Stofnmat á Íslenska lundastofninum - Samantekt helstu niðurstaða

Hansen (2023) skýrði frá samdrætti lundastofnsins síðustu tvo áratugi og tengdi við hækkun hita sjávar og fæðuskort á ungatíma. Einnig var bent á að veiðar á lunda væru sennilega stofnvistfræðilega ósjálfbærar og yrðu það líklega áfram næsta áratug. Vegna þýðingu þessa niðurstaða fyrir veiði og verndaráætlun, óskaði Umhverfisstofnun við Dr. Fred Johnson og Carl Walters til að kanna hvort áframhaldandi veiði væri líkleg til að auka fækkunina vegna veiða.

Nokkrar mismunandi aðferðir voru notaðar til stofnmats. Einfaldasta aðferðin notar þekkingu á lífssögu og skölun eftir líkamsstærð til að meta hámarks sjálfbærs veiðihlutfalls og reikna líkur með hermun á því að veiði síðustu áratuga hefðu verið ósjálfbærar. Næsta líkan notaði fylkjareiking með tölum frá Hansen (2023). Flóknasta aðferðin sem beitt var "stofnfækkunargreining" (E: Stock Reduction Analysis). Þessi aðferð var þróuð til að meta stærðarbil heildarstofnstærðar yfir tíma með því að spyrja hver stofnstærð hefði þurft að vera til þess að endurspegla séð veiðimynstur og þar með bein áhrif veiðana. Nánari skýringar á öllum þrem aðferðunum og niðurstöðum þeirra fylgja hér á eftir á Ensku.

- Lundar eru ófrjósamir, langlíf tegund með lágan stofnvaxtarhraða, jafnvel við bestu umhverfisskilyrði. Langtíma sjálfbært veiðihlutfall er ólíklegt að fari yfir 4-5% af veiðanlegum stofni.

- Mikil dreifing ungfugla gerir svæðabundna veiðistjórnun marklausa. Jafnvel þótt að svæðabundinn munur sé á viðkomu, þá dreifast ungfuglar, sem eru uppistaðan í veiðinni, víða.

- Mild ofveiði hefur líklega átt sér stað frá nítjándu öld. Langtíma fækkun í lundastofninum is líklega að hluta til vegna hægra en uppsafnaðra áhrifa veiða, auk tímabíla með óhagstæðum umhverfisskilyrðum.

- Það erum miðlungs til háar líkur að veiðar hafi stuðlað að stofnfækkun síðasta áratug. Áframhaldandi veiðar eins og undanfarin síðustu ár eru líkleg til að valda frekari fækkun nema að viðkoma batni.

- Mikilvæg spurning um stefnumótun er hvort best væri að hætta alfarið veiðum á tímabilum þegar viðkoma er lág, eða að halda áfram veiðum en hóflegum. Röksemd fyrir hinu síðarnefnda er það, ef tímabil með lágri viðkomu eru ekki of löng, er ekki líklegt að hófleg veiði myndi valda mikilli fækkun í varpstofninum, sem er ekki eins auðveiðanlegur og ungfuglarnir. Röksemd fyrir hinu fyrrnefnda er að líkurnar á heildastofnstærð myndi aukast og veiði samhliða með tímabundum stöðvunum veiða.

- Að lokum, leggjum við til eftirtaldar tillögur að vöktun sem er nauðsynlega til að bæta stofnmat og til grundvallar veiðistjórnun:

  - Er til ákjósanleg aðferð til að mæla beint stofnstærð lundastofnsins;
  - Öðlast betri skilning á hvernig hægt er að hagnýta veiðitölur til að meta breytingar í stofnstærð;
  - Áframhaldandi merkingar á bæjarpysjum í Eyjum (og á öðrum svæðum ef mögulegt er) til að gera mæingu á veiðiálagi mögulega.
  - Halda áfram að mæla viðkomu, að meðtöldum áhrifum sjávarhita og varptímasetningu; og
  - Athuga hvort hægt sé að meta lífslíkur fyrsta árið betur.

Icelandic Puffin Stock Assessments

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Hansen (2023. Stofnvöktun lunda 2020-2022. Lokaskýrsla til Umhverfisstofnunar. Náttúrustofa Suðurlands. 43s.) reported a decline in puffin abundance over the last two decades and attributed the decline largely to warm sea-surface temperatures and accompanying lack of forage. He further suggested that recent harvests were unsustainable, and likely to remain so over the next decade. Because of the policy implications of that report, the Environment Agency of Iceland (Umhverfisstofnun) requested Drs. Fred Johnson and Carl Walters to examine whether continued harvests are likely to contribute to further population declines.

Several approaches were used for these additional puffin stock assessments. The simplest used life-history information and allometric relationships to estimate a maximum sustainable harvest rate and the probability that recent harvests have been unsustainable. A slightly more complex method involved the construction of a matrix population model, which was parameterized by demographic information provided by Hansen (2023). The most complex method was a stock reduction analysis (SRA). SRA was developed to provide bounds on absolute population size over time by asking how large the population would have to have been to exhibit assumed changes in relative abundance and to have sustained the observed historical removals. Details of all three methods and their results follow this summary.

Key conclusions from the assessments include:

- Puffins are unproductive, long-lived species with a low intrinsic population growth rate, even under favorable environmental conditions. A long-term sustainable harvest rate is unlikely to exceed 4-5% per year of the vulnerable segments of the population.

- Juvenile dispersal creates a "commons problem" for managing harvest. Although there is regional variation in reproductive success, dispersal of juveniles that are vulnerable to harvest could make regional harvest management ineffective.

- Modest over-harvesting has likely occurred since the late 1800's. The long-term decline in the puffin population is likely due in part to the slow, cumulative effects of harvests, as well as periods of unfavorable reproductive conditions.

- There is a moderate to high probability that harvest contributed to the decline in abundance over the last decade. Continued harvest at current levels is likely to contribute to further declines unless reproduction improves.

- An important policy question is whether it is best to completely suspend hunting during periods of low productivity or to continue hunting at some modest level. An argument for the latter is that, as long as the period of low productivity is not too long, modest harvests would not be expected to severely erode abundance of the breeding population, which is less vulnerable to harvest than juveniles. An argument for the former is the likelihood that long-term puffin abundance and harvest would be higher with periodic hunting closures.

- Finally, we make the following recommendations concerning monitoring needed to improve stock assessments and to guide harvest policy:
    - determine if there is a feasible method for empirically estimating the current size of the Icelandic population;
    - gain a better understanding of how harvest statistics can be used to reflect changes in population size;
    - continue to ring puffin chicks in the Westmans (and in other areas if practical) to facilitate the monitoring of harvest pressure;
    - continue to monitor reproductive success, including its relationship to ocean temperature and phenology; and
    - determine if fledgling survival to age 1 year can be better estimated.

Icelandic Puffin Stock Assessment

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Two approaches were used to help determine the sustainability of puffin harvests in Iceland. Both approaches relied heavily on the demographic information provided by Hansen (2023) and through personal communication with him.

Using the R package *popharvest*

The R package *popharvest* is useful when demographic data are limited, and it provides a first approximation of harvest sustainability in birds (Eraud et al. 2021, Johnson et al. 2024). We used *popharvest* to calculate the probability that puffin harvests were unsustainable, first during 2004 – 2013, and then during 2014 – 2023 when harvests were much reduced. Estimates of harvest were provided by the Environment Agency, and the size of the puffin population that was vulnerable to harvest was taken from the stock-reduction analysis conducted by Dr. Walters (see the last document in this report). The following R code is all that is needed to run this analysis.

```
install.packages("popharvest")
library(popharvest)
ptl = PTL(full.option=TRUE,NSp=1,Nsim=20000,Fobj=1,
      surv.beta=TRUE,mean.surv=0.92,sd.surv=0.0544, # Hansen (2023)
      alpha.fixed=5.424,
      theta.fixed=1,
      #estim.theta='random',
      living.rate="long",
      #pop.fixed=1070000, # mean vulnerable pop 2004-2013 (C Walters)
      pop.fixed=671000, # mean vulnerable pop 2014-2023 (C Walters)
      #harvest.fixed=60444) # mean harvest 2004-2013
      harvest.fixed=30131) # mean harvest 2014-2023

output.summary(ptl)
hMSY = ptl$Rmax*ptl$theta/(ptl$theta+1) # hMSY
quantile(hMSY,p=c(0.025,0.50,0.975))
```

A rather critical parameter in using *popharvest* is theta, which is the functional form of density dependence. Frequently it is assumed to be linear, such that theta.fixed=1. However, the program can also estimate this parameter based on life history characteristics (estim.theta='random'). Because of the large uncertainty concerning the form of density dependence in puffins, we examined both approaches. For theta.fixed=1, the harvest rate at maximum sustained yield is $h_{MSY} = 0.04 \ (0.02 - 0.06)$ under the average environmental conditions in which the species evolved (note that recent ecological conditions may differ from

this evolutionary context). Under the assumption of linear density dependence, there is an 86% probability that harvest was unsustainable during 2004 – 2013, and a 53% probability during 2014 – 2023. If we allow the program to estimate theta, the estimated mean is $\theta = 4.3$, suggesting that the strongest density dependence occurs when abundance is near carrying capacity. In this case, $h_{MSY} = 0.06 \ (0.02 - 0.11)$, and the probability that harvest was unsustainable was 46% and 28% during 2004 – 2013 and 2014 – 2023, respectively. Whether these probabilities are deemed too high depends on the risk attitude of those responsible for puffin harvest management.

Age-structured matrix model

A key limitation of *popharvest* is that it uses a scalar logistic model that does not admit any age-specificity in demography or harvest vulnerability (beyond age at first breeding). This can be problematic in long-lived birds with delayed sexual maturity, and which have age-specific vulnerabilities to harvest. To help address this limitation, we constructed a pre-breeding matrix model for puffins aged 1 to 6+ years. The model was parameterized using demographic rates provided by Hansen (2023), with rates applicable mostly to the period 2010 – 2022. It should be noted that this period began with sea surface temperatures much greater than optimal for puffin reproduction (Hansen et al. 2021), but significant cooling occurred during the latter part of this period. After parameterizing the matrix, we calculated the asymptotic growth rate in the absence of harvest. Finally, we projected the puffin population 10 years into the future assuming the mean harvest that was observed during 2010 – 2022. For each simulation, we randomly drew demographic rates each year from their statistical distributions. We simulated population trajectories 10,000 times and examined the mean population growth rate, the probability that the growth rate <1, and the percentage change in population size over the next 10 years. R code for the matrix model is provided at the end of this document.

The pre-breeding (female only) matrix had the form:

$$
\begin{bmatrix}
0 & 0 & (Pb_3P/2)S_1 & (Pb_4P/2)S_1 & (Pb_5P/2)S_1 & (Pb_6P/2)S_1 \\
S_a & 0 & 0 & 0 & 0 & 0 \\
0 & S_a & 0 & 0 & 0 & 0 \\
0 & 0 & S_a & 0 & 0 & 0 \\
0 & 0 & 0 & S_a & 0 & 0 \\
0 & 0 & 0 & 0 & S_a & S_a
\end{bmatrix}
\cdot
\begin{bmatrix}
N_1 \\
N_2 \\
N_3 \\
N_4 \\
N_5 \\
N_{6+}
\end{bmatrix}
$$

We used the following values to parameterize the matric model:

- Survival (and permanent emigration) of 1st year birds S1 ~ beta with mean = 0.5 and sd = 0.2; due to high uncertainty about survival of fledglings, we also used a value of 0.7 (sd = 0.2) suggested by Dr. Walters' model
- Survival of older birds Sa ~ beta with mean = 0.92 and sd = 0.0544

- Probability of breeding for 3- and 4-year-olds $P_b = 0.067$, 5-year-olds $P_b = 0.7$, and 6+ year-olds $P_b = 1$
- Young produced per breeder $P \sim$ gamma with mean = 0.293 and sd = 0.1434, representing the country-wide average for 2010 – 2023; we also examined productivity from the nine best years during this period with mean = 0.385 and sd = 0.0741
- Initial pre-breeding population size in 2022 for birds aged 1 – 6+ was N = [242000, 69700, 187000, 298000, 189000, 3446000] (C Walters)
- Average female harvest during 2010 – 2021 assuming an even sex ratio in the harvest of 2-4-year-olds $H \sim$ gamma with mean = 27846/2 and sd = 1505/2, and 5-6+ year-olds $H \sim$ gamma with mean 4235/2 and sd = 229/2

The following table provides the deterministic, asymptotic growth rate with no harvest, as well as the results of the stochastic simulations with harvest for the scenarios involving different fledgling survival and productivity. The asymptotic growth rates in the absence of harvest are <1 using the average productivity observed during 2010 –2023, regardless of the two fledgling survival rates; this suggests there was likely no sustainable harvest during the last decade. Only if fledgling survival and productivity were both high, would there be any sustainable harvest and it would be expected to be quite low. If the recent harvests were continued over the next 10 years, the population would be expected to continue to decline under all scenarios except in the case where both productivity and fledgling survival remain high.

S1	P	Harvest = 0	Harvest = 32081		
		λ	λ	P(λ<1)	pop. change
0.5	0.293	0.977	0.968	94%	-26%
0.7	0.293	0.995	0.988	70%	-10%
0.5	0.385	0.991	0.984	79%	-14%
0.7	0.385	1.011	1.010	35%	+9%

Both the *popharvest* and matrix-model analyses suggest a moderate to high probability that harvests over the last decade were unsustainable. A continuation of recent harvests for the next ten years is likely to reduce population size further unless both productivity and fledgling survival remain high.

Literature Cited

Eraud, C., T. Devaux, A. Villers, F. A. Johnson, and C. Francesiaz. 2021. popharvest: An R package to assess the sustainability of harvesting regimes of bird populations. Ecology & Evolution:16562– 16571.

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Johnson, F. A., C. Eraud, C. Francesiaz, G. S. Zimmerman, and M. D. Koneff. 2024. Using the R package popharvest to assess the sustainability of offtake in birds. Ecology and Evolution 14:e11059.

Matrix-model R code

```
library(popbio)
library(matrixcalc)

# Beta method of moments
MOM.beta=function(mu,var) {
  sum_ab=(mu*(1-mu)/var)-1
  a=sum_ab*mu
  b=sum_ab*(1-mu)
  answer=list(a,b)
  names(answer)[[1]]="a"
  names(answer)[[2]]="b"
  return(answer)
}
# Gamma method of moments
MOM.gamma = function(mean,var) {
  shape = mean^2/var
  rate = mean/var
  answer=list(shape,rate)
  names(answer)[[1]]="shape"
  names(answer)[[2]]="rate"
  return(answer)
}

#####  PARAMETER VALUES ##################################################
s = c(0.5, 0.7)
sd.s = 0.2
s1 = s[1]
s1beta = MOM.beta(s[1],sd.s^2)
curve(dbeta(x,s1beta$a,s1beta$b),xlab='S1',ylab='Density')

sa = 0.92
sd.sa = 0.0544
sabeta = MOM.beta(sa,sd.sa^2)
curve(dbeta(x,sabeta$a,sabeta$b),xlab='Sa',ylab='Density')

pb3 = pb4 = 0.067 # probability of breeding
pb5 = 0.75
pb6 = 1

# productivity
# p = c(0.666,0.399,0.448,0.246,0.278) # Table 6 Hansen 2023 report (4 regions + Country)
```

```
# sd.p = c(0.0256,0.0765,0.0696,0.0605,0.0393)
# annual productivity 2010-2023 from Hansen 9Mar2024
pall = c(0.092,0.059,0.179,0.160,0.146,0.331,0.288,
      0.386,0.286,0.428,0.380,0.511,0.440,0.416)
pall = sort(pall)
p = c(mean(pall), mean(pall[6:14])); sd.p = c(sd(pall), sd(pall[6:14]))

Pg = MOM.gamma(p[1],sd.p[1]^2)
curve(dgamma(x,shape=Pg$shape,rate=Pg$rate),xlim=c(0,1),xlab='P',ylab='Density')

Npre = matrix(c(2.42E+05,   6.97E+04,    1.87E+05,    2.98E+05,    1.89E+05,
          (1.10E+05  + 1.70E+05 + 1.16E+05      + 3.05E+06),
        rep(0,60)),byrow=FALSE,nrow=6) # 2022 CWalters



#####  ASYMPTOTIC MATRIX PROPERTIES ####################################
P = p[1] # choose P
s1 = s[1] # choose s1

# pre-breeding matrix
pre = matrix(c(0,0,s1*pb3*P/2,s1*pb4*P/2,s1*pb5*P/2,s1*pb6*P/2,
        sa,0,0,0,0,0,
        0,sa,0,0,0,0,
        0,0,sa,0,0,0,
        0,0,0,sa,0,0,
        0,0,0,0,sa,sa),byrow=TRUE,nrow=6)

A=eigen.analysis(pre)
A$lambda1

# age-specific vulnerabilities
#Table SI Hansen 2021 article
pSI = c(0.002,0.163,0.339,0.206,0.080,0.027+.024+.021+.018+.016+.014+.012)
pSI = c(pSI[1:5],1-sum(pSI[1:5]))
v = pSI/A$stable.stage
vul = round(v/max(v),2)

# post-breeding matrix
post = matrix(c(0,0,sa*pb3*P/2,sa*pb4*P/2,sa*pb5*P/2,sa*pb6*P/2,sa*pb6*P/2,
        s1,0,0,0,0,0,0,
        0,sa,0,0,0,0,0,
        0,0,sa,0,0,0,0,
        0,0,0,sa,0,0,0,
```

```
                 0,0,0,0,sa,0,0,
                 0,0,0,0,0,sa,sa),byrow=TRUE,nrow=7)


E = eigen.analysis(post)

#####  STOCHASTIC PROJECTIONS ################################################
Htot = 32081 #avg harvest 2010-2021
Hsd = 6008
Hage = pSI*Htot
Hg = MOM.gamma(Htot,Hsd^2)

Pg = MOM.gamma(p[2],sd.p[2]^2) # choose productivity
s1beta = MOM.beta(s[2],sd.s^2) # choose s1

sims = 10000 # number of simulations
t = 10 # number of years beyond 2022
lambda = delta = NULL

for (j in 1:sims) {
 for (i in 2:(t+1)) {
  s1 = rbeta(1,s1beta$a,s1beta$b)
  sa = rbeta(1,sabeta$a,sabeta$b)
  P = rgamma(1,shape=Pg$shape,rate=Pg$rate)

  pre = matrix(c(0,0,s1*pb3*P/2,s1*pb4*P/2,s1*pb5*P/2,s1*pb6*P/2,
            sa,0,0,0,0,0,
            0,sa,0,0,0,0,
            0,0,sa,0,0,0,
            0,0,0,sa,0,0,
            0,0,0,0,sa,sa),byrow=TRUE,nrow=6)

  Htot = rgamma(1,shape=Hg$shape,rate=Hg$rate) #avg 2010-2021
  H = pSI*Htot

# choose harvest level
#   H = round(0.0*H)
#   H = round(0.25*H)
#   H = round(0.50*H)
  H = round(H)
#   H = round(1.25*H)

  Npre[,i] = pmax(0, round(pre%*%Npre[,(i-1)])) - H)
 }
```

```
 N = apply(Npre,2,sum)
 lambda[j] = (N[11]/N[1])^(1/10)  # finite t-year growth rate
 delta[j] = (N[11]-N[1])/N[1]     # proportional population change over t years
 }

mean(lambda); quantile(lambda,probs=c(0.025,0.975))
mean(lambda<1) # probability that lambda < 1 over number of sims
mean(delta); quantile(delta,probs=c(0.025,0.975))
```

A stochastic stock reduction analysis for Icelandic puffin population estimation

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May 2024

Introduction

A common problem in fisheries stock assessment has been to estimate historical population changes given total catch removals over time but only estimates at one or more times of relative population size. Stock reduction analysis (SRA) was developed to provide bounds on absolute population size over time by asking how large the population had to have been in order to have exhibited the assumed changes in relative abundance and to have sustained the observed historical removals, given assumptions about production parameters (birth and survival rates) and "random" environmental influences on production rates (Walters, et al. 2006). The basic idea in SRA is to propose a reasonable population model structure that includes catch removals, then run (or fit) that model with alternative assumptions about production parameters so as to at least estimate the initial population size and likely production rates over time.

SRA model structures for mature population numbers

I developed two SRA model structures, first a simple, age-aggregated "balance model" for total age 3+ abundance and second an age structured model accounting separately for abundances at age up to age 9+. Comparing these models helps to understand effect of assuming more detail, hence having to provide estimates of more uncertain parameters, on estimated abundance patterns.

For the simple balance model, the basic structure for the total number $N(t)$ of age 3 and older birds at the start of each breeding season (t) is given by the basic the basic survival-recruitment equation

$$N(t) = [N(t-1)-H(t-1)]S + BN(t-3)f(SST) e^{w(t)} \qquad (1).$$

Here, $H(t)$ is harvest in year t, B is a base production rate per breeding bird of age 3 offspring under ideal conditions, S is average annual survival rate (assumed to be 0.92 and constant oer years), $f(SST)$ is a dome-shaped function of sea surface temperature scaled to 1.0 at SST=7.1 C and with spread to match Figure 3 in Hansen et al. 2021, and $w(t)$ is a mean-0 "process anomaly" representing effects on reproductive success not accounted for in the SST function.

The age-structured version of the SRA (basically a life table model) follows the structure recommended in Walters et al (2006), while treating birds aged 9 and older as a "plus group". Life table parameter estimates for this model were extracted by Fred Johnson from Hansen (2023), and the basic results to date appear generally similar to those obtained with the age-aggregated model above while utilizing additional information on age-dependent rates and vulnerability to harvest. The basic age-structured SRA equation for predicting numbers at age $N(a,t)$ is

N(1,t+1)= BN(t)f(SST)2e^{w(t)} (same as aggregate model, but with N(t)=∑_aN(a,t)m(a)

$N(1,t+1)= BN(t)f(SST)2e^{w(t)}$ (same as aggregate model, but with $N(t)=\sum_a N(a,t)m(a)$

$N(a+1,t+1)=N(a,t)S(a)[1-v(a)U(t)]$ ages 1-7   (3)

$N(9,t+1)= N(8,t)S(8)[1-v(8)U(t)]+N(9,t)S(9)[1-v(9)*U(t)]$ age 9 plus group

Here, $m(a)$ is age-specific proportion of mature birds and $S(a)$ is age-specific survival rate, and $v(a)$ is age-specific vulnerability to exploitation (allowing exploration of effects of younger birds being much more vulnerable to harvesting). Exploitation rate $U(t)$ is set to observed harvest over predicted number of vulnerable birds, i.e. $U(t)=H(t)/VN(t)$ where $VN(t)= \sum_a N(a,t)v(a)$ is the vulnerable abundance. The harvest-based abundance index H/days for this model is assumed to be proportional to the vulnerable abundance rather than to the total breeding population size.

For initial tests of the age-structured model, I assumed the age-specific rate parameters shown in Table 1, provided by Fred Johnson based on data in Hansen (2023). These rates imply dome-shaped vulnerability, birds mostly mature by age 5, and age-specific survival rates that are high (0.92) for all age 1 and older birds.

Table 1. initial assumed values of relative vulnerability at age v(a), proportion mature m(a), and annual survival rates S(a)

Age	1	2	3	4	5	6	7	8	9+
v(a)	0.01	0.45	1.00	0.64	0.26	0.04	0.04	0.04	0.04
m(a)	0	0	0.067	0.5	0.75	1	1	1	1
S(a)	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92

(note that the annual survival rates for ages 1-2 bird should probably be at least somewhat lower)

For both models, I constrained the $w(t)$ values to be less than about 0.8, implying maximum recruitment per breeding bird about 2x the average. The long-term average recruitment to age 1 per breeding bird (B) was assumed to be 0.5x0.45x0.6=0.135 (sex ratio 50:50 times 45% of nests producing a chick times 60% average first year survival from fledging to age 1). So 2x that average would require higher survival to hatching along with up to 100% survival after leaving the nest hole as a theoretical maximum for chicks that encountered very favorable provisioning and subsequent feeding conditions. Lower values of the maximum allowable $w(t)$ result in smoother predictions of recruitment variation with less extreme positive responses in years when harvest data suggest that rapid abundance increases occurred.

I fit the models to a relative abundance time series $I(t)$ equal to $H(t)/days(t)$, where $days(t)$ is the number of days open to harvest in year t. Presumably $I(t)$ is a better "catch per effort" index of abundance than just the harvests $H(t)$. For this index, I assumed it to be proportional to $N(t)$ with lognormal sampling variation, i.e.

$$I(t)=qN(t)e^{v(t)}$$ (2).

For model fitting, I used a relative log-likelihood function consisting of an inverse-variance weighted sum of $\sum_t w(t)^2$ and $\sum_t v(t)^2$, i.e. observed relative abundances were assumed to have varied due to a combination of ecological process and observation errors. Additional squared

error terms were included to allow penalties for model departures from particular estimates of recent total breeding population sizes.

The analysis was set up in Excel, in a copy of the time series data spreadsheet provided as supplementary material by Hansen et al. 2021 so as to insure use of exactly the same data. All needed information was in that spreadsheet, including past harvests H(t), SST, and season lengths (days(t)), so the SRA was set by just adding columns to the Hansen et al spreadsheet to calculate f(SST), I(t), and solve the SRA equation (1) over spreadsheet rows representing years from 1880-2010.

Excel's nonlinear search procedure Solver was used to search for maximum values of the relative likelihood function by varying the initial N(1880), mean recruitment rate (B), and the production anomalies w(t). In most test runs, the B was frozen at 0.135 as noted above and N(1880) was simply varied manually so as to give reasonable estimates of recent (2010) total breeding population size or was strongly penalized for deviating from prior estimates for recent years based on burrow numbers and observed burrow occupancy rates in the Westmann Islands population. Note that given particular values for N(t) from eq.(1) and the search parameters, the v(t) of the likelihood function can be calculated using eq. (2) as just v(t)=ln(I(t)/N(t))-lnq, where lnq is the logarithm of q given by just the average of the "Z statistics" ln(I(t)/N(t)). The most credible results to date have been obtained with B frozen to 0.135, a reasonable value based on sex ratio, fecundity, and first-year survival estimates; without this constraint on productivity, the model fits tended to overestimate B and to correspondingly underestimate breeding population sizes N(t) relative to recent estimates based on estimates of nest hole numbers.

The age-structured model was fit to harvest data from both the Westmann Islands alone and from a reconstruction of total Iceland harvest. Copies of both spreadsheets are available upon request to the authors.

Preliminary results

When fit to the abundance index data with N(1880) set large enough for the Westmann population to end up with near 2 million breeding birds in 2010 as estimated by Hansen, both models fit the data reasonably well and are in agreement that historical exploitation rates (harvest/population size) have been relatively low, on order 10% per year or less of the vulnerable population and have not varied in a way that could explain observed abundance fluctuations. For the total country age-structured model, similar exploitation rate histories were estimated when N(1880) was set so as to give a national total breeding population of near 6 million birds in 2010. However, the life table rates imply that the long-term sustainable harvest rate is unlikely to be greater than 4-5% per year of the vulnerable population, so there quite likely has been modest overharvesting since the late 1800s. Still, the main cause of long-term population fluctuations appears to be persistent regime changes in reproductive success, with higher success generally in years of lower sea surface temperature as expected from a variety of observations about changes in availability of sand lance prey. Further, the models agree with findings in Hansen (2024) that population decline likely continued until at least 2020 so that the future of the populations is entirely unclear.

Basic model fitting results are shown below for the two model structures. The fits are certainly credible, showing large fluctuations in abundance of younger birds but smoother changes over time in the breeding population (that smoothing has to happen considering the large number of year-classes contributing to the overall adult abundance.

Figure 1. Model fit diagnostics for the age-structured model for the Westmann population. Black dots in the top right panel show direct estimates of Westmann breeding numbers from number of nesting holes and occupancy rates.
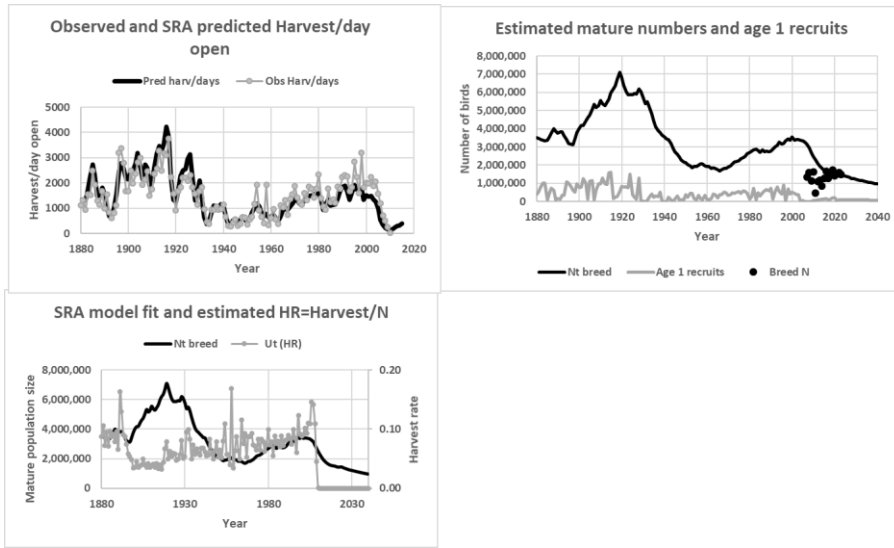
Figure 2. Model fit diagnostics for the total Iceland age-structured population model; note that harvest data after 2010 made it possible to fit the model to a longer time series of relative abundances. Black dots in the top right panel show direct estimates of Westmann breeding numbers from number of nesting holes and occupancy rates
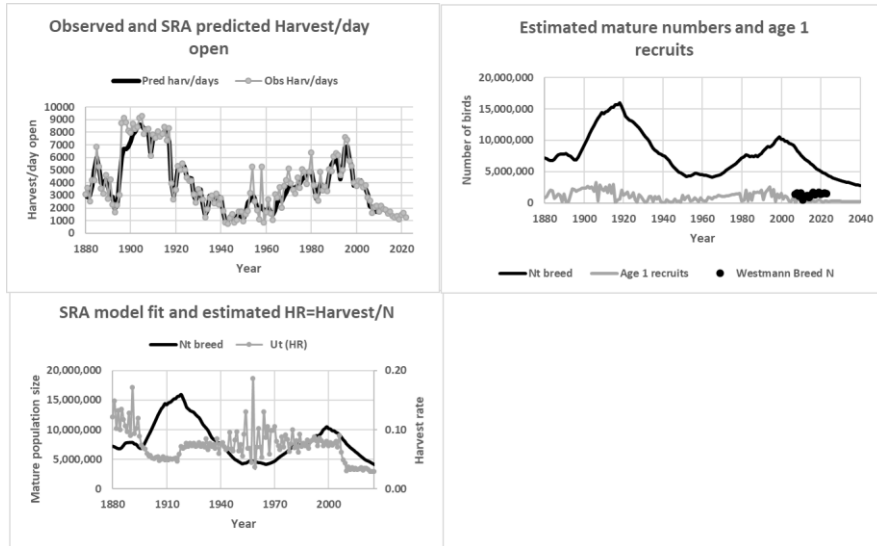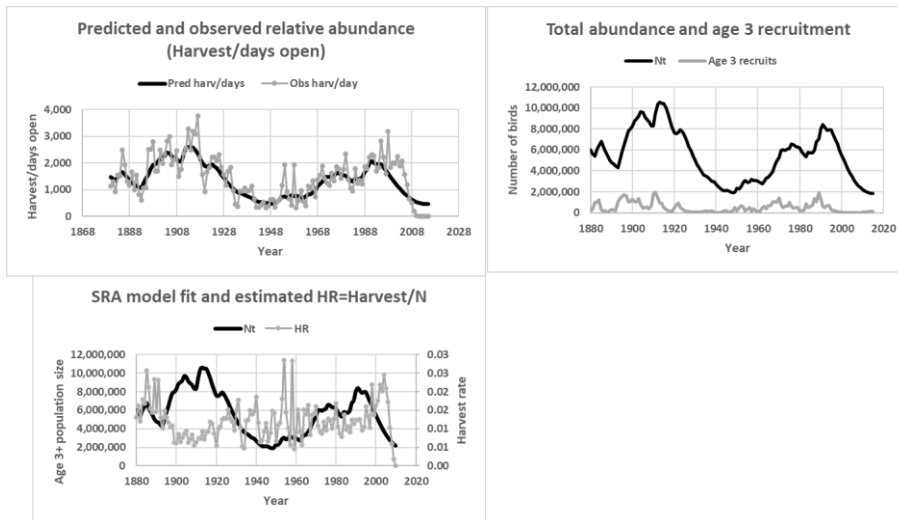

Figure 3. Model fit diagnostics for the simple balance model

For these fits, reproductive rate parameter B was frozen at 0.135 for the age model and was estimated to be lower for the balance model for recruitment to age 3 (0.11) as expected since births are multiplied by three rather than two years of survival rates.

It must be emphasized that the good fits to data obtained with the model do not in any way imply that the model has correctly reconstructed historical absolute abundances and exploitation rates. Three key parameters determine those absolute estimates: (1) the initial (1880) abundance estimate, (2) the assumed decline in abundance as represented by credible independent estimates of recent breeding population size, and (3) assumed productivity, as represented by the life table

rates and importantly by the B parameter. So for example, if we increase B (assume higher age-0 survival rates), we then have to lower the N(1880) and later population sizes in order to predict a declining trend, and those lower abundances in turn imply higher historical exploitation rates. The only independent check we have on the credibility of the resulting exploitation rate estimates is from ringing data, in particular total recapture rates of birds banded as chicks. Even with the help of such data, there remains substantial uncertainty about just how high exploitation rates have been. I experimented with a model version that tried to force a good fit to the average recapture rates for 1959-1999 (cohorts with nearly complete ring recoveries over ages), and this version indicated that the B parameter may be larger than the 0.135 default, perhaps as high as 0.16 (implying best model fits with somewhat lower abundances, higher productivity, and higher exploitation rates averaging around 0.1 on the most vulnerable age (3). However, I am not confident about the fitting procedure used in that model version; it needs more work before I would be willing to assert with any confidence that exploitation rates have in fact been as high as it indicates.

But as a positive note, scenarios that result in higher exploitation rate estimates also result in higher estimates of the best long term exploitation rate, i.e. estimates of relatively how much exploitation rates need to be reduced from historical levels are quite stable, at around 50% lower rates than prevailed over the 20th century.

Recommendations

While the annual exploitation rates estimated by the SRA models have generally been low (averaging less than 10% of the vulnerable juvenile birds), those rates have impacted the pre-breeding survival of a very unproductive, long-lived species that has a low intrinsic population growth rate even under favorable conditions. A simple way to measure that impact is with "retrospective analysis", i.e. by running the SRA models from 1880 forward in time, with the estimated productivity anomaly pattern, but with the H(t)/VN(t) exploitation rate estimates replaced with all zeros. For the age-structured model, doing this retrospective simulation results in population growth averaging only about 1% per year over the 1880-2010 period, and rarely exceeding 5% per year even during the most favorable periods for juvenile survival. Put another way, the broad pattern of decline over time has very likely been due in part to slow, cumulative effects of harvesting as well as periods of unfavorable reproductive conditions.

While lower sea surface temperatures in at least the Westmann Islands area since 2017 have possibly created favorable locally conditions for population growth, declining harvests for Iceland as a whole warn that such favorable conditions may not be occurring in all areas and that other factors like reproductive timing may now be more important causes of recent low reproductive success. A key issue is whether the declining harvests in recent years do actually reflect declining local populations, or instead actions by hunters and landowners aimed at slowing or reversing declines by reducing harvesting effort or simply difficulty in finding enough birds to make hunting worthwhile. Fortunately, dispersal of juvenile birds across colonies will likely help to minimize impacts of local overharvesting by people not willing to take further action to reduce local rates of population decline; but on the other hand, juvenile dispersal also

creates a "commons" problem since owners cannot expect to be the main beneficiaries of their local conservation efforts. This is a very difficult policy situation.

Hopefully more information can be gathered from landowners on their harvesting effort, perceptions of recent trends, and reasons for reducing hunting effort. With a bit of luck, it might be found that local trends in relative abundance have been positive in at least some areas and that more successful reproduction is occurring in other colonies besides the Westmann ones. For both long term and local population management, harvesting effort and other information to inform indices of trend in relative abundance is certainly an important need, even if such data show that the recent declines have reversed and that limited sustainable harvest is possible again as occurred over the period from 1950-1990.

It is unclear from the standpoint of harvest management theory whether the best policy during declines is to stop harvesting until populations have recovered. If the interests of harvesters are represented by a risk-averse utility function (for which the marginal utility of having at least some income is high, with increments to higher incomes being less important), harvest optimization studies have shown that it may be better to continue harvesting at lower rates over periods of low productivity than to just stop entirely for long periods (eg, see Walters and Parma, 1986; Hawkshaw and Walters 2006). Such options can easily be examined using retrospective simulations with the fitted models, to basically ask whether higher total utility could have been had over the last century of increases and declines by following some policy involving complete closures.

To further examine alternative policy choices for very long-term management, I set up 400-year simulations for the total Iceland population model, with the historical productivity anomaly patterns from Figure 2 repeated every 130 years; this results in a simulation with multiple (6) "cycles" of high and low productivity (Figure 4). For these very long simulations, I assumed a carrying capacity for age 1 juvenile production equal to twice the maximum estimated by model fitting to have occurred since 1880. I then harvested this simulated population using harvest control rules that have been recommended in the fisheries literature, namely ones that specify annual total harvest as linear function of total abundance, with a minimum or "limit reference" abundance (LRP) below which harvesting is not allowed. For LRP=0, i.e. for constant annual exploitation rates over time, these simulations give the highest total yield and utility at an annual exploitation rate of about 4% of the vulnerable young birds. When Solver is used to seek the utility-maximizing policy, it recommends the policy shown in Fig. 4, namely, to take no harvest at lower population sizes then to allow harvest rate increases at higher abundances. But the predicted gain in yield by having such closures is not large (about 25%) compared to that predicted by allowing a 4% harvest rate every year even during low productivity periods.

> Figure 4. Results from very long term (400 year) simulations with the total Iceland population fitted model, where estimated historical productivity anomaly patterns are repeated every 130 years and where exploitation rates are managed starting in simulation year 1880 using a harvest control rule that maximizes predicted total long-term utility of the harvest. Note that the harvest control rule would have stopped all harvesting over the 1950-70 period of low productivity, possibly not a socially or legally viable option.
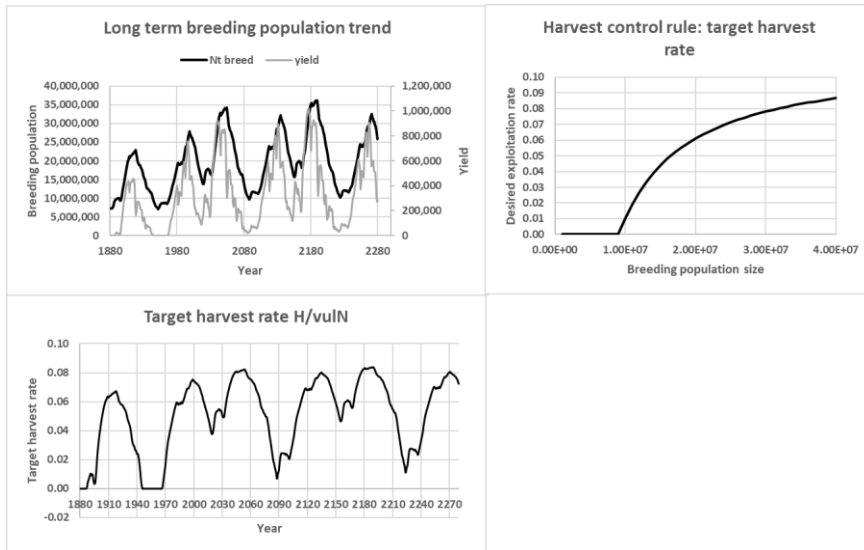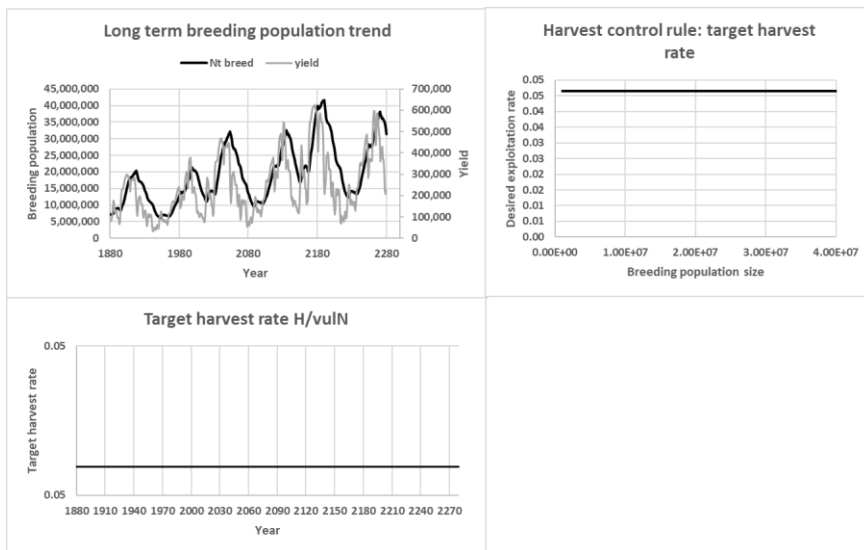
Figure 5. Results from same model setup as Figure 4, but with constant 4.6% annual exploitation rate (which maximized 400-year yield given no allowable variation in exploitation rate from year to year)


One argument in favor of allowing modest exploitation rates even during the current period of decline is that total breeding population sizes will not decline all that rapidly given the high longevity of puffins. That is, there will still be a substantial population base for rebuilding, even if breeding is largely unsuccessful for at least another decade. The problem with this argument, of course, is that we have no credible way to predict just how long the current unfavorable conditions may persist.

It is really difficult to interpret recent statistics provided by the Environmental Agency on regional harvests and numbers of hunters. As shown in Fig. 6, total harvest and hunter numbers are declining, but the kill per hunter has actually increased since 2010. Does this mean that the average hunter has experienced stable or increasing relative abundance, or that only the most

skilled and determined hunters are still going out? Ambiguities like this in interpretation of available harvest statistics emphasize the need mentioned above to find better harvest-based indices of recent population trend, and to use those indices in making decisions about the urgency of further reductions in exploitation rates.

Figure 6. Harvest and harvest per hunter estimates from the Environmental Agency
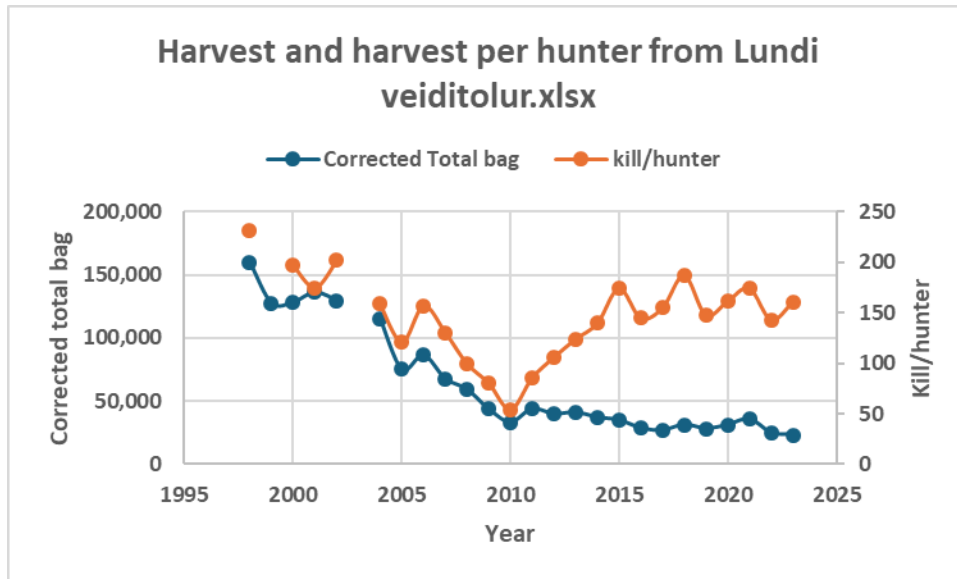
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