The Effect of Egg Capsule Clustering on Embryonic Survival in the Dogwhelk Nucella lapillus Connor F. White and Jonathan D. Allen Department of Biology, College of William and Mary, Williamsburg, VA 23187



Abstract

Observations of several species from a taxonomically diverse group of amphibians, reptiles, arachnids, coleopterans, lepidopterans and molluscs have suggested that clustering of eggs is a survival strategy through which rates of predation or desiccation are decreased. The dogwhelk *Nucella lapillus* is an intertidal predatory snail that deposits egg capsules under intertidal rocks in clusters of up to 1000 capsules. These benthic egg capsules are then left to develop undefended for up to four months. This study investigated the adaptive significance of clustering eggs capsules by manipulating cluster size in the field over a five week span. In this study and previous work it was found that capsules themselves provide little direct protection against predators. However, it was found that clustering of egg capsules is beneficial and significantly reduces predation relative to uniformly spaced egg capsules. Similarly, it appears that encapsulation is an ineffective means to prevent desiccation induced mortality in the embryos. However, this study found that clustering of capsules significantly reduced mortality due to desiccation. Overall, clustering increased survival among egg capsules and the increase in survival was roughly proportional to cluster size. In addition we conducted laboratory predation trials to identify potential predators on N. lapillus egg capsules. We found that lobsters, green crabs and rock crabs all consumed N. lapillus capsules in the lab but hermit crabs did not.

Introduction

Nucella lapillus is a common predatory snail in the rocky intertidal throughout the North Atlantic. *N. lapillus* deposits small egg capsules, approximately 10 mm high and 3 mm in diameter, from which 12-36 juveniles emerge (Feare 1970; Crothers 1985; Costello and Henley, 1971). Encapsulation of the embryos alone has proved to be ineffective at deterring predation as well as desiccation (JDA unpub., Spight 1977, Pechenick 1983). Adults cluster these capsules in aggregations, which can grow to be quite large and contain over 1000 egg capsules (Crothers 1985). In some amphibian and insect species clustered eggs have greater rates of survival when climate conditions promote water loss (Clark and Faeth1998). Observations of several species have shown that clustered eggs have lowered rates of predation (Agarwala and Dixon 1993, Faraji et al. 2002). We tested whether the size of egg capsule clusters affected rates of mortality due to predation and desiccation.

Methods

Field Experiments

•Egg capsules were glued onto rocks in 3 possible arrangements: 1 cluster of 100 capsules, 2 clusters of 50 capsules, and 100 capsules uniformly spaced 1 cm apart

•Rocks were deployed at the low tide line

•The number of capsules that were clipped, missing or discolored were recorded every week for 5 weeks

Lab Experiments

•Hermit crabs, lobsters, green crabs, and rock crabs were placed in cages with 9 egg capsules spaced on a rock in a uniform distribution

•The number of capsules eaten were recorded every day for four days

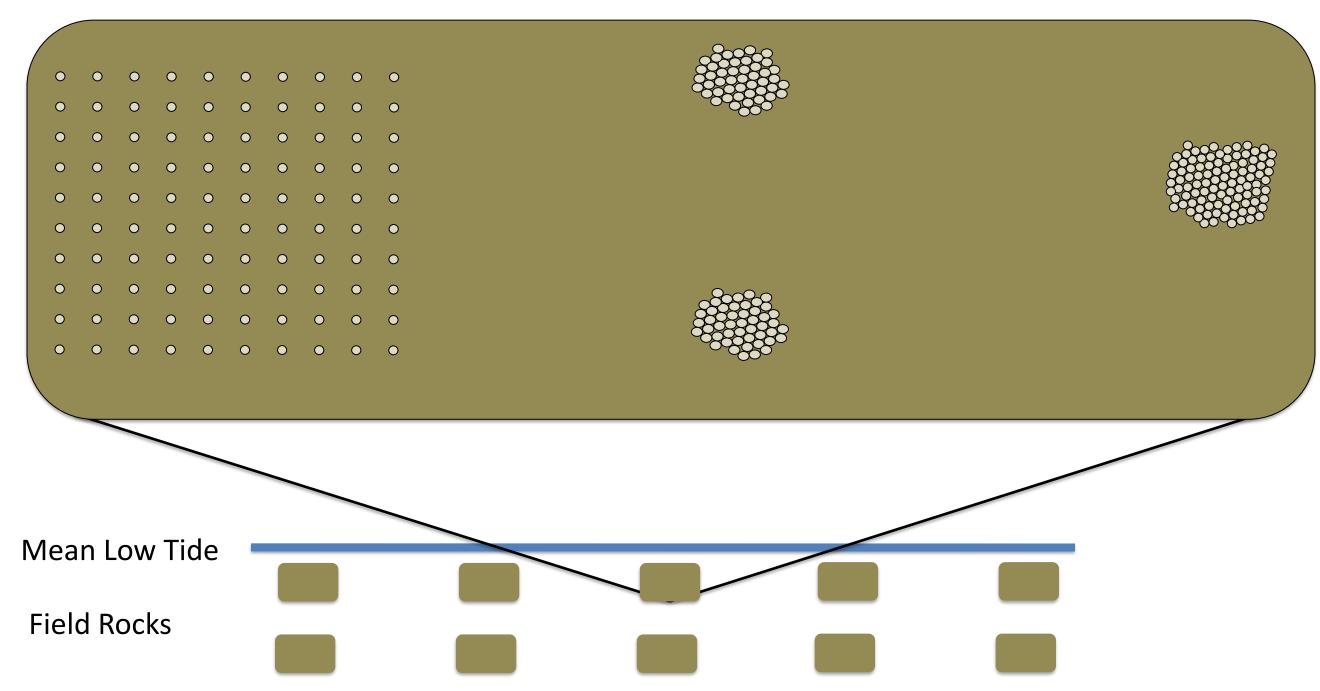


Fig. 1. Field arrangements of rocks on the shore of Orr's Island, Maine at the Bowdoin College Coastal Studies Center. Five rocks were placed along the mean low tide line on July 1st 2010. Five more rocks were placed one meter higher in the intertidal one week later on July 8, 2010. Each rock had two clusters of 50 capsules, one cluster of 100 capsules, and 100 eggs in an uniform distribution.



Results

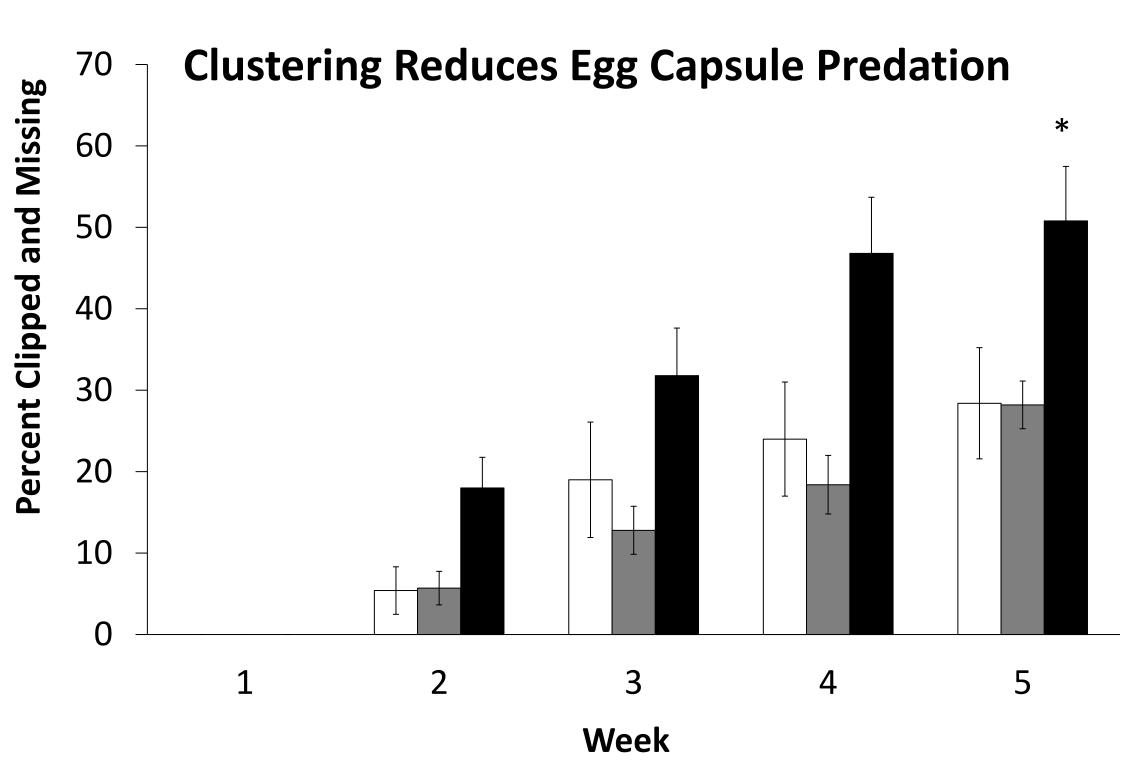


Fig. 2. Percent of capsules clipped and missing by week. There was a significant effect of cluster type (2-way ANOVA, F_{2.16}=7.448, P=0.005) but not tidal height (2-way ANOVA, $F_{2,16}=1.735$, P=0.208) on the number of capsules missing and eaten. Since there was no significant effect of tidal height, data were pooled and the cumulative data graphed. The ANOVA was only run on data from week 5. An asterisk (*) indicates a significant difference from clustered treatments based on post-hoc tests.



Clustering Increases Survivorship

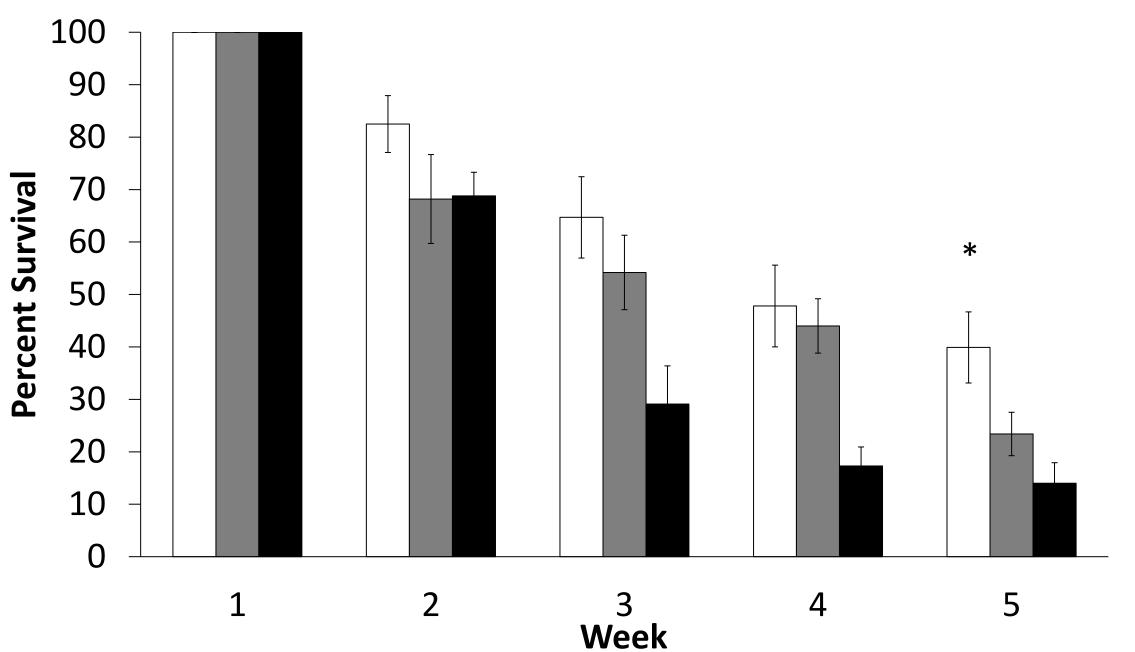


Fig. 4. Percent of capsules alive by week. There was a significant effect of cluster type (2way ANOVA, F_{2.16}=12.530, P=0.001) but not tidal height (2-way ANOVA, F_{2.16}=0.486, P=0.505) on the number of capsules missing and eaten. Since there was no significant effect of tidal height, data were pooled and the cumulative data graphed. The ANOVA was only run on data from week 5. An asterisk (*) indicates a significant difference between the cluster of 100 and the remaining treatments based on post-hoc testing.



Fig. 6. Egg capsules were scored as either present, clipped, discolored or missing. Panel A shows a clipped capsule next to an intact capsule. Panel B shows a discolored/desiccated egg capsule (far right) next to two living, intact capsules . Panel C shows a green crab with a N. lapillus capsule in its left claw.

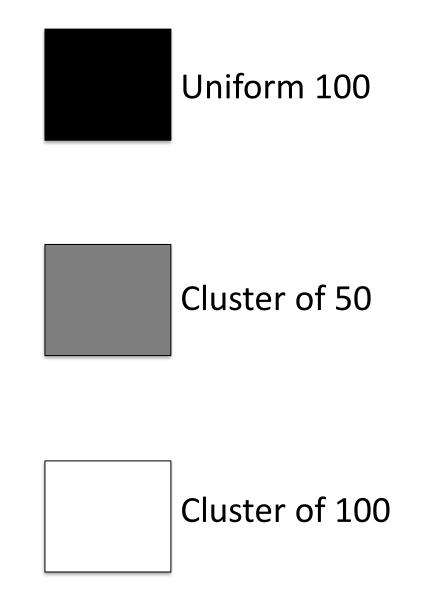




Fig. 3. (A) The field site along Harpswell Sound, Maine. (B) Rock used for the field experiment. (C) Rock with egg capsules in a uniform distribution used for lab predation xperiments

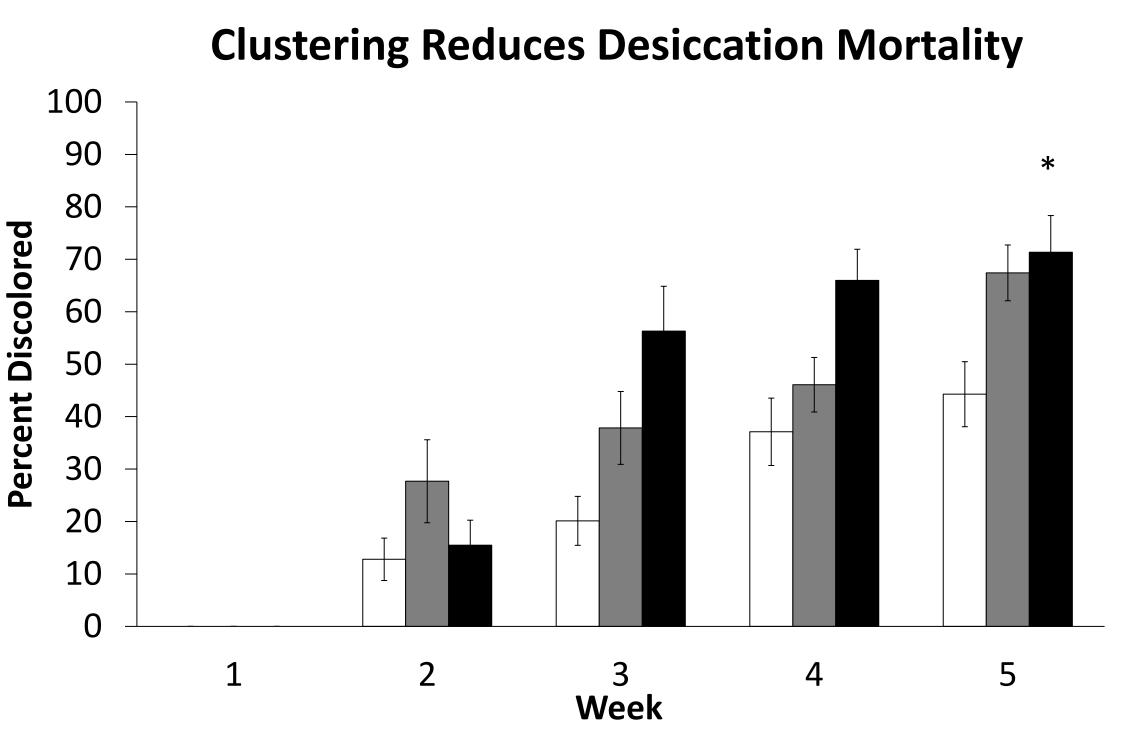


Fig. 5. Percent of intact capsules desiccated by week. There was a significant effect of cluster type (2-way ANOVA, F_{2.16}=7.181, P=0.006) but not tidal height (2-way ANOVA) F_{2 16}=0.229, P=0.645) on the number of capsules missing and eaten. Since there was no significant effect of tidal height, data were pooled and the cumulative data graphed. The ANOVA was only run on data from week 5. An asterisk (*) indicates a significant difference between uniform capsules and clusters of 100.

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Increasing cluster size increases egg capsule survivorship

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Lobsters, Rock Crabs and Green Crabs eat Egg Capsules Control Hermit Crab A **Green Crab** B **Rock Crab** B,C Lobster 20 10

Fig. 7. The percent of capsules surviving each day in laboratory experiments. Juvenile lobsters (Homarus americanus), green crabs (Carcinus maenus), rock crabs (Cancer borealis) or hermit crabs (Pagurus longicarpus) were placed in cages with nine egg capsules. The number of capsules remaining were recorded daily for four day. There was a significant effect of predator type (1-way ANOVA, F_4 =16.243, P<0.001), letters indicate significance.

Conclusions

- Clustering decreases the rate of predation on egg capsules
- Clustering reduces the rate of desiccation experienced by egg capsules
- There are high rates of mortality for capsules deposited in the intertidal zone regardless of cluster size
- Desiccation and predation appear to be roughly equivalent threats to encapsulated embryos.
- Green crabs, rock crabs, and juvenile lobsters are likely natural predators on egg capsules

Acknowledgements

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