Chapter 20
Hector's and Māui Dolphins: Small Shore-Living Delphinids with Disparate Social Structures

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Abstract Hector's dolphins (*Cephalorhynchus hectori hectori*) are a small (~1.5 m long) marine dolphin, primarily inhabiting turbid, coastal waters discontinuously around the South Island of New Zealand. The Māui dolphin (*C. h. maui*) is a critically endangered subspecies of Hector's dolphin, only found along a small part of their original range spanning the west coast of the North Island of New Zealand. Both subspecies have small alongshore home ranges of around 50 km, with high levels of site fidelity and low levels of gene flow. Despite this, some individuals have traveled distances of at least 400 km, interacting with local animals. Hector's dolphins exhibit seasonal movements linked to prey availability and social aggregation behaviors associated with the summer mating and calving period. They typically occur in small groups of 2–10, with high levels of fission-fusion and low levels of association among individuals. Sex segregation occurs in small groups (<5 individuals) of Hector's dolphins throughout the year, but this same pattern does not hold for larger groups. Mother-calf pairs are typically associated with other females, a common pattern for delphinids. Māui dolphins do not show the same pattern, with mixed-sex aggregations of dolphins independent of group size, perhaps an artifact of the extremely small population size. Hector's dolphins largely communicate with ultrasonic clicks, with different vocalizations among social groups and during feeding. Their echolocation clicks are important when foraging in their preferred habitat of low visibility. They forage on a wide range of benthic and demersal fishes and squids, with most prey <10 cm long and some regional differences in species composition, but overall similarities in prey preferences. Despite their distribution around New Zealand and variation in local population sizes, Hector's and Māui dolphins have broad similarities in behavior, association patterns, and habitat use. Where differences exist, the habitat, prey movements, and population size are potential explanatory factors. In New Zealand, a hot spot for cetacean diversity, these dolphins occupy a small and

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specific niche that is typical for *Cephalorhynchus* elsewhere in the Southern Hemisphere. Because they occur close to shore in waters affected by humans, they are vulnerable to anthropogenic disturbance. But with recognition of dangers and appropriate protections, the species should flourish in New Zealand's productive coastal waters.

Keywords Hector's dolphin · Māui dolphin · *Cephalorhynchus* · New Zealand · Behavior

20.1 Introduction

The genus *Cephalorhynchus* is represented by four species of small, coastal dolphins in Southern Hemisphere waters, all sharing a common ancestor (Pichler et al. 2001; Dawson 2018). The *Cephalorhynchus* dolphins have similar behavioral characteristics and are typically found in smaller groups, feeding on a wide range of benthic and demersal prey. Their coastal habitat preference exposes them to predation risk from sharks and killer whales (*Orcinus orca*), as well as anthropogenic threats of boat strikes and interactions with fishing gear.

New Zealand has only one species of endemic cetacean, the Hector's and Māui dolphin (*Cephalorhynchus hectori*). They are recognized as subspecies (*C. h. hectori* and *C. h. maui*) based on morphological and genetic differences as a result of around 15,000 years of isolation after the last glacial maxima and low natural dispersal by the species (Baker et al. 2002). Despite this long period of separation, both sister taxa display similar behaviors with variations between populations in different habitats rather than between the two subspecies. For the purposes of this chapter, I refer to them as Hector's dolphins unless there are direct differences between the two subspecies.

20.2 Habitat Preference and Home Range

Hector's dolphins occur discontinuously around the coastal waters of the South Island of New Zealand, with three recognized regional populations along the west, east, and south coasts (Hamner et al. 2012). The North Island is currently populated by the Māui dolphins along only part of their historical range spanning the west coast (Oremus et al. 2012), with occasional reports of Hector's dolphins on the west and east coasts of the North Island, although the provenance of the east coast dolphins remains unknown (Freeman 2003; Hamner et al. 2014).

In almost all areas throughout their range, Hector's dolphins are associated with turbid waters often in association with major watersheds such as river outflows, estuaries, harbors, and/or areas with glacial meltwater (e.g., Rodda and Moore 2013; Derville et al. 2016). These are areas of higher productivity and nutrient flows and therefore are attractive to dolphins as prey hot spots. While adept at swimming in rough coastal waters, often playing in waves just before they crash ashore, Hector's dolphins move away from areas with large ocean swell, perhaps in response to movements in prey toward more turbid waters (Dittmann et al. 2016). As expected with their coastal habitat preference, they usually occur in shallow waters but will use deeper waters if near the coast (Weir and Sagnol 2015). There are suggestions that the turbid waters are preferred habitat because they provide the dolphins protection from predation by sharks and killer whales. While predation by killer whales has not been reported, white sharks (*Carcharodon carcharias*) and seven-gill sharks (*Notorhynchus cepedianus*) have been found with Hector's dolphin remnants in their stomachs (Cawthorn 1988; Hamner et al. 2012). The levels of predation remain largely unknown, but a recent analysis of scars and marks on the bodies of living Māui dolphins suggests that either predation events are successful and result in the death of animals or alternatively that the low level of scars from shark bites indicates low levels of predation (Garg 2017).

Hector's dolphins inhabit cool temperate waters influenced by warm and cool seasonal currents with sea surface temperature (SST) trends around the South Island showing a marked increase over the past 50 years (Shears and Bowen 2017). With SST an important indicator of dolphin distribution (Bräger et al. 2003; Derville et al. 2016), likely a proxy for productivity and prey distribution, it will be interesting to see how dolphins respond as temperatures continue to increase. Hector's have a broad range of thermal tolerance, from approximately 8 to 21 °C, as evidenced by their wide spatial distribution, year-round fidelity to small home ranges, and no long-distance migrations (Rayment et al. 2011a). This, along with their generalist diet (Miller et al. 2013), suggests that changes in SST may not have wide impacts upon this species' distribution as long as there is potential prey. What may influence their behavior is changes in runoff, in particular the west coast South Island regions where glacial meltwater is an important source of turbid water. If there is less turbidity, dolphins need to adapt or move to another habitat that suits their requirements, and this may be challenging given their low dispersal rates. If turbidity is important for evading predators and dolphins remain in less turbid waters, they may form larger groups for predator vigilance, leading to possible shifts in association patterns.

South Island Hector's dolphins along the east and south coasts have seasonal differences in distribution, with smaller, more dispersed groups of dolphins further offshore in winter compared to summer (Dawson and Slooten 1988; Bräger et al. 2003; Turek et al. 2013; Slooten et al. 2006; Rodda 2014; MacKenzie and Clement 2014). Hector's dolphins occur up to ~35 km offshore, often in areas where there is shallow habitat across an extensive continental shelf (MacKenzie and Clement

2014). This pattern is less prevalent for west coast South Island dolphins, where the habitat differs markedly with deeper less turbid water, and the dolphins remain closer to shore across all seasons (Bräger et al. 2003; Rayment et al. 2011a; MacKenzie and Clement 2016). Prey dispersal during winter is likely to be a contributing factor to offshore distribution in the shallower, continental shelf waters, but the summer breeding season is another important driver of clustered social aggregations. Warmer coastal waters provide ideal habitat for females to calve, and thermal demands on newborns may be less than in cooler water.

Despite some seasonal inshore-offshore movement, Hector's dolphins, like other *Cephalorhynchus*, have small home ranges averaging about 50 km alongshore (Rayment et al. 2009a; Oremus et al. 2012). There are some individuals that undertake movements of ~100 km (Bräger et al. 2002), but these are considered unusual for the species. With dorsal fin mark rates typically around 10–20%, the feature most frequently used to identify individual dolphins, we detect only a small proportion of the animals ranging further. There is recent evidence of genetic connectivity between populations, with individuals crossing less optimal habitat (e.g., from the west coast to the south coast South Island) (Hamner et al. 2012). The greatest dispersal distance is a conservative estimate of a $\geq$400 km movement by two female Hector's dolphins from the west coast South Island population to the core range of Māui dolphins, where they were in mixed groups of Māui and Hector's dolphins (Hamner et al. 2014). One of the females remained in the west coast North Island habitat for at least 6 years. There are also other genetically identified South Island dolphins interacting with Māui dolphins (Baker et al. 2016) (Fig. 20.1).

There is no evidence of hybrid offspring between the two subspecies, and with similarities in social structure, size, genetics, and vocalizations, there should not be boundaries to interbreeding (Baker et al. 2002). It is possible that there are more dolphins dispersing from the South Island to the North Island, along the east coast. The origins of these dolphins have yet to be determined, but they are likely to come from the large population of animals from Cloudy and Clifford Bay, east coast South Island (MacKenzie and Clement 2014; Hamner et al. 2017). Although there are few records of longer range dispersals, there is no apparent sex bias in animals ranging further than expected (Bräger et al. 2002; Oremus et al. 2012). Similarly, there appears to be no clear sex bias for dispersal within the normal ranging behavior of Hector's dolphins, with males and females broadly distributed in these coastal subpopulations. With the ability of Hector's dolphins to disperse long distances, as long as they find good-quality prey, they could enhance the gene pool and social structure of the population they move to. This may bode well for the species' future.

Fig. 20.1 A typical short-term aggregation of Māui dolphins, *Cephalorhynchus hectori maui*, swimming in turbid waters off the west coast, North Island. Image credit: Courtesy of Steve Hathaway and the Harbers Family Foundation

20.3 Group Living

Hector's dolphins live in small groups typically numbering between two and ten dolphins, although larger aggregations occur in summer (Dawson 2018). Like most other delphinids, they have a fission-fusion society, but even though they have small home ranges, Hector's have very weak associations between individuals within a population, not different from random (Slooten et al. 1993; Bejder et al. 1998; Bräger 1999). This fluid pattern of association is reflected in field studies where small groups of dolphins occur in close proximity to one another, within a few hundred meters, yet functioning as independent units with regular exchanges of individuals between groups. Males interact with more dolphins than females, suggesting that males might be moving between groups to find females in estrous (Slooten et al. 1993). One of the challenges is that the low mark rate on Hector's dolphin dorsal fins may limit conclusions about the group dynamics of some populations (e.g., Bräger 1999). Nonetheless, the areas with long-term research reveal a persistent pattern of fission-fusion and low individual rates of association, so should be considered typical for the species. In areas with deeper nearshore waters, Hector's have slightly higher levels of association possibly linked to their more limited dispersal patterns compared to east coast dolphins (Bräger 1999).

There are different patterns of age- and sex-class group composition. In the longest-studied population of Hector's dolphins at Banks Peninsula on the east coast South Island, there were clear patterns of sex segregation during spring, summer, and winter. Females were more likely alone and small ($\leq$5 dolphins) groups were typically either all male or all female (Webster et al. 2009). Mother-calf pairs were accompanied by other females, but once groups contained more than five dolphins, they were more likely to be mixed-sex aggregations. This pattern did not hold for Māui dolphins, where mixed-sex groups occurred across all group sizes, noting that there is a female dominant sex bias in this population (Baker et al. 2016). The mixed-sex groups may be due to the very small population size of Māui dolphins (63 dolphins aged 1+, CL 57–75) (Baker et al. 2016) that potentially disrupts typical social structure and breeding aggregations. Whether this variation in sex-biased grouping occurs elsewhere, or if Māui dolphins are an exception, has yet to be determined.

Hector's dolphins often occur in nursery groups, with mother-calf pairs alone, with one or two other female group members, or in loose association with other mother-calf pairs (Bräger 1999; Webster et al. 2009; Oremus et al. 2012). This is a typical pattern for delphinids in a number of other species. Females have a 2- to 3-year inter-birth interval, so the period of calf dependency is short but similar to other small delphinids (Chap. 1). Despite the species' small size, calves grow rapidly within their first years of life, up to adult size at 5 to 6 years old (Webster et al. 2010). It is possible that some of the other females associated with mother-calf pairs may be previous offspring who remain in some association with their mother until they reach sexual maturity.

In summer, high levels of activity occur, indicative of mating competition as part of a multi-mate (often incorrectly termed "promiscuous") breeding system (Slooten et al. 1993). Hector's dolphins regularly engage in jumps clear of the water, repetitive side-slaps, head-slaps, and chases (Fig. 20.2). They use ultrasonic clicks

Fig. 20.2 Hector's dolphins, *Cephalorhynchus hectori hectori*, leaping in Cloudy Bay, South Island. Image credit: Courtesy of Oregon State University and the University of Auckland Collaborative Research Programme

to communicate and produce more complex click types and pulse rates in larger, active groups (Dawson 1991). With only a proportion of the females in estrous, competition by males is likely to be high, and males and females engage in active social behaviors. With their relatively large testes and dynamic larger group aggregations, the summer is an important time for males, when they actively attempt to encounter as many females as possible to increase their chance of fathering offspring (Slooten 1991; Slooten et al. 1993). It is also an important time for females, to produce calves most likely to survive (see Chap. 4).

In winter, groups of Hector's dolphins become more evenly dispersed, and group sizes decrease slightly. Dolphins also move offshore, with the overall winter range generally larger than the summer range as it has a wider offshore and alongshore distribution, most notably along the east coast, South Island (Dawson and Slooten 1988; Bräger et al. 2003; Rodda 2014; MacKenzie and Clement 2014). With social groupings largely driven by breeding behavior rather than the formation of long-term, complex social alliances, once this season has passed, there is no benefit for Hector's dolphins to remain in proximity to other dolphins, hence the change in social structure.

There are several poorly studied small populations dispersed around coastal waters that may reveal a greater disparity in social associations and patterns of group structure than currently understood. With habitat playing an important role in prey availability, water turbidity, and risk of predation, this may influence association rates between isolated populations (e.g., Kaikoura, Hamner et al. 2012; Weir and Sagnol 2015) or the potential for different "inshore" and "offshore" cohorts in areas where the population is widely dispersed (e.g., Cloudy and Clifford Bays, MacKenzie and Clement 2014; Hamner et al. 2017).

20.4 Foraging

Because Hector's dolphins live in turbid waters and only occasionally forage near the sea surface, it is difficult to make direct field observations of foraging events, so our knowledge of diet comes mainly from analysis of gut contents from dead beachcast individuals and as bycatch or entanglement in fishing gear. They are generalist foragers that eat a variety of benthic, demersal, and pelagic fishes and squids throughout the water column (Miller et al. 2013). As they are typically found in shallow, coastal waters, Hector's are able to take advantage of their entire vertical and horizontal habitat within diving range. They are primarily solitary foragers with rare observations of communal foraging behaviors (Dawson 2018). They feed mainly on prey items ranging from <1 to >60 cm, with most prey <10 cm in length. Even though 29 different prey species have been identified, 6 species made up 77% of their total diet (Miller et al. 2013). The patterns of prey types are similar throughout the species' range, although prey species composition varies in particular between the west and east coasts of the South Island (Miller et al. 2013). Observations of deep dives, accompanied by more forceful exhalations upon surfacing, are indications that dolphins are foraging in mid- or benthic waters. Sometimes individuals swim rapidly near the surface, presumably chasing prey, but our behavioral observations of foraging events are limited.

Hector's dolphins have high fidelity to particular coastal or harbor locations, areas of high productivity (Bejder and Dawson 2001; Rayment et al. 2009a, b; Miller et al. 2013; Rodda and Moore 2013). In Akaroa Harbor, Banks Peninsula, the dolphins undertake some diel movements entering the harbor in the morning and leaving at night, most likely in response to prey movements or availability (Stone et al. 1995). Reliable, good-quality prey availability is important (Spitz et al. 2012), and the dolphins move in response to seasonal movements of preferred prey. The summer inshore presence of dolphins is correlated with movements of preferred prey such as red cod (*Pseudophycis bacchus*), which follow their prey into harbors and coastal waters. One of the challenges when determining drivers behind dolphin movements is our poor understanding of marine food webs and dynamics associated with noncommercial fish species.

On the west coast, South Island of New Zealand, the dolphins have a more similar winter and summer distribution than east coast Hector's dolphins and are found considerably closer to shore (<6 nm) than east coast dolphin populations (Rayment et al. 2011a; MacKenzie and Clement 2014, 2016). The exposed west coast has a steep drop-off to deeper waters close to the coast, which may not be a suitable habitat for preferred prey or pose a limitation on the ability of these small dolphins to dive deep enough to capture benthic prey (Schreer and Kovacs 1997). As with the west coast Hector's dolphins, Māui dolphins of the North Island have a limited offshore range (Du Fresne 2010) and similar preferred prey (Miller et al. 2013). One difference is the range of potential preferred habitat on the west coast North Island compared to the South Island, with harbors, turbid waters, and juvenile fish nursery grounds largely underutilized by the population, possibly due to the severely reduced population size and range contraction (Dawson et al. 2001; Rayment et al. 2011b; Oremus et al. 2012; Derville et al. 2016). The current Māui dolphin core range is adjacent to these easily accessible harbors, therefore the low use may reflect a limitation on their current socially transmitted knowledge of these habitats. It is possible that the fisheries closure in core habitat (as part of a marine mammal protected area) has removed prey competition by humans for coastal species, and the small population is able to obtain its nutritional needs from the coastal waters.

Hector's dolphins have not been observed taking fish from gill nets, but some feed behind trawlers (Rayment and Webster 2009). As observed in other species (Chilvers and Corkeron 2001), average group size was significantly larger for trawl-fishing than groups not associated with trawlers (Rayment and Webster 2009). There is an increased availability of prey as fish either are disturbed by the trawl activities or escape from the net, making this an important source of prey for all dolphins, including mothers with calves (as discussed for other dolphins by Fertl and Leatherwood 1997). Hector's dolphins in association with trawlers also increase levels of aerial and sexual behaviors, likely a result of larger numbers of dolphins aggregating (Rayment and Webster 2009). As some Hector's dolphins die from entanglement in trawl nets, it is a risky behavioral strategy, but energetic payoffs must be considerable. Some dolphins feed near trawlers year-round, and it is possible that different communities develop social ("cultural") proclivities for such feeding, as has been observed in other species (e.g., Chilvers and Corkeron 2001; Ansmann et al. 2012; see Chap. 10).

20.5 Interactions

Hector's dolphins are vulnerable to anthropogenic impacts due to their coastal habitat. They are vulnerable to fisheries bycatch and entanglement that has led to significant declines in abundance (Reeves et al. 2013). They are a social dolphin known for boat approaches and are a popular species for dolphin-based tourism operations and/or people swimming out from beaches after they see them from shore (Bejder et al. 1999; Martinez et al. 2010). Hector's dolphins appear to be more interactive with humans during summer, the season when they are most socially active. Overall, Hector's dolphins have similar responses to boats and swimmers as occurs with other small delphinids (Constantine and Bejder 2008). They are attracted to novel stimuli (Martinez et al. 2011) and often play with seaweed, approaching swimmers while engaged in active behaviors, jumping out of waves, and bow-riding boats.

20.6 Concluding Thoughts

Hector's dolphins have social lives typically characterized by small home ranges, weak associations between individuals, an active summer breeding season, and movements largely linked to prey availability. But there are disparities between the east and west coasts of the South Island and the west coast North Island subspecies. The type of social aggregation varies depending on time of year, e.g., short-term male-female associations are linked to breeding, and mother-calf pairs are often associated with other females year-round, perhaps part of younger females' learning associated with calf rearing or as a strategy to minimize risk from predation. In other areas, males and females are equally mixed. Hector's dolphin ranging behavior varies depending on the offshore characteristics with shallow, continental shelf areas leading to greater dispersal and different aggregation behaviors than those living near deeper nearshore waters. Cooperative foraging is rarely observed even in the longest running studies, removing one important driver of delphinid social behavior and affiliations between conspecifics (see Gowans et al. 2007). As far as is known at this time, they do not appear to have complex communication systems characteristic of some larger delphinids, although they may "eavesdrop" on the echolocation signals of other dolphins to locate or secure prey in turbid waters (Gregg et al. 2007), but this is an area requiring more investigation. If the Māui dolphin population recovers, perhaps they will return to the sex-specific social grouping in larger populations of South Island Hector's dolphins, but this is presently unknown. Changes in human land use have resulted in increased runoff, degrading harbor habitats for potential prey. Whether the reduced use of harbors by Māui dolphins is due to small population size influencing social "knowledge" of these habitats or as a result of reduced prey quality remains unknown. Hector's are under threat from anthropogenic impacts, including most recently deaths from the cat-borne disease toxoplasmosis (Roe et al. 2013), but management decisions that act to protect them are having some positive effect on the species and hopefully their future survival (Gormley et al. 2012; MacKenzie and Clement 2014, 2016).

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