morphological approximations. Vogel (1994) reports drag

coefficients of 0.74 for a rectangular solid, 0.76 for an erect cylinder and 0.32 for a hemisphere. Such approximations may prove useful for some organisms in animal forests (e.g. hemisphere-like stony corals, Hench and Rosman 2013) but, in general, canopies present the additional complexities of (a) significant morphological complexity, including variation over height and (b) organisms potentially existing in the wake of upstream elements, which can greatly affect the drag coefficient. Drag estimation becomes complicated further when animal forests are comprised of organisms with a range of ages, and hence a range of sizes and shapes, as is frequently observed in highly diversified tropical environments. Thus, quantification of canopy drag coefficients has remained elusive. Values of canopy drag coefficients ranging from 0.01 (Reidenbach et al. 2006) to 0.8 (MacDonald et al. 2006) have been estimated from flow measurements over coral reefs while values used in reef flow modelling ranged from 0.02 to 0.1 (Rosman and Hench 2011).

Variation of a steady flow with canopy density

Qualitatively, three regimes of flow within and immediately above animal forests have been identified. These regimes are distinguished by the packing density of the forest, and are schematized in two dimensions in Figure 5 (adapted from Vogel 1994). At low density, each individual in the forest is not in the wake of the closest upstream individual, and the forest impacts the mean velocity profile only in the vicinity of the individual canopy elements. Both the displacement height and roughness length remain small in this regime. As packing density increases, organism wakes begin to interact, such that individual wakes can no longer be identified. The in-canopy flow becomes strongly three-dimensional and local velocities depend strongly on the precise arrangement of organisms. The apparent roughness increases in this regime, but the displacement height remains small. As packing density increases further, forest drag produces a sufficiently strong blockage that a ‘skimming’ flow (where the strength of the in-canopy flow is minimized) occurs above the canopy. This corresponds to a decrease in the roughness length together with a rapid increase in the displacement height. Density thresholds delineating these three flow regimes in real canopies depend on the size of the wake that develops behind each organism, thus varying with organism size and shape as well as flow speed. In the case of atmospheric flows over vegetation canopies, the onset of skimming flows occurs for frontal area density (i.e. the canopy frontal area per unit bed area) larger than 0.2 (MacDonald 2000).

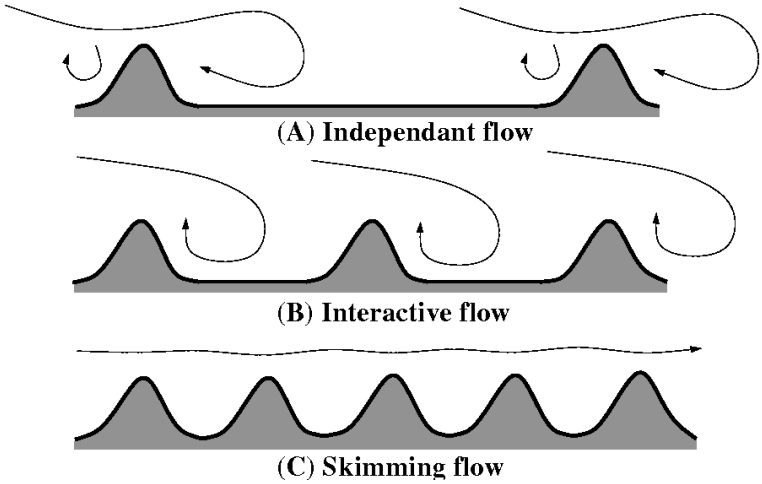


Figure 5: Three typologies of flow modification in the vicinity of obstacles for increasing packing density (adapted from Vogel 1994).

Variation of a steady flow with canopy flexibility

A significant complication in predicting the flow structure in animal forest canopies arises when dealing with flexible organisms like soft-corals (Ghisalberti and Nepf 2006). It has been seen that, eve in steady flows, flexible canopies exhibit a coherent, large-amplitude waving (Ghisalberti and Nepf 2002, Ghisalberti and Nepf 2004, termed the *monami* in vegetation canopies (Ackerman and Okubo 1993). The generation mechanism of the *monami*, although still under debate (Singh et al. 2015), has been explained by the passage of the vortices at the top of the canopy, which create strong sweeping motions as they pass (Ghisalberti and Nepf 2006). This coherent waving of flexible canopies significantly modifies the structure of the mean and turbulent flow above and inside the canopy, increasing (relative to rigid canopies) mean velocities inside the canopy and reducing the friction velocity (Ghisalberti and Nepf 2009).

Structure of the benthic boundary layer in oscillatory flows

Marine animal forests are not exposed only to steady unidirectional flows (i.e. currents), but also to oscillatory flows driven by wind-waves (shorter periods) and swell waves (longer periods). A complete description of wave-driven flow requires two parameters: the amplitude of the orbital velocity, U_w, and the wave period, T. As in steady flow, a boundary layer forms near the bed, within which the wave orbital velocity decreases as the bed is approached.

In the absence of a canopy, boundary layers in oscillatory flow are considerably thinner than their unidirectional counterparts. While tidal boundary layers frequently extend over several meters, the boundary layer under a 10-second wave may extend over only a few centimeters. The thickness of a turbulent oscillatory boundary layer can be approximated by $\sqrt{\square_{\square}}$ $\sqrt{\nu_t T}$ where ν_t is the eddy viscosity (Nielsen 1992). With flow energy dissipated in such a thin layer, maximum bottom friction velocities are generally an order of magnitude larger in wave flows than in the corresponding unidirectional flow (Jonsson 1966). However, bottom friction velocities as all turbulent quantities within a wave boundary layer exhibit oscillatory variations at half the wave periodicity (Sleath 1987). As a consequence of these time variations, and in contrast with steady boundary layers in which turbulence intensity is fairly constant throughout fully developped boundary layers, time-averaged turbulence intensity decay inversely with distance to the bed within a wave boundary layer (Sleath 1987). However, when velocities are phase-averaged i.e. keeping track of the flow phase along the periodic flow outside the boundary layer, the law of the wall (velocity log decay and linear increase of mixing length) applies along a large part of the wave cycle (Jenssen et al. 1989). These experiments partly validated various quasi-steady modelling of wave boundary layer (e.g. Grant and Madsen 1979). However, describing with accuracy turbulent quantities within a turbulent oscillatory bounday layer, and particularly the phase lagging of turbulent quantities across it, motivated many more complex numerical modelling (reviewed by Fredsoe and Deigaard 1992, Guizien et al., 2003).

In the presence of a canopy, a wave boundary layer is considerably less affected than a steady flow boundary layer. The porous nature of the canopy, even at high densities, offers comparatively little resistance to pressure transmission within the canopy, and velocity reduction inside the canopy will be much smaller than in unidirectional flow (Lowe et al. 2005). No simple description exists for the vertical profile of orbital velocity inside a canopy under wave-driven flow, although Lowe et al. (2007) have developed a unique model for prediction of the overall velocity attenuation of canopies in oscillatory flows. The model is based on wave energy dissipation from two sources, friction at the top of the canopy and canopy element drag. Ultimately, however, its use relies on estimation of friction and drag coefficients.

Similarly to steady flows, vortex generation at the top of the canopy is also observed under oscillatory flows. This occurs when two key dimensionless parameters, namely the Reynolds number and Keulegan-Carpenter number (the ratio of the timescale of flow oscillation to that of

shear layer formation), exceed threshold values such that an unstable shear layer forms on each wave half-cycle (Ghisalberti and Schlosser 2013). This means that vortices are preferentially seen in long and energetic waves over dense canopies.

In summary, developing predictive capability for the structure of the mean and turbulent flow in real marine canopies remains challenging. Nevertheless, a qualitative classification of the effect of the canopy on flow velocity and mixing can be proposed for animal forests (Table 1).

	Low population density	High population density
Wave-dominated flow	No significant attenuation of flow within canopy, enhanced mixing in canopy due to unsteady wakes.	Moderate flow attenuation within canopy, greatly enhanced mixing at top of canopy
Current-dominated flow	Flow speed reduced within canopy, fairly uniform rates of mixing through the canopy.	Flow speed strongly reduced within canopy, strong turbulent mixing in upper region of canopy, with reduced mixing near the bed.

Table 1: Summary of the key aspects of flow modification by animal forests.

3. The biogeochemistry inside and above the canopy of the animal forest

From a biogeochemical perspective, the analogy between terrestrial forests and marine animal forests is not straightforward given their opposite trophic pathways: trees as autotrophs synthesize organic matter from inorganic nutrients, absorbing CO_2, while animals degrade organic matter into inorganic compounds, releasing CO_2 (N.B. the analogy works somewhat better with tropical corals whose symbiotic association with autotrophic algae put them in the category of semi-autotrophs). Despite their reversed trophic pathways, an analogy between trees and marine animal forests can be based on their life-span; long-lived biota, either autotrophs or heterotrophs, act as carbon-sinks through carbon sequestration (albeit temporarily) as long as they grow, and thus influence the global carbon cycle in a similar manner. Furthermore, an increasing density of aquatic canopies is likely to shift their role in global biogeochemical cycles from carbon sink to carbon source. While the reduced flow and low turbulence deep in dense aquatic canopies can promote burial of undegraded particulate organic matter due to hypoxic conditions (carbon sink), higher levels of turbulence within canopies of intermediate density can maintain an oxygen supply sufficient to enhance the degradation of sedimenting organic matter (carbon source). The role of marine animal forests in

global biogeochemical cycles is also linked to their stability and to the diversity they host. Biogeochemical conditions are essential drivers of the growth of large organisms and cell division in micro-organisms. Therefore, it is critical that we understand how the regulation of mass transfer inside and above canopies controls the uptake of biogeochemical compounds necessary for the development of organisms living in or forming canopies, in order to predict their resilience to disturbances (Holling 1973).

Bulk mass transfer rates across canopy boundaries

At the canopy scale, turbulent mixing regulates the exchange of dissolved and particulate species across the top of the canopy boundaries. Indeed, mass transfer across the top of the canopy is typically related by analogy to turbulent momentum transfer, which is governed by the interfacial hydrodynamics. Turbulent momentum transfer (indicated by u_*) between the in-canopy and above-canopy flows has been described through a momentum exchange velocity, U_E (Bentham and Britter 2003):

$$u_*^2 = U_E (U_{ref} - U_c) \quad (6)$$

where U_{ref} is the flow velocity at $z = 2.5h$ (i.e. near the bottom of the logarithmic layer) and U_c is the depth-averaged velocity inside the canopy.

By analogy, the rate of mass transfer (ϕ) of a dissolved compound across the top of the canopy is thought to be controlled by the same exchange velocity as momentum and expressed by :

$$\phi = U_E (C_c - C_{ref}) / Sc \quad (7)$$

(Moulin et al. 2007) where C_{ref} is the compound concentration at $z = 2.5h$ and C_c is the depth-averaged concentration inside the canopy. The compound is characterized by its Schmidt number (*Sc*), equal to the ratio of the kinematic viscosity of sea water (ν) to the diffusion coefficient of the compound in sea water (*D*). This characterisation of mass transfer can also be described in terms of the Stanton number (*St*), which represents the ratio of the mass transfer coefficient $\phi/(C_c - C_{ref})$ to fluid advection (U_{ref}):

$$St = \phi / [U_{ref} (C_c - C_{ref})] = U_E/(U_{ref}\, Sc), \quad (8)$$

and depends only on the mean flow structure (and a Schmidt number correction). Given its practical utility, formulations of the Stanton number as a function of canopy drag coefficient (as used by Bilger and Atkinson 1992) have been developed to avoid the necessity of explicitly measuring the in-canopy flow and mass transfer rate.

Uptake inside the canopy

For all the progress in understanding rates of mass transfer across canopy boundaries, downscaling bulk fluxes at the canopy scale to the micro-scale heterogeneity of concentration within the canopy remains a challenge. Within the canopy, transfer to organismal surfaces is expected to be regulated by molecular diffusion in the organism's diffusive boundary layer, which extends over a portion (approximately 10%) of the viscous sublayer. In canopies, the developed surface area where a diffusive boundary layer (DBL) can be present is considerably enhanced compared to uncovered beds and can reach 15 times the planar reef area (Dahl, 1973).

With the thickness of the DBL proportional to the viscous sublayer thickness, it decreases with the local Reynolds number around the organism and will vary between canopy elements based on the local flow speed and turbulence intensity. The lower the Reynolds number, the thicker the DBL. Hence, the DBL is likely thicker on the upstream face of organisms spacing is large than in the wake on the downstream face where turbulent detachment occurs and streamlines spacing is smaller (Figure 6, upper panel). Active motile cilia on the epidermis of an organism disrupt the viscous and diffusive boundary layers (Figure 6), increasing mass transport locally; up to a five-fold enhancement of mass transfer rates to organism surfaces has been observed due to vortical ciliary flows (Shapiro et al. 2014). Among cnidarians which often form animal forests, motile epidermal cilia are present in scleratinian corals (Yonge 1930), but absent in octocorals (Lewis 1982). It is worth noting that not all erected species rely on the physical disruption of the diffusive boundary layer to increase mass transfer; many are active filter-feeders that create biomixing (Riisgard and Larsen, this book).

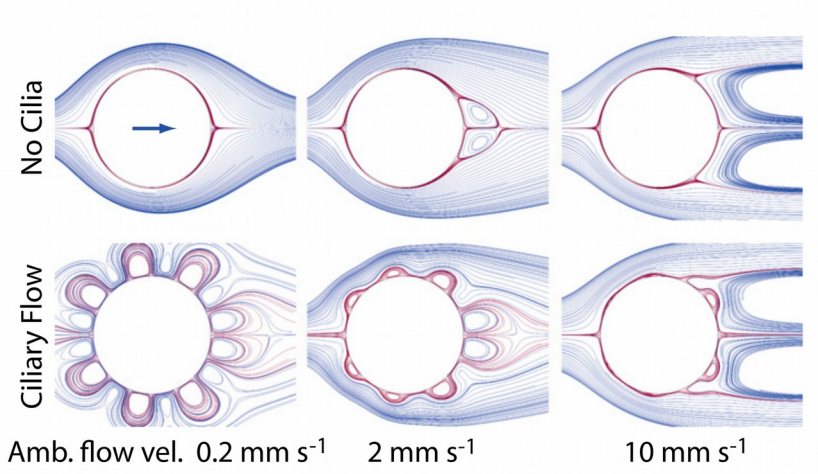


Figure 6: Streamlines (shown in blue) from numerical simulations of flow around a coral branch (diameter = 5 mm). Streamline spacing can be taken as proxy for DBL thickness: the greater the spacing, the thicker the DBL. Ciliary vortical flows (lower panel) significantly impact the flow topology and decrease the DBL thickness at low-to-moderate ambient flow velocities, relative to the no-cilia case (upper panel). The arrow marks the direction of the ambient flow. Streamlines shown in red are those passing within 50 μm of the branch (from Shapiro et al. 2014, with kind permission of PNAS Editions)..

In addition to the spatial heterogeneity of mass transfer inside the canopy, the canopy organisms contribute to strong concentration gradients through their consumption or production. Coral polyps (indicated by red dots in Figure 7A), where biogeochemical transformations take place through respiration, calcification, uptake and release of organic and inorganic forms of phosphorous and nitrogen, form a complex three-dimensional distribution of concentration (Figure 7B).

Mapping the micro-scale physical and chemical environment that organisms experience requires high-resolution, 3D measurements of both flow and concentration. The current capacity is limited to simultaneous 2D visualization of flow and concentration through a combination of Particle Image Velocimetry (PIV) and Particle Laser Induced Fluorescence (PLIF, e.g. Koehl and Reidenbach 2007, Figure 7B). Significant advances should be sought to improve the 3D mapping of flow and concentration, which may come from medical (Positron Emission Tomography) or material science (Raman spectrometry, Du et al. 2015) technologies.

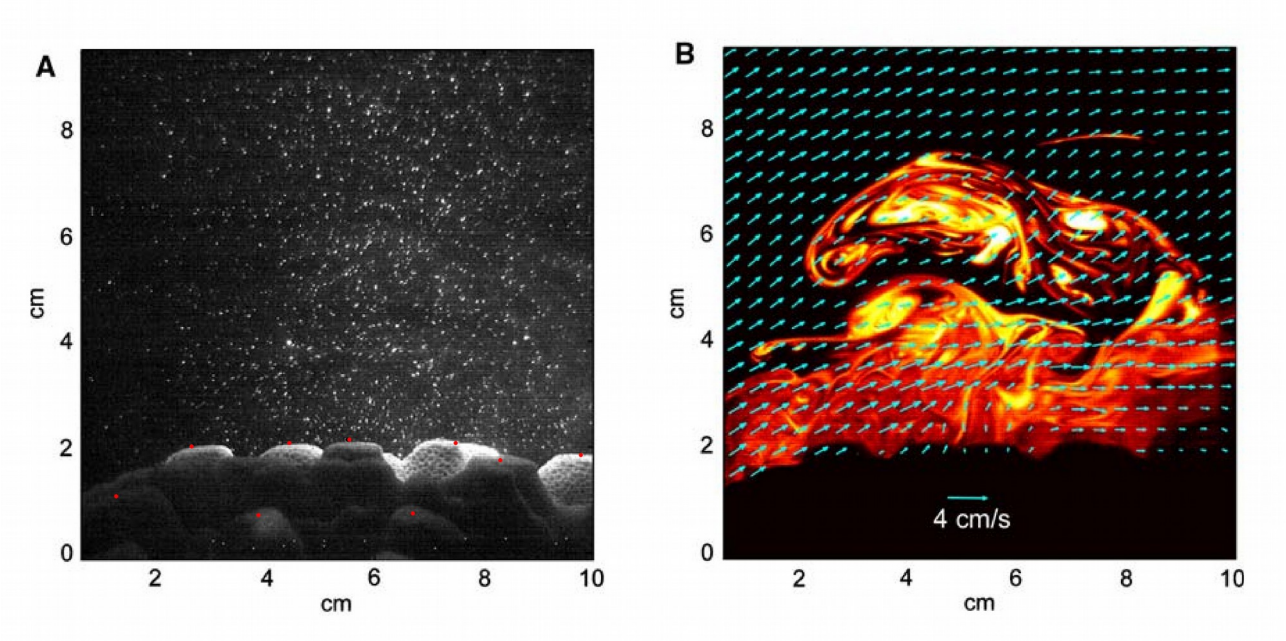


Figure 7: Example of simultaneous PIV and PLIF measurements over *Porites compressa* coral in a wave-dominated flow (with a weak current present) in a flume. (A) A PIV frame, on which opening polyps are indicated by red dots. (B) A PLIF image of dye concentration released from the coral coating, recorded 0.02 s after the image shown in A. The velocity vectors during this interval are shown in blue (from Koehl and Reidenbach, 2007, with kind permissions of Springer).

Relating bulk mass transfer across the canopy to local mass transfer limitations

An important application of the Stanton number characterisation of bulk mass transfer across canopies was in the demonstration that local nutrient uptake by coral reef organisms is frequently mass-transfer-limited, and not biologically-controlled. It has been shown that Stanton numbers for phosphate in experimental coral reefs (assuming infinitely rapid uptake, i.e., taking $C_c = 0$) agree well with those estimated from engineering formulations that only consider the hydrodynamic influence of the reef roughness (Bilger and Atkinson 1992). Other methods for quantifying the influence of fluid-canopy interactions on nutrient supply can be based on comparisons of timescales of nutrient consumption (if known) and canopy flushing (e.g. Kregting et al. 2011). Mass transfer limitation on reef flats has been shown for ammonia and nitrate, including under waves (Falter et al. 2004), demonstrating the high demand for these compounds in coral reefs. Similarly, mass transfer limitation has been shown for ammonia in seagrass and macroalgae canopies (Cornelisen and Thomas 2009; Stephens and Hepburn 2014). For heterotrophic forest-forming species, such as Mediterranean gorgonians, the validity of assuming mass transfer limitation for basic resources

(oxygen and organic compounds) must be investigated.

Canopy uptake will not always be physically-limited, however; in such cases, direct measurements of mass transfer into the canopy are required. Eddy correlation techniques allow direct measurement of turbulent diffusive fluxes of a compound, provided a high-frequency, small-scale technique exists to measure the compound concentration and its turbulent fluctuations. In marine systems, such measurements can only be provided by micro-electrode sensors, which effectively limits the technique to quantification of fluxes of dissolved oxygen (Berg et al. 2003). Importantly, eddy correlation techniques allow quantification of local fluxes under both wave- and current-dominated flows, unlike the exchange velocity model in (6), which only applies to steady flows. The eddy correlation approach was used to monitor spatial and temporal variability of respiration and photosynthesis rates over the slope and crests of a coral reef (Long et al. 2013). In this study, respiration rates increased with current velocity, suggestive of mass transfer limitation. Rates of respiration and gross primary production were higher on the reef crest (dominated by gorgonians and soft-corals) than on the reef slope (dominated by sand and pavement).

4. Living in the canopy of the animal forest

Habitat complexity has long been recognized as increasing biodiversity and biomass, explained through the provision of a diversity of niches (MacArthur and MacArthur 1961). Aquatic canopies built by flora or fauna display structural complexity and have been shown to host higher diversity and biomass than bare beds (Benedetti-Cecchi et al. 2001; Emslie et al. 2014). Yet, the relationship between canopy complexity (measured through precise canopy descriptors) and the hosted diversity and biomass still needs to be defined. In a recent study, the overall fish population biomass (driven by large fishes) was positively correlated with the density of kelp stipes forming a canopy over temperate rocky reefs (Trebilco et al. 2015). The fish population structure, however, was more closely correlated to the roughness of the under-canopy rocky substratum. While this study is clearly a step towards more quantitative description of understorey species habitat, it highlights the lack of a mechanistic conceptualization of habitat complexity, one that integrates the effects of the underlying substratum roughness and the canopy to predict the overall flow structure. Moreover, although canopy density likely influences the living conditions of fishes inside the canopy, the increase of fish biomass with canopy density is not straightforward given the nonlinear effect of density on the canopy flow structure. Indeed, turbulence intensity first increases with density (as indicated by an increase in roughness length) but then suddenly decreases with the onset of

skimming flow in dense canopies (a decrease in roughness length, Vogel 1994).

Elucidating the functional role of canopies requires consideration of the combination of all physical and chemical factors that are (1) locally- or globally-modified within a canopy and (2) that define the fundamental niche of a hosted species. A fundamental niche (*sensu* Hutchinson 1957) is defined as the set of abiotic conditions in which a species can live. Fundamental niche explorations should rely on different experimental or observational strategies according to the motility of hosted species. For sessile species, fundamental niches should be sought with an Eulerian approach; that is, monitoring in fixed locations, determining regions where temporal variations in physical and chemical conditions are within acceptable ranges. For mobile species, fundamental niches should be sought with a Lagrangian approach; that is, monitoring conditions along potential organism paths.

Living in a sparse animal forest

In marine animal forests with low population density, the flow intensity will display localized variations, creating a dependence on organism arrangement of rates of mass transfer to organism surfaces. Hosted and more precisely-associated fauna and flora are expected to display a spatial structure reflecting the wakes developing behind each individual. In such open forests, mass transfer into the canopy will not be significantly affected and the biogeochemical conditions are expected to be similar to those in the absence of the animal forest(except in individuals wake), such that the physical conditions will be dominant in structuring the biota, particularly in determining colonization processes (settlement and post-settlement survival). Individual wakes should increase local larval retention and could potentially facilitate densification of the forest by self-recruitment of the canopy-forming species as long as intra-specific competition remains small. However, such densification may be slow compared to algal growth in photic areas, suggesting that shallow animal forests would be less resilient to perturbation than deeper ones.

Living in a moderately populated animal forest

In marine animal forests of intermediate population density, in which there is significant wake interaction, the patchiness of mass transfer into the canopy and flow intensity (together with some light penetration) should promote diversification of trophic niches, enabling the development of slow growing sessile autotrophs competing for space with sessile heterotrophs. In this context, despite high local retention of larvae by the animal forest, recruitment success will probably be low due to strong intra- and inter-specific competition. The settlement of sessile heterotroph larvae in these environments should be favored in regions of rapid mass transfer into the canopy. The larvae

582 of some species are able to respond sufficiently quickly to turbulent fluctuations so as to change and
583 adapt their locomotory behaviour to more precisely follow chemical cues to appropriate sites
584 (Koehl et al. 2007). The ability of larvae with low motility to maintain themselves in the appropriate
585 Lagrangian niche seems to depend on the larval sinking speed: only those larvae with a sufficiently
586 high density or rapid behavioural changes (e.g. velum retraction, cessation of swimming) will settle
587 rapidly enough. Patchy flow conditions and visual occlusion in less dense canopies should limit the
588 size of highly mobile species (like fishes) seeking low-flow refuge in animal forests. In summary,
589 marine animal forests of intermediate population density are expected to be characterized by (1) a
590 high diversity of sessile species, autotrophic and heterotrophic, whose distribution could reflect the
591 colonization ability of larvae advected from distant sites, and (2) strong intra- and inter-specific
592 competition. Hosted mobile species are expected to be diversified, due to the variety of trophic
593 resources associated with the diversity of sessile species and the spatial variability of the flow
594 (Finelli et al. 2009). Such hosted species are expected to be limited in number and size, depending
595 on the size and shape of the canopy-forming organisms. In marine animal forests of intermediate
596 density, the choice of spatial and temporal scales used to describe in-canopy conditions is incredibly
597 important, as canopy-averaged values may differ greatly from those actually experienced by
598 organisms. Upscaling procedure should take into account not only average but also variance and co-
599 variance descriptors. Quantile descriptors should also be considered as to express the proportion of
600 time or space over which given conditions are experienced.
601
602 *Living in a dense animal forest*
603 In dense canopies (of either autotrophs or heterotrophs), the reduction of rates of mass transfer near
604 the bed associated with the low in-canopy flow is expected to lead to the accumulation of
605 compounds excreted by the canopy-forming species. Similarly, the consumption of compounds
606 useful to the canopy-forming species can lead to their depletion. Local modification of the
607 biogeochemical and mass transfer conditions below dense assemblages of macroalgae growing on
608 sessile corals was found to be deletereous to the development of sessile corals, due to the reduction
609 in oxygen concentration and increase in dissolved organic carbon concentration (Hauri et al. 2010).
610 Combining limited diffusion and high rates of consumption, sessile species hosted in dense
611 canopies are expected to be limited to those having a different trophic regime than the canopy-
612 forming species. However, near the bed in dense heterotrophic marine forests, low light conditions
613 should also prevent the development of algae. In the absence of competition with algae in a low
614 flow environment, bacteria associated with hypoxic environments will likely be favored, in turn
615 leading to low biomass and a uniform composition of sessile species. One could expect a dense

canopy to be monospecific, or at least formed by species sharing similar growth traits. Indeed, a canopy will adjust so as to have a large surface area in the the high-velocity, turbulent region of the canopy flow, where the DBL around the organism surface is thin. Such a mechanism was proposed recently to explain the existence of the oldest known marine animal forest in the deep ocean of the Precambrian era (Ghisalberti et al. 2014). In the low-flow and nutrient-rich conditions of the Precambrian ocean, tall rangeomorphs could have grown up to 2 m relying on osmotic uptake only, due to an increased mass transfer to the organism surface resulting from a thinned DBL. As a consequence of limited diffusion and flow velocity in the lower part of the canopy, one can expect dense canopies to be cleared of smaller sessile species, freeing space for mobile species like fishes looking for shelter from predators and low flow conditions to rest. The amount of open space in the lower canopy might even increase as the canopy grows, as some canopy-forming species with a tree-like shape experience population density decay though a self-thinning mechanism (Cau et al. 2016). In this case, the hosted biomass is expected to increase with the growth of the canopy-forming species. In summary, one could expect dense marine animal or vegetal forests to (1) be composed of sessile species of similar height, (2) host a diverse and large biomass of highly mobile species like fishes that are using the canopy as a refugia, and (3) a diverse microbiota subsisting on by-products of macrobiota function. .

5. Conclusions and Future directions

Local modification of the physical and biogeochemical environment by erect animals living on the sea floor has long been recognized as a key factor generating high biodiversity and biomass in the understorey. While there is a fairly comprehensive understanding in the environmental fluid mechanics community of the modification of the flow structure generated by these animal forests, these modifications are not well-known amongst the biological community studying these diverse assemblages. In this sense, marine animal forests are archetypal of ecosystems whose study requires more interdisciplinarity and reciprocal pedagogy to advance knowledge. Indeed, going beyond the term ‘habitat complexity’ to explain species associations in a unified framework to yield a typology of forest requires an understanding of physically-relevant parameters such as canopy planar and frontal density, roughness and drag coefficients, and non-dimensional parameters such as the Reynolds, Keulegan-Carpenter and Stanton numbers.

Research into the physical and biogeochemical environments around scleratinians has demonstrated

the relevance of such an interdisciplinary approach in explaining species function. Drawing scientific attention to scleratinians in the last 40 years was possible given the climatic and overfishing threats that they face. However, other marine animals, such as gorgonians, soft-corals and sponges (Maldonado et al., in this book), form animal forests that may colonize places freed up by scleratinians and provide an alternative complex habitat for understorey species. The flexibility of soft-coral species contrasts with the stiffness of scleratinian species, making their hydrodynamic influence similar to that of vegetation canopies.

The ultimate goal of such interdisciplinary research should be to develop models of marine animal forest functioning, and to compare predictions and observations of niche extent in a meta-community approach. Such models will then be useful in the prediction of biodiversity evolution under climatic and anthropogenic stresses, thereby assisting conservation efforts.

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