Introduction

Bioluminescence is a fascinating biological phenomenon, which can be found in terrestrial and oceanic environments. Numerous bioluminescent taxa were described from the marine environment [1-2]. Bioluminescence is especially abundant in the deep-sea. The majority of luminescent taxa are invertebrate animals. In contrast to the high diversity in invertebrates, vertebrates lack bioluminescent light organs, with the exception of an amazing diversity in teleosts and some shark species. A recent paper reported that bioluminescence appeared in ray finned fishes in 27 independent evolutionary events [3]. Bioluminescent light is generated in specialized light organs based on an oxidation of a light emitting luciferin in the presence of oxygen and the enzyme luciferin [1,4]. Most of the bioluminescent species produce blue green light in the wavelength range around $\lambda_{\text{max}} \approx 475\text{nm}$ [1]. Luminescence in fishes can be divided in two different types of light production. Fish species with intrinsic bioluminescence show their own luciferin-luciferase system in specialized light organs. Nitric oxide was suggested to modulate adrenaline stimulated light emission in hatchet fishes of the genus Argyropelecus [5].

In case of cartilaginous fishes, luminescence is controlled by the application of melatonin as reported for the pygmy shark *Squaliolus allii* [6]. Fish species with extrinsic bioluminescence are not able to control their light emission directly. These species host bioluminescent bacterial species in specialized light organs. The bioluminescent bacteria produce a constant light and fishes with extrinsic luminescence use mechanical structures to cover the light organs and produce impressive blink patterns during the night. The flashlight fishes (Anomalopidae) for example use different mechanisms to close their light organs [7]. Numerous studies that describe the anatomy, diversity, function and evolution of bioluminescent light organs in fishes were published in the last 100 years. The objective of this review is to give a short overview about the functions of extrinsic and intrinsic luminescence in fishes.

Fishes with Intrinsic Bioluminescence

Fish species with intrinsic luminescence use their own luciferin-luciferase system to produce light. Many different types of light organs and functions of light organs were described. Bioluminescent sharks use ventral photophores to mimic residual light from the water surface and remain unseen by potential predators. This function is called counterillumination. The sharks produce a constant glow and swim up and down in the water to remain unseen and follow a so called «iso luminance depth» [8]. The small deep-sea lantern-shark *Etmopterus spinax* was suggested to use a light organ on the dorsal spine as a visual signal that deter predators in addition to the ventral light organs for counter illumination [9]. The tiny cookie-cutter shark *Isistius brasiliensis* show a unusual feeding behavior. The small shark bites small round pieces flesh from pelagic predators like swordfish and tunas. One study suggested that *Isistius brasiliensis* use the ventral photophores to lure pelagic predators instead of the usual function of counterillumination [10]. Lantern fishes (Fam: Myctophidae) show a high diversity and are highly abundant in the mid water column. Lantern fishes have photophores that glow to the sides and downward. In addition lantern fishes show a large photophore that produce strong and short (400ms) light flashes [2,11].

The dragonfishes (Order: Stomiiformes) is an amazing group of bioluminescent fishes. In addition of emitting blue-greenish light, like the most luminescent fish species, dragon fishes produce long wavelength red light. The three dragonfish genera Malacosteus, *Pachystomias* and Aristostomias show suborbital photophores that emit long wavelength red light and postorbital photophores that glow blue. In addition the genus show a preorbital photophore that produce red light [12]. The function of red bioluminescence might be related to intraspecific communication [12] and it has been suggested that dragonfish Malacosteus Niger use red luminescence to see without seen by other animals [13].

Fishes with Extrinsic Bioluminescence

Fishes with extrinsic luminescence lack their own luciferine-luciferase system. They host symbiotic bacterial species in specialized light organs that can either be appendages of the
alimentary tract or they show light organs under the eyes (Fam.: Anomalopidae), in a specialized dorsal fin ray (Fam.: Ceratioidei) or light organs at the anterior angle of the lower jaw (Fam.: Monocentridae) [1-4, 14, 15]. Less is known about the transport of symbionts from one generation to the next and about the ontogenetic development of luminescence onset in fishes. The cardinalfish (Fam.: Apogonidae) Sphimia tubifera show a ventral light organ and is active during twilight. It has been suggested that Sphimia use the light to detect and find zooplankton [16]. The mouth breeding Sphimiahost the luminescent symbiotic bacterial species Photobacterium mandapamensis and one study described that the symbiosis was initiated 8-10 days after the release of the parents mouth [17]. Many deep-sea anglerfishes (Fam: Ceratioidei) use a luminescent lure at the tip of a modified dorsal fin ray and host symbiotic bacteria related to the genus Vibrio. Angler fishes are generally thought to use the lure to attract prey organisms in the deep-sea [18-21]. Prey capture was also suggested for Gazza minuta (Fam: Leignonathidae) display a discrete projected luminescence and it was proposed that Gazza minuta attract and locate the fish on which Gazza minuta nocturnally feeds. The flashlight fishes (Fam: Anomalopidae) comprises 6 genera including 9 valid species [22-29]. Anomaloskaptopteryx, Photoblepharon palpebratum and Photoblepharon steinitzi live in relatively shallow waters of coral reefs and feed on zooplankton during the night. Flashlight fishes show enhanced activity during the night. They show bean-shaped light organs under the eyes and host bacteria of the genera Candidatus Photodesmus in Anomalos katoptron [30] and Candidatus Photodesmus blepharus in Photoblepharon [31]. Interestingly the related species Anomalos katoptron and Photoblepharon palpebratum/steinitzi use different mechanisms to close their light organs. Anomalopsrotate the light organ down and backwards whereas Photoblepharon use an eyelid like shutter [7]. Several functions of light organs and blink patterns in flashlight fishes have been proposed [32,33].

(a) The light organs assist in predation, i.e. to see or attract prey organisms.
(b) To avoid predators, i.e. evasive swimming behavior coordinated with rapid blinking (blink-and-run pattern).
(c) Intraspecific communication, i.e. school formation, territorial behavior and courtship behavior. Photoblepharon live in pairs or small groups between corals and rocks [34,35].

In contrast, A. katoptron swim in schools of up to 200 specimens near the water surface [34,35]. Several functions of biluminescence like communication, feeding behaviour and territorial behaviour were suggested for Photoblepharon steinitzi [32]. The split finfish light fish Anomalops katoptron us their light organs to illuminate small zooplankton organisms during the night. They display a high frequent blink pattern during the night and switched to constant glowing in the presence of planktonic prey organisms. The blink pattern of the light organs also follow an exogenous control by the ambient light, i.e. during dim light conditions the light organ is mainly closed [14]. Bioluminescence in fishes is highly diverse and needs further laboratory and field studies to investigate the exact functions of luminescence in fishes especially in deep-sea and coral reef ecosystems.

Summary

Bioluminescence in fishes is a widespread phenomenon in oceanic environments. Bioluminescenc ecan be found in ray finned fishes and also in some small shark species. Fishes can either display intrinsic bioluminescence, i.e. the have their own luciferin-luciferase system or extrinsic luminescence, i.e. they host symbiotic luminescent bacteria in specialized light organs. Bioluminescence in fishes has diverse functions and it is used for illuminating prey organisms, attracting prey, communication, counter illumination and territorial behaviour.

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