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Shining a Light on Fish at Night: An Overview of Fish and Fisheries in the Dark of Night, and in Deep and Polar Seas

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introduction

Shining a light on fish at night: an overview of fish and fisheries in the dark of night, and in deep and polar seas

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ABSTRACT.—In aquatic environments, what one observes during the day can differ substantially by night. The species composition and associated ecological processes that occur during the day are often different than night. In polar seas and at great depths, "night" can span, months, years, and beyond. Teleosts and elasmobranchs have evolved unique sensory and behavioral modalities for living in darkness. As a consequence, fishers have adopted unique strategies for exploiting fish at night or in dark systems. We propose that neglecting the night has led to an incomplete understanding of aquatic organismal ecology, population/community dynamics, and ecosystem function with consequences for fisheries conservation management. To address this knowledge gap and stimulate the exchange of new data and ideas on behaviors, patterns, and processes relating to fish and fisheries in darkness, Fish at Night: an International Symposium was held in Miami, Florida (USA), from 18 to 20 November, 2015. Here, we synthesize the findings from the symposium, providing an overview on the state-of-knowledge of fish studies in the dark, identifying critical information gaps, and charting a course for future research. We focus our commentary and synthesis on six areas: (1) nocturnal fish behavior and ecology; (2) fishing, fisheries, and enforcement; (3) deep and polar seas; (4) diel fish distribution and abundance comparisons; (5) methods for studying fish in darkness; (6) human threats to fish at night; and (7) larval fish at night. Taken together, we attempt to "shine a light" on fish at night, generating a greater interest and understanding of fishes and fisheries during darkness.

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As the sun sets, most aquatic researchers pack up their gear and head home from the field. Yet this is precisely the time when many fish are most active. Indeed, some of the planet's greatest migrations occur at night when organisms rise toward the surface, creating massive pulses of biodiversity and biomass. In nearly every aquatic environment, from pelagic waters to coral reefs to headwater streams, what one observes by day can differ markedly from what is happening under the cover of darkness. In polar seas, "night" can span months, and in deep seas and caves, it is perpetually "night." Fish and fishers in these dark systems have adopted tactics and strategies that take advantage of low-light conditions. Although it is generally recognized that the activity of fish (teleosts and elasmboranchs) at night differs from the day, studies of fish and fisheries in the dark are relatively limited as is our understanding of these processes. This shortfall is primarily due to the logistical and technological challenges of working at night in aquatic environments and the difficulties in interpreting community dynamics that can differ significantly at night and in polar and deep seas.

There is growing evidence that night may be the most ecologically relevant time period for many aquatic organisms, and that deep and polar seas are unique biological hotspots. Consequently, fish in darkness can be vulnerable to human threats, which are rarely considered in fisheries management, such as light pollution. Thus, failure to take these processes into account may lead to an incomplete understanding of fish ecology, physiology, behavior, community dynamics, and ecosystem function with profound consequences for conservation. However, recent technological advances and research developments have provided an opportunity to "shine a light on fish at night," improving our understanding of the biology, ecology, management, and conservation of fish in the dark.

Fish at Night: an International Symposium was held in Miami, Florida (USA), from 18 to 20 November, 2015. This was the first organized international meeting devoted to understanding fish and fisheries in the dark. The overall goal of the symposium was to stimulate the exchange of new knowledge, data, and ideas on behaviors, patterns, and processes relating to fish and fisheries operating underwater in darkness. Symposium themes included: (1) nocturnal fish behavior and ecology; (2) night fishing, fisheries, and enforcement; (3) deep and polar seas ("perpetual night") fish and fisheries; (4) diel fish distribution and abundance comparisons; (5) methods for studying fish in darkness; (6) human threats to fish at night; and (7) larval fish at night.

The symposium attracted high quality presentations from countries around the world, including contributions from industry, government, and academic institutions. The results of the symposium are published in this special issue of the *Bulletin of Marine Science*. Here, we summarize the symposium findings and provide an overview of the current state of knowledge regarding fish studies in the dark. This information is presented in the following sections: (1) methods for studying fish in darkness; (2) sensory physiology and life in the dark; (3) nocturnal fish behavior and ecology, (4) polar seas, (5) deep seas, (6) diel fish distribution and habitat use; (7) larval fish at night; (8) human threats to fish at night; and (9) night fishing, fisheries, and enforcement. Taken together with the other papers in this special issue, we detail new research developments and research prospects, identify critical knowledge gaps, and provide a framework for understanding fish and fisheries in the dark.

Methods for Studying Fish in Darkness

Our earliest insights into the nocturnal habits of fish come from observations made by fishers. For example, the second-century Greco-Roman poet Oppian described fishers who concluded that parrotfish [*Sparisoma cretense* (Linnaeus, 1758)] sleep at night because they are never caught in fishing nets during the hours of darkness (Mair 1928). Sampling at night using fishing gears or related scientific devices such as plankton trawls (Bowen and Sutton this issue), or light traps (Kough et al. this issue) remains an important method both for determining patterns of fish occurrence and abundance (Bangley and Rulifon this issue, Chiappa-Carrara this issue), and also for obtaining information on feeding and reproductive status of fishes (Reubens et al. 2014, Koenig et al. this issue), and is increasingly being combined with newer sampling technologies to provide a more detailed understanding of the ecology of fish at night (Reubens et al. 2014).

Insights from fisheries and other direct observations by humans (Verrill 1897) continued to be the dominant source of information on fish behavior during the hours of darkness until the mid-twentieth century when a new era of remote observation of fish began with the accidental discovery of the deep scattering layer (DSL) by sonar scientists during World War II (Duvall and Christensen 1946). The DSL results from sonar bouncing off the swim bladders of mesopelagic fish, whose diel vertical migrations result in the cyclic rise and fall of this layer in the water column (Barham 1966). Subsequent decades have seen substantial development and refinement of sonar systems for surveying fish in both marine and fresh water (Petreman et al. 2014, Bollinger and Kline 2015), and more recently, the application of airborne lidar for this purpose (i.e., using laser light instead of sound, Churnside et al. this issue). For smaller individuals [≤12 cm total length (TL)], the use of sonar systems remains a primary method for remotely studying their abundance and movements because they are too small to carry most current models of electronic telemetry tags. Sophisticated, high-resolution multi-beam sonar devices (e.g., DIDSON and ARIS, Fig. 1) now function as acoustic cameras producing near-video quality images of fish in dark and turbid waters (McCauley et al. 2014). With the advent of underwater, broad-spectrum acoustic recorders, the sounds made by fish themselves can also provide clues to their activities at night or in deep waters below the photic zone (Koenig et al. this issue, Ricci this issue, Rice this issue, Spence this issue).

Light-based camera systems have also been used to study fish in darkness (Goebel et al. this issue a,b, Milisen this issue), although challenges remain in illuminating the visual field without altering the behavior of fish present (Whitmarsh et al. this issue). The most widely used systems for scientific purposes are various forms of drop-cam, which record a fixed-field of view at their deployment location, but mobile cameras have also been used successfully to observe fish in darkness, variously carried by divers (Milisen this issue), or deployed on submersibles (Stoner et al. 2008), remotely operated vehicles (Lorance and Trenkel 2006), autonomous underwater vehicles (Seiler et al. 2012), or on fishes themselves (Nakamura et al. 2015a,b). Camera systems capable of recording in far red light beyond the visual spectrum of fish may have the lowest impact on fish behavior in dark environments (Whitmarsh et al. this issue).

The development of telemetry and biologging technology over the last five decades has provided a growing suite of tools for studying fish in darkness. These devices

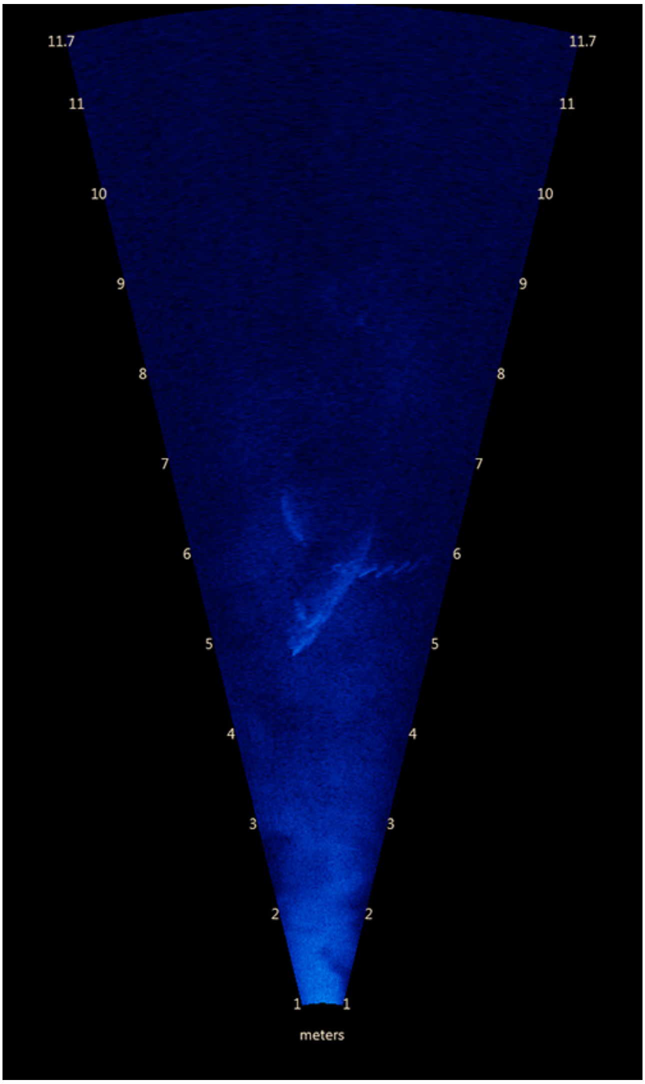


Figure 1. High resolution sonar image of a white shark [*Carcharodon carcharias* (Linnaeus, 1785)] at night using ARIS imaging sonar (Sound Metrics).

range from simple acoustic pingers for manually tracking the movements of individual fish (Lonsdale and Baxter 1968, Meyer and Holland 2005), to autonomous arrays of receivers for tracking long-term movements of multiple individuals (Bangley and Rulifon this issue, Hammerschlag et al. this issue, Stump this issue), and multi-sensor, data-logging devices capable of providing high-resolution insights into fish activity levels, swimming patterns, body orientation, spatial dynamics, and habitat use (Nakamura et al. 2011, 2015a,b). Some of these devices (except acoustic tags and small biologgers) are currently too large for use on fish ≤15 cm TL, but ongoing miniaturization of batteries and electronics is greatly reducing the size of telemetry devices, making them more suitable for use on smaller fish (e.g., Hussey et al. 2015, Meyer this issue).

Beyond simple positioning, the capabilities of telemetry tags are determined by their onboard sensors. For several decades, telemetry tags have been capable of quantifying depth and temperature (Carey et al. 1982), and newer generations of devices also quantify ambient light levels, swimming speed, tri-axial acceleration, compass bearing, and dissolved oxygen concentration (Nakamura et al. 2011, 2015a, Coffey and Holland 2015). These sensors collectively quantify the fish' physical environment and behavioral responses, but with the exception of intramuscular thermistors (Carey et al. 1982, Nakamura et al. 2015b), good tools for remotely studying the physiology of free-ranging fish in their natural habitats are lacking.

Where field studies are not possible, gaps in our understanding of the influence of darkness on fish can be filled by carefully-designed laboratory experiments, where a variety of tools can be used to measure physiological and genomic responses of fish under natural or artificial light-dark cycles (López-Olmeda et al. 2013, Lazado et al. 2014, Kopperud and Grace this issue). Overall, studying fish at night and in deep waters is becoming easier as technology advances and the number of tools available to researchers increases, but significant challenges remain in extending telemetry studies to the smallest fish, ground-truthing remotely-sensed data, and measuring physiological responses of fish in their natural habitats.

Sensory Physiology and Life in the Dark

Why some fishes evolve to be nocturnally active, while others do not, remains unknown. Such a knoweldge gap in our understanding of fish circadian rhythms is largely due to challenges of quantifying diel activity patterns of fish across environments, which has led to phylogentic and geographic sampling biases (Dornburg et al. this issue). However, what is becoming apparent from recent research regarding the behavior and ecology of nocturnal fishes, is that these animals require a suite of sensory adaptations for being nocturnally active. Fish, like all animals, utilize a variety of sensory information to modulate physiology and behavior in context-relevant manners. Visual, chemical, pressure, tactile, thermal, and electromagnetic cues generate reflexive responses that drive decision-making in scenarios, including conspecific recognition, mate finding and reproduction, prey localization and targeting, predator avoidance, navigation, selection of appropriate habitat, and identification and utilization of refugia. While different types of sensory information are conveyed to the central nervous system by distinct neural channels, sensory information streams of distinct modalities often merge in the brain, providing a comprehensive analysis of the external world that underlies reflexive responses and effective decision-making.

Vision is an image-forming system that begins with photoreceptor cells (rods and cones) in the retina, and visual information ultimately projects to a region of the fish brain known as the optic tectum, where a spatial representation of the world is created. That is, the optic tectum literally contains a functional, real-time map of visual space. In addition, fish possess non-visual light-detecting cells that provide information to a variety of neural systems that regulate complex behavior and physiology; these include circadian timing systems that regulate daily rhythms, and light serves to keep slightly imprecise biological clocks synchronized with real-world time (Kopperud and Grace this issue).

All aspects of the visual system are subject to adaptation, beginning with the anatomical features of eyes. Schmitz and Wainwright (2011) examined ocular optical characteristics of 256 species of marine fish that occupied either a diurnal or a nocturnal niche, and found that nocturnal species exhibit significantly less divergence in measured optical characteristics than diurnal species. Just as the array of diurnal fish species exhibit much greater trophic diversity than do nocturnal species, they also express a higher diversity of morphological and optical characteristics. This should not be surprising given the tremendous range of photic microhabitats available to diurnal species. On the other hand, nocturnal species (constrained under natural conditions to very low ambient light levels) exhibit larger eye size relative to body size than do diurnal species, relatively large lenses, and generally more circular pupils than diurnal species possess (Schmitz and Wainwright 2011), all of which would be predicted (Schmitz and Motani 2010), as all serve to enhance light-gathering capacity under scotopic conditions. Moreover, the range of variability in these characteristics is narrower in nocturnal vs diurnal species, suggesting that activity in the dark constrains ocular diversity to maximize light sensitivity (Schmitz and Wainwright 2011).

Similarly, the retinas of fish are also remarkably varied, including the functional characteristics of retinal photoreceptor arrays. Some fish retinas contain as few as one or two classes of visual photoreceptor cells, to systems with rods and at least five types of cone photoreceptors. This extensive variation correlates with the complexity of light environments in aquatic habitat; light intensity and spectrum vary tremendously with depth, turbidity, and dissolved materials (Jerlov 1976). The opsin proteins that detect light in retinal photoreceptors provide further variation, with different sets of opsins providing different ranges of spectral (color) sensitivity. Through gene duplications and amino-acid-substituting point mutations, extant fishes (particularly teleosts) possess a diversity of opsin genes and, therefore, spectral sensitivities that may be unmatched by any other vertebrate animal group (Hofman and Carleton 2009). This genetic diversity is reflected in the diversity of light-detecting systems, the constructs of which correlate with the qualities of available light in fish habitats. Deep sea fishes have few opsins (often only one), while littoral species possess a variety of opsins, the spectral sensitivities of which are aligned with the spectrum of light available in the local environment (Loew and Lythgoe 1978, Partridge et al. 1989).

Even greater diversity in retinal function is provided by the remarkable ability of fish nervous systems, including the retina, to change over the course of time. In elopomorph fishes, for example, retinal light detection capability changes in dramatic ways over the course of development (Taylor et al. 2011, 2015). As elopomorphs (and likely many other species) migrate to new, optically distinct aquatic habitats over the course of development, new photoreceptor cells and opsin proteins emerge on the retina. Ultimately, fish may develop a variety of species-specific retinal specializations, including light-reflective tapeta, spectral profiles of light harvesting photoreceptor cells, stacked and bundled photoreceptors that enhance photon capture, and retinomotor movements, that provide effective vision even in very low-light conditions (Grace and Taylor this issue). Retinal changes in elopomorph species appear to happen in correlation with habitat shifts (Taylor and Grace 2005, Taylor et al. 2011, 2015), and preliminary evidence suggests that both genetic and environmental factors may drive these changes (Taylor et al. 2015). The possibility that environment plays a role in retinal form and function has important implications for conservation of fish in the face of climate change, and other natural and anthropogenic changes that can profoundly alter light intensity and spectrum in aquatic environments.

Light is used not only for seeing, but through a series of parallel neural pathways, it also drives daily and seasonal changes in the functional biology of fishes. For example, in fish and other vertebrates, some of these parallel light-processing pathways feed back to the eye, thereby regulating pupil diameter. Regulation of pupil diameter provides vertebrate animals the ability to adjust light intensity at the retina under varying lighting conditions, and it also modulates visual resolution and depth of field. Interestingly, while some fishes have strong pupillary responses to light (Douglas et al. 1998), many others have little or none. The significance of this variation is unknown.

Perhaps the most broadly important non-visual function of light in fish is the regulation of timed activities, including daily and seasonal rhythms. Because the daily light-dark cycle is among the most reliable temporal signals (certainly the most reliable daily signal), all vertebrate taxa possess well-developed circadian timing systems that produce a wide variety of important daily changes in physiology and behavior. Locomotor activity, the daily activity-rest cycle, feeding, and a host of other processes are regulated not only by direct sensory input from the environment, but also by internal biological timekeeping mechanisms (Menaker 1969). Light's role in regulating daily rhythms is to synchronize these internal clocks with the daily light-dark cycle, and it does so through pathways completely distinct from those used for vision. In fact, non-mammalian vertebrates, including fish, contain a variety photoreceptors and biological clocks in distinct regions of the central nervous system and elsewhere (Whitmore et al. 1998). Light-regulated biological clocks control not only daily changes in behavior and physiology (Kopperud and Grace this issue), but also photoperiodic timing of fish reproduction (Duston and Bromage 1986), which may be utilized to artificially control maturation and thus enhance reproductive output of fish in captivity (Bromage et al. 1992, Taranger et al. 2010).

Alteration of the natural light environment may have profoundly important effects on fish and other vertebrates. Changes in water quality because of eutrophication, pollution, storms, and temperature alteration can produce changes in the optical qualities of water that may affect the health and normal function of fishes. Decreased water clarity and changes in the spectrum of available light may decrease food and mate-finding abilities that may ultimately lead to reduced fecundity, death, or forced movement to new habitats that maintain suitable optical conditions. In addition to the quality of available light, the timing of light availability also has important effects on fish. Exposure to light at inappropriate times, for example in developed coastal regions, may alter the timing of important daily and seasonal events, which in turn may harm the health and fecundity of fish. Conversely, manipulation of light quality and the timing of light cycles in aquaculture situations may be used to increase reproductive output, enhance growth rates, and prepare aquaculture-raised fish for release into the wild (Bromage et al. 2001).

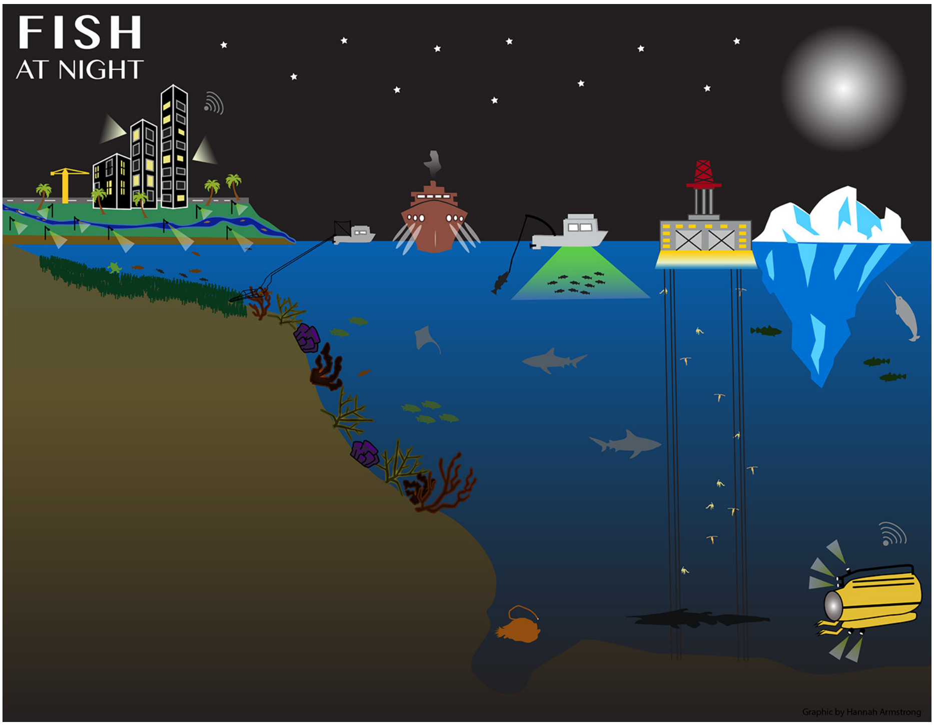
Nocturnal Fish Behavior and Ecology

While it has long been recognized that many fishes are nocturnal, the behavior and ecology of fish at night remains relatively understudied. This is largely due to the logistical and technological challenges of studying fish in darkness. Among the first empirical field research focused on nocturnal fish behavior and ecology was dedicated to documenting and understanding foraging migrations of reef fish at night (e.g., Hobson 1973, 1974, Ogden and Buckman 1973). Much of this early comprehensive work on fish behavior at night was summarized in Helfman (1986). This paper focused primarily on direct observations of fish behavior in the wild, particularly related to changes in ambient light levels. Studies explicitly investigating the nocturnal behavior and ecology of fishes since this seminal paper by Helfman (1986) have been diffuse, but increasing due in large part to technological advances. This work, including the research reported in this symposium proceedings, have generated the following two primary insights. First, nocturnal behaviors among fishes are highly variable. Not only can these patterns differ among species, but they can also vary within a species and among life-stages, as well as between and within habitats (e.g., Bangley and Rulifon this issue). Second, for fishes that are nocturnally active, failure to conduct nocturnal sampling can significantly overlook key aspects of their behavior and ecology, with implications for ecosystem processes and conservation (e.g., Sikkel et al. this issue).

Based on available data, aspects of fish behavior and ecology that are most likely to be influenced by night include foraging, predation, and reproduction. For example, snappers and grunts will leave the safety of coral reef refuges at night to feed in shallow seagrass beds on the invertebrates that emerge there at night (Goebel et al. this issue a,b). While such seagrass habitats have typically been considered nursery areas for juvenile fish, characterized by high food availability and low predation risk, recent research suggests that predation risk to juvenile fish from larger fish at night may be significant and thus juvenile fish experience food-risk trade-offs by foraging within these habitat at night (Hammerschlag et al. 2010a,b). However, the occurrence of fish predators in these seagrass habitats can vary by species, life-stage and even distance from shore (Goebel et al. this issue a,b). It is likely that such predator-prey interactions and associated food-risk trade-offs will vary by season and also according to moon phase, given that increased lunar illumination could affect the ability of predators to detect prey and vice versa (Mougeot and Bretagnolle 2000, Penteriani et al. 2011, Prugh and Golden 2014).

For some fishes, night time may be particularly important for reproduction, especially for those species that time their nocturnal spawning activities with lunar phases. While many species of fish have been found to spawn during full moon periods (e.g., Koenig et al. this issue), Atlantic goliath grouper [*Epinephelus itajara* (Lichtenstein, 1822)] spawn at night during new moon periods (dark-night spawning) (Koenig et al. this issue). It is possible that dark-night spawning may be an adaptation for minimizing egg predation by smaller fish (Koenig et al. this issue). However, there remain few studies that have revealed the drivers underlying spatial and temporal differences in nocturnal spawning events by fish.

Nocturnal fish migration is common in coral reef associated species. It is widely assumed that such movement is related to increased food or decreased predation risk. Sikkel et al. (this issue) show that nocturnal migrations of French grunt [*Haemulon flavolineatum* (Desmarest, 1823)], from coral reefs to neighboring seagrass beds, could be a mechanism to reduce exposure to blood-feeding gnathiid isopods. As a direct or indirect consequence of parasitism, French grunt populations may indirectly alter trophic connectivity between habitats (Sikkel et al. this issue). Moreover, when French grunts move from reefs to seagrass beds at night, some gnathiids are



Graphic by Hannah Armstrong

Figure 2. Infographic demonstrating human-driven threats to fish at night or in deep and polar seas, including coastal, industrial or boat-based light and noise pollution, sedimentation and nutrient runoff, fishing, habitat destruction, climate change, as well as deep and polar sea research exploration, oil drilling, and mining.

deposited in the seagrass, which may provide another base food source for trophic transfer up the food web by other species (Sikkel et al. this issue).

Emerging research is revealing that the nocturnal behaviors of fish can be altered in numerous ways by humans, either directly or indirectly. These anthropogenic factors can include light pollution (discussed further below), noise, tourism, sedimentation, habitat degradation, and fishing (Fig. 2). For example, whitetip reef sharks [*Triaenodon obesus* (Rüppell, 1837)] are normally nocturnally active, but show increased levels of diurnal vertical activity at dive sites during daytime provisioning tourism operations (Fitzpatrick et al. 2011), which can have negative consequences for their energy budgets (Barnett et al. 2016). Additionally, overfishing and subsequent declines of large diurnal predators on coral reefs can result in a shift in diel activity pattern of fishes, with nocturnal fish becoming more abundant during daylight hours (McCauley et al. 2012).

While nocturnal fisheries and management is discussed in a separate section below, it is worth considering how diel changes in the behavior and ecology of invasive species can affect efforts to control their populations. For example, lionfish (*Pterois* spp.) are invasive within the western Atlantic Ocean, with potentially marked impacts on coral reef fishes and their habitats. There are several efforts underway to both evaluate the ecosystem impacts of lionfish, as well as eradicate these invasive fish. However, these efforts rely primarily upon diurnal observations and removals from the reef. McCallister et al. (this issue) have revealed that lionfish are most active during crepuscular periods when they emerge from coral refuges to forage. Accordingly, diurnal observations of lionfish may thus underestimate their ecological impacts on coral reefs. As such, eradication efforts for this species may be most effective if conducted during crepuscular periods when lionfish emerge from shelter and are most active. Eradication efforts using capture methods may need to account for diel differences in catchability.

There has been a significant amount of recent research focused on determining "essential fish habitat" and associated habitat-specific secondary production rates of fish for conservation and management purposes (Beck et al. 2001, Mumby et al. 2004, Valentine-Rose et al. 2007). However, these secondary production estimates are based mostly on diurnal sampling during which many fish occupy refuges in a single habitat (e.g., mangroves or coral reefs). However, increasing nocturnal sampling is revealing that many fishes leave refuges at night to feed where they may use multiple habitats (coral reefs, mangroves, and seagrasses). Therefore, attributing secondary production to a single habitat based on diurnal sampling alone may be flawed (Hammerschlag and Serafy 2010). Thus, for identifying essential fish habitats and/or for generating estimates of habitat-specific secondary production, nocturnal sampling is needed for fishes that are active at night (Hammerschlag and Serafy 2010).

Diel Patterns of Fish Distribution and Habitat Use

Nocturnal movements of fishes are well known by recreational and commercial fishers who target certain species at night, often catching larger fish of commercially and recreational important species than they would during the day (Diogo and Pereira 2016, Cooke et al. this issue, Blankinship et al. this issue). Nocturnal teleosts and elasmobranchs represent approximately one third of the fish within any ecosystem (Helfman 1978, 1986), but in some habitats, such as tropical mangroves, they can represent over half (57%) of the species present and approximately 75% of the fish abundance (Ley and Halliday 2007). However, the majority of studies on the distribution, abundance, and habitat use of fish are based on diurnal sampling (but see Rooker et al. 1997, Annese and Kingsford 2005, Azzurro et al. 2007, Holzman et al. 2007, Hammerschlag and Serafy 2010, Matheson et al. this issue, Arena and Anderson this issue). This is probably due to the logistical challenges of sampling fish at night in a repeatable manner (Meyer this issue).

Some species of fish exhibit nocturnal movements between habitats (Lowry and Suthers 1998, Platell and Potter 2001, Grace and Taylor this issue, Hammerschlag et al. this issue). These diurnal and nocturnal migrations may be driven by feeding or reproductive behavior (Hobson 1973, 1974, Lowry and Suthers 1998, Platell and Potter 2001, Diaz-Carballido and Chiappa-Carrara this issue, Hammerschlag et al. this issue, Koenig et al. this issue) and can be influenced by the presence of predators (Hammerschlag et al. 2010a,b).

The use of passive and active acoustics (Meyer this issue) has greatly increased our understanding of fine scale fish movements. For example Lowry and Suthers (1998) found that Red morwong (*Cheilodactylus fuscus* Castelau, 1879) doubled their home range at night as they moved from their predominant daytime habitat of boulders out over a variety of habitats to feed. A similar pattern has been documented for *Lethrinus miniatus* (Forster, 1801) (Currey et al. 2015), for mullids, haemulids, and lutjanids (Meyer et al. 2000, Hitt et al. 2011, Topping and Szedlmayer 2011). These diel migrations between feeding grounds and sheltered areas have been documented for other reef affiliated species (Hobson 1973, 1974, Ogden and Buckman 1973, Gladfelter 1979, Luo et al. 2009, Hammerschlag and Serafy 2010).

Many of the quantitative studies investigating nocturnal changes in the distribution and habitat use of fish have focused on movements between mangroves and other nearby habitats. It is well documented that during the day, mangroves have high densities of fish (particularly juveniles), which use the prop roots for shelter reducing risk of predation (Robertson and Blaber 1992). Using seine nets, Hammerschlag and Serafy (2010) found that the abundance of species at night, such as early and late juvenile gray snapper [*Lutjanus griseus* (Linneaus, 1758)] increased with distance from the mangroves suggesting that this species moved out of the mangroves to feed in seagrass beds at night. Acoustic tracking data supported these findings (Luo et al. 2009). Other studies have found that circadian diel cycles interact with the tidal cycle to influence the behavior, movement, and feeding of coastal fishes (Wilcockson and Zhang 2008, Krumme 2009, Grace and Taylor this issue). High tides at night facilitate foraging opportunities on sand flats and in mangroves, which are inaccessible or less accessible at low tide, without the higher risk of predation that occurs during the day. In general, greater numbers of species and fish are sampled on high tides at night than high tides during the day (Krumme et al. 2015). In micro-tidal areas, such as the Caribbean and Mediterranean seas, the diel cycle is the primary cue triggering fish movements across habitats (Gibson 1992, Castellanos-Galindo and Krumme 2015).

Demersal fishes often have strong affiliations with a specific benthic habitat (Fitzpatrick et al. 2012, Harvey et al. 2013). Using a baited remote underwater stereo-video system with artificial lights to illuminate the field of view at night, Harvey et al. (2012) showed that generally more species and greater numbers of fish were recorded in six benthic habitats during the day than at night. This was because 31% of the species viewed at night were seen on multiple habitats, but were only seen in a single habitat during the day. This tends to support the notion that some species of fish are more active at night as they disperse from their diurnal habitat and forage across several benthic habitats.

With the exception of some of the electronic tracking studies, many sampling programs that investigate the movements and changes in the distribution and abundance of fishes between day and night investigate only specific time periods. Myers et al. (2016) used replicate remote underwater videos equipped with a blue light and a timer to record 9 min of video every hour throughout a 24-hr cycle on a temperate reef off Western Australia. They observed more species and fish during the day than at night, with the greatest number of species and fish recorded at dawn and dusk when both nocturnal and diurnal fish were recorded. The diurnal fish assemblage was characterized by benthic invertivores and the nocturnal assemblage by zooplanktivores and generalist feeders. An interesting observation from that study was the presence of juvenile fish belonging to species only seen diurnally in the water column feeding on plankton during the middle of the night (E Myers, Massey University, New Zealand, pers comm). Nocturnal sampling using baited remote underwater videos is increasing (see; Goebel et al. this issue a,b, Whitmarsh et al. this issue).

A large quantity of fishes are active nocturnally and make significant vertical and horizontal migrations to feed and reproduce. These migrations increase their vulnerability to predation and to harvesting. Some nocturnal species are important to commercial and recreational fishers, while others are important components in marine food webs and the transfer of energy and resources within and among pelagic and benthic habitats. In the context of ecologically sustainable development and ecosystem-based fisheries management (Fletcher et al. 2010, Norse 2010), there is a need for spatial management that incorporates assemblages and communities, not just populations of single species. For marine fisheries and biodiversity management, which are spatially explicit, it is important to understand diurnal and nocturnal habitat usage (e.g., Matheson et al. this issue) to ensure that essential fish habitat and the behavior and movements of fish are incorporated into management plans.

Fish in Polar Night

For many years, the common perception among scientists and governments had been that aquatic habitats in the polar regions were largely devoid of biological activity and in a state of dormancy during the polar night (Berge et al. 2015b). Despite the emerging sub-field of polar night biology, field studies focused in the winter months are still very rare, largely due to the associated logistical difficulties of working in the polar regions during this time. Investigations into fish species present in the polar night are extremely limited, and are often opportunistic observations, lacking spatial and/or temporal resolution. However, theories of winter ecosystem dormancy have been rebutted by studies, particularly in the last decade, demonstrating continued biological activity throughout the winter months, and even particular biological processes occurring seasonally at this time (Johnsen et al. 2014, Berge et al. 2015a). Several fish species have been speculated to maintain feeding activities throughout the entire polar night, and this was demonstrated for Arctic char [*Salvelinus alpinus* (Linnaeus, 1758)] in high Arctic lakes (Svenning et al. 2007), despite this species being considered a primarily visual predator.

In the absence of strong light-dark cycles, polar fish seasonally lack the clearest zeitgeber of circadian rhythms. This could result in disruptions to both behavioral and physiological processes (Williams et al. 2015). A notable physiological process controlled by circadian clocks is the regulation of melatonin levels. Arctic char were found to maintain diel melatonin rhythms during the polar night, which actually ceased during the polar day (Strand et al. 2008). This indicates that light regimes in shallow water polar regions, although minimal during polar night, may be sufficient to entrain daily circadian rhythms. Indeed, ambient light still influences aquatic biota during the polar night. Important prey items, such as zooplankton and krill, can detect changes in light intensity under ice in the polar night and actively respond, exhibiting vertical movements associated with the lunar schedule (Cohen et al. 2015, Tarling 2015). Similarly, some species of polar fish have adaptation for facilitating activity in both high and low light conditions (e.g., Eastman and DeVries 1985, La Mesa and Eastman 2012). That said, the ability of polar fish to detect changes in ambient light during the winter months is poorly understood and an area in need of significant research. Indeed, it may not be visual cues that fish are responding to, but rather nonvisual photoreceptional cues that are connected to biological clocks. In addition to ambient light, bioluminescence is another source that has been speculated to play a role in facilitating continued feeding by polar fish during the polar night (Benoit et al. 2010, Johnsen et al. 2014), but again, to what extent is poorly understood. It would be logical that polar fish would have physiological and sensory adaptations specific to the unique light regimes they experience on a seasonal basis, similar to their relatively well investigated cold adaptations. The lateral line system of the bald notothen [*Pagothenia borchgrevinki* (Boulenger, 1902)] responds to the movements of its swimming crustacean prey, and the consistent presence of mud in the stomachs of Arctic char led Svenning et al. (2007) to speculate the dominant use of non-visual senses during the polar night. To date, little research focus has been placed on the non-visual sensory adaptations of polar fish that would aid continued feeding in vastly reduced light conditions.

Despite the absence of strong altering light regimes, several accounts of diel vertical migrations by Arctic cod [*Boreogadus saida* (Lepechin, 1774)] have been documented during the polar night (Benoit et al. 2010, Geoffroy et al. 2011) and circadian timing systems can be highly sensitive to even low light levels that repeat in daily fashion. Seasonal niche and habitat switching between polar day and night have been observed for polar fish. For example, freshwater alpine sculpins (*Cottus poecilopus* Heckel, 1837) and European bullhead (*Cottus gobio* Linnaeus, 1758) switch from diurnal to nocturnal, and Arctic switch from whole lake distribution to the littoral zone (Klemetsen et al. 2003). Finally, a common adaption for polar fish appears to be the ability to focus reproduction during the polar night (Berge et al. 2015b). Wienerroither et al. (2011) reported that 20% of the fish species observed in the Barents Sea and Svalbard region were reproducing in the winter months. Arctic cod spawning is widely believed to occur in January–February (Hop et al. 1995), though this is largely inferred from laboratory studies. In Antarctic waters, the hatching of icefish larvae was observed during winter (Kellermann and Schadwinkel 1991). Berge et al. (2015b) recently speculated that it is in fact the ability to reproduce during the polar night, rather than visual adaptations, which dictates the composition of polar fish communities.

Our understanding of polar ecosystems is very poor overall, and data to date have been collected predominantly during the polar day. As a result, our relative understanding of polar fish during the polar night is extremely limited. For example, it remains unknown if patterns of nocturnal activity in Artic fishes are similar or different from Antarctic fishes. A statement common to most, if not all, articles on polar fish, regardless of focus, is "knowledge is lacking." Berge et al. (2015b) recently highlighted the great importance of this emerging field of research in the statement: "Research into the polar-night biology of the Arctic has the potential for radically altering our perception of the Arctic marine ecosystem, mechanisms governing ecosystems processes, and how a continued warming of the Arctic will affect ecosystem structure and function." Given the rapidly changing sea ice dynamics in response to climate change, it is predicted that ecosystem structure and productivity in the polar regions will be substantially altered in the next few decades (Berge et al. 2015b). Ice extent greatly influences ambient light penetration in polar aquatic ecosystems, and in the absence of a comprehensive understanding of biology and ecology during the polar night, it will be virtually impossible to predict future changes and invoke effective management strategies. With such a void of data on all elements of polar fish biology and ecology, any avenue of focused research is desirable. Of particular importance is investigation into the visual and other sensory systems of polar fish, movement ecology, and the identification of physiological adaptations that permit the persistence of circadian rhythms.

Fish in Deep Seas

In coastal marine and freshwater bodies, the length of the day/night cycle is determined by Earth's rotation and orbit. In deep bodies of water, length of "nighttime" (i.e., darkness) is also a function of depth. The classical pelagic vertical zonation schema of the open ocean includes three major depth zones, all defined primarily by sunlight penetration (Angel 1993, Herring 2002, Robison 2004): the epipelagial (0–200 m depth), the mesopelagial (200–1000 m), and the bathypelagial (>1000 m, though some recognize the abyssopelagial, with depths >4000 m). Of these, the epipelagial receives 1%–100% of surface solar irradiance during daylight, the mesopelagial receives approximately 0%–1%, and the bathypelagial, representing the majority of the World Ocean (>65%), receives 0% and can truly be considered "perpetual night" (reviewed in Sutton 2013).

The ecological demarcation of these zones is based primarily on the presence of characteristic fauna within each layer (reviewed in Sutton 2013), and on the daytime vertical distributions of adults. Nighttime patterns have proved much more complex. During daytime, the epipelagial is dominated by diverse assemblages of larval and juvenile fishes (e.g., Bowen et al. this issue, Malarky and Sutton this issue), beloniform fishes (e.g., Churnside et al. this issue), flotsam/jetsam associated fishes (e.g., juvenile Carangidae, Tetraodontiformes, Coryphaenidae), "baitfishes" (e.g., Clupeiformes, some Carangidae), and a limited number of large, highly migratory species (e.g., Lamniformes, Scombriformes). At night the ichthyofaunal diversity of the epipelagial increases several-fold with the upward active flux of vertically migrating fishes from the mesopelagial (e.g., Stomiiformes, Myctophiformes; Bowlin et al. this issue), who use the cover of darkness to feed in the relatively food-rich surface waters (Roe and Badcock 1984, Hopkins et al. 1996). Thus, Earth's largest biome in terms of area (by far), the epipelagial, undergoes an unparalleled ichthyofaunal day/night transformation, with the euphotic epipelagic fauna inexorably linked to the disphotic mesopelagic fauna according to time of day. Recent evidence has even demonstrated active linkage of the epi- and the aphotic bathypelagial zones at night (Cook et al. 2013, Sutton et al. this issue).

The use of quantitative, discrete-depth sampling methods, along with advancements in tagging technologies (for larger fishes), has changed our perceptions of the ecological connectivity of the oceanic ichthyofauna in a vertical sense, with much of this connectivity occurring at night by vertically migrating fishes. Recent estimates using larger trawling gear and acoustics have up-scaled our global estimates of mesopelagic fishes by an order of magnitude (Koslow 1997, Brodeur and Yamamura 2005, Sutton et al. 2008, Kaartvedt et al. 2012). Integrating this with the finding that the efficiency of energy transferred from primary producers to higher trophic levels through deep-pelagic fishes appears to be higher than previously thought (Irigoien et al. 2014), one quickly sees that the trophic interactions of fish and their prey at night in the oceanic epipelagial zone is a major component of the biologically-driven sequestration of increasingly high atmospheric CO_2 into the deep ocean (Passow and Carlson 2012). Pelagic food web models are also now emphasizing the importance of mid-trophic level species in overall oceanic ecology (Brodeur et al 2011, Ruzicka et al 2012), again with most trophic interactions happening at night (Hopkins et al. 1996).

Despite concerted efforts in the last few decades (e.g., Census of Marine Life; McIntyre 2010), the largest data gap in fish research in the "perpetual night" of the deep-sea remains the incompleteness of the global faunal inventory, both in a qualitative and quantitative sense, and particularly at bathypelagic depths (Webb et al. 2010). We must improve our sampling methodologies and quantitative rigor, and must endeavor to sample a broader spectrum of the deep-sea fish fauna using multiple gear types. Missing the larger individuals of the deep-pelagic fauna may significantly underestimate pelagic biomass (i.e., biomass being a cubic function of length). Concomitant with this data gap is the lack of information on ecological process rates, such as trophodynamics (reviewed in Gartner et al. 1997), growth (Allain and Lorance 2000), and reproduction (Marks and Sutton this issue). These are necessary parameters used in population dynamics to characterize ecosystem structural dynamics, quantify oceanic carbon flow, and assess the increasing footprint of anthropogenic disturbance (Mengerink et al. 2014). Integrating the diel temporal component of these rate estimates, one of the subjects of this symposium, is essential if we are to accurately model and predict oceanic ecosystem function and the intermediate services this function provides.

Larval Fish at Night

Recent studies focusing on larval reef fish navigation have shown a wide diversity of behavioral and sensory strategies across species including the use of a sun compass for orientation to settlement habitat, detection of polarized downwelling light, increased swimming speeds when in groups, and discrimination between settlement odors, which can trigger changes in swimming behavior (Mouritsen et al. 2013, Paris et al. 2013, Berenshtein et al. 2014, Irisson et al. 2015, Leis et al. 2015). However, these studies have mostly been carried out during short observational periods during the day. In contrast, very little is known about the temporal aspects of larval fish behavior, especially at night, despite some larval species being known to be more active at night and larval settlement from pelagic habitats to nearshore reefs often occurring at night and correlated with lunar phases (Fisher and Bellwood 2003). For example, while it is known that larval fish are capable of orienting relative to settlement habitats during the day, possibly from chemical, visual, or sound cues, it remains unknown what cues they may use at night for orientation and to trigger movement, such as chemical cues or possibly even celestial bodies (Brooker et al. this issue). There is only one published account of larval fish orientation at night, and that comes from behavioral chambers moored on coastal reefs (Stobutzki and Bellwood 1998).

Although limited, recent research has revealed some unique aspects of larval behavior at night. For example, Staaterman et al. (2014) provided the first in situ record of sounds emitted by larval fish (gray snapper, *L. griseus*) off the coast of Miami, Florida, at night. Interestingly, these larval vocalizations occurred only during the nighttime, leading the authors to speculate that fish larvae may vocally communicate for maintaining group cohesion when unable to see each other under the cover of darkness. Paris et al. (this issue) found that the swimming behavior of larval *L. griseus* deployed in the drifting in situ chamber (DISC, Paris et al. 2008, 2013) changed significantly after dusk, orienting offshore at night and onshore during day, questioning the paradigm that fish larvae settle exclusively at night. Malarky and Sutton (this issue) investigated diel and depth patterns of larval fish abundance (primarily flatfish, *Bothus* sp.) in the Gulf of Mexico. They found that overall larval fish abundance was much greater at night, even in the epipelagic zone. Surprisingly, larvae were found even at depths >1000 m.

While diel vertical migration has been previously documented in deep sea ichthyoplankton, such as some fish larvae, relatively few studies have investigated potential species- and life-stage-specific differences in this behavior. Conducting surveys of mesopelagic larval fish in the California current, Bowlin et al. (this issue) found strong evidence for ontogenetic differences in diel vertical distribution of fish larvae, suggesting the ontogenetic development of diel vertical migration. The authors suggested that the documented ontogenetic variation in diel vertical distribution may be related to differences in food-risk trade-offs of species at different life stages (Bowlin et al. this issue). However, other studies on coral reef fish larvae have failed to find any evidence of diel vertical migration (Irisson et al. 2010). Thus, despite these recent advances in understanding larval fish behavior at night, many questions still remain.

Light Pollution and Fish at Night

The burgeoning human population has led to a number of dramatic alterations of ecosystems (Vitousek et al. 1997). One the most obvious, especially when viewed from space, is light pollution arising from human infrastructure and activities (Elvidge et al. 2001), and this pollution is regarded as a threat to biodiversity (Hölker et al. 2010). Ecological light pollution is defined as the alteration of natural light regimes because of chronic or periodically increased illumination, unexpected changes in illumination, and direct glare (Longcore and Rich 2004). In an aquatic context, nearshore light pollution arises largely from coastal development, while offshore light is emitted from fishing boats, offshore oil platforms, and shipping vessels, and cruise ships (Davies et al. 2014). For some taxa, there is extensive mechanistic research on the ways that ecological light pollution alters organismal physiology and behavior, population-level processes, and community and ecosystem interactions (reviewed in Gaston et al. 2013). However, for most fish, whether freshwater or marine, little is known about how light influences their biology or ecology (Nightingale et al. 2006, Perkin et al. 2011, Davies et al. 2014), and what is known tends to be incomplete in terms of providing a comprehensive understanding of effects that span from the individual to the population to the ecosystem.

Some of the earliest work on fish was indirect and focused on zooplankton with the assumption that the vertical distribution of zooplankton in the water column would influence the vertical distribution of fish (Moore et al. 2000). Mechanistic studies on fish are quite varied using a variety of species and life-stages with diverse endpoints in both freshwater and marine systems (Nightingale et al. 2006). A recent example involving freshwater European perch (*Perca fluviatilis* Linnaeus, 1758) revealed significant alterations of light pollution on circadian rhythms, but no evidence of a physiological stress response (Brüning et al. 2015). In a subsequent study (Brüning et al. 2016), the authors examined gonadotrophic gene expression relative to different colors and intensities of light, and revealed that some light sources not only had the potential to disturb the melatonin cycle, but also the reproductive rhythm, which could have direct population- and ecosystem-level consequences. Newman et al. (2015) examined the influence of artificial light on Atlantic salmon (*Salmo salar* Linneaus, 1758) eggs and fry, but failed to detect a significant physiological stress responses (measured via cortisol). One of the few examples focused explicitly on a coastal marine fishes was a study of constant lighting (e.g., dock lighting) vs intermittent lighting (e.g., vehicular traffic) on juvenile bonefish [*Albula vulpes* (Linnaeus, 1758)] (Szekeres et al. this issue). The authors documented a physiological effect of both light sources, but the behavior of fish was consistent across both light regimes. Given the importance of epifaunal invertebrates to marine fish and fish habitat, research on epibenthos is also relevant. Davies et al. (2015) reported the first evidence of ecological light pollution altering the composition of temperate epifaunal marine invertebrate communities by either inhibiting or encouraging colonization rates of both sessile and mobile species. These examples represent much of what is known about light pollution on fish to date (see Nightingale et al. 2006 for conceptual review), but it is anticipated that such research will increase rapidly in the coming decades.

One of the most well-known examples of light pollution comes from the marine realm—the recognition that newly-hatched sea turtles orient toward land-based light sources rather than heading to sea (Witherington and Bjorndal 1991a). Mechanistic research on their sensory physiology (e.g., Witherington and Bjorndal 1991b; reviewed in Lohmann et al. 1997) provided the link between different forms of light and the disruption of turtle navigation. After the problem was identified (which ended up being a truly global issue; reviewed in Kamrowski et al. 2012) and public awareness and political will were fostered, there were a number of successful initiatives that reduced land-based light pollution in coastal zones where turtles are common (e.g., Salmon 2006). This example is relevant to marine fish in two ways. First, the reductions in light pollution, even if only seasonal, presumably reduced light pollution for coastal marine fish in areas where turtle nesting occurred. Second, the model used to document and then address the impacts of light pollution on sea turtles can presumably be exported to marine fish. For example, step one is documenting a problem such as change in physiology or behavior. Step two is documenting any change in population size/structure or community structure as a result. Step three is conducting mechanistic research to understand the pathway of effect between the putative pollutant (light) and the behavioral/physiological and subsequent population- or community-level responses. That mechanistic component might include detailed studies of sensory physiology, visual ecology, anatomy, behavior, and energetics (see Gaston et al. 2013). After the pathway of effect is established, potential solutions should become evident (Cooke et al. 2014). At such a point, it would be necessary to understand what logistical, societal or political barriers might exist to the solutions being implemented which would likely involve engagement with human dimensions researchers and stakeholders (Mascia et al. 2003).

An inherent limitation with research on ecological light pollution is the need to understand the "natural" biology and ecology of animals in the absence of light pollution (Gaston et al. 2015). Given the extent of ecological light pollution, particularly in coastal areas, it is difficult to find "pristine" systems. Moreover, as discussed in other parts of this synthesis, there is very little research on fish at night, although that is changing. Collectively, these issues present important challenges in moving forward with identifying the extent to which ecological light pollution is or is not a problem for fish and aquatic ecosystems.

Fish and Fisheries at Night

Commercial and recreational fisheries exist targeting species at night (e.g., Yuen 1979, Hamilton et al. 2012, Orbesen et al. this issue). However, directed fisheries that occur at night are generally a numerical minority in a global context, but their data can still be valuable in terms of either detailing significant landings quantities (e.g., pelagic longline fisheries targeting swordfish, *Xiphias gladius* Linnaeus, 1758) or as auxiliary indicator trends of the stocks (e.g., swordfish tournament fisheries, Davis et al. this issue, Kerstetter et al. this issue), assuming that any gear and other technical changes in the respective fishery are adequately documented. Nighttime commercial fisheries present specific technical challenges regarding the monitoring of target landings, bycatch, or secondary target catch characteristics, such as length or sex composition data. Beyond the at-sea observer issues noted elsewhere for all fisheries, such as ensuring representative temporal and spatial coverage of the respective programs, the poor lighting on most fishing vessels at night can also result in misidentification of released or discarded species even for experienced crew and observers. However, the challenges of electronically monitoring catch via video are currently being addressed through improvements in technology (e.g., Wallace this issue).

Recreational fisheries that occur at night present additional issues for reporting beyond the usual ones (diffuse angling locations, etc.), including the difficulty for enforcement agency personnel to visually locate or question participating anglers. In nighttime fisheries, there is also usually no set end-time, but fishing instead ends when the tide changes, the regulatory limit is caught, or the angler is simply tired. Thus, characterization of the recreational at-night fisheries themselves is essential prior to utilization of any fisheries-dependent data—something that rarely occurs, even in daytime US fisheries. A key addition to the characterization issue is that, although daytime fishing activities may share similarities and gear types, nighttime hook-and-line fisheries may result in differences in hooking location on the individual fish, especially if the anglers are using passive techniques (Cooke et al. this issue). If deep-hooking events tend to result in lower post-release survival rates, even in catch-and-release fisheries (Bartholomew and Bohnsack 2005), diel differences in fisheries may also result in differing mortality rates. A freshwater study on several teleost fish species revealed that one species [i.e., pumpkinseed, *Lepomis gibbosus* (Linnaeus, 1758)] was hooked more deeply at night than during the day (Bower et al. this issue). To our knowledge, that is the sole study on the topic.

However, the real issue is not the fisheries activities themselves, but how best to address the underlying vulnerability question, referring to a capacity for capture by a particular technique or gear type. For example, escolar [*Lepidocybium flavobrunneum* (Smith, 1843)] may be caught incidentally at night during pelagic longline sets for swordfish, but is it really a species that is only nocturnally active or is it captured at night because that is when fishing is occurring? In other words, particular fish may only be caught at night when the fishery operates, but the fish may also be foraging at other times, when they would also be vulnerable to exploitation by other fisheries. As an example, swordfish, which were previously captured only in night sets of pelagic longlines, are now being caught off the southeastern United States during daylight hours at deep depths using so-called "deep-drop gear" (Davis et al. this issue), which changes the conversation regarding a formerly "nighttime" species. Vulnerability is thus a question that needs to be addressed via better understanding the biology and behavior of fish that interact—or even just potentially so—with fisheries activities. Studies of fisheries interactions at night, such as the pelagic longline fisheries in Orbesen et al. (this issue) and Gallagher et al. (2014), therefore only provide insights into the diurnally variable vulnerability of these species. As these studies do not necessarily provide any information about vulnerability at other time periods or in different fisheries, caution should be used in making any adjustment of fishing behavior (i.e., a switch from night to day) to alter exploitation rates. Fishes that occur incidentally in commercial fisheries also often have particularly poorly-understood life-histories, such that current fisheries could be inadvertently mining these resources rather than engaging in sustainable management. Fisheries exist at night because of a productive combination of fisher accessibility and fish behavior (usually nocturnal feeding). If nighttime fisheries catches are driven primarily by increases in fish activity at night, then targeted species would be more vulnerable to overexploitation at night than during the day. Characterizing those vulnerabilities for species targeted in nighttime fisheries will not only provide additional warnings about overexploitation, but also contribute to greater understandings of the underlying biology of the affected stocks.

Conclusions and Research Priorities

Fish at Night: an International Symposium was organized to assess and advance the current understanding of fishes and fisheries in darkness. Here, we have synthesized key themes from the symposium, provided a basis for understanding fish and fisheries in darkness, and identified knowledge gaps and research priorities that we hope will help chart a course for future science on fish at night. The identified research priorities, grouped according to the topical areas reviewed above, include:

Methods for Studying Fish in Darkness

- Further miniaturization of telemetry and biologging technologies to permit use on the smallest fish
- Development of new tools for remotely measuring physiological responses of fish in their natural habitats
- Development of new camera systems capable of recording fish behavior in darkness without using visible light

Sensory Physiology and Life in the Dark

- Determination of spectral and absolute visual sensitivities in different fish taxa, particularly with respect to the light environment during times of behavioral activity
- Comprehensive analysis of light quality (spectrum and intensity) in aquatic habitats throughout the day/night cycle and across seasons
- Determination of the intensity and spectral qualities of light pollution in aquatic environments and comparison with visual sensitivities of fish species in those environments
- Examination of the effects of natural photo cycle alteration on behavioral and physiological rhythms

- Evaluation of the effects of artificial light and un-natural photoperiods on the development and visual function of captive reared fish, especially for restocking programs
- Assessment of ontogenetic changes in visual function
- Examination of the capacity of developmental plasticity and adult neural plasticity to compensate for changes in light environments caused by natural and anthropogenic habitat disturbance

Nocturnal Fish Behavior and Ecology

- Determination of inter- and intra-specific variation in nocturnal behavior among fishes and habitats
- Evaluation of the importance of darkness for predatory fish and the extent to which their peak activity occurs at night
- Examination of the relevance of night and subsequent lunar illumination for predator-prey interactions
- Evaluation of the influence of lunar phase on nocturnal spawning behavior and success
- Determination of the effects of noise and fishing activities on the behavior and ecology of nocturnal fishes
- Examination of the effectiveness of diurnal monitoring programs and eradication efforts focused on invasive species
- Quantification of “essential fish habitat’ that includes consideration of nocturnal habitat use patterns
- Evaluation of why some fishes evolve to be nocturnally active, while others do not

Diel Patterns of Fish Distribution and Habitat Use

- Quantification of the movement range and associated behavior of fish at night
- Collection of fine scale behavioral data throughout the course of the night rather than just day/night comparisons
- Quantification of potential changes in fish behavior due to illuminated video monitoring cameras and the resulting implications for biodiversity studies

Fish in Polar Night

- Completion of field-based surveys of fish behavior during the months of polar night
- Investigation of visual and non-visual sensory adaptations of polar fish in laboratory settings
- Evaluation of physiological mechanisms that allow for the persistence of circadian rhythms during polar night
- Evaluation of fish abilities to detect or respond to visual or non-visual photoreceptional cues that are connected to biological clocks
- Investigation of the distribution and movement ecology of fish under ice during the polar night
- Evaluation of nocturnal activity in Arctic and Antarctic fishes to determine consistency in patterns
- Completion of comparative behavioral and ecological studies of species that inhabit tropical, temperate, and polar regions

Fish in Deep Seas

- Completion of quantitative sampling day and night, from the surface to bathypelagic depths, to assess the active flux of fish biomass in oceanic ecosystems
- Investigation of diel variation in ecological rate processes (feeding, digestion, egestion, and metabolism) in the deep sea
- Estimation of daytime or nighttime avoidance of sampling gears by fishes and its effect on abundance/biomass assessments

Larval Fish at Night

- Investigation of the generality of larval fish vocalization at night and the reason behind this behavior
- Determination of the cues that larval reef fish use for orientation, movement, and settlement at night
- Evaluation of the effects of moon phase and celestial cues on the nocturnal behavior of larval fishes
- Examination of species-specific and ontogenetic variation in diel vertical migration of larval fishes
- Observations of larval fish swimming and orientation during the night in the pelagic environment and during settlement

Light Pollution and Fish at Night

- Evaluation of the extent to which light pollution alters organismal biology with a particular emphasis on understanding the factors that influence whether light will attract or repel fish and whether light pollution is indeed a stressor across life stages (including larvae)
- Characterization of the ecosystem-level consequences of light pollution with a particular focus on how it mediates predator-prey interactions
- Completion of studies to understand the adaptive capacity of fish that inhabit areas of high light pollution
- Identification of opportunities for mitigating light pollution in aquatic ecosystems (e.g., different light types and spectra)

Fish and Fisheries at Night

- Estimation of respective fishing effort during diel periods for commercial and recreational fisheries
- Evaluation of variation in fish behavior across diel periods for estimating their vulnerability to various fishing gear types
- Development of improved video monitoring systems for increased observational coverage of fisheries under low-light conditions

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