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Enhancing Coral Settlement Through a Novel Larval Feeding Protocol

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Intensifying anthropogenic stressors have contributed to declines in reef-building corals in many regions. These disturbances result in reduced live coral cover, impacting key population-level processes such as coral larval settlement and recruitment that are essential for reef recovery. Reef restoration efforts that rely on enhanced larval supply provide a pathway for the recovery of degraded reefs. However, corals at very early life stages experience high post-settlement mortality bottlenecks, which impede stock-recruitment processes. Overcoming these bottlenecks is a high priority goal in coral restoration. Some coral larvae are known to be capable of gaining exogenous nutrients. Therefore, we hypothesised that the capacity to access exogenous nutrients may confer advantages to larval survival, settlement and post-settlement success. The present study aimed to quantify the effect of larval feeding on coral larvae settlement and early post-settlement survival. We completed an *ex-situ* experiment using aposymbiotic larvae of two broadcast spawning reef-building coral species - *Acropora tenuis* and *Acropora millepora.* Larvae were randomly assigned to either fed or unfed treatment groups for each species. Fed larvae received homogenised *Artemia* once a day, for three days. Results show that for both species, feeding significantly increased larval settlement. Feeding *A. millepora* larvae more than doubled mean settlement (13.0 ± 1.17 SE vs 31.4 ± 2.88 SE; p <0.001). Similarly, feeding *A. tenuis* larvae increased mean settlement from 18.2 (± 1.85 SE) to 29.9 (± 2.22 SE; p <0.001). Larval feeding had an immediate positive effect on spat survival, such that *A. millepora* and *A. tenuis* spat from fed treatments had increased survival three days post-settlement (89.5% ± 3.75 SE vs 70.6% ± 2.59 SE, p <0.001; 88.8% ± 2.21 SE vs 71.4% ± 3.80 SE, p <0.001, respectively). Therefore, enhancing settlement and early post-settlement survival by feeding larvae homogenised *Artemia* has the potential to improve the effectiveness of larval rearing protocols and coral restoration efforts.

Keywords: recruitment, post-settlement survival, coral restoration, reef restoration, facultative planktotrophy, larval energetics, aquaculture

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INTRODUCTION

Coral reefs are vulnerable ecosystems impacted by a range of environmental disturbances across small and large spatial scales (Bellwood et al., 2004) and from natural and anthropogenic sources (Hughes et al., 2003; Burke et al., 2011). Intensifying anthropogenic impacts, including climate change, have contributed to recent declines in reef-building corals (Hoegh-Guldberg et al., 2007;

De'Ath et al., 2012; Hughes et al., 2018). Declines in live coral cover can impact key population-level processes, including reproductive capacity and concomitant replenishment of corals *via* coral larval recruitment, a primary driver of recovery on degraded reefs (Harrison and Wallace, 1990; Mumby and Harborne, 2010; Gouezo et al., 2019). These early life stages often represent a bottleneck in the successful reproduction and recruitment process for marine invertebrates (Pineda, 2000). Therefore, negatively impacted stock-recruitment processes reduce the overall ability for coral communities and reefs to naturally recover (Hughes et al., 2019).

Reef restoration is a pathway to recover degraded reefs and is increasingly included in natural resource management (Edwards, 2010; Omori, 2019; Boström-Einarsson et al., 2020). Coral restoration has routinely relied on using asexually produced coral fragments to restore corals (Rinkevich, 2005), but the use of sexually derived coral larvae for coral and reef restoration is rapidly increasing (dela Cruz and Harrison, 2017; Doropoulos et al., 2019; dela Cruz and Harrison, 2020; Harrison et al., 2021). Using coral larvae for restoration relies on the high fecundity of broadcast spawning coral colonies (Harrison and Wallace, 1990), allowing collection of millions of gametes on reefs and in laboratory settings. Collected gametes enable the mass culture of larvae which allows restoration efforts to supply sufficiently high numbers of larvae to degraded reefs. Equally critical is ensuring settlement of coral larvae and metamorphosis into settled polyps, and survival and growth into juvenile corals. These early life stages are an essential step in recruitment to adult populations (Harrison and Wallace, 1990; Richmond, 1997) and dictate the effectiveness of restoration efforts (Boström-Einarsson et al., 2020).

Most wild-spawned coral larvae die or are lost from reef systems during their planktonic larval phase or in the first few weeks and months post-settlement (Harrison and Wallace, 1990; Wilson and Harrison, 2005; Doropoulos et al., 2016; dela Cruz and Harrison, 2017; Harrison et al., 2021), and there remain many questions around the biological determinants of settlement and recruitment processes for corals. For example, endogenous energy stores in non-feeding larvae are a limiting factor that dictate settlement outcomes (Strathmann, 1985; Marshall and Keough, 2003; Botello and Krug, 2006; Graham et al., 2013a). Egg provisioning impacts larval competency and the initial stages of settlement and post-settlement survival. Prolonged larval phases are thought to decrease settlement rates as energy stores are depleted, thereby compromising the potential to complete metamorphosis with increasing age (Wilson and Harrison, 1998; Graham et al., 2008). Therefore, the dynamic interplay between larval endogenous energy stores, settlement success and the latent effects on recruitment success highlight the importance of understanding the link between larval energetics and restoration efforts (Harrison and Wallace, 1990; Graham et al., 2013b).

While coral larvae are considered lecithotrophic, provisioned with sufficient energy needed during their larval phase, competency periods for broadcast spawning coral larvae are often longer than energetic models predict (Tranter et al., 1982; Wilson and Harrison, 1998; Nozawa and Harrison, 2002). As a result, some researchers suggest that certain species of coral larvae gain exogenous nutrients to bridge these gaps (Fadlallah, 1983; Arai et al., 1993; Zaslow and Benayahu, 1996; Graham et al., 2013a; Rivest et al., 2017). One important source of nutrients for coral larvae appears to be dissolved organic material (DOM) (Sorokin, 1973; Fadlallah, 1983; Graham et al., 2013a). Moreover, there is evidence that free amino acids contribute up to 11% of the metabolic needs of coral larvae (Zaslow and Benayahu, 2000) and may play a role in inducing settlement (Baird and Morse, 2004). Other nutrients may also be physiologically important, for example, *Pocillopora damicornis* larvae have been found to lack sufficient quantities of nitrogen and phosphorous necessary for metamorphosis (Titlyanov et al., 1998). Similarly, when deprived of all sources of exogenous nutrients, *Porites porites* larvae cannot settle successfully (Fadlallah, 1983).

In addition to the assimilation of DOM, there is evidence that some coral larvae actively feed on particulate matter *via* ciliary currents and mucus strings (Tranter et al., 1982; Harii et al., 2009). The use of ciliary currents to move particulate matter to the oral pore has been observed in the larvae of *Stylophora pistillata* (Rinkevich and Loya, 1979), *Cyphastrea ocellina* (Wright, 1986), *Pocillopora damicornis* (Richmond, 1985) and *Fungia scutaria* (Krupp, 1983), and is common in other single-banded ciliated invertebrates (Strathmann et al., 1972; Paulay et al., 1985). In conjunction with ciliary currents, larvae have been observed using mucus strings to capture food particles (Tranter et al., 1982; Schwarz et al., 1999; Harii et al., 2009) in a process known as mucociliary transport (Young, 1971; Brown and Bythell, 2005). In this process, nutritive particulate matter is captured in mucus and transported to the oral pore, where it is then ingested (Tranter et al., 1982; Schwarz et al., 1999; Harii et al., 2009). With evidence that certain species of coral larvae are capable of gaining exogenous nutrients, the capacity to access exogenous nutrients may confer advantages to larval survival, settlement and post-settlement success.

Therefore, a strict dichotomy of binary nutritional modes - feeding *or* non-feeding - does not suit the wide biological variation seen among coral larvae. Alternatively, researchers have proposed an intermediate nutritional mode - facultative planktotrophy - to account for similar variation in other non-coral marine invertebrates (Allen and Pernet, 2007; Collin, 2012; Pernet, 2018). This nutritional mode is characterised by larvae capable of feeding but which are not required to do so to complete metamorphosis (Boidron-Métairon, 1995). Furthermore, when fed, facultative planktotrophic larvae often metamorphose into larger juveniles and exhibit increased post-metamorphic survivorship (Boidron-Métairon, 1995; McEdward, 2000; Allen and Pernet, 2007). However, to date, there are limited data that examine the relationships between the supply of exogenous nutrients and settlement in coral larvae. Therefore, these critical aspects of coral larval biology and ecology warrant more detailed investigation. Hence, the present study aims to quantify the effect of feeding on coral larval settlement and early post-settlement survival. Specifically, we hypothesise that rearing larvae with access to exogenous nutrients will enhance settlement and potentially improve post-settlement survival.

MATERIALS AND METHODS

This experiment was conducted on Bindal country at the Australian Institute of Marine Science's (AIMS) National Sea Simulator (SeaSim) in Townsville, Australia, to assess the effect of supplying nutrients to coral larvae on their settlement and early post-settlement survival. Aposymbiotic larvae of two broadcast spawning corals were used - *Acropora tenuis* and *Acropora millepora*. Both species are widespread in the Indo-Pacific region and common on a range of reef sites (Wallace, 1999). *Acropora tenuis* has been previously used in *ex-situ* larval restoration studies (dela Cruz and Harrison, 2017; Cameron and Harrison, 2020; Harrison et al., 2021). Furthermore, both species have been successfully spawned and reared in aquaria with well-established culturing and settlement techniques (Heyward and Negri, 1999; Humanes et al., 2016; Conlan et al., 2017; Pollock et al., 2017).

Coral Collection

Gravid colonies of each species were collected from near-shore and mid-shelf reefs on Wulgurukaba and Bindal Sea Country on the central Great Barrier Reef in the days leading up to the November 2020 full moon and transported to SeaSim (GBRMPA Permit G12/35236.1).

Larval Culture

On arrival at SeaSim, colonies were transferred to outdoor flow-through holding tanks and maintained at 27°CC (± 0.5°CC) under 30% shaded natural sunlight until spawning occurred. Once spawning occurred, gamete bundles were skimmed from the surface, and a 60µm mesh sieve was used to separate eggs and sperm. Eggs were then transferred to a separate 60L tank filled with 1µm filtered seawater. Sperm were then added at a concentration of 1 x 10^6 sperm/ml (Willis et al., 1997), and after two hours, when embryos were observed to be cleaving, they were rinsed and transferred to a 500L culture tank. Light aeration was added after 24hrs.

Experimental Design

Rearing

Thirty-six hours after spawning, larvae were transferred to individual rearing tanks, which consisted of 14L aerated cone-shaped plastic flow-through tanks. All tanks had a 12L per hour flow rate using 1µm filtered seawater, equating to a complete water turnover every 70 mins. Fluorescent lights over the tanks were set on a 12:12 hr timer with the first light at 6 am and the last light at 6 pm. The average light level over the rearing tanks was 40 µmoles m^{-2} s^{-1}. Water temperature in the tanks remained at 27°CC (± 0.5°CC) for the duration of the experiment. *Acropora tenuis* larvae were added at one larva per 5 ml, resulting in approximately 2800 larvae per tank. *Acropora millepora* larvae were added at a concentration of 0.16 larvae per ml, with about 2250 larvae per tank.

All tanks with larvae were randomly assigned to one of two treatments, either unfed or fed for each species. Both species had the same number of unfed replicates (n = 4). However, due to larval supply differences, there was an uneven number of fed replicates for *A. millepora* larvae (n = 3) and *A. tenuis* larvae (n = 5). In the unfed treatment, larvae were reared without exogenous food supplied in ultrafiltered seawater (<0.05 µm). In the fed treatment, larvae received 50ml of homogenised *Artemia* at 4,185 nauplii per ml daily for three days. Food was provided on days six, seven, and eight after the spawning period and the onset of embryo and larval development. The water supply remained on when the food was administered to maintain water quality and avoid a build-up of organic matter that could lead to diseases. Therefore, the food was cleared approximately 70 mins after being provided.

Settlement

Nine days after spawning, larvae were transferred from rearing tanks to settlement tanks. Replicates were kept consistent between the rearing and settlement phases. Each settlement tank consisted of a 5L rectangular flow-through plastic container that housed custom made PVC settlement trays (300mm x 150mm x 20mm) with a grid of 50 holes (dia. 20mm) drilled into the top surface so that aragonite settlement plugs (dia. 20mm) could be inserted flush with the surface of the tray. Each settlement tray had twenty-five settlement plugs that had been biologically conditioned in a flow-through seawater system for six weeks prior to experiments to develop biofilms and crustose coralline algae (CCA) which are known settlement inducers for *A. tenuis* and *A. millepora* larvae. The remaining 25 plugs were not conditioned prior to experiments and therefore contained no CCA. Unconditioned plugs were rinsed in freshwater before being added to the settlement tray to remove any loose aragonite. The unconditioned plugs were used to fill the remaining plug holes to create a level surface across the settlement tray. Coral larvae settle preferentially on conditioned plugs. Light over each settlement tray was provided by Aqua Illumination Sol LED lights, simulating daylight and day length cycles. The mean light intensity over the settlement containers was 40 µmoles m^{-2} s^{-1}. The first light occurred at 6 am with a 5-hour ramp up time. The light remained at maximum intensity for 2 hours from 11 am until 1 pm, at which point light intensity decreased until the last light at 6 pm. Water temperature remained consistent at 27°CC (± 0.5°CC).

Data Collection and Statistical Analysis

At days three and seven, after introducing larvae into the settlement tanks, coral settlement plugs within each tank were photographed using a high-resolution Nikon camera system attached to a pre-programmed robotic mechanism. The first timepoint approximated the ecological time frame for settlement to occur, including searching for a settlement surface and metamorphosing into a coral spat. The second time point was arbitrarily chosen to aid in logistical planning allowing for the capture of early mortality. Each photo was analysed by counting the coral spat present on each conditioned settlement plug. Coral spat were identified as larvae that had fully attached to the settlement plug and metamorphosed into a single polyp with a

mouth and skeletal structure (**Figure 1**). Spat were included in plug counts if they were attached to the conditioned plug or in the crevice between the plug and tray if it was clearly attached to the settlement plug. Spat attached to the settlement tray, or an unconditioned plug, were counted separately. Additionally, any spat that had lost colour and appeared white and displayed tissue deterioration were presumed to be dead (**Figure 1**). Three days post-settlement, for each conditioned plug, all coral spat were counted and identified as either alive or dead. At seven days post settlement, only live coral spat were counted.

Spat counts of each species were calculated for each treatment. The three-day settlement counts resulted in a mean number of live, dead, and total spat per conditioned plug for each fed and unfed treatment. Together, spat on the tray, unconditioned plugs, and conditioned plugs were combined yielding total settlement for each replicate. The number of dead recruits at and the difference between the number of spat at three days post settlement was used to calculate a three-day survival rate. At seven days post-settlement, the spat counts yielded the mean number of surviving recruits per plug for each treatment. The difference in numbers of spat present between each plug at three days compared to seven days was used to calculate the percentage of surviving spat. As with mean settlement, the percentage of surviving spat was calculated for each treatment, yielding the mean survival within treatment groups.

The mean settlement of each category of spat between the unfed and fed treatment groups was analysed using a paired sample t-test. To meet the variance assumption of the test, variances were tested using an F-test for variance. The variance was found to vary, and therefore, the paired-sample t-test assuming unequal variances was used. T-tests were run on the mean settlement at three days post-settlement, and seven days post-settlement for each species. The mean survival between the unfed and fed treatment groups was also measured using a paired sample t-test assuming unequal variances for each species.

RESULTS

Larval Settlement

Total larval settlement was first censused three days after exposure to settlement cues. For both *A. millepora* and *A. tenuis* larval settlement was significantly higher in fed treatments compared to unfed treatments (**Table 1**; **Figure 2**). At the first census period, the total mean settlement, including both alive and dead spat, was significantly higher in fed *A. mille*pora larvae than unfed larvae (31.4 ± 2.88 SE vs 13.0 ± 1.17 SE, respectively $t(65) = 5.91$, $p < 0.001$) (**Figure 2A**). The mean number of alive spat was also significantly different between the fed and unfed treatments for *A. millepora* (**Figure 3**) whereby the mean number of alive *A. millepora* spat was higher in the fed treatments than in the unfed treatments (29.2 ± 3.05 SE vs 10.6 ± 1.22 SE, $t(65) = 5.65$, $p < 0.001$) (**Figure 3A**).

Similarly, three days after larvae were exposed to settlement cues, the total mean settlement of fed *A. tenuis* larvae that settled was significantly higher than unfed larvae (29.9 ± 2.22 SE vs 18.2 ± 1.85 SE, $t(198) = 4.04$, $p<0.01$) (**Figure 2C**). The mean number of settled *A. tenuis* larvae alive at the three-day census period was significantly higher in the fed treatments than in the unfed treatments (28.3 ± 2.28 SE vs 14.5 ± 1.77 SE, $t(198) = 4.78$, $p < 0.001$) (**Figure 3B**). This trend remained consistent over the first-week post-settlement.

In *A. millepora* larvae, the trend of higher settlement in fed treatments was maintained when all spat were counted. The average number of settled larvae, including those on unconditioned surfaces in the unfed treatment, was more than half that of the fed larvae (436.3 ± 74.53 SE vs 1000.5 ± 34.50 SE, respectively, $t(2) = 5.37$ $p = 0.017$). Of the total number of *A. millepora* spat across all fed treatments, 78.4% settled on conditioned settlement surfaces (1569 vs 432 spat). Meanwhile, A. millepora larvae across all unfed treatments settled on an unconditioned settlement surface 74.4% of the time (1299 vs 446 spat). The mean total spat

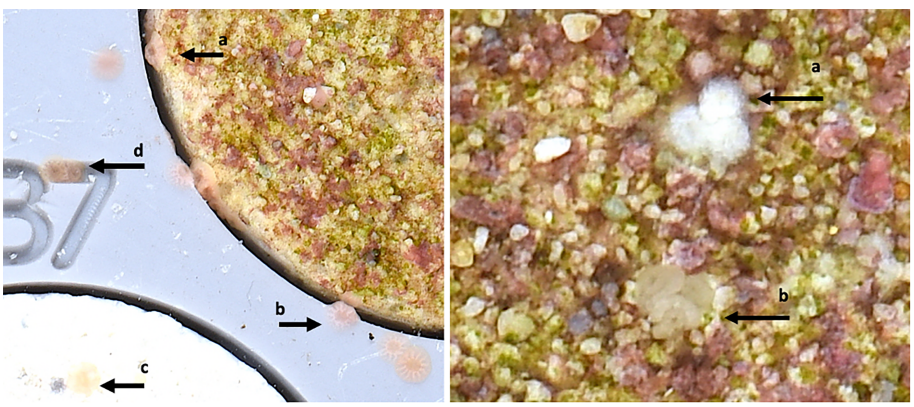

FIGURE 1 | (Left) *Acropora tenuis* spat showing various settlement locations, (a) spat on a conditioned settlement plug (b) spat on the PVC settlement tray, (c) spat on an unconditioned settlement plug, (d) spat in the crevice of the plug identification number. (Right) Examples of a cluster of opaque white dead *A. millepora* spat (a), and a cluster of alive *A. millepora* spat (b) on a conditioned settlement plug.

TABLE 1 | Observed mean, standard deviation (SD), standard error (SE), t-statistic, degrees of freedom (df), and *p* values for each t-test performed at either three (t_{3days}) or seven days (t_{7days}) after the introduction of settlement cues.

	t_{3days}						t_{7days}					
	Mean	**SD**	**SE**	**t-stat**	**df**	**p-value**	**Mean**	**SD**	**SE**	**t-stat**	**df**	**p-value**
Alive spat												
A. millepora												
Fed	29.16	21.56	3.05	5.65	65	<0.001*	13.60	15.36	2.17	3.45	72	<0.001*
Unfed	10.61	12.22	1.22				5.29	10.30	1.03			
A. tenuis												
Fed	28.26	25.51	2.28	4.78	198	<0.001*	15.99	21.26	1.90	3.98	191	<0.001*
Unfed	14.45	15.30	1.77				7.04	10.31	1.19			
Dead spat												
A. millepora												
Fed	2.85	4.67	0.66	0.56	59	0.58						
Unfed	2.38	3.80	0.38									
A. tenuis												
Fed	1.64	4.07	0.36	3.15	134	0.001*						
Unfed	3.76	4.90	0.57									
Total spat												
A. millepora												
Fed	31.38	11.66	1.17	5.91	65	<0.001*						
Unfed	12.99	20.39	2.88									
A. tenuis												
Fed	29.90	24.80	2.22	4.04	198	<0.001*						
Unfed	18.21	16.00	1.85									
Survival												
A. millepora												
Fed							45.56	30.84	4.26	2.17	107	0.016*
Unfed							33.55	33.38	3.34			
A. tenuis												
Fed							49.75	33.29	2.98	0.86	123	0.19

Asterisk denotes significant *p*-value.

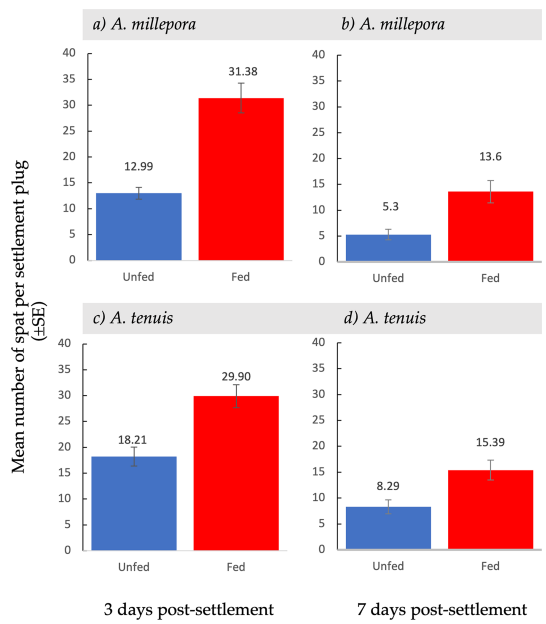

FIGURE 2 | Mean settlement (± SE) of unfed and fed *Acropora millepora* **(A, B)** and *Acropora tenuis* larvae **(C, D)**, after three days **(A, C)** and after seven days (B, D) after larvae were provided with settlement surfaces

per settlement tray was significantly higher in *A. millepora* larvae (p = 0.016). Similarly, the mean totalsettlement per settlement tray in *A. tenuis* larvae was twice as high in the fed treatments (1146.2 ± 279.00 SE) than those in the unfed treatments (619.3 ± 244.06 SE). However, the difference in the mean total settlement per settlement tray was not statistically significant between the fed and unfed treatments (t(6) = 1.42, p = 0.21). As with the *A. millepora* larvae, *A. tenuis* larvae from fed treatments settled on conditioned settlement surfaces 65.2% of the time (3737 vs 1994 spat) while 73.5% of larvae from unfed treatments settled on conditioned settlement surfaces (1366 vs 492).

Post-Settlement Survival

Three Days After Exposure to Settlement Cues

At the first census period, survival and mortality were recorded. The mean number of dead spat per conditioned plug varied between *A. millepora* and *A. tenuis* (**Figure 3**). Specifically, the mean number of dead *A. tenuis* spat was significantly higher in the unfed treatments than in the fed treatments (t(134) = 3.15, p = 0.001) (**Figure 3B**). The mean number of dead *A. millepora* spat was consistent between fed and unfed treatments (2.9 ± 0.66 SE vs 2.4 ± 0.38 SE, t(59) = 0.56, p = 0.58) (**Figure 3B**).

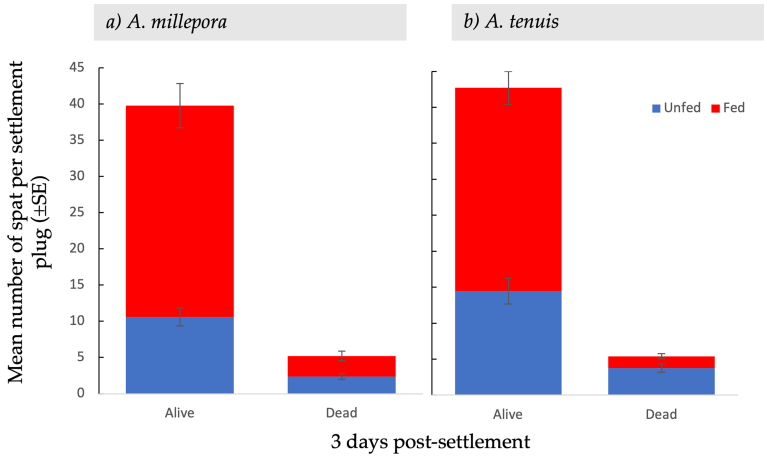

FIGURE 3 | Mean settlement (± SE) of alive and dead *Acropora millepora* **(A)** and *Acropora tenuis* spat **(B)**, from unfed and fed treatments, three days after the introduction of settlement cues.

Spat survival three days post-settlement varied between fed and unfed treatments (**Figure 4**). Mean survival of *A. millepora* spat three days post-settlement was significantly higher in fed treatments than in unfed treatments ($t(146) = 4.11$, $p < 0.001$) (**Figure 4A**). Spat from fed treatments exhibited an 89.5% (± 2.59 SE) survival rate while spat from unfed treatments had a 70.6% (± 3.75 SE) survival rate. Three days post settlement, *A. tenuis* spat from fed treatments, also had a significantly higher survival rate than spat from unfed treatments ($t(120) = 3.91$, $p < 0.001$) (**Figure 4C**). Spat from fed treatment had a survival rate of 88.8% (± 2.21 SE) while spat from unfed treatments had a 71.4% (± 3.80 SE) survival rate.

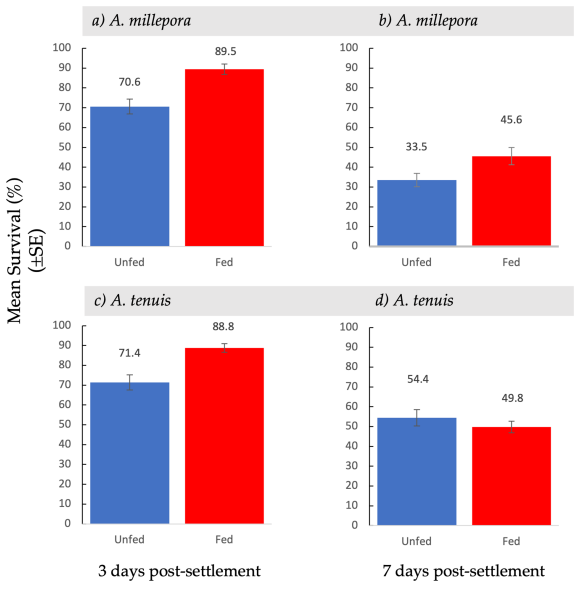

FIGURE 4 | Mean survival (± SE) of *Acropora millepora* **(A, B)** and *Acropora tenuis* spat **(C, D)** from unfed and fed treatments, three days **(A, C)** and seven days **(B, D)** after larvae were provided with settlement surfaces.

Seven Days After the Exposure to Settlement Cues

At the second census period, seven days after the introduction of settlement cues, survival was recorded again. Feeding treatments had a variable effect on spat survival seven days post-settlement (**Figure 4**). *Acropora millepora* spat from fed treatments had a significantly higher survival rate than spat from unfed treatments ($t(107) = 2.17$, $p < 0.05$) (**Figure 4B**). Spat from fed treatments showed a 45.6% (± 4.36 SE) survival rate, while spat from unfed treatments had a 33.5% (± 3.34 SE) survival rate. There was a 30% increase in survival of fed *A. millepora* larvae compared to unfed larvae. An increased early post-settlement survival rate, combined with a higher mean settlement in fed larvae, resulted in a larger difference in mean settlement over time (**Figure 2B**). Consequently, mean settlement of living *A. millepora* larvae remained significantly higher in the fed treatments than in the unfed treatments at seven days (13.6 ± 2.17 SE vs 5.30 ± 1.03 SE, respectively $p < 0.001$) (**Figure 2B**). In contrast, there was no significant difference in seven-day survival between treatments in *A. tenuis* spat ($t(123) = 0.86$, $p = 0.19$) (**Figure 4D**). However, due to the similar survival rates in both the fed and unfed larval treatments but overall higher settlement in the fed treatments, the mean settlement of alive spat in fed *A. tenuis* larvae remained higher than settlement in unfed larvae seven days post-settlement (15.4 ± 1.92 SE vs 8.3 ± 1.35 SE, respectively $t(191) = p < 0.001$) (**Figure 2D**).

DISCUSSION

The results of this study demonstrate that rearing larvae with homogenised *Artemia* as a source of nutritive particulate matter doubled settlement rates for *Acropora tenuis* larvae and were 2.5 times higher for *Acropora millepora* larvae. This result suggests that endogenous energy content may be a limiting factor

affecting larval settlement patterns. It has been demonstrated that *Acropora tenuis* larvae can typically lose between 30% and 75% of their energy stores within the first week of development (Harii et al., 2007; Figueiredo et al., 2012; Graham et al., 2013a), a result which is reflected in lipid depletion across other *Acropora* species (Harii et al., 2007; Okubo et al., 2008; Harii et al., 2010; Figueiredo et al., 2012; Graham et al., 2013a). Previous studies have shown that some coral larvae have the ability to feed (Tranter et al., 1982; Titlyanov et al., 1998; Schwarz et al., 1999; Harii et al., 2009). Therefore, by providing access to exogenous nutrients, larvae could supplement their endogenous energy stores, extending their potential to settle successfully and survive. This advantage is clearly seen in corals that produce larvae with photo-symbionts, which use photosynthetically derived nutrition to enhance survival and settlement (Harii et al., 2010). Photosymbiotic larvae reared under light were more likely to survive until settlement than larvae reared in the dark, as light-reared larvae could supplement up to 40% of their metabolic demands with exogenous nutrients (Harii et al., 2010). The results of the present study are consistent with the results of previous studies examining enhanced settlement associated with increased nutritional potential (Richmond, 1985; Schwarz et al., 1999; Harii et al., 2010).

In addition to increased settlement of fed larvae, another key finding from the present study was the increased post-settlement survival in *A. millepora* and *A. tenuis* spat. Mortality in the first year after settlement can be extremely high (Babcock and Heyward, 1986; Babcock and Mundy, 1996; Wilson and Harrison, 2005; Davies et al., 2013; dela Cruz and Harrison, 2017; Suzuki et al., 2018) and is highest immediately following settlement, declining markedly as coral spat increase in size (Martinez and Abelson, 2013; Doropoulos et al., 2016; Harrison et al., 2021). High early mortality may be due to the energy investment required for larvae to complete metamorphosis, as this process represents a significant energy investment for corals (Harrison and Wallace, 1990; Graham et al., 2013a). Therefore, coral larvae with lower energy stores may deplete these energy stores during metamorphosis and die shortly thereafter. However, for larvae provisioned with ample energy stores, metamorphosis into a coral spat should allow sufficient energy reserves to meet metabolic demands until they acquire photosymbiotic Symbiodiniaceae and gain photosynthetically derived nutrition (Harii et al., 2007; Harii et al., 2009; Harrison et al., 2021). Once the coral spat gain symbionts and develop tentacles, they can begin to feed in the same manner as adults, namely through autotrophy and planktotrophy, respectively. The high early mortality of coral spat from the unfed treatments in this study supports the hypothesis that some larvae run out of energy shortly after metamorphosis. Furthermore, the increased early post-settlement survival of both *A. millepora* and *A. tenuis* spat derived from larvae that were supplied with homogenised *Artemia* in this study, highlights the potential for supplying exogenous food to supplement energy stores to enhance post-settlement survival.

Although there was an initial difference in survival between *A. tenuis* spat from fed and unfed treatments, by seven days post-settlement, survival was similar between treatments. Fed *A. tenuis* larvae settled in much higher numbers than unfed larvae, even with consistent settlement surface availability, resulting in a higher density of spat in the fed treatments than the unfed treatments. Therefore, similar survival rates among recruits from both the fed and unfed *A. tenuis* larvae (**Figure 4**) may have been influenced by post-settlement competition for space rather than metabolic demands. Juvenile survival after settlement can be affected by various ecological processes such as predation, sedimentation, and density-dependent competition (Ritson-Williams et al., 2009; Ricardo et al., 2017; Cameron and Harrison, 2020; Randall et al., 2021) While accidental grazing and predation are large sources of mortality in *in-situ* environments (Baria et al., 2010; Gallagher and Doropoulos, 2017), those pressures were not present in the current laboratory experiment and therefore, unlikely to influence the observed survival rates. Alternatively, density-dependent processes are known to impact survival as spat compete for space (Martinez and Abelson, 2013; Cameron and Harrison, 2020; Randall et al., 2020). With overall higher settlement in the fed *A. tenuis* larval treatment compared with the unfed larvae (**Figure 2**), mortality due to space competition could have been higher in the fed than in the unfed treatment, resulting in less spat from fed treatments surviving overall. Moderate densities reduce space competition among newly settled spat (Cameron and Harrison, 2020). Therefore, more research is needed to optimise settlement density to maximise recruitment success.

While *A. tenuis* and *A. millepora* larvae benefit from being reared with access to exogenous nutrients, the exact feeding mechanism could not be determined during this study. Whether larvae assimilate nutrients *via* osmotrophy or ingest particulate matter through direct planktotrophy is yet to be resolved. However, due to their ability to utilise nutrients, *A. tenuis* and *A. millepora* are likely facultative planktotrophic rather than strictly lecithotrophic. Regardless of the feeding mechanism, the ecological relevance of enhanced settlement is clear- as is the importance of this approach for developing new larval rearing protocols for mass culture of coral larvae in future. Species-specific differences in larval quality impact settlement success in marine invertebrates (Marshall and Keough, 2004) with egg size and lipid composition influencing post-metamorphic performance (Pechenik, 2006; Pechenik, 2018). Furthermore, egg size, lipid composition, and lipid depletion are known to vary across acroporid coral larvae (Richmond, 1987; Zaslow and Benayahu, 2000; Graham et al., 2013a). For example, *A. tenuis* has been shown to deplete energetic lipids at a faster rate than other *Acropora* coral larvae examined (Graham et al., 2013a). These differences in egg quality may have resulted in a differential benefit of exogenous nutrients between *A. tenuis* and *A. millepora*. Therefore, differential utilisation of exogenous nutrients may be contributing to the differences in the mean settlement between *A. tenuis* and *A. millepora*. However, direct uptake of nutrients between species was not measured in the present experiment.

Overcoming high post-settlement mortality bottlenecks is a high priority goal in coral restoration (Boström-Einarsson et al., 2020; Randall et al., 2020). Current larval restoration techniques supply large numbers (often millions) of cultured

larvae to degraded reefs (dela Cruz and Harrison, 2017; dela Cruz and Harrison, 2020; Harrison et al., 2021). Once on the reef, cultured larvae face the same barriers to settlement, survival and recruitment as wild-spawned larvae. Therefore, rearing cultured larvae with access to exogenous nutrients could produce energetically enhanced larvae with an increased capacity for settlement and post-settlement survival, thereby significantly increasing the efficiency of larval restoration efforts.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

PH provided the overall rationale for the study. CR, SW, and PH conceived and designed the experiment. CR and CH conducted the experiments. CR analysed the data and wrote the draft manuscript. PH obtained the primary research funding. All authors edited and approved the final draft.

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