



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

Katell Guizien, Marco Ghisalberti

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Katell Guizien, Marco Ghisalberti. Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects. Sergio Rossi; Lorenzo Bramanti; Andrea Gori; Covadonga Orejas. Marine Animal Forests. The Ecology of Benthic Biodiversity Hotspots, Springer International Publishing, pp.1-22, 2016, 10.1007/978-3-319-17001-5_14-1 . hal-03999703

HAL Id: hal-03999703

<https://hal.science/hal-03999703>

Submitted on 21 Feb 2023

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1 Living in the Canopy of the Animal forest: Physical and Biogeochemical Aspects

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3 Katell GUIZIEN

4

5 Sorbonne Universités, CNRS, UPMC Univ Paris 06, Laboratoire d'Ecogéochimie des
6 Environnements Benthiques (LECOB), Observatoire Océanologique, F-66650, Banyuls/Mer,
7 France

8 e-mail : guizien@obs-banyuls.fr

9

10 Marco GHISALBERTI

11

12 Department of Infrastructure Engineering, University of Melbourne, Parkville, Melbourne, Victoria
13 3010, Australia

14

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

17

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36 Abstract

37

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

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

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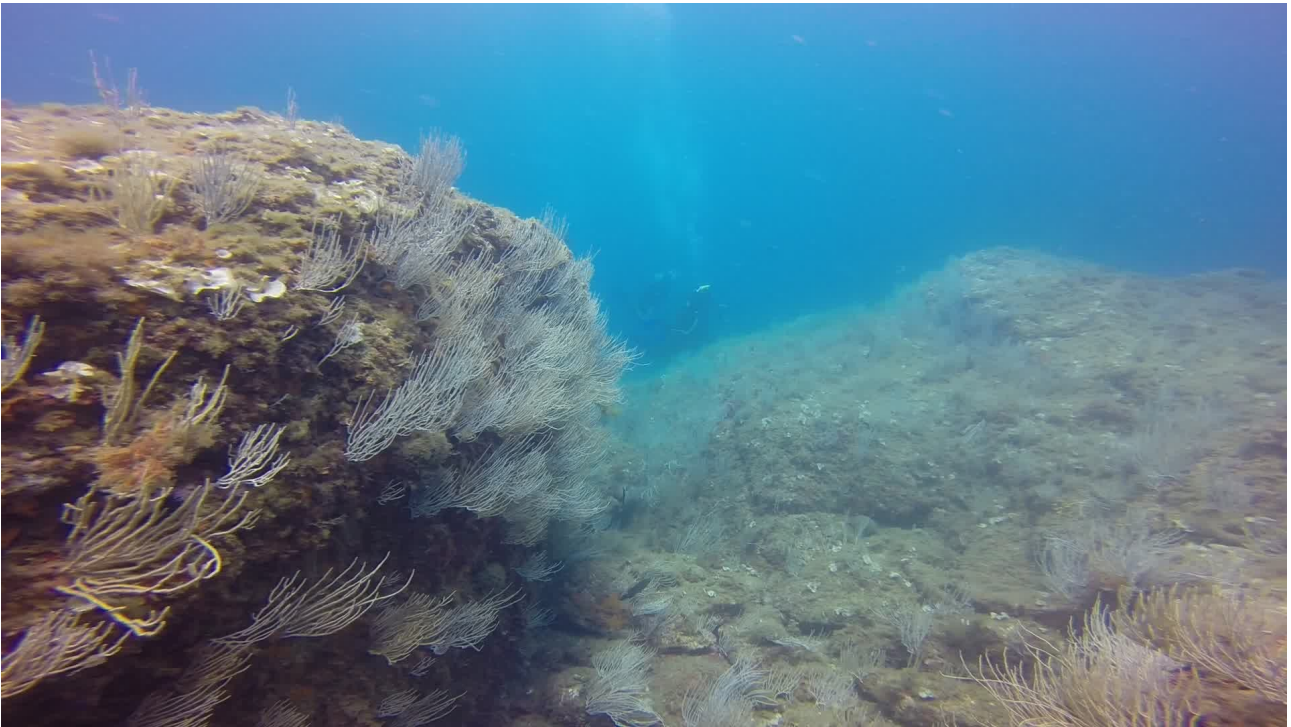
51 Keywords : Benthic boundary layer, flow instability, drag, micro-niche, spatial heterogeneity,
52 gradients, filaments, biotic-abiotic interactions, ecosystem engineers

53

54 1. Introduction

55

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



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

73

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

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

88 Marine animal forests have been shown to act as autogenic ecosystem engineers in marine systems
89 through the provision of habitat, colonization opportunities and increasing habitat complexity. For
90 corals, these effects are well-established in shallow tropical environments, but also recognized in
91 temperate (Scinto et al. 2009 ; Cerrano et al. 2010) and deep-water environments (Cordes et al.
92 2008; Freiwald and Roberts 2005). Animal forests also act as autogenic ecosystem engineers
93 through modification of the mean and turbulent flow structure. The lower levels of turbulence
94 inside the canopy increase sedimentation (Luckenbach 1986), causing the retention of propagules
95 and enhancing larval settlement (Eckman 1985; Smith and Witman 1999; Bruno 2000). At the top
96 of the canopy, the enhanced turbulence generated by the large canopy roughness augments the
97 delivery of food and critical metabolites by reducing the thickness of the diffusive boundary layer
98 on organism surfaces (Dennison and Barnes 1988; Thisle and Eckman 1990; Shashar et al. 1996).
99 Flow modification by marine forests encompasses a wide range of processes on a range of spatial
100 scales (reviewed for coral reefs by Monismith 2007) and it is now clear that the hydrodynamics of
101 marine forests demonstrate strong similarities, regardless of whether the forest is comprised of
102 plants (e.g. kelp forests or seagrass meadows, Eckman et al. 1989; Duarte 2000) or animals. This
103 flow modification likely leads to the creation of highly dynamic micro-environments, which
104 ultimately select those organisms able to feed, grow and reproduce within the marine forest.

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

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

116

117 2. The hydrodynamics inside and above the marine animal forest

118

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

127

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

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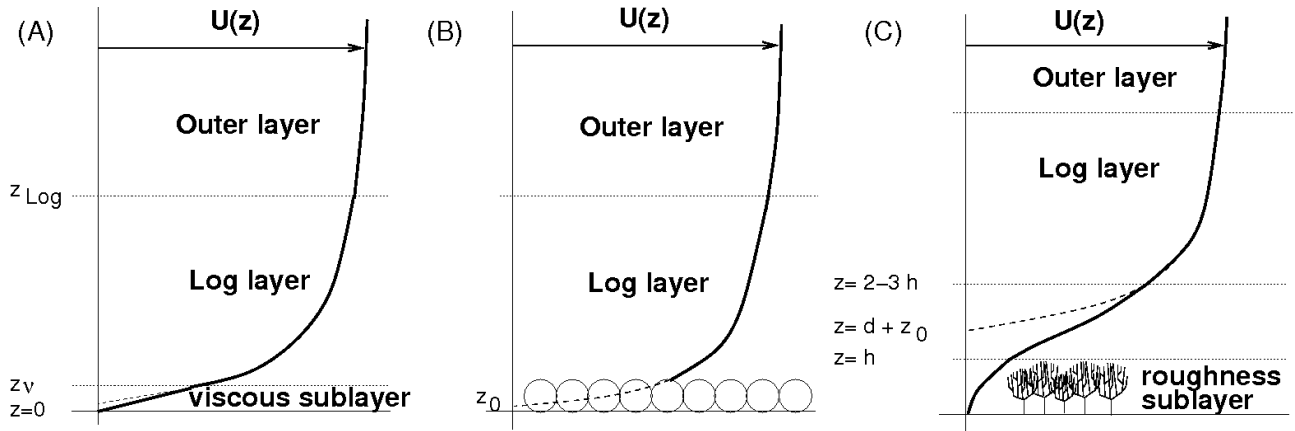
130 The bottom boundary layer is the region where the flow velocity is impacted by the bed and where
131 flows dissipate their energy into heat by viscous friction to reach a zero velocity at the bottom.
132 Under unidirectional steady flows, the thickness (δ) of a turbulent boundary layer decreases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

$$149 \quad U(z) = u_*/\kappa \ln [z/z_0] \quad \text{for } k_N < z < z_{Log}=600 \nu/u_* \quad (1)$$

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

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

152



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

157

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

159

160 When ocean beds are covered by large obstacles (i.e. a canopy) which extend into the theoretical
161 logarithmic layer of the unobstructed flow, the classical boundary layer structure can be
162 significantly modified when obstacles height is larger than 10 % of its drag length scale (see
163 definition below, Nepf et al. 2007). This is typically the case in animal forests formed by erect
164 organisms larger than a few centimeters. The wakes produced by these obstacles create strong
165 spatial variations in the flow, over a region (embedded within the boundary layer) known as the
166 roughness sublayer (RSL, Figure 2C). In an homogeneous canopy (of elements of height h), the
167 RSL is estimated to extend to approximately $2-3h$ above the bed (MacDonald 2000). Above the
168 RSL, where the flow is horizontally homogeneous, there is again a logarithmic dependence of
169 velocity on height; the profile in (1) is shifted upwards by a displacement height, d (Raupach et al.,
170 1980). Within the canopy (i.e. in the lower part of the roughness sublayer, below $z = h$), the vertical
171 profile of horizontally-averaged flow velocity has been approximated by an exponential decay from
172 its value at the top of the canopy (U_h) down to the bed (MacDonald 2000, Cheng and Castro 2002).
173 The mean flow velocity, $U(z)$, inside and above animal forests is thus typically modelled as:

174

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

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

177

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

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

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200 A)

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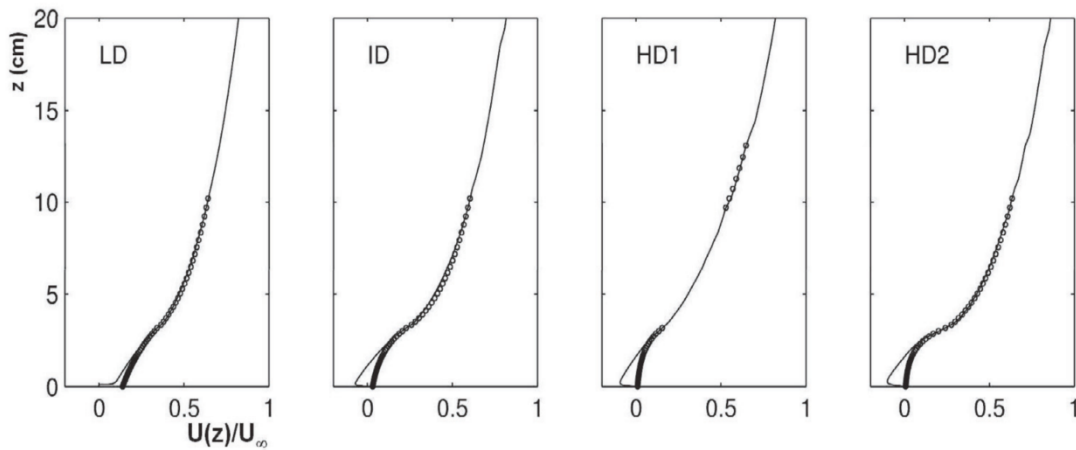
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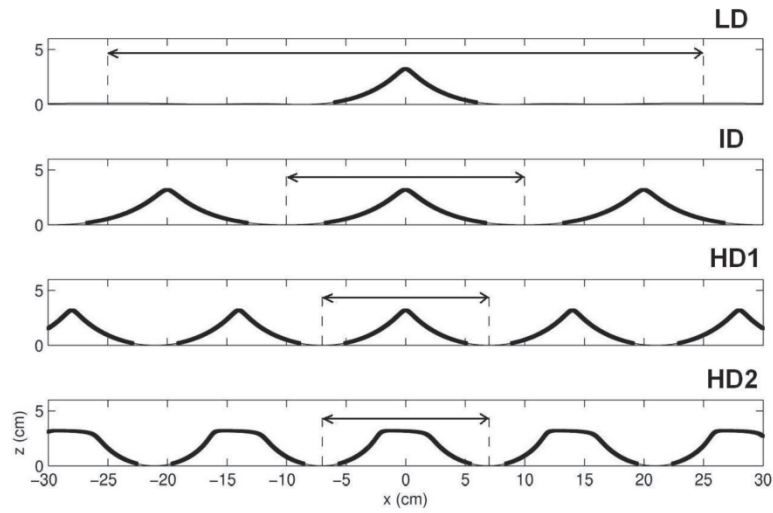


Figure 3: (A) Vertical profiles (solid lines) of the non-dimensional temporally- and horizontally-averaged longitudinal velocity ($U(z)/U_\infty$) for a steady flow of strength U_∞ above rippled beds with different densities. Fits for the logarithmic layer and for the exponential decay of velocity within 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).

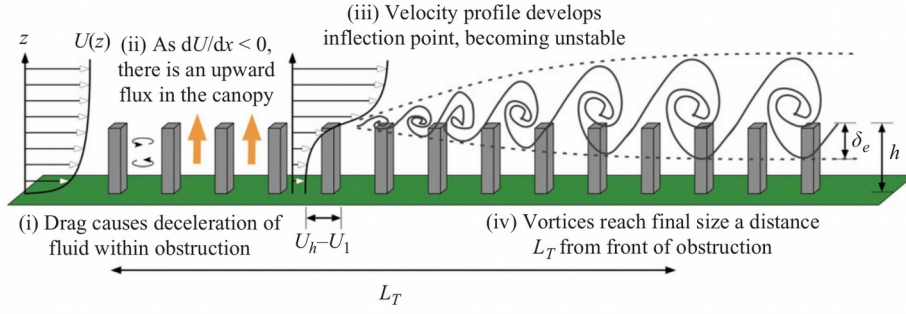


FIGURE 3. The evolution of flow along a submerged permeable medium. The distance required for full flow development L_T scales upon the drag length scale of the obstruction.

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 $O(\text{mm})$ – $O(10 \text{ m})$) 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:

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

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:

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

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).

285

Variation of a steady flow with canopy density

287

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).

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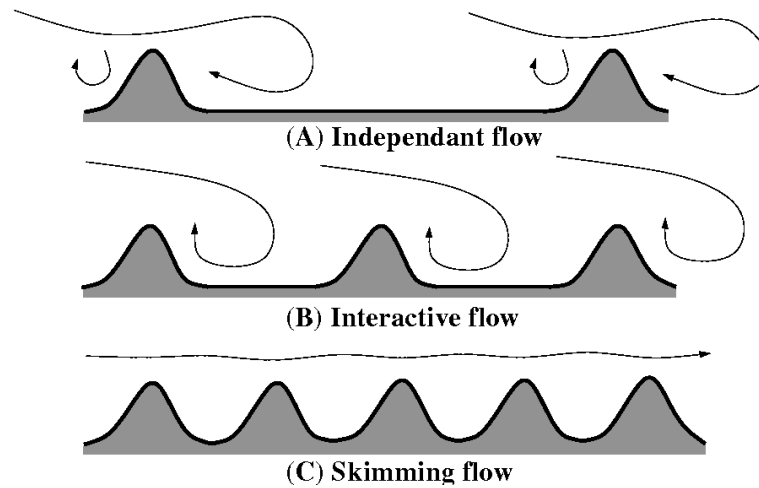


Figure 5: Three typologies of flow modification in the vicinity of obstacles for increasing packing density (adapted from Vogel 1994).

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, even 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.

341 In the absence of a canopy, boundary layers in oscillatory flow are considerably thinner than their
 342 unidirectional counterparts. While tidal boundary layers frequently extend over several meters, the
 343 boundary layer under a 10-second wave may extend over only a few centimeters. The thickness of a
 344 turbulent oscillatory boundary layer can be approximated by $\sqrt{\frac{\nu_i T}{\pi}}$ where ν_i is the eddy
 345 viscosity (Nielsen 1992). With flow energy dissipated in such a thin layer, maximum bottom friction
 346 velocities are generally an order of magnitude larger in wave flows than in the corresponding
 347 unidirectional flow (Jonsson 1966). However, bottom friction velocities as all turbulent quantities
 348 within a wave boundary layer exhibit oscillatory variations at half the wave periodicity (Sleath
 349 1987). As a consequence of these time variations, and in contrast with steady boundary layers in
 350 which turbulence intensity is fairly constant throughout fully developed boundary layers, time-
 351 averaged turbulence intensity decay inversely with distance to the bed within a wave boundary layer
 352 (Sleath 1987). However, when velocities are phase-averaged i.e. keeping track of the flow phase
 353 along the periodic flow outside the boundary layer, the law of the wall (velocity log decay and
 354 linear increase of mixing length) applies along a large part of the wave cycle (Jenssen et al. 1989).
 355 These experiments partly validated various quasi-steady modelling of wave boundary layer (e.g.
 356 Grant and Madsen 1979). However, describing with accuracy turbulent quantities within a turbulent
 357 oscillatory boundary layer, and particularly the phase lagging of turbulent quantities across it,
 358 motivated many more complex numerical modelling (reviewed by Fredsoe and Deigaard 1992,
 359 Guizien et al., 2003).

360

361 In the presence of a canopy, a wave boundary layer is considerably less affected than a steady flow
 362 boundary layer. The porous nature of the canopy, even at high densities, offers comparatively little
 363 resistance to pressure transmission within the canopy, and velocity reduction inside the canopy will
 364 be much smaller than in unidirectional flow (Lowe et al. 2005). No simple description exists for the
 365 vertical profile of orbital velocity inside a canopy under wave-driven flow, although Lowe et al.
 366 (2007) have developed a unique model for prediction of the overall velocity attenuation of canopies
 367 in oscillatory flows. The model is based on wave energy dissipation from two sources, friction at
 368 the top of the canopy and canopy element drag. Ultimately, however, its use relies on estimation of
 369 friction and drag coefficients.

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

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

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

379

	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.

380

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

382

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

384

385 From a biogeochemical perspective, the analogy between terrestrial forests and marine animal
 386 forests is not straightforward given their opposite trophic pathways: trees as autotrophs synthesize
 387 organic matter from inorganic nutrients, absorbing CO₂, while animals degrade organic matter into
 388 inorganic compounds, releasing CO₂ (N.B. the analogy works somewhat better with tropical corals
 389 whose symbiotic association with autotrophic algae put them in the category of semi-autotrophs).
 390 Despite their reversed trophic pathways, an analogy between trees and marine animal forests can be
 391 based on their life-span; long-lived biota, either autotrophs or heterotrophs, act as carbon-sinks
 392 through carbon sequestration (albeit temporarily) as long as they grow, and thus influence the global
 393 carbon cycle in a similar manner. Furthermore, an increasing density of aquatic canopies is likely to
 394 shift their role in global biogeochemical cycles from carbon sink to carbon source. While the
 395 reduced flow and low turbulence deep in dense aquatic canopies can promote burial of undegraded
 396 particulate organic matter due to hypoxic conditions (carbon sink), higher levels of turbulence
 397 within canopies of intermediate density can maintain an oxygen supply sufficient to enhance the
 398 degradation of sedimenting organic matter (carbon source). The role of marine animal forests in

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

405

406 *Bulk mass transfer rates across canopy boundaries*

407

408 At the canopy scale, turbulent mixing regulates the exchange of dissolved and particulate species
409 across the top of the canopy boundaries. Indeed, mass transfer across the top of the canopy is
410 typically related by analogy to turbulent momentum transfer, which is governed by the interfacial
411 hydrodynamics. Turbulent momentum transfer (indicated by u_*) between the in-canopy and above-
412 canopy flows has been described through a momentum exchange velocity, U_E (Bentham and Britter
413 2003):

414

$$415 \quad u_*^2 = U_E (U_{ref} - U_c) \quad (6)$$

416

417 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
418 depth-averaged velocity inside the canopy.

419

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

422

$$423 \quad \phi = U_E (C_c - C_{ref}) / Sc \quad (7)$$

424

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

431

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

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).

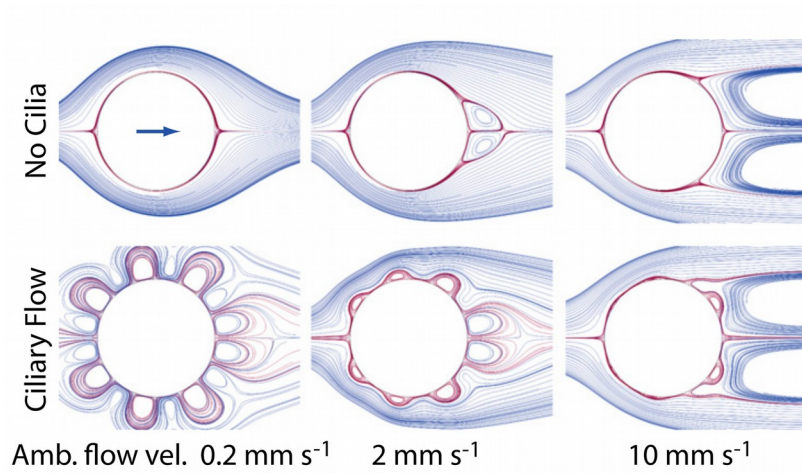


Figure 6: Streamlines (shown in blue) from numerical simulations of flow around a coral branch (diameter = 5 mm). Streamline spacing can be taken as proxy for DBL thickness: the greater the spacing, the thicker the DBL. Ciliary vortical flows (lower panel) significantly impact the flow topology and decrease 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.

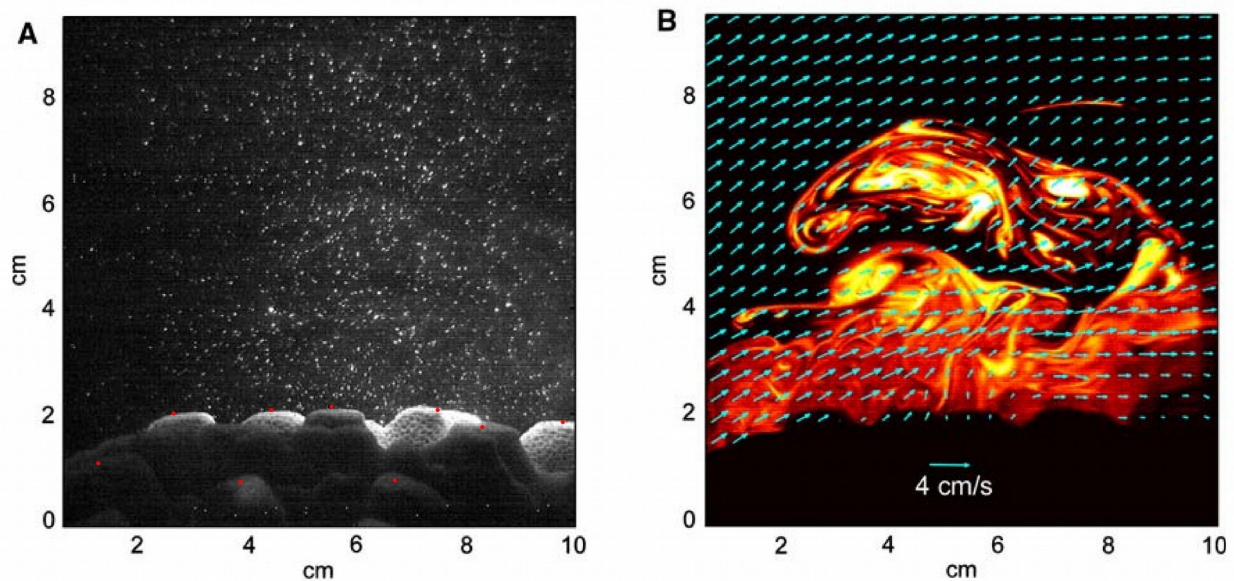


Figure 7: Example of simultaneous PIV and PLIF measurements over *Porites compressa* coral in a wave-dominated flow (with a weak current present) in a flume. (A) A PIV frame, on which opening polyps are indicated by red dots. (B) A PLIF image of dye concentration released from the coral coating, recorded 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

516 (oxygen and organic compounds) must be investigated.

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

530

531 4. Living in the canopy of the animal forest

532

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

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

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

559

560 *Living in a sparse animal forest*

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

573

574 *Living in a moderately populated animal forest*

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

633

634

635 5. Conclusions and Future directions

636

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 understory. 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

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

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

660

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