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**Title:** Global fishery dynamics are poorly predicted by classical models

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Running title: Global fishery dynamics

**Abstract:**

Fisheries dynamics can be thought of as the reciprocal relationship between an exploited population and the fishers and/or managers determining the exploitation patterns. Sustainable production of protein of these coupled human-natural systems requires an understanding of their dynamics. Here, we characterized the fishery dynamics for 173 fisheries from around the globe by applying general additive models to estimated fishing mortality and spawning biomass from the RAM Legacy Database. GAMs specified to mimic production models and more flexible GAMs were applied. We show observed dynamics do not always match assumptions made in management using 'classical' fisheries models and the suitability of these assumptions varies significantly according to large marine ecosystem, habitat, variability in recruitment, maximum weight of a species, and minimum observed stock biomass. These results identify circumstances in which simple models may be useful for management. However, adding flexibility to classical models often did not substantially improve performance, which suggests in many cases considering only biomass and removals will not be sufficient to model fishery dynamics. Knowledge of the suitability of common assumptions in management should be used in selecting modeling frameworks, setting management targets, testing management strategies, and developing tools to manage data-limited fisheries. Effectively balancing expectations of future protein production from capture fisheries and risk of undesirable outcomes (e.g. 'fisheries collapse') depends on understanding how well we can expect to predict future dynamics of a fishery using current management paradigms.

Key words: coupled human-natural systems, effort dynamics, population dynamics, production models, stock assessment

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42

43      **Introduction**

44      Approximately twenty percent of worldwide dietary protein is derived from the sea (FAO, 2016).

45      Global population is projected to increase to over 9 billion by 2050 (from a current population of

46      ~7 billion; UN-DESA, 2015), but production from capture fisheries stabilized at 85-95 million

47      metric tonnes (mmt) in the 2000s (FAO, 2016). Fisheries managers are often tasked with

48      ensuring the fish and invertebrate populations that support these fisheries remain productive and

49      attempt to do so by modeling the dynamics of exploited populations to determine sustainable

50      catches.  Models of fishery dynamics often assume the number of individual fish entering a

51      population is related to spawning biomass (SB) and that decreases in spawning biomass occur

52      due to natural mortality and fishing mortality (F).  Most management strategies for fisheries are

53      predicated on the assumption that management can manipulate fishing pressure to achieve

54      changes in a fished population. However, shifts in population dynamics over time (Szuwalski et

55      al. 2015) can influence the response of a population to fishing and these responses likely vary by

56      region and species (Neubauer et al., 2013; Thorson et al. 2012).  Effectively balancing

57      expectations of future protein production and risk of undesirable outcomes (e.g. 'fisheries

58      collapse') requires an ability to understand and predict the dynamics of a fishery.

59

60      'Fisheries dynamics' are defined here as the manner in which F and SB change at different levels

61      of F and SB.  Changes in F can be seen as the response of management or fishers to changes in

62      the population and the perceived level of exploitation; changes in SB can be seen as the response

63  of the population to exploitation, density-dependence (i.e. the existence of a 'carrying capacity'),

64  and/or environmental forcing. Fisheries managers make assumptions about the way SB and F

65  change when developing strategies for management. For example, SB is expected to decrease on

66  average when F increases, and F might be assumed to decrease when SB is low due decreases in

67  the profitability of fishing (Thorson et al., 2014) or management action. The validity of these

68  assumptions and the predictability of fishery dynamics can influence the performance of a given

69  management strategy, but these assumptions are not often checked.

70

71  Here we characterize the fishery dynamics for 173 stocks from the RAM Legacy Stock

72  Assessment Database (Ricard et al, 2012) by fitting generalized additive models to estimates of

73  SB and F. Using these fitted models, we ask, "If today's SB and F are known, can changes in SB

74  and F next year be predicted based on the past responses of the fishery?" We then link stock

75  characteristics to a measure of predictability and identify stocks with expected fishery dynamics

76  given common assumptions of density-dependence, stationary dynamics, active management,

77  and/or cost-based constraints on fishing effort. Finally, we discuss implications for management

78  and potential strategies for coping with different levels of predictability and unexpected fishery

79  dynamics.

80

81  **Materials and methods**

82  <u>Global fisheries data</u>

83  Time series' of SB and F from the RAM Legacy Stock Assessment Database were used based on

84  the criteria that the recruitment estimates for the years extracted must not come directly from a

85  stock-recruit curve (i.e. predictions of F and SB derived deterministically from assumed structure

86  of stock assessment models were not used) and at least 18 contiguous years of F and SB were

87  available. The RAM Database is the most up-to-date compilation of stock assessments for

88  stocks fished worldwide. Exploring relationships between potentially dependent, model-derived

89  quantities can be fraught with statistical pitfalls (Thorson et al., 2015). However, these are the

90  best available estimates of F and SB and fisheries management is routinely conducted using

91  these estimates as accurate representations of reality. Therefore, assumptions made about

92  fisheries dynamics by managers should be consistent with the dynamics compiled in this

93  database. In total, 173 stocks were included in the analysis and time series' of SB were rescaled

94  from 0 to 1 before analysis to improve comparability. Rescaling was not done for F because

95  fishing mortality already represents a rate that is approximately comparable among stocks

96  (differences in selectivity will impact the comparability of Fs (Cordue 2011), but selectivities

97  were not reported in the RAM database).

98

99  <u>Population dynamics, GAMs, and predictability</u>

100 Dynamics of the SB and F of a population can be characterized as:

$$B_{t+1}, F_{t+1} = B_t, F_t + f(B_t, F_t) + N(0, \Sigma)$$

Eq 1a

101 where $B_t$ and $B_{t+1}$ are SB in years $t$ and $t+1$, $F_t$ and $F_{t+1}$ are fishing mortality in years $t$ and $t+1$,

102 $f(B_t, F_t)$ represents the coupled natural and human dynamics of SB and F, and $N(0, \Sigma)$ is a

103 multivariate normal "process error" arising from our model $f(B_t, F_t)$ failing to include all relevant

104 processes. We seek to estimate $f()$, and take the first difference of F and SB:

$$B_{t+1}, F_{t+1} - B_t, F_t = f(B_t, F_t) + N(0, \Sigma)$$

Eq 1b

105 Given the assumption that $\Sigma$ is diagonal, we can decompose these dynamics into two

106 independent equations:

$$B_{t+1} - B_t = g(B_t, F_t) + N(0, \sigma_B^2)$$

Eq 1c

$$F_{t+1} - F_t = h(B_t, F_t) + N(0, \sigma_F^2)$$

107 where $g()$ represents "population dynamics" and $h()$ represents "effort dynamics" (Thorson et al.,

108 2013). Both $g$ and $h$ can be estimated using non-parametric models given the assumption that $F_t$

109 and $B_t$ are known without error. We used two strategies to fit the fishery dynamics data (Eq. 1c)

110 here. First, we estimated $g()$ and $h()$ using generalized additive models (GAMs), but restricted

111 the number of knots allowed for each to a maximum of 3. Three knots allowed for quadratic

112 models to be fit, which represents the prevailing dynamics assumed by most fisheries models (i.e.

113 the dynamics between SB and F can be described by at most a dome-shaped curve). Second, we

114 again estimated $g()$ and $h()$ using GAMs, but the number of knots was increased to 5. Five was

115 chosen to offer more flexibility in estimation, but also increased the potential for overfitting with

116 some of the shorter time series.

117

118  Predictability of changes in F and SB for both methods was evaluated by excluding the last year

119  of data, fitting the GAMs, predicting the excluded year using the fitted models and calculating

120  the absolute relative error of the observed vs. the prediction.  This process was repeated for each

121  of the last five years of data and the mean absolute relative error over those five years (MARE) is

122  used here to represent the predictability of changes in F and SB. Excluding the last year from the

123  analysis and predicting the change mimics the management process in which SB is estimated one

124  year out and a target F is set. MARE was recorded for the 'traditional' dynamics models (i.e.

125  restricted to quadratic relationships between F and SB) and the 'flexible' dynamics model (i.e.

126  the model in which the number of knots allowed was increased).

127

128  <u>Fishery dynamics and expectations</u>

129  Each of the fitted relationships between SB and F represent a different 'process effect' in the

130  human-natural coupled system of a fishery. Models fit to changes in F describe the way in which

131  fishers and fisheries managers perceive and interact with a stock, while models fit to changes in

132  SB  describe  how  the  stock  responds  to  exploitation  as  well  as  density-dependent  and

133  environmental changes.

134

135  Before applying the GAMs described above to the observed data, they were fitted to data drawn

136  from  simulated  populations  to  understand  1)  what  fishery  dynamics  are  'expected'  given  a

137  common model of fishery dynamics used in fisheries management (e.g. Beverton and Holt, 1957)

138  and 2) how well the GAMs could be expected to reflect the underlying dynamics of a system.  A

139  production  model  (equation  2)  undergoing  an  exploitation  history  in  which  'effort  dynamics'

140  (equation 3; Thorson et al., 2013) determine fishing mortality was used to simulate data.  The

141  effort dynamics model defines a point at which economic equilibrium is reached (i.e. profits =

142  costs) and posits an unregulated fishery will converge upon this point.  The dynamics of a system

143  driven by effort dynamics (i.e. a spiral in F vs. SB phase space converging on a target over time)

144  are very similar to those observed in a system managed to a reference point like $B_{MSY}$. Once a

145  stock target is specified in management (e.g. $B_{MSY}$), managers endeavor to maintain the stock at

146  that point. However, due to errors in the management process (e.g. implementation, process, or

147  observation), the realized fishing mortality rarely equals the target. Consistent course correction

148  through management action would therefore be expected to produce a spiral path through F vs.

149 SB space, and, consequently, the effort dynamics model is also appropriate to apply to managed

150 stocks (i.e. all those in this analysis). Models (Eq. 1c) were fit to the changes in F and SB from

151 data sets simulated for different numbers of observed years and beginning observation of the

152 fishery at different time in the exploitation.

153

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{K}\right) - C_t \qquad \text{Eq 2}$$

154 Where:

$B_t$     Biomass at time $t$

$r$     Intrinsic rate of population growth (set to 0.2)

$K$     Carrying capacity (set to 1000)

$C_t$     Catch from the fishery at time $t$

155

$$C_{t+1} = \frac{C_t}{B_t} \left(\frac{B_t}{a * B_0/2}\right)^x B_{t+1} \qquad \text{Eq 3}$$

156 Where:

$a$     Indicates what fraction of $B_{MSY}$ economic equilibrium occurs (set to 0.5)

$B_0$     Equilibrium biomass in the absence of fishing

$x$     Adjusts the fraction of last year's catch applied based on the relationship of current biomass to the biomass at economic equilibrium (set to 0.2)

157

158 <u>Random forests: linking stock characteristics to predictability</u>

159 The predictability of fisheries as a coupled human-natural system (measured as MARE for

160 predictions based on Eq. 1c) may vary among stocks based on life history characteristics of the

161 species, or for other reasons. We therefore conduct a post-hoc analysis of predictability based on

162 biological and fishery characteristics. To do so, we use 'random forest', which is an efficient

163 statistical method for estimating nonlinear responses and interactions among many potential

164 predictors (Brieman, 2001). Random forests boast high classification accuracy, can model non-

165 linear relationships between predictor and response variables, can model complex interactions

166 among predictor variables, and provide a method for determining variable importance (Cutler et

167  al., 2007).  Random forests were an appropriate choice for analysis here because functional

168  forms and interactions for the variables tested here were not obvious, nor was the analysis

169  balanced.  When compared to other methods, such as generalized linear models, random forests

170  are able to reveal more complicated relationships (De'ath and Fabricius, 2000). Random forests

171  were implemented here using the R package "randomForest" (Breiman et al. 2013).

172

173  *Data for classification*

174  Maximum weight, maximum length, maximum age, and habitat type were drawn from FishBase

175  (Froese and Pauly, 2015*;* references 39-68 were used to fill gaps in FishBase) and large marine

176  ecosystem, managing body, phylogenetic order, average F, minimum observed spawning

177  biomass, and length of time series were drawn or calculated from the RAM Legacy Database

178  (Ricard et al. 2012) to be tested as explanatory variables for predictability of changes in F and

179  SB (Table 1). The Spearman's cross-correlation (1904) between spawning biomass and

180  recruitment (where the zero lag correlation represent the influence of spawning biomass on

181  recruitment and the largest correlation of the negatively lagged correlations represents the

182  influence of recruitment on spawning biomass), the average length of recruitment regimes, and

183  the coefficient of variation in recruitment were taken from Szuwalski et al. (2015).

184

185  Variables important for determining the predictability of stocks were identified using a stepwise

186  method similar to Genuer et al. (2010).  Random forests were fit to the data using all identified

187  predictor variables (table 1) and the variance explained (a 'pseudo-$r^2$) was calculated as 1-mean

188  square error divided by the variance of the response variable.  The predictor with the lowest

189  importance score was dropped and random forests were fit to the data again.  The resulting

190  trajectory of percent variance explained can be used to indicate which variables are important. A

191  vector of random numbers was also included as a predictor in each random forest to aid in the

192  identification of important variables. Variables that performed more poorly than the random

193  number vectors were not considered for inclusion in the final model.

194

195  **Results**

196  *Simulation and defining expected fishery dynamics*

197    Consistent patterns arose in the estimated relationships between F and SB when GAMs were fit

198    to data simulated from surplus production and effort-dynamics models (Eq. 2-3) regardless of the

199    number of data points included.  These consistent patterns form the basis for the 'expected

200    dynamics' against which the RAM Legacy data will be compared. For example, the influence of

201    F on changes in SB (which tracks the impact of fishing on the population) shows an inverse

202    relationship (i.e. as F increases, SB decreases for the simulated data sets; solid lines; Figure 1).

203    Consequently, we defined expected dynamics for this model class as only negative monotonic

204    relationships.  If this expectation is violated (i.e., no influence of F on SB) then this implies that

205    fisheries management cannot affect SB by changing F, which would render fisheries

206    management ineffective.

207

208    The influence of SB on changes in SB reflects density-dependent effects manifested in the

209    endogenous dynamics of the population.  The relationship between changes in SB and SB was

210    negative and monotonic for most simulated data sets (dot and dash line; Figure. 1).  The

211    mechanism behind this relationship can stem from different sorts of density dependence (e.g.

212    direct cannibalism or competition for resources).  Depensation at low stock sizes could also

213    result in a concave relationship, but there is little evidence for depensation in fished marine

214    stocks (Liermann, et al., 2001).  Still, for the purposes of this analysis, expected relationships are

215    defined as negative monotonic or concave relationships between changes in SB and SB.

216

217    The influence of SB on the change in F indicates how managers (or fishers) change F based on

218    the perceived size of the stock.  The change in F decreased as SB decreased in the simulated data

219    sets (dotted line; Figure 1).  This is conceptually intuitive because, even in the absence of

220    management, as SB decreases the profitability of the fishery should decrease with a decreasing

221    CPUE.  If management is active, its primary job is to decrease F when SB decreases past a

222    certain point. However, hyperstability in the CPUE resulting from schooling behavior may allow

223    F to remain high as SB decreases in open access situations and some management strategies

224    eschew biomass-based metrics for constant fishing mortality rates.  For this analysis, the

225    'expected' dynamic between changes in F and SB is one in which F decreases at low SB sizes

226    because it is most consistent with management goals and open-access—however the size at

227 which this decrease occurs can be different between unregulated effort-dynamics and active
228 fisheries management.

229

230 The influence of F on the change in F indicates the way in which managers (or fishers) change F
231 in response to a perceived level of exploitation. For the simulated data sets, this relationship is
232 either flat or convex with respect to SB (dashed line; Figure 1). However, any relationship
233 between F and changes in F could be plausible, depending on the history of fishing and
234 management. Consequently, we have placed no expectations on this relationship in this analysis
235 (i.e. all forms of the relationship can be 'expected').

236

237 The results of this simulation exercise show that the GAMs can be used to estimate the
238 relationship between SB and F, given the underlying dynamics of the system follow those that
239 are most often assumed by fisheries managers. Predictions of changes in SB and F were nearly
240 perfect for the longest simulated time series (60 years; RMSE <0.001 for both) using only the
241 'traditional dynamics' models from above (i.e. those in which the number of knots was construed
242 to be 3 or fewer). This exercise also produced a baseline for 'expected dynamics' given a
243 'traditional' management paradigm.

244

245 *Application to global fisheries*
246 For each stock, the functions *g()* and *h()* that describe the population and effort dynamics were
247 estimated from the data with varying degrees of explanatory power. The predictability of
248 changes in F and SB based on these fitted models varied significantly across large marine
249 ecosystem (LME), recruitment variability, maximum weight of the species fished and the ratio of
250 minimum and maximum observed SB, as indicated by the applied random forests (see Table 1
251 for a description of tested variables). Predictability of changes in SB also varied across
252 maximum length of the species fished, while predictability of changes in F also varied among
253 habitat types. In general, changes in SB were more predictable than changes in F, but there was a
254 larger variety in predictability of F (0.17 vs. 0.73 MARE; compare top rows of figure 2). The
255 average F over the history of the fishery also influenced the predictability of changes in SB to
256 some extent and the influence of recruitment on SB influenced the predictability of changes in F
257 (figure 3).

258

259 Observed fishery dynamics often did not match the classical assumptions of fishery dynamics.

260 Sixty-two percent of stocks displayed one of three patterns in fishery dynamics: 22% displayed

261 all expected dynamics, 21% showed density dependence, but SB did not decrease as F increased,

262 and 19% showed density dependence, but F did not increase as SB increased. In total, dynamics

263 consistent with density-dependence appeared in 73% of stocks, and SB decreased as F increased

264 for 54% of stocks. The proportion of stocks that displayed all expected dynamics varied

265 significantly according to LME, the influence of recruitment on spawning biomass (as seen

266 through the most significant lagged cross correlation), variability in recruitment, and average F

267 (figure 4). Predictability did not markedly improve when moving from models with 3 knots to 5

268 knots (figure 5).

269

270 *Case studies*

271 Predictability was often relatively high when a fishery responded as expected to changes in F and

272 SB (and hence identifying and managing toward a target level of SB and F was possible).

273 Sablefish (*Anoplopolma fimbria*, Anoplopmatidae) in the eastern Bering Sea presented a good

274 example of expected fishery dynamics (figure 6). SB began relatively high while F was low, SB

275 decreased as F increased, then F decreased as SB declined further, after which SB subsequently

276 rebounded. The resulting spiral in F vs. SB phase space was centered around the management

277 target for the stock (Hanselman et al. 2013). Survey and CPUE data do not start until 1979, so

278 the early part of the time series' of F and SB do not have informative data driving them.

279 However, they could be removed and the same spiral (though a truncated version of it) would be

280 seen in F vs. SB phase space. This spiral is what produces the 'predictability' of the system with

281 classical models. Errors in predictions of changes in SB were 4% on average for the last 5 years

282 of data (88th percentile out of all stocks); errors in predicted Fs were 6% on average (97th

283 percentile).

284

285 Prediction was very difficult for some stocks, particularly short-lived species with variable

286 recruitment. Pacific herring (*Clupea pallasii,* Clupeidae) in the Gulf of Alaska, was a good

287 example of a stock with poor predictability (2nd percentile and 1st percentile for predictability in

288 SB and F, respectively). A relatively long history of exploitation was captured in the assessment

289      for herring and large swings in abundance and fishing pressure were observed, during which

290      much of the F vs SB phase space was explored (figure 6). However, the responses in a given

291      area of the phase space were not consistent through the history of the fishery, which translated to

292      poor predictive performance.

293

294      Some stocks were fished to low levels and never rebounded, even when fishing pressure was

295      relaxed (a "one-way trip"). Ten percent of stocks in the analysis showed one-way trips, but

296      determining if shifts in population dynamics or overfishing caused the collapses is often difficult.

297      Walleye pollock (*Theragra chalcogramma,* Gadidae; figure 6) around the Aleutian Islands

298      exhibits a 'one-way trip' hailed by some as the "most spectacular fishery collapse in North

299      American history" and was attributed to overfishing (Bailey, 2011). However, changes in F for

300      pollock were as expected (i.e. F decreases when SB was low), SB did not respond as expected

301      (i.e. increase when F was low). Although changes in F were as expected, the timing of these

302      changes was not immediate—there were several years during which SB was low, but F was still

303      high, which suggests a lagged management response.

304

305      Counter-intuitive responses to fishing were common. For example, changes in F for skipjack

306      tuna (*Katsuwonus pelamis,* Scombridae) in the Pacific Ocean produced very little change in

307      SB—spawning biomass actually increased with increases in F (figure 6). This could be a result

308      of relatively light fishing pressure and changes in the environment, but European plaice

309      (*Pleuronectes platessa,* Pleuronectidae) on the Celtic-Biscay Shelf experienced relatively high

310      and steady F and showed similarly counter-intuitive patterns—SB changed independently of F

311      (figure 6). Responses like these run counter to the assumptions of most management strategies

312      and corroborate evidence that population dynamics for many exploited species are influenced

313      more strongly by the factors other than SB over the range of observed stock sizes (Szuwalski et

314      al. 2015). Plots for all fisheries included in the analysis and supplementary references can be

315      found in the supplementary materials.

316

317      **Discussion**

318      *Quantified gradients of predictability*

319    Gradients of predictability imply gradients in both manageability and the appropriate precaution
320    to be taken when calculating sustainable catches.  This may be particularly important for stocks
321    that have little management or are poorly understood, particularly when attempting to manage
322    under the traditional paradigm of fishery dynamics.  Quantifying and placing fishery dynamics in
323    a global context (as we have done here) will allow for more appropriate incorporation of
324    uncertainty in the study and management of exploited populations. The Precautionary Approach
325    (i.e. when estimates of spawning biomass are uncertain, err on the side of conserving the stock;
326    FAO 1996) is often invoked to address some of the uncertainty in estimates of SB and F due to
327    model misspecification and process error, but there is no standardized way of determining an
328    appropriate amount of precaution (although forecasting error may sometimes be a useful proxy;
329    Ralston et al, 2011). Our finding suggest less-predictable stocks should be evaluated with greater
330    caution than more-predictable stocks, given that SB or F is more likely to change unexpectedly
331    for unpredictable stocks.

332

333    Climate change and increased variability has the potential to drastically influence the
334    predictability of stocks.  Fisheries managers' main sources of information when managing stocks
335    are time series of catch, indices of abundance, and samples of the age and size distribution, from
336    which the productivity and response of a population to exploitation can sometimes be inferred.
337    However, if stock productivity is influenced by factors other than SB and large environmental
338    changes occur, past observations of catch and estimates of abundance will be less informative
339    about expected future productivity (Szuwalski and Hollowed, 2016).  Changing trophic
340    interactions over time may have similar influences on the predictability (Szuwalski et al., 2016).
341    Under all the myriad influence, one-way trips (and the opposite circumstance in which
342    productivity increases; e.g. Arrowtooth flounder in the Gulf of Alaska, Figure S6) may become
343    more prevalent as the oceanic environment continues to change (Doney et al., 2012).

344

345    *Drivers of predictability*
346    In general, variables identified by this analysis as important for predicting changes in SB and F
347    make intuitive sense. Longer maximum lengths and higher maximum weights (which both are
348    related to older maximum ages) buffer against large inter-annual changes in SB and therefore
349    improve predictability of changes in SB.  Higher CVs of recruitment can make predicting F and

350   SB more difficult, particularly if recruitment comprises a relatively large fraction of exploitable

351   biomass. The influence of habitat on predictability of changes in F may stem from differential

352   selectivity of gear types used in different habitats and differences in management (consider the

353   targeting ability of a demersal trawl fishery and a pelagic purse seine fishery). LME was

354   important for both changes in F and SB, perhaps due to differences in fisheries management or

355   environmental forcing by geographic area. Higher minimum observed SB improved

356   predictability in F and SB, perhaps because relatively low SB is correlated with increased

357   variability in recruitment and hence less-predictable biomass dynamics (Minto et al. 2008).

358   Stocks with all 'expected' fishery dynamics were more likely to have lower minimum observed

359   SB, higher CVs around recruitment and a higher average F. These are all factors that predispose

360   a stock to explore the F vs SB phase space more thoroughly.

361

362   *Implications for model suitability*

363   We show 'classical' production models do not effectively predict the dynamics of a large

364   fraction of global fisheries, but many fisheries have sufficient data to perform assessments that

365   incorporate age-at-length sampling data, tagging data, or other information. Additional biological

366   information may improve predictability for changes in SB in many cases and the stock

367   assessments from which the estimated time series of F and SB were drawn would likely predict

368   changes in SB better than the presented models. For example, age-composition information will

369   inform estimates of past recruitment and provide information regarding somatic growth in a

370   given year (Ono et al., 2015; however, incorporation of additional biological data does not

371   always decrease uncertainty in management quantities, Kell et al. 2016). Similarly, information

372   regarding fishery characteristics (profitability, management changes, nominal effort) may

373   increase predictability for F (Sethi et al, 2010; Menychuk, et al., 2013). Nevertheless, our results

374   provide a lower-bound on predictability and can be used to identify relatively unpredictable

375   stocks, which could then be managed with greater precaution. Furthermore, the concept

376   encapsulated by our analysis (e.g. testing the predictability of a given modeling framework for

377   both simulated and real data) should occupy a central point of any management effort.

378

379   Upwards of 80% of worldwide fisheries are unassessed and minimally managed, and interest is

380   high in improving assessment and management for these fisheries (Thorson et al., 2012; Costello

381 et al., 2012). However, data for assessment are often few. Methods that only require catch time
382 series are being explored to assess and manage fisheries (Martell and Froese, 2012; MacCall,
383 2009), but the debate concerning the information content of catch time series' is ongoing
384 (Hilborn and Branch, 2013 vs. Pauly, 2013). Catch only methods can be justified if fisheries
385 dynamics match the assumed dynamics of the prevailing fisheries paradigm (Thorson et al.,
386 2013), yet this match is only apparent in 22% of assessed fisheries in our analysis. This suggests
387 that, although there is a subset of stocks for which catch-only methods might be possible, catch is
388 often not a reliable indicator of biomass in the larger scale fisheries examined here (this may not
389 be the case for small scale and subsistence fisheries).

390

391 *Implications for management strategies*

392 Simulation frameworks (e.g. management strategy evaluation, Smith et al, 1999) are often used
393 to test harvest strategies under a variety of assumed population and effort dynamics. However,
394 simulation testing requires speculation about what scenarios are plausible or likely (Carpenter,
395 2002; Rochet and Rice, 2009). Region-specific meta-analysis may provide improved baselines
396 for simulating scenarios, but our study shows that unpredictable fishery dynamics are more the
397 rule than the exception, and hence rapid changes in F or SB independent of the current level of F
398 or SB should be explored. Similarly, environmental and/or regime shift scenarios for biomass
399 dynamics are common in the populations analyzed here and management strategies should be
400 explored that are robust to these changes (e.g. Szuwalski and Punt, 2013). For many of the
401 unassessed stocks globally, collection of data required for assessment can be prohibitively
402 expensive. Simulation studies are increasingly being suggested for use to identify management
403 strategies that are robust to a range of fishery dynamics (Bentley and Stokes, 2009; Punt, 2008),
404 but have been criticized for the lack of variety in the assumed simulation dynamics (Rochet and
405 Rice, 2009). We therefore recommend that future simulation studies explore both predictable
406 dynamics (i.e., density dependent population dynamics combined with endogenous effort
407 dynamics), unpredictable dynamics (i.e., regime-based population dynamics combined with
408 rapid shifts in fishing pressure), and non-linear dynamics (as those suggested by Glaser et al.,
409 2015).

410

411 Successful fisheries management requires an understanding of a population's response to
412 exploitation and changes in the environment, if not on a mechanistic level, at least on a
413 predictive level. Some failures in fisheries management can be traced to incorrect assumptions
414 about population dynamics (e.g. Walters and Maguire, 1999). Consequently, regular checks that
415 the dynamics of F and SB (and recruitment dynamics) in a population are operating as assumed
416 should become a regular part of assessment and management. The ability of capture fisheries to
417 continue to support global protein needs depends on our ability to sustainably manage exploited
418 populations; fisheries managers must more thoroughly examine the way in which they expect a
419 population to behave to ensure sustainable harvest.

420 **Acknowledgments:**

425

426 **Supplementary materials:**

427 Plots similar to figure 6 for all stocks in the analysis and supplementary references used to
428 populate the databased used to identify gradients in predictability in are available online.

429

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535

536

537   Table 1. Description of variables linked to predictability of changes in F and SB.

| Predictor | Description |
|---|---|
| Maximum length | Maximum body length achieved by a species |
| Maximum weight | Maximum body weight achieved by a species |
| Maximum age | Maximum age achieved by a species |
| Habitat | Major habitat occupied by a species (e.g. coral reef, pelagic, demersal) |
| LME | Large marine ecosystem |
| Management | Managing body for the stock (e.g. DFO, NMFS, ICCAT) |
| Assessment | Method of assessment (e.g. VPA, SCAA, Production model) |
| Order | Phylogenetic order (e.g. Scorpaeniformes) |
| Average F | Average estimated fishing mortality experienced of the period of assessment |
| Ratio of minimum and maximum observed SB | Minimum estimated spawning biomass over the period of assessment, calculated as a fraction of the maximum observed spawning biomass |
| Lagged CCF | Most significant negatively lagged crosscorrelation between spawning biomass and recruitment (indicates the influence of recruitment on SB) |
| Recruitment Drivers | Drivers of recruitment dynamics as indicated by Szuwalski et al. 2015 |
| Length | Length of the time series for a given stock in this analysis |
| Zero CCF | Magnitude of the Spearman's correlation of between spawning biomass and recruitment |
| Coefficient of variation in recruitment | Quantifies the variability in recruitment |

538

539

540   **Figure legends:**

541　Figure 1. Simulated fishing mortality (F. mort), spawning biomass (Sp.Bio.) from a production

542　model with effort dynamics determining catch. The middle row plots the trajectory of the stock

543　through F and SB phase space; white are the oldest observations, black are the newest. The

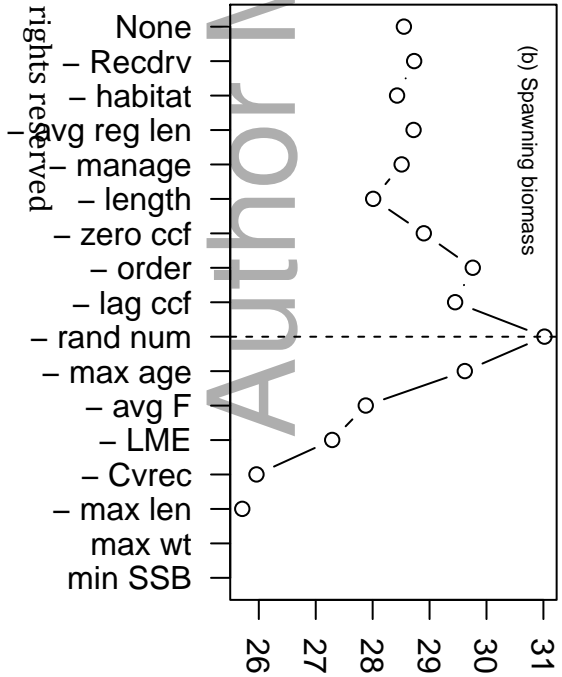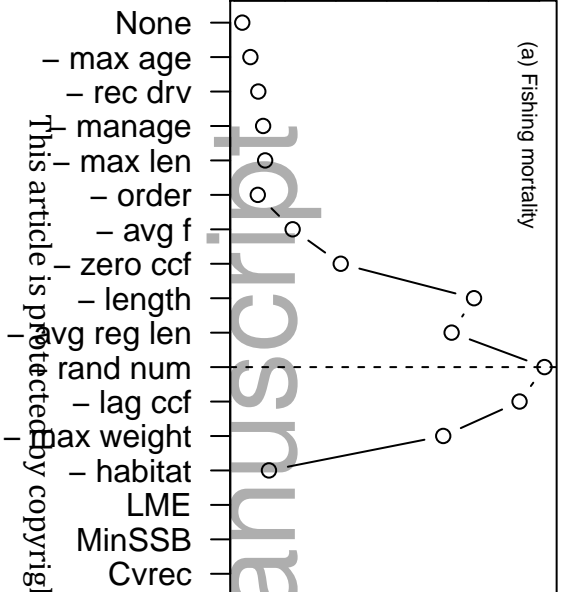544　bottom row plots the fitted relationship between changes in F or SB to current F or SB. Each

545　column represents a different number of years of simulated data and/or starting observation at

546　different points in the exploitation history.

547

548　Figure 2. Variables identified as important in predicting changes in F and SB via random forest.

549　Changes in F or SB are increasingly predictable (measured in mean absolute relative error

550　[MARE]) towards the right of the graph. LMEs for which data for at least 5 stocks were

551　included in the LME plot.

552

553　Figure 3. Percent variability explained for changes in fishing mortality (F) and spawning biomass

554　(SB) via random forest as terms are removed from the model. Vertical dashed line in each

555　represents the random number vector and the variables to the right were retained in the models

556　presented.

557

558　Figure 4. Frequency of combinations of fishery dynamics and probability of all expected

559　dynamics. Below the histogram of observed dynamics (top), the probability of observing all

560　expected dynamics (i.e. active management and stationary, density-dependent population

561　dynamics) given 4 variables identified as important by random forests (lagged CCF indicates the

562　most significant negatively lagged cross correlation). Shaded areas represent 95% confidence

563　intervals.

564

565　Figure 5. Changes in root mean square error (RMSE) when moving from estimating the

566　dynamics of SB and F using GAMs with 3 knots to 5 knots. A decrease in RMSE indicates

567　improved predictive ability.

568

569　Figure 6. Example stocks on the spectrum of predictability. Estimated fishing mortality (F mort),

570　spawning biomass (Sp.Bio.) and recruits are in the top row. The middle row plots the trajectory

571　of the stock through F and SB phase space; white are the oldest observations, black are the

572    newest.  The bottom row plots the fitted relationship between changes in F or SB to current F or

573    SB.
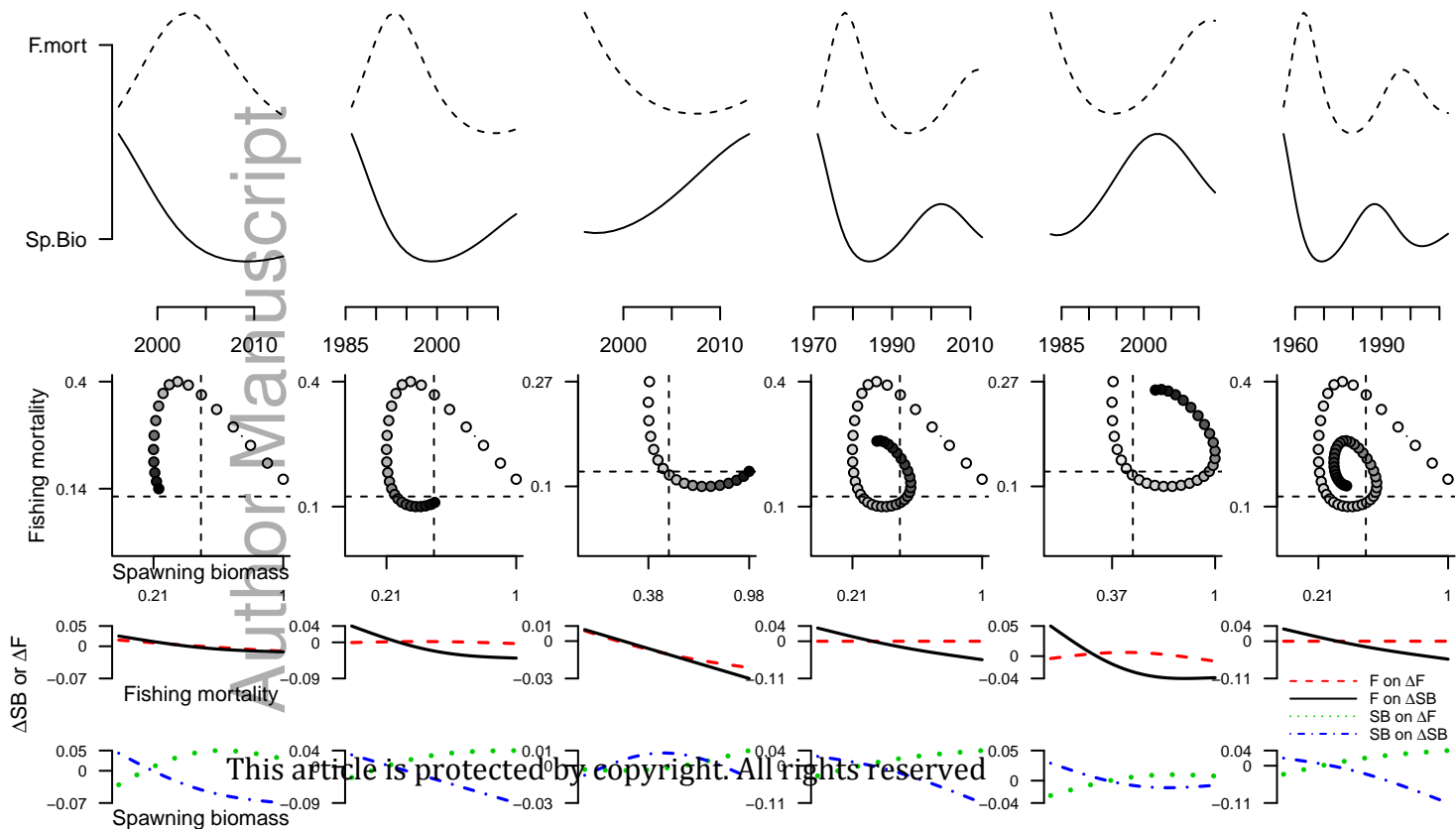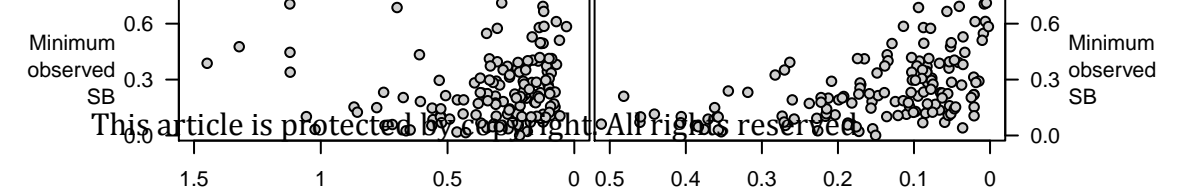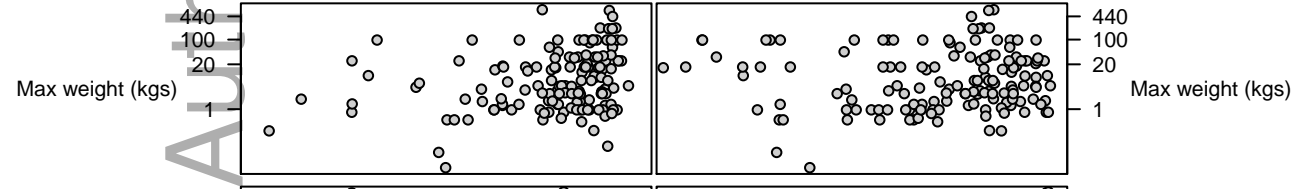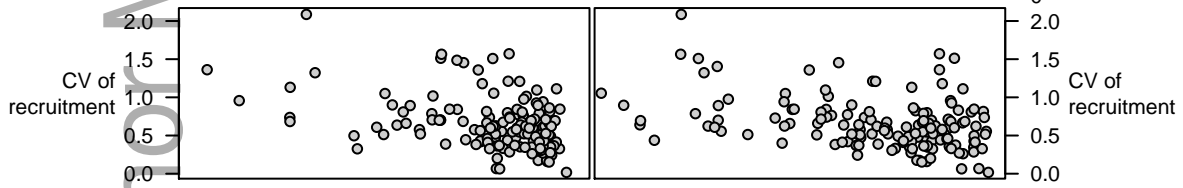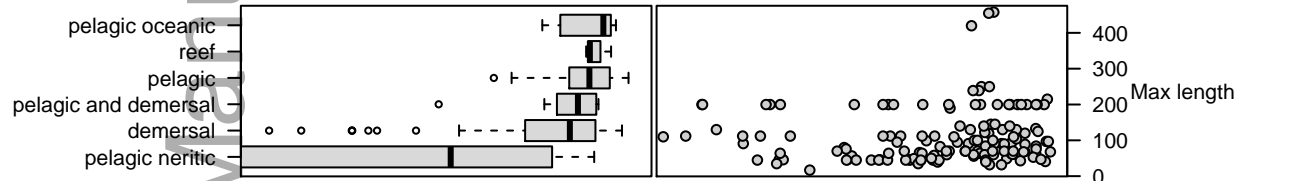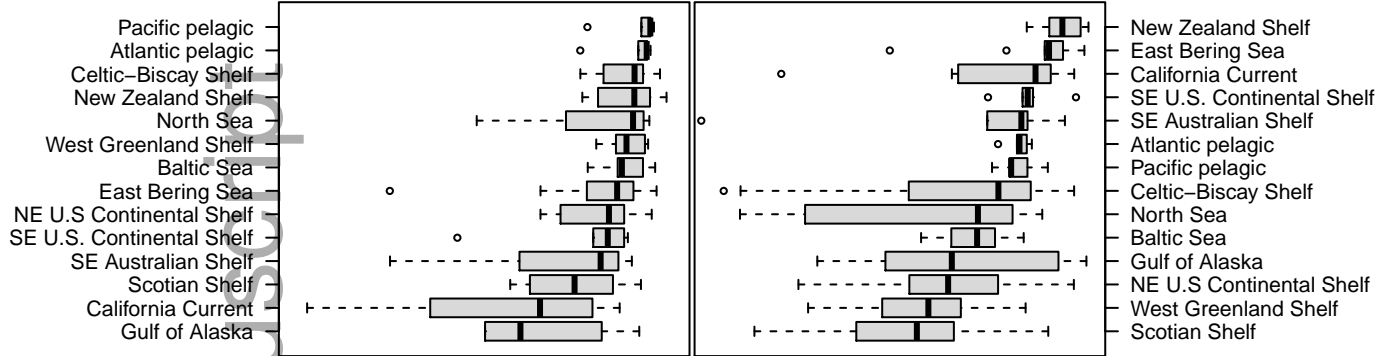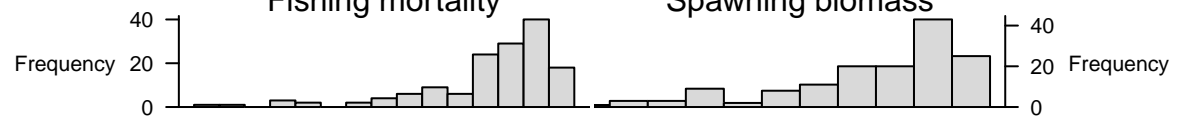
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(a)   x = Expected

Frequency

SB on ΔSB    X    X         X              X
F on ΔSB                X    X    X    X
SB on ΔF     X                X    X                        X
F on ΔF      X    X    X    X    X    X    X    X

Atlantic pelagic
NE U.S Continental Shelf
East Bering Sea
Gulf of Alaska
Celtic–Biscay Shelf
North Sea
Scotian Shelf
Baltic Sea
California Current
New Zealand Shelf
Pacific pelagic
SE Australian Shelf
SE U.S. Continental Shelf
West Greenland Shelf

(b)

Average F

(c)

Coefficient of variation in Recruitment

(d)

Lagged CCF

(e)
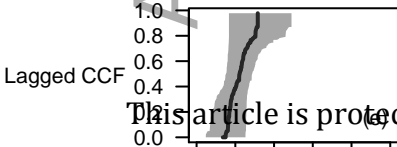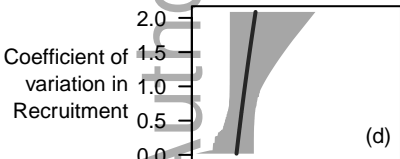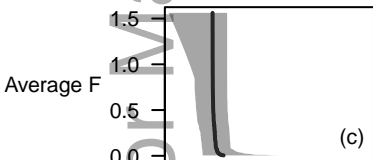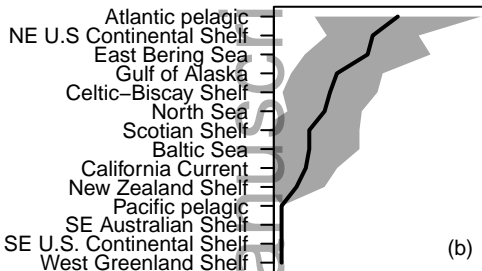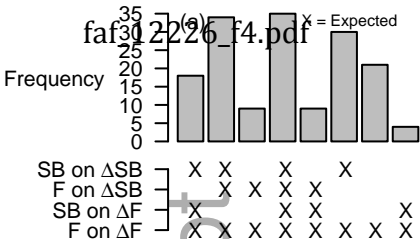
Probability of expected dynamics

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(a) Spawning biomass

(b) Fishing mortality

$\Delta$RMSE
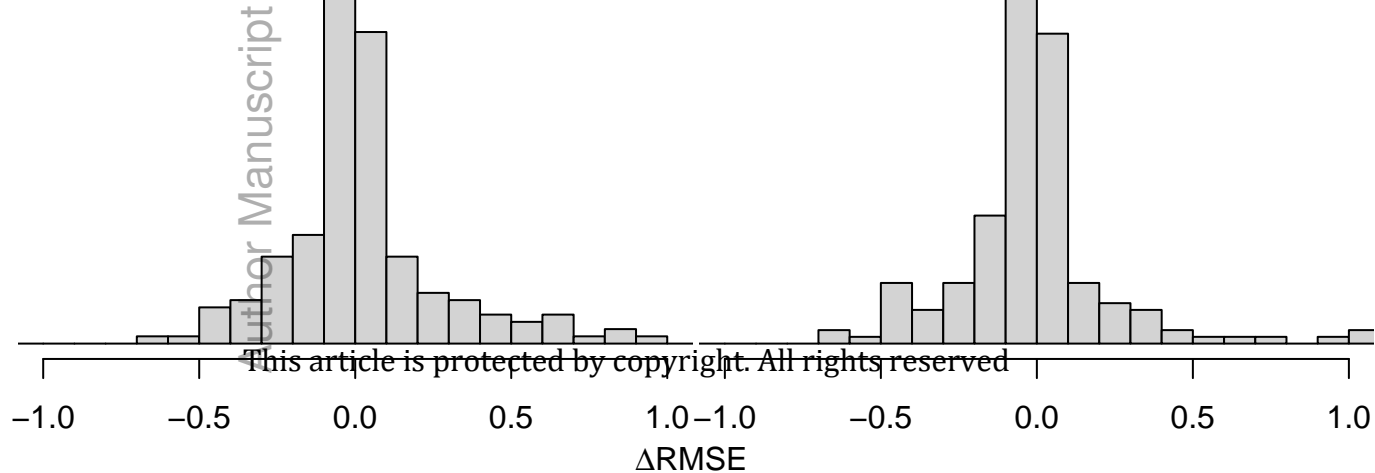
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| Common name | Sablefish | Pacific herring | Walleye pollock | Skipjack tuna | European Plaice |
|---|---|---|---|---|---|
| Species | *Anoplopoma fimbria* | *Clupea pallasii* | *Theragra chalcogramma* | *Katsuwonus pelamis* | *Pleuronectes platessa* |
| Order | Scorpaeniformes | Clupeiformes | Gadiformes | Perciformes | Pleuronectiformes |
| LME | East Bering Sea | Gulf of Alaska | East Bering Sea | Pacific pelagic | Celtic–Biscay Shelf |
| RAM ID | AFSC–SABLEFEBSAIGA–1956–2008–MEL | DFO–PAC–HERRPRD–1951–2007–COLLIE | AFSC–WPOLLAI–1976–2008–MELNYCHUK | SPC–SKJCWPAC–1972–2006–JENSEN | WGSSDS–PLAICCELT–1976–2006–JENNIN |

F.mort

Sp.Bio

Recruits

oldest obs
newest obs

Fishing mortality

Spawning biomass

ΔSB or ΔF

Fishing mortality

Spawning biomass

F on ΔF
F on ΔSB
SB on ΔF
SB on ΔSB