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**Diversity and function of fluorescent molecules in marine organisms**

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14 **Abstract**

15 Fluorescence in marine organisms has mainly been studied in corals but is found in many different  
16 phyla such as Annelida, Crustacea, Mollusca, and Chordata. While many fluorescent proteins and  
17 molecules have been identified, very little information is available about the biological function of  
18 fluorescence. In this review, we focus on describing the occurrence of fluorescence in marine animals  
19 and the behavioural and physiological functions of fluorescent molecules based on experimental  
20 approaches. These biological functions of fluorescence range from prey and symbiont attraction,  
21 photoprotection, photoenhancement, stress mitigation, mimicry, aposematism to inter- and  
22 intraspecific communication. We provide a comprehensive list of marine taxa that utilize fluorescence,  
23 including demonstrated effects on behavioural or physiological responses. On one hand, this review  
24 describes the numerous known functions of fluorescence in anthozoans and their underlying  
25 molecular mechanisms in detail. On the other hand, it highlights which marine taxa should be further  
26 studied regarding their functions of fluorescence. We suggest that an increase in research effort in this  
27 field could contribute to understanding the capacity of marine organisms in mitigating negative effects  
28 of climate change.

29

30 *Keywords:* Fluorescent proteins, marine biodiversity, corals, functions of fluorescence, marine ecology,  
31 GFP

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73

74 **I. Introduction**

75 Light in the marine environment is an important ecological factor and becomes crucial under visually  
76 restricted conditions. Adaptations to these conditions include the emission of light by organisms  
77 themselves (bioluminescence) and/or the absorption and subsequent emission of lower energy light  
78 (i.e. a shift from shorter to longer wavelengths). This process is called fluorescence. Fluorescent light  
79 is emitted by molecules such as porphyrins, chlorophyll, phycobiliproteins, chitin or GFP-like  
80 fluorescent proteins (FPs), which are excited by sunlight during the day or moonlight during the night  
81 (García-Plazaola *et al.*, 2015; Macel *et al.*, 2020). More than 300 different fluorescent molecules have  
82 been described in different phyla (Figure 1, Appendix I). While fluorescence of many biological  
83 molecules is just an intrinsic physical property of the molecule itself (NADH, tryptophane, or  
84 chlorophyll) and has most likely no biological functions, various fluorescent molecules including their

85 cellular structures have evolved during evolution to adapt to specific environments and behaviours  
86 (Table 1) (Marshall & Johnsen, 2017; Mazel, 2017). Suggested functions of these molecules include  
87 attraction of prey or symbionts, photoprotection, photoenhancement, light harvesting, stress  
88 mitigation, mimicry, aposematism, and communication (Figure 2) (Salih, 2000; Mazel *et al.*, 2004;  
89 Michiels *et al.*, 2008; Palmer, Modi & Mydlarz, 2009a; Gittins *et al.*, 2015; Haddock & Dunn, 2015;  
90 Macel *et al.*, 2020). In the following sections, we will review the different functions and explain the  
91 underlying fluorescent systems across various taxa.

92

## 93 **II. Functions of fluorescence**

### 94 (1) Nutritional function - Prey attraction

#### 95 ((a)) Cnidaria – Medusozoa (jellyfish) and Anthozoa (corals & sea anemones)

96 The first discovered FP, the green fluorescent protein (GFP) was isolated from the cnidarian jellyfish  
97 *Aequorea victoria*. Here, GFP acts as an acceptor/antenna molecule for the luciferase Aequorin  
98 (Shimomura, Johnson & Saiga, 1962; Shimomura, 2006). In this bioluminescent-fluorescent system GFP  
99 shifts the blue light produced by Aequorin to longer wavelengths, i.e. green light (Eremeeva, Van Berkel  
100 & Vysotski, 2016). Various bioluminescent-fluorescent systems have been developed in jellyfish  
101 (Fourrage *et al.*, 2014). In *Clytia hemispherica*, for example, the light emitting GFPs are located in  
102 tentacle bulbs and tentacles ideally placed to lure prey (Fourrage *et al.*, 2014). It has been  
103 demonstrated that fluorescent light is used for prey attraction in the hydrozoan *Olindias formosa*. It  
104 expresses dfGFP that has a 33 % homology with *A. victoria* GFP (Shinoda *et al.*, 2018). Blue light  
105 illumination of the green fluorescence in the tentacles attracts juvenile rockfish in laboratory settings,  
106 while white or yellow light has no effect. The attraction of juvenile rockfish in the laboratory was  
107 comparable to in situ observations of benthic fish species (i.e. *Enchelyurus* spp., *Synodus jaculum* &  
108 *Mulloidichthys* sp) that chased green light, resembling fluorescence-like stimuli (Haddock & Dunn,  
109 2015). Whether the fish reacted to green light or just the movement of light was not addressed. The  
110 authors hypothesize that the use of fluorescent lures might be a common mechanism to attract prey

111 in non-visual and visual organisms (Haddock & Dunn, 2015). For example, the non-visual cnidarian  
112 predator, the siphonophore *Rhizophysa eysenhardti*, has green fluorescent spots on the tips of the  
113 tentacles and along the gastrozooids, which potentially aid in prey capturing of larval fish (Purcell,  
114 1981; Haddock & Dunn, 2015). Similar strategies were suggested for other siphonophores:  
115 *Resomia ornicephal*, *Diphyes dispar* and *Rosacea plicata* to capture euphausiid shrimp (Haddock &  
116 Dunn, 2015).

117 Mesophotic corals also use fluorescence to attract prey. For example, the green fluorescent morph of  
118 the *Fimbriaphyllia (Euphyllia) paradivisa* shows a higher predation rate than the orange morph (Ben-  
119 Zvi *et al.*, 2022). This correlates with the phenomenon that zooplankton show a positive phototaxis to  
120 green fluorescence. The combination of the bright green fluorescence against dark background and  
121 potentially fluorescent patterns highlighting tentacles and/or the oral part of a polyp further suggest  
122 a role in prey attraction in corals and an increase in nutrition supply (Ben-Zvi *et al.*, 2022).

123 In benthic cnidarians that are neither bioluminescent, nor have algal symbionts (Haddock & Dunn,  
124 2015), green fluorescence is found in tentacles of hydroids of the genus *Cytaeis* (Prudkovsky *et al.*,  
125 2016), in the deep-sea anemone *Cribrinopsis japonica* (Actinaria;  $\lambda_{em}$  510 nm) (Tsutsui, Hatada &  
126 Tsuruwaka, 2014; Tsutsui *et al.*, 2016) and in cerianthid tube anemones (*Cerianthus*) (Haddock & Dunn,  
127 2015) suggesting a role for prey attraction. *Cytaeis* polyps live on shells of the nocturnal gastropod  
128 *Nassarius margaritifer* in the Red Sea (Egypt) and emit green fluorescent light ( $\lambda_{em}$  518 nm) when  
129 illuminated by moonlight or during sunrise and sunset (Prudkovsky *et al.*, 2016).

130

131 ((b)) Chordata - Cephalochordata – Branchiostomatidae (lancelets)

132 Cephalochordates are the only deuterostomes that express endogenous GFP (Deheyn *et al.*, 2007).  
133 Deuterostomian GFP was first found in three species of lancelets (Deheyn *et al.*, 2007) and GFP-  
134 encoding genes most likely existed in an ancestral cephalochordate, as these genes occur across  
135 distantly related genera of amphioxus (Yue *et al.*, 2016). With 16 different identified GFP genes, the  
136 amphioxus *Branchiostoma floridae*, is the species with the highest diversity of GFPs known so far

137 (Bomati, Manning & Deheyn, 2009; Bomati *et al.*, 2014) and red fluorescence is known from the  
138 congeneric *B. lanceolatum* (Pletnev *et al.*, 2013). In *B. floridae*, the various GFPs exhibit different  
139 fluorescence intensities, extinction coefficients and absorption profiles, which makes the species an  
140 interesting organism for studying the function and evolution of GFP (Bomati *et al.*, 2014). In adult  
141 lancelets GFP is concentrated in the oral cirri implicating its role in planktonic prey attraction (Deheyn  
142 *et al.*, 2007; Yue *et al.*, 2016).

143

144 ((c)) Chordata - Vertebrata – Osteichthyes (fish)

145 In marine fish, the brightness of fluorescence can be regulated, suggesting that fluorescent signals are  
146 used to attract and detect prey and/or sexual partners. The black-faced blenny *Tripterygion delaisi*, for  
147 example, regulates the brightness of the red-fluorescent iris by dispersal and aggregation of black-  
148 pigmented melanosomes within melanophores. These melanophores encase fluorescent iridophores  
149 on the anterior side of the iris. The movement of the melanosomes leads to the covering or revealing  
150 of red fluorescent iridophores, which is most likely controlled neuronally (Wucherer & Michiels, 2014).  
151 That the change in fluorescent brightness is used for prey attraction or localization is supported by the  
152 fact that fluorescence increases during foraging and decreases during inactivity or stress (Wucherer &  
153 Michiels, 2014). Possessing red fluorescent irises is common in small predatory fishes (Anthes *et al.*,  
154 2016).

155

156 (2) Nutritional function - Symbiont attraction

157 ((a)) Cnidaria – Anthozoa (corals)

158 *Echinophyllia aspera* (Scleractinia) that fluoresce bright green ( $\lambda_{em}$  492 and 505 nm) under blue light,  
159 attract their symbiotic dinoflagellates of the genus *Symbiodinium* under laboratory conditions (Aihara  
160 *et al.*, 2019). The dinoflagellate shows maximum positive phototactic responses towards 510 nm  
161 (green) and 680 nm (red) light and negative phototaxis towards strong purple blue ( $\lambda_{em}$  380-475 nm)  
162 light. These experiments suggest that the symbiont avoids light-induced photodamage of the

163 photosynthetic machinery and is maximally attracted by green fluorescence. The attraction hypothesis  
164 between corals and symbionts is also supported by the fact that GFP fluorescence is higher in larvae  
165 and juvenile coral polyps than in adult colonies and in bleached than in non-bleached corals (Kenkel *et*  
166 *al.*, 2011; Ricaurte *et al.*, 2016; Aihara *et al.*, 2019). Strong fluorescence in bleached corals may help to  
167 attract new symbiont communities for improving survival strategies (Baker, 2001). This has also been  
168 suggested for colourful coral bleaching, where upregulated FPs may improve recolonization of the  
169 symbionts (Bollati *et al.*, 2020).

170

171 ((b)) Mollusca – Gastropoda – Heterobranchia (slugs)

172 Several Heterobranchia also live in symbiosis with red fluorescent dinoflagellates. Slugs feed on algae  
173 or soft corals and store the dinoflagellates (zooxanthellae, *Symbiodinium*) in their cerata (Rudman,  
174 1981; Hirano & Ito, 1998). Species known to have dinoflagellate symbionts are in the families  
175 Facelinidae, Tethydidae, Aeolidiidae, Trinchesiidae and Arminidae (Burghardt & Wägele, 2014; Avila,  
176 Ballersteeros, Slattery, 1998; Burghardt, Stemmer & Wägele, 2008). *Symbiodinium* provides a cryptic  
177 appearance and supplies metabolites that help the slug survive periods of food shortage (Burghardt *et*  
178 *al.*, 2008; Burghardt & Wägele, 2014).

179

180 (3) Defensive or regulatory function - Photoprotection

181 FP mediated photoprotection involves light absorption, screen scattering, and antioxidation (Salih *et*  
182 *al.*, 2000; Gilmore *et al.*, 2003; Mazel *et al.*, 2003a; Bou-Abdallah, Chasteen & Lesser, 2006; Palmer *et*  
183 *al.*, 2009a). FP mediated photoprotection has mainly been described and investigated in cnidarians  
184 (Scleractinia and Actinaria) and has been suggested in Cephalochordata (Yue *et al.* 2016) and  
185 Polychaeta (Rodrigo *et al.*, 2022).

186



187 ((a)) Cnidaria – Anthozoa (corals)

188 In cnidarians the light environment plays a central role in the symbiosis between a heterotrophic host  
189 and its autotroph endosymbiont, e.g. the symbiosis between scleractinian corals and dinoflagellates  
190 (*Symbiodinium*) (Roth, Fan & Deheyn, 2013). Green fluorescence has been shown to be positively  
191 correlated with the photobiology of the symbionts and with coral growth (Roth & Deheyn, 2013).  
192 *Symbiodinium* is involved in the photosynthetic fixation of carbon, which is used as food supply and  
193 Ca<sup>2+</sup> carbonate resource in skeleton growth by the coral. In return, the coral provides ammonium as  
194 nutrient for the dinoflagellates. For a vital symbiosis it is important to reduce photodamage, while  
195 balancing light harvesting for photosynthesis is maximized (Muscatine, 1990). Corals living in shallow  
196 reefs benefit from physiological systems that absorb high-intensity sunlight and emit at longer  
197 wavelength to reduce the production of reactive oxygen species (Bou-Abdallah *et al.*, 2006; Palmer *et al.*,  
198 2009a).

199 Reactive oxygen species can cause damage in the coral tissue, while high-intensity light can cause  
200 photoinhibition of photosynthesis by dinoflagellates (Hoegh-Guldberg & Jones, 1999; Gorbunov *et al.*,  
201 2001). Therefore, mechanisms reducing oxidative stress are vital for the coral. Coral FPs have been  
202 shown to quench oxygen radicals most likely to prevent or reduce oxidative stress in coral tissue (Bou-  
203 Abdallah *et al.*, 2006; Palmer *et al.*, 2009a). The potential role of FPs as oxygen radical quenchers in a  
204 coral stress response may explain the variation in the temporal and spatial localization of the FPs as an  
205 adaptive mechanism (Dove, Hoegh-Guldberg & Ranganathan, 2001; Palmer, Roth & Gates, 2009b).

206 Chromoproteins (CP) and FPs are expressed in the ectoderm, facing the external environment and  
207 shielding the zooxanthellae in the endoderm. Thus, light that reaches the zooxanthellae through the  
208 ectoderm is shifted to a longer wavelength, reducing harmful, high-energy radiation for the symbionts  
209 (Salih *et al.*, 2000; Mazel *et al.*, 2003b; Oswald *et al.*, 2007). That CPs play an important role in  
210 mitigating light stress in shallow water by absorbing light has been demonstrated with optical  
211 microsensor measurements in symbiotic reef building corals. Here, the upregulation of pink CPs during

212 bleaching leads to a reduction of orange light within the tissue by 10 to 20% compared to low CP-  
213 expressing tissue (Bollati *et al.*, 2022).

214 An optical feedback loop involving dinoflagellate symbionts and corals has been proposed to induce  
215 the expression of FPs during colorful bleaching, a world wide reoccurring phenomenon in coral reefs.  
216 The upregulation of the photoprotective molecules is driven by increased internal light fluxes after the  
217 loss of the symbionts. The upregulation of FPs in bleached coral tissue has been suggested to be  
218 important for the recolonization of reef-building corals by symbionts (Bollati *et al.*, 2022).

219 Different colour morphs of FPs are known from various coral species (Alieva *et al.*, 2008; Meyers, Porter  
220 & Wares, 2013; Eyal *et al.*, 2015; Gittins *et al.*, 2015). Fluorescent proteins often exist as multicopy  
221 genes, contributing to high levels of FP production and allowing adjustment of transcript levels in  
222 response to the light environment. Thus, transcription of multicopy genes in reef corals allows for fast  
223 changes in the colour combinations within an FP population, most likely to adapt to environmental  
224 changes in the habitat. This has been demonstrated for the red amilFP597 from *Acropora millepora* in  
225 which transcript levels increase with light intensity and vary among colour morphs (Gittins *et al.*, 2015).

226 In addition, Satoh *et al.* (2021) show that different colour morphs of *Acropora tenuis* with different  
227 expression of fluorescent proteins could play a role in physiological response of environmental stress  
228 (Satoh *et al.*, 2021). These findings suggest that colour polymorphism in reef corals depends on  
229 environmental factors. It may contribute to the reduction in photodamage and to diversification and  
230 optimization of physiological responses (Shagin *et al.*, 2004; Meyers *et al.*, 2013; Gittins *et al.*, 2015).

231 High GFP levels have also been suggested to provide protection of RNA from oxidative damage by UV-  
232 light. An upregulation of GFP could help avert damage by scattering UV-light (Grinblat *et al.*, 2018).

233 Green fluorescent protein is not only expressed in adult coral colonies but also in planula larvae,  
234 particularly in regions undergoing high cell differentiation with high transcription levels (D'Angelo *et*  
235 *al.*, 2012). High expression of FPs has also been observed in injured and regenerating growth areas of  
236 corals, which also reveal high transcription and DNA synthesis (D'Angelo *et al.*, 2008, 2012; Grinblat *et*

237 *al.*, 2018). In cephalochordates, GFP is upregulated in oocytes and spawned eggs (Deheyn *et al.*, 2007;  
238 Yue *et al.*, 2016), suggesting a similar role in photoprotection of RNA/DNA as in coral larvae.  
239 Another dinoflagellate-host system where photoprotection is discussed as function of FPs occurs in  
240 actinarians. At least five different morphs of the actinarian *Anemonia viridis* (*var. rustica*, *smaragdina*,  
241 *rufescens*, *viridis* and *vulgaris*) as well as *Condylactis gigantea* and *Heteractis crispa* express FPs and  
242 non-fluorescent pink-red and purple-blue CPs in the tips of their tentacles (described for  
243 *Anemonia viridis var. smaragdina*, *rufescens* and *viridis*) (Wiedenmann, Röcker & Funke, 1999;  
244 Wiedenmann *et al.*, 2000; Lukyanov *et al.*, 2000; Labas *et al.*, 2002; Leutenegger *et al.*, 2007b; Mallien  
245 *et al.*, 2018).

246 In contrast to the studies above, it has also been suggested that FPs may not improve photoprotection  
247 and photosynthesis in mesophotic corals (Eyal *et al.*, 2015; Ben-Zvi, Eyal & Loya, 2019). Studies on  
248 different fluorescent colour morphs of the mesophotic coral *Fimbriaphyllia* (*Euphyllia*) *paradivisa*  
249 revealed no differences in enhancement of photoprotection and photosynthesis, when exposed to  
250 high-intensity photosynthetic active radiation or UV light (Ben-Zvi *et al.*, 2019). Examining the spectra  
251 and kinetics of FP populations and chlorophyll a (Chl a) from colour morphs of *Acropora spp.* or  
252 *Plesiastrea versipora* and their corresponding zooxanthellae revealed energy transfer between FPs  
253 within the FP population but not between the FP and the Chl a. The experiments contradict the  
254 function of FPs in photoprotection in the respective coral-symbiont system (Gilmore *et al.*, 2003).

255

256 ((b)) Annelida (segmented worms)

257 The intertidal worm *Eulalia sp.* secretes a mucus containing a proteinaceous fluorescent complex  
258 including the fluorescent protein ubiquitin and antioxidant protein peroxiredoxin. This mucus/complex  
259 when excited by UV light emits light in the blue-green spectrum, where intensity of light emission is  
260 dependent on the redox state. The authors suggest an antioxidant function where the mucus  
261 containing the fluorescent complex protect the worm against high-energy radiation during foraging at  
262 daylight (Rodrigo *et al.*, 2022).

263

264 ((c)) Chordata - Cephalochordata – Branchiostomatidae (lancelets)

265 Besides its presence in cirri of adult lancelets, in *Asymmetron lucayanum* fluorescent GFP is also  
266 present in oocytes and spawned eggs of where it is suggested to fulfil photoprotective functions (Yue  
267 et al., 2016).

268

269 (3) Photoenhancement

270 ((a)) Porifera (sponges)

271 Fluorescence mediated photoenhancement is discussed in Porifera (Read, Davidson & Twarog, 1968).

272 In the mediterranean sponge *Aaptos aaptos* ultraviolet excited fluorescence occurs in the  
273 archaeocytes (amoebocytes) (Liaci, 1962). The yellow tube sponge *Aplysina fistularis* has a green-  
274 yellow colour at a depth of 40 m due to a fluorescent pigment that has been identified in the lamellar  
275 portion of the sponge fibres. In addition, *Halisarca dujardini*, an intertidal, non-tropical, spiculeless  
276 sponge, contains fluorochromes similar to those in *Aplysina fistularis* (Read et al., 1968).

277

278 ((b)) Cnidaria – Anthozoa (corals)

279 The occurrence of colour polymorphism in reef corals supports the hypothesis that FPs may enhance  
280 the light environment in the mesophotic reef, which is characterized by areas of low light penetration.

281 Green or red light reaches vaster in the coral tissue to the symbionts and complements the  
282 predominantly blue light spectrum in deeper water layers (Schlichter, Fricke & Weber, 1986; Salih et  
283 al., 2000, 2006; Eyal et al., 2015; Smith et al., 2017). Photoconvertible red fluorescent proteins can

284 contribute to 50% of orange/red light, that is available to the symbionts at mesophotic depths.

285 Measurements with microsensors placed directly in the coral tissue showed that red light penetrates

286 deeper into the tissue than green light and could be available for photosynthetic symbionts located in

287 deeper layers (Bollati et al., 2022).

288 It was shown that fluorescence is shifted to longer wavelengths of light (orange and red) in deeper  
289 reefs, while green fluorescence is more common in shallow reefs. Interestingly, yellow fluorescence  
290 has only been observed in mesophotic reef corals so far (Eyal *et al.*, 2015). Yellow FPs (e.g. zFP538 from  
291 *Zoanthus sp.* or ccalYFP1 from *Corynactis californica*) have also been found in non scleractinian corals  
292 in shallow reefs (Matz *et al.*, 1999; Schnitzler *et al.*, 2008). Notably, FPs found in coral species from  
293 lower light habitats are biochemically, photophysically and functionally distinct to FPs from coral  
294 species dominating in high-light habitats (Salih *et al.*, 2000; Alieva *et al.*, 2008; Eyal *et al.*, 2015; Roth  
295 *et al.*, 2015; Smith *et al.*, 2017; Bollati *et al.*, 2020).

296

297 ((c)) Annelida (segmented worms)

298 Photoenhancement has also been suggested for annelids and involves a shift of bioluminescent light  
299 (Hastings, 1996). In the putative light organs of *Tomopteris spp.* (pelagic annelids) a fluorescent signal  
300 is correlated with the emission of bioluminescent light (Gouveneaux *et al.*, 2017). It has been proposed  
301 that the fluorescence is most likely produced by a breakdown product of the chemiluminescent  
302 reaction, which was first demonstrated in the polynoid worm *Acholoe astericola* (Bassot & Bilbaut,  
303 1977; Bassot & Nicolas, 1995; Gouveneaux *et al.*, 2017). *Tomopteris spp.* that exhibit a unique, yellow-  
304 orange luminescence in their parapodia, a quinone derivative (anthraquinone; Aloe-emodin) has been  
305 isolated and is suggested to be involved in bioluminescent light emission. In the tubeworm  
306 *Chaetopterus variopedatus* blue and green luminescence have been described in the mucus of the  
307 worm (Deheyn *et al.*, 2013; Branchini *et al.*, 2014). The green fluorescence is most likely emitted by  
308 riboflavin ( $\lambda_{em}$  525 nm) or a related derivative, which has been isolated from the mucus (Branchini *et*  
309 *al.*, 2014). Interestingly, riboflavin cannot be synthesized by tubeworms themselves and needs to be  
310 acquired from an external source. Therefore, it has been proposed that annelids may acquire  
311 fluorescent molecules with their nutrition (Fox *et al.*, 1952). In addition, intense blue fluorescence after  
312 emission of bioluminescent light was detected in the mucus of the fireworm *Odontosyllis phosphorea*,  
313 suggesting that an oxidized product resulting from light production mediates fluorescence (Deheyn &

314 Latz, 2009; De Meulenaere, Puzanghera & Deheyn, 2020). While these studies suggest that  
315 fluorescence increases the bioluminescent spectra, the ecological implications of these  
316 bioluminescence-fluorescence systems need to be further explored.

317

318 (4) Stress mitigation and regulatory mechanisms

319 ((a)) Cnidaria – Anthozoa (corals)

320 Fluorescence can be found very early during coral development within eggs, embryos, larvae and  
321 polyps (Hirose, Kinzie & Hidaka, 2000; Leutenegger *et al.*, 2007a; Roth *et al.*, 2007; D'Angelo *et al.*,  
322 2008). In fact, fluorescence can be used to detect coral recruits (Piniak *et al.*, 2005; Baird, Salih &  
323 Trevor-Jones, 2006). Larvae of *Acropora millepora* can express red and green fluorescent proteins, with  
324 no correlation between fluorescent colour of the parent colony to the larvae (Kenkel *et al.*, 2011).  
325 Interestingly, larvae with red fluorescence have lower colonization success than those with green  
326 fluorescence and heat stress reduces the red fluorescence (Kenkel *et al.*, 2011). In *Seriatopora hystrix*,  
327 a developmental change from two green (larvae) to one cyan (adult) fluorescing protein occurs. In the  
328 larvae, two GFPs co-exist, with the peak emission of one GFP (499 nm) overlapping with the peak  
329 excitation of the second GFP (504 nm), which may allow energy transfer if the GFPs are in close  
330 proximity (Roth, Fan & Deheyn, 2013). Larvae showed large ranges in GFP fluorescence, dinoflagellate  
331 abundance and size, suggesting that coral larvae have the physiological capacity to adapt to many  
332 different light microhabitats ( Roth, Fan & Deheyn, 2013).

333 Red fluorescence in larvae (e.g. *Acropora millepora*) has been associated with a reduction in sensitivity  
334 to settlement cues, suggesting a function in long-range dispersal (Kenkel *et al.*, 2011). In addition, the  
335 red colour morphs reveal a reduced expression of genes involved in cell division, accompanied by an  
336 upregulation of ribosomes and stress-tolerance involving genes important for deactivation of reactive  
337 oxygen species. This suggest that red colour morphs have increased antioxidant protection which could  
338 be beneficial for long-term survival at the water surface during sunlight exposure (Strader, Aglyamova  
339 & Matz, 2016). Interestingly, the change in gene expression patterns in the red colour morph

340 resembles changes in gene expression of the long-lived dauer stage of *Caenorhabditis elegans*,  
341 suggesting a role of FPs in the regulation of diapause-like states in coral larvae (Strader *et al.*, 2016).

342

343 (5) Bilirubin binding to reduce cellular, oxidative stress

344 ((a)) Chordata - Vertebrata - Osteichthyes (fish)

345 Green and red fluorescent patterns have been observed in moray eels (e.g. Muraenidae) (Guarnaccia  
346 *et al.*, 2021), false morays (Chlopsidae) (Sparks *et al.*, 2014) and freshwater eels (Anguillidae) (Hayashi  
347 & Toda, 2009; Kumagai *et al.*, 2013). The FPs are believed to have regulatory functions in stress  
348 mitigation (Funahashi *et al.*, 2016). Japanese freshwater eels *Anguilla japonica* express fluorescent  
349 green proteins of a different family (UnaG) (Kumagai *et al.*, 2013). UnaG belongs to the family of fatty  
350 acid binding proteins. Green fluorescence is mediated by noncovalent binding of an endogenous ligand  
351 bilirubin, a membrane-permeable heme metabolite in a non-conjugated form (Kumagai *et al.*, 2013).  
352 The entire bilirubin molecule is closely coordinated within the holoprotein complex, located deep in  
353 the barrel structure. UnaG emits green fluorescence independent of oxygen (Kumagai *et al.*, 2013). In  
354 young *A. japonica* UnaG is expressed in the white muscles, particularly in small fibres. These muscle  
355 fibres represent the late developing fibres during muscle growth, and it is assumed that the expression  
356 of the FP is attenuated with the onset of juvenile muscle growth. The long-distance migration cycle of  
357 the eel from freshwater to the Philippine Sea puts considerable demands on the metabolic physiology  
358 of the skeletal muscles (Kumagai *et al.*, 2013). Due to the non-covalent binding of bilirubin to the  
359 fluorescent protein, it has been suggested that the accumulation of this metabolite is regulated, which  
360 could constitute benefits for the permanent strain on the muscles during migration. Bilirubin  
361 molecules, whose degradation as ligands has been found to be significantly slowed down, potentially  
362 provide antioxidant activities, while fatty acid binding proteins are involved in metabolism and the  
363 homeostasis of oxidative stress (Kumagai *et al.*, 2013). Accordingly, the fluorescent holoprotein in the  
364 eel may contribute to muscle metabolism and to the reduction of cellular, oxidative stress that arises  
365 during long-distance migration (Kumagai *et al.*, 2013; Funahashi *et al.*, 2016). Due to the migration

366 cycle of the genus *Anguilla*, it has been suggested that the eel blood plasma containing biliverdin  
367 (abundant form of heme metabolite) is enzymatically reduced in skeletal muscle cells to bilirubin. It  
368 binds to the protein, expresses green fluorescence and functions as a complex, like a scavenger of  
369 hydrogen peroxide and/or hydroxyl radical. After the cells are exposed to oxidative stress during the  
370 long-distance migration, bilirubin is oxidized in biliverdin and transported to blood circulation  
371 (Funahashi *et al.*, 2016). Other members of the bilirubin binding GFPs have also been identified in two  
372 chlopsid eels *Kaupichthys hyoprroides* and *Kaupichthys n. sp.* (Chlopsid FP I and II) and in the moray  
373 eel *Gymnothorax zonipectis* (GymFP) (Gruber *et al.*, 2015; Guarnaccia *et al.*, 2021). Since most moray  
374 eels do not show fluorescence in a comparable habitat and do not migrate for long-distances the  
375 ecological and physiological function of GymFP should be investigated further.

376

377 (6) Immune response

378 ((a)) Cnidaria – Anthozoa (corals)

379 In corals, FPs have also been suggested to play a role in the immune response. The immune response  
380 in corals is mediated by pathogen recognition receptors that recognize microbes and activate several  
381 downstream signalling pathways. During infection with the trematode *Podocotyloides stenometre*, the  
382 expression of green FPs changes towards red FPs in trematodiasis-compromised tissue (Palmer *et al.*,  
383 2009b). Pigmentation at alternatively compromised tissue has been described in other corals (Willis,  
384 Page & Dinsdale, 2004; Bongiorno & Rinkevich, 2005; Ravindran & Raghukumar, 2006a, 2006b; Palmer,  
385 Mydlarz & Willis, 2008). The increased expression of CPs and FPs in immunocompromised coral tissues  
386 suggests a role in coral immunity (Palmer *et al.*, 2008, 2009b; Chudakov *et al.*, 2010).

387

388 ((b)) Chordata - Vertebrata - Chondrichthyes – (sharks)

389 Green fluorescence is also found in the skin of sharks. The swell shark *Cephaloscyllium ventriosum* from  
390 the eastern Pacific and the chain catshark *Scyliorhinus retifer* from the western Atlantic reveal a high-  
391 intensity green fluorescence in the lighter colored areas of the skin (catshark) and the dark spots of



392 the skins (swell shark) (Park *et al.*, 2019). This fluorescence is produced by brominated tryptophan-  
393 kynurenine metabolites. In phosphate buffered saline these compounds reveal excitation peaks in the  
394 UV-blue range ( $\lambda_{ex}$  360-438 nm) and emission peaks in the blue-green range ( $\lambda_{em}$  400-507 nm) (Park *et*  
395 *al.*, 2019). The authors suggest that the fluorescent molecules may play a role in immune response,  
396 since kynurenine metabolism regulates host-microbiome signaling and immune response in humans.

397

398 (7) pH regulation and skeleton deposition

399 ((a)) Cnidaria - Medusozoa (jellyfish) and Anthozoa (corals)

400 Wildtype (wt)-GFP from *A. victoria* might be involved in the acidification of proteins or organelles as it  
401 may function as a light-driven non-membrane-bound proton pump (Agmon, 2005, 2007; Shinobu &  
402 Agmon, 2017). Thus, FPs might be involved in regulating the deposition of the calcium carbonate  
403 skeleton in corals, a strongly pH-dependent process. Although most coral GFPs have a permanent  
404 anionic chromophore (Alieva *et al.*, 2008) and, therefore, do not exhibit the GFP-like photocycle from  
405 *A. victoria*, their accumulation in the calcioblastic ectoderm supports the hypothesis. An upregulation  
406 of FP expression is also induced by acidification. This has been shown in *Stylophora pistillata*, where a  
407 non-stressful decrease in pH results in increased fluorescence. Here, the increase in fluorescence  
408 correlates with an increase in total protein concentration (Krief *et al.*, 2010; Grinblat *et al.*, 2018).

409

410 (8) Light-driven electron transfer

411 Various phyla. Another possible function of FPs is their active role in light-driven electron transfer  
412 (Bogdanov *et al.*, 2009). It has been observed that under anaerobic conditions GFP undergoes  
413 photoconversion into a red fluorescent state (Elowitz *et al.*, 1997), a process called “redding”  
414 (Bogdanov *et al.*, 2009). During this process, GFP of diverse origin can act as light-induced electron  
415 donor in photochemical reactions with electron acceptors such as cytochrome c, FMN, FAD or NAD+.  
416 The green to red photoconversion can also be induced by 488 nm light irradiation in vivo in  
417 *Zoanthus sp.* Light-induced electron transfer seems to be a common feature of FPs of different phyla

418 (e.g. jellyfish, anthozoans, copepods and lancelets) (Chudakov *et al.*, 2010; Povarova *et al.*, 2017) and  
419 is dependent on the chromophore. The electron transfer only takes place in natural Tyr66-based  
420 chromophores, while mutants with artificial Trp66- or His66-based chromophores are inactive. This  
421 suggests a high evolutionary pressure if FP-mediated redox reactions are involved in specific cellular  
422 processes. This hypothesis has been challenged because the light-induced transfer of two electrons  
423 from a FP to an oxidant such as NAD<sup>+</sup> leads to an irreversible inactivation of the FP. However, sensory  
424 function might still be a possible explanation, since it does not require excessive electron transfer  
425 (Chudakov *et al.*, 2010; Povarova *et al.*, 2017).

426

#### 427 (9) Mimicry and aposematism

428 Fluorescence in marine environments can be perceived by other species with appropriate  
429 photoreceptors or filters (like intraocular filters) such as fish, copepods, mantis shrimps and  
430 dinoflagellates (Sparks *et al.*, 2014). It has been suggested that these fluorescent signals may have an  
431 aposematic function to warn or repel predators and to hide symbionts from herbivorous fish  
432 (Chudakov *et al.*, 2010).

433

#### 434 ((a)) Mollusca – Gastropoda – Heterobranchia (slugs)

435 Non-endosymbiont mediated fluorescence in Heterobranchia has also been described (Betti,  
436 Bavestrello & Cattaneo-Vietti, 2021). The authors suggest that the common occurrence of green  
437 fluorescence in the cerata of Cladiobranchia could originate from ingested food, which is partly stored  
438 in the cnidosacs, that enhance the aposematic coloration. Moreover Betti *et al.* (2021) found  
439 fluorescence in the dorsal rim of the heterobranchs genus *Diaphorodoris spp.*. In behavioral assays,  
440 the dorsal rim of a related Heterobranchia species *Goniobranchus splendidus* has been demonstrated  
441 to function as aposematic signal. Here, a potential fish predator recognized the yellow rim as a warning  
442 signal (Winters *et al.*, 2017). Therefore, it seems likely, that the fluorescence in the genus  
443 *Diaphorodoris* is involved in aposematism as well (Betti *et al.*, 2021).

444

445 ((b)) Chordata - Vertebrata – Osteichthyes (fish)

446 Fluorescence shows a high prevalence in crypto-benthic fish species and has been presumed to  
447 facilitate background matching (Sparks *et al.*, 2014; Brauwer *et al.*, 2018). A first study highlighting this  
448 correlation showed that the red fluorescence of scorpionfish was influenced by background luminance  
449 (John, Santon & Michiels, 2023). Furthermore, the red fluorescent scorpionfish  
450 (*Scorpaenopsis papuensis*) perch on red fluorescing algae, while the green fluorescent two-lined  
451 monocle bream (*Scolopsis bilineata*) can be found near green fluorescing coral heads of *Acropora*  
452 (Sparks *et al.*, 2014). In general, fluorescence of a patchy distribution across the body can be found  
453 more often in sit-and-wait predators than in mobile fish (Anthes *et al.*, 2016).

454

455 (10) Intraspecific communication

456 Fluorescence can play a role in recognition of conspecifics, warning and threatening, mate choice and  
457 mating behaviour (Herring, 1988; Mazel *et al.*, 2004; Shagin *et al.*, 2004).

458

459 ((a)) Mollusca – Cephalopods (squids)

460 In cephalopods, fluorescent signals may play a role in intraspecific communication. The squids  
461 *Allotheutis subulata* and *Loligo vulgaris* have fluorescent “eyespot”. These brightly coloured eyespots  
462 consist of two layers - the lower iridescent layer and a fluorescent layer on top (Mäthger & Denton,  
463 2001).

464

465 ((b)) Arthropoda – Copepoda

466 In copepods FPs have been isolated and characterized from *Chiridius poppei* (CpYGFP) (Masuda *et al.*,  
467 2006), *Pontelina plumata* (ppluGFP1, ppluGFP2 (Evdokimov *et al.*, 2006)), *Pontella meadi* (pmeaGFP1,  
468 pmeaGFP2), *Pontella mimocerami* (pmimGFP1, pmimGFP2), *Labidocera aestiva* (laesGFP), and an  
469 unidentified species (pdae1GFP) (Shagin *et al.*, 2004; Hunt *et al.*, 2010). Pontellidae have elaborate

470 eyes and show sexual dimorphism in eye design with different fluorescent patterns (e.g.  
471 *P. mimicerami*). It has been proposed that detection of fluorescent pattern might be involved in  
472 intraspecific recognition (Ohtsuka & Huys, 2001; Shagin *et al.*, 2004; Evdokimov *et al.*, 2006). Herring  
473 (1988) described a sexual dimorphism of fluorescent patches, which are associated to bioluminescent  
474 glands of calanoid copepods (*Oncaea conifera*). But whether fluorescence or other factors such as body  
475 size enhances mating success or is only a side effect of bioluminescence remains to be determined  
476 (Herring, 1988). Blue fluorescent (in the open ocean) or green fluorescent (in nearshore waters)  
477 pigments were suggested to work as countershading mechanism for copepods (as suggested for  
478 *L. aestiva*) (Shagin *et al.*, 2004). In the mantis shrimp *Lysiosquilla glabriuscula* fluorescent displays  
479 enhance visual communication. Here, antennal scales and the carapace show yellow fluorescing  
480 patches. Fluorescent patches accentuate weapons and are discussed as a threat display towards  
481 potential predators or males of the same species (Mazel *et al.*, 2004).

482

483 ((c)) Chordata - Vertebrata – Osteichthyes (fish)

484 In marine fish, little is known about the ability to perceive fluorescence. Several studies, however,  
485 suggest the perception of red fluorescence, which requires red shifted photoreceptors. The red  
486 fluorescent goby *Eviota pellucida*, the blenny *Tripterygion delaisi* and the fairy wrasse  
487 *Cirrhilabrus solorensis* reveal maximum absorbance in the visual pigments of 460-540 nm (Michiels *et*  
488 *al.*, 2008; Gerlach *et al.*, 2016; Bitton *et al.*, 2017). The retina of *C. solorensis* possesses one class of  
489 rods and three spectrally distinct classes of cones with maximum absorbance around 530 nm (Gerlach  
490 *et al.*, 2016). It has been suggested that the absorption spectrum of the long-wavelength opsins ( $\lambda_{\text{abs}}$   
491 530-540 nm) are sufficiently overlapping with the emission spectra of red fluorescence ( $\lambda_{\text{em}}$  600-650  
492 nm) (Michiels *et al.*, 2008; Anthes *et al.*, 2016). In addition, red shifted photoreceptors ( $\lambda_{\text{abs}}$  550-580  
493 nm) have been described in *Thalassoma dupery*, several seahorses and pipefish (Syngnathidae) and  
494 the goby *Gobiusculus flavescens* (Barry & Hawryshyn, 1999; Utne-Palm & Bowmaker, 2006; Mosk *et*  
495 *al.*, 2007; Anthes *et al.*, 2016). The triggerfish *Rhinecanthus aculeatus*, *C. solorensis* and the blenny

496 *T. delaisi* recognize red fluorescence > 600 nm wavelengths as has been tested in physiological and  
497 behavioural assays. In these behavioural assays the wrasse *C. solorensis*, for example, showed more  
498 aggressive behaviour by recognizing possible fluorescent rivals in comparison to non-fluorescent rivals.  
499 In addition, the triplefin *T. delaisi* showed an increase in choice behaviour to a red fluorescent cue,  
500 that is similar to their own fluorescence (Cheney *et al.*, 2013; Gerlach, Sprenger & Michiels, 2014;  
501 Gerlach *et al.*, 2016; Kalb *et al.*, 2015; Bitton *et al.*, 2017).

502 Many marine, diurnal fish including species with fluorescent patterns possess intraocular filters in the  
503 lenses or corneas (Heinermann, 1984; Sparks *et al.*, 2014). It has been proposed that these filters are  
504 used as long-pass filters to detect or enhance the perception of green to red fluorescence. Therefore,  
505 trichromatic vision in combination with long pass filters allows the perception of red-shifted visible  
506 signals as cues for behavioural responses (Wucherer & Michiels, 2014). Red light attenuates with depth  
507 and distance. Thus, in deeper marine environments red fluorescent signals for communication can only  
508 be perceived over short distances. Therefore, it has been proposed that red fluorescent irises are more  
509 common in small rather than large fish, because small fish communicate over shorter distances  
510 (Michiels *et al.*, 2008; Anthes *et al.*, 2016). Other wavelengths of light such as green or yellow light is  
511 detected over a longer distance and might therefore be involved in communication for bigger fish living  
512 in groups (e.g. group coherence or a distraction for predators) (Michiels *et al.*, 2008; Anthes *et al.*,  
513 2016). The fluorescence of the lumpfish *Cyclopterus lumpus* has been suggested to be a  
514 communication signal for territorial claims because of the strong fluorescence in high crest and ridges,  
515 which may be seen from a competitor at a distance (Juhasz-Dora *et al.*, 2022). The nocturnal moray  
516 eel *Gymnothorax zonipectis* reveals bilirubin inducible fluorescence (GymFp). It has been suggested  
517 that the visual detection of this fluorescence might be involved in synchronized spawning during full  
518 moon (Munz & McFarland, 1973; Lee *et al.*, 2008; Wang, Tang & Yan, 2011; Guarnaccia *et al.*, 2021).

519 Fluorescent patterns among closely related reef fish show species-specific variations, for example in  
520 *Eviota* and *Enneapterygius* (Michiels *et al.*, 2008). In addition, interspecific variation has been observed  
521 for members of the lizardfish *Synodus*, the goby *Eviota* and in the juvenile arctic snailfish *Liparis gibbus*

522 (Sparks *et al.*, 2014; Gruber & Sparks, 2021) and investigations regarding fluorescent body patterns in  
523 pseudocheilnid wrasses varied greatly across species (Gerlach *et al.*, 2016). These findings suggest a  
524 role of fluorescent patterns in intraspecific recognition (Sparks *et al.*, 2014). Moreover, fins, i.e. the  
525 anal fin (Gobiidae), the first dorsal fin (Tripterygiidae) or the caudal fin (Syngnathidae) can be  
526 fluorescent. These fins have been shown to be involved in intraspecific signalling (Michiels *et al.*, 2008).  
527 Differences in fluorescence intensity and patterns are observed between males and females of  
528 different vertebrate species and suggest an involvement in sexual communication (Anthes *et al.*, 2016;  
529 Gerlach *et al.*, 2016). Flatfish possess different fluorescent patterns on an individual's blind and sight  
530 surface. During mating, flatfish flash their blind sides to each other (Sparks *et al.*, 2014). In general,  
531 sexually dimorphic fish show an increased abundance of fluorescent fins (Anthes *et al.*, 2016). Recently,  
532 green and red fluorescent leucosome-like pigment organelles (fluoroleucophores) have been  
533 described in embryos of the Arabian Killifish *Aphanius dispar* (Hamied *et al.*, 2020). Knock-out of GTP  
534 cyclohydrolase abolishes the fluorescence, suggesting that fluorescence involves molecules associated  
535 with the pterine biosynthesis pathway. The authors suggest that the Arabian Killifish may have  
536 developed strong reflecting leucophores as a photoprotection mechanism or that this fluorescence  
537 could be a visual signal involved in mating (Hamied *et al.*, 2020).

538

### 539 **III. Other observations of fluorescence**

540 Besides the studies mentioned above, which provide evidence or hypothesis for the function of  
541 fluorescence in marine animals, there is an additional number of studies reporting fluorescence in  
542 other marine organisms including Hexacorallia (scleractinian corals, black corals, sea anemones,  
543 corallimorphs and zoanthids). In fact, the first fluorescent proteins not coupled to bioluminescence  
544 were described in scleractinian corals (Matz *et al.*, 1999) and many different other fluorescent proteins  
545 were isolated later (Labas *et al.*, 2002; Mazel *et al.*, 2003a; Alieva *et al.*, 2008; D'Angelo *et al.*, 2008;  
546 Gittins *et al.*, 2015). To date, more than 200 different FPs are known from Hexacorallia, Crustacea,

547 Hydrozoa, Cephalochordata and fish (Figure 1, Appendix II). In addition, fluorescent molecules have  
548 also been described in soft corals, blue corals, sea pens and gorgonians (Alcyonacea, Helioporacea,  
549 and Pennatulacea). Some Octocorallia are azooxanthellat filter-feeders but some, mostly those found  
550 in shallow depths, possess symbiotic algae (Ruppert, Fox & Barnes, 2004). In Octocorallia,  
551 bioluminescent species are found in pennatulaceans, alcyonaceans (in *Paraspaerasclera grayi*, in the  
552 genera *Anthomastus*, and *Iridogorgia*) and in gorgonians (in the genera *Halypterus*, *Iridogorgia*, and  
553 *Chrysogorgia*) with some species expressing fluorescent antenna proteins (Panceri, 1872; Parker, 1920;  
554 Harvey, 1952; Nicol, J., A., C., 1955; Haddock, Moline & Case, 2010; Raddatz *et al.*, 2011; Frank, Tamara,  
555 M. *et al.*, 2016). Luciferases, for example, coexist with GFPs in *Renilla mülleri*, *Renilla köllikeri*,  
556 *Stylatula elongate*, *Acanthoptilum gracile*, and *Ptilosarcus guernyi*, (Wampler *et al.*, 1973; Shimomura  
557 & Johnson, 1975; Matz *et al.*, 1999; Labas *et al.*, 2002; Alieva *et al.*, 2008; Haddock *et al.*, 2010). In  
558 addition, FPs have been identified in the genera *Clavularia*, *Dendronephyta*, and *Sarcophyton* (all  
559 Alcyonacea) (Matz *et al.*, 1999; Labas *et al.*, 2002; Alieva *et al.*, 2008). Red fluorescence has also been  
560 described in octocorallians, but most likely originates from chlorophyll (Alderslade & McFadden, 2007;  
561 Zawada & Mazel, 2014; Leal *et al.*, 2015; Holm & Heidelberg, 2016).

562 Various Crustaceans express fluorescent substances like lipofuscin (Sheehy, 1990) or tryptophan  
563 associated molecules (Erker, Hübler & Decker, 2008) in addition to FPs. Cuticular autofluorescence has  
564 also been described (Michels, 2007). In addition, Isopods of the genus *Santia* live in symbiosis with  
565 fluorescent unicellular microalgae. These isopods are fully covered with red fluorescent cyanobacteria,  
566 where red fluorescence may serve as a warning colour for predators (Lindquist, Barber & Weisz, 2005).

567 In marine gastropods and bivalves, the structural composition of the mussel shell plays an important  
568 role of absorbing, transmitting and reflecting light (Prudkovsky *et al.*, 2016). The shell of the oyster  
569 *Pinctada vulgaris* contains a lamellar pattern of red fluorescence that consists of red and black parallel  
570 zones (Arma *et al.*, 2014). The fluorophore porphyrin causes the red fluorescence seen when the  
571 prismatic layer of the shell is exposed to a certain wavelength of light (Arma *et al.*, 2014). Giant clams  
572 of the genus *Tridacna* and *Hippopus* (Bivalvia) live in a symbiosis with photosynthetic algae of the genus

573 *Symbiodinium* and reveal a red fluorescence. These symbiotic algae are hosted in the clam's mantle  
574 tissue and produce nutrients (Carlos, Baillie & Maruyama, 2000; Maxwell & Johnson, 2000; Yau & Fan,  
575 2012). Photosynthetic algae show a far-red fluorescence associated to chlorophyll photosystem II  
576 (Jeffrey & Haxo, 1968; Maxwell & Johnson, 2000). The symbionts' fluorescence can be studied to better  
577 understand the symbiosis and to assess the current state of health of bivalves or even entire reefs  
578 (Maxwell & Johnson, 2000; Rowan, 2004; Yau & Fan, 2012).

579 Many marine fish reveal fluorescence with unknown function and often unknown origin. These include  
580 cartilaginous (such as sharks and rays) as well as bony, especially ray-finned fish such as scorpionfish  
581 (Scorpaenoidei), blennie (Blennioidei), gobie (Gobioidei), flatfish (Pleuronectiformes) and numerous  
582 other tropical reef fish (Sparks *et al.*, 2014). Families like pipefish and seahorses (Syngnathidae), and  
583 dragonets (Callionymidae) reveal red fluorescence with emission patterns ranging from small defined  
584 areas to an irregular and interspersed distribution across the body (Anthes *et al.*, 2016). Out of 665  
585 fish species examined 40% (272 species) showed red fluorescence. Emission of red fluorescence  
586 involves iridophores with fluorescent guanine crystals (Michiels *et al.*, 2008; Wucherer & Michiels,  
587 2014), fluorescent chromatophores (Wucherer & Michiels, 2012), fluorescent scales and fin rays  
588 (Michiels *et al.*, 2008) (summarized in (Anthes *et al.*, 2016)).

589

#### 590 **IV. Conclusion**

591 (1) Fluorescent molecules in marine organisms fulfil a broad range of functions across various  
592 taxa.

593 (2) Most hypotheses regarding the function of fluorescence have been surmised from the  
594 morphology of the animal. Very few experiments mainly conducted in corals and fish have  
595 been performed specifically to identify and verify the functions of fluorescence.



596 (3) The number of fluorescent molecules published in different taxa reflects limited knowledge of  
597 the taxonomic distribution of fluorescence. Most fluorescent molecules are known either from  
598 terrestrial plants or Cnidarians.

599 (4) The well-studied functions of FPs in corals and their importance for photoprotection,  
600 photoenhancement, symbiont and prey attraction, and stress mitigation demonstrate how  
601 important it is to better understand the mechanisms that help corals cope with climate change  
602 and how these are related to fluorescent molecules.

603 (5) It is possible that important functions in mitigating climate change effects can be found in more  
604 marine taxa than corals. Research on fluorescent marine organisms, therefore, holds an  
605 unknown potential for marine conservation.

606

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612

## 613 **VI. Competing interests**

614 The authors declare that they have no competing interests.

615

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619

## 620 **VIII. Authors' contributions**

621 All authors developed the initial framework together, and contributed to the writing of the first draft,  
622 the revision and editing.

623

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1021 **X. Supporting Information**

1022 Supplementary material may be found online in the supporting information section at the end of the  
1023 article.

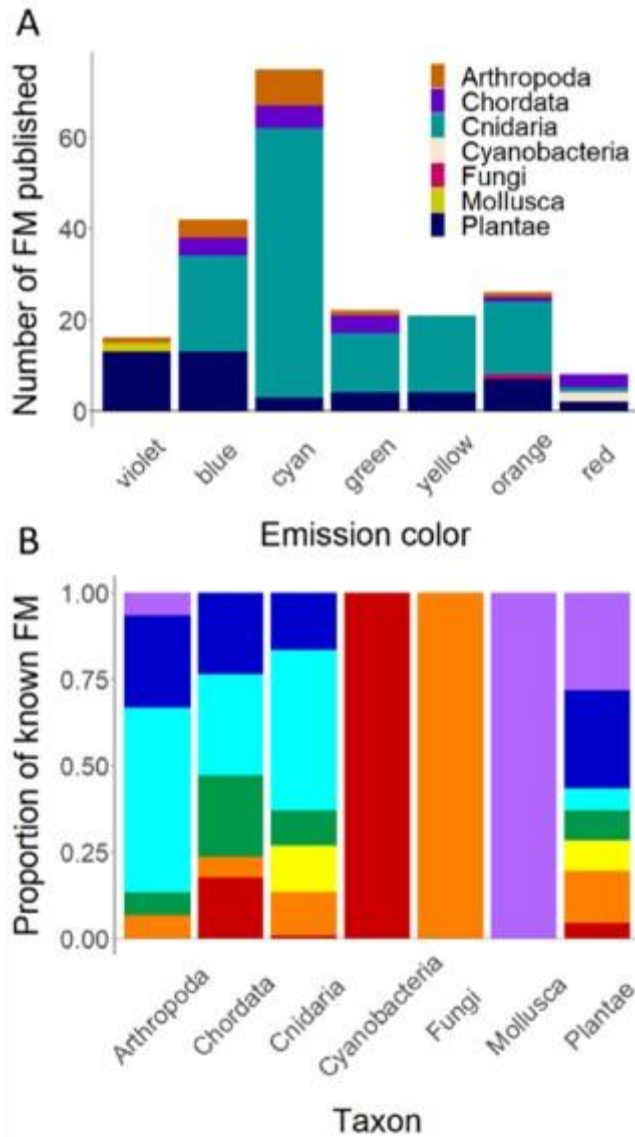
1024 Appendix I: List of fluorescent molecules (marine and terrestrial), including excitation and emission  
1025 wavelengths, emission colour and respective references.

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1027 Appendix II: List of fluorescent proteins that naturally occur in marine organisms. Details on the  
1028 published name, maximum excitation and emission wavelength, molecular weight, number of amino  
1029 acids and references of first publication are given.

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1031 **Table and figure headings:**



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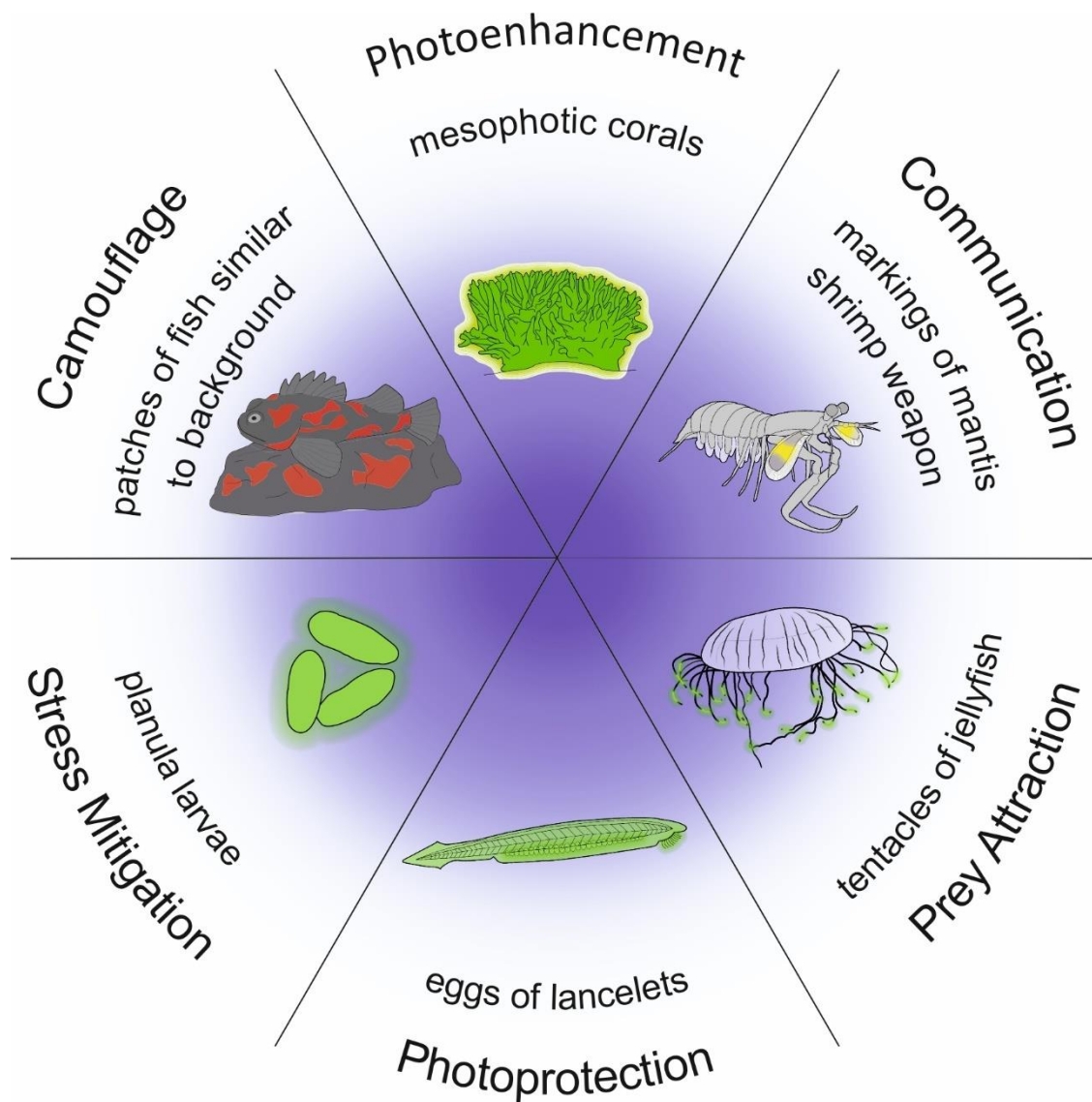
1033 Figure 1: Distribution of fluorescent molecules across taxa. (A) Number of published fluorescent

1034 molecules (FM) sorted by emission wavelength and taxa. (B) Relative occurrence of fluorescent

1035 molecules of different emission wavelengths across taxa (violet = 380-434 nm, blue = 435-499 nm,

1036 cyan = 500-519 nm, green = 520-564 nm, yellow = 565-589 nm, orange = 590-624 nm, red = 625-739

1037 nm).



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1039 Figure 2: Schematic functions of fluorescence in marine organisms. Examples were selected to  
 1040 represent different taxa but are not exclusive to those taxa.

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1045 Table 1: Detailed list of functions of fluorescence in marine organisms and their demonstrated effects  
 1046 on behavioural and physiological responses.

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Class or Order	Family or Species	Localization and Physiological function	Fluorescent signal/molecule	Demonstrated fluorescent mediated behaviours and/or physiological response	Citations
<b>Prey attraction</b>					
Hydrozoa	<i>Olindias formosa</i>	Acceptor molecule for bioluminescent light in tentacles.	dfGFP $\lambda_{ex/em}$ 505/524 nm	Attraction of juvenile rockfish; green vs white or red preference.	(1)
Siphonophores	<i>Rhizophysa eysenhardt</i> , <i>Resomia ornicephal</i> , <i>Diphyes dispar</i>	Fluorescence on tips of tentacles, gastrozooids on bracts and nectophores (swimming bells).	Green, orange $\lambda_{em}$ 518-536 nm	<i>Rhizophysa eysenhardt</i> only feed on fish larvae in the presence of light.	(1–3)
Scleractinia	<i>Fimbriaphyllia (Euphyllia) paradivisa (green morph)</i>	Tentacles and oral part of the polyps.	Green	Higher predation rates in green fluorescing morphs; plankton is attracted by green vs orange fluorescent cues.	(4)
Osteichthyes	<i>Tripterygion delaisi</i> , 114 different fish species	Red fluorescent iris; melanophores encase fluorescent iridophores on the anterior side of the iris.	$\lambda_{em}$ 600 nm <i>T.delaisi</i> $\lambda_{em}$ 580-740 nm (114 species)	Fluorescence increases during foraging and decreases during inactivity or stress.	(5, 6)
<b>Symbiont attractions</b>					
Scleractinia	<i>Echinophyllia aspera</i>		Green $\lambda_{em}$ : 492 and 505 nm	Attraction of <i>Symbiodinium</i> ; green, red vs blue preference.	(7)
<b>Photoprotection</b>					
Scleractinia	<i>Acropora youngei</i>	Adult corals: CP and FPs expressed in ectoderm; light absorption, screen scattering and antioxidation.	GFP $\lambda_{ex/em}$ 470/517 nm	Positive correlation between green fluorescence and increased photobiology of symbiont and growth rate of coral in cold-treated vs heat-treated corals.	(8, 9)
Hydrozoa	<i>Aequorea victoria</i>	Reduction of oxidative stress.	wt-GFP $\lambda_{ex/em}$ 395/509 nm	Quenching oxygen radicals; quenching of superoxide radicals and exhibition of SOD like activity by competing with cytochrome c for reaction with superoxide radicals.	(10)
Scleractinia	<i>Acropora millepora</i> , <i>Porites massive sp.</i> , <i>P. astreoides</i> , <i>Montastraea annularis</i> , <i>M. faveolata</i> , <i>M. cavernosa</i> , <i>Diploria strigosa</i> , <i>Dichocoenia stokseii</i> , <i>Sidastrea siderea</i>	CFP is located in small areas in tentacle tips; GFP is localized throughout the tissue; RFP is upregulated in areas of infected or compromised coral tissue; CP is localized to extremities of colonies (branch tips and basal boundaries).	CFP $\lambda_{em}$ 465-500 nm GFP $\lambda_{em}$ 505-515 nm RFP $\lambda_{em}$ 575-590 nm	Naturally occurring and pure coral FPs and CPs have H <sub>2</sub> O <sub>2</sub> scavenging activity (CFP<GFP<RFP, CP).	(11)
<b>UV protection of RNA and DNA</b>					
Scleractinia	<i>Montipora foliosa</i> , <i>Acropora pulchra</i> , <i>Porites lobata</i> , <i>Stylophora pistillata</i>	Fluorescence in adult corals: in injured and regenerating tissue and growth zones. Fluorescence in planula larvae: in regions undergoing cell differentiation.	mfolCP $\lambda_{abs}$ 577 nm; mfolFP $\lambda_{em}$ 483 nm; apulFP $\lambda_{em}$ 584 nm; apulFP $\lambda_{em}$ nm483; plobFP $\lambda_{em}$ 610nm; plobFP $\lambda_{em}$ 490 nm	Upregulation of FPs in bleached, injured, regenerating and differentiating corals and larvae; higher fluorescence at lower pH (pH7.6 vs pH8.15; <i>S. pistillata</i> ).	(12, 13)

Scleractinia	<i>Pocillopora damicornis</i> , <i>Montastraea cavernosa</i>	High ectodermal expression of CPs in areas of low symbiont density.	CP <i>P. damicornis</i> $\lambda_{abs}$ 565 nm CP <i>M. foliosa</i> purple	Alteration of intra-tissue light environment in CP expressing corals; upregulation of pink CP during bleaching leads to 10-20% reduction of orange light	(14)
Scleractinia	<i>Porites lichen</i> , <i>Pocillopora damicornis</i>		CFP <i>P. lichen</i> $\lambda_{ex/em}$ 466/489 nm GFP <i>P. lichen</i> $\lambda_{ex/em}$ 489/519 nm CP <i>P. damicornis</i> $\lambda_{abs}$ 565 nm	Upregulation of green/cyan fluorescence ratio during light acclimation, bleaching and recovery and downregulation of chlorophyll fluorescence emission during bleaching; upregulation of CPs after bleaching and recovery.	(15)
Annelida	<i>Eulalia sp.</i>	Protection against high energy radiation; mucus contains FPs, ubiquitin and antioxidant protein peroxiredoxin.	Mucus $\lambda_{ex}$ 285-374 nm $\lambda_{em}$ 507-513 nm	Secretion of a mucus containing a proteinaceous fluorescent complex.	(16)
<b>Photoenhancement</b>					
Scleractinia	<i>Montastraea cavernosa</i> , <i>Echinophyllia sp.</i>	Ectodermal pcRFP in mesophotic corals; enhancement of photosynthesis in mesophotic habitats via wavelength conversion.	pcRFP $\lambda_{em}$ 514 <sub>unconverted</sub> , 582 <sub>converted</sub> nm	pcRFP emission contribute >50 of orange-red light available for photosynthesis; ectodermal pcRFPs increase the illumination of deeper tissue layers exposed to mesophotic light.	(14)
<b>Stress mitigation and regulatory mechanisms</b>					
Scleractinia	<i>Acropora millepora</i>	RFP leads to a reduction in settlement cues important for long-range dispersal; green fluorescence at oral pole and red fluorescence in ectodermal cells in aboral pole in larvae and recruits.	4 CPs and 8 FPs, amilCPs $\lambda_{abs}$ 580, 586, 604 nm amilFPs $\lambda_{em}$ 484, 490, 497, 504, 512, 513, 593, 597 nm	Larvae with red fluorescence have lower colonization success than those with green fluorescence; heat stress reduces the red fluorescence.	(17-19)
<b>Bilirubin binding to reduce cellular, oxidative stress</b>					
Osteichthyes	<i>Anguilla japonica</i>	In young eel expression in white muscles in small fibers and binding of bilirubin is involved in metabolism and homeostasis of oxidative stress during long-distance migration.	UnaG - fatty acid binding proteins Binding of bilirubin $\lambda_{ex/em}$ 498/527 nm	Bilirubin is a break down product of hemoglobin in red blood cells. Bilirubin bound to GFP can act as a scavenger of hydrogen peroxide and/or hydroxyl radical.	(20, 21)
<b>Immune response</b>					
Scleractinia	<i>Porites compressa</i>	expression of green FPs changes towards red FPs in trematodiasis-compromised tissue.	GFP, RFP $\lambda_{em}$ 590 nm in compromised tissue	Increased and alteration of FP expression in compromised tissue.	(22)
Chondrichthyes	<i>Cephaloscyllium ventriosum</i> , <i>Scyliorhinus retifer</i>	High intensity green fluorescence in the lighter colored areas of the skin for the catsharks and the dark spots of the skins for the swell shark.	Brominated tryptophan-kynureinine $\lambda_{ex}$ 360-438 nm $\lambda_{em}$ 400-507 nm	Kynureinine metabolism regulates host-microbiome signaling and immune response in human.	(23)
<b>pH regulation and skeleton deposition (pH dependent process)</b>					

Hydrozoa	<i>Aequorea victoria</i>	GFP mediated light-driven non-membrane-bound proton pump for light driven acidification.	wt-GFP $\lambda_{ex/em}$ 395/509 nm	Proton motion within GFP.	(24–27)
<b>Light-driven electron transfer</b>					
Anthozoa	<i>Zoanthus sp.</i>	Light-induced electron donor in photochemical reactions with electron acceptors such as cytochrome c, FMN, FAD or NAD <sup>+</sup> ; highly mobile cytoplasmic localization and spindle-shaped aggregates in cells.	Various FPs, Tyr66-based chromophores	Light-induced electron transfer of FPs.	(28, 29)
<b>Mimicry and aposematism</b>					
Heterobranchia	<i>Goniobranchus splendidus</i> , 16 mediterranean Heterobranchia	Green fluorescence in particular in the cerata stored in the cnidosacs to enhance the aposematic coloration (warning function). In addition fluorescence is found in rhinophores, dorsum and gills.	Mainly green, but also yellow, pink, orange, red	The dorsal rim of <i>Goniobranchus splendidus</i> induces an avoidance response in the Picasso triggerfish; unpalatable secondary metabolites and yellow rim as apoptotic signals for predators.	(30, 31)
<b>Intra/interspecific communication</b>					
Osteichthyes	<i>Cirrhilabrus solorensis</i>	Red fluorescent body coloration.	$\lambda_{em}$ 650-700 nm	Increased aggressive behaviour by recognizing possible fluorescent rivals in comparison to non-fluorescent rivals in <i>C. solorensis</i> . <i>C. solorensis</i> express four visual photoreceptors: one rod ( $\lambda_{em}$ 492 nm) and three classes of cones ( $\lambda_{em}$ 497, 514, 532) which should be sensitive to their own fluorescence.	(32, 33)
Osteichthyes	<i>Tripterygion delaisi</i>	Red fluorescent eye rings.	$\lambda_{em}$ 600 nm	<i>T. delaisi</i> can perceive and respond to levels of fluorescence that are similar to its own (positive correlation to a red fluorescent but not grey cue) <i>T. delaisi</i> express four visual photoreceptors: one rod ( $\lambda_{em}$ 502 nm) and three classes of cones ( $\lambda_{em}$ 468, 517, 532) which should be sensitive to their own fluorescence.	(5, 34, 35)
<b>Sexual communication</b>					
Osteichthyes	<i>Cirrhilabrus solorensis</i> , pseudocheiliniid wrasses (13 species), 185 different fish species	Differences in the fluorescence pattern between males and females.	<i>C. solorensis</i> $\lambda_{em}$ 640-670 nm, 185 fish species $\lambda_{em}$ 580-750 nm	Red fin fluorescence associated with sexual dimorphism photoreceptors: one rod ( $\lambda_{abs}$ 492 nm), three classes of cones ( $\lambda_{abs}$ 497, 514, 532).	(33, 36)

- 1048 According to Marshall and Jonson (2017) and Mazel (2017) various criteria have to be fulfilled to support an ecological function of fluorescence in animals (37) (38). These include
- 1049(1) the presence of a fluorescent molecule in a visible location, that can be sufficiently excited under natural lighting conditions to induce fluorescence with high enough energy to be received by
- 1050 photoreceptors.
- 1051(2) The overlap of the emission wavelength of the fluorophore with the spectra sensitivity range of the organism.
- 1052(3) Visually guided behaviours that are driven or supported by the fluorescent signal.

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In addition, we included in this table the physiological function of fluorescent molecules irrespective of light emission, when physiological responses have been correlated with an increase or decrease in molecule expression.

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1122 Appendix I: List of fluorescent molecules (marine and terrestrial), including excitation and emission wavelengths, emission colour and respective references

Molecule	Organism	Taxon	Molecule type	Fluorescence	$\lambda_{exc}$ (nm)	$\lambda_{em}$ (nm)	Colour(em) (nm)	Reference
Acridone	Alkaloids plants	plantae			381	427	430	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Aesculin	Roskastanie	plantae	Glucosid (alcohol & Phenol and Glycose bonded)	blue under UV-light	NA	NA	450	J. C. Poggendorf (Hrsg.): <i>Annalen der Physik</i> , Bd. 4, Verlag J. A. Barth, Leipzig 1854. S. 313.
Allophycocyanin	cyanobacteria & red algae	cyanobacteria	Pigment belonging to the Phycobilinen, Protein		633	680	680	Luttmann, W., Bratke, K., Küpper, M., & Myrtek, D. (2014). <i>Der Experimentator: Immunologie</i> . Springer-Verlag
Anthocyanins	plants, flowers	plantae	NA	NA	533	624	620	A. Iriel and M. G. Lagorio, Biospectroscopy of Rhododendron indicum flowers. Non-destructive assessment of anthocyanins in petals using a reflectance-based method, <i>Photochem. Photobiol. Sci.</i> , 2009, 8, 337, all sources in Lagorio 2015 Reviewing the relevance of fluorescence in biological systems
Anthranilic acid	plants	plantae	acid		300	405	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Aurones	plants, flowers	plantae	flavonoids	NA	430	560	570	Ono, M. Fukuchi-Mizutani, N. Nakamura, Y. Fukui, K. Yonekura-Sakakibara, M. Yamaguchi, T. Nakayama, T. Tanaka, T. Kusumi and Y. Tanaka, Yellow flowers generated by expression of the aurone biosynthetic pathway, <i>Proc. Natl. Acad. Sci. U. S. A.</i> , 2006, 103, 11075, N. Shanker, O. Dilek, K. Mukherjee, D. W. McGee and S. L. Bane, Aurones: small molecule visible range fluorescent probes suitable for biomacromolecules, <i>J. Fluoresc.</i> , 2011, 21, 2173
Azulene	plants	plantae	Terpenoids		360 - 380	420, 620, 725	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Berberin	Berberitze	plantae	Alkaloid	yellow under UV-light	NA	NA	570	<a href="http://www.chemie.uni-jena.de/institute/oc/weiss/naturstoffe.htm">http://www.chemie.uni-jena.de/institute/oc/weiss/naturstoffe.htm</a>
Beta-Carboline	Scorpions	arthropoda	indole alkaloid	blue-green under UV-light	375	450	450	S. J. Stachel, S. A. Stockwell and D. L. Van Vranken, The fluorescence of scorpions and cataractogenesis, <i>Chem. Biol.</i> , 1999, 6, 531
Beta-Carotene	plants, flowers	plantae	Terpenoids		360, 480	500-525, 580	520	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Betacyanins	plants, flowers	plantae	pigments	NA	524	570	570	all sources in Lagorio 2015 Reviewing the relevance of fluorescence in biological systems

Betaxanthins	plants, flowers	plantae	pigments	NA	NA	NA	570	all sources in Lagorio 2015 Reviewing the relevance of fluorescence in biological systems
Bromo-tryptophan-kynurenines	shark	vertebrata			375	439, 447	450	Park, H. B., Lam, Y. C., Gaffney, J. P., Weaver, J. C., Krivosihk, S. R., Hamchand, R., ... & Crawford, J. M. (2019). Bright Green Biofluorescence in Sharks Derives from Bromo-Kynurenine Metabolism. <i>Iscience</i> , 19, 1291-1336.
Caffeic acid	plants	plantae	Phenolics		206, 310	281, 432	410	H. K. Lichtenthaler and J. Schweiger, Cell wall bound ferulic acid, the major substance of the bluegreen fluorescence emission of plants, <i>J. Plant Physiol.</i> , 1998, 152, 272
Calcein	NA	NA	fluorescein complex		494	517	520	Horobin, RW. und Kiernan, JA. (2002): <i>Conn's Biological Stains: A Handbook of Dyes, Stains and Fluorochromes for Use in Biology and Medicine</i> . BIOS Scientific Publ., 10. Auflage; ISBN 1-85996-099-5)
Crustacyanin	lobster	arthropoda	pigments		530	580	595	T. Gillbro and R. J. Cogdell, Carotenoid fluorescence, <i>Chem. Phys. Lett.</i> , 1989, 158, 312, O. Völker, Ueber fluoreszierende, gelbe federpigmente bei papagein, eine neue klasse von federfarbstoffen, <i>J. Ornithol.</i> , 1937, 85, 136, K. J. McGraw and M. C. Nogare, Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots, <i>Comp. Biochem. Physiol., B: Biochem. Mol. Biol.</i> , 2004, 138, 229, Chayen, N. E., Cianci, M., Grossmann, J. G., Habash, J., Helliwell, J. R., Nneji, G. A., ... & Zagalsky, P. F. (2003). Unravelling the structural chemistry of the colouration mechanism in lobster shell. <i>Acta Crystallographica Section D: Biological Crystallography</i> , 59(12), 2072-2082.)
Cianidin	plants	plantae	phenolics, flavonoids		547	595	595	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Cicutotoxin	plants	plantae	lipids		360-380	580	595	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Cinnamic acid	plants	plantae	phenolics		360	405-427	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Chinin	plants	plantae	Chinolin-alkaloids	brightblue under UV-light	315-380		470	F. von Bruchhausen: <i>Hagers Handbuch der Pharmazeutischen Praxis: Drogen A–K</i> . 5. Auflage. Springer Verlag, Berlin 1998, ISBN 3-540-61618-7, S. 101.
Chlorogenic acid	plants	plantae			330	440	450	H. K. Lichtenthaler and J. Schweiger, Cell wall bound ferulic acid, the major substance of the bluegreen fluorescence emission of plants, <i>J. Plant Physiol.</i> , 1998, 152, 272

Chlorophyll-a	plants	plantae	Tetrapyrrole, protein		465, 480, 665, 680	675-690, 730-740	680	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Colchicine	plants	plantae	Alkaloids		360	435	430	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Coumarin	spiders, cockroaches	arthropoda	Alkaloids		280, 410	415-445	430	H. K. Lichtenthaler and J. Schweiger, Cell wall bound ferulic acid, the major substance of the bluegreen fluorescence emission of plants, <i>J. Plant Physiol.</i> , 1998, 152, 272, L. M. Frost, D. R. Butler, B. O'Dell and V. Fet, A coumarin as a fluorescent compound in scorpion cuticle, in <i>Scorpions 2001: in Memoriam, Gary A. Polis</i> , British Arachnological Society, Burnham Beeches, Buckinghamshire, UK, 2001, pp. 365–368)
Coumarin-dyes	plants	plantae	coumarin derivatives				NA	Ulrich Brackmann: <i>Lambdachrome: Laser Dyes</i> . 3. Auflage. Lamda Physik AG, Göttingen 2000, M. Sauer, J. Hofkens, J. Enderlein: <i>Handbook of Fluorescence Spectroscopy and Imaging: From Single Molecules to Ensembles: From Ensemble to Single Molecules</i> . Wiley-VCH Verlag, Weinheim 2011, ISBN 978-3-527-31669-4 , S. 39 ff.
Epicocconon	fungi	fungi		weak green to red	395		620	P. J. Bell, P. Karuso: Epicocconone, a novel fluorescent compound from the fungus <i>epicoccumnigrum</i> . In: <i>Journal of the American Chemical Society</i> . Band 125, Nummer 31, August 2003, S. 9304–9305, doi:10.1021/ja035496+, J. A. Mackintosh, D. A. Veal, P. Karuso: Fluoroprofile, a fluorescence-based assay for rapid and sensitive quantitation of proteins in solution. In: <i>Proteomics</i> . Band 5, Nummer 18, Dezember 2005, S. 4673–4677, doi:10.1002/pmic.200500095
Esculetin	plants	plantae	phenolics		360	475	470	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
UnaG	eels	vertebrata	protein		500	527	520	Kumagai, A., Ando, R., Miyatake, H., Greimel, P., Kobayashi, T., Hirabayashi, Y., ... & Miyawaki, A. (2013). A bilirubin-inducible fluorescent protein from eel muscle. <i>Cell</i> , 153(7), 1602-1611.
Ferulic acid	plants	plantae	acid		240. 340	400-480	470	P. J. Harris and R. D. Hartley, Detection of bound ferulic acid in cell walls of the Gramineae by ultraviolet fluorescence microscopy, <i>Nature</i> , 1976, 259, 508, H. K. Lichtenthaler and J. Schweiger, Cell wall bound ferulic acid, the major

								substance of the bluegreen fluorescence emission of plants, <i>J. Plant Physiol.</i> , 1998, 152, 272
Flavine/Flavonoids	plants	plantae	phenolics	yellow	365	445-461	450	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Flavoproteins	plants	plantae	Flavins		365	520-540	520	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Fluorescent Proteins	cnidaria	cnidaria	protein				NA	O. Shimomura, The discovery of aequorin and green fluorescent protein, <i>J. Microsc.</i> , 2005, 217, 3, Y. A. Labas, N. G. Gurskaya, Y. G. Yanushevich, A. F. Fradkov, K. A. Lukyanov, S. A. Lukyanov and M. V. Matz, Diversity and evolution of the green fluorescent protein family, <i>Proc. Natl. Acad. Sci. U. S. A.</i> , 2002, 99, 4256, N. O. Alieva, K. A. Konzen, S. F. Field, E. A. Meleshkevitch, M. E. Hunt, V. Beltran-Ramirez, D. J. Miller, J. Wiedenmann, A. Salih and M. V. Matz, Diversity and evolution of coral fluorescent proteins, <i>PLoS One</i> , 2008, 3, e2680, S. H. D. Haddock, C. W. Dunn, P. R. Pugh and C. E. Schnitzler, Bioluminescent and red-fluorescent lures in a deep-sea siphonophore, <i>Science</i> , 2005, 309, 263)
Fluorescent skeletons/bones	frogs, chamelions	vertebrata	collagen, tetracyclines, apartit				NA	Bachman, C. H., & ELLIS, E. H. (1965). Fluorescence of bone. <i>Nature</i> , 206(4991), 1328-1331
Folic acid	plants	plantae	phenolics		365	450	450	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Gaillardine	plants	plantae	Terpenoids		360	415	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Galangin	plants	plantae	phenolics		365	447-461	450	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Gallic acid/valonic acid	plants	plantae	phenolics		360-380	500	520	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Gentinsic Acid	plants	plantae	phenolics		340	450	450	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.

Guanine	fish	vertebrata	nucleobase		500-570	584-699	595	N. K. Michiels, N. Anthes, N. S. Hart, J. Herler, A. J. Meixner, F. Schleifenbaum, G. Schulte, U. E. Siebeck, D. Sprenger and M. F. Wucherer, Red fluorescence in reef fish: A novel signalling mechanism?, <i>BMC Ecol.</i> , 2008, 8, 16
Hyloin	frogs	vertebrata	Dihydroisoquinolinones	blue-green under UV-light			490	Taboada, C., Brunetti, A. E., Pedron, F. N., Neto, F. C., Estrin, D. A., Bari, S. E., ... & Faivovich, J. (2017). Naturally occurring fluorescence in frogs. <i>Proceedings of the National Academy of Sciences</i> , 114(14), 3672-3677.
Kaempferol	plants	plantae	phenolics	green	260-270. 360-380	520	520	W. A. Peer, D. E. Brown, B. W. Tague, G. K. Muday, L. Taiz and A. S. Murphy, Flavonoid accumulation patterns of transparent testa mutants of arabidopsis, <i>Plant Physiol.</i> , 2001, 126, 536
Kinetin	plants	plantae	cytokinins		380	410-430	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbelo, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Kynurenic acid	plants	plantae	Alkaloids		325	405	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbelo, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Sandercyanine	fish	vertebrata	Lipocalin (protein)	red	375	630	620	Ghosh, S., Yu, C. L., Ferraro, D. J., Sudha, S., Pal, S. K., Schaefer, W. F., ... & Ramaswamy, S. (2016). Blue protein with red fluorescence. <i>Proceedings of the National Academy of Sciences</i> , 113(41), 11513-11518.
Lipofuscin	plants, fruits, cockroaches	arthropoda			360-380	440-470	450	Y. P. Maguire and N. F. Haard, Fluorescent product accumulation in ripening fruit, <i>Nature</i> , 1975, 258, 599, M. R. J. Sheehy, Widespread occurrence of fluorescence morphological lipofuscin in the crustacean brain, <i>J. Crustacean Biol.</i> , 1990, 10, 613
Luciferin	fireflies	arthropoda			327	530	520	Marques, S. M., Esteves da Silva, J. C. G. (2009) Firefly Bioluminescence: A Mechanistic Approach of Luciferase Catalyzed Reactions. <i>Life</i> , 61(1), 6-17
Matlaline	plants	plantae			283, 307, 382, 430	466	470	Lagorio 2015 Reviewing the relevance of fluorescence in biological systems
Malvidin-O-glucosid	plants	plantae			530	630	620	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbelo, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Menthol	plants	plantae	Terpenoids		360	415-420	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbelo, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.

Minerals	NA	NA	Minerals				NA	for all fluorescent minerals see: <a href="https://www.uvminerals.org/minerals/common-fluorescent-minerals/">https://www.uvminerals.org/minerals/common-fluorescent-minerals/</a> )
Mucous-like secretions	amphibians	vertebrata		green			520	Lamb 2020 Salamanders and other amphibians are aglow with biofluorescence
Parietin	plants	plantae	phenolics		442	600	595	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Petunidin	plants	plantae	phenolics		510-585	610	620	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Pheophorbide-a	fish	vertebrata			400	670	680	R. H. Douglas, C. W. Mullineaux and J. C. Partridge, Long-wave sensitivity in deep-sea stomiid dragonfish with far-red bioluminescence: evidence for a dietary origin of the chlorophyll-derived retinal photosensitizer of <i>Malacosteus niger</i> , <i>Philos. Trans. R. Soc. London, Ser. B</i> , 2000, 355, 1269
Phycobilliprotein	Cyanobacteria	cyanobacteria	protein		642	670	680	Rodríguez, E. A., Tran, G. N., Gross, L. A., Crisp, J. L., Shu, X., Lin, J. Y., & Tsien, R. Y. (2016). A far-red fluorescent protein evolved from a cyanobacterial phycobiliprotein. <i>Nature methods</i> , 13(9), 763-769
Porphyrins	cnidaria	cnidaria	prophyrines	red	410	620	620	R. Bonnett, E. J. Head and P. J. Herring, Porphyrin pigments of some deep-sea medusa, <i>J. Mar. Biol. Assoc.</i> , 1979, 59, 565
Psittacofulvin	birds	vertebrata	carotenoids		420-450	527	520	K. J. McGraw and M. C. Nogare, Carotenoid pigments and the selectivity of psittacofulvin-based coloration systems in parrots, <i>Comp. Biochem. Physiol., B: Biochem. Mol. Biol.</i> , 2004, 138, 229, R. Stradi, E. Pini and G. Celentano, The chemical structure of the pigments in <i>Ara macao</i> plumage, <i>Comp. Biochem. Physiol., B: Biochem. Mol. Biol.</i> , 2001, 130, 57
Pterins	Arthropods	vertebrata	pterins				450	Lagorio 2015 Reviewing the relevance of fluorescence in biological systems
Pteric acid	plants	plantae	phenolics		360	435	430	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Pyridoxine	plants	plantae	pyridines		340	400	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Pyridoxamine	plants	plantae	pyridines		335	400	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015).

								Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Quercetin	plants	plantae	phenolics		250, 370	500-540	520	A. P. Nifli, P. A. Theodoropoulos, S. Munier, C. Castagnino, E. Roussakis, H. E. Katerinopoulos, J. Vercauteren and E. Castanas, Quercetin exhibits a specific fluorescence in cellular milieu: A valuable tool for the study of its intracellular distribution, <i>J. Agric. Food Chem.</i> , 2007, 55, 2873
Quinine	plants	plantae			347	450	450	M. Honigsbaum and M. Willcox, in <i>Cinchona in Traditional Medicinal Plants and Malaria</i> , ed. M. Willcox, G. Bodeker and P. Rasoanaivo, CRC Press, Boca Raton, Florida, USA, 2005, ch. 2, p. 22, Lagorio 2015 Reviewing the relevance of fluorescence in biological systems
Resilin	Arthropods	arthropoda	protein				450	S. Donoughe, J. D. Crall, R. A. Merz and S. A. Combes, Resilin in dragonfly and damselfly wings and its implications for wing flexibility, <i>J. Morphol.</i> , 2011, 272, 1409
Riboflavin	plants	plantae	Flavins		377	526	520	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Rhodopin	plants	plantae	carotenoids		500-550	560-600	595	T. Gillbro and R. J. Cogdell, Carotenoid fluorescence, <i>Chem. Phys. Lett.</i> , 1989, 158, 312
Rosmarinic acid	plants	plantae	acid		60-380	440-450	450	H. K. Lichtenthaler and J. Schweiger, Cell wall bound ferulic acid, the major substance of the bluegreen fluorescence emission of plants, <i>J. Plant Physiol.</i> , 1998, 152, 272
Rutacridone	plants	plantae	Alkaloids		381	590-595	595	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Sepiapterin	fish	vertebrata	Pteridin		UV	450-490	450	Le Guyader S, Jesuthasan S. Analysis of xanthophore and pterinosome biogenesis in zebrafish using methylene blue and pteridine autofluorescence. <i>Pigment Cell Res</i> 2002;15:27–31
Serotonin	plants	plantae	Alkaloids		360	410-420	410	García-Plazaola, J. I., Fernández-Marín, B., Duke, S. O., Hernández, A., López-Arbeloa, F., & Becerril, J. M. (2015). Autofluorescence: biological functions and technical applications. <i>Plant Science</i> , 236, 136-145.
Schiff-bases	bees	arthropoda	imines		360	450	450	R. G. Young and A. L. Tappel, Fluorescent pigment and pentane production by lipid peroxidation in honey bees, <i>Apis Mellifera</i> , <i>Exp. Gerontol.</i> , 1978, 13, 457
Spheniscin	birds	vertebrata	beta-defensins		370-400	450-500	470	K. J. McGraw, M. B. Toomey, P. M. Nolan, N. I. Morehouse, M. Massaro and P. Jouventin, A description of unique fluorescent yellow pigments in penguin feathers, <i>Pigm. Cell Res.</i> , 2007, 20, 301, D. B. Thomas, C. M. McGoverin, K. J. McGraw, H. F. James and O. Madden, <i>Vibrational</i>

								spectroscopic analyses of unique yellow feather pigments (spheniscins) in penguins, J. R. Soc. Interface, 2013, 10, 20121065
Spheroidenone	plants	plantae	carotenoids		520	570-610	595	T. Gillbro and R. J. Cogdell, Carotenoid fluorescence, Chem. Phys. Lett., 1989, 158, 312

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1124 Appendix II: List of fluorescent proteins that naturally occur in marine organisms. Details on the published name, maximum excitation and emission wavelength,

1125 molecular weight, number of amino acids and references of first publication are given.

Taxon	Species	Fluorescent Protein	Max. Excitation (nm)	Max. Emission (nm)	Molecular Weight (kDa)	Number of amino acids	Accession No.	Paper doi	Paper
<b>Anthozoa</b>	Acanthastrea sp. (Micromussa lordhowensis)				25.86	226	<a href="#">KY806741</a>		Chen 2017 - Molecular cloning and characterization of fluorescent proteins in the stony coral Acanthastrea lordhowensis
	Acanthastrea sp. (Micromussa lordhowensis)				26.11	227	<a href="#">KY806740</a>		Chen 2017 - Molecular cloning and characterization of fluorescent proteins in the stony coral Acanthastrea lordhowensis
	Acropora digitifera	AdRed	567	612	26.10	231	<a href="#">LC125067</a>	<a href="https://doi.org/10.1002/pro.3540">https://doi.org/10.1002/pro.3540</a>	Kim 2018 - Spectral and structural analysis of a red fluorescent protein from Acropora digitifera
	Acropora aculeus	aacuGFP1	478	502	25.70	231	<a href="#">AY646069</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora aculeus	aacuGFP2	502	513	26.09	231	<a href="#">AY646066</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora aculeus	aacuCP	580	NA	24.98	221	<a href="#">AY646077</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.



	Acropora eurostoma	aeurGFP	504	515	26.02	231	<a href="#">EU498722</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora hyacinthus	ahyaCP	580	NA	24.96	221	<a href="#">AY646076</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora millepora	amilFP484	420	484	26.08	231	<a href="#">EU709808</a>	<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Acropora millepora	amilCFP	441	489	25.95	231	<a href="#">AY646070</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora millepora	amilFP497	477	497	25.90	231	<a href="#">EU709809</a>	<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Acropora millepora	amilFP512	500	512	25.93	231	<a href="#">EU709810</a>	<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Acropora millepora	amilGFP	503	512	25.99	231	<a href="#">AY646067</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora millepora	amilCP506	506	516	2.43	21	<a href="#">JQ009184</a>	<a href="https://doi.org/10.1111/mec.13041">https://doi.org/10.1111/mec.13041</a>	Gittins 2015 - Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments
	Acropora millepora	amilFP597	558	597	26.12	232	<a href="#">JX258844</a>	<a href="https://doi.org/10.1111/mec.13041">https://doi.org/10.1111/mec.13041</a>	Gittins 2015 - Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments

	Acropora millepora	amilFP597	558	597	26.09	232	<a href="#">EU709811</a>	<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Acropora millepora	amilFP605 (Ala)	559	605		232	KJ729554	<a href="https://doi.org/10.1111/mec.13041">https://doi.org/10.1111/mec.13041</a>	Gittins 2015 - Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments
	Acropora millepora	amilRFP	560	593	26.15	232	<a href="#">AY646073</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora millepora	amilCP564	564	599		231	JX258846	<a href="https://doi.org/10.1111/mec.13041">https://doi.org/10.1111/mec.13041</a>	Gittins 2015 - Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments
	Acropora millepora	amilCP	588	NA	26.09	232	<a href="#">AY646075</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora millepora				26.10	232	<a href="#">AY650288</a>	DOI: 10.1007/s10126-007-9049-6	Smith-Keune 2008 - Gene expression of a green fluorescent protein homolog as a host-specific biomarker of heat stress within a reef-building coral
	Acropora millepora				25.56	227	<a href="#">DQ206400</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora millepora				1.98	18	<a href="#">KM101115</a>	<a href="https://doi.org/10.1111/mec.13041">https://doi.org/10.1111/mec.13041</a>	Gittins 2015 - Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments

	Acropora millepora				2.42	21	<a href="#">JQ009183</a>	<a href="https://doi.org/10.1111/mec.13041">https://doi.org/10.1111/mec.13041</a>	Gittins 2015 - Fluorescent protein-mediated colour polymorphism in reef corals: multicopy genes extend the adaptation/acclimatization potential to variable light environments
	Acropora millepora				24.99	221	<a href="#">KC411500</a>	DOI 10.1007/s00338-012-0994-9	Smith 2013 - Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae
	Acropora millepora				25.01	221	<a href="#">KC411499</a>	DOI 10.1007/s00338-012-0994-9	Smith 2013 - Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae
	Acropora millepora				25.02	221	<a href="#">KC349891</a>	DOI 10.1007/s00338-012-0994-9	Smith 2013 - Screening by coral green fluorescent protein (GFP)-like chromoproteins supports a role in photoprotection of zooxanthellae
	Acropora nobilis		462	490	25.90	231	<a href="#">AY646072</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora nobilis	anobCFP2	477	495	25.70	231	<a href="#">AY646071</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora nobilis	anobGFP	502	511	25.88	231	<a href="#">AY646068</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Acropora pulchra	apulFP483	420	483	25.93	231	<a href="#">EU709806</a>	<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Acropora pulchra	apulCP584	584		24.97	221	<a href="#">EU709807</a>	<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals

	Acropora tenuis	atenFP	504	515	24.60	220	<a href="#">BAM08940</a>	<a href="https://doi.org/10.1016/S1096-4959(02)00025-8">https://doi.org/10.1016/S1096-4959(02)00025-8</a>	Papina 2002 - Separation of highly fluorescent proteins by SDS-PAGE in Acroporidae corals
	Agaricia fragilis	afraGFP	494	503	25.69	226	<a href="#">AY647156</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Agaricia fragilis				30.02	259	<a href="#">AY037765</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Matz 2002 - Diversity and evolution of GFP-like fluorescent proteins
	Agaricia fragilis				6.89	58	<a href="#">KC248482</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.87	58	<a href="#">KC248497</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.90	58	<a href="#">KC248483</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.82	58	<a href="#">KC248491</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.92	58	<a href="#">KC248499</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.89	58	<a href="#">KC248492</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.86	58	<a href="#">KC248495</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.91	58	<a href="#">KC248484</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals

	Agaricia fragilis				6.88	58	<a href="#">KC248493</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.88	58	<a href="#">KC248485</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Agaricia fragilis				6.93	58	<a href="#">KC248498</a>	<a href="https://doi.org/10.1093/jhered/est028">https://doi.org/10.1093/jhered/est028</a>	Wares 2013 - Genetic diversity of fluorescent proteins in Caribbean Agariciid corals
	Anemonia majano	amFP486	458	486	25.32	229	<a href="#">AF168421</a>	<a href="https://doi.org/10.1038/13657">https://doi.org/10.1038/13657</a>	Matz 1999 - Fluorescent proteins from nonbioluminescent Anthozoa species.
	Anemonia sulcata	asCP	568	595 (none)	25.92	232	<a href="#">AF246709</a>	<a href="https://doi.org/10.1074/jbc.C000338200">https://doi.org/10.1074/jbc.C000338200</a>	Lukyanov 2000 - Natural animal coloration can be determined by a nonfluorescent green fluorescent protein homolog.
	Anemonia sulcata	asFP499	403/480	499	25.37	228	<a href="#">AF322221</a>	<a href="https://doi.org/10.1073/pnas.97.26.14091">https://doi.org/10.1073/pnas.97.26.14091</a>	Wiedenmann 2000 - Cracks in the beta-can: fluorescent proteins from Anemonia sulcata (Anthozoa, Actinaria).
	Anemonia sulcata				25.92	232	<a href="#">EF587182</a>	<a href="https://doi.org/10.1016/j.jembe.2007.09.013">https://doi.org/10.1016/j.jembe.2007.09.013</a>	Leutenegger 2007 - Analysis of fluorescent and non-fluorescent sea anemones from the Mediterranean Sea during a bleaching event
	Anemonia sulcata				25.96	232	<a href="#">AF322222</a>	<a href="https://doi.org/10.1073/pnas.97.26.14091">https://doi.org/10.1073/pnas.97.26.14091</a>	Wiedenmann 2000 - Cracks in the beta-can: fluorescent proteins from Anemonia sulcata (Anthozoa, Actinaria).
	Astrangia lajollaensis	alajGFP3	494	504	25.20	226	<a href="#">AAS18272</a>	<a href="https://doi.org/10.1021/bp034308g">https://doi.org/10.1021/bp034308g</a>	Bessette 2004 - Flow Cytometric Screening of cDNA Expression Libraries for Fluorescent Proteins

	<i>Astrangia lajollaensis</i>	alajGFP1	509	517	25.00	223	<a href="#">AAS18270</a>	<a href="https://doi.org/10.1021/bp034308g">https://doi.org/10.1021/bp034308g</a>	Besette 2004 - Flow Cytometric Screening of cDNA Expression Libraries for Fluorescent Proteins
	<i>Astrangia lajollaensis</i>	alajGFP2	509	517	24.70	219	<a href="#">AAS18271</a>	<a href="https://doi.org/10.1021/bp034308g">https://doi.org/10.1021/bp034308g</a>	Besette 2004 - Flow Cytometric Screening of cDNA Expression Libraries for Fluorescent Proteins
	<i>Ceriantharia</i> sp.	OFP	548	573	25.10	222	<a href="#">AAP55761</a>	DOI: 10.1007/s10126-007-9005-5	Ip - 2007 - Characterization of Novel Orange Fluorescent Protein Cloned from Cnidarian Tube Anemone <i>Cerianthus</i> sp.
	<i>Clavularia</i> sp	cFP484	456	484	30.45	266	<a href="#">AF168424</a>	<a href="https://doi.org/10.1038/13657">https://doi.org/10.1038/13657</a>	Matz 1999 - Fluorescent proteins from nonbioluminescent Anthozoa species.
	<i>Condylactis gigantea</i>	cgigGFP	399/482	496	25.74	229	<a href="#">AY037776</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	<i>Condylactis gigantea</i>	cgCP	587 (571)	622 (none)	25.42	227	<a href="#">AF363775</a>	<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">https://doi.org/10.1016/S0014-5793(01)02930-1</a>	Gurskaya 2001 - GFP-like chromoproteins as a source of far-red fluorescent proteins. ; Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	<i>Condylactis gigantea</i>				25.38	227	<a href="#">AY037777</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Matz 2002 - Diversity and evolution of GFP-like fluorescent proteins
	<i>Condylactis passiflora</i>	cpCP	571	none	25.45	227	<a href="#">AF383155</a>	<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">https://doi.org/10.1016/S0014-5793(01)02930-1</a>	Gurskaya 2001 - GFP-like chromoproteins as a source of far-red fluorescent proteins.
	<i>Corynactis californica</i>	ccalGFP1	504	517	24.80	221	<a href="#">AAZ14788</a>	<a href="https://doi.org/10.1007/s10126-007-9072-7">https://doi.org/10.1007/s10126-007-9072-7</a>	Schnitzler 2008 - Spectral Diversity of Fluorescent Proteins from the Anthozoan <i>Corynactis californica</i>
	<i>Corynactis californica</i>	ccalGFP3	505	517	24.80	221	<a href="#">ABI58282</a>	<a href="https://doi.org/10.1007/s10126-007-9072-7">https://doi.org/10.1007/s10126-007-9072-7</a>	Schnitzler 2008 - Spectral Diversity of Fluorescent Proteins from the

									Anthozoan <i>Corynactis californica</i>
	<i>Corynactis californica</i>	ccalOFP1	508	561	25.50	226	<a href="https://doi.org/10.1007/s10126-007-9072-7">AAZ14789</a>	<a href="https://doi.org/10.1007/s10126-007-9072-7">https://doi.org/10.1007/s10126-007-9072-7</a>	Schnitzler 2008 - Spectral Diversity of Fluorescent Proteins from the Anthozoan <i>Corynactis californica</i>
	<i>Corynactis californica</i>	ccalYFP1	514	523	25.00	221	<a href="https://doi.org/10.1007/s10126-007-9072-7">AAZ67343</a>	<a href="https://doi.org/10.1007/s10126-007-9072-7">https://doi.org/10.1007/s10126-007-9072-7</a>	Schnitzler 2008 - Spectral Diversity of Fluorescent Proteins from the Anthozoan <i>Corynactis californica</i>
	<i>Corynactis californica</i>	ccalRFP1	568	598	24.80	221	<a href="https://doi.org/10.1007/s10126-007-9072-7">AAZ67342</a>	<a href="https://doi.org/10.1007/s10126-007-9072-7">https://doi.org/10.1007/s10126-007-9072-7</a>	Schnitzler 2008 - Spectral Diversity of Fluorescent Proteins from the Anthozoan <i>Corynactis californica</i>
	<i>Cyphastrea microphthalma</i>	VFP	491	503	25.60	225	<a href="https://doi.org/10.1111/j.1742-4658.2010.07618.x">CBI12485</a>	<a href="https://doi.org/10.1111/j.1742-4658.2010.07618.x">https://doi.org/10.1111/j.1742-4658.2010.07618.x</a>	Ilagan 2010 - A new bright green-emitting fluorescent protein - engineered monomeric and dimeric forms
	<i>Dendronephthya</i> sp.	dendGFP	492	508	25.81	225	<a href="https://doi.org/10.1073/pnas.06255229">AF420591</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	<i>Dendronephthya</i> sp.	dendRFP	557	575	26.83	234	<a href="https://doi.org/10.1073/pnas.06255229">AF420591</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	<i>Dipsastraea (Favia) favus</i>	KikG	507	517	25.88	227	<a href="https://doi.org/10.1038/sj.embor.7400361">AB193294</a>	<a href="https://doi.org/10.1038/sj.embor.7400361">https://doi.org/10.1038/sj.embor.7400361</a>	Tsutsui 2005 - Semi-rational engineering of a green-emitting coral fluorescent protein into an efficient highlighter
	<i>Dipsastraea (Favia) favus</i>	KikGR	390/507	517	25.76	227	<a href="https://doi.org/10.1038/sj.embor.7400361">AB193293</a>	<a href="https://doi.org/10.1038/sj.embor.7400361">https://doi.org/10.1038/sj.embor.7400361</a>	Tsutsui 2005 - Semi-rational engineering of a green-emitting coral fluorescent protein into an efficient highlighter
	<i>Dipsastraea (Favia) favus</i>	KikGR	583/360	593				<a href="https://doi.org/10.1038/sj.embor.7400361">https://doi.org/10.1038/sj.embor.7400361</a>	Tsutsui 2005 - Semi-rational engineering of a green-emitting coral fluorescent protein into an efficient highlighter

	Discosoma sp.	dis3GFP	503	512	26.02	231	<a href="#">AF420593</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Discosoma sp.	drFP583	558	583	26.05	225	<a href="#">AF168419</a>	<a href="https://doi.org/10.1073/pnas.182157199">https://doi.org/10.1073/pnas.182157199</a>	Wiedenmann 2002 - A far-red fluorescent protein with fast maturation and reduced oligomerization tendency from Entacmaea quadricolor (Anthozoa, Actinaria).
	Discosoma sp.	drFP583	558	583	25.93	225	<a href="#">AF168419</a>	<a href="https://doi.org/10.1038/13657">https://doi.org/10.1038/13657</a>	Matz 1999 - Fluorescent proteins from nonbioluminescent Anthozoa species.
	Discosoma sp.	dsFP593	573	593	26.37	230	<a href="#">AF272711</a>	<a href="https://doi.org/10.1016/S0014-5793(00)01895-0">https://doi.org/10.1016/S0014-5793(00)01895-0</a>	Fradkov 2000 - Novel fluorescent protein from Discosoma coral and its mutants possesses a unique far-red fluorescence.
	Discosoma sp.				26.69	236		<a href="https://doi.org/10.1021/bi0607731">https://doi.org/10.1021/bi0607731</a>	Shu 2006 - Novel chromophores and buried charges control color in mFruits
	Discosoma sp.				25.59	226	<a href="#">AY786537</a>	<a href="https://doi.org/10.1073/pnas.0407752101">https://doi.org/10.1073/pnas.0407752101</a>	Wang 2004 - Evolution of new nonantibody proteins via iterative somatic hypermutation.
	Discosoma sp.				25.51	226	<a href="#">AY786536</a>	<a href="https://doi.org/10.1073/pnas.0407752101">https://doi.org/10.1073/pnas.0407752101</a>	Wang 2004 - Evolution of new nonantibody proteins via iterative somatic hypermutation.
	Discosoma sp.				27.10	236	<a href="#">DQ301560</a>	<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Carter 2003 - Cnidarian fluorescent proteins
	Discosoma sp.				25.79	225	<a href="#">AF545828</a>	<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Wiedenmann 2002
	Discosoma sp.				27.03	236	<a href="#">AY679107</a>	<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Carter 2004 - Cloning of Anthozoan Fluorescent Protein Genes
	Discosoma sp.				27.04	236	<a href="#">AY679106</a>	<a href="https://doi.org/10.1073/pnas.0909204106">https://doi.org/10.1073/pnas.0909204106</a>	Carter 2004 - Cloning of Anthozoan Fluorescent Protein Genes
	Discosoma sp.				26.77	236		<a href="https://doi.org/10.1038/13657">https://doi.org/10.1038/13657</a>	Subach 2009 - Photoactivation mechanism



									of PAmCherry based on crystal structures of the protein in the dark and fluorescent states
	Discosoma striata	dsFP483	443	483	26.44	232	<a href="https://doi.org/10.1016/j.cca.2004.07.002">AF168420</a>	<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Matz 1999 - Fluorescent proteins from nonbioluminescent Anthozoa species.
	Discosoma striata				25.64	227	<a href="https://doi.org/10.1016/j.cca.2004.07.002">AY679108</a>		Carter 2004 - Cloning of anthozoan fluorescent protein genes
	Echinophyllia echinata	eechGFP1	497	510	26.11	229	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206383</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Echinophyllia echinata	eechGFP2	506	520	25.50	224	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206395</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Echinophyllia echinata	eechGFP3	512	524	25.91	228	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206396</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Echinophyllia echinata	eechRFP	574	582	25.60	225	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206387</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Echinopora forskaliana	efor/RFP	589	609	25.66	227	<a href="https://doi.org/10.1371/journal.pone.0002680">EU498726</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Entacmaea quadricolor		552	578	25.50	226		<a href="https://doi.org/10.1038/nmeth1062">https://doi.org/10.1038/nmeth1062</a>	Merzlyak 2007 - Bright monomeric red fluorescent protein with an extended fluorescence lifetime
	Entacmaea quadricolor	eqFP611	559	611	25.93	231	<a href="https://doi.org/10.1073/pnas.182157199">AY130757</a>	<a href="https://doi.org/10.1073/pnas.182157199">https://doi.org/10.1073/pnas.182157199</a>	Wiedenmann 2002 - A far-red fluorescent protein with fast maturation and reduced oligomerization tendency from Entacmaea quadricolor (Anthozoa, Actinaria).
	Entacmaea quadricolor				26.32	233		<a href="https://doi.org/10.1107/S0907444909020927">https://doi.org/10.1107/S0907444909020927</a>	Pletnev 2009 - Rotational order-disorder structure of fluorescent protein FP480.
	Entacmaea quadricolor				24.97	223		<a href="https://doi.org/10.1107/S0907444912020598">https://doi.org/10.1107/S0907444912020598</a>	Pletnev 2012 - Structural basis for bathochromic shift of fluorescence in far-red

									fluorescent proteins eqFP650 and eqFP670
	Entacmaea quadricolor				26.08	231		<a href="https://doi.org/10.1002/pro.654">https://doi.org/10.1002/pro.654</a>	Pletneva 2011 - Crystallographic study of red fluorescent protein eqFP578 and its far-red variant Katushka reveals opposite pH-induced isomerization of chromophore
	Entacmaea quadricolor				25.98	231		<a href="https://doi.org/10.1002/pro.654">https://doi.org/10.1002/pro.654</a>	Pletneva 2011 - Crystallographic study of red fluorescent protein eqFP578 and its far-red variant Katushka reveals opposite pH-induced isomerization of chromophore
	Entacmaea quadricolor				25.86	230	<a href="#">AAQ11988.1</a>	<a href="https://doi.org/10.1073/pnas.182157199">https://doi.org/10.1073/pnas.182157199</a>	Wiedenmann 2002
	Euphyllia ancora				25.54	226	<a href="#">KT452623</a>	<a href="http://doi:10.1038/srep25868">http://doi:10.1038/srep25868</a>	Shikina 2016 - Oocytes express an endogenous red fluorescent protein in a stony coral, Euphyllia ancora: a potential involvement in coral oogenesis.
	Eusmilia fastigiata	efasCFP	466	490	25.86	229	<a href="#">DQ206397</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Eusmilia fastigiata	efasGFP	496	507	24.42	220	<a href="#">DQ206385</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Favites abdita	fabdGFP	508	520	25.45	224	<a href="#">EU498723</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Fimbriaphyllia (Euphyllia) ancora	EaGFP	506	514	25.90	226	<a href="#">QAU55049.1</a>	<a href="https://doi.org/10.1002/mrd.23157">https://doi.org/10.1002/mrd.23157</a>	Chiu 2019 - Testicular somatic cells in the stony coral Euphyllia ancora express an endogenous green fluorescent protein
	Galaxea fascicularis	Azami-Green	492	505	25.96	225	<a href="#">AB107915</a>	<a href="https://doi.org/10.1074/jbc.M304063200">https://doi.org/10.1074/jbc.M304063200</a>	Karasawa 2003 - A green-emitting fluorescent protein

									from Galaxeidae coral and its monomeric version for use in fluorescent labeling.
	Galaxea fascicularis	mAzami-Green	492	505	25.85	225	<a href="https://doi.org/10.1074/jbc.M304063200">AB108447</a>	<a href="https://doi.org/10.1074/jbc.M304063200">https://doi.org/10.1074/jbc.M304063200</a>	Karasawa 2003 - A green-emitting fluorescent protein from Galaxeidae coral and its monomeric version for use in fluorescent labeling.
	Galaxea fascicularis	gfasGFP	492	506	25.99	225	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206389</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Galaxea fascicularis	gfasCP	577	NA	24.95	221	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206394</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Goniopora djiboutiensis	gdjiCP	583	NA	24.84	221	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206376</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Goniopora tenuidens	gtenCP (gtCP)	580	none	24.92	221	<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">AF383156</a>	<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">https://doi.org/10.1016/S0014-5793(01)02930-1</a>	Gurskaya 2001 - GFP-like chromoproteins as a source of far-red fluorescent proteins.
	Heteractis crispa	HcRed	592	645	25.60	227		<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">https://doi.org/10.1016/S0014-5793(01)02930-1</a>	Gurskaya 2001 - GFP-like chromoproteins as a source of far-red fluorescent proteins.
	Heteractis crispa	hcriGFP	405/481	500	25.34	225	<a href="https://doi.org/10.1073/pnas.06255229">AF420592</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Heteractis crispa	hcCP	492 (578)	645 (none)	25.64	227	<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">AF363776</a>	<a href="https://doi.org/10.1016/S0014-5793(01)02930-1">https://doi.org/10.1016/S0014-5793(01)02930-1</a>	Gurskaya 2001 - GFP-like chromoproteins as a source of far-red fluorescent proteins.
	Heteractis magnifica	hmGFP	490	510	25.90	228	<a href="https://doi.org/10.1016/S0006-291X(03)00019-6">AAO16871</a>	<a href="https://doi.org/10.1016/S0006-291X(03)00019-6">https://doi.org/10.1016/S0006-291X(03)00019-6</a>	Tu 2003 - A naturally enhanced green fluorescent protein from magnificent sea anemone (Heteractis magnifica) and its functional analysis
	Hydnophora grandis	hgraFP492	443	492				<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals

	Hydnophora rigida	HriGFP	507	527		132		<a href="https://doi.org/10.1016/j.bbrc.2014.04.042">https://doi.org/10.1016/j.bbrc.2014.04.042</a>	Indrees 2014
	Lobophyllia hemprichii	EosFP (Green)	506	516	25.79		<a href="#">AY765217</a>	<a href="https://doi.org/10.1073/pnas.040366810">https://doi.org/10.1073/pnas.040366810</a>	Wiedenmann 2004 - EosFP, a fluorescent marker protein with UV-inducible green-to-red fluorescence conversion
	Montastraea cavernosa	mcavGFP	506	516	26.74	234	<a href="#">AY037769</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Montastraea cavernosa	mcavRFP	508/572	520/580	25.87	225	<a href="#">AY037770</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Montastraea cavernosa				25.79	225	<a href="#">EU035530</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.89	225	<a href="#">EU035527</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.84	225	<a href="#">AY181556</a>	<a href="https://doi.org/10.1093/molbev/msg130">https://doi.org/10.1093/molbev/msg130</a>	Kelmanson 2003 - Molecular basis and evolutionary origins of color diversity in great star coral Montastraea cavernosa (Scleractinia: Faviida).
	Montastraea cavernosa				25.83	225	<a href="#">AY181557</a>	<a href="https://doi.org/10.1093/molbev/msg130">https://doi.org/10.1093/molbev/msg130</a>	Kelmanson 2003 - Molecular basis and evolutionary origins of color diversity in great star coral Montastraea cavernosa (Scleractinia: Faviida).
	Montastraea cavernosa				26.81	234	<a href="#">AY181554</a>	<a href="https://doi.org/10.1093/molbev/msg130">https://doi.org/10.1093/molbev/msg130</a>	Kelmanson 2003 - Molecular basis and evolutionary origins of color diversity in great star coral Montastraea cavernosa (Scleractinia: Faviida).

	Montastraea cavernosa				25.82	225	<a href="#">AY181552</a>	<a href="https://doi.org/10.1093/molbev/msg130">https://doi.org/10.1093/molbev/msg130</a>	Kelmanson 2003 - Molecular basis and evolutionary origins of color diversity in great star coral <i>Montastraea cavernosa</i> (Scleractinia: Faviida).
	Montastraea cavernosa				25.74	224	<a href="#">EU035531</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				26.74	234	<a href="#">AY037768</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Matz 2002 - Diversity and evolution of GFP-like fluorescent proteins
	Montastraea cavernosa				25.68	224	<a href="#">EU035534</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.71	224	<a href="#">EU035528</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.77	224	<a href="#">EU035532</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.66	225	<a href="#">EU035536</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.88	225	<a href="#">AY362545</a>	<a href="https://doi.org/10.1016/j.febslet.2004.06.043">https://doi.org/10.1016/j.febslet.2004.06.043</a>	Sun 2004 - Biophysical characterization of natural and mutant fluorescent proteins cloned from zooxanthellate corals.
	Montastraea cavernosa				25.78	225	<a href="#">AY056460</a>	<a href="https://doi.org/10.1016/j.febslet.2004.06.043">https://doi.org/10.1016/j.febslet.2004.06.043</a>	Sun 2004 - Biophysical characterization of natural and mutant fluorescent proteins cloned from zooxanthellate corals.
	Montastraea cavernosa				25.85		<a href="#">AF384683</a>	<a href="https://doi.org/10.4319/lo.2003.48.1_part_2.0402">https://doi.org/10.4319/lo.2003.48.1_part_2.0402</a>	Lesser 2003 - Green fluorescent proteins in

									Caribbean Scleractinian corals
	Montastraea cavernosa				25.88	225	<a href="#">AY679111</a>	<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Carter 2004 - Cloning of anthozoan fluorescent protein genes
	Montastraea cavernosa				25.97	227	<a href="#">EU035535</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				26.04	227	<a href="#">AF406766</a>	<a href="https://doi.org/10.4319/lo.2003.48.1_part_2.0402">https://doi.org/10.4319/lo.2003.48.1_part_2.0402</a>	Lesser 2003 - Green fluorescent proteins in Caribbean Scleractinian corals
	Montastraea cavernosa				26.02	227	<a href="#">EU035529</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				26.04	227	<a href="#">EU035533</a>	<a href="https://doi.org/10.1007/s10126-007-9025-1">https://doi.org/10.1007/s10126-007-9025-1</a>	Kao 2007 - Dynamic regulation of fluorescent proteins from a single species of coral.
	Montastraea cavernosa				25.96	227	<a href="#">AY679110</a>	<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Carter 2004 - Cloning of anthozoan fluorescent protein genes
	Montastraea cavernosa				26.02	227	<a href="#">AY181553</a>	<a href="https://doi.org/10.1093/molbev/msg130">https://doi.org/10.1093/molbev/msg130</a>	Kelmanson 2003 - Molecular basis and evolutionary origins of color diversity in great star coral Montastraea cavernosa (Scleractinia: Faviida).
	Montastraea cavernosa				26.06	227	<a href="#">AY181555</a>	<a href="https://doi.org/10.1093/molbev/msg130">https://doi.org/10.1093/molbev/msg130</a>	Kelmanson 2003 - Molecular basis and evolutionary origins of color diversity in great star coral Montastraea cavernosa (Scleractinia: Faviida).
	Montipora digitata	mdigFP486	470	486	24.91	221		<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals

	Montipora digitata	mdigFP514	508	514				<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Montipora digitata	mdigFP572	556	572				<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Montipora efflorescens	meffCFP	467	492	25.99	232	<a href="#">DQ206381</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Montipora efflorescens	meffGFP	492	506	26.54	233	<a href="#">DQ206393</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Montipora efflorescens	meffRFP	560	576	26.51	234	<a href="#">DQ206379</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Montipora efflorescens	meffCP	574	NA	24.97	221	<a href="#">DQ206377</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Montipora foliosa	mfolCP577	577					10.1007/s00338-012-0926-8	D'Angelo 2012 - Locally accelerated growth is part of the innate immune response and repair mechanisms in reef-building corals as detected by green fluorescent protein (GFP)-like pigments
	Montipora foliosa				14.70	133		10.1007/s00338-012-0926-8	D'Angelo 2012 - Locally accelerated growth is part of the innate immune response and repair mechanisms in reef-building corals as detected by green fluorescent protein (GFP)-like pigments
	Montipora millepora	mmilCFP	404	492	25.57	227	<a href="#">DQ206392</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.

	Mycedium elephantotus	meleCFP	454	485	25.90	227	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206382</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Mycedium elephantotus	meleRFP	573	579	25.84	226	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206386</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Platygira lamellina	plamGFP	502	514	26.50	230	<a href="https://doi.org/10.1371/journal.pone.0002680">EU498724</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Pocillopora damicornis				25.09	222		<a href="https://doi.org/10.1016/j.cca.2004.07.002">https://doi.org/10.1016/j.cca.2004.07.002</a>	Carter 2004 - Cloning of anthozoan fluorescent protein genes
	Porites lobata	plopFP490	420	490				<a href="https://doi.org/10.1007/s00338-012-0926-8">https://doi.org/10.1007/s00338-012-0926-8</a>	D'Angelo 2012 - Locally accelerated growth is part of the innate immune response and repair mechanisms in reef-building corals as detected by green fluorescent protein (GFP)-like pigments
	Porites lobata	plobFP610	530	610				<a href="https://doi.org/10.1007/s00338-012-0926-8">https://doi.org/10.1007/s00338-012-0926-8</a>	D'Angelo 2012 - Locally accelerated growth is part of the innate immune response and repair mechanisms in reef-building corals as detected by green fluorescent protein (GFP)-like pigments
	Porites lobata	plobRFP	576	614	26.45	233		<a href="https://doi.org/10.1007/s10126-019-09931-9">https://doi.org/10.1007/s10126-019-09931-9</a>	Bridges 2020 - Expression and Characterization of a Bright Far-red Fluorescent Protein from the Pink Pigmented Tissues of Porites lobata
	Porites porites	pporGFP	495	507	24.73	220	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206391</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Porites porites	pporRFP	578	595	26.05	231	<a href="https://doi.org/10.1371/journal.pone.0002680">DQ206380</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.



	Psammocora sp.	psamCFP	404	492	25.88	230	<a href="#">EU498721</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Ptilosarcus sp.	ptilGFP	500	508	27.05	238	<a href="#">AY015995</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Szent-Gyorgyi 2001 - Luciferases, fluorescent proteins, nucleic acids encoding the luciferases and fluorescent proteins and the use thereof in diagnostics, high throughput screening and novelty items
	Ptilosarcus sp.	ptilGFP	500	508	27.00	238	<a href="#">AAG54097</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family
	Renilla muelleri	rmueGFP	498	510	27.12	238	<a href="#">AY015996</a>		Szent-Gyorgyi 2001 - Luciferases, fluorescent proteins, nucleic acids encoding the luciferases and fluorescent proteins and the use thereof in diagnostics, high throughput screening and novelty items
	Renilla muelleri				36.11	311	<a href="#">AY015988</a>		Szent-Gyorgyi 2001 - Luciferases, fluorescent proteins, nucleic acids encoding the luciferases and fluorescent proteins and the use thereof in diagnostics, high throughput screening and novelty items
	Renilla reniformis	rrenGFP	485	508	26.00	233	<a href="#">Q96319</a>	<a href="https://doi.org/10.1007/s10126-007-9072-7">https://doi.org/10.1007/s10126-007-9072-7</a>	Schnitzler 2008 - Spectral Diversity of Fluorescent Proteins from the Anthozoan <i>Corynactis californica</i>
	Ricordea florida	rfloGFP	508	518	26.01	231	<a href="#">AY037772</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.

	Ricordea florida	rFloRFP	506/566	517/574	25.70	231	<a href="#">AY037773</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Ricordea florida				26.00	231	<a href="#">AY037774</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Matz 2002 - Diversity and evolution of GFP-like fluorescent proteins
	Ricordea florida				25.99	231	<a href="#">AY646065</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Sarcophyton sp.	sarcGFP	483	500	25.83	225	<a href="#">EU498725</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Sarcophyton sp.				25.77	224	<a href="#">AB425088</a>	doi: 10.1038/nmeth.1235	Tsutsui 2008 - Improved membrane voltage measurements by FRET using novel coral fluorescent proteins
	Scolymia cubensis	scubGFP2	497	506	26.61	235	<a href="#">AY037771</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Scolymia cubensis	scubGFP1	497	506	26.63	234	<a href="#">AY037767</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Scolymia cubensis	scubGFP1	497	506		234	<a href="#">AAK71333</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family
	Scolymia cubensis	scubGFP2	497	506		235	<a href="#">AAK71337</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family
	Scolymia cubensis	scubRFP	570	578	26.06	230	<a href="#">AY646064</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Scolymia cubensis	scubRFP	570	578	26.10	230	<a href="#">AAU06843</a>	<a href="https://doi.org/10.1073/pnas.062552299">https://doi.org/10.1073/pnas.062552299</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family
	Seriatopora hystrix	shysCP562	562					<a href="https://doi.org/10.3354/meps07588">https://doi.org/10.3354/meps07588</a>	D'Angelo 2008 - Blue Light Regulation of GFP-Like Protein Expression in Reef-Building Corals
	Stylocoeniella armata	SAASoti	510	519				<a href="https://doi.org/10.1142/S1793545815500285">https://doi.org/10.1142/S1793545815500285</a>	Lapshin 2015 - Fluorescence color diversity of great barrier reef corals

	Stylocoeniella armata	SAASoti	510	589				<a href="https://doi.org/10.1142/S1793545815500285">https://doi.org/10.1142/S1793545815500285</a>	Lapshin 2015 - Fluorescence color diversity of <u>grat</u> barrier reef corals
	Stylocoeniella sp.	stylGFP	485	500	24.99	224	<a href="#">DQ206390</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Stylocoeniella sp.	stylCP	574	NA	24.95	221	<a href="#">DQ206378</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Stylophora pistillata	spisCP	560	NA	24.95	224	<a href="#">DQ206398</a>	<a href="https://doi.org/10.1371/journal.pone.0002680">https://doi.org/10.1371/journal.pone.0002680</a>	Alieva 2008 - Diversity and evolution of coral fluorescent proteins.
	Stylophora pistillata				21.88	192	<a href="#">LSMT01000557</a>	<a href="https://doi.org/10.1038/s41598-017-17484-x">https://doi.org/10.1038/s41598-017-17484-x</a>	Voolstra 2017 - Comparative analysis of the genomes of Stylophora pistillata and Acropora digitifera provides evidence for extensive differences between species of corals
	Stylophora pistillata				17.63	159		<a href="https://doi.org/10.1038/s41598-017-17484-x">https://doi.org/10.1038/s41598-017-17484-x</a>	Voolstra 2017 - Comparative analysis of the genomes of Stylophora pistillata and Acropora digitifera provides evidence for extensive differences between species of corals
	Stylophora pistillata				12.32	109		<a href="https://doi.org/10.1038/s41598-017-17484-x">https://doi.org/10.1038/s41598-017-17484-x</a>	Voolstra 2017 - Comparative analysis of the genomes of Stylophora pistillata and Acropora digitifera provides evidence for extensive differences between species of corals
	Stylophora pistillata				42.43	374		<a href="https://doi.org/10.1038/s41598-017-17484-x">https://doi.org/10.1038/s41598-017-17484-x</a>	Voolstra 2017 - Comparative analysis of the genomes of Stylophora pistillata and Acropora digitifera provides evidence for extensive differences between species of corals
	Trachyphyllia geoffroyi	Kaede green	508	518	25.70	225	<a href="#">BAC20344</a>	<a href="https://doi.org/10.1073/pnas.202320599">https://doi.org/10.1073/pnas.202320599</a>	Ando 2002 - An optical marker based on the UV-induced green-to-red

									photoconversion of a fluorescent protein
	Trachyphyllia geoffroyi	Kaede red	572	580	25.70	225	<a href="#">BAC20344</a>	<a href="https://doi.org/10.1073/pnas.202320599">https://doi.org/10.1073/pnas.202320599</a>	Ando 2002 - An optical marker based on the UV-induced green-to-red photoconversion of a fluorescent protein
	Zoanthus sp.	zFP506	496	506	26.11	231	<a href="#">AF168422</a>	<a href="https://doi.org/10.1038/13657">https://doi.org/10.1038/13657</a>	Matz 1999 - Fluorescent proteins from nonbioluminescent Anthozoa species.
	Zoanthus sp.	zFP538	528	538	26.17	231	<a href="#">AF168423</a>	<a href="https://doi.org/10.1038/13657">https://doi.org/10.1038/13657</a>	Matz 1999 - Fluorescent proteins from nonbioluminescent Anthozoa species.
	Zoanthus sp.	zoan2RFP	552	576	26.41	231	<a href="#">AY059642</a>	<a href="https://doi.org/10.1073/pnas.06255229">https://doi.org/10.1073/pnas.06255229</a>	Labas 2002 - Diversity and evolution of the green fluorescent protein family.
	Zoanthus sp.				25.95	231	<a href="#">AF482451</a>	DOI 10.1007/s12033-008-9131-y	Yanushevich 2003 - Green fluorescent protein from Zoanthus
	Zoanthus sp.				25.94	229	<a href="#">EU625506</a>	DOI 10.1007/s12033-008-9131-y	Bogdanova 2009 - DSN depletion is a simple method to remove selected transcripts from cDNA populations
	Zoanthus sp.				26.04	231	<a href="#">EU625505</a>		Bogdanova 2009 - DSN depletion is a simple method to remove selected transcripts from cDNA populations
<b>Crustacea</b>	Chiridius poppei	CpYGFP	508	518	24.70	219	<a href="#">AB185173</a>	<a href="https://doi.org/10.1016/j.gene.2005.11.031">https://doi.org/10.1016/j.gene.2005.11.031</a>	Masuda 2006 - A novel yellowish-green fluorescent protein from the marine copepod, Chiridius poppei, and its use as a reporter protein in HeLa cells
	Pontella meadi	pmeaGFP2	487	502	24.90	222	<a href="#">AAQ01187</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional

									Features and Structural Complexity
	Pontella meadi	pmeaGFP1	489	504	25.00	222	<a href="https://doi.org/10.1093/molbev/msh079">AAQ01186</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional Features and Structural Complexity
	Pontella mimocerami	pmimGFP1	491	505	25.10	222	<a href="https://doi.org/10.1371/journal.pone.0011517">ACT99046</a>	<a href="https://doi.org/10.1371/journal.pone.0011517">https://doi.org/10.1371/journal.pone.0011517</a>	Hunt 2010 - Very Bright Green Fluorescent Proteins from the Pontellid Copepod <i>Pontella mimocerami</i>
	Pontella mimocerami	pmimGFP2	491	505	25.10	222	<a href="https://doi.org/10.1371/journal.pone.0011517">ACT99047</a>	<a href="https://doi.org/10.1371/journal.pone.0011517">https://doi.org/10.1371/journal.pone.0011517</a>	Hunt 2010 - Very Bright Green Fluorescent Proteins from the Pontellid Copepod <i>Pontella mimocerami</i>
	Pontellidae sp.	pdae1GFP	491	511	24.90	222	<a href="https://doi.org/10.1093/molbev/msh079">AAQ01188</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional Features and Structural Complexity
	Pontellina plumata	ppluGFP1	480	500	24.60	222	<a href="https://doi.org/10.1093/molbev/msh079">AAQ01183</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional Features and Structural Complexity
	Pontellina plumata	ppluGFP2	482	502	24.70	222	<a href="https://doi.org/10.1093/molbev/msh079">AAQ01184</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional Features and Structural Complexity
<b>Hydrozoa</b>	<i>Aequorea australis</i>	AausGFP	398	503	26.20	234		Lambert 2019 - <i>Aequorea victoria</i> 's secrets	Lambert 2019 - <i>Aequorea victoria</i> 's secrets
	<i>Aequorea australis</i>	AausFP1	504	510	26.40	234		Lambert 2019 - <i>Aequorea victoria</i> 's secrets	Lambert 2019 - <i>Aequorea victoria</i> 's secrets
	<i>Aequorea australis</i>	AausFP3	587		26.40	234		Lambert 2019 - <i>Aequorea victoria</i> 's secrets	Lambert 2019 - <i>Aequorea victoria</i> 's secrets

	Aequorea australis	AausFP2	609		25.80	232		Lambert 2019 - Aequorea victoria's secrets	Lambert 2019 - Aequorea victoria's secrets
	Aequorea coerulescens	aceGFP	480	505	24.90	222	<a href="#">AAN41637</a>	<a href="https://doi.org/10.1074/jbc.M109.09232">https://doi.org/10.1074/jbc.M109.09232</a>	Pletneva 2010 - Structural Evidence for a Dehydrated Intermediate in Green Fluorescent Protein Chromophore Biosynthesis
	Aequorea victoria	AcS-CFP	440	480	26.40	235	<a href="#">JX472997</a>	<a href="https://doi.org/10.1007/s00253-014-5975-1">https://doi.org/10.1007/s00253-014-5975-1</a>	Aliye 2015 - Engineering color variants of green fluorescent protein (GFP) for thermostability, pH-sensitivity, and improved folding kinetics.
	Aequorea victoria	GFP	395/471	508	25.60	232	<a href="#">M62653</a>	<a href="https://doi.org/10.1016/0378-1119(92)90691-H">https://doi.org/10.1016/0378-1119(92)90691-H</a>	Prasher 1992 - Primary structure of the Aequorea victoria green-fluorescent protein.
	Aequorea victoria	FF-GFP	400(prot)/490(dep rot)	514	26.60	237	<a href="#">JX472995</a>	<a href="https://doi.org/10.1007/s00253-014-5975-1">https://doi.org/10.1007/s00253-014-5975-1</a>	Aliye 2015 - Engineering color variants of green fluorescent protein (GFP) for thermostability, pH-sensitivity, and improved folding kinetics.
	Aequorea victoria	FFTS-YFP	400(prot)/510(dep rot)	528	26.60	233	<a href="#">JX472996</a>	<a href="https://doi.org/10.1007/s00253-014-5975-1">https://doi.org/10.1007/s00253-014-5975-1</a>	Aliye 2015 - Engineering color variants of green fluorescent protein (GFP) for thermostability, pH-sensitivity, and improved folding kinetics.
	Aequorea victoria				25.70	232	<a href="#">X83960</a>	DOI: <a href="https://doi.org/10.1007/s11693-010-9062-3">https://doi.org/10.1007/s11693-010-9062-3</a>	Raab 2010 - The GeneOptimizer Algorithm: using a sliding window approach to cope with the vast sequence space in multiparameter DNA sequence optimization.
	Aequorea victoria				25.60	232	<a href="#">X83959</a>		Watkins J.N., Campbell A.K. 1994
	Aequorea victoria				25.50	232	<a href="#">JN800726</a>		Mendoza E., Scharff C. 2011
	Anthoathecata	anm2CP	572	597	27.50	241	<a href="#">AAR85352</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily:

									Evolution of Functional Features and Structural Complexity
	Clytia gregaria	cgreGFP	485	500	26.80	238	<a href="#">ADI71929</a>	DOI: 10.1039/C0PP00023J	Markova 2010 - Green-fluorescent protein from the bioluminescent jellyfish Clytia gregaria: cDNA cloning, expression, and characterization of novel recombinant protein
	Clytia hemisphaerica	CheGFP1	488	500	25.90	232	<a href="#">AEP19814</a>	<a href="https://doi.org/10.1098/rsob.130206">https://doi.org/10.1098/rsob.130206</a>	Fourrage 2014 - An endogenous green fluorescent protein-photoprotein pair in Clytia hemisphaerica eggs shows co-targeting to mitochondria and efficient bioluminescence energy transfer
	Clytia hemisphaerica	CheGFP4	488	500	26.89	238	<a href="#">AEP19817</a>	<a href="https://doi.org/10.1098/rsob.130206">https://doi.org/10.1098/rsob.130206</a>	Fourrage 2014 - An endogenous green fluorescent protein-photoprotein pair in Clytia hemisphaerica eggs shows co-targeting to mitochondria and efficient bioluminescence energy transfer
	Clytia hemisphaerica	CheGFP2	488	508			<a href="#">AEP19815</a>	<a href="https://doi.org/10.1098/rsob.130206">https://doi.org/10.1098/rsob.130206</a>	Fourrage 2014 - An endogenous green fluorescent protein-photoprotein pair in Clytia hemisphaerica eggs shows co-targeting to mitochondria and efficient bioluminescence energy transfer
	Labidocera aestiva	laesGFP	491	506	28.07	251	<a href="#">AAQ01185</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional Features and Structural Complexity

	Obelia sp.	obeCFP	400	499	28.13	251	<a href="#">AEL17649</a>	DOI: 10.1039/C1PP05068K	Aglyamova 2011 - Multi-colored homologs of the green fluorescent protein from hydromedusa Obelia sp.
	Obelia sp.	obeCGFP	502	515	26.87	238	<a href="#">AEL17650</a>	DOI: 10.1039/C1PP05068K	Aglyamova 2011 - Multi-colored homologs of the green fluorescent protein from hydromedusa Obelia sp.
	Obelia sp.	obeYFP	514	528	26.95	238	<a href="#">AEL17651</a>	DOI: 10.1039/C1PP05068K	Aglyamova 2011 - Multi-colored homologs of the green fluorescent protein from hydromedusa Obelia sp.
	Olindias formosus	dfGFP	505	524	28.13	251	<a href="#">BBC28143</a>	<a href="https://doi.org/10.1016/j.chembiol.2017.12.005">https://doi.org/10.1016/j.chembiol.2017.12.005</a>	Shinoda 2018 - Acid-Tolerant Monomeric GFP from Olindias formosa
	Phialidium sp.	phiYFP	525	537	4.93	44	<a href="#">AY485333</a>	<a href="https://doi.org/10.1093/molbev/msh079">https://doi.org/10.1093/molbev/msh079</a>	Shagin 2004 - GFP-like Proteins as Ubiquitous Metazoan Superfamily: Evolution of Functional Features and Structural Complexity
<b>Fish</b>	Branchiostoma floridae	bfloGFPa1	500	512	24.60	219		<a href="https://doi.org/10.1038/srep05469">https://doi.org/10.1038/srep05469</a>	Bomati 2014 - Spectral and structural comparison between bright and dim green fluorescent proteins in Amphioxus
	Branchiostoma floridae	bfloGFPc1	493	521				<a href="https://doi.org/10.1038/srep05469">https://doi.org/10.1038/srep05469</a>	Bomati 2014 - Spectral and structural comparison between bright and dim green fluorescent proteins in Amphioxus
	Branchiostoma floridae	LanFP1	500	510	24.60	220		<a href="https://doi.org/10.1186/1745-6150-3-28">https://doi.org/10.1186/1745-6150-3-28</a>	Baumann 2008 - A family of GFP-like proteins with different spectral properties in lancelet Branchiostoma floridae
	Branchiostoma floridae	LanFP2	500	516	23.70	223		<a href="https://doi.org/10.1186/1745-6150-3-28">https://doi.org/10.1186/1745-6150-3-28</a>	Baumann 2008 - A family of GFP-like proteins with



									different spectral properties in lancelet <i>Branchiostoma floridae</i>
	<i>Branchiostoma lanceolatum</i>	LanYFP	513	524	24.70	219	<a href="https://doi.org/10.1038/nmeth.241">ACA48232</a>	<a href="https://doi.org/10.1038/nmeth.241">https://doi.org/10.1038/nmeth.241</a>	Shaner 2013 - A bright monomeric green fluorescent protein derived from <i>Branchiostoma lanceolatum</i>
	<i>Anguilla japonica</i>	UnaG	498	527	15.60	139	<a href="https://doi.org/10.1016/j.cell.2013.05.038">AB763906</a>	<a href="https://doi.org/10.1016/j.cell.2013.05.038">https://doi.org/10.1016/j.cell.2013.05.038</a>	Kumagai 2013 - A Bilirubin-Inducible Fluorescent Protein from Eel Muscle
	<i>Kaupichthys hyoproroides</i>	Chlopsid FP I	498	523	15.80	136		<a href="https://doi.org/10.1371/journal.pone.0140972">https://doi.org/10.1371/journal.pone.0140972</a>	Gruber 2015 - Adaptive Evolution of Eel Fluorescent Proteins from Fatty Acid Binding Proteins Produces Bright Fluorescence in the Marine Environment
	<i>Kaupichthys hyoproroides</i>	Chlopsid FP II	498	523	15.80	136		<a href="https://doi.org/10.1371/journal.pone.0140972">https://doi.org/10.1371/journal.pone.0140972</a>	Gruber 2015 - Adaptive Evolution of Eel Fluorescent Proteins from Fatty Acid Binding Proteins Produces Bright Fluorescence in the Marine Environment
	<i>Gymnothorax zonipectis</i>	GymFP	496	532	15.60	139		<a href="https://doi.org/10.3389/fmars.2021.678571">https://doi.org/10.3389/fmars.2021.678571</a>	Guanaccia 2021 - Discovery and characterization of a bilirubin inducible green fluorescent protein from the moray eel <i>Gymnothorax zonipectis</i>