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19 **Abstract**

20 This study has determined the diet of the demersal Knifefish *Oplegnathus woodwardi* in depths
21 of 50 - 200 m off the southern coast of Western Australia, where the benthic invertebrate
22 epifauna is overwhelmingly dominated by sponges. The many fused teeth that form the parrot-
23 like beak of *O. woodwardi* are used in conjunction with strong muscular plate-like jaws to
24 shear/chop off pieces of sponge and crush the spicule-containing skeleton. Despite the
25 potentially formidable physical and chemical defences (siliceous spicules and secondary
26 metabolites) of sponges, these invertebrates constitute the main prey of *O. woodwardi*. Sponges
27 were thus ingested by 44% of *O. woodwardi* and contributed 38% to the volume of the stomach
28 contents across a wide length range of fish. The volume of sponges was, however, far less in
29 the stomachs than intestines, whereas the reverse was true for teleosts. This is presumably due
30 to sponges undergoing less digestion than the externally soft-bodied teleosts as food passes
31 through the gut, which is consistent with the large numbers of mainly intact spicules present in
32 the intestine. Since the poriferan prey consisted almost exclusively of species of the
33 Tetractinellida, even though there are three other speciose sponge orders in the region where
34 *O. woodwardi* feeds in south-western Australia, this predator apparently selects the sponge taxa
35 it ingests. The length of the siliceous spicules of the Tetractinellida often exceeds 2000 μm , a
36 value nearly ten times that which acts as a deterrent in another fish predator-sponge interaction.
37 Thus, despite possessing formidable defence mechanisms, tetractinellinids are palatable to
38 *O. woodwardi*. The next most important prey after sponges was teleost fish (among which
39 clupeids were relatively abundant), being ingested by 35% of individuals and comprising 28%
40 of the stomach contents. The other major invertebrate prey comprises both hard-bodied
41 crustaceans (mainly decapod crabs), echinoderms, bivalve molluscs and cephalopod molluscs
42 (with their hard beaks and internal shells), all of which were probably associated with the
43 particular habitat occupied by tetractinellid sponges. These hard-bodied prey are processed by
44 *O. woodwardi* through the crushing action of its strong jaw mechanism. It is beneficial for
45 *O. woodwardi* to feed on tetractinellid sponges because they are sessile, palatable to
46 *O. woodwardi* and very abundant in the environment of this predator and thus do not incur a
47 high energetic cost of foraging.

48 **Keywords:** benthic environment; epifaunal invertebrates; sponge defences; predation; Oplegnathidae;
49 Australia.

50

51 **1. Introduction**

52 Sponges (Phylum Porifera) are abundant and play an important functional role in many marine
53 epibenthic communities in a range of water depths and latitudes worldwide (McClintock et al.,
54 2005; Heyward et al., 2010; Berman and Bell, 2016; Garcia-Hernández et al., 2018). These
55 sessile invertebrates are, however, not commonly ingested by marine predators (Randall and
56 Hartman, 1968) including demersal fish species (Bulman et al., 2001; French et al., 2013; Park
57 et al., 2017). The relative neglect of sponges as suitable prey has been attributed to their
58 possession of defence mechanisms. These include chemical defences, such as those produced
59 by toxic secondary metabolites (Beccero et al., 2003; Loh and Pawlik, 2014; Rohde and
60 Schupp, 2018), and structural defences and particularly those provided by their siliceous
61 spicules, which, together with the proteinaceous fibres (spongin), also potentially limits
62 digestibility (Bjorndal, 1990; Burns and Ilan, 2003; Burns et al., 2003).

63 The effectiveness of the above defence mechanisms varies among sponge taxa. For
64 example, the spicules of Red Sea sponges deter predation by Klunzinger's wrasse *Thalassoma*
65 *klunzingeri* when their spicules are longer than $\sim 250 \mu\text{m}$ (Burns and Ilan, 2003), whereas those
66 of the sponge *Geodia neptuni* that were longer than $500 \mu\text{m}$ did not have a similar deterrent
67 effect on fish predation (Chanas and Pawlick, 1995). The physical and chemical defences of
68 Red Sea sponges were more effective against predation when combined than when employed
69 separately (Burns and Ilan, 2003). Fish that feed predominantly on poriferans consume a wide
70 range of sponge species, whereas those that consume sponges as part of a broader diet tend to
71 prey on a particular species of sponge (Randall and Hartman, 1968; Wulff, 2016).

72 The monogeneric Oplegnathidae (Knifejaws), which has a temperate Indo-Pacific
73 distribution (Bray and Hoese, 2006; Nelson, 2006), contains seven species that includes the
74 Cape Knifejaw *Oplegnathus conwayi*, which has been shown to be a spongivore (Chater et al.,
75 1995). The latter study showed that sponges constituted as much as 63% of the dietary volume
76 of this species in water depths $< 25 \text{ m}$ on the southern coast of Africa. In contrast, the sponges

77 in the diet of the Natal Knifejaw *Oplegnathus robinsoni*, the only other demersal oplegnathid
78 for which there are dietary data, constituted only 1.5% by volume in the waters of the lower
79 east coast of Africa (Chater et al., 1995). Instead, the diet of *O. robinsoni* contained large
80 volumes of hard-shelled invertebrates, i.e. barnacles, bivalve and gastropod molluscs and
81 bryozoans.

82 The Knifejaw *Oplegnathus woodwardi* (Waite 1900) is the only representative of the
83 Oplegnathidae in Australia, where its distribution extends throughout the southern region of
84 this continent, including Tasmania (Gomon et al., 2008). This demersal species, which lives in
85 water depths of 50 - 400 m and thus in a mesophotic environment, is considered an excellent
86 food fish that is caught in moderate numbers by commercial fishers (McAuley and
87 Simpfendorfer, 2003; Knuckey et al., 2009) and infrequently by recreational fishers
88 (P. Coulson pers., observ.). Preliminary observations of the gut contents of *O. woodwardi* in
89 south-western Australian waters showed that, like *O. conwayi*, this oplegnathid ingests large
90 volumes of both sponges, which are by far the most abundant of the invertebrate phyla in those
91 waters (Fromont et al., 2012), and also teleosts. The teeth in the small terminal mouth of
92 *O. woodwardi* are fused to form a powerful parrot-like beak (Kakizawa et al., 1980; Gomon
93 et al., 2008), similar to those of the hawksbill turtle *Eretmochelys imbricata* and of teleosts
94 such as parrotfishes, angelfishes and leatherjackets that likewise “bite off” and ingest large
95 amounts of sponges and other hard-bodied invertebrates (Randall and Hartman, 1968; Meylan,
96 1988; Wulff, 1997; León and Bjorndal, 2002; Rodgers et al., 2013; Wood et al., 2017; Pawlik
97 et al., 2018).

98 While the study of *O. conwayi* provided details of the food consumed by this spongivore
99 (Chater et al., 1995), it did not explore whether the diet underwent seasonal and size-related
100 changes and did not determine the taxonomic composition of the sponge prey. The diets of
101 many fish predators change markedly as their mouth size, jaw strength and swimming ability
102 increase (Werner and Gillam, 1984; Platell et al., 2010; Park et al., 2017). Indeed, the diet of
103 the omnivorous silver trevally *Pseudocaranx georgianus*, the carnivorous foxfish *Bodianus*
104 *frenchii* and three piscivorous species of the Platycephalidae underwent both seasonal and size-

105 related changes on the same coast as *O. woodwardi* (Platell et al., 2010; French et al., 2012;
106 Coulson et al., 2015).

107 The aim of the present study was to determine the feeding biology of *O. woodwardi*,
108 which is atypical in that it involves ingesting large volumes of sponges. The hypothesis was
109 tested that differential digestion of the various prey items during their passage through the gut
110 leads to the intestine containing relatively greater volumes of spiculose sponges than the
111 stomachs, whereas the reverse is true for the externally soft-bodied teleost fishes. Having found
112 this to be true, the dietary composition of *O. woodwardi*, and the extent to which, if any, it
113 changes with season and increasing body length, were then determined using data derived
114 solely from the stomach contents. Next, the sponges were identified using the morphology of
115 their spicules, thereby enabling the contribution made to the volume of prey by poriferans at
116 the family, genus and species levels to be estimated. The morphology of the jaws and teeth of
117 *O. woodwardi* are described and used, in conjunction with data on its dietary composition and
118 reports on the benthic macroinvertebrates present in the region (McEnnulty et al., 2011;
119 Fromont et al., 2012), to elucidate how and where this species feeds.

120

121 **2. Materials and methods**

122 *Oplegnathus woodwardi* was obtained in each season, between the winters of 2011 and 2013,
123 from the catches of commercial fishers operating on the south coast of Western Australia
124 between 36°S, 117°E and 34°S, 124°E. The benthic epifauna, at a depth of ~ 200 m on the
125 south coast of Western Australia where *O. woodwardi* occurs, is dominated by sponges, with
126 at least five conspicuous erect forms of sponges shown in Fig. 1 from left to right on the
127 midground, and encrusting species of sponges attached to the bedrock. Other organisms
128 (including other sponges) about the sandy substrate and two ascidian-like stalked sponges are in
129 the right hand foreground.

130 The vast majority of *O. woodwardi* (n = 258) were caught using sunken monofilament
131 gillnets (stretched meshes of 165 - 178 mm), following the methods of McAuley and
132 Simpfendorfer (2003). Nets were typically set for up to 17 h during the night over relatively
133 flat substrata and in water depths of 50 - 150 m. In addition, 54 *O. woodwardi* were caught in

134 the same south coast waters by commercial line-fishers using three bait sources, i.e. Australian
135 herring *Arripis georgianus*, Australian pilchard *Neopilchardus sagax* and imported squid *Illex*
136 *argentinae*. All *O. woodwardi* were provided as filleted frames with their viscera intact.

137 2.1. Laboratory analyses

138 The upper and lower jaws of an *O. woodwardi* of ~ 300 mm total length were immersed in hot
139 water to soften their tissues, which were then removed using tweezers. The jaws and their
140 dentition were photographed using a Nikon 5500 digital single reflex camera and a macro lens.

141 Each *O. woodwardi* from each corresponding season of the calendar year were grouped
142 for use in subsequent analyses. The total length (TL) of each *O. woodwardi* was measured to
143 the nearest 1 mm. Each gut, in which either or both of its stomach and intestine contained food,
144 was removed and stored at -18°C and later defrosted for dissection. The relative fullness of
145 each of those stomachs and/or intestines was scored visually on a range from 1 to 10, i.e. from
146 10 to 100% full (Hynes, 1950; Hyslop, 1980).

147 The contents in the stomach and/or intestine were removed, examined under a
148 dissecting microscope and the invertebrate contents (apart from sponges) identified to the
149 lowest taxonomic level, employing one or more of the following references: Hale (1929),
150 Hinton (1978), Shepherd and Thomas (1982a,b), Coleman (1994), Lamprell and Healy (1998),
151 Wells and Bryce (2000), Jones and Morgan (2002), Lu and Ickeringill (2002), Wilson (2002)
152 and Poore (2004).

153 The identification of sponges requires analysis of skeletal characters, such as spicule
154 types and arrangement, and thus requires microscopy (Bergquist, 1978; Hooper and van Soest,
155 2002). Sponges are also renowned for exhibiting highly variable growth form, colour and
156 ability to incorporate other material, such as sand or spicules from other sponge species
157 (Shepherd and Thomas, 1982a; Edgar, 1997). These species can only be identified in the field
158 if they have highly distinctive characteristics or when the local fauna is well known and
159 described (Hooper and van Soest, 2002). Sponges were removed from the guts of each fish,
160 stored separately in 70% ethanol and later identified by examining their morphological features
161 (skeletal structure and spicule morphology) using light microscopy. They were identified to
162 genus using Hooper and van Soest (2002) and references therein.

163 For examining skeletal structure, a representative segment of sponge was cut at right
164 angles to the surface of the sponge, dehydrated through an ascending ethanol series, cleared in
165 Histolene (Fronine Laboratory Supplies) and embedded in paraffin wax (Shandon Histoplast)
166 using an automatic tissue processor on a 9 h cycle. The sponge segment was further infiltrated
167 with paraffin wax under a vacuum of 635 mm Hg for 30 min prior to embedding. The blocks
168 were sectioned at 90 μm thickness and placed on a glass slide smeared with egg albumin, dried
169 overnight at 60°C and dehydrated in two changes of Histolene. Sections were mounted in
170 Shandon EX-Mount and examined employing light microscopy, with digital images recorded
171 using a Leica DFC420 camera on a Leica DME microscope. For examining their morphology,
172 spicules were prepared for examination by dissolving small fragments of each sponge in nitric
173 acid (58% w/w), followed by centrifugation through two washes of both distilled water and
174 100% ethanol. The spicule extracts were dried on a glass slide and mounted in Shandon EX-
175 Mount (Thermo Electron Corporation). The dimensions of 10 randomly-selected spicules of
176 each spicule type of every specimen examined were measured using an eyepiece graticule with
177 an Olympus BX50.

178 The teleost prey in the stomachs and intestines were identified, when possible, to
179 species and then aggregated to family (Hutchins and Swainston, 1999). The ability to identify
180 teleosts in gut contents was enhanced by using descriptions of the otoliths of many fish species
181 in the marine waters of south-western Australia (Dowling et al., Department of Primary
182 Industries and Regional Development, Western Australia, unpublished data) and southern
183 Australia (Furlani et al., 2007).

184

185 2.2. Analyses of stomach and intestinal contents

186 Since the bait in the stomach contents of *O. woodwardi* caught by line fishing had been cut into
187 well-defined segments and was undigested, it was readily distinguishable in those contents and
188 could thus be disregarded in analyses. The overall percentage frequency of occurrence (%*F*) of
189 each major taxon, dietary category and dietary item in a stomach and/or intestine containing
190 food was calculated using the data for individual fish. The volumetric contribution (%*V*) of
191 each major taxon, dietary category and dietary item to the contents of each stomach and each

192 intestine in which there was food was estimated visually, using a grid-marked petri dish and
193 the methods described by Hynes (1950), Hyslop (1980) and Lek et al. (2018). The data for the
194 various dietary items were aggregated by dietary category and their major taxa.

195 When both the stomach and intestine of *O. woodwardi* contained food, paired *t*-tests
196 were used to test whether 1) the fullness of those two gut regions and 2) the volumetric dietary
197 contributions of sponges and of fish to the contents of these two regions differed.

198 Stacked bar graphs were constructed to compare visually the mean percentage
199 volumetric contributions of the dietary categories to the contents of both the stomachs and the
200 intestines of *O. woodwardi* in sequential 50 mm TL classes between < 300 mm and > 500 mm
201 TL. They thus covered the full TL range of fish (271 - 565 mm) caught with identifiable food
202 in their guts. As the volumetric contributions made by Cirripedia and algae were very small
203 (< 0.1%), they are not shown in those bar graphs.

204 All of the following multivariate analyses were conducted using PRIMER v7 with the
205 PERMANOVA+ add on (Anderson et al., 2008; Clarke and Gorley, 2015). Because the
206 contents of an individual gut region typically contained only a few of the 16 dietary categories
207 recorded, their compositions could differ markedly among individual gut regions. The
208 similarity coefficients calculated for individual fishes can thus prevent effective multivariate
209 analysis (Lek et al., 2011). The samples from each of these two gut regions in each length class
210 of fish in each season were thus randomly sorted into groups of three or four, depending on the
211 total number of fish in the samples, after which the volumetric dietary contributions for each
212 dietary category in each group were averaged (Platell and Potter, 2001; Lek et al., 2011). The
213 volumetric data for each of these ‘replicate’ groups were square-root transformed and used to
214 construct a Bray-Curtis resemblance matrix, which was subjected to Permutational Analysis of
215 Variance (PERMANOVA, Anderson et al., 2008) using Type III sums of squares. This three-
216 way analysis determined whether the dietary compositions of the stomachs and intestines
217 differed ($P < 5\%$), taking into account the potentially confounding effects of Length Class (six
218 levels) and Season (four levels). All factors were fixed.

219 The above Bray-Curtis resemblance matrix was used in two ways to visualise the extent
220 of any differences between the compositions of the stomach and intestinal contents. First, a

221 non-metric Multidimensional Scaling (nMDS) ordination was constructed in which the
222 replicates were coded for Gut Region, i.e. stomach or intestine (Clarke and Gorley, 2015).
223 Secondly, this matrix was subjected to the Bootstrap Averages Routine to bootstrap samples in
224 metric multi-dimensional scaling (mMDS) space (Clarke and Gorley, 2015). The averages of
225 those repeated bootstrap samples (bootstrapped averages) for stomachs and intestines were
226 used to construct a mMDS ordination plot. For both the stomach and intestinal data sets in this
227 latter plot, group average (i.e. the average of the bootstrapped averages) and the associated,
228 smoothed and the marginally bias-corrected bootstrap region, in which 95% of the bootstrapped
229 averages fell, were superimposed on the plot.

230 As the above analysis showed that the dietary compositions of the stomach and intestine
231 of *O. woodwardi* differed significantly (see Results), the next analysis was restricted to data
232 for the stomachs, which reflects more accurately the composition of the food ingested than
233 those for the intestine, in which the different food sources would have undergone variable
234 degrees of digestion during their passage through the gut. Two-way PERMANOVA was
235 therefore employed to determine whether the dietary composition of the stomachs differed
236 among Length Class and/or Season and whether there was an interaction between these two
237 factors (Anderson et al., 2008). RELATE tests (Clarke et al., 2014a) were then used to
238 determine whether the dietary composition of *O. woodwardi* changed significantly ($P < 5\%$)
239 in a serial manner through successive length classes in each calendar season. The strength of
240 any seriation was measured by the size of the Rho (ρ) value, which ranges from ~ 0 to 1. The
241 ‘distances among centroids’ approach, using the same matrix as for the above PERMANOVA,
242 was employed to construct a nMDS ordination plot displaying the distribution of the dietary
243 samples according to Length Class and Season and showing the extent of any interaction
244 (Anderson et al., 2008).

245 Shade plots (Clarke et al., 2014b) were constructed to display the volumetric data for
246 the dietary categories in the stomach contents of *O. woodwardi* according to Length Class and
247 Season. Dietary categories (y axis) were clustered employing the Whittaker’s Index of
248 Association (Somerfield and Clarke, 2013) and therefore aligned in their optimum serial order,
249 while sequential length classes in each season from austral Summer to Spring were arranged

250 on the x axis. The range of shading from grey to black for each dietary category in each length
251 class and season combination represents increasing contributions of that dietary category,
252 while a white space denotes that the dietary category was not recorded (Clarke et al., 2014b).

253

254 **3. Results**

255 *3.1. Morphology of the head, jaws and dentition*

256 The head of *Oplegnathus woodwardi* possesses a terminal parrot-like beak formed from fused
257 teeth, a prominent flesh-covered maxilla (upper jaw) that extends upwards over the snout, and
258 a large eye (Fig. 2a). The upper and lower jaws comprise tooth plates that contain many fused,
259 roughly hexagonal teeth (Fig. 2b-d). The upper jaw ‘sits’ outside the lower jaw, creating an
260 overbite when the jaws close (Fig. 2b, c). There are patches on the inside of the upper and lower
261 jaws containing prominent molars that are particularly numerous on the upper jaw (Fig. 2d).

262

263 *3.2. Major taxa, dietary categories and dietary items*

264 Among the 312 *O. woodwardi* examined, the guts of 174 (55.7%) contained food. The majority
265 (114) of those 174 guts contained food in both their stomach and intestine, while 35 contained
266 food only in their stomachs and 25 had food solely in their intestine. Food was thus present in
267 149 stomachs and 139 intestines (Table 1). The mean fullness of the stomach (5.8) and the
268 intestine (5.5) were not significantly different (paired $t = 1.614$, $df = 114$, $P = 10.9\%$).

269 Sponges, crustaceans and teleosts were by far the most frequently found major taxa in
270 both gut regions (Table 1). Sponges were present in 43.6% of the stomachs of *O. woodwardi*
271 and contributed 37.9% to the overall dietary volume of stomachs that contained food, with the
272 corresponding values for the intestines containing food being 65.7%*F* and 58.0%*V* (Table 1).
273 A paired t -test showed that sponges made a greater contribution to the intestine than stomach
274 contents, i.e. 37.9 vs 58.0% ($t = 4.529$, $df = 114$, $P = < 0.1\%$).

275

276 *3.3. Sponge taxa ingested by Oplegnathus woodwardi*

277 At least seven species of sponge were identified in the gut contents of *O. woodwardi*,
278 representing four genera within the Class Demospongiae, i.e. *Ecionemia*, *Stelletta* and

279 *Rhabdastrella* (Order Tetractinellida) and *Monanchora* (Order Poecilosclerida) (Table 1). An
280 additional sponge fragment, which made a very small contribution to the total volume of
281 sponges, could not be further identified. *Ecionemia* sp. 2 was the most frequently represented
282 species in both the stomachs and intestines (14.8 and 23.4%*F*, respectively) and made the
283 greatest volumetric contribution in those two regions (12.1 and 18.8%*V*; Table 1). The next
284 most numerous sponge, cf *Ecionemia* sp. 2, contributed 6.9% to the stomach contents and
285 16.7% to those of the intestine. Detailed descriptions and spicule measurements are provided
286 for each of these taxa in Supplementary Material.

287

288 3.4. Contribution of dietary categories other than Porifera

289 In contrast to the Porifera, the Chordata, consisting predominantly of teleosts, among which
290 the Clupeidae was prominent, was more frequently found (37%) and made a greater volumetric
291 contribution (29.6%) to the stomachs than intestines (11.7%*F* and 10.0%*V*, respectively;
292 Table 1). Teleosts made a significantly greater contribution to the volume of the stomach than
293 intestinal contents, i.e. 27.8 vs 6.2% (paired $t = 2.779$, $df = 114$, $P = 0.6\%$).

294 Crustaceans, consisting mainly of decapod crabs, were present in 24.2 and 33.6% of
295 the stomachs and intestines, respectively, and contributed 16.2 and 21.6% to the dietary volume
296 of the stomach and intestines, respectively (Table 1). Echinoderms, molluscs and particularly
297 polychaetes were less frequently ingested and made lesser volumetric contributions than
298 poriferans, teleosts and crustaceans (Table 1).

299

300 3.5. Contributions of different dietary categories to stomach and intestinal contents of different 301 length classes of fish

302 The few stomach samples from the smallest *O. woodwardi* consisted mainly of decapods,
303 teleosts and sponges, while those of the similarly few intestinal samples from the smallest fish
304 comprised exclusively sponges (Fig. 3a,b). The stomach contents of each TL class of
305 *O. woodwardi* were dominated by sponges, decapods (crabs) and teleosts, with these groups
306 collectively contributing between 72 and 89% to the overall volume (Fig. 3a). The volumetric
307 contribution made by sponges to the stomach contents was significantly and positively

308 correlated with the body size of *O. woodwardi* ($r^2 = 0.725$, $P = 5\%$). Sponges contributed
309 similar or lesser volumes than teleosts to the volume of the stomach contents of each of the TL
310 classes, whereas sponges clearly contributed relatively greater volumes than teleosts to the
311 intestinal contents of those length classes (Fig. 3a,b).

312 Dietary compositions of the stomach and intestinal contents of *O. woodwardi* were
313 significantly different ($P = 0.1\%$) and there was a significant Length Class \times Season interaction
314 ($P = 2.4\%$, Table 2a). The difference between gut regions contributed, however, far more to the
315 total mean squares (66%) than that of the interaction (7%). The marked difference between the
316 dietary compositions of the two gut regions is reflected on the nMDS ordination plot in Fig. 4a,
317 by the replicates for the stomachs lying predominantly to the left of those for the intestines. The
318 regions in which 95% of the bootstrapped averages of the stomach and intestinal data fall do
319 not overlap on the mMDS plot (Fig. 4b).

320 Overall, the percentage frequency of occurrence and volumetric contribution of
321 sponges was far greater in the intestine than in the stomach, reflecting relatively larger amounts
322 of relatively indigestible siliceous spicules, whereas the reverse was true for teleosts, which
323 contained soft-bodied components. This difference in the relative compositions of the food in
324 the stomach and intestines is assumed to reflect the fact that the siliceous spicules and other
325 hard components of sponges are less digestible than the softer body parts of teleosts. Thus
326 inferences of the prey of *O. woodwardi* should be based on the contents of the stomachs rather
327 than the intestines.

328

329 3.6. Dietary composition of stomachs in different seasons and length classes

330 When the dietary data for just the stomachs of *O. woodwardi*, derived from the dietary data for
331 the stomach contents of each length class of fish in each season, were subjected to two-way
332 PERMANOVA, a significant Length Class \times Season interaction was detected ($P = 0.6\%$,
333 Table 2b). On the corresponding nMDS ordination plot, all but one of the dietary samples for
334 spring lie in the left-hand upper part of the plot to the right of all but one of those for summer,
335 with those for autumn occupying an intermediate position (Fig. 5). The atypical location of one
336 summer sample and one spring sample both represented the length class of smallest fish in

337 those respective seasons, which, together with the widely dispersed sample of smallest fish for
338 autumn, help account for the Length Class \times Season interaction.

339 RELATE showed that, in spring, the dietary composition of *O. woodwardi* changed
340 progressively as the length of this predator increased ($\rho = 0.697$ and $P = 0.8\%$), reflecting the
341 trend for the volumetric contributions of sponges to increase and for those of teleosts to
342 decrease, as shown in the shade plot (Fig. 6). Dietary compositions did not undergo significant
343 changes with body size of predator in other seasons ($P = 22.4$ to 43.6%). The shade plot
344 emphasises that sponges were typically ingested by all length classes of *O. woodwardi*
345 throughout the year and that the same was largely true for teleosts and, to a lesser extent, for
346 decapods (Fig. 6). The other dietary categories were infrequently ingested.

347

348 **4. Discussion**

349 This study has demonstrated that *Opleognathus woodwardi* consumes a very substantial
350 volume of sponges. This was facilitated by its possession of a highly specialised beak-like
351 mouth formed by fused teeth and strong plate-like jaws, which enable this predator to extract
352 food material from its poriferan prey that potentially possesses formidable physical and
353 chemical defence mechanisms. The feeding mechanisms also facilitate the ingestion and
354 mastication of other prey with hard-bodied parts such as decapod crabs, echinoderms and
355 molluscs. The following sections discuss the characteristics of sponges that make poriferans
356 such an important contributor to the diets of *O. woodwardi*, focussing, in particular, on the
357 characteristics of the sponge species that are ingested by this predator and of those of its other
358 prey.

359

360 *4.1. Sponges as a food source*

361 Sponges are abundant and ecologically dominant members of many benthic marine
362 communities in a range of water depths (Diaz and Rützler, 2001; McClintock et al., 2005;
363 Heyward et al., 2010; Berman and Bell, 2016; Garcia-Hernández et al., 2018). Indeed, during
364 a first assessment of poriferans on Australia's south-western margin of the continental shelf
365 (100 - 1100 m depth), this taxon was found to overwhelmingly dominate (86%) the biomass of

366 the benthic invertebrate epifauna in these temperate waters and in which the Knifejaw
367 *Oplegnathus woodwardi* lives (McEnnulty et al., 2011; Fromont et al., 2012). The large
368 abundance of sponges in those hard-bottom mesophotic waters are targeted by *O. woodwardi*
369 and thus account for the Porifera being the most frequently ingested dietary category of that
370 predator in those waters (44%) and to making the greatest volumetric contribution to the food
371 consumed by the wide size range of its individuals examined (38%).

372 Despite their possession of a formidable range of potential defence mechanisms, certain
373 species of Porifera sometimes make particularly large contributions to the diets of the few
374 predators that are well adapted for spongivory. Sponges comprise for example, as much as 95%
375 of the dry mass of the diets of the hawksbill turtle *Eretmochelys imbricata* in tropical
376 environments (Meylan, 1988). Although invertebrates have been regarded as the main
377 predators of sponges in temperate waters (Wulff, 2006), sponges did contribute 74% to the
378 dietary mass of the horseshoe leatherjacket *Meuschenia hippocrepis* over rocky reefs in
379 temperate southern Australia (Rodgers et al., 2013). Furthermore, a few abundant fish species
380 feed so extensively on sponges that they exert a top-down control on the benthic communities
381 in their environment (Pawlik et al., 2018).

382 As sponges are relatively long-lived (McMurray et al., 2008), sessile and abundant
383 (Diaz and Rützler, 2001, Fromont et al., 2012), they are consistently available for predation.
384 They also heal readily from injuries, such as those caused by the bites of predators (Wulff,
385 2006; 2016), and thereby persist as potential prey following attack. Despite their potentially
386 beneficial characteristics as a food source, sponges only form a major component of the diet of
387 a small number of predators, which includes a few highly-evolved teleost species (Randall and
388 Hartman, 1968), such as now shown to include *O. woodwardi*. This has generally been
389 attributed to their possession of chemical and physical defence mechanisms and to the low
390 digestibility of their skeletal materials (Barthel, 1995; Burns and Ilan, 2003; Burns et al., 2003;
391 Rohde and Schupp, 2018).

392

393 4.2. Feeding mechanisms and characteristics of sponge prey

394 The parrot-like beak and strong jaws of *O. woodwardi* are ideally adapted for removing
395 substantially large pieces of sponge, with the movement of the upper jaw over the lower jaw
396 creating a shearing action. The sponges and other prey are then crushed through the combined
397 action of the powerful jaws and strong molariform dentition (Nelson, 2006). The type of teeth
398 and jaw arrangement, along with the well-developed musculature of *O. woodwardi* produces a
399 particularly strong bite force, similar to that of species of the Scaridae, which eat hard-
400 structured corals (Marcus et al., 2017). These morphological and functional features, which are
401 characteristic of the Oplegnathidae, also account for the ability of the congeneric *Oplegnathus*
402 *conwayi* to consume large volumes of sponges in coastal waters of southern Africa (Chater
403 et al., 1995). A similar parrot-like beak and strong jaws facilitates a comparable function in
404 extensive spongivory by *E. imbricata* and *M. hippocrepis* (Meylan, 1988; Rodgers et al., 2013).

405 Although the spicules of Red Sea sponges with lengths exceeding ~ 250 µm acted as a
406 deterrent to predation by the wrasse *Thalassoma klunzingeri* (Burns and Ilan, 2003), those of
407 the tetractinellid *Geodia neptuni* with lengths longer than 500 µm did not deter predation by
408 another labrid, i.e. *Thalassoma bifasciatum* (Chanas and Pawlik, 1995). It is thus relevant that
409 the sponge component of the diet of *O. woodwardi* consisted almost entirely of species
410 belonging to the Order Tetractinellida, i.e. *Ecionemia*, *Stelletta* and *Rhabdastrella* spp, and that
411 the length of their spicules ranged upward to as high as 2000 µm. Tetractinellids also constitute
412 a substantial component of the diet of the hawksbill turtle (Meylan, 1988; León and Bjorndal,
413 2002) and dorid nudibranchs (Chu and Leys, 2012). Thus, as with some other species, the long
414 spicules of the Tetractinellida do not deter ingestion of large volumes of this sponge species by
415 *O. woodwardi*. Although the orders Haplosclerida and Dictyoceratida were the most speciose
416 in the mesophotic waters of south-western Australian waters (McEnnulty et al., 2011; Fromont
417 et al., 2012), they were not found in the gut contents of *O. woodwardi*. The species in these
418 orders therefore presumably possess deterrent mechanisms and/or did not occupy precisely the
419 same habitat.

420 The overwhelming dietary contribution made by species of Tetractinellida to the diet
421 of *O. woodwardi*, together with the substantial abundances of species from other orders in the

422 same environment as *O. woodwardi*, means that this fish predator targets certain species in that
423 taxonomic order, rather than ingesting a range of the potentially available sponge species. Such
424 targeting is consistent with the conclusion of Randall and Hartman (1968) that this is a
425 characteristic of spongivores that also ingest substantial volumes of prey other than sponges.
426 In contrast, fishes that feed very extensively on sponges use a smorgasbord approach by
427 ingesting a greater diversity of poriferan species (sensu Randall and Hartmann, 1968; Wulff,
428 2016).

429

430 4.3. Other prey of *Oplegnathus woodwardi*

431 Although the Porifera was the most frequently ingested of the major prey taxa and made the
432 greatest volumetric contribution to the stomach contents, teleosts dominated the remaining
433 component of the diet, being ingested by 37% of fish and comprising 30% of the volume. While
434 most of the teleosts could not be identified, the fact that the Clupeidae was by far the most
435 frequently identified of the five teleost families recorded in the stomach contents suggests that
436 it might well have been the main family in the unidentified material as well. Although clupeids
437 are typically pelagic (Nelson, 2006), some clupeids feed in the benthic environment under
438 certain circumstances (Domermuth and Reed, 1980; Hourston et al., 2004). The Scorpaenidae,
439 which was the next most important of the teleost families, contains relatively sedentary species
440 of “ambush” predators that ingest some of the same (non-sponge) prey as *O. woodwardi* in
441 waters slightly to the north on the lower west coast (Platell and Potter, 1998).

442 The possession by *O. woodwardi* of a beak-like mouth and plate-like jaws, which are
443 ideally adapted for crushing hard-bodied prey, enables this species to process the major
444 invertebrate prey of this predator other than sponges. These prey include appreciable volumes
445 of crustaceans (mainly decapod crabs), echinoderms and molluscs (particularly bivalves and
446 sepiolid cephalopods with their beak and internal shell), all of which have been recorded as
447 part of the endofauna of poriferan species (e.g. Wulff, 2006; Abdo, 2007). Furthermore, the
448 largest contributor to the diet of the congeneric *O. conwayi*, other than sponges (which
449 volumetrically constituted nearly two thirds of the diet) was the Holothuroidea (Chater et al.,

450 1995), a taxon whose leathery body wall contains numerous calcareous ossicles and spicules
451 (Edgar, 1997; Brusca and Brusca, 2003).

452 The food ingested by *Oplegnathus robinsoni* contains only a very small volume of
453 sponges and thus differs markedly from that of *O. conwayi* at a higher latitude in South Africa
454 (Chater et al., 1995) and of *O. woodwardi* in south-western Australia. *Oplegnathus conwayi*
455 does likewise consume, however, mainly tough-bodied prey, and particularly cirripedes,
456 holothuroids, bivalves and ophiuroids, which can be obtained and processed using the
457 specialised feeding mechanism of the Oplegnathidae, as described in the current paper. They
458 also represent taxa that are likely to be found in close association, including as part of the
459 endofauna, with sponges (e.g. Wulff, 2006; Abdo, 2007).

460

461 4.4. Relationship between diet with body size and season

462 On the basis of univariate analyses, using pooled data for season, the volumetric contributions
463 of sponges to the diet of *O. woodwardi* increased significantly with body size. At a finer scale
464 and employing multivariate analyses, the dietary composition only changed significantly with
465 body size in spring, reflecting the trend for the volumetric contributions of sponges in the
466 stomach contents in that season to increase with body size and for those of teleosts to decrease.
467 As sponges are sessile and long-lived, these inverse trends suggest that the availability of
468 teleost prey for larger fish in this season declined. The size-related seasonal decline in the
469 teleost dietary component may reflect the larger individuals of more pelagic species, such as
470 clupeids, becoming concentrated in the water column in spring for spawning and/or capitalising
471 on their zooplankton prey when they would be likely to be most abundant. Consequently, these
472 teleosts may become beyond the reach of the larger individuals of the demersal *O. woodwardi*.
473 Many studies have demonstrated a link between clupeid predators and their zooplankton prey,
474 including two species of clupeid in the Baltic Sea, which fed increasingly on copepods during
475 the boreal spring (e.g. Möllmann and Köster, 2002).

476 Although the dietary composition of *O. woodwardi* did not change over a wide range
477 in body sizes in three of the four seasons, that range did not include the smallest individuals of
478 this species. As these individuals would have been unable to handle or ingest the prey of the

479 larger individuals and/ or occupied a different habitat, they were presumably feeding on a
480 different suite of prey. Small individuals (< 100 mm TL) of two other oplegnathids, i.e. the
481 Barred Knifejaw *Oplegnathus fasciatus* and the Spotted Knifejaw *Oplegnathus punctatus*,
482 occupied surface drifting algae and fed on planktonic prey (e.g. Yamasaki et al., 2014;
483 Hasegawa et al., 2016). As with *O. woodwardi*, the adults of these other knifejaws possess
484 fused beaklike teeth and jaws that are adapted for crushing hard-bodied prey which in these
485 species are molluscs (National Oceanic and Atmospheric Administration – National Ocean
486 Service, 2019).

487

488 *4.5. Implications of spongivory for Oplegnathus woodwardi*

489 The large volumes of sponges by ingested by *O. woodwardi*, which is well adapted for
490 spongivory, is facilitated by the dominance and abundance of sponges in the benthic
491 environment of this Knifejaw species (Gomon et al., 2008; Fromont et al., 2012). In other
492 words, it would be beneficial for this species to feed extensively on this very abundant and
493 sessile prey as large amounts could be ingested without incurring the heavy energy cost of
494 either searching for or chasing that prey. This would be consistent with optimal foraging theory
495 (Hughes, 1980). It would also be beneficial, however, for the diet to be relatively diverse as
496 this would provide a wider and better-balanced range of dietary components. Such diversity is
497 achieved by ingesting substantial volumes of a range of benthic invertebrate and teleost species,
498 which would incur some metabolic cost in foraging, and moderate volumes of sessile molluscs,
499 crustaceans and echinoderms. Thus, as with the small number of other spongivorous fish
500 species, *O. woodwardi* is essentially an opportunist feeder that belongs to a highly specialised
501 family, suggesting that spongivory has evolved relatively recently (Randall and Hartman,
502 1968).

503

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514

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711 western Japan. *Estuar. Coast Shelf Sci.* 147, 32-41.

Tables

Table 1. Frequency of occurrence (%*F*) and volumetric contributions (%*V*) and \pm SE of major taxa (boldface), dietary categories (*) and dietary items in the stomachs and intestines of *Oplegnathus woodwardi* in mesophotic waters off the southern coast of Western Australia.

Major taxa, dietary categories & dietary items	Stomachs		Intestines	
	% <i>F</i>	% <i>V</i>	% <i>F</i>	% <i>V</i>
Bryozoa*	1.3	< 0.1 (0.0)	2.2	0.8 (0.9)
Cnidaria*	0.7	0.7 (0.7)	0.7	0.7 (0.9)
Porifera*	43.6	37.9 (3.7)	65.7	58.0 (4.3)
<i>Ecionemia</i> sp.	28.2	23.6 (3.3)	50.4	43.3 (4.1)
<i>Ecionemia</i> sp. 1	1.3	0.9 (0.7)	0.7	0.2 (0.0)
cf <i>Ecionemia</i> sp. 1	4.7	3.7 (1.5)	9.5	7.6 (2.3)
<i>Ecionemia</i> sp. 2	14.8	12.1 (2.5)	23.4	18.8 (3.4)
cf <i>Ecionemia</i> sp. 2	8.1	6.9 (2.0)	20.4	16.7 (3.2)
<i>Monanchora</i> sp.	-	-	0.7	< 0.1 (0.0)
<i>Rhabdastrella</i> sp.	3.4	2.8 (1.3)	3.6	2.6 (1.6)
<i>Stelletta</i> sp.	11.4	10.4 (2.4)	11.7	10.7 (2.9)
Unidentifiable poriferans	1.3	1.1 (0.8)	1.5	1.5 (1.2)
Polychaeta*	3.4	1.1 (0.7)	0.7	< 0.1 (0.0)
Mollusca	12.1	6.3 (1.8)	8.8	2.9 (1.5)
Gastropoda*	1.3	< 0.1 (0.0)	0.7	0.7 (0.9)
Bivalvia*	4.7	1.1 (0.7)	7.3	1.5 (0.9)
Cardiidae	-	-	2.2	0.2 (0.2)
Limidae	-	-	1.5	0.1 (0.1)
Mactridae	0.7	0.7 (0.7)	0.7	< 0.1 (0.0)
Pectinidae	2.0	0.4 (0.3)	2.2	0.2 (0.2)
Veneridae	1.3	< 0.1 (0.0)	-	-
Unidentifiable bivalves	0.7	< 0.1 (0.0)	1.5	0.8 (0.9)
Cephalopoda*	6.7	5.1 (1.7)	0.7	0.7 (0.9)
Sepiolida	2.0	1.7 (1.0)	0.7	0.7 (0.9)
Unidentifiable cephalopods	4.7	3.4 (1.4)	-	-
Crustacea	24.2	16.2 (2.8)	33.6	21.6 (3.5)
Cirripedia*	-	-	1.5	0.1 (0.1)
Isopoda*	5.4	1.8 (1.0)	6.6	3.1 (1.5)
Decapoda (crabs)*	20.8	14.4 (2.7)	27.7	18.4 (3.3)
Echinodermata	12.8	8.2 (2.1)	8.8	5.9 (2.0)
Asteroidea*	4.7	4.1 (1.6)	4.4	3.0 (1.3)
Ophiuroidea*	2.7	1.1 (0.7)	-	-
Echinoidea*	5.4	3 (1.2)	4.4	2.9 (1.5)
Chordata	36.9	29.6 (3.5)	11.7	10.0 (2.7)
Ascidiacea*	2.7	1.8 (0.9)	4.4	3.8 (1.9)
Teleostei*	34.9	27.8 (3.4)	7.3	6.2 (2.0)
Arripidae	0.7	0.5 (0.5)	-	-
Aulopodidae	0.7	0.7 (0.7)	-	-
Clupeidae	6.0	4.8 (1.7)	-	-
Scorpaenidae	2.7	2.7 (1.3)	-	-
Triglidae	0.7	0.6 (0.6)	0.7	0.7 (0.0)
Unidentifiable teleosts	24.2	18.6 (3.0)	6.6	5.5 (2.0)
Algae*	0.7	< 0.1 (0.0)	0.7	< 0.1 (0.1)
Number with food		149		139
Mean (SE) fullness		5.8 (0.2)		5.5 (0.2)

Table 2. Results of PERMANOVA tests, employing the Bray-Curtis similarity matrix derived from the mean percentage volumetric contributions of the dietary categories for the contents of (a) both the stomachs and intestines (3-way) and (b) stomachs only (2-way), of *Oplegnathus woodwardi* in mesophotic waters off the southern coast of Western Australia. df, degrees of freedom; MS, mean squares; %MS, percentage mean squares, pseudo-*F* ratios; *P* (%) significance level. *P* (%) showing significant results (< 5 %) are displayed in bold

(a) Stomach and intestinal contents	df	MS	%MS	Pseudo-<i>F</i>	<i>P</i> (%)
Main effects					
Gut region	1	30,651	66.13	14.86	0.1
Length class	5	1,565	3.37	0.76	71
Season	3	3,297	7.11	1.59	12.1
Interaction					
Gut region × Length class	13	1,259	2.72	0.61	85.1
Gut region × Season	3	3,373	7.28	1.63	9.4
Length class × Season	13	3,222	6.95	1.56	2.4
Gut region × Length class × Season	13	1,630	3.52	0.79	79.4
Residual	18	1,351	2.92		
(b) Stomach contents	df	MS	%MS	Pseudo-<i>F</i>	<i>P</i> (%)
Main effects					
Length class	5	1,405	16.33	1.04	44.1
Season	3	3,042	35.36	2.25	26.0
Interaction					
Length class × Season	13	2,806	32.61	2.07	0.6
Residual	18	1,351	15.7		

712 **Figure legends**

713

714

715 **Fig. 1.** Photograph of the mesophotic benthic environment at a depth of ~ 200 m at 35°S off the
716 temperate southern coast of Western Australia, over which *Oplegnathus woodwardi* lives, highlighting
717 the overwhelming presence of sponges in the epifauna. Photograph supplied by CSIRO.

718

719

720 **Fig. 2.** Head and jaws of *Oplegnathus woodwardi*. (a) Lateral view of intact head showing fused teeth
721 and the large eye. (b) Lateral view and (c) frontal view of upper jaw passing downwards and outside
722 (over-biting) that of lower jaw. (d) View of the rear-sides of the upper (above) and lower (below) jaws.
723 (a) Photo supplied by Mark McGrouther/Australian Museum (License: CC by Attribution-
724 NonCommercial-ShareAlikeIn), (b-d), flesh has been removed. Scale bars = 10 mm.

725

726 **Fig. 3.** Stacked bar graphs showing the mean percentage volumetric contributions of the predominant
727 prey groups in (a) stomach and (b) intestinal contents of sequential length classes of *Oplegnathus*
728 *woodwardi*. Numbers above bars represents the number of guts for each length class.
729 **NEEDS COLOUR**

730

731 **Fig. 4.** Multidimensional scaling ordination plots, derived from the Bray-Curtis matrix of the mean
732 volumetric ‘replicate’ data for the various dietary categories in the stomach and intestinal contents of
733 each length class of *Oplegnathus woodwardi* in each season, and coded for each gut region, with (a) a
734 non-metric (nMDS) plot displaying those ‘replicates’ and (b) the metric (mMDS) plot, constructed from
735 bootstrap averages for each gut region, i.e. ‘sample’. Group averages (larger circles) and approximate
736 95% region estimates fitted to the bootstrap averages (shaded region) are provided.

737

738 **Fig. 5.** Non-metric multidimensional scaling (nMDS) ordination plot, derived from the Bray-Curtis
739 matrix of the mean volumetric data for the various dietary categories in the stomach contents of each
740 length class of *Oplegnathus woodwardi* in each season, coded for length class and season.

741

742 **Fig. 6.** Shade plot, showing the square-root transformed volumetric contributions of each dietary
743 category in the stomach contents of each sequential length class of *Oplegnathus woodwardi* in each
744 calendar season of the year. Above the cells, in order, are the length class and season (as shown in
745 Fig. 5) and the number of stomachs for that length class in that season.

746

747 **Fig. 7.** Images of sponge dietary items of *Oplegnathus woodwardi*. (a) Fragments of *Ecionemia* sp. 2.
748 (b) Sponge skeleton showing dense spicule palisade typical of the sponge surface (*Ecionemia* sp. 2).
749 (c) Anatriaene spicule from *Ecionemia* sp. 2. (d) Fragments of *Stelletta* sp. showing dense spicule
750 clusters internally. (e) Plagiotriaene spicule and (f) strongylaster microscleres, each from *Stelletta* sp.

751



752

753 Figure 1

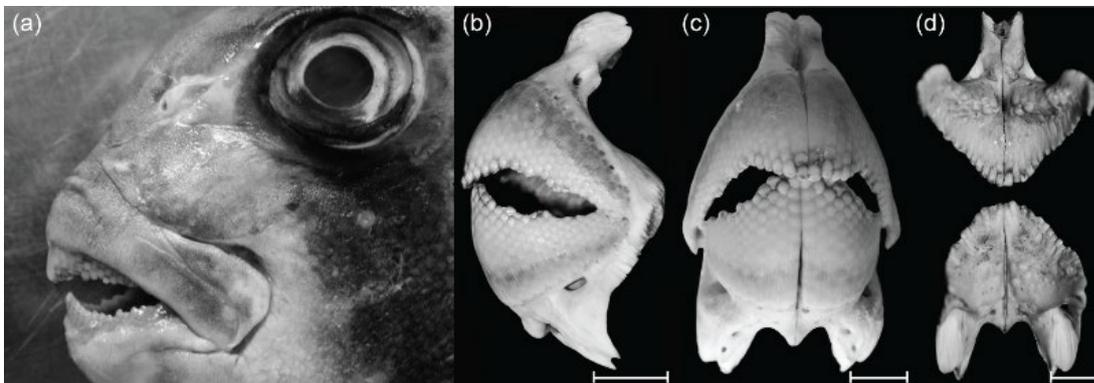
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760 Figure 2

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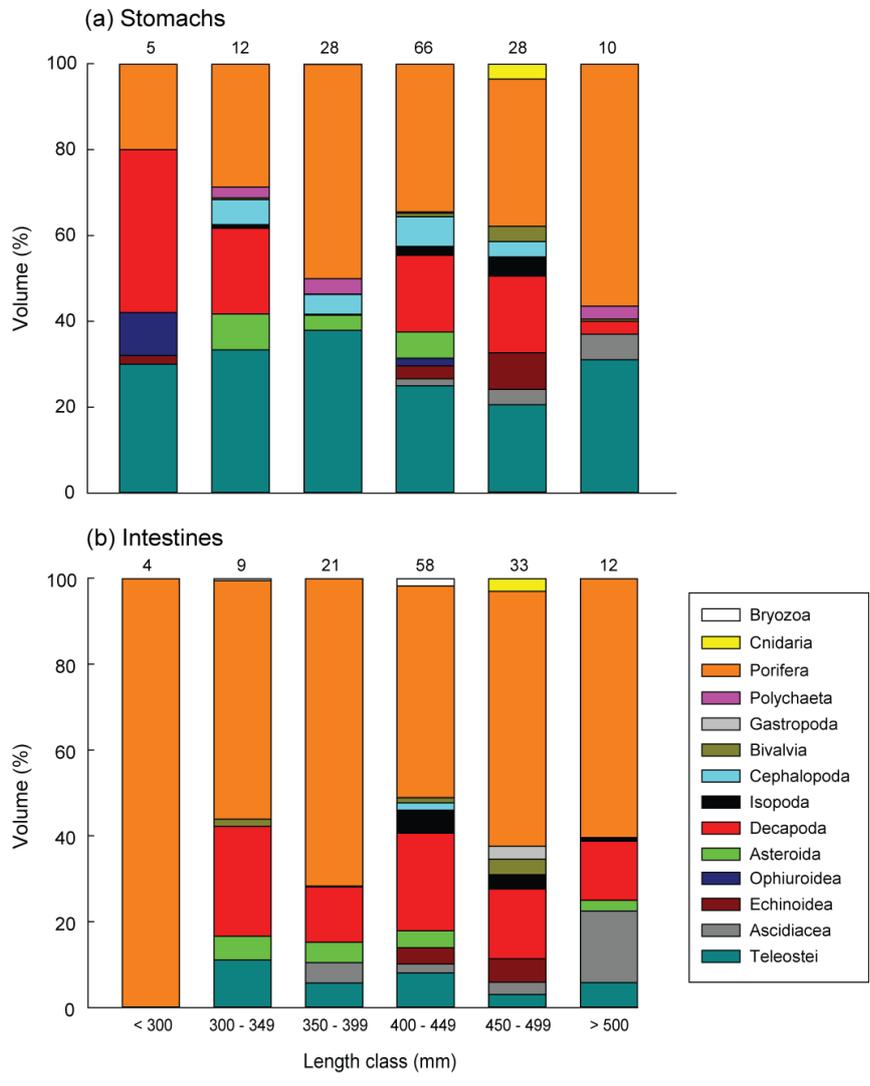
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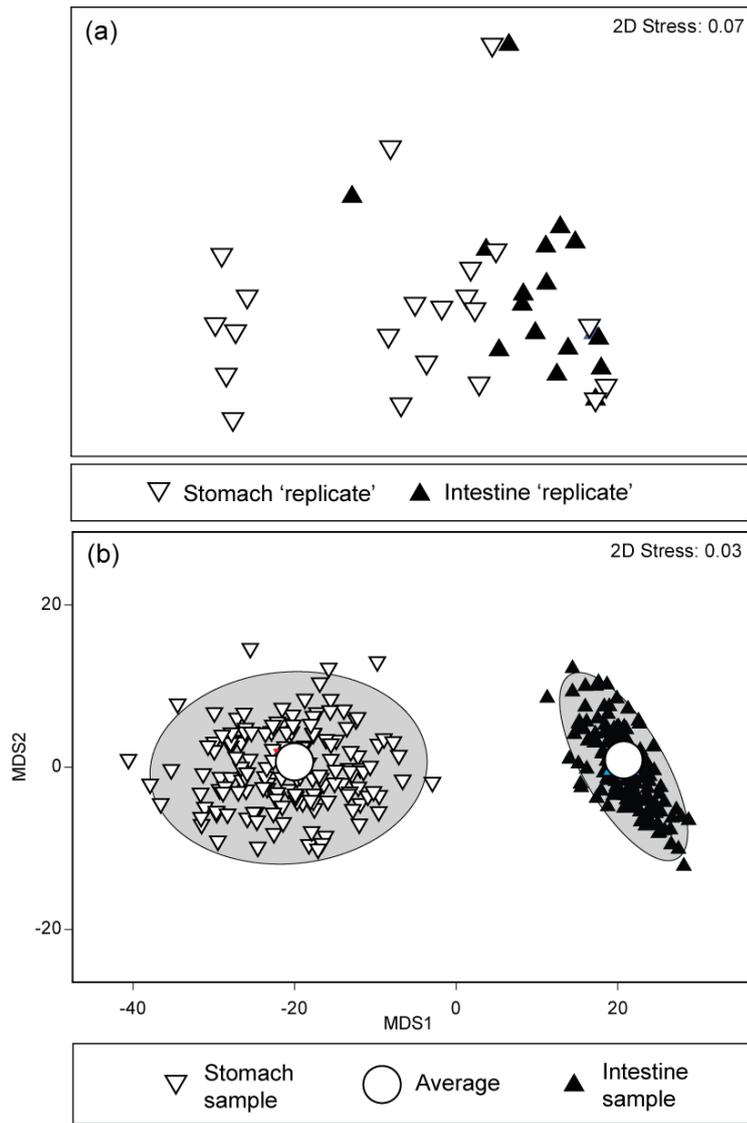
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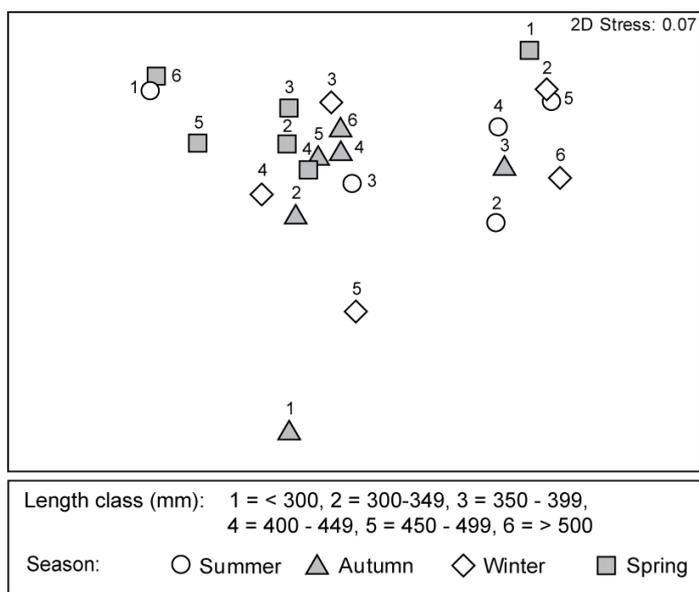


772
 773 **Figure 3**



774

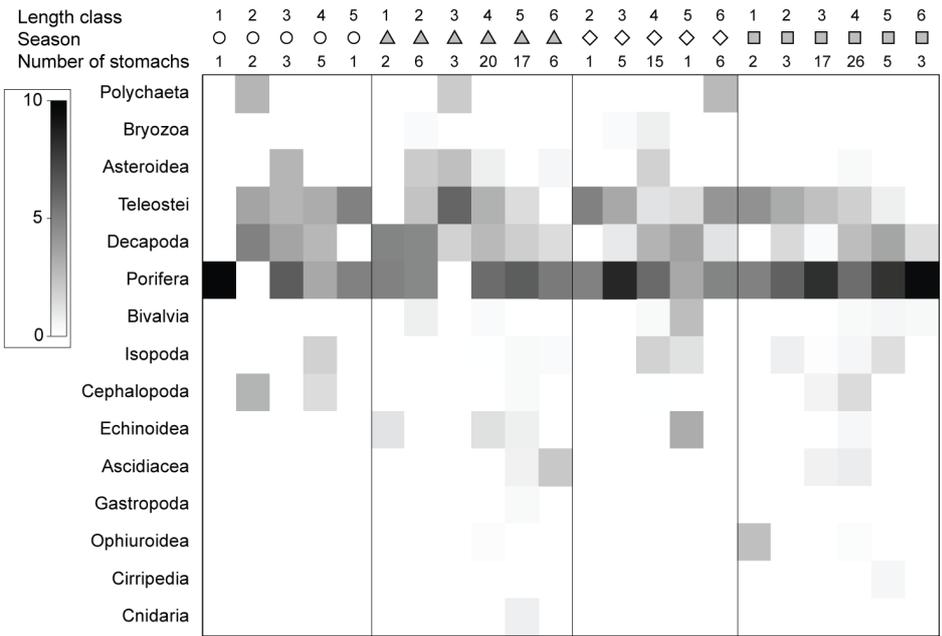
775 Figure 4



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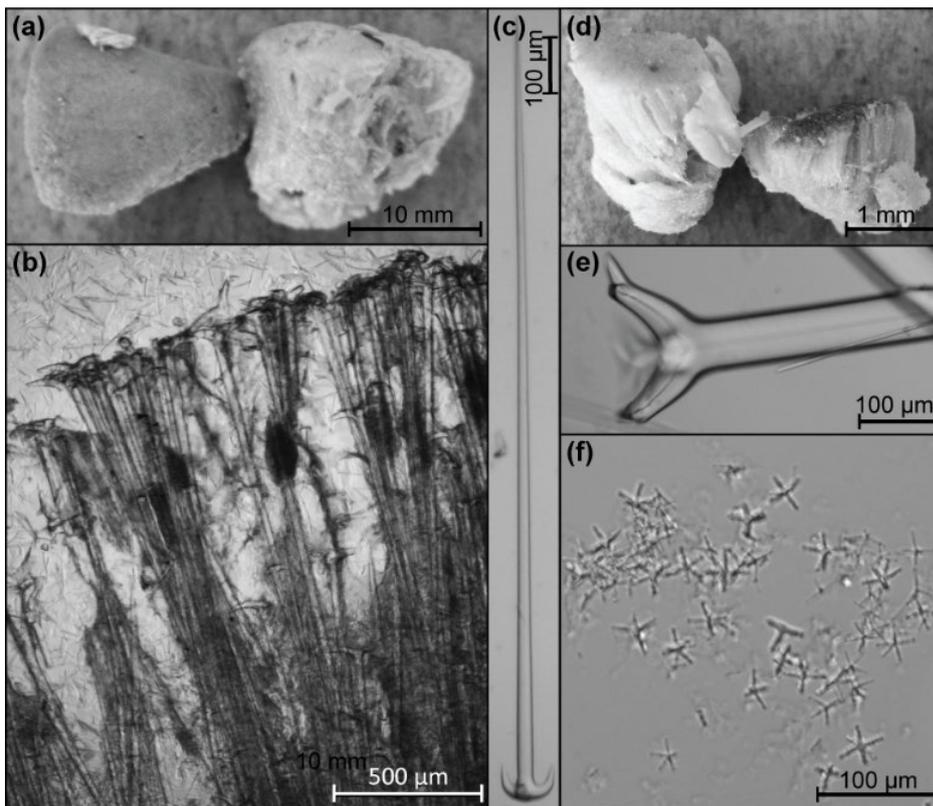
777 Figure 5

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780 Figure 6



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782 Figure 7

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785 **Supplementary Material**

786 *Ecionemia* sp. 1. The voucher specimen WAM Z65354 is a small fragment with a
787 macroscopically hispid surface, firm and incompressible texture that is spikey from spicules
788 extending beyond the surface, and light brown in colour when preserved. No oscules are
789 apparent and there is no distinct superficial cortex. The choanosomal skeleton is dense and
790 compact. Principal megascleres, mean and (SE), are triaenes with reduced rhabds $1127 (\pm 79) \times$
791 $27 (\pm 3) \mu\text{m}$, orthotriaenes/ plagiortriaenes $1619 (\pm 89) \times 45 (\pm 4) \mu\text{m}$ and oxeas with stepped
792 ends $2213 (\pm 83) \times 46 (\pm 3) \mu\text{m}$. Microscleres are microrhabds with small microspines $9 (\pm 0.3)$
793 μm long and tylasters $16 (\pm 1) \mu\text{m}$ wide. Two additional specimens are identified as *Ecionemia*
794 cf. sp. 1, WAM Z65363 has no visible microscleres and WAM Z65364 has rare microscleres
795 and some sand in the ectosome, although both specimens have the large stepped oxeas found
796 in the species.

797 *Ecionemia* sp. 2. The specimens are small fragments with smooth but microscopically
798 hispid surfaces (Fig. 7a). The sponges are firm and incompressible and light brown in colour
799 when preserved. No oscules are apparent on the sponge surfaces. There is no distinct superficial
800 cortex, except for a narrow 1 mm thick compact porous region, otherwise the ectosomal
801 skeleton intergrades into the choanosomal skeleton (Fig. 7b). The choanosomal skeleton is
802 dense, radial and compact except where there are canals. It is very spicule dominated. Principal
803 megascleres, mean and (SE), are orthotriaenes $1758 (\pm 217) \times 27 (\pm 2) \mu\text{m}$, anatriaenes 1517
804 $(\pm 64) \times 24 (\pm 1) \mu\text{m}$ (Fig. 1c), and oxeas $1664 (\pm 112) \times 28 (\pm 2) \mu\text{m}$, and microscleres are
805 microspined microrhabds $40 (\pm 2) \mu\text{m}$ long and slender tylasters of $16 (\pm 0.5) \mu\text{m}$. Voucher
806 specimens in the collections of the Western Australian Museum, Perth, Australia are WAM
807 Z65353, WAM Z65358, WAM Z65359, WAM Z65360. Two specimens are cf. to this species
808 because they have rare microrhabds 15 - 20 μm long, their voucher specimens are WAM
809 Z65361 and WAM Z65362 and are in the collections of the Western Australian Museum.

810 *Stelletta* sp. The specimens are small fragments with a macroscopically smooth surface
811 that microscopically is hispid and uneven (Fig. 7d). The sponges are firm and slightly
812 compressible and are prickly to the touch from spicules extending beyond the surface. The

813 sponges are fawn in colour when preserved. No oscules are apparent. The ectosomal skeleton
814 has slightly different colouration and texture to the choanosomal skeleton. The choanosomal
815 skeleton is dense (Fig. 7d), compact and radial with an abundance of megascleres. Principal
816 megascleres are dichotriaenes and plagiotriaenes $2293 (\pm 229) \times 39 (\pm 5) \mu\text{m}$ (Fig. 7e), slender
817 anatriaenes $2302 (\pm 112) \times 17 (\pm 1) \mu\text{m}$, and oxeas with occasional stylote modifications 2509
818 $(\pm 134) \times 49 (\pm 5) \mu\text{m}$. Microscleres are microspined strongylasters $20 \mu\text{m} (\pm 1)$ wide (Fig. 7f),
819 and less common tylasters $17 (\pm 0.8) \mu\text{m}$ wide. Specimen numbers are WAM Z65365, WAM
820 Z65355, WAM Z65366, WAM Z65367 and WAM Z65368.

821 *Rhabdastrella* sp. One specimen is a small fragment (WAM Z65356) and the other has
822 only the surface crust remaining (WAM Z65369). The specimens have a sand crust and
823 collagenous interior and are medium to dark brown after preservation. The texture is firm and
824 incompressible and no oscules are apparent. Principal megascleres are occasional, rare triaenes
825 with reduced rhabds $867 (\pm 11) \times 11 (\pm 0.4) \mu\text{m}$ and strongyloxeas $869 (\pm 26) \times 14 (\pm 1) \mu\text{m}$.
826 Microscleres are two sizes of oxyasters, the large forms are $30 \mu\text{m}$ wide, and the small ones
827 have very fine rays and are $15 - 20 \mu\text{m}$ wide, and oxysphaerasters that are $21 (\pm 2) \mu\text{m}$ wide.

828 *Monanchora* sp. The specimen is a very degraded fragment (WAM Z65370) that is
829 light brown when preserved. The choanosomal skeleton is plumoreticulate with fibres cored
830 by very fine, smooth styles with some strongylote modifications and echinated by irregularly
831 spined acanthoxeas. The styles are $166 (\pm 5) \times 3 (\pm 0.2) \mu\text{m}$ and the acanthoxeas $84 (\pm 4) \times 8$
832 $(\pm 0.4) \mu\text{m}$. There are no microscleres.

833

834