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Coral farming: effects of light, water motion and artificial foods

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*Improved coral cultivation will facilitate the reduction of wild harvesting, reef restoration, preservation of biodiversity, and the use of corals as model experimental organisms. In this study, we examine species-specific responses in growth and survival of corals from the effects of light, water motion and artificial (i.e. non-living aquarium trade) food supplements. Three species representing distinct, diverse and abundant coral genera were chosen (*Montipora capitata*(Mc),* Porites compressa *(Pc)* and Pocillopora damicornis *(Pd)) for three experiments to examine: (1) the interaction of water flow and light on growth and survival of Mc and Pc; (2) the effects of artificial foods on Mc, Pc and Pd; and (3) the effects of increasing dosage of artificial foods in an open system on Mc and Pc. Pc thrived at the highest light levels with low flow, while Mc exhibited bleaching and reduced growth in the same conditions and grew best in shaded treatments. High constant flow (~11 cm s^{-1}) resulted in slightly less overall growth than low constant flow (~4 cm s^{-1}). Some artificial foods resulted in a significant increase in growth in Mc and Pd, but not in Pc. These combined results suggest that Mc may be more heterotrophic than Pc. This study illustrates that each species has unique requirements for optimal growth conditions that can be determined by relatively simple and low cost experiments, but that ideal conditions for one species might not be generalized to others.*

Keywords: coral aquaculture, coral foods, light, water flow, *Porites compressa*, *Pocillopora damicornis*, *Montipora capitata*

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INTRODUCTION

Improved coral cultivation has a variety of potential benefits including: preservation of biodiversity; rehabilitation of disturbed coral reefs (e.g. Rinkevich, 1995, 2000, 2005); reversing coral–algal phase shifts (e.g. McManus & Polsenberg, 2004); and reduction of wild harvesting for the aquarium and curio trades. Coral restoration projects have widely varying efficacy (Edwards & Clark, 1998; Rinkevich, 2005) that could be improved by more cost-effective means of 'farming' coral at a larger scale (Clark & Edwards, 1995; Delbeek, 2001; Rinkevich, 2005). Coral farming not only has the potential to benefit a wide variety of studies that use corals as model experimental organisms, the process of cultivation itself is likely to provide important insights to coral ecology and organismal biology.

One of the first steps of cultivating any organism is to determine a range of physical and biological parameters that optimize growth and survivorship. Compared to many terrestrial organisms of similar economic, cultural, or scientific interest, corals have a relatively recent history of cultivation (Delbeek, 2001). Scleractinian corals primarily receive their nutrition from symbiotic photosynthetic dinoflagellates (zooxanthellae) (Goreau *et al.*, 1971; Buddemeir & Kinzie, 1976; Muscatine, 1990). Even though phototrophy is often the primary nutritional mode, at least some scleractinian corals are capable of heterotrophy to varying degrees (e.g. Wellington, 1982; Sebens *et al.*, 1996; Bak *et al.*, 1998; Anthony, 1999; Ferrier-Pagès *et al.*, 2003; Grotolli *et al.*, 2006).

Studies have shown that for some coral species, nutritional modes of heterotrophy versus phototrophy can be plastic (e.g. Anthony & Fabricius, 2000; Titlyanov *et al.*, 2001). Heterotrophic and phototrophic plasticity is suggested to aid in maintaining carbon energy requirements when environmental stressors affect corals. For example, *Goniastrea retiformis* increased its heterotrophic capacity with decreased light availability (Anthony & Fabricius, 2000), *Stylopora pistillata* required zooplankton to acclimate to low light (Titlyanov *et al.*, 2001) and *Montipora capitata* recovered from bleaching faster when fed (Grotolli *et al.*, 2006). It is not yet clear to what degree phototrophic and heterotrophic capacities are affected by environmental conditions, morphology and taxonomy (i.e. phylogenetic history).

Live food has been shown to be important for increasing growth and survivorship for a variety of scleractinian coral genera (e.g. Grotolli *et al.*, 2006; Goldman, 2007; Sawall *et al.*, 2011), but far less is known about artificial foods. Artificial foods have the potential to be less expensive and labour-intensive than live food and are the only option available to many aquarists. However, artificial foods from the aquarium trade contain a wide variety of formulations that are poorly or not regulated, and are rarely evaluated for efficacy, with a few exceptions (e.g. Toonen *et al.*, 2002). Artificial foods, if not consumed, can decay and have undesirable consequences such as supplying nutrients for bacteria and

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algae (Larned, 1998; Stambler *et al.*, 1991). It is therefore not surprising that coral aquarists have a variety of experiences and opinions regarding artificial food supplements.

The purpose of this study was to examine a range of basic physical parameters and commercially available artificial (non-living) food supplements from the hobby trade for *Porites compressa*, *Montipora capitata* and *Pocillopora damicornis*. All three species are abundant throughout the Hawaiian Archipelago and are among the most abundant reef building genera in the Pacific. These corals can reproduce asexually via fragmentation with very high survivorship (Highsmith, 1982; Forsman *et al.*, 2006), which is an experimental advantage that can provide large sample sizes of genetically identical fragments of uniform size. We conducted three experiments to examine the interaction between light and water motion (Experiment 1), the effects of artificial foods on coral growth (Experiment 2) and the effects of increased doses of artificial food (Experiment 3). Our explicit null hypotheses were that there were no differences in each species response to light and water flow (Experiment 1), that artificial foods have no effect on growth (Experiment 2) and that increasing the dose of artificial foods will have no effect on growth (Experiment 3).

MATERIALS AND METHODS

Experiment 1: light and water motion

Sixteen clear plastic buckets (18 l capacity) were arrayed in a 10 cm deep seawater bath in a 1 m × 3 m fibreglass holding tank (Figure 1A). The seawater supply was filtered with a 500 micron nylon bag filter in a housing (Aquatic Ecosystems) and distributed by irrigation tubing with 16 micro-sprinkler-emitters arrayed to inject water to provide constant circular flow (Figure 1B). A total of 480 1 cm^2 nubbins, 240 from *P. compressa* and 240 from *M. capitata*, were arrayed onto 1 cm^2 plastic mesh and held in place with the weight of 15 cm × 15 cm glossy white ceramic tiles (Figure 1C). The experiment included two replicates of a two-factor design (light and water motion), with four levels for light (0X, 1X, 2X and 3X layers of 50% shade cloth) and two levels for flow (high and low). Each bucket contained 30 nubbins (15 per species), taken from three colonies per species. The nubbins were arrayed on each mesh in 5 rows by 6 columns, alternating by species, then by colony of origin. The experiment had two replicate buckets for each treatment, and the position of each treatment was assigned by pseudo-random numbers generated in MS Excel 2003. The buckets were cleaned and each nubbin array was photographed weekly. Bi-weekly flow rates were measured with 2 methods: (1) time to fill 10 ml graduated cylinder; and (2) time for one rotation of a drop of 10 mg/ml fluorescein dye. Water motion over the nubbins was estimated by dividing the time in seconds per rotation of dye, by the bucket circumference (74 cm).

Photosynthetically active radiation (PAR) was measured bi-weekly at noon, for each of the shade treatments with a Li-Cor PAR omnidirectional quantum light sensor and light meter. The area covered by coral tissue was measured with the program Image J, V 10.2, from top-down digital images calibrated to scale with the ruler attached to a

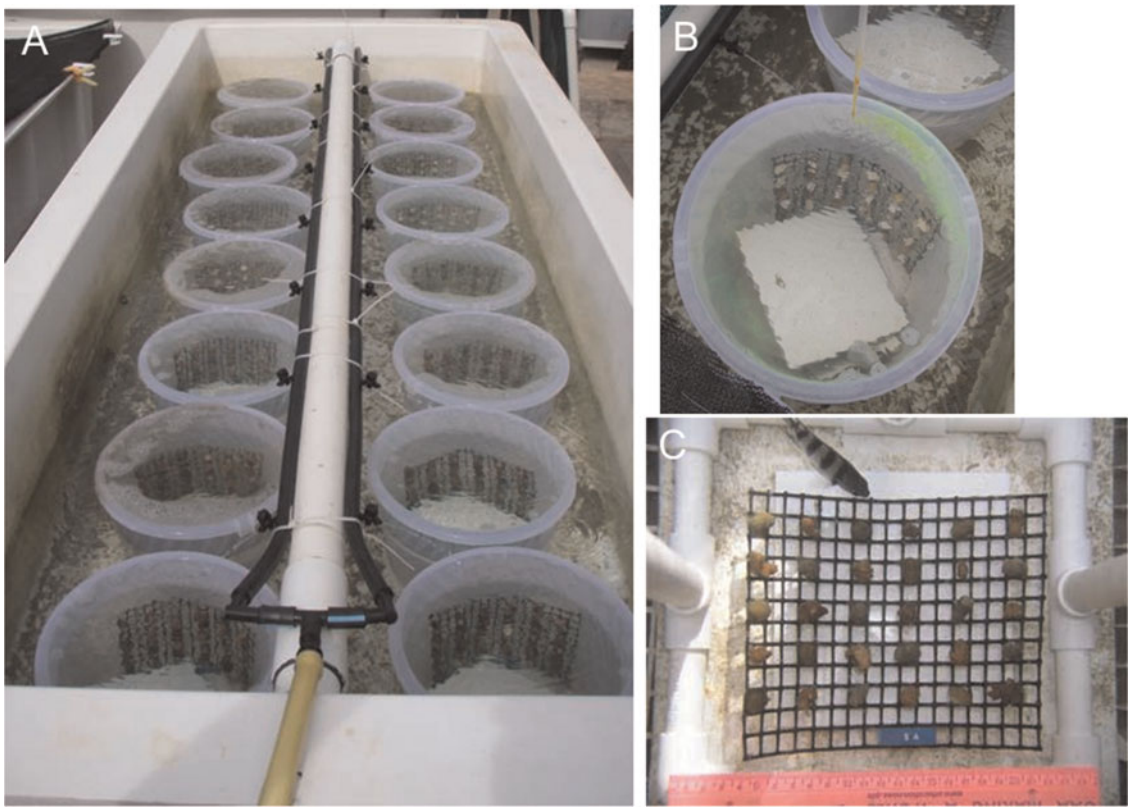

Fig. 1. Experiment 1 (light and water motion) set up. (A) Plastic buckets with layers of shade cloth removed; (B) water flow measured by fluorescein dye; (C) close-up of an array of coral fragments.

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photo framer. Area measurements were taken after the experiment was set up on 7 October 2006, at 19 days (26 October 2006), and at 41 days (17 November 2006). Four Hobo pennant temperature loggers (Onset Computer Corporation) recorded temperature at 10 minute intervals for the duration of the experiment. Statistical analysis was performed in SPSS 17.0

Experiment 2: effects of artificial foods

Ten nine gallon tanks were set up in natural light with Hydor Koralia 1 (~200 gph) water pumps to maintain water flow and circulation. Feeder tubes supplied 5 micron filtered water into each of the tanks at a rate of 0.38 l per hour (0.1 gph) creating a flow through system. Tanks were conditioned for two days before adding coral fragments. Thirty coral fragments of each species (*P. compressa, M. capitata* and *P. damicornis*) were collected from fringing reef surrounding Coconut Island (N = 90). For each species, five fragments were taken from each of six different colonies. A random number generator in MS Excel was used to determine the treatment in each tank and each fragment was placed in a Latin square randomized design within each treatment tank. Fragments of coral were set into plastic mesh at the bottom of each of the ten plastic tanks. One fragment from each of three different colonies was placed into each replicate tank for each species, totalling 6 fragments per species per treatment. Four foods were tested (Oyster Eggs, Roti-Feast, Reef Chili and Reef-Roids), as well as a control (filtered seawater), and each treatment had two replicates. Corals were fed four times a week, at the food manufacturers' recommended dosages (Table 1). Tanks were also cleaned weekly to control algal growth. Corals were fed for 12 consecutive weeks. During the first month of the experiment, the tanks were in direct sunlight, and subsequently placed under shade cloth to decrease the algal growth in the tank. The water and pumps were turned off for 2–3 hours each day to allow corals to feed. A species of nudibranch (*Phestilla* sp.) was found inhabiting several of the tanks. This nudibranch specifically feeds on *Porites* coral species, eating its outer tissues (Gochfeld & Aeby, 1997) and was removed from tanks when seen. Measurements of wet weight (g) and displacement (ml) were taken at the start of the experiment, and again at the end of the three month period. Weight of fragments was measured using an electronic balance and displacement was measured by a graduated cylinder. Weight and displacement data were analysed as percentage increase, to account for relationships between growth rate and size of fragment.

Table 1. Food type, dosage and average growth (g) over a 12 week period.

Food type	Dose	Species	N	Average net growth (g) ± SE
Filtered seawater	na	P.c.	6	0.0579 ± 0.020
		M.c.	6	0.022 ± 0.014
		P.d.	6	−0.015 ± 0.016
		Total	18	0.021 ± 0.012
Oyster Eggs	0.18 ml	P.c.	6	0.048 ± 0.018
		M.c.	6	0.058 ± 0.030
		P.d.	6	−0.024 ± 0.016
		Total	18	0.027 ± 0.012
Roti-Feast	1.33 ml	P.c.	6	0.023 ± 0.014
		M.c.	6	0.079 ± 0.020
		P.d.	6	−0.008 ± 0.007
		Total	18	0.031 ± 0.018
Reef Chili	0.0135 g	P.c.	6	0.042 ± 0.019
		M.c.	6	0.134 ± 0.030
		P.d.	6	0.031 ± 0.019
		Total	18	0.065 ± 0.018
Reef-Roids	0.17 g	P.c.	6	0.073 ± 0.030
		M.c.	6	0.114 ± 0.023
		P.d.	6	0.041 ± 0.022
		Total	18	0.076 ± 0.016

P.c., *Porites compressa*; M.c., *Montipora*; *capitata* P.d., *Pocillopora damicornis*.

Experiment 3: increased doses of artificial foods

The experiment was conducted between October and December 2006 at Kewalo Marine Laboratory in Honolulu Hawaii. Sixteen grey plastic buckets (18 l capacity) were arrayed in a fibreglass water table and supplied with seawater filtered through a 500 micron bag filter (Aquatic Ecosystems). The seawater table was shaded with garden-variety 50% shade cloth, and water motion and aeration was supplied to each bucket by irrigation tubing, micro-sprinkler emitters and aquarium tubing. Each bucket contained a 6 × 6 inch glossy white ceramic tile with nubbins attached with Z-spar splash-guard marine epoxy. A total of 480 ~1 cm^2 nubbins, 240 from *P. compressa* and 240 from *M. capitata*, were arrayed onto the tiles. Each tile contained 30 nubbins (5 nubbins from three donor colonies for each species, alternating between species and donor colonies). A stand-pipe was constructed out of 3 inch PVC, with a 3 inch sleeve, such that water levels could be raised above the level of the buckets (to allow water circulation between buckets), or below the level of the buckets to allow dosing of different commercial coral foods (Figure 2). The experimental treatments consisted of four foods (MicroVert, MarineSnow Plankton Diet, Phytoplan and Salifert Coral Food) and four doses (0X = filtered seawater, 1X = manufacturers' recommended dosage, 3X = 3 times recommended dosage, 10X = 10 times recommended dosage) (Table 2). The plastic buckets were cleaned and each nubbin array was photographed weekly. Each week, the position of each treatment was randomized using the pseudo-random number generator in MS Excel. The area covered by coral tissue was measured with the program Image J, V 10.2, from digital images calibrated to scale with the ruler attached to the photo framer. Area measurements were taken after the experiment was set up on 7 October 2006 and at 45 days (21 November 2006).

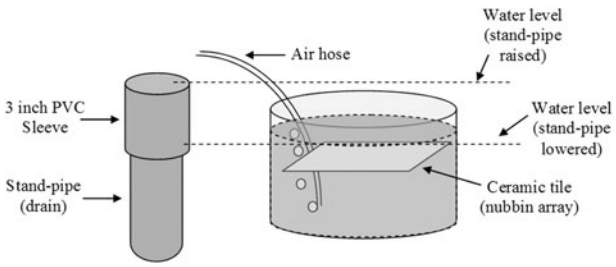

Fig. 2. Diagram of dosing compartment (Experiment 3).

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Table 2. Food type, dose and average net tissue increase over 41 days (Experiment 3).

Food type	Dose	Amount	N	Average net growth (cm^2) ± SE
Prorites				
None	na	na	60	0.695 ± 0.052
Microvert	1X	50 ul	14	0.717 ± 0.072
	3X	150 ul	15	0.763 ± 0.113
	10X	1.5 ml	15	0.565 ± 0.117
Marine Snow	1X	660 ul	15	0.651 ± 0.106
	3X	1.98 ml	15	0.586 ± 0.076
	10X	6 ml	15	0.857 ± 0.142
Phytoplan	1X	0.04 g	15	0.675 ± 0.202
	3X	0.12 g	14	0.444 ± 0.094
	10X	0.4 g	14	0.489 ± 0.091
Salifert	1X	300 ul	15	0.885 ± 0.101
	3X	900 ul	15	0.585 ± 0.092
	10X	3 ml	15	0.433 ± 0.069
Total			237	0.653 ± 0.028
Montipora				
None	na	na	35	0.378 ± 0.053
Microvert	1X	50 ul	9	0.272 ± 0.069
	3X	150 ul	8	0.489 ± 0.07
	10X	1.5 ml	7	0.287 ± 0.063
Marine Snow	1X	660 ul	8	0.381 ± 0.062
	3X	1.98 ml	7	0.285 ± 0.106
	10X	6 ml	10	0.245 ± 0.109
Phytoplan	1X	0.04 g	8	0.375 ± 0.077
	3X	0.12 g	7	0.246 ± 0.054
	10X	0.4 g	8	0.286 ± 0.058
Salifert	1X	300 ul	7	0.406 ± 0.064
	3X	900 ul	5	0.221 ± 0.19
	10X	3 ml	10	0.269 ± 0.12
Total			129	0.331 ± 0.024

RESULTS

Experiment 1: light and water motion

This experiment resulted in high overall survivorship (99.4%, N = 480) for both species over a period of 41 days (Table 3). Overall net tissue increase was ~50% for *P. compressa* and 9% for *M. capitata*. Average light (PAR) values and 95% confidence intervals (CI) for the shaded treatments were as follows; 0X = 1252 ± 371 μ mol m^{-1} s^{-1}, 1X = 457 ± 110 μ mol m^{-1} s^{-1}, 2X = 145 ± 30μ mol m^{-1} s^{-1} and 3X = 82.86 ± 19.20 μ mol m^{-1} s^{-1}. Average fill rates and rotation rate of fluorescein dye had an inverse relationship ($r^2 = 0.8798$, $P < 0.001$, data not shown), and the two measures showed consistent differences among treatments; the dye travelled on average 3.93 ± 0.37 cm s^{-1} for the low flow treatments, and 11.10 ± 0.69 cm s^{-1} for the high flow treatments (average ± 95% CI). Temperature logger data were only available for four of the 16 treatments. Average temperature differences between these treatments over the course of the experiment only differed by a tenth of a degree C (the lowest average was 26.81 ± 0.01°C for a high flow 1X shade cloth treatment, and the highest average was 26.98 ± 0.02°C for a full sun, low flow treatment).

Higher water motion resulted in slightly less tissue growth, in both species, for both 19 and 41 day measurements; however, the comparisons were not statistically significant. Levene's statistic indicated that the high flow treatments resulted in significantly higher variance in net tissue growth (for all comparisons except *Porites* on day 19, not shown). The relationship between light and net tissue increase, is approximately linear in *Porites* (Figure 3). Average *P. compressa* tissue area increased by approximately 40% in the lowest light treatments, and was greater than 60% in the highest light treatments over 41 days. There was no evidence of bleaching of the *P. compressa* nubbins, despite exposure to full sunlight in only a few inches of water. *Montipora capitata*, on the other hand, exhibited bleaching of the upper surfaces in the full sun treatments, and this resulted in less growth (Figure 3), in the full sun treatment (0X shade cloth).

An analysis of variance (ANOVA) across light and flow treatments indicated significant differences between species, light treatments, flow treatments (within replicates), and a significant interaction between light, water motion and species (Table 4). In other words, each species responded differently to the light and flow treatments, and light, water motion and species interacted. The growth response for the two

Table 3. Growth and survivorship in light by flow treatments.

Flow	Light	N(start)	N(end)	Initial size (mm^2 ± 95%CI)	End size (mm^2 ± 95%CI)	Net increase (mm^2 ± 95%CI)
Porites compressa						
Low	0X	30	30	1.07 ± 0.06	1.72 ± 0.12	0.65 ± 0.10
	1X	30	30	1.03 ± 0.06	1.61 ± 0.09	0.57 ± 0.08
	2X	30	30	0.98 ± 0.09	1.47 ± 0.10	0.49 ± 0.09
	3X	30	29	1.02 ± 0.08	1.35 ± 0.13	0.36 ± 0.08
High	0X	30	29	1.06 ± 0.09	1.53 ± 0.18	0.47 ± 0.16
	1X	30	30	1.09 ± 0.09	1.62 ± 0.13	0.52 ± 0.09
	2X	30	30	1.04 ± 0.09	1.48 ± 0.15	0.44 ± 0.14
	3X	30	30	1.01 ± 0.08	1.47 ± 0.12	0.46 ± 0.13
Montipora capitata						
Low	0X	30	30	1.14 ± 0.08	1.17 ± 0.09	0.03 ± 0.03
	1X	29	29	0.97 ± 0.12	1.13 ± 0.14	0.16 ± 0.07
	2X	30	30	0.95 ± 0.10	1.12 ± 0.11	0.16 ± 0.06
	3X	30	30	0.98 ± 0.12	1.06 ± 0.13	0.08 ± 0.05
High	0X	30	30	1.09 ± 0.10	1.13 ± 0.13	0.11 ± 0.06
	1X	30	30	1.00 ± 0.09	1.18 ± 0.13	0.09 ± 0.07
	2X	30	30	0.97 ± 0.10	1.04 ± 0.11	0.07 ± 0.09
	3X	30	30	0.98 ± 0.09	1.00 ± 0.10	0.02 ± 0.11

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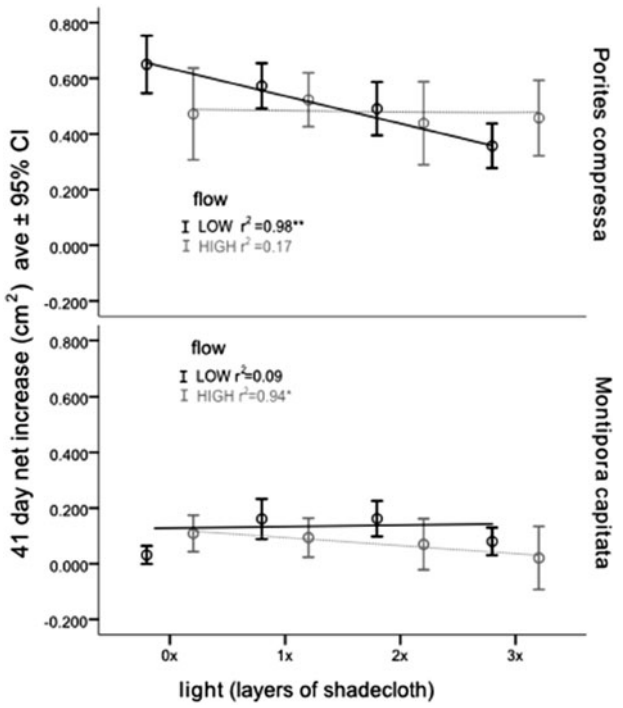

Fig. 3. Species responses to light and flow treatments (Experiment 1).

species clearly differed in response to light and water flow (Figure 3). *Montipora capitata* grew poorly and bleached in high light and low flow, while *P. comressa* did the best under these same conditions. High flow resulted in greater variation within most of the treatments.

Experiment 2: effects of artificial foods

The average overall (pooled across species) weight increase for the control (filtered seawater) was 2.1%, which was lower than all other treatments. The tanks fed with Oyster Eggs, and Roti-Feast had slightly higher overall mean weight increase (2.7% and 3.1% respectively), but these differences were not significant according to *post-hoc* tests. Reef Chili and Reef-Roids on the other hand show a comparatively large overall weight increase (6.5% and 7.5% respectively). When the contribution of each species was examined, it became clear that *M. capitata* showed the highest increase in weight, followed by *P. damicornis*, with Reef Chili and Reef-Roids showing the largest increases (Figure 4). *Porites compressa* however did not appear to be influenced by feeding, with similar growth between the control and artificial food treatments. An ANOVA indicated significant differences between food types and coral species (Table 5).

Table 4. Analysis of variance of light, flow and species interactions after 41 days of net growth (Experiment 1).

Source	Type III sum of squares	df	Mean square	F
R(F)	0.188	2	0.094	5.752**
L	0.159	3	0.053	3.238*
S	3.923	1	3.923	239.629***
C(S)	0.101	4	0.025	1.549
L * F	0.031	3	0.010	0.629
F * S	0.001	1	0.001	0.034
F * C(S)	0.020	4	0.005	0.311
L * S	0.078	3	0.026	1.598
L * C(S)	0.059	12	0.005	0.302
L * F * S	0.138	3	0.046	2.818*
L * F * C(S)	0.068	12	0.006	0.348

L, light; F, flow; S, species; R, replicate; c, colony. *, $P<0.05$; **, $P < 0.01$; ***, $P < 0.001$.

The fastest growing fragment according to weight increase was a fragment of *M. capitata* which had a 24% increase in a tank being treated with Reef Chili. According to increase in displacement, the fastest growing fragments were two *M. capitata* fragments which had a 47% increase in displacement, and were also in the same replicate of the tank being treated with Reef Chili. Water displacement generally showed similar overall patterns as weight (not shown); however, weight had much lower variance and was presented here.

Experiment 3: increased doses of artificial foods

Overall survivorship was high for *P. compressa* (98.7%), however nearly half (49%) of *M. capitata* nubbins died shortly after they were fixed onto the ceramic tiles, most likely due to excessive handling time. The feeding experiment was set up following the light/flow experiment (Experiment 1), which resulted in a long delay between fragmentation and attachment which is most likely the cause for the higher mortality. The two experiments were performed with the same randomized pool of nubbins, so that inferences could be made about the relative importance of light, flow and doses of artificial foods. In spite of high initial mortality, overall net tissue area increase was high (*P. compressa* 65% and *M. capitata* 35%).

Adding food supplements (MicroVert, MarineSnow Plankton Diet, Phytoplan, and Salifert) at the manufacturers' recommended dosages, resulted in no significant difference to the controls (ANOVA, $P = 0.604$). Unlike the feeding experiments in filtered seawater above, these comparisons among the types of coral food (pooled over dose) indicated no significant differences with controls (ANOVA: *M. capitata* $P = 0.30$, *P. compressa* $P = 0.368$). Adding either 3 or 10 times the recommended dose generally resulted in a decrease in growth (Figure 5). There was a significant trend towards decreased growth with increasing dosage (pooled over food types) for *M. capitata* ($r^2 = 0.95$, $P < 0.024$). Although the trends for *P. compressa* ($r^2 = 0.59$, ns) and for both species pooled together ($r^2 = 0.80$, ns) were not significant (Figure 6), the trends were in the same direction and had a similar slope. Phytoplan and Salifert treatments consistently had the lowest growth rates for both species although these differences were not significant.

DISCUSSION

This study examined species-specific responses to light, water motion, and supplementation with artificial foods using relatively simple metrics such as changes in weight or top-down area measurements. We were able to gain insights in a relatively short time, with minimal cost, by exploiting the clonal nature of corals in a series of straightforward and inexpensive experiments.

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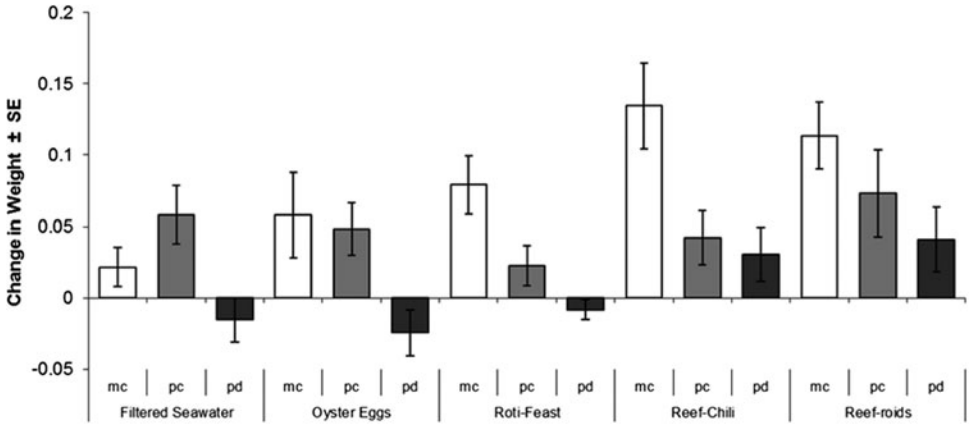

Fig. 4. Species-specific change in weight by artificial foods (Experiment 2). mc, *Montipora capitata*; pc, *Porites compressa*; pd, *Pocillopora damicornis*.

Experiment 1: light and water motion

This experiment illustrated that light and water motion interact to effect growth, and that different species respond differently to changes in these parameters. *Porites compressa* grew best in high-light, low-flow conditions, while *M. capitata* did the worst under these same conditions. These differences were unlikely to be due to morphology (e.g. Jokeil, 1978; Lesser *et al.*, 1994) since the small fragments were very similar in size and shape. The interaction between light and water motion has been a subject of study in a variety of corals (e.g. Dennison & Barnes, 1988; Kuffner, 2000, 2002; Fabricius, 2006), although most of these studies have focused on manipulations involving a single species per study. Species-specific effects of light and water motion are not particularly surprising however, since these factors are thought to play an important role in species zonation patterns (e.g. Wellington, 1982; Titlyanov & Titlyanova, 2002; Vermeij & Bak, 2002; Anthony & Connolly, 2004, but see Titlyanov *et al.*, 1990 for an example of three Pacific species with largely overlapping light ranges).

Interestingly, the high flow treatments (~11 cm s^{-1}) consistently resulted in slightly less (though not significant) growth for both species. These experimental flow conditions are highly artificial and likely to be far more unidirectional and less variable than natural conditions; nevertheless the flow conditions in this experiment are relatively slow; for example lagoons fluctuate between 1 and 16 cm/sec, while exposed reefs can be far higher (Sebens & Done, 1992). Constant rates of unidirectional flow in such a small circular volume may have hydrodynamic properties that prevent suspension feeding or otherwise inhibit coral growth. Increased flow at high light levels reduced the effects of bleaching for *M. capitata*, which has been seen in previous studies on photo-inhibition (Finelli *et al.*, 2005; Nakamura *et al.*, 2005). This reduction could be due to a variety of factors such as decreased irradiance from increased surface turbulence, an increased rate of gas exchange, or a slight decrease in temperature (although temperature loggers showed only slight differences between treatments).

Table 5. Analysis of variance of percentage weight increase for corals feed on an artificial diet (Experiment 2).

Source	Type III sum of squares	df	Mean square	F
Species	0.104	2	0.052	18.407***
Treatment	0.044	4	0.011	3.884***
Species * treatment	0.040	8	0.005	1.724
Tank (treatment)	0.003	5	0.001	0.270
Species * tank (treatment)	0.015	10	0.001	0.521
Error	0.169	60	0.003	
Total	0.549	90		
Corrected total	0.373	89		

R Squared = 0.548 (adjusted R squared = 0.329). *, $P<0.05$; **, $P < 0.01$; ***, $P < 0.001$.

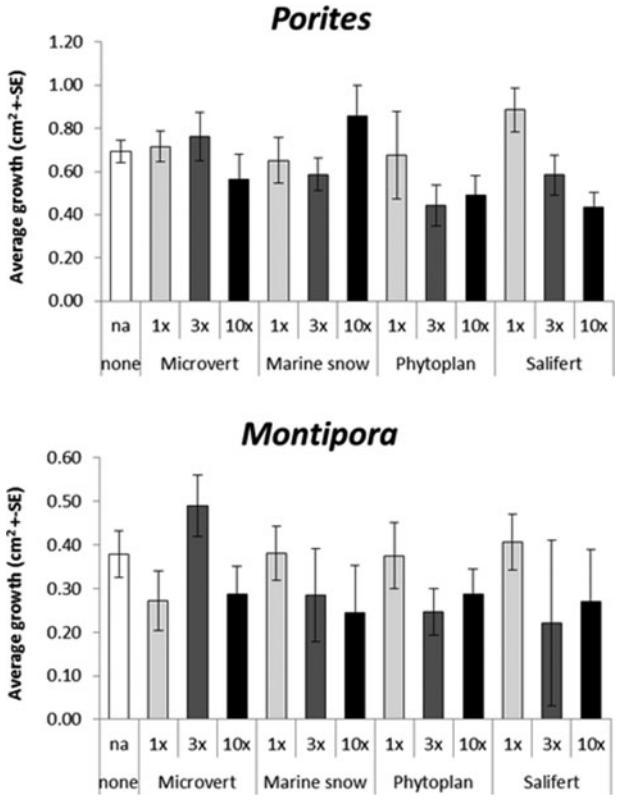

Fig. 5. Effects of artificial food type and dose on growth of *Porites* and *Montipora* in an open system (Experiment 3).

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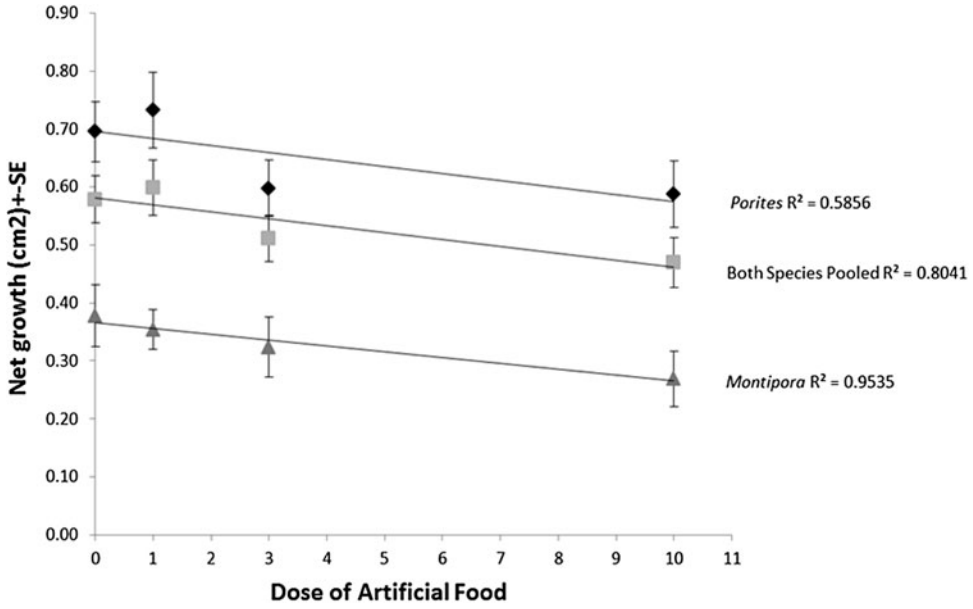

Fig. 6. Effects of dose of artificial foods pooled by food type (Experiment 3).

Experiment 2: effects of artificial foods

This study demonstrated that some commercially available artificial coral foods can have a large positive effect on the growth of some species of scleractinian corals. These foods can be fairly expensive, although they are generally less expensive and labour intensive than live food. According to the growth data (by weight and displacement), Roti-Feast, Reef Chili and Reef-Roids increased the average growth rates of the *M. capitata* and *P. damicornis* fragments (Figure 4). Although being one of the more expensive and natural products, the tanks fed with the Oyster Eggs did not differ significantly from the control tank. According to the product labels, Reef Chili contains zooplankton, copepods and rotifers; Reef-Roids contains zooplankton, Roti-Feast contains rotifers and rotifer eggs, and Oyster Eggs contain actual oyster eggs.

The three test species clearly responded quite differently to foods (Figure 4). *Porites compressa* did not appear to benefit from feeding, because growth rates did not vary significantly among any of the treatments. *Montipora capitata*, however, was much more sensitive to the addition of food and all treatments resulted in increased growth relative to the controls. Finally, *P. damicornis* showed variable responses, losing weight in the controls and with two of the foods, whereas there was significant growth in tanks treated with Reef Chili and Reef-Roids. These species-specific differences most likely correspond to differences in heterotrophic ability. *Porites compressa* may rely more on phototrophy, which would also explain why this species did so well in the highest light treatments in Experiment 1. *Montipora capitata* shows the opposite trend in each experiment and appears amply capable of using heterotrophy to fuel growth. Although the coral fragments of *M. capitata* and *P. damicornis* grew faster in the Reef-Roids and Reef Chili treatments, it is important to note that there was also an abundance of algal growth in these treatment tanks relative to other treatments. There is likely to be a fine line between feeding and overfeeding. Regardless of the dose, coral fragments that are fed nutrient rich foods will require more herbivores or frequent cleaning to prevent algal overgrowth.

Experiment 3: increased doses of artificial foods

This experiment was designed to examine the effects of increasing doses of artificial foods on coral growth. For this experiment, we chose readily available and widely distributed coral foods with long shelf lives as opposed to the specialty foods with limited distribution used in the previous experiment. According to the product labels Microvert contains spirulina and kelp; Marine Snow contains phytoplankton, (*Nannochloropsis*, *Tetraselmis*, *Isochrysis*, Spirulina, *Schyzochitrium*, dried seaweed meal and zooplankton); Phytoplan contains a spray-dried blend of phytoplankton; and Salifert contains encapsulated and dissolved fatty acids, carbohydrates, proteins, vitamins and minerals. At the manufacturers' recommended dose we saw no effect of these foods on coral growth above the negative control (filtered seawater). It is important to note that this experiment took place in an open system, with coarsely filtered seawater, and these results may differ in a closed system. Interestingly, although no food treatments were significantly different from the negative control (filtered seawater) the consistent trend was decreased coral growth with increased feeding across both species and all food products (Figure 6). At concentrations higher than the manufacturers' recommended levels, the foods appear to inhibit coral growth, although this trend is only statistically significant for *M. capitata*. This result is surprising, because even the highest doses of foods were relatively dilute (6 ml in 18 l), and dosing only occurred overnight, followed by flushing with fresh seawater each morning. Although there were few consistent patterns aside from decreased growth with increasing dose, the Phytoplan and Salifert coral food treatments contained noticeably higher algal growth, and the lowest coral growth when averaged over all doses for the coral species we tested.

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Overall conclusions

This study shows that light and water motion interact and have species-specific effects on coral growth rates and that some artificial coral foods clearly have the potential to increase coral growth rates in some coral species, while having little or even negative effect on others. Some of the most commonly available and inexpensive coral foods in the aquarium trade were found to have no significant effect on coral growth at recommended dosage, and increased doses resulted in decreased coral growth. Effects of light, water motion and food were in some cases species-specific: *P. compressa* appears to grow best in bright light regardless of supplemental feeding, whereas *M. capitata* and *P. damicornis* showed significant growth in response to some (but not all) artificial foods, and *M. capitata* tended to grow faster at lower light levels. Strong species-specific effects imply that corals are adapted to specialize on a particular niche in a highly heterogeneous environment. Further studies are needed to explain the mechanisms behind these differences (such as polyp and particle size, tentacle and or nematocysts size and arrangement, or zooxanthellae type and density). The overall implication from this study is that abiotic conditions and artificial feeds can be optimized to have large beneficial effects on coral growth. A systematic examination of the requirements for a given species of reef building coral can result in more successful cultivation of that variety, and may yield interesting insights into basic ecology and organismal biology in the process.

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REFERENCES

Anthony K.R.N. (1999) Coral suspension feeding on fine particulate matter. *Journal of Experimental Marine Biology and Ecology* 232, 85–106.

Anthony K.R.N. and Connolly S.R. (2004) Environmental limits to growth: physiological niche boundaries of corals along turbidity–light gradients. *Oecologia* 141, 373–384.

Anthony K.R.N and Fabricius K. E. (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology* 252, 221–253.

Bak R.P.M., Joenje M., de Jong I., Lambrechts D.Y.M. and Nieuwaland G. (1998) Bacterial suspension feeding by coral reef benthic organisms. *Marine Ecology Progress Series* 175, 285–288.

Buddemeir R.W. and Kinzie R.A. (1976) Coral growth. *Oceanography and Marine Biology: an Annual Review* 14, 183–225.

Clark S. and Edwards A.J. (1995) Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. *Coral Reefs* 14, 201–213.

Delbeek J.C. (2001) Coral farming: past, present and future trends. *Aquarium Sciences and Conservation* 3, 171–181.

Dennison W.C. and Barns D.J. (1988) Effect of water motion on coral photosynthesis and calcification. *Journal of Experimental Marine Biology and Ecology* 155, 67–77.

Edwards A.J. and Clark S. (1998) Coral transplantation: a useful management tool or misguided meddling? *Marine Pollution Bulletin* 37, 474–487.

Fabricius K.E. (2006) Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: implications for coral bleaching? *Limnology and Oceanography* 51, 30–37.

Ferrier-Pagès C., Witting J., Tambutté E. and Sebens K.P. (2003) Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. *Coral Reefs* 22, 229–240.

Finelli C.M., Helmuth B.S., Pentcheff N.D. and Wethey D.S. (2005) Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* 25, 47–57.

Forsman Z., Rinkevich B. and Hunter C. (2006) Investigating fragment size for culturing reef-building corals (*Porites Lobata and P. Compressa*) in *ex situ* nurseries. *Aquaculture* 261, 89–97.

Gochfeld D.J. and Aeby G.S. (1997) Control of populations of the coral feeding nudibranch *Phestilla sibogae* by fish and crustacean predators. *Marine Biology* 130, 63–69.

Goldman L. (2007) Evaluation of live food versus artificial food on the growth of juvenile *Pocillopora damicornis* cultured from planulae. *Advanced Aquarist Online Magazine VI*. http://www.advancedaquarist.com/2007/6/aafeature1

Goreau T.F., Goreau N.I. and Yonge C.M. (1971) Reef corals: autotrophs or heterotrophs. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 141, 247–260.

Grotolli A.G., Rodriguez L.J. and Palardy J.E. (2006) Heterotrophic plasticity and resilience in bleached corals. *Nature* 440, 1186–1189.

Highsmith R.C. (1982) Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7, 207–226.

Jokiel P.L. (1978) Effects of water motion on reef corals. *Journal of Experimental Marine Biology and Ecology* 35, 87–97.

Kuffner I.B. (2000) Effects of ultraviolet radiation and water motion on the reef coral *Porites compressa* Dana: a flume experiment. *Marine Biology* 138, 467–476.

Kuffner I.B. (2002) Effects of ultraviolet radiation and water motion on the reef coral *Porites compressa* Dana: a transplantation experiment. *Journal of Experimental Marine Biology and Ecology* 270, 147–169.

Larned S.T. (1998) Nitrogen-versus phosphorous-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology* 132, 409–421.

Lesser M.P., Weis V.M., Patterson M.R. and Jokiel P.L. (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *Journal of Experimental Marine Biology and Ecology* 178, 153–179.

McManus J.W. and Polsenberg J.F. (2004) Coral–algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60, 263–279.

Muscatine L. (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In Dubinsky Z. (ed.) *Ecosystems of the world: coral reefs*. Amsterdam: Elsevier, pp. 75–87.

Nakamura T., van Woesik R. and Yamasaki H. (2005) Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral *Acropora digitifera*. *Marine Ecology Progress Series* 301, 109–118.

Rinkevich B. (1995) Restoration strategies for coral reefs damaged by recreational activities: the use of sexual and asexual recruits. *Restoration Ecology* 3, 241–251.

Rinkevich B. (2000) Steps towards the evaluation of coral reef restoration by using small branch fragments. *Marine Biology* 136, 807–812.

Rinkevich B. (2005) Conservation of coral reefs through active restoration measures: recent approaches and last decade progress. *Environmental Science and Technology* 39, 4333–4342.

Sawall Y., Teichberg M.C., Seemann J., Litaay M., Jompa J. and Richter C. (2011) Nutritional status and metabolism of the coral *Stylophora subseriata* along a eutrophication gradient in Spermonde Archipelago (Indonesia). *Coral Reefs* 30, 841–853. DOI:10.1007/s00338-011-0764-0.

Sebens K.P., Vandersall K.S., Savina L.A. and Graham K.R. (1996) Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure. *Marine Biology* 127, 303–317.

Sebens K.P., and Done T.J. (1992) Water flow, growth form and distribution of scleractinian corals: Davies Reef (GBR), Australia. *Proceedings of the Seventh International Coral Reef Symposium* 1, 557–568.

Stambler N., Popper N., Dubinsky Z. and Stimson J. (1991) Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. *Pacific Science* 45, 299–307.

Titlyanov E.A., Leletkin V.A., Ermak V.D. and Voskoboinikov G.M. (1990) Light adaptation of mass species of reef-building corals. *Soviet Journal of Marine Biology* 16, 25–31.

Titlyanov E.A., Titlyanova T.V., Yamazoto K. and van Woesik R. (2001) Photo-acclimation of the hermatypic coral *Stylophra pistillata* while subjected to either starvation or food provisioning. *Journal of Experimental Marine Biology and Ecology* 257, 163–181.

Titlyanov E.A. and Titlyanova T.V. (2002) Reef-building corals—symbiotic autotrophic organisms: 1. general structure, feeding pattern, and light-dependent distribution in the shelf. *Russian Journal of Marine Biology* 28, 51–515.

Toonen RJ., Batchelor K. and Mai T. (2002) Planktonic foods for the reef aquarium: if you feed the tank, are these foods for you? *Marine Fish & Reef USA Annual 2002* 4, 18–31.

Wellington G.M. (1982) An experimental analysis of the effects of light and zooplankton on coral zonation. *Oecologia* 52, 311–320.

and

Vermeij M.J.A. and Bak R.P.M. (2002) How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. *Marine Ecology Progress Series* 233, 105–116.

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