# Range Utilization and Movement Patterns of Coastal Hector's Dolphins (*Cephalorhynchus hectori*)

Stefan Bräger and Zsuzsanna Bräger

Deutsches Meeresmuseum, 18439 Stralsund, Germany E-mail: Stefan.Braeger@gmx.net

This article is dedicated to Bernd Würsig, friend and mentor, who continues to do so much for cetacean research off Kaikoura and around New Zealand.

#### Abstract

Home range sizes have been determined for few odontocete populations, although the understanding of comparative trends in range utilization is important for conservation. Most of the published knowledge of the Hector's dolphins (Cephalorhynchus hectori) of New Zealand, originates from one wellstudied population around Banks Peninsula. Its ranging behavior has been described previously by a decades-long photo-identification (ID) study and by a shorter radio-telemetry study. Little is known, however, about how the dolphins utilize their home range in other coastal areas around the South Island of New Zealand. We used an intensive three-year photo-ID study to define the movement patterns of Hector's dolphins over diel and seasonal scales. Significant differences in the average movement behavior between the East Coast populations off Kaikoura and Moeraki and the West Coast populations off Westport-Greymouth and in Jackson Bay are identified. Movement patterns optimizing range utilization in relation to prey abundance and accessibility are discussed. At the Kaikoura study area, the mean distances between consecutive sightings and speeds of dolphins were considerably reduced compared to other coastal areas. Therefore, the photo-ID study was extended off Kaikoura to cover a total of 14 years. Those findings can be explained by the existence of an environmental barrier (i.e., the deep-water Kaikoura Canyon) that almost completely interrupts Hector's dolphin movements over the short distance of 15 km and very likely has led to a reduced genetic exchange. In conjunction with two recent studies, we present evidence of the impact of an environmental barrier on the population structure and foraging behavior of this shallow-water dolphin.

**Key Words:** environmental barrier, home range, Kaikoura Canyon, South Island of New Zealand, migration, site fidelity

#### Introduction

A *home range* is defined as the area normally traversed by an individual animal or group of animals during activities associated with feeding, resting, reproduction, and seeking shelter (Burt, 1943). A multitude of methods has been developed to estimate home range size (e.g., Oshima & Santos, 2016), but the true meaning of home range to an individual may not be well understood (Powell & Mitchell, 2012).

The Hector's dolphin (*Cephalorhynchus hectori*) is a small, coastal odontocete endemic to New Zealand. Most of the populations live along the east and west coasts of the South Island and are known to prefer a habitat determined by shallow (< 39 m depth), murky (< 4 m visibility), and relatively warm (> 14° C) water (Bräger et al., 2003). Furthermore, their small-scale habitat selection is influenced by river mouths, underwater reefs, and prominent headlands (Bräger et al., 2003). Distribution around Banks Peninsula is concentrated in nearshore waters with sightings more than 15 to 20 km offshore being rare in summer and slightly more common in winter (e.g., Rayment et al., 2010; MacKenzie & Clement, 2014).

Up to now, most of the knowledge about the ranging behavior of this species comes from the population around Banks Peninsula near Christchurch. Along-shore home ranges defined by multiple years of data have been estimated around Banks Peninsula to measure on average 31.0 km in a straight line along the coast (for n = 32 individuals over 13 y; Bräger et al., 2002) or 49.7 km for 95% of the density estimate (for n = 20 individuals over 22 y; Rayment et al., 2009). Within the home range, diurnal movements have been observed (Stone et al., 1995, 2005) as well as a seasonal offshore–onshore distribution shift (Dawson & Slooten, 1988; Bräger & Schneider, 1998; Rayment et al., 2010; MacKenzie & Clement, 2014).

For long-distance movements within the Banks Peninsula population, the farthest recorded straightline distances between two sightings amounted to 61 km (Smith, 1992), 63 km (Stone, 1992), and 106 km (Bräger et al., 2002), respectively. These distances were confirmed by a telemetry study of Hector's dolphins, also off Banks Peninsula. Three individuals were caught and equipped with satellite transmitters in March 2004. The maximum diameters of their short-term home ranges (i.e., straightline distances between the most extreme localizations) were between 50.9 and 66.5 km over 3 to 6 mo (Stone et al., 2005). However, Hamner et al. (2014) provided genetic evidence for movements over 400 km from extralimital records along North Island shores where at least two of six members of the nominate subspecies originated from the west coast of the South Island.

Photo-identification (ID) results from several other Hector's dolphin study populations were analyzed for association patterns (e.g., Bräger, 1999) but not yet for movement patterns. In this article, resighting data from the east and west coasts of the South Island are analyzed to define Hector's dolphin home ranges over temporal (i.e., days to months) and spatial scales. Differences in movement patterns among the East and West Coast populations, and the ecological impact of an environmental barrier near Kaikoura are discussed. The underlying processes may be relevant for a better understanding of population fragmentation in this endangered species (e.g., due to anthropogenic impacts such as bycatch in set-nets).

## Methods

Between November 1993 and April 1997, small boat surveys at a speed of 12.5 ( $\pm$  2.5) kts under good weather and sea conditions ( $\leq$  Beaufort State 4) were used to locate dolphins. Individual Hector's dolphins were photographically identified in these areas using SLR cameras with an 80-200 mm zoom lens from a 4.5-m research vessel equipped with a 40-hp outboard engine. Field effort varied between 10 and 210 d on the water at each of the different study areas, totaling 434 d in a 42-mo period (Table 1). The photographic quality of the identification photographs was standardized, and photos were matched manually (for details, see Bräger et al., 2002, 2003). Only photographic re-identifications were used to record movements. Hence, all distances and speeds are minimum estimates as no information is available on the likely detours between sightings. Consecutive resightings of the same animal were treated as being independent for the purpose of this analysis (Table 2).

Originally, seven study areas were chosen along the east and west coasts of the South Island of New Zealand to cover a range of possible movements within (up to 230 km) and between (120 to 600 km) them (Figure 1). The analysis concentrates on resightings from only four of the six study areas: (1) Kaikoura, (2) Moeraki, (3) Westport-Greymouth, and (4) Jackson Bay. The study areas off Westport and Greymouth overlapped slightly near Punakaiki and, thus, were treated as one study area from here on (with a total length of about 230 km of coastline between Karamea and Ross; Bräger & Schneider, 1998). The four study areas were visited usually every 6 mo in summer and in winter for 1 to 2 wks at a time. The data from Porpoise Bay were sparse (due to little long-range effort) and were used only to give examples of extraordinary movements. Resightings from Banks Peninsula extended over a much longer time span and were used to document multi-year home ranges (Bräger et al., 2002).

The local population of Hector's dolphins off Kaikoura has been estimated to consist of 304 (Weir & Sagnol, 2015) to 358 (MacKenzie & Clement, 2014) individuals, respectively. The unusual results—for example, particularly short movements—obtained from this population between March 1994 and April 1997 prompted a continuation of the photo-ID effort with another 33 survey days between May 1997 and May 2002 (not included in Table 1). Opportunistic photo-ID information from

Table 1. Survey effort at the seven original study areas from 1993 to 1997

Study area	Study period	Study period Number of field days			
Kaikoura	March 1994–April 1997	80	153		
Banks Peninsula	Nov 1993–March 1997	210	1,346		
Moeraki	Sept 1994–Dec 1996	37	102		
Porpoise Bay	Feb 1996–Feb 1997	10	28		
Westport	Feb 1995–Jan 1997	34	244		
Greymouth	Feb 1995–Feb 1997	30	271		
Jackson Bay	Feb 1995–Feb 1997	33	116		
Total	Nov 1993–April 1997	434	2,260		

Study population	Number of resighted individuals	Total number of sightings	Mean distance between sightings ± SE (km)	Mean distance between sightings per day ± SE (km/d)
Kaikoura	51	201	$3.9 \pm 0.58 \ (n = 81)$	$0.1 \pm 0.03 \ (n = 73)$
Moeraki	24	131	$6.3 \pm 0.45 \ (n = 107)$	$1.5 \pm 0.24 \ (n = 107)$
Westport-Greymouth	30	69	$17.7 \pm 2.36 \ (n = 38)$	$4.0 \pm 1.38 \ (n = 38)$
Jackson Bay	38	108	$10.8 \pm 1.89 \ (n = 70)$	$2.2 \pm 0.75 \ (n = 70)$

Table 2. Mean distances and transit speeds between consecutive sightings in four study populations between 1994 and 1997



Figure 1. Location of the study areas along the coasts of the South Island, New Zealand

local photographers from Kaikoura was also available from 1988 to 1993 for five resighted individual Hector's dolphins. These five sightings from the Kaikoura study area (not included in Table 1) were included in the analysis.

#### Results

In the 42 mo between November 1993 and April 1997, a total of 2,260 dolphin groups were studied (Table 1), of which 886 from the four study areas were included in the analysis. These groups provided 509 sightings of 143 identifiable individuals (Table 2). Almost half of these individuals were only sighted twice (i.e., resighted only once), whereas 9% of individuals were resighted a maximum of six to 13 times.

### Distances

Consecutive sightings of Hector's dolphins provided 296 straight-line distances between 0.0 and 61.4 km over a period of 2 y (Figure 2). Most of these distances were relatively short with  $51.7\% \le 5$  km and 38.2% > 5 to 20 km. No movements > 62 km were documented. There was also no indication of a seasonal trend in the alongshore distances traversed by Hector's dolphins (Figure 2). Even the longest distances recorded of 30 to 62 km were equally likely traveled within a few days and after 2 y. These distances corresponded with the summer home ranges from the Banks Peninsula (Bräger et al., 2002; Rayment et al., 2009). Long-distance movements of 62 to 600 km were not observed in this study.

Not included in these long-range movements was the resighting of a female that was seen in Porpoise Bay, Southland, on 25 February 1996 without a calf. Three days later, she was accompanied by a neonate calf near Waipapa Point, 20 km west of Porpoise Bay. During the following 17 d, the presumed mother and her calf made their way back to Porpoise Bay where they were photographed together again on 17 March and 1 April 1996 (L. Bejder, pers. comm., 1996). These sightings showed that extensive movements can occur during pregnancy and with very young calves.

The minimum distance between two consecutive sightings within 1 d ranged from 0.0 to 46.8 km. With the assumption that these animals covered a straight path, this reflects a potential speed of up to 2 kmh<sup>-1</sup>. On 22 January 1998, one easily identifiable individual covered 4.8 km in 30 min (9.58 kmh<sup>-1</sup>) off Westport. Other "fast" individuals covered an average of 21.5, 4.8, and 3.5 km, respectively, within a day based on resightings within the same day.

#### Short-Term Movement Patterns

In general, Hector's dolphins appear to have used the same stretch of a maximum of 62 km coastline for 2 y or longer. In fact, one individual in Kaikoura was resighted frequently in the same area for 10 y between January 1992 and May 2002. Within their home range, Hector's dolphins appeared to use smaller subareas over a matter of days. Two days after an initial sighting, the average straight-line distance covered is about 11 km, whereas it contracts again to about 3 km after 4 to



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 (±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 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 SE per day, whereas they covered  $\bar{x} = 2.8 \text{ km} \pm$ 0.69 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<sup>-1</sup>).

#### 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 subareas (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<sup>-1</sup> 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 km ± 1.92 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 km<sup>2</sup> ( $\bar{x}$  = 35.6 km<sup>2</sup>) and 3 to 13 km<sup>2</sup> ( $\bar{x} = 8.4$  km<sup>2</sup>), 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 km<sup>2</sup> and 302 to 1,028 km<sup>2</sup> 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 longterm 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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