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Experimental assessment of the effects of cold-water coral patches on water flow

F. Mienis[1*], T.J. Bouma[2], R. Witbaard[2], D. van Oevelen[2], G.C.A. Duineveld[1]

[1] NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, 1790 AB Den Burg, Texel, the Netherlands

[2] NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, 4401 NT Yerseke, The Netherlands

*Corresponding author:

Furu Mienis

NIOZ Royal Netherlands Institute for Sea Research and Utrecht University

P.O. Box 59

1790 AB Den Burg

The Netherlands

e-mail: furu.mienis@nioz.nl

Abstract

Despite the importance for ecosystem functioning, little is known about flow patterns at the cold-water coral-patch scale (i.e., centimetre-meter). In-situ flow speed measurements using moorings or landers only provide general near reef flow patterns and experimental studies so far focussed on single coral branches for feeding and behavioural studies. We address this knowledge gap by means of a flume study. The effect of different coral patches (4, 10 and 25 cm height, respectively) created from dead coral branches on the ambient flow field and the refreshment rate of water within a patch was assessed, using three realistic current speeds (0.05, 0.15 and 0.3 m s^{-1}). High bottom roughness in combination with strong currents increased current velocity and turbulence in the wake of all patches, even with very low relief. The formation of two dynamically different environments was observed. The framework-water interface was characterised by high turbulence and enhanced vertical turbulent transport of momentum, while in the wake reduced turbulence and vertical mixing activity was observed, characterised by near stagnant flows. Subsequently, water-refreshment rates within a patch drastically decreased at current speeds less than 0.2 m s^{-1}, while near to unobstructed stream conditions were observed at current speeds above 0.2 m s^{-1}. Combining flume observations with available in-situ data suggest that heterogeneity and patchiness of cold-water coral growth is likely induced by flow patterns at the coral patch scale, influencing the fate of particulate and dissolved matter as well as oxygen exchange rates in and around the reef.

Introduction

Benthic ecosystems are governed by interactions between organisms and their chemical and physical environment. On the one hand, physical processes strongly affect the distribution of benthic fauna (Jumars & Nowell 1984, Cozzoli et al. 2014). Conversely, through their structural components (e.g. tubes, skeletons, leaves) protruding from the seafloor, organisms can modify the local near-bed flow and fate of dissolved and suspended matter (Bouma et al. 2007, Borsje et al. 2014). Organisms that modify their physical environment are generally referred to as ecosystem engineers (Jones et al. 1997). Colony-forming cold-water corals are a clear example of globally occurring ecosystem engineers. Reef forming cold-water corals, like the commonly occurring species *Lophelia pertusa* (Linnaeus, 1758) can modify the seafloor landscape at large scales (Buhl-Mortensen et al. 2010). They have developed in a wide variety of growth forms, ranging from isolated individuals, to compact thickets, reefs and kilometres long and wide carbonate mounds of several 100 m's height (Roberts et al. 2006). Such mounds, which are composed of a mixture of sediment and coral fragments (Mienis et al. 2009), are for instance found on the eastern slope of Rockall Bank (Logachev mound province). In many, if not most cold-water coral habitats there is substantial small-scale variation in framework height and patchiness is high, whereby dense erect thickets alternate with low relief rubble (Buhl-Mortensen et al. 2010).

In general cold-water coral reefs and mounds occur in areas characterized by strong bottom currents (Roberts et al. 2006, Mienis et al. 2007), which increases the potential for corals to alter flow and fluxes. The giant carbonate mounds on Rockall Bank (Kenyon et al. 2003), for instance, are considered a result of baffling of the flow by the corals, leading to accumulation of sediment between the coral framework (Dorschel et al. 2005). At mounds and reefs where coral growth outpaces sedimentation, the framework consists of a layer of dead coral framework protruding above the sediment, with the living cold-water coral polyps

found at the distal ends of the framework (Mortensen et al. 2008). The preference for cold-water corals to live on the outer parts of the framework is likely related to several factors. Corals will experience the highest food particle encounter rate at the distal ends of the framework and the lowest chance of depletion of food particles (Orejas et al. 2016a), which is important for their food supply. In addition living on open framework not being in close contact with the sediment will prevent the living polyps of corals from suffocation at times of high sediment load (Brooke et al. 2009). Furthermore, the dead coral framework forms a substrate for many epi-benthic species like sponges, hydroids, anemones and foraminifera as well as a shelter and nursery for mobile fauna, like fish, gastropods and echinoderms (Buhl-Mortensen et al. 2010, Lessard-Pilon et al. 2010, Soeffker et al. 2011). As a result cold-water coral habitats are generally characterized by elevated biodiversity, benthic biomass and are sites of enhanced carbon mineralisation (Henry & Roberts 2007, Van Oevelen et al. 2009). Various observations support the contention that processes at the intermediate scale (e.g. food supply, oxygen refreshment, sedimentation rates) are important for the functioning and distribution of live corals, associated biota and structure of the habitat (e.g. heterogeneous distribution of corals) (Comeau et al. 2014, Findlay et al. 2014). For example the microbial community composition within the cold water coral framework differs significantly from that in the water above the reef. This was explained by the dense coral framework constraining exchange of water and solutes between reef and overlying water mass (van Bleijswijk et al. 2015). Other studies showed that at *L. pertusa* reefs in areas with a dominant unidirectional current regime (e.g. Traena-Norway, Cape Lookout-USA) live corals are only found at the upstream site of structures, facing the strongest currents (Buhl-Mortensen et al. 2010, Mienis et al. 2014). Apparently organic matter in the water flow does not reach beyond the first frontier of live corals either because of distortion of the flow or depletion of food particles and

nutrients (Wagner et al. 2011). These observations emphasize the need for detailed understanding of flow patterns within and around coral patches.

Recent studies suggest that turbulence might be a factor of importance for cold-water coral distribution on medium to large spatial scales (van Haren et al. 2014). For instance, a large-scale hydrographic model of the Logachev coral mounds predicted intensified bottom currents at mound slopes caused by internal tides interacting with topography. Distribution patterns of live cold-water coral seems to match with such high energy slopes (Mohn et al. 2014). Actual in-situ measurements on a Logachev mound slope confirmed the intensified mixing which was 100 fold values in the open ocean (van Haren et al. 2014). A successive field and model study by Cyr et al. (2016) illustrated the interaction between coral mounds of different heights and flow resulting in enhanced tidal currents on the slopes where corals were found to be most abundant.

Contrary to slopes of the Logachev Mounds with their extensive cover of cold-water coral framework, many coral habitats are composed of a collection of coral thickets. Most likely, also the extensive coral habitat on Rockall Bank once started as individual thickets that merged into an extensive framework (Wilson 1979). To understand the onset of coral cover growth and its subsequent evolution to heterogeneous habitats or mounds, it is important to obtain insight into coral-water flow interactions at a scale intermediate between the landscape-scale represented by a mound province, (e.g. Mohn et al. 2014, or whole reef studies e.g. Guihen et al. 2013), and the smallest scale represented by responses of individual polyps to flow (Purser et al. 2010, Gori et al. 2014, Orejas et al. 2016a). To our knowledge, there is scant information on this subject in the context of colony forming cold-water corals such as *Lophelia pertusa*. This in contrast with large number of studies on flow alteration by

underwater vegetation and consequences for sedimentation (e.g. Bouma et al. 2007, Kondziolka & Nepf 2014).

As cold-water corals form vulnerable hotspot ecosystems, better insight is required into factors that affect where and even more importantly how corals grow (e.g. thickets, continuous coral cover). Collecting in-situ measurements in close vicinity of coral framework is a technical challenge. Only one study is known (Guihen et al. 2013) where in-situ measurements were made of near-bed current speeds inside and outside a cold-water coral reef in a 200 m deep coastal reef (Tisler, Norway). This showed that the roughness of coral structures created a thicker bottom mixed layer above the reef potentially allowing for more vertical transport of particles towards the polyps. However, so far it has not been possible to obtain detailed in-situ current measurements around individual coral patches or colonies in a deep coral reef or mound habitat. We aim to address this knowledge gap by means of a flume study, in which we assess the effect of cold-water coral patches of different dimensions (4, 10 and 25 cm height) on the ambient flow field and turbulence levels, using three realistic current speeds (0.05, 0.15 and 0.3 m s^{-1}) measured on the Irish margin (cf. field data by Dorschel et al. 2007 and Mienis et al. 2007). With these measurements we intend to expand insight into processes that influence transport of particulate and dissolved matter, and corresponding exchange rates between the coral framework and overlying water relevant for food capture, oxygen supply and particle settling.

Methods

Coral patches

Fossil cold-water coral branches of non-eroded framework were collected with a box-corer in the Logachev mound province on the SE Rockall Bank margin during a cruise (64PE360) with the RV Pelagia in 2012. Sites with a dense coral framework were selected based on

video recordings and subsequently sampled with a squared NIOZ box-corer (55 cm height and 50 cm wide). Video observations and bottom samples collected with the box-corer showed great heterogeneity in cold-water coral cover on the mounds (Figure 1). To simulate the in-situ structures observed, coral patches were made with different characteristics (height and density) using various sized coral branches (Figure 1 and 2). Selected branches that were used were part of overlying unburied framework and therefore showed no signs of erosion. Only branches that were not covered by epifauna were selected and if present epifauna was removed.

As observed in box-core samples, branch size decreased towards the seafloor, which has been related to bio-erosion of coral debris (Beuck & Freiwald 2005). Centimetre sized coral branches, representing coral rubble, were used as base for all patches, which were placed on top of steel plates of 50 cm in length and 58 cm in width. Patches were created as homogenous as possible, whereby the whole width of the flume was filled with a similar coral density and height. Three different patch types were created, representing different environmental settings as observed on in-situ video images (Figure 1 and 2). The low relief patch type (LP) consisted of a thin layer (maximum 4 cm above bottom) of centimetre sized coral branches. The middle relief patch type (MP) consisted of a layer of cm sized coral patches with some larger erect coral colonies on top (maximum 10 cm above bottom). The high relief patches (HP, maximum 25 cm above bottom) were created using even larger decimetre sized coral colonies (Figure 2). No sediment cover was present at the bottom of the flume. Only a small amount of fine sediment was kept in suspension in the flume to create backscatter, needed for the measurements with the Acoustic Doppler Velocimeter (ADV).

Hydrodynamic measurements

The effect of flow on the different cold-water coral patches was measured in a large racetrack flume at the NIOZ laboratory in Yerseke (Figure 2). The water column height (z) was 0.4 m and the total volume of the flume was 10 m³ (for a detailed description see Bouma et al. 2005). Flow velocity components in the downstream (u), cross stream (v) and in the vertical direction (w) were measured at 20 Hz with a Nortek AS Acoustic Doppler Velocimeter (ADV) mounted on a 3-dimensional positioning system. Measurements were performed at three free stream velocities ($\bar{u}$ at z=0.3) of 0.05, 0.15 and 0.3 ms⁻¹, which are representative current speeds for cold-water coral habitats on the Irish margin (Dorschel et al. 2007, Mienis et al. 2007). Vertical hydrodynamic profiles were measured in front, above and behind the different patch types and ranged from close to the bed (z = 0.01 m) to 0.3 m above the bed with step sizes of 0.02 m (Figure 2). Time averaged components ($\bar{u}$, $\bar{v}$ and $\bar{w}$) and their fluctuations (u', v' and w') were calculated by averaging the temporal measurements at each sampling location (n=200). Data points with correlations less than 70% (indicating unreliable data) and obvious outliers were filtered and removed (Morris et al. 2008). Subsequently, turbulent kinetic energy (TKE, $0.5(\bar{u}'^2+\bar{v}'^2+\bar{w}'^2)$ in m s⁻¹), was calculated to define vertical mixing, which potentially influences vertical fluxes of food as caused by turbulence (Folkard & Gascoigne 2009). In addition the vertical flux of momentum, the Reynolds Stress ($-\rho(u'w')$ in Pa, was calculated, which is an indicator of vertical mixing activity and is thus a measure of access to water column resources, whereby a positive Reynolds stress indicates momentum flux towards the bed (Hendriks et al. 2008).

Dye measurements

In addition to flow measurements, the refreshment rate of water expressed as the residence time of water was measured in a high coral patch. A fluorescent dye Uranine (Na-salt of Fluorescein; $C_{20}H_{10}Na_2O_5$, M=376.28 g mol⁻¹) was used as a conservative tracer. Uranine is a

relatively cheap, non-toxic tracer that can be monitored at low concentrations using a fluorosensor. Three fluorosensors (Cyclops-Turner designs) were placed at 4 cm above the bottom within the coral framework of a high coral patch at 10, 30 and 45 cm from the leading edge of the patch, respectively (Figure 1F and 2). A solution of 2 mg Uranine mixed in a litre of seawater collected from the flume was prepared and 10 ml of this solution was injected in one pulse at the leading edge of the patch at 4 cm above the bottom of the flume (Figure 2). Residence time of the solution was measured at a range of current speeds (0.05, 0.1, 0.15, 0.2, 0.25 and 0.3 m s^{-1}), resembling current speeds as measured in-situ near cold-water coral areas on the Irish margin (Dorschel et al. 2007, Mienis et al. 2007). Measurements were repeated 5 times at each setting. The residence time was calculated by subtracting the arrival time after release of the dye at a specific sensor from the total time that dye was observed in front of a sensor until it disappeared. Peaks were integrated and analysed with the Origin Pro 9.1 peak analyser software. The Uranine solution was also injected in front of the second and third sensor in line to quantify the reduction in flow, due to presence of the coral framework, mimicking the effect of flow on dissolved and particulate matter that is captured in between the coral framework (e.g. from vertical settling). For comparison a blank measurement (i.e. without a coral patch) was also carried out, whereby the fluorosensors were placed in the same configuration.

A second set-up was created, whereby the sensors were placed behind the coral patch at 4 and 10 cm above the bottom, respectively. Uranine was injected at 4 cm above the bed at the leading edge of the patch and measurements were repeated 5 times. Again the residence time was calculated as well as the respective arrival time of the dye at the different sensors. Data from the Cyclops fluorosensors were continuously recorded with a frequency of 1 Hz.

Statistics

To test whether velocity profiles measured in front and behind the patch differed significantly among each other and to the mean of all, a series of Generalized Additive Models (GAM) (Wood, 2006) was fitted through the velocity data over the measured depths. In a GAM, a penalized smoother function (spline regression) is fitted. In this case it was fitted through the velocity profiles describing the change of current speed (or TKE or residence time) over depth. No specific linear relationship between current speed or other variables is assumed but a smoother function is estimated, which fits the data best. The use of GAM, enables the simultaneous statistical comparison of the entire velocity profiles (smoother functions) instead of post hoc comparison of single measurements or means at specific depths and distances (treatments). The disadvantage is that no simple parametric function is derived by which the profiles can be predicted on basis of other parameter values. It is a best description of the observed patterns and differences therein under the tested conditions.

In the first analyses the measured current speed in relation to depth (Z) and distance (X) are analysed. Measurements immediately above the patch were excluded, due to absence of data in a large part of the profile. A series of four nested models with increasing complexity were tested and the best of these 4 models (Equation1) was selected on basis of the lowest value of the Akaike Information Criterion statistic (AIC).

$U_p = \alpha + f(Z:X) + \beta_l (X) + \varepsilon$ (**Equation 1**)

$\quad\quad$ with $\varepsilon \sim N(0, \sigma^2)$

where U_p, is defined as a constant (α) and a function of depth (Z) and distance (X) for each distance separately. β_l is the coefficient of the mean (common) current-depth profile for all distances (X), and the error (ε) is normally distributed. The model fit was checked by plotting residuals against fitted values and by checking for homogeneity of variance between the

tested factors. The resulting smoother functions for each distance (X) were statistically compared with an F-test and used to evaluate the effect of the factor Distance.

A similar procedure was followed to test whether the relationship between residence time of the fluorescent dye with current speed differed between an experimental setup with and without a coral patch.

$$log(t_{res}) = \alpha + f(U : Patch) + \beta_1 (Patch) + \beta_2 (X_{inj}) + \beta_3 (X_{Sensor}) + \varepsilon \quad (\textbf{Equation 2})$$

$$\text{with } \varepsilon \sim N(0, \sigma^2)$$

where α is a constant, residence time is a function of velocity and presence or absence of the patch, β are coefficients and ε is the error. The residence time was modelled as being dependent on current speed (U) and the absence or presence of a coral patch (*patch*), the location of the injection point (X_{inj}) and position of the sensor (X_{sensor}) (Equation 2). To fulfil the requirements of a good fit, the residence times (t_{res}) were log transformed to obtain normal distributed residuals and homogeneity of variances.

Results

Hydrodynamic measurements

Velocity vector plots of $\bar{u}$ and $\bar{w}$ clearly showed different patterns depending on patch type and velocity treatment. The high patch caused the largest changes in flow pattern. At high current speeds (0.3 m s^{-1}), flow is deflected upwards and accelerated above the patches, resulting in a fast flowing upper layer and reduced velocities immediately behind the patches (Figure 3). Mean water velocity increased to 0.45, 0.23 and 0.06 m s^{-1} above the high patch at velocity treatments of 0.3, 0.15 and 0.05 m s^{-1}, respectively (Figure 4). The accelerated upper layer was still detectable 2.2 m behind the patch in the 0.15 and 0.3 m s^{-1} velocity treatments while at 0.05 m s^{-1} free stream velocities were observed at 1.2 m behind the high patch. Flow

speeds in the wake of the coral patch (z=0.01-0.18) were reduced to almost 0, only to increase again at 2.2 m behind the patch (Figure 4). The mid patch had a smaller influence on the flow velocity as compared to the high patch. However, also here velocities were reduced to almost 0 behind the patch and the division between fast flowing upper water and slow flowing water near the bottom of the flume could still be observed 2.2 m behind the patch (Figure 4). The low patch showed qualitatively similar patterns at all velocity treatments. At velocity treatments of 0.3 m s^{-1} mean water velocities at z=0.03 decreased to 0.12 m s^{-1} behind the low patch and showed a minor increase at 2.2 m behind the patch up to 0.2 m s^{-1}, which shows that even a low relief, like coral rubble, already affects the flow within and near a reef system (Figure 3). At low velocity treatments of 0.05 and 0.15 m s^{-1} changes in flow behind the low patch were minimal (Figure 4).

In all treatments, Reynolds stress showed positive peaks immediately behind the patches just below the maximum height of the patches, corresponding with the boundary between the fast and slow flowing layers. This distinct Reynold stress showed that this region is dynamically different from the area above and below, indicating that fluxes in this area are oriented towards the bed (Figure 5). The zone of positive Reynolds Stress became wider moving away from the patches, indicating increased mixing between the two hydrodynamically different environments.

Turbulent kinetic energy (TKE) levels, a measure of turbulent activity, strongly increased above and specifically behind all patches (Figure 6). However, the position of the TKE maxima differed between velocity treatments and patch type. Maxima were again observed just below the maximum patch height at the boundary between the fast and slow flowing water layers, indicating increased mixing just below the height of the top of the patch. Prominent peaks in TKE were observed between 10 and 20 cm above the bottom behind the high patch at current speeds of 0.15 and 0.3 m s^{-1}. At greater distance behind the high patch,

TKE values remained relatively high towards the bottom of the flume, indicating increased mixing. At 0.05 m s^{-1} a small TKE peak was observed immediately behind the high patch and only a minor peak at 2 m (Figure 6). The same patterns were observed for the mid patch, although TKE values were a factor two lower. At current speeds of 0.3 and 0.15 m s^{-1} the low relief patch showed a distinct TKE peak right behind the patch at 5 cm above the bottom, and a peak twice as small at 2 m behind the patch (Figure 6). At a current speed of 0.05 m s^{-1} changes in TKE were observed immediately behind the low patch. However, no changes were observed at greater distance behind the patch.

In all combinations of patch-type and flume current speed, the model as given in equation 1 provided the best fit. The resulting model fits with confidence bands are shown in Figure 7 and in the supplementary Figures 1 and 2. The p-values belonging to the significance test of the factor Distance are summarized in Table 1 together with the Rsq and percentage deviance explained.

Dye measurements

Dye was injected at the leading edge of a high patch and the refreshment rate expressed as the residence time of water was measured inside the coral patch and compared to measurements without a coral patch (blanks). Measurements were conducted under different velocities at three sensor positions, i.e. at 15, 30 and 45 cm from the front of the patch (Figure 2). In general residence times showed a tendency to decrease with increasing speed and increasing distance from the leading edge (Figure 8). A GAM model incorporating (log-transformed) residence times with speed and sensor position as covariates shows all parameters to have a significant effect on residence time. In figure 9 a comparison of the recalculated residence times excluding the effects of injection point or sensor is given showing an evident difference between the absence or presence of a coral patch.

At velocities above 0.2 m s^{-1} the influence of the coral patch on the residence time of the dye became minimal, implying that all water within the coral framework is renewed at a relatively constant rate. At velocities less than 0.1 m s^{-1} the coral patch increased residence times at the positions of the second and third sensor with a factor three as compared to blank (without patch) measurements (Figure 9). The effect of sensor position is clearly visible in Figure 8. At the first sensor position the increase of residence times compared to blank measurements, were minimal. However, at the second and third sensor residence times increased at velocities of 0.05 m s^{-1} with up to 25 and 35 seconds, respectively (Figure 9). This difference of about 10 seconds between sensors most likely reflects flow inside the framework (not measured) becoming weaker with increasing distance from the leading edge. Dye injected at 4 cm before the second and third sensor showed an increase in residence time of the dye within the patch. Longest residence times were measured at the injection before the third sensor, whereby the average residence at 0.05 m s^{-1} time increased from 58 seconds at injection before the first sensor to 100 seconds at injection before the third sensor.

A second experiment was carried out whereby dye was injected at the front of the high-relief patch and sensors were mounted in a vertical position behind the patch at 4 and 10 cm above the bottom, respectively. Longest residence times were observed at the lowest velocity treatments. Compared to blank measurements the presence of the coral patch increased the residence time with more than 15 seconds at the strongest current velocities (Figure 10). Dye arrived slightly earlier at the sensor mounted at 10 cm above the bottom of the flume and also the residence time was shorter at all velocity treatments, pointing to mixing and exchange at the boundary between framework and overlaying water, which was also observed in high TKE values at the boundary between the coral patch and the overlying water (Figure 5).

Discussion

By using realistic flow velocities, the present flume experiments start to provide us with a basic understanding of how various forms of cold-water coral patches with different characteristics affect mixing and turbulence patterns. Such insights are needed to bring us closer to explaining water flow within and around coral patches, which strongly affect ecosystem functioning. So far flow patterns at the intermediate coral-patch scale are poorly studied due to technical limitations hampering in-situ studies and lack of experimental studies beyond the coral branch scale (Guihen et al. 2013, Gori et al. 2014). The flume tank experiments in this study thus provide novel insights in the quantitative near-bed flow processes and interactions around and within a coral patch. The experiments clearly showed that different sized coral patches changed flow patterns around and within patches and turbulence downstream of patches, as well as the refreshment rate of water within patches.

These alterations on coral patch scale and specifically the turbulence that is created will affect particulate and dissolved matter supply to living corals, exchange of matter within the coral framework with the associated reef fauna and particle settlement as has been shown for tropical coral reefs (Reidenbach et al. 2006; Genin et al. 2002). This will ultimately steer coral distribution patterns, and might explain the heterogeneous mosaic of living and dead coral patches often observed on mounds and reefs (Buhl-Mortensen et al. 2010). In the discussion below reference is made to comparable flume studies using tropical corals. Though latter studies support the relevance of studying small and medium scale water movement, it needs to be stressed that the morphology of tropical corals strongly differs from the structures that cold-water corals build. Moreover, environmental conditions (i.e. turbulent shallow versus quiescent deep-sea) and physiology and resources (i.e. light versus suspended particles) in cold and tropical reefs strongly differ. These fundamental differences preclude quantitative comparison of results from the two types of studies.

Hydrodynamic patterns and implications for coral growth

Small scale turbulence on a coral patch scale (centimetres to meters) might influence (larval) dispersal processes and food acquisition, depending on the exchange rates between a reef and the surrounding ocean (Baird & Atkinson 1997, Reidenbach et al. 2006). Observations on shallow water tropical coral reefs have shown that topographic roughness greatly enhances turbulence and mixing within the benthic boundary layer, which plays an important role in replenishing the reef with particles (plankton), nutrients and even having an effect on ocean acidification (Genin et al. 2002, Comeau et al. 2014). This so called mass transfer limitation is affected by the roughness of the surface and current speed, whereby exchange rates increase with increasing roughness and current speed (Abelson et al. 1993; Reidenbach et al. 2007; Chang et al. 2009). The current study implies that most likely similar mechanisms apply to cold-water coral habitats where current speed attains similar levels as in the study of Genin et al. (2002) and roughness is sufficient to enhance shear stress (Guihen et al. 2013).

In this study the presence of a cold-water coral patch in combination with high bottom roughness of the coral branches and enhanced currents, increased the current velocity and turbulence in the wake of all coral patches, even with very low relief. The formation of two dynamically different environments was also observed near other epi-benthic structures, like sea grass beds and tropical coral reefs (Baird & Atkinson 1997, Weitzman et al. 2015) and in flume experiments with artificial obstacles blocking the flow (Chen et al. 2012; Kondziolka & Nepf, 2014). One region is characterised by high turbulence and enhanced vertical turbulent transport of momentum at the framework-water interface. This is the part of the framework where living cold-water coral polyps are mostly observed, growing on the distal ends of the framework (Rogers 1999, Mortensen et al. 2008). This is also the part of the reef that has the highest potential to exchange metabolites (Baird & Atkinson 1997).

In the wake of the coral patch between the bottom of the flume and maximum framework height reduced turbulence and vertical mixing activity were observed, whereby mass transfer was reduced. Within the wake, immediately behind the patch, increased momentum fluxes to the seabed were observed as indicated by elevated values of Reynolds stress. This wake region is characterised by near stagnant flows which are suboptimal for coral growth due to reduced access to particle flux (see Chang et al. 2009). This effect is most likely exacerbated by gradual depletion of food resources (particulate matter and nutrients) and oxygen in the flow during passage over the frontal and distal parts with live corals. Moreover in areas with high sediment loads, stagnant flow induces sedimentation (cf. Bouma et al. 2007), which could negatively influence coral growth (Brooke et al. 2009). In conclusion, strongly reduced velocities behind the patches do not provide ideal environments for coral growth, which likely explains the occurrence of living corals at the current facing site of mound and reefs dominated by unidirectional flow (e.g. Cape Lookout (Mienis et al. 2014), Tisler reef (Lavaleye et al. 2009)).

Wake effects related to the presence of the different patch types reach up to several meters in the high velocity treatments, while they dissipate quickly at velocity treatments at 0.05 m s^{-1}. In the wake of the patches increased mixing and fluxes were observed towards the bottom of the flume, which can have a positive effect on deposition in close vicinity to the patch and inhibit deposition of particles further away from the patch due to enhanced levels of turbulence (Chen et al. 2012). Especially at current velocities above 0.15 m s^{-1} applied to the middle and high patch, wake effects were still clearly present at 2.2 m behind the patches. This flow diversion reduces the velocity in the wake downstream of the patch, which could lead to lateral expansion of patches through the interactions of patch wakes as has been modelled for aquatic vegetation (Kondziolka & Nepf 2014) and tropical coral canopies (Reidenbach et al. 2007). At some distance where vertical mixing in the benthic boundary

layer has replenished resources, new patches may arise leading to a series of spatially separated reefs as was observed at larger scales in Traena (Norway) (Cathalot et al. 2015), Florida slope (USA) (Grasmueck et al. 2006) or Darwin Mounds (NE Atlantic) (Masson et al. 2003).

Cold-water corals are highly dependent on currents that transport pelagic food (Duineveld et al. 2007) and they mainly feed on (phyto)detritus, suspended particulate organic matter or zooplankton (Duineveld et al. 2007, Becker et al. 2009, Wagner et al. 2011). Laboratory studies have shown that cold-water corals might exploit different food sources depending on the flow rate (Purser et al. 2010, Orejas et al. 2016b). They found that the net capture rate of zooplankton by *L. pertusa* decreases when flow velocity exceeds 0.07 m s^{-1}. However, such optimal conditions for plankton capture clearly do not fit with field observations, showing most living polyps to be distributed on top of framework (Mortensen et al. 2008), which is subject to the highest current speed and turbulence as shown in this experiment. In addition, in many reef locations average current velocities exceed 0.1 m s^{-1} (Duineveld et al. 2007, Mienis et al. 2014, Kenchington et al. 2017). In fact, *Lophelia pertusa* has been observed in-situ with fully extended tentacles in current speed of 0.1 m s^{-1} and much higher (Buhl-Mortensen et al. 2015).

Water renewel within coral patches and its ecological implications

In a laboratory flume study (Chang et al. 2009) measured decreased flow and stagnant patches of water inside a single colony of a tropical coral. The alteration of the flow in the experiment by Chang et al. was especially strong at the highest velocity they applied (0.07 m s^{-1}) and downstream in the colony, and according to the authors could cause depletion of nutrients and reduced access to particulate matter. Likewise, in this study it was shown that within a coral patch residence time of water and conversely flow rates within the coral patch increased up to

3 times at velocities below 0.2 m s^{-1} with the effect becoming stronger at lower velocities. This could have a positive effect on the ability of associated epifauna to settle on or attach to the framework and exchange dissolved and particulate matter (Koehl & Hadfield 2010). However, if the flow is diverted and water resides too long between the coral framework depletion of particulate matter, nutrients and oxygen might occur. The high respiration rates of the framework community and notably of the underlying sediment at the Rockall coral mounds (van Oevelen et al. 2009) promote a rapid depletion of oxygen within the framework. Such conditions might explain why van Bleijswijk et al. (2015) found a completely different microbial community in the water in between the framework compared to both the water overlaying the reef and the sediment and why active N$_2$ fixation (a process inhibited by oxygen) may take place within the coral holobiont (Middelburg et al. 2015).

In contrast to Chang et al. (2009) who found increased stagnancy with increased velocity, the residence time of dye at the highest realistic velocities that we applied, i.e. above 0.2 m s^{-1} dropped towards nearly unobstructed flow conditions. Under these circumstances water in a patch of this size will potentially become refreshed and oxidized, which is important for the epifauna living on the dead coral framework, such as sponges, bryozoans, hydrocorals, and molluscs. Indeed periods of strong flow seem to relate to higher oxygen uptake rates in Norwegian reefs (Rovelli et al. 2015). For some suspension feeders that live in between the dead coral framework like sponges strong currents are equally important. For example the common glass sponge *Aphrocallistes* a common species on cold-water coral reefs uses current-induced flow during bouts of high current speed (>0.15 m s^{-1}) to filter up to 2/3 of its daily total filtration volume (Leys et al. 2011), but at the same time may stimulate water exchange by autonomous pumping in times of low current velocities. Beside energy requirements sponges are also dependent on the ambient flow for oxygenation (Schlaeppy et al. 2010).

It has been shown that cold-water coral reefs act as a filter depleting the overflowing water of high quality particulate organic matter. For example, at Tisler reef (Sweden) the amount of particulate organic carbon was depleted across the reef in spite of an increase in quality due to admixture of coral produced mucus (Lavaleye et al. 2009, Wagner et al. 2011). While accelerated flow over corals thickets promotes particle pick-up and respiration, the strongly reduced flow and collision with coral branches within coral patches will induce settlement of inorganic and organic particles as was shown by the increased residence times of water when dye was released within the framework before the second and third fluorosensor. The high respiration rates of the underlying sediment point at an enhanced input of organic material. This deposition, though essential for mound build-up (De Haas et al. 2009), also tends to deplete resources within the framework and limits its extension. Depletion through combined acceleration over and reduction of flow in the framework is most likely responsible for the observed heterogeneity of coral coverage in habitats which have a unidirectional current (~ resource supply) such as Traena where coral thickets alternate with bare sediment. Replenishment of resources through turbulent mixing behind the coral thickets is essential for the repetitive re-occurrence of thickets (Kondziolka & Nepf 2014). More in general, also in areas with tidally alternating current direction depletion of resources will at some point hamper framework development. For instance at the Logachev Mounds with a strong diurnal currents, the most extensive framework is found on the sloping faces of the mounds with a 100-fold turbulent mixing (Mohn et al. 2014, van Haren et al. 2014). On flat mound tops, the framework is patch-like organized (Mienis, pers. Obs,).

Summary

Field measurements revealed heterogeneity of framework in many coral habitats notably those with unidirectional currents. Our flume experiments show that once heterogeneity is created,

flow patterns at the patch scale are likely to maintain and even enhance such heterogeneity. That is, some regions of the reef become more suitable for coral growth (fast flowing upper layer) and other regions less suitable (lee site of coral patches) due to low turbulence levels, increased sedimentation rates and depletion of dissolved and particulate matter. The different sets of hydrodynamic conditions above, inside and behind a coral patch found in this study in combination with consequences for coral feeding and sedimentation, match with observed heterogeneity in the field. This pertains specifically to live coral distribution in areas with a dominant unidirectional current regime, like in the West Atlantic along the US continental margin at the Miami terrace and near Cape Lookout (Correa et al. 2012, Mienis et al. 2014) and along the Norwegian coast at the Tisler and Stjernsund reefs (Lavaleye et al. 2009, Rüggeberg et al. 2011). In these areas live cold-water corals solely occur at sites of the reef that are influenced by the strongest currents, where (food) particle encounter rates are highest (Thiem et al. 2006). Downstream, conditions for live coral apparently become less favourable giving rise to a zone with erect dead coral and coral rubble (Cathalot et al. 2015). Although in this part growth of live coral could be hampered by sedimentation, as indicated by our flume results, we assume that resource depletion is also an important factor here.

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Figure and table captions

Table 1: GAM models fitted through velocity data over the measured depth. Corresponding p-values belonging to the significance test of the factor Distance, Rsq and percentage deviance of the different patch types are indicated.

Figure 1: Areas with different characteristics in coral cover as observed in the Logachev mound area on the Irish margin, NE Atlantic. A. coral debris on top of sediment. B. Coral fragments on top of coral debris. C. Dense cold-water coral patches with living colonies on top of coral fragments. D. Box core taken in the Logachev mound area for collection of corals used in this study. E. High coral patch created in the laboratory. F. Positioning of the fluorosensors in the high patch.

Figure 2: A. Representation of the low, middle and high relief coral patches. B. Schematic overview of the racetrack flume used to asses effects of unidirectional flow on coral patches (for details (Bouma et al. 2005). C. Representation of dye experiments, indicating position of dye injection and fluorosensors. Experiments were carried out whereby either sensors were placed within a high relief patch (dots) or behind the patch (squares).

Figure 3: Vector plots of horizontal ($\overline{u}$) and vertical ($\overline{w}$) mean current speed (m s^{-1}) over the low, middle and high relief coral patches. Patches were subjected to three velocity treatments

A. 0.3 m s^{-1}, B. 0.15 m s^{-1} and C. 0.05 m s^{-1}. Patch size and height is denoted by the grey contours.

Figure 4: Velocity profiles (U) at free stream velocities of 0.05, 0.15 and 0.3 m s^{-1}. Velocities were measured 0.5 m in front, above, 0.5 m behind and 3.0 m behind the different patch types.

Figure 5: Reynold stress profiles at free stream velocities of 0.05, 0.15 and 0.3 m s^{-1}, which were measured 0.5 m in front, above, 0.5 m behind and 3.0 m behind the different patch types.

Figure 6: Turbulent kinetic energy profiles at free stream velocities of 0.05, 0.15 and 0.3 m s^{-1}, which were measured 0.5 m in front, above, 0.5 m behind and 3.0 m behind the different patch types.

Figure 7. GAM models fitted through velocity data over the measured depth. A. High patch with 0.3 cm s^{-1} velocity. B. Low patch with 0.05 m s^{-1} velocity. Data of the different treatments are presented in supplement A.

Figure 8: Residence times of dye injected at different positions in front and within a high relief coral patch at free flow velocities of 0.05, 0.1, 0.15, 0.2, 0.25 and 0.3 m s^{-1}. A. Blank measurement with no coral patch. B. Dye injected in front of high relief coral patch. C. Dye injected in front of sensor 2 (S2). D. Dye injected in front of sensor 3 (S3).

Figure 9: A. Plot showing increased residence times at position S1, S2 and S3, due to the presence of the high relief coral patch in the flume. B. GAM model data show modelled residence time (y-)axis being dependent on current speed and presence or absence of a coral

patch. A comparison of the recalculated residence times excluding the effects of injection point or sensor is given.

Figure 10: Dye experiment with sensors placed behind the patch at 4 and 10 cm at free flow velocities of 0.05, 0.1, 0.15, 0.2, 0.25 and 0.3 m s^{-1}. A. Residence and arrival time of blank measurement with no patch. B. Residence and arrival time of dye at sensor placed at 4 cm above bottom with presence of high coral patch. C. Residence and arrival time of dye at sensor placed at 10 cm above bottom with presence of high coral patch.

Supplementary figure 1: GAM models fitted through velocity data over the measured depth in order to test whether velocity profiles measured in front and behind the patch differed significantly among each other. Penalized smoother functions are fitted through the velocity profiles describing the change in current speed over depth. Note that measurements immediately above the patch were excluded, due to absence of data in a large part of the profile.

Supplementary figure 2: GAM models fitted through the TKE data over the measured depth in order to test whether TKE profiles measured in front and behind the patch differed significantly among each other. Penalized smoother functions are fitted through the TKE profiles describing the change in TKE over depth. Note that measurements immediately above the patch were excluded, as well as other measurements that showed absence of data in a large part of the profile.

Tables and figures

U	Patch type	fDist p-value	R-sq	% Dev expl
0.05	High	7.70E-05	0.94	96.2
	Medium	3.84E-07	0.95	97.2
	Low	1.16E-03	0.87	90.8
0.15	High	3.07E-10	0.98	98.9
	Medium	0.705	0.74	80.1
	Low	0.691	0.91	93.7
0.3	High	2.23E-15	0.99	99.6
	Medium	8.74E-06	0.93	95.7
	Low	0.0719	0.97	98.3

Table 1

Figure 1

A.

Low Patch 4 cm

Mid Patch 10 cm

High Patch 25 cm 40 cm Water level in flume

B.

Drive belt

Carriage with ADV

Coral patch

Flow direction →

Test section

17.55 m

C.

Dye injection →

S1 S2 S3 25 cm

Dye injection →

P2
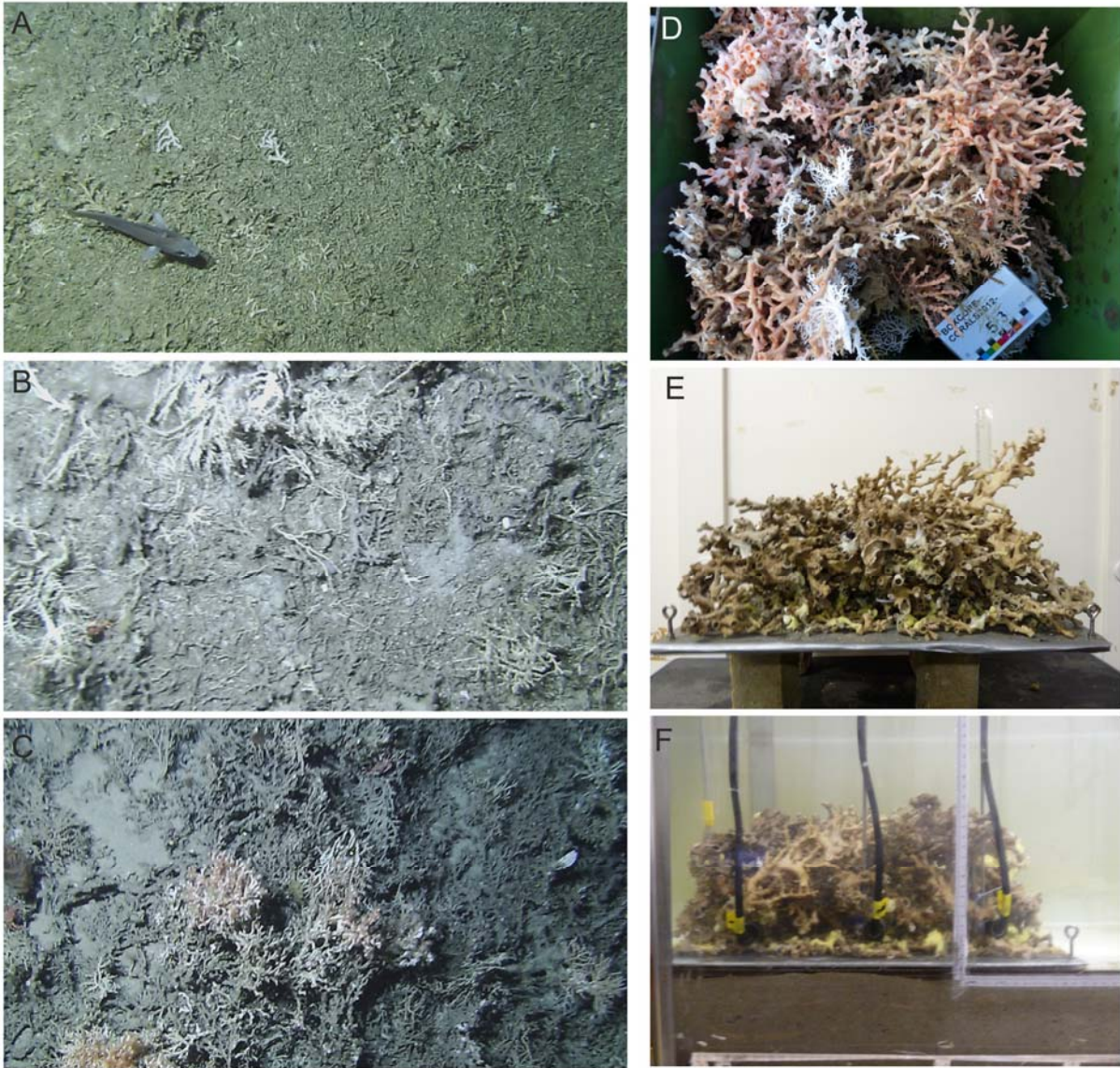
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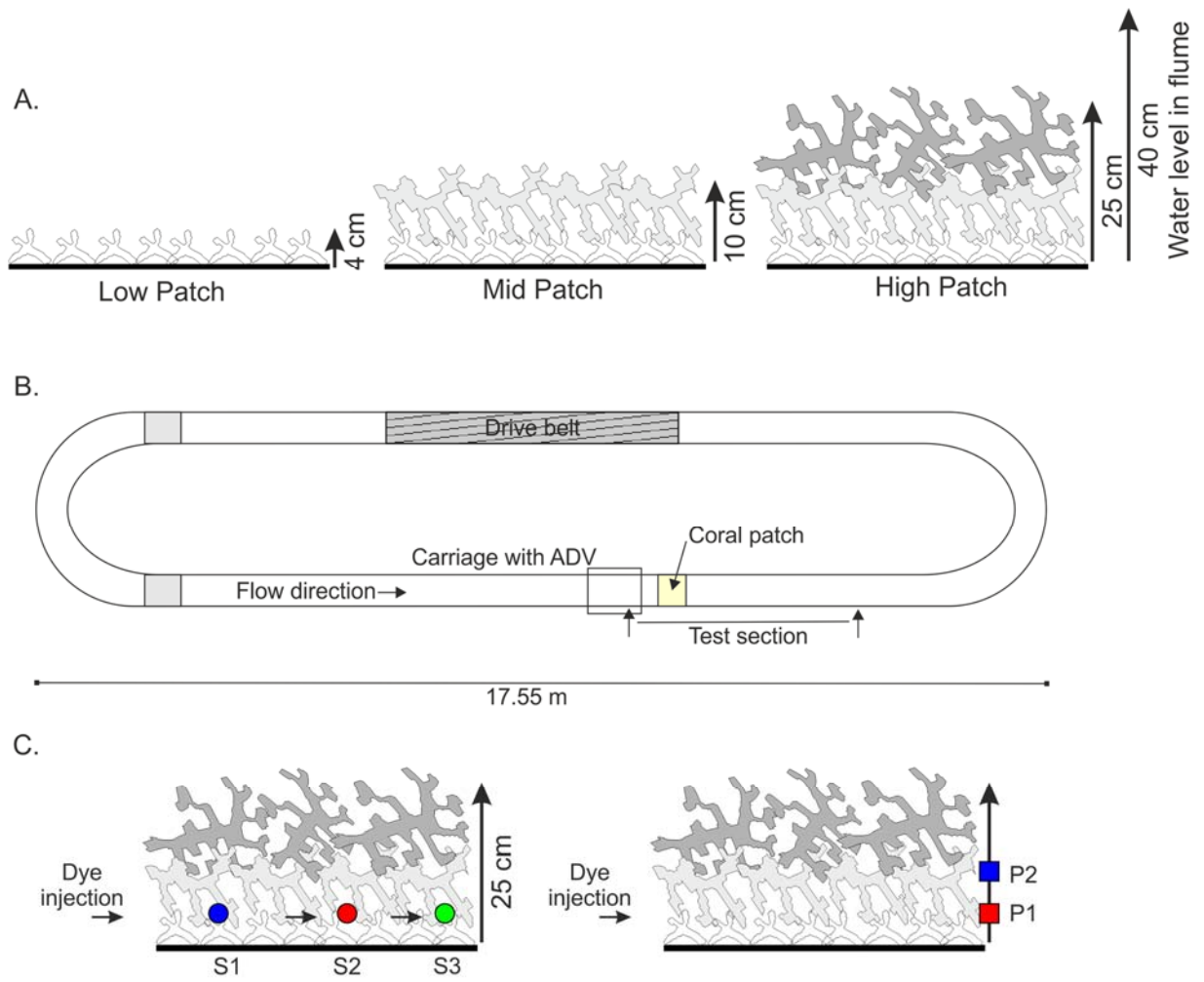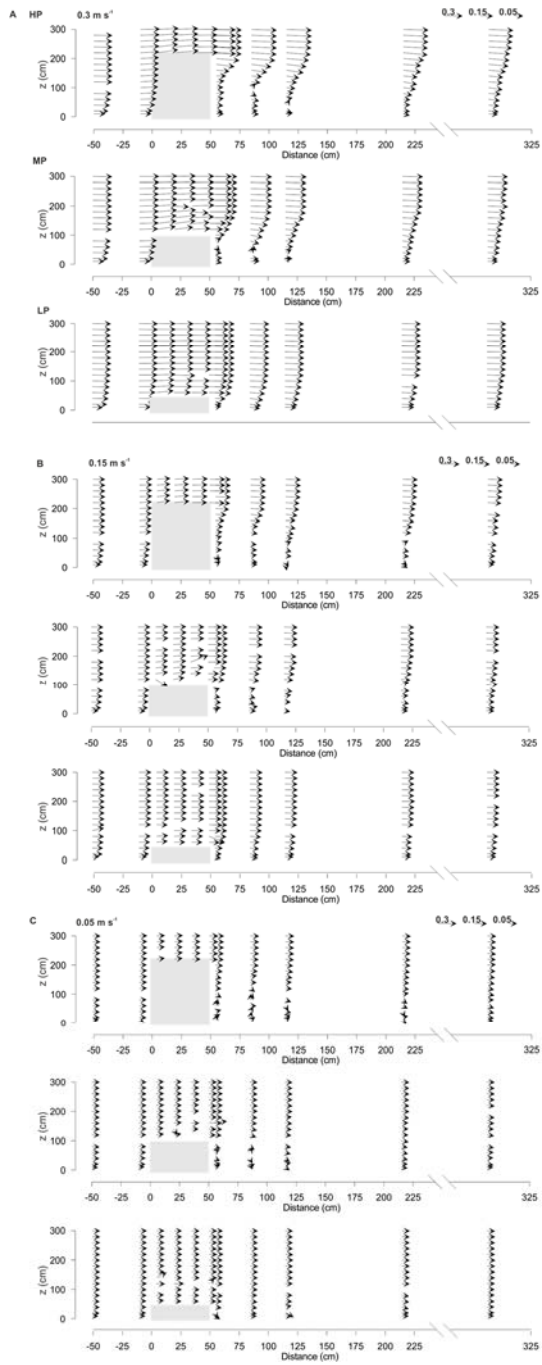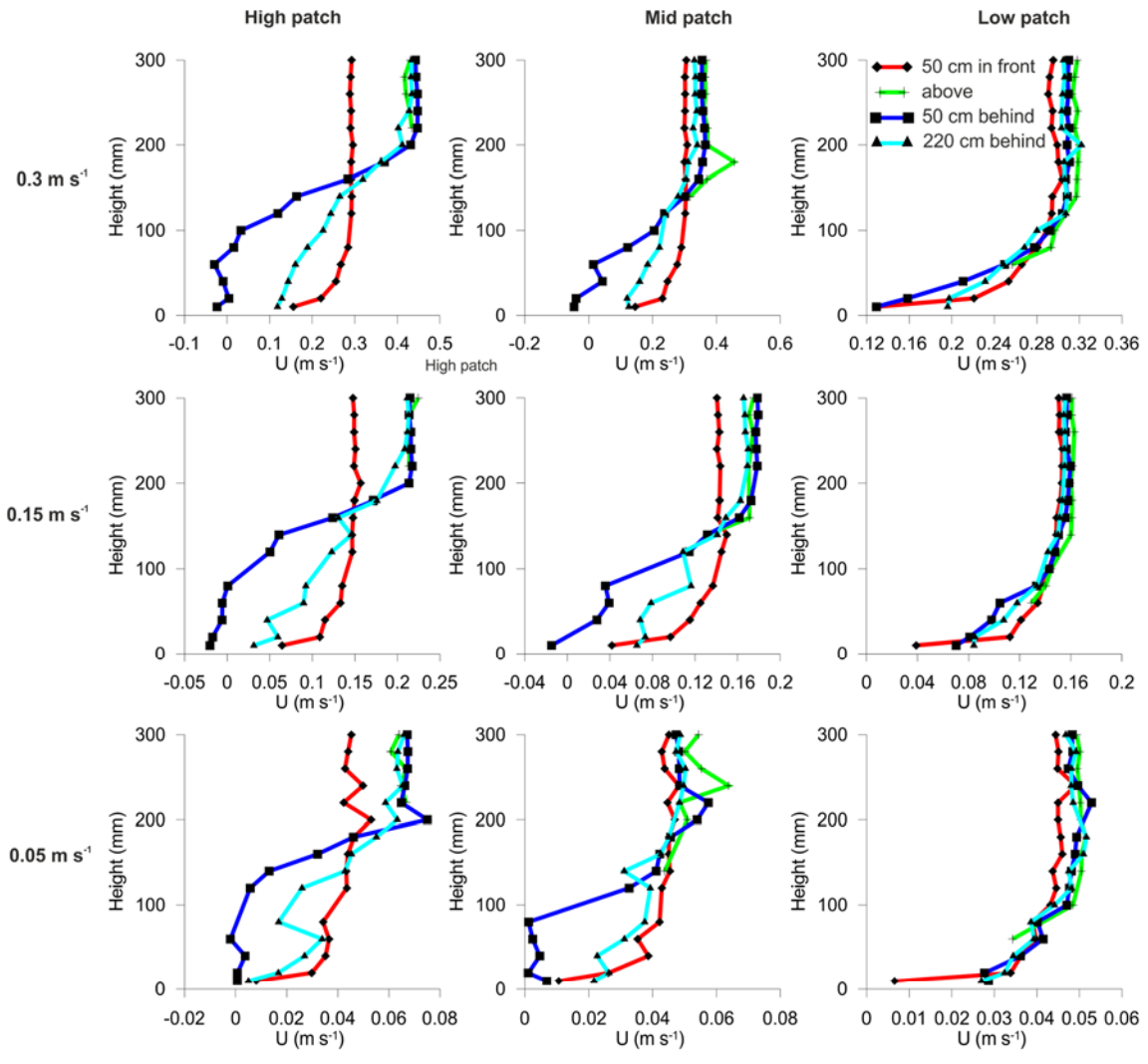
Figure 2

Figure 3

Figure 4
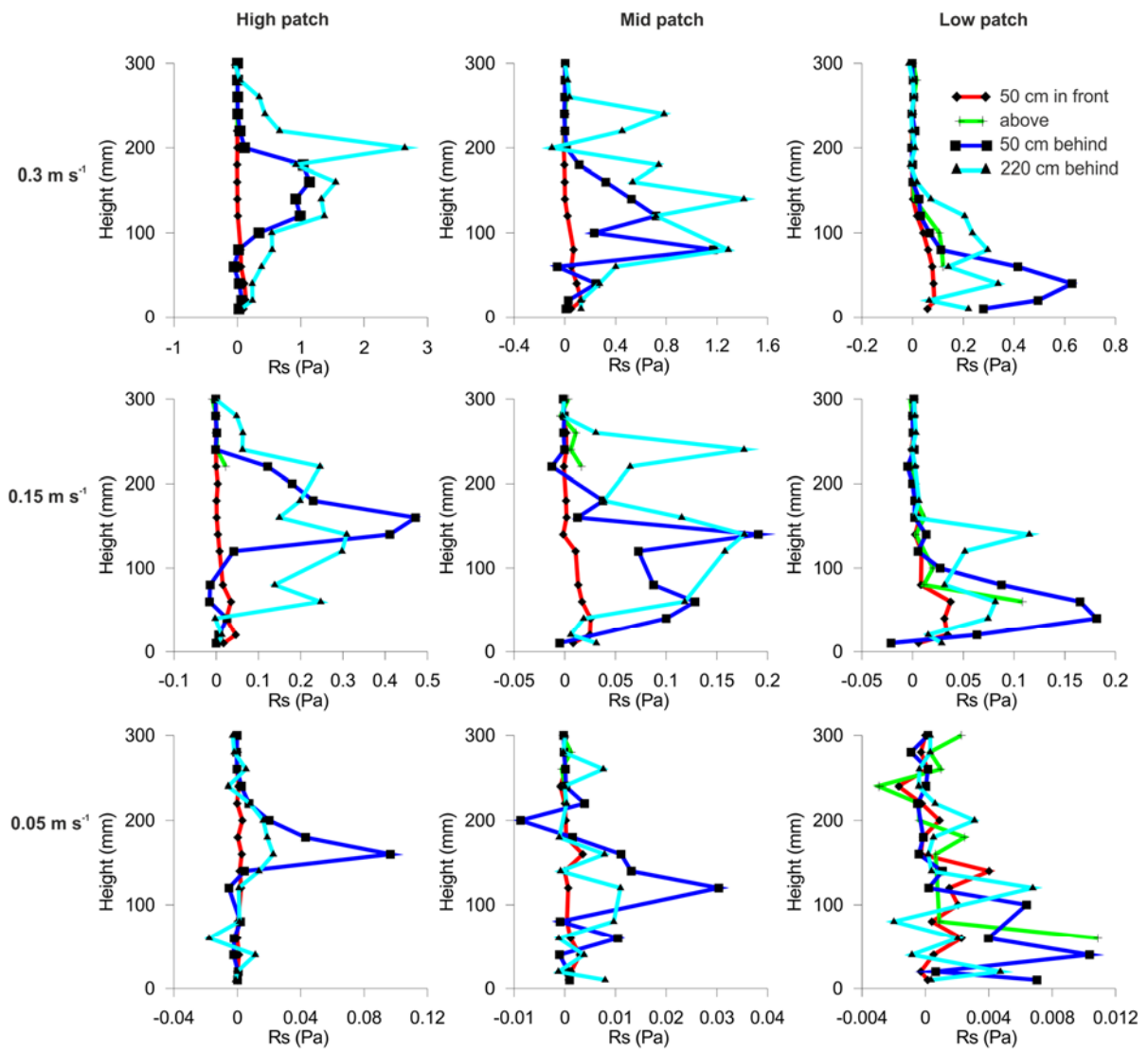
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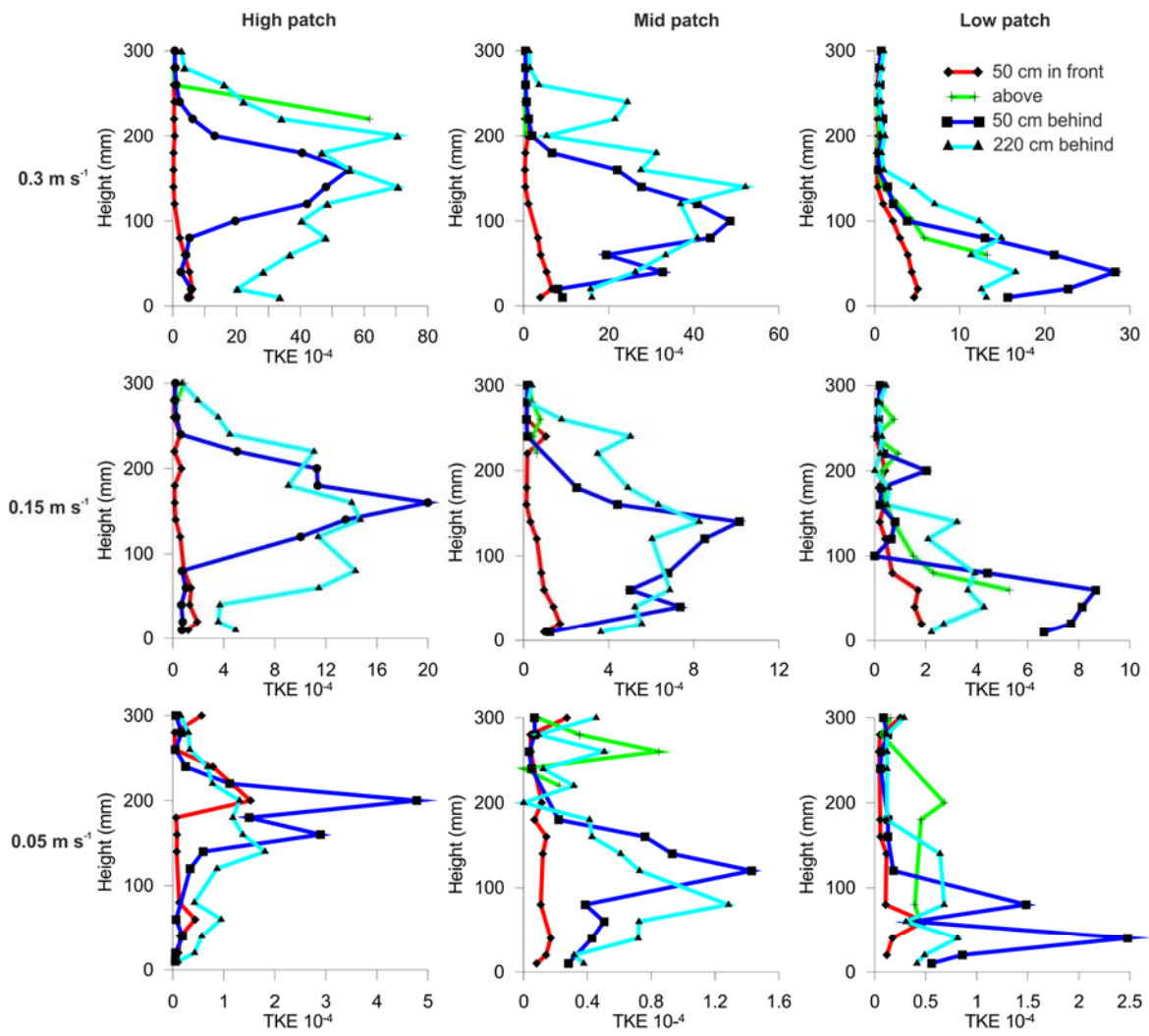
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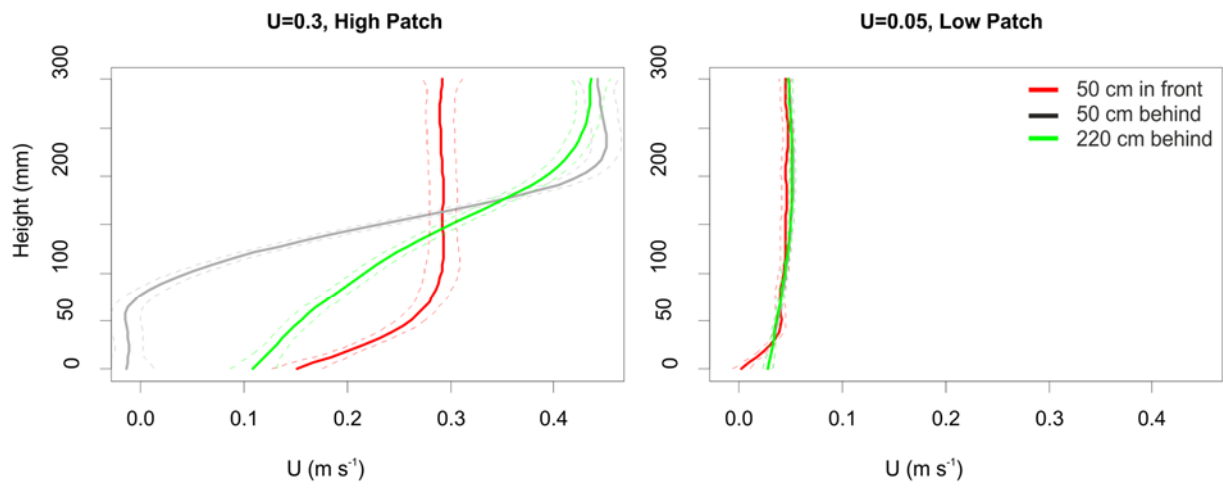
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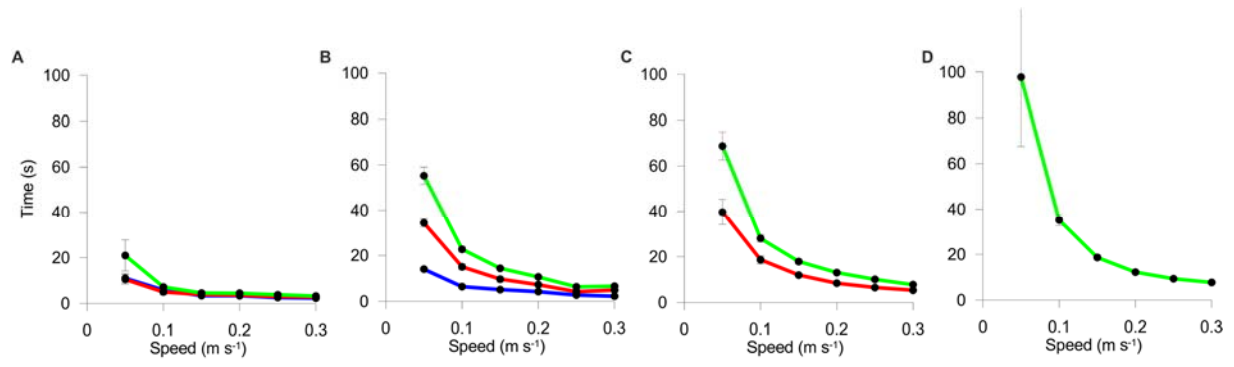
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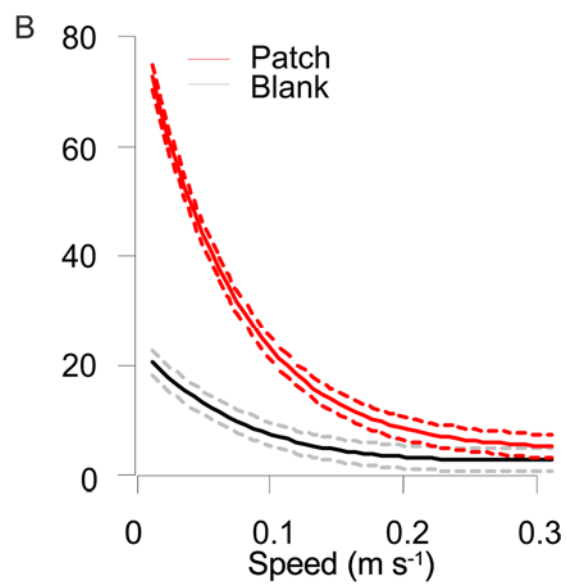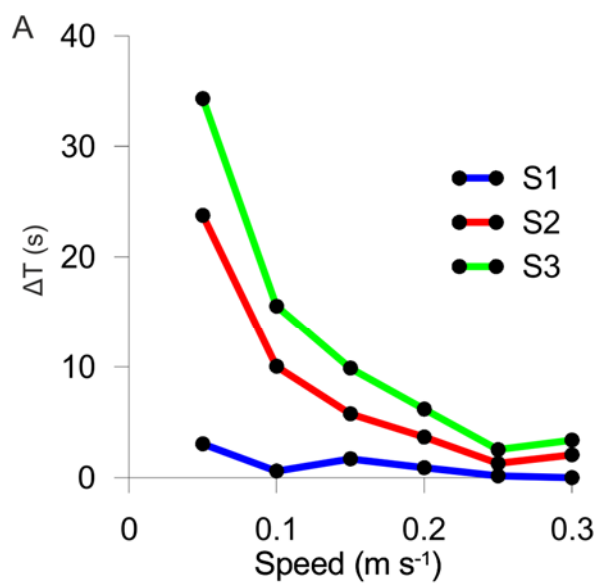
Figure 9
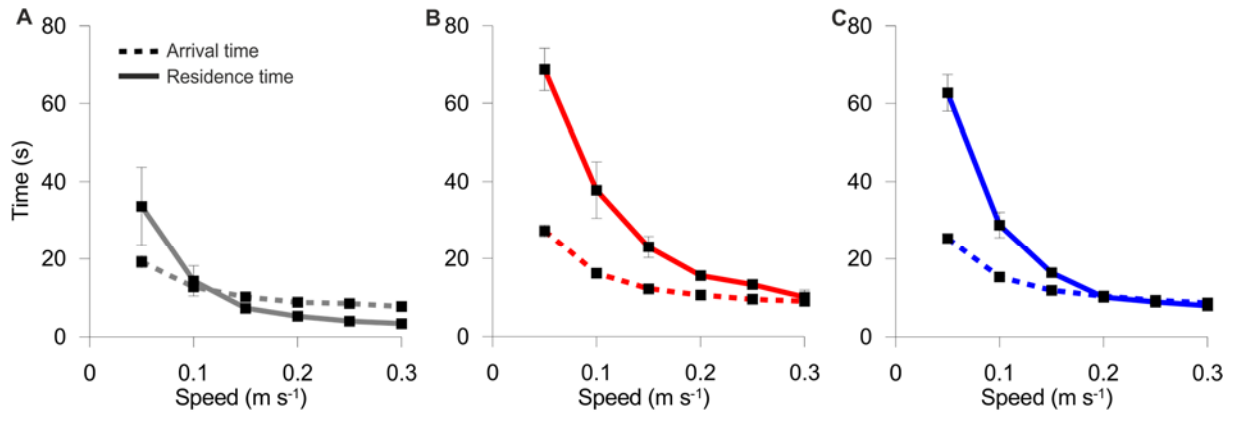
Figure 10

Supplementary material Fig. 1

High Patch   Medium Patch   Low Patch

50 cm in front
50 cm behind
220 cm behind

Supplementary material Fig. 2