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Bivalves as Model Organisms to Elucidate Patterns of Predation

by

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Abstract

Understanding fluctuations in exploited marine stocks has been
difficult due to our inability to directly census, observe and
experiment with discrete populations in a three dimensional
environment. Utilizing an infaunal bivalve species as a model
organism, we conducted manipulative experiments to test specific
hypotheses concerning predator- mediated variations in prey
mortality. These manipulations demonstrated that:
(i) predator-induced escape responses of prey can reduce growth
rates of individual prey and subsequently increase
susceptibility to predation, (ii) variations in prey aggregation
scale (i.e. patch size) can significantly change mortality rates
at overall constant densities, and (iii) diel predator distribution
around shelter sites significantly affects spatial mortality
patterns in prey populations.

Introduction

Potential causal mechanisms for exploited marine stock

fluctuations has had a long history of study. Such studies are

often restricted to a correlative approach, in which various

large-scale physical factors are related to production or catch,

due to the insurmountable difficulty of directly censusing most

populations and following the fate of individuals[1]. While

some physical events may directly cause mortality in a

population, it is generally believed that large scale physical

factors act as forcing agents on small-scale phenomena (e.g.

temperature variations affecting larval development rates).

Recent process-oriented investigations, focusing on the larval

stage, have concentrated on the success of prey location and

first feeding by fish larvae (e.g. the critical period

hypothesis)[2] and larval transport from nursery areas[3] as

possible causal mechanisms to explain year-class variation.

However, there is a general lack of correlation between larval

abundance and year-class strength[4].

Predation is believed to be a major cause of pre-adult mortality

in marine populations[5]. This is inferred from the presence of

eggs, larvae and juveniles in gut contents of predatory species

and by the apparent absence of starved larvae in the water

column. While it is generally difficult in finfish populations

to study predation events due to potential large scale individual

movement, bivalve mollusks are more easily studied because they are usually sessile. Distributions and interactions with predators are more easily observable using bivalves, and individuals are easily manipulated for process oriented studies.

Since predation events occur on the scale of meters (i.e. patches within populations), we have taken the approach that predation phenomena are best evaluated at this level. Studies of small-scale predation phenomena could lead to understanding causes of larger stock and population variations. Direct underwater observations of crustacean predation on bivalve prey in nearshore areas of the northeast U.S. continental shelf have revealed that interactions occur at a variety of spatial scales[6]. At the smallest scale, that of the individual, foraging activity by predators can elicit escape responses by intended prey. As predator density increases, the frequency of escape responses can increase to the point where feeding, and subsequently growth, of the prey individual is affected. On the scale of prey patches, crustacean predators (Cancer spp. and Carcinus maenus in particular) utilize a hierarchical foraging strategy. Dactyl probing locates individual prey items which are removed, and if prey are sufficiently abundant this is followed by an excavation approach which exposes all potential prey in a patch of bottom. These alternative search patterns imply some critical density/patch size which will elicit the change in

foraging response. The largest scale we consider is the spatial distribution of predation, as influenced by the distribution of predator shelter sites. Heterogeneous distributions of shelters and the predators that use them may potentially affect the spatial pattern of mortality of infaunal prey [1].

Manipulative Experiments

In a series of field and laboratory experiments we utilized the hard clam Mercenaria mercenaria as a model infaunal prey item to test hypotheses concerning the scale of interactions of crustacean predators and infaunal prey. All clams used were within 0-group size ranges to elicit effects which would occur during the first year of growth.

At our smallest scale, that of the individual, possible sublethal effects of foraging activity were examined using groups of approximately 2000 juvenile clams of 1.23mm (+/- 0.16mm) shell length (SL) (shell length is the tangential length from the umbo to the longest ventral region). Each group was placed into screened azoic sand in 37.9 liter aquaria supplied with ambient flowing seawater. The hermit crab, Pagurus longicarpus, was introduced into the tanks at densities of 0, 2,

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[1] Our hypothesis was generated after making a series of observations in several habitats (shallow subtidal sand flats and deep sand plains to 50 m) along the northeast coast of the U.S. Quantitative observations, showed that shelter use by crustacean predators (Cancer borealis, Cancer irroratus, Carcinus maenus, juvenile Pagurus longicarpus) was affected on a diel basis. Tests of homogeneity of distribution showed that diurnal distributions were significantly (Chi-square test, p <0.05) related to the availability of shelter while nocturnal patterns were not (Chi-square test, p >0.10). Shelter, in these cases, consisted of large bivalve shells (Mercenaria mercenaria, Arctica islandica, Placopecten magellanicus) or large worm tubes (e.g. Diopatra spp.) on open sand plans where no greater topographical relief (e.g. rock, cobble, boulders) was available.

5, and 10 crabs/tank   (0, 17.9, 44.7, 89.4 crabs/m^2)[2],   with

three replicates per density treatment.   The dactyl portion of

the crab's chelae was removed such that the crabs were free to

exhibit foraging behavior but were unable to consume the

clams[3].

The experiment was run for 30 days, at which time the control

treatment (no predators) showed significant (t= 13.37, p <

0.0001) growth.   Subsamples of 100 individuals from each

replicate were taken and measured for SL.   There was a

significant (F = 15.06, p < 0.005) detrimental effect on clam

growth as crab density increased.

At our intermediate scale, that of the prey patch, a field

experiment was conducted to determine the covarying effects of

patch size and density on hard clam survivorship.   Clams 3.45 mm

(+/- 0.38) SL were deployed in a complete factorial design in

triplicate using three densities (25, 150, and 300 clams/0.25 m^2)

and four patch sizes (0.25, 0.50, 1.0 and 2.0 m^2).   Clams were at

large for a period of one week in ambient sediments[4].   This

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[2] These densities are within a range of densities we have observed in the field.
We must raise a note of caution, however, because the field measured densities
are instanteneous measures and we do not have any data regarding persistence
of aggregation of foraging crabs.

[3] Verified by initial observations, P. longicarpus can consume clams up to 1.1 mm
SL by using their chelae to chip away at the shell margin and hinge. Without
the dactyl, individuals can only manipulate, but not consume, clams of this size
with their mandibles. Observations of clam siphons in these treatments showed
foraging crabs to elicit normal escape responses in the prey.

[4] Ambient, rather than azoic, sediments were used to: (1) retain the sedimentary
cohesiveness necessary for crustacean predators to use both the dactyl probing
and excavation foraging strategies, and (2) reduce the disturbance level and
the subsequent attraction of predators, while setting the experiment out.

time frame was chosen to eliminate long-term multiple predation
events which would mask the patterns caused by initial prey
densities[5].   Survivorship was determined by counting all
live clams remaining in each quadrat[6].   Patch size had a
highly significant effect (F = 10.47 p = 0.0001) on
survivorship, with mortality increasing with patch size. Density
had a slightly significant effect (F = 2.58 p = 0.097) with
mortality increasing with density. There was no significant
interaction between density and patch size.

Our largest scale of predation examined the effect of shelter-
induced predator distributions on differential predation between
patches. Our working hypothesis was that predation is more
intense around shelters, since these areas are available for the
entire diel period, while areas more distant from shelters are
available only on a nocturnal or periodic basis. A site was
selected with a mud sand substrate which covered an area in
excess of 100 m^2. Four bushels of adult hard clam valves were
distributed in a circular area (with a radius of 2 m) and left
for three weeks[7].   Subsequent observations showed that the

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[5] Longer time frames would greatly affect the densities that predators would
perceive when encountering the patch. In situ observations of predators
indicate residence times in patches to be on the scale of minutes. Subsequent
predators therefore encounter patches of reduced prey density.

[6] Clams were recovered separately from each replicate patch by a diver operated
air-lift device. Recovery rates in excess of 99% were obtained in an initial
experiment (n=3) where protected clams from the experimental treatments were
at large for 1 week in 0.25 m^2 quadrats. We assume unrecovered clams from the
experimental treatments were preyed upon and removed from the patch.

[7] The clam valves are representative of a death assemblage from a dense patch
of adults. We have observed these assemblages previously during SCUBA,
submersible, and ROV dives on the northeast continental shelf of the U.S.
Although relatively rare when compared to shelters consisting of only single
or double valves, the dense valve assemblage was chosen to accentuate the
available shelter for predators for the purpose of this experiment.

shelter site was utilized by, and had a higher overall density of

crustacean predators than the surrounding area.

Juvenile clams (approximately 5mm SL) were distributed into

ambient sediment at densities of $150/0.25m^2$ quadrant. Six

replicate quadrants were deployed at increasing distances (0, 2,

6, 14 m) from the shell site. Clams were recovered after one

week and enumerated as in the previous experiment. A significant

increase (F = 5.08 p < 0.001) in log-transformed survivorship was

noted as distance from the predator shell refuge increased.

Discussion

Our results demonstrate the effects of predation at a variety of

scales. At the level of the individual, predator activity and

subsequent escape responses of prey can decrease individual

growth rates in prey populations. Reduction in growth leaves

individual prey organisms within susceptible size ranges for

subsequent predation longer than if no reduction in growth had

occurred. The pattern becomes circular: higher predator density

--> less growth --> increased time of susceptibility to predators

--> continued attraction of predators to prey patches.

At the level of prey aggregations in patches, the larger a patch

at any specific density, the higher overall mortality rate (i.e.

at least over the ranges used in this experiment). The pattern

of predation intensity we have shown may be caused by the

formation of sub-patches within the larger experimental

treatment. As predation events reduce densities in one part of a large patch, other portions retain the higher density. The presence of high density sub-patches continues to attract predators which forage in the overall patch for longer periods than the average density would predict. Prey in lower density areas between subpatches are still located due to the continual foraging activity, and are preyed upon. In smaller patches, the lower number of clams are less likely to be located and do not retain foraging predators in the patch. This pattern of activity would cause higher mortality in larger patches than in smaller patches starting at the same density.

The diel distribution of predators at levels greater than patch size is the largest scale we examined. Figure 1 illustrates a simple conceptual model of the "sphere of influence" caused by heterogeneous predator distribution. Predation is most intense around shelter sites since these areas are always accessible (i.e. foraging is possible over 24 hours). The distal areas around shelters are only accessible during nocturnal foraging when predators move away from shelters, probably due to the reduced threat from visual predators. These results may apply only to the case at hand: that is, in shelter - poor environments with little topographic relief on the small-scale. Shelter-rich environments (e.g. coral reefs, seagrass beds, boulder reefs) may, and probably do, have much different patterns of predator activity and foraging strategies.

The role of density-dependent predation has been firmly

established [7].   However, if density-dependent predation solely

governed predation impacts on a population, the summation of the

resultant interactions would, after some time, yield uniform prey

distributions provided all patches are located.   This obviously

is not the case.   A possible explanation may be that differential

predatory interactions on several spatial scales result in

spatial heterogeneity among prey populations.

Effects such as we have demonstrated may, in concert, influence

naturally occurring densities of both prey and predators, which

will also result in non-uniform distributions.   While our work

has focused on a two-dimensional system (e.g. benthic), the

hypotheses we generated from observations of this system are

similar to others concerning larval and juvenile fishes which

have been generated in a three-dimensional system [8].

Here we have demonstrated predator induced effects of growth and

distribution on a single prey species.   However, these are only

basic patterns and future efforts will be required to relate

predation pressure to recruitment models.   These areas include

the effects of: i) multiple predator species on size (age)-

specific prey mortality rates, ii) overlapping predator refuges or

aggregations on prey mortality patterns, iii) variations in

predator density on growth of prey of different sizes (ages), and

iv) synergistic interactions over all spatial levels on prey

distribution and abundance. Additionally, further field observations may reveal new scales of interactions which will require elucidation.

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   for small-scale investigations into recruitment processes.

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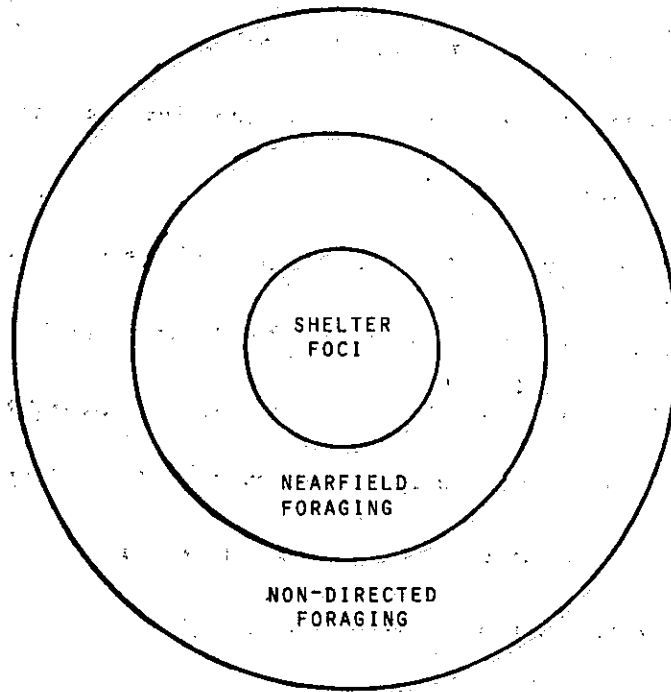
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Figure 1.   A conceptual model of the effects of heterogeneous

predator distributions on the spatial-temporal

aspects of foraging. During diurnal periods,

foraging is limited to areas directly around the

shelter site. Shelter affinities break down

during nocturnal periods and foraging occurs at

more distal sites. The solid lines do not imply

any fidelity of the predators to particular

shelter sites.