Front Formation in Starfish

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Abstract

Consumer fronts are a well-known and often devastating occurrence that can alter entire ecosystems. One organism that is known to form such fronts is the common starfish, *Asterias rubens*, which is an important predator of the blue mussel, *Mytilus edulis*, and could have a huge impact on commercial mussel cultivation. One theory for how these fronts might form is through density-dependent movement, where starfish move fast on bare substrate, and slow down as they reach the mussel bed. However, this theory is purely based on field observations of starfish behaviour, and until now has never been experimentally tested. To test this theory we first performed mesocosm experiments, designed to study the movement of starfish under different circumstances. Using the results of these experiments we then developed an individual-based model designed to simulate the movements of starfish on or near a mussel bed. Our simulations show that it is possible for starfish to form fronts through density-dependent movement alone, without the need for additional outside factors. Due to climate change, the impact of *A. rubens* on mussel seedbeds is likely to increase, as rising winter temperatures lengthen the period *A. rubens* is active. This insight into how starfish form feeding fronts thus becomes ever more important for the conservation of mussel beds for both ecological and commercial purposes.

Introduction

Consumer fronts are a well-known and often devastating occurrence that can alter entire ecosystems. Such fronts are triggered by universal mechanisms: top-down control is increased beyond prey carrying capacity, and resource-dependent movement leads consumers to aggregate along the edge of the prey population (Silliman et al. 2013). The front then moves through the system as a self-propagating wave, which are reinforced via over-exploitation and density-dependent feedback. Given enough space, these fronts can quickly decimate the entire area and even lead to regime shifts. For instance, sea urchins can reduce an entire sea grass meadow

to barren seabed, and swarms of locusts can be so devastating that they're even described in the Bible as a punishment from God.

One type of organism that is known to form consumer fronts are starfish (Witman et al. 2003). The common starfish, *Asterias rubens*, is an important predator of the blue mussel, *Mytilus edulis*, especially young ones (García 2015). Thus, the formation of fronts could have a huge impact on commercial mussel cultivation and fisheries, potentially eliminating entire seedbeds before they have a chance to grow to commercial size.

Unfortunately, due to climate change, the impact of *A. rubens* on mussel seedbeds may increase. Currently, they are not very active in winter, since they are poikilotherms. However, climate change could likely increase the occurrence of milder winters, thus lengthening the period *A. rubens* is active (García 2015). Thus, mussel seedbeds could increasingly be eliminated before they grow big enough to attain size refuge. Because of this likely increased impact on both aquaculture and biodiversity, it's important to know how starfish-fronts form. This knowledge could hopefully be used to protect mussel beds from over-predation, preserving them for both economic and ecological purposes.
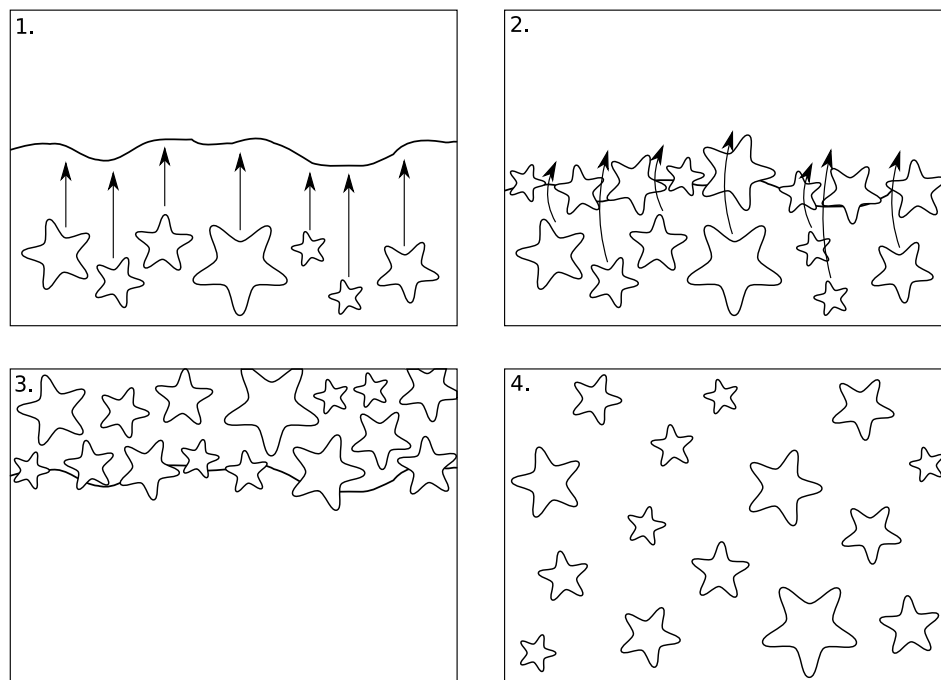

Figure 1: The formation of a front. 1) Starfish move quickly until they reach a mussel bed. 2) Individuals 'leap-frog' over each other, forming a front. 3) The front moves across the bed, eating all the mussels. 4) Once all the mussels are gone, the front dissipates.

One theory for how these fronts might form (Silliman et al. 2013) can be found in **figure 1**. Front formation starts when an aggregation of starfish forms near a mussel bed (**Figure 1.1**). The starfish move fast on bare substrate, but slow down when they encounter the edge of the mussel bed (**Figure 1.2**). The ones behind then climb over the ones in front to also reach the mussels, forming a front on the edge of the mussel bed. This process continues across the mussel bed, until all the mussels have been consumed (**Figure 1.3**). Finally, the front breaks up as movement speed increases on the now bare substrate (**Figure 1.4**).

However, this theory is based on field observations of starfish behaviour, and has not been experimentally tested. Therefore this project aims to conduct behavioural experiments in the lab, and subsequently develop a model in which this behaviour might be reproduced. To do this, we need more information on the movement of starfish under different circumstances.

First of all, we want to know whether starfish can detect their prey from a distance, and if so, from how far away. This influences at what distance starfish will switch from random movement to a directed movement toward the mussel bed. We also want to know their movement speed when moving towards a mussel bed. These to factors together influence whether the first step in the process will occur.

Second, we want to know if starfish have a particular preference for clustered or solitary mussels. A preference for either could influence how much starfish will spread out on the mussel bed, since the amount of clustering differs across the bed. If they have a strong preference, they may spread out across the bed, instead of forming a front.

Lastly, we want to know if starfish have a tendency to aggregate. If they do, they would be more likely to stay close together and form a front. But it would also mean that step 4 is less likely to occur, since they would stay together as a group rather than separate and spread out.

To acquire this data, we will perform a series of mesocosm experiments, which we will record using time-lapse photography. We will then analyse this footage to collect data we can use to answer our research questions. Using both the collected data and data from existing literature, we will develop an individual-based model. In this model we will attempt to replicate front formation by tuning different parameters. This way we can get an idea whether this process could occur in their natural environment, and under what circumstances.

Methods

This project consists of two phases, where the results of the first phase are used in the second; therefore, this section is set up as follows. First, a description of the

methods for the mesocosm experiments. Second, the results of these experiments. Third, a description of the model and the simulations run. The final results of these simulations are covered in their own section.

Mesocosm Experiments
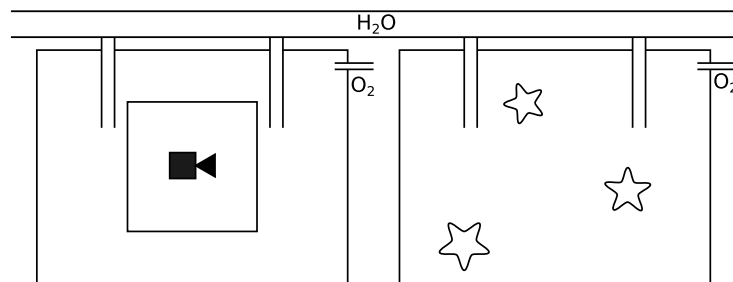
Experimental Setup

Figure 2: Experimental setup for mesocosm experiments

We used two plexiglass tanks, one to keep the starfish and one to perform experiments. The tanks were continually supplied with unfiltered seawater from the nearby Eastern Scheldt. The experimental tank contained a raised platform of 59 cm x 59 cm, on which most of the experiments were performed. A camera was mounted above the tank. The tank were the starfish where kept was supplied with extra oxygen. Starfish were by-catch from the company next door, who pick up plenty of starfish when harvesting their mussels. Mussels were supplied by Wageningen Marine Research, and kept in a tank outside.

First the ability of starfish to detect prey at a distance was tested. This was done by placing some mussels in the middle of four starfish. If the starfish moved towards the mussels, rather than random directions, this would indicate an ability to detect prey. The distance of the starfish to the mussels was varied somewhat to get an idea from what distance they might be able to detect their prey.

Next was their preference for size of mussel clusters. For this, clusters of 1, 8 and 32 mussels were placed on the platform, as well as several starfish. At first there were 2 clusters of each size and 3 starfish. This was later changed to 3 groups of each size and 6 starfish. At the same time the individual mussels were replaced with clusters of 2, to reduce their movement. Here we simply observed which clusters starfish chose to feed on.

Lastly, the starfish's preference for congregating with conspecifics was tested. Unfortunately, these experiments didn't seem to work very well, because the starfish seemed very keen to move toward one end of the tank. The reasons for this are still unclear. Instead, we removed the platform and placed a large amount

of mussels at one end of the tank and starfish at varying distances. This was meant to see if the starfish did indeed form a front under experimental conditions.

For the first two rounds of experiments, the starfish were kept hungry to ensure their interest in mussels. They were then fed before the third round of experiments to remove the element of hunger. Since starfish can resort to cannibalism when they get too hungry, the results might otherwise have been influenced by their attempts to eat each other.

Experiments lasted one hour and were recorded with one of two cameras, both of which took a picture every ten seconds:

- A Canon Powershot D30, using a time-lapse script (McCrossan et al. 2013) for the Canon Hack Development Kit (CHDK Development Team 2015).

- A Browning Spec Ops Platinum FHD trail camera, with a built-in time-lapse function.

Image Analysis

Image analysis was done in Fiji (Schindelin et al. 2012), a distribution of ImageJ (Schindelin et al. 2015), including the Manual Tracking plug-in (Cordeliéres 2006, Cordeliéres and White 2005).

For the first round of experiments, the locations of all starfish were tracked, as well as the original location of the group of mussels and any individual mussels that separated from the group and seemed relevant to the experiment. Tracking was done in micrometers per second, using the edge of the platform to calibrate distances.

For the second round, only the starfish were tracked. For the location of the mussels, a binary image was produced for each experiment, where the areas covered by mussels were coloured black, and the background coloured white.

For the final round of experiments, only the starfish were tracked.

Unfortunately, only the second round of experiments yielded any useful data for the development of the model, thus only this data was further analysed.

An R-script was developed to analyse the area of mussel cover under each starfish during the course of the experiment, based on the Matlab script used by van de Koppel et al. (2008). In addition to the change from Matlab to R, the following changes were made to the script:

The original script uses a mussel radius and eight additional radii which are simply multiplication factors of the mussel radius. Mussel cover under these eight additional radii is calculated by the script. The modified script uses one radius for the core of the starfish, later used to determine whether the starfish was on a clump of mussels. Like the original script, it uses 8 additional radii, but instead

of multiplying the core radius, these radii are absolute numbers based on typical starfish sizes. The mussel cover under all these radii is calculated, not just the additional ones.

Because the modified script was used to analyse black-and-white images instead of color, the part of the script that analysed color also had to be modified to analyse grayscale images. Once all the tracks had been analysed, another R-script was used to collect the data into one csv-file. A third script was used to plot the movement speeds of starfish against the mean mussel cover of radius 2 through 9.
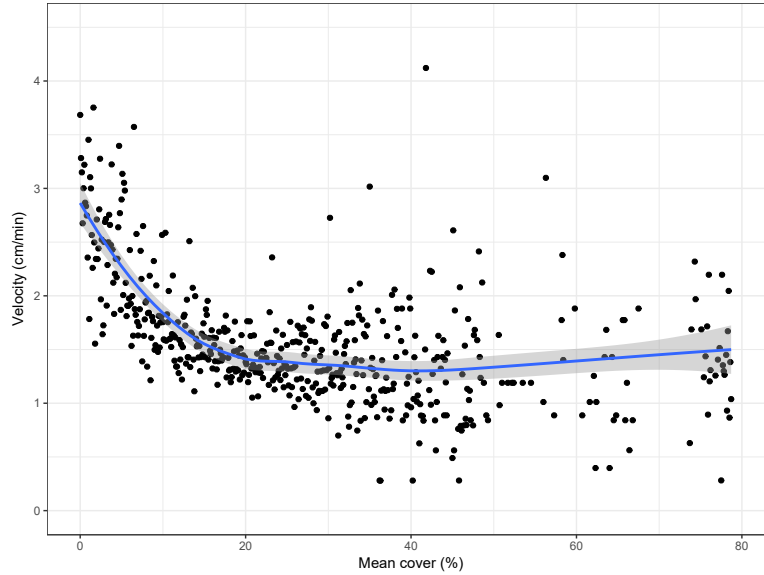
Behavioural Results

Figure 3: Starfish movement velocity plotted against mussel cover

As seen in **figure 3**, starfish speed decreases approximately logarithmically with mussel cover, with no indication of any influence besides mussel cover directly under the starfish. Thus a general linear model was fitted using a gamma distribution. From this model the intercept was extracted, indicating the base speed, and the coefficient for cover, indicating the change in speed with an increase in cover.

$$f(x, \beta) = \frac{1}{\beta \cdot e^{-x/\beta}} \tag{1a}$$

$$\beta = \frac{1}{(P_1 \cdot cover + P_2)} \tag{1b}$$

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Distance covered per minute follows an exponential distribution (1a), where the scale parameter β is a function of mussel cover under the starfish (1b). Here, P_2 is the base speed and P_1 is the change in speed with mussel cover.

Our analysis gives us a P_1 of 1.83 and a P_2 of 0.30. When we plug these values into equation (1b), we get the following formula for β (**Figure 4**):
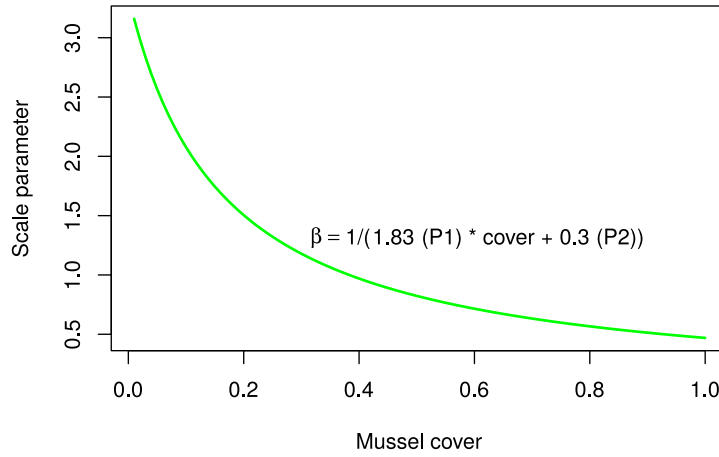
$$\beta = \frac{1}{1.83 \cdot cover + 0.30}$$

Figure 4: Scale-parameter β plotted against mussel cover

Modelling

The Model

The model simulates starfish movement on and near a mussel bed. It is a random-walk model where stepsize follows an exponential gamma-distribution, based on the amount of mussel cover under each starfish. Simulations take place in an arena, the top 3/4 of which are covered by mussels. Starfish are randomly distributed around the bottom quarter. Starfish then move around the arena eating mussels, while the mussels remain stationary. Several aspects of the model can be changed to test different assumptions. The measure of slowdown based on mussel cover can be changed. Starfish chemotaxis can be turned on or off. Time needed to capture and consume a mussel can be changed. And mussels can be spread

around the arena randomly or form a clustered pattern. The inner workings of the model are described below.

The model was made in R (R Core Team 2015). It is largely based on the model developed by van de Koppel et al. (2008), which simulates the formation of self-organising patterns in mussel beds. This model has been adapted to simulate the movement of starfish instead of mussels. Unlike the mussels in the original model, starfish have only two P-values, one for the base speed and one to reduce speed with increasing mussel density. For each starfish, the model first determines mussel cover under the starfish, then determines movement speed based on equation (1).

Starfish direction can be either random or directional. Random direction simulates starfish that cannot detect prey, directional movement simulates starfish who can detect their prey. If prey detection is turned off, direction is determined by generating a random movement angle. If prey detection is turned on, direction is determined by first setting it towards the nearest mussel, then adding noise if mussel cover is 0. This noise increases with distance, to simulate chemotaxis. Starfish start eating a mussel once it's covered by the center of the starfish. Starfish are given a handling time once they start eating a mussel. During this time, the starfish stays in the location where it started eating. The mussel is immediately removed by setting its location far outside the arena, to prevent other starfish from interacting with it.

At the start of the simulation, mussels are either randomly placed in the top three-quarters of the arena, or mussel locations can be loaded from a previous simulation. If mussels are randomly placed, they can either be left to form natural patterns before adding starfish, or starfish can be added immediately, depending on the given parameters. The positions of mussels can also be saved for later use before adding starfish to the simulation. In this manner, a simulation can be run with the mussels either homogeneously spread or clustered.

Generating Output

Simulations were run using the parameters in **table 1**. P_2 was set to 1 to increase the overall speed of the starfish. This gives the starfish from our experiments a P_1 of 6. Each combination of parameters was run 5 times. Each time, the amount of front formation was given a value between 0 and 1 in steps of 0.25, where 0 was no front formation and 1 was a clearly defined, dense front (**Figure 5**). This was done instead of just front or no front, first because of the difficulty of determining where exactly the line is between front or no front, and second to more clearly see the influence of different parameters on front formation.

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Parameter	Value(s)
Starfish size (cm)	1.5
Starfish core (cm)	0.5
P_2	1
Handling time (minutes)	0, 1, 5, 10, 30, 60
P_1^*	1, **5**, **10**, 50, 100, 150
Clustered mussels	yes, no
Chemotaxis	yes, no

*Runs with handling time 0 use all P_1 values, runs with handling time >0 use only P_1 values in bold.

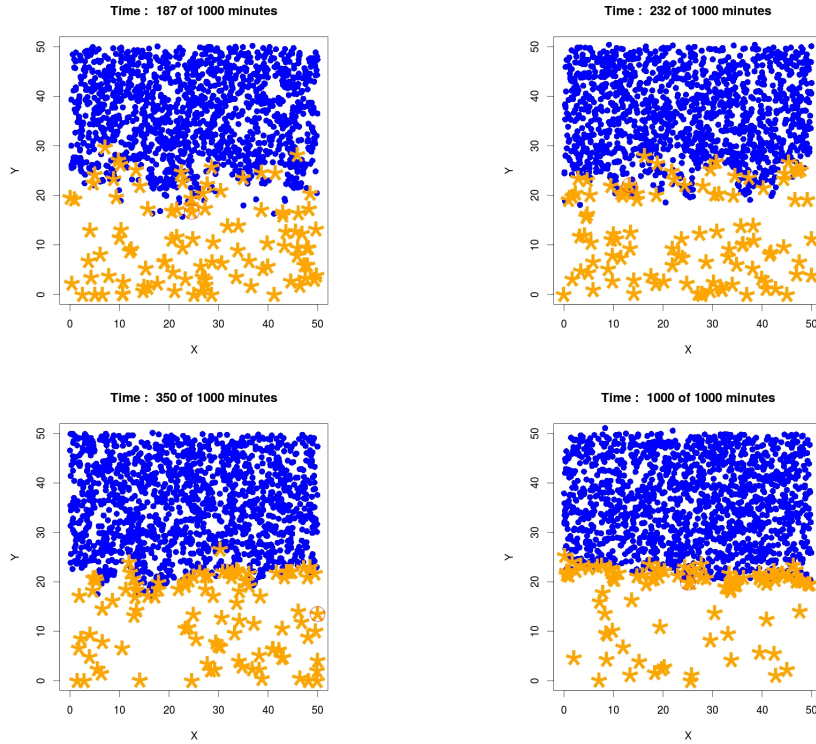**Table 1:** Parameters used in the model

Figure 5: Examples of different amounts of front formation. From top left to bottom right: 0.25, 0.50, 0.75, 1

Data Analysis

For each combination of parameters, the amount of front formation of all 5 runs was averaged, giving us the measure of front formation for each combination.

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These values were plotted to determine the influence of the different parameters on front formation.

Results

The value of P_1 is clearly the most significant factor influencing front formation, with higher values slowing the starfish down more when mussel cover increases and making the formation of a front more likely. The addition of chemotaxis increases this effect, as does a longer handling time. Clustering of mussels, on the other hand, inhibit the formation of fronts, especially in the absence of chemotaxis.
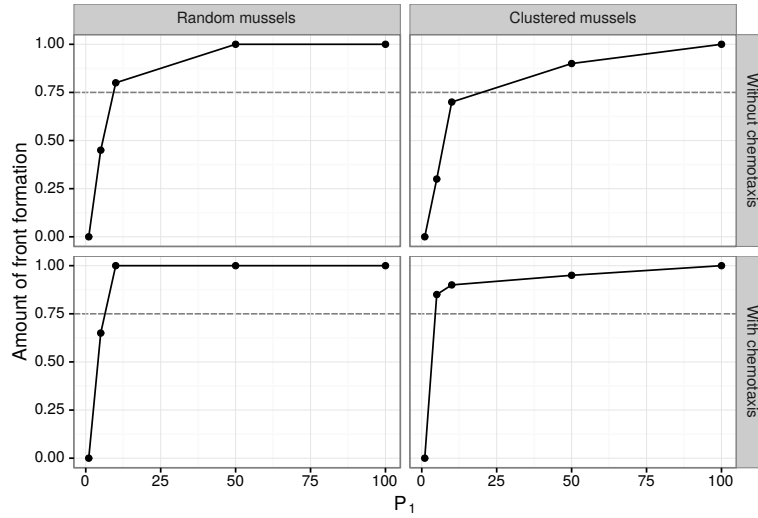

Figure 6: Front formation plotted against P_1, with handling time 0, where 0 means no front formation and 1 means a very dense front

In **figure 6** front formation is plotted against P_1, with handling time=0, with homogeneous or clustered mussels and with or without mussel detection. P_1=150 has been left out of the graph, since front formation always maxed out at P_1=100. We see an approximately logarithmic increase in front formation with increasing P_1. Front formation is inhibited my mussel clustering but stimulated by the addition of prey detection.

In **figure 7** we look at the effect of handling time on front formation. Because a P_1 of 6 only triggered full front formation in 1 out of 4 cases, we concluded that the addition of a handling time was necessary. We chose to use P_1's of 5 and 10 rather than just 6 to account for differences with movement speed of starfish in
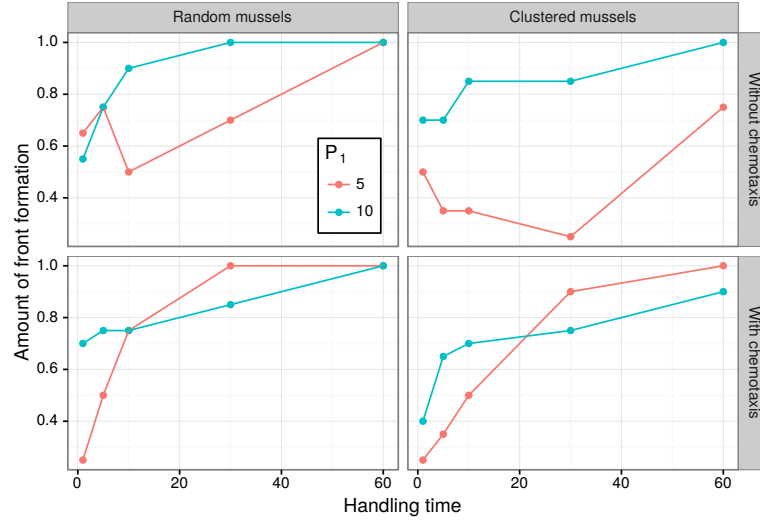
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Figure 7: Front formation plotted against handling time, for P_1=5 and P_1=10

the wild. In this case we see a pretty erratic pattern of front formation, especially when mussels are clustered and starfish can't detect prey.
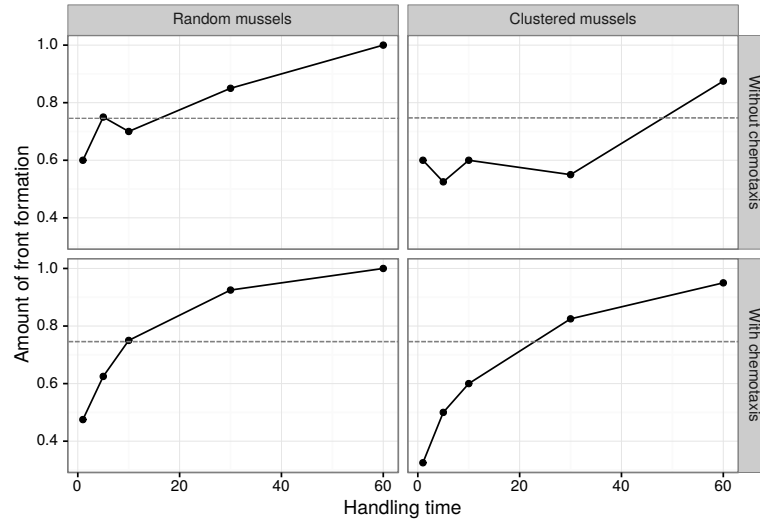

Figure 8: Front formation plotted against handling time, for P_1=5 and P_1=10 combined

Since it seems reasonable to assume that starfish in the wild would have a P_1 between 5 and 10, we also plotted the average of the two values. This takes care of most of the erratic trends we see for the individual values. We again see something akin to a logarithmic increase with handling time, with similar influences of clustering and prey detection.

Discussion

Do starfish form fronts on mussel beds through density dependent movement? From our experiments it's clear that starfish exhibit density-dependent movement, slowing down from their base speed when they encounter mussels, and slowing down more as mussel cover increases. But is this enough? Density-dependent movement clearly has significant influence on front formation in starfish on mussel beds. Front formation is also influenced by clustering of the mussels in the bed and the ability of starfish to detect their prey. However, patterns tend to be unclear for simulations with clustered mussels but no prey detection. We hypothesize that this is due to the influence of random chance on the movement direction of starfish. Prey detection makes the movement more directional, reducing the influence of chance, while clustering means that starfish are more likely to end up in a place with no mussel cover, increasing their speed and thus their chances of ending up far away from other starfish. All of this together explains why trends for simulations with clustered mussels and no prey detection are the most erratic, while those with homogeneous mussels and prey detection are the most straightforward.

Although we ran simulations with homogeneous mussels and without prey detection, these results don't translate to the real world. Mussels are known to cluster (van de Koppel et al. 2008), and starfish are known to employ chemoreception to detect prey (Anger et al. 1977, Beer et al. 2016, Lauzon-Guay et al. 2008, McClintock and Lawrence 1985, Petie et al. 2016), although high water perturbation may make chemotaxis impossible (Lauzon-Guay et al. 2008). It would thus be reasonable to assume that the version with clustered mussels and prey detection is the most likely scenario. If we posit that the P_1-value of starfish in the wild is indeed between 5 and 10, and any value for front formation of at least 0.75 constitutes a front, then density dependent movement alone is enough to trigger front formation in starfish, even without a handling time. If we assume, however, a situation in which chemotaxis is impossible due to water turbulence, density-dependent movement alone is not sufficient. In this case, a handling time of 10-60 minutes is sufficient to trigger front formation, depending on the value of P_1. Since handling times for real starfish can easily be several hours (Anger et al. 1977, García 2015, personal observations), this is well within the realm of possibility. Thus we can conclude, under the circumstances proposed in these experiments, that density-dependent movement is a viable mechanism for causing front formation in starfish.

These results are similar to those found in related species. Lauzon-Guay et al. (2008) found that both cushion sea stars and green sea urchins can form fronts through density-dependent movement, with no need for prey detection. However, like in our model, the addition of prey detection increased the speed of front for-

mation. Lauzon-Guay and Scheibling (2009) also found front formation through resource-dependent movement in periwinkles. In all of these cases, front formation occurs in a similar manner (Silliman et al. 2013): First, the food source becomes patchy, often due to over-consumption. This patchiness then causes resource-dependent movement towards the food source. The front then persists due to negative density-dependent movement. Finally, the resource is depleted and there is no more density-dependent movement, causing the front to disperse. In all of these species, the occurrence of feeding fronts has a huge impact on the local ecosystem, as the complete removal of the resource in question has a cascading effect on other local species. Often, this ecological damage translates to economic damage as well, causing a loss in fisheries or tourist revenue.

Unfortunately, this research has its limitations. First, the area in which the experiments where conducted, as well as the area used in the model, were both limited and enclosed. This means the starfish are always in close proximity to the mussel bed, and were thus more likely to find them than they probably would be in the wild. Also, it was impossible to determine from what distance starfish would be able to detect mussels, if at all, and so the distance required for prey detection had to be estimated. There is still a lot more to be done in order to fully understand the mechanisms for front formation in starfish. In addition to the issues mentioned above, we did not vary the number of starfish or mussels, meaning we have no idea how these influence front formation. Also, due to both space constraints and strange behaviour by the starfish (either due to lack of acclimation or their known abnormal behaviour in captivity (Anger et al. 1977)), a lot of our data was unusable, particularly relating to prey detection.

Despite these limitations this project still gave us some very interesting results. Similar to previous research, we have shown that density-dependent movement can cause the formation of feeding fronts. This is yet another example of small-scale behaviour such as movement speed can eventually have huge effects on an ecosystem. The simple act of slowing down by an individual causes a cascade of effects, eventually altering the entire ecosystem. Unfortunately, this simplicity makes the occurrence of feeding fronts hard to prevent or stop. It's very easy for a front to form under the right circumstances, and it only stops once the resource is depleted. In addition, the resource affected often has an important role in the ecosystem, and is not easily replaced. All in all, feeding fronts pose a serious threat to ecosystem resilience in many habitats; a deeper understanding of how they form and how they might be prevented is necessary to protect both biodiversity and economic interests in affected regions.

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