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Towards an Abundance Estimate for New Zealand Fur Seal in New Zealand

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ABSTRACT

A lack of population abundance and trajectory data is a conservation and management issue relevant to numerous pinniped species, many of which are exposed to a variety of threats. New Zealand fur seal (*Arctocephalus forsteri*; 'NZFS') populations in different parts of New Zealand have experienced both substantial increases and decreases to their abundance over the last 50 years, since the last nationwide census. Here, existing data and stage-structured matrix modelling were used to provide a contemporary nationwide estimate of NZFS abundance. Graphical depictions demonstrate the spatial inconsistencies in NZFS monitoring in New Zealand through time. A minimum population estimate of 131,338–168,269 NZFS was calculated by combining the most recently available pup production data from around New Zealand and using established multipliers. A second estimate of 181,646–239,473 NZFS was calculated using stage-structured matrix models to project contemporary abundance. Inconsistent NZFS population monitoring and sparse vital rate data for New Zealand's NZFS limited this study, and both population ranges are likely underestimates. However, they still represent substantial increases on the most cited nationwide abundance figure (100,000 NZFS). From these findings, we suggest that a regularised program of monitoring is adopted for New Zealand's NZFS, as has been achieved for similar species in other countries. This would both aid in the management of NZFS in the face of emerging risks, such as H5N1 avian influenza, and enable their use as a sentinel for the health of New Zealand's marine ecosystems.

1 | Introduction

Population abundance estimates are important to species management and conservation (Wittmer et al. 2010; Wege et al. 2016). Without contemporary abundance estimates, it can be difficult to prioritise species for conservation interventions (Bland et al. 2015) or identify emerging threats (Zipkin and DiRenzo 2022; Campagna et al. 2024). Outdated understandings of population size and trajectory can lead to risks being missed and interventions delayed, sometimes with devastating consequences (Voyles et al. 2014). Widely distributed, or wide-ranging, species often experience varying population trajectories (Roberts and Neale 2016), and differing threats through space (Lascelles et al. 2014; Wright et al. 2022). Macro understandings of abundance are required to recognise the impacts of disparate threats on a species, and because policies and agreements governing conservation action, and other relevant anthropogenic activities, are often set at national or supranational levels (Robinson et al. 2014).

A lack of population abundance and trajectory data is common to many pinniped species around the world, making population level change hard to detect (Kovacs et al. 2012). Other than Otago (MacDiarmid and Lalas 2014) and three colonies on the West Coast of the South Island (WCSI) (Roberts and Neale 2016) (Figure 1), there is no longitudinal New Zealand

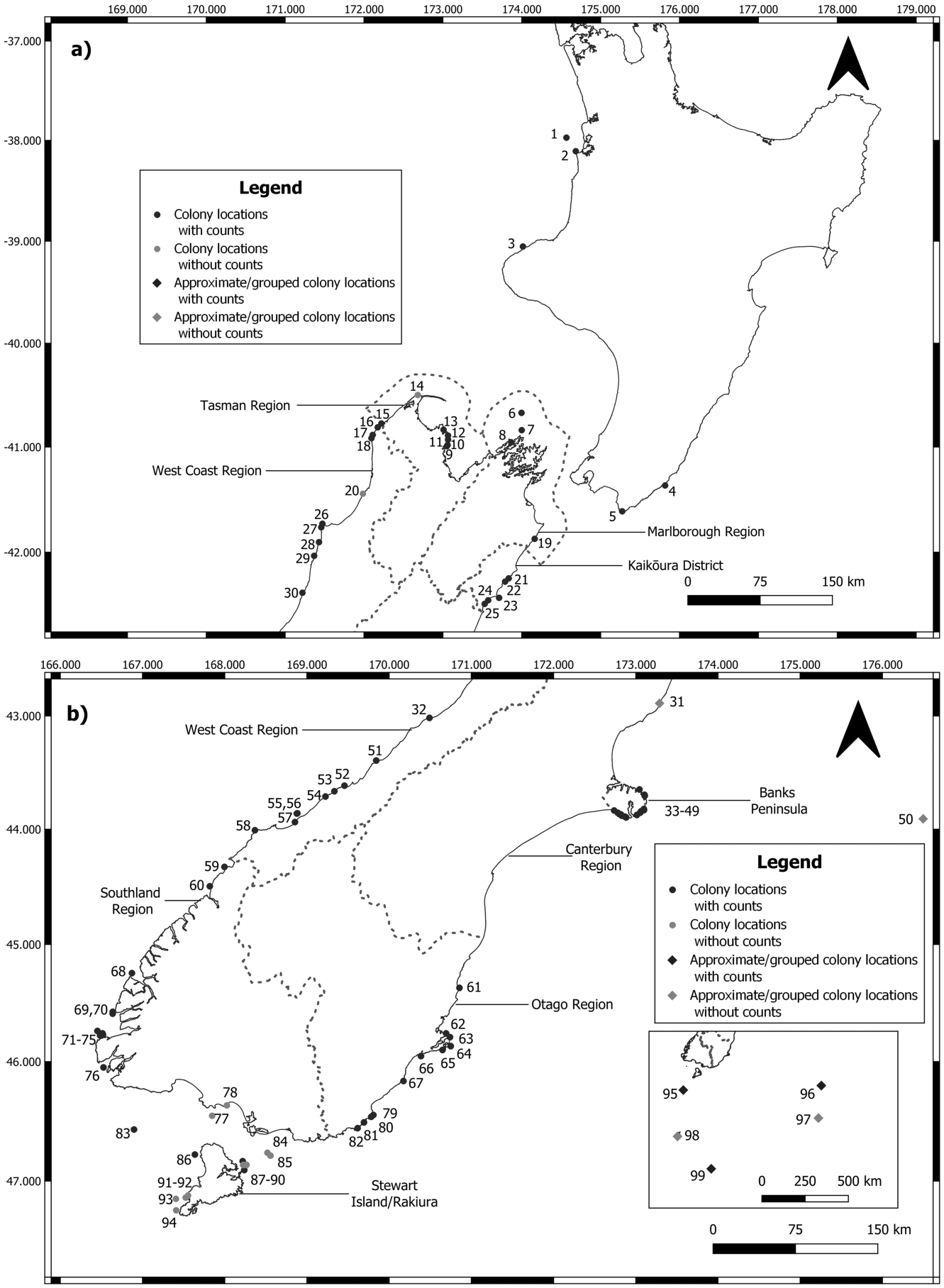

FIGURE 1 | Legend on next page.

FIGURE 1 | Known New Zealand fur seal colonies in New Zealand. 1. Gannet Island, 2. Albatross Point, 3. Sugarloaf Islands, 4. Honeycomb Rock, 5. Cape Palliser, 6. Stephens Island, 7. Trio Islands, 8. Admiralty Bay, 9. Fisherman Island, 10. Adele Island, 11. Pinnacle Island, 12. Tonga Island, 13. Separation Point–Shag Harbour, 14. Cape Farewell, 15. Kahurangi Point, 16. Otukoroiti Point, 17. Steep Point, 18. Wekakura Point, 19. Needles Point, 20. Kongahu Point, 21. Ōhau Point, 22. South Rakautara, 23. Kaikōura Peninsula, 24. Kaikōura South Coast, 25. Otumatu, 26. Black Reef, 27. Cape Foulwind, 28. Charleston, 29. Seal Island, 30. Point Elizabeth, 31. North Canterbury, 32. West of Pukutuaro Cliff, 33. Tokoroa Bay, 34. Te Oka Bay, 35. Robin Hood Bay, 36. Peraki Bay, 37. Horseshoe Bay, 38. Island Bay, 39. Whakamoa Bay, 40. Pōhatu Bay, 41. Reef Nook, 42. Sleepy Bay, 43. Otanerito Bay, 44. Shell Bay, 45. Goat Pt, 46. Paua Bay, 47. Ducksfoot Bay, 48. Pa Bay, 49. Long Lookout Point, 50. Chatham Islands, 51. Gillespie's Point, 52. Hanata Island, 53. Abbey Rocks, 54. Rock off Knight's Point, 55. Taumaka Island, 56. Popotai Island, 57. Jackson Bay, 58. Cascade Point, 59. Long Reef Martins Bay, 60. Yates Point, 61. Moeraki Peninsula, 62. Heyward Point, 63. Otago Peninsula–North, 64. Otago Peninsula–Centre, 65. Otago Peninsula–South, 66. Green Island, 67. Quoin Point, 68. Nee Island, 69. Breaksea Island, 70. Wairaki Island, 71. Five Finger Peninsula, 72. Anchor Island, 73. Many Islands, 74. Outer Islands, 75. Seal Island, 76. Chalky Island, 77. Rarotoka/Centre Island, 78. Rocks, Riverton, 79. Nugget Point, 80. Tucks Cove, 81. Penguin Bay, 82. Cosgrove Island, 83. Solander Island, 84. Ruapuke Island, 85. Breaksea Islands, 86. Whenhua Hou/Codfish Island, 87. Edwards Island, 88. Herekopare Island, 89. Bunkers Islets, 90. Bench Island, 91. Kundy Island, 92. Big Island, 93. Mokinui/Big Moggy Island, 94. Taukihepa/Big South Cape Island, 95. Snares Island, 96. Bounty Islands, 97. Antipodes Islands, 98. Auckland Islands, 99. Campbell Island. Note: NZFS breed in most bays and headlands on the southern and south-eastern coasts of Banks Peninsula (24–40). To keep this as concise as possible, only colonies with 50+ pups (Hall et al. 2025) in this area are labelled here. Where colony locations are not precisely known, or multiple colonies have been grouped for an area, for example on the subantarctic islands, this has been made shown in the key.

fur seal/kekeno (*Arctocephalus forsteri*; 'NZFS') abundance data collection for colonies within New Zealand waters. Here, New Zealand waters refers to mainland New Zealand, plus all nearshore and offshore islands within its Exclusive Economic Zone. Most colonies/regions have only been surveyed sporadically, and, in extreme examples, some have gone unassessed for nearly 40 years (Taylor 1992). Additionally, differing survey methodologies (Taylor et al. 1995; Gooday et al. 2018; Chilvers 2021) make it challenging to compare results. For example, counts conducted from aeroplanes (Baker et al. 2009) have been shown to produce underestimates relative to ground counts (Stringell et al. 2014). Counts from boats (Taylor et al. 1995) are also typically less reliable than those conducted terrestrially (personal observation). There has also been little demographic parameter data collection for NZFS in New Zealand (Mattlin 1978; Lalas and Harcourt 1995; Bradshaw 1999; Dickie and Dawson 2003; Boren 2005), although such data do exist for NZFS in Australia (Goldsworthy 1994; McKenzie et al. 2005; McKenzie 2006; Goldsworthy and Page 2007). The lack of NZFS vital rate data from New Zealand means that multipliers borrowed from elsewhere in the species' range (Goldsworthy and Page 2007), or from other *Arctocephalus* spp. (Taylor 1992) have been used to scale up NZFS pup production estimates into population estimates (Chilvers 2021; Hall et al. 2024). The most commonly used multiplier (Goldsworthy and Page 2007) derives from lifetables of NZFS from Australia and allows estimation of an entire colony or population abundance from the numbers of pups produced (Goldsworthy and Page 2007). Pup production estimates are the most common way of assessing pinniped population abundance (Berkson and DeMaster 1985) (see Materials and Methods), although there are drawbacks to such approaches (Karamanlidis 2024).

There is currently no comprehensive estimate for NZFS abundance within New Zealand waters (hereafter, 'nationwide abundance'), as the species continues its post-exploitation recovery (Dussex et al. 2016). A figure of 100,000 is the most cited nationwide abundance estimate (Taylor et al. 1995; Wickens and York 1997; Harcourt 2001), and 200,000 has been suggested for the combined New Zealand–Australia NZFS population for over 20 years (Harcourt 2001; Goldsworthy and Gales 2008; Chilvers and Goldsworthy 2015). These figures are based on the last attempted nationwide census, which estimated a population of 30,000–50,000 NZFS (Wilson 1981). However, this census was incomplete, and count reliability varied between sites (Wilson 1981). The uncertainty of the subsequent estimates is demonstrated by the fact that 200,000 NZFS has been estimated for both New Zealand's population (Emami-Khoyi et al. 2018), and for the combined New Zealand–Australia population (Harcourt 2001; Goldsworthy and Gales 2008; Chilvers and Goldsworthy 2015). Consequently, these figures can be best thought of as guesstimates. Comparatively recently, an estimate of 117,400 individuals was suggested for Australia's NZFS abundance (Chilvers and Goldsworthy 2015), a population which has increased by approximately 60% in the last 20 years (Shaughnessy and Goldsworthy 2015). Recent studies, based on robust pup production estimates, have provided NZFS abundances for New Zealand regions that had not been assessed for some time, such as lower Fiordland (Chilvers 2021), Kaikōura (Hall et al. 2024) and Banks Peninsula (Hall et al. 2025). The locations of currently known NZFS colonies are shown in Figure 1, based on a literature review and discussions with NZFS researchers and local conservation managers. Of the limited number of recently assessed sites, nearly all are thought to be growing (Chilvers 2021; Hall et al. 2024, 2025). However, three colonies on the WCSI (Cape Foulwind, Wekakura Point and Taumaka Island; Figure 1) are documented as in decline (Roberts and Neale 2016). Overall, the monitored colonies in New Zealand are unlikely to be representative of some areas that have gone unassessed for long periods—such as New Zealand's subantarctic islands, where environmental and ecological conditions are very different to the mainland.

The current highly pathogenic avian influenza (HPAI) H5N1 avian influenza pandemic, which has killed birds and mammals (Plaza et al. 2024), and been diagnosed in humans (Pulit-Penaloza et al. 2024), is among the most compelling contemporary reasons for monitoring New Zealand's NZFS abundance. HPAI H5N1 has caused catastrophic mortality in southern elephant seals (*Mirounga*

leonina) (Campagna et al. 2024) and harbour seals (*Phoca vitulina*) (Puryear et al. 2023), and correlates with a similar event in South American sea lions (*Otaria flavescens*) (Ulloa et al. 2023). Given HPAI H5N1's detection within Antarctic and subantarctic regions (Bennison et al. 2023), and within *Arctocephalus* spp., the virus will likely reach New Zealand (Gartrell et al. 2024). Otariids can be effective indicators for the presence of pathogens (Donahoe et al. 2014), and sentinels for changes to the marine environment (Brock et al. 2013; Elorriaga-Verplancken et al. 2016; Taylor et al. 2018), which can aid effective species and wider ecosystem management.

Substantial difficulties exist when assessing wildlife abundances at large geographic scales, particularly for long-lived species (Baker et al. 2016; Christie et al. 2016; Torney et al. 2019), with modelling often offering the best approaches (McDonald et al. 2014; Ureña-Aranda et al. 2015; Fleming et al. 2022). Here, we provide an updated nationwide abundance estimate for New Zealand's NZFS, by combining recent surveys and population modelling. We simultaneously highlight longstanding inconsistencies in NZFS monitoring methodologies and make suggestions on how this could be improved.

2 | Materials and Methods

Three approaches were undertaken to estimate NZFS's nationwide abundance in New Zealand: a minimum population abundance estimate (Section 2.1), a density-independent projection model (Section 2.2.1) and a density-dependent projection model (Section 2.2.2) (Table 1).

NZFS abundance estimates are typically extrapolated from pup production estimates (Boren 2005; Roberts and Neale 2016; Chilvers 2021), because pups younger than ca. 3–4 months are easily identifiable and confined to their natal colonies. Thus, theoretically, this entire cohort can be counted, unlike older individuals, of which an unknown proportion may be at sea during surveys (Berkson and DeMaster 1985). Direct counts (Taylor et al. 1995; Taylor 1996; Gooday et al. 2018) and mark-recapture (Boren, Muller, and Gemmell 2006; Chilvers 2021) are the two most common ways of estimating NZFS pup production. Direct counts are suitable at smaller colonies (Chilvers 2021) but produce underestimates compared with mark-recapture at larger sites (Watson et al. 2009), although the former are quicker, cheaper, less invasive and require fewer personnel.

TABLE 1 | Parameter description for the matrix population models used to estimate New Zealand fur seal abundance.

Symbol	Parameter
φ_1	Pup survival
φ_2	Juvenile survival
φ_3	Adult survival
ω	Adult fecundity
σ	Juvenile transition

2.1 | Minimum Nationwide Abundance Estimate

A minimum nationwide NZFS abundance estimate was calculated using the most recent pup production estimate from colonies/regions for which data were available (Table 2) without any projection forward. Where only pup counts were provided, these were scaled up to population estimates using Goldsworthy and Page's multiplier (2007) (Chilvers 2021). Where provided in the original study, population estimates were used directly. For populations where abundance ranges were provided, the lower and upper bounds were separately summed with the single estimates from the remaining sites to produce a total range.

Pup production and population estimates were collected through a literature review and by seeking unpublished data from researchers. Figure 2 provides a summary of the geographic distribution of NZFS abundance research in New Zealand over time. A more detailed breakdown is given in Supplementary Information (SI) 1.

2.2 | Population Projection Modelling

Two modelling approaches were applied using stage-structured matrix models (Lefkovitch 1965; Caswell 2001). Both defined three stages of NZFS ontogeny: 'pups' (0–1 years old), 'juveniles' (1–4 years old), 'adults' (4+). The cutoff between juvenile and adult is arbitrary, but age 4 was used in many of the studies from which vital rate data were derived (SI 2). The models can be described as:

$$\boldsymbol{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

With $\mathbf{n}_t$ and $\mathbf{n}_{t+1}$ representing the number of individuals in each stage at time intervals t and $t+1$ respectively, and $\mathbf{A}$ representing the population matrix:

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & \omega \\ \varphi_1 & \varphi_2\sigma & 0 \\ 0 & \varphi_2(1-\sigma) & \varphi_3 \end{pmatrix}$$

Vital rate data are required for matrix models; however, these are highly limited for New Zealand's NZFS (Mattlin 1978; Dickie and Dawson 2003). As such, additional vital rate data were applied from other fur seal species (SI 2).

Additional to survival rates for each stage, and fecundity rates for adults, a transition rate was required from the juvenile–adult stages, calculated as:

$$1 - \frac{1}{x_j - x_i}$$

where x_i is the first age class in stage i (juveniles; 1) and x_j is the first age class in stage $i+1$ (adults; 4) (Fujiwara and Diaz-Lopez 2017). In this instance, giving 0.66.

To be forward projected, colonies/regions had to:

TABLE 2 | Most recent New Zealand fur seal pup counts and derived minimum population estimates.

Colony/region	Year of most recent pup production estimate	Count method	Pup production estimate	Source	Minimum population estimate
Gannet Island and Albatross Point	2023	Boat direct counts	15	C. Hansen (personal communication)	71
Sugarloaf Islands	2023	Boat direct counts	25	Chaddy's Charters (personal communication)	119
Honeycomb Rock	1999	Direct count	10	(Baird 2011)	48
Cape Palliser	2023	Direct count	600	L. Boren, personal communication	2856
Stephens Island	1994	Direct count	276[a]	(Taylor et al. 1995)	1314
Trio Islands	2007	Boat direct counts	50	(Baird 2011)	238
Admiralty Bay	2021	Direct counts	100	L. Boren, personal communication	476
Tasman Region (Separation Point to Onetahuti, Tonga Island, Adele Island, Pinnacle Island and Fisherman Island)	2023	Direct counts	101	L. Boren, personal communication	481
Kahurangi/Otukoroiti	2009	Aerial direct count	63	(Baker et al. 2009)	300
Steep Point	2009	Aerial direct count	25	(Baker et al. 2009)	119
Wekakura Point	2023	Mark-recapture	144	(Department of Conservation 2023)	685
Black Reef	2010	Direct counts	200[a]	(H. Best, *unpublished data*)	952
Cape Foulwind	2023	Mark-recapture	93	(Department of Conservation 2023)	443
Charleston	2010	Direct counts	476[a]	(H. Best, *unpublished data*)	2266
Seal Island	2009	Aerial direct counts	6	Baker et al. 2009)	29
Point Elizabeth	2003	Direct count	10	(Baird 2011)	48
Needles Point	2023	Direct count	36	L. Boren (personal communication)	171
Kaikōura (Ōhau Point–Otumatu)	2023	Mark recapture and direct counts	4400–5781	(Hall et al. 2024)	20,944–27,518[b]
Banks Peninsula (all colonies)	2024	Mark recapture and direct counts	2762–3713	(Hall et al. 2025)	13,147–17,675[b]
West of Pukutuaro Cliff	2009	Aerial direct counts	16	(Baker et al. 2009)	76
Gillespie's Point	2009	Aerial direct counts	3	(Baker et al. 2009)	14
Hanata Island	2009	Direct counts	66	(Baker et al. 2009)	314

(Continues)

TABLE 2 | (Continued)

Colony/region	Year of most recent pup production estimate	Count method	Pup production estimate	Source	Minimum population estimate
Abbey Rocks	2009	Aerial Direct counts	12	(Baker et al. 2009)	57
Rock off Knights Point	2009	Aerial direct counts	13	(Baker et al. 2009)	62
Taumaka Island	2023	Mark-recapture	776	(Department of Conservation 2023)	3694
Popotai[c]	2009	Aerial direct counts	118	(Baker et al. 2009)	NA
Jackson Head	2009	Aerial direct counts	21	(Baker et al. 2009)	100
Cascade Point	2009	Aerial direct counts	1466[a]	(Baker et al. 2009)	6978
Long Reef, Martins Bay	2009	Aerial direct counts	163[a]	(Baker et al. 2009)	776
Yates Point	2009	Aerial direct counts	1228[a]	(Baker et al. 2009)	5845
Lower Fiordland (Doubtful/Pateā, Dusky and Breaksea Sounds, and Chalky Inlet)	2021	Mark recapture and direct counts	2935–5042	(Chilvers 2021)	13,971–24,000[b]
Otago and the Catlins (Oamaru to Slope Point)	2009	Direct counts	2993–5294	(MacDiarmid and Lalas 2014)	13,000–28,800[b]
Solander Island	2009	Aerial direct counts	1107	(Baker et al. 2009)	5269
Rakiura/Stewart Island (and surrounding islands)	2003	Mark recapture and direct counts	2694[a]	(Watson et al. 2015)	12,823
Snares Islands	1997	Direct counts	188	(Carey 1998)	895
Bounty Islands	1994	Direct counts	4380[a]	(Taylor 1996)	20,849
Antipodes Islands	1985	Direct counts	7	(Taylor 1992)	33
Campbell Islands	1988	Direct counts	126[a]	(Moore and Moffat 1990)	600
Minimum estimate totals			**27,798–34,538**		**131,338–168,219**

[a]Sites that met the criteria to be projected to 2024.
[b]Population estimates provided in the original study.
[c]The 2009 estimate for Popotai was not used in any calculations due to declining pup numbers on nearby Taumaka Island but is included here for completeness.

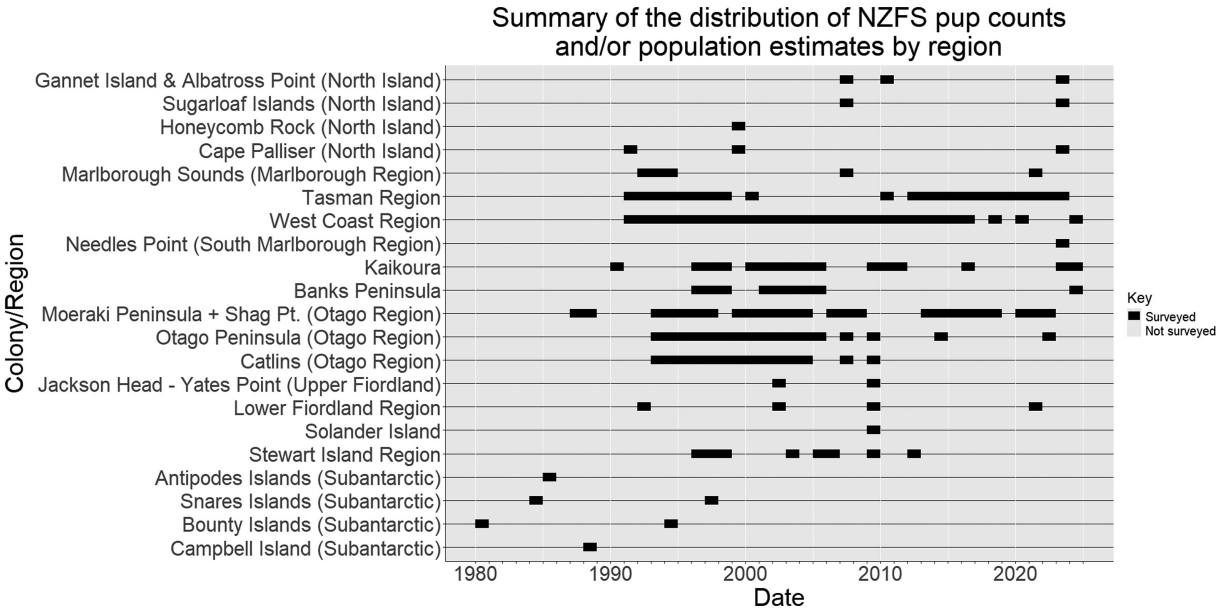

FIGURE 2 | Summary of the geographic distribution of New Zealand fur seal population size assessments through time in New Zealand since Wilson (1981). Years marked as 'surveyed' mean that one or more pup count or population estimate was undertaken in that region in that year. Mostly, these studies did not cover the entire region. Where isolated colonies occur, these are included individually—this comprises all North Island colonies and Needles Point.

- Have gone unassessed for the last 5 years (before the year of writing; 2024).
- Have more than 100 pups at their last count.
- Not represent counts listed as 'guesstimates' in the literature.
- Not represent populations which are thought to have stabilised.

These criteria were selected for the following reasons. Due to the limitations of the modelling approach (see Discussion), it was decided that estimates from colonies/regions assessed within the last 5 years would likely be more accurate than projected population estimates. Of the 12 colonies/regions assessed within the last 5 years (Table 2), 10 were assessed in either 2023 or 2024.

Colonies with fewer than 100 pups at their last count were excluded due to the instability of small populations (Davison et al. 2019). Counts listed as 'guesstimates' in the literature (e.g. some counts in Baird 2011) were excluded due to a lack of information on how these figures were reached. Finally, colonies/regions with populations that are thought to have stabilised were not included, as it seemed inappropriate to project their numbers forward, when evidence suggests they are no longer growing. Three populations with previous pup counts are thought to have stabilised: Snares Island, Otago/the Catlins and Solander Island. For Snares Island and Otago/the Catlins, determinations of the populations having stabilised were based on the conclusions of the researchers who studied them (Carey 1998; MacDiarmid and Lalas 2014). For Solander Island, this determination was based upon the results of two population assessments, made 36 years apart, which indicated no substantial change in local NZFS abundance (Wilson 1981; Baker et al. 2009).

The only other count excluded was that from Popotai Island, where 118 pups were counted from a plane in 2000 (Baker et al. 2009). Popotai is approximately 500 m from Taumaka, where regular monitoring (Department of Conservation 2023) has shown consistent declines in pup production.

2.2.1 | Density-Independent Projection Model

As insufficient data exist documenting density-dependent impacts on NZFS population growth, a density-independent modelling approach was trialled using the *pop.projection* function within the *popbio* package (Stubben and Milligan 2007) in R Studio (R Core Team 2022). This method produced such improbably large results (see Section 4.2) that a full description of the methods and results is not included.

2.2.2 | Density-Dependent Projection Model

The density-dependent modelling approach utilised the *stoch.proj* (Stubben 2020) function in the *popbio* package (Stubben and Milligan 2007) in R Studio.

Minimum, average and maximum values were selected for each required vital rate, from the data in SI 2. The juvenile–adult transition rate was calculated at 0.66, as outlined above (Fujiwara and Diaz-Lopez 2017). Five matrices were then created. The 'low', 'average' and 'high' matrices contained, respectively, the lowest, the average and the highest values for each vital rate. The fourth matrix (high survival, low fecundity) contained average rates for all inputs, except adult survival rates were high and adult fecundity rates were low. The final matrix (high fecundity, low survival) was the inverse regarding adult fecundity and survival. These final two

matrices were included due to evidence of reproductive costs on female Antarctic fur seal (*Arctocephalus gazella*) survival (Boyd et al. 1995).

Starting abundances are required for each ontogenetic cohort to initiate the projections. These were calculated for the juveniles and adults in each projected region/colony by using popbio's *stable.stage* function (Stubben and Milligan 2007). To do this, stable stages were first calculated for each of the five matrices, and then a single stable stage calculated by averaging those results for each respective ontogenetic cohort. As the starting abundances for pups were already known, the proportions provided by the stable stage could be used to provide the same for juveniles and adults.

The *stoch.proj* function permits inclusion of simple density-dependence by providing a maximum number of individuals (*nmax*) that the projections cannot exceed (Stubben 2020). Given the lack of data, for individual colonies (e.g. Stephens Island), *nmax* was set as the largest pup production estimate hitherto obtained for a single NZFS colony in New Zealand (2471 at Ōhau Point in 2015; (Gooday 2016)) multiplied by 4.76 (Goldsworthy and Page 2007), giving an *nmax* of 11,761. For multiple colonies across regions, e.g. Stewart Island, the Otago/Catlins area population estimate (28,800) was used. This is the largest regional NZFS population estimate recorded in New Zealand (MacDiarmid and Lalas 2014). The impacts of selecting these *nmax* values are reported for each projection (Table 3), and a discussion of the limitations of this approach is provided in Section 4.3.

stoch.proj also enables the prescription of a weighted probability vector for matrix selection at each iteration. Little data exist on the frequency with which NZFS experience variation in vital rates through time, making it difficult to select values for this vector. Expert opinion indicates that the 'average' vital rate matrix should occur more frequently than any other matrix. As such, this was given a higher probability weighting, and the remaining four matrices were given equal weightings. Nineteen possible integer combinations exist whereby one value is largest, and the remaining four equal, with all five summing to 100. To demonstrate the impacts of varying the probability weightings on the final population estimates, three results are presented for each projection (Tables 3 and 4). These represent the 'high difference' (average = 0.96, other = 0.01), 'median difference' (average = 0.6, other = 0.1) and 'low difference' (average = 0.24, other = 0.19) relative differences in the probability values ascribed to the average versus the other four (low; high; high survival, low fecundity; high fecundity, low survival) matrices.

Each projection ran for 1000 iterations, and the respective projection intervals equalled the numbers of years elapsed between the last local NZFS survey and 2024.

2.2.3 | Model Testing

The results of the model were tested using data collected from Moeraki Peninsula in the Otago/Catlins region by C. Lalas (personal communication), and results from Te Oka Bay on Banks Peninsula (Boren, Muller, and Gemmell 2006; Hall et al. 2025).

The Moeraki data set contains pup count estimates for 23 of the years between 1987 and 2021, with pups first recorded in 1988 (C. Lalas, unpublished data). This dataset was projected from 2001, when 96 pups were estimated, until the most recent survey in 2021, when 782 pups were estimated (plausible range 606–964) (C. Lalas, unpublished data).

The Te Oka Bay record is less complete, with data available in 1997, 2001–2005 and 2024. The value of 84 pups from 2003 (Boren, Muller, and Gemmell 2006) was used to initiate the projection, and model results were compared with those from 2024 (Hall et al. 2025), where 418 ± 1 SE pups were estimated at Te Oka Bay in 2024.

The initiation years for Moeraki (2001) and Te Oka Bay (2003) were selected as the pup counts in these respective years were the closest to the minimum 100-pup rule described in Section 2.2. The methodology was as described in Section 2.2.2, and *nmax* for both was set at 11,761.

3 | Results

3.1 | Minimum Nationwide Abundance Estimate

A total minimum nationwide pup count of 27,798–34,538 was calculated, based on the most recently available, unprojected pup counts listed in Table 2.

From this, a minimum nationwide abundance of 131,338–168,269 NZFS was calculated, derived from the sum of the most recent pup counts, multiplied by 4.76 (Goldsworthy and Page 2007), or population totals provided in the original studies.

3.2 | Density-Dependent Estimate

When summed, the sites that did not meet the criteria to be projected (Table 2) produced an unmodelled population range of 77,375–125,044. The results of the projected sites/colonies are presented below (Table 3), combined with number of times the *nmax* ceiling was reached in the 1000 iterations.

Using the results from the 'high difference' scenario, which appear likely to be the most accurate (as shown in Section 3.3), the projected populations of the modelled colonies/regions totalled 104,271–114,429 (Table 3). When combined with the unmodelled colonies, a nationwide abundance range of 181,646–239,473 NZFS was calculated.

3.3 | Model Testing Results

The results of the model testing from Moeraki Peninsula and Te Oka Bay are presented in Table 4. The figures in this table refer to pup counts, rather than population estimates, in contrast to Table 3, as pup counts are comparable with the observed results from the original studies. Across the 'High', 'Median' and 'Low' probability weightings, the population *nmax* of 11,761 was hit just once out of the 1000 iterations on the 'High' scenario for Moeraki, and not at all in the others.

TABLE 3 | Estimated 2024 New Zealand fur seal population abundances for modelled colonies/regions.

Colony/ region	Latest recorded pup count (year)	Projected 2024 pup abundance (mean ± SD) 'High difference'	Projected 2024 population abundance (mean ± SD) 'High difference'	No. times nmax reached (/1000) 'High difference'	Projected 2024 pup abundance (mean ± SD) 'Median difference'	Projected 2024 population abundance (mean ± SD) 'Median difference'	No. times nmax reached (/1000) 'Median difference'	Projected 2024 pup abundance (mean ± SD) 'Low difference'	Projected 2024 population abundance (mean ± SD) 'Low difference'	No. times *nmax* reached (/1000) 'Low difference'	Maximum range
Stephens Island	276 (1994)[a]	2427–3134	9414–11,946	190	1319–2905	5214–10,865	166	736–2516	3031–9290	77	3031–11,946
Black Reef	200 (2010)[b]	525–654	2038–2488	0	329–730	1325–2700	0	239–752	981–2738	0	981–2738
Charleston	476 (2010)[b]	1260–1578	4908–5983	0	817–1761	3242–6521	0	591–1748	2433–6368	2	2433–6521
Cascade Point	1466 (2009)[c]	2913–3201	11,523–11,936	903	2379–3457	9646–12,381	578	1919–3423	7968–12,183	357	7968–12,381
Long Reef, Martins Bay	163 (2009)[c]	460–583	1787–2205	0	298–677	1203–2464	0	206–644	842–2353	0	842–2464
Yates Point	1228 (2009)[c]	2905–3210	11,432–11,994	908	2220–3364	8896–12,317	479	1740–3361	7133–11,955	307	7133–12,317
Stewart Island Region	2694 (2003)[d]	7158–7806	28,143–29,275	883	5910–8345	23,847–30,406	558	4583–8316	18,888–29,847	335	18,888–30,406
Bounty Islands	4380 (1994)[e]	7178–7810	28, 229–29,224	847	6259–8408	26,075–29,806	611	5471–8575	28,842–30,051	446	22,842–30,051
Campbell Island	126 (1988)[f]	1758–2458	6797–9378	0	713–2487	2806–9333	0	813–8228	813–8228	1	813–9378
Projected site totals		26,584–30,434	104,271–114,429		20,244–32,134	82,256–116,792		16,298–37,563	64,932–113,013		64,932–118,202
Total from unmodelled sites											77,375–125,044
Grand total[g]											181,646–239,473

Note: 'High difference', 'Median difference' and 'Low difference' refer to the probability weightings assigned to the matrices, explained in Section 2.2.2.

[a]Taylor et al. (1995).

[b]Baird (2011).

[c]Baker et al. (2009).

[d]Watson et al. (2015).

[e]Taylor (1996).

[f]Moore and Moffat (1990).

[g]This figure combines the unmodelled total with the modelled results from the 'high difference' scenario, which appears likely to be the most accurate (Section 3.2).

TABLE 4 | Results of the model testing.

Colony/region	Pup count in year initiated	True pup count in final year of study	Projected pup abundance (mean ± SD) 'High difference'	Projected pup abundance (mean ± SD) 'Median difference'	Projected pup abundance (mean ± SD) 'Low difference'	Maximum range (based on means ± SD)
Moeraki Peninsula	96 (2001)[a]	782 (2021)	457 ± 62	396 ± 172	343 ± 204	111–717
Te Oka Bay	84 (2003)[b]	418 ± 1 SE[c] (2024)	432 ± 59	370 ± 158	327 ± 210	117–537

[a]C. Lalas (unpublished data).
[b]Boren, Muller, and Gemmell (2006).
[c]Hall et al. (2025).

4 | Discussion

This study is the first empirical effort to update our understanding of New Zealand's nationwide NZFS abundance since Wilson (1981). A minimum nationwide NZFS abundance estimate of 131,338–168,269 was calculated using the latest unmodelled population figures and pup production estimates, combined with Goldsworthy and Page's (2007) population multiplier. A second estimate of 181,646–239,473 NZFS was produced using stage-structured matrix models that projected previous pup production estimates forward to 2024. Combining the modelled abundance figure with Australia's NZFS population estimate (117,400; (Chilvers and Goldsworthy 2015), gives a range-wide abundance estimate for NZFS of 299,046–356,873.

Uncertainties around some existing pup production figures, and the methodologies' limitations, discussed below, highlight the need for more regular and methodologically consistent NZFS monitoring within New Zealand. Such monitoring would benefit both NZFS management and wider understandings of New Zealand's marine ecosystems (Donahoe et al. 2014; Elorriaga-Verplancken et al. 2016; Fulham et al. 2018).

4.1 | Minimum Nationwide Abundance Estimate

The minimum nationwide abundance estimate (131,338–168,269) is an increase on the most cited nationwide abundance estimate of 100,000 (Taylor et al. 1995; Harcourt 2001), but smaller than the 200,000 NZFS figure cited in Emami-Khoyi et al. (2018). It is worth remembering, however, that much of the data input for these earlier population estimates are guesstimates. While the new minimum nationwide abundance estimate presented here provides a baseline, it is unlikely to accurately reflect New Zealand's current NZFS abundance, as some pup production estimates are outdated—by up to 39 years at the most extreme, for the Antipodes Islands (Taylor 1992). Pup production can change dramatically over such periods—for example, between 1990 and 2023, pup production at Ōhau Point (Figure 1b), increased from three pups (M. Morrissey, unpublished data) to 2401 (± 99) (Hall et al. 2024). While it is possible that some of the colonies/regions projected forward in this study may have, in fact, declined since their most recent assessments, as has occurred on the WCSI (Roberts and Neale 2016), the preponderance of the evidence from NZFS population studies across New Zealand and Australia over several decades suggests population growth, or stabilisation following a period of growth, are the most likely trajectories for the colonies/regions modelled here (MacDiarmid and Lalas 2014; Shaughnessy and Goldsworthy 2015; Chilvers 2021; Hall et al. 2024).

Given the survey gaps at some sites and known growth rates from other NZFS colonies (Lalas and Harcourt 1995; Lalas and Murphy 1998; Lalas and Bradshaw 2001; Boren, Muller, and Gemmell 2006) (Table 2), the minimum nationwide abundance figure is likely an underestimate. Additionally, some NZFS colonies have never been formally assessed (Baird 2011), and others may not have been discovered. The former was true of several colonies in Fiordland prior to 2021 (Chilvers 2021), Kaikōura prior to 2023 (Hall et al. 2024), and Banks Peninsula prior to

2024 (Hall et al. 2025). Additionally, known sites where no reliable pup count data exist, such as the Auckland Islands, were excluded.

The use of uncalibrated direct counts (Table 2) is another reason for suspecting that the minimum abundance figure is an underestimate (Watson et al. 2009). As no appropriate calibration indices exist for most parts of New Zealand, this could not be avoided. Additionally, some sites (Table 2) were assessed through photographs taken from aircraft (Baker et al. 2009). Aerial counts can be an unreliable way to survey seal populations (Phillips and Mathews 2007) and may produce underestimates even relative to terrestrial direct counts (Stringell et al. 2014). Surveying from boats also tends to produce underestimates relative to terrestrial direct counts (personal observation). As no other data exist for these locations, these counts were included.

4.2 | The Density-Independent Projection Model

The results from the density-independent projections were also unsatisfactory. For example, a pup production estimate of 1,222,605 was projected for the Bounty Islands in 2024. This seems impossible, given that, at the last assessment (4380 pups in 1994), 50% of the available breeding habitat was already occupied (Taylor 1996).

Such overestimates emphasise the importance of including density-dependence in NZFS population projections. Like other species (Noad et al. 2019; Tanasovici et al. 2020), NZFS populations can grow exponentially (Boren, Muller, and Gemmell 2006), sometimes for extended periods (Shaughnessy and Goldsworthy 2015). However, this is not indefinite, and growth rates eventually slow (Roux 1987; Carey 1998; MacDiarmid and Lalas 2014). Thus, projections ignoring density-dependence are likely to overestimate NZFS abundance.

4.3 | The Density-Dependent Projection Model

When combined with the summed estimates from the unmodelled colonies, the density-dependent model produced a nationwide abundance estimate of 181,646–239,473. No recent nationwide abundance estimates are available for comparison, meaning its validity must be assessed in other ways.

The result of the sensitivity testing using C. Lalas' (unpublished) Moeraki Peninsula data found that the model projections substantially underestimated the true number of pups born in 2021 (Table 4). However, the results from the test using Te Oka Bay were closer to reality (Table 4). For both test sites, the 'high difference' probability weighting results, whereby the average scenario was given a 0.96 probability, and the remaining scenarios were each given a 0.01 probability, were the closest to reality. Calculating average annual pup production rates at the two test colonies helps explain why the Te Oka projection was relatively accurate, while Moeraki Peninsula was not. The Moeraki Peninsula projection ran over 20 years (2001–2021), during which the actual average annual exponential rate of increase in pup numbers (calculated as per Lalas and Murphy (1998) was 0.1. Over the 21 years (2003–2024) covered in the Te Oka test, the actual average annual exponential rate of increase in pup numbers was 0.08. The model, thus, failed to replicate the faster average growth rate at Moeraki compared to Te Oka. As such, if the colonies/regions projected in Table 3 experienced similar, lengthy periods of substantial year-on-year growth, these results could also be underestimates. Notably, MacDiarmid and Lalas (2014) state that the Otago/Catlins region, where Moeraki Peninsula is situated (Figure 1b) experienced particularly rapid NZFS recolonisation. As such, this growth rate may not have been replicated elsewhere in New Zealand. Local factors, such as food availability, likely influence NZFS population trajectories, meaning trends through space are not uniform (Boren, Muller, and Gemmell 2006). In addition, Roux (1987) showed that fur seal colonies typically take some time to enter a phase of rapid growth, thus if a colony takes longer to arrive at that phase, its overall growth will be slower. A factor that further complicates direct comparisons between colony growth rates is the concept of spillover breeding, whereby density-dependent factors at established breeding sites lead to new colonies being founded nearby (Bradshaw, Lalas, and Thompson 2000). Therefore, pup production increases at Te Oka Bay could have been higher than the 2003–2024 comparison suggests, but this breeding may have spilled over into neighbouring bays, and thus not been assigned to Te Oka Bay's 2024 total (Hall et al. 2025). Indeed, this seems likely, given that Te Oka Bay, in the years following the 2003 count of 84 pups, grew rapidly to 210 (2004) and then 301 (2005) (Boren, Muller, and Gemmell 2006), with the next estimate being 418 ± 1 in 2024, when several colonies in proximal bays were recorded for the first time (Hall et al. 2025).

Immigration could also engender varying NZFS population growth rates around New Zealand. NZFS recolonisation likely spread northwards from refugia colonies on the South Island's south-western coast (Dussex et al. 2016), with no North Island breeding recorded until 1991 (Dix 1993). As founders are more likely to establish new breeding sites close to existing ones (Bradshaw, Lalas, and Thompson 2000), immigration likely followed the same staggered northwards expansion. Therefore, colonies in southern areas of mainland New Zealand are likely to have consistently received immigrants at a faster rate, and thus to have grown faster than colonies further north. Indeed, much of the substantial annual population increases recorded in Otago colonies, such as Moeraki Peninsula (Figure 1b), has been attributed to immigration (Lalas and Bradshaw 2001; MacDiarmid and Lalas 2014), perhaps partly explaining the difference in the model test results.

Historic sealing records (Ling 1990), and notes made during previous assessments, provide other ways to analyse some of the model results. For example, the upper bound of the Bounty Islands pup production estimate (8575) seems reasonable, given that ca. 50% of the available breeding habitat was occupied when the last estimate was made (4380 in 1994) (Taylor 1996). In the intervening years, NZFS may have colonised the remaining habitat, with pup production approximately doubling. Additionally, between 1807 and 1809, ca. 53,500 NZFS skins were taken from the Bounty Islands (Ling 1990). As competition from fisheries and changed environmental conditions may mean that the Bounty Islands can

no longer support that many NZFS, a total projected population estimate of 28,229–29,224 ('high difference' scenario result) is not improbable.

Overall, the modelled projections should be treated with caution, due to the significant underestimation of Moeraki Peninsula's 2021 pup production. However, the model test results from Te Oka Bay, together with information available from other modelled locations, such as the Bounty Islands, suggests other projections may be realistic. If sensitivity tests were conducted on other colonies, it is likely that there would have been substantial diversity in the reliability of their respective results. This, again, is largely a result of the dearth of region-specific vital rate data for most of New Zealand's NZFS colonies.

Another limitation of the projection model is setting *nmax*. This argument provides simple density-dependence (Stubben 2020) and has been used previously in this capacity (Crain et al. 2019). Ideally, *nmax* would differ by site based on knowledge of local factors impacting NZFS population growth, including available breeding habitat (Boren, Muller, and Gemmell 2006), predation (Boveng et al. 1998), food availability and bycatch mortality (Roberts and Neale 2016; Pavanato et al. 2023), past disruptions (Hall et al. 2024), and anthropogenic impacts on the marine environment (Brock et al. 2013). However, very little such data exist for New Zealand's NZFS, and certainly not sufficient to apply a different, justifiable *nmax* to each projection. Thus, it was deemed best to apply two consistent *nmax* figures, based on knowledge of the respective sites. The impacts of *nmax* were greatest on the larger colonies/regions, and particularly prevalent on the 'high difference' runs, where the 'average' vital rate scenario had a probability of 0.96. For both Cascade Point and Yates Point, *nmax* (11,762) was reached in over 90% of the 'high difference' projection runs, and *nmax* (28,800) was reached in nearly 85% of the 'high difference' runs for Bounty Islands, and over 88% of 'high difference' runs for Stewart Island (Table 3). This stands to reason, given that these colonies/regions' populations were already substantial at the time of their respective most recent assessments and so should experience the limitations of density-dependence more frequently in the simulations (Roux 1987). However, it is not ideal that *nmax* had such a substantial impact on these results, since the selection of the two *nmax* values had limited support, and had the *nmax* ceiling been set higher, the results that were constrained by *nmax* (Table 3) would have also been greater. That said, there is some justification for the selection of these figures. Single colonies used the 11,761-population figure, based on Gooday's (2016) study at Ōhau Point near Kaikōura. Ōhau Point experienced particularly rapid pup production increases, growing at ca. 32% per annum between 2002 and 2005, and pups there likely have a buffer against low food supply periods, thanks to proximity to the highly productive Kaikōura Canyon (Boren, Muller, and Gemmell 2006). This may mean that Ōhau Point has some immunity to growth-restraining resource limitation that might, at times, limit pup production increases elsewhere in New Zealand (Boren, Muller, and Gemmell 2006). Importantly, NZFS abundance at Ōhau Point also appears to have largely escaped lasting negative impacts from the 2016 Kaikōura earthquake (Hall et al. 2024). At the time of their study, Bradshaw, Davis, Lalas, and Harcourt (2000) found that NZFS pups on the East Coast of the South Island, where both Ōhau Point and the Otago/Catlins Region are located (Figure 1b), were in generally better condition than those on the West. Of the nine colonies projected forward to 2024, five are on the West Coast, including the two (Cascade Point and Yates Point) where *nmax* was reached most frequently. Given the links between pup survival and condition in fur seals (Majluf 1992), and the possibility that the Kaikōura Canyon has promoted particularly rapid, and sustained growth rate at Ōhau Point (Boren, Muller, and Gemmell 2006), it is possible that the Cascade Point and Yates Point colonies have not surpassed Ōhau Point's population, thus rendering 11,761 a reasonable *nmax* to apply as an upper limit. The other two regions where *nmax* was reached in most of the 'high difference' runs (Stewart Island and the Bounty Islands) had already surpassed 11,761 (Table 2), meaning this could not be used as a population *nmax*. The 28,800 figure used as the regional *nmax* was derived from MacDiarmid and Lalas' (2014) study of the Otago/Catlins region (Figure 1b). NZFS recolonisation of this area was particularly rapid (MacDiarmid and Lalas 2014), and this region is also on the South Island's East Coast, where pups appear to be in better condition (Bradshaw, Davis, Lalas, and Harcourt 2000) and thus, potentially, have better survival rates than in other areas (Majluf 1992). As such, it was the best option for *nmax* for the remaining projected sites. The need for a ceiling for sites such as the Bounty Islands was demonstrated by the impossible pup production estimate of 1,222,605 projected for this region in 2024 by the density-independent approach.

Assigning probability weightings to the matrix selections was another difficult element of designing the methodology, given the lack of data. The main difference in the results generated by the 'high difference', 'median difference' and 'low difference' scenarios was in the standard deviation around the means. Consistently, the standard deviation was least for the 'high difference' scenario, and greater for the other two. This makes sense because, in the 'high difference' runs, the average scenario was being selected with a probability of 0.96, whereas the other two ('median difference' and 'low difference') had greater opportunity to vary. By presenting three sets of results from each projected colony/region, the uncertainty of the estimations is demonstrated.

Finally, stage-structured models inherently risk oversimplifying study species' ontogeny. This is likely here, as vital rates can vary substantially within the three stages prescribed. For example, prime breeding years for adult female NZFS are thought to be ages 8–13, sandwiched between ages of lower fecundity, potentially due to, initially, inexperience and, latterly, senescence (McKenzie et al. 2007). While this variation was captured in the adult fecundity data (SI 2), separate stages were not created, as there were insufficient corresponding survival data. Similarly, the juvenile age category was not further divided, despite evidence from other *Arctocephalus* spp. that post-weaners suffer higher mortality rates than older juveniles (Beauplet et al. 2005). The vital rates used came from studies of NZFS and other fur seal species (SI 2). Sharing vital rate data between taxonomically or ecologically comparable species is not unusual where such information is lacking (Kindsvater et al. 2018; Fleming et al. 2022); however, it is not ideal, as these inputs can clearly impact matrix projections. That said, similarities in vital rates between different fur seal species across large geographic areas have been noted (Wickens and York 1997), and this relative

homogeneity is evident in the vital rates selected for this study (SI 2), lending support to this approach.

4.4 | Management Implications

Understanding contemporary NZFS abundance has several important management implications. NZFS can act as marine ecosystem sentinels, due to their conspicuousness and elevated trophic position (Moore 2008; Bossart 2011). The usefulness of pinnipeds as sentinels has been demonstrated with threats including climate change (Elorriaga-Verplancken et al. 2016), pollutants (Taylor et al. 2018) and zoonotic diseases (Donahoe et al. 2014).

NZFS species management would also benefit from updated contemporary abundance estimates. As animals making regular use of two environments, NZFS face a complex range of threats, both anthropogenic and natural. In New Zealand, these include very high rates of bycatch (Pavanato et al. 2023), entanglement (Boren, Morrissey, Muller, and Gemmell 2006), human infrastructure (Hall et al. 2023), illegal killings (Department of Conservation 2022), fisheries competition (Roberts and Neale 2016), changes to the marine environment (Elorriaga-Verplancken et al. 2016) and oil spills (Mearns et al. 1999). Regular abundance estimates promote understandings of the cumulative risks of such threats on the species, and thus enable appropriate responses (Soykan et al. 2008; Kobayashi et al. 2014).

Regular NZFS population monitoring would also benefit understandings of climate change impacts on New Zealand's coastal species and ecosystems. NZFS risk habitat loss due to increases to global sea levels (Kovacs et al. 2012), which could lead to habitat inundation, as predicted for northern elephant seals (*Mirounga angustirostris*) in California (Funayama et al. 2013). Rising sea levels will likely act synergistically with storm surges to inundate larger quantities of Australian fur seal habitat more regularly (McLean et al. 2018), and, as some NZFS inhabit space-limited reefs and islets (pers. obs.), and other sites have been spatially squeezed by anthropogenic infrastructure (Hall et al. 2024), sea level rise may force site abandonment.

4.5 | Future Monitoring of NZFS in new Zealand

The largely opportunistic monitoring of New Zealand's NZFS populations since Wilson (1981) has engendered lasting uncertainty over the species' abundance. Notably, regions at both extremes of NZFS' New Zealand range have received less attention than central areas such as the WCSI (Roberts and Neale 2016) and Otago/Catlins (MacDiarmid and Lalas 2014) (Figure 1). Estimates from New Zealand's subantarctic islands are between 27 years (Snares Islands; Carey 1998) and 39 years old (Antipodes Islands; Taylor 1992), and as previous estimates from some of these islands would make up a significant proportion of the total New Zealand NZFS population estimate (Table 2), they should be prioritised for future surveys.

Similarly, the Stewart Island region was last assessed 12 years ago, when only one island was evaluated (Watson et al. 2015). Although Chilvers (2021) assessed several colonies within lower Fiordland, much of this region has never previously been surveyed. Fiordland colonies likely provided refugia from which recolonisation began (Dussex et al. 2016), meaning that unknown, and potentially large, colonies possibly exist there today.

A regularised program of NZFS monitoring is strongly advised for New Zealand. The benefits of such approaches have been demonstrated on the WCSI (Roberts and Neale 2016), and with Australian fur seal, where switching from ad hoc monitoring to a co-ordinated approach meant trends could be more reliably detected (McIntosh et al. 2018). Such monitoring would also enable detection and study of unusual mortality events, as noted at Ōhau Point in 2024 (J. Weir, unpublished data). The improvements to Australian fur seal monitoring (McIntosh et al. 2018) involved a range wide census of the species. While, ideally, this would be replicated for NZFS in New Zealand, practically, this is unlikely. With many endangered species, some of which are the subject of resource, personnel and time-intensive conservation programs (Digby et al. 2023; Manno and Young 2023; Agnew 2024), currently, New Zealand is unlikely to be able to support a nationwide NZFS monitoring program. This is exacerbated by the extreme difficulty of accessing NZFS colonies in remote locations, such as those on some of New Zealand's subantarctic islands.

As such, the next-best, and most realistic, approach to future NZFS monitoring in New Zealand should comprise regular assessments of several baseline sites, using consistent methodologies, to enable trend detection. Given the value of long-term data sets for population level studies (Clutton-Brock and Sheldon 2010), it is suggested that these baseline sites should include Kaikōura, the Otago/Catlins and the three colonies on the WCSI already monitored regularly (Taumaka, Cape Foulwind and Wekakura Point). Kaikōura, Otago/Catlins and the three WCSI colonies currently represent the most complete records of NZFS colonies in New Zealand (Figure 2), and the WCSI is also a priority due its declining pup production rate (Roberts and Neale 2016). Additionally, Cape Palliser should be included among the regularly monitored sites, as it is the only substantial NZFS colony on New Zealand's North Island and is proximal to the busy Cook Strait fishing and shipping channel. Given that the records for many of these sites include counts around the time of their respective origins, not only would ongoing assessment enable future trend detection, it may also reveal insights into the impacts of density-dependence as the colonies age (Bradshaw, Lalas, and Thompson 2000). As WCSI colony monitoring currently occurs every 2–3 years (Department of Conservation 2023), and because large-scale longitudinal surveys can be expensive and resource intensive, the same timeframe is suggested as a minimum for the monitoring at these other baseline sites. Consistent survey methodologies are important and will likely comprise direct counts and mark-recapture (Chilvers 2021). Importantly, at least one site per region should be assessed by both mark-recapture and direct counts to enable calibration index calculation (Watson et al. 2009). It is also recommended that updated abundance estimates are made for New Zealand's subantarctic islands, given the risk that these sites act as a conduit to mainland New Zealand for HPAI H5N1 (Gartrell et al. 2024). The difficulties and expense involved in accessing these sites mean they are unlikely to be monitored regularly. At the same time as baseline site monitoring occurs, it is suggested

that vital rate data are collected from the northernmost (Cape Palliser) and southernmost (Otago/Catlins) of the regularly assessed sites. These data are key to constructing lifetables for New Zealand's NZFS, which would benefit future population modelling. Here, Goldsworthy and Page's (2007) multiplier was used to convert pup production counts into population estimates. However, this multiplier derives from a study in South Australia (Goldsworthy and Page 2007) making it suboptimal for use in New Zealand, as vital rates can vary spatially (Raithel et al. 2007).

5 | Conclusion

This study highlights the current difficulties of estimating New Zealand's nationwide NZFS abundance, largely due to ad hoc population monitoring in most regions since Wilson (1981), large gaps in the record, and a lack of data on important parameters such as vital rates and the impacts of density-dependence on population dynamics. The minimum nationwide population abundance of 131,338–168,269 NZFS calculated here is likely a significant underestimate, based on knowledge from recent regional surveys (MacDiarmid and Lalas 2014; Chilvers 2021; Hall et al. 2024). The second estimate of 181,646–239,473 NZFS, produced using stage-structured matrix projection models, may also be an underestimate; however, projections for some regions, such as the Bounty Islands, appear to be reasonable.

A regular program of NZFS monitoring is strongly suggested in New Zealand to benefit the management NZFS and enable their use as a sentinel for the health of New Zealand's marine environments (Elorriaga-Verplancken et al. 2016).

Author Contributions

Alasdair A Hall: conceptualisation, investigation, writing – original draft, methodology, validation, visualisation, writing – review and editing, formal analysis, project administration, data curation, resources, software. **B Louise Chilvers:** conceptualisation, investigation, methodology, validation, writing – review and editing, project administration, supervision, resources. **Jody Suzanne Weir:** conceptualisation, methodology, writing – review and editing, supervision, project administration.

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Ethics and Permit Approval Statement

No ethics permissions or permits were required to produce this study.

Conflicts of Interest

The authors declare no conflicts of interest.

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.