

# Flow velocity and nutrient uptake in marine canopies

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**ABSTRACT:** Marine canopies can reduce velocities within the canopy, promoting the settling of particles, increasing the residence time of dissolved nutrients and providing a refuge for biota. Increased velocities have also been shown to enhance nutrient uptake, which has been attributed to a decrease in the thickness of the diffusive boundary layer adjacent to plant cells. In this paper, we attempted to unify the varying effects of velocity on nutrient uptake in canopies into a simple framework. We analyzed the interaction between flow conditions and nutrient uptake in marine canopies (coral, macroalgal and seagrass) by synthesizing data from 13 previously published studies conducted over the past 20 yr. We present a conceptual framework for the relationship between canopy uptake of nutrient pulses and flow velocities using a canopy control volume approach combined with analysis of non-dimensional Damköhler and Reynolds numbers, identify 4 possible regimes and explore velocity thresholds that trigger regime transitions. All data showed increasing nutrient uptake with increasing flow velocities, though many data sets showed saturation of uptake rates. The relationship between flow velocity and nutrient uptake varied with canopy species, nutrient species and canopy density. We found evidence for 2 of the proposed regimes; however, the remaining 2 regimes, though suggested in the literature, were not evidenced by the data. The analysis highlighted that our understanding of canopy function under disturbed conditions is currently based on experimental data from ecosystems under a relatively narrow range of flow and canopy conditions that are unlikely to be stressful to the organism. We are therefore unlikely to fully understand the response of canopies to strong perturbations of the external hydrodynamics.

**KEY WORDS:** Marine canopy · Nutrient uptake · Flow velocity · Seagrass · Corals · Macroalgae

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## 1. INTRODUCTION

The local hydrodynamic environment has long been recognized as a significant factor impacting nutrient uptake within marine canopy communities (Atkinson & Bilger 1992, Sanford & Crawford 2000, Thomas & Cornelisen 2003, Larkum et al. 2006). Hydrodynamic-canopy interactions can impact nu-

trient uptake in several ways and canopy species can adapt to optimize uptake (Larkum et al. 2006). Marine canopy species can modify their morphologies to reduce velocities within the canopy to 30% of external velocities (Nepf 2012a, Abdolahpour et al. 2018), providing shoot protection from high-energy storms (Vogel 1984), promoting the settling of organic and inorganic particles (Granata et al. 2001, Agawin &

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Duarte 2002) and increasing the residence time of dissolved nutrients (Ackerman & Okubo 1993, Koch & Gust 1999). Additionally, canopies provide refuge for fish, invertebrates and plankton (Koch 2001) that subsequently enhance organic matter concentration and availability. As a consequence, coastal ecosystems that contain canopies, such as macroalgae (e.g. kelp forests), coral reefs and seagrass meadows, are among the most productive ecosystems in terms of net primary production per unit area and time, with high biodiversity (Hughes et al. 2002).

The attenuation of both unidirectional and oscillatory velocities by canopies is a function of plant shoot density, morphology, stiffness and the ratio of canopy height to water depth (Pujol et al. 2013, Rominger & Nepf 2014), all of which can be adaptive responses of canopy species to ambient hydrodynamic conditions. Such adaptations can ameliorate the negative impacts of high-energy flows on canopy health, nutrient uptake and growth. For example, the ambient flow condition has shown a significant impact on particle capture in coral canopies (Helmuth & Sebens 1993, Helmuth et al. 1997, Sebens et al. 1997), the absorption characteristics of the aggregate (Kaandorp et al. 1996), local productivity (Carpenter et al. 1991, Patterson et al. 1991) and gas exchange (Patterson & Sebens 1989) in these environments.

Flow velocities have also been shown to impact rates of nutrient uptake in seagrasses canopies (Cornelisen & Thomas 2006, Morris et al. 2008) and coral communities (Shashar et al. 1993, Hearn et al. 2001, Badgley et al. 2006). Lei & Nepf (2016) proposed that canopy blade surfaces were increasingly exposed during higher flows and this promoted nutrient uptake. However, the increased uptake has classically been attributed to the effect of flow on the thickness of the diffusive boundary layer (DBL) (Carpenter et al. 1991, Shashar et al. 1993). When fluxes across the DBL concentration gradient are not limited by supply, they are controlled by molecular diffusion, an extremely inefficient transport mechanism (Denny 1988, Hurd 2000, Stevens et al. 2003). However, as water velocity increases, the DBL becomes thinner, diffusive transport becomes faster and nutrient uptake more rapid (Atkinson & Bilger 1992, Thomas & Cornelisen 2003). This effect has also been observed under turbulent flows as the DBL is distorted and deformed by small-scale eddies (Huang et al. 2011, Barton et al. 2014, Rominger & Nepf 2014). Transport across the DBL then becomes sufficiently fast that nutrient fluxes into the cell are controlled by the speed of enzymatic reactions or the availability of

uptake sites in the cells adjacent to the DBL (Cornelisen & Thomas 2004).

Thus, uptake can be conceptualized as a 2-step process: (1) transport across the DBL, governed by Fick's First Law and (2) uptake of the nutrient across the cell wall via active uptake sites. The overall nutrient uptake rate,  $R$ , was parameterized by Aksnes & Egge (1991) as:

$$R = \frac{nh^{-1}[N]}{(A_s\beta h)^{-1} + [N]} \quad (1)$$

where  $n$  is the number of uptake sites per unit biomass,  $\beta$  is the mass transfer coefficient ( $\text{m s}^{-1}$ ),  $A_s$  is the catchment area of the uptake site ( $\text{m}^2$ ),  $[N]$  is the nutrient concentration in the medium outside the DBL ( $\mu\text{mol m}^{-3}$ ) and  $h$  is the time taken (s) by an uptake site to transport, or handle, an ion across the cell wall (Aksnes & Egge 1991). Note that we have used consistent nomenclature throughout this paper (Table 1), while compiling literature and equations across multiple disciplines. Nomenclature may therefore be different from that used in the cited source.

$R$  is more frequently described by Michaelis-Menten kinetics (Sanford & Crawford 2000):

$$R = R_{\max} \frac{[N]}{K_{[N]} + [N]} \quad (2)$$

where  $R_{\max}$  is the maximum uptake rate ( $\mu\text{mol m}^{-3} \text{s}^{-1}$ ) and  $K_{[N]}$  is the nutrient concentration ( $\mu\text{mol m}^{-3}$ ) at which  $R = 0.5R_{\max}$ . We use the generalized parameter  $K$  to denote the value of the variable indicated in the sub-script that is required to reach 50% of the maximum uptake,  $R_{\max}$ .  $K_{[N]}$  is commonly denoted  $K_{SAT}$  in biological literature; however, for consistency across disciplines we have denoted it herein as  $K_{[N]}$ . Comparing Eqs. (1) and (2), we find:

$$\begin{aligned} R_{\max} &\equiv nh^{-1} \\ K_{[N]} &\equiv (A_s\beta h)^{-1} \end{aligned} \quad (3)$$

Note that Eq. (1) encompasses both passive and active uptake and we assume that Michaelis-Menten kinetics can also describe the chemical and biological factors that impact  $R$ . Peters et al. (2006) modelled nutrient uptake under turbulent conditions and proposed that hydrodynamics impact  $K_{[N]}$  (through the thinning or thickening of the DBL), however not  $R_{\max}$ . Michaelis-Menten kinetics assume that  $R_{\max}$  and  $K_{[N]}$  are constant over the timescale of an experiment, and care must therefore be taken that  $n$ ,  $h$ ,  $A_s$  and  $\beta$  remain constant (Aksnes & Egge 1991). Biological processes and adaptation could allow manipulation of  $n$

Table 1. Notation

Symbol	Unit	Definition
$A_C$	$m^2$	Planar surface area of the canopy
$A_S$	$m^2$	Catchment area of uptake site
$\beta$	$m\ s^{-1}$	Mass transfer coefficient
$Da$		Damköhler number
$FR$		Dimensionless flushing ratio
$h$	$s$	Time taken by an uptake site to transport ion across the cell wall
$k'$	$s^{-1}$	First-order rate coefficient
$K_{[N]}$	$\mu mol\ m^{-3}$	Nutrient concentration
$K_{[T]}$	$m^2\ s^{-3}$	Turbulent level at which $R = 0.5R_{max}$
$K_{[U]} \equiv U_{0.37}$	$m\ s^{-1}$	Velocity at which $R = 0.5R_{max}$
$l_e$	$m$	The effective canopy length
$L_C$	$m$	Canopy length
$M_B$	$g\ dry\ wt\ m^{-2}$	Tissue biomass
$n$		Number of uptake sites per unit biomass
$[N]_F$	$\mu mol\ l^{-1}$	Final external concentration
$[N]_0$	$\mu mol\ l^{-1}$	Initial concentration of B
$R$	$\mu mol\ m^{-3}\ s^{-1}$	Uptake rate
$R_{max}$	$\mu mol\ m^{-3}\ s^{-1}$	Maximum uptake rate
$R_0$	$\mu mol\ m^{-3}\ s^{-1}$	Uptake rate at zero velocity
$R_B$	$mol\ g\ dry\ wt^{-1}\ s^{-1}$	Nutrient uptake per unit of biomass
$Re$		Reynolds number
$St$		Stanton number
$t$	$s$	Time
$\tau_{depletion}$	$s$	Timescale of depletion
$\tau_E$	$s$	Exposure timescale
$\tau_{flushing}$	$s$	Timescale of flushing
$\tau_P$	$s$	Processing timescale
$\tau_T$	$s$	Transport timescale
$U$	$m\ s^{-1}$	Mean water velocity far above the canopy
$U_C$	$m\ s^{-2}$	Flow speed through canopy
$U_e$	$m\ s^{-1}$	The effective velocity scale
$U^{rms}$	$m\ s^{-1}$	The root-mean-square of the oscillatory velocity far above the canopy
$V_C$	$m^3$	Canopy control volume
$\nu$	$m^2\ s^{-1}$	Kinematic viscosity

via shoot density, and  $A_S$  via flexibility and waving (Nepf 2012a, Lei & Nepf 2016);  $h$  would be impacted by nutrient status and is also expected to be species-specific (Babourina & Rengel 2010).

We note the similarity between the response of  $R$  to increasing velocities and the response of  $R$  to increasing nutrient concentrations. Aksnes & Egge (1991) and Peters et al. (2006) both proposed that  $R_{max}$  is constant for a given canopy species; i.e. once  $R_{max}$  is reached, uptake will not be increased by either increasing velocities or increasing nutrient concentrations. In parallel to  $K_{[N]}$ ,  $K_{[U]}$  is the velocity at which  $R = 0.5R_{max}$ ; and  $K_{[T]}$  is the turbulence level at which  $R = 0.5R_{max}$  (Barton et al. 2014). We stress that as  $R_{max}$  changes, so do  $K_{[N]}$ ,  $K_{[U]}$  and  $K_{[T]}$ . Affinity,  $\alpha = R_{max}/K$ , has been suggested as a more robust indicator of effectiveness of uptake, particularly under low nutrient conditions, compared to either  $R_{max}$  or  $K$  individually (Peters et al. 2006).

According to Michaelis-Menten kinetics,  $R$  will be independent of concentration (i.e. zero-order kinetics) when  $[N] \gg K_{[N]}$  or will be linearly dependent on concentration (i.e. first-order kinetics) when  $[N] \ll K_{[N]}$  (Fechner-Levy & Hemond 1996). The first- and zero-order relationships between nutrient uptake and concentration can be conceptualized as 2 different regimes (Regime I and II respectively), and threshold nutrient concentrations are explicit in Michaelis-Menten parameterization of  $K_{[N]}$ .  $K_{[N]}$  has been extensively investigated for a wide range of canopy species and therefore in most contexts we can assess whether first-order (Regime I) or zero-order (Regime II) kinetics is appropriate. We have seen that similar relationships have been proposed between  $R$  and velocity; however  $K_{[U]}$  and  $K_{[T]}$  are much less understood, and threshold velocities that indicate transition between first-order kinetics (Regime I) and zero-order kinetics (Regime II) have not previously been explored.

Hurd et al. (1996) and Kregting et al. (2011) explored the saturating relationship between flow velocity and nutrient uptake in the macroalgae *Macrocystis integrifolia*, and empirically derived  $R_{\max}$  and the inflection point on the saturation curve, defined by the authors as  $U_{0.37}$ , by fitting data to:

$$R = R_0 + (R_{\max} - R_0) \left[ 1 - \exp\left(-\frac{U}{U_{0.37}}\right) \right] \quad (4)$$

where  $R_0$  is the estimated uptake rate at zero velocity if the DBL is allowed to form over a 1–2 h period and  $U$  is flow velocity ( $\text{m s}^{-1}$ ). While they used  $U_{0.37}$  as the inflection point rather than  $K_{[U]}$ , similarities with the Michaelis-Menten saturating relationship are evident.

The impacts of substrate concentration and velocity on nutrient uptake have frequently been observed at a canopy scale (see e.g. Morris et al. 2008), despite being conceptualized at the cellular scale. At a canopy scale, any factor that impacts the DBL thickness (e.g. epiphyte cover, topography or surface roughness) would also affect nutrient fluxes (Thomas & Atkinson 1997, Cornelisen & Thomas 2004). In an investigation of the impact of canopy–fluid interactions on nutrient uptake, Kregting et al. (2011) translated across scales, using a ratio of depletion and flushing timescales in the canopy ( $\tau_{\text{depletion}}$  and  $\tau_{\text{flushing}}$  respectively):

$$\text{FR} = \frac{\tau_{\text{depletion}}}{\tau_{\text{flushing}}} = \frac{([N]V_C)/(M_B A_C R_B)}{L_C/U_C} \quad (5)$$

where  $V_C$  is the canopy control volume ( $\text{m}^3$ ),  $M_B$  is the tissue biomass ( $\text{g dry wt m}^{-2}$ ),  $A_C$  is the planar area of a typical canopy ( $\text{m}^2$ ),  $R_B$  is the nutrient uptake rate per unit of biomass ( $\mu\text{mol g}^{-1} \text{ dry wt s}^{-1}$ ) (assuming it is independent of concentration; i.e. zero-order),  $L_C$  is the canopy length ( $\text{m}$ ) and  $U_C$  is the flow speed through the canopy ( $\text{m s}^{-1}$ ). By simplifying the problem and reducing the number of variables, FR can be used to assess whether nutrient uptake is limited by the supply of nutrients to the plants (in which case it would be sensitive to changing hydrodynamic conditions), or by biological uptake processes alone. This ratio of timescales is similar to the dimensionless uptake rate used by Sanford & Crawford (2000) and the Damköhler number (Da), which is defined as the balance between transport ( $\tau_T$ ) and reaction or processing timescales ( $\tau_P$ ) in a defined volume. Da has been used extensively in chemical engineering (Fogler 1999) and more recently by Oldham et al. (2013) in environmental contexts. Such dimensionless ratios are applied across a wide range of conditions to provide insights into the

system. In canopies, Da quantifies the relative impacts of the 2 most important timescales (i.e.  $\tau_P$  and  $\tau_T$ ) and facilitates an understanding of different nutrient uptake regimes across a wide range of field conditions. By transferring the previously proposed flushing ratio into a Da, we seek to take advantage of conceptual framing provided by a larger body of research.

In the present study, we used published nutrient uptake data from 12 studies to explore the relationship between  $R$  and velocity above the canopy,  $U$ , to determine  $R_{\max}$  and  $K_{[U]}$  for a range of canopy species (coral, seagrass and macroalgae) and nutrients. Note that while Kregting et al. (2011) used the in-canopy flow speed for their parameterization, this value is rarely reported in nutrient uptake studies, and we therefore used the above-canopy velocity; we expect these to be the same order of magnitude (Lowe et al. 2005, Abdollahpour et al. 2018). We then used a Da analysis to explore different flow–nutrient uptake regimes, discuss possible controls on transitions between regimes and propose potential ecological consequences.

## 2. METHODOLOGY

### 2.1. Experimental data

An array of previously published data from field and laboratory experiments in canopies were selected to explore how  $R$  varied across a range of hydrodynamic conditions, nutrient species and canopy species (Table 2). While there has been a very large body of research investigating controls on nutrient uptake, a surprisingly small subset reported both the nutrient uptake and flow variables required for our analysis. There were differences in experimental approach across the utilized data sets; however, typically a pulse of nutrients was released into the water column at the canopy boundary under oscillatory or unidirectional flow conditions. Water samples were removed from the flume over time, analyzed for nutrient concentrations and nutrient uptake was determined as the decline in water column nutrient concentration. Water velocities were measured using an acoustic Doppler velocimeter or similar. The experiments covered a wide range of flow velocities (from  $2 \times 10^{-3}$  to  $600 \times 10^{-3} \text{ m s}^{-1}$ ), canopy marine species (corals, seagrasses and macroalgae) and different nutrient species ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ). Some experiments were carried out using a mix of canopy communities. In these cases, we specified the predomi-

Table 2. Overview of published data used in our analysis

Authors	Canopy	Nutrients	Experiments	Flow regime
Atkinson & Bilger (1992)	Corals <sup>a</sup> : <i>Porites compressa</i> , <i>Porites lobata</i> , <i>Pocillopora damicornis</i> , <i>Pocillopora meandrina</i> , <i>Montipora verrusco</i> , <i>Montipora patula</i> , <i>Fungia scutario</i> Macroalgae: <i>Dictyosphaeria cavernosa</i> , <i>Halimeda opuntia</i> , <i>Lyngbia majuscula</i> , <i>Lobophora variegata</i> , <i>Padina australis</i> , <i>Sargassum polypheylum</i> , <i>Turbinaria ornate</i> Macroalgae: <i>Nerocystis leutkeana</i> , <i>Macrocystis integrifolia</i> Corals: organisms included corals, coralline algae, attached microalgae, rubble and all associated cryptofauna, epifauna and epiphytes	$\text{PO}_4^{3-}$	Laboratory experiments	Unidirectional flow
Hurd et al. (1994)		$\text{NH}_4^+$ , $\text{NO}_3^-$	Laboratory experiments	Unidirectional flow
Bilger & Atkinson (1995)		$\text{NH}_4^+$ , $\text{PO}_4^{3-}$	Laboratory experiments	Unidirectional flow
Thomas & Atkinson (1997)	Corals: <i>Porites compressa</i> , <i>Pocillopora damicornis</i>	$\text{NH}_4^+$	Laboratory experiments	Unidirectional flow
Larned & Atkinson (1997)	Macroalgae: <i>Dictyosphaeria cavernosa</i>	$\text{NH}_4^+$ , $\text{PO}_4^{3-}$	Laboratory experiments	Unidirectional flow
Thomas et al. (2000)	Seagrasses: <i>Halodule wrightii</i> , <i>Thalassia testudinum</i>	$\text{NH}_4^+$	Field experiments with field flume	Unidirectional flow
Atkinson et al. (2001)	Macroalgae <sup>b</sup> : Calcareous and non-calcareous macroalgae belonging to the Chlorophyta, Rhodophyta and Phaeophyta. Corals: 25 genera of coral Sponges: <i>Leuconia</i> sp., 12 % total Seagrasses: <i>Thalassia testudinum</i>	$\text{NH}_4^+$ , $\text{PO}_4^{3-}$	Laboratory experiments	Oscillatory flow
Cornelisen & Thomas (2002)	Seagrasses: <i>Thalassia testudinum</i>	$\text{NH}_4^+$	Field experiments with field flume	Unidirectional flow
Thomas & Cornelisen (2003)	Seagrasses: <i>Thalassia testudinum</i>	$\text{NH}_4^+$	Field experiments with field flume	Unidirectional flow, Oscillatory flow
Cornelisen & Thomas (2006)	Seagrasses: <i>Thalassia testudinum</i>	$\text{NH}_4^+$ , $\text{NO}_3^-$	Field experiments with field flume	Unidirectional flow
Cornelisen & Thomas (2009)	Seagrasses: <i>Thalassia testudinum</i> , <i>Syringodium filiforme</i> <sup>c</sup> Ahermatypic coral: <i>Porites</i> spp., <i>Manicina areolata</i> Calcareous algae: <i>Penicillus</i> spp., <i>Halimeda</i> spp., <i>Rhipocephalus</i> spp. Sponges: <i>Chondrilla nucula</i> , <i>Tedania ignis</i> Macroalgae: <i>Adamsiella chauvinii</i>	$\text{NH}_4^+$	Field experiments with field flume	Unidirectional flow
Kregting et al. (2011)		$\text{NH}_4^+$ , $\text{NO}_3^-$	Laboratory and field experiments	Unidirectional flow
Weitzman et al. (2013)	Seagrasses: <i>Thalassia testudinum</i> , <i>Syringodium filiforme</i> <sup>d</sup> Macroalgae: <i>Halimeda</i> spp., <i>Laurencia</i> spp., <i>Penicillus</i> spp. Corals: <i>Porites</i> spp.	$\text{NH}_4^+$ , $\text{NO}_3^-$	Field experiments with field flume	Unidirectional flow, Oscillatory flow

<sup>a</sup>One-third of the flume was covered with coral and coralline algae; <sup>b</sup>Macroalgae was the dominant species;<sup>c</sup>This represents 70 % of the benthic community; <sup>d</sup>Dominant benthic community

nant canopy community for each experiment. We used a consistent methodological approach to compare experimental data across disparate canopy types and to assess whether a saturating relationship between nutrient uptake and flow velocity was universally observed.

## 2.2. Reynolds number

The non-dimensional Reynolds number,  $Re$ , provides the balance between inertial and viscous forces and is used to characterize environmental flow conditions, e.g. as laminar or turbulent. Specifically, low  $Re$  represents low-flow conditions and high  $Re$  represents high flows with turbulent characteristics. When comparing data from multiple marine systems, it is important to estimate  $Re$  to determine significant differences in their ambient hydrodynamic conditions. Since  $Re$  is a dimensionless ratio, characterizing  $Re$  also enables generalization of the results to a wide range of field conditions. Here,  $Re$  is defined as:

$$Re = \frac{UL_C}{\nu} \quad (6)$$

where  $\nu$  is the kinematic viscosity ( $10^{-6} \text{ m}^2 \text{ s}^{-1}$ ). Note the difference between  $Re$  used here and those used in previous studies; e.g. Kregting et al. (2011) who used a blade-scale  $Re$  to characterize nutrient uptake. Since  $L_C$  is the length scale over which  $R$  has been measured, we used  $L_C$  as the characteristic length for characterizing  $Re$  in this study (see details in Section 2.3.1).

## 2.3. Damköhler number

The non-dimensional Damköhler number,  $Da_E$  was defined as:

$$Da_E = \frac{\tau_E}{\tau_p} \quad (7)$$

where  $\tau_E$  is the exposure timescale and  $\tau_p$  is a generalized processing (or nutrient uptake) timescale (Oldham et al. 2013). When  $Da_E \ll 1$ ,  $\tau_p$  is longer than  $\tau_E$  and the material does not have sufficient time to react during transport. The process can therefore be considered non-reactive (conservative) and there will be no uptake within the canopy. When  $Da_E \gg 1$ ,  $\tau_p$  is shorter than  $\tau_E$  and the material has ample time to react during transport. The process can therefore be considered reactive and uptake occurs within the canopy. If  $Da_E \approx 1$  the system can be considered

highly dynamic ( $\tau_E \approx \tau_p$ ); the balance for a given process will be very sensitive to hydrodynamic conditions and may fluctuate between conservative and reactive. Sanford & Crawford (2000) highlighted that under these conditions any change in controlling parameters can significantly affect uptake.

### 2.3.1. Exposure timescales

The exposure timescales for each experiment was estimated as the ratio of mean velocity to system length scale:  $\tau_E = U_e/l_e$  (where  $l_e$  and  $U_e$  are the effective length and velocity scales, respectively). For canopies exposed to unidirectional flows,  $U_e$  is equivalent to  $U$ . For canopies exposed to oscillatory flows, the root-mean-squared (RMS) of the orbital velocity far above the canopy ( $U^{\text{rms}}$ ) was used as the relevant velocity scale. This velocity scale is conveniently used to represent the mean value of the orbital velocity where a direct comparison with unidirectional flow is needed (Lowe et al. 2005, Reidenbach et al. 2007, Abdolahpour 2017). Additionally,  $l_e = L_C$  in unidirectional flows and  $l_e = A_\infty$  in oscillatory flows (where  $A_\infty$  is the horizontal excursion length of the orbital velocity) (Fig. 1). Note, in unidirectional flows, the flume length was used as the characteristic length scale where the length of the canopy was not available.

### 2.3.2. Uptake rates

The estimation of  $\tau_p$  for each study was more challenging as it was impacted by kinetic assumptions and therefore by ambient nutrient concentrations relative to half-saturation conditions. Initially, values of  $R$  were extracted or derived from each published data set. Because of different assumptions made by authors, the unknowns may be different from one study to another. To facilitate extraction of as much information as possible from canopy data sets, we present below a step-by-step derivation of  $R$ . We note that Kregting et al. (2011) assumed a zero-order relationship between  $R$  and concentration (our Regime II), while Oldham et al. (2013) assumed that for most natural environmental systems  $[N] \ll K_{[N]}$  and therefore first-order nutrient uptake dominates (Regime I). For marine systems with  $[N] \ll K_{[N]}$ , we assumed first-order kinetics, such that:

$$R = \frac{d[N]}{[N]dt} = -k'dt \quad (8)$$



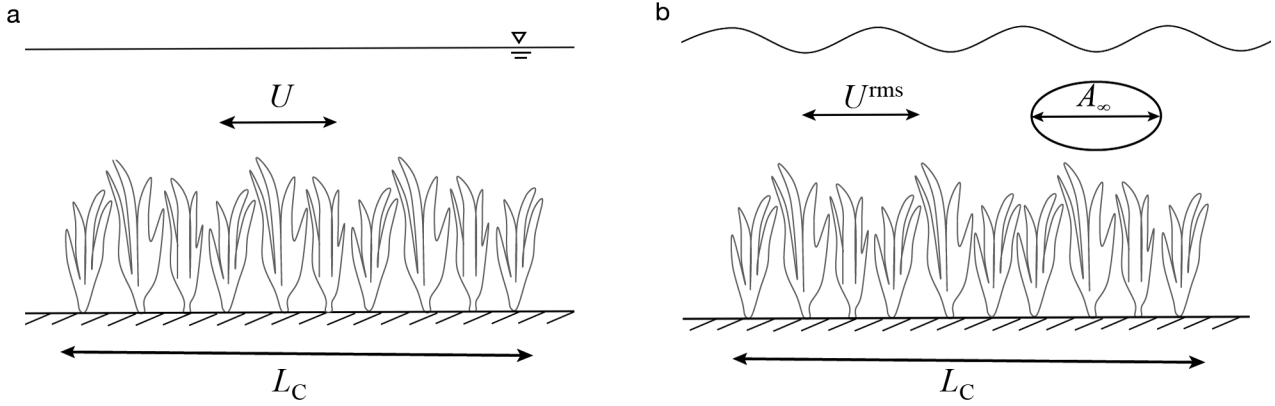


Fig. 1. Schematic view of the test sections for (a) unidirectional and (b) oscillatory flow conditions. See Table 1 for symbol definitions

where  $k'$  is the assumed (or pseudo) first-order rate coefficient ( $s^{-1}$ ). By integrating both sides of the equation, we get:

$$\int_{[N]_0}^{[N]_F} \frac{d[N]}{[N]} = -\int_{t_0}^t k' dt \quad (9)$$

where  $[N]_F$  and  $[N]_0$  are the final and initial concentrations of chemical ( $\mu\text{mol m}^{-3}$ ), respectively. Solving the equation and expressing it as the variation of the concentration on time (also known as the integrated rate law), we get:

$$\ln[N]_F = \ln[N]_0 - k't \quad (10)$$

Therefore,

$$k' = \frac{\ln\left(\frac{[N]_F}{[N]_0}\right)}{t} \quad (11)$$

Finally, we assumed that  $\tau_p \sim O(1/k')$ . In some flume experiments  $[N]_F$  or  $[N]_0$  were not reported, however we could proceed if the Stanton number ( $St$ ) was provided:

$$St = \frac{\beta}{U} \quad (12)$$

thus,  $k'$  (and therefore  $\tau_p$ ) could be then found by:

$$\beta = \frac{k' V_C}{A_C} \quad (13)$$

### 3. RESULTS AND DISCUSSION

For the experiments with coral and seagrass communities (using a recirculating flume under unidirectional flow) there was a positive relationship between  $R$  (measured as  $-d[N]/dt$ ) and  $U$  (Fig. 2a,b). There were fewer published studies for macroalgal communities and the experiments were performed over a

smaller range of flow velocities, yielding a less obvious relationship between  $R$  and  $U$  (Fig. 2c). We also note that the experiments by Hurd et al. (1994) used a single macroalgal blade, whereas other experiments on coral reefs, seagrass meadows or macroalgae used canopies. Thus, we may expect a degree of underestimation of  $R$  in macroalgal communities using Hurd et al. (1994).

For all types of communities,  $R$  generally followed a saturating (power regression, suggested by the best fitting curve) relationship with increasing water velocity, with high values of  $r^2$  and  $p < 0.05$  (Table 3). While most communities reached maximum  $R$  when  $U$  was in the range  $0.02$ – $0.4 \text{ m s}^{-1}$ , the maxima for  $\text{NH}_4^+$  were highly variable. In particular, seagrass communities reached maximum  $R$  when  $U$  was in the range  $0.002$ – $0.2 \text{ m s}^{-1}$  and generally had a tighter fit than the coral data. For seagrass communities,  $r^2$  was typically  $>0.7$ , while for coral communities  $r^2$  was lower. Additionally, while coral canopies are deemed to reach maximum saturation at higher velocities ( $>0.2 \text{ m s}^{-1}$ ) when subjected to unidirectional flows (Fig. 2a), they exhibit similar behavior as other communities under oscillatory flows (Fig. 2d). Experiments on macroalgal communities were conducted with  $U$  ranging from  $0.02$ – $0.16 \text{ m s}^{-1}$ , with some studies showing saturating  $R$  while others showed no obvious relationship between  $R$  and  $U$  (Fig. 2c,d).

The relationship between  $R$  and  $U$  (i.e. the slope of the data lines in Fig. 2) and  $R_{\max}$  (i.e. the plateau value of nutrient uptake) varied with nutrient species ( $\text{PO}_4^{3-}$ ,  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ). The saturation nutrient uptake of  $\text{NO}_3^-$  was lower than  $\text{NH}_4^+$  for the same canopy community and flow conditions. This agrees with the results of Cornelisen & Thomas (2006), who found that under unidirectional flow, seagrass nutrient uptake rates for  $\text{NH}_4^+$  were faster than for  $\text{NO}_3^-$ . They attributed this to the increased energy required

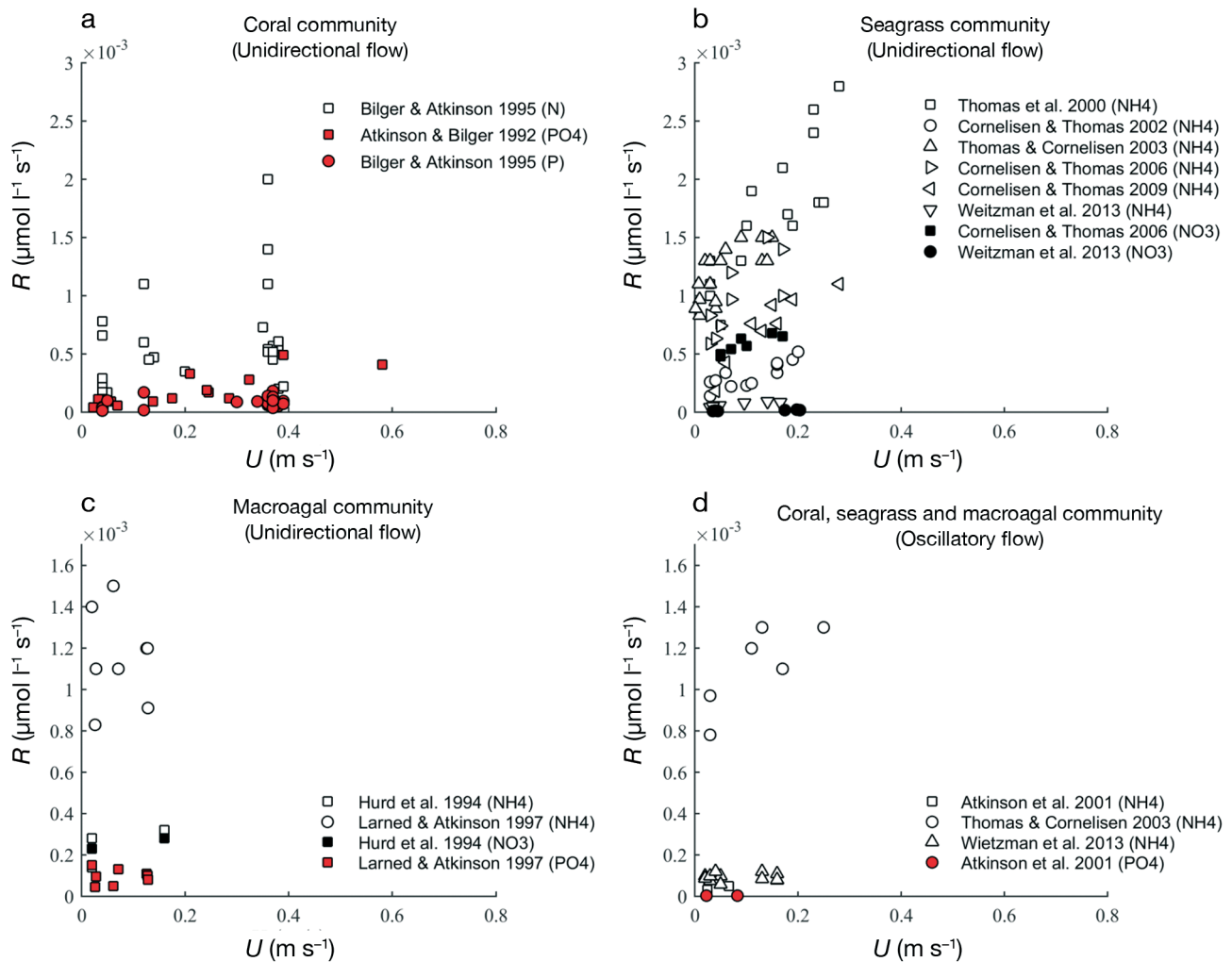


Fig. 2. Rate of nutrient uptake ( $R$ ) versus velocity ( $U$ ) for different experiment types: (a) coral communities under unidirectional flow; (b) seagrass communities under unidirectional flow, (c) macroalgal communities under unidirectional flow and (d) aquatic canopies under oscillatory flow

to reduce nitrate to nitrite and then to ammonia before being assimilated by the canopy (Touchette & Burkholder 2000).

There was also a large variation in  $R$  for seagrasses; this may be explained in part by shoot density (shoot  $\text{m}^{-2}$ ) examined in different studies (Fig. 2b). The data from Thomas et al. (2000) were collected from a dense seagrass community (dominated by *Halodule wrightii* and *Thalassia testudinum* at 10 200–48 500 blades  $\text{m}^{-2}$ ) which showed high sensitivity to flow conditions with less evident uptake saturation. In contrast, data from Weitzman et al. (2013) were collected from a sparse seagrass community (dominated by *T. testudinum* at 280–1100 blades  $\text{m}^{-2}$ ) and showed uptake saturation at the lowest  $R$  under very low-flow conditions. The densest canopy community continued to be sensitive to flow conditions at high

flows while the sparse canopy only responded to flow conditions at very low flows.

The faster saturation observed in sparse canopies can be described by (1) the higher  $U_c$  and (2) the greater turbulence levels in these environments. For the same value of  $U$ ,  $U_c$  is greater in the sparse canopy compared to the dense canopy (Nepf 2012b, Abdolahpour et al. 2017). Thus, we expect that  $R$  (and ultimately saturation) will be faster in sparse canopies compared to the dense canopies when subjected to the same flow velocities. Additionally, the higher  $U_c$  will increase turbulence levels within the sparse canopies (Abdolahpour et al. 2018) which can positively impact  $R$  by constantly thinning or removal of the DBL (Denny & Roberson 2002, Stevens et al. 2003). Note that the experiments of Weitzman et al. (2013) were carried out in summer while Thomas et



Table 3. Fit of power regression to data. Note, no  $r^2$  is provided in runs indicated by (–) due to small number of data obtained from these experiments. The high p-values in runs indicated with (\*\*) are due to the small number of data obtained from these experiments

Canopy	Authors	Flow regime	$r^2$	p-value
Coral community	Atkinson & Bilger (1992) ( $\text{PO}_4^{3-}$ )	Unidirectional flow	0.69	<0.05
	Bilger & Atkinson (1995) (P)	Unidirectional flow	0.25	<0.05
	Bilger & Atkinson (1995) (N)	Unidirectional flow	0.19	<0.05
Seagrass community	Thomas et al. (2000) ( $\text{NH}_4^+$ )	Unidirectional flow	0.84	<0.05
	Cornelisen & Thomas (2002) ( $\text{NH}_4^+$ )	Unidirectional flow	0.58	<0.05
	Thomas & Cornelisen (2003) ( $\text{NH}_4^+$ )	Unidirectional flow	0.47	<0.05
	Thomas & Cornelisen (2003) ( $\text{NH}_4^+$ )	Oscillatory flow	0.72	<0.05
	Cornelisen & Thomas (2006) ( $\text{NH}_4^+$ )	Unidirectional flow	0.71	<0.05
	Cornelisen & Thomas (2006) ( $\text{NO}_3^-$ )	Unidirectional flow	0.86	<0.05
	Cornelisen & Thomas (2009) ( $\text{NH}_4^+$ )	Unidirectional flow	0.89	<0.05
	Weitzman et al. (2013) ( $\text{NH}_4^+$ )	Oscillatory flow	0.03	<0.05
	Weitzman et al. (2013) ( $\text{NH}_4^+$ )	Unidirectional flow	0.85	<0.05
	Weitzman et al. (2013) ( $\text{NO}_3^-$ )	Unidirectional flow	0.91	<0.05
Macroalga community	Hurd et al. (1994) ( $\text{NH}_4^+$ )	Unidirectional flow	0.42	>0.05**
	Larned & Atkinson (1997) ( $\text{NH}_4^+$ )	Unidirectional flow	0.01	<0.05
	Hurd et al. (1994) ( $\text{NO}_3^-$ )	Unidirectional flow	–	>0.05**
	Larned & Atkinson (1997) ( $\text{PO}_4^{3-}$ )	Unidirectional flow	0.01	<0.05
	Atkinson et al. (2001) ( $\text{NH}_4^+$ )	Oscillatory flow	–	>0.05**
	Atkinson et al. (2001) ( $\text{PO}_4^{3-}$ )	Oscillatory flow	–	>0.05**

al. (2000) was done in autumn. Although the details of light availability, epiphytes, etc. of these 2 studies were not available, the seasonality (e.g. plant physiology) may have an impact on the results obtained here.

In order to understand the unifying trend of aquatic canopies under a wide range of flow conditions, values of  $\text{Da}_E$  were plotted as a function of  $\text{Re}$ . The range of  $\text{Re}$  examined here covered a broad range of conditions from low- ( $\text{Re} = 7.3 \times 10^3$ ) to high-flow environments ( $\text{Re} = 3.3 \times 10^6$ ) (Fig. 3). This allowed the characterization of  $\text{Da}_E$  (and thus, reactive and non-reactive processes) across a wide range of field conditions. Our results revealed that  $\text{Da}_E$  ranged from about 0.1–10 for all communities, highlighting the wide range of environmental conditions that can exist in the real system. Specifically,  $\text{Da}_E$  calculated for corals was distributed homogeneously and did not show a clear trend with  $\text{Re}$  (Fig. 3). In contrast, data from seagrasses and from most macroalgae showed significant positive relationships ( $p < 0.001$  in both cases) between  $\text{Da}_E$  and  $\text{Re}$ . Importantly, under steady flow conditions, most communities showed  $\text{Da}_E < 1$  (i.e.  $\tau_E < \tau_p$ ), suggesting insufficient exposure time in these communities. Under wave action, however,  $\text{Da}_E \sim O(1)$ . This is an important result as it suggests that under wave action (such as those found in coastal ecosystems), canopies respond to highly dynamic environments. This is consistent with previous studies that showed exposure times in wave-driven flows in-

variably exceed those in corresponding unidirectional flows (see, e.g. field and laboratory studies by Thomas & Cornelisen 2003 and Abdolhahpour et al. 2017, respectively). These greater exposure times under wave flows may explain why a greater  $\text{Da}_E$  is observed for all canopies under these conditions.

#### 4. CONCEPTUAL FRAMEWORK OF REGIMES

We now conceptually explore the impact of increasing flows on nutrient uptake of a nutrient pulse. For simplicity, we assume that all nutrient pulses occur via transport into the canopy; i.e. allochthonous sources. We proposed above that, in analogy to the nutrient uptake and concentration relationships, there are 2 regimes in the relationship between  $R$  and  $U_c$ . In Regime I,  $R$  is linearly dependent on  $U$ , while in Regime II  $R$  is independent of  $U$ . Conceptually, we proposed the existence of 2 additional  $R$ – $U$  regimes. Increasingly high flows have the potential to trigger fragmentation and destruction of the canopies, ultimately resulting in zero nutrient uptake; we call this Regime IV. We also propose a transition between the maximum uptake of Regime II and the zero uptake of Regime IV; we label this transition as Regime III. Thus, we arrive at 4 potential regimes (Fig. 4).

We can also conceptualize sub-regimes. The Michaelis-Menten approach proposes that for a

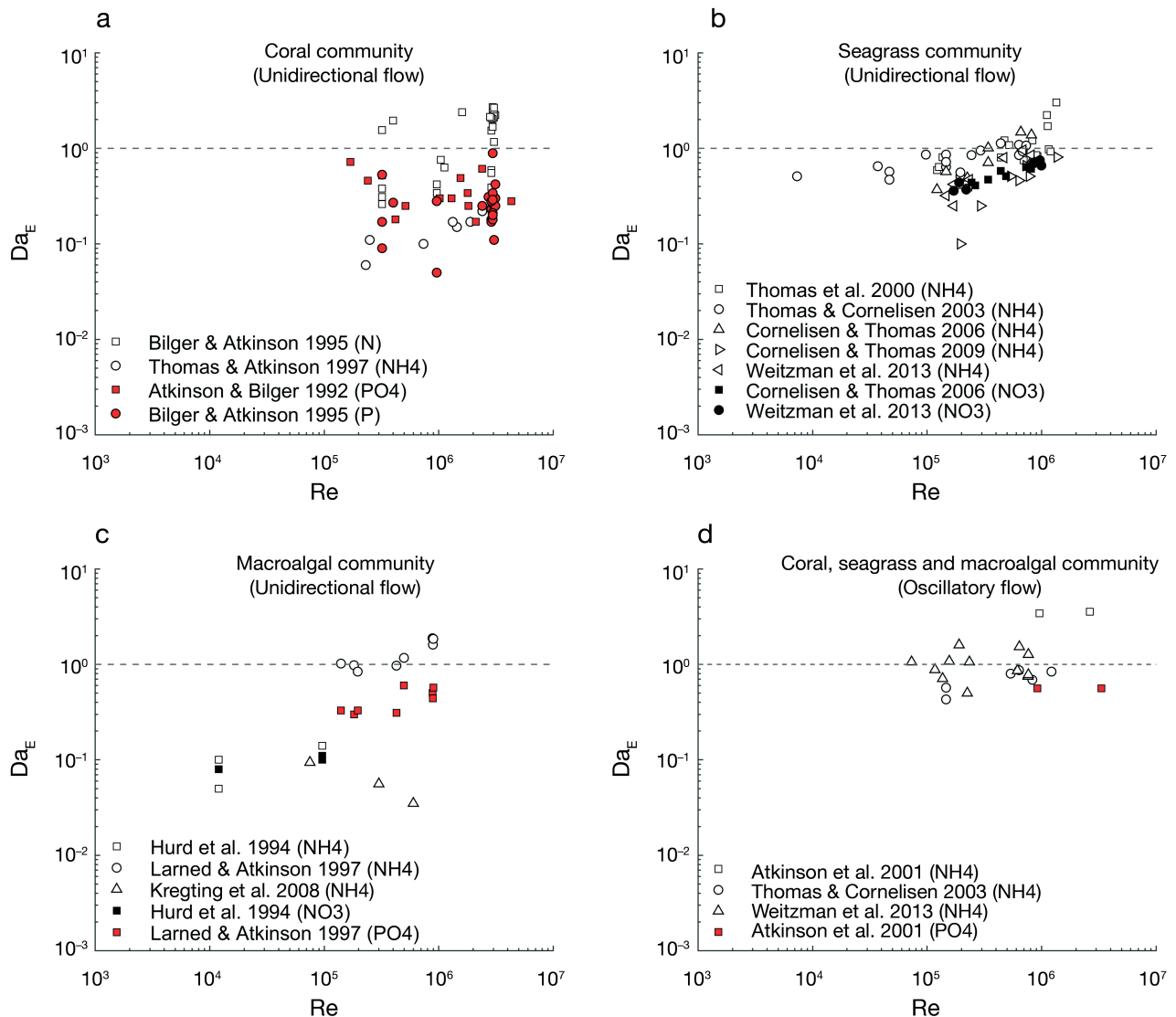


Fig. 3. Damköhler number versus Reynolds number for experiments carried out within (a) coral communities under unidirectional flow, (b) seagrass communities under unidirectional flow, (c) macroalgal communities under unidirectional flow and (d) various marine canopies under oscillatory flow conditions

given canopy density, at very low velocities, nutrient uptake is only mildly impacted by increasing velocity (Regime Ia; Fig. 4). As velocities increase, but while  $U < K_{[U]}$ ,  $R$  increases linearly with increasing  $U_C$  (Regime Ib; Fig. 4). Once  $R_{\max}$  is reached, uptake rates will again be independent of  $U$  (Regime II, Fig. 4). From the perspective of a nutrient pulse, we suggest that in this regime, nutrients are supplied as fast as they are taken up by the canopy community; i.e. supply and uptake are in balance (Regime II, Fig. 4). This optimal window may be of variable 'widths' depending on the community of interest. While a Michaelis-Menten approach goes no further than this plateau, if we again consider a nutrient

pulse, higher velocities would move the nutrients rapidly past the uptake receptors and the pulse would be flushed through the canopy prior to uptake (Regime III, Fig. 4). Under extreme flow conditions (Regime IV, Fig. 4), canopy communities would not remain anchored and we would not expect canopies to be present in areas where such velocities are common.

#### 4.1. Transitions and thresholds

The transition between different regimes would be initiated at different velocities, referred to as the crit-

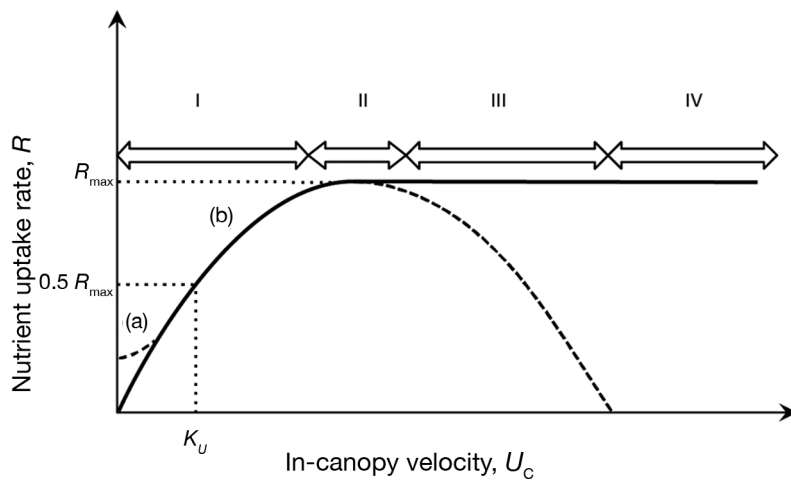


Fig. 4. Conceptual framework for transitional regimes (I–IV) based on Michaelis-Menten approach. See Section 4 for a description of Regimes Ia and Ib

ical velocities. In Regime I and at low flow velocities, nutrient supply becomes limited by the transport across the DBL (Thomas et al. 2000) and increasing flow velocities thin the DBL and increase  $R$ . Hurd et al. (1996) showed that transport within the DBL appeared to constrain nutrient supply when flow velocities were less than  $0.06 \text{ m s}^{-1}$ . More recently, Ghisalberti et al. (2014, Supplemental information) used a modeling approach to show that transport across the DBL became independent of flow at velocities greater than  $\sim 0.04 \text{ m s}^{-1}$ . The data compiled here clearly shows continued effect of flow velocity on nutrient uptake at velocities higher than  $0.06 \text{ m s}^{-1}$ , suggesting that nutrient uptake may be constrained by nutrient supply outside the DBL. The critical velocities for the Regime I to II transition vary between experiments (Fig. 2) and are likely impacted by canopy species, chemical species and canopy density.

The compiled data showed a range of flow velocities up to  $0.3 \text{ m s}^{-1}$  (with flows reaching  $0.6 \text{ m s}^{-1}$  over coral reef systems); however transition to Regime III was not observed in any of the data. Therefore, we cannot validate the existence, or not, of Regime III; however, Fonseca et al. (1983) and Fonseca & Bell (1998) showed that current speeds above  $0.25\text{--}0.53 \text{ m s}^{-1}$  induced spatial fragmentation of *Zostera marina* meadows. Koch (2001) suggested that current velocities between  $0.05$  and  $1 \text{ m s}^{-1}$  were needed to support the growth and distribution of healthy seagrass beds. The transition from Regime II to III may occur with the initiation of canopy fragmentation, but nutrient uptake under these conditions is rarely measured.

The transition to Regime IV was also not observed in the compiled data; however, Infantes et al. (2009) reported that an increase in wave energy caused a decrease of *Posidonia oceanica* cover, and that seagrass was not present when wave velocities were greater than  $0.38\text{--}0.42 \text{ m s}^{-1}$ . They proposed that this critical velocity determined the upper depth limit of *P. oceanica*. We suggest that this is an example of transition to Regime IV. In summary, while the compiled nutrient uptake data does not show evidence of Regimes III and IV, other published studies support the existence of these regimes.

#### 4.2. Ecological consequences

The conceptual model presented here assumes that the canopy community uses externally sourced (allochthonous) nutrients. Under this assumption, canopy communities would struggle to survive under both low and high flow velocities (both ends of the conceptual framework). However, alternative ecological strategies are likely used to survive under these conditions. As an example, if we consider canopies situated for prolonged periods in Regime I, when uptake is faster than nutrient supply, we might expect that canopies would rely on alternative sources of nutrients, for example nutrient recycling mechanisms within the canopy, or resort to modifying their structural characteristics to significantly increase the exposure times. Kaandorp et al. (1996) observed that corals tend to adapt their morphological characteristics based on the nutrient uptake regimes that they were exposed to; i.e. corals represented more compact cluster shapes in high-flow (or advection-dominated) environments and more branching shapes in low-flow (or diffusion-dominated) environments. The hydrodynamic drag and sheltering impacts observed in many canopies provide another example of such processes with an implied assumption that canopies can engineer their structural characteristics to increase in-canopy sheltering and optimize nutrient exposure timescales (Sand-Jensen & Pedersen 1999, Bornette & Puijalon 2011).

Hurd (2000) showed that under low-flow conditions macroalgae may acquire nutrients from sources other than the mainstream seawater. Koch (2001) also showed that physiological adaptation to stagnant con-

ditions can trigger the release of  $H^+$  on one side of the leaf blade, reducing the pH in the DBL (Prins et al. 1982) and increasing the  $CO_2$  concentration gradient across the DBL resulting in an increased flux of  $CO_2$  into the plant. If canopies resort to alternative mechanisms to ensure supply of nutrients, we would expect a broader window for Regime II, where nutrient uptake is balanced by nutrient supply and little effect of increasing velocities is observed. In these cases, we might expect a direct transition from Regime II to Regime IV. We suggest that when increasing chemical uptake occurs independently of flow velocities, an alternative physiological strategy may exist for accessing nutrients (Helmuth et al. 1997).

All the canopy communities show  $Da_E$  between 0.1 and 10 (Fig. 3). We expect conceptually that the  $Da_E$  threshold between conservative and non-conservative (or reactive) processes would be where  $Da_E$  is on the order of 1. However, the data compiled in Figs. 2 & 3 highlight that nutrient uptake (i.e. reactive transport) occurred across this range of  $Da_E$ . The data from corals and macroalgae under unidirectional flow align with Regime I and II whereas the data from seagrasses aligns with Regime I. We therefore suggest that observations will continue to show nutrient uptake until  $\tau_E \ll \tau_p$ , and therefore a threshold occurs not where  $Da_E$  is in the order of 1, rather uptake will continue to be measured until  $Da_E \sim O(10)$ . This can be considered the threshold between conservative and reactive processes. The absence of data for higher water velocities does not allow us to validate the transition between Regime II and III and therefore to define a threshold value of  $Da_E$  for conservative processes.

It is important to note that while we have endeavored to bring together observations from a wide range of flow and canopy conditions, natural systems are normally associated with a high level of complexity. This includes variation in the background nutrients, light and uptake kinetics (passive or active). Seasonal variation can significantly alter  $R$  by a direct impact on canopy morphology, light intensity and nutrient availability. Additionally, natural canopies (e.g. seagrasses, coral reefs and kelp forests) may be composed of communities with different species which possess abundant variation in both their morphologies and roughness scales (Duarte 2000, Weitzman et al. 2015). Previous studies have shown that the effect of high structural complexity in seagrasses is an important driver of macroinvertebrate density; in particular, that provided by algal epiphytes (Orth et al. 1984, Gartner et al. 2013). This intra-canopy variability is deemed to influence the

length scale of the meadow and subsequently alter interactions between species composition, canopy height, density and patchiness within the meadow (Lavery & Vanderklift 2002). All of these can significantly alter  $R$  by the canopy. Additionally, our recently improved understanding revealed that flexibility alone can significantly increase (by up to 35 %) the exposure time in flexible canopies (e.g. seagrasses, macroalgae and kelp forests) compared to corresponding rigid canopies (e.g. hard and stony corals) (Abdolahpour et al. 2018). Thus, it is conceivable to expect that further complexities associated with natural canopies will have a non-negligible impact on important ecological and biological processes such as exposure and reaction time. It remains to be ascertained which of these canopy characteristics affect  $R_{max}$ , and which affect  $K_{[U]}$ . More detailed investigation of the relationships between canopy characteristics, local hydrodynamics and nutrient uptake is required; our proposed regimes provide a framework for these investigations and a methodology for estimating threshold velocities.

## 5. CONCLUSIONS

The impact of above- and within-canopy hydrodynamics on canopy nutrient status has been frequently explored, however that research has used a variety of conceptual frameworks, nomenclature and experimental approaches. In this paper, we have consolidated data and findings from more than a dozen studies into a consistent conceptual model. The framework allowed us to explore the potential impact of hydrodynamics and canopy characteristics on nutrient uptake across 4 regimes that would contribute to the ecological health of the canopy. Placing the published literature within the conceptual framework also highlighted the relatively narrow range of conditions under which the experimental data were collected. Care must be taken when extrapolating nutrient uptake data collected from the relatively benign Regimes I and II, to conditions that may stress canopies, trigger fragmentation and ultimately produce unfavorable environments for canopy growth.

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research design and assisted with interpretation of results for ecological and biological implications. C.O. provided significant advice on model development, data analysis, interpretation as well as manuscript writing.

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