Top Photo: HIPc301, a member of Cluster 3 of the endangered main Hawaiian Islands population, with a very large mahimahi off Kona, Hawai'i Island, in October 2011. *Photo by Robin W. Baird/ Cascadia Research.*

ALWAYS ON THE MOVE:

THE COMPLEX MOVEMENT ECOLOGY OF FALSE KILLER WHALES

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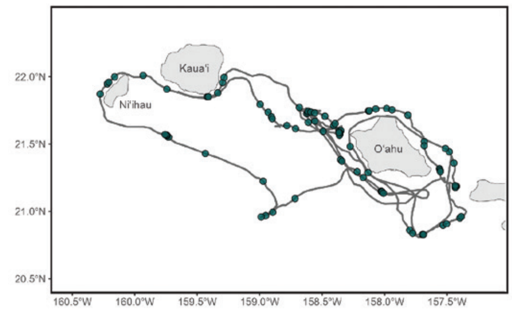
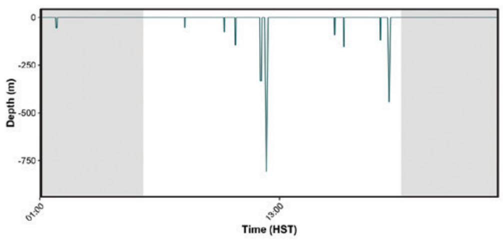
Movement is a universal requirement for survival: all animals must move to find and obtain food and mates, and avoid predators. For false killer whales, it's more complicated than this: as a highly social, group-living species, they also find, capture, and share prey with their companions, all in a dynamic and unpredictable environment. The movement decisions of a false killer whale are thus a balance between these two needs—physical and social—and studying these decisions is not only interesting, but also critical for conservation and management efforts. In practice this is quite challenging, because you need extensive information on both movements and sociality. Fortunately, Cascadia's research on Hawaiian false killer whales over the past 26 years has produced such datasets, which I'm using to answer questions on movements and space use for my PhD at Oregon State University's Marine Mammal Institute.





An example snapshot of the information we get on horizontal and vertical movements from satellite tag data.

Top Photo: False killer whale HIPc431 from the northwestern Hawaiian Islands population, tagged off Kaua'i in 2015. *Image by Brenda K. Rone/Cascadia Research.*

Middle Map: Movement track (gray line) with estimated dive positions (green circles) from HIPc364, a member of Cluster 3 of the main Hawaiian Islands population, tagged with a SPLASH10-F tag

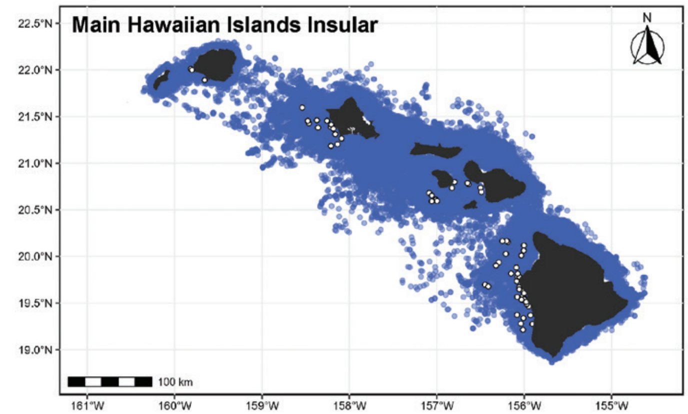
Bottom Graph: Dive profile (dive depth vs time) for one day, with the grey shading indicating nighttime.

Cascadia Research Collective started deploying satellite tags, specifically "LIMPET" tags, on false killer whales in Hawaiʻi in 2007 (see Robin Baird's tagging history article in this issue). My go-to analogy for these tags are "ear-piercings" on the dorsal fin that provide location data to satellites which can then be downloaded from our computers. As Robin explains in his article, these tags greatly advanced our ability to study the movements of false killer whales, and especially in Hawaiʻi where the unique geography of the islands creates some areas that are great for small-boat work and others that are much the opposite. With only a few tag deployments we quickly learned that false killer whales use both windward and leeward sides of the islands (Baird et al. 2010), confirming that limitations to surveying windward waters do result in a loss of information on where false killer whales spend their time. Secondly, these whales move a lot. Those first tagged animals and nearly every one of the 70 individuals from the main Hawaiian Islands insular population tagged since then have shown extensive movement rates (e.g., 450 km over 4 days) and island-hopping behavior (Baird et al. 2010, 2012). Considering low sighting rates of false killer whales during small boat surveys, this all makes sense: they aren't likely to stay in one area for very long and can cover a lot of distance in little time. This also taught us that while these resident whales seem to primarily use nearshore waters, they do foray into offshore habitats as well (Baird et al. 2010, 2012).

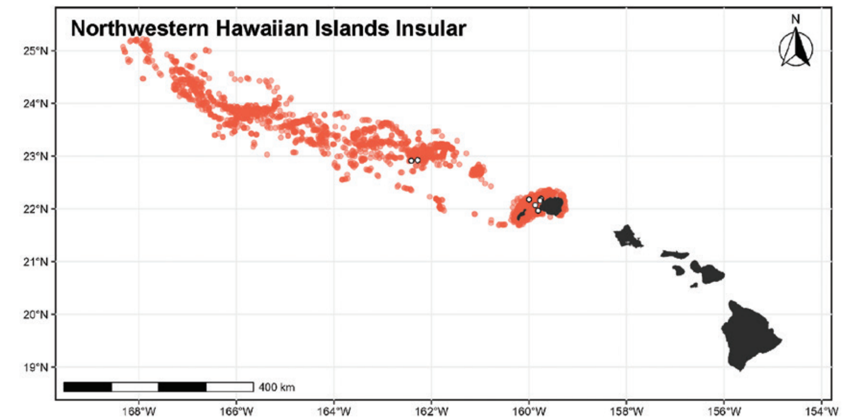
Why do they move so much? The short answer: highly mobile prey means highly mobile predators. False killer whales in Hawaiʻi are known to feed on large fish, including (but not limited to) mahimahi, a number of tuna species, reef-associated gamefish, and some billfish. Many of these species are highly mobile themselves and require quite the pursuit to successfully capture. While the satellite tags can't give us any proof of when they are feeding or not, there are some ways we can infer possible feeding behavior. For example, from about a dozen dive behavior-logging satellite tags we know that false killer whales spend a lot of their time in the top 50 meters of the water column, likely targeting surface-oriented prey (Kratofil et al. in prep). When they do dive deeper, it's typically between 100-400 meters deep, but they can and do dive much deeper (1,000+ meters; Kratofil et al. in prep). These deeper dives are likely for prey that we haven't been able to document them feeding on at the surface. In fact, remnants of squid have been found in the stomachs of some stranded false killer whales that were examined by Kristi West and her team at the University of Hawaiʻi, so this deep diving behavior could indicate that false killer whales pursue deep-dwelling prey, like some species of squid, more often than we previously assumed. False killer whales also don't seem to have a predictable diel pattern in their dive behavior, which could be attributed to their diverse diet. Dive behavior logs from some other delphinid species in Hawaiʻi suggest they track the vertical and horizontal migration of the mesopelagic boundary community, but we don't see such a pattern that would suggest the same for false killer whales.

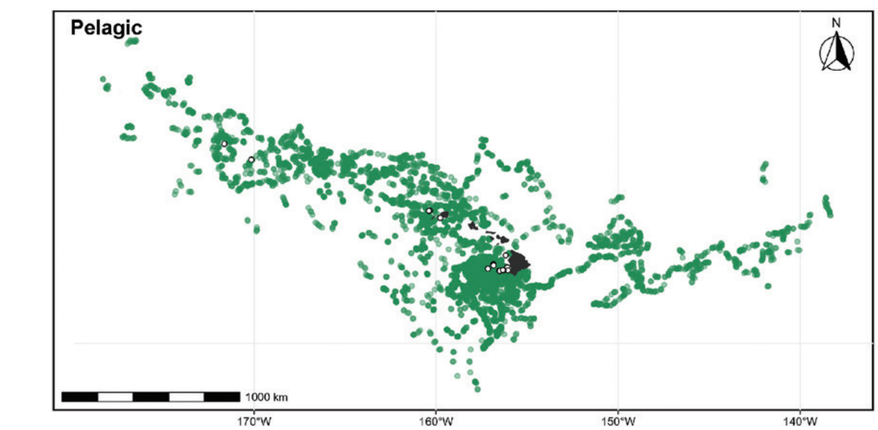
All three false killer whale populations have been documented feeding on similar prey. However, we know from tagging data that prey alone does not explain the movements and space use of false killer whales. Population membership plays a big role in this: individuals from the two insular stocks (main Hawaiian Islands, Northwestern Hawaiian Islands) have similar spatial behavior in the way that they primarily use nearshore shelf/slope waters around the islands that are within their respective ranges, but occasionally use offshore habitats (Baird et al. 2012, 2013; Kratofil et al. 2023). Pelagic false killer whales, in contrast, are typically much more nomadic. Just over two thirds of the tags on this population have been deployed offshore of Hawaiʻi Island, and most tend to move on to the high seas post-tagging. I say "most" because this was the case until the fall of 2023, when a number of pelagic false killer whales were tagged off Hawaiʻi Island and remained in the area offshore of Hawaiʻi Island for a considerable amount of time. It felt like they knew I had been calling them nomads and decided to prove us wrong. Nevertheless, the different movement strategies we see among the three populations could be a result of adaptations to the different ecological contexts they experience. This was hypothesized in Karen Martien's research on the genetic differentiation between the different populations: that the unique geography resulting from island mass effects could have promoted different behavioral adaptations, and these different adaptations could have driven genetic divergence (Martien et al. 2014). Assessing this empirically using satellite tag data from all three populations is one of the objectives of my PhD research.

Population membership will largely determine the general movement strategy and range of any given tagged false killer whale, but within a population, there remains a lot of variation. This variation is likely driven by a combination of factors relating to environmental conditions, resource availability, and social dynamics. Teasing apart these factors is easier for the main Hawaiian Islands insular population that has the most tag deployments and extensive information on social structure. To date, we know that some social clusters use slightly different habitats than others (e.g., deeper waters) and appear to have different high-use areas within the main Hawaiian Islands (Baird et al. 2012, 2023; Mahaffy et al., 2023). Further, although seasonal changes in the Hawaiian environment are not as stark as in other regions around the world, there is some evidence that at least one social cluster (Cluster 1) has seasonal variation in space use (Baird et al. 2019). My PhD research digs further into these dynamics: I'm using models that treat each individual tagged false killer whale as their own data point on what habitat features (e.g., seafloor depth, oceanographic variables) they used during their tag attachment period, compared to what was available to them at the time. Using this individual-level information, we can look for patterns among social clusters across the entire study period, but also during shorter periods (~3 months) when multiple social clusters were tagged at the same time. This second analysis on restricted time periods is especially interesting, because although social cluster membership is stable in the long-term, we often see dynamic association/dis-association patterns—moving in concert, separation, then coming back together—among multiple individuals during these shorter time scales (e.g., Baird et al. 2010). I'm also assessing whether individual geographic space use (what we call "home ranges") is more similar to those in the same cluster than other clusters; perhaps they all use somewhat similar habitats, but in different places. Lastly, in collaboration



Maps: Satellite tag locations from false killer whales across the three different populations, showing the variability in space use. White points represent the locations where the whales were tagged.

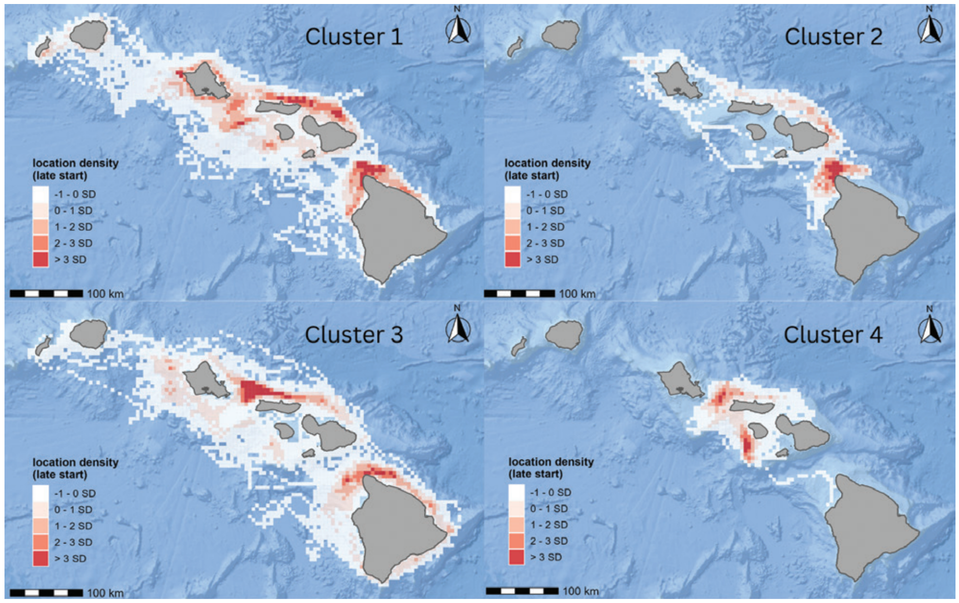




with Jeremy Kiszka and Michelle Caputo at Florida International University, we're looking further into their trophic ecology with stable isotope analysis, to see if some clusters have broader diets than others. While I'm still in the midst of my analyses, we're finding some interesting results that ultimately emphasize that social clusters are unique and should be considered units of conservation.

Another aspect of false killer whale movement dynamics is the role of human activities, and particularly fishing for Hawaiian false killer whales. Common prey of false killer whales are also commonly sought by recreational and commercial fishermen, and this competition unfortunately results in harmful interactions between false killer whales and fishers. This is an ongoing issue: while false killer whales have been documented interacting with nearshore fisheries in Hawaiʻi since the 1960s (Pryor, 1975), we continue to see evidence of such interactions in individuals today (Baird et al. 2015; Harnish et al. 2024). As I mentioned above, many false killer whale prey species are highly mobile and require a lot of energy and group effort to capture. When a fisherman hooks one of these species, it essentially creates a buffet for false killer whales, or at least significantly reduces the energetic cost of naturally pursuing prey themselves. From the energetics standpoint, it would make sense for false killer whales to depredate – take the bait or target fish off the line – and thus their movement decisions are likely mediated by fishing activity. For the main Hawaiian Islands insular population, this is difficult to observe because there is no observer program or ability to track the movements of nearshore commercial and recreational fishing vessels from which we could compare our satellite tag data with. However, as this population is endangered and declining (Badger et al. 2024) and has the highest rate of fisheries-related injuries (Harnish et al. 2024), it is essential to investigate relationships between movements and fishing activity to better manage their recovery. In our study published in 2021, we took this first step by identifying areas of high overlap between main Hawaiian Islands insular false killer whales and nearshore commercial fishing effort using our long-term satellite tag dataset and commercial fishing logs (Baird et al. 2021). In my PhD research, I'll be assessing false killer whale movement patterns in relation to fish aggregating devices (FADs) – anchored buoys designed to attract fish – as another plausible indicator of overlap with fishing activity.

Pelagic false killer whales are also known to take fish off lines, and this has been a contentious issue with the Hawai‘i deep-set longline fishery that operates in their offshore domain. There is an observer program for this fishery (although with very low and declining coverage) and vessel movement information is available to analyze with tagged whale movement data. It's much more challenging to study the movements of pelagic false killer whales because they are usually in offshore waters that aren't always accessible by small boats, so the satellite tag sample size is much smaller. A study using data from the first three groups of tagged pelagic false killer whales (including five tagged individuals) found that individuals only infrequently came in close proximity of longline vessels during the tag attachment period (Anderson et al. 2020). They did find that movements of one tagged group towards active vessels was extensive during the hauling phase, suggesting that hauling gear could be a cue that false killer whales use to initiate interactions (Anderson et al. 2020). With two additional tag deployments, Fader et al. (2021) showed that pelagic false killer whales have very high rates of movement (up to 75 km in 4 hours, 335 km in one day) and thus can easily keep up with the pace of longline vessels. This essentially means that "move-on rules", where fishermen move away from an area with false killer whales or post-depredation, are unlikely to be effective unless they move extensive distances and wait at least a week before resuming fishing (Fader et al. 2021). The sample size of pelagic false killer whale satellite tag deployments has grown substantially since then (now up to 14 deployments by Cascadia, largely thanks to our tagger, Colin Cornforth and his rapid response efforts out of Kona, and an additional eight deployments by colleagues with the Pacific Islands Fisheries Science Center). With these newer deployments, I'll be assessing their movement patterns in relation to longline vessels as previous studies have, and also environmental predictors of both pelagic false killer whales and longline vessel space use to understand factors that could drive co-occurrence.



While most of what we know of false killer whale movement ecology comes from our research in Hawai‘i, studies in other areas around the world have also shed light on the factors that drive their whereabouts. Carol Palmer and colleagues have used LIMPET satellite tags to study false killer whales in the Northern Territory of Australia and found similar movement patterns with respect to travel rates, use of coastal and pelagic habitats (albeit much shallower than in Hawai‘i), and dynamic group association patterns (Palmer et al. 2017). More recently, using a combination of satellite tag data, sightings, and genetics, they provided evidence for this resident population of false killer whales being demographically independent from offshore false killer whales in the region (Palmer et al. 2023; see Carol Palmer's article in this issue, "*Pseudorca* research summary for the Northern Territory, Australia"). Interestingly, the genetic mitochondrial haplotype that typifies this population is most similar to those found in the main Hawaiian Islands insular false killer whale population, providing evidence for an evolutionary relationship between these two populations (Palmer et al. 2023). Further, Martien et al. (2019) documented an immigrant in the main Hawaiian Islands insular population that had a haplotype found in false killer whales in Australia. This genetic evidence adds interesting context to the complex and extensive movements of false killer whales as a species (see Karen Martien's article in this issue). As Robin mentions in his tagging article, the only other satellite tag work on false killer whales has been one deployment off Madeira that remained in the general area but also made extensive movements offshore. Outside of satellite tagging, other studies have documented extensive movements of false

killer whales through re-sighting data. For example, Douglas et al. (2023) documented a maximum distance between an individual re-sighting between Mexico and southern Nicaragua (2,265 km, or 1,407 miles).

There is still much to learn about false killer whale movements and space use, both within Hawai'i and in other regions around the globe. For example, as Jochen Zaeschmar mentions in his article, "Life on the edge: the ecology of false killer whales at the limit of their natural range", false killer whales have a seasonal presence in New Zealand waters and their whereabouts during the cold season remain unknown. Investigating this seasonal movement pattern would certainly add to our knowledge of false killer whale movement ecology, particularly because most information on movements comes from regions with comparatively little seasonal variation in the environment. In Hawai'i, we now have the fewest tag deployments on Northwestern Hawaiian Islands false killer whales. From available satellite tag data we know that they spend time around Kaua'i and Ni'ihau (Baird et al. 2013; Kratofil et al. 2023), and while rare, they have been sighted further east in the main Hawaiian Islands (CRC unpublished). Their ranging patterns make encounters with them during small-boat efforts sparse, but additional tag deployments in the future will help inform their risk to fisheries interactions, for which there is currently little photographic evidence (Harnish et al. 2024), as well as their space use dynamics, especially if the main Hawaiian Islands insular population continues to decline.

Top Photo: A false killer whale from the endangered main Hawaiian Islands population with an ulua aukea, a giant trevally, off Kona, Hawai'i. *Photo by Colin J. Cornforth/Captain Zodiac.*

Page 32 Maps: The four social clusters of the main Hawaiian Islands population have different but overlapping high-use areas. These maps show location density (calculated as the number of locations per grid cell) from satellite tag deployments (from Baird et al. 2023).

Capturing the complexities of what drives false killer whale movements – their environment, their group dynamics, and human activities – will always be a challenge, but with multi-faceted research, collaborations, and some patience, we'll continue to fill in these knowledge gaps. Even with our extensive satellite tag dataset in Hawai'i, every tag deployment seems to teach us something new.

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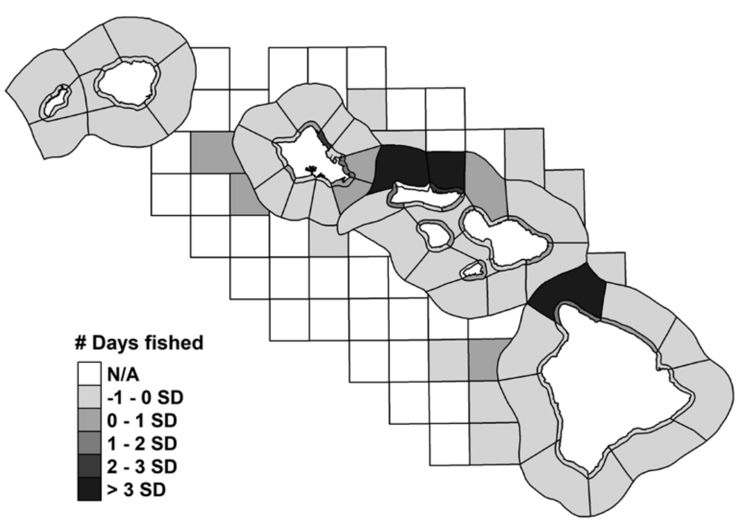

Bottom Map: This map shows the areas where individual fishermen are most likely to have interactions with false killer whales from the main Hawaiian Islands population, with the darkest areas having the highest estimated overlap. These indices were developed by overlapping commercial fishing effort data (represented here as the number of days fished in each area) with satellite tag data from the main Hawaiian Islands population, and are represented by standard deviations above/below the mean value. indices from Baird et al. 2021.

Page 35 Photo: False killer whales approaching a freediver off Kona, Hawai'i in April 2018. This group is part of the Hawai'i pelagic population and several individuals matched to groups seen in October 2013 and May 2020. *Photo by Paul Okumura.*

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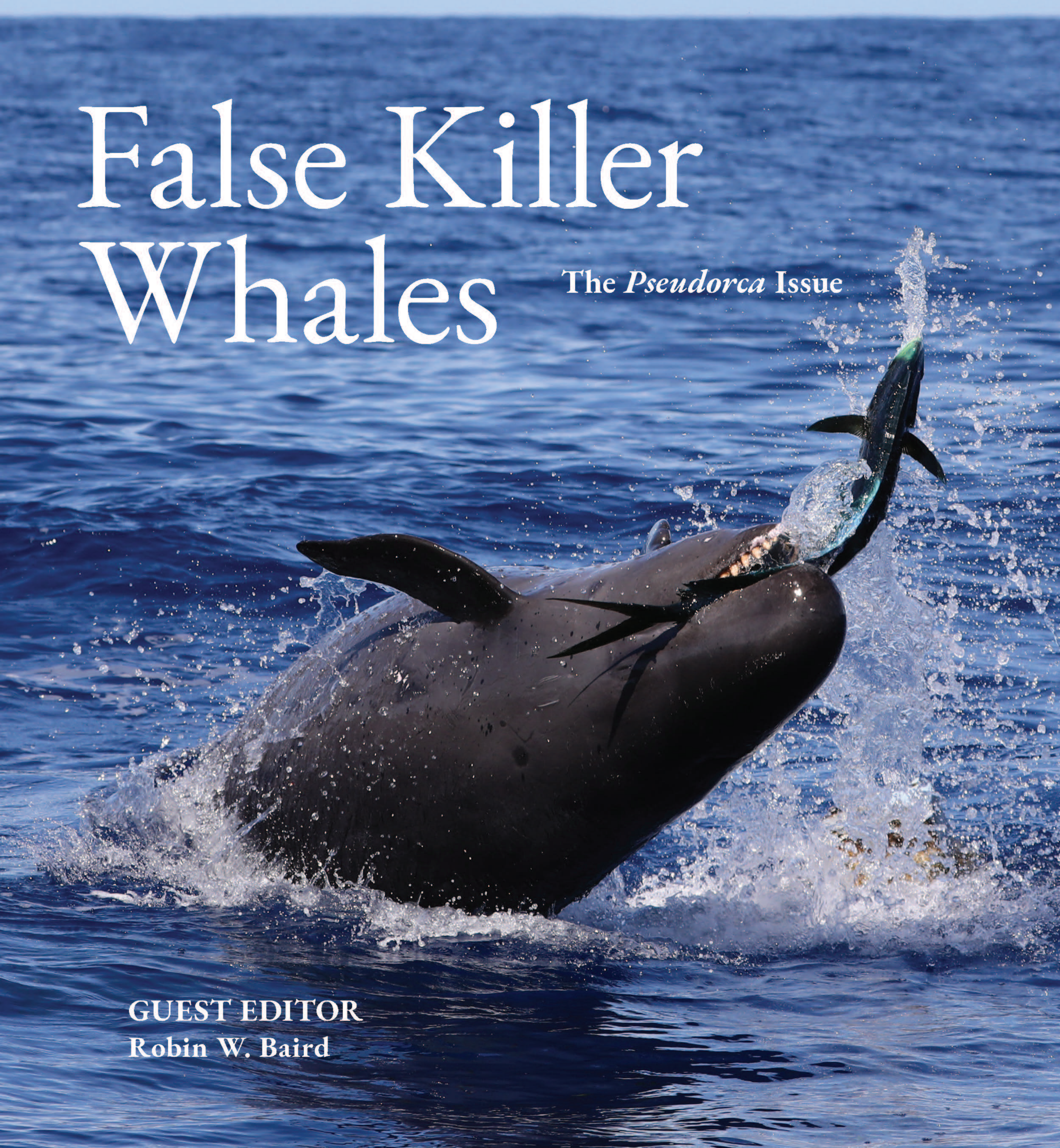

False Killer Whales

The *Pseudorca* Issue

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