



Lunar cycle effects on pelagic predators and fisheries: insights into tuna, billfish, sharks, and rays

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Abstract The lunar cycle has a major influence on the daily structure of marine ecosystems. As the moon orbits the earth across an approximate 29.5 day cycle, it influences these systems by altering nighttime light availability and shaping the strength and timing of tides. Numerous studies have documented the effects of the lunar cycle on large epipelagic fishes (here referring to tuna, billfish, sharks and rays), however, there has been no concerted effort to systematically compare these patterns across studies. Here, we review 190 studies documenting the effects of the lunar cycle on the ecology of large epipelagic fishes and discuss the potential underlying factors that contribute to the observed patterns. Most studies focused on fisheries science and movement ecology, examining metrics such as catch rate and depth of tagged individuals, respectively. A smaller proportion of studies delved into foraging behaviors and behavioral

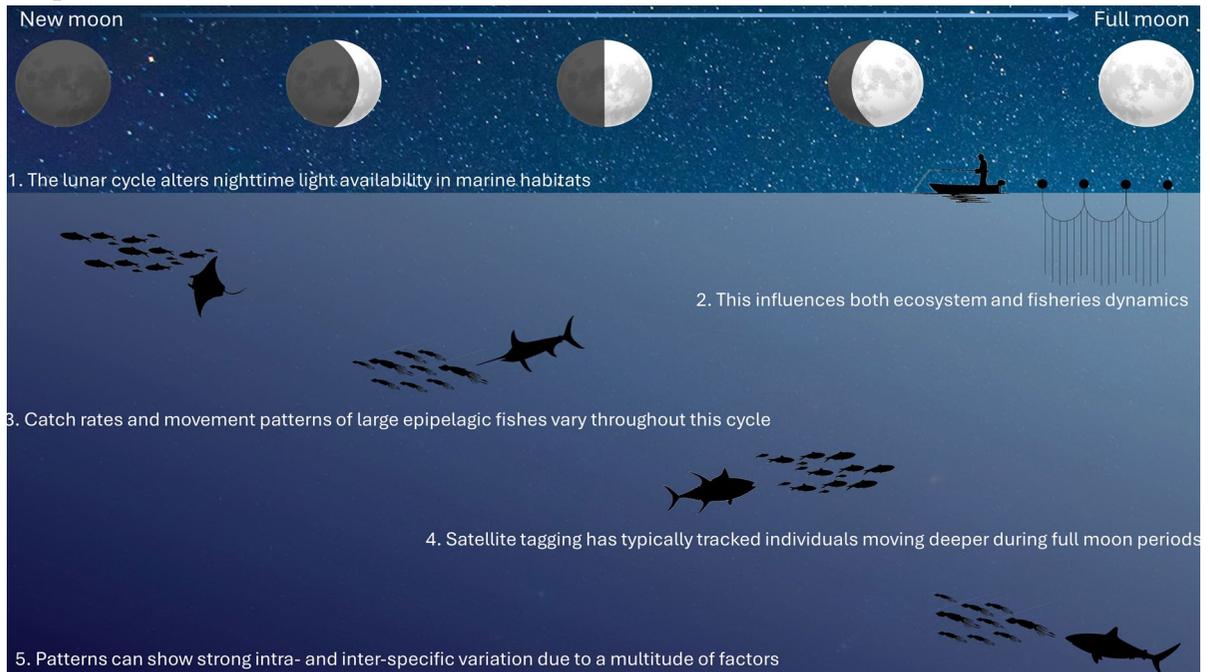
patterns. The effects observed varied among study types and taxa, yet vertical movement patterns consistently indicated a trend of deeper movements with increasing lunar illumination. Many factors likely contribute to this variation, including study specific methods (both field and analytical), other light sources or obstructions in the marine environment (such as bioluminescence and cloud cover), local site variation (such as local oceanography and prey distribution), species specific traits (such as distribution and foraging strategy) and individual traits (such as ontogenetic stage and body condition). We propose best practices for future studies on lunar effects, aimed at addressing this variation and promoting comparative analyses.

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Graphical abstract



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Introduction

The moon's influence on marine ecosystems has been a long-standing observation within fishing communities, and continues to be a subject of discourse in popular media (e.g. Olander 2022). In several Pacific Islands, for example, indigenous fishing knowledge informs fishing methods and gears based on day of the lunar cycle (e.g., Kiribati, New Caledonia, Papua New Guinea, Solomon Islands; Kitolelei et al. 2021), and the Māori fishing calendar predicts superior angling success on specific lunar days (Best 1929). In contemporary studies, a substantial body of research has documented relationships between migratory, spawning, and foraging behaviors across phases of the moon for a wide range of marine taxa (e.g. Benoit-Bird, Au & Wisdom 2009; Hamilton et al. 2012; Last et al. 2016; Ravache et al. 2020). These trends, however, are complex, with multiple pathways through which lunar cycles can impact

marine ecosystems. In brief, the lunar cycle refers to the regular sequence of changes in the appearance of the moon as it orbits the earth, shifting its relative position to the sun across a span of approximately one month (~29.5 days; see Figure 1 for a visualization of this cycle). Throughout the lunar cycle, nighttime light availability increases from the new moon to full moon. Additionally, gravitational interactions between the earth, moon and sun influence the strength and timing of tides, with full and new moons linked to spring tides (i.e., greater tidal range), and first and last quarter phases linked to neap tides (i.e., lower tidal range).

Understanding how this cycle influences marine ecosystems is important for fisheries management and conservation efforts. For commercially and recreationally important species, perceived knowledge of lunar effects on catch (see Olander 2022) can factor into decision making for trip planning with consequences for success that may impact overall catch and profit (Lerner, Levesque & Talaue-McManus 2017). Lunar-driven aggregations like spawning events, that predictably concentrate individuals during specific lunar phases, raise concerns about potential targeting of aggregations and subsequent overexploitation (Hamilton et al. 2012). These examples underscore the importance of unraveling lunar cycle patterns

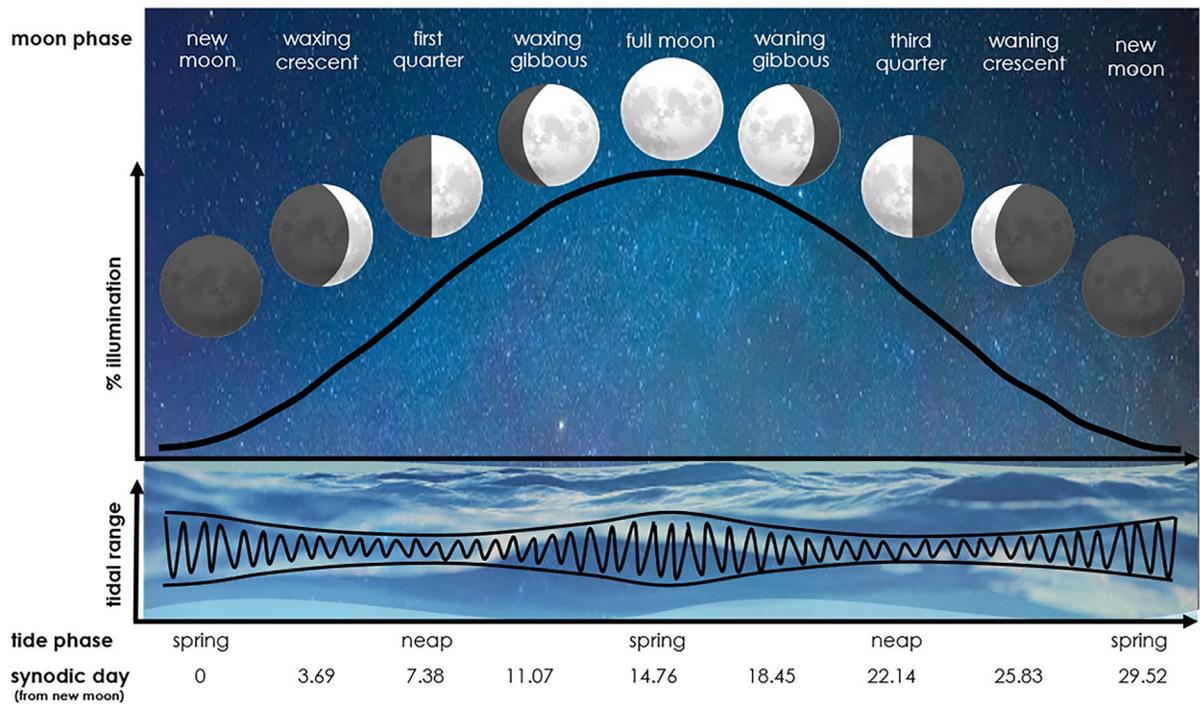


Fig. 1 Variation in moon appearance, % moon illumination and tidal range throughout the lunar cycle.

to guide marine spatial planning and conservation efforts. For threatened species, knowledge of lunar-related patterns may inform bycatch mitigation strategies. For example, if nighttime depth distributions of a bycatch species are governed by moonlight, modifying target depths over a lunar cycle may assist in reducing interaction rates (Andrzejaczek et al. 2022). From an ecological perspective, understanding behavioral changes throughout the lunar cycle can further our knowledge in elucidating environmental drivers of behavior (Schlaff, Heupel & Simpfendorfer 2014) while also advancing our insights into intra- and interspecific interactions. In the context of the latter, this may involve discerning whether behaviors are a direct response to lunar-related variables, or in response to the reactions of a prey species.

Large, epipelagic fishes are highly mobile marine species that demonstrate spatial movement and diving behaviors influenced by environmental conditions and prey landscapes. In this way, this diverse group of predators present an ideal system through which to study lunar-related effects on behavior. We define this group as species that attain maximum sizes >30 kg and spend the majority of their

lives traversing the top 0–200 m of marine habitats (Andrzejaczek et al. 2019), and restrict our discussion to tuna, billfish, shark and ray species. These taxa experience light and tidal related lunar effects throughout their habitats. For instance, moonlight can penetrate to the bottom of their primary vertical habitat in the epipelagic zone during a full moon in offshore environments aiding visual predators in nighttime foraging (Young et al. 1980; Kaartvedt, Langbehn & Aksnes 2019). Conversely, in coastal habitats, such effects also interplay with those of the tidal cycle. As these animals are large enough to be tracked with electronic tags, their long-term movement patterns over the course of the lunar cycle have been well documented (e.g. Block et al. 2011; Braun et al. 2015; Queiroz et al. 2016). In addition, for many regions there is temporal catch data associated with these species, as tuna and billfish form the basis of important commercial and recreational fisheries and sharks and rays represent a large part of targeted and incidental bycatch (Worm et al. 2024). For these reasons, many studies have investigated the effect of the lunar cycle on various aspects of the ecology of large, epipelagic fishes. However,

there has been no consistent or standardized method for documenting these effects, inhibiting comparisons among studies.

Here, we aim to provide a synthesis of the existing knowledge of the effects of the lunar cycle on the ecology of large, epipelagic fishes. We quantify the scale and scope of published studies, investigate trends with increasing lunar illumination across taxa, and discuss the hypothesized drivers of these relationships. Finally, we document the different ways lunar relationships were measured in these previously published studies and provide best practices for future studies to facilitate comparisons.

Methods

This literature review is based on keyword and title searches of library and electronic databases, including *Google scholar* and *Web of Science*, using combinations of the words 'lunar', 'moon', 'tuna(s)', 'billfish(es)', 'shark(s)', and 'ray(s)' published prior to April 2023. Search terms and resulting studies were limited to the English language. Relevant studies cited in papers found through database searches were also incorporated. For each study the following information was documented: (1) if a primary focus of the study was to investigate the lunar cycle; (2) study species/taxa and location; (3) habitat type of the study (offshore, coastal, estuarine or transient); (4) the type of study; (5) how the lunar cycle was measured and the source of the measurement; (6) the response variable; (7) the type of analysis used; (8) the descriptive lunar effect; (9) the relationship with increased lunar illumination and (10) the hypothesized process underlying the observed relationship (see Table 1 for more detailed descriptors of these obtained variables; and Supplementary File 1 for the collected data). Where it was unclear where a method and/or result fit under a given variable, it was listed as 'NA' to avoid ambiguity. All papers and the documented information were evaluated by a minimum of two reviewers.

Results and discussion

Section 1: Meta-analysis overview

A total of 190 ecological studies were identified that investigated the effect of the lunar cycle on tuna, billfish, shark and/or ray taxa (Supplementary File 1). Of these studies, only 33 (~17%) identified lunar effects as a primary research objective. Across all studies, 147 investigated the lunar effect on a single species and 43 looked at the effect across multiple species. The degree to which taxon were examined varied with 43 studies on tunas, 57 studies on billfishes, 92 studies on sharks and 20 studies on rays (Figure 2). These studies explored a range of relationships with the lunar cycle, with 84 studies categorized as fisheries science, 83 studies as movement ecology, 12 as foraging ecology, 12 as behavioral ecology and one as chronobiology (Figure 2C). Additionally, one study investigated both fisheries and foraging ecology, while another focused on both fisheries science and movement ecology. The most common variables examined in response to the lunar cycle were catch rate ($n = 66$) and depth of movement of a tagged individual ($n = 54$), followed by acoustic detection rate of a tagged individual ($n = 16$). Shark species dominated movement ecology studies, whereas commercially important billfish and tuna species occurred more frequently in fisheries science studies (Figure 2C). Only 9% of studies investigated rays, likely influenced, in part, by the challenges in attaching a tag to these dorso-ventrally compressed taxa (Ward et al. 2019). Additionally, the predominance of pelagic catch methods (such as longlining, utilized in 62% of fisheries studies) may have contributed, as such techniques may not yield high catch rates of this primarily benthic taxon. Swordfish (*Xiphias gladius*) were the most studied species, occurring in 33 studies. Since these fish constituted the majority of the billfish studies and are targeted using distinct catch methods, they were analyzed separately. We also note that several relevant studies have been published since April 2023 (e.g. Tracey et al. 2023; Laurioux et al. 2024), enriching the discussion of this review, however, were not included in our meta-analysis.

Collectively, these studies covered a large global range, with notable gaps in study coverage including at extreme latitudes and the west coasts of Canada, South America and Africa (Figure 2). The highest

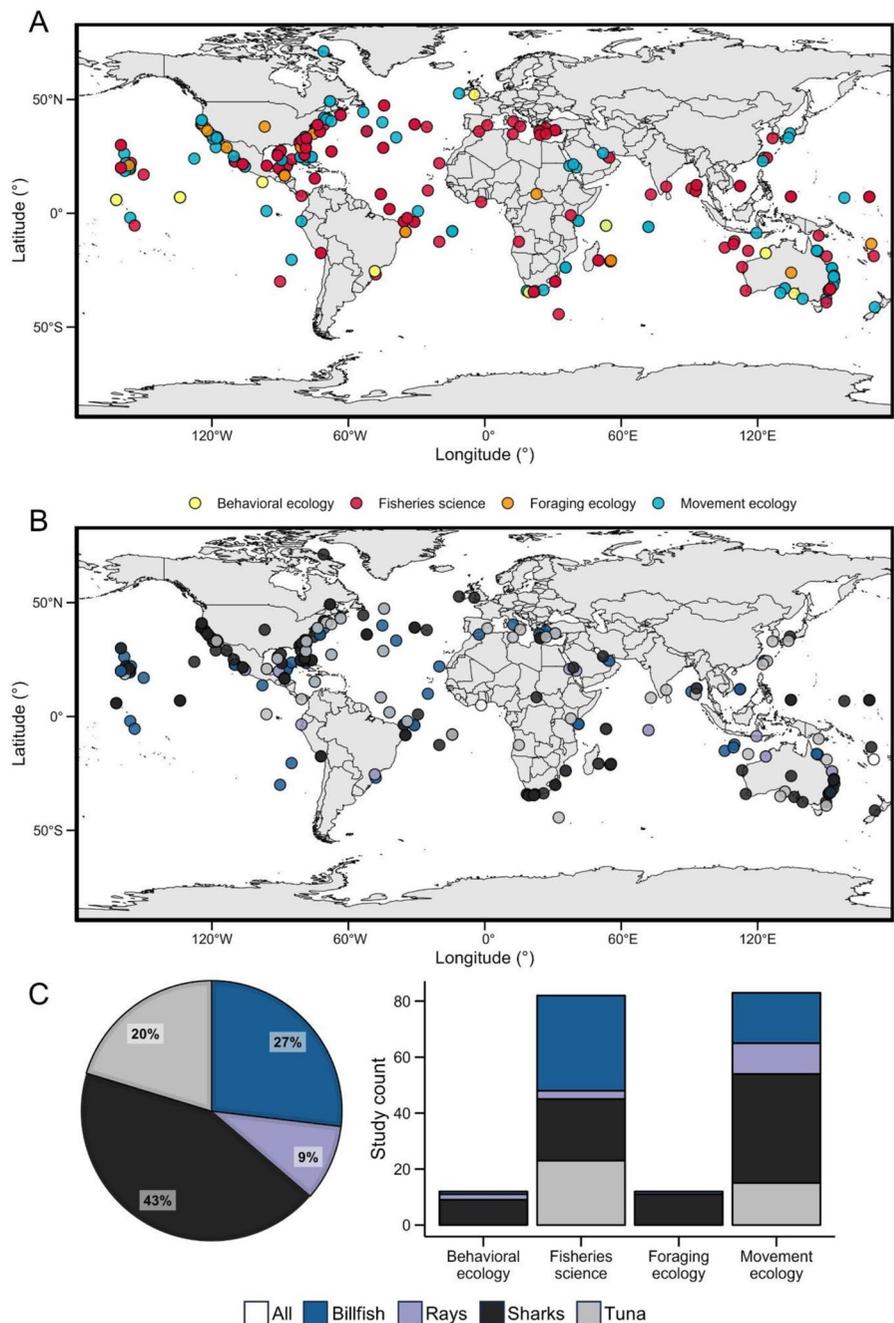
Table 1 Detailed descriptions of the variables obtained from each study reviewed in our meta-analysis.

Variable name	Variable type	Description
1. Primary lunar focus	Category (n = 2)	If a primary objective of the study was clearly defined as assessing the effects of the lunar cycle on specific variable(s). If the study explicitly stated that they were investigating lunar effects in their objectives/hypotheses, this was listed as 'yes'. However, if the study simply included the lunar cycle as a variable, this was listed as 'no'
2. Study taxa and location	Descriptive and numerical	Taxa was recorded to the highest order classification possible. The broad study region was noted, as well as a more specific latitude and longitude. For the latter, this may have been approximated if not noted in the study or averaged if the study occurred across a broad region. For tagging studies, tag deployment location was used.
3. Primary habitat type	Category (n = 4)	Primary habitat type was split into 'Estuarine', 'Coastal', 'Offshore' or 'Transient'. 'Estuarine' was recorded where studies occurred in estuaries, while all others were based on distribution of the data collection on continental shelf habitats with studies distributed exclusively on the continental shelf assigned as 'Coastal' (e.g., coastally deployed acoustic receivers, or fishing exclusively in coastal areas), those off the continental shelf as 'Oceanic' (e.g., fishing or tagging exclusively in offshore regions), and those moving between the two and/or resident in both as 'Transient' (e.g., fishing in both coastal and offshore regions; Andrzejczek et al. 2022).
4. Type of study	Category (n = 5)	Type of study was split into (A) movement ecology, (B) fisheries science, (C) foraging ecology, (D) behavioral ecology or (E) chronobiology.
5. Measurement and source of the lunar cycle	Category (n = 16 for measurement; n = 20 for source)	The measurement of the lunar cycle used in the paper and where this was obtained from. Example measurements include categorical lunar phases (e.g., new moon, first quarter, full moon, third quarter), continuous daily lunar illumination, and synodic day of the lunar cycle starting at the new moon (1-29). See Figure 1 for schematic of the lunar cycle.
6. Response variable	Descriptive	The ecological variable responding to the lunar cycle.
7. Analysis type	Category (n = 49)	The statistical analysis used to compare the lunar cycle with the ecological response variable. 'Descriptive' was recorded where no statistical analysis was used.
8. Descriptive lunar effect	Descriptive	The relationship described between the lunar cycle and the response variable discussed in the study.
9. Relationship with increased lunar illumination	Category (n = 5)	The relationship between the response variable and lunar illumination. This was split into 'Increase', 'Decrease', 'No effect' or 'Variable effect' where this relationship could be assessed. 'Variable effect' was used in situations where the result was either non-linear, or varied among individuals and/or groups.

Table 1 (continued)

Variable name	Variable type	Description
10. Hypothesized process	Descriptive	The hypothesized process underlying the observed relationship between lunar illumination and the response variable reported in the study (e.g., increased light available, or tidal effects)

Fig. 2 Summary of studies investigating the effect of the lunar cycle on billfish, ray, shark and tuna species. 'All' refers to studies that investigated all four taxa. **A** and **B** Geographic distribution of studies by study type **A** and taxa **B**. Where studies included a wider region (e.g. an entire country or continent), the point was placed in the middle of the respective region, resulting in some points being placed on land. **C** Proportional and count distribution of taxa and study type, respectively, to the total study count



concentration of studies, particularly those for movement ecology, occurred around North America and Australia, potentially reflecting variation in research funding (i.e., a pattern that is also noted in large collaborative tagging studies such as Queiroz et al. (2019) and Andrzejaczek et al. (2022)). In contrast, fisheries science studies exhibited a broader geographical distribution (Figure 2).

Section 2: Lunar trends and hypothesized processes

Vertical movement

The effect of the lunar cycle on vertical movement patterns was investigated by 79 independent analyses across 54 studies. Electronic tagging methods were used to assess depth changes across all these studies, with 38 using pop-up satellite archival tags (PSATs), nine using archival tags, and seven using acoustic tags. Overall, depth showed the clearest patterns with lunar illumination across this meta-analysis (Figure 3), with 51% ($n = 40$) of analyses revealing deeper movements with increasing lunar illumination, and just 5% ($n = 4$) recording shallower movements (Figure 4). This pattern was most consistent for tuna species (see species-specific findings in Supplementary File 1), with 12 of the 15 tagging studies

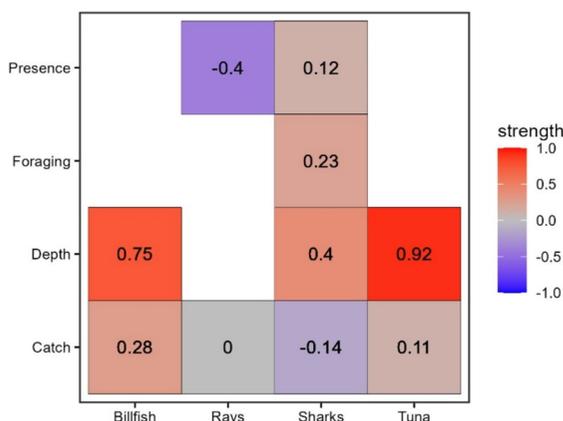


Fig. 3 Summarized directional relationships between major response variables and increased lunar illumination, displayed across the four major taxa. The strength of the associated relationship is computed as the average over a given group, where each individual study finds either a positive relationship (1), negative relationship (-1), or no effect (0) with increased lunar illumination. Mixed relationships and groups with $n \leq 5$ were excluded from this analysis.

displaying deeper movements with increased illumination (Figure 4A), as demonstrated by the mean nighttime depth of a Pacific bluefin tuna (*Thunnus orientalis*) increasing towards full moon periods in Figure 4C (Kitagawa et al. 2007). Billfish showed more variability, with 63% of the 19 studies revealing deeper movements, 21% no effect, and 15.8% a variable effect with increasing lunar illumination (Figure 4A). For nine of the ten studies for swordfish, however, a deeper effect was recorded (Figure 5). Sharks demonstrated the most variable depth effect with lunar illumination, with high intraspecific variation documented (Figure 4A, B). For instance, white sharks (*Carcharodon carcharias*; four of five studies) and blue sharks (*Prionace glauca*; four of five studies) showed consistent deeper patterns, while other species such as the whale shark (*Rhincodon typus*) and the porbeagle shark (*Lamna nasus*), showed more variable patterns with lunar illumination. Four species displayed shallower patterns with increasing lunar illumination: the bull shark (*Carcharhinus leucas*), Galapagos shark (*Carcharhinus galapagensis*), oceanic whitetip shark (*Carcharhinus longimanus*) and the largetooth sawfish (*Pristis microdon*).

Deeper movements with increasing lunar illumination are likely predominantly driven by light-based predation strategies. Analogous to patterns of diel vertical migration (DVM), whereby individuals are deeper in the day and shallower at night in order to avoid visual predation (Hays 2003), animals may exhibit ‘lunar vertical migrations’ (LVM), following isolumes deeper with increasing lunar illumination (Last et al. 2016). For visual animals, full-moon nights can aid predators in detecting prey and/or prey in detecting predators (Palmer et al. 2022). Indeed, some of the clearest patterns of LSM in this study were from known visual predators with high visual acuity, such as white sharks (Strong Jr 1996) and swordfish (Fritsches, Brill & Warrant 2005). These patterns were also particularly evident among offshore epipelagic species, such as tuna, perhaps as such habitats are not constrained by bottom depth and are less influenced by tides. Conversely, for animals that move between coastal and offshore habitats, patterns became more variable, a pattern also noted in the DVM for such transient species. For instance, porbeagle sharks have shown plasticity in diel depth changes as a function of habitat type, demonstrating reverse DVM (shallower in the day and deeper

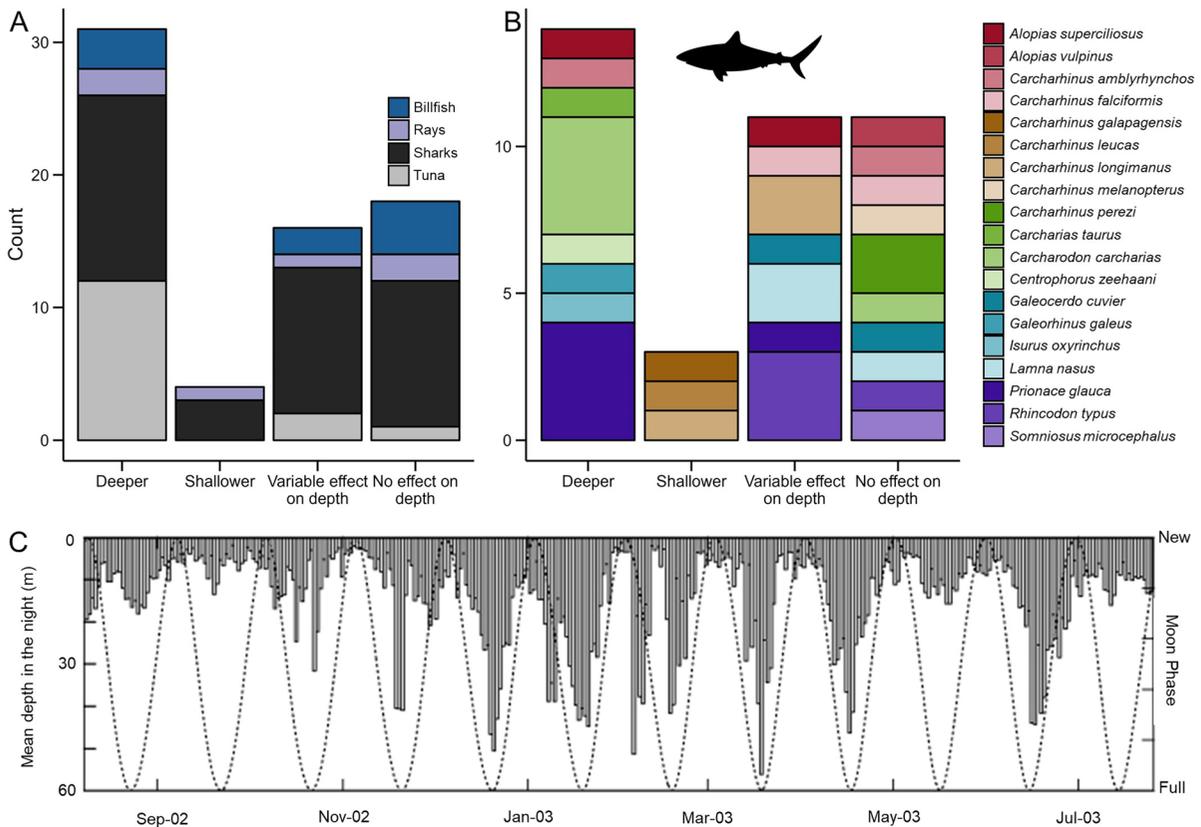


Fig. 4 Trends in depth with increased lunar illumination in published electronic tracking studies. **A** Depth trends observed across the four study taxa with increasing lunar illumination (excluding swordfish). Count refers to the number of studies recording each respective relationship. **B** Depth trends observed across shark species with increasing lunar illumina-

tion. **C** Lunar illumination and daily average nighttime depth of a tagged juvenile Pacific bluefin tun (*Thunnus orientalis*) in the eastern Pacific Ocean, revealing deeper movements during full moon periods. Figure reproduced, with permission, from Kitagawa et al. 2007.

at night) in well-mixed coastal waters and normal DVM in deeper, thermally well-stratified waters, likely reflecting patterns of their prey (Pade et al. 2009). Similarly, LVM may become less apparent in influencing the distribution and availability of prey as such transient species move inshore. For the few taxa that demonstrated reverse patterns of LVM (i.e., shallower with increasing lunar illumination), it has been suggested that individuals may be following prey into shallower water during a full moon (Whitty et al. 2009; Madigan et al. 2020). Though the motivation in such cases is somewhat unclear, it may be that a full moon provides a certain threshold of light required for such predators to visually hunt in shallow waters.

Catch

The effect of the lunar cycle on fisheries catch patterns was investigated by 134 independent analyses across 66 studies. Catch rate with increasing lunar illumination did not reveal consistent or clear directional patterns across taxa (Figure 3). However, looking at individual groups, billfish recorded the strongest directional relationship, indicating higher catch with increasing lunar illumination (Figure 3). This was likely due to the large representation of swordfish studies ($n = 29$) that were dominated by higher catch (Figure 5B), compared to ‘no effect’ prevailing among other billfish studies ($n = 18$; Figure 6A). For shark taxa, the absence of any significant effect of lunar illumination on catch was also the most

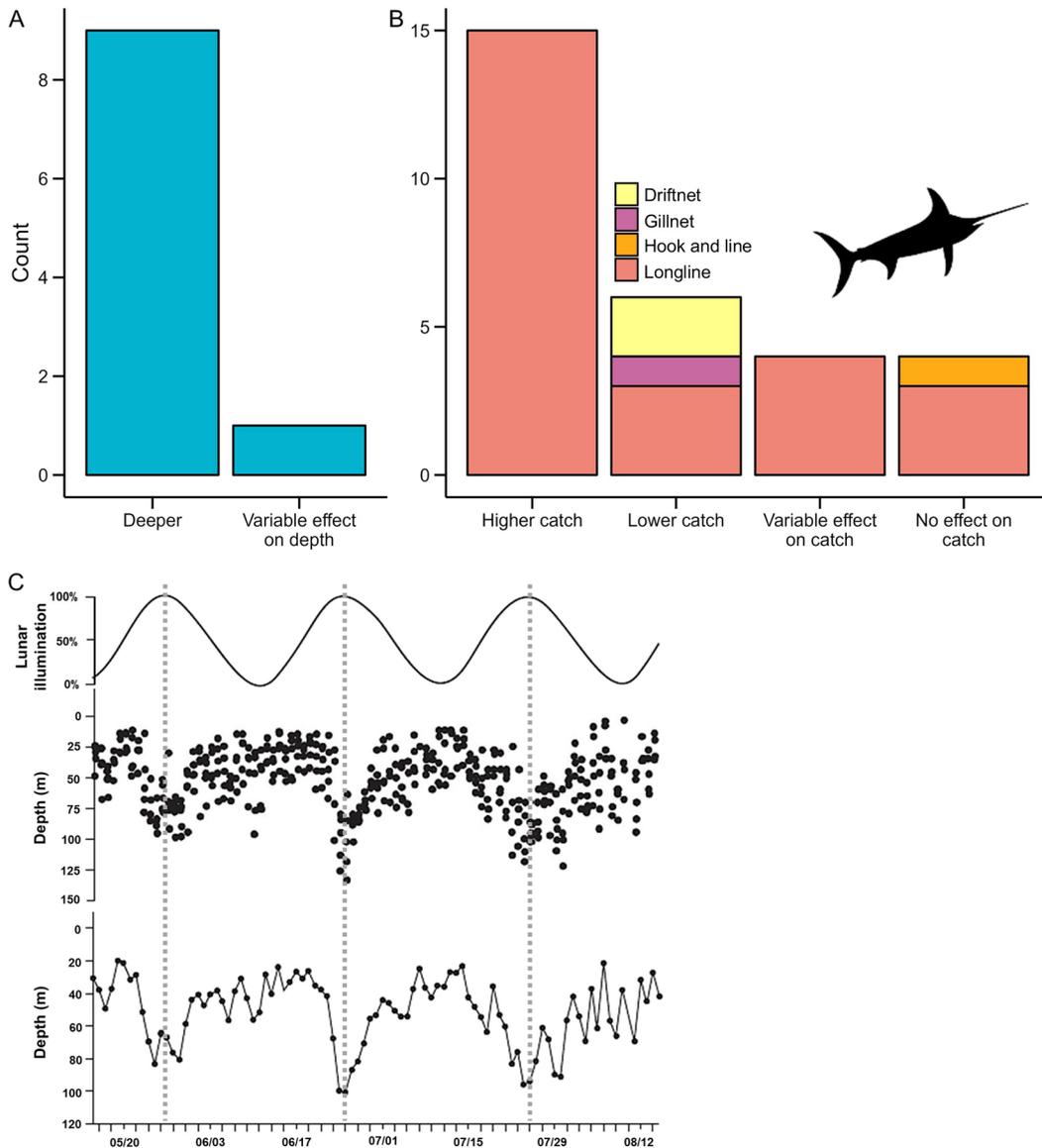


Fig. 5 Trends with increasing lunar illumination for swordfish (*Xiphias gladius*). Swordfish was the most studied species identified in this study, with 46 individual analyses from 33 unique studies evaluating the effect of the lunar cycle on patterns of swordfish movement or catch. **A** Depth trends with increasing lunar illumination. **B** Catch trends with increasing

lunar illumination colored by gear type. **C** Depth of a swordfish tracked over three lunar cycles in the western North Atlantic by Loefer et al. (2007). The top panel displays the lunar cycle, the middle panel the hourly mean of nocturnal depths, and the bottom panel the nightly mean depth. The dotted lines highlight the full moon period for each panel.

common relationship, being recorded in 50.8% of the 63 analyses. Conversely, tuna (n = 37) and ray (n = 7) catch showed no dominant trend with lunar illumination across analyses (Figure 6). For species that had a higher sample size of catch analyses (≥ 5), swordfish remained the only taxa with a clear pattern with

lunar illumination (Figure 6B). When incorporating gear type into catch patterns, some trends became more apparent (Figure 5B, 6C). Longline gears, for instance, resulted in higher catch with increasing lunar illumination for swordfish and many tuna taxa,

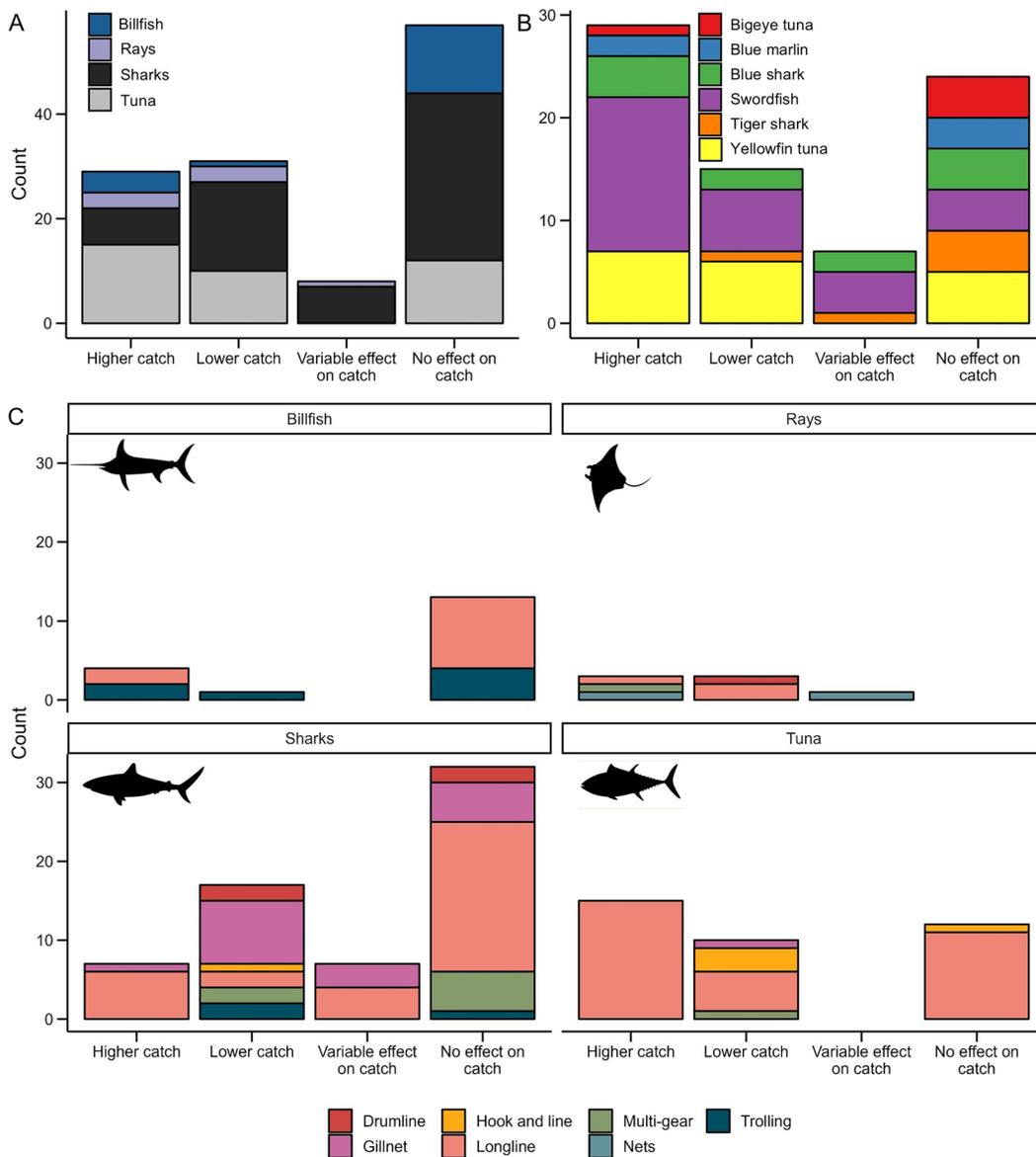


Fig. 6 Trends in catch with increased lunar illumination in published electronic tracking studies. **A** Catch trends observed across the four study taxa (excluding swordfish). **B** Catch

trends observed across species with ≥ 5 catch studies. **C** Trends in catch faceted by taxa and colored by fishing gear type.

while net gears (i.e. driftnets and gillnets) resulted in lower catch across shark taxa and swordfish.

Similar to vertical movement, the variation in catch rate observed throughout the lunar cycle may be attributed to visual cues. In the case of baited hooks associated with longlines, the full moon may

enhance visibility, aiding fish in locating bait, stimulating feeding activity, and consequently increasing the likelihood of being hooked (Draganik & Cholyst 1988; Hernandez-Milian et al. 2008). Conversely, for larger gears such as nets, the increased illumination may instead enhance the ability of fish to detect gear and therefore avoid capture (Akyol 2013; Lee et al. 2018). In contrast to the discernable

patterns in vertical movement associated with lunar illumination, catch patterns were relatively weak. This is likely due to the nuances and confounding factors of fishery-dependent approaches that we could not account for given the available data. Notably, the type and depth of gear deployed, type of bait used, set technique, time of day spent fishing, and adaptive behavior of fishers in response to the lunar cycle, are unlikely to be consistent between studies. For instance, the Italian swordfish gillnet fleet was recorded to stay in the harbor during full moon phases (Di Natale & Mangano 1995) and commercial swordfish fishers in the Florida Strait have previously been observed to adjust hook depth according to the lunar cycle (Lerner et al. 2013). Analyzing catch reports from large ranging fisheries (e.g. whole ocean basins) also introduces complexity in disentangling the variables that may impact catch outcomes. We hypothesize that, in general, fisheries catch is likely to be impacted by the lunar cycle, however, this will vary with gear, the target species of the fishery and environmental conditions.

Acoustic detections

The effect of the lunar cycle on acoustic detection data was investigated by 19 independent analyses across 16 studies on sharks ($n = 11$) and rays ($n = 5$). Approximately half of these studies revealed no effect ($n = 10$; Supplementary File 1), but several species-specific studies found significant directional responses to lunar illumination. Reef manta rays (*Mobula alfredi*), for instance, were highly represented in these significant responses ($n = 7$), yet relationships remained variable both within and between studies. Where directional responses did occur, they were often assumed to be associated with inshore-offshore movements between moon phases. For example, reef manta rays in island habitats were hypothesized to travel offshore (i.e. away from coastal receiver arrays) during full moon periods to follow the migration of zooplankton prey into deeper waters during these periods (Peel et al. 2019). Alternatively, mantas may select to spend more time in coastal waters during a new moon, coinciding with periods when demersal plankton emerge from the sediment in response to lower light conditions (Alldredge & King 1980; Couturier et al. 2018). Collectively, the high variability in the influence of lunar illumination

across acoustic studies may be due to the predominant deployment of acoustic receivers in coastal regions where patterns are also susceptible to influence from tides and other fine-scale coastal processes (Spaet et al. 2020).

Shark-human interactions

Global analyses of data from public shark attack files from 1970–2016 recorded no relationship between shark-human interactions and lunar illumination (Ritter, Amin & Zambesi 2013; French et al. 2021). However, location- and species-specific analyses produced mixed results. No effect on interactions were recorded in California (Ugoretz, Hellmers & Coates 2022) and Reunion Island (Taglioni et al. 2019), while lower rates of interactions were recorded in Florida with higher illumination (Burgess et al. 2010) and non-linear effects were reported in Brazil, with higher shark-human interaction rates predicted at both high and low lunar illumination (Hazin, Burgess & Carvalho 2008). Given that overlap between sharks and humans will predominantly occur in coastal habitats, patterns of presence here will, as described for acoustic detections, be dependent on other fine-scale coastal processes for both humans and sharks. For instance, for surfers, activity peaks will be heavily influenced by the tide and season, with ideal tide being site dependent. Overall, these interactions appear to have mixed relationships with lunar illumination, suggesting that they may be location and/or species specific.

Spawning rates

Spawning rates were analyzed in relation to lunar illumination in three studies (Margulies et al. 2007; Shimose, Yokawa & Tachihara 2013; Hazen et al. 2016). While lunar-influenced spawning has been documented in several coastal fish species (Taylor & Mills 2013), the extent to which pelagic fish species similarly respond to these cues is less clear. Pacific bluefin tuna increased their spawning fraction around the new moon (i.e. lower lunar illumination; Shimose, Yokawa & Tachihara 2013). However, higher lunar illumination increased the likelihood of spawning for Atlantic bluefin tuna in the Gulf of Mexico (*Thunnus thynnus*; Hazen et al. 2016) and increased egg production for yellowfin tuna in Panama (*Thunnus albacares*; Margulies et al. 2007). Additionally,

acceleration data from PSATs deployed on mahi-mahi (*Coryphaena hippurus*) were used to predict spawning events (Schlenker et al. 2021). Models trained on data from captive spawning mahi-mahi indicated that spawning predominantly occurs during the new moon phase. While this taxa was not a focus of this review, the methods used by Schlenker et al. (2021) could be applied to other spawning pelagic fish species, such as tuna.

Activity rates

Given the likely influence of water column illumination on visual predation, it was unsurprising that several studies noted correlations between activity, defined as heightened movement, and lunar illumination. For instance, researchers documented increased activity, as measured by accelerometers, in sailfish (*Istiophorus platypterus*) during the full moon, attributing this to increased light availability facilitating nighttime foraging (Pohlot & Ehrhardt 2018). Conversely, for sand tiger sharks (*Carcharias taurus*), higher activity was observed during the new moon, possibly reflecting their preference for hunting in low ambient light conditions (Kneebone et al. 2018). Tidal rhythms may also play a role in driving patterns in activity. Mixed vertical activity patterns were recorded in basking sharks (*Cetorhinus maximus*) in relation to lunar illumination, with tidal influences hypothesized as playing a significant role (Shepard et al. 2006). A more distinct pattern was observed in gray reef sharks (*Carcharhinus amblyrhynchos*), where activity in a French Polynesian atoll channel peaked during the full and new moons (Laurieux et al. 2024). During these periods, the sharks likely experienced heightened turbulence caused by stronger tidal currents.

Other relationships

Several additional response variables to lunar illumination were recorded in our meta-analysis, each supported by a single study (Supplementary File 1). Amongst many of these, no consistent relationships were found with lunar illumination. For example, sex ratios (white sharks; Robbins 2007), swimming orientation (scalloped hammerhead sharks (*Sphyrna lewini*); Klimley 1993), body temperature (blacktip reef sharks (*Carcharhinus melanopterus*);

Papastamatiou et al. 2015) and hooking time (shark sp.; Gulak & Carlson 2021) showed no clear relationship.

Section 3: Drivers of variability

Collectively, variation in response to lunar illumination among and within taxa was a common theme in this review. However, it is important to note that (1) the methods employed to measure the relationships between the lunar cycle and response variables exhibited considerable variability across studies, complicating comparisons, and (2) patterns are dynamic and likely influenced by a multitude of additional factors.

Methods varied among studies in several aspects, including how the lunar cycle was measured, whether additional lunar related variables (e.g. tide strength and direction) were considered, and how relationships were quantified. Firstly, it is important to acknowledge that understanding lunar relationships was not the primary goal of most studies (~83%), likely influencing the extent to which analyses were conducted. The most common measurements used were daily lunar illumination as a continuous variable (41.8%), closely followed by categorical lunar phases (e.g., new moon, quarter moon, full moon, three quarter moon; 40.3%). Approximately 6% of studies used lunar or synodic day as the measured lunar variable. Additionally, a few studies used irradiance data recorded directly from tagged sharks to estimate the stage of the lunar cycle (e.g. Klimley 1993), while one study developed a comprehensive moonlight index, incorporating in the percentage of lunar illumination, the angle of the moon, topographical features and percentage of cloud cover (Niella et al. 2021). For many studies, there was ambiguity regarding whether the data analysis focused solely on nighttime patterns or encompassed both diel periods, especially in fisheries research. For catch data, this is not surprising considering that reporting typically occurs at broader spatial and temporal scales, often prohibiting segregation of data into specific diel periods. For depth data, which is often recorded at a higher frequency and is therefore easier to parse into such periods, a majority of studies (61%) exclusively considered nighttime depth with lunar illumination. Conversely, eight studies modeled day and night separately and two considered the interaction between diel phases and lunar illumination. While we also originally aimed to assess tidal

effects across lunar studies, they were predominately discussed in a qualitative manner and measured separately or as an interaction in only a handful of studies, thus preventing detailed evaluation.

Several biological and environmental processes may also explain variation in responses to lunar illumination. Intraspecific variation is a common theme among movement and fisheries studies on large epipelagic fish species (e.g. Towner et al. 2016; Andrzejczek et al. 2020). Untangling the drivers behind these patterns can be challenging without detailed, species-specific analyses. However, they are likely linked to a combination of factors including geographic distribution, local prey availability and diversity, specific oceanographic conditions influencing water column structure, ontogenetic stage of the individual, and temporal scope of the study. In addition, investigating how individual size or body condition influences vertical distributions throughout the lunar cycle could offer insights within a state-dependent risk framework (Beltran et al. 2021; Palmer et al. 2022). For example, individuals with superior body condition may prioritize safety in the deeper and darker depths during a full moon, whereas others may risk a higher chance of predation to forage in shallower, more illuminated

depths during this period. Interspecific variation in catch and movement patterns is also prevalent among multi-species comparative studies, driven by factors such as geographic and vertical distribution, foraging strategies, and sensory perception (e.g. Block et al. 2011; Andrzejczek et al. 2022; Haulsee et al. 2022). For instance, the degree to which a species can utilize its visual system to perceive its environment (i.e. see Collin 2018) is likely to play a role in determining its vertical distribution and susceptibility to fishing gears under varying lunar illuminations. Furthermore, the response of prey to the lunar cycle is expected to vary among species, thereby potentially influencing the distribution of their predators. The extent to which species adhere to an endogenous biological rhythm or a ‘circalunar’ clock, as opposed to merely responding to direct external cues (e.g., changing light levels), will further contribute to individual variability observed across the lunar cycle (Benoit-Bird, Au & Wisdom 2009; Ikegami, Takeuchi & Takekura 2014). While these rhythms are well studied for synchronized spawning events, especially in coral species, they may also play a role in shaping movement behaviors, such as diel migration patterns. For instance, the nocturnal horizontal migration of a

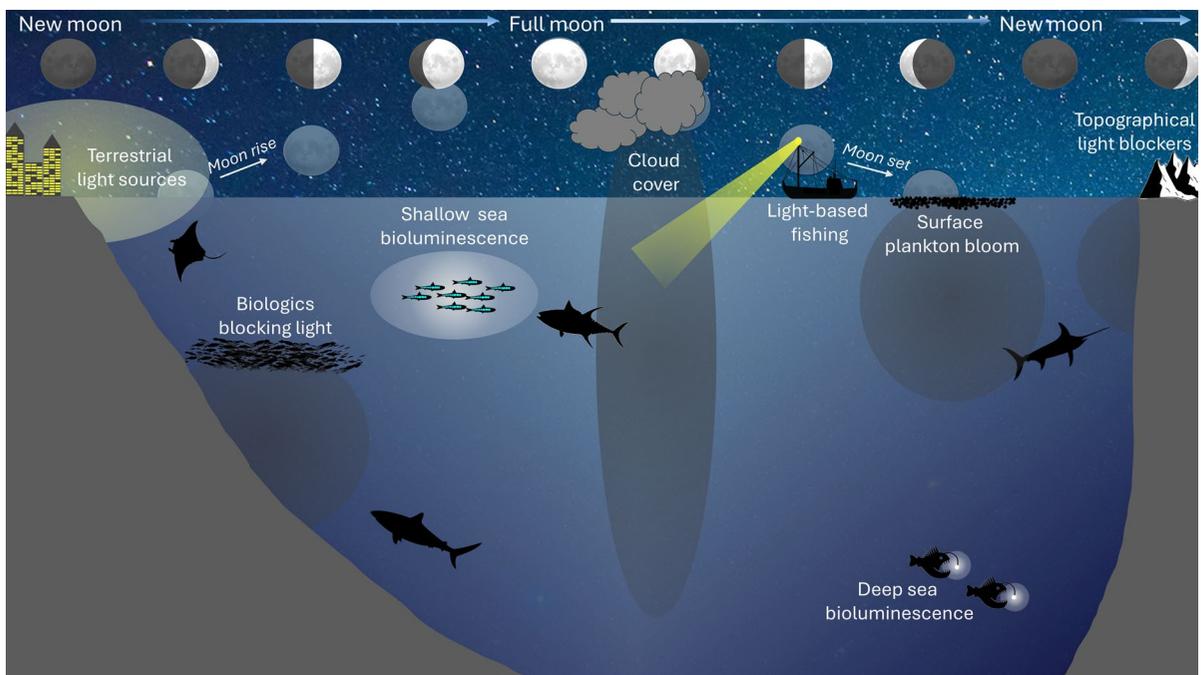


Fig. 7 Simplified representation of light sources in the marine environment throughout the lunar cycle.

nearshore scattering layer in Hawaii was influenced by the lunar phase, even when light availability and the lunar cycle were decoupled, suggesting an endogenous lunar rhythm rather than a direct causation by the lunar cycle (Benoit-Bird, Au & Wisdom 2009). Applying this decoupling approach in other systems could enhance our understanding of these ‘circalunar clocks’.

For those species responding to external light cues, fine-scale factors influencing light availability in the water column will likely affect the degree of a lunar response (e.g., cloud cover, turbidity, topography, day length; Figure 7). In addition, the timing of moonrise and moonset will influence light availability throughout the night (Tracey et al. 2023). Considering that these factors are likely to vary significantly across time and space, they likely contribute substantially to the variability observed across the studies in this meta-analysis.

Section 4: Best practices for future studies

Ideally, future studies investigating responses to the lunar cycle would incorporate all aforementioned sources of variability within their analyses. However, this is logistically infeasible, especially in studies where lunar responses are not the primary focus. In lieu of this, we propose practical and analytical priorities that would not only aid in uncovering the underlying processes driving the observed patterns, but also standardize methods to facilitate comparisons between studies.

In practice, studies would be best served by measuring lunar-related variables directly in the field. For instance, measuring both light availability and tidal parameters such as tidal phase, time to high tide, and tidal range *in situ* would assist in disentangling the effects of these two processes. Tagging studies, which typically collect finer-scale temporal and positional data, inherently possess greater capacity to accomplish this when compared to fisheries studies that are based on catch records. For PSATs, the most common tag type used for recording vertical movements in epipelagic fish, harnessing the existing and highly sensitive light sensors on the tags could provide a direct and accurate means of assessing whether individuals maintain a consistent isolume throughout the lunar cycle. Similarly, deploying light sensors on fishing gears could provide a tool to evaluate

how catch rates fluctuate in response to nighttime light availability. This approach will help disentangle other factors that affect light availability at depth, such as cloud cover and water turbidity. Additionally, comparing trends in *in situ* light data across a lunar cycle with predictions based on daily lunar illumination metrics will help assess how accurately the latter approximates variability in light input into the marine environment. Collecting positional information where applicable will also be beneficial for aligning with relevant tide data (further discussed below), such as the nearest tide gauges. Where possible, detailed information pertaining to catch records should be taken, especially in relation to deployment period and depth.

As our analytical toolbox grows, so do the strategies for effectively using lunar data to examine animal behaviors at sea. Overall, we recommend using modeling approaches, such as generalized additive models, that can account for non-linear and spatially and/or temporally correlated data and random effects, when modeling environmental associations (Zuur et al. 2009; Mull et al. 2022). If feasible, we advise testing relationships across individual animals to account for intraspecific variation. Indeed, several tagging studies that adopted this approach found variable effects among individuals (e.g. Musyl et al. 2011; Braun et al. 2014). The response variable should be measured at the highest frequency possible, such as hourly for depth data or by diel phase for catch data. However, we recognize that achieving this level of precision may not always be feasible due to limitations in available data resolution. For explanatory variables, we firstly recommend modeling daily lunar illumination as a continuous variable (when ambient light cannot be measured directly), a variable most frequently obtained in our review from the United States Naval Observatory website (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). This approach reduces the loss of statistical power that occurs when this continuous variable is instead treated as categorical (deBruyn & Meeuwig 2001; Stevenson & Millar 2013). Where accurate positional and cloud coverage data is available, we instead recommend considering the moonlight index (Niella et al. 2021), although we acknowledge that such data is often unavailable (but see Copernicus Climate Change Service (C3S), Climate Data Store (CDS), (2022)). For tidal variables, we suggest using continuous variables of time to high

tide and tidal range. These data can be acquired either from local tidal gauges (if available) or from tidal models, such as the Oregon State University Tidal Model Driver (Egbert & Erofeeva 2002; Peel et al. 2019). Finally, we also suggest incorporating interaction effects, such as ‘lunar illumination and diel phase’ and ‘lunar illumination and tidal phase’ (e.g. see Couturier et al. 2018), to more thoroughly disentangle the various processes involved in the lunar cycle.

Concluding paragraph

This is the first comprehensive review to examine the effects of the lunar cycle on the ecology of large, epipelagic fishes. Our meta-analysis revealed substantial variability within and across studies, likely attributable to a multitude of factors, including inconsistencies in methodologies, analyses and reporting standards. Notably, tagging studies revealed the clearest trends, likely due to the higher resolution of available information facilitating the detection of behavioral changes. Adhering to the best practices proposed in this study will be instrumental for advancing our understanding of the complex dynamics of lunar effects in marine ecosystems. Incorporating these more detailed methods may reveal that trends observed in earlier studies using coarser resolutions of lunar-related variables may change or strengthen upon re-analysis.

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Data availability All data used in this manuscript are provided in Supplementary File 1.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

References

Akyol O (2013) The influence of the moon phase on the CPUEs of Swordfish Gillnet Fishery in the Aegean Sea, Turkey. *Turkish J Fish Aquat Sciences* 13:54

- Allredge AL, King JM (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. *J Exp Marine Biol Ecol* 44:133–156
- Andrzejaczek S, Chapple TK, Curnick DJ, Carlisle AB, Castleton M, Jacoby DMP, Peel LR, Schallert RJ, Tickler DM, Block BA (2020) Individual variation in residency and regional movements of reef manta rays *Mobula alfredi* in a large marine protected area. *Marine Ecol Prog Ser* 639:137–153
- Andrzejaczek S, Gleiss AC, Pattiaratchi CB, Meekan MG (2019) Patterns and drivers of vertical movements of the large fishes of the epipelagic. *Rev Fish Biol Fish* 29:335–354
- Andrzejaczek, S., Lucas, T.C.D., Goodman, M.C., Hussey, N.E., Armstrong, A.J., Carlisle, A., Coffey, D.M., Gleiss, A.C., Huvneers, C., Jacoby, D.M.P., Meekan, M.G., Mourier, J., Peel, L.R., Abrantes, K., Afonso, A.S., Ajemian, M.J., Anderson, B.N., Anderson, S.D., Araujo, G., Armstrong, A.O., Bach, P., Barnett, A., Bennett, M.B., Bezerra, N.A., Bonfil, R., Boustany, A.M., Bowlby, H.D., Branco, I., Braun, C.D., Brooks, E.J., Brown, J., Burke, P.J., Butcher, P., Castleton, M., Chapple, T.K., Chateau, O., Clarke, M., Coelho, R., Cortes, E., Couturier, L.I.E., Cowley, P.D., Croll, D.A., Cuevas, J.M., Curtis, T.H., Dagorn, L., Dale, J.J., Daly, R., Dewar, H., Doherty, P.D., Domingo, A., Dove, A.D.M., Drew, M., Dudgeon, C.L., Duffy, C.A.J., Elliott, R.G., Ellis, J.R., Erdmann, M.V., Farrugia, T.J., Ferreira, L.C., Ferretti, F., Filmlalter, J.D., Finucci, B., Fischer, C., Fitzpatrick, R., Forget, F., Forsberg, K., Francis, M.P., Franks, B.R., Gallagher, A.J., Galvan-Magana, F., García, M.L., Gaston, T.F., Gillanders, B.M., Gollock, M.J., Green, J.R., Green, S., Griffiths, C.A., Hamerschlag, N., Hasan, A., Hawkes, L.A., Hazin, F., Heard, M., Hearn, A., Hedges, K.J., Henderson, S.M., Holdsworth, J., Holland, K.N., Howey, L.A., Hueter, R.E., Humphries, N.E., Hutchinson, M., Jaine, F.R.A., Jorgensen, S.J., Kanive, P.E., Labaja, J., Lana, F.O., Lassaue, H., Lipscombe, R.S., Llewellyn, F., Macena, B.C.L., Mambrasar, R., McAllister, J.D., McCully Phillips, S.R., McGregor, F., McMillan, M.N., McNaughton, L.M., Mendonça, S.A., Meyer, C.G., Meyers, M., Mohan, J.A., Montgomery, J.C., Mucientes, G., Musyl, M.K., Nasby-Lucas, N., Natanson, L.J., O’Sullivan, J.B., Oliveira, P., Papastamtiou, Y.P., Patterson, T.A., Pierce, S.J., Queiroz, N., Radford, C.A., Richardson, A.J., Richardson, A.J., Righton, D., Rohner, C.A., Royer, M.A., Saunders, R.A., Schaber, M., Schallert, R.J., Scholl, M.C., Seitz, A.C., Semmens, J.M., Setyawan, E., Shea, B.D., Shidqi, R.A., Shillinger, G.L., Shipley, O.N., Shivji, M.S., Sianipar, A.B., Silva, J.F., Sims, D.W., Skomal, G.B., Sousa, L.L., Southall, E.J., Spaet, J.L.Y., Stehfest, K.M., Stevens, G., Stewart, J.D., Sulikowski, J.A., Syakurachman, I., Thorrold, S.R., Thums, M., Tickler, D., Tolloti, M.T., Townsend, K.A., Travassos, P., Tyminski, J.P., Vaudo, J.J., Veras, D., Wantiez, L., Weber, S.B., Wells, R.J.D., Weng, K.C., Wetherbee, B.M., Williamson, J.E., Witt, M.J., Wright, S., Zilliaccus, K., Block, B.A. & Curnick, D.J. (2022) Diving into the vertical dimension of elasmobranch movement ecology. *Science Advances*, 8, eabo1754.

- Beltran RS, Kendall-Bar JM, Pirota E, Adachi T, Naito Y, Takahashi A, Cremers J, Robinson PW, Crocker DE, Costa DP (2021) Lightscales of fear: how mesopredators balance starvation and predation in the open ocean. *Sci Adv* 7:eabd9818
- Benoit-Bird KJ, Au WWL, Wisdom DW (2009) Nocturnal light and lunar cycle effects on diel migration of micronekton. *Limnol Oceanogr* 54:1789–1800
- Best, E (1929) Fishing methods and devices of the Maori. *Dominion Museum Bulletin No. 12*. Government Printer, Wellington.
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Braun CD, Kaplan MB, Horodysky AZ, Llopiz JK (2015) Satellite telemetry reveals physical processes driving billfish behavior. *Anim Biotelemetry* 3:2
- Braun CD, Skomal GB, Thorrold SR, Berumen ML (2014) Diving behavior of the reef manta ray links coral reefs with adjacent deep pelagic habitats. *PLoS One* 9:e88170
- Burgess, G.H., Buch, R.H., Carvalho, F., Garner, B.A. & Walker, C.J (2010) Factors contributing to shark attacks on humans: A Volusia County, Florida, case study. *Sharks and their Relatives II* (eds J. Carrier, J. Musick & H. M.), pp. 557–582. CRC Press, Boca Raton.
- Collin SP (2018) Scene through the eyes of an apex predator: a comparative analysis of the shark visual system. *Clin Exp Optometry* 101:624–640
- Couturier LIE, Newman P, Jaine FRA, Bennett MB, Venables WN, Cagua EF, Townsend KA, Weeks SJ, Richardson AJ (2018) Variation in occupancy and habitat use of *Mobula alfredi* at a major aggregation site. *Marine Ecol Prog Ser* 599:125–145
- deBruyn AMH, Meeuwig JJ (2001) Detecting lunar cycles in marine ecology: periodic regression versus categorical ANOVA. *Marine Ecol Prog Ser* 214:307–310
- Di Natale A, Mangano A (1995) Moon phases influence on CPUE: a first analysis of swordfish driftnet catch data from the Italian fleet between 1990 and 1991. *Col Vol Sci Pap ICCAT* 44:264–267
- Draganik B, Cholyst J (1988) Temperature and moonlight as stimulators for feeding activity by swordfish. *Col Vol Sci Pap ICCAT* 27:305–314
- Egbert GD, Erofeeva SY (2002) Efficient inverse modeling of barotropic ocean tides. *J Atmospheric Oceanic Technol* 19:183–204
- French LA, Midway SR, Evans DH, Burgess GH (2021) Shark side of the moon: are shark attacks related to lunar phase? *Front Marine Sci* 8:745221
- Fritsches KA, Brill RW, Warrant EJ (2005) Warm eyes provide superior vision in swordfishes. *Curr Biol* 15:55–58
- Gulak SJB, Carlson JK (2021) Less soak time saves those upon the line: capture times and hooking mortality of sharks caught on bottom longlines. *North Am J Fish Manag* 41:791–808
- Hamilton RJ, Giningele M, Aswani S, Ecochard JL (2012) Fishing in the dark-local knowledge, night spearfishing and spawning aggregations in the Western Solomon Islands. *Biol Conserv* 145:246–257
- Haulsee DE, Blondin HE, Logan RK, Crowder LB (2022) Where do the billfish go? Using recreational catch data to relate local and basin scale environmental conditions to billfish occurrence in the Eastern Tropical Pacific. *Fish Oceanogr* 31:135–148
- Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163–170
- Hazen EL, Carlisle AB, Wilson SG, Ganong JE, Castleton MR, Schallert RJ, Stokesbury MJW, Bograd SJ, Block BA (2016) Quantifying overlap between the deepwater horizon oil spill and predicted bluefin tuna spawning habitat in the Gulf of Mexico. *Sci Rep* 6:33824
- Hazin FH, Burgess GH, Carvalho FC (2008) A shark attack outbreak off Recife, Pernambuco, Brazil: 1992–2006. *Bull Marine Sci* 82:199–212
- Hernandez-Milian G, Goetz S, Varela-Dopico C, Rodriguez-Gutierrez J, Romón-Olea J, Fuertes-Gamundi JR, Ulloa-Alonso E, Tregenza NJC, Smerdon A, Otero MG, Tato V, Wang J, Santos MB, López A, Lago R, Portela JM, Pierce GJ (2008) Results of a short study of interactions of cetaceans and longline fisheries in Atlantic waters: environmental correlates of catches and depredation events. In: Valavanis VD (ed) *Essential Fish Habitat Mapping in the Mediterranean*. Springer, Netherlands, Dordrecht, pp 251–268
- Ikegami, T., Takeuchi, Y. & Takemura, A (2014) Lunar Clock in Fish Reproduction. *Annual, Lunar, and Tidal Clocks: Patterns and Mechanisms of Nature's Enigmatic Rhythms* (eds H. Numata & B. Helm), pp. 163–178. Springer Japan, Tokyo.
- Kaartvedt S, Langbehn TJ, Aksnes DL (2019) Enlightening the ocean's twilight zone. *ICES J Marine Sci* 76:803–812
- Kitagawa T, Boustany AM, Farwell CJ, Williams TD, Castleton MR, Block BA (2007) Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean. *Fish Oceanogr* 16:409–421
- Kitolelei S, Thaman R, Veitayaki J, Breckwoldt A, Piovano S (2021) Na vuku makawa ni qoli: indigenous fishing knowledge (IFK) in Fiji and the Pacific. *Front Marine Sci* 8:684303
- Klimley A (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biol* 117:1–22
- Kneebone J, Winton M, Danylchuk A, Chisholm J, Skomal GB (2018) An assessment of juvenile sand tiger (*Carcharias taurus*) activity patterns in a seasonal nursery using accelerometer transmitters. *Environ Biol Fish* 101:1739–1756
- Last KS, Hobbs L, Berge J, Brierley AS, Cottier F (2016) Moonlight drives ocean-scale mass vertical migration of zooplankton during the Arctic Winter. *Curr Biol* 26:244–251
- Laurioux A, Huvneers C, Papastamatiou Y, Planes S, Ballesta L, Mourier J (2024) Abiotic drivers of the space use and activity of gray reef sharks *Carcharhinus amblyrhynchos* in a dynamic tidal environment. *J Fish Biolog.* <https://doi.org/10.1111/jfb.15825>

- Lee KA, Roughan M, Harcourt RG, Peddemors VM (2018) Environmental correlates of relative abundance of potentially dangerous sharks in nearshore areas, southeastern Australia. *Marine Ecol Prog Ser* 599:157–179
- Lerner J, Levesque JC, Talaue-McManus L (2017) Recreational swordfish (*Xiphias gladius*) fishery: angler practices in South Florida (USA). *Fishes*. <https://doi.org/10.3390/fishes2040018>
- Lerner JD, Kerstetter DW, Prince ED, Talaue-McManus L, Orbesen ES, Mariano A, Snodgrass D, Thomas GL (2013) Swordfish vertical distribution and habitat use in relation to diel and lunar cycles in the western North Atlantic. *Trans Am Fish Soc* 142:104
- Loefer JK, Sedberry GR, McGovern JC (2007) Nocturnal depth distribution of western North Atlantic swordfish (*Xiphias gladius*, Linnaeus, 1758) in relation to lunar illumination. *Gulf Caribbean Res* 19(2):83–88
- Madigan DJ, Richardson AJ, Carlisle AB, Weber SB, Brown J, Hussey NE (2020) Water column structure defines vertical habitat of twelve pelagic predators in the South Atlantic. *ICES J Marine Sci* 78:867
- Margulies D, Sutter JM, Hunt SL, Olson RJ, Scholey VP, Wexler JB, Nakazawa A (2007) Spawning and early development of captive yellowfin tuna (*Thunnus albacares*). *Fish Bull* 105:249–265
- Mull, C.G., Andrzejczek, S., Udyawer, V. & Dwyer, R.G. (2022) Advances in Methods, Understanding, and Applications of Elasmobranch Movement Ecology. *Biology of sharks and their relatives* (eds J.C. Carrier, C. Simpfendorfer, M.R. Heithaus & K.E. Yopak). CRC Press.
- Musyl MK, Brill RW, Curran DS, Fragoso NM, McNaughton LM, Nielsen A, Kikkawa BS, Moyes CD (2011) Post-release survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fish Bull* 109:341–368
- Niella Y, Wiefels A, Almeida U, Jaquemet S, Lagabrielle E, Harcourt R, Peddemors V, Guyomard D (2021) Dynamics of marine predators off an oceanic island and implications for management of a preventative shark fishing program. *Marine Biol* 168:42
- Olander, D (2022) How Moon Phase Affects Fishing Success. *Sport Fishing*.
- Pade NG, Queiroz N, Humphries NE, Witt MJ, Jones CS, Noble LR, Sims DW (2009) First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: area fidelity, wider-scale movements and plasticity in diel depth changes. *J Exp Marine Biol Ecol* 370:64–74
- Palmer MS, Gaynor KM, Becker JA, Abraham JO, Mumma MA, Pringle RM (2022) Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends Ecol Evolution* 37:911–925
- Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? *PLoS One* 10:e0127807
- Peel LR, Stevens GMW, Daly R, Keating Daly CA, Lea JSE, Clarke CR, Collin SP, Meekan MG (2019) Movement and residency patterns of reef manta rays *Mobula alfredi* in the Amirante Islands, Seychelles. *Marine Ecol Prog Ser* 621:169–184
- Pohlot BG, Ehrhardt N (2018) An analysis of sailfish daily activity in the Eastern Pacific Ocean using satellite tagging and recreational fisheries data. *ICES J Marine Sci* 75:871–879
- Queiroz N, Humphries NE, Couto A, Vedor M, da Costa I, Sequeira AMM, Mucientes G, Santos AM, Abascal FJ, Abercrombie DL, Abrantes K, Acuña-Marrero D, Afonso AS, Afonso P, Anders D, Araujo G, Arauz R, Bach P, Barnett A, Bernal D, Berumen ML, Bessudo Lion S, Bezerra NPA, Blaison AV, Block BA, Bond ME, Bonfil R, Bradford RW, Braun CD, Brooks EJ, Brooks A, Brown J, Bruce BD, Byrne ME, Campana SE, Carlisle AB, Chapman DD, Chapple TK, Chisholm J, Clarke CR, Clua EG, Cochran JEM, Crochelet EC, Dagorn L, Daly R, Cortés DD, Doyle TK, Drew M, Duffy CAJ, Eriksson T, Espinoza E, Ferreira LC, Ferretti F, Filmlalter JD, Fischer GC, Fitzpatrick R, Fontes J, Forget F, Fowler M, Francis MP, Gallagher AJ, Gennari E, Goldsworthy SD, Gollock MJ, Green JR, Gustafson JA, Guttridge TL, Guzman HM, Hammerschlag N, Harman L, Hazine FHV, Heard M, Hearn AR, Holdsworth JC, Holmes BJ, Howey LA, Hoyos M, Hueter RE, Hussey NE, Huvneers C, Irion DT, Jacoby DMP, Jewell OJD, Johnson R, Jordan LKB, Jorgensen SJ, Joyce W, Keating Daly CA, Ketchum JT, Klimley AP, Kock AA, Koen P, Ladino F, Lana FO, Lea JSE, Llewellyn F, Lyon WS, MacDonnell A, Macena BCL, Marshall H, McAllister JD, McAuley R, Mejer MA, Morris JJ, Nelson ER, Papastamatiou YP, Patterson TA, Peñaherrera-Palma C, Pepperell JG, Pierce SJ, Poisson F, Quintero LM, Richardson AJ, Rogers PJ, Rohner CA, Rowat DRL, Samoilyns M, Semmens JM, Sheaves M, Shillinger G, Shivji M, Singh S, Skomal GB, Smale MJ, Snyders LB, Soler G, Soria M, Stehfest KM, Stevens JD, Thorrold SR, Tolotti MT, Towner A, Travassos P, Tyminski JP, Vandeperre F, Vaudo JJ, Watanabe YY, Weber SB, Wetherbee BM, White TD, Williams S, Zárte PM, Harcourt R, Hays GC, Meekan MG, Thums M, Irigoien X, Eguiluz VM, Duarte CM, Sousa LL, Simpson SJ, Southall EJ, Sims DW (2019) Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* 572:461–466
- Queiroz N, Humphries NE, Mucientes G, Hammerschlag N, Lima FP, Scales KL, Miller PI, Sousa LL, Seabra R, Sims DW (2016) Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proc Natl Acad Sci* 113:1582
- Ravache A, Bourgeois K, Thibault M, Dromzée S, Weimerskirch H, de Grissac S, Prudor A, Lorrain A, Menkes C, Allain V, Bustamante P, Letourneur Y, Vidal É (2020) Flying to the moon: lunar cycle influences trip duration and nocturnal foraging behavior of the wedge-tailed shearwater *Ardenna pacifica*. *J Exp Marine Biol Ecol* 525:151322
- Ritter E, Amin R, Zambesi A (2013) Do lunar cycles influence shark attacks? *Open Fish Sci J* 6:71–74
- Robbins RL (2007) Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia. *J Fish Biol* 70:1350–1364
- Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement,

- behaviour and habitat use: a review. *Rev Fish Biol Fish* 24:1089–1103
- Schlenker LS, Faillettaz R, Stieglitz JD, Lam CH, Hoenig RH, Cox GK, Heuer RM, Pasparakis C, Benetti DD, Paris CB, Grosell M (2021) Remote predictions of mahi-mahi (*Coryphaena hippurus*) spawning in the open ocean using summarized accelerometry data. *Front Marine Sci* 8:626082
- Shepard EL, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecol Prog Ser* 328:205
- Shimose T, Yokawa K, Tachihara K (2013) Higher catch rates around the full moon for blue marlin, *Makaira nigricans*, in a diurnal trolling fishery. *Bull Marine Sci* 89:759–765
- Spaet JLY, Manica A, Brand CP, Gallen C, Butcher PA (2020) Environmental conditions are poor predictors of immature white shark *Carcharodon carcharias* occurrences on coastal beaches of eastern Australia. *Marine Ecol Progr Ser* 653:167–179
- Stevenson BC, Millar RB (2013) Promising the moon? Evaluation of indigenous and lunar fishing calendars using semiparametric generalized mixed models of recreational catch data. *Environ Ecol Statistics* 20:591–608
- Strong Jr, W.R (1996) Shape Discrimination and Visual Predatory Tactics in White Sharks *Great white sharks: the biology of Carcharodon carcharias* (eds A.P. Klimley & A.D. Ainley), pp. 229–240. Academic Press, New York.
- Taglioni F, Guiltat S, Teurlai M, Delsaut M, Payet D (2019) A spatial and environmental analysis of shark attacks on reunion Island (1980–2017). *Marine Policy* 101:51–62
- Taylor BM, Mills JS (2013) Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. *Coral Reef* 32:1077–1087
- Towner AV, Leos-Barajas V, Langrock R, Schick RS, Smale MJ, Kaschke T, Jewell OJD, Papastamatiou YP (2016) Sex-specific and individual preferences for hunting strategies in white sharks. *Funct Ecol*. <https://doi.org/10.1111/1365-2435.12613>
- Tracey SR, Wolfe BW, Hartmann K, Pepperell J, Williams SM (2023) Movement behavior of swordfish provisions connectivity between the temperate and tropical southwest Pacific Ocean. *Sci Rep* 13:11812
- Ugoretz J, Hellmers EA, Coates JH (2022) Shark incidents in California 1950–2021; frequency and trends. *Front Marine Sci*. <https://doi.org/10.3389/fmars.2022.1020187>
- Ward CRE, Bouyoucos IA, Brooks EJ, O’Shea OR (2019) Novel attachment methods for assessing activity patterns using triaxial accelerometers on stingrays in the Bahamas. *Marine Biol* 166:53
- Whitty JM, Morgan DL, Peverell SC, Thorburn DC, Beatty SJ (2009) Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. *Marine Freshw Res* 60:306–316
- Worm B, Orofino S, Burns ES, D’Costa NG, Manir Feitosa L, Palomares MLD, Schiller L, Bradley D (2024) Global shark fishing mortality still rising despite widespread regulatory change. *Science* 383:225–230
- Young RE, Kampa EM, Maynard SD, Mencher FM, Roper CFE (1980) Counterillumination and the upper depth limits of midwater animals. *Deep Sea Research Part A. Oceanogr Res P* 27:671–691
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M (2009) *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

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