1 *A new species of the cheilostome bryozoan* Chiastosella *in the*

2 *Southern Ocean, past and present*

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12

13 **Abstract**

14 Understanding whether marine calcifying organisms may acclimatize to climate change is

15 important with regard to their survival over the coming century. Because cold waters have a

16 naturally higher $CO_2$ uptake,the Southern Ocean provides an opportunity to study the

17 potential impact of climate change. In 2011, anew cheilostome bryozoan species –

18 C*hiastosella ettorina* sp. nov. – was dredged from Burdwood Bank, Southern Ocean, at 300

19 metres depth during the *Nathaniel B Palmer* Cruise. *C. ettorina* had previously been collected

20 in 1902 from the same area at 100 metres depth, but was incorrectly identified as *Chiastosella*

21 *watersi*, which is an encrusting species from New Zealand. The availability of samples of the

22 same species, from the same general location, but collected 109 years apart allowed us to

23 investigate morphological modifications potentially arising from environmental changes. We

24 found a significant difference in zooid size, with the oldest and shallowest specimens having

25 smaller zooids than the recently collected, deeper specimens in disagreement with the

26 temperature-size rule. This difference in zooid size appears to be unrelated to known sources

27 of environmental variation such as temperature and salinity and it could represent the

28 extremes of the zooid size range of C. *ettorina*. Analternative explanation is that the

29 acidifying waters may cause zooids to grow more slowly, resulting in a final larger size.

32    **Introduction**

33    There is a currently great interest in the predicted effect of climate change on calcifying

34    marine organisms around the world. Climate change is an important factor in determining the

35    past and future distributions of biodiversity (Rosenzweig et al. 2008). The high sensitivity of

36    polar and sub-polar species to temperature increase and pH decrease renders the responses of

37    taxa in these regions particularly important. Analyses of geographical distributional patterns

38    of several groups of marine organisms (e.g., Clarke and Crame 1989; Gray 2001; Linse et al.

39    2006) have disproved the paradigm that biodiversity in all taxonomic groups decreases

40    towards the poles (Sanders 1968). Indeed, some parts of the Southern Ocean, such as

41    Burdwood Bank, seem to be hotspots for biodiversity, with an ever-increasing number of new

42    species being discovered, from hydrocorals to gorgonians to (Häussermann and Försterra

43    2007; Zapata-Guradiola  and López-González 2010; López-Gappa 2000). These discoveries

44    contribute to the 700 additional new species described from the Southern Ocean since 2002,

45    mostly from deep waters (Brandt et al. 2007).

46         Bryozoans comprise a phylum of benthic colonial invertebrates that are widely

47    distributed throughout the world's oceans (Hayward  and Ryland 1999; Wood *et* et al. 2012).

48    They are a major component of the Southern Ocean benthos (Hayward 1995) and significant

49    carbonate producers on the Antarctic shelf (Henrich et al. 1995). The phylum comprises

50    about 5900 described living species, of which most belong to the order Cheilostomata ( Bock

51    and Gordon 2013). Bryozoan colonies demonstrate morphological differentiation of

52    constitutent individuals, called zooids, with zooids specialised for feeding (autozooids),

53    reproduction (ovicells and gonozooids) and defence (avicularia). Bryozoans are also capable

54    of adopting appropriate morphological responses to environmental changes (McKinney and

55    Jackson 1989) that can be expressed at genotypic or phenotypic levels. Differences in zooid

56    size and shape, for example, have been related to growth rates, feeding resources, salinity,

57    extreme hydrodynamic conditions, oxygen concentrations and temperature (Okamura 1992;

58    O'Dea and Okamura 1999; Atkinson et al. 2006; O'Dea 2003; Okamura and Partridge 1999;

59    Hunter and Hughes 1994). Many features, including general zooid size and shape, are fixed

60    in the carbonate skeleton at the time that the zooid is budded (O'Dea and Okamura 2000). All

61    these features make bryozoans valuable recorders of environmental changes in the present

62    day as well as over geological time (e.g. O'Dea et al. 2011).

During the *Nathaniel B Palmer* Cruise in 2011 a new species, named here as *Chiastosella ettorina*, was collected from two different dredge hauls on the Burdwood Bank at a depth of 324-329 metres. It was the most abundant of bryozoans collected in these dredges together with *Microporella sp.*. The Burdwood Bank is a submerged plateau forming part of the Scotia Arc and located about 200 km south of the Falkland Islands. After examining the material it became evident that this new species had already been found on Burdwood Bank in 1902, but was misidentified in the literature (Hayward 1980). The discovery of these older specimens in the National Scottish Museum from the same location gave us the opportunity to compare the morphology of the species in samples collected 109 years apart.

**Materials and methods**

The study material from 2011 (six colonies) obtained during a cruise of the RVIB *Nathaniel B Palmer* (11-03; May 9–June 11, 2011). The bryozoan colonies were collected using dredges at 324-219 metres depth on the Burdwood Bank (54°28.88'S; 62°18.08'W). Historical material (one colony) originated from the *Scotia* (1902-1904) expedition, also collected on the Burdwood Bank, but at a shallower depth of 56 fms (~100 metres) (Fig.1).

Zooid size in a single colony was measured by randomly choosing 15 zooids outside the zone of astogenetic change (O'Dea & Okamura 2000) and measuring their maximum lengths and maximum widths. The same procedure was used to measure size of 10 ovicells per colony.

Three colonies of the recently collected bryozoans were bleached to remove the organic material and then prepared for scanning electron microscopy (SEM) using a CamScan-CS-44 at the University of Bristol and a low-vacuum microscope (LEO VP-1455) at the Natural History Museum, London. From the SEM images, three transects per colony were selected and zooid sizes were measured along these transects using ImageJ analysis software (Rasband 2008). For the historical material, SEM was carried out on one unbleached and uncoated colony using a low-vacuum microscope (LEO VP-1455) at the Natural History Museum, London. Replication of material for study was highly constrained by the lack of colonies sufficiently large to enable sampling zooid and ovicell sizes.

Surface areas (maximum length x maximum width) and elongation (maximum length/ maximum width) of both feeding zooids and ovicells from recent and historical material were

95  compared using a Student's t-test. A Mann-Whitney Rank Sum Test was used to analyse

96  ovicell surface areas since the data were not normally distributed.

97  Specimen repositories and their abbreviations are as follows: NHMUK, Natural

98  History Museum, London; NSM, National Scottish Museum, Edinburgh; NMNH, National

99  Museum of Natural History, Smithsonian Institution, Washington DC.

100

101  **Results**

102

103  *Taxonomy*

104  Family ESCHARINIDAE Tilbrook 2006

105  Genus CHIASTOSELLA Canu & Bassler, 1934

106  CHIASTOSELLA ETTORINA SP. NOV.

107  **Synonymy:** *Chiastosella watersi* (Stach, 1937): Hayward 1980, p. 704, fig. 1D.

108  **Material:** Holotype: NMNH ****. Paratypes: NHMUK ****, NSM 1921.143.1809 [material

109  studied by Hayward]

110  **Etymology:** Named for the late father of the first author, Ettore Ragazzola.

111  **Description:** Colony erect, bilamellar, foliaceous, comprising broad fronds; large in size,

112  with fragments up to 6 cm long. Colony base and early astogenetic stages unknown.

113  Autozooids polygonal in outline, usually longer than broad (L = 0.94 ± 0.057 mm, W = 0.86

114  ±0.0.59 mm, mean L/W = 1.05) (n = 50). Frontal shield evenly covered by small round pores,

115  often missing from a tongue-shaped area proximal of the orifice. Primary orifice small, semi-

116  circular, usually wider than long (L = 0.19± 0.013 mm, W = 0.27± 0.005 mm) (n = 50), with

117  a rounded median sinus. Three to four oral spines developed. Ovicell helmet-like,

118  hyperstomial, fairly prominent, as long as wide (L = 0.43± 0.02 mm, W = 40± 0.006 mm) (n

119  = 10), with a narrow border containing a row of pores surrounding a central smooth,

120  depressed area of entooecium. Spines lacking in ovicellate zooids. Bands of ovicells usually

121  present, although rare isolated ovicells can be found. Avicularia adventitious, long, acute,

122  usually situated along one or both of the distolateral edges of the polygonal autozooids and

123 directed proximolaterally; rostrum acute and generally elevated at the tip; pivotal bar

124 complete.

125 **Remarks:** This species was originally identified by Hayward (1980) as *Chiastosella watersi*

126 Stach, 1937, an encrusting species from New Zealand. Aside from the erect, foliaceous

127 colony-form, it differs in having considerably larger zooids (mean W = 0.86 mm in *C.*

128 *ettorina* vs. mean W = 0.55 mm in *C. watersi*) (see Gordon 1989, p. 44, pl. 22E). Another

129 important difference between the two species is orifice shape, which in *C. ettorina* lacks the

130 straight proximal rim with a narrow, rectangular median sinus described for *C. watersi*. In

131 contrast, the sinus in *C. ettorina* is rounded.

132 Paratypic material of this new species, originally identified by Hayward (1980) as *C.*

133 *watersi*, was collected from Burdwood Bank at 103 metres depth between 1902 and 1904

134 (Fig. 2a, b). These specimens have smaller zooids than those collected in 2011 from 324

135 metres depth (Fig. 2c, d) (L = 0.79 ± 0.063 mm, W = 0.70 ± 0.041 mm vs. L = 0.94 ± 0.057

136 mm, W = 0.86 ±0.059 mm), but exhibit a similar orifice size (L = 0.22 ± 0.024 mm, W =

137 0.25± 0.024 mm vs L = 0.19 ± 0.013 mm, W = 0.27 ± 0.006 mm). Both the average surface

138 area of the autozooids of *C. ettorina* and the surface area of the ovicells show a significant

139 difference (p<0.001) between the recently collected (0.85 ±0.07 mm) and the historical

140 material (0.60 ±0.10 mm) (Fig 3). The reduced size of the zooids could be ecophenotypic as

141 the earlier collection was made from much shallower waters where the temperature is likely

142 to have been higher. The size of bryozoan zooids is known to be inversely proportional to the

143 temperature at which they are budded (Okamura et al. 2011) and smaller zooids therefore

144 indicate warmer waters. However, the magnitude of the difference in this instance is large.

145 The new species *C. ettorina* is unusual for this genus in having erect, foliaceous

146 colonies with broad fronds. This colony-form contrasts with the typically small encrusting

147 colonies seen in other species, many of which occur in New Zealand and have been described

148 or revised by Gordon (1989). It differs from *Chiastosella umbonata* Gordon, 1989 in having

149 larger zooids (mean W = 0.86 mm in *C. ettorina* vs. mean W = 0.53 mm in *C. umbonata*) and

150 a multiporous frontal shield; the frontal shield of *C. umbonata* Gordon, 1989 is largely

151 smooth and imperforate. The new species lacks oral spines in ovicellate zooids but these are

152 present and typically number two in both *C. enigma* Brown, 1954 and *C. umbonata*. The

153 frontal shield has fewer pores in *Chiastosella duplicata* Gordon, 1989 and the autozooids

154 may be larger (up to 1.07 mm long) but otherwise the zooidal morphology is quite similar to

155 that of *C. ettorina*. A less porous frontal shield and larger zooids characterize *Chiastosella*

156    *exuberans* Gordon, 1989 and this species also has tubercles on the frontal shield. In

157    *Chiastosella dissidens* Gordon, 1989 the frontal shield has only marginal pores and avicularia

158    are lacking. Ovicellate zooids have distinctly larger orifices than infertile zooids in the

159    Australian species *Chiastosella daedala* (MacGillivray, 1882); there is some indication that

160    ovicellate zooids usually have somewhat larger orifices in *C. ettorina* but this is not

161    consistent (see Fig. 2d). *Chiastosella gabrieli* Stach, 1937 has very large zooids (mean L =

162    1.30 mm in *C. gabrieli* cf. L = 0.94 ± 0.057 mm in *C. ettorina*). In *Chiastosella conservata*

163    (Waters 1881) the ovicell has a pair of pores in the proximal part of the endooecium and

164    autozooidal frontal shields are sparsely porous (see Bock

165    http://www.bryozoa.net/cheilostomata/escharinidae/chiacon.html).

166    **Distribution:** Burdwood Bank, Falkland Islands, South Atlantic.

167    *Morphometric analyses*

168    The average surface area of both the feeding zooids and the ovicells of *C. ettorina* showed

169    significant differences (feeding zooids: t = 7.128; p<0.001; ovicell: t = 280.00; p = <0.001)

170    between the recently collected (0.95 mm$^2$ ±0.02) and the historical material (0.6 mm$^2$ ±0.1)

171    (Fig 5). In contrast, the elongation of both feeding zooids and ovicells did not show any

172    significant differences between the recently collected and the historical material (feeding

173    zooids: t = 1.744 p = 0.087; ovicell: t = 187.00; p = 0.742). Transects taken from three

174    different colonies of similar size of the recently collected specimens showed no obvious

175    cyclic pattern in the surface area of the feeding zooids (Fig. 3).

176

177    **Discussion**

178    In keeping with the temperature-size rule (Atkinson et al. 2006; O'Dea 2003), bryozoan

179    zooids generally show an inverse relationship between temperature and size at the time of

180    budding, larger zooids being formed in cooler waters. This makes it possible to infer seasonal

181    variation in temperatures experienced by the bryozoan colonies by measuring within-colony

182    variations in zooid size (O'Dea and Okamura 2000). Likewise, cyclical patterns in zooid size

183    should be evident in transects, with peaks in size corresponding to the cold, winter season and

184    small zooid sizes associated with the warm, summer season. However, parallel transects from

185    different colonies of *C. ettorina* revealed no evidence for coordinated cyclical patterns in

186   zooid size in the recently collected material (Fig. 3). This result was not surprising given the

187   ~ 0.6°C seasonal temperature difference (Southern Ocean Atlas 2004).

188   Unexpected, however, is the significant and surprisingly large difference in zooid size

189   between the recently collected and the historical material, the former having appreciably

190   larger zooids than the latter. Although the material comes from different depths (historical:

191   100 metres; recent: 219–324 metres), the difference in annual temperature of ~ 0.5°C (Fig. 4)

192   between the two sites is similar to the seasonal variation at each site and was not associated

193   with cyclicity in zooid size. As the historical material has smaller zooids (Fig. 5), this would

194   imply a cooling trend between 1902 and 2011 in stark disagreement with a large body of

195   work showing warming in the Southern Ocean (Meredith and King 2005; Turner et *al.* 2005).

196   Furthermore, the difference in zooid size is surprisingly large, in the order of zooid size

197   changes associated with changing thermal regimes of a much greater range. For instance,

198   differences in zooid areas recorded for *Conopeum seurati* in the Severn Estuary (United

199   Kingdom) during the summer and winter months (O'Dea and Okamura 1999) are roughly

200   similar to those observed here for *C. ettorina* colonies from different depths (ratio of

201   large:small zooid sizes approximately 1.5 and 1.4 for *C. seurati* and *C. ettorina*,

202   respectively). However, the zooid size changes observed for *C. seurati* colonies were

203   associated with an approximately 12$^o$C difference in temperature through the year. Similarly,

204   seasonal patterns of zooid size variation (based again on ratio of large:small zooid sizes) in

205   cupuladriid bryozoans are roughly 1.7 and 1.1 from the Pacific (temperature range ~ 6$^o$C) and

206   Caribbean (temperature range ~ 2$^o$C) coasts of Panama, respectively (O'Dea and Jackson

207   2002). The opposite direction of zooid size change with time relative to the known difference

208   in temperature and the magnitude of size variation observed here together imply that

209   temperature is unlikely to explain directly the notable variation in zooid size in colonies

210   collected during the two time periods.

211   Salinity is also unlikely to have influenced zooid size given the similar salinity

212   profiles in the two collection sites (Fig. 4) over the time period and with depth. Water flow is

213   another factor that can exert strong effects on zooid size. In particular, it has been shown that

214   rapid flow regimes lead to a miniaturization along with changes in zooid shape (measured as

215   zooid elongation) in bryozoan colonies (Okamura and Partridge 1999). Such miniaturization

216   may be adaptive in effecting suspension feeding from similar flow microhabitats. However,

217   zooid shape (as measured by zooid elongation) in *C. ettorina* is identical in the recent and

218   historical material (Fig. 5 c), suggesting that variation in current flow is unlikely to explain

219 our results. Furthermore, the increase in size from the historical to the modern material would

220 be associated with a reduction in ambient flow regimes by a factor of 3x (Okamura and

221 Partridge 1999). Even if sampling sites are located at the northern end of the ACC (Antarctic

222 circumpolar current), with the AAOI (Antarctic oscillation index) indicating a strengthening

223 and weakening of circumpolar westerly flow since 1920 (Jones and Widman 2004), we

224 suggest this magnitude of difference in flow on regional scale is unlikely to characterise the

225 depths (100 and 219–324 metres) from which colonies were collected for this study. It is

226 possible that the observed, very large difference in zooid size could represent the extremes of

227 the size range in *C. ettorina* if this species is particularly variable. Unfortunately this can only

228 be ascertained by obtaining further specimens for examination. Alternatively, it may indicate

229 phenotypic plasticity in response to some unidentified factor. An intriguing additional

230 possibility is that acidifying waters may cause zooids to grow more slowly, resulting in a

231 final larger size, particularly if acidification has an even stronger effect on development than

232 on growth.

233

234 It would be desirable to obtain material from a range of depths at Burdwood Bank for

235 morphological examination in order to characterise more fully the spectrum of morphological

236 variation present in this species. Sequence data of course would also be highly informative.

237 For the material presently at hand, it is likely to be difficult to obtain sequences from the

238 historical samples that were probably subject to formaldehyde-based fixation at some stage,

239 making DNA extraction and amplification highly problematic. Questions for future

240 investigation include whether other Antarctic taxa exhibit similarly large ranges in zooid size

241 at different depths and the influence of acidification on zooid size.

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332

**Figure captions**

**Fig. 1** Location of the sampling area.

335

**Fig. 2** Scanning electron micrographs of *Chiastosella ettorina* sp. nov. from Burdwood Bank. (**a**), (**b**) holotype colony (NMNH *****) collected in 2011; (**a**) Part of colony with reparative growth of zooids on the left side from a fracture running vertically through the centre of the image; (**b**) three ovicellate zooids (O) and scattered small avicularia (A). (**c**), (**d**) Paratype colony (NMSZ 1921.143.1809); (**c**) Part of unbleached colony with opercula closing autozooidal orifices; (**d**) Transverse band of ovicells.

**Fig. 3** Zooid surface areas sampled alongtransects from the distal, recently-developed zooids at colony edges to progressively older zooids away from colony edges in  three different colonies of *Chiastosella ettorina* that were alive at the time of collection in 2011.

**Fig. 4** Hydrological parameters for the two different collecting sites for *Chiastosella ettorina* (Ocean Data View). The triangle is the 1902 collection site and the square the 2011 collection site. The bands display the depth of the 1902 sample and the depth of the 2011 sample.

**Fig. 5** Mean surface areas and elongation of autozooids (a, c) and ovicells (b, d) of *Chiastosella ettorina* sp. nov. from Burdwood Bank collections made during 2011 at 324–319 m depth and 1902 at ~100 metres depth (n=15 zooids from six different colonies and from a single colony, respectively; error bars = standard deviations).

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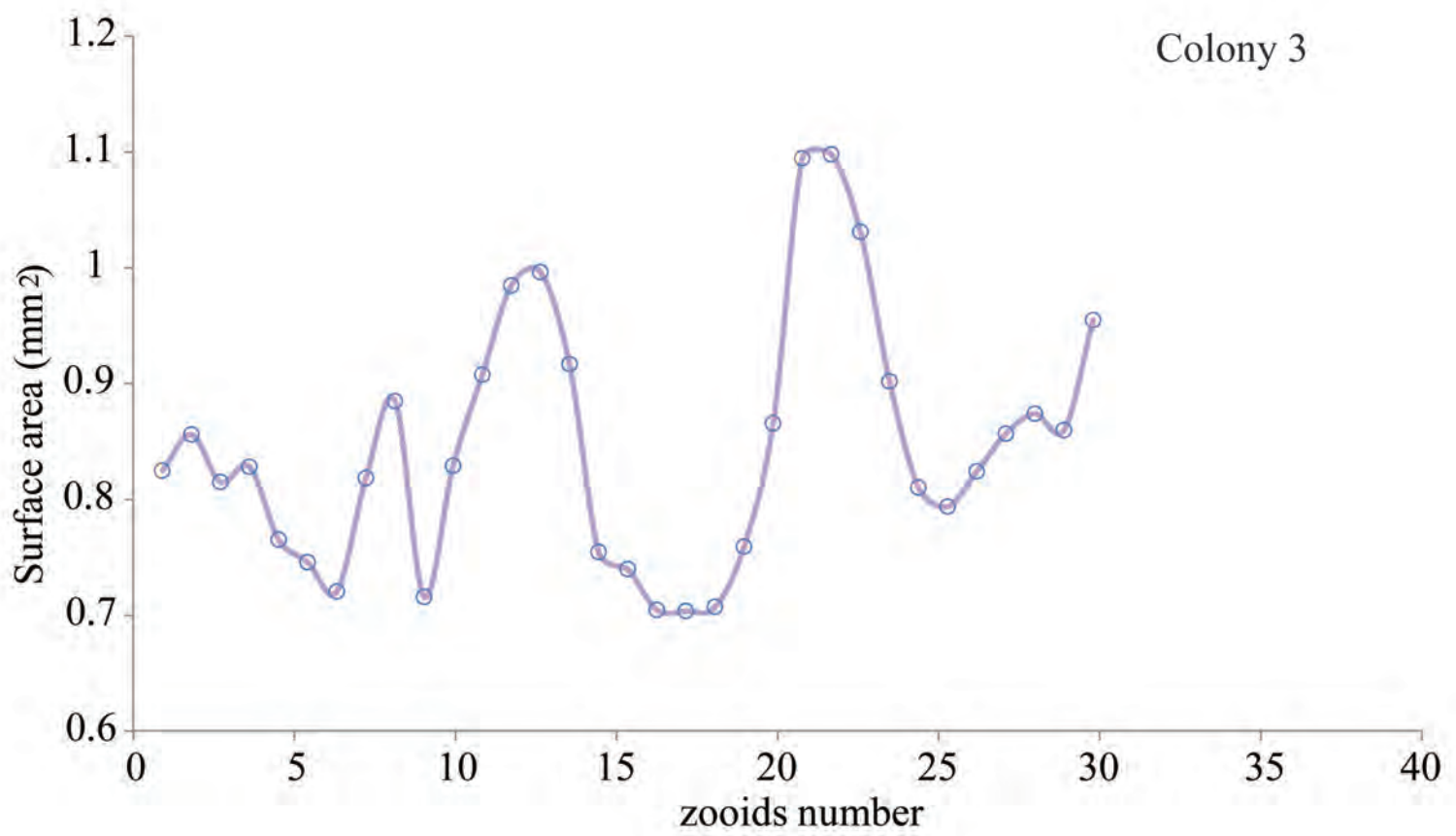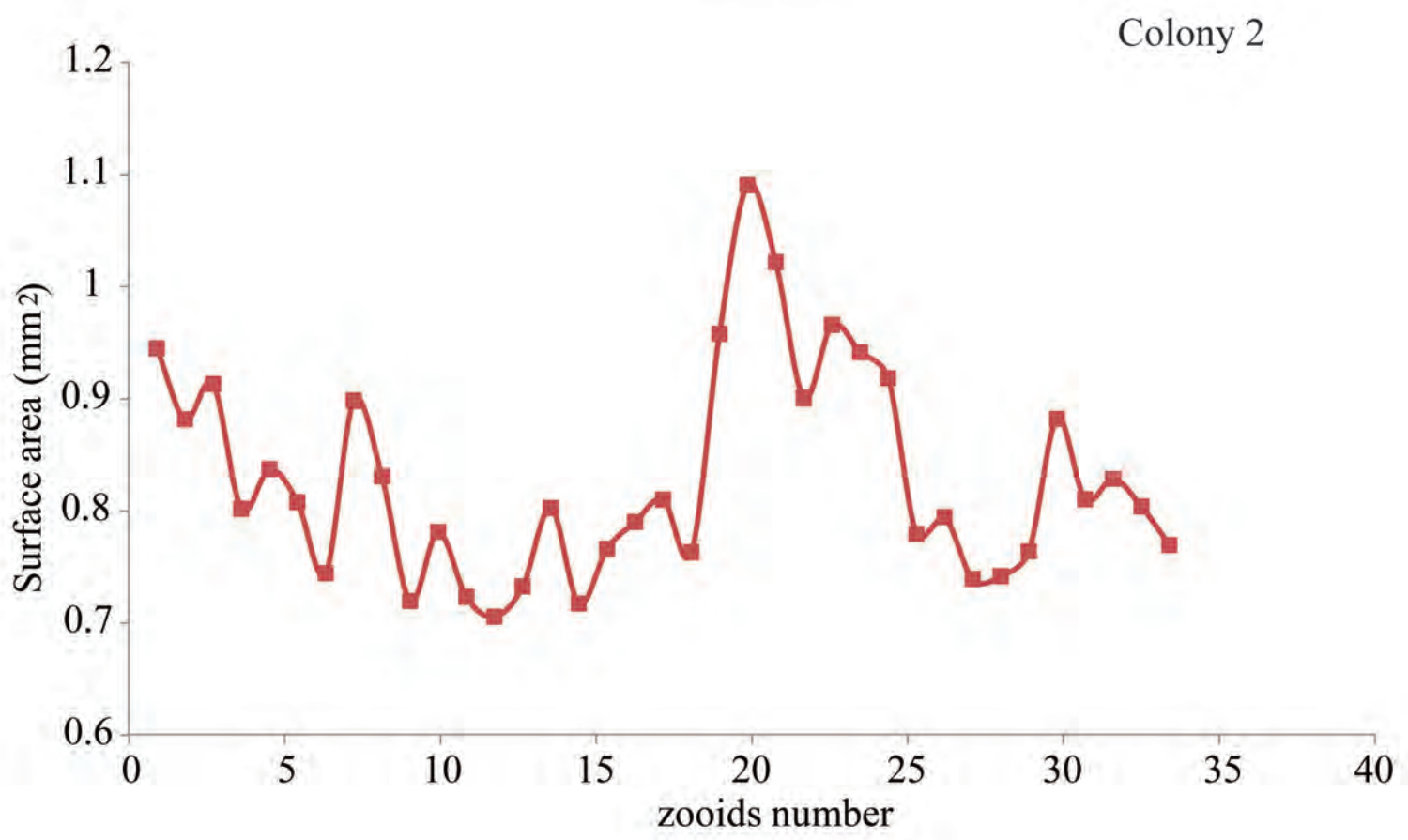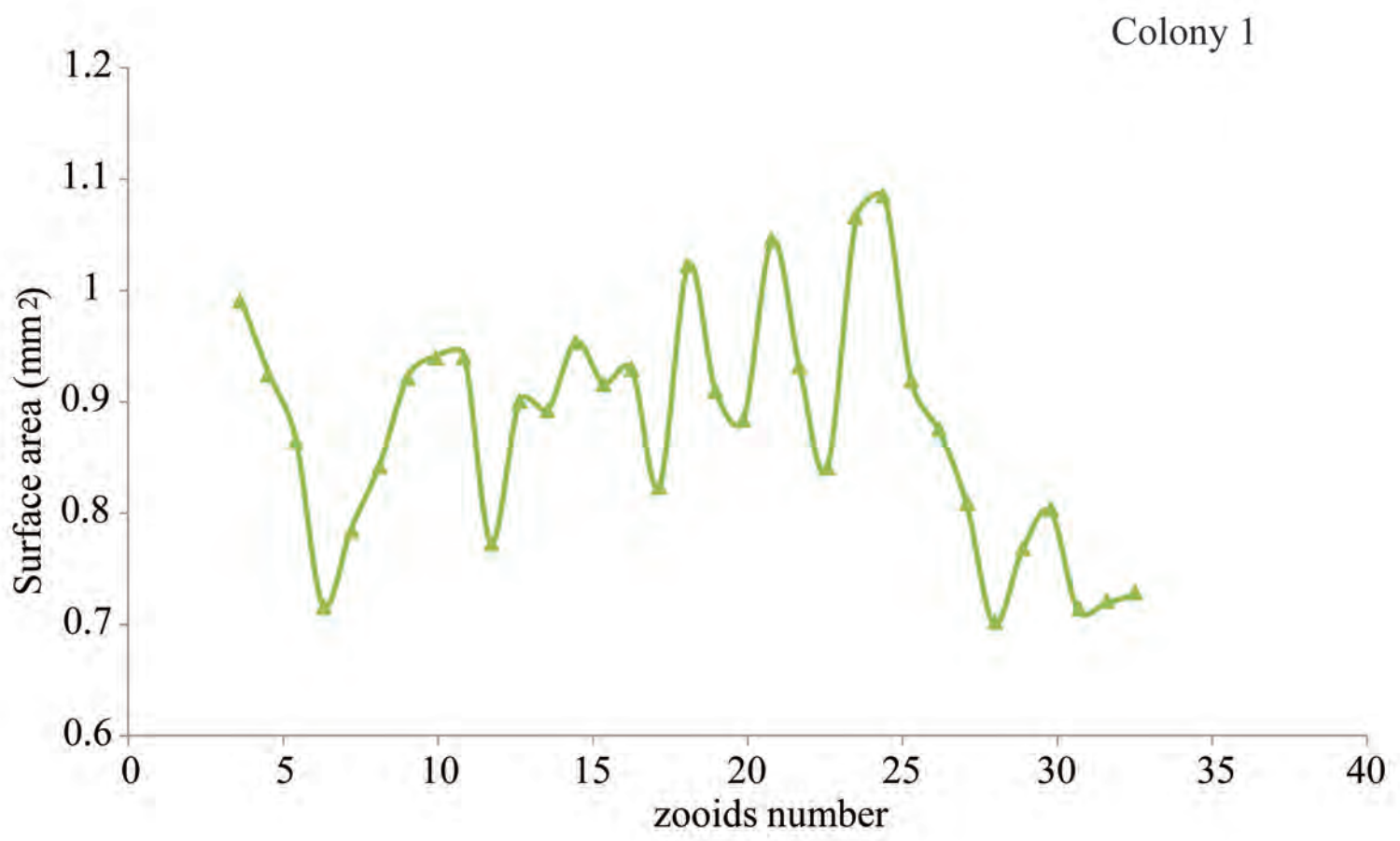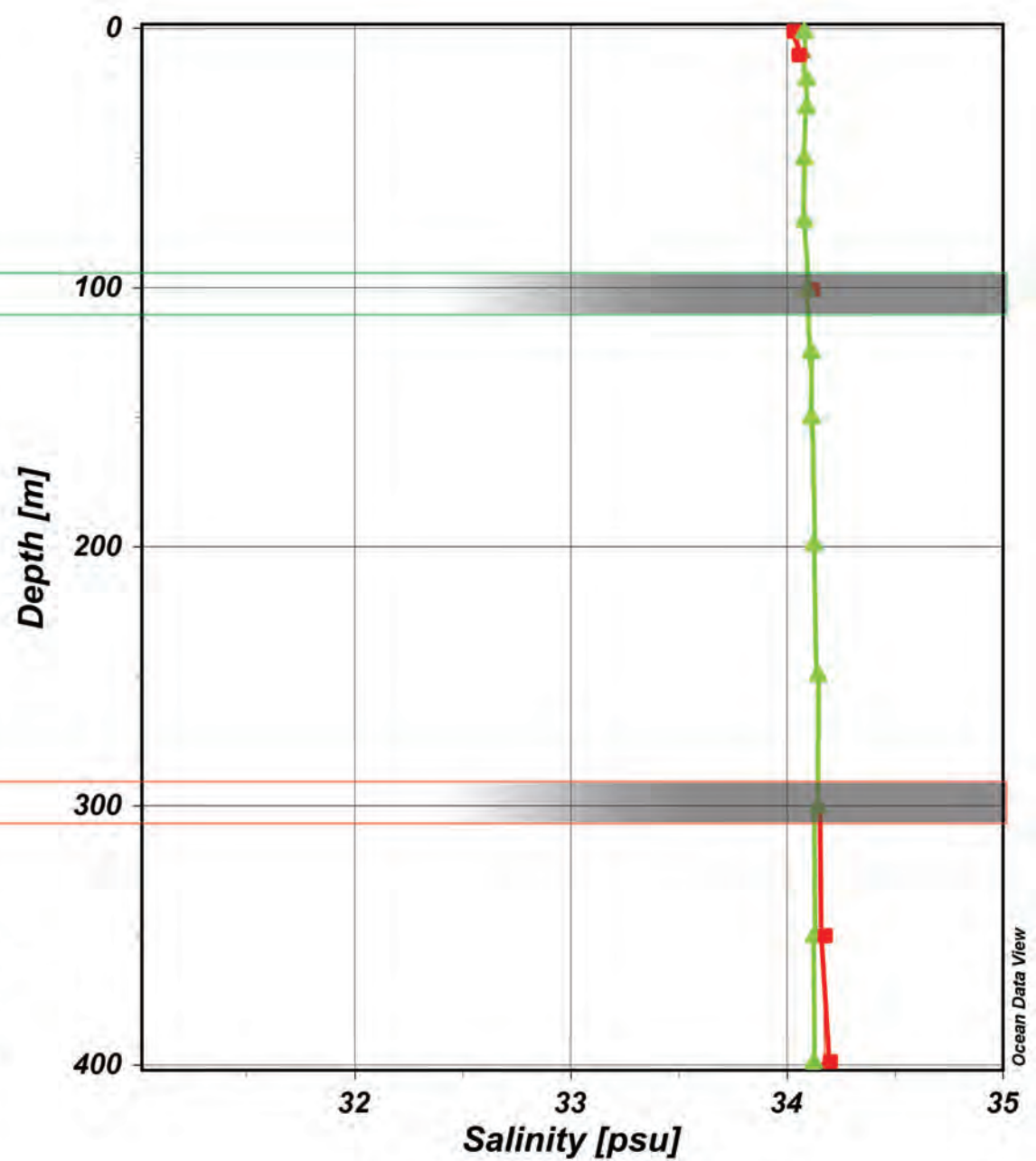
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Colony 1

Colony 2

Colony 3