Evaluating the Influence of Proportional Entrainment Loss on Subadult Delta Smelt Survival Using the Maunder and Deriso in R (MDR) Model

Analysis by:

Michael Tillotson, Senior Fisheries Biologist, ICF (Mike.Tillotson@icf.com)

John Brandon, Senior Biometrician, ICF

For:

Metropolitan Water Department of Southern California

November 29th, 2023

Executive Summary

The marked and persistent decline in Delta Smelt abundance across multiple decades has been accompanied by massive changes in the Sacramento - San Joaquin Delta ecosystem, including both to physical habitats and trophic conditions, and also substantial changes in water management. Clarifying the relative influence of these various factors on Delta Smelt population dynamics is critical for understanding the effectiveness of past management actions, and for prioritizing current and future recovery efforts. Of particular interest is the degree to which the abundance and population dynamics of Delta Smelt are influenced by direct entrainment into large-scale water diversions in the Delta, and whether historic changes to water operations have been sufficient to reduce entrainment risk. Multiple modeling efforts have previously attempted to address this issue of key management importance, including the model published by Maunder and Deriso (2011) where the authors evaluated models including total salvage as a covariate of both survival and recruitment, but the results of this effort were ambiguous with regard to the effect of salvage. This report describes an effort to clarify entrainment effects on Delta Smelt population dynamics using an updated and generalized version of Maunder and Deriso's analysis (hereafter referred to as the Maunder and Deriso in R or MDR model), along with 10 additional years of data and an updated approach to quantifying Delta Smelt entrainment.

The MDR is a statistical life-cycle model that is fit to data, including indices of stage-specific Delta Smelt abundance, and can also accommodate covariates in a flexible manner. Entrainment of Delta Smelt during the sub-adult phase has been hypothesized to appreciably effect the population's survival through this stage, and various metrics of entrainment were therefore considered as covariates of sub-adult survival. Expanded salvage estimates (i.e. the total number of sub-adult Delta Smelt entrained on an annual basis) were used in Maunder and

Deriso's 2011 analysis, but this metric may underestimate the effect of entrainment at low population sizes (e.g. 100 fish entrained is likely consequential for a population of 1,000, but not for a population of 1,000,000). Proportional entrainment loss (PEL) accounts for this by estimating the proportion of a life stage entrained annually. This analysis considered both entrainment metrics, in addition to a large set of other candidate covariates previously identified as potential determinants of Delta Smelt population dynamics, to evaluate the effects of entrainment on the survival of sub-adult Delta Smelt using several related applications of the MDR.

As a statistical model, the MDR is suitable for identifying and evaluating the strength of correlations between each of the modeled vital rates and one or more candidate covariates. An extensive model comparison and selection effort was first undertaken to identify one or more significant covariates for each survival or recruitment transition (i.e. identify the "best" model, given the candidate covariates). The overall best model included density-dependence in sub-adult survival, but this model was only marginally preferred to a density-independent model. In the interest of clarity and consistency with other modeling efforts, the density-independent model was used for this analysis. This best model was then iteratively modified to include only one covariate of sub-adult survival, and the resulting coefficient estimates were compared to evaluate the strength of survival-entrainment relationships relative to other potential covariates. Although both expanded salvage and PEL were identified as significant covariates of sub-adult survival, the "best" model did not include any of the direct metrics of entrainment and instead retained indirect metrics of entrainment, South Delta turbidity and combined Old and Middle River flow (OMR), as covariates of this transition.

A modified version of the "best" model, which included PEL as the sole covariate of sub-adult survival, was then used to project Delta Smelt population dynamics forward for 21 years, recycling 1995-2015 covariate values for all variable except PEL, was evaluated under seven scenarios ranging in average annual loss from <1% to ~19%. The relative trajectories of the projected populations were intuitive, with the lowest PEL scenarios seeing the largest population growth. Even in the high PEL scenarios, positive population growth was achieved through the first six years of the projections (with non-PEL covariate values from the "best" model, including temperature, turbidity and food variables equivalent to the 1995-2000 period). Thereafter, the population trajectories diverged with higher PEL scenarios resulting in declines while lower PEL scenarios had increasing or stable populations.

This analysis reveals that, at least within the MDR life-cycle model framework, sub-adult Delta Smelt survival is significantly and negatively correlated with PEL. Moreover, the strength of this effect is equal or larger than that of any other single covariate. However, PEL was excluded from the "best" model as identified through an extensive model selection procedure; the conditions associated with greater likelihood of sub-adult and adult Delta Smelt being present in the South Delta (i.e. low OMR and high turbidity) were instead preferred by the model. This finding is consistent other recent studies that found South Delta turbidity and OMR were most strongly associated with entrainment mortality throughout the Delta Smelt life cycle. Comparison of projected scenarios indicated that consistently low rates of PEL could result in a stable or growing Delta Smelt population. In the scenarios in which the population did not markedly decline, PEL never rose above 4%. Since 2009, estimated PEL has remained in this same range, indicating that entrainment of sub-adults is unlikely to be limiting population growth at present, but could have contributed to declines that occurred during the early 2000s.

Persistently low Delta Smelt abundances in recent years in spite of substantial reductions in entrainment suggest that other conditions now constrain Delta Smelt population growth. Nevertheless, the results of this work indicate that in the absence of efforts to reduce Delta Smelt entrainment population declines between 2009 and 2016 likely would have been more severe.

1. Introduction

The factors contributing to a multi-decade decline in the survival and abundance of Delta Smelt have received considerable attention since the early 2000s. A wide range of analytical approaches have been applied in an attempt to partition the influence of a broad suite of potential drivers while accounting for substantial uncertainty associated with sampling pelagic species, changes in data availability, an evolving regulatory and water operations landscape and a Delta ecosystem that has experienced multiple larger perturbations (e.g. invasions, drought). The variables identified as most strongly associated with declines in Delta Smelt have varied somewhat between studies; likely owing to differences in analytical approach, covariates considered and/or the time periods analyzed. An ongoing Structured Decision-Making (SDM) effort by the Collaborative Adaptive Management Team (CAMT) is attempting to interrogate these differences through application of four previously published Delta Smelt life-cycle models using a shared dataset, candidate covariates and hypothetical management actions.

Among the many potential covariates of Delta Smelt survival and abundance that have been evaluated, of particular management relevance is the influence of direct mortality resulting from entrainment into large, South Delta water diversions. Because of its emphasis on evaluating management options, the CAMT SDM effort is testing the influence of covariates hypothesized to drive such entrainment (e.g. South Delta turbidity, OMR) rather than observed entrainment itself. An alternative analytical approach is to treat direct metrics of entrainment derived from observations of Delta Smelt in South Delta fish salvage facilities as covariates of life stage-specific survival. The influence of entrainment on post-larval and sub-adult Delta Smelt survival was evaluated directly by Maunder and Deriso (2011) by including total annual salvage as a candidate covariate of survival during either the March-July or December-April period. Although salvage during the December-April period (i.e. sub-adult and adult entrainment) was identified to have a substantial influence on recruitment (i.e. the coefficient for adult entrainment was among the largest estimated), models including salvage were deemed by the authors to have problematic characteristics, and so no conclusions on the role of entrainment were ultimately drawn. Annual indices of the absolute number of fish observed in the salvage facilities may also be inappropriate for evaluating impacts on population dynamics because, for a given number of fish salvaged, the impact on the population will vary depending on the current population size. Salvage as a proportion of some population estimate may therefore be a more realistic reflection of any impacts on entrainment on Delta Smelt dynamics.

Refined estimates of proportional Delta Smelt loss to entrainment during the winter and early spring (i.e. adult Proportional Entrainment Loss or PEL) have recently been produced (Smith et al. 2022), and so it is now possible to readily compare the influence of relative (PEL), absolute (Annual salvage) and indirect (e.g. OMR, South Delta turbidity) metrics of entrainment on Delta Smelt population dynamics. The objective of this study was to undertake such a comparison using an updated version of Maunder and Deriso's Delta Smelt life cycle model, in order to clarify a) whether entrainment of sub-adult and adult Delta Smelt during the winter and early spring has a measurable influence on survival, and b) which, if any, metric(s) of entrainment have the strongest support as covariates of survival during this period.

2. Methods

2.1 Model Background

In 2021 and 2022 Mark Maunder developed a generalized life cycle model based on extending the model described by Deriso and Maunder (2011) [henceforth referred to as the M&D model] and applied the resulting model to Delta Smelt, with candidate covariates and several of the model extensions borrowed from Polansky et al. (2021). Important differences between the original M&D model and the application of Polansky et al. nevertheless remain, and include model structure, survey indices used, inference method, covariates tested and consideration of density dependence; these differences are summarized in Table 1. The updated model, hereafter referred to as the MDR, is programmed in Template Model Builder (TMB; Kristensen et al., 2016) within R (R Core Team, 2017) in a Frequentist, state-space framework allowing for both process variation and observation error. Transition between stages (i.e. survival and the stock-recruitment relationship) can be a function of density and covariates, in addition to unexplained temporal variation (process error).

To best allow for comparison with the results of Polansky et al. (2021), the MDR was modified from the original M&D model to include an additional stage (adults; with the other stages adjusted appropriately) and estimate catchability (survey bias). The MDR is also fit to two additional indices of abundance for adults (spring midwater trawl prior to 2001 and spring Kodiak trawl for 2001 and later), and the likelihood function was changed to a log-normal likelihood (see Table 1 for additional detail). The period (1995-2015) and the covariates used by

Polansky et al. (2021) are different than those used in Maunder and Deriso (2011), and so were also updated in the MDR. A user guide along with a more complete description of the MDR model updates are included in Appendix A.

Table 1. Comparison of MDR model characteristics with the USFWS Delta Smelt LCM and the original Maunder and Deriso model.

Characteristic	M&D	Polansky et al.	MDR
Time frame	1972-2006	1995-2015 (1994 adults also included)	1995-2015
Stages	3 (larvae, juveniles, adults)	4 (post larvae, juveniles, sub-adults, adults)	4 (post larvae, juveniles, sub-adults, adults)
Stock-recruitment survival process variation (Adult to larvae survival)	Lognormal	Lognormal	Lognormal
Other survival process variation	Lognormal	Logit-normal	Lognormal
Density dependence	Beverton-Holt, Ricker, or Deriso-Schnute	None	Beverton-Holt (Ricker and Deriso-Schnute are also possible)
Indices of abundance	3 (20mm, summer tow net, fall midwater trawl)	4 (20mm, summer tow net, fall midwater trawl, spring Kodiak trawl, and spring midwater trawl)	4 (20mm, summer tow net, fall midwater trawl, spring Kodiak trawl, and spring midwater trawl)
Catchability (survey bias)	Catchability fixed at 1 (assumes can’t estimate absolute abundance)	Catchability fixed at one for 20mm and for spring Kodiak trawl (2001 and later), estimated for other surveys and years, but spring midwater trawl is assumed equal to the fall midwater trawl.	Catchability fixed at one for 20mm and for spring Kodiak trawl (2001 and later), estimated for other surveys and years, but fall and spring MWT are assumed equal. However, this had confounded parameters, so just

			estimated the catchability for Adult spring midwater tow
Observation error	Normal with known standard deviation that varies by year	Lognormal with known CV that varies by year (also investigated estimating CV scaler)	Lognormal with known CV that varies by year
Inference framework	Frequentist state-space	Bayesian state-space	Frequentist state-space
Model selection	Two at a time selection based on model averaging of AICC weights (density dependence model selection was based on full factorial without covariates)	Include all covariates and evaluate Bayesian interval coverage of zero	Stochastic exploration of covariate combinations followed by stepwise, AICc-based model selection.
Covariates	Various (see Appendix A)	Various (see Appendix A)	Various (see Table 3)

2.2 Application of MDR to Management Scenario Evaluation

Building from Mark Maunder's recent work, ICF began working with the MDR in 2022 in support of CAMT structured decision-making efforts. The underlying population dynamics model, and the statistical model fitting procedures, as coded in C++ were not modified for the analyses described here. Rather, ICF significantly expanded upon the R code used to fit, validate, and project the population dynamics model given alternative sets of environmental covariate values and associated model parameter estimates. Primary extensions include streamlined processing of covariate data to allow for rapid iteration between model formulations, an automated process for generating scenarios with modified covariate values based on hypothetical management actions, a series of functions for producing visualizations that aid in model interpretation and validation, and a function-based approach to model projection under multiple scenarios.

Within this framework the MDR has been utilized for the CAMT structured decision-making (SDM) process to evaluate the influence of proposed management actions and portfolios on Delta Smelt population growth rates. The general workflow for these evaluations as follows:

1) Select candidate covariates of each life-stage transition.
    a. An initial, extensive set of candidate covariate data based on the Smith et al. (2021) analysis was provided by USFWS. To this set ICF added a lagged effect of fall X2 on recruitment which was evaluated, and found to be a significant predictor of recruitment, in the original USFSW life cycle model publication (Polansky et al., 2021), but not evaluated in the Smith et al., (2021) analyses.
2) Select a base model.
    a. Initial evaluations used a base model that included covariates intended to match those reported in Smith et al. (2022) as closely as possible. This facilitated the most direct comparison of results between the two models.
    b. Subsequently, it was suggested that the MDR be optimized via a separate model selection procedure so that any important differences between models could be better evaluated. The "best" model identified through model selection (described below) was therefore used for later action/portfolio evaluations. Depending on the specifics of an action or portfolio, the "best" model was adapted to include as many of the managed covariates as possible in the event that they were not already included.

3) Fit the model with and without density dependence.
    a. The model is fit using maximum likelihood with optimization algorithms provided by Template Model Builder (TMB).
4) Project the model with baseline and alternative covariate values.
    a. Although theoretically possible, the state-space nature of the MDR poses challenges for backward-looking projection. That is to say, it is difficult to “rewind” the model to the beginning of the time-series used in model fitting and project forward from the historical abundances. As a result, model runs were projected forward from 2015, the last year in the data used for fitting.
    b. For each model and portfolio/action, baseline projections were produced by projecting Delta smelt abundance forward using unmodified covariate values; the covariates timeseries used for fitting were simply recycled, and the projections were run forward 21 years (i.e. the number of years used in model fitting). For density dependent models, additional years were projected to allow population equilibrium to be achieved before covariate effects were applied. This was achieved by adding 30 years to the beginning of the projection period with all covariates held at their mean values. Following this stabilization period, the covariate data were recycled as described above.
    c. The predicted effect of various management actions or portfolios of actions was evaluated by modifying the historical covariates to reflect alterations in water operations, water quality and/or food availability. Modified timeseries of covariates were then used in the model projection phase. The development of portfolios and their predicted effects on covariate values was undertaken by

CAMT and will not be further described here; neither salvage nor proportional entrainment were evaluated via the CAMT SDM process. Scenarios for evaluating the influence of proportional entrainment are discussed below in section 2.5.

5) Compare population trajectories between baseline and modified projections.
    a. Projected populations trajectories for each scenario were compared with one another and with the baseline (i.e. projection with unmodified historic covariates) to evaluate the relative performance of Delta Smelt under varying levels of entrainment loss during December-April.
    b. Note that the projections should be used only for comparative purposes and should not be interpreted as accurate predictions of future abundances. In developing and evaluating the MDR, Mark Maunder noted that forward projection resulted in highly uncertain abundance estimates because even after the inclusion of covariates and density dependence, a large amount of unexplained temporal variation in survival remains (see the discussion in Appendix A).

In contrast to this recent application of the MDR for management action evaluation via the CAMT SDM process, the goal of this analysis was to evaluate the impact of a single factor on population viability. In light of these differing objectives, several additions were made to the workflow above, and these are described in the following sections.

2.3 Comparison and Selection of Entrainment Indices

The appropriate metric for measuring the impact of entrainment on Delta Smelt requires some consideration. Given a relatively stable population, raw salvage can provide a useful proxy for the impact of entrainment on Delta Smelt. However, in a scenario where long-term directional change in abundance is occurring, raw salvage may be a poor proxy for this impact. For example, salvaging 1,000 fish would have a markedly different impact on a population of 1,000,000 versus a population of 10,000 Delta Smelt. With the estimated sub-adult population of Delta Smelt declining by more than two orders of magnitude since the 1990s, it seems possible that raw salvage is an inappropriate metric for evaluating entrainment effects. In a population with highly variable or directionally changing abundance the proportion of the population entrained is likely to be a much more relevant and direct index of impact. Such proportional estimates have recently been produced for adult Delta Smelt (i.e. loss during the December-April period; Smith et al. 2022) and these values were used for the present analysis.

Estimates of adult Delta Smelt proportional entrainment loss (PEL) were obtained from Smith et al. (2022) and detailed methods are provided therein. Briefly, PEL was calculated by dividing daily counts of adult Delta Smelt observed in the state and Federal salvage facilities by estimated daily populations of adult Delta Smelt during the winter entrainment season (typically December through April); daily estimates were then aggregated to produce annual PEL values. For years prior to the initiation of the Spring Kodiak Trawl (SKT) in 2002 an additional modeling step was required for estimating daily population size. In order to account for the additional uncertainty introduced by this step, high and low bookends are reported for PEL estimates prior to 2002. Two separate time-series of PEL were therefore considered for this analysis by incorporating these bookend values. Additionally, each PEL covariate was evaluated both in its raw, proportional form as an unbounded variable in logit space. As with all other covariates, all entrainment metrics were standardized to zero-mean and unit variance prior to use in the MDR model. Note that adult PEL is modeled as a covariate of sub-adult survival because this transition is bounded by the sub-adult (FMWT) and adult (SKT/SMWT) abundance indices.

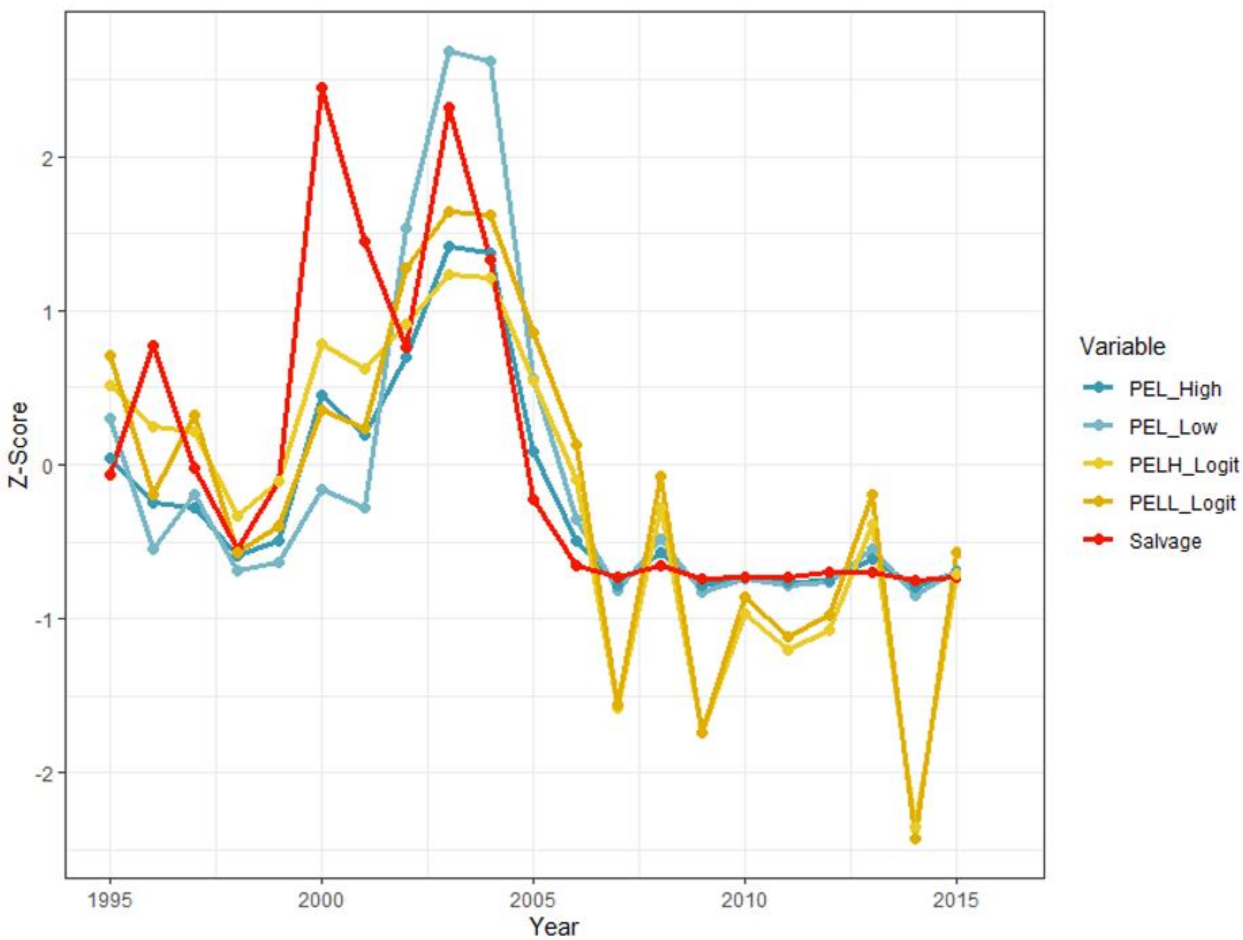

Figure 1. Standardized entrainment covariate values, 1995-20165

Although minor differences exist between the resulting covariate time series, the general patterns are similar: intermediate values with a declining trend prior to 2000, a period of markedly higher values from 2000-2005 and very low values since 2006. An exploratory comparison of results using either proportions or logit-transformed PEL values was made with little impact on the results, and so the logit-transformed values were used in subsequent analyses.

2.4 Model selection

A wide range of environmental and operational covariates have been hypothesized to impact recruitment and/or life-stage specific survival in Delta Smelt. As a statistical model, the MDR is suitable for identifying and evaluating the strength of correlations between each of the modeled vital rates and one or more candidate covariates. In contrast to a mathematical simulation, such as the Delta Smelt individual based model (IBMR), the form and strength of any covariate influence cannot be manually specified, and so hypothetical management scenarios can only be compared through projection when a managed covariate is found to significantly influence one or more vital rate. A commonly used approach for selection of an optimal model is to begin with all candidate covariates included and then sequentially remove variables based on some selection criterion. However, this stepwise approach has several important limitations when applied to the MDR model:

1) Inclusion of multiple correlated covariates of a single life-stage transition in the model tends to produce poor fits and obscure the influence of such covariates. Stepwise selection must therefore be initiated from a candidate set where covariates of a given transition are not highly correlated (i.e. $r > \sim 0.6$-0.7).
2) The importance of a covariate may depend on the inclusion of another covariate in the same, or a separate life-stage transition, and in such cases a stepwise approach to model selection can exclude an important covariate.

3) Retention of a covariate may depend on whether density dependence is included in one or more of the life-stage transitions.

A global model selection approach where all potential combinations of covariates are evaluated would theoretically overcome these limitations, but such an approach is precluded by computational time: given a large pool of potential survival and recruitment covariates, and four separate transitions to which covariates may be applied, the number of potential model parameterizations is extremely large. As an alternative approach, a stochastic model selection procedure was therefore developed that attempts to realize the benefits of global model selection (i.e. identifying potential synergies or dependencies between covariates) within a reasonable amount of computational time. The stochastic approach involved random selection of two covariates per transition from the complete set of candidates (Table 2) and random selection of which, if any, life stages were subject to density dependence (options for density dependence were weighted such that there was equal probability of no density dependence and *any* density dependence).

Table 2. Candidate Covariates included in Model Selection

Covariate^	**Impacted Transition**	**Covariate aggregate months***
X2	Post-larval survival	June-August
Delta Outflow	Post-larval survival	June-August
Delta mean Temperature	Post-larval survival	June-August
Delta mean Secchi depth	Post-larval survival	June-August
Food (small)	Post-larval survival	June-August
Food (small/large)	Post-larval survival	June-August
Inland Silverside Index	Post-larval survival	June-August
Threadfin Shad Index	Post-larval survival	June-August
Tridentiger Goby Index	Post-larval survival	June-August
South Delta Secchi Depth	Post-larval survival	April-June
OMR	Post-larval survival	April-June
X2	Juvenile Survival	September-November

Delta Outflow	Juvenile Survival	September-November
Delta mean Temperature	Juvenile Survival	September-November
Delta mean Secchi depth	Juvenile Survival	September-November
Food (large)	Juvenile Survival	September-November
Food (small/large)	Juvenile Survival	September-November
Age 1+ Striped Bass Index	Juvenile Survival	September-November
OMR	Sub-adult Survival	December-February
Delta Outflow	Sub-adult Survival	December-February
South Delta Secchi Depth	Sub-adult Survival	December-February
Delta mean Temperature	Sub-adult Survival	December-February
Delta mean Secchi depth	Sub-adult Survival	December-February
Proportional Entrainment (Low Bookend)	Sub-adult Survival	December-February
Proportional Entrainment (High Bookend)	Sub-adult Survival	December-February
Salvage	Sub-adult Survival	December-February
Age 1+ Striped Bass Index	Sub-adult Survival	December
Food (large)	Sub-adult Survival	December-February
Delta Outflow	Recuitment	March-May
Delta mean Temperature	Recuitment	March-May
Delta mean Secchi depth	Recuitment	March-May
Food (small)	Recuitment	March-May
Food (large)	Recuitment	March-May
Inland Silverside Index	Recuitment	March-May
Tridentiger Goby Index	Recuitment	March-May
X2	Recuitment	Prior September-November

^ Covariate data were obtained from USFWS; sources are summarized in Smith et al. (2021)
*Aggregation periods based on methods from Smith et al. (2021)

For each randomly generated model, Akaike's Information Criterion corrected for small sample sizes (AICc) was calculated as an index of overall model performance. Next, 80% confidence intervals were calculated for each covariate in the model, and were evaluated for significance (i.e. overlap of zero). This stochastic model fitting procedure was repeated 400,000 times. After completion of stochastic model building, the results were summarized by calculating, for each candidate covariate, the proportion of times the covariate was significant in a model, given that it was selected (i.e. 80% confidence interval excluding zero), and the average AICc of the models in which a covariate was included. In addition, the model with the lowest overall AICc score was used as a starting point for a final, stepwise model selection approach in order to evaluate whether a better model could be produced by including more or less than two covariates per transition.

2.5 Evaluating the Magnitude of Sub-Adult Entrainment Effects

Examination of correlations between candidate covariates and sub-adult survival can provide some guidance on the likely influence of the covariates on Delta Smelt population dynamics. Pearson correlation coefficients of the log-transformed ratio of the adult and sub-adult indices (i.e. log(N_Adults/N_SubAults)) and candidate covariates were calculated. Because adult index values prior to 2001 were derived from the Spring Midwater Trawl survey, these earlier values were adjusted based on the model-estimated catchability coefficient (q = 0.144) prior to the calculation of correlation. While these raw correlations are readily interpretable, they do not account for the complexities and dependencies of the Delta Smelt life cycle. In contrast, the estimated coefficients for each modeled covariate do account for such complexities, and because covariates are standardized prior to model fitting the resulting coefficients give a general picture of the relative magnitude of their influence on sub-adult survival in the context of the broader life cycle. Further comparison of entrainment impacts with other potential covariates of sub-adult Delta Smelt survival was therefore achieved by modifying the “best” model identified through the model selection procedure to include only one covariate for the sub-adult to adult transition and then refitting each model; covariate for all other transitions were left unchanged during this exercise. Coefficient estimates for each of the potential sub-adult survival covariates were then extracted from the model results. The resulting single-covariate results were also compared with the coefficient estimates from the “best” model which included two covariates of sub-adult survival.

While the coefficient estimates allow for evaluation of the relative importance of covariates, and their confidence intervals indicate whether a covariate has *any* significant effect on survival, they do not allow for straightforward interpretation of the magnitude of impact on the abundance or population growth. Of ultimate interest here is the degree to which modifying a survival covariate within a realistic range impacts the long-term trajectory of the Delta Smelt population. Following the workflow described in Section 2.2, seven scenarios of entrainment were therefore projected forward for 21 years (Table 3). The model formulation used for these projections was modified from the “best” model covariates shown in Table 4 by replacing the sub-adult survival covariate with the high bookend estimates of logit-transformed PEL; the other PEL time-series including the low bookend values and non-transformed were also tested, but with only minor impact on results, and for simplicity are not reported here.

It is important to note that hypothetical entrainment scenarios were unrealistically simplified, and as noted previously, the projections are inherently uncertain and should not be taken as actual predictions of future Delta Smelt abundance, but instead used only for comparative purposes. The seven scenarios include a baseline projection in which historic covariate values are simply reused without modification, four constant scenarios where PEL is held at the 5^{th} (low), 25^{th}, 50^{th} (median) or 75^{th} (high) percentile of the historic estimates, and two additional scenarios with PEL values held constant only before or after 2008/2009. These final two scenarios are intended to capture management changes which appear to have effectively limited Delta Smelt since 2009: the ReducePreBiOp scenario simulates a situation in which entrainment was also reduced pre-2009 while the NoBioOp scenario simulates conditions in which management did not change and entrainment continued at the pre-2009 average.

Table 3. Proportional Entrainment Loss Scenarios Used in Forward Projection of MDR Model

Scenario Name	PEL Low Value	PEL High Value	Modified Period
Base	N/A	N/A	None
Entrainment_Low	0.6%	0.8%	All
Entrainment_ReducePreBiOp	1.0%	1.0%	1995-2008
Entrainment_25th	1.7%	1.9%	All
Entrainment_Median	4.8%	7.6%	All
Entrainment_NoBiOp	12%	15%	2009-2015
Entrainment_High	14%	19%	All

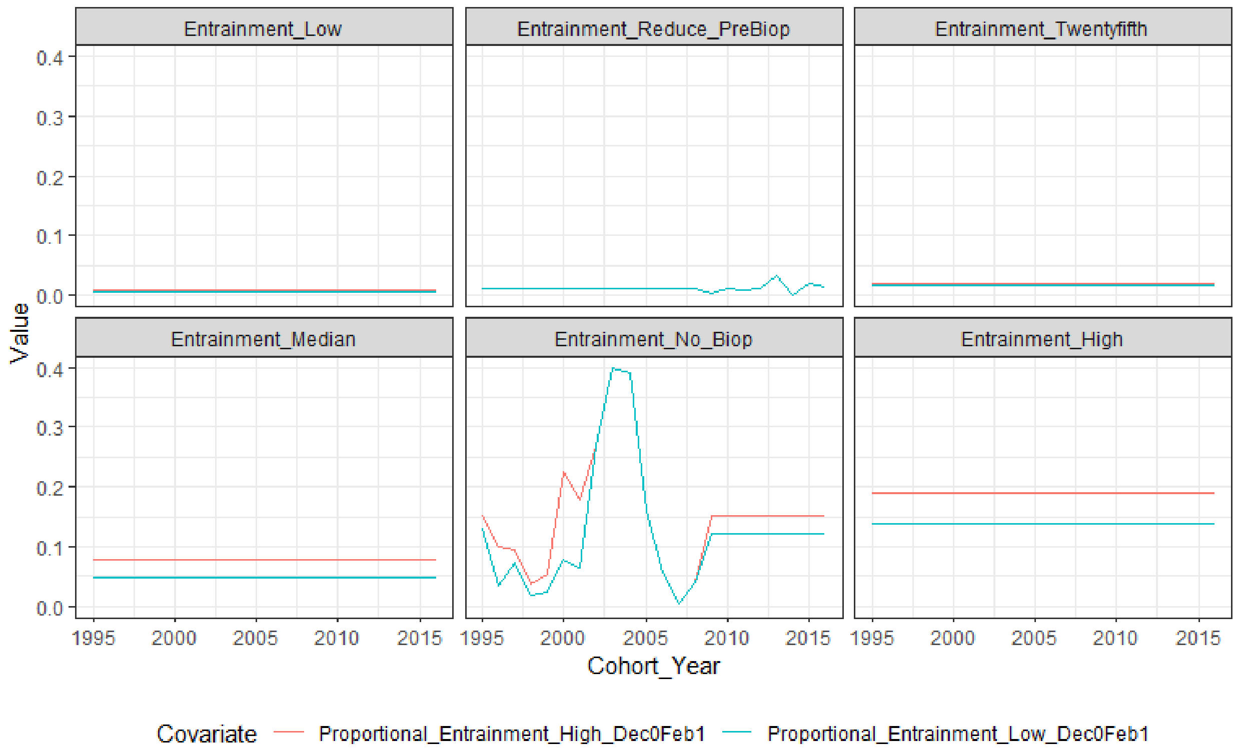

Figure 2. Time-series of PEL non-transformed scenario covariate values

3. Results

3.1 Model Selection

The overall "best" model identified after application of the hybrid stochastic-stepwise model selection process included South Delta Secchi depth and Beverton-Holt density dependence for the sub-adult survival transition. The lowest AICc model excluding density dependence also included OMR as a significant covariate of sub-adult survival (Table 4.). Models where ΔAICc <2 are generally considered to be essentially equal in terms of parsimony, and so based on this analysis the role of density dependence remains equivocal. Notably, direct measures of sub-adult entrainment were not included in the best model.

Table 4. Summary of "best" models as identified through a hybrid stochastic and stepwise model selection procedure.

	With Density-Dependence	**No Density-Dependence**

Density Dependent Transition	Sub-adult Survival	N/A
Post-Larval Survival	Temperature_mean_Jun0Aug0 NJACM_BPUV_Jun0Aug0*	Temperature_mean_Jun0Aug0 NJACM_BPUV_Jun0Aug0*
Juvenile Survival	Secchi_mean_Sep0Nov0 Temperature_mean_Sep0Nov0	Secchi_mean_Sep0Nov0 Temperature_mean_Sep0Nov0
Sub-Adult Survival	SouthSecchi_mean_Dec0Feb1	OMR_Dec0Feb1 SouthSecchi_mean_Dec0Feb1
Recruitment	Fall_X2_Lag	N/A
Minimum AICc	215	217

*Summer X2 or Outflow can be substituted for summer food with negligible impact on AICc

Direct and indirect metrics of sub-adult Delta Smelt entrainment were nevertheless both consistently identified to be significant covariates of survival. Ranked by the frequency with which a covariate was found to be significant (given that it was randomly selected to be included in a model), the five highest ranked variables are all relevant to South Delta entrainment for density independent models. OMR was the covariate most frequently identified to be significant in the absence of density dependence and was retained in nearly all randomly generated models in which it was included. South Delta Secchi depth was also retained in nearly every model where it appeared, regardless of density dependence. PEL high, salvage and PEL low followed with each being retained in more than 75% of the density-independent models. Models that included OMR had substantially lower average AICc values than for any other variable (Figures 3 and 4). Inclusion of density dependence substantially reduced the likelihood the PEL variables would be significant covariates of survival but increased the likelihood of raw salvage being significant.

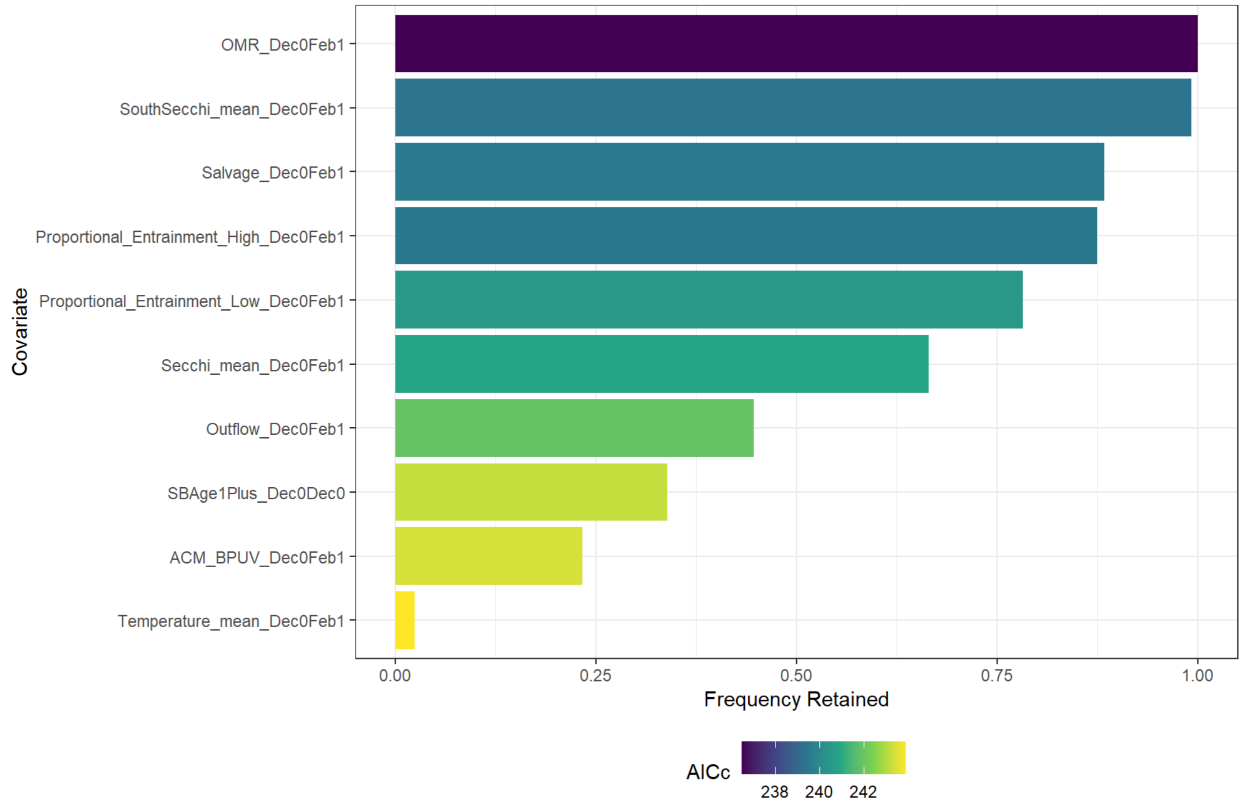

Figure 3. Results of stochastic model selection with no density dependence

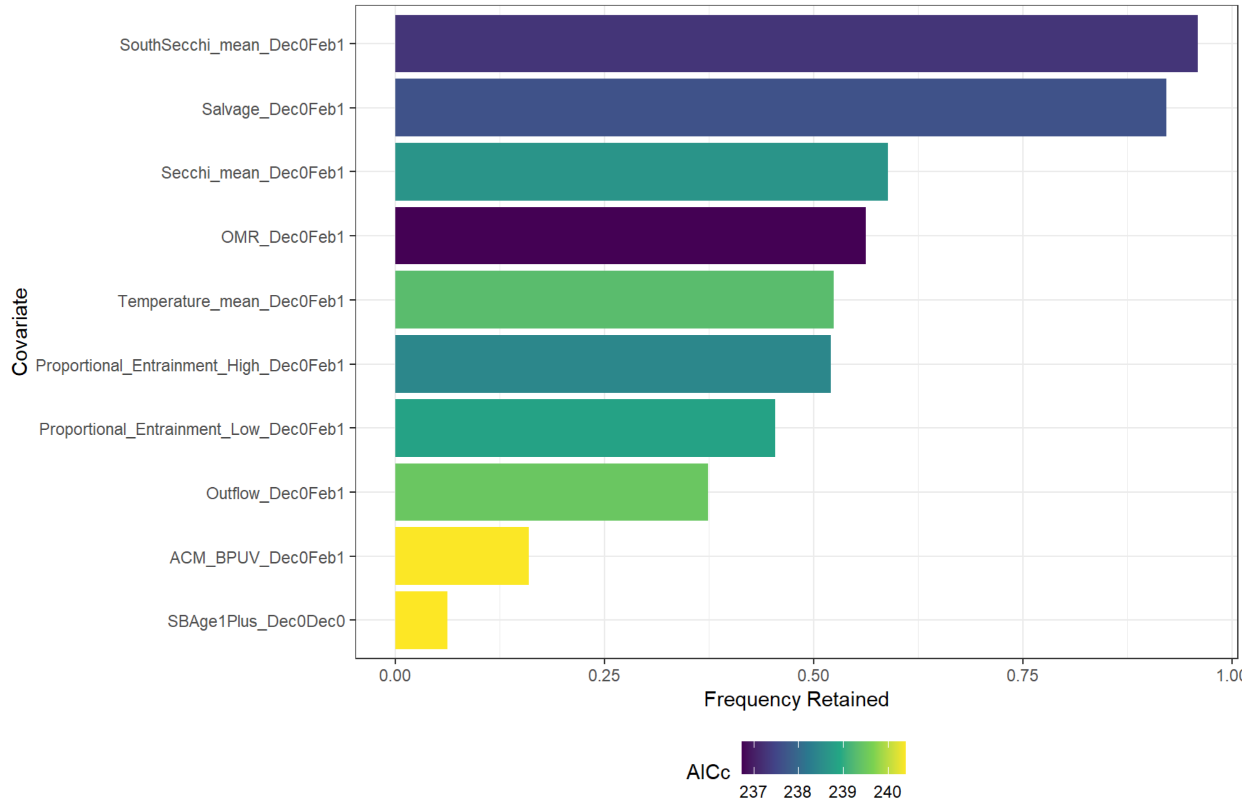

Figure 4. Results of stochastic model selection with density dependence

3.2. Correlation with Covariates and Comparison of Estimated Coefficients

Comparison of candidate covariates and the log ratio of adult to sub-adult Delta Smelt abundance indices revealed modest correlations for all entrainment related covariates including indirect (OMR and South Delta Secchi depth), absolute (Salvage) and relative (PEL) metrics (Table 5). The direct metrics all had the largest, and similar Pearson correlation coefficients ranging from -0.63 to -0.67. The indirect entrainment metrics showed somewhat weaker correlation and the remaining candidate covariates showed minimal correlation.

Table 5. Pearson Correlation Coefficients (*r*) for sub-adult survival (log(Adults/sub-adults)) and candidate covariates

Covariate	Correlation Coefficient
OMR	0.40
Delta Outflow	-0.03
South Delta Secchi Depth	0.49
Delta mean Temperature	-0.09
Delta mean Secchi depth	0.42
Proportional Entrainment (Low Bookend)	-0.63
Proportional Entrainment (High Bookend)	-0.67
Salvage	-0.65
Age 1+ Striped Bass Index	-0.17
Food (large)	0.22

For fitted models containing a single sub-adult survival covariate, the high bookend proportional entrainment variable was found to have the largest individual effect on sub-adult survival. When both OMR and South Delta turbidity were included, as is the case in the “best” model, the resulting coefficients were somewhat larger than for PEL (Figure 5), suggesting some potential synergistic effect between these two indirect entertainment covariates.

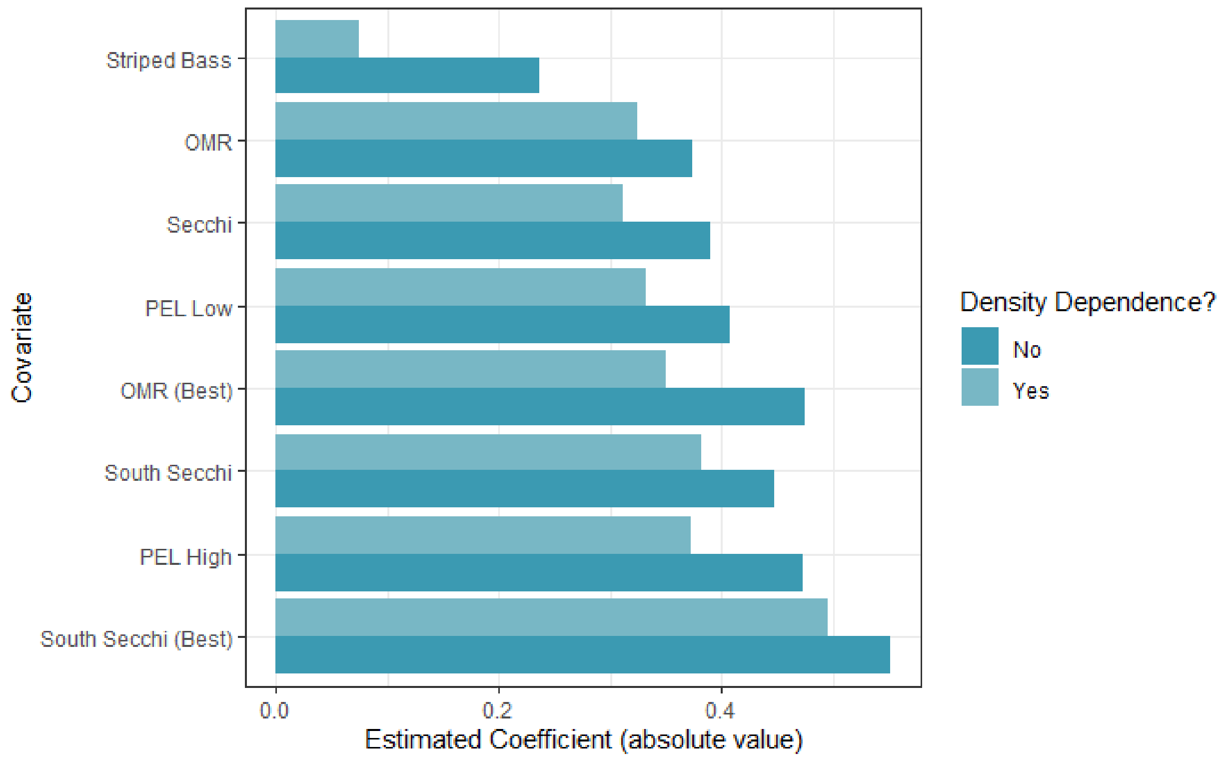

Figure 5. Comparison of estimated model coefficients for selected candidate covariates of Delta Smelt sub-adult survival

3.3. Comparison of Projected Adult Abundance Across Entrainment Scenarios

Based on the marginal improvement of AICc with the inclusion of density dependence and apparently reduced influence of PEL for these models, projections were run only without density dependence. This decision is not intended to ignore the need to clarify what, if any, role density dependence has played in Delta Smelt population dynamics, and this issue is addressed further in the discussion. However, without stronger AIC-based evidence supporting the inclusion of density dependence, we have chosen to avoid the added complexity for this analysis. Forward projection of PEL scenarios indicates a substantial impact of entrainment on Delta Smelt population trajectory. Predictably, the scenarios with the lowest entrainment (Low and

Reduce_PreBiOp) resulted in consistently larger adult populations than the other scenarios (Figure 6).

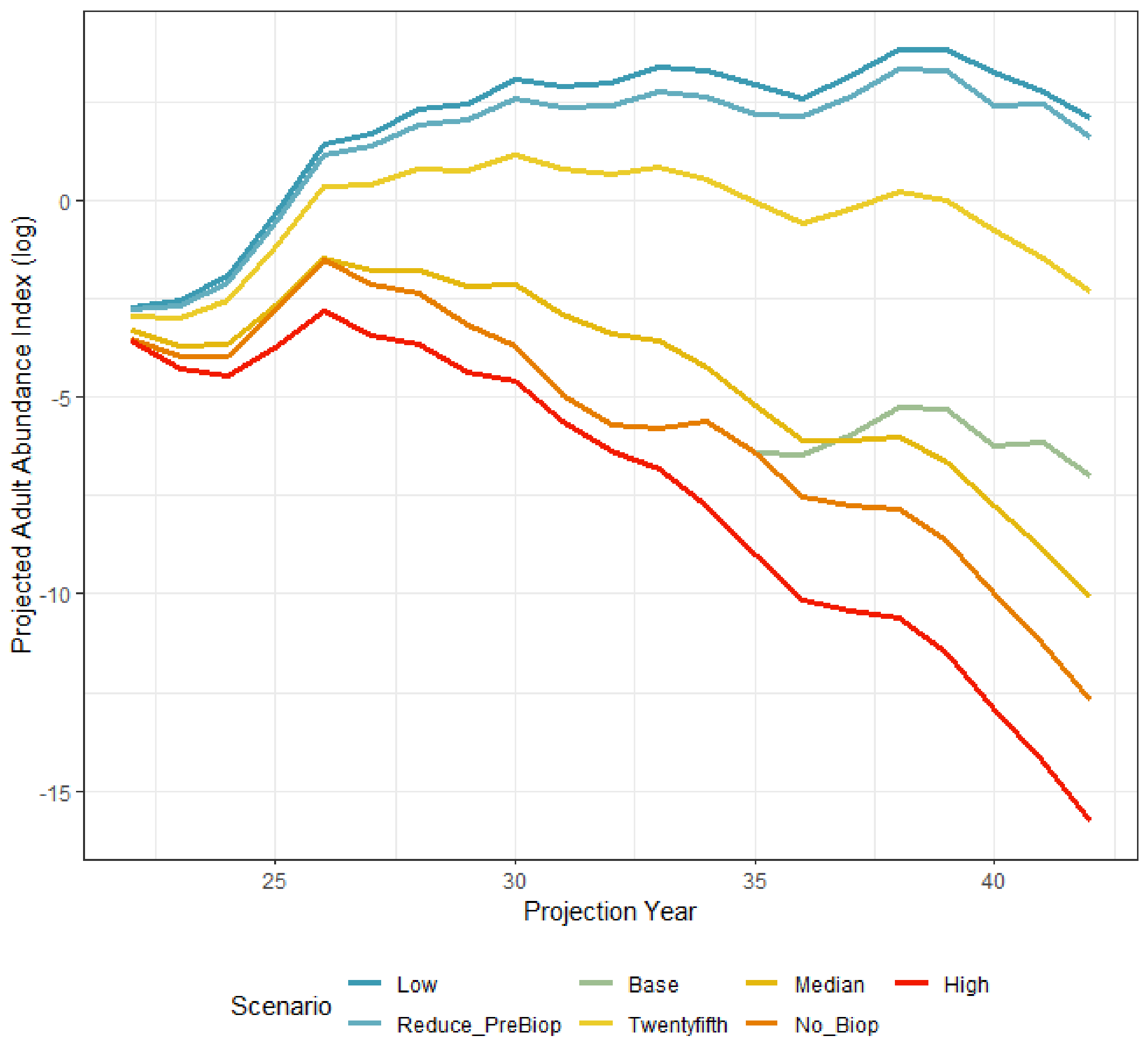

Figure 6. Modeled adult Delta Smelt log abundance indices across 21 years of forward projection

In these consistently low entrainment scenarios, the populations grew rapidly to very large sizes and then remained largely stable across the final 10 years of projection. In contrast, models projected continuing declines in the higher entrainment scenarios. The magnitude of differences between these scenarios and the baseline projection are thus extreme, and for low entrainment scenarios are almost certainly unrealistically optimistic. One result of interest is the comparison between the baseline and No_BiOp scenarios, which as expected, overlap completely through the first 15 years of projection. However, the two projections show strong divergence when the pre-2009 mean entrainment is assumed for the later projection years, suggesting that further declines in Delta Smelt would have occurred in the absence of entrainment reductions. Figure 7 shows the distribution of scenario population growth rates relative to baseline projections. These figures further highlight that population growth was frequently improved relative to baseline, in some cases substantially, when entrainment loss was consistently low.

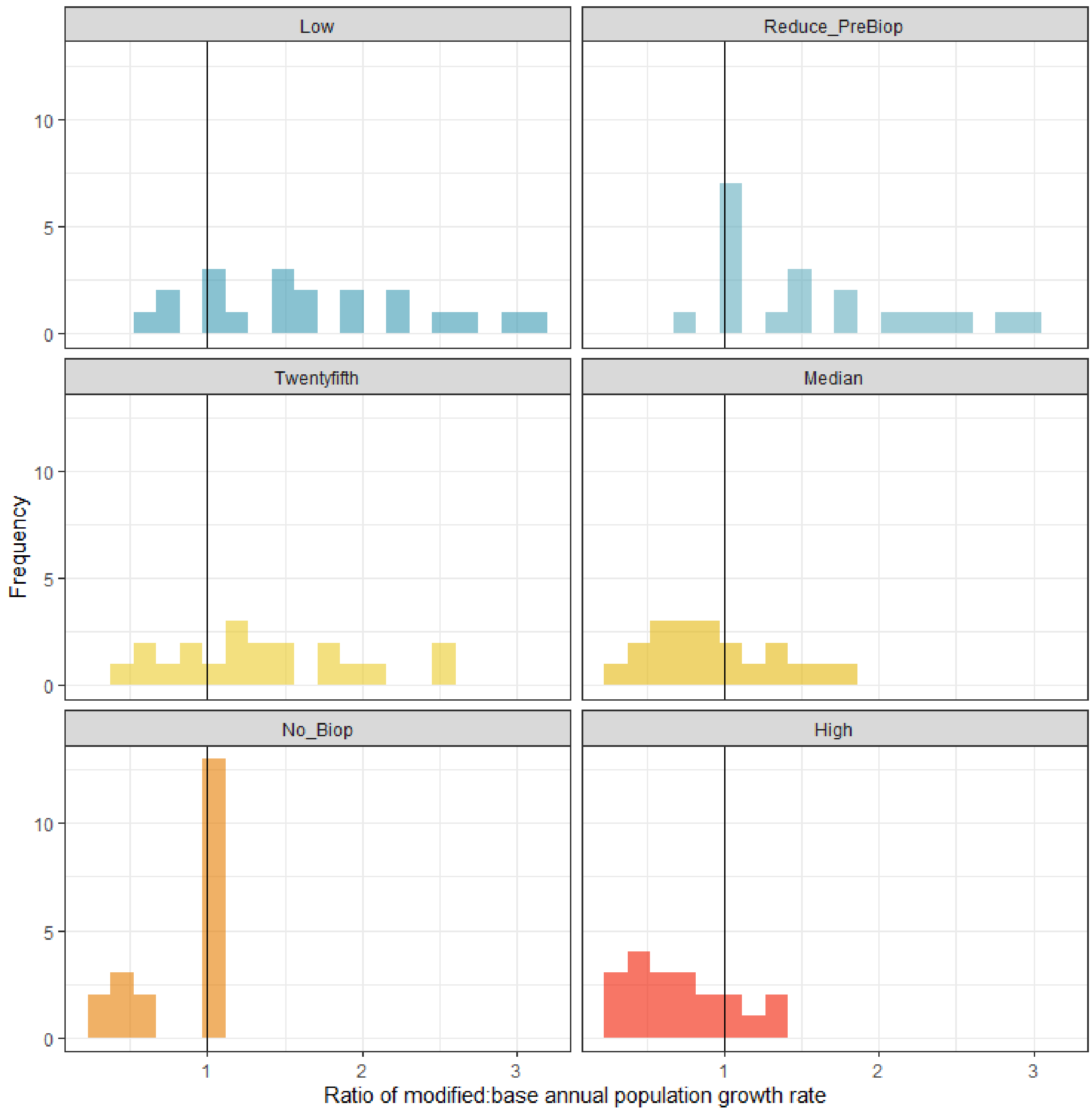

Figure 7. Ratios of annual population growth rates from modified and baseline projections. Values larger than 1 indicate a scenario resulted in greater population growth than with baseline entrainment conditions.

4. Discussion

It is clear from this modeling exercise that, within the MDR life-cycle model framework, sub-adult Delta Smelt survival is significantly and negatively correlated with indices of entrainment, including absolute, relative, and indirect metrics. As a single covariate of sub-adult survival, proportional entrainment loss showed a stronger influence than any other single covariate considered (but note that OMR and turbidity have larger coefficients when included together). The model selection procedure made an implicit comparison of absolute (salvage counts), relative (PEL) and indirect (OMR, South Delta Turbidity) metrics of entrainment, and the covariates included in the "best" model suggest that the conditions associated with greater likelihood of sub-adult and adult Delta Smelt being present in the South Delta (i.e. low OMR and high turbidity) are better predictors of sub-adult survival than a direct metrics (PEL/salvage). Exclusion of PEL salvage from the best model does not indicate that these factors are unimportant, but rather that they explain less of the variability in sub-adult survival than other variables considered. This could result from the fact that many smelt are likely lost in the South Delta before ever arriving in the vicinity of the salvage facilities or uncertainty arising from the salvage sampling process. It may also indicate that OMR and South Delta turbidity have impacts on survival independent of their association with entrainment risk. In any case, this finding is consistent with Smith et al. (2021), where South Delta turbidity and OMR were most strongly associated with entrainment mortality throughout the Delta Smelt life cycle.

Results from forward projections should be interpreted cautiously and used only for comparative purposes (See Appendix A for further discussion of uncertainties associated with projecting the MDR). Nevertheless, projection of adult Delta Smelt abundance under a range of PEL scenarios indicated that, given the historically observed patterns in the other model covariates, consistently low rates of PEL could result in a stable or growing Delta Smelt population. In the scenarios in which the population did not markedly decline, PEL never rose above 4%. Since 2009, estimated PEL has remained in this same range, suggesting that entrainment of sub-adults is unlikely to be limiting population growth at present, but was correlated with changes in sub-adult survival that occurred in the past including declines during the early 2000s. The contrast between the baseline conditions and the scenario in which no entrainment reductions occurred during the later years of projection (Figure 6) indicate that entrainment management has likely helped to prevent further declines in Delta Smelt abundance. However, consistent with observations in the real world, in spite of persistently low entrainment loss none of the projections show a notable increase in abundance during this low-entrainment loss period. This suggests that some other factor(s) have constrained Delta Smelt population growth despite low entrainment. In the model described here, the other included covariates are summer temperature and zooplankton food density and autumn turbidity and temperature, though these potentially correlate with many other aspects of the Delta ecosystem.

The results described here are based on a model assuming no density dependence in survival or recruitment. Given the depleted state of the Delta Smelt population, density independence has been generally assumed in other life cycle models and the original Maunder and Deriso model was criticized for its inclusion of density dependence. Nevertheless, in both the analysis described in Appendix A and the model selection procedure described above, support remains for the potential of density dependent processes acting on subadult survival. It was beyond the scope of this analysis to try and resolve this critical issue, and since density-independent models had nearly as strong support as the best density-dependent bases on a comparison of AICc, we chose to avoid the added complexity of density dependence. However, inclusion of density dependence has substantial impacts on the model results, including which covariates are retained, the strength of their influence on survival, and the trajectory of projected populations. In the best density dependent model, inclusion of Beverton-Holt density dependence acting on sub-adult survival can serve as a substitute for OMR as a covariate. These two results have potentially very different management implications, and a broader discussion and analysis of density dependence in the Delta Smelt life cycle therefore seems prudent.

5. Literature Cited

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., Bell, B.M., 2016. TMB: automatic differentiation and laplace approximation. *J. Stat. Softw*. 70, 1–21.

Maunder, M.N., and Deriso, R.B. 2011. A state–space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (*Hyposmesus transpacificus*). *Can. J. Fish. Aquat. Sci*. 68(7): 1285–1306.

Polansky, L., Newman, K. B., & Mitchell, L. (2021). Improving inference for nonlinear state-space models of animal population dynamics given biased sequential life stage data. *Biomet.*, *77*(1), 352-361.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Smith, W. E., Polansky, L., & Nobriga, M. L. (2021). Disentangling risks to an endangered fish: using a state-space life cycle model to separate natural mortality from anthropogenic losses. *Can. J. Fish. Aquat. Sci*, *78*(8), 1008-1029.

Smith, P.E., Donovan, J.M., Gross, E.S., Korman, J, McNamara, B.J. & Grimaldo, L.F. (2022). Adult Delta Smelt Proportional Entrainment Losses at the State and Federal Export Facilities within the Sacramento-San Joaquin Delta. DRAFT REPORT, May 4, 2022.

Appendix A. Report from Mark Maunder: Illustration of the Generalized Life Cycle Model (GLCM) with application to the delta smelt data from Polansky et al. (2021)

By Mark Maunder

Introduction

We develop a generalized life cycle model based on extending the model described by Deriso and Maunder (2011) [henceforth referred to as the M&D model] and applied to Delta smelt. Several of the extensions are taken from Polansky et al. (2021). The differences between the original M&D model and the application of Polansky et al. include model structure, surveys used, inference method, and covariates tested. The differences are listed in Table 1.

The model is programmed in Template Model Builder (TMB; Kristensen et al., 2016) within R (R Core Team, 2017). The original M&D model was programmed in AD Model Builder (ADMB; Fournier et al. 2012) and hypothesis testing was applied manually. TMB provides a more efficient method of analyzing random effects (the approach to implementing the state-space model and the associated process error) and the R programming environment allows automation of the hypothesis tests.

The code to implement the following analyses is included in file "`USFWS working.r`", which in turn sources several r scripts with additional calculations and functions, and compiles the TMB code "`LHmodel.cpp`", which implements the model.

The Generalized Life Cycle Model

The Generalized Life Cycle Model (GLCM) represents a single cohort life strategy species that dies after it reproduces (i.e. the final transition is from adults to recruits and very few adults survive to the next time period e.g. an annual species), but can have any number of stages that the cohort passes through. It is modelled in a Frequentist (but Bayesian inference is possible in TMB) state-space framework allowing for both process variation and observation error. Transition between stages (i.e. survival and the stock-recruitment relationship) can be a function of density and covariates, in addition to unexplained temporal variation (process error). Covariates can also be used to influence the density dependent relationship or the survey catchability (bias). The model can be fit to any number of surveys representing any of the stages. There is also flexibility in the timing of density dependence, surveys, process error and covariates. The covariates can be estimated as random variables to represent uncertainty in the measurement of the covariates, dealing with missing covariates, or allowing for uncertainty in projections, but this is not illustrated here.

Application to delta smelt

The GLCM is illustrated with application to Delta smelt following Polansky et al. (2021) as far as practical by modifying the approach of M&D model. The model of M&D was modified to include an additional stage (pre-adults), with stages adjusted appropriately, fit to two additional indices of abundance for adults (spring midwater trawl prior to 2001 and spring Kodiak trawl for 2001 and later), catchability (survey bias) estimated for summer tow net and fall midwater tow, the catchability for the spring midwater trawl was set equal to the fall midwater trawl, and the likelihood function was changed to a log normal (see Table1). [estimation of catchability was confounded with other parameters so in the final model only catchability for adult abundance in the spring midwater trawl was estimated] The time period (1995-2015) and the covariates used by Polansky et al. (2021) are different than those used in Maunder and Deriso (2011). See table 2 for a list of covariates from Polansky et al. (2021) used in this application. [the single interaction of covariates used in Polansky et al. was not used in this application] The surveys were fit at the start of the stage before any other processes occurred. Covariates and process variation were included after density dependence.

Several different analyses were conducted some with and without density dependence. The density dependence included in the model was based on running all combinations of Ricker, Beverton-Holt, and density independence combinations for all the stages.

Four different approaches for model selection were used:

1) Calculating the correlation between the log of the ratio of indices of consecutive life stages and covariates
2) Running the model for all covariates and determining the confidence intervals on coefficients that excluded zero
3) Simple forward stepwise regression
4) Two at a time AICC weights based model averaging

Steps in doing the analysis

Compile and load the TMB code

TMB must be installed on the computer to run the model. TMB is installed as an R package and the library loaded (see `https://cran.r-project.org/web/packages/TMB/index.html`).

Once installed, load the library using `library(TMB)`

Read in the R functions

There are several R functions that have been created to automate the model selection. The scripts containing these functions must be loaded into R. The scripts include:

`USFWS_functions.R`

`LHM functions.R`

`Test2by2.R`

`TwoByTwo.R`

`DD.R`

Read in the data and set up the TMB lists

Read in the survey indices of abundance and the covariates. These need to be formatted in the correct way so they can be included in the TMB data list in the right format. The indices of abundance were divided by 1,000,000 to improve parameter estimation (avoiding the b parameter of the density dependence function from being excessively small), so the results are all in millions of fish, where relevant.

The Polansky et al. model starts with the adults in model year 1994 with the first “recruitment” covariate being for the transition from Adults in model year 1994 to juveniles in model year 1995. Since the GLCM model starts with post larvae in model year 1995, the survey index for adults in 1994 is not used and the covariate for the transition should be removed from the data and the whole set of covariate values used for “recruitment” in Polansky et al. were therefore lagged appropriately. This also means that there should be a covariate for “recruitment” in the last year, but it is not used.

The TMB model requires a list of data (`data`), a list of initial parameter values (`pars`), a list of parameters that are treated as random (integrated out using Laplace approximation; `random`), and a list defining what parameters are to be fixed and what parameters are shared (`map`).

The probability of converging on the global optima will be improved by providing reasonable initial values for the parameters. Care should be taken to make sure that there are the correct number of initial values for the covariate coefficients (vector `beta`).

Two scrips are used to read in the data and set up the TMB lists:

```
USFWS data.R
```

```
USFWS setup.R
```

Look at the raw correlations

The correlation between the log of the ratio of indices of consecutive life stages and covariates is calculated. The correlations that include adult abundance are only calculated from 2001 due to the different surveys used and therefore catchability is not consistent. The correlation is provided in Table 1 and illustrated in Figures 1-4. Many covariates have a correlation greater than 0.3, although some of them have the wrong sign. These types of correlations should be interpreted with care because they do not take into consideration the variation in observation error among indices and with time.

Run the model with no covariates

The parameters are estimated using the nonlinear function minimizer `nlminb` provided in R using the analytical gradient produced by TMB (other nonlinear optimizers or Bayesian inference methods could be used).

```
nlminb(obj$par,obj$fn,obj$gr)
```

The model passes the `nlminb` convergence criteria returning `0`. The maximum gradient component is `1.976633e-4`, which is reasonable. The model fits the survey data reasonably well (Figure 5). However, the standard errors (SEs) for some of the parameters are extremely large indicating that the parameters are confounded.

Parameter	Estimate	Std. Error
`ln_a` (post-larvae)	-0.8256441	5.707725e+05
`ln_a` (Juveniles)	-0.2525674	5.707725e+05
`ln_q` (adults in spring midwater trawl)	-0.6295874	5.707725e+05

It is not necessary to estimate the catchability to evaluate the effect of the covariates on survival, unless a covariate (e.g. entrainment) is used in absolute number of individuals. Therefore, the confounding can be eliminated by fixing the catchability. However, since there are two indices for the adult stage and the catchability is only known for one of them, the catchability for the other index must be estimated.

Changing which catchability parameters are estimated is controlled by the TMB `map` list, where `NA` means do not estimate and a number means estimate. [two or more parameters with the same number means estimate a single value and share it among those paramaters] The following estimates the catchability for the adult abundance in the spring midwater trawl and fixes the other catchabilities.

```
USFWS_map$ln_q <- factor(c(NA,NA,NA,1,NA))
```

The model passes the `nlminb` convergence criteria returning `0`. The maximum gradient component is `8.51522e-05`, which is reasonable. The model fits the survey data the same as when the two catchabilities were estimated (Figure 6). The standard errors (SEs) are now all reasonable. The parameters are essentially the same for all the parameters when the two catchabilities were estimated, except for some of the "`a`" parameters for the density dependence function. This model with a single catchability estimated is used in the rest of this report.

Run the model with all the covariates

The covariates are turned on by removing the `beta` parameter from the `map` list (`USFWS_map$beta` can be commented out using the `#` sign). The model passes the `nlminb` convergence criteria returning `0`. The maximum gradient component is `2.502899e-4`. The model fits the survey data similar to when no covariates are included (Figure 7).

The 80% confidence intervals for the estimates of the covariate coefficients (vector `beta`) are examined to see if they include zero. If they don't, it suggests that these covariates are significant. Ten of the covariates have 80% confidence intervals that don't cover zero (Table 2 and Figure 8), but two of them have the wrong sign.

Run the forward stepwise model selection

The forward stepwise model selection requires setting up the matrix of hypotheses, which includes identifying the covariate, process that is impacted, stage, and the sign of the relationship. The processes include survival before density dependence "`BDD`", survival after density dependence "`ADD`", survey catchability "`q`", and the density dependence "`b`". The sign can be restricted to be positive "`pos`", negative "`neg`", or either "`both`". The forward stepwise model selection is run using function "`LHM.forward`".

The forward stepwise model selection procedure found 7 covariates that provide an AICc within 4 units of the best AICc (Tables 2 and 3).

The model was run with only these covariates included. This is done by modifying the "`design_in_*`" matrices (e.g. `design_in_after`). The number of initial values for the covariate coefficients (vector `beta`) also needs to be adjusted appropriately.

None of the covariates had confidence intervals for their coefficient that included zero (Figure 9).

Run the two-by-two model averaging model selection

The two-by-two model averaging model selection requires setting up the matrix of hypotheses as described above and is run using function "`LHM.twobytwo`".

The two covariates at a time AICc model averaging procedure selects some covariates with the wrong sign as they can be the right sign when combined with remaining covariates, but none of these were included in the models that had an AICc within 4 units of the best model. The models selected are the same as selected in the forward stepwise model selection, but the first three covariates were selected in a different order.

Including density dependence

The full combination of density dependence possibilities which included the Beverton-Holt, Ricker, and density independence for each stage were evaluated using the function `LHM.DD` for the model with no covariates. The best AICc model had density independent processes between all stages except Beverton-Holt between sub-adults and adults. The AICc was 217.71, which is 15.73 units less than the density independent model with no covariates (233.44). Adding density dependence in any of the other transition between stages could only reduce the likelihood further by a miniscule amount.

Using the Beverton-Holt model for the transition from sub-adults to adults requires setting the "`g`" parameter to -1 and turning on the estimation of the "`b`" parameter for sub-adults. The initial values for the "`b`" parameters should also be adjusted appropriately (e.g. set to `−1`). Turning on the parameters requires removing the `NA` factors from the `map` list for those parameters, which may require setting the value to an integer factor if not all parameters in a parameter vector are estimated (e.g. `ln_b=factor(c(NA,NA,1,NA))`). The shape of the Beverton-Holt relationship can be seen in figure 11.

Including all the covariates in the density dependent model converged with a maximum gradient component of 1.225248e-4, but the process error for sub-adults was estimated to be zero and the standard errors could not be estimated for the associated variance parameter and one of the covariate coefficients.

The forward stepwise model selection was applied to the model with density dependence. The forward stepwise model selection procedure found 7 covariates that provide an AICc within 4 units of the best AICc (Tables 2 and 4). Running the model with the chosen covariates included did not find any covariate coefficient (beta) with 80% confidence intervals that covered zero (Figure 10). The shape of the Beverton-Holt relationship can be seen in figure 12. The two at a time AICc model average procedure had convergence issues.

Comparison among model selection approaches

The empirical correlations found 10 covariates with the right sign and a correlation of 0.3 or higher. The 0.3 was an arbitrary value and the observation error was not taken into consideration. The model with all covariates included found 7 covariates with 80% confidence intervals that did not include zero and the right sign. Only four of the selected covariates were common between the empirical correlations and the full model. The forward stepwise and two at a time AICc weights model averaging approach found the same 7 covariates within 4 units of the best AICc model and 5 of these were the same covariates selected using the full model 80% confidence interval approach. Including density dependence selected 7 covariates, including 6 of those chosen using the density independent model. The density independent model selected OMR for Sub-adult survival while the density dependent model selected X2 for the stock-recruitment relationship. The two at a time AICc weights model averaging approach had convergence issues for the density dependence model.

Projections

The model was projected 10 years into the future with the outflow covariate for post-larvae survival at "average" levels (covariate set to zero) versus increased outflow (covariate set to 1) for both the density dependent and density independent models. The density independent model showed a linear decline in the log abundance, and increasing the OMR reversed the trend. The density dependent model showed an abrupt increase for both levels of OMR which reduced over time due to the density dependence. Because the covariates were not treated as random effects (i.e. the input values for the covariates were not treated as data with observation error) in this implementation, the uncertainty about the unspecified covariates is not taken into consideration. However, the results still showed substantial uncertainty in the projections.

Covariate impacts

The temporal impacts of the covariates are illustrated in Figures 15 (without density dependence) and 16 (with density dependence) by simply showing the exponent of each covariate multiplied by its associated estimate of the coefficient. The cumulative effect of all the covariates is simply calculated by taking the product of the individual effects. The impact of density dependence was not account for in these illustrations.

Discussion

There are some differences between the different methods used to select covariates and whether density dependence is included. The best density dependent model is 6.56 AICc units better than the best density independent model and the results (Figures 11 and 12) suggest that the density dependence curve for survival from sub-adults to adults is supported by several data points. Unfortunately, the index for the adult abundance is split and the high density points are mostly in the early index, making interpreting the relationship from the empirical data difficult. Maunder and Deriso (2011) found evidence for density dependence between juveniles and adults, but this corresponds to the surveys used in this model for survival between juveniles and sub-adults.

The inclusion of density dependence is most influential on the projections. Given the low current levels of abundance, the survival rate under average conditions in the model with density dependence is very high causing the population to rapidly increase in size. However, under no density dependence the population continues to decline.

There is a large amount of uncertainty in the projections even though the uncertainty about the future values of the covariates was not included. This is because of the large amount of unexplained temporal variation in survival for the different stages and suggests that it is not possible to predict the future abundance under different management actions with any certainty. However, it may be possible to evaluate the relative effects of the different management actions and this needs to be further investigated.

The projections did not consider the correlation among the covariates. Management action designed to influence one covariate is likely to influence some or even all of the other covariates. This correlation among covariates could be modelled through the approach that treats the covariates as random effects and fit to the input covariate data. The covariates could be modelled as a multivariate time series process. This approach might be best conducted outside the GLCM to estimate the multivariate distribution to avoid convergence issues.

The selection of the density dependence form and stage was conducted using a model with no covariates. It is possible that including covariates might change the support for the form or stages that have density dependence. Convergence issues were found using a model with all the covariates. Testing the density dependence using a model with he selected covariates and/or some iterative modelling approach between selecting covariates and selecting density dependence should be considered to determine the sensitivity of the results to the approach.

The two at a time AICc model average covariate selection procedure selected the same covariates as the forward stepwise model selection for the density independent model and encountered convergence issues with the density dependent model. It is possible that removing some covariates from the density dependent model may improve the convergence (note the all covariate model had difficulty estimating mating a process error and one of the covariate coefficients). The approach also selects covariates that have the wrong sign because including remaining covariates result in estimates with the right sign. This model selection approach needs further investigation, but in this application supports the models selected.

References

Fournier, D.A., Hans, H.J., Acheta, J., Ianelli, J.N., Magnuson, A., Maunder, M., Nielsen, J.L., Sibert, J., 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27, 233–249.

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., Bell, B.M., 2016. TMB: automatic differentiation and laplace approximation. J. Stat. Softw. 70, 1–21.

Maunder, M.N., and Deriso, R.B. 2011. A state–space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (Hyposmesus transpacificus). Can. J. Fish. Aquat. Sci. 68(7): 1285–1306.

Polansky, L., Newman, K.B., Mitchell, L. 2021. Improving inference for nonlinear state-space models of animal population dynamics given biased sequential life stage data. Biometrics, 77:352–361.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

794 Table 1. Differences between the M&D and Polansky et al. models.

Characteristic	M&D	Polansky et al.	This application
Time frame	1972-2006	1995-2015 (1994 adults also included)	1995-2015
Stages	3 (larvae, juveniles, adults)	4 (post larvae, juveniles, sub-adults, adults)	4 (post larvae, juveniles, sub-adults, adults)
Stock-recruitment survival process variation (Adult to larvae survival)	Lognormal	Lognormal	Lognormal
Other survival process variation	Lognormal	Logit-normal	Lognormal
Density dependence	Beverton-Holt, Ricker, or Deriso-Schnute	None	Beverton-Holt (Ricker and Deriso-Schnute are also possible)
Indices of abundance	3 (20mm, summer tow net, fall midwater tow)	4 (20mm, summer tow net, fall midwater tow, spring Kodiak trawl, and spring midwater tow)	4 (20mm, summer tow net, fall midwater tow, spring Kodiak trawl, and spring midwater tow)
Catchability (survey bias)	Catchability fixed at 1 (assumes can't estimate absolute abundance)	Catchability fixed at one for 20mm and for spring Kodiak trawl (2001 and later), estimated for other surveys and years, but spring midwater tow is assumed equal to the fall midwater tow.	Catchability fixed at one for 20mm and for spring Kodiak trawl (2001 and later), estimated for other surveys and years, but spring midwater tow is assumed equal to the fall midwater tow. However, this had confounded parameters, so just estimated the catchability for Adult spring midwater tow
Observation error	Normal with known standard deviation that varies by year	Lognormal with known CV that varies by year (also investigated estimating CV scaler)	Lognormal with known CV that varies by year (other options available)
Inference framework	Frequentist state-space	Bayesian state-space	Frequentist state-space

Model selection	Two at a time selection based on model averaging of AICC weights (density dependence model selection was based on full factorial without covariates)	Include all covariates and evaluate Bayesian interval coverage of zero	Empirical correlations, full covariate model, forward stepwize selection, two at a time selection based on model averaging of AICC weights
Covariates	Various (see Table of M&D)	Various (see Table 2 and Table C1 of Polansky et al.)	Various (see Table 2 and Table C1 of Polansky et al.)

Table 2. Results of the alternative model selection procedures. "Empirical" is the correlation between the log of the ratio of the appropriate indices and the covariate. Green represents a covariate that is "selected". Red represents a covariate that has the wrong sign. The value in the empirical column is the correlation coefficient. The value in the forward and two at a time AICc weights model average columns is the order in which the covariate was selected. The two covariates at a time AICc model averaging procedure selects some covariates with the wrong sign as they can be the right sign when combined with remaining covariates, only the covariates included in the models that had an AICc within 4 units of the best model are listed here (none of these had the wrong sign).

Covariate	Stage	Covariate	Lagged	Sign	Empirical	80%	Forward	Two at a time	BH JtoSA
1	PLsurvival	Outflow_Jun0Aug0	no	pos	0.5		1	3	1
2	PLsurvival	Secchi_mean_Jun0Aug0	no	neg	-0.46		8		9
3	PLsurvival	Temperature_mean_Jun0Aug0	no	neg	-0.47		4	4	3
4	PLsurvival	ISS_Jun0Aug0	no	neg	-0.45		14		11
5	PLsurvival	TriGoby_Jun0Aug0	no	neg	-0.58				
6	Jsurvival	X2_Sep0Oct0	no	neg	0				
7	Jsurvival	Secchi_mean_Sep0Nov0	no	neg	-0.14		6	6	5
8	Jsurvival	Temperature_mean_Sep0Nov0	no	both	0.27		7	7	6
9	Jsurvival	ACM_BPUV_Sep0Nov0	no	pos	-0.07				
10	SAsurvival	Outflow_Dec0Feb1	no	pos	-0.25		15		
11	SAsurvival	OMR_Dec0Mar1	no	pos	0.64		3	1	
12	SAsurvival	SouthSecchi_mean_Dec0Mar1	no	pos	0.58		2	2	7
13	SAsurvival	Temperature_mean_Dec0Feb1	no	both	-0.07		5	5	4
14	SAsurvival	ACM_BPUV_Dec0Feb1	no	pos	0.43		12		
15	SAsurvival	SBAge1Plus_Dec0Dec0	no	neg	-0.21		11		
16	Recruitment	Outflow_Mar0May0	yes	pos	0.28				
17	Recruitment	Secchi_mean_Mar0May0	yes	neg	0.02		3		8
18	Recruitment	Temperature_mean_Mar0May0	yes	neg	-0.39		9		
19	Recruitment	ACM_BPUV_Mar0May0	yes	pos	-0.09		10		10
20	Recruitment	NJ_BPUV_Mar0May0	yes	pos	-0.34				
21	Recruitment	TFS_Mar0May0	yes	neg	-0.14				
22	Recruitment	ISS_Mar0May0	yes	neg	0.55				
23	Recruitment	TriGoby_Mar0May0	yes	neg	-0.54				
24	Recruitment	X2_lag	yes	neg	-0.13		13		2

Table 3. Results of each stage of the forward stepwise regression for the model without density dependence. The yellow shaded values are the covariates included up to the step that is within 4 AICC units of the best AICC model.

Hypothesis	nlnL	npar	AIC	ndata	AICC	beta	dif
0	105.2132	10	230.4265	84	233.4402	NA	
1	101.8838	11	225.7677	84	229.4343	0.465516	10.33267
12	99.15309	12	222.3062	84	226.7005	0.405453	7.598883
11	93.95083	13	213.9017	84	219.1017	0.434852	0
3	92.60051	14	213.201	84	219.288	-0.29652	0.186309
13	91.62269	15	213.2454	84	220.3042	-0.16186	1.202545
7	90.91235	16	213.8247	84	221.9441	-0.25409	2.842433
8	89.08489	17	212.1698	84	221.4425	0.45952	2.340837
2	88.78198	18	213.564	84	224.087	-0.13447	4.985381
18	88.55078	19	215.1016	84	226.9766	-0.09286	7.874897
19	88.35094	20	216.7019	84	230.0352	0.087099	10.93356
15	88.18182	21	218.3636	84	233.2669	-0.07572	14.1652
14	87.87021	22	219.7404	84	236.3306	0.109267	17.22892
24	87.80026	23	221.6005	84	240.0005	-0.05326	20.89885
4	87.7897	24	223.5794	84	243.9184	-0.03363	24.81672
10	87.78969	25	225.5794	84	247.9932	0.001003	28.89152

Table 4. Results of each stage of the forwards stepwise regression for the model with density dependence using the Beverton-Holt model for survival from adult to post-Larvae (stock-recruitment) and the Beverton-Holt model for survival from Juveniles to sub-Adults. The yellow shaded values are the covariates included up to the step that is within 4 AICC units of the best AICC model.

Hypothesis	nlnL	npar	AIC	ndata	AICC	beta	dif
0	96.02281	11	214.0456	84	217.7123	NA	5.17467
1	92.51946	12	209.0389	84	213.4333	0.491709	0.895651
24	90.66881	13	207.3376	84	212.5376	-0.27322	0
3	89.34835	14	206.6967	84	212.7837	-0.29939	0.246028
13	87.98183	15	205.9637	84	213.0225	0.178036	0.484859
7	86.86237	16	205.7247	84	213.8442	-0.34099	1.306527
8	85.96191	17	205.9238	84	215.1966	0.347114	2.658932
12	85.00267	18	206.0053	84	216.5284	0.204876	3.990789
17	84.16867	19	206.3373	84	218.2123	-0.20036	5.674718
2	83.868	20	207.736	84	221.0693	-0.14179	8.531711
19	83.86383	21	209.7277	84	224.6309	0.012864	12.09326
4	83.85977	22	211.7195	84	228.3097	-0.02171	15.77208

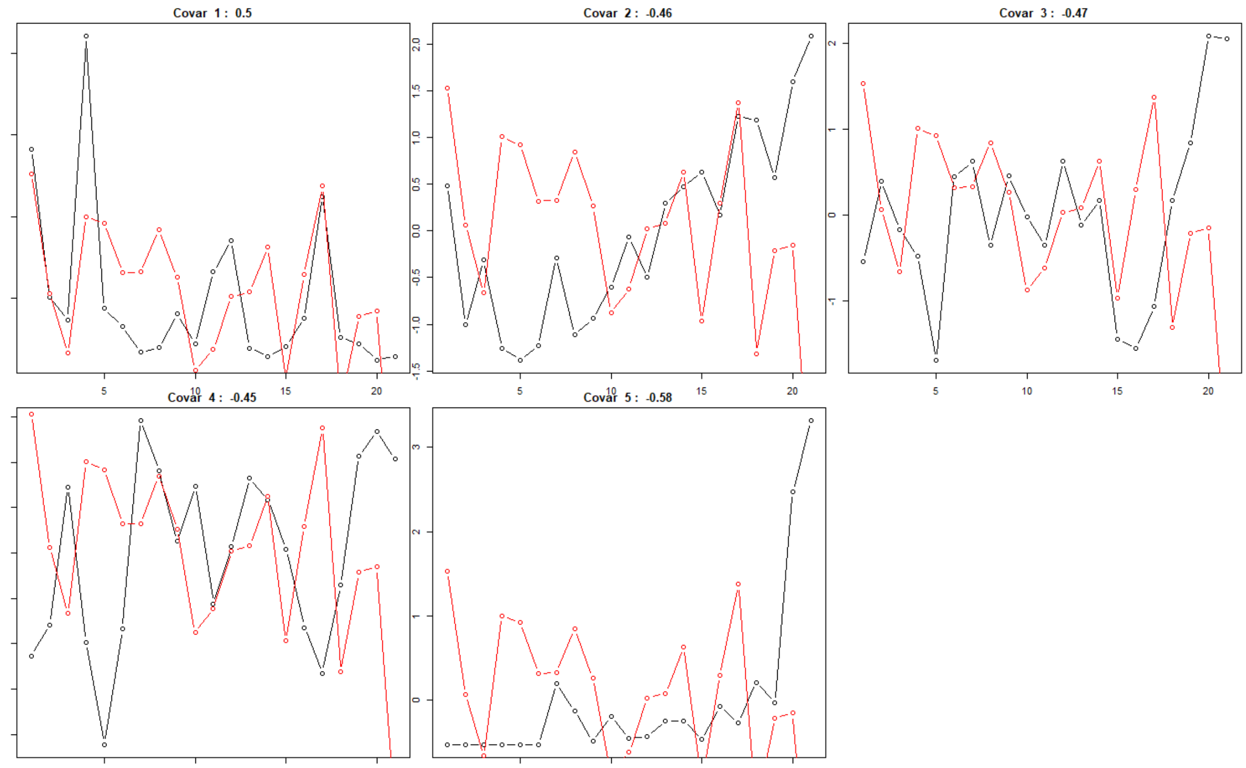

Figure 1. Correlation between log(J/PL) and the covariates for PL survival

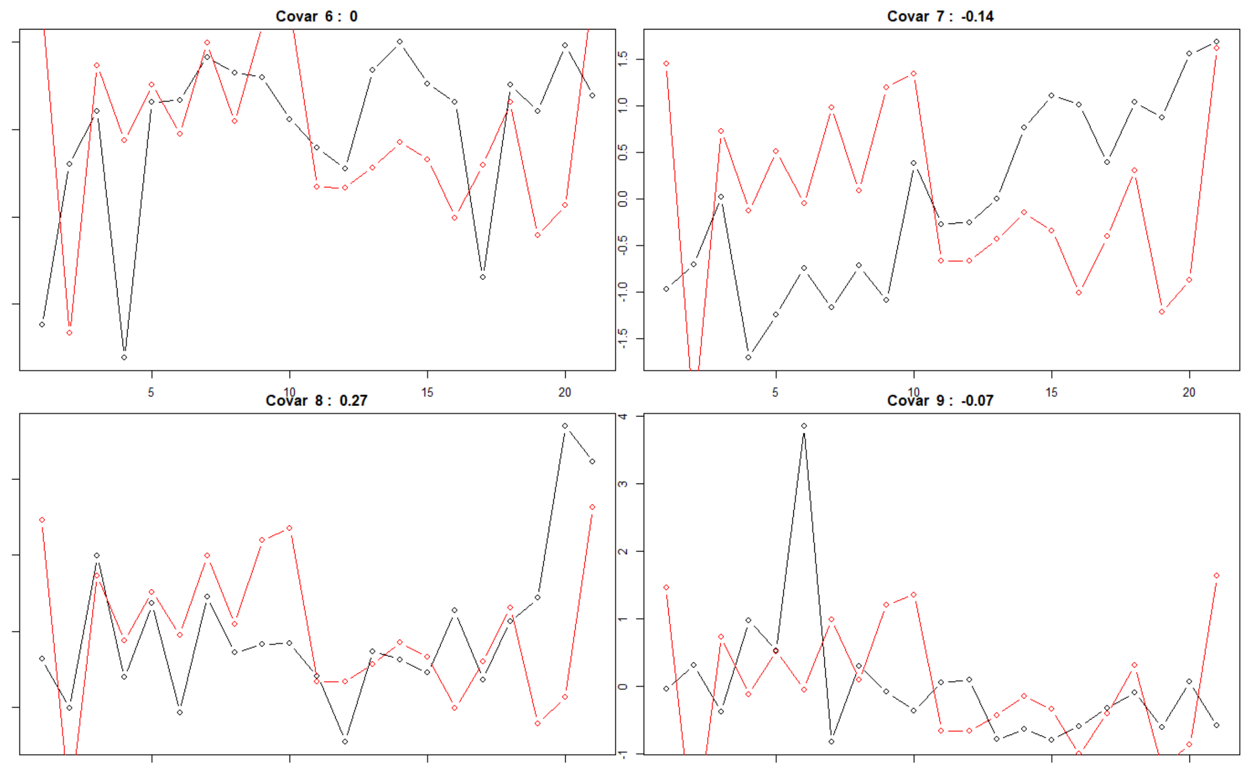

Figure 2. Correlation between log(PA/J) and the covariates for J survival

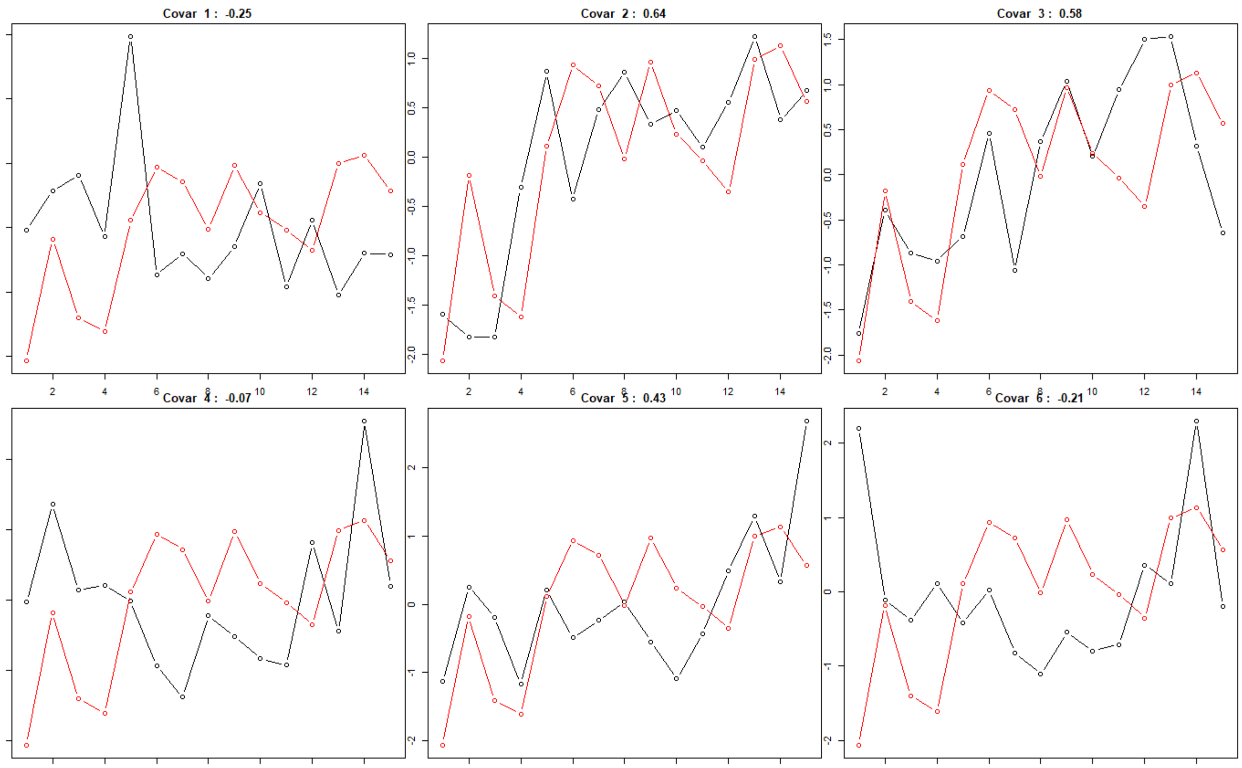

Figure 3. Correlation between log(A/PA) and the covariates for PA survival. Only data from 2001??? is used because of the change in the gear used for the adult survey. Covariates labeled 1-6 are covariates 10-15.

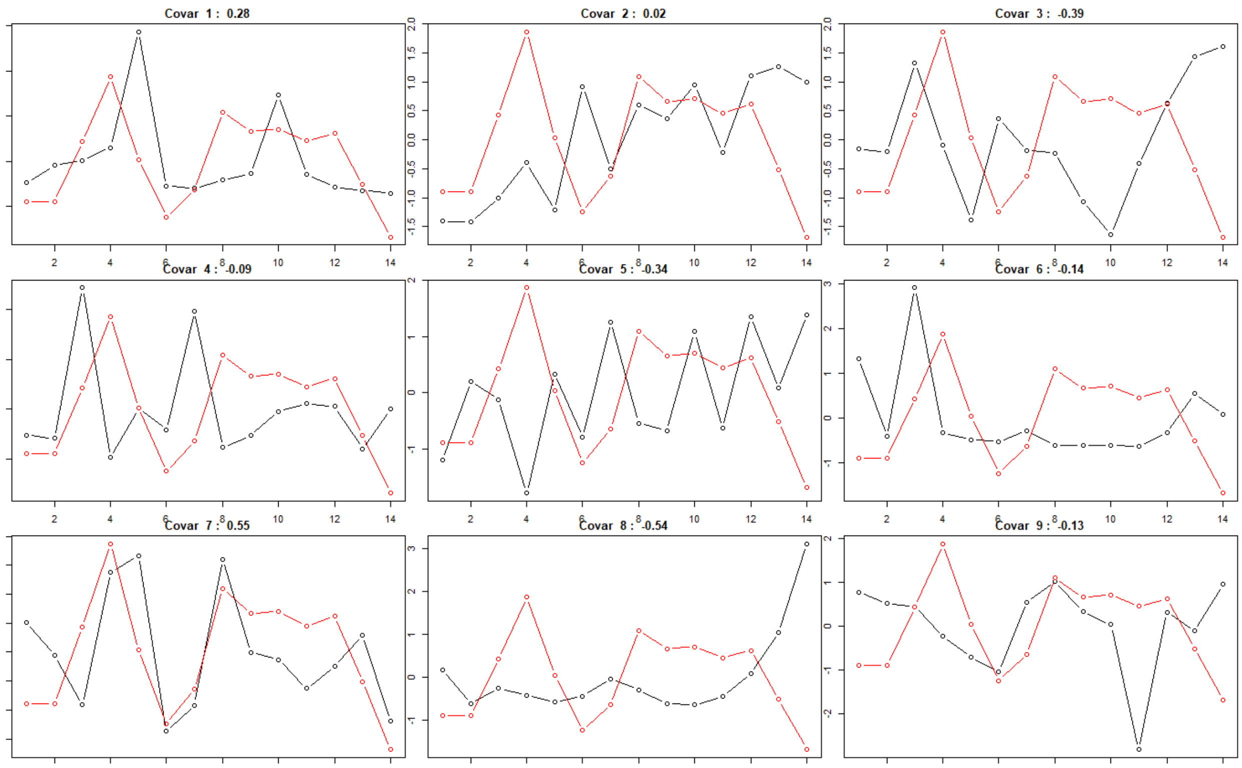

Figure 4. Correlation between log(PL/A) and the covariates for A survival/stock-recruitment relationship. Only data from 2001 are used because of the change in the gear used for the adult survey. The data for the juveniles was lagged appropriately. Covariates labeled 1-9 are covariates 16-24.

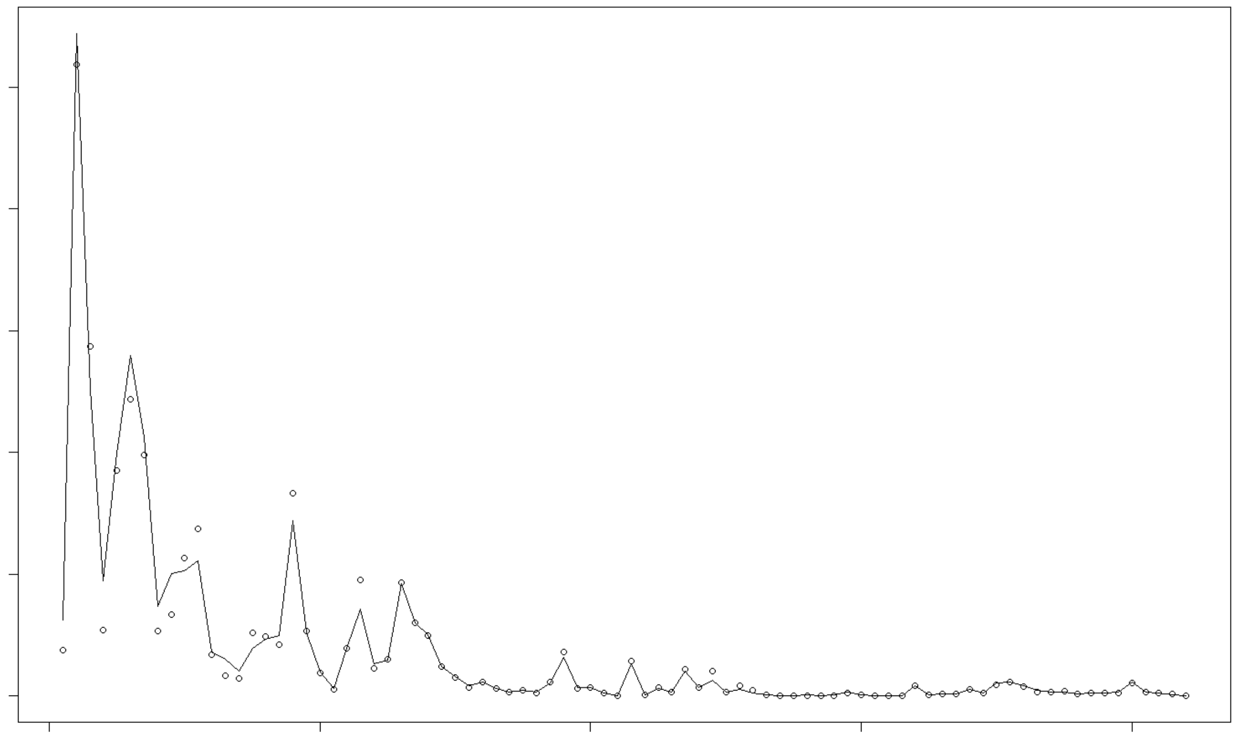

Figure 5. Fit to the survey data without covariates and two catchability parameters estimated. All surveys are plotted in a single figure to quickly check for any obvious misfits.

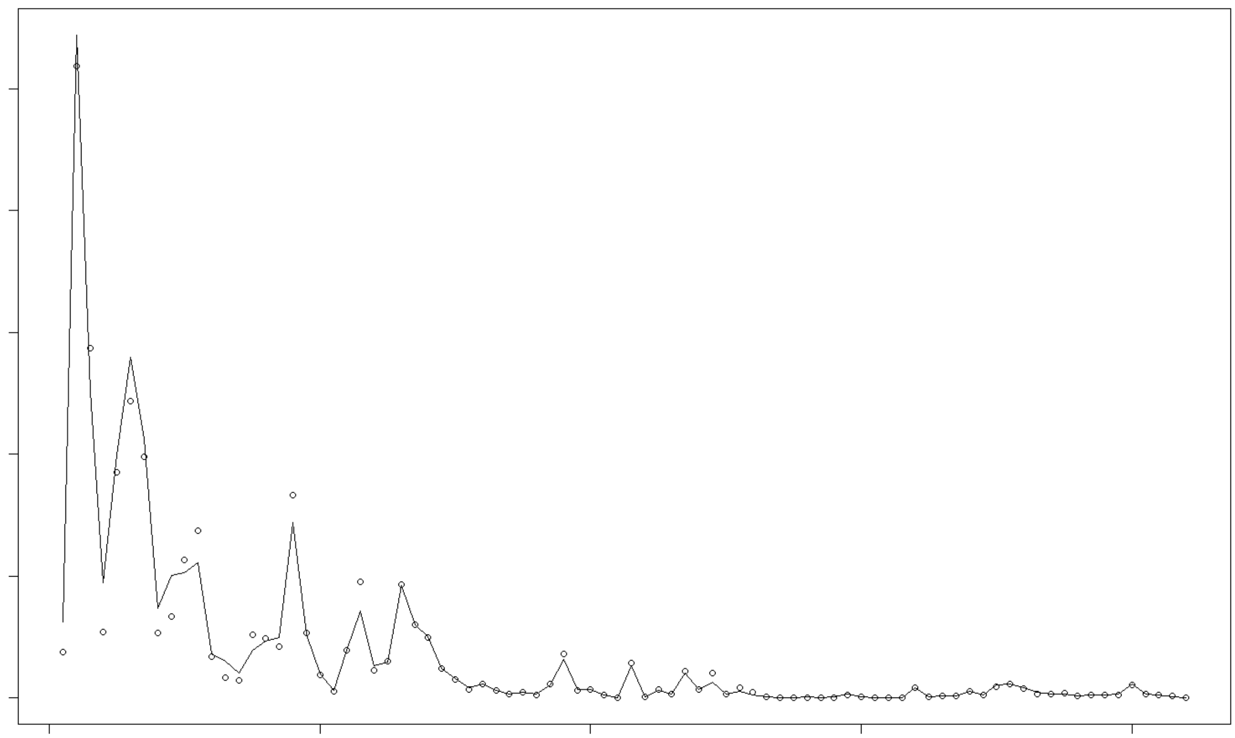

Figure 6. Fit to the survey data without covariates and only one catchability parameter is estimated. All surveys are plotted in a single figure to quickly check for any obvious misfits.

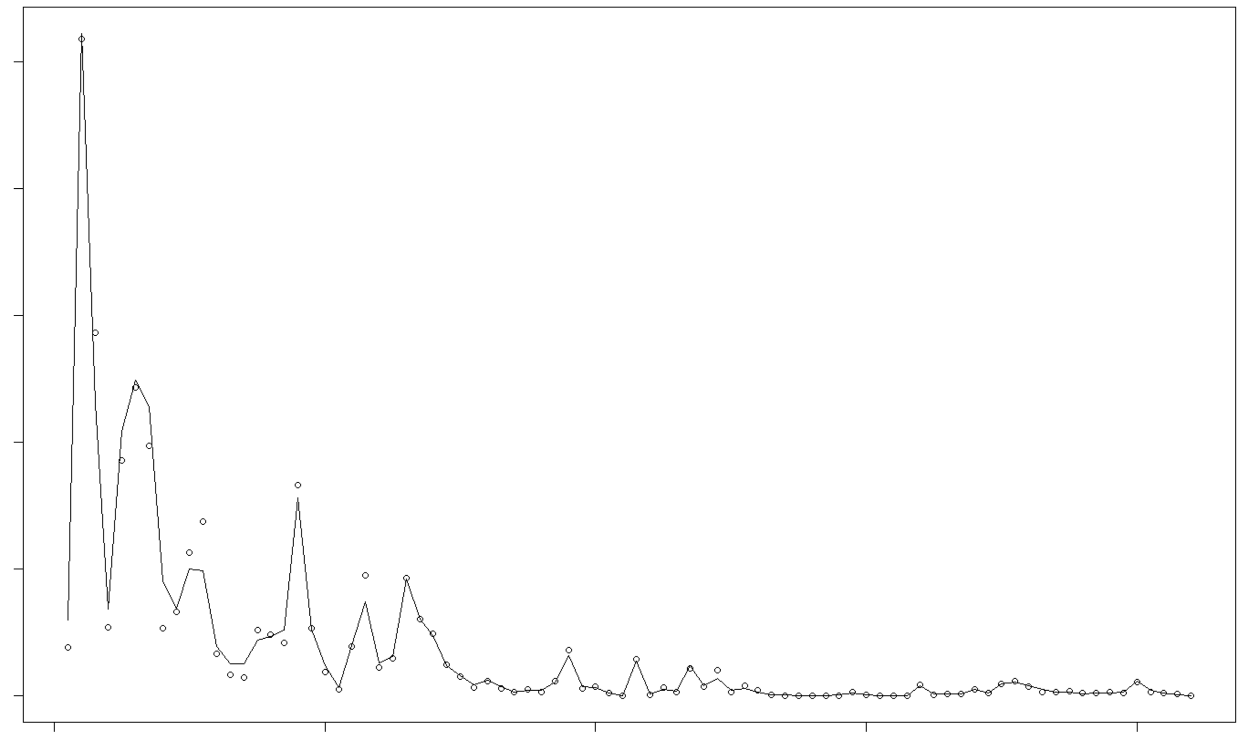

Figure 7. Fit to the survey data including all covariates and only one catchability parameter is estimated. All surveys are plotted in a single figure to quickly check for any obvious misfits.

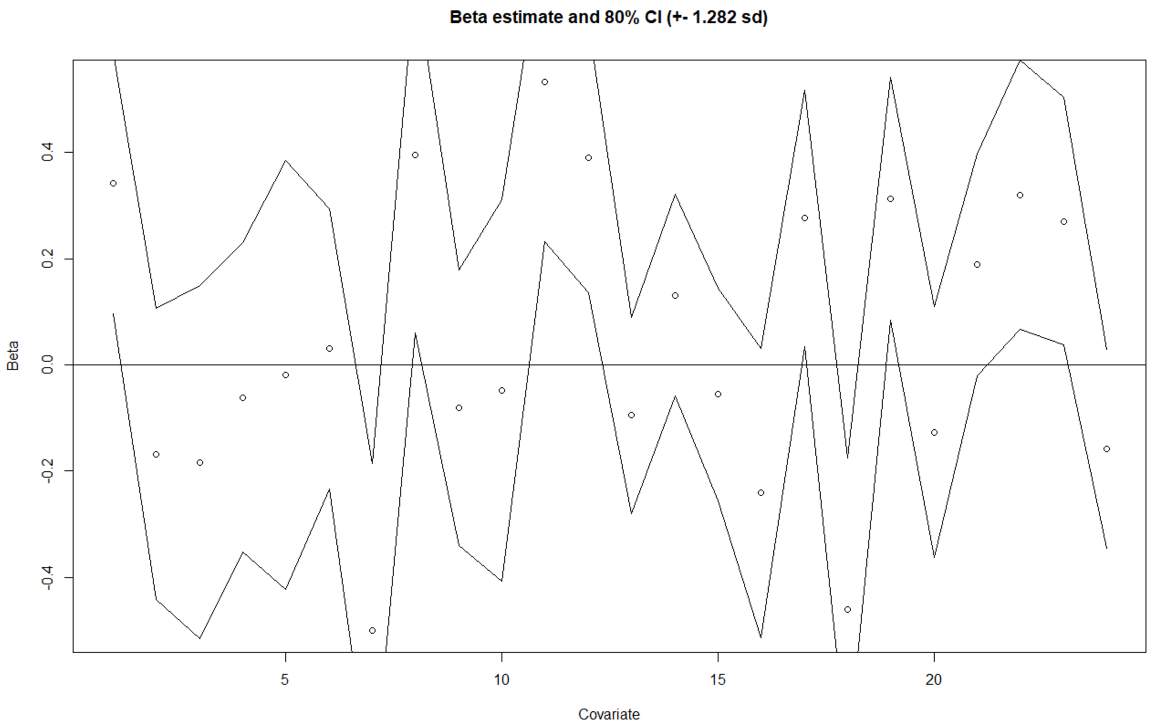

Figure 8. Estimates of the covariate coefficients and their approximate 80% confidence intervals (+- 1.282 se) from a model that includes all the covariates and estimates only one catchability (survey bias).

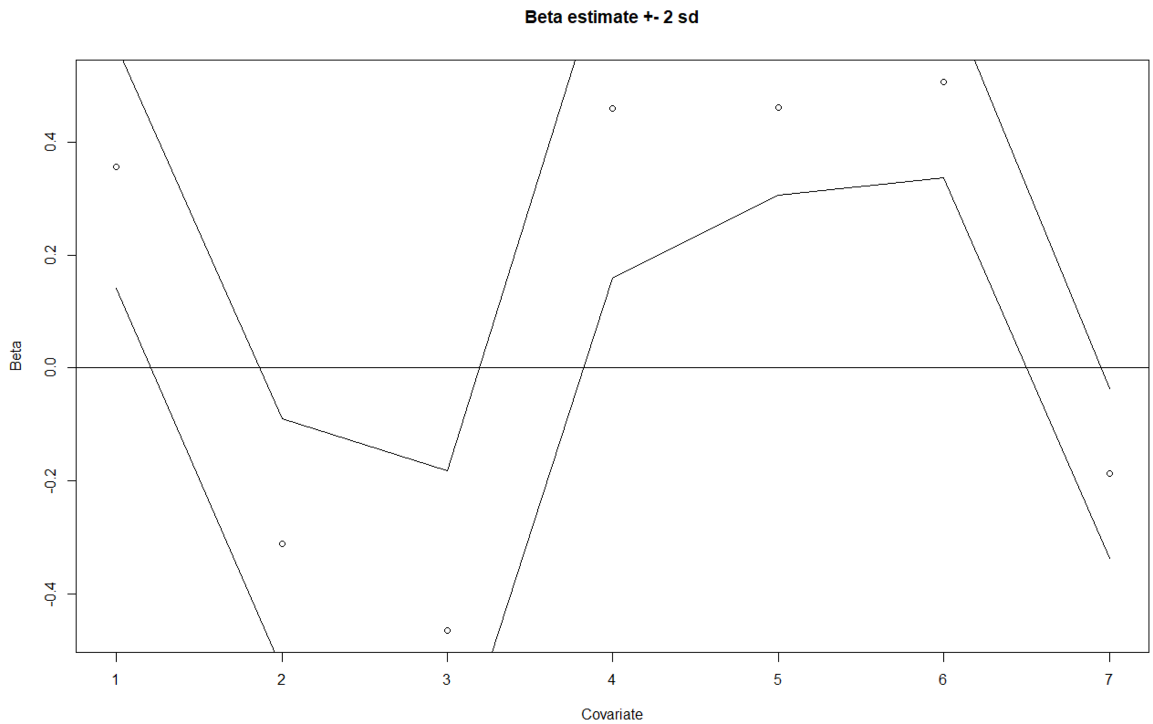

Figure 9. Estimates of the covariate coefficients and their approximate 80% confidence intervals (+- 1.282 se) from a model that includes only the covariates selected in the forward model selection procedure. The numbering of the models is related to the models included (1,3,7,8,11,12,13).

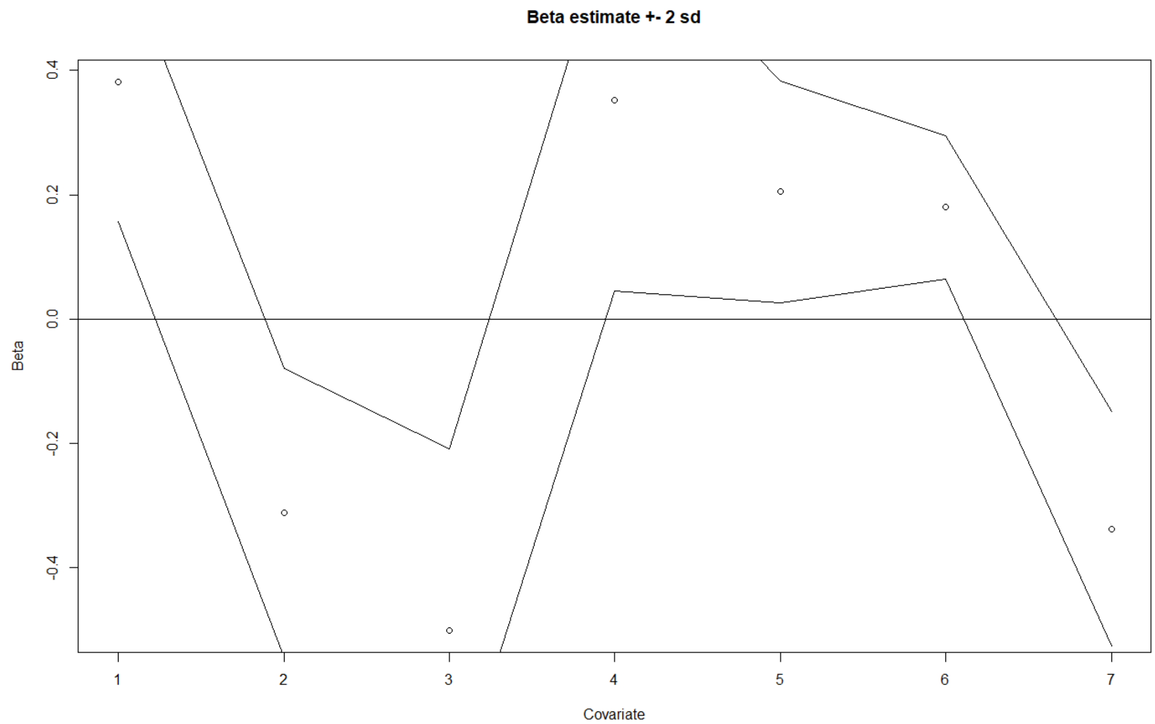

Figure 10. Estimates of the covariate coefficients and their approximate 80% confidence intervals (+- 1.282 se) from a model that includes only the covariates selected in the forward model selection procedure using the model with density dependence. The numbering of the models is related to the models included (1, 3, 7, 8, 11, 12, 15, 17, 24).

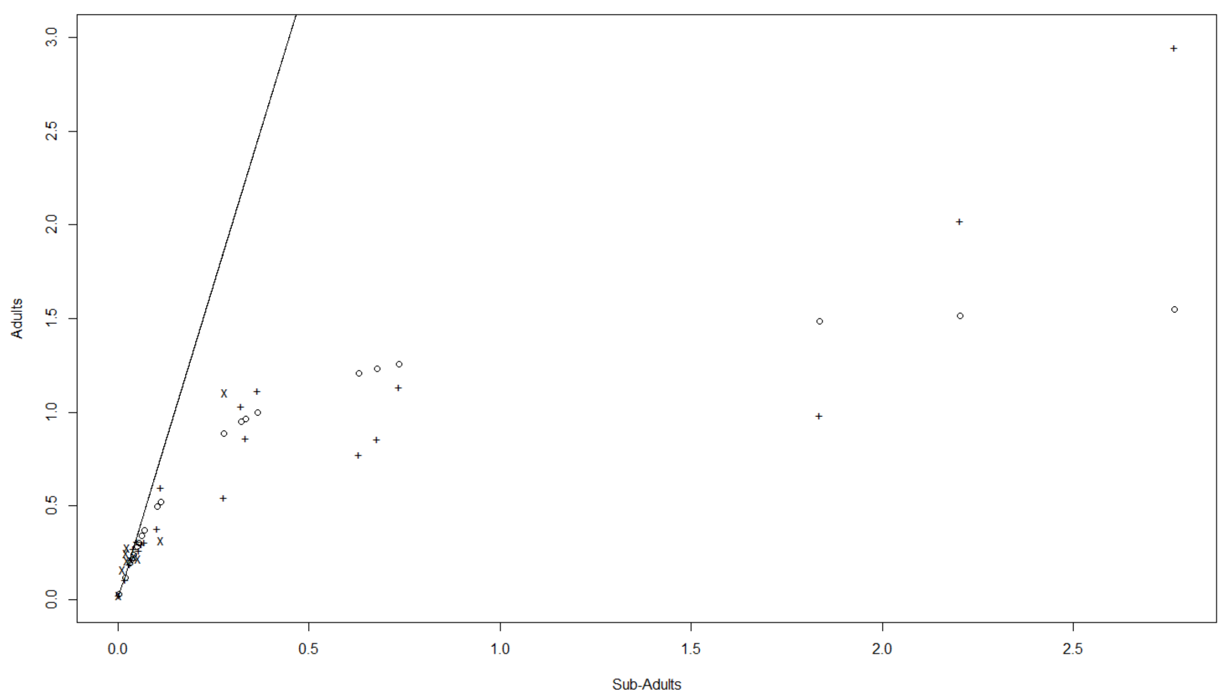

Figure 11. The density dependence function from juveniles to sub-adults estimated in a model **without** covariates. The circles are the density dependent function, the crosses are the estimated abundance, the x's are the survey data, and the line is density independence.

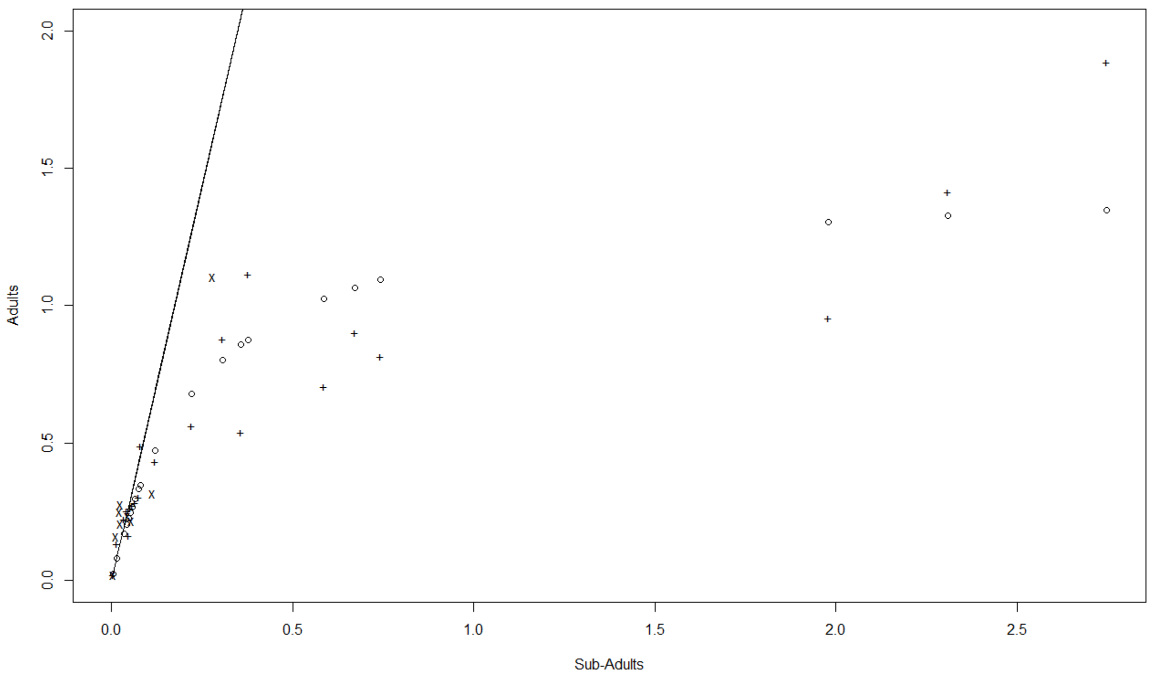

Figure 12. The density dependence function from juveniles to sub-adults estimated in a model **with** covariates. The circles are the density dependent function, the crosses are the estimated abundance, the x's are the survey data, and the line is density independence.

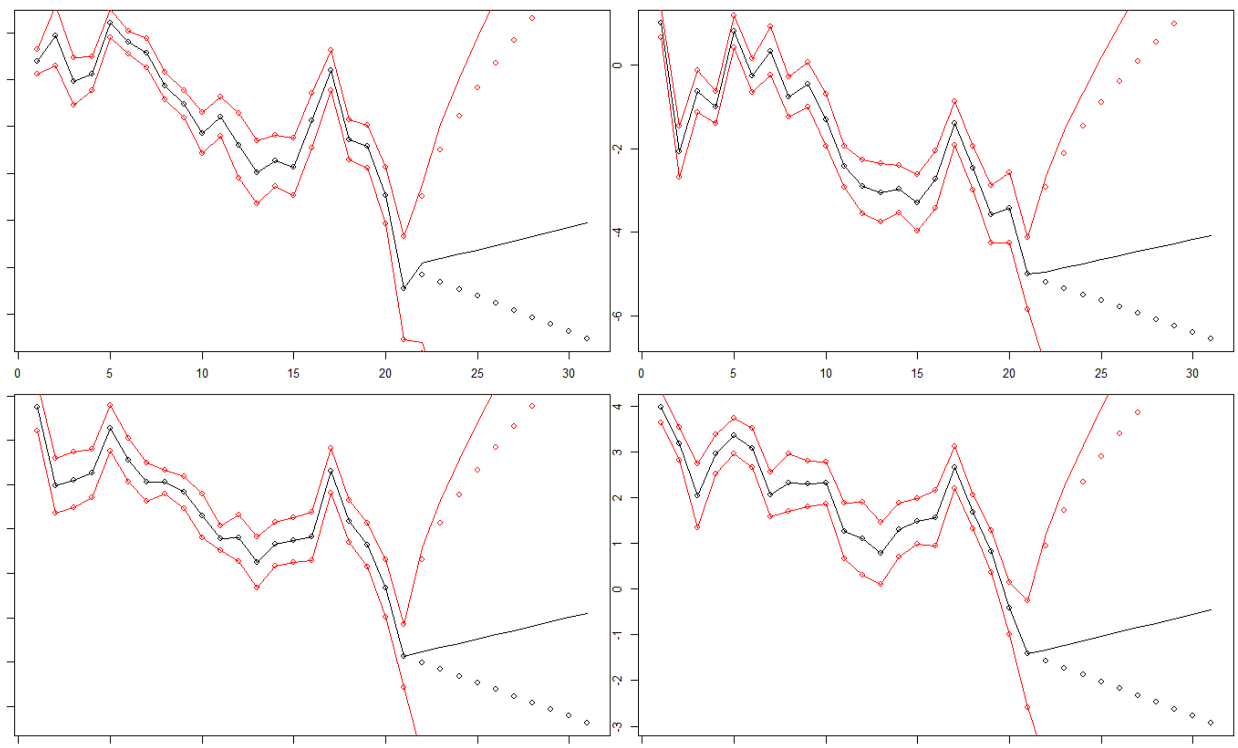

Figure 13. Ten year projections and approximate 95% confidence intervals from a model that includes only the covariates selected in the forward model selection procedure using the model **without** density dependence. The circles are with “mean” values for the covariates (set to zero) and the lines are with the outflow covariate effect doubled (covariate = ln(2)). The panels are the 4 stages.

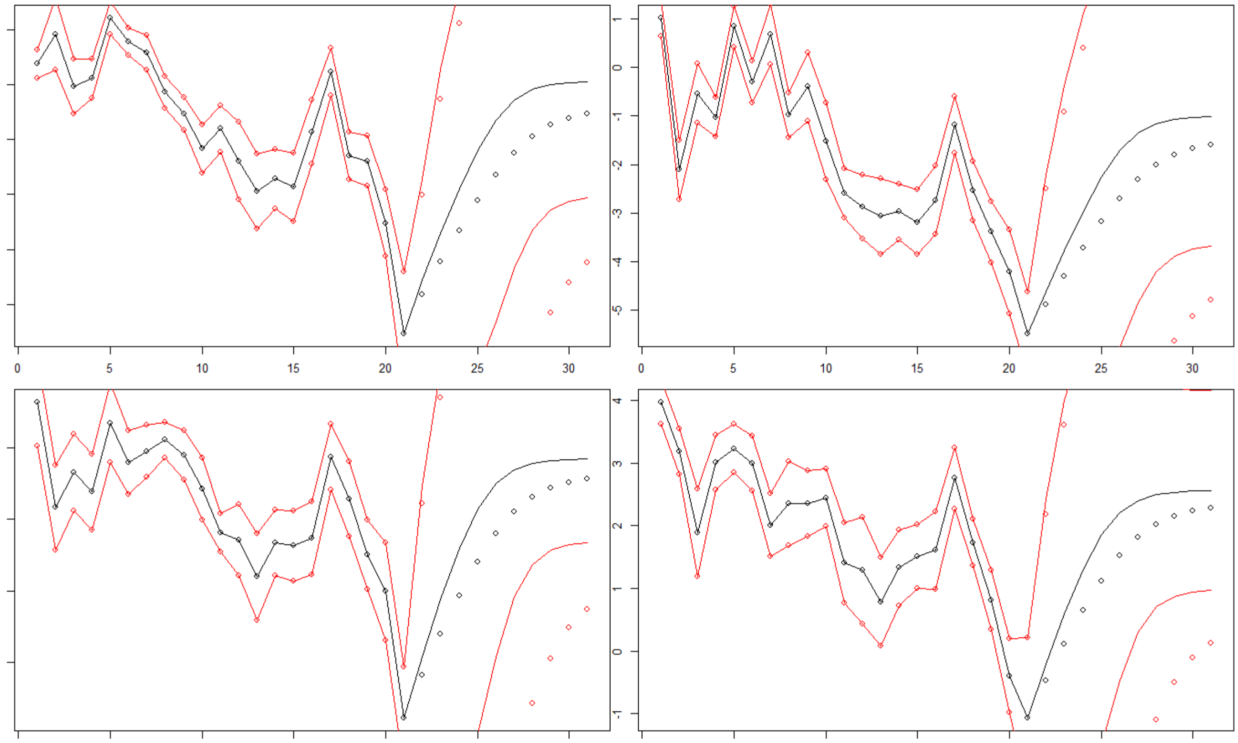

Figure 14. Ten year projections and approximate 95% confidence intervals from a model that includes only the covariates selected in the forward model selection procedure using the model **with** density dependence. The circles are with “mean” values for the covariates (set to zero) and the lines are with the outflow covariate effect doubled (covariate = ln(2)). The panels are the 4 stages.

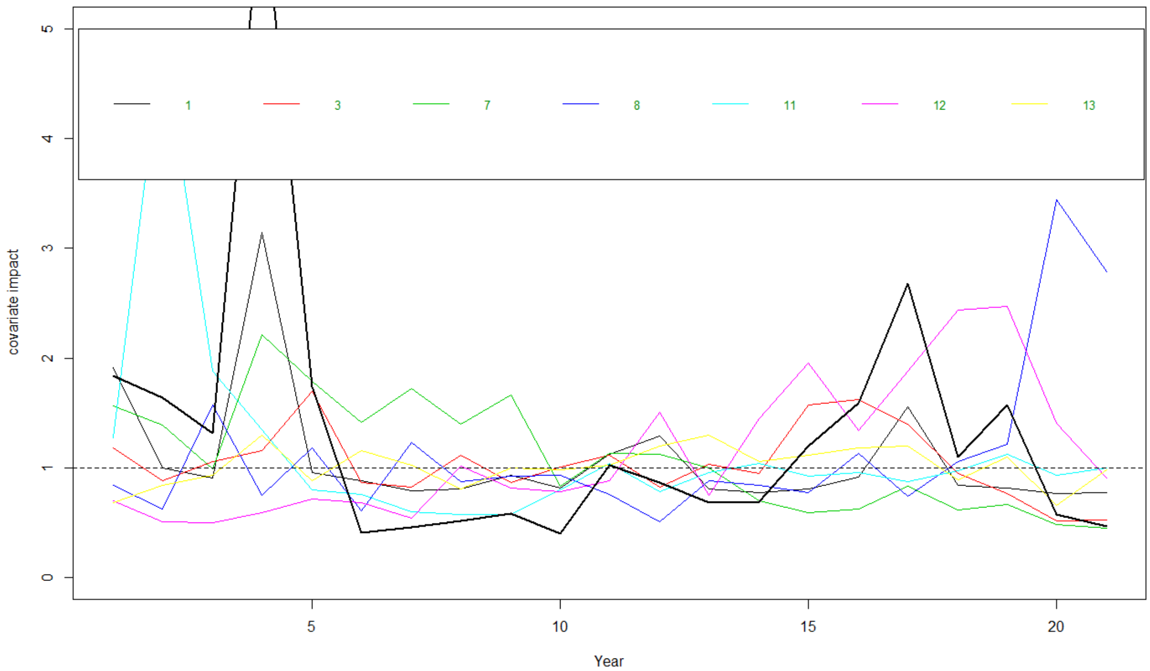

Figure 15. Illustration of the temporal trend in the covariate effect (exp(beta*X)) for the model **without** density dependence. The thick black line is the product of all the effects. The unexplained variation (the process error) is not shown.

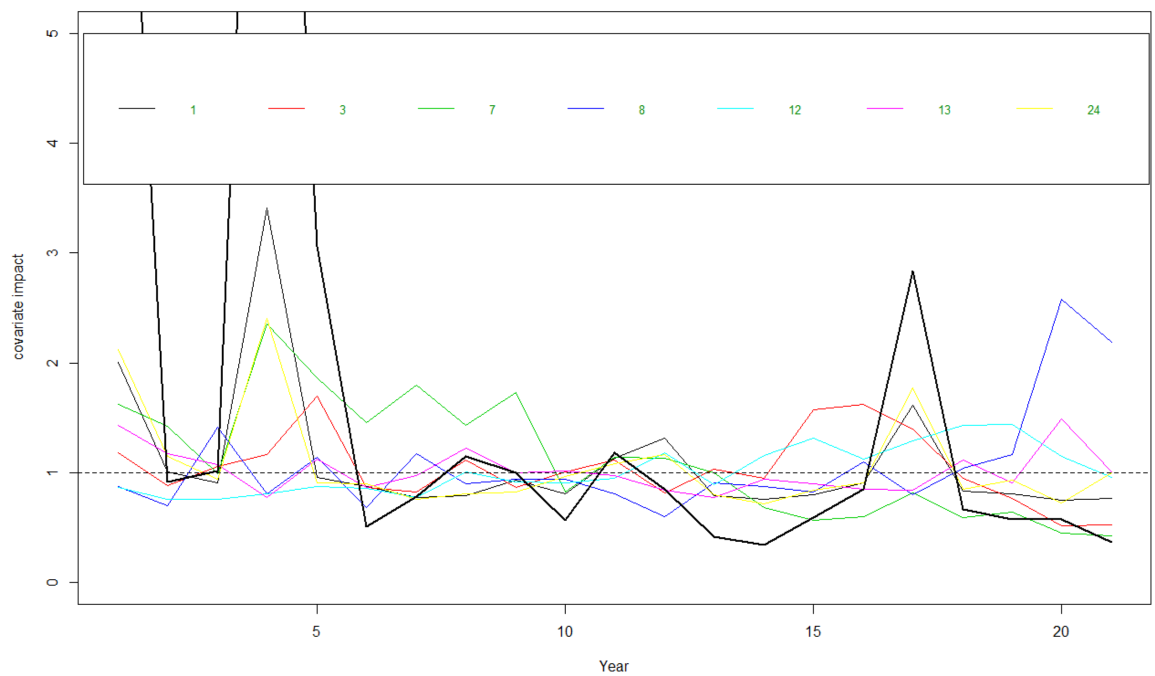

Figure 16. Illustration of the temporal trend in the covariate effect (exp(beta*X)) for the model **with** density dependence. The thick black line is the product of all the effects. The unexplained variation (the process error) is not shown. The effects of the covariates will also be impacted by the density dependence, which is not taken into consideration in this figure. (note the colors differ somewhat with those used for figure 15)