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Prevalence, Faunal Composition, and Vertical Distribution of Bioluminescence in the Pelagic Gulf of Mexico: Fishes, Crustaceans, Cephalopods and Gelatinous Megaplankton

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Abstract

Bioluminescence is the phenomenon of light emission by living organisms. It occurs through a chemical reaction within an organism and serves various purposes. The diversity of bioluminescent capabilities and occurrence in unrelated taxa suggest that bioluminescence has evolved independently numerous times amongst taxa thriving in certain environments. One such environment is the deep ocean, where little to no sunlight penetrates the water column, specifically in the mesopelagic (200-1000 m depth) and bathypelagic (> 1000 m) zones. The mesopelagic and bathypelagic zones have been extensively sampled and well documented in the Gulf of Mexico (GoM), one of the few places globally where this has occurred. Currently, no detailed faunal inventory of bioluminescence for the deep-pelagic GoM exists. This study is the first to quantitatively characterize the prevalence (both taxonomic and numerical), faunal composition, and vertical distribution of bioluminescence among major taxonomic groups at intermediate trophic levels. This large cumulative dataset of fishes, crustaceans, and cephalopods (micronekton hereafter) provides the basis for the current study with the following aims: (1) create an inventory of the bioluminescent micronekton and net-caught gelatinous megaplankton in the "upper mile" (0-1500 m depth) of the northern and eastern GoM; (2) quantitatively assess the vertical partitioning of bioluminescence as a function of taxonomic composition and organismal abundance; and (3) investigate variability in the vertical partitioning of bioluminescence as a function of diel cycle. Additionally, these topics will provide insight for discussing the relationship between the distribution of bioluminescence and the overall vertical ecology of a low-latitude, oceanic ecosystem. Quantification of abundance amongst bioluminescent organisms within the GoM revealed that approximately 75.5% of all captured individuals were capable of bioluminescence. The expression of bioluminescence was found to be most prominent vertically between 200-1000 m, representing the upper and lower mesopelagic zones, with ~87% of all individuals capable of bioluminescence. The mesopelagic also contained the largest percentages of bioluminescent fishes in this study. In the upper mesopelagic (200 to 600 m) ~67% of fish taxa in this depth interval were bioluminescent during daytime, while at night time values decreased to approximately 54%. Day and nighttime percentages of bioluminescent individuals in this depth zone were very similar and very high (97-98%). The most numerically abundant bioluminescent taxon was fishes, notably the Order Stomiiformes (genus *Cyclothone*). Alone, *Cyclothone* comprised approximately 72% of all bioluminescent fishes. Regarding crustaceans, a vertical 'gradient' of bioluminescent was exhibited, reaching a maximum 93.4% in the 200-1600 m depth stratum. Below this depth, the percentage of bioluminescent individuals decreased. While pelagic cephalopods are characterized by rapid swimming speeds and avoidance behavior, making sampling quite difficult, this study found that approximate 94% of all individuals collected were bioluminescent, with these distributed evenly throughout the water column. Finally, as predicted, there was a profound shift in bioluminescent organisms from deeper zones towards the epipelagic zone at night, highlighting the tight connections between diel vertical migration and bioluminescence in Earth's largest ecosystem type.

Keywords: Bioluminescence, cephalopods, crustaceans, gelatinous megaplankton, bathypelagic ecology, Gulf of Mexico, vertical distribution

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Introduction

Bioluminescence

Bioluminescence, defined as the light created through a chemical reaction within a living organism, is a form of *chemiluminescence*, the production of light by a chemical reaction (Syed & Anderson, 2021). Previously seen as an idiosyncrasy in the natural world, more interesting than functional, bioluminescence has evolved in nearly every Class of marine organisms (Haddock & Case, 1994, 1999; Hastings, 1983). Aristotle was the first to record observations of the self-luminous properties of bioluminescent organisms, recognizing the oddity of the light production without heat (Lee, 2008). Deep-sea bioluminescence has been documented since the days of the *Challenger* expedition (Haddock et al., 2010). Bioluminescence serves a variety of functions, both offensive and defensive, even within a single organism (Haddock et al., 2010). Quantifying the abundance of taxa that exhibit this functional trait provides further insight into a trait-based approach to understanding ecosystem dynamics.

Bioluminescence is the product of an enzyme-catalyzed oxidation reaction within the organism (Brodl et al., 2018). The reaction occurs when the light-emitting organic molecule, luciferin, and its accompanying enzyme, luciferase, interact with molecular oxygen (Shimomura, 2006). Luciferin can also react with a photoprotein, an enzyme variation of luciferase that produces light upon co-binding with another ion such as calcium or magnesium (Krasitskaya et al., 2020). Various types of luciferin are known in unrelated chemical pathways, further suggestive of bioluminescence evolving independently. A catalyzed luciferase combined with oxidized luciferin molecules produces a palette of light-emitting reactions in an array of colors, catalysis rates, and dependence on ATP (Fleiss & Sarkisyan, 2019). Major taxa of fishes, cephalopods and crustaceans are often able to modify the intensity, wavelength and even color of their light (Haddock & Case, 1999). Just as adaptations and capabilities of some luminescent specimens are much more sophisticated than others, the high variability in the delivery of light including color, intensity, and kinetics, is equally impressive (Widder, 2010). The sophisticated physiological and behavioral mechanisms for controlling bioluminescence are evidence of its ecological importance.

Bioluminescence has evolved independently numerous times, with the majority of bioluminescent organisms residing in the deep sea, defined as depths > 200 m (Herring, 1987;

Shimomura, 2006; Widder, 2010). The array of colors emitted by organisms identified within the bioluminescent spectra spans the entire visible range. However, the majority of bioluminescence evolved in the open ocean, resulting in blue being the most common wavelength of light emitted (λ_{max} ~ 475 nm) as it penetrates the farthest in seawater (Jerlov, 1976). Green is the second most frequently emitted color, found primarily in benthic and shallow coastal areas where turbidity rates tend to scatter blue light, creating a need for transmission of longer wavelengths (Herring, 1983). These green wavelengths are also common among the minor percentage of terrestrially luminescent organisms including fireflies, beetles, and fungi (Sharifian et al., 2017). The green fluorescent protein found in *Aequorea victoria*, (i.e., jellyfish) emits green light through energy transfer between a stable luciferase intermediate photoprotein (aequorin) and green fluorescent protein (Love & Prescher, 2020; Shimomura et al., 1962, 1963), and is a well documented and utilized tool for biomedical and biotechnical studies. Other wavelengths of light emitted do exist and include violet, yellow, orange, and red; however, their occurrence is rare (Widder, 2010).

Types of luciferin

The main luciferins found in most luminescent genera in the sea are coelenterazine, dinoflagellate, Vargulin (or cypridinid-type), and bacterial luciferin. Coelenterazine is the most abundant luciferin molecule in marine ecosystems and is regularly employed as a substrate by many independently evolved luciferases in phylogenetically diverse groups of animals (Bessho-Uehara et al., 2020; Fleiss & Sarkisyan, 2019). Trophic interactions contribute to coelenterazine's widespread presence in marine species, as it is not generally synthesized by an organism itself but acquired through dietary means (rare exceptions of intrinsically synthesized coelenterazine include the decapod shrimp *Systellaspis debilis* and the copepod *Metridia pacifica (*Oba et al., 2009a; Thomson et al., 1995). All known coelenterazine-dependent systems emit blue-wavelength light and most do not require a cofactor other than oxygen, except for gelatinous fauna that use it in conjunction with photoproteins (Ohmiya & Hirano, 1996). In some cases, a fluorescent protein interacts with the luciferase to change the hue of bioluminescence. The plethora of genera utilizing coelenterazine includes radiolarians, cnidarians, ctenophores, cephalopods, copepods, decapod shrimp, lophogastrids, chaetognaths, certain ophiuroids, and some fishes (Haddock et al., 2010).

Dinoflagellate bioluminescence contrasts with cypridinid- and coelenterazine-driven bioluminescence by emitting light using complex organs (Fleiss & Sarkisyan, 2019). The luciferin found in dinoflagellates is similar to chlorophyll (Dunlap et al., 1981), suggestive of derivation from photosynthetic organisms, although the specific ecological purpose of this adaptation is unknown (Johnsen, 2005). The intensity of light emitted from dinoflagellate-type luciferin is dependent on the amount of sunlight the organism receives during the day. This mechanism allows dinoflagellates to recharge their chemicals to flash again the next night. Dinoflagellates and krill (which also contain dinoflagellate-type luciferin) both produce blue-green wavelengths of light (Haddock et al., 2010). Bioluminescent dinoflagellate ecosystems are uncommon in the open ocean, occurring largely in warm-water lagoons with limited access to the open sea (Kendall et al., 2005). Bioluminescence from this type of luciferin-luciferase complex results in flashes of light induced by electrical or mechanical stimulation in dinoflagellates (Valiadi & Iglesias-Rodriguez, 2013) and euphausiids (Fregin & Wiese, 2022).

Cypridinid-type luciferin, like coelenterazine, also emits a blue wavelength light and is thought to be acquired through a dietary ingestion, producing what is known as semi-intrinsic luminescence (Mirza & Oba, 2021). Although biosynthesis of this luciferin is not entirely known (Fleiss & Sarkisyan, 2019), all known instances of semi-intrinsic luminescence involve either coelenterazine or cypridinid-type luciferin as the substrate (Mirza & Oba, 2021). Luminous genera exhibiting use of cypridinid-type luciferin include ostracods, the midshipman fishes (*Porichthys* spp.) and a species of sweeper fish, *Parapriacanthus ransonneti* (Delroisse, 2021; Haddock et al., 2010).

The entire mechanism of bacterial luciferin production has been known since the late 1980s, making the lux operon the only genetically encodable bioluminescent system available in the last three decades (Meighton, 1991). Bacterial bioluminescence is uniform in the sense of all organisms utilizing bacterial luciferin exude the same light emission mechanism whereby photons are created in a series of reactions that require flavin mononucleotide (FMN), myristic aldehyde, oxygen, and nicotinamide adenine dinucleotide (NADH) (Fleiss & Sarkisyan, 2019). Myristic aldehyde is oxidized during luciferin processing; however, the main light source in bacterial bioluminescence is the flavin mononucleotide derivative (Fleiss & Sarkisyan, 2019). Most bacterial bioluminescence is blue, although red-shifted forms of the bacterial system exist both naturally and synthetically (Fleiss & Sarkisyan, 2019). Bacterial luciferin may occur in free-living or symbiont bacteria and is found in certain species of bacteria, squid, fishes, and most recently, pyrosomes (Haddock et al., 2010).

Adaptations of bioluminescence

Although the light-emitting chemicals are extensive and unique, the methods of controlling light emission are even more diverse in nature. The numerous examples of evolutionary convergence connected to bioluminescence attest to the trait's survival benefits (Widder, 2010). Organisms with bioluminescent capabilities emit light either through an intrinsic, self-luminescent capability (autogenically) that allows the organism to regulate their light activities or by symbiotic bacteria contained in light organs (Tanet et al., 2020). Both systems can be utilized in one organism, such as in female linophrynid anglerfishes (Sutton & Milligan, 2019), though it is more common that organisms produce bioluminescence intrinsically rather than by bacterial symbionts (Haddock et al., 2010). As the method of bioluminescence varies in organisms, so does the purpose, ranging from reproduction to defense.

While the origin and function of some bioluminescent systems remain ambiguous, research assessing the function, physiology and evolution of bioluminescence has exponentially expanded insight into the mechanisms driving this chemical generation of light among organisms (Widder, 2010). The phenomenon is widespread and diverse, including habitats ranging geographically from tropical to polar, and vertically from the sea surface to the sea floor (Haddock, 2010). The widespread occurrence paired with the impressive array of taxa that possesses bioluminescent capabilities provides evidence that bioluminescence is essential for fulfilling ecological roles within the pelagic ocean (Martini & Haddock, 2017).

Zones of the ocean and bioluminescence

In a vertical sense, the pelagic ocean consists of depth zones referred to as the epipelagic, mesopelagic, bathypelagic, abyssopelagic and hadalpelagic zones (Figure 1). This zonation relates to light availability, as described below, and is the main factor determining the vertical distribution of pelagic communities, and inherently, bioluminescence among these assemblages (Martini & Haddock, 2017).

The epipelagic (euphotic) zone is characterized by ample sunlight and is populated by photosynthetic organisms (Figure 2). The mesopelagic (dysphotic) zone is characterized by a gradient of light from 1% to 0% of surface solar light (Jerlov, 1976) and serves as a transition zone from primarily solar to primarily organismal light production. This transition of light source dependency makes this zone an oceanic 'bioluminescent hotspot,' where more than 80% of the species present are predicted to be bioluminescent (Paitio et al., 2016). The mesopelagic zone is a highly structured habitat vertically due to the exponential rate of sunlight attenuation with increasing depth. This creates a visual-adaptation-heavy environment where organisms have developed various strategies to optimize light detection (Claes et al., 2014b). The final zone, the bathypelagic (aphotic) zone, encompassing depths too great for sunlight to penetrate, has been subdivided into the bathypelagic (1000-4000 m), abyssopelagic (4000-6000 m) and hadalpelagic (6000 m and deeper) zones. Despite being the least-studied major ecosystem type on Earth (Webb et al., 2010), the bathypelagic zone occupies 7.5 times the total volume of all terrestrial ecosystems combined, while also containing over 60% of the ocean's volume (review in Sutton, et al., 2010). In this zone, bioluminescent micronekton species are characterized by a reduction in both number and size of photophores (Herring & Morin, 1978). While bioluminescence is most abundant in the pelagic ocean, bioluminescence in coastal regions is exhibited by only approximately 1 to 2% of taxa, with the majority of these organisms being microorganisms such as dinoflagellates and marine diatoms (Morin, 1983). While there is greater abundance of bioluminescent species in the mesopelagic and bathypelagic zones, it appears that total bioluminescence intensity is greatest in the epipelagic zone, possibly due to the prevalence of photosynthetic bioluminescent organisms (Paitio et al., 2016).

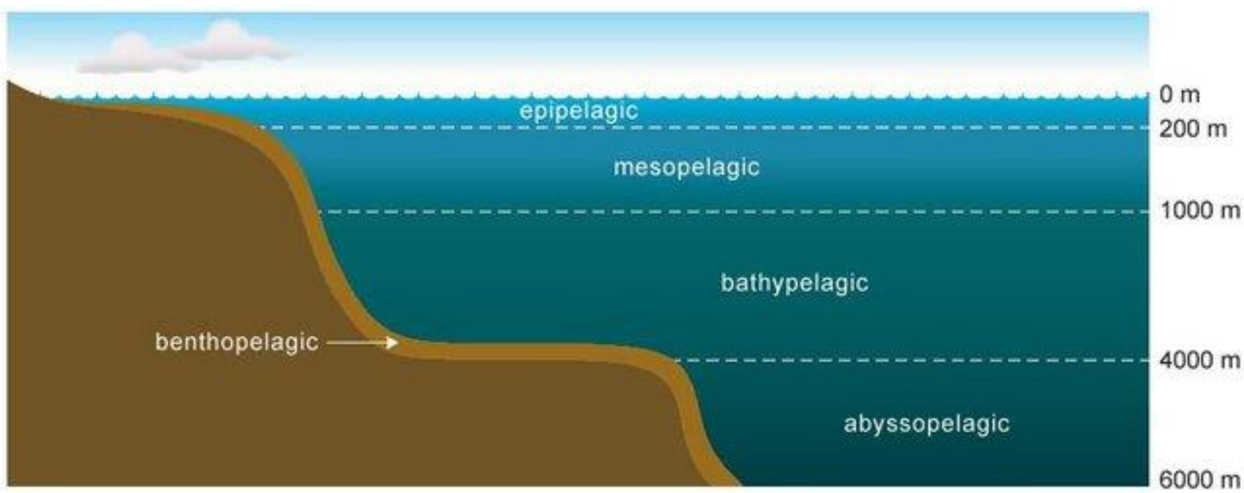

Figure 1. The depth zones of the pelagic ocean (www.fao.org).

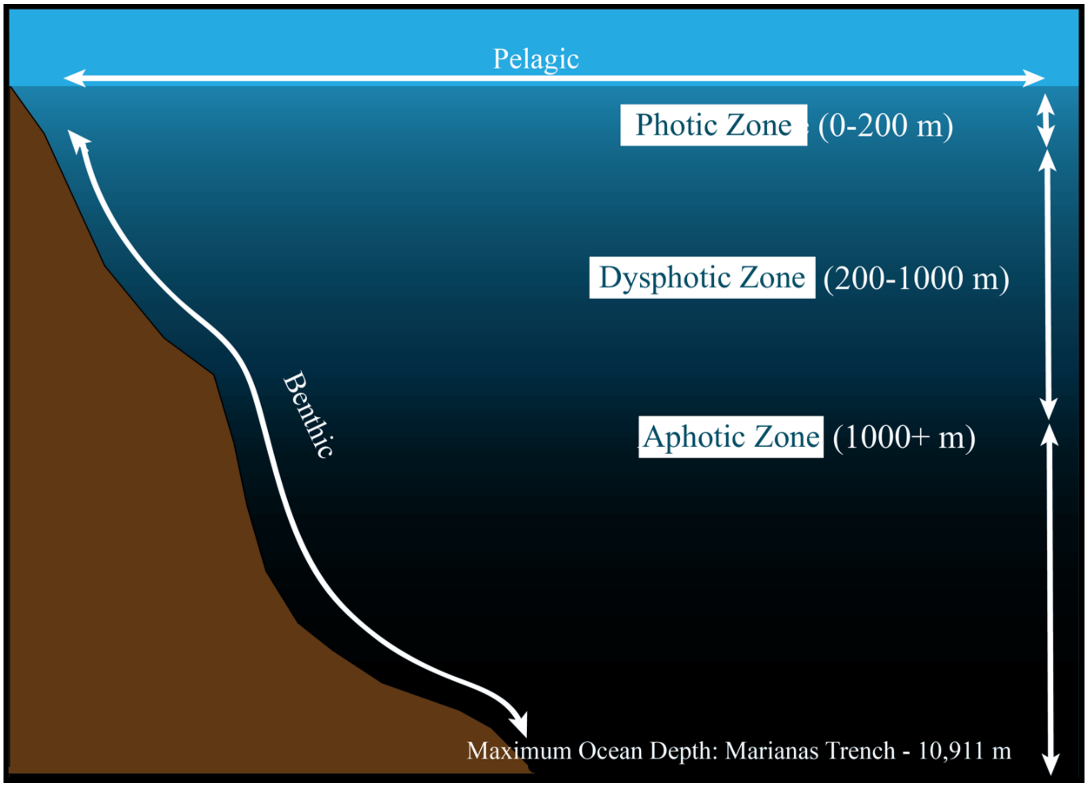

Figure 2. Pelagic oceanic zones defined by light availability (www.tigerweb.towson.edu).

Bioluminescence in marine organisms

Bioluminescence in fishes

Studies of bioluminescence in fishes indicate that the ability to generate light developed dozens of times in unrelated clades (Paitio et al., 2016), with bioluminescence most likely evolving at least 29 times in fishes (Davis et al., 2016; Srivastava & Katiyar, 2021). At least 43 families among 11 orders of bony fishes emit bioluminescence, either intrinsically or via bacterial symbionts (Paitio et al., 2016). Bioluminescence is particularly prominent in bony fishes which possess a complexity and diversity of light organs with their accompanying biological and ecological functions (Ghedotti, 2018). Approximately 1510 species of fishes are known to possess bioluminescence (Davis et al., 2016; Paitio et al., 2016). There are many cases where entire fish families exhibit bioluminescent qualities, including the Myctophidae, Leiognathidae, Anomalopidae, and multiple anglerfish families (Davis et al., 2014; Paitio et al., 2016; Pietsch, 2009). In addition, every species in the order of Stomiiformes is capable of bioluminescence (Sutton, 2003).

The structure and positioning of light organs in bony fishes belies their function, namely defense (counterillumination, startling), offense (prey attraction), and communication (Paitio et al., 2016). Photophores can be incredibly sophisticated, with a single fish containing both thousands of microscopic simple photophores and a few sizable photophores (Paitio et al., 2016) as presented below.

Teleostei. The repeated evolution of bioluminescence is widespread across teleost (bony) fishes (Davis et al., 2016). The high number of independent origins of bioluminescence in vertebrates is documented only among marine fishes. Intrinsic bioluminescence constitutes more than half of all known bioluminescent fish species, using either cypridinid- or coelenterazine-type luciferin systems (Paitio et al., 2016). Control of intrinsic bioluminescence via neural light emission is present in dragonfishes (Stomiidae), lanternfishes (Myctophidae), *Porichthys*, slickheads (Alepocephalidae), and pearleyes (Scopelarchidae) (Claes & Mallefet, 2015; Paitio et al., 2016). Fishes that use bacterial symbionts, which emit light continuously, have developed a plethora of anatomical features such as chromatophores and tissue patch “shutters" that focus, broadcast, or even restrict the light produced by the bacteria.

Chondrichthyes. While bioluminescence is not as commonly found in cartilaginous fishes compared to teleosts, three families within one order of Chondrichthyes express luminosity: Etmopteridae, Dalatiidae and Somniosidae (Mallefet et al., 2021; Straube et al., 2015). Bioluminescence in sharks differs from the typical process in teleosts; in sharks, photogenic organs are predominantly controlled by hormones rather than under neural control (Duchatelet et al., 2021). Bioluminescence in Chondrichthyes serves multiple purposes such as counterillumination, aposematism, and conspecific recognition (Claes & Mallefet, 2009b; Claes et al., 2014a). While the first descriptions of shark light emission date back to the nineteenth century, bioluminescence studies that focus on physiological control and photophore form and function have only recently been undertaken. Although previous studies describe the evolution, ecology, and physiology of shark luminescence, the interplay between hormonal regulatory system and neuromodulation, as well as the chemistry of shark luminescence, currently remains poorly known (Duchatelet et al., 2021).

Bioluminescence in Crustaceans

The Crustacea, a subphylum of the diverse phylum Arthropoda, contains an extensive group of bioluminescent taxa, including ostracods, copepods, euphausiids and decapods (Frank et al., 2012; Haddock et al., 2010). Bioluminescent crustacea live primarily above 1000 m depth (krill, mesopelagic shrimp), while non-bioluminescent deep-sea Crustacea (isopods, decapods) live below 2500 m, with a gradient in between (Haddock et al., 2010).

Euphausiids are particularly prominent with respect to the number of bioluminescent species, with only one known non-luminescent exception (Harvey, 1952). Furthermore, euphausiids employ the same luciferin as dinoflagellates (Nakamura et al., 1989), implying trophic connections at some point in their evolution. Decapod bioluminescence has only been reported in meso- and bathypelagic taxa, with the family Sergestidae having an abundance of luminescent species (Review in Golightly et al., 2022). Sergestids that possess organs of Pesta, a type of autogenic internal photophore, are able to tilt these structures to keep their downward position, regardless of body orientation, for counterillumination (Latz, 1995). Within the family Oplophoridae, three genera are known to exhibit not only secretory spews of luminescence, but also a mechanism of bioluminescence in the form of cuticular photophores that function for counterillumination (Herring, 1985; Wong et al., 2014). The majority of decapods, ostracods and copepods utilize coelenterazine-type luciferin, while a variety of ostracods have been found to use cypridinid-type luciferin (Widder, 2010). The morphology and position of crustacean photophores highlight functions of bioluminescence, such as the use of ventral photophores for counterillumination and mate recognition (Johnsen et al., 2012; Widder, 2010).

Bioluminescence in marine Mollusca

Bioluminescent molluscs demonstrate at least seven ways to generate light intrinsically (Haddock et al., 2010). Most luminous molluscs produce light using coelenterazine or highly derived or modified versions of coelenterazine (Rees, 1998). While this is primarily intrinsic, several species appear to obtain coelenterazine via dietary means. Bacterial symbionts generate light in several genera in the families Sepiolidae and Loliginidae (Guerrero-Ferreira & Nishiguchi, 2009; Jones & Nishiguchi, 2004; Ruby & McFall-Ngai, 1992). The intrinsic output derived from bacterial luciferin does not create a uniform level of luminescence but rather exhibits predictable cyclic oscillations in the amount of light emitted per cell (Brodl, 2018). The oscillation rhythm resembles a circadian pattern in that it causes an increase in the intensity of symbiont luminescence throughout the day (Boettcher et al., 1996). Within the Mollusca, bioluminescence occurs across a wide range of taxa, including the Gastropoda, Bivalvia, and Cephalopoda. Although the pelagic environment is certainly the one in which luminescence has been most frequently observed, there are some molluscs residing in the pelagic zone with no known examples of luminescence, including holoplanktonic gastropods (heteropods and pteropods) (Herring, 1987).

Among the luminescent molluscs, the most prominent are the cephalopods, with squid alone representing at least 70 luminous genera (Haddock et al., 2010). Squids can generate an impressive range of luminous displays, with complex photophores on various parts of the body emitting long displays of light, flashes of light, secreting luminous “ink” clouds, and glowing tentacles (Review in Widder, 2010). Many species are thought to employ their ventral photophores to provide counterillumination for both predatory and defensive purposes (Davis et al., 2016). Given the variety of methods that cephalopods utilize to produce bioluminescence, the number of independent evolutionary origins in this group, and in Mollusca in general, is likely to be far larger than previously thought (Lindgren et al., 2012).

Bioluminescence in gelatinous megaplankton

Gelatinous fauna such as ctenophores and cnidarians are notable for their ability to produce light (Haddock & Case, 1994; 1995; Herring, 1987). While cnidarians and ctenophores are among the simplest invertebrates, they have refined bioluminescent expression numerous times and in numerous ways (Morin & Hastings, 1971; Shimomura et al., 1962).

Ctenophores. Ctenophores have the highest proportion of bioluminescent species, with more than 90% of genera known to produce light (Haddock & Case, 1995; Haddock et al., 2010). In a study of bioluminescence in the Pacific, 91.8% of ctenophores were found to be bioluminescent (Martini & Haddock, 2017). Ctenophores are strictly carnivorous, but do not possess stinging cells to stun prey, as are found in Cnidaria, leading the phylum to be extremely diverse to accommodate a wide trophic breadth (Martini & Haddock, 2017). Typically, ctenophores feed using strategies such as their tentacles, lobes, engulfment, mucus, colloblasts, or their large cilia, which are used to engulf and swallow specific species of prey. Many ctenophores have red coloring, a form of iridescence, which is hypothesized to block light emitted by consumed bioluminescent prey (Review in Jékely, 2015).

Cnidaria. Martini & Haddock (2017) quantified bioluminescence potential among cnidarian taxa and reported over 97% of species to be bioluminescent. Within the phylum, the most notable are the Hydrozoa (including hydromedusae and siphonophores), with 100% of known species predicted to be bioluminescent (Martini & Haddock, 2017). Benthic cnidarians including corals and anemones also exhibit bioluminescence (Johnson et al., 2012). All luminous cnidarians studied to date utilize coelenterazine as their light-emitting substrate (Haddock et al., 2010).

Purpose of bioluminescence

Predation reduction

One of the most common uses of bioluminescence is presumed to be defense against predators in a dark environment. Predation reduction mechanisms of bioluminescence are presented in a variety of forms, with one of the most widely known being the use of counterillumination (Brodl et al., 2018), in which organisms utilize ventral photophores to replace downwelling light blocked by their bodies. In this manner, they camouflage their silhouette from visual predators below them (Claes et al., 2014a). If a counterilluminating organism resides in an area with variable light input such as the upper mesopelagic, the intensity of light can be adjusted to match the changing light field. Autogenic light organs in deep-sea shrimp autogenic light organs exhibit light-detecting abilities that may explain how the organism can fine-tune their light emission to match the downwelling of light (Bracken-Grissom et al., 2020). Photophores on eyestalks potentially act as feedback mechanisms to determine how well their ventral photophores match background light (Herring & Locket, 2009). These, like most photophores, are controlled by the nervous system, with serotonin being modulated by nitric oxide (Haddock et al., 2010; Krönström et al., 2007). While counterillumination serves as a long-term adaptation to evade predators, there are also encounter-based defenses such as flashes of bioluminescence or bioluminescent clouds produced to confuse or startle a predator (Widder, 2010). *Vampyroteuthis infernalis* (i.e., vampire squid), similar to many other deep-sea squid, lacks ink sacs and instead ejects sticky bioluminescent mucus that startles, confuses and delays predators, allowing the squid to flee (Haddock et al., 2010). Similarly, many of the planktonic, luminous species of copepods, ostracods, crustaceans, siphonophores, ctenophores and cnidarians produce luminous secretions in the water as a defensive cloud for distraction (Haddock et al., 2010). Most hydrozoans employ bioluminescence as a warning, producing flashes, waves, and glowing periods of light.

Bioluminescent slime is often used to mark predators so that something else might consume the predator rather than the primary prey item. Luminous brittle stars and sea cucumbers are capable of detaching parts of the body that luminesce independently or attach to passing organisms, redirecting the predator to trail that organism instead, providing an escape for the brittle star or sea cucumber (Widder, 2010). This action is thought to be strictly for defense because sea stars and sea cucumbers do not possess image-forming eyes (Haddock et al., 2010).

Offensive

In contrast to defensive uses of bioluminescence, many predatory deep-sea fishes utilize lures or headlights to help attract or find food. Myctophids belonging to the genus *Diaphus* employ larger photophores around their eyes to illuminate prey in the water column (Paitio et al., 2016). Females of many species of deep-sea anglerfishes are notorious for using their bioluminescent lure to attract prey (Pietsch, 2009). The ability of some loosejaws (i.e., *Malacosteus*) to emit red light is a unique adaptation of offensive and defensive bioluminescence; most pelagic animals can only detect blue light, allowing *Malacosteus* to illuminate their prey while remaining undetected (Herring & Cope, 2005; Widder et al., 1984). Counterillumination, while generally considered to be a defensive mechanism, may also be considered a predatory technique used by cookiecutter sharks (Mallefet et al., 202l; Widder, 1998).

Communication

Bioluminescence may also be used to locate potential mates by species-specific or spatial and temporal emissions of light, although the only verified example of this in the marine environment is in ostracods, which use a species specific pattern of luminescent spew to attract mates (Morin, 1983). All of the other examples are based on correlation, not experimental data. For example, many meso- and bathypelagic fishes, crustaceans, and squid have species-specific and/or gender specific photophore patterns (Herring, 2007). In particular, lateral photophores are hypothesized to assist in inter/intraspecies communication (Haddock et al., 2010). *Taningia danae* (i.e., Dana Octopus squid), a cephalopod with light organs at the extremities of its arms, possesses clawlike hooks instead of suckers and enormous light organs at the tips of its arms (Haddock et al., 2010). They are hypothesized to use light for intraspecific communication as well as to possibly stun victims. Bioluminescence has also been hypothesized to play a role in mating, as females of the pelagic deep-sea octopods *Japetella* and *Eledonella* develop a glowing greenish-yellow ring around their mouth when sexually mature (Herring et al., 1987). In certain deep-pelagic shrimp genera, such as *Systellaspis*, *Oplophorus*, and *Janicella*, that possess both photophores and secretory spews of bioluminescence, also possess blue-green and near-UV-sensitive visual pigments, that may provide these shrimps with the ability to differentiate between their different modes of bioluminescence (Frank & Case, 1988; Frank & Widder, 1999).

Depending on conditions, a bioluminescent flash is detectable from tens to hundreds of meters away, making bioluminescence one of the most effective ways for organisms to communicate in the deep sea (Turner et al., 2009; Warrant & Locket, 2004). For example, nighttime schooling of flashlight fishes using synchronized bioluminescent flashing displays only requires small bioluminescent flashes in a small percentage of individuals for school cohesion to be maintained. The use of bioluminescence by flashlight fishes suggests that schooling behavior in mesopelagic bioluminescent fishes may be facilitated by luminescent flashing displays (Gruber et al., 2019).

Bioluminescence and diel vertical migration

The daily, synchronized movement of marine animals between the surface and deep layers of the open ocean is referred to as diel vertical migration (DVM) and is thought to be the largest net animal movement on the planet (Hays, 2003; Longhurst, 1976). The migratory assemblage includes a wide range of deep-sea biota, including many micronektonic crustaceans, fishes, and cephalopods. DVMs are primarily driven by the need to avoid the elevated risk of visual predation during the day in the enhanced-prey environment in shallow waters. (Bollens & Frost, 1989; Hays et al., 2010; Marshall, 1955). Depth- and light-related niche partitioning may generate a series of synchronized vertical movements of predators and prey within depth strata (i.e., staged migrations) (Vinogradov, 1962).

Significance of work and project aims

Bioluminescence is known to have a strong influence on species interactions via predator-prey relationships and in reproductive strategy (Haddock et al., 2010), making the trait a distinguishing feature in ecological function. Trait-based approaches assessing the similarity of organisms based on functional and morphological traits is becoming more relevant in community ecology to address general ecological rules (Martini et al., 2019). It has been hypothesized that bioluminescence is utilized more frequently and in more complex ways in the pelagic environment than in the benthic realm (Morin, 1983). Thus, an understanding of organismal bioluminescence abundance is central to understanding the ecology of the deep-sea and processes of diel vertical migration.

Utilizing one of the most highly resolved (taxonomically and spatiotemporally) datasets in oceanographic history, the aims of this project are to: (1) create an inventory of the bioluminescent micronekton and net-caught gelatinous megaplankton of the northern and eastern Gulf of Mexico from the surface to 1500 m depth; (2) quantitatively assess the abundance and vertical distribution of bioluminescent micronekton (gelatinous taxa are considered quantitative only at the level of taxon, not of individuals due to sampling damage); (3) investigate the vertical distribution of micronektonic bioluminescence as a function of diel cycle; and (4) discuss how the distribution of bioluminescence relates to the overall vertical ecology of a low-latitude, oceanic ecosystem.

The quantitative characterization of bioluminescence using this highly resolved data set will provide ecological insight into the taxonomic scope, distribution, and variability of micronekton bioluminescence in the GoM, which may serve as an analog to the world's low-latitude deep pelagial (by far Earth's largest ecosystem type).

Methods

Data and sample collection

Following the *Deepwater Horizon* Oil Spill (DWHOS) in 2010, two programs were established to examine the spill's consequences on the Gulf of Mexico (GoM). The first program, ONSAP (Offshore Nekton Sampling and Analysis Program; Cook et al., 2020; Sutton et al., 2020), was supported by NOAA and involved a series of seven surveys undertaken between 2010 and 2011. Four of the seven surveys were conducted on the NOAA FRV *Pisces* as part of this program: Pisces 8 (PC8), Pisces 9 (PC9), Pisces 10 (PC10), and Pisces 12. (PC12). Each *Pisces* sampling survey lasted three weeks (Cook et al., 2020). A total of 17 stations were sampled obliquely using a series of high-speed rope trawls (Cook et al., 2020). Because the trawl utilized in *Pisces* sampling were non-closing, discrete-depth bins could not be sampled. "Shallow-depth" samples were typically taken from the surface to 800 m, while "deep samples" were routinely fished from the surface to a depth of 1300-1500 m, with concentration between 700-1500 m. There were 84 "shallow" trawls and 87 "deep" trawls in total (Cook et al., 2020).

The remaining three ONSAP surveys were conducted on a second research vessel, the M/V *Meg Skansi*: Meg Skansi 6 (MS 6), Meg Skansi 7 (MS 7), and Meg Skansi 8 (MS 8). From January to September 2011, this vessel sampled continuously, with a total of 47 locations sampled day and night (Cook et al., 2020). A 10-m^2 Multiple Opening/Closing Net and an Environmental Sensing System (MOCNESS; MOC-10) was used for micronekton sampling (Cook et al., 2020). Unlike the nets used on the *Pisces* deployments, this net was remotely opened and closed at various depths to sample discrete depth bins (Cook et al., 2020). The MOC-10 net sampled five discrete depth bins: N1 = 1500 m-1200 m; N2 = 1200 m-1000 m; N3 = 1000 m-600 m; N4 = 600 m-200 m; and N5 = 200 m-surface (Cook et al., 2020).

Following ONSAP, the GoM Research Initiative (GoMRI) funded the Deep Pelagic Nekton Dynamics (DEEPEND) Consortium. Sampling was conducted over eight cruises onboard the R/V *Point Sur* in the northern GoM (Cook et al., 2020). Deep-pelagic species were sampled using MOC-10 nets at the same discrete depth intervals as the *Meg Skansi* surveys (Cook et al., 2020). Cruise DP01 occurred in May 2015, DP02 in August 2015, DP03 in May 2016, DP04 in August 2016, DP05 in May 2017, DP06 in July/August 2017, DP07 in April/May 2021, and DP08 in July/August 2022. The data from cruises DP01-DP07 were included for this project and all micronektonic specimens collected from ONSAP and DEEPEND cruises and sample locations (Figure 3) were utilized for this project. DP08 cruise data was omitted as the data had not been processed entirely prior to the synthesis of this project. Across DEEPEND cruises DP01-DP07, trawl deployments were conducted at 33 stations using MOC-10 nets. A total of 7,554,002 cubic meters of water were sampled at five discrete depth intervals from surface to 1500 m centered around solar noon and midnight. The total trawl deployments for sampling per cruise series are noted in **Table 1**.

Table 1: Cruise series and count of samples.

Cruise Series	Number of Samples
Pisces	171
Meg Skansi	94
DEEPEND	142

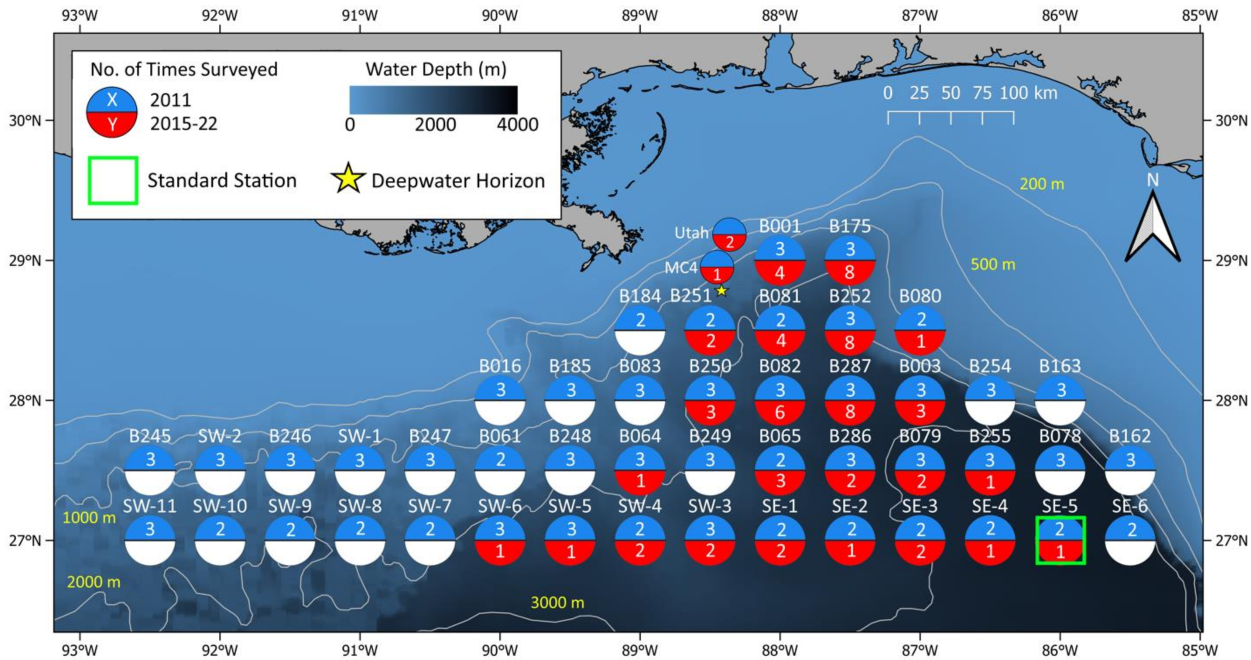

Figure 3. Sample grid and station identifications used during the ONSAP and DEEPEND programs in the northern GoM: placement of the star represents the *Deepwater Horizon* oil spill location. Blue colored half-circles represent ONSAP sample sites, while red colored half-circles represent DEEPEND sample sites. Sites with both red and blue were sampled during each cruise series. Numbers indicated inside the circle represent the number of times the site was sampled during cruises. The light to dark blue coloration represents the depth of the GoM at sample locations. **Figure from Cook et al., 2020.**

Faunal inventory of bioluminescent taxa

All specimens from ONSAP and DEEPEND cruise series were identified to the lowest taxonomic level possible. Bioluminescence capability of each taxon was determined by morphological characteristics such as the presence of photophores, luminescent lures, appendages, or any other light organs. Additionally, the ability to secrete or expel bioluminescent clouds or slime were determined via an extensive literature search. In addition to the scientific literature, information from large scientific databases was utilized, including FishBase, CephBase, the World Register of Marine Species, ITIS, The Tree of Life, Systematic Distribution of Bioluminescence in Living Organisms (Herring, 1987; Suntsov et al., 2008; Widder and Sutton, 2008), and the most recent additions to luminous taxa from a review of bioluminescence by Haddock et al. (2010). Finally, species with "speculated bioluminescent capabilities" e.g., *Gennadas*, were considered bioluminescent for this appendix. All data collected from this study were then compiled to create a bioluminescent oceanic micronekton inventory to provide a starting point for quantitative analysis. All species that were found to be bioluminescent were supported with a reference to the claim and added to **Appendix Table 1.**

Bioluminescence as a function of taxon and organismal abundance

Discrimination of taxonomic units for further quantitative analyses

All taxa were required to meet the "unique" standard in order to be considered for the bioluminescent faunal inventory (i.e., there was no lower taxonomic identification of the specimen within their taxon). The previously created bioluminescent inventory was utilized to create a second appendix table (**Appendix Table 2**) denoting counts of bioluminescent taxa, non-bioluminescent taxa, and total taxa among all cruise series.

Quantitative assessment of bioluminescence

All samples of fishes, crustaceans, and cephalopods collected from DEEPEND cruises DP01-DP07 that had accurate flow data and conformed to standardized depth bins were selected for quantitative analysis. These analyses specifically considered standardized abundance (no. volume^{-1}) and depth of occurrence, both day and night. The previously created bioluminescent inventory was utilized to calculate bioluminescence ratios of individuals and taxa among the quantitative DEEPEND samples and was organized in **Appendix Table 3** by major faunal group (Fishes, Crustacea and Cephalopoda).

Gelatinous macrozooplankton exclusion from organismal abundance analyses. Sampling throughout the ONSAP and DEEPEND cruises with the high-speed rope trawl net and MOC-10 nets targeted fishes, crustaceans and cephalopods. During this process, “net-caught gelata,” ctenophores, cnidarians, chaetognaths, echinoderms, gastropods, annelids, and Urochordata (tunicates) were also collected, albeit non-quantitatively (net sampling can destroy fragile gelatinous forms, leaving only the large and robust taxa in cod ends). These taxa were included in the comprehensive bioluminescent inventory but were not included in quantitative analyses.

Vertical distribution of bioluminescence

Bioluminescence vertical distributions were plotted in R Studio using modified t-plots that compared day and night sampling efforts. The plot displayed the relative abundance of bioluminescent micronekton as a percentage of individuals and percentage of all taxa caught at each depth interval and time of day. These plots were separately created for fishes, crustaceans and cephalopods. The change in the vertical distribution of bioluminescent taxa during the diel cycle was reflected in these plots, with specific emphasis on a predicted “epipelagic transition” from a sparse bioluminescent environment during daytime to a highly bioluminescent environment at night.

Results

Faunal inventory of bioluminescent micronekton and net-caught gelatinous zooplankton in the deep-pelagic Gulf of Mexico

Of the 1451 unique taxa (defined in 2.2.1.) collected during ONSAP and DEEPEND sampling, 636 (43.8%) are considered bioluminescent. Fishes comprised the majority of bioluminescent taxa (317), while net-caught gelata (164), crustaceans (94), and cephalopods (61) represented the remainder of bioluminescent taxa (**Figure 4).**

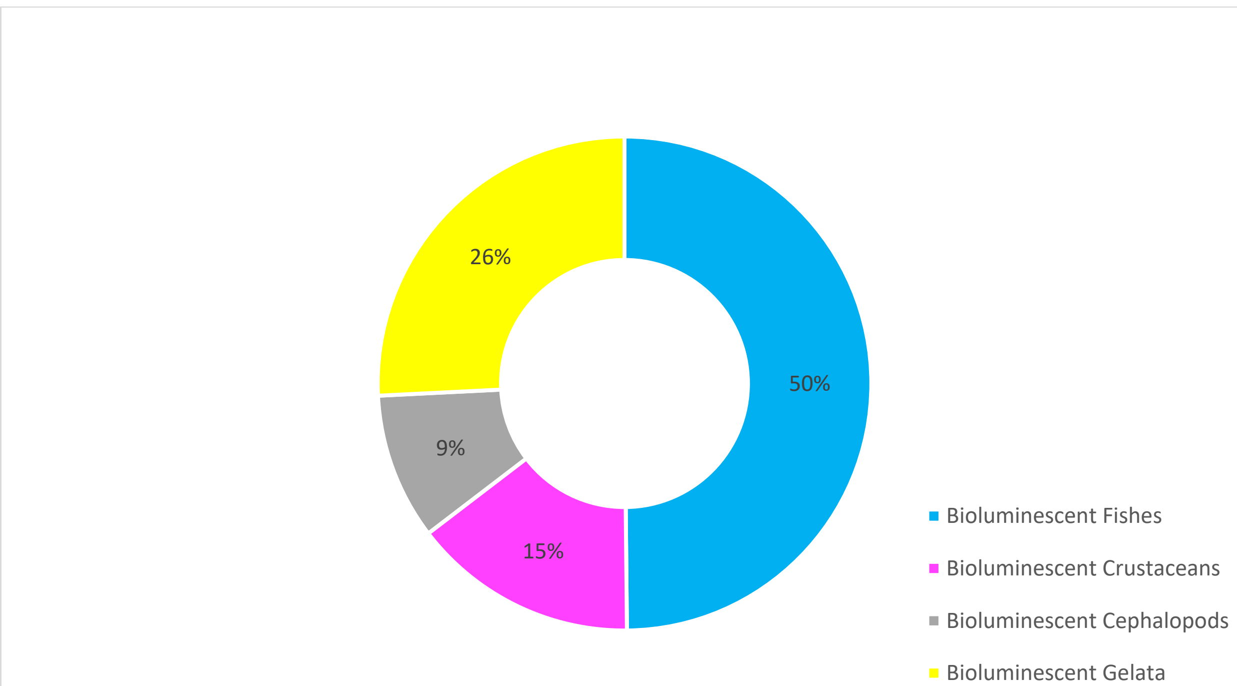

Figure 4: Taxonomic breakdown of bioluminescent taxa in the deep-pelagic Gulf of Mexico.

Fishes contributed the most taxa to the total micronekton/macrozooplankton assemblage (65.6%), as well as the highest number and percentage of bioluminescent taxa (317, 49.8%, respectively). Of the 952 total fish taxa collected, approximately 33.3% are considered bioluminescent**.** Stomiiformes accounted for ~45% of luminous fish species, Myctophiformes ~20%, Lophiiformes (specifically, ceratioid anglerfishes) ~19%, and Alepocephaliformes ~7% of luminous species. Other Orders contributing less than 7% of the total bioluminescent species included, in decreasing order, Gadiformes, Scombriformes, Aulopiformes, Squaliformes, Argentiniformes, Acropomatiformes, and Saccopharyngiformes**.**

Net-caught gelatinous macrozooplankton accounted for 243 unique taxa of the 1451 micronekton/macrozooplankton taxa collected. A total of 164 taxa (67.4%) of all gelatinous macrozooplankton taxa are considered bioluminescent. Members of Class Hydrozoa comprised 131 of the 164 (79.8%) bioluminescent taxa, with the majority of species belonging to the Order Siphonophorae.

Crustaceans accounted for 165 taxa of the total micronekton/macrozooplankton assemblage. Bioluminescent taxa (94) represented ~59% of crustacean taxa collected. Members of the Order Decapoda comprised about 60% of the bioluminescent taxa, the majority of which came from Superfamily Oplophoroidea (consisting of the Acanthephyridae and Oplophoridae) (~27%) and Sergestidae (~20%). Euphausiidae comprised 31% of bioluminescent crustacean taxa.

Class Cephalopoda accounted for 91 taxa of the total micronekton/macrozooplankton assemblage (6.2%). Bioluminescent taxa (61) represented approximately 67% of cephalopod taxa collected. The majority of bioluminescent cephalopods (87%) belong to the Order Oegopsida.

Vertical partitioning of bioluminescence as a function of taxon and organismal abundance

Quantitative Assessment of Bioluminescence among taxa and individuals

During DEEPEND cruises, 579 taxa were collected, with 264 (45.5%) being bioluminescent. Collectively, 64,991 individuals of micronekton (fishes, crustaceans and cephalopods) were captured. Fishes made up of the majority of total individuals (35,803), followed by crustaceans (28,779), and then cephalopods (409 individuals). Of the total number of individuals collected, bioluminescence taxa contributed 49,065 individuals (75.5% of the total).

Fishes. A total of 427 fish taxa (148 bioluminescent [34.7%]) and 35,803 individuals (28,003 bioluminescent [78.2%]) were collected during DEEPEND cruises. The percentages of bioluminescent taxa and total individuals with respect to depth and diel cycle are shown in Figures 5 and 6, respectively.

Among bioluminescent fishes, the most frequently caught taxon was the genus *Cyclothone* (Family Gonostomatidae), captured day and night in all depth bins. Individuals from the genus

Cyclothone accounted for 72.3% of all (20,255) bioluminescent fishes. Members of the sternoptychid genera *Sternoptyx*, *Argyropelecus*, *Valenciennellus*, and the myctophid genera *Lampanyctus*, *Diaphus*, *Ceratoscopelus*, and *Benthosema* made up 23.0% of the total bioluminescent fishes captured. Other genera within Gonostomatidae (*Sigmops* and *Gonostoma*) contributed ~ 1% of all bioluminescent individuals. Additional abundant bioluminescent fish taxa included individuals of the families Sternoptychidae and Myctophidae, contributing to approximately 11% and 9% of all bioluminescent individuals, respectively.

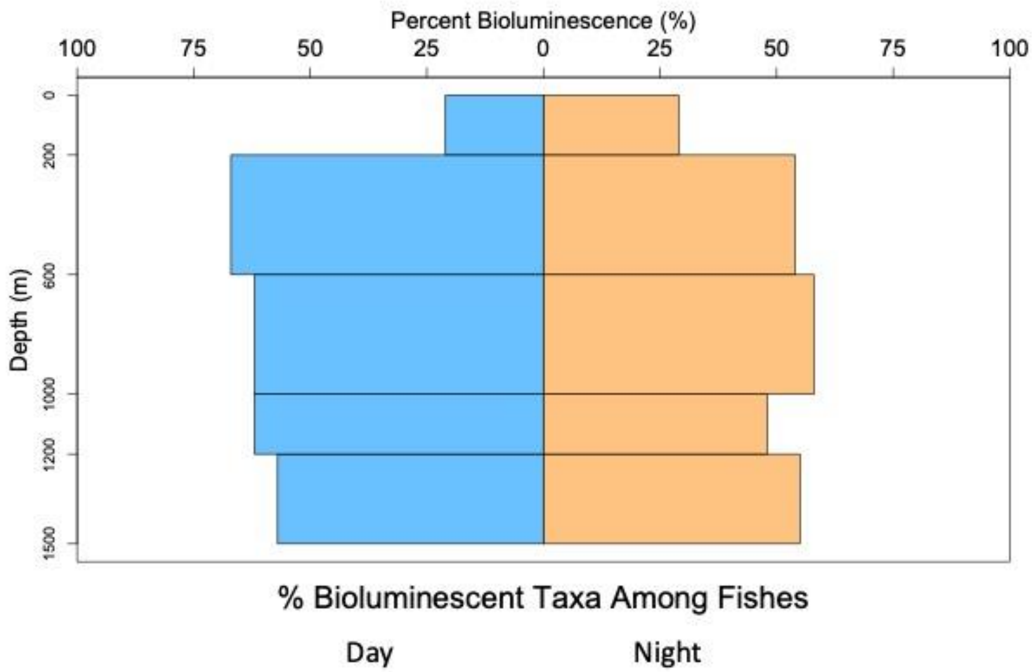

Figure 5. Vertical partitioning of fish taxon bioluminescence in the Gulf of Mexico. Percentages reflect the portion of bioluminescent taxa among all taxa collected in each depth bin during daytime (left) and nighttime (right).

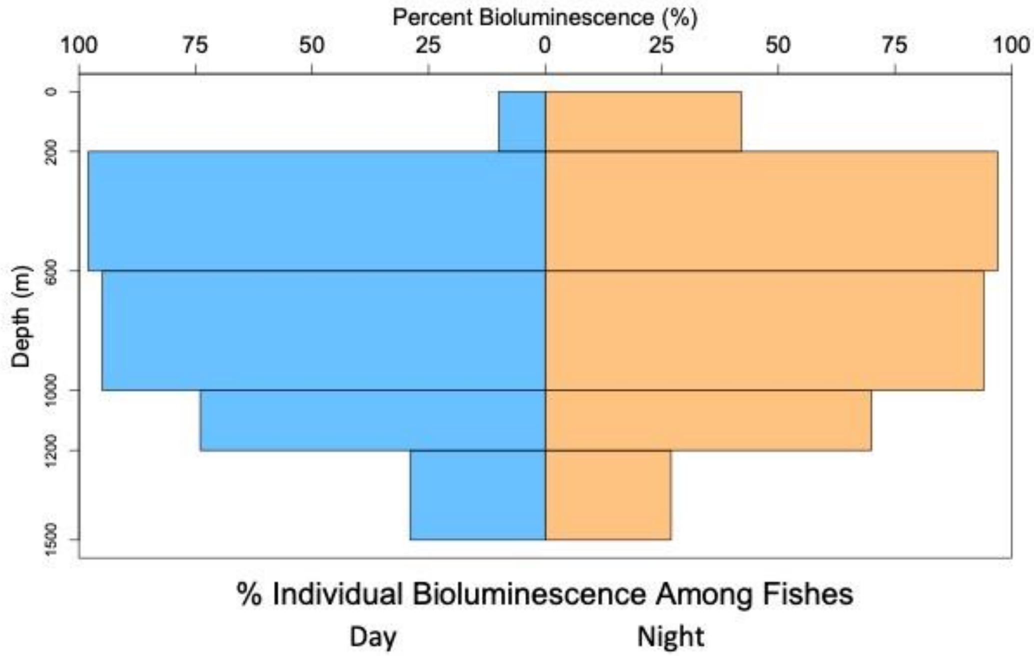

Figure 6. Vertical partitioning of individual fish bioluminescence in the Gulf of Mexico. Percentages reflect the portion of bioluminescent individuals among all individuals collected in each depth bin during daytime (left) and nighttime (right)

Crustaceans. A total of 105 crustacean taxa were caught throughout cruises DP01-DP07 at all depth bins and time of day, with 78 possessing bioluminescent capabilities (~74%). A total of 28,779 individuals were collected and of these, 20,678 individuals are bioluminescent (~72%). The percentages of bioluminescent taxa and total individuals with respect to depth and diel cycle are shown in **Figures 7 and 8**. The largest contribution of crustacean bioluminescence was made by individuals of the genera *Allosergestes, Challengerosergia, Deosergestes, Gardinerosergi, Neosergestes Parasergestes, Thysanopoda, Nematobrachion, Gennadas, Acanthephyra, Nematoscelis,* and *Systellaspis.* Collectively, these luminous taxa accounted for nearly 57% of crustacean bioluminescence in the GoM and were found at all five depth intervals and during both day and nighttime collections.

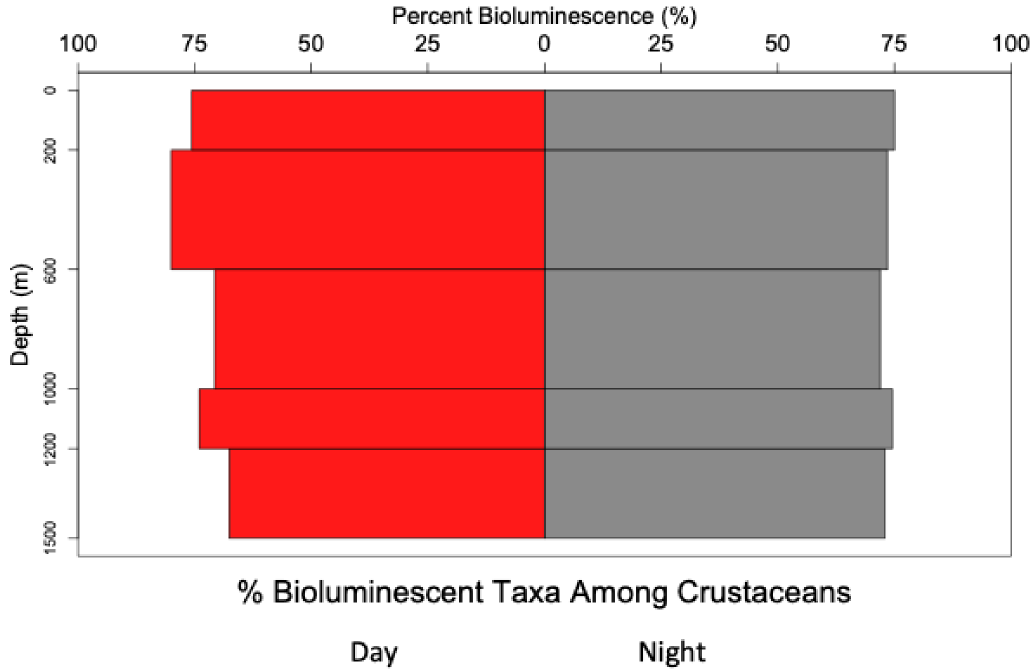

Figure 7. Vertical partitioning of crustacean taxon bioluminescence in the Gulf of Mexico. Percentages reflect the portion of bioluminescent taxa among all taxa collected in each depth bin during daytime (left) and nighttime (right).

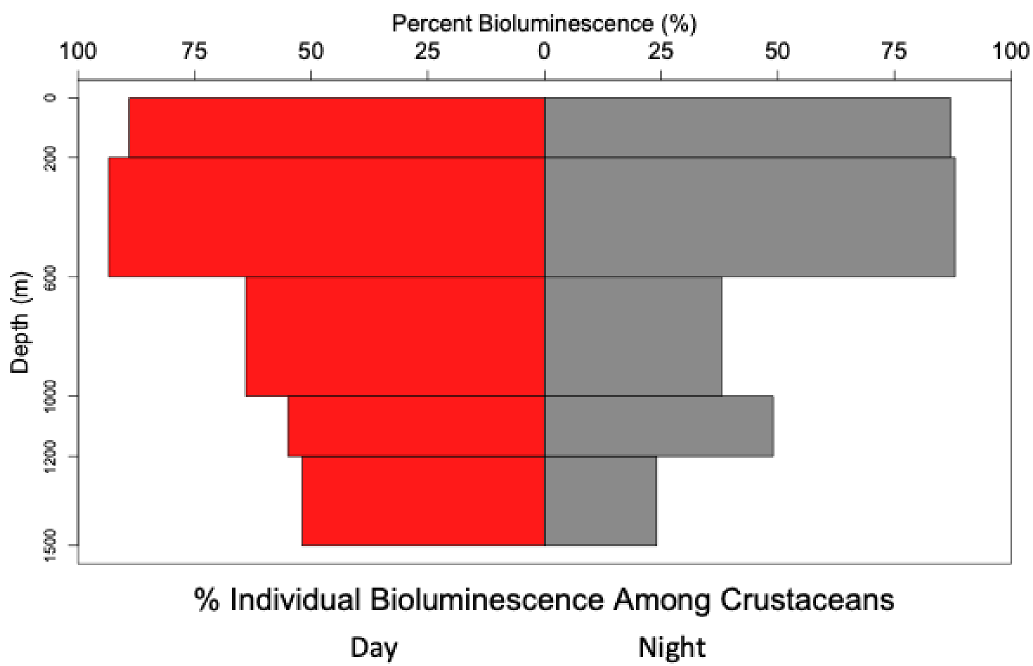

Figure 8. Vertical partitioning of individual crustacean bioluminescence in the Gulf of Mexico. Percentages reflect the portion of bioluminescent individuals among all individuals collected in each depth bin during daytime (left) and nighttime (right)

Cephalopods. The total number of cephalopod taxa caught throughout cruises DP01-DP07 at all depth bins and time of day totaled 47 taxa, with 38 possessing bioluminescent capabilities (~81%). A total of 409 individuals were collected, of which 384 individuals were identified as bioluminescent (~94%). The percentages of bioluminescent taxa and total individuals with respect to depth and diel cycle are shown in **Figure 9 and 10**.

Members of the genus *Pterygioteuthis* and species such as *Japetella diaphana*, *Bolitaena pygmaea*, *Vampyroteuthis infernalis*, *Cranchia scabra*, and *Pyroteuthis margaritifera*, represented almost 59% of all luminous individuals among the cephalopods. The majority of luminous cephalopod individuals were primarily squids, but there was an abundance of two octopods as well (*Japetella diaphana* and *Bolitaena pygmaea*).

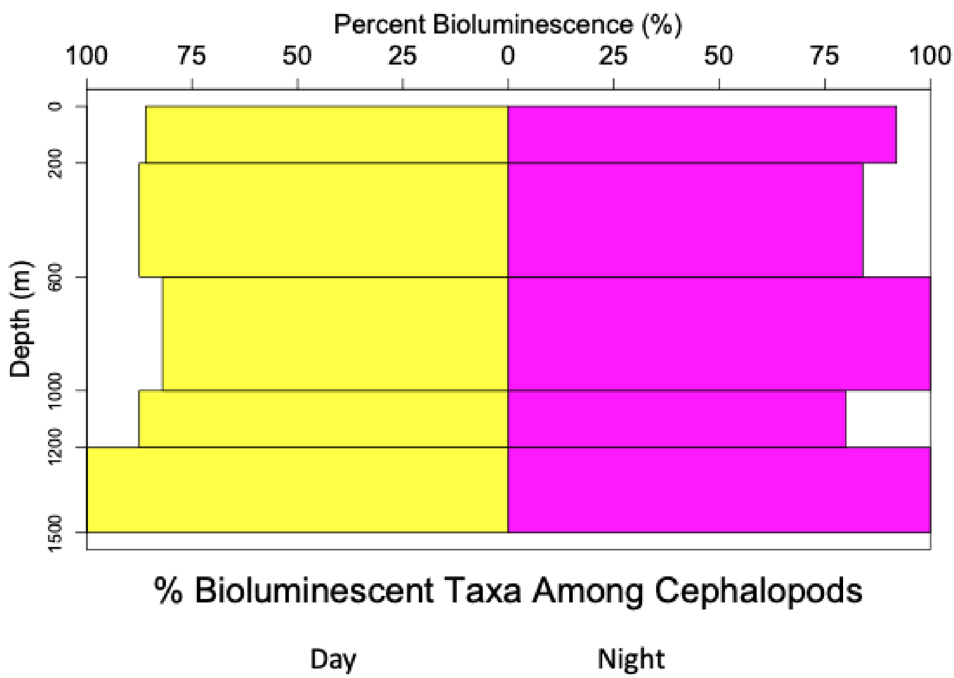

Figure 9. Vertical partitioning of cephalopod taxon bioluminescence in the Gulf of Mexico. Percentages reflect the portion of bioluminescent taxa among all taxa collected in each depth bin during daytime (left) and nighttime (right).

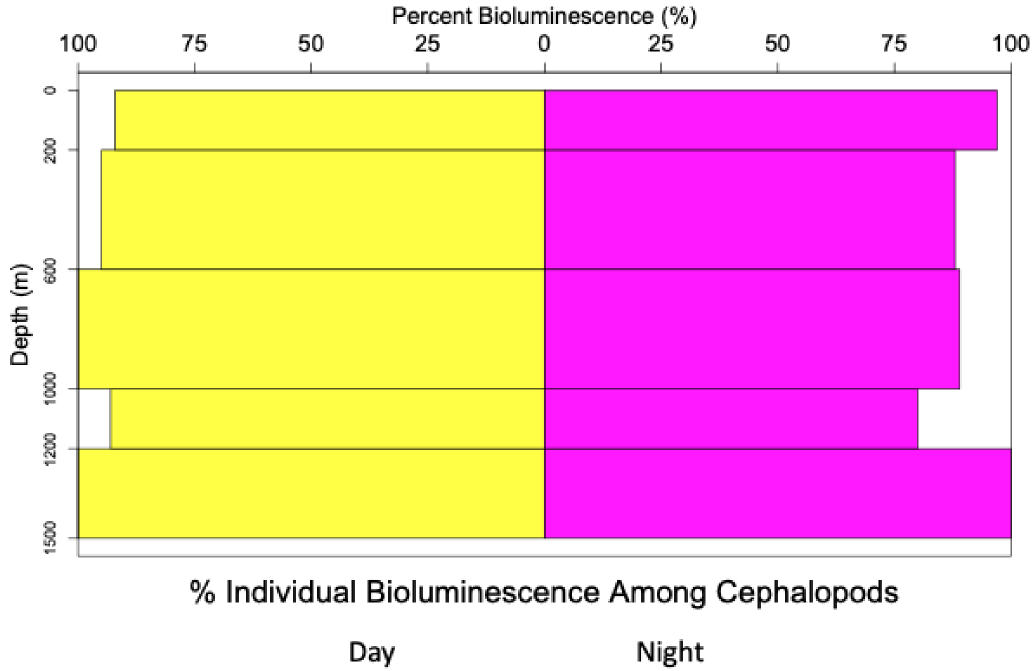

Figure 10. Vertical partitioning of individual cephalopod bioluminescence in the Gulf of Mexico. Percentages reflect the portion of bioluminescent individuals among all individuals collected in each depth bin during daytime (left) and nighttime (right).

Discussion

Prior to the *Deepwater Horizon* Oil Spill (DWHOS) in 2010, the deep-pelagic fauna and their distributions in the GoM were poorly known (Sutton et al., 2022). Since DWHOS, research efforts have identified the GoM as one of the world's most diverse mesopelagic ecosystems (Sutton et al., 2017a; 2020; 2022). Deeper zones of the GoM, including the bathypelagic, support a diverse variety of fauna adapted to life in total darkness, relying heavily on light production from bioluminescence (Burghart et al., 2007; Sutton et al., 2022). Despite the dramatic increases in our understanding of the deep-pelagic GoM, little is known about the faunal and spatial prevalence of bioluminescence in this habitat. While previous research has surveyed and quantified deep-pelagic life (e.g., Cook et al., 2020, Frank et al., 2020; Judkins & Vecchione, 2020; Sutton et al., 2020),no literature exists devoted to the relative abundance of bioluminescent fauna.

Bioluminescence in the GoM

Organismal bioluminescence spanned the entire vertical range of this study (0 - 1500 m) and included about 75.5% of all micronektonic individuals collected with a midwater trawl, reflecting the ubiquity of bioluminescence in the oceanic GoM. This ubiquity has been shown in other systems using different censusing techniques. For example, an ROV-based study utilizing 350,000 observations in Monterey Canyon (0-3900 m depth) found that 76% of all individuals were capable of generating light (Martini & Haddock, 2017). That study differed in having more taxonomic categories (13) despite being a much lower-diversity ecosystem overall (Sutton et al., 2017a), and in the finding that the largest percentage of bioluminescence was contributed by the gelatinous fauna. The quantitative exclusion of gelatinous zooplankton in this study due to gear type bias likely underestimates the true ubiquity of bioluminescence in the oceanic GoM. The following discussion will detail the ecology of bioluminescence among the major taxonomic groups and their distributions within the GoM. Results of this study may provide a foundation for future research using bioluminescence partitioning in the GoM, or other bodies of water, in trait-based approaches to assess ecological processes.

Specific examples of studies utilizing bioluminescence in other bodies of water include that of Vacquié-Garcia et al., (2012), revealing female southern elephant seals to have low- light-adapted vision to detect bioluminescent organisms such as myctophids, their main prey. These authors related depth and bioluminescence to foraging intensity. The results suggested that bioluminescence likely provides these predators with valuable indications of prey occurrence and are thus a major driver of predator-prey interactions in deep, dark marine environments (Vacquié-Garcia et al., 2012).

Bioluminescence abundance among major taxa

Fishes. A total of 78% of all individual fish specimens collected were from bioluminescent taxa. This ratio of bioluminescent fishes in the GoM was higher than that of fishes reported in Monterey Canyon (~54%; Martini & Haddock, 2017). The difference between the GoM and Monterey Canyon values may be a function of the latter study taking place only during the daytime, but more likely, the difference probably reflects differences in methods – ROV-based surveys allow for detailed observations of gelatinous forms *in situ*, but are prone to missing more mobile, darkly covered fauna such as fishes (Sutton, pers. comm.).

The most abundant fishes captured in the GoM were *Cyclothone,* a genus of bristlemouths within family Gonostomatidae. *Cyclothone* consists of 13 extant species worldwide, 12 of which were found to be bioluminescent. *Cyclothone obscura*, the only non-luminous species and the numerically dominant bathypelagic fish of the GoM, bears minute photophores, though they are not known to be functional (Davis et al., 2020). The loss of photophore function among *C. obscura* may be attributed to their abundance in depths below 1000 m and the non-migratory behaviors of *Cyclothone* species (Sarmiento-Lezcano et al., 2023). Many species bear ventral photophores for migratory "invisibility," however, since *C. obscura* does not migrate and remains in bathypelagic depths, the energy needed to emit light may be limiting for the species. In the GoM *Cyclothone* alone was responsible for approximately 72% of all bioluminescent fishes, with individuals caught in all depth bins and times of day, though they were most abundantly caught between 200 to 1000 m depths. *Cyclothone* are estimated to be the most abundant vertebrates on earth, accounting for more than 50% of total vertebrate abundance in mid-water habitats (~100 to 1,000 m) (Davis et al., 2014; Sutton et al., 2010).

Myctophids (lanternfish) are endemic to pelagic deep-sea environments and are consistently among the most abundant and species-rich taxa in these systems (Davis et al., 2014; Eschmeyer, 2013; Sutton et al., 2010;). While individuals of Gonostomatidae, particularly those belonging to *Cyclothone*, contributed the most individuals, myctophids and dragonfishes of the family Stomiidae contributed the most species (Sutton et al., 2010). The impressive variability of myctophid and stomiid light-organ systems, including photophore patterns, sexually dimorphic luminescent organs on the tail or head, and bioluminescent appendages, may provide evidence for bioluminescence being a direct contributor to the reproductive isolation of such speciose diversification (Davis et al., 2014; Paxton 1972).

Crustaceans. Crustaceans contributed the second highest number of individuals of all taxonomic groups collected throughout the DEEPEND cruises**.** Bioluminescent individuals comprised approximately 72% of all individual crustaceans. Pelagic crustacean specimens belonging to families Euphausiidae, Sergestidae, Oplophoridae, and the genus *Gennadas* contributed approximately 89% of all bioluminescence individuals among crustaceans in the Gulf of Mexico. Euphausiids were the most abundant bioluminescent crustaceans collected, accounting for approximately 60% of all crustacean bioluminescence alone, and were captured at all depth intervals and times of day. Euphausiids are notably both speciose and bioluminescent. Euphausiids, like many mesopelagic fishes, possess light organs along the ventral surface of the body to function as a counterillumination technique. Ecologically, euphausiids are a major mid-trophic pathway for energetic transfer between primary producers and predators (Rockwood et al., 2020), making their abundance and vertical migration patterns an important ecological component of the pelagic GoM.

Decapod shrimp such as the family Sergestidae made up approximately 18.5% of all bioluminescent individuals, while individuals of the superfamily Oplophoroidea (consisting of Oplophoridae and Acanthephyridae) made up roughly 10% of luminous individuals. Decapod shrimps are notable for their ability to make use of their intrinsically bioluminescent systems in a variety of ways. Sergestids use photophores that tilt to maintain their downward orientation regardless of which way the animal is swimming (Latz, 1995). Oplophoroidea, which includes the abundantly caught genera *Systellaspis, Acanthephyra,* and *Oplophorus*, can expel large amounts of luminous fluid as part of a distress response (Inouye et al., 2000). Additionally, the bioluminescent systems of the oplorphorid genera *Systellaspis, Oplophorus* and *Janicella* are considered the most highly resolved, possessing autogenic photophores along the ventral regions of the body for counterillumination during diel vertical migration. The ability to fine-tune their counterillumination to match downwelling light via intensity, angle, and spectral distribution is likely an evolutionary driver of deep-sea decapod shrimps (Bracken-Grissom et al., 2020). Adults' visual systems are tuned to detect bioluminescence with respect to both temporal and spectral properties (Frank, 1999; Frank & Widder, 1999).

Cephalopods. Few studies have specifically focused on the GoM's cephalopod abundance in the meso- and bathypelagic zones (e.g., Judkins & Vecchione, 2020; Passarella, 1990; Voss, 1956) and in particular, the bioluminescent capabilities among this class of invertebrates. Among the DEEPEND cruises, nearly 81% of all captured cephalopod taxa were found to be capable of light emission. Individual abundance of these bioluminescent taxa accounted for ~94% of all individual cephalopods captured throughout all depth bins and time of day. Cephalopods were the least abundant taxonomic group captured throughout the DEEPEND cruises, with only 409 total individuals collected. Cephalopods have been reported to exhibit avoidance behavior as a reaction to bright artificial light, motor noise, electrical fields and induced water motion in the water column (Martini & Haddock, 2017). Additionally, previous midwater trawls found that different gear types had an effect on the catchability of cephalopods. Large midwater trawls and MOC-10 nets have been found equally effective at estimating overall species richness of midwater cephalopods (Judkins et al., 2017). However, the large midwater trawl (LMT) gear type collected close to the expected diversity for the region, whereas the MOC-10 (the gear type used by DEEPEND) had not reached asymptote (Judkins et al., 2017). To optimize cephalopod capture, incorporating multiple net systems has been found to improve documentation of cephalopod biodiversity within a region (Judkins et al., 2017; Vecchione et al., 2010). In future studies, this sampling method may provide a more accurate abundance of cephalopods and thus, bioluminescent potential among this phyla group.

Pterygioteuthis and *Cranchia* individuals accounted for approximately 25% of bioluminescent cephalopods captured at all depths and time of day. *Pterygioteuthis* (firefly squid) and *Cranchia* (glass squid), are abundant pelagic squid species with global distribution. *Pterygiotetuthis* are exceptionally small and characterized by arms with hooks, along with an abundance of photophores on the body cavity, around the eyes, and along the arms (Lindgren, 2010). Members of the family Cranchiidae are known for ontogenic migrations, with a change in their distribution from epipelagic depths during their juvenile and subadult life, to deep-pelagic realms as mature adults (Evans, 2018). Members of the genus *Cranchia* possess a body composition and photophore arrangement relatively similar to *Pterygioteuthis*, although they are not known to vertically migrate.

Vampyroteuthis infernalis (vampire squid), also have global distributions and accounted for approximately 11% of all luminous individuals. While the common name suggests them to be "squid", these unique molluscs fit into their own order due to having anatomy similar to both an octopus and a squid. These extremophile-type molluscs occupy meso- to bathypelagic depths and employ a variety of bioluminescent capabilities. Using a plethora of photophores located on the posterior end of each fin, the mantle, the funnel, the head, and aboral surface, they produce luminescent clouds of glowing particles (Grzimek, 1972; Wood & Ellis, 1999). The arm tips and the base of the fins are also luminescent, glowing, or flashing, which is usually followed by an escape response (Portner et al*.*, 1994; Seibel et al., 1997). Both modes of light production are apparently linked to anti-predation strategies (Robison et al., 2003).

Deep-sea octopods *Bolitaena* and *Japetella* are prominent deep-water genera and accounted for roughly 22% of all luminous cephalopod individuals throughout the DEEPEND cruises. Not all individual *Bolitaena* were able to be identified to the species level, however. The only species captured during the trawls was identified as *Bolitaena pygmaea*. *Bolitaena pygmaea* and *Japetella diaphana* are extremely similar, characterized by a laterally compressed small-body, wide-set eye stalks, and females possessing unique ring-shaped light organs around the mouth notable for changing to a bright yellow glow when sexually mature. This organ is found only in females approaching sexual maturity, suggesting that it acts to attract a mate. Both *Japetella diaphana* and *Bolitaena pygmaea* mate at the lower end of their vertical range (Young, 1978). At these great depths (~1000 m and 1400 m) reduced predation pressure may make sexual signaling less risky. The color and shape of the yellow-colored oral organ of females is not as noticeable as characteristic blues or greens of other luminous organisms, thus making it poorly visible to predators. Other cephalopods do not possess these unique, orally directed photophores.

When pelagic cephalopods die after reproduction, some sink to the seafloor and are consumed by deep-sea bottom scavengers (Hoving et al., 2017). Other deep-water species float up to become important food for seabirds, reversing the typical vertical flow of energy (Croxall & Prince, 1994; Rodhouse et al., 1987; Xavier et al., 2013). The critical role these pelagic cephalopods play as vectors of energy transfer from zooplankton and micronekton to pelagic top predators is suggestive of their extreme ecological importance in deep-pelagic food webs (de la Chesnais et al., 2019; Passarella & Hopkins, 1991)

Vertical partitioning of bioluminescence

Bioluminescent distribution patterns within the GoM were found to be variable over both depth and time of day in bioluminescent taxa and individuals. Fishes were observed to have a greater proportion of bioluminescent taxa at mesopelagic depths. The number of taxa among crustaceans was lowest in the epipelagic and greatest at mesopelagic depths; however, the ratio of luminous to non-luminous taxa remained consistent with depth. Cephalopod taxa had a uniform distribution of bioluminescent taxa throughout the water column during the day and at night. The proportion of bioluminescent individuals among fishes was greatest at mesopelagic depths while individual bioluminescent crustaceans were found in the highest percentages in the upper mesopelagic zone. Bioluminescent cephalopod individuals had a uniform distribution throughout the water column.

Approximately 45.5% of all taxa captured in the GoM were found to possess some sort of bioluminescent capability, with most found in more than one depth bin or time of capture. Bioluminescent taxa and individuals were found to be most abundant in 200 m - 1000 m depth ranges, with an approximate 87% of all individuals expressing some capability of bioluminescence.

The vertical distribution of bioluminescence during the day differed substantially from nighttime patterns, as expected. During the day, the sea surface - 200 m depth interval contained 14% of **all bioluminescent taxa**, increasing to 26% in the 200 - 600 m range. This percentage increased again in the 600 - 1000 m depth stratum, before declining to 17.7% in the 1000-1200 m depth interval and 13% in the 12000 - 1500 m depth interval.

The vertical distribution of **all bioluminescent individuals** during the day followed a similar pattern. The epipelagic zone contained ~2% of bioluminescent individuals, with a sharp increase to 41% in the 200 - 600 m depth range and then a moderate increase to 43.5% in the 600 – 1000 m stratum. The proportion of bioluminescent individuals decreased in the 1000 - 1200 m depth range, comprising only 9.4% of all bioluminescent individuals and only 4.3% of bioluminescent individuals from 1200 – 1500 m in depth.

The vertical distribution of bioluminescence greatly shifted upwards during nighttime. The epipelagic zone contained 29% of bioluminescent **taxa**, decreasing slightly in the 200 – 600 m depth interval to 24.5% and 21.5% in the 600 – 1000 m stratum. Only ~12.5% of all bioluminescent taxa were found at night from 1000-1500 m in depth. Approximately 34.6% of bioluminescent **individuals** were found in the epipelagic zone at night. This value decreased slightly to ~30% between 200 – 600 m and again to 26.1% between 600 – 1000 m. The depth interval 1000 – 1200 m contained 6.6% of all bioluminescent individuals while the 1200 – 1500 m range contained only 2.9% of all bioluminous individuals.

Fishes. Investigations of the macroevolutionary processes of bioluminescent fish lineages, both inshore and deep-sea, suggest the use of bioluminescence for communication, feeding, and reproduction (Davis et al., 2016). The majority of this species richness occurs in deep-sea fishes with intrinsic bioluminescent systems, as well as in both shallow and deep-sea lineages with luminescent communication systems (Davis et al., 2016). Based on previous studies, 90% of fishes found below 500 meters in the North Atlantic were thought to be bioluminescent (Herring, 2002; Herring & Morin, 1978; Martini & Haddock, 2017). This study provides evidence that a range of 95-98% of fishes between 200 and 1000 m possess some form of bioluminescent capability.

In the epipelagic zone during daytime, approximately 21% of fish taxa collected were bioluminescent. At night, this value increased ~29%. In this same depth interval, ~10% of daytime-captured individuals were bioluminescent, while at night, a sharp increase in bioluminescent individuals (~42%) was observed. The sharp nighttime increase in both bioluminescent taxa and individuals in this depth interval is explained by the influx of diel vertical migrators (Sutton et al., 2010). Fishes captured at these depths a night were mainly myctophids and bristlemouths, the latter also seen at mesopelagic depths during the day.

The upper and lower regions of the mesopelagic zone contained the largest percentages of bioluminescent fishes in this study. In the upper mesopelagic (200 to 600 m) ~67% of fish taxa in this depth interval were bioluminescent during daytime, while nighttime values decreased to approximately 54%. Day and nighttime percentages of individuals in this depth zone were very similar and very high (97-98%). The upper mesopelagic light is sourced from downwelling sunlight, making the characteristic silver body coloration of fishes in this realm an advantageous form of camouflage, acting as mirrors (Paitio et al., 2016). As daytime light subsides, these fishes often possess photophores to provide further camouflage via counterillumination while migrating towards the surface. Major fishes found in the depth interval 200 – 600 m included *Cyclothone*, sternoptychids, and myctophids. A large portion of sternoptychids were found in this depth interval, providing evidence that the silver body coloration is both abundant and advantageous for this realm.

Samples from 600 to 1000 m in depth represented the lower region of the mesopelagic zone. During the day, approximately 62% of fish taxa inhabiting this depth interval were found to possess bioluminescent capabilities, with an observable decrease to ~54% at night. Individual bioluminescence abundance in this depth interval ranged from ~95% during the day to ~94% at night. The decrease in bioluminescence abundance at night in this depth range may also be explained by diel vertical migration patterns seen in mesopelagic fishes. The majority of fishes inhabiting the lower mesopelagic and upper bathypelagic commonly possess very dark bodies to prevent the reflection of bioluminescence in the deeper regions of the sea (Paitio et al., 2016). Common fishes found at these depths included species of *Cyclothone*, Phosichthyidae, Stomiidae, and Myctophidae, all possessing the characteristic dark-colored bodies to conceal their reflection, while also allowing for counterillumination when vertically migrating to the surface at night. An additional bioluminescent feature found amongst the dragonfishes in this region is a luminous chin barbel, serving as a sort of "fishing lure" to attract prey (Sutton, 2003). Additionally, sternopychids were seen in abundance in this interval, most commonly at night.

The deepest intervals represented bathypelagic depths (1000 m to 1500 m). Approximately 62% of daytime taxa from 1000– 1200 m were bioluminescent, with a sharp decrease to 48% at night. Individual bioluminescence abundance was approximately 74% during the day, dropping off to ~70% at night. Although the bathypelagic fauna is not known for diel vertical migration, previous studies present evidence of deep-water, synchronous migrations occurring in the afternoon, with populations departing from bathypelagic depths in a coherent pattern prior to sunset and deeper residing individuals starting the ascent even earlier in the afternoon (Kaartvedt et al., 2020). These findings apply to the current study regarding a decreasing percentage of bioluminescent specimens found in the upper bathypelagic realm due to potential vertical migration. Their study also mentioned that these vertical migrators often did not necessarily ascend to the surface, often only to mesopelagic depths (Kaartvedt et al., 2020). This provides a further explanation for the high percentages of bioluminescence abundance still seen in mesopelagic depth intervals, despite many bioluminescent taxa that inhabit those ranges vertically migrating above such depths at night.

Bioluminescent fish taxa caught in depth interval 1200 – 1500 n during the day represented approximately 57% of all fish taxa caught in this depth stratum, decreasing slightly to 55% at night. Bioluminescent individual abundance at this depth encompassed ~29% of all individuals during the day and ~27% at night. Vereshchaka et al., (2019) reported that vertical migrations are nearly absent from the lower bathypelagic Atlantic zone due to rapid declines in concentration of planktonic food (Chatzievangelou et al., 2021). This observation is supported by this study, with very small decreases in both bioluminescent taxa and individuals between day and nighttime sample collections in the depth interval. Major fish taxa dominating these two intervals included *Cyclothone* and myctophids.

Crustaceans: Bioluminescent crustacean taxa were uniformly abundant throughout depth intervals and during solar noon and solar midnight collections. While the number of taxa in depth intervals varied, the ratio of bioluminous and nonluminous species remained consistent. However, there was a larger percentage of individual abundance in the upper mesopelagic depth interval with variations in abundance mainly observed in depth ranges 200 – 600 m before individual values began to decline with depth. Previous studies revealed bioluminescent Crustacea distributions are primarily above 1000 m depth (krill, mesopelagic shrimp), while non-bioluminescent Crustacea (isopods, decapods) live below 2,500 m with a gradient of some bioluminescence in-between. In addition, previous research found that approximately 80% of crustaceans found between the surface to 500 m depth are bioluminescent, while only 41% are bioluminescent between 500 -

1000 m depth (Herring, 2002; Martini & Haddock, 2017). This study agrees with these high individual bioluminescent percentages. Furthermore, the ‘gradient’ of bioluminescent Crustacea between the abundance from 0 - 500 m and non-luminous species below 2500 m (Herring, 2002; Martini & Haddock, 2017) may be represented in the GoM in depth intervals 200 – 600 m, where approximately 80% of all individuals were luminous while only 34% of all individuals in the 1200 – 1500 m range were bioluminescent.

In the epipelagic zone, approximately 75% of all taxa were bioluminescent across day and nighttime collections. Bioluminescent epipelagic individuals represented 89% of all individuals in this depth interval while a similar 87% were so night. Abundantly caught bioluminescent specimens in this interval included euphausiids, particularly at night, and members of the Sergestidae. Diel vertical migrations from deeper waters to the surface at night likely play a major role in this increase of bioluminescence in the epipelagic zone. For example, Greene et al., (1992) reported that during the day, euphausiids segregate partially by size, with a group of smaller individuals remaining relatively shallow while the majority of the population occurred deeper than 200 m. Both groups of euphausiids merged during their evening migration just below the surface (Greene et al., 1992).

At depths between 200 and 600 m there was a relatively uniform distribution of bioluminescence among taxa. During the day, 80% of taxa caught were bioluminescent, decreasing to ~73.5% at night. This slight decrease could be attributed to the smaller-sized bioluminescent euphausiids migrating from their semi-shallow depths to the surface along with their larger-size populations at night. During the day, approximately 93.4% of individuals within this depth range were bioluminescent. With respect to individuals, the higher daytime value decreased to approximately 88% at night, with individuals of euphausiids, sergestids and *Gennadas* comprising the majority of bioluminescent specimens in the depth interval. The high percentages of bioluminescence in this depth interval coincide with previous studies that found approximately 80% of crustaceans from the surface to 500 m are capable of bioluminescence (Herring, 2002; Martini & Haddock, 2017).

The 600 to 1000 m depth interval contained nearly identical percentages of bioluminescent taxa, ~71%, but the percentage of individuals were lower during nighttime (38%) than daytime (~64%). *Gennadas* individual abundance dominated this depth interval during the day and dwindled at night, mostly found in shallower depth intervals at night. In this region of the water column, *Gennadas* undergo diel migration with most of the population aggregating at 500-1500 m throughout the day and migrating to 200–500 m at night (Fine, 2016; Frank et al., 2020; Vereshchaka et al., 2017).

The relative abundance among taxa in depth interval 1000 to 1200 m was similar to depth interval 200 to 600 m. In depth ranges of 200 to 600 m, roughly 74% of all taxa across day and nighttime catches were bioluminescent, while individual bioluminescence was lower; approximately 55% during the day and dropped to 49% at night. Again, the values of decreasing individuals at night may be contributed to the vertical migration patterns of many deep-pelagic crustaceans and decapods. Decapod shrimp, particularly genera of *Acanthephyra* and *Gardinerosergia,* broadly spanned this interval. Depth interval 1200 to 1500 m exhibited a similar degree of bioluminescence among taxa, ~68% during the day and 73% at night. However, the individual bioluminescence was less prominent; approximately 52% during the day and 24% at night. These findings align with previous studies reporting that bioluminescent pelagic crustacea are primarily found above 1000 m, with about 41% being bioluminescent between 500 and 1000 m (Herring, 2002; Martini & Haddock 2017).

Cephalopods. Previous studies off the coast of California reported cephalopod bioluminescence to be relatively uniform over depth, with approximately 53.3% of cephalopod taxa found to be bioluminescent (Martini & Haddock, 2017). The current study revealed a higher proportion, with 94% of all **individuals** being bioluminescent, distributed evenly throughout the water column. Pelagic squid and octopods are most notable for bioluminescent capabilities. However, it is worth noting that due to fast swimming speeds and avoidance behavior (York, 2016), cephalopods are more difficult to capture in abundance and thus, the values in this dataset may be much lower than the actual faunal composition, bioluminescent capabilities, and distribution of cephalopods found within the pelagic GoM.

The surface to 200 m depth interval contained ~ 86% bioluminescent capable taxa during the day with an increase to ~92% at night. Approximately 92% of all daytime-captured individuals were bioluminescent, with an increase at nighttime (97%). Abundant bioluminescent individuals captured in this depth range included *Pterygioteuthis, Pyroteuthis margaritifera* and *Cranchia scabra. Pterygioteuthis* individual abundance occurred mostly in nighttime catches, agreeing with previous studies reporting that the genus primarily resides in the upper mesopelagic during the day, then migrates to the epipelagic nightly (Judkins & Vecchione, 2020).

In the 200 – 600 m depth interval, *Pterygioteuthis* was still found in abundance as well as *Japetella diaphana*. During the day, 87.5% of taxa were found to be bioluminescent with a slight decrease (84%) at night. Individual bioluminescent abundance was higher during the day in this stratum (~95%) than at night (88%). The 600 – 1000 m depth range contained a larger percentage of taxon bioluminescence, approximately 82% during the day and rising to 100% at night. Conversely, 100% of individuals captured during the day were capable of light emission with a decrease to 88% of individuals at night. Abundant bioluminescent taxa within this depth range included *Japetella diaphana*, *Bolitaena pygmaea* and *Vampyroteuthis infernalis.* Judkins & Vecchione, (2020), investigated the vertical distribution of pelagic cephalopods within the Gulf of Mexico and found that octopod species *Bolitaena pygmaea*'s distribution ranged from 0 to 1500 m in depth while *Japetella diaphana* individuals most resided in depths greater than 600 m. Additionally, neither of the octopod species seemed to follow any vertical migration behavior. However, ontogenetic shifts of large, mature *B. pygmaea* and *J. diaphana* individuals were found in deeper regions of the water column. This study supports the increasing abundance of octopods with depth, contrasting the general diel vertical migration patterns seen in many fishes and crustaceans. Thomas, (2018), found that maximum depths in bioluminescent cephalopods were significantly higher than in non-bioluminescent cephalopods. Maximum depth optima for bioluminescent cephalopods were 880 m versus 290 m for non-bioluminescent cephalopods. However, the maximum depth optimum for bioluminescent species is near the lower limit of the mesopelagic zone, where animals can still detect dim, downwelling daylight. This could be due to the optimization of bioluminescent functions in the lower mesopelagic ocean for both camouflage and signaling (Thomas, 2018).

The 1000 - 1200 m depth stratum contained similar luminous species as the 600 – 1000 m depth interval (*Vampyroteuthis infernalis, Japetella diaphana* and *Bolitaena pygmaea*). However, the overall representation of bioluminescence in this depth range was reduced compared to other depths. Roughly 87.5% of daytime taxa were found to be capable of light emission, with a slight decrease to 80% at night. This could be contributed to the ontogenetic shifts of larger octopods. Nearly 93% of all individuals in depth interval 1000 – 1200 m down were found to be luminous, with a decline to 80% at night. It is worth noting that the abundance of taxa caught throughout cruises at this depth interval was relatively low and may limit representing the true abundance of bioluminescence in this depth interval. From 1200 – 1500 m in depth, there was also a very limited capture abundance, however 100% of both taxa and individuals caught in this depth interval during the day exhibited bioluminescent capabilities. Cephalopods provide a unique opportunity for investigating how bioluminescence may affect the evolution of other traits. They are highly visual animals, important members of marine food webs, and exhibit rich behavioral repertoires of visual signaling and camouflage (Hanlon & Messenger, 1998). Kubodera et al., (2007), presented the first *in situ* observation of the deep-pelagic squid species *Tangia danae* hunting, highlighting the use of bioluminescence during hunting. The light emission was extremely short, possibly serving as a blinding flash for the prey, as well as a source of illumination and measurement of target distance in a dark environment. More interestingly, several short luminous glows separated by intervals when wandering around the bait without attacking may be a behavioral attempt to communicate with conspecifics through bioluminescence (Kubodera et al., 2007). This provides evidence that cephalopods, especially pelagic squid, may heavily rely on bioluminescence for feeding and reproductive ecology.

Conclusions

Given the slow-progressing nature of deep-sea studies, the true abundance of bioluminescence among midwater taxa and species accumulation curves obtained from previous studies have yet to reach an asymptotic plateau (Chatzievangelou et al., 2021; Costello et al., 2012; Webb et al., 2010). This is the first quantitative examination of bioluminescence in the pelagic GoM, specifically the prevalence, faunal composition, and distribution of bioluminescence among major taxonomic groups at intermediate trophic levels. Quantifying the abundance of bioluminescent organisms in the GoM revealed that approximately 75.5% of all captured individuals were bioluminescent. With 87% of all individuals capable of bioluminescence, the expression of bioluminescence was found to be most prominent vertically between 200-1000 m, representing the upper and lower mesopelagic zones.

The mesopelagic had the highest percentage of bioluminescent fishes; daytime bioluminescent fishes comprised 67% of fish taxa in the upper mesopelagic (200 to 600 m), while at night, the value dropped to around 54%. The percentages of individuals in this depth zone during the day and night were very similar and very high (97-98%). Fishes, particularly the Order Stomiiformes (genus *Cyclothone*), were the most abundant bioluminescent taxon (72% of all bioluminescent fishes). A vertical 'gradient' of bioluminescent crustaceans was observed, with increasing percentages of total bioluminescent individuals between 200 and 600 m depth and decreasing below this depth. This study revealed that approximately 94% of all cephalopod individuals collected were bioluminescent and distributed evenly throughout the water column. These results are indicative of diel vertical migrations in the pelagic GoM.

This study highlights the major ecological role bioluminescent organisms play in a hyper-diverse, deep-pelagic oceanic ecosystem such as the GoM. Bioluminescent organisms and their predators, for example, are thought to play an important role in the biological carbon pump through preferential consumption of luminous particles by high-level consumers. This can affect the former's sinking rates, remineralization, and availability in deeper waters (Tanet et al., 2020), or it can lead to higher success rates of visual predation for macroorganisms (Chatzievangelou et al., 2021). Furthering bioluminescence abundance studies within deep-pelagial zones may also be a key factor in advancement of trophic food web studies. This research provides key evidence that bioluminescence, both extremely abundant and ecologically relevant in the GoM, is a quantitatively understudied, yet functionally important trait in deep-sea ecosystems.

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Appendices

Appendix Table 1: Faunal inventory of bioluminescent micronekton and gelatinous zooplankton collected in the Gulf of Mexico organized in descending taxonomic abundance order.

Systematic Level	No. BL Taxa	References
Chordata	**324**	
Vertebrata	**317**	
Actinopterygii	315	
Stomiiformes	**143**	
Stomiidae	110	
Aristostomias grimaldii		Suntov, et al., 2008
Aristostomias polydactylus		Suntov, et al., 2008
Aristostomias tittmanni		Suntov, et al., 2008
Aristostomias xenostoma		Suntov, et al., 2008
Astronesthes atlanticus		Suntov, et al., 2008
Astronesthes decoratus		Suntov, et al., 2008
Astronesthes gemmifer		Suntov, et al., 2008
Astronesthes gudrunae		Suntov, et al., 2008
Astronesthes haplophos		Suntov, et al., 2008
Astronesthes macropogon		Suntov, et al., 2008
Astronesthes micropogon		Suntov, et al., 2008
Astronesthes neopogon		Suntov, et al., 2008
Astronesthes niger		Suntov, et al., 2008
Astronesthes oligoa		Suntov, et al., 2008
Astronesthes richardsoni		Suntov, et al., 2008
Astronesthes similus		Suntov, et al., 2008
Astronesthes undes. TS1		Suntov, et al., 2008
Astronesthes zetgibbsi		Suntov, et al., 2008
Astronesthes zharovi		Suntov, et al., 2008
Bathophilus altipinnis		Suntov, et al., 2008
Bathophilus brevis		Suntov, et al., 2008
Bathophilus digitatus		Suntov, et al., 2008
Bathophilus filifer		Suntov, et al., 2008
Bathophilus longipinnis		Suntov, et al., 2008
Bathophilus nigerrimus		Suntov, et al., 2008
Bathophilus pawneei		Suntov, et al., 2008
Bathophilus proximus		Suntov, et al., 2008
Bathophilus schizochirus		Suntov, et al., 2008
Borostomias elucens		Suntov, et al., 2008
Borostomias mononema		Suntov, et al., 2008
Chauliodus danae		Suntov, et al., 2008
Chauliodus sloani		Suntov, et al., 2008
Echiostoma barbatum		Suntov, et al., 2008

Eustomias (Biradiostomias) undescribed TS1	Suntov, et al., 2008
Eustomias (Dinematochirus) undescribed TS1	Suntov, et al., 2008
Eustomias (Spilostomias) undescribed TS1	Suntov, et al., 2008
Eustomias achirus	Suntov, et al., 2008
Eustomias acinosus	Suntov, et al., 2008
Eustomias bibulbosus	Suntov, et al., 2008
Eustomias bigelowi	Suntov, et al., 2008
Eustomias bimargaritatus	Suntov, et al., 2008
Eustomias bituberatus	Suntov, et al., 2008
Eustomias brevibarbatus	Suntov, et al., 2008
Eustomias contiguus	Suntov, et al., 2008
Eustomias dendriticus	Suntov, et al., 2008
Eustomias enbarbatus	Suntov, et al., 2008
Eustomias filifer	Suntov, et al., 2008
Eustomias fissibarbis	Suntov, et al., 2008
Eustomias furcifer	Suntov, et al., 2008
Eustomias hulleyi	Suntov, et al., 2008
Eustomias hypopsilus	Suntov, et al., 2008
Eustomias kreffti	Suntov, et al., 2008
Eustomias lipochirus	Suntov, et al., 2008
Eustomias longibarba	Suntov, et al., 2008
Eustomias macronema	Suntov, et al., 2008
Eustomias macrophthalmus	Suntov, et al., 2008
Eustomias medusa	Suntov, et al., 2008
Eustomias melanostigma	Suntov, et al., 2008
Eustomias micraster	Suntov, et al., 2008
Eustomias monoclonus	Suntov, et al., 2008
Eustomias monodactylus	Suntov, et al., 2008
Eustomias patulus	Suntov, et al., 2008
Eustomias schmidti	Suntov, et al., 2008
Eustomias triramis	Suntov, et al., 2008
Eustomias undescribed TS1	Suntov, et al., 2008
Eustomias undescribed TS2	Suntov, et al., 2008
Eustomias variabilis	Suntov, et al., 2008
Eustomias xenobolus	Suntov, et al., 2008
Flagellostomias boureei	Suntov, et al., 2008
Grammatostomias circularis	Suntov, et al., 2008
Heterophotus ophistoma	Suntov, et al., 2008
Idiacanthus fasciola	Suntov, et al., 2008
Idiacanthus undescribed TS1	Suntov, et al., 2008
Leptostomias bermudensis	Suntov, et al., 2008
Leptostomias bilobatus	Suntov, et al., 2008
Leptostomias gladiator	Suntov, et al., 2008

Leptostomias haplocaulus		Suntov, et al., 2008
Leptostomias leptobolus		Suntov, et al., 2008
Leptostomias longibarba		Suntov, et al., 2008
Leptostomias undescribed TS1		Suntov, et al., 2008
Leptostomias undescribed TS2		Suntov, et al., 2008
Malacosteus niger		Suntov, et al., 2008
Melanostomias bartonbeani		Suntov, et al., 2008
Melanostomias biseriatus		Suntov, et al., 2008
Melanostomias macrophotus		Suntov, et al., 2008
Melanostomias margaritifer		Suntov, et al., 2008
Melanostomias melanopogon		Suntov, et al., 2008
Melanostomias melanops		Suntov, et al., 2008
Melanostomias tentaculatus		Suntov, et al., 2008
Melanostomias undescribed TS1		Suntov, et al., 2008
Melanostomias valdiviae		Suntov, et al., 2008
Pachystomias microdon		Suntov, et al., 2008
Photonectes (Melanocetes) undescribed TS1		Suntov, et al., 2008
Photonectes (Trachinostomias) undescribed TS1		Suntov, et al., 2008
Photonectes achirus		Suntov, et al., 2008
Photonectes braueri		Suntov, et al., 2008
Photonectes caerulescens		Suntov, et al., 2008
Photonectes dinema		Suntov, et al., 2008
Photonectes gracilis		Suntov, et al., 2008
Photonectes leucospilus		Suntov, et al., 2008
Photonectes margarita		Suntov, et al., 2008
Photonectes parvimanus		Suntov, et al., 2008
Photostomias goodyeari		Suntov, et al., 2008
Photostomias guernei		Suntov, et al., 2008
Stomias affinis		Suntov, et al., 2008
Stomias boa		Suntov, et al., 2008
Stomias brevibarbatus		Suntov, et al., 2008
Stomias longibarbatus		Suntov, et al., 2008
Thysanactis dentex		Suntov, et al., 2008
Thysanactis undescribed TS1		Suntov, et al., 2008
Gonostomatidae	15	
Bonapartia pedaliota		McEachran & Fechhelm, 1998
Cyclothone acclinidens		McEachran & Fechhelm, 1998
Cyclothone alba		McEachran & Fechhelm, 1998
Cyclothone braueri		McEachran & Fechhelm, 1998
Cyclothone microdon		McEachran & Fechhelm, 1998
Cyclothone pallida		McEachran & Fechhelm, 1998
Cyclothone parapallida		Suntov, et al., 2008
Cyclothone pseudopallida		McEachran & Fechhelm, 1998

Diplophos taenia		McEachran & Fechhelm, 1998
Gonostoma atlanticum		McEachran & Fechhelm, 1998
Manducus maderensis		McEachran & Fechhelm, 1998
Margrethia obtusirostra		McEachran & Fechhelm, 1998
Sigmops bathyphilus		Suntov, et al., 2008
Sigmops elongatus		Suntov, et al., 2008
Triplophos		McEachran & Fechhelm, 1998
Sternoptychidae	11	
Argyropelecus aculeatus		Suntov, et al., 2008
Argyropelecus affinis		Suntov, et al., 2008
Argyropelecus gigas		Suntov, et al., 2008
Argyropelecus hemigymnus		Suntov, et al., 2008
Argyropelecus sladeni		Suntov, et al., 2008
Maurolicus weitzmani		Suntov, et al., 2008
Polyipnus asteroides		Suntov, et al., 2008
Polyipnus clarus		Suntov, et al., 2008
Sternoptyx diaphana		Suntov, et al., 2008
Sternoptyx pseudobscura		Suntov, et al., 2008
Valenciennellus tripunctulatus		Suntov, et al., 2008
Phosichthyidae	7	
Ichthyococcus ovatus		Suntov, et al., 2008
Pollichthys mauli		Suntov, et al., 2008
Polymetme thaeocoryla		Suntov, et al., 2008
Vinciguerria attenuata		Suntov, et al., 2008
Vinciguerria nimbaria		Suntov, et al., 2008
Vinciguerria poweriae		Suntov, et al., 2008
Yarrella blackfordi		Suntov, et al., 2008
Myctophiformes	**64**	
Myctophidae	62	
Benthosema suborbitale		McEachran & Fechhelm, 1998
Bolinichthys distofax		McEachran & Fechhelm, 1998
Bolinichthys photothorax		McEachran & Fechhelm, 1998
Bolinichthys supralateralis		McEachran & Fechhelm, 1998
Centrobranchus nigroocellatus		McEachran & Fechhelm, 1998
Ceratoscopelus warmingii		McEachran & Fechhelm, 1998
Dasyscopelus asper		McEachran & Fechhelm, 1998
Dasyscopelus obtusirostris		McEachran & Fechhelm, 1998
Dasyscopelus selenops		McEachran & Fechhelm, 1998
Diaphus anderseni		McEachran & Fechhelm, 1998
Diaphus bertelseni		McEachran & Fechhelm, 1998
Diaphus brachycephalus		McEachran & Fechhelm, 1998
Diaphus dumerilii		McEachran & Fechhelm, 1998
Diaphus effulgens		McEachran & Fechhelm, 1998

Diaphus fragilis	McEachran & Fechhelm, 1998
Diaphus garmani	McEachran & Fechhelm, 1998
Diaphus holti	McEachran & Fechhelm, 1998
Diaphus lucidus	McEachran & Fechhelm, 1998
Diaphus minax	McEachran & Fechhelm, 1998
Diaphus mollis	McEachran & Fechhelm, 1998
Diaphus perspicillatus	McEachran & Fechhelm, 1998
Diaphus problematicus	McEachran & Fechhelm, 1998
Diaphus rafinesquii	McEachran & Fechhelm, 1998
Diaphus splendidus	McEachran & Fechhelm, 1998
Diaphus subtilis	McEachran & Fechhelm, 1998
Diaphus taaningi	McEachran & Fechhelm, 1998
Diaphus termophilus	McEachran & Fechhelm, 1998
Diaphus vanhoeffeni	McEachran & Fechhelm, 1998
Diogenichthys atlanticus	McEachran & Fechhelm, 1998
Electrona risso	McEachran & Fechhelm, 1998
Gonichthys cocco	McEachran & Fechhelm, 1998
Hygophum benoiti	McEachran & Fechhelm, 1998
Hygophum hygomii	McEachran & Fechhelm, 1998
Hygophum macrochir	McEachran & Fechhelm, 1998
Hygophum reinhardtii	McEachran & Fechhelm, 1998
Hygophum taaningi	McEachran & Fechhelm, 1998
Lampadena anomala	McEachran & Fechhelm, 1998
Lampadena luminosa	McEachran & Fechhelm, 1998
Lampadena speculigera	McEachran & Fechhelm, 1998
Lampanyctus achirus	McEachran & Fechhelm, 1998
Lampanyctus alatus	McEachran & Fechhelm, 1998
Lampanyctus ater	McEachran & Fechhelm, 1998
Lampanyctus cuprarius	McEachran & Fechhelm, 1998
Lampanyctus festivus	McEachran & Fechhelm, 1998
Lampanyctus lineatus	McEachran & Fechhelm, 1998
Lampanyctus nobilis	McEachran & Fechhelm, 1998
Lampanyctus photonotus	McEachran & Fechhelm, 1998
Lampanyctus pusillus	McEachran & Fechhelm, 1998
Lampanyctus tenuiformis	McEachran & Fechhelm, 1998
Lepidophanes guentheri	McEachran & Fechhelm, 1998
Lobianchia dofleini	McEachran & Fechhelm, 1998
Lobianchia gemellarii	McEachran & Fechhelm, 1998
Loweina interrupta	McEachran & Fechhelm, 1998
Myctophum affine	McEachran & Fechhelm, 1998
Myctophum nitidulum	McEachran & Fechhelm, 1998
Notolychnus valdiviae	McEachran & Fechhelm, 1998
Notoscopelus caudispinosus	McEachran & Fechhelm, 1998

Notoscopelus resplendens		McEachran & Fechhelm, 1998
Symbolophorus rufinus		McEachran & Fechhelm, 1998
Taaningichthys bathyphilus		McEachran & Fechhelm, 1998
Taaningichthys minimus		McEachran & Fechhelm, 1998
Taaningichthys paurolychnus		McEachran & Fechhelm, 1998
Neoscopelidae	2	
Neoscopelus macrolepidotus		McEachran & Fechhelm, 1998
Neoscopelus microchir		McEachran & Fechhelm, 1998
Lophiiformes	**59**	
Oneirodidae	21	
Chaenophryne draco		Pietsch, 2009
Chaenophryne longiceps		Pietsch, 2009
Chaenophryne melanorhabdus		Pietsch, 2009
Chaenophryne ramifera		Pietsch, 2009
Chirophryne xenolophus		Pietsch, 2009
Danaphryne nigrifilis		Pietsch, 2009
Dolopichthys dinema		Pietsch, 2009
Dolopichthys jubatus		Pietsch, 2009
Dolopichthys longicornis		Pietsch, 2009
Dolopichthys pullatus		Pietsch, 2009
Dolopichthys undescribed TS1		Pietsch, 2009
Lophodolos acanthognathus		Pietsch, 2009
Lophodolos indicus		Pietsch, 2009
Microlophichthys microlophus		Pietsch, 2009
Oneirodes bradburyae		Pietsch, 2009
Oneirodes carlsbergi		Pietsch, 2009
Oneirodes eschrichtii		Pietsch, 2009
Oneirodes macrosteus		Pietsch, 2009
Oneirodes schmidti group		Pietsch, 2009
Oneirodes theodoritissieri		Pietsch, 2009
Spiniphryne gladisfenae		Pietsch, 2009
Linophrynidae	10	
Haplophryne mollis		Herring & Munk, 1994
Linophryne algibarbata		Hansen & Herring, 2009
Linophryne arborifera		Hansen & Herring, 2009
Linophryne brevibarbata		McEachran & Fechhelm, 1998
Linophryne densiramus		McEachran & Fechhelm, 1998
Linophryne macrodon		Hansen & Herring, 2009
Linophryne pennibarbata		Hansen & Herring, 2009
Linophryne racemifera		Hansen & Herring, 2009
Linophryne undescribed TS1		Hansen & Herring, 2009
Photocorynus spiniceps		Pietsch, 2009
Gigantactinidae	10	

Gigantactis gargantua		Pietsch, 2009
Gigantactis gracilicauda		Pietsch, 2009
Gigantactis herwigi		Pietsch, 2009
Gigantactis longicauda		Pietsch, 2009
Gigantactis longicirra		Pietsch, 2009
Gigantactis macronema		Pietsch, 2009
Gigantactis microdontis		Pietsch, 2009
Gigantactis undescribed TS1		Pietsch, 2009
Gigantactis vanhoeffeni		Pietsch, 2009
Gigantactis watermani		Pietsch, 2009
Thaumatichthyidae	4	
Lasiognathus beebei		Pietsch, 2009
Lasiognathus dinema		Pietsch, 2009
Lasiognathus saccostoma		Pietsch, 2009
Thaumatichthys binghami		Pietsch, 2009
Ceratiidae	4	
Ceratias undescribed AB1		McEachran & Fechhelm, 1998
Ceratias undescribed TS1		McEachran & Fechhelm, 1998
Ceratias uranoscopus		McEachran & Fechhelm, 1998
Cryptopsaras couesii		Pietsch, 2009
Himantolophidae	4	
Himantolophus albinares		McEachran & Fechhelm, 1998
Himantolophus brevirostris group		McEachran & Fechhelm, 1998
Himantolophus groenlandicus		McEachran & Fechhelm, 1998
Himantolophus paucifilosus		McEachran & Fechhelm, 1998
Diceratiidae	3	
Bufoceratias undescribed TS1		Pietsch, 2009
Bufoceratias wedli		Pietsch, 2009
Diceratias pileatus		Pietsch, 2009
Melanocetidae	2	
Melanocetus johnsonii		Munk et al., 1998
Melanocetus murrayi		Munk et al., 1998
Centrophrynidae		
Centrophryne spinulosa		Pietsch, 2009
Alepocephaliformes	**21**	
Platytroctidae	18	
Barbantus curvifrons		McEachran & Fechhelm, 1998
Holtbyrnia anomala		Matsui & Rsenblatt, 1988
Holtbyrnia cyanocephala		Matsui & Rsenblatt, 1988
Holtbyrnia innesi		Matsui & Rsenblatt, 1988
Holtbyrnia macrops		Matsui & Rsenblatt, 1988
Maulisia acuticeps		McEachran & Fechhelm, 1998
Maulisia argipalla		Matsui & Rsenblatt, 1988

Maulisia mauli		Matsui & Rsenblatt, 1988
Maulisia microlepis		McEachran & Fechhelm, 1998
Mentodus crassus		McEachran & Fechhelm, 1998
Mentodus facilis		Poulsen, 2019
Mentodus longirostris		McEachran & Fechhelm, 1998
Mentodus mesalirus		McEachran & Fechhelm, 1998
Mentodus rostratus		McEachran & Fechhelm, 1998
Normichthys operosus		McEachran & Fechhelm, 1998
Platytroctes apus		McEachran & Fechhelm, 1998
Sagamichthys schnakenbecki		Poulsen, 2019
Searsia koefoedi		Matsui & Rsenblatt, 1988
Alepocephalidae	3	
Photostylus pycnopterus		McEachran & Fechhelm, 1998
Rouleina maderensis		McEachran & Fechhelm, 1998
Xenodermichthys copei		McEachran & Fechhelm, 1998
Gadiformes	**12**	
Macrouridae	10	
Hymenocephalus billsam		Schwarzhans, 2014
Hymenocephalus italicus		Schwarzhans, 2014
Malacocephalus laevis		McEachran & Fechhelm, 1998
Malacocephalus occidentalis		McEachran & Fechhelm, 1998
Nezumia longebarbata		McEachran & Fechhelm, 1998
Nezumia suilla		McEachran & Fechhelm, 1998
Odontomacrurus murrayi		Nakayama, 2020
Sphagemacrurus grenadae		Merett, 2003
Trachonurus sulcatus		Merett, 2003
Ventrifossa macropogon		Merett, 2003
Steindachneriidae		
Steindachneria argentea		McEachran & Fechhelm, 1998
Moridae	1	
Physiculus kaupi	1	Pires et al., 2019
Scombriformes	**7**	
Chiasmodontidae	7	
Pseudoscopelus altipinnis		McEachran & Fechhelm, 2006
Pseudoscopelus aphos		McEachran & Fechhelm, 2006
Pseudoscopelus cordilluminatus		McEachran & Fechhelm, 2006
Pseudoscopelus obtusifrons		McEachran & Fechhelm, 2006
Pseudoscopelus sagamianus		McEachran & Fechhelm, 2006
Pseudoscopelus scriptus		McEachran & Fechhelm, 2006
Pseudoscopelus scutatus		McEachran & Fechhelm, 2006
Aulopiformes	**4**	
Paralepididae	2	
Lestidium atlanticum		Ghedotti et al., 2015

Lestrolepis intermedia		Ghedotti et al., 2015
Evermannellidae	2	
Coccorella atlantica		McEachran & Fechhelm, 1998
Odontostomops normalops		Paitio et al., 2016
Acropomatiformes	**2**	
Howellidae	1	
Howella atlantica		Herring, 1987
Epigonidae	1	
Epigonus macrops		Ghedotti et al., 2018
Argentiniformes	**2**	
Opisthoproctidae	2	
Opisthoproctus soleatus		Wagner et al., 2022
Winteria telescopa		Wagner et al., 2022
Saccopharyngiformes	**1**	
Eurypharyngidae	1	
Eurypharynx pelecanoides		Houde & Zastrow, 1993
Chondrichthyes	2	
Squaliformes	**2**	
Dalatiidae	2	
Isistius brasiliensis		Claes & Mallefet, 2009b
Isistius plutodus		Claes & Mallefet, 2009b
Urochordata	**7**	
Thaliacea	7	
Salpida	**6**	
Salpidae	6	
Cyclosalpa bakeri		Sunwoo et al., 2012
Cyclosalpa danae		van Soest, 1975
Cyclosalpa floridana		van Soest, 1974
Cyclosalpa pinnata		van Soest, 1974
Cyclosalpa polae		Sunwoo et al., 2012
Helicosalpa virgula		van Soest, 1974
Pyrosomida	**1**	
Pyrosomatidae	1	
Pyrosoma atlanticum		Martini & Haddock, 2017
Cnidaria	**145**	
Medusozoa	**145**	
Hydrozoa	131	
Siphonophorae	**68**	
Diphyidae	16	
Chelophyes appendiculata		Haddock & Case, 1999
Dimophyes arctica		Haddock & Case, 1999
Diphyes bojani		Haddock & Case, 1999
Diphyes dispar		Haddock & Case, 1999

Eudoxoides mitra		Haddock & Case, 1999
Eudoxoides spiralis		Haddock & Case, 1999
Lensia exeter		Haddock & Case, 1999
Lensia fowleri		Haddock & Case, 1999
Lensia hotspur		Haddock & Case, 1999
Lensia multicristata		Haddock & Case, 1999
Muggiaea kochi		Haddock & Case, 1999
Sulculeolaria biloba		Haddock & Case, 1999
Sulculeolaria chuni		Haddock & Case, 1999
Sulculeolaria quadrivalvis		Haddock & Case, 1999
Sulculeolaria turgida		Haddock & Case, 1999
Agalmatidae	13	
Agalma elegans		Haddock & Case, 1999
Agalma okenii		Haddock & Case, 1999
Erenna richardi		Haddock & Case, 1999
Halistemma amphytridis		Haddock & Case, 1999
Halistemma cupulifera		Haddock & Case, 1999
Halistemma foliacea		Haddock & Case, 1999
Halistemma maculatum		Haddock & Case, 1999
Halistemma rubrum		Haddock & Case, 1999
Halistemma striata		Haddock & Case, 1999
Halistemma transliratum		Haddock & Case, 1999
Marrus orthocanna		Haddock & Case, 1999
Melophysa melo		Haddock & Case, 1999
Nanomia bijuga		Haddock & Case, 1999
Abylidae	11	
Abyla bicarinata		Haddock & Case, 1999
Abyla haeckeli		Haddock & Case, 1999
Abyla trigona		Haddock & Case, 1999
Abylopsis eschscholtzi		Haddock & Case, 1999
Abylopsis tetragona		Haddock & Case, 1999
Abylopsis trigona		Haddock & Case, 1999
Bassia bassensis		Haddock & Case, 1999
Ceratocymba dentata		Haddock & Case, 1999
Ceratocymba leuckarti		Haddock & Case, 1999
Ceratocymba sagittata		Haddock & Case, 1999
Enneagonum hyalinum		Haddock & Case, 1999
Prayidae	11	
Amphicaryon acaule		Haddock & Case, 1999
Amphicaryon ernesti		Haddock & Case, 1999
Amphicaryon peltifera		Haddock & Case, 1999
Lilyopsis medusa		Haddock & Case, 1999
Maresearsia praeclara		Haddock & Case, 1999

Nectadamas diomedeae		Haddock & Case, 1999
Nectopyramis natans		Haddock & Case, 1999
Praya dubia		Haddock & Case, 1999
Praya reticulata		Haddock & Case, 1999
Rosacea cymbiformis		Haddock & Case, 1999
Rosacea plicata		Haddock & Case, 1999
Hippopodiidae	5	
Hippopodius hippopus		Haddock & Case, 1999
Vogtia glabra		Haddock & Case, 1999
Vogtia pentacantha		Haddock & Case, 1999
Vogtia serrata		Haddock & Case, 1999
Vogtia spinosa		Haddock & Case, 1999
Pyrostephidae	4	
Bargmannia amoena		Haddock & Case, 1999
Bargmannia elongata		Haddock & Case, 1999
Bargmannia lata		Haddock & Case, 1999
Pyrostephos		Mapstone, 2014
Rhizophysidae	2	
Bathyphysa conifera		Haddock & Case, 1999
Rhizophysa		Herring, 1987
Clausophyidae	2	
Chuniphyes moserae		Haddock & Case, 1999
Chuniphyes multidentata		Haddock & Case, 1999
Apolemiidae	1	
Apolemia		Herring, 1987
Stephanomiidae	1	
Stephanomia amphytridis		Haddock & Case, 1999
Spaeronectidae	1	
Sphaeronectes koellikeri		Haddock & Case, 1999
Physophoridae	1	
Physophora hydrostatica		Haddock & Case, 1999
Forskaliidae	1	
Forskalia contorta		Haddock & Case, 1999
Anthoathecatae	**22**	
Bythotiaridae	9	
Bythotiara capensis		Haddock et al., 2010
Bythotiara depressa		Haddock et al., 2010
Calycopsis chuni		Haddock et al., 2010
Calycopsis papillata		Haddock et al., 2010
Calycopsis simulans		Haddock et al., 2010
Calycopsis typa		Haddock et al., 2010
Pseudotiara tropica		Haddock et al., 2010
Protiaropsis anonyma		Haddock et al., 2010

Protiaropsis minor		Haddock et al., 2010
Bougainvilliidae	4	
Bougainvillia carolinensis		Haddock et al., 2010
Bougainvillia frondosa		Haddock et al., 2010
Bougainvillia platygaster		Haddock et al., 2010
Koellikerina fasciculata		Haddock et al., 2010
Pandeidae	4	
Halitholus intermedius		Haddock et al., 2010
Cirrhitiara superba		Haddock & Case, 1999
Leuckartiara		Herring, 1987
Stomotoca		Herring, 1987
Zancleopsidae	2	
Zancleopsis dichotoma		Haddock et al., 2010
Zancleopsis undescribed TS1		Haddock et al., 2010
Proboscidactylidae	1	
Proboscidactyla ornata		Haddock et al., 2010
Corymorphidae	1	
Corymorpha furcata		Haddock et al., 2010
Oceaniidae	1	
Oceania armata		Haddock et al., 2010
Trachymedusae	**16**	
Rhopalonematidae	12	
Aglantha digitale		Haddock et al., 2010
Amphogona apicata		Haddock et al., 2010
Arctapodema ampla		Haddock et al., 2010
Arctapodema antarctica		Haddock et al., 2010
Benthocodon pedunculatus		Haddock et al., 2010
Colobonema sericeum		Haddock et al., 2010
Crossota alba		Haddock et al., 2010
Crossota rufobrunnea		Haddock et al., 2010
Pantachogon haeckeli		Haddock et al., 2010
Pantachogon scotti		Haddock et al., 2010
Rhopalonema velatum		Haddock et al., 2010
Sminthea eurygaster		Haddock et al., 2010
Geryoniidae	2	
Geryonia proboscidalis		Haddock et al., 2010
Liriope tetraphylla		Haddock et al., 2010
Halicreatidae	2	
Botrynema brucei		Haddock et al., 2010
Halicreas minimum		Haddock & Case, 1999
Leptothecata	**15**	
Aequoreidae	5	
Aequorea forskalea		Haddock & Case, 1999

Aequorea globosa		Haddock & Case, 1999
Aequorea macrodactyla		Haddock & Case, 1999
Rhacostoma atlanticum		Haddock et al., 2010
Zygocanna vagans		Haddock et al., 2010
Eirenidae	3	
Eirene pyramidalis		Haddock et al., 2010
Eutima gracilis		Haddock et al., 2010
Eutonina scintillans		Haddock et al., 2010
Campanulariidae	2	
Clytia lomae		Haddock & Case, 1999
Clytia simplex		Haddock et al., 2010
Eucheilotidae	1	
Eucheilota ventricularis		Haddock et al., 2010
Malagazziidae	1	
Tetracanna octonema		Haddock et al., 2010
Melicertidae	1	
Netocertoides brachiatum		Haddock et al., 2010
Mitrocomidae	1	
Mitrocomella		Haddock & Case, 1999
Orchistomatidae	1	
Orchistoma pileus		Haddock et al., 2010
Narcomedusae	**9**	
Solmarisidae	4	
Pegantha martagon		Haddock et al., 2010
Pegantha triloba		Haddock et al., 2010
Solmaris flavescens		Haddock et al., 2010
Solmaris solmaris		Haddock et al., 2010
Cuninidae	4	
Cunina duplicata		Haddock et al., 2010
Cunina frugifera		Haddock et al., 2010
Cunina octonaria		Haddock et al., 2010
Solmissus incisa		Haddock & Case, 1999
Aeginidae	1	
Aegina citrea		Haddock & Case, 1999
Limnomedusae	**1**	
Olindiidae	1	
Aglauropsis kawari		Haddock et al., 2010
Scyphozoa	14	
Coronatae	**9**	
Nausithoidae	3	
Nausithoe punctata		Haddock et al., 2010
Nausithoe rubra		Haddock et al., 2010
Nausithoe maculata		Haddock et al., 2010

Periphyllidae	2	
Periphylla periphylla		Haddock & Case, 1999
Periphyllopsis braueri		Haddock & Case, 1999
Atollidae	2	
Atolla vanhoeffeni		Haddock & Case, 1999
Atolla wyvillei		Haddock & Case, 1999
Linuchidae	1	
Linuche unguiculata		Haddock et al., 2010
Paraphyllinidae	1	
Paraphyllina ransoni		Haddock & Case, 1999
Semaeostomeae	**5**	
Ulmaridae	3	
Aurelia aurita		Haddock et al., 2010
Deepstaria reticulum		Haddock et al., 2010
Tiburonia granrojo		Haddock et al., 2010
Pelagiidae	2	
Chrysaora quinquecirrha		Haddock et al., 2010
Pelagia noctiluca		Haddock et al., 2010
Arthropoda	**94**	
Crustacea	**94**	
Malacostraca	93	
Decapoda	**56**	
Sergestidae	19	
Allosergestes pectinatus		Vereshchaka et al., 2014
Allosergestes sargassi		Vereshchaka et al., 2014
Challengerosergia challengeri		Herring, 1985
Challengerosergia hansjacobi		Vereshchaka & Shirshov, 2000
Challengerosergia talismani		Vereshchaka & Shirshov, 2000
Cornutosergestes cornutus		Vereshchaka et al., 2014
Deosergestes corniculum		Vereshchaka et al., 2014
Deosergestes henseni		Vereshchaka et al., 2014
Deosergestes paraseminudus		Vereshchaka et al., 2014
Eusergestes arcticus		Vereshchaka et al., 2014
Gardinerosergia splendens		Vereshchaka & Shirshov, 2000
Neosergestes edwardsii		Vereshchaka et al., 2014
Parasergestes armatus		Vereshchaka et al., 2014
Parasergestes vigilax		Vereshchaka et al., 2014
Phorcosergia grandis		Vereshchaka & Shirshov, 2000
Phorcosergia filicta		Vereshchaka & Shirshov, 2000
Robustosergia regalis		Vereshchaka & Shirshov, 2000
Robustosergia robusta		Vereshchaka & Shirshov, 2000
Sergestes atlanticus		Vereshchaka et al., 2014
Acanthephyridae	19	

Acanthephyra acanthitelsonis		Herring, 1985
Acanthephyra acutifrons		Wong et al., 2015
Acanthephyra brevirostris		Herring, 1985
Acanthephyra curtirostris		Wong et al., 2015
Acanthephyra eximia		Wong et al., 2015
Acanthephyra pelagica		Wong et al., 2015
Acanthephyra purpurea		Wong et al., 2015
Acanthephyra quadrispinosa		Wong et al., 2015
Acanthephyra stylorostratis		Varela et al., 2021
Ephyrina benedicti		Varela et al., 2022
Ephyrina ombango		Wong et al., 2015
Hymenodora glacialis		Wong et al., 2015
Hymenodora gracilis		Wong et al., 2015
Meningodora marptocheles		Varela et al., 2021
Meningodora miccyla		Herring, 1985
Meningodora mollis		Wong et al., 2015
Meningodora vesca		Wong et al., 2015
Notostomus elegans		Wong et al., 2015
Notostomus gibbosus		Wong et al., 2015
Benthesicymidae	7	
Amalopenaeus elegans		Herring, 1987
Gennadas bouvieri		Herring, 1987
Gennadas capensis		Herring, 1987
Gennadas propinquus		Herring, 1987
Gennadas scutatus		Herring, 1987
Gennadas talismani		Herring, 1987
Gennadas valens		Herring, 1987
Oplophoridae	6	
Janicella spinicauda		Wong et al., 2015
Oplophorus gracilirostris		Wong et al., 2015
Oplophorus spinosus		Wong et al., 2015
Systellaspis braueri		Wong et al., 2015
Systellaspis cristata		Varela et al., 2021
Systellaspis debilis		Wong et al., 2015
Solenoceridae	3	
Hadropenaeus affinis		Chan et al., 2008
Hymenopenaeus aphoticus		Chan et al., 2008
Hymenopenaeus debilis		Herring, 1985
Pandalidae	2	
Heterocarpus ensifer		Wong et al., 2015
Parapandalus		Johnsen et al., 2012
Euphausiacea	**32**	
Euphausiidae	32	

Euphausia americana		Keen, 2012
Euphausia brevis		Keen, 2012
Euphausia gibboides		Keen, 2012
Euphausia hemigibba/pseudogibba		Keen, 2012
Euphausia krohnii		Keen, 2012
Euphausia mutica		Keen, 2012
Euphausia tenera		Keen, 2012
Nematobrachion boopis		Keen, 2012
Nematobrachion flexipes		Keen, 2012
Nematobrachion sexspinosum		Keen, 2012
Nematoscelis atlantica		Keen, 2012
Nematoscelis megalops		Keen, 2012
Nematoscelis microps		Keen, 2012
Nematoscelis tenella		Keen, 2012
Stylocheiron abbreviatum		Keen, 2012
Stylocheiron affine		Keen, 2012
Stylocheiron carinatum		Keen, 2012
Stylocheiron elongatum		Keen, 2012
Stylocheiron longicorne		Keen, 2012
Stylocheiron maximum		Keen, 2012
Stylocheiron robustum		Keen, 2012
Stylocheiron suhmi		Keen, 2012
Thysanoessa gregaria		Keen, 2012
Thysanopoda acutifrons		Keen, 2012
Thysanopoda aequalis		Keen, 2012
Thysanopoda cristata		Keen, 2012
Thysanopoda egregia		Keen, 2012
Thysanopoda monacantha		Keen, 2012
Thysanopoda obtusifrons		Keen, 2012
Thysanopoda orientalis		Keen, 2012
Thysanopoda pectinata		Keen, 2012
Thysanopoda tricuspidata		Keen, 2012
Lophogastrida	**4**	
Gnathophausiidae	4	
Fagegnathophausia gracilis		Herring, 1985
Gnathophausia zoea		Herring, 1985
Neognathophausia gigas		Herring, 1985
Neognathophausia ingens		Herring, 1985
Amphipoda	**1**	
Scinidae	1	
Scina curvidactyla		Herring, 1987
Ostacoda	1	
Myodocopida	**1**	

Cypridinidae	1	
Vargula		Delroisse et al., 2021
Mollusca	**63**	
	61	
Cephalopoda	59	
Oegopsida	**51**	
Cranchiidae	13	
Bathothauma lyromma		Carpenter & Niem, 1998
Cranchia scabra		Thomas, 2018
Egea inermis		Carpenter & Niem, 1998
Galiteuthis armata		Thomas, 2018
Helicocranchia papillata		Carpenter & Niem, 1998
Helicocranchia pfefferi		Carpenter & Niem, 1998
Leachia atlantica		Thomas, 2018
Leachia lemur		Thomas, 2018
Liguriella podophthalma		Carpenter & Niem, 1998
Liocranchia reinhardti		Carpenter & Niem, 1998
Sandalops melancholicus		Carpenter & Niem, 1998
Taonius pavo		Thomas, 2018
Teuthowenia megalops		Thomas, 2018
Enoploteuthidae	6	
Abralia redfieldi		Carpenter & Niem, 1998
Abralia veranyi		Thomas, 2018
Abraliopsis atlantica		Carpenter & Niem, 1998
Abraliopsis hoylei		Carpenter & Niem, 1998
Enoploteuthis anapsis		Carpenter & Niem, 1998
Enoploteuthis leptura		Thomas, 2018
Chiroteuthidae	6	
Asperoteuthis acanthoderma		Judkins et al., 2009
Asperoteuthis sp. A		Judkins et al., 2009
Chiroteuthis joubini		Mensch, 2010
Chiroteuthis mega		Thomas, 2018
Chiroteuthis spoeli		Mensch, 2010
Chiroteuthis veranii		Thomas, 2018
Grimalditeuthis bonplandi		Thomas, 2018
Lycoteuthidae	5	
Lampadioteuthis megaleia		Berry, 1916
Lycoteuthis diadema		Berry, 1920
Lycoteuthis lorigera		Thomas, 2018
Lycoteuthis springeri		Carpenter & Niem, 1998
Selenoteuthis scintillans		Thomas, 2018
Ommastrephidae	4	
Hyaloteuthis pelagica		Roper & Jereb, 2010

Ommastrephes bartramii		Thomas, 2018
Ornithoteuthis antillarum		Thomas, 2018
Sthenoteuthis pteropus		Roper & Jereb, 2010
Histioteuthidae	4	
Histioteuthis bonnellii		Thomas, 2018
Histioteuthis corona		Thomas, 2018
Histioteuthis reversa		Thomas, 2018
Stigmatoteuthis arcturi		Gomes-Pereira et al., 2016
Mastigoteuthidae	3	
Echinoteuthis atlantica		Thomas, 2018
Mastigopsis hjorti		Thomas, 2018
Mastigoteuthis agassizii		Thomas, 2018
Pyroteuthidae	3	
Pterygioteuthis gemmata		Thomas, 2018
Pterygioteuthis giardi		Thomas, 2018
Pyroteuthis margaritifera		Butcher et al., 2009
Octopoteuthidae	3	
Octopoteuthis danae		Carpenter & Niem, 1998
Octopoteuthis megaptera		Thomas, 2018
Taningia danae		Kubodera et al., 2007
Cycloteuthidae	2	
Cycloteuthis sirventi		Thomas, 2018
Discoteuthis discus		Thomas, 2018
Ancistrocheiridae	1	
Ancistrocheirus lesueurii		Carpenter & Niem, 1998
Brachioteuthidae	1	
Brachioteuthis		Shea et al., 2019
Onychoteuthidae	1	
Onychoteuthis banksii		Thomas, 2018
Bathyteuthoidea	**2**	
Bathyteuthidae	1	
Bathyteuthis abyssicola		Thomas, 2018
Chtenopterygidae	1	
Chtenopteryx sicula		Thomas, 2018
Octopoda	**2**	
Amphitretidae	2	
Bolitaena pygmaea		Thomas, 2018
Japetella diaphana		Thomas, 2018
Sepioidea	**2**	
Sepiolidae	2	
Heteroteuthis dagamensis		Judkins et al., 2016
Heteroteuthis dispar		Judkins et al., 2016
Vampyromorpha	**1**	

Vampyroteuthidae	1	
Vampyroteuthis infernalis		Robison et al., 2003
Spirulida	**1**	
Spirulidae	1	
Spirula spirula		Thomas, 2018
Gastropoda	2	
Nudibranchia	**2**	
Phylliroidae	2	
Phylliroe bucephala		Haddock et al., 2010
Phylliroe lichtensteinii		Haddock et al., 2010
Ctenophora	**7**	
Nuda	4	
Beroida	**4**	
Beroidae	4	
Beroe cucumis		Haddock & Case, 1999
Beroe forskalii		Haddock & Case, 1999
Beroe mitrata		Haddock & Case, 1999
Beroe ovata		Haddock & Case, 1999
Tentaculata	3	
Lobata	**2**	
Bolinopsidae	2	
Bolinopsis infundibulum		Haddock & Case, 1999
Mnemiopsis leidyi		Ward & Seliger, 1974
Cydippida	**1**	
Bathyctenidae	1	
Bathyctena chuni		Haddock & Case, 1999
Annelida	**1**	
Medusozoa	**1**	
Polychaeta	1	
Phyllodocida	**1**	
Tomopteridae	1	
Tomopteris		Francis et al., 2014
Chaetognatha	**1**	
Sagittoidea	1	
Phragmophora	**1**	
Eukrohniidae	1	
Eukrohnia bathypelagica		Thuesen et al., 2010
Echinodermata	**1**	
Echinozoa	**1**	
Holothuroidea	1	
Elasiopodida	**1**	
Pelagothuriidae	1	

Appendix Table 2. Relative contributions to total bioluminescent counts with respect to taxon abundance.

Systematic level	BL	Non-BL	Total
Chordata	**324**	**660**	**984**
Actinopterygii	**315**	**635**	**950**
Stomiiformes	143	1	144
Gonostomatidae	**15**	**1**	**16**
Bonapartia pedaliota	1		1
Cyclothone acclinidens	1		1
Cyclothone alba	1		1
Cyclothone braueri	1		1
Cyclothone microdon	1		1
Cyclothone obscura		1	1
Cyclothone pallida	1		1
Cyclothone parapallida	1		1
Cyclothone pseudopallida	1		1
Diplophos taenia	1		1
Gonostoma atlanticum	1		1
Manducus maderensis	1		1
Margrethia obtusirostra	1		1
Sigmops bathyphilus	1		1
Sigmops elongatus	1		1
Triplophos	1		1
Phosichthyidae	**7**		**7**
Ichthyococcus ovatus	1		1
Pollichthys mauli	1		1
Polymetme thaeocoryla	1		1
Vinciguerria attenuata	1		1
Vinciguerria nimbaria	1		1
Vinciguerria poweriae	1		1
Yarrella blackfordi	1		1
Sternoptychidae	**11**		**11**
Argyropelecus aculeatus	1		1
Argyropelecus affinis	1		1
Argyropelecus gigas	1		1
Argyropelecus hemigymnus	1		1
Argyropelecus sladeni	1		1
Maurolicus weitzmani	1		1
Polyipnus asteroides	1		1
Polyipnus clarus	1		1

Sternoptyx diaphana	1	1
Sternoptyx pseudobscura	1	1
Valenciennellus tripunctulatus	1	1
Stomiidae	**110**	**110**
Aristostomias grimaldii	1	1
Aristostomias polydactylus	1	1
Aristostomias tittmanni	1	1
Aristostomias xenostoma	1	1
Astronesthes atlanticus	1	1
Astronesthes decoratus	1	1
Astronesthes gemmifer	1	1
Astronesthes gudrunae	1	1
Astronesthes haplophos	1	1
Astronesthes macropogon	1	1
Astronesthes micropogon	1	1
Astronesthes neopogon	1	1
Astronesthes niger	1	1
Astronesthes oligoa	1	1
Astronesthes richardsoni	1	1
Astronesthes similus	1	1
Astronesthes undescribed TS1	1	1
Astronesthes zetgibbsi	1	1
Astronesthes zharovi	1	1
Bathophilus altipinnis	1	1
Bathophilus brevis	1	1
Bathophilus digitatus	1	1
Bathophilus filifer	1	1
Bathophilus longipinnis	1	1
Bathophilus nigerrimus	1	1
Bathophilus pawneei	1	1
Bathophilus proximus	1	1
Bathophilus schizochirus	1	1
Borostomias elucens	1	1
Borostomias mononema	1	1
Chauliodus danae	1	1
Chauliodus sloani	1	1
Echiostoma barbatum	1	1
Eustomias (Biradiostomias) undescribed TS1	1	1
Eustomias (Dinematochirus) undescribed TS1	1	1
Eustomias (Spilostomias) undescribed TS1	1	1
Eustomias achirus	1	1

Eustomias acinosus	1	1
Eustomias bibulbosus	1	1
Eustomias bigelowi	1	1
Eustomias bimargaritatus	1	1
Eustomias bituberatus	1	1
Eustomias brevibarbatus	1	1
Eustomias contiguus	1	1
Eustomias dendriticus	1	1
Eustomias enbarbatus	1	1
Eustomias filifer	1	1
Eustomias fissibarbis	1	1
Eustomias furcifer	1	1
Eustomias hulleyi	1	1
Eustomias hypopsilus	1	1
Eustomias kreffti	1	1
Eustomias lipochirus	1	1
Eustomias longibarba	1	1
Eustomias macronema	1	1
Eustomias macrophthalmus	1	1
Eustomias medusa	1	1
Eustomias melanostigma	1	1
Eustomias micraster	1	1
Eustomias monoclonus	1	1
Eustomias monodactylus	1	1
Eustomias patulus	1	1
Eustomias schmidti	1	1
Eustomias triramis	1	1
Eustomias undescribed TS1	1	1
Eustomias undescribed TS2	1	1
Eustomias variabilis	1	1
Eustomias xenobolus	1	1
Flagellostomias boureei	1	1
Grammatostomias circularis	1	1
Heterophotus ophistoma	1	1
Idiacanthus fasciola	1	1
Idiacanthus undescribed TS1	1	1
Leptostomias bermudensis	1	1
Leptostomias bilobatus	1	1
Leptostomias gladiator	1	1
Leptostomias haplocaulus	1	1
Leptostomias leptobolus	1	1
Leptostomias longibarba	1	1
Leptostomias undescribed TS1	1	1

Leptostomias undescribed TS2	1		1
Malacosteus niger	1		1
Melanostomias bartonbeani	1		1
Melanostomias biseriatus	1		1
Melanostomias macrophotus	1		1
Melanostomias margaritifer	1		1
Melanostomias melanopogon	1		1
Melanostomias melanops	1		1
Melanostomias tentaculatus	1		1
Melanostomias undescribed TS1	1		1
Melanostomias valdiviae	1		1
Pachystomias microdon	1		1
Photonectes (Melanocetes) undescribed TS1	1		1
Photonectes (Trachinostomias) undescribed TS1	1		1
Photonectes achirus	1		1
Photonectes braueri	1		1
Photonectes caerulescens	1		1
Photonectes dinema	1		1
Photonectes gracilis	1		1
Photonectes leucospilus	1		1
Photonectes margarita	1		1
Photonectes parvimanus	1		1
Photostomias goodyeari	1		1
Photostomias guernei	1		1
Stomias affinis	1		1
Stomias boa	1		1
Stomias brevibarbatus	1		1
Stomias longibarbatus	1		1
Thysanactis dentex	1		1
Thysanactis undescribed TS1	1		1
Anguilliformes		120	120
Anguillidae		**4**	**4**
Anguilla anguilla		1	1
Anguilla rostrata		1	1
Type I sp. B FWNA		1	1
Type II sp. FWNA		1	1
Chlopsidae		**6**	**6**
Chilorhinus suensonii		1	1
Chlopsis bicolor		1	1
Chlopsis dentatus		1	1
Kaupichthys hyoproroides		1	1

Kaupichthys nuchalis	1	1
Robinsia catherinae	1	1
Congridae	**30**	**30**
Acromycter perturbator	1	1
Ariosoma anale	1	1
Ariosoma balearicum	1	1
Ariosoma coquettei	1	1
Ariosoma selenops	1	1
Bathycongrus dubius	1	1
Bathycongrus sp. A FWNA	1	1
Bathyuroconger vicinus	1	1
Conger esculentus	1	1
Conger oceanicus	1	1
Conger triporiceps	1	1
Congridae genus c species b	1	1
Congridae sp. c	1	1
Congridae sp. f	1	1
Congridae sp. g	1	1
Congridae sp. h	1	1
Congridae sp. i	1	1
Congridae sp. j	1	1
Congridae sp. k	1	1
Congridae sp. l	1	1
Gnathophis	1	1
Heteroconger longissimus	1	1
Heteroconger luteolus	1	1
Parabathymyrus oregoni	1	1
Paraconger caudilimbatus	1	1
Pseudophichthys splendens	1	1
Rhynchoconger flavus	1	1
Rhynchoconger gracilior	1	1
Uroconger syringinus	1	1
Xenomystax congroides	1	1
Derichthyidae	**2**	**2**
Derichthys serpentinus	1	1
Nessorhamphus ingolfianus	1	1
Moringuidae	**2**	**2**
Moringua edwardsi	1	1
Neoconger mucronatus	1	1
Muraenidae	**18**	**18**
Anarchias similis	1	1
Channomuraena vittata	1	1
Gymnothorax conspersus	1	1

Gymnothorax funebris	1	1
Gymnothorax kolpos	1	1
Gymnothorax miliaris	1	1
Gymnothorax moringa	1	1
Gymnothorax nigromarginatus	1	1
Gymnothorax ocellatus	1	1
Gymnothorax saxicola	1	1
Gymnothorax sp. A FWNA	1	1
Gymnothorax sp. jam1	1	1
Gymnothorax sp. jam2	1	1
Gymnothorax sp. jam3	1	1
Gymnothorax vicinus	1	1
Monopenchelys acuta	1	1
Muraena retifera	1	1
Uropterygius macularius	1	1
Nemichthyidae	**4**	**4**
Avocettina infans	1	1
Labichthys carinatus	1	1
Nemichthys curvirostris	1	1
Nemichthys scolopaceus	1	1
Nettastomatidae	**12**	**12**
Facciolella oxyrhynchus	1	1
Facciolella sp. B FWNA	1	1
Facciolella sp. C FWNA	1	1
Hoplunnis diomediana	1	1
Hoplunnis macrura	1	1
Hoplunnis similis	1	1
Hoplunnis sp. C FWNA	1	1
Hoplunnis tenuis	1	1
Nettastoma melanura	1	1
Nettastomatidae sp. a	1	1
Nettenchelys pygmaea	1	1
Venefica procera	1	1
Ophichthidae	**31**	**31**
Ahlia egmontis	1	1
Aplatophis chauliodus	1	1
Aprognathodon platyventris	1	1
Apterichtus kendalli	1	1
Bascanichthyini sp. fwna	1	1
Bascanichthys bascanium	1	1
Bascanichthys scuticaris	1	1
Callechelys guineensis	1	1
Callechelys muraena	1	1

Echiophis punctifer		1	1
Gordiichthys randalli		1	1
Letharchus aliculatus		1	1
Letharchus velifer		1	1
Myrichthys breviceps		1	1
Myrichthys ocellatus		1	1
Myrophis platyrhynchus		1	1
Myrophis punctatus		1	1
Ophichthini sp. 1 fwna		1	1
Ophichthini sp. 2 fwna		1	1
Ophichthini sp. 3 fwna		1	1
Ophichthini sp. 5 fwna		1	1
Ophichthini sp. 7 fwna		1	1
Ophichthus gomesii		1	1
Ophichthus melanoporus		1	1
Ophichthus puncticeps		1	1
Ophichthus rex		1	1
Pseudomyrophis frio		1	1
Pseudomyrophis fugesae		1	1
Quassiremus ascensionis		1	1
Quassiremus sp. B JAM		1	1
Stictorhinus potamius		1	1
Serrivomeridae		**2**	**2**
Serrivomer beanii		1	1
Serrivomer lanceolatoides		1	1
Synaphobranchidae		**9**	**9**
Dysomma anguillare		1	1
Dysommina proboscideus		1	1
Ilyophinae sp. b5		1	1
Ilyophinae sp. c1 fwna		1	1
Simenchelys parasitica		1	1
Synaphobranchid sp. a5 fwna		1	1
Synaphobranchidae JAM6		1	1
Synaphobranchidae sp. 11 jam		1	1
Synaphobranchus oregoni		1	1
Scombriformes	7	70	77
Ariommatidae		**3**	**3**
Ariomma bondi		1	1
Ariomma melanum		1	1
Ariomma regulus		1	1
Bramidae		**7**	**7**
Brama caribbea		1	1
Brama dussumieri		1	1

Pterycombus brama		1	1
Taractes asper		1	1
Taractes rubescens		1	1
Taractichthys longipinnis		1	1
Taractichthys steindachneri		1	1
Caristiidae		**4**	**4**
Caristius		1	1
Paracaristius maderensis		1	1
Paracaristius nudarcus		1	1
Platyberyx andriashevi		1	1
Centrolophidae		**2**	**2**
Centrolophus niger		1	1
Schedophilus medusophagus		1	1
Chiasmodontidae	**7**	**12**	**19**
Chiasmodon braueri		1	1
Chiasmodon microcephalus		1	1
Chiasmodon niger		1	1
Chiasmodon pluriradiatus		1	1
Dysalotus alcocki		1	1
Dysalotus oligoscolus		1	1
Kali colubrina		1	1
Kali falx		1	1
Kali indica		1	1
Kali kerberti		1	1
Kali macrodon		1	1
Kali parri		1	1
Pseudoscopelus altipinnis	1		1
Pseudoscopelus aphos	1		1
Pseudoscopelus cordilluminatus	1		1
Pseudoscopelus obtusifrons	1		1
Pseudoscopelus sagamianus	1		1
Pseudoscopelus scriptus	1		1
Pseudoscopelus scutatus	1		1
Gempylidae		**9**	**9**
Diplospinus multistriatus		1	1
Epinnula magistralis		1	1
Gempylus serpens		1	1
Lepidocybium flavobrunneum		1	1
Nealotus tripes		1	1
Neoepinnula americana		1	1
Nesiarchus nasutus		1	1
Promethichthys prometheus		1	1
Ruvettus pretiosus		1	1

Nomeidae		**7**	**7**
Cubiceps capensis		1	1
Cubiceps pauciradiatus		1	1
Nomeus gronovii		1	1
Psenes arafurensis		1	1
Psenes cyanophrys		1	1
Psenes maculatus		1	1
Psenes pellucidus		1	1
Pomatomidae		**1**	**1**
Pomatomus saltatrix		1	1
Scombridae		**15**	**15**
Acanthocybium solandri		1	1
Auxis rochei		1	1
Auxis thazard		1	1
Euthynnus alletteratus		1	1
Katsuwonus pelamis		1	1
Sarda sarda		1	1
Scomber colias		1	1
Scomberomorus cavalla		1	1
Scomberomorus maculatus		1	1
Scomberomorus regalis		1	1
Thunnus alalunga		1	1
Thunnus albacares		1	1
Thunnus atlanticus		1	1
Thunnus obesus		1	1
Thunnus thynnus		1	1
Scombrolabracidae		**1**	**1**
Scombrolabrax heterolepis		1	1
Stromateidae		**2**	**2**
Peprilus burti		1	1
Peprilus paru		1	1
Tetragonuridae		**2**	**2**
Tetragonurus atlanticus		1	1
Tetragonurus cuvieri		1	1
Trichiuridae		**5**	**5**
Aphanopus carbo		1	1
Aphanopus intermedius		1	1
Benthodesmus simonyi		1	1
Benthodesmus tenuis		1	1
Trichiurus lepturus		1	1
Lophiiformes	59	13	72
Antennariidae		**3**	**3**
Antennarius striatus		1	1

Fowlerichthys radiosus		1	1
Histrio histrio		1	1
Caulophrynidae		**1**	**1**
Caulophryne		1	1
Centrophrynidae	**1**		**1**
Centrophryne spinulosa	1		1
Ceratiidae	**4**		**4**
Ceratias undescribed AB1	1		1
Ceratias undescribed TS1	1		1
Ceratias uranoscopus	1		1
Cryptopsaras couesii	1		1
Chaunacidae		**2**	**2**
Chaunacops roseus		1	1
Chaunax suttkusi		1	1
Diceratiidae	**3**		**3**
Bufoceratias undescribed TS1	1		1
Bufoceratias wedli	1		1
Diceratias pileatus	1		1
Gigantactinidae	**10**	**2**	**12**
Gigantactis gargantua	1		1
Gigantactis gracilicauda	1		1
Gigantactis herwigi	1		1
Gigantactis longicauda	1		1
Gigantactis longicirra	1		1
Gigantactis macronema	1		1
Gigantactis microdontis	1		1
Gigantactis undescribed TS1	1		1
Gigantactis vanhoeffeni	1		1
Gigantactis watermani	1		1
Rhynchactis leptonema		1	1
Rhynchactis macrothrix		1	1
Himantolophidae	**4**		**4**
Himantolophus albinares	1		1
Himantolophus brevirostris group	1		1
Himantolophus groenlandicus	1		1
Himantolophus paucifilosus	1		1
Linophrynidae	**10**		**10**
Haplophryne mollis	1		1
Linophryne algibarbata	1		1
Linophryne arborifera	1		1
Linophryne brevibarbata	1		1
Linophryne densiramus	1		1
Linophryne macrodon	1		1

Linophryne pennibarbata	1		1
Linophryne racemifera	1		1
Linophryne undescribed TS1	1		1
Photocorynus spiniceps	1		1
Lophiidae		**1**	**1**
Lophiodes reticulatus		1	1
Melanocetidae	**2**		**2**
Melanocetus johnsonii	1		1
Melanocetus murrayi	1		1
Neoceratiidae		**1**	**1**
Neoceratias spinifer		1	1
Ogcocephalidae		**3**	**3**
Dibranchus atlanticus		1	1
Halieutichthys aculeatus		1	1
Ogcocephalus pantostictus		1	1
Oneirodidae	**21**		**21**
Chaenophryne draco	1		1
Chaenophryne longiceps	1		1
Chaenophryne melanorhabdus	1		1
Chaenophryne ramifera	1		1
Chirophryne xenolophus	1		1
Danaphryne nigrifilis	1		1
Dolopichthys dinema	1		1
Dolopichthys jubatus	1		1
Dolopichthys longicornis	1		1
Dolopichthys pullatus	1		1
Dolopichthys undescribed TS1	1		1
Lophodolos acanthognathus	1		1
Lophodolos indicus	1		1
Microlophichthys microlophus	1		1
Oneirodes bradburyae	1		1
Oneirodes carlsbergi	1		1
Oneirodes eschrichtii	1		1
Oneirodes macrosteus	1		1
Oneirodes schmidti group	1		1
Oneirodes theodoritissieri	1		1
Spiniphryne gladisfenae	1		1
Thaumatichthyidae	**4**		**4**
Lasiognathus beebei	1		1
Lasiognathus dinema	1		1
Lasiognathus saccostoma	1		1
Thaumatichthys binghami	1		1
Myctophiformes	64	1	65

Myctophidae	**62**	**62**
Benthosema suborbitale	1	1
Bolinichthys distofax	1	1
Bolinichthys photothorax	1	1
Bolinichthys supralateralis	1	1
Centrobranchus nigroocellatus	1	1
Ceratoscopelus warmingii	1	1
Dasyscopelus asper	1	1
Dasyscopelus obtusirostris	1	1
Dasyscopelus selenops	1	1
Diaphus anderseni	1	1
Diaphus bertelseni	1	1
Diaphus brachycephalus	1	1
Diaphus dumerilii	1	1
Diaphus effulgens	1	1
Diaphus fragilis	1	1
Diaphus garmani	1	1
Diaphus holti	1	1
Diaphus lucidus	1	1
Diaphus minax	1	1
Diaphus mollis	1	1
Diaphus perspicillatus	1	1
Diaphus problematicus	1	1
Diaphus rafinesquii	1	1
Diaphus splendidus	1	1
Diaphus subtilis	1	1
Diaphus taaningi	1	1
Diaphus termophilus	1	1
Diaphus vanhoeffeni	1	1
Diogenichthys atlanticus	1	1
Electrona risso	1	1
Gonichthys cocco	1	1
Hygophum benoiti	1	1
Hygophum hygomii	1	1
Hygophum macrochir	1	1
Hygophum reinhardtii	1	1
Hygophum taaningi	1	1
Lampadena anomala	1	1
Lampadena luminosa	1	1
Lampadena speculigera	1	1
Lampanyctus achirus	1	1
Lampanyctus alatus	1	1
Lampanyctus ater	1	1

Lampanyctus cuprarius	1		1
Lampanyctus festivus	1		1
Lampanyctus lineatus	1		1
Lampanyctus nobilis	1		1
Lampanyctus photonotus	1		1
Lampanyctus pusillus	1		1
Lampanyctus tenuiformis	1		1
Lepidophanes guentheri	1		1
Lobianchia dofleini	1		1
Lobianchia gemellarii	1		1
Loweina interrupta	1		1
Myctophum affine	1		1
Myctophum nitidulum	1		1
Notolychnus valdiviae	1		1
Notoscopelus caudispinosus	1		1
Notoscopelus resplendens	1		1
Symbolophorus rufinus	1		1
Taaningichthys bathyphilus	1		1
Taaningichthys minimus	1		1
Taaningichthys paurolychnus	1		1
Neoscopelidae	**2**	**1**	**3**
Neoscopelus macrolepidotus	1		1
Neoscopelus microchir	1		1
Scopelengys tristis		1	1
Perciformes		53	53
Acropomatidae		**1**	**1**
Acropomatidae		1	1
Anthiadidae		**8**	**8**
Anthias nicholsi		1	1
Anthias woodsi		1	1
Baldwinella aureorubens		1	1
Baldwinella vivanus		1	1
Choranthias tenuis		1	1
Hemanthias leptus		1	1
Plectranthias garrupellus		1	1
Pronotogrammus martinicensis		1	1
Bembropidae		**2**	**2**
Bembrops anatirostris		1	1
Bembrops gobioides		1	1
Callionymidae		**3**	**3**
Diplogrammus pauciradiatus		1	1
Foetorepus agassizii		1	1
Paradiplogrammus bairdi		1	1

Epinephelidae	**3**	**3**
Cephalopholis cruentata	1	1
Mycteroperca	1	1
Pseudogramma gregoryi	1	1
Gobiidae	**1**	**1**
Ctenogobius boleosoma	1	1
Haemulidae	**1**	**1**
Haemulidae	1	1
Labridae	**5**	**5**
Clepticus parrae	1	1
Halichoeres cyanocephalus	1	1
Scarinae	1	1
Thalassoma bifasciatum	1	1
Xyrichtys	1	1
Liopropomatidae	**2**	**2**
Bathyanthias mexicanus	1	1
Liopropoma olneyi	1	1
Peristediidae	**1**	**1**
Peristedion imberbe	1	1
Polynemidae	**1**	**1**
Polynemidae	1	1
Scaridae	**1**	**1**
Sparisoma	1	1
Scorpaenidae	**7**	**7**
Pontinus castor	1	1
Pontinus longispinis	1	1
Pontinus rathbuni	1	1
Pterois volitans	1	1
Scorpaena agassizi	1	1
Scorpaena plumieri	1	1
Scorpaenidae undescribed TS1	1	1
Sebastidae	**1**	**1**
Helicolenus dactylopterus	1	1
Serranidae	**13**	**13**
Anthiinae	1	1
Centropristis striata	1	1
Cephalopholis fulva	1	1
Diplectrum bivittatum	1	1
Epinephelus cruentatus	1	1
Epinephelus itajara	1	1
Epinephelus striatus	1	1
Gonioplectrus hispanus	1	1
Hyporthodus flavolimbatus	1	1

Hyporthodus mystacinus		1	1
Hyporthodus nigritus		1	1
Hyporthodus niveatus		1	1
Serranus		1	1
Setarchidae		**2**	**2**
Ectreposebastes imus		1	1
Setarches guentheri		1	1
Uranoscopidae		**1**	**1**
Xenocephalus egregius		1	1
Aulopiformes	4	48	52
Alepisauridae		**2**	**2**
Alepisaurus brevirostris		1	1
Alepisaurus ferox		1	1
Anotopteridae		**1**	**1**
Anotopterus pharao		1	1
Bathysauridae		**2**	**2**
Bathysaurus ferox		1	1
Bathysaurus mollis		1	1
Chlorophthalmidae		**2**	**2**
Chlorophthalmus agassizi		1	1
Parasudis truculenta		1	1
Evermannellidae	**2**	**2**	**4**
Coccorella atlantica	1		1
Evermannella balbo		1	1
Evermannella melanoderma		1	1
Odontostomops normalops	1		1
Giganturidae		**2**	**2**
Gigantura chuni		1	1
Gigantura indica		1	1
Ipnopidae		**5**	**5**
Bathypterois bigelowi		1	1
Bathypterois phenax		1	1
Bathypterois viridensis		1	1
Bathytyphlops marionae		1	1
Ipnops murrayi		1	1
Notosudidae		**6**	**6**
Ahliesaurus berryi		1	1
Scopelosaurus lepidus		1	1
Scopelosaurus mauli		1	1
Scopelosaurus meadi		1	1
Scopelosaurus smithii		1	1
Scopelosaurus undescribed TS1		1	1
Omosudidae		**1**	**1**

Omosudis lowii		1	1
Paralepididae	**2**	**17**	**19**
Lestidiops affinis		1	1
Lestidiops jayakari		1	1
Lestidiops mirabilis		1	1
Lestidium atlanticum	1		1
Lestrolepis intermedia	1		1
Macroparalepis affinis		1	1
Magnisudis atlantica		1	1
Paralepis brevirostris		1	1
Paralepis coregonoides		1	1
Stemonosudis bullisi		1	1
Stemonosudis gracilis		1	1
Stemonosudis intermedia		1	1
Stemonosudis rothschildi		1	1
Stemonosudis siliquiventer		1	1
Stemonosudis undescribed TS1		1	1
Sudis atrox		1	1
Sudis hyalina		1	1
Uncisudis advena		1	1
Uncisudis quadrimaculata		1	1
Scopelarchidae		**4**	**4**
Scopelarchoides danae		1	1
Scopelarchus analis		1	1
Scopelarchus guentheri		1	1
Scopelarchus michaelsarsi		1	1
Synodontidae		**4**	**4**
Saurida brasiliensis		1	1
Synodus poeyi		1	1
Synodus synodus		1	1
Trachinocephalus myops		1	1
Carangiformes		44	44
Bothidae		**5**	**5**
Bothus		1	1
Chascanopsetta lugubris		1	1
Engyophrys senta		1	1
Monolene sessilicauda		1	1
Trichopsetta ventralis		1	1
Carangidae		**21**	**21**
Alectis ciliaris		1	1
Carangoides bartholomaei		1	1
Caranx crysos		1	1
Caranx hippos		1	1

Caranx ruber	1	1
Chloroscombrus chrysurus	1	1
Decapterus macarellus	1	1
Decapterus punctatus	1	1
Decapterus tabl	1	1
Elagatis bipinnulata	1	1
Hemicaranx amblyrhynchus	1	1
Pseudocaranx dentex	1	1
Selar crumenophthalmus	1	1
Selene brownii	1	1
Selene setapinnis	1	1
Selene vomer	1	1
Seriola dumerili	1	1
Seriola rivoliana	1	1
Trachinotus carolinus	1	1
Trachurus lathami	1	1
Uraspis secunda	1	1
Coryphaenidae	**2**	**2**
Coryphaena equiselis	1	1
Coryphaena hippurus	1	1
Cyclopsettidae	**6**	**6**
Citharichthys cornutus	1	1
Citharichthys spilopterus	1	1
Cyclopsetta chittendeni	1	1
Cyclopsetta fimbriata	1	1
Etropus crossotus	1	1
Syacium papillosum	1	1
Echeneidae	**2**	**2**
Remora osteochir	1	1
Remora remora	1	1
Istiophoridae	**1**	**1**
Istiophorus platypterus	1	1
Poecilopsettidae	**1**	**1**
Poecilopsetta beanii	1	1
Sphyraenidae	**5**	**5**
Sphyraena barracuda	1	1
Sphyraena borealis	1	1
Sphyraena guachancho	1	1
Sphyraena picudilla	1	1
Sphyraena sphyraena	1	1
Xiphiidae	**1**	**1**
Xiphias gladius	1	1
Beryciformes	41	41

Barbourisiidae	**1**	**1**
Barbourisia rufa	1	1
Berycidae	**2**	**2**
Beryx decadactylus	1	1
Beryx splendens	1	1
Cetomimidae	**14**	**14**
Ataxolepis apus	1	1
Cetomimus compunctus	1	1
Cetomimus gillii	1	1
Cetomimus hempeli	1	1
Cetomimus picklei	1	1
Cetomimus teevani	1	1
Cetostoma regani	1	1
Danacetichthys	1	1
Ditropichthys storeri	1	1
Eutaeniophorus festivus	1	1
Gyrinomimus bruuni	1	1
Gyrinomimus grahami	1	1
Gyrinomimus myersi species group	1	1
Gyrinomimus parri	1	1
Gibberichthyidae	**1**	**1**
Gibberichthys pumilus	1	1
Melamphaidae	**20**	**20**
Melamphaes ebelingi	1	1
Melamphaes eulepis	1	1
Melamphaes longivelis	1	1
Melamphaes polylepis	1	1
Melamphaes pumilus	1	1
Melamphaes simus	1	1
Melamphaes suborbitalis	1	1
Melamphaes typhlops	1	1
Poromitra "Gibbsi" Keene undescribed JM1	1	1
Poromitra crassiceps	1	1
Poromitra kukuevi	1	1
Poromitra megalops	1	1
Scopeloberyx "americanus"	1	1
Scopeloberyx bannikovi	1	1
Scopeloberyx opisthopterus	1	1
Scopeloberyx robustus	1	1
Scopeloberyx rubriventer	1	1
Scopeloberyx sp. JAM1	1	1
Scopelogadus beanii	1	1
Scopelogadus mizolepis	1	1

Rondeletiidae		**2**	**2**
Rondeletia bicolor		1	1
Rondeletia loricata		1	1
Stephanoberycidae		**1**	**1**
Stephanoberyx monae		1	1
Alepocephaliformes	21	14	35
Alepocephalidae	**3**	**14**	**17**
Photostylus pycnopterus	1		1
Rouleina attrita		1	1
Rouleina maderensis	1		1
Xenodermichthys copei	1		1
Alepocephalus bairdii		1	1
Asquamiceps caeruleus		1	1
Bajacalifornia megalops		1	1
Bathylaco nigricans		1	1
Bathytroctes		1	1
Conocara salmoneum		1	1
Herwigia kreffti		1	1
Leptochilichthys microlepis		1	1
Leptochilichthys pinguis		1	1
Narcetes stomias		1	1
Rinoctes nasutus		1	1
Talismania antillarum		1	1
Talismania homoptera		1	1
Platytroctidae	**18**		**18**
Barbantus curvifrons	1		1
Holtbyrnia anomala	1		1
Holtbyrnia cyanocephala	1		1
Holtbyrnia innesi	1		1
Holtbyrnia macrops	1		1
Maulisia acuticeps	1		1
Maulisia argipalla	1		1
Maulisia mauli	1		1
Maulisia microlepis	1		1
Mentodus crassus	1		1
Mentodus facilis	1		1
Mentodus longirostris	1		1
Mentodus mesalirus	1		1
Mentodus rostratus	1		1
Normichthys operosus	1		1
Platytroctes apus	1		1
Sagamichthys schnakenbecki	1		1
Searsia koefoedi	1		1

Ophidiiformes		33	33
Bythitidae		**4**	**4**
Barathronus bicolor		1	1
Cataetyx laticeps		1	1
Diplacanthopoma		1	1
Grammonus claudei		1	1
Carapidae		**3**	**3**
Carapus bermudensis		1	1
Echiodon dawsoni		1	1
Snyderidia canina		1	1
Ophidiidae		**26**	**26**
Abyssobrotula galatheae		1	1
Barathrites iris		1	1
Bassogigas gillii		1	1
Bassozetus compressus		1	1
Bassozetus taenia		1	1
Bathyonus laticeps		1	1
Benthocometes robustus		1	1
Brotula barbata		1	1
Brotulotaenia crassa		1	1
Brotulotaenia nigra		1	1
Dicrolene introniger		1	1
Dicrolene kanazawai		1	1
Lamprogrammus niger		1	1
Lepophidium		1	1
Luciobrotula corethromycter		1	1
Monomitopus agassizii		1	1
Neobythites gilli		1	1
Neobythites marginatus		1	1
Ophidiidae sp.1 jam		1	1
Ophidion josephi		1	1
Otophidium omostigma		1	1
Parophidion schmidti		1	1
Penopus microphthalmus		1	1
Porogadus miles		1	1
Pycnocraspedum phyllosoma		1	1
Spectrunculus grandis		1	1
Gadiformes	12	14	26
Bathygadidae		**3**	**3**
Bathygadus favosus		1	1
Bathygadus macrops		1	1
Gadomus longifilis		1	1
Bregmacerotidae		**3**	**3**

Bregmaceros atlanticus		1	1
Bregmaceros mcclellandii		1	1
Bregmaceros undescribed TS1		1	1
Macrouridae	**10**	**2**	**12**
Coelorinchus		1	1
Coryphaenoides mediterraneus		1	1
Hymenocephalus billsam	1		1
Hymenocephalus italicus	1		1
Malacocephalus laevis	1		1
Malacocephalus occidentalis	1		1
Nezumia longebarbata	1		1
Nezumia suilla	1		1
Odontomacrurus murrayi	1		1
Sphagemacrurus grenadae	1		1
Trachonurus sulcatus	1		1
Ventrifossa macropogon	1		1
Melanonidae		**1**	**1**
Melanonus zugmayeri		1	1
Moridae	**1**	**4**	**5**
Gadella imberbis		1	1
Laemonema barbatulum		1	1
Laemonema goodebeanorum		1	1
Physiculus fulvus		1	1
Physiculus kaupi	1		1
Phycidae		**1**	**1**
Urophycis		1	1
Steindachneriidae	**1**		**1**
Steindachneria argentea	1		1
Tetraodontiformes		26	26
Balistidae		**6**	**6**
Balistes capriscus		1	1
Balistes vetula		1	1
Canthidermis maculata		1	1
Canthidermis sufflamen		1	1
Melichthys niger		1	1
Xanthichthys ringens		1	1
Diodontidae		**5**	**5**
Chilomycterus antillarum		1	1
Chilomycterus reticulatus		1	1
Chilomycterus schoepfii		1	1
Diodon holocanthus		1	1
Diodon hystrix		1	1
Monacanthidae		**9**	**9**

Aluterus monoceros	1	1
Aluterus schoepfii	1	1
Aluterus scriptus	1	1
Cantherhines macrocerus	1	1
Cantherhines pullus	1	1
Monacanthus ciliatus	1	1
Monacanthus tuckeri	1	1
Stephanolepis hispidus	1	1
Stephanolepis setifer	1	1
Ostraciidae	**1**	**1**
Acanthostracion quadricornis	1	1
Tetraodontidae	**4**	**4**
Canthigaster jamestyleri	1	1
Canthigaster rostrata	1	1
Lagocephalus lagocephalus	1	1
Sphoeroides spengleri	1	1
Acanthuriformes	24	24
Acanthuridae	**3**	**3**
Acanthurus bahianus	1	1
Acanthurus chirurgus	1	1
Acanthurus coeruleus	1	1
Antigoniidae	**2**	**2**
Antigonia capros	1	1
Antigonia combatia	1	1
Chaetodontidae	**2**	**2**
Chaetodon sedentarius	1	1
Prognathodes aya	1	1
Ephippidae	**1**	**1**
Chaetodipterus faber	1	1
Lobotidae	**1**	**1**
Lobotes surinamensis	1	1
Luvaridae	**1**	**1**
Luvarus imperialis	1	1
Pomacanthidae	**5**	**5**
Centropyge argi	1	1
Centropyge aurantonotus	1	1
Holacanthus bermudensis	1	1
Holacanthus ciliaris	1	1
Holacanthus tricolor	1	1
Priacanthidae	**4**	**4**
Cookeolus japonicus	1	1
Heteropriacanthus cruentatus	1	1
Priacanthus arenatus	1	1

Pristigenys alta		1	1
Sciaenidae		**4**	**4**
Cynoscion nothus		1	1
Leiostomus xanthurus		1	1
Micropogonias undulatus		1	1
Sciaenops ocellatus		1	1
Sparidae		**1**	**1**
Stenotomus caprinus		1	1
Argentiniformes	2	17	19
Argentinidae		**1**	**1**
Argentina		1	1
Bathylagidae		**2**	**2**
Dolicholagus longirostris		1	1
Melanolagus bericoides		1	1
Microstomatidae		**7**	**7**
Microstoma microstoma		1	1
Nansenia atlantica		1	1
Nansenia groenlandica		1	1
Nansenia longicauda		1	1
Nansenia pelagica		1	1
Nansenia undescribed TS1		1	1
Xenophthalmichthys danae		1	1
Opisthoproctidae	**2**	**7**	**9**
Monacoa grimaldii		1	1
Opisthoproctus soleatus	1		1
Winteria telescopa	1		1
Bathylychnops brachyrhynchus		1	1
Bathylychnops exilis		1	1
Dolichopteroides binocularis		1	1
Dolichopteryx longipes		1	1
Duolentops rostrata		1	1
Rhynchohyalus natalensis		1	1
Beloniformes		17	17
Belonidae		**2**	**2**
Ablennes hians		1	1
Platybelone argalus		1	1
Exocoetidae		**10**	**10**
Cheilopogon cyanopterus		1	1
Cheilopogon exsiliens		1	1
Cheilopogon furcatus		1	1
Cheilopogon melanurus		1	1
Exocoetus obtusirostris		1	1
Hirundichthys affinis		1	1

Hirundichthys rondeletii		1	1
Parexocoetus hillianus		1	1
Prognichthys gibbifrons		1	1
Prognichthys occidentalis		1	1
Hemiramphidae		**5**	**5**
Hemiramphus balao		1	1
Hemiramphus brasiliensis		1	1
Hyporhamphus		1	1
Oxyporhamphus micropterus		1	1
Oxyporhamphus similis		1	1
Incertae sedis in Eupercaria		15	15
Emmelichthyidae		**1**	**1**
Emmelichthys ruber		1	1
Latilidae		**2**	**2**
Caulolatilus cyanops		1	1
Lopholatilus chamaeleonticeps		1	1
Lutjanidae		**11**	**11**
Etelis oculatus		1	1
Lutjanus analis		1	1
Lutjanus campechanus		1	1
Lutjanus griseus		1	1
Lutjanus mahogoni		1	1
Lutjanus synagris		1	1
Ocyurus chrysurus		1	1
Pristipomoides aquilonaris		1	1
Pristipomoides freemani		1	1
Pristipomoides macrophthalmus		1	1
Rhomboplites aurorubens		1	1
Malacanthidae		**1**	**1**
Malacanthus plumieri		1	1
Acropomatiformes	2	12	14
Bathyclupeidae		**2**	**2**
Bathyclupea schroederi		1	1
Neobathyclupea argentea		1	1
Epigonidae	**1**	**5**	**6**
Brephostoma carpenteri		1	1
Epigonus denticulatus		1	1
Epigonus macrops	1		1
Epigonus pandionis		1	1
Epigonus pectinifer		1	1
Sphyraenops bairdianus		1	1
Howellidae	**1**	**1**	**2**
Bathysphyraenops simplex		1	1

Howella atlantica	1		1
Symphysanodontidae		**1**	**1**
Symphysanodon berryi		1	1
Synagropidae		**3**	**3**
Caraibops trispinosus		1	1
Parascombrops spinosus		1	1
Synagrops bellus		1	1
Syngnathiformes		11	11
Callionymidae		**2**	**2**
Synchiropus agassizii		1	1
Synchiropus goodenbeani		1	1
Centriscidae		**1**	**1**
Macroramphosus gracilis		1	1
Dactylopteridae		**1**	**1**
Dactylopterus volitans		1	1
Draconettidae		**1**	**1**
Centrodraco acanthopoma		1	1
Fistulariidae		**2**	**2**
Fistularia petimba		1	1
Fistularia tabacaria		1	1
Mullidae		**3**	**3**
Mulloidichthys martinicus		1	1
Pseudupeneus maculatus		1	1
Upeneus parvus		1	1
Syngnathidae		**1**	**1**
Hippocampus erectus		1	1
Notacanthiformes		8	8
Halosauridae		**7**	**7**
Aldrovandia affinis		1	1
Aldrovandia gracilis		1	1
Aldrovandia oleosa		1	1
Aldrovandia phalacra		1	1
Halosaurus guentheri		1	1
Halosaurus ovenii		1	1
Tiluropsis		1	1
Notacanthidae		**1**	**1**
Leptocephalus giganteus		1	1
Lampriformes		7	7
Lampridae		**1**	**1**
Lampris guttatus		1	1
Lophotidae		**1**	**1**
Lophotus lacepede		1	1
Radiicephalidae		**1**	**1**

Radiicephalus elongatus	1	1
Regalecidae	**1**	**1**
Regalecus glesne	1	1
Trachipteridae	**3**	**3**
Desmodema polystictum	1	1
Trachipterus arcticus	1	1
Zu cristatus	1	1
Holocentriformes	6	6
Holocentridae	**6**	**6**
Holocentrus	1	1
Myripristis jacobus	1	1
Neoniphon vexillarium	1	1
Ostichthys trachypoma	1	1
Sargocentron bullisi	1	1
Sargocentron coruscum	1	1
Trachichthyiformes	6	6
Anoplogastridae	**1**	**1**
Anoplogaster cornuta	1	1
Diretmidae	**3**	**3**
Diretmichthys parini	1	1
Diretmoides pauciradiatus	1	1
Diretmus argenteus	1	1
Trachichthyidae	**2**	**2**
Gephyroberyx darwinii	1	1
Hoplostethus mediterraneus	1	1
Zeiformes	6	6
Grammicolepididae	**2**	**2**
Grammicolepis brachiusculus	1	1
Xenolepidichthys dalgleishi	1	1
Parazenidae	**2**	**2**
Cyttopsis rosea	1	1
Parazen pacificus	1	1
Zeidae	**1**	**1**
Zenopsis conchifer	1	1
Zeniontidae	**1**	**1**
Zenion hololepis	1	1
Clupeiformes	5	5
Clupeidae	**2**	**2**
Dorosoma petenense	1	1
Sardinella aurita	1	1
Engraulidae	**2**	**2**
Anchoviella perfasciata	1	1
Engraulis eurystole	1	1

Spratelloididae		**1**	**1**
Jenkinsia		1	1
Kurtiformes		5	5
Apogonidae		**5**	**5**
Apogon aurolineatus		1	1
Apogon maculatus		1	1
Apogon pseudomaculatus		1	1
Astrapogon		1	1
Paroncheilus affinis		1	1
Scorpaeniformes		3	3
Peristediidae		**2**	**2**
Peristedion gracile		1	1
Peristedion miniatum		1	1
Triglidae		**1**	**1**
Triglidae		1	1
Cichliformes		3	3
Pomacentridae		**3**	**3**
Abudefduf saxatilis		1	1
Azurina cyanea		1	1
Stegastes partitus		1	1
Elopiformes		3	3
Elopidae		**2**	**2**
Elops saurus		1	1
Elops smithi		1	1
Megalopidae		**1**	**1**
Megalops atlanticus		1	1
Albuliformes		2	2
Albulidae		**2**	**2**
Albula goreensis		1	1
Albula vulpes		1	1
Saccopharyngiformes	1	1	2
Eurypharyngidae	**1**		**1**
Eurypharynx pelecanoides	1		1
Saccopharyngidae		**1**	**1**
Saccopharynx		1	1
Polymixiiformes		2	2
Polymixiidae		**2**	**2**
Polymixia lowei		1	1
Polymixia nobilis		1	1
Gobiiformes		1	1
Microdesmidae		**1**	**1**
Microdesmus		1	1
Pleuronectiformes		1	1

Cynoglossidae		**1**	**1**
Symphurus		1	1
Stylephoriformes		1	1
Stylephoridae		**1**	**1**
Stylephorus chordatus		1	1
Mugiliformes		1	1
Mugilidae		**1**	**1**
Mugil cephalus		1	1
Appendicularia		**2**	**2**
Copelata		2	2
Oikopleuridae		**2**	**2**
Mesochordaeus		1	1
Oikopleura		1	1
Chondrichthyes	**2**		**2**
Squaliformes	2		2
Dalatiidae	**2**		**2**
Isistius brasiliensis	1		1
Isistius plutodus	1		1
Thaliacea	**7**	**23**	**30**
Salpida	6	19	25
Salpidae	**6**	**19**	**25**
Brooksia rostrata		1	1
Cyclosalpa affinis		1	1
Cyclosalpa bakeri	1		1
Cyclosalpa danae	1		1
Cyclosalpa floridana	1		1
Cyclosalpa pinnata	1		1
Cyclosalpa polae	1		1
Helicosalpa virgula	1		1
Iasis cylindrica		1	1
Iasis zonaria		1	1
Ihlea punctata		1	1
Metcalfina hexagona		1	1
Pegea bicaudata		1	1
Pegea confederata		1	1
Ritteriella amboinensis		1	1
Ritteriella retracta		1	1
Salpa aspera		1	1
Salpa cylindrica		1	1
Salpa fusiformis		1	1
Salpa maxima		1	1
Thalia cicar		1	1
Thalia democratica		1	1

Thalia orientalis		1	1
Thetys vagina		1	1
Traustedtia multitentaculata		1	1
Pyrosomida	1	2	3
Pyrosomatidae	**1**	**2**	**3**
Pyrosoma atlanticum	1		1
Pyrostremma agassizi		1	1
Pyrostremma spinosum		1	1
Doliolida		2	2
Doliolidae		**2**	**2**
Dolioletta gegenbauri		1	1
Doliolina (Doliolinetta) intermedia		1	1
Arthropoda	**94**	**71**	**165**
Copepoda		**2**	**2**
Calanoida		2	2
Euchaetidae		**1**	**1**
Paraeuchaeta		1	1
Calanoida		**1**	**1**
Calanoida		1	1
Malacostraca	**93**	**69**	**162**
Decapoda	56	48	104
Acanthephyridae	**19**		**19**
Meningodora miccyla	1		1
Acanthephyra acanthitelsonis	1		1
Acanthephyra acutifrons	1		1
Acanthephyra brevirostris	1		1
Acanthephyra curtirostris	1		1
Acanthephyra eximia	1		1
Acanthephyra pelagica	1		1
Acanthephyra purpurea	1		1
Acanthephyra quadrispinosa	1		1
Acanthephyra stylorostratis	1		1
Ephyrina benedicti	1		1
Ephyrina ombango	1		1
Hymenodora glacialis	1		1
Hymenodora gracilis	1		1
Meningodora marptocheles	1		1
Meningodora mollis	1		1
Meningodora vesca	1		1
Notostomus elegans	1		1
Notostomus gibbosus	1		1
Aristeidae		**2**	**2**
Cerataspis monstruosus		1	1

Hepomadus tener		1	1
Benthesicymidae	**7**	**4**	**11**
Altelatipes carinatus		1	1
Amalopenaeus elegans	1		1
Bentheogennema intermedia		1	1
Benthesicymus carinatus		1	1
Benthoecetes bartletti		1	1
Gennadas bouvieri	1		1
Gennadas capensis	1		1
Gennadas propinquus	1		1
Gennadas scutatus	1		1
Gennadas talismani	1		1
Gennadas valens	1		1
Bresiliidae		**1**	**1**
Lucaya bigelowi		1	1
Disciadidae		**1**	**1**
Disciadidae		1	1
Hippolytidae		**1**	**1**
Latreutes fucorum		1	1
Luciferidae		**1**	**1**
Lucifer typus		1	1
Nematocarcinidae		**3**	**3**
Nematocarcinus cursor		1	1
Nematocarcinus ensifer		1	1
Nematocarcinus rotundus		1	1
Nephropidae		**1**	**1**
Nephropidae		1	1
Oplophoridae	**6**		**6**
Janicella spinicauda	1		1
Oplophorus gracilirostris	1		1
Oplophorus spinosus	1		1
Systellaspis braueri	1		1
Systellaspis cristata	1		1
Systellaspis debilis	1		1
Palaemonidae		**1**	**1**
Leander paulensis		1	1
Pandalidae	**2**	**8**	**10**
Plesionika edwardsii		1	1
Plesionika ensis		1	1
Plesionika holthuisi		1	1
Plesionika martia		1	1
Heterocarpus ensifer	1		1
Parapandalus	1		1

Plesionika polyacanthomerus		1	1
Plesionika richardi		1	1
Plesionika willisi		1	1
Stylopandalus richardi		1	1
Pasiphaeidae		**7**	**7**
Eupasiphae gilesii		1	1
Eupasiphae paucidentata		1	1
Eupasiphae serrata		1	1
Parapasiphae cristata		1	1
Parapasiphae sulcatifrons		1	1
Pasiphaea merriami		1	1
Pasiphaea princeps		1	1
Penaeidae		**5**	**5**
Funchalia villosa		1	1
Metapenaeus		1	1
Parapenaeus americanus		1	1
Penaeopsis serrata		1	1
Penaeus monodon		1	1
Physetocarididae		**1**	**1**
Physetocaris microphthalma		1	1
Scyllaridae		**1**	**1**
Scyllarides		1	1
Sergestidae	**19**	**4**	**23**
Acetes americanus		1	1
Allosergestes pectinatus	1		1
Allosergestes sargassi	1		1
Challengerosergia challengeri	1		1
Challengerosergia hansjacobi	1		1
Challengerosergia talismani	1		1
Cornutosergestes cornutus	1		1
Deosergestes corniculum	1		1
Deosergestes henseni	1		1
Deosergestes paraseminudus	1		1
Eusergestes arcticus	1		1
Gardinerosergia splendens	1		1
Neosergestes edwardsii	1		1
Parasergestes armatus	1		1
Parasergestes vigilax	1		1
Phorcosergia filicta	1		1
Phorcosergia grandis	1		1
Phorcosergia wolffi		1	1
Robustosergia regalis	1		1
Robustosergia robusta	1		1

Sergestes atlanticus	1		1
Sergia remipes		1	1
Sergia tenuiremis		1	1
Solenoceridae	**3**	**3**	**6**
Hadropenaeus affinis	1		1
Hymenopenaeus aphoticus	1		1
Hymenopenaeus debilis	1		1
Hymenopenaeus laevis		1	1
Mesopenaeus tropicalis		1	1
Pleoticus robustus		1	1
Stenopodidae		**1**	**1**
Stenopus		1	1
Pleocyemata		**3**	**3**
Achelata		1	1
Brachyura		1	1
Galatheoidea		1	1
Euphausiacea	32	2	34
Bentheuphausiidae		**1**	**1**
Bentheuphausia amblyops		1	1
Euphausiidae	**32**	**1**	**33**
Euphausia americana	1		1
Euphausia brevis	1		1
Euphausia gibboides	1		1
Euphausia hemigibba/pseudogibba	1		1
Euphausia krohnii	1		1
Euphausia mutica	1		1
Euphausia tenera	1		1
Nematobrachion boopis	1		1
Nematobrachion flexipes	1		1
Nematobrachion sexspinosum	1		1
Nematoscelis atlantica	1		1
Nematoscelis megalops	1		1
Nematoscelis microps	1		1
Nematoscelis tenella	1		1
Stylocheiron abbreviatum	1		1
Stylocheiron affine	1		1
Stylocheiron carinatum	1		1
Stylocheiron elongatum	1		1
Stylocheiron longicorne	1		1
Stylocheiron maximum	1		1
Stylocheiron robustum	1		1
Stylocheiron suhmi	1		1
Thysanoessa gregaria	1		1

Thysanopoda acutifrons	1		1
Thysanopoda aequalis	1		1
Thysanopoda cornuta		1	1
Thysanopoda cristata	1		1
Thysanopoda egregia	1		1
Thysanopoda monacantha	1		1
Thysanopoda obtusifrons	1		1
Thysanopoda orientalis	1		1
Thysanopoda pectinata	1		1
Thysanopoda tricuspidata	1		1
Lophogastrida	4	6	10
Eucopiidae		**4**	**4**
Eucopia australis		1	1
Eucopia grimaldii		1	1
Eucopia sculpticauda		1	1
Eucopia unguiculata		1	1
Gnathophausiidae	**4**		**4**
Fagegnathophausia gracilis	1		1
Gnathophausia zoea	1		1
Neognathophausia gigas	1		1
Neognathophausia ingens	1		1
Lophogastridae		**2**	**2**
Lophogaster		1	1
Pseudochalaraspidum hanseni		1	1
Amphipoda	1	6	7
Caprellidae		**1**	**1**
Caprellidae		1	1
Cystisomatidae		**1**	**1**
Cystisoma		1	1
Oxycephalidae		**1**	**1**
Oxycephalus clausi		1	1
Phronimidae		**1**	**1**
Phronima sedentaria		1	1
Phrosinidae		**1**	**1**
Phrosina semilunata		1	1
Pronoidae		**1**	**1**
Parapronoe crustulum		1	1
Scinidae	**1**		**1**
Scina curvidactyla	1		1
Mysida		3	3
Mysidae		**3**	**3**
Boreomysis		1	1
Coifmanniella mexicana		1	1

Gastrosaccinae		1	1
Isopoda		2	2
Cirolanidae		**1**	**1**
Bahalana geracei		1	1
Sphaeromatidae		**1**	**1**
Sphaeroma terebrans		1	1
Stomatipoda		1	1
Leptostraca		1	1
Nebaliidae/nebaliopsidae		**1**	**1**
Nebaliidae/nebaliopsidae		1	1
Ostacoda	**1**		**1**
Myodocopida	1		1
Cypridinidae	**1**		**1**
Vargula	1		1
Cnidaria	**145**	**6**	**151**
Anthozoa		**1**	**1**
Actiniaria		1	1
Cubozoa		**1**	**1**
Carybdeida		1	1
Carybdeidae		**1**	**1**
Tamoya haplonema		1	1
Hydrozoa	**131**	**4**	**135**
Siphonophorae	68		68
Abylidae	**11**		**11**
Abyla bicarinata	1		1
Abyla haeckeli	1		1
Abyla trigona	1		1
Abylopsis eschscholtzi	1		1
Abylopsis tetragona	1		1
Abylopsis trigona	1		1
Bassia bassensis	1		1
Ceratocymba dentata	1		1
Ceratocymba leuckarti	1		1
Ceratocymba sagittata	1		1
Enneagonum hyalinum	1		1
Agalmatidae	**13**		**13**
Agalma elegans	1		1
Agalma okenii	1		1
Erenna richardi	1		1
Halistemma amphytridis	1		1
Halistemma cupulifera	1		1
Halistemma foliacea	1		1
Halistemma maculatum	1		1

Halistemma rubrum	1	1
Halistemma striata	1	1
Halistemma transliratum	1	1
Marrus orthocanna	1	1
Melophysa melo	1	1
Nanomia bijuga	1	1
Apolemiidae	**1**	**1**
Apolemia	1	1
Clausophyidae	**2**	**2**
Chuniphyes moserae	1	1
Chuniphyes multidentata	1	1
Diphyidae	**15**	**15**
Chelophyes appendiculata	1	1
Dimophyes arctica	1	1
Diphyes bojani	1	1
Diphyes dispar	1	1
Eudoxoides mitra	1	1
Eudoxoides spiralis	1	1
Lensia exeter	1	1
Lensia fowleri	1	1
Lensia hotspur	1	1
Lensia multicristata	1	1
Muggiaea kochi	1	1
Sulculeolaria biloba	1	1
Sulculeolaria chuni	1	1
Sulculeolaria quadrivalvis	1	1
Sulculeolaria turgida	1	1
Forskaliidae	**1**	**1**
Forskalia contorta	1	1
Hippopodiidae	**5**	**5**
Hippopodius hippopus	1	1
Vogtia glabra	1	1
Vogtia pentacantha	1	1
Vogtia serrata	1	1
Vogtia spinosa	1	1
Physophoridae	**1**	**1**
Physophora hydrostatica	1	1
Prayidae	**11**	**11**
Amphicaryon acaule	1	1
Amphicaryon ernesti	1	1
Amphicaryon peltifera	1	1
Lilyopsis medusa	1	1
Maresearsia praeclara	1	1

Nectadamas diomedeae	1	1
Nectopyramis natans	1	1
Praya dubia	1	1
Praya reticulata	1	1
Rosacea cymbiformis	1	1
Rosacea plicata	1	1
Pyrostephidae	**4**	**4**
Bargmannia amoena	1	1
Bargmannia elongata	1	1
Bargmannia lata	1	1
Pyrostephos	1	1
Rhizophysidae	**2**	**2**
Bathyphysa conifera	1	1
Rhizophysa	1	1
Spaeronectidae	**1**	**1**
Sphaeronectes koellikeri	1	1
Stephanomiidae	**1**	**1**
Stephanomia amphytridis	1	1
Anthoathecatae	22	22
Bougainvilliidae	**4**	**4**
Bougainvillia carolinensis	1	1
Bougainvillia frondosa	1	1
Bougainvillia platygaster	1	1
Koellikerina fasciculata	1	1
Bythotiaridae	**9**	**9**
Bythotiara capensis	1	1
Bythotiara depressa	1	1
Calycopsis chuni	1	1
Calycopsis papillata	1	1
Calycopsis simulans	1	1
Calycopsis typa	1	1
Pseudotiara tropica	1	1
Protiaropsis anonyma	1	1
Protiaropsis minor	1	1
Corymorphidae	**1**	**1**
Corymorpha furcata	1	1
Oceaniidae	**1**	**1**
Oceania armata	1	1
Pandeidae	**4**	**4**
Halitholus intermedius	1	1
Cirrhitiara superba	1	1
Leuckartiara	1	1
Stomotoca	1	1

Proboscidactylidae	**1**		**1**
Proboscidactyla ornata	1		1
Zancleopsidae	**2**		**2**
Zancleopsis dichotoma	1		1
Zancleopsis undescribed TS1	1		1
Leptothecata	15	3	18
Aequoreidae	**5**		**5**
Aequorea forskalea	1		1
Aequorea globosa	1		1
Aequorea macrodactyla	1		1
Rhacostoma atlanticum	1		1
Zygocanna vagans	1		1
Campanulariidae	**2**		**2**
Clytia lomae	1		1
Clytia simplex	1		1
Eirenidae	**3**	**1**	**4**
Eirene pyramidalis	1		1
Eirene viridula		1	1
Eutima gracilis	1		1
Eutonina scintillans	1		1
Eucheilotidae	**1**		**1**
Eucheilota ventricularis	1		1
Laodiceidae		**1**	**1**
Laodicea brevigona		1	1
Malagazziidae	**1**		**1**
Tetracanna octonema	1		1
Melicertidae	**1**		**1**
Netocertoides brachiatum	1		1
Mitrocomidae	**1**		**1**
Mitrocomella	1		1
Orchistomatidae	**1**		**1**
Orchistoma pileus	1		1
Tiaropsidae		**1**	**1**
Octogonade		1	1
Trachymedusae	16	1	17
Geryoniidae	**2**		**2**
Geryonia proboscidalis	1		1
Liriope tetraphylla	1		1
Halicreatidae	**2**		**2**
Botrynema brucei	1		1
Halicreas minimum	1		1
Rhopalonematidae	**12**	**1**	**13**
Aglantha digitale	1		1

Amphogona apicata	1		1
Arctapodema ampla	1		1
Arctapodema antarctica	1		1
Benthocodon pedunculatus	1		1
Colobonema sericeum	1		1
Crossota alba	1		1
Crossota rufobrunnea	1		1
Pantachogon haeckeli	1		1
Pantachogon scotti	1		1
Rhopalonema funerarium		1	1
Rhopalonema velatum	1		1
Sminthea eurygaster	1		1
Narcomedusae	9		9
Aeginidae	**1**		**1**
Aegina citrea	1		1
Cuninidae	**4**		**4**
Cunina duplicata	1		1
Cunina frugifera	1		1
Cunina octonaria	1		1
Solmissus incisa	1		1
Solmarisidae	**4**		**4**
Pegantha martagon	1		1
Pegantha triloba	1		1
Solmaris flavescens	1		1
Solmaris solmaris	1		1
Limnomedusae	1		1
Olindiidae	**1**		**1**
Aglauropsis kawari	1		1
Scyphozoa	**14**		**14**
Coronatae	9		9
Atollidae	**2**		**2**
Atolla vanhoeffeni	1		1
Atolla wyvillei	1		1
Linuchidae	**1**		**1**
Linuche unguiculata	1		1
Nausithoidae	**3**		**3**
Nausithoe punctata	1		1
Nausithoe rubra	1		1
Nausithoe maculata	1		1
Paraphyllinidae	**1**		**1**
Paraphyllina ransoni	1		1
Periphyllidae	**2**		**2**
Periphylla periphylla	1		1

Periphyllopsis braueri	1		1
Semaeostomeae	5		5
Pelagiidae	**2**		**2**
Chrysaora quinquecirrha	1		1
Pelagia noctiluca	1		1
Ulmaridae	**3**		**3**
Aurelia aurita	1		1
Deepstaria reticulum	1		1
Tiburonia granrojo	1		1
Mollusca	**63**	**72**	**135**
Cephalopoda	**61**	**30**	**91**
Oegopsida	53	18	71
Ancistrocheiridae	**1**		**1**
Ancistrocheirus lesueurii	1		1
Architeuthidae		**1**	**1**
Architeuthis dux		1	1
Brachioteuthidae	**1**		**1**
Brachioteuthis	1		1
Chiroteuthidae	**7**	**2**	**9**
Asperoteuthis acanthoderma	1		1
Asperoteuthis sp. A	1		1
Chiroteuthis joubini	1		1
Chiroteuthis mega	1		1
Chiroteuthis spoeli	1		1
Chiroteuthis veranii	1		1
Grimalditeuthis bonplandi	1		1
Planctoteuthis danae		1	1
Planctoteuthis lippula		1	1
Cranchiidae	**13**		**13**
Bathothauma lyromma	1		1
Cranchia scabra	1		1
Egea inermis	1		1
Galiteuthis armata	1		1
Helicocranchia papillata	1		1
Helicocranchia pfefferi	1		1
Leachia atlantica	1		1
Leachia lemur	1		1
Liguriella podophthalma	1		1
Liocranchia reinhardti	1		1
Sandalops melancholicus	1		1
Taonius pavo	1		1
Teuthowenia megalops	1		1
Cycloteuthidae	**2**		**2**

Cycloteuthis sirventi	1		1
Discoteuthis discus	1		1
Enoploteuthidae	**6**		**6**
Abralia redfieldi	1		1
Abralia veranyi	1		1
Abraliopsis atlantica	1		1
Abraliopsis hoylei	1		1
Enoploteuthis anapsis	1		1
Enoploteuthis leptura	1		1
Histioteuthidae	**4**		**4**
Histioteuthis bonnellii	1		1
Histioteuthis corona	1		1
Histioteuthis reversa	1		1
Stigmatoteuthis arcturi	1		1
Joubiniteuthidae		**1**	**1**
Joubiniteuthis portieri		1	1
Lepidoteuthidae		**2**	**2**
Lepidoteuthis grimaldii		1	1
Pholidoteuthis adami		1	1
Lycoteuthidae	**5**		**5**
Lampadioteuthis megaleia	1		1
Lycoteuthis diadema	1		1
Lycoteuthis lorigera	1		1
Lycoteuthis springeri	1		1
Selenoteuthis scintillans	1		1
Magnapinnidae		**1**	**1**
Magnapinna pacifica		1	1
Mastigoteuthidae	**3**	**1**	**4**
Echinoteuthis atlantica	1		1
Magnoteuthis magna		1	1
Mastigopsis hjorti	1		1
Mastigoteuthis agassizii	1		1
Neoteuthidae		**3**	**3**
Narrowteuthis nesisi		1	1
Neoteuthis nesisi		1	1
Neoteuthis thielei		1	1
Octopoteuthidae	**3**		**3**
Octopoteuthis danae	1		1
Octopoteuthis megaptera	1		1
Taningia danae	1		1
Ommastrephidae	**4**		**4**
Hyaloteuthis pelagica	1		1
Ommastrephes bartramii	1		1

Ornithoteuthis antillarum	1		1
Sthenoteuthis pteropus	1		1
Onychoteuthidae	**1**	**5**	**6**
Moroteuthopsis ingens		1	1
Onychoteuthis banksii	1		1
Onykia aequatorialis		1	1
Onykia carriboea		1	1
Onykia ingens		1	1
Walvisteuthis jeremiahi		1	1
Pholidoteuthidae		**1**	**1**
Pholidoteuthis massyae		1	1
Pyroteuthidae	**3**		**3**
Pterygioteuthis gemmata	1		1
Pterygioteuthis giardi	1		1
Pyroteuthis margaritifera	1		1
Thysanoteuthidae		**1**	**1**
Thysanoteuthis rhombus		1	1
Octopoda	2	11	13
		1	**1**
Octopus undescribed HJ1		1	1
Alloposidae		**1**	**1**
Haliphron atlanticus		1	1
Amphitretidae	**2**		**2**
Bolitaena pygmaea	1		1
Japetella diaphana	1		1
Argonautidae		**1**	**1**
Argonauta argo		1	1
Octopodidae		**6**	**6**
Callistoctopus macropus		1	1
Macrotritopus defilippi		1	1
Octopus vulgaris		1	1
Pteroctopus tetracirrhus		1	1
Scaeurgus unicirrhus		1	1
Tetracheledone spinicirrhus		1	1
Ocythoidae		**1**	**1**
Ocythoe tuberculata		1	1
Tremoctopodidae		**1**	**1**
Tremoctopus violaceus		1	1
Bathyteuthoidea	2	1	3
Bathyteuthidae	**1**	**1**	**2**
Bathyteuthis abyssicola	1		1
Bathyteuthis devoleii		1	1
Chtenopterygidae	**1**		**1**

Chtenopteryx sicula	1		1
Sepioidea	2		2
Sepiolidae	**2**		**2**
Heteroteuthis dagamensis	1		1
Heteroteuthis dispar	1		1
Vampyromorpha	1		1
Vampyroteuthidae	**1**		**1**
Vampyroteuthis infernalis	1		1
Spirulida	1		1
Spirulidae	**1**		**1**
Spirula spirula	1		1
Gastropoda	**2**	**42**	**44**
Pteropoda		32	32
Cavoliniidae		**17**	**17**
Cavolinia gibbosa		1	1
Cavolinia inflexa		1	1
Cavolinia tridentata		1	1
Cavolinia uncinata		1	1
Cuvierina columnella		1	1
Diacavolinia constricta		1	1
Diacavolinia deblainvillei		1	1
Diacavolinia deshayesi		1	1
Diacavolinia flexipes		1	1
Diacavolinia limbata		1	1
Diacavolinia longirostris		1	1
Diacavolinia ovalis		1	1
Diacavolinia souleyeti		1	1
Diacavolinia strangulata		1	1
Diacavolinia vanutrechti		1	1
Diacria major		1	1
Diacria trispinosa		1	1
Cliidae		**5**	**5**
Clio andreae		1	1
Clio cuspidata		1	1
Clio polita		1	1
Clio pyramidata		1	1
Clio recurva		1	1
Creseidae		**2**	**2**
Creseis acicula		1	1
Styliola subula		1	1
Cymbuliidae		**4**	**4**
Corolla spectabilis		1	1
Cymbulia parvidentata		1	1

Cymbulia peronii		1	1
Gleba cordata		1	1
Desmopteridae		**1**	**1**
Desmopterus papilio		1	1
Limachinidae		**1**	**1**
Limacina		1	1
Peraclidae		**2**	**2**
Peracle bispinosa		1	1
Peracle reticulata		1	1
Littorinimorpha		8	8
Atlantidae		**1**	**1**
Oxygyrus inflatus		1	1
Carinariidae		**3**	**3**
Cardiapoda placenta		1	1
Carinaria lamarckii		1	1
Carinaria pseudorugosa		1	1
Pterotracheidae		**4**	**4**
Firoloida desmarestia		1	1
Pterotrachea coronata		1	1
Pterotrachea hippocampus		1	1
Pterotrachea scutata		1	1
Gymnosomata		2	2
Clionidae		**1**	**1**
Clione limacina		1	1
Cliopsidae		**1**	**1**
Cliopsis krohnii		1	1
Nudibranchia	2		2
Phylliroidae	**2**		**2**
Phylliroe bucephala	1		1
Phylliroe lichtensteinii	1		1
Ctenophora	**7**		**7**
Nuda	**4**		**4**
Beroida	4		4
Beroidae	**4**		**4**
Beroe cucumis	1		1
Beroe forskalii	1		1
Beroe mitrata	1		1
Beroe ovata	1		1
Tentaculata	**3**		**3**
Lobata	2		2
Bolinopsidae	**2**		**2**
Bolinopsis infundibulum	1		1
Mnemiopsis leidyi	1		1

Cydippida	1		1
Bathyctenidae	**1**		**1**
Bathyctena chuni	1		1
Chaetognatha	**1**	**4**	**5**
Sagittoidea	**1**	**4**	**5**
Aphragmophora		4	4
Sagittidae		**4**	**4**
Flaccisagitta enflata		1	1
Flaccisagitta hexaptera		1	1
Parasagitta megalophthalma		1	1
Sagitta		1	1
Phragmophora	1		1
Eukrohniidae	**1**		**1**
Eukrohnia bathypelagica	1		1
Annelida	**1**	**1**	**2**
Polychaeta	**1**		**1**
Phyllodocida	1		1
Tomopteridae	**1**		**1**
Tomopteris	1		1
Sipuncula		**1**	**1**
Sipuncula		1	1
Echinodermata	**1**		**1**
Holothuroidea	**1**		**1**
Elasiopodida	1		1
Pelagothuriidae	**1**		**1**
Enypniastes eximia	1		1
Hemichordata		**1**	**1**
Enteropneusta		**1**	**1**
Tornaria		1	1

Appendix Table 3. Numerical contributions to total bioluminescent per individuals (exclusions: ONSAP data and gelatinous zooplankton)

Taxonomic Distinction	No. Bioluminescent Individuals
FISHES	**28003**
Cyclothone pallida	12076
Cyclothone pseudopallida	3263
Cyclothone acclinidens	1502
Cyclothone alba	1337
Cyclothone braueri	1247
Cyclothone	825
Sternoptyx	613
Argyropelecus hemigymnus	605
Sternoptyx diaphana	564
Valenciennellus tripunctulatus	545
Lampanyctus alatus	498
Ceratoscopelus warmingii	471
Argyropelecus aculeatus	413
Benthosema suborbitale	317
Sigmops elongatus	317
Sternoptyx pseudobscura	263
Diaphus dumerilii	256
Lepidophanes guentheri	245
Chauliodus sloani	199
Notolychnus valdiviae	196
Vinciguerria poweriae	138
Pollichthys mauli	116
Hygophum taaningi	103
Diaphus mollis	99
Myctophum affine	94
Linophrynidae	88
Hygophum benoiti	78
Vinciguerria nimbaria	72
Notoscopelus resplendens	65
Lampanyctus	64
Photostomias guernei	58
Stomias affinis	54
Lobianchia gemellarii	54
Bolinichthys photothorax	49
Lampanyctus lineatus	48
Polyipnus clarus	43
Bonapartia pedaliota	37
Argyropelecus gigas	37

Diaphus	34
Diogenichthys atlanticus	33
Diaphus lucidus	32
Lampadena luminosa	31
Myctophidae	31
Diaphus splendidus	31
Hygophum hygomii	30
Cryptopsaras couesii	28
Hygophum macrochir	27
Eustomias	25
Bolinichthys supralateralis	24
Howella atlantica	24
Stomiidae	23
Oneirodidae	22
Taaningichthys bathyphilus	21
Maurolicus weitzmani	20
Margrethia obtusirostra	19
Stomiiformes	16
Astronesthes niger	15
Lampanyctus nobilis	15
Astronesthes macropogon	14
Platytroctidae	13
Coccorella atlantica	13
Lampanyctus cuprarius	12
Vinciguerria attenuata	11
Echiostoma barbatum	10
Aristostomias xenostoma	9
Bathophilus pawneei	9
Malacosteus niger	9
Leptostomias	9
Gonostoma atlanticum	9
Centrobranchus nigroocellatus	8
Haplophryne mollis	8
Argyropelecus affinis	8
Lestrolepis intermedia	8
Melanocetus johnsonii	7
Argyropelecus	7
Aristostomias	7
Lampanyctus ater	7
Ichthyococcus ovatus	7
Diaphus rafinesquii	7
Astronesthes similus	7
Photonectes leucospilus	7

Diaphus perspicillatus	7
Gonichthys cocco	7
Mentodus facilis	6
Melanocetus	6
Himantolophidae	6
Diaphus brachycephalus	6
Hygophum reinhardtii	6
Astronesthes richardsoni	5
Polyipnus	5
Astronesthes	5
Lampanyctus tenuiformis	5
Platytroctes apus	5
Oneirodes	5
Myctophum nitidulum	5
Bathophilus digitatus	4
Pseudoscopelus scutatus	4
Notoscopelus caudispinosus	4
Dasyscopelus selenops	4
Diaphus subtilis	4
Nezumia	4
Argyropelecus sladeni	4
Ceratias	4
Astronesthes undescribed TS1	3
Melanocetus murrayi	3
Dasyscopelus asper	3
Ceratias undescribed TS1	3
Lampanyctus festivus	3
Barbantus curvifrons	3
Diaphus taaningi	3
Diaphus termophilus	3
Eustomias fissibarbis	3
Lobianchia dofleini	3
Leptostomias bermudensis	3
Photostylus pycnopterus	3
Cyclothone microdon	3
Melanostomias tentaculatus	3
Taaningichthys	3
Pseudoscopelus altipinnis	2
Diaphus problematicus	2
Cyclothone parapallida	2
Stomias longibarbatus	2
Astronesthes gemmifer	2
Macrouridae	2

Oneirodes carlsbergi	2
Bathophilus proximus	2
Diplophos taenia	2
Idiacanthus fasciola	2
Eustomias schmidti	2
Chaenophryne draco	2
Diaphus fragilis	2
Symbolophorus rufinus	2
Eustomias acinosus	2
Flagellostomias boureei	2
Borostomias mononema	2
Pseudoscopelus scriptus	2
Dolopichthys	2
Astronesthes oligoa	2
Borostomias	2
Eustomias variabilis	2
Odontostomops normalops	2
Astronesthes micropogon	2
Gigantactis microdontis	2
Centrophryne spinulosa	2
Holtbyrnia	2
Chauliodus danae	1
Malacocephalus occidentalis	1
Maulisia	1
Vinciguerria	1
Lophodolos indicus	1
Linophryne	1
Xenodermichthys copei	1
Oneirodes theodoritissieri	1
Photonectes margarita	1
Lestidium atlanticum	1
Photonectes achirus	1
Leptostomias gladiator	1
Epigonus macrops	1
Hygophum	1
Photonectes	1
Oneirodes macrosteus	1
Hymenocephalus italicus	1
Melanostomias	1
Gigantactis gargantua	1
Himantolophus	1
Taaningichthys minimus	1
Oneirodes eschrichtii	1

Aristostomias polydactylus	1
Bathophilus longipinnis	1
Eustomias brevibarbatus	1
Diaphus effulgens	1
Lampadena anomala	1
Bathophilus brevis	1
Isistius brasiliensis	1
Spiniphryne gladisfenae	1
Dolopichthys pullatus	1
Haplophryne	1
Ceratioidea	1
Gonostomatidae	1
Photocorynus spiniceps	1
Taaningichthys paurolychnus	1
Photostomias goodyeari	1
CRUSTACEANS	**20678**
Euphausiidae	2021
Nematoscelis atlantica/microps	1925
Gennadas valens	1885
Gennadas	1182
Thysanopoda obtusifrons/aequalis	1127
Allosergestes pectinatus	878
Gardinerosergia splendens	868
Thysanopoda acutifrons/orientalis	730
Thysanopoda tricuspidata	660
Stylocheiron abbreviatum	572
Acanthephyra stylorostratis	563
Sergestidae	551
Euphausia gibboides	496
Systellaspis debilis	478
Nematobrachion boopis	466
Nematobrachion flexipes	377
Oplophoridae	330
Gennadas capensis	313
Neosergestes edwardsii	310
Sergestes atlanticus	308
Hymenodora gracilis	287
Parasergestes vigilax	274
Acanthephyra purpurea	263
Stylopandalus richardi	247
Allosergestes sargassi	237
Nematoscelis microps	227
Acanthephyra curtirostris	183

Deosergestes corniculum	181
Nematobrachion sexspinosum	177
Deosergestes henseni	176
Robustosergia regalis	137
Thysanopoda monacantha	128
Nematoscelis atlantica	125
Sergestes	124
Stylocheiron maximum	111
Parasergestes armatus	105
Gennadas scutatus	104
Thysanopoda pectinata	95
Gennadas bouvieri	95
Phorcosergia grandis	95
Thysanopoda aequalis	65
Notostomus gibbosus	63
Euphausia mutica	61
Janicella spinicauda	60
Oplophorus spinosus	58
Challengerosergia hansjacobi	57
Challengerosergia talismani	52
Acanthephyra brevirostris	51
Nematoscelis tenella	50
Robustosergia robusta	45
Acanthephyra acutifrons	43
Stylocheiron robustum	42
Notostomus elegans	36
Thysanopoda	34
Thysanopoda orientalis	34
Thysanopoda acutifrons	33
Acanthephyra	33
Oplophorus gracilirostris	32
Meningodora vesca	31
Euphausia hemigibba/pseudogibba	30
Gennadas talismani	25
Gnathophausia zoea	25
Meningodora mollis	25
Ostracoda	23
Neognathophausia ingens	22
Ephyrina ombango	22
Thysanopoda obtusifrons	15
Gnathophausiidae	14
Ephyrina benedicti	14
Calanoida	13

Systellaspis cristata	13
Hymenopenaeus debilis	11
Nematobrachion	11
Hymenodora	9
Stylocheiron	9
Nematoscelis	9
Acanthephyra acanthitelsonis	8
Neonathophausia gigas	7
Acanthephyra quadrispinosa	6
Notostomus	6
Thysanopoda cristata	6
Euphausia	6
Ephyrina	6
Fagegnathophausia gracilis	5
Cornutosergestes cornutus	5
Stylocheiron elongatum	5
Paraeuchaeta	5
Thysanopoda egregia	4
Euphausia tenera	4
Meningodora miccyla	4
Parasergestes armatus	3
Scina	3
Vargula	3
Stylocheiron longicorne	2
Amalopenaeus elegans	2
Systellaspis braueri	1
Meningodora marptocheles	1
Sergia	1
Euphausia brevis	1
Systellaspis	1
Thysanoessa gregaria	1
Deosergestes paraseminudus	1
CEPHALOPODS	**384**
Japetella diaphana	53
Pterygioteuthis	48
Vampyroteuthis infernalis	41
Cranchia scabra	25
Bolitaena pygmaea	23
Pterygioteuthis gemmata	20
Pyroteuthis margaritifera	14
Helicocranchia pfefferi	10
Bolitaenidae	9
Abralia redfieldi	9

Selenoteuthis scintillans	8
Histioteuthidae	8
Stigmatoteuthis arcturi	7
Histioteuthis corona	7
Cycloteuthis sirventi	7
Mastigoteuthis agassizii	7
Grimalditeuthis bonplandi	7
Octopoteuthis	5
Abraliopsis atlantica	5
Chiroteuthidae	4
Taoniinae	4
Leachia atlantica	4
Helicocranchia	4
Heteroteuthis	3
Cranchiidae	3
Ornithoteuthis antillarum	3
Sandalops melancholicus	2
Onychoteuthis	2
Echinoteuthis atlantica	2
Mastigopsis hjorti	2
Taningia danae	2
Chiroteuthis mega	2
Ancistrocheirus lesueurii	2
Abralia	2
Enoploteuthis	2
Enoploteuthidae	2
Onychoteuthis banksii	2
Ommastrephidae	2
Bathothauma lyromma	1
Spirula spirula	1
Abraliopsis	1
Lycoteuthis lorigera	1
Pyroteuthis margaritifera	1
Lycoteuthidae	1
Galiteuthis armata	1
Discoteuthis discus	1
Chiroteuthis	1
Heteroteuthis dagamensis	1
Brachioteuthis	1
Cycloteuthidae	1
Sthenoteuthis pteropus	1
Liguriella podophthalma	1
Asperoteuthis sp. A	1

Teuthowenia megalops	1
Pterygioteuthis giardi	1
Chiroteuthis veranyi	1
Octopoteuthis megaptera	1
Mastigoteuthidae	1
Enoploteuthis anapsis	1
Histioteuthis	1