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► **To cite this version:**

Nicolas Djeghri, Philippe Pondaven, Herwig Stibor, Michael N. Dawson. Review of the diversity, traits, and ecology of zooxanthellate jellyfishes. *Marine Biology*, 2019, 166 (11), pp.147. 10.1007/s00227-019-3581-6 . hal-02868573

HAL Id: hal-02868573

<https://hal.science/hal-02868573>

Submitted on 5 Jul 2023

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Review of the diversity, traits, and ecology of zooxanthellate jellyfishes

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Abstract :

Many marine organisms form photosymbioses with zooxanthellae, but some, such as the medusozoans, are less well known. Here, we summarize the current knowledge on the diversity of zooxanthellate jellyfishes, to identify key traits of the holobionts, and to examine the impact of these traits on their ecology. Photosymbiosis with zooxanthellae originated at least seven times independently in Medusozoa; of these, five involve taxa with medusae. While most zooxanthellate jellyfishes are found in clades containing mainly non-zooxanthellate members, the sub-order Kolpophorae (Scyphozoa: Rhizostomeae) is comprised-bar a few intriguing exceptions-of only zooxanthellate jellyfishes. We estimate that 20-25% of Scyphozoa species are zooxanthellate (facultative symbiotic species included). Zooxanthellae play a key role in scyphozoan life-cycle and nutrition although substantial variation is observed during ontogeny, or at the intra- and inter-specific levels. Nonetheless, three key traits of zooxanthellate jellyfishes can be identified: (1) zooxanthellate medusae, as holobionts, are generally mixotrophic, deriving their nutrition both from predation and photosynthesis; (2) zooxanthellate polyps, although capable of hosting zooxanthellae rarely depend on them; and (3) zooxanthellae play a key role in the life-cycle of the jellyfish by allowing or facilitating strobilation. We discuss how these traits might help to explain some aspects of the ecology of zooxanthellate jellyfishes-notably their generally low ability to outbreak, and their reaction to temperature stress or to eutrophication-and how they could in turn impact marine ecosystem functioning.

35 **Acknowledgements** First we would like to thank Patricia Kremer and Alan Verde who
36 provided some unpublished data on *Linuche unguiculata* and *Cassiopea xamachana*
37 respectively. We would also like to thank Ferdinando Boero and André Cararra Morandini for
38 pointing us to some hard to find literature. Finally, we thank Bella Galil, Ilka Straehler-Pohl
39 and Sho Toshino for details about some of their work.

40 We also thank two anonymous reviewers for their valuable comments and suggestions.

41 Finally, we thank Natalia Llopis Monferrer for the artwork in Fig. 3.

42

43 **Funding** This work is part of the Ph.D. project of Nicolas Djeghri, funded by the University of
44 Western Brittany (UBO).

45 **1. Introduction**

46 Many organisms, from corals and giant clams to protists, form photosymbioses with
47 endosymbiotic, autotrophic dinoflagellates or “zooxanthellae” (Venn et al. 2008; Stoecker et
48 al. 2009). Most of our knowledge on this kind of relationships comes from the study of
49 photosymbiotic scleractinian corals, but other cnidarians also form photosymbioses
50 including jellyfishes (e.g. Arai 1997). Zooxanthellate jellyfishes are historically linked to the
51 study of cnidarian-zooxanthellae symbiosis as the zooxanthellae first described as
52 *Symbiodinium* was obtained from the upside-down jellyfish *Cassiopea* (Freudenthal 1962).
53 This jellyfish genus *Cassiopea* is still relevant today as a model organism (Ohdera et al. 2018)
54 while other symbiotic scyphozoan species have potential to illuminate pelagic symbioses (e.
55 g. Muscatine et al. 1986). Moreover, their relevance is increasing as zooxanthellate
56 jellyfishes’ populations have also increased in some environments (Arai 2001; Pérez-Ruzafa
57 et al. 2002) raising the question of their roles in ecosystem functioning (see e.g. Pitt et al.
58 2009).

59 However, despite increasing interest, zooxanthellate jellyfish remain little studied relative to
60 other, non-zooxanthellate, jellyfishes or to scleractinian corals. Zooxanthellate jellyfishes are
61 of particular interest for two, often distinct, communities of scientists: the first, focused on
62 jellyfishes, the second focused on photosymbiosis. This has led to a somewhat scattered
63 literature with few works bridging the gap. Our goal with this review is to establish a more
64 integrative, synthetic, foundation for future studies focusing on the diversity and on the
65 ecology of zooxanthellate jellyfishes.

66 All zooxanthellate jellyfishes share two key characteristics. First a metagenetic life-cycle, as
67 many other, non-zooxanthellate, jellyfishes, with two distinct body-plans and ecologies: the
68 polyp and the medusa (Box 1). Second a photosymbiotic relationship with zooxanthellae, as
69 in scleractinian corals (Box 2). The combination of these two characteristics and their
70 interplay is likely to give zooxanthellate jellyfishes a unique set of ecological traits. Indeed,
71 zooxanthellate jellyfishes have a variety of unique morphologies and behaviors (Arai 1997), a
72 narrower latitudinal distribution (e.g. Holland et al. 2004; Swift et al. 2016), a propensity to
73 not bloom (Dawson and Hamner 2009), and a different nutrition (e.g. Verde and McCloskey
74 1998; Kremer 2005) from their non-zooxanthellate counterparts. However, these jellyfishes
75 also occupy multiple branches of the cnidarian tree of life. This raises the question of

76 whether these characteristics are attributable to the symbiosis itself or to other lineage-
77 specific evolutionary history.

78 To better understand these characteristics of zooxanthellate jellyfishes, we divide our review
79 into three parts. First, we review the phylogenetic distribution of zooxanthellate jellyfishes.
80 Second, we review the roles of zooxanthellae in zooxanthellate jellyfishes, primarily with
81 respect to their complex life-cycle and in their nutrition. Finally, once the key traits have
82 been characterized, we review how these traits could impact the ecology of zooxanthellate
83 jellyfishes and their influence on marine communities and ecosystem functions.

Box 1: Jellyfishes and their Metagenetic Life-Cycle

Jellyfish may be seen as an ambiguous word. Here, we refer to jellyfish as pelagic cnidarians (Lucas and Dawson 2014). Many of these organisms display a complex life-cycle with an alternation of a benthic, asexually reproducing, polyp phase and a pelagic, sexually reproducing, medusa phase. Differences in the details of the life-cycle exist between groups. For instance, the transition between the polyp and the medusa phase is generally done by lateral budding in Hydrozoa, by metamorphosis in Cubozoa, and by strobilation in Scyphozoa (see e.g. Boero et al. 2016). Many variations from this general depiction of life-cycles exist; for instance, reduction or loss of one of the phases (very common in Hydrozoa, Bouillon et al. 2006).

The alternation of polyp and medusae phases has important repercussions for the ecology of these organisms. Generally, populations of asexually reproducing polyps are perennial, and represent the source of the pelagic medusae populations. Then, pelagic medusae, may bloom, aggregate, or swarm (see e.g. Lucas and Dawson 2014), with potential for ecological and human consequences.

84

Box 2: Cnidarian-Zooxanthellae Photosymbiosis

Photosymbiosis can be defined predominantly as a mutualistic nutritional association. In the case of the cnidarian-zooxanthellae photosymbiosis the symbionts are found within host cells (endosymbionts). This involves complex processes of symbiont recognition, acquisition and regulation (see Davy et al. 2012). The main advantage of this kind of symbiosis is nutritional. Zooxanthellae photosynthesize and share some of the photosynthates with their host. These photosynthates include diverse molecules such as carbohydrates, lipids and amino-acids that can be metabolized by the host (Davy et al. 2012). The symbionts can then use the host excretion and respiration products (CO₂, dissolved inorganic nitrogen) for their autotrophic metabolism (Yellowlees et al. 2008, Davy et al. 2012). Consequently, these associations allow a recycling of nutrients within the holobiont (symbionts + host). They are thus considered particularly advantageous in nutrient poor environments (Yellowlees et al. 2008).

Box 3: Glossary

We give here some of the technical terms used in this review. For more information on jellyfish anatomy, development and taxonomy, see Arai 1997 and Bouillon et al. 2006.

Ecology:

Bloom: A true, natural, jellyfish bloom is defined as an increase in jellyfish biomass linked to phenology (see Lucas and Dawson 2014).

Development:

Planula: The larval stage of cnidarians. Generally pyriform, ciliated, and motile.

Planuloid budding: A mode of asexual reproduction in scyphozoan polyps. A planuloid bud is formed by a polyp, detaches and swims to finally reattach to the substrate and form a new polyp. This is the dominant mode of polyp formation in Kolpophorae, a group of monodisk strobilating, often photosymbiotic, jellyfishes.

Ephyra: Young medusa-like stage in Scyphozoa.

Strobilation: A mode of asexual reproduction whereby a scyphozoan polyp forms ephyrae through transverse fission (see Helm 2018). Strobilation can be monodisc, when one ephyra is formed at a time or polydisc, when multiple ephyrae are formed at the same time.

Anatomy:

Mesoglea: An extracellular matrix, primarily composed of collagen, located between the endoderm and ectoderm in cnidarian. In medusae, the mesoglea can be thick and generally provides most of the volume of the animal.

Oral arms: In medusae, expansions of the mouth involved in prey capture and, at times, digestion. Not to be confounded with tentacles.

Exumbrella: In medusae, the superior (aboral) part of the umbrella.

Subumbrella: In medusae, the inferior (oral) part of the umbrella.

Coronal muscle: A circular muscle that ensures umbrella contractions.

87 2. Diversity of Zooxanthellate Jellyfishes

88

89 2.1. Diversity of Hosts

90 Jellyfish (i.e. pelagic cnidarians, Lucas and Dawson 2014) belong to the taxon Medusozoa.
91 Albeit the aim of this review is to focus on zooxanthellate jellyfishes, their evolutionary
92 history cannot be separated from either: (1) other medusozoans that lack zooxanthellae and,
93 (2) other medusozoans that lack a pelagic phase. Thus, all groups of medusozoans are taken
94 in account, at this first stage, to discuss phylogenetic patterns of zooxanthellate
95 medusozoans (Table 1, Fig. 1).

96 Considering only confirmed reports of zooxanthellate presence (Table 1), we estimate that
97 symbiosis between medusozoans and zooxanthellae originated independently at least seven
98 times (Fig. 1). Of these seven originations, five involved groups containing pelagic taxa (i.e.
99 jellyfishes) (Fig. 1): one in Cubozoa (two species of Carybdeid jellyfish), two in Hydrozoa (in
100 Capitata with the family Porpitidae and in Loadiceida with the genus *Wuvula*) and two in
101 Scyphozoa (in Coronatae with the Linuchidae plus some *Nausithoe* and in Kolpophorae). The
102 two other originations are from hydrozoan groups lacking a medusae phase (see Bouillon et
103 al. 2006): in Filifera I (family Eudendriidae) and in Macrocolonia (e.g. *Aglaophenia*, *Halecium*,
104 *Pseudoplumaria*). No zooxanthellate staurozoans have been found.

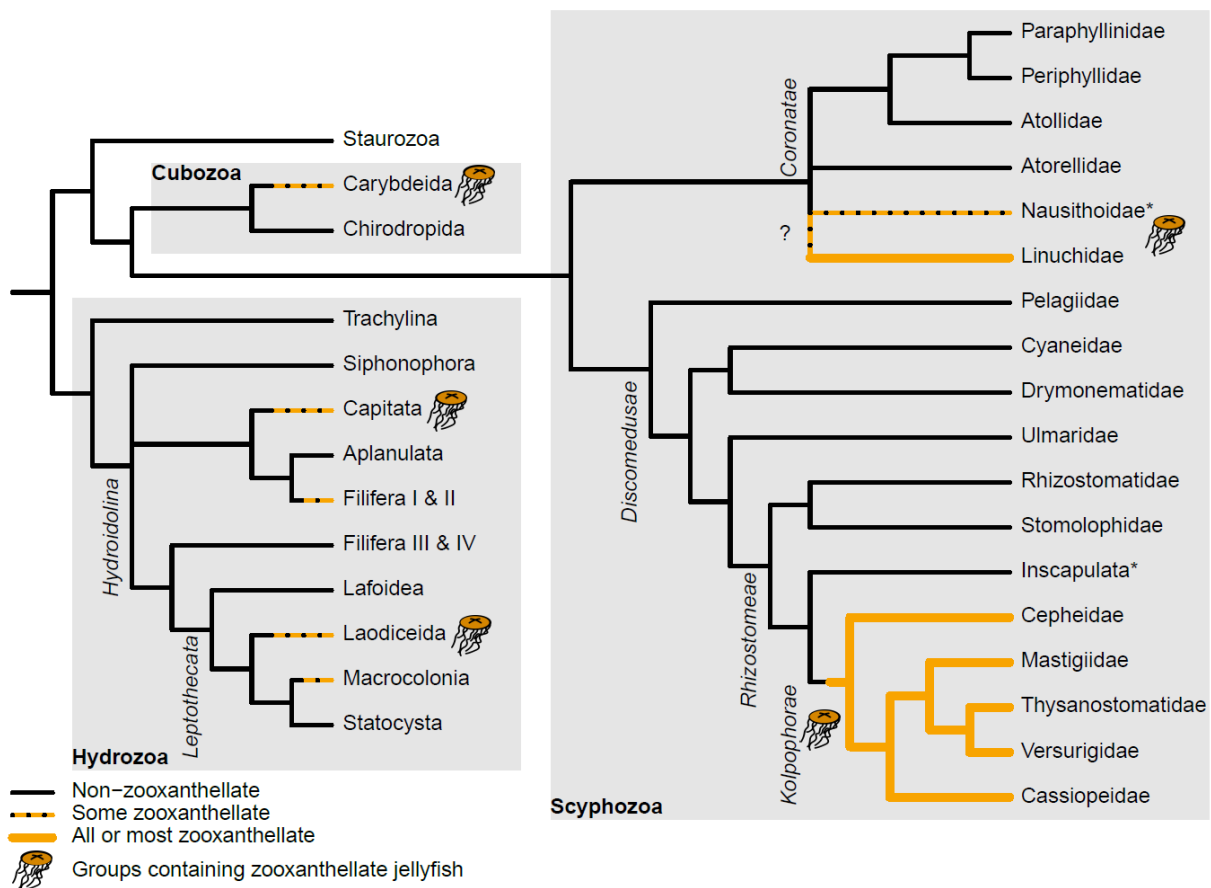
105 It is important to emphasize that seven originations of symbiosis with zooxanthellae in
106 Medusozoa is a minimum. Firstly, symbioses between zooxanthellae and medusozoans are
107 often little documented in the literature. It is thus likely that we have underestimated the
108 number of zooxanthellate species. Secondly, the phylogeny of hydrozoans in particular is
109 more complex than presented here. Thus, some zooxanthellate groups may be subdivided
110 more finely phylogenetically as more data are gathered. For instance, Macrocolonia is a very
111 diversified group (Maronna et al. 2016) and it is likely that the macrocolonian genera
112 reported to be zooxanthellate are not closely related (see Maronna et al. 2016; Moura et al.
113 2018). Similarly, the Porpitidae family and the genus *Millepora* (fire corals) both belong to
114 Capitata and host zooxanthellae but might not be closely related (Nawrocki et al. 2010). This
115 remark is also valid for zooxanthellate Coronatae until phylogenetic relationships are better
116 resolved (Fig. 1). Finally, *Dichotomia cannoides* (Hydrozoa, Leptothecata, Dipleurosomatidae)

117 may represent another origination of the medusozoan-zooxanthellae symbiosis. However,
118 until its phylogeny is better resolved (Maronna et al. 2016), it cannot be confirmed.

119 Despite multiple originations, only a minority of medusozoans are found in symbiosis with
120 zooxanthellae. Often, photosymbiotic species are clustered in mostly non-zooxanthellate
121 clades. Even in close relatives (within a family or a genus) it is common that some species are
122 zooxanthellate while most others are not (see e.g. *Aglaophenia* - Svoboda and Cornelius
123 1991, *Alatina* - Carrette et al. 2014, *Eudendrium* - Marques et al. 2000, Laodiceidae - Bouillon
124 et al. 2006, *Nausithoe* - Silveira and Morandini 1997). In these groups, symbiosis with
125 zooxanthellae does not appear to have favored adaptive radiation. In which context,
126 Kolpophorae appears as an exception: it is a diversified group with ca. 40–50 species in five
127 families (Daly et al. 2007) and likely many more yet to be described (Gómez Daglio and
128 Dawson 2017), that is predominantly, and possibly only, constituted of zooxanthellate
129 species. Six of the nine genera of Kolpophorae are reported to be zooxanthellate,
130 photographic evidence suggest that two other genera might have zooxanthellae (ESM 1). We
131 hence infer parsimoniously that all Kolpophorae might be zooxanthellate (facultative
132 included; Table 1).

133

134 Considering all Kolpophorae plus the zooxanthellate Coronatae we estimate that between
135 20 and 25% of scyphozoan species are zooxanthellate (including facultative symbionts,
136 species richness obtained from Daly et al. 2007). Such an estimate is hard to give at present
137 for hydrozoans and cubozoans as their zooxanthellate representatives are less documented.



138

139 **Fig. 1** Phylogenetic position of zooxanthellate medusozoans with emphasis on Scyphozoa.
 140 The topology used here is based on Kayal et al. (2018) for the relationships among major
 141 groups, Kayal et al. (2015) for Hydroidolina, Maronna et al. (2016) for Leptothecata, Bayha et
 142 al. (2010) for Coronatae and Gómez Daglio and Dawson (2017) for Discomedusae. ‘*’ = non-
 143 monophyletic group. ‘?’ = unclear origin of symbiosis with zooxanthellae in Coronatae. See
 144 Table 1 for the literature identifying zooxanthellae presence. Only confirmed reports are
 145 taken into account in this figure with the exception of Kolpophorae where we
 146 parsimoniously infer the presence of zooxanthellae in all or most species (possibly
 147 facultative, see ESM 1)

148

149 **2.2. Diversity of Symbionts**

150 Zooxanthellae associated with jellyfish species belong mostly to the family Symbiodiniaceae
 151 (see the recent revision of the family, LaJeunesse et al. 2018). The most common symbionts
 152 found in zooxanthellate scyphozoan jellyfishes in the field appear to belong to the genera
 153 *Symbiodinium* (previously *Symbiodinium* clade A) and *Cladocopium* (previously

154 *Symbiodinium* clade C) although other Symbiodiniaceae can be found (LaJeunesse et al.
155 2001; Santos et al. 2003; Thornhill et al. 2006; Mellas et al. 2014). Furthermore, laboratory
156 experiments have demonstrated that the associations between the jellyfish *Cassiopea* spp.
157 and Symbiodiniaceae genera are not specific. Indeed, *Cassiopea* spp. polyps have been
158 successfully infected with a variety of isolated and mixed Symbiodiniaceae genera including
159 *Symbiodinium*, *Cladocopium*, *Breviolum* (previously *Symbiodinium* clade B) and *Durusdinium*
160 (previously *Symbiodinium* clade D) (Thornhill et al. 2006; Mellas et al. 2014; Lampert 2016).
161 However, adult medusae tend to harbour only one phylotype of symbiont suggesting that a
162 mechanism such as competitive exclusion occurs within the host (Thornhill et al. 2006). Thus
163 some flexibility appears to exist in the zooxanthellae-jellyfish association. This is further
164 illustrated by the symbionts found in the hydrozoan *Velella velella*. Zooxanthellae from
165 *Velella velella* can indeed belong to Symbiodiniaceae (LaJeunesse et al. 2001) but they can
166 also belong to the genera *Brandtodinium* and *Scrippsiella* (or *Ensiculifera*) from the family
167 Thoracosphaeraceae (Banaszak et al. 1993; Probert et al. 2014).

168

169 **2.3. Biogeography and Habitat**

170 Generally, zooxanthellate jellyfishes are found in tropical and sub-tropical waters between
171 40° N and 40° S (see e.g. Bieri 1977; Bouillon et al. 1988; Bolton and Graham 2004; Holland
172 et al. 2004; Bayha and Graham 2014; Heins et al. 2015; Straehler-Pohl and Toshino 2015;
173 Boero et al. 2016; Swift et al. 2016). The zooxanthellate coronates and kolpophoran
174 rhizostomes in particular are tropical clades (Dawson and Hamner 2009). However,
175 exceptions can exist as some zooxanthellate jellyfishes may be found in temperate waters
176 either occasionally (e.g. Purcell et al. 2012a) or possibly as resident species (see Brinckmann-
177 Voss and Arai 1998).

178 At finer geographic scales, zooxanthellate jellyfishes are typically shallow-water species
179 (Dawson and Hamner 2009). They have been reported in a number of coastal habitats
180 including lagoons, estuaries, coral reefs, mangroves or marine lakes (see e.g. García 1990;
181 Kikinger 1992; Fleck and Fitt 1999; Pitt et al. 2004; Swift et al. 2016; Morandini et al. 2017).
182 Such coastal habitats are most likely linked to the fact that most zooxanthellate jellyfishes
183 have a benthic polyp phase, which limits their extension toward the open ocean. However,

184 the medusa phase in some instances has been reported in the open sea (e.g. in Cepheidae –
185 Tokioka et al. 1964; Boero et al. 2016, in *Linuche* – Larson 1992). Furthermore, hydrozoans of
186 the family Porpitidae realize their whole life-cycle in the open ocean (Bieri 1977),
187 exemplifying that the presence of benthic polyps in the life-cycle, rather than symbiosis with
188 zooxanthellae, more likely restricts jellyfishes to coastal waters.

189

190 **3. Roles of the Zooxanthellae in Jellyfish Symbioses**

191

192 ***3.1. Acquisition, Location, Transmission and Abundance of Zooxanthellae along the*** 193 ***Jellyfish Life-Cycle***

194 *3.1.1. Acquisition of the zooxanthellae*

195 The acquisition of zooxanthellae is the first step of the symbiosis. A host may acquire
196 zooxanthellae by two means: (1) vertical transmission, where the symbiont is directly
197 transferred from the parents to the offspring (usually from the mother to the egg), or (2)
198 horizontal transmission, where the symbiont is taken from the environment. While vertical
199 transmission may occur in zooxanthellate hydrozoans (see e.g. Mangan 1909; Bouillon 1984;
200 Lewis 1991), it is likely that most other zooxanthellate jellyfishes acquire their symbionts via
201 horizontal transmission. In Kolpophorae, the symbiont is not provided by parents but
202 acquired from the environment at the polyp stage (e.g. Sugiura 1963; Ludwig 1969; Sugiura
203 1969; Fitt 1984; Colley and Trench 1985; Kikinger 1992; Astorga et al. 2012; Newkirk et al.
204 2018). The coronate *Linuche unguiculata* presents a somewhat intermediate mode of
205 acquisition of the symbiont since fertilized eggs are released in mucus strand replete with
206 maternal zooxanthellae that contaminate the larvae very early in development, generally
207 before the 128 cells stage (Montgomery and Kremer 1995).

208

209 *3.1.2. Location of zooxanthellae in jellyfishes*

210 In hydromedusae, zooxanthellae are found in endodermal cells (Bouillon et al. 1988;
211 Banaszak et al. 1993; see also Brooks 1903; Brinckman-Voss and Arai 1998, Fig. 2a). In

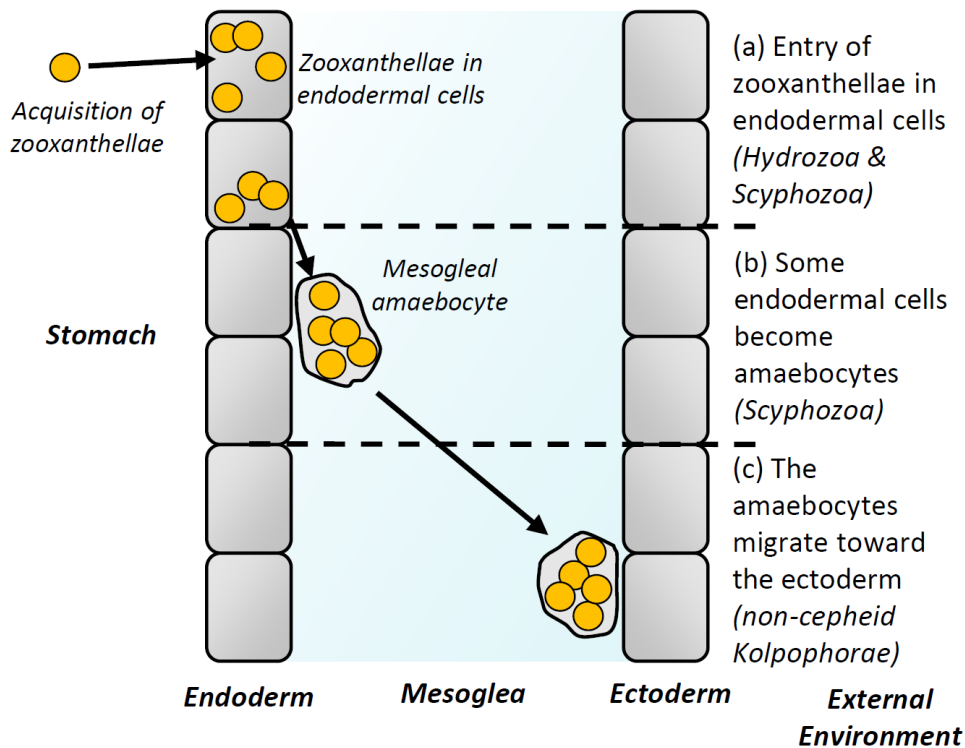
212 scyphozoans, zooxanthellae first enter polyps' endodermal cells, which then migrate and
213 become mesogleal amaebocytes (Colley and Trench 1985, Fig. 2a and b). In ephyrae, these
214 amaebocytes filled with zooxanthellae stay mostly closely associated with the endoderm
215 (see Kikinger 1992; Silveira and Morandini 1998; Straehler-Pohl and Jarms 2010). This
216 remains the case for later stage medusae in the Coronatae (*Linuche unguiculata*; Costello
217 and Kremer 1989), and in the Cepheidae (*Cotylorhiza tuberculata*; Kikinger 1992). In other,
218 non-cepheid, Kolpophorae, the zooxanthellae end up closely associated with the ectoderm
219 (e.g. coronal muscle, subumbrella, exumbrella, oral arms; Blanquet and Riordan 1981;
220 Muscatine et al. 1986; Blanquet and Phelan 1987; Estes et al. 2003; Souza et al. 2007; Fig.
221 2c). This suggests that the close association of zooxanthellae with the ectoderm could be a
222 synapomorphy of the clade of non-cepheid Kolpophorae. The reason for this evolution is
223 unclear, but perhaps could have adaptive value in allowing better exposure of zooxanthellae
224 to light or nutrients, or providing energy more directly to the host tissues that require it the
225 most.

226

227 *3.1.3. Abundance and transmission of the zooxanthellae during the jellyfish life-cycle*

228 Zooxanthellae abundance in their hosts is affected by the complex life-cycles of jellyfishes. In
229 the best studied zooxanthellate jellyfishes, the Kolpophorae, the symbionts are taken up at
230 the polyp stage. At this stage, the abundance of zooxanthellae can range from zero
231 (aposymbiotic polyp) to tens of thousands of zooxanthellae per polyp (Newkirk et al. 2018).
232 Polyps form other polyps asexually through a variety of processes (e.g. Schiariti et al. 2014)
233 and in Kolpophorae, the dominant process is by far the production of planuloid buds
234 (Schiariti et al. 2014; Heins et al. 2015). During this process, zooxanthellae are transferred
235 from the parent polyp to the forming bud. Thus polyps formed asexually by zooxanthellate
236 polyps are also zooxanthellate (e.g. Sugiura 1964; Ludwig 1969; Silveira and Morandini 1998;
237 Heins et al. 2015). Then, during strobilation, zooxanthellae multiply in the oral region of the
238 polyp where the ephyra is formed (Ludwig 1969). The ephyrae formed are thus also
239 zooxanthellate (e.g. Sugiura 1964; Ludwig 1969; Sugiura 1969; Kikinger 1992; Silveira and
240 Morandini 1997, 1998; Straehler-Pohl and Jarms 2010). Finally, during the growth of
241 medusae, zooxanthellae densities tend to stay constant or to decrease slightly in most
242 species (densities in the order of 10^7 cells.g⁻¹ wet mass, see Muscatine et al. 1986; Kremer et

243 al. 1990; Verde and McCloskey 1998). However, some species such as *Cephea cephea* may
 244 lose their zooxanthellae at the medusae stage (Sugiura 1969); this is likely the case of many
 245 other Cepheidae too (see ESM 1). The ontogenic loss of zooxanthellae suggests that the
 246 symbiosis might present trade-offs and might not always be advantageous (see e.g. Lesser et
 247 al. 2013). The presence or absence of zooxanthellae during the life-cycle of some
 248 zooxanthellate jellyfish have been compiled in Table 2.



249
 250 **Fig. 2** Positions of zooxanthellae in jellyfishes' tissues as a function of taxa and ontogeny. (a)
 251 Zooxanthellae enter in endodermal cells. (b) Some endodermal cells filled with
 252 zooxanthellae become mesogleal amaebocytes. (c) The mesogleal amaebocytes migrate
 253 toward the ectoderm at the medusae stage in non-cepheid Kolpophorae. In brackets are the
 254 taxa that perform a given step

255
 256 **3.2. Nutrition of Zooxanthellate Jellyfishes**

257 **3.2.1. Photosynthesis**

258 Zooxanthellate jellyfishes differ from non-zooxanthellate jellyfishes by the additional energy
 259 source they can access through the photosynthesis of their zooxanthellae (either through

260 exchange of metabolites but also through digestion of zooxanthellae, see Davy et al. 2012).
261 In polyps however, only a small part of photosynthates is directed to the host (Hofmann and
262 Kremer 1981). At the medusae stage, by contrast, photosynthesis can constitute an
263 important, if not the major part, of the nutrition of zooxanthellate medusae. Photosynthetic
264 rates are often equal or superior to respiration rates (Drew 1972; Cates 1975; Mergner and
265 Svoboda 1977; Kremer et al. 1990; Kikinger 1992; McCloskey et al. 1994; Verde and
266 McCloskey 1998; Welsh et al. 2009; Jantzen et al. 2010). This indicates that in most cases,
267 respiration requirements in carbon may be fulfilled, and even exceeded, by the
268 photosynthetic activity.

269 When the holobiont's photosynthesis rates exceed respiration rates, the host's metabolites
270 cannot fulfill the photosynthetic demand of zooxanthellae. Thus zooxanthellate jellyfishes
271 must take additional inorganic nutrients (inorganic carbon, nitrogen or phosphorus) from the
272 surrounding water (reviewed in Pitt et al. 2009; see Hofmann and Kremer 1981; Muscatine
273 and Marian 1982; Wilkerson and Kremer 1992; Pitt et al. 2005; Todd et al. 2006; Welsh et al.
274 2009; Jantzen et al. 2010; Freeman et al. 2016). Uptake rates of various nutrients can be
275 influenced by some environmental factors. For instance, darkness can induce net nitrogen
276 excretion (Cates and McLaughlin 1976; Pitt et al. 2005; Welsh et al. 2009 but see Muscatine
277 and Marian 1982; Wilkerson and Kremer 1992), while light has been found to increase
278 ammonium and inorganic carbon uptake (Jantzen et al. 2010; Freeman et al. 2016). All this
279 indicates that photosynthetically active zooxanthellae play an important role in inorganic
280 nutrient uptake.

281 Given the nutritional importance of the symbionts, it is not surprising that their hosts
282 present some behavioral and morphological characteristics that help their zooxanthellae
283 (see e.g. Furla et al. 2011 for scleractinian corals). Zooxanthellate jellyfishes, for instance,
284 tend to maximize their light exposure by swimming near the surface (e.g. Hamner et al.
285 1982; Larson 1992; Haddad and Nogueira Júnior 2006 but see Bieri 1977), but also by
286 performing more complex horizontal and vertical daily migrations (Hamner and Hauri 1981;
287 Hamner et al. 1982; Dawson and Hamner 2003). Similarly, zooxanthellae patches found in
288 *Linuche unguiculata* tissue contract with a daily rhythm (Costello and Kremer 1989). One
289 consequence of these behaviors is high exposure to potentially damaging UV radiation. It has
290 thus been hypothesized that some zooxanthellate jellyfishes' pigments might have a

291 photoprotective role (Blanquet and Phelan 1987; Dawson 2005 but see Lampert et al. 2012)
292 as might small behavioral adjustments of depth (Dawson and Hamner 2003). Others
293 behavioral and morphological characteristics of zooxanthellate medusae have been
294 suggested to help their zooxanthellae to access inorganic nutrients. For instance,
295 zooxanthellae within their hosts are found in high concentration near the coronal muscle,
296 which is an important source of excretion products (Blanquet and Riordan 1981; Muscatine
297 et al. 1986; Blanquet and Phelan 1987). The zooxanthellate jellyfish *Mastigias papua*
298 performs reverse diel vertical migrations which help it to access deep nutrients at night
299 (Hamner et al. 1982; Muscatine and Marian 1982), possibly imprinting a daily rhythm in the
300 cell division of its symbionts (Wilkerson et al. 1983). And finally, the pumping action of
301 *Cassiopea* facilitates its access to nutrient-rich pore water (Jantzen et al. 2010). Additional
302 access to nitrogen might also be provided by symbiotic nitrogen fixing bacteria (Freeman et
303 al. 2017).

304

305 3.2.2. Predation

306 Zooxanthellate jellyfishes are predators that can eat a variety of prey. Both the polyp and
307 the medusae stages do feed on zooplankton. Information on the polyp diet in the field is
308 scarce, but they are routinely fed zooplankton such as *Artemia* sp. nauplii in the laboratory
309 (e.g. Schiariti et al. 2014). In zooxanthellate medusae, it has been suggested that some of the
310 characteristics that favor their autotrophy might be detrimental to their heterotrophy (Arai
311 1997). An extreme case might be the modified body shape of the benthic *Cassiopea* sp.,
312 which might reduce its contact efficiency with prey as compared to other rhizostomes (see
313 Bezio et al. 2018). For planktonic zooxanthellate jellyfishes, behaviors such as a reversed diel
314 vertical migration might induce spatial mismatch with zooplanktonic prey during the day
315 (Hamner et al. 1982). Zooxanthellate medusae might also have less stinging ability than non-
316 zooxanthellate medusae from other species (Peach and Pitt 2005), or even non-
317 zooxanthellate conspecifics (Bolton and Graham 2004), possibly affecting the amount of
318 captured prey. However, zooxanthellate medusae have been found to feed on a large variety
319 of prey from large diatoms to fish larvae (see e.g. Kikinger 1992; Larson 1997; Pérez-Ruzafa
320 et al. 2002; Graham et al. 2003; Kremer 2005; Peach and Pitt 2005; Purcell et al. 2012a;
321 Zeman et al. 2018). Moreover, the clearance rates of zooxanthellate jellyfishes are often

322 comparable to those of similarly sized non-zooxanthellate jellyfishes (García and Durbin
323 1993; Santhanakrishnan et al. 2012; Bezio et al. 2018). Finally, while several studies indicate
324 that photosynthesis can provide most if not all the carbon requirement, predation seems
325 necessary to meet nitrogen and phosphorus requirements (Kremer 2005; Welsh et al. 2009).

326

327 **3.3. Variability in the Roles of Zooxanthellae in Jellyfish Symbioses**

328 In previous sections we noted that the abundance and position of zooxanthellae can vary
329 during the jellyfish life-cycle or as a function of the jellyfish species (Table 2). In terms of
330 nutrition, zooxanthellate jellyfishes appear to be generally mixotrophic deriving their
331 nutrition from both photosynthesis and predation. However, variations of the relative
332 importance of autotrophy versus heterotrophy can be identified. This variability can be
333 detected along the ontogeny of jellyfishes but also at the intra- and inter-specific level,
334 particularly at the medusae stage.

335

336 *3.3.1. Reduced role of zooxanthellae at the polyp stage*

337 At the polyp stage, the zooxanthellae transmit only a small fraction of the photosynthates to
338 the host (Hofmann and Kremer 1981). Most studies also show that zooxanthellae presence
339 or activity have little impact on polyp's budding or survival (Sugiura 1963; Hofmann et al.
340 1978; Rahat and Adar 1980; Prieto et al. 2010; but see Mellas et al. 2014). Moreover, the
341 zooxanthellae *Durusdinium* (previously *Symbiodinium* clade D) can increase the mortality of
342 *Cassiopea* sp. polyps (Lampert 2016). All this suggests that, at the polyp stage, symbionts
343 and autotrophy are of little direct importance for most zooxanthellate jellyfishes. However,
344 zooxanthellae in polyps can still provide some benefits for the host such as resistance to
345 hypoxia or acidification (Klein et al. 2017). Such reduced importance of zooxanthellae has
346 also been reported for coral larvae, indicating that importance of the symbiosis can vary
347 through host life-cycle (Hartmann et al. 2019).

348 This limited importance of zooxanthellae for polyps is further confirmed by the ecology of
349 zooxanthellate jellyfish polyps in the field. Zooxanthellate jellyfish polyps tend to be found
350 more often on the undersides of surfaces (Kikinger 1992; Fleck and Fitt 1999; see also

351 Astorga et al. 2012) and the settlement of planulae appears favored in the dark (Duarte et al.
352 2012). These observations indicate that the polyps are generally poorly exposed to sunlight
353 in the field.

354

355 *3.3.2. Important, but still unclear, role of zooxanthellae during strobilation*

356 Several environmental cues control the strobilation in scyphozoans but one of the most
357 important is temperature (Lucas et al. 2012). This is also true of zooxanthellate scyphozoans
358 (Sugiura 1965; Sugiura 1969; Rahat and Adar 1980; Rippingale and Kelly 1995; Prieto et al.
359 2010; Purcell et al. 2012b). However, zooxanthellae appear also involved in the strobilation
360 process. Indeed, zooxanthellae tend to multiply and accumulate into the forming ephyra
361 during strobilation (Ludwig 1969). Several laboratory studies show that the presence of
362 zooxanthellae helps, and is even often indispensable, for the onset of strobilation (Sugiura
363 1964; Ludwig 1969; Sugiura 1969; Hofmann et al. 1978; Rahat and Adar 1980; Hofmann and
364 Kremer 1981, Fitt 1984; Colley and Trench 1985; Kikinger 1992; see also Hofmann et al. 1996
365 and Astorga et al. 2012) though exceptions apparently exist (e.g. Dawson et al. 2001).
366 Interestingly, zooxanthellae still favor strobilation when they are unable to photosynthesize
367 (Sugiura 1969; Hofmann and Kremer 1981; Hofmann et al. 1996) and time to strobilation is
368 independent of zooxanthellae density in *Cassiopea xamachana* (Newkirk et al. 2018). This
369 suggests that the role of zooxanthellae during strobilation is not only to provide
370 photosynthates (Hofmann et al. 1996). However, their exact role is still unclear and warrants
371 further research.

372

373 *3.3.3. Variable role of zooxanthellae during the medusa stage*

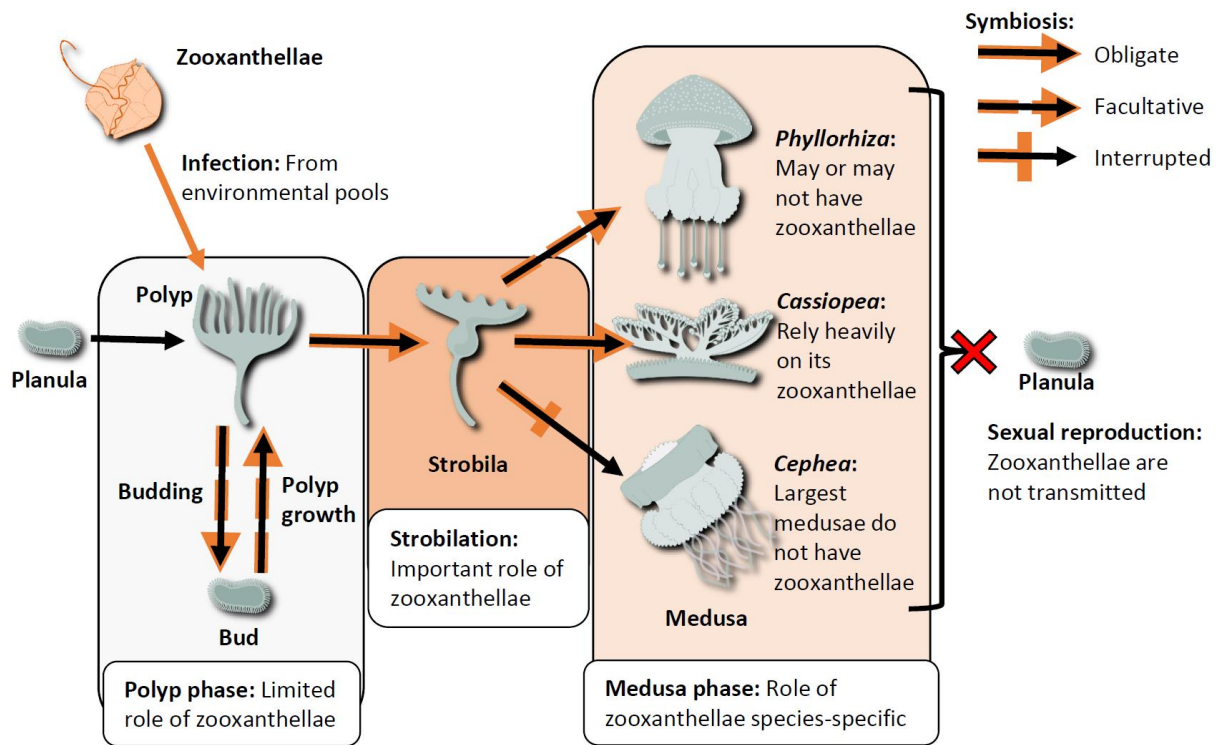
374 At the medusa stage there can be important variation in the relative importance of
375 autotrophy and heterotrophy among populations or individuals of the same species. The
376 most extreme case may be *Phyllorhiza punctata* where some populations have
377 zooxanthellae while others do not (Bolton and Graham 2004). Similarly, individuals or
378 populations of *Mastigias papua* can occasionally be non-zooxanthellate (Dawson et al.
379 2001). Beyond these extreme cases, it is expected that variations in the
380 autotrophy/heterotrophy balance can vary depending on physiologic (e.g. abundance of

381 zooxanthellae) or environmental (e.g. light exposure, availability of prey) conditions. For
382 instance, populations of *Mastigias papua* appear to differ in the proportion of their
383 energetic demand that can be met by their zooxanthellae (McCloskey et al. 1994). However,
384 few comparative data exist to confirm this point. Individual size can also impact the relative
385 importance of heterotrophy and autotrophy. In some species, the photosynthesis can
386 increase faster than the respiration with medusae size suggesting that larger individuals are
387 more autotrophic than small ones (McCloskey et al. 1994). On the other hand, some other
388 species such as *Cephea cephea* can lose their symbionts at some point in their development
389 (Sugiura 1969) suggesting that smaller individuals rely more on their zooxanthellae than
390 large ones.

391 Variation in reliance on zooxanthellae can also be seen inter-specifically. Some species
392 appear to be heavily dependent on their zooxanthellae such as *Cassiopea* spp. (e.g. low level
393 of light can induce shrinking; Mortillaro et al. 2009). At the other extreme, *Cephea cephea*
394 (and probably many Cepheidae, ESM 1) may lose its symbionts at the medusae stage
395 (Sugiura 1969) and becomes then strictly heterotrophic. The fact that both zooxanthellate
396 and non-zooxanthellate individuals and populations can be found in *Mastigias papua* and
397 *Phyllorhiza punctata* (Dawson et al. 2001; Bolton and Graham 2004) leads us to hypothesize
398 that Kolpophorae are generally ordered Cassiopeidae > Mastigiidae > Cepheidae from the
399 most to the least dependent on zooxanthellae. However, this hypothesized order stays
400 speculative as relevant information exists for only a limited number of species.

401

402 From the information compiled here, it is possible to summarize the life-cycle of
403 Kolpophorae, indicating the transmission, and variation of the role of zooxanthellae (Fig. 3).
404 Due to the little information available it is however impossible to propose such a synthetic
405 view for zooxanthellate cubozoans or hydrozoans.



406

407 **Fig. 3** Synthetic representation of zooxanthellate Kolpophorae (Scyphozoa: Rhizostomeae)
 408 life-cycle with presence and importance of zooxanthellae. Black arrows indicate jellyfish life-
 409 cycle while orange arrows indicate presence of the symbiont. The infection occurs at the
 410 polyp stage. The symbiont is transmitted during asexual reproduction (budding and
 411 strobilation) but not during sexual reproduction. Symbionts are generally important for
 412 strobilation but not for budding. During the medusae phase, the nutritional importance of
 413 the symbiont is species specific (three examples are given)

414

415 **3.4. Zooxanthellate Jellyfishes as a Unique Combination of Traits**

416 Although evolution is typically considered to proceed through the gradual acquisition of
 417 small modifications, the evolution of photosymbioses in the jellyfishes combined traits that
 418 previously were present only in very distinct lineages. The novel zooxanthellate jellyfishes
 419 thus can be compared and contrasted with other groups of cnidarians—non-zooxanthellate
 420 jellyfishes, and photosymbiotic scleractinian corals—with which they share newly assorted
 421 characteristics. The novel combination brought together (1) the complex life-cycle, the body-
 422 plan, and the mobility of the former with (2) the often oligotrophic, shallow-water,
 423 photosymbiosis of the latter. We believe that the integration, in zooxanthellate jellyfishes, of

424 these two characteristics became more than the sum of the parts: this unique combination
425 of complex traits originated three major novelties in the ecologies of zooxanthellate
426 jellyfishes.

427 *Large pelagic mixotrophs:* The combination of the medusa and photosymbiosis not
428 only conjoined a pelagic life-style with mixotrophy, but additionally did so in relatively large
429 and fast growing, annual, organisms. Other pelagic photosymbioses are found in protists
430 (Stoecker et al. 2009), but zooxanthellate jellyfishes are orders of magnitudes larger; corals
431 in contrast, are benthic, perennial and slow growing. In this regard, zooxanthellate jellyfishes
432 occupy a unique ecological niche, which, for some (especially Kolpophorae), may have
433 represented a new adaptive zone (sensu Simpson 1953).

434 *Heterotrophic benthic photosymbioses:* In spite of their ability to host zooxanthellae,
435 zooxanthellate jellyfish polyps generally do not rely much on them. They can thus be seen as
436 (mostly) heterotrophic benthic photosymbioses, in stark contrast to the mixotrophic benthic
437 corals. One can speculate on why it is the case. Scyphozoan polyps are generally found on
438 undersides of surfaces (e.g. Arai 1997) where they are not exposed to light and
439 zooxanthellate jellyfish polyps may simply have retained this trait from their non-
440 zooxanthellate ancestors. Irrespective of the reason, this implies that the polyp would most
441 likely behave more as a non-zooxanthellate jellyfish polyp than as a small scleractinian coral.

442 *A symbiont-dependent strobilation:* The strobilation process in zooxanthellate
443 jellyfishes is facilitated or permitted by the symbionts. The underpinning process is still
444 unknown but it is not only due to energetic requirements. This may be due to the fact that
445 the medusae needs the symbionts more than the polyp but cannot acquire them; that the
446 polyp is not competent to strobilate without zooxanthellae assures that the medusae would
447 have the symbionts. Irrespective of the mechanism, this implies that the transition from the
448 polyp to the medusa is under the control of a supplementary factor as compared with non-
449 zooxanthellate jellyfishes.

450 These three novel complex traits are likely shared to differing degrees by different
451 zooxanthellate jellyfishes. They are most characteristics of the large zooxanthellate
452 scyphozoans (e.g. *Cassiopea*, *Mastigias*) from which most of the data were gleaned.

453 Exploring the extent to which these conclusions can be applied to other, less studied,
454 zooxanthellate hydrozoan and cubozoan jellyfishes is a key research agenda.

455

456 **4. Ecology of Zooxanthellate Jellyfishes**

457 The unique combination of traits found in zooxanthellate jellyfishes is expected to shape
458 various aspects of their ecology. Notably, differences in strobilation, nutrition and
459 dependencies on environmental conditions might impact their population dynamics as
460 compared to non-zooxanthellate jellyfishes. Likewise, differences in life-cycle or nutrition
461 might impact the way zooxanthellate jellyfishes react to environmental perturbations as
462 compared with non-zooxanthellate jellyfishes or corals. Finally, their unique combination of
463 traits could lead to unique impacts on marine ecosystems and communities.

464

465 **4.1. Population Dynamics**

466 *4.1.1. Phenology*

467 Across their range of habitats, zooxanthellate jellyfishes can exhibit varied phenology. In
468 some cases, medusae are present year-round (Hamner and Hauri 1981; Hamner et al. 1982;
469 Fitt and Costley 1998) sometimes with mixed size-classes, suggesting long or continuous
470 recruitment periods. Contrastingly, in other environments, the medusae are present
471 seasonally (García 1990; Pérez-Ruzafa et al. 2002; Pitt et al. 2004; Purcell et al. 2012b) with
472 generally one cohort identifiable each year (e.g. Ruiz et al. 2012). On top of these intra-
473 annual population fluctuations, recruitment differences (Ruiz et al. 2012) or long term
474 environmental variations such as El Niño Southern Oscillation (Dawson et al. 2001; Martin et
475 al. 2006) can shape populations sizes over years or decades. Such phenology and population
476 fluctuations are also observed in non-zooxanthellate jellyfishes (e.g. Dawson and Martin
477 2001; Purcell et al. 2012b; Condon et al. 2013).

478

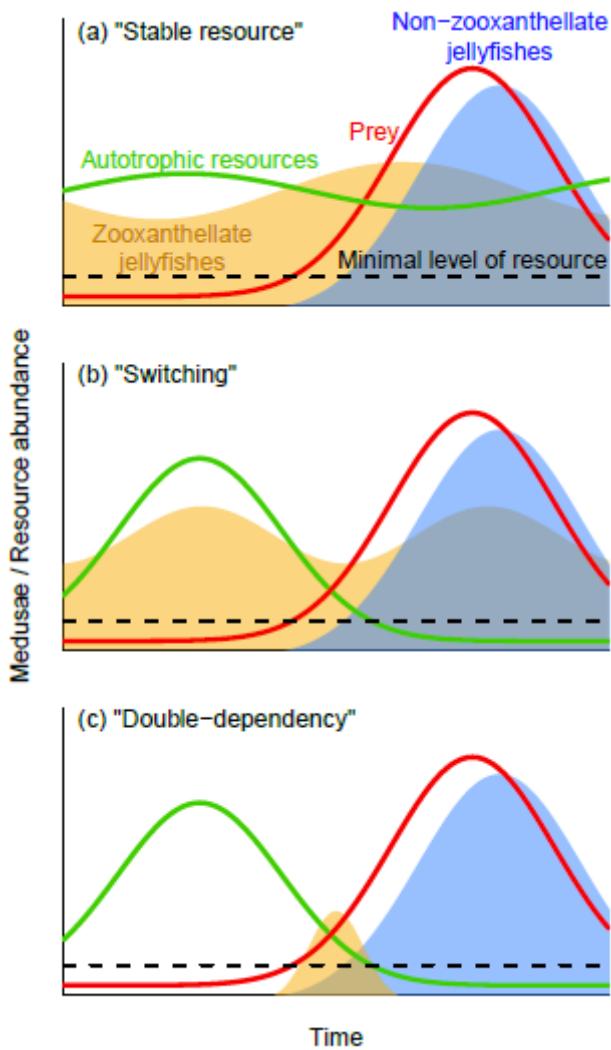
479 *4.1.2. Blooming ability*

480 An important aspect of many jellyfish species population dynamics is their tendency to
481 bloom (Dawson and Hamner 2009; Lucas and Dawson 2014). Blooms are defined as sudden
482 increases of medusa biomass linked with seasonal life-cycle (Lucas and Dawson 2014). These
483 “true blooms” are a consequence of the coincidence of favorable environmental conditions
484 (e.g. a pulse in prey abundance) with a jellyfish species whose traits enable it to take
485 advantage of the conditions (Dawson and Hamner 2009). Zooxanthellate jellyfishes,
486 however, are generally unlikely to bloom to the same degree as non-zooxanthellate
487 jellyfishes, suggesting that the photosymbiosis limits their ability to respond to, or benefit
488 from, pulses of prey (Dawson and Hamner 2009). Due to the correlated nature of character
489 complexes—e.g. zooxanthellate scyphozoans are also predominantly monodisc strobilators
490 whereas bloom forming, non-zooxanthellate scyphozoans are predominantly polydisc
491 strobilators—it is challenging to identify the cause of this low blooming ability. Nonetheless,
492 we believe that it would be valuable to formulate testable hypotheses to give a foundation
493 for future research. Dawson and Hamner (2009) hypothesized several possible causes for the
494 low blooming ability of zooxanthellate jellyfishes, as follows.

495 One hypothesis is that the mixotrophy of zooxanthellate jellyfishes implies trade-offs that
496 physiologically limit their ability to take advantage of pulses of prey. For instance, several
497 behavioral characteristics of zooxanthellate jellyfishes may limit their predation efficiency
498 (see section 2.2.2.). The strobilation of many zooxanthellate jellyfishes is regulated by
499 zooxanthellae (see section 2.3.2.) potentially decorrelating strobilation period from pulse of
500 prey. Moreover, evidence from zooxanthellae-coral symbioses suggests that zooxanthellae
501 can at times have negative effects on their hosts (Lesser et al. 2013, Hartmann et al. 2019).
502 The existence of such trade-offs might also explain why many Cepheidae apparently tend to
503 lose their symbionts at the medusa stage (Sugiura 1969, ESM 1). These trade-offs are,
504 however, little known in zooxanthellate jellyfishes and more studies are needed to
505 characterize them.

506 The other hypotheses relate to the ecological availability of resources and how
507 zooxanthellate jellyfishes can use them. Dawson and Hamner (2009) proposed two
508 mechanisms: (1) zooxanthellae may access a more stable resource stream as compared to
509 prey abundances (Fig. 4a); (2) zooxanthellate jellyfishes may be able to switch from one
510 resource to another (see section 2.3.3., Fig. 4b). In both cases, the generalism of

511 zooxanthellate jellyfishes allow them to achieve a temporally smoother energetic income (as
512 opposed to non-zooxanthellate jellyfishes which, in this context, may be seen as specialists).
513 This would in turn result in smoother population dynamics and thus less abrupt population
514 increase, i.e. no unusual blooms. Along with these two hypotheses from Dawson and
515 Hamner (2009) we propose a third one: that some zooxanthellate jellyfishes might need
516 both autotrophy and heterotrophy (e.g. Kremer 2005; Welsh et al. 2009). Thus to bloom,
517 zooxanthellate jellyfishes would need both resources concomitantly in abundance. In the
518 context of the match-mismatch hypothesis developed for fisheries (see e. g. Cushing 1990)
519 the success of a given cohort is function of the timing between the spawning and a peak in
520 available prey. This can be transposed directly to non-zooxanthellate jellyfishes (Dawson and
521 Hamner 2009) where the strobilation corresponds to the spawning event. Zooxanthellate
522 jellyfishes, however, under the hypothesis that they need both autotrophic and
523 heterotrophic resources to bloom, would be dependent on appropriate timing of not one,
524 but two matching peaks of resources. Thus, because they rely on more diverse resources,
525 zooxanthellate jellyfishes would be more likely to encounter a mismatch than non-
526 zooxanthellate jellyfishes (Fig. 4c). Elevated possibility of mismatch for zooxanthellate
527 jellyfishes might also arise as a consequence of the additional control of zooxanthellae on
528 strobilation as compared to non-zooxanthellate jellyfishes (e.g. temperature cue for
529 strobilation and zooxanthellae presence might not always match, see section 2.3.2.) or
530 changing seasonality and phenology in the oceans (e. g. Mackas et al. 2012). This higher
531 chance of getting a mismatch would reduce zooxanthellate jellyfishes' likeliness to bloom.



532

533 **Fig. 4** Three hypotheses on zoxxanthellate jellyfishes' blooming ability as compared to non-
 534 zoxxanthellate jellyfishes. Zoxxanthellate jellyfishes (orange) are able to exploit both
 535 autotrophic resources (light, dissolved inorganic nutrients; green) and prey (red) whereas
 536 non-zoxxanthellate jellyfishes (blue) can only exploit prey. Black dashed line indicates the
 537 minimum level of any resource to support a medusae population. (a) Hypothesis 1:
 538 Zoxxanthellae provide access to a more stable resource (the autotrophic resources),
 539 smoothing population dynamics. (b) Hypothesis 2: Zoxxanthellae allow a diversification of
 540 resources, when one is insufficient, the other might compensate; again smoothing
 541 population dynamics. (c) Hypothesis 3: Zoxxanthellate jellyfishes need both resource
 542 streams which exposes them to higher chances of mismatches reducing their likeliness to
 543 bloom. Schematics are illustrative only, and provided in simplified form to emphasize key
 544 circumstances that may shape jellyfish population responses

545 These different hypotheses might not be mutually exclusive. For instance, resource
546 availability might vary across ecosystems or from year to year. The hypothesis in which
547 zooxanthellate jellyfishes are able to switch resources (Fig. 4b) might represent a species
548 that can tolerate a lot of variation in its nutrition (e.g. *Phyllorhiza punctata* - Bolton and
549 Graham 2004). By opposition, the hypothesis in which zooxanthellate jellyfishes need both
550 resources (Fig. 4c) would represent a species that cannot tolerate much variation in its
551 nutrition. Thus, rather than being opposed these hypotheses might represent extremes of a
552 continuum. It is also important to note that some species might not be within the scope of
553 these hypotheses. For instance, *Cephea* (and possibly other Cepheidae; see ESM 1) loses its
554 zooxanthellae at the medusa stage (Table 2), and might thus bloom (e.g. Cruz-Rivera and El-
555 Regal 2015) as many other, non-zooxanthellate, jellyfishes. Similarly, *Phyllorhiza punctata*
556 has invasive, non-zooxanthellate, populations that have been reported to bloom (Graham et
557 al. 2003; Verity et al. 2011). Disentangling the conditions, species and environments in which
558 a given hypothesis might best describe population dynamics and blooming ability is an
559 important direction for future research on zooxanthellate jellyfishes.

560

561 **4.2. Reaction to Environmental Perturbations**

562 *4.2.1. Temperature driven bleaching*

563 As scleractinian corals, zooxanthellate jellyfish also can bleach (expel zooxanthellae) in
564 response to a heat stress (Dawson et al. 2001; McGill and Pomoroy 2008; Newkirk et al.
565 2018; Klein et al. 2019). Few jellyfish bleaching event have been documented in the field; it
566 is unclear whether such events are rarer, or simply less reported than in corals, but this
567 would be an important question to resolve. The first report was of *Mastigias papua* from
568 Clear Lake, a marine lake in Palau (Dawson et al. 2001). Subsequent experimental
569 manipulations also elicited bleaching in conspecific polyps from nearby lakes at
570 temperatures higher than 31.5 °C, providing a possible explanation for the subsequent
571 *Mastigias papua* population collapse in the adjacent Ongeim'l Tketau marine lake during the
572 extreme El Niño-La Niña oscillation of 1997-1999. Interestingly, the co-occurring non-
573 zooxanthellate *Aurelia* sp. population did not experience such a collapse (Dawson et al.
574 2001). Another jellyfish bleaching event—of *Cassiopea* sp. medusae in the Red Sea, Saudi

575 Arabia—occurred during a heat wave, after three consecutive days of atmospheric
576 temperatures > 44 °C. Mass mortality of the medusae occurred five to seven days after the
577 bleaching event (Klein et al. 2019).

578 Recovery of a medusa population following a bleaching-induced collapse depends on
579 replenishment from polyps and raises an intriguing scenario. As polyps do not rely on
580 zooxanthellae to sustain their populations (section 3.3.1.) it can be expected that the
581 requisite polyp populations will not have been depleted even if they bleached. However,
582 because strobilation usually depends on zooxanthellae (section 3.3.2.), even a large
583 population of bleached polyps may not be able to replenish the medusae population. In such
584 cases, the recovery of the medusa population would depend on the reacquisition of
585 zooxanthellae by the polyps (excepting the strobilation of aposymbiotic medusae, see
586 Dawson et al. 2001).

587 However, as some zooxanthellate jellyfish species can sometimes realize their life-cycle
588 without zooxanthellae (Table 2), bleaching may not always result in a population collapse.
589 This is confirmed by observation of populations of apparently bleached, heterotrophic,
590 mixed size-classes (from ca. 1 to 20 cm bell diameter) of *Mastigias papua* in Clear Lake, in
591 Palau (Djeghri, Dawson, unpublished data). Moreover, remaining zooxanthellae in artificially
592 bleached *Cassiopea* medusae are able to recolonize their host (Estes et al. 2003). Thus
593 zooxanthellate jellyfishes might be able to survive a bleaching event either by the recovery
594 of their zooxanthellae or by switching their nutrition towards predation.

595

596 4.2.2. Eutrophication

597 Some zooxanthellate jellyfish populations have been reported to increase after
598 eutrophication events (García 1990; Arai 2001; Pérez-Ruzafa et al. 2002) or to have higher
599 abundances in human-impacted sites, possibly due to higher nutrient concentrations (Stoner
600 et al. 2011). This contrasts with what is seen in other photosymbiotic animals such as
601 scleractinian corals (Fabricius et al. 2005; Lapointe et al. 2019) but is consistent with the
602 tendency of some jellyfish species to be favored by eutrophication (Arai 2001; Purcell 2012).
603 This apparent contradiction can be resolved if we consider that, generally speaking,
604 zooxanthellate jellyfishes are less likely than benthic photosymbiotic organisms (such as

605 corals) to suffer from the usual negative effects of eutrophication. For example,
606 zooxanthellate medusae are not subject to competition with macroalgae. They can also
607 compensate for turbidity by adjusting their depth either by swimming in planktonic species
608 (Dawson and Hamner 2003), or by settling in shallower waters in the case of the benthic
609 *Cassiopea*. Water turbidity could affect benthic polyps but, as discussed in previous sections,
610 they do not rely much on their zooxanthellae and therefore, do not need much light.
611 Moreover, scyphozoan polyps tend to be resistant to the conditions associated with
612 eutrophication (Purcell 2012; see also Klein et al. 2017). Eutrophic ecosystems could even
613 present advantages for zooxanthellate jellyfishes as they are characterized by a greater
614 availability of nutrients, which can promote the growth of zooxanthellae in zooxanthellate
615 jellyfishes (see e.g. Freeman et al. 2017) and may, in normal circumstances, be limiting (see
616 section 3.2.).

617

618 **4.3. Impacts on Ecosystems**

619 In some ecosystems, zooxanthellate jellyfish populations reach densities up to tens or
620 hundreds of medusae per 1000 m⁻³ (e.g. Hamner et al. 1982; García 1990; Pérez-Ruzafa et al.
621 2002; Gueroun et al. 2014; Cimino et al. 2018). Such densities likely strongly impact these
622 ecosystems in various ways. Some of these impacts can be very similar to those induced by
623 non-zooxanthellate jellyfishes such as high predation pressure on zooplankton (e.g. García
624 and Durbin 1993). However, due to their particular traits, zooxanthellate jellyfishes could
625 impact ecosystems in ways that differ from what is known from their non-zooxanthellate
626 counterparts.

627

628 **4.3.1. Primary productivity**

629 Individual zooxanthellate jellyfishes can reach primary productivity levels comparable to
630 those of scleractinian corals (Kremer et al. 1990). Therefore, when abundant, zooxanthellate
631 jellyfishes can represent an important fraction of the primary productivity of the ecosystem
632 they inhabit. For instance, *Mastigias papua* medusae can contribute 16 % of the primary
633 productivity in the marine lake Ongeim l'Tketau in Palau (McCloskey et al. 1994). However,
634 this high contribution may approach the upper bound of primary production contributions

635 by zooxanthellate jellyfishes: the population density of *Mastigias papua* medusae in Ongeim
636 l'Ŧketau can be very high (on average ca. 1000 medusae per 1000 m⁻³; Hamner et al. 1982;
637 Cimino et al. 2018). In other ecosystems, even when zooxanthellate jellyfishes are numerous
638 they rarely attain densities as high (maximum densities of ca. 100 medusae per 1000 m⁻³ e.
639 g. García 1990; Pérez-Ruzafa et al. 2002). Moreover, whereas jellyfish productivity can be
640 directed towards higher trophic levels (Hays et al. 2018), when their populations attain high
641 densities, most of their production may be instead directed towards microbial respiration
642 (Condon et al. 2011) or exported (e. g. Billet et al. 2006). Hence, it is unlikely that
643 zooxanthellate jellyfishes would contribute as much as scleractinian corals to productivity in
644 their ecosystems.

645

646 4.3.2. Nutrient cycling

647 Zooxanthellate jellyfishes can affect nutrient cycling in the ecosystems they inhabit. One
648 example already mentioned is the pumping action of the benthic medusae *Cassiopea* spp.
649 which releases nutrient-rich pore water for its zooxanthellae but also for the pelagic
650 community (Jantzen et al. 2010). However, this positive impact of zooxanthellate jellyfishes
651 on pelagic nutrient fluxes should probably be considered as an exception. Pitt et al. (2009)
652 suggested that the recycling and uptake of nutrients by zooxanthellate jellyfishes implies
653 that they act more as sinks for nutrients than as sources (unlike non-zooxanthellate
654 jellyfishes). This, in turn, can impact planktonic communities.

655

656 4.3.3. Planktonic communities

657 Pitt et al. (2009) suggested that if zooxanthellate jellyfishes act as sinks for dissolved
658 inorganic nutrients, then this implies fewer nutrients are available for phytoplankton growth.
659 Moreover, some characteristics of zooxanthellate jellyfishes might reduce their predation
660 efficiency (Dawson and Hamner 2009; see section 2.2.2.). Thus Pitt et al. (2009) concluded
661 that the presence of zooxanthellate jellyfish would reduce phytoplankton population
662 densities by two means. First, a bottom-up effect where the zooxanthellate jellyfishes makes
663 nutrients unavailable to phytoplankton. Second, a top-down effect where predation on
664 zooplankton by zooxanthellate jellyfishes is relatively low (as compared with non-

665 zooxanthellate jellyfishes); zooplankton populations would thus be larger and predation
666 pressure on phytoplankton would increase. This hypothesis has been successfully tested in
667 mesocosm experiments (West et al. 2009).

668

669 It is however important to stress that the impacts discussed here concern mainly quite
670 specific ecosystems (i.e. lagoons) that are characterized by important densities of jellyfishes
671 and that are more or less enclosed. In more open coastal areas, or in the open ocean, only
672 little is known of zooxanthellate jellyfishes' population fluctuations and potential impacts on
673 community dynamics and ecosystem functioning.

674

675 **5. Summary and Knowledge Gaps**

676 Zooxanthellate jellyfishes can be found in lineages across the medusozoan phylogeny (Fig.
677 1). Most of the zooxanthellate jellyfish species are isolated in mostly non-zooxanthellate
678 clades with the notable exception of Kolpophorae (Rhizostomeae: Scyphozoa).

679 Zooxanthellate jellyfishes' reliance on their symbionts can vary across species, populations
680 and ontogeny (Fig. 3, Table 2). Three key traits can be identified: (1) As holobionts, the
681 medusae are generally mixotrophic, although many variations can be observed; (2) in
682 contrast, the polyps, although being able to host zooxanthellae, do not rely much on
683 zooxanthellae for survival, growth and budding; and (3) zooxanthellae play a key role during
684 strobilation. Due to these traits, zooxanthellate jellyfishes may have different ecologies
685 when compared to non-zooxanthellate jellyfishes (e.g. different blooming ability, Fig. 4) or to
686 other photosymbiotic cnidarians such as scleractinian corals (e.g. reaction to
687 eutrophication).

688 However, there are still substantial gaps in our current understanding of zooxanthellate
689 jellyfish ecology. Hydrozoan and cubozoan zooxanthellate jellyfishes are, in most cases, only
690 described to occur, with no in depth study of their ecology. Basic information on the life-
691 cycle and nutrition is still lacking for most species. Most of our knowledge comes from large,
692 coastal, scyphozoan species which may not be representative of other groups or of other
693 environments such as the open ocean. The best studied genus is *Cassiopea* since it has been
694 used as a model organism for the study of cnidarian-zooxanthellae symbiosis (see recent

695 review; Ohdera et al. 2018). However, due to the benthic life-style of its medusae, this genus
696 may not be the best model for understanding pelagic zooxanthellate jellyfish ecology. Our
697 understanding of zooxanthellate jellyfish diversity and ecology would benefit from more
698 systematic assessment—e. g. using microscope study or molecular methods—of the
699 presence of zooxanthellae in a wide range of medusozoans. Albeit generally mixotrophic,
700 zooxanthellate medusae display a great variability in their nutrition, which also needs to be
701 characterized better given its implications for the ecologies of these species. Traditional
702 measures of predation, photosynthesis, respiration and excretion (e. g. Kremer 2005) would
703 be beneficial though time consuming. More recent methods, involving trophic markers such
704 as stable isotopes or fatty acids have been applied successfully to other photosymbiotic
705 animals such as corals (see e. g. Ferrier-Pagès and Leal 2018; Mies et al. 2018) and would
706 usefully be applied to zooxanthellate jellyfishes (e. g. Mortillaro et al. 2009; Freeman et al.
707 2017; Zeman et al. 2018). The last, but possibly major caveat with the study of
708 zooxanthellate jellyfishes may be due to the way we divide our scientific fields.
709 Zooxanthellate jellyfishes are somewhat caught between jellyfish focused researchers and
710 coral focused researchers. To gain insight of zooxanthellate jellyfishes' biology and ecology,
711 we need to bring together ideas from these two communities.

712

713 **Compliance with ethical standards:**

714 **Conflict of interest** All authors declare that they have no conflict of interest.

715 **Ethical approval** This article does not contain any work involving animals performed by any
716 of the authors

717

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1138 bloom year: insight from gut contents and stable isotope analysis. *Mar Biol* 165:120

1139 **Table 1** List of zooxanthellate medusozoan genera found in the literature and inferred in this
 1140 study (including facultative symbionts). The inference of the presence of zooxanthellae was
 1141 made for the members of the sub-order Kolpophorae where all the genera on which
 1142 relevant information is available are zooxanthellate. Unless stated otherwise, it is assumed
 1143 that all species in each genus may have zooxanthellae. This list is likely far from complete as
 1144 many groups, particularly in Hydrozoa remain little known. Reports of zooxanthellae
 1145 presence are classified as follows: “Confirmed”: when zooxanthellae have been directly
 1146 observed and/or studied (e.g. microscopic imagery, zooxanthellae presence used as a
 1147 taxonomic criterion, measures of photosynthesis available). “Potentially”: when authors
 1148 where unsure that the observed structure were zooxanthellae. “Indirect report”: report of
 1149 the presence of zooxanthellae without direct observation. “Doubtful”: indirect reports with
 1150 contradicting direct observations. Additional indirect evidence (photographs) for the
 1151 presence of zooxanthellae in some little studied Kolpophorae is discussed in electronic
 1152 supplementary material (ESM 1)

CLASS, Order, Family	Genus	Presence of zooxanthellae? (Reference(s))
CUBOZOA		
Carybdeida		
Alatinidae	<i>Alatina</i>	Confirmed in <i>Alatina morandinii</i> (Straehler-Pohl and Jarms 2011; Straehler-Pohl and Toshino 2015)
Carukiidae	<i>Malo</i>	Confirmed in <i>Malo maxima</i> (only in a minority of polyps; Underwood et al. 2018)
HYDROZOA		
Anthoathecata		

Capitata incertae sedis	<i>Paulinum</i>	Potentially (see Kramp 1961 (as <i>Dicodonium</i>); Brinckmann-Voss and Arai 1998)
Eudendriidae	<i>Eudendrium</i> *	Confirmed in some species (Marques et al. 2000)
	<i>Myrionema</i> *	Confirmed (Fitt and Cook 2001)
Milleporidae	<i>Millepora</i> **	Confirmed (Lewis 2006)
Porpitidae	<i>Porpita</i>	Confirmed (Bouillon et al. 2006)
	<i>Veleva</i>	Confirmed (Larson 1980; Bouillon et al. 2006; Lopes et al. 2016)
Ptilocodiidae	<i>Hydrichtella</i> *	Indirect report (Muscatine 1974)
Stylasteridae	<i>Sporadopora</i> *	Indirect report (Muscatine 1974)
Leptothecata		
Agloapheniidae	<i>Aglaophenia</i> *	Confirmed in some species (Svoboda and Cornelius 1991)
Dipleurosomatidae	<i>Dichotomia</i>	Confirmed (Brooks 1903; Bouillon 1984)
Haleciidae	<i>Halecium</i> *	Confirmed in some species (Pagliara et al. 2000)
Laodiceidae	<i>Wuvula</i>	Confirmed (Bouillon et al. 1988)
Plumulariidae	<i>Pseudoplumaria</i> *	Confirmed in <i>Pseudoplumaria marocana</i> (Medel and Vervoort 1995)
Sertularellidae	<i>Sertularella</i> *	Indirect report (Muscatine 1974; see also Calder 1990)
Sertulariidae	<i>Dynamena</i> *	Potentially (Galea and Ferry 2015)
Thyrosocyphidae	<i>Symmetrosyphus</i> *	Confirmed (Calder 1990)

Siphonophorae		
Physaliidae	<i>Physalia</i>	Doubtful (Wittenberg 1960 but see Lopes et al. 2016)
SCYPHOZOA		
Coronatae		
Linuchidae	<i>Linuche</i>	Confirmed (Ortiz-Corp's et al. 1987; Kremer et al. 1990)
Nausithoidae	<i>Nausithoe</i>	Confirmed in some species (Werner 1973; Silveira and Morandini 1997)
Rhizostomeae		
Catostylidae	<i>Catostylus</i>	Doubtful (Muscatine 1974 but see Pitt et al. 2005)
Rhizostomatidae	<i>Rhizostoma</i>	Doubtful (Trench 1971 but see Fuentes et al. 2011)
Cassiopeidae (Kolpophorae)	<i>Cassiopea</i>	Confirmed (Freudenthal 1962; Mergner and Svoboda 1977; Verde and McCloskey 1998)
Cepheidae (Kolpophorae)	<i>Cephea</i>	Confirmed (Sugiura 1969) see also ESM 1
	<i>Cotylorhiza</i>	Confirmed (Kikinger 1992) see also ESM 1
	<i>Marivagia</i>	No photographic evidence of the presence of zooxanthellae in the medusa (ESM 1) – inference: zooxanthellae likely present in the polyp as in close relatives

	<i>Netrostoma</i>	Confirmed (Straehler-Pohl and Jarms 2010) see also ESM 1
Mastigiidae (Kolpophorae)	<i>Mastigias</i>	Confirmed (Sugiura 1964; McCloskey et al. 1994)
	<i>Phyllorhiza</i>	Confirmed (Pitt et al. 2005)
Thysanostomatidae (Kolpophorae)	<i>Thysanostoma</i>	Photographic evidence for the presence of zooxanthellae available (ESM 1)
Versurigidae (Kolpophorae)	<i>Versuriga</i>	Photographic evidence for the presence of zooxanthellae available (ESM 1)
?	<i>Bazinga</i>	Confirmed (Gershwin and Davie 2013)

1153 * = groups with no medusae phase (see Bouillon et al. 2006). ** = group with short lived

1154 medusae phase (see Soong and Cho 1998)

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1158 **Table 2** Presence of zooxanthellae along the life-cycle in some species of zooxanthellate

1159 jellyfish. Brackets indicates a state inferred from closely related species but without direct

1160 confirmation found in the literature

Species	Planula	Polyp	Ephyra	Medusa	Reference(s)
CUBOZOA					
Carybdeida					
<i>Alatina morandinii</i>	?	present	N/A	present	Straehler-Pohl and Jarms 2011; Straehler-Pohl and Toshino 2015

<i>Malo maxima</i> *	?	present	N/A	?	Underwood et al. 2018
HYDROZOA					
Anthoathecata					
<i>Porpita porpita</i>	?	present	N/A	present	Bouillon et al. 2006
<i>Velella velella</i>	?	present	N/A	present	Larson 1980; Bouillon et al. 2006
Leptothecata					
<i>Wuvula fabietii</i>	?	?	N/A	present	Bouillon et al. 1988
SCYPHOZOA					
Coronatae					
<i>Linuche unguiculata</i>	present	present	present	present	Ortiz-Corp's et al. 1987; Montgomery and Kremer 1995; Silveira and Morandini 1998
<i>Nausithoe aurea</i>	?	present	present	present	Silveira and Morandini 1997
Rhizostomeae					
<i>Cassiopea</i> spp.	absent	present	present	present	Ludwig 1969; Hofmann et al. 1996; Verde and McCloskey 1998
<i>Cephea cephea</i> *	absent	present	present	absent	Sugiura 1969
<i>Cotylorhiza tuberculata</i>	absent	present	present	present	Kikinger 1992

<i>Mastigias papua</i> **	absent	present	present	present	Sugiura 1963 ; Sugiura 1964 ; Dawson et al. 2001
<i>Phyllorhiza punctata</i> **	(absent)	present	present	present	Bolton and Graham 2004; Schiariti et al. 2014

- 1 ? = unknown. * = species where presence of the symbiont is facultative. ** = species with
- 2 some populations without zooxanthellae. N/A = not applicable (cubozoans and hydrozoans
- 3 do not have ephyra)

Review of the diversity, traits, and ecology of zooxanthellate jellyfishes (Electronic Supplementary Material)

Nicolas Djeghri, Philippe Pondaven, Herwig Stibor, Michael N Dawson

ESM 1: Photographic evidence of zooxanthellae presence or absence in less studied Kolpophorae medusae

Method

In the absence of samples that could be tested using a suite of modern techniques (see main text) possible presence of zooxanthellae was assessed using photographs of the less studied genera (or species) of Kolpophorae. Photographs were searched for in scientific publications (as priority) and online. These genera and species belong to the families Cepheidae, Thysanostomatidae and Versurigidae. Brown coloration was considered as potential evidence for the presence of zooxanthellae. Absence of brown coloration was considered as evidence for few or no zooxanthellae.

The genera and species investigated for photographs were the following:

Cepheidae: *Cephea* spp., *Cotylorhiza erythraea*, *Marivagia stellata*, *Netrostoma* spp.

Thysanostomatidae: *Thysanostoma* spp.

Versurigidae: *Versuriga* spp.

Importantly, this method does not allow us to conclude that a species is or is not zooxanthellate as photos generally are of insufficient resolution to see zooxanthellate and, also, zooxanthellae may still be present in the polyp.

Results and Discussion

Cepheidae:

Cephea spp.: The photographs show generally very clear medusae, with possibly a few zooxanthellae in the tip of oral arms (Cruz-Riveira and El-Regal 2015; Gul et al. 2015a, b). Zooxanthellae are however present in the polyp and ephyra (Sugiura 1969). This supports the conclusion of Sugiura (1969) stating that *Cephea cephea* lose most of its symbionts during the medusa phase.

See also:

http://thescyphozoan.ucmerced.edu/Syst/Rhi/C_cephea_i.html

Cotylorhiza eythraea: Photographs of both clear and brownish individuals found (Galil et al. 2016) suggesting that this species is a facultative symbiont at the medusa stage. Zooxanthellae apparently present in oral arms.

Marivagia stellata: The photographs found show only very clear individuals (Galil et al. 2010) suggesting that this species is not zooxanthellate at the medusa stage (zooxanthellae may still be present in polyps and ephyra, see *Cephea* spp. and *Netrostoma* spp.).

Netrostoma spp.: The photographs found show very clear individuals, with possibly a few zooxanthellae in the tip of oral arms (Gul et al. 2015a). Zooxanthellae present in polyp and ephyra (Straehler-Pohl and Jarms 2010). This suggests that this genus loses most of its symbionts at the medusae stage, as does its close relative *Cephea* spp.

Thysanostomatidae:

Thysanostoma spp.: No color photograph found in scientific papers. Online photographs suggest the presence of zooxanthellae in oral arms and coronal muscle:

https://fr.wikipedia.org/wiki/Thysanostoma#/media/File:Thysanostoma_loriferum_Maldives.JPG

[http://doris.ffesmm.fr/Especies/Thysanostoma-cf.-loriferum-Thysanostome-bleue-4883/\(rOffset\)/0](http://doris.ffesmm.fr/Especies/Thysanostoma-cf.-loriferum-Thysanostome-bleue-4883/(rOffset)/0)

[http://doris.ffesmm.fr/Especies/Thysanostoma-thysanura-Thysanostome-rouge-3539/\(rOffset\)/1](http://doris.ffesmm.fr/Especies/Thysanostoma-thysanura-Thysanostome-rouge-3539/(rOffset)/1)

http://thescyphozoan.ucmerced.edu/Syst/Rhi/T_Thysanura_i.html

Versurigidae:

Versuriga spp.: Photographs of brown individuals (Sun et al. 2018) suggest this genus is zooxanthellate. Zooxanthellae apparently present in oral arms and along the coronal muscle. Another photograph shows a pale individual, suggesting that the genus may be a facultative symbiont:

http://thescyphozoan.ucmerced.edu/Syst/Rhi/V_anadyomene_i.html

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