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Influence of wave-induced disturbance on seasonal spawning patterns in the sabellariid polychaete *Phragmatopoma lapidosa*

Daniel A. McCarthy^{1,2,*}, Craig M. Young¹, Roland H. Emson²

¹Department of Larval Ecology, Harbor Branch Oceanographic Institute, 5600 North, Fort Pierce, Florida 34946, USA

²Division of Life Sciences, King's College, University of London, 150 Stamford Street, London SE1 9NN, United Kingdom

³Present address: Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, Florida 34949-3140, USA

ABSTRACT: The effect of wave-induced disturbance on seasonal spawning patterns of the opportunistic polychaete *Phragmatopoma lapidosa* (Kinberg, 1867) was investigated by comparing seasonal fecundity, egg size and adult size between intertidal and subtidal worms at Boynton Beach, Florida. Fecundity patterns showed spawning peaks in summer and fall in both habitats, with reduced spawning in late fall and early winter. Subtidal females averaged 1015.2 eggs mm⁻¹ body length (range 0 to 2000 eggs mm⁻¹), while intertidal females averaged 607.4 eggs mm⁻¹ (range 0 to 1520 eggs mm⁻¹). Mean egg diameters were not significantly different between worms from the 2 habitats, ranging between 90.4 µm (SD = 3.7) and 89.5 µm (SD = 4.3) for intertidal and subtidal worms respectively. Inter- and intra-census comparisons of egg diameter, fecundity and adult length revealed few statistically significant relationships, suggesting that intertidal and subtidal worms were the same age. Adult lengths in both habitats did change seasonally. The smallest adult worms were found shortly after massive fall recruitment replaced a large percentage of individuals in both intertidal and subtidal populations. Stepwise multiple regression indicated that 76.2% of the variance in intertidal fecundity was explained by a negative correlation with wave height (40.4%), and a positive correlation with day length (34.7%). In contrast, 85.5% of the variance in subtidal fecundity was explained by a positive correlation with day length (77.4%), and a negative correlation with chlorophyll a concentration (8.1%). While habitat-specific differences in energy available for gametogenesis probably contribute towards the observed fecundity trends, the force of crashing waves could also influence fecundity, as it may affect frequency of spawning in intertidal but not subtidal habitats.

KEY WORDS: *Phragmatopoma* · Polychaetes · Fecundity · Spawning · Reproductive plasticity

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INTRODUCTION

Predictable and unpredictable disturbances in natural communities are known to be important in shaping the life-history patterns of both terrestrial and aquatic species (Pickett & White 1985, Hildrew et al. 1994). Space is often at a premium for sedentary animals and disturbance creates space for colonization by new individuals in otherwise crowded habitats (Osman 1977, Sousa 1984, Connell & Keough 1985). Opportunistic species can take advantage of sudden avail-

ability of space because they have the ability to reproduce quickly in response to a disturbance event. Thus, disturbance may in theory provide space for colonization while simultaneously cueing a reproductive response that permits the occupation of that new space.

Few studies of marine invertebrates have quantitatively demonstrated a tight link between seasonal disturbances that create space for settlement and reproductive responses of species that take advantage of the newly opened space (Barry 1989). Several correlative

Statistical correlations and regressions. Potential relationships between measured life-history and reproductive characteristics of *Phragmatopoma lapidosa* were investigated for each habitat by statistical correlations using 2 types of data—inter- and intracensus. In both sets of correlations, individual mean values of fecundity, egg diameter and adult length were separately correlated with Pearson correlations for each habitat (SYSTAT 1992).

The relationships between several seasonal environmental factors and the measured life-history character-

istics of *Phragmatopoma lapidosa* from intertidal and subtidal habitats were also investigated using statistical correlations. Mean values of each environmental factor were used in separate Pearson correlations with census means of fecundity, egg length and adult diameter for each habitat (SYSTAT 1992).

Stepwise multiple regression (linear fit) was used to determine which combination of environmental factors best accounts for the variation in fecundity, egg size and adult lengths (SYSTAT 1992). The relative importance of each environmental factor in affecting dependent factors was assessed by evaluation of the adjusted r-square value after its addition to a regression model.

RESULTS

Study sites and sampling

Statistical analyses of life-history characteristics were only carried out from June 1997 through March 1999 because of the negative effects of a neighboring beach restoration project. In spring 1998, 783 000 m³ of offshore sand were deposited at Ocean Ridge Beach (1.6 to 2.4 km north of the study sites). During subsequent collections at Boynton Beach, it was observed that gray restoration sand had been transported south, affecting the subtidal sites and covering a significant amount of the hard-bottom/worm reef habitat. Subtidal collections ceased in June 1999 because no live worms could be found in the diminishing habitat, although the worm mounds were still present. By August 1999 there was minimal hard-bottom habitat, and no visible worm mounds were exposed in the subtidal study area. Consequently, statistical comparisons between life-history characteristics of intertidal and subtidal individuals were only possible for collections made during 22 of the 32 months of the study.

Day length and seawater temperature exhibited low inter-annual variability (Fig. 2A,B), while chlorophyll a and wave height were generally more variable (Fig. 2C,D). Maximum daylight hours of approximately 13.5 h were from June through August, and minimum daylight hours of approximately 10.5 h from December through January (Fig. 2A). Seawater temperatures varied seasonally, with high values ranging between 25.6 and 30.0°C between July and October and low values ranging between 20.0 and 23.3°C from January to April (Fig. 2B).

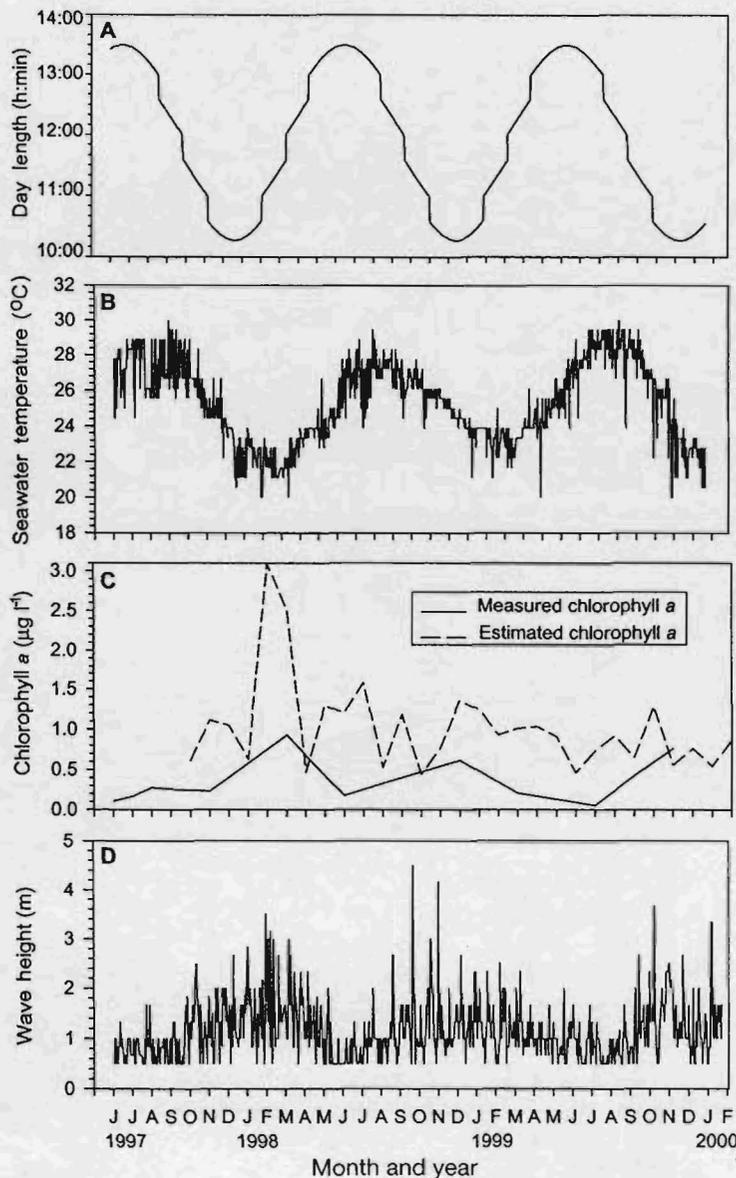


Fig. 2. Seasonal mean values of (A) day length, (B) seawater temperature, (C) chlorophyll a and (D) wave height for the southeast Florida area. Measured and estimated chlorophyll a values are from Fowey Rocks and Boynton Beach respectively

A positive correlation ($r = 0.521$) was found between Fowey Rocks chlorophyll *a* measurements and Boynton Beach chlorophyll *a* estimates. Seasonal peaks in chlorophyll *a* values at Fowey Rocks were between 0.600 and 0.875 $\mu\text{g l}^{-1}$ and occurred during late fall and early winter. Satellite estimates for Boynton Beach were higher, ranging between 1.100 and 3.097 $\mu\text{g l}^{-1}$, with peaks during late fall, early summer and early winter. Low values of chlorophyll *a* at Fowey Rocks were between 0.050 and 0.175 $\mu\text{g l}^{-1}$ and occurred during late spring and summer (Fig. 2C). Low values at Boynton Beach were between 0.446 and 0.629 $\mu\text{g l}^{-1}$ and occurred mostly during late summer and fall.

Increased wave activity occurred from October 1997 to May 1998, July 1998 to May 1999 and September 1999 to February 2000 (Fig. 2D). The highest values were recorded in February and March 1998 (3.0 to 3.7 m), October and November 1998 (4.0 to 4.3 m), October 1999 (2.7 to 3.7 m) and January 2000 (1.7 to 3.3 m). The calmest periods of the study were in the summer, from May to August, with mean values ranging between 0.5 and 2.0 m.

Fecundity, egg diameter and adult size

The log-transformed fecundity values were significantly different between females from the 2 habitats (Table 1). Subtidal females averaged 1015.2 eggs mm^{-1} (SD = 1209.8), while intertidal females averaged 607.4 eggs mm^{-1} (SD = 717.1) (Fig. 3A). Within each site, except for Site 3, intertidal worms had significantly fewer eggs than subtidal worms (Fig. 3A). Adult size was not significant as a covariate in the analysis (Table 1).

Egg number fluctuated in a similar manner in both habitats through the year for *Phragmatopoma lapidosa*, although fecundity was often higher subtidally than intertidally (Fig. 4A,B). Generally standardized fecundity was highest in late spring and summer with means between 700 and 2000 eggs mm^{-1} (i.e. 17 500 and 50 000 total fecundity for a 25 mm worm, respectively). Fecundity was lowest in fall and early winter, with means between 0 and 575 eggs per mm (0 and 14 375 total fecundity for a 25 mm worm).

Table 1. *Phragmatopoma lapidosa*. Results of nested ANOVAs comparing means of fecundity, egg diameter and adult length. Independent factors are habitat, time period, and site nested within habitat. Adult length is used as a covariate in the ANOVAs comparing fecundity and egg diameter. Fecundity and egg diameter means were log-transformed to fit assumptions of ANOVA

Dependent variable Source	SS	df	MS	F-ratio	p
Fecundity					
Habitat	52.596	1	52.596	49.361	0.001
Time period	372.059	13	28.620	26.859	0.001
Site (Habitat)	25.214	6	4.202	3.944	0.001
Time period \times Habitat	113.580	13	8.737	8.200	0.001
Adult length	0.032	1	0.032	0.030	0.863
Error	509.330	478	1.066		
Egg diameter					
Habitat	0.004	1	0.004	0.877	0.350
Time period	2.284	13	0.176	34.255	0.001
Site (Habitat)	0.020	6	0.003	0.665	0.678
Time period \times Habitat	0.216	13	0.017	3.235	0.001
Adult length	0.001	1	0.001	0.041	0.839
Error	2.452	478	0.005		
Adult length					
Habitat	14.777	1	14.777	1.867	0.172
Time period	4612.00	13	354.769	44.815	0.001
Site (Habitat)	90.824	6	15.137	1.912	0.077
Time period \times Habitat	366.170	13	28.167	3.558	0.001
Error	3791.892	479	7.916		

Subtidal worms had significantly (Tukey pairwise probability = 0.05) higher numbers of eggs than intertidal worms in October 1997, May 1998, November 1998 and March 1999 (Fig. 4A,B). Although not significant, the trend continued, with 6 additional months (June 1997, September 1997, December 1998, February 1998, April 1998 and March 1999) displaying higher subtidal than intertidal means of fecundity (Fig. 4A,B).

There were no habitat differences between log-transformed mean egg sizes of *Phragmatopoma lapidosa*. Mean egg sizes were 90.4 μm (SD = 3.7) and 89.5 μm (SD = 6.9) for intertidal and subtidal worms respectively (Fig. 3B). Egg diameter did not covary with adult size nor were there any site differences. Seasonally, egg diameters were largest in the fall and winter, with peaks in December 1997, February 1998 and March 1999. Egg diameters were smallest in summer and early fall, with lowest values in July 1997, July 1998 and November 1998 (Fig. 4C,D, Table 1). Egg diameters were significantly larger subtidally than intertidally in the month of July 1997 (Fig. 4C,D).

High seasonal variability in adult size was characteristic of both intertidal and subtidal *Phragmatopoma lapidosa*. Female *P. lapidosa* were similar sized with intertidal and subtidal lengths averaging 23.6 mm

(SD = 4.10) and 22.9 mm (SD = 4.11) respectively (Fig. 3C). Seasonally, the mean length of *P. lapidosa* changed similarly in both habitats (Fig. 4E,F, Table 1). However, adults were significantly larger intertidally than subtidally in July 1998 (Fig. 4E,F). The largest individual worms were obtained in late spring and through the summer, with lengths varying between 26 and 32 mm. The smallest worms were measured in late fall and early winter, and ranged from 15 to 20 mm in length.

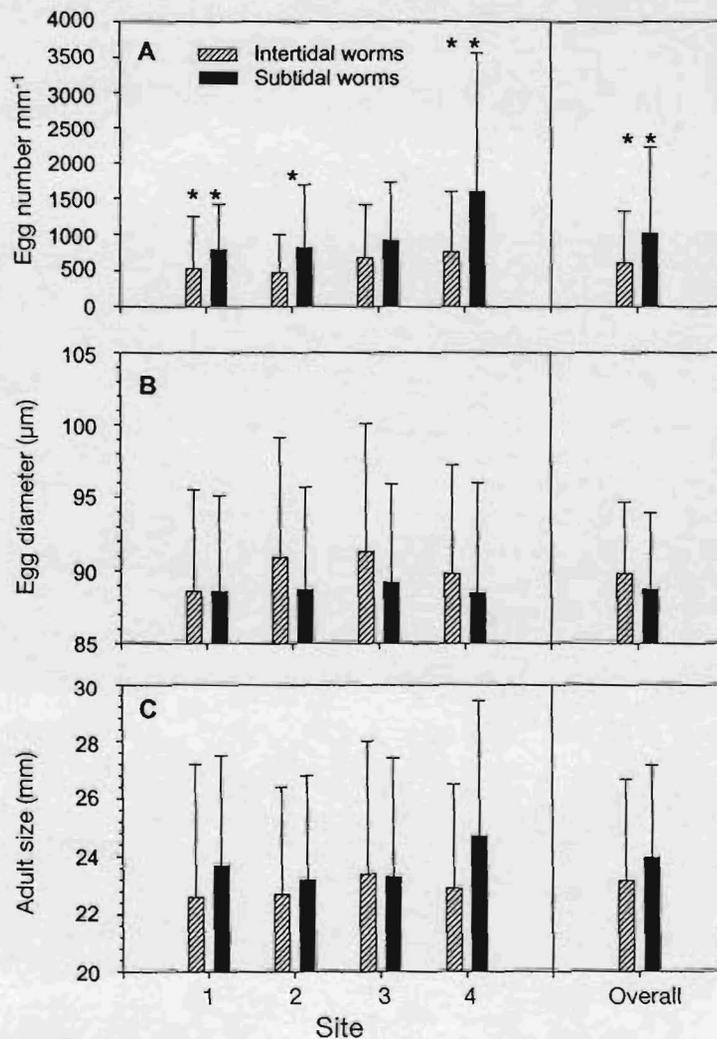


Fig. 3. *Phragmatopoma lapidosa*. Site and overall mean (± 1.0 SD) fecundity, egg diameter and adult length at 4 intertidal and 4 subtidal sites; $n = 70$ in all cases. (A) Fecundity: subtidal worms were significantly more fecund than intertidal worms ($p < 0.001$); within each site, except for Site 3, intertidal (i) worms had fewer eggs than subtidal (s) worms (Tukey pairwise probabilities between sites: 1i and 1s = 0.001, 2i and 2s = 0.008, 3i and 3s = 0.983, 4i and 4s = 0.001). (B) Egg diameters: no significant differences were found among site and habitat treatments. (C) Adult lengths: no significant differences were found among habitat site and treatments. Asterisks indicate significant difference between treatment means (*: $p < 0.01$; **: $p < 0.001$)

Statistical correlations and regressions

The majority of within-census correlations between egg diameter and egg number, and between egg diameter and adult length of *Phragmatopoma lapidosa* were not significant. Positive correlations were found between mean egg diameter and egg number in intertidal worms during December 1997 and March 1999 (Table 2). A negative correlation was found between egg diameter and mean egg number for intertidal worms collected in January 1999 (Table 2). Egg number was negatively correlated with adult length in intertidal worms obtained in January 1999 and positively correlated for subtidal worms collected in March 1998 (Table 2). Adult length correlated positively with intertidal egg diameter in March 1999 (Table 2).

There was only 1 significant seasonal correlation involving the measured life-history characteristics of *Phragmatopoma lapidosa* (Table 2). Egg number was positively correlated with adult length for intertidal worms (Table 2). All other correlations were non-significant.

Several significant correlations were found between mean fecundity, egg diameter and adult length and the observed environmental factors. Intertidal fecundity was negatively correlated with wave height and positively correlated with day length (Table 3). In contrast, subtidal fecundity was not significantly correlated with any environmental factor (Table 3). Both intertidal and subtidal egg diameter correlated only with sea temperature (Table 3). Adult size correlated positively with day length for both intertidal and subtidal worms (Table 3), and negatively with wave height for intertidal worms alone (Table 3). We also ran additional correlations incorporating 1 to 2 month lags of the environmental factors. However, none of these analyses revealed new trends among the measured life-history characteristics and environmental factors.

The stepwise regression analyses accounted for fairly high percentages of the variation in several of the dependent factors. Regression analysis revealed that 76.2% of the variance in intertidal fecundity ($F = 27.7$; $df = 2, 16$; $p < 0.001$) was explained by a negative correlation with wave height (40.4%; $p < 0.001$), and a positive correlation with day length (34.7%; $p < 0.001$). In contrast, 85.5% of the variance in subtidal fecundity ($F = 21.1$; $df =$

2, 16; $p < 0.001$) was explained by a positive correlation with day length (77.4%; $p < 0.004$), and a negative correlation with chlorophyll *a* (8.1%; $p < 0.398$). For egg size, 37% of the intertidal ($F = 10.3$; $df = 1, 15$; $p < 0.005$) and 49% of the subtidal ($F = 13.5$; $df = 1, 12$; $p < 0.03$) variance was explained by a negative correlation with seawater temperature at p values of 0.05 and 0.001 respectively. The analyses also revealed that 64.4% of intertidal adult length variance ($F = 17.3$; $df = 2, 17$; $p < 0.001$) was explained by positive relationships with day length (59.0%; $p < 0.001$) and sea temperature (5.4%; $p < 0.08$). Subtidally, 83.3% of the adult length variance ($F = 24.3$; $df = 3, 11$; $p < 0.001$) was explained positively by day length (65.1%; $p < 0.001$) and negatively by wave height (14.6%; $p < 0.01$).

DISCUSSION

Temporal variation in spawning patterns

There was high seasonal variability in the fecundity of *Phragmatopoma lapidosa* in the Boynton Beach area. Fecundity of both intertidal and subtidal worms was high from early summer through fall and was followed by drastic decreases in late fall and early winter. Consequently, while some individual *P. lapidosa* can be induced to spawn year-round, spawning potential is highest during summer and early fall.

The analysis of seasonal changes in mean egg diameter also suggests summer and early fall spawning peaks. Smaller oocytes coincided with higher fecundi-

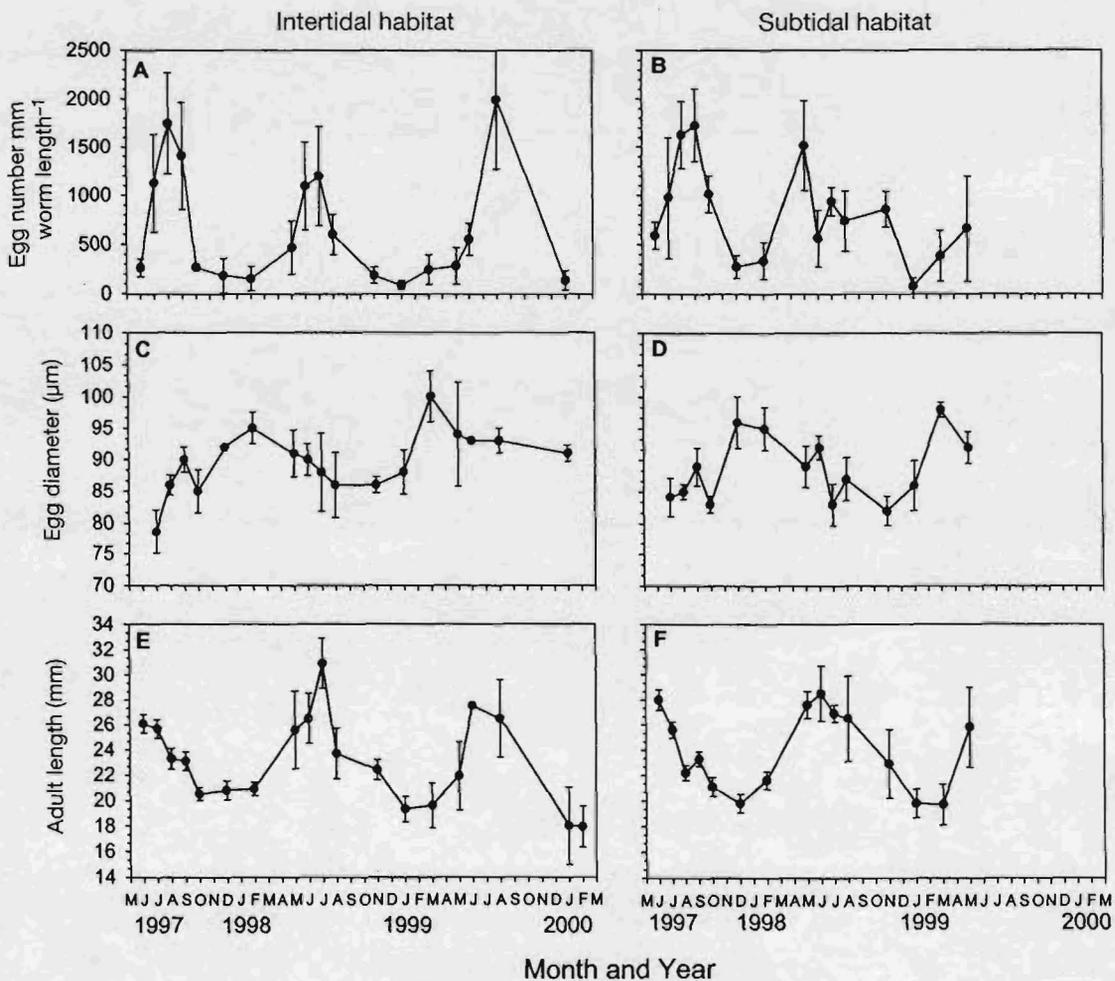


Fig. 4. *Phragmatopoma lapidosa*. Seasonal changes in mean (± 1.0 SD) fecundity, egg diameter and adult length of intertidal and subtidal worms (A,B) Subtidal worms were more fecund than intertidal worms in October 1997, May 1998, November 1998 and March 1999 (Tukey pairwise probabilities between habitats = 0.001, 0.004, 0.001 and 0.036 respectively). (C,D) Egg diameters were significantly larger subtidally than intertidally in month of July 1997 (Tukey pairwise probability = 0.005). (E,F) Adults were significantly larger intertidally than subtidally in July 1998 (Tukey pairwise probability = 0.002). Subtidal sites were completely covered by sand after March 1999

Table 2. *Phragmatopoma lapidosa*. Pearson correlation coefficients of within and between census values of fecundity and egg diameter, fecundity and adult length and egg diameter and adult length for intertidal and subtidal worms. *Statistically significant at 0.05 level

Comparison Census date	Egg diam./Egg no.		Egg no./Adult size		Egg no./Adult size	
	Intertidal	Subtidal	Intertidal	Subtidal	Intertidal	Subtidal
Within census						
Jun 97	-0.341	0.201	-0.104	-0.322	-0.441	0.044
Jul 97	0.041	0.361	0.256	0.274	0.281	0.281
Aug 97	0.033	-0.122	0.144	-0.236	-0.079	-0.029
Sep 97	0.145	-0.425	0.049	-0.497	0.091	0.538
Oct 97	0.387	-0.192	-0.080	-0.381	-0.182	0.036
Dec 97	0.491*	-0.434	0.011	-0.105	-0.049	-0.353
Feb 98	0.085	-0.273	-0.192	0.210	0.198	-0.102
Mar 98	-0.081	-0.193	0.128	0.415	0.032	-0.273
Jun 98	-0.169	-0.107	-0.190	-0.321	0.260	0.153
Jul 98	0.409	0.045	-0.192	-0.321	-0.047	0.101
Aug 98	0.103	-0.069	-0.018	0.011	0.220	-0.027
Nov 98	-0.295	0.259	0.010	-0.005	-0.012	0.044
Jan 99	-0.558*	0.255	-0.518*	-0.239	0.381	-0.076
Mar 99	0.551*	-0.007	0.382	0.534*	0.467*	-0.226
May 99	-0.006	0.373	-0.348	-0.338	0.074	-0.272
Between census	-0.244	-0.244	0.568*	0.282	-0.222	-0.239

ties during summer and early fall, suggesting that the larger oocytes are spawned frequently during this period. It is unlikely that a decrease in mean egg size would be the result of an ontogenetic change in egg size and egg number because seasonal and within-census correlations between egg diameter and adult size were generally not significant. Also, although eggs could be fertilized year-round in the laboratory, higher percentages were fertilized during the spring, summer and early fall (D.A. McCarthy pers. obs.). This could be because a fraction of the gametes were not mature at other times of the year.

of these environmental factors has been documented for polychaetes (Clark 1988, Chu & Levin 1989, Giangrande 1997) and other invertebrates (see Giese & Kanatani 1987 for a review). The multiple stepwise regression did reveal that day length was important in explaining fecundity variance for both intertidal and subtidal *P. lapidosa*. The proximity of habitats, combined with the very oligotrophic waters derived from the nearby Florida Current (approximately 1.6 km away), makes it likely that both light penetration and sea temperature are similar in the 2 habitats, thus affecting gametogenesis in similar ways.

Seasonal entrainment of gametogenesis

It is likely that both day length and sea temperature are important in the seasonal entrainment of gametogenesis for *Phragmatopoma lapidosa*. The importance

Spatial variation in spawning pattern

Fecundity of *Phragmatopoma lapidosa* tended to be higher in subtidal than intertidal worms during most of the study period. The difference was most obvious

Table 3. *Phragmatopoma lapidosa*. Seasonal correlations of intertidal and subtidal fecundity, egg diameter and adult length means with chlorophyll a, sea temperature, wave height and day length. Measured and estimated chlorophyll a values are from Fowey Rocks and Boynton Beach respectively. *Statistically significant at 0.05 level; **significant at 0.001 level

Environmental factors	Fecundity		Egg diam.		Adult length	
	Intertidal	Subtidal	Intertidal	Subtidal	Intertidal	Subtidal
Day length	0.610**	0.430	-0.349	-0.439	0.783**	0.822**
Sea temperature	0.427	0.433	-0.639*	-0.728**	0.196	0.140
Chlorophyll a (measured)	-0.219	-0.445	0.080	0.180	-0.496	-0.378
(estimated)	-0.012	-0.241	0.396	0.334	0.068	-0.076
Wave height	-0.672**	-0.394	0.399	0.420	-0.579**	-0.505

from fall through spring, with intertidal and subtidal fecundities becoming virtually equal in summer. While habitat-specific differences in age could be responsible for the observed fecundity trends, these trends could also result from differences in food availability and/or the frequency of spawning cues between the 2 habitats.

Habitat-specific differences in size or age

Given the absence of a significant size difference between intertidal and subtidal worms, it is unlikely that between-habitat differences in fecundity were size-related. No significant difference in size occurred between intertidal and subtidal worms. Further, the majority of within-census correlations between egg number and adult length were not significant.

The observation that juveniles essentially replaced established adults in both habitats supports the idea that all worms were similar in age. There were cyclical changes in the sizes of both intertidal and subtidal worms (Fig. 4E,F) that corresponded with fall recruitment peaks. Sometimes unavoidable delays in sampling occurred in the fall because of storm activity. During these periods, newly settled recruits grew tubes so quickly (0.42 mm h^{-1} in the laboratory) that juvenile tubes rapidly became indistinguishable from those of established adults. It was only apparent that the worms were smaller when tubes were dissected in the laboratory. The combined observations of cyclical size changes and massive recruitment in both habitats suggest that individuals of *Phragmatopoma lapidosa* spawn gametes for a single season before dying. This observation is in line with Kirtley's (1966) prediction that they have a lifespan of approximately 1 to 2 yr.

Food availability

Habitat-specific differences in food concentration or duration of feeding time could explain the observed fecundity patterns. Studies have demonstrated relationships between food quantity or quality and reproductive output in spionid polychaetes (Levin 1986, Grémare et al. 1989, Levin 1991, Qian & Chia 1991) as well as other invertebrates (McKillup & Butler 1979, George et al. 1990, George 1994). For example, Walker & Heffernan (1994) observed differences in time to spawning and gonad index with relation to level of tidal exposure of the northern quahog *Mercenaria mercenaria*. Differences in immersion times between intertidal and subtidal *Phragmatopoma lapidosa* could affect the amount of energy available for reproduction. However, if this were the only variable responsible

for the apparent difference in rate of egg production between intertidal and subtidal *P. lapidosa*, fecundity would be expected to covary in the 2 habitats. Additionally, if food availability were solely responsible, it would be expected that seasonal correlations between fecundity and chlorophyll *a* would be significant. They were not. While a non-significant correlation between fecundity and chlorophyll *a* does not negate the importance of seasonal food availability for reproduction, it does imply that other environmental factors that vary between habitats have an effect on fecundity.

Disturbance

Differences in wave energy that affect spawning provide the most likely explanation for the observed differences in fecundity patterns between intertidal and subtidal *Phragmatopoma lapidosa*. During this study, both intertidal and subtidal hard-bottom habitats with *P. lapidosa* reefs were affected by wave-induced disturbance. Wave-induced disturbance was most severe during the hurricane season in late summer and early fall, and to a lesser extent during the winter. Wave action damaged worm reefs in both habitats by either breaking them apart and/or smothering them with sand. Intertidal worm reefs were more obviously affected by physical destruction during periods of increased wave activity than subtidal reefs. This is because intertidal reefs were exposed to the full force of waves crashing on them at low tide. In contrast, subtidal worms were always at least a few meters deep, so they were not exposed to the same level of destructive force as intertidal worms. Numerous intertidal colonies displayed cracks caused by the force of crashing waves. In addition, sand movement was high during storms and scoured intertidal colonies. No comparable cracks were observed in subtidal reefs, but sand-scouring did occur. These observations suggest that sublethal disturbances might be somewhat more frequent and unpredictable intertidally than subtidally. Such differences in sublethal disturbance between intertidal and subtidal habitats are likely to affect adult energy investment in reproduction by diverting energy to regeneration of body parts. However, as the individual worms used in our study appeared to be undamaged and were of similar sizes, the effects of sublethal disturbance on the energy available for reproduction may possibly not be important in explaining the observed fecundity trends.

Disturbance is very likely to contribute to the observed differences in fecundity between worms from the 2 habitats by affecting the frequency in spawning. When spawning occurs, eggs free in the coelomic cavities of a female of *Phragmatopoma lapi-*

dosa will be spawned; eggs still attached and developing in gonads will not be released. Ultrastructural research has revealed that *P. lapidosa* has vitellogenic mechanisms that produce mature eggs in just a few days (Eckelbarger 1979). Individual worms that have been spawning more frequently may have produced fewer new cohorts and thus appear to have lower numbers of eggs. In contrast, worms that have been holding gametes because they have not received the cue to spawn would appear to have higher fecundities.

Summary

We found that seasonal spawning in *Phragmatopoma lapidosa* was very tightly linked to day length and wave activity. We also found that intertidal worms generally spawned more often than subtidal worms. Both observed patterns could simply reflect food availability; however, the evidence suggests that surviving worm colonies are likely to have spawned gametes in response to sublethal disturbance caused by waves, and that intertidal worms probably do so more often than subtidal worms. These spawning differences are indeed expected, because the levels of sublethal and lethal disturbances which stimulate spawning are higher intertidally than subtidally (McCarthy 2001). The ability of *P. lapidosa* to produce eggs rapidly may allow it to respond plastically to varying intensities of disturbance, and thereby enhance the chance that larval recruitment will occur when space is available for colonization.

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