Nocturnal and crepuscular behavior in elasmobranchs: a review of movement, habitat use, foraging, and reproduction in the dark

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ABSTRACT.—It is commonly assumed that elasmobranchs (sharks, skates, and rays) are most active during dark periods (dawn, dusk, night). However, this assertion has not been critically evaluated. It is also unclear whether dark periods are primarily utilized for the performance of important life-history events, such as mating. If this were the case, low-light periods would be of significance to elasmobranch conservation as some anthropogenic activities (night fishing, lighting) could disproportionately impact fitness of species that are more active in the dark. Here, we review and summarize previous studies on elasmobranch behavior during nocturnal and crepuscular periods focusing on patterns of movement, habitat use, foraging, and reproduction. A review of 166 studies provided mixed results for widely-assumed increased elasmobranch activity when dark. Frequency of foraging and horizontal movement (distance travelled, activity space) were reported as greater only during crepuscular periods in the majority (>50%) of reviewed studies (28 of 43 and 78 of 125 studies, respectively), a pattern not evident during night. No pervasive patterns emerged for increased habitat use or reproductive behaviors during dark. We did not find any particular habitat type consistently supporting increased activity during dark, nor did we find evidence that higher trophic level elasmobranchs were more active when dark. Thus, generalizations about increased elasmobranch activity during dark periods are currently not supported. While research on the behavior of elasmobranchs during dark periods has been increasing, many knowledge gaps remain and we present a set of research priorities to assist in the development of future investigations.

The life cycles of most living species are governed by the periodicity of light and dark, which is perhaps the most consistent and predictable environmental cue (Moore 1997, McClung 2006). As such, species will be most active during the periods that offer them the greatest opportunities to maximize feeding for growth and development (Boeuf and Le Bail 1999), opportunities for reproduction (Fraser et al. 2004), and predator avoidance (Bollens and Frost 1991, Moreno et al. 1996), and will be less active during portions of the 24-hr cycle that are less favorable to these activities.

Differences in biological processes along the nocturnal/diurnal continuum have long been of interest to zoologists, posing questions of central importance to ecology and evolution about how environments may affect animal physiology and behavior (Panda et al. 2002, Panda and Hogenesch 2004). Researchers have investigated many related questions in smaller aquatic species [e.g., Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum, 1792); sockeye salmon, *Oncorhynchus nerka* (Walbaum, 1792); steelhead trout, *Oncorhynchus mykiss* (Walbaum, 1792); Pacific lamprey, *Entosphenus tridentatus* (Richardson, 1836); and American shad, *Alosa sapidissima* (Wilson, 1811) (Keefer et al. 2013); sharpsnout seabream, *Diplodus puntazzo* (Walbaum, 1792) (Vera et al. 2006); teleost reef fish (Schmitz and Wainwright 2011)]. However, comparing day/night/crepuscular activity in large marine fishes presents unique challenges, largely due to the highly migratory behavior of many species and the concealing nature of the environment.

It is widely assumed and commonly reported (e.g., Andrews et al. 2009, Fitzpatrick et al. 2011) that elasmobranchs are most active during low-light periods (dawn, dusk, night). For example, media often warn beachgoers to stay out of the water during nocturnal and crepuscular periods to avoid risk of encounters with large sharks, which are assumed more active and feeding at dark. Such assumptions have likely developed due to a suite of sensory adaptations (visual, olfactory, auditory, electrical, and magnetic) possessed by elasmobranchs that may permit increased activity during low-light periods (Hueter et al. 2004). These dark-adapted sensory systems include, for example, a light-adjusting iris/pupil, a tapetum lucidum behind the retina that reflects light back through the retina, and a high concentration of rod cells in the eye with irradiance-sensitive opsin pigments (Lisney et al. 2012). However, there are more than 1000 species of elasmobranchs (Dulvy et al. 2014) and it remains unknown how widespread possible increases in nocturnal and/or crepuscular activity might actually be in this group of fishes. It is also unclear whether dark periods are generally utilized more by elasmobranchs for the performance of important life-history events such as mating or pupping, which, if the case, would then be helpful in informing fisheries management for conservation of imperiled elasmobranch species. Therefore, it is important to assess whether the generalizations made about increased activity of elasmobranchs during dark periods are accurate and appropriate.

To address these knowledge gaps, we present the results of a comprehensive review of previous studies of elasmobranch behavior and habitat use during nocturnal and crepuscular periods (referred to as "dark"), focusing specifically on patterns of movement, habitat use, foraging, and reproduction. Where possible, we compared these activity patterns with those from daytime to assess whether diel differences in behavior or habitat use patterns exist. We also used these findings to address the following questions relating to elasmobranch behavior and habitat use: (1) What is the scale and scope (geographic and topical) of studies that have investigated the behavior of elasmobranchs during dark periods and do any disparities exist in the

Table 1. Terms used for literature search; each search string included three terms (from each of term one, term two, and term three).

Term 1	Term 2	Term 3			
		Movement	Habitat use	Foraging	Reproduction
Night	Shark	Habitat	Density	Predation	Mating
Diel	Skate	Satellite tag	Aggregation	Feeding	Copulation
Crepuscular	Ray	Acoustic tag	Catch per unit effort	Foraging	Reproduction
Dawn	Elasmobranch	Movement	Catch per unit area	Eating	Breeding
Dusk		Vertical	Kernel density	Hunting	Courtship
Nocturnal		Spatial	Population		Sexual
		Migration	Abundance		
		Locomotion	Number		
		Diving			
		Home range			
		Activity space			

taxa surveyed, research areas investigated, and locations studied? (2) What research methods have been most used for studying elasmobranch behavior during dark? (3) Are elasmobranch activity levels higher during dark periods compared to day? (4) Do any habitats consistently support the presence of increased activity levels during dark periods? and (5) Are higher trophic level elasmobranchs (i.e., apex predatory sharks) more active during dark periods as commonly reported? Based on the ability of the available published literature to answer these questions, we identified gaps in our knowledge of elasmobranch nocturnal or crepuscular behavior and also generated a set of research priority questions to assist in the development of future investigations.

Methods

To facilitate a review of the literature, we investigated four broad categories that relate to elasmobranch behavior and activity: movement, habitat use, foraging, and reproduction. A search of the literature was conducted with the Web of Science (in search field "Topic"), as well as Aquatic Sciences and Fisheries (ASFA) databases (in search field "Anywhere"), using all combinations of the search terms given in Table 1. There were a total of 264 search combinations for the category movement, 192 for habitat use, 120 for foraging, and 144 for reproduction.

We restricted the review to only peer-reviewed publications appearing in scientific journals (i.e., excluding book chapters, unpublished conference presentations, student theses, agency reports, etc.). The search generated papers that fell between January 1975 and June 2015 (the literature search was completed in July 2015). The references cited in each relevant article were examined for new items and this process was continued until no additional publications emerged. All results from the searches were scrutinized to determine relevance for further review as follows. A paper was retained only if it met three criteria: (1) empirically considered the topic in question (movement, habitat use, foraging, or reproduction), (2) addressed at least one elasmobranch as a study species (specified in methods), and (3) included time of day (either actual time and/or photoperiod, e.g., night) in the study design or results including, at minimum, night or crepuscular periods. Papers that were applicable to

multiple time periods (night, crepuscular, or both) were considered under both periods. Additionally, papers that were applicable to multiple topics (i.e., a foraging paper containing movement search terms) were analyzed under both topics.

The final list of publications was analyzed for the following variables: (1) year of publication; (2) type(s) of elasmobranch(s) assessed (shark, skate, ray, or multiple); (3) size, sex, and life-history stage of the elasmobranch(s) if given; (4) trophic level; (5) topic variable type (movement, habitat use, foraging, reproduction); (6) frequency of behavior or activity (see below for metrics); (7) diel period (nocturnal, crepuscular, or both); (8) study climatic zone (tropical, subtropical, temperate, or polar) based on study latitude; (9) study geographic location (see below for analysis); (10) study habitat type (pelagic; coastal; reef; small island/atoll; estuarine including mangroves, lagoons, and seagrass; and/or "other" such as ice-covered habitats and rivers, or multiple habitat types); (11) primary methodological approach [acoustic telemetry, satellite telemetry, archival telemetry, visual survey such as diver survey or baited remote underwater video, or fisheries sampling (gill netting, traps, longline, rod-and-reel)]; and (12) whether environmental (e.g., lunar and tidal cycles), biological (sex), or life-history (maturity status) factors influenced activity or habitat use.

For movement, the following data were extracted from published studies where reported: (1) home range, (2) activity space, (3) speed, (4) distance, and (5) direction of movement. For habitat use, reported data extracted included information on presence/absence, density/biomass, counts or total or mean numbers, and catch per unit effort or area within a specific habitat. For foraging behavior, we identified reported predation events, incidences of tag or logger consumption, correlation of predator with prey movement and abundance, and stomach content analysis. For reproduction, metrics included reported incidences of egg laying, mating, courtship or parturition. For all studies, reports of vertical migration toward or away from the surface associated with the diel-nocturnal cycle were also recorded.

We used these data to separately calculate the percent of reviewed studies that reported increased activity levels or habitat use and/or higher frequency of a behavior performed during night, crepuscular periods, or both dark periods (night and crepuscular) combined. For analyses regarding day vs dark differences, we excluded "dark-only" studies that did not have comparative daytime data. For studies that did find increased movement, habitat use, foraging, or reproduction during crepuscular and/or nighttime periods compared to daytime periods, we further explored the results for differences by habitat type and trophic level. Trophic levels were assigned for each species according to Cortés (1999), Ebert and Bizzarro (2007), or FishBase (Froese and Pauly 2016) using values calculated from diet composition of original samples if available. We considered an activity or behavior to be more frequent during a dark period if greater than or equal to 50% of reviewed studies, which provided comparable light vs dark data, reported increased frequency of a given behavior performed during a dark period and/or increased activity levels at that time. An analysis of variance (ANOVA) was not performed as these data and its classification (i.e., yes, there was increased activity, or no, there was not more activity at night) did not lend itself to this type of statistical test, rather a simple probability inference (as a percentage) was used.
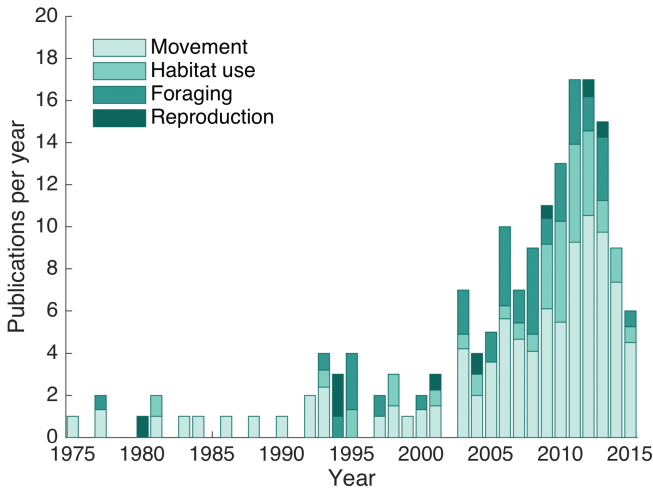
Figure 1. Temporal trends in the number of scientific papers published that reported elasmobranch behavior during dark (night and crepuscular periods).

Spatial Analysis.—To assess the scale of research being done on elasmobranch behavior during dark periods, geographic coordinates were identified for each study. If coordinates were not explicitly stated in the text and could not be determined from an included figure, Google Earth was used to determine a study's approximate geographic coordinates. One representative location was recorded per study. Given that we were interested in where studies were occurring geographically, for tagging studies, we used the location of the tag deployment even if the tagged animals dispersed from the general study location over time.

ArcGIS 10.3 was used to identify geographic trends in research locations. First, point data were imported into ArcGIS to determine where sharks, skates, and rays have been studied during dark periods. Next, kernel density estimates were created to illustrate the global research trends observed in our review. Kernel density maps were created for all of the studies combined as well as for each individual topic under investigation (movement, habitat use, foraging, and reproduction). If a study focused on two variables (e.g., movement and foraging) the study was included in each topic's kernel density calculation, but was only included in the overall kernel density calculation once. Each map was classified using natural breaks (Jenks), an algorithm that optimizes for minimal within-class deviance from the class mean (Slocum 1999). While this classification scheme obscures the true density values, it is the most effective way of illustrating the trends observed in our review.

Results

Scale and Scope.—Literature searches yielded 4199 results for movement, 670 for habitat use, 422 for foraging, and 83 for reproduction. Following refinement according to the criteria listed above, a total of 166 relevant papers, published between 1975 and 2015, were retained for subsequent analyses (Online Appendix 1, Fig. 1). There were few published reports on elasmobranch behavior during dark periods until the early 2000s (32 from 1975 to 1999), with an exponential increase, peaking
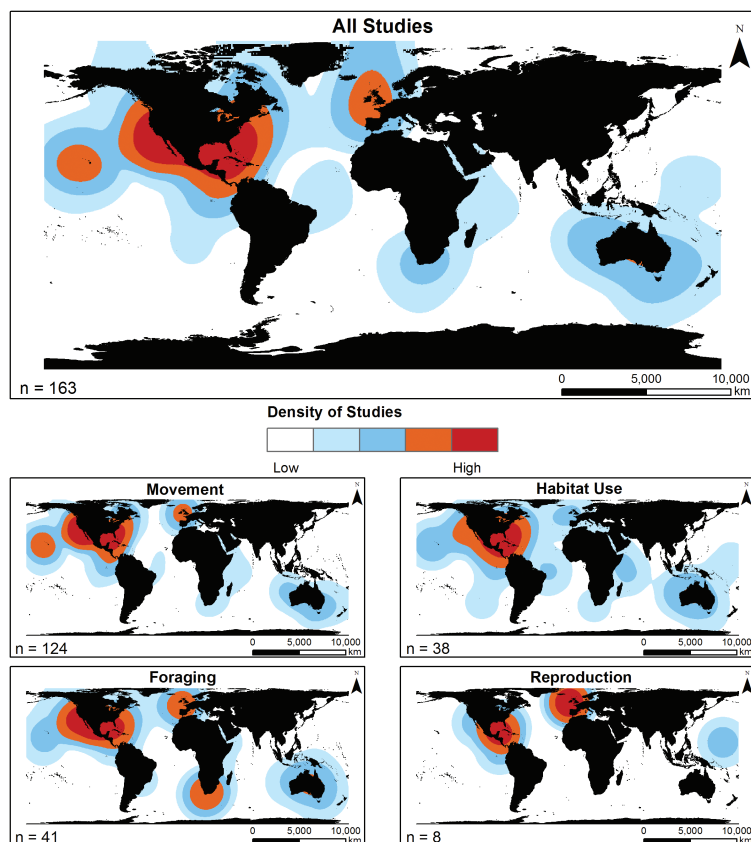
Figure 2. Density of elasmobranch behavioral studies during dark periods by region.

in more recent years (Fig. 1). Papers that were applicable to multiple topics (i.e., a foraging paper containing movement search terms) were considered under both topics. Thus, of the 166 papers identified, 125 were on movement, 40 on habitat use, 43 on foraging, and 8 related to reproduction (Online Appendix 1).

SAMPLING PERIOD.—One-hundred-and-forty-eight papers compared study metrics between day and night; 51 papers compared day, night, and crepuscular periods; 10 papers included only crepuscular periods; and 6 papers considered only night periods.

SPATIAL ANALYSES.—Geographic coordinates were determined for 163 of the 166 studies included in our review. Shark behavior and habitat use in the dark has been studied on all continents except Antarctica (142 studies; Fig. 2). Spatially, research on ray and skate behavior in the dark is limited. Ray behavior was studied in North America, South America, Asia, and Australia (22 studies), while skates were exclusively studied in North America and Europe (five studies). All of the studies included in this specific analysis were either coastal or pelagic, with the exception of one inland study on stingrays from the Paraná River, Brazil (Garrone Neto and Uieda 2012).

While studies took place on almost every continent, our review suggested that most of them occurred in North America (Fig. 2), followed by Europe, Australia,
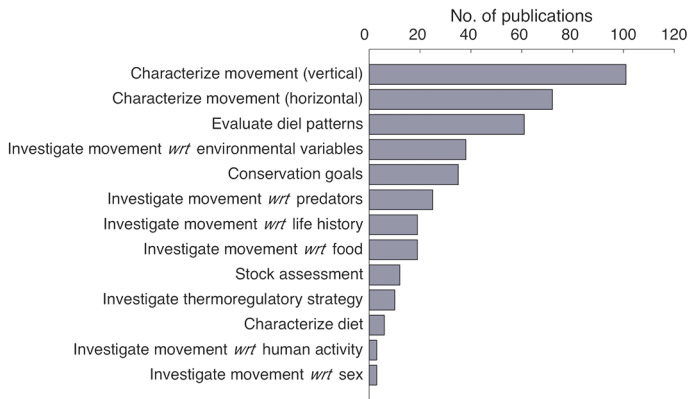
No. of publications

Characterize movement (vertical)
Characterize movement (horizontal)
Evaluate diel patterns
Investigate movement *wrt* environmental variables
Conservation goals
Investigate movement *wrt* predators
Investigate movement *wrt* life history
Investigate movement *wrt* food
Stock assessment
Investigate thermoregulatory strategy
Characterize diet
Investigate movement *wrt* human activity
Investigate movement *wrt* sex

Figure 3. Objective of studies that included data on elasmobranch behavior during night or crepuscular periods. "*wrt*" = "with respect to."

and Africa. Our review also indicated that elasmobranchs of central East Asia, West Africa, and the Mediterranean were not subject to nighttime or crepuscular study. Individual patterns in study density were observed for each of the four behaviors recorded in this review (Fig. 2). Movement, foraging, and habitat use studies were prominent among all major countries where nighttime studies occurred; however, reproductive studies were far more rare and geographically limited (Fig. 2).

Species and Families.—Of published studies on elasmobranch behavior and habitat use during dark periods, 145 (87%) have been on sharks, 25 (15%) included rays, and 5 (3%) included skates. Of shark studies that included dark periods, 99 (68%) had observations at night, 20 (14%) had observations during crepuscular periods, and an additional 26 (18%) included observations from both night and crepuscular periods. Overall, 125 (86%) included observations at night and 46 (32%) included observations from crepuscular periods. For rays, 19 (76%) had observations at night, 3 (12%) had observations during crepuscular periods, and an additional 3 (12%) included observations from both night and crepuscular periods. Overall, 22 (88%) were at night and 6 (24%) included crepuscular periods. For skates, overall 4 (80%) occurred at night and 2 (40%) considered crepuscular periods, with 1 (20%) study including both night and crepuscular periods. Certain studies fit multiple criteria, resulting in instances, here and elsewhere in the present study, such that percentages across categories summed to >100%.

Twenty-eight elasmobranch families were studied; the three most common were Carcharhinidae (56 studies), Lamnidae (20 studies), and Sphyrnidae (14 studies). In total, 109 species were studied, with the most common species being the blue shark [*Prionace glauca* (Linnaeus, 1758)] and white shark [*Carcharodon carcharias* (Linnaeus, 1758)] (12 studies each), scalloped hammerhead [*Sphyrna lewini* (Griffith and Smith, 1834), 11 studies], and whale shark (*Rhincodon typus* Smith, 1828, 10 studies).

Aims of Reviewed Studies.—The characterization of elasmobranch movement was represented as the primary study aim for a total of 110 studies (66%, Fig. 3). Evaluating diel behavioral patterns (61 studies, 37%) and how environmental variability affected behavior (38 studies, 22%) were also relatively common aims (Fig. 3).
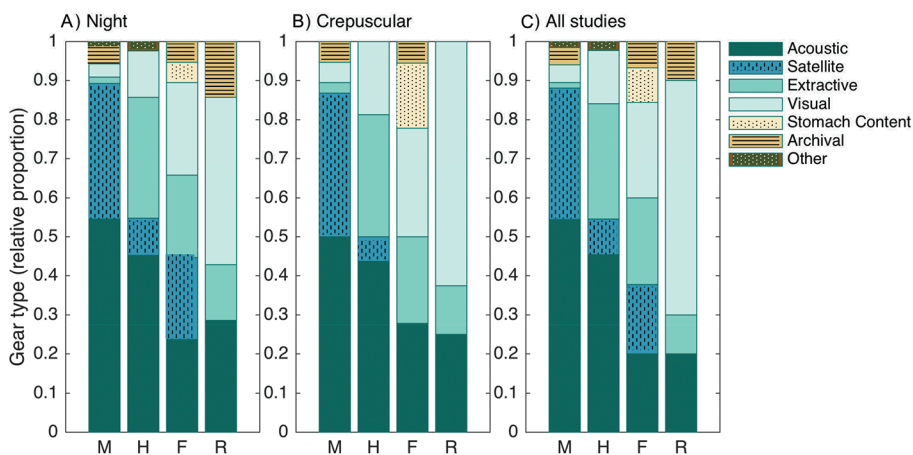
Figure 4. Proportion of studies using different sampling gear types where data on elasmobranch behavior was reported during (A) night, (B) crepuscular periods, and (C) both night and crepuscular periods combined. Behaviors investigated in studies are displayed separately, where M = movement, H = habitat use, F = foraging, and R = reproduction. "Visual" refers to visual observation (e.g., diver observation, baited remote underwater video), and "extractive" refers to the use of fishing gear (e.g., longlines for abundance assessment).

Least specifically investigated were movement with respect to a human disturbance, such as fishing, and movement with respect to elasmobranch sex (three studies each, 2%).

Sampling Methods and Gear.—Acoustic (76 studies, 46%) and satellite (46 studies, 28%) telemetry were the most common methods used for examining patterns of movement, habitat use, foraging, and reproduction in dark periods, although fisheries sampling methods (gillnetting, longlines) were often used for monitoring habitat use (13 studies, 33%) and ascertaining foraging patterns (10 studies, 23%; Fig. 4). Direct visual observation was most common in reproductive (six, 75%) studies (Fig. 4).

Activity Level.—Of the movement studies, we found that 38% (44 studies) detected increased activity during night while 65% (24 studies) detected evidence of increased movement during crepuscular periods (Fig. 5). This increased crepuscular activity was attributed to a greater propensity for horizontal movements (23 studies, 62%) vs vertical movements (6 studies, 16%). Of the studies evaluating habitat use, we found that 35% of studies suggested increased habitat use at night or during crepuscular periods (23%) (Fig. 5). Elasmobranchs showed evidence of increased foraging during dark periods (Fig. 5): we found that 64% (28 studies) of reviewed studies documented increased foraging during crepuscular periods. Forty-nine percent of studies (21 studies) showed increased foraging at night, resulting in a pooled 55% of studies showing increased foraging during dark. Only five studies evaluated aspects of elasmobranch reproduction at night, three of which found increased activity (Fig. 5).

Activity Level × Habitat Type.—There were no consistent patterns when comparing habitat type and activity level or frequency of behavior during dark periods (Fig. 6). The majority of increased foraging activity during dark periods was reported
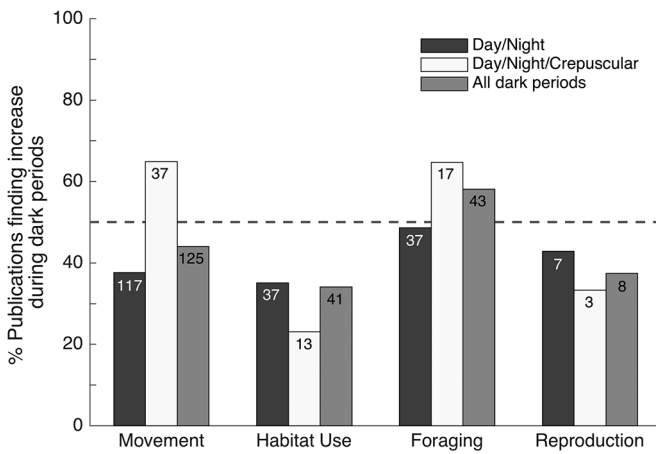
Figure 5. Proportion of studies that found activity during night, crepuscular and all dark periods combined for movement, habitat use, foraging and reproduction. Numbers in bars are total number of publications per category in the given time period. For reference, the dotted line across the graphs indicates were 50% of studies reported increased activity levels, at or above which we considered a majority of studies reporting heightened activity during a dark period.

from reef habitats as well as in coastal habitats at night (83% and 47% of studies in these habitats found an increase, respectively). Similarly, the majority of increased reproductive activity at night occurred in coastal habitats (60% of studies in this habitat found an increase; Fig. 6).

ACTIVITY LEVEL × TROPHIC LEVEL.—There were no consistent patterns when comparing elasmobranch trophic level and activity level during dark periods (Fig. 7). Moreover, there was little evidence of higher trophic level predators being more active during dark, with one exception: elasmobranchs with a trophic level of >4.1 were implicated in 55% of studies that found increased foraging during crepuscular periods (Fig. 7).

DIEL VERTICAL MIGRATION.—Of the 77 reviewed studies that investigated diel vertical swimming behavior, 42 studies (55%) reported diel vertical migration (DVM; occupying shallower habitat at night than day) and 10 studies (13%) reported reverse diel vertical migration (rDVM; occupying deeper habitat at night than day).

ENVIRONMENTAL INFLUENCES.—Lunar phase was found to influence diel behavior in 14 studies across movement [e.g., greater acceleration near full and new moon by *Carcharhinus melanopterus* (Quoy and Gaimard, 1824); Papastamatiou et al. 2015] and habitat use [*Carcharhinus falciformis* (Müller and Henle, 1839) were more present at night during full moon; Clarke et al. 2011]. In nine of these cases, elasmobranchs used deeper depths as lunar phase progressed toward full. Water temperatures experienced by the animals were found to be different from night to day in 13 studies, concurrent with a change in depth. Tidal cycle was implicated in 12 studies, influencing the magnitude and direction of movement (2 and 3 studies, respectively) and habitat use (6 studies), with the latter higher at low or slack tide in 4 studies.
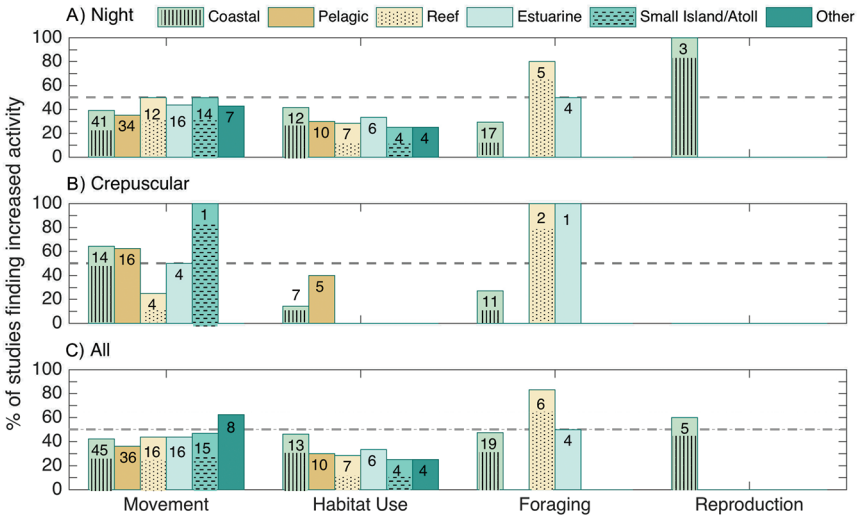
Figure 6. Proportion of studies that found elevated activity during dark periods for movement, habitat use, foraging and reproduction, according to habitat type. Numbers in or above bars are number of publications per category in the given time period. For reference, the dotted line across the graphs indicates 50% of studies reported increased activity levels, at or above which we considered a majority of studies reporting heightened activity during a dark period.

Discussion

We found mixed results for increased activity by elasmobranchs during dark periods across variables assessed. With respect to habitat use, diel shifts by marine and terrestrial organisms are well documented. These shifts occur in response to numerous intrinsic and extrinsic environmental drivers, including predator avoidance, food availability, and reproduction. For instance, sockeye salmon (*O. nerka*) have been found to alternate habitat use from lakes to streams at night to reduce predation risk from brown bears (*Ursus arctos* Linnaeus, 1758) during spawning periods (Bentley et al. 2014). Several species of dung beetles (*Onthophagus* spp.) have been shown to shift habitat use from diurnal to crepuscular periods in disturbed but recovering tropical lowland forests, suggesting resource partitioning among sympatric species in a changing environment (Boonrotpong et al. 2012). Elasmobranchs could similarly optimize their use of habitat during dark periods to achieve favorable conditions for a variety of factors; however, our review did not demonstrate any clear, general patterns in habitat use with respect to diel periods.

Our review found that some species, including common thresher sharks [*Alopias vulpinus* (Bonnaterre, 1788); Cartamil et al. 2010] and prickly sharks (*Echinorhinus cookei* Pietschmann, 1928; Dawson and Starr 2009) have been found to exhibit higher abundance in shallow waters at night. However, evidence does not support increased use of specific habitats during dark periods across elasmobranchs. In contrast, elasmobranchs do appear to exhibit increased movement activity during crepuscular periods (Fig. 5). Interestingly, increased crepuscular movements appear to be largely horizontal. For example, horizontal movement of blacktip reef sharks
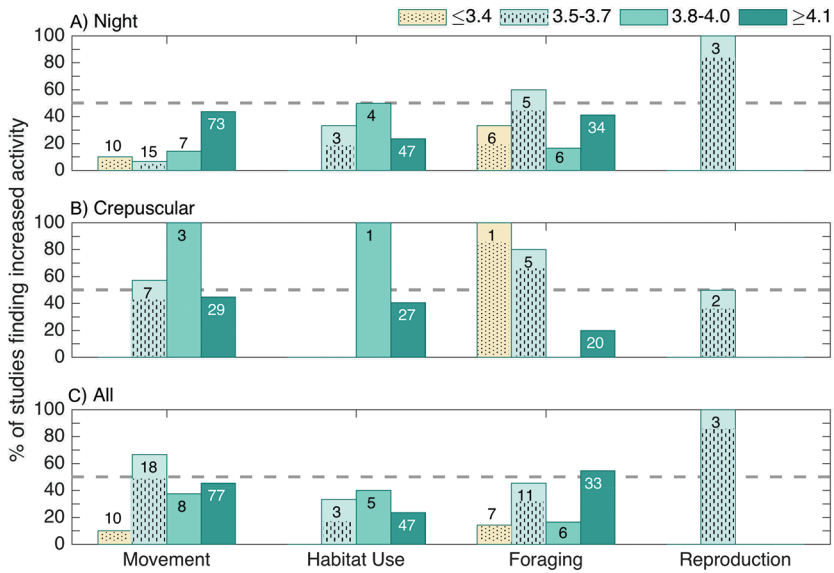
Figure 7. Proportion of studies that found elevated activity during dark periods for movement, habitat use, foraging and reproduction, according to trophic level of the elasmobranch(s) studied. Numbers in or above bars are number of publications per category in the given time period. For reference, the dotted line across the graph indicates 50% of studies reported increased activity levels, at or above which we considered a majority of studies reporting heightened activity during a dark period. Trophic levels were assigned according to Cortés (1999), Ebert and Bizzarro (2007), or Fishbase (http://www.fishbase.us, using values calculated from diet composition of original samples if available).

(*C. melanopterus*) at a tropical atoll peaked in early evening to pursue herbivorous reef fish (Papastamatiou et al. 2015). This result suggests that rather than increasing movement up or down throughout the water column, elasmobranchs may generally expand their range or move to different areas during crepuscular periods. Considered in conjunction with foraging studies, which found increased feeding activity during crepuscular periods, and recognizing the sensory advantages elasmobranchs may have over their prey in low light conditions, it seems plausible that increased crepuscular movements may relate to foraging efforts. Additionally, increased movement of smaller and lower trophic level shark species during dark periods could be associated with attempts to reduce predation risk. Plains zebras [*Equus quagga burchelli* (Gray, 1824)] have been shown to adapt their habitat use in response to the presence of lions [*Panthera leo* (Linnaeus, 1758)] at night (Fischhoff et al. 2007). Overall, while many studies identified some degree of increased horizontal movement during crepuscular periods, few were able to identify the cause of this increased activity or determine where the animals moved. Future work may consider combining research tools or developing new techniques to better assess these questions.

It is generally accepted that elasmobranchs exhibit diel vertical swimming behavior, which has been documented in several species for which it has been assessed (Sims et al. 2005, 2006). Our results show that DVM appears to be more common than rDVM (at least for the studies of this kind to date). Elasmobranchs showed some evidence of increased foraging activity during dark periods (Fig. 5). For instance, Segura-Zarzosa et al. (1997) found that stomachs of horn sharks [*Heterodontus*

francisci (Girard, 1855)] contained greater volume and number of prey items at night than during the day, suggesting nocturnal foraging. However, there were few empirical studies evaluating diel differences in foraging or predator-prey interactions (18 studies total). This is likely due to logistical challenges of visual observation or stomach content analysis, although foraging was commonly suggested as a likely driver of DVM (e.g., Carlisle et al. 2011).

Prey species may be less able to detect or avoid predators at night. For example, the observed prey capture efficiency of brown bears was 16% higher at night, which was attributed to decreased evasion behavior of salmon (Klinka and Reimchen 2002). Some prey species may be more accessible to predators at nighttime. For example, White Pelicans (*Pelecanus erythrorhynchos* Gmelin, 1789) caught more large fish during the night when those fish were closer to the surface (McMahon and Evans 1992). Foraging during crepuscular hours may permit predators to hunt both diurnal and nocturnal prey during the limited time that both groups are simultaneously accessible. Bats are known to take advantage of crepuscular foraging to access diurnal and nocturnal insects (Pavey et al. 2001). However, only three studies in our review directly measured elasmobranch predation rates during dark periods. Of the latter, Hammerschlag et al. (2006) found white shark success rate of seal capture was highest during crepuscular periods (dawn), and Lowe et al. (1994) found Pacific electric rays [*Tetronarce californica* (Ayres, 1855)] to be extremely active at night, more actively hunting and seeking prey (shown by decreased latency times in rays attacking prey at night vs the day).

Our review found 34 studies that inferred possible foraging behavior from overlap between distributions of elasmobranchs and their prey or from predation events inferred from tag transmissions. In one such instance, Béguer-Pon et al. (2012) reported possible consumption of tagged eels by porbeagle sharks [*Lamna nasus* (Bonaterre, 1788)] based on tag measurements of increases in temperature assumed to be associated with being consumed by a "warm-gutted" predator, and also a change in depth distributions similar to that of DVM behavior in porbeagle sharks. Visual observation (scuba divers, underwater video cameras) was mostly limited to daylight hours, and could not occur during some of the deeper dives when foraging was inferred. Thus, further research is needed to directly assess both feeding behavior and predator-prey interactions during dark periods. Multi-instrument telemetry tags incorporating an internal pH sensor (e.g., Papastamatiou et al. 2007) or cameras (e.g., Crittercams, e.g., Heithaus et al. 2001) were used to provide confirmation that tagged elasmobranchs were consuming (via internal pH readings) or pursuing (via Crittercam imagery) prey. In the absence of such confirmation, researchers should be wary of assuming that spatial overlap between predators and prey equates to foraging or feeding events.

Elasmobranchs could potentially perform mating behaviors at night due to the cover of darkness affording reduced predation risk (for mating sharks or eggs being laid). This could serve to maximize fitness of the individuals, and could depend on the habitat, season, and species composition. Previous work observed eggs of the Pacific sergeant major damselfish [*Abudefduf troschelii* (Gill, 1862)] to hatch after dusk, near the new moon, which may synchronize with the timing of tides that transport the eggs away from reef-associated predation (Foster 1987). While some studies reported increased elasmobranch reproductive activity at night, this came only from 3 of 5 studies that considered day and night periods. However, these studies found

mating behavior (courtship, pre-coupling, copulation) occurred at either dawn or night (Tricas 1980, Carrier et al. 1994, Whitney et al. 2010). Carrier et al. (1994) observed nurse shark [*Ginglymostoma cirratum* (Bonnaterre, 1788)] mating behavior over a diel cycle; however, the vast majority of observations were conducted during the light hours despite the noted occurrence of a mating event at night. Additional research is necessary to develop a more complete understanding of the mechanics and spatial and temporal distribution of reproductive activity for elasmobranch fishes.

Fourteen of the reviewed studies found suggestive evidence for the influence of lunar phase on elasmobranch behavior, including changes in abundance, diving, and acceleration. Moon phase has been previously found to influence fish behavior (e.g., Rooker and Dennis 1991, Domeier and Colin 1997, deBruyn and Meeuwig 2001). In one study, nocturnal depths of grey reef sharks [*Carcharhinus amblyrhynchos* (Bleerker, 1856)] at outer coral reef slopes off Palau, Micronesia, increased from the new to full moon (Vianna et al. 2013). However, the existing studies only hint at the possible effects of moon phase and other environmental factors on diel elasmobranch behavior, and not the mechanics behind such patterns.

There are likely numerous other factors and scenarios that affect behavior during dark periods that were not directly explored in our review. For example, how behaviors during dark periods may differ according to individual life-stage or energetic condition, and behaviors in perpetually dark habitats. It is possible that juvenile elasmobranchs may reduce nocturnal activities to lower predation risk from larger conspecifics that actively forage during dark periods (Hammerschlag et al. 2010). Individuals may also base their foraging decisions on body condition and health, as individuals in poor energetic condition may opt to assume increased predation risk in exchange for access to food resources and increases in probability of hunting success under low light conditions (Brown and Kotler 2004).

It also remains unknown if and how circadian rhythms of elasmobranchs could be influenced by the absence of normal diel environmental cues (Hammerschlag et al. 2017). For example, it is unknown whether elasmobranchs exhibit diel behavior patterns (e.g., DVM) when living in deep waters void of light, or under sea ice or in polar areas where it is perpetually dark for long periods of time. Suggestively, DVM of zooplankton continues throughout perpetual dark periods in the Arctic Ocean, and bluntnose sixgill sharks [*Hexanchus griseus* (Bonaterre, 1788)] undergo DVM at very low light levels (Comfort and Weng 2015), likely due to diel variations in lunar and solar illumination that persist beyond the threshold of human perception (Berge et al. 2009). Unfortunately, our review did not provide us with enough data to assess all these possibilities.

In addition to the knowledge gaps described above, few studies have assessed the impacts of potential anthropogenic stressors on elasmobranch behavior during dark periods. However, noise and light pollution, boat traffic, and fishing occurring at different times of day or night could have significant consequences for some species of elasmobranchs. 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). It is possible that such alterations in nocturnal activity could have energetic or fitness consequences; however, this remains unknown (Gallagher et al. 2015). It is also feasible that the loss of elasmobranch prey or predators could alter diel

behaviors. Indeed, fisheries depletion of coral reef predators has been shown to result in increased abundances of nocturnal fishes during the day, thought to be a response to the reduction in diurnal predation risk to these individuals (McCauley et al. 2012).

There are significant conservation and management implications of nocturnal or crepuscular changes in elasmobranch behavior, although they are rarely discussed. Only 2% of reviewed movement studies involving dark period were directly related to stock assessments or fisheries management (Strong et al. 1992, Zanella et al. 2012, Vanderklift et al. 2014). However, some elasmobranch species may be more or less vulnerable to exploitation at dark (Gallagher et al. 2014). For example, individuals that use marine protected areas during the day, but disperse across larger areas at dark may be more vulnerable to fishing pressure at night (Hearn et al. 2010). Similarly, elasmobranchs that exhibit vertical migration at night may become more vulnerable to interacting with fishing gear at or near the surface (e.g., Doyle et al. 2015). For example, Gallagher et al. (2014) evaluated survival of sharks as bycatch in pelagic longline fisheries targeting tuna during the day and swordfish at night. For blue sharks and silky sharks (*C. falciformis*), survival was lower in swordfish sets, which are deployed at sunset to take advantage of vertically migrating swordfish (Gallagher et al. 2014). With greater knowledge of diel patterns of elasmobranch movement, fishers could alter the timing and location of fishing activity (e.g., gear deployment/retrieval time and/or gear depth) to reduce or increase catch rates of elasmobranchs. However, it is important to note that our review found intraspecific variation in habitat use at night (a given species may exhibit DVM in one habitat and reverse DVM elsewhere; Sims et al. 2005), suggesting that a study of a species from one region should not necessarily be used to set conservation management regulations for that species in a different region.

While studies on elasmobranchs at night are occurring globally, most are from a handful of developed countries. This is not only a trend with respect to studies of nocturnal behaviors, but studies of elasmobranchs and their associated fisheries in general, and few studies occur in developing nations despite these countries typically having higher shark biodiversity (Lack and Sant 2011, Gallagher et al. 2012). For example, in the past 20 yrs, 261 papers focusing on life history and population status of sharks have been published focusing on the US and Australia, but only nine focusing on Indonesia, the world's top shark fishing nation by biomass caught (Momigliano and Harcourt 2014). Thus, there remains a large disparity between the scale of elasmobranch research at dark vs the diversity and threat to elasmobranchs.

Our review shows that research on the behavior of elasmobranchs at night and during crepuscular periods is increasing. However, the focus of these studies was mostly on sharks, with relatively few relevant studies on rays and skates. This is a pattern that has been observed by others for the study and conservation of elasmobranchs more generally (Simpfendorfer et al. 2011). Similarly, of the studies including investigations of elasmobranch behavior at night, the focus has been on movement, whereas studies on reproduction are lacking. This is likely attributed to the widespread use of biotelemetry (Hammerschlag et al. 2011, Papastamatiou and Lowe 2012) and the relative feasibility of remotely studying the movements of elasmobranchs in the dark compared to reproductive aspects of behavior. However, recent advances in non-lethal reproductive assessment tools for elasmobranchs (e.g., Hammerschlag and Sulikowski 2011, Sulikowski et al. 2016), bioltelemety and biologging (Whitney et al. 2010), and animal-borne cameras (Marshall 1998) make studying reproduction

much more feasible. Biotelemetry, for example, has been used to identify small-spotted catsharks [*Scyliorhinus canicula* (Linnaeus, 1758)] depositing eggs at night (Wearmouth et al. 2013).

Conclusions and Research Priorities

While our analysis found that research on the behavior of elasmobranchs at night and during crepuscular periods is increasing, many significant knowledge gaps remain. It is generally assumed that elasmobranchs, especially large sharks, are more active under dark conditions, but we found mixed empirical evidence for this supposition. Our review found that frequency of foraging and horizontal movement were reported to be higher during crepuscular periods in the majority of relevant studies; however, there seem to be no clear patterns among studies related to habitat use and reproduction, with relatively small sample sizes limiting our ability to draw meaningful inferences about these variables. Our queries also do not provide evidence for any strong relationships between behavior and habitat type or trophic level. Thus, our review suggests that generalizations about increased elasmobranch behavior during nocturnal or crepuscular periods is inappropriate at this time and many notable knowledge gaps remain.

In terms of addressing knowledge gaps on elasmobranch behavior during dark periods, we particularly recommend increased research to evaluate the crepuscular and nocturnal behaviors of rays and skates and an increased effort to examine aspects of reproduction, foraging, and predator-prey interactions during these periods. Future research should also include data collection to help understand how life-stage, health, condition, and environmental factors may influence nocturnal and crepuscular behaviors. Specific recommended future research priorities include:

- Investigate for life-history and sex differences in nocturnal and crepuscular behaviors
- Investigate for potential variation in behavior and activity level throughout the diel cycle
- Examine to what extent vertical movements are tied to thermoregulation and foraging
- Continue evaluating the influence that environmental factors (salinity, temperature, oxygen, lunar phase) may have on diel behavior
- Further develop new technologies to remotely assess behaviors of elasmobranchs during low-light conditions
- Investigate for potential impacts of anthropogenic stressors (e.g., light pollution, fishing, noise) on the nocturnal behavior of elasmobranchs
- Examine for diel variation in vulnerability of elasmobranchs to fisheries exploitation

Given the scale of threats to elasmobranchs and the magnitude of reported population declines of many species, improving our understanding of their nocturnal and crepuscular behaviors and incorporating this knowledge into conservation and

management is timely. Our review demonstrates that empirical investigation of nocturnal and crepuscular behavior in elasmobranchs remains a relatively understudied, yet potentially valuable area of research within the increasingly established field of elasmobranch biology and ecology.

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