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1 **Effect of wharves on intertidal assemblages on seawalls in Sydney Harbour, Australia**

2

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4

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11

12 **Abstract**

13 Worldwide, urbanisation has resulted in extensive replacement of natural habitats with man-
14 made habitats. In Sydney Harbour, Australia, approximately half of the natural foreshore has been
15 replaced by seawalls. Many of these have wharves built over part of their length, which could affect
16 intertidal assemblages on seawalls beneath the wharves. This was tested by sampling and
17 comparing assemblages under and not under wharves in Sydney Harbour. Assemblages differed
18 between the two habitats, with greater cover of macro-algae and abundance of grazing molluscs on
19 seawalls without a wharf and, to a lesser extent, greater cover of sessile invertebrates on seawalls
20 under a wharf. There was, however, considerable spatial variability among locations in composition
21 of assemblages and the species dominating differences between the two habitats. The impact of
22 multiple artificial structures in close proximity and the variability among apparently homogeneous
23 artificial habitats must be considered for the management of urbanised estuaries.

24

25 *Keywords:* Algae; Artificial habitats; Coastal structures; Grazing molluscs; Sessile invertebrates

26 Shading; Sydney Harbour; Temperature; Urbanisation

27

28 **1. Introduction**

29 Urbanisation of coastal waters has resulted in proliferation of a variety of different artificial
30 marine structures (e.g. pontoons, pilings and seawalls), each supporting different assemblages
31 (Connell & Glasby, 1999; Glasby & Connell, 1999). Seawalls are among the most common marine
32 habitat within urbanised estuaries and bays (Davis, Levin & Walther, 2002; Chapman, 2003), but
33 often have other types of artificial structures built in close proximity, such as wharves (Blockley &
34 Chapman, In press). These structures might influence the assemblage living on the seawall by
35 increasing or decreasing abundances or covers of different species.

36 The sections of seawalls under wharves are potentially subject to different environmental
37 conditions (e.g. light, temperature, rain and wind) to those in the open. Wharves, jetties and similar
38 structures have been found to reduce the growth of seagrasses (Short & Burdick, 1996; Burdick &
39 Short, 1999) and density of salt marsh plants (Sanger, Holland & Gainey, 2004). The effect of
40 wharves and jetties on assemblages living on other artificial habitats has also been examined in
41 subtidal habitats (e.g. for pilings), with reductions in the cover and types of algae in shaded areas
42 and an increase in sessile invertebrates (Glasby, 1999a; 1999b). The effect of wharves on intertidal
43 hard substrata has not, however, received much attention. This is an important consideration
44 because wharves are most profuse in areas that are already urbanised and so are most likely to be
45 built in association with other artificial structures, frequently seawalls (Blockley & Chapman, In
46 press).

47 This study was done in Sydney Harbour, Australia, where most wharves are built over parts
48 of the extensive network of seawalls. Sections of seawalls that were either shaded or unshaded by
49 wharves were predicted to have different assemblages and covers or abundances of individual taxa
50 would differ between shaded or unshaded seawalls. Specifically, it was predicted that; (1) the cover
51 of algae would be greater on unshaded seawalls where there is more light (e.g. Clark, Edwards &
52 Foster, 2004), (2) grazing invertebrates would be more abundant on unshaded seawalls because this

53 is where their food source was predicted to be greater and (3) sessile invertebrates would have
54 greater cover on shaded seawalls because they would not have to compete for space with algae, nor
55 be dislodged by mobile invertebrates and might be benefited by the presence of a wharf (e.g.
56 reduction of thermal stress and desiccation). It was also predicted that these patterns would be
57 spatially and temporal consistent throughout Sydney Harbour.

58

59 **2. Methods**

60 This study was done at seven locations in Sydney Harbour: Athol Bay, Cremorne Point,
61 Rushcutters Bay, Hermit Point, Parriwi Head, Little Manly Point and Quarantine Station (Figure 1).
62 All locations had seawalls with adjacent sections either with or without wharves. At each location,
63 one section of seawall, approximately 5 m wide, under a wharf and one not under a wharf were
64 sampled. Despite considerable variability in the design of wharves in this study, each 5 m section
65 under a wharf was completely in shade and at least 1 m from the edge of the wharf. For each
66 section, ten replicate 20 x 25 cm quadrats were sampled at the mid- (0.9 - 1.1 m above chart datum)
67 and low-tidal (0.6 - 0.8 m above chart datum) heights. Percentage cover of all algae and sessile
68 invertebrates were measured and all mobile invertebrates counted. Where possible, without
69 destructive sampling, organisms were identified to species. Where complexes were formed, so that
70 individual species could not be distinguished (e.g. some of the small foliose algae and sponges),
71 these were assigned to broad groups (e.g. mixture of sponges referred to as “orange sponge”).
72 Sampling was repeated four times; in March, June, October, 2003 and February, 2004. Even though
73 the same sections of seawall were sampled each time, these times are far enough apart to provide
74 independent data (Underwood & Chapman, 1998; Bulleri, Chapman & Underwood, 2005).
75 Replicates were sampled randomly across the wall each time, so quadrats were not fixed. At the
76 low-tidal height, only six of the locations were sampled because the lower shore of Parriwi Head
77 was buried by a sand bank after the first sampling.

78 Environmental conditions on seawalls under or not under wharves were measured, with
79 incident light on the wall and the surface temperature of the substratum the two variables recorded.
80 These variables were considered to most likely differ between seawalls under or not under a wharf
81 and are known to be important in structuring assemblages. The amount of incident light has a strong
82 influence on the growth and survival of algae (Glasby, 1999a; Goldberg & Foster 2002; Clark et al.,
83 2004) and recruitment of invertebrates (Pomeroy & Reiner, 1942; Saunders & Connell, 2001).
84 Incident light was measured (in Lux) using a light meter placed at 10 random areas on seawalls
85 under or not under wharves at each of the 7 locations. Sampling was repeated 5 times each month
86 from April, 2003 until March, 2004.

87 Surface temperature of the substratum has been closely linked to the body temperature of
88 many sessile invertebrates (Wetthey, 2002) and is an important indirect measure of thermal stress.
89 The surface temperature of the seawall was also recorded for each habitat and location using an
90 infra-red electronic thermometer. This measures the temperature of the surface of the substratum
91 directly and is unaffected by air temperature or whether or not the device is in the sun. As for
92 incident light, 10 random areas were sampled in each habitat for each of the 7 locations, with
93 sampling repeated 5 times each month for a year.

94 All measurements of light and temperature throughout the sampling period were collected at
95 approximately the same time of day and during low tide. It was not possible to collect incident light
96 data during high tide and it would not have made sense to collect thermal data when organisms
97 were immersed. During high tide, the surface temperature would have been controlled by water
98 temperature and would not have differed between shaded and unshaded seawalls. For each month,
99 there were 50 replicate measures of surface temperature and incident light collected for each habitat
100 and location. These were averaged to give a mean monthly value. Collection of continuous data was
101 not feasible with the resources available over such a large number of sites. There are also many
102 restrictions on what can be attached to seawalls, being publically or privately owned structures.

103 The assemblages were compared using PERMANOVA (Anderson, 2001). Matrices of

104 dissimilarity among samples were calculated using the Bray-Curtis dissimilarity coefficient (Bray &
105 Curtis, 1957). The method of permutation used for all analyses was the permutation of residuals
106 under a full model because this gives the best power and accurate Type 1 error while being
107 reasonably quick (Anderson & Legendre, 1999). Each of the 4 times of sampling was treated as an
108 independent test of the hypothesis that difference between assemblages on seawalls shaded or
109 unshaded by wharves was general to all locations, while in separate analyses each of the 7 locations
110 were used as independent tests of the hypothesis that patterns would be temporally consistent. The
111 data were visualised with nMDS ordinations (Clarke, 1993). Analyses of variance tested hypotheses
112 that covers or abundances of taxa differed between the two habitats (fixed, orthogonal), among
113 locations (random, orthogonal) and through time (random, orthogonal) for algae, mobile
114 invertebrates and sessile invertebrates. Generally, it was found that heterogeneous variances for
115 percentage covers could not be stabilised by transformation and so analyses were done on
116 untransformed data with a more conservative significance level (see tables). ANOVA is, however,
117 robust to heterogeneity of variance and non-normal data and so is an appropriate analytical
118 technique (Underwood, 1999).

119

120 **3. Results**

121 *3.1. Comparisons among assemblages*

122 In general, at each time, the assemblages of the two habitats plotted apart on the nMDS
123 graph for each location (Figure 2). Despite some pattern of grouping by habitat, particularly at times
124 1 and 4, there was a great deal of overlap between habitats shown in the plots among locations (i.e.
125 some points representing assemblages on shaded seawalls plotted close to the cluster of points
126 representing those on unshaded seawalls from different locations (Figure 2)).

127 There was a significant interaction of Location and Habitat for the mid- and low-tidal
128 heights for the analyses of each time (Table 1a). Therefore, the hypothesis that the patterns of
129 difference would be general to all locations was rejected, although *a posteriori* pairwise

130 comparisons showed that these habitats were always different for each location. This result is
131 supported by the Bray-Curtis dissimilarities, which show that the dissimilarity between habitats is
132 much greater than the average dissimilarity within each habitat for both tidal heights (Table 2). The
133 dissimilarity among locations for each habitat is also large, supporting the lack of generality of the
134 pattern among locations (hence the variability in Figure 2). Furthermore, the variability among
135 locations for seawalls under wharves was greater than for seawalls not under a wharf at the mid-
136 tidal height, but similar at the low tidal height (Table 2).

137 The analyses of each location separately across all times gave interactions between time and
138 habitat for both heights in each location (Table 1b) showing that patterns of difference changed
139 through time. Nevertheless, the plot for each location shows strong separation between habitats
140 across all times indicating differences between the habitats remained large (Figure 3). The temporal
141 changes, illustrated in the nMDS plots, did not show a consistent pattern among locations or
142 between habitats.

144 3.2. Comparisons of individual taxa

145 Despite no general pattern of difference between habitats for whole assemblages, it was
146 evident that there were consistent patterns for individual taxa among locations at the mid- (Table 3,
147 Figure 4) and low-tidal height (Table 4, Figure 5). The encrusting alga, *Hildenbrandia rubra* was
148 the dominant alga at the mid-tidal height (Figure 4a), while the turf, *Corallina officinalis* or foliose
149 green algae, formed by complex patches of *Enteromorpha intestinalis*, *Ulva lactuca*, *Cladophora*
150 sp., *Chaetomorpha* sp. and *Bryopsis* sp., dominated the low-tidal height (Figure 5a). *Hildenbrandia*
151 *rubra* showed Time x Location and Location x Habitat interactions (Table 3a) while the low-shore
152 algae had significant Time x Location x Habitat interactions (Table 4a). Despite this, the general
153 patterns did not vary much among times, as shown by *Hildenbrandia rubra* (Figure 4a). For this
154 reason and for the sake of brevity, only one time is shown to illustrate patterns for the other two
155 alga (Figure 5a). There were large differences in cover among locations and the difference between

156 habitats was only significant at some times and locations, but there was a strong pattern of greater
157 cover on seawalls not under wharves (Figure 4a & 5a). Binomial tests indicated that, despite the
158 lack of significant differences at some locations or times, the general pattern was significant (Figure
159 4a & 5a).

160 The oyster *Saccostrea glomerata* was the dominant sessile invertebrate at most locations at
161 the mid-tidal height. The mussel *Mytilus galloprovincialis*, the tubeworm *Galeolaria caespitosa*, the
162 barnacles *Tesseropora rosea* and *Tetraclitella purpurascens* and an encrusting orange sponge also
163 had relatively large covers at many locations (Figure 4b). The pattern was similar at the low-tidal
164 height, although *S. glomerata* was not as dominant and the barnacle *Austrobalanus imperator* was
165 also present (Figure 5b). As for the algae, there were significant Time x Location x Habitat
166 interactions for most analyses of cover of sessile invertebrates (Table 3b & 4b). Exceptions were *M.*
167 *galloprovincialis* at the mid-tidal height and *A. imperator* and *T. rosea* at the low-tidal height,
168 which showed higher-order interactions. Despite this, the patterns were fairly consistent through
169 time, shown for *S. glomerata* and so only one time is presented for the remaining taxa to illustrate
170 the pattern (Figure 4b). There was, however, considerable difference in the covers of the various
171 species among locations.

172 Covers of *S. glomerata* were most consistent among locations mid-tidally and were
173 significantly greater on seawalls that were not under a wharf (binomial tests, Figure 4b). This is
174 opposite to the pattern predicted. Similarly, mid-tidally *T. rosea* had a greater cover on seawalls not
175 under wharves at many locations, although the general pattern was not significant (Figure 4b). The
176 other sessile invertebrates showed the predicted pattern of greater covers on seawalls under wharves
177 at many, but not all locations, however the difference was still significant (Figure 4b).

178 The cover of *S. glomerata*, *M. galloprovincialis*, *G. caespitosa*, and *A. imperator* did not
179 differ between habitats significantly at the low-tidal height, although the cover of *A. imperator* was
180 significantly greater on walls under wharves at Athol Bay and Cremorne Point at all times (Table
181 4b, Figure 5b). *T. rosea* showed a significant pattern, although as for the mid-tidal height, it was

182 opposite to that predicted (Figure 5b). *T. purpurascens* and orange sponge, however, showed a
183 significant pattern of greater cover on walls under wharves as predicted (Figure 5b).

184 Of the mobile invertebrates, only *Chiton pelliserpentis* and the limpet, *Siphonaria*
185 *denticulata* occurred in large enough numbers to be analysed. Analyses showed that each were
186 more abundant on walls not under a wharf, although not significantly at all locations or times (Table
187 3c, Figure 6). Nevertheless the general pattern was consistent through time (Figure 6). There were
188 many locations with a significantly greater abundance of both species on unshaded seawalls (Table
189 3c, Figure 6), although, at some times and locations, the opposite was found. Despite this, the
190 predicted pattern of greater abundance of grazing invertebrates was significant (Figure 6).

191

192 3.3. Measurements of surface temperature and light on seawalls

193 The mean surface temperature on walls not under wharves was greater than on walls under
194 wharves at each location (Figure 7). Nevertheless, the magnitude of the difference between the two
195 habitats was not consistent among locations (e.g. the difference between the two habitats at Athol
196 Bay was relatively small, while the difference at Hermit Point was much larger). There was also a
197 difference in range of mean temperatures among locations (e.g. the seawall not under a wharf at
198 Rushcutters Bay had a maximum temperature of approximately 28° C, while the same habitat at
199 Cremorne Point was about 23° C).

200 Despite the mean surface temperature on seawalls not under wharves being greater than that
201 on walls under wharves, the magnitude of the difference in temperature between habitats changed
202 through time. The greatest difference was in the Austral summer months (December through to
203 February), when the greatest mean surface temperatures were recorded.

204 The change in mean light, measured in Lux, on seawalls shows some similarity to the
205 pattern seen for mean temperature (Figure 8). Incident light was, as would be expected, greater on
206 seawalls not under wharves at all locations and at all times. There was considerable variability
207 among locations in the magnitude of difference between the two habitats, as well as the range of

208 values recorded and a great deal of variability through time. Unlike temperature, there was no easily
209 discernible pattern for the temporal variability of the light. There did not appear to be a consistent
210 pattern among locations or in relation to seasonal change.

211

212 **Discussion**

213 In the current study, algae were virtually absent from walls under wharves and there was
214 considerable covers of algae, such as *Corallina officinalis* and foliose green algae (e.g.
215 *Enteromorpha intestinalis*), on unshaded seawalls. Shade can be important in structuring
216 assemblages and has been shown to have important effects on the growth and survival of terrestrial
217 plants (Weih & Karlsson, 1987; Valladares & Pearcy, 1997; Sans, Escarré, Lepart, & Hopkins,
218 2002), marine algae (Glasby, 1999b; Goldberg & Foster, 2002; Clark et al, 2004) seagrasses
219 (Burdick & Short, 1999) and saltmarsh (Sanger et al., 2004). Animals on intertidal shores have also
220 been shown to be affected by shading, with greater recruitment or survival where there is shade
221 (Denley & Underwood, 1979; Harper & Williams, 2001). Shading alone may, therefore, explain the
222 absence of algae and the greater cover of most species of sessile invertebrates under wharves in the
223 present study, although this can not be concluded categorically without manipulative experiments.

224 Unlike many other sessile invertebrates in this study, the barnacle *T. rosea* had greater cover
225 on unshaded walls. Denley & Underwood (1979) found that *T. rosea* would settle on unshaded and
226 shaded shores, but survived better in the sun. The oyster *S. glomerata*, one of the dominant space
227 occupiers, also had greater cover on unshaded walls. Bulleri et al. (2005) found that *S. glomerata*
228 was able to dominate space on seawalls in Sydney Harbour, although the pattern was variable
229 among locations. Beds of *S. glomerata* can be quite thick, providing oysters with protection from
230 environmental extremes (e.g. thermal stress) in a similar way to the presence of a wharf. The lesser
231 cover of other sessile invertebrates on unshaded seawalls may also have meant that oysters had less
232 competition for space and so were able to maintain greater covers than on shaded seawalls.

233 The present study has shown that there is less incident light reaching seawalls with wharves
234 compared to sections without wharves. Glasby (1999b) found that the degree of shading may be
235 important in structuring assemblages of epibiota on subtidal pier pilings, with similar results as in
236 the present study. The amount of shade can also influence the surface temperature of rocky
237 intertidal areas, with unshaded areas having much greater surface temperatures than adjacent shaded
238 areas during low-tide leading to physiological affects (e.g. greater mortality through desiccation or
239 thermal stress (Garrity, 1984; Harper & Williams, 2001)). The provision of shade can ameliorate
240 thermal stress and increase recruitment and survival (Denley & Underwood, 1979; Williams, 1994;
241 Bertness, Leonard, Levine, & Bruno, 1999). According to Helmuth and Hofmann (2001), however,
242 it is extreme temperature events (extremes of heat and cold) rather than the mean temperature that
243 causes physiological stress. The design of the experiment was unlikely to capture temperature
244 extremes because it unavoidably involved “snap-shot” measurements. The data collected does give
245 a good indication that these extreme high temperatures would occur on unshaded seawalls, where
246 surface temperature was always greater, whereas wharves would buffer seawalls beneath them from
247 these events.

248 Recruitment of algae and invertebrates to seawalls has been shown to be affected by
249 wharves, which shade the wall directly under them (Blockley & Chapman, In press). The greater
250 cover of most sessile animals in the lower light conditions under wharves might represent a
251 negative phototactic response at the time of settlement (e.g. Pomerat & Reiner, 1942; Wisely,
252 1959). O’Donnell (1984) showed that *G. caespitosa* recruit in greater numbers to shaded habitats,
253 possibly explaining the patterns in the current study. Algae has also been shown to have greater
254 recruitment to unshaded habitats (Goldberg & Foster, 2002; Clark et al, 2004). It is, therefore,
255 possible that the patterns found in the present study are determined at the time of recruitment rather
256 than by post-recruitment processes.

257 Despite support for patterns of difference between assemblages on seawalls under or not
258 under wharves, there was great variability among locations and to, a lesser extent, among times.

259 Large-scale spatial (at the scale of km) and temporal differences in intertidal assemblages are a
260 feature of the rocky shores of New South Wales, Australia (Dakin, Bennett, & Pope, 1948;
261 Underwood & Chapman, 1998; Benkendorff & Davis, 2002). However, seawalls, unlike rocky
262 shore, are homogeneous structures and so would be predicted to be less variability among locations.
263 Previous research on seawalls in Sydney Harbour by Bulleri et al. (2005) has, however, shown that
264 the variability of assemblages on seawalls can be as great as, or greater than that found on rocky
265 shores among locations. Although Bulleri et al. (2005) found that the taxa responsible for patterns
266 on seawalls varied among locations, general patterns were consistent for each location,. This is
267 similar to the present study, with assemblages consistently differing between the shaded and
268 unshaded seawalls at each location, but species responsible for patterns differing, resulting in the
269 overall variability among locations. In their study, Bulleri et al. (2005) only examined three
270 locations and did not directly compare among locations. The present study has therefore expanded
271 on this by examining a greater number of locations, comparing among locations and studying a
272 common, yet so far largely ignored, artificial habitat, that is seawalls under wharves.

273 One explanation for the large-scale spatial variability is that the orientation and position
274 within the harbour of seawalls differed among locations, such that physical conditions on the
275 seawalls could have varied among locations. Seawalls that faced north, for example, would be
276 subject to more direct sunlight than those facing south, resulting in greater surface temperatures.
277 This is evident in the measures of incident light and surface temperature of unshaded seawalls (e.g.
278 Hermit Point and Quarantine Station, north facing wall, compared to Cremorne Point and Athol
279 Bay, south facing wall). In locations where seawalls were oriented towards the sun, the difference in
280 temperature between shaded and unshaded seawalls would be expected to be greater than where
281 seawalls were not oriented towards the sun. In the present study, the difference in temperature
282 between shaded and unshaded sections of seawall that faced north, towards the sun, was up to 10°C,
283 while the difference between habitats for south facing walls was less than 5°C. This could explain
284 some of this dissimilarity in the composition of assemblages among locations.

285 Urbanised waterways are heavily impacted by anthropogenic activity, with many sources of
286 disturbance (Kullenberg, 2001; Vallega, 2001; Kennish, 2002). The multiple impacts of artificial
287 structures built on, or in the vicinity of, other artificial structures and the additive effects of their
288 associated impacts has generally been overlooked in studies of disturbance ecology. Although this
289 study did not examine how the assemblages associated with two different types of artificial
290 structures (i.e. seawalls and wharves) differed from those on natural shores, previous studies have
291 shown that assemblages differ between seawalls and natural shores (Chapman & Bulleri, 2003;
292 Chapman, 2003; Bulleri et al., 2005). The present study has shown that the presence of another
293 structure (wharves) can further alter assemblages on seawalls. Whether the difference to
294 assemblages on seawalls caused by the presence of wharves translates to making assemblages more
295 or less different from those on natural shores is an area of further study.

296 The potential of wharves to provide or alter habitats for marine organisms needs to consider
297 the possible positive effects against negative impacts. The presence of a wharf not only means that
298 the composition of assemblages or relative covers or abundances of taxa differs from adjacent
299 unshaded seawalls, but also results in assemblages that are more variable at small and large spatial
300 scales. The shaded surfaces may act as substitutes for microhabitats that are missing from seawalls,
301 as well as adding to the amount and variety of habitats because of structures, such as pilings,
302 associated with wharves. The negative impacts on surrounding habitats and the fact that the
303 assemblages on these structures do not necessarily represent natural assemblages must, however, be
304 considered. If seawalls with wharves do not support assemblages that are representative of those on
305 natural shores, then they cannot necessarily be said to have a positive impact, regardless of
306 increasing local diversity. This is an important issue if, as Cole, Glasby & Holloway (2005) suggest,
307 we attempt to apply ecological theories from the study of natural shores to the management of
308 artificial structures.

309

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ACCEPTED MANUSCRIPT

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ACCEPTED MANUSCRIPT

448 Table 1. Results from analyses by non-parametric MANOVA on assemblages on sections of seawall under or not under
 449 wharves (a) among locations for each time of sampling and (b) through time at each location, at mid-and low-tidal
 450 heights. 5000 permutation of residuals were used for all analyses. NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P <$
 451 0.001.

452
 453 (a)

454 Mid-tidal height

Source	df	<i>F</i> Time 1	<i>F</i> Time 2	<i>F</i> Time 3	<i>F</i> Time 4
Location = L	6	-	-	-	-
Habitat = H	1	-	-	-	-
L x H	6	23.84***	18.23***	15.14***	14.28***
Residual	126				

455

456 Low-tidal height

Source	df	<i>F</i> Time 1	<i>F</i> Time 2	<i>F</i> Time 3	<i>F</i> Time 4
Location	5	-	-	-	-
Habitat	1	-	-	-	-
L x H	5	12.10***	10.98***	10.03***	11.13***
Residual	119				

457

458

459

460 (b) Mid-tidal Height

Source	df	<i>F</i> Athol Bay	<i>F</i> Cremorne Point	<i>F</i> Rushcutters Bay	<i>F</i> Hermit Point	<i>F</i> Parriwi Head	<i>F</i> Little Manly Pt	<i>F</i> Quarantine Station
Time = T	3	-	-	-	-	-	-	-
Habitat = H	1	-	-	-	-	-	-	-
T x H	3	3.54***	11.07***	5.14***	6.75***	4.71***	2.64**	3.53***
Residual	72							

461

462 Low-tidal Height

Source	df	<i>F</i> Athol Bay	<i>F</i> Cremorne Point	<i>F</i> Rushcutters Bay	<i>F</i> Hermit Point	<i>F</i> Little Manly Pt	<i>F</i> Quarantine Station
Time	3						
Habitat	1						
T x H	3	3.18 ***	2.80 ***	7.55 ***	8.39 ***	6.66***	5.98***
Residual	72						

463

464

465

466 Table 2. Average Bray-Curtis dissimilarities within and among locations for each habitat and between the two habitats
 467 at each time for mid- and low-tidal height. W= Wharf and NW = No-wharf habitats.
 468

	WHARF		Between W/NW	NO-WHARF	
	Within	Among		Within	Among
Time 1	41.2	75.9	71.4	23.1	64.0
Time 2	41.5	80.2	74.4	29.3	60.6
Time 3	44.5	82.9	72.6	27.2	50.5
Time 4	48.0	85.2	79.6	36.9	60.4

	WHARF		Between W/NW	NO-WHARF	
	Within	Among		Within	Among
Time 1	58.6	85.0	90.1	38.5	79.2
Time 2	54.4	85.4	78.0	44.7	87.5
Time 3	61.0	87.3	88.5	45.5	79.3
Time 4	52.7	83.9	83.3	48.5	82.7

469 Table 3. Analyses of individual taxa of (a) algae, (b) sessile invertebrates and (c) mobile invertebrates on sections of
 470 seawall under or not under wharves at the mid-tidal height.
 471

(a)		<i>H. rubra</i>	
Source	df	MS	<i>F</i>
Time = T	3	178.1	
Location = L	6	3767.1	
Habitat = H	1	10386.8	
T x L	18	281.8	2.7 *
T x H	3	85.4	0.4 NS
L x H	6	3333.0	14.1 *
T x L x H	18	237.1	2.3 NS
Residual	504	104.3	
Transformation		None	
Cochran's test		**	

(b)		<i>S. glomerata</i>		<i>M. galloprovincialis</i>		<i>G. caespitosa</i>		<i>T. rosea</i>	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time = T	3	2795.5		42.8		1767.6		35.8	
Location = L	6	49571.3		1469.9		6301.4		2151.8	
Habitat = H	1	207587.9		1980.2		13519.5		192.5	
T x L	18	1481.0		29.2	1.2 NS	646.6		18.9	
T x H	3	927.3		68.4	1.2 NS	1823.2		224.1	
L x H	6	13918.3		1329.2	22.6 *	11220.4		82.1	
T x L x H	18	1683.8	5.9 *	58.9	2.4 NS	730.0	4.14 *	199.9	5.1 *
Residual	504	286.0		25.0		176.2		39.0	
Transformation		None		None		None		None	
Cochran's test		*		**		**		**	

		<i>T. purpurascens</i>		Orange sponge	
Source	df	MS	<i>F</i>	MS	<i>F</i>
Time	3	441.0		26.0	
Location	6	13137.8		124.3	
Habitat	1	40683.8		536.3	
T x L	18	243.7		18.5	
T x H	3	639.4		27.2	
L x H	6	10876.1		113.6	
T x L x H	18	313.8	3.2 *	18.6	3.2 *
Residual	504	97.5		5.9	
Transformation		None		None	
Cochran's test		**		**	

(c)		<i>C. pelliserpentis</i>		<i>S. denticulata</i>	
Source	df	MS	<i>F</i>	MS	<i>F</i>
Time	3	3.5		1.3	
Location	6	9.1		2.0	
Habitat	1	11.4		11.8	
T x L	18	1.3		0.5	
T x H	3	2.8		0.2	
L x H	6	7.1		5.9	
T x L x H	18	1.2	5.4 ***	0.8	2.9 ***
Residual	504	0.2		0.3	
Transformation		Ln(X + 1)		Ln(X + 1)	
Cochran's test		NS		NS	

472 Where analyses showed significant interactions, *F*-ratios are not given for main effects and lower order interactions
 473 because these cannot be logically interpreted. NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ except where
 474 Cochran's test was significant (for *C* with $P < 0.05$, * = $P < 0.01$, ** = $P < 0.001$; for *C* with $P < 0.01$, * = $P < 0.001$)

475 Table 4. Analyses of individual taxa of (a) algae and (b) sessile invertebrates on sections of seawall under or not under
 476 wharves at the low-tidal height.
 477

(a)		<i>C. officinalis</i>		Foliose green algae	
Source	df	MS	<i>F</i>	MS	<i>F</i>
Time = T	3	4468.2		4.2	
Location = L	5	10590.6		13.3	
Habitat = H	1	76329.8		44.7	
T x L	15	1163.2		3.9	
T x H	3	4446.4		7.5	
L x H	5	10518.0		5.5	
T x L x H	15	1164.7	6.5 *	2.7	7.1 *
Residual	432	179.4		0.4	
Transformation		None		None	
Cochran's test		**		**	

(b)		<i>S. glomerata</i>		<i>M. galloprovincialis</i>		<i>G. caespitosa</i>		<i>A. imperator</i>	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time = T	3	2129.6		721.5		977.9		56.8	
Location = L	5	10070.7		698.2		3987.7		450.1	10.6 *
Habitat = H	1	8535.0		286.8		1117.3		763.4	
T x L	15	2270.7		756.4		415.9		^P 35.9	
T x H	3	6362.0		799.4		58.1		71.6	1.7 NS
L x H	5	7786.4		969.5		2347.6		299.7	7.1 *
T x L x H	15	2610.3	10.1 *	736.1	41.9 *	316.0	2.6 *	^P 45.8	
Residual	432	259.3		17.6		122.0		42.6	
Pooled	462							42.5	
Transformation		None		None		None		None	
Cochran's test		**		**		**		**	

		<i>T. rosea</i>		<i>T. purpurascens</i>		Orange sponge	
Source	df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time	3	110.4		12.4		45.2	
Location	5	809.5		1252.6		6107.6	
Habitat	1	145.8		3370.8		18710.1	
T x L	15	109.8	4.3 *	285.4		258.2	
T x H	3	18.0	0.7 NS	10.3		107.1	
L x H	5	105.7	4.1 *	1084.2		4437.5	
T x L x H	15	^P 19.5		289.2	7.9 *	364.3	3.2 *
Residual	432	25.9		74.4		113.5	
Pooled	447	25.7					
Transformation		None		None		None	
Cochran's test		**		**		**	

478 ^P indicates pooling ($P > 0.25$). Where analyses showed significant interactions, *F*-ratios are not given for main effects
 479 and lower order interactions because these cannot be logically interpreted. Because Cochran's test was significant ($P <$
 480 0.01) a conservative significance level was used was used NS = $P > 0.01$, * = $P < 0.001$
 481

482 **Figure captions**

483

484 Figure 1. Map of field sites within Sydney Harbour, Australia

485

486 Figure 2. nMDS ordination of centroids of assemblages on seawalls under wharves (filled shapes)
487 or not under wharves (empty shapes) at each location: Athol Bay (circle); Cremorne Point (square);
488 Rushcutters Bay (downward triangle); Hermit Point (upward triangle); Parriwi Head (diamond);
489 Little Manly Point (small circle); Quarantine Station (small square). Each sampling times and
490 height is graphed separately.

491

492 Figure 3. nMDS ordination of centroids of assemblages on seawalls under wharves (circles) or not
493 under wharves (squares) through time (1-4) for selected locations as examples of general patterns at
494 the mid- and low-tidal heights.

495

496 Figure 4. Mean (+SE) percentage cover of algae and sessile invertebrates on seawalls under
497 (shaded) or not under (hashed) wharves at the mid-tidal height. Only one time is shown to illustrate
498 general patterns, except for *H. rubra* and *S. glomerata*. A = Athol Bay; C = Cremorne Point; R =
499 Rushcutters Bay; H = Hermit Point; P = Parriwi Head; M = Little Manly Point; Q = Quarantine
500 Station. Text in bold indicate number of times the mean was greater under a wharf (W) or where
501 there was no wharf (NW), with number of these that were significantly greater, from SNK tests,
502 given in brackets. *P* values (with number of comparisons in subscript) are from binomial tests of
503 means.

504

505 Figure 5. Mean (+SE) percentage cover of algae and sessile invertebrates on seawalls under
506 (shaded) or not under (hashed) wharves at the low-tidal height. Only one time is shown to illustrate
507 general patterns. A = Athol Bay; C = Cremorne Point; R = Rushcutters Bay; H = Hermit Point; M =

508 Little Manly Point; Q = Quarantine Station. Text in bold indicate number of times the mean was
509 greater under a wharf (W) or where there was no wharf (NW), with number of these that were
510 significantly greater, from SNK tests, given in brackets. *P* values (with number of comparisons in
511 subscript) are from binomial tests of means.

512

513 Figure 6. Mean (+SE) abundance of mobile invertebrates on seawalls under (shaded) or not under
514 (hashed) wharves at the mid-tidal height. A = Athol Bay; C = Cremorne Point; R = Rushcutters
515 Bay; H = Hermit Point; P = Parriwi Head; M = Little Manly Point; Q = Quarantine Station. Text in
516 bold indicate number of times the mean was greater under a wharf (W) or where there was no wharf
517 (NW), with number of these that were significantly greater, from SNK tests, given in brackets. *P*
518 values (with number of comparisons in subscript) are from binomial tests of means.

519

520 Figure 7. Mean surface temperature (\pm S.E.) of seawalls under (circle, solid line) or not under
521 (triangle, hashed line) wharves at each location from April 2003 until March 2004.

522

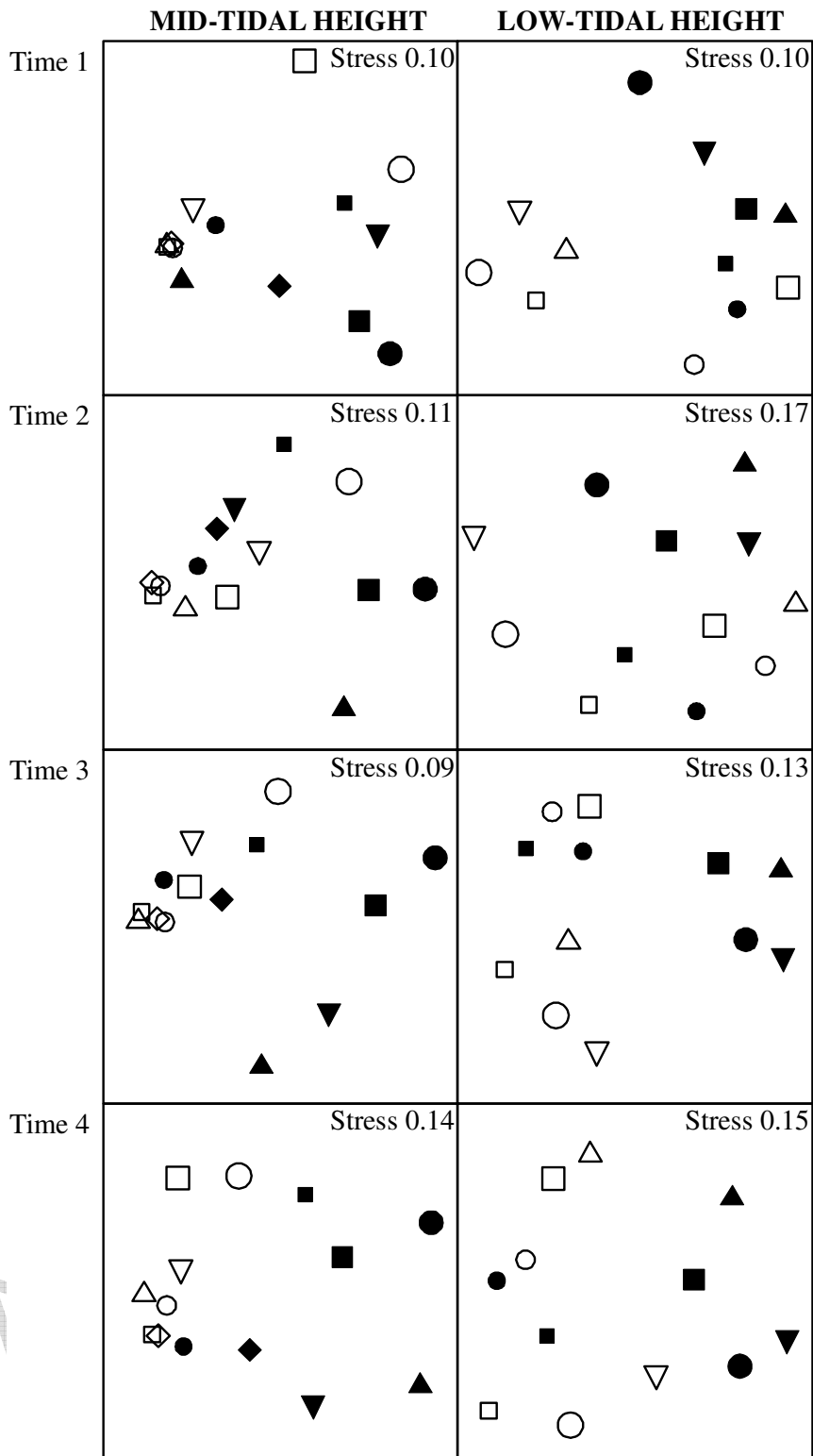
523 Figure 8. Mean light (Lux) on seawalls under (circle, solid line) or not under (triangle, hashed line)
524 wharves at each location from April 2003 until March 2004.

525 Fig. 1

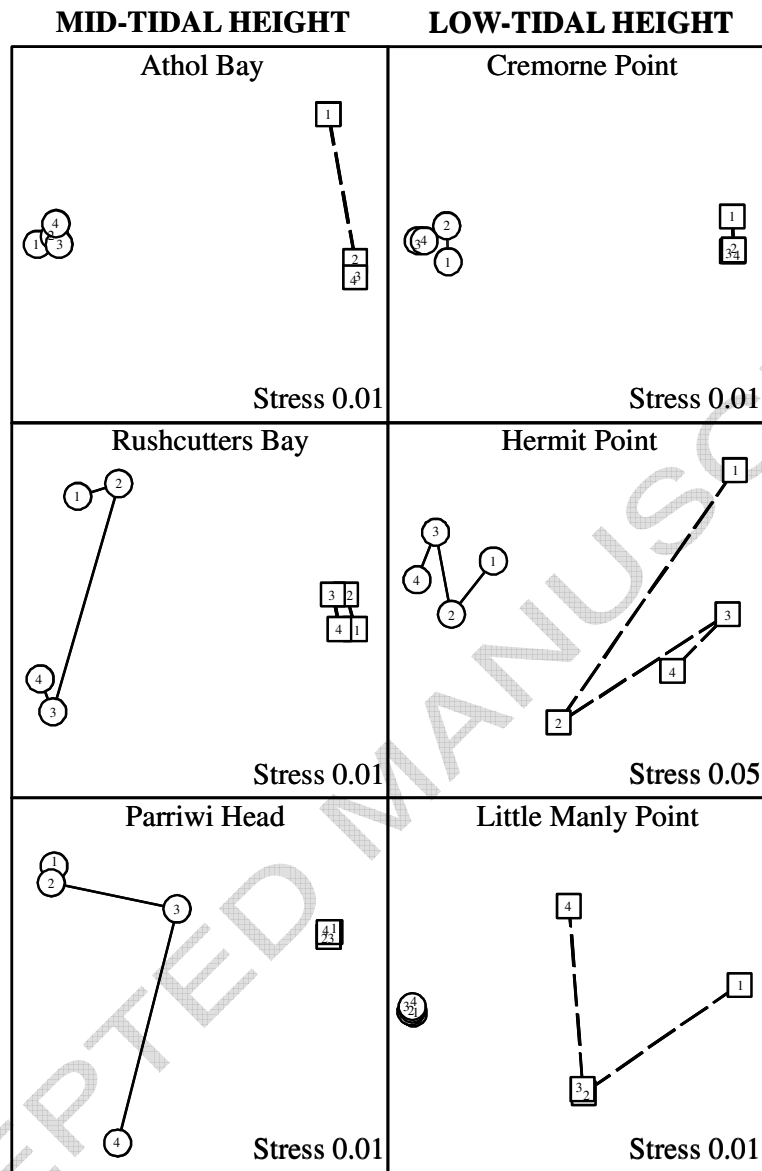


526

527 Fig. 2



529 Fig. 3



530

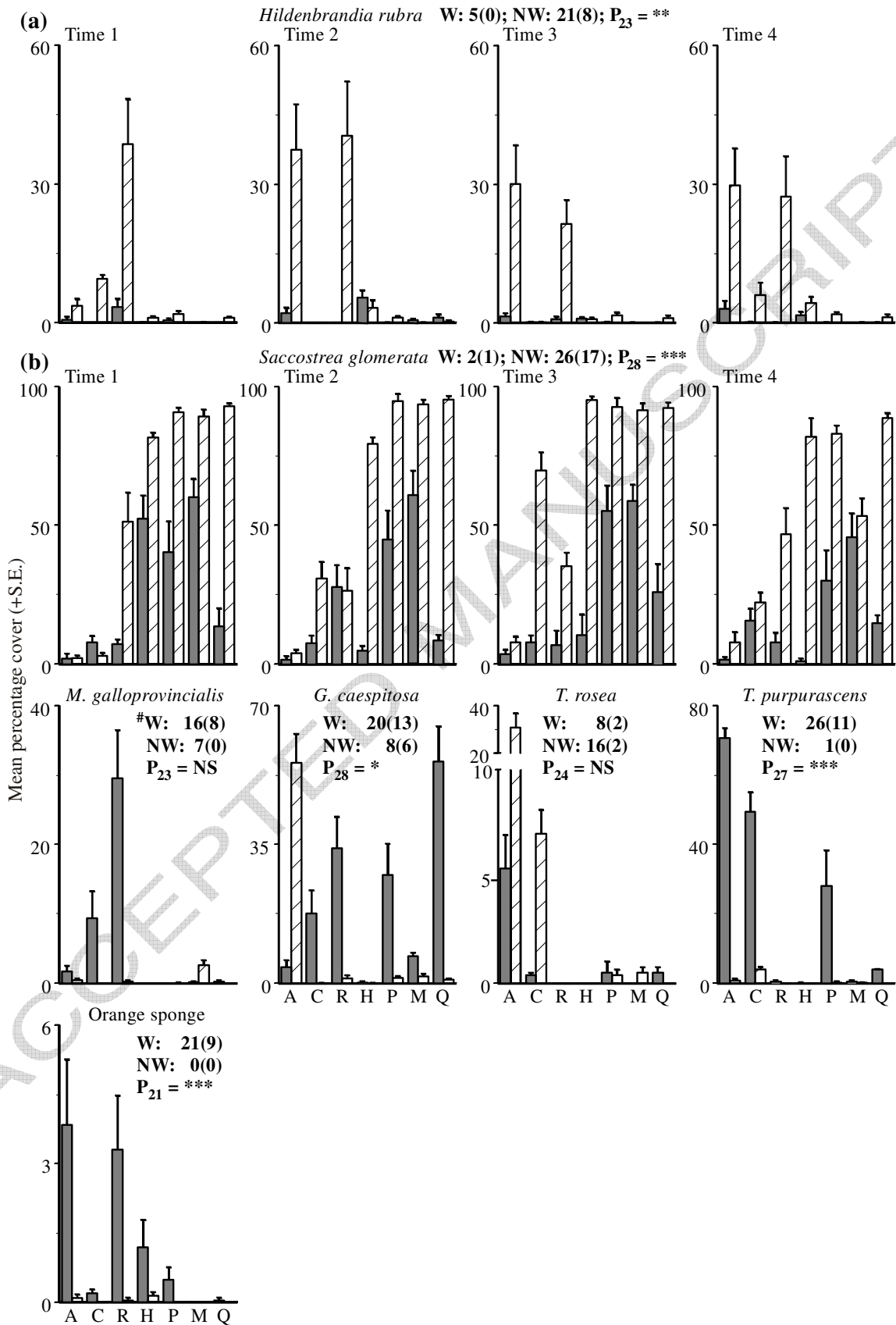
531

532 Fig. 4

533

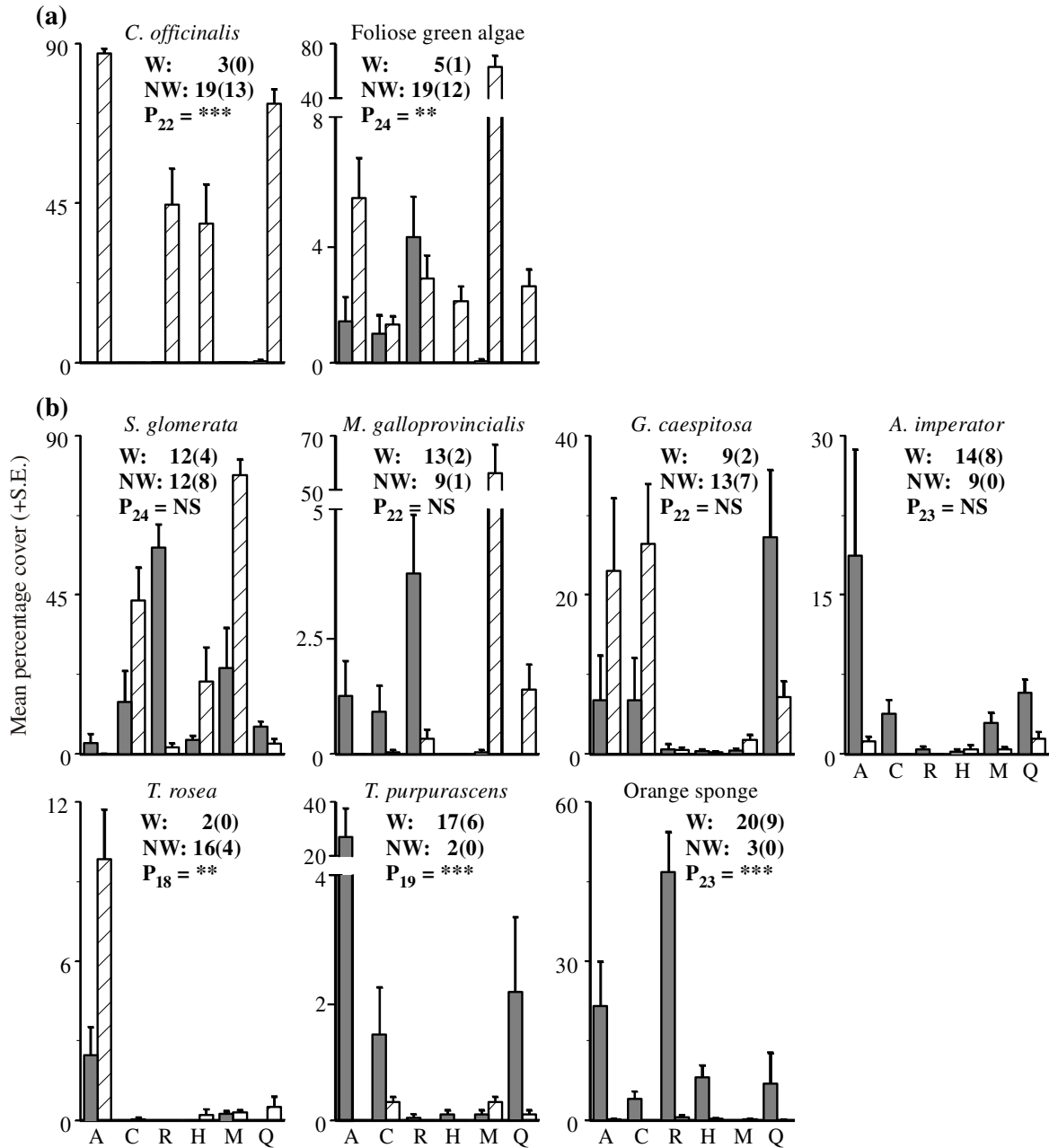
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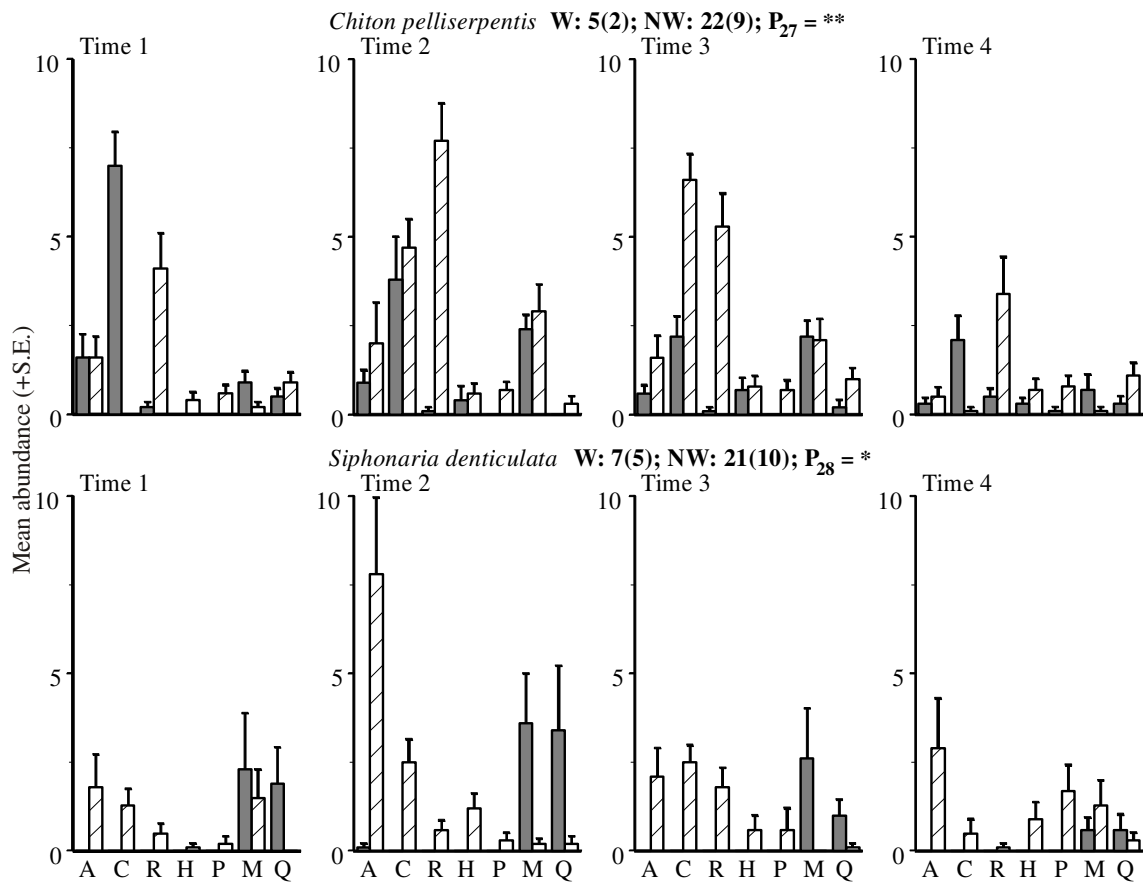
536

537 Fig. 5



538

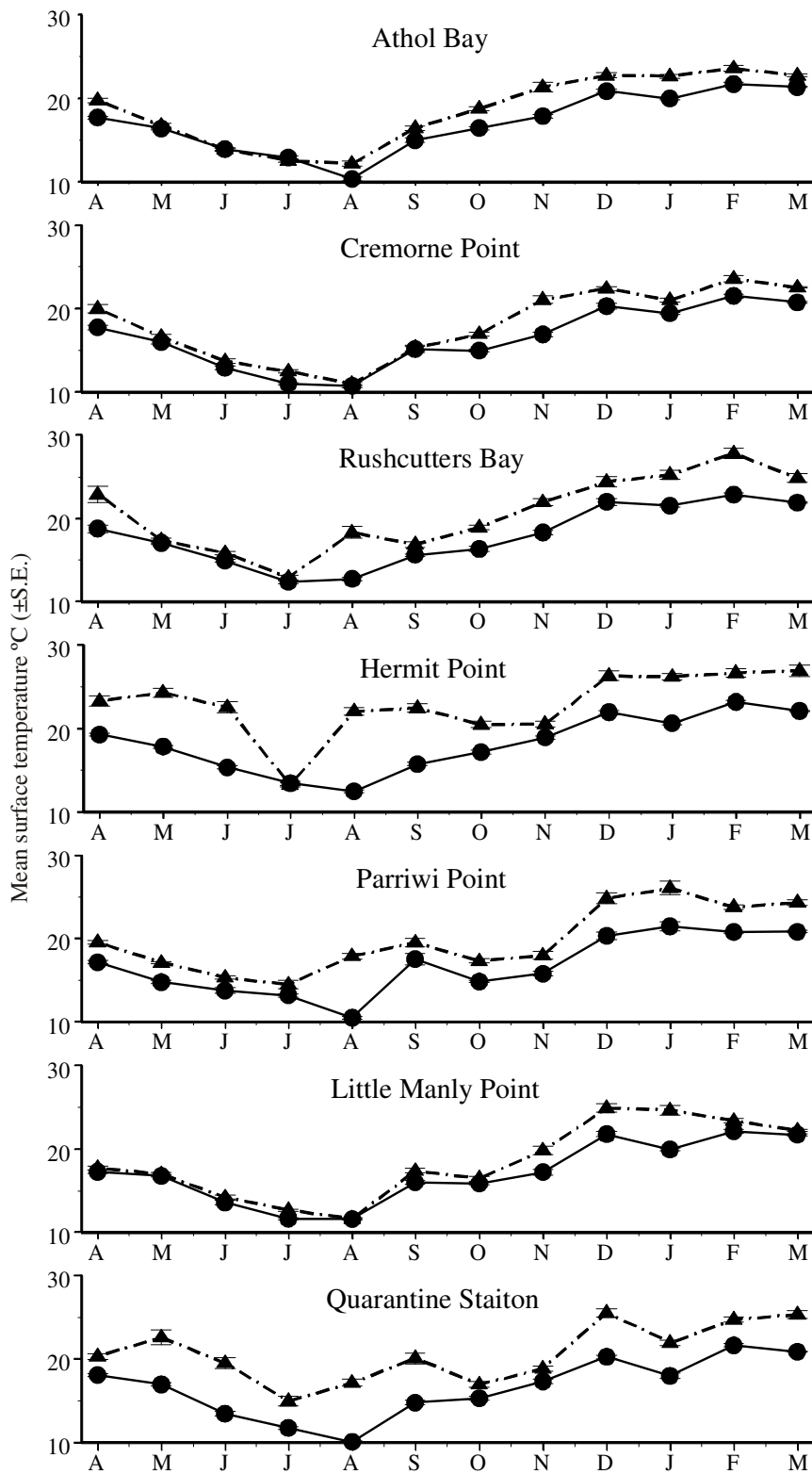
539 Fig. 6



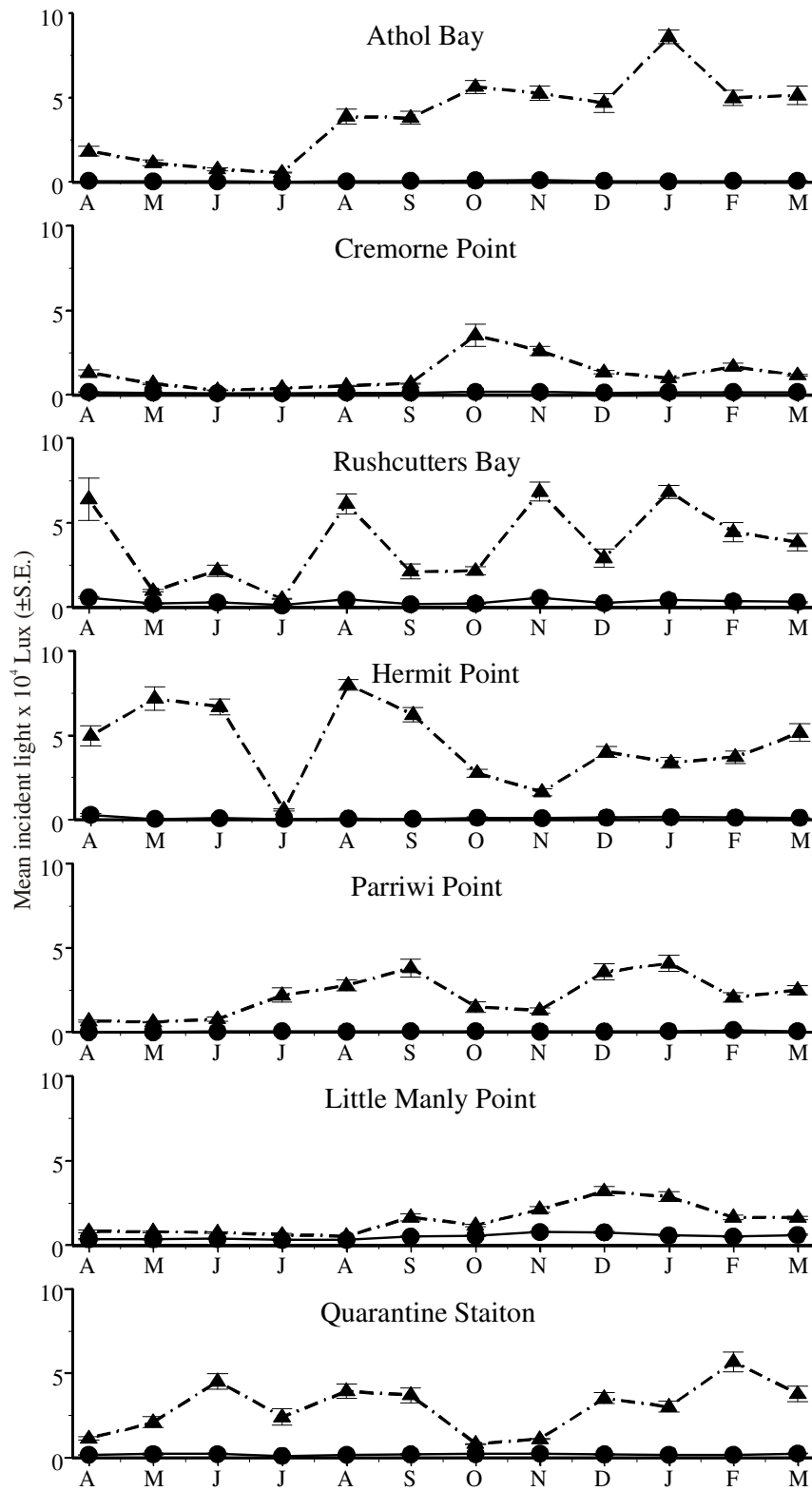
540

ACCEPTED

541 Fig. 7



543 Fig. 8



544

545