No Tradeoff between Sexual and Asexual Investments in the Sea Anemone *Aiptasia pulchella* (Anthozoa: Actiniaria)

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Chienhsiun Chen, Herng-Yuan Chang, and Keryea Soong (2012) No tradeoff between sexual and asexual investments in the sea anemone *Aiptasia pulchella* (Anthozoa: Actiniaria). *Zoological Studies* **51**(7): 996-1005. Classic examples of tradeoffs between sexual and asexual reproduction include rotifers, aphids, and water fleas, in which reproduction is either sexual or asexual depending on the season. In marine organisms capable of simultaneously reproducing in both modes, the same rules presumably apply despite a lack of evidence. In this study, we analyzed the sea anemone *Aiptasia pulchella* in southern Taiwan, which continuously produces asexual lacerates from pedal disks while developing gonads in the mesenteries. Investments in the 2 reproductive modes under different feeding frequencies, local densities, temperatures/photoperiods, and light intensities/presence of zooxanthellae were compared. Three of the 4 above comparisons revealed simultaneous increases in both reproductive investments, whereas no correlation was observed in controlling photoperiod and temperature. There may be little competition for resources when both reproductive modes are simultaneously exhibited. The critical resource that results in classic examples of tradeoff is apparently not energy or materials, but rather the organs shared by the 2 reproductive modes. http://zoolstud.sinica.edu.tw/Journals/51.7/996.pdf

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Ageneral assumption about life-history evolution is that sexual and asexual modes of reproduction greatly overlap in resource requirements (Abrahamson 1980). A tradeoff between the 2 modes results in only 1 mode being favored for any given set of environmental conditions (Roff 1992, Stearns 1992).

Classical examples of a tradeoff between the 2 modes of reproduction include monogonont rotifers, parthenogenic aphids, and water fleas. These species exhibit obligate parthenogenesis but switch to sexual reproduction under challenging environmental conditions (Birky and Gilbert 1971, Innes and Singleton 2000, Simon et al. 2002). Experimental evidence indicates that such a transition is a response to overcrowding in the case of rotifers (Bell 1982, Yoshinaga et al. 1999), to overcrowding, food deficiencies, and a shortened day-length in aphids (Lees 1967 1990, Dixon and Glen 1971), and to a shortened day-length in water fleas (Ferrari and Hebert 1982, Deng 1996). All 3 organisms generally switch to sexual reproduction under stressful environments.

Tradeoffs between the 2 reproductive modes are obvious in the above organisms since only one is expressed at any given time. What is less clear is what the critical resource is, i.e., the common "currency", that the 2 modes of reproduction require. Although energy and material requirements in developing gametes and propagules are default candidates (Calow 1979, Zera and Harshman 2001), other possibilities, such as a limited supply of undifferentiated cells, were also suggested (Rinkevich 1996). All of these hypotheses predict that the same tradeoff is

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applicable to organisms simultaneously capable of both modes of reproduction. However, it is unclear whether the prediction is borne out.

Many environmental factors, including darkness, food availability, photoperiod, population density, and temperature, were proven to be proximate cues that regulate reproduction in many marine invertebrates (Chu and Levin 1989, Stocker and Underwood 1991, Lin et al. 1992a, Barker and Scheibling 2008, Schlesinger et al. 2010). These; however, could be simple responses of individuals to environmental factors (see Knop et al. 2007) without the need to invoke allocation tactics. To examine possible tradeoff implications, both modes must be examined simultaneously. Until now, no experiment has explicitly tested whether investments in sexual and asexual reproduction were negatively correlated or whether a tradeoff occurs in marine species capable of simultaneously reproducing in both modes.

Many sea anemones simultaneously reproduce sexually and asexually, and their respective occurrences are indeed related to environmental factors (reviewed in Chia 1976, Shick 1991, Fautin 1992). For example, darkness, high population densities, high feeding frequencies, high temperatures, and the presence of zooxanthellae are all known to reduce asexual reproduction in sea anemones under laboratory conditions (Table 1). However, no experimental study has investigated how these factors affect sexual reproduction. Specifically, no study has directly compared sexual and asexual investment by sea anemones.

In practice, comparing sexual and asexual reproduction is difficult. For example, since the gametogenesis cycle often spans a long period with no known spawning date (Jennison 1979), estimating investment may be impractical. In asexual reproduction, division is relatively shorter, but the investment period and amount are often hard to define, e.g., in binary fission (Minasian 1982, Hand and Uhlinger 1995). Thus, although many species are capable of both modes, evaluating potential tradeoffs between sexual and asexual reproduction is often difficult (Ayre 1984, Hand and Uhlinger 1992, Schlesinger et al. 2010).

The sea anemone *Aiptasia pulchella* Carlgren

Table 1. Effects of exogenous factors on frequencies of asexual reproduction of sea anemones under laboratory conditions

Exogenous factor	Species	Reference
Food availability		
Positive correlation	*Anthopleura dixoniana*	Lin et al. 1992a
	Haliplanella lineata	Minasian 1979
	Haliplanella luciae	Minisian 1976
	Metridium exilis	Bucklin 1987b
	Metridium senile	Bucklin 1987a
	Nematostella vectensis	Hand and Uhlinger 1995
Negative correlation	*Aiptasia pallida*	Clayton and Lasker 1985
	Aiptasiogeton pellucidus	Smith and Lenhoff 1976
	Anthopleura elegantissima	Sebens 1980
No effect	*Aiptasia pulchella*	Hunter 1984
Photoperiod		
Negative correlation	*Aiptasia pulchella*	Hunter 1984
	Anthopleura elegantissima	Sebens 1980
No effect	*Anthopleura dixoniana*	Lin et al. 1992a
Population density		
Positive correlation	*Aiptasia pallida*	Clayton 1983
Temperature		
Positive correlation	*Anthopleura elegantissima*	Sebens 1980
	Anthopleura dixoniana	Lin et al. 1992a
	Haliplanella lineata	Minasian 1982
	Haliplanella luciae	Minasian 1979
Zooxanthellae presence		
Positive correlation	*Aiptasia pallida*	Clayton and Lasker 1985

1943 produces propagules asexually via pedal laceration (Chia 1976, Lin et al. 1992b). During this process, the basal discs constrict, and lacerates are pinched off. Lacerates, which are continually produced, are considerably smaller (at 1-2 mm in diameter) than the parent sea anemones (pers. observ.). They reorganize and form tentacles within days (Lin et al. 1992b).

Studies of sexual reproduction of *A. pulchella* in southern Taiwan show that synchronous reproductive activities occur monthly and throughout the year. Eggs are released in the 4th quarter of the lunar cycle, i.e., about 8-14 d after the full moon (Chen et al. 2008). Thus, the short cycles and easily identifiable products provide an opportunity to test whether investments in the 2 reproductive modes are negatively correlated.

This study performed laboratory analyses of 6 factors affecting sexual and asexual reproduction and their possible tradeoffs in the sea anemone *A. pulchella*. The objective was to determine whether the investments in 2 reproductive modes were negatively correlated in species capable of simultaneously performing both modes. However, no such pattern was found in any experiments, and just the opposite patterns were found in some.

MATERIALS AND METHODS

Acclimation

Aiptasia pulchella specimens were collected from a marine station outlet at Tungkang (22.25°E, 120.26°N) in southern Taiwan. Once transported to the laboratory, they were allowed to acclimate for 4-5 wk in artificial seawater (30‰-32‰ salinity, Corallife Scientific Grade Marine Salt AF 70) at 25 ± 1°C under a 12-h light: 12-h dark photoperiod with a light intensity of 2200 ± 200 lux. Cultured sea anemones were fed 3 times per week with freshly hatched nauplii of *Artemia* brine shrimp.

Aposymbiotic sea anemones were produced by culturing in 10^{-5} M of 3-(3,4 dichlorophenyl)-1,1 dimethyl urea (DCMU) for 4-5 wk. Individuals cultured by this method showed loss of coloration, and a microscopic study of homogenized tissues at 400x showed the complete loss of zooxanthellae.

Except for the 4s/beaker density treatment, all other treatments and experiments used 1 sea anemone in a glass beaker containing 250 ml of artificial seawater as a replication unit. In the 4s/beaker treatment, 4 sea anemones were kept in a beaker with 250 ml of artificial seawater. The

seawater in each beaker was changed daily. All beakers were bathed in a water table, and a constant water temperature, salinity, photoperiod, and light intensity were maintained during acclimation. Each experiment began with 10 or 15 replicates in each treatment (Table 2).

Experimental design

After acclimation, 48-d experiments were performed. Healthy sea anemones with pedal disc diameters of 8-14 mm (calculated by averaging the longest disc axis and the longest axis perpendicular to the longest disc axis) were selected for use in the experiments.

Six factors, including the feeding frequency, sea-anemone density, temperature, photoperiod, light intensity, and the presence or absence of zooxanthellae were analyzed to determine the tradeoff between sexual and asexual reproduction (Table 2).

In the feeding-frequency experiment, 4 feeding frequencies were compared: none (0x/wk), and once (1x/wk), 3 times (3x/wk), and 6 times per week (6x/wk). Sea anemones were fed nauplii from 1 g of *Artemia* eggs per 30 sea anemones.

In the density experiment, sea anemones were raised in 2 densities: 1 or 4 specimens per 250-ml beaker (1s/beaker and 4s/beaker, respectively). Specimens were given the above described rations 3 times weekly. The food supplied was proportional to the number of individuals in the beakers.

The 3rd experiment used a factorial design with varying temperatures (22 and 29°C) and photoperiods (9-h light: 15-h dark and 15-h light: 9-h dark) (Table 2). Temperatures and photoperiods were intended to approximate monthly averages of cooler and warmer months in southern Taiwan.

The factorial design in the 4th experiment analyzed 2 factors: light intensity and the presence or absence of zooxanthellae (Table 2). Healthy sea anemones were chosen from each of 2 cultured stocks (symbiotic and aposymbiotic) and then raised under 3 light intensities (0, 2200, and 11,000 lux). In the 0-lux treatment, sea anemones were raised in darkness without disturbance except for a daily 1-h maintenance and feeding period.

All sea anemones survived until the end of the experiment except for a few individuals in the 3rd and 4th experiments. Additionally, 4 specimens spawned gametes in the 3rd experiment. The weights of gonads and lacerates in dead and

spawned specimens were excluded from the following analyses.

Estimation of sexual and asexual reproductive investments

The wet weight of total gonads was used as a parameter of sexual investment, whereas that of lacerates a parameter of asexual investment. Lacerates produced by each sea anemone were collected daily and fixed in 10% neutral seawater formalin. At the end of the experiment, the total wet weight of all lacerates of each sea anemone was weighed to the nearest milligram using an electronic balance accurate to a precision of 0.1 mg. After the experiment, all sea anemones were anesthetized and relaxed in a 7% $MgCl_2$-seawater solution with 5-methyl-2-(1-methyl-ethyl) cyclohexanol (menthol) and then fixed in a 10% neutral buffered formalin solution for at least 24 h before being preserved in 70% ethanol. Reproductive mesenteries of each sea anemone, i.e., primary and secondary mesenteries, were examined under a microscope. The gonads were then removed from the mesenteries, blotted dry, and weighed on an electronic balance. The relative investment in sexual reproduction was quantified by calculating the ratio of the wet weight of total gonads to that of total gonads and lacerates.

Data analyses

In each experiment, differences in the wet weights of total gonads and total lacerates between various treatments were analyzed using ANOVA followed by Dunn's post-hoc pairwise test with Bonferroni's correction. Differences in relative investments between various treatments were analyzed by a nonparametric Mann-Whitney U test (2-group comparisons) or by the Kruskal-Wallis test (> 2-group comparisons) followed by the Mann-Whitney pairwise test (between treatment pairs) with Bonferroni's correction. Statistical tests were conducted using StatView 5.01 (SAS Institute, Cary, NC, USA) or PAST 1.86 (Hammer et al. 2001).

RESULTS

Feeding frequencies

Gonad and lacerate weights of sea anemones significantly differed among treatments with different feeding frequencies (Table 3a). Sea anemones under higher feeding frequencies produced heavier gonads and lacerates than did those in treatments with lower feeding frequencies (Table 4a). For example, the average mean wet weights of total gonads in sea anemones fed 3x/wk

Table 2. Experimental design, labels of treatments, and sample sizes

Experiment	Treatment	Sample size at the beginning (end)
Feeding frequency	0x/wk (no feeding)	10 (10)
	1x/wk (once per week)	10 (10)
	3x/wk (3 times per week)	10 (9)
	6x/wk (6 times per week)	10 (10)
Densities of sea anemone	4s/beaker (4 specimens per beaker)	10 (10)
	1s/beaker (1 specimen per beaker)	10 (10)
Temperature × Photoperiod	22-9L (22°C with 9-h light: 15-h dark photoperiod)	15 (14)
	22-15L (22°C with 15-h light: 9-h dark photoperiod)	15 (15)
	29-9L (29°C with 9-h light: 15-h dark photoperiod)	15 (13)
	29-15L (29°C with 15-h light: 9-h dark photoperiod)	15 (10)
Light intensity × Zooxanthellae	S/0 (symbiotic and constant darkness)	10 (10)
	S/2.2K (symbiotic with 2200-lux light intensity)	10 (10)
	S/11K (symbiotic with 11,000-lux light intensity)	10 (9)
	A/0 (aposymbiotic and constant darkness)	10 (9)
	A/2.2K (aposymbiotic with 2200-lux light intensity)	10 (10)
	A/11K (aposymbiotic with 11,000-lux light intensity)	10 (9)

and 6x/wk were at least 25-times heavier than those of sea anemones fed 0x/wk. The mean wet weights of total lacerates in anemones fed 3x/wk and 6x/wk were on average ~4-times heavier than those fed 0x/wk and 80% heavier than those fed 1x/wk. Although wet weights of total gonads and lacerates simultaneously increased, investment in sexual reproduction was proportionally higher than that observed at lower feeding frequencies (Fig. 1A). The mean relative investments in sexual reproduction in sea anemones fed 3x/wk and 6x/wk were about 89% and were on average 20% and 60% higher than those fed 1x/wk and 0x/wk, respectively (Table 5a).

Density

Differences in gonad and lacerate weights were significantly associated with the density treatment (Table 3b). Sea anemones produced heavier gonads and lacerates at a low density than at a high density (Table 4b), even though the food supply was proportional to the number of individuals. For example, the mean wet weight of total gonads in the 1s/beaker was ~30% higher than that of total gonads in the 4s/beaker, and the mean wet weight of total lacerates in the 1s/beaker was ~70% higher than that of total lacerates in the 4s/beaker. Although the wet weights of total gonads and lacerates simultaneously increased, sea anemones invested more in sexual reproduction than in asexual reproduction as the density of individuals increased (Fig. 1B). The mean relative investment in sexual reproduction in the 4s/beaker was 25%, which was ~30% higher than that observed in the 1s/beaker (Table 5b).

Temperature and photoperiod

A two-way ANOVA analysis of gonad weight

Table 3. *Aiptasia pulchella*. Summaries of ANOVA results. Effects of (a) feeding frequency, (b) sea anemone density, (c) temperature and photoperiod, and (d) the presence of zooxanthellae with light intensity, on the wet weight (wt.) of total gonads and lacerates

Experiment	Source of variation	d.f.	MS	F	p
a. Feeding frequency					
Gonad wt.	Treatment	3	62,200.0	32.8	< 0.01
	Error	36	1895.4		
Lacerate wt.	Treatment	3	403.7	11.7	< 0.01
	Error	36	34.5		
b. Density					
Gonad wt.	Treatment	1	29.8	6.2	0.02
	Error	18	49.8		
Lacerate wt.	Treatment	1	2161.1	64.9	< 0.01
	Error	18	33.3		
c. Temperature (T) × Photoperiod (P)					
Gonad wt.	Treatment (T)	1	4066.1	8.8	< 0.01
	Treatment (P)	1	18,199.7	39.4	< 0.01
	Interaction	1	495.2	1.1	0.31
	Error	48	461.7		
Lacerate wt.	Treatment (T)	1	1439.4	15.7	< 0.01
	Treatment (P)	1	11.5	0.1	0.73
	Interaction	1	175.1	1.9	0.17
	Error	48	91.9		
d. Light intensity (L) × Zooxanthellae (Z)					
Gonad wt.	Treatment (L)	2	66,313.5	39.3	< 0.01
	Treatment (Z)	2	100,628.1	59.7	< 0.01
	Interaction	2	12,338.3	7.3	< 0.01
	Error	51	1686.3		
Lacerate wt.	Treatment (L)	2	39.1	7.0	< 0.01
	Treatment (Z)	2	109.4	19.5	< 0.01
	Interaction	2	4.8	0.9	0.43
	Error	51	5.6		

revealed that the wet weight of total gonads was significantly influenced by the temperature and photoperiod (Tables 3c, 4c). Sea anemones under a lower temperature (22°C) on average produced ~30% heavier gonads than did those under a higher temperature (29°C). In sea anemones raised with a long photoperiod (15-h light: 9-h dark), the wet weight of gonads was ~60% higher than that in anemones raised with a short photoperiod (9-h light: 15-h dark).

For lacerate weight, a two-way ANOVA revealed that the wet weight of total lacerates was significantly influenced only by temperature, and not by photoperiod (Table 3c). The mean wet weight of total lacerates in the 22°C treatment, for example, was ~50% higher than that in the 29°C treatment (Table 4c).

Although no correlation between gonad and lacerate weights was found in this experiment (Fig. 1C), analyses revealed that the relative investment in sexual reproduction was significantly influenced by the photoperiod ($Z = -2.9$, $p < 0.01$, $n = 52$, Mann-Whitney U-test, Table 5c). The mean relative investment in sexual reproduction with the long photoperiod (15-h light: 9-h dark) was

80% and was ~10% higher than that with the short photoperiod (9-h light: 15-h dark).

Light intensity and zooxanthellae

Gonad weight in *A. pulchella* was affected by light intensities and zooxanthellae (Table 3d). Although the two-way ANOVA revealed a significant interaction between light intensity and zooxanthella treatments (Table 3d), similar trends were detected in among-group differences (Table 4d). For example, in both symbiotic and aposymbiotic *A. pulchella* groups, those given an intermediate light intensity (2200 lux) had heavier gonads compared to those given treatments with 0 or 11,000 lux (Table 4d). Additionally, gonad weights of symbiotic individuals were heavier than those of aposymbiotic ones under the various light intensities (Table 4d).

A two-way ANOVA showed that lacerate weights were affected by light intensities and zooxanthellae (Table 3d). Total lacerate weight was lower in the treatment at 11,000 lux than in treatments at 0 and 2200 lux (Table 4d). Sea anemones with zooxanthellae produced heavier

Table 4. *Aiptasia pulchella.* Wet weight (wt.) of total gonads and total lacerates (mean ± SE) under (a) 4 feeding frequencies, (b) 2 sea-anemone densities, (c) 2 temperatures with 2 photoperiods, and (d) 3 light intensities with and without zooxanthellae. Means with the same superscripts do not significant differ (Dunn's post-hoc pairwise test with the Bonferroni correction)

Reproductive investment	Treatment					
a. Feeding frequency	0x/wk	1x/wk	3x/wk	6x/wk		
Gonad wt. (mg)	4.7 ± 1.1[a]	33.0 ± 4.8[a]	133.2 ± 9.7[b]	169.9 ± 25.3[b]		
Lacerate wt. (mg)	3.9 ± 0.8[a]	9.8 ± 1.6[ab]	16.3 ± 2.0[bc]	17.7 ± 2.6[c]		
b. Density of sea anemone	1s/beaker	4s/beaker				
Gonad wt. (mg)	12.0 ± 0.8[a]	9.6 ± 0.5[b]				
Lacerate wt. (mg)	49.5 ± 2.1[a]	28.7 ± 1.4[b]				
c. Temperature × Photoperiod	22°C	29°C		9-h light: 15-h dark	15-h light: 9-h dark	
Gonad wt. (mg)	93.4 ± 5.3[a]	72.1 ± 5.9[b]		65.5 ± 4.9[a]	104.0 ± 4.1[b]	
Lacerate wt. (mg)	30.3 ± 2.2[a]	19.7 ± 1.1[b]		24.5 ± 1.9[a]	26.8 ± 2.4[a]	
d. Zooxanthellae × Light intensity	0 lux	2200 lux	11,000 lux			
Gonad wt. (mg) -aposymbiotic	25.1 ± 3.8[a]	87.0 ± 12.8[b]	35.3 ± 9.5[a]			
-symbiotic	70.1 ± 5.5[a]	227.8 ± 13.5[b]	101.9 ± 24.9[a]			
	0 lux	2200 lux	11,000 lux		Aposymbiosis	Symbiosis
Lacerate wt. (mg)	5.4 ± 0.5[a]	4.5 ± 0.8[a]	2.5 ± 0.5[b]		2.8 ± 0.3[a]	5.6 ± 0.6[b]

lacerates compared to those without zooxanthellae (Table 4d).

Increases in wet weights of both total gonads and total lacerates were observed (Fig. 1D). Aposymbiotic sea anemones treated with 2200 lux invested more in sexual reproduction compared to those treated with 0 lux (Z = -3.59, $p < 0.01$, n = 19, Mann-Whitney U-test with Bonferroni's correction). The mean relative investments in sexual reproduction with treatment at 2200 lux was 97% vs. 85% and 73% under respective treatments at 0 and 11,000 lux (Table 5d). With treatments at 2200 and 11,000 lux, symbiotic sea anemones invested more in sexual reproduction compared to those given 0 lux (for 2200 lux, Z = -3.78, $p < 0.01$, n = 20 and for 11,000 lux, Z = -2.53, p = 0.04, n = 19; Mann-Whitney U-test with Bonferroni's correction). The mean relative investments in sexual reproduction were 91%, 97%, and 94% in treatments with 0, 2200, and 11,000 lux, respectively (Table 5d). Additionally, relative investments did not significantly differ between symbiotic and aposymbiotic sea anemones (for 0 lux, Z = -1.63, p = 0.10, n = 19; for 2200 lux, Z = -0.68, p = 0.50, n = 20; and for 11,000 lux,

Z = -0.75, p = 0.45, n = 18; Mann-Whitney U-test).

DISCUSSION

The sexual and asexual reproduction modes of the sea anemone *Aiptasia pulchella* were sensitive to factors tested in this investigation. However, no evidence of a negative correlation between gonad and lacerate investment was found in this study of *A. pulchella* after treatments with 4 environmental variables and 2 biotic variables. *Aiptasia pulchella* did not switch between sexual and asexual reproduction as observed in rotifers, water fleas, and aphids. Instead, it simultaneously increased or decreased investment in both reproductive modes when environmental conditions changed (Table 4). It is likely that the same may well apply in nature where sea anemones are subject to natural fluctuations of environmental factors.

An obvious question is why has *A. pulchella* not evolved the ability to switch between reproductive modes when both are obviously flexible? One hypothesis is that the marine envi-

Table 5. *Aiptasia pulchella*. Percentage of relative investment in sexual reproduction (weight wet of total gonads vs. those of total gonads and lacerates) under (a) 4 feeding frequencies, (b) 2 sea-anemone densities, (c) 2 temperatures with 2 photoperiods, and (d) 3 light intensities with and without zooxanthellae. Ranges with the same superscripts do not significant differ (Mann-Whitney pairwise test with the Bonferroni correction)

Reproductive investment reproduction (%)	Treatment					
a. Feeding frequency	0x/wk	1x/wk	3x/wk	6x/wk		
Range	37.2-73.8[a]	56.3-90.5[ab]	80.8-99.5[bc]	75.6-94.1[c]		
Mean ± S.E.	(55.4 ± 3.6)	(75.5 ± 3.4)	(88.7 ± 1.5)	(89.3 ± 1.7)		
b. Density of sea anemones	1s/beaker	4s/beaker				
Range	12.0-26.0[a]	19.8-28.3[b]				
Mean ± S.E.	(19.5 ± 1.2)	(25.0 ± 1.0)				
c. Temperature × photoperiod	22°C	29°C			9-h light: 15-h dark	15-h light: 9-h dark
Range	46.7-97.6[a]	60.1-90.7[a]			46.7-96.0[a]	67.8-97.6[b]
Mean ± S.E.	(74.4 ± 2.1)	(76.5 ± 2.0)			(71.5 ± 2.1)	(79.5 ± 1.6)
d. Zooxanthellae × Light intensity	0 lux	2200 lux	11,000 lux			
aposymbiotic - Range	70.7-93.1[a]	93.1-99.1[b]	0-98.2[a]			
Mean ± S.E.	(85.2 ± 2.4)	(96.8 ± 0.6)	(73.3 ± 13.9)			
symbiotic - Range	85.3-95.1[a]	95.2-99.5[b]	77.0-99.0[b]			
Mean ± S.E.	(90.7 ± 0.8)	(97.4 ± 0.5)	(94.4 ± 2.3)			

ronment inhabited by sea anemones may be more stable, e.g., in terms of a smaller magnitude of temperature fluctuations between seasons, compared to terrestrial and freshwater habitats inhabited by rotifers, water fleas, and aphids. Additionally, some seasonal patterns observed in terrestrial environments result from moisture fluctuations (Wolda 1978), which in itself is unlikely to be relevant in the marine environment.

Therefore, lacerates and sexual propagules produced throughout the year may each experience mortality or success rates independent of season. Differential selective pressures may simply be insufficient to favor different modes of reproduction in tropical seas, seasonally.

Second, the lack of a physiological tradeoff does not exclude the possibility that a tradeoff is exhibited in other levels of comparisons. For
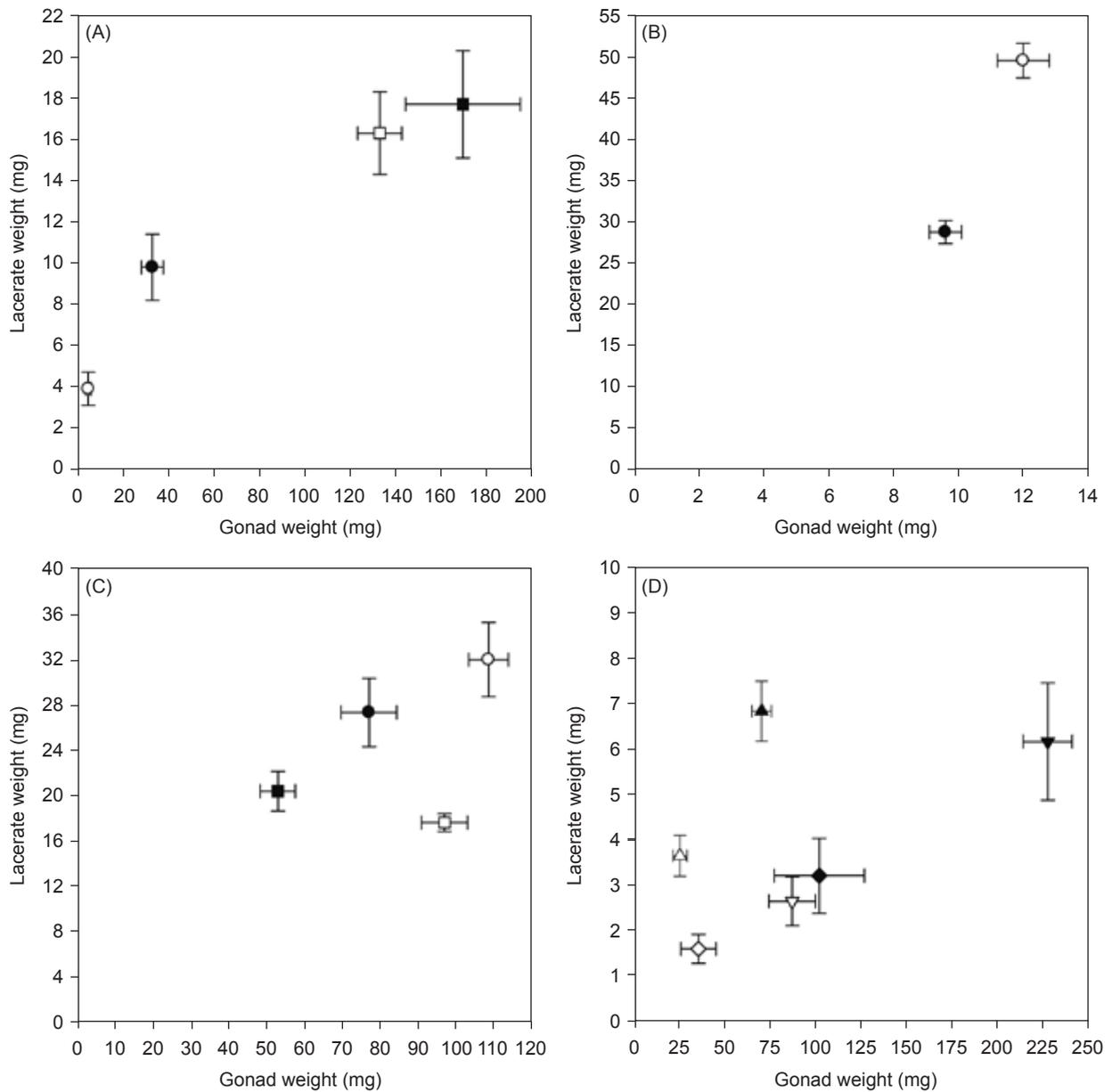

Fig. 1. Relationships between gonad weight and lacerate weight of individual sea anemones under various treatments of (A) 4 feeding frequencies (■, 6x/wk; □, 3x/wk; ●, 1x/wk; and ○, 0x/wk); (B) 2 sea-anemone densities (●, 4s/beaker and ○, 1s/beaker); (C) 2 temperatures with 2 photoperiods (■: 29°C-9-h light; □, 29°C-15-h light; ●: 22°C-9-h light; and ○: 22°C-15-h light); and (D) 3 light intensities (11,000, 2200, and 0 lux) with (S) and without (A) zooxanthellae (◆, S/11K; ◇, A/11K; ▼, S/2.2K; ▽, A/2.2K; ▲, S/0; and △, A/0). Error bar: ± standard error of the mean.

example, the reaction norms of different genotypes may vary widely (Via et al. 1995), and tradeoffs may be detected when comparing different genotypes and/or different populations (Nylin and Gotthard 1998, Piquot et al. 1998, Ronsheim and Bever 2000). Genotypes with different allocation ratios between sexual and asexual reproduction may be favored in other environments (Roff 1992, Stearns 1992). Similarly, evidence of a tradeoff may be found when comparing species (Sutherland and Vickery 1988).

Third, *A. pulchella* uses very different organs for each reproductive mode. Gonads are produced in mesenteries, whereas lacerates are pinched off along the periphery of pedal discs (Lin et al. 1992b). The lack of overlap in participating body parts allows both modes to occur simultaneously, and this may be the critical factor determining whether an organism has to switch between reproductive modes. The actual positive correlation between investments in the 2 modes suggests that despite the need to share resources, such as energy and nutrients, no competition or tradeoffs occur at the individual level, which is unlike aphids (Dixon 1973), rotifers (Nogrady et al. 2002), and water fleas (Hebert 1978), in which the same organs or body parts produce both sexual and asexual propagules. Therefore, simultaneous production of both is constrained by space in these latter groups. In other words, the critical resource in short supply is the "machinery" for which the reproductive modes compete in these organisms. Conversely, no such constraint requires *A. pulchella* to focus on only 1 reproductive mode at a time.

Since *A. pulchella* begins laceration before maturation (Lin et al. 1992b), the earliest reproductive investment is asexual. Although absolute investment may increase in both modes, the proportion allocated to laceration decreases as the proportion of sexual investment in the gonads increases. Rather than invoking this as an evidence of a tradeoff, the allometric investment ratios may result from a dimensional constraint. Lacerates are produced only along the periphery of pedal discs, and their production may be limited to a linear relationship with the circumference of pedal discs. Gonads developing in mesenteries, on the other hand, may be limited by the number of primary and secondary mesenteries (Sebens 1981, Chen et al. 2008) and the volume of mesentery cavities; they can potentially increase cubically with linear body dimensions. This argument suggests that what limits the asexual modes of reproduc-

tive investment is not the sexual mode, but the locations of laceration itself. Competition in energy or materials between sexual and asexual modes was invoked in classical examples of tradeoffs. Here, we suggest that the organs responsible for reproduction are the critical resource. When different organs are used, as in the case of *A. pulchella*, no tradeoff need occur between sexual and asexual modes at the individual level.

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