POPULATION STRUCTURE, RESIDENCY, AND INTER-ISLAND MOVEMENTS OF COMMON BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) OFF O‘AHU AND MAUI NUI

by

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ABSTRACT

Population Structure, Residency, and Inter-Island Movements of Common Bottlenose Dolphins (*Tursiops truncatus*) off Oʻahu and Maui Nui

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Accurate descriptions of population structure are critical to inform effective management of protected species. Here I present the results of a reassessment of the population structure and residency of two common bottlenose dolphin (*Tursiops truncatus*) stocks from the main Hawaiian Islands. Previous photo-identification and genetic studies have shown that bottlenose dolphins in the main Hawaiian Islands live in four small (~100-200 individulas) demographically independent and genetically differentiated island-associated populations designated as stocks centered around Kauaʻi/Niʻihau, Oʻahu, Maui Nui (Maui, Lānaʻi, Kahoʻolawe, and Molokaʻi), and Hawaiʻi. However, photo-identification and satellite-tagging data has shown that some individuals do occasionally move between island areas, especially between Oʻahu and Maui Nui. These movements may have important consequences, as even a few dispersing individuals can impact genetic diversity and allow for the transmission of culturally-mediated behaviors, both of which could impact long-term population health..

I reassessed the population structures of the Oʻahu and Maui Nui stocks by analyzing over two decades' worth of photo-identification data representing 472 individuals, and satellite-tag data from five individuals. While I found that social connections between the two populations were minimal, there was geographic overlap in spatial use that crossed stock boundaries. This was caused by a subset of individuals (n=14) from the Oʻahu population that occasionally travel between island areas, using SW Oʻahu, SW Molokaʻi, and SW Lānaʻi. Satellite-tag data from two suspected inter-island travelers reveals that these animals made extensive use of Penguin Bank, indicating that this area may be of importance to inter-island travelers. Inter-island travelers were sighted in both island areas at all times of the year, though they were consistently sighted more frequently off Oʻahu than off Maui Nui. Further research will be needed to identify the possible drivers of this behavior.

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Dedication

For my mother, Celeste, who first taught me the love of nature.

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Chapter One: Literature Review: The Population Biology of Odontocetes and Global Population Structures of Common Bottlenose Dolphins

Introduction

As human populations and their consequent impact to the environment grow, conservation efforts are becoming increasingly important to ensure the preservation of wildlife species worldwide. Desirable conservation outcomes for wildlife are facilitated through effective communication and feedback between scientists and managers, as well as broad scale support from the public and policymakers. Scientists can identify and advocate for conservation priorities and act as a source of knowledge for managers, who may then utilize scientists' data and insights to craft new policy solutions or management strategies whose outcomes can then be evaluated by scientists as part of a continuous feedback loop. When considering conservation efforts at the species-level, population information such as distribution, population structure, and abundance are especially relevant, and these types of measures are assessed regularly for heavily managed species, including several species of marine mammals. The literature review portion of this thesis will explore and analyze how population structure is studied and evaluated among toothed whales and dolphins (parvorder *Odontoceti*) and how this information is used by managers, with particular emphasis on the common bottlenose dolphin (*Tursiops truncatus*).

Population Biology of Odontocetes

Toothed whales and dolphins include some of the most charismatic and highly intelligent species on Earth. At the moment there are over 70 different identified species of odontocetes, and continuing advances in genetics and taxonomy are likely to result in the classification of additional species. Many species of odontocetes have wide distributions at a global scale, but distribution is rarely continuous, and even when it is divisions within a species can quickly become apparent with closer observation. These divisions create cohesive groups of individuals within a species that are called populations, the exact definitions of which will be discussed at length.

Factors that influence the division of populations

Several factors have been hypothesized to influence the division of odontocete species into populations. Physical boundaries that separate populations in marine environments are not as obvious as in terrestrial environments, but evidence indicates that land barriers, salinity, and depth all limit dispersal ability of several marine species (Costello et al., 2017). While odontocetes have the capacity for long-range movements, geographic boundaries do seem to influence dispersal as has been shown for bottlenose dolphins in the Northeast Atlantic (Natoli et al., 2005). Additionally, fine-scale population structure among odontocetes has been repeatedly documented worldwide, proving that the capacity to disperse does not necessarily equate to actual dispersion (e.g., Mirimin et al., 2011; Kiszka et al., 2012; Mirimin et al., 2011; Möller et al., 2007; Urian et al., 2009).

Habitat preferences are suspected to limit dispersal between odontocete populations in some circumstances. For example, populations of inshore and offshore ecotypes of common bottlenose dolphins off Northwest Ireland have distributions that appear to be restricted by distance from shore, with the inshore ecotype only sighted within the 3 km closest to the shoreline, and the offshore ecotype only sighted at distances greater than 4 km from the shoreline (Oudejans et al., 2015). Inshore vs. offshore habitat preferences among common bottlenose dolphins are also reflected in dietary studies from United States East Coast, where the stomach contents of stranded inshore animals were found to contain near-shore species of fish, while the stomach contents of offshore animals had deep-water and pelagic species of fish and squid (Mead & Potter, 1995). Habitat preferences between different bottlenose dolphin ecotypes have been proposed as a driver of ecological specialization at an evolutionary scale, which will continue to increase their behavioral, morphological, and genetic divergence (Louis et al., 2014a, 2014b).

Habitat preferences have also been identified within populations of the same species and ecotype. For example, Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) populations along the southeast coast of Australia show significant genetic differentiation between coastal and bay habitats, and a high degree of site fidelity in spite of their very close proximity (Möller et al., 2007). Additionally, a genetic study of several U.S. East Coast bottlenose dolphin populations by Richards et al. (2013) found significant genetic differentiation between inshore populations occupying different habitat types along the coastline (Richards et al., 2013). The most startling example of fine-scale habitat preference the authors identified in this study was in the Indian River Lagoon of Florida, where one population of dolphins has a distribution restricted to the northernmost regions of the lagoon even while a second, partially sympatric population is seen throughout the entire range of the lagoon (Richards et al., 2013). The authors of both the southeast Australia and the U.S. East Coast studies hypothesized that the genetic differences between populations were the direct result of their specific habitat preferences (Möller et al., 2007; Richards et al., 2013).

Behavior, in conjunction with habitat preference, may also play a role in the development of population structures. Many odontocete populations have complex and specific social structures and behavioral patterns that have come be viewed as cultures, and cannot be explained by genetics alone (Rendell & Whitehead, 2001). Some aspects of culture are highly specialized to particular habitats, and may affect the willingness of populations to disperse to new habitats. For example, the Indo-Pacific bottlenose dolphins of Shark Bay exhibit habitat preferences that coincide well with different foraging strategies and genetic haplotypes (Kopps et al., 2014). In this case, social transmission of foraging strategies (usually from mother to calf) and a high degree of site fidelity has increased habitat specialization among different groups (Kopps et al., 2014). This in turn has increased philopatry, reduced mixing and led to genetic differentiation between groups (Kopps et al., 2014). Additionally, complex social structures may limit dispersal between populations. For example, Rosel et al. (2009) suggested that social relationships between common bottlenose dolphins on the U.S. Atlantic coast might limit their dispersal to new populations due to the relative cost of building new relationships.

Population definitions

In spite of its significance for both biological science and management, the precise definition of a population has been hotly debated within science for decades. Two major paradigms have emerged within this debate: the ecological paradigm, and the evolutionary paradigm (Waples & Gaggiotti, 2006). The ecological paradigm states that a population is defined by shared space and time and the opportunity to interact (demographic cohesion), while in contrast the evolutionary paradigm states that populations are defined by proximity and the opportunity to mate (reproductive cohesion) (Waples & Gaggiotti, 2006). The ecological paradigm is especially relevant for exploring population structure among intelligent species with a high degree of sociality, as has been frequently documented in odontocetes. Among these species, population cohesion is largely determined by behavioral patterns, rather than proximity or mating opportunity. A prime example of this is the existence of different sympatric ecotypes of killer whales (*Orcinus orca*) in the nearshore waters of the eastern North Pacific. While both fish-eating and mammal-eating ecotypes of killer whales frequently utilize the same territory, their group sizes and foraging tactics differ in accordance with their prey (Baird et al., 1992). Mating between ecotypes does not occur as a hypothesized consequence of these cultural differences, and it has been proposed that the cultural differences between ecotypes will eventually lead to their speciation (Baird et al., 1992; Riesch et al., 2012). In spite of their close proximity and the opportunity to mate, these two ecotypes of killer whale clearly represent different populations, and require different management strategies as such.

However, neither paradigm is ever "correct" to the exclusion of the other, and both perspectives are useful to managers. The evolutionary paradigm's emphasis on reproduction as a cohesive factor makes it well-suited to examining questions about long-term evolution and natural selection, and favors genetic approaches (Waples & Gaggiotti, 2006). In contrast, the ecological paradigm is more adapted to exploring short-term conservation-oriented questions, and can incorporate a larger range of methods, including studies of demographic connectivity (Waples & Gaggiotti, 2006). Under the ecological paradigm, a population is best defined through demographic independence (Waples & Gaggiotti, 2006; Martien et al., 2019). This occurs when population trends such as abundance are more strongly influenced by internal birth and death rates, rather than by emigration and immigration of individuals into/out of other populations. Such populations are referred to as demographically independent populations (DIPs).

Quantitative measures for evaluating population structure also differ between paradigms. Waples and Gaggiotti (2006) suggested that the most appropriate measure to define population boundaries in the ecological paradigm is the migration rate (m), also known as a dispersal rate, which is the percentage of individuals within a population that will disperse from their natal population into a new population. The precise cutoff where demographic independence occurs is highly dependent upon the species in question, but one estimate is that the cutoff occurs somewhere around m = 10% (Hastings, 1993). In contrast, rather than describing a single specific cutoff for demographic independence, Lowe and Allendorf (2010) argue that the type of connectivity being evaluated must be taken into account when determining a cutoff point. For example, while a low migration rate might be sufficient to theoretically prove ecological connectivity, it does not necessarily demonstrate actual connectivity to a degree that is relevant for conservation managers, unless the context in which migrants interact with the population is further explored (Lowe & Allendorf, 2010).

One important caveat of migration rates is that they mean little in a genetic context; even migration rates below 1% can reduce genetic differentiation within populations to the degree where they are hard to distinguish using genetic methods and conversely, high migration rates may not impact genetic differentiation at all if migrants fail to interbreed with a population (Martien et al., 2019; Waples & Gaggiotti, 2006). For example, killer whales live in stable matrilineal pods with only very rare dispersal of individuals between social groups, but population-level genetic analyses indicate an appreciable degree of relatedness within the population as a whole (Pilot et al., 2010). In this case, low dispersal between groups does not result in low gene flow rates between groups as predicted, demonstrating that migration rates do not necessarily equate to equivalent rates of gene flow. For this precise reason, Waples and Gaggiotti (2006) suggested that analysis of genetic datasets should be redirected towards more suitable approaches under the evolutionary paradigm, such as the number of migrants per generation (Nm). Nm is typically determined using genetic data, and can be used in two ways to determine if populations are demographically independent. First, Nm can be used to reject the assumption of panmixia, in which all individuals in the populations are interbreeding, or it can be proven that Nm falls below an arbitrarily set value for demographic independence (Waples & Gaggiotti, 2006). The value of the different approaches has been contested though. Palsbøll et al. (2007) caution that relying on a rejection of panmixia increases the risk of incorrectly designating management units, especially when statistical power is low, while Lowe and Allendorf (2010) again argue that any cutoff point for genetic connectivity must be considered in light of the type of connectivity being assessed.

Metapopulation theory adds another layer of complexity to finding an operational definition for a population. In metapopulation theory distinct localized populations of a species may remain connected through periodic dispersal events, forming a larger metapopulation. Classically, metapopulations are comprised only of isolated populations separated by unsuitable habitat, without any large populations to act as a reservoir of immigrants (Levins, 1969). Metapopulation theory is compatible with both the ecological and evolutionary paradigms, and can have significant biological and conservation implications for the persistence of populations in that it allows for even struggling localized populations to persist because of influxes of new animals from surrounding populations (Hanski, 1991). However, metapopulation theory has little relevance for delineating demographically independent populations for management purposes. Quantitative methods for studying the dynamics of metapopulations usually involve assessing both dispersal (i.e., m or Nm, as previously described) and connectivity (the ease of movement between localized populations). Calabrese and Fagan (2004) separated measures of connectivity into three flavors: 1) structural connectivity, which describes the physical spaces between populations, 2) potential connectivity, which predicts connections between populations by integrating dispersal information with spatial descriptions, and 3) actual connectivity, which is derived directly from observation. Measures of structural connectivity can incorporate information on the distance between suitable habitat spaces, the type of habitat, and the area of different types of habitat, while potential connectivity measures usually incorporate knowledge of behavioral responses to habitat type and dispersal ability, and actual connectivity measures directly incorporate observational data of movements between populations (Calabrese & Fagan, 2004; Kindlmann & Burel, 2008).

Datasets that are useful in evaluating population structure

Several different types of data can be used to study population structure in odontocetes, and have been broadly reviewed in Martien et al. (2019). The most reliable conclusions are drawn from morphometric, genetic, and movement datasets, while moderately reliable conclusions can be drawn from distributional data, contaminant ratios, habitat preferences, and association data (Martien et al., 2019). However, these different lines of evidence are relevant at different time scales and levels of divergence, and inherent tradeoffs also exist in data collection.

Morphometric and genetic datasets can be used to draw some of the most reliable long-term conclusions about population structure. Morphometric differences only emerge after a long period of isolation between populations, while genetic differences can appear after a much shorter period of isolation. For example, morphometric differences have been regularly used to differentiate between stranded individuals of inshore and offshore ecotypes of common bottlenose dolphins, which differ in their body size, bone structure, and hematology (Duffield et al., 1983; Mead & Potter, 1995). However, morphometric differences between inshore populations of common bottlenose dolphins are often subtle at best, and genetic methods are more commonly applied to differentiate between these populations (e.g., Natoli et al., 2004).

Movement and distributional data can be used to draw reliable and moderately reliable conclusions about population structure, but both may vary temporally, which presents a challenge in interpreting these types of data. Movement data may vary both over time and according to demographic variables. For example, adult male common bottlenose dolphins and subadults of both sexes in Sarasota Bay, Florida, have been shown to explore larger areas of their home ranges than the adult females within the same population (Wells et al., 1987). Additionally, even if movement data reveals possible spatial overlaps between populations, the significance of those overlaps cannot be interpreted without additional data to provide context (Martien et al., 2019). For example, Baird et al. (2016) reports that a common bottlenose dolphin tagged off Kaua‘i in October 2014 dispersed to O‘ahu nine days after being tagged, but a lack of further resightings of the tagged animal makes it unclear whether this movement between islands represents a permanent or temporary dispersal. Distributional hiatuses, when larger than home ranges, can be especially helpful in defining stock boundaries, though careful consideration must also be applied to where distributions change seasonally or over time (Martien et al., 2019). For example, the U.S. East Coast migratory stocks of common bottlenose dolphins are most clearly defined by their distributions during the summer months, when they have the smallest degree of overlap with other stocks, whereas in the winter months a high degree of overlap between stocks makes defining them by distribution very difficult (Hayes et al., 2018).

Habitat preferences and contaminant ratios can also be used to draw moderately reliable conclusions about population structure. The use of habitat preferences as a line of evidence in defining populations is informed by the idea that different populations will specialize in using separate habitats, and contaminant ratios in individual animals may reflect this specialization as well, provided that the habitat is contaminated. For example, common bottlenose dolphins in the Indian River Lagoon in Florida are divided into two genetic clusters, with one restricted to the northern portion of the lagoon while the other, partially sympatric cluster ranges primarily in the southern portion of the lagoon, reflecting differences in habitat preference between these two clusters (Richards et al., 2013). A 2015 study of blood samples from both clusters also showed that these habitat preferences may be driving differences in contaminant ratios, as mercury concentrations exist along a gradient that decreases from north to south (Schaefer et al., 2015). Habitat preferences and contaminant ratios may also vary with demographic factors, and visiting transient animals may further complicate attempts to define populations with these datasets (Martien et al., 2019).

Association data have been repeatedly used to demonstrate the demographic independence of populations (e.g., Baird et al., 2009; Mahaffy et al., 2015), but is not always practical because of the need for long-term and intensive efforts to identify individual members of a population (Martien et al., 2019). Additionally, association data is useful only for species with a high degree of sociality, which may limit its applicability for certain species. Regardless of the approach taken to explore population structure, the products of these efforts, and their consequences all come down to the interpretation of results by policy makers.

Legislative Definitions and Applications of Population Structure for Managing Odontocete Populations

Legislative definitions of populations may not necessarily equate to biological distinctions, and may leave little room for nuanced explanations or the incorporation of scientific uncertainty. However, these definitions form the basis for management decisions regarding different species and have significant consequences for conservation efforts.

Within the U.S., odontocetes are primarily managed under the Marine Mammal Protection Act (MMPA) of 1972, which utilizes the best available scientific information about population structure to designate management units called stocks. The definition of a stock under the MMPA has gradually evolved. The 1994 amendments to the MMPA first defined stocks as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature", a definition that falls under the evolutionary paradigm because of its emphasis on interbreeding. However, in 2005 NMFS refined this definition by stating that stocks should be DIPs (NMFS, 2005). This refinement shifted the stock concept towards the ecological paradigm, and emphasizes the importance of dispersal over genetic differentiation (Martien et al., 2019).

The National Marine Fisheries Service (NMFS) is responsible for designating odontocete stocks based on the best available scientific evidence. Once designated, a new stock assessment report is supposed to be produced every three years that incorporates the best available scientific information to ensure that the abundance of designated stocks remains at the optimum sustainable population level for ecological sustainability, though some vulnerable stocks are assessed more frequently. However, it is also important to acknowledge that politics, both internal and external to NMFS, can also play a role in determining the frequency with which stocks are reassessed. The language of the MMPA makes clear that the conservation of stocks to preserve ecosystem functionality is a priority for managers, but stock designation initially favored large stock designations often corresponding with geopolitical boundaries, rather than taking a precautionary approach that favored small stock designations (Martien et al., 2019). This was problematic for achieving conservation goals, as the comparatively large allowable losses in improperly designated large stocks may be devastating for small populations that are disproportionately impacted. As a result, revisions have since broken many large stocks into smaller stocks as scientific evidence shows that divisions are warranted (Martien et al., 2019). This highlights the importance of accurate scientific information to guide management.

Population structure information is also utilized in the Endangered Species Act (ESA) of 1973, which is applied in addition to the MMPA for some odontocete species. In contrast to the MMPA concept of stocks, the ESA utilizes management units called Distinct Population Segments (DPS). This unit may not necessarily equate to a stock, and in practice DPSs are frequently larger units because of different genetic divergence thresholds. One of the reasons for this is that the MMPA prioritizes ecological function over genetic differentiation, while the ESA prioritizes preserving genetic diversity to conserve small populations (Martien et al., 2019). Regardless of the technical definition for management units however, both acts are dependent on accurate assessments of population structure in order to be effective in achieving conservation goals.

Common Bottlenose Dolphins – Globally Observed Population Structures

Common bottlenose dolphins are one of the most easily recognizable and well-studied cetacean species in the world. They are globally distributed throughout tropical and temperate waters, and divided into both inshore and offshore ecotypes that are occasionally sympatric. Site fidelity is variable in this species, and various populations have been described as either migratory or resident (e.g., Hayes et al., 2018). Inshore resident populations of common bottlenose dolphins in particular have been identified as an ideal sentinel species for monitoring changes in ecosystem health because of their long lifespans, high trophic level, and tendency to store environmental pollutants in their blubber (Bossart, 2011; Wells et al., 2004).

Indo-Pacific bottlenose dolphins are the only other long-recognized species within the same genus as common bottlenose dolphins, though their distribution is currently thought to be limited to the Indian and Western Pacific oceans. While there is some evidence of hybridization between the two species, genetic studies have shown that Indo-Pacific bottlenose dolphins are more closely related to species within the *Stenella* genus than to common bottlenose dolphins, indicating that perhaps this species has been misplaced taxonomically (Martien et al., 2011; Möller et al., 2008). While many characteristics are shared between the two species, this review will be limited to common bottlenose dolphins (hereafter just "bottlenose dolphins") from this point.

A defining characteristic of bottlenose dolphins is their well-developed cognitive intelligence, which has allowed bottlenose dolphins to develop novel strategies for foraging that are well-suited to their specific environments. For example, bottlenose dolphins in the Florida Keys practice mud-plume feeding in shallow areas, where dolphins intentionally stir fine sediments into a suspended plume, then lunge through the plume to capture fish inside (Lewis & Schroeder, 2003). Further north in Florida, the bottlenose at Cedar Key practice fish herding, where groups of dolphins work together to drive fish towards one another (Gazda et al., 2005). Additionally, bottlenose dolphins in U.S. East Coast salt marshes have been observed stranding themselves to drive fish onto mud banks for easier capture (Hoese, 1971; Rigley et al., 1981). Each of these foraging strategies are uniquely suited to the habitat where they are practiced, and constitute a form of ecological niche specialization within populations that may limit dispersal and reinforce population structure (Hoelzel, 2009).

A recurring trend among bottlenose dolphin populations is the mixing of several different residency categories within one geographical region, which can create confusion in delineating populations. Bottlenose dolphins live within fission-fusion societies, where group sizes and their individual compositions regularly fluctuate, though some long-term relationships between individuals are maintained (Connor & Wells, 2000). An interesting consequence of this type of social structure is the regular mixing of resident, transient, and migrant animals within the same geographic area, which has been documented in several populations of bottlenose dolphins (e.g., Dinis et al., 2016; Estrade & Dulau, 2020; Silva et al., 2008; Speakman et al., 2010). While these overlaps may increase the opportunities for gene flow, they do complicate the process of delineating populations because they increase the chances of incorporating individuals that are part of a separate population that is not actually resident to the area. To counter this, Martien et al. (2019) recommends that associations be interpreted in the context of additional information. Estrade and Dulau (2020) accomplished this by assigning residency classes to the individuals that they studied, and by evaluating differences in observed movement patterns.

As previously mentioned, behavioral traits in conjunction with habitat preferences can be a driver of population structure. The combined global distribution and widespread ecological niche specialization of bottlenose dolphins has helped to establish an impressive array of population structures within this species, several of which are reviewed below. These classifications are broadly defined, but they do not necessarily capture the entire spectrum of possible population structures.

Offshore Populations

Offshore bottlenose dolphins have been the subject of comparatively few studies, mostly because of inherent difficulties in conducting deep-water surveys, and limited information is available about their population structures and behaviors (Klatsky et al., 2007). Offshore bottlenose populations have a high degree of genetic diversity based on samples taken from stranded animals, which may be indicative of large, undifferentiated populations (Costa et al., 2015; Hoelzel et al., 1998; Oudejans et al., 2015). There is also evidence that offshore bottlenose may regularly travel long distances and show minimal site fidelity, covering up to 89 km/day in extensive journeys that have been documented to reach 4,200 km (Wells et al., 1999). However, only limited conclusions can be drawn from these two lines of evidence. The stranded animals sampled in genetic studies may represent members of multiple offshore populations that have drifted to strand at the same location (Hoelzel et al., 1998). Additionally, studies of movement data for offshore bottlenose have had contradictory results: Wells et al. (1999) tagged two animals that moved 89 km/day and 48 km/day, while Klatsky et al. (2007) tagged three dolphins that travelled much smaller distances, averaging only 28 km/day. Klatsky et al. (2007) suggested that their comparatively shorter average daily travel distances were the result of their tagged animals lingering at specific sites during the time frame where movements were recorded, possibly to take advantage of available prey. Additionally, differences in their movements may have been driven by habitat differences in the areas where Wells and Klatsky tagged or released dolphins; Klatsky deployed tags off the Bermuda pedestal, while Wells tagged dolphins that had been previously stranded in Florida (Klatsky et al., 2007; Wells et al., 1999). Further studies of offshore bottlenose dolphins will be needed to elucidate accurate information about their population structures.

Coastal and Migratory Coastal Populations

Some inshore populations of bottlenose dolphins live in populations characterized by long-distance movements and regular mixing. The best documented examples of this type of population structure are found on the U.S. West and East Coasts. On the U.S. West Coast, the Coastal California Stock of bottlenose dolphins has an extensive range that stretches from San Francisco into northern Baja, Mexico (Carretta et al., 2019; Defran et al., 2015). Photo identification studies have shown that individuals in this stock regularly travel long distances along the shoreline, sometimes moving up to 95 km/day (Defran & Weller, 1999; Hwang et al., 2014). In spite of its large range this stock remains genetically distinct from offshore populations, and has more limited genetic diversity than offshore animals, indicating its cohesiveness as a population (Lowther-Thieleking et al., 2014). Defran et al. (2015) suggested that the long-distance movements within this population may be a consequence of limited prey predictability, as animals are forced to travel farther in pursuit of foraging opportunities.

On the U.S. East Coast, two migratory stocks of bottlenose dolphins have been delineated that perform seasonal migrations along the coastline (Hayes et al., 2018). The Western North Atlantic Northern Migratory Coastal Stock spends the summer months between Assateague, Virginia and Long Island, New York, then moves south between Cape Lookout, North Carolina, and the North Carolina/Virginia border for the winter months (Garrison et al., 2017). The Western North Atlantic Southern Migratory Coastal Stock, on the other hand, spends its summer months to the north of Cape Lookout, North Carolina and Assateague, Virginia, then moves south between Cape Lookout and northern Florida for the winter months (Garrison et al., 2017). Between the two stocks, differences also exist in their abundance, and the number and type of overlapping commercial fisheries, warranting their separate management (Hayes et al., 2018).

However, knowledge of the population structure of these two stocks is still evolving. Initially, all Atlantic coast bottlenose dolphins were treated as members of a single depleted stock, but this notion that was later disproven with genetic methods and stock designations were consequently reassigned by NMFS (Rosel et al., 2009, 2011). Even with genetic methods the ease of delineating these two migratory stocks changes seasonally due to spatiotemporal overlap though, and understanding of the demographics and movement patterns of the Southern Migratory stock remains especially limited (Hayes et al., 2018). Toth et al. (2012) has suggested that additional divisions may even exist in the comparatively well-understood Northern Migratory Stock, based on sighting locations, behavior, morphology, and the occurrence of a commensal barnacle.

Transient Archipelago-Associated Populations

Some archipelago-associated populations of inshore ecotype bottlenose dolphins also live in transient populations with regular movement between islands and little genetic differentiation. One example of this comes from the Canary Islands, Spain, where a photo-identification study identified a small population of bottlenose dolphins (Tobeña et al., 2014). Over the course of ten years, 313 individual dolphins were identified in the islands, 36 (10%) of which moved between islands at least once, travelling distances between 30-130 km (Tobeña et al., 2014). Another example comes from the Azores, Portugal, where out of 966 bottlenose dolphins identified in a photo-identification study, 66 (7%) individuals moved between island areas (Silva et al., 2008). While the average distance between sightings was only 25 km in the Azores study, movements of up to 291 km were repeatedly detected (Silva et al., 2008). This suggests that the population is not divided between island areas, as the distance between island groups ranges from 160-230 km, well within the range of movement displayed by these animals (Silva et al., 2008). A third example of this type of population structure comes from the Madeira Archipelago, Spain, where out of 501 documented individuals, only 15 (4%) were resighted in more than one year, and regular inter-island movements of approximately 50 km were likely based on calculated movement probabilities (Dinis et al., 2016). Additionally, no genetic differentiation has been detected within the Madeira Archipelago, indicating a lack of island-associated population structuring (Quérouil et al., 2007). Interestingly, different portions of the Madeira archipelago had varying probabilities of immigration and emigration, especially areas with shallow-water habitats, where prey is likely more readily available (Dinis et al., 2016). This raises the question of why bottlenose dolphins move between islands so readily.

Reasons suggested for inter-island movements include seeking out foraging or mating opportunities (Hooker & Gerber, 2004). The waters surrounding both the Canary Islands and the Azores are oligotrophic, which may contribute to limited prey availability that forces animals to travel farther distances to forage (Baird et al., 2009; Silva et al., 2008; Tobeña et al., 2014). In contrast, while in the Madeira archipelago there are shallow-water areas with assumed high prey availability, the high rate of immigration and emigration in these areas suggests that other factors, such as anthropogenic impacts or exposure to predators are preventing the establishment of a resident population in this region (Dinis et al., 2016). Limited genetic differentiation within the Azores population and within the North Atlantic region as a whole also suggests that movement between islands increases mating opportunities, though this is more likely a consequence rather than a driver of movements (Quérouil et al., 2007; Silva et al., 2008).

Resident Coastal Populations

Resident coastal populations of bottlenose dolphins have been repeatedly described in the literature worldwide. These populations are characterized by a high degree of site fidelity and genetic differentiation from neighboring populations, and frequently live within easily distinguishable habitats like estuaries or lagoons. Fourteen distinct resident coastal populations have been recognized along the U.S. East Coast alone, 11 of which are localized to estuarine systems or embayments (Hayes et al., 2018). Globally, additional resident populations of bottlenose have also been described in western Ireland (Mirimin et al., 2011; Nykänen et al., 2018), Greece (Bearzi et al., 2008), the Black Sea (Gladilina et al., 2018), New Zealand (Tezanos-Pinto et al., 2009), the Caribbean (Caballero et al., 2012), and southern Brazil (Costa et al., 2015; Fruet et al., 2014), just to name a few.

Some of the most well-described populations of resident bottlenose dolphins are located in the Gulf of Mexico, where 32 bay, sound, and estuarine stocks are currently recognized by NMFS (Rosel et al., 2011). In particular, a 50 year examination of the Sarasota Bay, Florida resident bottlenose has yielded incredibly detailed information that is fairly representative of resident bottlenose communities described elsewhere. This population is small, with approximately 160 individuals, and has been thoroughly documented over 40 years of study (Wells, 2009). Both female and male Sarasota dolphins show site fidelity to the bay, though males occasionally disappear for short periods, and have been seen in association with members of neighboring populations (Wells et al., 1987; Wells & Scott, 1990). Immigration and emigration are rare in spite of this however, and the dynamics of the population are thus dependent on births and deaths (Wells & Scott, 1990). This degree of insularity has led to significant genetic differentiation from other neighboring populations, and may be maintained through specialized foraging behaviors (Sellas et al., 2005). Most of the population traits described for the Sarasota Bay animals (small population size, high site fidelity, genetic distinctiveness, and habitat-specific behaviors) are also represented in other documented coastal resident populations, though variation does occur.

Resident Island-Associated Populations

Other than the main Hawaiian Islands stocks (reviewed in chapter two), resident island-associated populations of bottlenose dolphins have only been described a few times. One of these populations is found off the Little Bahama Bank in the Bahamas (Parsons et al., 2006). In contrast to other island-associated populations discussed in this review however, Little Bahama Bank is a single sand-bank system, meaning that the two major islands that comprise the bank are not separated by deep-water channels (Parsons et al., 2006). This may increase the ability of animals to move between areas in the islands because there is no break in suitable habitat between areas (Parsons et al., 2006). However, photo-identification surveys of the population revealed that dolphins showed site fidelity to surveyed sites on East and South Abaco, with only infrequent movements between areas (Parsons et al., 2006). Additionally, genetic analyses revealed that gene flow is limited between East Abaco, South Abaco, and a third study site at White Sand Ridge, all of which are less than 200km apart (Parsons et al., 2006).

Recently, a resident island-associated population of bottlenose dolphins off Reunion Island was described for the first time using photo-identification data collected over six years (Estrade & Dulau, 2020). Dolphins were present at the island year-round, though only 1/3 of animals were classified as residents, and immigration and emigration occurred regularly (Estrade & Dulau, 2020). In spite of the documented presence of resident animals, there is still a sizable proportion of individuals that are transient that associate with resident animals (Estrade & Dulau, 2020). An island-associated population of bottlenose dolphins similar to the Reunion population has been described off São Tomé, in the Gulf of Guinea along the western coast of Africa (Pereira et al., 2013). A photo-identification study of cetaceans off this island has revealed that the bottlenose dolphin population there is very small, with only an estimated 37 individuals, and regular resightings of roughly only 1/3 of the total number of identified animals (Pereira et al., 2013). While the dataset used in the São Tomé study was limited in its scope, the regular resightings of a few individuals do suggest some degree of residency (Pereira et al., 2013). However, the high proportion of non-resident animals sighted off both Reunion and São Tomé indicates that perhaps these populations as a whole should not be considered as truly resident to the island, but may fall somewhere between the classifications of resident and transient island- or archipelago-associated populations given in this review.

Additional resident island-associated populations of bottlenose dolphins may be described in the future, but the present rarity of this particular type of population structure indicates that the ecological conditions which favor it are generally uncommon.

Metapopulation Structures

Metapopulations are clasically defined as a series of connected but isolated habitat patches surrounded by unsuitable habitat and no unlimited large population to provide a constant influx of immigrants (Levins, 1969). This is compatible with many described resident bottlenose dolphin populations, which show site fidelity to areas that are separated from one another by habitat either unsuitable for foraging or where predation risk is increased. Additionally, most resident bottlenose dolphin populations have no nearby large stock constantly supplying new immigrants, though there is frequently some small degree of movement between populations. This suggests, therefore, that metapopulation theory may be useful in evaluating the population structures of this species, though to date it has only rarely been applied. Two metapopulation structures of bottlenose dolphins have been identified by Gladilina et al. (2018): the well-connected migratory Coastal California Stock (described earlier), and the slightly less well-connected northwestern and central Mediterranean basin populations. The Mediterranean basin populations fall somewhere between the previously explored classifications of migratory and resident populations, and are characterized by regular long-distance movements of individuals between stocks that generally show site-fidelity, resulting in genetic differentiation between the western and eastern portions of the basin that becomes less apparent at a closer scale (Bearzi et al., 1997; Bearzi et al., 2010; Gaspari et al., 2015; Gnone et al., 2011; Natoli et al., 2005). Interestingly, Carnabuci et al. (2016) described the northwestern Mediterranean basin populations as a metapopulation, but elsewhere the Coastal California Stock and Mediterranean basin populations are generally not described as metapopulations in the literature. Metapopulation structure has also been hinted at to describe the loosely connected resident populations of Western Ireland and the United Kingdom, though this suggestion has drawn criticism (Ingram & Rogan, 2003; Louis et al., 2014a; Nichols et al., 2007; Nykänen et al., 2018). In general, metapopulation theory has not been regularly applied to examine population structure and dynamics among bottlenose dolphins. This might be occurring because of ambiguity over how to define metapopulations of bottlenose dolphins, the lack of relevance that metapopulation theory has in delineating DIPs for management purposes, or because of geographic limitations in study designs that restrict scientists to single localized populations and prevent identification of connections between populations.

Conclusion

Common bottlenose dolphins exist in a variety of population structures worldwide that are influenced by geography, oceanographic conditions, habitat preferences, behavior, and social structure. While the precise definition of a population remains subject to debate, the most relevant definition for this highly charismatic species is the DIP, which is theoretically intended to be analogous to the MMPA's definition of stocks. Accurate designation of stocks, performed by NMFS, is of paramount importance to inform effective management, and is informed by the best available scientific knowledge. This may include conclusions drawn from any number of datasets, including morphometric, genetic, movement, and distributional data, as well as contaminant ratios and habitat preferences (Martien et al., 2019).

Chapter Two: Introduction: Hawaiian Resident Common Bottlenose Dolphins

The Hawaiian Islands are one of the most isolated archipelagos in the world, located in the middle of the Pacific Ocean and surrounded by a vast expanse of oligotrophic tropical waters. Despite their isolation however, the islands and waters surrounding them have been repeatedly colonized by wildlife of all varieties, and as a result are rich in biodiversity and home to many endemic species (Eldredge & Evenhuis, 2003). One of the hypothesized factors driving the marine diversity of the region is the comparatively high rate of productivity of the waters surrounding the islands, known as the "island mass effect" (Doty & Oguri, 1956; Gove et al., 2016). This effect is driven primarily by upwelling, but is also influenced by reef ecosystem processes and natural and anthropogenic nutrient runoff (Gove et al., 2016).

One of the remarkable aspects of Hawai'i's biodiversity is the presence of 11 species of odontocetes with resident populations that remain in the islands year-round, including dwarf sperm whales (*Kogia sima*), Blainville's beaked whales (*Mesoplodon densirostris*), Cuvier's beaked whales (*Ziphius cavirostris*), false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), melon-headed whales (*Peponocephala electra*), short-finned pilot whales (*Globicephala macrorhynchus*), rough-toothed dolphins (*Steno bredanensis*), pantropical spotted dolphins (*Stenella attenuata*), spinner dolphins (*Stenella longirostris*), and bottlenose dolphins (Baird et al., 2015). These populations were likely established from offshore populations that "discovered" the islands and remained to take advantage of the increased availability of prey that they found surrounding the islands compared to in offshore habitats (Baird, 2016). The resident bottlenose dolphin populations, for example, show evidence of genetic relatedness to offshore animals sampled in the area (Martien et al., 2011).

Ecotypes, Distribution, Population Structure, and Status

Both inshore and offshore ecotypes of bottlenose dolphins can be found in Hawaiian waters, and are currently divided into one offshore pelagic stock and four inshore island area associated stocks, centered around Kaua‘i/Ni‘ihau, O‘ahu, Maui Nui (Maui, Lāna‘i, Kaho‘olawe, and Moloka‘i), and Hawai‘i (Figure 1; Carretta et al., 2019). Boundaries for the four island-associated stocks are currently drawn at the 1,000 m depth contour, with the exception of the O‘ahu and Maui Nui stocks, which are separated at the Ka‘iwi Channel between the islands at approximately 500 m depth (Carretta et al., 2019). A 2009 abundance estimate based on photo-identification data placed the abundance of each of the four island-associated stocks in the low hundreds, with the exception of O‘ahu, which was placed around 700 (Baird et al., 2009). However, the relatively high abundance estimate for the O‘ahu stock in the 2009 estimate was likely a consequence of data limitations, and a more recent abundance estimate has placed the O‘ahu stock’s abundance in the low hundreds as well (Baird et al., 2009; Van Cise et al., 2021).

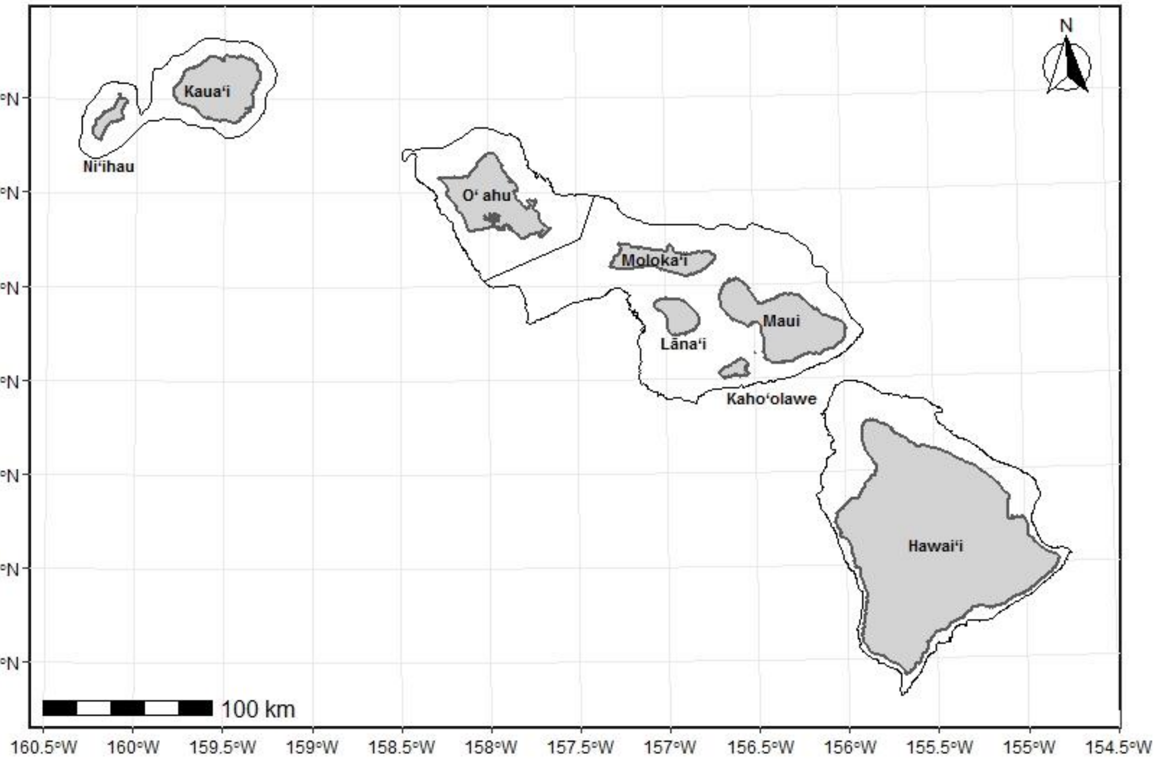


Figure 1. Stock boundaries of the four resident island-associated stocks of common bottlenose dolphins. Stock boundaries are drawn at the 1,000 m bathymetric depth contour, with the exception of the O'ahu and Maui Nui stock boundary, which is drawn at approximately the 500 m bathymetric depth contour.

Hawaiian inshore bottlenose dolphins are distributed primarily throughout shallow waters, with over 95% of sightings taking place at depths shallower than 1,000 m, and over 50% of sightings taking place at depths shallower than 500 m (Baird et al., 2013; Baird, 2016). Sightings have occurred year-round at each island area, with high resighting rates indicative of resident populations (Baird et al., 2009; Baird, 2016). Additionally, genetic analyses have revealed that the island-associated populations are genetically differentiated from one another (Martien et al., 2011). Both satellite-tagging efforts and photo-identification have shown that animals rarely leave their island areas, though occasional inter-island movements have been documented through both methodologies, especially between Maui Nui and O'ahu, which are the two island areas that are closest in proximity (Baird, 2016). The significance of these inter-island movements remains unknown at present, but one possible consequence is that it increases the exposure of some individuals to spatially variable anthropogenic threats.

There is evidence that three of the four resident stocks are in decline, with significant declines in the Maui Nui stock, and non-signficant declines in the O‘ahu and Kaua‘i/Ni‘ihau stocks (Van Cise et al., 2021). Model-derived apparent survival rates are also lower than expected in all four stocks, with the lowest apparent survival rate in the O‘ahu stock (0.84, se = 0.023; Van Cise et al., 2021). The factors driving these declines are uncertain at present, but exposure to anthropogenic stressors likely plays a role.

Anthropogenic Threats

Today, the State of Hawai‘i, comprising the eight major islands at the southeastern end of the archipelago, is home to over 1.4 million people, and boasts a booming economy largely rooted in natural resources and tourism (State of Hawai‘i DBEDT, 2019). Dense human inhabitation is known to have negative consequences for wildlife populations however, and bottlenose dolphins in Hawai‘i are exposed to a variety of anthropogenic stressors, many of which vary by island area (Figure 2).

Figure 2. Examples of potential anthropogenic stressors to Hawaiian insular bottlenose dolphins that vary spatially, including fisheries interactions, tour boats, and military vessel activity. Photo credits clockwise from top left: Deron Verbeck, Alicia Ward, Jessica Aschettino/CRC, and Tori Cullins.

One example of a spatially-variable stressor is ambient noise from anthropogenic activities. Shipping activity is most frequent in the Hawaiian Islands off the island of O‘ahu, where Honolulu functions as a major port city, and there are considerable volumes of small boat traffic off Maui Nui and Hawai‘i. Large commercial ships are especially significant noise generators that can produce up to 195 dB of ambient noise, though even small boats can produce up to 160 dB (Hildebrand, 2009). Increased ambient noise may interfere with the ability of animals to communicate with one another by masking their vocalizations, as has been documented in other species (e.g., Van Parijs & Corkeron, 2001). Increased boat traffic has also been shown to induce changes in breathing among bottlenose dolphins, possibly as part of an anti-predator response to boat noise (Hastie et al., 2003). Additional noise may come from military activities, which are especially prevalent around Kaua‘i and Ni‘ihau. Military mid-frequency sonar can produce sound levels on the order of 235 dB, and is regularly used on the

Pacific Missile Range Facility off Kaua‘i, where resident bottlenose dolphins may be repeatedly exposed to sonar (Baird et al., 2014; Hildebrand, 2009). Exposure response studies in bottlenose dolphins have shown that exposure to high levels of sound may induce behavioral changes, which could have significant consequences for survival (Houser et al., 2013).

Bottlenose dolphins are also impacted by fisheries activity off the main Hawaiian Islands. Their shallow distribution places them into regular contact with nearshore fisheries, and there is evidence that animals are at least occasionally hooked or entangled, likely when trying to steal bait or catch (Baird, 2016; Sims, 2013). Additionally, fishermen may sometimes attempt to retaliate against animals that try to depredate lines, with potentially lethal consequences (Baird, 2016; Harnish et al., 2019). Another source of potential fisheries interactions is an offshore fish farm on Hawai‘i Island’s Kona coastline, which has drawn repeated, long-term associations by bottlenose dolphins (Harnish et al., 2021; Sims, 2013). Elsewhere, regular associations with fish farms have caused changes in social structures and association patterns (Díaz López & Shirai, 2008). Similarly, there is evidence that the Kona farm may also be inducing behavioral changes, including increased inter-species aggression and smaller group sizes (Harnish et al., 2021). Additionally, long-term associations with the Kona farm hint at potential dependency, which could have a devastating impact in the case that the farm is ever removed (Harnish et al., 2021). Overall, the spatial variation in anthropogenic impacts to the resident bottlenose dolphins emphasizes the need for accurate stock delineation to inform management efforts for these populations, which is especially critical now given the evidence that some of these stocks may be in decline.

Conclusion

One of the rarest types of population structure documented for bottlnose dolphins are resident island-associated populations, four of which have been documented off the main Hawaiian Islands and are designated as separate stocks for management. The long-term residency of these stocks makes them vulnerable to island-specific anthropogenic threats, and a recent abundance estimate indicates that three of these stocks may be in decline. Appropriate management strategies must take into account any possible connections between stocks that could allow for increased gene flow or the spread of socially transmitted behaviors. Long-term photo-identification and satellite-tagging efforts off the islands of O‘ahu and Maui Nui have shown that occasionally individual animals do move between areas, meaning that these populations may not be demographically independent, though the significance of these inter-island movements remains unknown at present (Cascadia Research Collective, unpublished data).

The aim of this thesis will be to provide an updated assessment of the residency patterns and possible connections between the O‘ahu and Maui Nui stocks. This information will help to inform accurate management of these populations, which is especially critical now, given the recent evidence of declines and lower-than-expected survival rates in both stocks.

Chapter Three: Methods

Primary Datasets

Photo-identification

Cascadia Research Collective (CRC) encounters with bottlenose dolphins took place as part of a larger effort to study multiple species of Odontocetes through small boat surveys from 2000-2018. Survey effort varied both between island areas and over time, and was both nonrandom and nonsystematic, though efforts were made to cover the greatest area and variety of habitats possible, given limitations imposed by weather conditions. While surveying, GPS locations of the survey vessel were recorded every five minutes. Whenever the survey vessel detected a group of odontocetes, the group was approached until it was in range for species identification, and the location, behavior, and estimated group size was recorded. Depending on the species, photographs were taken of as many individuals as possible within the group, including non-distinctive animals. Additional photographs of bottlenose dolphins were taken by other researchers and community members from Hawai‘i from 1996-2018, and contributed to CRC. An encounter is considered an observation of a group of animals, and encounters ended either when the group was lost, or the survey vessel left the group. A single day of survey effort could include multiple encounters with the same group of animals. The circumstances of encounters contributed by other researchers and community members varied widely, and locations of encounters were not always recorded, though information about the island area where encounters took place was always available.

All photographs of bottlenose dolphins were sorted within encounters by individual, using the unique pattern of natural marking on each animal (notches on dorsal fin, pigmentation, scarring, etc.). Then, following the protocols in Baird et al., (2009), individuals were compared against the long-term CRC catalog of bottlenose dolphins to establish sighting histories. Each individual was assigned a distinctiveness score between 1 and 4 (1 = not distinctive, including unmarked fins; 2 = slightly distinctive, with 1-2 notches; 3 = distinctive, with 3-5 notches; 4 = very distinctive, with 5 or more notches), and a best photo quality score between 1 and 4 (1 = poor, 2 = fair, 3 = good, 4 = excellent) for every encounter (Figure 3). All unique individuals were named using the following system: HITt####, where HI stands for Hawai‘i, Tt for *Tursiops truncatus*, and #### is a unique four digit number.

Figure 3. Examples of distinctiveness and photo-quality scores. Clockwise from top left: distinctiveness 4, photo-quality 3, photo by Paul Johnson; distinctiveness 3, photo-quality 2, photo by Tori Cullins; distinctiveness 1, photo-quality 4, photo by Tori Cullins; distinctiveness 2, photo-quality 1, photo by Lynn Opritoiu.

Satellite-Tags

Satellite-tags were deployed on bottlenose dolphins by CRC staff on one occasion off O‘ahu, and on four occasions off Maui Nui, in accordance with protocols described elsewhere (Schorr et al., 2009). Tags were manufactured by Wildlife Computers, and included one MK10-A tag (deployed in 2012 off Maui Nui, yielding location and dive data), one SPOT5 tag (deployed in 2012 off Maui Nui, yielding location data only), and three SPOT6 tags (deployed once in 2016 off O‘ahu and twice in 2017 off Maui Nui, yielding location data only). Briefly, tags were deployed onto slow-moving adults via air rifle in the LIMPET configuration, using two 4.7 cm titanium darts with backwards-facing petals that attach to the dorsal fin (Figure 4). Tags were preprogrammed to maximize the number of transmissions during predicted Argos satellite overpasses, extending battery life. Following deployment, tags transmitted location information to Argos satellites when the tagged animal surfaced, following the preprogrammed schedule. Tags were designed to remain on the animals and transmit for only a short time frame (usually less than a month), and naturally worked their way out of the dorsal fin afterwards. Photos of tagged individuals were compared against the catalog to determine sighting histories, providing context for which to later interpret the tagging results.

Figure 4. Example of a satellite-tag deployed on HITt0788 off Maui Nui in the LIMPET configuration, December 2012. Photo by CRC/Annie Douglas.

Satellite-tag processing was performed by CRC staff following established internal protocols (e.g., Baird et al., 2021). Briefly, location data were processed by Argos with the Kalman smoothing algorithm in the Wildlife Computers portal (Lopez et al., 2015), then with a Douglas-Argos filter through Movebank (Kranstauber et al., 2011) to clean the location data of any apparent errors based on a realistic measure of speed, with higher-quality locations (Argos location-quality 2 or 3) exempt from filtering (Douglas et al., 2012). The user-defined settings of the Douglas-Argos filter set the maximum sustainable rate of movement (MINRATE) at 20 km per hour, the maximum distance between consecutive locations (MAXREDUN) at 3 km, and the tolerance for turning (RATECOEF) at 25.

Biopsy Samples for Sex Determination

Skin biopsy samples were collected from 29 adult bottlenose dolphins on 32 occasions between 2000-2010, 19 (representing 17 individuals) off Maui Nui, and 13 (representing 13 individuals) off Oʻahu. Briefly, a stainless steel dart (8 mm diameter and ~18 mm long) with backwards-facing barbs, mounted onto an arrow with a float, was fired from a crossbow onto the body of a passing animal when it surfaced, removing a small amount of skin and blubber. The arrow and sample was retrieved, and frozen prior to subsampling and laboratory analysis. Genetic analysis of the samples for sex determination was undertaken by Southwest Fisheries Science Center.

Survey Effort, Quality Control, and Coverage

Survey effort by CRC and contributed encounters were evaluated to assess whether the data represents a comprehensive sample of the Oʻahu and Maui Nui bottlenose dolphin populations. Aspects of coverage that were examined include the spatial distribution of CRC and non-CRC effort, the distribution of encounters across years, the distribution of encounters across seasons, and the distribution of encounters across depths when GPS coordinates were available. All depths were determined using the R package marmap v. 1.0.5 (Pante & Simon-Bouhet, 2013) in conjunction with imported NOAA bathymetric data at a 1-minute resolution. Additionally, discovery curves comparing the number of unique individuals against the number of total identifications over time were constructed to evaluate the extent to which populations have been comprehensively sampled.

To ensure that the data was robust and included no misidentifications or duplicate identifications, and in accordance with previously established protocols (e.g., Baird et al., 2009), the dataset was restricted to include only individuals with photo quality scores of 3 or 4, and distinctiveness scores of 3 or 4.

The season in which encounters took place were defined by the month, with March-May for Spring, June-August for Summer, September-November for Fall, and December-February for Winter.

Demographics

Group size was considered only for CRC encounters where estimates of group size were recorded in the field, in order to minimize any bias in photographic effort (i.e., partial coverage of groups in contributed photographs). Group sizes for O‘ahu and Maui Nui encounters were first tested for normality with the Shapiro-Wilk test, and then group sizes were compared using a Mann-Whitney U test.

Sex was determined based on recorded calf presence, morphology (e.g., clear view of the genital slit or penis), or on genetic analysis of biopsy samples undertaken at the Southwest Fisheries Science Center. Sex distribution by island area was tested to examine whether it differed significantly from random using Pearson's X^2 test.

Residency Assignments and Social Networks

Residency was initially assigned to each ID based on the island(s) and span of years that each was encountered across. Individuals with a sighting history span greater than three years on a single island were classified as long-term residents. Individuals with a sighting history span greater than one year, but less than three years were classified as short-term residents, and individuals with a sighting history spanning less than one year were classified as visitors. Individuals that were seen off both Oʻahu and Maui Nui were classified as inter-island.

Residency assignments were then reassessed based on their social associations. A social network containing all individuals with photo quality scores of 3 or 4 and distinctiveness scores of 3 or 4 was built using a half-weight association index in SOCPROG 2.4 (Whitehead, 2008), and visualized using Netdraw 2.158 (Borgatti, 2002) with spring embedding. Any visitors that connected to the main components of the network were reassigned as associative residents for the component that they most closely linked to (i.e., Oʻahu or Maui Nui), to account for the fact that these individuals may be resident animals that were infrequently sampled, rather than true visitors. Residency assignments for visitors that did not connect to the main components were not revised.

Subarea Stratification

To explore how spatial use impacts residency, encounters with GPS locations were divided into five different geographic subareas based on demographic and geographic separation, three of which are located within the Oʻahu island area, and two of which are located in the Maui Nui island area (Figure 5). These subareas are: Oʻahu North (ON), Oʻahu West (OW), Oʻahu East (OE), Molokaʻi/Penguin Bank (MPB), and Maui Nui (MN, representing Maui, Lānaʻi , and Kahoʻolawe). These subareas align with the subareas designated in Van Cise et al. (2021), though the Oʻahu East subarea does represent a new addition. The Oʻahu North subarea encompasses the northwest coast of Oʻahu, northward of Kaʻena Point (~21.6° N, 158.3° W), and West of Kahuku Point (~21.7° N, 158.0° W). The Oʻahu East subarea encompasses the northeast coast of Oʻahu, eastward of Kahuku Point and southward to Makapuʻu Point (~21.3°

N, 157.7° W). The Oʻahu West subarea encompasses both the west and south coasts of Oʻahu, south of Kaʻena Point along the Waiʻanae coast, and southwest of Makapuʻu Point along the south coast. The Molokaʻi/Penguin Bank subarea includes the waters surrounding Penguin Bank (a large shallow water area to the southwest of the the island of Molokaʻi), and the waters surrounding the island of Molokaʻi itself, extending to midway between Molokaʻi and Lānaʻi and between Molokaʻi and Maui. The Maui Nui subarea is geographically the largest subarea, encompassing the waters surrounding the islands of Maui, Lānaʻi, and Kahoʻolawe. Subareas were further divided based on depth at the 500 m bathymetric contour in subareas where deepwater encounters (i.e., encounters in water deeper than 500 m) took place, resulting in the creation of three additional subareas: Oʻahu West Deep (OWD), Oʻahu East Deep (OED), and Maui Nui Deep (MND).

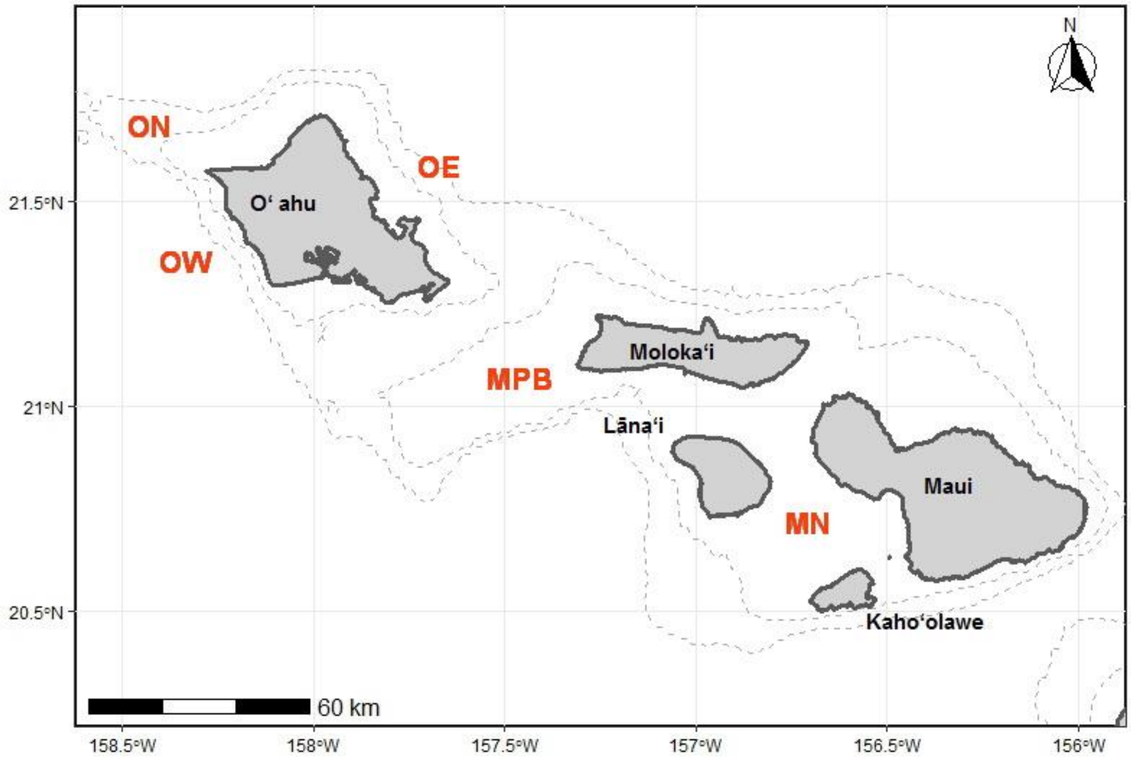


Figure 5. Subarea locations (red text). Abbreviations are as follows: ON = O‘ahu North, OW = O‘ahu West, OE = O‘ahu East, MPB = Moloka‘i/Penguin Bank, MN = Maui Nui (subarea). Subarea divisions based on depth (O‘ahu West Deep, O‘ahu East Deep, and Maui Nui Deep) are not shown. Depth contours (grey dashed lines) are shown for 500 m and 1,000 m bathymetric depth.

To explore how characteristics of subareas might impact bottlenose dolphin distribution, subareas were characterized by measuring the area within different depth ranges, and by describing seasonal fluxes in chlorophyll-a concentrations. These particular variables were chosen because Pittman et al. (2016) demonstrated that both are important predictors of bottlenose dolphin distribution in the Hawaiian Islands, especially depth. The area within various depth ranges was measured in 100 m bins using the R package marmap v. 1.0.5 and imported NOAA bathymetric data at a 1-minute resolution. Chlorophyll-a concentrations were evaluated using data from the National Aeronautics and Space Administration’s Aqua satellite, which measures surface reflectance of blue and green light to indirectly gauge chlorophyll-a concentrations (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, 2018). This data was mapped by season for three randomly selected years spanning the study period with Oceanic Niño indices between -1.0 and 1.0 (2006, 2013 and 2018), using the R package oceanmap v. 0.1.1 (Bauer, 2020).

The subareas where individuals were encountered were mapped on the social network to explore how spatial stratification impacts social relationships, and the distribution of residency classifications by subarea was described. A rough estimate of “density” was calculated for each subarea by dividing the total number of individuals encountered in a subarea by the total area. However, as this measure does not account for variations in the presence or absence of individuals over time or the amount of effort expanded in each subarea, it cannot be considered a true measure of density. Discovery curves were also constructed for each subarea to examine sampling coverage, and demographics were explored by comparing group sizes where CRC encounters were available. Group sizes were first tested by subarea for normality using a Shapiro-Wilk test, then tested for significant differences between subareas using a Kruskal-Wallis ranked sums test in conjunction with Dunn’s test.

Inter-Island Movements

Inter-island movements were described at the individual level and summarized seasonally. An inter-island movement was considered to be any movement that crossed the stock boundary between island areas (Figure 1), either from Maui Nui to O‘ahu, or from O‘ahu to Maui Nui. Inter-island individuals were also identified on both the residency class and subarea social networks to explore social connections.

Movements and Spatial Use

Photo-Identification Data

To explore possible variation in movement patterns, mean inter-annual travel distances were calculated for all individuals identified at any point within each island area, subarea and residency class, following the methods from Van Cise et al. (2021). This value reflects the mean distance between resightings from each year that an animal has been documented as a means of assessing overall site fidelity. Briefly, one location was randomly selected using the sample_n() function in R for each individual per year, and the distance between locations for each individual was calculated using the Geosphere package (Hijmans, 2019). Then the mean was calculated for all individuals sighted within the particular island area, subarea or residency class being examined. Because this method samples individuals sighted over multiple years, all visitors and associative residents were excluded from this analysis, as well as the Oʻahu East and Oʻahu East Deep subareas.

Additionally, mean inter-annual travel distances were calculated for a simulated randomly mixed population for both island areas as well as each island area separately, using the encounter locations from the actual dataset while ignoring resightings, as in Van Cise et al. (2021). Locations were randomly selected from the data for the same number of actual individual sightings in each year, and the distances between locations were calculated using the Geosphere package (Hijmans, 2019).

Satellite-Tag Data

Individual tracklines of Douglas-filtered datasets were first mapped to evaluate overall spatial use. Previously conducted CRC distance analyses have shown that none of the animals moved in concert while tags were deployed, so pseudoreplication of location data was not a concern (CRC, unpublished data). To explore broad trends in spatial use, core home ranges were constructed using probability-density distribution analysis, following the methods from Baird et al. (2021). The first 24 hours of data from each tag deployment were excluded from the data to reduce any bias in spatial use stemming from where the animals were tagged, and the data was arbitrarily trimmed to include only every fourth record to reduce the effects of spatial autocorrelation. Then kernel densities were constructed for individuals tagged off each island area with AdehabitatHR (Calenge, 2006), and used to estimate 50, 95, and 99 percent home ranges.

Individual Habitat Preferences

To explore whether there were individual habitat preferences, the distribution of depths where each individual was encountered were determined for a small sample (n=6) of the individuals with the greatest number of resightings with GPS coordinates. The distribution of depths was also determined for all five satellite-tagged individuals, using the depths of all Douglas-filtered locations between 0 and 1,000 m bathymetric depth. Significant differences in depth preferences between individuals were tested among both the six individuals with the greatest number of resightings and the five satellite-tagged individuals with a Kruskal-Wallis ranked sums test, in conjunction with Dunn’s test.

Interchange Indices

Dispersal rates were calculated as the interchange index both between areas and subareas, based on the methods of Urbán et al., 2000. Interchange indices increase when populations are small, as well as when there is a high degree of movement between areas, and decrease when populations or large or there is minimal movement between areas. First, to contextualize the interchange indices, within-area resighting indices were calculated as:

$$R_{WA} = (N_R / (N_A^2)) \times 1{,}000$$

where R_{WA} is the within-area or within-subarea resighting index, N_R is the number of animals resighted over multiple years within the area or subarea, and N_A is the total number of animals seen in an area. Interchange indices were then calculated as:

$$R_{AB} = (N_{AB} / (N_A \times N_B)) \times 1{,}000$$

where R_{AB} is the interchange index for areas A and B, N_{AB} is the number of animals sighted in both areas, N_A is the total number of animals sighting in area A, and N_B is the total number or animals sighted in area B. Interchange indices that fall within the same magnitude as within-area resighting rates for the corresponding areas indicate that movements between areas are just as likely as movements within-areas, and are especially significant.

Chapter Four: Results

This study presents the results of a reassessment of the population structure and residency of bottlenose dolphins off O‘ahu and Maui Nui, based on over two decades’ worth of photo-identification data, as well as satellite-tagging efforts. Several approaches were used to analyze these datasets, including assigning residency classes based on sighting histories, social networks, and spatial analysis.

Survey Effort, Quality Control, and Coverage

CRC Survey Effort

From 2000-2018, CRC conducted 588 hours and 9,626 km of survey effort off O‘ahu, and 969 hours and 14.021 km of survey effort off Maui Nui (Table 1; Figure 6). Survey effort was heavily biased towards the leeward sides of the islands, owing to restrictions caused by weather conditions on the windward side, but covered a wide range of depths and potential habitats. During this time, bottlenose dolphins were encountered on 18 occasions off O‘ahu and on 65 occasions off Maui Nui. When restricted to the number of photographed encounters with at least one individual of photo quality score ≥ 3 and distinctiveness score ≥ 3, these numbers drop to 14 encounters off O‘ahu, and 63 encounters off Maui Nui (Table 1).

The number of CRC encounters with bottlenose dolphin varied across years on both islands in accordance with research goals over time (Figure 7). The most CRC encounters took place off Maui Nui in 2001, with 17 encounters, and off O‘ahu in 2003, with seven encounters. CRC encounters occurred most frequently off both islands in the early 2000s.

Table 1. CRC and non-CRC survey effort and encounters. Two CRC encounters from the Maui Nui island area lack corresponding GPS coordinates, but GPS coordinates are available for all other CRC encounters. PQ = photo quality score, Dist = distinctiveness score.

Island Area	Total km of CRC Survey Effort (on effort)	Total Hours of CRC Survey Effort	Total # of CRC Bottlenose Encounters With at Least 1 Individual PQ ≥ 3, Dist ≥ 3	Total # of Non-CRC Encounters With at Least 1 Individual PQ ≥ 3, Dist ≥ 3	Total # of Non-CRC Encounters With Corresponding GPS Locations
O‘ahu	9,626	588	14	234	19
Maui Nui	14,021	969	63	294	199

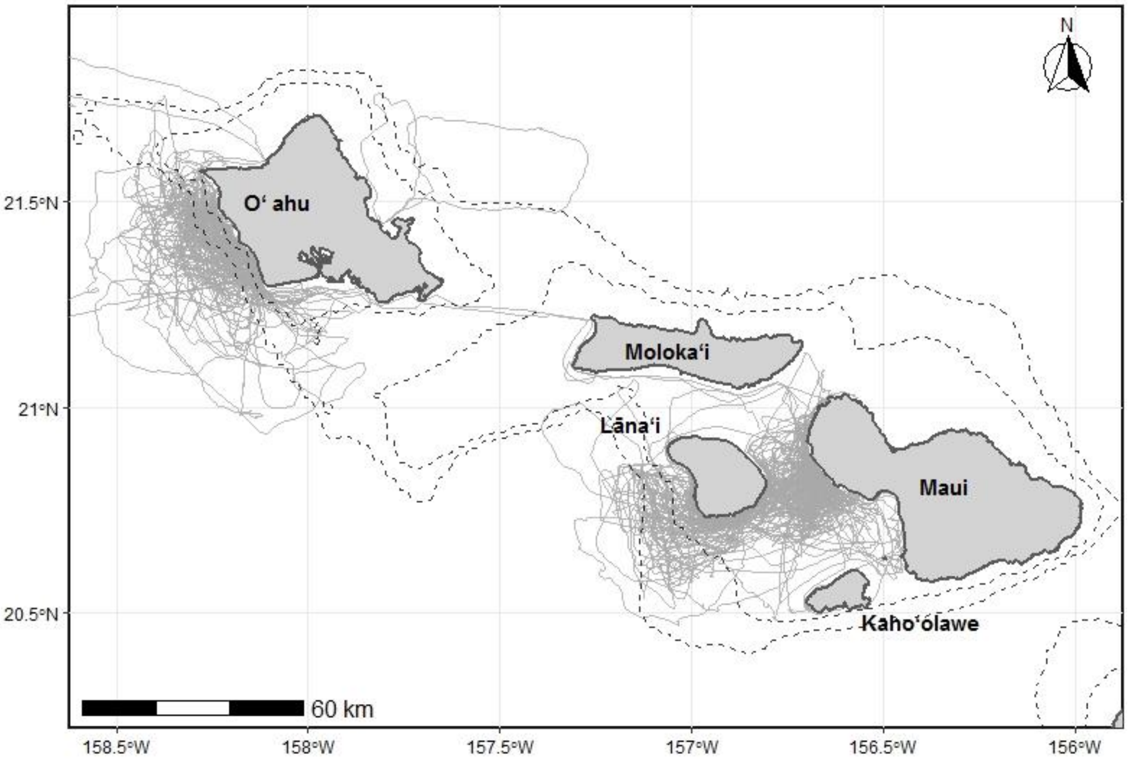


Figure 6. CRC effort tracklines (grey) off O‘ahu and Maui Nui from 2000-2018. Depth contours (black dashed lines) are shown for the 500 m and 1,000 m bathymetric depth.

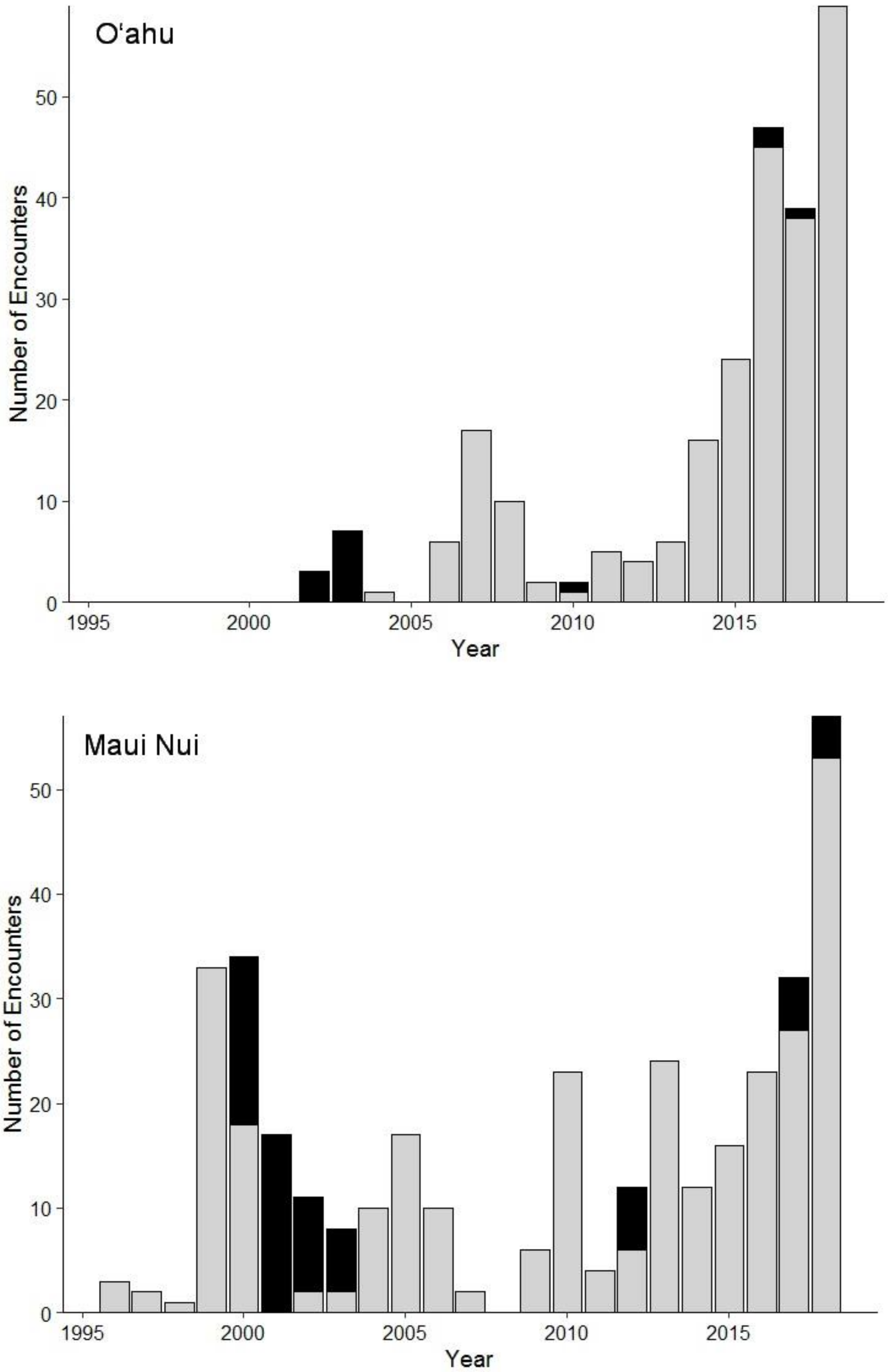


Figure 7. Barplots of encounters by year for each island area, including both CRC (black) and non-CRC (grey) encounters. Top: O‘ahu. Bottom: Maui Nui.

Contributed Encounters

From 1996-2018, other researchers and community scientists have contributed photos from over 700 encounters with bottlenose dolphins to CRC. When these are restricted to the number of encounters with at least one individual with a photo quality score ≥ 3 and a distinctiveness score ≥ 3, 234 encounters from Oʻahu and 294 encounters from Maui Nui were retained (Table 1). Contributions off Maui Nui are in large part from the Pacific Whale Foundation, while off Oʻahu they were largely from tour boat operators. Contributions off Oʻahu especially have gradually increased over time (Figure 7b).

GPS Location Availability and Depth

GPS locations were available for all but two CRC encounters off Maui Nui (97% of all CRC encounters), but were not available for all contributed encounters. Overall, of the total 528 contributed encounters, 218 (41%) had corresponding GPS locations. Of the 234 contributed Oʻahu encounters, 19 (8%) had associated GPS location data, while of the 294 contributed Maui Nui encounters, 199 (68%) had associated GPS location data (Table 1; Figure 8). Among the encounters with associated GPS location data, depths for encounters off Maui Nui ranged from 1 m to 1,629 m, and off Oʻahu from 3 m to 872 m. However, encounters were heavily skewed in favor of shallower encounters, with the vast majority (96%) of encounters taking place at depths < 500 m (Figure 9). While the distribution of encounter depths generally resembled the distribution of survey effort depth, encounters were more strongly skewed in favor of shallow water (Figure 9).

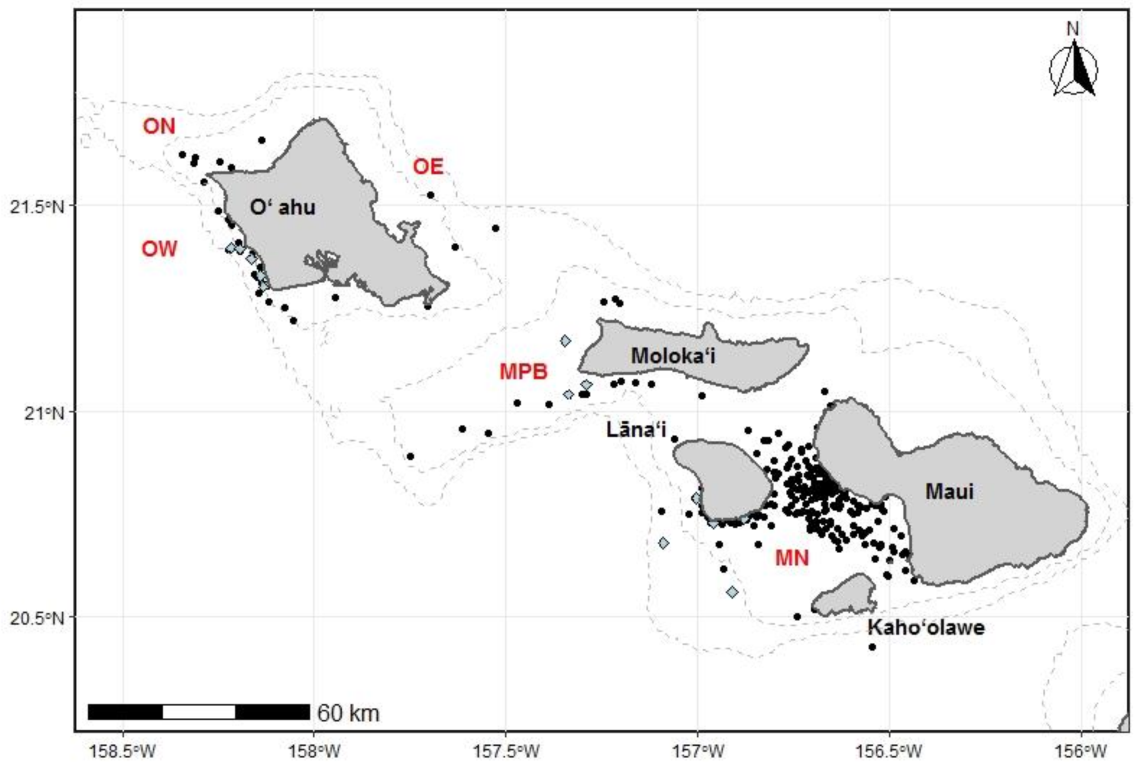


Figure 8. Encounter locations and subareas. Encounter locations are represented by black dots, with encounters where inter-island individuals were present shown as light blue diamonds. Subareas are abbreviated in red, with ON for O‘ahu North, OW for O‘ahu West, OE for O‘ahu East, MPB for Moloka‘i/Penguin Bank, and MN for Maui Nui (subarea). Subarea divisions based on depth (O‘ahu West Deep, O‘ahu East Deep, and Maui Nui Deep) are not shown. Depth contours (grey dashed lines) are shown for the 500 m and 1,000 m bathymetric depth.

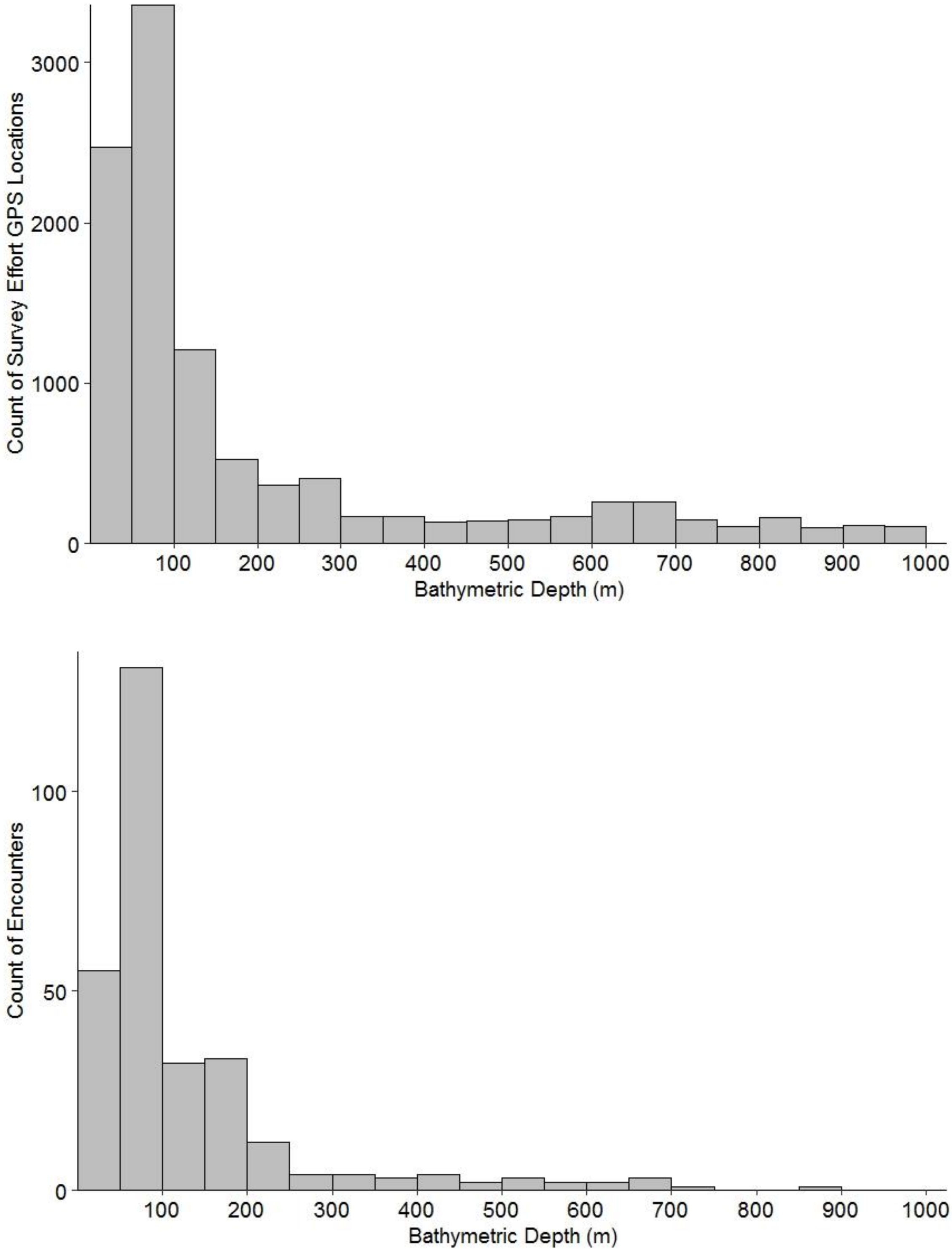


Figure 9. Histogram of bathymetric depths for CRC survey effort (top) and all encounters with corresponding GPS locations, including CRC and non-CRC encounters (bottom). One encounter from the south side of Kaho‘olawe that took place in 1,629 m bathymetric depth has been excluded from the bottom panel.

Photo-Identification Results and Quality Control

After encounters were processed by CRC staff, 3,278 total identifications representing 775 individuals from 748 encounters were part of the original dataset. However, resighting rates varied substantially between different levels of distinctiveness and photo quality, with rates improving as distinctiveness and photo quality increased (Table 2). Quality control measures were therefore applied to restrict the dataset to only those individuals with photo quality scores of 3 or 4, and distinctiveness scores of 3 or 4. This reduced the overall size of the dataset to 1,830 total identifications (56% of the original 3,278 total identifications) from 605 encounters (81% of the original 748 encounters), representing 472 individuals (61% of the original 775 individuals).

Table 2. Resighting rates with varying levels of restrictions on distinctiveness and photo quality for all encounters. Percentages indicate the proportion of the total number of individuals identified within the same distinctiveness and photo-quality score range, rounded to the nearest integer.

	No Photo Quality Restrictions			**Photo Quality ≥ 3 Only**		
Highest Distinctiveness	**# Individuals**	**# (%) Seen More Than Once**	**# (%) With Over 1 Year Resighting Span**	**# Individuals**	**# (%) Seen More Than Once**	**# (%) With Over 1 Year Resighting Span**
1 (Not Distinctive)	110	37 (34%)	15 (14%)	86	36 (42%)	15 (17%)
2 (Slightly Distinctive)	129	48 (37%)	25 (19%)	110	42 (38%)	25 (23%)
3 (Distinctive)	259	136 (53%)	102 (39%)	220	132 (60%)	102 (46%)
4 (Very Distinctive)	277	151 (55%)	128 (46%)	252	144 (57%)	125 (50%)
Total	775	372 (48%)	270 (35%)	668	354 (53%)	267 (40%)

Coverage

Between CRC surveys and contributed photos, encounters off both Oʻahu and Maui Nui have comprehensive coverage across years, though the overall number of encounters does increase over time (Figure 7). The greatest number of encounters within a single year took place off both Oʻahu and Maui Nui in 2018, with 57 encounters off Maui Nui, and 59 encounters off Oʻahu. The mean number of encounters per year was 16 off Maui Nui (sd = ± 13.8, min = 0, max = 57) , and 11 off Oʻahu (sd = ± 16.4, min = 0, max = 59).

The number of encounters varied seasonally off both Oʻahu and Maui Nui, with the highest number occurring off Maui Nui during the Spring, and the lowest number occurring off Maui Nui during the Fall (Figure 10). For Oʻahu the greatest number of encounters took place in the summer, while the lowest number took place in the winter (Figure 10). For Maui Nui, the number of encounters by season was Spring = 151 (42%), Summer = 69 (19%), Fall = 34 (10%), Winter = 103 (29%), while for Oʻahu Spring = 76 (31%), Summer = 79 (32%), Fall = 46 (19%), and Winter = 47 (19%).

A discovery curve displaying the number of unique individuals encountered over time shows that coverage off Maui Nui is approaching an asymptote, indicating comprehensive sampling (Figure 11). In contrast, the discovery curve for Oʻahu has mostly inflected, but continues to rise and is higher overall, indicating a continued influx of new IDs in spite of fair sampling effort (Figure 11).

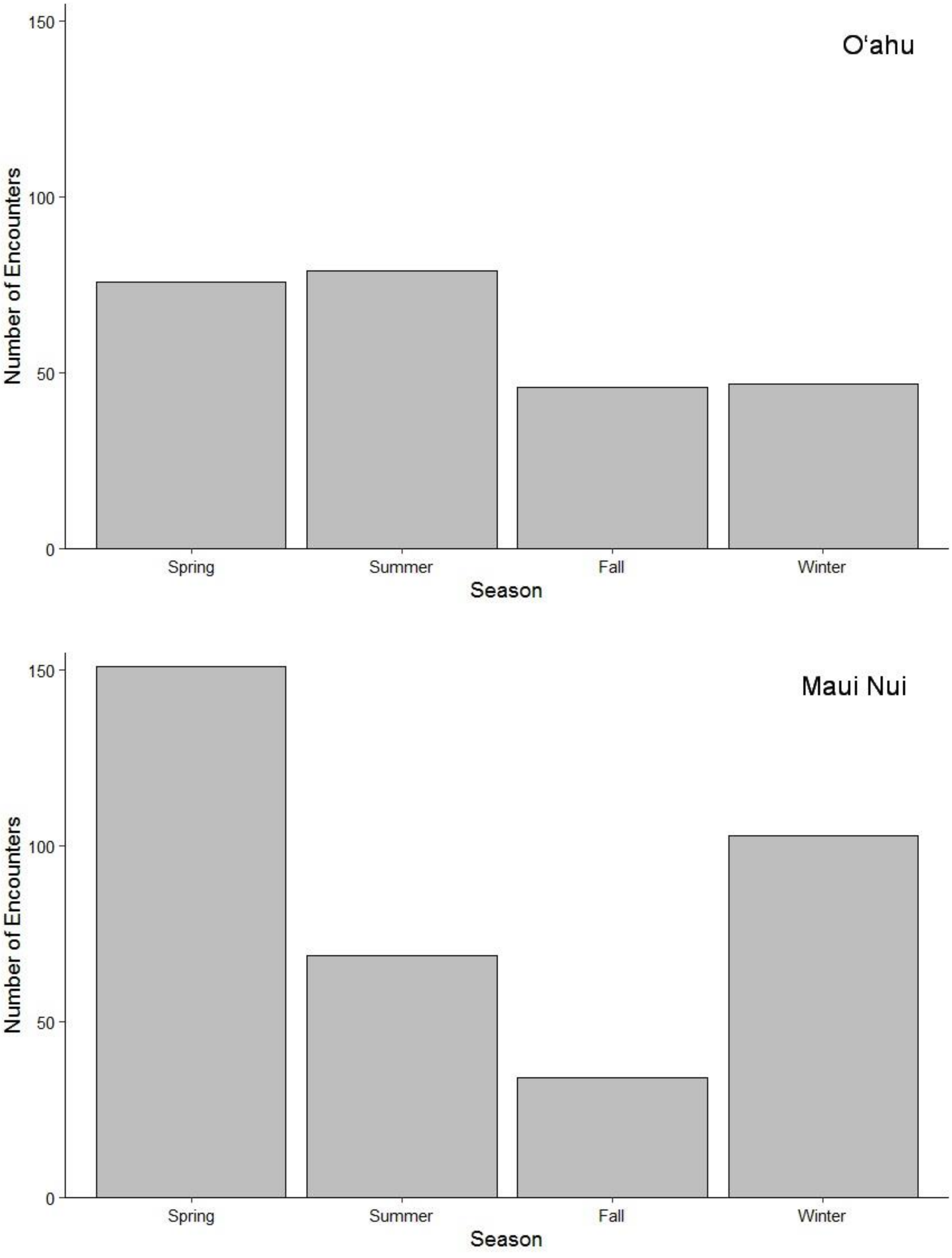
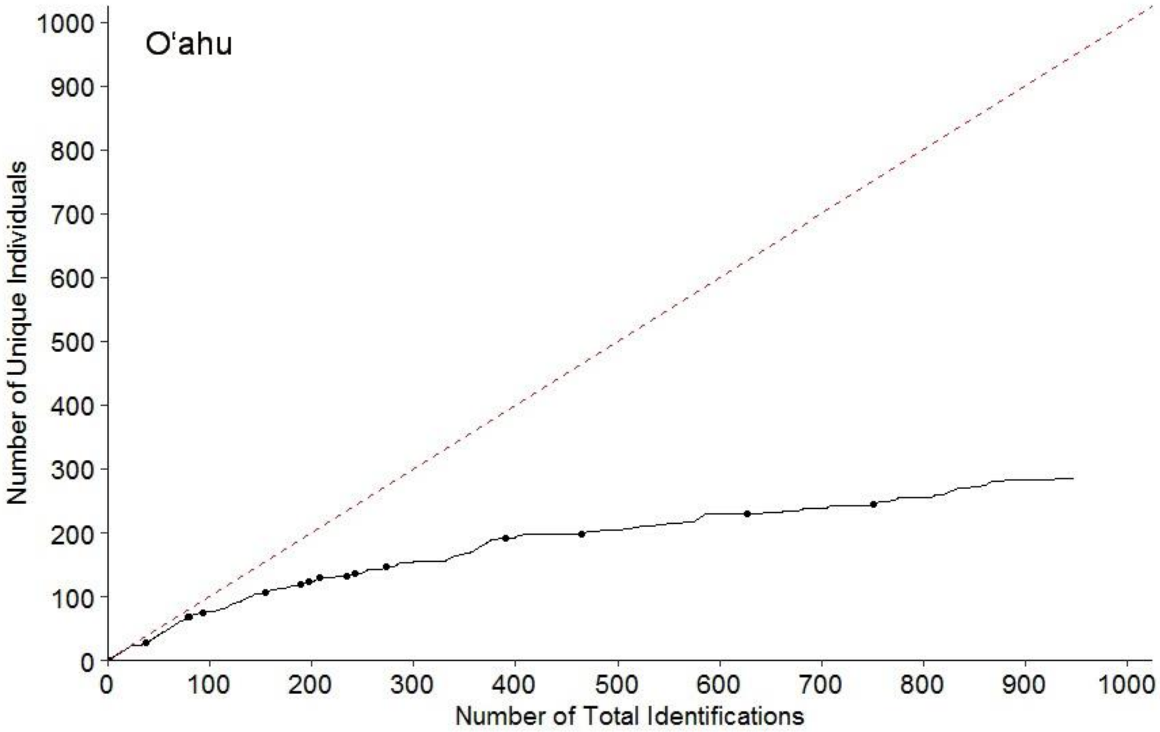


Figure 10. Histograms of encounters by season for each island area, with seasons defined by the month in which encounters took place (Spring = March-May, Summer = June-August, Fall = September-November, Winter = December-February). Top: Oʻahu. Bottom: Maui Nui.



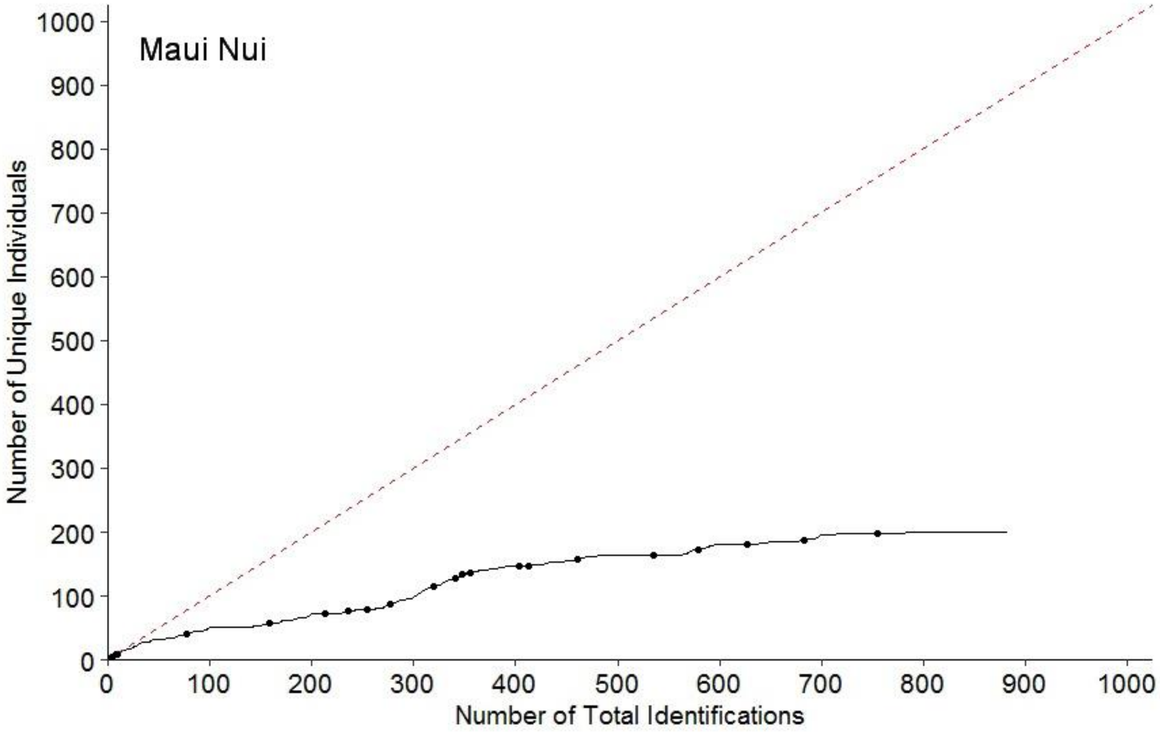


Figure 11. Discovery curves of individuals by island area, restricted to distinctive or very distinctive individuals with good or excellent quality photographs, with a reference 1:1 dashed trendline shown in red. Curves are constructed chronologically, with black dots showing the start of each year. Top: O‘ahu (2002-2018). Bottom: Maui Nui (1996-2018).

Demographics

CRC group sizes of O‘ahu encounters tended to be larger than Maui Nui encounters. The mean group size for O‘ahu encounters was 12.8 (sd = ± 10.4, min = 1, max = 40), and the mean group size for Maui Nui encounters was 6.1 (sd = ± 4.4, min = 1, max = 18). Based on Shapiro-Wilk tests, the group sizes for O‘ahu were normally distributed ($p = 0.061$), but the group sizes for Maui Nui encounters were not normally distributed ($p < 0.001$). Due to the mixed results regarding normality, a Mann-Whitney U test was used to test whether the differences in group sizes were statistically significant. The results of the Mann-Whitney showed that group sizes were significantly different between island areas ($p = 0.008$).

Sex was determined for a total of 49 individuals, 25 of which were seen off O‘ahu, 21 of which were seen off Maui Nui, and three of which were seen off both island areas (Appendix Table A). In all three groups sexes skewed heavily towards females, with 20 females identified off O‘ahu (80% out of the 25 sexed individuals total), 15 females identified off Maui Nui (71% out of the 21 sexed individuals total), and three females identified off both island areas (100% out of the three sexed individuals total). Calf presence and morphology contributed heavily toward the high ratio of females vs. males for all three groups, but even when restricting to individuals sexed through genetic sampling ($n = 24$), sexed individuals still included more females than males for both O‘ahu and Maui Nui.

To examine whether the distribution of sexes differed significantly from random, a Pearson’s X^2 test was performed on the data. This test excluded the individuals seen off both islands because of the small sample size, the fact that no males were documented off both islands, and because these individuals could not be incorporated into the totals for both island areas without counting them twice. The X^2 statistic was 0.11015, with an associated p-value of 0.74, indicating that the variation in distribution of sexes did not differ from random.

Residency Assignments and Social Networks

Initial Residency Assignments

Island areas where individuals were encountered were mapped onto a social network of all 472 individuals included in the study to evaluate initial impressions of connectedness between island areas (Figure 12). The entire network includes 6,356 ties linking the 472 individual nodes, and includes two easily identifiable main components that represent animals encountered largely off O‘ahu, and animals encountered off Maui Nui. When restricted to the main components, there are 5,966 ties connecting 380 nodes. Only two ties (representing $< 0.1\%$ of all ties in the network) link the main O‘ahu and Maui Nui components. There are 17 peripheral clusters including more than one connected individual, and 16 individuals that are unconnected to any other individuals on the network. Of the 16 individuals unconnected to any other animals in the network, eight were encountered by themselves, and the remaining eight were artifacts of quality control measures (i.e., they linked to the main cluster when no restrictions were applied).

Initial residency assignments are fully reported in Appendix Table B for reference. Briefly, of the 271 individuals encountered solely in the O‘ahu area, 59 are long-term residents, 22 are short-term residents, and 190 are visitors. Of the animals encountered solely in the Maui Nui area, 66 are long-term residents, 26 are short-term residents, and 95 are visitors. Only 14 individuals were encountered off of both O‘ahu and Maui Nui, and therefore assigned as inter-island individuals. Initial residency assignments were mapped onto the same social network diagram as the island areas, revealing that most Maui Nui long and short-term residents cluster together, and that most O‘ahu long and short-term residents also cluster together (Appendix Figure A).

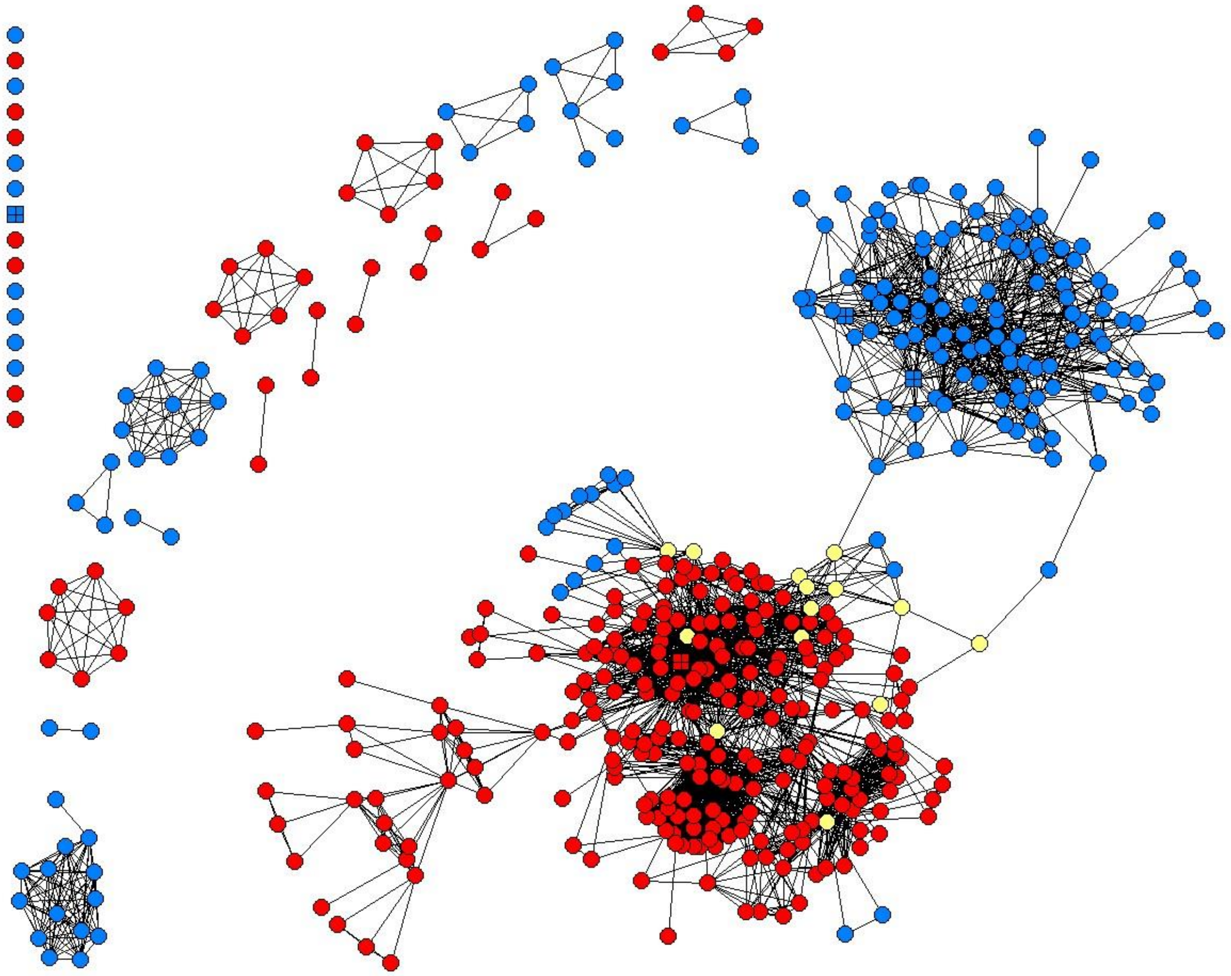


Figure 12. Social network with island areas of the individual nodes indicated by color, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. All tagged animals (n=4) are indicated by a square node shape. Red nodes are animals encountered only off O‘ahu, blue nodes are animals encountered only off Maui Nui, and yellow nodes are animals encountered in both island areas.

Revised Residency Assignments

Revised residency assignments are summarized in Table 3. Briefly, 152 of the 190 O‘ahu visitors were reassigned as O‘ahu associative residents on the basis of their connection to the main O‘ahu component of the network, along with the 16 of the 95 Maui Nui visitors that linked most closely to the O‘ahu cluster through connections with inter-island individuals. These results were also mapped onto the same social network diagram as the initial residency assignments (Figure 13). All Maui Nui long-term residents were connected to one another in the social network, along with all but two Maui Nui short-term residents. O‘ahu long-term residents were not all connected to one another – they divided into three groups with 55 individuals, three individuals, and one individual. These groups remained separate even with the addition of O‘ahu short-term residents, which also resulted in the creation of another group with one individual. When O‘ahu visitors were added to the social network, the two larger groups became connected through a single individual, HITt1703 (seen twice off O‘ahu, both times in 2018).

Table 3. Revised residency assignment results by island area. Percentages indicate the proportion of the total number of unique identified individuals from all island areas combined, rounded to the nearest integer.

Island Area	Total # (%) of Individuals	# (%) Long-Term Residents	# (%) Short-Term Residents	# (%) Associative Residents	# (%) Visitors
O‘ahu	287 (61%)	59 (13%)	22 (5%)	168 (36%)	38 (8%)
Maui Naui	171 (36%)	66 (14%)	26 (6%)	29 (6%)	50 (11%)
Inter-Island	14 (3%)	-	-	-	-
All Island Areas	**472**	125 (26%)	48 (10%)	196 (42%)	88 (19%)

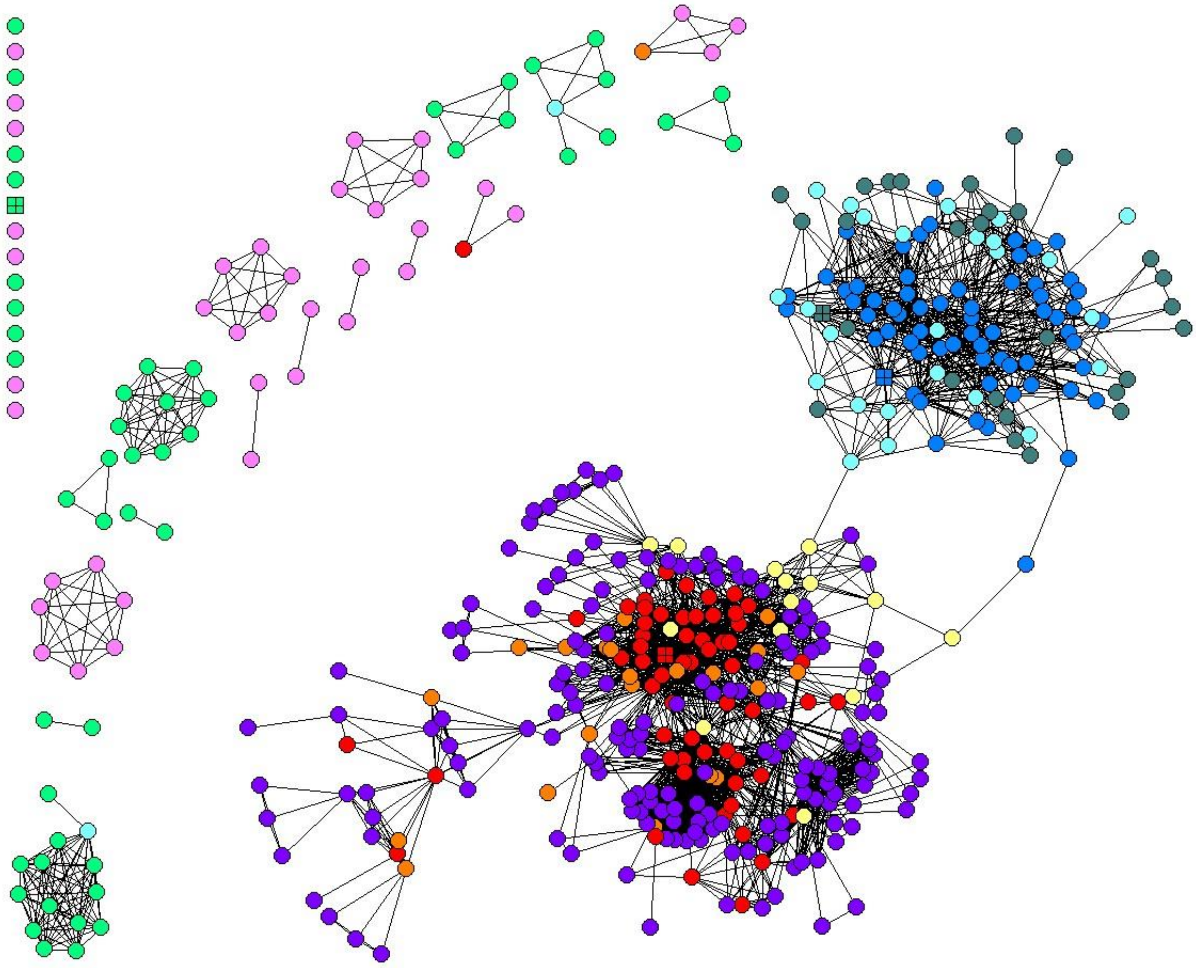


Figure 13. Social network with revised residency assignments of the individual nodes indicated by color, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. All tagged animals (n=4) are indicated by a square node shape. Red nodes are Oʻahu long-term residents, orange nodes are Oʻahu short-term residents, purple nodes are Oʻahu associative residents, pink are Oʻahu visitors, blue are Maui Nui long-term residents, light blue are Maui Nui short-term residents, teal are Maui Nui associative residents, and green are Maui Nui visitors.

Most individuals in the peripheral clusters were visitors, with two exceptions: HITt1145, classified as an O‘ahu long-term resident, and HITt1169, classified as an O‘ahu short-term resident. HITt1145 was first seen in 2008, then again in 2018, both times in the company of one other individual. HITt1169 was first seen in 2016 by itself, then again in 2017 in the company of three other individuals.

Interestingly, all inter-island individuals clustered most closely with the O‘ahu component, and only represented a link between the two main components twice. These two links were identified as HITt1095 (seen three times off Maui Nui in 2012, 2014, and 2017, and once off O‘ahu), and HITt1152 (seen once off Maui Nui in 1997, and twice off O‘ahu in 2015 and 2016). Additionally, several Maui Nui visitors clustered more closely with the O‘ahu component than the Maui Nui component. When inter-island individuals were filtered out of the social network, the two main components were completely separated, and all Maui Nui visitors that clustered with the O‘ahu component became isolated from both main components.

Sex Determination

Consistent with the results for island areas, sex was biased towards females across all residency classes (Appendix Table A). This trend was particularly apparent for sexed long-term residents off O‘ahu, all nine of whom were female. This was also true for sexed inter-island individuals, all three of whom were female. The sexed Maui Nui long-term residents had the largest number of males (five males out of 16 sexed individuals total), and the highest proportions of males identified were among the O‘ahu visitors (one male out of two sexed individuals total), and the Maui Nui associative residents (one male out of two sexed individuals total), though both of these groups had very limited sample sizes.

Subarea-Stratification

Spatial stratification of the dataset resulted in the creation of five distinct geographic subareas: O‘ahu North (ON), O‘ahu West (OW), O‘ahu East (OW), Moloka‘i/Penguin Bank (MPB), and Maui Nui (MN; representing Maui, Lāna‘i , and Kaho‘olawe; Figure 8). Three of these subareas were further divided at the 500 m bathymetric depth (O‘ahu West (OW)/O‘ahu West Deep (OWD), O‘ahu East (OE)/O‘ahu East Deep (OED), and Maui Nui (MN)/Maui Nui Deep (MND)). This resulted in a total of eight subareas.

Subarea Characterization

The total area of each subarea ranged from 934 km^2 (O‘ahu West) to 6,174 km^2 (Maui Nui), with all three of the O‘ahu subareas smaller than the Maui Nui subareas (Table 4). All subareas had more shallow water (0-500 m bathymetric depth) than deep water (500-1,000 m bathymetric depth), but the Maui Nui and Moloka‘i/Penguin Bank subareas in particular had extensive shallow water habitat, with 4,030 km^2 and 2,570 km^2 of shallow water respectively.

Table 4. Total area (in km^2) by depth (m) for each island area and subarea. Values have been rounded to the nearest integer. For island areas, O = O‘ahu island area, MN = MN island area. For subareas, OE = O‘ahu East, OW = O‘ahu West, ON = O‘ahu North, MN = Maui Nui subarea, MPB = Moloka‘i/Penguin Bank.

Island Area	**Sub-area**	**Amount of available habitat (km^2) by depth (m) range**												
		0-1000	**0-500**	**500-1000**	**0-100**	**100-200**	**200-300**	**300-400**	**400-500**	**500-600**	**600-700**	**700-800**	**800-900**	**900-1000**
O	**-**	3041	1683	1358	748	174	180	284	297	368	270	281	255	184
MN	**-**	10103	6600	3503	2497	1283	1031	917	872	1049	1001	590	415	448
O	**OE**	1145	612	533	296	58	74	100	84	126	132	152	71	52
O	**OW**	962	559	403	262	32	42	94	129	155	90	52	74	32
O	**ON**	934	512	422	190	84	64	90	84	87	48	77	110	100
MN	**MN**	6174	4030	2144	1267	801	707	652	603	541	603	419	253	328
MN	**MPB**	3929	2570	1359	1230	482	324	265	269	508	398	171	162	120

The shape and relative exposure of shallow water within subareas varied substantially (Figure 8). The O‘ahu West and O‘ahu West Deep subareas consist of a narrow band of habitat along the west coast of O‘ahu that widens off the south coast, while the O‘ahu North subarea consists of a broader expanse of shallow water. O‘ahu East consists of intermediate-sized bands of shallow and deep water compared to O‘ahu West/O‘ahu West Deep and O‘ahu North. Moloka‘i/Penguin Bank consists of an extensive shallow-water shelf (Penguin Bank) and shallow area surrounding Moloka‘i, with a band of deep water encompassing Penguin Bank. The Maui Nui subarea has a broad shallow-water area, with some nearshore deepwater habitat off the west coast of Lāna‘i and the south shore of Kaho‘olawe. All of the O‘ahu subareas are highly exposed to the open ocean, while a large portion of the Maui Nui subarea is enclosed by the islands of Maui, Lāna‘i, and Kaho‘olawe. Penguin Bank is also highly exposed, but the waters to the south of Moloka‘i are partially enclosed by Maui and Lāna‘i.

Chlorophyll-a concentrations varied substantially both between seasons and between years, though all were consistently oligotrophic (Appendix Figure B). During the summer months, chlorophyll-a concentrations rose markedly across all years examined, and generally appeared to be lower during the fall and winter months. Within subareas, chlorophyll-a concentration trends fluctuated within the same season between years, with no immediately obvious recurring spatial patterns.

Social Networks, Residency, and Demographics by Subarea

Subareas where individuals were encountered were mapped onto the social network to explore social consequences of spatial stratification. Spatial stratification between subareas generally aligned with social relationships (Figure 14). O‘ahu North animals in particular clustered together almost entirely separate from the main Oʻahu cluster, connected by one individual, HITt1703, which was seen twice off Oʻahu in 2018, and only once with GPS coordinates recorded. Individuals seen in both the Oʻahu West and Oʻahu West Deep subareas were frequently intermixed with Oʻahu West individuals, though there was some peripheral partitioning of a few Oʻahu West Deep individuals within the main Oʻahu cluster. Individuals seen in the Molokaʻi/Penguin Bank subarea were generally located in peripheral clusters, though a few were located on the periphery within the main Oʻahu cluster, and deep within the Maui Nui cluster. Additionally, a couple of individuals with GPS locations in both the Molokaʻi/Penguin Bank and Maui Nui subareas acted as cutpoints between the Oʻahu and Maui Nui main clusters. These two individuals were identified as HITt0027 and HITt0070, both of whom were classified as Maui Nui long-term residents.

Based on encounters with recorded GPS locations, two individuals were sighted in subareas corresponding to two different island areas (Figure 15). One individual, HITt1104, was sighted twice in the Oʻahu West and once in the Maui Nui Deep subarea. The other individual, HITt0232 , was sighted once in the Oʻahu West Deep and once in the Maui Nui Deep subarea. Neither individual was of known sex, and both individuals clustered within the main Oʻahu cluster (Figure 14). Exchange between subareas within the same island area was repeatedly documented, most frequently between the Oʻahu West and Oʻahu West Deep subareas, with nine individuals documented in both subareas. Four individuals were documented in both the Maui Nui and Molokaʻi/Penguin Bank subareas, two individuals were documented in both the Maui Nui and Maui Nui Deep subareas, and one individual was documented in both the Oʻahu North and Oʻahu West subareas.

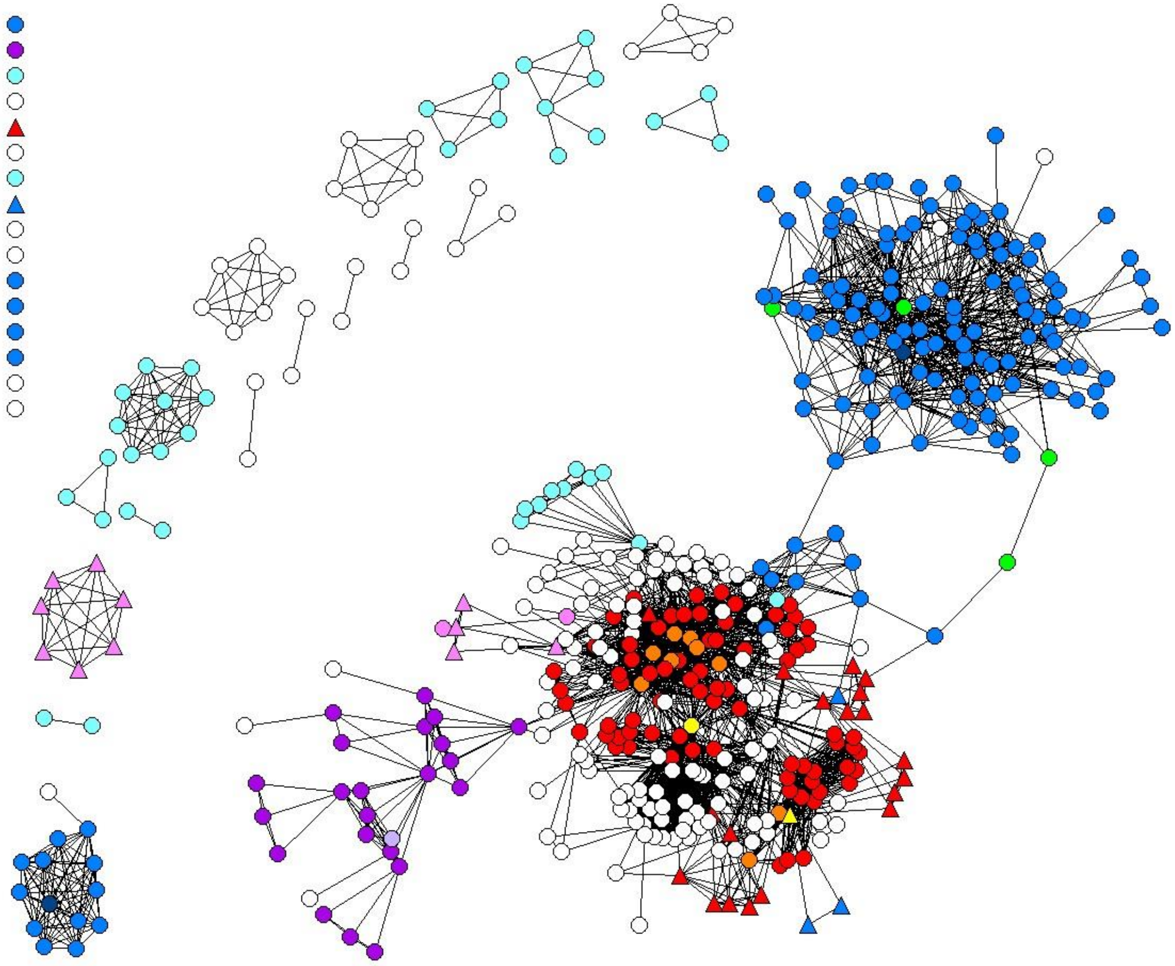


Figure 14. Social network with subareas where individuals were encountered indicated by color and shape, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. Blue circles indicate the Maui Nui subarea, dark blue indicate both the Maui Nui and Maui Nui Deep suabreas, blue triangles indicate the Maui Nui deep subarea, light blue circles indicate the Moloka‘i/Penguin Bank subarea, green ciricles indicate both the Maui Nui and Moloka‘i/Penguin Bank subareas, yellow circles indicate both the Maui Nui Deep and O‘ahu West subareas, yellow triangles indicate both the Maui Nui Deep and O‘ahu West Deep subareas, red triangles indicate the O‘ahu West Deep subarea, red circles indicate the O‘ahu West subarea, orange circles indicate both the O‘ahu West and O‘ahu West Deep subareas, light purple circles indicate both the O‘ahu North and O‘ahu West subareas, dark purple circles indicate the O‘ahu North subarea, pink circles indicate the O‘ahu East subarea, pink triangles indicate the O‘ahu East Deep subarea, and white circles indicate an individual lacking any GPS coordinates to assign subareas.

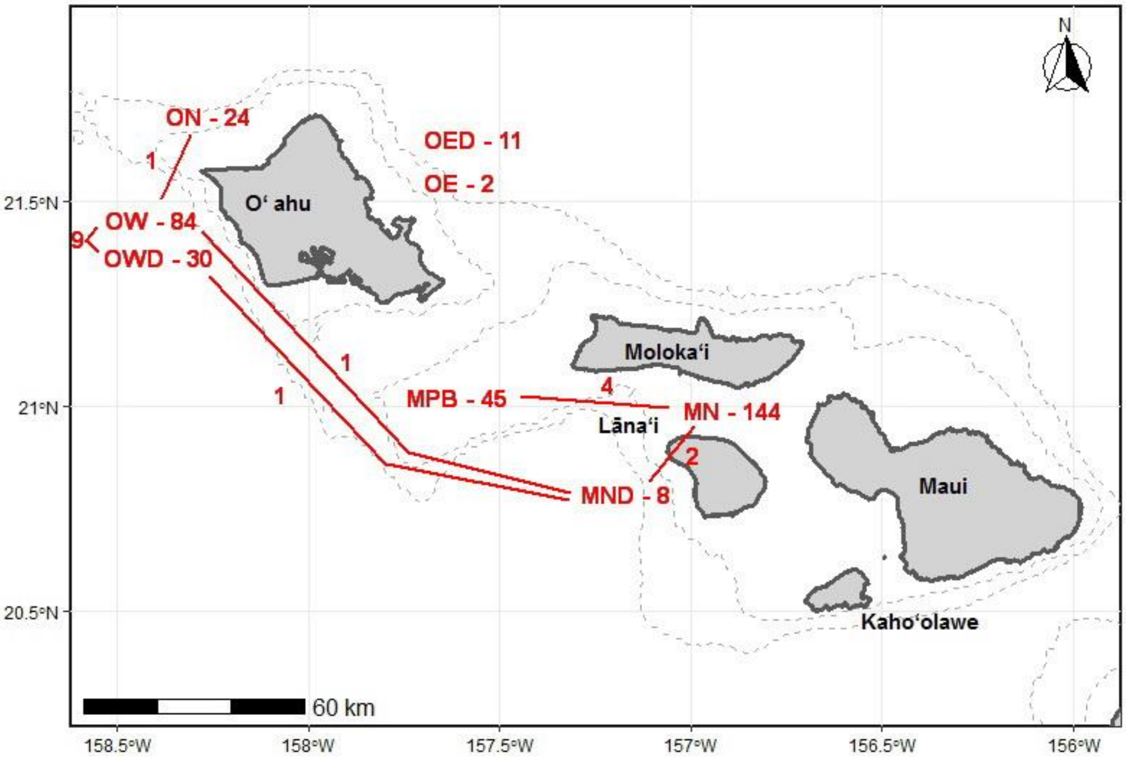


Figure 15. Map of subareas with the total number of animals identified within each subarea following the subarea abbreviation in red, and the number of individuals identified within both subareas adjacent to the red lines connecting subareas. Depth contours (grey dashed lines) are shown for the 500 m and 1,000 m bathymetric depth. ON = O‘ahu North, OW = O‘ahu West, OWD = O‘ahu West Deep, OE = O‘ahu East, OED = O‘ahu East Deep, MPB = Moloka‘i/Penguin Bank, MN = Maui Neui (subarea), MND = Maui Nui Deep.

The distribution of different residency classes between subareas varied substantially, and is reported in full in Table 5. The greatest proportion of inter-island individuals (38%) was in the Maui Nui Deep subarea, although the greatest number of inter-island individuals were documented within the Maui Nui subarea. The greatest numbers of long-term residents were documented within the Maui Nui and O‘ahu West subareas (66 and 32 individuals, respectively), and the greatest number and proportion of short-term residents were documented within the Maui Nui subarea (25 individuals, 17%). The greatest proportions of long-term residents were in the O‘ahu East and O‘ahu West Deep subareas (50% each). Associative residents were most frequently documented within the O‘ahu West subarea (41 individuals), and the greatest number and proportion of visitors were documented within the Moloka‘i/Penguin Bank subarea (30 individuals, 67%). The greatest proportion of associative residents, however, was within the O‘ahu North subarea (71%).

Table 5. Subareas versus revised residency classifications for all encounters where corresponding GPS location data were available. Percentages indicate the proportion of the total number of unique individuals identified within that particular subarea, rounded to the nearest integer. Rough density is calculated as the total number of individiauls identified within a subarea, divided by the total area (km^2) for the appropriate depth range (0-500 m, 500-1,000 m, or 0 – 1,000 m).

Sub-area	# Encounters	Total # Identified Individuals	Rough Density	# Individuals Resighted Within the Subarea > 1 yr	# (%) Inter-Island	# (%) Long-Term Residents	# (%) Short-Term Residents	# (%) Associative Residents	# (%) Visitors
OE	1	2	0.003	0	0 (0%)	1 (50%)	0 (0%)	1 (50%)	0 (0%)
OED	2	11	0.021	0	0 (0%)	0 (0%)	1 (9%)	3 (27%)	7 (64%)
OW	18	84	0.150	12	2 (2%)	32 (38%)	9 (11%)	41 (49%)	0 (0%)
OWD	6	30	0.074	1	1 (3%)	15 (50%)	1 (3%)	12 (40%)	1 (3%)
ON	6	24	0.026	3	0 (0%)	3 (13%)	3 (13%)	17 (71%)	1 (4%)
MN	235	144	0.036	88	7 (5%)	66 (45%)	25 (17%)	29 (20%)	17 (12%)
MND	7	8	0.004	0	3 (38%)	1 (13%)	0 (0%)	2 (25%)	2 (25%)
MPB	18	45	0.011	2	2 (4%)	4 (9%)	1 (2%)	8 (18%)	30 (67%)

Rough calculations revealed that the greatest “density” of animals (0.150 animals/km^2) was within the O‘ahu West subarea, followed by the O‘ahu West Deep subarea (0.074 animals/km^2), and then the Maui Nui subarea (0.036 animals/km^2; Table 5). The lowest “density” was within the O‘ahu East subarea, with 0.003 animals/km^2. However, these calculations should not be treated as true measures of density, as they fail to account for variation in survey effort and spatial use, as well as variation in the number of animals over time. Discovery curves constructed for each of the subareas revealed that sampling was not comprehensive for the vast majority of subareas, with the exception of the Maui Nui and perhaps the O‘ahu West subareas (Figure 16). This means that the densities of the remaining subareas are likely biased low, due to a potentially large portion of the animals that use the area not having been identified yet. However, differences in subarea “densities” may also reflect genuine differences in habitat use.

Group sizes varied between subareas, with larger groups generally found in the O‘ahu West subarea and O‘ahu West Deep subareas, and smaller groups found in the O‘ahu North, Maui Nui, and Maui Nui Deep subareas (Appendix Table C). Group sizes were normally distributed for only the Maui Nui and Maui Nui Deep subareas based on the results of Shapiro-Wilk tests, so to test whether group sizes differed significantly between groups, a Kruskal-Wallis ranked sums test was applied. This test revealed significant differences in group size by subarea (KW = 9.544, p = 0.049). Post-hoc pairwise comparison using Dunn’s test with the Benjamini-Hochberg method revealed that the only significant difference in group sizes by subarea was between the Maui Nui and O‘ahu West subareas at the 0.1 significance level (Dunn’s test p-adjusted = 0.074).

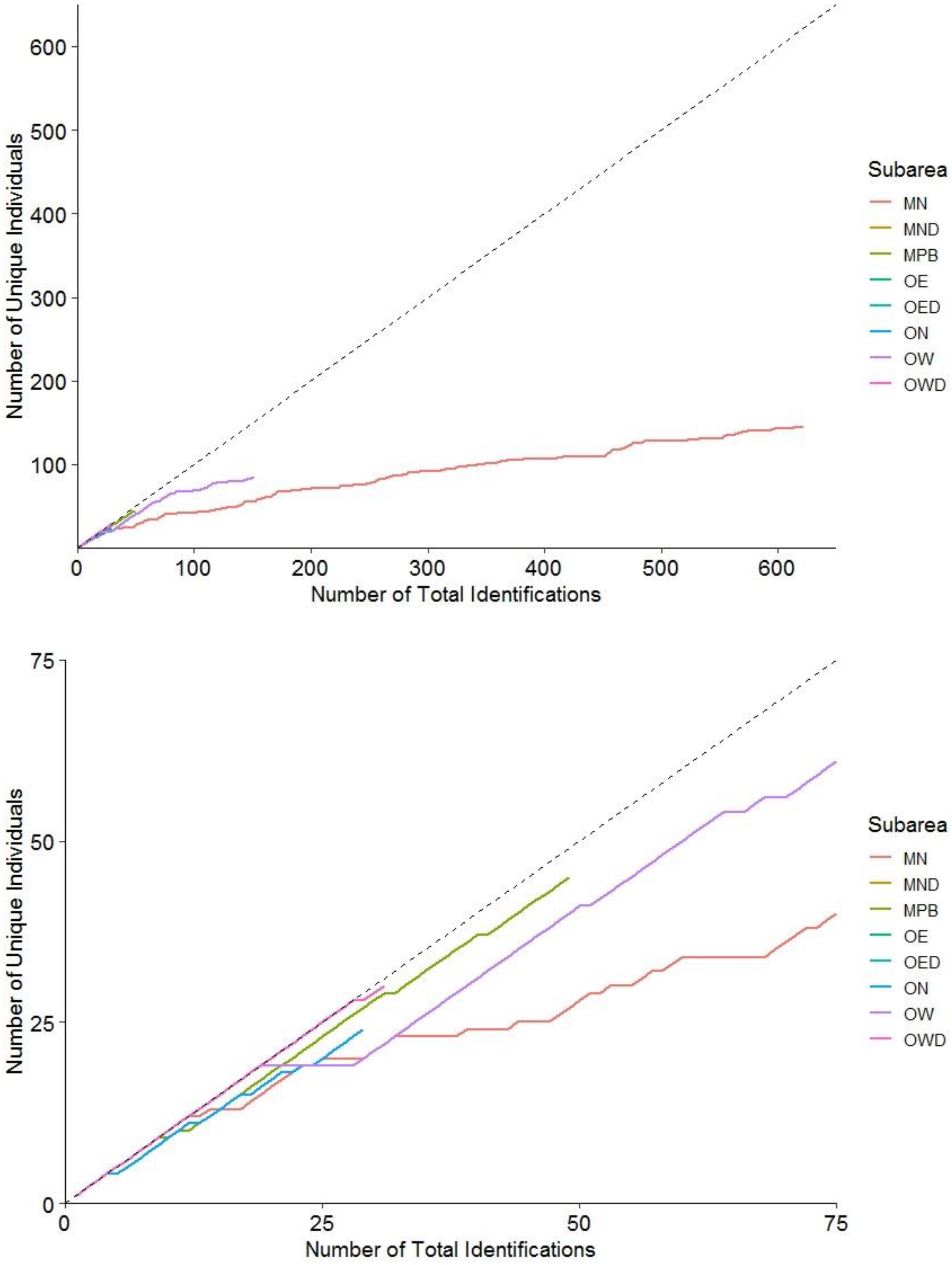


Figure 16. Discovery curves by subarea (indicated by color) for all encounters with corresponding GPS location data, with a reference 1:1 dashed trendline in black. Curves are constructed chronologically. Top: Full view of all discovery curves. Bottom: Zoomed-in view of the bottom left corner of the graph. ON = O‘ahu North, OW = O‘ahu West, OWD = O‘ahu West Deep, OE = O‘ahu East, OED = O‘ahu East Deep, MPB = Moloka‘i/Penguin Bank, MN = Maui Neui (subarea), MND = Maui Nui Deep.

Inter-Island Movements

Fourteen individuals were documented moving between island areas based on photo-identification. Only three of the 14 were sexed, all of whom were identified as females based on calf presence. HITt0518, one of the confirmed adult females, was seen the greatest number of times, with 20 total sightings between 2006 and 2018, 19 of which took place off Oʻahu, and one of which took place off Molokaʻi in 2007. Of the inter-island individuals, six were sighted off Oʻahu in multiple years, and two were sighted off Maui Nui in multiple years. Inter-island individuals were seen in association during eight encounters, of the 47 total encounters where at least one inter-island individual was present. The mean number of sightings for inter-island individuals was 4.4 (sd = ± 4.6), though the majority of resightings were often within the same island area.

Most individuals were documented moving between island areas only once (e.g., moving from Oʻahu to Maui Nui), but three individuals moved between island areas more than once (e.g., moving from Oʻahu to Maui Nui and back to Oʻahu). The three individuals that moved between island areas more than once were HITt1095 (sighted first off Maui Nui in December 2012, then off Oʻahu in June 2014, and then again off Maui Nui in November 2014), HITt1104 (first sighted twice off Oʻahu in June 2014 and February 2016, then off Maui Nui in March 2017, and again off Oʻahu in November 2017) and HITt1439 (sighted first off Oʻahu in September 2012, then twice off Maui Nui in December 2012 and November 2014, and then again off Oʻahu in June 2017). The two inter-island individuals documented moving between islands in encounters with corresponding GPS locations were HITt0232 (sighted in the Maui Nui Deep subarea in 2002, then in the Oʻahu West Deep subarea in 2003) and HITt1104 (sighted first in the O‘ahu West subarea in 2016, then in the Maui Nui Deep subarea in March 2017, and then again in the O‘ahu West subarea in November 2017).

There were no strong seasonal trends to encounters with inter-island individuals (Table 6). Encounters with inter-island individuals most frequently took place off O‘ahu, and were less frequent off Maui Nui. The proportion of total encounters with inter-island individuals was greatest in O‘ahu during the summer (18%), and at its lowest during the spring (12%), while off Maui Nui it was greatest during the Fall (6%), and at its lowest during the summer (1%) and winter (1%).

Table 6. Inter-island movements by season from photo-identification data. Percentages are of the total number of encounters for that particular island area and seaon. II = Inter-Island.

Season	**Total # Encounters off O‘ahu**	**# Encounters with II off O‘ahu (%)**	**Total # Encounters off Maui Nui**	**# of Encounters with II off Maui Nui (%)**
Spring	76	9 (12%)	151	6 (4%)
Summer	79	14 (18%)	69	1 (1%)
Fall	46	7 (15%)	34	2 (6%)
Winter	47	7 (15%)	103	1 (1%)

Movements and Spatial Use

Photo-Identification Data

Mean inter-annual movement distances varied between island areas, subareas, and residency classes, though the vast majority fell below 20 km (Table 7; Figure 17). The mean overall inter-annual movement distance for all individuals was 16.5 km (sd = ± 16.8 km, rsd = 102%), but when broken down by island area was markedly lower for O‘ahu (10.3 km, sd = ± 8.5 km, rsd = 83%) than for Maui Nui (17.4 km, sd = ± 9.4 km, rsd = 54%). Inter-island individuals had substantially larger inter-annual movement distances, with a mean of 65.0 km (sd

= ± 78.4 km, rsd = 121%), due the influence of the inter-island movements. When broken down by subareas, the O‘ahu North, O‘ahu West, and Maui Nui subareas all had relatively small mean inter-annual travel distances, at 8.0 km (sd = ± 1.5 km, rsd = 19%), 10.0 km (sd = ± 8.8 km, rsd = 88%), and 16.9 km (sd = ± 9.2 km, rsd = 54%) respectively. In contrast, the O‘ahu West Deep and Moloka‘i/Penguin Bank had mean inter-annual movement distances that exceeded the mean for all individuals, at 25.4 km (sd = ± 49.1 km, rsd = 193%) and 26.3 km (sd = ± 12.5 km, rsd = 48%) respectively, and by far the largest mean inter-annual movement distance was for individuals seen in the Maui Nui Deep subarea (86.9 km, sd = ± 74.8 km, rsd = 86%). When broken down by residency class, O‘ahu long-term and short-term residents also had smaller mean inter-annual movement distances when compared to Maui Nui long and short-term residents, with the smallest distance for O‘ahu short-term residents (9.2 km, sd = ± 1.2 km, rsd = 13%), and the greatest distance for Maui Nui long-term residents (17.5 km, sd = ± 8.3 km, 47%).

Mean inter-annual movment distances for a simulated randomly mixing population were also calculated to provide a point of reference for comparison between actual populations (Table 7). For the simulated population with random mixing between island areas, the mean inter-annual travel distance was 66.9 km (sd = ± 43.5 km, rsd = 65%). For the simulated populations with random mixing within island areas, mean inter-annual travel distances were 19.5 km (sd = ± 13.3 km, rsd = 68%) for O‘ahu, and 22.0 km (sd = ± 9.6 km, rsd = 44%) for Maui Nui.

Table 7. Mean inter-annual travel distances for individuals seen in more than one year for all encounters where corresponding GPS locations were available. For island area calculations, all inter-island individuals have been excluded. Distances could not be calculated for the Oʻahu East or Oʻahu East Deep subareas, or any associative residents or visitors.

Island Area, Subarea, or Residency Class	# Individuals	Mean (SD) Inter-Annual Travel Distance (km)
Simulated Random (All Encounters)	NA	66.9 (± 43.5)
Simulated Random (Oʻahu Island Area)	NA	19.5 (± 13.3)
Simulated Random (Maui Nui Island Area)	NA	22.0 (± 9.6)
All Individuals	116	16.5 (± 16.8)
Oʻahu (Island Area)	23	10.3 (± 8.5)
Maui Nui (Island Area)	88	17.4 (± 9.4)
Inter-island	5	65.0 (± 78.4)
Oʻahu North	4	8.0 (± 1.5)
Oʻahu West	22	10.0 (± 8.8)
Oʻahu West Deep	10	25.4 (± 49.1)
Molokaʻi/Penguin Bank	6	26.3 (± 12.5)
Maui Nui (subarea)	88	16.9 (± 9.2)
Maui Nui Deep	4	86.9 (± 74.8)
Oʻahu Long-Term Resident	20	10.5 (± 9.0)
Oʻahu Short-Term Resident	2	9.2 (± 1.2)
Maui Nui Long-Term Resident	64	17.5 (± 8.3)
Maui Nui Short-Term Resident	19	16.0 (± 10.6)

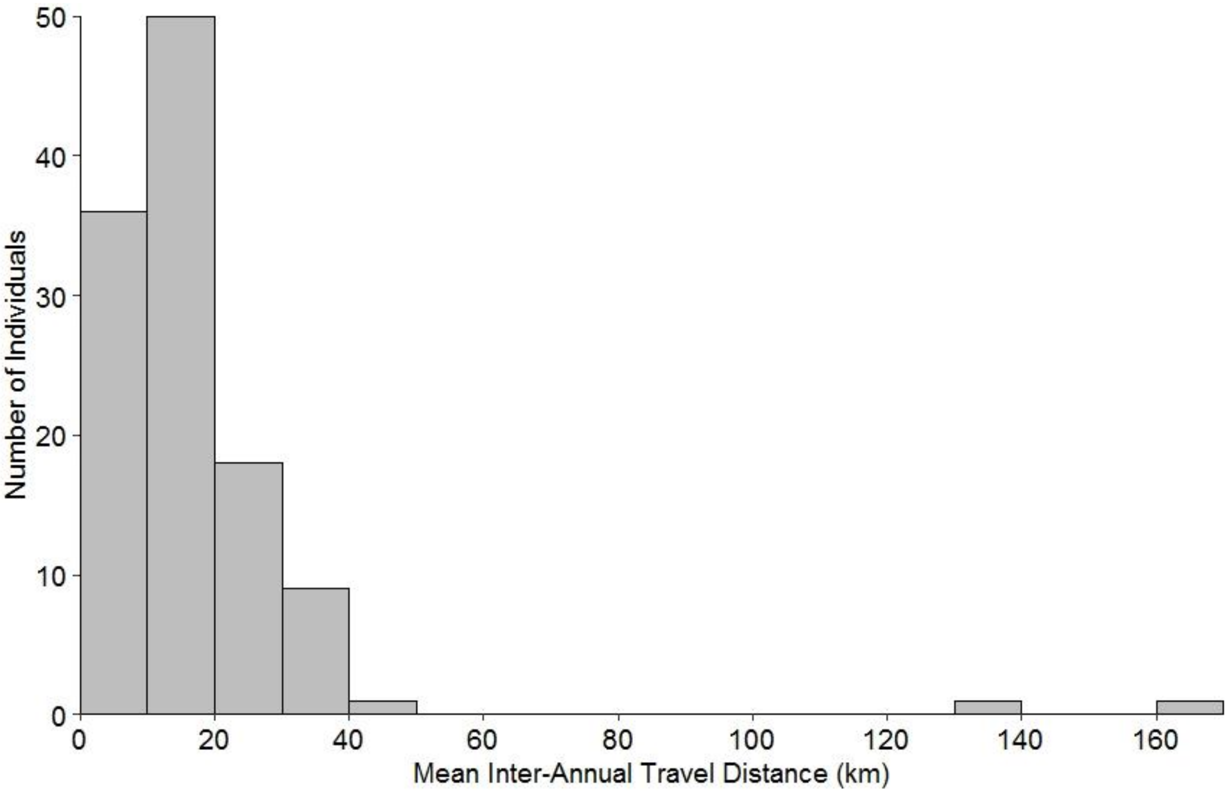


Figure 17. Histogram of mean inter-annual travel distances for all individuals (n=116) seen in more than one year for all encounters where corresponding GPS locations were available.

Satellite-Tag Data

Satellite-tags were deployed off both island areas over the course of three different years, and in a wide range of depths (Table 8). TtTag006 (HITt0788) and TtTag007 (HITt0794) were both deployed in December 2012. HITt0788 (TtTag006) is a male dolphin classified as a Maui Nui long-term resident, and has only been documented through photo-identification in the Maui Nui subarea. On the social network, it is located within the main Maui Nui cluster, where it is tied to 25 other individuals. This animal generally remained within the Maui Nui subarea over the course of the 17.7 days where the tag was transmitting, though it did briefly cross up into the Moloka‘i/Penguin Bank subarea when it moved to the south shore of Moloka‘i (Figure 18). HITt0794 (TtTag007) is classified as a Maui Nui associative resident, and has only been documented through photo-identification in the Maui Nui subarea as well. On the social network, this individual is also located within the main Maui Nui cluster, where it shares ties with nine other individuals. During the 9.0 days of signal contact, the animal generally remained within the Maui Nui subarea, though it did venture out into the Maui Nui Deep subarea briefly (Figure 18).

Table 8. Summary of tag data. Sex was determined for only two individuals: TtTag006 was identified as a male based on genetic analysis, and TtTag030 was identified as a female based on calf presence.

Tag ID	Individual ID	Date Tagged	Tag Deployment Location	Bathymetric Depth Tagged (m)	Tag Type	Duration of Contact (Days)	# Kalman Locations (Unfiltered)	# Douglas Filtered Locations
TtTag006	HITt0788	13-Dec-2012	Southeast Lāna‘i	140	MK 10-A	17.7	345	337
TtTag007	HITt0794	19-Dec-2012	West Lāna‘i	93	SPOT 5	9.0	131	130
TtTag030	HITt0604	17-Oct-2016	West O‘ahu	479	SPOT 6	13.0	236	230
TtTag031	HITt1094	07-Mar-2017	Offshore West Lāna‘i	708	SPOT 6	16.3	343	332
TtTag032	HITt1096	17-Mar-2017	West Lāna‘i	72	SPOT 6	13.0	253	246

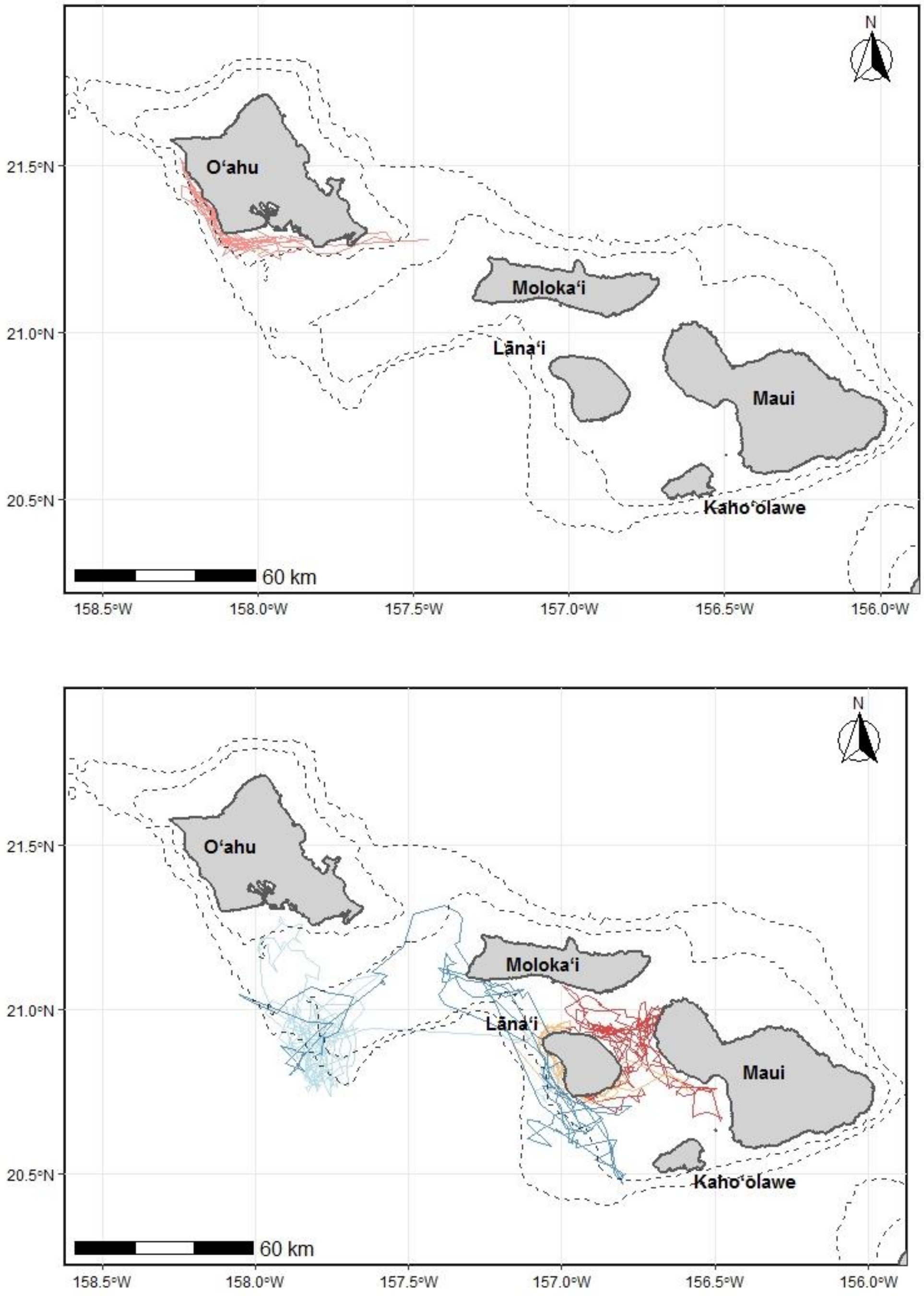


Figure 18. Douglas-filtered Argos tracklines of the five satellite-tagged invividuals, one from O'ahu (top), and four from Maui Nui (bottom). In the top panel, TtTag030 (HITt0604, deployed off west O'ahu, 17-30 October 2016) is colored red. In the bottom panel, TtTag006 (HITt0788, deloyed off southeast Lāna'i, 13-31 December 2012) is colored red, TtTag007 (HITt0794, deployed off west Lāna'i, 19-28 December 2012) is colored orange, TtTag031 (HITt1094, deployed offshore from west Lāna'i, 7-24 March 2017) is colored light blue, and TtTag032 (HITt1096, deployed off west Lāna'i, 17-30 March 2017) is colored dark blue. Depth contours (black dashed lines) are shown for the 500 m and 1,000 m bathymetric depth.

TtTag030 (HITt0604) was deployed off O‘ahu in October 2016 onto a female O‘ahu long-term resident documented through photo-identification in both the O‘ahu West and O‘ahu West Deep subareas. This animal spent the duration of the 13.0 days of signal contact within the O‘ahu West and O‘ahu subareas, with most locations in the O‘ahu West subarea (Figure 18).

The final two tags, TtTag031 (HITt1094) and TtTag032 (HITt1096), were both deployed off Maui Nui in March 2017, onto two animals of unknown sex. HITt1094 (TtTag031) is classified as a Mui Nui visitor, and has only ever been documented through photo-ID in the Maui Nui Deep subarea. On the social network, it is disconnected from the main components, and shares no ties with any individuals. Over the 16.3 days of signal contact, HITt1094 (TtTag031) moved around extensively, crossing into the O‘ahu West, O‘ahu West Deep, Moloka‘i/Penguin Bank, Maui Nui Deep, and Maui Nui subareas, with the majority of locations taking place on the south end of Penguin Bank (Figure 18). HITt1096 (TtTag032) was not assigned a residency class or included in the social network, on account of its distinctiveness falling below a score of Dist = 3. This individual has only been encountered once, on the day when it was tagged, when it was encountered with three other individuals, HITt1095, HITt1097, and HITt1098. HITt1098 was also not assigned a residency class or included in the social network on account of a low distinctiveness score, but HITt1095 and HITt1097 were classified as an inter-island individual and a Maui Nui short-term resident, respectively. On the social network, these two individuals occupy locations on the periphery of the O‘ahu and Maui Nui clusters, and represent one of the two links connecting the main clusters. Over the 13.0 days of signal contact, HITt1096 also moved around extensively, moving between the Maui Nui and Maui Nui Deep subareas, as well as the Moloka‘i/Penguin Bank and O‘ahu West Deep suabreas (Figure 18).

Probability densities were constructed for both island areas where tags were deployed (Figure 19). The core area for the single animal tagged off O‘ahu was centered around the southwest coast, incorporating parts of the O‘ahu West and O‘ahu West Deep subareas, while the core area for the four animals tagged off Maui Nui were primarily centered around the island of Lāna‘i, though a second, smaller core area existed on the south end of Penguin Bank. The 95 and 99% density polygons for Maui Nui-deployed tags extended to include the south shore of O‘ahu, and overlapped with all three of the O‘ahu polygons.

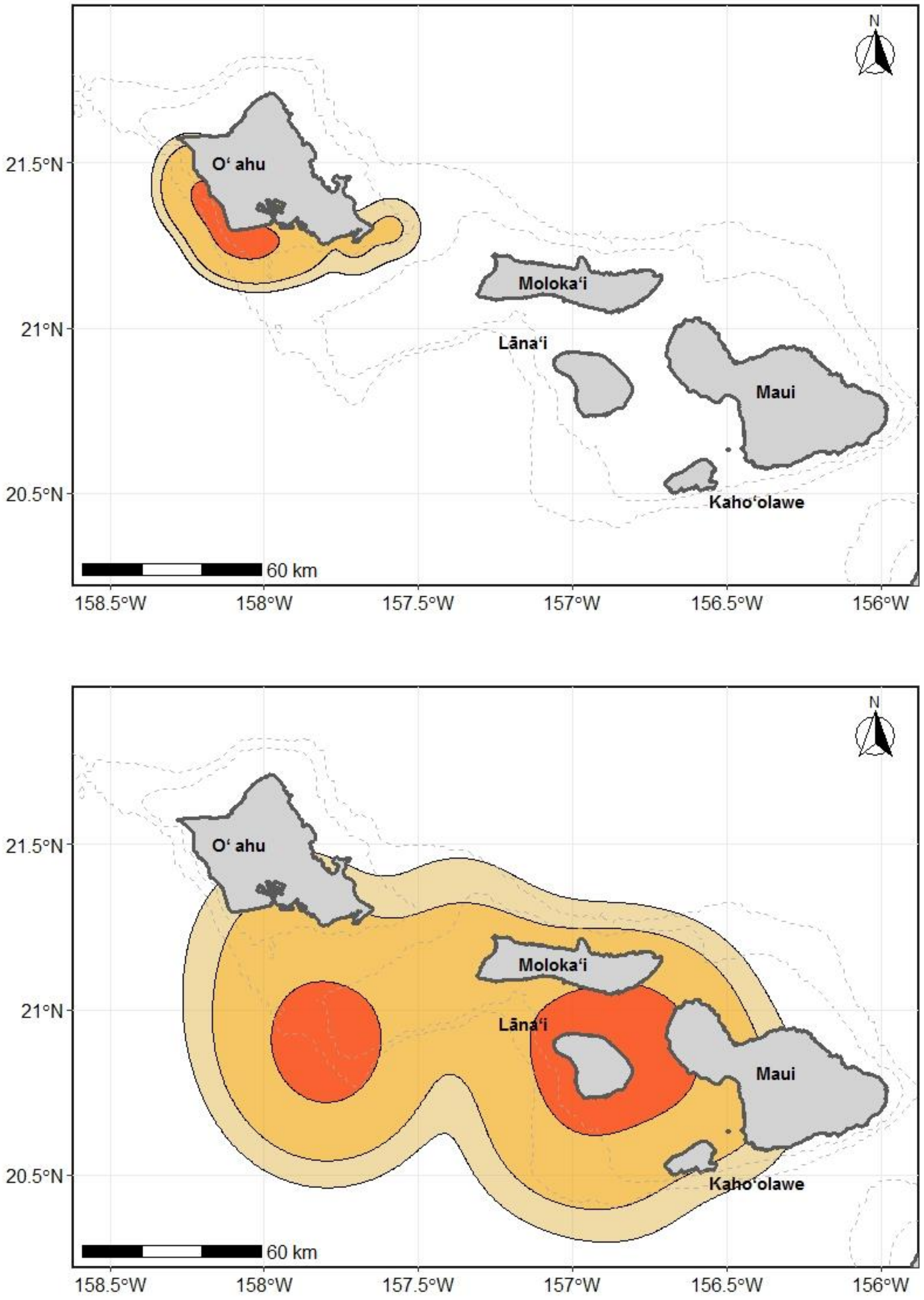


Figure 19. Probability density representation of bottlenose dolphin home ranges by island area where the animal was tagged, based on trimmed data from one satellite-tag deployed off O'ahu (top) and four off Maui Nui (bottom). Location data from the first 24 hours of each deployment were discarded to reduce tagging area bias. Dark orange indicates the 50% polygon, orange indicates the 95% polygon, and light orange represents the 99% polygon. Depth contours (grey dashed lines) are shown for the 500 m and 1,000 m depth contours.

Individual Habitat Preferences

An examination of depth distributions for the six individuals with the greatest number of sightings with corresponding GPS coordinates revealed a slight degree of individual preference for different depth ranges (Figure 20). All six individuals (HITt0006, HITt0008, HITt0024, HITt0044, HITt0056, and HITt0062) were Maui Nui long-term residents with sightings exclusively in the Maui Nui subarea, and four of the six were identified as females based on genetic sampling. Yet even within this mostly homogenous group, sightings of individuals were distributed differently by depth. HITt0006, HITt0024, HITt0044, and HITt0056 exhibited a strong preference for depths ≤ 100 m, with mean depths at 69 m (sd = ± 42 m), 101 m (sd = ± 93 m), 58 m (sd = ± 21 m), and 81 m (sd = ± 83 m) respectively. HITt0008 and HITt0062, on the other hand, exhibited a preference for depths ≥ 100 m, with mean depths at 119 m (sd = ± 58 m) and 147 m (sd = ± 50 m) respectively. Across the entire group, however, all sightings took place in depths < 500 m, echoing the overall distribution of bottlenose sightings for all island areas (Figure 9). A Kruskal-Wallis ranked sums test was performed to test whether encounter depths differed by ID, revealing significant differences (KW = 23, $p < 0.001$). Post-hoc comparison of IDs using Dunn's test with the Benjamini-Hochberg method revealed significant differences in encounter depths between HITt0006 and HITt0008 (Dunn's test p-adjusted = 0.006), HITt0008 and HITt0044 (Dunn's test p-adjusted = 0.007), HITt0008 and HITt0056 (Dunn's test p-adjusted = 0.012), HITt0006 and HITt0062 (Dunn's test p-adjusted = 0.006), HITt0044 and HITt0062 (Dunn's test p-adjusted = 0.010), and between HITt0056 and HITt0062 (Dunn's test p-adjusted = 0.008).

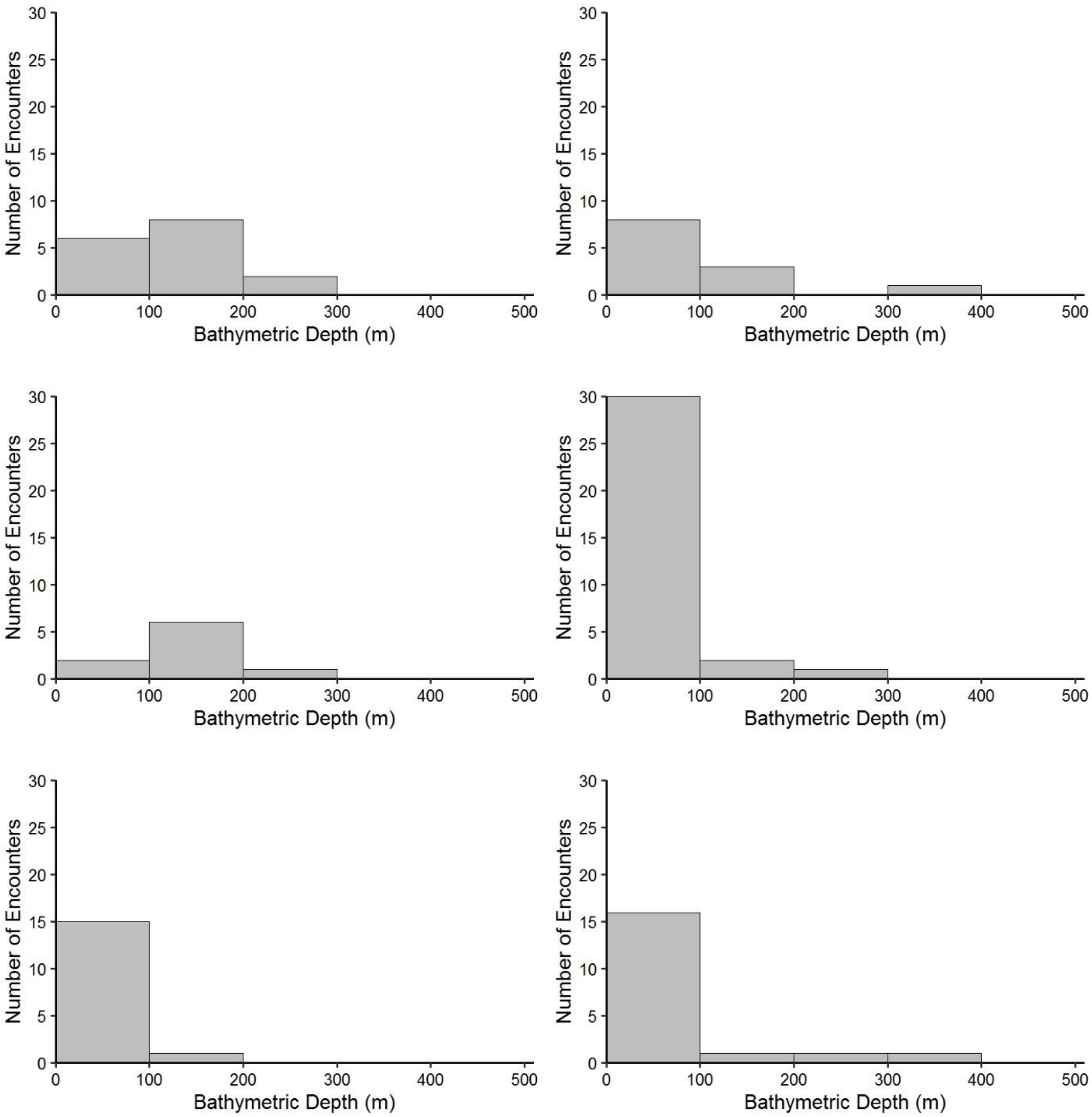


Figure 20. Range of depths from photo-ID encounters for six Maui Nui long-term residents. Top left: HITt0008. Top right: HITt0024. Middle left: HITt0062. Middle right: HITt0006. Bottom left: HITt0044. Bottom right: HITt0056.

Tagged individuals also showed preferences for different depth ranges, though these tended to be more extreme (Figure 21). TtTag006 (HITt0788) and TtTag007 (HITt0794) were both tagged off Maui Nui in relatively shallow water (< 150 m), and had the majority of their Douglas-filtered Argos locations in depths ≤ 100 m, with mean depths of 75 m (sd = ± 74 m) and 78 m (sd = ± 151 m) respectively. However, a third individual tagged off Maui Nui in shallow water at 72 m depth, TtTag032 (HITt1096), spent a significant portion of its time in waters deeper than 100 m, and had a mean depth of 448 m (sd = ± 397 m). The remaining individual tagged in relatively shallow water off O‘ahu in 479 m, TtTag030 (HITt0604), also displayed a preference for waters ≤ 500 m, with a mean depth of 373 m (sd = ± 212 m) though it did spend extensive time in deeper water. The one individual tagged in deep water off Maui Nui at 708 m, TtTag031 (HITt1094), spent the majority of its time in water ≥ 500 m, with a mean depth of 809 m (sd = ± 545 m), though it did cross into shallow water areas as well. Another Kruskal-Wallis ranked sums test was performed to determine whether the differences in tag location depths were significant, revealing that they are (KW = 573.46, $p < 0.001$). Post-hoc pairwise comparison using Dunn’s test with the Benjamini-Hochberg method revealed significant differences in tag location depths between all pairs, with the exception of TtTag006 (HITt0788) and TtTag007 (HITt0794), and TtTag030 (HITt0604) and TtTag032 (HITt1096; Appendix Table D).

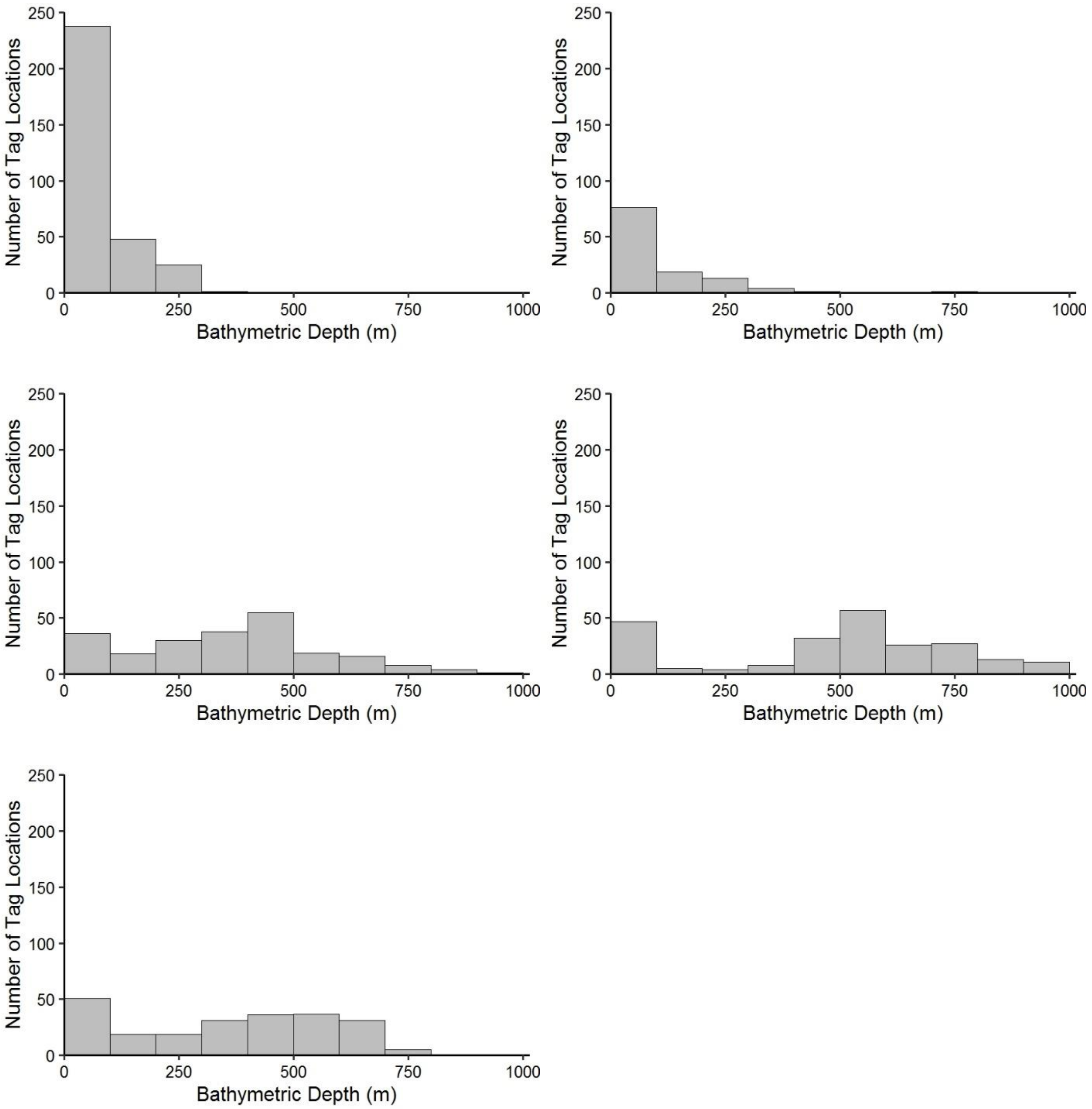


Figure 21. Range of depths from satellite-tag data for five individuals. Top left: TtTag006 (HITt0788, deployed off southeast Lāna‘i, 13-31 December 2012). Top right: TtTag007 (HITt0794, deployed off west Lāna‘i , 19-28 December 2012). Middle left: TtTag030 (HITt0604, deployed off west O‘ahu, 17-30 October 2016). Middle right: TtTag031 (HITt1094, deployed offshore from west Lāna‘i, 7-24 March 2017). Bottom left: TtTag032 (HITt1096, deployed off west Lāna‘i, 17-30 March 2017).

Interchange Indices

Within-area resighting indices and interchange indices for island areas were calculated using the entire photo-identification dataset after quality control. Resighting indices were 1.07 for Oʻahu, and 2.33 for Maui Nui, indicating that a higher proportion of individuals are resighted off Maui Nui than off Oʻahu, and reconfirming the earlier results of the discovery curves for these areas (Figure 11). The interchange index between island areas was 0.28, falling an order of magnitude below the Maui Nui and Oʻahu within-area resighting indices. This means that movement between the island areas does occur, but not at levels that make it as likely as movement within the island areas.

Within-area resighting indices by subarea for encounters with GPS coordinates ranged from 0 to 5.21, with the lowest indices in the Oʻahu East (0.00), Oʻahu East Deep (0.00), and Maui Nui Deep (0.00) subareas, and the highest index within the Oʻahu North subarea (5.21). The second highest within-area resighting index was for the Maui Nui subarea (4.24), and values for remaining subareas were 1.70 for Oʻahu West, 1.11 for Oʻahu West Deep, and 0.99 for Molokaʻi/Penguin Bank. Sample sizes of resighted individuals in several subareas were very small, including for the Oʻahu North, Oʻahu West Deep, Oʻahu East, Oʻahu East Deep, Molokaʻi/Penguin Bank, and Maui Nui Deep Subareas, all of which had three or fewer individuals resighted across multiple years. Total sample sizes of individuals within subareas were comparatively small for all of the subareas as well, however. The greatest number of within-area resighted individuals was within the Maui Nui subarea, with 88 out of 144 total individuals having resightings across multiple years. Even with the generally small sample sizes, however, movements between subareas were identified.

Interchange indices between subareas that were of the same or greater magnitude as both within-area resighting indices for those subareas were found for four pairs of subareas: O‘ahu West/O‘ahu West Deep, O‘ahu West/Maui Nui Deep, O‘ahu West Deep/Maui Nui Deep, and Maui Nui/Maui Nui Deep (Table 9). This indicates that movements between these pairs of subareas is as likely as movements within each of the subareas that compromise the pairs. Interchanges indices between subareas that were not of the same or greater magnitude as both within-area resighting indices for those subareas were calculated for two pairs of subareas: O‘ahu West/O‘ahu North, and Maui Nui/Moloka‘i/Penguin Bank. Movements between these pairs of subareas are therefore not as likely as movements within each of the individual subareas that comprise the pairs, but do still occur. The interchange indices between all remaining pairs of subareas were calculated to be zero, indicating that either no movement between those subareas takes place, or that movement is infrequent enough that it was never documented.

Table 9. Within-area resighting and interchange indices for individuals with designated subareas based on GPS coordinates. Resighting indices are based on the number of individuals seen across multiple years, and located along the diagonal. Interchange indices that are of the same magnitude as within-area resighting indices for both of the same subareas are shaded in grey. ON = Oʻahu North, OW = Oʻahu West, OWD = Oʻahu West Deep, OE = Oʻahu East, OED = Oʻahu East Deep, MPB = Molokaʻi/Penguin Bank, MN = Maui Neui (subarea), MND = Maui Nui Deep.

Subarea (# Within-Area Resighted Individuals, # Total Individuals)	**ON**	**OW**	**OWD**	**OE**	**OED**	**MPB**	**MN**	**MND**
ON (3, 24)	5.21	-	-	-	-	-	-	-
OW (12, 84)	0.49	1.70	-	-	-	-	-	-
OWD (1, 30)	0	3.57	1.11	-	-	-	-	-
OE (0, 2)	0	0	0	0	-	-	-	-
OED (0, 11)	0	0	0	0	0	-	-	-
MPB (2, 45)	0	0	0	0	0	0.99	-	-
MN (88, 144)	0	0	0	0	0	0.62	4.24	-
MND (0, 8)	0	1.49	4.17	0	0	0	1.74	0

Chapter Five: Discussion

Introduction

Accurate information about population structure is critical for effective management of protected species. Bottlenose dolphins are found worldwide in tropical and sub-tropical waters in a wide variety of population structures, including offshore, non-resident coastal, migratory, transient archipelago-associated, resident coastal, and resident island-associated populations, as well as possible metapopulation structures. While still subject to debate, the most relevant definition for management purposes of a population for this species is the demographically-independent population (DIP), which is intended to be analogous to the NMFS-designated stocks under direction of the MMPA.

Four small, demographically-independent and genetically differentiated populations of resident island-associated bottlenose dolphins have been designated as stocks in the main Hawaiian Islands, three of which showed evidence of decline in a recent abundance estimation (Van Cise et al., 2021). These four stocks are centered around Kauaʻi/Niʻihau, Oʻahu, Maui Nui (Maui, Lānaʻi, Kahoʻolawe, and Molokaʻi), and Hawaiʻi, with statistically significant declines occurring in the Maui Nui stock, and non-significant declines occurring in the Kauaʻi/Niʻihau and Oʻahu stocks (Van Cise et al., 2021). These stocks are subject to unique anthropogenic stressors that vary spatially, including shipping activity off Oʻahu, small boat traffic off Maui Nui and Hawaiʻi, military activity off Kauaʻi and Niʻihau, and fisheries activity off Oʻahu and Hawaiʻi. To ensure effective management, stock designations must therefore utilize accurate spatial boundaries that encompass these spatially variable threats.

Long-term photo-identification and satellite-tagging efforts have revealed that some resident dolphins may move between Oʻahu and Maui Nui (CRC, unpublished data). However, the relative importance and impacts of these movements has remained unknown up to this point, in spite of their potential for altering levels of genetic diversity, and transmitting culturally-mediated behaviors. I used photo-identification and satellite-tag data on resident bottlenose dolphins collected over the course of more than two decades to evaluate the population structure, spatial use, and residency patterns of the Oʻahu and Maui Nui stocks using several approaches. This sizable dataset, incorporating encounters from several areas, years, and seasons, allowed for a robust evaluation. Dividing island areas into subareas allowed for greater resolution, and helped to identify areas where minimal survey effort might bias conclusions.

Residency classifications revealed that while the number of long-term and short-term residents in each island area were similar, there was a vast disparity in the number of visitors, with a substantially larger number identified off Oʻahu. I also found that while social connections between the two populations were minimal, there was geographic overlap in spatial use. This was caused by a subset of individuals from the Oʻahu population that move between the west and south coasts of Oʻahu, southwest Molokaʻi, Penguin Bank, and southwest Lānaʻi. Generally, however, most individuals exhibited much more strict site fidelity and preference for specific depth ranges, with mean inter-annual travel distances for the Oʻahu population at 10.3 km, and for the Maui Nui population at 17.4 km, compared to 65.0 km for animals that used both island areas. There was no clear seasonal driver of inter-island movements, with inter-island animals identified in both island areas at all times of the year. However, the drastically higher number of visitors off Oʻahu in spite of a smaller total area of shallow-water habitat suggests that perhaps this behavior is a response to limited resource availability caused by a high density of bottlenose dolphins.

Survey Coverage, Encounter Characteristics, and Depth Preferences

Data spanned over two decades between CRC surveys and contributions from other researchers and community scientists, allowing for a robust examination of residency and movements. While CRC had considerable survey effort off Maui Nui in 2000-2001, the vast majority of encounters (87%) were from groups other than CRC (Figure 7). This expansion of the dataset allowed for a much more thorough evaluation of both residency and population structure than would have been possible with CRC encounters alone, and improved the likelihood of detecting inter-island movements. Additionally, contributed encounters increased coverage in areas where CRC survey effort was not extensive, such as Penguin Bank and the waters around Molokaʻi. However, both CRC effort and contributed encounters were heavily biased towards the leeward sides of the islands due to weather conditions, likely excluding bottlenose that primarily use the windward sides (Figure 6; Figure 8). Discovery curves for north and east Oʻahu, two regions with minimal coverage, continue to rise at a steep incline, indicating that either sampling has not been comprehensive or that there is a lower degree of site fidelity on the windward sides (Figure 16). Additionally, the few encounters from the windward sides (six from north Oʻahu, and three from east Oʻahu, as well as the three encounters from north of Molokaʻi) were comprised of animals that were seen only in those areas, with the single exception of an animal seen off both north and west Oʻahu. Furthermore, animals from these areas cluster together, largely separate from the main components in the social network (Figure 14). This strongly suggests that additional groups of bottlenose dolphins are present on the windward sides of the islands that are largely isolated from the leeward side groups, and may therefore be demographically independent. Future survey efforts in these areas would be beneficial in understanding whether windward side groups exist, and if so, what their relationships to the leeward side groups are.

Dividing the island areas into subareas allowed for a more detailed analysis of population structure and spatial use, and also helped to identify areas where encounter rates were low or survey coverage was poor. Perhaps unsurprisingly given the small calculated mean inter-annual travel distances (mean = 16.5 km for all resighted individuals), social stratification aligned well with spatial stratification between subareas (Figure 14). Satellite-tag data also revealed spatial stratification among tagged resident animals from the main island area clusters, with the two Maui Nui residents generally remaining within shallow waters around Maui and Lāna‘i, and the O‘ahu resident remaining in the waters around west and south O‘ahu (Figure 18). These five tagged individuals help to demonstrate that Hawaiian resident bottlenose dolphins generally have strict site fidelity, as previously reported by Baird et al. (2009), supported by Martien et al. (2011), and later confirmed by Van Cise et al. (2021), something that is likely behaviorally driven by distinct habitat preferences. Different subareas have unique degrees of open-ocean exposure, total areas, and different expanses of nearshore habitat that could favor niche specialization, as has been observed in other bottlenose dolphin populations worldwide (Hoelzel, 2009). Over a long time period, the limited mobility of Hawaiian bottlenose, in conjunction with their social and spatial stratification, may continue to gradually increase the genetic and cultural differentiation between groups. Already, the populations between island areas are genetically differentiated (Martien et al., 2011), and future work to investigate how genetic haplotype ratios differ between subareas would be informative.

Generally, encounter rates were highest in shallow subareas with extensive survey coverage, including O‘ahu West, and Maui Nui, lowest in subareas with minimal survey coverage, including Oʻahu North, Oʻahu East, and Molokaʻi/Penguin Bank. However, this trend did not hold true for deep water areas, where in spite of extensive CRC survey effort, encounters with bottlenose dolphins were less frequent than expected. This indicates that Hawaiian bottlenose dolphins exhibit a general preference for shallow waters, especially waters shallower than 200 m bathymetric depth, where the vast majority of encounters took place. These results are well in line with previous work among other populations of inshore bottlenose dolphins (Dinis et al., 2016; Silva et al., 2014). This also reaffirms conclusions in previous work on Hawaiian bottlenose dolphins by Pittman et al. (2016), who demonstrated that depth is the single most important predictor of bottlenose dolphin distribution in the Hawaiian Islands, with animals exhibiting a strong preference for shallow water. This is likely driven by prey distribution, as bottlenose are known to feed on nearshore and reef fish species (Baird, 2016).

A few encounters did take place in waters deeper than 500 m, raising the question of whether the individuals in these encounters were from separate populations or social groups than the shallow water animals. To explore this, subareas were further divided at the 500 m bathymetric contour when encounters in both shallow and deep water were available. We found that interchange between shallow and deep water subareas was generally high, with interchange indices demonstrating that movements between Oʻahu West and Oʻahu West Deep, as well as between Maui Nui and Maui Nui Deep were just as likely as movements within each subarea (Table 9). Movements were not detected between the Oʻahu East and Oʻahu East Deep subareas, but sample sizes in these subareas were small, limiting the ability to accurately assess movements. This suggests that most bottlenose encounters in deep water (at least up to 1,000 m bathymetric depth) likely do not represent different populations or social groups, but are occasional excursions of the same resident populations that prefer shallow water.

Encounter characteristics and tag data revealed behavioral differences between animals in different island areas. Significant differences in group size were detected between island areas, with larger groups of animals encountered off O‘ahu compared to the groups encountered off Maui Nui (Mann-Whitney U Test, p = 0.008). Additionally, satellite-tag data reveals possible differences in depth preference. The two tagged animals that are positioned within the main Maui Nui component of the social network remained exclusively in shallow water, never venturing beyond 500 m depth, while in contrast the single animal tagged off O‘ahu and the remaining two tagged animals from Maui Nui frequently ventured into deeper waters (Figure 18; Figure 21). The two tags from Maui Nui that do not cluster with the main Maui Nui component are more likely inter-island animals than members of the Maui Nui stock based on their association and movement patterns, explaining the differences between the distributions of their tag location depths and those of the other two animals tagged off Maui Nui. The similar depth distribution between their tag locations and that of the single tagged O‘ahu animal lends further support to the idea that they are inter-island animals, as all inter-island individuals are clustered within the O‘ahu component of the social network and appear to represent a subset of this population (Figure 13). However, tag data is inherently short-term, and caution must used in interpreting these results. Crucially, the significant interchange between the Maui Nui and Maui Nui Deep subareas revealed by photo-identification and interchange indices suggests that members of the Maui Nui population do in fact make use of deep water, something which the tag data failed to capture (Table 9).

Beyond population-level preferences, there is also evidence that preferences for different depth ranges may exist at the individual level. An examination of the distribution of encounter depths for the six Maui Nui long-term residents with the most encounters demonstrates that there were significant differences in encounter depths between individuals (Figure 20; Kruskal-Wallis ranked sums test, $p < 0.001$). This occurred in spite of the fact that these individuals are all members of the same encountered only within the same subarea, and all are clustered together within the Maui Nui main component of the social network (Figure 13). Significant differences were primarily between individuals most frequently encountered between 100-200 m depth and those most frequently encountered in ≤ 100 m depth. An analysis of the distribution of tag location depths for the five satellite-tagged animals also revealed stark differences in tag location depths between individuals (Figure 21). Almost all pairwise comparisons of tag location depths between tagged individuals revealed significant differences, with only two exceptions – once between two animals from the same island area, and once between two animals from different island areas (Appendix Table D). This further highlights the need for caution in drawing conclusions about population identity only from spatial use, and vice versa, as tremendous variation can exist even within the same populations. Multiple lines of evidence in this case produced slightly contradictory results regarding depth preferences, but in general the findings of this study indicate that Oʻahu and inter-island animals tend to use deep water more regularly than Maui Nui animals. This may be a behavioral adaptation indicative of ecological niche specialization, though to some degree this may also reflect the greater total area of shallow water habitat around Maui Nui compared to Oʻahu (Table 4).

Residency Assignments

Residency assignments were undertaken to explore potential variations between island areas. There were similar numbers of long- and short-term residents for both island areas, though there were almost six times as many associative residents in the Oʻahu island area compared to the Maui Nui island area. The greatest numbers of both long- and short-term residents were found in the Oʻahu West and Maui Nui subareas (Table 5). This is unsurprising given that these subareas had both the greatest survey coverage and numbers of encounters, and improved survey coverage increases the likelihood of repeated encounters with the same individuals, allowing for a better assessment of how long individuals remain in a particular area. In contrast, the Oʻahu East, Oʻahu East Deep, Oʻahu North subareas, all with poor coverage, have low numbers of long- and short-term resident animals compared to the number of associative residents and visitors. Interestingly, the Molokaʻi/Penguin Bank subarea had the greatest number of visitors and one of the lowest resighting rates, in spite of having the second-largest number of encounters within the subarea, and the third largest number of total identified individuals. This implies that perhaps the animals using this subarea tend to be more transient, something reaffirmed by the fact that the mean inter-annual travel distance of Molokaʻi/Penguin Bank animals is greater than the mean inter-annual travel distances for all other subareas, with the exception of Maui Nui Deep (Table 7).

Within the social network, two large main components representing the two main island areas were easily distinguishable, along with several peripheral clusters (Figure 12). Of the 472 total animals included in the study, 380 (81%) individuals are part of the main components, while 92 (19%) individuals are part of the peripheral clusters. Almost all long- and short-term residents clustered within the main components, while the peripheral components were comprised almost entirely of visitors (Figure 13). This is not unexpected, as their limited number of resightings reduces the number of social relationships represented in the network. Peripheral clusters may therefore be an artifact of inadequate sampling, but it is also possible that they represent visiting dolphins from the pelagic stock, or from Kauaʻi or Hawaiʻi Island, though no such movements have been identified to date through photo-identification studies (Baird et al., 2009; CRC, unpublished data). In terms of spatial use, most peripheral clusters were comprised of individuals identified in the Moloka‘i/Penguin Bank subarea, though Moloka‘i/Penguin Bank animals were also identified in both main components (Figure 14). Connections to the Maui Nui component seem to be an artifact of the way that the subareas were drawn, however. HITt0075 and HITt0437 (the two Moloka‘i/Penguin Bank subarea animals deeply embedded within Maui Nui component), and HITt0070 and HITt0027 (the two Moloka‘i/Penguin Bank animals connecting the O‘ahu and Maui Nui components) were all encountered in the easternmost portion of the Moloka‘i/Penguin Bank subarea, directly adjacent to the boundary of the Maui Nui subarea. Revised subarea boundaries may counter this effect, and the further division of the Maui Nui and Moloka‘i/Penguin Bank subareas should be considered in future work. The connections to the O‘ahu component cannot be explained by subarea boundaries however, suggesting that they are not artifacts of study design. This issue will be further discussed below.

The large number of associative residents within the O‘ahu island area is particularly striking given how similar the relative numbers of other residency classes are for both island areas (Table 3). All of these individuals are connected to the main O‘ahu component of the social network, and of similar morphology to the other animals present around O‘ahu (CRC, unpublished data), so they are likely not visiting offshore groups, but members of an inshore population. Additionally, most associative residents were identified in either the O‘ahu West or O‘ahu West Deep subareas (Table 5). These animals have all only been seen over time spans of less than one year however, so they are either visitors from less frequently surveyed O‘ahu subareas, or are not resident to the island at all. This raises the question of what draws these individuals to the more heavily surveyed O‘ahu West subarea. Ecological conditions within the

O‘ahu West subarea are not markedly better than the ecological conditions elsewhere on O‘ahu and Maui Nui, and in many ways are actually worse given the heavy volume of shipping traffic, military activity, fishing activity, and the assorted environmental issues associated with dense coastal human settlement. There is therefore no immediately identifiable ecological attractant to explain such a large number of individuals passing through. An alternative explanation is that the associative residents utilize certain areas of O‘ahu with high survey coverage (such as the west coast of O‘ahu) as shallow-water travel corridors on their way to somewhere else with lower survey coverage, and mingle along the way with the resident animals that use the area more consistently. This would explain the limited resightings of these individuals and provide a possible explanation for the larger group sizes encountered off O‘ahu. This still begs the question, however, of where these animals are coming from and where they are going. Additional tagging efforts dedicated to non-resident animals off O‘ahu may shed light on the identity of these individuals.

Inter-Island Movements

Based on photo-identification evidence, very few individuals (14 out of 472 animals included in this study, 3%) moved between island areas, all of which clustered within the main O‘ahu component in the social network (Figure 12; Figure 13). In spite of over two decades worth of data, and almost 400 identified animals with almost 6,000 links in the main components, inter-island individuals only connected the two main components twice. Inter-island travelers have associated with several individuals only seen once off Maui Nui, but without additional resightings and social association data for these animals it is impossible to confirm whether they are members of the Maui Nui stock, or travelers from the O‘ahu stock. Social associations between the stocks, even with occasional inter-island movements occurring, therefore appear infrequent at best. The fact that animals from separate stocks do not seem to interact aligns well with the results of Martien et al. (2011), which found significant genetic differentiation between the O‘ahu and Maui Nui stocks. Geographically, however, the areas used by inter-island animals does overlap with the areas used by Maui Nui residents, indicating that there is potential for interactions, and raising the question of why animals from different stocks do not interact. A possible factor is the relative likelihood that separate groups of animals will encounter one another. The Maui Nui stock is small (and declining), with only an estimated abundance of 48-85 individuals (95% CI) in 2018 (Van Cise et al., 2021). The Maui Nui island area has over 10,000 km^2 of water between 0 and 1,000 m bathymetric depth, and over 6,000 km^2 of water between 0 and 500 m of bathymetric depth, so this low abundance should theoretically result in a very low density of bottlenose dolphins for the island area as a whole. Combined with the fact that inter-island movements have only been captured a handful of times through photo-ID, it seems unlikely that both an inter-island group and a Maui Nui group would happen to be in the same place at the same time, allowing them the opportunity to interact. An alternative explanation is that even in circumstances which spatially allow for interactions, behavioral differences between groups may limit their ability or willingness to interact with one another. Similar situations have been documented with different ecotypes of killer whales in the nearshore waters of the temperate eastern North Pacific, where in spite of sympatry between mammal-eating and fish-eating populations, the two ecotypes do not interact because of behavioral differences (Baird et al., 1992). Similar to the different killer whale populations, group sizes also significantly differ between the O‘ahu and Maui Nui stocks (Mann-Whitney U Test, $p = 0.008$), suggesting that there is at least some degree of behavioral differentiation between the two. Further research will be needed to explore whether there are additional behavioral differences between the two stocks, such as different vocalization or communication patterns or unique foraging specializations which might explain the lack of interaction between them.

In spite of the lack of social interactions between stocks, there is clearly spatial overlap, driven by the inter-island travelers. Compared to other island areas in the main Hawaiian archipelago, connectivity between the Oʻahu and Maui Nui areas is quite good for bottlenose dolphins. The channel between Hawaiʻi and Maui Nui is almost 2,000 m deep and 28 km across, and the channel between Oʻahu and Kauaʻi exceeds 3,000 m depth and is 116 km wide. While distance is not necessarily an issue in that bottlenose dolphins are physically capable of travelling long distances (e.g., Wells et al., 1999), most bottlenose in the Hawaiian islands have fairly limited movements. The mean inter-annual travel distance of all bottlenose in the study was only 16.5 km, far smaller than the distances across the larger channels and the mean inter-annual travel distance of a simulated population that randomly mixes across both island areas (Table 7). Additionally, as previously discussed, bottlenose show a distinct preference for shallow water, and especially water under 200 m bathymetric depth (Figure 9). This suggests that movements across the larger channels are very unlikely, given that bottlenose dolphins are not likely to travel that far or traverse into such deep waters. Only one movement of a tagged individual between Kauaʻi and Oʻahu has been documented in the two decades that CRC has studied bottlenose in the Hawaiian Islands (Baird, 2016), supporting this conclusion. In contrast, the Kaʻiwi channel between Oʻahu and Maui Nui presents a much less significant barrier to movement. It reaches only ~700 m depth, and is 42 km wide. While the distance across the channel does exceed the mean inter-annual travel distance for all individuals, it is much smaller than the other channels.

Also, the much shallower depth does fall below the depths of the observed tag locations for three out of the five satellite-tagged animals from Maui Nui and Oʻahu, and three encounters with GPS locations that were included in this study. While bottlenose do not regularly move across the larger channels, at least 14 individuals have been identified that have crossed the Kaʻiwi channel, and the mean inter-annual travel distance for individuals confirmed to do this was 65.0 km, much higher than the mean for all animals in the study.

As previously mentioned, all of the inter-island travelers clustered within the main Oʻahu component in the social network, yet utilized both island areas. Encounters with GPS locations where inter-island animals were identified were centered around southwest Oʻahu, southwest Molokaʻi, and southwest LānaʻI (Figure 8). Interchange indices based solely on photo-identification data with GPS locations also revealed that movements between the Oʻahu West/Oʻahu West Deep subareas and the Maui Nui Deep subarea were just as likely as movements within each of these areas (Table 9). Furthermore, based on associations and spatial use, the two satellite-tags deployed on suspected inter-island animals (TtTag031 and TtTag032) also made use of south Oʻahu, southwest Molokaʻi, west Lānaʻi, and south Lānaʻi. These tagged animals also made extensive use of Penguin Bank, hinting that this area may also be of importance to inter-island travelers (Figure 18). Combined, these data indicate that the inter-island travelers seem to have a much larger range than the current Oʻahu stock boundaries, extending from southwest Oʻahu, across Penguin Bank and southwest Molokaʻi to south Lānaʻi. However, this range does not seem to extend into the more insular waters between western Maui and eastern Lānaʻi, where the vast majority of encounters with Maui Nui stock members are concentrated. Given the relative spatial use of the inter-island travelers versus the Maui Nui residents, future research should incorporate revisions to the subarea boundaries (i.e., breaking the Maui Nui subarea down into Maui Nui West and Maui Nui East subareas) to explore movement patterns with a more refined lens.

The Moloka‘i/Penguin Bank subarea presents a few unique issues in regards to assessing population structure. Animals identified in this subarea cluster within both the Maui Nui and O‘ahu main components of the social network (Figure 14). The individuals clustered within the Maui Nui component were all seen in the easternmost portion of the Moloka‘i/Penguin Bank subarea, and therefore most likely an artifact of the way subarea boundaries were drawn, but connections to the O‘ahu main component cannot be explained by subarea boundaries. Instead, connections to the O‘ahu main component appear to be linked to inter-island movements. This aligns well with the satellite-tag data of the two suspected inter-island travelers, which made extensive use of the the Moloka‘i/Penguin Bank subarea. The area also has one of the greatest proportions of visitors and lowest resighting rates, in spite of having 18 encounters, and the discovery curve for this subarea is still sharply rising at almost a 1:1 ratio (Figure 16). This suggests that the majority of animals within this subarea have not been identified, or that residency to the area is very limited. This may be a result of inadequate sampling, but the sample size is almost twice as large, or larger than the other regions with steep discovery curves. The two regions with larger sample sizes (O‘ahu West and Maui Nui) had already shown some indicators of leveling by the time their numbers of total identifications approached the number of total identifications within the Moloka‘i/Penguin Bank subarea. This hints at either a larger population within the Moloka‘i/Penguin Bank subarea, or that there is a smaller degree of residency within the subarea. The large number of animals associated with peripheral clusters is a further source of perplexity, as the majority of animals from this subarea don’t associate with either the resident Maui Nui or O‘ahu animals. This could also be an effect of sample size, but the relative proportion of animals in peripheral clusters vs in the main components exceeds that of the other subareas with small sample sizes, making this theory less plausible. Instead, the most likely hypothesis seems that the Molokaʻi/Penguin Bank subarea is frequently visited by transient animals that do not remain in the area, though this cannot be proved without expanded survey effort in the region.

While this study identified 14 inter-island travelers through photo-identification, and two through satellite-tag data, it remains unclear what proportion of the Oʻahu stock moves between island areas. When currently identified inter-island travelers are excluded, the mean inter-annual travel distance of the Oʻahu stock is only 10.3 km, much smaller than the mean inter-annual travel distance of a simulated population randomly mixing around Oʻahu at 19.5 km,suggesting that at least while around Oʻahu animals do not tend to move about very much. Twelve individuals from the Oʻahu stock have been resighted within the Oʻahu West subarea in multiple years, sometimes dozens of times, so there is clearly an appreciable degree of site fidelity within that subarea at least. However, it is possible that these animals also travel occasionally between island areas, but that these movements are infrequent enough that they have not been documented. Tour guides based on the western Oʻahu coast have said that they believe the bottlenose dolphins in the region are not permanent residents, but regularly leave the area (R.W. Baird, personal communication, March 5, 2021). Additionally, the Oʻahu West subarea is comparatively small (962 km^2 of water between 0 and 1,000 m bathymetric depth), especially along the western coast where there is only a narrow band of shallow-water habitat (559 km^2 of water between 0 and 500 m bathymetric depth; Table 4). The Oʻahu West subarea also does not seem exceptionally productive compared to other subareas, based on seasonal chlorophyll-a data (Appendix Figure B). The limited availability of shallow-water habitat in the subarea may not have enough resources to sustain the O‘ahu West animals, especially with the constant influx of visiting animals that was previously discussed. It is possible, therefore, that these animals are occasionally forced to travel greater distances to locate foraging opportunities, driving inter-island movements. Similar circumstances have been identified among bottlenose dolphins in the Azores, where the average distance between sightings in 25 km, but movements of up to 291 km are repeatedly detected and hypothesized to be driven by limited prey availability (Silva et al., 2008). The forces driving inter-island movements in the Hawaiian Islands remain unclear at present though. Male sex-biased dispersal similar to that of the Sarasota resident bottlenose dolphins (e.g. Wells et al., 1987) seems unlikely, as the three sex-identified inter-island animals are females. There is also no obvious link between inter-island movements and seasonal chlorophyll-a concentrations in the Hawaiian Islands, and no immediately discernable seasonal trend to inter-island movements, with inter-island animals found in both island areas at all times of the year. Continued research will be required to identify the ecological drivers of this behavior.

Conclusion

Though somewhat constrained by uneven sampling across subareas, the broader patterns revealed by this study point towards several interesting conclusions. I found that there are limited social connections between the O‘ahu and Maui Nui island areas, which accounts for the significant genetic differentiation between stocks revealed by Martien et al. (2011). However, in spite of the limited social connections between stocks, there are important geographic overlaps that cross current stock boundaries. These overlaps are caused by a subset of the O‘ahu population that moves between island areas, using an expanded range that includes southwest

O‘ahu, Penguin Bank, southwest Moloka‘i, and the west and southwest coasts of Lāna‘i. This suggests that current stock boundaries may be inadequate for the O‘ahu stock, as they fail to account for exposure to any anthropogenic threats off Maui Nui. However, the proportion of the O‘ahu stock that uses this extended range and the ecological cues that drive this behavior remain unclear, and continued research will be required to address these factors. Continued research should also focus on subareas with minimal coverage, such as O‘ahu North and O‘ahu East, where social stratification in conjuction with spatial stratification suggests the possibility of additional demographically-independent populations of bottlenose.

Finally, the use of multiple datasets yielded different conclusions in this study, highlighting a general need to use multiple, long-term approaches in assessing population structure. While genetic and photo-identification data initially suggested that animals do not move across the Ka‘iwi channel, reassessment of long-term data and the inclusion of satellite-tag data points to a different conclusion. Continued reassessment of the population structure of these animals should be undertaken to test the accuracy of previous work, and ensure the effectiveness of current management strategies to preserve these charismatic animals for future generations.

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Appendix

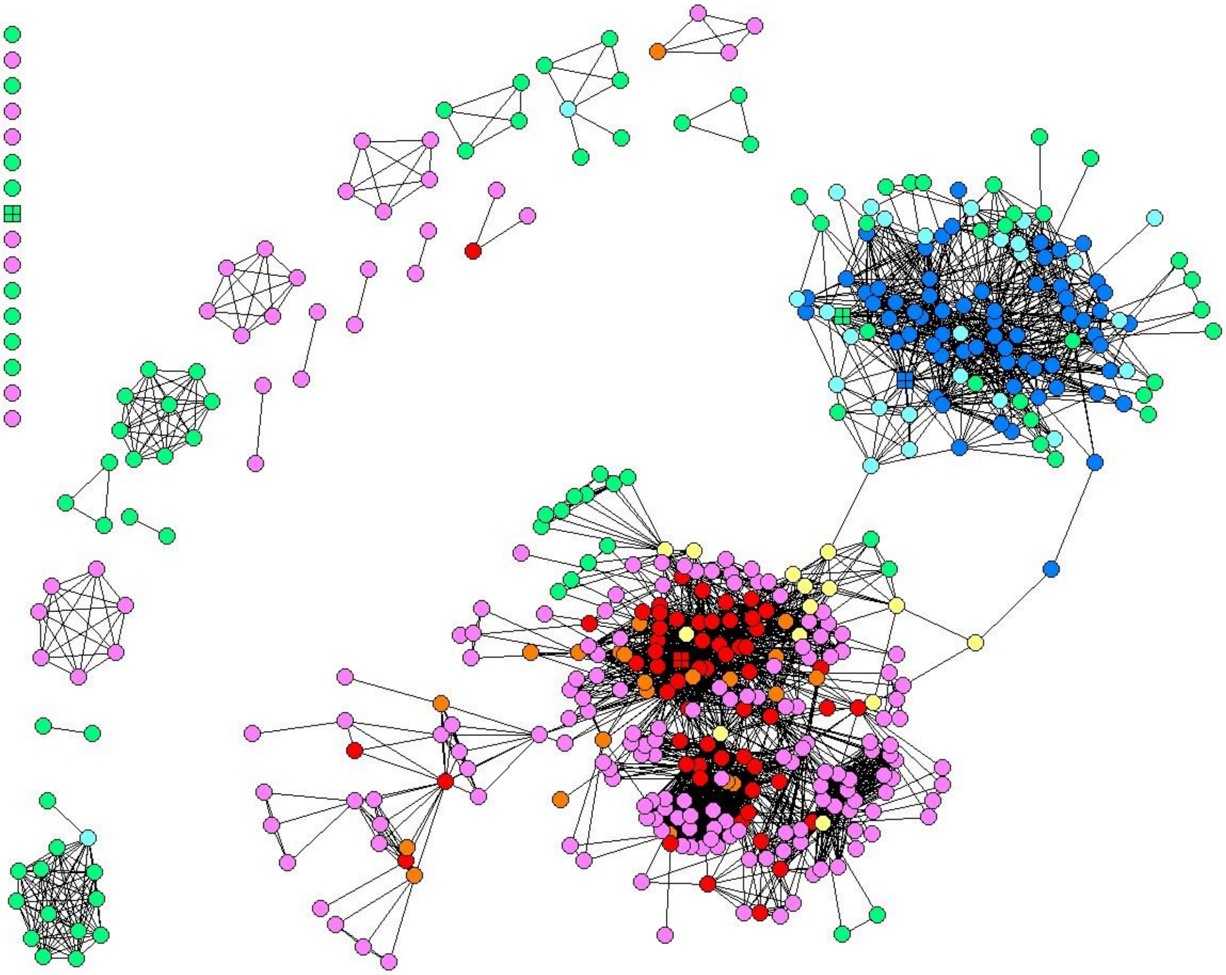

Figure A. Social network with initial residency assignments indicated by color, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. All tagged animals (n=4) are indicated by a square node shape. Red nodes are O‘ahu long-term residents, orange nodes are O‘ahu short-term residents, pink are O‘ahu visitors, blue are Maui Nui long-term residents, light blue are Maui Nui short-term residents, green are Maui Nui visitors, and yellow are inter-island animals.

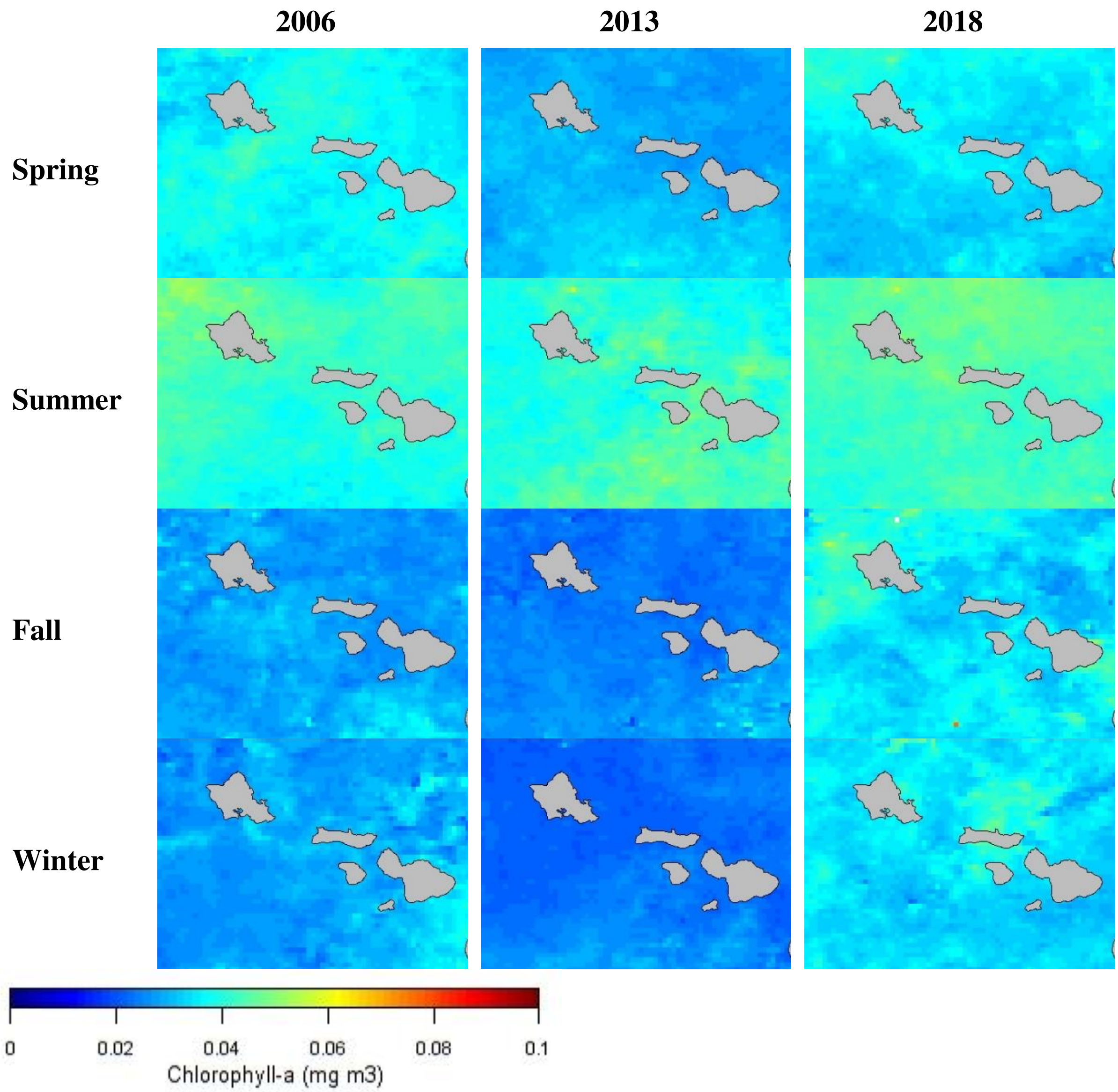

Figure B. Chlorophyll-a levels in mg/m^3 around O‘ahu and Maui Nui across different seasons from 2006, 2013, and 2018 at a 4 km resolution, based on data from NASA’s MODIS-Aqua satellite mission.

Table A. Sex distribution by island area and residency class for the 49 individuals where sex could be determined, representing 10% of the 472 total individuals included in the study.

Residency Class or Island Area	**# Individuals Sexed**	**# Males (Confirmed Through Genetics)**	**# Presumed Males (Confirmed Only Through Morphology)**	**# Females (Confirmed Through Genetics)**	**# Presumed Females (Confirmed Only Through Calf Presence or Morphology)**
O‘ahu (Island Area)	25	4	1	6	14
Maui Nui (Island Area)	21	6	0	8	7
Inter-Island	3	0	0	0	3
O‘ahu Long-Term Resident	9	0	0	2	7
O‘ahu Short-Term Resident	3	0	1	0	2
O‘ahu Associative Resident	11	3	0	4	4
O‘ahu Visitor	2	1	0	0	1
Maui Nui Long-Term Resident	16	5	0	7	4
Maui Nui Short-Term Resident	3	0	0	1	2
Maui Nui Associative Resident	2	1	0	0	1
Maui Nui Visitor	0	0	0	0	0

Table B. Initial residency assignment results by island area. Percentages indicate the proportion of the total number of unique identified individuals from all island areas combined, rounded to the nearest percentage.

Island Area	Total # (%) of Individuals	# (%) Long-Term Residents	# (%) Short-Term Residents	# (%) Visitors
O‘ahu	271 (57%)	59 (13%)	22 (5%)	190 (40%)
Maui Naui	187 (40%)	66 (14%)	26 (6%)	95 (20%)
Inter-Island	14 (3%)	-	-	-
All Island Areas	**472**	125 (26%)	48 (10%)	285 (60%)

Table C. Subareas versus group size for subareas with CRC encounters. Group sizes are best estimates from CRC encounters. CRC encounters were not available for the O‘ahu East, O‘ahu East Deep, or Moloka‘i/Penguin Bank subareas.

Subarea	# CRC Encounters	Mean Group Size (SD)	Minimum Group Size	Maximum Group Size
OW	7	17.3 (± 12.4)	2	40
OWD	3	11 (± 7.0)	6	19
ON	4	6.3 (± 4.1)	1	10
MN	52	6.3 (± 4.5)	1	18
MND	3	4.3 (± 2.9)	1	6

Table D. Post-hoc pairwise comparisons of tag location depths between tags.

Comparison	Dunn’s Test P-Adjusted
TtTag006 – TtTag007	8.055×10^{-1}
TtTag006 – TtTag030	2.058×10^{-29}
TtTag006 – TtTag031	1.687×10^{-99}
TtTag006 – TtTag032	2.549×10^{-40}
TtTag007 – TtTag030	1.955×10^{-19}
TtTag007 – TtTag031	5.553×10^{-58}
TtTag007 – TtTag032	7.039×10^{-26}
TtTag030 – TtTag031	4.842×10^{-15}
TtTag030 – TtTag032	1.076×10^{-1}
TtTag031 – TtTag032	6.164×10^{-10}