Hindawi Publishing Corporation
Journal of Marine Biology
Volume 2012, Article ID 854849, 7 pages
doi:10.1155/2012/854849

*Research Article*

# Water Flow Affects Zooplankton Feeding by the Scleractinian Coral *Galaxea fascicularis* on a Polyp and Colony Level

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Received 24 September 2012; Revised 11 November 2012; Accepted 14 November 2012

Academic Editor: Horst Felbeck



Several factors may affect heterotrophic feeding of benthic marine invertebrates, including water flow rate and polyp context (i.e., the presence of neighbouring polyps). We tested the interactive effects of water flow rate and polyp context on zooplankton feeding by the scleractinian coral *Galaxea fascicularis*. Single polyps and colonies were incubated in a flow cell for 30 minutes with an ambient *Artemia* nauplii concentration of 10,000 $L^{-1}$ and water flow rates ranging from 1.25 to 40 cm $s^{-1}$. Water flow rate and polyp context showed significant main and interactive effects on feeding rates of *G. fascicularis* polyps. More specifically, feeding rates were optimal at flow rates of 1.25 cm $s^{-1}$ for single polyps and 5 to 10 cm $s^{-1}$ for polyps inhabiting colonies. The presence of epizoic acoelomorph flatworms may have negatively affected the observed feeding rates, especially at high flow. Our results demonstrate that water flow affects coral feeding and thus heterotrophic nutrient input at both a polyp and colony level. These findings are of relevance to our understanding of how biotic and abiotic factors interact on coral heterotrophy and may serve to optimise coral aquaculture.

## 1. Introduction

Heterotrophy is vital to coral health, as it supplies the holobiont with essential nutrients including amino acids and fatty acids [1]. For scleractinian corals, profound effects of heterotrophy on the physiology of the coral host and its symbiotic dinoflagellates have been documented. Zooplankton feeding has been found to enhance coral calcification, organic matrix synthesis, and photosynthetic rates [2, 3]. Up to 100% of the daily metabolic carbon requirements can be supplied by zooplankton, both during bleaching episodes [4] or when high prey concentrations are used in aquaculture [5]. These findings fit well with the long-term effects of zooplankton feeding on corals, which show that heterotrophy can be a limiting factor to growth [1, 6].

Several factors may affect coral feeding rates, including bleaching status [4], prey density [7], symbiotic organisms such as epizoic flatworms [8], water flow rate [9–16], and colony size [12, 16]. Water flow is a key parameter in this respect, as sessile organisms including corals depend on water movement to provide them with prey items [17]. Increased flow rates will increase the encounter rate or flux of food particles [10, 14, 18, 19], but will also increase the kinetic energy of particles approaching coral polyps. A higher kinetic energy of food particles may constrain the capture abilities of coral polyps, as has been documented for octocorals [20–22]. Moreover, drag forces caused by water flow can result in deformed feeding structures, decreasing capture efficiency [9, 10, 15, 16, 22–24]. Furthermore, corals may contract their tentacles if extension is no longer cost-efficient [9]. These mechanisms explain why bell-shaped relationships between water flow rate and prey capture have been found for several coral species [9, 12, 13, 16].

Colony size may also affect individual polyp feeding rates, both in negative and positive ways, due to polyp interactions within colonies. Negative effects may include polyp shading (i.e., polyps covering and obstructing one another) and local particle depletion, resulting in decreased prey capture by

downstream polyps [19]. Positive effects may include the generation of intracolonial turbulence and mucus secretion by upstream polyps, enhancing prey capture by downstream polyps [5, 12, 16, 25].

More insight into how different factors interact on zooplankton feeding by corals will contribute to our understanding of benthic-pelagic coupling on coral reefs. Furthermore, as heterotrophy is a limiting factor to growth [1, 6], coral aquaculture may be optimised by taking factors that enhance coral feeding into consideration. Therefore, we determined how water flow rate affects zooplankton feeding by a scleractinian coral on both a polyp and colony level. To this end, we performed video analyses of the scleractinian coral *Galaxea fascicularis* (Linnaeus 1767) feeding on *Artemia* nauplii under different flow regimes. As this species experiences highly variable water flow in the field, ranging from approximately 5 to 50 cm $s^{-1}$ at the depths at which this species is commonly found (9–12 m) [26], we used a similar range of flow rates.

## 2. Materials and Methods

*2.1. Selected Species and Husbandry.* For this study, we used the Indo-Pacific scleractinian species *Galaxea fascicularis* (Linnaeus 1767). Corals were kept in a closed system of 400 L, with the following parameters: salinity 35 ± 0.5 g $L^{-1}$, temperature 26 ± 0.5°C, pH 8.2 ± 0.3, photon flux density 322 $\mu$mol $m^{-2}$ $s^{-1}$ (12 h/12 h light/dark regime), nitrate 0.25 ± 0.08 mg $L^{-1}$, phosphate 0.02 ± 0.01 mg $L^{-1}$, calcium 400 ± 23 mg $L^{-1}$, and magnesium 1300 ± 40 mg $L^{-1}$. Water flow was provided by four Turbelle nanostream 6045 circulation pumps (Tunze Aquarientechnik GmbH, Penzberg, Germany) and an Eheim 1260 return pump (Eheim GmbH Co. KG, Deizisau, Germany), providing a total flow rate of 20,000 L $h^{-1}$ or 5 to 10 cm $s^{-1}$. Both single polyps and colonies were used for video analysis.

*2.2. Preparation of Colonies and Single Polyps.* Single polyps (approximate corallite length of 10 mm and diameter of 5 mm, resp.) were individually and randomly removed from a parent colony by using pincers and subsequently glued onto 7 × 7 cm PVC plates with two-component epoxy resin (GroTech Aquarientechnik GmbH, Affalterbach, Germany). Small colonies of approximately 100 polyps (approximately 4 × 4 cm) were cut from a parent colony with an electrical hand saw (Dremel, Breda, The Netherlands). This size was chosen to ensure some distance (2.5–3 cm) between the corals and the walls of the flow cell, thereby reducing potential boundary layer effects. All single polyps and colonies were of the same genotype, since they all originated from a single parent colony.

*2.3. Video Analysis.* For video analysis, *G. fascicularis* single polyps ($n = 4$) and colonies ($n = 4$) were incubated in a respirometric flow cell (Wageningen UR, Wageningen, The Netherlands) for 30 minutes (Figure 1). The outer dimensions of the flow cell were 51.8 × 29.1 × 14.3 cm (length × width × height), and its internal volume was 3.5 L. Water flow was created using a modified paddle wheel that was powered by a DC motor (Maxon Motor Benelux B.V., Enschede, The Netherlands) with a three-channel incremental encoder and line driver that allows precise control of rotational speed. EPOS user interface software (version 2.3.1, Maxon motor benelux B.V., Enschede, The Netherlands) was used to create flow rates of 1.25, 5, 10, 20, 30, and 40 cm $s^{-1}$. Water flow rates were calibrated using particle tracking, according to Schutter et al. [27]. Water from the holding tank was used for the experiments to rule out artefacts resulting from changes in water chemistry. Temperature was kept at 26 ± 0.5°C by means of a water jacket connected to a TC20 water cooler (Teco SRL, Ravenna, Italy). Photon flux density was set to holding tank intensity (322 $\mu$mol $m^{-2}$ $s^{-1}$) with a T5 fluorescent lighting fixture containing four 24 W fluorescent tubes with a colour temperature of 14,000 Kelvin (Elke Müller Aquarientechnik, Hamm, Germany). An HDR-CX505VE handy cam (Sony Corporation, Tokyo, Japan) was used for recording still and moving images in high-resolution format (1440 × 1080 pixels, 25 fps). *Artemia* nauplii were hatched from cysts (Great Salt Lake Artemia cysts, Artemia International LLC, Fairview, USA) at a salinity of 25 g $L^{-1}$ and a temperature of 28°C and used immediately after hatching. Average nauplii size was 440 $\mu$m according to the manufacturer. A concentration of 10,000 *Artemia* nauplii $L^{-1}$ was used for all experiments. This prey concentration was chosen as it reflects aquaculture conditions and to ensure sufficient feeding events would occur during the short incubations. Polyps and colonies were acclimated in the flow cell for 15 minutes before the start of every incubation. Each polyp and colony was analysed individually, and once at each flow treatment. All treatments were randomised for each individual. Corals were allowed to rest in the holding aquarium for at least 48 hours between treatments, and they were never fed before any treatment. All experiments were carried out over a period of approximately four weeks. Capture, release, and retention of *Artemia* nauplii by coral polyps were scored by analysing videos after experiments. For polyps within colonies, the most central polyp was consistently selected for all analyses. Nauplii capture by polyps was defined as prey that attached to the polyp surface for at least 10 seconds. Nauplii release was defined as prey that detached from the polyp surface and remained in suspension for at least 10 seconds. Nauplii retention was defined as the number of nauplii that remained in contact with the polyp surface at the end of the incubation, where two or more clustered nauplii were considered an aggregate. Retention of nauplii in aggregates was quantified as *G. fascicularis* has been found to mainly digest prey externally using mesenterial filaments [5].

*2.4. Data Analysis.* Normality of data was tested by plotting residuals of each dataset versus predicted values and by performing a Shapiro-Wilk test. Homogeneity of variances was determined using Levene's test. Sphericity was determined with Mauchly's test. As capture and release data were not found to be normally distributed ($P < 0.050$), a log10 transformation was used. After transformation, all feeding data were found to be normally distributed ($P > 0.050$).

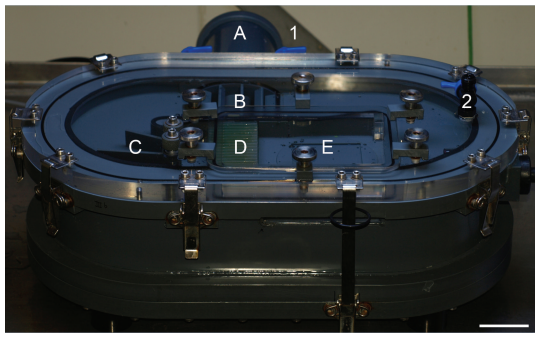


Figure 1: Overview of the respirometric flow cell used in this study. A: motor. B: paddle wheel. C: flow adjusters. D: flow laminator. E: coral plate holder. 1: water inlet. 2: water outlet. Scale bar: 5 cm.

Transformation also resulted in homogeneity of variance ($P > 0.050$) and sphericity ($P > 0.050$) of the data. We used a two-way mixed factorial ANOVA to test the (interactive) effects of water flow rate and polyp context on prey capture, release, and retention by *G. fascicularis* polyps, where water flow was considered a repeated measures factor (within-subjects factor). Bonferroni post hoc tests were used to determine capture, release, and retention differences between the various water flow rates, for both single polyps and polyps in colonies. Simple effects analysis was employed to infer capture, release and retention differences between single polyps and polyps in colonies at each water flow rate. A $P$ value $< 0.050$ was considered statistically significant. Statistical analyses was performed with IBM SPSS Statistics 19.0 (IBM Corp., Armonk, USA). Graphs were plotted with SigmaPlot 11.0 (Systat Software, Inc., San Jose, USA). Data presented are expressed as means ± sd unless stated otherwise.

## 3. Results

*3.1. Video Observations.* During all treatments, *G. fascicularis* polyps were active and well expanded. All single polyps and polyps within colonies captured prey (Figure 2). Mucus excretion was apparent and resulted in clustering of captured nauplii in mucus aggregates (not shown). No ingestion of nauplii was observed during any of the treatments. Instead, mesenterial filaments were expelled through the actinopharynx and temporary openings in the ectoderm of the oral disc, which enveloped single nauplii and nauplii aggregates. Filament expulsion seemed to be random; however, during several incubations this occurred in the vicinity of captured nauplii. On a few occasions, polyps that were part of colonies lost prey to neighbouring individuals, either passively by water current or actively by tentacle movement.

Deformation of polyps was observed at flow rates of 20 cm $s^{-1}$ and higher, for both single polyps and those within colonies. No significant polyp contraction was observed for any of the flow rates.

The presence of epizoic acoelomorph flatworms (tentatively identified as *Waminoa* sp.) was also observed for all polyps. These epizoic worms, approximately 1-2 mm in length, moved across coral polyps and actively preyed on *Artemia* nauplii.

*3.2. Feeding Rates.* Prey capture, release, and retention rates of *G. fascicularis* polyps were highly variable among the different flow treatments (Figure 2). Significant main effects of water flow rate and polyp context on prey capture rate were found (Table 1). A significant interactive effect was also found (Table 1), reflected by the fact that polyps in colonies captured significantly more prey compared to single polyps at water flow rates of 5, 10 and 30 cm $s^{-1}$ (simple effects, $P = 0.001$, $P = 0.007$, and $P = 0.049$, resp., Figure 2).

Significant main effects of water flow rate and polyp context on prey release rate were found (Table 1). A significant interactive effect was also found (Table 1), reflected by the fact that polyps in colonies released significantly more prey compared to single polyps at water flow rates of 5, 10, and 30 cm $s^{-1}$ (simple effects, $P = 0.011$, $P = 0.008$, and $P = 0.046$, resp., Figure 2).

Significant main effects of water flow rate and polyp context on prey retention rate were found (Table 1). A significant interactive effect was also found (Table 1), reflected by the fact that polyps in colonies retained significantly more prey compared to single polyps at water flow rates of 5, 10, and 20 cm $s^{-1}$ (simple effects, $P = 0.000$, $P = 0.016$, and $P = 0.050$, resp., Figure 2).

## 4. Discussion

*4.1. Effects of Water Flow and Polyp Context on Coral Feeding.* This study revealed a significant main effect of water flow rate on capture rates of *G. fascicularis* in a relationship that approximated a bell curve, although the interaction with polyp context demonstrated that this curve was affected by the presence of neighbouring polyps. This finding is in accordance with previous studies on corals [9, 12, 13, 16]. More generally, a significant effect of flow rate on particle capture has been found for various benthic marine invertebrates, including alcyonaceans [9, 10, 13], pennatulaceans [18], scleractinians [11, 12, 14, 16, 28], actiniarians [23], hydrozoans [19], bryozoans [29], crinoids [24], and barnacles [30]. The ability of *G. fascicularis* to feed on zooplankton under a wide range of flow rates also correlates well with the different reef habitats in which this species is found, which are exposed to flow rates of 5 to 50 cm $s^{-1}$ [26, 31]. Several authors have stated that the feeding capacity of suspension and filter feeding invertebrates can be affected by food particle encounter rate and deformation of feeding structures [9, 10, 13, 15, 16, 18, 19, 21, 23, 24]. In accordance with their claims, the initial positive effect of flow rate on prey capture rates we found for *G. fascicularis* is likely to have been caused by an increased encounter rate or particle flux of *Artemia* nauplii. At the same time, polyp deformation was absent under flow rates of 1.25 to 10 cm $s^{-1}$, favouring high capture rates. At flow rates of 20 cm $s^{-1}$ and higher, polyp tentacles deformed significantly due to drag forces, resulting in reduced filter area facing the flow. This may have negatively affected prey encounter rate

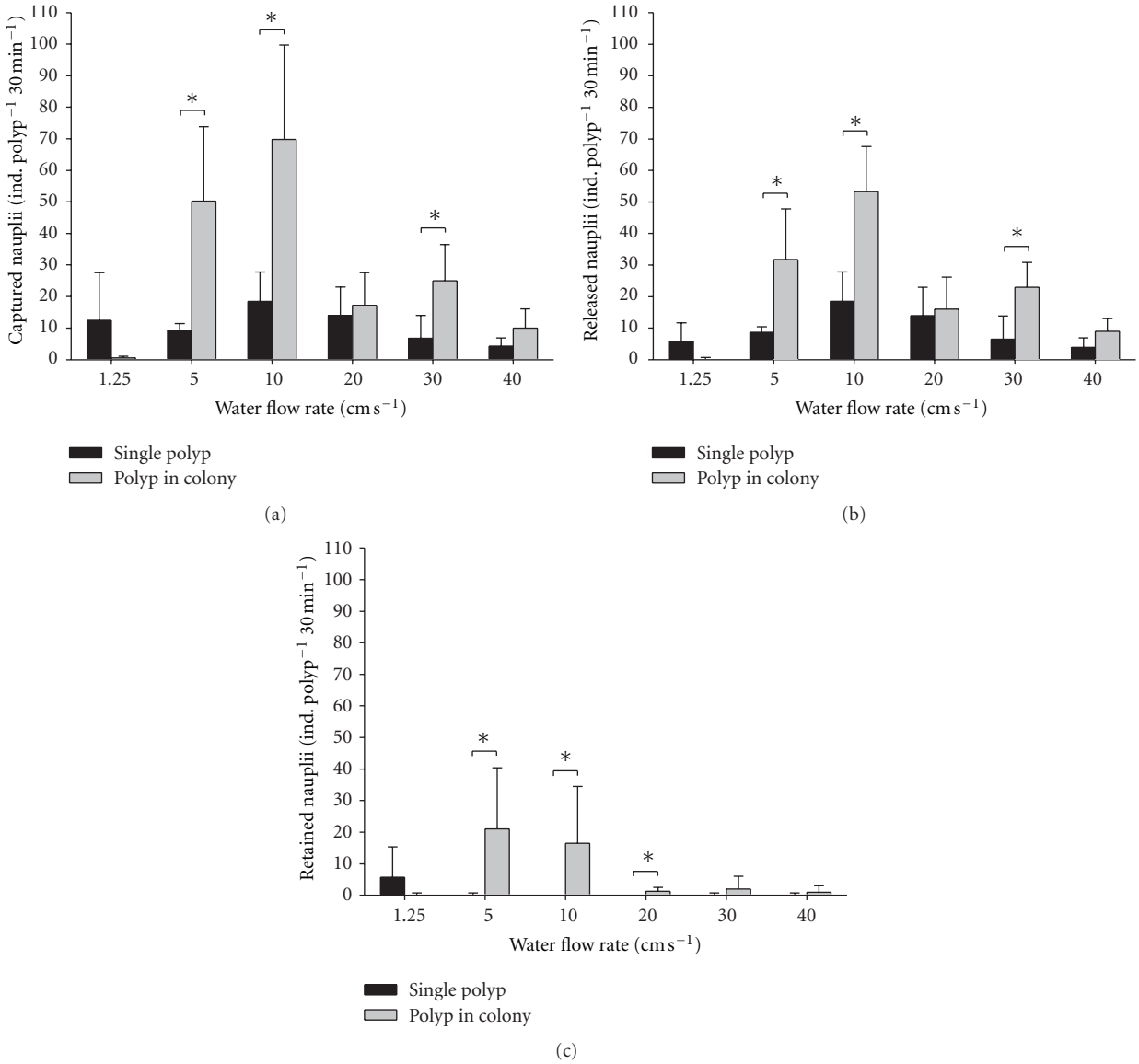


Figure 2: Prey capture (a), release (b), and retention (capture minus release, (c) rates of *Galaxea fascicularis* single polyps (black bars) and polyps in colonies (grey bars) at water flow rates of 1.25 to 40 cm s$^{-1}$. Values are means + sd ($n = 4$). *Indicates significant difference ($P < 0.050$, simple effects analysis).

Table 1: Two-way mixed factorial ANOVA, showing main and interactive effects of water flow rate and polyp context on prey capture, release, and retention by *G. fascicularis* polyps ($n = 4$).

| Variable | Factor | $F$ | df | Error | $P$ |
|---|---|---|---|---|---|
| Prey capture | Water flow rate | 9.67 | 5 | 30 | <0.001* |
| | Polyp context | 39.24 | 1 | 6 | 0.001* |
| | Water flow rate ∗ polyp context | 5.08 | 5 | 30 | 0.002* |
| Prey release | Water flow rate | 12.92 | 5 | 30 | <0.001* |
| | Polyp context | 17.73 | 1 | 6 | 0.006* |
| | Water flow rate ∗ polyp context | 4.65 | 5 | 30 | 0.003* |
| Prey retention | Water flow rate | 3.21 | 5 | 30 | 0.019* |
| | Polyp context | 45.14 | 1 | 6 | 0.001* |
| | Water flow rate ∗ polyp context | 6.08 | 5 | 30 | 0.001* |

*Indicates significant effect ($P < 0.050$).

and capture at flow rates of 20 cm $s^{-1}$ and above. Another limiting factor may have been the increased kinetic energy of nauplii at higher flow rates, which requires stronger adhesive and retention abilities of coral tentacles [20, 22]. This was illustrated by our observation that at higher flow rates, nauplii seemed effectively paralysed by cnidocytes, but were not as well retained by polyps. Hunter [19] suggested that both the flux and kinetic energy of particles increase when flow rates increase, with positive and negative effects on feeding, respectively. As capture rates decreased with higher flow rates, the positive effect of higher prey flux did not compensate for the negative effects of increased kinetic energy of food particles and polyp deformation.

A significant main effect of water flow rate on overall release rates of *G. fascicularis* polyps was also found, in a pattern that matched capture rates. In other words, increased prey capture was followed by increased prey release, which may not have been deliberate but a result of insufficient adhesive abilities of polyps (see below).

Water flow rate significantly affected overall prey retention rates, with much lower retention rates than previously found by Wijgerde et al. [5] ($6 \pm 10$ versus $32 \pm 33$ *Artemia* nauplii $polyp^{-1}$ 30 $min^{-1}$). This may have been due to the presence of epizoic acoelomorph flatworms, which were observed in high numbers during the incubations. Hii et al. [25] and Wijgerde et al. [5] showed that *Galaxea fascicularis* secretes copious amounts of mucus for zooplankton entrapment, whereas Naumann et al. [32] demonstrated that epizoic flatworms actively feed on this mucus. Therefore, mucus removal from the oral disc by epizoic flatworms could potentially affect the ability of the corals to capture and retain prey, especially at high flow rates. Indeed, Wijgerde et al. [33] recently demonstrated that epizoic flatworms reduce the capacity of *Galaxea* polyps to feed on zooplankton. Although Wijgerde et al. [5] also reported the presence of flatworms on polyps with high retention abilities, differences in flatworm hosting densities may explain the discrepancy. A reduced adhesive ability will especially affect single polyps, as no current shading effects of upstream polyps occur. Indeed, video analysis demonstrated that at flow speeds of 5 cm $s^{-1}$ and higher, single polyps were unable to successfully retain prey. Moreover, Wijgerde et al. [8] demonstrated that epizoic flatworms actively compete with their coral host for zooplankton, which could further reduce prey capture by *G. fascicularis*. Future studies may reveal a negative impact of epizoic acoelomorph flatworms on other coral species, in terms of feeding impairment, as flatworms are common symbionts of many coral taxa, both *in situ* and in captivity [32, 34, 35].

Next to flow rate, turbulence, and thus flow direction, played a role in zooplankton capture by the corals. On the leeward side of both single polyps and colonies nauplii concentrated, which was clearly the result of eddy formation. From these eddies, zooplankton was regularly propelled in the direction of the coral after which capture sometimes followed. During several measurements at 5 and 10 cm $s^{-1}$, the amount of nauplii captured directly from the water current was lower than the number captured from the eddy. Helmuth and Sebens [12] and Sebens et al. [16] described similar observations for the scleractinian corals *Agaricia agaricites* and *Madracis mirabilis*, respectively. They found that capture shifted from upstream to downstream regions with increasing flow rates. Based on their observations, they suggested that turbulent currents formed by polyps or branches aid in prey capture. This phenomenon contributed to the capture rates we observed (also see below on interactions).

Polyp context also had a significant main effect on prey capture, release, and retention rates, as polyps inhabiting colonies generally captured, released, and retained significantly more prey than single polyps. The apparent advantage of the presence of neighbouring polyps could be due to mucus secretion and paralysis of zooplankton prey by upstream polyps, allowing for more effective capture by downstream central polyps. This is in accordance with earlier findings by McFadden [20] on octocorals, who found that colony aggregations displayed enhanced prey capture, and Wijgerde et al. [5], who showed that *G. fascicularis* polyps within a single colony can develop significant *Artemia* nauplii aggregates. However, the latter authors also found that polyp capture rates within a colony are patchy, as only 7.7% of polyps accumulate aggregates. This finding demonstrates that although certain individual polyps in a colony may capture prey more efficiently compared to solitary polyps, the colony as a whole may become less efficient in terms of average prey capture per polyp. Thus, if we had preselected different polyps inhabiting colonies for our observations, the results could have revealed less efficient feeding compared to solitary individuals. Polyps inhabiting colonies which do not capture prey may still benefit from the shared internal anatomy of scleractinians which enables nutrient redistribution [36, 37]. The fact that polyps in the context of a colony capture less prey on average is in agreement with decreasing growth rates with size observed for *G. fascicularis* [38], possibly caused (in part) by decreased nutrient procurement per unit of biomass.

In this study, water flow rate and polyp context were found to have a significant interactive effect on prey capture, release, and retention rates, demonstrating that the effect of water flow on feeding rates was modified by polyp context and vice versa. The interaction resulted from the different ways in which single polyps and central polyps in colonies responded to flow in terms of prey capture, release, and retention. Polyps within colonies exhibited a distinct response to water flow, with virtually no prey capture, and release at 1.25 cm $s^{-1}$, highest capture/release rates at 5 to 10 cm $s^{-1}$, and intermediate capture/release at even higher flow rates. Single polyps displayed a different response to flow, especially when regarding prey retention. This occurred only at the lowest flow rate, whereas polyps within colonies retained significantly more prey at intermediate flow rates. The interactive effect can also be illustrated with the fact that prey capture, release, and retention rates were higher for polyps within colonies only at specific water flow rates. This interactive effect may be explained by intracolonial polyp interactions, including negative effects such as polyp shading and local particle depletion as described by Hunter [19] and positive effects such as intracolonial turbulence

and additional mucus production [5, 12, 16]. These negative and positive interactions are, turculence excluded, absent in single polyps. At low flow and thus low particle flux, upstream polyps may reduce particle availability for their downstream clone mates, which as a result capture less prey. This could explain the low capture and release rates we found for central polyps at 1.25 cm $s^{-1}$. This, however, seems unlikely at the high prey concentrations that were used. Another explanation may be that at low flow, a thicker boundary layer results in advection of prey around the massive, hemispherical colonies, resulting in less prey availability for the densely packed central polyps. At high flow rates, on the other hand, upstream polyps may cover downstream polyps due to deformation caused by drag forces, thereby shading the feeding structures of the latter. This could explain the distinctly lower capture and release rates we found for central polyps at high flow rates of 20 cm $s^{-1}$ and beyond. Indeed, video analysis showed that at flow rates of 20 cm $s^{-1}$ and higher, polyp deformation and thus shading, was significant. The reason why polyp interactions resulted in highest prey capture, release, and retention at an intermediate flow of 5 to 10 cm $s^{-1}$ may be that at these flow rates, an optimal trade-off exists between prey encounter rate on one hand and polyp shading effects and increased kinetic energy of prey on the other. As stated above, turbulence may further aid in prey capture, increasing contact time between prey and polyps. In a similar way, a favourable trade-off between prey encounter rate, drag force, and kinetic energy may explain higher feeding rates by single polyps at intermediate and low flow rates.

Finally, as we used only one genotype, the results obtained here may not reflect the behaviour of this species in general. Future studies may reveal genotypic variability in terms of feeding ability under different flow regimes.

## 5. Conclusions

This study demonstrates that water flow and polyp context exert an interactive effect on zooplankton feeding by *G. fascicularis*, with optimal feeding rates at 1.25 and 5 to 10 cm $s^{-1}$ for solitary and colonial polyps, respectively. These findings have implications for aquaculture of this species, as heterotrophic feeding can significantly enhance coral growth [1, 6]. Although the prey concentrations we used only exist in aquaculture, the relative differences reflect the important effects of water flow and polyp context on coral heterotrophy, which is relevant to the ecology of *G. fascicularis*. Exposure to high flow rates may significantly limit prey and nutrient acquisition by this species, and thus growth and survival, whereas low flow rates may enhance feeding rates of primary polyps. Future studies should address the potential interaction between water flow rate and prey concentration on the feeding rates of this species, similar to the study of Purser et al. [28] for *Lophelia pertusa*. In addition, determining the effect of flow pattern, that is, oscillating versus unidirectional flow, would be relevant as Hunter [19] demonstrated that this factor can affect feeding rates of benthic colonial invertebrates.

## Conflict of Interests

The authors declare that they have no conflict of interests.

## Acknowledgments

This work was funded by Wageningen UR. The authors wish to thank Evert Janssen and the staff of De Haar experimental facility for technical support, and the three reviewers whose comments substantially improved a draft version of the paper.

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