



# Nutritional drivers of adult locomotion and asexual reproduction in a symbiont-hosting sea anemone *Exaiptasia diaphana*

Samuel A. Bedgood<sup>1,2</sup> · Matthew E. S. Bracken<sup>2</sup> · Will H. Ryan<sup>1,3</sup> · Samantha T. Levell<sup>1,4</sup> · Janie Wulff<sup>1</sup>

Received: 22 May 2019 / Accepted: 9 January 2020  
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

## Abstract

Some sedentary marine invertebrates have the potential to modify the environments they experience by moving, even as adults. Of particular interest are sea anemones, which, despite appearing immobile, can move throughout their lives. Individual locomotion may mitigate changes in environment conditions and, therefore, play an important role in the natural history of sea anemones, especially in naturally variable and/or stochastic environments. Sea anemones that associate with algal endosymbionts may respond to changes in nutrition, both autotrophic (from algae) and heterotrophic (from prey). Here, we describe the adult movement behaviors and asexual reproduction of the sea anemone *Exaiptasia diaphana* in response to changes in food availability and photosymbiont density. Anemones were collected from mangrove roots in the Florida Keys USA (24° 49' 21.91" N, 80° 48' 37.95" W) during January 2016 and exposed to a factorial experiment in which food availability and exposure to temperature shock were manipulated. Sea anemones exhibited a variety of responses, including (1) increased crawling along the substrate in response to starvation, (2) increased detachment from the substrate and reattachment in a new location in response to starvation, and (3) increased production of motile asexual clones in response to both starvation and temperature-induced changes in symbiont density. These responses are shaped not only by the direct consequences to the sea anemone, but also by the effects on the symbiotic algae, which exchange sugars, lipids, and oxygen for nutrients within the host. Observed patterns of movement and reproduction are likely advantageous for life in the dynamic mangrove root fouling communities where this anemone species occurs. The ability to disperse as an adult may give this otherwise sedentary invertebrate an advantage in naturally stochastic conditions or in rapidly changing environments.

Responsible Editor: G. Chapman.

Reviewed by N. E. Chadwick, J. Cushman, A. Roark and undisclosed experts.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00227-020-3649-3>) contains supplementary material, which is available to authorized users.

✉ Samuel A. Bedgood  
sbedgood@uci.edu

<sup>1</sup> Department of Biological Science, Florida State University, 319 Stadium Dr., Tallahassee, FL 32306-4295, USA

<sup>2</sup> Department of Ecology and Evolutionary Biology, University of California, 321 Steinhaus Hall, Irvine, CA 92697-2525, USA

<sup>3</sup> Department of Biology, University of Alabama at Birmingham, 1300 University Blvd., Birmingham, AL 35233, USA

<sup>4</sup> Department of Evolution, Ecology, and Organismal Biology, University of California Riverside, Eucalyptus Dr. #2710, Riverside, CA 92521, USA

## Introduction

An organism faced with changing environmental conditions must acclimate, move, or perish. In marine invertebrates, changes in physiology, body size, reproductive behavior, individual movement, and dispersal can all play a role in response to environmental change (Harley et al. 2006; Brooker et al. 2007; Ryan 2018). The capacity for, and adaptive value of, differing response strategies is strongly shaped by the natural history of organisms. For example, dispersal is expected to be solely accomplished by larval or juvenile forms in most sedentary and sessile marine species (Cowen and Sponaugle 2009). As such, investigating adult movement as a potential response mechanism is often overlooked in favor of studies of physiological acclimation to changing environments in nominally sessile organisms, even for species known to be mobile throughout their lives (e.g., mussels, snails, sea anemones). We have a limited understanding of the ecological role of adult movement in many species, despite the potential for this behavior to

reduce environmental variability, whether that variability is caused by stochasticity, seasonal fluctuation, or climate change. Understanding all of the ways organisms cope with environmental variation is key to making accurate ecological predictions under both ordinary and novel circumstances (Fox et al. 2019).

Here, we measure the ability of a nominally sessile sea anemone to engage in both short- and potentially long-distance movement to escape unfavorable conditions. Sea anemones can disperse as larvae, as new settlers, and as adults. The potential for adult movement is well accepted by those who keep sea anemones in the aquarium trade and evidenced by several studies. Adult movement occurs in response to changes in light (Pearse 1974), to the threat of predators (Sund 1958; Edmunds et al. 1976), to agonistic behavior of conspecifics and other cnidarians (Sebens 1984; Chadwick 1987), or to ontogenetic changes as habitat requirements shift (Ottaway and Thomas 1971; Sebens 1981a). Individual sea anemones achieve directed movement through waves of muscular contractions that allow them to “crawl” along a surface (Parker 1916). The ability of sea anemones to travel short distances by crawling locomotion is well documented (McClendon 1906), but such behaviors are rarely integrated into eco-evolutionary hypotheses about the purpose or effects of movement (but see Fredericks 1976; Sebens 1981a; Chadwick 1987). Some anemones are also known to travel longer distances as adults. Distant dispersal may be achieved by detachment and drifting (Riemann-Zürneck 1998). We know that sea anemones can exhibit complex growth and reproductive responses to environmental fluctuations (Ryan 2018; Ryan and Miller 2019), but little is known about the potential roles of active movement or detachment in individual responses to changing environmental conditions, especially those that involve nutritional pathways.

Many tropical and temperate cnidarians, including sea anemones, host endosymbiotic dinoflagellate algae (Muller-Parker and Davy 2001). The responses of the holobiont—composed of a cnidarian host and its algal symbionts—to changing environmental conditions reflect both the host’s and symbiont’s environmental tolerances (Brown 1997). Algal symbionts can provide the animal with energy in the form of sugars and lipids in exchange for nitrogen produced by the animal (Smith et al. 1969; Yellowlees et al. 2008). In sea anemones, algal symbionts may also play a critical role in keeping animal tissues oxygenated when external conditions become hypoxic (Rands et al. 1992). The physical closeness of the two organisms can allow for rapid exchange of resources with minimal loss, a major advantage in resource-limited environments (Raven et al. 2009). The interaction between host and symbiont can also influence anemone movement. Pearse (1974) found that *Anthopleura elegantissima* individuals display phototactic movement

only when symbionts are present. Individuals from high-light environments move toward light, likely to increase photosynthetic products from symbionts. Fredericks (1976) found that phototactic behavior in *A. elegantissima* is associated with oxygen enrichment by photosynthesizing algal symbionts.

Resources from algal symbionts are supplemented by the prey that anemones capture via passive suspension feeding. The diets of sea anemones can be complex (Sebens 1981b) and highly variable between sites or through time (Quesada et al. 2014). Chintiroglou and Koukouras (1992) found that 99.15% of the coelenterons of *Anemonia viridis*, which lives symbiotically with algae, were empty during winter sampling; while, only 85.64% were empty during summer sampling, suggesting that sea anemone diets can be seasonal and highly variable. Anemones may go long periods of time with no success in capturing prey. The availability of planktonic food shapes competition among species (Svensson and Marshall 2015) and the distribution of species in space (Lesser et al. 1994), but no previous study that we know of has addressed how variation in diet could affect movement of sea anemones.

Many sea anemone species reproduce asexually, and movement can be an important component to asexual reproduction. For example, *Exaiptasia diaphana* reproduces asexually by pedal laceration. Small pieces of the pedal disc are detached from the adult and left behind, and these tissue pieces develop into new adult anemones. Unlike other species that create large clonal aggregations via asexual reproduction (e.g., *Anthopleura elegantissima*), *E. diaphana* adults move away from their clonemates (S. Bedgood, pers obs). Previous studies have revealed nutritional drivers of asexual reproduction in *E. diaphana*. Hunter (1984) reported increased pedal laceration when anemones were kept in the dark (no contribution from symbionts) but no difference between feeding regimes, and Clayton and Lasker (1985) found that anemones produced more pedal lacerates immediately after starvation. Clayton (1985) found an interaction between feeding and symbiont state where anemones that were starved and possessed symbionts produced the most pedal lacerates. Nutritional drivers may also impact asexual reproduction or mitigate the risk of movement by leaving behind clones.

As heterotrophic and autotrophic pathways both contribute to nutrient acquisition in these sea anemones, each pathway, as well as their potential interaction, on adult anemones has the potential to influence processes at the individual, population, and community levels. Previous work suggests that interactions between the host, its symbionts, and the environment likely influence movement of symbiotic sea anemones (Pearse 1974; Fredericks 1976). In this study, we explored the interactive effects of food limitation and symbiont density on the locomotion behavior of

the symbiont-hosting sea anemone, *Exaiptasia diaphana* (Rapp 1829; ICZN 2017) from the Florida Keys, commonly referred to as *Aiptasia* and formerly known as *Aiptasia pallida*. *E. diaphana* in this region are genetically distinct from other populations around the world and may host dinoflagellate algal symbionts from three different genera (*Symbiodinium*, *Breviolum*, and *Cladocopium*) in the family Symbiodiniaceae (Thornhill et al. 2013). By manipulating the contribution of two potential sources of nutrition, we tested the hypotheses (1) that anemones move more frequently in response to food-limited environments (i.e., anemones actively forage), (2) that a reduction in heterotrophic nutrition provokes a similar movement response as a reduction in autotrophic nutrition, and (3) that movement increases under dark versus light conditions for individuals with symbionts as a response to the reduction in photosynthate from algal symbionts. We also measured the influence of food limitation and symbiont density on body size and clonal reproduction as these outcomes may reflect changes in life history strategy in response to treatments alongside changes in movement.

## Methods

### Species description

The distribution of *E. diaphana* extends from subtropical to tropical shallow-water marine habitats, where they attach to hard substrates (Thornhill et al. 2013). There is currently no consensus on the local distribution of this species. The most common habitats where *E. diaphana* are found in the Florida Keys include biofouling communities on docks or buoys, boulders in shallow bays, and mangrove roots (S. Bedgood, pers obs). We have observed that mangrove roots have the highest density of anemones in this region. Invertebrates, including *E. diaphana*, attach to the submerged portion of the roots. The availability of hard substrate in this environment is in constant flux as new roots periodically enter the water and are then rapidly colonized by a diverse assemblage of sponges, ascidians, algae, and anemones (Wulff 2004). Light in this environment is highly variable due to shading by mangrove branches and macroalgae (S. Bedgood, unpubl data). Perhaps as a consequence of this dynamism, *E. diaphana* in the field have variable symbiont densities and are usually found on the outer edges of mangrove root stands in this region (S. Bedgood, pers obs).

### Cold-shock efficacy experiment

To manipulate symbiont density, we used a cold-shock protocol (Muscatine et al. 1991). This is a unique approach to manipulating symbiont density, as the majority of previous

studies have completely excluded symbionts as a control treatment. Here, we include low and high symbiont densities because aposymbiotic individuals are rare or absent in the field (S. Bedgood, pers obs). To determine the efficacy of a cold-shock treatment in reducing symbiont density in anemones from this region, we collected 14 adult individuals of *E. diaphana* from mangrove roots on the west side of Otter Key in Sarasota, Florida, USA (GPS coordinates 27° 18' 50.09" N, 82° 34' 11.62" W) in December 2017. For the purpose of this study, we define "adult" anemones as individuals with a pedal disc area of 15 mm<sup>2</sup> or larger. Sea anemones were divided into either ambient or cold-shock treatments and were housed individually in 0.5-l containers for 2 weeks. Ambient treatment anemones were maintained at room temperature (23 °C) throughout the experiment, which was similar to field conditions. Cold-shock treatment anemones were also kept at 23 °C except during a weekly cold shock of 4 °C for 4 h that was accomplished by placing aquaria in a temperature-controlled chamber. Water in the aquaria was ambient when placed in the chamber, and we completed water changes to all treatment groups after cold-shock anemones were removed from the chamber, rapidly increasing the temperature of cold-shock treatments to ambient temperature. We sacrificed and measured the symbiont density of all anemones after 2 weeks of treatment (total of two cold shocks).

We measured symbiont density by homogenizing whole sea anemones. The homogenate was diluted approximately 1:20 with deionized water, and cells were counted on a Brightline hemocytometer (Hausser Scientific, Horsham, Pennsylvania, USA). To standardize the symbiont density, we measured animal protein from the same diluted homogenate using the Lowry method for protein estimation (Lowry et al. 1951) with Bovine Serum Albumin as a standard. We report symbiont density in units of symbiont cells per µg protein (Muller-Parker 1984; Bergschneider and Muller-Parker 2008; Hiebert and Bingham 2012). Muscatine et al. (1991) reported a release of 40–55% of algal symbionts from the sea anemones after this treatment. We achieved similar results (details reported below).

### Nutrition and movement experiment

We collected 128 *E. diaphana* adult individuals from 26 mangrove roots along a 20-m stretch of Zane Grey Creek in the Florida Keys, USA (GPS coordinates 24° 49' 21.91" N, 80° 48' 37.95" W) in January 2016. A maximum of five sea anemones were collected from each root to avoid overrepresentation of a single genet (clonal group) due to *E. diaphana*'s prolific asexual reproduction (Cary 1911; Bellis et al. 2018).

Sea anemones were transported to the laboratory where they were randomly distributed among 16 plastic 2 L

aquaria, with eight sea anemones per aquarium. We chose these aquaria because they had a similar surface area to a small mangrove root and allowed for movement measurements across a flat clear surface. Air stones were used in each aquarium to provide water movement and oxygen, and six 27 W 6500 K compact fluorescent lights were used to illuminate the aquaria from above on a 12/12-h light cycle. Light intensity was no higher than  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  and no lower than  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ . These measurements were within the light intensities measured at the site during collections on a clear day at several roots ( $50\text{--}500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The water of each aquarium was changed twice per week using 35 ppt salinity water prepared using Instant Ocean Sea Salt (Blacksburg, Virginia).

We conducted a fully factorial experiment manipulating food availability (starved, fed) and symbiont density (high density, low density; achieved via a weekly cold shock). Starved sea anemones were given no food after field collection; whereas, fed sea anemones were given newly hatched brine shrimp nauplii (*Artemia*, Brine Shrimp Direct, Ogden, Utah, USA) twice weekly ad libitum, and Microvert Invertebrate Food (KENT Marine, Franklin, Wisconsin, USA) once weekly. Excess food was removed via water changes to all aquaria several hours after feeding. Symbiont density was manipulated as described above, using a weekly cold shock to create the low symbiont density treatment. Cold-shock treatments began immediately (first day of experiment) and continued to week three of the experiment for a total of three cold shocks applied to create and maintain the low symbiont density treatments.

To measure locomotion activity, we recorded movement every 4 min for all 3 weeks (see Supplemental Fig. 1), day and night, with a Canon Powershot S100 camera, operated with the automation software Canon Hackers Development Kit (CHDK). Photos were taken from below the aquaria, which were suspended from a structure one meter above the camera (see Supplemental Fig. 2). Photos were loaded into ImageJ (Schneider et al. 2012) as an image sequence for each 12-h night or day period. We traced the path of each sea anemone that moved, tracking the center of the pedal disc (see Supplemental Fig. 2C). We also recorded the number of sea anemone movements, which we defined as locomotion across the substrate punctuated by no movement for 30 min or more on either end of the path. Because individual sea anemones were not easily identifiable across days, the total distance each anemone moved along the bottom of the aquarium during each 12-h period was recorded and averaged for each aquarium. If anemones moved up the side of the aquarium, movement was not recorded and not included in the average, but this type of movement was rare (approximately, one anemone per tank per week).

We recorded detachment and reattachment of anemones in this study, a behavior observed in other sea anemone

species (see Riemann-Zürneck 1998) but previously undescribed in *E. diaphana*. We defined detachment and reattachment as occurring when the anemones expanded, detached, and became neutrally buoyant. They then became caught in the flow, tumbled around the aquarium for several minutes to hours, and reattached in a new location. These events were recorded only if the detached anemone was observed to expand, detach, and tumble in the water, eventually reattaching in a new location.

Photographs of each sea anemone were taken weekly throughout the experiment and used to measure pedal disc area using ImageJ software (Schneider et al. 2012). We used pedal disc area to measure growth because it was the least invasive method and correlated closely with freeze dried mass (Supplemental Fig. 3).

Anemones produced clonal fragments via pedal laceration. The number of pedal lacerates produced in each treatment was recorded once at the end of the second week because counting lacerates was intensive and invasive. Pedal lacerates were defined as physically isolated pieces of anemone tissue that separated from the parent adult and remained attached to the substrate (Cary 1911). At the time data were recorded, pedal lacerates varied in size and stage of regeneration; some had fully formed tentacles, while others were newly separated pieces of tissue. No difference in the apparent stage of pedal lacerates was observed among treatments; so, all stages were pooled for analysis. There was no way to determine which anemone produced which pedal lacerate; so, clonal reproduction was averaged for each aquarium containing eight individual adults.

## Darkness experiment

During the third week of the experiment, anemones were kept entirely in the dark for 3 days to determine if the absence of light affected movement. A black plastic tarp was draped over the entire system with only a small amount of light entering from below, so that long exposure times could capture images. Light intensity in all aquaria read as  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Movement recorded over the 3 days leading up to the dark period and the 3 days during the dark period was compared to test the effect of dark exposure. We measured movement and detachment during this time as described above.

## Statistical analyses

We conducted all analyses in R 3.4.2 (R Core Team 2017) using a variety of parametric and non-parametric tests. Data from the cold-shock efficacy experiment were replicated by individual anemone ( $n=6$  or  $7$ ), and data from the nutrition and movement experiment and the darkness experiment were pooled by aquarium with eight anemones in



each aquarium and a total of four aquaria in each treatment ( $n=4$ ). To verify the assumption of normality, we used a Shapiro–Wilk test on each set of data. Movement data and detachment data were not normally distributed; whereas, symbiont density, asexual reproduction, and anemone size data were normally distributed. We analyzed the data from the cold-shock efficacy experiment with a two-sample  $t$  test. We used several approaches with the anemone movement experiment. Movement data were transformed ( $\log_{10}[x+1]$ ) to achieve normality, and we analyzed movement and clonal reproduction data using a two-way ANOVA with feeding and symbiont density as main factors followed by Tukey HSD tests for multiple comparisons. Detachment data were non-normal regardless of transformations; so, we analyzed them via a Kruskal–Wallis rank sum test and used Dunn’s multiple comparisons test for post hoc evaluation of differences between treatments. We used a generalized linear mixed-effects model (GLMM) to analyze the size of sea anemones throughout the experiment, with tank identity as a random effect and feeding, temperature, and week as fixed effects. We analyzed differences in the darkness experiment by comparing movement and detachment data between the 3 days of darkness and the previous 3 days of light using a repeated-measures ANOVA.

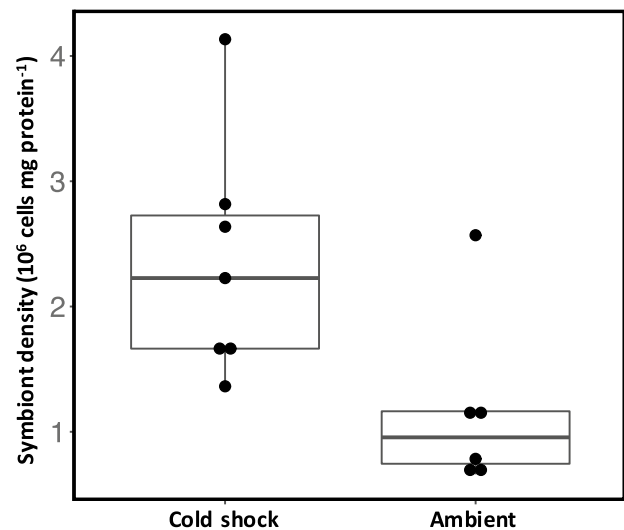
## Results

### Cold-shock efficacy experiment

Sea anemones that were cold-shocked had a lower symbiont density than those that were kept at an ambient temperature (two-sample  $t$  test,  $t(12)=2.56$ ,  $P=0.030$ ; Fig. 1). Our treatment reduced symbiont density to 47% of the symbiont density observed in the control on average, which was within the range reported by Muscatine et al. (1991). Cold-shocked sea anemones appeared lighter in color than ambient-temperature sea anemones throughout the experiment, suggesting that symbionts remained at a low density in this treatment for the duration of the experiment. Based on these results, hereafter we refer to the ambient treatments as “high symbiont density” and the cold-shocked treatments as “low symbiont density.”

### Nutrition and movement experiment

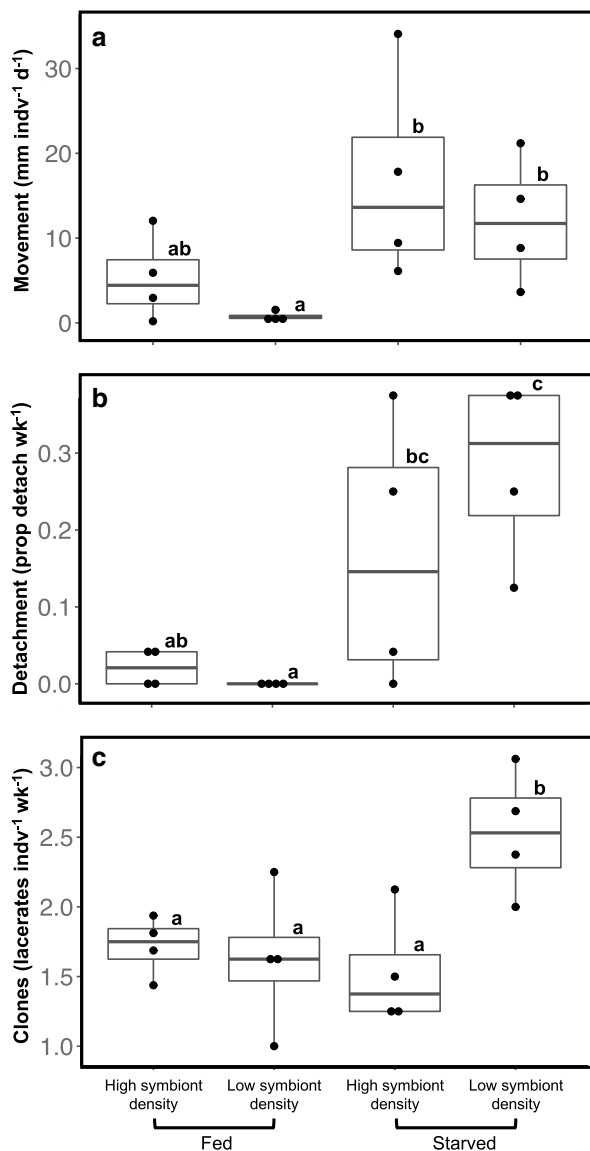
Anemones in all treatments increased movement when first introduced to aquaria, so we allowed 1 week for acclimation to aquaria and treatments before recording movement rates (see Supplemental Fig. 4). Movement of anemones via crawling across the substrate was greater in starved treatments than in fed treatments [two-way ANOVA,  $F(1,12)=15.90$ ,  $P=0.002$ ], but there was no effect of symbiont density on



**Fig. 1** Boxplot of symbiont density of anemones after being kept at an ambient temperature (23 °C) or cold-shocked for 4 h (4 °C). Symbiont density was determined by counting cells and standardizing with animal protein concentration. Data were analyzed with a two-sample  $t$  test. For each boxplot, lower and upper box boundaries are 25th and 75th percentiles, respectively, line inside box is the median, and lower and upper error lines are the smallest or largest data points within 1.5 times the interquartile range, respectively. Overlaid points are symbiont densities of individual anemones (cold shock  $n=7$ , ambient  $n=6$ )

movement [two-way ANOVA,  $F(1,12)=2.23$ ,  $P=0.162$ ; Fig. 2a] or interaction between feeding and symbiont density [two-way ANOVA,  $F(1,12)=0.86$ ,  $P=0.373$ ]. Fed anemones moved an average of  $3.03 \pm 1.46$  ( $\bar{x} \pm \text{SE}$ ,  $n=8$ ) mm per anemone per week; whereas, starved anemones moved an average of  $14.47 \pm 3.50$  ( $n=8$ ) mm per anemone per week, almost five times as much.

The path length of each anemone, measured by taking the length of a path defined by no movement at the start and end, and the number of anemone movements within a replicate (aquarium) both played a role in the average movement value (Fig. 2a). We analyzed path length and the number of anemone movements separately. Path distances of starved sea anemones were appreciably longer than those of fed anemones [two-way ANOVA,  $F(1,12)=5.96$ ,  $P=0.031$ ]; fed anemones moved an average of  $15.75 \pm 6.32$  mm per movement, and starved anemones moved an average of  $39.46 \pm 6.97$  mm per movement [two-way ANOVA,  $F(1,12)=5.96$ ,  $P=0.031$ ]. These path distances are larger than the movement rates because they exclude anemones that did not move. Starved sea anemones were also characterized by a greater number of movements than fed anemones [two-way ANOVA,  $F(1,12)=13.35$ ,  $P=0.003$ ]. We recorded an average of  $4.88 \pm 1.16$  movements per week in the fed treatments and an average of  $16.25 \pm 2.65$  movements per week in the starved treatments. Both the path length



**Fig. 2** Boxplot of movement, detachment, and reproduction of *E. diaphana* in four treatments. The high symbiont density treatments were kept at an ambient temperature and the low symbiont density treatments were cold-shocked weekly. **a** Average movement of each anemone analyzed with a two-way ANOVA and Tukey HSD. **b** The proportion of anemones that detached in each aquarium analyzed with a Kruskal–Wallis test and Dunn’s multiple comparisons test. **c** Average reproduction via asexual pedal laceration analyzed with a two-way ANOVA and Tukey HSD. Lowercase letters indicate significant differences among treatments. See Fig. 1 description for boxplot explanation. Overlaid points are the means of each aquarium ( $n=4$  for each treatment)

and number of movements in each replicate aquarium demonstrated the same result; starved anemones moved more frequently and farther than fed anemones. Symbiont density did not affect any metric of movement [two-way ANOVA, path— $F(1,12)=0.90$ ,  $P=0.362$ , number— $F(1,12)=0.002$ ,  $P=0.969$ ].

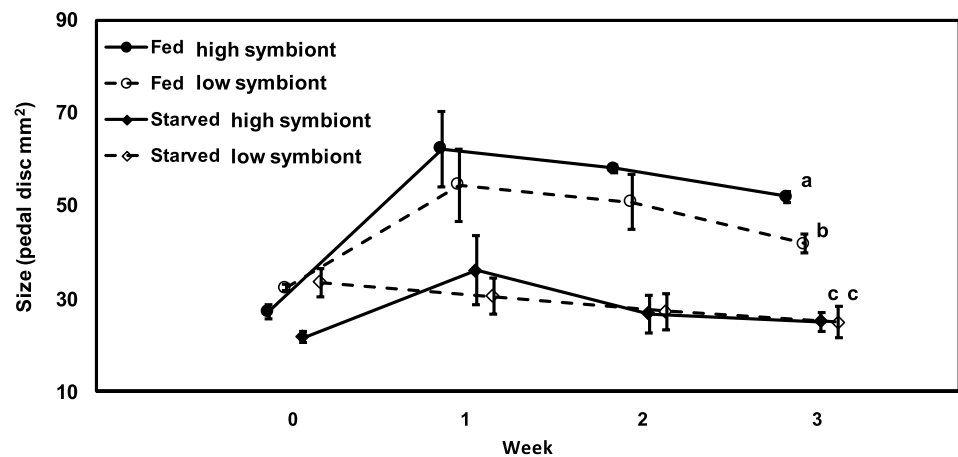
Because the behavior was rare, we pool and report detachment data collected over all 3 weeks during both the nutrition and movement experiment and the darkness experiment (Supplemental Fig. 1). Regardless of treatment,  $85.83 \pm 6.88\%$  ( $\bar{x} \pm \text{SE}$ ,  $n=6$ ) of anemones detached during the night rather than day. Feeding treatment had a significant effect on detachment (Kruskal–Wallis test,  $H1=8.24$ ,  $P=0.004$ ), but symbiont density did not (Kruskal–Wallis test,  $H1=0.03$ ,  $P=0.868$ ). We were not able to test for an interaction between feeding and symbiont density because detachment data were not normally distributed. An average of  $22.40 \pm 5.39\%$  ( $n=8$ ) of anemones detached per aquarium per week in starved treatments, while an average of only  $1.04 \pm 0.68\%$  ( $n=8$ ) of anemones detached per aquarium per week in fed treatments (Fig. 2b). A post hoc analysis revealed differences between the starved, low symbiont treatment, and fed, high symbiont (Dunn’s multiple comparisons test,  $Z=-2.15$ ,  $P=0.015$ ) and fed, low symbiont treatments ( $Z=-2.93$ ,  $P=0.002$ ). However, the fed, high symbiont treatment was not different from the starved, high symbiont treatment ( $Z=1.015$ ,  $P=0.155$ ) suggesting that an interaction between feeding and symbiont density was likely.

Anemones with low symbiont density produced more offspring via pedal laceration than those whose symbiont density was unmanipulated [two-way ANOVA,  $F(1,12)=4.82$ ,  $P=0.049$ ], but this effect was driven by an interaction with feeding [two-way ANOVA,  $F(1,12)=7.03$ ,  $P=0.021$ ; Fig. 2c]. The largest number of pedal lacerates was produced by the starved, low symbiont treatment, where each anemone produced an average of  $2.53 \pm 0.23$  ( $\bar{x} \pm \text{SE}$ ,  $n=4$ ) pedal lacerates per week. In contrast, sea anemones in other treatments produced an average of  $1.63 \pm 0.11$  pedal lacerates per week. We also observed that once tentacles were developed, lacerate-derived individuals moved just as far as large anemones, if not farther, and detached more frequently. However, because of their small size, movement and detachment were not always discernible in the time-lapse photo series; so, these attributes were not recorded for pedal lacerates.

Anemone size changed throughout the experiment (Fig. 3). A linear mixed-effects model used to analyze anemone size during all 3 weeks of the experiment showed that feeding (GLMM,  $X1=94.14$ ,  $P<0.001$ ) and time (GLMM,  $X3=47.41$ ,  $P<0.001$ ) were the main factors influencing anemone size during the experiment. There was also an interaction between feeding and time (GLMM,  $X3=29.60$ ,  $P<0.001$ ). Fed anemones quickly increased in size between week 1 and week 2; whereas, starved anemones remained the same size throughout the experiment.

Both feeding treatment [two-way ANOVA,  $F(1,12)=91.09$ ,  $P<0.001$ ] and symbiont density [two-way ANOVA,  $F(1,12)=4.93$ ,  $P=0.046$ ] affected final anemone size (Fig. 3). There was a marginally significant interaction

**Fig. 3** Mean ( $\pm$ SEM) sea anemone size for all four treatments measured at the end of each week analyzed with a GLMM and Tukey HSD. Points are offset horizontally to accommodate error bars. Lowercase letters indicate significant differences between treatments at end of week three. The sample size for each point is  $n=4$



between feeding and symbiont density [two-way ANOVA,  $F(1,12) = 4.61$ ,  $P = 0.053$ ]. Starved anemones remained the same size as they were when collected, whereas fed anemones almost doubled in size. Symbiont density did not influence size when anemones were starved but contributed to significantly larger anemones when coupled with feeding.

### Dark vs. light experiment

Patterns of anemone movement did not change during the period of complete darkness. Starved anemones continued moving more than fed anemones, and the magnitude of movement was not significantly different from movement before the dark period [repeated-measures ANOVA,  $F(1,12) = 0.226$ ,  $P = 0.643$ ].

### Discussion

Despite being considered largely sedentary, *E. diaphana* has the ability to crawl or even detach from and reattach to the substrate. This behavior allows anemones to escape deleterious conditions and potentially choose habitat. Here, we hypothesized that nutrition, both from captured food and from photosymbionts, would affect the movement of anemones. We predicted that starvation and a low symbiont density would increase movement relative to anemones that were fed ad libitum and had a high symbiont density, respectively.

Movement and detachment in *E. diaphana* are driven by food availability. We found that starved sea anemones moved more frequently and farther than those that were fed. This response might be advantageous because small movements could alter the amount of food available to the individual. In mangrove root communities and other fouling communities in which *E. diaphana* is found, there is a high risk of smothering by macroalgae, other *E. diaphana*, sponges, and other suspension-feeding invertebrates (Ellison and Farnsworth 1992; Wulff 2004). Anemones may use the decrease in food

availability that accompanies this smothering as a cue to move to a different location, escaping the low food environment. For example, *E. diaphana* individuals were regularly found attached to the outside of dense macroalgal growths, exposing their tentacles to higher water flow and potential zooplankton prey (S. Bedgood, pers obs).

How far can sea anemones move to escape deleterious environments? The fastest individuals measured travelled over 200 mm within 12 h, which could allow them to move substantial distances over longer time frames. The physiological cost of movement is currently unknown; so, movement over long distances without adequate food availability might be energetically limited. However, anemones in the starved treatments showed no decline in movement rate and in some cases increased their movement toward the end of our 3-week experiment. Anemone size may also play a role in movement. Previous work on Fungiidae corals found that smaller individuals could move farther (Chadwick-Furman and Loya 1992), but the effect of size on movement in sea anemones is currently unknown. The average anemone size was the same across all aquaria at the beginning of the experiment, but it did diverge during the experiment (see Fig. 3). Size likely did not influence movement results as the effect of treatments on movement was apparent before size diverged.

Detachment of *E. diaphana* from the substrate, drifting, and eventual reattachment appeared purposeful, occurred mostly during the night, and were driven by starvation. This behavior was rare and would not have been detected without time-lapse photography. There is risk in this strategy, at least in mangrove root habitats, as the area immediately surrounding most mangrove roots is predominately soft sediment, unsuitable for attachment. The timing of detachment could increase the potential for successful dispersal as the risk of predation is likely lower during the night. Anemones may also compensate for the risk of detaching by leaving pedal lacerates behind in the original location. There is some evidence for this strategy as the treatment group with

the highest asexual propagation rate also had the highest detachment rate. Given the intense competition for space on mangrove roots (Wulff 2017) and the regularity with which bare roots enter the water forming new patches, adult dispersal through drifting may be a reliable and important strategy for this species. Bellis et al. (2018) found genetically identical clones of *E. diaphana* on mangrove roots up to 50 m apart. Detachment and reattachment to a new root could explain this pattern. Future field studies that address movement between roots are needed to link genetic structure to anemone movements in the field.

Medium- to long-distance post-larval dispersal by nominally sessile animals is not uncommon. Individual polyps of some corals including *Seriatopora hystrix* and *Pocillopora damicornis* have been observed to detach from the colony during stressful conditions and resettle in a new location (Sammarco 1982; Fordyce et al. 2017). At least two coral-limbopharian species asexually produce buds that disperse in the water column to new locations (Chadwick-Furman and Spiegel 2000). Sea cucumbers can travel up to 90 km per day in a similar manner, expanding and increasing their water content by up to 700% (Hamel et al. 2019). The genetic structure of some *Metridium senile* (sea anemone) populations suggest that asexual clone dispersal is common (Shick et al. 1979). *Diadumene lineata* is known to occasionally detach from the substrate when exposed at low tide (Shick et al. 1979) or in fouled tanks (W. Ryan pers obs), just as our *E. diaphana* detached when food was limiting. Riemann-Zürneck (1998) has even suggested that free-living sea anemone individuals are common, frequently being found in plankton trawls in an expanded buoyant state. Though many such observations are scattered throughout the literature, no systematic effort to understand the role of adult dispersal in sea anemones has yet been undertaken. Such behaviors may alter predictions about genetic population structure or population growth rates and should be considered in future studies, especially with regard to expected environmental change scenarios.

To investigate the effect of algal symbiont density on movement in sea anemones, we experimentally manipulated symbiont density with weekly cold shocks. This method is commonly used to produce low-symbiont-density or aposymbiotic anemones (Muscatine et al. 1991; Weis 1991; Gates et al. 1992). Exposure to water cold enough to induce bleaching does occur in the Florida Keys, despite high average sea surface temperatures. Cold-water events occur periodically in the Florida Keys, causing large die-offs of corals, gorgonians, macroalgae, and sponges (Colella et al. 2012). The minimum water temperatures during January offshore of Long Key (our collection site) reach 8.7 °C (Colella et al. 2012). However, within Zane Grey Creek where our anemones were collected, water temperatures likely match air temperatures on outgoing tides because a large shallow

marsh empties through the creek (S. Bedgood, pers obs). Air temperatures periodically dip below 4 °C at Long Key, usually during January. Since 2000, air temperatures during January have dropped to 4 °C three times at Long Key (NOAA National Centers for Environmental Information, Asheville, North Carolina, USA). Although we could not separate the physiological effects of symbiont density from those of the brief cold shock itself, we interpret our results here in terms of symbiont density while acknowledging the potential effects of cold alone. Given the likely confounding of these two phenomena in field populations, we believe that our results reflect patterns relevant to the ecology of the animals in their natural setting.

The taxonomic identity of algal symbionts within anemones in this study is unknown, but sampling from adjacent sites (Crawl Key and Summerland Key) identified sea anemones with symbionts from three different genera including *Symbiodinium*, *Breviolum*, and *Cladocopium*. *Symbiodinium* was the most common genus, while the other two genera were fairly rare and usually found in combination with *Symbiodinium* (Thornhill et al. 2013). Symbiodiniaceae genera and species are known to have different temperature-specific limitations to symbiosis (LaJeunesse et al. 2010; McGinty et al. 2012) and different carbon fixation rates (Rädecker et al. 2018). Our cold-shock treatment may have changed the composition of symbiont genera or species within the anemones. However, measuring this change goes beyond the scope of this study. Future work should address how environmental fluctuations affect symbiont composition within the host.

The symbiont density manipulation did not influence either crawling rate or the likelihood of detachment on the timescale of the experiment, even though symbiont density was reduced in the cold-shock treatments to half of the original density (Fig. 1). Likewise, the absence of adequate light for photosynthesis over a short period did not substantially influence the movement of sea anemones. The absence of a difference may indicate that the 3-day duration of darkness was not sufficiently long to impact the dietary benefits from algal symbionts, that these sea anemones simply do not respond to the presence of light, or that we failed to capture an important variable as we were not able to measure directionality in the response to light. Previous studies in *Anthopleura elegantissima* have found that anemones with and without algal symbionts show similar movement rates (Pearse 1974), but anemones hosting symbionts are positively attracted to light. Fredericks (1976) showed that this positive phototaxis occurred when the surrounding water was hypoxic or normoxic, but when oxygen was super-saturated, anemones showed no attraction to light. Thus, phototactic behavior was hypothesized to increase oxygen availability by stimulating photosynthesizing symbionts (Pearse 1974; Fredericks 1976).



It may be that anemones alter movement rate when food is scarce, but that symbiont density affects the direction of that movement with regard to light. Additional studies are needed to understand this interaction.

The symbiont density manipulation did influence body size and asexual reproduction. Sea anemones are able to grow and shrink rapidly in response to environmental conditions, including food and oxygen availability (Sebens 1981b; Chomsky et al. 2004; Ryan 2018; Ryan et al. 2019). Our initial predictions assumed that both prey capture and translocated products from symbionts were comparable nutritional pathways in *E. diaphana*, as they are in other sea anemones (Fitt and Pardy 1981). After two weeks of growth, fed anemones were larger; however, the presence of symbionts only increased body size in fed anemones. Starved anemones remained the same size regardless of symbiont status. This result contrasts with some previous studies. Clayton and Lasker (1985) found that the presence of symbionts only affected growth in *E. diaphana* when anemones were starved, and Leal et al. (2012) found that growth of *E. diaphana* is maximized when fed and kept in the dark (no symbiont contributions). However, both of these studies used treatments that completely eliminated symbiont contributions; while, our study likely reduced the contributions of symbiont in one treatment (low symbiont density). We acknowledge that our study is limited by having no treatment that completely excluded the contribution from symbionts (aposymbiotic), but the low and high symbiont density manipulations that we include are realistic based on field observations. Future studies could include a variety of symbiont densities to resolve the effects of naturally varying symbiont densities and aposymbiotic controls.

Algal symbionts could influence anemone growth by two pathways: translocation of photosynthate or oxygen production. Without food, anemones have less nitrogen to translocate to their symbionts, potentially slowing the growth of those symbionts. Many cnidarians directly translocate nitrogen to their symbionts (Wang and Douglas 1998; Piniak et al. 2003). Symbionts within starved *E. diaphana* have a higher C:N ratio than those that were fed regularly (Cook et al. 1988), suggesting that symbionts are limited by anemone diet. However, Davy and Cook (2001) found that nutritional state did not affect the translocation of photosynthate from symbionts to host in *E. diaphana* even after 86 days of starvation. The reduction in nitrogen was mitigated by increased photosynthesis and increased carbon translocation per symbiont. Symbionts may be important as an internal source of oxygen in addition to nutritional enhancement, allowing the host anemone to grow larger without oxygen limitation. The interaction between nitrogen limitation and oxygen enrichment with the host warrants additional study, as even subtle differences in oxygen availability can also

influence the size and performance of sea anemones (Ryan et al. 2019) and their metabolic rates (Szczebak et al. 2013).

The rate of asexual reproduction was highest in the least favorable condition (i.e., starvation with low symbiont density), which agrees with previous work (Clayton and Lasker 1985). This increase in asexual reproduction is likely limited by the duration of starvation as Clayton and Lasker (1985) found a higher rate of asexual reproduction in their starved group during the first four weeks of treatment, but their fed treatments produced more pedal lacerates during the next four weeks of treatment, potentially as a result of increased size. Because pedal lacerates originate at the edge of the pedal disc, and larger anemones have a larger pedal disc circumference, size could play a role in asexual propagation (e.g., larger anemones produce more pedal lacerates). We found that size of anemones positively correlated with pedal laceration within the range of sizes included in the movement experiment (Supplemental Fig. 5). It is, therefore, likely that the larger anemones in the fed treatments (Fig. 2c) had a higher potential for offspring production. Despite being smaller, starved cold-shocked anemones produced more offspring than either of the fed treatments.

Asexual propagation can be an effective strategy to track phenotypic optima in a changing environment (Ryan 2018; Ryan et al. 2019). Under deteriorating conditions, rapid reproduction may increase the chances of escape, as each clone can travel in a different direction. Small individuals formed from laceration may also be able to survive periods of metabolic stress better than larger parent clones, as they require fewer resources and have a higher surface area to volume ratio. In addition, there was some evidence in this study for pedal lacerates moving more rapidly along the substratum than adults (S. Bedgood, pers obs); so, this behavior may aid in escaping poor conditions, but no quantitative data were taken.

The locomotive capabilities of adult sea anemones may play a critical role in habitat choice throughout life, and so may influence all aspects of growth, survival, and reproduction. Thus, considering movement is critical to understand the evolutionary ecology of these animals, including physiological measures, population structure, and species interactions. Furthermore, a species' ability to move directly affects how well it will be able to adapt to changing environmental conditions. Our study demonstrates the importance of considering multiple movement strategies, including both locomotion across substrates and more extreme—and risky—dispersal events (i.e., detachment), and reinforces the importance of environmental context in assessing the costs and benefits of symbiosis. It will become increasingly important to consider all forms of movement and dispersal at multiple stages of an organism's life, even in nominally sessile species such as sea anemones to predict species' distributions and abundances under changing environments.

**Acknowledgements** We thank Will Ballentine, Kate Hill, Katie Kaiser, Jessica Sandelli, Andrea Schmidt, and Kelly Vasbinder for assistance with fieldwork. They made this work wonderful. We thank the Keys Marine Laboratory for housing and laboratory space while working at our field site. We thank Dr. Joseph Travis for allowing us to use his aquaria and his laboratory, Dr. Thomas Miller for use of his laboratory, and Dr. Scott Burgess for his advice on our experimental design. We thank Genevieve Bernatchez, Laura Elsberry, and Amy Henry for their comments and suggestions on the manuscript as well as five anonymous reviewers that greatly improved the final manuscript. This research was supported by the John Mark Caffrey Endowed Scholarship (to S. Bedgood) and the Florida State University Mentored Research and Creative Endeavors Award (to S. Bedgood).

**Data availability** The datasets generated during and analysed during the current study are available in the Dryad Digital Repository, <https://doi.org/10.15146/R3509H>.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest. This research was made possible through funding provided by the John Mark Caffrey Endowed Scholarship (to S. Bedgood) and the Florida State University Mentored Research and Creative Endeavors Award (to S. Bedgood). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

## References

- Bellis ES, Edlund RB, Berrios HK, Lessios HA, Denver DR (2018) Molecular signatures of host specificity linked to habitat specialization in *Exaiptasia* sea anemones. *Ecol Evol* 8:5413–5426. <https://doi.org/10.1002/ece3.4058>
- Bergschneider H, Muller-Parker G (2008) Nutritional role of two algal symbionts in the temperate sea anemone *Anthopleura elegantissima* Brandt. *Biol Bull* 215:73–88. <https://doi.org/10.2307/25470685>
- Brooker RW, Travis JMJ, Clark EJ, Dytham C (2007) Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *J Theor Biol* 245:59–65. <https://doi.org/10.1016/j.jtbi.2006.09.033>
- Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16:S129–S138. <https://doi.org/10.1007/s003380050249>
- Cary LR (1911) A study of pedal laceration in actinians. *Biol Bull* 20:81–107. <https://doi.org/10.2307/1536038>
- Chadwick NE (1987) Interspecific aggressive behavior of the coral-limorpharian *corynactis californica* (cnidaria: anthozoa): effects on sympatric corals and sea anemones. *Biol Bull* 173:110–125. <https://doi.org/10.2307/1541866>
- Chadwick-Furman N, Loya Y (1992) Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea. *Mar Biol* 114:617–623. <https://doi.org/10.1007/BF00357258>
- Chadwick-Furman NE, Spiegel M (2000) Abundance and clonal replication in the tropical corallimorpharian *Rhodactis rhodostoma*. *Invertebr Biol* 119:351–360. <https://doi.org/10.1111/j.1744-7410.2000.tb00103.x>
- Chintiroglou Ch, Koukouras A (1992) The feeding habits of three Mediterranean sea anemone species, *Anemonia viridis* (Forsskål), *Actinia equina* (Linnaeus) and *Cereus pedunculatus* (Pennant). *Helgoländer Meeresunters* 46:53–68. <https://doi.org/10.1007/BF02366212>
- Chomsky O, Kamenir Y, Hyams M, Dubinsky Z, Chadwick-Furman NE (2004) Effects of temperature on growth rate and body size in the Mediterranean Sea anemone *Actinia equina*. *J Exp Mar Biol Ecol* 313:63–73. <https://doi.org/10.1016/j.jembe.2004.07.017>
- Clayton W (1985) Pedal laceration by the anemone *Aiptasia pallida*. *Mar Ecol Prog Ser* 21:75–80. <https://doi.org/10.3354/meps021075>
- Clayton WS, Lasker HR (1985) Individual and population growth in the asexually reproducing anemone *Aiptasia pallida* Verrill. *J Exp Mar Biol Ecol* 90:249–258. [https://doi.org/10.1016/0022-0981\(85\)90170-4](https://doi.org/10.1016/0022-0981(85)90170-4)
- Colella MA, Ruzicka RR, Kidney JA, Morrison JM, Brinkhuis VB (2012) Cold-water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys. *Coral Reefs* 31:621–632. <https://doi.org/10.1007/s00338-012-0880-5>
- Cook CB, D'Elia CF, Muller-Parker G (1988) Host feeding and nutrient sufficiency for zooxanthellae in the sea anemone *Aiptasia pallida*. *Mar Biol* 98:253–262. <https://doi.org/10.1007/BF00391203>
- Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annu Rev Mar Sci* 1:443–466. <https://doi.org/10.1146/annurev.marine.010908.163757>
- Davy S, Cook C (2001) The relationship between nutritional status and carbon flux in the zooxanthellate sea anemone *Aiptasia pallida*. *Mar Biol* 139:999–1005. <https://doi.org/10.1007/s002270100640>
- Edmunds M, Potts GW, Swinfen RC, Waters VL (1976) Defensive behaviour of sea anemones in response to predation by the opisthobranch mollusc *Aeolidia papillosa* (L.). *J Mar Biol Assoc UK* 56:65–83. <https://doi.org/10.1017/S0025315400020440>
- Ellison AM, Farnsworth EJ (1992) The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. In: Jaccarini V, Martens E (eds) *The ecology of mangrove and related ecosystems*. Springer, Dordrecht, pp 87–98
- Fitt WK, Pardy RL (1981) Effects of starvation, and light and dark on the energy metabolism of symbiotic and aposymbiotic sea anemones, *Anthopleura elegantissima*. *Mar Biol* 61:199–205. <https://doi.org/10.1007/BF00386660>
- Fordyce AJ, Camp EF, Ainsworth TD (2017) Polyp bailout in *Pocillopora damicornis* following thermal stress. *F1000Research*. <https://doi.org/10.12688/f1000research.11522.2>
- Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD (2019) Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philos Trans R Soc B Biol Sci* 374:20180174. <https://doi.org/10.1098/rstb.2018.0174>
- Fredericks CA (1976) Oxygen as a limiting factor in phototaxis and in intracolonial spacing of the sea anemone *Anthopleura elegantissima*. *Mar Biol* 38:25–28. <https://doi.org/10.1007/BF00391482>
- Gates RD, Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. *Biol Bull* 182:324–332. <https://doi.org/10.2307/1542252>
- Hamel J-F, Sun J, Gianasi BL, Montgomery EM, Kenchington EL, Burel B, Rowe S, Winger PD, Mercier A (2019) Active buoyancy adjustment increases dispersal potential in benthic marine animals. *J Anim Ecol*. <https://doi.org/10.1111/1365-2656.12943>
- Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. *Ecol Lett* 9:228–241. <https://doi.org/10.1111/j.1461-0248.2005.00871.x>
- Hiebert TC, Bingham BL (2012) The effects of symbiotic state on heterotrophic feeding in the temperate sea anemone *Anthopleura*

- elegantissima*. Mar Biol 159:939–950. <https://doi.org/10.1007/s00227-011-1871-8>
- Hunter T (1984) The energetics of asexual reproduction: Pedal laceration in the symbiotic sea anemone *Aiptasia pulchella* (Carlgren, 1943). J Exp Mar Biol Ecol 83:127–147. [https://doi.org/10.1016/0022-0981\(84\)90041-8](https://doi.org/10.1016/0022-0981(84)90041-8)
- ICZN (2017) Opinion 2404 (Case 3633)—*Dysactis pallida* Agassiz in Verrill, 1864 (currently *Aiptasia pallida*; Cnidaria, Anthozoa, Hexacorallia, Actiniaria): precedence over *Aiptasia diaphana* (Rapp, 1829), *Aiptasia tagetes* (Duchassaing de Fombressin & Michelotti, 1864), *Aiptasia mimosa* (Duchassaing de Fombressin & Michelotti, 1864) and *Aiptasia inula* (Duchassaing de Fombressin & Michelotti, 1864) not approved. Bull Zool Nomencl 74:130–132
- LaJeunesse TC, Smith R, Walther M, Pinzón J, Pettay DT, McGinley M, Aschaffenburg M, Medina-Rosas P, Cupul-Magaña AL, Pérez AL, Reyes-Bonilla H, Warner ME (2010) Host–symbiont recombination versus natural selection in the response of coral–dinoflagellate symbioses to environmental disturbance. Proc R Soc B Biol Sci 277:2925–2934. <https://doi.org/10.1098/rspb.2010.0385>
- Leal MC, Nunes C, Engrola S, Dinis MT, Calado R (2012) Optimization of monoclonal production of the glass anemone *Aiptasia pallida* (Agassiz in Verrill, 1864). Aquaculture 354–355:91–96. <https://doi.org/10.1016/j.aquaculture.2012.03.035>
- Lesser MP, Witman JD, Sebnens KP (1994) Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. Biol Bull 187:319–335. <https://doi.org/10.2307/1542289>
- Lowry OH, Rosebrough NJ, Farr AL, Randall RJ (1951) Lowry: protein measurement with the Folin phenol reagent. J Biol Chem 193:265–275
- McClendon JF (1906) On the locomotion of a sea anemone (*Medtridium marginatum*). Biol Bull 10:66–67. <https://doi.org/10.2307/1535667>
- McGinty ES, Pieczonka J, Mydlarz LD (2012) Variations in reactive oxygen release and antioxidant activity in multiple Symbiodinium types in response to elevated temperature. Microb Ecol 64:1000–1007. <https://doi.org/10.1007/s00248-012-0085-z>
- Muller-Parker G (1984) Photosynthesis-irradiance responses and photosynthetic periodicity in the sea anemone *Aiptasia pulchella* and its zooxanthellae. Mar Biol 82:225–232. <https://doi.org/10.1007/BF00392403>
- Muller-Parker G, Davy SK (2001) Temperate and tropical algal-sea anemone symbioses. Invertebr Biol 120:104–123
- Muscantine L, Grossman D, Doino J (1991) Release of symbiotic algae by tropical sea anemones and corals after cold shock. Mar Ecol Prog Ser 77:233–243
- Ottaway JR, Thomas IM (1971) Movement and zonation of the intertidal anemone *Actinia tenebrosa* Farqu. (Cnidaria: Anthozoa) under experimental conditions. Mar Freshw Res 22:63–78. <https://doi.org/10.1071/mf9710063>
- Parker GH (1916) Locomotion of sea-anemones. Proc Natl Acad Sci USA 2:449–450
- Pearse VB (1974) Modification of sea anemone behavior by symbiotic zooxanthellae: phototaxis. Biol Bull 147:630–640. <https://doi.org/10.2307/1540746>
- Piniak GA, Lipschultz F, McClelland J (2003) Assimilation and partitioning of prey nitrogen within two anthozoans and their endosymbiotic zooxanthellae. Mar Ecol Prog Ser 262:125–136. <https://doi.org/10.3354/meps262125>
- Quesada AJ, Acuña FH, Cortés J (2014) Diet of the sea anemone *Anthopleura nigrescens*: composition and variation between daytime and nighttime high tides. Zool Stud 53:26. <https://doi.org/10.1186/s40555-014-0026-2>
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 31 July 2019
- Rädecker N, Raina J-B, Pernice M, Perna G, Guagliardo P, Kilburn MR, Aranda M, Voolstra CR (2018) Using *Aiptasia* as a model to study metabolic interactions in cnidarian–*Symbiodinium* symbioses. Front Physiol 9:214. <https://doi.org/10.3389/fphys.2018.00214>
- Rands ML, Douglas AE, Loughman BC, Ratcliffe RG (1992) Avoidance of hypoxia in a cnidarian symbiosis by algal photosynthetic oxygen. Biol Bull 182:159–162. <https://doi.org/10.2307/1542191>
- Rapp W (1829) Über die Polypen im Allgemeinen und die Actinien. Grolsherzogl. Sdch, Weimar, p 62
- Raven JA, Beardall J, Flynn KJ, Maberly SC (2009) Phagotrophy in the origins of photosynthesis in eukaryotes and as a complementary mode of nutrition in phototrophs: relation to Darwin's insectivorous plants. J Exp Bot 60:3975–3987. <https://doi.org/10.1093/jxb/erp282>
- Riemann-Zürneck K (1998) How sessile are sea anemones? A review of free-living forms in the Actiniaria (Cnidaria: Anthozoa). Mar Ecol 19:247–261. <https://doi.org/10.1111/j.1439-0485.1998.tb00466.x>
- Ryan WH (2018) Temperature-dependent growth and fission rate plasticity drive seasonal and geographic changes in body size in a clonal sea anemone. Am Nat 191:210–219. <https://doi.org/10.1086/695496>
- Ryan WH, Miller TE (2019) Reproductive strategy changes across latitude in a clonal sea anemone. Mar Eco Prog Ser 611:129–141. <https://doi.org/10.3354/meps12862>
- Ryan WH, Adams L, Bonthond G, Mieszkowska PKE, Krueger-Hadfield SA (2019) Environmental regulation of individual body size contributes to geographic variation in clonal life cycle expression. Mar Biol 166:157. <https://doi.org/10.1007/s00227-019-3608-z>
- Sammarco P (1982) Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. Mar Ecol Prog Ser 10:57–65. <https://doi.org/10.3354/meps010057>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675 (PMID 22930834)
- Sebens KP (1981a) Recruitment in a sea anemone population: juvenile substrate becomes adult prey. Science 213:785–787. <https://doi.org/10.1126/science.213.4509.785>
- Sebens KP (1981b) The allometry of feeding, energetics, and body size in three sea anemone species. Biol Bull 161:152–171. <https://doi.org/10.2307/1541115>
- Sebens KP (1984) Agonistic behavior in the intertidal sea anemone *Anthopleura xanthogrammica*. Biol Bull 166:457–472. <https://doi.org/10.2307/1541154>
- Shick JM, Hoffmann RJ, Lamb AN (1979) Asexual reproduction, population structure, and genotype-environment interactions in sea anemones. Integr Comp Biol 19:699–713. <https://doi.org/10.1093/icb/19.3.699>
- Smith D, Muscantine L, Lewis D (1969) Carbohydrate movement from autotrophs to heterotrophs in parasitic and mutualistic symbiosis. Biol Rev 44:17–85. <https://doi.org/10.1111/j.1469-185X.1969.tb00821.x>
- Sund PN (1958) A study of the muscular anatomy and swimming behaviour of the sea anemone, *Stomphia coccinea*. J Cell Sci 3:399:401–420
- Svensson JR, Marshall DJ (2015) Limiting resources in sessile systems: food enhances diversity and growth of suspension feeders despite available space. Ecology 96:819–827. <https://doi.org/10.1890/14-0665.1>
- Szczepak JT, Henry RP, Al-Horani FA, Chadwick NE (2013) Anemonefish oxygenate their anemone hosts at night. J Exp Biol 216:970–976. <https://doi.org/10.1242/jeb.075648>

- Thornhill DJ, Xiang Y, Pettay DT, Zhong M, Santos SR (2013) Population genetic data of a model symbiotic cnidarian system reveal remarkable symbiotic specificity and vectored introductions across ocean basins. *Mol Ecol* 22:4499–4515. <https://doi.org/10.1111/mec.12416>
- Wang J, Douglas AE (1998) Nitrogen recycling or nitrogen conservation in an alga-invertebrate symbiosis? *J Exp Biol* 201:2445–2453
- Weis VM (1991) The induction of carbonic anhydrase in the symbiotic sea anemone *Aiptasia pulchella*. *Biol Bull* 180:496–504. <https://doi.org/10.2307/1542351>
- Wulff JL (2004) Sponges on mangrove roots, Twin Cays, Belize: early stages of community assembly. *Atoll Res Bull*. <https://doi.org/10.5479/si.00775630.519.1>
- Wulff J (2017) Bottom-up and top-down controls on coral reef sponges: disentangling within-habitat and between-habitat processes. *Ecology* 98:1130–1139. <https://doi.org/10.1002/ecy.1754>
- Yellowlees D, Rees TAV, Leggat W (2008) Metabolic interactions between algal symbionts and invertebrate hosts. *Plant Cell Environ* 31:679–694. <https://doi.org/10.1111/j.1365-3040.2008.01802.x>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.