Is bigger better? A study of competitive abilities in bryozoa in deep time.

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Sammendrag

Competition is a vital part of shaping communities and ecosystems. In short terms we know competition is important, but when it comes to competition and biotic factors' effect on evolution, there are still no full agreement on the matter. The difficultness of following interaction and competition over long scale time is unfortunate, but there exist a system where such a thing is possible. Bryozoa are colonial creatures who consists of many genetic identical zooids. They often encrusts spaces and thus compete for it when they meet other colonies or species. Bryozoa fossilize easily and their interactions are often fossilized too, which means scientists have an opportunity to observe interaction through time. In my study I have looked at bryozoan fossils from Nukumaru Limestone, Nukumaru Brown Sand and Upper Kai-Iwi Shellbed to study the interactions of Cheilostomes and Cyclostomes over time. My main goal is, however, to determine if the zooid size of a bryozoa affects the outcome of the competitions between the colony. After analysing the collected data, it sure looks like the bigger you are, the more advantage you have over your opponent. It was also observed that the competitive ablity of the bryozoan orders/species didn't change much over time. They were pretty stable.

Forord

I wish to thank my supervisors Lee Hsiang Liow and Kjetil Lysne Voje for their extremely valuable help with my thesis. I could not have wished for better supervisors. I would also like to thank Paul Taylor for helping me in the beginning of my Masters, but also for letting me visit the Natural History Museum in London and work with the Nukumaru Limestone samples over there. I would also thank Emanuela Di Martino for helping me during my labwork and helping me with in general with bryozoa related business. I would like to thank Nils Christian Stenseth for supporting our bryozoa related work in CEES. Last, but not least I want to thank my wonderful co-Master students Emily and Jeroen for being supportive and helpful!

Innholdsfortegnelse

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1 Introduction

Competition can be defined as an overlap in the ecological niches of populations from different or the same species, in which the demand for similar resources affects them negatively regarding reproduction and survival (Hickman *et al.*, 2008) (Krebs, 2009). Competition is a well-studied field in ecology as it is key to understand ecosystems and population dynamics (some refs here). There are lots of traits that might be a direct or indirect result of competition, or that even affects the competition itself. Size of different organs/body parts is often studied, perhaps especially the size of the testis and/or the size/length of sperm cells regarding sperm competition (Stockley *et al.*, 1997) (Gage, 1994).

Sexual selection, increased mortality and body size is, too, something scientists have studied over the years (Promislow, 1992), and reports/studies on how sexual selected traits and size work together (Emlen, 2001) are important to understand how competition and interactions can affect evolution, as that's something that for a long time has been poorly understood (Schluter, 1994).

On short time scales it is known that competition is important to shape the communities and ecosystems around the world, but we still don't know much about competition's affect on long term evolution. Some scientists agree that competition is necessary to drive the evolution forwards, others believe evolution happens mostly after fluctuations in the climate, after nature catastrophes and so on (Benton, 2009). One reason for this is that to be able to understand competition's effect on biological systems over a long time scale, you need long scale systems to study. And that's a part of why not many studies have been done on this subject yet. Interactions and competition is very rarely fossilized in good shape (Taylor, 2016). However, there is a system which can be used to study competition over a long time scale.

Bryozoans are colonial, filter-feeding invertebrates that often grow on sturdy substrates such as shells, rocks and seaweed (Taylor, 2005). The group is highly diverse morphologically and the phylum includes almost 6000 described extant species (Taylor

& Waeschenbach 2015). Each bryozoan colony is built up by tiny units called zooids. The zooids are genetically identical, but in many bryozoans, and perhaps especially in cheilostomes, the zooids are highly polymorphic and may look quite different from other zooids. Some of these zooids are used for feeding; some are used for reproduction and some for defense. Both colony size and size of these zooids vary greatly between species.

We know now that space is a limited factor that is one of the main forces that drives bryozoan competition (Barnes & Dick, 2000), and it is also believed that the competition for food affects the competition for space and the outcome itself (Okamura, 1988). Many bryozoan skeletons are made up of minerals like calcite and aragonite (Rucker & Carver 1969), which is a reason bryozoans with mineral skeletons often fossilize quite well, and are often well preserved. This means that if two or more colonies are involved in a competition against each other, and they fossilize like that, the competition will be preserved. This makes for a unique chance to study interactions in prehistoric times (Barnes & Dick, 2000)

There are several types of interactions that can occur between bryozoans although the type of interaction that happens most frequently is overgrowth, where one colony grows over the other (Jackson, 1979). Other types of bryozoan interactions are stand-off, where no colony manages to get the upper hand and overgrow the competitor, and reciprocal overgrowth where colony A grows over colony B at one point, while colony B grows over colony A at another point (Taylor 2016) (Rosso & Sanfilippo, 2005). SEM photos of overgrowth, fouling and standoff can be seen in figure 1a, b and c.

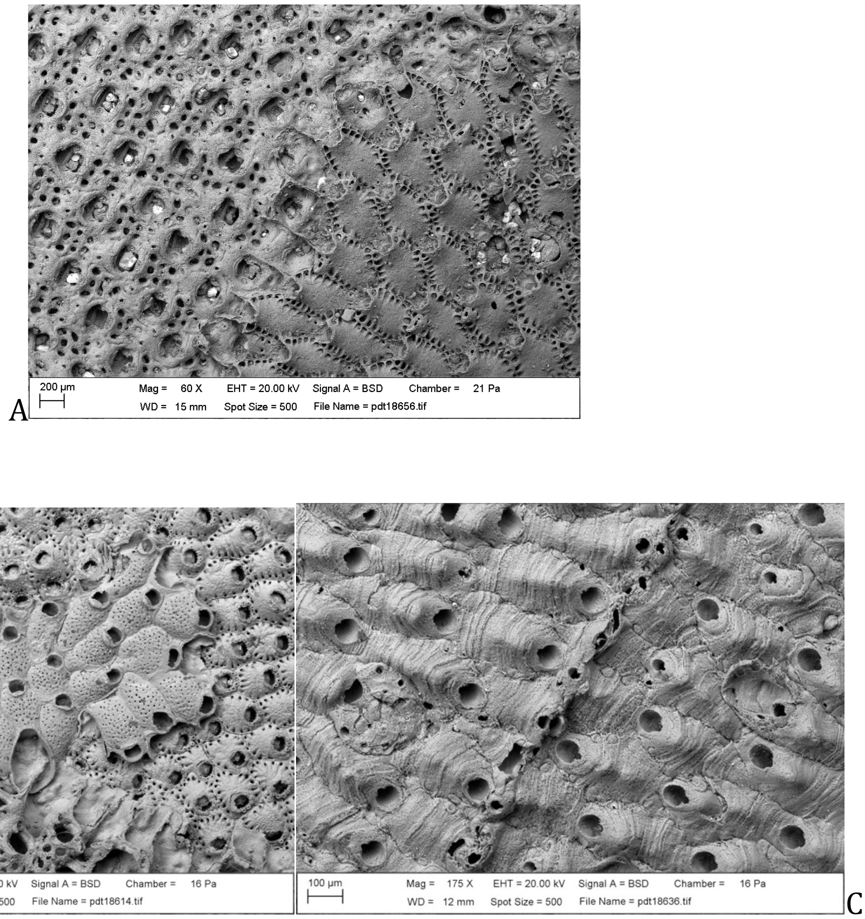


Figure 1: SEM Photos of different types of interactions between bryozoan colonies. A shows a nice example of overgrowth where an *Escharoides excavata* grows over an *Arachnopusia unicornis.* B shows a young *Emballotheca waipukurensis* who fouls an *Escharella spinosissima* and C shows a standoff between two *Antarctothoa tongima* colonies. Photos by Paul Taylor.

Previous studies on overgrowth between colonies have focused the angles of the encounter, location and time (Turner & Todd, 1994). One study, which takes encounter angle into consideration, shows that a tie is more likely if interacting colonies meet at the front, while overgrowth is more likely if colonies encounter other colonies in their terminal section (Turner & Todd, 1994). The same study also showed that competitive ability was affected by location. Some species would differ in interactions in different places (Turner & Todd, 1994).

Studies on prehistoric bryozoan interactions have mostly focused on the competition at clade level (Sepkoski Jr *et al.*, 2000) (Lidgard *et al.*, 1993) (c. These studies discovered a major change in bryozoan diversity in the past. This change started mid-Cretaceous and includes the

the two bryozoan orders Cheilostomata and Cyclostomata (Lidgard *et al.,* 1993) (McKinney, 1992). Before the mid-Cretaceous, the Cheilostomes had a small amount of diversity, but from this point in geological history, their species diversity increased (Sepkoski Jr *et al.,* 2000). So the Cheilostomata grew in diversity, while the opposite thing happened to the Cyclostomata (Jablonsky *et al.,* 1997).

Although these studies of clade level-competition are important and reveal interesting information on the evolutionary history of bryozoans, competition is inherently a phenomenon that happens between individuals, and not between higher taxonomic groups. Not many studies on bryozoan interactions have focused on the competition between individuals belonging to different species. Also, previous work on bryozoan competition regarding anything size related has only been investigating the effects of colony size on competitive outcomes (Nandakumar & Tanaka 1997). To what extent zooid size is an important trait in competitive ability is now known.

This study is the first to investigate the effect of zooid size on the outcome of species level Cheilostome interactions. Since zooid size is something that varies little among individuals of the same species, investigating the effect of the size of zooids on competition will also help us learn if some species actually are better competitors than others. I will look at interactions from the different time periods and see if any species change their competitive ability over time, which will be very interesting from an evolutionary point of view.

This will also be one of the first studies to look at competition over a long term scale at species level. I will investigate five species which area all present in all of the time periods I have chosen for my study, and I will also look at the Cheilostome/Cyclostome interactions through deep time as well as the Cheilostome/Cheilostome interactions to see if there are any differences in competitive abilities and if there are any differences, why might that be.

2 Materials and methods

The main material in this study comes from a geological formation called the Nukumaru Limestone Formation (NKLS) in New Zealand.

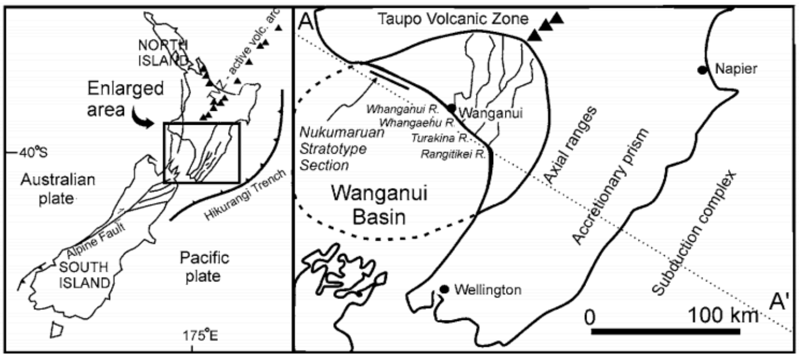


Figure 2: An overview of the Wanganui Basin where the study material has been collected (Abbott *et al.*, 2005)

This formation is approximately 2 million years old (Abbott *et al.*, 2005). The fossils were collected January 2014 from the Wanganui Basin in New Zealand. The material used in this study consist of fossilized bivalves with encrusting bryozoans (Liow *et al.*,2016). Data was also collected from specimens kept at the Natural History Museum in London. This material was collected from the same location in New Zealand, but at a different time and for a different purpose.

Scanning Electron microscope images

Not only was more data collected at the National History Museum, but there was also an opportunity to get some SEM photographs of shells picked out in advance taken. During the stay in London, two sessions of SEM photographing was conducted, with several shells, different colonies and different interactions being captured.

Not only did I use fossils from the NKLS, but I also used as data from the Nukumaru Brown Sand (NKBS) which is approximately between 1.80 and 1.99 Ma and the Upper Kai-iwi Shellbed which is approximately around 68 Ma (Abbott *et al.*, 2010) (Naish *et al.,* 2005) 5231 interactions from the NKLS samples was collected for this study specifically, while 1078 interactions were collected from the dataset for another study (Liow *et al.*, 2016). Data from NKBS and Upper Kai-Iwi Shellbed was also collected from this study. Distributions of interaction types and the angles in which the interactions happened were investigated, along with the number of cases where the cheilostome colony with the biggest and smallest zooids won. A Bootstrap method was used for every plot except for the distribution of Cyclostome and Cheilostome interactions and the distribution of interaction types. During the bootstrap I resampled the original data to test the strength and validity of your data.

Regarding the Cyclostomes and Cheilostomes, I analyzed both a data set containing all individual colonies measured and a smaller data set containing only the interactions where both participating colonies had been identified to species level. The competitive outcome of interactions involving the species *Antarctothoa tongima*, *Aimulosia marsupium, Arachnopusia unicornis, Microporella agonistes* and *Crepidacantha crinispina* were investigated to check if these species' competitive ability change or stay constant over time. All these five species are present in the three stratigraphic sections investigated.

Fossils where cleaned to increase the possibility of observing interactions between bryozoan colonies. Depending on the fragility of the fossils, different cleaning methods were used: Careful removal of sand/dirt by using a brush, carefully picking off the more difficult pebbles, washing the dirt off by putting the shell under running water, and ultrasonication was used for shells that contained a heavy amount of dirt or where the dirt was difficult to get off (Liow *et al*., 2016). After cleaning and drying of the study material, each fossil was given a unique number in order to keep the samples organized. To make a complete record of the study material, every shell was to be photographed. If bryozoan colonies grew on both sides of the shell, both sides were photographed.

Collecting data consisted of investigating photos of each shell, both sides if applicable, and register colonies and their interactions. Each separate colony was given a unique number so it was easy to keep the data organized. Writing down every single colony would take too much time, so I was only registering the colonies that interacted with other colonies. Both cheilostome and cyclostome bryozoans were included in the collected data. Cheilostome species were identified down to species level if possible, and to genus level if species identification wasn't possible due to poor preservation. Due to the difficulties of identifying cyclostome species because of fewer polymorphic traits, they were, if possible, only identified down to a genus level. The type of interaction and the outcome were registered. In cases of overgrowth, the winning colony was marked with a "W" and the losing colony was marked with an "L". Standoff interactions were marked with an "SO", fouling interactions with an "F" and reciprocal overgrowth interactions were marked with an "R". When observing an interaction between two cheilostome colonies, additional information was added as well. A comparison of zooid size between the involved cheilostome colonies was done by eye. The colony with the biggest zooids was marked with "B", while the one with the smaller zooids were marked with an "S". The zooid size was marked as "Similar" in cases when no clear difference in zooid size was observed. Zooid size was marked as "Equal" in interactions between two colonies of the same species. Interactions between two cheilostome colonies where the zooid size was not possible to determine were marked with a "?". This would be applied If the zooids were in so bad shape they were unrecognizable both in shape and/or in size. When it comes to cyclostomes, the zooid size would be close to impossible to determine due to their colony structure, so interactions between a cheilostome colony and a cyclostome colony or between two cyclostome colonies were just marked as "NA". Each interaction was carefully studied, and in cases where there were any uncertainties regarding the outcome of the interaction, like if a colony was fouling or not, or if it was uncertain if a colony was really winning over the other one, they would be marked as "U". Interactions with certainty in the outcome were marked as "C".

This procedure was done for every shell in every sample from the Nukumaru Limestone formation. The total amount of shell in the NKLS counted 497. The total number of interactions were 6309, and the number of colonies per shell varied tremendously; from cases with only one interaction to shells with over 80 interactions. After finishing a sample, the data which was written down on paper would be transferred to a computer and into a spreadsheet. Additional information like the date the data was added, the sample ID, the shell ID and information about on which side of the shell the interactions happened; marked as either "INT" (for interior side), and "EXT" (for exterior side), was also registered in the spread sheet.

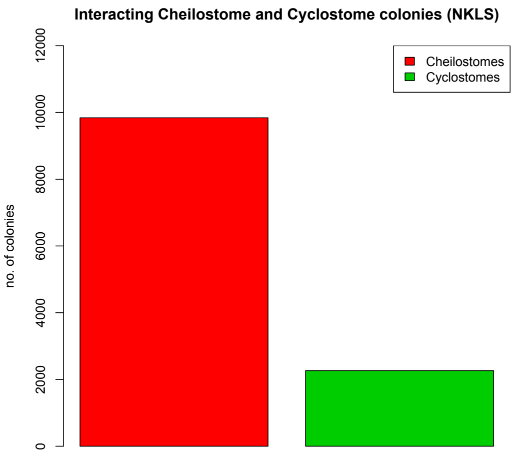
All analyses where conducted in the program R (R Core Team 2013) Removal of uncertain data was done early in the process, removing any buzz that might have affected the results of the analysis. Since most of my analysis would look at only cheilostomes, removing cyclostomes from the dataset in R was done quickly. During the analysis of the outcome between bigger zooid size versus smaller zooid size in overgrowth interactions, removal of the other interaction types was crucial, so every interaction marked with “F”, “R” and “SO” was left out. For the analysis that focused on interactions down to species level, any interaction where one or both colonies was not identified to species level was removed.

I analyzed data from the Nukumaru Limestone formation (NKLS) which is approximately 2 Ma, as well as data from the Nukumaru Brown Sand (NKBS) which is approximately between 1.80 and 1.99 Ma and the Upper Kai-iwi Shellbed which is approximately around 68 Ma (Abbott *et al.*, 2005) (Naish *et al.,* 2005. 5231 interactions from the NKLS samples was collected for this study specifically, while 1078 interactions were collected from the dataset for another study (Liow *et al.*, 2016). Data from NKBS and Upper Kai-Iwi Shellbed was also collected from this study. Distributions of interaction types and the angles in which the interactions happened were investigated, along with the number of cases where the cheilostome colony with the biggest and smallest zooids won. A Bootstrap method was used for every plot except for the distribution of Cyclostome and Cheilostome interactions and the distribution of interaction types. The number of replicates was set to 1000. During the bootstrap I resampled the original data to test the strength and validity of your data.

Regarding the Cyclostomes and Cheilostomes, I analyzed both a data set containing all individual colonies measured and a smaller data set containing only the interactions where both participating colonies had been identified to species level. The competitive outcome of interactions involving the species *Antarctothoa tongima*, *Aimulosia marsupium, Arachnopusia unicornis, Microporella agonistes* and *Crepidacantha crinispina* were investigated to check if these species' competitive ability change or stay constant over time. All these five species are present in the three stratigraphic sections investigated.

3 Results

The Nukumaru Limestone (NKLS) dataset consists of 6309 interactions in total, with 497 shells distributed from 18 samples. We observed 73 genera and 92 species. The distribution of Cheilostomes and Cyclostomes from the Nukumaru Limestone Formation, as seen in figure 3a, shows 10152 cases where you have cheilostome colonies involved in any interaction, and 2235 colonies where you have cyclostome colonies as part of an interaction. The number may seem confusing when compared to the number of interactions in total, as it is much bigger, but when the Cheilostomes and Cyclostomes were counted, it included colonies that have been involved in several interactions. The dataset contains, among other columns, two columns where the order of the two interactive colonies was written down. And sometimes two colonies of the same order interacted with each other, so those interactions counted as "double". And that's why the number of interactions containing Cheilostomes and Cyclostomes increased. These numbers count all interacting colonies in an interaction, which is why the numbers are higher that the number of interactions themselves. The distribution of Cheilostome and Cyclostome interactions from the Nukumaru Brown Sand samples is shown in figure 3b. The number of interactions that contain at least one Cheilostomes is 1925 and the number of interactions that contain at least one Cyclostome is 254. Figure 3c shows the interaction distribution of the Upper Kai-Iwi Shellbed. Here there are 2988 interaction that at least contain one Cheilostome and 268 interactions that contain at least one Cyclostome.



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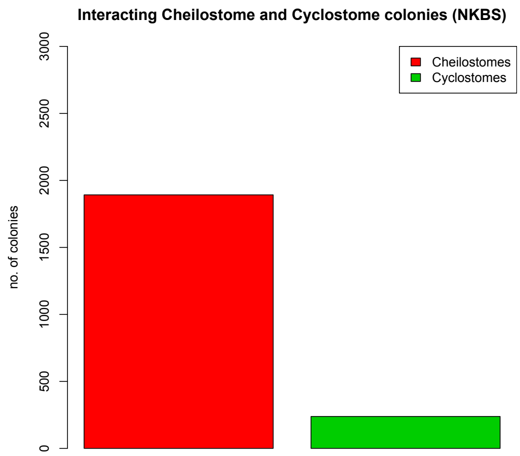

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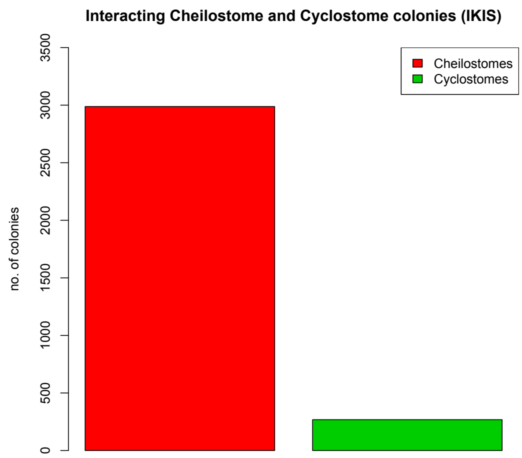

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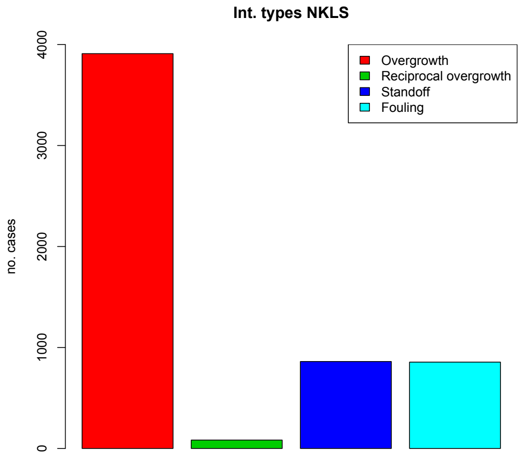
Figure 3a, b and c: Figure 3a shows the number of Cheilostome and Cyclostome colonies participating in interactions in the samples from the Nukumaru Limestone Formation. These numbers represent all competing colonies, so the numbers in the figures are higher than the count of total interactions in the data set. Figure 3b and 3c shows the number of Cheilostome and Cyclostome colonies participating in interactions in the NKBS and Upper Kai-Iwi Shellbed formations, respectively.

The distribution of the different types of interactions (overgrowth, reciprocal overgrowth, standoff and fouling) for both Cheilostomes and Cyclostomes from the NKLS formation can be seen in figure 4a with 3910 cases of overgrowth (counting both wins and losses), 83 cases of reciprocal overgrowth, 861 cases of standoff and 855 cases of fouling. Figure 4b shows the result from the NKBS formation and here the distribution counts: 604 cases of overgrowth, 5 cases of reciprocal overgrowth, 279 cases of standoff and 66 cases of fouling. Figure 4c shows the interaction type distribution from the Upper Kai-Iwi Shellbed and here it counts: 767 cases of overgrowth, 22 cases of reciprocal overgrowth, 145 cases of standoff and 147 cases of fouling.



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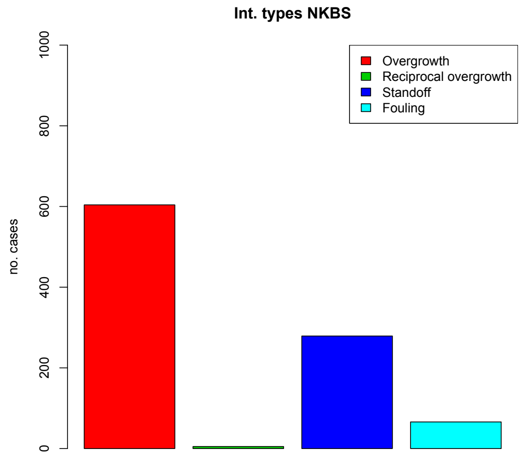

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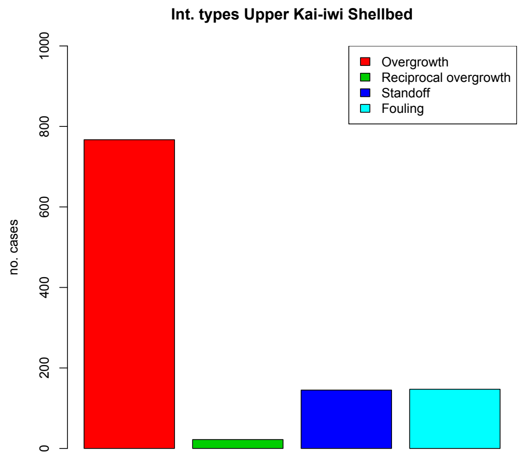

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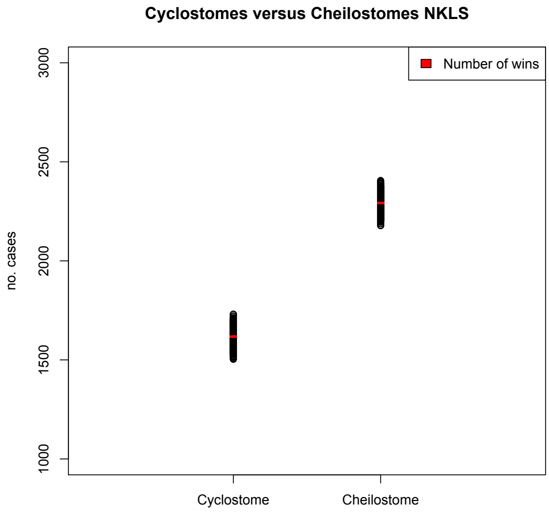
Figure 4a-c: 4a shows the distribution of the different interaction types in the Nukumaru Limestone samples including both Cheilostomes and Cyclostomes. The red bar shows the cases of overgrowth, the green bar shows the cases of reciprocal overgrowth, the blue bar shows the cases of standoff and the turquoise bar shows the cases of fouling. 4b shows the distribution from Nukumaru Brown Sand and 4c shows the distribution from Upper Kai-Iwi Shellbed.

There is a clear pattern that Cheilostome colonies win more often in interactions with Cyclostomes colonies in all three formations (figure 5a, b, c). There are 2292 cases of interactions where cheilostome colonies win and 1617 cases where the Cyclostome colonies win in the NKLS formation (figure 5a). In the data from NKBS (figure 5b) there are 362 cases where the Cheilostomes wins and 242 cases where the Cyclostomes win, and there are 493 cases where the Cheilostomes win, and 274 cases where the Cyclostomes win in the Upper Kai-Iwi Shellbed (5c).



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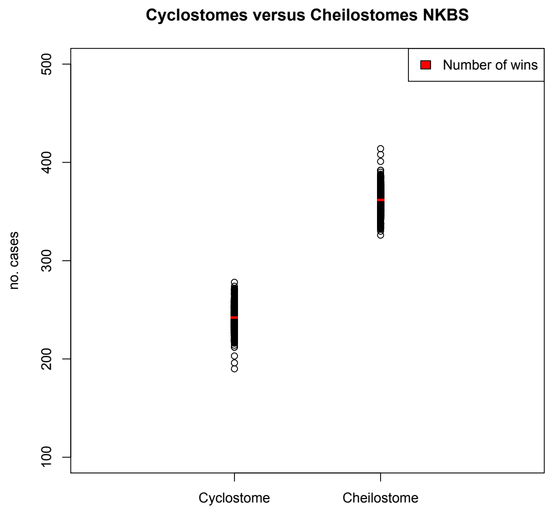

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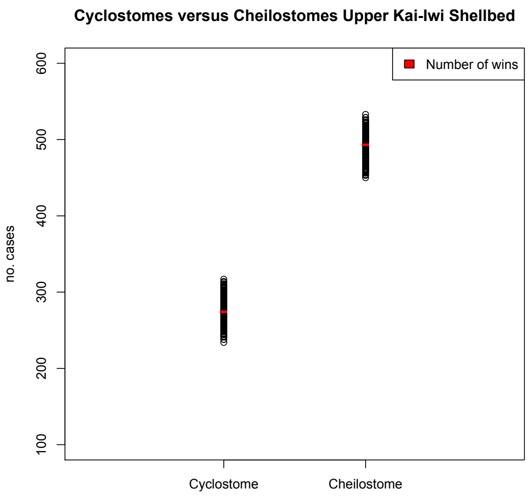

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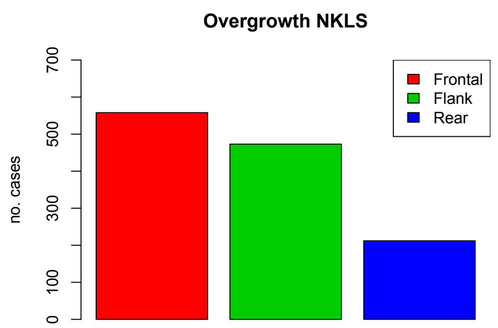
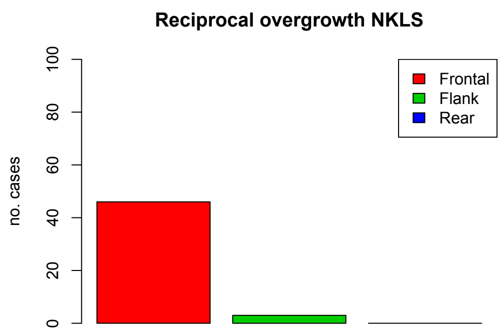
Figure 5a-c: Figure 5a shows number of wins for cheilostome bryozoans and cyclostome bryozoans from the NKLS formation. The red line shows the counted wins in the original data, while the black dots represent estimated wins in the bootstrap replicates. Non-overlapping distributions of the bootstrap data indicate difference in wins between

Cyclostomes and Cheilostomes. 5b shows the same, but with the data from NKBS and 5c shows the data from Upper Kai-Iwi Shellbed

Looking more detailed at the overgrowth interaction and from which angle it happens (flank, frontal or rear), the distribution of these in the NKLS samples are: 558 cases of overgrowth from a frontal angle, 473 cases from the flank and 212 cases of overgrowth happening at the rear of one of the colonies. When it comes to standoff interactions there are 626 cases of overgrowth from a frontal angle, 19 from the flank and 2 from a rear angle. Reciprocal overgrowth interactions have 46 cases from a frontal angle and 3 from the flank. No rear reciprocal overgrowth was found. This can be seen in figure 6a-c.





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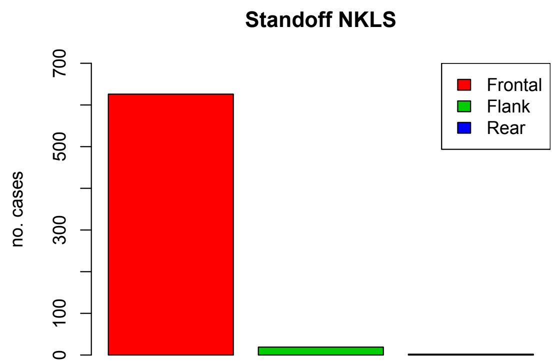

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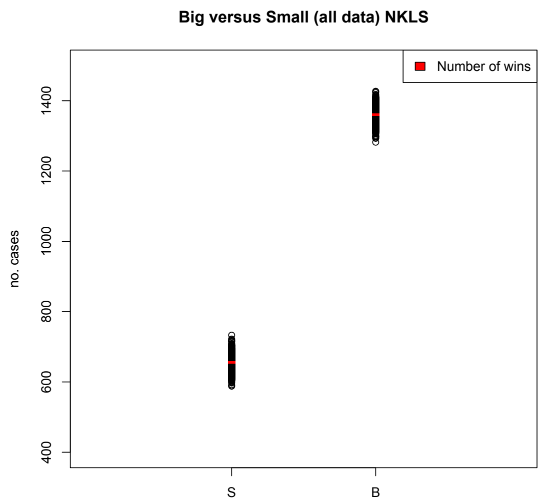
Figure 6a-c: The distribution of the different interaction angles for the different interaction types in the NKLS formation. Figure 6a shows the possible angles an overgrowth can happen from and the distribution of them in the NKLS samples. Figure 6b shows the distribution of the angles in cases of reciprocal overgrowth and figure 6c shows the same only in cases of standoff.

The colony with the biggest zooids tends to wins more often compared to colonies with smallest zooids (figure 7a-f). Both the plots containing all the data points (figure 7a, c, e) and the plots where only the interactions where both colonies had been identified to species were used (figure 7b, d, f) showed the same result. In the NKLS plot with all the data points, there are 1360 cases where the cheilostome with the bigger zooids won, and 655 where the cheilostome with the smaller zooids won, and in the plot where only the interactions with both interacting colonies have been identified to species there are 783 cases where the cheilostome with the biggest zooids won and 333 cases where the cheilostome with the smaller zooids won. In the NKBS plot with all the data points, there are 305 cases where the Cheilostome with the bigger zooids won, and 71 where the Cheilostomes with the smaller zooids won, and in the plot where only the interactions with both interacting colonies have been identified to species there are 214 cases where the Cheilostome with the biggest zooids won and 51 cases where the Cheilostome with the smaller zooids won. In the Upper Kai-Iwi Shellbed plot with all the data points, there are 330 cases where the cheilostome with the bigger zooids won, and 166 where the cheilostome with the smaller zooids won, and in the plot where only the interactions with both interacting colonies have been identified to species there are 169 cases where the cheilostome with the biggest zooids won and 79 cases where the cheilostome with the smaller zooids won.

and 79 cases where the cheilostome with the smaller zooids won.



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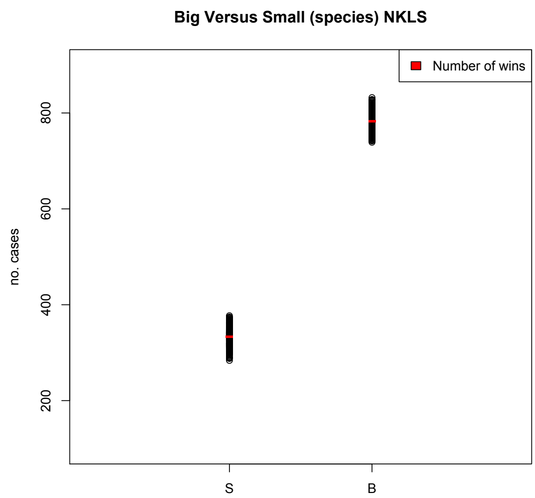

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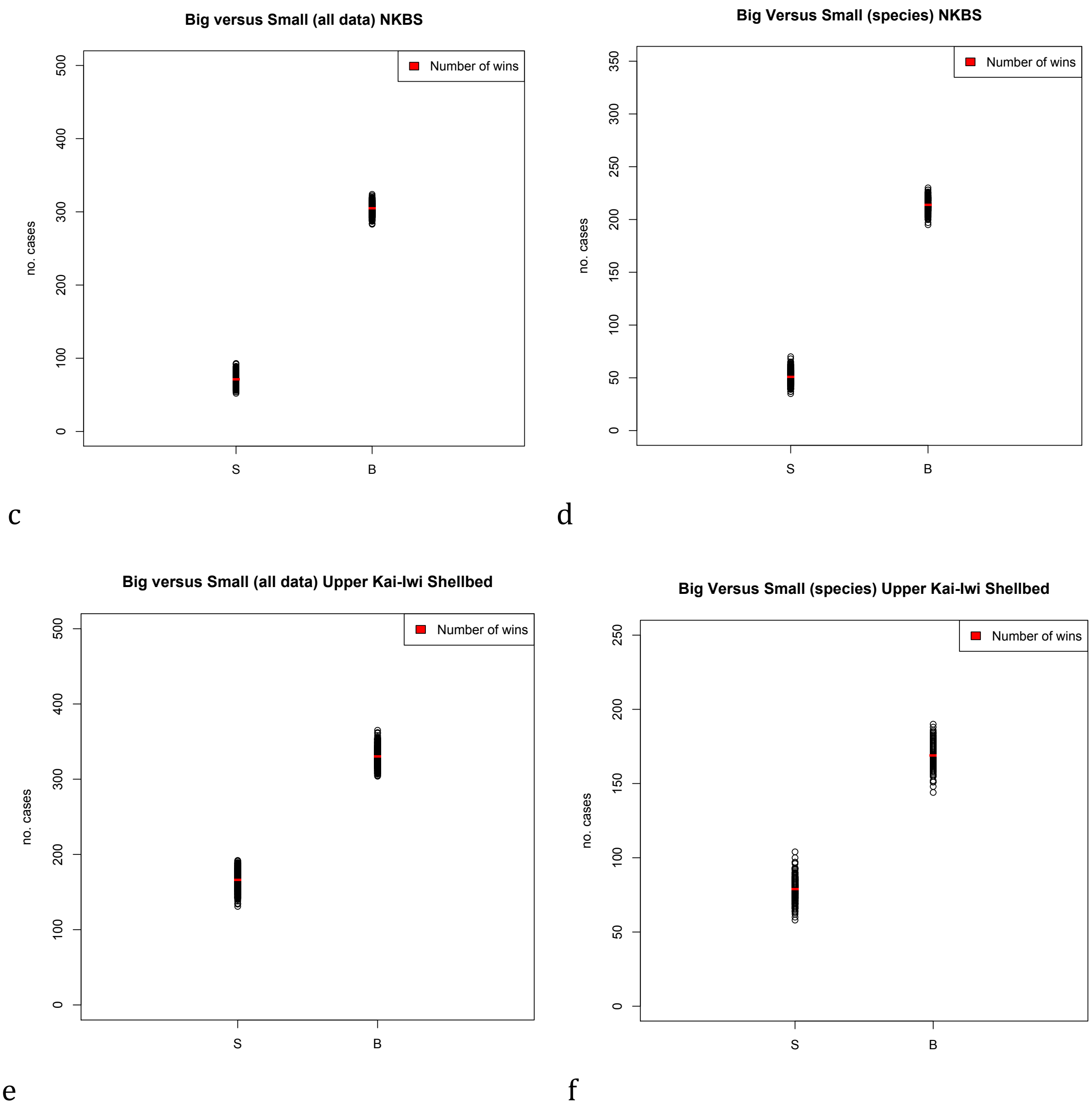
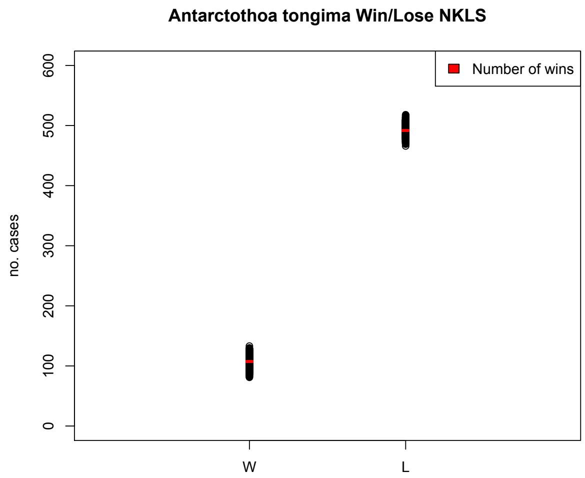


Figure 7a-f: Figure 7a and b shows the bootstrapped results of the interactions between cheilostome colonies with smaller and bigger zooids in the NKLS formation, showing how many cases the colony with the smallest and biggest zooids wins, respectively.. Figure 7a contains all the data points in the dataset while 7b shows the results when only focusing on interactions where both colonies in the interaction had been identified to species level. Figure 7c and d show the same analyses for the NKBA formation and Figure 7e and f show the same analyses for the Upper Kai-Iwi Shellbed formation.

Antarctothoa tongima

Figure 8a shows the distribution of wins/losses when *A. tongima* is involved in overgrowth interactions in the Nukumaru Limestone formation. The amount of wins counts 107 and the amount of losses counts 492. Figure 8b shows the cases where *A. tongima* wins and the distribution of wins when it is the biggest competitor and when it is the smallest competitor. The cases of wins while being the smallest competitor counts 23 and the cases of wins when it's the biggest competitor counts 30. Figure 8c and 8d shows the data from the NKBS samples and 8c shows that *A. tongima* wins 18 times and loses 99 times, and in figure 8d we see that the species wins 9 times when it is the bigger competitor and it wins 3 times while being the smallest competitor. Figure 8e and 8f show the data from the Upper Kai-iwi Shellbed. 8e shows us that *A. tongima* wins 23 times while it loses 57 times, and 8f shows that it wins 4 times while being the bigger competitor and wins 9 times while being the smallest competitor.



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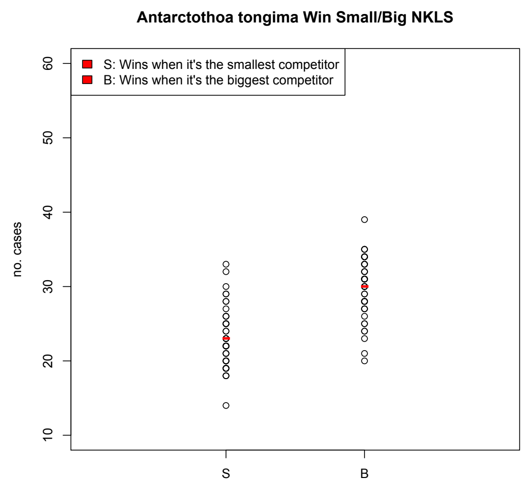

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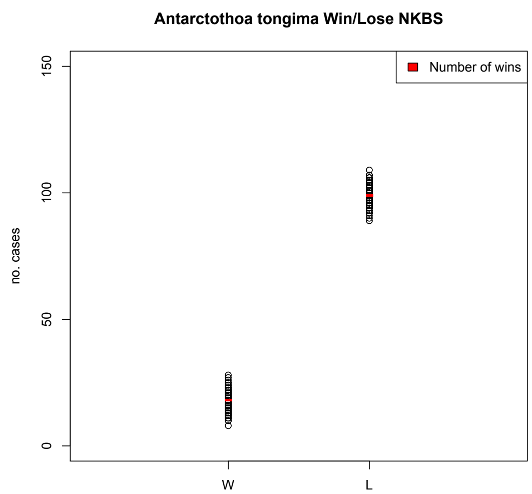

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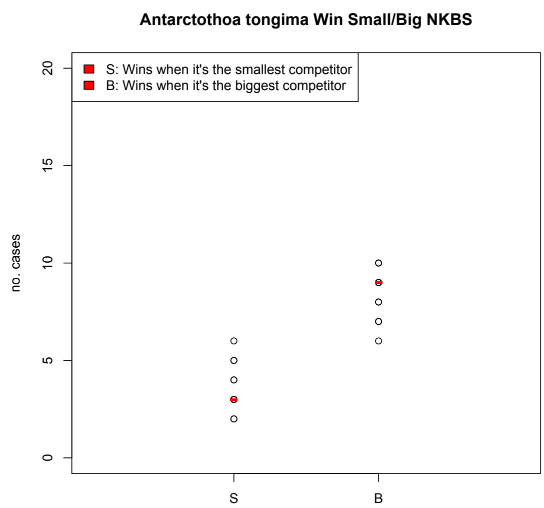
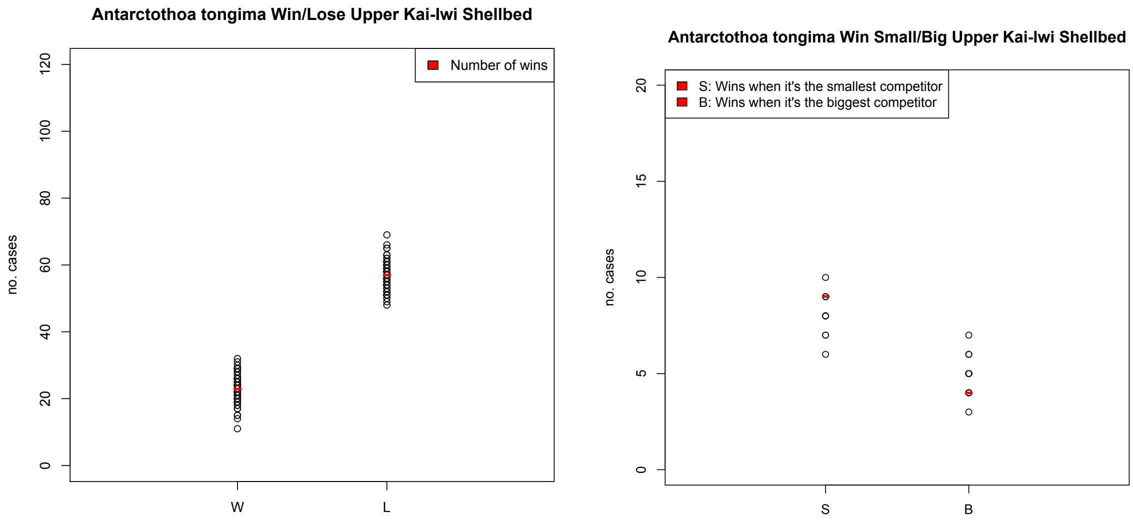


d



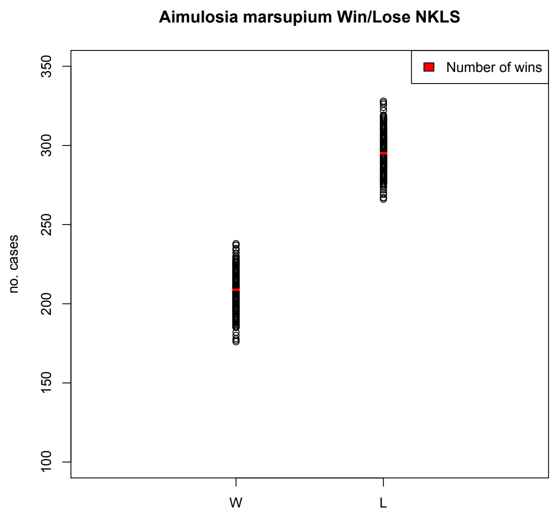
e f

Figure 8a-f: Figure 8a shows the bootstrapped NKLS distributions of wins/losses for *Antarctothoa tongima* while figure 8b shows the distributions of wins in NKLS when it is the colony with the bigger zooids and the cases where it wins and it has the smaller zooids. Figure 8c and 8d show the same plots for the NKBS formation and 8e and 8f show the same plots for the Upper Kai-Iwi Shellbed. Note the overlapping distributions of points in plots b, d, and f.

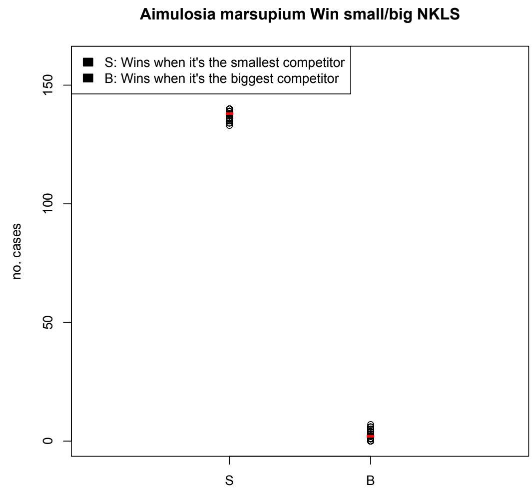
Aimulosia marsupium

Figure 9a shows the distribution of wins/losses when *Aimulosia marsupium* is involved in overgrowth interactions in the Nukumaru Limestone formation. The number of times *A. marsupium* wins is 209, while its losses counts 295. In figure 9b we see the distributions of wins when *A. marsupium* is the smallest competitor and when it's the biggest competitor. The number of wins when *A. marsupium* is the smallest competitor is 138, while the number of wins when it's the biggest competitor is 2. For the NKBS formation we have figure 9c and 9d, and in figure 9c we see that *A. marsupium* wins 34 times and loses 96 times. Figure 9d shows us that *A. marsupium* wins 3 times when it's the biggest competitor, and 19 times when it's the smallest competitor.

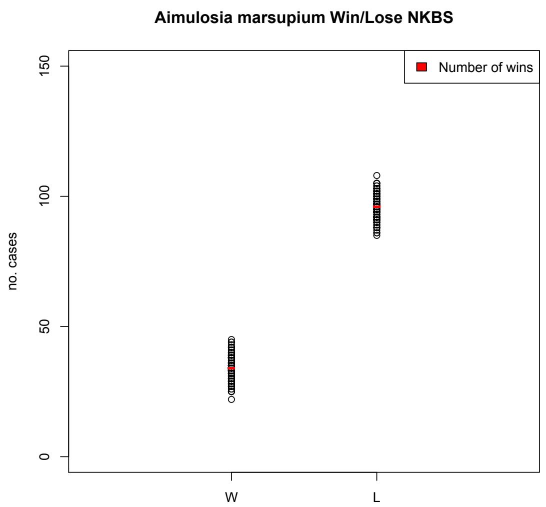
Figure 9e shows the amount of wins and losses for *A. marsupium* in the Upper Kai-iwi Shellbed samples. It wins 29 times and loses 47 times. Figure 9f shows the species' wins and whether or not it wins more as a small competitor than a big one, and here it wins 16 times when it is the smallest competitor and 0 times when it is the biggest one.


Aimulosia marsupium Win/Lose NKLS
Number of wins
no. cases
100
150
200
250
300
350
W
L

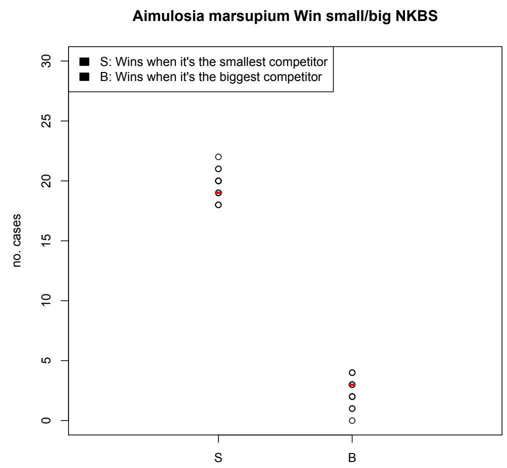
a


Aimulosia marsupium Win small/big NKLS
S: Wins when it's the smallest competitor
B: Wins when it's the biggest competitor
no. cases
0
50
100
150
S
B

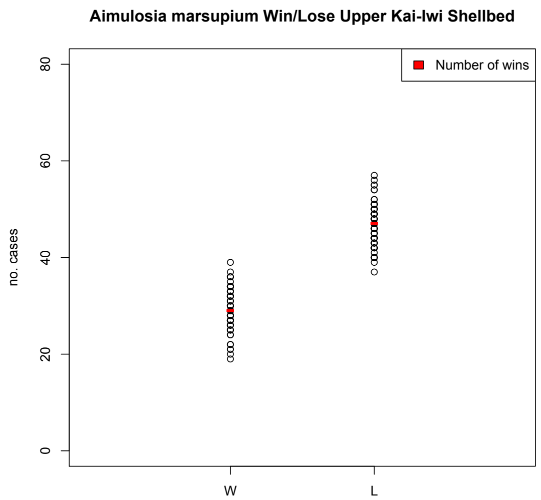
b


Aimulosia marsupium Win/Lose NKBS
Number of wins
no. cases
0
50
100
150
W
L

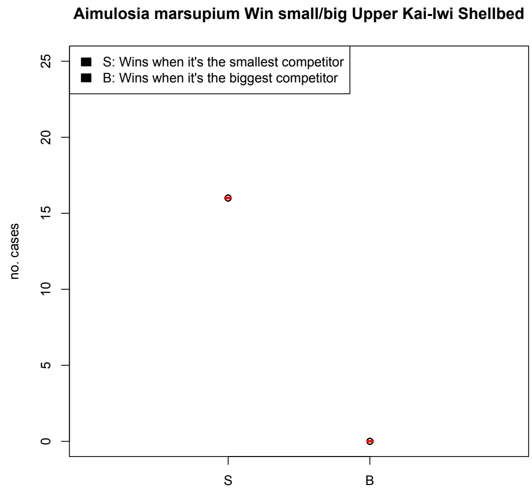
c


Aimulosia marsupium Win small/big NKBS
S: Wins when it's the smallest competitor
B: Wins when it's the biggest competitor
no. cases
0
5
10
15
20
25
30
S
B

d


Aimulosia marsupium Win/Lose Upper Kai-Iwi Shellbed
Number of wins
no. cases
0
20
40
60
80
W
L

e

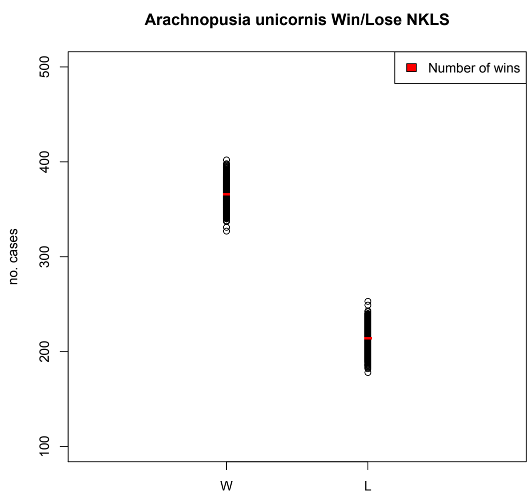

Aimulosia marsupium Win small/big Upper Kai-Iwi Shellbed
S: Wins when it's the smallest competitor
B: Wins when it's the biggest competitor
no. cases
0
5
10
15
20
25
S
B

f

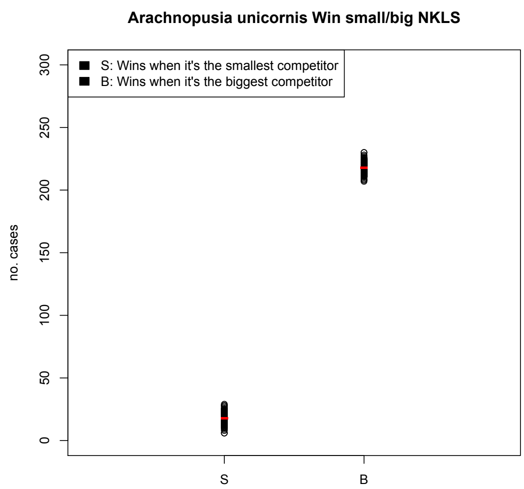
Figure 9a-f: Figure 9a shows the NKLS distributions of wins/losses for *Aimulosia marsupium* while figure 9b shows the NKLS distributions of wins when the species is the colony with the bigger zooids and the cases where it wins and it has the smaller zooids. Figure 9c and 9d show the same things, but with data from NKBS and figure 9e and 9f do the same with the Upper Kai-Iwi Shellbed data.

Arachnopusia unicornis

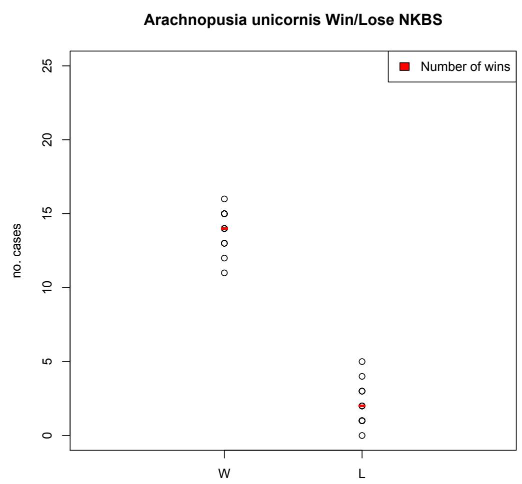
Figure 10a shows the amount of wins and losses for the interactions *Arachnopusia unicornis* is involved in from the NKLS formation. The number of wins count 366 while the amount of losses counts 214. In figure 10b where the distribution of wins when *A. unicornis* is the smaller competitor and when it's the bigger competitor. The amount of wins when it is the smaller competitor counts 18 while it counts 218 when it is the bigger competitor. In figure 10c (NKBS data) we see that *A. unicornis* wins 14 times and loses 2 times, while in 10d (NKBS data) we see that it wins 9 times when it is the bigger competitor and that it won 1 time when it is the smallest competitor. Figure 10e and 10f are from the Upper Kai-Iwi Shellbed data and 10e shows us that *A. unicornis* wins 19 times and loses 8 times, while 10f shows us that it wins 11 times when it's the biggest competitor while it won 1 interaction as the smaller competitor.



a



b



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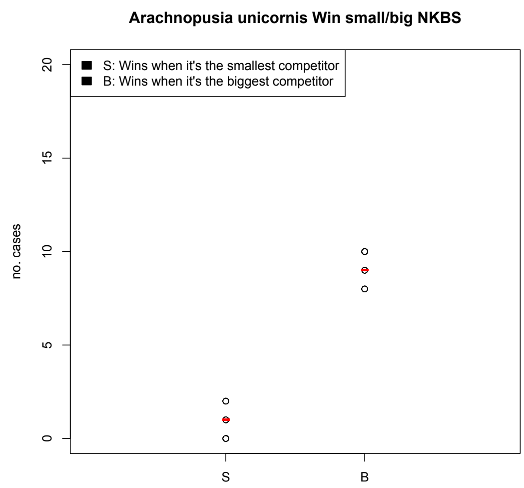

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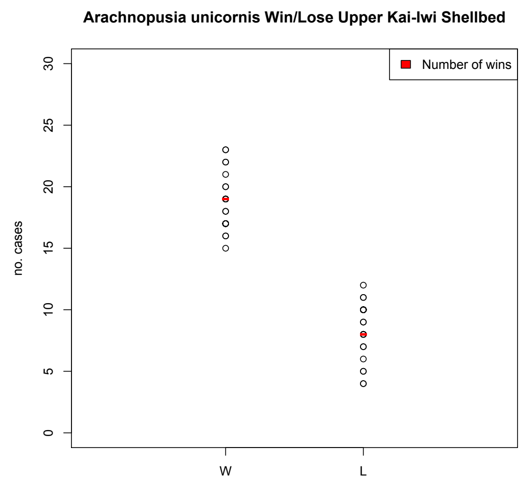

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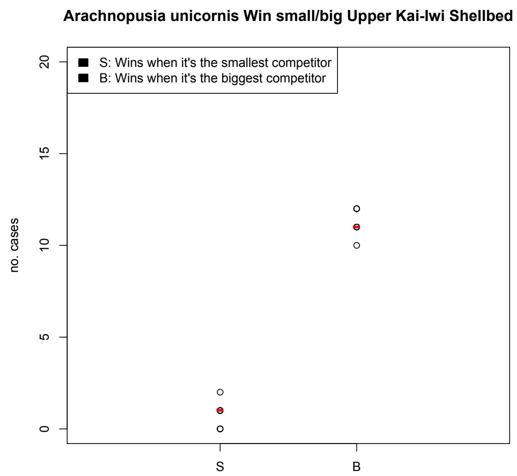
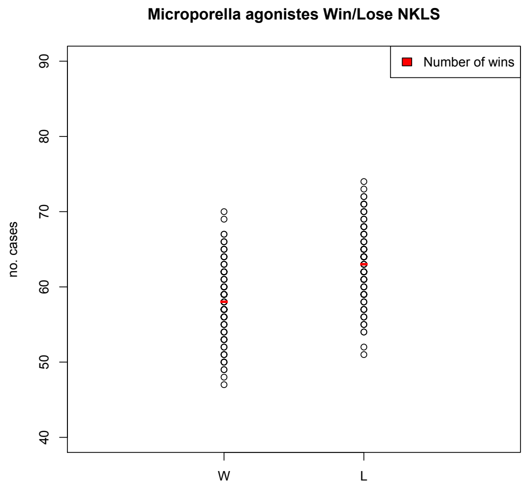


f

Figure 10a-f: Figure 10a shows the NKLS distributions of wins/losses for *Arachnopusia unicornis* while figure 10b shows the distributions of wins when it is the colony with the bigger zooids and the cases where it wins and it has the smaller zooids. Figure 10c and 10d show the same, only for the NKBS data and figure 10e and 10f show it for the Upper Kai-Iwi Shellbed data.

Microporella agonistes

Figure 11a shows the distribution of wins/losses when *Microporella agonistes* is involved in overgrowth interactions in the NKLS formation. The amount of wins counts 58 and the amount of losses counts 63. Figure 11b shows the cases where *M. agonistes* wins and the distribution of wins when it's the biggest competitor and when it's the smallest competitor. The cases of wins while being the smallest competitor counts 3 and the cases of wins when it is the biggest competitor counts 34. Figure 9c and 9d show the plots for the NKBS data and 11c shows that *M. agonistes* wins 39 times and loses 29 times, while 11d shows us that it wins 20 times when it is the bigger competitor and 1 time when it is the small competitor. Figure 11e and 11f shows the data for the Upper Kai-Iwi Shellbed. 11e shows us that *M. agonistes* wins 47 times and loses 51 and 11f shows us that the species win 27 times when it is the bigger competitor and 6 when it is the smallest competitor.



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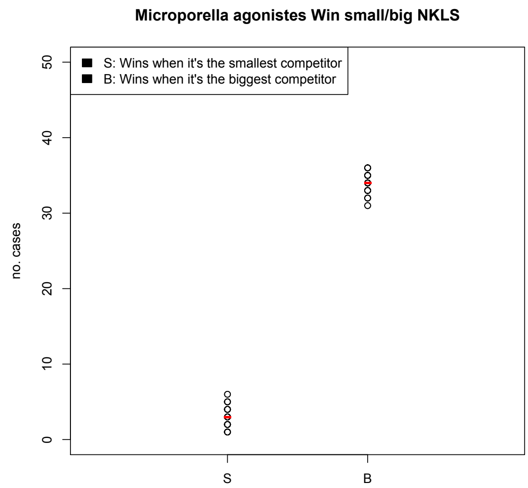
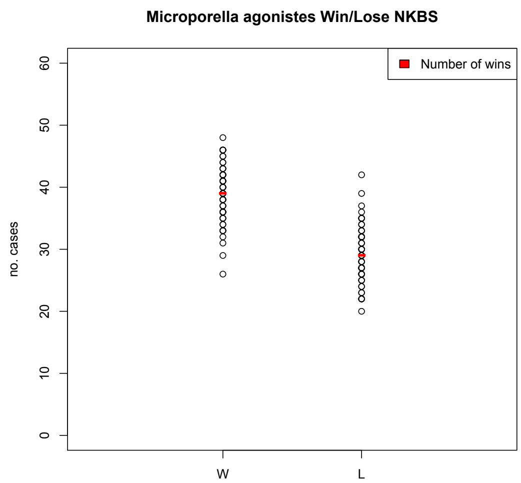


b



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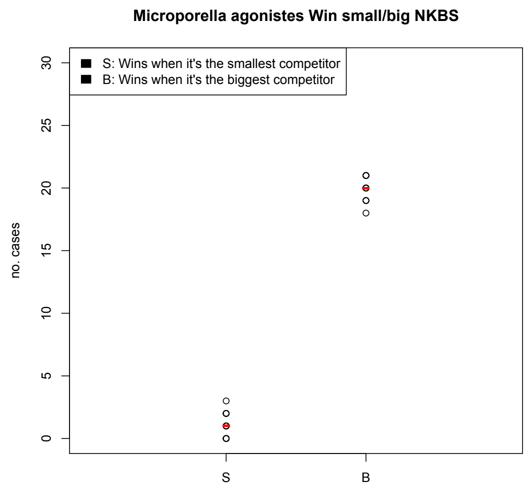

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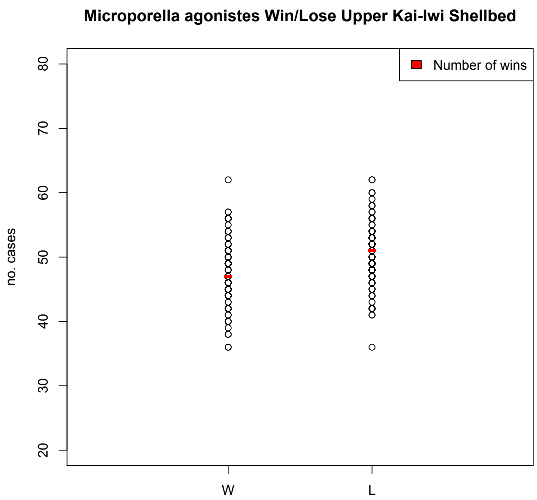

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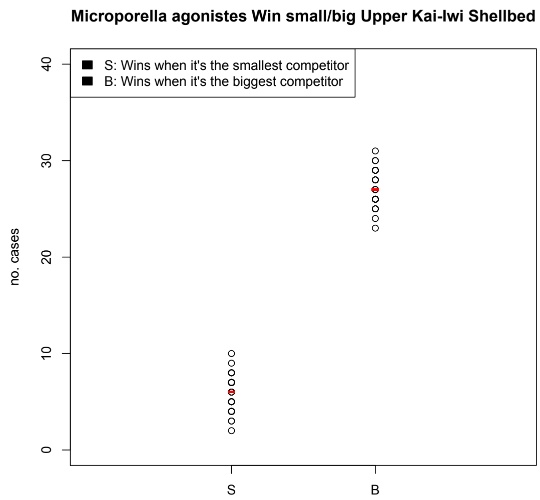
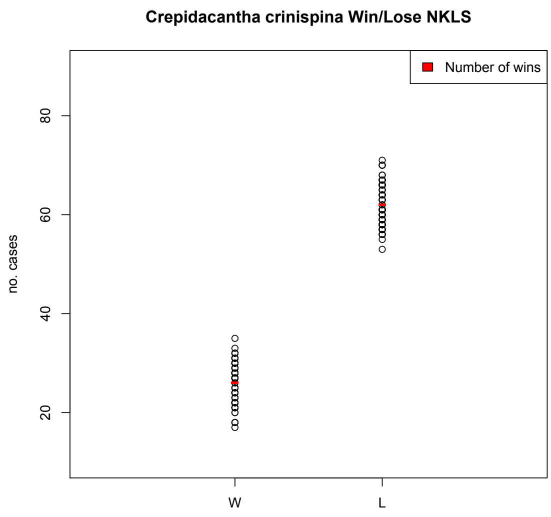


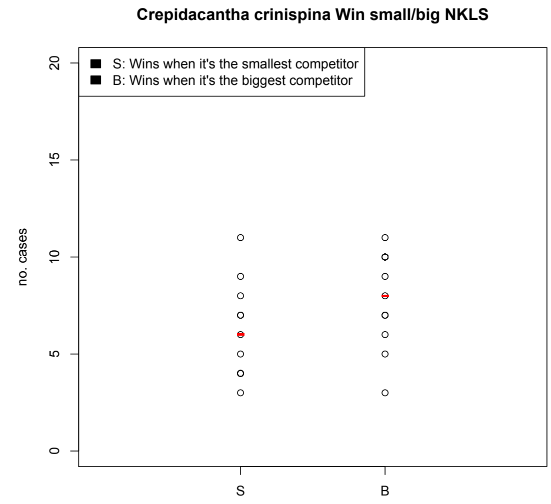
f

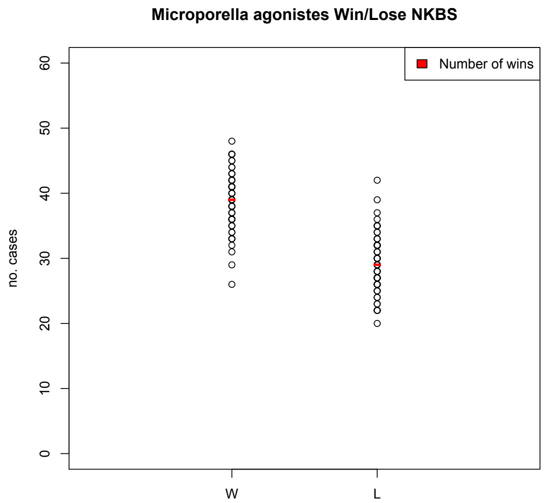
Figure 11a-f: Figure 11a shows the NKLS distributions of wins/losses for *Microporella agonistes* while figure 11b shows the distributions of wins when it is the colony with the bigger zooids and the cases where it wins and it has the smaller zooids. Figure 11c and 11d show the same, only for the NKBS data and figure 11e and 11f show it for the Upper Kai-Iwi Shellbed data. Note the overlapping distributions in plots a, c and e.

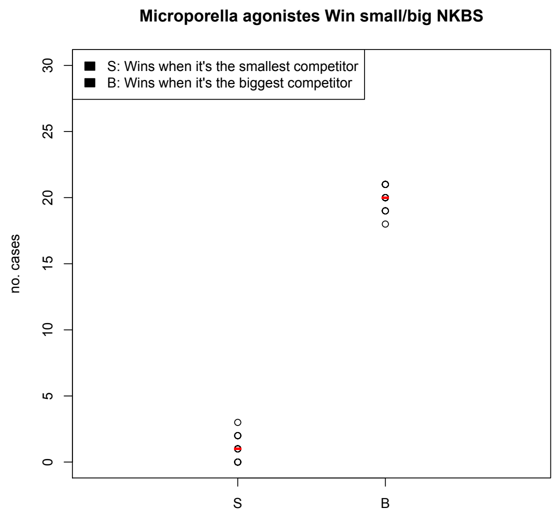
Crepidacantha crinispina

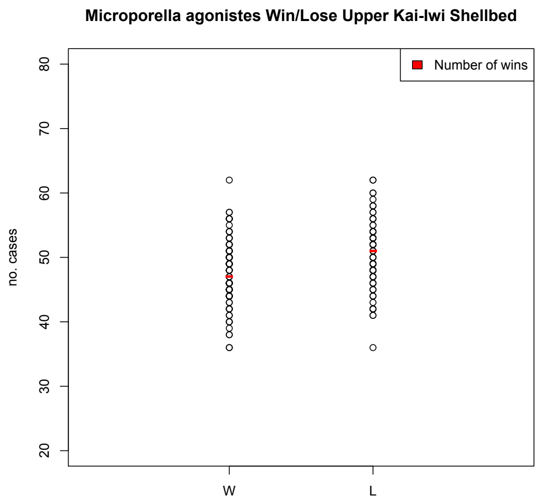
Figure 12a shows the NKLS distribution of wins/losses when *Crepidacantha crinispina* is involved in overgrowth interactions. The total amount of wins counts 26 and the amount of losses counts 62. Figure 12b shows the NKLS cases where *C. crinispina* wins and the distribution of wins when it is the biggest competitor and when it is the smallest competitor. The cases of wins while being the smallest competitor counts 6 and the cases of wins when i is the biggest competitor counts 8. Figure 12c and 12d shows the same plots for the NKBS data and in 12c we see that *C. crinispina* wins 5 times while it loses 20 times, and in 12d we see that it only wins 1 time when it is the bigger competitor and 2 times when it is the smaller competitor. Figure 12e and 12f show the plots for the Upper Kai-Iwi Shellbed, and in 12e we see that *C. crinispina* wins 85 times and loses 129 times. In 12f we see that the species win 16 times when it is the bigger competitor and 37 times when it is the smallest competitor.


Crepidacantha crinispina Win/Lose NKLS
Number of wins
no. cases
20
40
60
80
W
L


Crepidacantha crinispina Win small/big NKLS
S: Wins when it's the smallest competitor
B: Wins when it's the biggest competitor
no. cases
0
5
10
15
20
S
B


Microporella agonistes Win/Lose NKBS
Number of wins
no. cases
0
10
20
30
40
50
60
W
L


Microporella agonistes Win small/big NKBS
S: Wins when it's the smallest competitor
B: Wins when it's the biggest competitor
no. cases
0
5
10
15
20
25
30
S
B


Microporella agonistes Win/Lose Upper Kai-Iwi Shellbed
Number of wins
no. cases
20
30
40
50
60
70
80
W
L

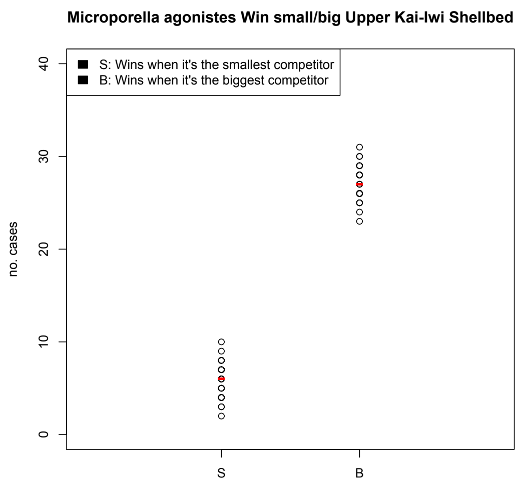

Microporella agonistes Win small/big Upper Kai-Iwi Shellbed
S: Wins when it's the smallest competitor
B: Wins when it's the biggest competitor
no. cases
0
10
20
30
40
S
B

Figure 12a-f: Figure 12a shows the distributions of wins/losses for *Crepidacantha crinispina in* NKLS while figure 12b shows the distributions of wins when it it the colony with the bigger zooids and the cases where it wins and it has the smaller zooids. Figure 12c and 12d show the same, only for the NKBS data and figure 12e and 12f show it for the Upper Kai-Iwi Shellbed data. Note the overlapping distributions in plots b, c and e.

4 Discussion

There have been remarkably few studies on bryozoan competition at a species level, and not many related to size and competition for that matter. One study looks at the colony size of the interacting colonies and how it might affect the outcome of the interactions (Nandakumar & Tanaka, 1997). Others have looked at the competition between clades like Cheilostomata and Cyclostomata and others (Barnes & Dick, 2000) (McKinney, 1994) (McKinney 1992), but as mentioned earlier in the introduction: This is the first study where zooid size is used to study Cheilostome interactions. This study presents brand new results regarding competition not only because it involves looking at a factor affecting competition (in this case zooid size), that no one has studied yet, but also because it looks at competition at species level as well.

If we look at the distribution of Cyclostomes and Cheilostomes involved in interactions, we see the consistency of there being more Cheilostome colonies in all of the three time periods investigated. There is also a clear pattern of Cheilostomes winning more interactions than Cyclostomes. If we take in the Cheilostomes' advantage in abundance, this might not be entirely surprising as they would be likely to have more winning interactions because of the sheer number of interacting cheilostomes. The figures showing the distribution of the different interaction types do also show almost the same result in all of the three time periods. The number of overgrowths is way more prominent than the other interaction types. In the Nukumaru Limestone and Upper Kai-iwi Shellbed samples standoff and fouling seem to be happening in a practically equal amount, but the distribution of standoff interactions and fouling interactions is not equal in the Nukumaru Brown Sand sample. Here, the amount of standoff interactions is higher than the number of fouling interactions. The reason behind this is unclear. It could have something to do with a lower number of data points, making the results somewhat randomly skewed. Or maybe the Nukumaru Brown Sand samples contain more intraspecific interactions which may end up in standoffs more often because of the same competitive ability between the two interacting colonies.

The main aim of this thesis was to discover if the zooid size of Cheilostome bryozoans affects the outcome of the overgrowth interactions. There is a clear trend that colonies with the biggest zooids in the interactions seem to win more often than a colony with the smallest zooids in the interaction. This seems to be the case for all the three time periods, even with the differences in the number of interactions. Also, whether the interacting species have been identified to the species level or not does not affect this result. There seems to be an advantage to be the biggest competitor in an interaction between Cheilostome colonies. Bigger zooids may help the colony growing over a smaller competitor because the sheer size is directly helping the colony to grow over the other one. Another reason might be that the larger species are just in general better at competing. *Arachnopusia unicornis* is a species with quite big zooids overall, and it's abundance in all the time periods made it possible to see how the species' competitive ability changes over time and if its size helps it win against smaller competitors. In all the three time periods, *A. unicornis* wins more often than it looses, and it seems to win more often when it is the bigger competitor than when it is the smaller one. This suggest it's advantageous to be bigger than your opponent, as it seems like most of the species in this study win more when they're bigger than their opponent.

Antarctothoa tongima is a relatively small species, and it was, as well as *A. unicornis*, found in all the time periods used in this study. Here the result is the opposite when it comes to the distribution of *A. tongima's* wins and losses. In all the time periods, it loses far more interactions than it wins which might be due to its smaller size and/or weaker competitive ability. *A. tongima* is a species with relatively high abundance, so that might be one way for the species to make up for its low competitive strength. When it comes to whether it wins the most when it is the bigger competitor or the smaller competitor, the results from NKLS and NKBS show that *Antarctothoa tongima* wins more when it is the biggest competitor, while the result from Upper Kai-iwi Shellbed shows the opposite. This might be due to low sampling size, which makes it difficult to make conclusive statements on the competitive ability of *A. tongima* over time. Since *A. tongima* generally does not win that much, it is not a surprise that the sampling size for number of wins is low. However, both NKLS and NKBS show the same trend, which may indicate that this species probably wins more often when it is the biggest species in the interaction compared to when it is the smaller one.

Aimulosia marsupium is another small species which happens to lose more interactions than it wins. This is a trend through all of the time periods, which may show evidence of a relatively stable competitive ability through the history. *Aimulosia marsupium* is one of the smallest species in my samples, which makes it a bit difficult to estimate the real proportion of wins when it is the bigger competitor, as most other species are larger than *A. marsupium*. The results show that it does win more often when it is the smaller competitor, and that is not a surprise since it's one of the smallest species in the data and doesn't often meet opponents that are smaller than itself. It is interesting to note that the

Microporella agonistes is one of the species with a size that falls in between small and big, and thus it would especially be interesting to see if it wins more often when it is the bigger competitor because it has more of a chance to meet and interact with species both bigger and smaller than itself. The small and big species is at a disadvantage when it comes to this, as they often do not meet colonies that are smaller/bigger than themselves. In the NKLS and Upper Kai-iwi Shellbed data shows that *Microporella agonistes* loses slightly more interactions than it wins, but in the data from NKBS, it wins more often than it loses, which is interesting. The sampling size is not very large, so that might potentially explain the different result from the different time periods. The conditions and environment during the NKBS period might have been better for *M. agonistes* than it was during the NKLS and Upper Kai-iwi Shellbed periods or the interspecific competition might have been less tough than during the NKLS and Upper Kai-Iwi Shellbed era. It is interesting to note that as a species that is not the biggest species, nor the smallest, *M. agonistes*' win/lose proportion is a lot closer than for the species that are big or small, which may make sense because it does not have a real size advantage like *A. unicornis*, nor a size disadvantage like *A. marsupium.* When one looks at the results that shows the amount of wins when it is the smaller and bigger competitor, there is a clear trend of it winning more often when it is the bigger competitor in the interactions, which supports the notion that being the bigger competitor is an advantage in Cheilostome interactions.

Crepidacantha crinispina is a relatively small species, although not the smallest one in the samples. This species is also losing more interactions than it wins, and this is seen in all the three time periods. It seems like its small size might be a disadvantage in competition with other species. It is also worth noting that in the NKLS samples it seems to win more often when it is the biggest competitor, but that is not the case for the NKBS and Upper Kai-iwi Shellbed samples. One reason for this difference might be due to low sample size. Especially the NKBS has a very low amount of data points, which makes it difficult to draw any firm conclusions. The Upper Kai-iwi Shellbed samples contain the most data points and thus is more reliable. That one shows that *C. crinispina* wins more often when it is the smaller competitor, which might be because the interactions where *C. crinispina* is involved and is the smaller competitor might outnumber the interactions where it is the bigger competitor since it is a relatively small species.

So in most of the cases, the competitive ability in the Cheilostomes and Cyclostomes seem to have stayed relatively the same through time, although we can't say anything for the time periods in between the Nukumaru Limestone, Nukumaru Brown Sand and Upper Kai-Iwi Shellbed. Even though the Cheilostomes have had a competitive advantage over the Cyclostomes through millions of years (McKinney, 1994), the Cyclostomes have not yet disappeared.

In addition to some low sample sizes, studies of prehistoric bryozoan interactions do not come without challenges. One of the most difficult aspects with fossilized bryozoan interactions is that we often cannot be sure if both colonies were alive at the time when the interaction happened (Liddell & Brett, 1982) (West & McKinney, 2011) (McKinney, 1995). This is a problem because a dead organism has no competitive ability, and thus would create a false picture of the interaction and lead us to make wrong conclusions. One way to reduce this problem is to choose interactions where both participants look equally preserved and thus more likely to have lived at the same time (Liddell & Brett, 1982). This again could, and would, create a subjective bias. To solve this problem in the least subjective way as possible, it is possible to look for signs that show that the colonies had a mutual interaction with each other, like standoffs and reciprocal overgrowth. Some of these signs could be mutual (reciprocal) overgrowth or mutual growth discontinuance where the colonies meet (McKinney, 1995).

5 Conclusion

This study is among the very first to look at competitive abilities on a species level over time. It is, to my knowledge, also the first study to look at how the zooid size affects the outcome of Cheilostome interactions, which might prove to be useful information for future studies on bryozoan competition.

The results of this study shows that zooid size seems to have an effect on Cheilostome interactions. By looking at the five species which was analyses in this study, it is pretty clear that in most cases if you're bigger than your opponent, that is an advantage for you, and that if you are smaller than your opponent, then that might be a disadvantage. The plots of the species used in this study show that if a species is the biggest competitor, it tends to win more often. And this seems like be the case with most of them. It's also pretty clear that the smaller species loses more often than they win, and the biggest species in this study wins more than it loses. And this study has also shown that a large species wins more often than it loses, so a bigger size might be an advantage in competition with other species. What is also interesting is that the species' competitive abilities seem to have remained the same/almost the same through the time periods. It's clear that the Cyclostome/Cheilostome competitive relationship has been somewhat stable through the time even though the Cheilostomes are better at competing.

This study has started to answer some question about competition in bryozoan, but there are still lot of unanswered question to ask. Given the potential for evolutionary research on bryozoa because of their well preserved fossils with fossilized interactions, there might be coming more interesting studies in the future.

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