Predator Induced Plasticity in Barnacle Shell Morphology

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A Thesis

Submitted in Partial Fulfillment of the

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<u>Abstract</u>

Organisms employ inducible defenses to prevent predation. This occurs when the

organism recognizes an environmental cue that leads to the expression of the

defensive trait. In marine systems this cue is often chemical in nature. Several

marine invertebrates have been shown to use inducible defenses, including:

bryozoans, mussels, snails, and barnacles (Harvell 1984, Lively 1986, Trussell 1996,

Leonard et al. 1999, Dalziel and Boulding 2005, Jarrett 2008). The purpose of this

study was to determine if the cue from exposure to *Mexacanthina lugubris*, a

predatory snail, causes the narrow operculum morphology in the barnacle

Chthamalus fissus.

Rocks containing juveniles of the species *C. fissus* were collected in La Jolla, CA. In

the laboratory the barnacles were assigned to one of three treatments: *M. lugubris*

(predator), *Tegula funebralis* (herbivore), or control. The barnacles in the predator

and herbivore treatment were exposed to cues from the snails for 28 days over a 35

day period. The barnacles in the control treatment were exposed to the same

conditions without the presence of any snails. Digital photographs of the barnacles

were taken on 1 August 2007 and 23 January 2008. Measurements of operculum

width, operculum length, and basal diameter were taken using Sigma Scan Pro 5[TM]

software and compared among the treatments.

Over the course of the experiment, barnacles that were exposed to *M. lugubris*

developed significantly narrower opercula than barnacles in the *T. funebralis* and

control treatments. This indicates that the narrow operculum morphology seen in *C. fissus* is an inducible defense triggered by a cue from its predator, *M. lugubris*. Future studies are needed to determine the cost of employing the narrow morphology, to investigate the nature of the cue and the effects of damaged conspecifics on the development of the narrow morphology, and to determine how genetic variation in populations of barnacles influences their ability to respond to invasive predators.

Introduction

Inducible defenses are adaptations used by organisms to prevent herbivory and predation. This form of phenotypic plasticity occurs when an organism responds to a cue that indicates the presence of a threat to the future survival of that organism. The cue may originate from the consumer, or from damaged conspecifics (Baldwin and Schultz 1983, Leonard et al. 1999, Dalziel and Boulding 2005). The resulting defense may take the form of a chemical or morphological change in the organism (Baldwin and Schultz 1983, Lively 1986b). Although all traits are governed by the genetic makeup of an organism, phenotypically plastic traits are regulated by a genotype that codes for the flexibility to express a trait in the presence of a stimulus in the local environment. These plastic traits are induced as a defense against a direct threat to the fitness and survival of the organism.

The existence of phenotypic plasticity has been well documented in many organisms. Plants produce chemicals in their tissues to deter herbivory when mechanical damage to the leaves occurs (Baldwin and Schultz 1983). Chemicals produced within algal tissues deter herbivores from grazing and limit further damage (Van Alstyne 1988, Cronin, G. and Hay, M. E. 1996). The use of induced defenses is not limited to plants and algae. The induction of chemical defenses is used by toads to protect from predation (Benard and Fordyce 2003). In addition to chemical defenses, morphological changes are used by organisms to reduce the threat of predation. These include spines on bryozoans (Harvell 1984) and rotifers (Gilbert 1966), crests on *Daphnia* (Grant and Bayly 1981), increased thickness in the shells of mollusks

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(Trussell 1996, Leonard et al. 1999, Dalziel and Boulding 2005), and alternate body forms in barnacles (Lively 1986).

If inducible defenses are effective at deterring predation, one can ask why these mechanisms are not employed in the general body form of the organism. The intermittent use of inducible defenses is related to the costs associated with these defenses. Developing an inducible defense may limit the energy available for allocation to growth (Lively 1986a, Appleton and Palmer 1988, Harvell 1992, Trussell and Nicklin 2002) and reproduction (Grant and Bayly 1981, Lively 1986a, Harvell 1992). Behavioral changes (i.e. reduced foraging) as well as morphological changes can impact the fitness of organisms in larval and adult stages (Harvell 1992, Van Buskirk 2000, Benard and Fordyce 2003). The presence of predators is unpredictable and can vary spatially and temporally in an environment (Trussell 1996, Leonard et al. 1999), therefore it is not adaptive to display the trait and incur the costs of doing so at all times.

For marine organisms, this is often determined through a chemical cue that is carried in the water (Harvell 1986, Appleton and Palmer 1988, Leonard et al. 1999, Trussell and Nicklin 2002, Dalziel and Boulding 2005). These cues are reliable and beneficial to individuals as they do not need to be damaged by the predator in order to sense them (Harvell 1992). The reliability of the cue is the key to using an inducible defense. Using a cue that is an accurate indicator of future predation reduces unnecessary allocation of energy (Trussell and Nicklin 2002). In order for the

inducible defense to be useful, the cost to the organism must be outweighed by the benefit of protection from predation (Harvell 1992, Trussell and Nicklin 2002).

Recently many studies have shown the importance of phenotypic plasticity in benthic marine communities. This is an important interaction, as the ability of a prey species to defend from predation can play a significant role in community assemblages. Water-borne cues from a crab predator and damaged conspecifics lead to larger spines in the snail *Thais lamellosa* (Appleton and Palmer 1988). Two species of *Littorina* grow thicker shells in the presence of a crab predator (Trussell 1996, Dalziel and Boulding 2005). Increased byssal thread attachment and shell thickening have been documented in *Mytilus edulis* in response to predator cues (Leonard et al. 1999). The mussel, *Semimytilus algosus*, shows the ability to react to the specific type of threat posed by a particular predator (Caro and Castilla 2004). In both cases, increased shell thickness leads to higher survival because the predator is not able to easily gain access to the soft tissue and consume the mussel (Leonard et al. 1999). Colonial marine invertebrates also exhibit phenotypic plasticity. For example, bryozoans grow spines in the presence of nudibranch predators, which decreases the rate of predation on the bryozoan colony (Harvell 1984, Harvell 1986).

Barnacles are crustaceans belonging to the family Cirripedia. Due to their sessile lifestyle they must assume a defensive role in order to survive the various predators that they may encounter in the rocky intertidal habitat. When a cyprid larva settles on a substrate, it secretes a cement that attaches it head-first to the surface. As the larva

metamorphoses into an adult it grows plates that resemble a volcano. The plates provide protection from the abiotic and biotic stresses in the barnacles' habitat. In order to feed, barnacles extend their cirri into the water through an opening in the plates, the operculum. As vital a purpose as the operculum serves, it is also the one weakness in the barnacles' armor. Predators of barnacles usually gain access to their prey through the operculum (Barnes and Powell 1954, Palmer 1982). The ability to fortify the opercular plates has been effective in deterring predators (Palmer 1982), and their survival depends on the ability to close the plates of the operculum against outside threats.

In the ever changing evolutionary arms race, the defensive strategy of one species is readily counteracted by an offensive strategy of a determined predator (Smith and Palmer 1994). As barnacles gain the capacity to better defend themselves against attack, predators adapt new techniques to counter them. *Acanthina angelica* is a predatory snail that uses a spine along the margin of its shell to penetrate the defensive plates of the barnacle operculum (Lively 1986b). In response to this varied method of attack, *Chthamalus anisopoma* shows typical conic shape and an alternate bent form, in which the plates grow such that the aperture of the operculum is perpendicular to the substrate. As a result of the orientation of the operculum, barnacles with the bent form resist predation better than those exhibiting the conical form.

Increased exposure to *A. angelica* leads to increased numbers of the bent body form in *C. anisopoma* (Lively et al. 2000). This finding suggests that the alternate morphology of *C. anisopoma* is an inducible defensive trait. As *A. angelica* feeds on adult barnacles it passes over nearby juveniles that are not eaten due to their small size. The juveniles of *C. anisopoma* are exposed to the mucus of the predator. This provides them with the cue needed to trigger the inducible defense before they reach the optimal size for predation.

A comparable interaction has been observed in another species of the genus *Chthamalus*. *Chthamalus fissus* is preyed upon by the snail, *Mexacanthina lugubris*, which accesses its prey in a similar fashion to *A. angelica*. In addition to the bent form a third morphology has been identified (Wu 1982, Miller et al 1989). The operculum of the third morphology occurs in the same orientation as the conical form, but the aperture of the operculum is much narrower than the typical oval shape. Barnacles in the presence of high predator density develop the narrow operculum morphology in the field. In addition, barnacles settling in areas that are less likely to encounter the predatory snail develop the typical conic form (Jarrett 2008). The intensity of the cue appears to determine the response of the prey in deploying the induced defense.

The cost of an inducible defense can impact the overall fitness of an organism (Harvell 1986, Harvell 1992). In *C. anisopoma*, the bent morphology leads to lower growth rates and consequently decreased fecundity (Lively 1986a). Likewise, *C.*

fissus individuals that develop the narrow morphology do so at a cost. They exhibit lower growth rates than the oval morphology (Jarrett, in review). However, the narrow operculum morphology significantly reduces mortality due to predation. The oval morphs are twice as likely to be preyed upon than the narrow morphs (Jarrett 2008). This provides further evidence that the cost in fitness is outweighed by the benefit of survival due to the inducible defense.

It remains to be seen whether all barnacles possess the ability to grow a distinct morphology in reaction to the presence of a predator. Barnacles disperse their offspring through a planktonic larval stage that allows nauplii to be carried by currents from their point of origin (Alexander and Roughgarden 1996). Therefore it can be assumed that a population of barnacles in a specific area represents a heterogeneous genetic background. Yet it is important to consider the potential impact that genetic variation could have on an inducible defense. Lively et al. (2000) showed that all members of the *C. anisopoma* population studied are not capable of growing the bent morphology in the presence of the predatory cue. Therefore it is likely that the morphologic changes seen in *C. anisopoma* are driven at least in part by genetics. Other studies have shown population differences in organisms with planktonic larvae (Freeman and Byers 2006). It is possible that genetic variation plays an important role in the use of inducible defenses.

A transplant study of *C. fissus* suggests that the response to *M. lugubris* is not population specific. When *C. fissus* is transplanted from an area that is not heavily

populated by *M. lugubris* to a location where the predator is common, the barnacles

exhibit the narrow morphology. Similarly the barnacles transplanted from an area

with high predator density to an area of low predator density exhibit the oval

morphology (Jarrett 2008). This indicates that the trait is not an adaptive response of

genetically distinct barnacles in a select community, but is a plastic response. It is

unclear what role genetic variation plays in the inducible defenses of barnacles, and

more work is needed to fully understand the relationship.

The role that genetics plays in induced defenses becomes increasingly important as

the number of species populating new areas continues to rise (Ruiz et al 2000, Solow

and Costello 2004). Selection pressure can lead to a shift in the population that

favors individuals with the genetic makeup to defend themselves against an invasive

organism by developing the inducible defense. *M. edulis* from northern New England

that have not been previously exposed to *Hemigrapsus sanguineus* do not thicken

their shells when exposed to this invasive predator, whereas their southern

counterparts who have experienced this predator for 15 years show significant shell

thickening when exposed to it (Freeman and Byers 2006). It is possible that *M.

lugubris* may continue to extend its range northward due to changing conditions

associated with climate change. Will the barnacle population further north be

equipped to deal with increased predation pressure?

The purpose of this study is to provide further understanding of phenotypic plasticity

in operculum morphology of the barnacle *C. fissus*. This will assist in explaining the

results of previous field experiments with this barnacle. While field studies have

shown that the defense can be induced, it is not clear what causes the change in the

barnacle morphology. The goal of this study is to provide a better understanding of

the induced defensive response in *C. fissus*.

Methods

Subjects Used

The subject of this study is the acorn barnacle *C. fissus*. This barnacle is common

along the rocky coasts of California, USA and south into Baja California, Mexico

(Jarrett 2008). The predator in this study is the snail *M. lugubris*, which is known to

feed on the *C. fissus* during low tide. The herbivorous common turbin snail, *Tegula*

funebralis, was used as a treatment to determine the effects of a non-predatory snail

on barnacle operculum morphology. The control treatment consisted of *C. fissus*

alone, without exposure to any type of snail.

Study Site

Juveniles of the species *C. fissus* were collected in the field in La Jolla, California,

USA (32°48' N Lat., 115°16' W Long.). The collection area is a boulder field with a

tidal range of ~ -0.6 m to +2.4 m MLLW. Small rocks were collected from the

intertidal region representing the typical habitat of the barnacles ~1.5 m above

MLLW. The rocks collected contained juvenile barnacles, and varied in size, shape,

and barnacle population density.   The study site is at the northern limit of the

traditional range of *M. lugibris* (Booth 2003). Therefore it can be assumed that the

juveniles were not exposed to predatory cues from *M. lugibris* prior to the laboratory experiment.

Barnacle and Snail Maintenance

The juvenile barnacles attached to rocks were randomly assigned to a treatment: predator, herbivore, or control. At the start of the experiment, each rock was tagged with a number for identification purposes and a scale for measurement purposes. The number tags and scales were affixed with cyanoacrylate to an area on the rock clear of barnacles. Before introduction to the assigned treatment, barnacles on each rock were photographed with a digital camera.

Barnacles were kept in separate containers, based on their treatment, and held at room temperature (~22° Celsius). The containers were filled with filtered sea water (collected from Avery Point, Groton, CT) and aerated. The water was maintained at approximately 30 ppt salinity, and the barnacles were fed a combination of *Skeletonema costatum* and *Isochrysis galbana* ad libitum. Water in the containers was changed every two to four days.

The two snail species were kept in separate aerated aquaria filled with man-made sea water, using deionized water and Instant Ocean. The predatory snails (*M. lugubris*) were fed stock barnacles (*Semibalanus balanoides*) collected from Long Island Sound. The herbivorous snails (*T. funebralis*) were fed *Ulva sp.* collected from Long Island Sound. Both snails were continuously allowed access to food in their aquaria.

Exposure Treatments

The barnacles were exposed to their treatments daily for 27 days in a 37 day period.

The rocks were removed from their holding containers and placed on a surface out of

the water to simulate low tide. Predator and herbivore exposures consisted of

covering the barnacles on the rocks with snails for up to three hours. Control

barnacles were exposed to air and did not have any snails placed on them. During the

exposure period the snails were kept on the rocks. Snails that moved were gently

replaced onto the rocks. After exposure, the rocks were returned to their respective

containers.

Photographs of the rocks were taken at the start and end of the experiment using a

digital camera. The operculum length, operculum width, and basal diameter of the

study barnacles was measured using Sigma Scan Pro 5^{TM} software. Basal diameter

was measured through the center of the operculum along the long axis. The smallest,

and presumably youngest, barnacles on each rock were measured. The measurements

were compared between the photographs from the start (1 August 2007) and end (23

January 2008) of the experiment to determine how the morphology of the barnacles

changed as they grew.

Statistical Analysis

Regression analyses were used to determine the relationship between operculum

width and operculum length for the control and each treatment. Analysis of

covariance was used to compare barnacle operculum width as a function of treatment

with operculum length as a covariate. Growth rates of barnacles in the three treatments were compared using ANOVA. Tukey's multiple comparison test was used to compare differences in growth between treatments.

Results

August 2007 Measurements

Photographs taken on 1 August 2007 were analyzed. Regression analysis of the relationship between operculum length and operculum width shows a positive correlation between these parameters (Figure 1). This relationship is typical of barnacle morphology and is seen in all three treatments.
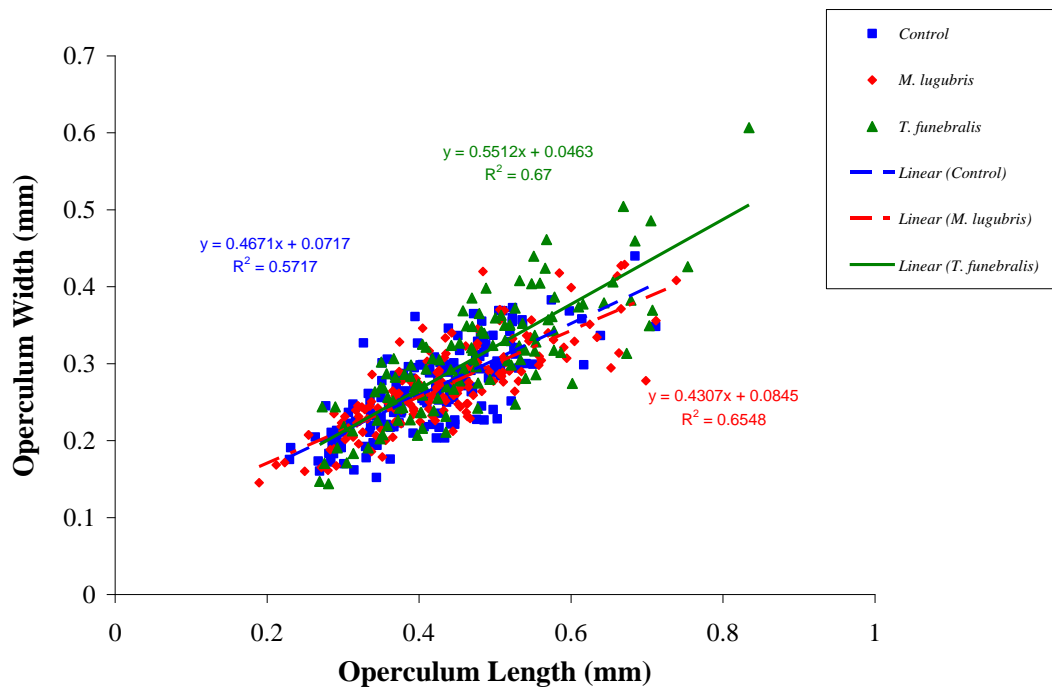

Figure 1. Linear regression of operculum width as a function of operculum length for juvenile *C. fissus* in all three treatments on 1 August 2007 (N=119-172).

There was no significant difference in the operculum width of the barnacles in the

control and *M. lugubris* treatments (p = 0.70556). There was a significant difference

in the operculum width of the barnacles in the *T. funebralis* treatment when compared

with the barnacles in both the control (p = 0.01) and *M. lugubris* treatments (p =

0.0009). Juveniles in the *T. funebralis* treatment had the largest adjusted mean

operculum width, 0.29017 mm, compared to the juveniles in the other two treatments

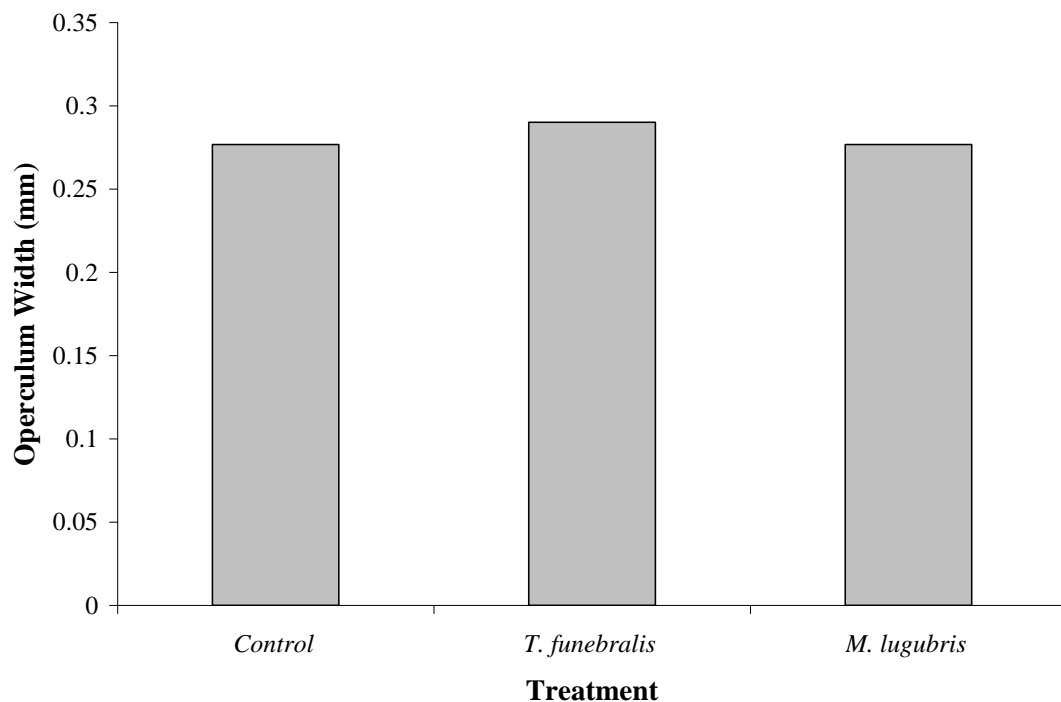(control = 0.27672 mm; *M. lugubirs* = 0.27337 mm; Figure 2).

Figure 2. Adjusted mean operculum width of juvenile *C. fissus* in all three treatments

on 1 August 2007 (N=119-172).

January 2008 Measurements

Photographs taken on 23 January 2008 were analyzed. Regression analysis of the relationship between operculum width and operculum length continued to show a positive correlation. A notable difference was seen in the height of the regression line for the barnacles in the *M. lugubris* treatment (Figure 3). The operculum width for barnacles in this treatment did not correspond with barnacles of similar operculum length in the control and *T. funebralis* treatments.
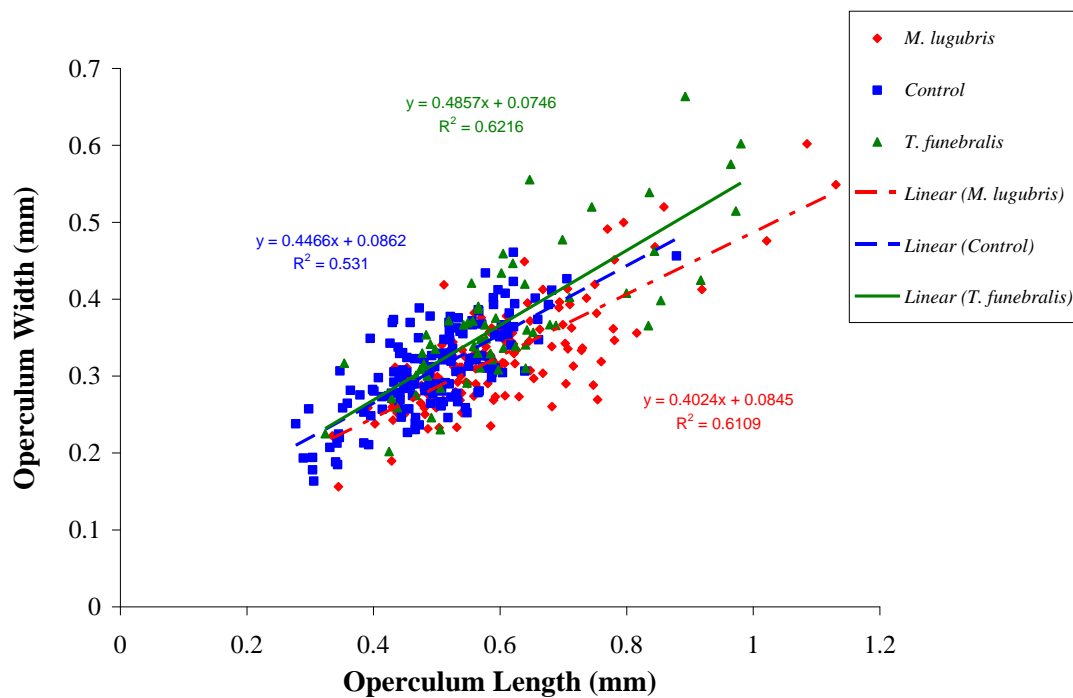

Figure 3. Linear regression of operculum width as a function of operculum length for juvenile *C. fissus* in all three treatments on 23 January 2008 (N=62-157).

The operculum width of barnacles exposed to *M. lugubris* was significantly smaller than the operculum width of the barnacles in both the control (p < 0.00001) and *T. funebralis* (p < 0.00001) treatments. There adjusted mean operculum width did not

differ between the control barnacles and the barnacles exposed to *T. funebralis* (p = 0.13). Juveniles in the *M. lugubris* treatment had the smallest adjusted mean operculum width, 0.30634 mm, compared to the juveniles in the other two treatments (control = 0.333 mm; *T. funebralis* = 0.34679 mm; Figure 4).
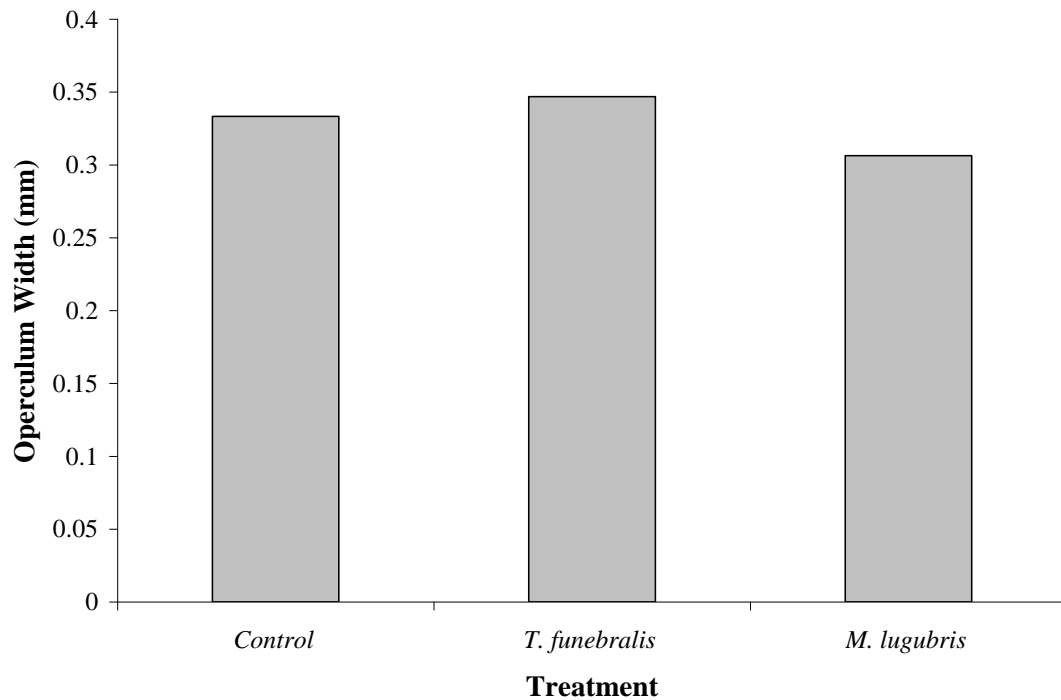

Figure 4. Adjusted mean operculum width of juvenile *C. fissus* in all three treatments on 23 January 2008 (N=62-157).

Comparisons of Change in Morphology

The change in operculum length from 1 August 2007 to 23 January 2008 varied among the treatments (Table 1). The mean growth of operculum length of the barnacles in the control treatment was 0.07558 mm ± 0.01113. This was significantly

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less than both the *T. funebralis* (mean 0.1873 mm $\pm$ 0.03977; p < 0.01) and *M. lugubris* barnacles (0.1506 mm $\pm$ 0.01482; p < 0.05; Figure 5).

Table 1. Results of ANOVA for differences in change in operculum length for *C. fissus* among the three treatments.

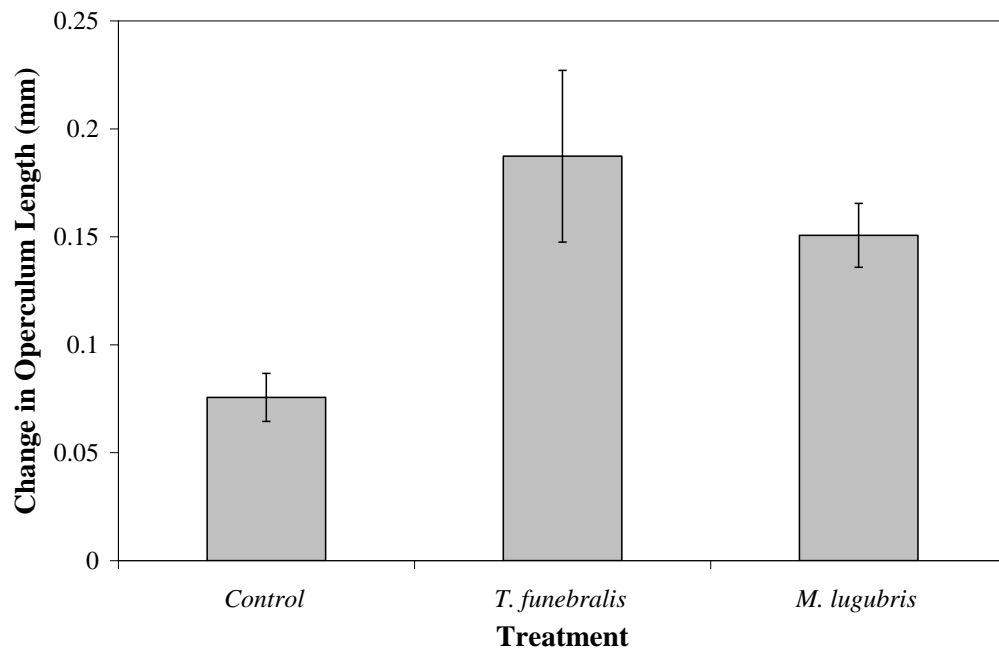|	SS	df	MS	F	P
Treatment	0.06328	2	0.03164	6.759	0.0042
Residual	0.1264	27	0.004681		
Total	0.1897	29			

Figure 5. Mean change in mm $\pm$ SE of operculum length for juvenile *C. fissus* in all three treatments from 1 August 2007 to 23 January 2008.

The change in operculum width differed among the three treatments (Table 2). The

mean change in the operculum width of the control barnacles was 0.03788 mm $\pm$

0.007140. This was not significantly different than the change in the operculum

width in the *M. lugubris* barnacles (mean 0.04351 mm $\pm$ 0.006965; $p > 0.05$). The

mean growth of the operculum of the barnacles in the *T. funebralis* treatment was

0.08744 mm $\pm$ 0.01358. This was significantly larger than either the control ($p <$

0.01) or *M. lugubris* treatments ($p < 0.01$).

Table 2. Results of ANOVA for differences in change in operculum width for *C.

fissus* among the three treatments.

	SS	df	MS	F	P
Treatment	0.01300	2	0.006498	8.250	0.0016
Residual	0.02126	27	0.0007876		
Total	0.03426	29			

Measurements of operculum width growth showed a different relationship than

operculum length. While the barnacles exposed to *T. funebralis* still showed a greater

change, the barnacles in the control and *M. lugubris* treatments showed similar

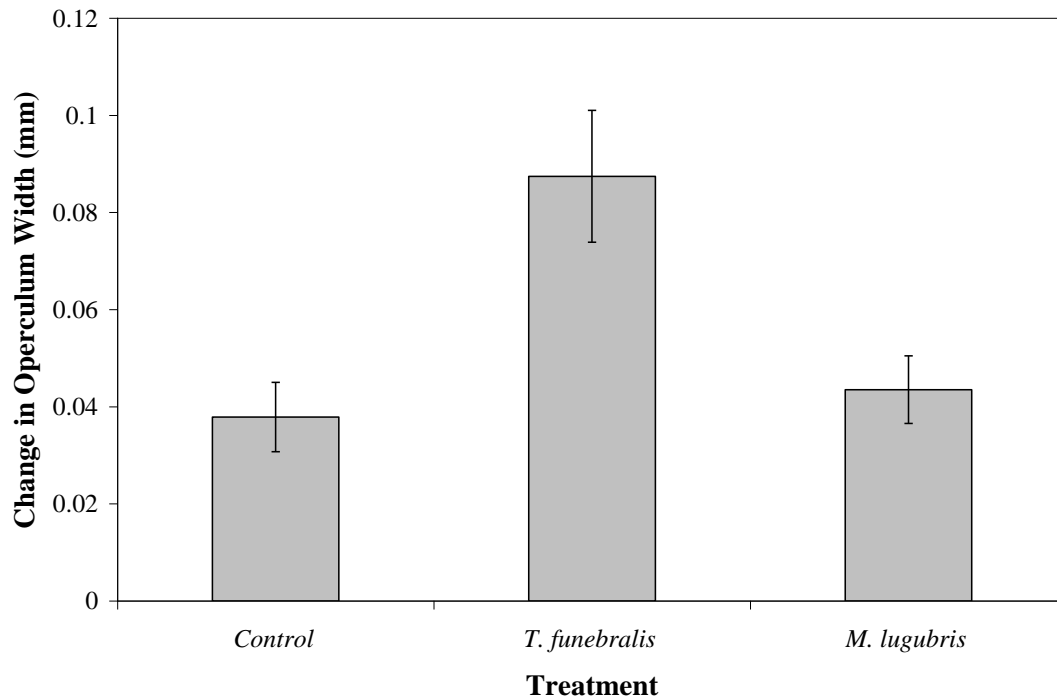change in operculum widths (Figure 6).

Figure 6. Mean change in mm ± SE of operculum width for juvenile *C. fissus* in all three treatments from 1 August 2007 to 23 January 2008.

The change of the basal diameter in barnacles from all three treatments was similar (Figure 7, Table 3). The mean growth of basal diameter in the control barnacles was 0.3327 mm ± 0.05078. The mean growth of the basal diameter in the *T. funebralis* barnacles was 0.6531 mm ± 0.1623. The mean growth of the basal diameter in the *M. lugubris* barnacles was 0.4920 mm ± 0.08957. The mean growth of the basal diameter was not significantly different among the three treatments (p = 0.1051).
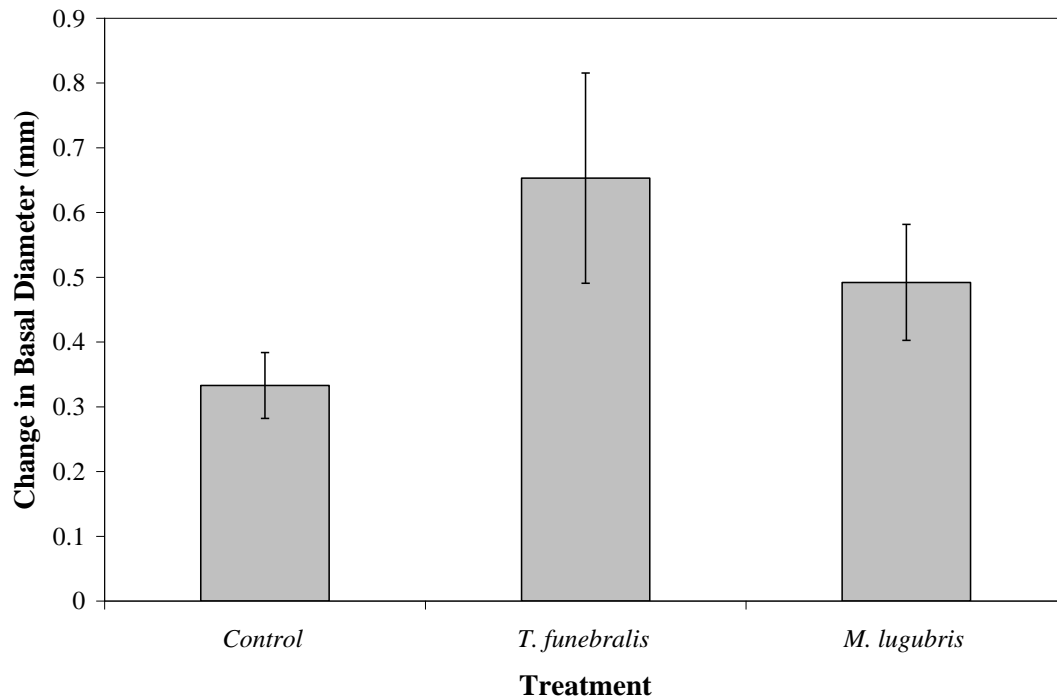
Figure 7. Mean change in mm $\pm$ SE of basal diameter for juvenile *C. fissus* in all three treatments from 1 August 2007 to 23 January 2008.

Table 3. Results of ANOVA for differences in change in basal diameter for *C. fissus* among the three treatments.

	SS	df	MS	F	P
Treatment	0.01300	2	0.006498	2.451	0.1051
Residual	0.02126	27	0.0007876		
Total	0.03426	29			

Discussion

Change in Morphology from August 2007 to January 2008

The presence of a predator is known to induce defenses in many marine organisms

(Harvell 1984, Trussell 1996, Leonard et al 1999, Dalziel and Boulding 2005). The

results of this study suggest that the operculum width of *C. fissus* is a trait that can

vary in response to cues from a common predator.   The mean operculum width of the

juvenile barnacles exposed to the predator was significantly less at the end of the

experiment than the operculum widths of the barnacles in the other two treatments

(control and herbivore). This supports the findings of field studies which indicate that

the morphology of the barnacle operculum is a phenotypically plastic trait (Lively

1986b, Jarrett 2008).

At the start of the experiment, barnacles in the *T. funebralis* treatment had wider

operculum openings than barnacles in both the control and *M. lugubris* treatments,

which did not differ from each other. If the predatory environmental cue did not

affect barnacle shell morphology, one would predict that similar comparative widths

would be measured at the end of the experiment. This, however, was not the case.

As the mean operculum width of the control and herbivore barnacles continued to

increase, the barnacles exposed to *M. lugubris* did not keep up. At the end of the

experiment, the mean operculum width of barnacles in the *M. lugubris* treatment was

significantly less than the other two treatments. Similar results were seen in field

studies of *C. fissus* (Jarrett 2008, Jarrett in review), and these findings provide further

evidence that this change in morphology is directly linked to the presence of *M. lugubris*.

Examination of the regression lines from August and January demonstrates this difference. In August, the data points and trendlines were overlapping. In January, the control and *T. funebralis* treatments had regression lines that were higher than the predator treatment. As the operculum length of the barnacles got larger, the operculum width of the barnacles in the predator treatment increased more slowly compared to barnacles in the control and herbivore treatments. Although there was still a positive correlation in the *M. lugubris* treatment, the opercula were narrower than those of barnacles in the control and *T. funebralis* treatment. These results were expected due to the exposure of those juveniles to the predatory cue.

Comparisons of Change in Morphology

Even though the operculum length of the barnacles showed similar growth in the *T. funebralis* and *M. lugubris* treatments, the growth in the operculum width was less in the *M. lugubris* treatment than the *T. funebralis* treatment. The ratio of change of the operculum length to operculum width was two to one for the barnacles in the control and *T. funebralis* treatments, while the barnacles in the *M. lugubris* treatment had a ratio of four to one. This is consistent with previous findings for growth rates of *C. fissus* when under predator exposure and predator exclusion conditions (Jarrett 2008). These data indicate that exposure to the predator causes the width of the opercula of juvenile *C. fissus* to grow at a slower rate.

Unexpected differences in overall growth of the barnacles may be attributed to population densities within each treatment. There were many more barnacles in the control treatment than in the *T. funebralis* treatment. Decreased competition for food may have allowed the barnacles in the *T. funebralis* treatment to grow more than those in the control treatment. In addition, fewer numbers of the barnacles in the *T. funebralis* treatment could have lead to measurements of barnacles that were older due to lack of smaller individuals on the rocks. This may explain the differences in overall size and growth seen in the *T. funebralis* treatment as compared to the control treatment.

Growth in basal diameter did not vary significantly among the three treatments. This may be due to the fact that the barnacles studied were juveniles. If the barnacles continued to grow I predict that differences in basal diameter would arise based on operculum morphology. The barnacles with the narrow operculum exhibit lower growth rates than their oval operculum counterparts (Jarrett in review). It is likely that the narrow operculum leads to reduced feeding capability and consequently a decrease in growth rate. If this is true, I would expect that as the barnacles mature the narrow operculum morphs would show a decrease in the growth of their basal diameter.

Conclusion

This study provides a better understanding of the change in shell morphology as a predator induced defense in the barnacle *C. fissus*. The results support previous field

work that indicates a link between a narrow operculum and exposure to the predatory

snail, *M. lugubris*. The demonstration of this in a controlled laboratory setting

excludes all other environmental factors, such as wave intensity and other organisms,

as possible causes for the induced trait.

If the narrow operculum morphology is successful in deterring predation, why doesn't

every individual express this phenotype? As with any inducible defense, there is a

cost associated with using it. In order for the defense to be beneficial, the advantages

must outweigh the disadvantages for the individual. In the case of *C. fissus*, a narrow

operculum may limit the ability of the barnacle to feed. This may in turn reduce their

growth rate and consequently their fecundity may be reduced. In the face of certain

death from predation these costs are readily assumed in order to ensure survival.

However, when the threat of predation is not present, there is no need to assume costs

that would lead to reduced individual success. Further investigation is needed to

determine the costs that individuals incur due to the expression of the narrow

morphology.

Although this study provides some insight to the workings of the predator induced

trait in *C. fissus*, many questions still remain. The exact nature of the exposure to the

predatory cue that is needed to induce the trait is unknown. This study does not

provide information on the amount of exposure or the age of the juveniles during the

exposure period that would be needed to induce a change in morphology.

In addition to chemical cues from the predator, cues from damaged conspecifics have also been shown to influence the expression of a plastic trait (Appleton and Palmer 1998, Leonard et al 1999, Trussell and Nicklin 2002). It is possible that a combination of cues from *M. lugubris* and damaged *C. fissus* could induce a greater expression of the narrow morphology. Perhaps the presence of both cues would induce the more costly bent morphology as a defense against a heightened threat.

The role of genetics in the barnacles' ability to respond to the predatory cue also remains to be seen. Are some individuals more genetically fit to respond with a change in morphology? A study of *C. anisipoma* found that every individual in a population was not capable of inducing the alternate body form (Lively et al 2000). It is possible that populations of barnacles could respond differently to exposure to *M. lugubris* based on their genetic makeup. Indeed, studies have shown that the history of exposure to a predator influences the ability of individuals within a population to respond with an inducible defense (Freeman and Byers 2006).

This leads to questions about the ability of barnacles that have not previously been exposed to *M. lugubris* to develop a narrow operculum. In southern California there are no physical barriers to the dispersal of the planktonic larvae of the barnacles. However different factors, such as seamounts and currents, may prevent larval dispersal to the northward. Data collected as part of an intertidal census show that *M. lugubris* is extending its range northward along the California coast (Booth 2003). Studies of *C. fissus* populations from points north of La Jolla, CA, where *M. lugubris*

is not commonly found, are needed to determine if there is a disparity in the ability of barnacles from different populations to express an alternate shell morphology in response to the threat of predation.

This study provides support to a growing list of marine organisms that exhibit predator-induced phenotypically plastic traits. Many questions regarding the exact nature of the inducible defense remain for future study.

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