Marine mammal population decline linked to obscured by-catch

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Declines of marine megafauna due to fisheries by-catch are thought to be mitigated by exclusion devices that release nontarget species. However, exclusion devices may instead conceal negative effects associated with by-catch caused by fisheries (i.e., unobserved or discarded by-catch with low postrelease survival or reproduction). We show that the decline of the endangered New Zealand (NZ) sea lion (*Phocarctos hookeri*) is linked to latent levels of by-catch occurring in sub-Antarctic trawl fisheries. Exclusion devices have been used since 2001 but have not slowed or reversed population decline. However, 35% of the variability in NZ sea lion pup production is explained by latent by-catch, and the population would increase without this factor. Our results indicate that exclusion devices can obscure rather than alleviate fishery impacts on marine megafauna.

by-catch | exclusion devices | fisheries management | megafauna | recovery

Global fisheries, particularly trawl fishing, have steadily expanded since the 1970s (1). Industrial fishing offers subsistence and prosperity for many communities (2) but poses risks to marine species, their habitats, and whole ecosystems (3). By-catch, the unintentional catch of nontarget species, is a global conservation problem for marine megafauna (4) such as cetaceans (5), turtles (6), and pinnipeds (7–9). For trawl fisheries, exclusion devices are an increasingly common tool to release nontarget species from nets without substantially affecting commercial landings (4). However, exclusion devices are contentious because they may bias by-catch estimates (10) and cause unknown postrelease mortality or reproductive failure due to injuries sustained during capture and release (11). Crucially, despite decades of use, there is scant empirical evidence to verify whether exclusion devices improve the population growth of by-caught species. Most analyses focus on changes in reported by-catch numbers (e.g., refs. 9, 12, 13, and 14), compliance levels of fishers (e.g., refs. 15 and 16), or simulated model predictions of population responses (e.g., refs. 17, 18, 19, and 20). In this study, we empirically analyze whether exclusion devices contribute to recovery or decline of the endangered New Zealand (NZ) sea lion (*Phocarctos hookeri*) (21).

Since 1998, the main subpopulations of NZ sea lions, which breed in the sub-Antarctic Auckland Islands (50°S, 166°E) (Fig. 1), have declined by 48% (22, 23) (Fig. 2), leading to a current total population size of 11,767 [95% Credible Interval (CrI): 10,790–12,923] sea lions (23). Hypotheses for the NZ sea lion decline include (*i*) neonatal mortality of pups due to bacterial epidemics, (*ii*) emigration from breeding sites, (*iii*) predation by great white sharks (the sole predator), (*iv*) genetic effects of overharvest during historic sealing, (*v*) a carrying capacity overshoot, (*vi*) environmental change, (*vii*) contaminants, (*viii*) prey depletion by fisheries, and (*ix*) direct by-catch of sea lions in trawl fisheries (24). Most hypotheses have been discounted due to NZ sea lions' philopatry to breeding sites, genetic diversity, historical population sizes, and contaminant levels in blubber (24, 25). Shark predation is considered poorly understood but an unlikely cause of the NZ sea lion population decline (24, 25). The pup disease hypothesis can be discounted because analyses of mark–recapture time series have not revealed an increase in

overall pup mortality during epidemic years, suggesting compensatory mortality (26), and elasticity analysis indicates a low response of the NZ sea lion population growth rate to pup survival compared with survival of adult females (27). In this paper, we analyze the hypotheses of prey depletion, environmental change, and fisheries by-catch using long-term time series of pup census data from the Auckland Islands subpopulations.

The main subpopulations of NZ sea lions that breed in the Auckland Islands contain 70% of the overall population (21) and are distributed among three breeding sites—Sandy Bay (Enderby Island), Dundas Island, and Figure of Eight Island (22, 23) (Fig. 1). Female NZ sea lions from the Auckland Islands usually breed between December and January at their natal sites (28) from which they predominantly forage northwest (individuals from Sandy Bay) and southeast (individuals from Dundas Island and Figure of Eight Island) of the Auckland Islands (29). Within these same areas, a trawl fishery for arrow squid occurs—the Auckland Islands squid fishery—which temporally overlaps with the first 4 mo of a 9-mo lactation period (30) between February and April (12). Pup production, considered a reliable index for the population dynamics of pinnipeds (31), has been estimated for NZ sea lions at the Auckland Islands through a 2-d mark–recapture program immediately following pupping in January in each year 1995–2016 (22, 23). Mortality or reproductive failure of mature NZ sea lions caused by the squid fishery will therefore directly impact the number of pups born—and therefore the pup production estimate—in the breeding season of the following year (30). We focused our analysis on pup production of the two principal subpopulations (Sandy Bay and Dundas Island; Figs. 1 and 2), together accounting for 97% (status 2016) of pup production at the Auckland Islands (22).

Significance

Declines of marine megafauna such as turtles, pinnipeds, and whales are often related to mortality caused by capture or entanglement in fisheries gear. To help recovery of these species, trawl fisheries have implemented exclusion devices that release nontarget species. Despite decades of use, there has been no empirical evaluation of whether or not exclusion devices aid recovery of affected species. Long-term data on the endangered New Zealand sea lion and a trawl fishery in the Southern Ocean indicate that exclusion devices have paradoxically contributed to ongoing decline rather than recovery. Exclusion devices obscure the postrelease impact of elevated mortality or reproductive failure; meanwhile, reduced levels of reported by-catch may mislead management that continued decline is not associated with fisheries.

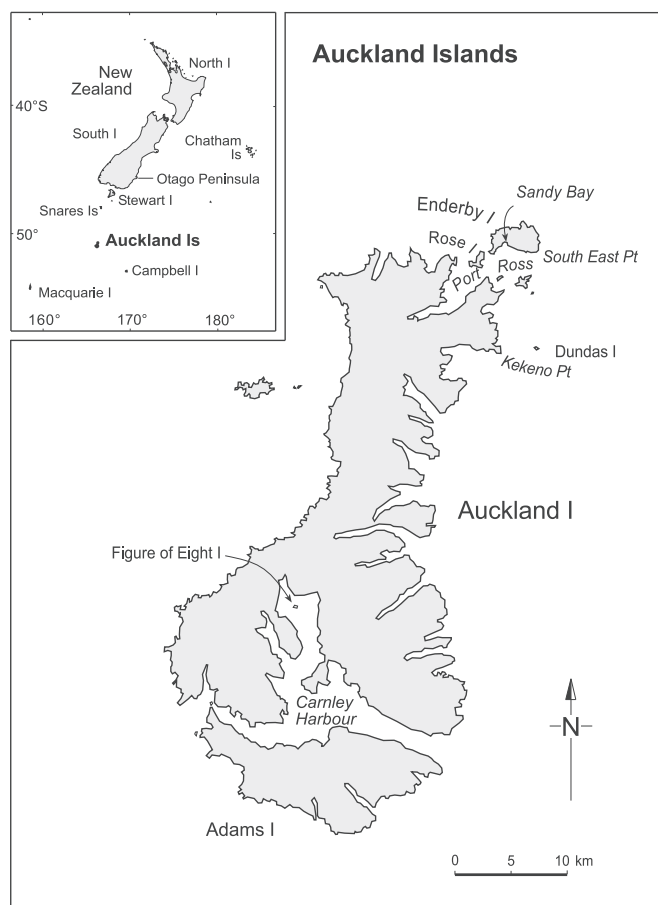POPULATION BIOLOGY

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Fig. 1. Main breeding area (Auckland Islands) of NZ sea lions with currently active subpopulations Sandy Bay (Enderby Island), Dundas Island, and Figure of Eight Island.

Sea lion exclusion devices (SLEDs) were first introduced into the Auckland Islands squid fishery in 2001 and were comprehensively used since 2004 (32). SLEDs consist of a grid that prevents sea lions from entering the end of the net and instead directs them to an opening at the top of the net (30). Since 1996, fishing vessels in the Auckland Islands squid fishery have been partially monitored by observers to estimate by-catch for the entire fishing fleet (33). We compiled two fishery variables for the Auckland Islands squid fishery: (*i*) the by-catch rate (BR) in year *t* and (*ii*) the interaction rate (IR) in year *t* (*SI Appendix,* Fig. S1 *A* and *B*). The BR is the estimated number of NZ sea lion captures that were landed on deck per unit fishing effort (a single tow), whereas the IR is the estimated total number of NZ sea lion captures per unit fishing effort (i.e., those landed on deck plus those that were ejected through SLEDs dead or alive with unknown postrelease survival and reproductive success) (see *Methods*). The hypotheses of prey depletion via environmental change or fisheries as well as carrying capacity overshoot imply density-dependent mortality or reproduction, and so we also tested for density dependence in the population growth rate. To account for variability in environmental conditions in general and resource depletion either naturally or due to commercial fishing, we also fitted the model to direct and lagged (by 1 y) covariates of sea surface temperature (SST) anomaly and catch of arrow squid per unit fishing effort (*SI Appendix,* Fig. S1 *C–F*). The SST anomaly is considered to integrate several environmental conditions such as prey abundance and prey distribution (for example, the Pearson correlation coefficient between squid

catch per unit fishing effort and 1-y lagged SST anomaly is −0.516), which could affect pup production in pinnipeds (34, 35), and arrow squid has been identified as a consistent prey species for NZ sea lions (30).

Results

Using a Bayesian approach, we fitted first-order autoregressive process [AR(1)] models that represent Gompertz population growth and that have previously been applied to time series of other sea lions (36) as well as several other taxa (37, 38). The model can be expanded into a multivariate form to simultaneously model multiple populations (36) and can also be expanded into a state-space process to separate variance of observed population trends into process error and observation error (38). The model is $log(n(i,t)) = log(n(i,t\text{-}1)) + u + d*D(t\text{-}1) + w(t)$, where $log(n(i,t))$ is the (natural) log-transformed pup production of subpopulation *i* in year *t*, *u* is the population growth rate, and *d* is the effect size in response to covariate *D*. $w(t)$ is a multivariate Normal distribution with mean zero, temporal SD (σ) of pup production, and the temporal correlation between both subpopulations (ρ) described by the variance–covariance matrix *Q* [i.e., $w(t) \sim MVN(0, Q)$]. The parameters *u*, *d*, and σ are the same for both subpopulations (*SI Appendix*). To include observation error of pup production, we modeled the observed pup production as being normally distributed with year-specific SDs that were supplied as data inputs and derived from the mark–recapture analysis used to estimate the pup production data (see *Methods* and *SI Appendix*). A preliminary exploration of the model structure (*SI Appendix*) suggests that NZ sea lion population dynamics were density-independent over the last two decades, which is consistent with a current population size that is an order of magnitude lower than the estimated historic population size (39). We additionally fitted the model without covariates to estimate the total temporal variance (σ^2_{total}) of pup production.

The model without covariates estimates a population growth rate (*u*) of −0.019 with 95% CrI: −0.079 to 0.039, reflecting currently a 74% risk of continued population decline (i.e., the proportion of posterior samples for *u* smaller than zero). The temporal correlation coefficient (ρ) of 0.721 (95% CrI: 0.442–0.870) indicates that both subpopulations have behaved similarly. The only covariate negatively correlated with pup production was the fishery IR (*d* = −4.195, 95% CrI: −6.280 to −2.132), explaining 35% of the total variance (σ^2_{total} = 0.022, 95% CrI: 0.014–0.040). This negative correlation remained when we considered reported 95% extremes of the confidence limits for IR (*SI Appendix,* Fig. S8), and in this case, IR explained 43% of total variance. To underpin our results, we conducted Gibbs variable selection (40) for the model with IR as covariate in various combinations with other predictor variables assessed here, which estimated a 0.95 or larger posterior model probability to only include IR in the model (*SI Appendix,* Table S2). Including an interaction between lagged SST anomaly and catch of arrow squid resulted in a 0.84 probability for including only IR (note that probabilities are distributed across many combinations when model interactions are included; see *SI Appendix,* Table S2). Furthermore, this result was not affected when adding observation effort (in the Auckland Islands squid fishery) as an interaction with IR (*SI Appendix,* Table S2). Models considering any of the other predictor variables without IR had close to zero probability (*SI Appendix,* Table S2). Similarly, there existed no support to include BR into the model (probability 0.06–0.08; see *SI Appendix,* Table S2). Predicted pup production, based on estimated parameters from the model including IR (*SI Appendix*), was consistent with observed time series of pup production (Fig. 2).

In the absence of fishery by-catch (i.e., when IR in the fitted model is set equal to zero), the model indicates that the NZ sea lion population would increase at rate *u* = 0.214 (95% CrI: 0.086–0.343). This is further emphasized by the empirical observations of annual
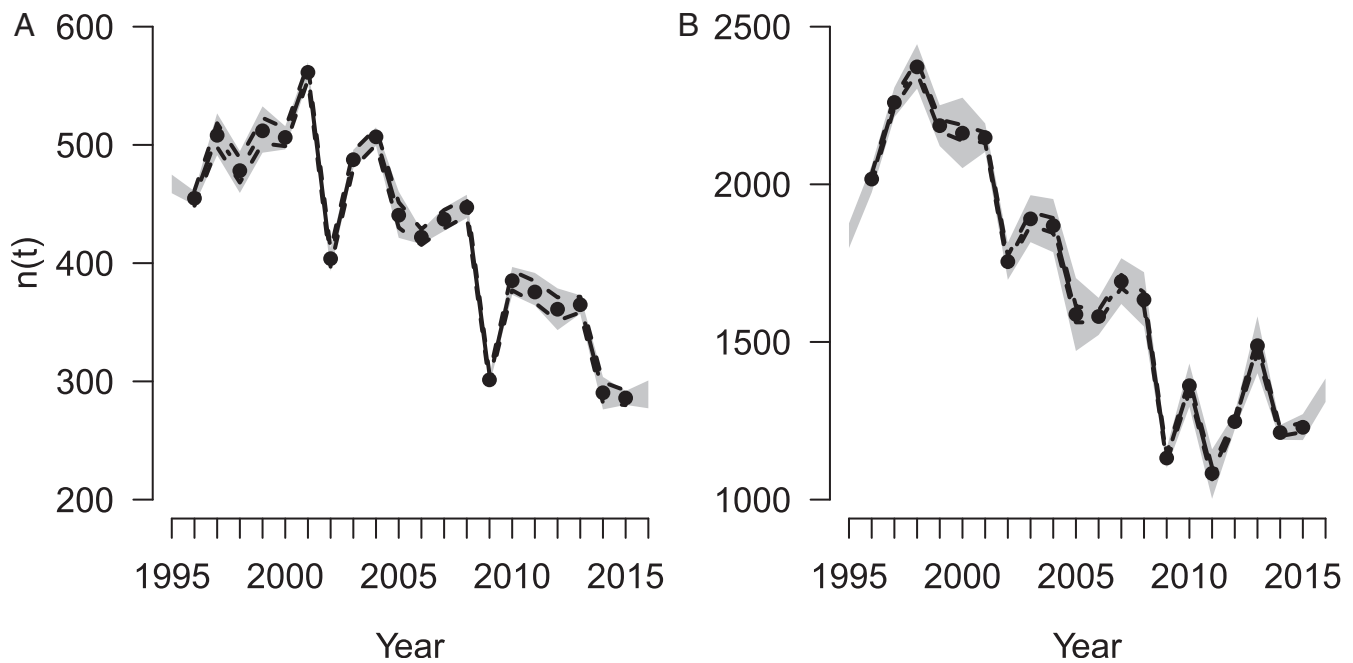
Fig. 2. Observed and predicted pup production for NZ sea lion subpopulations at Sandy Bay (*A*) and Dundas Island (*B*); gray area: 95% confidence interval of observed pup production (based on Petersen estimate) between 1995 and 2016; lines: predicted pup production based on the model with covariate IR (black dots: median; black dashed lines: 95% CrI) between 1996 and 2015.

growth rates $[log(n(t)/n(t-1))]$ for both subpopulations, which are negatively correlated with IR (Fig. 3 *A* and *B*; $t = -4.317$, df = 17, *P* value = 0.000468). In contrast, all other covariates we considered had negligible explanatory power of NZ sea lion population trends. BR and the environmental covariates explained each between -4% (i.e., in some cases σ^2 was negatively biased to σ^2_{total}) and 0% of the total variance. The mortality parameter (*d*) from the BR was -0.893 (and -0.725 when 95% confidence limits of BR were included), but the 95% CrI overlapped zero (*SI Appendix*, Fig. S8). The effect sizes for the environmental covariates were all close to zero (*SI Appendix*, Fig. S8). Estimated effect sizes as well as the Gibbs variable selection were not affected by the choice of prior distributions (*SI Appendix*, Figs. S6, S7, and S13–S16 and Table S2).

To further evaluate the sensitivity of our results to uncertainty in the IR covariate caused by the initial introduction of SLEDs in 2001 and comprehensive SLED use since 2004 (32), we also fitted the models to time series truncated at years 2001 through 2005. For these sections of the time series, the IR is equal to the BR up to 2001, but they then diverge by 2004 when SLEDs were widely implemented (Fig. 3*C*). None of these scenarios altered the estimated effects of IR on NZ sea lion population dynamics (*SI Appendix*, Fig. S11), whereas the correlation between pup production and BR eroded as the length of the time series increased (i.e., where IR and BR diverge) (*SI Appendix*, Fig. S12). These analyses of time series scenarios further reinforce the conclusion that it is the fishery interaction (IR) rather than landed by-catch (BR) that is influential for NZ sea lion population growth.

Discussion

Our results provide population-level empirical analysis of the effectiveness of exclusion devices for protecting an endangered marine megafauna from fisheries by-catch in a situation of high compliance. The results indicate that exclusion devices designed and implemented for the endangered NZ sea lion have likely failed to reverse population decline and instead contribute to imperilment by concealing mortality or reproductive failure caused by by-catch. There are other situations where exclusion

devices have been ineffective, but those are mainly due to noncompliance among fishers to install or correctly operate them, such as marine turtles (41). Many predictions exist from simulation models that marine megafauna, including NZ sea lions, should respond positively to by-catch reductions (e.g., refs. 15, 17, 18, and 20) and many empirical analyses indicate exclusion devices have reduced megafauna BRs (e.g., 13 and 42). The missing links in this body of work are that analyses do not account for postrelease mortality and/or failed reproduction, and the model predictions for improved population growth have not been empirically tested. Our analysis provides an empirical test of those predictions, and contrary to expectation, our results indicate that, under conditions of high compliance, exclusion devices may contribute to population decline rather than aid recovery.

It is difficult to determine the fate of individuals released through by-catch mitigation devices. Our results indicate that live NZ sea lions that are released from SLEDs suffer elevated subsequent mortality or reproductive failure, which would likely be caused by injuries sustained during collision with the exclusion grid or temporary entanglement (43). Autopsies of purposely retained individuals are inconclusive, because it is not possible to differentiate between trauma-related lesions, preexisting conditions, or artifacts owing to carcass freezing (44). It was further not possible to observe the fishery interaction via underwater video footage due to poor visibility at fishing depths (44). Moreover, data to simulate concussion probabilities of NZ sea lions that collide with the grid had to be derived from human crash tests and fur seals in Australian fisheries (44). Clearly, more research is needed on postrelease survival and reproduction to avoid underestimating population-level impacts of by-catch (45).

While we have focused on the Auckland Islands squid fishery, there also exist several, partially monitored, trawl fisheries (without SLEDs) that operate adjacent to the Auckland Islands (12, 33). Although those fisheries do not strongly overlap with female NZ sea lions' foraging ranges, they may nonetheless contribute a small amount of fishery mortality to NZ sea lion population dynamics (29, 30). There are also of course multiple other nonfishery factors that affect NZ sea lion demography, and
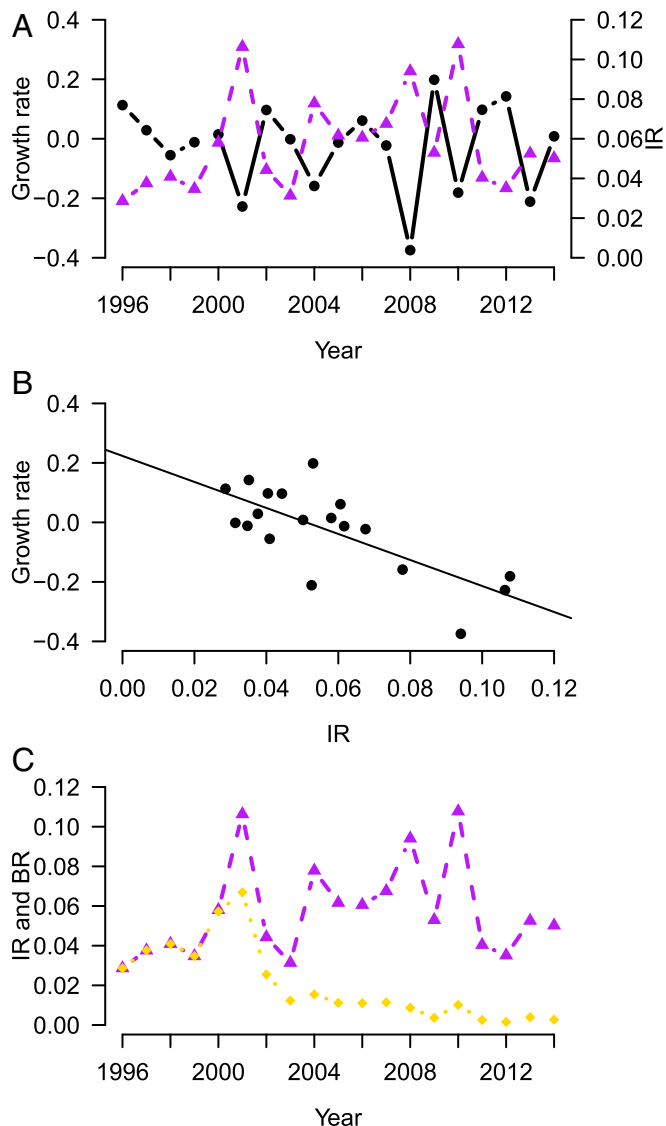
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Fig. 3. NZ sea lion fishery interactions compared with instantaneous population growth rate [i.e., *log[n(t)/n(t − 1)]*] of pup production (based on mean estimates): (*A*) Instantaneous population growth rate (black solid line) from year *t − 1* to *t* (*x* axis shows year *t − 1*) compared with IR (purple dashed line) in year *t − 1*. (*B*) Instantaneous population growth rate plotted against IR (solid line: slope of linear regression fit; see *Results*). (C) IR (purple dashed line) and BR (yellow dotted line) before SLED use (before 2001) and after SLED use (2001–2014).

we do not claim that fishery impact (i.e., mortality and/or reproductive failure) is the sole driver of NZ sea lion population dynamics. The nine hypotheses for the NZ sea lion population decline reviewed in the introduction may well affect NZ sea lion population dynamics, but by process of elimination, our results and the literature (24, 25) leave the fishery IR as the only hypothesis that can explain the ongoing decline of NZ sea lions. Overall, that 35% of the total variance in pup production is explained by IR alone indicates that the impact from the squid fishery is likely a key driver of the NZ sea lion decline, and importantly, this is a factor that is amendable to management intervention.

One alternative hypothesis for the NZ sea lion decline that is not mutually exclusive of fishery by-catch, and is currently a focus of NZ sea lion management (46), is neonatal mortality arising from bacterial epidemics of newborn to 2-mo-old pups that

occurred in 1998, 2002, and 2003 (47). The time series we have analyzed here are not suitable to test this hypothesis because any increase in pup mortality from the epidemics would be expressed in pup production time series over a 4- to 7-y distributed lag, which is the age at first reproduction for female NZ sea lions (48), causing any impact of the epidemics to widely overlap and occupy most of the time series length. However, another more detailed analysis of the age-structured mark–recapture time series data that exist for these populations has not revealed an increase in overall mortality of pups over their first year of life in association with the epidemics, indicating that disease-associated mortality is likely compensatory for pups (26). Further, even if epidemics affect overall pup survival (i.e., disease-induced mortality is not compensatory), the population-level effects of epidemics are likely to be small relative to by-catch impacts because elasticity analysis of NZ sea lion population growth has indicated a low response to pup survival compared with survival of adult females (27).

Our results also indicate that predictions from the models often used to inform modern fisheries and conservation management—complex integrated population models that have dozens to hundreds of parameters—can be diametrically opposed to observed outcomes. For NZ sea lions, the models currently used for management indicate that by-catch of NZ sea lions is not a major factor in their continuing decline (49, 50). In contrast, our statistical analysis of NZ sea lion abundance time series provides empirical evidence that fishery interactions are likely a primary cause of NZ sea lion decline. This discrepancy likely occurs because management models incorrectly assume high survival and reproductive rates of individuals ejected from SLEDs as well as structural inconsistencies such as density dependence in NZ sea lion survival (49) when there is no evidence for such effects (39). The fact that we found no evidence of food limitation (i.e., squid prey availability and/or SST anomaly) further underpins that the current NZ sea lion population dynamics are not density-dependent. Clearly, by-catch of adult females requires particular attention in NZ sea lion management, but this is not the current priority of NZ sea lion conservation management.

Empirical evidence of population recovery in response to conservation actions are relatively rare. Examples include positive population responses of African wildlife to policy that supports antipoaching programs (51), improved population trends of European birds due to several international policy interventions (52), recovery of Hawaiian green sea turtles after protection from human exploitation (53), and rebuilding of biomass of depleted fish stocks in response to management (54). For marine megafauna, Gormley et al. (55) found (for the first time) improved survival of Hector's dolphins (*Cephalorhynchus hectori*) due to mitigated by-catch via marine protected areas (MPAs). In contrast, Australian sea lions (*Neophoca cinerea*) continue to be at risk for population decline despite several management efforts, such as the implementation of a MPA to mitigate by-catch in shark gillnets (56). For Australian fur seals (*Arctocephalus pusillus doriferus*), unobserved mortality owing to interaction with fishing gear remains a key uncertainty (10). Overall, for the case of marine megafauna, there is scant empirical evidence to support the conservation value of properly implemented by-catch exclusion devices, and our results highlight the need for more extensive retrospective empirical analyses of population responses to exclusion devices.

Our findings indicate that the endangered NZ sea lion continues to decline due to fishery impacts that have been obscured by the implementation of exclusion devices that release sea lions with poor prospects for postrelease survival and/or reproduction. It is therefore insufficient that the efficacy of exclusion devices in general be evaluated by the extent of by-catch reduction (e.g., ref. 13) or through simulated model predictions of population

responses, as is often done (e.g., refs. 17, 19, 50). Rather, evaluations should be made in terms of empirically demonstrated population responses to by-catch and its mitigation. More broadly, our results imply that the common belief that exclusion devices in fisheries gear serve to protect marine megafauna from by-catch mortality may be false. Instead, exclusion devices may contribute to declines of marine megafauna by obscuring the impacts of by-catch mortality and reproductive failure, which can thereby forestall the design and implementation of alternative recovery strategies.

Methods

Data—NZ Sea Lion Abundance (Pup Production). The breeding season (i.e., mating and pupping) of NZ sea lions at the Auckland Islands spans from early December to early January the following year. The mean pupping date is December 26 or 27 (57), and most pups are born by January 2 (58). Here, we refer to the second year of the breeding season (e.g., 1997 refers to December 1996 until January 1997). For the period from 1995 to 2016, pup production estimates are based on mark–recapture experiments taking place at slightly variable dates between January 15 and January 21 at both subpopulations (22, 23). Pups were temporarily marked evenly across the breeding area and recaptured by three observers over a period of 2 d. These experiments occurred after pupping ceased and before pups disperse away from their natal birth beach (58, 59). The estimate for total pup production is based on a modified Petersen estimate (60). We calculated the mean Petersen estimate and SDs (to model observation error) from raw mark–recapture data for pup production estimates given in Childerhouse et al. (22) and previous reports (*SI Appendix*). The data used in this study were collected during a long-term study and permission for handling and capture of newborn NZ sea lion pups (*P. hookeri*; males and females) was obtained from the New Zealand Department of Conservation Animal Ethics Committee under the Animal Welfare Act 1999.

Data—Covariates. The NZ fishing year spans the dates October 1 to September 30 in the next year, and the Auckland Islands squid fishery mainly operates between February and April. Here, we refer to the second year of the fishing season (e.g., 1997 refers to October 1, 1996 until September 30, 1997). Within the Auckland Islands squid fishery, between 13% and 99% (mean: 41%; SD: 24) of annual fishing effort (effort is measured in number of tows) has been observed from 1996 to 2014 (12, 33) (*SI Appendix*, Fig. S2). Our preliminary analysis showed that our results are not influenced by the variability in observation effort (*SI Appendix*). During this time period, observed NZ sea lion by-catch ranged from 0 to 39 individuals (12, 33). To estimate the NZ sea lion by-catch and interactions in the Auckland Islands squid fishery (i.e., per unit effort in each year), Abraham et al. (12) fitted a Bayesian generalized linear model, including the following covariates: the distance to the breeding colony, tow duration, subarea for fishing, and whether a SLED was used (12). Estimates for by-catch on the observed fishing effort were then extrapolated to the unobserved fraction (12). Between 1996 and 2014, mean estimates for by-catch ranged from 2 to 140 (95% CrI ranged from 0 to 222) individuals, and estimated mean interactions were between 14 and 202 (95% CrI ranged from 2 to 535) individuals (12, 33).

To be clear, by-catch is the estimated number of NZ sea lions captured and landed on deck per fishing effort in year *t*, whereas the interaction is the estimated number of NZ sea lions that (*i*) were landed on deck plus (*ii*) those released through SLEDs with unknown fate (12) per fishing effort in year *t*. These estimates for by-catch and interactions do not distinguish between males and females, juveniles and adults, or NZ sea lions captured in different Auckland Islands squid fishing areas (12). We transformed these estimates for total by-catch and interactions into the BR (*SI Appendix*, Fig. S1A) and IR each year (*SI Appendix*, Fig. S1B), respectively, by dividing each estimate by the total fishing effort in the corresponding year. These covariates then represent the impact of a single unit of fishing effort on pup production, which includes factors such as variation in tow duration (12). Reported fishing effort and estimates for by-catch and interactions for the years 1996–2013 were taken from table B-80 in Abraham et al. (12), and the year 2014 was updated with estimates reported in table 3.5 in a technical report by the NZ Ministry for Primary Industries (33).

In addition to fishery variables, we considered two environmental variables that were publicly available and that may affect pup production: **SST_anomaly** (*SI Appendix*, Fig. S1C): This covariate provides annual SST anomalies for the Auckland Islands region (50°S, 166°E). SST data were available for the years 1870–2015. SST anomalies were calculated as follows: (*i*) For each year between 1870 and 2015, the monthly mean SST was

calculated. (*ii*) From *i* total monthly mean SSTs (i.e., 12 mean SSTs) were derived. (*iii*) The SST anomaly for all months in any year was calculated by subtracting *ii* from *i*. The annual SST anomalies were calculated by averaging monthly SST anomalies in *iii* over the austral year (i.e., July to June). The analysis considered SST anomalies between the years 1995 and 2015. SST data were based on Rayner et al. (61) and were downloaded at www.metoffice.gov.uk/hadobs/hadisst/. **SST_anomaly_m1** (*SI Appendix*, Fig. S1D): SST anomaly in the previous year. See description for SST_anomaly on how this covariate has been calculated. The analysis considered SST anomalies between the years 1995 and 2015. **CPUE_squid** (*SI Appendix*, Fig. S1E): This covariate was calculated for the Auckland Islands squid fishery as kg of caught squid in year *t*/total number of tows in year *t*. The analyzed time period for CPUE_squid ranged from 1995 to 2012. Data were requested by Bruce Robertson through the NZ Ministry for Primary Industries under the Official Information Act 1982. **CPUE_squid_m1** (*SI Appendix*, Fig. S1F): Same as CPUE_squid but for the previous year. The analyzed time period for CPUE_squid_m1 ranged from 1995 to 2013.

Note that the length of the analyzed time series for pup production varied depending on the time period available for each covariate (e.g., if the final year for a covariate was 2012, then we analyzed pup production until the year 2013). The covariates BR and IR were centered to the mean of corresponding time series [e.g., *BR(t) − mean(BR)*], and the model predictions with IR set to zero were based on *0 − mean(IR)*. CPUE_squid and CPUE_squid_m1 were additionally scaled on the SD [e.g., *[CPUE_squid(t) − mean(CPUE_squid)]/sd(CPUE_squid)*].

Model. We began by fitting a first-order autoregressive [AR(1)] state-space model of population dynamics that is derived from the Gompertz growth model and is commonly used for analyzing time series of animal abundances (including other sea lion species). The model is:

$$\log(n(i, t)) = \log(n(i, t\text{-}1)) + u(i) + w(t), \quad [1]$$

where *log(n(i,t))* is the (natural) log-transformed pup production of subpopulation *i* in year *t*, *u(i)* is the mean trend or population growth rate of subpopulation *i*, and *w(t)* is a multivariate Normal distribution with mean zero, subpopulation-specific variances, and temporal correlation described by the variance–covariance matrix *Q* [i.e., *w(t) ~ MVN(0, Q)*] (*SI Appendix*). The state-space structure of the model is such that the observed number of pups, on real scale, in any year *t* at subpopulation *i* (*y(i,t)*) was modeled as a normally distributed random observation process (38):

$$y(i, t) \sim N(n(i, t), \sigma_y), \quad [2]$$

where σ_y is the year-specific SD of observed pup production in each year 1996–2016, which has been supplied as input data to the model (*SI Appendix*). Preliminary analyses indicated the population growth rates and variances between both sites were equal and that population dynamics were density-independent (*SI Appendix*). We therefore proceeded with a simpler model:

$$\log(n(i, t)) = \log(n(i, t\text{-}1)) + u + d * D(t\text{-}1) + w(t), \quad [3]$$

where *d* is the effect size in response to covariate *D(t −1)*, *u* a single growth rate for both subpopulations, and *w(t)* is comprised of a temporal correlation coefficient and the same variance for both subpopulations. The model was fitted in a Bayesian framework implemented in JAGS (62). We used a burn-in of 80,000 iterations followed by another 80,000 iterations, and posterior samples were taken with a thinning interval of 6. Model convergence was assumed if the potential scale reduction factor for each parameter was less than 1.1 (63) (the potential scale reduction factor for all parameters ranged between 0.99 and 1.01). A full description of the model, including prior sensitivity analysis, and its implementation is detailed in *SI Appendix*.

Datasets and executable R-code are available in Datasets S1–S6.

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