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RESEARCH

Net illumination is more effective for reducing fisheries bycatch at night

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Abstract Coastal gillnet fisheries allow fishers to target multiple species, thus increasing their ability to handle variability and uncertainty. However, gillnets can incur high bycatch of threatened marine megafauna. One emerging strategy to reduce marine megafauna bycatch is net illumination, which is thought to utilize differences in behavior or visual capacity between bycatch and target species. Although testing of net illumination has expanded into multiple coastal gillnet fisheries over the past decade, its effects have only been studied at night. To address this important knowledge gap, we compared the effects of net illumination on total and species-specific bycatch, target fish catch, and catch value across day and night periods in a coastal gillnet fishery along Mexico's Baja California peninsula with among the highest reported marine megafauna bycatch rates worldwide. Using paired trials, we found that gillnet illumination significantly reduced total fisheries, elasmobranch, Humboldt squid, and finfish bycatch at night, with no reductions observed during the day. Furthermore, we found that the magnitude of nighttime bycatch reductions was significantly greater than the magnitude of daytime reductions for total fisheries and elasmobranch bycatch. By contrast, target fish catch and value were maintained across each illumination and time of day treatment. These results improve our understanding of this emerging bycatch reduction technology, while providing a framework to assess the effects of net

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illumination across day and night periods in passive net fisheries worldwide.

Keywords Bycatch reduction technology · Artificial illumination · Coastal gillnet fisheries · Elasmobranch · Fisheries management · Gear modification · Sea turtle · Visual cues

Introduction

Fisheries play a critical role in sustaining human livelihoods through food security and employment (FAO 2022; Rousseau et al. 2019). Yet modern fisheries are increasingly facing environmental and economic variability and uncertainty due to factors such as overfishing, globalization, emerging diseases and pandemics, and climate change (Finkbeiner 2015; Islam & Chuenpagdee 2022; Johnson & Welch 2009). Gillnets are a globally ubiquitous fishing gear that typically allow fishers to target multiple species in coastal systems (as opposed to specialist fisheries), thus increasing fisher resilience by reducing risk (Finkbeiner 2015; He et al. 2021). However, one of the most pronounced issues affecting the management of coastal gillnet fisheries is bycatch, or the unintended capture of non-target species (Davies et al. 2009; Lewison et al. 2004; Lively & McKenzie 2023; Northridge et al. 2017; Shester & Micheli 2011).

Bycatch can have important population-level effects on non-target species, which can lead to changes in species diversity and ecosystem function (Bonanomi et al. 2017; Crowder & Murawski 1998; Gray & Kennelly 2018; Hall et al. 2000; Lewison et al. 2004, 2014). Marine megafauna, such as sea turtles, seabirds, elasmobranchs, and marine mammals, are especially vulnerable to the detrimental effects of bycatch due to their life history characteristics (e.g., long lifespans, late maturity, and low reproductive output; Bonanomi et al. 2017; Hall et al. 2000; Lewison et al. 2004, 2014; Liles et al. 2017; Senko et al. 2014a). Relative to other gear types, small-scale gillnet fisheries incur some of the highest reported bycatch rates for marine megafauna and total bycatch (Gray & Kennelly 2018; Lewison et al. 2014; Senko et al. 2014a; Senko et al. 2022; Shester & Micheli 2011; Wallace et al. 2013).

Existing strategies to mitigate marine megafauna bycatch include time-area closures, gear modifications, and to a lesser extent, bycatch quotas and buyouts (Senko et al. 2014b). Among these, gear modifications may offer some comparative advantages (Senko et al. 2014b). For example, unlike spatial or temporal closures, gear modifications allow fishers to continue operating in their preferred locations and seasons, avoid redistributing bycatch impacts, and may be favored by fishers when target catch is maintained, as their use can prevent fishery closures (Senko et al. 2014b). In particular, illuminating gillnets at night has been shown to maintain target fish catch while reducing bycatch of sea turtles (Allman et al. 2020; Bielli et al. 2020; Darquea et al. 2020; Gautama et al. 2022; Kakai 2019; Ortiz et al. 2016; Snape et al. 2024; Virgili et al. 2018; Wang et al. 2010, 2013), seabirds (Bielli et al. 2020; Mangel et al. 2018), marine mammals (Bielli et al. 2020), elasmobranchs (Senko et al. 2022; Snape et al. 2024), Humboldt squid (Senko et al. 2022), and total fisheries bycatch (Senko et al. 2022). However, results have not been universally positive, with some studies reporting no effect or even increased bycatch (Field et al. 2019; Jančič et al. 2025; Martínez-Baños & Maynou 2018; Post et al. 2024; Sigurdsson 2023). These results and the limited number of studies highlight the need to conduct further research to better understand how bycatch and target catch respond to net illumination and the factors that drive these responses.

Despite over a decade of net illumination research, the mechanisms driving bycatch reductions remain unclear. Net illumination is thought to deter non-target species by providing a visual cue, with effectiveness likely influenced by changes in ambient light levels, such as differences between day and night. However, no study has compared the efficacy of net illumination during the day versus the night, limiting our understanding of how responses to net illumination may vary based on time of day. Here, we compare the effects of net illumination on bycatch (including elasmobranchs, loggerhead turtles, Humboldt squid, finfish, and total bycatch) as well as target fish catch and value across daytime and nighttime periods in a high-bycatch gillnet fishery off the Pacific coast of Baja California Sur, Mexico.

Material and methods

Study site

The study was conducted in the Gulf of Ulloa along the Pacific coast of Baja California Sur, Mexico (see Peckham et al. 2007 for map of study area). The Gulf of Ulloa has intense gillnet fisheries that overlap with a marine megafauna hotspot (Peckham et al. 2008, 2007; Senko et al. 2017; Wingfield et al. 2011), resulting in some of the highest recorded loggerhead sea turtle bycatch rates worldwide (estimated bycatch of > 1,500 loggerheads per year; Peckham et al. 2008, 2007; Senko et al. 2017). These fisheries primarily target California halibut (*Paralichthys californicus*), star-studded grouper (*Hyporthodus niphobles*), and gulf coney/rooster hind (*Hyporthodus acanthistius*), but opportunistically target several other demersal finfish species (Senko et al. 2022).

Study design and data collection

Controlled bottom-set gillnet illumination experiments were coordinated in partnership with local gillnet fishers and Mexico's National Fisheries and Aquaculture Institute (INAPESCA). Local fishers were contracted to build nets with a height of 6.1 m, a diagonal single-thread monofilament mesh size of 20 cm, and a length ranging from 153 to 199 m, with 1.5 m tie-downs connecting the float and sink lines every 2 m along the gillnets (Senko et al. 2022). The net specifications and materials were chosen to match those of the local bottom-set gillnet fleet.

During the summer of 2012, a total of 28 net pairs were deployed at sunrise and retrieved at sunset, while 28 net pairs were deployed at sunset and retrieved at sunrise. All nets were deployed, retrieved, and sorted by the same fishing crew throughout the study. Data on the nighttime sets are reported in Senko et al. (2022). Every net pair consisted of an illuminated gillnet attached to a control gillnet of similar size with a 200 m rope, a distance sufficient to prevent light pollution between illuminated and control nets. Green light-emitting diode (LED) lights of wavelength 500 nm and luminous intensity around 2,500 mcd (Centro Standard Fishing Light, Model SW-1, Centro Corporation, http://www.centrofishing.com/board/bbs/board.php?bo_table=products12&wr_id=7) powered by AA batteries were clipped to the treatment nets every 10 m along the float line and remained illuminated throughout the trials. The LED lights pointed downward to illuminate the monofilament mesh material of the gillnet. The control nets received inactive LED lights of the same model at the same 10 m intervals, with batteries reversed to maintain the same weight. Each net pair was set perpendicular to the shoreline in highly productive halibut and grouper fishing grounds at depths ranging from 10.9 to 43.9 m (Senko et al. 2022).

Each day, four net pairs were set across a range of fishing locations, spaced out by 1 to 5 km, all within the Gulf of Ulloa loggerhead turtle bycatch hotspot identified by Peckham et al. (2007). The replicates were set in the same spot for one day period (sunrise to sunset) and one night period (sunset to sunrise) to allow for paired analysis across daytime and nighttime sets and ensure consistent depths and bottom topography among paired day-night sets. To control for site effects, the location of the control and illuminated nets from each net pair was rotated after each pair was soaked for one full day and night deployment (Senko et al. 2022).

Bycatch was defined as any species that were either not retained in these fisheries or their take was prohibited during the study period (Senko et al. 2022). All bycatch and target fish catch were binned by their respective taxonomic groups, recorded, and weighed (Senko et al. 2022). For each gillnet set, bycatch rates (bycatch per unit effort, BPUE) were calculated for total fisheries bycatch, loggerhead turtles (*Caretta caretta*), elasmobranchs (i.e., sharks, rays, and skates), unwanted finfish, and Humboldt squid (*Dosidicus gigas*) using the following formula: BPUE = kg of bycatch group/([net length/100 m] × [net soak time/12 h]); and for loggerhead turtle counts: BPUE = number of turtles/([net length/100 m] × [net soak time/12 h]). Similarly, total target catch rates (catch per unit effort, CPUE) were calculated for each gillnet using: CPUE = kg of target catch group/([net length/100 m] × [net soak time/12 h]). Market value was used to determine the effects of illuminated nets on the catch value of target fish to assess impacts on fisher profit that may not be reflected in CPUE. These values were based on the 2012 market prices (i.e., value at the time of the study) and were determined by a local veteran fisher with over 30 years of experience gillnet fishing in the Gulf of Ulloa. Market value rates (market value per unit effort, MVPUE) were determined for total target catch rates of each net via the following formula: MVPUE = USD of target fish caught/([net length/100 m] × [net soak time/12 h]).

The animal use protocol for this research was reviewed and approved by the Institutional Animal Care and Use Committee at Arizona State University (IACUC protocol #12-1256R). All research activities were performed under the supervision of the National Fisheries and Aquaculture Institute of Mexico and authorized by the Mexican government through SEMARNAT permit SGPA/DGVS/05137/12.

Data analysis

To broadly understand how bycatch, target catch, and market value differed between illumination treatments and time of day, we first compared total BPUE, BPUE by species group, CPUE, and MVPUE among daytime control, daytime illuminated, nighttime control, and nighttime illuminated nets using Generalized Linear Models (GLMs) and Generalized Linear Mixed-Effects Models (GLMMs). Global models were fit using the ‘glmmTMB’ function in the “glmmTMB” package in R with either BPUE, CPUE, or MVPUE as a response variable (McGillycuddy et al. 2025). We selected a Tweedie distribution based on residual plots to account for our continuous zero-inflated data (Shono 2008). For each species group and for MVPUE, we fit all possible model combinations with: 1) treatment (i.e., control day, illuminated day, control night, illuminated night) included as a fixed effect in every model to quantitatively assess the effect of illumination and time of day, 2) varied inclusion of depth (fixed), day (fixed or random), and pair ID (random) as predictors, and 3) varied inclusion of an interaction between treatment and depth. We then used Alkaline Information Criteria to compare all models to find the best-fit model for each species group (Burnham & Anderson 2010). The assumptions for each model were verified by examining Q-Q and residual plots using the ‘simulateResiduals’ function from the “DHARMa” package (Hartig 2016). For each best-fit model, we used the ‘Anova’ function in the “car” package to extract p-values for each term (Fox & Weisberg 2019), then the ‘emmeans’ and ‘emtrends’ functions in the “emmeans” package to perform pairwise comparisons with a Tukey adjustment to identify significant differences among the four treatments (Lenth 2017). Best-fit models are summarized in Table 1, while detailed model results and pairwise comparison results are presented in Supplementary Tables 1 and 2, respectively.

Next, we assessed the effectiveness of net illumination during day versus night periods. For each taxonomic group, we compared daytime catch rates between control and illuminated nets for each gillnet pair set during the day by calculating a daytime normalized difference in catch rates between the treatments according to the Equation 1, where *kgPUE* represents the biomass per unit effort in kilograms captured during a trial (for loggerhead turtle counts, the number of turtles per unit effort was used in place of *kgPUE*). To compare nighttime catch rates between control and illuminated nets,

Table 1 Best-fit model specifications and significance of predictor terms

Species	Model specification[a]	Treatment	Depth	Treatment: Depth
Total bycatch	~ Treatment + day	< 0.001	–	–
Elasmobranchs	~ Treatment + depth	0.001	0.035	–
Humboldt squid	~ Treatment + (1|day) + (1|pair)	< 0.001	–	–
Finfish	~ Treatment × depth + day + (1|pair)	< 0.001	0.454	0.004
Loggerheads (biomass)	~ Treatment + depth	0.026	0.054	–
Loggerheads (counts)	~ Treatment + depth	0.024	0.034	–
Total target catch	~ Treatment + day + (1|pair)	0.775	–	–
MVPUE	~ Treatment × depth + day	0.576	0.104	0.028

Model specification and *p*-values for treatment, depth, and the interaction between treatment and depth for the best-fit GLMM or GLM for each species group. Full model results can be found in Supplementary Table 1, while detailed pairwise comparison results for species groups with significant differences among treatments can be found in Supplementary Tables 2 and 3

[a] A random effect is denoted by (1|Predictor)

we also calculated nighttime normalized differences for each gillnet pair set at night using Equation 2.

$$Daytime\quad normalized\quad difference = \frac{kgPUE_{DayControl} - kgPUE_{DayIlluminated}}{kgPUE_{DayControl} + kgPUE_{DayIlluminated}}$$

To compare nighttime catch rates between control and illuminated nets, we also calculated nighttime normalized differences for each gillnet pair set at night using a similar equation:

$$Nighttime\quad normalized\quad difference = \frac{kgPUE_{NightControl} - kgPUE_{NightIlluminated}}{kgPUE_{NightControl} + kgPUE_{NightIlluminated}}$$

These daytime and nighttime normalized differences account for variation in the magnitude of catch between nets, thereby representing the relative difference in catch between control and illuminated gillnets set at the same time of day. Normalized difference values (n = 28 for daytime sets, n = 28 for nighttime sets) range from − 1 to 1, where more positive values indicate lower catch rates in illuminated nets, more negative values represent higher catch rates in illuminated nets, and a value of zero represents identical catch rates in control and illuminated nets. For example, if we caught 100 kg of fish in a daytime control net and 50 kg of fish in a daytime illuminated net, the daytime normalized difference would be calculated as (100–50)/(100 + 150) = 0.33, representing a decrease in catch in the illuminated net during the day. When both the control and illuminated net of a paired gillnet set had zero catch, the normalized difference calculation resulted in "NaN" values. These 'NaN' values were manually replaced with a value of '0' to indicate no difference between bycatch or target catch biomass in the illuminated and control net of a paired gillnet set.

To assess whether net illumination affected bycatch and target catch rates differently during the day versus night, we compared the daytime normalized differences with the nighttime normalized differences using a Wilcoxon matched-pairs signed-rank test for each taxonomic group. Each matched pair consists of one daytime trial and the nighttime trial that immediately followed it, each set in the same location. Before tests were conducted, assumptions of normality and equal variance between day and night groups were checked using QQ plots and Levene's tests, respectively. The assumption of equal variance between groups was met for all taxonomic groups. However, QQ plots revealed highly skewed, non-normal catch data, necessitating the non-parametric Wilcoxon tests. Given that the Wilcoxon matched-pairs signed-rank test compares the difference between the daytime and nighttime normalized differences, this difference (i.e., nighttime normalized difference—daytime normalized difference) is presented alongside the Wilcoxon results and in Table 2. Data were analyzed in R version 4.0.3 (R Core Team 2022), with statistical significance inferred at a p-value of 0.05 or less.

Results

Overall effects of illumination, time of day, and depth on bycatch, target catch, and market value

We found significant differences in BPUE across the four illumination and time of day treatments for total bycatch ($p < 0.001$), elasmobranchs ($p = 0.001$), Humboldt squid ($p < 0.001$), finfish ($p < 0.001$), and loggerhead turtles by biomass ($p = 0.026$) and count ($p = 0.024$, Fig. 1; Table 1). By contrast, target catch rates ($p = 0.775$) and MVPUE ($p = 0.707$) did not significantly differ across treatments (Fig. 2; Table 1).

Pairwise comparisons revealed that BPUE in nighttime illuminated nets was significantly lower compared to nighttime control nets for total bycatch (night control mean BPUE = 32.13 ± 4.85 SE, night illuminated mean BPUE = 11.95 ± 2.29 SE, Tukey, $p = < 0.001$), elasmobranchs (night control mean BPUE = 4.09 ± 1.31 SE, night illuminated mean BPUE = 0.19 ± 0.13 SE, Tukey, $p = 0.002$), and Humboldt squid (night control mean BPUE = 7.59 ± 3.32 SE, night illuminated mean BPUE = 1.43 ± 0.73 SE, Tukey, $p = 0.004$, Fig. 1, Table 2, Supplementary Table 2). However, we found no significant differences between daytime control and daytime illuminated nets for any species group (Fig. 1, Table 2, Supplementary Table 2).

For finfish bycatch, the best-fit GLMM showed a significant interaction between treatment and depth ($p = 0.004$, Table 1). The effect of depth was significantly different depending on time of day, with finfish BPUE decreasing with depth during the day and slightly increasing with depth at night

Table 2 Difference in bycatch, target fish catch, and market value between control and illuminated nets during the day and at night

	Day			Night			Day vs. night	
Bycatch discards	Mean control BPUE ± SE	Mean illuminated BPUE ± SE	Mean normalized difference in BPUE ± SE[a]	Mean control BPUE ± SE	Mean illuminated BPUE ± SE	Mean normalized difference in BPUE ± SE[a]	Mean difference in normalized differences ± SE[b]	p^c
Elasmobranch biomass	4.77 ± 2.66	1.75 ± 0.86	0.06 ± 0.13	4.09 ± 1.31	0.19 ± 0.13	0.39 ± 0.12	0.33 ± 0.18	0.048*
Loggerhead turtle biomass	21.90 ± 5.67	21.37 ± 5.32	− 0.02 ± 0.12	11.54 ± 3.63	5.69 ± 2.08	0.10 ± 0.13	0.12 ± 0.17	0.429
Loggerhead turtle counts	0.64 ± 0.17	0.66 ± 0.16	− 0.03 ± 0.12	0.34 ± 0.11	0.17 ± 0.06	0.09 ± 0.13	0.12 ± 0.16	0.383
Unwanted finfish biomass	7.59 ± 2.46	5.66 ± 1.85	0.10 ± 0.11	8.91 ± 2.61	4.64 ± 0.79	0.21 ± 0.08	0.11 ± 0.13	0.254
Humboldt squid biomass	4.29 ± 3.11	0.10 ± 0.53	0.04 ± 0.06	7.59 ± 3.32	1.43 ± 0.73	0.18 ± 0.07	0.14 ± 0.10	0.155
Total bycatch biomass	38.55 ± 7.61	29.78 ± 6.64	0.04 ± 0.10	32.13 ± 4.85	11.95 ± 2.29	0.39 ± 0.10	0.35 ± 0.13	0.015*
Target fish catch	Mean control CPUE ± SE	Mean illuminated CPUE ± SE	Mean normalized difference in CPUE ± SE[a]	Mean control CPUE ± SE	Mean illuminated CPUE ± SE	Mean normalized difference in CPUE ± SE[a]	Mean difference in normalized differences ± SE[b]	p^c
Total target catch biomass	3.53 ± 1.66	4.19 ± 2.42	0.03 ± 0.11	2.55 ± 1.07	2.70 ± 0.84	− 0.08 ± 0.11	− 0.11 ± 0.16	0.667
Market value	Mean control MVPUE ± SE	Mean illuminated MVPUE ± SE	Mean normalized difference in MVPUE ± SE[a]	Mean control MVPUE ± SE	Mean illuminated MVPUE ± SE	Mean normalized difference in MVPUE ± SE[a]	Mean difference in normalized differences ± SE[b]	p^c
Total target fish value	8.80 ± 4.66	11.63 ± 7.19	0.006 ± 0.12	6.52 ± 2.52	6.91 ± 2.49	− 0.09 ± 0.12	− 0.09 ± 0.17	0.623

Comparison of bycatch per unit effort (BPUE), catch per unit effort (CPUE), and market value per unit effort (MVPUE) between control versus illuminated nets during both day and night. BPUE = kg of bycatch group/([net length/100 m] × [net soak time/12 h]); and for loggerhead turtle counts: BPUE = number of turtles/([net length/100 m] × [net soak time/12 h]); CPUE = kg of target fish catch/([net length/100 m] × [net soak time/12 h]); MVPUE = market value ($US) of target fish/([net length/100 m] × [net soak time/12 h])

[a] The mean normalized difference represents the change in catch between paired control and illuminated nets (normalized difference = [control biomass per unit effort − illuminated biomass per unit effort]/[control biomass per unit effort + illuminated biomass per unit effort]). Normalized difference values range from − 1 to 1, where positive values indicate lower catch rates in illuminated nets, negative values represent higher catch rates in illuminated nets, and a value of zero represents identical catch rates in control and illuminated nets

[b] The mean difference in normalized differences represents the mean difference between each trial's daytime normalized difference and nighttime normalized difference values (difference in normalized differences = nighttime normalized difference − daytime normalized difference). Normalized difference values range from − 1 to 1, where positive values indicate lower catch rates in illuminated nets, negative values represent higher catch rates in illuminated nets, and a value of zero represents identical catch rates in control and illuminated nets

[c] *P*-values are presented from the Wilcoxon tests assessing day vs. night performance of net illumination, with significant differences in catch between day and night indicated with an asterisk

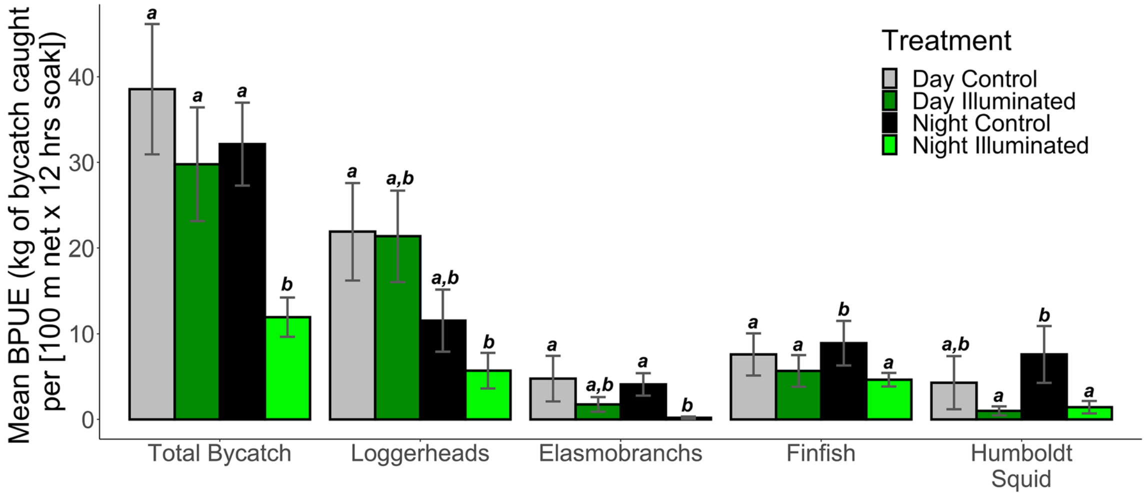
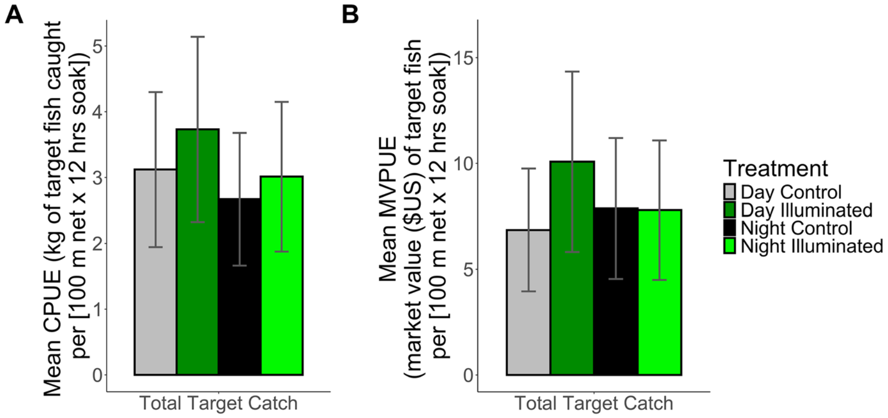


Fig. 1 Mean BPUE (kg of bycatch/[100 m net × 12 h soak]) for total, loggerhead turtle, elasmobranch, finfish, and Humboldt squid bycatch biomass. Error bars represent standard error. Lettering denotes significant differences in BPUE across treatments. For finfish, effects are averaged across depths due to the treatment × depth interaction predicted by the best-fit model (Supplementary Fig. 3A)

Fig. 2 Mean **A)** CPUE (kg of target catch/([net length/100 m] × [net soak time/12 h])) and **B)** MVPUE (USD of target fish caught/([net length/100 m] × [net soak time/12 h])) for total target fish catch for each net illumination treatment and time of day. Error bars represent standard error. There were no significant differences across treatments



(Supplementary Fig. 1A, Supplementary Table 3). When averaged across depths, finfish BPUE was significantly lower in nighttime illuminated nets (mean BPUE = 4.64 ± 0.79 SE) compared to nighttime control nets (mean BPUE = 8.91 ± 2.61 SE, Fig. 1, Table 2, Supplementary Table 2).

Depth was also included as a predictor in the best-fit models for elasmobranch bycatch, loggerhead turtle bycatch by biomass and count, and MVPUE (Table 1). Elasmobranch BPUE significantly increased with deeper depths ($p = 0.035$, Supplementary Fig. 1B). Loggerhead turtle BPUE decreased with depth and this relationship was nearly identical between biomass and count models, although significance differed (count $p = 0.034$, biomass $p = 0.054$, Table 1, Supplementary Fig. 1C). For MVPUE, there was a significant interaction between treatment and depth ($p = 0.028$, Table 1). Specifically, MVPUE in nighttime control nets had a significantly steeper positive relationship with depth compared to daytime control nets (Tukey, $p = 0.049$, Supplementary Fig. 1D, Supplementary Table 3).

Daytime versus nighttime effects of net illumination on total and multi-taxa bycatch

For total fisheries bycatch and elasmobranch bycatch, reductions in BPUE when comparing

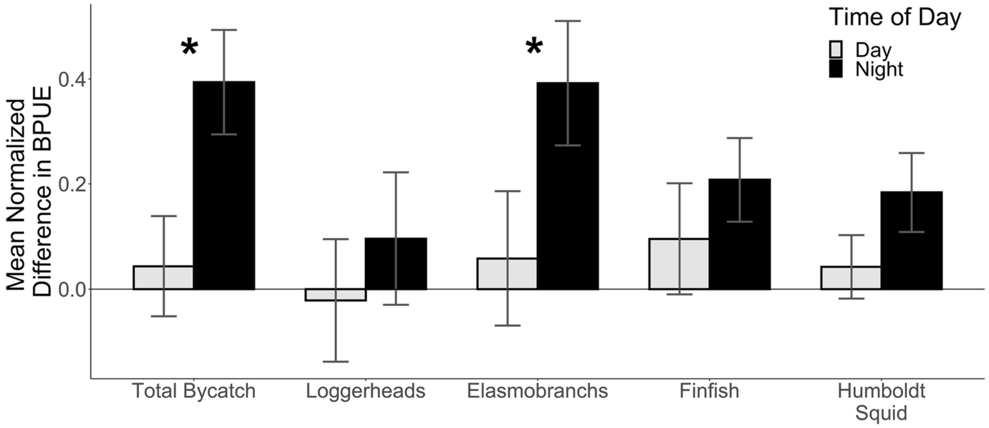


Fig. 3 Mean normalized difference in bycatch rates between control and illuminated nets for day and night periods for total, loggerhead turtle, elasmobranch, finfish, and Humboldt squid bycatch biomass. Normalized difference values range from − 1 to 1, where positive values indicate lower catch rates in illuminated nets, negative values represent higher catch rates in illuminated nets, and a value of zero represents identical catch rates in control and illuminated nets. Error bars represent standard error, while asterisks denote significant differences between day and night normalized differences. Normalized difference = (control biomass per unit effort—illuminated biomass per unit effort)/(control biomass per unit effort + illuminated biomass per unit effort)

control and illuminated gillnets were significantly greater at night than in the day. Specifically, total fisheries bycatch biomass was, on average, reduced by 4% during the day and 39% at night (mean difference in normalized differences = 0.35 ± SE 0.13, Wilcoxon, $p = 0.015$), whereas elasmobranch bycatch biomass was reduced by 6% during the day and 39% at night (mean difference in normalized differences = 0.33 ± SE 0.18, Wilcoxon, $p = 0.048$, Fig. 3, Table 2). The effectiveness of net illumination was not significantly different between day and night periods for loggerhead turtles by biomass (mean difference in normalized differences = 0.12 ± SE 0.17, Wilcoxon, $p = 0.429$) or counts (mean difference in normalized differences = 0.12 ± SE 0.16, Wilcoxon, $p = 0.383$), finfish bycatch (mean difference in normalized differences = 0.11 ± SE 0.13, Wilcoxon, $p = 0.254$), or Humboldt squid bycatch (mean difference in normalized differences = 0.14 ± SE 0.10, Wilcoxon, $p = 0.155$, Fig. 3, Table 2).

Effects of net illumination on target fish catch and market value during the day versus night

There were no significant differences in biomass of total target fish CPUE between control and illuminated nets during the day and at night (mean difference in normalized differences = − 0.11 ± SE 0.16, Wilcoxon, $p = 0.667$, Fig. 4, Table 2). The total target fish MVPUE was also not significantly different between day and night net treatments (mean difference in normalized differences = − 0.09 ± SE 0.17, Wilcoxon, $p = 0.623$, Fig. 4, Table 2).

Cost analysis for illuminating gillnets

At ~ 7–9 USD per light, the Centro lights we tested here would cost ~ 700–900 USD per 1000 m at 10 m spacing. Less expensive lights (which have not been tested), available at ~ 2 USD, could lower costs to 200 USD per 1000 m, provided comparable efficacy. Fishers in our study region typically fish 800–1000 m of net (Senko et al. 2022), so it would cost ~ 560–900 USD to equip them with Centro lights or ~ 160–200 USD for less expensive lights at the 10 m spacing used here.

There are also ongoing operational costs for replacing batteries and broken lights. At 0.50 USD per battery, replacement would cost 100 USD per 1000 m of net, with annual expenses reaching several hundred USD depending on battery life. However, solar-powered lights, currently in development, can eliminate this recurring operational expense (Senko

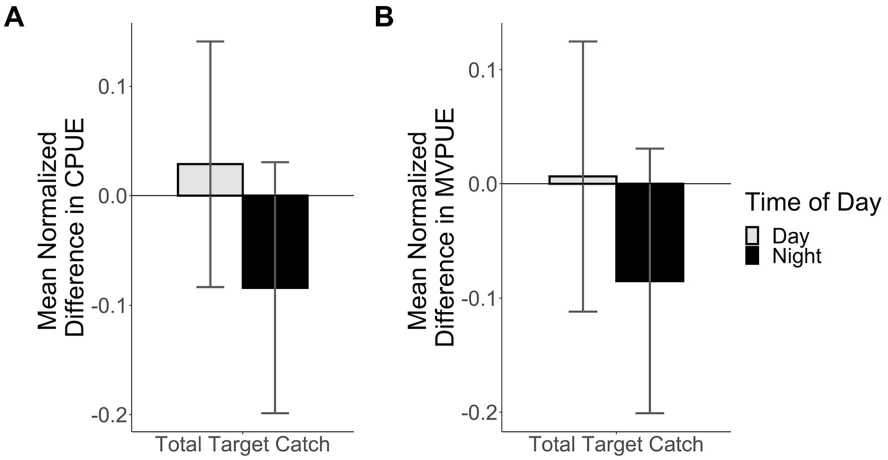


Fig. 4 Mean normalized difference in **A)** target catch and **B)** market value rates between control and illuminated nets for day and night for total target fish catch. Normalized difference values range from − 1 to 1, where positive values indicate lower catch rates in illuminated nets, negative values represent higher catch rates in illuminated nets, and a value of zero represents identical catch rates in control and illuminated nets. Error bars represent standard error. There were no significant differences between day and night. Normalized difference = (control biomass per unit effort—illuminated biomass per unit effort)/(control biomass per unit effort + illuminated biomass per unit effort)

et al. 2025). LED durability limits broken lights and the need for replacements; assuming 10 broken lights per year, replacements would cost ~ 20–90 USD annually. Overall, annual operational costs may range from < 100 USD with solar-powered lights to several hundred USD, depending on light type, batteries, and usage (e.g., duration, depth, storage, etc.).

Discussion

Over the past decade, net illumination has emerged as a promising multi-taxa bycatch reduction technology (Allman et al. 2020; Bielli et al. 2020; Darquea et al. 2020; Gautama et al. 2022; Kakai 2019; Mangel et al. 2018; Ortiz et al. 2016; Senko et al. 2022; Snape et al. 2024; Virgili et al. 2018; Wang et al. 2010, 2013), yet mixed results (Field et al. 2019; Jančič et al. 2025; Martínez-Baños and Maynou 2018; Post et al. 2024; Sigurdsson 2023) warrant further research into the effects of net illumination and the factors that drive variable responses (Yochum et al. 2024). Although testing of net illumination has expanded into multiple coastal gillnet fisheries over the past decade, no study has compared the efficacy of net illumination during the day versus the night. Here, we demonstrate that net illumination is more effective for reducing fisheries bycatch at night (Figs. 1 and 3, Table 2), with no significant effect on target catch rates or value (Figs. 2 and 4, Table 2). At night, gillnet illumination significantly reduced total fisheries, elasmobranch, Humboldt squid, and finfish bycatch (Fig. 1, Table 1). However, during the day, we observed no significant bycatch reductions in illuminated nets for any species group (Fig. 1, Table 1). When comparing the magnitude of bycatch reductions using illuminated nets between paired day and night trials, we found that the magnitude of nighttime reductions was significantly greater than the magnitude of daytime reductions for total fisheries and elasmobranch bycatch (Fig. 3, Table 2). Our results improve our understanding and inform conservation decision-making regarding this emerging bycatch reduction technology, while providing a framework to assess the effects of net illumination across day and night periods in other passive net fisheries. With this knowledge, fisheries managers can more sustainably manage gillnet fisheries to maintain resilience in the face of rising vulnerability, safeguarding both coastal livelihoods and marine ecosystems (Finkbeiner 2015; Islam and Chuenpagdee 2022).

We found that net illumination was more effective for reducing total fisheries bycatch at night, indicating that net illumination can be an effective bycatch reduction strategy in gillnet fisheries that operate at night. Senko et al. (2022) showed a 63% reduction in total bycatch in gillnets set during the night (for bycatch consisting of finfish and marine megafauna), while Martínez-Baños and Maynou (2018) showed no significant change in total bycatch rates (for bycatch consisting of invertebrates, finfish, and some elasmobranchs). However, several gillnet illumination studies have demonstrated reductions across multiple species when nets are set overnight (Bielli et al. 2020; Senko et al. 2022; Snape et al. 2024), and Lucas and Berggren (2022) showed that LEDs are the only bycatch reduction technology to show reductions across multiple marine megafauna groups. These reductions across species groups suggest the potential for reductions in total bycatch upon further assessment of this metric. Given the reductions in total bycatch presented here, net illumination may be an important solution for minimizing the harmful ecosystem impacts of bycatch, such as trophic downgrading and other effects on ecosystem structure and functioning. Fishers can also benefit from net illumination, as reductions in total fisheries bycatch can increase efficiency of fishing operations, prevent fishery closures or other government regulations, and reduce damage that bycatch species may impose on nets (Panagopoulou et al. 2017; Senko et al. 2014b; Senko et al. 2022). Furthermore, reductions in total bycatch may be important for encouraging fisher adoption of net illumination, as bycatch incidents involving protected species are typically rare and thus may not be a strong motivator for change; as such, fishers may be more likely to notice and respond to reductions in total bycatch (Senko et al. 2022). Future research should quantify the effects of net illumination on total bycatch to provide a comprehensive understanding of its effects.

Our results confirm previous research that found net illumination can reduce elasmobranch bycatch in passive net fisheries at night (Senko et al. 2022; Snape et al. 2024). However, our findings here suggest that net illumination may not be effective for reducing elasmobranch bycatch during the day. Elasmobranchs use a variety of sensory cues to navigate their environment, including visual, electrical, chemical, and mechanical cues (Jordan et al. 2013). Generally, elasmobranch visual systems are well-developed and can adapt to a wide range of light conditions (Gardiner et al. 2012; Hart and Collin 2015). Color vision is not present in all elasmobranch species, though many have retinas containing rhodopsins sensitive to light within the blue to green wavelengths (Gardiner et al. 2012; Southwood et al. 2008). Therefore, the green LEDs used in this study are likely visible to the elasmobranch species caught during these trials. Given that we did not find a significant reduction in elasmobranch bycatch during the day, the visual cue from the light, which is less visible during the daytime, may be the driver of the elasmobranch reductions seen here. However, elasmobranchs also possess electroreception, which may allow them to detect electrical fields generated by lights on illuminated nets. It is, therefore, unknown if elasmobranchs use primarily visual cues, or a combination of visual and electrical cues to avoid illuminated nets.

Elasmobranch physiology is highly variable between species, which may lead to variation in how different species respond to net illumination. Due to logistical limitations with this study, our results cannot be interpreted by species as we were unable to record species-specific bycatch rates (Senko et al. 2022). Given that elasmobranchs are globally threatened by bycatch and overfishing (Dulvy et al. 2014, 2017; Pacoureau et al. 2021; Worm et al. 2013), it is critical to find solutions for reducing elasmobranch bycatch across a variety of species. Therefore, more research is needed on species-specific elasmobranch responses to net illumination across day and night periods and the mechanisms driving these differences.

For Humboldt squid, finfish, and loggerhead bycatch, we did not find significant differences in bycatch reduction rates across day and night using illuminated nets. For loggerheads, bycatch rates in daytime control and illuminated nets were almost identical, and there was a nonsignificant reduction in nighttime illuminated nets compared to nighttime control nets (Fig. 1, Table 2). Given that several studies have shown that net illumination can reduce sea turtle bycatch (Allman et al. 2020; Bielli et al. 2020; Darquea et al. 2020; Gautama et al. 2022; Kakai 2019; Ortiz et al. 2016; Snape et al. 2024; Virgili et al. 2018; Wang et al. 2010, 2013), we expected to see similar results here. Although loggerheads are capable of detecting green light (Horch et al. 2008; Levenson et al. 2004; Wang et al. 2007), the nearly identical bycatch rates between control and illuminated daytime nets suggest that the LEDs used in this study may not have been strong enough for the turtles to detect or respond to in ambient light. For Humboldt squid and finfish, while there was no significant difference between day and night in the effectiveness of net illumination, we found significant reductions using net illumination at night (Figs. 1 and 3, Table 2). Relatively low catch rates for Humboldt squid and loggerheads, as well as highly variable catch rates for finfish, may have limited the power of statistical analyses. Therefore, additional sampling may reveal significant differences for these species. Furthermore, to optimize bycatch reductions across both day and night periods, future research could vary the wavelength or increase the intensity of lights to heighten visibility in photopic conditions.

The capability of an animal to detect fishing gear likely depends on the contrast of the gear in relation to its surroundings, which can be influenced by ambient light levels, depth, and turbidity (Arimoto et al. 2010; Kim and Wardle 1998; Martin and Crawford 2015). At night, illuminated nets are more likely to contrast against the dark background of the surrounding water, increasing their visibility and, thus, likely making it easier for animals to avoid the nets. During the daytime, however, high ambient light levels may effectively "drown out" the lights, reducing net contrast and visibility. This lack of contrast in high ambient light may help explain why net illumination was less effective for reducing bycatch during the day.

Similarly, depth may also influence the effectiveness of net illumination. Ambient light decreases at greater depths, which may enhance the contrast of illuminated nets, potentially making them more effective at reducing bycatch. We found that depth affected catch rates for elasmobranch bycatch, loggerhead turtle bycatch, finfish bycatch, and MVPUE (Table 1, Supplementary Fig. 1). Elasmobranch BPUE increased with depth and loggerhead BPUE decreased with depth uniformly across illumination and time of day treatments (Supplementary Fig. 1B, C). While models predicted a significant interaction between treatment and depth for finfish bycatch and MVPUE, these effects appear to depend more on time of day than illumination (Supplementary Fig. 1A, D, Supplementary Table 3). Overall, these depth-dependent catch rates likely reflect inherent species behavior, with the interactions for finfish and MVPUE potentially being influenced by differences in species composition during day and night. Despite finding no evidence for varying effects of depth between control and illuminated nets here, this may be due to the limited range of depths fished in our study or the limited power of statistical modeling due to relatively low catch rates for some species. Future studies should further assess how changes in ambient light levels due to depth and time of day affect responses to net illumination.

In addition to ambient light and depth, turbidity can also impact the ability of animals to perceive and respond to net illumination. Differences in turbidity levels can drastically modify how far light is transmitted through water, thereby affecting the capability of an animal to visually identify and respond to an illuminated net (Jerlov 1976; Lomeli et al. 2020). Underwater visual acuity is inversely related to turbidity for multiple species (Lunt and Smee 2015; Martin and Crawford 2015; Strod et al. 2004; Weiffen et al. 2006). Therefore, high turbidity may decrease the effectiveness of net illumination, especially if the light does not scatter far enough for animals to detect it in time to evade entanglement. In the relatively turbid waters at our study site, it is possible that the LED lights were not intense enough for some species to detect, especially when combined with high ambient light levels (Wang et al. 2007). Further research is needed to understand how turbidity and net illumination interact, as water clarity was not measured in this study. Combining illumination with net materials that have high contrast to the background color of the ocean could improve gillnet visibility and result in greater bycatch reductions during the day or under turbid conditions.

Target catch rates and market value did not exhibit significant differences across treatments (Figs. 2, and 4). Many species of fish can detect green light (Arimoto et al. 2010; Matsuda et al. 2009), although they may respond differently than bycatch species to light stimuli. Although artificial light has been used to attract fish for thousands of years, the mechanisms behind this attraction remain largely unknown (Arimoto et al. 2010; Nguyen and Winger 2019), although variations in visual systems of fish across species, life stages, and habitat depth may play a role (Arimoto et al. 2010; Bowmaker 1995; Britt 2009; Nguyen and Winger 2019). Our results are consistent with previous studies showing that target catch rates and market value can be maintained when using net illumination (Allman et al. 2020; Bielli et al. 2020; Darquea et al. 2020; Gautama et al. 2022; Kakai 2019; Mangel et al.

2018; Ortiz et al. 2016; Senko et al. 2022; Snape et al. 2024; Virgili et al. 2018; Wang et al. 2010, 2013).

Although gillnet illumination may be an effective strategy to reduce fisheries bycatch in gillnets at night while maintaining fish catch and value, there are several considerations to be made before this technology can be implemented on a large scale. While Senko et al. (2022) showed a reduction in haulback time using net illumination, the lights need to be managed (e.g., changing batteries, replacing broken lights, unentangling lights), which may be time-consuming. Cost is another important factor, as many small-scale fishers cannot afford to purchase lights without assistance, such as government subsidies (Ortiz et al. 2016; Senko et al. 2022). While the cost analysis presented here provides a rough estimate of costs, it highlights the need to lower the cost of adoption for fishers. Some studies have shown that spacing lights ~ 15 m apart can still be effective for reducing bycatch (Allman et al. 2020; Kakai 2019; Virgili et al. 2018). Thus, costs of net illumination could be reduced by optimizing light spacing, but additional research is needed to understand how efficacy varies at different spacing intervals. Furthermore, there are additional economic and environmental costs associated with the disposable batteries used by many lights on the market. Designing more practical lights may solve many of these issues. For example, solar-powered fishing lights could reduce the recurring costs associated with buying batteries, while also preventing batteries from being disposed of in the ocean (Senko et al. 2025). Solar-powered lights may be particularly advantageous for fishers who set their nets at night, as lights can charge out of water during the day and are most effective when used at night, as shown here. Further research should focus on reducing costs to fishers and optimizing this emerging technology.

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Data availability Data are permanently archived in the Open Science Framework.

Declarations

Conflict of interests The authors declare no conflict of interests.

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