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1 **Title**

2 Two decades of seawater acidification experiments on tropical scleractinian corals: overview, meta-
3 analysis and perspectives

4

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27 **Abstract**

28 Ocean acidification has emerged as a major concern in the last fifteen years and studies on the
29 impacts of seawater acidification on marine organisms have multiplied accordingly. This review
30 aimed at synthesizing the literature on the effects of seawater acidification on tropical scleractinians
31 under laboratory-controlled conditions. We identified 141 articles (published between 1999-2021)
32 and separated endpoints into 22 biological categories to identify global trends for mitigation and
33 gaps in knowledge and research priorities for future investigators. The relative number of affected
34 endpoints increased with pH intensity (particularly for endpoints associated to calcification and
35 reproduction). When exposed to pH 7.6-7.8 (compared to higher pH), 49% of endpoints were
36 affected. The diversity in experimental designs prevented deciphering the modulating role of coral
37 life stages, genera or duration of exposure. Finally, important bias in research efforts included most
38 experiments on adult corals (68.5%), in 27 out of 150 (18%) coral ecoregions and exclusively from
39 shallow-waters.

40

41 **Keywords**

42 Ocean acidification, Tropical scleractinian, pH, Calcification, Review

43

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50

1. Introduction

51 Due to the increasing emissions of carbon dioxide into the atmosphere, the Ocean is warming and
52 getting more acidic. Ocean acidification (OA) has been identified as a global environmental threat
53 and included as the United Nations' Sustainable Development Goal 14.3, as well as one of the nine
54 planetary boundaries (Jagers et al., 2019; Rockström et al., 2009). OA impacts on marine species and
55 ecosystems are well documented, including effect on marine calcifiers, threatening coral reefs as well
56 as broader marine ecosystems (Doney et al., 2009; Feely, 2004; Gattuso & Hansson, 2011; Hendriks
57 et al., 2010; Jiang et al., 2019; Kroeker et al., 2010, 2013; Orr et al., 2005).

58 Most of the available knowledge on the effects of OA on marine organisms comes from short-term
59 laboratory experiments on isolated organisms (Kroeker et al., 2010). Fixed-term studies have the
60 disadvantage of potentially under/overestimate the effects of OA, as some taxa may show
61 vulnerability/acclimatization in the long-term (Fantazzini et al., 2015). Similarly, other life stages than
62 those considered may show different vulnerability and controlled conditions does not consider the
63 indirect effects due to OA-driven ecological changes (Fabricius et al., 2011). In this context,
64 knowledge acquired through field experiments taking advantage of organisms that are naturally
65 exposed to OA (e.g. CO₂ vent systems) are very complementary as they account for the life-long
66 acclimatization of organisms. These studies already showed that OA may change reef community
67 composition and metabolism (Biscéré et al., 2019; Noonan et al., 2018). They also reported effects on
68 skeletal porosity (Prada et al., 2021) and a variety of responses to OA on calcification rate, suggesting
69 species-specific acclimatization to OA (Strahl et al., 2015).

70 Coral reefs have received particular attention as they are among the most severely threatened
71 ecosystem on Earth (Pandolfi, 2003; Raven, 2005). The effects of seawater acidification on corals
72 have been extensively studied (Chan & Connolly, 2013; Erez et al., 2011), but responses often differ
73 between studies depending on parameters such as tested populations, species and life-cycle stages
74 (Kawahata et al., 2019). These apparent conflicting results in the literature could also be attributed to
75 variations in experimental designs and methodologies. In this study, we reviewed the literature that
76 examined the effects of decreased pH on tropical scleractinian corals under laboratory-controlled
77 conditions. A meta-analysis based on 169 experiments conducted in 141 peer-reviewed articles
78 published since 1999 was performed, with four main objectives:

79 (1) To provide a semi-quantitative description of the evolution of research efforts testing the
80 effects of seawater acidification on tropical scleractinian corals,

81 (2) To evaluate the effect of seawater acidification on coral biological functions,

- 82 (3) To investigate the modulating influence of exposure duration, coral life stages and coral
83 genera on sensitivity to seawater acidification and,
84 (4) To highlight research gaps and bias.

85 Based on this review, we provide recommendations and perspectives for future research and an
86 updated baseline for scientists starting in this field of research.

87

88

2. Material and methods

89 The code used in this manuscript was based on Jacob et al. (2020):
90 <https://doi.org/10.5281/zenodo.3694955>.

91

92 2.1 Literature search

93 A literature search was performed using the following databases: Ocean Acidification – International
94 Coordination Centre portal for ocean acidification biological response data, Google Scholar, Scopus
95 (keywords such as “coral” AND “acidification”). We listed all experimental studies published before
96 2021, which mainly focused on the effects of experimental seawater acidification on tropical
97 scleractinian corals. Studies were selected according to the following criteria: 1) the experiment(s)
98 was(were) performed under laboratory-controlled conditions; 2) one treatment (at least) was
99 designed to test the effects of seawater acidification only (without interaction with another stressor);
100 3) a tropical scleractinian coral species (at least) was studied; 4) an acidified treatment was compared
101 with a control treatment (present-day conditions), with constant conditions (*i.e.* non-oscillating). *In*
102 *situ* experiment(s) of the effects of seawater acidification on biological functions were not included in
103 the database but were considered for the discussion. Higher than present-day (control) pH
104 conditions (e.g. pre-industrial pH conditions) were not included in the database. When the statistics
105 lacked clarity/transparency or did not allow to be adequately decomposed into the database, the
106 article was excluded. The completeness of the results obtained was considered as satisfactory based
107 on “snowballing” (*i.e.* checking citations on reference lists of relevant articles until no further
108 relevant article could be found; Sayers, 2007).

109

110 2.2 Main data extraction

111 For each experiment selected in the database, the following information was extracted: Study
 112 location(s), study duration(s), coral genus and species, coral life stage(s), number of studied species,
 113 tested pHs, pH scale and endpoints.

114

115 2.3 Data organization

116 For analyses, six pH classes were defined: Class 1 for pH between 7.8 and 8, Class 2 for pH between
 117 7.6 and 7.8, Class 3 for pH between 7.4 and 7.6, Class 4 for pH between 7.2 and 7.4, Class 5 for pH
 118 between 7 and 7.2, Class 6 for pH below 7. Recent studies highlight the importance of local
 119 adaptation to the present natural variability in the carbonate chemistry to define species sensitivity
 120 to OA (e.g. Vargas et al., 2017). As a consequence, the definition of pH scenarios or categories
 121 relevant in the context of OA should consider this natural variability. As diurnal and seasonal pH
 122 variability is low in coral reef environments (e.g. Cyronak et al., 2020), pH within class 1 to 6 are
 123 considered relevant in the context of OA. Similarly, duration, genus and life stage were also divided
 124 into classes. Four duration classes were defined: Class 1 for very short-term experiments (<1 week),
 125 Class 2 for short-term experiments (1-4 week(s)), Class 3 for medium-term experiments (1-3
 126 month(s)), Class 4 for long-term experiments (>3 months); Three genus classes: Class 1 for species
 127 from the genus *Acropora*, Class 2 for species from the genus *Porites*, Class 3 for species from the
 128 genus *Pocillopora*; and three life stage classes were chosen: Class 1 for free-living non-calcifying early
 129 life stages (Gametes, Gastrulae, Larvae), Class 2 for settled calcifying early life stages (Recruits,
 130 Primary polyps, Juveniles) and Class 3 for the adults. All classes are summarized in Table 1.

131

132 **Table 1.** pH, Duration, genus and life stage classes used to classify this review.

Parameters	Classes	
pH	Class 1	7.8-8
	Class 2	7.6-7.8
	Class 3	7.4-7.6
	Class 4	7.2-7.4
	Class 5	7.0-7.2
	Class 6	<7
Duration	Class 1	<1 week
	Class 2	1-4 week(s)
	Class 3	1-3 month(s)
	Class 4	>3 months
Genus	Class 1	<i>Acropora</i>
	Class 2	<i>Porites</i>
	Class 3	<i>Pocillopora</i>
Life stage	Class 1	Free-living early life stages
	Class 2	Settled early life stages
	Class 3	Adults

133

134 2.4 Endpoints

135 For each study and experiment, all measured endpoints were identified and divided into categories
 136 based on their biological significance. When the biological significance of an endpoint was not
 137 straightforward and/or when an endpoint could have several biological meanings, we attributed it to
 138 a single category based on the focus adopted by authors. In total, eight categories, divided into 22
 139 subcategories, were established (Table 2).

140

141 **Table 2.** List of the biological categories and subcategories used in the database, with one example of endpoint
 142 measured.

Biological category	Biological subcategory	Endpoint measured ¹
Feeding and excretion	Excretion	Ammonia excretion rate
	Feeding	Feeding rate
Fitness	Reproductive investment and success	Settlement rate
	Calcification	Net calcification rate
	Mortality	Total mortality
	Growth and development	Linear extension rate
Cellular stress-response mechanisms	Apoptosis	p53 expression level
	Oxidative stress	Glutathione reductase expression level
	Other molecular actors	HSP70
Biomolecules	Carbohydrate	Carbohydrate content
	Lipid	Total lipid content
	Protein	Protein content
	Energy content	Host ATP content
Respiration and photophysiology	Photophysiology	Net photosynthetic rate
	Respiration	Dark respiration rate
	Productivity	Net productivity
Microbiome and endolithic algae	Bacterial community composition	Gammaproteobacteria content
Metabolome		Metabolite profile
Epigenetic mechanism		DNA methylation level
Community	Community structure	Planar cover of the community
	Community calcification	Light community calcification
	Respiration	Community net oxygen consumption

143 ¹This is a non-exhaustive list of examples. See the database in Supplementary Material for the full list of endpoints
 144 measured.

145

146 For each endpoint, we reported the occurrence of a significant effect of exposure to pH as compared
 147 to the highest tested pH: YES if the endpoint was significantly affected by pH; NO elsewhere (Jacob et

148 al., 2020). If multiple pH treatments were used and the statistics in the study did not compare the
149 effect of each treatment with the control, but rather reported the result as a statistical trend, a YES
150 was attributed to an endpoint when the trend was significant. For each category and subcategory,
151 the percentage of affected endpoints was calculated by dividing the number of affected endpoints
152 (*i.e.* number of YES) by the total number of endpoints in this category or subcategory (Jacob et al.,
153 2020).

154

155 2.5 Database construction

156 All selected experimental studies were grouped in a common database gathering all relevant
157 information (main data, endpoints and effects as described from 2.2 to 2.4). The database is available
158 as Supplementary Material.

159

160

3. Results & Discussion

161 3.1 General trends in experimental seawater acidification research on tropical scleractinian corals

162 *Literature trend*

163 In our database, we identified 169 experiments in 141 articles (listed in Supplementary Material) that
164 have evaluated the effects seawater acidification under laboratory-controlled conditions on tropical
165 scleractinian corals. The six best studied regions account for 69% of the studies: Australia (15%),
166 Japan (14%), French Polynesia (14%), Hawaii (10%), the USA (excluding Hawaii, 8%) and Taiwan (8%;
167 Fig. 2A). Six percent of the studies were carried out on corals that have been maintained and
168 acclimated in aquaria for years (referred to as “Aquaria acclimated”; Fig. 2A). These included the
169 species *Stylophora pistillata* that were held in aquaria in Monaco (Liew et al., 2018; Reynaud et al.,
170 2003; Tambutté et al., 2015; Venn et al., 2013, 2019, 2020; Zoccola et al., 2016), but also by other
171 coral species obtained from commercial suppliers (Bove et al., 2020; Wijgerde et al., 2014).
172 Altogether, these data reveal that the effects of experimental seawater acidification on tropical
173 scleractinian corals have only been studied in 27 out of 150 coral ecoregions (18%; Veron et al., 2005,
174 2015). Certain parts of the world remain unexplored, with no study to date in the African reefs nor
175 around the coasts of India or Sri Lanka, and very few studies in the coral triangle (Figure 1), despite
176 being known as the most biodiverse area in the ocean, containing more than 76% of the world’s
177 shallow-water reef-building corals (Asaad et al., 2018). Moreover, no study has ever focused on the
178 impact of seawater acidification on tropical mesophotic corals, even though they represent 2/3rd of

179 the world coral reefs (Morais & Santos, 2018) and are expected to act as “deep refugia”, by providing
180 a viable reproductive source for shallow reefs after disturbance (Bongaerts et al., 2010).

181 Experimental seawater acidification research on tropical scleractinians is relatively recent and has
182 increased exponentially since the 21st century (Fig. 2B). Similarly, *in situ* studies have only started to
183 develop even more recently, with a majority of studies (70%) published over the five past years (Fig.
184 2B). Among these, 80% took advantage of coral communities living under naturally acidified waters
185 such as submarine springs in Mexico (Crook et al., 2012, 2013; Martinez et al., 2019; Wall et al.,
186 2019) and CO₂ vents in Papua New Guinea (Biscéré et al., 2019; Fabricius et al., 2011; Fantazini et al.,
187 2015 ; Marcelino et al., 2017 ; Morrow et al., 2015 ; Noonan et al., 2016, 2018 ; O’Brien et al., 2018 ;
188 Prada et al., 2021 ; Smith et al., 2016 ; Strahl et al., 2015 ; Wall et al., 2017). Other studies compared
189 adjacent reef sites with distinct pH conditions (Barkley et al., 2015, 2017; Camp et al., 2017). Finally,
190 20% of studies have performed *in situ* controlled CO₂ enrichment such as FOCE experiments (Free
191 Ocean CO₂ Experiments; Albright et al., 2016, 2018; Doo et al., 2019; Georgiou et al., 2015; Kline et
192 al., 2019; Srednick et al., 2020). *In situ* studies possess the great advantage of being more ecologically
193 realistic than laboratory-based studies, as they account for the complexity of species interactions of
194 the whole reef community, under natural abiotic conditions (Albright et al., 2018). Yet, naturally
195 acidified sites are not always available and possess their own set of limitations. They are not perfect
196 predictors of future ocean ecology owing to temporal variability in pH, spatial proximity with other
197 populations and changes in other parameters such as seawater temperature (Prada et al., 2021;
198 Riebesell, 2008). Moreover, the manipulation of seawater parameters *in situ* is technically
199 challenging and comes at great expenses, which greatly limits its reproducibility.

200

201 *pH scale*

202 Best practices recommend to measure seawater pH using the total hydrogen ion concentration scale
203 (Total scale; Dickson et al., 2007). Yet, only 54.4% of experiments used this scale (Figure 2I). The rest
204 of the experiments measured pH on the NBS scale (US National Bureau of Standards, now referred to
205 as the IUPAC scale, 29.2%) or on the seawater scale (SWS; 5.3%). A minority of experiments (3.5%)
206 did not measure the pH but estimated its value from the other seawater carbonate chemistry
207 parameters, via CO₂sys (Pierrot et al., 2006) or the R package seacarb (Gattuso et al., 2020). Finally, a
208 significant proportion (7.6%) did not specify how the pH was measured/calculated. Such
209 heterogeneity in the pH scales used to measure seawater pH probably lies in the fact that it is,
210 together with the study of acid-base reactions in seawater, one of the most confused areas of marine
211 chemistry (Dickson, 1993). Above all, it is essential that the pH is defined on the same pH scale as

212 that of all acid-dissociation constants that are used with it (Riebesell et al., 2011). We highly
213 recommend future studies to focus on measuring total scale pH following the complete procedure
214 and best practices in SOP6a and SOP6b (Dickson et al., 2007).

215

216 *Coral characteristics*

217 The vast majority of studies have evaluated the effects of seawater acidification on adult
218 scleractinians (68.4%; Fig. 2C). 16.7% of studies were devoted to free-living (non-calcified) early life
219 stages (mainly larvae -13.9%-, followed by gastrulae -1.7%- and gametes -1.1%). Then, the most
220 studied settled (calcified) early life stages were recruits (7.8%), followed by primary polyps (4.4%)
221 and juveniles (2.8%; Fig. 2C). This focus on adult corals is a common trend also generally observed for
222 other marine organisms (Kroeker et al., 2010). For corals, the high attention devoted to adult stages
223 is likely due to the convenience of collection and husbandry, compared to early life stages, which
224 require specific knowledge on spawning events and high expertise for a successful rearing. However,
225 future studies should put greater emphasis on early life stages as they are often inferred to be more
226 vulnerable to environmental conditions than adults (Byrne, 2011). However, as only 4.7% of studies
227 considered multiple life history stages, the susceptibility among life stages remains largely
228 underexplored. Multigenerational studies are thus crucial as they allow to compare the sensitivity of
229 a species among life stages and to evaluate transgenerational carry over effects. To the best of our
230 knowledge, very few studies have evaluated these effects with corals, as compared to other taxa
231 (e.g. mollusks; Hettinger et al., 2012; Parker et al., 2012) or other stressors (e.g. global warming;
232 Dixon et al., 2015). Studies on scleractinians suggested that exposure of the parents to stressful
233 conditions had positive influence on coral offspring performances, when subsequently re-exposed
234 (e.g. metabolic acclimation for *P. damicornis*, Putnam & Gates, 2015; greater larval settlement and
235 survivorship for *P. damicornis*, Putnam, 2021). Yet, this likely vary between species (e.g. *S. pistillata*,
236 Bellworthy et al., 2018). Multigenerational studies are thus required to investigate parental (carry-
237 over) effects, to decipher whether the exposure to seawater acidification in adults enhance offspring
238 tolerance, and to predict the future of coral reefs more accurately (Putnam et al., 2016, 2021).

239 Altogether, three genera stand for 65.1% of the experiments, with the most studied being *Acropora*
240 (30.4%), followed by *Porites* (18.3%) and *Pocillopora* (16.3%; Fig. 2D). The most studied species from
241 the database is *Acropora millepora*. Other well studied genera are *Montipora* (7.9%), *Stylophora*
242 (6.3%) and *Seriatopora* (4.6%), followed by studies that have evaluated the effects of seawater
243 acidification on the coral community (3.8%; Fig. 2D). The genera *Siderastrea*, *Pavona* and
244 *Psammocora* each accounted for 1.7, 1.7 and 1.3% of the database, respectively. Finally, 6.7% of

245 experiments were performed on less studied genera (<1%, referred to as “Others”; Fig. 2D). These
246 include species from the genera *Cyphastrea*, *Duncanopsammia*, *Favia*, *Favites*, *Fungia*, *Galaxea*,
247 *Goniopora*, *Isopora*, *Leptastrea*, *Litophyllon*, *Madracis*, *Montastrea*, *Mussismila*, *Orbicella*,
248 *Pseudodiploria* and *Turbinaria* (Fig. 2D). Overall, these data show that a small number of coral species
249 are favoured in experimental seawater acidification experiments. As previously reported for heat
250 stress experiments on corals (review by McLachlan et al., 2020), this may be due to the facility of
251 working on highly studied species (*i.e.* with the availability of their genome), the presence of these
252 species within each region or to logistical constraints (e.g. permits, easiness of maintenance in
253 captivity). This finding also means that many species, and so several functional traits which are likely
254 to drive differential responses to acidification, remain uninvestigated.

255

256 *Experimental design*

257 The majority of experiments (63.9%) considered a single species of coral (Fig. 2E). The remaining
258 experiments used two to four (30.8%) or five to eight species (3.0%) and only 2.3% evaluated the
259 effects of seawater acidification on the coral community (Fig. 2E). Undoubtedly, it limits and
260 oversimplifies our understanding of the effects of OA on the biologically complex assemblage
261 characterizing coral reefs. On top of that, species interactions can also decrease the predictability in
262 species response to seawater acidification, since different pairings and spatial organization of corals
263 might significantly influence the observed endpoints (Brien et al., 2016; Evensen et al., 2015, 2016).
264 For these reasons, designing experiments based on the local species assemblage in terms of diversity,
265 abundance and spatial organization, should be prioritized in future investigations.

266 Furthermore, most experiments lasted between 1 and 4 week(s) (39.6%), with the other experiments
267 lasting less than a week (26.4%), one to three month(s) (24.7%) and more than three months (9.3%),
268 for a minority (Fig. 2F). This trend is likely explained by the constraints associated with long-term
269 studies, in terms of time, logistical or even financial limitations. Nevertheless, the duration of
270 exposure may influence coral sensitivity to seawater acidification. For instance, corals are able to
271 counteract the negative effects of acidification for a specific period through energy-demanding
272 processes, until reaching a time-dependent threshold beyond which it will no longer be able to
273 counter these effects (Castillo et al., 2014; Schoepf et al., 2013). For these reasons, short-term
274 studies should be avoided, and long-term experimental studies prioritized, when possible. In that
275 aspect, field experimentations/observations at CO₂ vents have the benefit to provide natural long-
276 term studies (e.g. Biscéré et al., 2019; Fabricius et al., 2011; Martinez et al., 2019; Morrow et al.,
277 2015; Noonan et al., 2018; Noonan & Fabricius, 2016; Prada et al., 2021; Strahl et al., 2015).

278

279 *Endpoints*

280 Most experiments worked on the effects of seawater acidification on the fitness (57.3%), respiration
281 and photophysiology (23.9%) and biomolecules (7.1%) of tropical scleractinians (Fig. 2G). The other
282 endpoints studied were involved in cellular stress response mechanism(s) (4.3%), community
283 response(s) (3.5%), microbiome and endolithic algae composition (2.0%), epigenetic effect(s) (0.8%)
284 and/or feeding and excretion (0.8%; Fig. 2G). Among those that have worked on the effects of
285 seawater acidification on coral fitness, calcification was the most studied endpoint (52.6%), followed
286 by growth and development (25.5%), reproductive investment and success (10.9%) and mortality
287 (10.9%; Fig. 2H).

288

289 3.2 Biological effects of pH on tropical scleractinian corals

290 *General trends*

291 Overall, the relative number of affected endpoints increases with decreasing pH (Fig. 3). Twenty-six
292 percent of endpoints were affected between pH 7.8 and 8, 46.2% between pH 7.6 and 7.8, 48.3%
293 between pH 7.4 and 7.6, 46.3% between pH 7.2 and 7.4, 96.4% between pH 7.0 and 7.2 and 100%
294 below pH 7.0. However, it should be noted that the number of available articles and data is not the
295 same for each pH category. Studies have mainly focused on pH 7.8-7.6 (n endpoints=608), followed
296 by pH 8.0-7.8 (n=519), pH 7.6-7.4 (n=203), pH 7.4-7.2 (n=162), pH 7.2-7.0 (n=56) and below 7.0 (n=4).
297 Similarly, differences in experimental designs within each pH category is potentially a strong
298 confounding factor, mixing results from experiments of multiple duration of exposure, coral life-
299 stages, coral species, among others. This may particularly limit our interpretations for the less-
300 studied pH categories.

301

302 *Fitness*

303 The decrease in pH and $[\text{CO}_3^{2-}]$ through OA is believed to increase the energetic cost of calcification
304 for marine calcifiers (Gattuso & Hansson, 2011). Known as one of the biggest threats related to OA,
305 calcification, the ability to build and maintain calcium carbonate structures, was among the most
306 studied parameters (52.6% of studies). Results showed that 43.4% of endpoints related to
307 calcification were affected for pH 7.8-8.0 (n=152), 55.3% for pH 7.6-7.8 (n=244), 66.7% for pH 7.4-7.6
308 (n=96), 85.7% for pH 7.2-7.4 (n=42), 96.9% for pH 7.0-7.2 (n=33) and 100% for pH below 7.0 (n=2)
309 (Fig. 3). Similarly, growth and development (*i.e.* coral linear extension, biomass, larval size, recruits

310 diameter, etc.) were increasingly affected with decreasing pH, with 29.5% of affected endpoints for
311 pH 7.8-8.0 (n=44), 44.4% for pH 7.6-7.8 (n=63), 61.1% for pH 7.4-7.6 (n=18), 73.7% for pH 7.2-7.4
312 (n=19), 88.9% for pH 7.0-7.2 (n=9) and 100% for pH below 7.0 (n=1). Fewer studies worked on the
313 effects of seawater acidification on reproductive investment and success (10.9%). Yet, they showed
314 that 50.0% of reproductive endpoints were affected for pH 7.8-8.0 (n=20), 75.0% for pH 7.6-7.8
315 (n=16), 100% for pH 7.2-7.4 (n=1) as well as for pH below 7 (n=1). Noticeable effects on reproduction
316 included effects on sperm flagellar motility (Morita et al., 2010), time to gastrulation (Chua et al.,
317 2013) and larval settlement (Albright et al., 2010; Doropoulos et al., 2012; Jiang et al., 2020; Pitts et
318 al., 2020; Viyakarn et al., 2015). Finally, effects of seawater acidification on coral mortality were only
319 showed under pH 7.6-7.8 (37.5% of affected endpoints, n=24). Mortality on adult colonies included
320 partial mortality (local tissue loss; Bahr et al., 2016; Kavousi et al., 2016) and total mortality (death of
321 the colonies; Yang et al., 2020). Studies also showed mortality of coral larvae (Cumbo et al., 2013;
322 Doropoulos et al., 2012) and recruits (Dufault et al., 2012, 2013) under seawater acidification.

323

324 *Respiration and photophysiology*

325 Measurement of the coral host respiration rate is often used as an indicator of the metabolism's
326 state/activity level. Moreover, the proper functioning of the algal symbiont photosynthetic activity is
327 fundamental as it provides an energy source as photosynthates to the host (Muscatine et al., 1981).
328 As the host, coral has some control over the photosynthetic activity of the algal symbionts (by
329 contributing to the low pH of the symbiosome via H⁺-ATPase, Barott et al., 2015), maintaining this
330 vital function is thus critical. The endpoints related to coral host respiration rate and algal symbiont
331 photosynthetic activity were poorly affected by seawater acidification, regardless of the pH level (Fig.
332 3). Despite this, studies on the effects of seawater acidification on photosynthetic processes gave
333 ambiguous results, with multiple studies showing an increased photosynthetic rate under low pH
334 (Anderson et al., 2019; Biscéré et al., 2019; Langdon, 2005). Response heterogeneity could be linked
335 to strain-specific responses by distinct *Symbiodinium sp.* (Brading et al., 2011; Graham & Sanders,
336 2016) or even attributed to differences in experimental parameters such as light or nutrients, which
337 both contributes to photosynthesis (Chauvin et al., 2011). It is expected that the effect of seawater
338 acidification on the coral's metabolism is small as compared to the effect of increasing temperature
339 (Agostini et al., 2013; Cumbo et al., 2013; Edmunds & Burgess, 2016; Van der Zande et al., 2020).

340

341 *Biomolecules*

342 Quantification of biomolecules such as lipids, carbohydrates and proteins is often used as an
343 indicator of energetic reserves of organisms. As such, their depletion under stressful conditions is
344 often related to increased metabolic demands in ectotherms (Deutsch et al., 2008). Endpoints
345 related to lipid, protein and carbohydrate metabolisms seemed to remain relatively stable under
346 decreased pH (Fig. 3). Yet, for lipids, 55.6% of endpoints were affected for pH 7.6-7.8 (n=9) and 33.3%
347 for pH 7.4-7.6 (n=6). Reduction of lipid content may show that maintenance of coral performances
348 and calcification under seawater acidification increase energetic costs, which is met through
349 catabolism of energy reserves. The subcategory “energy content” (here, the sum of lipids,
350 carbohydrates and proteins) showed to be greatly affected at pH 7.6-7.8, but this requires further
351 attention as it has only been studied in one experiment (Wall et al., 2017).

352

353 *Cellular stress-response mechanism*

354 Changes in the environment, like OA, are likely to drive cellular stress response, a universally
355 conserved mechanism used to protect macromolecules within cells from the potential damage that
356 OA may cause (Kaniewska et al., 2012). Here, a number of studies indicated that endpoints involved
357 in cellular stress-response mechanisms were affected by seawater acidification (Fig. 3). In the
358 subcategory “other molecular actors”, 19.2% of endpoints were affected for pH 7.8-8.0 (n=26), 16.7%
359 for pH 7.6-7.8 (n=6), 0% for pH 7.4-7.6 (n=2) and 100% for pH 7.2-7.4 (n=1). These were attributed to
360 genes involved in innate immunity (Kaniewska et al., 2012) and heat shock response (Liew et al.,
361 2018; Moya et al., 2015; Putnam et al., 2013). Thirty-one percent of endpoints associated with
362 oxidative stress were affected at pH 7.8-8.0 (n=26) and 36.6% at pH 7.6-7.8 (n=41). These were
363 essentially affecting the activity level of antioxidant enzymes (Bielmyer-Fraser et al., 2018; Jiang et
364 al., 2019; Soriano-Santiago et al., 2013) or genes involved in the antioxidant response (Kaniewska et
365 al., 2012; Moya et al., 2015). These later studies also indicated up/down regulation of anti-apoptotic
366 genes, as showed with 50% of endpoints affected under pH 7.8-8.0 (n=2) and 100% under pH 7.6-7.8
367 (n=9).

368

369 *Other biological category*

370 Coral reefs form complex network of interactions between species. Each of its component plays a
371 role and contributes to the overall equilibrium of the reef as well as its resilience to environmental
372 change. Working on the coral community is therefore necessary as it allows considering the
373 interactions between coral species and therefore provides more realistic responses. Yet, few studies

374 have experimentally worked on the effects of seawater acidification on coral community, likely owing
375 to the difficulty of having a realistic community in an aquarium. For this aspect, we suggest to refer
376 to the numerous *in situ* studies, which naturally consider the coral community. Endpoints indicated
377 that community structure was changed under pH 7.6-8.0 (100% of affected endpoints, n=2; Edmunds
378 et al., 2019, 2020).

379 As acidifying conditions affect corals, their energy requirements increase and must be compensated
380 in order to sustain the proper biological functioning of the coral. This may be studied by looking at
381 feeding rate (the input of energy *via* heterotrophy) and excretion rate (ammonium ion
382 concentration; the output of energy through protein catabolism) of corals. Towle et al. (2015)
383 indicated that coral can buffer OA effects by increasing feeding rates under pH 7.8-8.0 and Edmunds
384 & Wall (2014) showed that catabolism of proteins and amino acids is accelerated by OA (pH 7.8-8.0),
385 supporting that OA may perturb protein metabolism.

386 Phenotypic plasticity has the potential to facilitate rapid acclimatization of corals, a requirement in
387 view of the rapid rate of change in the environment, driven by human activities. Mechanisms of rapid
388 acclimatization may include changes in microbial community, with 50% of endpoints affected for pH
389 7.8-8.0 (n=4), 50% for pH 7.6-7.8 (n=4), 50% for pH 7.6-7.4 (n=2) and 87.5% for pH 7.2-7.4 (n=16)
390 (Meron et al., 2011; Webster et al., 2013, 2016; Yang et al., 2020; Zhou et al., 2016). Another
391 potential mechanism is epigenetics (*i.e.* the heritable postsynthesis modification of DNA or DNA-
392 associated proteins, without a change in the DNA sequence itself, Feil & Fraga, 2012), with 50% of
393 endpoints affected for pH 7.6-7.8 (n=2) and 100% for pH 7.2-7.4 (n=1) (Liew et al., 2018; Putnam et
394 al., 2016). Finally, metabolomic profiling is a useful molecular tool that allows quantifying the
395 intermediates and products of many biochemical processes. Putnam et al. (2016) found lower
396 amount of metabolites under OA, suggesting a general suppression of metabolic activities. These
397 techniques have started to be used on corals recently and deserve more attention in future
398 investigations.

399

400 *Gene expression*

401 Understanding the fitness consequences of observed changes in endpoints is not always
402 straightforward. This is particularly evident for changes in gene expression. An over or
403 downregulations of a given gene does not implicitly translate into a positive or negative effect on
404 protein level, function or fitness (Feder & Walser, 2005; Koussounadis et al., 2015; Greenbaum et al.,
405 2003). Moreover, the intensity of an observed change at the gene expression level that is biologically
406 significant is often poorly understood. For example, a 200% change in the expression of genes

407 involved in calcification does not necessarily translate into a 200% change in calcification. For these
408 reasons, we did not use the gene expression data to infer biological impacts of seawater acidification.

409

410 3.3 Biological effects of pH 7.6-7.8 on tropical scleractinian corals

411 Many factors can modulate the biological response of tropical scleractinian corals to seawater
412 acidification, including the tested species, life-history stage, tested pH or duration of exposure. As
413 shown in the previous section, the effects on various endpoints tend to increase with decreasing pH.
414 To better understand the role of the other modulating factors while minimizing the effect of the pH
415 intensity, we decided to focus on pH class 2 (pH 7.6-7.8) for 2 reasons: (i) it is the class with the most
416 available data (n endpoints=608); and, (ii) this range of pH corresponds to projected scenarios
417 expected for 2100 (SSP3-7.0 and SSP5-8.5; IPCC, 2021).

418

419 *General trends*

420 Tested endpoints were only moderately affected under pH 7.6-7.8 (Fig. 4). No strong effects of the
421 duration of exposure, coral genus or life stage could be identified, even when endpoints were
422 separated into different categories.

423

424 *Effects of the duration of exposure*

425 The effect of the duration of the exposure in seawater acidification experiment is still poorly
426 understood (Cumbo et al., 2013). Time-dependent response patterns were previously documented
427 (Castillo et al., 2014; Schoepf et al., 2013). For example, Castillo et al. (2014) observed an increase in
428 the calcification rate of *S. siderea* until the 60th day of exposure to acidified conditions, which
429 thereafter started to decline. Similar results were reported for *A. millepora*, with a decrease of
430 calcification that appeared only during the second half of the experiment (viz. after 1 month; Schoepf
431 et al., 2013). In these specific cases, the parabolic responses to decreased pH would not have been
432 detected if the duration of the experiments was shorter. These results might result from the ability of
433 corals to compensate for the extra energy costs associated with the exposure to decreased pH, until
434 reaching a time-dependent threshold beyond which the organism does not have the energy reserve
435 allowing to counteract the extra costs associated with the stress. In other taxonomic groups, a
436 different pattern was observed with a milder effect observed over longer period of time. For
437 example, Dupont et al. (2013) showed that the strong negative effect of pH on adult sea urchin

438 fecundity observed after a 4-month exposure disappeared after 16 months. The negative effect
439 observed over the first part of the experiment was interpreted as short-term costs associated with
440 physiological acclimation to the new low pH environment. These examples highlight the value of
441 long-term experiments.

442

443 *Effects of the coral life stage*

444 Early life stages are generally more vulnerable to environmental conditions than adults (Byrne, 2011),
445 so dismissing the effects of decreasing pH on multiple life stages in current prediction models would
446 represent an important bias for the projection of the fate of coral reef ecosystems. Indeed, if pH
447 disrupts early-life processes, it would compromise sexual recruitment and therefore affect future
448 population dynamics and the ability of coral reefs to recover from a disturbance (Caroselli et al.,
449 2019). This question has received relatively poor attention and experiments that have considered
450 more than one life stage are few (5%). Albright et al. (2010) suggested that OA has the potential to
451 affect multiple, early-life history stages of *Acropora palmata*, with negative effects on gametes
452 fertilization, larval settlement and post settlement growth. More experiment addressing this
453 question and considering multiple life stages are thus crucial.

454

455 *Effects of the coral genera*

456 The biological responses of corals to decreased pH are highly variable and often considered to be
457 species-specific (Bahr et al., 2016; Bedwell-Ivers et al., 2017; Bove et al., 2019; Brown & Edmunds,
458 2016; Edmunds et al., 2012; Hoadley et al., 2015; Sekizawa et al., 2017; Strahl et al., 2015). Several
459 other parameters were proposed to explain the diversity of response observed between studies.
460 While methodological differences could contribute to the difference between studies such as light
461 intensities (Crawley et al., 2010; Dufault et al., 2013), feeding regime (Comeau et al., 2013; Edmunds,
462 2011; Houlbrèque et al., 2015) or water motion (Comeau et al., 2015), acclimation (*i.e.* their life
463 history; Strahl et al., 2015), competition (Brien et al., 2016; Evensen et al., 2015; 2016; Horwitz et al.,
464 2017), or even the size of the fragments used (Edmunds & Burgess, 2016), biological differences
465 between taxa could explain the variability in coral sensitivity to seawater acidification. First, the
466 “biomass plasticity” hypothesis (Edmunds, 2011) supports that corals reduce their sensitivity by
467 increasing tissue thickness at low pH (Comeau et al., 2013; 2014; Edmunds, 2011). Indeed, thicker
468 tissue allow isolating the site of calcification from the surrounding seawater, better protecting the
469 zooxanthellae by changing the intensity and internal properties of the internal light field (Dimond et

470 al., 2012; Loya et al., 2001), as well as providing more energy reserves, which may be advantageous
471 under low pH (as for *Turbinaria reniformis*, Hoadley et al., 2015). Massive *Porites* is known for having
472 an unusually thick tissue layer that penetrates deeply into the skeleton (Edmunds, 2011). Second, the
473 “pH regulation” hypothesis (Holcomb et al., 2015) suggests that scleractinians which have a high
474 control over the regulation of their calcifying fluid’s pH will be less affected by low pH conditions.
475 Indeed, as the concentration of H⁺ in seawater increases under OA, the concentration gradient
476 between seawater and the site of calcification increases accordingly (Cohen & McConnaughey, 2003;
477 Jokiel, 2011; Ries, 2011; Von Euw et al., 2017). Transporting H⁺ will require more energy for the coral,
478 which may alter calcification (McCulloch et al., 2012). As such, the coral’s capacity/strategy to
479 overcome higher energy requirements (through efficient zooxanthellae photosynthesis, McCulloch et
480 al., 2012) or increased heterotrophic feeding (Towle et al., 2015) under more acidic conditions is also
481 crucial in explaining interspecific differences in sensitivity. Despite this, increasing heterotrophic
482 feeding under low pH conditions was not experimentally proven in all coral genera yet (such as
483 *Porites*; Grottoli et al., 2006). This goes along with the hypothesis suggesting that differences in
484 skeletal porosity may also explain differences in sensitivity of calcification among species. Indeed,
485 scleractinians with highly porous skeletons require less CaCO₃ to calcify than corals that have low
486 porosity skeletons, so these species may be less susceptible to seawater acidification (Brown &
487 Edmunds, 2016; Jokiel, 2011). Finally, the “growth rate” hypothesis (Comeau et al., 2014) states that
488 species characterized by higher calcification rate will be more vulnerable. Previous studies suggested
489 that different calcification strategies exist across populations (Bove et al., 2019; Leong & Pawlik,
490 2010; Metcalfe & Monaghan, 2001). It relies on the theory that fast-growing coral species are more
491 likely to be impaired under stressful conditions as their energy requirements for growth are higher
492 than slow-growing species, which mainly store energy when the environment is favorable, allowing
493 them to calcify normally under less-favorable conditions. However, this trend was not verified by
494 Chan & Connolly (2013).

495

496 *Evolutionary potential of corals under OA: local adaptation, carry over effects, parental effects*

497 Overall, there is very little information on the potential of marine organisms to adapt to OA. To
498 better understand the evolutionary responses of scleractinians to global changes, the best approach
499 is to evaluate the effects of environmental drivers through multiple generations (Putnam et al.,
500 2016). While trans-generational effects of OA has received more attention in the previous years
501 (Allan et al., 2014; Donelson et al., 2012; Dupont et al., 2013; Hettinger et al., 2012; Kurihara et al.,
502 2019; Miller et al., 2012; Munday, 2014; Parker et al., 2012), studies evaluating these effects on

503 scleractinian corals are few, likely due to their long life span. Among the available studies, evidences
504 suggested that trans-generational acclimatization processes (e.g. epigenetics) have the potential to
505 influence the sensitivity of corals to changing conditions (Putnam et al., 2016). This approach is of
506 great importance to determine whether the exposure as an adult might enhance their descendant
507 tolerance in order to better assess the status of future coral reef ecosystems. A high variability of
508 response between individual corals and a high heritability for corals exposed to low pH conditions
509 was observed, suggesting an adaptation potential (Jury et al., 2019). As highlighted by Putnam
510 (2021), non-genetic, yet heritable phenotypic plasticity, will have significant ecological and
511 evolutionary implications for sessile marine organisms persistence under rapid environmental
512 changes. We support the need to consider the interactions of rapid and evolutionary responses
513 (microbiome, epigenetic effects, parental carry-over effects; see Putnam, 2021), that have been
514 overlooked so far, but deserve more attention as they provide additional avenues for rapid
515 acclimatization.

516

517 *The future of the reef: past environmental exposure, multiple stressors/drivers interactions*

518 OA acts in conjunction with a myriad of other stressors/drivers, which presence and intensity vary
519 locally. Among those, global ocean warming has received particular attention as it represents the
520 main stressor on the reefs, inducing coral bleaching and widespread mortality in multiple regions.
521 Studies considering a combination of increasing temperatures with seawater acidification often
522 showed additive effects, thus worsening the effects observed when considering a single stressor (e.g.
523 Albright & Mason, 2013; Anlauf et al., 2011; Anthony et al., 2008; Horvath et al., 2016; Kavousi et al.,
524 2016; Reynaud et al., 2003). Then, to predict more realistically the future of coral reefs, their
525 vulnerability must be assessed over long term and consider the stressors experienced by the reef
526 organisms in the past. There is a temporality in the action of stressors on the reef that will condition
527 the response of reef organisms. For example, multiple evidences showed that corals that have gone
528 through repeated heat stress events in the past may have become more tolerant to future heat
529 stress (Guest et al., 2012; Maynard et al., 2008; Thompson & van Woesik, 2009). Similarly, decreased
530 thermal susceptibility was described with corals preconditioned to mild heat stress for a short period
531 (Bay & Palumbi, 2015; Bellantuono et al., 2012a, 2012b; Middlebrook et al., 2008). In addition, OA
532 will impair coral reefs previously altered by several bleaching events. Coral reef communities will be
533 fragilized by the intensity and frequency of bleaching and it is likely that their capacity to endure
534 additional stressor as OA will be highly detrimental.

535

536

4. Research gaps and perspectives

537

538 Based on all aforementioned points, we selected a list of priorities and actions that should be
539 addressed for future experimental works investigating the effects of seawater acidification on
540 tropical scleractinians (Table 3).

541

542 **Table 3.** List of actions and priorities for future research on the effects of seawater acidification on tropical
543 scleractinians.

Type	Recommended action(s)
Coral characteristics	Investigate corals from less-studied ecoregions, mesophotic depths
Experimental design	Consider multigenerational approaches Use multiple life-history stages, including early stages Realism: select the diversity and abundance of species based on the local assemblage, favour multi-species approach Include key species interacting with the tested species Avoid short-term exposure, consider multiple duration of exposure when feasible
Carbonate chemistry and scenarios	Monitor and consider the local variability of carbonate chemistry while defining scenarios and rely on local projections Include the natural variability for the carbonate chemistry and other key environmental drivers (multiple stressors) Apply best practices for carbonate chemistry parameters measurement (Dickson et al., 2007). Report pH in total scale.
Biological endpoints	Focus on endpoints to better understand the acclimatization capacity: epigenetic effects, microbiome and endolithic algae composition Consider multiple complementary approaches: genetic and physiological tools

544

545

546

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551 **Figure legends**

552

553 **Figure 1.** World map of coral reefs that have been the subject of an experimental study (blue circles)
554 on the effects of seawater acidification. Circle size: number of experimental study. Red colour: Global
555 distribution of coral reefs (UNEP-WCMC, WorldFish Centre, WRI, TNC, 2010; version of March 2021).

556 **Figure 2.** General trends in the experimental research of the effects of seawater acidification on
557 biological functions of tropical scleractinian corals. **(A)** Number of experiments per country/location
558 that experimentally examined the effects of seawater acidification on tropical scleractinian corals
559 (total n=169). **(B)** Number of *ex situ* (total n= 169) and *in situ* (total n=27) studies published before
560 2021 that experimentally examined the effects of seawater acidification on tropical scleractinian
561 corals. Relative proportion of **(C)** coral life stages (n=180) and **(D)** coral genera (n=240) studied in the
562 169 experiments that looked at the effects of seawater acidification on tropical scleractinian corals
563 before 2021. Relative proportion of experimental design by **(E)** assemblages (n=169; i.e. number of
564 studied species per experiment) and **(F)** duration of exposure (n=182) to seawater acidification in the
565 same 169 experiments. **(G)** Relative proportion of the main biological categories studied in the same
566 169 experiments (n=255), with **(H)** specific focus on the fitness category. **(I)** Relative proportion of
567 the pH scale used in the 169 experiments. Some of these bar charts have a (n) superior to 169
568 because some of the 169 experiments that were selected used more than one life stage, genera,
569 duration of exposure and/or biological endpoint.

570 **Figure 3.** Effects of pH intensity on tropical scleractinian corals biological functions. Heatmaps
571 indicate the number of endpoints (circle size) and the proportion of affected endpoints (color, in %)
572 in each biological subcategory. Full red (100%) indicates that all endpoints are affected and full green
573 (0%) that no endpoints were affected.

574 **Figure 4.** Effects of pH 7.6-7.8 on tropical scleractinian corals biological functions according to the
575 duration of exposure, the coral genus and life stage. Heatmaps indicate the number of endpoints

576 (circle size) and the proportion of affected endpoints (color, in %) in each biological subcategory. Full
577 red (100%) indicates that all endpoints are affected and full green (0%) that no endpoints were
578 affected.

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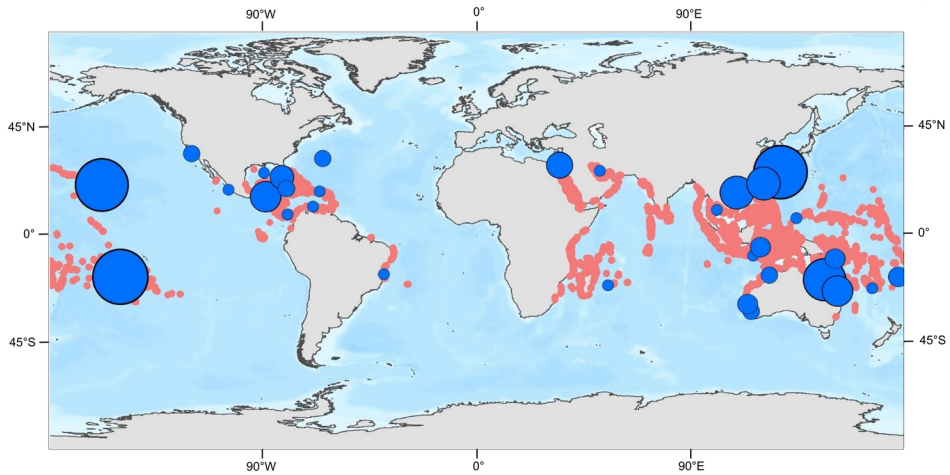
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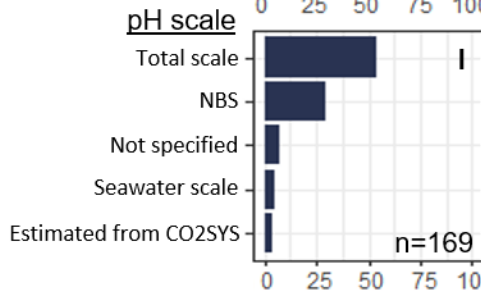
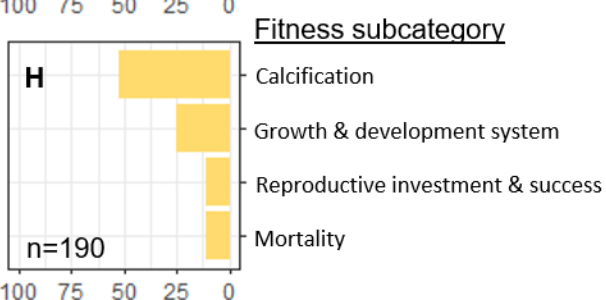
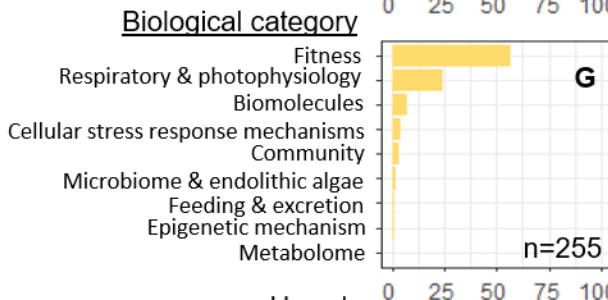
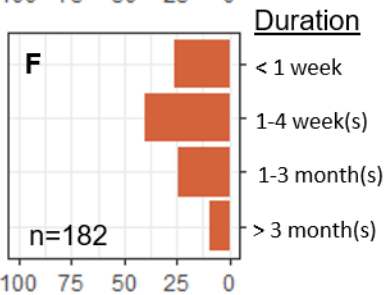
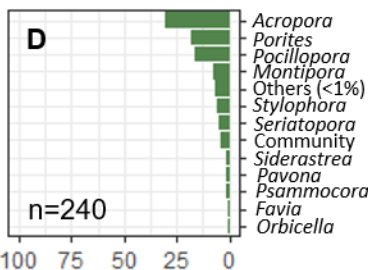
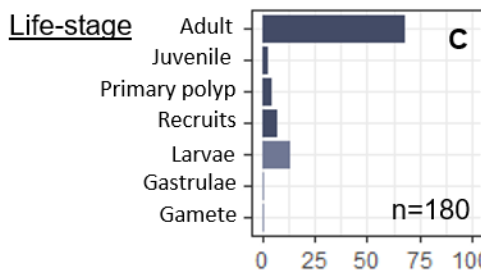
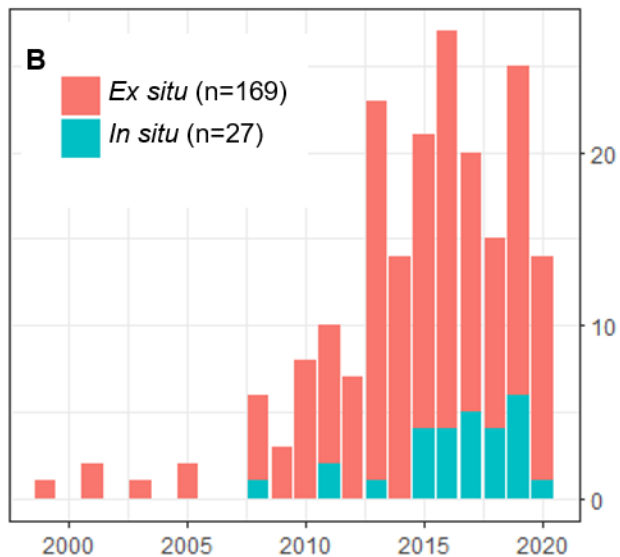
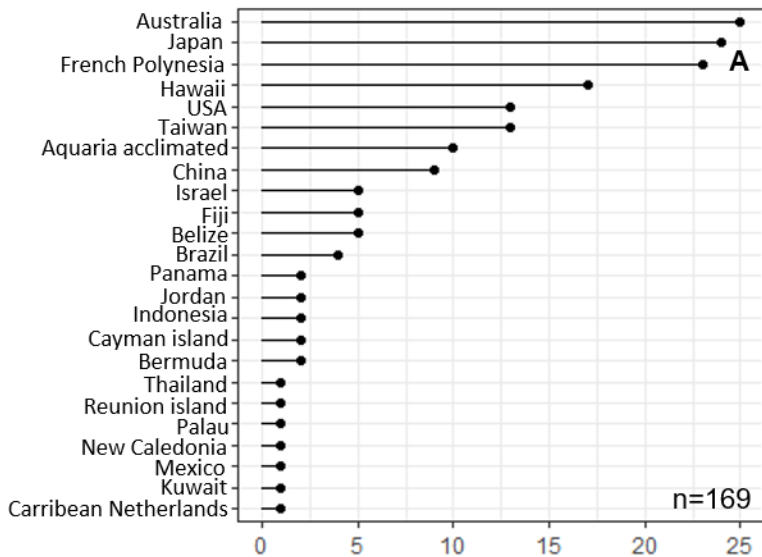
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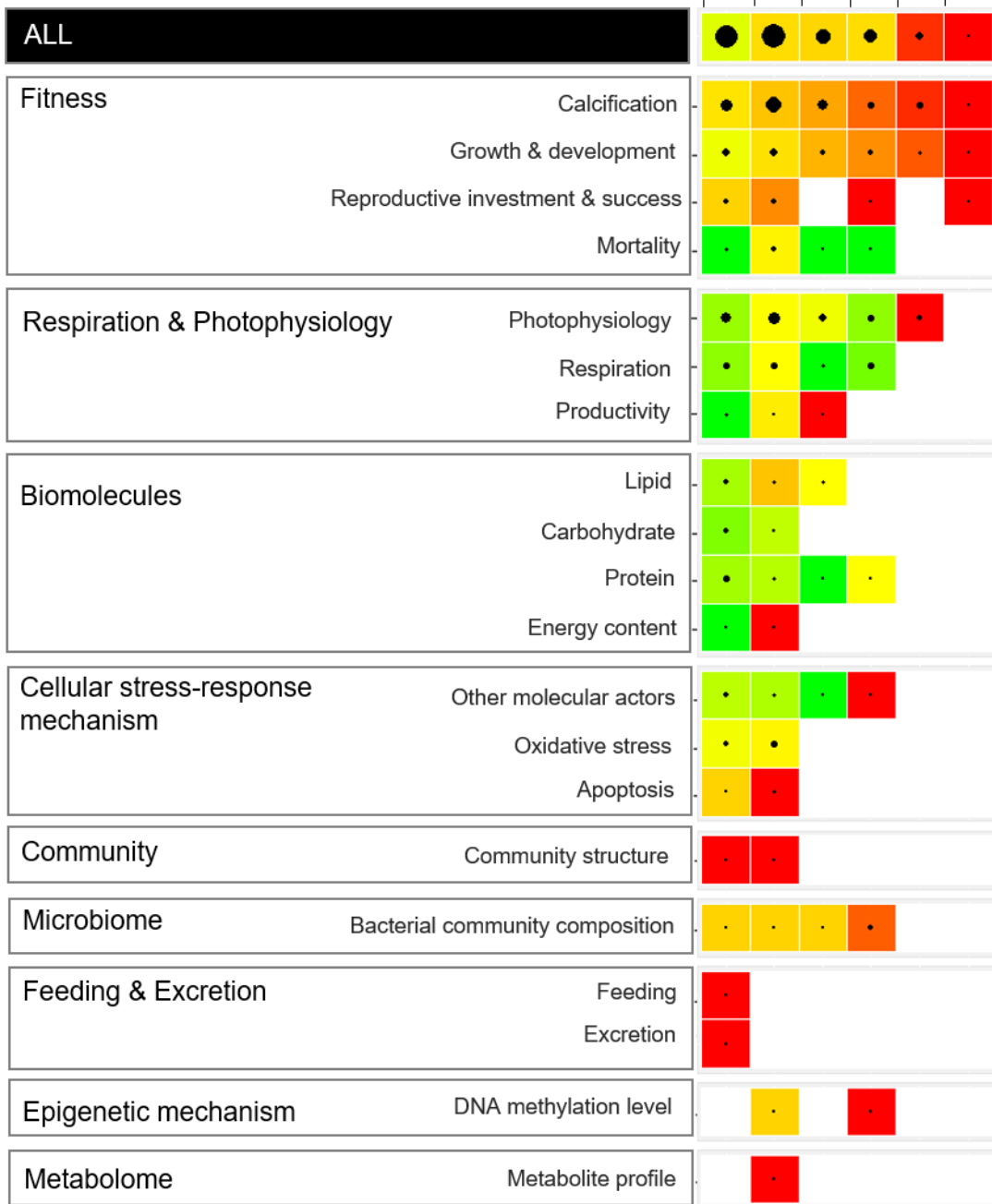
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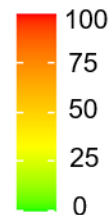


Proportion of experiment (%)

pH 8.0 7.8 7.6 7.4 7.2 7.0



Affected endpoints (%)



Number of endpoints

