Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER

Integrating Landscapes of Fear and Energy Reveals the Behavioural Strategies That Shape Predator–Prey Interactions

Michael A. Gil[1] | Cyril J. Michel[2,3] | Simone Olivetti[3] | Vamsi Sridharan[2,4] | Andrew M. Hein[5]

[1]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado, USA | [2]Institute of Marine Sciences' Fisheries Collaborative Program, University of California, Santa Cruz, California, USA | [3]Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, California, USA | [4]Tetra Tech Inc., Fairfax, Virginia, USA | [5]Department of Computational Biology, Cornell University, New York, New York, USA

Correspondence: Michael A. Gil (michael.gil@colorado.edu)

Received: 21 May 2024 | **Revised:** 20 December 2024 | **Accepted:** 24 December 2024

Funding: This work was supported by National Science Foundation Division of Emerging Frontiers (2222478), California Department of Fish and Wildlife (P1896007-01), National Science Foundation Division of Integrative Organismal Systems (1855956, 2338596).

Keywords: animal decision-making | diel activity patterns | energetics | fitness trade-offs | landscape of fear | migration | movement ecology | trait mediated interactions

ABSTRACT

Disparate bodies of literature implicate risk avoidance and energy conservation as important drivers of animal movement decisions. Theory posits that these phenomena interact in ecologically consequential ways, but rigorous empirical tests of this hypothesis have been hampered by data limitations. We fuse fluid dynamics, telemetry, and attack data to reconstruct risk and energy landscapes traversed by migrating juvenile salmon and their predators. We find that migrants primarily use midriver microhabitats that facilitate migration at night. During daylight, predators become more aggressive in the midriver, and prey reduce midriver use in favour of nearshore microhabitats, resulting in increased energy expenditure and decreased migration efficiency. Predators attack most when migrants are not prioritising threat avoidance and during ephemeral periods of low lighting. Our findings suggest that predator–prey interactions result from an interplay between landscapes of fear and energy, which can determine the degree to which predators affect prey through mortality or fear.

1 | Introduction

Animal movements influence the demography and evolution of animal populations by affecting a vast range of ecological processes (Bartoń et al. 2011; Borchering et al. 2017; Hein and Martin 2019; Hein and McKinley 2013; Lindström et al. 2013; Pawar, Dell, and Savage 2012). Determining the mechanisms by which animals make movement decisions has, thus, become a central goal in modern ecology (Kays et al. 2015; Nathan et al. 2022). Over the last half-century, many studies have implicated perceived risk, or 'fear,' as a driver of animal movement decisions, suggesting that the 'landscape of fear', or spatial variation in perceived risk, can determine how animals navigate their environments (Gaynor et al. 2019; Palmer et al. 2023). Over the same period, a second, but largely separate body of literature has suggested that animals make movement decisions based on the energetic costs of those movements (Darveniza et al. 2023; Gallagher et al. 2017; Shepard et al. 2013). Through this lens, animals navigate an 'energy landscape,' where they seek to exploit structure in the environment (e.g. environmental currents, flat terrain, Gallagher et al. 2017) that allows them to move efficiently, thereby conserving energy that can instead be allocated to critical life-history tasks such as reproduction.

The need to avoid predators and the need to move efficiently are examples of proximate objectives animals might seek to achieve that potentially trade off with one another. Classic fitness-optimization models in ecology posit that when energy is in sufficiently high demand (e.g. when an individual is close to starvation, or is engaged in demanding activities such as dispersal or migration), an organism must prioritise activities that meet this demand, even if this means lower investment in activities that reduce the risk of being killed by a predator (Brown and Kotler 2004; Lima 1998; McNamara and Houston 1987). Many empirical studies have tested this hypothesis in the context of organisms meeting energetic demands through energy intake; for example, via feeding (Brown and Kotler 2004; Lima and Dill 1990; Verdolin 2006). However, an animal's energetic state is also determined by how it uses energy. A primary way mobile animals use energy is through movement, and animals often have the option of choosing among microhabitats that confer very different energetic costs of movement (Darveniza et al. 2023; Shepard et al. 2013). Thus, an important hypothesis that extends from classic theory of energy-safety tradeoffs is that landscapes of fear and landscapes of energy interact to influence animal movement decisions (Gallagher et al. 2017, Papastamatiou et al. 2024), and as a consequence, whether predators affect prey via mortality or fear. Here, we test this hypothesis by fusing extensive movement, fluid dynamics, and predation data to reconstruct the landscapes of fear and energy wild animals experience as they make movement decisions.

In this study, we focus on animals in the midst of an energetically demanding migration: juvenile Chinook salmon 'smolts' (hereafter, referred to as 'migrants'), a species of critical management concern, migrate through riverine and estuarine habitat in the Sacramento-San Joaquin Delta to reach the Pacific Ocean, where they mature before returning to spawn. Like many other migrants that swim or fly, smolts use favourable flows to aid them in travel; river flows can advance individuals along their migratory route toward the ocean (Sridharan et al. 2023), while reducing energy expenditures (Liao 2007). Thus, the flows available to migrants within a river channel generate a dynamic energy landscape. At the same time, abundant invasive predators, heavily subsidised by invasive prey, impose a severe risk of mortality on migrants (Mahardja et al. 2017). Consequently, we hypothesize that migrants will exploit high seaward flows (e.g. in the midriver; McElroy, DeLonay, and Jacobson 2012) but that threat avoidance in the face of high predation risk could reduce this energy-saving behaviour. Using computational fluid dynamics modelling (Olivetti et al. 2021), we reconstructed dynamic flows within a key segment of the migration route with high densities of predators (Henderson et al. 2023). We used telemetry data from tagged predators to derive spatiotemporal patterns of predator space use, and combined this with extensive field predation assays. These rich, complementary data sources allowed us to reconstruct both the energy landscape, and the landscape of risk migrants encountered as they made movement decisions. We coupled these insights with migrant telemetry data, offering detailed information about migrant movement decisions, as they negotiated these landscapes. Our results allowed us to test whether and how migrants prioritise moving efficiently over avoiding predators, and to directly infer how movement strategies influence predator–prey interactions.

2 | Material and Methods

2.1 | Data Collection

2.1.1 | Telemetry and Environmental Data

Raw flow and animal tracking data were collected from a segment of the San Joaquin River in the California Central Valley (McQuirk, Simon, and Cane 2015). Four hundred and twenty-four Fall-run Chinook salmon (*Oncorhynchus tshawytscha*), 23 striped bass (*Morone saxatilis*) and 17 largemouth bass (*Micropterus salmoides*) were implanted with injectable HTI hydroacoustic tags (M800 and 795Lm models), which were detected at 13 HTI hydroacoustic detectors (model 590) deployed in a two-dimensional array extending over roughly 1 km of the San Joaquin River at the junction with Old River from April to June, 2012. The resultant dataset includes 120,249 relocations from 172 salmon smolts, 1,077,823 relocations from 13 largemouth bass, and 674,776 relocations from 19 striped bass.

We estimated river depth at each salmon relocation, using bathymetric data (Wang, Ateljevich, and Jaffe 2018) and river stage measured by an upstream data logger (CDEC 2024). We computed light availability for the study region using a celestial almanac and empirical estimates for the lux (lumens per area per second) values of sunlight, moon phases and twilight stages (Time and Date AS 2024a, 2024b). We were unable to obtain reliable data on cloud cover for our specific study location and dates, but regional data suggest low to nonexistent cloud cover during the months of our study (Meteoblue 2023).

We built a Computational Fluid Dynamics Model (CFDM) based on hydrodynamic and bathymetry data (*Supporting Information*, Wang, Ateljevich, and Jaffe 2018; Olivetti et al. 2021). We then used the hydrodynamic information from our CFDM and smolt relocation data to quantify the dynamics of individual fish motion.

2.1.2 | Predation Data

We measured relative predation rates on our focal prey species using predation assays in which a live juvenile Chinook salmon smolt (*O. tshawytscha*, hatchery raised) was tethered to a drifting buoy. Three thousand nine hundred and twenty-four predation assays were deployed over 3097 total hours throughout our study region (Supporting Information (Michel et al. 2020) (Figure S1)).

2.2 | Data Analysis

2.2.1 | Riverflow

We used the river midline to determine, at any point in the study region, which direction would achieve the greatest seaward progress (Figure S2). We used the direction of the nearest river midline with CFDM-generated flow magnitude and direction at each migrant relocation to compute the river flow vector in the seaward (migratory) direction. We verified that these data were approximately normally distributed and computed 95% confidence intervals as the sample mean ± 1.96*SE.

2.2.2 | Spatiotemporal Distributions of Predators and Migrants

We used telemetry data from smolts and two dominant piscivorous predators in our study system: largemouth bass and striped bass (Nobriga and Feyrer 2007), to determine microhabitat use over the diel light cycle. To eliminate biases driven by differences in the numbers of relocations sampled per individual and individuals sampled among light periods (and to normalise for differences in relocations per species for predators), we normalised the spatial occurrence probability distributions of each predator species and of migrants for night, twilight and day, such that all relocations for a given species in a given light period sum to 1.

2.2.3 | Migration Progress and Displacement

For each consecutive pair of relocations, we computed the magnitude of the migrant's movement vector in the migratory direction (i.e. displacement along the river midline, with positive and negative values indicating migration progression and regression, respectively). We divided this value by the displacement between the time steps to get migration efficiency. For migration efficiency, displacement, work, and predator exposure of migrants, we computed 95% confidence intervals around each mean via nonparametric bootstrapping, by sampling migrant trajectories with replacement 1000 times, computing the mean for each sample, and computing the 0.025 and 0.975 quantiles of this distribution of sampled means. We repeated this process to analyse migrant behaviour in response to moonlight.

2.2.4 | Calculation of Work

Given local flow conditions reconstructed with the CFDM, and given the instantaneous heading of each migrant revealed by the trajectory of relocations, we used Newton's Second Law to compute the locomotion force that each fish would have exerted to move in the way that it did (Supporting Information—Data S1). We used these estimates of locomotion force to compute the work (Joules) exerted by each fish between consecutive relocations.

2.2.5 | Prey Exposure to Predators

We subdivided our 5.3-ha study location into a grid of 3.5 × 3.5 m cells, for each of which we summed normalised predator relocations therein and divided this by area (12.5 m^2) to get normalised predator density. To obtain more general predator density estimates, not limited to the grid cells in which tagged predators were observed, we fitted a generalised additive model (GAM) to our normalised predator density data, using the 'gam' package in R (Hastie and Narasimhan 2023; R Core Team 2023), allowing us to use environmental predictor variables to estimate species-specific predator densities in every grid cell of our study location. We divided each predicted predator density in a given light period by the domain-wide sum of predicted predator densities for that light period, to control for differences between light periods. We fitted a model set that included all possible unique combinations of the main effects of distance from shore, depth, diel light period, predator species, and all two-way interactions thereof, yielding 112 candidate models. We compared model fits using the Akaike information criterion (AIC), which revealed five top models with AIC values within 2 units of one another, indicative of comparable fit (Table S1) (Burnham and Anderson 2002). All top models included two-way interactions that collectively involved all four predictor variables (Table S1). We used the best fitting GAM to compute density estimates for each predator species at each migrant relocation, using distance from shore, depth and diel light period thereof. We then took the sum of predator density estimates across migrant relocations for each combination of light period (night, twilight or day) and microhabitat (nearshore or midriver). To control for differences in sample size between light periods, we divided predator density sums for a given light period by the total number of relocations sampled from that light period, yielding the metric that we refer to as 'exposure' of prey to predators. Main text results come from the top model, and we reproduced all results using each of the top five models to test the sensitivity of our results (Supporting Information–Data S1).

2.2.6 | Counterfactual Analyses

To further contextualise patterns in migrant movement decisions across the diel light cycle, we analysed counterfactual scenarios, in which we superimposed the movement trajectories of migrants from one light period onto the map of estimated predator densities from a different light period. Specifically, we took nighttime salmon movement data and used our GAM to compute the predator exposure that would be expected if it were daytime, and we compared differences in predator exposure nearshore vs. midriver between actual and counterfactual scenarios. We computed 95% confidence intervals for predator exposure via nonparametric bootstrapping, in which we resampled tracks with replacement 1000 times and, in each case, computed the sum and the lower 0.025 and upper 0.975 quantiles of the resultant distribution of sums. For visual purposes, we report these findings as differences between actual and counterfactual predator exposure (normalised by median predator exposure), for which we present the most conservative estimate of the differences, by taking from the actual predator exposure estimate the confidence interval that yields the lesser effect size and subtracting from it the mean and lower and upper confidence intervals for the counterfactual predator exposure estimate.

2.2.7 | Field Predator Attack Assays

For each combination of microhabitat (nearshore vs. midriver) and diel light period (night, twilight, day; night without vs. with moonlight), we computed the mean predator attack rate (attack [0 or 1] over trial duration) and 95% confidence interval via nonparametric bootstrapping, based on sampling of assays with replacement 1000 times, computing the mean for each sample and the 0.025 and 0.975 quantiles of the distribution of sampled means. We normalised these rates to produce two additional metrics. Firstly, we divided predator attack rate by prey exposure to largemouth bass and striped bass for nearshore habitat (in which both species were identified as attackers in predation assays) and by prey exposure to striped bass only for midriver habitat (in which only striped bass were identified as attackers in predation assays). Secondly, to estimate variability in per-predator attack rate, we divided predator attack rate for each light period by the relative density of striped bass (from relocation data) normalised such that mean densities across the river summed to 1 for each light period examined (night without moonlight, night with moonlight, twilight, and day). We present findings on per-predator attack rate for striped bass only, because this species generally utilised the full cross section of the river; because largemouth bass were rarely found beyond nearshore microhabitat, we had low confidence in estimates of their per-predator attack rate in the midriver.

3 | Results

3.1 | Reconstructing Landscapes of Opportunity and Risk

In our study system, river flows in the seaward direction are generally higher in the midriver than they are nearshore (Figure 1a,b). Thus, opportunities for migrants to exploit seaward flows to facilitate migration are greater in the midriver. Concerning predators, telemetry data revealed that the two dominant fish predators in the system, largemouth bass and striped bass, exhibit different microhabitat use patterns. Largemouth bass strongly prefer nearshore microhabitats (0–32 m from shore), while striped bass are more evenly distributed across the river, utilising nearshore microhabitats more at night and midriver microhabitats (32–64 m from shore) more in the day (Figure 1c,d; patterns in Figure 1d were conserved across all top models: Figure S3). Predation assays revealed that attack rates varied considerably over space and time, but exhibited two clear spatiotemporal patterns. Firstly, attack rates peaked during twilight, the ephemeral, low-light transition period between day and night (Figure 1e). Secondly, attack rates were higher nearshore than in the midriver at night but more evenly distributed across the river under daylight and twilight (Figure 1e).

The patterns of flow and predator activity revealed by our analysis allow one to interpret observed movement patterns of migrants in the context of predator avoidance and energy objectives. For example, if migrants prioritise minimising energetic costs of migration, they should preferentially use the midriver across the diel cycle to exploit seaward flows that minimise the cost of migratory movements. If, instead, migrants seek only to minimise the risk of predation, they could minimise encounters with largemouth bass and total attack rates by avoiding nearshore microhabitat, but minimising encounters with striped bass would require avoidance of midriver microhabitat in the day. Thus, naïvely, it seems possible that migrants could optimise both threat avoidance and energy conservation by adopting a strategy in which they use the midriver over the entire diel cycle and avoid nearshore microhabitat altogether.

3.2 | Prey Decision-Making in the Face of Risk and Energy Savings

Contrary to the prediction that migrants should use the midriver across the diel cycle, we found that occurrence probability of migrants was higher nearshore than in midriver microhabitats throughout the diel cycle, but particularly during the day, when 75.6% of relocations were nearshore (Figure 2a). Use of the midriver was intermediate during twilight and greatest at night. Because midriver microhabitat facilitates migration (Figure 2b), the pattern of increased use of the midriver at night (Figure 2a) resulted in a 3-fold greater migration efficiency at night than during the day (Figure 2c). This effect was far greater than the relatively small difference in average flow between day and night in our dataset (Figure 1b). We further found that absolute displacement was greater (by 23.6%) and physical work performed during locomotion was much greater (by 260.4%) in daylight than at night (Figure 2d,e).

To understand what may drive migrant microhabitat use, we analysed exposure of migrants to the two dominant species of predators. Exposure to the nearshore-associated largemouth bass increased by 22% from night to day (Figure 2f, a pattern conserved across all top models: Figure S4). Conversely, exposure to striped bass was highest at night, decreasing by 38% from night to day (Figure 2g, a pattern conserved for three top models; two top models showed no clear effects of diel light period on exposure to striped bass: Figure S4). We further found that, despite migrants using the midriver least in daylight (Figure 2a), midriver encounters with striped bass were not lower in the day than they were at night (Figure 3a, a pattern conserved across all top models: Figure S5), indicating that these encounters were driven by increased use of the midriver by striped bass during the day (Figure 1d). To further elucidate the movement strategy of migrants, we performed a counterfactual analysis by computing the predator exposure migrants would experience if the observed patterns of migrant space use during day and night were reversed. This analysis revealed that if migrants adopted nighttime space-use patterns during the day, on average, they would have avoided 30% of actual daytime exposure to largemouth bass and 36% of actual daytime exposure to striped bass nearshore, but they would have experienced a 96% increase in exposure to striped bass in the midriver, relative to actual daytime midriver exposure to striped bass (Figure 3b and Figure S6, a pattern conserved across all top models: Figures S5 and S7). This finding suggests that, by avoiding midriver microhabitats in daylight, migrants reduce their exposure to striped bass in the midriver, but they forgo both a 3-fold increase in migration efficiency (Figure 2c) and a decrease in exposure to predators in other contexts (Figure 3b and Figure S6). One explanation for this pattern of behaviour is that midriver exposure to striped bass may be particularly dangerous for migrants. To test this hypothesis, we combined our estimates of prey exposure to predators with data from predation assays to compute a relative measure of the attack rate per unit exposure to each species of predator. The rate of attack per unit exposure to striped bass in the midriver in daylight is, on average, 10.6-fold greater than it is at night and 4.2-fold greater than that of striped bass and largemouth bass nearshore (Figure 4, a pattern conserved across all top models: Figure S8). The hypothesis that striped bass (and not largemouth bass) pose the primary threat during the day is also consistent

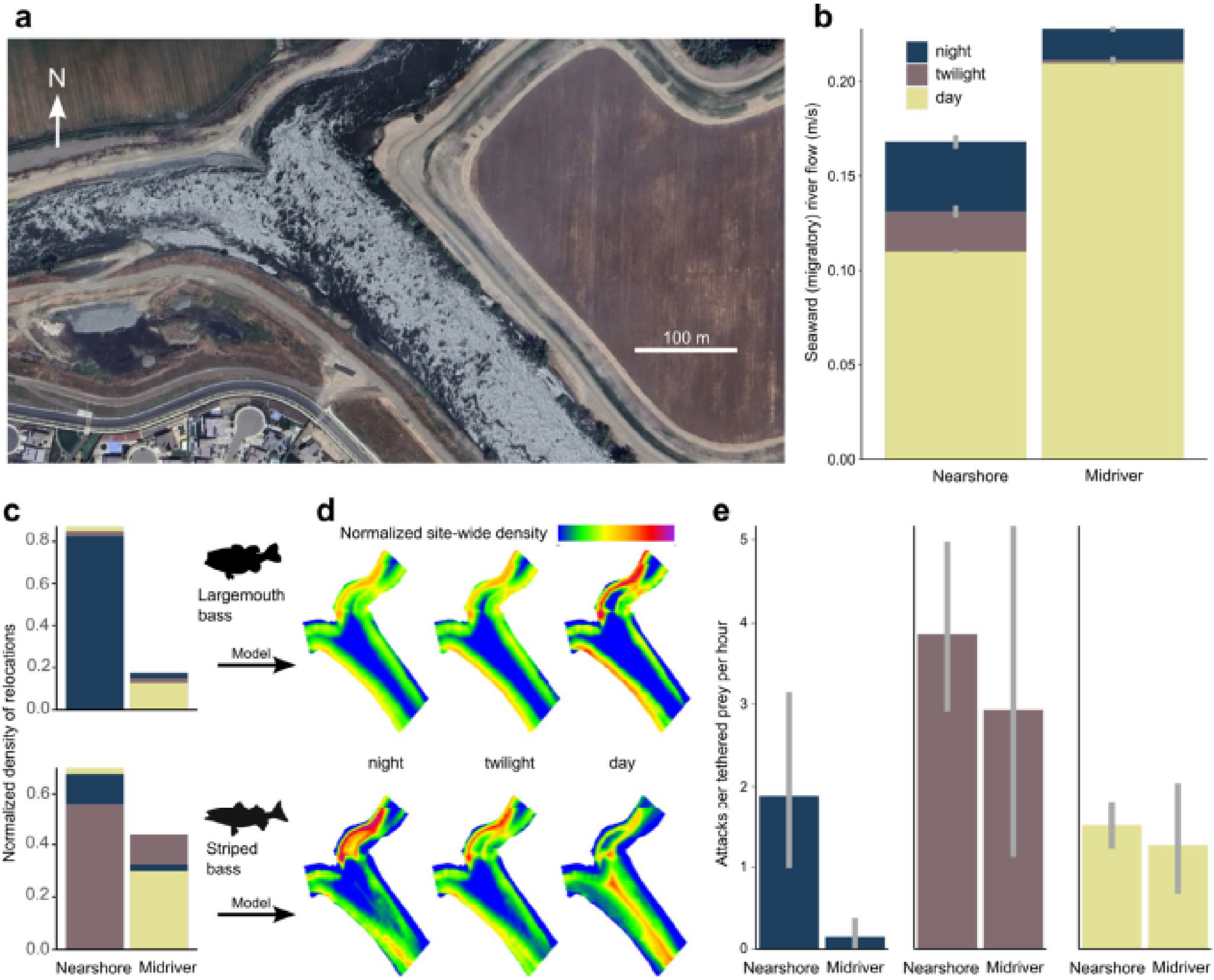

FIGURE 1 | Landscape traversed by juvenile Chinook salmon migrants (prey). (a) The 'Head of Old River' study area, at the junction of the San Joaquin River (flowing to the northeast) and Old River (flowing to the west), south of Stockton, California, USA, (b) velocity of river flow in the seaward (migratory) direction during migrant relocations, binned by distance from shore and diel light period (means +/− 95% confidence intervals, bars for each microhabitat are overlapping), (c) the distribution of the two putatively dominant predators of our focal prey species (juvenile Chinook salmon [smolts], *O. tshawytscha*, or 'migrants') in the system, binned by distance from shore (nearshore: <32 m from shore, midriver otherwise) and diel light period (bars for each microhabitat are overlapping), (d) site-wide densities (during median river depth) of both predator species estimated with generalised additive models fitted to predator relocation data (*Material and methods: Spatiotemporal distributions of predators and migrants*), and (e) predator attack rate from field presentations of tethered, live migrants of *O. tshawytscha* binned by distance from shore and diel light period (means ± 95% confidence intervals; lack of overlap in error bars denotes statistically significant differences).

with the analysis of a subset of predation assays, in which it was possible to determine predator identity (Figure S9). These data show that 197 of 213 (92%) identified attacks on migrants were by striped bass; moreover, all identified attacks in the midriver during the day were by striped bass.

3.3 | Spatiotemporal Dynamics of Predator Attack Behaviour

Predators also exhibited changes in behaviour from day to night; however, it was during twilight, the ephemeral period when prey transitioned between greater and lesser midriver microhabitat use, when the overall frequency of predator attacks was highest (Figure 1e). Furthermore, we found that attacks per unit exposure to striped bass were greatest in the midriver during twilight (4.7-fold greater than in the midriver in daylight; Figure 4), while twilight midriver use by migrants increased going from daylight to twilight (Figure 2a). Furthermore, on average, predators increase attack rate by a factor of 6.95 in the presence (vs. absence) of moonlight (Figure 5a), during which the system is exposed to a similar range of illuminance to that present during twilight. Indeed, over the diel cycle, the highest rates of attack occurred under twilight and moonlight, and these rates were similar in magnitude (Figures 1e and 5a). Furthermore, there was no detectable effect of moonlight on migrant behaviour (Figure 5b, and the pattern of predator exposure was conserved across all top models: Figure S10).

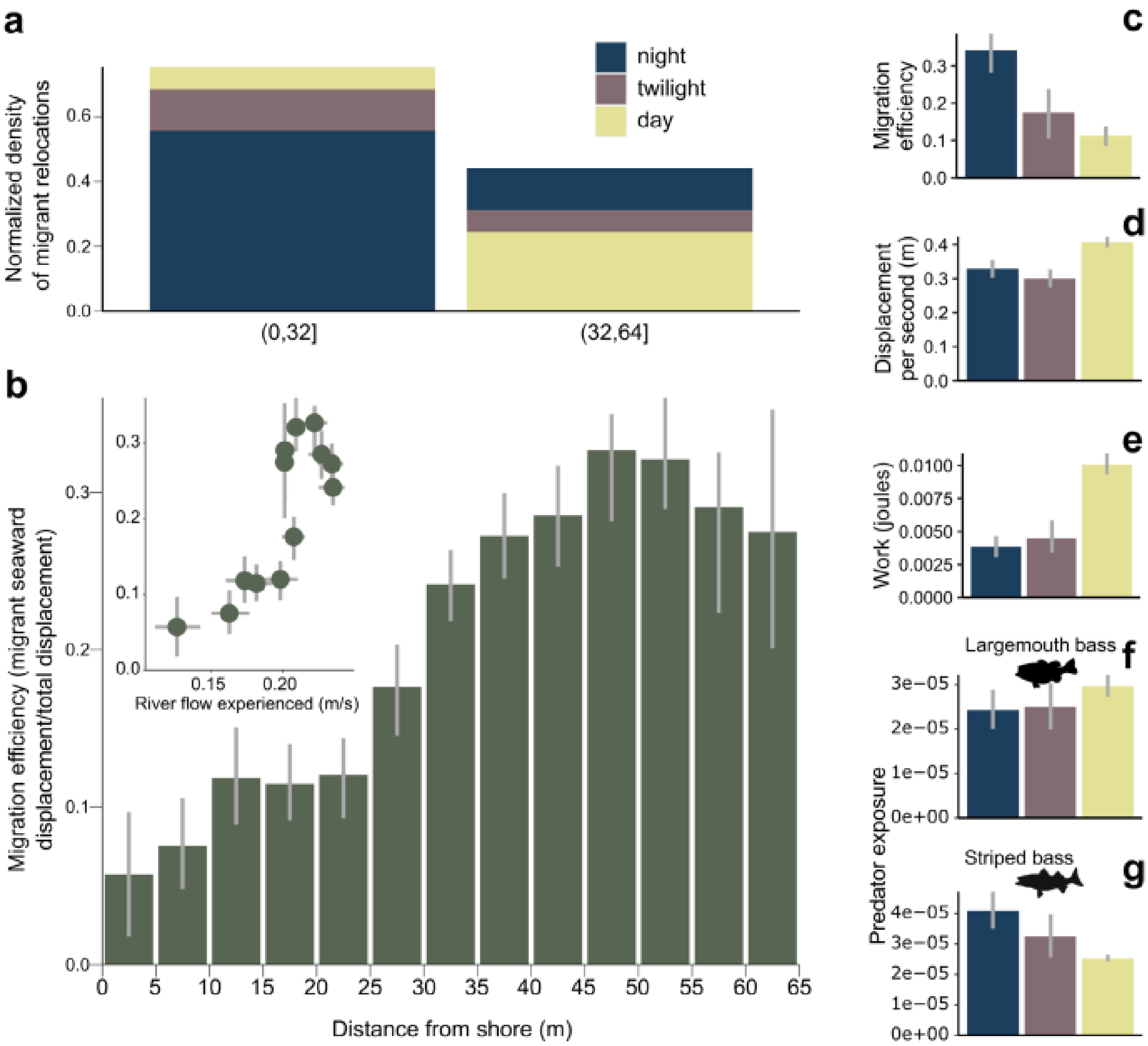

FIGURE 2 | Migrant (prey) behavioural responses to diel light period and flow and resultant predator exposure. (a) The distribution of migrants in the system over binned distances from shore and diel light periods (bars for each distance bin are overlapping), (b) migration efficiency (seaward displacement over total displacement) of prey (juvenile Chinook salmon [smolts], *O. tshawytscha*, or 'migrants') over both distances from shore (river bank) and, in the inset figure, the velocity of local river flow experienced (means ± 95% confidence intervals), and (c–g) migrant performance and behaviour over diel light periods (navy = night, maroon = twilight, yellow = day), from lowest to highest ambient light availability: Night, twilight, day (means ± 95% confidence intervals), measured with or derived from telemetry data (c–g), a computational fluid dynamics model (e), and modelled predator densities (f, g; Figure 1d, *Materials and methods: Prey exposure to predators*).

4 | Discussion

A classic prediction of ecological theory is that when energetic demands on prey are sufficiently high, prey should prioritise these demands over threat avoidance (Brown and Kotler 2004; Lima 1998; McNamara and Houston 1987). Our results allowed us to rigorously test this long standing hypothesis with respect to animal movement decisions in the wild. We find that prey employ a dynamic strategy in which they shift microhabitat use depending on both changing risk and the energetic cost of movement: prey appear to avoid risk at high energetic expense under daylight, but to effectively accept greater risk to improve the energetic efficiency of migration during twilight and nighttime. These results address a critical knowledge gap concerning how animals make decisions to both move with energetic efficiency and avoid predatory threats (Gallagher et al. 2017; Papastamatiou et al. 2024), a task that is likely to be particularly challenging during energetically demanding periods, such as dispersal or migration (Sabal et al. 2021). Our findings show that animals can dynamically prioritise threat avoidance and energetic efficiency (analogous to findings of prey dynamic prioritisation of threat avoidance and feeding; Poulin, Cherry, and Merkle 2023) within as narrow a time period as a diel cycle, demonstrating a movement strategy that falls between past observations that prey simply either prioritise threat avoidance (Matthews et al. 2020) or energy conservation (McCabe and Olsen 2015).

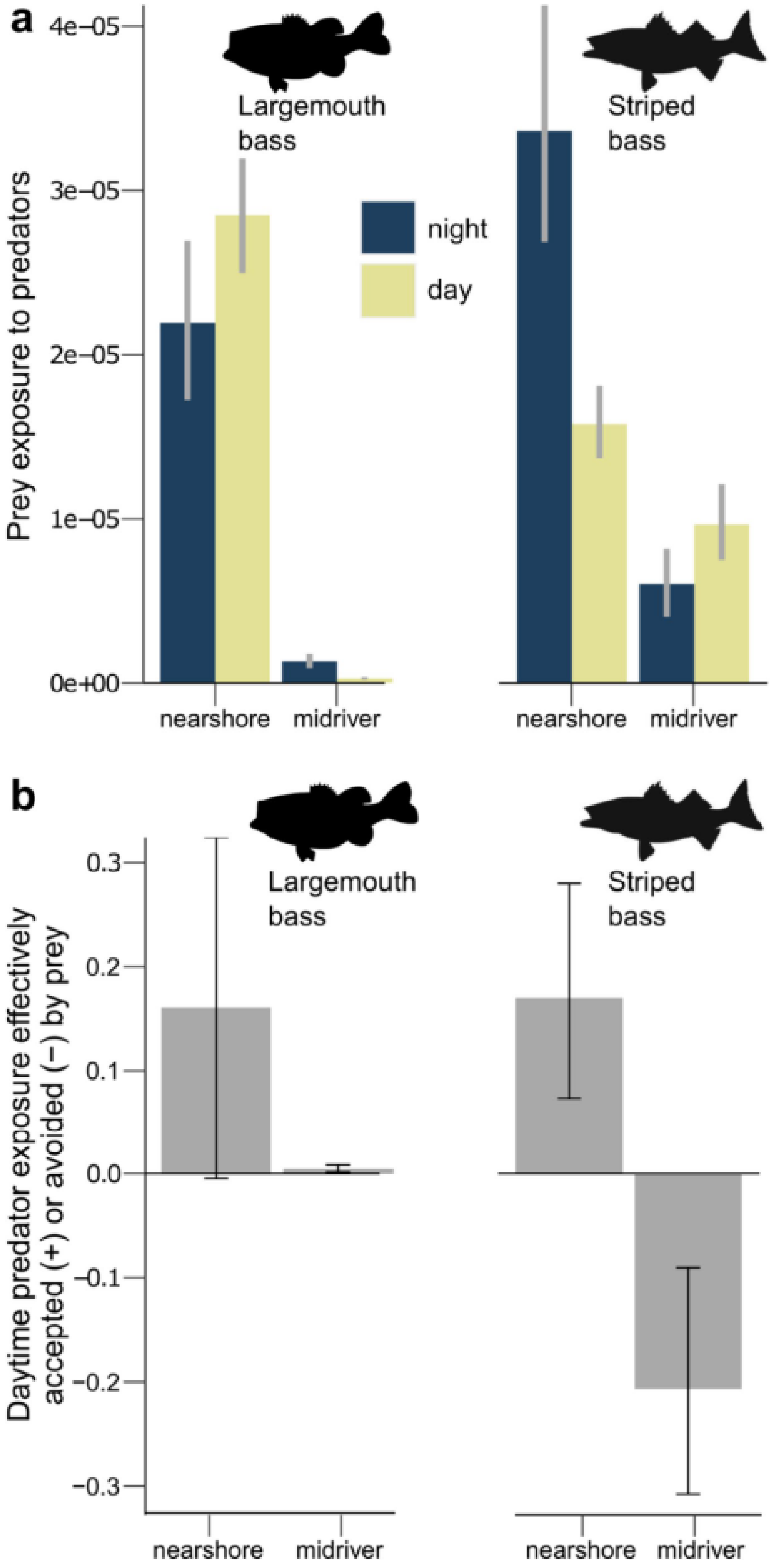

FIGURE 3 | Legend on next page.

FIGURE 3 | Migrant (prey) exposure to predators and effective acceptance or avoidance thereof. (a) Migrant exposure to predators, a normalised metric for risk, based on predicted predator densities (see *Material and methods: Prey exposure to predators*; means ± 95% confidence intervals) over binned distances from shore and over night (navy) and day (yellow), derived from telemetry data (see *Materials and methods: Prey exposure to predators*), and (b) the difference in estimated daytime predator exposure ((actual—counterfactual)/median predator exposure; means ± 95% confidence intervals, see *Materials and methods: Counterfactual analysis*) of migrant prey, indicative of effectively accepted (positive values) versus avoided (negative values) predator exposure.

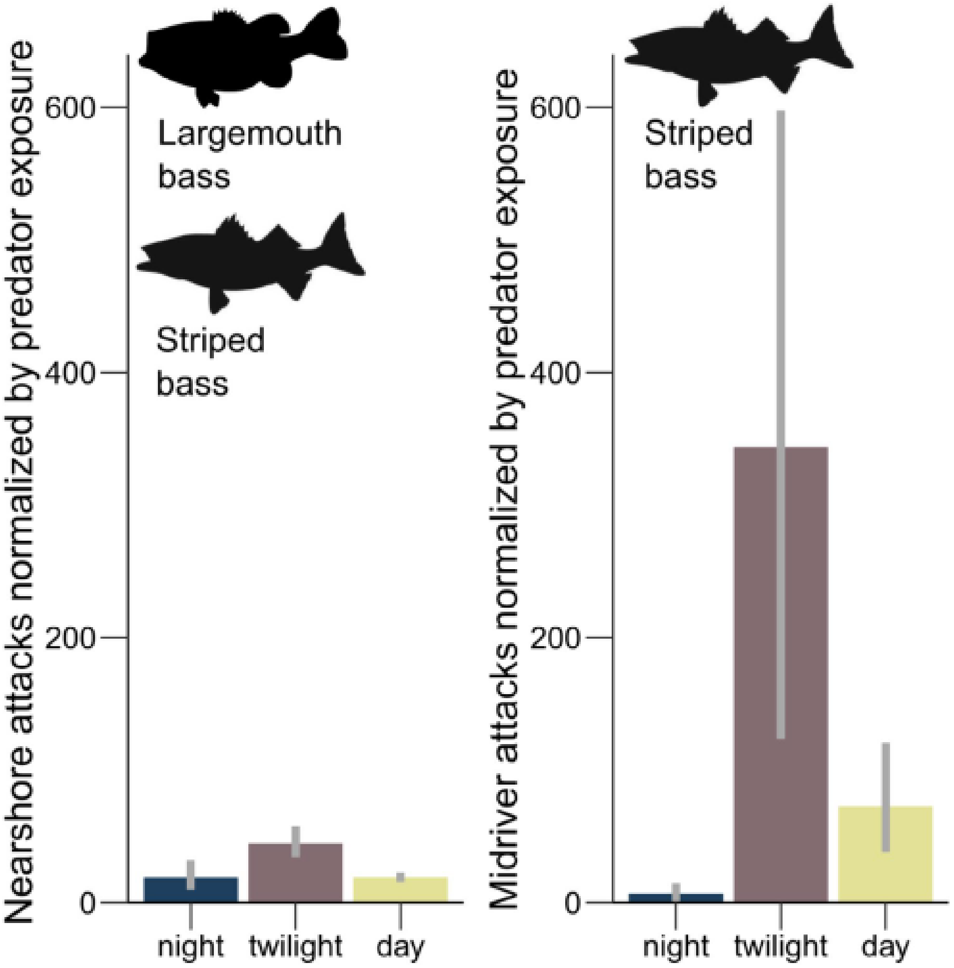

FIGURE 4 | The risk that exposure to a predator leads to an attack depends on predator species and spatiotemporal window. Attacks per unit of exposure of prey to predators (attacks per unit time on field presentations of tethered, live migrants of Chinook salmon (*O. tshawytscha*), divided by predator exposure per unit time derived from telemetry data; means ± 95% confidence intervals, see *Materials and methods: Field predator attack assays*) nearshore for largemouth bass and striped bass and midriver for striped bass.

By illustrating how prey negotiate the tradeoff between energy use and risk avoidance, our results address another fundamental question in ecology: *what determines whether predators affect prey primarily through fear or through direct mortality?* Our analyses suggest that predators are likely to affect prey populations most strongly when peaks in the landscape of risk have high spatiotemporal overlap with peaks in opportunities for energy savings across the landscape, resulting in strong conflict between movements that would optimise different demands. However, whether predators affect prey primarily by changing how prey use the energy landscape (i.e. through fear effects on prey behaviour) or through direct mortality, depends on how prey negotiate this tradeoff between conflicting demands. Our results show that prey in our system use a mixed strategy, wherein they avoid efficient but dangerous routes at some times (avoidance of the midriver during daylight, Figure 2c,e), but opt to use locations that confer efficient movement despite danger at other times (e.g. during twilight and moonlight, Figures 4 and 5). In the first case, predators affect prey through classic fear effects; prey pay both an opportunity cost of slowed migration and a high energetic cost when using safer microhabitats (Figure 2c,e). In the second case, predators are most likely to affect prey by imposing direct mortality, particularly during moonlight and twilight, when prey move more efficiently but appear unresponsive to heightened predation risk.

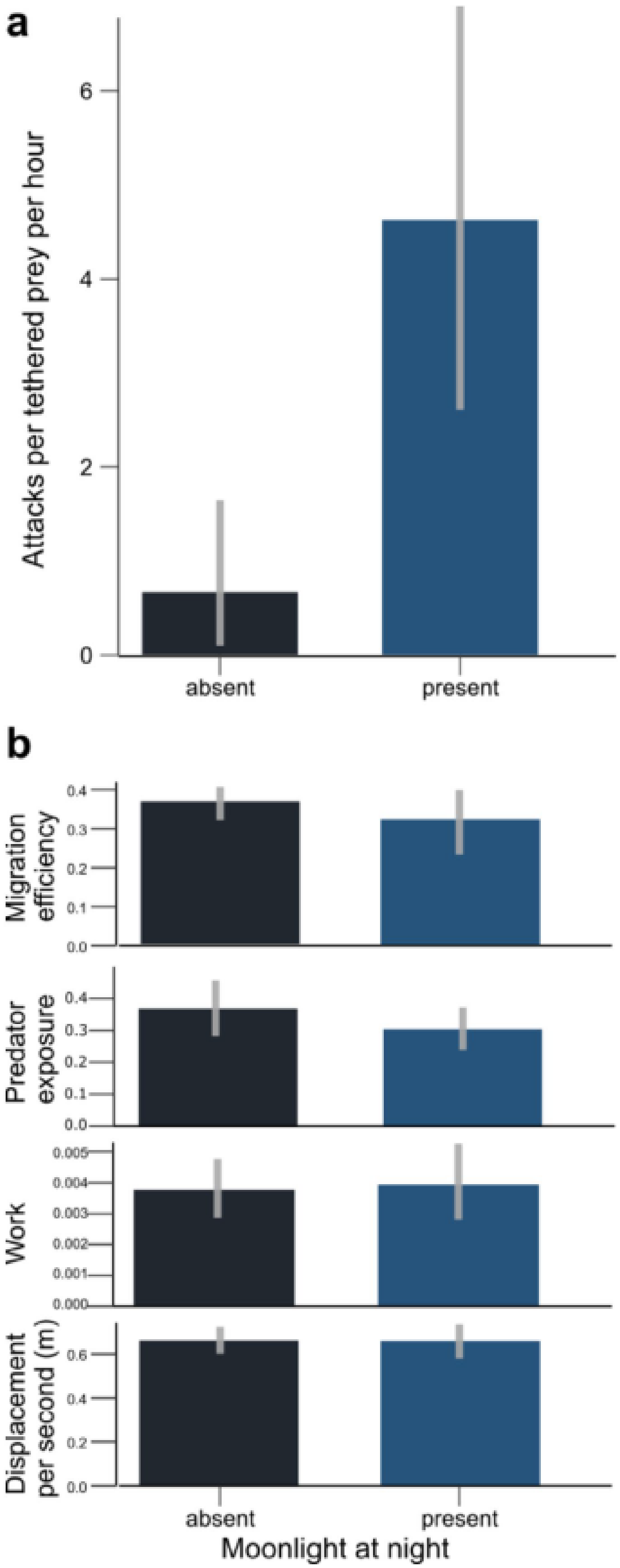

FIGURE 5 | Effects of moonlight differ between predators and prey. Effects of moonlight at night on (a) predator attack rate and (b) migrant performance and behaviour (means ± 95% confidence intervals).

We find that whether prey move in ways that prioritise energetic efficiency or minimise risk is tightly linked to the phase of the diel cycle; prey avoid risk during the day but prioritise efficiency during twilight and night. The idea that migratory animals may avoid travelling during the day to reduce predation risk has been widely invoked to explain patterns of nocturnal migration, including those observed in a number of salmon species (Chapman et al. 2013; Clark et al. 2016; Ibbotson, Beaumont, and Pinder 2011; Komal et al. 2017; Railsback et al. 2005). But it has also been argued more broadly that concentrating activity into nocturnal periods may be a general behavioural mechanism animals use to avoid threats (Berger and Gotthard 2008; Gaynor et al. 2018; Kronfeld-Schor and Dayan 2003). Our findings are consistent with these broad predictions, but the unique nature of our data allows us to add details to this picture of prey decision-making. For example, while prey migrate less efficiently during the day, they are not inactive but, instead, move frequently, cover significant distances, and expend substantial energy (Figure 2c–e). We also found that prey did not restrict their use of the microhabitats that confer efficient movement to dark night alone, when these locations are relatively safe, but also used these microhabitats during twilight, when attack risk per predator encounter reached its peak (Figure 4). These findings suggest that the strategies prey use to navigate tradeoffs between risk avoidance and energetic efficiency do not necessarily uniformly reduce risk, but may instead concentrate periods where prey are exposed to high risk into transient spatiotemporal windows.

The influence of ambient lighting on how prey navigate energy-safety tradeoffs is perhaps most evident in our findings that predatory attacks increase during twilight and moonlight (Figures 4 and 5a) but that there is an apparent lack of response by prey to these heightened threats (Figures 2a and 5b). Consistent with this, recent experimental manipulations of light levels at night in this system found that artificially increasing illuminance into a range that occurs naturally during moonlight and twilight (0.5–70 lx) caused a substantial increase in attack rates on salmon smolts (Nelson et al. 2021). A possible explanation for these patterns is that predators increase feeding activity during conditions of intermediate light precisely because they have a sensory advantage during these periods (Kronfeld-Schor et al. 2013; Ranåker et al. 2014). Striped bass, largemouth bass, and chinook salmon all exhibit limited visual perceptual capabilities at light levels below 10^{-4}—10^{-2} lx, corresponding to nocturnal conditions in the absence of moonlight, whereas perceptual capabilities of all three species increase dramatically with increasing light levels between 10^{-2} lx and roughly 50 lx—a range corresponding to moonlight and twilight (Hansen, Beauchamp, and Schoen 2013; Horodysky et al. 2010; McMahon and Holanov 1995). The limited experimental data that exist, however, suggest that this increase in visual capabilities occurs at lower light levels for striped bass and largemouth bass (Horodysky et al. 2010; McMahon and Holanov 1995) than it does for salmon (Hansen, Beauchamp, and Schoen 2013), consistent with the idea that intermediate light may create a sensory asymmetry between predators and prey. The extent to which such sensory asymmetries may occur across predator–prey systems, and whether they may explain the existence of diel or lunar predation windows remains an open question.

Understanding how the nature of predator–prey interactions emerges from the dynamic interplay between environmental contexts has been difficult historically because past studies of animal behaviour in the wild are limited not only by their lack of measurements of concurrent fear and energy landscapes, but also their lack of measurements of changes in prey and predator behaviour over time. Most previous studies have treated the landscape of fear as a static property of the environment (Kohl et al. 2018; Palmer et al. 2023). Moreover, many studies use the density or average density of predators as a proxy of risk, ignoring possible shifts in predator feeding behaviour (Lima 2002; Suraci et al. 2022). In our study, per-predator attack rates change by a factor of 20.8 over space and time (Figure S11), illustrating that predator density alone can be a poor proxy for risk. Instead, risk is determined by the interplay between behaviours of both predators and prey that vary over space and time. Importantly, the interactive effects of energy and fear landscapes were only apparent in our study because we were able to decouple attack risk in a given location from prey density, a variable that can confound risk estimates when they are based on variables like natural kill site locations or alarm call frequencies (Coleman and Hill 2014; Kauffman, Brodie, and Jules 2010; Perry et al. 2020). Our site-wide predator attack assays allowed us to assess relative predation risk even in locations that freely moving prey rarely or never visit, which is critical to understanding threat avoidance behaviour (e.g. prey avoidance of midriver habitat in daylight, where and when the risk of predation given prey exposure to a predator is particularly high; Figure 4).

While our analyses offer rich general insights, the observational nature of our datasets also imposes limitations on our inference. For example, because salmon smolts are only one of a range of possible prey species present in the system, we cannot determine definitively whether shifts in predator behaviour are a response to changes in the behaviour of salmon, per se. Despite these limitations, our analyses provide concrete evidence that energy landscapes can interact with dynamic landscapes of fear in ways that shape species interactions, for instance by determining when and where predators affect prey through density- (mortality) versus trait-mediated (fear) effects. Combining energy and fear landscapes, thus, has the potential to help resolve apparent discrepancies in the relative importance of these effects and their downstream ecological consequences (Kauffman, Brodie, and Jules 2010; Preisser, Bolnick, and Benard 2005; Sheriff et al. 2020). Our findings suggest that we may generally expect that density-mediated effects will dominate when energy-savings opportunities are substantial, or that fear effects will dominate when energy-savings opportunities are more limited.

Simultaneously quantifying prey and predator behaviour and energy landscapes in the wild has tremendous potential to further our understanding of the ecology and evolution of predator–prey interactions (Gallagher et al. 2017; Papastamatiou et al. 2024). Such work will be particularly critical for evaluating how anthropogenic changes like sensory pollution and habitat modifications that alter both risk and energy landscapes will impact ecosystems (Dickie et al. 2020; Dominoni et al. 2020; Abrahams and Kettenfeld 1997), for example, by changing the degree to which predators affect prey through mortality or fear. Building a deeper, data-driven understanding of prey and predator strategies and the sensory, energetic, and behavioural mechanisms that drive them has the potential to yield transformative insights for the disciplines of ecology, evolution, and conservation (Gaynor et al. 2021; Papastamatiou et al. 2024).

Author Contributions

M.A.G. and A.M.H. designed the study, M.A.G. performed all analyses, C.M. contributed predation data, S.O. contributed fluid dynamics models, M.A.G. and A.M.H. wrote the first draft of the manuscript, and all authors contributed to revisions.

Acknowledgements

This project was supported, in part, through the California Department of Fish and Wildlife from the Water Quality, Supply and Infrastructure Improvement Act of 2014 (CA Department of Fish and Wildlife grant No. P1896007-01), and the National Science Foundation (Grants IOS-1855956, IOS-2338596, and EF-2222478).

Data Availability Statement

The data and code supporting the results have been archived in a public repository: https://doi.org/10.5281/zenodo.14536270.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70068.

References

Abrahams, M. V., and M. G. Kattenfeld. 1997. "The Role of Turbidity as a Constraint on Predator-Prey Interactions in Aquatic Environments." *Behavioral Ecology and Sociobiology* 40: 169–174.

Bartoń, K. A., T. Hovestadt, B. L. Phillips, and J. M. J. Travis. 2011. "Risky Movement Increases the Rate of Range Expansion." *Proceedings of the Royal Society B: Biological Sciences* 279: 1194–1202.

Berger, D., and K. Gotthard. 2008. "Time Stress, Predation Risk and Diurnal–Nocturnal Foraging Trade-Offs in Larval Prey." *Behavioral Ecology and Sociobiology* 62: 1655–1663.

Borchering, R. K., S. E. Bellan, J. M. Flynn, J. R. C. Pulliam, and S. A. McKinley. 2017. "Resource-Driven Encounters Among Consumers and Implications for the Spread of Infectious Disease." *Journal of the Royal Society Interface* 14: 20170555.

Brown, J. S., and B. P. Kotler. 2004. "Hazardous Duty Pay and the Foraging Cost of Predation." *Ecology Letters* 7: 999–1014.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. New York, USA: Springer Verlag.

California Data Exchange Center (CDEC). 2024. *Sacramento-San Joaquin Delta*. Sacramento, USA: California Department of Water Resources.

Chapman, E. D., A. R. Hearn, C. J. Michel, et al. 2013. "Diel Movements of Out-Migrating Chinook Salmon (*Oncorhynchus tshawytscha*) and Steelhead Trout (*Oncorhynchus mykiss*) Smolts in the Sacramento/San Joaquin Watershed." *Environmental Biology of Fishes* 96: 273–286.

Clark, T. D., N. B. Furey, E. L. Rechisky, et al. 2016. "Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality." *Ecological Applications* 26: 959–978.

Coleman, B. T., and R. A. Hill. 2014. "Living in a Landscape of Fear: The Impact of Predation, Resource Availability and Habitat Structure on Primate Range Use." *Animal Behaviour* 88: 165–173.

Darveniza, T., S. I. Zhu, Z. Pujic, et al. 2023. "Behavioral adaptation to changing energy constraints via altered frequency of movement selection." *bioRxiv*. https://doi.org/10.1101/2023.11.08.566262.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. "Corridors or Risk? Movement Along, and Use of, Linear Features Varies Predictably Among Large Mammal Predator and Prey Species." *Journal of Animal Ecology* 89: 623–634.

Dominoni, D. M., W. Halfwerk, E. Baird, et al. 2020. "Why Conservation Biology can Benefit from Sensory Ecology." *Nature Ecology & Evolution* 4: 502–511.

Gallagher, A. J., S. Creel, R. P. Wilson, and S. J. Cooke. 2017. "Energy Landscapes and the Landscape of Fear." *Trends in Ecology & Evolution* 32: 88–96.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. "Landscapes of Fear: Spatial Patterns of Risk Perception and Response." *Trends in Ecology & Evolution* 34: 355–368.

Gaynor, K. M., M. J. Cherry, S. L. Gilbert, et al. 2021. "An Applied Ecology of Fear Framework: Linking Theory to Conservation Practice." *Animal Conservation* 24: 308–321.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. "The Influence of Human Disturbance on Wildlife Nocturnality." *Science* 360: 1232–1235.

Hansen, A. G., D. A. Beauchamp, and E. R. Schoen. 2013. "Visual Prey Detection Responses of Piscivorous Trout and Salmon: Effects of Light,Turbidity,and Prey Size." *Transactions of the American Fisheries Society* 142: 854–867.

Hastie, T., and B. Narasimhan. 2023. *Package: Gam: Generalized Additive Models*. CRAN.

Hein, A. M., and B. T. Martin. 2019. "Information Limitation and the Dynamics of Coupled Ecological Systems." *Nature Ecology & Evolution* 4: 82–90.

Hein, A. M., and S. A. McKinley. 2013. "Sensory Information and Encounter Rates of Interacting Species." *PLoS Computational Biology* 9: e1003178.

Henderson, M. J., C. M. Loomis, C. J. Michel, et al. 2023. "Estimates of Predator Densities Using Mobile DIDSON Surveys: Implications for Survival of Central Valley Chinook Salmon." *North American Journal of Fisheries Management* 43: 628–645.

Horodysky, A. Z., R. W. Brill, E. J. Warrant, J. A. Musick, and R. J. Latour. 2010. "Comparative Visual Function in Four Piscivorous Fishes Inhabiting Chesapeake Bay." *Journal of Experimental Biology* 213: 1751–1761.

Ibbotson, A. T., W. R. C. Beaumont, and A. C. Pinder. 2011. "A Size-Dependent Migration Strategy in Atlantic Salmon Smolts: Small Smolts Favour Nocturnal Migration." *Environmental Biology of Fishes* 92: 151–157.

Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. "Are Wolves Saving Yellowstone's Aspen? A Landscape-Level Test of a Behaviorally Mediated Trophic Cascade." *Ecology* 91: 2742–2755.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. "Terrestrial Animal Tracking as an Eye on Life and Planet." *Science* 348: aaa2478.

Kohl, M. T., D. R. Stahler, M. C. Metz, et al. 2018. "Diel Predator Activity Drives a Dynamic Landscape of Fear." *Ecological Monographs* 88: 638–652.

Komal, R., A. Khushboo Dwivedi, V. Vaish, and S. Rani. 2017. "Conquering the Night: Understanding Nocturnal Migration in Birds." *Biological Rhythm Research* 48: 747–755.

Kronfeld-Schor, N., and T. Dayan. 2003. "Partitioning of Time as an Ecological Resource." *Annual Review of Ecology, Evolution, and Systematics* 34: 153–181.

Kronfeld-Schor, N., D. Dominoni, H. de la Iglesia, et al. 2013. "Chronobiology by moonlight." *Proceedings of the Royal Society B: Biological Sciences* 280: 20123088.

Liao, J. C. 2007. "A Review of Fish Swimming Mechanics and Behaviour in Altered Flows." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 362: 1973–1993.

Lima, S. L. 1998. "Stress and Decision Making Under the Risk of Predation: Recent Developments From Behavioral, Reproductive, and Ecological Perspectives." In *Advances in the Study of Behavior*, edited by A. P. Møller, M. Milinski, and P. J. B. Slater, 215–290. Academic Press.

Lima, S. L. 2002. "Putting Predators Back Into Behavioral Predator–Prey Interactions." *Trends in Ecology & Evolution* 17: 70–75.

Lima, S. L., and L. M. Dill. 1990. "Behavioral Decisions Made Under the Risk of Predation: A Review and Prospectus." *Canadian Journal of Zoology* 68: 619–640.

Lindström, T., G. P. Brown, S. A. Sisson, B. L. Phillips, and R. Shine. 2013. "Rapid Shifts in Dispersal Behavior on an Expanding Range Edge." *Proceedings of the National Academy of Sciences* 110: 13452–13456.

Mahardja, B., M. J. Farruggia, B. Schreier, and T. Sommer. 2017. "Evidence of a Shift in the Littoral Fish Community of the Sacramento-San Joaquin Delta." *PLoS One* 12: e0170683.

Matthews, C. J. D., G. A. Breed, B. LeBlanc, and S. H. Ferguson. 2020. "Killer Whale Presence Drives Bowhead Whale Selection for Sea Ice in Arctic Seascapes of Fear." *Proceedings of the National Academy of Sciences* 117: 6590–6598.

McCabe, J. D., and B. J. Olsen. 2015. "Tradeoffs Between Predation Risk and Fruit Resources Shape Habitat Use of Landbirds During Autumn Migration." *Auk* 132: 903–913.

McElroy, B., A. DeLonay, and R. Jacobson. 2012. "Optimum Swimming Pathways of Fish Spawning Migrations in Rivers." *Ecology* 93: 29–34.

McMahon, T. E., and S. H. Holanov. 1995. "Foraging Success of Largemouth Bass at Different Light Intensities: Implications for Time and Depth of Feeding." *Journal of Fish Biology* 46: 759–767.

McNamara, J. M., and A. I. Houston. 1987. "Starvation and Predation as Factors Limiting Population Size." *Ecology* 68: 1515–1519.

McQuirk, J., K. Simon, and M. Cane. 2015. *An Evaluation of Juvenile Salmonid Routing and Barrier Effectiveness, Predation, and Predatory Fishes at the Head of Old River*, edited by AECOM. ICF International, and Turnpenny Horsefield Associates.

Meteoblue. 2023. Weather Archive Sacramento.

Michel, C. J., M. J. Henderson, C. M. Loomis, et al. 2020. "Fish Predation on a Landscape Scale." *Ecosphere* 11: e03168.

Nathan, R., C. T. Monk, R. Arlinghaus, et al. 2022. "Big-data Approaches Lead to an Increased Understanding of the Ecology of Animal Movement." *Science* 375: eabg1780.

Nelson, T. R., C. J. Michel, M. P. Gary, et al. 2021. "Effects of Artificial Lighting at Night on Predator Density and Salmonid Predation." *Transactions of the American Fisheries Society* 150: 147–159.

Nobriga, M. L., and F. Feyrer. 2007. "Shallow-Water Piscivore-Prey Dynamics in California's Sacramento–san Joaquin Delta." *San Francisco Estuary and Watershed Science* 5.

Olivetti, S., M. A. Gil, V. Sridharan, and A. M. Hein. 2021. "Merging Computational Fluid Dynamics and Machine Learning to Reveal Animal Migration Strategies." *Methods in Ecology and Evolution* 12: 1186–1200.

Palmer, M. S., K. M. Gaynor, J. O. Abraham, and R. M. Pringle. 2023. "The Role of Humans in Dynamic Landscapes of Fear." *Trends in Ecology & Evolution* 38: 217–218.

Papastamatiou, Y. P., B. M. Binder, K. M. Boswell, et al. 2024. "Dynamic Energy Landscapes of Predators and the Implications for Modifying Prey Risk." *Functional Ecology* 38: 284–293.

Pawar, S., A. I. Dell, and V. M. Savage. 2012. "Dimensionality of Consumer Search Space Drives Trophic Interaction Strengths." *Nature* 486: 485–489.

Perry, T. A., M. P. Laforge, E. Vander Wal, T. W. Knight, and P. D. McLoughlin. 2020. "Individual Responses to Novel Predation Risk and the Emergence of a Landscape of Fear." *Ecosphere* 11: e03216.

Poulin, M.-P., S. G. Cherry, and J. A. Merkle. 2023. "Dynamic Balancing of Risks and Rewards in a Large Herbivore: Further Extending Predator–Prey Concepts to Road Ecology." *Journal of Animal Ecology* 92: 1954–1965. https://doi.org/10.1111/1365-2656.13985.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. "Scared to Death? The Effects of Intimidation and Consumption in Predator-Prey Interactions." *Ecology* 86: 501–509.

R Core Team. 2023. R: A Language and Environment for Statistical Computing.

Railsback, S. F., B. C. Harvey, J. W. Hayse, and K. E. LaGory. 2005. "Tests of Theory for Diel Variation in Salmonid Feeding Activity and Habitat Use." *Ecology* 86: 947–959.

Ranåker, L., J. Persson, M. Jönsson, P. A. Nilsson, and C. Brönmark. 2014. "Piscivore-Prey Fish Interactions: Mechanisms Behind Diurnal Patterns in Prey Selectivity in Brown and Clear Water." *PLoS One* 9: e102002.

Sabal, M. C., M. S. Boyce, C. L. Charpentier, et al. 2021. "Predation Landscapes Influence Migratory Prey Ecology and Evolution." *Trends in Ecology & Evolution* 36: 737–749.

Shepard, E. L. C., R. P. Wilson, W. G. Rees, E. Grundy, S. A. Lambertucci, and S. B. Vosper. 2013. "Energy Landscapes Shape Animal Movement Ecology." *American Naturalist* 182: 298–312.

Sheriff, M. J., S. D. Peacor, D. Hawlena, and M. Thaker. 2020. "Non-consumptive Predator Effects on Prey Population Size: A Dearth of Evidence." *Journal of Animal Ecology* 89: 1302–1316.

Sridharan, V. K., D. Jackson, A. M. Hein, et al. 2023. "Simulating the Migration Dynamics of Juvenile Salmonids through Rivers and Estuaries using a Hydrodynamically Driven Enhanced Particle Tracking Model." *Ecological Modelling* 482: 110393.

Suraci, J. P., J. A. Smith, S. Chamaillé-Jammes, et al. 2022. "Beyond Spatial Overlap: Harnessing New Technologies to Resolve the Complexities of pREdator–Prey Interactions." *Oikos* 2022: e09004.

Time and Date AS. 2024a. Moonrise and Moonset Calculator.

Time and Date AS. 2024b. Sunrise and Sunset Calculator.

Verdolin, J. L. 2006. "Meta-Analysis of Foraging and Predation Risk Trade-Offs in Terrestrial Systems." *Behavioral Ecology and Sociobiology* 60: 457–464.

Wang, R. F., E. Ateljevich, and B. E. Jaffe. 2018. A Revised Continuous Surface Elevation Model for Modeling. Methodology for Flow and Salinity Estimates in the Sacramento-San Joaquin Delta and Suisun Marsh: 39th Annual Progress Report Bay-Delta Office, California Department of Water Resources and Pacific Coastal and Marine Science Center, United States Geological Survey.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.