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Interactions between *Cryptosula* and *Watersipora* (Bryozoa: Cheilostomata) on a ship's hull in Qingdao Harbour (South Yellow Sea) after five and a half years of immersion*

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Abstract The distributions of two ubiquitous fouling cheilostome bryozoans, *Cryptosula pallasiana* (Moll, 1803) and *Watersipora* sp., on a ship moored for almost six years in Qingdao Bay show differences with respect to illumination, *Cryptosula* being dominant on the side of the ship which was exposed to the sun and *Watersipora* dominating on the other side which was in shadow for most of the time. Competitive interactions for substrate space were nearly always won by *Watersipora*, which succeeded in overgrowing the edges of *Cryptosula* colonies regardless of the side of the ship. Reasons for the superiority of *Watersipora* in spatial competition with *Cryptosula* could include faster growth rate and the stronger feeding currents created by the larger lophophores of *Watersipora*.

Keyword: ecology; *Cryptosula*; *Watersipora*; spatial competition; Yellow Sea; Qingdao

1 INTRODUCTION

Cryptosula and *Watersipora* are two of the most ubiquitous and widely distributed genera of fouling cheilostome bryozoans (Gordon and Mawatari, 1992). They have been recorded from numerous harbours around the world and there are many papers dealing with their biology (e.g., Cohen, 2011; Vieira et al., 2014 and references there). However, there appear to have been no studies about the competition between colonies of these two genera for living space.

Cryptosula pallasiana (Moll, 1803), originally described from Mediterranean Sea, now occurs in almost all harbours and adjacent shallow waters globally. In New Zealand *C. pallasiana* was recorded as early as 1898 (Gordon and Mawatari, 1992), found on ships in 1960, and on non-transient substrates in 1967 (Cohen, 2011). It was first reported on the Pacific Coast of North America in the mid-1940s at Newport Bay and San Francisco Bay (Cohen, 2011). Subsequently it was found in Hawaii [first reported in 1968], Japan [first reported in 1963, although it was reported even earlier as *Hippodiplosia pallasiana* by Okada (1929) and Mawatari (1952)], Australia including South Australia [reported in 1977], Victoria [in Port Phillip Bay in the late 1800s], New South Wales and northern Queensland, Argentina [reported in 1965] and Chile (Gordon and Mawatari, 1992; Cohen, 2011). This ascophoran cheilostome was likely introduced either as a hull fouler or with shipments of Atlantic oysters, with which it occurs in Atlantic coastal regions. Since its larvae spend a very short time in the plankton, it is a poor candidate for inter-oceanic transport by ballast water (Cohen, 2011).

One of the most common species of *Watersipora* is *W. subtorquata* (d'Orbigny, 1852), originally

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described from Rio de Janeiro, Brazil, and later collected in the Pacific off southern California at Rincon Beach, Ventura County in 1963 (Cohen, 2011). It is possible that it was present at many more sites in the 1960s and 1970s but confused with other species of *Watersipora*, especially *W. subatra* and *W. cucullata*, (see Vieira et al., 2014), and with *W. arcuata* which was first collected in southern California at about the same time but was apparently much more common than *Watersipora subtorquata* until at least the late 1960s (Cohen, 2011). *Watersipora subtorquata* is now, however, reported predominantly from subtropical and tropical waters of the Atlantic and Mediterranean (Vieira et al., 2014), but occurs also in Korea. The similar species *W. subatra* differs mainly in the presence of multiporous septula and occurs mainly in the NE Atlantic (British Isles), Indo-West Pacific (Indonesia, Japan) and Pacific (New Zealand, Australia and California). The provenance for dispersal of *W. subatra* in the East China Sea may have been Japan, where it has been known for many years (Mawatari, 1952), while the source of *W. subtorquata* may have been Korea (Seo, 1999). As with *Cryptosula pallasiana*, *W. subtorquata* larvae spend less than a day in the plankton before settling (Cohen, 2011), so its transportation over long distances as larvae in oceanic currents or in ballast water is unlikely, although ships' ballasts can include locally sourced rocks which may theoretically be encrusted by this and other bryozoans. However, *W. subtorquata* more probably reached the west coast of North America by fouling ships' hulls. It has often been found on ships' bottoms as it is highly tolerant of copper-based, anti-fouling compounds (McKenzie et al., 2012). *Watersipora subtorquata* is also reported to be capable of self-fertilization, which would make it easier for one or a small number of colonies transported to a distant location to establish a viable population (Cohen, 2011). Due to the problems of distinguishing between *W. subtorquata* and *W. subatra* in the present paper, we refer to the studied specimens as *Watersipora* sp. Although one of the reviewers suggested that our species might be *Watersipora subatra*, the presence of strong calcification on the proximal lateral margin, and the shape of the operculum and sinus do not allow us to identify our specimens unequivocally as this species.

The aim of the present paper is to describe the distributions and competition for living space between these two common, sheet-like cheilostome bryozoan species that are important as invasive foulers, and to suggest factors that may influence the outcome of this competition.

2 MATERIAL AND METHOD

We studied six sections on the hull of the *Sea Gull* (*Hai'ou* in Chinese). This is a wharf ship used as a pontoon for mooring other ships, and has a metal hull, length 48.52 m, width 7.09 m and with a gross tonnage of 381 tons. The hull was treated with HJ 406 copper anti-fouling paint just before mooring.

This ship was anchored in Middle Harbour (Zhong Gang) in Qingdao Bay (GPS coordinates 36°05′N, 120°18′E) from September 2009 until its dockage in April 2015. It was oriented with the bow to the south and moored to the wharf by its stern. Therefore, the port side of the ship was exposed to the sun, while the starboard side was in shadow of the wharf throughout most of the five and a half-year period of anchorage. Water depth around the ship was 4–5 m. Water temperature (Fig.1) was measured using a portable CTD type AAQ1183-1F just under the ship from November to August. Unfortunately, the values for the other months are unavailable due to lack of access to the harbour. However, the values can be predicted from Fig.1. The measured values varied on average from 3.04°C during the winter to 24.19°C in the summer. While we studied the interaction after 5.5 years, temperature data only pertain to one year. Exposure to wave action and current flow did not differ on the port and starboard sides of the hull.

We scraped all fouling organisms off sections of the hull from the formerly submerged part of the ship, each section about 25 cm×25 cm in size. These samples were numbered 1 to 6, with even numbers used for samples from the port side (sunny) and odd numbers for samples from the starboard side (shaded). Each sample has two parts, A and B, part A being taken from the side of the hull near the waterline (vertically oriented), and part B from the bilge (inclined underside) of the hull at the corresponding position just under part A (Fig.2). Therefore, 12 samples were taken altogether.

Six of the samples (1A, 1B, 3A, 4B, 6A, and 6B) were fouled mainly by bryozoans. As the other samples contained mainly oysters, mussels, tunicates and only a few bryozoan colonies, but with no interactions between colonies of *Cryptosula pallasiana* and *Watersipora* sp., they were discarded for this study.

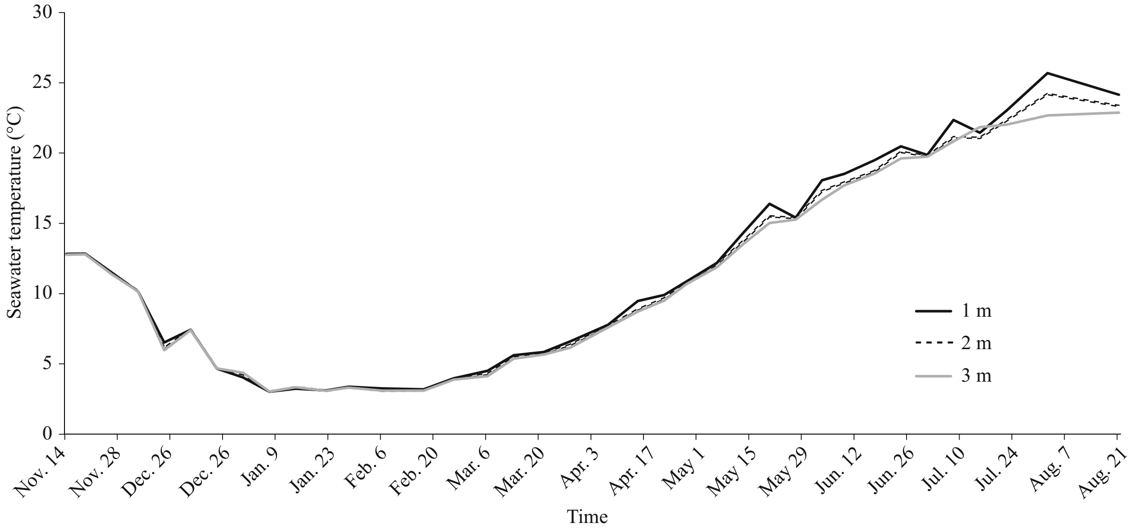

Fig.1 Seawater temperature at 1 m, 2 m and 3 m in Middle Harbour (Qingdao) during the period November 2012 to August 2013, measured using portable CTD type AAQ1183-1F just under the ship

Fig.2 Locations of the samples taken

The paper marks the position of Sample 1, comprising Sample 1A (grey arrow) from the vertical part of the hull near the former waterline, and Sample 1B (white arrow) from the inclined underside (bilge) of the hull.

Fig.3 Example of a typical contact between *Cryptosula pallasiana* (left) and *Watersipora* sp. (right) resulting in overgrowth by *Watersipora*

The arrow indicates the position of the contact. Note the presence of opercula in both colonies showing that they were alive at the time of the interaction.

We counted the number of colonies of *Watersipora* sp. and *Cryptosula pallasiana* from each sample; in the case of merged colonies, we tried to find the ancestrulae on the back-side of the colonies and counted the number. The maximum diameter of the encrusting colonies was small (45 mm), so colonies were collected almost intact when the samples were taken. Subsequently we searched for interactions between these two species along the edges of the colonies (Figs.3, 4). The overgrowing species for each interaction was recorded but only when there was evidence that the overgrown colony was alive at the time, i.e., it contained organic tissues or showed a clear morphological response (producing smaller or incompletely developed zooids, for example) to being overgrown. Only a few interactions involved reciprocal overgrowth in which the outcome was reversed along the line of contact between the colonies. In these cases, there was no clear winner (Fig.5). In one unusual example, contact between two colonies of the different species resulted in bifoliate erect growth, with one side being formed by *Cryptosula* and the other by *Watersipora* (Fig.6).

The coverage of the Bryozoa on the selected

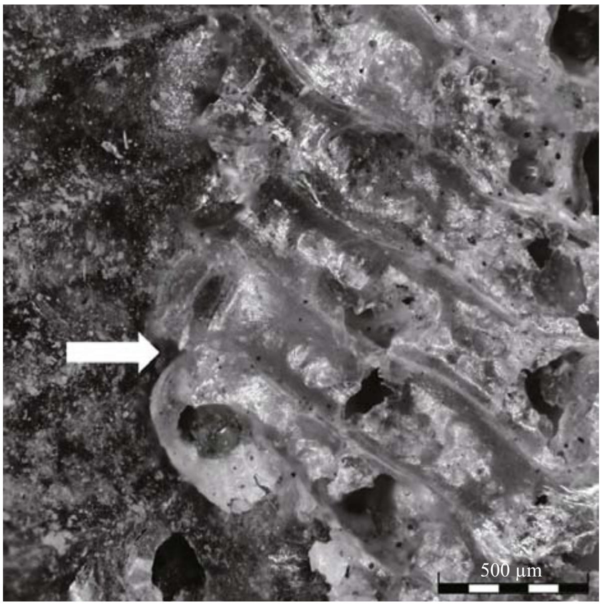

Fig.4 Example of overgrowth of *Cryptosula pallasiana* (right) by *Watersipora* sp. (left)

The picture is taken from the under side, because, the *Cryptosula* was completely overgrown by *Watersipora*, so on the frontal side, only *Watersipora* is observable. Note the reaction of the *Cryptosula* colony in producing smaller zooids (arrow) showing that it was alive at the time of the interaction.

samples was measured from photographic images using CorelDraw8 software. The sizes of *Cryptosula* and *Watersipora* zooids were measured using the integrated software with an Opto-digital microscope Olympus DSX500 system. We made 82 to 122 measurements on three to five colonies of each of four types (82 measurements on three colonies of *Cryptosula* from the sunny side, 122 measurements on five colonies of *Watersipora* from the sunny side, 112 measurements on four colonies of *Cryptosula* from the shaded side, and 82 measurements on four colonies of *Watersipora* from the shaded side). We used an online Chi-square test with one degree of freedom and a two-tailed *P* value to test the statistical significance of our results.

3 RESULT

3.1 Species composition

Altogether four bryozoan species were found fouling the ship's hull: *Watersipora* sp., *Cryptosula pallasiana*, *Pacificincola perforata* (Okada and Mawatari, 1937) and *Tricellaria occidentalis* (Trask, 1857). The dominant species were *Watersipora* sp. and *Cryptosula pallasiana*, whereas *Pacificincola perforata* was the least common.

Species composition and coverage by bryozoans differed on the starboard and port sides of the ship.

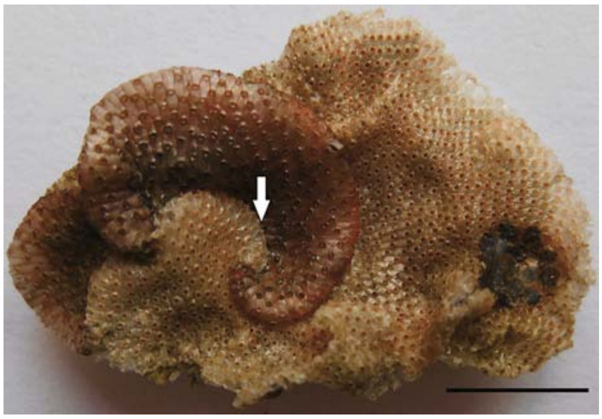

Fig.5 Example of an unclear winner in an interaction between *Cryptosula pallasiana* (pale coloured) and *Watersipora* sp. (red coloured)

Note reciprocal overgrowth between *Watersipora* and *Cryptosula* from one part of the contact between the colonies to another part close to the arrow. Scale bar 1 cm.

Fig.6 Example of an unusual contact between *Cryptosula pallasiana* (pale coloured) and *Watersipora* sp. (red coloured) that resulted in bifoliate erect growth of the combined colonies (arrowed)

Scale bar 1 cm.

The starboard vertical side, which was in shadow during mooring, was fouled by all four identified bryozoan species. However, on the port vertical side, which was exposed to the sun, only *Cryptosula* and *Watersipora* were found. The difference in the hull bilge (underside) was less pronounced: on the starboard side all four species were found, but on the port side *Tricellaria occidentalis* was found as well as *Cryptosula* and *Watersipora*.

The coverage of the Bryozoa on the vertical face of the hull ('A' samples) on the port side (sunny side) of the ship was approximately 22%–35% (measured from photographic images), while on the starboard (shaded) coverage was greater than 55%.

Table 1 Results of the interaction between *Watersipora* sp. and *Cryptosula pallasiana* in the different samples analysed

Sample	Illumination	# of colonies *Cryptosula pallasiana*	# of colonies *Watersipora* sp.	Interactions	*Cryptosula* wins	*Watersipora* wins	No clear winner
1A	Shaded	39	52	19	0	18	1
1B	Shaded	52	82	24	0	22	2
3A	Shaded	33	115	23	0	23	0
Total	**Shaded**	**124**	**249**				
4B	Sunny	58	20	13	0	13	0
6A	Sunny	53	11	5	0	0	5
6B	Sunny	76	26	16	2	12	2
Totals	**Sunny**	**187**	**57**	**100**	**2**	**88**	**10**

Bold numbers are the total number of colonies recorded in sunny and shaded sides, underlined numbers are the maximum number of colonies found in particular sample as referring in the text.

3.2 Distributions and interactions between *Cryptosula pallasiana* and *Watersipora* sp.

Overgrowth interactions between *Cryptosula pallasiana* and *Watersipora* sp. and the occurrence of these two species in the studied samples are summarised in Table 1. A significantly greater number of *Watersipora* sp. colonies were found on the starboard side of the ship, which was in shadow during the period of mooring (249 vs 57, Chi squared X^2=120.471, P<0.000 1). In contrast, *Cryptosula pallasiana* colonies dominated on the port side of the ship, which was exposed to the sun (187 vs 124; X^2=10.646, P=0.001 1). Despite the small number of samples (only six samples were suitable for studying interactions), these results show a strong contrast in the relative dominance of the two major fouling species between the shaded and sunny sides of the hull. The range of colony diameters (15–45 mm) in both species was limited, so the dominance in number of colonies corresponds to dominance in spatial coverage.

Watersipora sp. won almost all of its overgrowth interactions with *Cryptosula pallasiana* (Fig.3). Competitive dominance of *Watersipora* sp. was particularly pronounced on the shaded side (X^2=63.000, P<0.000 1). However, even in samples from the sunny (port) side where *Watersipora* sp. was less common and occasionally had the older parts of the colonies overgrown by *Cryptosula pallasiana*, it still won a significantly greater proportion of interactions (X^2=19.593, P<0.000 1).

3.3 Differences in size of zooids of *Cryptosula pallasiana* and *Watersipora* sp. from sunny and shaded sides

We measured the lengths and widths of *Cryptosula pallasiana* and *Watersipora* sp. zooids in samples from the sunny and shaded sides of the ship. As shown in Fig.7, there are considerable differences in the size of *C. pallasiana* zooids from sunny and shaded sides, while the average size of *Watersipora* sp. zooids is almost the same on both sides. The width of *C. pallasiana* zooids from the sunny side of the ship is slightly larger (362–609 μm, average 474 μm±57 μm) than zooids from the shaded site (334–504 μm, average 393 μm±52 μm), and length showed a similar pattern: 616–1 046 μm (average 875 μm±101 μm) on the sunny side vs. 522–827 μm (average 655 μm±52 μm) on the shaded side. The width of *Watersipora* sp. zooids on the sunny side was 341–605 μm (average 474 μm±54 μm), compared with 421–690 μm (average 540 μm±61 μm) on the shaded side. Zooid length was 910–1 459 μm (average 1 131 μm±116 μm) on the sunny side and 845–1 442 μm (average 1 069 μm±119 μm) on the shaded side.

3.3.1 Statistical analyses of size data (see Table 2)

Length of *Watersipora* zooids: according to two sample F-test for variance for alpha 0.01 the test criterion are 1.06; because critical value for 80 and 120 measurements are 1.60. The value shows that the standard deviations are not different. We used a two-sample t-test with equal variance to show that the average length is significantly smaller on the shaded side than on the sunny side. Test criterion is -3.67, one tail critical value for alpha 0.01 is -2.35, therefore the test criterion lies outside critical area (-2.35; infinity), so the null hypothesis is falsified and the average values of length are significantly different.

Width of *Watersipora*: according to two sample F-test for variance for alpha 0.01 the test criterion is 1.26. Therefore we used two-sample t-test with equal variance to show significant differences in average values in shaded and sunny sides. The null hypothesis

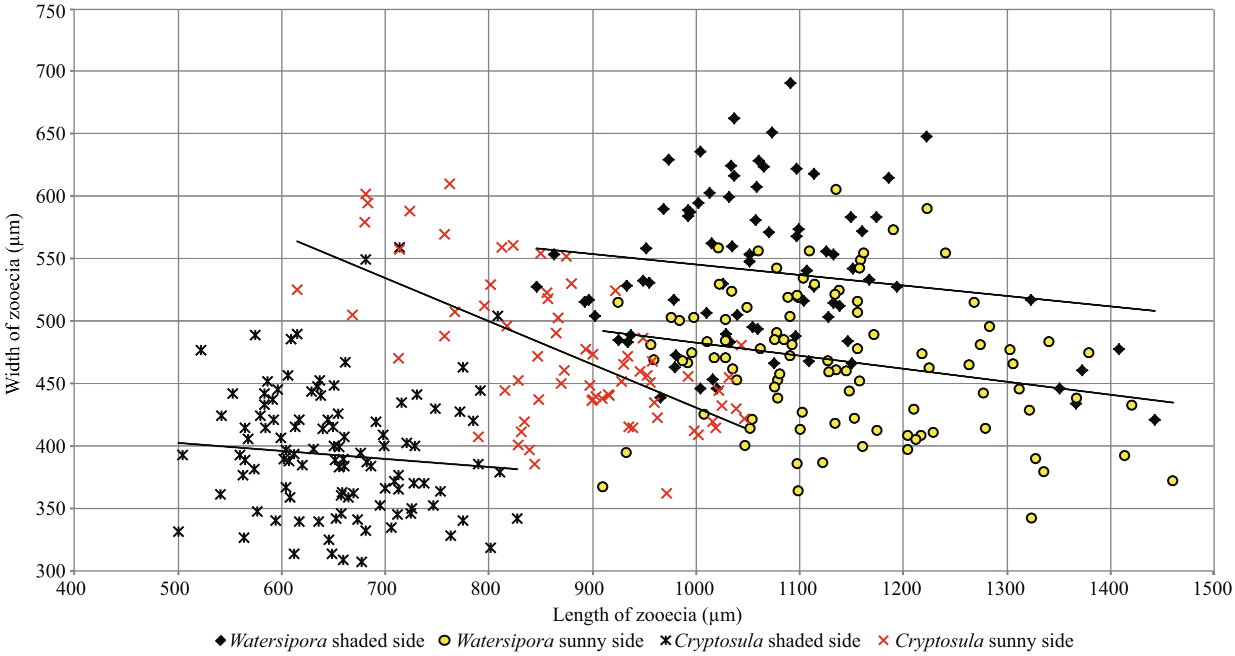

Fig.7 Chart showing the differences of size of *Cryptosula pallasiana* and *Watersipora* sp. zooecia from sunny and shaded sides of the ship

The lines show linear regressions of the values.

Table 2 Statistical analysis of length and width (μm) of *Cryptosula* and *Watersipora* on the shaded side versus the sunny side

Watersipora	Shaded side		Sunny side			Shaded side versus sunny side	
	Length	Width	Length	Width		Length	Width
Average	1 068.97	539.93	1 131.15	473.62	*F*-test criterion	1.06	1.26
Standard deviation	119.47	61.73	116.03	54.92	*F* critical value based on number of measurements	1.60	1.60
					t-test criterion	-3.67	7.96
					One tail critical value	-2.35	2.35
Cryptosula	Shaded side		Sunny side			Shaded side versus sunny side	
	Length	Width	Length	Width		Length	Width
Average	655.98	392.58	875.42	473.70	*F*-test criterion	2.00	1.20
Standard deviation	71.94	52.45	101.85	57.40	*F* critical value based on number of measurements	1.64	1.64
					t-test criterion	-15.70	-9.75
					One tail critical value	-2.36	-2.35

is that the average values are same. Test criterion is 7.96, one tail critical value for alpha 0.01 is 2.35. Because the test criterion lies outside critical area (minus infinity; 2.35), the null hypothesis is rejected and the average values of width are significantly different (the average width on the shaded side is smaller than on the sunny side).

Length of *Cryptosula*: according to two sample *F*-test for variance for alpha 0.01 the test criterion are 2.00; because critical value for 70 and 110 measurements are 1.64, this value shows that the standard deviations are different. Therefore we used a two-sample *t*-test with unequal variance to show statistically significant differences in average value between the shaded side, which is smaller and the sunny side. The null hypothesis is that the average values are the same. Test criterion is -15.70; one tail critical value for alpha 0.01 is -2.36, therefore, the test criterion lies outside critical area (-2.36; infinity), so the null hypothesis is rejected and the average values of length are significantly different.

Width of *Cryptosula*: according to two sample *F*-

test for variance for alpha 0.01 the test criterion are 1.20; because critical value for 70 and 110 measurements are 1.64, this value shows that the standard deviations are not significantly different. Therefore, we used a two-sample *t*-test with equal variance to show statistically significant differences in average value between the shaded side, which is smaller, and the sunny side. The null hypothesis is that the average values are the same. Test criterion is -9.75; one tail critical value for alpha 0.01 is -2.35, therefore, the test criterion lies outside the critical area (-2.35; infinity), so the null hypothesis is falsified and the average values of length are significantly different.

4 DISCUSSION

Species of *Watersipora* and *Cryptosula pallasiana* are invasive foulers (Gordon and Mawatari, 1992; Vieira et al., 2014), adapted for rapid growth and winning in competition for substrate space. Following previously published data (Jackson, 1983; Abdel-Salam and Ramadan, 2008 and many others; Cohen, 2011), these species can be categorized as r-strategists, allocating a relatively high proportion of their available energy to the rapid production of gametes capable of fouling surfaces as soon as they become available. Both normally lack polymorphs (although according to Winston (1982) small suboral avicularia are occasionally developed in *C. pallasiana*), and neither have ovicells for larval brooding (larvae are brooded internally, see Ostrovsky et al., 2009 and references therein).

Putative *Watersipora subovoidea* was found to be little affected by contact with neighbouring organisms in Tomioka Bay, Japan (Nandakumar and Tanaka, 1994). In this Japanese study, *Watersipora* showed significantly better growth than the two other studied bryozoans (*Celleporaria aperta* (Hincks, 1882) and *Schizoporella serialis* (Heller, 1867)) when growing close to neighbouring organisms such as algae, polychaetes, bryozoans and ascidians. In an earlier study on interspecific competition among sessile organisms from the same area, putative *W. subatra* was found to be higher in the competitive hierarchy for space than either *C. aperta* or *S. serialis* (see Nandakumar et al., 1993). Even though the species identity of the bryozoans used in these studies is not clear (see Vieira et al., 2014), the results may be applicable to species of *Watersipora*, including the *Watersipora* sp. in the current study.

Watersipora is apparently more immune than *Cryptosula* to the effects of various antifouling paints. A study in which a ship's hull was coated with three antifouling paints resulted in 64% of its surface being covered with *W. subtorquata* within 16 weeks; 22 other species (including *Cryptosula pallasiana*) occurred exclusively on top of the *W. subtorquata* colonies; no *Cryptosula* colonies were found directly encrusting the surface of the hull (Floerl et al., 2004). In our study, however, colonies of *Cryptosula* were found directly encrusting the surface of the hull on both sides. This might reflect depletion of the antifouling agent after a long period (>5 years) since its application.

An important difference between the Chinese *Watersipora* sp. and *Cryptosula pallasiana* may be in their growth rates. Amui-Vedel et al. (2007) gave the minimum specific growth rate (r) for *C. pallasiana* as 0.017 and the maximum rate as 0.092 (this study calculated specific growth rate as $r=\ln(N/N_0)/t$, where N_0 is the number of zooids at the beginning of the experiment, and N the number of zooids on day 27 at the end of the experiment). Lonhart (2012) reported the linear growth rate of putative *Watersipora subtorquata* to be 0.33 mm per day in California (Monterey Harbour). Fine and Loya (2003) gave the growth rate of *Watersipora* sp. in summer in the vermetid reefs of Sdot-Yam (Israel), at depths of 1–6 m, to be 6 mm±3 mm per month. The specific growth rate of *Watersipora* calculated from these linear growth rates by the method of Amui-Vedel et al. (2007) is 0.085–0.125, which is appreciably greater than the 0.017–0.092 reported in *C. pallasiana*. It should, however, be noted that these studies were undertaken in climatically different regions; Kuklinski et al. (2013), for example, found growth rates of sheet-like bryozoans to be greater in lower latitudes.

On the sunny side of the hull of the studied ship moored in Qingdao Harbour, temperatures were almost certainly higher. Our results show the production of larger zooids in *Cryptosula pallasiana* colonies on the sunny side compared to the shaded side. This is consistent with the findings of Amui-Vedel et al. (2007) that *Cryptosula* produces larger zooids in warmer waters, which is in contrast to previous studies on a number of other cheilostome species that bud smaller zooids in warm summer temperatures than in cold winter temperatures (Okamura, 1987; Okamura and Bishop, 1988; O'Dea and Okamura, 1999). Different genetically defined groups of *Watersipora* appear to show invasion patterns that can be predicted by ambient temperatures

(Mackie et al., 2012). Therefore, within this genus there are probably important variations in temperature-related adaptation. However, both survival and growth have been found to be temperature independent (Sorte et al., 2010). A zooid size-temperature relationship has been pointed out in *Watersipora* across multiple species and environments (Ryland et al., 2009).

It seems possible that the larger zooids budded by *C. pallasiana* may allow it to compete more successfully with *Watersipora* sp. on the sunny side of the ship during the summer. Moreover, the specific growth rates of *C. pallasiana* changed with temperature, ranging from 0.041 to 0.092, with an average rate of 0.066±0.015 8 (standard deviation) at 18°C, whereas the specific growth rate at 14°C, just 4°C less, was reduced by nearly half to 0.034± 0.009 7 (Amui-Vedel et al., 2007). In our samples the differences of size between *C. pallasiana* zooids growing on sunny and shaded sides were smaller than the seasonal differences described by Amui-Vedel et al. (2007) (Fig.7). The average difference in length was 138 μm (the length of zooids on the sunny side averaged 875 μm, while on samples from shaded side the average was 738 μm), and the average difference in width was 69 μm (the width of zooids on the sunny side averaged 474 μm, while samples from the shaded side averaged 405 μm) (see above Table 2 for the statistical significance of these differences). Even this small size increase may perhaps help *Cryptosula* to win at least some of its interactions with *Watersipora* on the sunny side. Although we do not know the exact differences in temperature between the sunny and shaded sides of the ship moored in Qingdao Harbour, we expect higher temperature on the side exposed to the sun.

The superiority of *Watersipora* sp. in competition for space with *Cryptosula pallasiana* could be linked with feeding intensity. Bryozoans with a greater number of tentacles are capable of creating more powerful feeding currents that may potentially deplete the shared food resources available to their spatial competitors (cf. McKinney, 1992): *Watersipora* sp. usually has 20–24 tentacles (Vieira et al., 2014), while *Cryptosula* has only 16–17 tentacles (Calvet, 1900) or 15–16 tentacles (Amui-Vedel et al., 2007).

5 CONCLUSION

The spatial distributions and competition for substrate space between two common fouling species of bryozoans (*Watersipora* sp. and *Cryptosula pallasiana*) were studied from different sites on the hull of a ship that had been moored in the water for five and a half years in Qingdao Harbour (China). The position of ship in the harbour meant that one side was exposed to the sun and the other was in the shade. On the shaded side of the ship, a maximum of 115 colonies of *Watersipora* sp. were recorded in the sample taken (altogether 249 colonies were recorded from all studied samples), compared with 52 colonies of *C. pallasiana* from the same sample (altogether 124 colonies were recorded from all studied samples). On the sunny side, only 26 colonies of *Watersipora* sp. were recorded from the sample taken (altogether 57 colonies were recorded from all studied samples), compared to 76 colonies of *C. pallasiana* in the same sample (altogether 187 colonies were recorded from all studied samples).

In a previous study (Amui-Vedel et al., 2007) of *Cryptosula pallasiana*, average specific growth rate doubled with an increase of 4°C, while another study (Sorte et al., 2010) has shown *Watersipora* to have a growth rate that is temperature independent. Unusually for a bryozoan, *Cryptosula* produces larger zooids in warmer water, which may help it to compete with *Watersipora* on the sunny (and presumably warmer) side of the hull

Therefore, we can conclude that:

1) colonies of *C. pallasiana* on the sunny side of the ship were found to have considerably longer zooids than those from the shaded side. The result is consistent with a previous study (Amui-Vedel et al., 2007) and might be related with differences in ambient temperatures;

2) zooids of *Watersipora* do not show significant differences in size on the sunny vs. shaded sides, which agrees with previously published data (Sorte et al., 2010);

3) regardless of location on the sunny or shaded side of the ship's hull, *Watersipora* sp. invariably won spatial competitive interactions with *Cryptosula pallasiana*, although the latter performed slightly better on the sunny side of the hull, which may correlate with the larger size of the zooids in colonies of *C. pallasiana* on this side.

Reasons for the superiority of *Watersipora* sp. in spatial competition with *Cryptosula pallasiana* might include:

a) faster growth rate: previous studies have determined a specific growth rate of 0.085–0.125 in *Watersipora* sp. (Lonhart, 2012) compared with 0.017–0.092 in *Cryptosula pallasiana* (Amui-Vedel et al., 2007);

b) stronger feeding currents: lophophores of *Watersipora* sp. have 20–24 tentacles, while those of *Cryptosula pallasiana* have 15–17 tentacles.

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