Are all patterns created equal? Cooperation is more likely in spatially simple habitats.

Running title: Cooperation in landscapes of fear

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Abstract

Cooperative behaviours, such as aggregation with neighbouring conspecifics, can enhance resilience in habitats where risks (i.e. predation, physical disturbances) are high, exerting positive feedback loops to maintain a healthy population. At the same time, cooperation behaviours can involve some extra energy expenditures and increasing resource competition. For sessile reefs, like mussels, simulation models predict increased cooperation under increasing levels of environmental stress. Predation risk is viewed as a behaviour-modifying stressor, but its role on cooperation mechanisms, such as likelihood of reciprocity, has not yet been empirically tested. This study harnesses this framework to understand how cooperation changes under different perceived levels of predation risk, using mussel beds as model of a complex 'self-organised' system. Hence we assessed the context-dependency of cooperation response in different 'landscapes of fear', created by changes in predator cues, substratum availability and body-size. Our experiments demonstrated that *i)* cooperation in a mussel bed system increases when predator cues are present, but that this relationship was found to be both *ii)* strongly context-dependent, particularly upon substratum availability and *iii)* size-dependent. That is, while cooperation is in general greater for larger individuals, the response to risk results in greater cooperation when alternative attachment substratum is absent, meaning that simpler landscapes may be perceived as riskier. The context-dependency of structural complexity is also an essential finding to consider in a changing world where habitats are losing complexity and cooperative strategies should be maximised.

Keywords: Aggregation, Behaviour, NCE, Mussel beds, Predation risk, Self-organisation

Introduction

Cooperative behaviour has been shown to be present at every level of biological organisation, from cells, to microbes, to macro-organisms (Guichard, 2017). Cooperation, resulting in the formation of gregarious patterns (Buss, 1981), is believed to bring benefits to individuals, such as increased survival rates but can also carry associated costs like reduced growth rates as result of competitive interactions (Bertness & Grosholz, 1985; Fréchette & Lefaivre, 1990; P. Turchin & Kareiva, 1989; Wilson & Agnew, 1992). Spatially self-organised systems may have evolved as a special mechanisms of cooperation, resulting in a trade-off between competition and facilitation (Hui, Zhang, Han, & Li, 2005; Nowak, Bonhoffer, & May, 1994) .

Spatial distribution of conspecifics can act as a mediator of this cooperation. The attraction towards conspecifics (Turchin, 1989) is greater initially when individuals are spaced apart, and leads to formation of clusters. As the number of neighbours increases, competition is intensified and cooperative behaviour diminishes (de Jager, Weissing, & van de Koppel, 2017; Doebeli & Hauert, 2005; Hauert & Doebeli, 2004). A clear example of spatially structured habitat, where habitat-formers are cooperating to form self-organised patterns according to different environments and neighbours size, is given by mussel beds (Commito et al., 2014; Commito, Gownaris, Haulsee, Coleman, & Beal, 2016; Q.-X. Liu, Weerman, Herman, Olff, & van de Koppel, 2012; Quan-Xing Liu et al., 2014; Snover & Commito, 1998; van de Koppel et al., 2008; van de Koppel, Rietkerk, Dankers, & Herman, 2005). Natural mussel beds are also spatially structured with regards to sizes of individuals within, with the basal structure made by larger individuals with younger individuals being more motile (Wiegemann, 2005) and finding refuge within the matrix provided (Commito et al., 2014; Bertolini, Montgomery, & O'Connor, 2018).

The aggregation into patches can be considered as a form of cooperation (Buss, 1981; Doebeli & Hauert, 2005), forming attachment with neighbouring mussels via production of byssal threads (Pearce & Labarbera, 2009). Attachment should protect mussels from dislodgement and predation (Bertness & Grosholz, 1985; Carrington, Moeser, Thompson, Coutts, & Craig, 2008; Hunt & Scheibling, 2001; van de Koppel et al., 2008), and mussels ability to reorganise has consequences for system persistence (Bertolini, Cornelissen, Capelle, Van de Koppel, & Bouma, 2019) and habitat boundary formation at whole systems-scale which may ultimately determine species distribution in terms of its realised niche (Donahue, Desharnais, Robles, & Arriola, 2011). However, not all patterns may be created equal, and some patterns might appear similar while hiding differences in their strength. Because of the high costs associated with thread production (i.e., up to 44% of total carbon and 21% of total nitrogen assimilated; Hawkins & Bayne, 1985), byssal threads may only be produced when perceived as a necessity (Garner & Litvaitis, 2013b), with some mussels benefitting from passive attachment and not actively engaging in thread production. Increased levels of cooperation, where more mussels produce threads, should result in overall stronger aggregations. More vulnerable individuals may be also the more likely to cooperate (Brown, Aronhime, & Wang, 2011; Garner & Litvaitis, 2013a). Studying cooperation under real-life empirical scenarios can give insights into energetic budgets of a population, thus its likelihood of survival.

For mussels, the degree of aggregation, overall byssal thread production and the strength of the byssal threads produced, are all known to vary with different environmental conditions (such as temperature, hydrodynamic conditions, food availability, Lachance, Myrand, Tremblay, Koutitonsky, & Carrington, 2008), and to be strongly enhanced by perceived risk (Cote & Jelnikar, 1999; Garner & Litvaitis, 2013a; Nicastro, Zardi, & McQuaid, 2007). Non-consumptive predator effects, arising from fear of predation, can have negative impacts on population dynamics, altering, amongst other traits, individual growth rates (Preisser & Bolnick, 2008). Prey perception of 'fear' may vary according to the background landscape settings, according to the theory of the "landscape of fear" (Laundre, Hernandez, & Ripple, 2010).

Different 'landscapes of fear' can be generated by multiple mechanisms. Firstly, cues can be either chemical or tactile (Ferrier, Zimmer, & Zimmer, 2016; Nicastro et al., 2007; Richardson & Brown, 1992) and can vary in intensity across the habitat depending on predators density, position and mechanisms responsible for cue propagation (Coleman & Hill, 2014; Mella, Banks, & McArthur, 2014). Similarly, degrees of structural complexity, provided by the substratum or by the bed itself, can provide refuge spaces (Commito et al., 2014; Maas Geesteranus, 1942), causing differences in fear perception across different settings (Matassa & Trussell, 2011). In riskier landscapes, individuals may invest more in stronger anti-predator behaviour. Understanding how risk is perceived under multiple ‘landscape of fear’ scenarios is essential to fully understand population and ecosystem dynamics.

It is still unclear how fear of predation will shape self-organisation patterns. It can be hypothesised that previously observed increased strength of attachment within clumps (Brown et al., 2011; Garner & Litvaitis, 2013a; O. Reimer & Harms-Ringdahl, 2001; Olof Reimer & Tedengren, 1997) is due to a greater amount of cooperation, as the number of reciprocally attached individuals increases, creating stronger clumps while evenly distributing investment. In this study, we aim to gain an understanding of this process, to provide further insights in the spatial ecology of mussel beds in fear landscapes. Hence two laboratory experiments were conducted to test the hypotheses that under perceived risk: (*i*) there will be greater attachment to conspecific (aggregation) compared to alternative attachment substratum in simple habitats; (*ii*) aggregations will consist of a greater number cooperative individuals that reciprocally attached to each other, *(iii)* smaller, more mobile , mussels will aggregate and cooperate more than larger, less mobile mussels; (*iv*) when tactile cues are added, potentially increasing the overall cue intensity, the cooperative response will be stronger than when only chemical cues are present.

Methods

Experiments

Common starfish *Asterias rubens* were kept in a separate tank with fresh aerated seawater and *ad libitum* food supply (live blue mussels, *Mytilus edulis*). Starfish were fed a mussel diet to standardise the release of cues but were left to starve for 24 hours prior each experimental trial to standardise hunger levels which may also influence the amount of emanated cues (Cheung, Luk, & Shin, 2006). New starfish were used for each trial.

Exp 1: Testing cooperation under perceived predation risk in landscapes offering alternative attachment substrata

To investigate how mussel attachment and cooperation behaviour changed under perceived risk, we set up an experiment with two different size classes of mussels presented with and without alternative attachment substrata and recorded their behaviour. The experiment was set up as follows. Eight experimental arenas were set up in two experimental tanks (four arenas per tank) with aerated seawater from the Oosterschelde held at a constant temperature (15 ºC). Over eight days in October 2017, a new experimental trial was set up daily, for a total of 64 experimental trials being ran. One tank was set up to expose mussels to chemical cue from a common predator, the starfish *Asterias rubens*, by adding two starfish in a fenced off area in the middle of the tank (Appendix 1) at least two hours before the start of the experimental trials. In each tank, two out of the four arenas were layered with empty shell material, while the other two offered only the bare substratum of the tank (plastic). These substrata were chosen to represent a simple hard substratum where movement is maximised but attachment is limited (bare plastic tank) and a complex hard substratum where attachment is possible and often preferred (mixed cockles and mussels shell material, in pieces > 3cm, Capelle, Leuchter, Wit, Hartog, & Bouma, 2019, Bertolini, Geraldi, Montgomery, & Connor, 2017). Fifty mussels of either small (20.52 ± 0.61mm, mean ± SE) or large (38.75 ± 0.54mm, mean ± SE) size classes were then added and spread evenly in one of the arenas (chosen at random) to obtain a density of 200 mussels/m^2, representative of a natural low-medium density (Bertolini et al., 2019), and were left for two hours to form byssal attachment. At the end of each two hours the total number of aggregated mussels was counted. The duration of the trials was long enough to elicit byssal production but short enough to allow quantification of threads by visual inspection. The number of byssal threads produced was therefore recorded and whether the attachment was towards conspecifics, tank or shells. To quantify ‘cooperation’, the number of reciprocal attachments was noted.

Exp 2: Disentangling the importance of chemical and tactile cues for cooperative behaviour

To investigate the role of chemical and tactile cues on mussel cooperative behaviour, a laboratory experiment was run as follows. One experimental arena (70 x 120 cm) with fresh flowing seawater held at a constant temperature (15 ºC) was used to run 48 continuous subsequent trials in October 2017. Trials were conducted in a randomised order and were either controls (only mussels), chemical cue or chemical + tactile cue (mussels + 5 starfish inside the mesh fence). Trials were conducted both on bare tank substrate and by lining the tank with soft-sediment to represent a more realistic, yet simple, substratum, where movement is slower and attachment to the substratum itself not possible (Camilla Bertolini et al., 2017; Young, 1983). To obtain chemical cues only, a fenced mesh was used to isolate one area of the tank (70 x 23 cm) where the mussels were placed, while five starfish were placed on the other side. For the tactile cue, five small starfish were added to the mussels, in order to give out an additive tactile cues on top of chemical cues, while being small enough thus minimising real consumption which would have affected density of mussels in the experiment (Appendix 2). For all treatments, 100 mussels were used (23.38 ± 0.6 mm, mean length ± SE) with new mussels used in each trial, and they were distributed, always in the same area of the tank, at the estimated density of 600 mussels/m^2, considered to be representative of a naturally occurring medium-high density (C Bertolini et al., 2019), in a manner to not be in contact with each other while being within reach of each other (Camilla Bertolini et al., 2017). Trials lasted one hour, after which mussels were taken out of the arena. Number of mussels in aggregations and nature of aggregations as in number of clumps, maximum and average number of mussels in clumps, was noted and to quantify aggregation the number of byssal threads produced were visually counted from all mussels. Furthermore, to assess levels of cooperation number of reciprocal attachments (two mussels reciprocally attached are counted as one reciprocal attachment) and number of non-cooperating individuals (considered as those that were part of a clump but did not produce any threads) were also counted. At the end of each trial the tank was flushed with fresh seawater to remove any cues before .

Statistical analyses

All statistical analyses were performed in R. Statistical tests were chosen based on raw data and residual distributions. Data were explored for normality and homogeneity of variances, using data observations, Shapiro-Wilk’s test and Levene’s tests (Quinn & Keough, 2002; Zuur, Ieno, & Elphick, 2010).

Exp 1: Testing cooperation under perceived predation risk in landscapes offering alternative attachment substrata

A linear model was run for the number of aggregated mussels, generalised linear model with negative binomial distribution was run for the total byssal threads, and with a Poisson distribution for the between-mussels number of threads and reciprocal attachment. Models initially included all of the three fixed factors: predator cue (two levels: ‘present’, ‘absent’), substratum (two levels: ‘plastic tank’, ‘shells added’), mussel size (two levels: ‘small’, ‘large’) and all possible interactions. Models were then simplified according to AIC scores (Zuur, Hilbe, & Ieno, 2013). Final models for number of aggregated mussels and number of clumps included all three single factors and the interaction between predator cue and mussel size, for total number of byssal threads produced the final model included all single factors and the interaction between predator cue and substratum, for the number of byssal attached to other mussels the final model included all terms and their three-way interaction, while the model testing the number of reciprocal byssal attachment only included predator cue and mussel size. Models were validated by exploring plots of model residuals (Zuur et al., 2013). Anova tables, with type III sums of square when interactions were significant and type II where there was no interaction, were then produced to obtain overall factor significance values, using chi squared tests for significance in case of Poisson models and F-tests in all other cases.

Exp 2: Disentangling the importance of chemical and tactile cues for cooperative behaviour

Generalised linear model with negative binomial error distribution were run for the number of aggregated mussels, number of clumps, total number of byssal threads, number of reciprocal attachments and maximum number of mussels per clump, while an inverse Gaussian distribution was used for the average number of mussels per clumps. Models initially included the two fixed factors: predator cue (three levels: ‘absent’, ‘chemical’ and ‘tactile’), substratum type (‘plastic tank’, ‘sediment added’) and their interaction. Models were then simplified according to AIC scores (Zuur et al., 2013). Final models for number of aggregated mussels, number of clumps, total number of byssal threads and number of reciprocal attachments included both factors and their interaction, while for average and maximum number of mussels the models only included the effect of substratum. using chi squared tests for significance in case of Poisson models and F-tests in all other cases.

RESULTS

Evaluating cooperation: predation cuess, presence/absence of alternative substrata & mussel size

Our experiments revealed that mussel aggregation to other mussels was greater, when they perceived cues about predator presence. The number of aggregated mussels increased when predator cue was present ($F_{1,59}$=9.01, $p < 0.01$, Fig. 1A), with a tendency for the larger mussel size class being the one responding to predation cue (predator x size interaction: $F_{1,59}$=3.8, $p = 0.057$, Fig. 1A). Contrary to our hypothesis, larger mussels generally aggregated more than smaller ones ($F_{1,59}$= 13.9, $p < 0.001$, Fig. 1A). In line with our hypothesis, the number of aggregated mussels was generally greater when there was no alternative substratum (shells) ($F_{1,59}$= 10.3, $p < 0.01$, Fig. 1A),

The number of byssal threads produced increased when shells were added as alternative substratum for mussels to attach to ($F_{1,59}$= 166.5, $p < 0.001$, Fig. 1B). However, it was only in absence of shells that mussels responded to predation threat by increasing byssal production (predator x substratum interaction: : $F_{1,59}$=6.7, $p < 0.05$, predator: $F_{1,59}$= 6.04, $p < 0.05$, Fig.1B, Appendix 3a). Size mattered, with larger individuals found to produce an overall greater number of threads than small ones ($F_{1,59}$= 27.2, $p < 0.001$, Fig.1B). As a result, larger mussels responded to predators by increasing their conspecific attachment in both presence and absence of alternative substratum (predator x substratum x size interaction:, χ^2 =7.33 ,$p < 0.01$; size: χ^2=31.2, $p < 0.001$, substratum: χ^2= 3.8, $p < 0.05$, Fig. 1C, Appendix 3a). Small mussels responded to predators by increasing attachments with conspecifics only in the absence of shells (substratum: χ^2=3.9, $p<0.05$, predator: χ^2=7.98, $p < 0.01$, Fig 1C, Appendix 3a). Predation responses did not change reciprocity, which was observed more in large mussels (size: χ^2= 14.55, $p < 0.001$, Fig. 1D).

Disentangling the importance of chemical and tactile cues for cooperative behaviour

We observed a clear effect of predator cues on cooperative behaviour. When mussels were placed on either the tank bottom or soft sediments, we observed that the number of threads connecting mussels increased in the presence of predator cues (predator: $F_{2,39}$= 5.2p < 0.01, Fig. 2a), both for chemical and tactile cues compared to no cue (all post-hoc $p< 0.001$, Appendix 3b). While the total number of threads was the same across both substratum types (substratum: $p > 0.05$) , aggregation patterns where shaped by predator cues only when mussels were placed on the soft-sediments (substratum x predator interaction, N of aggregated mussels $F_{2,39}=3.1$, $p = 0.057$, Fig. 2b; N of clumps $F_{2,39}= 3.15$, $p = 0.054$, Fig. 2c), with no differences between chemical-only or tactile cues compared to no cue (all post-hoc $p< 0.001$, Appendix 3b). It should be noted that mussels aggregated less in soft sediment compared to the tank substratum alone (N of aggregated mussels $F_{1,39}=17.1$, $p < 0.001$, Fig. 2b; N of clumps $F_{1,39}= 12.1$, $p < 0.001$, Fig. 2c). The nature of the aggregations was only dependent upon substratum type, with overall fewer mussels in clumps in soft sediments compared to bare tank (average number of mussels: $F_{1,39}=20.1$, $p < 0.001$; max number of mussels $F_{1,39}=21.8$, $p < 0.001$, Fig 2d-e). Attachment to substratum was not quantified, as it was rarely observed (pers. obs.). The number of cooperative mussels, measured as the number of reciprocally attached mussels, was higher when starfish cue was present ($F_{2,39}= 14.1$, $p < 0.001$, Fig. 2f) in both sediment types (substratum x predator interaction= $p > 0.05$). This was true for both chemical and tactile cues (all post-hoc $p < 0.001$, appendix 3b). Greater reciprocity was found when no sediments were added ($F_{1,39}= 12.2$, $p < 0.01$, Fig. 2f).

Discussion

In nature, finding optimal levels of cooperative behaviour is a delicate balance between maximising protection while minimising competition (Buss, 1981; Nowak et al., 1994). These optimal levels can change with different levels of risk perception, which in itself can depend upon environmental settings given by habitat degradation (Hui et al., 2005). In the present study we identified that the presence of a predator, giving out a chemical cue, may be enough to elicit a fear response that can result in increased cooperation. Moreover, we found a landscape-dependency of this cooperative behaviour (Donelan, Grabowski, & Trussell, 2016), where organisms were less cooperative in relatively safer environment, represented by more structurally complex settings. Investigating cooperation as trade-offs between aggregation (facilitation) and competition as a responses to fear is a novel approach that should be granted further investigations.

Mussel movement strategy is one of the factors determining aggregation (de Jager, Weissing, Herman, Nolet, & van de Koppel, 2011). Mussels move more on ‘simple’ hard substrates compared to ‘simple’ soft substrates and ‘complex’ hard surfaces provided by empty shells (Bertolini et al., 2017). Thus, on a simple hard substrate such as that offered by the tanks, there is an overall greater chance to encounter conspecifics to form aggregations with, independently of risk. However, behavioural response to risk in ‘simple’ habitats should cause an increase in aggregation with conspecifics to gain safety in number (Cote & Jelnikar, 1999; Olof Reimer & Tedengren, 1997). In our experiment we found an enhanced selectivity for conspecifics in bare sedimentary substrata, which by themselves provide no alternative attachment (Young, 1983). Consequently, when mussels were presented with an additional alternative (shell) substratum, they produced an increased number of byssal threads attaching to empty shells and aggregating to conspecifics less, independently from the predation risk, a strategy that can maximise survival from both predation and hydrodynamic stress (Capelle et al., 2019) while limiting competition for resources (Christensen et al., 2015).

Cooperation, here intended as reciprocated byssal attachment, thus as a two-way investment, was found under perceived predation risk. Smaller mussels cooperated less than their larger counterpart. This result was opposing our hypothesis that smaller mussels, being naturally most vulnerable to predation (Hummel, Honkoop, & van der Meer, 2011), would not only be the ones responding more to risk with inducible defences (Brown et al., 2011; Johnson & Smee, 2012) but also cooperate more. However, cooperation response in smaller mussels was dependent upon availability of complexity of substratum. Smaller mussels may obtain greater refuge from shells (Eschweiler & Christensen, 2011; Strain et al., 2017), lessening the need to cooperate, and should benefit from being selfish due to greater needs for growth at this stage. This suggests that mechanisms of cooperation and competition may operate with different strengths at different ontogenetic stages (Miriti, 2006).

The response to predator risk, both in terms of aggregation and cooperation was the same regardless of the nature of the cue. We were expecting a much greater response with tactile cue, as found for barnacle whelk interaction (Ferrier et al., 2016), with fear perception by bivalves usually related to predator proximity (Stephen Gosnell, Spurgin, & Levine, 2017). Present findings indicate that the aggregative response of *M. edulis* may have adapted to recognise both types of cues. Moreover, because tactile cues cannot be fully disentangled from chemical cues, it is possible that chemical cues are enough to create a ‘landscape of fear’ in this scenario. Moreover, the starfish used for tactile cues may have been too small to be perceived as a real threat and elicit a response. This shows the importance of considering the multi-faceted aspects of predator-prey interactions, which are complex in nature.

Using an empirical approach we found greater aggregation in presence of predation risk. We further showed that this strategy is highly dependent upon environmental background and settings. Environmental background can modify the level of perceived risk, with more complex habitats providing increased refuge thus lowering the needs for ‘social protection’ (e.g. Orpwood, Magurran, Armstrong, & Griffiths, 2008). Interestingly, even organisms that tend to be sessile, such as mussels, show differential behaviour according to structural habitat complexity. This adds on to the body of evidence that also semi-sessile species show some degree of selectivity (Shin, Liu, Liu, & Cheung, 2008) similar to that shown by typically more mobile species (Grabowski, 2004; Lima & Dill, 1990; Orpwood et al., 2008) which allows the organisms to create a balance between predation and competition avoidance.

Cooperation, when studied in the context of predation avoidance, provides an interesting extension of the concept of landscapes of fear. Different landscapes of fear might be provided by different degrees of complexity in the environment which may be already existing in the habitat or generated by the organisms themselves. When cooperation generates spatial aggregations that provide a greater degree of safety, individuals within these aggregations will likely in turn experience lower ‘fear levels’ then those outside of such aggregations, or in weaker ones, creating spatial differentiation - a landscape - in the degree of fear. These findings are important in changing world scenario where habitat structural complexity is being increasingly lost (Agostini et al., 2018; Fabricius, De’ath, Noonan, & Uthicke, 2014; McCormick & Lönnstedt, 2013), and empirically demonstrate that cooperation can be a strategy that maximises chances of maintaining population levels in decaying habitats (Hui et al., 2005; Zhang, Hui, Han, & Li, 2005).

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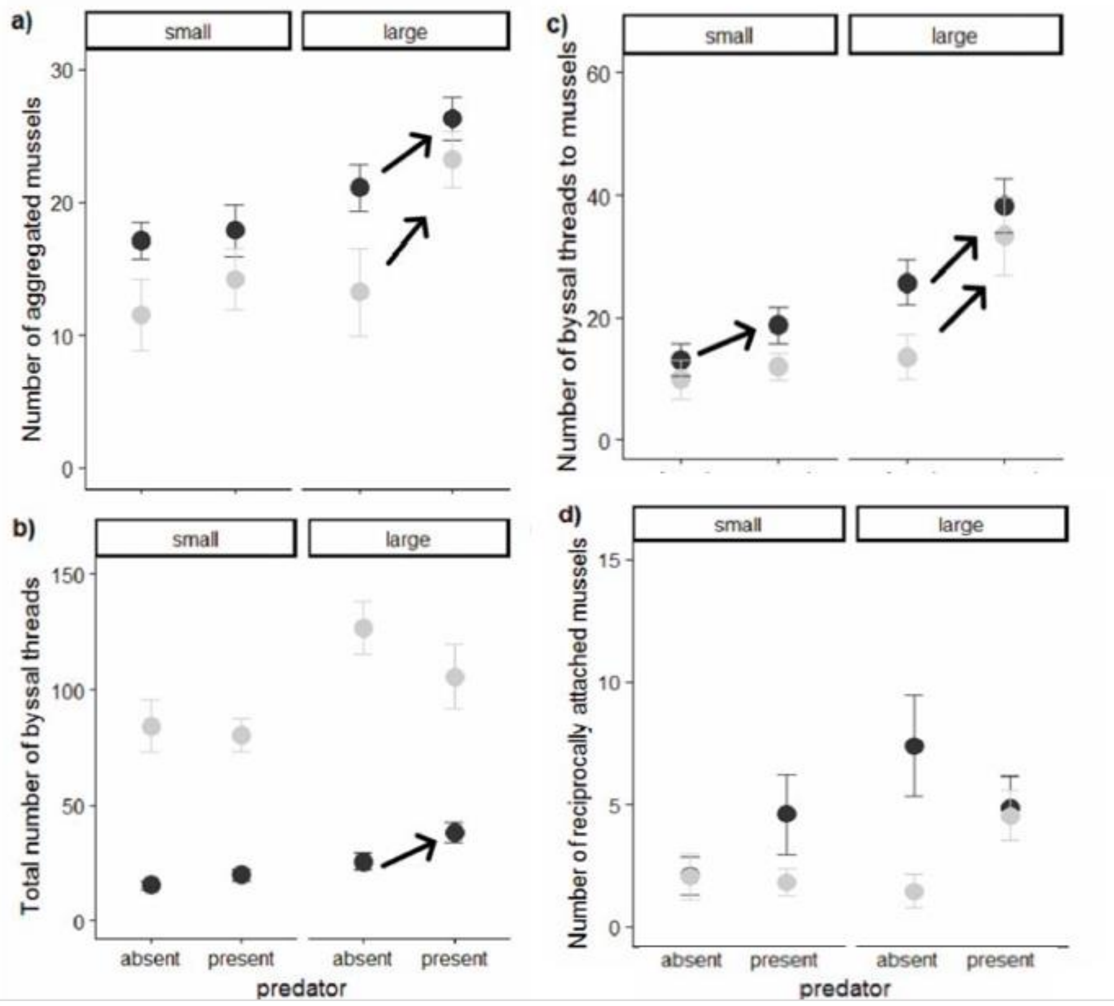
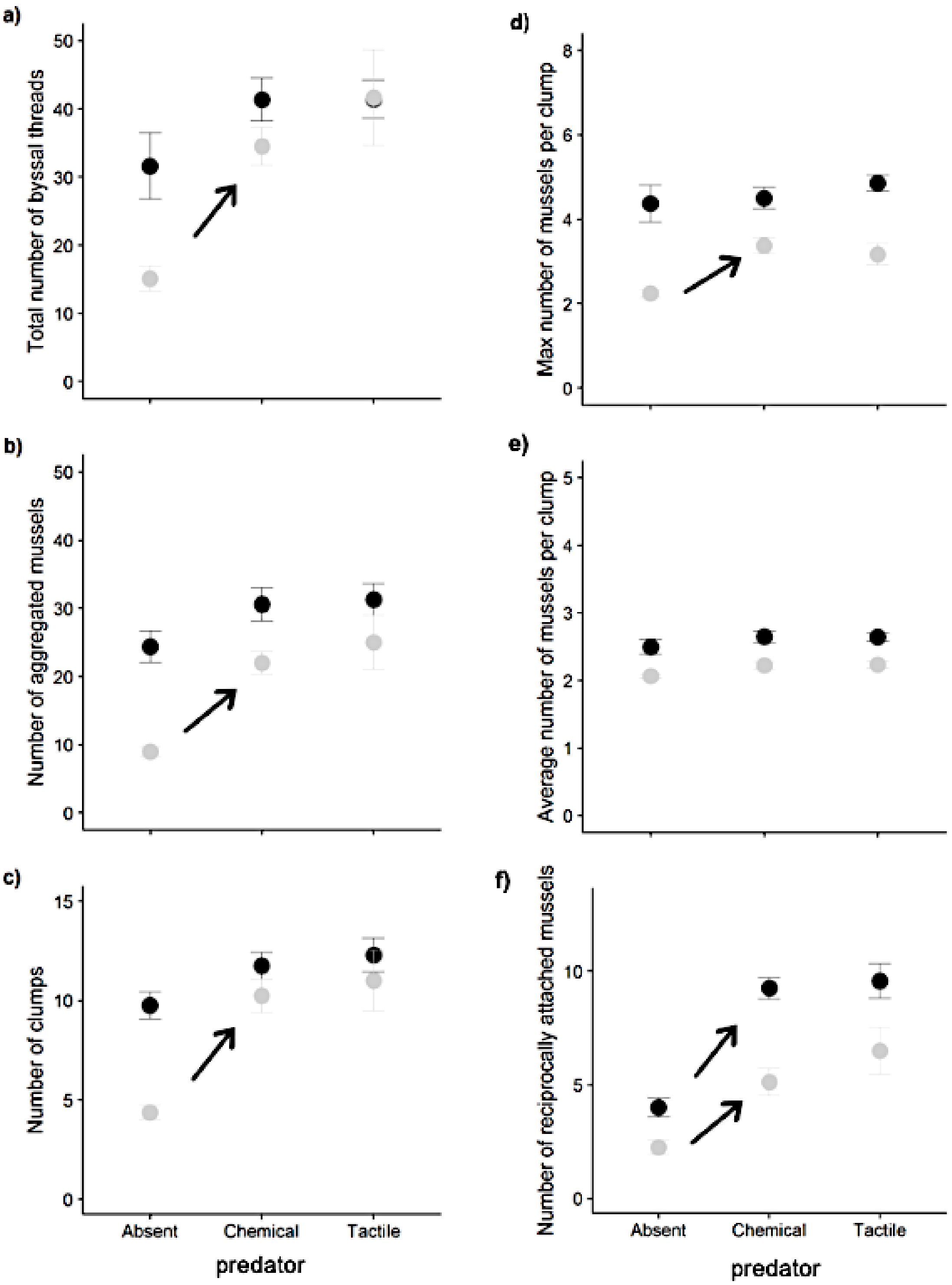
Fig.1 Effects of predator cues, substratum type (black: plastic tank, grey: addition of shells) and mussel size on a) Total number of mussels forming aggregations; b) total number of byssal threads produced; c) Number of byssal threads connecting mussels and d) number of reciprocally attached mussels. Arrows represent direction of significant differences. All plots show mean and standard errors.

Fig 2 Effects of types of predator cues and substratum type (black: plastic tank, grey: soft sediment) on a) total number of byssal threads, b) number of aggregated mussels, c) number of clumps, d) maximum number of mussels in each clump, e) average number of mussels in each clump, f) number of reciprocally attached mussels. All plots show mean and standard errors.



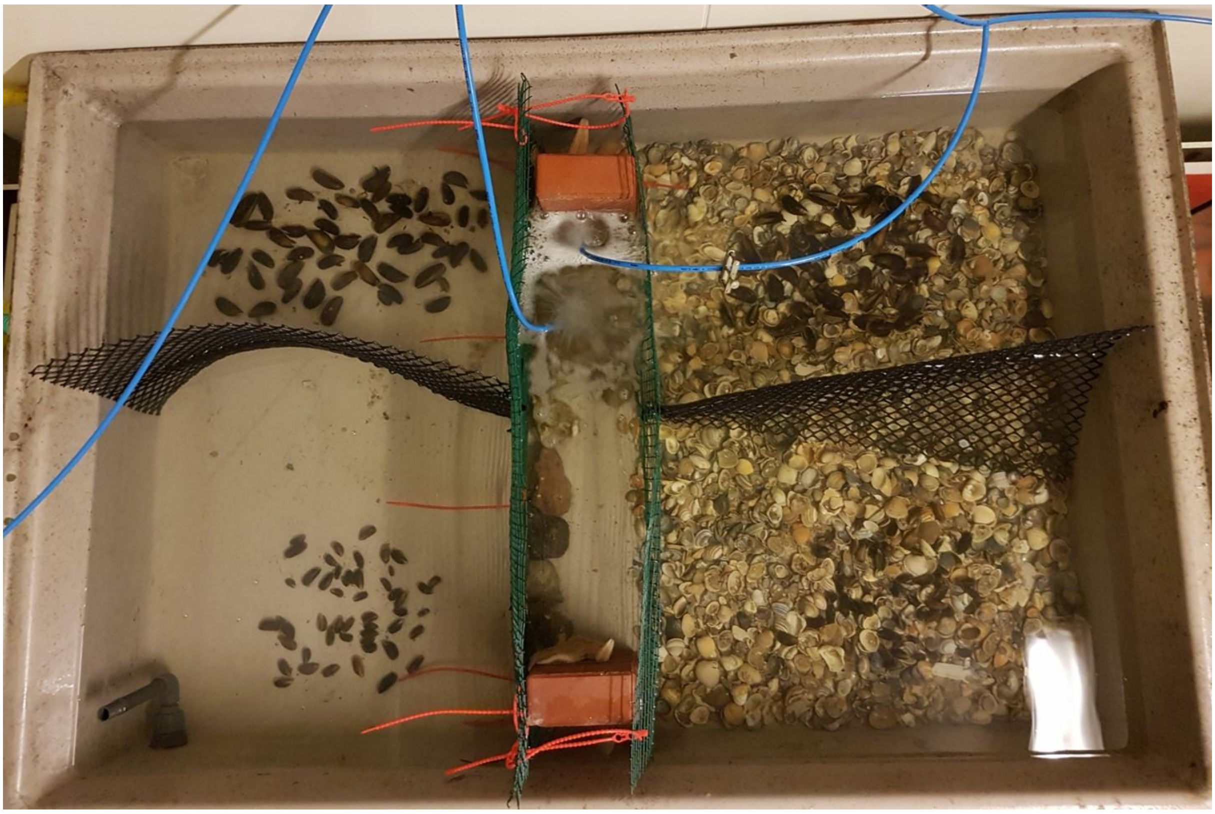

a)
Total number of byssal threads
0
10
20
30
40
50
b)
Number of aggregated mussels
0
10
20
30
40
50
c)
Number of clumps
0
5
10
15
Absent
Chemical
Tactile
predator
d)
Max number of mussels per clump
0
2
4
6
8
e)
Average number of mussels per clump
0
1
2
3
4
5
f)
Number of reciprocally attached mussels
0
5
10
Absent
Chemical
Tactile
predator

Appendix 1 – Experimental tank example for experiment one showing compartments with mussels and middle compartment with predators. Top left and clockwise: large, plastic tank; large, shells added; small, shell added; small, plastic tank.

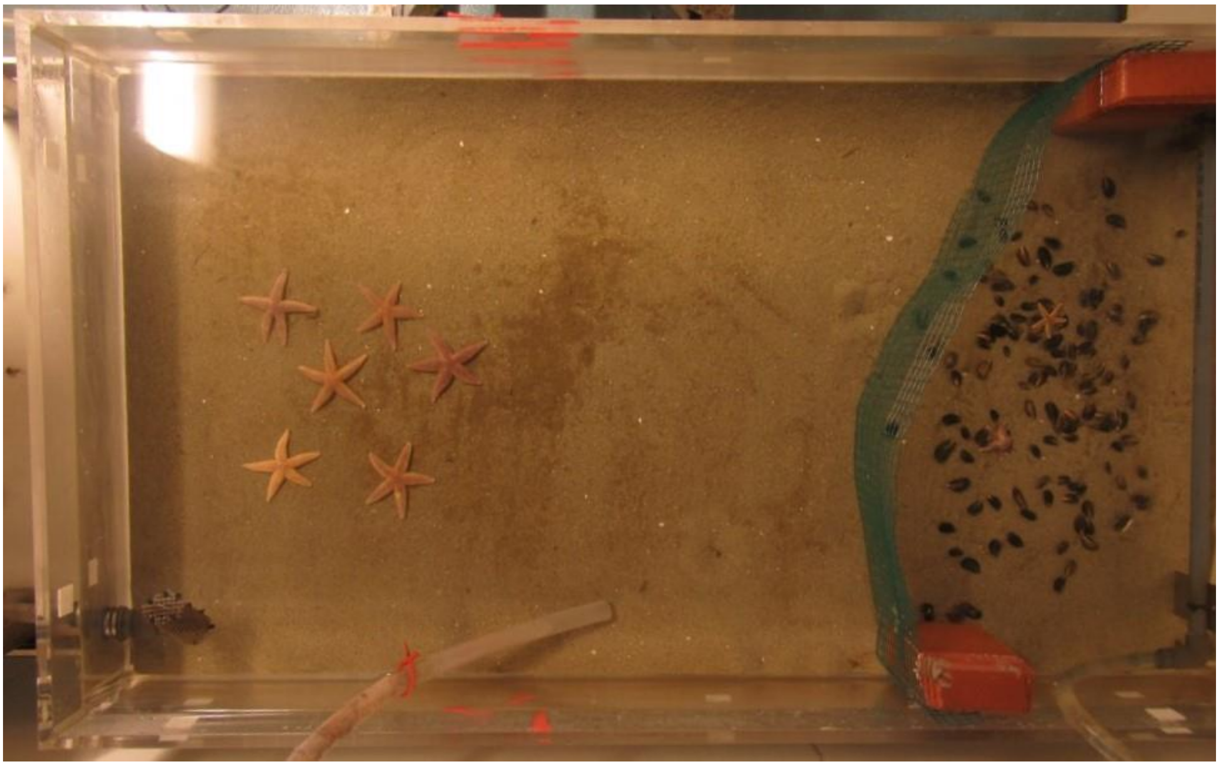
Appendix 2 – Experimental tank example for experiment two, showing experiment with soft sediment addition and both a chemical cue given by the starfish present on the left of the net and tactile cue from the starfish enclosed on the right side of the net.

Appendix 3 – results of post-hocs analysis from a) experiment one and b) experiment two.

Appendix 1



Appendix 2



Appendix 3a

Number of aggregated individuals	**Number of threads**	**Number threads between conspecifics**
Small: NS **Large: No < Cue, 0.0009**	Bare: No < Cue 0.02 Shells: NS	Small Bare: No < Cue 0.026 Shells: NS Large Bare: No < Cue 0.0002 Shells: No < Cue <0.0001

Appendix 3b

Number of threads	**Number of aggregated individuals**	**Number of clumps**	**Reciprocally attached (cooperative)**
Bare: NS **Sediment:** **No < Chemical 0.0003** **No < Tactile 0.0021** **Chemical=Tactile**	Bare: NS Sediment: No < Chemical 0.0002 No < Tactile 0.0003 Chemical= Tactile	Bare: NS Sediment: No < Chemical 0.0002 No < Tactile 0.0003 Chemical=Tactile	Bare: No < Chemical 0.0006 No < Tactile 0.0004 Chemical=Tactile Sediment: No < Chemical 0.012 No < Tactile 0.001 Chemical=Tactile