CrossMark

COMMENT AND REPLY

Reply to Comment on "Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*" by Middleton and Breen (2016)

Stefan Meyer[1] · Bruce C. Robertson[1] · B. Louise Chilvers[2] · Martin Krkošek[3]

A general result in population ecology is that species characterized by long lifespan and slow reproduction have population growth rates that are highly sensitive to changes in adult survival (Heppell et al. 1996; Gaillard and Yoccoz 2003; Linares et al. 2007; Pol et al. 2010; Rotella et al. 2012; Maniscalco et al. 2015). In Meyer et al. (2015), we analysed the demography of the endangered New Zealand sea lion (NZSL) *Phocarctos hookeri*, and concluded that survival of breeding-age females was a main determinant of population growth. Our result is in line with the general understanding of how life history affects population dynamics; however, it has generated a management controversy because adult female sea lions are commonly captured as bycatch in trawl fisheries that are of economic importance (Chilvers 2008). Our results call into question the current model developed for the New Zealand

Responsible Editor: G. Pierce.

Reviewed by an undisclosed expert.

This reply refers to the comment available at doi:10.1007/s00227-016-2864-4.

✉ Stefan Meyer
  stefan.meyer@otago.ac.nz

1 Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

2 WILDBASE, Institute of Veterinary, Animal and Biomedical Science, Massey University, Palmerston North, New Zealand

3 Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada
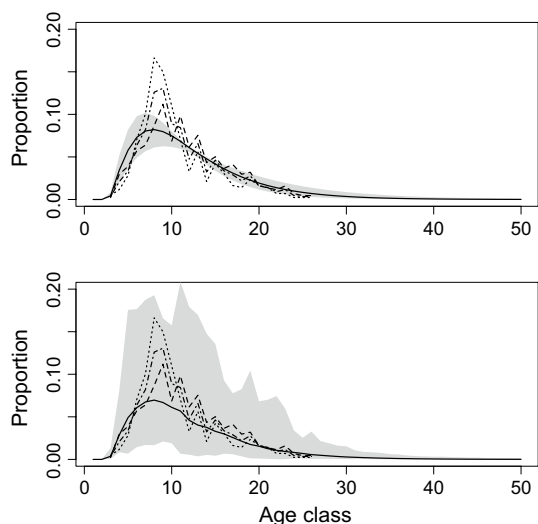
government for managing NZSL bycatch; a model that indicates elevated adult mortality due to fishing is not a problem for the recovery of the species (Breen et al. 2011).

Middleton and Breen (2016) commented that our data were too limited; the modelling approach too simplistic to reliably estimate demographic parameters; and they suggested that we misinterpreted our results. Here, we show their claims to be false and that they are based on misleading statements, obfuscating arguments, and a misinterpretation of our work. Furthermore, we arrive at the same conclusions as our original analysis even when one uses the model structure and parameter values that they claim to be superior. Below, we summarize our rebuttal of their claims and provide more detailed analyses in the electronic supplementary material.

We completely disagree with Middleton and Breen (2016) that the mark-recapture data we used leads to estimated demographic parameters that are inconsistent with other NZSL data. First and importantly, the model predictions for population growth showed excellent agreement with the time-series of pup abundances (Meyer et al. 2015). This is a compelling validation of the model because the pup abundance data used for the validation are independent and at a different scale (population) than the individual-level mark-recapture data used to parameterize the model (Thomson et al. 2008; Arlot and Celisse 2010).

Middleton and Breen (2016) rightfully point out that a stage-structured model implies a distribution of ages within stages that may not agree with senescence in the adult stage. They suggest instead that an age-structured model of adults would be more appropriate. Such model would require the same assumption of shared demographic rates amongst age groups as our model, but differ in that they truncate the age distribution. We show in Online Resource A that such an age-structured model returns the same

Springer

Fig. 1 Age-within-stage distribution of breeding New Zealand sea lions [stage 4 in Meyer et al. (2015)]. *Top panel* deterministic prediction; *bottom panel* stochastic prediction. Given are the median (*solid line*) and 95 % credible interval (*grey area*). Furthermore provided are the age distribution of lactating New Zealand sea lions (pooled for the years 1999–2001) for Sandy Bay (*dotted line*), Dundas Island (*dashed line*) and both sub-colonies combined (*dotted* and *dashed line*) as reported in Childerhouse et al. (2010). See Online Resource B for methods

conclusions as our original analysis. To address other possible age-within-stage issues, we provide additional validation of our original model for the age distribution of lactating NZSLs [stage 4 in Meyer et al. (2015)] (Online Resource B). Figure 1 shows that both the deterministic and the temporal stochastic model accurately predict the observed age distribution of lactating NZSLs, where the highest proportion of lactating NZSLs occurs at age 8 (95 % CrI 7–9) years. In comparison, Childerhouse et al. (2010) found that the age distribution of lactating females peaks at age 8 or 9 years.

Middleton and Breen (2016) have misrepresented the applicability of integrated modelling approaches in their criticism of our study. Abadi et al. (2010) show that integrated population models (IPM) can increase the precision of demographic estimates, but this is only relevant if data sets are small (200 individuals, simulations carried out over 10 years; Abadi et al. 2010). In comparison, our dataset comprised 2928 individuals marked over 14 years (marked between 1998 and 2011; recaptured between 1999 and 2012). Another application of IPM is to estimate undetected permanent or temporary emigration (Abadi et al. 2010). Middleton and Breen (2016) suggest that temporary emigration of individuals occurs between 1 and 3 years of age, but neither of the integrated NZSL models highlighted by the authors attempted to explicitly deal with temporary emigration of juvenile NZSLs. Overall, the claim that their

IPM (i.e. Breen et al. 2011) is a superior approach simply because it is more complex is baseless; it has crucial untested assumptions such as density dependence (Bradshaw et al. 2013), is sensitive to prior information, for example for the population growth rate (Breen and Kim 2006; Breen et al. 2011), and it has been suggested that the model attempts to estimate more information than provided by the data (Fletcher 2004). It is now well understood that such complex models suffer from estimation issues and can be misleading (Brooks et al. 2000; Gimenez et al. 2009).

The authors suggest that our survival estimates are biased. For example, they imply that adult survival might be biased through senescence, but they omitted to mention that estimates of survival after 14 years are highly uncertain in most NZSL studies [e.g. see Fig. 25 in MacKenzie (2012); but see Roberts et al. (2014)]. Given that the probability of adult recapture is high (Meyer et al. 2015) and senescence is not likely to start before 15 years (Roberts et al. 2014), we would not expect a bias of adult survival larger than 1 % (Fletcher and Efford 2009). Moreover, Middleton and Breen (2016) say that our estimated pup survival is "much lower than was estimated in other studies", but ignore the effect of model structure. If we expand our stage-structured model to age-specific juvenile survival (age 1–3 years) (Online Resource C), the survival at one year is not estimable as indicated by a 41 % overlap between the marginal prior and posterior distribution (Gimenez et al. 2009). However, we show in Online Resource C that estimated pup survival varies with model complexity, but the population growth rate and elasticities across the different model parameterisations were nearly identical to those we originally reported. This is because model complexity had no effect on the proportion of individuals surviving to adulthood (i.e. 4 years).

Middleton and Breen (2016) claim that, with a hypothetical adult survival of 0.953, a simple simulation would show that 31 % of adults would be 28 years or older, but this claim is not supported if we use our actual estimates. For example, the resulting age-within-stage distribution (Online Resource B) after increasing the value for adult survival to 0.953 (95 % CrI 0.929–0.973) shows that the proportion of breeding adults (stage 4) older than 27 years and older than 35 years would only be 11.83 % (95 % CrI 8.24–17.09 %) and 5.18 % (95 % CrI 3.27–8.31 %), respectively. This suggests that even if some proportion of adults becomes older than the maximum reported age of 28 years for female NZSLs (Childerhouse et al. 2010), the impact on the predicted population growth rate will be small. This is further verified by our analysis of the age-structured model that is analogous to our stage-structured model (Online Resource A).

Middleton and Breen (2016) also use a ratio of survival probabilities for the declining and the hypothetically stable

population (Meyer et al. 2015) to suggest that only a 25 % decrease of actual pup mortality is required as opposed to a 60 % decrease in adult mortality. They implicitly contrast this to a percentage increase in pup survival of 110 % as opposed to an 8 % increase in adult survival. However, these calculations are misleading because the absolute difference between survival probabilities or mortality rates is the appropriate metric to measure the difference between two mutually independent probabilities (Sheps 1959; Keyfitz and Caswell 2005). Hence, in Meyer et al. (2015), we stated the absolute difference of survival probabilities between the declining population and the hypothetically stable population is 0.203 (95 % CrI 0.098–0.295) and 0.069 (95 % CrI 0.030–0.111) for pups and adults, respectively. Naturally, the absolute difference between the corresponding mortality is equivalent rather than grossly different as Middleton and Breen (2016) suggest.

Finally, Middleton and Breen (2016) provide a misleading example when they calculate the annual number of adult deaths per year. They state that with an adult survival of 0.883 (i.e. mortality = 0.117) and a starting population of 6000 [in fact it is 4784 (95 % CrI 4383–5277)] adult individuals, 702 females would die per year at the Auckland Islands. The authors ignore that the population size has declined since 1998 and thus so would the number of adult deaths. Consequently, the proportion of the population that is bycaught would increase if the bycatch per unit effort remains constant over time. A possible increase in the proportion of bycatch that is female indicates that this may have occurred (Robertson and Chilvers 2011; Bradshaw et al. 2013). The current management policy based on Breen et al. (2011) allows for a relatively constant fishery-related mortality limit (FRML) of 68 male and female NZSLs each year (Ministry for Primary Industries 2013). Estimating the overlap between fishery bycatch and the number of sea lion deaths that need to be averted to stabilize the population should be a focus of future research, but we did not pursue that estimation in our paper. Our results indicate that estimating the efficacy of NZSL bycatch mitigation devices (Bradshaw et al. 2013; Robertson 2015), and finding ways to reduce fishery interactions with adult female NZSLs (e.g. Kahui 2012) could be helpful. Finally, we suggest that the precautionary principle should be applied in relation to allowable NZSL bycatch.

We acknowledge the large efforts that have gone into IPM modelling of NZSL population dynamics and the various working groups and meetings on the management of NZSLs. However, to our knowledge, our work is the first elasticity analysis of NZSL demography. Our analysis and the more general basic life history result that population growth of long-lived and slowly reproducing species is highly sensitive to adult survival raises the possibility that the IPM model of Breen et al. (2011) may be misleading

fisheries management and contributing to endangerment of NZSLs. This should prompt a rethinking of current management and the tools used to inform it, rather than this misleading attempt of Middleton and Breen (2016) to cast doubt on our conclusions. Meanwhile, the NZSL continues its decline.

References

Abadi F, Gimenez O, Arlettaz R, Schaub M (2010) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. Ecology 91(1):7–14. doi:10.1890/08-2235.1

Arlot S, Celisse A (2010) A survey of cross-validation procedures for model selection. Stat Surv 4:40–79. doi:10.1214/09-SS054

Bradshaw CJA, Haddon M, Lonergan M (2013) Review of models and data underpinning the management of fishing-related mortality of New Zealand sea lions (*Phocarctos hookeri*), in the SQU6T trawl fishery. Unpublished report to the Ministry for Primary Industries, Wellington NZ, July 2013. Available on request from Pamela.Mace@mpi.govt.nz

Breen PA, Kim SW (2006) An integrated Bayesian evaluation of Hooker's sea lion bycatch limits. In: Trites AW, Atkinson SK, DeMaster DP, Fritz LW, Gelatt TS, Rea LD, Wynne KM (eds) Sea lions of the world. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, pp 471–493. doi:10.4027/slw.2006.30

Breen PA, Fu D, Gilbert DJ (2011) Sea lion population modelling and management procedure evaluations: report for project SAP2011-14, objective 2. Technical report, National Institute of Water and Atmospheric Research Ltd. (NIWA), Wellington, New Zealand

Brooks SP, Catchpole EA, Morgan BJT, Barry SC (2000) On the Bayesian analysis of ring-recovery data. Biometrics 56(3):951–956. doi:10.1111/j.0006-341X.2000.00951.x

Childerhouse SJ, Dawson SM, Slooten E, Fletcher DJ, Wilkinson IS (2010) Age distribution of lactating New Zealand sea lions: interannual and intersite variation. Mar Mamm Sci 26(1):123–139. doi:10.1111/j.1748-7692.2009.00330.x

Chilvers BL (2008) New Zealand sea lions *Phocarctos hookeri* and squid trawl fisheries: bycatch problems and management options. Endanger Species Res 5(2–3):193–204. doi:10.3354/esr00086

Fletcher D (2004) Review of modelling approaches for the New Zealand Sea Lion PMP. Unpublished report. http://www.doc.govt.nz/documents/conservation/marine-and-coastal/fishing/review-modelling-appr-pmp.pdf. Accessed at 10 Feb 2016

Fletcher D, Efford MG (2009) Effect of senescence on estimation of survival probability when age is unknown. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 1037–1053. doi:10.1007/978-0-387-78151-8_47

Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84(12):3294–3306. doi:10.1890/02-0409

Gimenez O, Morgan BJT, Brooks SP (2009) Weak identifiability in models for mark-recapture-recovery data. In: Thomson DL, Cooch EG, Conroy MJ (eds) Modeling demographic processes in marked populations. Springer, New York, pp 1055–1067. doi:10.1007/978-0-387-78151-8_48

Heppell SS, Crowder LB, Crouse DT (1996) Models to evaluate headstarting as a management tool for long-lived turtles. Ecol Appl 6(2):556–565

Kahui V (2012) A bioeconomic model for Hooker's sea lion bycatch in New Zealand. Aust J Agric Resour Econ 56(1):22–41. doi:10.1111/j.1467-8489.2011.00566.x

Keyfitz N, Caswell H (2005) Applied mathematical demography, 3rd edn. Springer, New York, p 558. doi:10.1007/b139042

Linares C, Doak DF, Coma R, Díaz D, Zabala M (2007) Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology 88(4):918–928. doi:10.1890/05-1931

MacKenzie DI (2012) Estimation of demographic parameters for New Zealand sea lions breeding on the Auckland Islands—Final Report: 1997/98–2010/11. Proteus Wildlife Research Consultants report for Department of Conservation project POP2010/1. http://www.doc.govt.nz/Documents/conservation/marine-and-coastal/marine-conservation-services/demographic-parameters-of-nz-sea-lions.pdf. Accessed 5 Jan 2016

Maniscalco JM, Springer AM, Adkison MD, Parker P (2015) Population trend and elasticities of vital rates for Steller sea lions (*Eumetopias jubatus*) in the eastern Gulf of Alaska: a new life-history table analysis. PLoS One 10(10):e0140982. doi:10.1371/journal.pone.0140982

Meyer S, Robertson BC, Chilvers BL, Krkošek M (2015) Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*. Mar Biol 162(8):1587–1596. doi:10.1007/s00227-015-2695-8

Middleton DAJ, Breen PA (2016) Comment on "Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*" by Meyer, Robertson, Chilvers and Krkošek (2015). Mar Biol

Ministry for Primary Industries (2013) Aquatic environment and biodiversity annual review 2013. Compiled by the Fisheries Management Science Team, Ministry for Primary Industries, Wellington

Pol MVD, Vindenes Y, Sæther BE, Engen S, Ens BJ, Oosterbeek K, Tinbergen JM (2010) Effects of climate change and variability on population dynamics in a long-lived shorebird. Ecology 91(4):1192–1204. doi:10.1890/09-0410.1

Roberts J, Fu D, Doonan I, Francis C (2014) NZ sea lion: demographic assessment of the causes of decline at the Auckland Islands. Unpublished NIWA Client Report WLG2014-60 to the Department of Conservation, Wellington NZ. October 2014. http://www.doc.govt.nz/Documents/conservation/marine-and-coastal/marine-conservation-services/reports/NZ-sea-lion-demographic-assessment-causes-decline-auckland-islands-part-1.pdf. Accessed 5 Jan 2016

Robertson BC (2015) Comment on "Review of research and assessments on the efficacy of sea lion exclusion devices in reducing the incidental mortality of New Zealand sea lions *Phocarctos hookeri* in the Auckland Islands squid trawl fishery". Fish Res 165:127–129. doi:10.1016/j.fishres.2014.12.003

Robertson BC, Chilvers BL (2011) The population decline of the New Zealand sea lion *Phocarctos* hookeri: a review of possible causes. Mamm Rev 41(4):253–275. doi:10.1111/j.1365-2907.2011.00186.x

Rotella JJ, Link WA, Chambert T, Stauffer GE, Garrott RA (2012) Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark–recapture data. J Anim Ecol 81(1):162–173. doi:10.1111/j.1365-2656.2011.01902.x

Sheps MC (1959) An examination of some methods of comparing several rates or proportions. Biometrics 15(1):87–97. doi:10.2307/2527603

Thomson DL, Cooch EG, Conroy MJ (eds) (2008) Modeling demographic processes in marked populations, vol 3. Springer, New York, p 1132. doi:10.1007/978-0-387-78151-8