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Earthquake impacts on a protected pinniped in New Zealand

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Abstract

1. The impacts of natural disasters on marine mammals are poorly understood and difficult to study, which can hamper management responses following such events.
2. This study provides the first distribution and abundance assessment of New Zealand fur seal (NZFS: *Arctocephalus forsteri*) colonies around Kaikōura, New Zealand, since a 7.8 magnitude earthquake in November 2016 caused substantial changes to both the local marine and terrestrial environments, and led to the reconstruction of a major highway that runs adjacent to NZFS colonies.
3. Mark–recapture and direct counts in the 2022–2023 breeding season estimated pup production for NZFS breeding colonies along the Kaikōura coast. Using established multipliers, pup estimates were used to provide the first comprehensive population estimate for Kaikōura's NZFS population since the earthquake.
4. Three new colonies and three new subcolonies were assessed and recorded, additional to reassessments of two established colonies. Overall, Kaikōura's NZFS population has grown and spread post-earthquake, with an upper total population estimate of between 21,560 and 28,327 animals in the 2022–2023 breeding season. Some sites, such as Lynch's Reef, appear to have benefited from earthquake-induced coastal uplift, with pup production increasing. Contrastingly, the estimated 2,401 (± 99) pups produced at Ōhau Point in 2023 is similar to pre-earthquake estimates. This indicates that the earthquake has disrupted previously documented growth at this site. The distribution of NZFS breeding at Ōhau Point has also changed substantially since the last pre-earthquake assessment.
5. From these findings, alterations to the Ōhau Point New Zealand Fur Seal Sanctuary and similar protections at other locations on the Kaikōura coast are suggested, as greater numbers of NZFSs are now accessible to human interaction and disturbance. The results demonstrate both how natural disasters and subsequent infrastructure modifications can impact coastal species and how conservation measures may need to be amended accordingly.

KEYWORDS

abundance, *Arctocephalus forsteri*, breeding distribution, mark–recapture, natural disaster, New Zealand fur seal

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1 | INTRODUCTION

Understanding the size and distribution of wildlife populations is key to successful management (Robinson et al., 2011; Laidre et al., 2015). Without effectively monitoring such parameters, important population trends can be masked (McIntosh et al., 2018), and interventions can come too late to achieve the desired outcomes (Voyles et al., 2014). Frequently, the logistics and costs of long-term monitoring programmes make them difficult to maintain (McIntosh et al., 2018), and gaps in the record can be exposed following catastrophic events (Schwing et al., 2020; Southwell et al., 2022) as attempts are made to understand their ecological impacts.

Natural disasters can have a range of impacts on wildlife populations, the most immediate being mortality during the event itself. For example, an estimated 40,000 Hutton's shearwaters (*Puffinus huttoni*) were killed during the landslides caused by the Kaikōura earthquakes (Cuthbert, 2019), and approximately 80% of Kangaroo Island's koala (*Phascolarctos cinereus*) population is thought to have perished in the 2019–2020 Australian bushfires (Dunstan et al., 2021). However, disaster-induced changes to habitats can also have long-term impacts on wildlife populations (Jolly et al., 2022). For example, nest counts in colonies of erect-crested penguins (*Eudyptes sclateri*) on the Antipodes Islands in October 2014 showed significantly greater declines in the numbers of nests in breeding areas impacted by storms in January 2014 compared with colonies that were unaffected or only partially impacted (Chilvers & Hiscock, 2019). The loss of habitat and resources likely also explains why bald eagles (*Haliaeetus leucocephalus*) and peregrine falcons (*Falco peregrinus*) failed to breed on an Alaskan island following a volcanic eruption (Williams, Drummond & Buxton, 2010). Following this 2008 eruption, Steller's sea lions (*Eumetopias jubatus*) were the only species to breed successfully one year later (Williams, Drummond & Buxton, 2010), demonstrating the differential impacts of natural events on affected species.

The impacts of the 2016 Kaikōura earthquake on other local wildlife populations have been studied. Additional to the substantial mortality of Hutton's shearwaters (Cuthbert, 2019), there was mass mortality among benthic invertebrate species such as black-footed pāua (*Haliotis iris*) (Schiel et al., 2019) caused by the uplift and exposure of the benthos. The foraging distribution and dive behaviour of sperm whales (*Physeter macrocephalus*) in the Kaikōura Canyon also changed for at least a year post-earthquake, likely due to disturbances to marine food chains (Guerra et al., 2020). The longest lasting impact of the 2016 earthquake to human populations was the damage to State Highway 1 (SH1), New Zealand's longest road. The earthquake damaged 194 km of SH1 (New Zealand Transport Authority, 2017), and it took approximately 17 months for the road to reopen for travel at all hours in both directions after the earthquake (Blake et al., 2019). Sections of the rebuilt road were moved away from the base of slopes, where landslips occurred, and closer to the coast (Green et al., 2018). At the geographical midpoint of the pre-earthquake Ōhau Point New Zealand fur seal (NZFS) colony (Boren, Muller & Gemmell, 2006), this shift was approximately 35 m seaward.

NZFSs (*Arctocephalus forsteri*) were hunted to the brink of extinction in the 18th and 19th centuries, with the population declining to less than 1% of the size it had attained prior to the arrival of humans in New Zealand (Emami-Khoyi et al., 2018). Since the cessation of sealing, NZFSs have been expanding in area and numbers, recolonizing parts of their former range (Dix, 1993; Bouma, Hickman & Taucher, 2008). However, colonies on the West Coast of the South Island have experienced declining pup production since 1991 (Roberts & Neale, 2016).

Estimating wildlife population abundances typically requires extrapolating data to produce an estimate for the wider population (Hammond, 2001). In pinnipeds, pup production estimates are the most reliable indicator for the overall population size (Berkson & DeMaster, 1985; Boren, Muller & Gemmell, 2006; Roberts & Neale, 2016; Chilvers, 2021). Pups are the only instantly recognizable age cohort and are confined to the colony until they wean, meaning that this group can, theoretically, be counted in its entirety (Berkson & DeMaster, 1985; Chilvers, 2021).

With NZFSs, abundance estimates involving pups have typically involved mark–recapture (Boren, Muller & Gemmell, 2006; Chilvers, 2021) and/or direct counts (Lalas & Harcourt, 1995; Taylor et al., 1995; Gooday et al., 2018). Though direct counts minimize disturbance to the animals, they produce underestimates, as pups may be concealed from the surveyors. Therefore, this methodology can only provide insights into relative population sizes and trends, and only then if executed consistently (Watson, Lalas & Seddon, 2009). As such, mark–recapture provides the most accurate method for estimating pup production, and thus population size (Boren, Muller & Gemmell, 2006; Watson, Lalas & Seddon, 2009; Chilvers, 2021).

Mark–recapture involves capturing and marking a subset of pups at a site and subsequently releasing them to mix with the remaining population (Boren, Muller & Gemmell, 2006; Chilvers, 2021). Following an interval of, typically, 24 h, the colony is revisited and a walk-through conducted to count the number of marked and unmarked pups. This ratio can be used in the formula later herein to calculate pup production. For NZFSs, marking is typically achieved through haircuts (e.g. Boren, Muller & Gemmell, 2006), livestock markers (e.g. Chilvers, 2021), or flipper tagging (e.g. Roberts & Neale, 2016). The limited time between marking and recapturing means that mortality in the intervening period can be assumed to be zero (Chilvers, 2021). However, dead pups observed during walk-throughs should be added to the live total to account for pre-survey mortality (Watson, Lalas & Seddon, 2009; Chilvers, 2021).

Pups included in walk-through counts must be categorized with certainty as either marked or unmarked, or else discounted (Chilvers, 2021). Similarly, marking and recapturing should be spread evenly through the study area, to help ensure that marked and unmarked pups have equal probabilities of being recaptured (Shaughnessy, Goldsworthy & Libke, 1995).

Despite its greater accuracy, mark–recapture is more expensive, labour intensive, and disruptive to NZFSs than direct counts (Watson, Lalas & Seddon, 2009). As such, calibration indices have been devised to estimate absolute pup production numbers from direct counts

(Watson, Lalas & Seddon, 2009; Chilvers, 2021). Though estimates of pup production based on these indices are not as reliable as those calculated from mark-recapture, together with their respective confidence limits, they provide greater accuracy than untransformed direct counts (Watson, Lalas & Seddon, 2009).

Following the demise of commercial sealing, large aggregations of NZFSs were observed in Kaikōura in the late 1950s (Street, 1964), with breeding recorded from the 1990s at three sites: Ōhau Point, Lynch's Reef, and Barney's Rock (Boren, Muller & Gemmell, 2006) (Figure 1). The most recent local NZFS abundance study (Gooday, 2016) estimated that 2,471 pups were born in the 2014–2015 breeding season at Ōhau Point, an increase from the ~600 pups estimated in 2005 (Boren, Muller & Gemmell, 2006). In their study, Boren, Muller & Gemmell (2006) determined that the Ōhau Point colony was growing at a rate of 32% per annum, whereas the Lynch's Reef colony, on the Kaikōura Peninsula, had a consistent annual pup production of 8–12 pups per year.

No comprehensive assessments of Kaikōura's NZFS population have been conducted since a magnitude 7.8 earthquake struck the region in November 2016. This event had significant impacts on the terrestrial and marine habitats used by NZFSs, including substantial uplift of coastal substrate by up to 6 m (Alestra

et al., 2019) and triggering over 10,000 landslides over approximately 10,000 km² (Massey et al., 2018). Additionally, 39×10^6 kg of benthic biomass was lost from the Kaikōura submarine canyon through an earthquake-induced flushing event (Mountjoy et al., 2018), disrupting local marine food chains (Guerra et al., 2020).

Given the impacts of this earthquake and the associated reconstruction efforts on SH1, which runs adjacent to several NZFS colonies, an updated evaluation of Kaikōura's NZFS population abundance and distribution is required to assess whether current management initiatives continue to effectively protect the local population.

2 | MATERIALS AND METHODS

Assessments of NZFS colonies were made along approximately 46 km of Kaikōura's coastline between Otumatu and Paparaoa Point on the north east of New Zealand's South Island (Figure 1). The definition of an NZFS colony as described by Shaughnessy et al. (1994) and Shaughnessy, Goldsworthy & Mackay (2015) is adopted here, whereby aggregations of breeding NZFSs are referred to as colonies, and when such aggregations occur within 2 km of each other they are

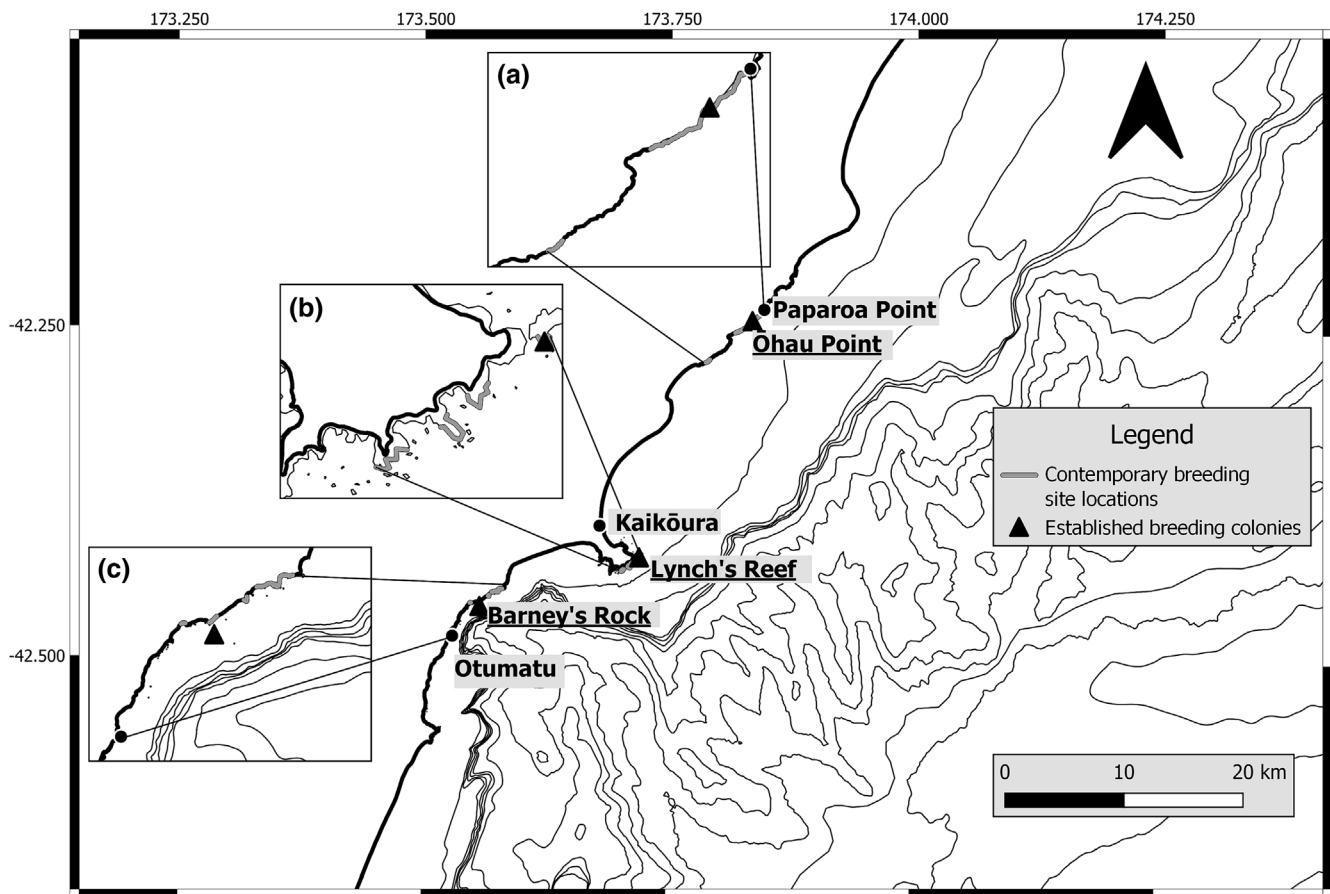


FIGURE 1 Map of the study area showing the location of the established breeding colonies Ōhau Point, Lynch's Reef and Barney's Rock, and insets showing the locations of the breeding colonies (a) north of Kaikōura, (b) on the Kaikōura Peninsula, and (c) south of Kaikōura assessed in this study. The benthic topography off the Kaikōura coast is shown to indicate the position of the deepwater Kaikōura Canyon.

categorized as a single colony. Distinct aggregations within colonies are referred to as subcolonies (Shaughnessy, Goldsworthy & Mackay, 2015).

Under this definition, the study focuses on five breeding colonies, two of which consist of multiple subcolonies (Figures 2–4). The ‘Ōhau Point’ colony includes the pre-earthquake Ōhau Point colony (Boren, Muller & Gemmell, 2006; Gooday, 2016), hereafter ‘Old Ōhau’, which had covered an approximately 800 m length of coastline (Figure 2).

2.1 | Breeding colony distribution

The location of NZFS breeding within the study area was established using direct counts of pups in the 2021–2022 and 2022–2023 breeding seasons. Typically, these direct counts involved at least two surveyors walking past the colonies and recording pup numbers using handheld tally counters. When only one surveyor was available to survey, counts were conducted twice so that a mean could be calculated.

The study area (Figure 1) was divided into three zones: ‘north of Kaikōura’ (between Paparoa Point and the northern end of Half Moon Bay; Figure 2), the ‘Kaikōura peninsula’ (between Kean Point

and Whalers Bay; Figure 3), and ‘south of Kaikōura’ (between SC Subcolony 1 and Otumatu; Figure 4). These zones were assessed at least once per month during the NZFS breeding season (December, January, and February) in both 2021–2022 and 2022–2023 to try to gain a full picture of where breeding takes place through time. Upon discovery of the South Rakautara colony in December 2021, this site was surveyed as frequently as possible when surveying other sites north of Kaikōura.

Direct counts were conducted from a distance or point of elevation above the colonies and did not involve walking through NZFS colonies. On the Kaikōura Peninsula, except for Whalers Bay, counts were conducted from the clifftops using binoculars. Barney's Rock, an offshore islet (Figure 4), could not be accessed for counts. However, continued pupping at this site was confirmed through binocular scans from headland vantage points.

2.2 | Abundance estimates

Abundance estimates were calculated using direct counts and mark-recapture (Table 2) between February 16 and 26, 2023. Abundance estimates for NZFSs typically take place from late January to March (e.g. Boren, Muller & Gemmell, 2006; Chilvers, 2021) as, at this stage,

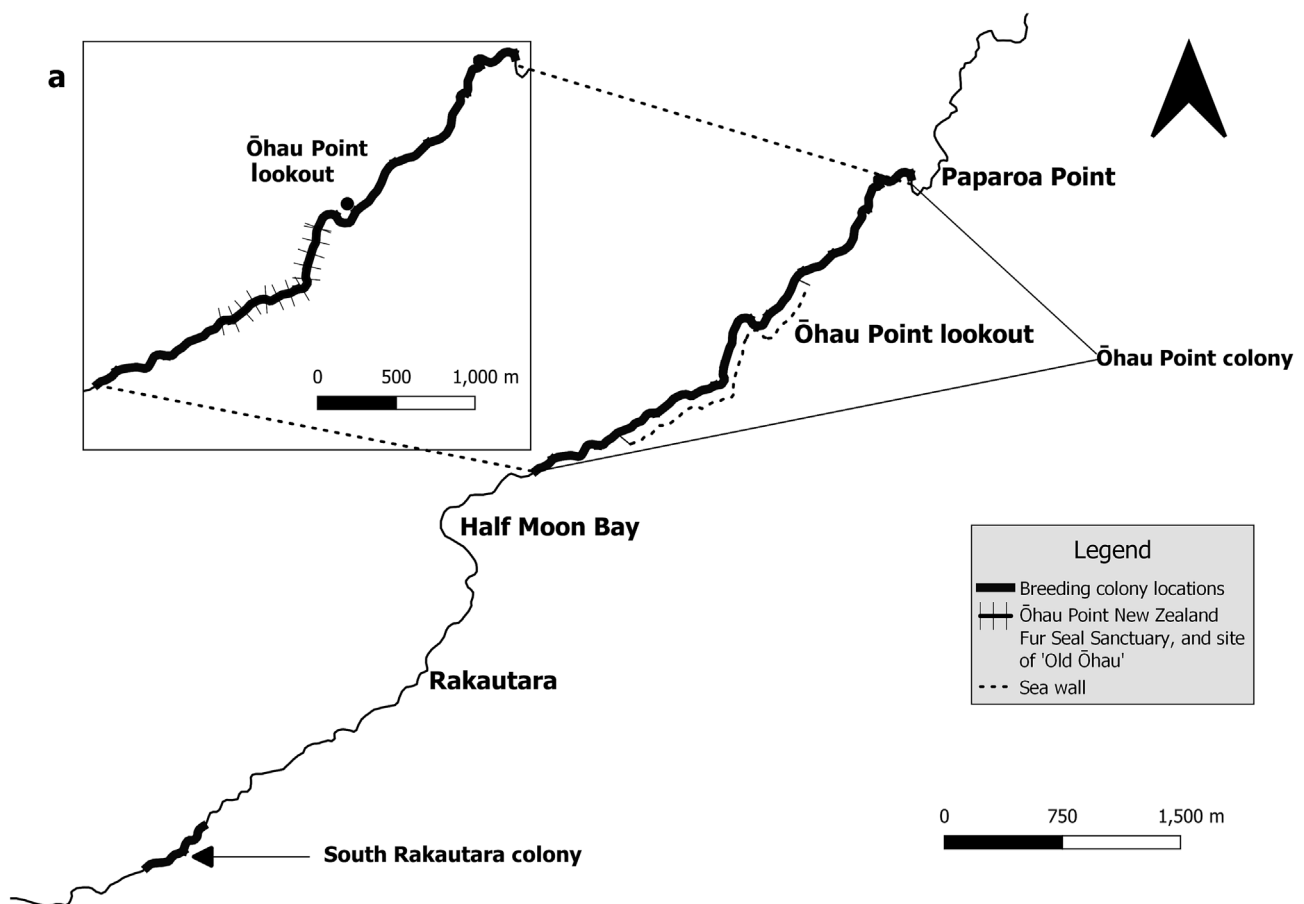


FIGURE 2 Location of Ōhau Point and South Rakautara colonies. The location of the sea wall is projected out from the coast for clarity.

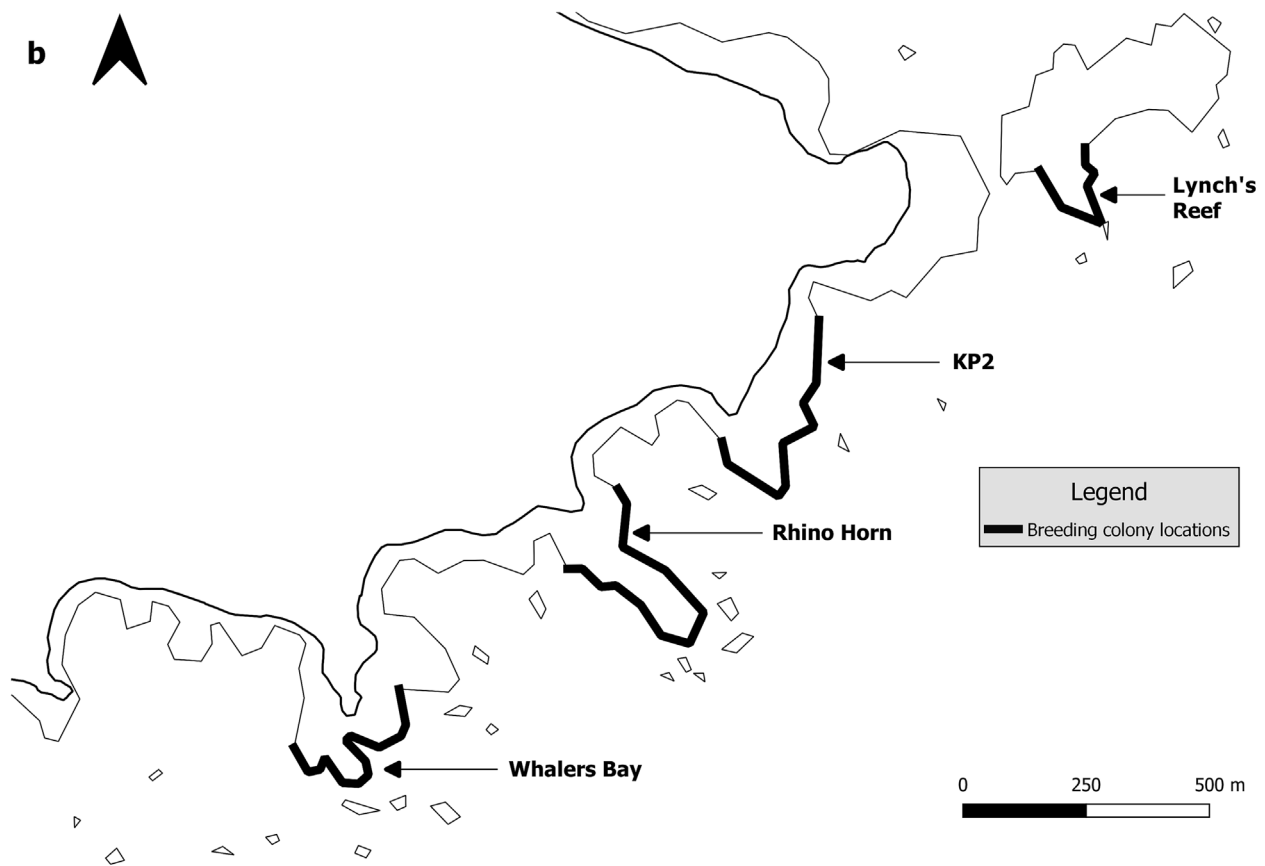


FIGURE 3 Location of the Kaikōura Peninsula subcolonies.

all pups will have been born and still have their instantly recognizable black pelage (Chilvers & Goldsworthy, 2015).

These direct counts were additional to the previously described survey efforts and involved groups of two to seven observers moving systematically through the colonies together and counting every NZFS pup they could find. This methodology was employed at the smaller South Coast subcolony sites (SC3, SC5, and Otumatu), where the small number of pups born (the largest single count was 37 ± 2 at SC3) made mark-recapture unnecessary, and at the Kaikōura Peninsula. Though the pup numbers and terrain complexity of the peninsula subcolonies warrant mark-recapture, the loss of fieldwork days due to Cyclone *Gabrielle* left insufficient time for mark-recapture here. Two sites, SC Subcolonies 1 and 4, were assessed using both direct counts and mark-recapture to enable the creation of calibration indices (Watson, Lalas & Seddon, 2009).

Mark-recapture analysis was conducted to obtain pup production estimates at larger sites. Marking was achieved through trimming a patch of fur on the pups' heads. All pups caught for marking were sexed to establish sex ratios. NZFS handling was subject to ethics approval by the Massey University Animal Ethics Committee.

Recaptures involved teams of four or five surveyors systematically moving through the colonies to count marked versus unmarked pups (Boren, Muller & Gemmell, 2006; Chilvers, 2021). Though this was done simultaneously, count independence was

achieved by surveyors recording the numbers of marked and unmarked pups individually, using handheld counters. Surveyors avoided double counting pups that were running ahead of them by only counting animals as they were passed. Owing to time constraints, only a single pass was made at each site. Effort was made to check all potential hiding places for pups.

The numbers of marked and unmarked pups in each recapture sample were used to calculate a modified Petersen pup production estimate (Chapman, 1952) as follows:

$$P_i = \left[\frac{(M+1)(C_i+1)}{R_i+1} \right] - 1$$

where, for each replicate i , M represents the number of marked NZFS pups, C_i is the total number of pups included in the recapture sample, and R_i is the number of marked pups recorded in the recapture sample. From this, the grand total estimate of pup production P is calculated from the mean of the Q Petersen estimators:

$$\frac{\sum_{i=1}^Q P_i}{Q}$$

Estimating pup production and extrapolating to a population estimate (Table 2) involved two calculations. First, mark-recapture

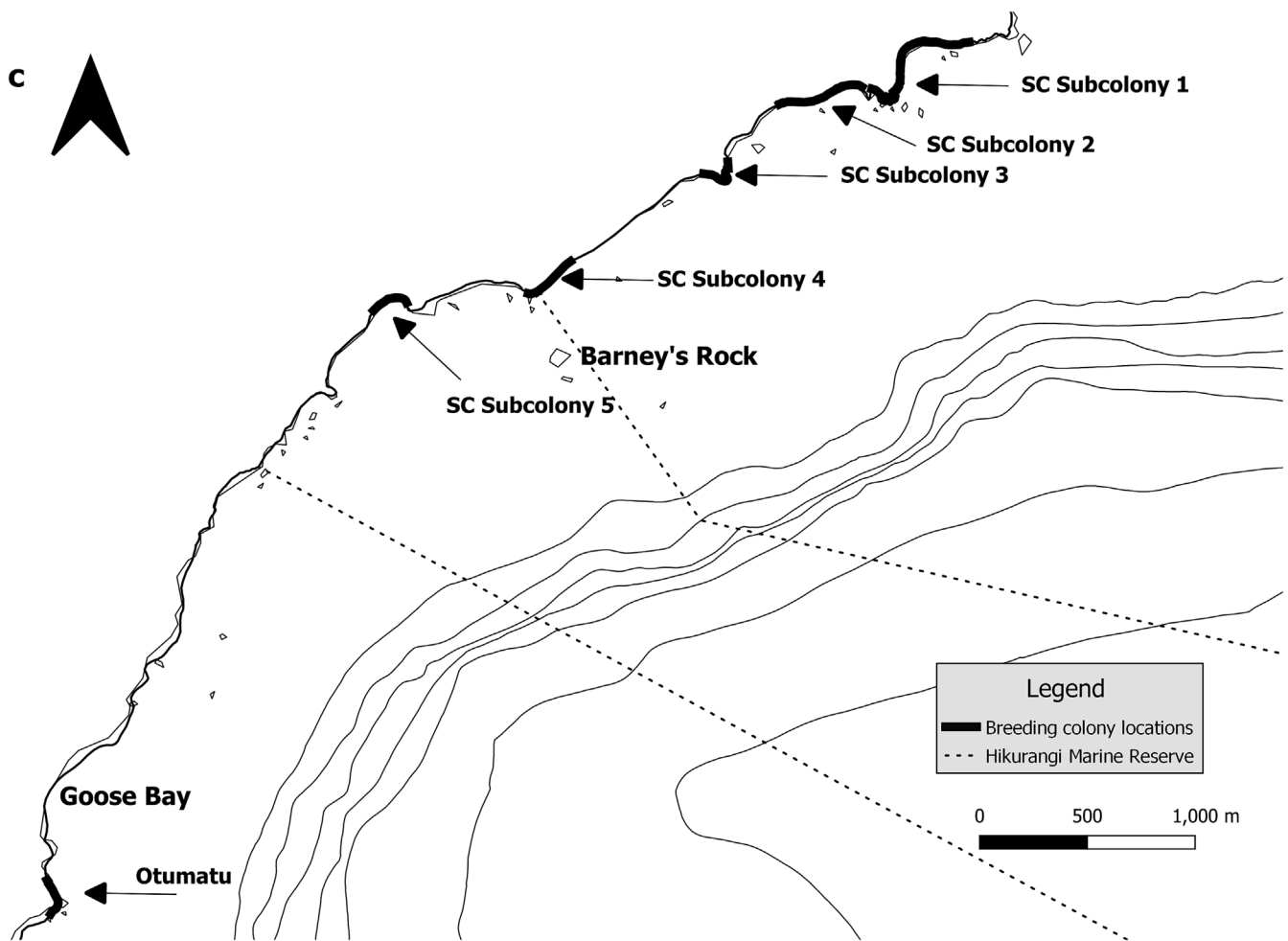


FIGURE 4 The location of the South Coast (SC) subcolonies and Otumatu breeding colony.

estimates plus all direct counts undertaken at sites where mark-recapture was not done were summed to calculate a minimum pup estimate. Second, direct counts from sites where mark-recapture was not done were multiplied by 1.57 (the mean of the differences between the direct counts and mark-recaptures at SC1 and SC4), and this total was added to the sum of the mark-recapture estimates.

Standard errors for mark-recaptures and direct counts (Table 2) were calculated as follows:

$$\sum_{i=1}^j (j - \bar{x}) \sqrt{\frac{1}{n(n-1)}}$$

where j is each surveyor's Petersen estimator or direct count, \bar{x} is the mean Petersen estimator or direct count for that site, and n is the number of surveyors.

Calculating population abundance estimates for NZFSs has typically involved using multipliers to convert pup production estimates (Shaughnessy et al., 1994; Shaughnessy, Goldsworthy & Libke, 1995; Campbell et al., 2014; Chilvers, 2021). The previously applied multipliers of 4.76 (Goldsworthy & Page, 2007) and 4.9 (Taylor, 1982) were used here (Table 2).

3 | RESULTS

3.1 | Breeding colony distribution

The distribution of NZFS breeding colonies in the 2022–2023 breeding season along the Kaikōura coastline is shown in Figures 2–4.

Old Ōhau is now two-thirds narrower than it was pre-earthquake due to the relocation of SH1 closer to the coastline. The linear extent of the colony is now approximately 3.3 km, compared with the approximately 800 m length of Old Ōhau. This includes an extension of approximately 800 m south of the southern boundary of Old Ōhau and approximately 1,770 m north of the northern boundary of Old Ōhau.

The area available at Lynch's Reef has also increased from the ~500 m² estimated by Boren, Muller & Gemmill (2006) to closer to ~10,000 m², although not all of this is currently used for breeding.

South of Kaikōura there are now two colonies: the South Coast colony and Otumatu. The South Coast colony includes six subcolonies: the five new sites SC1–SC5, shown in Figure 4, and Barney's Rock, which existed pre-earthquake. The mainland portion of

TABLE 1 Numbers of New Zealand fur seal pups marked at different sites along the Kaikōura coast.

Site	Pups marked	
	Number	Percentage of total (%)
Ōhau Point	384	15.9
South Rakautara	60	21
SC1	51	18.9
SC2	110	25.7
SC4	50	22

the South Coast colony stretches along approximately 3.8 km of coastline, with gaps of less than 2 km between each subcolony. Breeding at Otumatu occurs over approximately 180 m.

3.2 | Abundance estimates

The first new-born pups were recorded on December 8 in the 2021–2022 breeding season, and December 9 in the 2022–2023 breeding season.

During mark–recapture, a total of 655 pups were marked across five sites (Table 1). The total estimated pup production for these sites was $3,609 \pm 62$ (Table 2). The total pup production at sites assessed through direct counts alone was 830 ± 13 (Table 2). Combined, the mark–recapture estimates and direct counts provided a minimum pup estimate of 4,400–4,478 pups (Table 2), indicative of the mean plus/minus the standard error.

When the direct count only sites were subjected to the 1.57 multiplier and added to the mark–recapture site estimates (Ōhau Point, South Rakautara, SC1, SC2, and SC4), the pup count estimate for Kaikōura was 5,703–5,781 (Table 2), indicative of the mean plus/minus the standard error. A regional population estimate of between 20,944 and 27,518 was calculated using Goldsworthy & Page's (2007) 4.76 multiplier, and a regional population estimate of between 21,560 and 28,327 was calculated using Taylor's (1982) 4.9 multiplier (Table 2).

3.3 | Sex ratios

Sex ratios between the colonies and subcolonies where marking took place are presented in Table 3. A chi-squared test was used to test for deviation from an expected 1:1 sex ratio between sites within the 2022–2023 breeding season. This test found no significant deviation ($\chi^2 = 6.6353$, $df = 4$, $P = 0.1565$).

4 | DISCUSSION

This study provides the first comprehensive population assessment of Kaikōura's NZFSs since the November 2016 earthquake and subsequent road reconstruction.

4.1 | Limitations of the study

Two multipliers were used to convert pup production estimates into population estimates. Taylor's (1982) multiplier derives from research from the Bounty Islands and is based on assumptions and knowledge of Antarctic fur seal (*Arctocephalus gazella*) vital rates (Payne, 1977). Goldsworthy & Page's (2007) multiplier is derived from life-tables of South Australian NZFSs. Evidently, applying these multipliers can only produce coarse population estimates with wide confidence intervals (Chilvers, 2021). However, as many of the data used by Taylor (1982) and Goldsworthy & Page (2007) do not exist for NZFSs in New Zealand (Chilvers, 2021), the more generalized multipliers have been adopted to make the results comparable to other studies.

The 1.57 multiplier was derived from direct counts and mark–recapture at SC1 and SC4. Ideally, a separate index would have been created to convert direct counts from the Kaikōura Peninsula, as the terrain here is different to that in the South Coast colony, which can impact index suitability (Watson, Lalas & Seddon, 2009). However, loss of study days due to Cyclone *Gabrielle* made it impossible to conduct mark–recapture on the Kaikōura Peninsula. Future assessments of the Kaikōura Peninsula should attempt to create such an index, as this would likely improve result accuracy.

4.2 | Abundance estimates

Kaikōura's total NZFS abundance has increased since the last pre-earthquake assessment (Gooday, 2016). However, pup production at Ōhau Point has not. There is some evidence for growth stalling at Ōhau Point prior to the 2016 earthquake, with L. Boren (unpublished data) estimating 2,390 (± 227) pups produced in 2011, comparable to the 2,471 estimated in 2015 (Gooday, 2016). At that point, NZFS density within Old Ōhau was much greater than it is today across the larger post-earthquake breeding site, and Old Ōhau may have been approaching carrying capacity, with a concomitant reduction to the pup production growth rate (Roux, 1987). With NZFS density at Ōhau Point now considerably lower than it was pre-earthquake, and given the overall NZFS population growth in Kaikōura and across New Zealand (Emami-Khoyi et al., 2018; Chilvers, 2021), we would have expected Ōhau Point to revert to pup production growth. The fact that it has not likely relates to the extreme disruption to this colony caused by the 2016 earthquake. Much of the colony habitat was covered by landslip debris, causing loss of favourable habitat features (Gooday & Goldstien, 2018), and likely mortality. Additionally, there was disturbance and NZFS mortality caused by the road reconstruction (North Canterbury Transport Infrastructure Recovery, unpublished data) with some NZFSs relocated prior to the roadworks commencing, and the width of the colony reduced by the road's repositioning (Gooday & Goldstien, 2018). Despite all of this, Ōhau Point has surpassed Gooday & Goldstien's (2018) expectations by achieving pre-earthquake pup production. Given the lower density of NZFSs at Ōhau Point compared with before the earthquake, and the availability of suitable yet unused breeding habitat to the

TABLE 2 New Zealand fur seal pup counts and mark–recapture estimates for Kaikōura in the 2022–2023 breeding season.

Location	Pup direct count mean \pm SE	Pup mark–recapture estimate \pm SE	Area-specific pup production ranges
Ōhau Point		2,401 \pm 99	
South Rakautara		285 \pm 25	
Total north of Kaikōura		2,686 \pm 97	2,589–2,783
Kaikōura Peninsula subcolonies			
Lynch's Reef	41 \pm 1		
KP2	159 \pm 9		
Rhino Horn	323 \pm 10		
Whalers Bay	245 \pm 4		
Totals on Kaikōura Peninsula	768 \pm 15		1,182–1,229
South Coast subcolonies			
SC1	159 \pm 1	269 \pm 11	
SC2		427 \pm 13	
SC3	37 \pm 2		
SC4	157 \pm 11	227 \pm 4	
SC5	12		
Otumatu (separate colony)	13		
Totals south of Kaikōura	378 \pm 7	923 \pm 17	977–993 ^a 1,074–1,090 ^b
Total	830 \pm 13 ^c	3,609 \pm 62	
Minimum pup estimate		4,400–4,478	
Pup direct count to mark–recapture estimate (multiplier: 1.57) ^d		5,703–5,781	
Coarse estimated total population range (multiplier: 4.76) ^e		20,944–27,518	
Coarse estimated total population range (multiplier: 4.9) ^f		21,560–28,327	

Note: Empty cells denote where no count was done for that type/location.

^aMinimum pup estimate: equal to the sum of mark–recapture estimates plus all direct counts where mark–recapture was not undertaken.

^bDirect count to mark–recapture estimate: equal to the sum of the mark–recapture estimates plus the sum of the direct counts where mark–recapture was not done multiplied by 1.57.

^cThis total represents the sum of the direct counts for the sites where mark–recapture was not also conducted.

^dThis total represents the sum of the mark–recapture estimates added to the sum of the products of each respective direct count multiplied by 1.57.

^eThis coarse estimated total population range equals the range between the minimum pup estimate multiplied by 4.76 and the direct count to mark–recapture pup estimate multiplied by 4.76 (Goldsworthy & Page, 2007).

^fThis coarse estimated total population range equals the range between the minimum pup estimate multiplied by 4.9 and the direct count to mark–recapture pup estimate multiplied by 4.9 (Taylor, 1982).

TABLE 3 Pup sex ratios at the five sites where mark–recapture took place.

Site	No. of pups sexed	Sex ratio (F:M)
Ōhau Point	384	1:1.19
South Rakautara	60	1:1
SC1	51	1:1.55
SC2	110	1:1.04
SC4	50	1:2.33

immediate north and south of the current breeding distribution, it is expected that pup production at the Ōhau Point colony could grow further. Lynch's Reef, the other site for which comparable

pre-earthquake abundance data exist, produced substantially more pups in 2022–2023 than it did pre-earthquake (Boren, Muller & Gemmill, 2006).

The lack of recent population monitoring means it is impossible to establish the growth rate of the colonies studied here, nor estimate when previously unrecorded sites were founded. Gooday & Goldstien (2018) collated both published and unpublished NZFS data from the Kaikōura region going back to 1995. Whereas these data show, for example, that NZFSs were observed at Otumatu in 2001, no indication of whether they were adults or pups or precise location data is provided. Direct counts in the 2021–2022 and 2022–2023 breeding seasons suggest that Kaikōura's pup production has remained relatively stable across these two years (see [Supporting](#)

Information). However, data from other New Zealand NZFS colonies, and from New Zealand sea lion (*Phocartos hookeri*) colonies on the Auckland Islands, indicate that 2022–2023 was a low-productivity breeding season (L. Boren, personal communication). Though the causes of this are unknown, climate factors associated with a La Niña event may have contributed. The productivity of the Kaikōura Canyon likely provides local NZFS colonies with some buffer against the changing environmental and biological conditions associated with El Niño Southern Oscillation events (Boren, Muller & Gemmill, 2006), so it cannot be assumed that Kaikōura pup numbers were similarly impacted.

These uncertainties underscore the need for regular monitoring of wildlife populations. Gaps in the record are typical of NZFS monitoring across New Zealand (Chilvers, 2021), and declining pup production at West Coast colonies (Roberts & Neale, 2016) suggests that no single trajectory exists for New Zealand's NZFS colonies, demonstrating the need for more consistent and frequent assessments. It was fortunate, here, that Gooday's (2016) study provided relatively proximate 'before' data to allow inferences to be drawn as to the effects of the earthquake on Kaikōura's NZFSs. As substantial natural disasters are uncommon and unpredictable, missing baseline data often impedes such analyses (Southwell et al., 2022). McIntosh et al. (2018) describe the improvements made to population monitoring of Australian fur seals (*Arctocephalus pusillus doriferus*) when a coordinated, range-wide five-yearly census approach was adopted in 2002, replacing previous sporadic and opportunistic surveys. Currently, three-yearly NZFS mark–recapture monitoring is conducted at declining colonies on the West Coast of the South Island (Roberts & Neale, 2016), and it is suggested that a similar programme is adopted in Kaikōura to continue assessments of the population's trajectory post-earthquake. Given the large interannual variation in *Arctocephalus* spp. pup production (McIntosh et al., 2018), supplementary direct counts could also be conducted annually.

4.3 | Breeding colony distribution

NZFS breeding distribution around Kaikōura has expanded beyond that described previously (Figure 1) (Bradshaw, Lalas & Thompson, 2000a; Boren, Muller & Gemmill, 2006; Gooday, 2016). The Ōhau Point colony is now approximately 3.3 km long, compared with the approximately 800 m of Old Ōhau, although it is much narrower, and there is now a colony south of Rakautara that had not been described previously. Similarly, the Kaikōura Peninsula currently supports three previously unrecorded subcolonies additional to Lynch's Reef (Boren, Muller & Gemmill, 2006; Gooday, 2016). South of Kaikōura, pre-earthquake, Barney's Rock was the only recorded breeding site within the study area (Boren, Muller & Gemmill, 2006; Gooday, 2016). Today, there is also breeding in the mainland South Coast colony, and at Otumatu.

There are several likely explanations for these expansions. First, New Zealand's NZFS population is continuing to recover from exploitation (Emami-Khoyi et al., 2018; Chilvers, 2021). As such, the

founding of new colonies is expected as resources are stretched at existing sites (Roux, 1987). NZFSs are highly philopatric (Bradshaw, 1999; Chilvers, 2021), and Bradshaw et al. (2000b) suggested that new colonies should develop near existing ones in a 'spillover effect' representing a compromise between philopatry and density-dependent factors that may impact breeding success (Bradshaw et al., 2000b). This has been demonstrated in NZFS colonies on Kangaroo Island, South Australia (Shaughnessy & Goldsworthy, 2015), and newer subcolonies within the South Coast and Kaikōura Peninsula colonies also appear to follow this pattern. Breeding at SC4 is likely a spillover from Barney's Rock (Figure 4), an established breeding site with limited breeding space directly offshore from SC4. SC4 had previously been an adult haul-out site (Boren, 2005), and thus appears to have followed a documented pattern whereby sites evolve from haul-outs into breeding sites (Dix, 1993; Ryan, Hickling & Wilson, 1997). Similarly, KP2, Rhino Horn, and Whalers Bay on the Kaikōura Peninsula may represent spillover from Lynch's Reef, another established and previously spatially limited breeding area (Figure 3). Alternatively, these sites could have been founded by migrants from elsewhere in New Zealand, or from Ōhau Point post-earthquake.

Other sites, however, are unlikely to represent spillover. For example, South Rakautara is over 5 km from the southernmost extent of Ōhau Point, and a substantial amount of apparently suitable, yet unused, breeding habitat exists between the two colonies. This is also true of the coastline between SC5 and Otumatu. An alternative explanation for these new colonies is immigration of NZFSs, either from Ōhau Point, following the earthquake, or from elsewhere in the country (Robertson & Gemmill, 2005). Immigrating animals from further afield would be uninfluenced by local philopatry when selecting breeding habitat (Bradshaw et al., 2000b).

Earthquake-induced changes to breeding habitats have also likely impacted NZFS breeding distribution. The earthquake caused variable uplift of up to 6 m at different locations along the coastline (Alestra et al., 2019; Hay, 2020), creating additional breeding space at some sites. Pup production at Lynch's Reef has increased from the consistent 8–12 pups between 2002 and 2005 (Boren, Muller & Gemmill, 2006), which was believed to be close to the site's spatial limit, to 41 ± 1 pups in the 2022–2023 breeding season. However, uplift also has a potentially deleterious implication for NZFSs at Lynch's Reef. This subcolony is now substantially more accessible to people, as the uplift greatly reduced the depth of a channel that formerly separated the colony from a popular tourist carpark (Gooday & Goldstien, 2018). As such, additional protection measures, perhaps in the form of sanctuary protections, should be considered to protect NZFSs there from disturbance.

The earthquake, and subsequent anthropogenic responses, also had negative impacts on NZFS habitat quality at other sites around Kaikōura. For example, at Ōhau Point, uplift, combined with landslides dumping over 100,000 m³ of debris (Barrett & Hayes, 2019), destroyed important habitat features, including caves. Additionally, SH1 was rebuilt closer to the ocean, decreasing the width of the habitat between the road and the ocean by two-thirds (Gooday &

Goldstien, 2018). The resultant loss of caves, crevices, and rock pools led Gooday & Goldstien (2018) to downgrade the habitat's suitability, as per Taylor et al.'s (1995) scoring system, from 9 (the highest possible) to 6. The fact that the Ōhau Point colony is now approximately four times the length of Old Ōhau (Figure 2), but that pup production today ($2,401 \pm 99$) is comparable to the 2014–2015 breeding season (2,471; Gooday, 2016), suggests that the breeding population is now distributed more linearly along the coastline, likely in response to the changes to the physical habitat. Additionally, NZFSs were deliberately relocated prior to the commencement of roadworks on SH1 (Gooday & Goldstien, 2018). As there is now insufficient room for the pre-earthquake breeding population within Old Ōhau, some relocated NZFSs may not have returned.

Whether animals remain in a habitat impacted by a natural disaster depends on several factors. Immediately, members of the population must survive, although even when populations are extirpated (Rodríguez-Lozano et al., 2015) they can later return and repopulate former habitats (do Rosário & Mathias, 2007). Resource and habitat loss can also inhibit population persistence, even if members survived the initial event (Williams, Drummond & Buxton, 2010).

In Kaikōura, enough NZFSs survived the earthquake and enough local habitat remained suitable for the population to remain in situ. Indeed, NZFSs bred at Ōhau Point immediately after the earthquake (Gooday & Goldstien, 2018). How many NZFSs died as a direct result of the earthquake is unknown, although its timing at around midnight on November 14, 2016 (Furlong & Herman, 2017), likely reduced mortality compared with if it had happened a few weeks later, or during daylight hours. Previous studies of Ōhau Point's colony dynamics indicate that few, if any, of that season's pups would have been born when the earthquake occurred (Boren, 2005). Had the earthquake happened in late November or early December there may have been substantial pup mortality, as the median pupping date at Ōhau Point was December 16, 2002, December 5, 2003, and December 7, 2004 (Boren, 2005) and, once born, pups are initially relatively immobile (Crawley & Wilson, 1976). Further, as NZFSs are predominantly nocturnal foragers (Page, McKenzie & Goldsworthy, 2005), fewer adults would have been ashore when the earthquake occurred relative to daylight hours. However, there would have almost certainly been mortalities in the initial earthquake-induced landslips. In particular, there may have been substantial numbers of heavily pregnant females ashore at Ōhau Point when the earthquake occurred (Boren, 2005). Mortality among experienced female breeders may help to explain the continued stagnation of growth at Ōhau Point despite reduced population density. Discoveries of deceased individuals under rubble in 2017 suggests additional mortality during subsequent landslips, and NZFS were also accidentally killed during the road reconstruction by, for example, heavy machinery (North Canterbury Transport Infrastructure Recovery, unpublished data).

Though continued use of pre-earthquake sites suggests their continued suitability despite the disruptions, philopatric species can make maladaptive decisions to remain in diminished habitats

following natural disasters (Lai, Shieh & Kam, 2007; Dudley et al., 2022). Given Ōhau Point's reduced habitat quality (Gooday & Goldstien, 2018), this possibility should be considered for Kaikōura's NZFSs. With amphibious marine species, the ongoing suitability of both marine and terrestrial habitats should be appraised following a natural disaster. The highly productive Kaikōura Canyon (De Leo et al., 2010) provides a year-round food source for species such as dusky dolphins (*Lagenorhynchus obscurus*) (Benoit-Bird, Wursig & McFadden, 2004) and sperm whales (*P. macrocephalus*) (Sagnol et al., 2015) and is within easy foraging range of NZFSs from all colonies assessed in the present study (Boren, 2005) (Figure 1). Its presence may explain why Kaikōura's pups have previously been shown to be in better condition than those born in many other parts of New Zealand (Bradshaw, Lalas & Thompson, 2000a; Boren, Muller & Gemmell, 2006), perhaps because cows can make shorter foraging trips more energetically profitable, and thus nurse their pups more regularly and reduce pup fasting periods (Boren, 2005). Pups at Ōhau Point also wean later than at other NZFS colonies in New Zealand and Australia (Boren, 2005) despite being born at a similar time, potentially because females can remain in better condition while lactating, allowing them to extend the weaning period without severe energy penalties, and thus wean pups in better body condition (Boren, 2005). Though the earthquake-induced flushing of benthic biomass from the Kaikōura Canyon (Mountjoy et al., 2018) had observable impacts on local marine food chains, these effects appear to have been temporary (Guerra et al., 2020). Further, NZFSs' foraging plasticity (Baylis et al., 2012) may have enabled them to adjust to any changes to their foraging habitat. The Kaikōura Canyon likely provides such a bountiful resource that, even if the quality of some terrestrial habitats has been reduced, Kaikōura remains an excellent habitat for NZFSs. The habitat suitability criteria (Taylor et al., 1995) that Gooday & Goldstien (2018) used to reassess Ōhau Point following the earthquake only considers terrestrial features, perhaps explaining why, post-earthquake, Ōhau Point has surpassed their expectations for pup production.

5 | IMPLICATIONS FOR CONSERVATION

Changes to NZFS abundance and breeding distribution have implications for the management of the local population. This study highlights the reality that human–NZFS interactions are likely to become more frequent and occur in different locations due to the numeric and spatial expansion of the local NZFS population.

The linear expansion of NZFS breeding at the Ōhau Point colony means that most breeding now occurs outside the boundaries of the Ōhau Point New Zealand Fur Seal Sanctuary (Figure 2). This sanctuary was established under the Kaikōura (Te Tai ō Marokura) Marine Management Act 2014, with the intention of reducing anthropogenic impacts on the colony, particularly disturbance from tourists. The entirety of Old Ōhau, which is contained within the sanctuary boundaries, is now far harder for tourists to access due to the construction of the 8–10 m high sea wall (Figure 2). However, post-

earthquake breeding expansion means that substantial areas of the colony do not benefit from either the legal protections of the 2014 legislation or the physical barrier of the sea wall, and are, therefore, at risk of disturbance. The Kaikōura (Te Tai ō Marokura) Marine Management Act 2014 is due for a review commencing in 2024, and it is recommended that the existing Ōhau Point New Zealand Fur Seal Sanctuary be extended.

Such extensions should not only incorporate where NZFSs currently breed, but also consider where they may colonize next, should breeding continue expanding along the coastline. The narrowness of sections of the Ōhau Point colony, combined with the newly constructed sea wall, makes this site particularly vulnerable to sea-level rise. The Old Ōhau section is the contemporary colony's narrowest point (Figure 2), and so it is likely that there will be continued redistribution of breeding to both the north and south of Old Ōhau if sea levels rise as predicted (Kulp & Straus, 2019). As such, to help futureproof the sanctuary, the entirety of Paparoa Point (Figure 2) should be considered for sanctuary protections. Currently, only the southern face of Paparoa Point experiences NZFS breeding; however, the entire point features excellent NZFS breeding habitat (Ryan, Hickling & Wilson, 1997); and, given the typical spillover pattern of NZFS breeding colony expansion (Bradshaw et al., 2000b), this site is likely to be colonized in future. Similarly, at the southern end of the current Ōhau Point breeding distribution, we recommend that sanctuary protections are extended to the northern terminus of the Half Moon Bay sea wall (Figure 2). The habitat available up to this point is very similar to that already occupied in the contemporary Ōhau Point colony and is also likely to be colonized in the future. Half Moon Bay itself is not, as it does not contain suitable NZFS breeding habitat.

Sanctuary protections would also be beneficial for some of the other Kaikōura NZFS breeding sites identified in this study that are at particular risk from human disturbance. In particular, NZFSs on the Kaikōura Peninsula are a draw for tourists (Acevedo-Gutiérrez et al., 2010), and these colonies are particularly accessible. People have also been observed walking into subcolonies SC1 and SC4 on the south coast, where there is either no or minimal signage alerting people to the presence of NZFSs, or existing local regulations regarding interacting with these animals. If signage is to be employed to encourage compliance with current New Zealand regulations regarding maintaining appropriate distances from seals (20 m), then teleological signs are recommended as these have been shown to be more effective than ontological signs (Marschall, Granquist & Burns, 2017).

Additional to providing human access to road-abutting colonies, SH1 is a direct threat to Kaikōura's NZFSs (Hall et al., 2023). The numbers of live and dead NZFSs recorded on SH1 have increased from an average of 12 per year between 1996 and 2005 (Boren, Morrissey & Gemmill, 2008) to 59 per year (± 16.9 SD) between 2012 and 2022 (Hall et al., 2023). Much of this increase is likely due to local NZFS population growth, meaning the problem is likely to worsen without effective mitigation, such as more effective barriers, if local NZFS abundance continues to increase (Hall et al., 2023). Continued increases to New Zealand's nationwide NZFS numbers (Emami-Khoyi

et al., 2018; Chilvers, 2021), and expansions of pinniped populations in other countries (Kirkwood et al., 2010; Milano et al., 2020) mean that mitigating similar deleterious interactions between such species and humans is likely to require greater consideration and resources in the future.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception, methodology design, and data collection. Alasdair Hall and Louise Chilvers contributed to funding acquisition, data analysis, and visualization. The first draft of the manuscript was written by Alasdair Hall, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The datasets analysed during the current study are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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