

Figure 2. Consecutive sightings of Hector's dolphins (*Cephalorhynchus hectori*) in time and space from Kaikoura, Moeraki, Westport-Greymouth, and Jackson Bay (1994-1997)

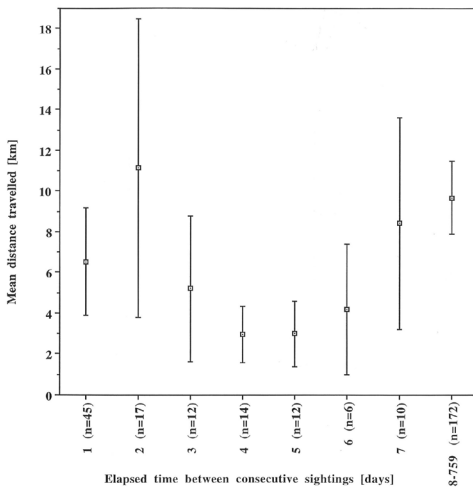


Figure 3. Mean distance of Hector's dolphin resightings (\pm 95% CI) from Kaikoura, Moeraki, Westport-Greymouth, and Jackson Bay (1994-1997)

5 d. Seven days after the initial sighting, the average distance to the next resighting is 9 km (Figure 3 with 95% confidence intervals [CI]). When comparing extremes (Figure 3), the distances after 1 to 2 d were significantly different from those after 4 to 5 d (Mann-Whitney U-test: $p = 0.0375$), which are significantly different again from those after 8

to 759 d (Mann-Whitney U-test: $p = 0.0005$). This could indicate a cyclical pattern in area use within a home range or—albeit less likely—a case of “trap response” to the first sighting.

Differences in Movement Patterns Among East Coast and West Coast Populations

The mean distances covered between sightings differed considerably between study areas (Table 2) and were considerably shorter in the two east coast areas ($\bar{x} = 5.42 \text{ km} \pm 0.380 \text{ SE}$) than in the two west coast areas ($\bar{x} = 13.19 \text{ km} \pm 1.506 \text{ SE}$). Moreover, all resightings over $> 30 \text{ km}$ (4.2%) were recorded on the west coast (Figure 4). The difference between mean distances covered is also caused by the restricted home range sizes at the Kaikoura study area (see below for details).

Time intervals between consecutive sightings, however, did not differ much between east coast ($\bar{x} = 122.7 \text{ d} \pm 10.74 \text{ SE}$) and west coast ($\bar{x} = 164.0 \text{ d} \pm 19.28 \text{ SE}$) sightings, possibly also reflecting slightly more survey effort at the east coast study areas (i.e., 117 vs 97 field days on the water at the west coast; Table 1). In general, most sightings were either less than 14 d (i.e., the duration of a seasonal visit to each area) or 6 or 12 mo apart because the study areas were visited usually on a semi-annual basis (Figure 2). However, in Kaikoura, individuals had the longest mean time interval between sightings while covering the shortest mean distance between them (Table 2).

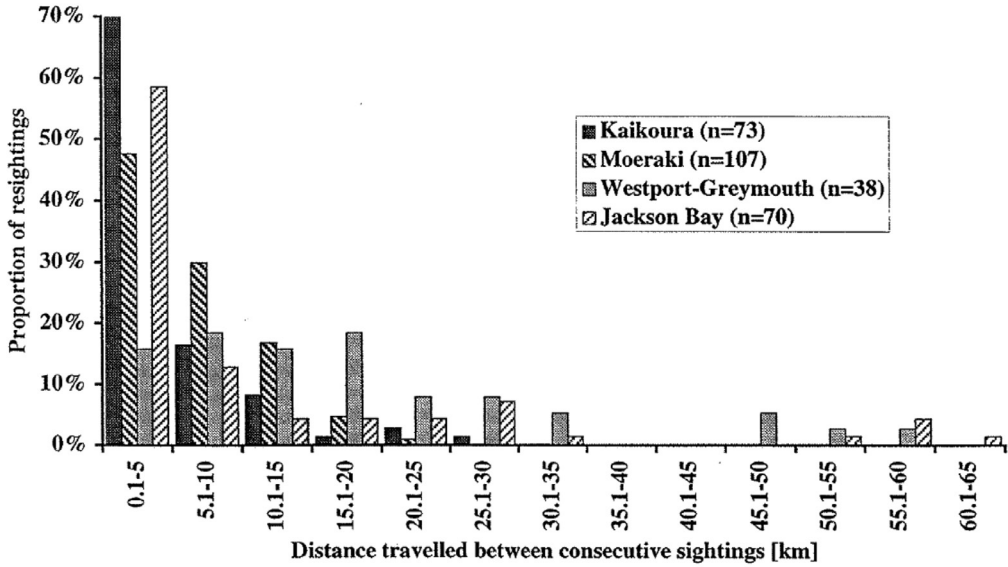


Figure 4. Frequency distribution of distances between consecutive sightings of Hector's dolphins in four different study areas: Kaikoura, Moeraki, Westport-Greymouth, and Jackson Bay (1994-1997)

The West Coast population of Hector's dolphins not only covered longer distances on average, they also did so at significantly higher mean transit speeds (i.e., distances per day) than their East Coast counterparts (Table 2). Off Kaikoura and Moeraki, Hector's dolphins covered $\bar{x} = 0.9 \text{ km} \pm 0.15 \text{ SE}$ per day, whereas they covered $\bar{x} = 2.8 \text{ km} \pm 0.69 \text{ SE}$ per day off Westport-Greymouth and in Jackson Bay. The highest transit speed was 46.8 km from Greymouth to Ross, covered in less than 28 h (i.e., 1.69 kmh⁻¹).

Ecological Impact of an Environmental Barrier

The Hector's dolphins off Kaikoura move only relatively short distances and, hence, appeared to be particularly slow (Table 2). In this study area, the suitable habitat is fragmented by the deep water of the Kaikoura Canyon (Figure 5), dividing the available shallow-water habitat into two with apparently separate subpopulations. The northern subpopulation extends at least from the mouth of the Hapuku River in the north to the mouth of the Kahutara River south of Kaikoura Peninsula and contains 55 resighted individuals (this geographic designation depends on the majority of the individuals' sightings). The southern subpopulation extends from the Haumuri Bluffs at least to the mouth of the Conway River and contains 16 resighted individuals. The actual home ranges of both subpopulations, however, are very likely to extend to the north and to the

south, respectively, beyond the boundaries of the study area.

Over the course of 8 y, only seven of these 71 individuals moved from north to south ($n = 6$) or from south to north ($n = 2$); one individual crossed from south to north and back south within 9 mo. On average, this equates to an exchange rate of only one exchange per year over a distance of about 15 km (i.e., a distance Hector's dolphins can easily cover in less than 1 d). The pooled sightings of these 71 individuals amount to 310 from 1988 to 2002, out of which only eight resulted in an exchange between sub-areas (2.6%).

Discussion

Resighting data for dolphins are time consuming to collect, especially on a large geographic scale. Using 509 sightings of 143 different individuals, we analyzed various aspects of the range utilization and movement patterns of the coastal Hector's dolphin—in particular, the distances covered, short-term movement patterns, the differences in movement patterns among East and West Coast populations, and the impact of an environmental barrier. In the following, we will attempt to put our findings in context by comparing them to available knowledge of this and other *Cephalorhynchus* species.

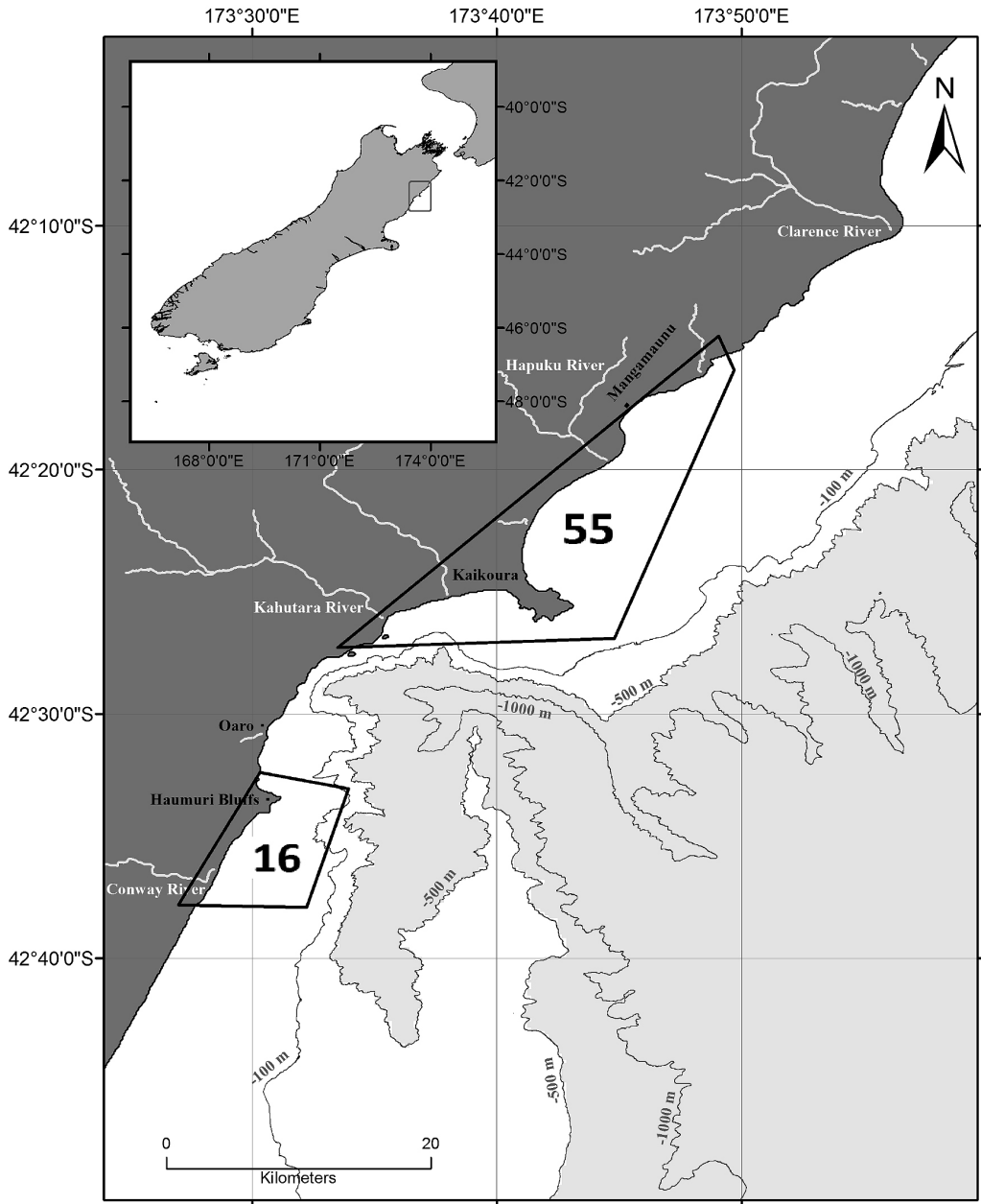


Figure 5. Northern and southern subpopulation (with numbers of repeatedly identified individuals) north and south of the Kaikoura Canyon, South Island of New Zealand; quadrangles indicate areas of sightings but not necessarily subpopulation boundaries.

Temporal and Spatial Scale of Hector's Dolphin Movements

We recorded movements of Hector's dolphins from 0.0 to 61.4 km, with almost 90% under 20 km and no resightings from 62 to 600 km. Maximum

speeds recorded were 46.8 km in 28 h or almost 10 kmh⁻¹ over one-half hour. Average distances covered after 2 d of the initial sightings were three times longer than those after 4 to 5 d, congruent with a cyclical pattern in range utilization.

Hector's dolphins consistently used relatively small home ranges within a maximum length of 67 km along shorelines (Smith, 1992; Stone, 1992; Bräger et al., 2002; Stone et al., 2005; Rayment et al., 2009) that are less than 100 m deep. Individual movements beyond 67 km appear to be rare (Bräger et al., 2002; Hamner et al., 2014).

For example, ten individually identifiable Hector's dolphins off Banks Peninsula that were sighted 14 to 27 times covered maximum distances of 14 to 39 km (Stone, 1992). Less frequently observed individuals covered up to 63 km between their most extreme sightings (Stone, 1992). Smith (1992) studied the same population and recorded maximum distances of 61 km between resightings for 21 individuals. These along-shore movements compiled by Smith (1992) and Stone (1992) likely represent trips within the individuals' seasonal home range. The results of Stone et al. (2005) show a zig-zag pattern of shifting monthly centers within the home ranges of three tagged animals. These may indicate—albeit on a scale of weeks rather than days—a cyclical pattern in home range use. However, comparable small-scale analysis of the spatio-temporal use of home ranges by odontocetes, in general, are surprisingly scarce and usually not based on individuals (e.g., Schaffeld et al., 2016; Williamson et al., 2017). Data from tagged individuals demonstrate substantial individual differences in movement patterns (Carneiro et al., 2017; van Beest et al., 2018). Our present hypothesis of cyclical range utilization by a coastal delphinid with a rather small home range may be only one of several explanations for our data, but this appears to be a promising avenue warranting additional research.

For a predator that hunts benthic prey, it might be expedient to cover its home range in the pattern discussed above and to return frequently (e.g., every 4 to 5 d). This period is too short to allow prey populations to replenish, but it may be sufficient to reduce the cautionary effects of fear and for other nonconsumptive predator effects to subside (*cf.* Brown et al., 1999; Stankowich & Blumstein, 2005; Clinchy et al., 2013; Moll et al., 2017). If a predator depletes a food patch by frightening prey rather than by actually killing it, then forgetful prey are likely to become less vigilant and, thus, increasingly more catchable during a subsequent visit by the predator.

Significance of Movement Patterns

Habitat preferences and movements of marine mammals in general are frequently assumed to be linked directly to their prey (as reviewed by Stevick et al., 2002; Stern, 2009). Hector's dolphins exhibit at least two recurring movement patterns that clearly differ in temporal and spatial

scale. First, they roam within their home range, sometimes covering it in a matter of days. Second, in spring, each population appears to shift its home range inshore, and then offshore in autumn, apparently without much mixing with neighboring populations (Dawson & Slooten, 1988; Bräger & Schneider, 1998; Stone et al., 2005; Rayment et al., 2010; MacKenzie & Clement, 2014). We presume that these two patterns are predominantly governed by food availability. Several of Hector's dolphins' main prey species have been found to increase in density inshore in areas 30 to 100 m deep during the summer, with lower densities recorded in winter (Miller et al., 2013). According to the authors, small and juvenile prey are targeted, the movements of which appear to determine Hector's dolphins' coastal distribution to a large degree (Miller et al., 2013).

The four species of the genus *Cephalorhynchus* live in the southern hemisphere and, to varying degrees, share a preference for small home ranges in coastal habitats. However, there appears to be a trend towards increased home range sizes with more exposed coastal habitats and pelagic foraging. Chilean dolphins (*Cephalorhynchus eutropia*) live in the protected bays and fjords of southern Chiloé where they occupy maximum ranges of 4 to 45 km ($\bar{x} = 23.1 \text{ km} \pm 1.92 \text{ SE}$; $n = 42$; Heinrich, 2006). The longest along-shore range was 70 km for a male in central Chiloé. Fixed kernel ranges (95% UD) and core areas (50% UD) were calculated for 11 individuals to be 22 to 46 km² ($\bar{x} = 35.6 \text{ km}^2$) and 3 to 13 km² ($\bar{x} = 8.4 \text{ km}^2$), respectively (Heinrich, 2006). These values are somewhat smaller than those cited for Hector's dolphins (Smith, 1992; Stone, 1992; Bräger et al., 2002; Stone et al., 2005; Rayment et al., 2009) but may vary for Chilean dolphins living along the less protected mainland coastline north of Chiloé.

Heaviside's dolphins (*Cephalorhynchus heavisidii*) have been tagged twice off western South Africa: three individuals in 1997 (Davis et al., 2014) and six individuals in 2004 (Elwen et al., 2006). These instrumentations resulted in estimated home range sizes of 672 to 2,347 km² and 302 to 1,028 km² for 90% minimum convex polygons, respectively. Furthermore, both studies recorded strong diurnal onshore-offshore movement patterns and linked them to the diel vertical migration of the principal prey. Lastly, several Commerson's dolphins (*Cephalorhynchus commersonii*) off Argentina alternated between two areas 250 km apart with on average 15 d in the prime study area and 73 d outside of it (Coscarella et al., 2011). The shortest time between consecutive sightings of an individual in both areas was only 5 d. In conclusion, *Cephalorhynchus* ranging distances appear to be governed by

habitat properties, prey availability, and possibly by socio-ecological factors such as group size.

Differences in Movement Patterns Among East and West Coast Populations

Recorded mean resighting distances from the west coast were more than twice as long as those from the east coast (13.2 vs 5.4 km), with mean transit speeds of 2.8 vs 0.9 km per day, respectively. The shorter resighting distance along the east coast can only partially be explained by the restricted home ranges off Kaikoura (Table 2) because the majority of east coast sightings originated from Moeraki where resighting distances were 60% longer than off Kaikoura, but still only 48% of the distance of west coast resightings.

The coastal and nearshore waters along the east and west coasts provide considerably different habitats with, among other conditions, warmer water temperatures and a narrower strip of shallow waters along the more exposed west coast (Bräger et al., 2003; Rayment et al., 2011). According to stomach content analysis, prey composition is less diverse but more pelagic along the west coast (Miller et al., 2013). This variability of environmental conditions together with long-term isolation has allowed the two populations to differ significantly in their haplotype composition (Pichler et al., 1998; Hamner et al., 2012, 2017).

As a consequence of their adaptation to these conditions, the two populations display significant differences in movement patterns. Additionally, both mean and maximum short-term movements are longest and fastest along the west coast. It remains unclear whether this is due to the more uniform habitat or the more pelagic prey consumed.

Impact of an Environmental Barrier

Fourteen years of photo-ID data on 71 individually identifiable Hector's dolphins resulted in 310 sightings of which only eight verified an exchange between subareas (2.6%) or less than one exchange per year. In recent years, these results were corroborated by additional photo-ID and genetic studies in the same study area.

Weir & Sagnol (2015) studied the distribution of Hector's dolphins around Kaikoura in 2013 and compared their results with opportunistic sightings between 2005 and 2012. They found no exchanges of individuals between the northern and southern subpopulations. They were, however, able to re-identify two individuals first sighted 18 years earlier during our study reported herein.

Hamner et al. (2016) biopsy-sampled 157 Hector's dolphins near Kaikoura in 2014 and 2015 to analyze the local population structure using microsatellite genotyping. They confirmed

that Hector's dolphins north and south of the Kaikoura Canyon belong to demographically and genetically differentiated subpopulations and that the barrier presented by the Kaikoura Canyon appears strong enough to create a disjunct in the overall isolation-by-distance pattern observed in the regional subpopulations with very few individuals dispersing per generation (Hamner et al., 2016). Their findings appear to confirm our low resighting rates between locations north and south of the Kaikoura Canyon barrier from 1988 to 2002, as well as the short distances and apparently low speeds observed for Kaikoura individuals from 1994 to 1997 due to the restricted home range covered by individuals.

The permanent existence of an environmental barrier (i.e., the deep-water canyon) thus appears to largely inhibit movements (only seven individuals moved between 1988 and 2002) and genetic exchanges (one northern individual sired by a southern individual; Hamner et al., 2016). It is not known whether water depth alone or some other factor (e.g., prey accessibility and/or predatory pressure) is/are creating this separation. If the isolating factors are sufficiently strong and persistent, however, they may lead to an increasing separation of the two subpopulations as may have happened in earlier times between the North and South Island populations. Cook Strait between the North and South Island and the deep Fiordland waters have long been suspected as ecological barriers for Hector's dolphins, effectively separating the populations off the east and west coasts of the South Island as well as the North Island from the south (Dawson & Slooten, 1988). Pichler et al. (1998) were able to show that no reproductive females migrated between these populations for many generations, possibly 10,000 years (F. Pichler, pers. comm., 1998).

In conclusion, our study provided evidence that the genetically isolated populations along the east and west coasts of South Island also display distinct differences in range utilization and movement patterns. These and related aspects of their differing behavioral ecology are expected to be driven by prey accessibility. The deep-water areas of Cook Strait and Fiordland have long been suspected to act as environmental barriers disrupting Hector's dolphin gene flow. The same mechanism also appears to work—on a smaller scale—off Kaikoura as can be seen by local population fragmentation.

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