AN ABSTRACT OF THE DISSERTATION OF

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Abstract approved:

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Mauricio Cantor

Animal movement directly reflects how individuals navigate resources and risks in their environment to survive and reproduce. Environments span both spatial (e.g., habitat) and social (e.g., population density) domains, and their intersection shapes movement across scales—from short-term individual-level behavior to group-level collective decisions to long-term population-level distribution. Understanding how this ‘spatial-social interface’ manifests in wild populations is thus imperative for predicting adaptability to environmental change, interpreting population dynamics, and guiding conservation strategies. This PhD dissertation explores the causes and consequences of such scale-dependent spatial-social processes in false killer whales (*Pseudorca crassidens*) around the Hawaiian Archipelago, where three partially sympatric, demographically independent populations occur: Main Hawaiian Islands (MHI) insular, Northwestern Hawaiian Islands (NWHI) insular, and pelagic.

Integrating long-term (1999-2025) datasets on movement (satellite-linked tags), demographic information (photo-identification, social networks), and biomarkers (stable isotopes), I quantify spatial and social drivers of movement patterns—and the feedback between them—across scales to then examine how these feedback mechanisms underlie behavior and distribution, including conflict with fisheries. In Chapter 2, I first examine the ecological contexts of diving behavior to reveal fundamental information on vertical movements and foraging strategies. Whales predominantly used the epipelagic zone—a key vertical habitat of known prey—but also exploited deeper habitats, including a record maximum for the species (>1,400 m). Despite high among-individual variability in behavior across populations, there were shared patterns with environmental proxies of vertical prey availability and accessibility. These findings collectively suggest that false killer whales adopt an ecologically-driven adaptive foraging strategy. With this understanding on foraging flexibility, in Chapter 3 I then develop and empirically apply a scale-explicit conceptual framework for testing how resource ephemerality and social reliance govern top-down versus bottom-up processes between movement and sociality. Here I focus on the well-documented endangered MHI population, which is structured into four stable social clusters of kin and non-kin associates. I found that strong social bonds drive bottom-up emergence of short-term intra-cluster movements, but ephemeral, island-structured prey landscapes impose top-down constraints on inter-social cluster dynamics across scales. These synergistic processes translated to long-term spatial fidelity in some social clusters and differentiated feeding niches among them. Importantly, these long-term effects reveal areas that serve as joint ecological resources and social arenas, with empirical evidence for effects on gene flow. Lastly, in Chapter 4 I apply a multiscale analytical framework to identify oceanographic features that may drive co-occurrence of, and conflict risk between, pelagic false killer whales and commercial longline fishing activity to inform bycatch and depredation mitigation measures. Whales and longline vessels exhibited similar range-wide affinities for proxies of productive mesoscale eddies. At intermediate scales, whales' ranging behavior was associated with metrics of biological productivity and prey accessibility; these relationships mapped similarly to fine-scale co-occurrences with longliners, suggesting that whales seek out longline gear for alternative foraging opportunities, supported by confirmed co-occurrences resulting in depredated gear by either tagged whales or distant associates. Together, the findings of this PhD dissertation enhance understanding on the environmental, behavioral, and anthropogenic factors shaping the movement decisions of highly intelligent and social top predators. These findings have direct implications for management in support of false killer whale population recovery and bycatch mitigation strategies in Hawaiʻi. More broadly, and beyond real-world application, I demonstrate an effective framework for integrating different, albeit complementary, data streams to develop a comprehensive depiction of animal movements across ecological and demographic scales. This research, therefore, makes a direct contribution to the emerging body of empirical and theoretical research bridging spatial and social behavior in Ecology.

Movement as a Spatial-Social Process: Multiscale Patterns in Hawai‘i’s False Killer Whales

by
Michaela A. Kratofil

A DISSERTATION

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APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries, Wildlife, and Conservation Sciences

Dean of Graduate Education

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Michaela A. Kratofil, Author

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ranging from sharing bad drafts first and crafting succinct narratives on beefy, complex results, to really taking a step back to look at the bigger picture—and I've grown so much from my time working with you. I'm very much looking forward to continuing our friendship and collaboration.

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CONTRIBUTION OF AUTHORS

Chapter 2: Michaela A. Kratofil processed the SPLASH data, conducted statistical analyses, created visualizations, and wrote and edited the paper; Jacquelyn F. Shaff processed TDR data, helped create visualizations, and wrote and edited the paper; Holly K. Hoffbauer helped process SPLASH data, helped create visualizations, and wrote and edited the paper; Mauricio Cantor provided conceptual guidance and edited the paper; Marie C. Hill contributed tag data and edited the paper; Robin W. Baird acquired funding, collected the data, provided conceptual guidance, and edited the paper. All authors read and approved the final manuscript.

Chapter 3: Michaela A. Kratofil, Robin W. Baird, and Mauricio Cantor conceptualized the ideas. Devin S. Johnson helped design the tag-based analytical framework. Colin J. Cornforth deployed satellite tags and collected biopsy samples. Sabre D. Mahaffy matched individuals and processed association data, Michelle Caputo and Jeremy J. Kiszka processed biopsy samples for stable isotopes and assisted with associated data analysis, and Karen K. Martien processed biopsy samples for genetic relatedness. Robin W. Baird acquired funding and conducted fieldwork. Michaela A. Kratofil conducted all statistical analyses with the supervision of Mauricio Cantor and Devin S. Johnson. Michaela A. Kratofil wrote the first draft of the manuscript and all authors reviewed and edited subsequent drafts.

Chapter 4: Michaela A. Kratofil: conceptualization, investigation, methodology, formal analysis, visualization, writing - original draft, funding acquisition; Robin W. Baird: conceptualization, writing - review and editing, data curation, investigation, funding acquisition; Colin J. Cornforth: investigation, data curation, writing – review and editing; Amanda L. Bradford: investigation, writing - review and editing; Mauricio Cantor: conceptualization, supervision, writing - review and editing.

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DEDICATION

I dedicate my dissertation to the wild things, who are completely ignorant of this dissertation, but have been an ever-present source of inspiration in my life and the reason why I do what I do.

1. GENERAL INTRODUCTION

1.1 Movement in the ecology of life

Movement is central to animal life: animals move to find food and mates, socially interact with others, and avoid predators and competitors, all of which are necessary to survive and reproduce. Thus, movement is fundamental to individual fitness and has important implications for population structure and persistence (Morales et al., 2010; Nathan et al., 2008). Animals also impose effects on their surrounding environment through their movements, thereby playing a key role in ecosystem functioning, community dynamics, and diversity (Lima and Zollner, 1996; Schmitz et al., 2018). Naturally, understanding the causes and consequences of animal movements is a central goal in ecological research.

An animal's movement path reflects how they respond to variation in their environment. In their seminal paper, Nathan et al. (2008) presented a unifying paradigm for contextualizing such responses in movement ecology through four mechanistic components (Figure 1.1): (1) internal state—why move?; (2) motion capacity—how to move?; (3) navigation capacity—where to move?; and (4) external factors in the surrounding environment (Nathan et al., 2008). The interactions among these components ultimately generate the movement paths that we observe and by empirically investigating interactions between different components (e.g., external environment and internal state), we can glean key processes that shape individual-level movements and population-level processes across scales. Importantly, this framework provides a foundation for quantifying movement-mediated responses to anthropogenic disturbance and environmental change, which is central to assessing adaptability and resilience in the Anthropocene (Gomez et al., 2025).

With improvements in tracking technology over recent decades, empirical studies centered in the movement ecology paradigm have revealed key causes and consequences of animal movement—such as the role of environmental variability (Riotte-Lambert and Matthiopoulos, 2020; Sequeira et al., 2018), cognition and memory (Fagan et al., 2013; Kashetsky et al., 2021), and other species traits (Beltran et al., 2025; Beumer et al., 2026)—among diverse taxa and ecological systems around the globe (Joo et al., 2022; Nathan et al., 2022). However, until recently, studies have predominantly contextualized the 'external factors' component of the movement ecology paradigm (Figure 1.1) through the physical environment, often overlooking important behavioral processes operating within animals' social environments.

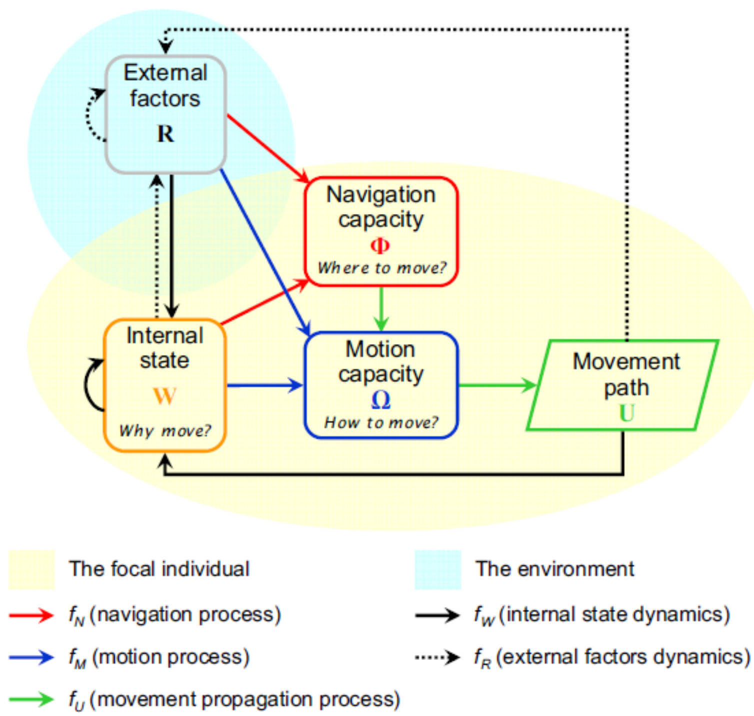

Figure 1.1. The general conceptual framework for movement ecology from Nathan et al. (2008). The framework is composed of three individual-level components (yellow background) and a fourth environmental-level component (blue background).

1.2 Spatial and social dimensions of movement

Animals navigate environments that span both spatial (e.g., habitat) and social (e.g., population density) domains. These are inextricably linked with spatial (e.g., home range) and social (e.g., preferred associations) behaviors (Webber et al., 2023). This intersection, termed the 'spatial-social interface', has only recently been formally recognized in ecological research as the fields of spatial ecology and behavioral ecology have largely evolved independent of one another despite shared theoretical and empirical foundations (Webber et al., 2023). For example, centered in optimality theory and the movement ecology paradigm, animals' movements should reflect behaviors to successfully acquire resources while minimizing energetic costs, thereby maximizing fitness (Charnov, 1976; MacArthur and Pianka, 1966). These spatially mediated mechanisms on individual movement can scale up to landscape-level species distributions and population ranges (Morales et al., 2010). Hence, a myriad of studies and methodologies have been developed for quantifying environmental drivers and consequences of movement (Hooten et al., 2017; Joo et al., 2022; Manly et al., 2002; Riotte-Lambert and Matthiopoulos, 2020). Advancements in the understanding of spatial drivers of animal movement have been integral in the management and conservation of wild populations (Matthiopoulos et al., 2023), but neglecting characteristics of the social environment results in partial depictions of the ecological processes sustaining populations (Webber et al., 2023; Webber and Vander Wal, 2018).

Social behaviors can evolve to optimize foraging strategies (e.g., cooperative foraging) and navigate risky environments (e.g., anti-predator behavior), thereby maximizing individual fitness (Krause and Ruxton, 2002a; Silk, 2007). These behaviors can scale up and generate diverse social structures—from solitary-living to dynamic fission-fusion systems to stable multi-level societies (Aureli et al., 2008; Grueter et al., 2020; Makuya and Schradin, 2024)—and their consequences on population persistence and community dynamics (e.g., spread of disease, information) are well-documented (Farine et al., 2015b; Gil et al., 2018; Sah et al., 2018; Weiss et al., 2023). Hence, there has been extensive research into describing and quantifying the mechanisms underlying social behaviors and the structures emerging from them in behavioral ecology (Croft et al., 2008; Farine and Whitehead, 2015; Kappeler, 2019). Movement is necessary for these social behaviors to occur: collective behaviors—such as group foraging—but also individual behaviors—such as eavesdropping on cues from conspecifics—directly reflect responses to animals' social environments (Kohles et al., 2022; Spiegel and Crofoot, 2016; Strandburg-Peshkin et al., 2015). Therefore, individuals both constitute and respond to their social environment, but how this feedback is also influenced by their spatial environment—which provides both resources and risks—is a central question in the spatial-social interface framework (Figure 1.2).

The intersection between spatial and social processes jointly affects all components of the movement ecology paradigm (Figure 1.1): animals move through space that includes both spatially (e.g., habitat, food, predators, interspecific competitors) and socially (e.g., associates, intraspecific competitors) mediated resources and risks (Gaynor et al., 2019; Webber et al., 2023). Because both spatial and social behaviors contribute to population structure, studying movements in spatial-social contexts can offer deeper insight into the mechanisms determining population persistence and resilience to environmental changes (Gaynor et al., 2024; Gomez et al., 2025; Webber et al., 2023; Webber and Vander Wal, 2018). Studying movements, therefore, requires tractable conceptual and analytical approaches to quantifying spatial and social processes in empirical systems, which independently vary across scales, and thus their coupled effects should also be scale dependent.

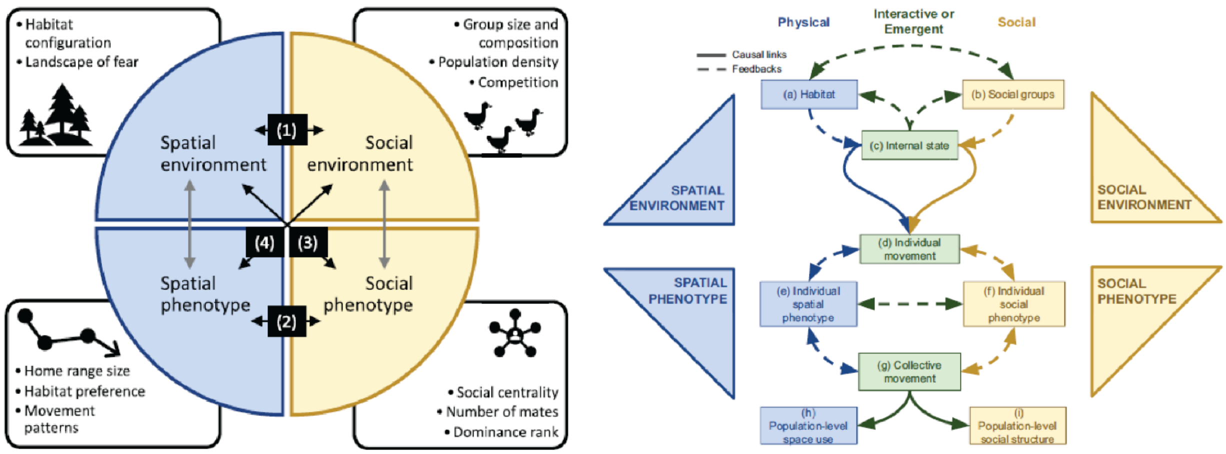

Figure 1.2. Conceptual figures from Webber et al. (2023) illustrating the links between the spatial and social dimensions of ecology. Left: conceptual symmetry of the spatial-social interface, with examples for both spatial and social environments and phenotypes. Right: framework linking movement ecology to the spatial-social interface, demonstrating how movement can both affect and be affected by spatial and social domains at individual- and population-levels.

Scale is fundamental in ecology. It serves as the lens through which ecological patterns and processes are observed and interpreted (Levin, 1992). Explicitly identifying scales of inquiry in the spatial-social interface is thus required. The recent call for consideration of ecological scales promises to generate more refined hypotheses to advance understanding of the roles of spatial and social behaviors—and their environments—on individual fitness and population dynamics (Picardi et al., 2024). Scale-dependence has been formalized in spatial ecology, whereby habitat selection (i.e., animals' disproportionate use of habitat or resource types relative to their availability) is depicted in a hierarchical framework of four "orders" (Johnson, 1980): (1) the geographic range selected by a species ("first order"); (2) the home range selected by an individual or population ("second order"); (3) the various habitat components selected by an individual within its home range ("third order"); and (4) the procurement of resources within habitat components of the home range ("fourth order"). These 'ecological scales' define the spatial and temporal scopes of inquiry (e.g., home range versus movement behavior within home ranges), yielding a direct analytical framework for testing hypotheses (Manly et al., 2002; McGarigal et al., 2016). Picardi et al. (2024) extended this hierarchy to couple spatial phenotypes (e.g., individual space use, movement patterns) and environments with social phenotypes (e.g., individual social position) and environments, where at the finest scales (fourth order) individuals select social preferences from their group environment/resource items from foraging sites, and at the coarsest scales (first order) individuals are affiliated with a specific population out of all conspecifics/population range within the species' range. This scale-explicit framework reveals avenues for quantifying the feedback between spatial and social processes, including the causal directionality—whether coarse-scale spatial/social behaviors emerge from or constrain fine-scale spatial/social behaviors (Picardi et al., 2024).

While the framework presented by Picardi et al. (2024) provides a foundation for investigating scale-dependent mechanisms linking animals' spatial and social behaviors, empirical demonstrations of these feedback links across scales remain in its infancy (although see Merkle et al., 2024). Critically, this framework has primarily focused on spatial and social scales, recognizing that temporal scales likely play an essential role in regulating spatial-social processes with cascading effects at other scales (e.g., individuals to population; Picardi et al., 2024). The extent to which temporal scales have an impact on inferences within the spatial-social interface framework is likely related to both ecosystem-level and species-level temporal variability (or predictability) in spatial and social environments. Together, scale-explicit empirical studies are needed across a variety of systems to unravel generalizable insights in the spatial-social interface, but particularly so for ecological systems where both resource dynamics and social behaviors can be extreme or complex across spatial, temporal, and social scales.

1.3 Oceans: home of spatial and social extremes

Oceans are characterized by comparatively low resource concentrations relative to terrestrial ecosystems, yet they clearly sustain a rich diversity of species, yielding ‘the paradox of the sea’ (Benoit-Bird, 2024; Steele, 1985). In addition to low resource concentrations overall, resources in marine environments are naturally and perpetually in flux: large scale water masses and atmospheric forces shape basin-wide patterns in productivity, and oceanographic processes at finer scales generate narrow hotspots of biological activity that other animals rely upon, particularly predators (Benoit-Bird, 2024; Boyd, 1996; Lalli and Parsons, 1997; Steele, 1978). Relating these dynamic environments with marine animal movements has generated key insights into the ways that animals navigate such unpredictable and ephemeral conditions (Block et al., 2011; Sequeira et al., 2018). However, understanding of the role of social environments in marine animal movements has comparatively lagged behind those in terrestrial environments, largely due to logistical challenges of observing social behaviors and tracking movements necessary for such inquiry (He et al., 2023) in marine systems.

Some of the most socially complex species occur in marine environments. Cetaceans are well-represented in this social complexity, ranging from mysticetes forming temporary groups (Tyack, 2022), to delphinids living under greater fission-fusion dynamics (Gowans, 2019), and long-lived odontocetes exhibiting stable, matrilineally structured societies (Rendell et al., 2019). Strong sociality in cetaceans likely evolved as a means to overcome the challenges of resource acquisition in marine environments, particularly in the face of predation; this is especially the case for large-bodied animals with increased energetic demands (Benoit-Bird, 2024; Whitehead, 2007). This evolutionary scale of social complexity, coupled with the extreme ephemerality in their environment, makes the spatial-social interface critically relevant to their ecology; simultaneously, theoretical and empirical understandings of spatial-social ecology are likely limited without explicitly considering these socially complex species living in spatially stochastic environments. Despite the logistical challenges of obtaining necessary data for spatial-social interface inquiries, longitudinal datasets on spatial and social behavior exist for some species and can be leveraged to address key knowledge gaps in the emerging field of spatial-social ecology.

1.4 Study system: false killer whales of the Hawaiian Archipelago

False killer whales (*Pseudorca crassidens)* represent a compelling case for investigating scale-dependent spatial-social feedback mechanisms in the oceanic environment. These highly intelligent and socially complex apex predators are distributed in sub-tropical and tropical pelagic waters worldwide with some records in temperate waters (Zaeschmar and Baird, 2025).

Much like other ‘blackfish’ (Meyer et al., 2026), false killer whales are long-lived (well into their 60s), slow to mature (10-15 years old at sexual maturity), and slow to reproduce (~6-8-year calving intervals; Ferreira et al., 2014; Photopoulou et al., 2017). They are strongly social, known to travel in large groups (20-100 individuals), and populations exhibit structure with long-term, stable groups of regular associates and kin (Baird et al., 2008a; Mahaffy et al., 2023; Zaeschmar, 2014; Zaeschmar and Baird, 2025). As a species, false killer whales are known to consume a wide variety of fishes and cephalopods (Zaeschmar and Baird, 2025). The most well-studied false killer whales occur around the Hawaiian Islands (Baird, 2016).

The Hawaiian Archipelago, spanning the main Hawaiian Islands (MHI)—from Hawai‘i Island to Kaua‘i and Ni‘ihau—to the shallow atolls of the Northwestern Hawaiian Islands (NWHI), is surrounded by an expansive area of deep, unproductive waters (Ziegler, 2002). The central North Pacific is often characterized as a biological desert as it lacks an abundance of phytoplankton and zooplankton that typically support productive ecological communities (Gove et al., 2016; Polovina et al., 2008b). Despite this, the Hawaiian Islands interrupt wind and ocean currents in a manner that produces biologically favorable conditions. This “island mass effect” (Figure 1.3) involves several localized causative mechanisms, such as upwelling, precipitation patterns, and island-associated inputs (e.g., groundwater discharge), that collectively enhance productivity in the marine environment immediately surrounding the islands (Doty and Oguri, 1956; Gilmartin and Revelante, 1974; Gove et al., 2016). As a result, the Hawaiian Islands have an ecologically diverse community of marine predators, including pelagic fishes, sharks, and marine mammals

(Baird, 2016; Meyer et al., 2018; Worm et al., 2003), and their distribution in accessible nearshore waters has enabled longitudinal multi-species studies (Baird et al., 2024). The cetacean community is particularly diverse, with island-associated populations of 11 different species—including several "blackfish" [e.g., false killer whales, short-finned pilot whales (*Globicephala macrorhynchus*), melon-headed whales (*Peponocephala electra*)], beaked whales [e.g., goose-beaked whale (*Ziphius cavirostrosis*), Blainville's beaked whales (*Mesoplodon densirostris*)], and delphinids [e.g., common bottlenose dolphins (*Tursiops truncatus*), pantropical spotted dolphins (*Stenella attenuata*), rough-toothed dolphins (*Steno bradanensis*)]—many of which exhibit different yet complex social structures (Baird, 2019, 2016; Corsi et al., 2026; Kratofil et al., 2023; Mahaffy et al., 2015). Together, the Hawaiian Archipelago is a uniquely rich case for examining the causes and consequences of spatial-social processes on false killer whale movement with context on the surrounding ecological community.

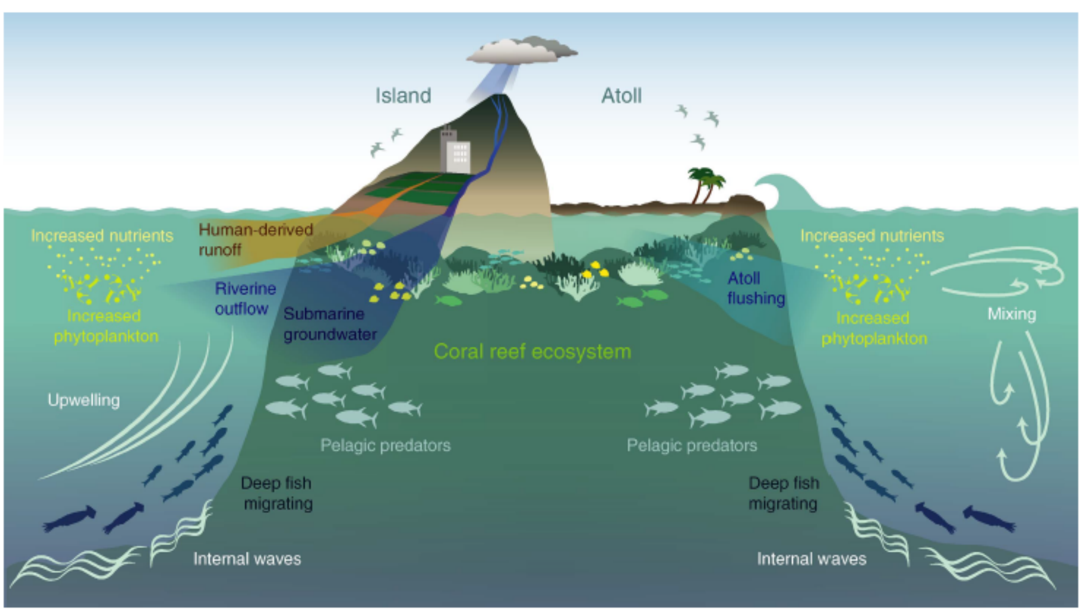

Figure 1.3. Schematic of the island mass effect (source: Gove et al., 2016).

The unique ecological contexts created by the archipelago and surrounding oceanographic conditions likely enable the coexistence of the three demographically independent, partially sympatric populations of false killer whales: the MHI insular, the NWHI insular, and the pelagic population (Bradford et al., 2015). The insular populations generally remain in the nearshore environments of their respective island chains, while pelagic false killer whales have a predominantly offshore distribution, often ranging widely in the central North Pacific (Anderson et al., 2020; Baird et al., 2013a, 2012, 2010; Fader et al., 2021; Kratofil et al., 2023). These differentiated movements and distribution, combined with evidence from genetics (Chivers et al., 2007; Martien et al., 2014) and social networks (Baird, 2016; Baird et al., 2008a; Mahaffy et al., 2026, 2023), collectively supported the designation of these three populations as separate stocks recognized by the U.S. National Marine Fisheries Service (NMFS; Bradford et al., 2015). False killer whales from all three populations have been observed feeding on pelagic game fishes (Baird et al., 2008a; Zaeschmar and Baird, 2025), including (but not limited to) yellowfin tuna (ʻahi, *Thunnus albacares*), bigeye tuna (ʻahi poʻonui, *Thunnus obesus*), albacore tuna (ʻahi palaha, *Thunnus alalunga*), skipjack tuna (aku, *Katsuwonus pelamis*), mahimahi (*Coryphaena hippurus*), wahoo (ono, *Acanthocybium solandri*), broadbill swordfish (aʻu ku, *Xiphias gladius*), and moonfish (opah, *Lampris guttatus*). The depth of information on movements, distribution, and social structure is variable among the three populations, largely due to the correspondingly variable accessibility of their ranges for small boat-based research.

The MHI false killer whale population is the most well-studied and is structured into four stable social groups (clusters, hereafter) consisting of kin and non-kin associates (Mahaffy et al., 2023; Martien et al., 2019). Previous studies have indicated that these social clusters exhibit different space use patterns (Baird et al., 2012; Mahaffy et al., 2023), very similar to what is known for pods of killer whales (*Orcinus orca ater*; e.g., Hauser et al., 2007) and clans of sperm whales (*Physeter macrocephalus*; e.g., Eguiguren et al., 2019). However, the spatial and social mechanisms underlying these coarse scale observations, and how they might vary across temporal scales and feed back on each other, remain unresolved. There is emerging evidence for similar social structure in the NWHI and pelagic populations (Mahaffy et al., 2026), although sample sizes of tag deployments are comparatively limited. The MHI population thus represents an ideal case study to test hypotheses in a scale-explicit spatial-social conceptual framework, and additional insights can be gained from available data on the other populations.

Addressing knowledge gaps on the movement ecology of Hawaiian false killer whales will also inform several ongoing conservation efforts. The MHI population was listed as "endangered" under the U.S. Endangered Species Act in 2012 (Oleson et al., 2010) and abundance has declined since the listing (Badger et al., 2025). Threats facing this population's viability include interactions with nearshore fisheries (Harnish et al., 2024), reduced genetic diversity (Chivers et al., 2007; Martien et al., 2014), health consequences associated with exposure to persistent organic pollutants (Kratofil et al., 2020; Ylitalo et al., 2009), entanglement in marine debris

(Douglas et al., 2026), and decreased prey biomass and size (Oleson et al., 2010). Pelagic false killer whale depredation of catch and bycatch in the Hawaiian deep-set longline fishery has been frequently documented and is an active area of conservation and economic concern for NMFS (Anderson et al., 2020; Fader et al., 2021; Forney et al., 2011). Therefore, a comprehensive assessment of the role of spatial-social processes on false killer whale movements—and their consequences on within-population connectedness—are needed to understand factors influencing survival, conflict risk, and persistence.

Collectively, the strong sociality, life history, and ranging behavior of false killer whales make them an ideal species to study the effect of spatial and social processes on movement patterns across scales. Hawaiian false killer whales are especially suitable models for such ecological research questions as they are the most well-studied false killer whales in the world and there exist long-term datasets on their movements, social structure, and demographics that can be used to fill such socioecological knowledge gaps. Moreover, there are clear conservation needs that can be readily informed by deeper empirical understanding of factors shaping their movement patterns.

1.6 Aims of this dissertation

This dissertation characterizes scale-dependent spatial-social processes in Hawai‘i’s false killer whales with the goal of elucidating the drivers and consequences of their movement and distribution. By analyzing these dynamics, this dissertation also evaluates adaptability to changes in the physical and social environments, and ultimately population persistence, with the applied goal of informing data-driven conservation strategies for the species. The next chapters draw upon long-term (1999-2025) datasets on false killer whale movements (satellite tracking), social associations (social networks), demographic information (photo-identification catalog, genetics), and biomarkers (stable isotopes) to achieve this objective. Chapter 2 examines diving behavior at both fine and coarse scales and in demographic and ecological contexts to elucidate the factors shaping vertical movements and foraging strategies employed by false killer whales. Building off fundamental information on foraging ecology gained from Chapter 2, Chapter 3 develops and applies a scale-explicit conceptual framework that tests how resource ephemerality and social reliance govern top-down and bottom-up processes between movement and sociality in the MHI population, from short-term individual-level movements to long-term population distribution. Chapter 4 applies this framework to the co-occurrence and conflict risk between pelagic false killer whales and commercial longline fisheries, identifying scale-dependent oceanographic contexts that drive whale movement patterns as they relate to fisheries depredation behavior.

These chapters step through scales and scopes of ecological inquiry, demonstrating an effective framework for integrating disparate, albeit complementary, data streams to better understand the movement ecology of social marine predators. Findings from these chapters also provide critical context for developing effective recovery plans and mitigation measures for false killer whale management in Hawaiʻi and inform topics for future research. Together, this body of work provides a novel contribution to the emergent field of spatial-social ecology while also supporting conservation initiatives for Hawai‘i’s false killer whales.

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2. ECOLOGICAL CONTEXTS OF DIVING BEHAVIOR IN HAWAIIAN FALSE KILLER WHALES

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2.1 Abstract

Background

Predator movements vary across different ecological contexts, offering valuable insights into their foraging strategies. However, studying these contexts in marine predators is challenging due to the difficulty of observing them and their prey over sufficient spatiotemporal scales. Using bio-loggers and detailed life history information, we investigated abiotic and biotic factors shaping the diving behavior of a highly social apex predator—the false killer whale (*Pseudorca crassidens*)—around the Hawaiian Archipelago where three partially sympatric, genetically differentiated populations coexist.

Methods

We deployed time-depth recorders (n=5) and depth-transmitting satellite tags (n=16) on false killer whales between 1999–2025 to describe diving at multiple spatiotemporal scales and ecological contexts. We fit generalized additive mixed-effects models to examine relationships between dive metrics and temporal and spatial proxies of prey distribution. Dive metrics were compared across demographic traits (sex, population, relative size) to assess potential drivers of behavioral variability.

Results

False killer whales spent most of their time in near-surface waters and frequently dove within the epipelagic zone. Individuals exhibited various dive types within and among different habitats, including near-seafloor and deep (> 1,000 m; record maximum of 1,424 m) diving behavior. Dive rates and depths were highest during daylight hours and full moons, although with significant inter-individual variation. Dive depth increased with current magnitude and mixed layer depth and decreased with lagged surface chlorophyll-a concentration. Larger individuals tended to dive deeper, although with high variation across demographic groups. These findings offer key insights into potential drivers of diving behavior, albeit with small effect sizes.

Conclusions

We present the first comprehensive description of diving behavior for this species, which was characterized by variable temporal patterns, in contrast to sympatric species that are known to exploit diel vertically migrating prey. The diversity of dive types across habitats, along with trends between dive metrics and oceanographic variables, suggests that false killer whales may adjust their vertical movements to target different prey and environmental conditions.

Hōʻuluʻulu Manaʻo (Hawaiian language abstract)

Ke Kahua

ʻOkoʻa ka holo ʻana o ke poʻiiʻa ma nā ʻano honua kaiaola like ʻole, a hiki nō ke ʻike ʻia kā lākou kaʻakālai ʻai. Paʻakikī naʻe ke kilo ʻana i kēia mau honua o nā poʻiiʻa kai ʻoiai, paʻakikī ka nānā ʻana iā lākou me kā lākou ʻai ma nā pālākiō henua kaime. Ma o ka hoʻohana ʻana aku i nā lēpili ola a me nā ʻikepili ola kikoʻī, noiʻi mākou i hiki i nā mea ʻōnaeao a me nā mea ola kino ke pā i ke ʻano o ka luʻu ʻana o ke poʻiiʻa keu ma ka lauana ʻana - ke koholā ʻāhuka iwi poʻo like

(*Pseudorca crassidens*) - a puni ka pae‘āina Hawai‘i i noho pū ‘ekolu pū‘uo ‘ano pili a ‘oko‘a ma ke ōewe ho‘i.

Ki‘ina Hana

Ua ho‘opa‘a mākou i nā mīkini ana kaime a hohonu (n=5) a me nā pepili ho‘oili ukali hohonu (n-16) ma nā koholā ‘āhuka iwi po‘o like mai nā makahiki 1999–2025 i mea e wehewehe aku ai i kalu‘u ‘ana ma nā pālākiō henua kaime a me nā pō‘aiapii kaiaola. Ua ho‘ohana mākou i nā ana pilina kaulike a me nā ana kaulele no ke kālailai ‘ana aku i ka pilina wa ma waena o nā ‘ikepili lu‘u a me nā mea kaime a henua ho‘i o ka ho‘omalele ‘ana o ka ‘ai. Ho‘ohālikelike ‘ia nā ‘ikepili lu‘u ma nā wae‘anona ‘ano (ke keka, ka pū‘uo, ka nui) i mea e kālailai ai i nā mea e hiki ke pā aku i nā ‘oko‘a o ka lawena.

Nā Hua

I ka hapanui o ko lākou ola, noho pinepine nā koholā ‘āhuka iwi po‘o like i ka ‘ili kai a lu‘u lākou i loko o ka wao mālamalama. Ma ka ho‘okahi, hō‘ike ‘ia nā ‘ano lu‘u like ‘ole i loko o nā kaianoho ‘oko‘a, e like ho‘i me ka pili papakū a hohonu (>1,000m; ma ka hohonu loa 1,424m) lawena lu‘u. ‘O ka pinepine a me ka hohonu o ka lu‘u ‘ana, ua ki‘eki‘e loa ma nā hola ao a me nā wā mahina poepoe, me ka loa‘a pū na‘e o ka ‘oko‘a o kēlā me kēia. Ua pi‘i ka hohonu o ka lu‘u ‘ana i ka nui o ke au a me ka hohonu o ka wao pā lewa a ua iho i ka lohi o ka aea ‘ana o ke kolopila-‘ā. ‘Oi a‘e ka hohonu o ka pi‘i ‘ana o nā mea ‘oi aku o kona nui, eia na‘e, me ka nui o ka loli ʻana ma nā pūʻuo ʻano. Ma o kēia mau hua, loaʻa nō nā ʻike koʻikoʻi no nā e pā ana i ke ʻano o ka luʻu, i loko nō naʻe o ka liʻiliʻi o ka hopena.

Nā Manaʻo Hope

Hōʻike aku mākou ka wehewehena piha mua o ka hana luʻu o kēia ʻano lāhui, i kuhikuhi ʻia ma nā lauana kaime ʻokoʻa, i hoʻohālikelike ʻia me ka lāhui ʻano pili a ʻokoʻa ma ke ōewe hoʻi, kekahi lāhui i ʻike ʻia e luʻu a piʻi e ʻai i ka ʻai neʻena. Ma o ka ʻokoʻa o nā ʻano luʻu ma nā kaiaola, a me ke ʻano o nā ʻikepili luʻu a me nā ʻano mea kai, hoʻololi paha nā koholā ʻāhuka iwi poʻo like i ko lākou neʻena kū i mea e loaʻa ʻai kekahi ʻano ʻai ma nā ʻano pōʻaiapili kaiapuni like ʻole.

2.2 Introduction

Foraging decisions are informed by predator (e.g., morphology; (Schoener, 1971)) and prey traits—type and size (Werner and Hall, 1974), mobility (Sih and Christensen, 2001), and behavior (Brown et al., 1999; Lima and Dill, 1990). The physical environment interacts with these factors and shapes the availability, abundance, and patchiness of prey and competitors across different scales, thereby mediating the predator foraging strategy (Charnov, 1976; Iwasa et al., 1981) and movement decisions (Benoit-Bird et al., 2013; Schwarz et al., 2021). For example, in resource-sparse or unpredictable environments, predators adopt flexible strategies such as covering large distances to locate dispersed prey patches (e.g., (Weimerskirch et al., 2005)) or adjusting movements to target diverse prey types (e.g., (Courbin et al., 2018; Kuhn et al., 2010)). Competition between species can also modulate foraging flexibility, with predators switching prey or habitat types to maintain success in the presence of competing specialists (e.g., (Fossette et al., 2017)). The interplay between physical and ecological contexts therefore shapes individual predator decisions, which can scale up to population diversity and persistence, community dynamics, and ecosystem function (Fryxell and Lundberg, 1993; Schmitz et al., 2008; Spiegel et al., 2017). However, understanding how these contexts modulate marine predator movements remains challenging due to the logistical difficulty of observing predators and prey over sufficient time and spatial scales (Block et al., 2011).

In the marine environment, foraging occurs in three dimensions and thus predators must track the structuring of their prey through both horizontal and vertical movements (i.e., diving). Ocean physical properties are constantly in flux, forcing predators to effectively navigate the interactions between oceanographic and atmospheric conditions that shape biological productivity and patchiness across spatiotemporal scales (Benoit-Bird, 2024; Boyd, 1996; Steele, 1978). Foraging in such environments is also limited by predator-specific physiological constraints (e.g., respiration in mammals and birds, (Kooyman and Ponganis, 1998); thermoregulation in fish, e.g., (Holland et al., 1992)). These challenges result in diverse foraging strategies across marine taxa (Benoit-Bird, 2024; Sequeira et al., 2018). For example, many marine predators closely track vertical migrations of prey that are known to vary over diel and lunar cycles (e.g., the deep scattering layer (DSL); e.g., rough-toothed dolphins, *Steno bredanensis,* (Shaff and Baird, 2021)*,* broadbill swordfish or aʻu ku, *Xiphias gladius,* (Dewar et al., 2011)). Both static (e.g., seafloor topography, reefs) and dynamic habitat features (e.g., mesoscale eddies) can also promote variable foraging tactics among marine predators, and such tactics can be reflected in vertical movement patterns (e.g., (Cox et al., 2018; Hays et al., 2006; Wyles et al., 2022)). Unraveling marine predator foraging strategies fills key behavioral and life history knowledge gaps in species that are hard to study—which is essential for interpreting their resilience to environmental fluctuations (e.g., (Ford et al., 2009))—and sheds light into the dynamics of ecologically and economically (i.e., for fisheries) important biomes (Braun et al., 2022; Kiszka et al., 2015).

The false killer whale (*Pseudorca crassidens*) is a long-lived, highly social apex predator found in sub-tropical and tropical oceans worldwide (Baird, 2018; Zaeschmar and Baird, 2025). Most information on their ecology and behavior comes from long-term studies in the Hawaiian Islands where three genetically differentiated but partially sympatric populations are recognized: two resident to insular waters—Main Hawaiian Islands (MHI) and Northwestern Hawaiian Islands (NWHI) populations—and one open-ocean population ranging broadly offshore (Anderson et al., 2020; Baird et al., 2013a, 2008a; Bradford et al., 2015; Martien et al., 2014). The MHI population is the most well-studied, within which four stable social clusters composed of relatives and regular associates have been identified (Baird et al., 2012; Mahaffy et al., 2023; Martien et al., 2019). Understanding false killer whale foraging strategies is crucial for conserving these populations, which face negative health effects from pollutant exposure (Kratofil et al., 2020; Ylitalo et al., 2009), harmful fisheries interactions (particularly for the MHI and open-ocean populations; (Baird et al., 2015; Harnish et al., 2024)), and reductions in prey size and quality (Oleson et al., 2010; Polovina et al., 2009). This is especially the case for the endangered MHI population (estimated at 139 individuals (95% credible interval: 114–162) in 2022), which has continued to decline at an annual rate of 3.51% since 2013 (Badger et al., 2025). Identifying key foraging drivers can inform conservation strategies and mitigate cumulative threats to their survival. Based on visual observations and limited stomach content samples, false killer whales in Hawaiʻi appear to have a generalist diet, primarily feeding on large epipelagic game fish (e.g., tunas, dolphinfish or mahimahi, *Coryphaena hippurus*, wahoo or ono, *Acanthocybium solandri*) and some squid (Baird et al., 2021; Zaeschmar and Baird, 2025). Outside of these observations, the vertical movement behavior and foraging strategies employed by false killer whales in Hawai‘i or anywhere are poorly understood (although see Minamikawa et al. (Minamikawa et al., 2013) for 3-d of dive data).

Here, we advance the understanding of the vertical movement ecology of false killer whales around the Hawaiian Islands by assessing diving behavior collected with two different types of tags at different scales and across ecological contexts. Short-term Time-Depth-Recorders (TDRs) collect fine scale dive information at the expense of geolocation data and deployment longevity, while long-term satellite-linked depth-transmitting tags remain attached for longer durations, collect geolocation and summarized dive data, but at the expense of fine scale depth information. Together, data from these tags allowed us to address three objectives: (1) describe dive behavior to advance species-specific knowledge; (2) compare dive behavior across demographic groups and individual traits (e.g., population, sex, relative body size) to understand potential drivers of inter-individual variation; and (3) assess dive metrics in relation to temporal and environmental variables to generate hypotheses on strategies as they relate to potential prey behavior and distribution.

2.3 Methods

All data processing and analysis detailed throughout were completed using the program R (R Core Team, 2025) unless noted otherwise. The ocean basemap image used in map figures is the intellectual property of Esri and is used throughout with permission (Copyright © 2025 Esri and its licensors, all rights reserved).

2.3.1 Tagging procedures and programming

Tagging and small boat-based surveys throughout the main Hawaiian Islands took place from 1999 through 2025 as a part of a long-term study of odontocetes undertaken by Cascadia Research Collective (CRC; (Baird et al., 2024, 2013b)). When false killer whales were encountered, photographs were taken of all individuals present, and information on group size, behavior, and any foraging events were recorded. Tag deployments from NOAA Pacific Islands Fisheries Science Center (PIFSC) used the same methods, albeit tagging occurred during a large-scale ship-based false killer whale survey in 2024 (Bradford, 2024a).

Tags used to record diving behavior were attached in one of two ways. In the first part of the study (1999–2008), suction-cup attached time-depth recorder (TDR)/VHF radio tags (Mk6, Mk9, Wildlife Computers, Redmond, WA) were deployed on five individuals following methodology described in Baird et al. (Baird et al., 2001). These tags sampled depth once per second at 1 m (Mk6) or 2 m (Mk9) increments (+/- 1–2 m accuracy, respectively). We defined dives from the TDRs as periods when the individual went beyond two body lengths in depth (≥ 10 m). Maximum depth ranges of the tags were 250 m or 500 m, respectively, although due to temperature-related drift in the sensor this value is empirically shallower. Swim speed was also recorded by Mk6 tags (with a paddle wheel) and are presented as relative velocity (uncalibrated units) because readings vary with the position of the tag on the body (Baird, 1998) and likely with body size (Baird et al., 2001). The TDRs used in this study do not record information on the geographic position of the animal, only dive depth (and relative velocity for Mk6 tags), although TDR-tagged individuals were tracked over some or all of the duration of tag attachments.

For the second part of the study (2010–2025), sixteen depth-transmitting satellite tags were deployed in the Low-Impact Minimally-Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al., 2008) on or near the dorsal fin with two gas sterilized 6.7-cm surgical grade titanium darts, using a pneumatic projector. Tags were either SPLASH10 tags that transmitted dive behavior data and location data from Argos satellites or SPLASH10-F tags that transmitted the same data streams in addition to Fastloc®-GPS location data (hereafter, both referred to as "SPLASH" tags; Wildlife Computers, Redmond, WA). Programming regimes varied throughout the study period, but tags were generally programmed to optimize data transmission (e.g., based on satellite coverage). Post-2013 deployments benefitted from one or more land-based Argos receivers (MOTEs; (Jeanniard-du-Dot et al., 2017)) that enhance reception of behavior data.

Transmitted dive behavior from SPLASH tags was in the form of behavior logs, consisting of "dive" and "surface" periods summarized by the start and end times of each period, the duration of each period, the maximum depth reached during each dive, and the shape of the dive. Dive shape was categorized onboard the tags, defined by the total duration of the dive relative to the "bottom time" of the dive (i.e., any depth greater than or equal to 80% of the maximum dive depth; square = bottom time duration > 50%; u = bottom time duration > 20% but ≤ 50%; v =

bottom time duration ≤ 20%). Dives were defined as any submergence greater than the user-programmed depth threshold (0–5 m), but the tags were programmed to ignore dives shallower than an additional depth and duration threshold to characterize deep dive behavior while optimizing battery life and minimizing gaps in the behavior data (i.e., increasing likelihood of reception of archived data by satellites). These latter two thresholds varied throughout the study period as lessons were learned from different programming regimes. Any submergence shallower and shorter than these pre-defined depth and duration thresholds were considered "surface" periods. To maintain consistency in our analyses given the variable dive settings across tags, we considered dive records shallower than 50 meters and shorter than two minutes in duration as surface periods. Surface periods thus include shorter and shallower dives (e.g., inter-ventilation dives, foraging on surface-oriented prey). Dive durations and depths were reported in the behavior log with minimum and maximum estimates for each dive and surface record (depth sensor accuracy is +/- 1%) and we used the means of each parameter for analyses.

2.3.2 Data processing

Tagged individuals were photo-identified following Baird et al. (Baird et al., 2008a), assigning them to recognized populations (MHI, NWHI, or open-ocean) and to social groups derived from social network analyses (social clusters for MHI and NWHI individuals, and social components for open-ocean individuals; (Mahaffy et al., 2023), CRC unpublished). Sex was determined genetically (if biopsy sampled; (Martien et al., 2014)), by morphological characteristics (e.g., head shape) if adequate photographs were available, or by the calf associations. If neither type of information were available, sex was assigned as "unknown". Age class (calf, juvenile, sub-adult, adult) was determined based on field and photographic assessments and photo-identification catalog information (Kratofil et al., 2026b). For SPLASH deployments, fin base length was measured from photographs (using known tag dimensions, following (Yahn et al., 2019)) and in some cases camera-based laser photogrammetry (Durban and Parsons, 2006) to assess relative body size effects on dive behavior, as body size can vary substantially even within adults (Ferreira et al., 2014) and fin base length should be generally correlated with body length (Sergeant, 1962; Yahn et al., 2019). Fin base length was presented as the mean of the measurements from all photographs of adequate quality.

After tag recovery, TDR data were processed using the manufacturer (Wildlife Computers) provided software *Minimum-Maximum-Mean* (Version 1.22) and *Zero-Offset-Correction* (Version 1.30) to correct for temperature-related drift in surface values. Those files were then processed with *Dive Analysis* (Version 4.08) to define and summarize statistics (maximum depth, duration, bottom time, ascent rate, descent rate) for each dive.

Behavior log data from the SPLASH satellite tags were examined for any indication of tag pressure transducer failures, drift (e.g., see (Baird et al., 2019; Cioffi et al., 2023)), or other indicators of tag malfunctioning that could invalidate dive behavior data (e.g., see (Shearer et al., 2019)). Our protocol and associated code are provided in a public repository (Kratofil et al., 2025).

Argos and Fastloc®-GPS location data from SPLASH tags were filtered in Movebank (Argos and GPS; (Kranstauber et al., 2011)) and R (GPS only; (Dujon et al., 2014)) to remove unrealistic locations based on speed and turn angles using species-specific settings specified in Kratofil et al. (Kratofil et al., 2023). Filtered locations were subsequently fit to a continuous-time correlated random walk (CTCRW) model using the package *crawl* (Johnson et al., 2008; Johnson and London, 2018) and used to estimate locations at behavior log event times. Any locations on land were rerouted around the 20-meter isobath with the *pathroutr* package (London, 2020).

2.3.3 Data analysis

We used both TDR and SPLASH datasets to describe and visualize dive behavior at their respective scales and in relation to variables of interest. Formal statistical analysis was limited to the SPLASH behavior logs as this dataset includes more individuals and longer-duration deployments. Additionally, the TDR tags do not provide location data, and thus no assessment of spatial variables in relation to these data could be undertaken. A summary of datasets used for each broad analytical objective is provided in Table 2.4 (Supplementary Materials).

2.3.3.1 Dive metrics

Focal behavior metrics from the SPLASH tags included dive depth, dive duration, and dive rate, and these were each assessed in relation to spatial, temporal, and demographic variables. Dive depth can provide insight into different prey types that false killer whales may target, while dive duration may reflect foraging effort, such as the time spent searching for and pursuing prey during a given dive. Dive rate (i.e., the frequency of dives) may also be a measure of foraging effort. Dive rate was calculated as the total number of dives divided by the total duration of dive and surface periods. While we cannot explicitly infer foraging behavior from these dive metrics, we examine them in the context of foraging given that they are defined by dives 50+ m and 2+ min—extending to depth distributions of several known prey species (e.g., (Lam et al., 2020; Musyl et al., 2003; Polovina et al., 2008a))—and thus are unlikely to reflect other behaviors (e.g., travelling, socializing). However, we acknowledge the possibility that shallower dives (e.g., ~ 50 m) could include other behaviors such as prey sharing. Median values of dive depth and duration were calculated for each individual, and individual medians were averaged for overall and group-level (e.g., demographic, temporal categories) means (following (Barlow et al., 2020; Schorr et al., 2014)). We also provided the standard deviation (SD) and coefficient of variation (CV, expressed as percent) for group-level summaries. In addition to these descriptive summaries, statistical models were used to quantify relationships between dive metrics and spatial and temporal variables for SPLASH tag data (detailed in subsequent sections). Formal statistical analyses were not undertaken to examine dive behavior across demographic groups due to limited sample size.

2.3.3.2 Temporal and spatial variables

We assessed dive metrics by civil diel categories (i.e., dawn/dusk defined by -6/6 degrees above/below the horizon, day/night in between) to account for seasonal and geographic shifts in the timing of diel periods and allow comparisons with other studies. Sun angles were calculated using the *suntools* package (Bivand and Luque, 2023). Dive rate by diel category was calculated using the method described above, and extended surface periods spanning multiple diel categories were split by category using a custom R script to correctly calculate dive rate per category. Dive rates were also visualized across hours of the day (i.e., clock hour), and thus this same process was applied to split surface periods by clock hour when necessary. This approach ensures that dive rates are calculated without including any data gaps

While the abiotic and biotic characteristics vary across the ranges of the three populations, there are some spatial features common to all populations' ranges (e.g., seafloor slope, chlorophyll-a levels, ocean current dynamics) and thus generalizable patterns could be inferred. Therefore, we constructed multivariate models relating dive metrics (i.e., dive depth, duration, hourly rate) to spatial and temporal predictors relevant to all populations and conducted separate univariate sub-analyses on additional spatial predictors relevant to each range-type (i.e., insular or open-ocean). For modeling hourly dive rate, the unit of observation was the number of dives per hour within each day of each tag deployment (e.g., 2010-10-28 01:00:00 – 01:59:59, 2010-10-28 02:00:00-02:59:59, etc.). For each individual tag deployment, hour-day units with less than 75% data coverage (i.e., summed duration of dives and surface periods in that hour < 0.75) were removed prior to modeling. Spatial predictors were not included in the hourly dive rate model as this would require fine-scale information on space use within each hour per day that is not typically available from satellite tags.

Candidate predictors included time-of-day, moon phase (in radians), day of the year, contemporaneous and 30-day lagged daily surface chlorophyll-a concentration (both log-10 transformed following (Glover et al., 2018)), daily mixed layer depth, daily sea surface temperature (SST), daily horizontal surface current magnitude, and seafloor slope. These dynamic oceanographic variables were selected because of their correlation with biological productivity and distribution of known false killer whale prey fish (e.g., yellowfin tuna or ‘ahi, *Thunnus albacares*, (Brill et al., 1999; Lam et al., 2020)). Time-of-day was modeled as a continuous variable as opposed to the categorical diel period to better assess non-linear relationships. Day of the year is confounded by individual variability as tags were deployed during different times of the year and durations were relatively short, and thus was not considered further. Moon phase was extracted using the *lunar* package (Lazaridis, 2022). Seafloor depth and slope were extracted from the 30 arc-second (~1 km resolution) GEBCO Grid[1], and daily chlorophyll-a concentration (4 km horizontal resolution) and all other dynamic oceanographic variables (i.e., mixed layer thickness (hereafter mixed layer depth), SST, current magnitude; 8 km horizontal resolution) were obtained from the Copernicus Marine Data Store[2,3]. The chlorophyll-a product includes a “flag” variable to identify grid cells that overlap or partially

[1] https://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_30_second_grid/

[2] https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_104/description

[3] https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/description

overlap with land; dives within these cells were removed prior to modeling. Surface current magnitude was derived from zonal and meridional current velocity components following Woodworth et al. (Woodworth et al., 2012). The 30-day lagged version of chlorophyll-a was derived using the value 30 days prior to that of the dive record. Seafloor depth was not included in multivariate models as this variable was not similarly relevant among the three populations (e.g., seafloor depth is not limiting to dive depth and is less variable for open-ocean false killer whales), but was explored for insular populations in a sub-analysis (details in the subsequent section). Spatial variables were extracted using the *stars* package (Pebesma and Bivand, 2023).

Prior to analyses of dive behavior in relation to spatial features, we excluded dive records with positional error ellipse estimates greater than 4 km so that retained dives would not exceed the spatial resolution of the dynamic oceanographic variables of interest, or drastically influence inference on static variables (e.g., slope). To assess whether this data restriction obscured any temporal patterns in dive behavior, we also fit all models with temporal predictors only, using the full dive records.

2.3.3.3 Generalized additive mixed effects models

Dive metrics were modeled in relation to several temporal and spatial variables using generalized additive mixed effects models (GAMMs) to allow for non-linear trends. GAMMs were fitted using the *mgcv* R package (Wood, 2017) with the restricted maximum likelihood method. Response variables dive depth and dive duration were each modeled with a Gamma distribution and log link function. Hourly dive rate was modeled as dive count per hour with a negative binomial distribution and log link function, and an offset for log hours of behavior data per hour to effectively model dive rate. Correlation among predictor variables was assessed prior to modeling; if predictors were highly correlated (Pearson's correlation > 0.5), only one of the predictors was retained in the model. Time-of-day and moon phase were modeled with smooth cyclic cubic regression splines (bs = "cc"), while all spatial predictors were modeled with thin plate regression splines (bs = "tp"). For each smooth term, we examined the model outcomes across different basis dimension sizes (k = 5… 20) and ultimately constrained this value to five (k = 5) to balance model fit and interpretability (Wood, 2017). Variable selection was conducted with a shrinkage approach that penalizes non-significant variables to zero (Marra and Wood, 2011). We evaluated the importance of individual-level variation by fitting two models with different random effects structures: (1) a model with random intercepts for tag ID (i.e., PcTag + tag deployment number; bs = "re"); and (2) a model with random factor smooths for tag ID (bs = "fs") on time-of-day to allow for individual-level variation in diel trends (Pedersen et al., 2019); the same shrinkage approach described above was applied to both models. An individual-level factor smooth term of tag ID with other predictors was not evaluated as not all tagged whales experienced the same range of predictor values (in contrast to time-of-day). We used conditional Akaike's Information Criterion (AIC) (Wood et al., 2016) and percent deviance explained to determine the best fit between these two random effects structures. Models were validated by visually inspecting residuals and through the gam.check() function (i.e., to assess adequacy of basis dimension size), and model performance was assessed through the percentage of the deviance explained. Following recent statistical recommendations (Wasserstein and and Lazar, 2016), we report covariate-specific p-values quantified in the GAMMs to aid interpretation, but these were not used as the sole basis of covariate significance. We additionally calculated covariate-specific contributions to the total percent deviance explained using the *gam.hp* package (Lai et al., 2024); currently, there is no functionality to obtain these values from models with offsets, so these were not determined for the hourly dive rate model. Model prediction plots were created using the *marginaleffects* R package (Arel-Bundock et al., 2024). For these prediction plots, covariate-specific relationships were conditioned upon the mean value of all other covariates in the model, and thus represent the functional relationship for a "typical" individual (Arel-Bundock et al., 2024).

2.3.3.4 Near-seafloor diving behavior

Insular false killer whales often use shallow, nearshore waters where the seafloor is accessible, and thus they have the potential to target prey near the seafloor. To explore this further, we needed to discern whether dives near the seafloor were an artifact of tag positional uncertainty or if the animals were truly diving near the seafloor. We first generated 20 imputations from the fitted CTCRW models for each individual, such that we obtained 20 possible routes that each individual could have taken given the parameterized movement model (e.g., CTCRW process, location error, time between locations, etc.; see (Scharf et al., 2017)). Positions were then estimated for each dive record from each of the 20 imputations using the method described previously, such that each dive record had 20 plausible geographic locations. Seafloor depths were extracted for each of the 20 dive locations using higher resolution bathymetry grids available for the ranges of insular false killer whales (MHI: 50-meter MHI Multibeam Bathymetry Grid[4]; NWHI: 60-meter NWHI Falkor Bathymetry grid[5]). We narrowed the subset to dives within the spatial uncertainty restriction criteria applied for the modeling (described above), then calculated the standard deviation and maximum seafloor depth values across the 20 imputations for each dive record. To focus on dives with reasonable spatial precision, probable seafloor dives were isolated by removing dives that had a standard deviation of seafloor depth values greater than 100 m. We then subset dives with a maximum depth difference (i.e., maximum seafloor depth minus dive depth) of +/-100 m or less to narrow down a window of the water column where dives could be close to the seafloor while accounting for the fact that seafloor depth can vary substantially around some habitat features. These were further examined visually and quantitatively (e.g., through assessing distributions of seafloor depth between imputed dives and estimated dive locations, the ratio of dive depth to seafloor depth) to assess the likelihood of dives occurring to or close to the seafloor.

2.4 Results

2.4.1 Tag deployment summary

Five individuals were tagged with TDR tags between 1999 and 2008, and sixteen individuals were tagged with SPLASH satellite tags between 2010 and 2025 (Table 2.1). Based on photo-

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[4] https://www.soest.hawaii.edu/hmrg/multibeam/bathymetry.php
[5] https://www.soest.hawaii.edu/hmrg/multibeam/grids.php

identification, all tags were deployed on different individuals. All TDR deployments and eight SPLASH satellite tag deployments were on individuals from the MHI population, five SPLASH tags were on individuals from the NWHI population, and the remaining three SPLASH tags were on open-ocean false killer whales. Within the MHI population, tagged individuals represented three of the four recognized social clusters (Table 2.1; (Mahaffy et al., 2023)). For the NWHI population, tagged individuals represented three of seven identified clusters (CRC unpublished). For the open-ocean population, there was one pair of tagged individuals that belong to the same component in the social network, and one individual from a separate component (Table 2.1). Sex was known for 14 individuals (TDR: three males, one female; SPLASH: seven males, three females, Table 2.1). All but two of the SPLASH tag deployments were on adults (the remaining deployments were on a sub-adult and juvenile), while only two of the five TDR deployments were on adults (Table 2.1).

2.4.2 Short-term, fine-scale dive behavior

TDR attachment duration ranged from 1.1 to 28.9 h for a combined 54.3 h across all deployments (Table 2.1). Of the 54.3 h of data, there were 1.0 h during dawn, 32.2 h during the day, 2.9 h during dusk, and 18.2 h during night. TDR-tagged whales spent an overall mean of 70.5% of their time in the top 10 m of the water column (range = 49.5–90.5%), with almost all their time spent in the top 50 m of the water column (Table 2.5, Figure 2.7, Supplementary Material). Out of all 716 dives to 10 m or deeper, dives were relatively shallow with an overall mean dive depth of 15 m (range of individual median depths = 11–19 m; SD = 3 m; CV = 21.8) and duration of 1.5 min (range of individual median durations = 0.9–1.9 min; SD = 0.4 min; CV = 26.7). The longest and deepest dive was 234 m deep and 12.0 min long; however, based on the dive profile at this time and the depth range of the tag sensor, this individual (PcTDR04) had maxed out the depth sensor for this tag. Thus, while the duration of this dive is accurate, the true dive depth was deeper than 234 m. Dives exceeding 230 m depth from this individual were thus excluded from further analyses. The deepest dive after this exclusion was 210 m (5.4 min long). No comparisons were made across demographic groups (i.e., social cluster, age, sex) due to limited tag deployments by groups and highly variable amounts of behavior data among individuals (Table 2.1).

For the three tags (PcTDR02, PcTDR04, and PcTDR05) that had data available across different times of day, mean time spent in water depths greater than 50 m was low during the day (1.0%; SD = 0.4%; CV = 40.1) and night (4.0%; SD = 4.9%; CV = 121.1). Overall mean dive depths during the day (17.7 m; SD = 1.5 m; CV = 8.6) and night (17.7 m; SD = 4.9 m; CV = 27.9) were similar and both deeper than those during dusk (13.3 m; SD = 2.5 m; CV = 18.9; Figure 2.8, Supplementary Material). Trends in dive durations followed a similar pattern, with overall mean durations during the day (1.6 min; SD = 0.3 min; CV = 17.0) and night (1.9 min; SD = 1.1 min; CV = 55.2) being longer than at dusk (1.2 min; SD = 0.1 min; CV = 10.0; Figure 2.8). Descent rates were higher than ascent rates, and this trend was consistent across diel periods (Figure 2.8). There were 37 dives with greater than 2 m/s descent rates. The maximum descent rate recorded was 5.8 m/s and associated with a daytime dive to 30 m. Mean relative velocity readings for

PcTDR02 were highest at night (0.61), followed by day (0.47) and dusk (0.31), but the maximum was recorded during the day (6.8). Mean relative velocity readings were higher overall for PcTDR04, and throughout the diel period, were highest during dawn and day (1.3, 1.3, respectively) compared to dusk (0.84) and night (0.40); the maximum relative velocity for this individual (6.6) was also recorded during the day.

One tagged individual (PcTDR02) was observed chasing a mahimahi shortly after tag deployment and dove within the top 50 m of the water column during this pursuit (Figure 2.1). There were two bouts of increased velocity during this prey chase, which reached maximums of 4.0 and 6.6 (uncalibrated units), respectively. No feeding events were observed post-tagging for the remaining individuals, but tagged animals were not systematically followed post-tagging to record such behavioral information due to other research priorities.

2.4.3 Long-term, coarse-scale dive behavior

Tag transmission durations of SPLASH tags ranged between 8.7 and 47.6 days (median = 20.1 d). Two deployments likely failed due to low battery voltage, while the others presumably failed due to the tag becoming detached. Coverage of behavioral data (i.e., proportion of data obtained out of the total data transmission period) was variable, ranging from 40.3 to 100 percent (Table 2.1). Excluding gaps in the behavior log data, there were 201.1 days of behavior data combined across all deployments (median = 9.7 d, range = 3.8–26.2 d; Table 2.1). By diel period, there were 7.3 days of data during dawn, 93.0 days during day, 8.1 days during dusk, and 92.7 days during night. There were no indications of pressure transducer failures for any of the tags.

All tagged whales spent most of their time in the top 50 m of the water column (range = 89.5-99.0% time at "surface"; Table 2.6, Supplementary Material). A total of 2,112 standardized dives (50 m or deeper, 2 min or longer) were recorded, ranging from 32 to 303 dives per individual (Table 2.6, Supplementary Material). For dives 50 m deep or greater, the overall mean dive depth was 246 m (range of individual median depths = 112–744 m, SD = 164 m, CV = 66.5.9) and overall mean dive duration was 5.8 min (range of individual median durations = 3.8–13.4 min, SD = 2.2 min, CV = 37.4; Table 2.6). The deepest dive recorded was 1,424 m from an open-ocean false killer whale; this was also the longest dive recorded (19.1 min; Table 2.6). This individual (PcTagP09) had visually different diving behavior from all other tagged whales, having higher proportions of deeper (greater than 750 m) dives than observed in other whales (Figure 2.2). The deepest dive recorded in the MHI population was 1,272 m (14.7 min) and the longest dive was 18.6 min (1,264 m; Table 2.6). The deepest dive for NWHI individuals was also the longest dive, recorded at 1,104 m and 18.2 min. Dive durations were positively correlated with dive depths (Spearman's rank correlation coefficient = 0.72); there were no apparent breaks that would indicate the existence of distinct dive types within the range of dive depths and durations we standardized herein (i.e., ≥ 50 m deep, ≥ 2 min long; Figure 2.9, Supplementary Material). Mean dive rate was 0.45 dives per hour (SD = 0.17, CV = 37.8) and ranged from 0.12 dives per hour to 0.75 dives per hour (Table 2.6). The mean time spent in the top 50 m of the water column between dives greater than 50 m was 51.0 min (range of individual medians = 19.3–86.5 min, SD = 21.1 min, CV = 41.1). Two individuals remained in the top 50 m for multiple days: one individual from the MHI population (max surface period duration = 3.1 d) and one individual from the open-ocean population (max surface period duration = 5.1 d).

2.4.3.1 Demographic comparisons

In the following results, descriptive summaries reflect those of the sample (i.e., data from SPLASH-tagged whales presented in this study), as limited group-specific sample sizes preclude generalizations on the respective between-group comparisons. Sample population-level summary statistics indicate that open-ocean false killer whales dove deeper (group mean = 390 m, SD = 317 m, CV = 81.2) and longer (group mean = 8.0 min, SD = 4.8 min, CV = 0.60) than NWHI (group means = 220 m, 5.5 min; SDs = 99 m, 0.7 min; CVs = 44.9, 12.0, respectively) and MHI false killer whales (group means = 208 m, 5.2 min; SDs = 110 m, 1.0 min; CVs = 53.1, 19.7, respectively), however this was driven by the one open-ocean individual with the greatest dive depths (PcTagP09; open-ocean group means with PcTagP09 excluded = 214 m, 5.3 min; SDs = 116 m, 1.3 min; CVs = 54.3, 23.8, respectively). Mean dive rates were lower in open-ocean false killer whales compared to MHI and NWHI false killer whales (group means = 0.33, 0.45, 0.51 dives/h, respectively), but variability within this metric was highest for open-ocean false killer whales compared to the other two populations (SDs = 0.21, 0.15, 0.17 dives/h; CVs = 62.2, 33.9, 33.7, respectively). Males dove deeper (group mean = 350 m, SD = 200 m, CV = 57.1) and longer (group mean = 6.8 min, SD = 3.0 min, CV = 44.1) than females (group means = 182 m, 4.9 min; SDs = 98 m, 1.2 min; CVs = 54.0, 24.2, respectively) and those of unknown sex (group means = 156 m, 5.2 min, SDs = 32 m, 0.9 min; CVs = 20.6, 17.5, respectively), although within-group variation was apparent and sample size varied by group (Table 2.1; Figure 2.10, Supplementary Material). Excluding PcTagP09, the group mean for males was still deeper (285 m, SD = 109 m, CV = 38.4) than that for females and unknown sex individuals (with the sample size caveats noted above), but mean dive duration (group mean = 5.7 min, SD = 0.7 min, CV = 12.4) was more comparable to females and those of unknown sex. Dive rates were highest in individuals of unknown sex (mean = 0.60, SD = 0.15, CV = 25.3), followed by males (mean = 0.38, SD = 0.07, CV = 18.5), and females (mean = 0.29, SD = 0.16, CV = 54.1), although variation was highest in females (Figure 2.10). Between-social cluster comparisons were not made for MHI individuals due to limited representation among clusters (Cluster 1, n = 3; Cluster 3, n = 4; Cluster 4, n = 1; Table 2.1). Within Cluster 3, the coefficient of variation for median dive depth was moderate (CV = 44.3; SD = 121 m) and low for median dive duration (CV = 24.6; SD = 1.3 min) and dive rate (CV = 28.8; SD = 0.13 dives/h). No age class comparisons were made as all but two SPLASH-tagged individual were adults (Table 2.1), however we assessed the potential influence of relative body size using fin base length as a proxy. Fin base length ranged from 55.2 cm to 68.0 cm; known males had fin base lengths greater than 65 cm and known females were less than 60 cm; individuals of unknown sex had some of the smallest fin base lengths (Table 2.1). There was a positive correlation between fin base length and median dive depth (Spearman's rank correlation = 0.39) and median dive duration (Spearman's rank correlation = 0.38). Five of six individuals that dove greater than 1,000 m deep had fin base lengths greater than 65 cm, but some individuals with longer fin bases did not dive as deep (Table 2.1; Table 2.6, Supplementary Material).

2.4.3.2 Spatial and temporal patterns in dive behavior

Dives occurred in a variety of habitats with differences among populations (Figure 2.3). MHI false killer whales dove in both nearshore and offshore environments, with the most dives recorded off the windward side of Maui Nui, around O‘ahu, and on Penguin Bank, all areas where the tagged individuals spent most of their time (Figure 2.11, Supplementary Material). These areas include island shelf/slope transitions of varying degrees and submarine canyons (north of Moloka‘i; Figure 2.3). NWHI false killer whales also dove primarily in nearshore habitats, with most dives concentrated around Kaua‘i, Ni‘ihau, Middle Bank, and Nihoa (Figure 2.3), where tagged animals spent most of their time (Figure 2.11, Supplementary Material). The 2023 tagged pelagic false killer whales dove around the Geologists Seamounts west of Hawai‘i Island (e.g., Perret, Cook, Jaggar Seamounts), and the 2024 individual dove around chains of seamounts and abyssal plains farther from the islands (Figure 2.3; Figure 2.11, Supplementary Material). While mean dive depth was typically shallower in island shelf and slope habitats, there was also high variability in dive depth within these habitats (CV of dive depth > 50%), including both shallow and very deep dives (Figure 2.4).

Univariate summaries of dive metrics by diel period indicate that mean dive depth and duration were similar across diel categories (Table 2.2). In contrast, dive rates were highest at dawn and dusk, intermediate during the day, and lowest at night (Table 2.2, Figure 2.5). This trend persisted across most depth bins, but became less apparent for deeper dives (500 m+, 750 m+, Figure 2.5). While dives greater than 750 m were generally infrequent, they occurred most often early in the morning and otherwise at relatively similar rates within the diel cycle (Figure 2.5). The average proportion of square-, u-, and v-shaped dives were similar throughout the diel cycle, with slightly higher proportions of u-shaped dives during dusk and v-shaped dives during night (8–10% more; Table 2.2). However, there was high variability in nearly all of these univariate summaries (Table 2.2). Dive metrics by shape and diel category were highly comparable to the patterns observed in dive metrics across diel categories irrespective of dive shape (Figure 2.12, Supplementary Material).

2.4.3.3 Spatiotemporal drivers of dive metrics

A total of 1,775 dives were available for the full models (i.e., both spatial and temporal predictors) after removing dives with positional uncertainty greater than 4 km (337 dives) and those with missing covariate values (19 dives). Contemporaneous daily chlorophyll-a concentration and SST were correlated with 30-day lagged chlorophyll-a concentration (Pearson's correlations = 0.7, 0.5, respectively) and thus we selected the latter variable (i.e., 30-day lagged chlorophyll-a) for subsequent modeling and excluded the former two. Correlations among all remaining pairs of predictor variables were low (Pearson's correlations < 0.5), and thus these variables were retained in the models. The GAMM models indicated that individual variation was notable across all models. The best fit model for each dive metric included the random factor smooth structure for time-of-day and individual tag ID, with the percent of deviance explained increasing by 1.0–4.6% compared to the random intercept model (Table 2.7, Supplementary Material). Therefore, we only report results on the models including the random factor smooth term throughout the rest of this section.

The dive depth model (32.2% deviance explained) indicated that tagged false killer whales generally dove deeper during daylight hours with a peak around mid-day (Table 2.3, Figure 2.6a). However, this relationship varied significantly across individuals, with individual-level random effects contributing 25.6% of the total deviance explained by the model (Table 2.3, Figure 2.6a). Most tagged individuals had little to no trend in dive depth across time-of-day (Figure 2.6a). The individual with the most apparent diel trend in diving depth (PcTag049) was from the NWHI population, reflecting the overall trend of diving deeper in the middle of the day. Two individuals from the MHI population appeared to have slightly deeper dives at dawn (PcTag028) or dusk (PcTag074; Figure 2.6a). Chlorophyll-a concentration (30-d lag) had the next highest contribution to the model's deviance explained (3.3%), where dives became shallower from low to intermediate chlorophyll-a concentrations, were no affected at intermediate values, followed by another decrease in dive depth with higher concentrations (Figure 2.6a). The model also indicated that whales dove deepest during full moons, however the predicted effect was relatively weak (0.08% deviance explained; Table 2.3, Figure 2.6a). Dive depths varied non-linearly with current magnitude (2.0% deviance explained; increase in depth with magnitude but asymptotes at higher values) and mixed layer depth (1.0% deviance explained), with no change in dive depth up to approximately 30 meters mixed layer depth, followed by an increase in dive depth with deeper mixed layers (Figure 2.6a). Seafloor slope had a minimal effect on dive depths (0.2% deviance explained), with little change in dive depth with slope until higher slope values, where depth slightly decreased (Figure 2.6a). However, this decreasing trend was driven by few observations with higher slopes (Figure 2.6a).

The model for dive duration (28.0% deviance explained) showed similar trends for time-of-day, where dives were generally longer at mid-day with significant among-individual variation (24.4% deviance explained; Table 2.3, Figure 2.6b). The individual-level trends observed in the dive depth model largely align with those in the dive depth model, albeit at slightly lower magnitude than observed in dive depths (Figure 2.6a, 2.6b). Similar to the dive depth model, chlorophyll-a concentration (30-d lag) had the second highest contribution to the overall deviance explained (1.8%), although the predicted relationship was slightly different for dive duration (Figure 2.6b). Dives were the longest at low chlorophyll-a concentrations and decreased at intermediate concentrations; however, this final portion of the predicted curve was driven by only a few observations (Figure 2.6b). Current magnitude contributed a similar proportion of deviance explained to the model (1.1%) with an estimated positive relationship between dive duration with increasing current magnitude (Figure 2.6b). The remaining covariates (moon phase, slope, mixed layer depth) had no estimated effect on dive duration (Table 2.3, Figure 2.6b).

The trends observed in the full models with the restricted dataset were nearly identical to those in the temporal predictors-only models fit with the complete dataset (n = 2,112 dives; Figure 2.6a, 2.6b; Table 2.8, Supplementary Material). Statistically, the dive duration model with the restricted dataset and all predictors estimated no effect of time-of-day ($p = 0.129$; Table 2.3, Figure 2.6b), while the temporal predictors-only model estimated a significant relationship ($p = 0.017$; Figure 2.6b; Table 2.8, Supplementary material). Visually, the predicted effects of this relationship were highly comparable between the two datasets (Figure 2.6b). Additionally, models without data from PcTagP09 (the individual with the most different dive behavior) showed the same trends as the models with all individuals (Table 2.9, Supplementary Material).

Hourly dive rates were highest between approximately 06:00 and 18:00 (Hawaiian Standard Time) and the model estimated a bimodal distribution within this period (Table 2.3, Figure 2.6c). The first peak in this bimodal distribution was around 07:00, with a slight decrease in rates until 12:00, followed by a second peak between 14:00–16:00 (Figure 2.6c). Dive rates decreased linearly after this time (i.e., into the night), and a similar increase was seen leading up to the first morning peak (Figure 2.6c). Individual-level variation was significant as in the other models (Table 2.3), but there was more conformity to this bimodal functional relationship with dive rate and time-of-day, unlike the models for depth and duration (Figure 2.6c). This includes nearly all individuals from the MHI population and one individual from the open-ocean population. Four individuals (three NWHI, one open-ocean) had higher hourly dive rates in the morning (i.e., had unimodal relationships), while one individual (NWHI population) had higher dive rates at night

(Figure 2.6c). There was evidence for an effect of moon phase on hourly dive rate (Table 2.3), although the predicted effect was minimal (Figure 2.6c).

2.4.3.4 Near-seafloor diving behavior

All tagged individuals from the MHI and NWHI populations had dives that initially appeared to be close to the seafloor, but for many dives, this appeared to be an artifact of tag location error (i.e., high variation in seafloor depth across 20 imputed dive positions; Figure 2.13, 2.14, Supplementary Material). Out of the 1,620 candidate dives (i.e., those with positional uncertainty < 4 km) from all tagged insular whales, there were 287 dives that were considered probable near-seafloor dives (i.e., standard deviation of seafloor depths < 100 m, max depth < 100 m from seafloor). The proportion of probable near-seafloor dives out of all candidate dives was low (mean = 16.9%, Table 2.4). Five individuals had proportions greater than this mean, ranging from 21% to 48% of all candidate dives as probable near-seafloor dives (Table 2.4). The overall mean dive depth and duration for dives that were likely at or close to the seafloor were 321 m and 7.4 min, respectively, and ranged from shallow dives (52 m) to very deep dives (1,272 m), with all but three of the thirteen insular individuals having probable seafloor dives deeper than 500 m (Table 2.4). Most seafloor dives were square- or u-shaped, but this varied among individuals (Table 2.4). Spatially, seafloor dives occurred on shallow banks, shelves, and both gradual and steep slopes (Figure 2.7). The most seafloor dives occurred on Penguin Bank, along the north and west shelf/slopes of Oʻahu, and in the leeward waters of Maui Nui, all of which are relatively shallow areas (< 500 m; Figure 2.7). Three individuals, all from the MHI population, had probable near-seafloor dives exceeding 1,000 m: PcTag026 had one 1,272 m dive recorded along the steep slope off southeastern Hawai‘i Island, adjacent to the Papa‘u Seamount (Figure 2.7); PcTag032 dove to 1,168 m around the north Moloka‘i submarine canyons; and both PcTag032 and PcTag099 dove to 1,264 m and 1,020 m, respectively, along the deep slope off northwest Hawai‘i Island (Figure 2.7). Temporally, median probable seafloor dive rates were highest during the day and at night, while the maximum rates occurred during dawn; however, there was high variability in dive rates by time-of-day, as several individuals had near-seafloor dives during some diel categories but not others (Table 2.4; Figure 2.15, Supplementary Material). Median depths of near-seafloor dives were slightly deeper at dawn and dusk than night or day, although the distribution of dive depths and durations were broadly similar across diel categories (Table 2.4; Figure 2.15, Supplementary Material).

2.5 Discussion

Using two types of bio-logging tags, we described the vertical movements of false killer whales at both fine- and coarse-scales and in relation to ecological contexts. We found that false killer whales spend most of their time in the epipelagic zone (i.e., surface to approximately 200 m depth) and exhibit a diversity of dive types across different habitats, with substantial variation over time and across individuals and demographic groups. These findings, combined with observed spatial patterns, suggest that false killer whales adapt their vertical movements to different prey types and environmental conditions. This study fills critical species-specific knowledge gaps and reveals surprisingly deep diving behavior in false killer whales. In the following sections, we discuss the potential ecological and demographic drivers of observed inter-individual variation in vertical movements, and hypothesize how they collectively provide emerging insight into this species' foraging ecology.

2.5.1 Vertical movements: diving behavior of false killer whales

Our study presents the first comprehensive description of diving behavior for false killer whales, providing a foundation for the vertical dimension of their movement ecology. All tagged false killer whales—both short-term, fine-scale TDR and long-term, coarse-scale SPLASH-tagged—spent a high proportion of time in the top 50 m of the water column and their median dives depths were typically in the top 300 m. This preference for the upper portions of the water column aligns with visual observations of behavior, including the variety of surface-oriented prey they have been documented feeding on (Baird et al., 2021, 2008a), and with insights from suction-cup tagged false killer whales elsewhere (Minamikawa et al., 2013). Despite their clear near-surface tendencies, the SPLASH-tagged false killer whales were capable of diving much deeper and did so more often than previously assumed. All these individuals performed dives exceeding 700 m, nearly half of them performed dives deeper than 1,000 m, and the maximum depth observed (1,424 m) was more than twice that known for the species (Minamikawa et al., 2013). Such extensive vertical movements suggest false killer whales actively forage at depth. While we cannot infer definitive feeding events from SPLASH tags, similar deep diving behavior is known to occur in foraging contexts of related, similar-sized and sympatric species, such as short-finned pilot whales (*Globicephala macrorhynchus*; (Owen et al., 2019)), goose-beaked whales (*Ziphius cavirostris*, (Baird, 2019)), and Blainville's beaked whales (*Mesoplodon densirostris*, (Baird, 2019)). Elucidating the function of these deep dives and their frequency across individual traits will require additional tag deployments, including satellite tags and other bio-loggers (e.g., those equipped with 3D accelerometers, acoustic sensors).

2.5.2 Demographic contexts of movement: from individuals to populations

Individual traits such as morphology (e.g., body size), age, and sex can shape the physiological capacities for diving in marine mammals (Noren and Williams, 2000). Consequently, individual traits modulate access to some prey communities at depth, thus contributing to inter-individual variation in foraging behavior (e.g., (Bird et al., 2024; Joyce et al., 2017)). We found a positive but weak correlation between relative body size (i.e., dorsal fin base length) and diving (i.e., depth and duration), and most individuals that undertook the deepest dives also had longer fin base lengths. The weak correlation is unsurprising, as nearly all tagged whales were adults and thus differences in relative body size are smaller than expected between younger individuals and adults. However, the estimated difference in body length between the smallest and largest adults could exceed one meter (Ferreira et al., 2014), and thus even a weak correlation in the data could indicate meaningful differences in dive capacity with body size. Additionally, while fin base length is a proxy for body size, it may not scale linearly or identically for both sexes. Males dove deeper and longer than females and those of unknown sex, but there are some caveats in these sex-based differences in diving capacities—largely driven by an outlier individual (PcTagP09) and only three of the satellite-tagged whales were known to be females and six were of unknown sex. Similar limitations preclude robust inference on age-based differences. Among all satellite-tagged individuals, only two were non-adults (juvenile and sub-adult) because adults are targeted for this type of tag due to their larger body size (and thus target area) and more predictable surfacing behavior. Ontogenetic shifts in diving behavior are thus not currently discernable but could be evaluated in the future with additional deployments on younger individuals with these tags or less invasive tag types. Further assessment of morphology-driven variation in diving behavior will also benefit from future drone-based photogrammetry (e.g., (Bird et al., 2024)).

Inter-individual variation in behavior, such as vertical movements, can also scale up to population-level foraging strategies, even among sympatric populations (e.g., (Tennessen et al., 2023)). Our available tag data suggest high within-population variability in vertical movements, even though our current sample size precludes a robust assessment of specializations or strategies at the population level. For example, PcTag049 primarily dove at night, a notably different diel pattern than the other four tagged NWHI false killer whales. Similarly, PcTagP09 dove deeper and much more frequently than all other tagged individuals combined, including the others from the open-ocean population. There was high variability in diving behavior within the MHI population as well, including the spatial distribution of dives, diel trends, and dive metrics. Such variation in diving behavior currently precludes generalization of population-level patterns, which will require more tag deployments. Additional genetic analyses of biopsy samples would help unravel within-population structuring (particularly for open-ocean false killer whales), and the extent to which differences in dive behavior reflect the degree of relatedness. Further, stable isotope analysis of biopsy samples from all three populations would help identify whether all populations exhibit similarities in diet breadth, or if some exhibit narrower trophic niches that reflect resource specialization (e.g., (Fossette et al., 2017)).

Group-specific movement strategies can emerge from inter-individual variation in behavior (Sheppard et al., 2021), particularly if individuals cooperatively hunt and behaviors can be socially learned (e.g., (Daura-Jorge et al., 2012)). Insights on social cluster contexts emerge from the available tag data, even though identifying cluster-level strategies in MHI false killer whales would also necessitate additional tag deployments. Most SPLASH-tagged MHI false killer whales were members of Cluster 3, and we found moderate variability in dive metrics within this social cluster, including diel trends. The number of dives was the most spatially constrained metric, and regions with the most dives overlapped with known high-use areas for Cluster 3 (Badger et al., 2025; Baird et al., 2023). However, individuals from other clusters also spent time and dove > 50 m in these habitats, and Cluster 3 high-use areas have high overlap with that estimated for the overall population (Kratofil et al., 2023). We additionally highlight the frequent near-seafloor diving behavior of PcTag055 (nearly 50% of all dives) as a potential indicator of cluster-level foraging tactics. This whale is the only individual in our dataset that belongs to Cluster 4 of the MHI population. Compared to the other social clusters, Cluster 4 has the most restricted space use, primarily using habitats within Maui Nui (Badger et al., 2025; Baird et al., 2023; Mahaffy et al., 2023). In contrast, high-use areas for the other clusters are found along the windward sides of Maui Nui, O‘ahu, and off northern Hawai‘i Island, and individuals from two of these clusters are known to move widely throughout the main Hawaiian Islands (Baird et al., 2023, 2012). Variation in persistent organic pollutant levels and stable isotopes also suggest that foraging habitats may slightly differ among the social clusters (Kratofil et al., 2020). Foraging site fidelity is often correlated with foraging specializations when prey availability is consistent and abundant (e.g., (Wakefield et al., 2015)), and perhaps this is the case for Cluster 4. Indeed, the high-use area of this social cluster also contains a large proportion of bottom fish (e.g., green jobfish or uku, *Aprion virescens*) habitat in the MHI region (Nadon et al., 2020); this shallow water habitat could additionally make near-seafloor dives more accessible. However, tagged whales from other clusters also exhibited near-seafloor diving behavior, and the deployment duration for PcTag055 was relatively short (approximately 1 week). Additional SPLASH tag deployments coupled with more comprehensive diet information will help discern social cluster-level foraging behavior.

2.5.3 Ecological contexts of movement: prey and niche partitioning

Across all tagged individuals combined, we found that false killer whales predominantly occupy the epipelagic zone. While definitive prey captures cannot be inferred from either TDR or satellite tags, visual observations of foraging on surface-oriented epipelagic fish support these findings (Baird, 2016; Baird et al., 2008a). We observed one of the whales chasing a mahimahi shortly after being equipped with a TDR tag, and its use of the near-surface waters (< 50 m) during this time validates foraging in the epipelagic zone from tag-derived measurements. Mahimahi spend most of their time in the top 50–150 m of the water column but will use much shallower waters when associated with floating objects (Whitney et al., 2016), which false killer whales have regularly been observed hunting mahimahi around (RWB, personal observation). The lower ascent rates (compared to descent rates) reported by the TDR tags could reflect a hunting tactic for such surface-oriented prey—or a predator avoidance tactic as suggested for beaked whales (e.g., (Baird et al., 2008b))—where false killer whales slow their ascent rates to visually scan for prey (or predators) near the surface. This pattern could also be a mechanism for preventing the formation of gas bubbles in blood or tissues (Fahlman et al., 2006), however, this hypothesis is more relevant for deeper dives (e.g., (Hooker and Baird, 1999; Martin and Smith, 1992)). Combined with the high proportion of time spent above 50 m, the significant relationship between dive depth and mixed layer depth in the multivariate model additionally suggests foraging on prey that occupy the epipelagic zone, or prey that respond to variation in the mixed layer (although this only explained 1% of the model deviance). Many mid- and upper-trophic level epipelagic fish included in false killer whales' diet are known to spend high proportions of their time in the surface mixed layer and epipelagic zone more broadly (e.g., ʻahi, (Brill et al., 1999; Lam et al., 2020)). Other large game fish, such as bigeye tuna or ʻahi poʻonui (*Thunnus obesus*), occupy deeper depths (300–500 m) during the day, with excursions to the surface mixed layer within this time period (Musyl et al., 2003). Thus, together with the temporal findings (discussed further in subsequent sections), false killer whale dives within the 200–300 m depth range could be targeting prey moving between epi-/mesopelagic zones such as ʻahi poʻonui, or pursuing prey within the epipelagic zone that attempt to flee by diving deeper (e.g., ʻahi, (Lam et al., 2020)). Overall, these findings indicate that information inferred from surface observations of false killer whale predation events or prey sharing likely reflect the majority of their diet, although given their observed deep diving behavior, surface observations are not reflective of their entire diet.

Tagged false killer whales exhibited a diversity of dive types when they were not using near-surface waters or diving within the epipelagic zone. Deeper, albeit comparatively infrequent dives outside of the epipelagic zone could reflect foraging on other prey species or types. For example, false killer whales have been observed feeding on monchong (lustrous pomfret or mukau, *Eumegistis illustris*; (Baird et al., 2008a)) which occur along deep slopes (> 900 m) and near seamounts (Chave and Mundy, 1994), and moonfish or opah (*Lampris guttatus*; (Baird et al., 2021)) which utilizes the mesopelagic zone (Polovina et al., 2008a). The island-associated mesopelagic boundary layer occupies the 400–700 m depth zone during the day (Reid et al., 1991) and it is possible that dives to these depths (or deeper) could reflect foraging for such mesopelagic or interzonal species knowing that false killer whales have consumed squid that occupy these vertical habitats (from stomach contents: diamondback squid, *Thysanoteuthis rhombus,* and purpleback flying squid, *Sthenotheuthis oualaniensis*; K. West personal communication; (Jereb and Roper, 2010; Parry, 2003). Although inconclusive, probable predation events on tagged yellowfin tuna in Hawaiian waters—inferred from isolated, uncharacteristically deep dives of up to 1,500 m [Lam et al.]—raise the possibility that they were fleeing from predators that can pursue prey at depth, including false killer whales.

We documented probable seafloor dives in all MHI and NWHI false killer whales, and the depth of near-seafloor dives were variable. Penguin Bank, where these dives were most common and limited to within 200 m, is known critical habitat for bottom fish, such as uku (Tanaka et al., 2022), which MHI false killer whales have been observed feeding on (Baird et al., 2021). Probable near-seafloor dives also occurred in deeper habitats, including steep slopes, gradual deep slopes, and submarine canyons, reflecting potential pursuit of deep slope associated prey (e.g., monchong; (Chave and Mundy, 1994)). Submarine canyons in Hawaiʻi are biological hotspots, where dynamic interactions between currents and topography enhance local nutrient availability and thus aggregate a variety of mobile fish (Vetter et al., 2010). The submarine canyons off Oʻahu and Molokaʻi in particular are known to have increased species richness relative to nearby slopes (Vetter et al., 2010). Thus, the probable seafloor dives near these features could potentially reflect foraging on these localized prey aggregations. This near-seafloor diving tactic does not appear to comprise a high proportion of their diving activity (with one exception discussed above), although it is possible that it occurs more frequently than reported here due to the restrictions applied for location uncertainty. Other bio-loggers, such as those equipped with acoustic sensors or cameras, could inform the function of these near-seafloor dives.

Our multivariate findings suggest that temporal cycles, serving as proxies of prey movement, are not a primary driver of false killer whale diving behavior. Although we found evidence for a common trend of diel and lunar patterns in dive depth where dives were deeper (by approximately 50 m) in the middle of the day and during full moons, the shape of this diel trend varied significantly among individuals. Several individuals had contrasting patterns in dive depth and duration with time-of-day (e.g., nocturnal versus diurnal, some deeper during dawn, others during dusk), even within a population. Minamikawa et al. (Minamikawa et al., 2013) did report deep dives (> 200 m) predominantly occurring during the daytime, although their sample of dive data was only for one individual for three days. Diel patterns in hourly dive rate, however, were more generalizable across all tagged false killer whales, where dives > 50 m occurred most frequently during daytime (except for one NWHI individual) with peaks just after dawn and prior to dusk. Increased frequency of dives during the day, but across variable depths and durations, could suggest that false killer whales forage deeper more often during the daytime but on a variety of prey that may or may not exhibit diel vertical migrations. High variation and complex relationships in diel patterns have been observed in other marine predators that exploit a diversity of prey types and whose availability may change across habitats (e.g., belugas, *Delphinapterus leucas,* (Storrie et al., 2022); leatherback sea turtles, *Dermochelys coriacea,* (Hays et al., 2006)). Further, a recent study documented the occurrence of a deep, non-migratory micronekton (fish, squid) layer in the leeward waters of Hawaiʻi Island (Drazen et al., 2023); false killer whales may exploit this non-migratory prey field, which could additionally explain the high variability in their diving behavior.

Niche partitioning among sympatric predators may also influence diel patterns in false killer whale diving behavior. Twenty-six species of cetacean have been documented around the

Hawaiian Archipelago, eleven of which are odontocetes that are resident year-round and geographically overlap with false killer whales (Baird, 2016; Kratofil et al., 2023). Several sympatric predators, including spinner dolphins, rough-toothed dolphins, short-finned pilot whales, pantropical spotted dolphins, and melon-headed whales, exhibit vertical movements that appear to track diel vertically migrating prey (Baird et al., 2001; Benoit-Bird and Au, 2003; Owen et al., 2019; Shaff and Baird, 2021; West et al., 2018), which contrasts to the high variation and weak diel patterns we found for false killer whales. Some of these studies have also found strong effects of lunar phase on diving behavior (Owen et al., 2019; Shaff and Baird, 2021), which again differs from our findings. Thus, it is possible that these sympatric delphinids fill a niche as predators on the DSL prey community that false killer whales only opportunistically exploit. This could be additionally inferred by contrasting movement and space use patterns observed in these other species: the high movement rates exhibited by false killer whales among all populations (Baird et al., 2012, 2010) are either infrequent or rare in the other resident odontocetes, which typically exhibit site fidelity to only one or few islands (Baird, 2016; Kratofil et al., 2023). Prey species comprising the diel vertically migrating DSL are typically less mobile than large epipelagic prey, and thus the stronger site fidelity and diel foraging behavior of sympatric predators could point to spatial and temporal partitioning with more generalist and higher trophic level false killer whales.

Our multivariate model results shed further light on the importance of dynamic oceanographic variables on false killer whale vertical movement behavior. On average, false killer whales dove deeper and longer when lagged surface chlorophyll-a concentrations were low and when surface current magnitude was high. Unlike the dive depth model results, the estimated trend between dive duration and lagged chlorophyll-a concentrations plateaued at higher values. These findings suggest that when surface productivity is low, false killer whales dive deeper (and thus longer), presumably targeting alternative prey deeper in the water column. High surface chlorophyll-a concentrations could also indicate reduced visibility in near-surface waters, which could subsequently affect prey pursuit and capture efficiency. Variance in chlorophyll-a concentrations could be confounded by seasonal climatic variation; however, the Central North Pacific lacks strong seasonal variability in primary productivity (Uitz et al., 2010), making prey dynamics or visibility more plausible explanations for our findings. Areas with stronger horizontal current magnitude can indicate the presence of oceanographic fronts or edges of mesoscale eddies, which are typified by vertical mixing and known to be hotspots of biological activity (Chelton et al., 2011; Prants, 2022). Other pelagic predators have been observed modifying their vertical movements and foraging at these features (e.g., seabirds, (De Pascalis et al., 2021); pinnipeds, (Abrahms et al., 2018)), and thus it is plausible that our results on false killer whales reflect similar behavior. Collectively, the diversity of prey and dive types, our findings on epipelagic tendencies and variable diel and lunar patterns in diving behavior, and the observed relationships between vertical movements and oceanographic variables all support a hypothesis for an ecologically driven, flexible foraging strategy.

2.5.4 Conclusions

Our study provides the first comprehensive description of false killer whale diving behavior and enhances understanding of their movement ecology. We highlight that our study takes place in a unique marine ecosystem—the Hawaiian Archipelago—where long-term multi-species studies have developed critical ecological context for interpreting false killer whale vertical movement behavior. Both fine-scale, short duration and coarse-scale, intermediate-long duration tags showed that false killer whales primarily occupy the epipelagic zone, a vertical habitat that many large, upper trophic level prey inhabit. Satellite tags additionally documented dives to a wide range of depths—including surprisingly deep (>1,000 m) diving behavior and a record maximum of 1,424 m—and within a variety of habitats. Temporal proxies of prey availability do not appear to shape false killer whale diving behavior; inter-individual variation in diel trends and proxies of biological productivity (i.e., surface chlorophyll-a concentration, current magnitude) and upper trophic level fish habitat (i.e., mixed layer depth) captured the most variation in the data, albeit with small effect sizes. There was also high variability in dive metrics among individuals of different age/sex classes, social clusters, and populations. These findings, paired with false killer whales' diverse diet and sympatry with predators known to exploit the DSL, support the hypothesis of a flexible, ecologically driven foraging strategy in this social pelagic predator. While additional tag deployments are needed to better characterize drivers of behavioral variability and more explicitly link diving with foraging behavior, our results provide emerging insights into the role of ecological context on the vertical movements of false killer whales. Our findings also serve as a foundation for interpreting false killer whale movements in the context of various conservation-oriented goals (e.g., energetics, important foraging habitats, fisheries interactions), particularly for the endangered MHI population that has declined over the recent decade (Badger et al., 2025).

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Tag data used in this study can be visualized on Movebank (https://movebank.org) and are available from the corresponding author on reasonable request. All code developed to process, analyze, and visualize the data in this study are available at https://github.com/makratofil/fkw-dive-behavior.

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2.8 Figures

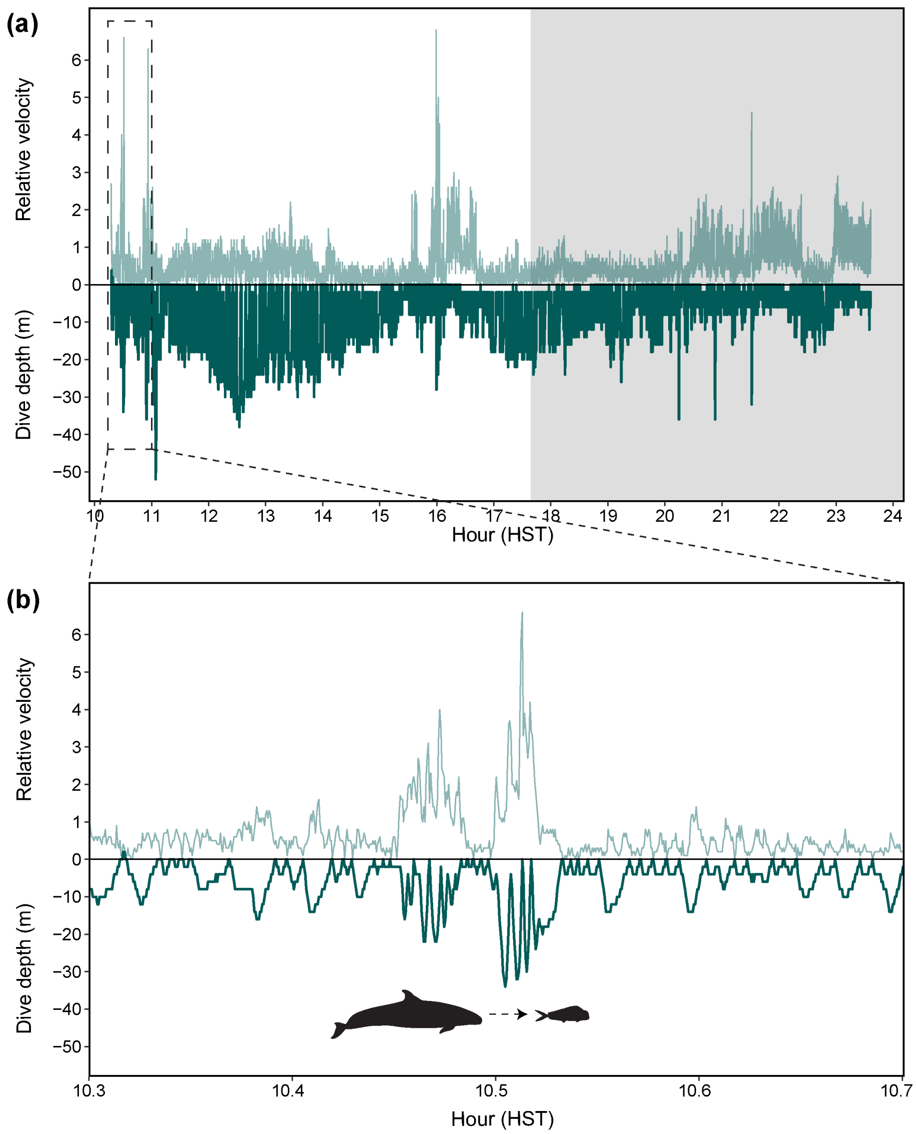

Figure 2.1. Dive depth and relative velocity profile from false killer whale PCTDR02 tagged in November 1999. Dives are represented by dark green lines and swim speed by light green lines. Night periods are indicated by gray shading and hours are in Hawaiian Standard Time (HST). (a) dive and velocity measurements over the entire deployment period; (b) dive and velocity profiles during a short period of time when the animal was observed chasing a mahimahi (indicated by the mahimahi icon).

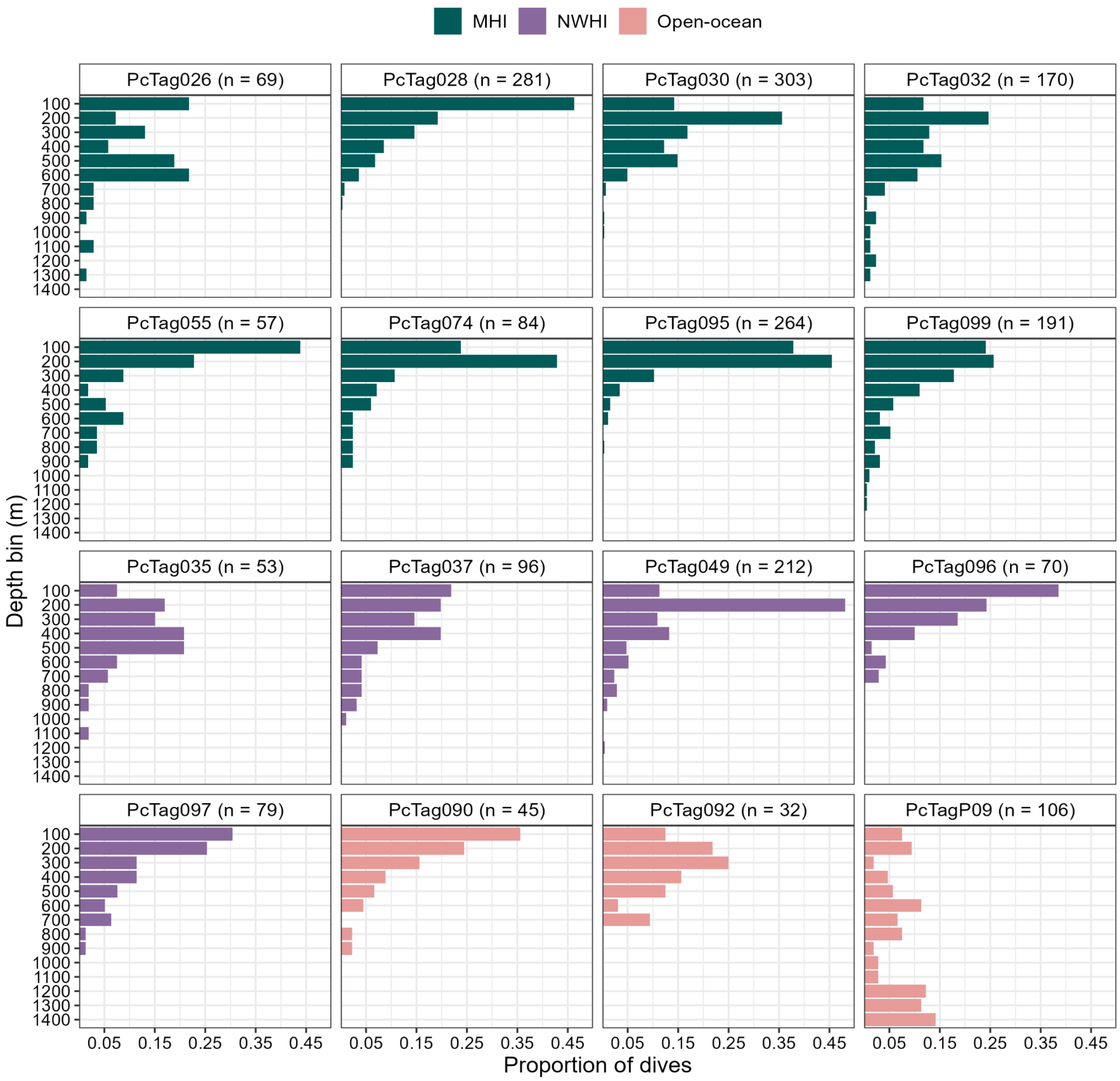

Figure 2.2. Proportions of dives by depth bin for each SPLASH-tagged false killer whale. The first depth bin labeled as "100" on the y-axis represents dives between 50–100 meters deep; the subsequent bin ("200") therefore represents dives 101–200 meters deep. MHI = main Hawaiian Islands; NWHI = Northwestern Hawaiian Islands. The number of dives for each tag are shown in plot headers.

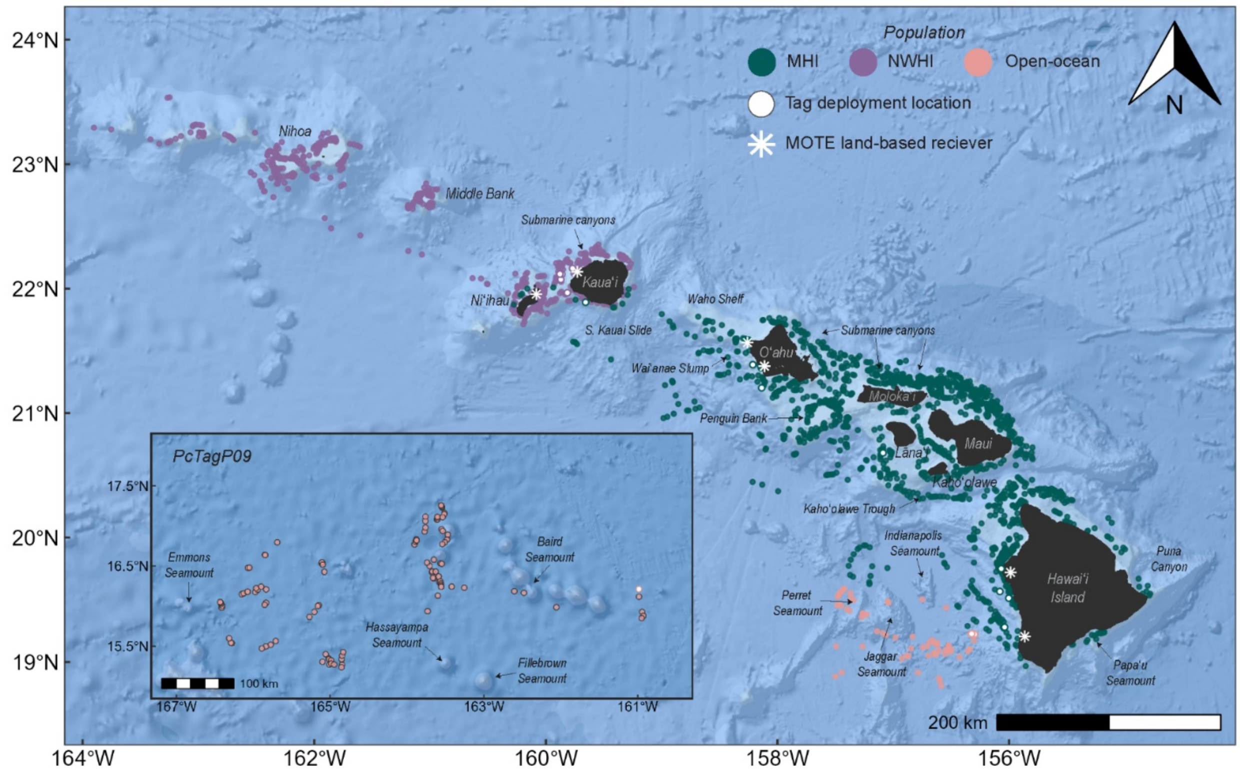

Figure 2.3. Estimated dive locations from sixteen SPLASH-tagged false killer whales in the study area. Dives (≥ 50 m, ≥ 2 min) are represented by circles. Note that the two deployment locations for open-ocean false killer whales off west Hawai‘i Island overlap. The inset map shows dive locations for PcTagP09 which occurred much farther offshore from the islands. Select topographic features are labeled.

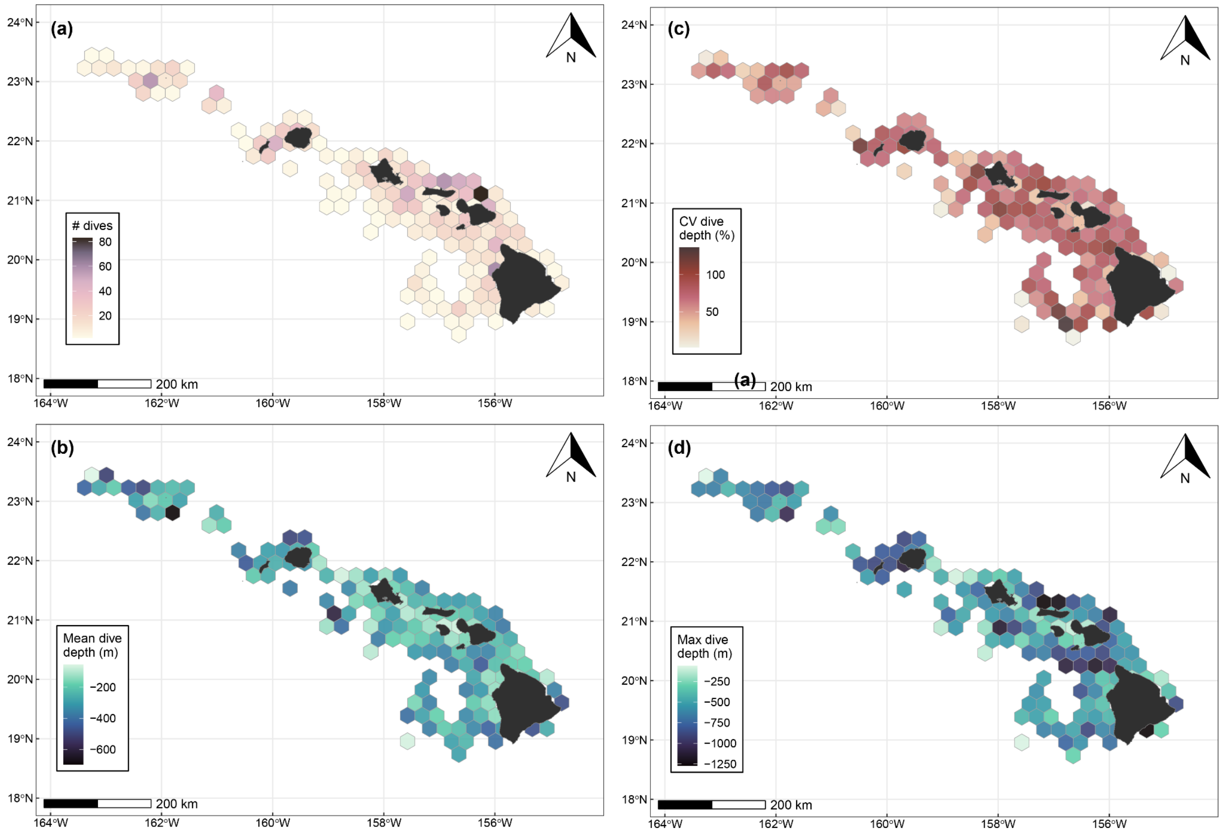

Figure 2.4. Gridded spatial distribution of dives from SPLASH-tagged false killer whales. (a) number of dives; (b) mean dive depth; (c) coefficient of variation (CV) in dive depth; and (d) maximum dive depth. Hexagon cell size (for those not intersecting with land) is 750 km^2, and cells with only one dive were excluded from these summaries. PcTagP09 was not included in these visual summaries because it was the only individual that occurred in its geographic range, precluding among-individual spatial summaries of dive metrics.

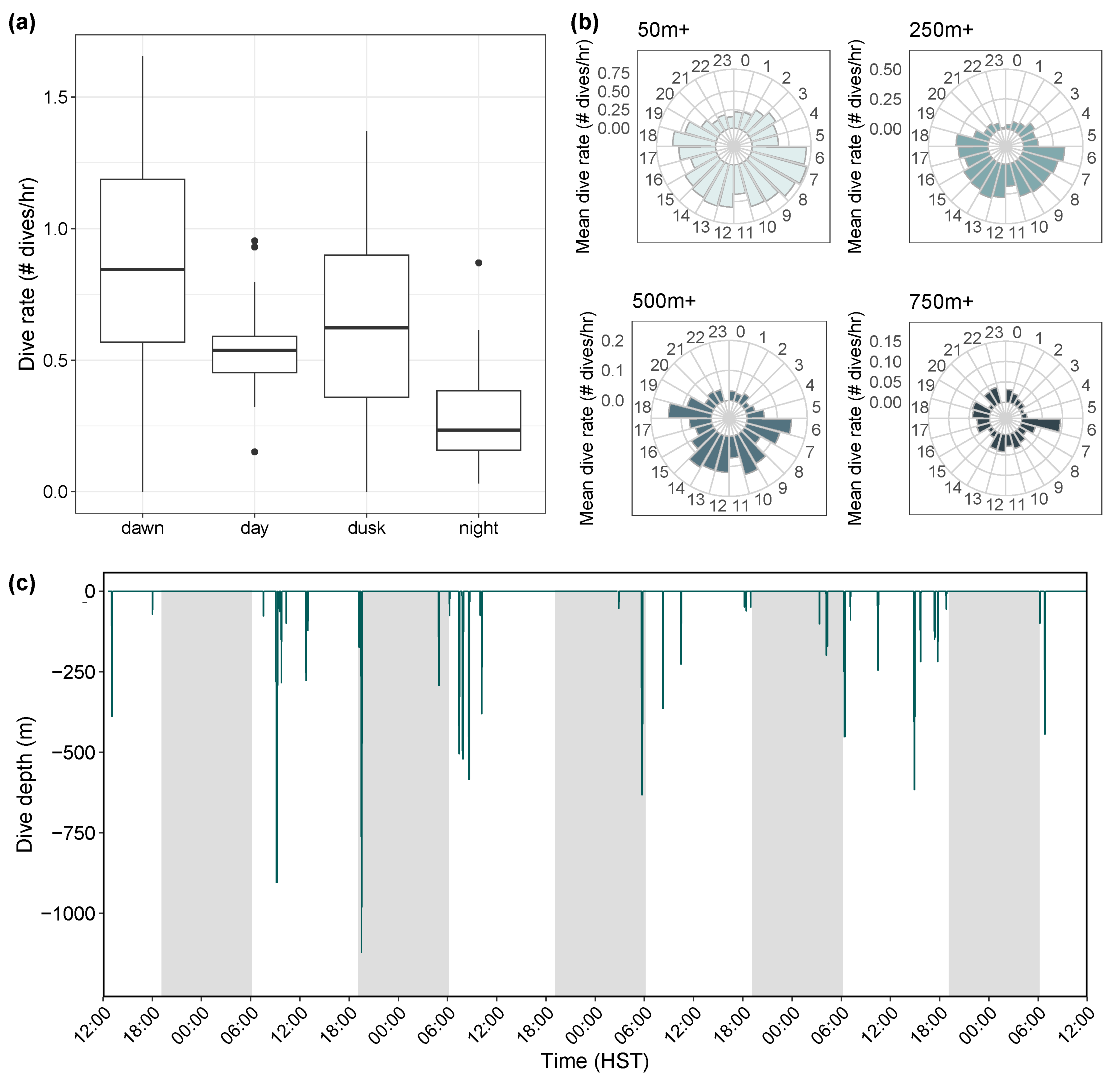

Figure 2.5. Grand mean dive rates throughout the diel cycle and across dive depth bins. Dive rates (# dives per hour; dives ≥ 50 m and ≥ 2 min) for (a) each diel category and (b) hourly, across different depth bins. A single value per individual and diel category was used for (a) and overall mean values were used for (b). Panel (c) shows the dive depth profile over five days for one tagged whale (PcTag099), with nighttime represented by the grey shaded rectangles (HST = Hawaiian Standard Time). Boxplots: the middle line in each box represents the median, the lower and upper extents of the box the first and third quartiles (respectively), the lower and upper whiskers the minimum and maximum (quartiles +/- 1.5*interquartile range), and any values outside of the box/whiskers are shown as points.

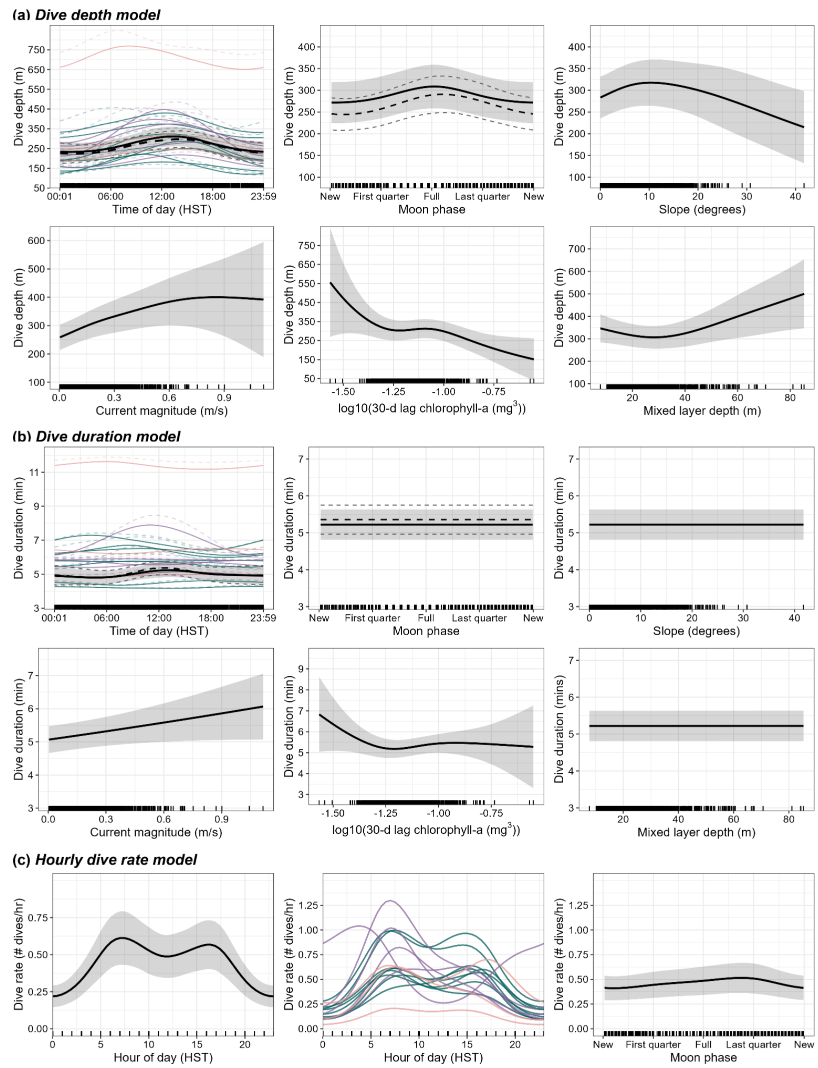

Figure 2.6. Predicted relationships from generalized additive mixed effects models. (a) dive depth; (b) dive duration; and (c) hourly dive rate in relation to spatial and temporal predictors (temporal only for (c)). The mean predicted functional response curve for each covariate is conditional upon the mean value for all other covariates, and is represented by the solid black line and associated 95% confidence intervals are represented by the shaded gray ribbon. Panels with colored lines show the random smooths for each individual and time of day, colored by population assignment (green = MHI, purple = NWHI, pink = open-ocean). Observed predictor values are shown as vertical black ticks along the x-axis. Dashed lines in time of day and moon phase panels in (a) and (b) represent the predicted response curves for those predictors in the model fit with the full dataset (i.e., no data restriction applied) and only temporal predictors.

2.9 Tables

Table 2.1 False killer whale dive behavior tag deployment summary. Social network cluster for MHI individuals was from Mahaffy et al. (2023). Sex was either genetically determined from a biopsy sample[1], inferred from presence of calf or morphological characteristics[2], or unknown if neither source of information were available. Percent behavior data coverage for SPLASH tags represents the summed duration of behavior log records out of the total time of behavior log data transmission (i.e., first message to last message), and thus provides an indication of gaps in transmissions. Individuals with multiple photos for dorsal fin base length measurements have an associated standard deviation (SD) with the mean of measurements. There is no dorsal fin base measurement for PcTag095 due to a lack of sufficient quality photographs for measurements. MHI = Main Hawaiian Islands; C=Cluster; NWHI = Northwestern Hawaiian Islands; MC=Main Component; IC = Isolated Component; A = adult; SA = sub-adult; J = juvenile; F = female; M = male; U = unknown. Maui Nui includes the islands of Maui, Moloka‘i, Lāna‘i, and Kaho‘olawe.

Table 2.1 False killer whale dive behavior tag deployment summary.

Tag ID	Tag type	Population–cluster/component	Age class	Sex	Fin base length mean ± SD (cm)	Deployment date	Deployment locality	Behavior data available (% coverage)
PcTDR01	Mk6 TDR	MHI – C3	A	U	-	29-Mar-1999	Maui Nui	1.1 h
PcTDR02	Mk6 TDR	MHI – C4	A	F[2]	-	17-Nov-1999	Maui Nui	13.4 h
PcTDR03	Mk6 TDR	MHI – C1	J	M[1]	-	28-Feb-2001	Maui Nui	3.6 h
PcTDR04	Mk6 TDR	MHI – C3	SA	M[1]	-	6-Oct-2004	Hawai‘i Island	28.9 h
PcTDR05	Mk9 TDR	MHI – C1	J	M[1]	-	16-Jul-2008	Hawai‘i Island	7.3 h
Total								54.3 h
PcTag026	SPLASH10	MHI – C3	A	M[1]	68.0 (0.1)	15-Oct-2010	O‘ahu	7.0 d (64.1)
PcTag028	SPLASH10	MHI – C1	SA	U	57.3 (0.4)	22-Oct-2010	O‘ahu	15.7 d (40.3)
PcTag030	SPLASH10	MHI – C3	A	U	55.2 (NA)	11-Dec-2010	Hawai‘i Island	20.0 d (66.8)
PcTag032	SPLASH10	MHI – C3	A	M[1]	65.8 (0.5)	11-Dec-2010	Hawai‘i Island	20.1 d (77.1)
PcTag055	SPLASH10-F	MHI – C4	A	M[1]	68.0 (NA)	9-Mar-2015	Maui Nui	6.5 d (78.4)
PcTag074	SPLASH10-F	MHI – C3	A	U	56.5 (0.2)	8-Aug-2021	Kaua‘i	9.2 d (95.7)
PcTag095	SPLASH10-F	MHI – C1	J	F[1]	NA (NA)	20-Jan-2025	Hawai‘i Island	26.2 d (84.7)
PcTag099	SPLASH10-F	MHI – C1	A	M[1]	67.3 (NA)	13-Jul-2025	Hawai‘i Island	25.7 d (86.7)
Total								130.5 d
PcTag035	SPLASH10	NWHI – C5	A	M[1]	66.7 (NA)	13-Jun-2012	Kaua‘i	6.6 d (100.0)
PcTag037	SPLASH10	NWHI – C4	A	M[2]	66.8 (0.2)	26-Jul-2013	Kaua‘i	10.2 d (67.0)
PcTag049	SPLASH10	NWHI – C2	A	U	57.9 (NA)	6-Sep-2015	Kaua‘i	14.5 d (98.6)
PcTag096	SPLASH10-F	NWHI – C4	A	U	55.7 (NA)	17-Feb-2025	Kaua‘i	3.8 d (59.4)
PcTag097	SPLASH10-F	NWHI – C4	A	U	56.6 (NA)	17-Feb-2025	Kaua‘i	7.1 d (94.0)
Total								42.2 d
PcTag090	SPLASH10-F	Open-ocean – MC1	A	F[1]	56.8 (NA)	31-Oct-2023	Hawai‘i Island	16.3 d (99.6)
PcTag092	SPLASH10-F	Open-ocean – MC1	A	F[1]	56.7 (NA)	31-Oct-2023	Hawai‘i Island	3.8 d (45.4)
PcTagP09	SPLASH10-F	Open-ocean – IC2	A	M[1]	65.9 (0.4)	16-May-2024	E. Johnston Atoll	8.4 d (69.1)
Total								28.4 d

Table 2.2. Summary of dives metrics from SPLASH-tagged false killer whales by diel category. Grand mean (mean of medians or proportions) ± the standard deviation (SD) and coefficient of variation (CV, expressed as %) of dive metrics from SPLASH-tagged false killer whales by diel category. Dives were considered those 50 m or deeper and 2 min or longer. The number of dives column includes the grand mean, SD, and CV across individuals and the total number of dives for the diel category. Dive shapes are determined by different proportions of bottom time within dives.

				Mean ± SD (CV)			
Diel category	# dives / total	Dive depth (m)	Dive duration	Rate (# dives ≥50 m /h)	% Square-shaped dives	% U-shaped	% V-shaped dives
Dawn	10 ± 7 (69.7) / 155	273 ± 186 (68.2)	6.3 ± 3.1 (49.3)	0.92 ± 0.39 (42.6)	34.5 ± 28.7 (83.1)	52.7 ± 26.7 (50.7)	12.8 ± 12.6 (98.2)
Day	74 ± 51 (68.7) / 1179	270 ± 162 (59.9)	6.0 ± 2.3 (39.2)	0.55 ± 0.21 (37.5)	27.1 ± 20.2 (74.6)	63.1 ± 18.1 (28.6)	9.8 ± 5.3 (53.9)
Dusk	10 ± 7 (66.5) / 137	292 ± 171 (58.3)	6.3 ± 2.5 (40.5)	0.72 ± 0.32 (45.2)	19.7 ± 27.5 (139.6)	70.9 ± 29.1 (41.0)	9.4 ± 12.5 (133.1)
Night	40 ± 38 (95.4) / 641	216 ± 235 (109.1)	5.6 ± 2.4 (43.1)	0.29 ± 0.21 (71.6)	25.6 ± 22.6 (88.3)	56.0 ± 22.6 (40.4)	18.3 ± 10.6 (58.0)

Table 2.3. Generalized additive mixed effects model outputs for dive behavior metrics. Dives with positional uncertainty of 4 km and greater were removed prior to analyses for dive depth and duration models that include both spatial and temporal predictors. All dives were used for the hourly dive rate model. The percent deviance explained by covariates for the hourly dive rate model are not included, as there is currently no functionality to obtain this metric from a model that includes an offset term. EDF = estimated degrees of freedom.

Model	Covariate	EDF	F-value	p-value	Deviance explained (%) by covariate
Dive depth	Time-of-day (HST)	2.260	4.683	<0.001	0.01
	Moon phase	1.739	1.769	0.032	0.08
	Slope	1.775	1.606	0.020	0.24
	Current magnitude	2.012	5.382	<0.001	2.03
	Chlorophyll-a (30-d lag)	3.153	3.233	0.003	3.28
	Mixed layer depth	2.052	2.962	<0.001	1.00
	Random: time-of-day x ID	31.973	2.712	<0.001	25.56
	Total	-	-	-	32.21
Dive duration	Time-of-day (HST)	0.207	0.076	0.129	0.05
	Moon phase	0.006	0.002	0.465	0.04
	Slope	0.001	0.000	0.712	0.34
	Current magnitude	0.830	1.186	0.015	1.08
	Chlorophyll-a (30-d lag)	2.693	1.676	0.045	1.84
	Mixed layer depth	0.004	0.001	0.520	0.25
	Random: time-of-day x ID	27.890	3.387	<0.001	24.4
	Total	-	-	-	28.00
Hourly dive rate	Hour-of-day (HST)	2.914		<0.001	-
	Moon phase	2.023		0.011	-
	Random: hour-of-day x ID	45.241		<0.001	-
	Total	-			14.70

2.10 Supplementary Materials

Table 2.4. Summary of primary analytical objectives and corresponding datasets used in the study.

Analysis	Tag type	Description of data used
Description of short-term, fine-scale dive behavior, comparisons across diel categories	TDR	All available dives (0- 230 m)
Description of long-term coarse-scale dive behavior, comparisons across demographic groups, diel categories, and spatial distributions	SPLASH	All available dives (≥ 50 m, ≥ 2 min)
Analysis of spatial and temporal predictors of dive behavior metrics (GAMMs)	SPLASH	All dives (≥ 50 m, ≥ 2 min) with estimated spatial uncertainty < 4 km.
Analysis of temporal predictors of dive behavior metrics (GAMMs; sensitivity assessment for data restriction above)	SPLASH	All available dives (≥ 50 m, ≥ 2 min)
Identifying probable near-seafloor dives	SPLASH	Dives (≥ 50 m, ≥ 2 min) from MHI and NWHI individuals only, with estimated spatial uncertainty < 4km; multiple imputations of dive locations restricted to dives with ± 100 m SD of seafloor depth

Table 2.5. Summary of dive information from five TDR tags deployed on false killer whales from the main Hawaiian Islands. Time at <50 m dives (%) represents the time the TDR individuals would have as "time at surface" as defined for the SPLASH satellite tags. PcTDR04 had a few dives exceeding the maximum value of the tag's depth sensor (approximately 230 m), and thus, while the dive durations are accurate, these dives were deeper than the reported value (indicated by the asterisk). Relative velocity is reported as uncalibrated units, given known influence of tag location and likely body size on swim speed measurements (see Baird et al. 2001).

			Metric mean (SD) / median / maximum				
Tag ID	Time at <50 m dives (%)	Number of dives (≥10 m)	Dive depth (m)	Dive duration (min)	Relative velocity (uncalibrated units)	Descent rate (m/s)	Ascent rate (m/s)
PcTDR01	100.0	7	13(5) / 11 / 22	1.5(0.4) / 1.7 / 2.0	0.5(0.4) / 0.5 / 3.5	0.5(0.2) / 0.4 / 0.9	0.7(0.3) / 0.6 / 1.1
PcTDR02	99.7	260	17(7) / 16/ 52	1.4(0.8) / 1.3 / 4.0	0.5(0.5) / 0.4 / 6.8	1.3(0.7) / 1.2 / 5.8	0.7(0.7) / 0.6 / 5.8
PcTDR03	99.2	35	17(10) / 13 / 53	1.1(0.5) / 0.9 / 3.0	1.9(0.7) / 1.9 / 6.9	1.3(0.6) / 1.2 / 2.6	0.9(0.3) / 1.0 / 1.9
PcTDR04	95.7	367	24(31) / 18 / 234*	2.4(1.7) / 1.9 / 12.0	0.9(0.9) / 0.8 / 6.6	0.8(0.5) / 0.7 / 4.8	0.5(0.4) / 0.5 / 5.1
PcTDR05	97.7	47	23(26) / 19 /180	1.8(0.7) / 1.7 / 3.6	-	1.0(0.6) / 0.9 / 3.1	0.7(0.6) / 0.6 / 3.6

Table 2.6. Summary of behavior data from SPLASH satellite tag deployments on both insular (MHI = Main Hawaiian Islands; NWHI = Northwestern Hawaiian Islands) and open-ocean false killer whales. Dive rate was calculated by dividing the total number of dives by the total duration of behavior log data (i.e., summed durations of surface and dive records, excluding gaps). All dive metric values are restricted to those dives of 50 m or deeper and 2 min or longer.

Population	Tag ID	% Time in "surface" periods (< 50 m)	Total # dives ≥ 50 m, ≥ 2 min	Dive depth (m) mean (SD) / median / max	Dive duration (min) mean (SD) / median / max	Dive rate (# dives ≥ 50 m/h)	# dives for spatial analyses (< 4 km error)
MHI							
	PcTag026	95.4	69	384 (259) / 424 / 1272	6.8 (2.9) / 6.4 / 14.7	0.41	53
	PcTag028	92.4	281	181 (150) / 112 / 728	6.1 (2.2) / 5.8 / 12.5	0.75	204
	PcTag030	94.6	303	251 (156) / 204 / 992	5.1 (1.9) / 4.9 / 11.2	0.63	267
	PcTag032	95.8	170	362 (269) / 316 / 1264	7.1 (3.6) / 6.6 / 18.7	0.35	131
	PcTag055	96.3	57	224 (223) / 128 / 816	6.0 (2.8) / 5.1 / 13.2	0.36	54
	PcTag074	97.1	84	221 (187) / 152 / 864	4.5 (2.4) / 3.8 / 11.8	0.40	84
	PcTag095	97.1	264	143 (96) / 120 / 752	4.2 (1.5) / 4.0 / 8.6	0.42	254
	PcTag099	97.0	191	277 (234) / 208 / 1136	5.8 (2.7) / 5.4 / 14.0	0.31	188
NWHI							
	PcTag035	96.5	53	369 (207) / 376 / 1040	6.2 (3.2) / 5.9 / 16.7	0.34	33
	PcTag037	96.2	96	298 (225) / 260 / 928	5.8 (3.2) / 4.8 / 15.2	0.39	86
	PcTag049	93.1	212	253 (186) / 172 / 1104	6.9 (2.8) / 6.4 / 18.2	0.61	121
	PcTag096	93.4	70	189 (146) / 132 / 640	5.2 (2.0) / 5.1 / 12.7	0.76	68
	PcTag097	95.5	79	252 (200) / 164 / 832	5.8 (2.8) / 5.3 / 13.6	0.46	77
Open-ocean							
	PcTag090	99.0	45	219 (196) / 132 / 896	5.0 (2.2) / 4.4 / 11.2	0.12	42
	PcTag092	96.4	32	295 (170) / 296 / 688	6.2 (2.5) / 6.2 / 12.4	0.36	30
	PcTagP09	89.5	106	780 (450) / 744 / 1424	11.9 (5.0) / 13.4 / 19.1	0.53	102

Table 2.7. Comparison of generalized additive mixed effects model performance between two different random effect structures (individual tag ID; random intercept versus random smooth) for each modeled dive behavior metric. Percent deviance explained and conditional AIC values are bolded for the highest performing model structure for each dive metric. Full model sets include both temporal and spatial predictors.

Model set	Modeled dive behavior metric	Random effect structure	% deviance explained	AIC
Temporal predictors only	Dive depth	Random intercept	27.2	26962.6
	Dive depth	Random smooth	**30.3**	**26916.4**
	Dive duration	Random intercept	24.2	26868.9
	Dive duration	Random smooth	**26.2**	**26851.8**
	Hourly dive rate	Random intercept	10.1	7788.4
	Hourly dive rate	Random smooth	**14.7**	**7672.6**
Full (spatial & temporal predictors)	Dive depth	Random intercept	30.2	22646.5
	Dive depth	Random smooth	**32.2**	**22633.9**
	Dive duration	Random intercept	26.3	22570.3
	Dive duration	Random smooth	**28.0**	**22567.4**

Table 2.8. Outputs of generalized additive mixed effects models examining relationships between dive behavior metrics and temporal predictors only. All dives (n =2,112) were included in these models.

Model	Covariate	EDF	F-value	p-value	Deviance explained (%) by covariate
Dive depth	Time-of-day (HST)	2.410	4.339	<0.001	0.02
	Moon phase	2.033	4.044	0.001	0.06
	Random: time-of-day x ID	40.124	4.454	<0.001	30.21
	Total	-	-	-	30.30
Dive duration	Time-of-day (HST)	0.938	0.516	0.017	0.01
	Moon phase	0.014	0.001	0.799	0.04
	Random: time-of-day x ID	33.649	4.558	<0.001	26.14
	Total	-	-	-	26.20

Table 2.9. Outputs of generalized additive mixed effects models examining relationships between dive behavior metrics and temporal and spatial predictors, but with data from PcTagP09 excluded (n = 1,673 dives). For dive depth and duration models, dives with positional uncertainty of 4 km and greater were removed prior to analyses. All dives were used for the hourly dive rate model (n = 2,006 dives). The percent deviance explained by covariates for the hourly dive rate model are not included, as there is currently no functionality to obtain this metric from a model that includes an offset term. EDF = estimated degrees of freedom.

Model	Covariate	EDF	F-value	p-value	Deviance explained (%) by covariate
Dive depth	Time-of-day (HST)	2.403	6.164	<0.001	0.00
	Moon phase	1.760	1.718	0.035	0.07
	Slope	1.980	1.918	0.012	0.16
	Current magnitude	2.040	5.500	<0.001	1.10
	Chlorophyll-a (30-d lag)	3.414	4.160	0.001	1.01
	Mixed layer depth	2.044	2.842	<0.001	0.27
	Random: time-of-day x ID	28.321	1.767	<0.001	18.49
	Total	-	-	-	21.10
Dive duration	Time-of-day (HST)	0.583	0.244	0.084	0.07
	Moon phase	0.006	0.001	0.508	0.01
	Slope	0.004	0.000	0.786	0.01
	Current magnitude	0.839	1.246	0.013	0.33
	Chlorophyll-a (30-d lag)	3.072	2.342	0.016	0.18
	Mixed layer depth	0.008	0.001	0.452	0.18
	Random: time-of-day x ID	26.011	1.826	<0.001	14.86
	Total	-	-	-	15.50
Hourly dive rate	Time-of-day (HST)	2.912	-	<0.001	-
	Moon phase	2.171	-	0.006	-
	Random: hour-of-day x ID	41.73	-	<0.001	-
	Total	-	-	-	15.0

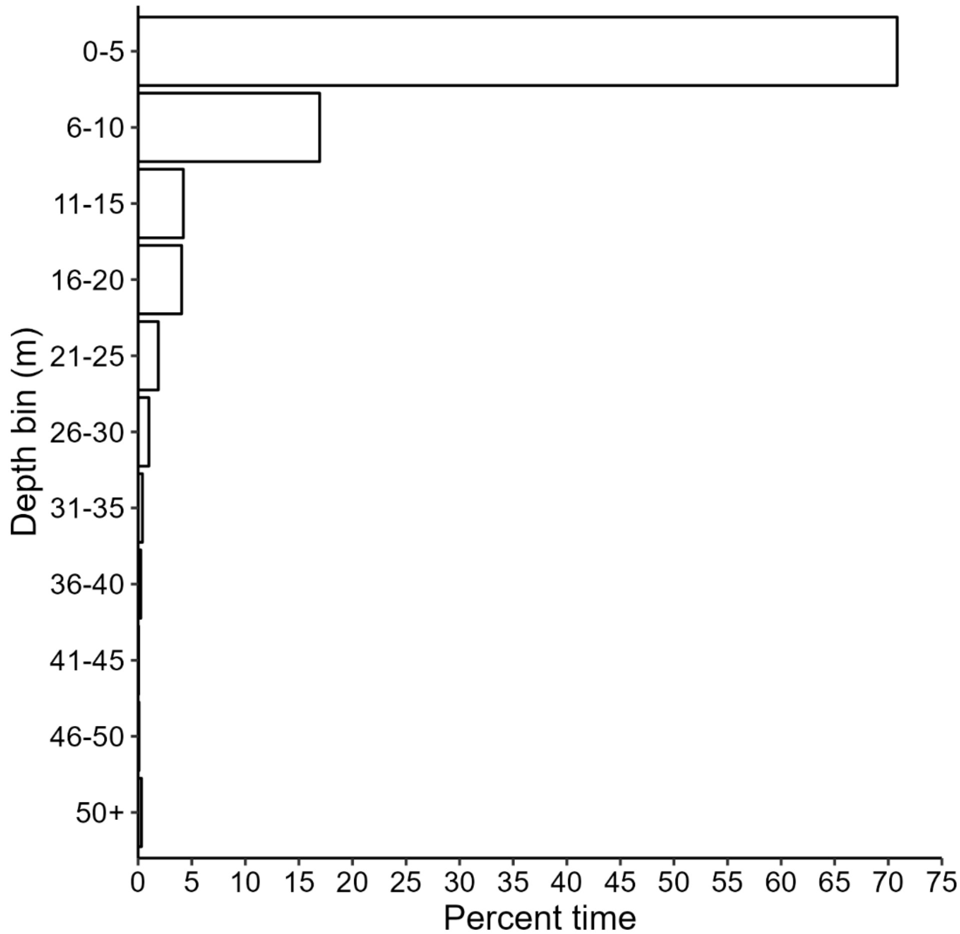

Figure 2.7. Proportion of total summed time spent at depth from five TDR tagged false killer whales belonging to the Main Hawaiian Islands population. Note: the last depth bin represents dives 50 m or deeper.

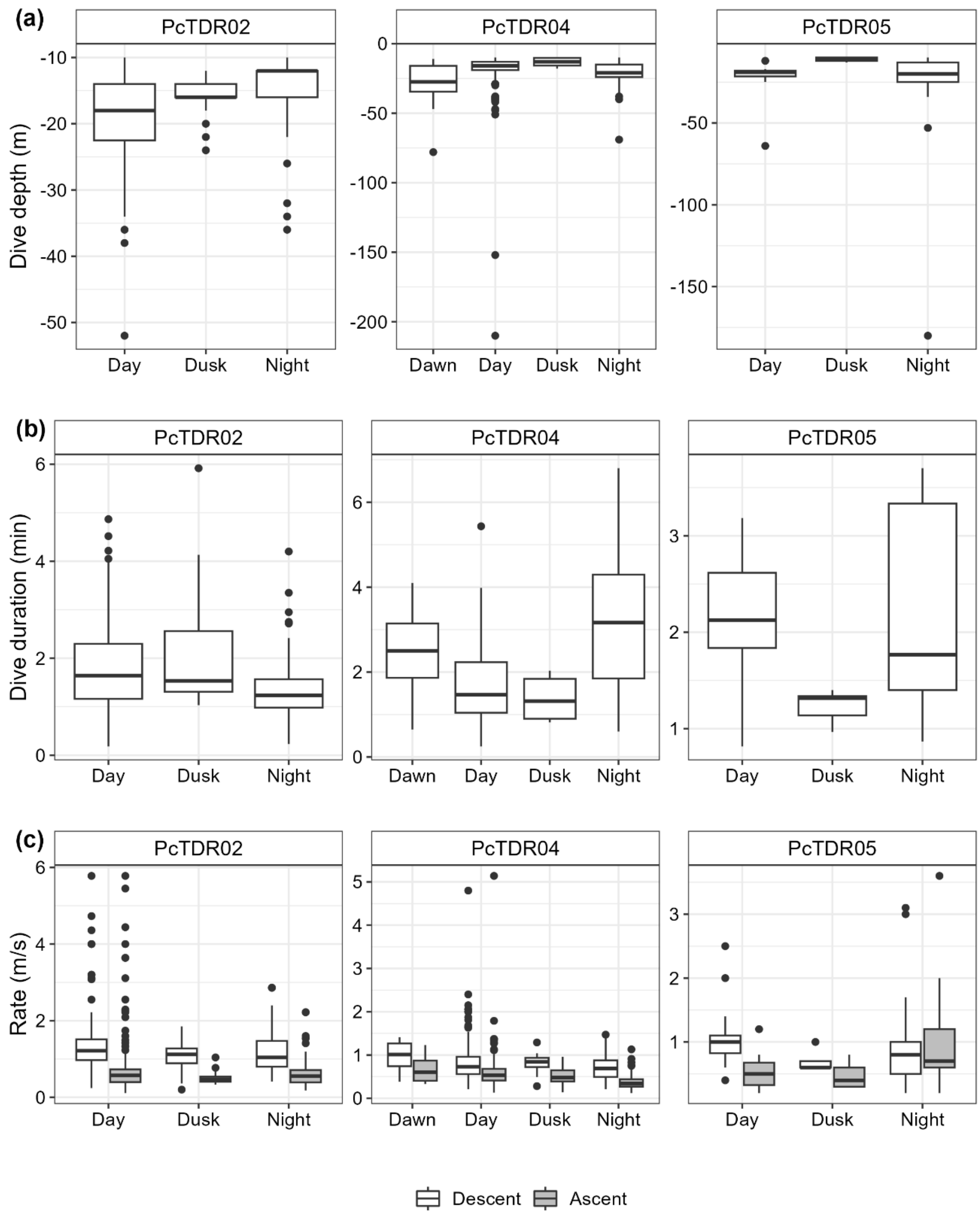

Figure 2.8. Box plots of (a) dive depth, (b) duration, and (c) ascent and descent rates across time of day (for dives ≥ 10 m) for PcTDR02, PcTDR04, and PcTDR05. Middle line shows median value, lower and upper lines of the boxes show 25th and 75th percentiles, respectively. The ends of the vertical line indicate minimum and maximum values, and outliers are indicated by black points.

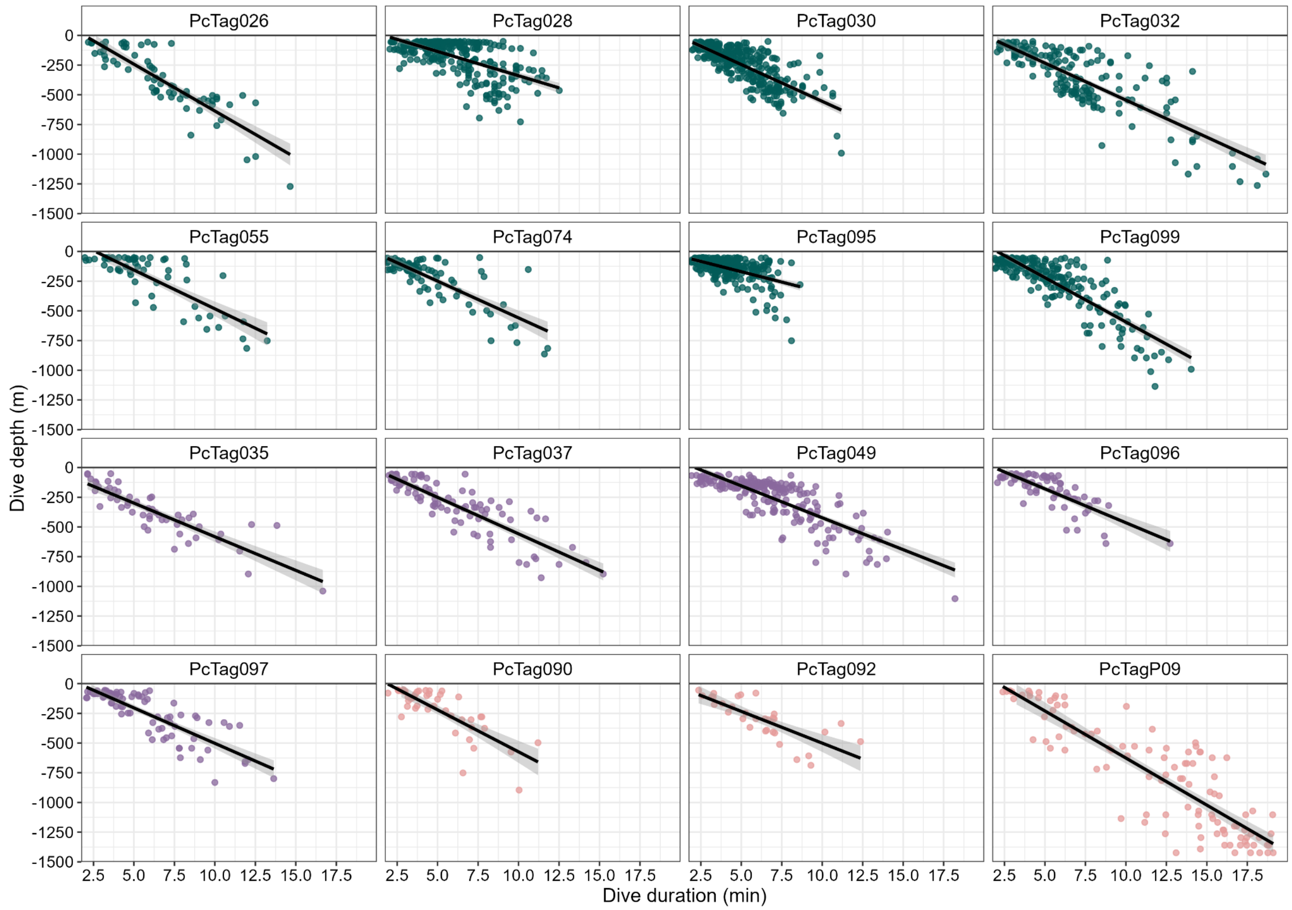

Figure 2.9. All dives (50 m or deeper, 2 min or longer) from SPLASH-tagged false killer whales by dive depth (y-axis, meters) and dive duration (x-axis, minutes). Panels are separated by individual, and points are colored by population (green = main Hawaiian Islands; purple = Northwestern Hawaiian Islands; pink = open-ocean). A linear smooth line (estimated from *ggplot2*'s geom_smooth() function) is shown for each individual.

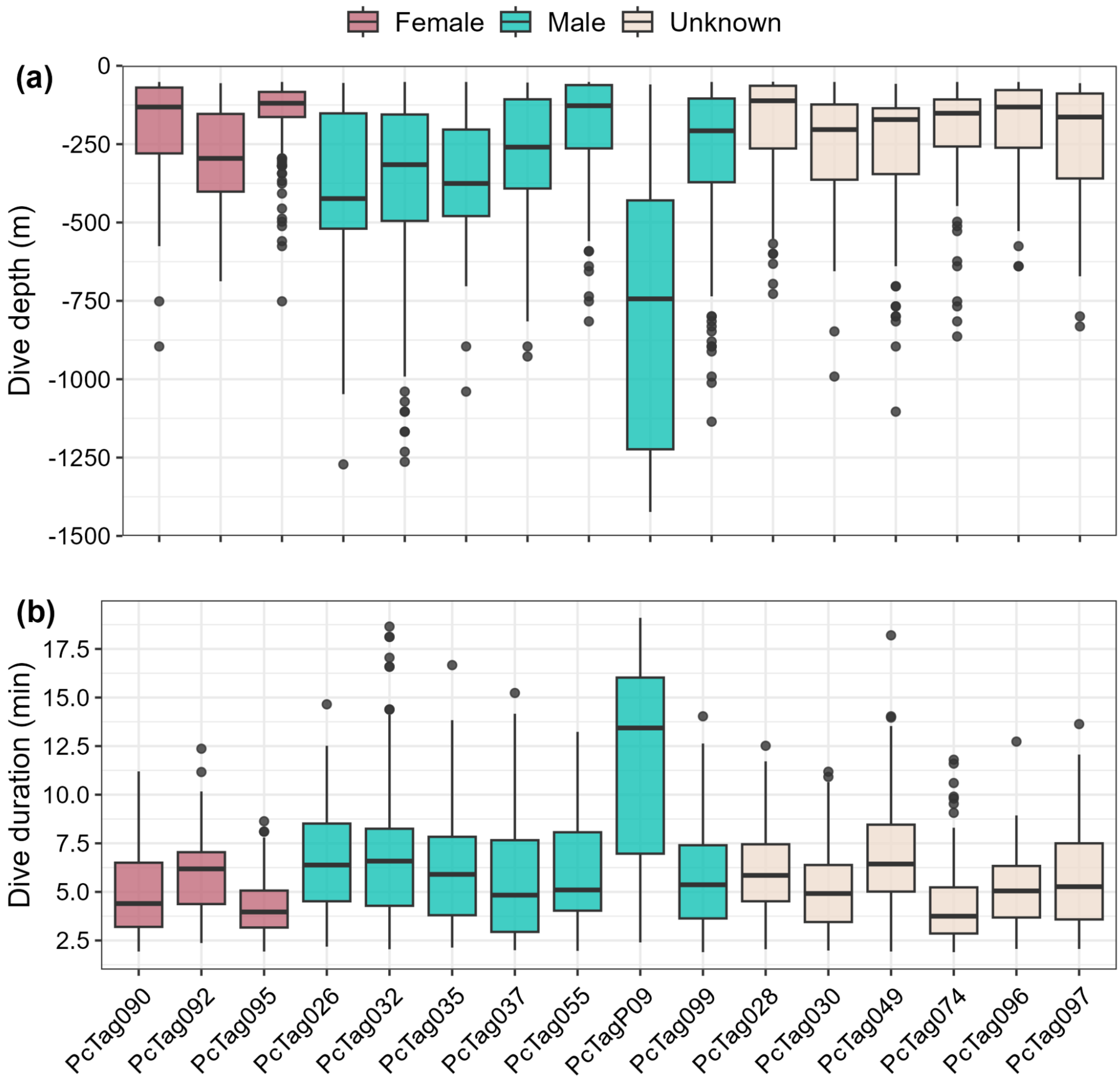

Figure 2.10. Boxplots of (a) dive depth and (b) duration of SPLASH-tagged false killer whales, colored by sex. The middle line in each box represents the median, the lower and upper extents of the box the first and third quartiles (respectively), the lower and upper whiskers the minimum and maximum (quartiles +/- 1.5*interquartile range), and any values outside of the box/whiskers are shown as points. See Table 1 for information on population identity.

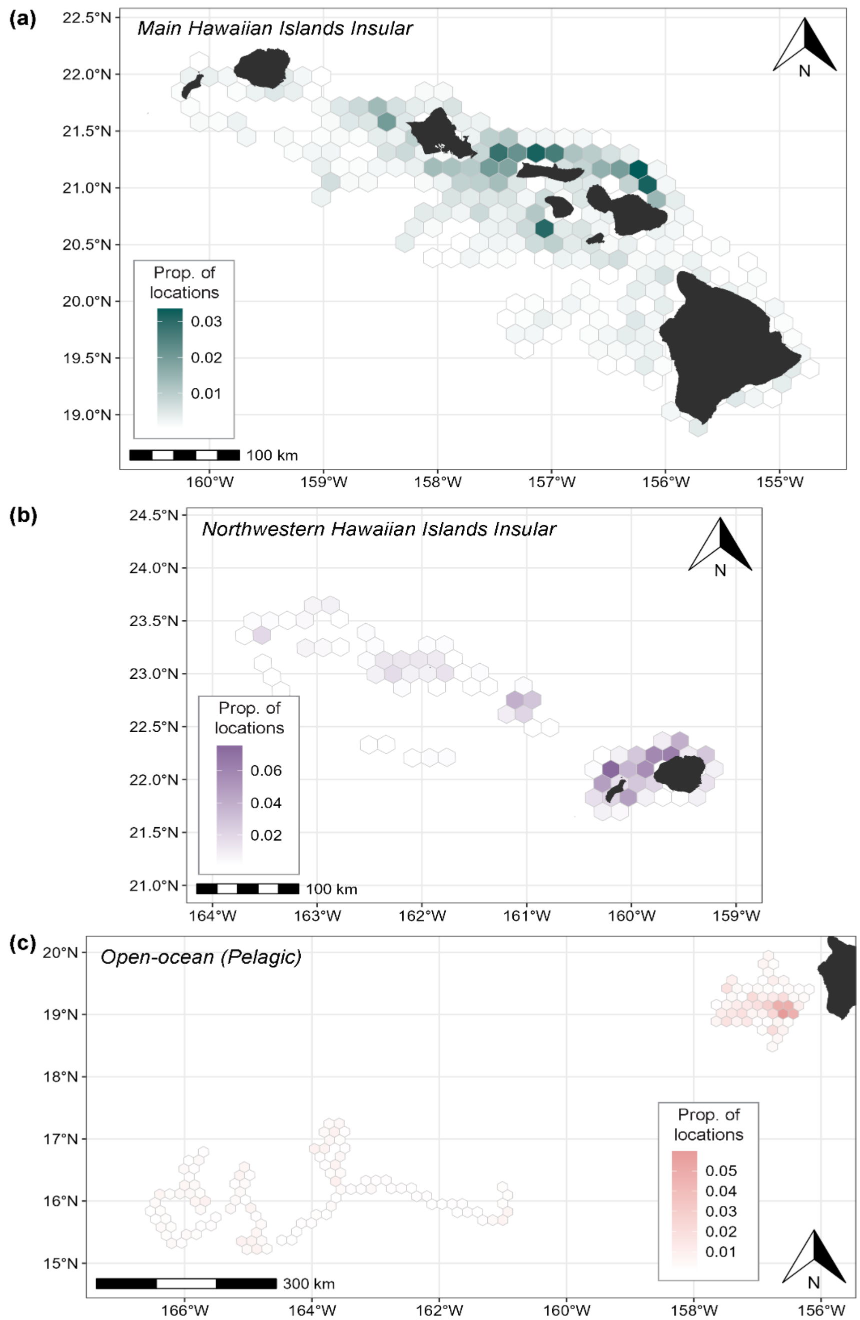

Figure 2.11. SPLASH satellite tag location density maps for (a) MHI insular, (b) NWHI insular, and (c) open-ocean false killer whales. Grids are colored by the proportion of all locations for that population contained within each cell. Original (i.e., non-interpolated) filtered locations were used, and only locations that occurred within the time range of available behavior log data.

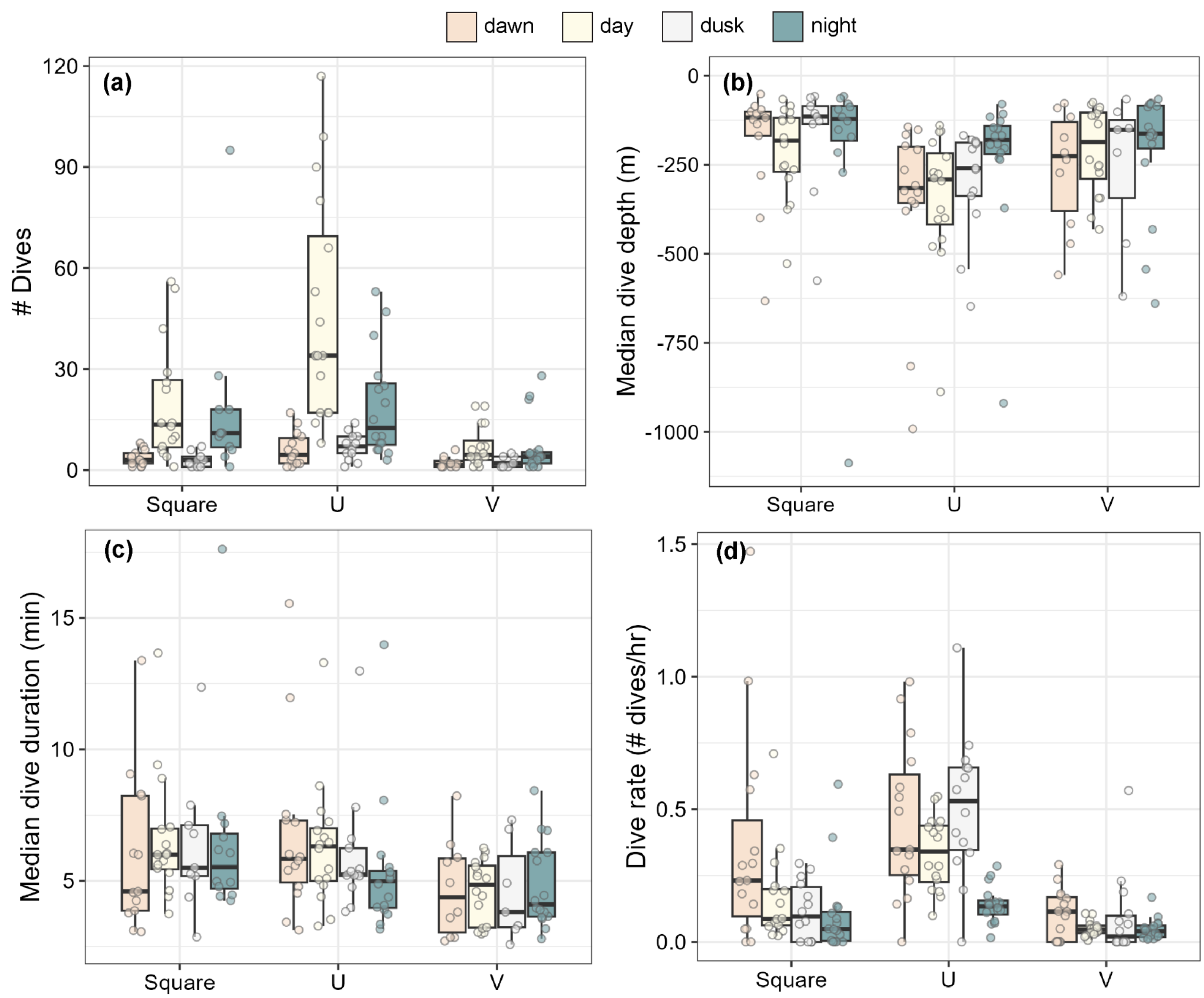

Figure 2.12. Dive metrics by dive shape and diel category; each jittered point represents a value for each individual (count or median of the individual). (a) the number of dives per category and shape; (b) dive depth; (c) dive duration; and (d) dive rate (number of dives per hour). All metrics represent dives 50 m or deeper and 2 min or longer. The middle line in each box represents the median, the lower and upper extents of the box the first and third quartiles (respectively), the lower and upper whiskers the minimum and maximum (quartiles +/- 1.5*interquartile range), and any values outside of the box/whiskers are shown as points.

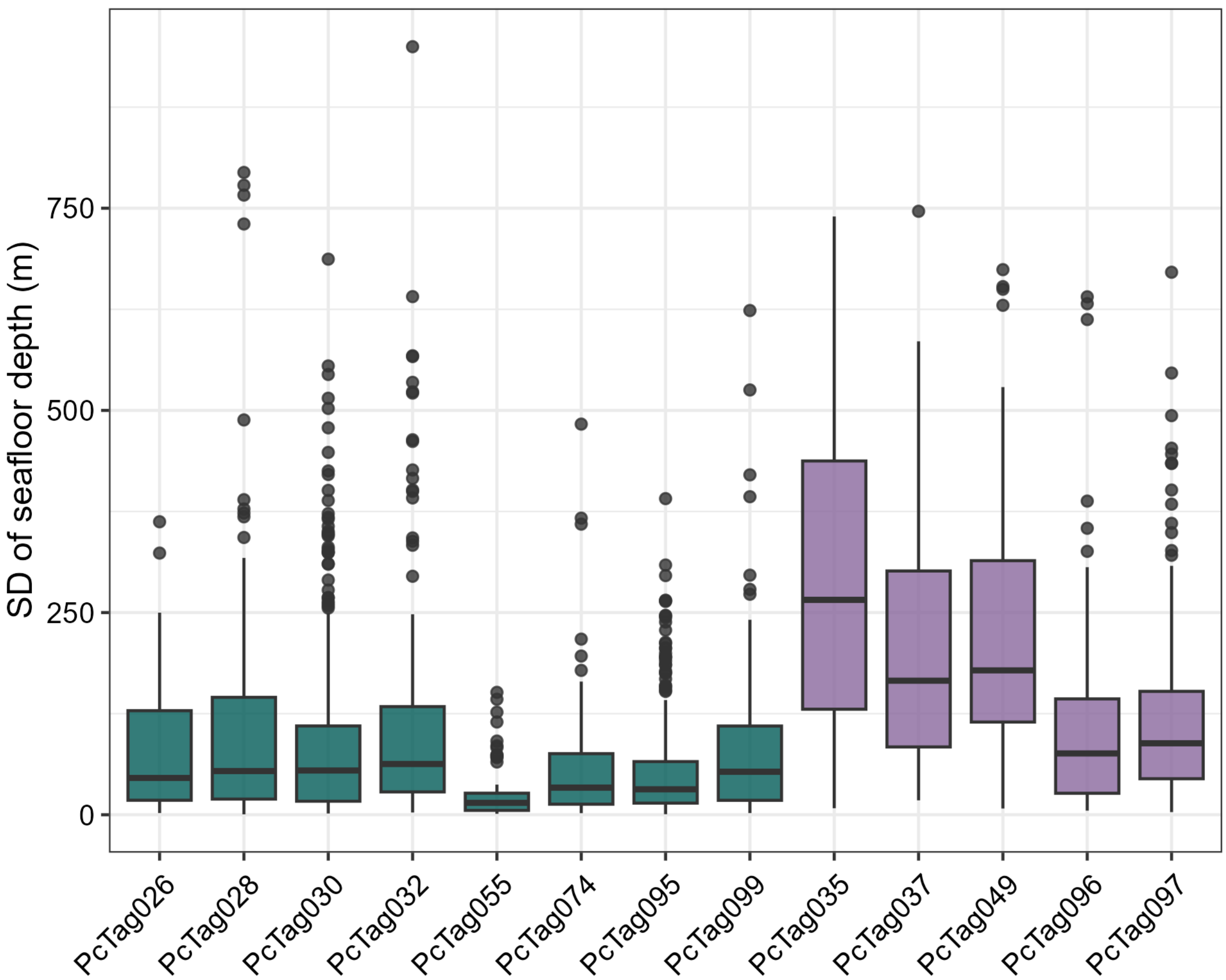

Figure 2.13. Distribution of standard deviation in seafloor depth values (calculated across all 20 imputed dive positions) for all dives with less than 4 km of positional uncertainty by insular false killer whales. This indicates that many are likely an artifact of positional uncertainty rather than truly benthic diving behavior. Boxplots are colored by population assignment (green = MHI; purple = NWHI). The middle line in each box represents the median, the lower and upper extents of the box the first and third quartiles (respectively), the lower and upper whiskers the minimum and maximum (quartiles +/- 1.5*interquartile range), and any values outside of the box/whiskers are shown as points.

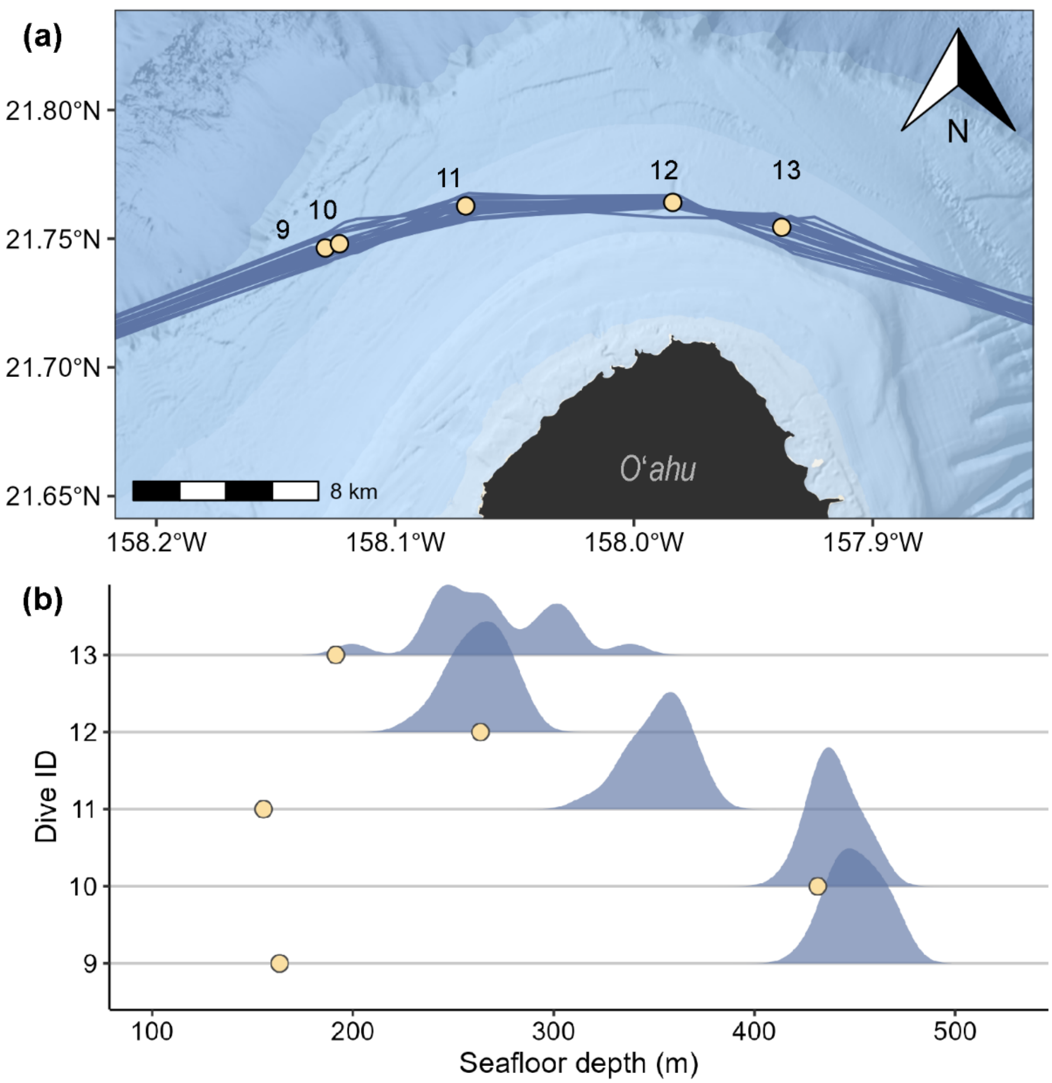

Figure 2.14. Example of using multiple imputations of dive locations to assess relationships between dive depth and seafloor depth using data from false killer whale tag deployment PcTag074. (a) Map of locations of five dives with estimated locations (yellow circles) and the 20 imputed tracks (gray lines). (b) Density plots of seafloor depth values across the 20 imputed dives (blue shaded density curves) and the recorded dive depth (yellow circle) for each of the dives shown in panel (a). Dives 9 and 11 were much shallower than the seafloor depth, while the remaining dive depths overlapped with their seafloor depths; dives 10 and 12 are probable seafloor dives, while dive 13 has higher uncertainty.

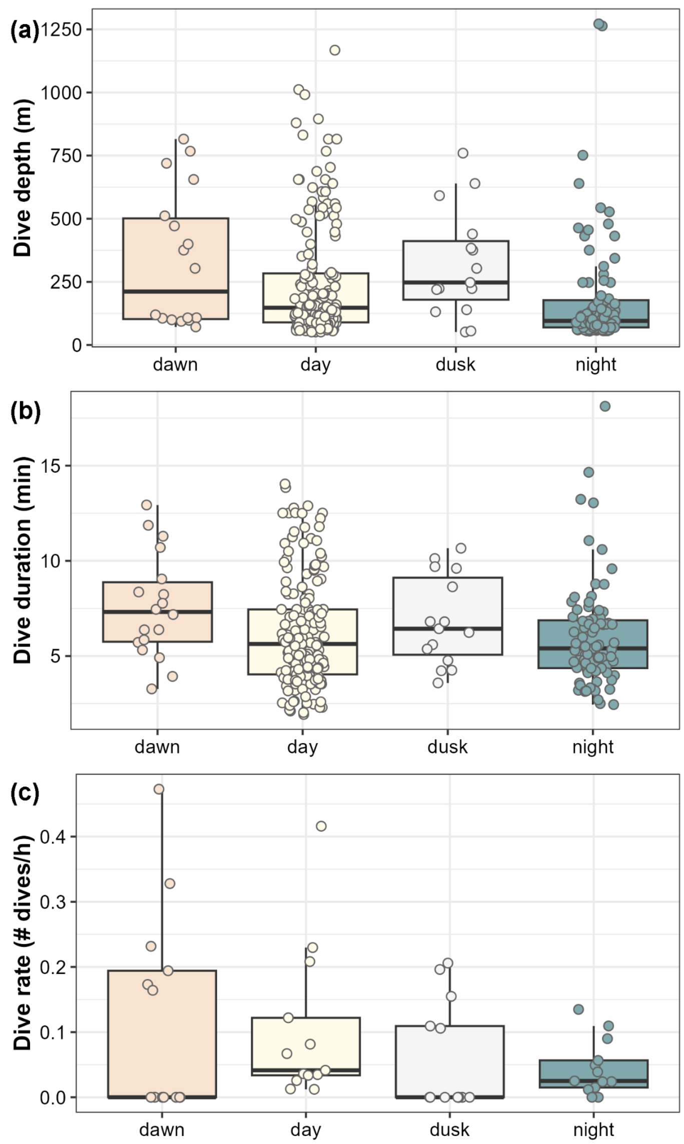

Figure 2.15. Distribution of (a) dive depths, (b) durations, and (c) rates of probable near seafloor dives by diel period for MHI and NWHI insular false killer whales. For dive rates (c), each point represents a single individual (as in Figure 5a), and thus the number of points across diel categories is the same in this panel. The middle line in each box represents the median, the lower and upper extents of the box the first and third quartiles (respectively), the lower and upper whiskers the minimum and maximum (quartiles +/- 1.5*interquartile range). Data points are plotted as jittered points.

3. SCALE-DEPENDENT FEEDBACK BETWEEN SPACE USE AND SOCIALITY IN A LONG-LIVED MARINE PREDATOR

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3.1 Abstract

Spatial and social behaviours in animals are intertwined, yet the causal direction of this feedback—and how it varies across scales—remains largely unresolved. Using long-term data from false killer whales (*Pseudorca crassidens*) in the main Hawaiian Islands, we developed and applied a scale-explicit analytical framework to test how social reliance and resource ephemerality govern top-down versus bottom-up processes linking movement and sociality. Movements, association networks, genetic relatedness, and isotopic niches reveal that strong social bonds drive bottom-up emergence of short-term intra-group movements, while ephemeral and likely island-associated prey landscapes impose top-down constraints on inter-group dynamics across scales. These complementary processes generate persistent, fine-scale fidelity within some groups and relatively well-differentiated feeding niches among them. Our findings highlight a general mechanism by which life-history strategies and environmental stochasticity jointly determine the scale and direction of feedback between space use and sociality—shaping population structure and connectivity in mobile social predators.

3.2 Introduction

Animal space use and social behaviour are both shaped by and feed back onto their spatial and social environments (Webber et al., 2023). Individual movements depend on the distribution of resources and risks in the spatial environment; this resulting space use determines opportunities for social interactions because individuals can interact if they share the same space (i.e., a top-down effect; Farine, 2015; Macdonald and Johnson, 2015). At the same time, individuals might incorporate social information indirectly (e.g., eavesdropping on cues) or directly (e.g., tracking signals and cooperating) to find food (Aplin et al., 2012), initiate movements (Oestreich et al., 2022), and avoid predators (Atkinson et al., 2025) or competitors (Mourier et al., 2024). Thus, space use inherently emerges from social processes. Inferring the direction of causality in this feedback—whether space use shapes social behaviours or *vice versa*—is critical, given the implications for both immediate effects on survival and long-term consequences for population structuring and persistence (Farine et al., 2015a; Webber and Vander Wal, 2018). Recent conceptualisation of scale-dependence in this spatial-social interface provides a framework for disentangling causal directions, specifically top-down (i.e., coarse scale spatial/social components constrain fine-scale behaviour) versus bottom-up processes (i.e., fine-scale spatial/social components give rise to coarse-scale behaviour; Picardi et al., 2024). However, there is limited empirical understanding of what biological or ecological characteristics mediate the predominance of top-down versus bottom-up effects, and how this scale-dependent directionality relates to both short- and long-term consequences.

The degree of dependence on conspecifics throughout an individual's lifespan (hereafter, "social reliance") provides a foundation for identifying scale-dependent bottom-up and top-down processes in the spatial-social interface. In several species that forage alone, interactions between individuals result from resource-driven co-occurrence (i.e., predominance of top-down effect of spatial on social behaviour; Carr and Macdonald, 1986; Newsome et al., 2013), while drivers of interactions in species that live in societies with high fission-fusion dynamics (i.e., where individuals frequently split parties and merge again) can be context-dependent (e.g., influenced by resource heterogeneity; Peignier et al., 2019; Ramos-Fernández et al., 2006). In contrast, bottom-up emergence of space use from social processes should be predominant in species that rely on group members to overcome most life-history challenges (Krause and Ruxton, 2002a). This is especially the case in long-lived and predominantly matrilineal species with advanced cognitive abilities, as longevity enables investment in differentiated social relationships that directly benefit survival (Brent et al., 2015; McComb et al., 2011; Silk and Hodgson, 2021). Inherent in the spectrum of social reliance is resource availability: predictable and defensible resources (e.g., prey) and risks (e.g., predation) can reduce social reliance, whereas heterogenous and ephemeral resource and risk landscapes can increase social reliance (Gaynor et al., 2019; Kohles et al., 2022; Kun and Dieckmann, 2013; Macdonald and Johnson, 2015). Thus, on an evolutionary timescale, ecological dynamics have shaped species-level diversity in social complexity (Krause and Ruxton, 2002a); in contemporary contexts, this established social reliance, combined with variation in the environment, likely mediates the predominance of causal directions in the spatial-social interface.

The synergistic effects of social reliance and resource ephemerality on animal spatial and social behaviour can have implications for long-term population dynamics. Specifically, where long-term variability in spatial (e.g., resource availability) and social environments (e.g., population density) results in unequal fitness among individuals (Bolnick et al., 2003), niche variation (e.g., habitat or diet specialisation, site fidelity) can develop at individual- (e.g., Sheppard et al., 2018; Strickler, 1979) or group-levels where social reliance is strong (e.g., De Stephanis et al., 2008; Eguiguren et al., 2019). Within-population niche variation can influence the distribution of individuals or groups, and consequently, the probability of inter-individual or inter-group interactions that give rise to population-level social structure (Araújo et al., 2011; He et al., 2019; Webber et al., 2024). This population-level outcome reciprocally influences how individuals navigate their spatial and social environments in the short term (e.g., days to weeks; Cantor et al., 2021; Farine et al., 2015a). Collectively, this implies that causal directions between spatial and social processes could structure a feedback loop linking short-term individual-level patterns with long-term population-level consequences (Figure 3.1). While similar eco-evolutionary feedback mechanisms have been proposed (Webber and Vander Wal, 2018), there has yet to be an explicit examination of how causal directions and scale-dependence regulate this feedback. Identifying the scales at which causal directions are predominant in this feedback would not only shed light on evolutionary causes and consequences in the spatial-social interface but also help elucidate relevant units of conservation and a population's adaptability to environmental change.

We empirically explored the scale-dependent feedback between bottom-up and top-down effects on the spatial-social dynamics of a strongly social and long-lived apex predator, the false killer whale *Pseudorca crassidens*. We developed a multi-scale analytical framework combining longitudinal information on social structure, movements, trophic ecology, and genetic relatedness on a small and endangered population occurring around the main Hawaiian Islands. Dyadic social bonds and group membership were obtained from long-term photo-identification (Mahaffy et al., 2023) and related to movements inferred from satellite-linked transmitters to derive individual-level spatial behaviours and group-level spatial niches. We used stable carbon and nitrogen bulk isotope analysis from skin biopsy samples to characterize group-level trophic niches and relative dietary contributions of prey. We then used these movement, social, and niche metrics to test our predictions that the longevity and strong social reliance of false killer whales would result in bottom-up emergence of within-group spatial behaviour in the short-term (Figure 3.1-i), while resource ephemerality and their island-associated habitat configuration would promote/impede between-group interactions in both the short-term (spatial partitioning) (Figure 3.1-ii) and long-term (niche variation) (Figure 3.1-iii), with consequences on relatedness and population structure (Figure 3.1-iv).

3.3 Methods

3.3.1 Study system

False killer whales live into their 60s, are slow to mature, invest significant care into rearing offspring, and are one of a few non-human species that undergo reproductive senescence (Ellis et al., 2024; Ferreira et al., 2014; Photopoulou et al., 2017). This species is resident around the main Hawaiian Islands and have been studied since the late 1990s (Baird et al., 2008a). The population is small and declining (<160 individuals; Badger et al., 2025), and is listed as endangered under the U.S. Endangered Species Act. The population is structured into four stable social groups (hereafter clusters) comprised of kin and non-kin associates (Mahaffy et al., 2023). Mating occurs both within and between clusters, and natal fidelity to clusters is strong (Martien et al., 2019). While the marine environment around the main Hawaiian Island is generally considered oligotrophic, the island-mass effect promotes enhancement of biological productivity, resulting in more consistent prey availability for marine predators (Gove et al., 2016). False killer whales' prey landscape is, however, much more ephemeral; many of their known prey—such as tunas, billfish, mahimahi *Coryphaena hippurus*—are highly migratory, fast, and difficult to capture. In response, false killer whales undertake extensive movements (up to 150 km/day), cooperatively hunt, and share prey with group members (Baird et al., 2010, 2008a; Bradford et al., 2014).

3.3.2 Empirical data

3.3.2.1 Satellite tagging and tissue sampling

Empirical data types and processing workflows are summarized in Figure 3.6 (Supplementary Material). Satellite tagging and biopsy sampling were undertaken during small boat-based surveys in Hawai‘i from 2000 to 2025 (Baird et al., 2024, 2013b). Tagging (Baird et al., 2012, 2010), biopsy sampling (Ylitalo et al., 2009), stable isotope (Kratofil et al., 2020; Supplementary

Material), and genetic (Martien et al., 2019, 2014) laboratory procedures followed standard protocols.

3.3.2.2 Deriving individual-level traits

Photographs of all tagged and biopsy sampled individuals were matched to a long-term photo-identification catalogue to determine individual identity and social cluster membership (Baird et al., 2008a; Mahaffy et al., 2023). We used a temporally-constrained half-weight index (HWI) as a metric for dyadic associations, which accounts for periods when individuals' sighting histories overlapped (Whitehead, 2009). Sex was either determined genetically from biopsies, inferred from morphological (e.g., head shape) or social characteristics (i.e., individuals consistently accompanied by calves), or assigned as "unknown". Age class was determined from photo-identification-derived metrics (see Kratofil et al., 2026b). Movement was tracked using satellite-linked transmitters (n=69 deployments; median transmission time=41 days, range=9-229; Cluster 1, n=31 deployments/25 individuals; Cluster 2, n=9/9; Cluster 3, n=20/20; Cluster 4, n=9/8). The bulk stable carbon and nitrogen isotopes dataset included 80 samples (Cluster 1, n=27 samples/22 individuals; Cluster 2, n=22/22; Cluster 3, n=12/10; Cluster 4, n=19/19). Pairwise genetic relatedness was available for a subset of tagged individuals (n=23) and calculated using the data and methods from Martien *et al.* (2014, 2019).

3.3.3 Quantifying individual-level spatial metrics

We derived individual-level spatial metrics (movements, ranges, habitat selection) from satellite tracks as the basis for subsequent analyses (Figure 3.6, Supplementary Material). All analyses were completed in R v4.5.0 (R Core Team, 2025). Tag location data were processed following Kratofil et al. (2023) and subsequently fit to continuous-time movement models using the *ctmm* and *ctmmUtils* packages (Fleming and Calabrese, 2023; Johnson and London, 2025; Supporting Information). All models described in the following sections follow the same fitting (see Supporting Information) and performance check procedures (e.g., R-hat values<1.05, mixing of chains, and posterior predictive checks) unless otherwise specified.

We characterized the spatial ranges used by tagged individuals through optimally weighted and area-corrected autocorrelated kernel density estimators (wAKDE UDs) in the *ctmm* package (Fleming and Calabrese, 2023), which accounts for irregular sampling in time (Fleming et al., 2018; Silva et al., 2022). Because these tracks only reflect a comparatively brief portion of an individual's life, we refrain from referring to these ranges as "home ranges", which reflect long-term space use (Péron, 2019). We defined core ranges as the 50% isopleth of the wAKDE UD.

We quantified individual-level habitat selection through a "used-available" framework within each tagged individual's spatial range (i.e., third order, Manly et al., 2002), which we defined as the 95% isopleth of their wAKDE UD. Tag locations represented "used" locations, and "available" locations were randomly sampled within each individual's spatial range at a 1:20 ratio (Northrup et al., 2013). We used 6-hourly locations (predicted using *ctmm*) to mitigate autocorrelation effects while also reflecting a relevant scale of habitat selection given false killer whale movement rates. Locations with error ellipses greater than 20 km were removed prior to modelling. Environmental variables related to biological productivity were extracted for each location; where two variables were correlated (Pearson's correlation>0.5), only one was included for subsequent modelling, and selected based on the most direct ecological interpretation (Table 3.1, Supplementary Material). Resource selection functions (RSFs) were fit as logistic regressions (Bernoulli distribution with logit link; Table 3.2, Supplementary Material; Manly et al., 2002) in the *brms* package (Bürkner, 2018).

3.3.4 Short-term within-cluster emergence and between-cluster overlap of space use

To test predictions (i) and (ii) (Figure 3.1), we compared spatial metrics of individuals tracked simultaneously in relation to their pairwise HWIs and cluster membership. We first calculated the pairwise distances between temporally overlapping tracks using the *ctmm* package (Fleming and Calabrese, 2023). We then modelled pairwise median distance apart in relation to HWI using a Bayesian generalized linear mixed effects model (bGLMM) in *brms* (Bürkner, 2018) with a gamma response distribution (log link) and multi-membership random effect for the pair of catalogued identifications (Hart et al., 2022; Table 3.2). We limited the dataset to individuals sighted five or more times.

We then selected seven periods with reasonable coverage of tagged individuals (1-4 months) within the same cluster or of different clusters to examine all spatial metrics. For these cases, we truncated tracks so that all tracks covered the exact same period; all spatial metrics were re-calculated with these equal-length tracks and qualitatively assessed (Figure 3.1). Overlap between spatial ranges was estimated using the bias-corrected Bhattacharyya's coefficient (BC) within the *ctmm* package (Fleming and Calabrese, 2023; Winner et al., 2018). To estimate overlap between core ranges, we first calculated the area of intersection between core range polygons using the *sf* package (Pebesma, 2018), and then defined overlap as two times the ratio of this area out of the combined core range areas for each pair.

3.3.5 Long-term within-cluster fidelity and between-cluster overlap

For prediction (iii) (Figure 3.1), we quantified long-term spatial and core range overlap (described above) between all pairs of tagged individuals across the entire study period. We fit bGLMMs to model spatial range overlap (BC; beta distribution, identity link function) in relation to unique cluster pairs (e.g., C1-C1, C1-C2, etc.) and a multi-membership random effect for each pair of individuals. We also included fixed effects for year (same/different) and difference in transmission duration (scaled) to account for any effects these variables may have on our inferences. We ran separate models on a subset of dyads for which pairwise genetic relatedness information was available to assess the potential influence of genetic similarity on space use (Table 3.2). We excluded pairs where the mean overlap estimates suggested range overlap (BC >0.5) but there was low confidence in this estimate (lower CI <0.1; Winner et al., 2018). The same model was fit for core range overlap, albeit with a zero-inflated beta distribution (Table 3.2).

We additionally assessed spatial fidelity by comparing spatial metrics within six individuals that have been tagged more than once during the study period. Within each individual, we truncated their unique tracks to the length of the shortest track and recalculated spatial metrics (following section 3.3.4).

3.3.6 Long-term cluster-level spatial and dietary niches

3.3.6.1 Spatial niches

We derived cluster-level home ranges from individual-level wAKDE UDs using the *ctmm* package (Fleming and Calabrese, 2023) and considered the 50% isopleth of these outputs as the cluster-level core range. Cluster-level home and core range overlap were determined following the same overlap methods described in section 3.3.4.

Cluster-level habitat selection was estimated using a two-stage approach following Johnson *et al.* (2022). The individual-level RSFs from section 3.3.3 constituted the first stage; posterior means and covariance matrices were extracted from the posterior samples and subsequently modelled as observations in a meta-mixed effects regression model (with a multivariate normal distribution) in relation to cluster membership and a random effect for tag ID; models were fit using the *mixmeta* package (Sera et al., 2019).

3.3.6.2 Isotopic niches and diet estimates

No temporal or demographic effects on $\delta^{13}C$ and $\delta^{15}N$ values were found (Supporting Information). We estimated bivariate ($\delta^{13}C$ and $\delta^{15}N$) isotopic niche space (95% probability overall region) and pairwise niche overlap (95% and 40% probability region) among social clusters using the *nicheROVER* R package (Lysy et al., 2023; Swanson et al., 2015).

We used stable isotope mixing models to estimate the relative dietary proportions of prey among social clusters. $\delta^{13}C$ and $\delta^{15}N$ values of 13 known false killer whale prey were compiled from the literature (Table 3.6, Supplementary Material) and aggregated into groups *a posteriori* to increase the discrimination power and interpretability of the mixing model (Phillips et al., 2014, 2005; Stock et al., 2018). We defined four groups based largely on ecological and functional traits (Table 3.7, Supplementary Material): (1) epipelagic predatory fish; (2) mesopelagic predatory fish; (3) reef-associated predatory fish, and (4) mesopelagic cephalopods. Mixing models were fit using the *MixSIAR* package (Stock et al., 2018; Stock and Semmens, 2016), with social cluster used as a random effect. We ran models with 300,000 iterations (200,000 burn-in, thinned every 50 samples) over three Markov chain Monte Carlo (MCMC) chains. Model convergence was checked using the R-hat (estimates <1.05) and Geweke diagnostic values ($<5\%$ of estimates less than $\pm$ 1.96).

3.3.7 Population connectivity

To assess prediction (iv), we derived the conditional distribution of encounters (CDE) across all individuals, which identifies areas with the highest probability of individuals encountering one another (Fleming and Calabrese, 2023; Noonan et al., 2021). We then mapped cluster-level core ranges on top of the population-wide CDE and descriptively related CDE hotspots to core range overlaps and the composition of mitochondrial haplotypes among clusters (Mahaffy et al., 2023).

3.4 Results

3.4.1 Short-term space use is an emergent property of social bonds

Pairs of tagged false killer whales (n=80 pairs with ≥10 d overlap) that were more strongly associated were more spatially cohesive (posterior median of bGLMM coefficient: -4.51, 95% credible interval (CrI): [-5.64; -3.36]; Figure 3.2; Table 3.3, Supplementary Material). There were some pairs who were associates (Half-weight index, or pairwise social association strength>0.2) in the same cluster (either Cluster 1 or 3) but did not remain spatially associated throughout their common tracking period (Figure 3.7, Supplementary Material). A single pair involving individuals from different clusters (Clusters 1-3) had a median distance of less than 10 km over 10 days. Pairs from Clusters 2 and 4 exhibited cohesive movements more than that observed for Clusters 1 and 3 (Figures 3.7, 3.8, Supplementary Material). Even when same-cluster pairs were not consistently spatially associated, spatial fidelity persisted (Figure 3.3a,b), and RSF coefficients were highly similar (Figure 3.3c,d; Figure 3.8, Supplementary Material).

3.4.2 Short-term spatial partitioning between social clusters

Spatial overlap between clusters was typically low during restricted periods (Figure 3.3e-l; Figure 3.8, Supplementary Material). Where overlap occurred, individuals of different clusters rarely, if ever, encountered one another. For example, individuals from Cluster 3 and Cluster 4 had high range overlap, but only occasionally came within 5 km of one another (Figure 3.3i-l). RSF coefficients between clusters during restricted periods were similar; while variation in individual coefficient estimates occurred, the 95% CrIs between individuals were highly overlapping (Figure 3.3e-l; Figure 3.8, Supplementary Material).

3.4.3 High short-term spatial and dietary overlap but distinct long-term core niches

Long-term within-cluster fidelity and between-cluster spatial overlap were high (Figure 3.4a). Pairwise cluster membership (i.e., CX-CY) had the strongest effect on spatial range overlap, specifically pairs from Cluster 4 (Figure 3.4a; Table 3.3, Supplementary Material). Cluster 4 also exhibited the lowest posterior mean, but the largest posterior uncertainty in range fidelity (Figure 3.4a). Core range fidelity and overlap were lower than that for spatial ranges (Figure 3.4a). Within-cluster fidelity was highest for Clusters 2 and 4 (albeit with overlapping credible intervals), and between-cluster overlap was lowest between Cluster pairs 1-4, 2-4, and 3-4 (Figure 3.4a). For both models, there was either no (core) or minimal (spatial) estimated effect of tag duration difference on overlap, while overlap was higher between pairs tagged in the same year (Table 3.3, Supplementary Material). There was no evidence for an effect of genetic relatedness on spatial nor core range overlap for relevant pairs (Table 3.3, Supplementary Material).

Cluster-level home ranges were variable in size and overlap (Figure 3.4a,b). Clusters 1 and 3 had the largest home ranges and Clusters 2 and 4 had the smallest (Figure 3.4b). There were minor differences in RSF coefficients between clusters, however, confidence intervals almost always overlapped (Figure 3.4c). Selection for shallower waters dominated habitat selection patterns (*depth*: Figure 3.4c), while selection for dynamic habitat features was minimal at this scale (Figure 3.4c). Cluster-level isotopic niches highly overlapped among all clusters (Figure 3.4d; Table 3.5, Supplementary Material). Isotopic niche spaces were similar in size among Clusters 1, 2 and 3, whereas Cluster 4 had a wider isotopic niche, mainly driven by a broader range in δ^{13}C values (Figure 3.4e). Estimated prey contributions were similar among clusters—leading with epipelagic predatory fish, then mesopelagic predatory fish, and small proportions (<20%) of reef-associated predatory fish and mesopelagic cephalopods (Figure 3.4f; Table 3.8, Supplementary Material). Clusters 1 and 2 had slightly higher proportions of mesopelagic predatory fish compared to the other clusters, while Clusters 3 and 4 had slightly higher proportions of epipelagic predatory fish (Figure 3.4f). These results were robust to prey grouping choices and source data (Supplementary Material).

Within-individual spatial range fidelity was variable. Only three of six individuals had high overlap between successive spatial ranges (HIPc145, HIPc202, HIPc272; Figure 3.9, Supplementary Material), one of which was tagged three times (HIPc145) and only the third range was more disparate (Figure 3.9, Supplementary Material).

3.4.4 Range-wide hotspots and habitat structure mediate between-cluster dynamics

The CDE revealed two primary areas where false killer whales are most likely to co-occur: one off northwestern Hawai‘i Island (including the ‘Alenuihāhā Channel) and the other being the Kaiwi Channel, between O‘ahu and Moloka‘i, both of which are characterized by high wind stress and current velocity (Figure 3.5). The core ranges of Cluster 1, 2, and 3 overlapped with the region off Hawai‘i Island, while those of Cluster 1, 3, and 4 included the Kaiwi Channel hotspot (Figure 3.5). Clusters 3 and 4 have only mitochondrial haplotype 1, while Clusters 1 and 2 have both haplotype 1 and 2 (Mahaffy *et al.* 2023).

3.5 Discussion

Using a novel scale-explicit conceptual framework with a longitudinal study of false killer whales, we demonstrated how strong sociality yields bottom-up emergence of intra-social cluster spatial behaviour from social bonds in the short term, while their ephemeral resource landscape regulates both short- and long-term inter-cluster dynamics. Most importantly, we show how these bottom-up and top-down processes may synergistically affect long-term population structure.

3.5.1 Social reliance mediates bottom-up emergence of spatial behaviour

As we hypothesised, false killer whale dyads that have stronger associations tended to move more cohesively. In highly social animals, movements reflect collective decisions and coordination among group members (Strandburg-Peshkin et al., 2015), a process that requires some level of spatial cohesion (Conradt and Roper, 2005). Spatial cohesion is especially important for predators that cooperatively hunt, share prey, or care for offspring (Hansen et al., 2023), as effective group coordination underlies individual success and survival. Consequently, cohesive movements should arise from the social bonds that form from the reliance on group members for these behaviours, and our findings are consistent with this expected directionality. By using longitudinal re-sightings data to measure pairwise social association strength, we captured bonds between individuals at time scales relevant to this long-lived species. Paired with snapshots of movements from satellite-linked transmitters, our findings validate the influence social reliance on short-term movement patterns. While spatial cohesion observed herein was often over several kilometres, false killer whales likely acoustically communicate over this range, as they are known to exhibit coordinated movements over extensive distances (>20 km; Baird et al., 2008a; Bradford et al., 2014).

The dyads that did not conform to this relationship (a subset of Cluster 1 and 3 members) could reflect cluster-specific behavioural properties unmeasured in our study. For example, group size or composition can influence intra-group spatial behaviour if sub-optimal sizes or certain demographic classes (e.g., younger, slower individuals) decrease the efficiency or performance of group-level decision making (Cantor et al., 2020; Fryxell et al., 2025; Papageorgiou and Farine, 2020) or are more likely to disperse (e.g., males; Clutton-Brock, 2016). Evidence for sub-clustering within Cluster 3 (Mahaffy et al., 2023) may explain some dyad's more diffuse spatial association patterns, while higher association strengths within Clusters 2 and 4 (Mahaffy *et al.* 2023) could explain these groups' more cohesive movements. Given that mating occurs both within and between clusters (Martien *et al.* 2019), sex and reproductive status may play a role in dyad-level movement patterns, as some less spatially cohesive dyads that occasionally associated in space included an adult male (Figure 3.3). While social processes shape fine-scale cohesion within clusters, the broader structuring of space among clusters is likely governed by ecological constraints, particularly the ephemerality and distribution of resources.

3.5.2 Resource ephemerality regulates short-term inter-cluster space use

Social clusters spatially partitioned themselves in the short-term at different scales. Large-scale spatial partitioning (e.g., low range overlap over weeks to months) theoretically reduces indirect intra-cluster resource competition (Fretwell and Lucas, 1969), particularly when resources are ephemeral and distributed across disparate patches of sufficient quality to sustain separate foraging groups. Indeed, our findings from stable isotopes show that all false killer whale clusters feed across the same prey trophic levels, suggesting that large-scale spatial partitioning may be a necessary tactic to maintain intra-cluster foraging success when prey is patchily distributed and relatively unpredictable.

In contrast, cases where different clusters exhibited high spatial range overlap but tagged dyads were rarely in close proximity (i.e., small-scale partitioning) could reflect temporary access to high-quality prey patches that can sustain multiple clusters simultaneously (Macdonald, 1983). Such ephemeral resource hotspots may promote temporary inter-cluster associations (Papageorgiou et al., 2019). Because false killer whales are highly social but not territorial, such periods of high spatial overlap could also provide opportunities for mutually beneficial inter-cluster interactions, such as cooperative foraging, social learning, and mating. In this sense, foraging hotspots may function not only as ecological resources but also as social arenas, a dual role increasingly recognized in highly social terrestrial mammals (Strauss et al., 2024).

While logistically infeasible in our system, measuring patch quality would provide a more robust basis for testing resource ephemerality and density-dependent effects on false killer whale inter-cluster dynamics. Nonetheless, high similarity in habitat selection across clusters during short periods—combined with the isotopic evidence—indicate that clusters share the same prey base. These results collectively support the hypothesis that resource ephemerality exerts a top-down influence on inter-cluster spatial and social behaviours in the short-term (Figure 3.1-ii). Over longer timescales, however, resource dynamics may not only modulate short-term associations but also shape persistent patterns of spatial fidelity and niche differentiation among clusters.

3.5.3 Long-term integration of spatial, social, and ecological processes

Consistent use of space over time can provide a variety of benefits, including efficient resource exploitation, familiarity with resource and predator landscapes, and reduced movement costs (Piper, 2011; Switzer, 1993). Over the 18-year study period, within-cluster spatial fidelity was most variable in Clusters 1 and 3 and least variable in Clusters 2 and 4. With the exception of Cluster 4, intra-cluster fidelity was highly comparable to inter-cluster overlap, suggesting that, in the long term, the population shares a common geographic range, while Cluster 4 occupies a more distinct spatial niche. Lower core range fidelity overall indicates that a cluster's core area at a given time may be more variable and sensitive to fluctuations in short-term prey availability and density-dependent effects, with some clusters (2, 4) exhibiting greater temporal consistency than others (although see discussion on caveats below). The low within-individual spatial fidelity among some re-tagged whales, and lack of effect of genetic similarity on range overlap, further supports the notion that short-term space use can shift dynamically in response to local conditions.

Similar to the short-term patterns, these long-term differences in space use and fidelity among clusters likely reflect both ecological variability and cluster-specific behavioural properties. For example, within-group core range fidelity is greater when group composition is stable in terrestrial group-living species (Ogino et al., 2025), suggesting that demographic turnovers can influence how groups make collective decisions. In species that maintain stable social membership, group turnover can imply the loss of older, experienced individuals with knowledge of alternative resource hotspots (Kopf et al., 2024), further influencing collective movement and cluster-level space use; this is a plausible process for our study population, which has declined over the past decade (Badger et al., 2025). Thus, both social and environmental processes that occur at finer temporal scales—such as group composition and resource variability—may contribute to the observed temporal variability in cluster-level space use, while enduring cluster-level behavioural traits may underpin the long-term temporal consistency seen in Clusters 2 and 4.

At coarser scales, cluster-level home and core ranges mirrored these spatial patterns. Whales from Clusters 1 and 3 occupied larger, more overlapping areas, whereas the ranges of those from Clusters 2 and 4 were more restricted. All clusters selected for similar habitats and had largely similar trophic ecologies, with some differences in habitat variables (primarily depth), isotopic niche widths, and prey groups consumed. While overlapping cluster-level niches are expected given that high prey field stochasticity constrains resource specialisation in marine predators (Courbin et al., 2018), we further found that Clusters 2 and 4 appear to have adopted more distinct spatial and dietary niches than Clusters 1 and 3. Cluster 4 exhibits the widest isotopic niche—driven by a broader range of δ^{13}C values consistent with feeding on more nearshore prey. This aligns with Cluster 4's home and core ranges encompassing shallower, coastal habitats than the other clusters. These findings, combined with limited evidence for use of other islands outside of their core range, potentially suggest that increased site fidelity and diversified trophic niche may represent effective strategies for optimizing spatial and social environments.

While limited tag sample sizes for Cluster 2 and Cluster 4 (9 tracks each) introduce caveats, both clusters included very long deployments (>80 days) showing consistent ranging behaviour across years. These patterns, coupled with rare sightings of these clusters outside their core ranges (Mahaffy et al., 2023), reinforce the hypothesis that spatial and dietary differentiation among clusters is stable over time. Future high-resolution tracking could test whether fine-scale habitat preferences further partition space among clusters within their shared ranges. Collectively, the current results suggest that both short- and long-term processes shape how social clusters interact in space, ultimately influencing the degree of connectivity and potential for population structuring.

3.5.4 Linking spatial-social dynamics to population structuring and connectivity

How individuals and groups navigate their spatial and social environments—with both short-term decisions and in long-term strategies—determines the probability of encounters among individuals or groups (Aureli et al., 2008; Webber et al., 2023). These processes collectively shape population-level social structure, including patterns of information transfer, mating and ultimately gene flow (Albery et al., 2021; He et al., 2019; Spiegel et al., 2017). In Hawaiian false killer whales, overlap between cluster-level core ranges was highest in two population-wide hotspots (proxied by the CDE), suggesting that these areas are consistently valuable and may serve as arenas for inter-cluster encounters. Critically, pairwise core range overlaps correspond with cluster-level mitochondrial haplotype composition (Mahaffy et al., 2023). While these are broad descriptive correlations, they offer rare empirical evidence that feedback mechanisms between spatial and social processes across scales can shape both population connectivity and genetic structuring.

The unique habitat configuration of the Hawaiian Islands likely reinforces these patterns. Compared to the surrounding open ocean, the archipelago likely promotes site fidelity through stable local resource patches and memory-based foraging, while the distances separating them are sufficient to limit constant inter-cluster contact—allowing for partial divergence among social clusters that can persist within distinct portions of the island chain. At the same time, proximity among island areas (particularly Oʻahu, Maui Nui, Hawaiʻi) maintains opportunities for social contact, information sharing, and mating, thereby at least partially mitigating potential inbreeding risks. Interestingly, while false killer whales use all the main Hawaiian Islands, their home ranges remain concentrated in these central islands, possibly reflecting higher resource abundance or the shorter inter-island distances. Alternatively, limited ranging near Kauaʻi and Niʻihau may instead result from competition with the Northwestern Hawaiian Islands false killer whale population (Baird et al., 2013a; Kratofil et al., 2023) or other ecological differences yet to be examined. Collectively, these results indicate that spatial and social processes interact across scales to generate a balance between cohesion and differentiation within this population—a dynamic equilibrium that promotes both local adaptation and population connectivity.

3.5.5 Conclusions

Together, our findings illuminate general mechanisms by which life-history strategies and environmental stochasticity jointly determine both the scale and direction of feedback links between space use and sociality. In Hawaiian false killer whales, this interplay yields a dynamic balance between cohesion and differentiation—promoting population connectivity while maintaining socially mediated structure. Beyond this system, this framework offers a tractable approach for examining how behaviour scales up to shape population structure in mobile species. Identifying the relative influence of these feedback mechanisms across systems of varying social complexity, resource predictability, and habitat heterogeneity will be key to revealing more general principles linking individual behaviour, group dynamics, and the evolution of population structure.

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3.8 Figures

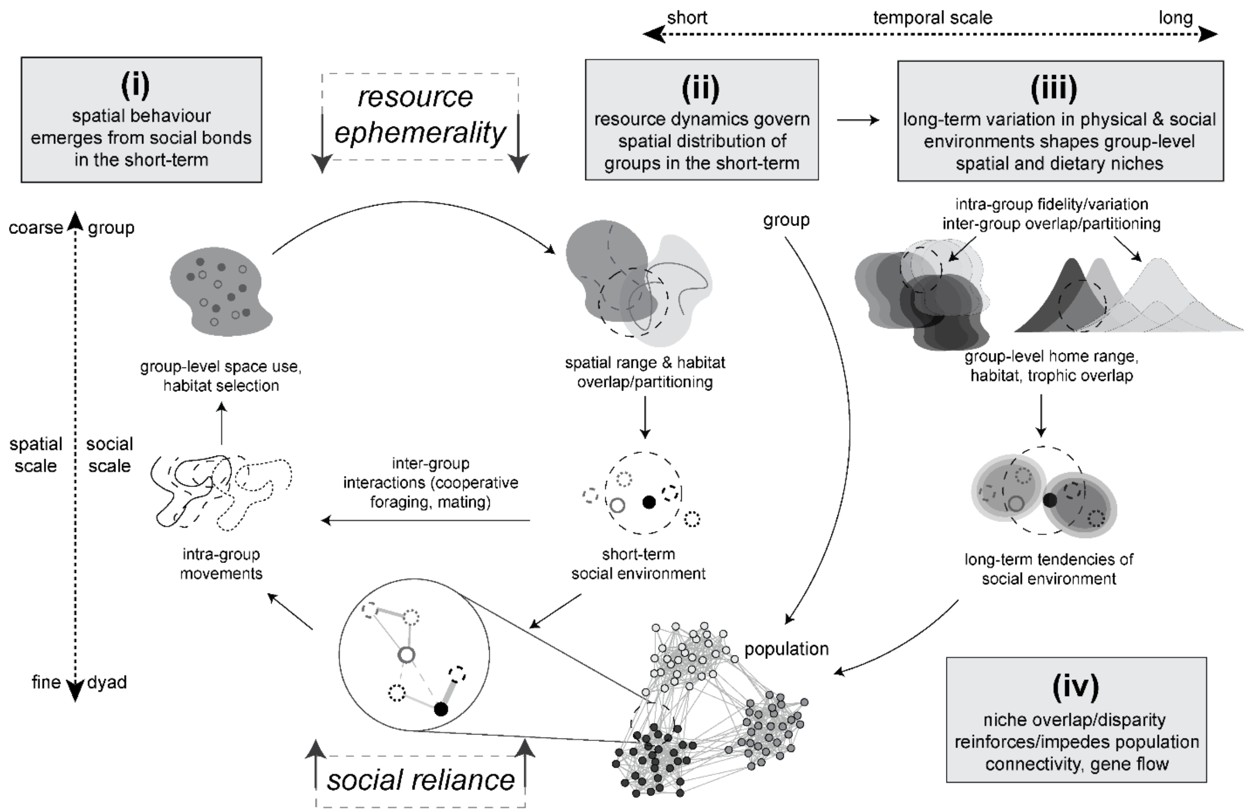

Figure 3.1. Conceptual diagram proposing social reliance and resource ephemerality as regulators of spatial-social directional feedback mechanisms (i.e., bottom-up versus top-down effects) across spatial, temporal, and social scales. We predict that (i) where social reliance is high, intra-group space use emerges from social bonds in the short-term; (ii) resource ephemerality (interacting with habitat configuration) determines the spatial distribution of social groups in the short-term (e.g., through density-dependent effects), which subsequently influences inter-group interactions in this time scale; (iii) long-term variation in the dynamics of physical and social environments (i.e., predictions (i) and (ii)) shapes niche variation among social groups, which can be measured through intra-group fidelity (or variation) and inter-group overlap in spatial and dietary niches; and (iv) niche overlap/disparity influences long-term tendencies of the social environment (i.e., probability of groups interacting with one another), and thus population connectivity and gene flow.

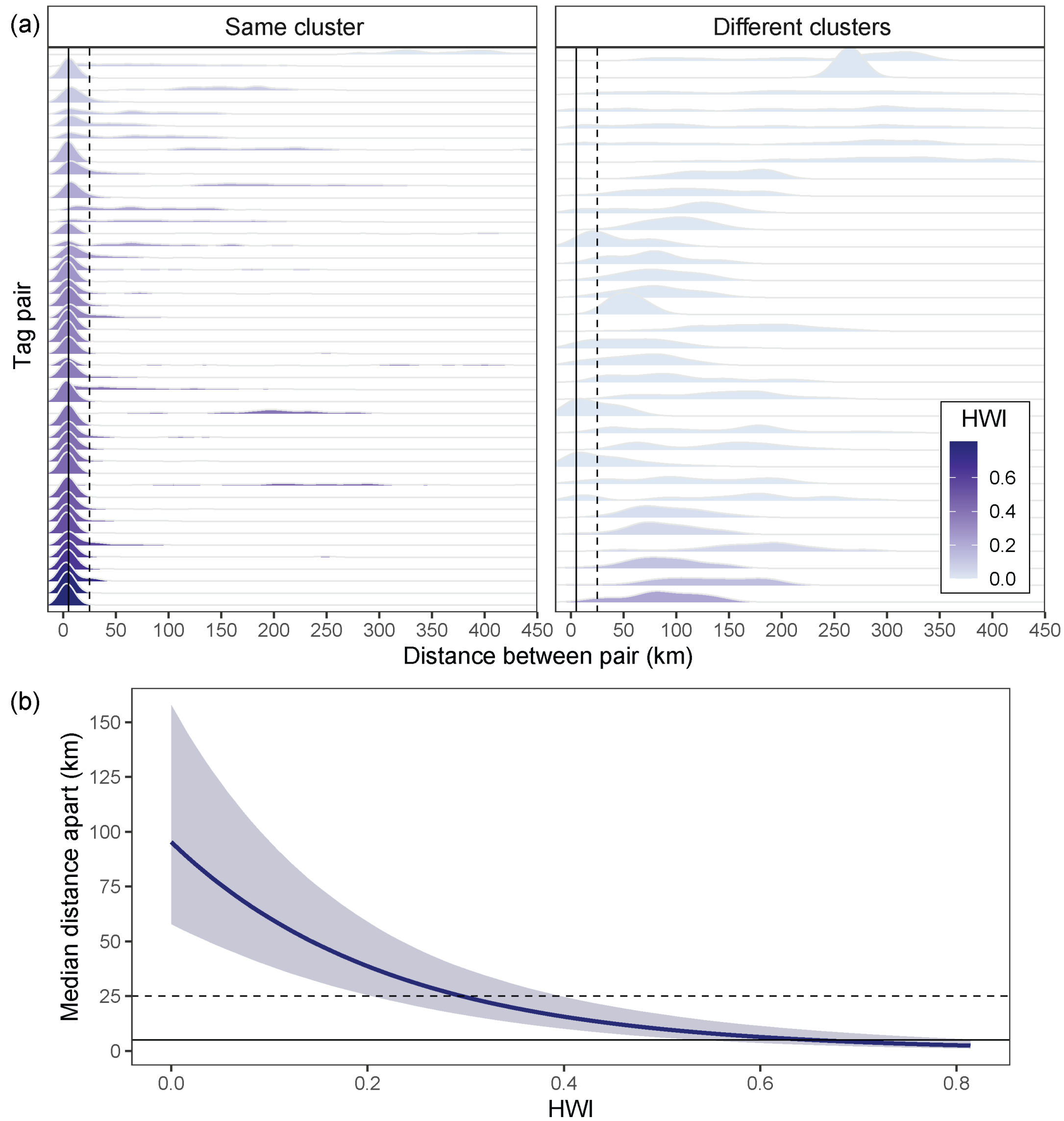

Figure 3.2. Relationship between social associations and spatial cohesion in tagged false killer whales. (a) Distribution of distance between tagged dyads sorted by decreasing pairwise association strength (half-weight index, HWI) for same-cluster pairs (left) and different-cluster pairs (right; vertical solid line = 5 km; vertical dashed line = 25 km); (b) conditional effects plot from the fitted model relating median distance between dyads and pairwise association strength (dark line = estimate; shaded ribbon = 95% credible interval; solid lines = 5 km; dashed lines = 25 km).

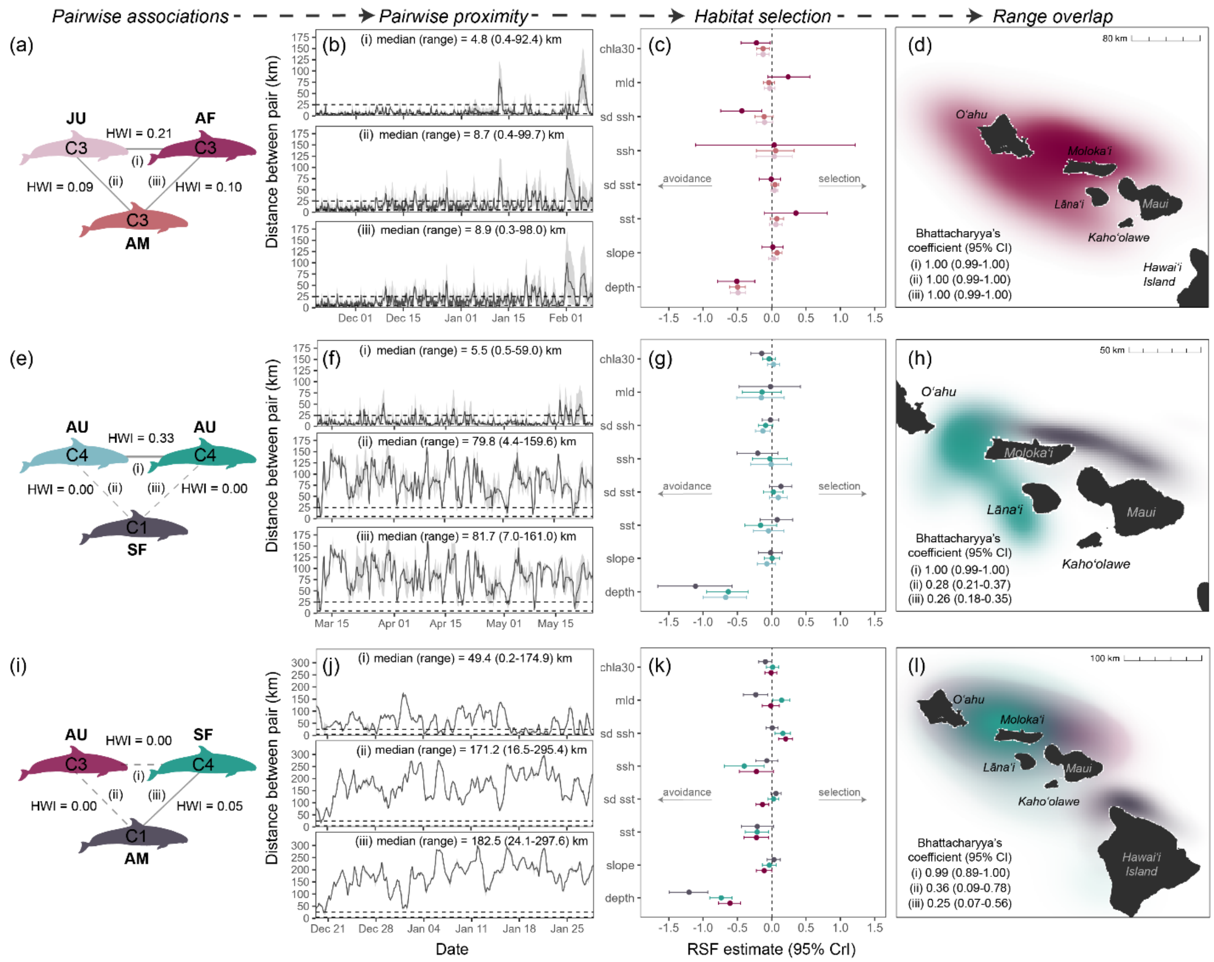

Figure 3.3. Short-term intra- and inter-cluster false killer whale social associations and spatial behaviour across scales. Emergence of intra-cluster space use from social bonds (a-h) from fine to coarse scales (left to right) and between-cluster partitioning (e-l) in the short-term. Each panel shows (1st column) pairwise association strength (half-weight index, HWI) among the focal individuals (i, ii, iii) with cluster membership (colour and “C#”) and age-sex class (A = adult, S = sub-adult, J = juvenile; F = female, M = male, U = unknown); (2nd column) pairwise proximity (distance between each pair) for the period of overlap, with 5-km and 25-km indicated by horizontal dashed lines; (3rd column) habitat selection coefficients of individuals (estimates and 95% credible intervals, CrI; mld = mixed layer depth, chla30 = 30-d lagged surface chlorophyll-a concentration, sd ssh = standard deviation of sea surface height, ssh = sea surface height, sd sst = standard deviation of sea surface temperature, sst = sea surface temperature, slope = seafloor slope, depth = seafloor depth); and (4th column) spatial range overlap, with the Bhattacharyya’s coefficient values and 95% confidence intervals (CI) shown for each pair.

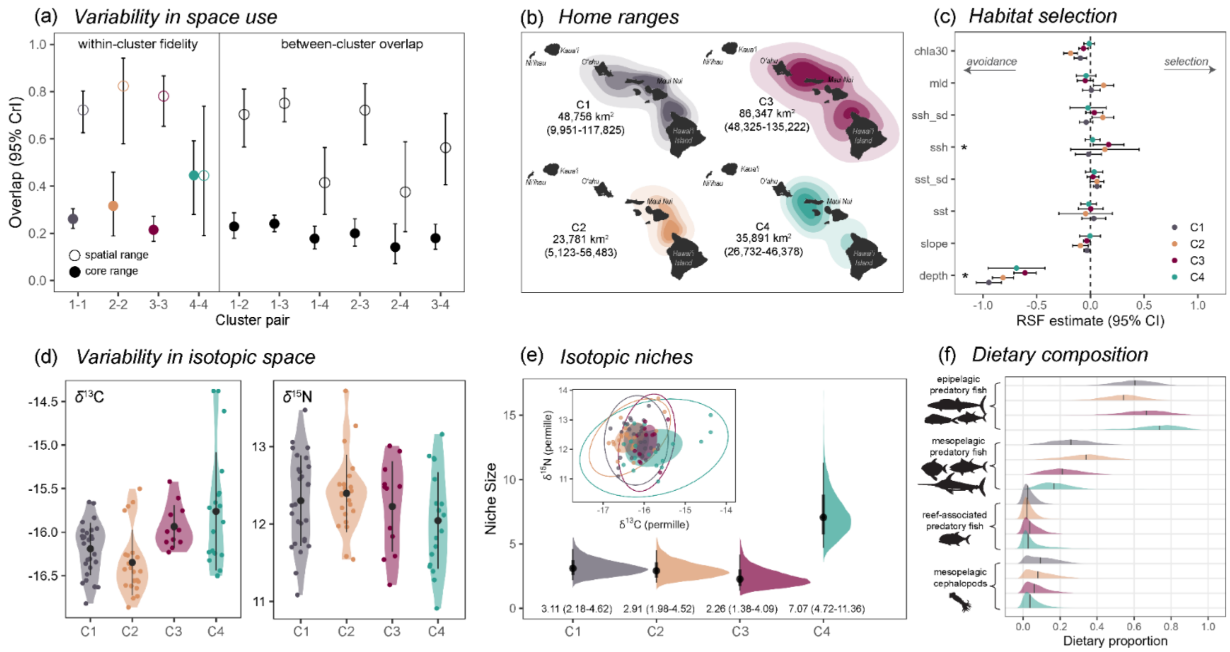

Figure 3.4. Spatial and trophic niches among false killer whale social clusters. (a) Conditional effects (posterior estimates, 95% credible intervals, CrI) of pairs of social clusters (x-axis) on spatial (open circles) and core range (filled circles) overlap models, showing within-cluster fidelity and between-cluster overlap; (b) cluster-level home ranges defined by population-level wAKDEs (95%, 75%, 50%, and 25% contours shown), with area estimates and associated 95% confidence intervals (CI) shown for each cluster. Maui Nui includes the islands of Maui, Molokaʻi, Lānaʻi, and Kahoʻolawe (see Figure 3.3); (c) cluster-level habitat selection coefficients (estimate, 95% confidence interval, CI; mld = mixed layer depth, chla30 = 30-d lagged surface chlorophyll-a concentration, sd ssh = standard deviation of sea surface height, ssh = sea surface height, sd sst = standard deviation of sea surface temperature, sst = sea surface temperature, slope = seafloor slope, depth = seafloor depth) with variables where cluster membership had a significant effect on selection (relative to Cluster 1, from mixed-meta regression) indicated by asterisks; (d) distribution of δ^{13}C and δ^{15}N isotopes by social cluster (mean and standard deviation plotted in centre); (e) cluster-level posterior isotopic niche size (point = median; line range = 95% CrI; shown in text) and inset ellipses (overall/95% outlined; core/40% shaded); (f) posterior densities of dietary proportions of prey groups among social clusters (median shown by vertical line) based on stable isotopes analysis of skin samples.

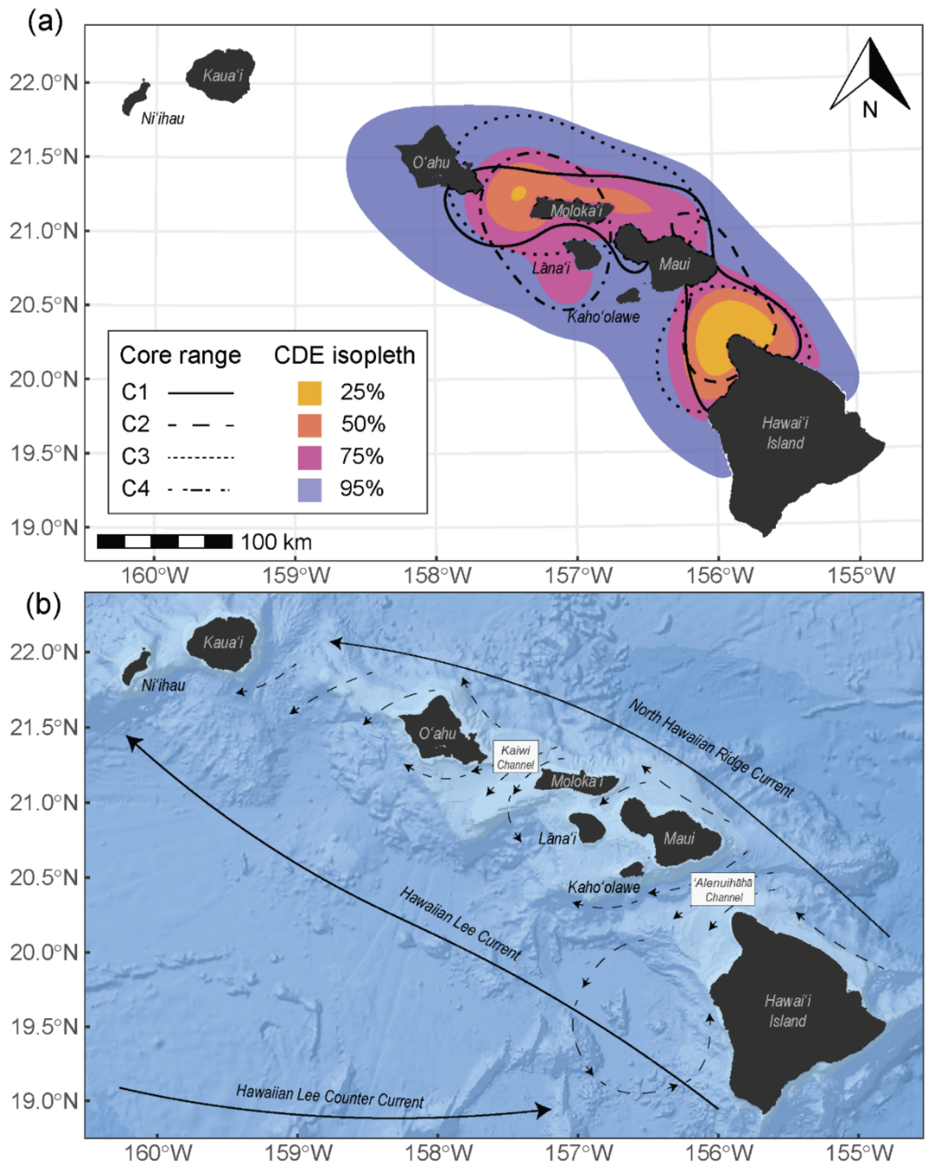

Figure 3.5. Co-occurrence hotspots of false killer whales in relation to broad scale habitat features around the Main Hawaiian Islands. (a) Overlap between population-wide spatial hotspots (proxied by the conditional distribution of encounters, CDE) and social cluster-level core ranges (C1 = Cluster 1, C2 = Cluster 2, C3 = Cluster 3, C4 = Cluster 4; outlined). (b) Primary currents (solid lines) and wind, current directions (dashed lines), and channels (outlined boxes) relevant to observed space use in panel (a). Current and wind lines were adapted from Lindo-Atichati et al. (2020).

3.9 Supplementary Materials

Supporting Information S1: Analytical framework

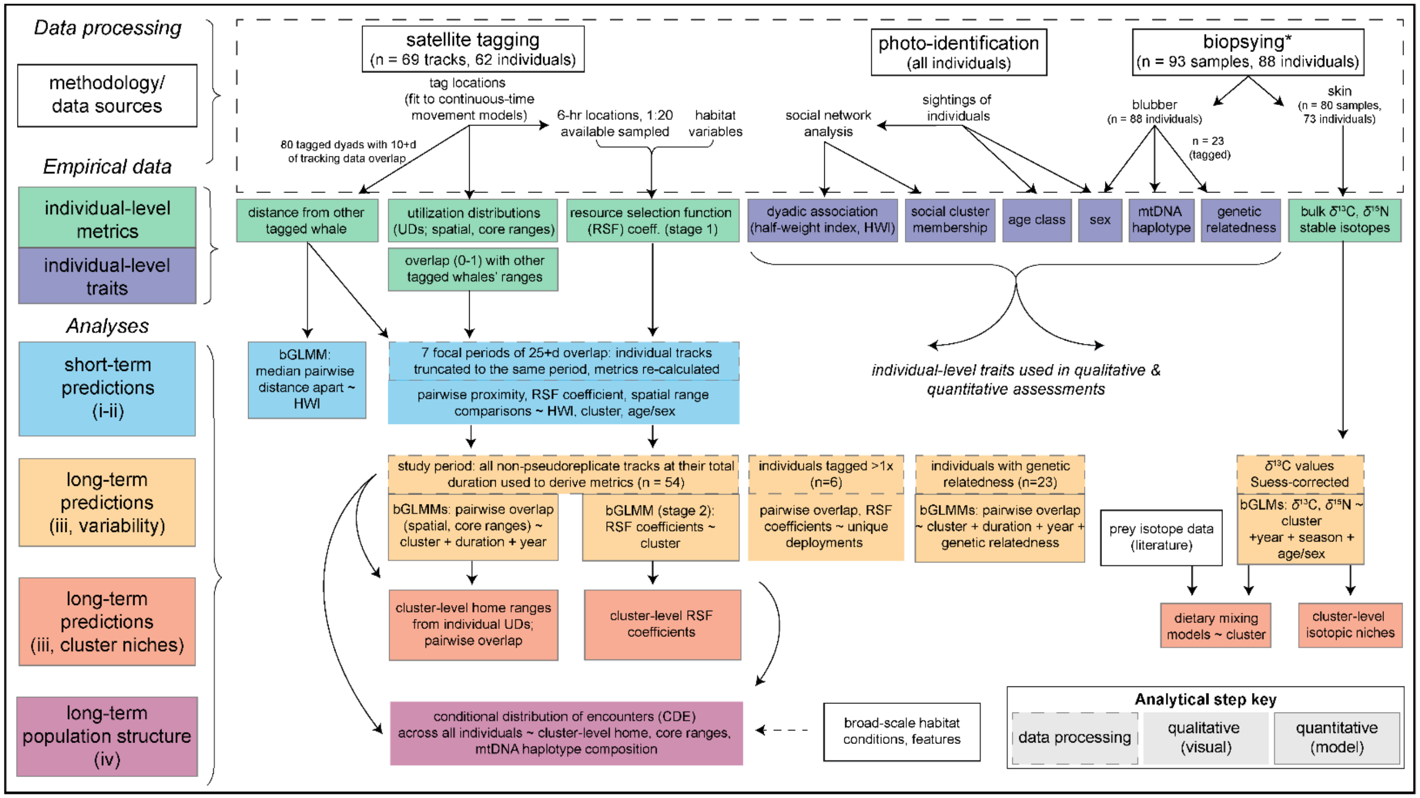

Figure 3.6. Conceptual overview of data sources and processing, resulting individual-level empirical data, and subsequent analytical steps used to test predictions corresponding to Figure 3.1 in the main text. *All biopsied individuals have genetic sex and mtDNA haplotype. Genetic pairwise relatedness was only assessed for tagged whale space use, and thus the sample size reflects the number of whales tracked, biopsied, and for which pairwise genetic relatedness information is available. The stable isotopes dataset primarily reflects data from individuals not tagged (n=56); while some individuals with stable isotopes were also tagged (n=17), the temporal window reflected by the two data sources does not overlap. Definitions: mtDNA = mitochondrial DNA; bGLMM = Bayesian Generalised Linear Mixed Effects Model; bGLM = Bayesian Generalised Linear Model; spatial range overlap = estimated through Bhattacharyya's coefficient; core range overlap = estimated as twice the area of intersection divided by the combined area of each dyad's core ranges.

Supporting Information S2: Biopsy sample collection and laboratory procedures

Stable isotope analysis

Biopsy and skin sample preparation methods follow that reported in Ylitalo et al. (2009) and Kratofil et al. (2020). Skin samples from Kratofil et al. (2020) (n = 54; 2008-2011) were included in this study as well as 26 additional samples collected between 2015 and 2020. The Kratofil et al. (2020) samples were analysed for bulk carbon and nitrogen (δ^{13}C and δ^{15}N) stable isotopes at NOAA Northwest Fisheries Science Center and the more recent 26 samples at the Institute of Environment's Stable Isotope Facility at Florida International University (North Miami, FL). Stable isotope analyses of skin samples from Kratofil et al. (2020) and this study were conducted in a similar manner: skin samples were first dried and homogenized into a fine powder, lipids were extracted because they are ^{13}C depleted (DeNiro and Epstein, 1977), and samples subsequently processed using a ThermoFinnigan Delta V isotope ratio mass spectrometer (IRMS) coupled with a NA 1500 Ne elemental analyzer. Lipid extractions were done chemically for both Kratofil et al. (2020) samples (with two cell volumes of dichloromethane at 25°C, 500 psi) and the samples analysed herein (following Caputo et al. 2025, with a 2:1 chloroform: methanol mixture). Specific laboratory lipid extraction methods can be found in Kratofil et al. (2020) and Caputo et al. (2025).

Supporting Information S3: Supplemental spatial metric methods & results

Continuous-time movement model fitting

Filtered satellite tag location data were fit to continuous-time movement models using the *ctmmUtils* and *ctmm* R packages (Fleming and Calabrese, 2023; Johnson and London, 2025). Argos error ellipse measurements were incorporated into the model. For tags deployed in 2007, where only location quality class was available, we used corresponding class-specific estimates of ellipsoidal uncertainty from Vincent et al. (2002). Additionally, some tags (n = 3) transmitted both Argos and Fastloc-GPS locations; for these tags, we assigned GPS locations error ellipses based on the number of satellites that were used to estimate the position, following values from Dujon et al. (2014). Any locations on land were rerouted around the 20-meter isobath using the *pathroutr* package (London, 2020).

Resource selection functions

Stage 1 resource selection functions (RSFs; i.e., individual-level) were fit with environmental variables reflecting seafloor topography and dynamic ocean activity. Correlations between environmental variables were assessed prior to modeling; where two variables were correlated (Pearsons' correlation > 0.5), only one was included for subsequent modeling. In these cases, the variable with the more direct ecological interpretation (e.g., known proxy of upwelling processes) was selected. Details on the variables, their resolution, source, and whether or not they were included in final RSFs are provided in Table 3.1. Variable selection was not undertaken at the stage 1 RSF level as the goal of the two-stage approach in our study was to assess among-individual variation (and among-cluster variation) in habitat selection of common habitat features.

Table 3.1. Environmental variables and source information for variables considered in resource selection functions (RSFs).

Variable	Spatial resolution	Temporal resolution	Source	Included/excluded in RSF models
Seafloor depth (depth)	1 km	NA	GEBCO[1]	Included
Seafloor slope (slope)	1 km	NA	GEBCO[1]	Included
Sea surface temperature (sst)	9 km	Daily	Copernicus Global Ocean Physics Re-analysis[2]	Included
Standard deviation of SST (sst_sd)	27 km	Daily	Calculated across 3 pixels using SST data	Included
Sea surface salinity (sss)	9 km	Daily	Copernicus Global Ocean Physics Reanalysis[2]	Excluded; correlated with ssh
Mixed layer depth (mld)	9 km	Daily	Copernicus Global Ocean Physics Re-analysis[2]	Included
Sea surface height (ssh)	9 km	Daily	Copernicus Global Ocean Physics Re-analysis[2]	Included
Standard deviation of SSH (ssh_sd)	27 km	Daily	Calculated across 3 pixels using SSH data	Included
Current magnitude (cmag; derived from u- and v- components of horizontal current velocity)	9 km	Daily	Copernicus Global Ocean Physics Re-analysis[2]	Excluded; correlated with ssh_sd
30-day lagged Surface chlorophyll-a concentration (logged; chla30)	4 km	Daily	Copernicus Ocean Color[3]; value extracted for date 30 days prior to date of locations	Included

[1]https://www.gebco.net/data-products/gridded-bathymetry-data
[2]https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/description
[3]https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_104/description

Spatial metric model specifications

Models examining the influence of social factors on space use metrics are detailed in Table 3.2.

All models were fit in a Bayesian framework using the *brms* package (Bürkner, 2018) with 6,000 iterations and a 3,000 warm-up period. We specified diffuse priors for all models as we did not have strong prior knowledge on the parameter distributions (Table 3.2). For RSF models, habitat variables were centered/scaled prior to model fitting.

For models assessing long-term predictions (i.e., predictions iii in Figure 3.1, 3.6), we only included one individual of same-cluster tagged dyads that remained spatially associated during their period of overlap based on findings from the dyadic distances model (i.e., to mitigate pseudoreplication).

The stage 2 RSFs did not include covariates for tag deployment year or duration, as was done for the spatial and core range overlap models. The random effect for tag ID in the stage 2 RSF accounts for any differences due to that individual (including tag deployment year), and the covariance matrices incorporated from stage 1 RSFs will generally reflect differences in among individuals in the amount of data (i.e., deployment length).

Only a subset of tagged dyads (n = 273 dyads) had pairwise genetic relatedness information available and thus separate spatial/core range overlap models were ran for this sub-analysis. Due to limited sample size across unique cluster pairs in the genetic similarity models, a binary predictor for same/different cluster was included in place of unique cluster pair.

Table 3.2. Spatial metric model parameters and priors. Note: stage 2 RSFs (i.e., meta-mixed effects models) were not fit in a Bayesian framework and thus no priors are listed. Parameter types: intercepts (a), slopes (b), distributional parameters (shape, phi, zi).

Model (family, link function)	Parameter	Prior
Median distance between dyad (gamma, log link)	a	student_t(3, 4.1, 2.5)
	b(HWI)	flat
	a(mmid1-id2)	student_t(3, 0, 2.5)
	sd(mmid1-id2)	student_t(3, 0, 2.5)
	shape	gamma(0.01, 0.01)
Spatial range overlap (beta, identity link)	a	student_t(3, 0, 2.5)
	phi	gamma(0.01, 0.01)
	b(coeffs): cluster pair, same/different year, duration difference (genetic subset: same/different cluster, year, duration difference, genetic relatedness)	flat
	a(mmtagid1-tagid2)	student_t(3, 0, 2.5)
	sd(mmtagid1-tagid2)	student_t(3, 0, 2.5)
Core range overlap (zero-inflated beta, identity link)	a	student_t(3, 0, 2.5)
	phi	gamma(0.01, 0.01)
	zi	beta(1, 1)
	b(coeffs): cluster pair, same/different year, duration difference (genetic subset: same/different cluster, year, duration difference, genetic relatedness)	flat
	a(mmtagid1-tagid2)	student_t(3, 0, 2.5)
	sd(mmtagid1-tagid2)	student_t(3, 0, 2.5)
Stage 1 RSFs (Bernoulli, logit link)	a	student_t(3, 0, 2.5)
	b(coeffs): RSF coefficients (Table S1)	flat
Stage 2 RSFs (multivariate normal, meta-mixed effects)	a	NA
	b(coeffs): cluster	NA
	a(tagid)	NA

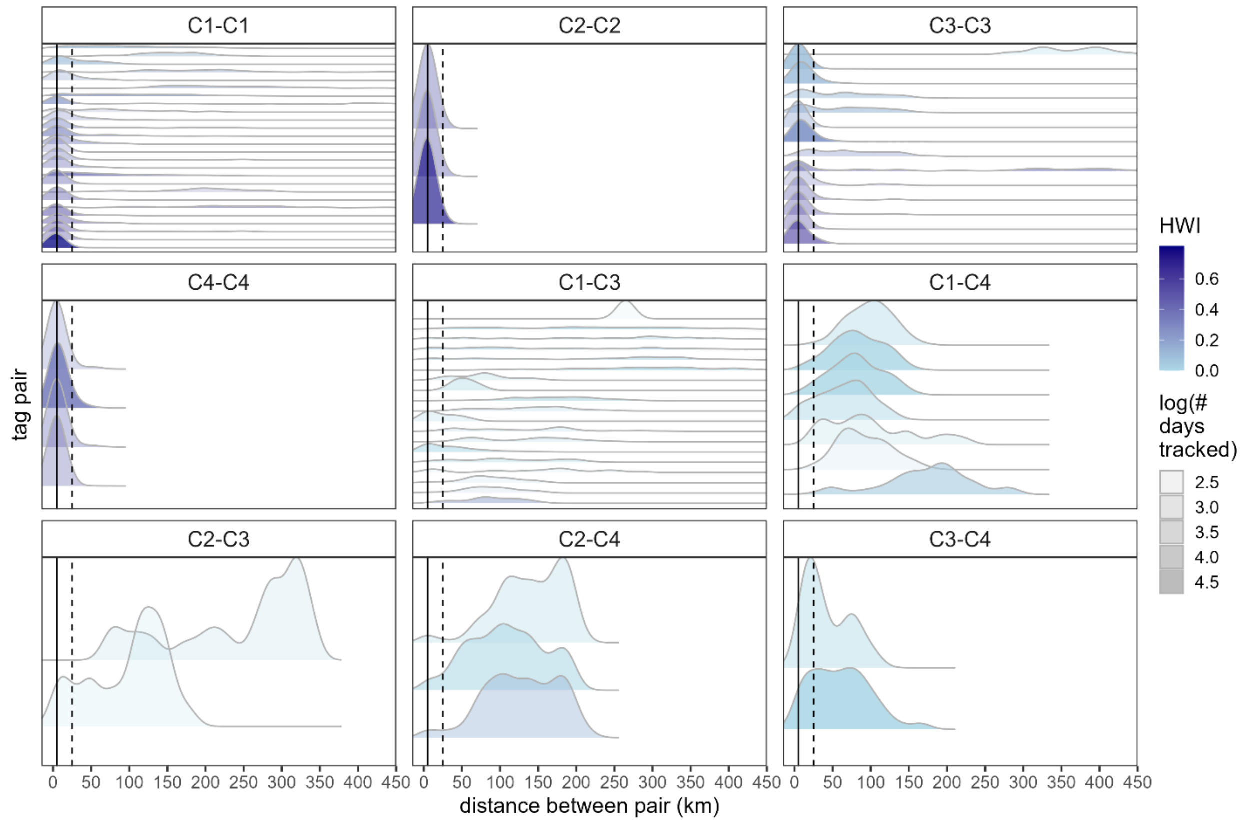

Figure 3.7. Distribution of distances between tagged dyads sorted by decreasing pairwise association strength (half-weight index, HWI) and faceted by cluster pair (i.e., C#-C#). The transparency of density distributions is scaled by the logged number of days tracked for the pair, so that longer tracking durations are less transparent. The solid vertical line represents 5 km, and the dashed vertical line represents 25 km.

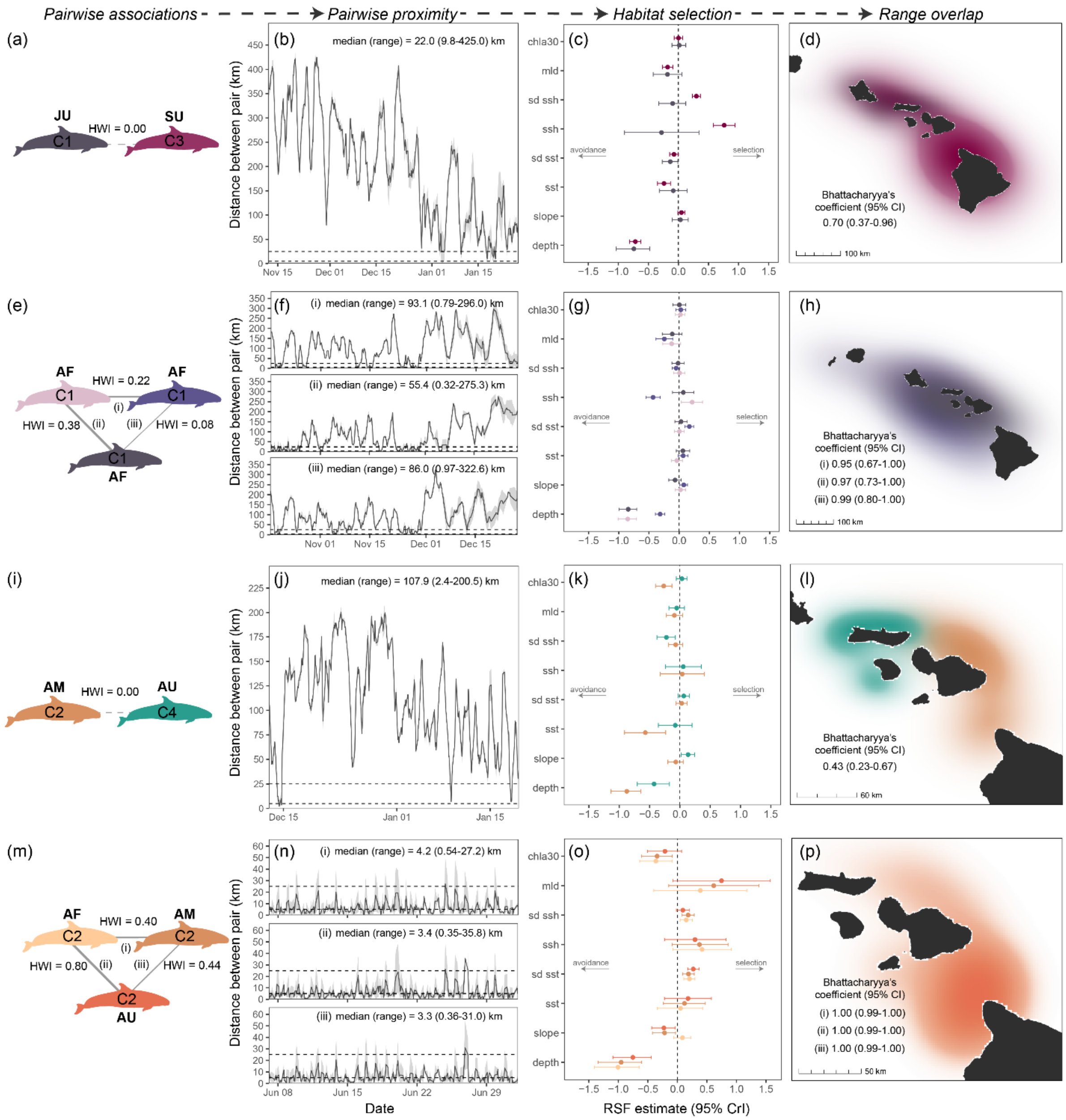

Figure 3.8. Additional cases exhibiting short-term intra- and inter-cluster social associations and space use. Emergence of intra-cluster space use from social bonds (e-h; m-p) from fine to coarse scales (left to right) and between-cluster partitioning (a-c; i-l) in the short-term. Each panel shows (1st column) pairwise association strength (half-weight index, HWI) among the focal individuals (i, ii, iii) with cluster membership (colour and "C#") and age-sex class (A = adult, S = sub-adult, J = juvenile; F = female, M = male, U = unknown); (2nd column) pairwise proximity (distance between each pair) for the period of overlap, with 5-km and 25-km indicated by horizontal dashed lines; (3rd column) habitat selection coefficients of individuals (estimates and 95% credible intervals, CrI; see Table 3.1 for variable codes); and (4th column) spatial range overlap, with the Bhattacharyya's coefficient values and 95% confidence intervals (CI) shown for each pair.

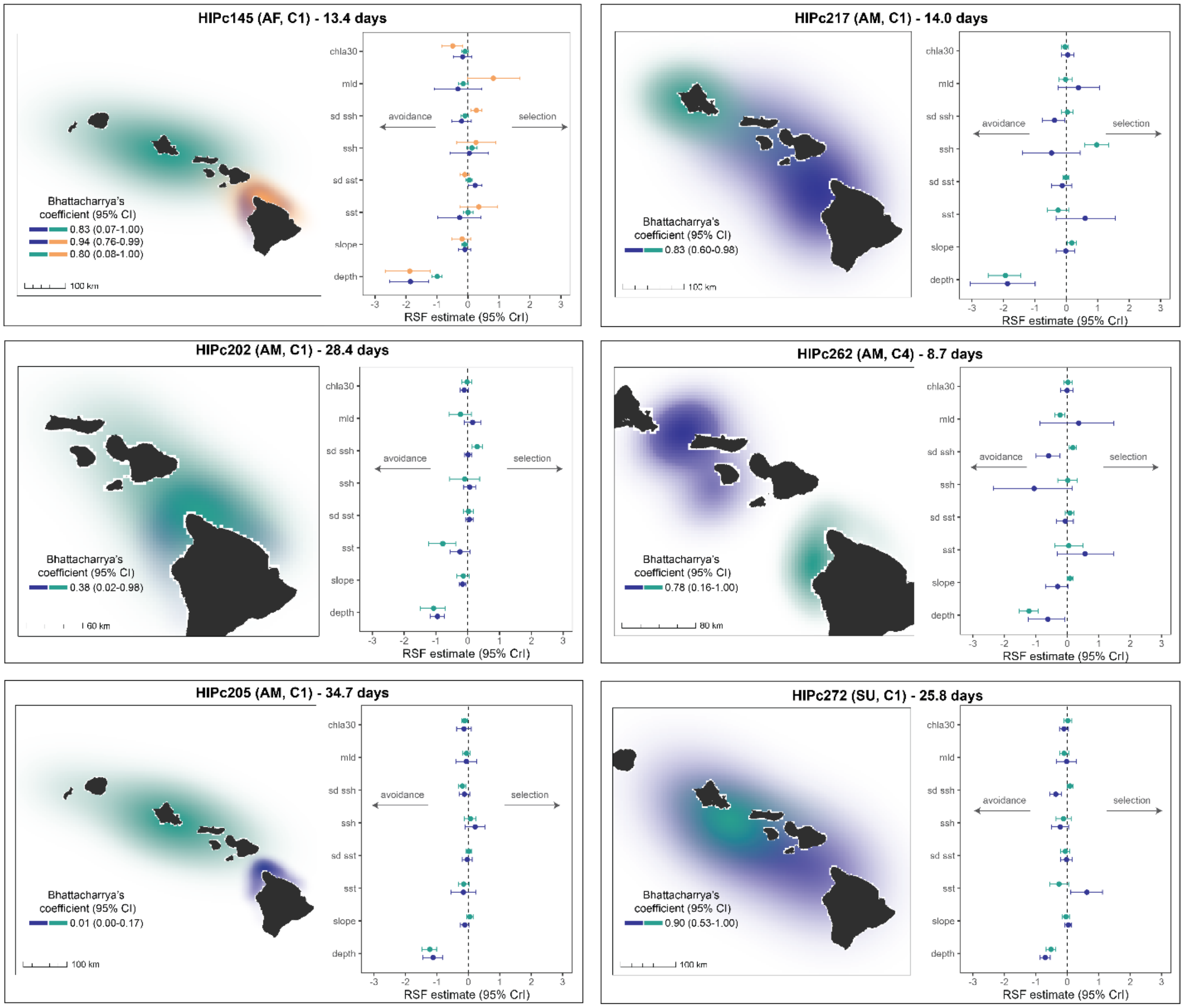

Figure 3.9. Comparative spatial behaviour (spatial range: left sub-panels, resource selection: right sub-panels) of individuals tagged more than once during the study period. Catalogue ID, age/sex class (A = adult, S = sub-adult, F = female, M = male), cluster membership (C#) and duration are indicated within each panel. Overlap between spatial ranges (Bhattacharyya's coefficient) and associated confidence intervals (CI) are provided in each map. Resource selection function coefficient names are provided in Table 3.1.

Table 3.3. Spatial metric model parameter estimates. Coefficient estimates (i.e., b parameters) that have 95% credible intervals (CrI) excluding zero are shown in bold. See Table 3.2 for parameter definitions. For models including coefficients for unique cluster pair (i.e., CX-CY), the reference level was set to C1-C1; C1 was set as the reference level for models including cluster. For the stage 2 RSF model, confidence intervals (CR) are provided.

Model (sample size)	Parameter	Estimate	Lower 95% CrI	Upper 95% CrI
Median distance between dyads (n=80 dyads)	a	4.56	4.06	5.06
	b(HWI)	**-4.51**	**-5.64**	**-3.36**
	sd(mmid1-id2)	1.26	0.89	1.70
	shape	2.09	1.35	3.04
Spatial range overlap (n=1,423 dyads)	a	0.96	0.51	1.40
	b(C1-C2)	-0.09	-0.69	0.52
	b(C1-C3)	0.14	-0.24	0.53
	b(C1-C4)	**-1.30**	**-1.88**	**-0.72**
	b(C2-C2)	0.59	-0.71	1.94
	b(C2-C3)	0.00	-0.77	0.78
	b(C2-C4)	**-1.46**	**-2.40**	**-0.50**
	b(C3-C3)	0.31	-0.46	1.07
	b(C3-C4)	-0.70	-1.45	0.05
	b(C4-C4)	-1.17	-2.45	0.13
	b(same_year = TRUE)	**0.53**	**0.31**	**0.75**
	b(duration_diff)	**-0.10**	**-0.18**	**-0.02**
	sd(mmtagid1-tagid2)	1.19	0.97	1.47
	phi	3.86	3.58	4.14
Core range overlap (n=1,423 dyads)	a	-0.60	-0.85	-0.36
	b(C1-C2)	-0.20	-0.55	0.16
	b(C1-C3)	-0.13	-0.37	0.11
	b(C1-C4)	**-0.55**	**-0.92**	**-0.18**
	b(C2-C2)	0.32	-0.49	1.14
	b(C2-C3)	-0.39	-0.85	0.07
	b(C2-C4)	**-0.86**	**-1.67**	**-0.10**
	b(C3-C4)	-0.29	-0.74	0.13
	b(C4-C4)	**-0.54**	**-1.01**	**-0.07**
	b(same_year = TRUE)	**1.02**	**0.05**	**1.99**
	b(duration_diff)	**0.26**	**0.05**	**0.47**
	sd(mmtagid1-tagid2)	0.59	0.45	0.77
	phi	3.86	3.55	4.19
	zi	0.26	0.24	0.29
Spatial range overlap – genetic relatedness subset (n=273 dyads)	a	0.78	0.18	1.38
	b(same_clust = TRUE)	0.22	-0.02	0.47
	b(same_year = TRUE)	**0.55**	**0.05**	**1.07**
	b(duration_diff)	-0.03	-0.29	0.23
	b(genetic_relatedness)	-0.20	-1.43	1.08
	sd(mmtagid1-tagid2)	1.40	1.01	1.94
	phi	4.53	3.80	5.33
	a	-0.96	-1.38	-0.55

Core range overlap – genetic relatedness subset (n=273 dyads)	b(same_clust = TRUE)	0.21	-0.07	0.49
	b(same_year = TRUE)	0.22	-0.32	0.74
	b(duration_diff)	-0.10	-0.33	0.12
	b(genetic_relatedness)	-0.18	-1.64	1.24
	sd(mmtagid1-tagid2)	0.87	0.54	1.30
	phi	4.70	3.81	5.68
	zi	0.24	0.19	0.30
Stage 2 RSF variable	**Parameter**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
depth	a	-0.94	-1.04	-0.84
	b(C2)	0.07	-0.20	0.34
	b(C3)	**0.33**	**0.17**	**0.50**
	b(C4)	0.23	-0.03	0.50
slope	a	-0.02	-0.05	0.003
	b(C2)	-0.04	-0.11	0.03
	b(C3)	-0.01	-0.05	0.04
	b(C4)	0.03	-0.04	0.10
sst	a	0.03	-0.06	0.13
	b(C2)	-0.10	-0.33	0.13
	b(C3)	-0.04	-0.20	0.11
	b(C4)	-0.05	-0.29	0.19
sst_sd	a	0.05	0.02	0.09
	b(C2)	0.001	-0.09	0.09
	b(C3)	-0.03	-0.09	0.03
	b(C4)	-0.03	-0.12	0.06
ssh	a	-0.02	-0.14	0.09
	b(C2)	0.09	-0.19	0.38
	b(C3)	**0.20**	**0.01**	**0.38**
	b(C4)	0.01	-0.27	0.30
ssh_sd	a	-0.04	-0.10	0.02
	b(C2)	0.15	-0.004	0.30
	b(C3)	0.07	-0.03	0.17
	b(C4)	0.02	-0.14	0.18
mld	a	-0.002	-0.07	0.07
	b(C2)	0.12	-0.04	0.28
	b(C3)	-0.04	-0.15	0.06
	b(C4)	-0.04	-0.20	0.11
chla30	a	-0.09	-0.14	-0.04
	b(C2)	-0.12	-0.24	0.004
	b(C3)	0.03	-0.05	0.10
	b(C4)	0.08	-0.04	0.19

Supporting Information S4: Supplemental stable isotopes data analysis methods & results

Isotopic summaries, temporal and demographic effects

Prior to formal data analyses, carbon isotope values were Suess-corrected using the *SuessR* R package (Clark et al., 2021) to account for anthropogenic-driven changes in baseline ocean carbon levels over the 12-year sampling period. This package includes built-in regional baseline values to inform correction factors; we used the Aleutian Islands region to Suess-correct our samples as the carbon levels are the same for the Hawaiian Islands (Velasquez-Vacca et al., 2024). We corrected values to the year of the most recent samples (2020) so that values reported herein will be comparable to other contemporary studies in Hawai‘i.

We assessed potential temporal and demographic effects on $\delta^{13}C$ and $\delta^{15}N$ values using Bayesian generalised linear regression models in the *brms* package (Bürkner, 2018). Out of the 80 total samples, 14 represented individuals sampled twice (i.e., seven individuals) over the study period; for analytical purposes, we considered these samples to be independent given they were obtained in separate years. Separate models were fit for $\delta^{13}C$ and $\delta^{15}N$ values assuming a Gaussian error distribution and identity link function, and considering sample year, sample season, age class, sex, and social cluster as fixed effects. We aggregated sampling year into two sampling periods to attempt to alleviate uneven sample sizes across years (2008-2011, n = 54 samples; 2015-2020, n = 26 samples). Samples were categorised into oceanographic seasons (Flament, 1996) based on one month prior to that of sampling to reflect the season during which foraging is reflected by the sample (i.e., approximately one month tissue turnover rate; Giménez et al., 2016). Due to low sample size during the winter compared to all other seasons, we combined samples into summer/fall (n = 43 samples) and winter/spring (n = 37 samples) seasons. Similarly, there were limited juveniles (n = 12) and sub-adults sampled (n = 9) compared to adults (n = 59), and thus juveniles and sub-adults were combined into one category. Sample size by sex was less skewed (males, n = 33; females, n = 47). Models were fit with four chains with 6,000 iterations and a 3,000-iteration warm-up phase. Model convergence was ensured through $\hat{R}$ values (<1.05), mixing of chains, and posterior predictive checks.

There was evidence for an effect of sampling period, with samples from 2015-2020 having higher δ^{13}C and δ^{15}N values (posterior estimates = 0.48, 0.50, 95% CrIs = 0.29 to 0.67, 0.22 to 0.79, respectively) compared to 2008-2011 samples; however, sample size between periods was skewed (n = 54, 26; Table 3.4) and the difference in mean values was within 1‰ (Figure 3.10). Samples from summer/fall season had lower δ^{15}N values compared to winter/spring (posterior estimate = -0.61, 95% CrI = -0.97 to -0.24), although the observed difference was less than 1‰; there was no evidence for an effect of season on δ^{13}C values (Table 3.4). Sub-adults/juveniles had higher δ^{13}C values than adults (posterior estimate = 0.23, 95% CrI = 0.03 to 0.44), although sample size was skewed (Table 3.4; Figure 3.10). There was no estimated effect of age class on δ^{15}N values, or sex on δ^{13}C or δ^{15}N values (Table 3.4).

Table 3.4. Bayesian generalised linear model parameter estimates for $\delta^{13}C$ and $\delta^{15}N$ in relation to temporal and demographic covariates. Covariates with a 95% credible interval (CrI) that crosses zero are bolded.

Model	Parameter	Estimate	Lower 95% CrI	Upper 95% CrI
$\delta^{13}C$	a	-16.35	-16.52	-16.19
	b(Period: 2015-2020)	**0.48**	**0.29**	**0.67**
	b(Season: summer-fall)	0.20	-0.04	0.45
	b(Cluster 2)	-0.15	-0.36	0.06
	b(Cluster 3)	-0.04	-0.34	0.26
	b(Cluster 4)	0.00	-0.26	0.26
	b(Age class: sub-adult/juv)	**0.23**	**0.04**	**0.43**
	b(Sex: male)	-0.01	-0.19	0.16
$\delta^{15}N$	a	12.33	12.09	12.58
	b(Period: 2015-2020)	**0.50**	**0.22**	**0.78**
	b(Season: summer-fall)	**-0.61**	**-0.97**	**-0.25**
	b(Cluster 2)	0.00	-0.31	0.31
	b(Cluster 3)	0.25	-0.19	0.68
	b(Cluster 4)	-0.14	-0.52	0.25
	b(Age class: sub-adult/juv)	0.03	-0.27	0.32
	b(Sex: male)	0.06	-0.19	0.32

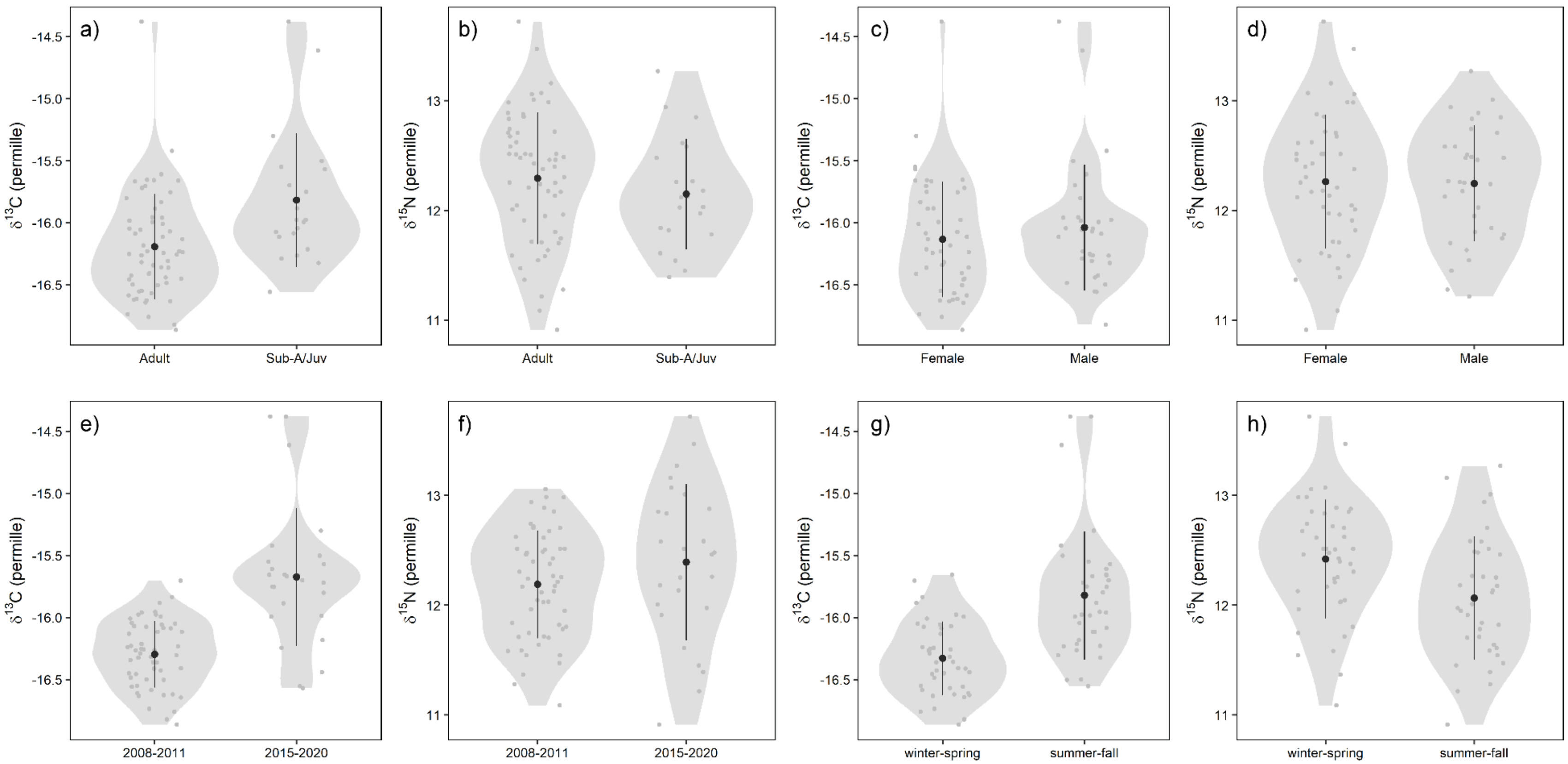

Figure 3.10. Violin plots of $\delta^{13}C$ and $\delta^{15}N$ values by (a, b) age class, (c, d) sex, (e, f) sampling period, and (g, h) sampling season, respectively. Points represent the mean value, and lines represent the standard deviation of the mean. Observations are shown as jittered points.

Cluster-level isotopic niches

Cluster-level isotopic niches were quantified in a Bayesian framework using the *nicheROVER* R package (Lysy et al., 2023; Swanson et al., 2015). For each social cluster, we fit a single model with 10,000 Markov chain Monte Carlo (MCMC) iterations and a flat Normal-Inverse-Wishart prior (Lysy et al., 2023). Niche size was considered the region of the posterior distribution with a 95% probability of containing individuals from each social cluster (Swanson et al., 2015). Pairwise niche overlap was assessed as the percentage probability of an individual from one social cluster falling within the niche space of another social cluster's niche (Swanson et al., 2015). We quantified the posterior distribution of niche overlap for both the overall niche space (95% probability region) and the core niche space (40% probability region) among social clusters (Table 3.5; Swanson et al., 2015).

Table 3.5. Mean posterior probability of bivariate $\delta^{13}C$ and $\delta^{15}N$ isotopic niche overlap (with 95% credible intervals) among social clusters for the overall niche (95% region) and core niche (40% region).

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Overall (95% region)				
Cluster 1	-	86.0 (68.5-97.5)	87.8 (65.6-99.0)	51.9 (32.6-72.5)
Cluster 2	83.1 (65.0-96.3)	-	71.8 (41.7-94.9)	41.3 (21.8-64.3)
Cluster 3	70.7 (45.8-92.9)	54.3 (27.7-84.6)	-	47.8 (28.3-71.4)
Cluster 4	92.3 (76.1-99.7)	90.9 (68.6-99.8)	95.5 (80.0-100.0)	-
Core (40% region)				
Cluster 1	-	33.3 (19.1-51.0)	29.8 (11.5-53.9)	13.1 (6.4-22.6)
Cluster 2	30.7 (17.7-47.2)	-	14.5 (2.5-35.1)	9.1 (3.5-17.4)
Cluster 3	20.9 (9.6-38.3)	12.6 (3.4-27.6)	-	12.6 (6.0-22.6)
Cluster 4	36.4 (13.0-63.4)	21.5 (3.1-53.0)	54.3 (27.5-80.7)	-

Mixing models: prey data, methods, and sensitivity analyses

We completed a literature search and compiled bulk $\delta^{13}C$ and $\delta^{15}N$ values available for 13 of 19 known false killer whale prey species that have been identified from observations of feeding events or stomach contents (Baird et al., 2021, Table 3.6; K. West Unpublished; 2008a; Zaeschmar and Baird, 2025). The six species that were unaccounted for either had another species in their functional group with stable isotope data (e.g., cephalopods, pelagic-oceanic fishes, neritic reef fish) or current evidence suggests they comprise a very small proportion of false killer whales' diet (elasmobranchs; Zaeschmar and Baird, 2025). Thus, our available data were reasonably representative of their known diet.

Prey $\delta^{13}C$ isotope values were Suess-corrected following the same methods described above for the false killer whale samples, particularly to account for temporal changes in anthropogenic CO^2 emissions. Studies accounted for the potential effect of lipids on $\delta^{13}C$ either through chemical extraction (Carlisle et al., 2021; Graham, 2007) or mathematical correction (Blum et al., 2013; Choy et al., 2015), while two studies reported low lipid content removing the necessity of lipid extraction (squid, Gloeckler et al., 2018; reef-associated fish, Sackett et al., 2015). There were several prey species with multiple studies reporting stable isotope values. For some of these studies, raw stable isotope values were made available, while others only reported means and standard deviations (SDs) for each prey species. Therefore, to comprehensively integrate values from all relevant studies, we resampled 1,000 values from the distributions of $\delta^{13}C$ and $\delta^{15}N$ for each prey/study and combined them into a cumulative distribution (and single mean and SD) for each prey species following Carlisle et al. (2021).

To discern whether differences in stable isotope methods across studies could potentially confound mixing model results, we ran a second version of the mixing model using only single-study prey data (i.e., data for each species comes from only one study). These studies also sampled prey during the same general time period (except for reef-associated fish), which mitigates any large-scale interannual variation in isotope values. We used values from Gloeckler et al. (2018) for mesopelagic cephalopods (purpleback flying squid, *Sthenoteuthis oualaniensis*, sampled in 2011 and 2014), Sackett et al. (2015) for neritic reef fish (uku, kahala, ulua; sampled 2003-2004 (uku, kahala) and 2009 (ulua)), and Carlisle et al. (2021) for all other prey species listed in Table 3.6 (sampled in 2011-2013).

Table 3.6. Summary of known false killer whale prey species sampled in Hawaiian waters or Central North Pacific region more broadly. Sample size (n*) reflects the number of samples from the referenced studies combined. Mean and standard deviation (SD) isotope values reflect the cumulative distribution of raw and resampled isotope distributions. Carbon isotope values ($\delta^{13}C$) were Suess-corrected to the year 2020 prior to summarizing the data. DVM = diel vertical migration.

Hawaiian name (common name; scientific name)	**n* all / n single**	**Mean (SD) δ^{13}C**	**Mean (SD) δ^{15}N**	**Evidence for DVM**	**Mean (SD) trophic position**	**Habitat zone: vertical/horizontal**	**Data, trophic level, and habitat references §**
A‘u ku (broadbill swordfish; *Xiphias gladius*)	28/9	-17.6 (1.7)	13.1 (1.7)	X	4.9 (0.9)	Epi-mesopelagic/oceanic	1,2,3 / 3,7,8
A‘u (shortbill spearfish; *Tetrapturus angustirostris*)	8/8	-17.2 (0.7)	11.3 (2.1)		4.5 (0.8)	Epipelagic/oceanic	2 / 9,10,22
‘Ahi po‘onui (bigeye tuna; *Thunnus obesus*)	55/9	-16.9 (0.7)	11.3 (1.1)	X	5.0 (0.6)	Epi-mesopelagic/oceanic	1,2,3,5 / 3,11
Ono (wahoo; *Acanthocybium solandri*)	11/11	-17.4 (0.4)	12.0 (1.4)		4.3 (0.2)	Epipelagic/oceanic	2 / 12,22
Mahimahi (dolphinfish; *Coryphaena hippurus*)	30/9	-16.7 (1.1)	10.7 (1.6)		4.3 (0.5)	Epipelagic/oceanic	1,2,3 / 3,13
‘Ahi (yellowfin tuna; *Thunnus albacares*)	30/9	-16.5 (1.0)	9.8 (1.9)	X	4.6 (0.1)	Epipelagic/oceanic	1,2,3,5 / 3,14,15
Aku (skipjack tuna; *Katsowonus pelamis*)	24/12	-17.0 (0.8)	9.9 (1.8)	X	4.3 (0.5)	Epipelagic/oceanic	1,2,3 / 3,16
‘Ahi palaha (albacore tuna; *Thunnus alalunga*)	3/3	-18.5 (0.4)	11.4 (0.6)	X	4.3 (0.2)	Epi-mesopelagic/oceanic	2 / 17,22
Opah (moonfish; *Lampris guttatus*)	40/10	-18.6 (1.1)	11.7 (1.0)	X	4.5 (0.1)	Mesopelagic/oceanic	1,2,3 / 3,18
Purpleback flying squid (*Sthenoteuthis oualaniensis*) †	28/3	-18.6 (0.5)	9.7 (2.1)	X	2.9 (NA)	Meso-bathypelagic/oceanic	2,4,25 / 19
Uku (blue-green snapper; *Aprion virescens*)	24/24	-16.3 (0.5)	9.5 (0.5)		4.3 (0.2)	Benthopelagic/coastal	6 / 20,21,23,24

Kahala (amber, almaco jack; *Seriola dumerili, rivoliana*)	8/8	-16.7 (0.2)	11.2 (0.2)	4.4 (0.03)	Benthopelagic/coastal	6 / 23,24
Ulua (giant trevally; *Caranx ignobilis*)	8/8	-13.7 (1.3)	11.5 (1.4)	3.8 (0.3)	Benthic/coastal	6 / 23,24

* Sample size reflects all available samples (i.e., all data references) and single studies of prey data (“single”) used in the sensitivity analyses

§ References: 1 Blum et al. (2013); 2 Carlisle et al. (2021); 3 Choy et al. (2015); 4 Gloeckler et al. (2018); 5 Graham (2007); 6 Sackett et al. (2015); 7 Abecassis et al. (2012); 8 Dewar et al. (2011); 9 Arostegui et al. (2019); 10 Arostegui et al. (2024); 11 Musyl et al. (2003); 12 Sepulveda et al. (2011); 13 Whitney et al. (2016); 14 Brill et al. (1999); 15 Lam et al. (2020); 16 Shaefer & Fuller (2007); 17 Domokos et al. (2007); 18 Polovina et al. (2008a); 19 Jereb & Roper (2010); 20 Tanaka et al. (2022); 21 Asher et al. (2017); 22 FishBase (n.d.); 23 Sackett et al. (2017); 24 HI DLNR; 25 Carlisle et al. (2015)

† Sample size for purpleback flying squid: one of the referenced studies (26) notes a sample size of 25 for squid with carbon and 127 for nitrogen, and we conservatively report the sample size of 25 (n = 28 with data from an additional reference) here.

We aggregated the 13 prey sources into groups *a posteriori* to increase the discrimination power and interpretability of the mixing model (Phillips et al., 2014, 2005; Stock et al., 2018). We defined four prey groups based largely on ecological and functional traits (Table 3.7): epipelagic predatory fishes (shortbill spearfish/a‘u, wahoo/ono, mahimahi, yellowfin tuna/‘ahi, skipjack tuna/aku, almaco jack/kahala, blue-green snapper/uku); mesopelagic predatory fishes (broadbill swordfish/a‘u ku, bigeye tuna/‘ahi po‘onui, moonfish/opah, albacore tuna/‘ahi palaha); reef-associated predatory fish (giant trevally/ulua), and mesopelagic cephalopods, using purpleback flying squid as model species. Mixing models were fit using the *MixSIAR* R package following the specifications detailed in the main text (Stock et al., 2018; Stock and Semmens, 2016). Trophic discrimination factors (TDFs) are incorporated into mixing models to account for discrimination in isotopes between the consumer and prey. We used the TDF values for carbon and nitrogen derived from a related species (bottlenose dolphins, *Tursiops truncatus*; δ13C = 1.01 ± 0.37‰, δ15N = 1.57 ± 0.52‰; Giménez et al., 2016) for our model on false killer whales, the closest species based on phylogeny and with a comparable metabolism (McGowen et al., 2020). Adequacy of prey sources and the TDF in capturing the consumers (i.e., false killer whales’) diet was assessed using simulated mixing polygons (Smith et al., 2013) and visually inspecting tracer plots (i.e., bivariate isotopic space with TDF corrections applied). Simulated mixing polygons and tracer plots indicated that all false killer whale isotope values fell within the isotopic space defined by the prey species with TDFs incorporated (Figures 3.11, 3.12). Posterior proportions of groups (and prey within those groups) for each social cluster and the population are provided in Table 3.8.

Table 3.7. Summary of false killer whale prey groups summarized *a posteriori* in mixing models.

Group	Species	Description
Epipelagic predatory fish	a‘u, ono, mahimahi, ‘ahi, aku, kahala, uku	Primarily occur and forage in the epipelagic zone; associate with surface mixed layer; limited diel vertical migrations; oceanic; includes benthopelagic fish
Mesopelagic predatory fish	a‘u ku, ‘ahi po‘onui, opah, ‘ahi palaha,	Primarily occur and forage in the mesopelagic zone, but some may migrate to the epipelagic zone over the diel cycle; oceanic
Reef-associated predatory fish	ulua	Primarily occur and forage in benthic or benthopelagic zones in shallow coastal habitats
Mesopelagic cephalopods	purpleback flying squid	Cephalopods that primarily occur and forage in the meso-bathypelagic zone, known to undertake diel vertical migrations

Two species—kahala and uku—overlap in habitat with ulua (separate group representing reef-associated game fish) but also use pelagic waters to an extent and isotopically were confounded with several epipelagic species (Figure 3.12, Table 3.8). Therefore, these species were grouped with epipelagic predatory fish in the model presented in the main text while ulua was kept separate (most isotopically distinct). To examine the effect of this decision, we also assessed outputs from a simplified mixing space with three prey sources: (1) epipelagic predatory fishes (as in Table 3.7), (2) shallow and deep reef-associated predatory fish (kahala, uku, and ulua), and (3) mesopelagic prey (mesopelagic predatory fishes from Table 3.7 combined with mesopelagic cephalopods). We acknowledge that aggregating 13 species into only three to four groups results in coarser depictions of sources to false killer whales' diet, and that some groups include prey species with slightly variable ecology or trophic level. However, we find these groupings still informative for our research questions as they are largely based on vertical and horizontal foraging habitat use of prey.

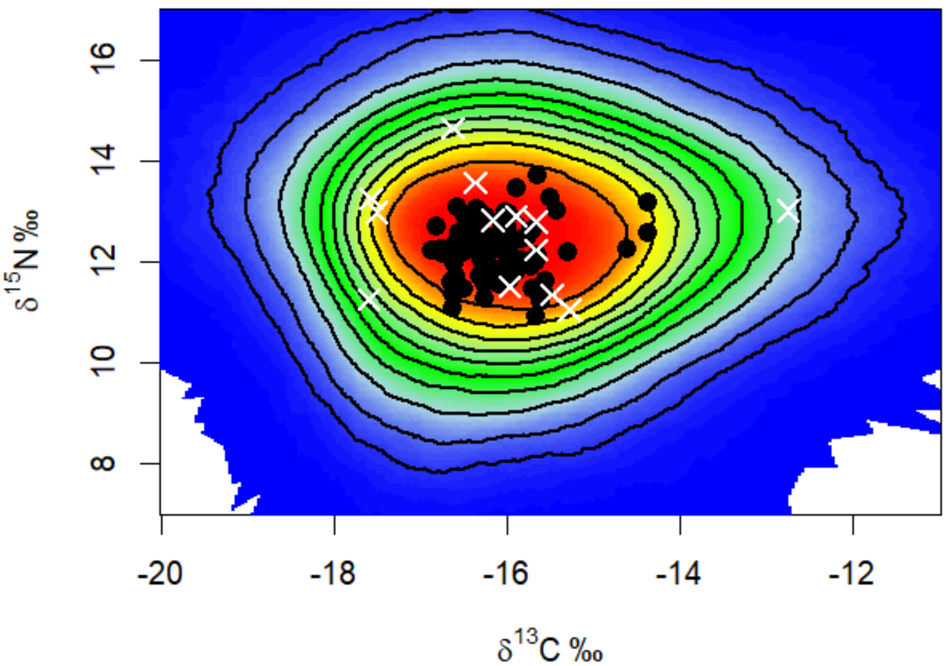

Figure 3.11. Simulated mixing polygon of prey species (white x's) and false killer whales (black dots). The probability that the prey fall within the consumer diet (i.e., false killer whales') increases with each inwards contour line (10% lines).

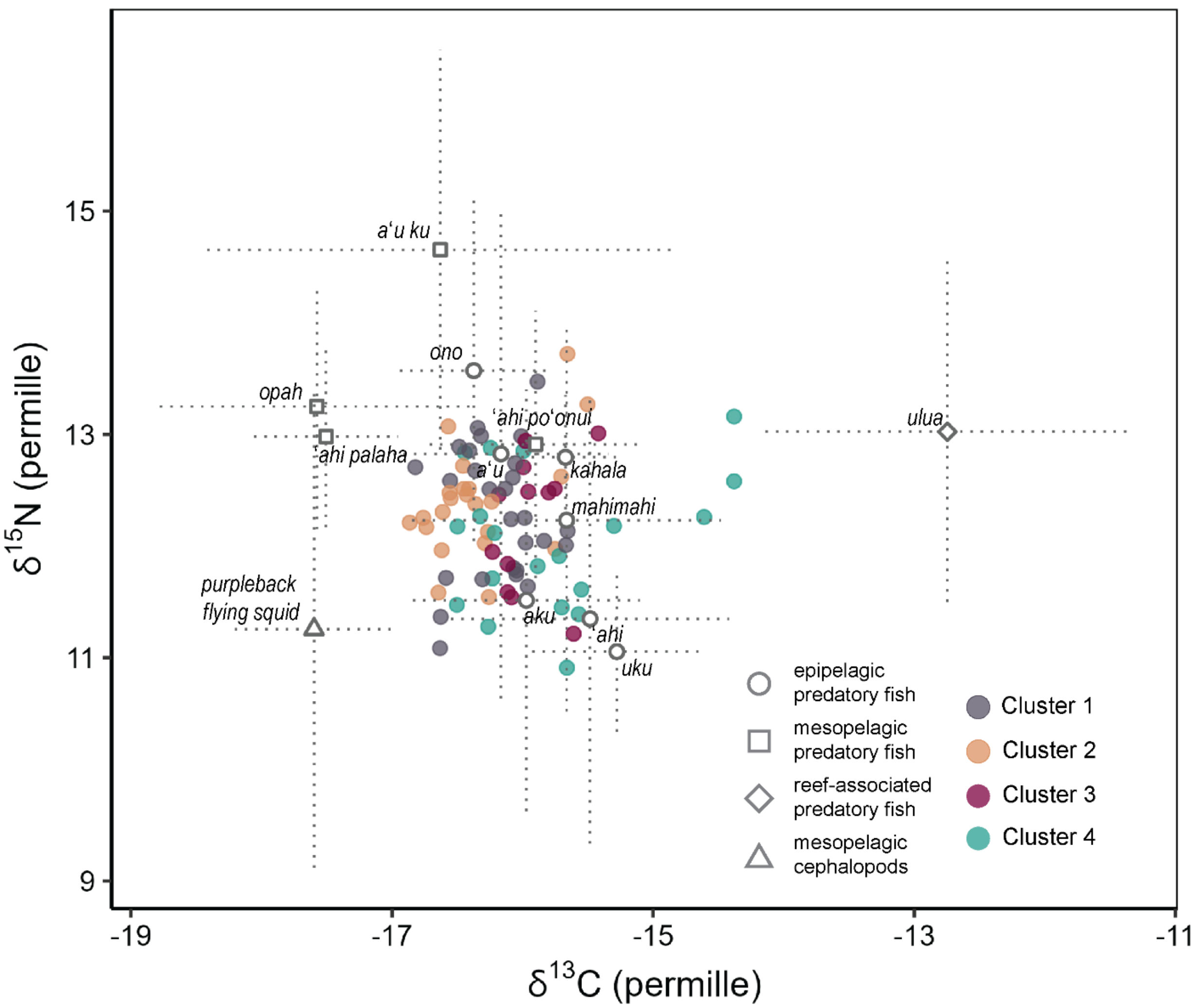

Figure 3.12. Bivariate δ^{13}C and δ^{15}N isotopic space of sampled false killer whales (points) and their prey (white shapes = means, dotted lines = standard deviations; trophic discrimination factors are incorporated).

Table 3.8. Stable isotope mixing model results with posterior mean (95% credible interval; CrI) predicted proportion of each prey group and individual prey species to false killer whales' diet for the population and by social cluster.

	Posterior mean proportion (95% CrI)				
Prey group, *species*	**Population**	**Cluster 1**	**Cluster 2**	**Cluster 3**	**Cluster 4**
Epipelagic predatory fish	0.611 (0.385-0.792)	0.600 (0.350-0.817)	0.538 (0.112-0.755)	0.658 (0.390-0.880)	0.715 (0.393-0.921)
Mahimahi	0.092 (0.001-0.286)	0.072 (0.001-0.250)	0.081 (0.001-0.280)	0.081 (0.001-0.293)	0.175 (0.001-0.616)
'Ahi	0.105 (0.005-0.298)	0.089 (0.003-0.263)	0.081 (0.002-0.258)	0.106 (0.002-0.320)	0.167 (0.002-0.551)
Ono	0.072 (0.003-0.219)	0.084 (0.001-0.323)	0.074 (0.001-0.286)	0.074 (0.001-0.277)	0.045 (0.001-0.163)
A'u	0.068 (0.003-0.223)	0.078 (0.001-0.300)	0.066 (0.001-0.266)	0.073 (0.002-0.289)	0.050 (0.001-0.231)
Aku	0.087 (0.004-0.267)	0.092 (0.002-0.318)	0.078 (0.002-0.263)	0.094 (0.002-0.319)	0.086 (0.001-0.446)
Uku	0.107 (0.002-0.315)	0.095 (0.001-0.286)	0.084 (0.001-0.261)	0.124 (0.001-0.364)	0.136 (0.001-0.568)
Kahala	0.082 (0.003-0.255)	0.091 (0.001-0.339)	0.075 (0.002-0.267)	0.106 (0.002-0.398)	0.056 (0.001-0.223)
Mesopelagic predatory fish	0.256 (0.108-0.440)	0.261 (0.067-0.475)	0.335 (0.107-0.551)	0.221 (0.060-0.431)	0.177 (0.040-0.372)
'Ahi palaha	0.093 (0.004-0.245)	0.106 (0.002-0.302)	0.145 (0.002-0.398)	0.075 (0.002-0.232)	0.053 (0.001-0.179)
'Ahi po'onui	0.068 (0.002-0.214)	0.071 (0.001-0.272)	0.068 (0.001-0.266)	0.072 (0.001-0.276)	0.054 (0.001-0.251)
A'u ku	0.038 (0.002-0.130)	0.030 (0.001-0.109)	0.038 (0.001-0.152)	0.029 (0.001-0.106)	0.031 (0.001-0.156)
Opah	0.058 (0.002-0.178)	0.054 (0.001-0.182)	0.084 (0.001-0.291)	0.044 (0.001-0.156)	0.039 (0.001-0.151)
Reef-associated predatory fish (*Ulua)*	0.047 (0.001-0.151)	0.034 (0.001-0.116)	0.031 (0.001-0.108)	0.047 (0.001-0.156)	0.053 (0.000-0.231)
Mesopelagic cephalopods (*Purpleback flying squid)*	0.086 (0.004-0.227)	0.104 (0.003-0.269)	0.096 (0.002-0.274)	0.074 (0.002-0.227)	0.055 (0.001-0.202)

Mixing model outputs using single-study prey isotope values generally had similar findings as the mixing models that used prey isotope values from all available studies. Estimated proportions of the four prey sources (Table 3.9) in the single-study prey isotope model were close or equal to the proportions estimated by the model using all prey isotope values (Table 3.8). The biggest differences were slightly increased proportions of reef-associated predatory fish for all clusters (differences in mean posterior proportions between 0.4-0.9) and higher epipelagic predatory fish proportions for Cluster 4 in the single-study model (difference in mean posterior proportion = 0.13; Table 3.9). Further, kahala and uku had the highest estimated proportions within the epipelagic group, albeit with higher uncertainty (Table 3.9). These observed differences are likely driven by sample sizes per prey species in the mixing model. The model fitted with single-study prey data had lower sample sizes of most epipelagic and mesopelagic predatory fishes that were more similar to, or even less than, the sample size of the reef-associated predatory fish (Table 3.6). The *MixSIAR* package incorporates uncertainty in prey source sample size into the mixing models, and thus prey source isotope summaries with higher sample sizes will have less uncertainty compared to those with lower sample sizes (Stock et al., 2018; Stock and Semmens, 2016). Additionally, the isotopic signatures of some epipelagic predatory fish that had higher proportions in the all-prey isotope value model (e.g., mahimahi, ‘ahi) were lower when only including the data from Carlisle et al. (2021) (Table 3.9). This additionally suggests an influence of sample size, and potentially a confounding effect of multiple prey occurring in similar isotopic space (Figure 3.12). Therefore, we can confidently infer that prey occurring in the defined epipelagic isotopic space make up a majority of false killer whales’ diet, but inferring prey-specific contributions within this space should be cautionary.

Table 3.9. Stable isotope mixing model results with four prey sources defined using prey data from only one study/source. Posterior mean (95% credible interval; CrI) predicted proportion of each prey group to false killer whales' diet for the population and by social cluster.

	Mean posterior proportion (95% CrI)				
Prey group, *species*	Population	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Epipelagic predatory fish	0.577 (0.336-0.796)	0.602 (0.336-0.835)	0.542 (0.295-0.789)	0.622 (0.340-0.856)	0.593 (0.269-0.878)
Mahimahi	0.057 (0.002-0.183)	0.067 (0.001-0.261)	0.055 (0.002-0.191)	0.059 (0.001-0.214)	0.044 (0.001-0.163)
'Ahi	0.080 (0.003-0.233)	0.088 (0.002-0.285)	0.088 (0.002-0.299)	0.075 (0.002-0.252)	0.063 (0.001-0.238)
Ono	0.058 (0.002-0.186)	0.063 (0.002-0.219)	0.063 (0.002-0.241)	0.057 (0.002-0.202)	0.045 (0.001-0.178)
A'u	0.045 (0.002-0.147)	0.047 (0.001-0.165)	0.039 (0.001-0.138)	0.045 (0.001-0.166)	0.037 (0.001-0.150)
Aku	0.064 (0.002-0.197)	0.067 (0.001-0.229)	0.062 (0.001-0.223)	0.062 (0.001-0.217)	0.055 (0.001-0.236)
Uku	0.174 (0.018-0.380)	0.158 (0.012-0.337)	0.137 (0.012-0.321)	0.201 (0.013-0.429)	0.278 (0.011-0.613)
Kahala	0.098 (0.007-0.267)	0.113 (0.005-0.357)	0.098 (0.005-0.328)	0.123 (0.004-0.409)	0.070 (0.003-0.226)
Mesopelagic predatory fish	0.243 (0.104-0.410)	0.236 (0.082-0.411)	0.298 (0.110-0.481)	0.211 (0.067-0.377)	0.184 (0.058-0.342)
'Ahi palaha	0.067 (0.004-0.195)	0.065 (0.002-0.209)	0.089 (0.002-0.301)	0.054 (0.002-0.178)	0.054 (0.002-0.192)
'Ahi po'onui	0.053 (0.002-0.173)	0.051 (0.001-0.179)	0.063 (0.001-0.236)	0.045 (0.001-0.160)	0.039 (0.001-0.141)
A'u ku	0.060 (0.002-0.194)	0.060 (0.002-0.205)	0.059 (0.002-0.210)	0.062 (0.001-0.223)	0.046 (0.001-0.173)
Opah	0.063 (0.002-0.188)	0.060 (0.001-0.199)	0.087 (0.001-0.277)	0.050 (0.001-0.163)	0.046 (0.001-0.163)
Reef-associated predatory fish (*Ulua*)	0.091 (0.007-0.218)	0.066 (0.004-0.162)	0.066 (0.003-0.162)	0.086 (0.004-0.208)	0.142 (0.003-0.323)
Mesopelagic cephalopods (*Purpleback flying squid*)	0.089 (0.005-0.238)	0.095 (0.003-0.260)	0.095 (0.003-0.258)	0.082 (0.003-0.231)	0.081 (0.002-0.279)

Mixing model outputs with the three-prey source model—where kahala and uku were grouped with ulua as reef-associated predatory fish—largely showed similar findings as the four-prey source model, where epipelagic predatory fish contributed the most to false killer whales' diet followed by mesopelagic prey and reef-associated predatory fish (Table 3.10). The movement of kahala and uku from the epipelagic to reef-associated predatory fish group naturally resulted in slightly higher proportions of reef-associated predatory fish in the three-prey source model (population posterior mean = 0.24, 95% CrI = 0.07 to 0.46) compared to the four-prey source model (population posterior mean = 0.05, 95% CrI = 0.00 to 0.15). This also resulted in lower proportions of epipelagic predatory fish across all social clusters (Table 3.10). Despite these differences, cluster-specific trends in dietary proportions were largely preserved: Clusters 1 and 2 had the highest proportions of mesopelagic prey, and slightly lower proportions of reef-associated predatory fish (Table 3.10). Similar to the four-prey source model, Cluster 4 had the lowest proportion of mesopelagic prey sources and highest proportion of epipelagic predatory fish in the three prey-source model (Table 3.10).

Table 3.10. Stable isotope mixing model results with three prey sources defined. Sources: epipelagic predatory fish = a‘u, ono, mahimahi, ‘ahi, aku; mesopelagic prey = a‘u ku, ‘ahi po‘onui, opah, ‘ahi palaha, purpleback flying squid; reef-associated predatory fish = kahala, uku, ulua; posterior mean (95% credible interval; CrI) predicted proportion of each prey group to false killer whales’ diet for the population and by social cluster. Prey-specific contributions to diet are provided in Table 3.9 but note the potential confounding effect of multiple prey occurring in similar isotopic space (Figure 3.12).

	Posterior mean proportion of diet (95% CrI)		
	Epipelagic predatory fish	Mesopelagic prey	Reef-associated predatory fish
Population	0.42 (0.17-0.66)	0.34 (0.18-0.52)	0.24 (0.07-0.50)
Cluster 1	0.41 (0.14-0.72)	0.37 (0.17-0.58)	0.22 (0.04-0.46)
Cluster 2	0.38 (0.13-0.66)	0.43 (0.24-0.63)	0.19 (0.03-0.41)
Cluster 3	0.43 (0.15-0.73)	0.30 (0.11-0.51)	0.28 (0.06-0.55)
Cluster 4	0.52 (0.10-0.85)	0.23 (0.07-0.46)	0.25 (0.03-0.65)

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4. SCALE-DEPENDENT OCEANOGRAPHIC DRIVERS OF CO-OCCURRENCE AND CONFLICT RISK BETWEEN PELAGIC FALSE KILLER WHALES AND LONGLINE FISHERIES

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4.1 Abstract

Co-occurrence between marine predators and fisheries can result in competition for resources, depredation, bycatch and economic loss, making mitigation of such potential conflicts a central challenge in applied ecology. Developing effective mitigation strategies requires understanding the ecological factors that promote co-occurrence. However, obtaining such information is challenging in the open ocean where resources are highly ephemeral and predators and fishing vessels move over extremely large scales, as the case of pelagic false killer whales (*Pseudorca crassidens*) and Hawai‘i's commercial longline fleet. With satellite-tagged false killer whales (n=19 whales/11 groups; 864 combined days tracked; 2013-2025), vessel logbooks (n=170 vessels; 53,220 sets), and satellite-derived AIS products (n=81,228 fishing events), we quantified spatial behavior of both whales and longliners relative to oceanographic features at multiple scales to identify the ecological contexts underlying co-occurrence and potential conflict. Habitat selection models show high similarity between whales and longliners in their range-wide selection for increased sea surface height—indicative of prey-aggregating anticyclonic eddies—but also some differences. Whales selected for areas reflective of submesoscale features (e.g., meanders, fronts) compared to longliners, who consistently selected for areas with static features (e.g., more seamounts). Whale habitat selection models did not improve with the addition of longline covariates suggesting their distribution is not directly driven by fishing activity. At intermediate scales, whales moved more widely when ecological conditions were unfavorable—indicative of increased search effort for alternative prey patches. At finer scales, some of these oceanographic drivers corresponded with co-occurrence patterns, where whales were more likely

to be within 50km of a fishing event when prey accessibility was lower—which was further supported by confirmed co-occurrences that resulted in depredated gear. However, groups were infrequently within 50km of longliners (median percent of days=14.7%), limiting the explanatory power of these models. Together, these findings suggest that shared affinities for mesoscale eddies can result in broad co-occurrence of whales and longliners, while fine-scale interactions are likely to occur under ecologically poor conditions. As such, mitigation strategies should consider dynamic oceanographic contexts by incorporating environmental indicators into spatial management or fleet advisories to improve proactive conflict reduction.

4.2 Introduction

Co-occurrence of marine predators and fisheries can generate competition for shared prey resources and escalate into negative interactions, including bycatch mortality and economic losses from depredation. Such conflicts remain both a management priority and a persistent challenge (Drymon et al., 2024; Tixier et al., 2021). Effective mitigation therefore requires understanding the ecological and behavioral circumstances conducive to co-occurrence and conflict (Wade et al., 2021). Yet, the often narrow focus on documenting spatial overlap or conflict events (e.g., depredation rates) fails to capture the independent decision-making processes of fishers and predators that underpin co-occurrence in the first place (Tixier et al., 2021). It becomes imperative, then, to consider the perspectives of each actor—fishers, predators, prey. Fishers select fishing grounds for multiple reasons (Dorn, 2001; Guiet et al., 2019), including forecasted oceanographic conditions that concentrate profitable target fish species and fidelity to historically productive fishing areas informed by experience or traditional ecological knowledge (Glazier, 2007; Teh et al., 2012). Prey fish and predators can sense such oceanographic conditions across spatial and temporal scales (Pinti et al., 2025; Torres, 2017), shaping movement decisions that can place them in close proximity to fishing activity. Indeed, fishers worldwide track the same aggregative, fine-scale physical oceanographic features used by marine predators, increasing the likelihood of bycatch (e.g., Scales et al., 2018; Watson et al., 2018). Thus, while co-occurrence may initially arise from independent pursuit of shared resources, it creates the ecological context in which neutral overlap can escalate into conflict.

In some systems, interactions go beyond passive overlap: predator species may intentionally respond to fishing activity. When fisheries provide predictable foraging opportunities (e.g., through hooked or discarded catch; Chilvers and Corkeron, 2001; fish aggregating devices; Patti et al., 2026), or when local prey patch quality is poor (Bankhead et al., 2026; Powell and Wells, 2011), predators may actively adopt fisheries-oriented foraging tactics. For example, the plausible “dinner bell” effect suggests that sperm whales (*Physeter macrocephalus*) changed their behavior and moved towards vessels in response to acoustic signatures of vessels’ fishing activity (Thode et al., 2007). These behaviors can be socially learned and spread to other members of the population (e.g., Schakner et al., 2014), sometimes with negative long-term consequences for individual fitness and population structuring (e.g., Auguin et al., 2024; Busson et al., 2019; Tixier et al., 2017). Fisheries-associated foraging is now commonplace in odontocetes worldwide (Hersh et al., 2025). Taken together, this evidence highlights that predator movements reflect both the ecological context of the physical environment (e.g., patch quality) and behavioral decisions influenced by the social environment (e.g., the foraging of conspecifics; Webber et al., 2023), which jointly can shape patterns of co-occurrence with fisheries across scales. These dynamics are particularly relevant in pelagic systems, where environmental variability is high and fisheries operate over broad spatial extents.

The high seas surrounding the Hawaiian Archipelago, home to the ‘pelagic’ stock of false killer whales (*Pseudorca crassidens*; hereafter ‘pelagic false killer whales’; Bradford et al., 2015), provides a compelling case study for understanding how these coupled environmental and social processes operate in real-world fisheries. False killer whales are upper trophic level predators, and members of this population are known to feed on large predatory game fish of high economic value (tuans, mahimahi *Coryphaena hippurus*, billfish; Zaeschmar and Baird, 2025). They are also strongly social: false killer whales live in social groups with relatives and non-kin associates, and those in Hawai‘i are known to cooperatively hunt for and share prey among companions (Baird, 2016; Baird et al., 2008a). Since pelagic false killer whales range widely in the central North Pacific region around the Hawaiian Archipelago (Anderson et al., 2020; Fader et al., 2021), they overlap with the operational range of Hawai‘i’s longline fisheries, excluding areas prohibited to longline fishing activity—the Main Hawaiian Islands year-round exclusion zone and the Papahānaumokuākea Marine National Monument (PMNM). The shallow-set longliners primarily target swordfish (a‘u ku, *Xiphius gladius*) while the deep-set targets bigeye tuna (‘ahi po‘onui, *Thunnus obesus*), but both often catch other marketable fishes (e.g., yellowfin tuna or ‘ahi *Thunnus albacares*, mahimahi, wahoo or ono *Acanthocybium solandri*; Boggs and Ito, 1993). Such overlap in whale diet and commercially targeted species has consequently led to depredation by and bycatch of false killer whales primarily in the deep-set longline fishery. In accordance with the U.S. Marine Mammal Protection Act, the high bycatch rates in the 1990s through early 2000s led to the establishment of the False Killer Whale Take Reduction Team (TRT) in 2010, a multi-stakeholder group of biologists, fishers, and managers. TRT members are tasked to develop a Take Reduction Plan (TRP) to reduce mortality and serious injury below the estimated Potential Biological Removal (PBR)—a reference point for how many individuals can be removed from the population while allowing it to reach or maintain its optimum sustainable size—within six months of implementation and to a level approaching zero (<10% of PBR) [16 U.S.C. 1387 (f) (2)].

Since the establishment of the TRT, there have been several studies undertaken to inform factors that may increase the probability of pelagic false killer whale bycatch and depredation in the commercial deep-set longline fishery. Acoustic studies indicate that pelagic false killer whales most frequently approach gear during the hauling phase of deep-set fishing, and that whales move along the line during this phase in tandem with the boat (Bayless et al., 2017; Thode et al., 2016); satellite transmitter-inferred movement data have also indicated that they tend to orient themselves towards vessels during the haul phase (Anderson et al., 2020). Vessel observer data indicate that depredation risk increased when vessels that already experienced depredation continued fishing in the same area following the first occurrence (i.e., repeat depredation on the same vessel), and that moving extensive distances (100 km) only slightly decreased this risk (Fader et al., 2021; Forney et al., 2011). While these same studies explored habitat covariates as predictors of bycatch or depredation rates, the predictive power of such habitat covariates in depredation models were poor, and operational covariates (i.e., aspects of catch and fishing activity) were stronger predictors (Fader et al., 2021; Forney et al., 2011). Despite such recent advancements, they are focused on directly modeling the probability of depredation or bycatch in the U.S. Hawaiian deep-set longline fishing fleet. However, other factors influencing the space use of pelagic false killer whales may not be apparent in these models due to several reasons: (1) behavioral decisions of pelagic false killer whales—whales may not always choose to pursue a vessel but rather exploit other habitat patches within their range, or could rely on social cues from distant associates; (2) incomplete fishery observer coverage, resulting in poor predictability of depredation rates; and (3) the presence of non-U.S. deep-set longline fishing vessels in the region that pelagic false killer whales may also interact with (although recent work indicates foreign fleets comprise <10% of longline effort in their range; Ahrens et al., 2026).

Here, we applied a multi-scale analytical framework to identify habitat features that may drive co-occurrence of, and conflict risk between, pelagic false killer whales and commercial longline fishing activity. We specifically assessed whale and fisher use of mesoscale (10-100 km) oceanographic features (e.g., anticyclonic eddies), which are known to enhance biological productivity and aggregate pelagic predatory fishes in the range of the fishery and pelagic false killer whales (Arostegui et al., 2022; Dufois et al., 2016). We analyzed locations from satellite-linked tags on pelagic false killer whales combined with longline vessel operations at three focal scales: (1) range-wide habitat selection patterns to infer the relative similarity in spatial behavior of whales and fishers; and (2) track-level movements to assess the extent to which oceanographic contexts may influence false killer whale multi-day spatial decisions, and whether these patterns relate to co-occurrence with longline vessels; and (3) fine-scale false killer whale movement behavior (e.g., directional changes) in relation to nearby fishing operations—as well as their social associates—to identify potential approaches to and interactions with longline gear. Our analysis differs from previous studies on pelagic false killer whale interactions with fisheries by focusing on the habitat selection of false killer whales independent of depredation or bycatch incidences, and thus provides a broad overview of relative probability of co-occurrence of false killer whales and fishers and the socioecological contexts surrounding them.

4.3 Methods

4.3.1 False killer whale data & processing

False killer whale movements were obtained through satellite-linked tagging and individual demographic information were derived from a combination of biopsy sampling (e.g., for sex, haplotype) and photo-identification based assessments. Satellite-linked tagging and biopsy sampling were undertaken through two survey methods: (1) small-scale boat-based surveys led by Cascadia Research Collective (CRC) throughout the main Hawaiian Islands (2000-present; Baird et al., 2024, 2013b) and (2) large-scale ship-based surveys led by NOAA PIFSC in 2013, 2017, and 2024 (Bradford, 2024a; Yano et al., 2018). Data from seven satellite-linked tags deployed on pelagic false killer whales from Anderson et al. (2020) and Fader et al. (2021) are included here in addition to data from 14 tags deployed since 2020 or earlier but not included in the aforementioned studies.

Photographs of tagged individuals were processed and matched to a long-term photo-identification catalog to determine catalog identification (ID) if previously sighted or previously tagged, or assigned a new catalog ID if never encountered before, following methods described in Baird et al. (2008a). Membership to the pelagic false killer whale stock was inferred through several lines of evidence: (1) social association patterns—whether individuals have been documented forming groups with known individuals from either of the insular stocks (Mahaffy et al., 2026); (2) genetics—for biopsy sampled individuals, whether their mitochondrial haplotype is shared with insular stocks or offshore North Pacific false killer whales (Martien et al., 2014); and (3) geographic locality and movement patterns—whether movements were in the known range and pattern of insular stocks, the latter of which exhibit clear and consistent island-associated movements (Baird et al., 2013a; Kratofil et al., 2026a, 2023). We re-iterate that the three false killer whale stocks are partially sympatric, meaning that there is some geographic overlap among their ranges (Bradford et al., 2015). Thus, the additional behavioral (social association patterns) and genetic (when available) lines of evidence were particularly useful for inferring stock of tagged whales that spent time within the vicinity of insular stocks. Social network analyses were then used to identify distinct social components, as sets of catalogued individual whales recurrently observed associated in groups (Mahaffy et al., 2026). Age class at tagging/sampling was assigned based on a combination of quantitative (i.e., time in catalog) and qualitative (e.g., relative size, markings) assessments following Kratofil et al. (2026b). Sex was either determined genetically (following Martien et al., 2014), inferred from the presence of sexually dimorphic features (Kratofil et al. 2026b) or presence of calf, or unknown.

Satellite-linked tags were deployed in the Low-Impact Minimally Percutaneous (LIMPET) configuration following methods detailed in Baird et al. (2012, 2010), and biopsy samples were obtained following Ylitalo et al. (2009). Satellite-linked tags included both Argos location-only tags (SPOT5, SPOT6, Wildlife Computers Inc, Redmond, WA) and Argos and Fastloc®-GPS location- and dive-depth transmitting tags (SPLASH10-F, Wildlife Computers Inc, Redmond, WA). While programming regimes varied over the years, all tags were generally programmed to transmit during hours with the best satellite coverage. Location-only tags were programmed to duty cycle later into the deployment to increase longevity, albeit with larger temporal gaps. Location data were filtered to remove erroneous locations (i.e., based on unrealistic speeds, turn angles) following the protocol in Kratofil et al. (2023). Filtered location data were fit to continuous-time movement models in the *ctmm* R package (Fleming and Calabrese, 2023), incorporating positional uncertainty, for subsequent analyses. Where more than one whale was tagged during a given period, we calculated pairwise distances (using the *ctmm* package) to identify non-independent tracks. Dive behavior data on three pelagic false killer whales from Kratofil et al. (2026c) were used here for inferring behavior relative to longline activity. The program R v4.5.2 (R Core Team, 2025) was used for all subsequent analyses.

4.3.2 Fishery data & processing

We used a combination of U.S.-based longline logbook, observer, and satellite-derived products as fishery data sources for subsequent analyses. Logbook and observer data are limited to the U.S. longline fleet (requested from and provided by the National Marine Fisheries Service (NMFS)), and thus we also incorporated Global Fishing Watch (GFW) satellite-derived products to account for fishing activity by foreign fleets.

Logbook data consist of each captain's recorded start and end dates, times, and locations (latitude, longitude) of longline gear setting and hauling operations (i.e., four times and four positions), as well as the number of hooks in the set, the length of the mainline, and the number of fish caught by species. A vessel 'proxy' variable was also provided for each operation, which represents a unique operator/vessel identification excluding personal identifiable information. The accuracy of logbook set and haul locations varies in quality, as some captains only reported a single location for each of the four operation time points. While false killer whale depredation predominantly occurs in the deep-set longline fleet (Bradford, 2024b), we incorporated logbook data from both shallow- and deep-set operations. Longline logbook data are confidential, and thus resulting data products incorporating this information were intentionally made vague to meet confidentiality requirements. There is a federal fishery observer program for the longline fleet, where observers are placed on vessels to collect data on catch (e.g., measurements, discards), weather conditions, depredation of bait or catch, bycatch (including marine mammals), and observations of protected species (e.g., marine mammals, sea turtles, seabirds). These observer data were obtained for assessing potential tagged whale approaches to longline gear, as observer records of depredation or bycatch on longline operations could ground truth tagged whale behavior. Observer coverage in the deep-set long-line fleet was approximately 20% from 2000 through 2023, reduced to 13% in 2024, and 7% in 2025; the shallow-set fleet has 100% observer coverage, but as noted above, false killer whale interactions with this fleet are comparatively rare. Thus, observer data was not available for all potential approaches to gear. Hereafter, we refer to vessels or trips with observer data as ‘observed vessels’.

We obtained fishing event data from GFW for periods overlapping with tag data post-2012, which is the earliest year that GFW data is available. GFW identifies fishing vessel types and presence using a combination of Automatic Identification System (AIS) data, a neural network classifier, vessel registry databases, and manual review (Kroodsma et al., 2018). Apparent fishing activity is then inferred from these vessels based on changes in vessel speed and direction. Fishing events summarize consecutive apparent fishing locations into a single ‘event’, with spatial and temporal restrictions applied to mitigate repeated observations or spurious event inferences (Kroodsma et al., 2018). Thus, summarized fishing events are somewhat similar to the logbook set and haul operation data. We downloaded GFW fishing event data using the *gfwr* R package (Sánchez-Tapia et al., 2026), and filtered fishing events to vessels that had any of the following gear type descriptions: ‘set longlines’, ‘drifting longlines’, ‘pole and line’, and ‘trollers’. We included the latter two gear types as false killer whales are also known to interact with these hook and line types. Resulting fishing events included the start and end date, time, vessel ID, a centroid position for the event (i.e., single latitude, longitude), and a bounding box for the event (i.e., two latitudes, two longitudes). All data sources were obtained for the same temporal extent of the false killer whale tag data, and the same spatial extent of the tag data plus a 1-degree buffer to allow analysis of tagged whale movements in relation to distant fishing operations.

4.3.3 Quantifying habitat selection

Broad scale habitat selection patterns were quantified using a similar approach for both tagged false killer whales and longline vessel operations. We fit resource selection functions (RSFs) in an “used-available” framework (Manly et al., 2002), where tag/vessel locations represented “used” locations and “available” locations were sampled from spatial availability domains (i.e., “third order”, within-home range selection; Manly et al., 2002). We defined the availability domain for each tagged false killer whale and unique vessel ID as the bounding box of their locations (buffered by 1 degree) and sampled available locations at a ratio of 1:25 used to available locations (Northrup et al., 2013). For false killer whales, we considered 6-hourly predicted locations (predicted in *ctmm*) as the used locations to mitigate spatial autocorrelation. We excluded predicted locations with estimated error ellipses exceeding 20 km prior to analyses. For longline vessels, we restricted this analysis to U.S. vessels from the logbook data which contains the most consistent and accurate information on within-vessel fishing operations (see Turner et al., 2025). We considered each unique longline set as the unit of selection as this reflects the captains' decision on where to catch fish. We used both the start and end locations of each set within a single "used" unit and weighted each location by 0.5 in the RSF to mitigate pseudoreplication and reflect uncertainty in the true position of the gear. In cases where captains only reported a single value for both the start and end of setting the gear, we assigned a weight of 1 for these used locations.

Environmental variables were then extracted for all used and available locations. We explored a variety of candidate oceanographic variables related to mesoscale (10-100 km) and sub-mesoscale (<10 km) processes as well as static habitat features (Table 4.1). Dynamic variables included sea surface temperature (SST) and its standard deviation (SST SD; calculated across the 3 nearest pixels in the *raster* R package Hijmans, 2025), sea surface height (SSH), mixed layer depth (MLD), sea surface salinity (SSS), eddy kinetic energy (EKE), surface chlorophyll-a concentration (CHLA), dissolved oxygen concentration at 150 m depth (OXY150), and wind speed above the sea surface (WIND). All surface and sub-surface variables were obtained at a daily resolution, and spatial resolutions varied between 4 km and 25 km (see Table 4.1 for source details). Eddy kinetic energy was derived from geostrophic current velocity vectors (*u, v*) as in equation (1) below.

$$EKE = \frac{(u^2 + v^2)}{2}$$

Surface chlorophyll-a concentration was log10 transformed prior to modeling following Glover et al. (2018). Static variables considered included seafloor slope, distance to the nearest seamount, and the number of seamounts within 25 km. Raster-based variables were extracted to whale and vessel operation locations using the *stars* package (Pebesma and Bivand, 2023), and distance-based variables were calculated using the *sf* package (Pebesma, 2018). Locations with missing covariates (e.g., those occurring in grid cells close to land, missing data) were removed, and available locations were re-sampled at a ratio of 1:20 used to available locations.

We used a two-stage approach to quantify habitat selection following Johnson et al. (2022) and Kratofil et al. (2026a): the first stage consisted of individual-level RSFs and the second stage modeled these outcomes in a multivariate meta-mixed effects model to estimate sample population parameters. This framework approximates a full Bayesian hierarchical model and thus robustly accounts for among-individual variation in habitat selection patterns (Johnson et al., 2022; Muff et al., 2020). Individual-level RSFs (stage 1) were fit using the *brms* package (Bürkner, 2018), with the response (used/available; likelihood-weighted for vessel sets as described above) modeled with a Bernoulli distribution (logit link) and environmental covariates as predictors. All environmental predictors were centered and scaled prior to model fitting. We assessed pairwise correlation among predictor variables prior to modeling; where two variables were correlated (Pearson's correlation > 0.5), we selected one of the variables for subsequent modeling based on the most direct ecological interpretation. We used default diffuse priors for all parameters. Stage 1 models were fit with 4 chains, 6,000 iterations, and a 3,000 warm-up period. Model convergence was assessed through mixing of chains, R-hat values, and posterior-predictive checks. Posterior means and (co)variance matrices were obtained from Stage 1 models and used to fit stage 2 models in the *mixmeta* package (Sera et al., 2019). Tagged whale

ID/vessel ID were specified as random effects in these models; where tagged whales moved in concert (see above), only the longest track was used in stage 2 models to represent the group's movements and avoid pseudoreplication. We explored several candidate RSFs based on hypotheses of environmental and operational variables (for whales). Thus, we specified the maximum likelihood method when fitting stage 2 models so that candidate models within the same dataset could be compared using AIC.

For the false killer whale RSF, we fit the top model with additional longline operation covariates (distance to the nearest set/haul) to determine whether longline fishing activity improved habitat selection models. We created spatial lines out of set and haul locations using the start/end locations for each, and calculated the distance of each false killer whale used/available point to the nearest set and haul on each day with the *sf* package (Pebesma, 2018). We additionally fit the same model but with a distance to the nearest fishing activity covariate, which represented the minima of the three distance-to-fishing variables: logbook set, logbook haul, and GFW fishing event. The GFW dataset has the advantage of incorporating information on foreign fishing vessels in addition to domestic vessels, but it did not always capture all of the longline operations recorded in the logbook data. Thus, using the minima of the three distance-to-fishing variables—as opposed to either logbook or GFW distance variables—ensures that all potential fishing activities within the vicinity of tagged whales were accounted for. Distances from tagged whale locations to the nearest GFW fishing event (using the centroid location) were calculated using the same method used for longline logbook sets and hauls described above.

4.3.4 Assessing within-range movement behavior

We examined ecological factors shaping false killer whale movement decisions at finer scales by deriving weekly range-use ratios and relating these ratios to environmental variables. Range-use ratios can be used to infer periods when tracked animals exhibited an area-restricted behavior (i.e., lower ratio) versus a more dispersive pattern (i.e., higher ratio) relative to a specific time period or range, and thus can inform potential ecological drivers of movement decisions (Spiegel et al., 2017; Webber et al., 2020). While many studies investigate fine scale movement-habitat relationships through methods such as step-selection functions and hidden Markov models (Beumer et al., 2023; Langrock et al., 2012), these approaches are not amenable to our available data: modeling step-level decisions in our study is limited by the spatial resolution of environmental covariates (9-27 km), and ultimately constrains the availability domain to few options and scales that may or may not be relevant to false killer whales. Hidden Markov models were explored, but often failed to converge, likely due to the temporal sampling of our satellite tags and the inherent coursing-type movement behavior of predators like false killer whales (i.e., foraging can occur during directed movements; Glennie et al., 2023). Range-use ratios, while coarse metrics, allowed us to explore ranging behaviors at scales relevant to and appropriate for our tagged false killer whales and available habitat covariates, and have been used for similar purposes in a variety of study systems (e.g., Barrios et al., 2024; Michelangeli et al., 2022).

To understand drivers of movement within each tagged whales' spatial ranges, we calculated weekly range-use ratios by dividing the area of the weekly 50% minimum convex polygon (MCP) by the overall 95% MCP for each tagged whale. We chose the weekly 50% MCP over the weekly 95% MCP to reflect the core areas of use during these time periods, and to also prevent artificially high range-use ratios resulting from shorter tag durations. We chose a weekly time step because it captures the temporal persistence of many oceanographic features spanning submesoscale and mesoscale ranges (Lévy et al., 2012; Taylor and Thompson, 2023), and to provide an adequate time window to capture shifts in false killer whale movement behavior while taking into account their known wide-ranging tendencies (moving up to 150 km/day; Bradford et al., 2014; Fader et al., 2021). We excluded weeks of data that had fewer than 3 days during which location data transmitted (e.g., when some tags were duty-cycled) to ensure range-use ratios were reasonably representative of weekly movements; across the 11 groups tracked, this resulted in a total of 99 weekly range-use ratios. MCPs were calculated using the *adehabitatHR* R package (Calenge, 2024) and using the model fitted locations (i.e., original timestamps from tags) to avoid artificial range dimensions that could result from model-predicted points that were interpolated during periods with large gaps in tag transmissions. Islands were removed from MCP spatial objects when necessary prior to area calculations using the *sf* package (Pebesma, 2018). The average values of daily oceanographic variables within each weekly 50% MCP range were extracted using the same methods as described above. Correlation among environmental predictors was assessed prior to modeling following the same approach applied to the habitat selection analyses. For this specific analysis, we focused on environmental variables reflective of dynamic oceanographic features, and not topographic features, to make inferences on relationships between movements and ephemeral habitats that both whales and fishers navigate.

We used generalized additive mixed effects models (GAMMs) to quantify the influence of environmental variables on weekly range-use ratios, which allow for non-linear relationships. GAMMs were fitted using the *mgcv* package in R (Wood, 2017). Range-use ratios were modeled as the response with a Gamma distribution and log link, and all environmental variables were modeled as smooth predictor terms (thin-plate regression splines). Individual tag ID was specified as a random effect; there was not enough data to model individual-specific random smooths (i.e., to fully account for among-individual variation; Pedersen et al., 2019). Weights were applied to each individual based on the number of weeks of data, so that individuals with fewer weeks tracked were downweighted relative to the tag with the longest tracking duration. We used the double penalty shrinkage approach to variable selection, which penalizes variables with little contribution to the model to zero (Marra and Wood, 2011). Model performance was assessed through visual inspection of residuals and the *gam.check()* function.

4.3.5 Examining drivers of co-occurrence

4.3.5.1 Environmental features promoting co-occurrence

We investigated how relationships between tagged whale ranging behavior and ecological contexts (i.e., analyses in section 4.2.4) might subsequently relate to co-occurrence with longline vessels. We fit a GAMM relating co-occurrence between tagged false killer whales and fishing activity within 50 km to the same set of environmental variables considered in the habitat selection and range-use ratio models. We defined 50 km as the scale of co-occurrence as this distance is well within the range of typical longline gear lengths (~30-100 km; Boggs and Ito, 1993). We also fit models with co-occurrences defined within 75 km, 100 km, and 125 km to infer any scale-dependent patterns. Longline fishing activity was defined as any operation from the combined data sources (i.e., a logbook set or haul operation, or a GFW-identified fishing event), and similar to the RSF models, we used the minima of the three distance-to-fishing variables—logbook set, logbook haul, and GFW event—as the distance to inform co-occurrence. Whale locations (6-hourly, predicted) were assigned a 1 if they were within 50 km of a set, haul, or GFW fishing event and otherwise a 0; this same dichotomy was applied for the other co-occurrence scales for the sensitivity analysis. We then modeled this metric (0 or 1 for co-occurrence) with a binomial distribution (logit link) and all environmental variables were fit as smooth predictors with thin-plate regression splines in the same manner described in Section 4.3.2.4. Individual tag ID was included as a random effect. The same model fitting and performance check procedures described above were used for this model. A first order autocorrelation structure was included in the models after preliminary results indicated the presence of temporal autocorrelation in the residuals; this was completed using the *itsadug* R package (van Rij et al., 2025) and *bam()* function in *mgcv* (Wood, 2017).

4.3.5.2 Case studies: potential approaches to gear

We qualitatively assessed tagged false killer whale approaches to longline gear, potential depredation events, and the environmental contexts surrounding them. We restricted the fishing data to the U.S.-based longline logbooks for this sub-analysis because the paired fishery observer data—which reports bycatch and depredation—can be used to validate potential false killer whale-fishery interactions. We narrowed down the analytical dataset by first identifying tagged whale locations within 100 km of a longline set or haul; for this analysis, we used all available locations (i.e., filtered and fitted to movement models) and all individuals (i.e., including those moving within the same group) to identify co-occurrence with vessels. We then identified periods where tagged whales appeared to come within closer proximity of a set or haul and descriptively examined movements relative to the timing and location of operations. We additionally assessed vertical movements during these scenarios for whales tagged whale depth-transmitting satellite-linked tags. We mapped potential approaches to gear with background environmental values (e.g., EKE) to contextualize behavioral patterns. We additionally inferred whether co-occurrences were likely neutral or negative based on the combination of tagged whale movement patterns, longline vessel setting and hauling locations, and observer data. For example, a neutral co-occurrence would describe a scenario where a tagged whale was within the vicinity of longline operations but did not make directed movements towards nor spatially overlap with the gear, and additionally supported if observer data were available and did not report any interactions or depredation damage. A probable negative co-occurrence would be a tagged whale moving towards and likely overlapping with gear, with an increased likelihood if the gear was from an observed vessel that recorded depredation damage. Depredation damage is reported as either ‘depredation damage’, ‘shark damage’, or ‘marine mammal damage’ on each fish caught. Lastly, we assessed whether individuals that approached gear, or other members of their social component, had any evidence for fisheries-related injuries as reported in Harnish et al. (2024).

4.4 Results

Between 2013 and 2024, 21 pelagic false killer whales were satellite-linked tagged with transmission durations ranging between 3-236 days (median = 17.5 days; Table 4.2; Figure 4.1). Nearly all tagged whales ranged widely, moving far from the nearshore island regions post-tagging (for those tagged closer to shore; Figure 4.1; Figure 4.6, Supplementary Material). Whales tagged during the fall of 2023 (n = 8 individuals) spent a large proportion of their time in the offshore lee of Hawai‘i Island and greater Geologist Seamounts region, with three individuals remaining entirely within this area (total of 36.4 days; overlapping with the year-round longline exclusion zone; Figure 4.7, Supplementary Material). The two individuals with the longest transmission durations during this period (PcTag088, PcTag091; Table 4.2) exhibited variable residency patterns, with periods of residency in this area followed by extended forays south of the main Hawaiian Island chain (i.e., outside of the longline exclusion zone; Figure 4.7, Supplementary Material). Just over half of all filtered locations (54.9% of 12,629 locations) were within permitted longline fishing zones (i.e., outside of the year-round exclusion zone and the PMNM), with a median of 58.8% of individual days tracked within longline fishing zones (range: 0.0-100%); two individuals tagged in 2013 were completely within the 2016-present

PMNM boundary, but partially outside of the pre-2016 boundary. The proportion of days tracked within longline fishing zones was variable among social components (median = 30.0%, range = 0.0-100.0%). We excluded two tags from statistical analyses due to their short transmission duration (Table 4.2). After assessing pairwise movements of whales tagged during the same period, there were a total of 11 unique groups tracked (representing seven social components; Table 4.2) which consisted of 9,382 filtered locations and 4,297 6-hourly predicted locations (1,810 with error ellipses <20 km).

Logbook data coinciding with false killer whale tracks between 2013 and 2025 consisted of 170 unique vessel proxies and 53,220 sets. Observer data was available for 8,380 (15.7%) of these sets. There were a total of 81,228 GFW fishing events during this same tagging periods and spatial extent, including vessels from the U.S. (57.5%), Chinese Taipei (TWN; 13.6%), the Republic of Korea (KOR; 13.5%), China (CHN; 5.6%), Vanuatu (VUT; 4.3%), Japan (JPN; 3.2%); 2.1% of events were from vessels with unknown flags, which is typically a result of invalid maritime identification numbers (see Global Fishing Watch, 2026), and the remaining 0.2% comprised minor contributions (<0.1%) by several Micronesian nations.

4.4.1 False killer whales and longline vessels select for similar habitats across their range

Tagged false killer whales selected for areas with high sea surface height—an indicator of anticyclonic eddies—within their spatial range, and this was consistent across all candidate models (Figure 4.2, Table 4.3; Table 4.4, Supplementary Material). Whales also selected for areas with increased slope (seafloor topography), as well as shallow mixed layers and high surface chlorophyll-a concentrations, but the strength of evidence for these latter two variables was weak (Table 4.3; Figure 4.8, Supplementary Material). Among-individual (or group) variation was high in all models, as indicated by the I-squared percentage, but lowest (85.6%) for the top ranking model (Table 4.3). Incorporating a predictor variable for the distance to the nearest logbook haul or fishing activity (minima of logbook set, haul, and GFW fishing event) did not improve model performance (Table 4.3), suggesting that their range-wide distribution is not directly driven by fishing activity.

Habitat selection patterns of longline gear sets were comparable to tagged false killer whales, with some minor differences (Figure 4.2). The most similar selection patterns between longline sets and false killer whales was the selection for areas with higher sea surface height and shallow mixed layers (Figure 4.2; Table 4.4, Supplementary Material). Differences in selection patterns primarily occurred in sub-surface properties: tagged whales selected for areas with high surface chlorophyll-a concentration, eddy kinetic energy, anomalous sea surface temperatures (SST SD), and slope compared to longline sets, although there was weak evidence for an effect for some these variables (e.g., confidence intervals included zero; Figure 4.2; Table 4.4, Supplementary Material). Interestingly, the top-ranking model for longline sets included the variable for number of seamounts within 25 km Table 4.3), with longline sets occurring in areas closer to seamounts at this scale (Figure 4.9, Table 4.4, Supplementary Material). The RSF estimate for this variable in the corresponding false killer whale model was similar to that of longline sets, albeit with higher uncertainty (Figure 4.9, Supplementary Material). These findings could potentially reflect longline vessel captains' affinity towards fixed habitat features compared to false killer whales that may rely on more dynamic features.

4.4.2 False killer whales ranged more widely during ecologically-poor conditions

The range-use ratio GAMM indicated that tagged false killer whales exhibited more dispersive behavior (i.e., larger range-use ratios) during weeks when proxies of biological productivity were lower, including mean chlorophyll-a concentration (estimated degrees of freedom (EDF) = 2.21, $p < 0.001$), variation in sea surface temperature (EDF = 1.10, $p = 0.029$), deeper mixed layers (EDF = 1.82, $p < 0.001$), and lower sea surface heights (i.e., indicative of less-productive cyclonic eddies, EDF = 0.85, $p < 0.001$; Figure 4.3). There was weak evidence for a non-linear effect of eddy kinetic energy (EDF = 1.37, $p = 0.121$), with smaller range-use ratios occurring at the lowest eddy kinetic energy values, followed by an increase at intermediate levels, and a subsequent decrease at the highest levels; however, uncertainty around this effect was high (Figure 4.3). The model deviance explained was 53.1%, indicating that the chosen environmental variables explained variation in ranging behavior at this scale reasonably well. Among-individual variation in range-use ratios (i.e., the random intercept) was high ($p < 0.0001$), likely due to variation in the number of weeks tracked across individuals. Mean sea surface temperature was not included in this model due to its strong correlation (Pearson's correlation > 0.7) with mean sea surface height.

4.4.3 Probability of co-occurrence was structured by scale-dependent ecological contexts

Tagged pelagic false killer whale groups were rarely within close proximity to longline fishing activity, with a median of 14.7% of days tracked (range = 0.0-27.8%) including at least one location within 50 km of a longline fishing vessel (Figure 4.10, Supplementary Material). Restricting the data to locations within permitted longline fishing zones, there was a median of 27.3% of days tracked (range = 0.0-56.5%) with at least one location within 50 km of a longline operation. There were 150 (8.3%) 6-hourly false killer whale locations within 50 km of GFW fishing events, 91.3% of which were with U.S. vessels, a small proportion from Japan (2.0%), and the remaining 6.7% of unknown flag.

Models quantifying the effects of environmental variables on co-occurrence had low predictive capacity overall (range of percent deviance explained: 9.7-17.7%; Table 4.5, Supplementary Material), which is likely due to the relatively rare co-occurrence documented from the tag data. Despite this, these models provide emerging insight on scale-dependent patterns (Figure 4.4): at the smallest scale examined (50 km), there was strong evidence for the probability of co-occurrence decreasing linearly with increasing chlorophyll-a concentrations (EDF = 0.906, p = 0.001) and weak evidence for an increase in co-occurrence with deeper mixed layers (EDF = 0.706, p = 0.063; Figure 4.4). There was weak evidence for a non-linear effect of eddy kinetic energy, with a higher probability of co-occurrence during both low and high eddy kinetic energy conditions (EDF = 1.38, p = 0.054; Figure 4.4). While there was a non-linear effect of sea surface temperature on the probability of co-occurrence, the uncertainty surrounding this effect was high (EDF = 1.202, p = 0.228; Figure 4.4). The model did not detect meaningful contributions for standard deviation in sea surface temperature nor sea surface height (i.e., shrunk to zero; Figure 4.4). Similar trends for sea surface temperature and mixed layer depth were estimated by models at larger spatial scales (Figure 4.4; Table 4.5, Supplementary Material). In the largest scale model (125 km), sea surface height was the most influential predictor; this model also had the highest percent deviance explained (Table 4.4, Supplementary Material). Effects of chlorophyll-a concentration on co-occurrence were only detected in the 50 km and 75 km models, the latter of which was non-linear (compared to the 50 km model) but shared an overall negative trend (Figure 4.4; Table 4.5, Supplementary Material).

4.4.4 Neutral and negative co-occurrences: individual versus group perspectives

Nineteen of all 21 tagged false killer whales occurred within 100 km of a U.S. longline operation at some point during their tracking period (n=2,680 locations) which represented 21.2% of all locations and 38.7% of locations within permitted longline fishing zones. Observer data was available for 23.9% of location-level co-occurrences within 100 km and consisted of 36 observed trips. Six of the seven social components (all but MC5/PcTag093, who spent little time in the longline zone; Table 4.2) were represented in these co-occurrences with observed vessels: four components only had observed or suspected neutral co-occurrences and two had a mix of both neutral and negative co-occurrences. None of the tagged whales had photographic evidence of fisheries-related injuries, but some tagged whales that potentially approached gear were part of social components that include individuals with some evidence of fisheries-related injuries (discussed below). We focused our detailed assessments on cases where tagged whales were 100 km or closer to an observed longline vessel, highlighting a subset of scenarios ranging from neutral co-occurrences, probable negative co-occurrences, and mixed cases. We do not refer to individual tagged false killer whales by their tag ID in subsequent narratives to maintain the confidentiality of longline fishing locations.

There were three probable negative co-occurrences, which had similar ecological and behavioral circumstances: tagged whales exhibited wide-ranging movement patterns in the days leading up to, during, and after approaches to gear, and the surrounding eddy kinetic energy field was low (Figure 4.5c, d, f). The whales in each case moved in the general region of the longlining activity in the day leading up to their close approaches to gear. In each case, the whales were between 30-80 km from the vessel at the start of the gear setting phase and were oriented towards the vessel (Figure 4.5c, d, f). The whales likely overlapped with gear at least several hours before (Figure 4.5c, d) or just prior to the start of the hauling phase (Figure 4.5f). Two of the cases reported marine mammal damage on catch (Figure 4.5c, d) and the other case (Figure 4.5f) reported shark damage on catch, although it is possible that the whales could have depredated bait or removed whole fish from the set (i.e., unobserved depredation). One of the whales (Figure 4.5c) likely overlapped with an unobserved vessel’s hauling phase after passing through the observed vessel’s gear, while in the other two cases, the whales moved away from the general area of fishing activity (Figure 4.5d, f). Both whales in these cases (Figure 4.5c) belong to social components that include individuals with some evidence of fisheries-related injuries (Harnish et al., 2024).

There were five cases of probable neutral co-occurrence, three of which were supplemented with information related to foraging behavior. A false killer whale with a depth-transmitting tag (Figure 4.5a) and its tagged associates were within 100 km of longline activity on one day, but based on horizontal movement patterns, none of the tagged whales appeared to approach longline gear (Figure 4.5a). During the closest proximity to a longline vessel (~25 km away), the whale with the depth-transmitting tag undertook deep dives (> 900 m), indicating that at least this individual was likely naturally foraging for deep prey. One of the distant vessels was observed and reported shark and general depredation damage (Figure 4.5a). The second case was similar, where two tagged whales moved into an area of high eddy kinetic energy (Figure 4.5b), and were likely cooperatively foraging based on their movement patterns; an unobserved vessel likely passed through this area while the whales were there, but the whales moved away from the vessel for the remainder of the setting phase. Similar neutral co-occurrences were observed, one in another pair of tagged whales (albeit in an area of lower eddy kinetic energy; Figure 4.11a, Supplementary Material) and another single tagged whale in the vicinity of an unobserved vessel but within an area of high eddy kinetic energy (Figure 4.11b, Supplementary Material). Lastly, one tagged whale was within 10 km of an observed vessel's setting phase but moved away from the vessel during the setting phase (Figure 4.11b, Supplementary Material); this whale is a member of a social component including two individuals with some evidence of fisheries-related injuries (Harnish et al., 2024). No damage was reported by the observer, but two days later, this same vessel reported a false killer whale hooking (with gear left on the animal).

There were three cases of neutral co-occurrence from the perspective of the tagged whales, but depredation or interactions were reported on nearby vessels and thus reveal key information on the social environment. Panel Figure 4.5e shows two tagged whales moving towards the general direction of an observed longline vessel that reported marine mammal damage, but based on the distances and timing of operations, this damage was caused by other animals within 20-50 km of the focal whales. There was one instance where an observed vessel reported false killer whale depredation of bait with a tagged whale approximately 50-60 km away (Figure 4.12a, Supplementary Material); on the following day, the same observer reported false killer whales following the vessel, and while the tagged whale was still at least 20-50 km away, it moved parallel to the vessel (Figure 4.12b, Supplementary Material). Lastly, there were multiple observed vessels in between two tagged whales shown in Figure 4.5f, and several of these vessels had some sort of depredation damage reported (shark, general depredation damage). While marine mammal depredation specifically was not reported, it’s clear that depredation was occurring in this range and the two tagged false killer whales were likely travelling with non-tagged associates.

4.5 Discussion

Our findings clarify the ecological drivers of pelagic false killer whale movements across scales and how their spatial behavior shapes co-occurrence with commercial longline fisheries in the central North Pacific. We found that both whales and vessels show similar range-wide selection for mesoscale oceanographic activity indicating that broad co-occurrence arises from independent responses to shared foraging habitats. We also found that while direct interactions are uncommon, they are more likely to occur under ecologically unfavorable conditions—characterized by proxies of biological productivity and prey accessibility—suggesting that fine-scale ecological context governs the risk of conflict. By simultaneously tracking multiple individual whales and vessels and mapping their interactions from fishery observer data, our study extends upon previous work (Forney et al. 2011; Fader et al. 2021) by linking movement ecology to empirically observed co-occurrence independent of depredation or bycatch events, and by revealing key insights on the role of the false killer whale social environment in fishery conflicts. Together, these results highlight the importance of considering environmental variability and social dynamics when predicting when and where whale-fishery conflicts are most likely to occur.

4.5.1 Oceanographic features shape whale and longliner movements across scales

At the largest scale, we found that false killer whales and longliners shared affinities for areas with higher sea surface height, a proxy for biologically-enhancing anticyclonic eddies in subtropical gyres like the central North Pacific (Dufois et al., 2016). This aligns with our hypothesis that mesoscale eddies are preferred habitat for both whales and fishers given their effects on aggregating pelagic prey targeted by both competitors in this region (Arostegui et al., 2022). Differences in habitat selection patterns at this scale primarily occurred between proxies of sub-mesoscale and static features, with captains setting in areas closer to seamounts than whales. These findings may reflect the differences between whales' and captains' ability to sense and detect environmental cues of prey aggregations. Longline fishing effort at the trip level is limited by a variety of logistical factors (e.g., distance from port, fuel, bait, ice, etc.), thus targeting areas with fixed cues (more seamounts) may be an effective strategy at this scale since seamounts are reliable indicators of enhanced local biological productivity (Clark et al., 2010). False killer whales are clearly not limited by the same trip-level constraints, and are also likely able to sense prey aggregations across a range of scales (Torres, 2017); thus they can adjust their foraging decisions to different dynamic ecological conditions (Kratofil et al., 2026c).

The importance of mesoscale eddy activity to false killer whale movement decisions was additionally highlighted by the range-use ratio analysis revealing that restricted ranging is associated with higher sea surface heights and other proxies of biological productivity. These relationships likely point to the coupled vertical and horizontal availability of prey at weekly scales, shaped by key biophysical processes underlying marine predator foraging success (Fahlbusch et al., 2024). For example, smaller range-use ratios associated with shallower mixed layers and higher chlorophyll-a concentrations could reflect more efficient foraging in the vertical dimension, which is validated by these variables' quantified relationships on their diving behavior (Kratofil et al., 2026c). The presence of a shallow scattering layer in our study region further supports the hypothesis that sub-surface properties and associated biological ‘zones’ can reduce foraging costs for marine predators (Arostegui et al., 2023), and thus could explain whales’ restricted ranging behavior in such conditions. Shifts in ranging behavior corresponding with ecologically unfavorable conditions is well known in a variety of taxa (Bégassat et al., 2026; Benoit-Bird et al., 2013; Irvine et al., 2025) and aligns with our findings of larger range-use ratios of pelagic false killer whales when metrics of biological productivity are lower. This suggests that ranging more widely under reduced patch quality or prey availability reflects whales searching for alternative prey patches, and longline fishing gear itself could function as alternative prey patches.

4.5.2 Whale and longliner co-occurrence are context-dependent and rare

The oceanographic drivers of pelagic false killer whale ranging behavior mapped similarly to whale and longliner co-occurrence patterns at finer scales, suggesting that under certain ecological contexts, whales likely seek out longline gear as alternative foraging opportunities. Specifically, whales ranged more widely and were more likely to co-occur with longliners within 50 km when mixed layers were deeper and chlorophyll-a levels were lower—indicative of low biological productivity, or potentially decreased prey accessibility (in terms of the mixed layer depth). The inference of longline gear as alternative foraging patches is additionally supported by the eddy kinetic energy trend in the 50-km co-occurrence model: although weak, the probability of co-occurrence was associated with both unfavorable (low energy) and favorable (high energy) conditions, which could correspond with targeted and passive overlap by whales, respectively. This was validated in the highlighted co-occurrence scenarios (Figure 4.5; Figure 4.11, Supplementary Material), where eddy kinetic energy was lower in the cases of overlap and conflict and higher in the probable neutral cases.

Interestingly, an effect of sea surface height was only detected in the 125km-scale co-occurrence model (although with weak evidence, Table 4.5, Supplementary Material) and implied the opposite of the habitat selection models: that co-occurrence at this scale was more probable when sea surface height is lower, which typically reflects cyclonic eddies that are less productive in our study region (Dufois et al., 2016). There are several explanations for this discrepancy. First, the co-occurrence analyses modeled true co-occurrences within each scale, while the habitat selection models estimated range-wide selection patterns for whales and longliners independently and thus do not directly reflect co-occurrence. Second, mesoscale eddies can be 100+ km in diameter (Dong et al., 2025), making it possible for both fishers and false killer whales to use these features without coming into close proximity to one another. Third, our findings herein, combined with quantified ecological relationships with diving behavior (Kratofil et al., 2026c), collectively imply that other (sub)mesoscale features are also important to false killer whales' movement decisions. It is thus likely that false killer whales are better able to exploit localized, ephemeral prey patches—within or adjacent to areas of higher sea surface height—than longliners and in doing so avoid co-occurrence. These inferences are caveated by the low explanatory power of the models—similar to models on depredation rates (Fader et al., 2021)—but insight from false killer whales' social environment help explain the nuances of fine-scale co-occurrences.

4.5.3 Depredation as an individual-level tactic within a social group-level strategy

Pooling foraging information from social interactions with, or observations of, others allows individuals in groups to collectively sense their environment at larger scales, and may be particularly important for exploiting resources with highly ephemeral dynamics (Boyd et al., 2016; Kohles et al., 2022; Oestreich et al., 2026; Spiegel and Crofoot, 2016). We identified several cases where tagged whales were likely exposed to social information about longliners, either by (a) passing through gear locations a few days prior to later depredation by other whales, or by (b) moving in the same general direction as operating longline vessels with an observed depredation event but (based on time and distance) were unlikely to be responsible. Taken together with the dynamic association patterns of some tagged groups, it is possible that some pelagic false killer whales have adopted a collective foraging strategy at the social group-level—where groups are spread out over extensive distances moving through clusters of longlining activity—but actual depredation events occur at the individual-level, with only some (tagged or not) individuals actually approaching gear during these wide ranging forays.

This hypothesis is further corroborated by observations of repeat depredation on longline vessels. Perceptions by longline captains (Ayers and Leong, 2022) and patterns of observed depredation rates (Fader et al. 2021) both indicate that depredation is most likely to occur on the same vessel if already depredated. However, based on our tag data, repeat depredation does not necessarily equate to repeat offenders (i.e., the same individual coming back to the same vessels), but rather groups spread out over a large area and passing through longlining activity over several days. There was one case where two individuals passed by, but did not overlap with, a longline set that had marine mammal damage (Figure 4.5e) but came back to that same vessel several days later (travelling over 300 km back) with a probable depredation (Figure 4.5d). While no tagged whales had photographic evidence of fisheries-related injuries, some of their associates did (i.e., other members within the same social component; Harnish et al., 2024), which provides potential evidence of within-group heterogeneity in depredation behavior (although see the discussion of caveats on detecting such injuries in Harnish et al., 2024). Thus, patch quality, information from their social environment, and memory of recent longline activity (within a limited spatiotemporal range) likely jointly determine the probability of an individual depredating gear.

Collective sensing over large scales in an oligotrophic system may offer a balance between individual fitness and social benefits. However, the available tag data suggests the possibility of inter-group variation in movement strategies: not all tagged groups exhibited such dynamic spatial association patterns, nor evidence of potentially cueing in on nearby interactions. For example, one group of three tagged whales remained tightly associated throughout their common deployment period (16 days), with one individual undertaking multiple deep dives during this time (Figure 4.5a), suggesting foraging on deep prey instead of interacting with nearby vessels. In contrast, several individuals in another group (representing a different social component) exhibited several periods of overlap with longline gear—with at least one probable depredation—although these tags transmitted longer than the former group (>16 days). Differences in the propensity of individuals or groups to interact with fisheries could feed back on how groups make decisions collectively (Bracken et al., 2022; Jolles et al., 2020). This feedback between sociality and space use can have cascading effects on long-term social structure (Kratofil et al., 2026a), and the influence of human-related foraging tactics on social structure has been documented in several odontocete populations (e.g., Bankhead et al., 2025; Esteban et al., 2016; Hersh et al., 2025). Given that longlining activity is a consistent, but ephemeral, characteristic of much of pelagic false killer whales' habitat—with 75% of their known range (Figure 4.1) open to longline fishing—it is plausible that it could socially aggregate whales, thereby further shaping their social structure in similar ways as clustered food subsidies (Beck et al., 2026; Gaynor et al., 2024) or physical habitat features (He et al., 2019).

4.5.4 Management implications and directions for future research

Our findings provide important context for developing bycatch mitigation measures. Negative co-occurrences were more likely to occur under ecologically unfavorable conditions based on quantified drivers of false killer whale ranging behavior and co-occurrence at different scales. This suggests that dynamic ocean management tools (Hazen et al., 2018) could help mitigate the probability of longliners experiencing false killer whale depredation. These tools (e.g., 'EcoCast[6]') use habitat suitability models to predict the distribution or bycatch of species of concern in near-real time to help fishers avoid areas where conflict is most likely to occur. Developing a predictive tool for Hawai'i could thus help identify when and where false killer whale depredation is most probable, and integrating movement-based relationships would enable more proactive mitigation through forecasting conditions underlying false killer whales' wide-ranging 'depredation forays'. While the explanatory power in our co-occurrence models and depredation models in previous studies were low (Fader et al., 2021; Forney et al., 2011), the use of electronic monitoring (e.g., Kindt-Larsen et al., 2012) could foster greater predictive capacity of 'EcoCast' type models by increasing the sample size of observed interactions to train models with. While dynamic ocean management tools would be a step forward in mitigating conflict between pelagic false killer whales and longline fisheries, their effectiveness could be limited by the capacity to integrate information on the social environment—a key factor shaping the decisions of false killer whales.

False killer whales are clearly able to maintain some level of cohesion across extensive scales (20+ km) based on previous observations (Baird et al., 2008a; Bradford et al., 2014) and paired movements reported here, so temporarily pausing fishing operations or moving to a new area within this scale might not be effective strategies for avoiding depredation or bycatch (c.f. Fader et al., 2021). However, we also found that some tagged groups exhibited more dynamic spatial

[6] https://coastwatch.pfeg.noaa.gov/ecocast/

association patterns and potentially propensities to overlap with longlining activity than others. Understanding the persistence of differentiated group-level spatial behavior requires repeated tracking of social groups over time (e.g., Kratofil et al., 2026a), which is a major challenge for studying pelagic false killer whales that typically range outside of areas accessible to researchers. Yet, as more group-level information is accrued moving forward, it could be potentially integrated into dynamic ocean management tools (e.g., down-weighting areas used by social groups with greater propensity to depredate). A tool that integrates both physical and social environmental drivers of behavior would not only be useful regionally (i.e., for false killer whales), but also globally, as odontocete depredation of commercially important fisheries is a widespread phenomenon (Tixier et al., 2021).

When negative co-occurrence is inevitable, other mitigation measures, such as handling techniques, guidance on fisher behavior, and gear modifications, are likely necessary to reduce serious injury and mortality of bycaught false killer whales—the mitigation target under the U.S. Marine Mammal Protection Act. Mitigation measures implemented by the Take Reduction Plan (TRP) in 2013 include gear requirements (e.g., weaker circle hooks, stronger terminal gear), spatial management (e.g., bycatch limit-triggered area closures), and measures for captain and crew response to handling hooked false killer whales (77 FR 71260; Federal Register, 2012), but the ineffectiveness of these measures has recently led to TRT recommendations for amendments to the existing TRP[7]. Our results empirically imply a value of longline gear as alternative foraging opportunities that social groups of pelagic false killer whales can collectively exploit over extensive spatial scales, beyond what may be feasible for individual longliners to adjust their behavior in response to. Collective behavioral responses of fishers longlining in the same area where false killer whale depredation occurs (e.g., several vessels moving far away and/or pausing operations), rather, could dilute opportunities for false killer whales and thus reduce depredation impacts (Fader et al., 2021; Gilman et al., 2006; Tixier et al., 2015). Aside from captains' behavior, continued exploration of gear handling methods or tools and gear modifications that reduce serious injury to bycaught whales will be important for short-term mitigation, and exploring measures that could decrease the strategic value of longline gear to false killer whales without compromising the fishery (e.g., fishing with more efficient gear but for shorter durations or lengths, Tixier et al., 2015, 2010) could be worth considering for long-term mitigation.

4.5.5 Additional analyses to support findings

Our study provides critical insight into the factors shaping co-occurrence and conflict risk between pelagic false killer whales and longline fisheries, but some additional analyses could help clarify the relative importance of these various factors. For example, modeling oceanographic drivers of longline catch data (e.g., using catch per unit effort, CPUE) will reveal

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[7] https://www.fisheries.noaa.gov/s3/2024-06/FINAL-KOM-FKWTRT-March2023-508.pdf

the robustness of our environmental proxies of biological productivity and their modeled relationships with whale and longliner habitat selection, whale ranging behavior, and co-occurrence with longline gear. If oceanographic drivers of CPUE are similar to those identified in our models of ranging behavior and co-occurrence, then we could reasonably assume that our environmental variables are capturing variation in prey patch quality. Additionally, we focused our fine-scale co-occurrence case studies on potential tagged whale approaches to gear from observed vessels, but there were other cases where tagged whales appeared to approach unobserved vessels. Expanding this analysis to incorporate unobserved vessels will thus more comprehensively depict the nature of false killer whale interactions with longline gear, including any cases with foreign vessels. While these cases lack observer data to confirm whether depredation damage occurred, they could still provide important insight on whale behavior (e.g., see Anderson et al., 2020), and the definitions of 'probable neutral' and 'probable negative' could be expanded to reflect the spectrum of available evidence on the nature of the interaction.

4.5.6 Conclusions

Our study demonstrates that shared responses to mesoscale oceanographic features create the conditions for broad spatial overlap between pelagic false killer whales and longline fisheries, and critically, how co-occurrence may translate to competition and conflict. Our results suggest that the probability of such negative interactions is governed by fine-scale ecological and behavioral contexts experienced by both whales and longliners over periods of days to weeks. These may include reduced prey availability and increased search effort or opportunistic foraging. As strongly social and highly mobile predators, we further highlight that pelagic false killer whales' wide-ranging movements as cohesive social groups can increase the spatial extent over which direct conflicts can occur. These findings together provide a mechanistic foundation for improving mitigation measures to reduce depredation and bycatch of false killer whales in Hawai'i's deep-set longline fishery, which is broadly relevant for interactions between other fisheries and socially foraging marine predators. In particular, our study supports the development of dynamic, environmentally informed management approaches to be implemented alongside operational guidance and handling practices that can reduce incentives for depredation and likelihood of fatal bycatch. More broadly, our study emphasizes that integrating multiscale movement and social ecology of marine predators with fishery data can improve prediction and management of fisher-wildlife conflict in highly variable pelagic environments.

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4.8 Figures

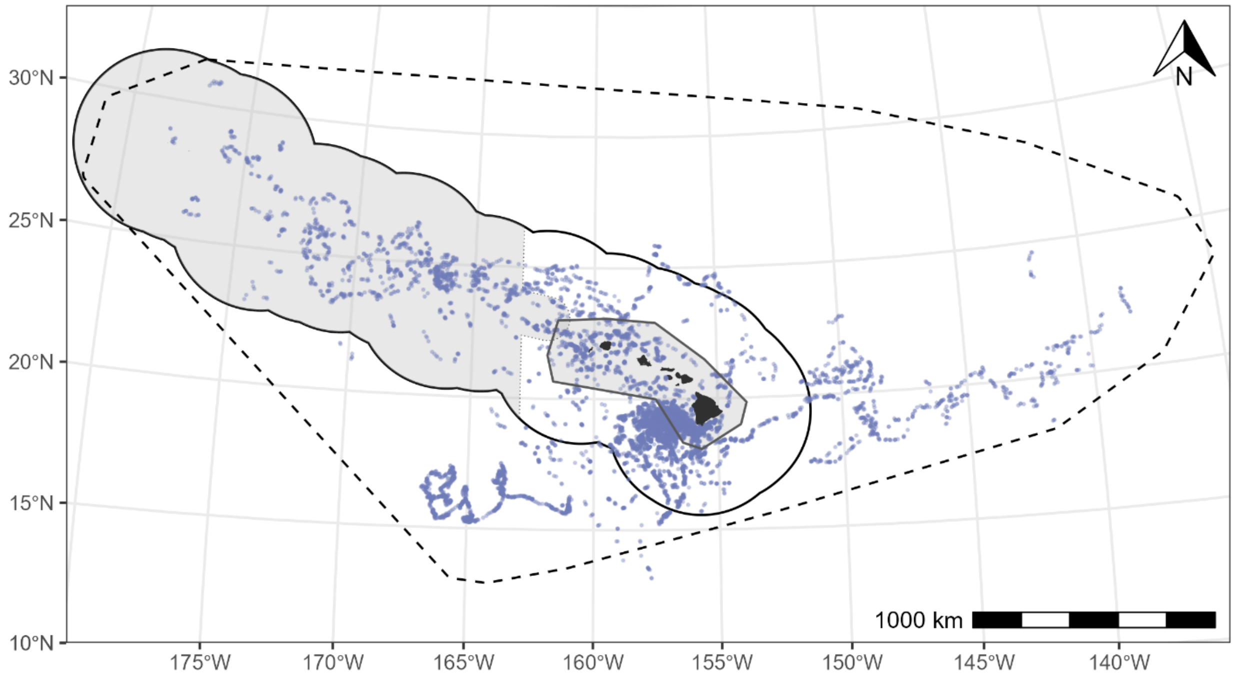

Figure 4.1. Satellite tag locations (purple) from all pelagic false killer whales tagged from 2013 through 2025. Areas where longlining is prohibited are shaded in light grey, including the year-round longline exclusion zone around the Main Hawaiian Islands (solid grey outline) and the Papahānaumokuākea Marine National Monument (dotted grey outline). The pelagic false killer whale assessment area is represented by the dashed black line and the U.S. Exclusive Economic Zone by the solid black line.

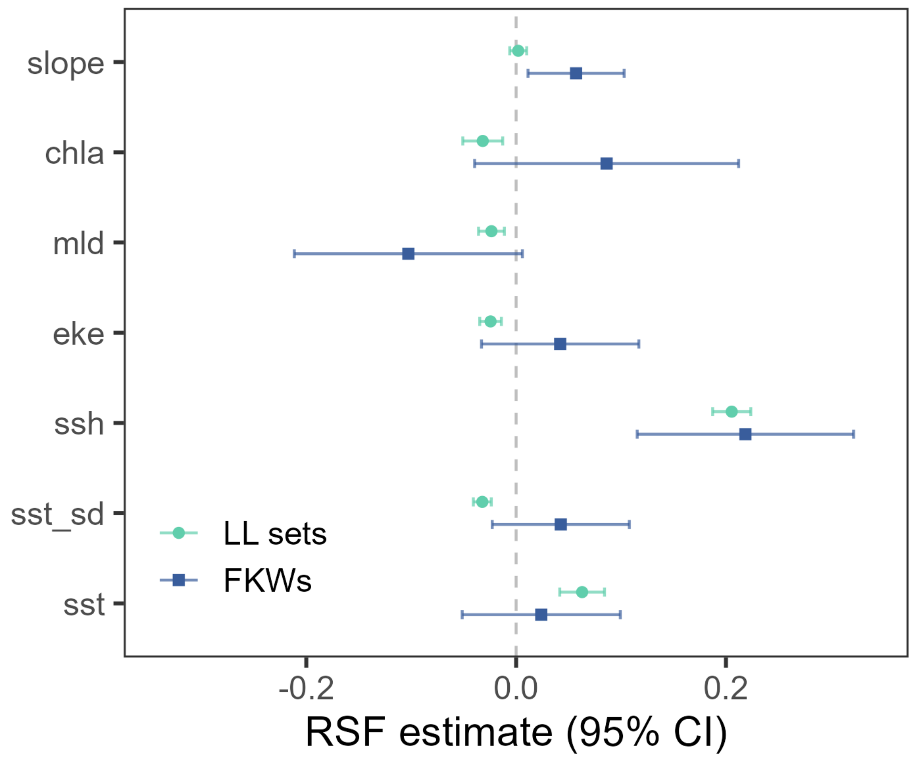

Figure 4.2. Comparison of sample population-level habitat selection patterns between pelagic false killer whales and longline vessel sets. Resource selection function (RSF) coefficient estimates (x-axis, with 95% confidence intervals) are shown for each environmental variable (y-axis), for the top false killer whale (FKW) RSF model (Table 4.3, 4.4) and longline (LL) set model fit to the same covariates. Estimates to the right of the dashed zero line indicate selection for positive/higher values of that variable (or attraction), while estimates to the left of the zero line indicate selection for negative/lower values (or avoidance). See Table 4.1 for environmental predictor descriptions.

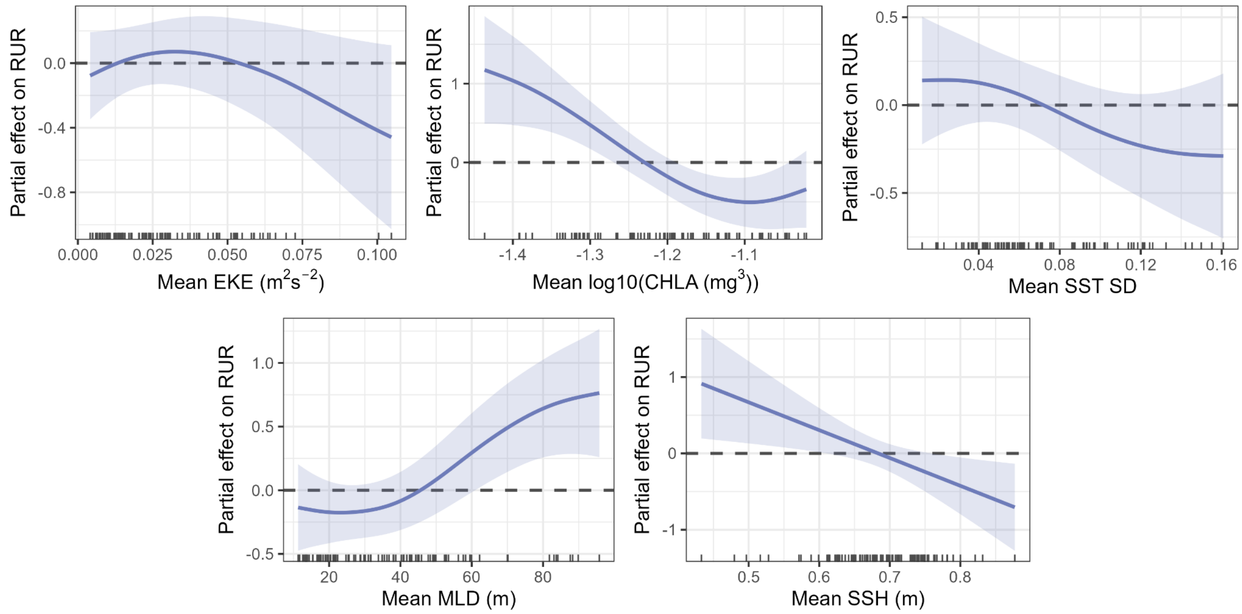

Figure 4.3. Relationships between weekly ranging behavior of pelagic false killer whales and environmental variables. Partial effects of weekly average environmental variables (x-axes) on weekly pelagic false killer whale range-use ratios (y-axes). Solid lines represent the estimated effect and the ribbons represent the 95% confidence intervals. Curves above the dashed zero line indicate a positive effect on range-use ratios while those below the dashed line indicate a negative effect on range-use ratios. The distribution of observations for each environmental variable are indicated by the vertical lines on the bottom of the x-axes.

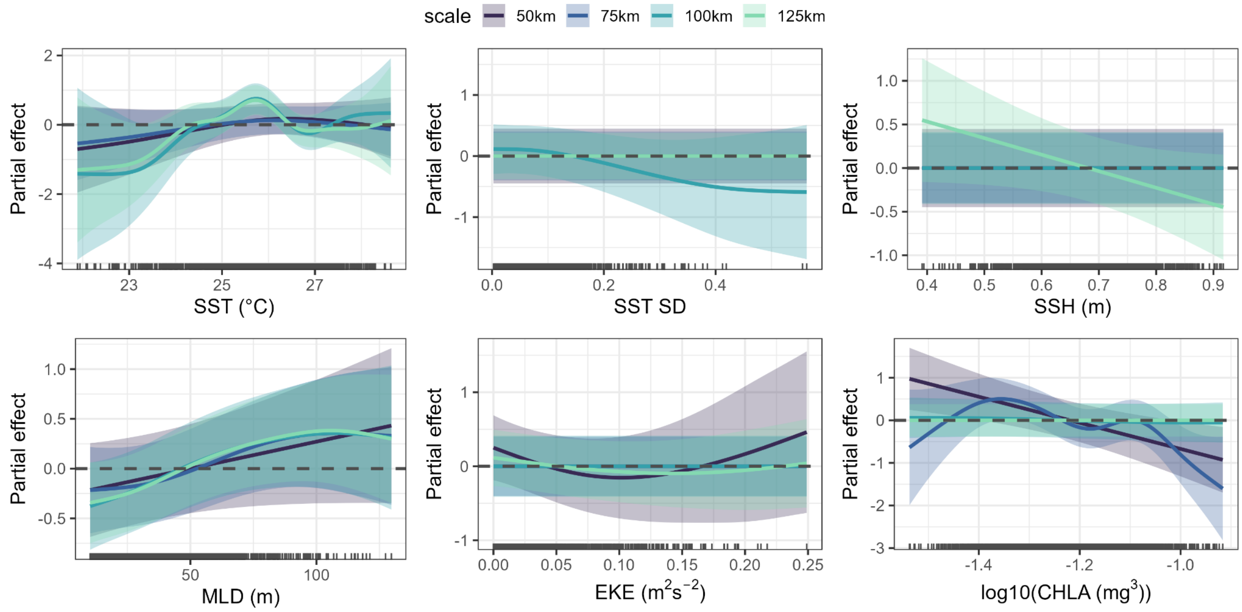

Figure 4.4. Relationships between pelagic false killer whale-fishing activity co-occurrence and environmental variables across scales. Partial effects of environmental variables (x-axes) on co-occurrence between false killer whales and fishing activity events (y-axes) defined at different scales (colors). Solid lines represent the estimated effect and the ribbons represent the 95% confidence intervals. Curves above the dashed zero line indicate a positive effect on the probability of co-occurrence while those below the dashed line indicate a negative effect on the probability of co-occurrence; those with flat lines were shrunk to zero (i.e., no estimated effect). The distribution of observations for each environmental variable are indicated by the vertical lines on the bottom of the x-axes.

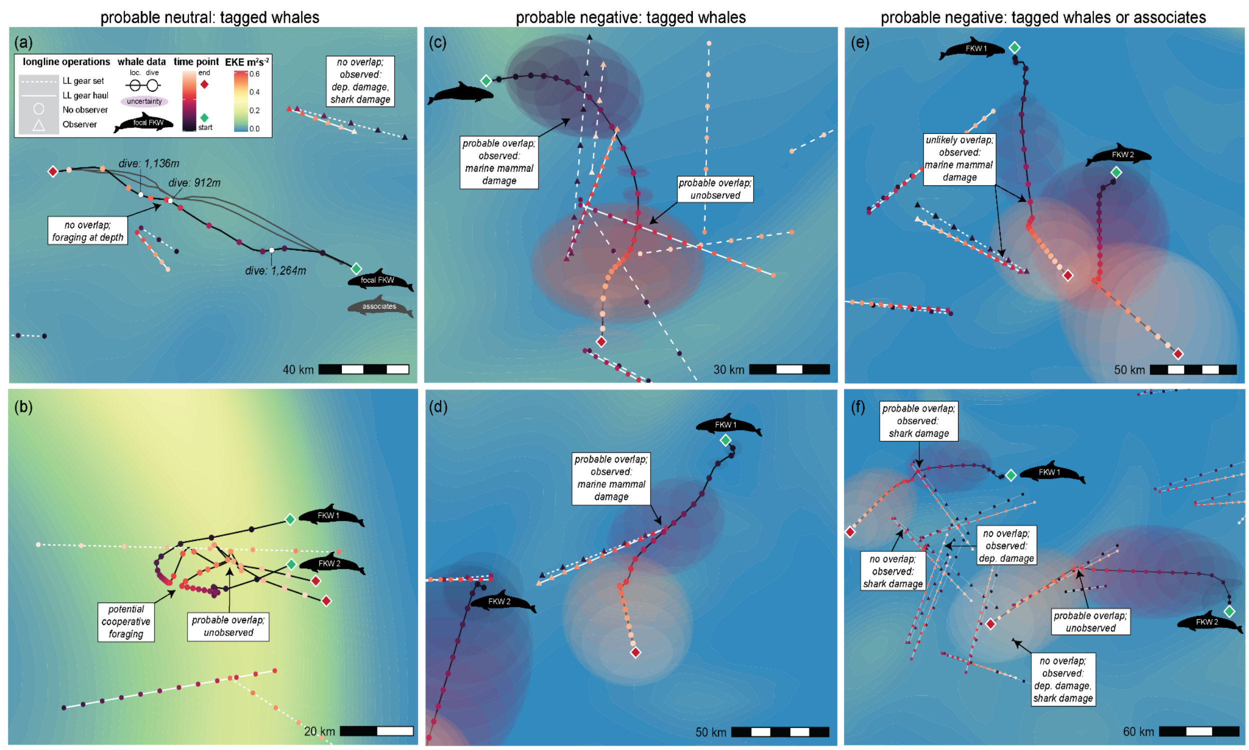

Figure 4.5. Case studies of neutral and negative pelagic false killer whale and longline vessel co-occurrences. Each panel shows movements of focal tagged false killer whales (FKW; black tracklines, 1-hourly predicted locations and associated error ellipses) relative to nearby longline set (LL; dashed white lines) and haul (solid white lines) operations for 12-24 hour periods where close approaches were observed (start and end of series indicated by green and red diamonds, respectively). The end points on each longline set and haul are captain-reported in the logbooks; points in between were interpolated (hourly) to provide a coarse visual estimate of the minimum trajectory of the vessel between trailing and retrieving gear locations, and thus should be interpreted with some level of discretion, particularly for hauling phases (i.e., when vessels are less likely to be moving at a consistent speed). All points (whale, vessel) are colored by the timestamp. Vessels that had an observer are indicated by triangle points and those without have circle points. The background raster is the eddy kinetic energy (EKE; Table 4.1) field for that day. Error ellipses are plotted in panel (a) but not visible due to the higher accuracy of that tag; ellipses are not shown in panel (b) for improving visualization.

4.9 Tables

Table 4.1. Candidate environmental variables for habitat selection models. For each variable, the spatial resolution, hypothesized relationship, and source are provided. All dynamic variables had a daily temporal resolution.

Variable	Spatial resolution	Hypothesized relationship	Source
Seafloor slope (SLOPE)	500 m	Topographic induced variation in vertical and horizontal water mass movement (e.g., upwelling)	GEBCO 2025 grid[1]
Distance to nearest seamount (DIST_SEAM)	NA	Distance to features known to enhance biological productivity	BlueHabitats[2]
# Seamounts within 25 km (NSEAMS25)	NA	The relative spatial clustering of seamounts in an area (25 km), which could relate to spatial clustering of biological enhancement	BlueHabitats[2]
# Seamounts within 50 km (NSEAMS50)	NA	The relative spatial clustering of seamounts in an area (50 km), which could relate to spatial clustering of biological enhancement	BlueHabitats[2]
Sea surface temperature (SST)	~9 km	Thermal preferences of target fish species	Copernicus GLORYS[3]
Standard deviation of SST (SST SD)	~27 km	Indicator of thermal fronts or anomalous thermal conditions	Calculated as SD of nearest 3 SST cells
Mixed layer depth (MLD)	~9 km	Depth of thermocline, related to water column stability and vertical structuring of prey fish	Copernicus GLORYS[3]
Sea surface salinity (SSS)	~9 km	Indicator of of water mass movement	Copernicus GLORYS[3]
Sea surface height (SSH)	~9 km	Indicator of cyclonic/anticyclonic eddies at mesoscale	Copernicus GLORYS[3]
Eddy kinetic energy (EKE)	~9 km	Indicator of intensity of mesoscale features (energy of eddies and meanders)	Derived from *u* and *v* geostrophic currents from GLORYS[3]
Surface chlorophyll-a concentration (CHLA; logged)	4 km	High surface biological productivity, proxy for potential prey aggregations	Copernicus Ocean Color[4]
Dissolved oxygen at 150 m depth (OXY150)	25 km	Indicator of the biogeographical split between North Equatorial Current/North Equatorial Counter Current; also related to mixing, productivity from eddies	Copernicus Ocean Biogeochemical Global Analysis and Forecast[5]
Windspeed above sea surface (WIND)	25 km	Influences horizontal and vertical water movement (e.g., vertical mixing, atmospheric exchange, upwelling)	NOAA Blended SeaWinds[6]

[1]https://www.gebco.net/data-products-gridded-bathymetry-data/gebco2025-grid
[2]https://bluehabitats.org/
[3]https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/description
[4]https://data.marine.copernicus.eu/product/OCEANCOLOUR_GLO_BGC_L4_MY_009_104/description
[5]https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_BGC_001_029/description
[6]https://coastwatch.noaa.gov/cwn/products/noaa-ncei-blended-seawinds-nbs-v2.html

Table 4.2. Pelagic false killer whale satellite tag deployment summary. Tag IDs with a superscript ‘x’ were excluded from formal analyses due to limited data, or because the individual was part of a tracked group and did not have the longest transmission duration. Alphabetic superscripts for tag IDs reflect individuals considered to be in the same ‘group’ based on inter-individual distances. Age/sex class: A = adult, S = sub-adult, U = unknown, F = female, M = male; if haplotype information is available, then sex was genetically determined. See Martien et al. (2014) for reference on mitochondrial haplotypes.

Tag ID	Social component	Haplotype	Age/sex class	Tag type	Date tagged	Deployment locality	Transmission duration (d)	# filtered locations
PcTagP01	MC4	9	AF	SPOT5	15-May-2013	E of Laysan	154.1	1074
PcTagP02	IC1	U	AU	SPOT5	26-May-2013	SE Maro Reef	13.6	152
PcTag039[a,x]	MC2	26	AF	SPOT5	22-Oct-2013	Hawai‘i Island	11.8	126
PcTag040[a,x]	MC2	26	AF	SPOT5	22-Oct-2013	Hawai‘i Island	15.8	182
PcTag041[a]	MC2	U	AU	SPOT5	22-Oct-2013	Hawai‘i Island	122.7	915
PcTagP03[b]	MC3	9	AF	SPOT5	12-Sep-2017	Kaua‘i	177.9	785
PcTagP04[b,x]	MC3	9	AM	SPOT5	13-Sep-2017	Kaua‘i	2.9	36
PcTagP05[b,x]	MC3	40	AF	SPOT5	13-Sep-2017	Kaua‘i	20.4	265
PcTag065	MC2	U	AM	SPOT6	15-May-2020	Hawai‘i Island	16.1	297
PcTag085[c,x]	MC1	U	AU	SPOT6	4-Sep-2023	Hawai‘i Island	25.4	539
PcTag086[c]	MC1	U	AU	SPOT6	4-Sep-2023	Hawai‘i Island	27.0	566
PcTag087[c,x]	MC1	U	AU	SPOT6	4-Sep-2023	Hawai‘i Island	5.0	101
PcTag088[d]	MC1	U	SU	SPOT6	24-Sep-2023	Hawai‘i Island	236.0	2522
PcTag089[d,x]	MC1	U	AF	SPOT6	24-Sep-2023	Hawai‘i Island	49.9	1090
PcTag090[e]	MC1	25	AF	SPLASH10-F	31-Oct-2023	Hawai‘i Island	19.0	579
PcTag091[f]	MC1	U	AF	SPOT6	31-Oct-2023	Hawai‘i Island	90.4	1794
PcTag092[e,x]	MC1	6	AF	SPLASH10-F	31-Oct-2023	Hawai‘i Island	12.4	303
PcTagP07[g,x]	IC2	9	AF	SPOT6	16-May-2024	E of Johnston Atoll	18.0	358
PcTagP08[g,x]	IC2	U	SU	SPOT6	16-May-2024	E of Johnston Atoll	10.5	239
PcTagP09[g]	IC2	9	AM	SPLASH10-F	16-May-2024	E of Johnston Atoll	17.0	499
PcTag093	MC5	U	AU	SPOT6	22-Dec-2024	Hawai‘i Island	10.9	191

Table 4.3. False killer whale and longline fishing activity habitat selection models and performance metrics. Models within each category (whale, longline) are ordered by increasing AIC (AIC, i.e., the top model is the best fit), shown with the Bayesian Information Criterion (BIC), log likelihood (logLik), and I^2 statistic (measure of heterogeneity in effect sizes across whales/vessels). See Table 4.1 for environmental predictor descriptions; DIST_HAUL = distance to the nearest longline logbook haul operation; DIST_FISH = distance to the nearest fishing activity (minima of logbook set, haul, and Global Fishing Watch fishing event). Variables WIND and OXY150 were not included in models due to their strong correlation with other candidate predictors.

Dataset	Model	AIC	BIC	logLik	I^2 %
False killer whales	SST + SST_SD + SSH + EKE + MLD + CHLA + SLOPE	-35.936	46.097	52.968	85.6
	SST + SST_SD + SSH + EKE + MLD + CHLA + NSEAMS25	-25.704	56.330	47.852	91.8
	SST + SST_SD + SSH + EKE + SSS + MLD + CHLA + SLOPE	-18.377	90.626	53.188	85.9
	SST + SST_SD + SSH + EKE + MLD + CHLA + SLOPE + DIST_FISH	-14.753	94.250	51.377	84.9
	SST + SST_SD + SSH + EKE + MLD + CHLA + NSEAMS50	-12.044	69.989	41.022	93.6
	SST + SST_SD + SSH + EKE + SSS + MLD + CHLA	-6.322	75.711	38.161	87.3
	SST + SST_SD + SSH + EKE + SSS + MLD + CHLA + NSEAMS25	-6.272	102.731	47.136	91.3
	SST + SST_SD + SSH + EKE + MLD + CHLA + NSEAMS25 + DIST_FISH	-2.478	106.525	45.239	91.1
	SST + SST_SD + SSH + EKE + MLD + CHLA + NSEAMS25 + DIST_HAUL	-1.065	107.938	44.533	91.4
Longline sets	SST + SST_SD + SSH + EKE + SSS + MLD + CHLA + NSEAMS25	-2499.151	-2269.680	1293.575	85.0
	SST + SST_SD + SSH + EKE + MLD + CHLA + SLOPE	-2349.271	-2171.411	1209.635	84.2
	SST + SST_SD + SSH + EKE + MLD + CHLA + NSEAMS25	-2227.978	-2050.741	1148.989	92.5
	SST + SST_SD + SSH + EKE + SSS + MLD + CHLA	-2083.916	-1906.056	1076.958	85.6

4.10 Supplementary Material

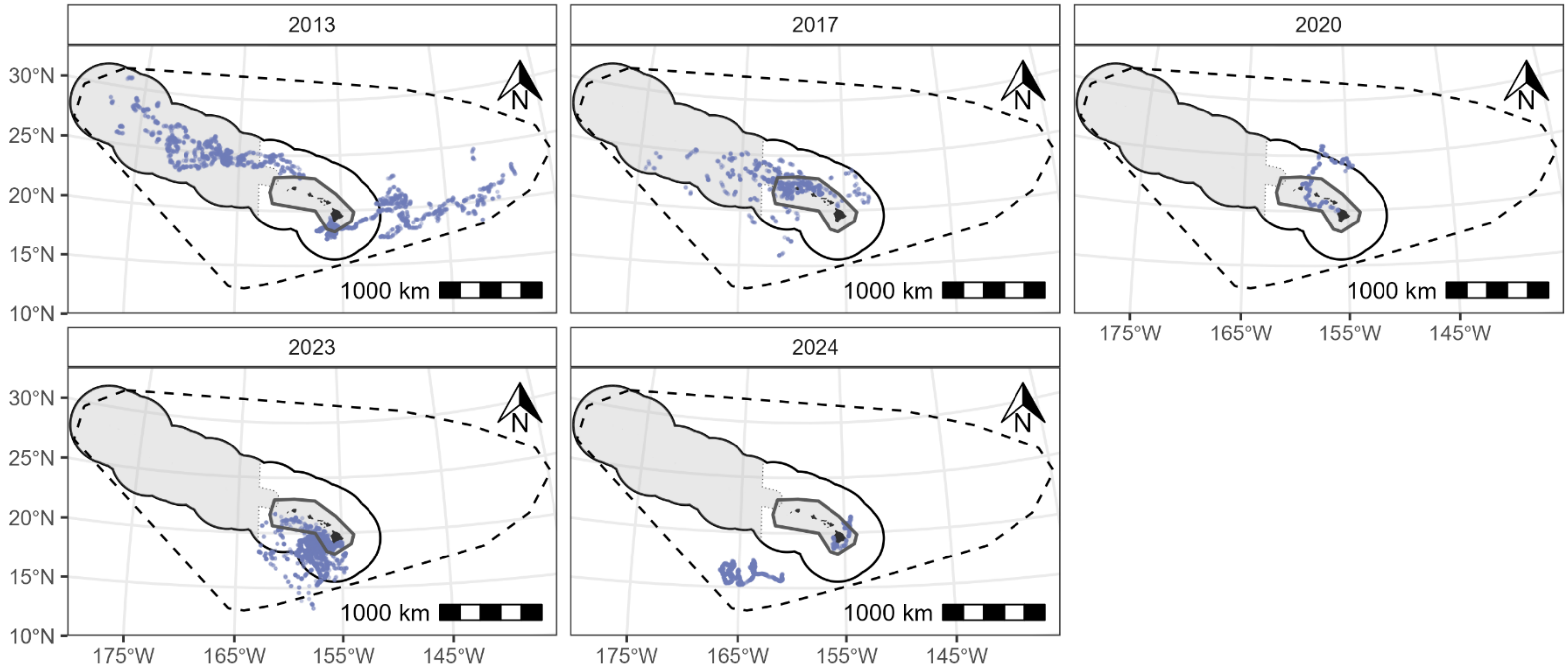

Figure 4.6. Map of pelagic false killer whale satellite tag locations (purple points) by deployment year. Areas where longlining is prohibited are shaded in light grey, including the year-round longline exclusion zone around the Main Hawaiian Islands (solid grey outline) and the Papahānaumokuākea Marine National Monument (dotted grey outline). The pelagic false killer whale assessment area is represented by the dashed black line and the U.S. Exclusive Economic Zone by the solid black line.

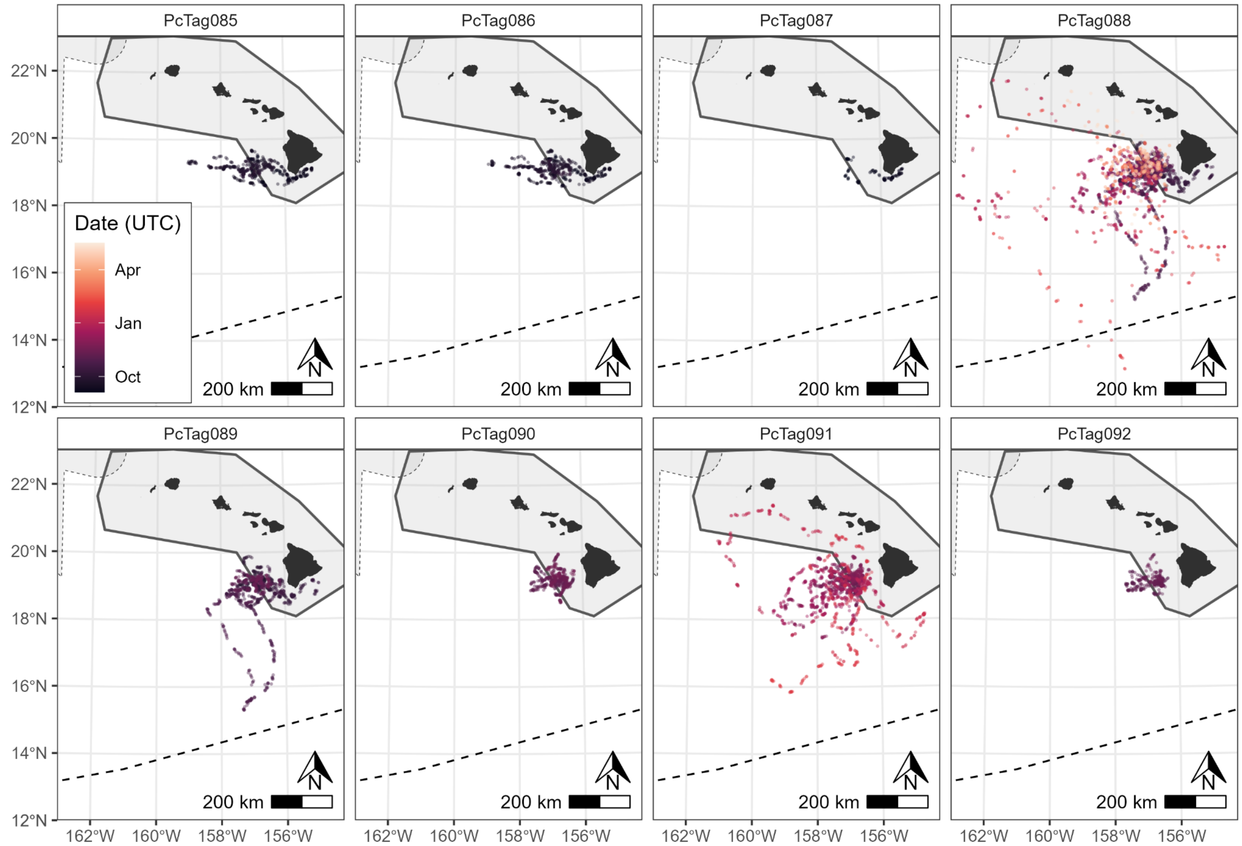

Figure 4.7. Maps of pelagic false killer whale satellite tag locations (colored points) for individuals tagged during the fall 2023 deployment period. Points are colored by date. Areas where longlining is prohibited are shaded in light grey, including the year-round longline exclusion zone around the Main Hawaiian Islands (solid grey outline) and the Papahānaumokuākea Marine National Monument (dotted grey outline), and the pelagic false killer whale assessment area is represented by the dashed black line.

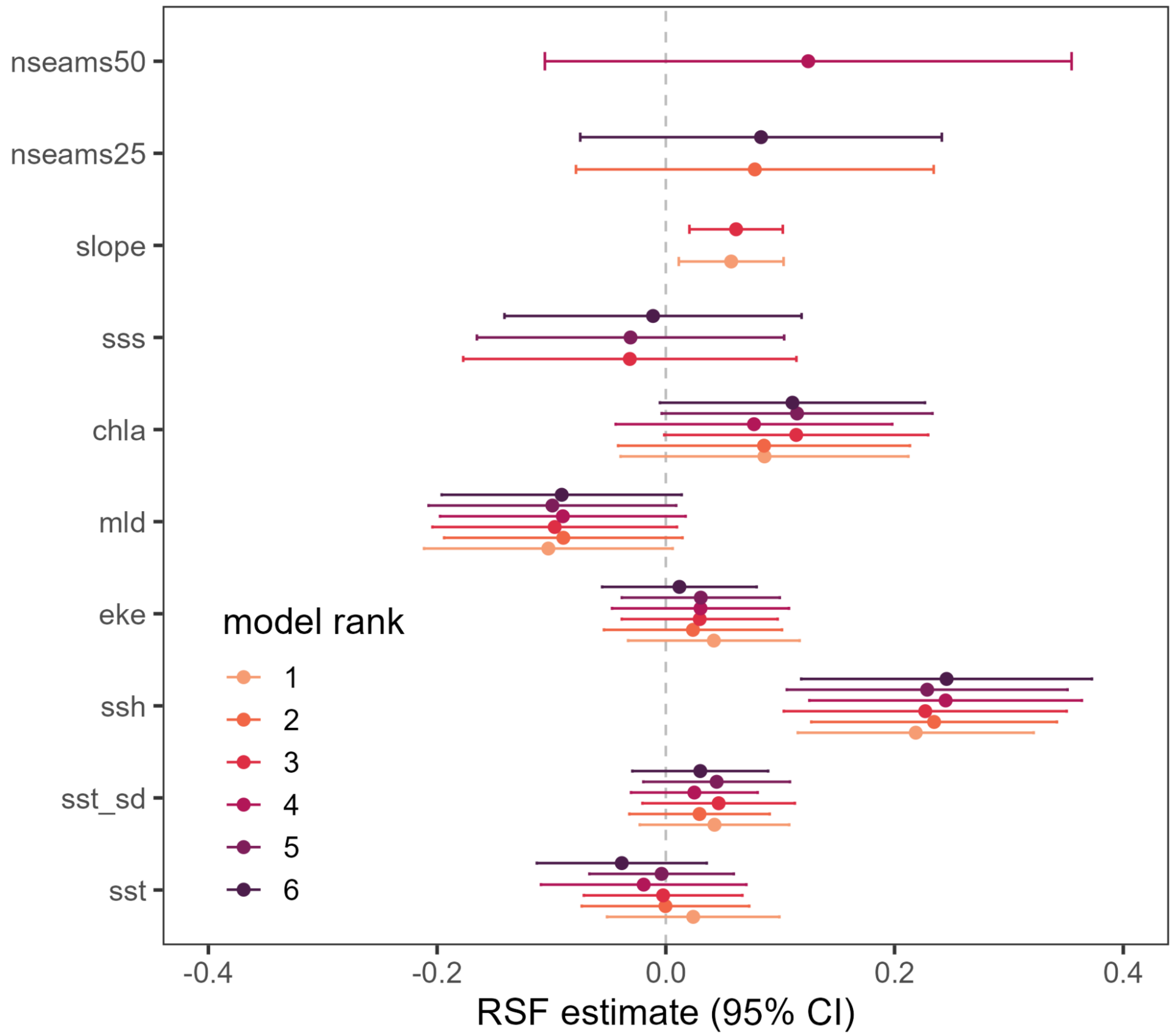

Figure 4.8. Comparison of sample population-level habitat selection patterns for pelagic false killer whales by model rank (environmental variables only). Resource selection function (RSF) coefficient estimates (x-axis, with 95% confidence intervals) are shown for each environmental variable (y-axis), for each environmental-variable only model (see Table 4.3). Estimates to the right of the dashed zero line indicate selection for positive/higher values of that variable (or attraction), while estimates to the left of the zero line indicate selection for negative/lower values (or avoidance).

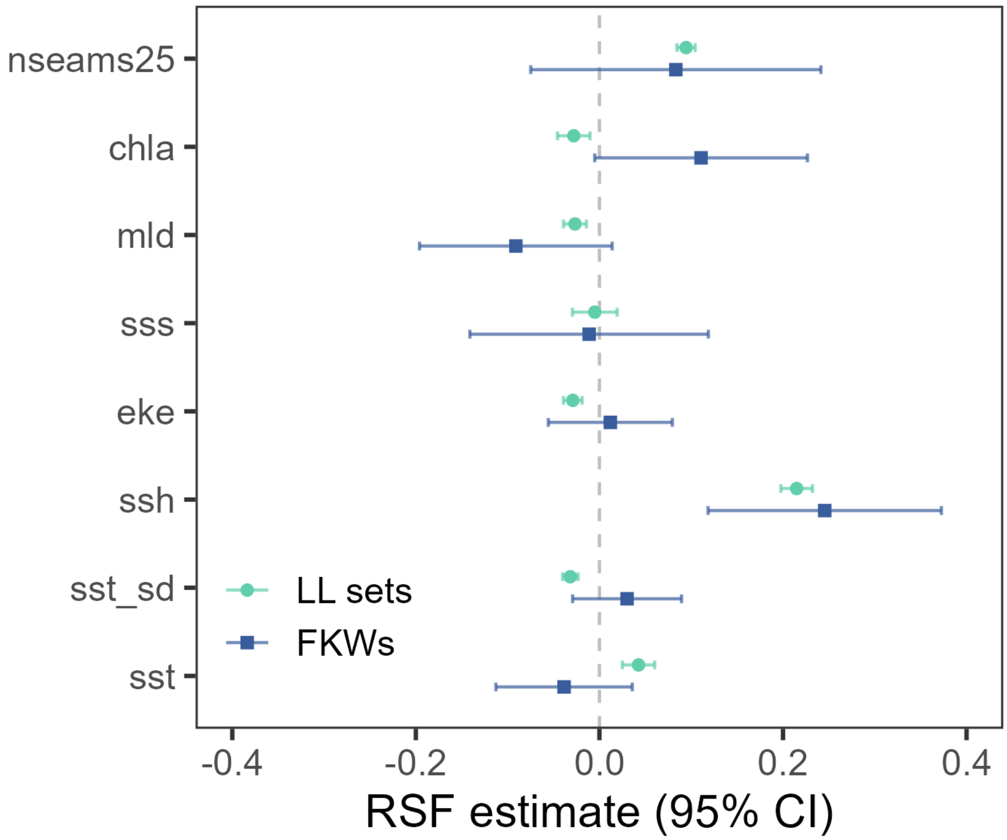

Figure 4.9. Comparison of sample population-level habitat selection patterns between pelagic false killer whales and longline vessel sets for the top ranking longline set model (Table 4.3, 4.4). Resource selection function (RSF) coefficient estimates (x-axis, with 95% confidence intervals) are shown for each environmental variable (y-axis). Estimates to the right of the dashed zero line indicate selection for positive/higher values of that variable (or attraction), while estimates to the left of the zero line indicate selection for negative/lower values (or avoidance).

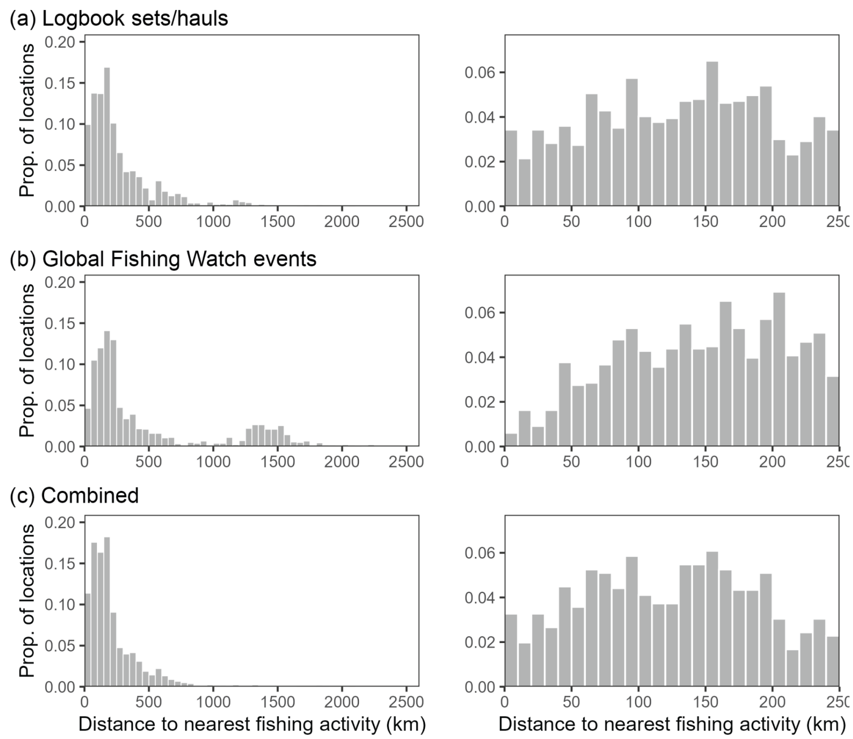

Figure 4.10. Distributions of the proportion of false killer whale tag locations and distance to the nearest daily fishing activity by activity types. (a) longline logbook sets/hauls, (b) longline fishing events identified by Global Fishing Watch (GFW), and (c) the two sources integrated (i.e., the minima of distances to longline set, haul, or GFW event). For each fishing activity type, both the entire distribution (left; 50 km bins) and distributions zoomed into 0 to 250 km distance (right; 10 km bins) are provided. 6-hourly predicted whale locations were used to mitigate pseudoreplication.

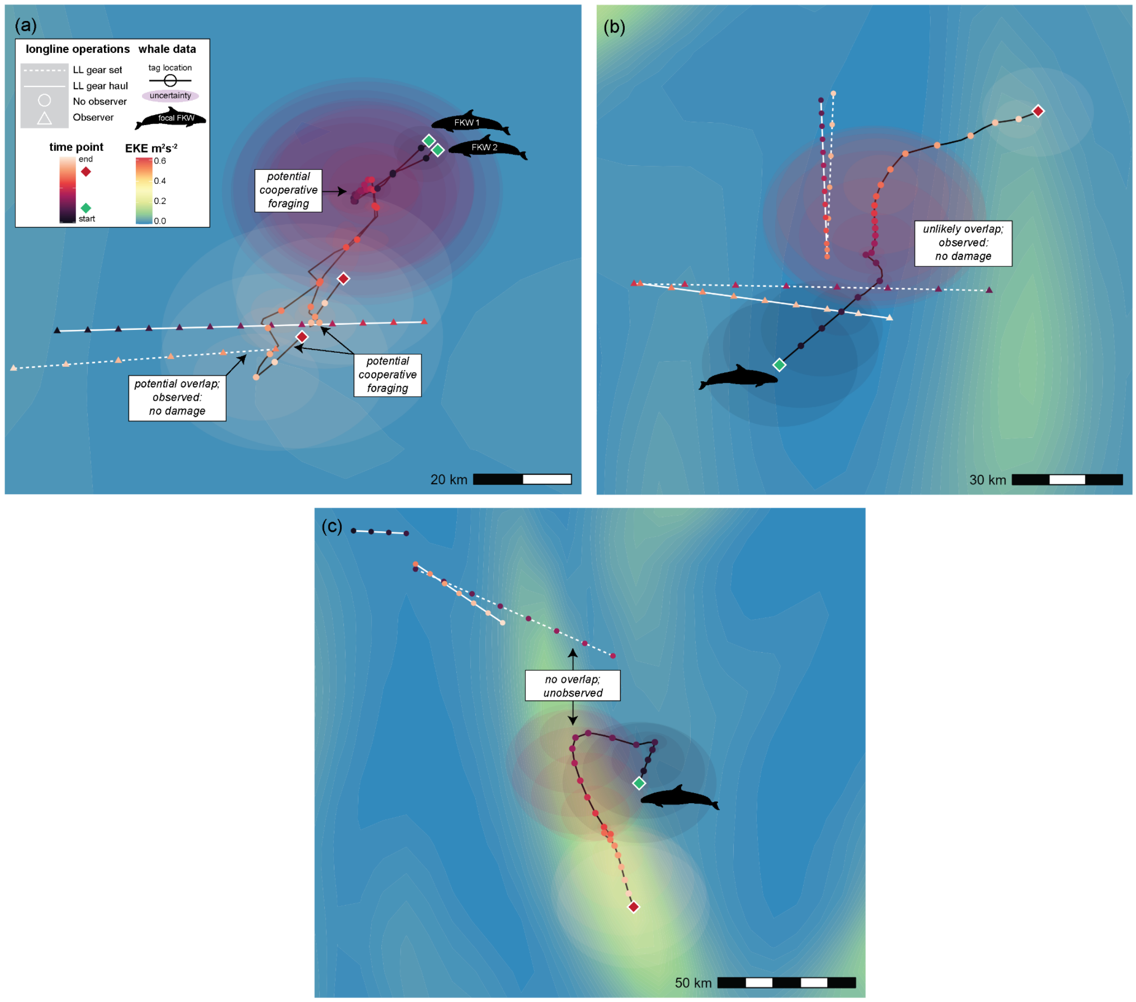

Figure 4.11. Cases of confirmed or probable neutral co-occurrence between tagged pelagic false killer whale (FKW) and longline vessels. Each panel shows movements of focal tagged FKWs (black tracklines, 1-hourly predicted locations and associated error ellipses) relative to nearby longline set (LL; dashed white lines) and haul (solid white lines) operations for 12-24 hour periods where close approaches were observed (start and end of series indicated by green and red diamonds, respectively). The end points on each longline set and haul are captain-reported in the logbooks; points in between were interpolated (hourly) to provide a coarse visual estimate of the minimum trajectory of the vessel between trailing and retrieving gear locations, and thus should be interpreted with some level of discretion, particularly for hauling phases (i.e., when vessels are less likely to be moving at a consistent speed). All points (whale, vessel) are colored by the timestamp. Vessels that had an observer are indicated by triangle points and those without have circle points. The background raster is the eddy kinetic energy (EKE; Table 4.1) field for that day.

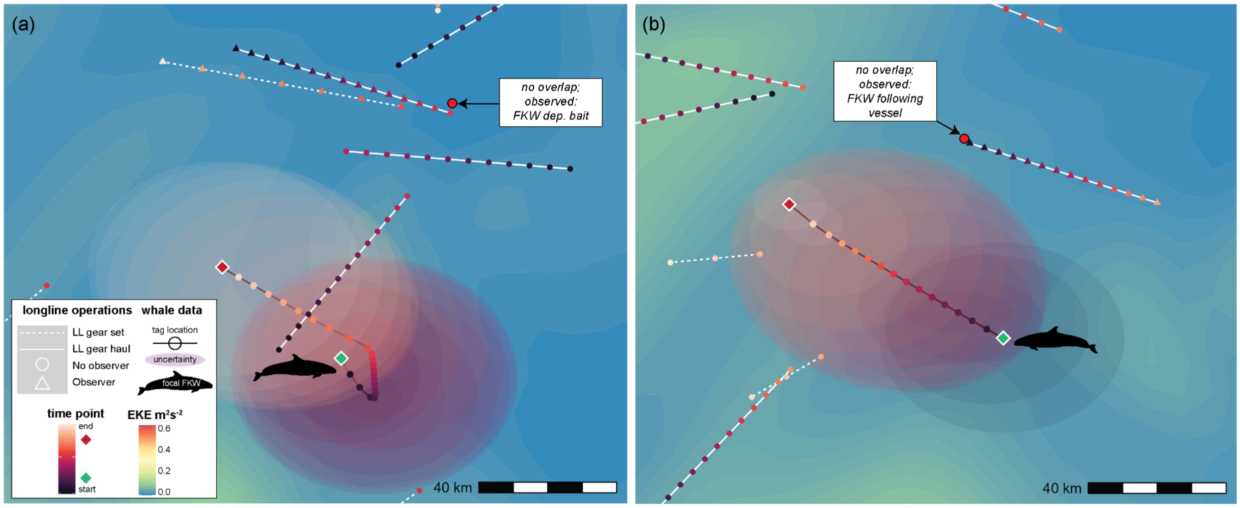

Figure 4.12. Case of neutral co-occurrence between tagged pelagic false killer whale (FKW) and longline vessels, but negative co-occurrence of distant FKWs based on observer data. (a) observed FKW depredation of bait; (b) observed FKW following the same vessel (no contact with gear) on the subsequent set. Each panel shows movements of focal tagged FKWs (black tracklines, 1-hourly predicted locations and associated error ellipses) relative to nearby longline set (LL; dashed white lines) and haul (solid white lines) operations for 12-24 hour periods where close approaches were observed (start and end of series indicated by green and red diamonds, respectively). The end points on each longline set and haul are captain-reported in the logbooks; points in between were interpolated (hourly) to provide a coarse visual estimate of the minimum trajectory of the vessel between trailing and retrieving gear locations, and thus should be interpreted with some level of discretion, particularly for hauling phases (i.e., when vessels are less likely to be moving at a consistent speed). All points (whale, vessel) are colored by the timestamp. Vessels that had an observer are indicated by triangle points and those without have circle points. The background raster is the eddy kinetic energy (EKE; Table 4.1) field for that day.

Table 4.4. Outputs from the top-ranking sample population-level habitat selection models for pelagic false killer whales and U.S. longline sets. Coefficient estimates, lower and upper 95% confidence intervals (CIs), and p-values are provided for each habitat variable. Model performance metrics are provided in Table 4.3.

Model	Estimate	Lower 95% CI	Upper 95% CI	p-value
False killer whales				
SST	0.024	-0.051	0.099	0.533
SST SD	0.043	-0.023	0.108	0.202
SSH	0.219	0.115	0.322	<0.001
EKE	0.042	-0.033	0.117	0.273
MLD	-0.103	-0.211	0.006	0.064
CHLA	0.086	-0.040	0.212	0.179
SLOPE	0.057	0.011	0.103	0.015
Longline sets				
SST	0.043	0.025	0.060	<0.001
SST_SD	-0.032	-0.040	-0.023	<0.001
SSH	0.215	0.198	0.232	<0.001
EKE	-0.029	-0.039	-0.019	<0.001
SSS	-0.005	-0.029	0.019	0.686
MLD	-0.027	-0.039	-0.014	<0.001
CHLA	-0.028	-0.046	-0.010	0.002
NSEAMS25	0.094	0.085	0.104	<0.001

Table 4.5. Outputs from generalized additive mixed effects models relating co-occurrence between tagged pelagic false killer whales and longline fishing activity across scales. For each scale of co-occurrence, model metrics and covariate-specific parameter estimates (estimated degrees of freedom, EDF, p-values) are provided. Note that some covariates have low p-values implying statistical significance, but are effectively flat and non-significant based on the confidence intervals surrounding the smooth estimates (see Figure 4.4).

	Modeled scale of co-occurrence			
Model metric	**50 km**	**75 km**	**100 km**	**125 km**
% deviance explained	9.7	12.6	16	17.7
Adjusted R-squared	0.054	0.102	0.164	0.192
Covariate	**EDF (p-value)**			
SST	1.202 (0.228)	1.188 (0.273)	5.384 (0.005)	5.605 (0.003)
SST SD	<0.001 (0.991)	<0.001 (0.003)	1.325 (0.054)	<0.001 (0.492)
SSH	<0.001 (0.758)	<0.001 (<0.001)	<0.001 (0.691)	0.771 (0.035)
MLD	0.706 (0.063)	1.588 (0.010)	1.780 (<0.001)	1.926 (<0.001)
EKE	1.375 (0.054)	<0.001 (0.307)	0.000 (0.538)	1.037 (0.072)
CHLA	0.906 (0.001)	4.750 (0.002)	0.416 (0.223)	<0.001 (0.062)
Random: Tag ID	6.035 (0.003)	7.110 (<0.001)	7.253 (<0.001)	7.810 (<0.001)

5. GENERAL DISCUSSION

5.1 Overview

This dissertation draws on a comprehensive long-term dataset—integrating movements, demographics, social networks, biomarkers, and genetics over 25 years—to reveal key and novel insight on the causes and consequences of spatial-social processes on marine predator movements across scales. Specifically, the chapters of my dissertation are structured to (1) address fundamental knowledge gaps in species-specific foraging strategies; (2) develop and evaluate multiscale spatial-social feedback mechanisms to better understand how populations persist; and (3) assess how foraging behavior and spatial-social processes jointly drive co-occurrence and conflict risk with human activities. In integrating empirical, conceptual, and applied approaches, this body of work provides a tractable approach for investigating similar questions beyond this study system.

Critically, my research deepens understanding of the mechanisms underlying false killer whale population dynamics in Hawaiʻi and offers new insights for developing conflict mitigation strategies. The findings in this study system—where multi-species studies on cetaceans have sustained for nearly three decades (Baird, 2016; Baird et al., 2024; Kratofil et al., 2023)—also benefit from a uniquely rich ecological context, underscoring the value of strategically designed long-term, individual-based research programs sustained across generations of long-lived animals (Clutton-Brock and Sheldon, 2010). Taken together, the work presented here represents a comprehensive synthesis of the processes shaping predator movement ecology, advances species- and population-specific knowledge, and serves as a novel contribution to the emerging body of research intersecting spatial and social ecology.

In the following sections I summarize key messages from each chapter (section 5.2); synthesize their implications in the context of false killer whale population dynamics (section 5.3); develop recommendations for socioecological indicators of population recovery (section 5.4); and discuss how the frameworks and findings in my dissertation could be developed to address remaining knowledge gaps in spatial and social ecology (section 5.5).

5.2 Data chapter-specific insights

Chapter 2 accomplishes two goals. It provides the first comprehensive description of false killer whale diving behavior, and demonstrates how behavioral variation among demographic groups and ecological contexts could shed light on foraging strategies (Kratofil et al., 2026c). Using two biologgers capturing different scales, I documented false killer whales' preference for the epipelagic zone, validated by visual observations of feeding on a variety of epipelagic predatory game fish. However, whales also dove much deeper (>1,000 m) and exhibited functional relationships with environmental proxies of prey, indicating they adjust foraging decisions to local prey landscapes. Interestingly, diel patterns in dive behavior were neither strong nor consistent, which contrasts to those found in sympatric predators known to exploit the island-associated deep scattering layer. Further, diving patterns between associated pairs suggest that observed inter-individual variation in vertical movements could partially be attributed to cooperative foraging behavior, where whales synchronized the timing of foraging bouts but not in exact dive depths or times (Appendix A). This chapter reveals how false killer whales meet their foraging needs in an oligotrophic environment—by adapting their behavior to the circumstances of their local physical and social environments. More broadly, this chapter reinforces the importance of interpreting variation in predator movement behavior through ecological, demographic, and social lenses.

In Chapter 3, I developed a conceptual framework to understand how resource dynamics and social reliance jointly regulate spatial-social feedback mechanisms across scales (Kratofil et al., 2026a). Applying this framework to MHI false killer whales, I found empirical support for socially driven short-term intra-cluster movements, while the whales' highly dynamic resource landscape regulates short-term inter-cluster space use at fine and coarse scales. Evidence for long-term processes was variable among clusters, with some clusters exhibiting more defined spatial and feeding niches than others. Lastly, long-term space use revealed two key areas where whales were most likely to co-occur and where long-term cluster-level core ranges overlapped. This pattern suggests that such areas are consistently important for foraging but also foster opportunities for inter-cluster interactions that reinforce population structure and gene flow. This work deepens understanding on the coupled spatial and social processes underling MHI false killer whale population structure, offering insights into socioecological factors promoting or impeding population persistence. Beyond this study system, this chapter illuminates general mechanisms by which both resource dynamics and life history strategies govern bottom-up and top-down processes linking sociality and space use.

Finally, in Chapter 4 I conceptually apply the framework developed in Chapter 3 to understand inter-specific interactions between pelagic false killer whales and commercial longliners to inform bycatch and depredation mitigation strategies. I found that shared affinities for areas with higher mesoscale activity can lead to broad scale co-occurrence between whales and longline fishers. However, ecological contexts at smaller spatiotemporal scales were more likely to govern fine-scale co-occurrence and conflict with longlining activity. Shared environmental drivers of whale ranging behavior and fine-scale co-occurrence with longline gear imply that whales seek out longline gear as alternative foraging opportunities and likely undertake ‘depredation forays’ when natural foraging opportunities are suboptimal at weekly scales. Fishery observers provided empirical data that further demonstrated the role of pelagic false killer whales’ social environment during depredation forays, where in some cases, tagged whales moved towards vessels that had been depredated by distant whales but did not cause the depredation themselves. These findings together suggest that predictive dynamic oceanographic tools and communication among captains could help reduce fine-scale co-occurrence, while gear modifications, handling techniques and tools to mitigate serious injury and mortality are necessary when bycatch does occur.

5.3 Contextualizing false killer whale population dynamics

These chapters collectively provide empirical evidence for the integral role of sociality on the foraging, movement patterns and distribution of Hawai‘i's false killer whales. It is therefore essential to interpret false killer whale population dynamics through both spatial and social lenses, particularly for the endangered MHI false killer whale population that has experienced a decline in abundance over the past decade (Badger et al., 2025). How do long-term changes in population density—their broad scale social environment—affect foraging success, social cluster-level space use, inter-cluster interactions, and ultimately population persistence? Are the determinants of population size environmentally mediated or behaviorally mediated, or both? These determinants, and the magnitude of various threats to population recovery (NOAA Fisheries, 2021), are likely regulated by scale-dependent spatial-social feedback mechanisms (Webber and Vander Wal, 2018). In the following sections, I synthesize what I have learned from the previous chapters with ecological theory to contextualize false killer whale population dynamics across scales. In particular, I explore how multiple Allee effects—a mechanism of the social environment—could synergistically impede or promote population persistence (Berec et al., 2007; Webber and Vander Wal, 2018).

5.3.1 Fine-scale, short-term foraging success and intra-cluster persistence

5.3.1.1 Behaviorally mediated effects: cooperative hunting

Cooperation is fundamental to the lives of false killer whales. It has likely enabled their persistence as large predators hunting highly mobile, difficult to capture, and patchily distributed prey in an oligotrophic environment (Benoit-Bird, 2024; Krause and Ruxton, 2002a; Silk, 2007). At the finest scales, group members cooperatively hunt in three-dimensional space (Chapter 2, Appendix A), and the social bonds reinforced by these cooperative behaviors drive individual-level movements up to cluster-level space use (Chapter 3). It is thus plausible to assume the existence of an optimal group size and composition for effective collective decision making and cooperative hunting of their prey (Cantor et al., 2020; Conradt and Roper, 2005; Markham et al., 2015; Papageorgiou and Farine, 2020). Suboptimal group sizes or composition resulting from demographic turnover (e.g., loss of knowledgeable or skilled individuals; Kopf et al., 2024) could result in inefficient cooperative hunting of large, energetically profitable prey and thus lower survival and fitness (Angulo et al., 2018). Hunting dangerous prey (e.g., billfish) without skilled individuals could also impact survival. This behaviorally mediated mechanism could have direct consequences on individual health; indeed, recent work (J. Currie personal communication) shows that individuals of this false killer whale population can experience large fluctuations in body condition. High levels of persistent organic pollutants (POPs) can further compound these negative effects, as blubber concentrations in many individuals sampled from this population exceeded thresholds for reproductive impairment and immunosuppression (Kratofil et al., 2020). Under nutritional stress, these POPs are mobilized from blubber storage to the bloodstream and other organs, exacerbating negative health effects; this phenomenon is likely occurring in the critically endangered Southern Resident killer whale (*Orcinus orca ater*) population (Lundin et al., 2016; Wasser et al., 2017). Thus, decreased population density at the social cluster level could potentially impose behaviorally mediated effects on fine-scale foraging success with cascading impacts on population recruitment via individual health and fecundity. The extent to which false killer whales can buffer against these effects of demographic turnover, however, is likely influenced by foraging plasticity and trends in prey landscapes.

5.3.1.2 Environmentally mediated effects: prey availability

MHI false killer whales' adaptive foraging strategy (Chapter 2) and generalist feeding niche (Chapter 3) could mitigate the cascading effects of decreased population density on fine-scale intra-cluster foraging success. The capacity for this strategy to effectively buffer impacts is likely tied to the availability of both primary and alternative prey, the latter of which false killer whales may or may not need to cooperatively hunt for. For example, I found that several whales exhibited near-seafloor diving behavior (Chapter 2), particularly over Penguin Bank which is a key habitat for deep reef-associated bottom fish like uku, and reef-associated predatory fish comprise a small proportion (<10%) of their diet (Chapter 3). I also found that mesopelagic cephalopods contribute a small, but non-negligible, proportion (<15%) to their diet (Chapter 3), and observed deep diving behavior could reflect foraging on such prey assemblages (Chapter 2). Stock assessments indicate uku abundance in the main Hawaiian Islands increased from 2005 through 2017 and has since remained stable (Nadon, 2024); no information is available on trends in mesopelagic cephalopod abundance. If behaviorally mediated changes to the efficacy of cooperative hunting for large epipelagic prey were to occur, then individual-level foraging on alternative prey could potentially allow individuals to meet energetic requirements for survival and reproduction, and thus reinforce the value of cooperative hunting for cluster-level success.

The plausibility of this environmentally mediated buffering mechanism not only depends on the availability of alternative prey on the landscape, but also that of preferred prey and potential competitors.

5.3.1.3 Behaviorally versus environmentally mediated effects: reliance on depredation

Depredation of fishing gear could also buffer false killer whales against behaviorally mediated Allee effects (i.e., on cooperative hunting), or changes in the availability of preferred prey over time, but with the risk of injury or mortality. While there are no observer programs for nearshore fisheries, indirect evidence—including photographs of fisheries-related injuries and documentation of hooks in stranded whales' stomachs—suggests MHI false killer whales interact with gear (Harnish et al., 2024). Fine-scale spatiotemporal information on nearshore fishing activity is not available as it is for the longline fleet, precluding the ability to quantify ecological drivers of co-occurrence and conflict risk for this endangered population as was possible for pelagic false killer whales (Chapter 4). However, insights from Chapter 4 and perceptions of longline fishers can help develop hypotheses on the degree to which MHI false killer whales rely on fisheries to supplement foraging needs.

Ecologically unfavorable conditions were more likely to result in wide-ranging behavior of pelagic false killer whales—by consequence, fine-scale co-occurrence with longline gear too—suggesting that depredation is an alternative, not primary, foraging tactic, at least for the pelagic population. Despite gaps in the understanding of drivers of MHI false killer whale ranging behavior, they exhibit broadly comparable movement patterns associated with the islands: tagged whales will often remain at one island area, moving within a limited range, before circumnavigating the island or moving to another island area within their range (Baird et al., 2012, 2010). If we apply the same logic from Chapter 4 to MHI false killer whales, their more dispersive movement behaviors outside of core ranges (Chapter 3) could reflect searching for alternative patches, including fishing activity. It is not possible to evaluate these hypotheses empirically without observer data in nearshore fisheries, but exploring differences in patch type and quality between the nearshore and offshore ranges (i.e., where data is available) may provide further insight.

There are operational differences in fishing practices between pelagic and MHI false killer whales' ranges that introduce caveats when contextualizing MHI false killer whale depredation behavior within Chapter 4 insights. For example, the presence of fish aggregating devices (FADs)—manmade, mostly anchored buoys designed to aggregate pelagic fishes—in nearshore waters could supplement patch quality for MHI false killer whales. Quantifying whale spatial behavior in relation to FADs remains a challenge due to the unknown distribution and abundance of private FADs combined with tag positional uncertainty. However, whales likely benefit from 'FAD patches', particularly through memory-based foraging (Fagan et al., 2013), and variation in natural prey availability could influence their reliance on such fixed features. This initial benefit imposes a potentially increased risk via passive overlap with fishers, but the frequency in which this type of co-occurrence escalates to conflict is unknown. Together, it is possible that false killer whale movement patterns relative to fishing activity are operationally dependent (e.g., fixed aggregative features with occasional fishers versus ephemeral longline gear which is the risk itself) and thus the findings from Chapter 4 are less transferrable to nearshore FADs or fisheries. Outside of FADs, other gear types used in nearshore fisheries are temporally less stable than longline gear (although the frequency of co-occurrence with nearshore fishing vessels could be higher), reducing the consistency of this alternative foraging opportunity to false killer whales. While this is likely a benefit for limiting harmful depredation and bycatch behavior in this endangered population, Chapter 4 also illustrates the difficulty of predicting drivers of fine-scale interactions (i.e., low explanatory power in models), particularly when they are rare and influenced by partially observed social environments.

In summary, the frequency in which MHI false killer whales depredate fisheries to meet or supplement energetic needs, and how population density could influence the propensity for this behavior, remains unresolved. This synthesis does not negate the threat of fisheries interactions to MHI false killer whales. Individuals matter: even if rare, injuries from interactions or mortality of a single individual can have cascading effects on population stability in this strongly social species (Angulo et al., 2018; Wade et al., 2012). Instead, this discussion contributes to the development of hypotheses on scale-dependent density-driven mechanisms—or compounding Allee effects—that could promote or impede population growth (Berec et al., 2007). These mechanisms, whether behaviorally mediated (i.e., cooperative foraging) or environmentally mediated (i.e., prey availability), can influence population stability through fine-scale, short-term survival, but may also contribute to broad-scale structuring and long-term persistence.

5.3.2 Long-term consequences of intra-cluster dynamics on population structure

Recent empirical evidence for the interplay between density dependence and spatial-social processes on individual fitness offers context for interpreting current and future false killer whale population dynamics. In their cross-taxa meta-analysis, Albery et al. (2025) found that high population density yielded higher within-population social connectedness, but that spatial connectedness occurred more readily than social connectedness. Webber et al. (2024) found similar empirical support in caribou (*Rangifer tarandus*), illustrating the adaptive value of habitat specialization and network centrality on maximizing individual-level fitness across population density gradients. Specifically, they found support for the Niche Variation Hypothesis (NVH; Van Valen, 1965) where under high population densities, individuals maximized fitness by specializing in habitats (e.g., to avoid competition) but were also less socially connected (Webber et al., 2024). While these studies focused on individual-level fitness, as opposed to the average fitness experienced at the social group-level, they provide a basis for generating hypotheses about how variation in false killer whale population density may shape social structure and the persistence of social clusters.

Taking insights from the aforementioned studies, under low population density I would expect false killer whales to become more generalist (e.g., reduced pressure to avoid competition), less spatially connected (e.g., lower local patch depletion rates), and potentially less socially connected (e.g., clusters become more spatially isolated). In the following sections I explore these outcomes in the context of false killer whales as strongly socially reliant species in a highly ephemeral resource landscape.

5.3.2.1 Changes in foraging or spatial strategies

False killer whales could generalize their diet or fine-scale habitat preferences in response to decreased population density. Under the broad implications from Albery et al. (2025) and Webber et al. (2024), the ultimate driver of this response would be the reduced pressure to avoid indirect competition. However, I expect changes in the generalization of false killer whales' foraging strategy to be first linked by behavioral processes (section 5.3.1.1), which are influenced by population (or group) density, and additionally shaped by variation in the physical environment (section 5.3.1.2). False killer whales are already generalist foragers, but in contrast to many of the systems presented in these studies (Albery et al., 2025; Webber et al., 2024), in Hawaiʻi cooperative behaviors on preferred large prey are key to their survival and thus fitness. Therefore, if false killer whales become even more generalist (e.g., consuming higher proportions of alternative prey or in alternative habitats), this could more likely result from behaviorally mediated Allee effects on cooperative hunting strategies and the availability of prey (both preferred and alternative) on the landscape. Interestingly, I found that Cluster 4 has a more generalist feeding niche in terms of their foraging habitat and also the most restricted space use (Chapter 3). It is difficult to discern whether this pattern could be a result of changes in population density over time, without consistent sampling across years and clusters, and without fine-scale details on the stability of cooperative foraging behavior over time. However, it is possible that Cluster 4's larger isotopic niche is shaped by density dependent spatial-social processes, consistent with the Niche Variation Hypothesis (Van Valen, 1965).

5.3.2.2 Changes in spatial and social connectedness

Decreasing population density could correspondingly decrease the spatial connectedness of false killer whale social clusters. In Chapter 3, I showed that Clusters 1 and 3 had the largest home ranges in the long-term and the most variable spatial patterns (i.e., low fidelity) over time. I discussed how cluster-specific behavioral properties, such as cluster size and composition, could explain these patterns and reflect mechanisms that mediate group size constraints on foraging success (Cantor et al., 2020). In other words, increased density at the cluster level likely drives higher fission-fusion dynamics, causing increased movement rates, and hence increasing the likelihood of inter-cluster contact rates—furthering the spatial connectedness among clusters. Therefore, if cluster-level densities decrease (i.e., under population decline), I would expect clusters to contract their ranges. This could have consequences for the frequency of inter-cluster interactions that define the population's social structure and support gene flow—mediating inbreeding risks—particularly for Clusters 2 and 4 whose core ranges are spatially separated by large channels between different island areas (He et al., 2019).

Because false killer whale sociality is strongly tied to their space use, density-dependent effects on spatial connectedness likely correlate with their effects on social connectedness (Albery et al., 2025). The extent to which this effect reduces inter-cluster connectedness will also depend on the extent to which their foraging strategy changes or remains the same (i.e., see the section above), and hence the capacity of the prey landscape to support the population. For instance, Chapter 3 revealed two key areas where overlaps between clusters' core ranges occur and are thus likely high quality foraging habitats. Reduced population density could potentially make it feasible for more (albeit smaller) clusters to co-occur in these high-quality patches and thus maintain important inter-cluster connections. Further, co-occurrences in high quality habitats could foster inter-cluster cooperative hunting behavior, and hence buffer against potential Allee effects on the efficiency of intra-cluster cooperative hunting. In this sense, behavioral and environmental processes could counteract some negative density-dependent effects.

5.4 Looking forward: indicators of population persistence

The synthesis above collectively points to social clusters being the units of conservation and sentinels to monitor population persistence of false killer whales. It also underscores the need to consider both behavioral (e.g., fine scale cooperation tactics, depredation behavior) and environmental (e.g., trends in preferred and alternative prey) determinants of population size when designing realistic recovery targets and strategies. Monitoring behavioral and demographic changes within and between clusters is necessary but challenging due to their rarity and frequent use of windward habitats that typically preclude small boat-based research. Therefore, combining existing survey approaches with other indicators could more efficiently reveal insight into population trends moving forward. In what follows, I highlight four key approaches forward.

5.4.1 Evaluating adaptability to environmental variation

More holistic characterizations of prey fish dynamics across MHI false killer whales' range will help determine what population-level outcomes (discussed in 5.3) could be more likely to occur. Does the environment contain enough prey to support more than four clusters of false killer whales? What are current trends in prey availability (abundance) and how do they vary across environmental gradients? It is difficult to obtain fisheries-independent data on large pelagic fish species, but integrating environmental modeling of fisheries-dependent landings data (e.g., Karp et al., 2023) could provide initial insight. Reported landings of pelagic fishes over the time series of MHI false killer whales' recent decline (2013-2022) do not indicate substantial changes in trends (although catch per unit effort, CPUE, for mahimahi has slightly declined for troll and longline fisheries; WPRFMC, 2023), but these data are caveated by fishery-dependent biases (see references within Karp et al., 2023). Together with continued analysis of false killer whale biomarkers (e.g., stable isotopes), these metrics on prey diversity and availability could help infer the extent to which environmental factors are limiting population recovery, and whether false killer whales could be adapting in response through their feeding behavior.

5.4.2 Monitoring persistence of social clusters

Continued monitoring of trends in abundance and spatial-social connectedness will provide insight into projected population viability and persistence. Trends in space use patterns (e.g., increased/decreased movement rates) could indicate whether density dependent effects are at play and could further impede or promote population recovery. This can be achieved through continued photo-identification and satellite-linked tagging, but it is also worth considering complementary approaches, such as passive acoustic monitoring in the core areas of the population, to determine the frequency of use and relative abundance. Some long-term passive acoustic monitoring efforts are in place in Hawaiʻi, however the hydrophones in these efforts are outside of MHI false killer whale core ranges (e.g., Baumann-Pickering et al., 2015; Ziegenhorn et al., 2023). Developing passive acoustic monitoring technology that could provide real time information on detections could also facilitate rapid response efforts to survey false killer whales. Assessing changes in within-cluster and between-cluster social associations over time would serve as an additional indicator for population stability/decline (e.g., are clusters becoming more connected or more disparate?) and associated consequences for recovery.

5.4.3 Contextualizing patterns in the greater ecological community

MHI false killer whales do not exist in a singular system, but rather a diverse community of other marine predators that are fully or partially sympatric and may indirectly compete with false killer whales to various extents (Baird 2016, Kratofil et al. 2023). Assessing trends in abundance and distribution of other species—within the spatial-social conceptual framework—could thus indirectly reveal factors contributing to the MHI false killer whale population decline or help predict or project population trajectories. For example, mesopelagic squid appear to be an alternative prey source for MHI false killer whales (Chapter 3), but are likely a primary prey source for other sympatric odontocetes including (but not limited to) short-finned pilot whales (more likely to overlap in squid diet; Gough et al., 2025) and melon-headed whales (less likely to overlap in squid diet; West et al., 2018). Increases in the abundance of these sympatric populations could reduce the availability of alternative prey to false killer whales, altering their ability to adapt via alternative prey landscapes, and thus limit population growth.

Another plausible indicator of population change in MHI false killer whales would be changes in the presence and distribution of partially sympatric NWHI and pelagic false killer whales. For example, if the MHI prey landscape is sufficient to sustain MHI false killer whales, but other factors—such as compounded Allee effects or incidental bycatch—continue to drive population decline, NWHI or pelagic false killer whales could potentially exploit the resulting ecological vacancy and expand their use of the MHI range. It is possible that the 2023 tagged pelagic false killer whale group (Chapter 4) is an emerging example of this effect: in contrast to all other tagged pelagic false killer whales, this group spent a large proportion of their time in the offshore lee of the MHI region. The island mass effect in the MHI is more prominent than in either of the other two populations' ranges, and the unique configuration of islands likely supports more efficient foraging strategies (e.g., larger island patches, more connected island patches, that reduce movement rates). Therefore, surveying areas where inter-population range overlap occurs (e.g., Kaua‘i/Ni‘ihau/O‘ahu, offshore Hawai‘i Island; see Mahaffy et al., 2026) and tracking

NWHI and pelagic populations (e.g., through continued satellite tagging efforts), could help elucidate whether such inter-population dynamics are occurring while also supporting other ongoing management needs (e.g., understanding pelagic whale interactions with fisheries).

5.4.4 Supporting sustainable conservation strategies

Understanding the extent to which various factors contribute to MHI false killer whale population trends can simultaneously inform management to support sustainable fisheries. Specifically, collaborating with fishers and agencies to better characterize the environmental and operational drivers of prey availability would not only improve understanding of the factors influencing false killer whale population growth, but also generate valuable insight into the fish stocks that sustain Hawaiian communities. Empirical data on the frequency and nature of direct competition with fisheries (i.e., fishery interactions) are also needed to evaluate how strongly this source of mortality contributes to population dynamics relative to other compounding pressures. At a minimum, providing clear guidance to commercial and recreational fishers on best practices for handling whales during interactions could help reduce serious injury and post-release mortality, as well as economic losses. Over the longer term, implementing observer programs or electronic monitoring will be essential for quantifying interactions and identifying the most effective strategies for mitigating whale-fishery conflicts.

5.5 Beyond false killer whales: broader implications in spatial-social ecology

Beyond its applied contribution to the conservation of Hawai‘i’s false killer whales, my dissertation advances a broader empirical and conceptual understanding of generalizable processes operating at the intersection of spatial and social ecology. Chapter 3 establishes a framework for testing scale-dependent mechanisms that link space use and sociality from individuals to populations, while the synthesis in section 5.3 explores potential ecological and demographic consequences of these feedback links. Together, these findings deepen understanding of how social individuals, groups, and populations persist, while also highlighting key unresolved questions in the broader field of spatial-social ecology.

Empirically testing the robustness of the spatial-social feedback framework I developed in Chapter 3 will help refine hypotheses at the interface of spatial and social ecology (Webber et al. 2023). For example, evaluating how well resource and life history characteristics across diverse systems and taxa align with the framework’s predictions will clarify its generalizability. This framework could be amended to include weights on the vectors linking scale-dependent processes to reflect the quantified predominance of social reliance versus resource dynamics at each spatial/social metric. In species that are gregarious but forage independently, for instance, resource ephemerality might exert more weight on individual spatial and social behavior than social reliance—either consistently or within specific temporal contexts (e.g., Peignier et al., 2019).

Extending this logic further, the framework also provides an opportunity to examine how variation in movement strategies—particularly in three-dimensional space—shapes emergent social structure and its population-level consequences. For example, other strongly social cetaceans, such as short-finned pilot whales and sperm whales (*Physeter macrocephalus*) which forage primarily through deep diving, likely have higher average movement rates in the vertical dimension than horizontal dimension. This constraint on horizontal movement rates may influence the frequency of inter-group interactions across larger spatial scales. This mechanism could explain the more clustered or hierarchical social networks in some populations of deep divers (e.g., as in short-finned pilot whales, Mahaffy et al., 2015; sperm whales, Whitehead et al., 2012). Such structural differences could, in turn, also influence information transfer and cultural transmission (Cantor et al., 2015; Cantor and Whitehead, 2013), individual fitness, and ultimately population persistence (Cantor et al., 2021). This mechanism may also help explain why short-finned pilot whales in Hawai‘i exhibit evidence of group-level acoustic dialects (and sperm whales; Cantor et al., 2015; Van Cise et al., 2018), whereas evidence for such dialects in false killer whales remains unresolved (Madrigal et al., 2026).

Lastly, exploring how long-term density-dependent processes shape spatial–social feedback mechanisms will be critical for understanding population resilience under accelerating environmental change and for refining adaptive management targets (Gaynor et al., 2024). Building on recent work by Webber et al. (2024) and Albery et al. (2025), there is growing empirical support for the adaptive value of density-dependent spatial behavior and social network centrality. In these studies, individuals adjusted space use and social positioning in ways that improved survival or resource access as local density fluctuated. However, this evidence comes largely from species that forage individually, where fitness consequences are primarily expressed at the level of the individual rather than the group.

This individual-centric perspective leaves two important gaps. First, it does not explicitly account for group-level processes. As demonstrated in Chapter 3, intra-cluster population scales can mediate both individual and collective fitness outcomes, suggesting that density-dependent feedbacks may operate differently within socially cohesive groups compared to loosely associated populations. In strongly social species, individual spatial positioning and network centrality are emergent properties of group-living structure, and their fitness consequences may depend on group cohesion, social stability, and demographic composition (Ebensperger et al., 2016; Heesen et al., 2015; Silk et al., 2003). Thus, the adaptive value of a given spatial–social strategy may vary not only with overall population density but also with the density and configuration of individuals within social clusters.

5.6 Conclusions

In conclusion, this dissertation contributes to a growing understanding of the integral role of spatial and social processes on individual behavior and population structuring (Webber et al. 2023), particularly on scale-dependent relationships (Picardi et al., 2024). By explicitly integrating movement ecology, social structure, and population demography, this work demonstrates that spatial and social dynamics are not parallel processes, but reciprocally linked components of population organization whose effects vary predictably across space and time.

This research also makes a novel contribution to the emergent spatial-social ecology literature by presenting a species and system that exemplify the extremes of sociality and resource ephemerality: false killer whales, a strongly social apex predator inhabiting a highly dynamic, patchy oligotrophic environment. The collective findings presented herein illuminate mechanisms explaining false killer whale movements and social structure across spatiotemporal scales; they also offer evidence-based insight into the factors driving cooperative intra-specific interactions (in MHI false killer whales) or conflictive inter-specific interactions (in pelagic false killer whales). These results underscore that population resilience or vulnerability cannot be understood from abundance alone; instead, they are emergent properties of spatial–social feedback links operating across nested scales.

5.7 References

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APPENDICES

Appendix A: Evidence for cooperative foraging in three dimensions

Overview

This appendix presents a brief extension from Chapter 2, presenting paired vertical and horizontal movements of false killer whales in the Hawaiian Islands over long (days to weeks) and large (several kilometers) spatiotemporal scales. False killer whale sub-groups have been documented coordinating their movements while foraging over extensive spatial scales (up to 35 km) and re-associating after capturing prey to share prey among companions (Baird, 2016; Baird et al., 2008a; Bradford et al., 2014). However, understanding of their cooperative foraging behavior has come from surface observations, which are limited in spatiotemporal scale—particularly for false killer whales, that regularly move up to 150 km per day (Baird et al., 2012, 2010; Fader et al., 2021)—and do not capture cooperative behaviors that may occur at depth. Thus, the extent to which these cooperative strategies extend into their vertical movements while foraging socially remains unknown.

Methods

Depth-transmitting satellite tag data for three pairs of false killer whales from Chapter 2 (Kratofil et al., 2026c) were used in this assessment and thus follow the same processing methods described in that section. In addition to using fitted movement models to estimate locations at behavior log record times, I also predicted locations at equal intervals (15-min) to examine pairwise distances over a more continuous time series. I then qualitatively assessed pairwise horizontal and vertical movements in the context of their known cooperative hunting behavior.

Results

There were three deployment events where two individuals were tagged with depth-transmitting tags in the same group and remained associated for some or all of their tag attachment period, one pair from each of the three recognized populations. Overlapping horizontal and vertical movement data between individuals ranged from 3.8 to 25.0 days after accounting for gaps in behavior logs. I provide highlights of findings herein, and more detailed, quantified assessments will be completed in future work.

The first pair (PcTag030, adult (unknown sex), and PcTag032, adult male; both from Cluster 3 of the MHI population) had 25 days of overlap in behavior log data with similar amounts of data coverage. These individuals remained associated for most of their period of overlap (median pairwise distance = 2.8 km; maximum pairwise distance = 27.9 km) and 73.4 percent of their combined 473 dives occurred within 5 km of each other. While these two individuals often undertook diving bouts (for dives ≥ 50 m and ≥ 2 min) during similar time periods, their dive behavior was only partially synchronous, with the number and depth of dives during a given period often differing between the pair. For example, between early morning and sunset on January 2, 2011, PcTag030 dove frequently, typically between 100–200 m in depth with three dives between 400–600 m (Figure A.1). In contrast, PcTag032 dove infrequently during this same period: three of these dives were the deeper (i.e., 400–600 m) dives, and the others were both shallow 100–200 m and very deep (> 800 m; Figure A.1). The pair remained associated (< 5 km) and coordinated in their horizontal movements during this 16 h period, with several periods of closer spatial proximity (Figure A.1). Greater straight-line distances between pairs occurred both longitudinally (i.e., one individual "in front" of the other) and latitudinally (i.e., individuals parallel but separated horizontally; Figure A.1); such dynamic association-reassociation behavior at this spatial scale occurred throughout the period of overlap.

These findings were highly similar to those observed in the pair of NWHI false killer whales (PcTag096, PcTag097), although both tags transmitted for shorter durations and one tag had lower data coverage. These individuals remained spatially associated throughout their overlapping transmission period (median distance apart = 1.1 km, maximum distance apart = 14.8 km; Figure A.2). These general findings were also observed in the third pair (PcTag090, PcTag092, both adult female open-ocean false killer whales), although there were fewer days of behavior log overlap (i.e., both durations were shorter) and one tag had lower data coverage, limiting assessment of pairwise patterns. These individuals were not as spatially cohesive during their period of data overlap as the first pair (median pairwise distance = 6.7 km, maximum pairwise distance = 82.0 km) and 40.3 percent of the 77 combined dives occurred within 5 km of each other. In contrast to the first pair, there were more periods with one individual not diving deeper than 50 m and the other diving during their period of overlap (Figure A.3). For all cases, there were likely group members that were not tagged but likely interacted with the tagged pairs we present herein.

Discussion

Sociality can be highly influential on the foraging behavior of predators that live in stable groups and where successful prey capture is dependent upon cooperation among group members (Krause and Ruxton, 2002b; Lang and Farine, 2017). False killer whales have been observed cooperatively hunting for prey, but this behavior has primarily been observed with surface-oriented and epipelagic prey (Baird et al., 2008a). Mechanisms of cooperative foraging on surface-oriented fish would not be discernable from the satellite tag data used in this study (which were restricted to dives ≥ 50 m and ≥ 2 min). However, our findings on within-group diving behavior suggest that false killer whales potentially cooperate when foraging at depth. We found that, despite coordination in horizontal movements (i.e., spatial cohesion over time) and in the timing of diving bouts (i.e., foraging in the same place and same block of time), pairwise vertical movements within bouts were largely asynchronous in time, depth, and duration. The lack of synchrony in dives during foraging bouts could point to collaborative behavior, where individuals serve different, but complementary, roles in group foraging (Bailey et al., 2013; Hansen et al., 2023; Lang and Farine, 2017). A similar social foraging strategy has been documented in long-finned pilot whales, where group members were synchronized in the timing of diving bouts but not always in their individual dives (Visser et al., 2014). Variability in the degree of synchrony in diving behavior could reflect cooperative herding of prey aggregations at depth (e.g., Benoit-Bird and Au, 2003), some individuals sampling the prey field and signaling feeding opportunities to other group members (e.g., acoustically, Dawson, 1991; specialized roles, Gazda et al., 2005; actively, Lusseau and Conradt, 2009). Alternatively, asynchrony in vertical movements, but maintained spatial cohesion, could reflect individuals foraging independently on vertically heterogenous prey (e.g., sperm whales, Irvine et al., 2017). The latter hypothesis may seem more plausible for false killer whales given the scale at which we describe spatial association here (i.e., several kilometers).

Despite that possibility, our findings are more likely linked to a social context than coincident individuals foraging independently, even with large inter-individual distances, for several reasons. First, false killer whales in Hawai‘i have frequently been observed rapidly converging, even when initially separated by several kilometers, and then documented sharing prey (RWB, personal observation). This often involves passing fish back and forth among group members before consuming it, after which the prey is shared among all companions (Baird, 2016; Baird et al., 2008a). Kin-directed food sharing has been documented in a killer whale population with a very similar social structure as MHI false killer whales and is hypothesized to serve inclusive fitness benefits in such highly natal philopatric social systems (Wright et al., 2016) like false killer whales (Martien et al., 2019). Such behavior may also serve to reinforce social bonds (e.g., Liévin-Bazin et al., 2019). Second, false killer whales are known to cooperatively hunt and exhibit coordinated movements over substantial distances (20 km or more; Baird et al., 2008a; Bradford et al., 2014), and dynamic spatial association patterns, as observed in our data, are typical for this species in Hawai‘i (Baird et al., 2010). Coordinating movements over such extensive spatial scales could reflect collective sensing (i.e., scanning or sampling) and exhaustive pursuit of prey that are large, fast, and difficult-to-capture (Hansen et al., 2023). This strategy may be particularly beneficial in Hawai‘i, where the oceanic environment is dynamic, patchy, and comparatively low in resource abundance (Benoit-Bird, 2024), and where prey refugia is shaped by the physiological limitations of predators (e.g., respiration, mobility) in the absence of physical barriers (Gaynor et al., 2019). While the spatial extent in which cooperative hunting behavior can occur over is often limited by visual abilities of predators in terrestrial systems (Hansen et al., 2023), false killer whales' echolocation and acoustic communication capacities likely facilitate coordination over large distances (e.g., Jacobs et al., 2024; Miller, 2002, 2006) during foraging bouts. We also highlight that the deepest dives in both pairs of whales occurred within 5 km of the other individual in the pair. This points to the importance of considering proximity to group members in both horizontal and vertical dimensions for group-living marine predators (e.g., Hessing et al., 2024; Kok et al., 2020).

Collectively, our findings on mostly asynchronous diving behavior, but synchronized timing of bouts and coordinated horizontal movements over extensive scales, provide key insights on the third dimension of cooperative foraging behavior by a highly social marine predator. Nevertheless, our interpretations are derived from only three pairs of tagged false killer whales, representing a bias from both limited sample size and from partial sampling of the group; our analysis did not capture other group members that were not tagged likely interacting with the tagged individuals. Sampling bias may also arise from fine-scale social preferences, where strongly associated pairs may be tagged together and subsequently more coordinated in their movements. However, the magnitude of this bias may be limited knowing false killer whales' highly dynamic spatial association patterns (Baird et al., 2010). For example, PcTag032 was tagged five hours after PcTag030, but the pair remained closely associated throughout their common deployment period. In contrast, PcTag090 and PcTag092 were tagged 30 minutes apart but were not as closely associated or coordinated as PcTag030/032. Further, there were several instances where the true proximity between pairs of tagged whales was slightly obscured by positional uncertainty (Figure A.1). Additional deployments on multiple individuals within a group—using higher accuracy Fastloc®-GPS tags—would facilitate understanding of vertical and horizontal coordinated foraging behavior. Information on fine-scale three-dimensional movements (e.g., from triaxial accelerometers) would additionally address knowledge gaps on the cooperative mechanisms these social marine predators employ at depth.

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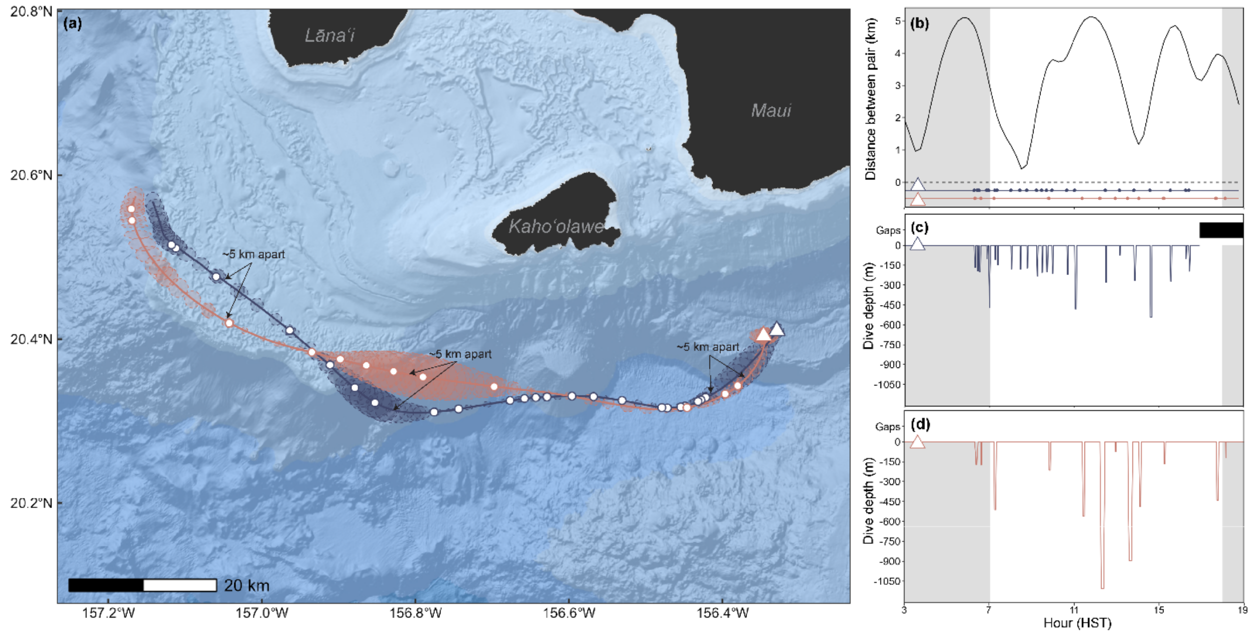

Figure A.1. Pairwise vertical and horizontal movements of two MHI false killer whales (PcTag030, PcTag032). One day example showing (a) movement paths (lines), dive positions (points), and error ellipses for locations (outlined ellipses) of the two individuals. Error ellipses aren't visible for some points, as they are the same or smaller in size of the point; periods with large error ellipses reflect gaps in transmitted location data. The outlined white triangles indicate the start of the time series for each individual for this day; (b) straight-line distances between the pair over time, with dive events indicated by points for each tag below the zero line; (c) and (d) dive profile plots for this day for PcTag030 and PcTag032, respectively; gray shading indicates nighttime, and the "Gaps" bar represents gaps in the behavior log data stream (i.e., dive behavior unknown during this time). Note that there were likely other untagged individuals interacting with this pair during this time.

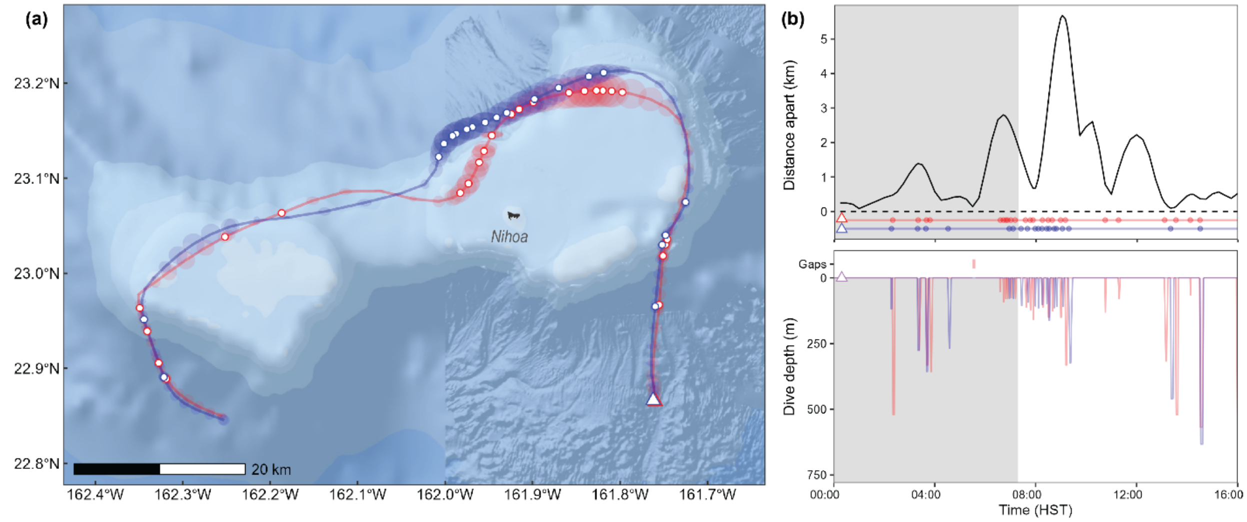

Figure A.2. Pairwise vertical and horizontal movements of two NWHI false killer whales (PcTag096, PcTag097). One day example of this pair showing (a) movement paths (lines), dive positions (points), and error ellipses for locations (shaded ellipses) of the two individuals. Error ellipses aren't visible for some points, as they are the same or smaller in size of the point; periods with large error ellipses reflect gaps in transmitted location data. The outlined white triangles indicate the start of the time series for each individual for this day; (b) straight-line distances between the pair over time, with dive events indicated by points for each tag below the zero line; (c) combined dive profile plots for this day for PcTag096 and PcTag097, respectively; gray shading indicates nighttime, and the "Gaps" bar represents gaps in the behavior log data stream (i.e., dive behavior unknown during this time). Note that there were likely other untagged individuals interacting with this pair during this time.

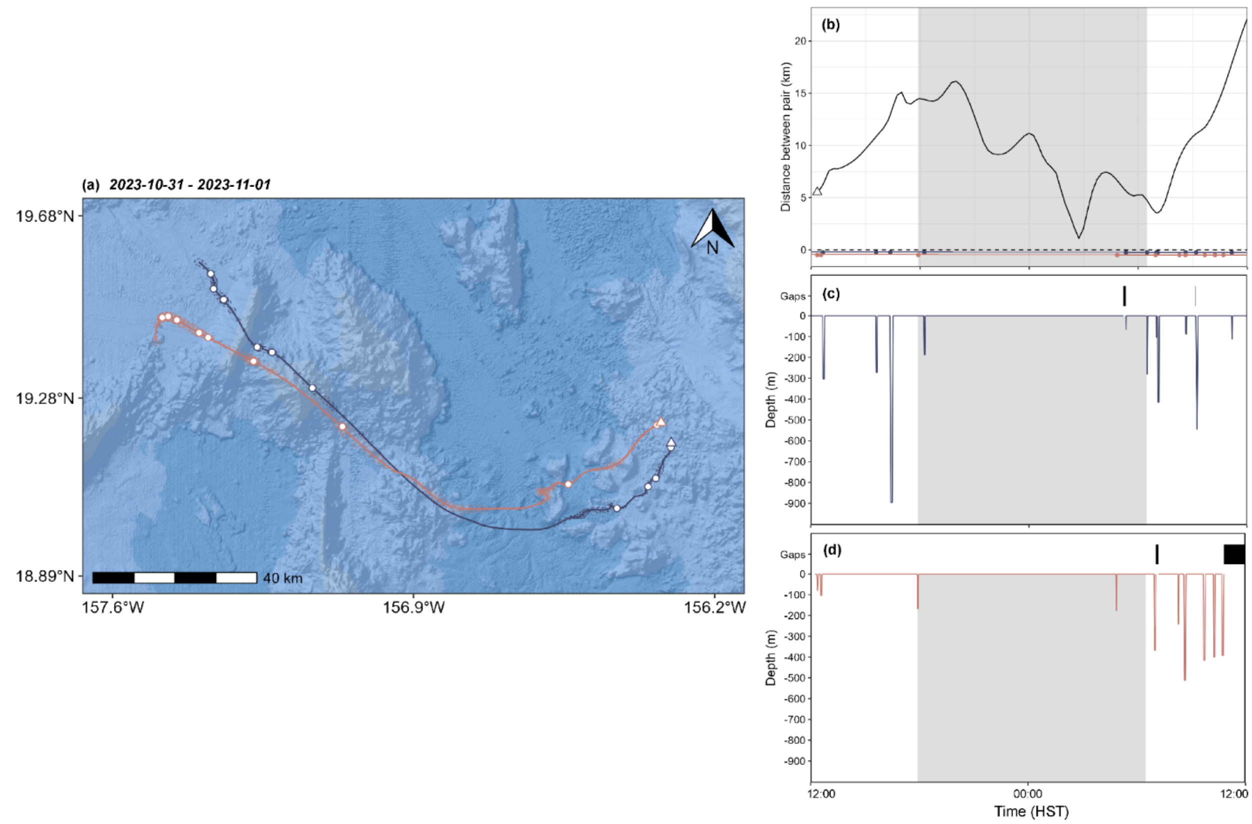

Figure A.3. Pairwise vertical and horizontal movements of two MHI false killer whales (PcTag090, PcTag092). One day example showing (a) movement paths (lines), dive positions (points), and error ellipses for locations (outlined ellipses) of the two individuals. Error ellipses aren't visible for some points, as they are the same or smaller in size of the point; periods with large error ellipses reflect gaps in transmitted location data. The outlined white triangles indicate the start of the time series for each individual for this day; (b) straight-line distances between the pair over time, with dive events indicated by points for each tag below the zero line; (c) and (d) dive profile plots for this day for PcTag090 and PcTag092, respectively; gray shading indicates nighttime, and the "Gaps" bar represents gaps in the behavior log data stream (i.e., dive behavior unknown during this time). Note that there were likely other untagged individuals interacting with this pair during this time.