Population and reproductive ecology of the directdeveloping sea stars *Parvulastra parvivipara* and *Cryptasterina hystera*

Lana M. Roediger

B. Sc. Mar. Biol. (Hons)

A thesis submitted for the degree of Doctor of Philosophy

School of Biological Sciences

Flinders University

November 2011

Table of Contents

List of Figures	V
List of Tables	viii
Abstract	xi
Declaration	xiii
Acknowledgements	xiv

Chapter 1	General l	Introduction	1
1.1	Overview	·	1
1.2	Diversity	of marine invertebrate life-histories	3
1.3	Evolution	ary ecology of marine invertebrate life-histories	5
	1.3.1	Fecundity and mortality	6
	1.3.2	Dispersal, population distributions, and population	
		structures	7
	1.3.3	Population stability over ecological and evolutionary	y time-
		scales	7
1.4	Intraspeci	fic variation in offspring size	9
1.5	Implicatio	ons of intraspecific variation in offspring size	13
1.6	Species e	xamined in the investigations presented here	14
1.7	Thesis air	ns	19
1.8	Thesis str	ucture	20

Chapter 2 Population dynamics of the direct-developing sea stars Parvulastra		
parvivipara and Cryptasterina hystera		
2.1 Abstract.	23	
2.2 Introduction	24	
2.3 Methods		

2.3.1	Study populations	
2.3.2	Distribution, abundance and size structure	29
2.3.3	Ecological variables	
2.3.4	Statistical analyses	
2.4 Results		36
2.4.1	Abundance and size structure	
	2.4.1.1 P. parvivipara	
	2.4.1.2 C. hystera	41
2.4.2	Ecological variables	44
	2.4.2.1 P. parvivipara	44
	2.4.2.2 C. hystera	46
2.5 Discussion		47
2.6 Tables		56

Chapter 3 Variation in offspring size and brood size in the direct-developing sea star *Parvulastra parvivipara* across the intertidal environment......70

•	al 1 ul vulusil u	pur vivipur u across the inter thuar environment	
3.1 Abstract.			70
3.2 Introduction			71
	3.3 Methods.		75
	3.3.1	Study populations	75
	3.3.2	Specimen collections	75
	3.3.3	Measurements of offspring size and brood size	76
	3.3.4	Density experiment	77
	3.3.5	Statistical analyses	79
	3.4 Results		80
	3.4.1	Adult size	80
	3.4.2	Brood size	83
	3.4.3	Offspring size	
	3.4.4	Coefficient of variation in offspring size	
	3.4.5	Adult density and sizes of offspring and broods	89
	3.4.6	Density experiment	91
3.5 Discussion			93
3.6 Tables			104

Chapter 4 Variation in offspring size in two species of sea stars exhibiting		
viviparity and direc	t development	109
4.1 Abstract.		109
4.2 Introducti	on	110
4.3 Methods.		113
4.3.1	Study populations	113
4.3.2	Specimen collections	113
4.3.3	Specimen dissections	114
4.3.4	Temperature variation	114
4.3.5	Statistical analyses	115
4.4 Results.		116
4.4.1	Variation in offspring size between species	116
4.4.2	Variation in offspring size within species	118
4.4.3	Temperature variation	121
4.5 Discussi	on	122
4.6 Tables		128

Chapter 5 Consequences of variation in offspring size within broods on offspring fitness during the first year of development in the direct-developing sea star Parvulastra parvivipara......130 5.3.1 5.3.2 Offspring growth and survivorship134 5.3.3 5.4.1 5.4.2 5.4.3 5.6 Tables......144

Chapter 6 General Discussion	
------------------------------	--

References 15	7
----------------------	---

List of Figures

Figure 1.1. Suggested evolutionary pathway from feeding pelagic larval development to viviparity and direct development in marine invertebrates.......5

 Figure 1.2. The viviparous, direct-developing sea stars (A) Parvulastra

 parvivipara, and (B) Cryptasterina hystera

Figure 1.3. Examples of variation in the size of offspring within broods released by (A) *P. parvivipara*, and (B) *C. hystera*......16

Figure 3.5. Mean (\pm SE, n = 127 - 793) coefficients of variation (CV) in offspring size within broods (black bars)) and among adults (white bars) among (A) three populations of *P. parvivipara*, and (B) among intertidal zones at Smooth Pool...89

Figure 4.2. Mean sizes (\pm SE, n = 120 - 46383) of (A) adults, (B) broods, and (C) offspring of *P. parvivipara* and *C. hystera*.....117

Figure 4.4. Linear regression analyses (n = 97 - 450) of adult size against (A, E) brood sizes, and (B, F) mean offspring sizes. Relationships between brood sizes and (C, G) the CV in offspring size within broods, and (D, H) mean offspring sizes are similarly analysed for *P. parvivipara* and *C. hystera*, respectively.....120

Figure 4.5. The mean temperature range recorded among tide pools in the temperate (*P. parvivipara*) and tropical (*C. hystera*) habitat......121

List of Tables

Table 2.10. Ecological variables identified by multiple logistic regression

 analyses as seasonal predictors of the presence or absence of *P. parvivipara*.....66

Table 2.13. Ecological variables that were identified as significant predictors of

 the presence or absence of *C. hystera* by multiple logistic regression analyses...69

Table 3.2. Size ranges of *P. parvivipara* adults, offspring and broods of three

 populations and intertidal zones

 105

Table 3.5. Linear regression comparisons between the density of *P. parvivipara*

 in tide pools at Smooth Pool and the sizes of adults and their brood

 characteristics
 108

The population dynamics and reproductive ecology of direct-developing marine invertebrates are poorly understood. The absence of an ecologically decoupling dispersive larval stage between adults and offspring in these species was thought to increase population stability relative to species with complex life-histories, but recent evidence suggests that they are less stable because population fluctuations are not dampened over time by recruitment of larvae from other populations. Recent studies have also shown that some marine invertebrates adaptively alter offspring phenotype (size) in response to environmental conditions experienced by the adults. Offspring size has profound implications for all life-history stages of marine invertebrates, as well as their population dynamics. The capacity to adaptively alter offspring phenotype should be greater among direct developers than species with dispersive larvae because their offspring are more likely to experience similar conditions to adults, and there are no conflicting selective pressures acting on life-history stages that occupy different ecological niches. I examined the population dynamics and brood characteristics of two Australian intertidal asterinids that reproduce via direct development-Parvulastra parvivipara (3 temperate populations, South Australia) and Cryptasterina hystera (4 tropical populations, Queensland). High structural complexity of tide pools predicted the likely presence and high abundances of both species; however, while population sizes of *P. parvivipara* and *C. hystera* were stable over 3 and 2-years, respectively, their distributions were highly dynamic. Both species disappeared from large proportions of tide pools that offered ideal conditions and recolonised these pools with no apparent periodicity. I suggest that metapopulation dynamics operating among tide pools stabilise population abundances in circumstances where unpredictable changes in tide pool conditions can lead to 100 % mortality. Small proportions of P. parvivipara gave birth during autumn and winter, but most individuals gave birth in late spring to summer. Offspring size was greatest and brood sizes smallest during summer. Experiments showed that larger

offspring had greater fitness (survivorship) than smaller offspring during this period. I suggest that *P. parvivipara* adaptively alters brood characteristics during summer to maximise offspring fitness during this period. Intragonadal cannibalism among siblings may facilitate these changes in brood characteristics. I also suggest that *P. parvivipara* exhibits plasticity in the timing of births; that is, mean offspring fitness is maximised by matching the characteristics of an individual's brood and timing of births to prevailing environmental conditions. The coefficients of variation in offspring sizes of both species were high, but based on this sampling P. parvivipara was more variable than C. hystera. The higher variability exhibited by *P. parvivipara* may be a bet-hedging strategy that maximises mean offspring fitness in a temperate habitat that is more variable than the tropical habitat of C. hystera. The CV in offspring size of P. parvivipara did not differ among intertidal zones as would be expected if a greater offspring size was used as a bet-hedging strategy in the more variable upper areas of its intertidal zone. I suggest that intertidal habitats are inherently variable and the high CV in their brood characteristics may increase mean offspring fitness via bethedging.

I certify that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Lana M. Roediger

Acknowledgments

I would like to thank my supervisor Dr. Toby Bolton for your support, encouragement and for introducing me to research at the Lincoln Marine Science Centre (LMSC). Thank you for your guidance, feedback and for all the discussions along the way. I have truly valued your support and enthusiasm towards my research, and I will continue to keep my 'sea star princess' crown in a safe place!

Thanks also to Professor Peter Fairweather for your feedback on draft versions of my thesis. Your encouragement and comments were very much appreciated in the latter stages of my thesis.

Numerous people have helped conduct field work throughout this study including Seb, Mum, Toby, Bridget and Louise. Thanks for the help through the wet, cold, windy, hot, slippery and often miserable conditions, and for the early morning starts we all hated. Thanks especially to Seb (my number one RA) and to Mum for helping in the field after my knee reconstruction, and for letting me boss you around when I was immobile.

I would like to thank the staff at the LMSC for your company and help around the lab. I feel that I was very lucky to have one of the best views from my office that one could ask for. The moments of day dreams were pleasant as pods of dolphins swum by, fishers passed, boats sailed out to sea and the odd submarine popped up. Being able to listen to the waves lap the shore from my desk is something that I will always miss.

Thank you to Professor Maria Byrne and the staff at One Tree Island Research Station for making my time and research on the island a great experience. It sure is a special place up there and I thank you for giving me the opportunity to research and experience it.

Thanks to my fellow students and colleagues Gemma, Nadine, Angela, Erin, Jenna, Andre, Dave and Shelley for your chats and de-briefs and for keeping me sane with non-work related conversations (especially during morning tea).

Thank you to my Dad and sister Em, who helped make the PVC containers for my experiments. We made a great production line in the workshop on the farm!

To Jenna and Bridget, thank you for your help with the tedious lab work. It was a long few days in the lab, and your help and company (along with Triple J) during them was very much appreciated.

Thanks to Jess and Squinty for trying to relocate my lost clipboard and data at Point Whittlebee. Sorry if I led you on a wild goose chase!

Thank you to the Department for Environment and Natural Resources: Wildlife Conservation fund, ANZ Trustees Foundation: Holsworth Wildlife Research Endowment, Nature Foundation of South Australia, Biology Society of South Australia, Field Naturalist Society of South Australia: Lirabenda Endowment fund, Eyre Peninsula Natural Resources Management Board and Flinders University for financial support to undertake this research. Without the support from your organisations this research may not have been possible.

To my best friend and husband Seb. Your support throughout my PhD and this past twelve years has been amazing and I cannot thank you enough for your help, encouragement, love, support and belief in me achieving my goals. You made the hard days so much better. Thanks so much for sacrificing your annual leave and your early morning surfs for field work. Don't worry - I won't make you do it again!

Finally, thank you so much to my friends and family for your love and friendship, to whom I could not have done this without. Your support has been so grateful

and there will now be plenty more time for wine, cheese and camping trips on the weekends! To Nan Oliver, I got there eventually, and I look forward to a celebratory glass of wine! To my Grandma, my hero: I recall telling you before you passed away that my dream was to come back home and undertake marine based research on the Eyre Peninsula. Well, I have now achieved that dream, and so much more. I am so stoked that I have been able to contribute to a small part in our understanding of the unique marine life on the Eyre Peninsula. I am also happy to continue living and working in this beautiful part of the world, that I am fortunate enough to call home.