Patterns of Odontocete Depredation and Bycatch in Pelagic Longline Fisheries

by

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University Program in Ecology
Duke University

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Rob Schick

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the University Program in Ecology in the Graduate School
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ABSTRACT

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Abstract

The leading threat to the conservation of whales and dolphins worldwide is incidental mortality (or bycatch) in fisheries. In longline fisheries, these interactions are commonly driven by an attraction to feed on bait or fish secured on fishing gear, a process known as depredation. Depredation is particularly common and costly in longline fisheries, where bait and catch are typically unprotected prior to gear retrieval. Bycatch of depredating whales can occur when animals become hooked or entangled in the gear while attempting to remove bait or catch. Depredation, and associated bycatch, is an exceedingly difficult problem to solve in open-ocean, or pelagic, longline fisheries, because the behavior often occurs at depth or at a large distance from the fishing vessel. Evidence of depredation may consist only of large stretches of missing bait or fish heads on hooks, because odontocetes have eaten the bodies of captured fish. Observations of bycatch are also rare and depend on on-board observers to carefully report details of the interactions.

In my dissertation, I examined two longline fisheries in the United States heavily impacted by depredation and bycatch of cetaceans: the Hawaiʻi deep-set longline fishery depredated by false killer whales (*Pseudorca crassidens*) and the Atlantic pelagic longline fishery depredated by short-finned pilot whales (*Globicephala macrorhynchus*). These two interactions are data rich (relative to most other pelagic longline fisheries), with detailed observations of cetacean-fishery interactions and long-term, dedicated behavioral research programs focused on the two depredator species. Both fisheries also benefit from resources and institutional will as a consequence of legislative mandates to reduce bycatch by the U.S. Marine Mammal Protection Act. Nevertheless, managers and stakeholders in both fisheries have struggled to fully resolve the problem. I used a variety of different data sources and interdisciplinary methods to better characterize depredation and bycatch interactions in both fisheries, with the ultimate goal to identify potential mitigation solutions that may help reduce the negative impacts of depredation and bycatch on both whales and fishermen.

In my first chapter, I reviewed common mitigation approaches to depredation and bycatch by marine mammals, and I conducted a case study analysis on the management process and its effectiveness in addressing depredation in the two focal fisheries. I identified past successes and failures and summarized the current situation for both fisheries and where bycatch management is going next.

The next two chapters focused in-depth on the Hawaiʻi deep-set pelagic longline fishery and depredation interactions by false killer whales. I first analyzed data collected by fisheries observers and from satellite-linked transmitters deployed on false killer whales to identify patterns of odontocete depredation that could help fishermen avoid overlap with whales. I identified several broad-scale patterns of depredation but found the best indicator of depredation to be the occurrence of depredation on a previous set of

the same vessel. I identified spatiotemporal scales of this ‘repeat’ depredation and analyzed satellite-tagged false killer whale data to better understand fine scale whale movement that may be relevant to avoiding depredation. I brought this information together to provide simple recommendations to fishermen that could reduce the occurrence of depredation from 18% to 9% on average (a 50% reduction).

Next I used the same fishery-dependent data sources (observer-collected and logbook data) and a novel, multi-stage modeling approach to derive quantitative estimates of catch losses by depredating odontocetes in the Hawaiʻi deep-set longline tuna fishery. Although depredation is relatively rare and variable on a per set basis, I estimated the total lost biomass and economic value of the top three catch species to average 100 t and one million USD per year, respectively. I also identified broad-scale spatiotemporal patterns where the relative losses of depredation by odontocetes are expected to be greatest, providing additional recommendations for how fishermen may be able to minimize costs of depredation.

My final chapter focused on the Atlantic pelagic longline fishery and depredation and bycatch of the short-finned pilot whale. I conducted a baseline analysis of pilot whale behavior from a rich satellite tag dataset, identifying a previously undetected diel behavioral pattern and adding additional novel insights to a growing body of research on this population of whales. I then described a novel behavioral state that occurred when whales were in close proximity to fishing activity (< 50 km).

Although the resolution of these data precluded a detailed characterization of depredation events, my observations that whales change their behavior when in the proximity of vessels may help inform move-on rules that fishermen could employ to reduce the occurrence of depredation and bycatch.

Dedication

I dedicate this dissertation to my parents, who have shown unconditional love and support throughout my long and winding educational and professional journey. And of course to Watson, who also showed unconditional love and support, in his own way, throughout this whole Ph.D.

Co-Authorship Statement

All of the work presented in this dissertation was collaborative and benefited greatly from the help of colleagues, some of whom are or will be co-authors on manuscripts submitted to peer-reviewed scientific journals. Versions of both chapters 1 and 2 have already been published. Chapter 1 was published in Frontiers in Marine Science in 2021 with Andy Read and Brianna Elliott as co-authors. Chapter 2 was also published in 2021 in the journal Ecosphere and was co-authored by Robin Baird, Amanda Bradford, Daniel Dunn, Karin Forney, and Andy Read. Rob Schick and Andy Read contributed significantly to Chapters 3 and 4. Funding provided by NOAA (Bycatch Reduction Engineering Program) and Duke University supported completion of much of this work.

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The rest of my committee also showed incredible support, patience, and mentorship. Jim Clark gave me an entirely new perspective on ecological modeling and

statistics right from my first semester as a Duke student, and he continued to provide constructive feedback and advice throughout. Daniel Dunn provided key inspiration and guidance on approaches to studying fishery bycatch interactions and is also a great role model in how to bridge the science and policy ocean science worlds. Rob Schick, although officially joining the team later on, has been a brilliant and valued collaborator and mentor for several years now. Finally, a very special thanks to Christophe Guinet, who welcomed me and hosted me in his research community in France and provided invaluable expertise on depredation interactions and marine mammal behavior throughout my dissertation.

Many other collaborators, mentors, and funders have contributed to this work and helped guide me on my professional journey. In particular, Amanda Bradford, Robin Baird, and Karin Forney have been incredibly generous with their time and expertise and have been wonderful role models. I also thank all the members of both Take Reduction Teams that I interacted with and who provided important feedback that improved this work. At Duke, Read Lab and Superpod members, past and present, have helped my work and taught me so much over these years. Special thanks to Danielle Waples, Heather Foley, Zach Swaim, Nicola Quick, Will Cioffi, Vivienne Foroughirad, Dave Haas, Austin Allen, Jeanne Shearer, and Greg Larsen. Thanks to Rachel Lo Piccolo, Danielle Wiggins, Jim Hench, and Lisa Campbell for tirelessly supporting the student community. I also thank NOAA and Duke for providing important funding opportunities that supported my work.

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Someone said that “everyone thinks they have the best dog, and none of them are wrong.” I am most certainly not wrong and I think there are a lot of people in the DUML community that agree that Watson is one of a kind. He entered my life right near the start of my Duke journey and made life so much richer, every step of the way. I can’t imagine doing it without him.

Finally, I also can’t imagine doing this, at least the last two years or so, without my very supportive partner Brianna (and her also very best dog, Brisbane). Through a global pandemic and the most intense and busy times of both of our lives, she has been a rock and endlessly supportive and caring. Her love, energy, and brilliant ideas and insights on global fisheries policy and bycatch mitigation, have vastly improved my life and my work. I can’t thank her enough.

1. Introduction: The challenges of managing depredation and bycatch of toothed whales in pelagic longline fisheries: two U.S. case studies.

1.1 Introduction

Direct interactions with fisheries are broadly recognized as the leading threat to the conservation of small cetaceans worldwide (Mitchell 1975, Read 2008, Brownell Jr. et al. 2019). Bycatch in gillnets is the most pressing problem (Read et al. 2006, Reeves et al. 2013), currently contributing to declines of 11 of the 13 critically endangered small-cetacean populations (Brownell Jr. et al. 2019) in freshwater, estuarine, and coastal environments. The threat is different in pelagic waters, where one of the primary gear types implicated in direct interactions with cetaceans is the pelagic longline (Lewison et al. 2014). Whereas some bycatch problems are a function of cetaceans failing to perceive gear (e.g., gillnets) or being actively entrapped by fishermen (e.g., purse seines), interactions between cetaceans and hook and line gear, such as longlines, are often driven by attraction of the animal to feed on bait or fish secured on the gear, a behavior known as *depredation* (Gilman et al. 2007a, Read 2008, Hamer et al. 2012). Many odontocete species are adept at depredation and can remove large quantities of catch, which can result in substantial economic costs to fishermen (Peterson et al. 2014, Tixier et al. 2020a). Switching from energetically costly, natural foraging on free-swimming prey to consumption of high-energy, restrained prey may provide energetic benefits to depredators and it has been shown that the reproductive output of depredating whales has increased in at least two populations (Tixier et al. 2015a, Esteban et al. 2016). However, this behavior also increases the risk of hooking or entanglement in fishing gear (e.g., Garrison 2007, Forney et al. 2011) or lethal retaliation or harassment by fishermen (Guinet et al. 2015), both of which have led to negative population consequences for depredating populations (Poncelet et al. 2010, Guinet et al. 2015, Tixier et al. 2020b).

Interactions between cetaceans and pelagic longlines have been documented as a concern for fishermen since shortly after the establishment of industrial longline operations in the 1950s (e.g., Sivasubramaniam 1964). An increase in published reports on depredation in the past two decades suggest that depredation is an increasing problem (Tixier et al. 2020b), and there has been strong interest in characterizing patterns of interactions between cetaceans and longlines to generate mitigation strategies (Werner et al. 2015, Tixier et al. 2020b). Numerous workshops involving fishermen, scientific experts, and fishery managers have assessed available mitigation strategies and considered approaches for research, testing, and implementation. These past efforts and general syntheses of odontocete-longline interactions and research have been summarized in several previous reviews (e.g., Gilman et al. 2007a, Hamer et al. 2012, Werner et al. 2015, FAO 2018, Hamilton and Baker 2019, Tixier et al. 2020b).

Many of these mitigation efforts have been motivated by a public desire to ensure that seafood is ethically and sustainably sourced (e.g., Roheim et al. 2018). In the

United States, for example, statutes such as the Marine Mammal Protection Act (MMPA) require fisheries to reduce incidental mortality or serious injury of marine mammals during fishing operations to ‘insignificant levels’ [16 U.S.C. § 1387]. International bodies such as the Food and Agriculture Organization of the United Nations (FAO) and regional fisheries management organizations (RFMOs), international governance bodies that manage fisheries in respective geographic regions, are increasingly addressing the bycatch of cetaceans and other vulnerable species (e.g., Clarke et al. 2014, Juan-Jordá et al. 2018, FAO 2020). Additionally, the mitigation of cetacean depredation and bycatch is motivated by a desire to reduce the direct economic impacts to the fisheries themselves (Werner et al. 2015, Tixier et al. 2020a).

Depredation and bycatch in pelagic longline fisheries are related, but separate and unique problems that have proven exceedingly difficult to solve. There has been little success in implementing effective strategies to protect target catch and reduce the economic costs of depredation to fishermen (Hamer et al. 2012, Werner et al. 2015, Tixier et al. 2020a). Likewise, it has been challenging to reduce injuries or mortalities due to hookings or entanglements of depredating cetaceans, even when mandated by legislation (e.g., Baird 2019). In many parts of the world, data limitations and scarce resources make it difficult to characterize the nature of these interactions and understand the scope of the problem (Hamer et al. 2012, Tixier et al. 2020b). In cases where bycatch occurs as a result of depredation, management mandates typically extend only to reducing bycatch or minimizing injury of bycaught cetaceans (e.g., the U.S. MMPA). Reducing depredation would result in a mutually positive outcome for industry and cetaceans, but in the absence of an effective strategy to reduce depredation, fishermen may be faced with costly measures to reduce bycatch that limit fishing effort, in addition to experiencing losses from depredation (Werner et al. 2015).

In this paper, we briefly outline the nature of these interactions and the primary mitigation strategies available, including recent findings relevant to mitigation and impacts on depredating odontocetes. We then explore two case studies from the United States in which attempts have been made to address the depredation and bycatch of small cetaceans. In the U.S., the MMPA requires Take Reduction Teams (TRTs) to develop methods to reduce the bycatch of marine mammals when mortality exceeds a biological reference point, known as Potential Biological Removal (PBR) [16 U.S.C. § 1362 (20)]. We situate these efforts in the context of global bycatch of odontocetes, in the hope that lessons learned from these well-funded, collaborative, and statutorily-mandated attempts may offer insights to other countries and international fisheries management bodies as they grapple with these complex issues.

1.2 Overview of the problem

1.2.1 Depredation

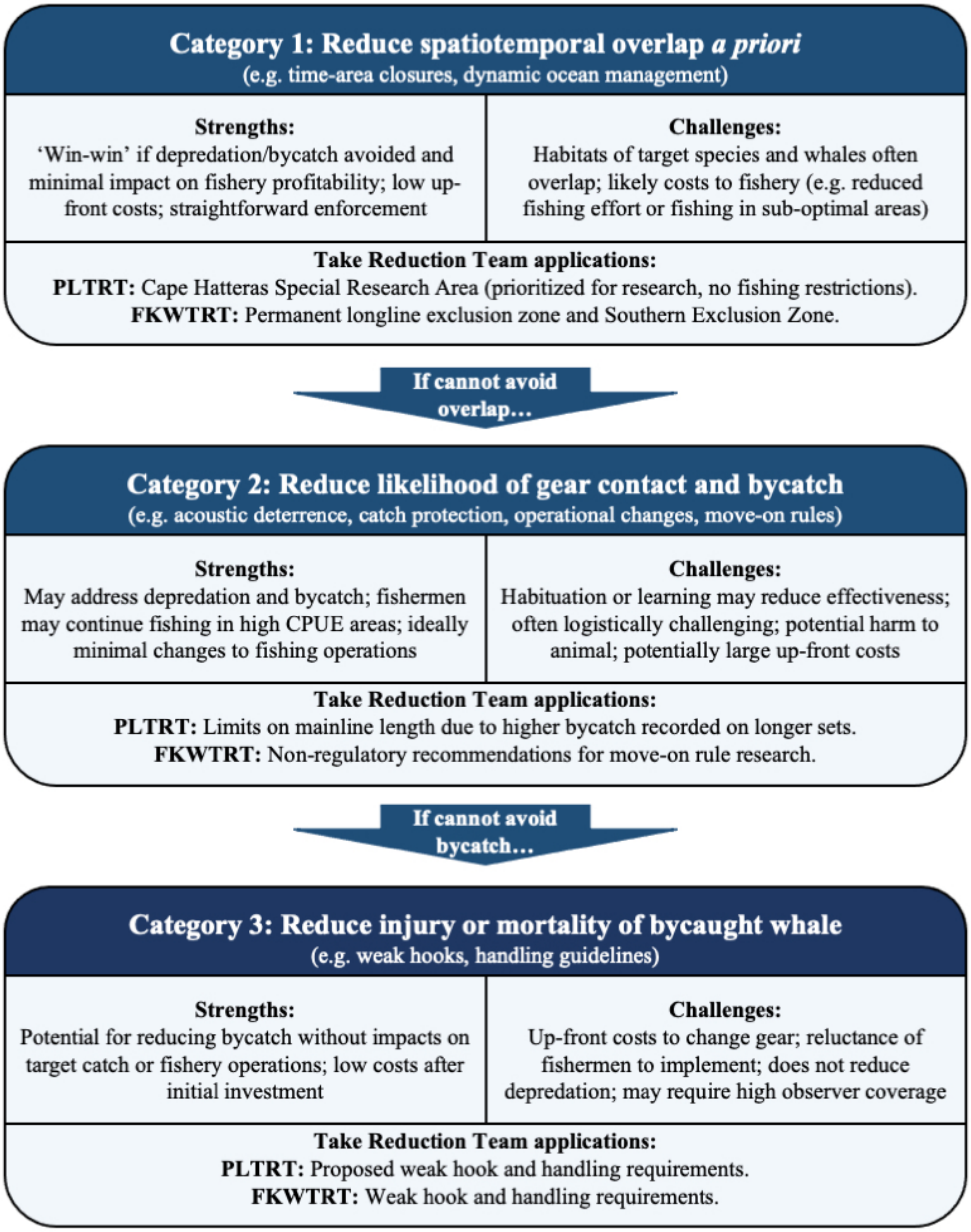
There are two distinct types of longline fishing, each susceptible to interactions with cetaceans in different ways. Demersal, or bottom, longlining is common in temperate to sub-polar ecosystems, in which gear is deployed on the sea floor to target species such as halibut (*Hippoglossus* spp.) or sablefish (*Anoplopoma fimbria*) in the Northern Hemisphere (Sigler et al. 2008, Peterson et al. 2013) and toothfish (mostly *Dissostichus eleginoides*) in the Southern Hemisphere (Ashford et al. 1996, Hucke-Gaete et al. 2004, Roche et al. 2007). The primary depredating odontocetes in these demersal longline fisheries in both hemispheres are killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) (Ashford et al. 1996, Hucke-Gaete et al. 2004, Roche et al. 2007, Sigler et al. 2008, Hamer et al. 2012, Peterson et al. 2013). Due to the depths in which gear is fished (500-2000 m), depredation occurs mostly during the hauling phase (but see Richard et al. 2020). Both odontocete species have been observed hooked or entangled in demersal gear, but bycatch appears relatively rare in demersal longline fishing (e.g., Ashford et al. 1996). Negative population impacts have been tied to active killing by fishermen. For example, killer whales in the Southern Ocean are thought to have experienced population declines from the use of explosive deterrents and lethal retaliation in Illegal, Unreported, and Unregulated (IUU) fishing in the 1980s and 1990s (Poncelet et al. 2010, Guinet et al. 2015). There are other important concerns related to the interaction, for example: (1) the economic and stock consequences of target catch lost to whales (Peterson et al. 2013, Peterson et al. 2014, Peterson and Hanselman 2017, Hanselman et al. 2018, Tixier et al. 2020a); and (2) possible indirect effects on depredator populations and their ecological communities driven by food subsidies (Tixier et al.

2017, Tixier et al. 2019). Two long-term collaborations among scientists, managers, and fishermen, one in the Gulf of Alaska (e.g., Straley et al. 2015) and one in the Crozet and Kerguelen Island fisheries (e.g., Guinet et al. 2015), have provided important data on the nature of these interactions.

In contrast, pelagic longlines typically target wide-ranging, pelagic species such as tunas (*Thunnus* spp.), swordfish (*Xiphias gladius*), and dolphinfish (*Coryphaenus hippurus*) by suspending baited hooks in the water column (Watson and Kerstetter 2006, Ward and Hindmarsh 2007). The gear is fished at depths that range from tens of meters for species such as swordfish, to over 400 meters for deeper species such as bigeye tuna (*Thunnus obesus*) (Watson and Kerstetter 2006, Ward and Hindmarsh 2007). Pelagic longline fishing is most common in tropical and sub-tropical habitats and is one of the primary gear types to interact with many species of oceanic cetaceans (Lewison et al. 2014). At least 20 odontocete species have been observed as bycatch in pelagic longline fisheries (Werner et al. 2015, Tixier et al. 2020b), including the false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Globicephala macrorhynchus*), killer whale, and, to a lesser extent, Risso's dolphins (*Grampus griseus*) (Hamer et al. 2012, Werner et al. 2015). As fishing operations and solutions to depredation vary greatly between these two fishery types, and because direct mortality of small cetaceans is currently a greater problem for pelagic than demersal longlines, we focus on depredation and bycatch mitigation in pelagic longlines in this paper.

1.2.2 Potential solutions

There are three, semi-hierarchical categories of approaches generally considered for addressing odontocete depredation and bycatch (Werner et al. 2015, Hamilton and Baker 2019): (1) reducing the spatiotemporal overlap between whales and fishing operations to minimize encounters *a priori*; (2) deterring whales from the gear or reducing their ability to perceive, locate, or access bait or catch, for example by disrupting the echolocation abilities of whales or deploying protective sleeves around captured fish; and (3) reducing the probability of injury and mortality despite becoming hooked or entangled, for example with weak terminal gear or hooks that allow cetaceans to break free but retain target catch (Figure 1). Many potential solutions covering these three categories have been critically evaluated by both fishermen and scientists and these are reviewed in detail elsewhere (Gilman et al. 2007a, Hamer et al. 2012, Werner et al. 2015, Hamilton and Baker 2019, Zollett and Swimmer 2019, Swimmer et al. 2020). Here, we briefly consider the range of options and recent findings relevant to pelagic longline fishery interactions and our two case studies.



Category 1: Reduce spatiotemporal overlap *a priori*
(e.g. time-area closures, dynamic ocean management)

Strengths:
'Win-win' if depredation/bycatch avoided and minimal impact on fishery profitability; low up-front costs; straightforward enforcement

Challenges:
Habitats of target species and whales often overlap; likely costs to fishery (e.g. reduced fishing effort or fishing in sub-optimal areas)

Take Reduction Team applications:
PLTRT: Cape Hatteras Special Research Area (prioritized for research, no fishing restrictions).
FKWTRT: Permanent longline exclusion zone and Southern Exclusion Zone.

Category 2: Reduce likelihood of gear contact and bycatch
(e.g. acoustic deterrence, catch protection, operational changes, move-on rules)

Strengths:
May address depredation and bycatch; fishermen may continue fishing in high CPUE areas; ideally minimal changes to fishing operations

Challenges:
Habituation or learning may reduce effectiveness; often logistically challenging; potential harm to animal; potentially large up-front costs

Take Reduction Team applications:
PLTRT: Limits on mainline length due to higher bycatch recorded on longer sets.
FKWTRT: Non-regulatory recommendations for move-on rule research.

Category 3: Reduce injury or mortality of bycaught whale
(e.g. weak hooks, handling guidelines)

Strengths:
Potential for reducing bycatch without impacts on target catch or fishery operations; low costs after initial investment

Challenges:
Up-front costs to change gear; reluctance of fishermen to implement; does not reduce depredation; may require high observer coverage

Take Reduction Team applications:
PLTRT: Proposed weak hook and handling requirements.
FKWTRT: Weak hook and handling requirements.

Figure 1: Hierarchical categories of bycatch mitigation. Outline of the hierarchical categories of bycatch mitigation solutions available to longline fisheries affected by depredation; including the strengths and weaknesses of each category and specific applications implemented by each Take Reduction Team.

Avoiding overlap between whales and longlines while maintaining target catch rates and fishery profitability (i.e., Category 1 listed above), is an ideal scenario. Many pelagic predators, including longline fishermen, range widely while tracking oceanographic conditions, and identifying the ecological drivers of co-occurrence could allow fishermen to avoid overlap and subsequent interactions. This 'dynamic ocean management' (Dunn et al. 2016) has been suggested as a means of reducing negative human-wildlife interactions, such as the bycatch of sea turtles (Howell et al. 2015) and ship strikes of migrating baleen whales (Hazen et al. 2017). Indeed, constantly improving oceanographic models and animal telemetry data have allowed unprecedented insights into habitat use by marine predators (Hays et al. 2019), including odontocetes that engage in depredation (e.g., Thorne et al. 2017, Anderson et al. 2020), and such information could be used to predict their overlap with pelagic longline fisheries. However, depredating whales may target similar oceanographic features as those sought by longline vessels. For example, short-finned pilot whales use the same shelf-break habitat and sea surface temperature patterns as the pelagic longline fleet along the U.S. east coast (Garrison 2007, Thorne et al. 2017, Stepanuk et al. 2018, Thorne et al. 2019). Similarly, false killer whale depredation and bycatch on Hawaiʻi pelagic longline vessels is likely driven by whales and fishermen targeting the same prey species (Forney et al. 2011). In such instances, the use of spatial and temporal avoidance would require fishing effort to relocate to sub-optimal areas with reduced rates of depredation and bycatch, but also lower catch rates of target species.

When broad-scale avoidance of depredators is not possible, the next logical strategy is to reduce the probability of gear contact and bycatch by deterring depredators, limiting their ability to detect or access catch, or altering fishing operations to limit contact (Category 2) (Werner et al. 2015, Swimmer et al. 2020). These strategies are all challenging due to the strong attraction that odontocetes can have towards longline gear (Werner et al. 2015), potentially driven by energetic incentives to feed on captured fish (Esteban et al. 2016). Physical harassment (e.g., explosives) and lethal retaliation have been reported in longline fisheries (e.g., Poncelet et al. 2010) but have questionable effectiveness, in addition to obvious negative conservation outcomes (Werner et al. 2015). Acoustic deterrents have garnered much interest by fishermen but have thus far proven impractical (Werner et al. 2015), as depredating whales likely quickly habituate and may even be attracted to the presence of deterrents that notify whales of the location of catch (Tixier et al. 2015b, Werner et al. 2015). Strategies to disrupt echolocation abilities or otherwise mask detection of gear can similarly be susceptible to learning and habituation (Mooney et al. 2009). Protecting target catch with sleeves or other physical barriers has shown promise in demersal longline fisheries, where they can be triggered to protect captured fish during hauling, when most depredation occurs (Moreno et al. 2008). The nature of pelagic longline gear makes this much more challenging as depredation does not occur exclusively during hauling and thus protective devices must be triggered by fish capture (Werner et al. 2015). These devices must also be cost effective and easy to store and deploy, both of which remain significant challenges; although further research may improve efficacy and feasibility (Rabearisoa et al. 2012, 2015; Hamer et al. 2015).

Catch protection devices also do not protect against odontocete depredation of bait, which has long been suspected by fishermen in some pelagic longline fisheries (Ayers and Leong 2020). The relative rate of depredation of bait *versus* catch is unknown and likely varies among fisheries, although small cetaceans are likely to engage in this behavior (Gilman et al. 2007a, Werner et al. 2015). Recent video and acoustic evidence confirmed that false killer whales depredate pelagic longline bait in the daytime using both visual and audio cues (Thode et al. 2016). Garrison (2007) also showed lower bycatch rates of Risso's dolphins in the U.S. East Coast pelagic longline fishery when fish bait was used in place of squid bait. These results suggest the potential for bait-focused mitigation strategies (e.g., chemicals to reduce palatability of bait or using artificial bait), although these techniques are untested and potentially challenging due to unintended impacts on target and non-target catch (Werner et al. 2015, Gilman et al. 2020).

Other avoidance strategies involve operational changes to limit opportunities for interaction, such as fishermen leaving areas of known depredation, a strategy formally known as 'move-on rules' (Dunn et al. 2014, Werner et al. 2015). This is a challenging strategy as odontocete depredators are highly mobile and may be able to perceive acoustic signatures from vessels over large distances. For example, sperm whales depredating demersal longlines in the Gulf of Alaska are attracted to cavitation noises of a ship's propeller when the engine is engaged to begin hauling gear and can detect these sounds at distances of several kilometers (Thode et al. 2007). Recent findings on interactions between false killer whales and the Hawai'i longline fishery suggest this mode of detection likely occurs with pelagic longlines as well. Passive acoustic monitoring of longline gear deployments detected false killer whales most commonly during the hauling phase, with whales potentially moving along the mainline away from the vessel as gear was being retrieved (Bayless et al. 2017). In another study, a group of satellite-tagged false killer whales was observed to show directed movements toward fishing gear during the hauling phase of some sets, although there was no apparent reaction to gear during other sets despite likely being within detection range (Anderson et al. 2020). Reducing the amount of gear set has also shown modest reductions in interaction rates in pelagic longline fisheries (Garrison 2007), and this technique could work synergistically with move-on strategies to limit possibilities for gear detection and contact by odontocetes (Tixier et al. 2015c). Together, these findings suggest that improved reporting of depredation interactions and communication among fishing vessels could help fleets avoid acoustic detection when depredation has been observed in a particular location.

If avoidance of depredators or minimizing contact with gear is not possible, modifying the terminal gear to release hooked animals or facilitating shedding of entangled gear may be the only option to mitigate bycatch impacts (Category 3) (Werner et al. 2015, Zollett and Swimmer 2019, Swimmer et al. 2020). In longline fisheries, this strategy generally entails guidelines to encourage fishermen to remove gear from hooked or entangled animals, or the use of hooks with a targeted bending strength, such that hooks are weak enough to straighten and release toothed whales but sufficiently strong to retain target catch (Bayse and Kerstetter 2010, Bigelow et al. 2012). This 'weak-hook' strategy has been used successfully to reduce bycatch of large, non-target bluefin tuna (*Thunnus thynnus*) by 46% in the U.S. Gulf of Mexico pelagic longline fishery, with no statistically significant impact on catch rates of yellowfin tuna (*Thunnus albacares*) (Walter 2017). Controlled mechanical tests of bending strengths and behavior of hooks under strain in the lip tissue of dead odontocetes have helped identify candidate weak hooks for minimizing cetacean bycatch (McLellan et al. 2015). Field trials in the U.S. Atlantic large pelagics longline fishery and Hawai'i deep-set longline fisheries have tested similar hook designs under controlled conditions (Bayse and Kerstetter 2010, Bigelow et al. 2012). The bycatch of cetaceans was too rare to determine whether weaker hooks had a positive influence on the outcome of such events, but weaker hooks were returned straightened more often than strong hooks in each study and one pilot whale was observed released by a straightened hook in the Atlantic (Bayse and Kerstetter 2010, Bigelow et al. 2012). Comparable rates of target catch were recorded in each study, although the Hawaiʻi study was not carried out during the season when the largest tuna are caught (Bigelow et al. 2012) and the size of swordfish was slightly smaller on weak hooks in some Atlantic trials (Bayse and Kerstetter 2010). One obstacle to implementation of such measures is the understandable reluctance of fishermen to modify their terminal tackle, particularly if such changes might reduce the catch rates of large and valuable target species (e.g., Bigelow et al. 2012, Ayers and Leong 2020). The post-release survival rates of animals hooked or entangled in pelagic longline gear are not well understood but have obvious and important implications for understanding population-level impacts (Garrison 2007, Werner et al. 2015).

1.3 Regulatory frameworks to address odontocete-longline interactions in the United States

1.3.1 U.S. Marine Mammal Protection Act and Take Reduction Teams

The U.S. MMPA of 1972 regulates the 'take' of marine mammals in commercial fisheries, with the term 'take' defined as to harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill any marine mammal [16 U.S.C. § 1362 (13)]. The general prohibition on taking under the MMPA has exemptions for certain activities, including commercial fishing, and authorizes the National Marine Fisheries Service (NMFS) to enforce this prohibition for all cetacean species in U.S. jurisdictions. Amendments to the MMPA passed in 1994 provide a mandate to assess the magnitude of bycatch relative to biological reference points and to implement conservation actions when takes exceed these thresholds [16 U.S.C. § 1387]. The MMPA also requires assessments for all marine mammal stocks in the U.S. Exclusive Economic Zone (EEZ) to characterize, among other parameters, range and population structure, minimum population estimates, and the magnitude of bycatch in fisheries and other sources of human-induced mortality [16 U.S.C. § 1386]. In addition to observed mortality, entangled or hooked marine mammals are considered takes if they are "likely to die", defined as experiencing a serious injury that presents a greater than 50 percent chance of death (NOAA Fisheries 2014). Precise estimates of post-release mortality are not available for most cetacean species and types of interactions (NOAA Fisheries 2014), but specific criteria for designating the probability of mortality to marine mammals due to fisheries interactions have been developed by NMFS in several workshops, using expert elicitation amongst marine mammal scientists and veterinarians (Angliss and Demaster 1998, Andersen et al. 2008). These criteria have been formalized in NMFS' Procedural Directive entitled "Process for distinguishing serious from non-serious injury of marine mammals (NOAA Fisheries 2014)," which provides guidance for estimating mortality using the best available scientific information when follow-up on the condition of the injured animal is unavailable, as is the case in the vast majority of fishery interactions with small cetaceans, including those with pelagic longlines (NOAA Fisheries 2014). Marine mammals experiencing either bycatch mortality or injury likely to lead to death are designated as Mortality and Serious Injury (M&SI). This parameter is then compared with a biological reference point, Potential Biological Removal (PBR) [16 U.S.C. § 1362 (20)], calculated for each stock as a product of minimum population size, maximum rate of population increase, and a recovery factor (Wade 1998). PBR represents the maximum number of individuals that can be removed while maintaining the stock at or above optimal sustainable population size [16 U.S.C. § 1362 (9)], typically defined as half of carrying capacity. If human-caused M&SI for a particular stock exceeds PBR, a Take Reduction Team (TRT) [16 U.S.C. § 1387 (f)] must be convened. A TRT is a stakeholder group which includes members of the fishing industry, environmental groups, academic scientists, and government managers and scientists.

Take Reduction Teams are asked to develop a Take Reduction Plan (TRP) to reduce M&SI to below PBR within six months of implementation and to a level approaching zero (the Zero-Mortality Rate Goal, ZMRG, defined as <10% of PBR) within 5 years [16 U.S.C. 1387 (f) (2)]. To reduce the effects of inter-annual variation, a five-year average of M&SI is applied against PBR. The Team is required to agree to a plan by consensus, and the plan is typically comprised of a suite of regulatory and non-regulatory measures. In the absence of a consensus plan, NMFS must generate a plan, so the impetus is on Team members to work together to craft a more effective strategy by consensus. Seven TRTs are currently active and their successes, failures, and the strengths and weaknesses of the TRT process have been reviewed elsewhere (McDonald and Rigling-Gallagher 2015, McDonald et al. 2016, Borggaard et al. 2017, Punt et al. 2018).

Two of these Teams directly address odontocete interactions with pelagic longlines and are reviewed here: the Pelagic Longline Take Reduction Team (PLTRT), addressing short-finned pilot whale bycatch in the Atlantic pelagic longline fishery, and the False Killer Whale Take Reduction Team (FKWTRT), addressing false killer whale bycatch in the Hawaiʻi pelagic longline fishery. Below, we describe these two teams, the strategies they have developed for addressing bycatch, and assess whether these measures are helping meet the goals of the MMPA. We draw on published peer-reviewed studies, NOAA technical documents, and summary information prepared following Team meetings that are publicly available through NOAA Fisheries[1,2].

1.3.2 Pelagic Longline Take Reduction Team

The U.S. large pelagics longline fishery targets pelagic swordfish, tunas, and billfish in the U.S. Atlantic and Gulf of Mexico EEZ. Both long-finned (*Globicephala melas*) and short-finned (*G. macrorhynchus*) pilot whales occur in the western North Atlantic, and both may depredate bait or catch from longlines and become hooked or entangled in gear as a result (Garrison 2007). Concern over bycatch of pilot whales in pelagic

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[1] False Killer Whale Take Reduction - Key outcomes memoranda and summaries. Accessed on 14 September 2020 at https://www.fisheries.noaa.gov/national/marine-mammal-protection/false-killer-whale-take-reduction.

[2] Pelagic Longline Take Reduction Plan - Key outcomes memoranda and summaries. Accessed on 14 September 2020 at https://www.fisheries.noaa.gov/national/marine-mammal-protection/pelagic-longline-take-reduction-plan.

longline fisheries emerged in the 1990s and 2000s (Waring et al. 2002), at a time when the demography and distribution of the two pilot whale species were not well understood. Initial stock assessments pooled abundance and takes of both species to calculate PBR and estimate M&SI (Waring et al. 2002). Subsequent research has identified the primary region of overlap to be along the continental shelf break between 38ºN and 40ºN latitude, with long-finned pilot whales occurring mostly north of this area and short-finned pilot whales primarily to the south (Garrison and Rosel 2017). Short-finned pilot whales make seasonal movements north of this area in summer months and are known to occur farther offshore into Gulf Stream waters (Garrison and Rosel 2017, Thorne et al. 2017). Most takes occur in times and locations where long-finned pilot whales are unlikely to occur, and all bycatch is thus assigned to the short-finned pilot whale. When takes occur farther north, a logistic regression model is used to estimate the probability of species occurrence and apply the take to each species as appropriate (Garrison and Rosel 2017, Hayes et al. 2019).

In June 2005 NMFS convened the first meeting of the PLTRT to develop a plan to reduce the bycatch of pilot whales to below ZMRG. The Team consists of approximately 20 members, including pelagic longline fishermen and other industry representatives, marine mammal and fisheries scientists, a representative from the U.S. Marine Mammal Commission, and representatives from environmental organizations and state and federal fisheries agencies. The Team held meetings every few months in 2005-2006, during which subject-matter experts provided briefings on pilot whale biology, fishery characteristics and experiences with interactions, and relevant mitigation research and efforts in other fisheries. Team members formed working groups to explore potential mitigation options in more depth and identify research priorities specific to the fishery. Discussions to clarify the goals and intended scope of the team and ensuing TRP were also conducted, e.g., whether to include Risso's dolphins in the scope of the plan or focus only on pilot whales; ultimately both species were included, but with a greater emphasis on pilot whales[3].

A draft TRP was agreed in June 2006, followed by a proposed rule open to public comment in 2008 and a final rule with regulations entering force in July 2009 (74 FR 23349) (Federal Register 2009). The Final PLTRP comprised a series of three regulatory and four non-regulatory measures intended to significantly reduce M&SI of pilot whales and Risso's dolphins in the Atlantic pelagic longline fishery (Table 1) (74 FR 23349) (Federal Register 2009). The regulatory measures included the designation of a region of particularly high bycatch rates as a priority area for future research and monitoring. To fish in this 'Cape Hatteras Special Research Area' (CHSRA), fishermen had to agree to carry observers who could conduct research targeted at bycatch reduction strategies (74 FR 23349) (Federal Register 2009). The second measure was a 20-nm (37-km) upper limit

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[3] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Meeting (January 25-27, 2006). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70623773.

on mainline length for pelagic longline sets in the Mid-Atlantic Bight (MAB), a region where bycatch is typically highest (74 FR 23349) (Federal Register 2009). This measure was informed by analyses conducted by NMFS scientists, who identified higher bycatch rates on sets greater than 20-nm in length in the MAB (Garrison 2007). Finally, an informational placard was required to be posted on every vessel outlining marine mammal careful handling and release guidelines (74 FR 23349) (Federal Register 2009). This measure was also informed by the Garrison (2007) study, which suggested that approximately equal proportions of observed pilot whale bycatch interactions involved hooking versus entanglement. In cases of entanglement, fishermen had some success in removing all trailing gear from animals using tools such as line cutters and, in such cases, entangled and released whales were typically not counted as serious injuries. Non-regulatory measures included a recommendation to increase observer coverage from ~8% to 12-15% of all trips in the Atlantic pelagic longline fishery; encouraging vessel operators to communicate with each other regarding interactions with protected species; advising NMFS to update careful handling and release guidelines; and a requirement for more frequent (quarterly) reporting of marine mammal interactions (74 FR 23349) (Federal Register 2009). Several additional research priorities were identified as well as an understanding that the PLTRT would regularly evaluate the success of the TRP and amend the Plan based on the results of ongoing research and monitoring (i.e., manage adaptively) (74 FR 23349) (Federal Register 2009).

Following implementation of the Plan, the Team continued to meet regularly to assess progress towards meeting the MMPA goals, industry compliance with regulations, and outcomes of ongoing mitigation research projects. Pilot whale bycatch remained below PBR from 2009 until 2015, when the estimated 5-year average from 2010-2014 exceeded PBR for the first time (M&SI 192/year; PBR 159) (Hayes et al. 2017). Updated abundance estimates resulted in an increase in PBR from 159 to 236 in 2016 (Hayes et al. 2019). The most recent 5-year annual average of M&SI (2015-2019) of 136 (Garrison, personal communication) is thus below PBR, although it is still above ZMRG (Figure 2).

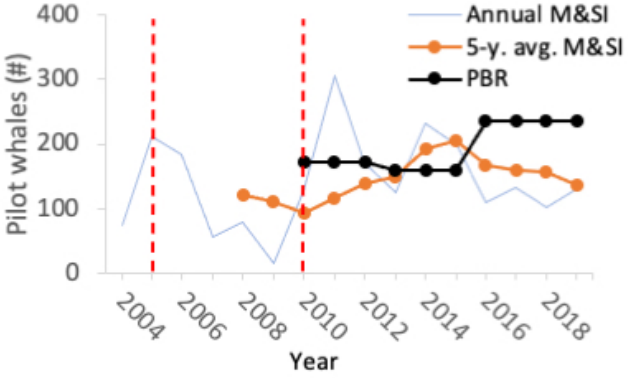

Figure 2: U.S. large pelagics longline fishery bycatch. Annual estimated mortality and serious injury (M&SI), 5-year moving average of M&SI, and potential biological removal (PBR) for short-finned pilot whales taken in the U.S. large pelagics longline fishery off the U.S. East Coast. The dashed red lines indicate the year of Pelagic Longline Take Reduction Team establishment (left, 2005) and year of publication of the final regulatory rule implementing the Pelagic Longline Take Reduction Plan (right, 2010).

Compliance with the mainline rule was less than 50% for the first 2-3 years of Plan implementation[4]. Compliance improved between 2012 and 2014, as fishermen began making sequential sets in which individual mainlines were less than 20-nm in length but separated by less than one nautical mile[5]. Considerable discussion has been devoted to whether this fishing strategy will lead to the intended reduction in bycatch rates and possible alternative strategies to limit mainline length. A modified consensus recommendation was reached in 2016, stipulating that a vessel may set no more than 30-nm of active gear, with only one piece of gear in the water at a time, and that any mainline more than 20-nm long must include at least 1-nm of hookless line[6].

Even with full compliance, the Team has recognized the mainline rule and other measures do not appear sufficient to meet ZMRG[7]. Thus, the Team has also discussed implementing a weak-hook approach to further reduce mortality and serious injury. This culminated in consensus recommendations at the 2015 meeting for the adoption of weak terminal gear (1.8 mm leaders, 300 lbs breaking strength, 16/0 circle hooks with maximum 4.05 mm diameter or 18/0 circle hooks with maximum 4.4 mm diameter) and

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[4] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Meeting (August 21-23, 2012). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70623617

[5] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Webinar (June 18, 2014). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70623614

[6] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Webinar (October 31, 2016). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70618731

[7] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Meeting (December 1-3, 2015). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70618735

to convene a workshop to develop better handling guidelines[8]. The Team also decided to repeal the CHSRA requirements, which has frustrated fishermen, as they have been required to call NMFS prior to fishing in the CHSRA to facilitate increased observer coverage in this area. However, no observers have been assigned for this purpose in over five years since the original recommendation[9]. In December 2020 NMFS published a proposed rule to reflect these changes (85 FR 81168) (Federal Register 2020).

1.3.3 False Killer Whale Take Reduction Team

The FKWTRT was convened in January 2010, when the five-year average of M&SI of false killer whales in the Hawaiʻi-based, pelagic longline fishery exceeded PBR (Carretta et al. 2009) (Table 1). False killer whales are social, mobile, apex predators that occur in tropical and subtropical oceans worldwide (Baird 2018). They are pursuit predators, known to feed on a range of pelagic fish species including tunas, mahi-mahi, and wahoo (*Acanthocybium solandri*) (Baird et al. 2008), all of which are commonly captured in the Hawaiʻi longline fishery. Three partially overlapping stocks of false killer whales occur around the Hawaiian Islands: an endangered, insular stock around the main Hawaiian Islands (MHIs) (Baird et al. 2008, Bradford et al. 2018), an insular stock closely associated with the Northwestern Hawaiian Islands (NWHIs) (Baird et al.

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[8] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Meeting (December 1-3, 2015). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70618735

[9] Pelagic Longline Take Reduction Team Key Outcomes Memorandum – PLTRT Meeting (December 1-3, 2015). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/70618735

2013), and a pelagic stock that ranges broadly within and beyond the U.S. EEZ (Bradford et al. 2015, Anderson et al. 2020). Most false killer whale bycatch in the Hawaiʻi longline fleet is from the pelagic stock, as vessels are currently restricted from fishing within the core range of the MHI population and not permitted to fish in the Papahānaumokuākea Marine National Monument, which encompasses the NWHIs. In rare cases of takes occurring in areas of overlap, bycatches are prorated to each stock based on relative stock occurrence and fishing effort (Carretta et al. 2019).

There are two distinct, Hawaiʻi-based, pelagic longline fisheries (WPRFMC 2020). Most effort is in the 'deep-set' fishery, which targets bigeye tuna year-round to the north and south of the Hawaiian Islands, both inside and outside of the U.S. EEZ. A smaller number of vessels fish with a 'shallow-set' configuration, targeting swordfish mainly north of the Hawaiian Islands. Both fisheries have experienced regulatory actions due to bycatch of several protected species. High bycatches of sea turtles led to closure of shallow-set operations in 2003-04 (Gilman et al. 2007b), and both fisheries have enacted operational and gear changes to mitigate the bycatch of sea turtles and seabirds (Gilman et al. 2007b, Gilman et al. 2008). Odontocete depredation and bycatch involving multiple species, but primarily the false killer whale, is a more common problem for the deep-set fishery (Forney et al. 2011) and is the main focus of the FKWTRT. Detailed bycatch information on bycatch and depredation is provided by on-board, independent observers present on approximately 20% of all deep-set trips (McCracken 2019).

NMFS convened and coordinated a series of meetings for the FWTRT, beginning with the first official in-person meeting in February 2010. At the time of Team formation, it was only possible for NMFS to calculate a PBR value for pelagic false killer whales inside the U.S. EEZ, so there was concern that fishing effort would increase outside of the EEZ to avoid punitive measures from the TRT (Federal Register 2010, 2012). Thus, in addition to the standard MMPA goals of reducing M&SI below PBR in 6 months and below ZMRG in 5 years, the FKWTRT had a third goal that fishery M&SI for the high-seas component of the pelagic false killer whale stock (i.e., outside the U.S. EEZ) should not increase (Federal Register 2010, 2012). As with the PLTRT, early meetings provided team members with essential background information on the fishery, false killer whale biology and ecology, and the latest research findings regarding possible depredation and bycatch mitigation options (Federal Register 2010).

Additional research specific to the deep-set fishery was commissioned by NMFS to inform team deliberations. One analysis assessed the influence of environmental and operational covariates on the occurrence of interactions of false killer whale depredation and bycatch between 2003-2009 (Forney et al. 2011). This research identified few clear patterns, except a seasonal incidence of lower depredation rates in summer months when the fleet typically fishes to the north, likely beyond the core range of pelagic false killer whales, and that sets were more likely to experience odontocete depredation if the preceding set was depredated, with a slight (~16%) decrease in risk by moving >100 km following previous depredation. There was also some evidence that circle hooks may slightly reduce false killer whale incidental takes. A concurrent field-based, weak-hook study (Bigelow et al. 2012) determined that smaller, weaker circle hooks had no effect on bigeye tuna catch rates in the longline fleet, although fishermen on the Team disputed these results, because the trials were not conducted in spring when the biggest tuna are caught. These studies strongly influenced subsequent Team deliberations, which focused on gear changes and strategies to reduce mortality and serious injury after hooking or entanglement.

The team met in person to develop a draft TRP with the Team's recommendations, which was ultimately published as a Final Rule in December 2012 (77 FR 71260) (Federal Register 2012) with regulatory and non-regulatory measures and a suite of research recommendations. The primary regulatory measure aimed at reducing the M&SI of false killer whales was to make the hook the weakest part of the terminal tackle, intended to release large animals (i.e., false killer whales) with minimal trailing gear. Specifically, the fishery is required to use circle hooks with round wire and a maximum wire diameter of 4.5 mm. Monofilament leaders and branch lines must be a minimum of 2.0 mm in diameter and 400 pounds breaking strength (77 FR 71260) (Federal Register 2012). Several additional regulatory measures were added to improve handling and release of bycaught false killer whales, such as expanding the content of existing Protected Species Workshops, requiring marine mammal handling and release informational placards to be displayed on all vessels, and requiring the captain to be notified by crew and to supervise all marine mammal bycatch interactions (77 FR 71260) (Federal Register 2012). Finally, two space-time management measures were included: a permanent longline exclusion zone around the MHI (previously a seasonal closure area only) and a "Southern Exclusion Zone" (SEZ) to be closed when specified levels of M&SI within the U.S. Hawaiian EEZ are exceeded (77 FR 71260) (Federal Register 2012).

The Team has continued to meet regularly to assess progress towards goals, fishery compliance, and research outcomes since Plan implementation. Annual M&SI for the pelagic stock inside the EEZ initially dropped from a pre-TRP five-year average of 13.3 (2008-2012) (Carretta et al. 2016) to 4.92 (2013-2017) (Carretta et al. 2019, Oleson 2020). It is currently 9.8 (2015-2019) and thus remains below PBR but above ZMRG (Table 1, Figure 3) (Oleson 2020). M&SI outside of the EEZ has shown a different pattern. In one year following Plan implementation, estimated M&SI for the pelagic stock outside of the U.S. EEZ rose from 6.6 whales in 2013 to 35.8 in 2014 (Carretta et al. 2019). With some annual variation, this level has remained relatively high (and generally increasing), with the five-year average currently at 28.8 takes per year (2015-2019) (Oleson 2020) compared to the pre-TRP average of 10.0 (2008-2012) (Figure 3). This increase is consistent with an ongoing trend of a fleetwide shift in fishing effort to the north and east, outside of the EEZ. This shift may be due to tracking of oceanographic conditions for improved target-species catch rates, rather than a reaction to the TRP (i.e., to avoid takes inside the EEZ that would lead to SEZ closure) (Woodworth-Jefcoats et al. 2018). Nonetheless, the third goal of takes not increasing outside of the EEZ is not being met. Also problematic is that closure of the SEZ (triggered by 2 or more false killer whale takes inside the EEZ in a calendar year) occurred in two consecutive years (2018 and 2019).

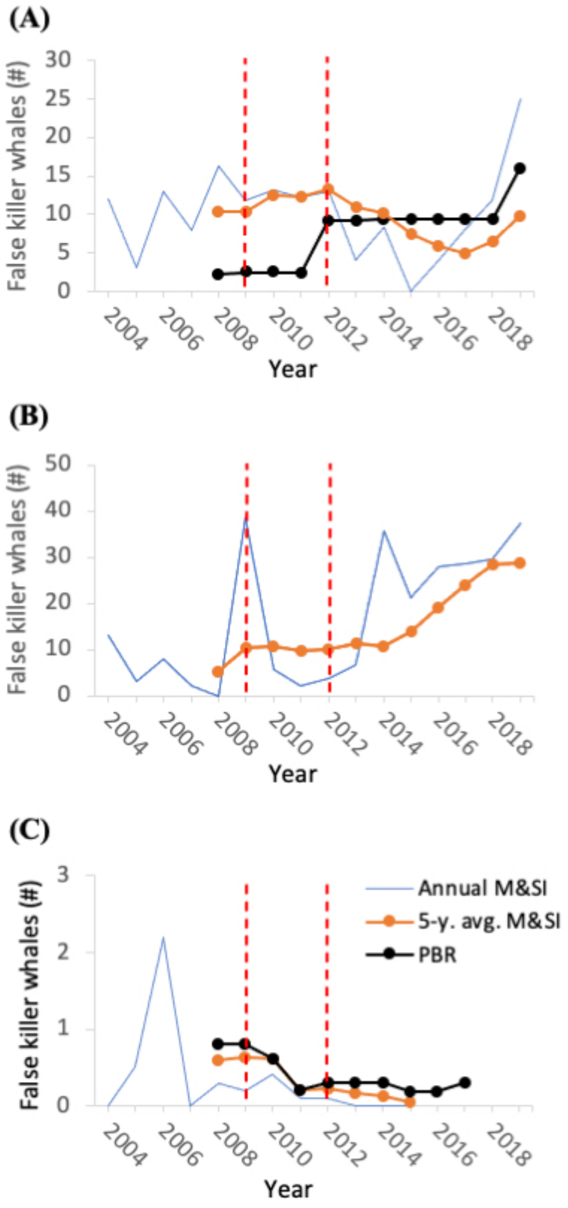

Figure 3: U.S Hawai'i pelagic longline deep-set fishery bycatch. Annual estimated mortality and serious injury (M&SI), 5-year moving average of M&SI, and potential biological removal (PBR) for three false killer whale stocks taken in the U.S Hawai'i pelagic longline deep-set fishery: (A) pelagic stock inside of the U.S. EEZ; (B) pelagic stock outside of the U.S. EEZ (no PBR available); and (C) insular, main-Hawaiian Islands stock. The dashed red lines indicate the year of False Killer Whale Take Reduction Team establishment (left, 2009) and year of publication of the final regulatory rule implementing the False Killer Whale Take Reduction Plan (right, 2012).

There has been some progress to mitigate false killer whale bycatch, but the Team has recognized that the weak-hook and handling guidelines are not fully adequate, at least as currently executed[10]. The Team has been provided with detailed reports of each observed false killer whale bycatch interaction in the deep-set fleet, assessing the details of the interaction and important outcomes such as captain and crew behavior, gear performance, and the fate of the animal[11]. Of 49 observed false killer whale interactions in the deep-set fishery between 2013-2018, the line was cut by captain or crew 19 times (39%) and broke 14 times (29%)[12]. In only four instances did the hook straighten as intended (~8% of interactions)[13]. In roughly half of the interactions the captain was not on deck, because the interaction was over before he reached the working deck or he was not notified of the interaction at all (Baird 2019).

The final regulation for a 4.5 mm hook is not as 'weak' as the initial Team consensus or hooks tested by Bigelow et al. (2012), which was 4.0 mm. This may partly explain observed hook performance, and the Team is now considering a transition to even weaker hooks and stronger branch line (4.2 mm hooks and 2.3 mm branch line),

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[10] False Killer Whale Take Reduction Team Key Outcomes Memorandum – FKWTRT Meeting (June 15, 2018). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/83268595

[11] False Killer Whale Take Reduction Team Key Outcomes Memorandum – FKWTRT Meeting (June 15, 2018). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/83268595

[12] False Killer Whale Take Reduction Plan – NOAA presentation given during 2019 Marine Mammal Commission Meeting. Accessed on 05 January 2021 at. https://www.mmc.gov/wp-content/uploads/False-Killer-Whale-2-GARRETT-2019_05_21_FKWTRP_MMC_final.pdf

[13] False Killer Whale Take Reduction Plan – NOAA presentation given during 2019 Marine Mammal Commission Meeting. Accessed on 05 January 2021 at. https://www.mmc.gov/wp-content/uploads/False-Killer-Whale-2-GARRETT-2019_05_21_FKWTRP_MMC_final.pdf

pending an additional field study to evaluate the impact of these measures on target catch rates and profitability[14]. There have also been concerns raised by Team members about captain and crew behavior during interactions. In particular, Baird (2019) has argued that the main bycatch reduction strategy of handling gear in a way to allow hooks to bend and release bycaught cetaceans is fundamentally flawed in the absence of full (100%) observer coverage. Even when observers were present, the line was cut in 39% of interactions and the captain was not present to supervise half of the interactions. Baird argues that appropriate handling methods or captain involvement are even less likely in the remaining 80% of trips when an observer is not present, and thus that the estimated M&SI levels are almost certainly biased low. This argument has led the scientific and conservation caucus to argue for increased electronic monitoring (EM) in the fleet[15], which has been trialed successfully for a small number of Hawaiʻi longline vessels (Stahl and Carnes 2020).

At time of writing, negotiations are ongoing but have been complicated by the emergence of the novel coronavirus which has caused large disruptions in the Hawaiʻi fleet and the observer program. Importantly, the fleet intended to execute a weak hook trial in 2020 but this experiment will now be delayed at least until 2021. Nonetheless,

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[14] False Killer Whale Take Reduction Team Key Outcomes Memorandum – FKWTRT Meeting (June 15, 2018). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/83268595

[15] False Killer Whale Take Reduction Team Key Outcomes Memorandum – FKWTRT Meeting (June 15, 2018). Accessed on 05 January 2021 at https://www.fisheries.noaa.gov/webdam/download/83268595

future Team discussions will likely, in some capacity, address the weak hook rules, EM, and the details of the SEZ agreement. NMFS is also working towards properly accounting for takes for the entire pelagic population (i.e., not just the portion inside the EEZ). Bradford et al. (2020) estimated, for the first time, pelagic false killer whale abundance for the entire central Pacific. A derivation of PBR for this portion of the population, as well as accounting of foreign fishery effort and potential takes in non-US fisheries, are still forthcoming. These results, when available, have the possibility to substantially alter the current PBR and M&SI situation and change the dynamics of the Team negotiations.

Table 1: Outline of objectives and policy actions relevant to each TRT. See Figures 2 and 3 for timelines and specific bycatch estimates.

	Pelagic Longline Take Reduction Team (PLTRT)	**False Killer Whale Take Reduction Team (FKWTRT)**
Fishery / Region	• U.S. large pelagics longline fishery / U.S. East Coast	• U.S. deep and shallow set longline fisheries / Hawai‘i USA
Focal Species	• Short and long-finned pilot whales • Risso’s dolphins	• False killer whale – Hawai‘i pelagic, insular (MHI), and NWHI stocks
Goals	• Below PBR in 6 months • Below ZMRG in 5 years	• Below PBR in 6 months • Below ZMRG in 5 years • M&SI of high seas component of pelagic stock does not increase (11.2 per year at time of final rule)

M&SI (5-year average) / PBR, when convened	- Pilot whales (both species pooled): 109 / 249 - Risso's dolphins: 20 / 129	- Pelagic Stock, inside EEZ: 13.6 / 9.1 - Pelagic Stock, outside EEZ: 11.2 / PBR not determined - MHI Stock: 0.5 / 0.3
M&SI (5-year average) / PBR, most recent	- Short-finned pilot whales: 136 / 236 (2015-2019) - Long-finned pilot whales: 21 (includes takes from non-longline fisheries) / 306 (2013-2017) - Risso's dolphin: 54.3 / 303 (2013-2017)	- Pelagic Stock, inside EEZ: 9.8 / 16 (2015-2019) - Pelagic Stock, outside EEZ: 28.8 / PBR not determined (2015-2019) - MHI Stock 0.01 / 0.3 (2011-2015)
Initial Plan	**Regulatory measures:** - Cape Hatteras Special Research Area (CHSRA) - 20-nm upper limit on mainline length within MAB - Informational placard for careful handling and release of marine mammals in wheelhouse and on working deck. **Non-regulatory measures:** - Increase observer coverage of all Atlantic pelagic	**Regulatory measures:** - Circle hooks with maximum wire diameter of 4.5 mm, 10 degree offset or less, round wire - Minimum 2.0 diameter for monofilament leaders and branchlines, with minimum breaking strength of 400 lbs (181 kg) - Longline exclusion zone around the MHI closed year-round - Expand existing, mandatory Protected

	longline fisheries that interact with pilot whales or Risso's dolphins to 12-15% • Encourage captains to communicate with other vessels about protected species interactions • Update careful handling/release guidelines • Provide quarterly reports of marine mammal interactions to the PLTRT	Species Workshop to include marine mammal interaction mitigation techniques • Informational placard on marine mammal handling and release posted on vessel • Captain must supervise handling and release of any hooked or entangled marine mammal • Require placard instructing crew to notify captain in event of MM interaction • Establish "Southern Exclusion Zone" (SEZ) closed when takes of FKWs meet thresholds **Non-regulatory measures:** • Increase precision of bycatch estimates • Notify team of observed interactions • Expedite process for species ID and injury determination

		• Make changes to observer training and data collection • Expedite processing 2010 HICEAS II survey data • Reconvene Team at regular intervals
New or proposed recommendations	• Implement weak hook approach • 16/0, 4.05 mm or 18/0 4.4 mm round circle hooks • 1.8 mm leaders with terminal tackle > 300 lbs breaking strength • Modified mainline requirements • ≤ 30-nm of active gear, continuous more than 20-nm must be separated by at least 1-nm of mainline • Repeal CHSRA • Working group for handling training • Better observer reporting of depredation, collect straightened hooks	• Further gear modifications • 4.2 mm diam. hooks • 2.3 mm diam. branchline • Electronic monitoring (EM) • Pending hook adoption and/or EM, removal of SEZ • More handling training • Move-on guidelines and research

1.4 Discussion

Odontocete depredation and bycatch continue to be challenging management problems, despite strong interest of fishermen in avoiding depredation (Ayers and Leong 2020) and serious conservation concerns regarding bycatch (Read 2008). The nature of odontocete behavior and realities of longline fishing contribute to the complexity of the issue. We have summarized two attempts to reduce odontocete bycatch in U.S. pelagic longline fisheries. These two Take Reduction Teams have achieved some of their goals, but even with robust funding, political will, and collaborative stakeholder involvement, and under the authority of a robust marine mammal protective statute, neither Team has fully achieved their bycatch reduction targets, nor resolved the depredation issue. Nevertheless, we hope that our description of these collaborative processes, their common struggles, and considered solutions may provide insight to other managers and scientists working on depredation and bycatch issues around the world.

Both take reduction teams invited participation from experts in marine mammal behavior, ecology, and bycatch as well as fishermen with practical knowledge of bycatch interactions and the respective fisheries. Together, they identified a comprehensive suite of potential mitigation solutions (e.g., Werner et al. 2015) that were considered carefully along with the specific nuances of each fishery. Additional research was commissioned to inform deliberations, much of which depended on high-quality, observer data on both depredation and bycatch events. Both Teams first prioritized options in Categories 1 and 2 (Figure 1), that is, limiting overlap with depredating odontocetes or preventing their contact with gear. For example, PLTRT analyses suggested that longer mainline length led to an increased interaction risk, and so the Team implemented a physical cap on mainline length. A high-interaction region was also designated a priority area for research, although no effort limitations were included that might directly reduce takes. The FKWTRT established a permanent area closure to protect the endangered, insular Main Hawaiian Island false killer whale stock, but no robust strategies for limiting overlap and avoiding interactions with the most commonly caught pelagic stock were identified. The other space-time measure (SEZ), in which high bycatch rates trigger closure of a large area important to the fishery, was meant as an incentive to limit bycatch more broadly. Interestingly, recent false killer whale density models suggest this may actually be an important area for the pelagic false killer whale population, and thus the SEZ may take on a new significance in future negotiations (Bradford et al. 2020). In general, fishermen in both Take Reduction Teams were reluctant to agree to any measure that restricted their ability to fish in particular times and areas, considering such measures as both punitive and unfair.

Ongoing research has continued to improve understanding of the overlap and nature of interactions between these fisheries and species. Recent studies comparing the distribution of short-finned pilot whales and pelagic longline fishing effort suggest that there might be some limited possibility of using extremely fine-scale spatial measures to avoid pilot whale bycatch, although areas of high bycatch generally correspond with high target catch rates (Stepanuk et al. 2018, Thorne et al. 2019). No clear environmental patterns have been identified that would help reduce false killer whale bycatch in the Hawaiʻi fleet (Forney et al. 2011). More recent research has begun to elucidate fine-scale behavior of false killer whales in the vicinity of deep-set longline gear, but thus far no clear mitigation strategies have emerged for reducing depredation or bycatch rates (Bayless et al. 2017, Anderson et al. 2020).

These research efforts have helped understand spatial and operational patterns of bycatch and suggest that avoidance strategies such as 'move-on rules' could help fishermen respond more effectively when interactions occur. However, none of these mitigation measures are considered likely to reduce interactions sufficiently to meet Team goals, and without clear options for limiting odontocete contact with gear (Categories 1 and 2), both Teams have resorted to reducing the number of serious injury determinations of bycaught animals (Category 3). The PLTRT initially specified guidelines for careful handling and release of marine mammals, although it did not include gear changes in its recommendations. Now, after several years with little progress in reducing pilot whale M&SI, a weak-hook strategy has emerged as the most acceptable solution. Together with plans for developing further improved handling guidelines, this measure is currently pending under a public comment period in a new set of proposed regulations (85 FR 81168) (Federal Register 2020).

The FKWTRT, with the advantage of learning from the PLTRT experience, adopted weak hook measures in its first round of recommendations in 2013. However, the implemented measures were not as stringent as initially agreed to by the Team (4.0 mm initially agreed on, 4.5 mm adopted in Final Rule), and are not meeting management objectives. Between 2013-2018, the most frequent outcome during false killer whale interactions was that the line was cut before straightening could occur. The line also broke nearly four times as often as the hook straightened. These patterns indicate that the hook is not weak enough, the captain and crew are not handling the line as intended in the regulations, or most likely, a combination of both. The Team is now exploring options for moving to even weaker hooks and improving handling guidelines.

The next few years will be important as both fisheries may implement these new or altered gear requirements. Yet, as Baird (2019) pointed out for the FKWTRT, weak-hook regulations for cetaceans depend critically on proper handling which, in the Hawaiʻi longline fleet, does not seem to occur, even in the presence of an independent observer[16]. Concerns over crew safety and economic expediency mean that the preferred

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[16] False Killer Whale Take Reduction - Key outcomes memoranda and summaries. Accessed on 14 September 2020 at https://www.fisheries.noaa.gov/national/marine-mammal-protection/false-killer-whale-take-reduction.

reaction to a hooked odontocete is often for a crew member to cut the line. Thus, there must be adequate incentives to ensure the necessary steps are taken, when safe and appropriate to do so, so that these interactions are resolved safely and effectively. Without comprehensive observer coverage to monitor the behavior of fishermen during interactions, this 'fatal flaw' (Baird 2019) in weak-hook and handling approaches for reducing bycatch mortality will be present in any fleet.

It is also worth noting the importance of specific statutory language and NMFS's "Process for distinguishing serious from non-serious injury of marine mammals (NOAA Fisheries 2014)" in shaping the resulting regulatory directives for each Team. The MMPA specifies that incidental mortality or serious injury of marine mammals occurring during commercial fishing operations must be reduced to insignificant levels [16 U.S.C. § 1387]. NMFS defines serious injury for marine mammals as one that is *more likely than not* to lead to mortality (NOAA Fisheries 2014). However, determining the fate of hooked or entangled cetaceans released alive from gear is exceedingly difficult and likely varies with species and gear type (NOAA Fisheries 2014). Odontocete interactions on pelagic longlines occur quickly and can be dangerous for the crew, providing little opportunity for fishermen or observers to collect identifying information (e.g., dorsal fin photos for photo-identification) or deploy location satellite-linked tags. This reduces the opportunity to collect data on survival outcomes of released whales (NOAA Fisheries 2014), as has been done for other taxa captured accidentally on longlines such as sea turtles (Swimmer et al. 2014), billfish (Musyl et al. 2015), and sharks (Musyl and Gilman 2019). In the absence of such empirical information, the criteria NMFS uses to categorize serious versus non-serious injury for these fleets (NOAA Fisheries 2014) have been developed almost entirely from expert opinion generated in a technical workshop held in 2007 (Andersen et al. 2008). The guidelines are based on scenarios that would lead directly to a determination of SI for a released marine mammal (e.g., an ingested hook) and have influenced the proposed strategies developed by each Team. For example, fishermen have been encouraged to remove hooks rather than minimizing the extent of trailing fishing line and leaving the hook in the animal. We note the importance of these 2014 guidelines for context, as they have been influential during the development of consensus recommendations by each Team. They also illustrate the challenges of understanding the population-level consequences of non-lethal bycatch which, in the case of the MMPA, provides the legal basis for fisheries management action on marine mammal bycatch. Further research on handling techniques and post-release mortality of odontocetes remains an important priority, so that the impacts of bycatch on cetacean populations can be more fully assessed (NOAA Fisheries 2014, Zollett and Swimmer 2019).

The examples presented here are specific to U.S. fisheries management under the auspices of the MMPA, but depredation and bycatch in pelagic longline fisheries are a global challenge. Some international instruments indirectly acknowledge the issue and, in some cases, charge fishing nations to address it. Foundationally, the United Nations Convention on the Law of the Sea obligates signatories to sustainably use and conserve marine living resources on the high seas and minimize impacts to other marine life, among other duties (UNCLOS 1982; e.g. Articles 61, 192, 194(5)). Other international instruments and agreements include non-binding measures and suggested guidelines to reduce marine mammal bycatch, such as, the Convention on the Conservation of Migratory Species (CMS) of Wild Animals (e.g., CMS Resolution 12.22 on Bycatch, CMS 2018), the FAO International Guidelines on Bycatch Management and Reduction of Discards (FAO 2011), and the draft FAO Technical Guidelines to Reduce Bycatch of Marine Mammals in Capture Fisheries (FAO 2020). The International Whaling Commission's recent Bycatch Mitigation Initiative is also currently working to reduce small cetacean bycatch globally. RFMOs also have authority and many have responsibilities to limit fisheries bycatch in their areas of jurisdiction. The tuna-based RFMOs have held joint meetings over the past decade, most recently in December 2019, to address bycatch in their fisheries (Joint t-RFMOs Bycatch Working Group 2019) and some have adopted conservation and management measures with relevance to reducing cetacean bycatch (Gilman et al. 2014, Juan-Jordá et al. 2018).

Despite these existing frameworks, these case studies represent, to our knowledge, two of the most direct, regulatory attempts to mitigate bycatch of small cetaceans caused by depredation on pelagic longlines. They offer important insights as other management bodies consider implementing their own strategies to reduce depredation and bycatch. They may also be relevant to non-U.S. pelagic longline fleets and in harvesting nations that export fisheries products into U.S. markets. The 2016 MMPA Import Provisions Rule (81 FR 54389) (Federal Register 2016) requires nations exporting fish and fish products to the U.S. to be held to comparable standards for reducing marine mammal incidental mortality and serious injury in fisheries as those stipulated by U.S. regulations. As countries work to comply with the Import Rule to continue exporting fish and fish products into the U.S., the TRT case studies presented here offer the current U.S. standard in regulatory and consensus-driven management that harvesting nations can consider in their own management.

Looking ahead: Depredation and bycatch are complex issues and will require a careful balance of monitoring, mitigation, and political will to reduce economic losses to fishermen and ameliorate population consequences for odontocetes. No mitigation measure will fully eliminate the problem, but there are a variety of mitigation and regulatory options that other fisheries can consider. We emphasize that, first and most importantly, high-quality observer programs are a crucial part of any mitigation strategy. Unbiased, independent, and representative data on fishing operations, catch, cetacean depredation, and bycatch are essential to accurately understand patterns of interactions and identify potential opportunities for mitigation. When mitigation strategies depend on gear changes and handling techniques, as in the two case studies considered here, such data are critical to ensure compliance across the fleet. It is unrealistic to expect full observer coverage across the world’s pelagic longline fleets, most of which currently operate at 5% observer coverage or lower (Ewell et al. 2020). However, rapidly improving electronic monitoring technologies can fill these gaps in highly capitalized fisheries. Addressing and acknowledging the issue of bycatch, including depredation, in fisheries regulations and incorporating a variety of stakeholder perspectives, will be a step forward for fisheries that encounter depredation. This will help the world’s pelagic longline fisheries reduce the economic cost of depredation and ameliorate the impact of bycatch on small cetaceans.

2. Patterns of depredation in the Hawai‘i deep-set longline fishery informed by fishery and false killer whale behavior.

2.1 Introduction

Many marine predators engage in depredation by consuming bait or fish secured on fishing gear. This behavior is very common and costly in longline fisheries worldwide (Read 2008, Hamer et al. 2012). Odontocetes, or toothed whales, are particularly adept at depredation and can remove large quantities of catch, often with substantial economic impacts (Tixier et al. 2020). Depredation reflects a switch from natural foraging behavior of prey pursuit to feeding on often high-energy but restrained prey. This behavior may reduce the energetic costs of foraging but increases the risk of hooking or entanglement in fishing gear. False killer whales (*Pseudorca crassidens*) depredate catch in a number of pelagic longline fisheries worldwide, including the Hawai‘i-based, deep-set longline fishery that targets bigeye tuna (*Thunnus obesus*) (Forney et al. 2011). False killer whales are the most frequently bycaught cetacean in this fleet and estimated fishery-related mortality and serious injury of this species has repeatedly exceeded allowable levels under the U.S. Marine Mammal Protection Act (MMPA) (Carretta et al. 2009). In the present study, we examine patterns of odontocete depredation in the Hawai‘i deep-set fishery and the behavior of tagged false killer whales to identify predictive factors that could be used to potentially reduce harmful interactions and the cost of depredation to fishermen.

At a global scale, depredation and subsequent marine mammal bycatch in longline fisheries has been an exceedingly difficult problem to solve, despite consideration of a wide range of mitigation strategies (e.g., Werner et al. 2015). The incentives to feed on large, energetically dense captured fish are likely high (Esteban et al. 2016), making it very difficult to create disincentives to this behavior. In addition, interactions are seldom observed directly, as they often occur at depth, at night, or far from the vessel (Werner et al. 2015). Acoustic harassment devices have been considered as a means of deterring marine mammals from engaging in depredation and reducing bycatch (Werner et al. 2015, Hamilton and Baker 2019), although in the case of longline depredation, odontocetes may habituate quickly to these signals and even be attracted to deterrents that notify whales of the location of catch, an apparent 'dinner bell' effect (Mooney et al. 2009, Tixier et al. 2015a). Many strategies thus focus on technological innovations that limit impacts after animals have encountered fishing gear. Gear modifications such as physical devices designed to protect catch (Rabearisoa et al. 2012) or weak hooks, designed to release hooked cetaceans, are in use in some fisheries (Bayse and Kerstetter 2010, Bigelow et al. 2012), including the Hawai'i deep-set fishery (weak hooks). However, these approaches can be costly and unwieldy to deploy (catch protection) or ineffective in reducing the incidence of depredation (weak hooks).

An alternative strategy is to adjust fishing behavior or operations to allow fishermen to avoid interactions with depredating species in the first place (e.g., Stepanuk et al. 2018, Tixier et al. 2019). Such an approach might be implemented at two spatial scales: (1) predicting interactions *a priori* from broad-scale environmental drivers of overlap between fisheries and bycatch; and (2) understanding fine-scale behavior of depredators around gear to avoid interactions despite whale co-occurrence. Many pelagic predators range widely and their patterns of distribution may be influenced by static (e.g., sea floor topography, (Lindsay et al. 2016, Thorne et al. 2017)) or dynamic oceanographic features (e.g., sea surface temperature (SST) fronts, (Howell et al. 2008, Woodworth et al. 2011, Hazen et al. 2017)). Pelagic fishing vessels also range widely, tracking specific oceanographic conditions, and when the distribution of fishing activities converges with the distribution of depredating species in space and time, interactions may occur (Howell et al. 2008, Thorne et al. 2017, Stepanuk et al. 2018, Thorne et al. 2019). Identifying the ecological drivers of this co-occurrence could help fishermen avoid overlap and subsequent interactions.

Given broad-scale spatiotemporal co-occurrence, depredation is further driven by the depredator’s behavior in the vicinity of fishing gear. The cues that depredating animals use to locate gear and their behavior during and around fishing operations are often species and fishery specific and thus are important to understand when developing mitigation strategies, such as limiting depredator access to gear or avoiding acoustic detection by depredators. For example, demersal longline fishing involves setting gear directly on the sea floor, and due to the extreme depths that this gear is fished (500-2000 m), depredation interactions are thought to occur mostly during the hauling phase (but see Richard et al. 2020, Richard et al. 2021). In contrast, pelagic longline gear is suspended in the water column closer to the surface, and thus the gear is potentially accessible to depredation for the full duration of a fishing event (Rabearisoa et al. 2012, Thode et al. 2016). Acoustic signatures from vessels or gear are likely important cues for depredating odontocetes in both fishery types, although there are surely nuances in each case. Sperm whales (*Physeter macrocephalus*) depredating demersal longlines in southeast Alaska appear to respond to very specific acoustic signatures from the cavitation of a ship's propeller when the engine is engaged to haul gear, detecting these sounds from several kilometers and arriving at a haul within minutes of a vessel beginning to retrieve gear (Thode et al. 2007, Thode et al. 2015). Passive acoustic monitoring of pelagic longline gear deployments detected false killer whales most commonly during the hauling phase, with whales moving along the mainline away from the vessel as gear was being retrieved (Bayless et al. 2017). Anderson et al. (2020) observed satellite-tagged false killer whales orienting their movements towards pelagic longline gear most commonly during the hauling phase, although they did not do so every time they were within likely detection range.

2.1.1 False killer whale depredation and bycatch

False killer whales are social, highly mobile, apex predators that occur in tropical and subtropical oceans worldwide. Independently of fisheries, they are known to feed on a range of pelagic fish species, including tunas (*Thunnus* spp.), mahi-mahi (*Coryphaenus hippurus*), and wahoo (*Acanthocybium solandri*) (Baird et al. 2008), all of which are commonly captured in the Hawaiʻi deep-set longline fishery. Three partially overlapping populations of false killer whales are recognized around the Hawaiian Islands: an endangered, insular population around the main Hawaiian Islands (MHIs) (Baird et al. 2008, Bradford et al. 2018), an insular population closely associated with the Northwestern Hawaiian Islands (NWHIs) (Baird et al. 2013), and a pelagic population that ranges broadly within and beyond the U.S. exclusive economic zone (EEZ) (Bradford et al. 2015, Anderson et al. 2020). Most false killer whale bycatch in the Hawaiʻi longline fleet involves the pelagic population, as vessels are restricted from fishing within the core range of the MHI population and are not permitted to fish in the Papahānaumokuākea Marine National Monument, which includes waters surrounding the NWHIs.

There are two distinct Hawaiʻi-based, pelagic longline fisheries. Most effort occurs in the deep-set fishery, which targets bigeye tuna and operates year-round to the north and south of the Hawaiian Islands, both inside and outside of the U.S. EEZ. A smaller, shallow-set fishery targets swordfish (*Xiphias gladius*), operating mainly north of the Hawaiian Islands. Hawaiʻi longline captains must fish with the same gear configuration (deep or shallow) for the duration of a trip. Regulations have been adopted to reduce the bycatch of several protected species in both fisheries. High rates of sea turtle bycatch led to the closure of shallow-set operations in 2003-04 (Gilman et al. 2007), and both fisheries have enacted operational and gear changes to mitigate sea turtle and seabird bycatch (Gilman et al. 2007, Gilman et al. 2008), primarily in response to litigation. Odontocete depredation and bycatch is a more common problem for the deep-set fishery (Forney et al. 2011), which is the focus of the current study. As in other pelagic longline fisheries experiencing odontocete depredation (e.g., Secchi and Vaske 1998, Rabearisoa et al. 2018), depredation by toothed whales is rarely observed directly in the deep-set fishery (Bayless et al. 2017), but rather inferred by characteristic damage to individual caught fish retrieved during the haul (Forney et al. 2011).

A variety of odontocete species have been observed as bycatch in this fishery, including false killer whales, short-finned pilot whales (*Globicephala macrorhynchus*), and Risso's dolphins (*Grampus griseus*) (Forney and Kobayashi 2007). High levels of false killer whale bycatch led to formation of the False Killer Whale Take Reduction Team (TRT) in 2010, a multi-stakeholder group charged with reducing mortality and serious injury of false killer whales below levels stipulated by the MMPA. The U.S. National Marine Fisheries Service (NMFS) published a final Take Reduction Plan in 2012 (77 FR 71260). The primary regulatory tool for mitigating bycatch was a requirement for vessels to use a combination of "weak" circle hooks (specified by a maximum shank diameter of 4.5 mm) and strong terminal gear (minimum 2.0 mm branch line diameter) to allow release of hooked false killer whales while retaining target catch. Recently, the team has acknowledged that these measures are not significantly reducing serious injury or mortality of false killer whales and have recommended studies to investigate the possibility of a transition to even weaker hooks (i.e., narrower diameter) and stronger (i.e., thicker diameter) branch lines[1]. This approach is designed to maximize the likelihood of survival for animals that become hooked, but it does not reduce the economic cost of depredation to the fishery.

Avoiding interactions outright would benefit both whales and fishermen, and there has been long-standing interest from the false killer whale TRT to identify patterns and proximate mechanisms driving depredation. To this end, Forney et al. (2011) conducted a multivariate analysis of false killer whale depredation and bycatch between 2003-2009 to assess the influence of environmental and operational covariates on the occurrence of interactions. The analysis identified few clear environmental covariates of depredation and bycatch, except for a seasonal pattern of lower depredation in summer when the fleet fishes farther to the north, likely beyond the primarily tropical and sub-tropical range of pelagic false killer whales. The authors found evidence that sets were more likely to experience odontocete depredation if the preceding set was depredated, and that moving 100 km following depredation led to a slight (~16%) decrease in the risk of subsequent depredation. These findings suggest either pursuit of fishing vessels by

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[1] False Killer Whale Take Reduction - Key outcomes memoranda and summaries. Accessed on 14 September 2020 at https://www.fisheries.noaa.gov/national/marine-mammal-protection/false-killer-whale-take-reduction

depredators or clumping of whales in space and time, although at the time there were insufficient data to assess patterns in space and time simultaneously.

This previous work has provided important insights into the processes driving false killer whale depredation, but this behavior remains poorly understood and unmitigated. Here, we incorporate nine years of additional fisheries observer data to expand the analysis of Forney et al. (2011). This larger dataset provides more power to explore environmental and operational covariates and the ability to examine patterns in repeat depredation in both space and time across the fleet. We also analyze typical speeds and distances traveled by satellite-tagged pelagic false killer whales, allowing comparison of depredator movement behavior to the spatiotemporal patterns of depredation observed from fishery-dependent data. An improved understanding of broad and fine-scale patterns of depredation, and the animal behavior driving these interactions, will help inform efforts to reduce the negative consequences of depredation and bycatch for both whales and fishermen.

2.2 Methods

2.2.1 Study area and fishery-dependent data sources

Hawaiʻi deep-set gear consists of a single monofilament mainline (3.2–4.0 mm diameter) suspended in the water column by a series of floats (Appendix A1: Figure A21). Individual branch lines with a mackerel-type bait on a single hook are regularly spaced along ~45–80 km of mainline (Boggs and Ito 1993). The target depth for bigeye tuna is around 400 m and a typical deployment of fishing gear ranges from 1,000-3,000 hooks. Deep-set fishermen generally deploy ('set'), their gear in the morning, allowing it to fish ('soak') until the retrieval ('haul'), begins around sundown. The hauling process may exceed 12 hours, depending on the catch and amount of gear deployed. We describe the full process of a single fishing event (i.e., the start of a set to the end of the haul) as a single 'deployment' or 'event', unless referring to a more specific step of the process.

Fishery dependent data were derived from two sources: logbook data recorded by vessel captains and data collected by fisheries observers. For each deployment, captains are required to record and submit to NMFS the times and GPS coordinates of the start and finish of setting and hauling of gear (i.e., four times and locations per fishing event), the number of hooks deployed, and counts of caught fish by species. By regulation, deep-set vessels are required to carry a federal observer, if requested, with a fleet-wide target coverage of 20% of all trips. Observers collect more detailed data on fishing effort, gear characteristics, and biological data from both target and non-target catch, including bycatch of protected species. Since late 2003, observers have also been trained to classify and systematically record depredation (i.e., damage to catch). Of interest in this study is odontocete depredation, which can be distinguished from other sources of depredation, such as squid or sharks, because toothed whales often predate the whole fish up to the gill plates, leaving only the head attached to the hook (e.g., Secchi and Vaske 1998). False killer whales are also known to depredate bait (Thode et al. 2016), but this is not systematically recorded by observers and is thus not reported here. Based on covariate data availability and model formulations, the multivariate analyses of depredation described below utilize observer-collected data from 2004-2017, while the spatial analyses utilize observer data from 2004-2018.

2.2.2 Derivation of covariates

We identified spatial, temporal, gear, operational, and environmental variables hypothesized to influence odontocete depredation rate (Appendix A1: Table A9). Space and time variables were associated with the start of the haul of the focal fishing deployment, as recorded by the on-board observer. Gear and operational variables were also based on observer-reported values for each fishing event, with the exception of vessel density, which utilized logbook data to calculate the number of all (i.e., not just observed) vessels that began a haul within 200 km and ±3 days of the observed (focal) haul. Number of hooks represents the total number of individual hooks deployed in the focal fishing event. Soak was calculated as the time (h) between the last piece of gear entering the water (end of set) to the last piece of gear removed from the water (end of haul). Minimum depth of gear (m) is the sum of all vertical pieces of gear (float line + branch line + leader), but due to shoaling and concatenation of the main line, actual depth of gear varies widely throughout the soak and haul (Bigelow et al. 2006). Hooks between floats was used as a secondary indicator of gear depth, as more hooks between floats generally means the gear sinks deeper. All catch and catch per unit effort (CPUE) variables were derived from observer-recorded counts of hooked (not necessarily landed or kept) target and non-target catch. CPUE (number of fish caught per 1,000 hooks) was based on all hooked bony fish (i.e., not including sharks) in a haul. As an indicator of catch on nearby vessels, we also calculated the CPUE of tuna species (number of tunas caught per 1,000 hooks) caught on observed vessels that began a haul within 100 km and ±1 day of the focal haul. We further identified, for each observed haul, whether odontocete depredation or bycatch of a false killer whale was recorded by the observer during the previous haul of the same vessel, with the first haul of each trip included but treated as an absence of previous depredation.

Environmental variables included both static and dynamic variables and most were associated with haul begin location, with any distances calculated as the great circle distance (km) from the haul-begin location to the feature. We acknowledge that haul-begin location is only an approximate representation of fishing location as longlines can be tens of kilometers long; however, we believe haul-begin location to be a reasonable characterization due to false killer whales evidently orienting most commonly to the hauling phase (Bayless et al. 2017, Anderson et al. 2020). The static variables depth and slope were derived from GEBCO 30 arc-second bathymetry data; and distance to nearest seamount was derived from the seamount database described in Allain et al. (2008).

Sea surface temperature (SST) range was calculated as the difference between the highest and lowest SST (ºC) for all four recorded fishing locations per deployment, with SST derived from Level 4 daily, nighttime interpolated SST provided by the Group for High Resolution Sea Surface Temperature (JPL 2010). Chlorophyll-a concentration (mg·m-3) was Level 3 monthly, 9-km resolution from the Aqua MODIS satellite (OBPG 2014). Absolute dynamic topography (adt, m), which is a measure of sea surface height, and total kinetic energy (tke, m2·s-2) were derived from the Archiving, Validation and Interpretation of Satellite Oceanographic data group hosted by the Copernicus Marine Environment Monitoring Service. Eddy distance and amplitude of the nearest eddy were derived from the database described in Chelton et al. (2011). Distance to oceanographic fronts was the distance to the nearest Cayula-Cornelius thermal front (Cayula and Cornillon 1992). El Niño-Southern Oscillation (ENSO) conditions were considered based on the Oceanic Niño Index (ONI) [3 month running mean of Extended Reconstructed Sea Surface Temperature (v4) anomalies in the Niño 3.4 region (5°N-5°S, 120°-170°W)]. We also conducted a lag-correlation analysis between the average monthly rate of odontocete depredation (centered and with seasonal trend removed) and monthly ONI, to assess if there was a delayed response to ENSO conditions. This identified a peak correlation in depredation 11 months following ONI (Appendix A1: Figure A22), and thus we included a variable for the 11-month lag value of ONI in addition to concurrent ONI in models. We used various tools in the Marine Geospatial Ecology Toolbox for extraction of many of the environmental variables (Roberts et al. 2010).

2.2.3 Multivariate data analysis

We conducted a detailed data exploration and analysis to examine the influence of potential predictor variables on the occurrence of odontocete depredation in the deep-set fishery from 2004-2017. We first assessed collinearity among explanatory variables by calculating Pearson correlation coefficients for all pairwise combinations of continuous variables, retaining only those with values less than 0.5. When two variables with similar ecological meaning were correlated, we retained the one with fewer missing values or a clearer ecological relationship to the response. After a first selection, we assessed the variables considered in the full models (Appendix A1: Table A9) using the Variance Inflation Factor (VIF), ensuring that none exceeded a threshold of 3. As the VIF of each variable depends on the other variables present, we recalculated VIF after model-selection, ensuring that no correlated variables were retained in the final models either. We also assessed concurvity (Wood 2006) amongst variables in candidate final models to ensure that no variables were non-linearly related.

We then used Generalized Additive Mixed Models (GAMMs) to examine the relationship between retained variables and the occurrence of odontocete depredation. GAMMs are a regression approach that calculate smooth functions to estimate relationships between predictor and response variables (Wood 2017). We chose GAMMs as we were interested in exploring the combined influence of a range of different variable types in a single model. The GAMM approach allows greater flexibility in specifying different terms within a single model, with fewer a priori assumptions on the nature of each relationship, than, for example, Generalized Linear Models (Wood 2017). A GAMM model uses a link function g() to relate a univariate response variable Y to a sum of smooth functions of the covariates Xi :

$$g(E(Y) = \alpha + \sum f_i(X_i)$$

where α is the intercept and f_i is a smooth function of the covariate X_i.

We used a logit link function to model the relationship between covariates and the binomial presence or absence of odontocete catch damage on at least one fish during a single set.. To increase sample size, we also included the occurrence of a hooked or entangled false killer whale as a ‘presence’, which added 29 observations. Although other odontocetes likely engage in depredation on Hawaiʻi deep-set gear, we included only false killer whale bycatch as this species is the most frequently bycaught odontocete, and we wanted the models to be as specific to false killer whales as possible. We explored two possibilities for a fully saturated model, one with no interactions (Appendix A1: Eqn. A1) and one including several interactions informed from exploratory analyses and a priori hypotheses (Appendix A1: Eqn. A2). These included interactions between month and latitude, month and ONI lag, and latitude and ONI lag. Following Zuur et al. (2009), we began model selection from the fully saturated models with penalized thin-plate regression splines used for all univariate smoothers and tensor product smooths for any interaction terms. We modeled month using a cyclic regression spline to ensure a smooth step from December to January. We treated the presence or absence of depredation on the previous set of the focal vessel as a categorical, parametric variable and vessel identity as a random effect to control for variation within vessels and individual trips. Penalized splines incorporate a penalty that drives the coefficients of non-contributing variables to zero (Wood 2006). These variables were removed after the first iteration, and then backward, stepwise selection was used on remaining variables using non-penalized splines, removing the variable with the highest p-value at each iteration until only variables with a $p\text{-value} < 0.001$ remained (Zuur et al. 2009). We explored model structures in which individual smoothed variables were constrained using ‘knots’, as well as formulations leaving variables unconstrained. Knots determine the complexity and flexibility of the curve and can limit over-fitting. Overall patterns and variable selection outcomes were similar for both strategies, but smooth terms were determined to be more realistic and interpretable when constrained to 5 knots, a common, conservative default. We present results only from the constrained version. Various other combinations of smoother types, parameter settings, and model selection algorithms were explored, without noticeable differences on the resulting inferences. The final, best fit models from both the interaction model and non-interaction model iterations were compared using AIC. All analyses were implemented in the package mgcv, version 1.8-31 (Wood 2006, 2007) in RStudio statistical software, version 1.2.5033 (R Core Team 2018).

2.2.4 Scale-dependent spatiotemporal analyses

We explored spatiotemporal patterns of depredation for all observed vessels simultaneously across a range of relevant space and time scales (maximum of 1,000 km and 20 days). We first used a variation of Ripley’s K function (Ripley 1977) to identify whether the occurrence of depredation exhibited spatiotemporal clustering across these scales. The technique treats the positions of specific events (e.g., depredation) as marked point processes to estimate the presence or absence of clustering of the event while controlling for the underlying distribution of all events (i.e., all fishing sets), as these are not randomly or evenly distributed themselves. By removing the effects of only space and only time, patterns of events due to space-time interactions can be identified (i.e., events that are close in both space and time). We also summarized the proportion of depredated or ‘marked’ fishing events amongst all vessels fishing within specified times and distances from where the focal depredation event occurred (using the same space and time scales as the K analysis). Space and time locations for these analyses were based on the beginning of the haul for all observed fishing deployments from 2004-2018.

For the clustering approach, we followed the approach of Dunn et al. (2014) and Bjorkland et al. (2015), applying the K function separately for all observed fishing deployments (all points, $\widehat{K}(s,t,st)_{all}$) and observed depredated deployments only (marked points, $\widehat{K}(s,t,st)_{mark}$), across a range of space-time thresholds (Gardner et al. 2008, Dunn et al. 2014):

where N is the total number of events, A is total area, T is total length of the time series, s_i is the spatial location of event I, t_i the time of event I, $w(s_i,s_j)v(t_i,t_j)$ an edge-correction factor, and I a function indicating events s_j,t_j within a distance s and time t of event s_i,t_i (Dunn et al. 2014). As the fishery operates on a daily time scale (i.e., typically one full set and haul per 24-hour period), we used one day as our time interval, from a minimum of one day to maximum of 20 days. Similarly, as the gear can spread over tens of kilometers, we used 50 km as a minimum distance step and interval to a maximum of 1,000 km. The maximum values for the distance and time steps were chosen to include all scales that could reasonably be considered actionable for mitigation purposes. We implemented $\widehat{K}$ calculations in the Splancs package, version 2.01-40 (Bivand et al. 2017) in RStudio statistical software, version 1.2.5033 (R Core Team 2018).

We calculated both $\widehat{K}(s,t,st)_{all}$ and $\widehat{K}(s,t,st)_{mark}$ across each possible space-time interval. Purely spatial and temporal effects ($\widehat{K}(s)$ and $\widehat{K}(t)$; Appendix A2: Eqns. A1 and A2) for all fishing sets and depredated sets were then subtracted from the respective $\widehat{K}(s,t,st)$ (Appendix A2: Eqn. A3) to isolate processes correlated in both space and time only (i.e., space-time interactions). Finally, the space-time clustering of the full dataset was subtracted from that of the marked points $\widehat{K}(st)_{mark} - \widehat{K}(st)_{all}$, to identify space-time effects of only the marked points (i.e., controlling for the nonrandom distribution of fishing events).

We then used random-labelling permutations to explore the spatiotemporal autocorrelation of depredation relative to randomly permuted fishing set events. This method builds envelopes of K by taking 1,000 random samples of the same size as the number of marked points from the overall dataset. These envelopes represent the range of expectations of K if there were no space-time structure to the data. We consider observed Ks that exceed the highest 95% threshold of these values at a particular space-time threshold to exhibit clustering. We acknowledge concerns of this method for assigning statistical significance (Loosmore and Ford 2006), and we considered this only as a data exploration exercise to identify plausible scales of correlation. For visualization purposes, at each space-time threshold, we subtracted the value of the highest 95th percentile of permuted Ks from the observed K and set all zero (random) or negative values (overdispersed) to zero. We then divided these subtracted K values by the highest K value across all space-time scales to standardize on a scale from zero to one, and we display this as a heat map to visualize specific space-time thresholds where aggregation is likely present (Gardner et al. 2008, Dunn et al. 2014).

While the K function provides information on the intensity of spatiotemporal clustering at different scales, it does not translate directly to a quantitative understanding of the change in risk of depredation relative to an observed depredation event. Thus, we also summarized the occurrence of depredation as a function of space and time from an observed depredation event. Specifically, we calculated the empirical proportion of depredation (fraction of total sets that are marked), within each space-time boundary, for every observed depredation event. In other words, when depredation occurs, what is the average rate of occurrence of additional depredation on all other nearby vessels, within each space and time window of the original event? We note that this method does not isolate combined space-time effects like the K-analysis, and thus independent time or space effects may be aggregated here as well, such as seasonal or static habitat correlates. To put these scales in context, we also explored the typical behavior of fishermen in response to interactions, calculating distances moved and time elapsed between sets (end of one haul to beginning of next set), following the presence or absence of odontocete depredation or false killer whale bycatch.

2.2.5 False killer whale movement analysis

Pelagic false killer whales were encountered and tagged with satellite tags during ship-based (Pacific Islands Fisheries Science Center, PIFSC) and small-boat (Cascadia Research Collective, CRC) cetacean surveys in 2013 (both), 2017 (PIFSC only), and 2020 (CRC only). See Appendix A3 in this paper, Baird et al. (2010), Baird et al. (2013), and Anderson et al. (2020) for further details on encounter, sampling, and tagging protocols. To avoid pseudo-replication, when multiple tags were deployed within a single group or animals tagged on separate days joined later, we included only the tag with the longest transmission time in subsequent analyses.

Filtered Argos data were further processed using a Correlated Random Walk state-space model (crw-ssm) using the foieGras package, version 0.4.0, implemented in RStudio version 1.2.5033 (R Core Team 2018) as described in Jonsen and Patterson (2019). The Correlated Random Walk model is a continuous time model that accounts for the irregular time intervals between positions available from Argos data. It estimates true locations while accounting for error in the Argos telemetry data and regularizing to consistent, pre-specified time intervals; in this case 4 hours. This allows data across multiple individuals to be normalized and as comparable as possible. False killer whale locations were regularized to four-hour intervals for up to the first 59 days after which tags began duty-cycling. We then summarized horizontal distance moved and average speed along four-hour interval tracks and horizontal distance moved, speed, and total displacement (straight-line distance from the first location of each day to the first location of the following day) for daily time steps.

2.3 Results

Between 2004 and 2018, a total of 267,231 sets [mean 17,815 per year, standard deviation (SD) 1,357] were made on 20,262 trips [mean 1,351 per year, SD 97] by 187 unique vessels [mean 132 per year, SD 7] in the Hawaiʻi deep-set longline fishery. Observers were present on 21.0% of trips covering 20.7% of sets, providing a dataset of 55,247 sets [mean 3,683 per year, SD 254] with detailed data. Fishermen set an average of 13.3 sets per trip [SD 3.7] and 2,355 hooks per set [SD 455.5] with an average soak time (end set to end haul) of 15.2 hours [SD 2.8]. Odontocete depredation on at least one captured fish was observed on 3,478 (6.3%) of all observed sets. Approximately half of trips (47.2%) experienced odontocete depredation on at least one set and 21.2% experienced odontocete depredation on two or more sets. The number of fish depredated per set was right-skewed, with a median of two and a maximum of 63 depredated fish recorded on sets with depredation. Odontocetes depredated a variety of fish species, mostly tunas (*Thunnus* spp., 68%), followed by billfish (11%), mahi-mahi (6%), and wahoo (5%). These species represented 28%, 4%, 8%, and 2% of total catch, respectively. Several species were depredated infrequently relative to their proportion of total catch. Notably, the most frequently caught species in this fishery, the longnose lancetfish (*Alepisaurus ferox*), comprised 23% of fish caught by number but less than 2%

of fish depredated by odontocetes. This may be due to avoidance by odontocetes or the gelatinous nature of their flesh, which makes this discard species easily damaged and difficult for observers to categorize the source of damage. In general, odontocetes did not feed on captured sharks. The blue shark (*Prionace glauca*) is the third most frequently caught species (~8% of total catch), but only 7 individual sharks of 3 species had evidence of odontocete depredation.

A diverse range of cetacean species were reported as hooked or entangled by observers, but most were odontocetes in the family Delphinidae (152 of 158 total animals). The most commonly caught cetacean was the false killer whale, representing approximately 70% of all bycaught cetaceans identified to species or genus (122 total). In total, 85 confirmed false killer whales were caught on 80 sets between 2004-2018, followed by 10 short-finned pilot whales (*Globicephala macrorhynchus*), 9 Risso's dolphins (*Grampus griseus*), and 7 common bottlenose dolphins (*Tursiops truncatus*). There were also 13 unidentified 'blackfish' species, likely false killer whales or short-finned pilot whales (McCracken 2010). Depredation of catch was observed on 51 of 80 (~64%) sets in which one or more false killer whales were hooked.

2.3.1 Multivariate Analysis

We used GAMMs to predict the presence or absence of odontocete depredation per set (occurrence of >= 1 depredated fish or false killer whale bycatch event as a proxy for depredation) as a function of variables hypothesized to influence interaction rates.

The parameters included in the 'best-fit' final models, and their functional relationships to depredation, were very similar for each model type (i.e., with interactions and with no interactions, Appendix A1: Eqns. A3 and A4). The main differences were that the month x latitude interaction term was significant in the interaction model and distance to seamount was marginally significant in the no-interaction model, but not kept in the interaction model. The interaction model had the lowest AIC value and highest deviance explained and thus was considered further. The final interaction model included the interaction between month and latitude, 11 additional quantitative variables, 1 categorical variable, and a random vessel identification effect, although overall deviance explained was still low at 8.11% (Table 2, Figure 4). There was a clear seasonal and spatial relationship, with a decrease in depredation occurrence in the second and third quarters of the year and at higher latitudes. Of the ONI variables, only the 11-month lagged version was kept in the final model and was positively associated with depredation. The only other significant oceanographic variable was a positive relationship between depredation and absolute dynamic topography.

Table 2: Results for the best-fit GAMM predicting odontocete depredation rates in the Hawai'i deep-set longline fishery from 2004-2017.

Parametric terms	Estimates	Standard Error	e.d.f.	Chi sq.	p-values
Intercept	-3.04	0.03			< 0.001
Depredation on previous set	0.90	0.06			<0.001
Smoothed terms					
Latitude x Month			14.0	302.10	< 0.001
Number of hooks set			1.91	110.93	< 0.001
Soak time (Hours)			2.35	30.26	< 0.001
Bigeye tuna (# caught)			3.93	379.51	< 0.001
Yellowfin tuna (# caught)			2.85	54.08	< 0.001
Mahi-mahi (# caught)			3.46	32.25	< 0.001
Wahoo (# caught)			2.06	27.61	< 0.001
Sharks (# caught)			1.00	17.39	< 0.001
CPUE (# fish / 1,000 hooks)			3.89	73.69	< 0.001
Nearby tuna CPUE (# tuna / 1,000 hooks)			3.49	141.22	< 0.001
ONI 11 mo. Lag			1.00	19.83	< 0.001
adt (m)			1.00	28.71	< 0.001
Vessel ID			65.95	124.16	< 0.001
n = 49,579 R-squared (adj.) = 0.048 Deviance explained = 8.11% UBRE = -0.571					

Operationally, the probability of depredation increased with the number of hooks set and more time the gear spent in the water. Depredation was also significantly more likely if the vessel experienced depredation on the previous haul of the same trip. These factors led to relatively large shifts in the model-predicted probability of depredation. For example, the predicted probability of depredation more than doubled when fishermen set 3,000 versus 1,500 hooks or when depredation occurred on the previous set. Finally, several catch-related variables were significant. There was a consistent, nonlinear relationship between depredation and catch of four of the most common target species (bigeye and yellowfin tuna, mahi-mahi, and wahoo) in which the likelihood of depredation decreased with increasing catch, and then leveled off or increased again at high levels of catch. Overall CPUE (number of bony fish per 1,000 hooks on the focal vessel) showed the same relationship, while average, tuna-only CPUE on vessels setting within 100 km and ±1 day had a linear, positive association with the risk of depredation. Number of sharks caught also had a linear, positive relationship with depredation occurrence, and vessel ID was highly significant as a random effect.

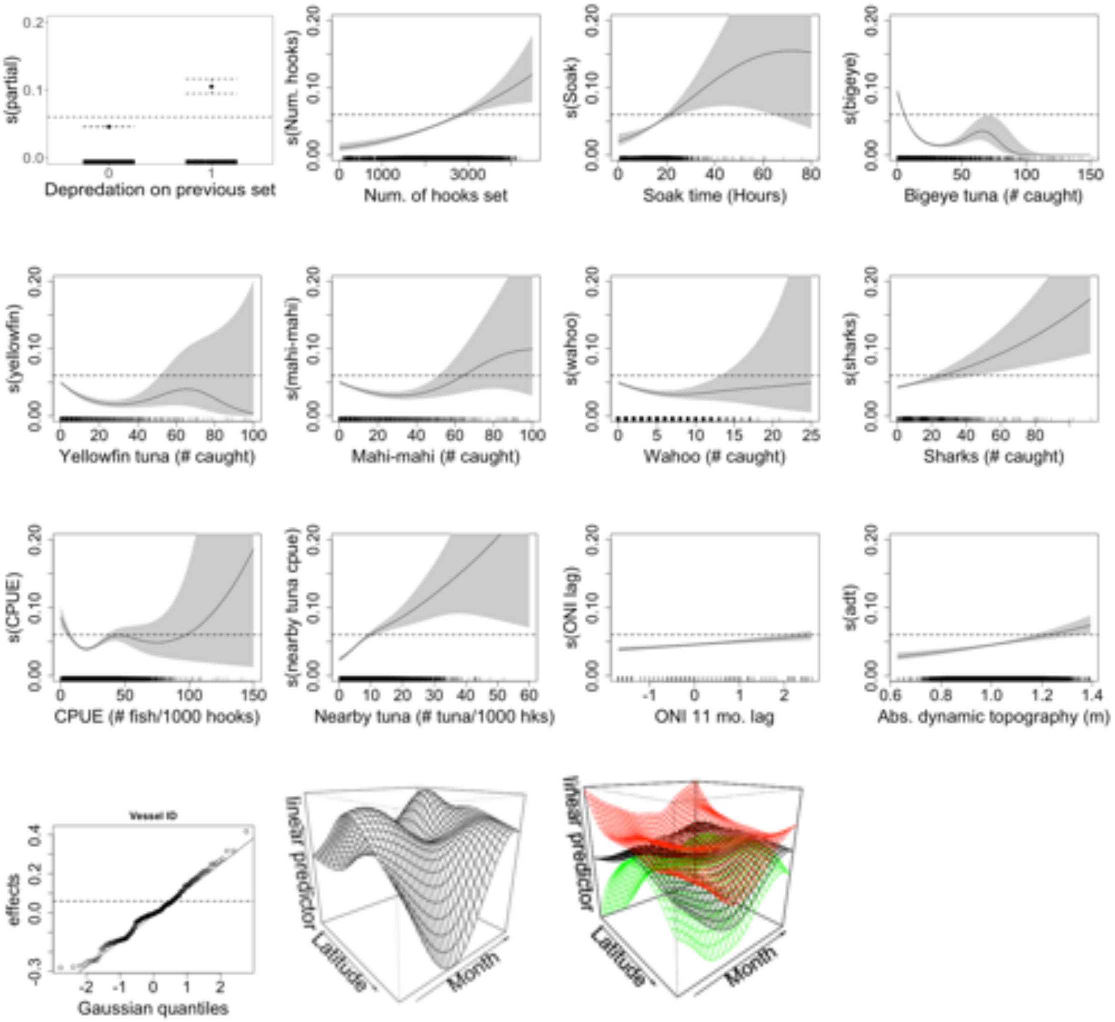

Figure 4: Depredation GAMM results. Smooth and parametric functions for variable output in binomial GAMM model of depredation occurrence. Figures represent presence/absence of odontocete depredation as function of each variable when all others are at their average value. Y-axis values are transformed from log-odds to probability scale and shifted by the model intercept to represent expected probability when all other variables are at their average value. The overall model-predicted probability (~0.06) of depredation is indicated by a dashed line in each figure so that the influence of each variable on probability of depredation can be directly assessed and compared. Distribution of observed values indicated by rug plot along x-axis. Shading reflects 2x standard error curves. Interaction term indicated by topographic 'perspective' plot.

2.3.2 Scale-dependent spatiotemporal analyses

The GAMM results showed an increased probability of depredation when a vessel experienced depredation on their prior set of the same trip. The modified Ripley's K method allows further exploration of this pattern by considering the occurrence of depredation across all co-occurring vessels that are close in space and time. This analysis showed a clear, spatiotemporal aggregation of depredation occurrence at most scales up to 1,000 km and 20 days (Figure 5a). The peaks in this surface indicate where clustering or aggregation is most intense – these occurred over areas of between 350-450 km and periods of 9-11 days. Our summary of empirical, or observed, depredation rates relative to distance and time since previous depredation events is consistent with the indicated spatiotemporal clustering. The observed depredation rate was 18% for vessels setting less than 50 km and 24 hours from previous depredation, but this rate dropped the farther away a vessel fished from a previous encounter. At the peaks from the Ripley's K, roughly 400 km and 9 days, the empirical depredation rate flattened to about 9% (a 50% reduction) and there was little additional benefit from moving farther (Figure 5b). Empirical depredation rates declined somewhat more rapidly with distance than time from the observed event, such that increased risk may be persistent for several days or more.

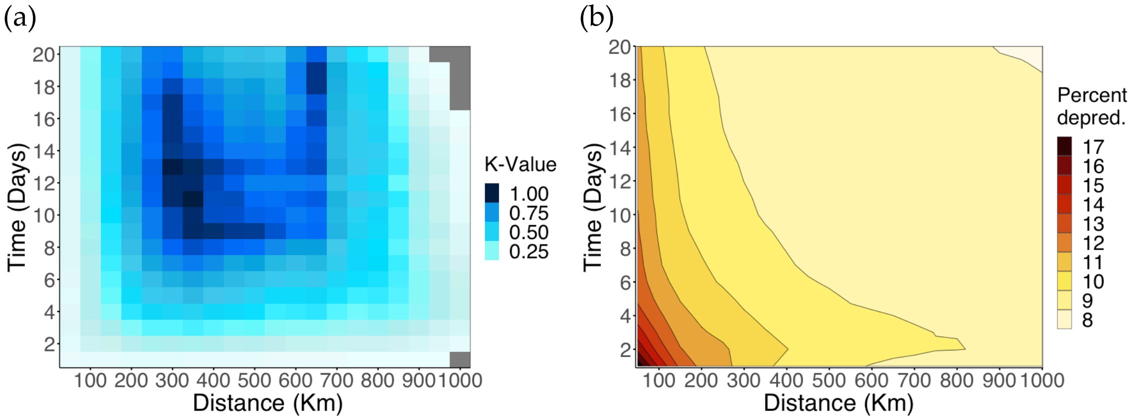

Figure 5: Spatiotemporal analysis of odontocete depredation. (a) Spatiotemporal clustering of odontocete depredation in the Hawaiʻi deep-set longline fishery from 2004-2018 represented by modified Ripley's K. Colored tiles are relative strengths of clustering, with any color-shaded tile (i.e., non-gray) representing spatiotemporal clustering above 95% random permutations at that space-time scale. The highest values represent the strongest levels of spatiotemporal clustering. (b) Percent occurrence of odontocete depredation based on time and distance (begin of haul) from a previous depredation event in the Hawaiʻi deep-set longline fishery.

The analysis of fishermen behavior showed that, in the absence of odontocete interactions, fishermen moved a median 35 km [interquartile range (IQR) 16–64 km] with a median duration of 4.3 h [IQR 2.9–6.1 h] from the end of that haul to the beginning of their next set. If depredation was experienced on a haul, they moved a median 46 km [IQR 24–83 km] in 4.7 h [IQR 3.2–7.3 h] before starting the next set, and 61 km [IQR 34–205 km] in 5.8 h [IQR 3.5–25.3 h] if a false killer whale bycatch event occurred.

2.3.3 False killer whale movement analysis

Tags were deployed on eight pelagic false killer whales during six encounters in 2013, 2017, and 2020. CRC deployed three tags in a group of approximately 16 individuals on 22 October 2013 and one tag in a group of 48 individuals on 14 May 2020 off of Hawaiʻi Island. PIFSC deployed one tag in a group of an estimated 23 individuals on 15 May 2013 and one tag in a group of estimated 15 individuals on 26 May 2013, both in the NWHIs. PIFSC deployed an additional two tags near the island of Kauaʻi, one in a group of approximately 32 individuals on 12 September 2017 and one in a group of approximately 19 individuals on 13 September 2017. Total tag durations, geographic use, and potential direct interactions with pelagic longline operations for the whales tagged in 2013 are described in greater detail in Anderson et al. (2020).

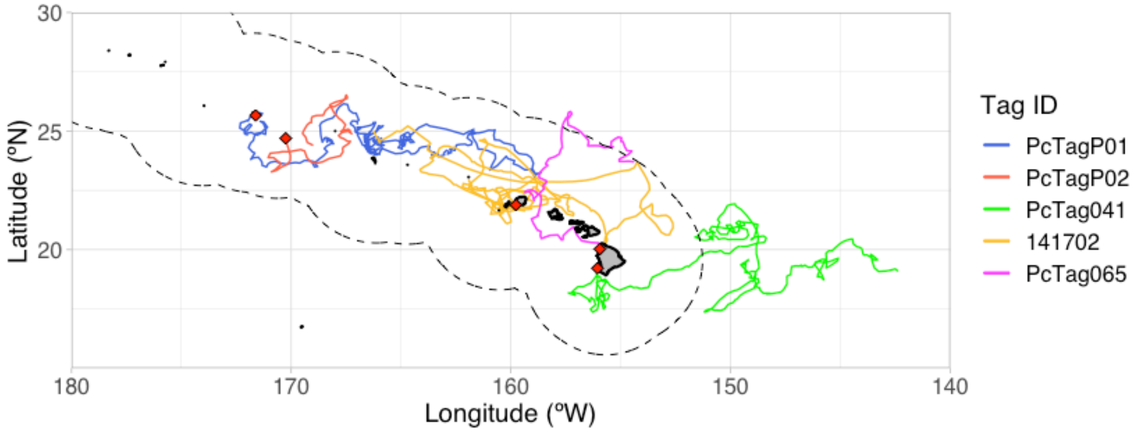

Figure 6: False killer whale satellite tag tracks. Red diamonds indicate tag-on locations. Dashed line represents the U.S. EEZ around the Hawaiian Islands. See text and Table 3 for further details.

There were five independent tags, with two (PcTagP02 and PcTag065) transmitting for about two weeks and the other three (141702, PcTag041, PcTagP01) transmitting beyond the 59 days of daily transmissions considered here (Figure 6). We included only full days of transmission, leaving 12 days for PcTagP02, 15 days for PcTag065, and 57 days each for the longer three (Table 3). Total distance traveled ranged from 1,653 km in 12 days for PcTagP02 to 8,099 km in 57 days for tag 141702. Median distance traveled in 4-hours for all animals was 19 km [range 1–75 km], translating to a median speed of 4.8 km/h [range 0.3–18.8 km/h] (Table 3, Figure 7). When considered at the daily scale, animals moved a median distance of 117 km [range 64–335 km] and median speed of 4.9 km/h [range 2.7–14.0 km/h]. Median displacement (straight-line distance from first location of day to first location of following day) was 81 km [range 2–333 km].

Table 3: Details on pelagic false killer whale tag deployments. Five tags were included in movement analysis after filtering through Douglas Argos-Filter and Correlated Random Walk state-space model.

Tag ID	Deployed by:	Deploy date	End date	# days	Cum. dist. (km)	Med. 4-h km [range]	Med. daily km [range]
PcTagP01	PIFSC	2013-05-16	2013-07-13	57	6,705	18 [2–54]	113 [64–203]
PcTagP02	PIFSC	2013-05-27	2013-06-09	12	1,653	21 [2–44]	125 [71–169]
PcTag041	CRC	2013-10-22	2013-12-19	57	6,602	17 [1–63]	112 [65–192]
141702	PIFSC	2017-09-12	2017-11-09	57	8,099	21 [1–75]	129 [64–335]
PcTag065	CRC	2020-05-15	2020-05-31	15	2001	21 [4–49]	121 [105–149]

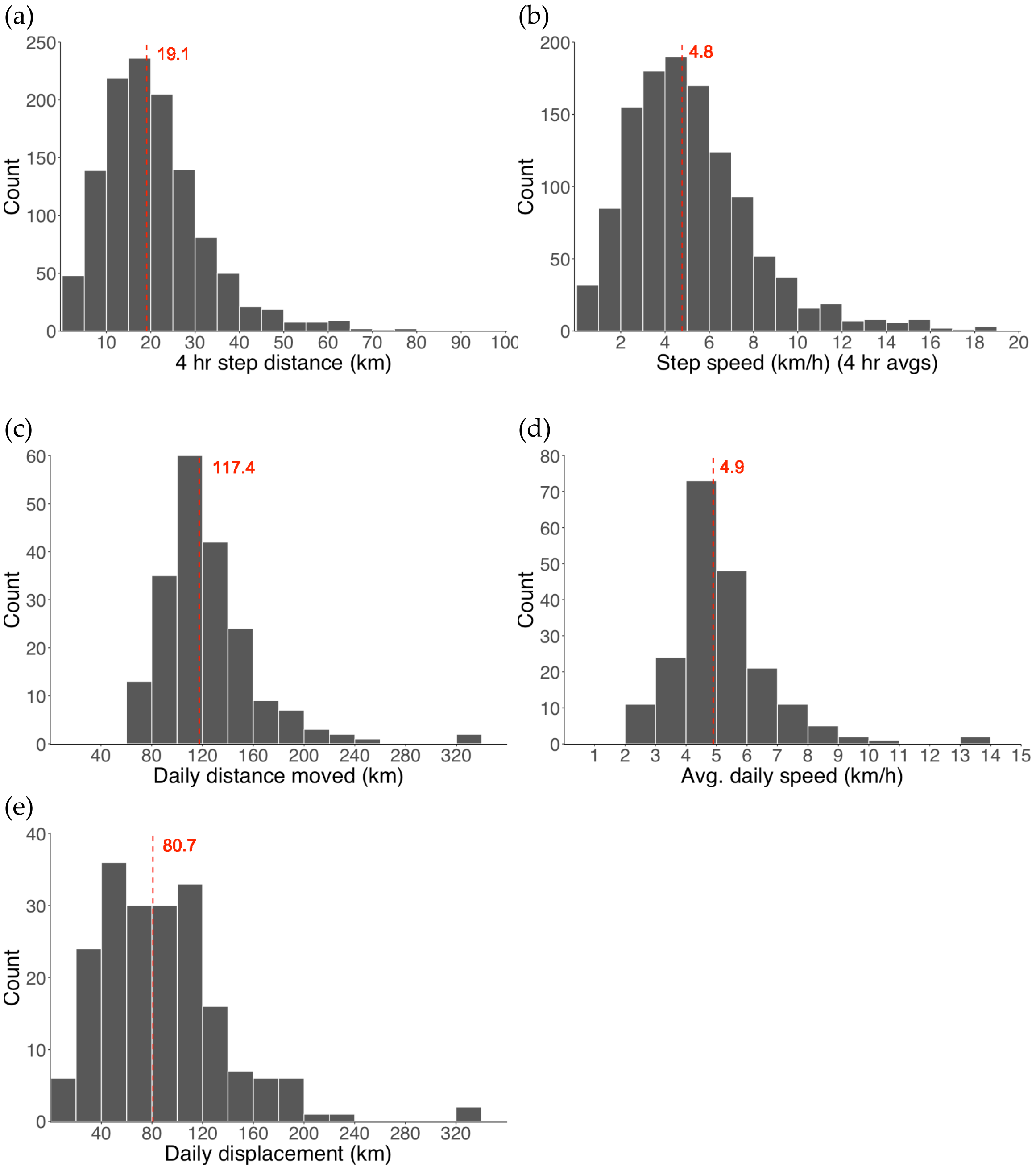

Figure 7: Summary histograms of false killer whale movement. Sub-daily (4-hour) track-line distance traveled and speed (a, b), daily track-line distance and speed (c, d), and total daily displacement (e) from five pelagic false killer whale satellite tags processed through Douglas Argos-Filter and Correlated Random Walk state-space models. Red values indicate median.

2.4 Discussion

We used several complementary approaches to explore patterns of odontocete depredation in the Hawaiʻi deep-set longline fishery. We first utilized a large observer dataset to explore relationships between odontocete depredation and environmental and operational covariates concurrent with deep-set fishing activity. These model outcomes largely corroborated those from an earlier analysis (Forney et al. 2011), with the larger dataset allowing for increased resolution of several patterns. The model did not identify environmental or operational covariates that could be used in a predictive management context, but it showed that the risk of depredation doubled if the previous set on the same trip experienced depredation. We explored whether the occurrence of depredation on other, nearby vessels also influenced depredation risk, and identified the space and time scales of such 'repeat' depredation to understand how risk changes with proximity to observed interactions. We also summarized false killer whale travel speeds and distances derived from satellite tags to help contextualize these scales of depredation and understand how movement of the depredating species contribute to the patterns we observed. Our analyses provide specific guidance on how fishermen can reduce the probability of repeated interactions following a depredation or bycatch event. Thus, our results have direct relevance to the ongoing deliberations of the False Killer Whale TRT and may inform management of other odontocete-longline interactions.

2.4.1 GAMM analysis of environmental and operational covariates

The overall explanatory power of the best-fit model was low, but several clear patterns emerged from the multivariate analysis of depredation occurrence. There was a marked decrease in interaction rates during the second and third quarters of the year and at higher latitudes, beyond around 18-20º N (Figure 4). This pattern was also observed by Forney et al. (2011) and is to be expected as the fleet extends north and east in these months (Woodworth-Jefcoats et al. 2018) into areas where false killer whale densities are predicted to be the lowest for this region of the Pacific (Forney et al. 2015, Bradford et al. 2020). Depredation is generally lowest at the northernmost extent of fishing effort, but it seemed to decrease at all latitudes during the Northern Hemisphere summer months (Figure 4). False killer whales likely move seasonally in response to changes in sea surface temperature (Bradford et al. 2020), and this could influence the intensity of overlap with fishing activity across the fleet's range. We also note that, although bycatch records and direct observation (Thode et al. 2016) suggest that false killer whales are the primary depredator species in this fishery, some depredation observations are likely due to other odontocete species. These broad space and time patterns may thus be partially influenced by interactions between these species' ranges, environmental conditions, and fishery behavior that cannot be disentangled here.

Depredation occurrence increased with absolute sea surface height, which is an indication of mesoscale features such as eddies and fronts (Chelton et al. 2011). This may relate to higher depredation in more productive habitats along these features, which is consistent with the higher depredation rates observed when target-species CPUE is high. We also documented a possible relationship between odontocete depredation and ENSO conditions. A weak but significant positive correlation (~0.14) was detected between the Oceanic Niño Index (ONI) and depredation 11 months later (Appendix A1: Figure A22), and this lagged ONI value was significantly positively associated with depredation rate in the GAMM analysis. It is unclear what ecological processes underlie this pattern. There could be a seasonal correlation component as El Niño events (ONI ≥ 0.5) disproportionately occurred in quarters 1 and 4 when there were higher rates of depredation. However, La Niña events (ONI ≤ -0.5) had a similar monthly distribution to El Niño and yet La Niña was associated with low depredation rates. A seasonal pattern would also not likely account for the apparent yearly fluctuations, and interaction terms between ONI lag and month and ONI lag and latitude were not significant in the depredation models. Strong El Niño events are known to disrupt oceanographic conditions and marine food webs, although effects on upper trophic level predators are not well understood (Lehodey et al. 1997, Stenseth et al. 2002). Perhaps false killer whales opportunistically target fishing vessels more frequently when El Niño periods destabilize their normal food webs, and this occurs at the observed lag due to impacts taking time to move through the prey community. However, it would be very difficult to empirically test this hypothesis and, for now, we simply note the pattern.

Operationally, we observed that the probability of depredation increased with number of hooks set and soak time in hours. Indeed, fishermen could reduce their risk by approximately 50% (~0.06 to ~0.03) by making sets less than 1,500 hooks or completing the haul in less than 10 hours. Soak time and the amount of gear have similarly been observed to influence depredation rates in demersal longline fisheries (Tixier et al. 2015b, Janc et al. 2018), reinforcing that simple strategies that reduce depredator access can be beneficial in reducing interactions. We also observed relationships between depredation and a number of catch indicators. For four of the most common target species there was a similar, non-linear relationship in which the probability of depredation decreased with catch, then leveled off at low probabilities or increased back to more neutral effects at high catch rates. We also observed an increase in the probability of depredation as the CPUE of tuna species by all vessels within 3 days and 200 km increased, as well as with the number of sharks caught. These patterns suggest that depredation is more common in areas where CPUE is high, which is to be expected, given false killer whales are apex predators that target many of the same species as the fishery (Baird et al. 2008). Most of the commonly caught shark species in this fishery are also apex predators and may similarly be drawn to regions that are favored by false killer whales. The nonlinear patterns at the focal vessel may be explained by generally low catch rates when depredation occurs. False killer whales are known to depredate bait in the deep-set fishery (Thode et al. 2016, Bayless et al. 2017), which could depress overall catch rates. The fish heads counted by observers are also an imperfect indicator of depredation and it is possible that the whole fish is sometimes removed by the depredating whale or falls off the line before the hook is hauled. This would also be consistent with the more linear trend for sharks, as sharks are almost never depredated by odontocetes (see also Oleson et al. 2010). The uptick in depredation at very high catch levels may be associated with the general pattern of false killer whales occurring in relatively productive areas.

2.4.2 Spatiotemporal depredation patterns

The GAMM shed light on finer scale patterns of depredation as well, such that depredation was significantly more likely if a vessel experienced depredation on the previous set of its same trip. This is consistent with the results reported by Forney et al. (2011) and reports from fishermen (TEC 2009), which suggest fishermen experience repeat depredation on trips and may actively move following depredation to reduce the probability of repeat occurrences. Forney et al. (2011) suggested that moving 100 km following a depredated set leads to slight reductions in risk (from 16% to 14% expected occurrence), but there was insufficient sample size in their analysis to assess time and space together and only interactions on the focal vessel were considered (i.e., not what is happening on other, nearby vessels).

We addressed these gaps using a variation of Ripley's K to estimate spatiotemporal autocorrelation of depredation simultaneously for all vessels across a range of actionable space and time scales. This approach has been used in other fisheries experiencing depredation or bycatch to identify scales of clustering, which can then be used to provide recommendations of distances to move, and/or times to wait, to avoid future negative encounters; these are commonly referred to as move-on rules. We identified spatiotemporal clustering of depredation in the deep-set fishery across most scales we considered, suggesting that a vessel should generally expect to encounter higher depredation rates near previously observed depredation events due to spatiotemporal clustering of events alone (i.e., independent of any effects of just time or just space).

To give a clearer picture of what fishermen could actually expect in terms of risk of depredation relative to the time and location of previous depredation, we also identified the average proportion of sets experiencing depredation (for all vessels simultaneously) within the same space-time thresholds from the observed depredation event (i.e., within 20 days and 1,000 km at increments of 24 hours and 50 km). As for a single vessel, the rate of depredation across all vessels is highest when a previous depredation event is observed nearby in space and time. On average, the proportion of sets experiencing depredation within 24 hours and 50 km of a previously observed depredation event is ~18%, compared to the overall background rate of ~6%. Consistent with the K-analysis, this proportion decreases with both space and time since the observed event. The peaks from the K-analysis indicate that ~400 km and ~9 days is the most effective distance to move and time to wait, respectively, for reducing repeat depredation. On average, the depredation rate decreased from 18% to 9% (~50% reduction) at this threshold, with little additional benefit gained by moving farther or waiting longer.

There also seems to be a greater benefit from moving rather than waiting, suggesting that these clusters of depredation activity may be relatively confined in space (still potentially over several hundred km), but persistent in time (i.e., lasting for up to several weeks). This may be beneficial to the fleet, as moving is likely to be a more practical strategy than simply waiting without fishing, although there are obvious costs associated with both. Indeed, past fishing practices suggest that pelagic longline fishermen tend to react to depredation and bycatch by moving but fishing again as soon as possible. Fishermen moved around 31% farther between sets when they experienced odontocete depredation and 74% farther when there was a false killer whale bycatch event, but the median times for each scenario were all under six hours, indicating a tendency to move but still set on the same day (so that a potential fishing day was not missed). We also note, however, that although the median times are similar, the upper quartile of time between sets increased to >24 hours following a false killer whale bycatch event, suggesting that at least some vessels or captains may be likely to both move and wait an extra day before fishing again. The K-analysis does suggest that any movement farther from an observed interaction will decrease the likelihood of repeat occurrences, but based on our move-on analysis, the distances typically moved may provide only very minor benefits when fishing again within 24 hours. For example, the average percentage of depredated sets within 61 km and 24 hours of a previously observed depredation event was 17% (compared to 18% within 50 km and 24 hours), while this decreased to 12% on the same day but 200 km away.

2.4.3 Depredator behavior and avoidance

The incidence of depredation is ultimately driven by the behavior of the depredator, and there have been important recent advances in understanding the nature of interactions between false killer whales and the Hawaiʻi deep-set longline fleet, and for interactions with odontocetes in other fisheries. For example, passive acoustic monitoring of longline gear deployments detected false killer whales most commonly during the hauling phase, with whales potentially moving along the mainline away from the vessel as gear was being retrieved (Bayless et al. 2017). Satellite-tagged false killer whales were also observed to show directed movements toward fishing gear during the hauling phase of some sets (from as far as 100 km away) and no apparent reaction to gear during other sets, despite being within apparent detection range (Anderson et al. 2020). It is still unclear how false killer whales locate gear, although work with other species and fisheries suggests that acoustic detection is very likely. Thode et al. (2007) showed that sperm whales depredating demersal longlines in southeast Alaska cue in on acoustic signatures from the cavitation of a ship's propeller when the engine is engaged to begin hauling gear, which they can detect from at least 4-8 km away. Thode et al. (2015) further point out that sperm whale clicks are more intense than the vessel noises themselves, and thus once at the gear location, depredating sperm whales may intentionally or unintentionally alert other whales from even farther away. Richard et al. (2021) recently identified clear acoustic signatures during setting operations of demersal longlines in a sub-Antarctic fishery. They argue that there may be multiple acoustic cues available to depredating whales for a given fishery and that different cues may travel different distances. This may help explain observations that killer whales in South Georgia orient to demersal longlines at 75-100 km (Towers et al. 2019), while they seem to orient to herring purse seine vessels in Norway when within 20 km (Mul et al. 2020).

Taken together, these studies demonstrate that false killer whales are likely capable of locating vessels from tens of kilometers away, following vessels, and moving along gear removing bait and target catch once found, although they do not always do so. Our spatiotemporal analysis identifies clear space-time aggregation of longline depredation, which could be a result of this type of active targeting and following of vessels by whales, simple overlap of whales and vessels targeting similar dynamic oceanographic conditions or, more likely, some combination of both. We provide a summary of baseline pelagic false killer whale movement behavior, using the same tags as Anderson et al. (2020) plus an additional tag from PIFSC in 2017 and CRC in 2020, to place in context the mobility of these pelagic predators and provide guidelines for what would be required to avoid or escape whales that are actively pursuing a vessel.

Over four-hour time periods, comparable to the typical duration between the end of a deep-set haul to beginning the next set, the median distance moved by the five focal whales was 19 km (median speed of 4.8 km/h). However, all five whales moved over 40 km in a four-hour period (speed of 10 km/h), two were observed to move over 60 km (15 km/h), and one exceeded 70 km in four hours on three different days (17.5 km/h). This compares to kinematic predictions of false killer whale speed based on morphology and cost of locomotion, which suggest cruising speeds of 11 km/h and highest efficiency of swimming at 13-14 km/h (Fish 1998). Burst speeds are likely much greater than could be maintained over four hours. Fish (1998) estimated maximum velocities for false killer whales of 27 km/h and Baird (personal observation) observed a group of false killer whales near Hawaiʻi maintaining speeds of 18 km/h for over 30 minutes.

Over daily time periods, the median along-path distance was 117 km with a median speed of 4.9 km/h. However, distributions were again right skewed with whales observed to move well over 200 km in 24-hour periods, maintaining speeds of at least 10 km/h. We note that reported along-path distances are all minimum values as whales are unlikely to move in straight lines for four or 24 hours. More accurate GPS-based tags, as well as better estimation of false killer whale cost of transport and aerobic capacity, could further inform how long animals are able to maintain high cruising speeds and how long they might be expected to pursue vessels.

False killer whales have a complex social structure and groups are often comprised of multiple sub-groups spread over distances up to at least 35 km (Baird et al. 2008, Bradford et al. 2014, Martien et al. 2019). Individuals within groups have been observed separating by over 100 km and rejoining the same group over a period of several days (Baird et al. 2010). Assuming a minimum detection range of 4-8 km for vessel noise and no movement by the depredating whales, it is thus possible that a vessel would have to move 40–50 km (acoustic propagation of vessel noise + spread of sub-groups) just to reach the edge of detection range for a large group of false killer whales. This distance could, of course, increase if individual whales disassociate and reassociate as observed by Baird et al. (2010) or follow the vessel as it moves to a new fishing location, which is known to occur in other odontocete-fishery interactions. Tixier et al. (2015b) demonstrated that a single pod of killer whales (*Orcinus orca*) could follow longline vessels for multiple days and suggest that the whales may even maintain their bearing, such that they can encounter and depredate gear several days later, despite likely losing contact with the acoustic signal of the vessel.

How long a vessel would have to move to outpace following whales depends on the speeds of the vessel and whale. The average maximum speed of Hawaiʻi longline vessels is about 15 km/h (obtained from MarineTracker.com), which is similar to the maximum speeds maintained in four hours by tagged false killer whales. Thus, it is possible that a vessel at maximum speed could still have following whales after four hours. Even if whales were moving at 10 km/h, which all tagged whales were easily capable of, a vessel moving at 15 km/h would only be 20 km from the following whales after four hours. As it could take three hours just to reach the conservative edge of detection range of 40-50 km, whales may be able to maintain detection well beyond four hours, even if the vessel moves at maximum speed. Our spatiotemporal analysis suggests that when fishing again within one day, vessels are unlikely to experience large decreases in depredation risk unless they move fairly large distances. We recognize constraints may limit a vessel's ability to move certain distances. Deep-set gear is typically deployed (set) in the morning with haul-back beginning around sunset and finishing in the early morning hours. A captain who wishes to fish two days in a row typically has only a few hours to redeploy gear at the optimal time of day, hence the median of ~4 hours from end of haul to beginning the next set. Unfortunately, even at the average maximum speed for these vessels, fishermen are unlikely to decrease their interaction risk within only four hours. We thus recommend that when depredation is known to occur, vessels move away as far and as quickly as practical. It may also benefit to diverge from the course of travel for 10-20 km before setting gear, as false killer whales may behave like killer whales and continue following in one direction after losing acoustic detection of the vessel (Tixier et al. 2015b). Vessels will experience greater reduction in risk if they wait to set until the following fishing day.

2.4.4 Recommendations and implications

Our work was motivated by the goal of identifying patterns of odontocete depredation and depredator behavior in a way that can be used by fishermen to mitigate these negative interactions. We detected some interesting patterns, but there were no unequivocal geographic, environmental, or operational covariates that could be used in a management context. As has been shown before, the probability of interaction increases with fishing effort (hooks set and time soaked). But, in general, odontocete depredation is likely driven at broad scales by convergence in space and time of fishing activities and the occurrence of these apex predators, which are both targeting similar prey fields. Both fishermen and whales are likely cueing on the same set of environmental factors to locate these areas. Nevertheless, depredation is still a relatively rare event, and thus high predictive accuracy based on a priori environmental factors alone is not currently possible.

Given the clumped occurrence of this behavior in space and time, it is not surprising that the best predictor of depredation is where and when it was observed previously. We characterize the boundaries of risk associated with previously observed events, which suggest that depredation risk consistently decreases until about 9 days later and 400 km away, with little expected reduction beyond that. Risk seems more persistent in time than in space. For example, the same proportion of sets were depredated within 50 km and 8 days of a depredated set than within 200 km only one day later. Thus, if vessels wish to fish again within 24 hours, they will experience the greatest reduction in risk by moving or staying as far away as possible, ideally 200-300 km.

We further considered the behavior of tagged pelagic false killer whales. False killer whales can pace fishing vessels for at least four hours. We recommend that fishermen steam at high speeds (> 15 km/h) for seven to eight hours if setting the same day, but again, they will experience further benefit if they wait until the next day to fish, allowing time to move even farther. This may be challenging under typical fishing operations, so fishermen who intend to fish on consecutive days may be able to capitalize on synergies between the reduction of risk at lower fishing effort and greater distances moved following depredation. By setting slightly less gear they should finish hauling earlier in the day. If depredation were to occur on that haul or be known to have occurred recently in their area, they would thus have more time to move to a safer location on the same day.

We also showed that risk is increased for all vessels in the vicinity of known interactions, suggesting that improved communication among vessels in the fleet would help reduce risk (Gilman et al. 2006). It may be difficult for a vessel at the center of a group of whales to escape detection within a day, but other vessels fishing in the same area can use that knowledge to reduce their own risk. Elevated depredation risk may persist within 100-200 km for a week or more, so it is important for other vessels to know where interactions occur so that they do not inadvertently fish again within high-risk areas. We understand that competition may reduce incentives to communicate among some vessels, and cooperation may be even less likely outside of the U.S. EEZ, where vessels from a number of other nations may also be longline fishing. However, reducing bycatch risk is in the best interest of all U.S. fleet members, given the potential management implications of high bycatch rates.

Finally, we recognize that although moving and waiting reduce odontocete interaction risks, they also incur costs themselves. Ultimately each captain must make decisions based on the perceived costs and the benefits of moving versus continuing to fish. We have attempted to provide information to help them evaluate part of this calculation, specifically the expected risk reduction from given avoidance measures. We hope that they can use this information to more precisely evaluate the tradeoffs in adopting these recommendations. Further work assessing the costs in terms of lost fish catch would be beneficial in helping fill in additional parts of these calculations that are not addressed here.

Depredation and associated bycatch are global issues but remain poorly understood in many ways, especially for pelagic longline fisheries where depredating animals are rarely seen in the vicinity of gear. Our study adds to a growing body of work for the Hawaiʻi longline fleet but is also relevant to pelagic longline depredation in other parts of the world. Unfortunately, depredation and bycatch will be difficult to avoid whenever the predators and fisheries target the same species. However, for species that occur in low densities with relatively low interaction rates, such as false killer whales, it may be possible to avoid areas of overlap and find other productive grounds to fish without whales. The tools used here can help identify the intensity and scale of risk where whales are known to occur, and the avoidance strategies most likely to be effective in minimizing further risk to the fishery. We demonstrate that rates of interaction can be reduced by up to 50% with appropriate avoidance measures. We hope that fishermen will add these measures to their toolkit for deciding where to fish, reducing economic burdens on the fleet and improving conservation outcomes for vulnerable bycatch species.

3. No free lunch: Estimating the biomass and ex-vessel value of target catch lost to depredation by odontocetes in the Hawaiʻi longline deep-set tuna fishery

3.1 Introduction

The expansion of human exploitation of marine living resources during the past century has created and exacerbated conflicts between fisheries and top predators (Lewison et al. 2004, Lewison et al. 2014, Guerra 2019). Some interactions are indirect, such as competition with predators for shared resources, or other trophic effects arising from exploitation of target species (Branch et al. 2010, Morissette et al. 2010). Others are more direct, such as entanglement and bycatch, or predators feeding on bait or fish secured on fishing gear, an interaction known as depredation (Gilman et al. 2007, Gilman et al. 2008, Tixier et al. 2020b). A wide range of marine predators are known to engage in depredation with a diverse array of fishing gear (Tixier et al. 2020b). The impacts of depredation extend to fishermen, predators, and ecosystem structure and function (Gilman et al. 2007, Gilman et al. 2008, Hamer et al. 2012, Mitchell et al. 2018).

Depredation can lead to substantial socioeconomic costs for affected fisheries (Peterson et al. 2014, Tixier et al. 2020a). These include direct costs from damage to gear and loss of bait or catch, and indirect costs caused by increasing fishing effort to make up for lost catch. Depredating species are also affected in multiple ways. Feeding on restrained catch may reduce energetic costs of foraging and create access to new foraging opportunities (Esteban et al. 2016). However, depredation also increases the risk of injury or mortality due to hooking or entanglement in fishing gear (Forney et al. 2011) and retaliatory responses from fishermen (Poncelet et al. 2010, Guinet et al. 2015). Depredation can have broader ecosystem consequences, including changes to predator-prey interactions. Finally, depredation can lead to higher exploitation rates of fish stocks and bias in stock assessments, as depredated catch is not typically included in estimates of fishing mortality (Peterson et al. 2013, Esteban et al. 2016, Peterson and Hanselman 2017, Hanselman et al. 2018). Thus, it is important to obtain accurate estimates of catch losses accruing from depredation to understand these diverse ecological and socioeconomic impacts.

Longline fisheries are particularly susceptible to depredation as bait and catch are suspended in the water column for long periods (Gilman et al. 2007, Gilman et al. 2008, Tixier et al. 2020b). Depredation has been reported in longline fisheries by cetaceans, sharks, squid, and seabirds (Tixier et al. 2020b). Depredation by odontocete cetaceans is particularly common and problematic for fishermen. Some odontocete species are skilled in locating fishing gear, sequentially removing fish as gear is hauled or traveling along lengths of gear to remove bait or catch (Towers et al. 2019, Anderson et al. 2020). These behaviors can lead to substantial economic cost to affected fishermen (Peterson et al. 2014, Tixier et al. 2020a).

In Hawai'i, two pelagic longline fisheries experience odontocete depredation and bycatch. The deep-set fishery targets bigeye tuna (*Thunnus obesus*) and operates year-round north and south of the Hawaiian Islands, both inside and outside of the U.S. EEZ. A smaller, shallow-set fishery operates mainly north of the Hawaiian Islands targeting swordfish (*Xiphias gladius*). Odontocete depredation and bycatch is more common in the deep-set fishery (Forney et al. 2011), where false killer whales (*Pseudorca crassidens*) depredate bait and catch and are the most common species of cetacean taken as bycatch (Thode et al. 2016, Bayless et al. 2017). Other odontocete species such as short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*) are also occasionally recorded as bycatch, likely driven by depredation as well (Forney and Kobayashi 2007, Forney et al. 2011, Fader et al. 2021). Unsustainable levels of false killer whale bycatch have led to regulatory actions by the National Marine Fisheries Service (NMFS), following recommendations from the False Killer Whale Take Reduction Team (FKWTRT), a multi-stakeholder group charged with reducing mortality and serious injury of false killer whales below levels stipulated by the U.S. Marine Mammal Protection Act (Federal Register 2010). The FKWTRT has recommended gear changes, handling requirements, and spatiotemporal closures that are triggered when false killer whale bycatch exceeds certain levels. These restrictions impart additional costs to the fishery beyond losses due to depredation itself.

There are a few video records of false killer whales depredating bait and acoustic recordings of false killer whales near depredated gear (Thode et al. 2016, Bayless et al. 2017) but, in general, depredation by odontocetes is rarely observed directly in the deep-set fishery. Instead, depredation of catch is inferred by characteristic damage to individual fish retrieved during the haul (Forney et al. 2011, Fader et al. 2021). Studies to date have focused on characterizing depredation patterns to inform potential mitigation solutions (Forney et al. 2011, Fader et al. 2021) and there have been no quantitative assessments of the economic impact that depredation has on the fishery or of the potential effects of these losses on target stocks. In this paper, we estimate aggregate and annual removals of target catch by odontocetes in the Hawaiʻi deep-set longline fishery and assess broad-scale spatial and temporal patterns of depredation across the range of the fishery.

3.2 Methods

3.2.1 Data sources and data preparation

3.2.1.1 Study area and fishery-dependent data sources

Hawaiʻi deep-set gear consists of a single monofilament mainline (3.2–4.0 mm diameter), suspended in the water column by a series of floats. Between each float, individual, monofilament branch lines are regularly spaced, each terminating with a single, mackerel-type bait attached to a circle hook (Boggs and Ito 1993). The target depth for bigeye tuna is around 400 m and typical deployment of fishing gear ranges from 1,000-3,000 hooks over ~45–80 km of mainline. When targeting bigeye tuna, deep-set fishermen typically deploy (ʻsetʼ), their gear in the morning, allowing it to fish (ʻsoakʼ) for several hours until the retrieval (ʻhaulʼ) begins around sundown. The hauling process may range from four to over 12 hours, depending on the catch and amount of gear deployed.

We derived fishery-dependent data from two sources: 'logbook' data recorded by vessel captains and 'observer' data collected by on-board, independent fisheries observers. All deep-set captains are required to record and submit logbooks to NMFS which record the times and GPS coordinates of the start and finish of each set and haul of gear (i.e., four times and locations per fishing event), the number of hooks deployed, and counts of captured fish by species. Deep-set vessels are also required to carry a federal fisheries observer, if requested by NMFS, with a fleet-wide target coverage of 20% of trips per year. Observers collect detailed data on fishing operations, gear characteristics, and biological data from both target and non-target catch. Observers monitor the entire haul-back of each gear deployment, identifying each captured species to the highest taxonomic level possible. Since 2009, observers also systematically measure to the nearest centimeter every third fish landed. Most bony fish are measured with standard fork-length, while billfish are measured using an eye-fork measurement. Observers are also trained to classify and systematically record incidences of depredation. Evidence of odontocete depredation is distinct from other sources, such as squid or sharks, because toothed whales typically consume the whole fish up to the gill plates, leaving only the head attached to the hook (e.g., Secchi and Vaske 1998) (Figure 8). False killer whales are also known to depredate bait from deep-set gear (Thode et al.

2016), but this is not systematically recorded by observers and is thus not considered or reported here. It is also likely that whales at times remove entire fish, in which case depredation may underestimated or not recorded at all.

Figure 8: Examples of odontocete depredation on three commonly depredated catch species: (a) unidentified tuna species, (b) mahi-mahi, and (c) unidentified billfish. Note characteristic tooth-rakes on top of the tuna head. Photos courtesy of the National Marine Fisheries Service.

3.2.1.2 Overview of multi-stage modeling approach

We utilized a multi-stage modeling approach to estimate the total biomass of target species lost to odontocete depredation in the deep-set fleet. We focused our analyses on bigeye tuna, yellowfin tuna (*Thunnus albacares*), and mahi-mahi (*Coryphaena hippurus*). The tuna species caught in this fishery cannot be reliably distinguished from the head and gills of individual depredated fish, so we first modeled expected species identity for the two target tuna species (Stage 1). There is only one common species of mahi-mahi caught in this fishery and thus this step was only necessary for tuna. We then estimated the expected biomass of each depredated fish, by species, by modeling its expected length and calculating its expected mass from established length-weight relationships (Stage 2). We aggregated the estimated biomass from individual fish for all observed sets in 5º x 5º x month cells and modeled the expected total biomass of depredated fish by species on observed sets (Stage 3). Finally, we used the best models of aggregated depredated biomass to predict total depredated biomass for the entire fishery (i.e., extrapolating to unobserved fishing sets using logbook records).

3.2.1.3 Derivation of covariates

We considered a suite of spatial, temporal, gear, operational, and/or environmental variables hypothesized to influence target species type, size, or aggregated depredated biomass for Stages 1, 2, and 3, respectively. Operationally, depth of gear has an important influence on both species and size composition of catch (Bigelow and Maunder 2007). As shoaling and concatenation of the main line makes it difficult to estimate the precise depth of gear directly (Bigelow et al. 2006), in both Stages 1 and 2 we utilized two gear-based variables that indicate the relative depth of an individual caught fish within a single set and relative to other sets. First, we calculated the standardized distance of each caught fish from the nearest float (HKDIST), such that a value of 0 is the first or last hook of the basket, while a value of 0.5 is the very middle of the basket. Due to the concatenation of mainline between floats, hooks closer to the middle of the basket are expected to be deeper in the water than those near the float (Bigelow et al. 2006). Secondly, we used the number of hooks between floats (HBF) for the entire fishing event (a parameter held constant as a boat deploys its gear across floats) as a general indicator of gear depth. More hooks between each float generally causes the gear to sink deeper (Bigelow et al. 2006).

We considered a range of static and dynamic environmental variables in all three stages including (detailed description and sources in Table 4): depth (DEP), sea surface temperature (SST), standard deviation of sea surface temperature (SSTDEV), the log of chlorophyll-a concentration (CHLA), mixed layer depth (MLD), sea surface salinity (SAL), absolute dynamic topography (ADT), total kinetic energy (TKE), Oceanic Niño Index (ONI), and lunar phase (Stages 1 and 2 only). The first four covariates were extracted for the 2009-2018 study period using NOAA ERDDAP servers (https://coastwatch.pfeg.noaa.gov/erddap/index.html) and the rerddapXtracto package in RStudio statistical software, version 1.4.1103 (R Core Team 2018). MLD, SAL, ADT, and TKE for 2009-2018 were derived and processed from the EU Copernicus Marine Service (https://marine.copernicus.eu/). Spatial resolutions of the data ranged from 1/12º–1/4º and temporal resolutions from days to months (Table 4).

For Stages 1 and 2, each environmental variable was associated with the spatial location of a single fishing set. As longlines can be tens of kilometers long, we derived the geographic centroid of each fishing set from the four observed spatial locations (set begin, set end, haul begin, haul end) and then created a bounding box of 0.25º x 0.25º around the centroid point, which encompasses the average spatial footprint of observed sets of 250 km². For environmental variables of a resolution higher than 0.25º x 0.25º, we used nearest neighbor resampling to take the average value within this box for each set. Similarly, in Stage 3, we used nearest neighbor resampling to standardize covariates to the desired spatiotemporal resolution of 5º x 5º x month.

Table 4: Description of environmental covariates included in this study.

Covariate	Units	Data name and source	Original spatial resolution	Original temporal resolution
Depth	m	General Bathymetric Chart of the Oceans (GEBCO) Grid[1]	15 arc-seconds	NA
Sea surface temperature (SST)	°C	NASA JPL Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1[2]	0.01°	Daily
SST Standard Deviation (SSTDEV)	NA	NASA JPL Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1[2]	0.01º	Daily
Chlorophyll-a concentration (CHL)	Natural log of $mg \bullet m^{-3}$	NASA Aqua MODIS Level 3[3]	4 km	Monthly
Mixed Layer Depth (MLD)	m	Global Ocean Physics Reanalysis GLORYS12V1[4]	1/12º	Daily
Surface Salinity (SAL)	1e-3	Global Ocean Physics Reanalysis GLORYS12V1	1/12º	Daily
Absolute Dynamic	m	Global ocean gridded L4 sea surface heights and	1/4º	Daily

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[1] https://coastwatch.pfeg.noaa.gov/erddap/info/GEBCO_2020/index.html

[2] https://coastwatch.pfeg.noaa.gov/erddap/info/jplMURSST41/index.html

[3] https://coastwatch.pfeg.noaa.gov/erddap/info/erdMH1chlamday/index.html

[4] https://resources.marine.copernicus.eu/product-download/GLOBAL_REANALYSIS_PHY_001_030

Topography (ADT)		derived variables reprocessed[5]		
Total Kinetic Energy (TKE)	$m^2 \cdot s^{-2}$	Global ocean gridded L4 sea surface heights and derived variables reprocessed	1/4º	Daily
Oceanic Niño Index (ONI)	NA	NWS Climate Prediction Center[6]	NA	3-month average
Lunar phase	NA	Package 'lunar'[7]	NA	Daily

3.2.2 Modelling approach

3.2.2.1 Data preparations

We conducted detailed data explorations prior to model fitting for each Stage to identify appropriate inclusion of predictor variables. We assessed collinearity among explanatory variables by calculating Pearson correlation coefficients for all pairwise combinations of continuous variables, retaining only those with values less than 0.7. When two variables with similar ecological meaning were correlated, we retained the one with fewer missing values or a clearer ecological relationship to the response. We also plotted covariates in histograms, against response variables, and in residual plots from preliminary models.

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[5] https://resources.marine.copernicus.eu/product-download/SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047

[6] https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php

[7] https://cran.r-project.org/web/packages/lunar/lunar.pdf

3.2.2.2 Generalized additive modeling approach

We used variations of generalized additive models (GAMs) in each of the three Stages. GAMs are a regression approach that calculate smooth functions to estimate relationships between predictor and response variables (Wood 2017). The GAM approach allows flexibility in specifying different terms within a single model, with minimal *a priori* assumptions on the nature of each relationship (Wood 2017). They allow for a wide range of distribution families, so that diverse types of response variables can be accommodated (Zuur et al. 2009). A link function $g()$ is used to relate a univariate response variable Y to a sum of smooth functions of the covariates X_i :

$$g(E(Y) = \alpha + \sum f_i(X_i)$$

where α is the intercept and f_i is a smooth function of the covariate X_i.

Following general approaches outlined in Zuur et al. (2009) and Dunn and Smyth (2018), for each species in each Stage, we began model selection from fully saturated models with cubic regression splines used for all univariate smoothers and tensor product smooths for any interaction terms. We used a cyclic cubic regression spline for month to ensure a smooth step from December to January. Splines were implemented with a shrinkage parameter, which incorporates a penalty on the null space that drives the coefficients of non-contributing variables to zero (Wood 2006). These variables were removed after the first iteration, and then backward, stepwise selection was used on remaining variables to arrive at a final model (Zuur et al. 2009).

All analyses were conducted in RStudio statistical software, version 1.2.5033 (R Core Team 2018). Stage 1 and 3 models were implemented with the package mgcv, version 1.8-31 (Wood 2006, 2007), and Stage 2 models were implemented using the gamm4 package, version 0.2-6 (Wood and Scheipl 2014). Further detail on each modeling Stage is provided below.

3.2.2.3 Stage 1 – Predicting tuna species for unknown depredated tuna

Tuna caught in the Hawaiʻi deep-set fishery include bigeye, yellowfin, skipjack, and albacore and these four species cannot be reliably identified from the head alone. Thus, we developed a classification model to predict the probability that each observed, odontocete-depredated tuna head was a particular tuna species. I utilized a GAM based on multinomial logistic regression, treating the species of tuna (one of four) as an unordered, categorical response variable. Covariates considered included gear (i.e., depth) and environmental variables described above, as well as space (i.e., latitude and longitude coordinates) and time (month) to account for spatial, seasonal, and inter-annual variation in distributions of tuna species. We also included covariates for set-specific tuna species proportions, calculated as the number of each tuna species caught on the focal set divided by the total number of all tuna caught on that set.

We removed several candidate variables that were highly correlated with other variables or did not have noticeable discriminatory capability for the different species (i.e., the histogram distributions were nearly identical for each species). The resulting, fully saturated GAM was of the form:

$$\text{Tuna Type} \sim \beta_0 + s(\text{YFT\_prop}) + s(\text{SKJ\_prop}) + s(\text{ALB\_prop}) + s(\text{Longitude}) + s(\text{Latitude}) + c(\text{Month}) + s(\text{Year}) + s(\text{SST}) + s(\text{HKDIST})$$

Multinomial GAMs produce p-values that indicate the ability to discern each class from a base or reference class (in this case, bigeye tuna). For the 4-class model, there were three sets of p-values for each variable. To arrive at an optimal model, we utilized backwards, stepwise model selection, sequentially removing variables that were not significant for any of the three other tuna classes. We assessed model fit and prediction accuracy by fitting models to a training set of half the available data, and then testing those models on out-of-sample test data. We selected models with a higher specificity and/or lower AIC. The resulting best model was used to predict, for each individual depredated fish, the probability that it was each of the four species of tuna.

3.2.2.4 Stage 2 – Predicting depredated fish length

To derive estimates of the length (and ultimately biomass) of observed, depredated fish heads, we modeled the length of all intact (i.e., non-depredated), observer-measured fish for each of the three focal fish species. We used fork length in centimeters for each fish species as a Gaussian-family response variable with an identity link function. Covariates considered included the two gear/depth variables from Stage 1, a time/space interaction between month and the latitude and longitude of the centroid of the fishing event, consecutive month from 2009-18, and the environmental covariates. We included the presence or absence of depredation on the same set of the focal vessel as a categorical, parametric variable. Finally, we included set and trip ID as nested, random effects to control for variation within a single set and across individual trips. The final, saturated GAMs were of the form:

$$\text{Fish Length}_{\text{species}} \sim \beta_0 + s(\text{Longitude, Latitude, Month}) + s(\text{Consecutive Month}) + s(\text{HBF}) + s(\text{HKDIST}) + s(\text{DEP}) + s(\text{SST}) + s(\text{SSTDEV}) + s(\text{CHLA}) + s(\text{MLD}) + s(\text{ADT}) + s(\text{TKE}) + s(\text{ONI}) + s(\text{LUN}) + \text{Depredation} + \text{random}(\text{Set ID} \mid \text{Trip ID})$$

We first removed all variables with a p-value > 0.1 and shrunken coefficients (expected degrees of freedom < 1). We then proceeded by removing the non-significant or the least significant covariates at each stage and refitting the model. We evaluated the prediction accuracy of candidate models at each stage using 5-fold cross-validation, fitting each candidate model to five different slices of the data, each time leaving out one fifth of the available data to test as novel data. We continued eliminating variables until we identified the model with the lowest average root mean squared error (RMSE) across the five folds, using the Akaike Information Criterion (AIC) to help decide between models in cases of very similar RMSE values.

GAMs allow various approaches for constraining the smoothness of individual variables to prevent overfitting. We left individual smoothed variables ‘unconstrained’ for initial formulations of all saturated models. Following model selection, we tested whether assigning a ‘gamma’ value, which constrains the flexibility of the model and counteracts overfitting by placing a heavier penalty on each degree of freedom (Wood 2007, Zuur et al. 2009, Wood 2017), led to further increases in prediction accuracy (RMSE) for the best candidate model.

We used the best candidate model by species to predict the expected fork length for each observed, depredated fish head and then used published length-weight relationships to convert predicted lengths into predicted mass in kilograms (Uchiyama and Kazama 2003, Uchiyama and Boggs 2006). For mahi-mahi, we summed the predicted depredated biomass into 5º x 5º x month strata. Given uncertainty in species identity for depredated tunas, we derived predicted biomass for both bigeye tuna and yellowfin tuna for every depredated tuna and assigned the predicted probability of tuna species from Stage 1 to each tuna head. We then resampled the dataset 5,000 times, randomly selecting at each iteration a species identity for each tuna head according to the predicted probabilities from the multinomial GAM. For each iteration we summed all bigeye and yellowfin tuna predicted biomass into 5º x 5º x month strata, and then chose the median biomass across the 5,000 samples as the best estimate of that tuna species in each stratum.

3.2.2.5 Stage 3 – Predicting aggregated depredated biomass

We used GAMs to model the aggregated, predicted biomass depredated per species derived in Stages 1 and 2, using kilograms of biomass per species per 5º x 5º x month strata as the response variable. Covariates considered included the environmental variables described above, as well as year, month, and a year x month interaction term. We used the total number of observed hooks as an offset term to account for variations in sampling intensity in each strata (Zuur et al. 2009). Fully saturated models for each species were of the form:

Catch Removals (kg) ~ β_0+ s(Year, Month) + s(Year) + s(Month) + s(DEP) + s(SST) + s(SSTDEV) + s(CHLA) + s(MLD) + s(ADT) + s(TKE) + s(ONI) + s(SAL) + offset(Number of hooks)

Distributions of the response variable for each species indicated many zeros and overdispersion. We thus explored two different model formulations suited to these types of data. We first used a tweedie distribution with a log link function, which is a flexible, non-negative, continuous distribution that can accommodate large numbers of true zeros (Shono 2008, Zuur et al. 2009, Dunn and Smyth 2018). We also explored a two-stage, delta approach commonly used for zero-inflated datasets (Shono 2008, Zuur et al. 2009, Sagarese et al. 2014). This approach involves first modeling the presence/absence of depredated biomass in each stratum using a binomial error distribution with a logit link function. A separate model is then used to model the conditional presence in non-zero strata. We used a gamma distribution with a log-link for the presence-only model. Both model formulations (tweedie and delta-gamma) were carried through full model-selection and diagnosis processes. We conducted model selection as described in Stage 2, basing decisions of best models on the average RMSE on out-of-sample test data from 5-fold cross-validation. We also tested whether including a gamma term improved prediction accuracy by restricting over-fitting. The tweedie model formulations had the highest accuracy for each species and were used in subsequent prediction steps.

3.2.2.6 Predictions of depredation loss across the fishery

For each species, the best selected model was applied to the logbook data to predict depredated biomass across 5º x 5º x month strata for the entire fishery. To avoid inappropriate extrapolations to novel environmental conditions, we constrained predictions to only the range of individual environmental covariates present in the observed sets. We then summed these predictions into month and year summaries.

To identify estimates of economic losses to depredation, we extracted data from the POP auction in Honolulu, HI, where deep-set fishermen sell their catch following each trip. These data were publicly available from POP Fishing and Marine in 2019[8], although they are no longer available from this location. The data include, for every day with auctioned fish catch from 2012–2018, the number of fish sold at auction, the total weight of fish sold that day, and the average price per pound. The data are separated into ahi (bigeye and yellowfin tuna) and 'miscellaneous', which includes any other species sold at auction. We calculated the average price per pound per month for each category of fish and applied this value to the total biomass losses by month predicted by the GAM models.

3.2.2.7 Detection of depredation hotspots

We used the model predictions for bigeye tuna removals to calculate the average depredation per unit effort (DPUE) across the range of the fishery. This was done by summing the predicted biomass in kilograms and the total number of hooks fished in each stratum across all years, and then dividing the total biomass by the number of hooks for each 5º x 5º cell. We then mapped the predicted DPUE for each month to visualize depredation hotspots for bigeye tuna throughout the year across the range of the fishery.

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[8] https://pop-hawaii.com/wp/

3.3 Results

Between 2009 and 2018, a total of 182,525 sets were made on 13,465 trips by 169 unique vessels in the Hawaiʻi deep-set longline fishery. Observers were present on 20.8% of trips covering 20.4% of sets, providing a dataset of 37,185 fishing events with detailed catch and depredation data. Approximately 85 different fish species were recorded as catch, although most were rarely observed. The top 10 caught species accounted for 87% of individually captured fish, and bigeye tuna and mahi-mahi accounted for nearly half of all retained fish (Table 5). Odontocete depredation on at least one captured fish was observed on 2,394 (6.4%) of all observed sets. The number of fish depredated per set was right-skewed, with a median of two and a maximum of 63 depredated fish recorded on sets that experienced depredation. Approximately half of trips (48.4%) experienced odontocete depredation on at least one set and 22.6% experienced odontocete depredation on two or more sets. Observers recorded 9,428 individual fish with damage from odontocete depredation, or around 1% relative to the total number of individual fish landed and kept for market. Tunas were the most commonly depredated fish (70%), followed by billfish (11%), wahoo (5%), and mahi-mahi (4%) (Table 5).

Table 5: Fish species encountered in the Hawai'i deep-set tuna longline fishery. Observations are organized by species as percent of total caught and identified, percent of caught species that were landed and kept by vessels, and percent by species depredated. Note depredated species are largely lumped into taxonomic categories to account for the difficulty of identifying remains of the most frequently depredated taxa.

	Total Caught			Total kept			Total Depredated		
	Species	% of total	cum. %	Species	% of total	cum. %	Species	% of total	cum. %
1	Longnose Lancetfish	24	24	Bigeye Tuna	35	35	Unidentified Tuna	70	70
2	Bigeye Tuna	19	43	Dolphinfish	14	49	Unidentified Billfish	11	81
3	Blue Shark	8	51	Sickle Pomfret	12	62	Wahoo	5	86
4	Snake Mackerel	8	59	Skipjack Tuna	6	68	Dolphinfish	4	90
5	Dolphinfish	8	66	Yellowfin Tuna	6	74	Opah	3	93
6	Sickle Pomfret	6	73	Escolar	6	80	Unidentified Pomfret	2	96
7	Escolar	5	78	Opah	4	85	Swordfish	1	96
8	Skipjack Tuna	4	81	Wahoo	4	89	Unidentified Bony Fish	1	97
9	Yellowfin Tuna	4	85	Shortbill Spearfish	3	91	Longnose Lancetfish	1	98
10	Opah	2	87	Albacore Tuna	3	94	Escolar	1	99

The selected model for the multinomial tuna discrimination analysis included the longitude and latitude of the centroid of the fishing set; year; month; the proportion of yellowfin, skipjack, and albacore tuna; and the standardized hook distance. The variables that showed the largest influence on species-discrimination were the proportion of species and hook location (Figure 9). Higher proportions of the overall less common tuna species (i.e., YFT, SKJ, ALB) occurring on the same set were associated with a higher probability of occurrence for that species. In other words, the more individuals of a particular species that were positively identified on the same set, the more likely an unknown tuna species was also that same species (Figure 9 a-c). Standardized hook distance, as a proxy for depth, was also influential for discriminating tuna species. Yellowfin and skipjack tuna, and to a lesser extent albacore tuna, were more likely to be caught in shallower portions of the set compared to bigeye tuna (Figure 9 d-e).

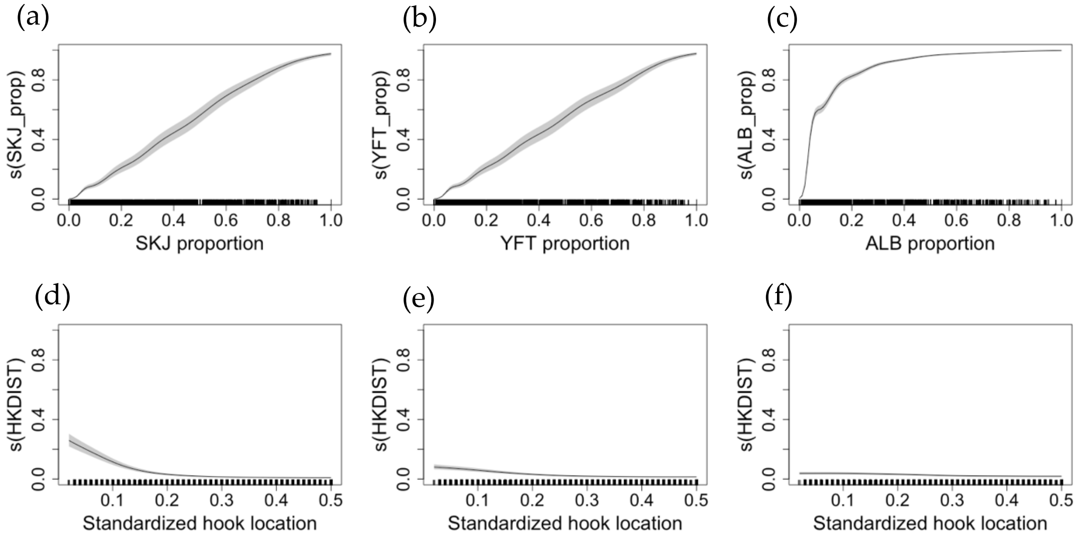


Figure 9: Statistical relationships between covariates and discrimination of three tuna species from bigeye tuna in multinomial GAM. Plots (a) and (d) represent discrimination of skipjack tuna from bigeye, (b) and (e) yellowfin from bigeye, and (c) and (f) albacore from bigeye. Y-axes are transformed to the probability scale to represent the expected probability of each species at particular covariate values. Distributions of observed values are indicated by a rug plot along each x-axis. Shading reflects 2x standard error curves.

The mean lengths of bigeye tuna, yellowfin tuna, and mahi-mahi were 111.9 cm [SD 23.1], 114.0 cm [SD 25.3], and 85.6 cm [SD 14.3], respectively. The length models that led to the best out-of-sample prediction included the interaction term between spatial location and month and the consecutive month term for each of the three focal species. The consecutive month variable indicated substantial interannual variation in predicted fish length for each species (Figure 10 a-c). The size of bigeye tuna showed a decreasing trend over the 10 years assessed, but yellowfin and mahi-mahi did not show clear long-term trends. The optimal yellowfin tuna model additionally included terms for SST and ONI, while the mahi-mahi model included SST, ONI, and MLD (Figure 10 d-h). Larger yellowfin tuna lengths were associated with more extreme ONI values, while the relationship between mahi-mahi length and ONI was less clear. Conversely, mahi-mahi showed a clear positive relationship between length and SST, while the relationship with yellowfin tuna was less clear. There was a slight unimodal relationship between mahi-mahi length and MLD, with the largest mahi-mahi associated with MLD values around 40m. For bigeye tuna, several variables that were considered significant in the GAMs ($p<0.01$) were dropped during model selection, as removing them led to increased prediction accuracy. These included ONI, SST, standardized hook distance, and the presence of marine mammal depredation on the same set.

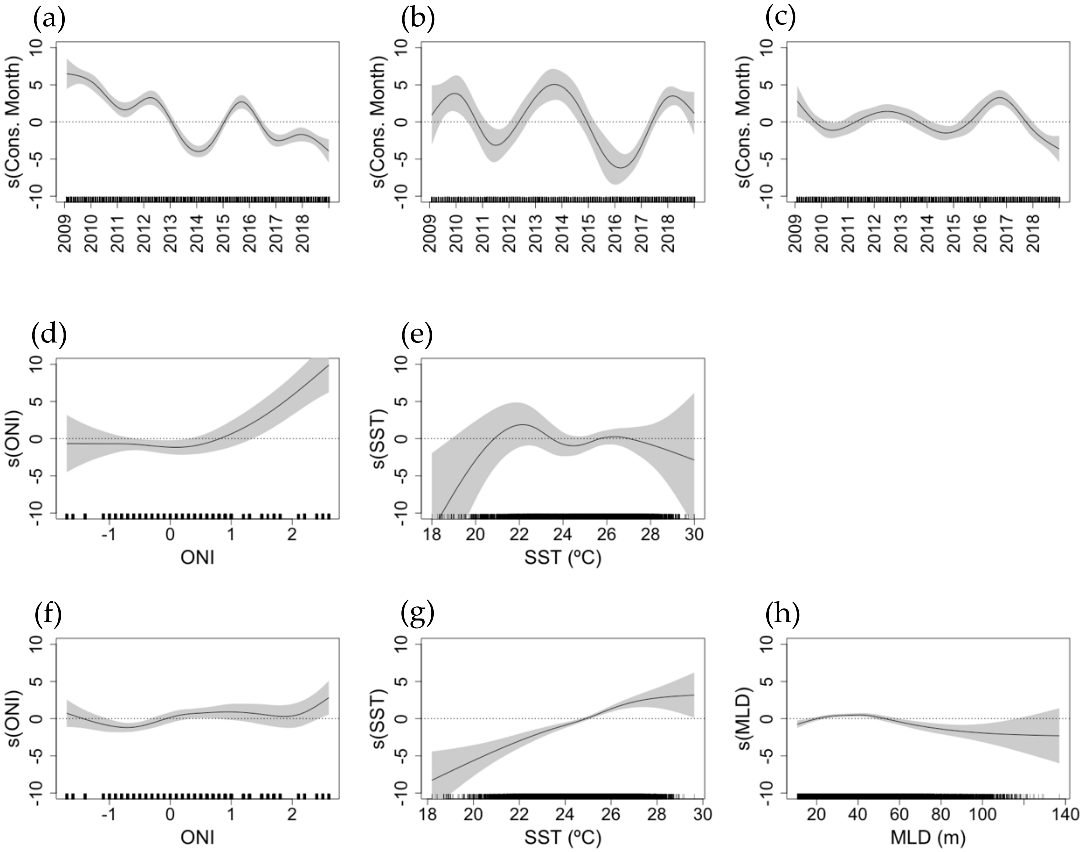
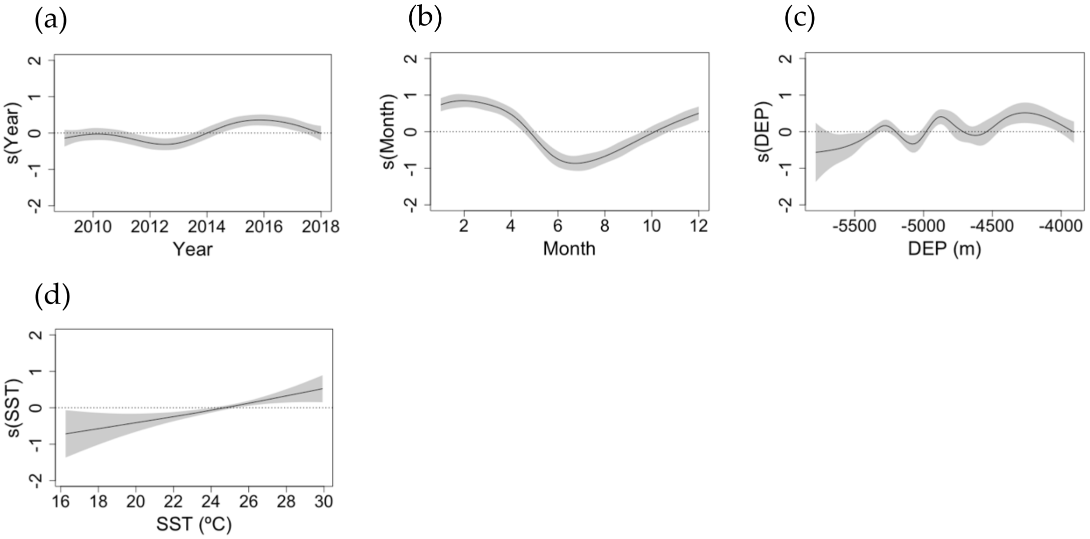


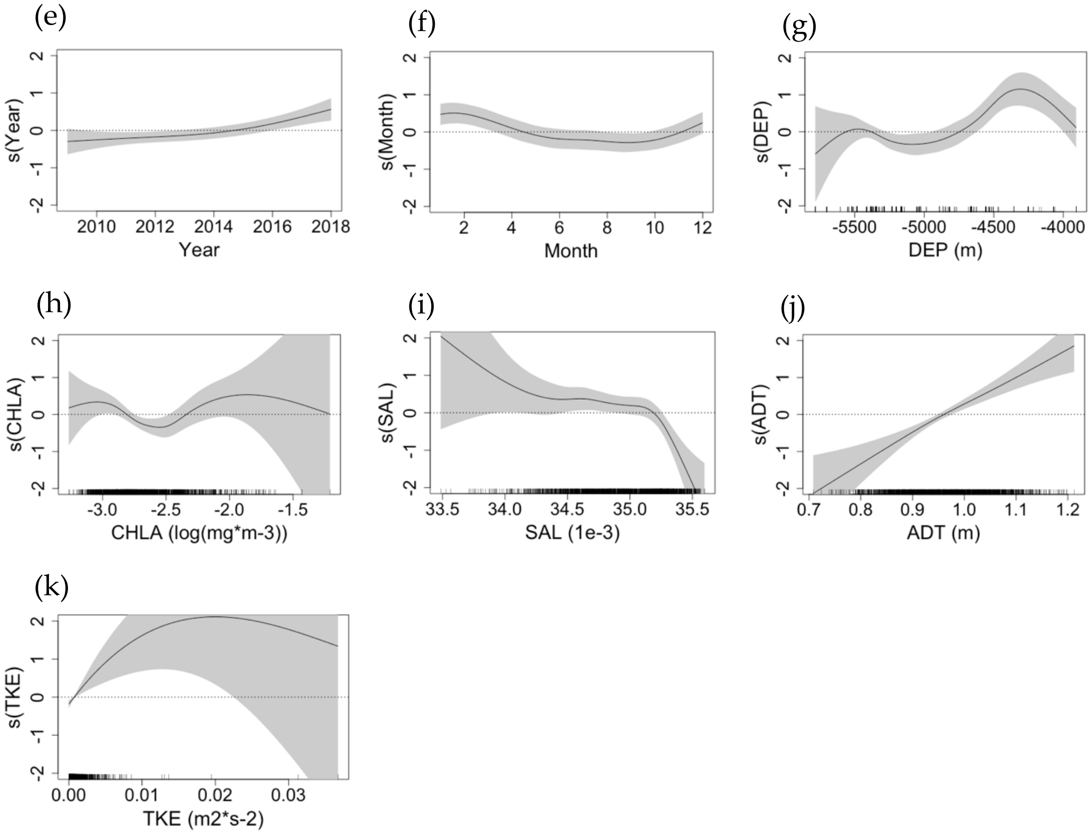
Figure 10: Statistical relationships between covariates and fork length (cm) for three target fish species. Plots (a-c) indicate the relationship between fish size and consecutive month for bigeye tuna (a), yellowfin tuna (b), and mahi-mahi (c). Plots (d-e) and (f-h) indicate additional environmental covariates included in best-fit models for yellowfin tuna and mahi-mahi, respectively. Y-axes are of the same scale to facilitate comparisons of variable importance on length for each species. Distributions of observed values are indicated by a rug plot along each x-axis. Shading reflects 2x standard error curves.

Depredation of bigeye tuna occurred in 34% of 5º x 5º x month strata for which fishing effort was observed. In strata with depredation, the mean estimated biomass of depredated bigeye tuna was 179.5 kg [SD 225.4] per cell per month. Yellowfin tuna were depredated in 13% of observed strata with a mean of 94.4 kg [SD 117.0] when present. Mahi-mahi were depredated in 11% of observed strata with mean of 9.3 kg [SD 7.1] when present. GAMs with a tweedie error distribution for the response variable and a log link had comparably higher prediction accuracy for each species than the two-step delta-gamma models. The best selected models for bigeye tuna, yellowfin tuna, and mahi-mahi had explained deviances of 18%, 32%, and 18%, respectively. All three included the single temporal covariates year and month (Figure 11), while the interaction between year and month was also included for both yellowfin tuna and mahi-mahi (not shown). All three species showed lower levels of depredation north of the equator in summer months, although this was most pronounced for bigeye tuna and mahi-mahi (Figure 11 b, f, and m). The bigeye tuna model indicated a variable and slightly positive relationship between predicted depredation and DEP and a nearly linear, positive relationship with SST (Figure 11 c-d). The yellowfin tuna model included the environmental covariates DEP, CHL, SAL, ADT, and TKE (Figure 11 g-k); and the best mahi-mahi model included ADT and MLD (Figure 11 l-o). Some of these patterns were relatively weak or showed variable and unclear relationships, while others were clearer. Yellowfin tuna and mahi-mahi depredation levels had clear positive associations with ADT (Figures 11 j and o). The significant effect between yellowfin depredation and salinity showed a mostly flat relationship with a sharp decline at high salinity levels (Figure 11 i).

Bigeye Tuna



Yellowfin tuna



Mahi-mahi

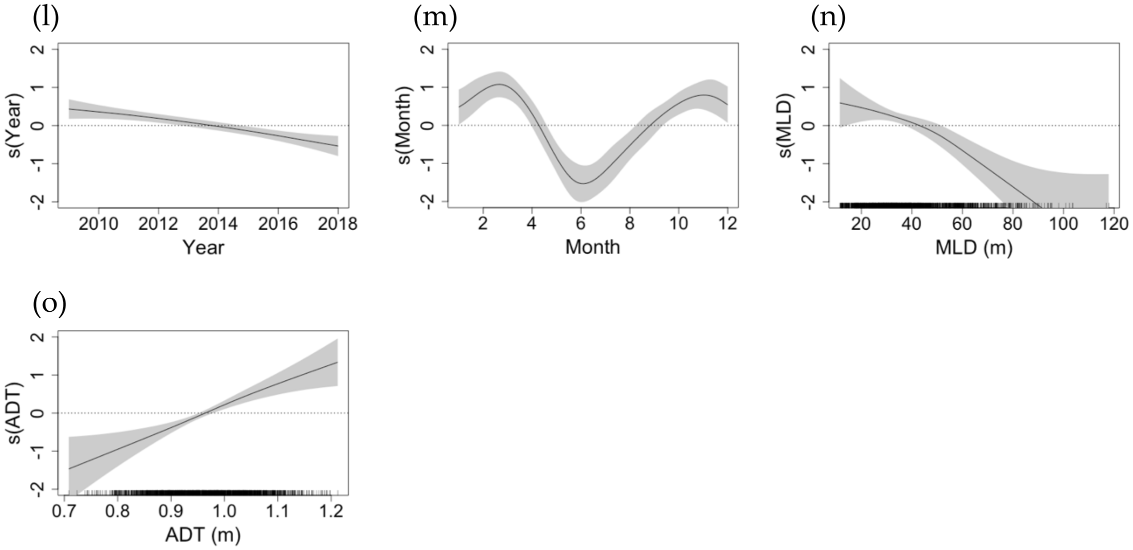


Figure 11: Statistical relationships between select covariates and predicted depredation (kg) for three target fish species. Plots (a-d) indicate the relationship between predicted bigeye tuna catch removals, plots (e-k) show relationships for yellowfin tuna, and plots (l-o) for mahi-mahi. Y-axes are of the same scale to facilitate comparisons of variable importance on length for each species. Distributions of observed values are indicated by a rug plot along each x-axis. Shading reflects 2x standard error curves.

We applied the best selected models for each species to equivalent hook and environmental data derived from the logbooks (i.e., all deep-set fishing effort) to predict depredated biomass for each species in each 5º x 5º x month strata. We then summed the predicted depredated mass for each species to explore monthly and yearly patterns (Figure 12a). We then applied monthly averages of auction prices for landed fish to estimate the economic costs associated with depredation on each species (Figure 12c). The predicted total depredated biomass of bigeye tuna, yellowfin tuna, and mahi-mahi from 2009-2018 was 781.8 t [95% CI 523.4–1040.3], 157.5 t [57.8–257.5], and 12.9 t [6.5–19.2] respectively, with annual means of 78.2 t [52.3–104.0], 15.8 t [5.8–25.7], and 1.3 t

[0.7–1.9], or 95.2 t [58.8–131.7] in aggregate. The average annual estimated cost across all three species from 2012-2018 was $1,117,000 USD [$694,000–$1,541,000]. On a finer scale, the median predicted catch removal for ahi tuna on sets that experienced odontocete depredation was 55.2 kg [52.0–57.9], corresponding to a median cost of $579 USD [$549–$614]. The median ahi catch removal on trips that experienced depredation at least once was 88.0 kg [83.7–92.9 kg] corresponding to $921 USD [$871–$971].

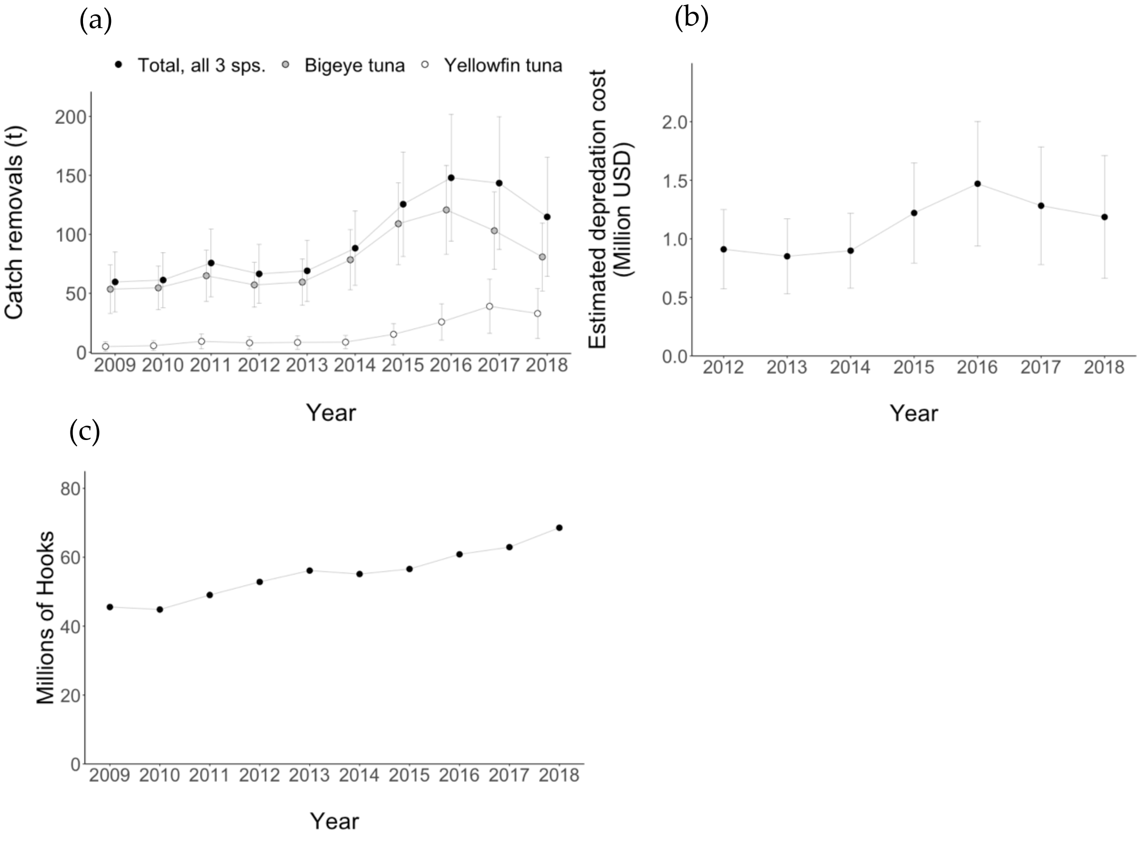


Figure 12: Predicted annual biomass lost by species (a) and total economic costs (b) resulting from catch removals by odontocetes in the deep-set fishery. Error bars indicate 95% confidence intervals. Also displayed is the total number of hooks set annually across the entire deep-set longline fishery (c).

Predicted catch removal rate or DPUE (kg depredated fish / fishing effort) for bigeye tuna was averaged across years and mapped for each 5º x 5º x month strata to visualize relative depredation rates over the year (Figure 13). Predicted bigeye tuna depredation rates were highest in the first and last quarters (November – April) and in the southwestern regions of the fishery. Depredation rates were lowest in the summer months (June – August).

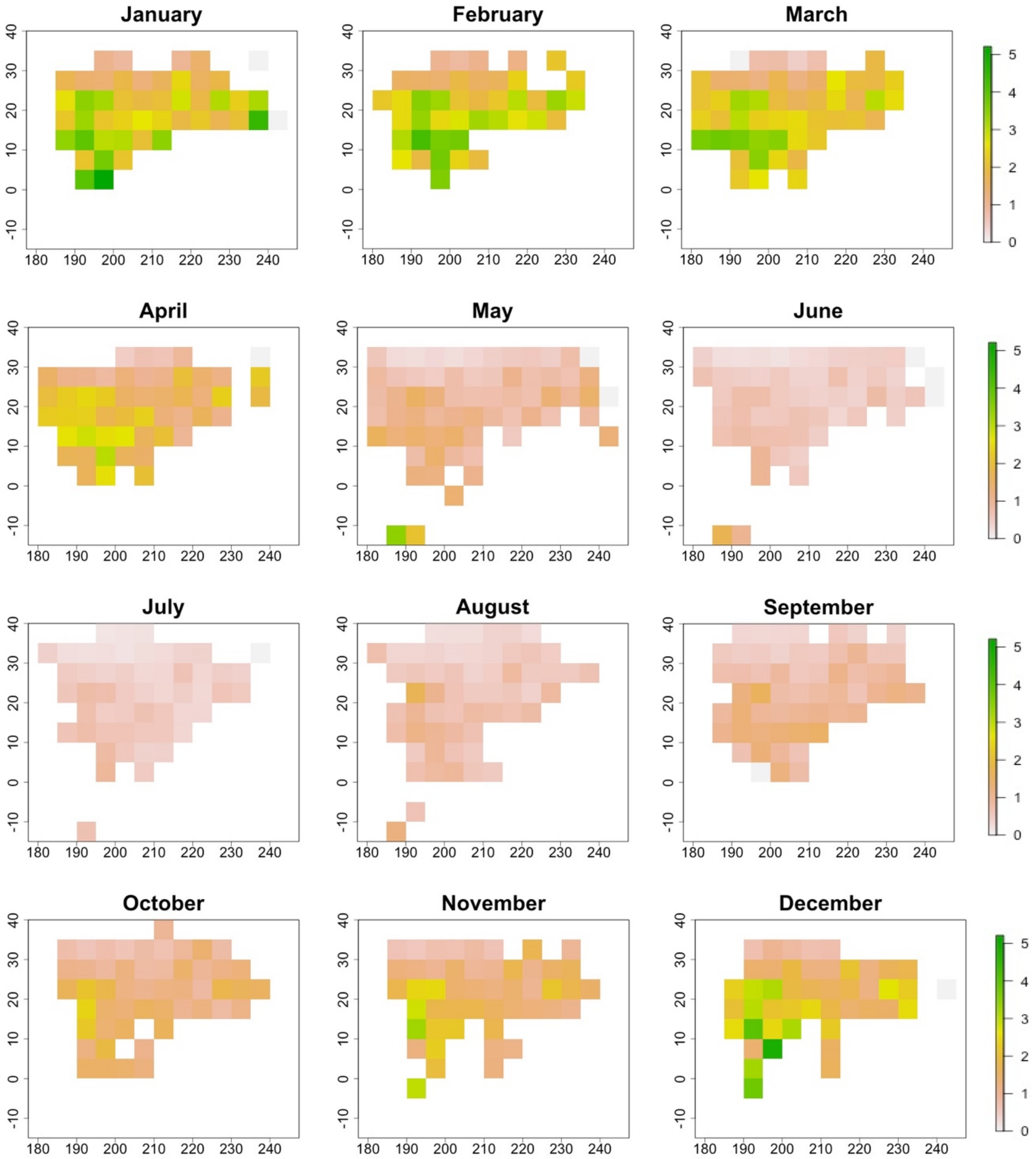


Figure 13: Predicted bigeye tuna depredation rates (kg bigeye tuna removed / 1000 hooks set) averaged across the 10 study years (2009-2018). The scale is the same for each figure, with the darkest green color corresponding to the highest observed depredation rate across all months (5.21 kg / 1000 hooks).

3.4 Discussion

We used a multi-stage, tiered modeling approach to derive quantitative estimates of catch losses by depredating odontocetes in the Hawai‘i deep-set longline tuna fishery. Depredation is relatively rare and variable on a per set basis, but lost catch and economic costs can be substantial when they do occur. Similarly, the intensity of depredation varies in time and space, but exceeded 100 t and one million USD in estimated costs to the fleet in each of the last four study years (2015-18). These values may be underestimates also, as fish entirely removed by the whales cannot be counted and we do not have a good estimate of the rate at which entire fish are lost or consumed. These findings demonstrate the broad-scale significance of odontocete depredation in this fishery and help quantify the ecological and economic implications of this interaction.

3.4.1 Depredation patterns

The estimated rates of occurrence of depredation on a per-set and per-trip level in this study are consistent with previous assessments of this fishery (Forney et al. 2011, Fader et al. 2021). Forney reported a nearly identical set-level depredation rate of 6% extending back to 2003. Summaries of catch rates by species, including depredated fish, have also been reported for this fishery and are largely consistent with the present study (Oleson et al. 2010, Fader et al. 2021). As shown here, tuna are consistently observed as the most frequently depredated species, but odontocetes consume a range of commonly caught species including mahi-mahi, wahoo, and billfishes. Most species were depredated at rates that were proportional to their composition of total catch, although some were depredated infrequently relative to their overall catch rates. For example, sharks, although a common non-target catch in this fishery, are virtually never depredated. Depredation on the longnose lancetfish (*Alepisaurus ferox*) was also rare, even though it was the most commonly caught species. This may be, at least in part, due to the gelatinous nature of their flesh, which makes it difficult for observers to categorize the source of damage for this discard species.

Most observed, depredated fish were either target species or non-target species commonly retained for sale (Table 5). However, to date there have been no detailed efforts to quantify the aggregate losses to depredation in this fishery. TEC 2009 reported estimates of fish biomass lost and economic implications due to odontocete depredation, but these estimates were based on estimates provided by fishermen of the proportion of total catch lost per depredated set. The present study utilizes a rich dataset that includes unbiased observations of catch and the occurrence of depredation. We built on observations of depredated fish to derive minimum estimates of catch removals by odontocetes. We also took advantage of the fact that there is a single auction in which the vast majority of Hawaiʻi deep-set fish are sold, allowing me to estimate the price fishermen could have expected to receive had they landed and sold depredated fish.

Despite the detailed observations of depredation described here, there were notable challenges in scaling up from observed fish remains to biomass estimates from the observer -collected data set. Odontocetes typically depredate the entire body of the fish, leaving behind only the jaws and gills. Some species, such as mahi-mahi, are still relatively identifiable when depredated. Tuna are more challenging, as several species are regularly caught and cannot be reliably distinguished by the head alone. We used multinomial GAMs to account for uncertainty in tuna species identification when aggregating predicted catch removals by species. The models provided strong out-of-sample classification accuracy on known tuna species, with the strongest predictors based on the proportion of species for positively identified, non-depredated fish as well as the relative depth on the set. Of note, bigeye tuna is more commonly caught on deeper gear than the next two most common tuna species, yellowfin, and skipjack. By utilizing this approach, we identified the most likely species to occur based on general catch trends and known operational characteristics, while incorporating the uncertainty in positive species identification.

An additional layer of complexity is that observers do not collect morphometric measurements that could be used to estimate the size of depredated fish. Bigeye tuna caught in this fishery range from 27 cm to 205 cm, and there is considerable variation in the size of captured fish seasonally, interannually, and geographically (Woodworth-Jefcoats and Wren 2020). Thus, simply applying an average mass for each species may be inappropriate as the true value varies greatly depending on where and when the vessel caught a particular fish. Since 2009, observers have systematically recorded the length of every third landed fish, providing a robust dataset of fish lengths for undamaged fish caught concurrently or in similar environmental conditions. We used this dataset to develop models predicting fish length for each focal species based on spatial, temporal, operational, and environmental covariates. Space and time covariates were consistently important in models for each species, indicating a likely cohort and recruitment structure, as has been observed in other studies in the region (Woodworth-Jefcoats and Wren 2020).

Our approach assumes that depredated fish are otherwise equivalent to non-depredated, measured fish, such that all fish are equally likely to be selected by a depredator species. It is possible that predators could preferentially select either smaller or larger fish, for example due to easier handling (smaller) or increased likelihood of detection and/or larger reward of capture (larger). Either scenario would bias estimates of fish length for unmeasured depredated fish. To better understand this possibility, we incorporated a categorical variable in the starting models for fish length indicating whether odontocete depredation occurred on the same set. This variable was not included in the best-predicting model for any of the three species, although it was marginally significant and one of the last variables to be removed from the bigeye tuna models during model selection. The direction of the effect suggested that non-depredated, measured bigeye tuna were slightly larger on sets where depredation did not occur. There are at least two mechanisms that could explain this pattern. It is possible that depredation occurs more commonly on sets where the fishery catches smaller tuna on average. This could be driven by space and time patterns of fishery effort and depredation occurrence, for example if fish were larger in northern areas where the fishery experiences lower depredation rates (Forney et al. 2011, Fader et al. 2021). The space, time, and/or environmental covariates would likely account for this pattern however, rather than a categorical predictor of depredation. An alternative explanation is that depredators are more likely to consume larger fish when they encounter a set, and thus any remaining, non-depredated fish on that set, which are the only ones available to be measured, are actually smaller than would otherwise be expected. False killer whales are known to attack and consume large, pelagic fish such as tunas, mahi-mahi, swordfish, and billfish in the wild (Baird et al. 2008, Baird 2009). There is little reason to suspect that this large predator would preferentially select smaller fish, and indeed, consuming hooked and restrained fish may allow them to consume even larger fish than they could capture if the prey was free-swimming. This hypothesis also aligns with reports by fishermen suggesting that whales prefer to depredate large ahi tuna (TEC 2009). Thus, this pattern may suggest a slight underestimate of depredated fish length and negatively bias the aggregated estimates of depredated biomass. Any effect is likely to be very small regardless, as the statistical effect of larger fish on non-depredated sets was approximately a one-centimeter difference.

The final step to estimate levels and patterns of depredation across the fishery was to scale estimates of catch removal from the observed dataset, representing approximately 20% of total deep-set effort, to the entire fleet. We utilized a catch standardization approach, commonly used in stock assessment analyses to estimate relative abundances from CPUE data (e.g., Shono 2008, Tascheri et al. 2010, Mateo and Hanselman 2014). This approach models CPUE relative to covariates, and then predicts abundance, or in this case, biomass of depredated fish, in areas with only effort and covariate data. To better detect and account for broad-scale patterns of depredation, and because depredation is relatively rare on a per-set basis, we aggregated observed depredation and environmental covariates into 5º x 5º x month strata. This still resulted in a high number of zero observations, and thus we explored several methods to account for zero-catch data.

Tweedie distributions in a GAM framework provided the best predictions, fit to model assumptions, and amount of deviance explained and were used to extrapolate depredation rates into all fished strata, including those without detailed observer data. This allowed estimates of catch removals for focal species across the fishery, as well as identification of potential hotspots of higher depredation risk. Several environmental covariates were influential in predictions for each species. Bigeye tuna catch removals increased with increasing SST, which is consistent with anecdotal reports of fishermen suggesting that depredation is less likely in waters cooler than 67-68ºF (~19–20ºC) (TEC 2009). Depredation intensity was positively associated with ADT for both yellowfin tuna and mahi-mahi, which is consistent with observations in Fader et al. (2021) that the probability of depredation is lower when fishing in waters with lower ADT values.

Predicted depredation intensity for bigeye tuna, aggregated by month across the 10 years of the study, indicated the highest rates of total bigeye catch removals from odontocete depredation in the first and last quarters of the year. There were also apparent spatial hotspots in the southwest and, to a lesser extent, the northeastern areas of the fishery, while depredation rates were low in the northernmost parts of the fishery in all months. These patterns are consistent with previous quantitative assessments, which have indicated relatively lower depredation rates north of the equator in summer months when the fleet fishes farther to the north (Forney et al. 2011, Fader et al. 2021), as well as anecdotal information from fishermen who have reported potential depredation hotspots in the south and southwest portions of the fishery (TEC 2009).

3.4.2 Catch removals and implications

The present study suggests that depredation is relatively rare on a per-set basis, but when it occurs, it can result in high rates of lost catch on individual fishing sets or trips. The median estimated cost, when depredation occurs on a set, was just under $600 USD, although the worst 10% of depredated sets experienced estimated losses of more than $2,300 USD. The worst 10% of depredated trips exceeded $3,500 in estimated losses. Due to the long durations and great distances traveled to reach fishing grounds, costs are already high in the Hawaiʻi longline fishery, regularly exceeding $30,000 per trip (Chan and Pan 2021). The prospect of losing several thousands of dollars in a single day of fishing is thus understandably a significant concern for longline fishermen. These estimates also do not account for additional costs of depredation that are difficult or impossible to quantify, such as bait lost to depredating whales or wasted on depredated fish. There are also opportunity costs such as lost gear, crew and vessel time, and costs likely incurred to make up for lost catch, as suggested in other fisheries subject to odontocete depredation (Gilman et al. 2007, Peterson et al. 2014, Tixier et al. 2020a).

When considered in aggregate, total losses to depredation by odontocetes are economically and ecologically meaningful. We estimate that between 100-150 t and over one million USD in losses of the three focal species were incurred in each of the last four years of the study period, mostly due to depredation on bigeye tuna. The Hawaiʻi longline fishery operates on regional catch limits for bigeye tuna set by two Regional Fisheries Management Organizations (RFMOs): the Inter-American Tropical Tuna Commission (IATTC) in the Eastern Pacific Ocean and the Western and Central Pacific Fisheries Commission (WCPFC). The fishery experienced partial closures in each of the 10 study years by reaching catch limits (Ayers et al. 2018). If catch removals from depredation were included in stock assessments, these limits would be reached more quickly, and the additional effort to account for depredated catch removals may indirectly increase fishing pressure on target stocks. The total annual loss of 100-150 t may seem relatively small on an ocean-basin scale in which 72,391 t of bigeye tuna was caught by longlines in 2019 in the WCPFC area alone, but the Hawaiʻi fishery accounts for only 5% of total landed bigeye in the Central Pacific Ocean (WCPFC 2019). If this analysis was extended to all fishing effort managed by these two RFMOs, the scale of catch losses caused by odontocete depredation is likely sufficiently large to warrant inclusion in stock assessments.

Finally, we documented an increase in catch removals and associated economic losses over the study period. Much of this increase is undoubtedly due to the increase in fishing effort observed in the fishery (Figure 12c). The peak in 2016-2017 is not entirely explained by aggregate fishing effort, however, and corresponds to an evident increase in depredation rates for bigeye tuna (Figure 12a). Interestingly, yellowfin tuna and mahi-mahi depredation rates show distinct patterns over the decade, with a small increase in yellowfin since 2016 and a general decline in the depredation rate for mahi-mahi. wet is unclear whether these patterns were driven by changes in distributions or behaviors of target species, odontocetes, the fishery itself, or some combination of these factors.

3.4.3 Conclusions

This study uses a novel approach for estimating catch removals from odontocete depredation in longline fisheries and identifying hotspots of depredation activity. The estimates of loss derived here can help fishery managers and fishermen to better understand the economic and ecological consequences of depredation and inform mitigation strategies by helping to understand drivers and predictors of depredation patterns at large spatial and temporal scales. Such information is important for improving ecosystem-based fisheries management and refining stock assessments to account for mortality of target species caused from depredation. This approach also demonstrates the importance of detailed observer data to document and contextualize patterns of relatively rare, but important, events such as depredation and bycatch.

4. Behavioral patterns of pilot whales near longline fishing vessels

4.1 Introduction

Direct interactions with fishing gear are a major conservation threat to marine mammal populations worldwide (Mitchell 1975, Read 2008, Brownell Jr. et al. 2019). Such interactions can be the result of passive entanglement or purposeful entrapment in gear, but bycatch of odontocetes, or toothed whales, may also be driven by whales feeding directly on bait or catch secured on fishing gear (Gilman et al. 2007, Read 2008, Hamer et al. 2012). This behavior, known as depredation, is particularly common and costly in longline fisheries, where bait and catch are typically unprotected prior to gear retrieval (Read 2008, Hamer et al. 2012). Bycatch of depredating whales can occur when animals become hooked or entangled in the gear itself.

Pelagic longline gear is suspended in the water column and targets fish at depths from tens to hundreds of meters, with gear extending horizontally over tens of kilometers in a single fishing event (Watson and Kerstetter 2006, Ward and Hindmarsh 2007). Thus, depredation events in pelagic longline fisheries are difficult to characterize, because the behavior may occur at depth or at some distance from the fishing vessel. Evidence of depredation may consist only of the absence of bait or heads of target fish remaining on retrieved hooks, because odontocetes have sequentially removed most or all baits (Thode et al. 2016, Bayless et al. 2017) or eaten the bodies of captured fish (e.g., Secchi and Vaske 1998). Observations of bycatch are also rare and depend on on-board observers to carefully report details of the interactions; events often occur so quickly that even the species of whale may be difficult to ascertain (Forney et al. 2011, Baird 2019).

Advances in satellite telemetry have provided important insights into the behavior of odontocetes around longline gear and, in some cases, into depredation events themselves. Such observations can provide insight into the spatial scales of interactions and the nature of whale behavior near fishing gear. For example, Anderson et al. (2020) observed satellite-tagged false killer whales (*Pseudorca crassidens*) orienting their movements towards pelagic longline gear most frequently during hauls, although they did not do so every time they were within detection range of the gear. Satellite-tagged killer whales (*Orcinus orca*) displayed attraction to Norwegian herring purse seine vessels at distances of up to 20 km (Mul et al. 2020), and a satellite-tagged killer whale and sperm whale (*Physeter macrocephalus*) followed a demersal longline vessel in the Southern Ocean for 302 km and 182 km, respectively (Towers et al. 2019). These insights can help provide behavioral context for interactions between fisheries and odontocetes and provide the basis for development of potential mitigation strategies.

The northeast continental shelf ecosystem off the East Coast of the United States is an important foraging ground and habitat for many cetaceans as well as key fishing grounds for commercial and recreational fisheries (Kenney et al. 1997, Thorne et al. 2017, Stepanuk et al. 2018). The U.S. large pelagics longline fishery targets pelagic swordfish, tunas, and sharks in this area, and both long-finned (*Globicephala melas*) and short-finned

(*Globicephala macrorhynchus*) pilot whales depredate bait and catch and become hooked or entangled in gear as a result (Garrison 2007). Short-finned pilot whales, in particular, inhabit the same shelf-break and canyon habitats that are heavily used by the pelagic longline fleet in the Mid-Atlantic Bight (MAB) area (Garrison 2007, Thorne et al. 2017, Stepanuk et al. 2018, Thorne et al. 2019).

Short-finned pilot whales are deep-diving odontocetes that forage on deep-water squid and fish in this area (Mintzer et al. 2008, Quick et al. 2017). Depredation on bait and target catch may reduce the energetic costs of foraging for pilot whales, but this behavior also increases the risk of serious injury or mortality through hooking or entanglement in fishing gear. Bycatch of short-finned pilot whales exceeded statutory limits in this fishery during eight of ten years from 2010-2018 (Fader et al. 2021b). As a result, a Take Reduction Team, mandated by the U.S. Marine Mammal Protection Act, implemented a number of mitigation measures intended to reduce the mortality of pilot whales in this fishery, including restrictions on the length of mainlines and training in safe handling and release of marine mammals (74 FR 23349) (Federal Register 2009). Despite these measures, depredation and bycatch of pilot whales continues to be a problem in this fishery, perhaps because the incentive to fish in prime pilot whale habitat, or the incentive for whales to depredate bait and catch is so strong.

Recent studies combining satellite telemetry of pilot whales and fishery-dependent data characterized the spatiotemporal overlap of whales and fishing vessels

(Thorne et al. 2017, Stepanuk et al. 2018, Thorne et al. 2019). These studies suggested that, at broad scales, pilot whales forage in the same areas targeted by the fishery, along the shelf break and in deep water canyons. The fine-scale behavior of individual whales near fishing gear is less-well understood but such information could help inform potential mitigation strategies such as move-on rules (Dunn et al. 2014, Werner et al. 2015). Here we use hidden Markov models (HMMs) to analyze a rich dataset of movements of satellite-tagged pilot whales in relation to the distribution of pelagic longline fishing activities. We first characterize the typical movement behavior of tagged whales and then explore whether whales react to or change their behavior near fishing gear. Our work is designed to inform conservation strategies to reduce the frequency and severity of such interactions.

4.2 Methods

4.2.1 Satellite telemetry

We deployed 19 Wildlife Computers SPLASH10 satellite-linked time-depth recording (SLTDR) tags in the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al. 2008) on short-finned pilot whales off Cape Hatteras in 2014-2017. Tags were deployed from a 9.1 m rigid-hulled boat using a pneumatic projector and secured to the dorsal fin or base of the dorsal fin with two titanium darts with backward facing petals. SPLASH10 tags deployed in 2014-2016 were programmed to transmit position data and compressed depth data through the Argos system for 10-17 hours/day for 20 days and were then duty-cycled to transmit on intervals of every three or five days. SPLASH10 tags deployed in 2017 were programmed to transmit for 17 hours per day and were not duty cycled. We restricted our analyses to full days of transmission before duty-cycling began. We also truncated the data record from one additional whale (GmTag182) because it was part of a controlled exposure experiment on September 12, 2017, in which the animal was exposed to mid-frequency active (MFA) sonar signals. All other tagged whales were greater than 300 km from the source of the signals at this time and thus their behavior was unlikely to have been affected by the sonar signals.

Argos SLTDR tags are prone to gaps in diving records due to data transmission limitations and the behavior of deep-diving animals (Quick et al. 2019) (Figure 14). We discarded data from any tags that had both more than three percent of the total records missing and if any single gap was greater than four hours. In a few cases, multiple whales were tagged in the same social group or on the same or subsequent days and some of these whales showed similar behavior over the course of their tracks. To avoid pseudoreplication, we removed duplicative tag records from either the animal with the shortest track or the track with the longest duration of diving gaps in the diving record. Ultimately, we removed five tags due to gaps in dive records and three tags due to pseudoreplication, leaving 11 tag records on which we focused subsequent analyses (Table 6).

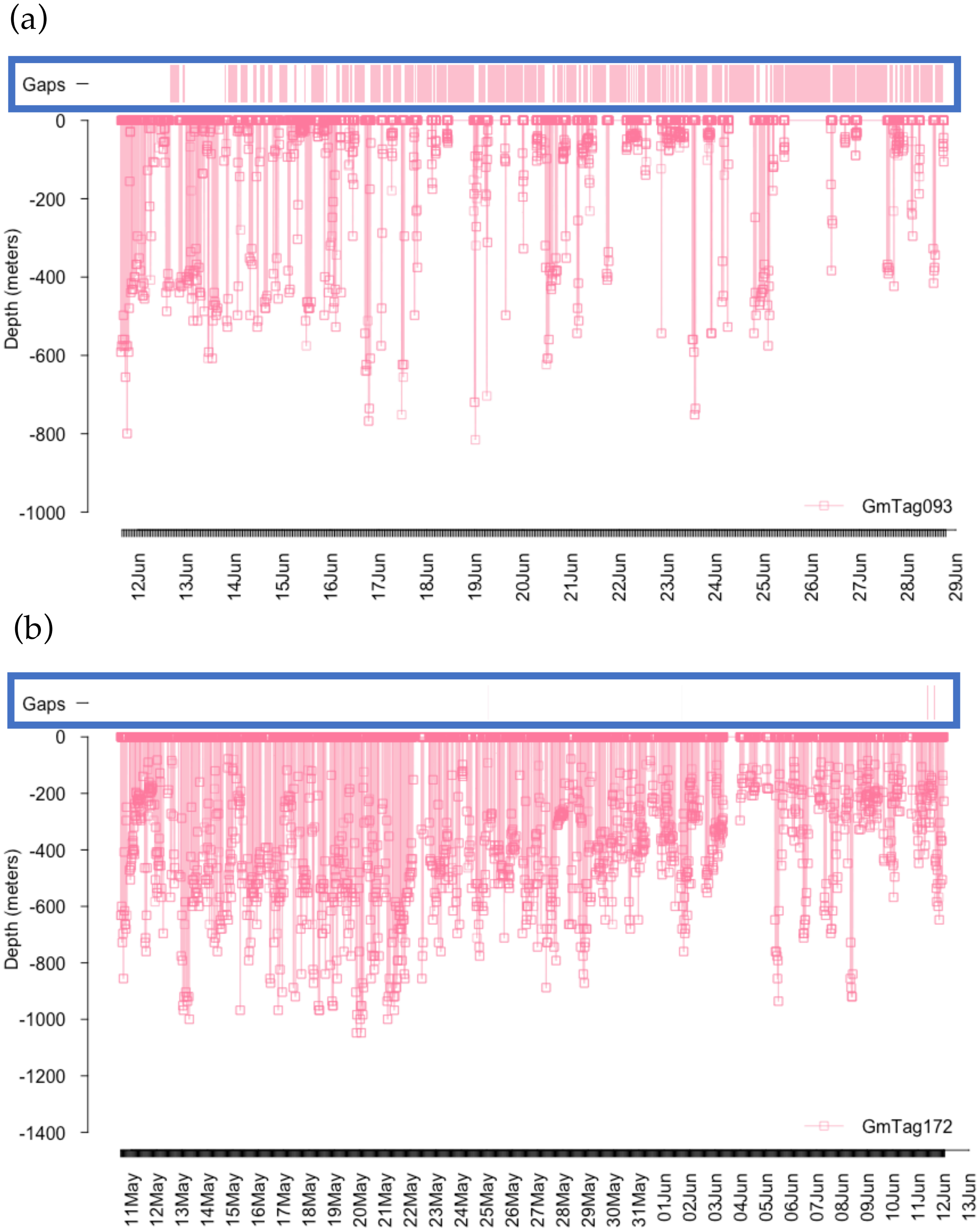


Figure 14: Two example tags, one with many gaps in the dive record (a) and one with very few gaps (b). Gaps are defined as any break in the dive record longer than two minutes.

4.2.2 Data processing

Estimates of animal locations were obtained through Service Argos using the Kalman algorithm and processed through the Douglas Argos-Filter (Douglas et al. 2012). All location class 'Z' positions and unreasonable positions based on the maximum rate of animal movement were discarded (Douglas et al. 2012; maximum rate of movements = 18 km h–1, maximum redundant distance = 5 km). The resulting filtered Argos data were then fitted to a continuous-time correlated random walk (CRW) model using the momentuHMM package, version 1.5.1 (McClintock and Michelot 2020), which uses a wrapper function to implement the Crawl package. The CRW model is a continuous-time model that accounts for the irregular time intervals between positions available from Service Argos. It estimates true locations while accounting for error in the Argos telemetry data and regularizing the output to consistent, specified time intervals. We used a three-hour time interval which we determined suitable based on an average lag between observed Argos locations of 93 minutes and an average number of 15 positions per day (Table 6).

Tags deployed in 2014-2015 were programmed to record all dives exceeding 20 (2014) or 30 m (2015) and 30 seconds. To minimize gaps in time series of deep diving data, 2017 tags were programmed to only record dives exceeding 75 m and 30 seconds. We standardized tags across all years by removing any recorded dives shallower than 75 m from all tags, counting these events as part of surface behavior in subsequent analyses. To associate diving behavior with the location information, which occurs at much coarser temporal resolution than individual dives, various summaries dive data were associated with each regularized three-hour time interval in the CRW locations. Specifically, we calculated the number of dives observed exceeding particular maximum depth thresholds (200 m, 400 m, and 600 m), as well as the total duration of time spent on dives that exceeded these thresholds, within a three-hour window of the predicted location.

Table 6: Summary of raw short-finned pilot whale SLTDR data considered for analysis.

Animal ID	Deployment Date	Pre-duty cycle duration (days)	No. of Locations	Avg. Locations d-1	Included in HMM analysis (Y/N)*
GmTag085	5/14/14	13.3	240	17.1	Y
GmTag093	6/11/14	19.0	311	16.4	N (gaps)
GmTag098	9/11/14	19.1	284	14.9	N (PR)
GmTag100	9/11/14	19.0	308	16.2	Y
GmTag123	5/16/15	13.9	225	16.1	N (gaps)
GmTag127	5/19/15	19.1	352	18.5	Y
GmTag135	10/15/15	19.1	331	17.4	Y
GmTag138	10/20/15	19.0	355	18.7	N (gaps)
GmTag172	5/10/17	32.8	512	15.1	Y
GmTag173	5/11/17	23.8	346	14.4	Y
GmTag174	5/11/17	31.4	492	15.4	Y
GmTag175	5/16/17	25.6	316	12.2	Y
GmTag176	5/16/17	11.8	163	13.6	N (PR)
GmTag177	5/17/17	28.3	444	15.3	N (gaps)
GmTag178	5/17/17	18.7	283	14.9	N (PR)
GmTag180	5/17/17	19.4	291	14.6	Y

GmTag181	8/20/17	30.9	444	13.9	Y
GmTag182	8/20/17	29.5	259	10.8	Y
GmTag183	8/20/17	32.2	474	14.4	N (gaps)
All tags		425.9	6,430	15.1	
Tags included in HMM		263.9	3,891	14.8	11

* 'gaps' were tags removed because of substantial gaps in diving data, 'PR' indicates tags remove because of concerns with pseudoreplication.

4.2.3 Pelagic longline fishery data

Pelagic longline captains are required to submit logbooks to the National Marine Fisheries Service (NMFS) recording the times and GPS coordinates of the start of each set of gear, the number of hooks deployed, and counts of captured fish by species. When requested by NMFS, vessels are also required to carry a federal fisheries observer, with a fleet-wide target coverage of 12-15% of trips per year (74 FR 23349) (Federal Register 2009). Observers collect detailed data on fishing operations, gear characteristics, and biological data from both target and non-target catch. To explore overlap with tagged whales and potential fishery-whale interactions, we obtained anonymized vessel logbook and observer-collected data for pelagic longline vessels fishing from 2014-2017 in the Mid-Atlantic Bight (MAB), South Atlantic Bight, Northeast Coastal, Florida East Coast, and Sargasso Sea fishing areas.

We used logbook data in the main analyses because this data set includes all fishing events. We utilized observer data for exploratory analyses and to summarize operational characteristics of fishing activity in more detail. Pelagic longlines can be tens of kilometers long and fishing events may exceed 24 hours from the beginning of setting gear until the last piece of gear is retrieved. The starting time and location of a fishing event is thus only an approximate representation of fishing activity. To better understand the spatial scale or footprint of a single fishing event, we calculated the maximum spread of the fishing gear for each observed set (i.e., the maximum Euclidean distance across all locations recorded by an observer for a single set). To assess whale behavior near fishing activity and best account for the full duration of a potential fishing event, we identified the distance and angle of each whale estimated position to the nearest fishing vessel within three hours before the start of fishing to 21 hours following the start of fishing. This accounts for the three-hour step-length of the estimated whale tracks and the potential for vessel movement to influence whale behavior before gear is placed in the water. We selected 21 hours following the beginning of the set as this captures the duration of fishing for most (75%) fishing events recorded by observers.

4.2.4 Whale behavior

We assessed whale behavior using hidden Markov models (HMMs), which are discrete, state space models that use unsupervised classification to infer unknown or hidden state sequences, such as behavioral patterns, from observed, state-dependent processes (McClintock et al. 2020). As we did not know *a priori* what effects, if any, fishing vessels may have on whale behavior, we conducted the analysis in two stages. We first modeled whale behavior without including information on nearby fishing activity to determine baseline behavioral patterns. We did this in two steps, first by modeling predicted whale locations and summary dive behavior in three-hour time steps. As a great deal of resolution in the dive time series is lost by summarizing over multiple hours, we also built a second model considering only the time series of dive data, thus ignoring location but accounting for every dive over 75 m for the entire tag record.

Following exploration of baseline pilot whale behavior, we incorporated additional data streams and covariates associated with nearby fishing activity, to test several hypotheses for how the presence of fishing activity might influence whale behavior. Specifically, we explored whether whales biased movement towards (i.e., were attracted to) the locations of fishing vessels, whether the presence of fishing vessels influenced the movement parameters of tagged whales (i.e., step length, angle of movement, and dive behavior), and whether the vessel distance influenced the transition probability between states.

We built models iteratively for each stage, starting with simple formulations of models and adding complexity to identify the best fitting models in each case, using Akaike's Information Criterion (AIC), examination of pseudo-residual plots, and assessment of parameter estimates to decide between competing models. Each candidate model included "data streams," or observed time-series of behavior, which were each modeled using an appropriate distribution. Covariates were then added to models to allow the potential influence of covariates on transition probabilities between identified states, the distribution parameters describing different data streams, or both. For the best supported models, we used the Viterbi algorithm (Forney 1973) to identify the most likely sequence of states based on the estimated state-dependent distributions for observed data streams and the transition probabilities between states. We fitted the models using maximum likelihood methods in the R package momentuHMM, version 1.5.1 (McClintock and Michelot 2020).

4.2.4.1 Stage one (no fishing activity)

In the location-based model in the first stage, we included step length, turning angle, and the number of dives as observed data streams, modeled as gamma, wrapped-Cauchy, and Poisson distributions, respectively. We first tested whether two-states (travel and area-restricted search (ARS)) or three-states (travel, ARS, and rest) provided a better fit to the data. In each case we constrained the traveling state to have longer step lengths and greater angle concentration of movement relative to ARS (2-state version) or resting behavior (3-state version). And, in each case, we explored whether including the number of dives exceeding 200 m, 400 m, or 600 m as the dive data stream led to the best model fit and discrimination of behavioral states. Model formulations with different dive formulations cannot be compared by AIC as the underlying data differs, thus we could only assess pseudo-residual plots and parameter estimates to make comparisons between models with different summary dive data metrics. We also used the cosinor function in MomentuHMM to incorporate a 24-hour, cyclical pattern as a covariate on dive behavior.

We approached the dive-only model in a similar way, testing two- and three-state models and building on complexity iteratively. We did not consider more than three states, because previous studies on the same population of pilot whales, using high-resolution, but short duration, digital acoustic recording tags (DTAGs), identified a four-state model as the best descriptor of behavior (Quick et al. 2017). Quick et al. (2017) included dives starting at 20 m and their shallowest state included dives occurring nearly exclusively below 75 m. As the dive records in our study were limited to dives greater than 75 m, we considered a maximum of three states. We included the maximum depth and total duration of the dive in the dive-only model, both modeled as gamma distributions. We tested the effect of including the 24-hour, cosinor variable on the state transition probabilities as well as on the individual parameter estimates.

4.2.4.2 Stage two (including fishing activity)

A three-stage model best described whale behavior in the absence of fishing activity information for the location-based model in the first stage. Thus, for the second stage, we added a fourth, "vessel-associated" state, to explore whether the presence of a fishing vessel influenced whale behavior. In addition to allowing the model to fit a new state, we also incorporated the distance to the nearest fishing vessel as an additional data-stream, modeled as a Weibull distribution. As the nearest fishing vessel to a whale location ranged from less than 5 km to greater than 1,000 km, we constrained the scale parameter of the distribution to be less than 35, which effectively restricted the vessel-associated state from occurring beyond approximately 100 km from the nearest fishing vessel. Because of this constraint, we did not include the effect of scaled boat distance as a separate covariate on transition probability parameters. We also constrained the shape parameter of the Weibull distribution for all four states to be less than three, which helps avoid excessively peaked distributions (McClintock et al. 2013).

We again started with a covariate-free model for the four-state model, including just the four states and data streams. We first added the same 24-hour cosinor covariate on dive behavior. To investigate the potential for bias of whale movement to fishing activity, we included the Euclidean distance between whale locations and the nearest fishing activity as a covariate on the turn angle concentration parameter of the wrapped Cauchy distribution for the boat-associated state. We also included the angle to the nearest vessel as an angular covariate, weighted by distance, to determine whether the strength of bias varied with distance. We also included distance to fishing activity as a covariate on the step mean parameter and dive lambda parameter.

4.3 Results

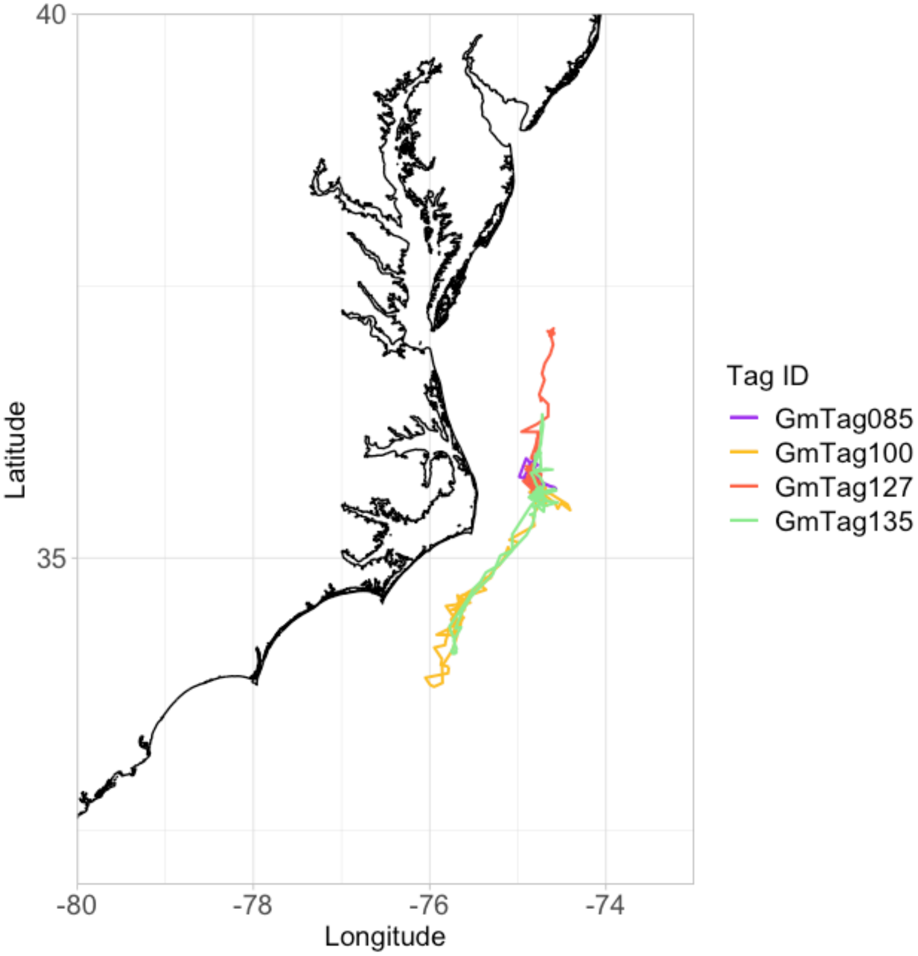
4.3.1 Data overview

The duration of tag records for the 11 whales prior to duty-cycling ranged from 11.8 to 32.8 days and included 3,891 Argos locations, averaging 14.8 location messages per day (Table 6). This corresponded to 2,032 regularized steps at three-hour intervals after processing as a CRW through the Crawl function. The total number of dives recorded (i.e., any submergence exceeding 75 m and 30 seconds) was 9,800, with 2,754 of these dives exceeding 600 m. The movements of tagged whales varied from following the continental shelf-break to swimming far offshore, and even traveling south to coastal waters off the Florida coast (Figure 15).

There were 19,056 pelagic longline sets deployed across the study area between 2014-2017, with 6,802 of these occurring in the Mid-Atlantic Bight. There was an observer present on 2,402 (~13%) of all fishing sets and 924 of the sets in the MAB (~14%). The median length of mainline deployed for a single fishing set, as reported by captains in logbooks, was 37 km (IQR 30–50) and the median number of hooks deployed per set was 694 (IQR 580–850). The median spatial spread, or maximum Euclidean distance, across a single set, was 35 km (IQR 25–46 km). The median time that a set was initiated was 18:23 Eastern Standard Time (EST), and the median set duration (from the time that gear was first placed in the water to the last piece of gear brought on board the vessel) of observed sets was 18.8 h (IQR 16.1–20.7 h). A total of 116 pilot whales were recorded as bycatch on 97 (4%) of the observed sets, with marine mammal depredation occurring on 6% of all observed sets (9% of sets had either bycatch or depredation). The median distance of CRW pilot whale locations to the nearest fishing event was 78 km

(IQR 27–166 km). Pilot whales spent approximately 60% of their time within 100 km of fishing activity and 18% of their time within 20 km.

(a)



(b)

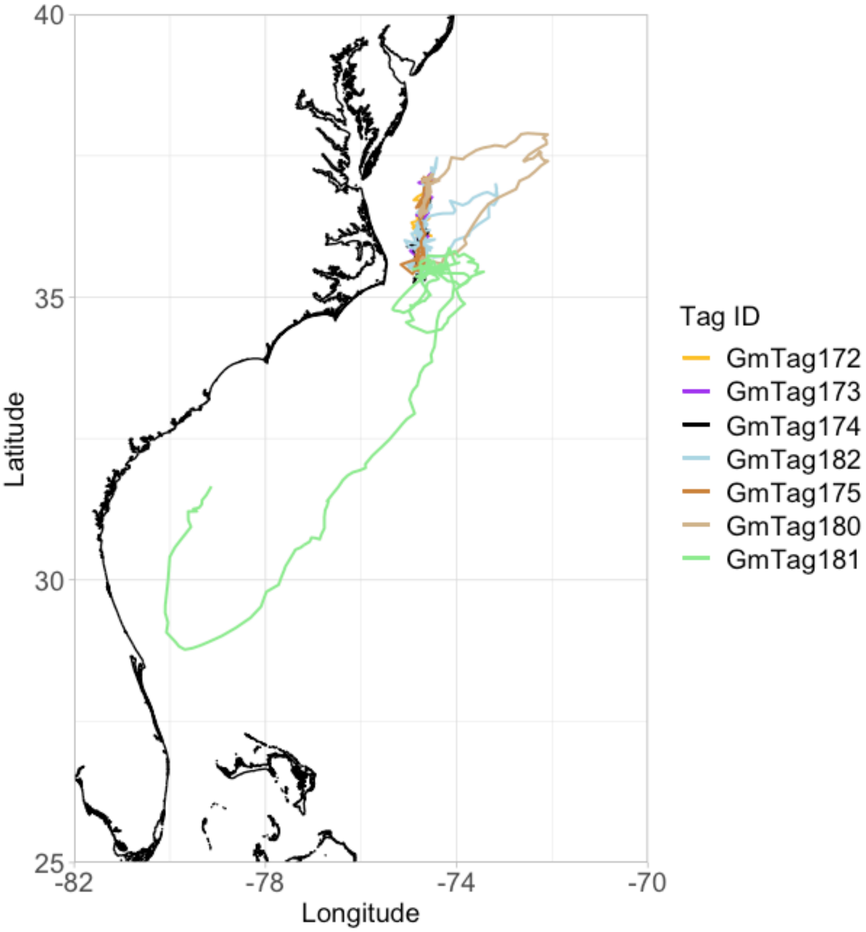


Figure 15: Map of individual tracks of short-finned pilot whales re-sampled to a three-hour time step in a continuous-time correlated random walk model. 2014-15 tags (a) and 2017 tags (b).

4.3.2 Whale behavior

4.3.2.1 Stage one (no fishing activity)

In the first analysis stage, there was strong support for a three-state model. Using the number of dives exceeding 600 m (deep dives) as the diving data stream provided the best state discrimination and model fit and was used in all remaining analyses. Additionally, the best-supported model included the effect of hour of day on the number of deep dives per three-hour interval. Including the hourly covariate in the formula for state transition probabilities was not favored by AIC relative to the single covariate version.

State 1 seemed to indicate a transiting or faster movement behavior, with the longest step lengths and highest angle concentration (indicating more directional persistence). State 2 had the shortest step lengths, smallest angle concentration, and the fewest number of deep dives, potentially indicating a resting phase. State 3 had the greatest number of deep dives, with moderate step lengths and angle concentration, possibly indicating a foraging phase. The effect of hour of day was most pronounced on state 3. The model indicated that tagged whales made more deep dives during the morning hours (EST) than in the late afternoon or evening (Figure 16d). Individual whales varied in the amount of time spent in each state, ranging from 10-47% for state 1, 4-68% for state 2, and 7-60% for state 3. Taken as a whole, the average time in each state across whales was 31%, 35%, and 35%, respectively.

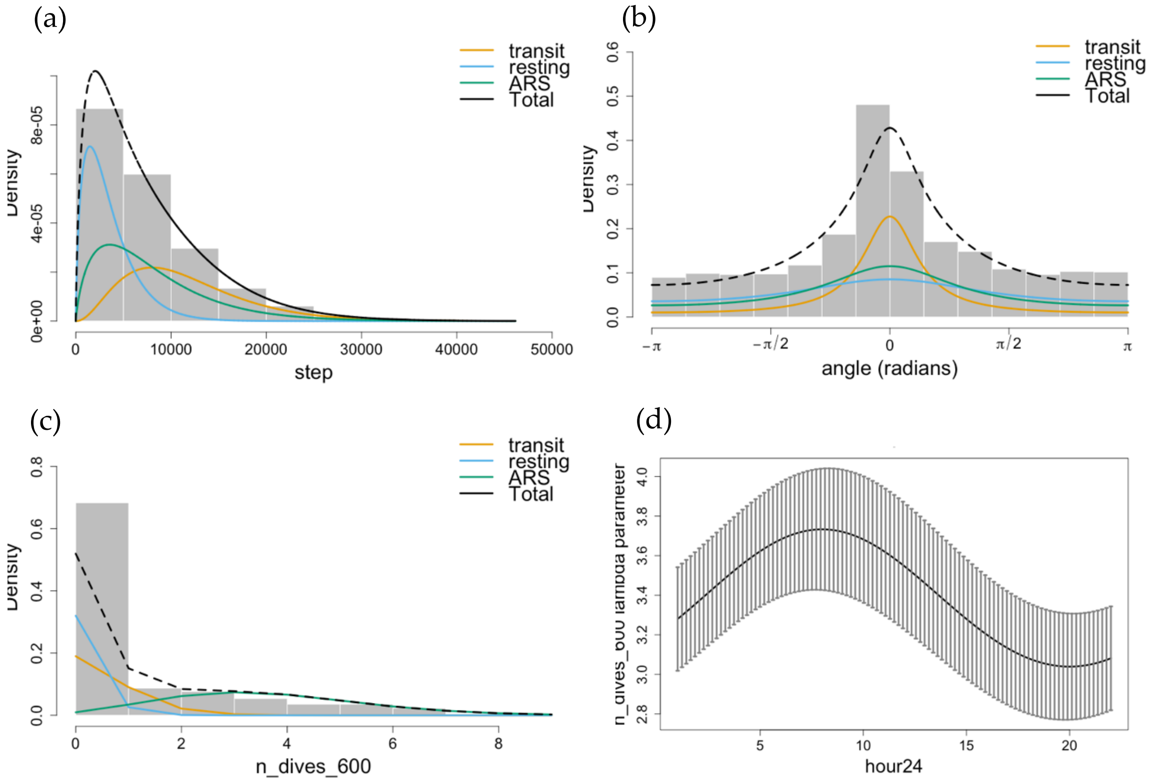


Figure 16: Results for the best Stage 1 model (no fishing effects). Fitted state dependent parameter distributions (colored lines) and observed data (gray bars) (a-c). Covariate effect of hour of day on number of deep dives (> 600 m) per three-hour interval in state three (ARS) (d).

The best dive-only model also supported three states and included the hourly covariate on the state transition probabilities. The best model did not include a direct effect on the depth or duration parameters themselves. The three states included a shallow dive state (state 1) with a mean depth of 209 m (SD 84.7 m) and duration of 9.0 minutes (SD 2.7 min), a medium dive state (state 2) with a mean depth of 439 min (SD 111 m) and duration 12.6 min (2.3 min), and a deep state (state 3) with a mean depth of 752 m (SD 132.1 m) and duration 16.9 min (SD 2.2 min) (Figure 17a-b). Hour of day had the largest effect on states 1 and 3, with state 3 slightly more likely in the morning hours (EST) and state 1 more likely from late afternoon to very early morning (Figure 17c). On average, state 2 was most common with an average of 48% of time spent across whales, followed by state 3 (29%) and state 1 (23%). All individual whales engaged in all diving states, ranging from 15-33%, 9-72%, and 11-55% for states 1, 2, and 3, respectively.

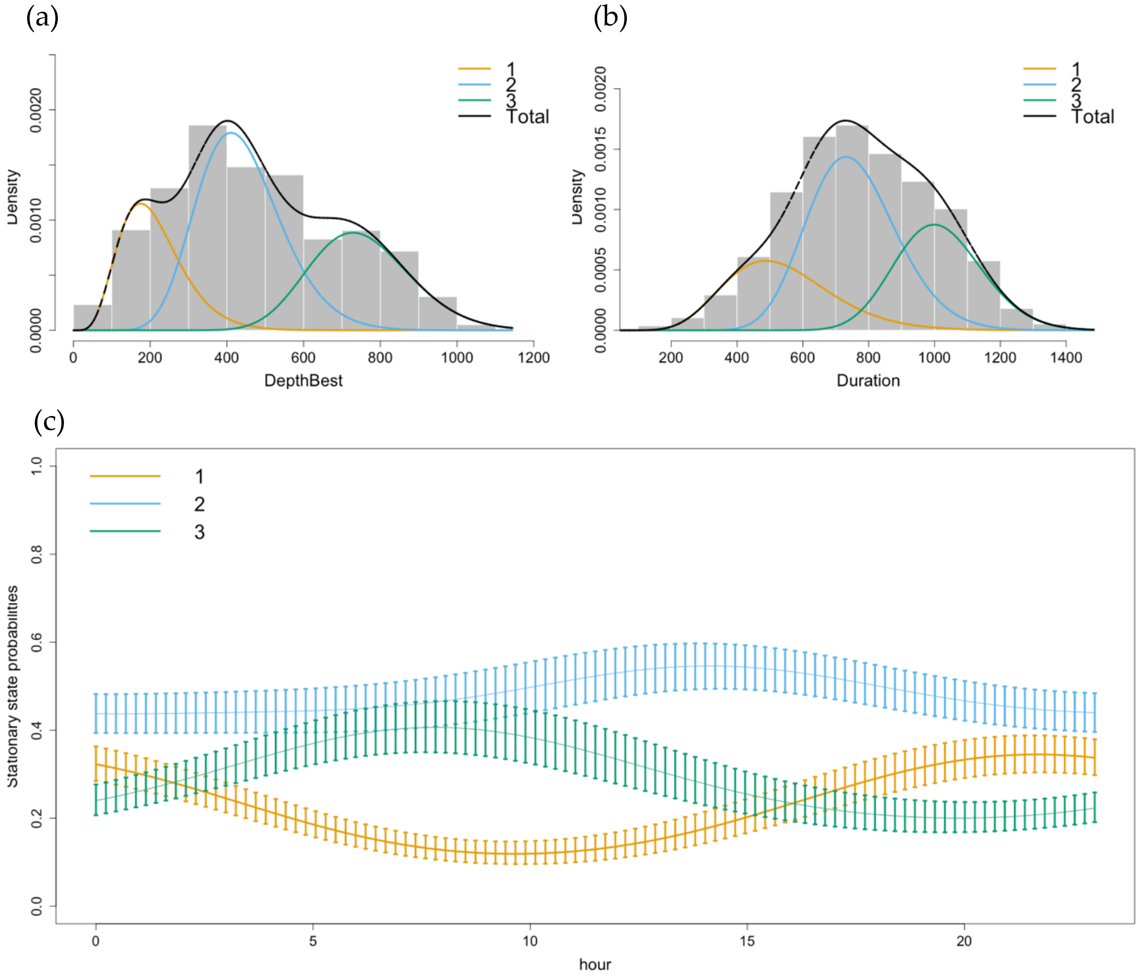


Figure 17: Results for the best-fit dive-only model. Fitted state dependent parameter distributions (colored lines) and observed data (gray bars) (a-b). Covariate effect and 95% confidence intervals of hour of day on the stationary probability of dive state for all tags (c).

4.3.2.2 Stage two (including fishing activity)

The relative parameter values for the baseline behavioral states (States 1, 2, and 3) were largely unchanged from the three-state compared to the four-state model, when we included proximity to fishing vessel as a data-stream (Figure 18a-c). The distribution for the vessel parameter indicated that a distinct fourth state occurred at distances up to no more than 50 km from the nearest fishing activity. The other three states all occurred over a greater range of distances from fishing activity, although state 2 (resting), and to a lesser extent state 3 (foraging), tended to occur most commonly within 100-200 km of fishing locations. At the mean distance to the nearest boat for the vessel state (~16 km), whales had relatively short step lengths, low angle concentration, and medium number of deep dives (Figure 18a-c).

We sequentially explored a range of possible model structures in which the distance and/or angle to the nearest vessel could influence the state-dependent probability distributions of parameters in the boat state. The best fit model based on AIC included the effect of scaled distance to nearest vessel on the number of deep dives and step length for state 4. The effects of vessel distance on the two parameters were marginal and characterized by high variance. However, the closer whales were to a fishing vessel, the shorter their step lengths and fewer dives beyond 600 m (Figure 19). An additional model that included the effect of vessel distance on angle concentration was nearly identical in AIC (< 1 AIC unit) to the best-fit model, and a third including angle and distance to vessel covariates on the mean angle movement parameter was also only slightly worse in AIC. However, the effects of vessel distance and angle on pilot whale movement angle were minor in both models, and thus, in combination with the worse AIC scores, there was not a strong reason to consider them further or to be better fits than the simpler model.

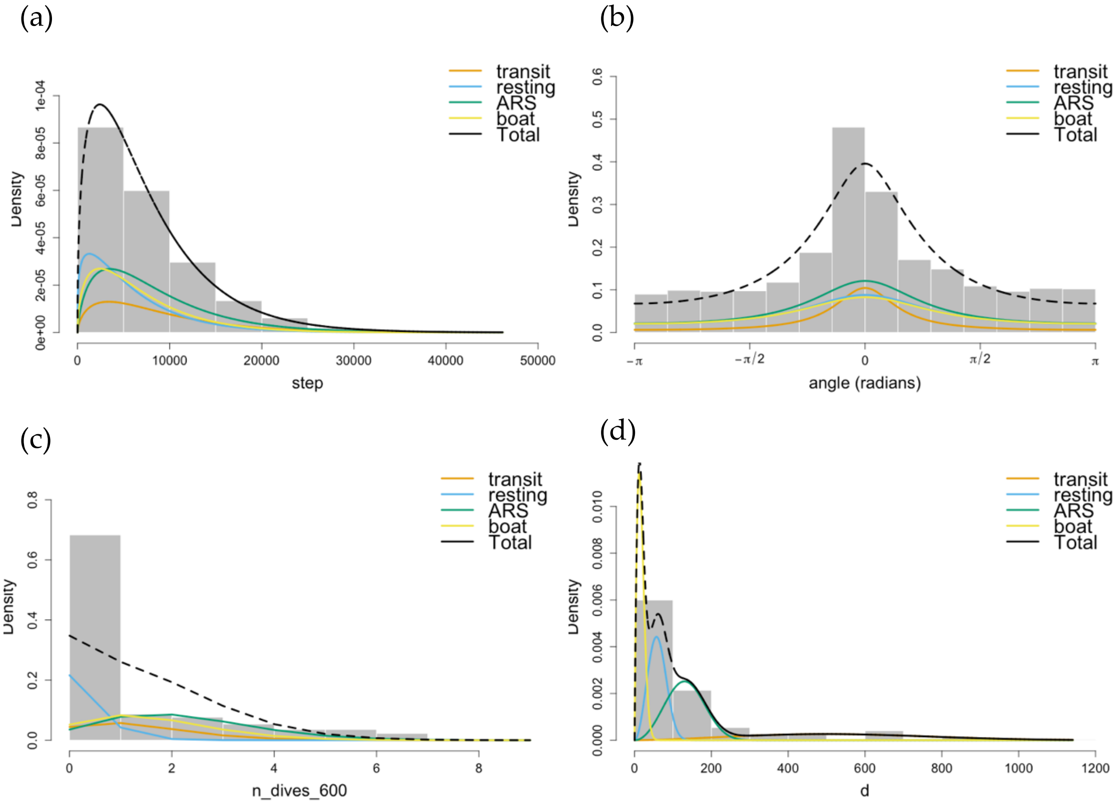


Figure 18: Results for the best Stage 2 model (with fishing effects). Fitted state dependent parameter distributions and observed data (gray bars), showing step length (a), angle (b), number of deep dives (c), and distance to nearest fishing boat (d) for each state.

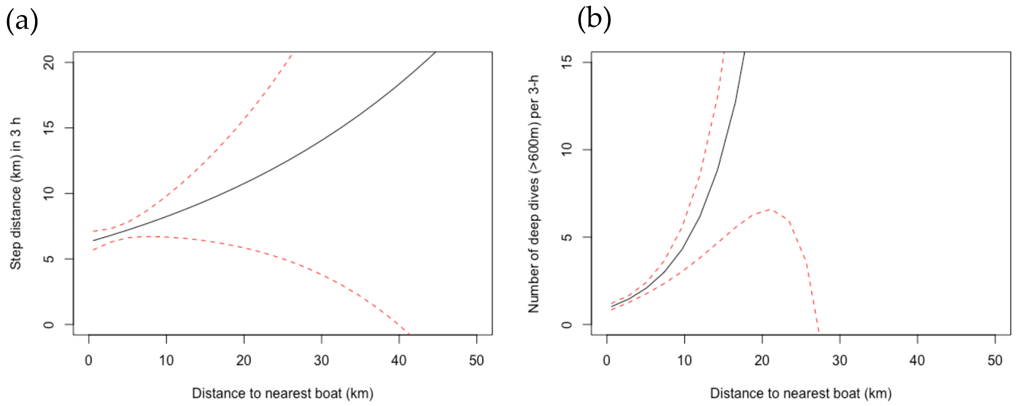


Figure 19: Estimated effects of distance to the nearest fishing activity on step length (a) and number of deep dives per 3 h interval (b).

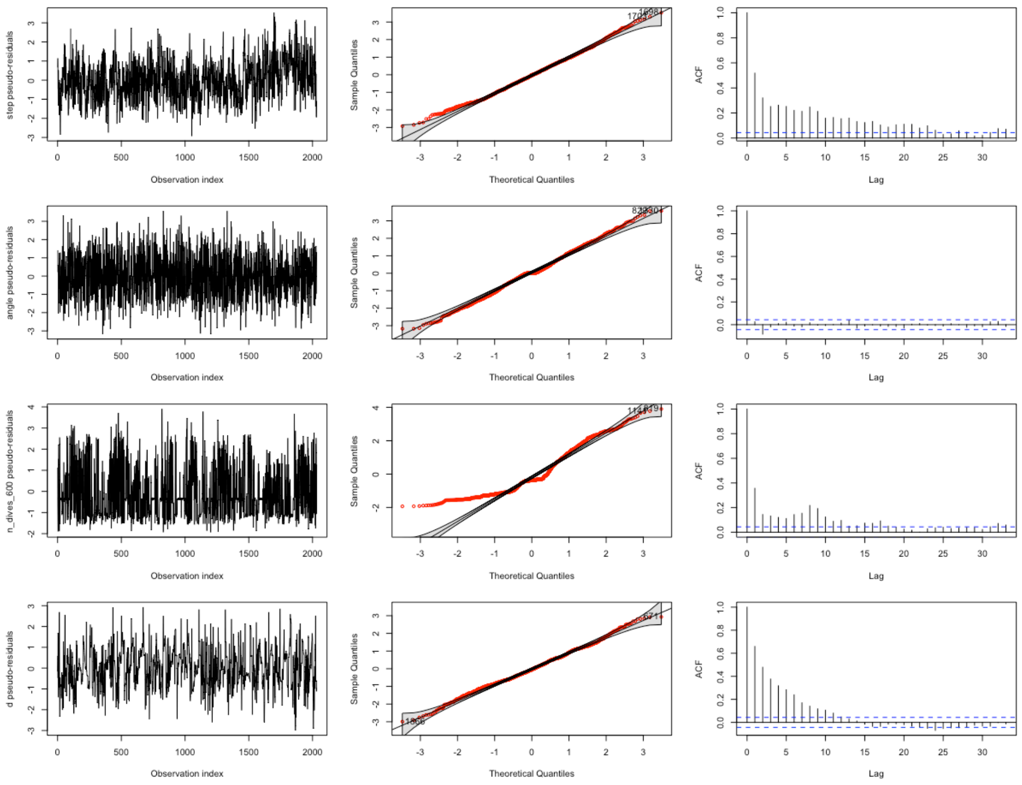


Figure 20: Time series, pseudo-residual plots, and auto correlation function for all four data streams (step length, angle, number of deep dives, and distance to nearest boat) for the best-fit four-state model.

Global state decoding using the Viterbi algorithm assigned 16% of the overall three-hour time steps to state 1, 26% to state 2, 32% to state 3, and 26% to state 4 (Table 7). Individual whales varied in the amount of time spent in each state, including the vessel state (state 4), in which tagged whales spent from 8 to 58% of time. State showed strong persistence, with the probability to persist in the same state from one time step to the next near or exceeding 90% for all four states (Table 8). Whales were most likely to enter state 4 from the resting state, but this with a low probability (~6%).

Table 7: Proportion of time steps assigned to each state in the four-state model. States were assigned by global state decoding of the hidden Markov model using the Viterbi algorithm.

	States (prop. time)			
Whale ID	**1**	**2**	**3**	**4**
GmTag085	0.03	0.54	0.04	0.39
GmTag100	0.16	0.03	0.51	0.30
GmTag127	0.05	0.20	0.17	0.58
GmTag135	0.01	0.22	0.33	0.44
GmTag172	0.07	0.32	0.42	0.20
GmTag173	0.12	0.41	0.39	0.08
GmTag174	0.07	0.22	0.37	0.34
GmTag175	0.12	0.36	0.43	0.08
GmTag180	0.37	0.42	0.08	0.13
GmTag181	0.42	0.20	0.23	0.15
GmTag182	0.28	0.04	0.35	0.33
Total	**0.16**	**0.26**	**0.32**	**0.26**

Table 8: Transition probabilities between all states (row -> column).

	State 1	State 2	State 3	State 4
State 1	0.950	0.017	0.029	0.003
State 2	0.003	0.886	0.051	0.060
State 3	0.020	0.045	0.931	0.004
State 4	0.005	0.061	0.016	0.918

4.4 Discussion

4.4.1 Baseline behavior

Our baseline analysis adds to a growing body of work describing the behavioral patterns of short-finned pilot whales in the Mid-Atlantic Bight. We demonstrate that pilot whales engage in several behavioral modes in this region, confirming previous work by Quick et al. (2017) and Thorne et al. (2017). We identified three distinct behavioral modes, including travel, resting, and foraging behavior. This is consistent with previous analyses of location-only tags for this same population of whales, which identified distinct behavioral stages of transit and area-restricted search (Thorne et al. 2017, Foley 2018). In our case, the addition of dive data allowed the distinction of the additional third state, which was similar to the foraging state in step length and angular movements, but had very few deep dives. Indeed, despite having the shortest step lengths of all states (mean 3.6 km, SD 2.6 km), often indicative of concentrated foraging behavior, whales in state 2 made only 98 total dives greater than 600 m compared to 2,466 dives to over 600 m in state 3. The use of summary dive data to other depths, for example dives over 200 m or 400 m, produced similar results, but the distinction between foraging and resting states, and overall model fit, was clearer when we used 600 m as the deep dive threshold.

The number of dives in a three-hour window is an imperfect metric regardless of the depth threshold employed, but given the nature of Argos-transmitting satellite tags and the deep-diving behavior of pilot whales it is not possible to obtain a temporal resolution equivalent to the frequency of individual dives in a location-based analysis. Therefore, we also assessed dive patterns on an individual dive basis without considering location. This is similar to the approach taken by Quick et al. (2017), who used HMMs to analyze short-finned pilot whale diving behavior from this same population using high-resolution DTAGs. DTAGs measure depth at high frequencies (e.g., 1 Hz), and record three-dimensional kinematic behavior and acoustic recordings. These authors identified four behavioral states, with the greatest number of foraging buzzes (rapid echolocation clicks employed by whales closing on prey) occurring in the two deepest dive states, and especially in the state characterized by dives mostly over 600 m. The best-fit HMM for our relatively coarse dive data indicated three distinct dive states, comparable to three of the dive states described by Quick et al. (2017).

Baseline models for location-based and dive-only HMMs indicated a diel pattern in dive behavior. The location model suggested that foraging whales dove to depths greater than 600 m more often during the morning to mid-day hours, and less often in the evening to nighttime. This effect was a difference of less than a single dive on average, but the model showed reasonably strong support for including the covariate. The dive-only model again suggested a pattern of deeper dives occurring in the early morning hours. In this case, the best-fit model included the effect of time of day on the probability of occurring in specific states, rather than on depth. The stationary state probability plot indicates a moderate but clear pattern of a higher probability of occurring in the deep state and lower probability of occurring in the shallow state in the morning, while this relationship flips in the late evening (Figure 17c).

Similar diel patterns are commonly observed in diving animals, including other populations of short-finned pilot whales, and have been suggested as an adaptation to the diel migration of prey (Baird et al. 2002, Aguilar de Soto et al. 2008). Interestingly, earlier studies on this population of pilot whales have failed to detect a diel diving pattern. Indeed, one analysis including some of these same tags (from 2014 and 2015) did not detect a discernible diel pattern in the number of dives or the maximum depth of dives (Bowers 2016). Quick et al. (2017) also did not detect clear diurnal patterns in their analysis of high-resolution DTAGs deployed on pilot whales from 2008 to 2014, although the maximum tag duration in this analysis was only ~18 hours. We conclude that the addition of seven additional tags to the data set analyzed by Bowers (2016) and the multi-day deployments made possible with SLTDR compared to DTAGs, helped identify this pattern, which is slight but clear. The fact that all three states occur throughout all hours, suggests that this observation may indeed be a response to shifting depths of prey throughout the day, although this is difficult to confirm without further information on foraging attempts or success (e.g., echolocation buzzes).

4.4.2 Behavior near fishing vessels

The broad-scale overlap between short-finned pilot whales and the pelagic longline fishery has been well-described, with the pelagic longline fleet favoring some of the same shelf-break and canyon habitats and sea surface temperature patterns as short-finned pilot whales (Thorne et al. 2017, Stepanuk et al. 2018, Thorne et al. 2019). Our objective was to better understand whether pilot whale behavior is modified when animals are in the vicinity of actively fishing vessels.

To explore whether there were effects of fishing vessel proximity on fine-scale whale behavior, we started from the same baseline model parameters as the three-state, non-fishing model, and added a fourth data stream (distance to fishing vessel) and fourth possible behavioral state. The fourth state was unrestricted with respect to any data stream parameters except for distance to vessel, in which a constrained scale parameter restricted the possibility that the "vessel state" could occur beyond approximately 100 km. The candidate models consistently constrained this fourth state to within a maximum of 50 km (mean of ~16 km) from the nearest fishing activity.

The best fit model additionally indicated slight decreases in both step length and the number of deep dives the closer whales were to the starting location of fishing activity. These patterns occurred over only short distances to fishing location (< ~20 km) and had wide confidence intervals, but the pattern, especially for number of deep dives, is consistent with what we expect during depredation behavior. The maximum length of vertical gear as measured by observers on pelagic longline vessels from 2014-2017 was 32.0 m (SD 12.5 m). The typical configuration of longline gear results in concatenation of gear so the actual fished depths are several times greater than this minimum vertical length (Bigelow et al. 2006), but the gear is highly unlikely to reach depths considered as deep foraging dives in the present study (i.e., 600 m). Tagged whales in the vessel phase had a similar number of deep dives to the deep foraging phase when averaged across the whole state (1.6 versus 2.1 per three-hour interval on average for the deep state). Yet, they appear to engage in shallower diving as they become very close to the best-known location of fishing activity. This may represent a change from normal deep foraging behavior to depredating on relatively shallow fishing gear.

The similar spatial scales of the occurrence of the vessel phase (mean 16 km) and potential influence of vessel proximity on actual movement behavior (no more than 10-20 km), may also suggest a response threshold or detection limit of whales to vessels and/or longline gear. How pilot whales locate gear to depredate is not known, although studies in several other systems and species indicate that acoustic detection of vessel sounds is likely. Thode et al. (2007) showed that sperm whales depredating demersal longlines in southeast Alaska are attracted to acoustic signatures from the cavitation of a ship’s propeller from at least 4-8 km away. Mul et al. (2020) showed that killer whales orient to herring purse seine vessels in Norway at ranges of up to 20 km.

Given the uncertainty in the locations of both pilot whale locations and longlines in this analysis, it is not possible to say with certainty whether the spatial patterns observed indicate a detection threshold. There was no strong support for a model that included the effect of vessel distance on movement angles, indicating there is no clear bias in movement towards fishing vessels, at least as identified in the current models. Nonetheless, the observation of distinct behavioral changes near fishing activity, despite the overall uncertainty and coarseness of data, was notable. Also notable is the fact that despite being within 20 km of fishing gear nearly 20% of the time, whales do not engage continuously in depredation. This is consistent with reports from our colleagues in the fishing industry, who report that depredation is stochastic and not necessarily predicted by the presence of pilot whales around their vessels. Combined rates of depredation and bycatch rates are still less than 10% per set, despite the heavy use of similar habitat by both whales and fishermen in this area (Stepanuk et al. 2018).

4.5 Conclusions

Using novel quantitative methods and a rich tagging dataset, we demonstrated several patterns of behavior of short-finned pilot whales. Tagged pilot whales exhibited deep diving behavior throughout the day but tended to dive to shallower depths during the nighttime than in the daytime. We also describe a novel behavioral state that occurred when whales were in close proximity to fishing activity (< 50 km). During this state, whales exhibited shorter step lengths and shallower dives, consistent with depredation behavior on longline gear. The resolution of our data precludes detailed characterization of depredation events, but our observations that whales change their behavior when in the proximity of vessels may help inform move-on rules that fishermen could employ to reduce the occurrence of depredation and bycatch. Improved observer coverage or access to more detailed vessel movements through vessel monitoring systems, combined with improvements in cetacean tagging technologies, would provide finer-grained insight into this difficult problem.

5. General Conclusions

Depredation and associated bycatch are global issues but remain poorly understood in many ways, especially for pelagic longline fisheries where depredating animals are rarely seen in the vicinity of gear. My dissertation brings together disparate data sources and novel quantitative methods to better characterize depredation and bycatch interactions in two U.S. fisheries, providing important insights into the nature of interactions and guidance on potential mitigation strategies that are not only useful in these fisheries, but potentially relevant to pelagic longline depredation in other parts of the world as well.

In my first chapter, I reviewed general mitigation approaches to depredation and bycatch by marine mammals, and I conducted a case study analysis on the management process and its effectiveness in addressing depredation in two U.S. fisheries heavily affected by odontocete depredation and bycatch. I highlighted that despite relatively robust research programs, observer coverage, legislative authority, and institutional will, these fisheries have largely failed to reduce bycatch interactions sufficiently below target bycatch limits. There has been even less success in reducing depredation interactions, which in turn would reduce bycatch rates, and thus both fisheries have largely resorted to efforts to reduce the mortality or injury of whales after they become caught in longline gear. This does not solve the problem for fishermen, whose main concern is understandably the financial repercussions of depredation behavior, rather than the hooking of a marine mammal.

My dissertation is largely motivated by the goal of identifying patterns of odontocete depredation and depredator behavior in a way that can be used by fishermen to avoid depredation interactions, and subsequent bycatch, in the first place. In my second and third chapters, I analyzed data from fisheries observers, environmental ocean observations, and satellite-linked transmitters deployed on false killer whales to identify patterns of odontocete depredation that could help fishermen avoid overlap with whales or better understand the consequences of interactions when they do occur. There were no unequivocal geographic, environmental, or operational covariates that could be used in a predictive management context. I did identify large spatial and temporal patterns of depredation risk which may help fishermen understand broad-scale patterns and expectations of depredation impacts. However, these results are unlikely to help fishermen precisely predict interaction risk on a set-by-set or daily basis.

Consistent with earlier studies, odontocete depredation in this fishery seems to be driven at broad scales by convergence in space and time of fishing activities and the occurrence of false killer whales, which are likely both cueing on similar environmental conditions to locate productive areas. However, the occurrence of depredation on a previous set of the same or a nearby vessel was a fairly strong predictor of depredation occurring on a later set. I characterized the boundaries of risk associated with these clumped depredation events and found that depredation risk consistently decreases until about 9 days later and 400 km away, with little expected reduction beyond that. Thus, although *a priori* forecasting may continue to be challenging, reactive avoidance and improving decision-making following known interactions can help alleviate the problem. Ultimately, these strategies could help reduce depredation rates by up to 50%, depending on the actions taken by fishermen.

My final chapter focused on the Atlantic pelagic longline fishery and depredation and bycatch of the short-finned pilot whale. Similar to the false killer whale interaction, pilot whales overlap heavily with pelagic longline vessels in their home ranges and habitat use. Although previous work has suggested some small adjustments in deciding where to fish could reduce immediate overlap and the probability of bycatch interactions, generally fishermen tend to fish in the same areas that whales are most concentrated, and it is difficult to reduce overlap to a large extent. Thus again, fine-scale behavior of fishermen and whales may be an important consideration for ways to reduce depredation interactions. Although whales may frequent particular habitats, they are patchily distributed and overall interaction rates are relatively low. Understanding the behavior of whales around fishing gear and whether there are thresholds of detection, could help fishermen make better decisions for how to respond and escape whales when they or another nearby fishing vessel encounters pilot whales.

I conducted an analysis of pilot whale behavior from a rich satellite tag dataset to better understand whale behavior in the vicinity of fishing gear. I identified a novel behavioral state that occurred when whales were in close proximity to fishing activity (< 50 km). Although the resolution of these data precluded a detailed characterization of depredation events or the mechanisms leading to behavioral changes, these observations help improve understanding of fine scale whale behavior in ways that may help design avoidance or reactive strategies.

Unfortunately, depredation and bycatch will be difficult to avoid whenever the predators and fisheries target the same species, as in the Hawaii fishery, or overlap heavily in habitat use, as is the case in both fisheries. However, for species that occur in low densities with relatively low interaction rates, such as false killer whales and pilot whales, understanding how best to react when whales are observed or known to be present in an area could substantially improve the ability of fishermen to avoid depredation interactions and find other productive grounds to fish without whales. The tools used here can help identify the intensity and scale of risk where whales do occur and the behavioral characteristics of whales that influence if and how a fisherman may avoid future depredation events. These insights would not be possible without high-quality observer data and difficult to obtain animal tagging data. Improved observer coverage or access to more detailed vessel movements through vessel monitoring systems, combined with improvements in cetacean tagging technologies, will provide finer-grained insight into this difficult problem. I hope that fishermen will add these measures to their toolkit for deciding where to fish, reducing economic burdens on fleets and improving conservation outcomes for vulnerable bycatch species.

Appendix A

Appendix A1

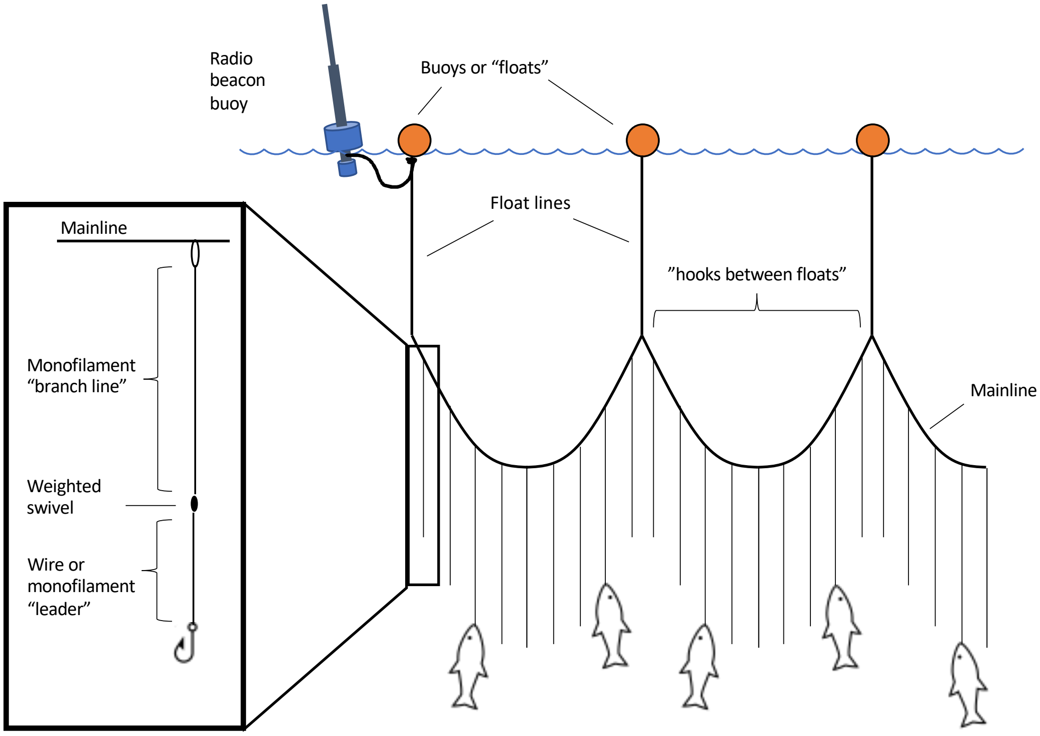


Figure A21: Schematic of pelagic longline gear used in the Hawai'i deep-set fishery.

Table A9: GAMM Variables. Variables considered in the fully-saturated generalized additive mixed model of probability of presence/absence of depredation. All variables represent characteristics relative to a single, observed longline deployment or environmental conditions at the haul-begin location of that set.

Space and time

- Haul begin location (Longitude, Latitude)
- Month

Gear and operational

- Vessel density (Number of all vessels within 200 km and ±3 days)
- Number of hooks set
- Soak time (Hours)
- Minimum depth of gear (length in m of float line + branch line + leader)
- Hooks between floats (number of hooks deployed between each pair of floats)
- Catch (# fish caught), each separately: Bigeye tuna, yellowfin tuna, mahi-mahi, wahoo, billfish, swordfish, sharks
- Catch per unit effort (CPUE, caught bony fish per 1,000 hooks)
- Nearby tuna CPUE –CPUE of tuna species across all observed vessels within 100 km and ±1 day
- Presence of depredation or false killer whale bycatch on previous set of same vessel
- Individual vessel (random effect)

Environmental

- Depth (m)
- Slope (m)
- Distance to seamount (km)
- SST range (difference between highest and lowest SST for all four fishing points, ºC)
- Chlorophyll-*a* ($mg \cdot m^{-3}$)
- Absolute dynamic topography (adt, m)
- Total kinetic energy (tke, $m^2 \cdot s^{-2}$)
- Distance to nearest eddy edge (km)
- Amplitude of nearest eddy (cm)

- Distance to nearest thermal Cayula-Cornelius front (km)
- Oceanic Niño Index (ONI)
    - Concurrent
    - 11-months prior to observed set
- Moon phase

Eqn. A1. Fully saturated model without interactions

$$
\begin{aligned}
(E(Y) = \alpha + \; & s(longitude) + s(latitude) + s(month) + s(vessel\ density) \\
& + s(num.hooks\ set) + s(soak) + s(min.gear\ depth) \\
& + s(hooks\ betw.floats) + s(\#\ bigeye\ tuna) + s(\#\ yellowfin\ tuna) \\
& + s(\#\ mahi\ mahi) + s(\#\ wahoo) + s(\#\ billfish) + s(\#\ swordfish) \\
& + s(\#\ sharks) + s(CPUE) + s(nearby\ CPUE) + prev.depredation \\
& + s(vessel\ ID, random) + s(depth) + s(slope) + s(seamount\ dist.) \\
& + s(SST\ range) + s(chl.a) + s(adt) + s(tke) + s(eddy\ dist.) \\
& + s(eddy\ amp.) + s(front\ dist.) + s(ONI) + s(ONI\ lag) \\
& + s(moon\ phase)
\end{aligned}
$$

Eqn. A2. Fully saturated model including interactions

$$
\begin{aligned}
(E(Y) = \alpha + \; & s(latitude\ x\ month) + s(latitude\ x\ ONI\ lag) + s(month\ x\ ONI\ lag) \\
& + s(longitude) + s(latitude) + s(month) + s(vessel\ density) \\
& + s(num.hooks\ set) + s(soak) + s(min.gear\ depth) \\
& + s(hooks\ betw.floats) + s(\#\ bigeye\ tuna) + s(\#\ yellowfin\ tuna) \\
& + s(\#\ mahi\ mahi) + s(\#\ wahoo) + s(\#\ billfish) + s(\#\ swordfish) \\
& + s(\#\ sharks) + s(CPUE) + s(nearby\ CPUE) + prev.depredation \\
& + s(vessel\ ID, random) + s(depth) + s(slope) + s(seamount\ dist.) \\
& + s(SST\ range) + s(chl.a) + s(adt) + s(tke) + s(eddy\ dist.) \\
& + s(eddy\ amp.) + s(front\ dist.) + s(ONI) + s(ONI\ lag) \\
& + s(moon\ phase)
\end{aligned}
$$

Eqn. A3. Final, best-fit model without interactions.

$$
\begin{aligned}
(E(Y) = \alpha + \; & s(latitude) + s(month) + s(num.hooks\ set) + s(soak) + s(\#\ bigeye\ tuna) \\
& + s(\#\ yellowfin\ tuna) + s(\#\ mahi\ mahi) + s(\#\ wahoo) + s(\#\ sharks) \\
& + s(CPUE) + s(nearby\ CPUE) + prev.depredation \\
& + s(vessel\ ID, random) + s(seamount\ dist.) + s(adt) + s(ONI\ lag)
\end{aligned}
$$

Eqn. A4. Final, best-fit model including interactions.

$$
\begin{aligned}
(E(Y) = \alpha + \; & s(latitude\ x\ month) + s(month) + s(num.hooks\ set) + s(soak) \\
& + s(\#\ bigeye\ tuna) + s(\#\ yellowfin\ tuna) + s(\#\ mahi\ mahi) \\
& + s(\#\ wahoo) + s(\#\ sharks) + s(CPUE) + s(nearby\ CPUE) \\
& + prev.depredation + s(vessel\ ID, random) + s(adt) + s(ONI\ lag)
\end{aligned}
$$

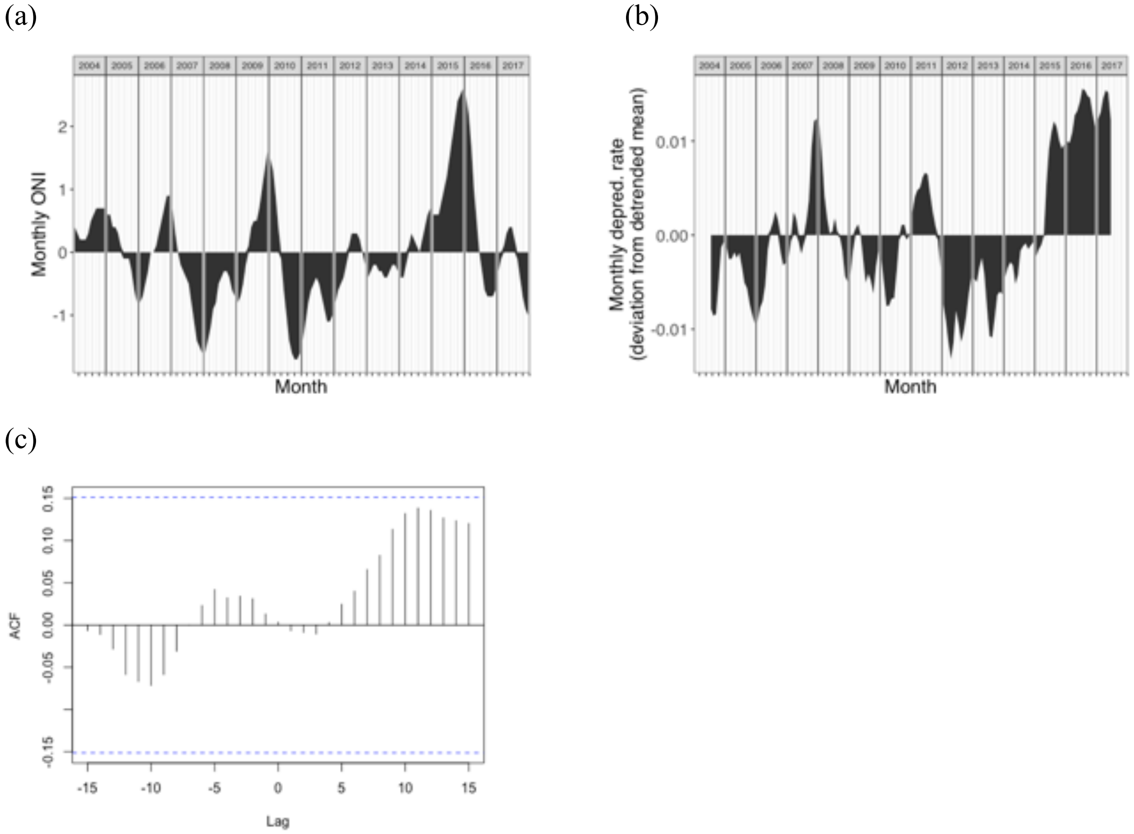


Figure A22: ENSO patterns. (a) Monthly Oceanic Niño Indicator (ONI) from 2004-2017; (b) monthly deviation from mean depredation rate on Hawai'i deep-set longline hauls after removing seasonal trend (i.e., 'trend' component in decompose function in RStudio, version 1.2.5033 (R Core Team 2018)); and (c) lag correlation analysis (auto-cross correlation function, ACF) between monthly ONI and average monthly depredation rate. The peak at 11 months following ONI was used in the GAMM models.

Appendix A2

Eqn. A1.

$$\widehat{K}(s) = \frac{A}{N^2}\sum_{i=1}^{N}\sum_{j\neq 1}^{N}\frac{I(\|s_i - s_j\| \leq d)}{w(s_i, s_j)}$$

Eqn. A2.

$$\widehat{K}(t) = \frac{T}{N^2}\sum_{i=1}^{N}\sum_{j\neq 1}^{N}\frac{I(\|t_i - t_j\| \leq t)}{v(t_i, t_j)}$$

Eqn. A3.

$$\widehat{K}(st) = \widehat{K}(s, t, st) - \widehat{K}(s) * \widehat{K}(t)$$

Appendix A3

Further details on false killer whale tagging protocols and data filtering

In a given sighting the group size was estimated, individuals were photographed for individual identification, and skin biopsy samples obtained for genetic analyses. All individuals considered in this analysis were confirmed to be from the pelagic population of false killer whales using established photo-identification and genetic databases and protocols (Baird et al. 2008, Martien et al. 2014). Individual whales in each group were tagged with SPOT5 Wildlife Computer satellite tags in the Low Impact Minimally Percutaneous External-electronics Transmitter configuration (Andrews et al. 2008) under relevant permits from the NMFS. Tags were deployed from a pneumatic projector and secured to the dorsal fin or base of the dorsal fin with two titanium darts. Tags were programmed to transmit daily position data through the Argos system for the first 60 days of deployment and then were duty-cycled to transmit every other or every several days. As we were interested in fine-scale, daily and sub-daily movement patterns, we focused our analyses on the first 59 days (or the maximum number of full days of transmission if tag-transmission ended prematurely). Estimates of animal locations were obtained through Service Argos using the Least Squares algorithm and processed through the Douglas Argos-Filter (Douglas et al. 2012) using the settings described by Baird et al. (2010) and Baird et al. (2013).

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