Computing wave impact in self-organised mussel beds

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Johan van de Koppel* Maarten Löffler† Tim Ophelders‡

Figure 1: Mussels organised in strips.

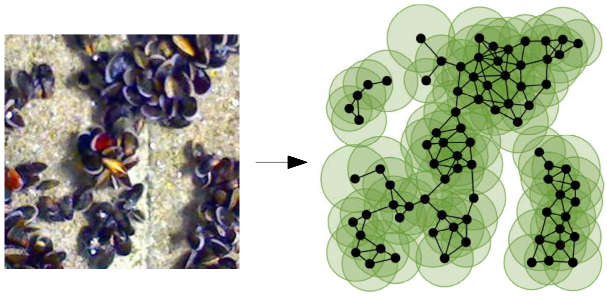

Figure 2: Mussels are modelled as a set of influence radius disks, and their relations define a disk graph.

Abstract

We model the effects of byssal connections made by mussels within patterned mussel beds on bed stability as a disk graph, and propose a formula for assessing which mussels, if any, would get dislodged from the bed under the impact of a wave. We formulate the computation as a flow problem, giving access to efficient algorithms to evaluate the formula. We then analyse the geometry of the graph, and show that we only need to compute a maximum flow in a restricted part of the graph, giving rise to a near-linear solution in practise.

1 Introduction

Mussel beds in the Waddenzee have attracted the interest of ecologists because they form typical self-organised patterns, consisting of strings of mussels that form reticulate networks, see Figure 1. Experimental studies have revealed that mussels form spatial patterns to provide stability against incoming waves, while still allowing enough access to food for individual mussels [3, 9]. To provide in-detail understanding of how the spatial structure of the mussel bed affects the persistence of individual mussels, the process of pattern formation has been modelled in individual-based models. However, these models simplify the impact of wave action on mussels, ignoring the protective effects of mussel clumps and strings on individual survival.

In order to run simulations on a large enough scale for macrobiological effects to become visible, efficient algorithms to compute the stability of given mussel configuration are needed [5]. For this, a suitable model for mussel beds is needed, as well as efficient algorithms to compute the effect of waves. Models that include a large-scale group/structure effect on mussel survival may provide a better understanding of self-organisation in mussels, and stability of mussel beds as a key habitat to many species.

Based on their size, mussels connect themselves to anything solid within a given radius around them using byssal threads. On sand, the only solid objects are other mussels. As such, the graph of connected mussels is naturally modelled as a disk graph [8, 9]. Disk graphs have been studied extensively in computational geometry and discrete mathematics [1, 2, 4, 6].

We set out to leverage this mathematical and computational knowledge to understand how the topological network formed by mussel byssal threads influences mussels' survival/persistence. An important focus is to understand whether and how net-shaped structures provide a more stable landscape than loose clumps, where wave vulnerability is lower. When waves exert force on a limited section of the bed (say 25×25 cm), small clumps can easily get dislodged, while larger clumps that are connected to the larger bed, may persist in the bed. For this we need a binary test, that checks whether the mussels within the wave impact zone are sufficiently connected not to break free.

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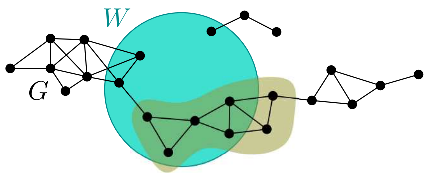


Figure 3: The wave impact zone W. In this case, the shaded set of mussels at the bottom might get dislodged: some mussels inside W stay because they are strongly connected to other mussels outside W, while some mussels outside W get pulled away along with mussels in W. In this case, two connections break.

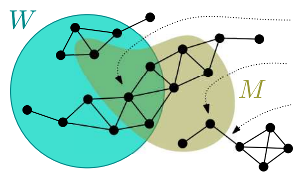


Figure 4: The potential of a given set M depends on $I(M)$, $O(M)$, and $C(M)$. In this particular case, the potential is most likely negative (depending on the weights), meaning this set of mussels would not get dislodged by W.

Contribution. We propose a model for approximating the impact of waves on mussel beds, and give a precise formulation of this model, including a formula for testing whether a given clump of mussels gets dislodged under influence of a given wave. We then show how to formulate the evaluation of this formula as a flow problem. Finally, we analyse the geometry of the underlying disk graph to speed up the computation of the maximum flow.

2 Modelling

We first present a mathematically precise formulation of the problem at hand.

2.1 Disk Graphs

Mussels grow connecting byssus threads to all other mussels within a given distance, depending on their age and size. Thus, we represent individual mussels by weighted points in $\mathbb{R}^2$. A set P of mussels then induces a graph G as follows. Each mussel (p_i, w_i) corresponds to a vertex at point p_i, and has edges to all mussels (p_j, w_j) for which $|p_ip_j| \leq w_i$. Note that the graph is undirected: once a byssus connection is established, it is no longer relevant which mussel created the connection.

Additionally, we know that mussels have a minimum and maximum size. The minimum size gives us a bound on the minimum distance δ^- between any two mussels, since mussels do not overlap; mussels vary in size from just under 1 cm in width up to 10 cm in length. The maximum size gives us a bound on the maximum distance δ^+ between two connected mussels, because threads do not grow longer than this distance; this length is not fully understood but it is not much longer than 10 cm. We define $\phi = \frac{\delta^+}{\delta^-}$ to be the ratio between this largest and smallest distance.

2.2 Wave Impact Zone

We are interested in what happens when a wave hits a part of the mussel bed. We model this by a disk W of radius r, which we call the *wave impact zone (WIZ)*. Figure 3 illustrates this.

We assume that when a wave hits a zone, all mussels in that zone are affected by the wave and start pulling on their neighbours to get washed away. Several things may happen:

- the mussels are washed away and pull their neighbours with them; or
- the neighbours keep the mussels anchored, and nobody is washed away; or
- some connections break, and some mussels are washed away while others stay behind.

2.3 Potential Function

Given G, W, and a set of mussels $M \subseteq P$, we define a function $F(M)$ that decides how much force is exerted on M by the wave. If $F(M)$ is positive, then there is enough force to dislodge M from G, breaking all connections between mussels in M and their neighbours outside M; if $F(M)$ is negative (or zero), then there is not enough force for this to happen. In order to define this $F(M)$, we are going to count three things:

The number of connections between M and the rest of the mussels:

$$C(M) = |\{(a, b) \in E : a \in M \wedge b \notin M\}|$$

The number of mussels of M that are inside the wave impact zone:

$$I(M) = |M \cap W|$$

The number of mussels of M that are outside the wave impact zone:

$$O(M) = |M \setminus W|$$

Figure 4 shows an example. The idea is that mussels in M that are in W are pulling on their neighbours, so they provide force. Mussels in M that are not in W need to be pulled, requiring force. Finally, connections that are broken require (significantly higher) force. This leads to a weighted formula, where w_C, w_I, and w_O are positive weights:

$$F(M) = w_I I(M) - w_O O(M) - w_C C(M)$$

2.4 Objective

To find out whether any mussels get dislodged, we take the maximum of $F(M)$ over all sets M, and see if this is a positive number. We also want to know *which* mussels get dislodged. If multiple sets of mussels have a positive potential, then it is not clear a priori which of the sets gets dislodged by the wave.

Lemma 1 *If we remove the set M that maximises F from G, then all remaining sets have negative or zero potential in the resulting graph.*

To prove the lemma, we first show some intermediate properties of the potential function.

Observation 1 *For sets of mussels A and B, we have $F(A \cap B) + F(A \cup B) = F(A) + F(B) + 2w_C E(A, B)$, where $E(A, B)$ counts the number of edges that have exactly one endpoint in A and exactly one endpoint in B.*

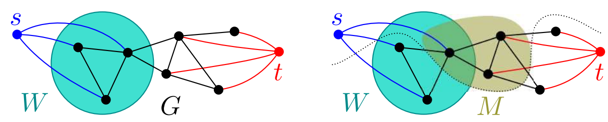
Proof. We verify the three components of F separately. The I term counts mussels inside W inside the sets. By definition, $W \cap A$ and $W \cap B$ overlap in $W \cap A \cap B$, so the sum of their cardinalities is the cardinality of the union plus the cardinality of the intersection. The same argument holds for the O term. Finally, for the C term, we observe that on both sides of the equation we count exactly those edges that cross the boundary of A or the boundary of B. ☐

This observation implies that whenever we have two candidate sets, either their intersection or their union has a higher potential than the lowest potential of the two. This allows us to prove Lemma 1.

Corollary 1 $F(A \cap B) \uparrow F(A \cup B) \geq F(A) \downarrow F(B)$.

Proof. [of Lemma 1] Assume for contradiction that M is the set of maximum potential, and that after removing M from G, another set N now has positive potential as well. Now consider the set $M \cup N$. By assumption, $F(M \cup N) \leq F(M)$. However, M and N are disjoint, so $F(M \cup N) = F(M) + F(N) + 2w_C E(M, N)$. This means $F(N) + 2w_C E(M, N)$ must be negative or zero. However, after removing M from G, the potential of N increases by only $w_C E(M, N)$, after which it should, by assumption, become positive. This is clearly a contradiction. ☐

Lemma 1 implies that the model is well-formed: if there are multiple sets of mussels with positive potential, we simply select the one with the maximum potential. Further note that if there are multiple mussel sets with maximum potential, then one of them contains all others; this is the one we wish to report.



(a) (b)

Figure 5: (a) The augmented graph G'. A new node s is connected to all nodes inside W, and a new node t is connected to all nodes outside W. Black edges have weight w_C, blue edges have weight w_I, and red edges have weight w_O. (b) The cut (dotted) associated with a given set M.

3 Algorithms

3.1 Constructing G

We first investigate how to construct the graph G from a given set of weighted points. We can easily construct the graph in $O(n^2)$ time, by testing, for each pair (p_i, w_i) and (p_j, w_j), whether $|p_i p_j| \leq \max(w_i, w_j)$.

However, we note that in realistic cases (such as cases where ϕ is bounded), the number of edges will be significantly smaller than n^2, and we can compute the graph more efficiently by first storing the points in a suitable data structure, and only testing pairs of points that are sufficiently close to each other.

We first compute a range tree with fractional cascading on P in $O(n \log n)$ time. We then search locally, for each point p_i, for all other points at distance at most w_i from p_i. Since $w_i \leq \delta^+$ and the minimum distance between points is δ^-, there are at most ϕ^2 such points. For each of these points, we add an edge.

Theorem 2 *Given a set P of n mussels in the plane, we can construct G in $O(n(\log n + \phi^2))$ time.*

Given additionally the wave impact zone W, we can easily augment G in linear time (see next section).

3.2 Min Cut Formulation

We can compute minimum value of F using a max flow algorithm, as follows.

We weight the original edges of G by w_C. We augment the graph G with two artificial nodes s and t. We add an edge from s to every node in W, weighted by w_I, and an edge from every node outside W to t, weighted by w_O. We call the resulting augmented weighted graph G'. Figure 5(a) shows an example.

Define $L = w_I |W \cap P|$ to be the maximum amount of force a given wave can exert on the mussels. The following lemma relates the value of a min cut in G' to $F(M)$ and L; see also Figure 5(b).

Lemma 3 *A minimum cut in G' that separates s from t corresponds with a set M that maximises $F(M)$. The value of $F(M)$ is L minus the weight of the minimum cut.*

Proof. Let M be any set of vertices of G. The cut in G' that separates $M \cup \{s\}$ from $P \setminus M \cup \{t\}$ has a total weight of $w_C C(M) + w_I|W \cap P \setminus M| + w_O|M \setminus W|$, which is equal to $L - F(M)$. Clearly, the set M that minimises the weight of the cut, maximises F. $\square$

Max flow can be solved in $O(|V|\cdot|E|)$ time or slightly faster (for instance, see [7]); we compute a minimum cut in G' in $O(|P| \cdot |E|)$ time, which gives us a $O(n^3)$ algorithm to solve the problem on arbitrary graphs. Assuming a bound on the mussel density ϕ, we can immediately improve this by observing that the maximum number of edges is only $O(\phi^2 n)$ instead of $O(n^2)$.

Theorem 4 *Given a set P of n mussels in $\mathbb{R}^2$, and a wave impact zone W, we can compute the set of mussels M that maximises $F(M)$ in $O(\phi^2 n^2)$ time.*

3.3 Geometric Analysis

By exploiting the geometry of unit disk graphs, and making reasonable assumptions about the wave impact zone and the weights w_I, w_O, and w_C, we can improve further on the running time of the above algorithm. The basic observation is that, in order to compute a maximum flow in G', we need never use any mussels that are too far from the boundary of W.

We assume that w_C, w_I, and w_O are within a constant factor of each other. We also assume that the wave impact zone W is a circle of radius r, where r is constant and $r > \delta^+$. For ease of presentation we assume W.L.O.G. that $\delta^- = 1$.

We claim that, to compute the min cut in G', we can restrict our attention to the graph G'' composed of those mussels that are at distance at most $\frac{w_C}{w_O} r\phi^3$ from W. There are at most $\frac{w_C}{w_O} r^2\phi^4$ nodes in G''.

Lemma 5 *The min cut in G' is the same as the min cut in G''.*

Proof. Let F be the set of edges of G that cross the boundary of W. First, we observe that any flow from s to t must use at least one edge of F. All mussels that contribute to edges in F must lie in an annulus centered at the boundary of W of width 2ϕ. Since the radius of W is r, there can be at most $r\phi$ mussels in this annulus, and each can have an edge to at most ϕ^2 other mussels. So, we have $|F| \leq r\phi^3$. Each edge has capacity w_C, so the maximum value the flow problem can have is bounded by $\mathcal{Q} = r\phi^3 w_C$.

Now, we argue that it never makes sense to use any mussels farther than $\mathcal{Q}\frac{\phi}{w_O}$ from W outside W, or farther than $\mathcal{Q}\frac{\phi}{w_I}$ from W inside W. Indeed, any path that long encounters enough edges to s or t to accommodate all the flow. $\square$

The number of mussels in this area is $\mathcal{Q}\frac{\phi}{w_O} r = \frac{w_C}{w_O} r^2 \phi^4$.

We can find those mussels easily once G is known. Therefore, we can substitute n in the result of the previous section, and arrive at the following result.

Theorem 6 *Given a set P of n mussels in $\mathbb{R}^2$, and a wave impact zone W, we can compute the set of mussels M that maximises $F(M)$ in $O(n \log n + n\phi^2 + (\frac{w_C}{w_O})^2 r^4 \phi^{10})$ time.*

4 Future Work

We modelled and analysed the effect of a single wave on a mussel bed, and gave efficient algorithms to compute it. The next step is to investigate whether we can calculate the value of F for multiple wave impact zones more efficiently, since a large number of waves need to be evaluated in a single simulation.

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