Diversity and function of fluorescent molecules in marine animals

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Abstract

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

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

Contents

I. Introduction

Light in the marine environment is an important ecological factor and becomes crucial under visually restricted conditions. Adaptations to these conditions include the emission of light by organisms themselves (bioluminescence) and/or the absorption and subsequent emission of lower energy light (i.e. a shift from shorter to longer wavelengths). This process is called fluorescence. Fluorescent light is emitted by molecules excited by light, such as porphyrins, chlorophyll, phycobiliproteins, chitin or green-fluorescent protein (GFP)-like fluorescent proteins (FPs) (García-Plazaola *et al.*, 2015; Macel *et al.*, 2020). More than 300 different fluorescent molecules have been described in different phyla (Figure 1, Appendix I). While fluorescence of many biological molecules is just an intrinsic physical property of the molecule itself (NADH, tryptophane, or chlorophyll) and has most likely no biological functions, various fluorescent molecules have evolved to adapt to specific environments and behaviours (Table 1) (Marshall & Johnsen, 2017; Mazel, 2017). Suggested functions of these molecules include attraction of prey or symbionts, photoprotection, photoenhancement, light harvesting, stress mitigation, mimicry, aposematism, and communication (Figure 2) (Salih, 2000; Mazel *et al.*, 2004; Michiels *et al.*, 2008; Palmer, Modi & Mydlarz, 2009a; Gittins *et al.*, 2014; Haddock & Dunn, 2015; Macel *et al.*, 2020, Ferreira *et al.,* 2023). In the following sections, we will review the different functions and explain the underlying fluorescent systems across various taxa.

II. Functions of fluorescence

(1) Nutritional function - Prey attraction

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

The first discovered FP, GFP was isolated from the cnidarian jellyfish *Aequorea victoria.* Here, GFP acts as an acceptor/antenna molecule for the luciferase aequorin (Shimomura, Johnson & Saiga, 1962; Morin & Hastings, 1971). In this bioluminescent-fluorescent system GFP shifts the blue light produced by aequorin to longer wavelengths, i.e. green light (Morin & Hastings 1971). Various bioluminescent-fluorescent systems have been developed in jellyfish (Morin & Hastings, 1971, Morise *et al.,* 1974, Fourrage *et al.*, 2014). In *Clytia hemispherica*, for example, the light emitting GFPs are located in tentacle bulbs and tentacles, and enhance the bioluminescent spectrum, which is used to lure prey (Fourrage *et al.*, 2014). It has been demonstrated that fluorescent light is used for prey attraction in the hydrozoan *Olindias formosa* (Haddock & Dunn, 2015). It expresses dfGFP that has a 33% homology with *A. victoria* GFP (Shinoda *et al.*, 2017). Blue light illumination of the green fluorescence in the tentacles attracts juvenile rockfish in laboratory settings, while white or yellow light has no effect. The attraction of juvenile rockfish in the laboratory was comparable to in situ observations of benthic fish species (i.e. *Enchelyurus* spp*., Synodus jaculum & Mulloidichthys* sp.) that chased green light, resembling fluorescence-like stimuli (Haddock & Dunn, 2015). Whether the fish reacted to green light or just the movement of light was not addressed. The authors hypothesize that the use of fluorescent lures might be a common mechanism to attract prey in non-visual and visual organisms (Haddock & Dunn, 2015). For example, the non-visual cnidarian predator, the siphonophore *Rhizophysa eysenhardti,* has green fluorescent spots on the tips of the tentacles and along the gastrozooids, which potentially aid in prey capturing of larval fish (Purcell, 1981; Haddock & Dunn, 2015). Similar strategies were suggested for other siphonophores: *Resomia ornicephal, Diphyes dispar* and *Rosacea plicata* to capture euphausiid shrimp (Haddock & Dunn, 2015).

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

In benthic cnidarians that are neither bioluminescent, nor have algal symbionts (Haddock & Dunn, 2015), green fluorescence is found in hydroids of the genus *Cytaeis* (Prudkovsky *et al.*, 2016), in the corallimorph *Corynactis californica* (Schnitzler *et al.,* 2008), and in cerianthid tube anemones (*Cerianthus*) (Wiedenmann *et al*., 2004). *Cytaeis* polyps live on shells of the nocturnal gastropod *Nassarius margaritifer* in the Red Sea (Egypt) and their hypostomes fluoresce green (λ_{em} 518 nm) (Prudkovsky *et al.*, 2016). Even though there is no experimental evidence, the localization of fluorescence in the hypostome may suggest a role for prey attraction.

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

Cephalochordates are the only deuterostomes that express endogenous GFP (Deheyn *et al.*, 2007). Deuterostomian GFP was first found in three species of lancelets (Deheyn *et al.*, 2007) and GFP-encoding genes most likely existed in an ancestral cephalochordate, as these genes occur across distantly related genera of amphioxus (Yue *et al.*, 2016). With 16 different identified GFP genes, the amphioxus *Branchiostoma floridae*, is the species with the highest diversity of GFPs known so far (Bomati, Manning & Deheyn, 2009; Bomati *et al.*, 2014). Red fluorescence emitted by lancelet red fluorescent protein (laRFP, λ_{em} 592 nm) is known from the congeneric *B. lanceolatum* (Pletnev *et al.*, 2013). In *B. floridae*, the various GFPs exhibit different fluorescence intensities, extinction coefficients and absorption profiles, which makes the species an interesting organism for studying the function and evolution of GFP (Bomati *et al.*, 2014). In adult lancelets GFP is concentrated in the oral cirri implicating its role in planktonic prey attraction (Deheyn *et al.*, 2007; Yue *et al.*, 2016).

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

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

(2) Nutritional function - Symbiont attraction

((a)) Cnidaria – Anthozoa (corals)

Echinophyllia aspera (Scleractinia) that fluoresce bright green (λ_{em} 492 and 505 nm) under blue light, attract their symbiotic dinoflagellates of the family Symbiodiniaceae under laboratory conditions (Aihara *et al.*, 2019). The dinoflagellate shows maximum positive phototactic responses towards 510 nm (green) and 680 nm (red) light and negative phototaxis towards strong purple blue (λ_{em} 380-475 nm) light. These experiments suggest that the symbiont avoids light-induced photodamage of the photosynthetic machinery and is maximally attracted by green fluorescence. The attraction hypothesis between corals and symbionts is also supported by the fact that GFP fluorescence is higher in larvae and juvenile coral polyps than in adult colonies and in bleached than in non-bleached corals (Kenkel *et al.*, 2011; Ricaurte *et al.*, 2016; Aihara *et al.*, 2019). Strong fluorescence in bleached corals may help to attract new symbiont communities for improving survival strategies (Bollati *et al.,* 2020). This has also been suggested for colourful coral bleaching, where upregulated FPs may improve recolonization of the symbionts (Bollati *et al.*, 2020).

Moreover, it is proposed that different GFP expression within coral larvae from different reef depths could attract and retain different dinoflagellates, increasing their fitness and chance of survival when arriving in new environments (Scucchia *et al.,* 2020)

(3) Defensive or regulatory function - Photoprotection

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

((a)) Cnidaria – Anthozoa (corals)

In cnidarians the light environment plays a central role in the symbiosis between a heterotrophic host and its autotroph endosymbiont, e.g. the symbiosis between scleractinian corals and dinoflagellates (Symbiodiniaceae) (Muscatine *et al*., 1984). Green fluorescence has been shown to be positively correlated with the photobiology of the symbionts and with coral growth (Salih *et al.* 2006, Roth & Deheyn, 2013). Symbiodiniaceae are involved in the photosynthetic fixation of carbon, which is used as food supply and Ca^{2+} carbonate resource in skeleton growth by the coral. In return, the coral provides ammonium as nutrient for the dinoflagellates. For a vital symbiosis it is important to reduce photodamage, while balancing light harvesting for photosynthesis is maximized (Muscatine, 1990, Takahashi *et al.,* 2009). The role of coral host pigments has recently been reviewed in detail by Ferreira *et al*. (2023). Corals living in shallow reefs may benefit from physiological systems that absorb high-intensity sunlight and emit at longer wavelength to reduce the production of reactive oxygen species (Bou-Abdallah *et al.*, 2006; Palmer *et al.*, 2009a).

Reactive oxygen species can cause damage in the coral tissue, while high-intensity light can cause photoinhibition of photosynthesis by dinoflagellates (Hoegh-Guldberg & Jones, 1999; Gorbunov *et* *al.*, 2001). Although controversially discussed in Cnidaria, mechanisms reducing oxidative stress are vital for an organism. In vitro experiments of Bou Abdallah *et al.* (2006) demonstrated weak scavenging by FPs (shown for avGFP), whereas results of Palmer *et al.* (2009a) do not provide conclusive evidence of an antioxidant role.

Non-fluorescent Chromoproteins (CP) and FPs are frequently, but not exclusively, expressed in the ectoderm, facing the external environment, and shielding the zooxanthellae in the endoderm. Thus, light that reaches the zooxanthellae through the ectoderm is shifted to a longer wavelength, reducing harmful, high-energy radiation for the symbionts or a part of the radiation is absorbed by the CPs (Salih *et al.*, 2000; Mazel *et al.*, 2003b; Oswald *et al.*, 2007, Smith *et al.,* 2013). Non-fluorescent chromoproteins, which are homologous to GFP, are crucial to the light microclimate and, therefore, play an important role in mitigating light stress in shallow water by absorbing light, which has been demonstrated with optical microsensor measurements in symbiotic reef building corals. Here, the upregulation of pink CPs during bleaching leads to a reduction of orange light within the tissue by 10 to 20% compared to low CP-expressing tissue (Bollati *et al.*, 2022).

An optical feedback loop involving dinoflagellate symbionts and corals has been proposed to induce the expression of FPs during colorful bleaching, a world wide reoccuring phenomenon in coral reefs. The upregulation of the photoprotective molecules is driven by increased internal light fluxes after the loss of the symbionts. The upregulation of FPs in bleached coral tissue has been suggested to be important for the recolonization of reef-building corals by symbionts (Bollati *et al.*, 2020).

Different colour morphs of FPs are known from various coral species (Alieva *et al.*, 2008; Meyers, Porter & Wares, 2013; Eyal *et al.*, 2015; Gittins *et al.*, 2014). The perception of specific colors by their emission wavelength may differ between observers. The classifications of the colors and names of the fluorescent proteins are not uniform and there are different divisions of the color classes (Alivea *et al.*, 2008, Chudakov *et al.*, 2010, Ferreira *et al.*, 2023). In this review we refer to the emission colors as follows: violet = 380 - 434 nm, cyan = 435 - 499 nm, green = 500 - 560 nm, yellow = 561 - 570 nm, orange = 571 - 590 nm, red = 591 - 739 nm (Figure 1). Fluorescent proteins often exist as multicopy genes, contributing to high levels of FP production and allowing adjustment of transcript levels in response to the light environment. Thus, transcription of multicopy genes in reef corals allows for fast changes in the colour combinations within an FP population, most likely to adapt to environmental changes in the habitat. This has been demonstrated for the red amilFP597 from *Acropora millepora* in which transcript levels increase with light intensity and vary among colour morphs (Gittins *et al.*, 2014). In addition, Satoh *et al.* (2021) show that different colour morphs of *Acropora tenuis* with different expression of fluorescent proteins could play a role in physiological response of environmental stress (Satoh *et al.*, 2021). These findings suggest that colour polymorphism in reef corals depends on environmental factors. It may contribute to the reduction in photodamage and to diversification and optimization of physiological responses (Shagin *et al.*, 2004; Meyers *et al.*, 2013; Gittins *et al.*, 2014).

High GFP levels have also been suggested to provide protection of RNA from oxidative damage by UV-light. An upregulation of GFP could help avert damage by scattering UV-light (as suggested by Grinblat *et al.*, 2018). Some FPs show a small, but recognizable absorbance of UV-light (Karasawa et al. 2003, Alieva 2009). However, UV-light (250- 400 nm) protection would be limited to shallow water levels since it is readily absorbed with increasing depth (Fleischmann 1989). Only limited amounts of UV-light are transmitted to mesophotic reefs as reported by Eyal et. al (2015). Furthermore, experiments testing different colour morphs did not find any significant decrease in DNA damage due to ultraviolet radiation (UVR) (Ben-Zvi et al. 2019). Green fluorescent protein is not only expressed in adult coral colonies but also in planula larvae, particularly in regions undergoing high cell differentiation with high transcription levels (Grinblat *et al.*, 2018). Planula larvae of *Stylophora pistillata* show stronger fluorescence in shallow than in mesophotic reefs (Scucchia et al. 2020). Fluorescence intensity was, however, not quantified but interpreted visually through photographs. Scucchia et al. (2020) also found that larvae from shallower colonies possess higher levels of GFP-like Chromoprotein. Although the GFP-like CP is not fluorescent, its absorption spectrum may help in photoprotection (Scucchia *et al.*, 2020). It should be noted that a discrimination of GFP and GFP-like chromoproteins is not consistent throughout the literature and both molecules are frequently intermingled and used as homologous.

High expression of FPs has also been observed in injured and regenerating growth areas of corals, which also reveal high transcription and DNA synthesis (D'Angelo *et al.*, 2012; Grinblat *et al.*, 2018). In cephalochordates, GFP is upregulated in oocytes and spawned eggs (Deheyn *et al.*, 2007; Yue *et al.*, 2016), suggesting a similar role in photoprotection of RNA/DNA as in coral larvae.

Another dinoflagellate-host system where photoprotection is discussed as function of FPs occurs in actiniarians. At least five different morphs of the actiniarian *Anemonia viridis* (*var. rustica*, *smaragdina, rufescens*, *viridis* and *vulgaris*) as well as *Condylactis gigantea* and *Heteractis crispa* express FPs and non-fluorescent pink-red and purple-blue CPs in the tips of their tentacles (described for *Anemonia viridis var. smaragdina*, *rufescens* and *viridis*) (Wiedenmann, Röcker & Funke, 1999; Wiedenmann *et al.*, 2000; Lukyanov *et al.*, 2000; Labas *et al.*, 2002; Leutenegger *et al.*, 2007b; Mallien *et al.*, 2018).

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

Converting light energy between different host pigments (e.g., CFP and GFP) via Förster resonance energy transfer (FRET) might act as a photoprotective mechanism (Gilmore et al., 2003, Salih et al., 2004). FRET occurs between two light sensitive molecules when the acceptor's absorption spectra and the donor's fluorescence emission spectra energetically overlap, they show the proper dipole-

dipole orientation, and they fall within the intermolecular distance (as described in Gilmore et al., 2003). This process was observed in *Acropora spp.* via fluorescence lifetime imaging (Gilmore et al., 2003, Cox et al., 2007) and FPs suitable for light conversion have been proposed in densely aggregated FP granules of other coral species (Salih et al., 2004). The absence of FRET among FPs in shade-acclimated samples (*Euphyllia ancora*) may reflect a reduction in the demand for photoprotection as a result of the transition from high light reef environments to shaded aquarium environments (Cox et al., 2007).

((b)) Annelida (segmented worms)

The intertidal worm *Eulalia sp.* secretes a proteinaceous fluorescent complex including ubiquitin, 14-3-3 protein and peroxiredoxin. This mucus/complex when excited by UV light emits light in the blue-green spectrum, where intensity of light emission is dependent on the redox state. The authors suggest that the mucous containing the fluorescent complex has an antioxidant function and protects the worm against high-energy radiation during foraging at daylight (Rodrigo *et al.*, 2022).

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

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

(4) Photoenhancement

((a)) Porifera (sponges)

Fluorescence mediated photoenhancement is discussed as providing better light conditions to photosynthesizing symbionts in Porifera (Read, Davidson & Twarog, 1968). It is mentioned as potential function but has not been shown experimentally, so far. In the Mediterranean sponge *Aaptos aaptos* ultraviolet excited fluorescence occurs in the archaeocytes (amoebocytes) (Liaci, 1962). The yellow tube sponge *Aplysina fistularis* has a green-yellow colour at a depth of 40 m due to a fluorescent pigment that has been identified in the lamellar portion of the sponge fibres. In addition, *Halisarca dujardini,* an intertidal, non-tropical, spiculeless sponge, contains fluorochromes similar to those in *Aplysina fistularis* (Read *et al.*, 1968).

((b)) Cnidaria – Anthozoa (corals)

The dominant occurrence of one colour morph in depth-specialistic coral species may hint that FPs may enhance the light environment in mesophotic reefs (Roth *et al.* 2015), which are characterized by areas of low light penetration. Green or red light reaches vaster in the coral tissue to the symbionts and complements the predominantly blue light spectrum in deeper water layers (Schlichter, Fricke & Weber, 1986; Salih *et al.*, 2000, 2006; Eyal *et al.*, 2015; Smith *et al.*, 2017). Photoconvertible red fluorescent proteins (pcRFPs) can contribute to 50% of orange/red light, that is available to the symbionts at mesophotic depths. Measurements with microsensors placed directly in the coral tissue showed that red light penetrates deeper into the tissue than green light and could be available for photosynthetic symbionts located in deeper tissue layers (Bollati *et al.*, 2022). Light transformation from green to red wavelengths via FRET in subunits of pcRFPs has been proposed to facilitate photosynthesis (note that this process is dependent on the photoconversion action spectrum of pcRFPs) (Bolatti et al., 2017, Wiedenman et al., 2004a). Additionally, FRET occurs under physiological conditions in non-photoconvertible RFPs, that evolve due to incomplete maturation (Matz et al., 1999).

It was shown that fluorescence is shifted to longer wavelengths of light (orange and red) in deeper reefs, while green fluorescence is more common in shallow reefs (Eyal *et al.*, 2015). Interestingly, yellow fluorescence has only been observed in mesophotic reef corals so far (Eyal *et al.*, 2015). So called yellow FPs (e.g. zFP538 (λ_{Em} 538nm) from *Zoanthus sp.* or ccalYFP1 (λ_{Em} 523nm), and ccalOFP (λ_{Em} 561 nm) from *Corynactis californica*) have also been found in non scleractinian corals in shallow reefs (Matz *et al.*, 1999; Schnitzler *et al.*, 2008).

((c)) Annelida (segmented worms)

Photoenhancement has also been suggested for annelids and involves a shift of bioluminescent light (Hastings, 1996). In the putative light organs of *Tomopteri*s *spp.* (pelagic annelids) a fluorescent signal is correlated with the emission of bioluminescent light (Gouveneaux *et al.*, 2017). It has been proposed that the fluorescence is most likely produced by a breakdown product of the chemiluminescent reaction, which was first demonstrated in the polynoid worm *Acholoe astericola* (Bassot & Bilbaut, 1977; Bassot & Nicolas, 1995; Gouveneaux *et al.*, 2017). In *Tomopteris spp.* that exhibit a unique, yellow-orange luminescence in their parapodia, a quinone derivative (anthraquinone; Aloe-emodin) has been isolated and is suggested to be involved in bioluminescent light emission. In the tubeworm *Chaetopterus variopedatus* blue and green luminescence have been described in the mucus (Deheyn *et al.*, 2013; Branchini *et al.*, 2014). The green fluorescence is most likely emitted by riboflavin (λ_{em} 525 nm) or a related derivative, which has been isolated from the mucus (Branchini *et al.*, 2014). Interestingly, riboflavin cannot be synthesized by tubeworms themselves and needs to be acquired from an external source. Therefore, it has been proposed that annelids may acquire fluorescent molecules with their nutrition (Fox *et al.*, 1952). In addition, intense blue fluorescence after emission of bioluminescent light was detected in the mucus of the fireworm *Odontosyllis phosphorea*, suggesting that an oxidized product resulting from light production mediates fluorescence (Deheyn & Latz, 2009; De Meulenaere, Puzzanghera & Deheyn, 2020). While these studies suggest that fluorescence increases the bioluminescent spectra, the ecological implications of these bioluminescence-fluorescence systems need to be further explored.

(5) Ontogenetic changes in FP patterns and potential functions in early life stages

((a)) Cnidaria – Anthozoa (corals)

Fluorescence can be found very early during coral development within eggs, embryos, larvae, and polyps (Hirose, Kinzie & Hidaka, 2000; Leutenegger *et al.*, 2007a; Roth *et al.*, 2007; D'Angelo *et al.*, 2008; Grinblat *et al.*, 2018). In fact, fluorescence can be used to detect coral recruits (Piniak *et al.*, 2005; Baird, Salih & Trevor-Jones, 2006). Larvae of *Acropora millepora* can express red and green fluorescent proteins, with no correlation between fluorescent colour of the parent colony to the larvae (Kenkel *et al.*, 2011). Interestingly, larvae with red fluorescence have lower colonization success than those with green fluorescence and heat stress reduces the red fluorescence (Kenkel *et al.*, 2011). In *Seriatopora hystrix*, a developmental change from two green (larvae) to one cyan (adult) fluorescing protein occurs. In the larvae, two GFPs co-exist, with the peak emission of one GFP (499 nm) overlapping with the peak excitation of the second GFP (504 nm), which may allow energy transfer if the GFPs are in close proximity (Roth, Fan & Deheyn, 2013). Larvae showed large ranges in GFP fluorescence, dinoflagellate abundance and size, suggesting that coral larvae have the physiological capacity to adapt to many different light microhabitats (Roth, Fan & Deheyn, 2013).

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

(6) Bilirubin binding to reduce cellular, oxidative stress

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

Green and red fluorescent patterns have been observed in moray eels (Muraenidae) (Guarnaccia *et al.*, 2021), false morays (Chlopsidae) (Sparks *et al.*, 2014) and eels (Anguillidae) (Hayashi & Toda, 2009; Kumagai *et al.*, 2013). The FPs are believed to have regulatory functions in stress mitigation (Funahashi *et al.*, 2016). Japanese eels *Anguilla japonica* express fluorescent green proteins of a different family (UnaG) (Kumagai *et al.*, 2013). UnaG belongs to the family of fatty acid binding proteins (FABPs). Green fluorescence is mediated by noncovalent binding of an endogenous ligand bilirubin, a membrane-permeable heme metabolite in a non-conjugated form (Kumagai *et al.*, 2013). The entire bilirubin molecule is closely coordinated within the holoprotein complex, located deep in the barrel structure. UnaG emits green fluorescence independent of oxygen (Kumagai *et al.*, 2013). In young *A. japonica* UnaG is expressed in the white muscles, particularly in small fibres. These muscle fibres represent the late developing fibres during muscle growth, and it is assumed that the expression of the fluorescent FABP is attenuated with the onset of muscle growth in juveniles. The long-distance migration cycle of the eel from freshwater to the Philippine Sea puts considerable demands on the metabolic physiology of the skeletal muscles (Kumagai *et al.*, 2013). Due to the non-covalent binding of bilirubin to the UnaG, it has been suggested that the accumulation of this metabolite is regulated, which could constitute benefits during the permanent strain on the muscles during migration. Bilirubin molecules, whose degradation as ligands has been found to be significantly slowed down, potentially provide antioxidant activities, while fatty acid binding proteins are involved in metabolism and the homeostasis of oxidative stress (Kumagai *et al.*, 2013). Accordingly, the fluorescent holoprotein in the eel may contribute to muscle metabolism and to the reduction of cellular, oxidative stress that arises during long-distance migration (Kumagai *et al.*, 2013; Funahashi *et al.*, 2016). It has been suggested that the eel blood plasma containing biliverdin (abundant form of heme metabolite) is enzymatically reduced to bilirubin in skeletal muscle cells. It binds to the protein, expresses green fluorescence and functions as a complex, like a scavenger of hydrogen peroxide and/or hydroxyl radical. After the cells are exposed to oxidative stress during the long-distance migration, bilirubin is oxidized in biliverdin and transported to blood circulation (Funahashi *et al.*, 2016). Other members of the bilirubin binding FPs have also been identified in two chlopsid eels *Kaupichthys hyoproroides* and *Kaupichthys n. sp.* (Chlopsid FP I and II) and in the moray eel *Gymnothorax zonipectis* (GymFP) (Gruber *et al.*, 2015; Guarnaccia *et al.*, 2021). Since most moray eels do not show fluorescence in a comparable habitat and do not migrate for long-distances the ecological and physiological function of GymFP should be investigated further.

(7) Immune response

((a)) Cnidaria – Anthozoa (corals)

In corals, FPs have also been suggested to play a role in the immune response. The immune response in corals is mediated by pathogen recognition receptors that recognize microbes and activate several downstream signalling pathways. During infection with the trematode *Podocotyloides stenometre*, the expression of green FPs changes towards red FPs in trematodiasis-compromised tissue (Palmer *et al.*, 2009b). Pigmentation at alternatively compromised tissue has been described in other corals (Willis, Page & Dinsdale, 2004; Bongiorni & Rinkevich, 2005; Ravindran & Raghukumar, 2006a, 2006b; Palmer, Mydlarz & Willis, 2008, D'Angelo *et al*., 2012). The increased expression of CPs and FPs in immunocompromised coral tissues suggests a role in coral immunity (Palmer *et al.*, 2008, 2009b; Chudakov *et al.*, 2010). It was also suggested that fluorescence can potentially serve as tool for monitoring coral health (Ramesh *et al*., 2019).

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

Green fluorescence is also found in the skin of sharks. The swell shark *Cephaloscyllium ventriosum* from the eastern Pacific and the chain catshark *Scyliorhinus retifer* from the western Atlantic reveal a high-intensity green fluorescence in the lighter colored areas of the skin (catshark) and the dark spots of the skins (swell shark) (Park *et al.*, 2019). This fluorescence is produced by brominated tryptophan-kynureinine metabolites. In phosphate buffered saline these compounds reveal exitation peaks in the UV-blue range (λ_{ex} 360-438 nm) and emission peaks in the blue-green range (λ_{em} 400-507 nm) (Park *et al.*, 2019). The authors suggest that the fluorescent molecules may play a role in immune response, since kynurenine metabolism regulates host-microbiome signaling and immune response in humans.

(8) Light-driven electron transfer

Various phyla. Another possible function of FPs is their active role in light-driven electron transfer (Bogdanov *et al.*, 2009). It has been observed that under anaerobic conditions GFP undergoes photoconversion into a red fluorescent state (Elowitz *et al.*, 1997), a process called “redding” (Bogdanov *et al.*, 2009). During this process, GFP of diverse origin can act as light-induced electron donor in photochemical reactions with electron acceptors such as cytochrome c, FMN, FAD or NAD+ (Bogdanov *et al.*, 2009). Light-induced electron transfer seems to be a common feature of FPs of different phyla (e.g. jellyfish, anthozoans, copepods and lancelets) (Chudakov *et al.*, 2010) and is dependent on the chromophore. The electron transfer only takes place in natural Tyr66-based chromophores, while mutants with artificial Trp66- or His66-based chromophores are inactive. This suggests a high evolutionary pressure if FP-mediated redox reactions are involved in specific cellular processes. This hypothesis has been challenged because the light-induced transfer of two electrons from a FP to an oxidant such as NAD+ leads to an irreversible inactivation of the FP. However, sensory function might still be a possible explanation, since it does not require excessive electron transfer (Chudakov *et al.*, 2010; Povarova *et al.*, 2017).

(9) Mimicry, aposematism and camouflage

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

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

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

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

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

(10) Intraspecific communication

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

((a)) Mollusca – Cephalopods (squids)

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

((b)) Arthropoda – Copepoda

In copepods FPs have been isolated and characterized from *Chiridius poppei* (cpYGFP) (Masuda *et al.*, 2006), *Pontelina plumata* (ppluGFP1, ppluGFP2 (Evdokimov *et al.*, 2006)), *Pontella meadi* (pmeaGFP1, pmeaGFP2), *Pontella mimocerami* (pmimGFP1, pmimGFP2), *Labidocera aestiva* (laesGFP), and an unidentified species (pdae1GFP) (Shagin *et al.*, 2004; Hunt *et al.*, 2010). Pontellidae have elaborate eyes and show sexual dimorphism in eye design with different fluorescent patterns (e.g. *P. mimicerami*). It has been proposed that detection of fluorescent pattern might be involved in intraspecific recognition (Ohtsuka & Huys, 2001; Shagin *et al.*, 2004; Evdokimov *et al.*, 2006). Herring (1988) described a sexual dimorphism of fluorescent patches, which are associated to bioluminescent glands of calanoid copepods (*Oncaea conifera*). But whether fluorescence, or other factors such as body size, enhances mating success or is only a side effect of bioluminescence remains to be determined (Herring, 1988). Blue fluorescent (in the open ocean) or green fluorescent (in nearshore waters) pigments were suggested to work as countershading mechanism for copepods (as suggested for *L. aestiva*) (Shagin *et al.*, 2004). In the mantis shrimp *Lysiosquillina glabriuscula* fluorescent displays enhance visual communication. Here, antennal scales and the carapace show yellow fluorescing patches. Fluorescent patches accentuate weapons and are discussed as a threat display towards potential predators or males of the same species (Mazel *et al.*, 2004).

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

In marine fish, little is known about the ability to perceive fluorescence. Several studies, however, suggest the perception of red fluorescence, which requires red shifted photoreceptors. The red fluorescent goby *Eviota pellucida,* the blenny *Tripterygion delaisi* and the fairy wrasse *Cirrhilabrus solorensis* reveal maximum absorbance in the visual pigments of 460-540 nm (Michiels *et al.*, 2008; Gerlach *et al.*, 2016; Bitton *et al.*, 2017). The retina of *C. solorensis* possesses one class of rods and three spectrally distinct classes of cones with maximum absorbance around 530 nm (Gerlach *et al.*, 2016). It has been suggested that the absorption spectrum of the long-wavelength opsins (λ_{abs} 530-540 nm) are sufficiently overlapping with the emission spectra of red fluorescence (λ_{em} 600-650 nm) (Michiels *et al.*, 2008; Anthes *et al.*, 2016). In addition, red shifted photoreceptors (λ_{abs} 550-580 nm) have been described in *Thalassoma dupery*, several seahorses and pipefish (Syngnathidae), and the goby *Gobiusculus flavescens* (Barry & Hawryshyn, 1999; Utne-Palm & Bowmaker, 2006; Mosk *et al.*, 2007; Anthes *et al.*, 2016). The triggerfish *Rhinecanthus aculeatus*, the wrasse *C. solorensis* and the blenny *T. delaisi* recognize red fluorescence > 600 nm wavelengths as has been tested in physiological and behavioural assays. In these behavioural assays the wrasse *C. solorensis,* for example, showed more aggressive behaviour by recognizing possible fluorescent rivals in comparison to non-fluorescent rivals. In addition, the triplefin *T. delaisi* showed an increase in choice behaviour to a red fluorescent cue, that is similar to their own fluorescence (Cheney *et al.*, 2013; Gerlach, Sprenger & Michiels, 2014; Gerlach *et al.*, 2016; Kalb *et al.*, 2015; Bitton *et al.*, 2017).

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

Fluorescent patterns among closely related reef fish show species-specific variations, for example in *Eviota* and *Enneapterygius* (Michiels *et al.*, 2008). In addition, interspecific variation has been observed in members of the lizardfish genus *Synodus* and the goby genus *Eviota* (Sparks *et al.*, 2014), while intraspecific variation has been described in the juvenile arctic snailfish *Liparis gibbus* (Gruber & Sparks, 2021). Investigations regarding fluorescent body patterns in pseudocheilinid wrasses varied greatly across species (Gerlach *et al.*, 2016). These findings suggest a role of fluorescent patterns in intraspecific recognition (Sparks *et al.*, 2014). Moreover, fins, i.e. the anal fin (Gobiidae), the first dorsal fin (Tripterygiidae) or the caudal fin (Syngnathidae) can be fluorescent. These fins have been proposed to be involved in intraspecific signalling (Michiels *et al.*, 2008).

Differences in fluorescence intensity and patterns are observed between males and females of different vertebrate species and suggest an involvement in sexual communication (Anthes *et al.*, 2016; Gerlach *et al.*, 2016). Flatfish possess different fluorescent patterns on an individual's blind and sight surface. During mating, flatfish flash their blind sides to each other (Sparks *et al.*, 2014). In general, sexually dimorphic fish show an increased abundance of fluorescent fins (Anthes *et al.*, 2016). Recently, green and red fluorescent leucosome-like pigment organelles (fluoroleucophores) have been described in embryos of the Arabian killifish *Aphanius dispar* (Hamied *et al.*, 2020). Knock-out of GTP cyclohydrolase abolishes the fluorescence, suggesting that fluorescence involves molecules associated with the pterine biosynthesis pathway. The authors suggest that the Arabian killifish may have developed strong reflecting leucophores as a photoprotection mechanism or that this fluorescence could be a visual signal involved in mating (Hamied *et al.*, 2020).

III. Other observations of fluorescence

Besides the studies mentioned above, which provide evidence or hypothesis for the function of fluorescence in marine animals, there is an additional number of studies reporting fluorescence in taxa where the functions have not – or hardly - been studied. To date, more than 200 different FPs are known from Hexacorallia, Crustacea, Hydrozoa, Cephalochordata, and fish (Figure 1, Appendix II). In addition, fluorescent molecules have also been described in soft corals, blue corals, sea pens, and gorgonians (Alcyonacea, Helioporacea, and Pennatulacea). Some Octocorallia are azooxanthellate filter-feeders but some, mostly those found in shallow depths, possess symbiotic algae (Ruppert, Fox & Barnes, 2004). In Octocorallia, bioluminescent species are found in pennatulaceans, alcyonaceans (in *Paraspaerasclera grayi*, in the genera *Anthomastus*, and *Iridogorgia*), and in gorgonians (in the genera *Halypterus, Iridogorgia*, *and Chrysogorgia*) with some species expressing fluorescent antenna proteins (Panceri, 1872; Parker, 1920; Harvey, 1952; Nicol, J., A., C., 1955; Haddock, Moline & Case, 2010; Raddatz *et al.*, 2011; Frank, Tamara, M. *et al.*, 2016). Luciferases, for example, coexist with GFPs in *Renilla mülleri, Renilla köllikeri, Stylatula elongate, Acanthoptilum gracile*, and *Ptilosarcus guernyi,* (Wampler *et al.*, 1973; Shimomura & Johnson, 1975; Matz *et al.*, 1999; Labas *et al.*, 2002; Alieva *et al.*, 2008; Haddock *et al.*, 2010). In addition, FPs have been identified in the genera *Clavularia*, *Dendronephyta*, and *Sarcophyton* (all Alcyonacea) (Matz *et al.*, 1999; Labas *et al.*, 2002; Alieva *et al.*, 2008). Red fluorescence has also been described in Octocorallia, but most likely originates from chlorophyll (Alderslade & McFadden, 2007; Zawada & Mazel, 2014; Leal *et al.*, 2015; Holm & Heidelberg, 2016).

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

In marine gastropods and bivalves, the structural composition of the mussel shell plays an important role of absorbing, transmitting and reflecting light (Prudkovsky *et al.*, 2016). The shell of the oyster *Pinctada vulgaris* contains a lamellar pattern of red fluorescence that consists of red and black parallel zones (Arma *et al.*, 2014). The fluorophore porphyrin causes the red fluorescence seen when the prismatic layer of the shell is exposed to a certain wavelength of light (Arma *et al.*, 2014). Giant clams of the genus *Tridacna* and *Hippopus* (Bivalvia) live in a symbiosis with photosynthetic algae of the family Symbiodiniaceae and reveal a red fluorescence. These symbiotic algae are hosted in the clam's mantle tissue (Carlos, Baillie & Maruyama, 2000; Maxwell & Johnson, 2000; Yau & Fan, 2012) and show a far-red fluorescence associated to chlorophyll photosystem II (Jeffrey & Haxo, 1968; Maxwell & Johnson, 2000). The symbionts' fluorescence can be studied to better understand the symbiosis and to assess the current state of health of bivalves or even entire reefs (Maxwell & Johnson, 2000; Rowan, 2004; Yau & Fan, 2012).

Many marine fish reveal fluorescence with unknown function and often unknown origin. These include cartilaginous (such as sharks and rays) as well as bony, especially ray-finned fish such as scorpionfish (Scorpaenoidei), blennie (Blennioidei), gobie (Gobioidei), flatfish (Pleuronectiformes), and numerous other tropical reef fish (Sparks *et al.*, 2014). Families like pipefish and seahorses (Syngnathidae), and dragonets (Callionymidae) reveal red fluorescence with emission patterns ranging from small defined areas to an irregular and interspersed distribution across the body

(Anthes *et al.*, 2016). Out of 665 fish species examined 40% (272 species) showed red fluorescence. Emission of red fluorescence involves iridophores with fluorescent guanine crystals (Michiels *et al.*, 2008; Wucherer & Michiels, 2014), fluorescent chromatophores (Wucherer & Michiels, 2012), fluorescent scales and fin rays (Michiels *et al.*, 2008) (summarized in (Anthes *et al.*, 2016)).

IV. Conclusion

(1) Fluorescent molecules in marine organisms fulfil a broad range of functions across various taxa.
(2) Most hypotheses regarding the function of fluorescence have been surmised from the morphology of the animal. Very few experiments mainly conducted in corals and fish have been performed specifically to identify and verify the functions of fluorescence.
(3) The number of fluorescent molecules published in different taxa reflects limited knowledge of the taxonomic distribution of fluorescence. Most fluorescent molecules are known from Cnidaria.
(4) The well-studied functions of FPs in corals and their importance for photoprotection, photoenhancement, symbiont and prey attraction, and stress mitigation demonstrate how important it is to better understand the mechanisms that help corals cope with climate change and how these are related to fluorescent molecules.
(5) It is possible that important functions in mitigating climate change effects can be found in more marine taxa than corals. Research on fluorescent marine organisms, therefore, holds an unknown potential for marine conservation.

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VI. Competing interests

The authors declare that they have no competing interests.

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VIII. Authors' contributions

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

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X. Supporting Information

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

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

Table and figure headings:

Table 1: Detailed list of functions of fluorescent molecules in marine animals and their effects on behavioural and physiological responses.

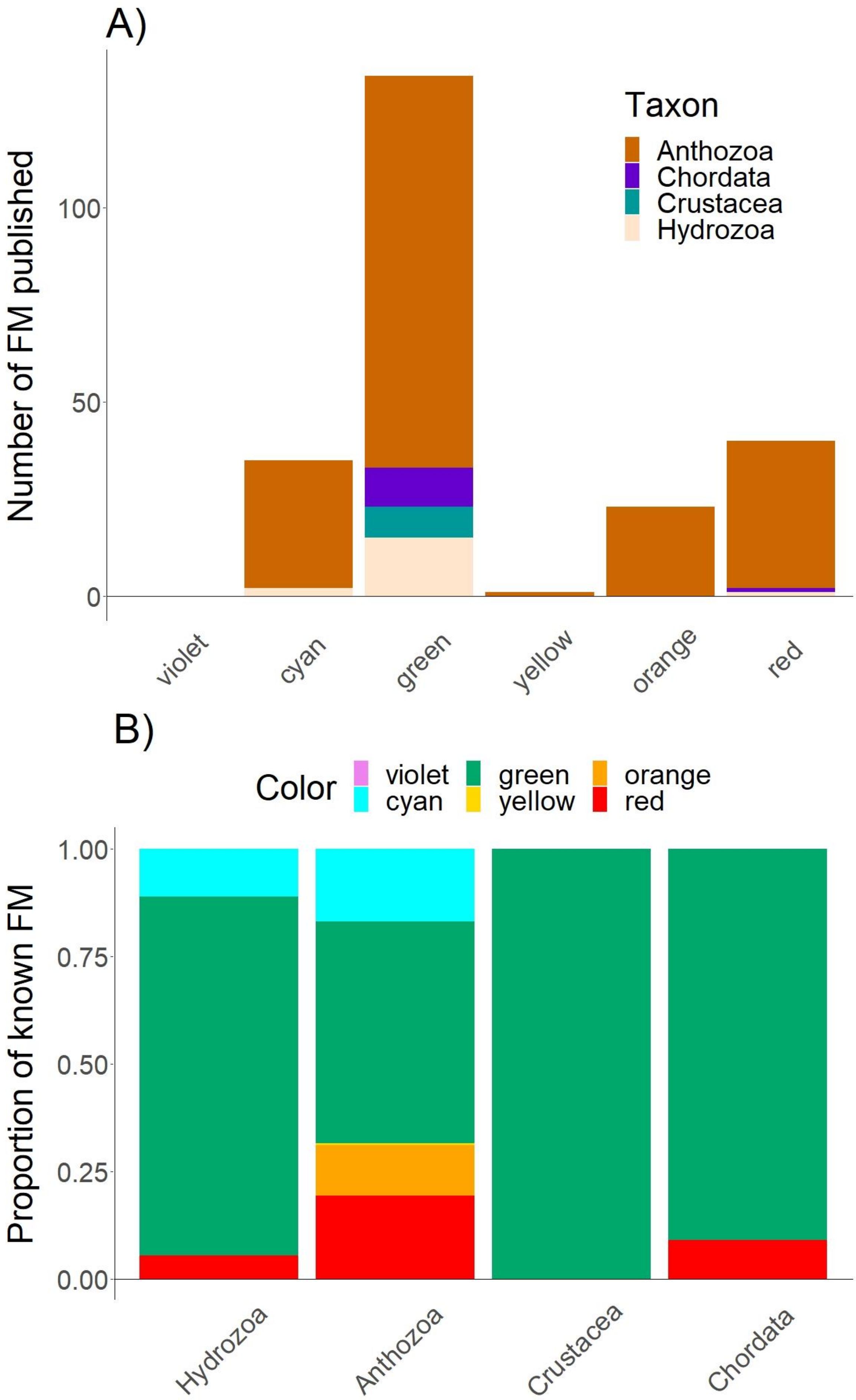
A)
Number of FM published
0
50
100
violet
cyan
green
yellow
orange
red
Taxon
Anthozoa
Chordata
Crustacea
Hydrozoa
B)
Color
violet
cyan
green
yellow
orange
red
Proportion of known FM
0.00
0.25
0.50
0.75
1.00
Hydrozoa
Anthozoa
Crustacea
Chordata

Figure 1: Distribution of fluorescent molecules across taxa. (A) Number of published fluorescent molecules (FM) sorted by emission wavelength and taxa. (B) Relative occurrence of fluorescent molecules of different emission wavelengths across taxa (violet = 380 - 434 nm, cyan = 435 - 499 nm, green = 500 - 560 nm, yellow = 561 - 570 nm, orange = 571 - 590 nm, red = 591 - 739 nm).

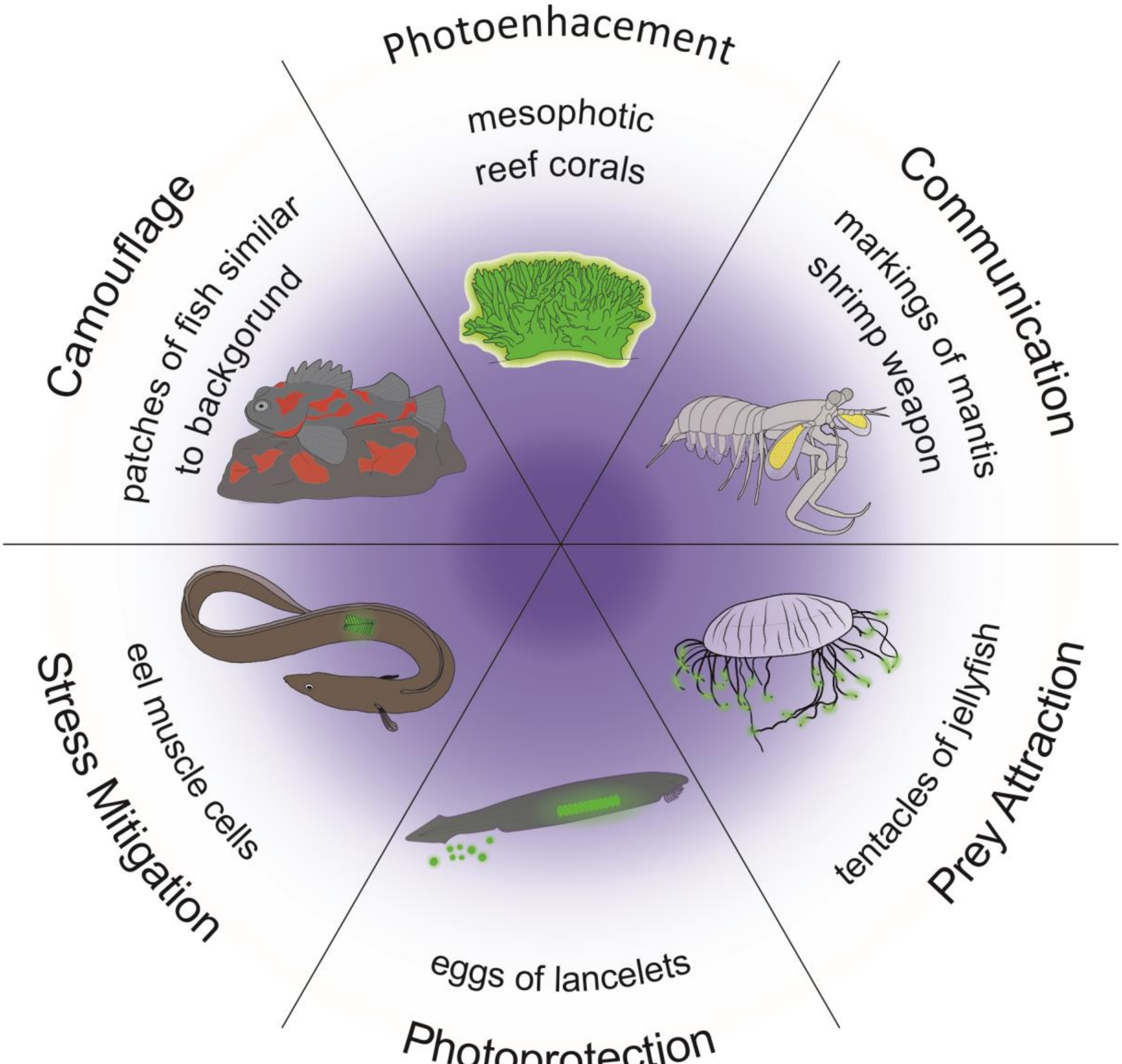

Figure 2: Scheme of proposed functions of fluorescence in marine animals. Examples were selected to represent different taxa but are not exclusive to those taxa. Furthermore, fluorescence might be an intrinsic property of the molecule itself without any described function.

Class or Order	**Family or Species**	**Localization and Physiological function**	**Fluorescent signal/molecule**	**Demonstrated fluorescent mediated behaviours and/or physiological response**	**Citations**
Prey attraction					
Hydrozoa	*Olindias formosa*	Acceptor molecule for bioluminescent light in tentacles.	dfGFP $\lambda_{ex/em}$ 505/524 nm	Attraction of juvenile rockfish; green vs white or red preference.	Haddock & Dunn, 2015
Siphonophores	*Rhizophysa eysenhardt, Resomia ornicephal, Diphyes dispar*	Fluorescence on tips of tentacles, gastrozooids on bracts and nectophores (swimming bells).	Green, orange λ_{em} 518-536 nm	*Rhizophysa eysenhardt* only feed on fish larvae in the presence of light.	Purcell 1981; Pugh & Haddock, 2010; Haddock & Dunn, 2015
Scleractinia	*Fimbriaphyllia (Euphyllia) paradivisa (green morph)*	Tentacles and oral part of the polyps.	Green	Higher predation rates in green fluorescing morphs; plankton is attracted by green vs orange fluorescent cues.	Ben-Zvi et al., 2022
Osteichthyes	*Tripterygion delaisi,* 114 different fish species	Red fluorescent iris; melanophores encase fluorescent iridophores on the anterior side of the iris.	Λ_{em} 600 nm *T.delaisi* λ_{em} 580-740 nm (114 species)	Fluorescence increases during foraging and decreases during inactivity or stress.	Wucherer & Michiels, 2014; Anthes et al., 2016
Symbiont attractions					
Scleractinia	*Echinophyllia aspera*		Green λ_{em}: 492 and 505 nm	Attraction of *Symbiodinium;* green, red vs blue preference.	Aihara et al., 2019
Photoprotection					
Scleractinia	*Acropora youngei*	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.	Roth et al., 2010; Roth et al., 2013
Hydrozoa	*Aequorea victoria*	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.	Bou-Abdallah et al., 2006
Scleractinia	*Acropora millepora, Porites massive sp., P. astreoides, Montastraea annularis, M. faveolata, M. cavernosa, Diploria strigosa, Dichocoenia stokseii, Sidastrea siderea*	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 λ_{em} 465-500 nm GFP λ_{em} 505-515 nm RFP λ_{em} 575-590 nm	Naturally occurring and pure coral FPs and CPs have H_2O_2 scavenging activity (CFP<GFP<RFP, CP).	Palmer et al., 2009
UV protection of RNA and DNA					
Scleractinia	*Montipora foliosa, Acropora pulchra,*	Fluorescence in adult corals: in injured and regenerating tissue and growth zones.	mfolCP λ_{abs} 577 nm; mfolFP λ_{em} 483 nm;	Upregulation of FPs in bleached, injured, regenerating and	D'Angelo et al., 2012; Schucchia et al., 2020

	Porites lobata, *Stylophora pistillata*	Fluorescence in planula larvae: in regions undergoing cell differentiation.	apulFP λ_{em} 584 nm; apulFP λ_{em} nm483; plobFP λ_{em} 610nm; plobFP λ_{em} 490 nm	differentiating corals and larvae; higher fluorescence at lower pH (pH7.6 vs pH8.15; *S. pistillata*).	
Scleractinia	*Pocillopora damicornis,* *Montastraea cavernosa*	High ectodermal expression of CPs in areas of low symbiont density.	CP $_{P. damicornis}$ λ_{abs} 565 nm CP $_{M.foliosa}$ 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	Bollati et al., 2022
Scleractinia	*Porites lichen,* *Pocillopora damicornis*		CFP$_{P.lichen}$ $\lambda_{ex/em}$ 466/489 nm GFP $_{P.lichen}$ $\lambda_{ex/em}$ 489/519 nm CP$_{P.damicornis}$ λ_{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.	Bollati et al., 2020
Annelida	*Eulalia sp.*	Protection against high energy radiation; mucus contains FPs, ubiquitin and antioxidant protein peroxiredoxin.	Mucus λ_{ex} 285-374 λ_{em} 507-513 nm	Secretion of a mucus containing a proteinaceous fluorescent complex.	Rodrigo et al., 2022
Photoenhancement					
Scleractinia	*Montastraea cavernosa,* *Echinophyllia sp.*	Ectodermal pcRFP in mesophotic corals; enhancement of photosynthesis in mesophotic habitats via wavelength conversion.	pcRFP λ_{em} 514$_{unconverted,}$ 582$_{converted}$ 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.	Bollati et al., 2022
Stress mitigation and regulatory mechanisms					
Scleractinia	*Acropora millepora*	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 λ_{abs} 580, 586, 604 nm amilFPs λ_{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.	Alieva et al., 2008; Kenkel et al., 2011; Smith et al., 2013
Bilirubin binding to reduce cellular, oxidative stress					
Osteichthyes	*Anguilla japonica*	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 UnaG can act as a scavenger of hydrogen peroxide and/or hydroxyl radical.	Kumagai et al., 2013; Funahashi et al., 2016
Immune response					

Scleractinia	*Porites compressa*	expression of green FPs changes towards red FPs in trematodiasis-compromised tissue.	GFP, RFP λ_{em} 590 nm in compromised tissue	Increased and alteration of FP expression in compromised tissue.	Palmer et al., 2009b
Chondrichthyes	*Cephaloscyllium ventriosum, Scyliorhinus retifer*	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 λ_{ex} 360-438 nm λ_{em} 400-507 nm	Kynurenine metabolism regulates host-microbiome signaling and immune response in human.	Park et al., 2019
Light-driven electron transfer					
Anthozoa	*Zoanthus sp*.	Light-induced electron donor in photochemical reactions with electron acceptors such as cytochrome c, FMN, FAD or NAD$^+$; highly mobile cytoplasmic localization and spindle-shaped aggregates in cells.	Various FPs, Tyr66-based chromophores	Light-induced electron transfer of FPs.	Chudakov et al., 2010; Povarova et al., 2017
Mimicry and aposematism					
Heterobranchia	*Goniobranchus splendidus* , 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 *Goniobranchus splendidus* induces an avoidance response in the Picasso triggerfish; unpalatable secondary metabolites and yellow rim as apoptotic signals for predators.	Winters et al., 2017; Betti et al., 2021
Intra/interspecific communication					
Osteichthyes	*Cirrhilabrus solorensis*	Red fluorescent body coloration.	Λ_{em} 650-700 nm	Increased aggressive behaviour by recognizing possible fluorescent rivals in comparison to non-fluorescent rivals in *C. solorensis. C. solorensis* express four visual photoreceptors: one rod (λ_{em} 492 nm) and three classes of cones (λ_{em} 497, 514, 532) which should be sensitive to their own fluorescence.	Gerlach et al., 2014; Gerlach et al., 2016
Osteichthyes	*Tripterygion delaisi*	Red fluorescent eye rings.	Λ_{em} 600 nm	*T. delaisi can perceive and respond to levels of fluorescence that are similar to its own (*positive correlation to a red fluorescent but not grey cue) *T. delaisi* express four visual photoreceptors: one rod (λ_{em} 502 nm) and three classes of cones (λ_{em} 468, 517, 532) which should be sensitive to their own fluorescence.	Wucherer et al., 2014; Kalb et al., 2015; Bitton et al., 2017
Sexual communication					

Osteichthyes	*Cirrhilabrus solorensis,* pseudocheilinid wrasses (13 species), 185 different fish species	Differences in the fluorescence pattern between males and females.	*C. solorensis* λ_{em} 640-670 nm, 185 fish species λ_{em} 580-750 nm	Red fin fluorescence associated with sexual dimorphism photoreceptors: one rod (λ_{abs} 492 nm), three classes of cones (λ_{abs} 497, 514, 532).	Anthes et al., 2016; Gerlach et al., 2016

According to Marshall and Johnson (2017) and Mazel (2017) various criteria have to be fulfilled to support an ecological function of fluorescence in animals. These include

(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 photoreceptors.

(2) The overlap of the emission wavelength of the fluorophore with the spectra sensitivity range of the organism.

(3) Visually guided behaviours that are driven or supported by the fluorescent signal.

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.

Molecule	**Organism**	**Taxon**	**Molecule type**	**Fluorescence**	**λexc (nm)**	**λem (nm)**
Acridone	Alkaloids plants	plantae			381	427
Aesculin	Rosskastanie	plantae	Glucosid (alcohol & Ph	blue under UV-light	NA	NA
Allophycocyanin	cynaobactria & re	cyanobacteria	Pigment belonging to the Phycobilinen, Prot		633	680
Anthocyanins	plants, flowers	plantae	NA	NA	533	624
Anthranilic acid	plants	plantae	acid		300	405
Aurones	plants, flowers	plantae	flavonoids	NA	430	560
Azulene	plants	plantae	Terpenoids		360 - 380	420, 620, 725
Berberin	Berberitze	plantae	Alkaloid	yellow under UV-light	NA	NA
Beta-Carboline	Scorpions	arthropoda	indole alkaloid	blue-green under UV-l	375	450
Beta-Carotene	plants, flowers	plantae	Terpenoids		360, 480	500-525, 580
Betacyanins	plants, flowers	plantae	pigments	NA	524	570
Betaxanthins	plants, flowers	plantae	pigments	NA	NA	NA
Bromo-tryptophan-k	shark	vertebrata			375	439, 447
Caffeic acid	plants	plantae	Phenolics		206, 310	281, 432
Calcein	NA	NA	fluorescein complex		494	517
Crustacyanin	lobster	arthropoda	pigments		530	580
Cianidin	plants	plantae	phenolics, flavonoids		547	595
Cicutotoxin	plants	plantae	lipids		360-380	580
Cinnamic acid	plants	plantae	phenolics		360	405-427
Chinin	plants	plantae	Chinolin-alkaloids	brightblue under UV-li	315-380	
Chlorogenic acid	plants	plantae			330	440
Chlorophyll-a	plants	plantae	Tetrapyrole, protein		465, 480, 665, 680	675-690, 730-740
Colchicine	plants	plantae	Alkaloids		360	435
Coumarin	spiders, cockroac	arthropoda	Alkaloids		280, 410	415-445
Cumarin-dyes	plants	plantae	coumarin derivatives			
Epicocconon	fungi	fungi		weak green to red	395	
Esculetin	plants	plantae	phenolics		360	475
UnaG	eels	vertebrata	protein		500	527
Ferulic acid	plants	plantae	acid		240. 340	400-480
Flavine/Flavonoids	plants	plantae	phenolics	yellow	365	445-461
Flavoproteins	plants	plantae	Flavins		365	520-540
Fluorescent Proteins	cnidaria	cnidaria	protein			
Fluorescent sceleton	frogs, chamelions	vertebrata	collagen, tetracyclines, apartit			

Folic acid	plants	plantae	phenolics			365		450
Gaillardine	plants	plantae	Terpenoids			360		415
Galangin	plants	plantae	phenolics			365	447-461	
Gallic acid/valonic ac	plants	plantae	phenolics		360-380			500
Gentinsic Acid	plants	plantae	phenolics			340		450
Guanine	fish	vertebrata	nucleobase		500-570		584-699	
Hyloin	frogs	vertebrata	Dihydroisoquinolinon	blue-green under UV-light				
Kaempferol	plants	plantae	phenolics	green	260-270. 360-380			520
Kinetin	plants	plantae	cytokinins			380	410-430	
Kynurenic acid	plants	plantae	Alkaloids			325		405
Sandercyanine	fish	vertebrata	Lipocalin (protein)	red		375		630
Lipofuscin	plants, fruits, coc	arthropoda			360-380		440-470	
Luciferin	firewflies	arthropoda				327		530
Matlaline	plants	plantae			283, 307, 382, 430			466
Malvidin-O-glucosid	plants	plantae				530		630
Menthol	plants	plantae	Terpenoids			360	415-420	
Minerals	NA	NA	Minerals					
Mucous-like secretio	amphibians	vertebrata		green				
Parietin	plants	plantae	phenolics			442		600
Petunidin	plants	plantae	phenolics		510-585			610
Pheophorbide-a	fish	vertebrata				400		670
Phycobilliprotein	Cyanobacteria	cyanobacteria	protein			642		670
Porphyrins	cnidaria	cnidaria	prophyrines	red		410		620
Psittacofulvin	birds	vertebrata	carotenoids		420-450			527
Pterins	Arthropods	vertebrata	pterins					
Pteroic acid	plants	plantae	phenolics			360		435
Pyridoxine	plants	plantae	pyridines			340		400
Pyridoxamine	plants	plantae	pyridines			335		400
Quercetin	plants	plantae	phenolics		250, 370		500-540	
Quinine	plants	plantae				347		450
Resilin	Arthropods	arthropoda	protein					
Riboflavin	plants	plantae	Flavins			377		526
Rhodopin	plants	plantae	carotenoids		500-550		560-600	
Rosmarinic acid	plants	plantae	acid		60-380		440-450	
Rutacridone	plants	plantae	Alkaloids			381	590-595	
Sepiapterin	fish	vertebrata	Pteridin		UV		450-490	

Serotonin	plants	plantae	Alkaloids		360	410-420	
Schiff-bases	bees	arthropoda	imines		360		450
Spheniscin	birds	vertebrata	beta-defensins	370-400		450-500	
Spheroidenone	plants	plantae	carotenoids		520	570-610	

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Taxon	Species	Fluorescent Protein	Max. Excitation (nm)	Max. Emission (nm)	Molecular Weigth (kDa)	Number of amino acids	Accession No.
Anthozoa	*Acanthastrea sp. (Micromussa lordhowensis)*				25.86	226	KY806741
	Acanthastrea sp. (Micromussa lordhowensis)				26.11	227	KY806740
	Acanthastrea sp. (Micromussa lordhowen	fluorescent prote	479	499		228	BBG58139.1
	Acropora aculeus	aacuGFP1	478	502	25.70	231	AY646069
	Acropora aculeus	aacuGFP2	502	513	26.09	231	AY646066
	Acropora aculeus	aacuCP	580	NA	24.98	221	AY646077
	Acropora digitifera	AdRed	567	612	26.10	231	LC125067
	Acropora digitifera		561	599		231	BAX00649.1
	Acropora digitifera		561	593		231	BAX00650.1
	Acropora digitifera		559	593		232	BAX00653.1
	Acropora digitifera		561	599		232	BAX00654.1
	Acropora digitifera		499	511		231	BAX00655.1
	Acropora digitifera		498	511		231	BAX00656.1
	Acropora digitifera		500	511		231	BAX00658.1
	Acropora digitifera		489	501		230	BAX00659.1
	Acropora digitifera		587	630		221	BAX00660.1
	Acropora digitifera		572	629		221	BAX00661.1
	Acropora digitifera		581	625		221	BAX00662.1
	Acropora digitifera		576	629		221	BAX00664.1
	Acropora digitifera		567	623		221	BAX00665.1
	Acropora digitifera		587	630		221	BAX00666.1
	Acropora digitifera		576	628		221	BAX00667.1
	Acropora digitifera		576	628		221	BAX00668.1
	Acropora digitifera		564	606		231	BAX00669.1
	Acropora digitifera		558	592		231	BAX00670.1
	Acropora digitifera		560	598		231	BAX00671.1

Acropora digitifera		490	501		231	BAX00672.1
Acropora digitifera		489	501		231	BAX00673.1
Acropora digitifera		577	630		221	BAX00675.1
Acropora digitifera		577	630		221	BAX00677.1
Acropora digitifera		502	512		231	BAX00690.1
Acropora digitifera		488	501		231	BAX00691.1
Acropora digitifera		448	491		231	BAX00790.1
Acropora digitifera		499	510		231	BAX00792.1
Acropora digitifera		489	501		231	BBC21269.1
Acropora digitifera		479	498		231	BBC21270.1
Acropora digitifera		561	593		231	BBC21271.1
Acropora digitifera		557	589		231	BBC21272.1
Acropora digitifera		521	593		232	BBC21273.1
Acropora digitifera		576	624		221	BBC21274.1
Acropora digitifera		577	630		221	BBC21275.1
Acropora digitifera		581	625		221	BBC21276.1
Acropora digitifera		447	492		203	FAA00738.1
Acropora digitifera		502	511		231	FAA00739.1
Acropora digitifera		480	499		220	FAA00740.1
Acropora digitifera		489	501		220	FAA00741.1
Acropora digitifera		541	577		215	FAA00746.1
Acropora digitifera		584	627		214	NP_00131011
Acropora eurostoma	aeurGFP	504	515	26.02	231	EU498722
Acropora hyacinthus	ahyaCP	580	NA	24.96	221	AY646076
Acropora millepora	amilFP484	420	484	26.08	231	EU709808
Acropora millepora	amilCFP	441	489	25.95	231	AY646070
Acropora millepora	amilFP497	477	497	25.90	231	EU709809
Acropora millepora	amilFP512	500	512	25.93	231	EU709810
Acropora millepora	amilGFP	503	512	25.99	231	AY646067
Acropora millepora	amilCP506	506	NA	2.43	21	JQ009184

Acropora millepora	amilFP597	558	597	26.12	232	JX258844
Acropora millepora	amilFP597	558	597	26.09	232	EU709811
Acropora millepora	amilFP605 (Ala)	559	605		232	KJ729554
Acropora millepora	amilRFP	560	593	26.15	232	AY646073
Acropora millepora	amilCP564	564	NA		231	JX258846
Acropora millepora	amilCP	588	NA	26.09	232	AY646075
Acropora millepora				26.10	232	AY650288
Acropora millepora				25.56	227	DQ206400
Acropora millepora				1.98	18	KM101115
Acropora millepora				2.42	21	JQ009183
Acropora millepora				24.99	221	KC411500
Acropora millepora				25.01	221	KC411499
Acropora millepora				25.02	221	KC349891
Acropora nobilis		462	490	25.90	231	AY646072
Acropora nobilis	anobCFP2	477	495	25.70	231	AY646071
Acropora nobilis	anobGFP	502	511	25.88	231	AY646068
Acropora pulchra	apulFP483	420	483	25.93	231	EU709806
Acropora pulchra	apulCP584	584	NA	24.97	221	EU709807
Acropora rubusta	arobGFP	501	512		231	AAU06847.1
Acropora rubusta	arobCFP	477	493		231	AAU06850.1
Acropora rubusta	arobCFP	449	490		231	AAU06851.1
Acropora tenuis	atenFP	504	515	24.60	220	BAM08940
Acropora tenuis	atenRFP	537	577		214	BBV24624.1
Acropora tenuis	atenGFP	425	481		216	BBV24626.1
Acropora tenuis	atenCP	547	NA		505	BBV24631.1
Acropora tenuis	atenCP	535	NA		356	BBV24632.1
Acropora tenuis	atenRFP	560	591		231	BBV24634.1
Acropora tenuis	atenGFP	479	498		220	BBV24635.1
Acropora tenuis	atenGFP	482	501		253	BBV24636.1

Acropora tenuis	atenGFP	499	513		220	BBV24637.1
Acropora tenuis	atenCP	566	NA		221	AAU06853.1
Agaricia fragilis	afraGFP	494	503	25.69	226	AY647156
Agaricia fragilis				30.02	259	AY037765
Anemonia majano	amFP486	458	486	25.32	229	AF168421
Anemonia sulcata	asCP	568	595 (none)	25.92	232	AF246709
Anemonia sulcata	asFP499	403/480	499	25.37	228	AF322221
Anemonia sulcata				25.92	232	EF587182
Anemonia sulcata				25.96	232	AF322222
Astrangia lajollaensis	alajGFP3	494	504	25.20	226	AAS18272
Astrangia lajollaensis	alajGFP1	509	517	25.00	223	AAS18270
Astrangia lajollaensis	alajGFP2	509	517	24.70	219	AAS18271
Catalaphyllia jardinei	cjarRFP	573	582		225	ABN41777.1
Ceriantharia sp.	OFP	548	573	25.10	222	AAP55761
Clavularia sp	cFP484	456	484	30.45	266	AF168424
Condylactis gigantea	cgigGFP	399/482	496	25.74	229	AY037776
Condylactis gigantea	cgCP	587 (571)	622 (none)	25.42	227	AF363775
Condylactis gigantea				25.38	227	AY037777
Condylactis passiflora	cpCP	571	none	25.45	227	AF383155
Corynactis californica	ccalGFP1	504	517	24.80	221	AAZ14788
Corynactis californica	ccalGFP3	505	517	24.80	221	ABI58282
Corynactis californica	ccalOFP1	508	561	25.50	226	AAZ14789
Corynactis californica	ccalYFP1	514	523	25.00	221	AAZ67343
Corynactis californica	ccalRFP1	568	598	24.80	221	AAZ67342
Cyphastrea microphthalma	VFP	491	503	25.60	225	CBI12485
Dendronephthya sp.	dendGFP	492	508	25.81	225	AF420591
Dendronephthya sp.	dendRFP	557	575	26.83	234	AF420591
Danafungia horrida	dhorRFP	507	538	26.04	221	ABB17957.1
Danafungia horrida	dhorGFP	501	512	24.10	231	ABB17972.1
Dipsastraea (Favia) favus	KikG	507	517	25.88	227	AB193294

Dipsastraea (Favia) favus	KikGR	390/507	517	25.76	227	AB193293
Dipsastraea (Favia) favus	KikGR	583/360	593			
Discosoma sp.	dis3GFP	503	512	26.02	231	AF420593
Discosoma sp.	drFP583	558	583	26.05	225	AF168419
Discosoma sp.	drFP583	558	583	25.93	225	AF168419
Discosoma sp.	dsFP593	573	593	26.37	230	AF272711
Discosoma sp.				26.69	236	
Discosoma sp.				25.59	226	AY786537
Discosoma sp.				25.51	226	AY786536
Discosoma sp.				27.10	236	DQ301560
Discosoma sp.				25.79	225	AF545828
Discosoma sp.				27.03	236	AY679107
Discosoma sp.				27.04	236	AY679106
Discosoma sp.				26.77	236	
Discosoma striata	dsFP483	443	483	26.44	232	AF168420
Discosoma striata				25.64	227	AY679108
Echinophyllia echinata	eechGFP1	497	510	26.11	229	DQ206383
Echinophyllia echinata	eechGFP2	506	520	25.50	224	DQ206395
Echinophyllia echinata	eechGFP3	512	524	25.91	228	DQ206396
Echinophyllia echinata	eechRFP	574	582	25.60	225	DQ206387
Echinopora forskaliana	efor/RFP	589	609	25.66	227	EU498726
Entacmaea quadricolor		552	578	25.50	226	
Entacmaea quadricolor	eqFP611	559	611	25.93	231	AY130757
Entacmaea quadricolor				26.32	233	
Entacmaea quadricolor				24.97	223	
Entacmaea quadricolor				26.08	231	
Entacmaea quadricolor				25.98	231	
Entacmaea quadricolor				25.86	230	AAQ11988.1
Euphyllia ancora				25.54	226	KT452623
Eusmilia fastigiata	efasCFP	466	490	25.86	229	DQ206397

Eusmilia fastigiata	efasGFP	496	507	24.42	220	DQ206385
Favites abdita	fabdGFP	508	520	25.45	224	EU498723
Fimbriaphyllia (Euphyllia) ancora	EaGFP	506	514	25.90	226	QAU55049.1
Galaxea fascicularis	Azami-Green	492	505	25.96	225	AB107915
Galaxea fascicularis	mAzami-Green	492	505	25.85	225	AB108447
Galaxea fascicularis	gfasGFP	492	506	25.99	225	DQ206389
Galaxea fascicularis	gfasCP	577	NA	24.95	221	DQ206394
Goniopora djiboutiensis	gdjiCP	583	NA	24.84	221	DQ206376
Goniopora tenuidens	gtenCP (gtCP)	580	none	24.92	221	AF383156
Heteractis cirspa	HcRed	592	645	25.60	227	
Heteractis crispa	hcriGFP	405/481	500	25.34	225	AF420592
Heteractis crispa	hcCP	492 (578)	645 (none)	25.64	227	AF363776
Heteractis magnifica	hmGFP	490	510	25.90	228	AAO16871
Hydnophora grandis	hgraFP492	443	492			
Hydnophora rigida	HriGFP	507	527		132	
Litophyllon concinna		545	554		217	BAD24721.1
Litophyllon concinna		547	559		218	BAD24722.1
Litophyllon concinna		511	522		218	BAF76140.1
Lobactis scutaria		496	509			ABB17961.1
Lobophyllia hemprichii	EosFP (Green)	506	516	25.79		AY765217
Lobophyllia hemprichii		511	544		231	ABN41776.1
Lobophyllia hemprichii		512	524		225	ACV52375.1
Lobophyllia hemprichii		520	522		226	ACV52375.1
Meandrina meandrites		413	507		214	AAO00732.1
Montastraea cavernosa	mcavGFP	506	516	26.74	234	AY037769
Montastraea cavernosa	mcavRFP	508/572	520/580	25.87	225	AY037770
Montastraea cavernosa	mc1	508	582	25.79	225	EU035530
Montastraea cavernosa	mcFP497	435	497	25.89	225	EU035527
Montastraea cavernosa	mc5	435	495	25.84	225	AY181556
Montastraea cavernosa	mc6	495	507	25.83	225	AY181557
Montastraea cavernosa	mc3	505	515	26.81	234	AY181554

Montastraea cavernosa	mc1	508	582	25.82	225	AY181552
Montastraea cavernosa	mcFP506	454	512	25.74	224	EU035531
Montastraea cavernosa		505	515	26.74	234	AY037768
Montastraea cavernosa		500	515	25.68	224	EU035534
Montastraea cavernosa	mcFP505	470	505	25.71	224	EU035528
Montastraea cavernosa		499.5782	514.88574	25.77	224	EU035532
Montastraea cavernosa				25.66	225	EU035536
Montastraea cavernosa	mcRFP			25.88	225	AY362545
Montastraea cavernosa	McCFP	432	477	25.78	225	AY056460
Montastraea cavernosa	McavFP	440	510	25.85		AF384683
Montastraea cavernosa	McaG2	492	502	25.88	225	AY679111
Montastraea cavernosa	McaG1	492	514	26.10	227	AAU04446.1
Montastraea cavernosa		502	514	25.97	227	EU035535
Montastraea cavernosa		505	516	26.04	227	AF406766
Montastraea cavernosa		502	516	26.02	227	EU035529
Montastraea cavernosa				26.04	227	EU035533
Montastraea cavernosa	McaG1ea	492	514	25.96	227	AY679110
Montastraea cavernosa	mc2	505	515	26.02	227	AY181553
Montastraea cavernosa		503	514	26.06	227	AY181555
Montipora digitata	mdigFP486	470	486	24.91	221	
Montipora digitata	mdigFP514	508	514			
Montipora digitata	mdigFP572	556	572			
Montipora efflorescens	meffCFP	467	492	25.99	232	DQ206381
Montipora efflorescens	meffGFP	492	506	26.54	233	DQ206393
Montipora efflorescens	meffRFP	560	576	26.51	234	DQ206379
Montipora efflorescens	meffCP	574	NA	24.97	221	DQ206377
Montipora foliosa	mfolCP577	577				
Montipora foliosa				14.70	133	
Montipora millepora	mmilCFP	404	492	25.57	227	DQ206392
Mycedium elephantotus	meleCFP	454	485	25.90	227	DQ206382

Mycedium elephantotus	meleRFP	573	579	25.84	226	DQ206386
Oxypora echinata		497	510		229	ABB17956.1
Oxypora echinata		569	573		225	ABB17960.1
Oxypora echinata		506	520		224	ABB17968.1
Oxypora echinata		509	520		228	ABB17969.1
Platygira lamellina	plamGFP	502	514	26.50	230	EU498724
Pocillopora damicornis		484	495		222	RMX40170.1
Pocillopora damicornis		501	508		245	RMX43351.1
Pocillopora damicornis		498	506		224	RMX43362.1
Pocillopora damicornis		462	526		341	RMX56440.1
Pocillopora damicornis		493	504		212	RMX59748.1
Pocillopora damicornis		486	496		299	RMX59762.1
Pocillopora damicornis		493	504		251	RMX59776.1
Pocillopora damicornis		484	495	25.09	222	AAU04450
Porites lobata	plopFP490	420	490			
Porites lobata	plobFP610	530	610			
Porites lobata	plobRFP	576	614	26.45	233	
Porites porites	pporGFP	495	507	24.73	220	DQ206391
Porites porites	pporRFP	578	595	26.05	231	DQ206380
Psammocora sp.	psamCFP	404	492	25.88	230	EU498721
Ptilosarcus sp.	ptilGFP	500	508	27.05	238	AY015995
Ptilosarcus sp.	ptilGFP	500	508	27.00	238	AAG54097
Renilla muelleri	rmueGFP	498	510	27.12	238	AY015996
Renilla muelleri				36.11	311	AY015988
Renilla reniformis	rrenGFP	485	508	26.00	233	Q963I9
Ricordea florida	rfloGFP	508	518	26.01	231	AY037772
Ricordea florida	rfloRFP	506/566	517/574	25.70	231	AY037773
Ricordea florida				26.00	231	AY037774
Ricordea florida				25.99	231	AY646065
Sarcophyton sp.	sarcGFP	483	500	25.83	225	EU498725

	Sarcophyton sp.				25.77	224	AB425088
	Scolymia cubensis	scubGFP2	497	506	26.61	235	AY037771
	Scolymia cubensis	scubGFP1	497	506	26.63	234	AY037767
	Scolymia cubensis	scubGFP1	497	506		234	AAK71333
	Scolymia cubensis	scubGFP2	497	506		235	AAK71337
	Scolymia cubensis	scubRFP	570	578	26.06	230	AY646064
	Scolymia cubensis	scubRFP	570	578	26.10	230	AAU06843
	Seriatopora hystrix	shysCP562	562				
	Stylocoeniella armata	SAASoti	510	519			
	Stylocoeniella armata	SAASoti	510	589			
	Stylocoeniella sp.	stylGFP	485	500	24.99	224	DQ206390
	Stylocoeniella sp.	stylCP	574	NA	24.95	221	DQ206378
	Stylophora pistillata	spisCP	560	NA	24.95	224	DQ206398
	Stylophora pistillata				21.88	192	LSMT0100055
	Stylophora pistillata				17.63	159	
	Stylophora pistillata				12.32	109	
	Stylophora pistillata				42.43	374	
	Trachyphyllia geoffroyi	Kaede green	508	518	25.70	225	BAC20344
	Trachyphyllia geoffroyi	Kaede red	572	580	25.70	225	BAC20344
	Zoanthus sp.	zFP506	496	506	26.11	231	AF168422
	Zoanthus sp.	zFP538	528	538	26.17	231	AF168423
	Zoanthus sp.	zoan2RFP	552	576	26.41	231	AY059642
	Zoanthus sp.				25.95	231	AF482451
	Zoanthus sp.				25.94	229	EU625506
	Zoanthus sp.				26.04	231	EU625505
Crustacea	*Chiridius poppei*	CpYGFP	508	518	24.70	219	AB185173
	Pontella meadi	pmeaGFP2	487	502	24.90	222	AAQ01187
	Pontella meadi	pmeaGFP1	489	504	25.00	222	AAQ01186
	Pontella mimocerami	pmimGFP1	491	505	25.10	222	ACT99046

	Pontella mimocerami	pmimGFP2	491	505	25.10	222	ACT99047
	Pontellidae sp.	pdae1GFP	491	511	24.90	222	AAQ01188
	Pontellina plumata	ppluGFP1	480	500	24.60	222	AAQ01183
	Pontellina plumata	ppluGFP2	482	502	24.70	222	AAQ01184
Hydrozoa	*Aequorea australis*	AausGFP	398	503	26.20	234	
	Aequorea australis	AausFP1	504	510	26.40	234	
	Aequorea australis	AausFP3	587		26.40	234	
	Aequorea australis	AausFP2	609		25.80	232	
	Aequorea coerulescens	aceGFP	480	505	24.90	222	AAN41637
	Aequorea victoria	AcS-CFP	440	480	26.40	235	JX472997
	Aequorea victoria	GFP	395/471	508	25.60	232	M62653
	Aequorea victoria	FF-GFP	)/490(deprot)	514	26.60	237	JX472995
	Aequorea victoria	FFTS-YFP	)/510(deprot)	528	26.60	233	JX472996
	Aequorea victoria				25.70	232	X83960
	Aequorea victoria				25.60	232	X83959
	Aequorea victoria				25.50	232	JN800726
	Anthoathecata	anm2CP	572	597	27.50	241	AAR85352
	Clytia gregaria	cgreGFP	485	500	26.80	238	ADI71929
	Clytia hemisphaerica	CheGFP1	488	500	25.90	232	AEP19814
	Clytia hemisphaerica	CheGFP4	488	500	26.89	238	AEP19817
	Clytia hemisphaerica	CheGFP2	488	508			AEP19815
	Labidocera aestiva	laesGFP	491	506	28.07	251	AAQ01185
	Obelia sp.	obeCFP	400	499	28.13	251	AEL17649
	Obelia sp.	obeCGFP	502	515	26.87	238	AEL17650
	Obelia sp.	obeYFP	514	528	26.95	238	AEL17651
	Olindias formosus	dfGFP	505	524	28.13	251	BBC28143
	Phialidium sp.	phiYFP	525	537	4.93	44	AY485333
Chordata	*Branchiostoma floridae*	bfloGFPa1	500	512	24.60	219	

Branchiostoma floridae	bfloGFPc1	493	521			
Branchiostoma floridae	LanFP1	500	510	24.60	220	
Branchiostoma floridae	LanFP2	500	516	23.70	223	
Branchiostoma lanceolatum	LanYFP	513	524	24.70	219	ACA48232
Branchiostoma lanceolatum	LaGFP	502	511	5.90	220	ACA48235.1
Branchiostoma lanceolatum	LanYFP	513	524	24.70	219	ACA48232
Branchiostoma lanceolatum	LaRFP	521	592	25.80	220	ACA48242.1
Kaupichthys hyoproroides	Chlopsid FP I	498	523	15.80	136	
Kaupichthys hyoproroides	Chlopsid FP II	498	523	15.80	136	
Gymnothorax zonipectis	GymFP	496	532	15.60	139	

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