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Title: Nonlinear dynamics and noise in fisheries recruitment - a global meta-analysis

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35

36 Abstract

37 The relative importance of environmental and intrinsic controls on recruitment in fishes
38 has been studied for over a century. Despite this, we are not much closer to predicting
39 recruitment. Rather, recent analyses suggest that recruitment is virtually independent of
40 stock size and, instead, seems to occur in distinct environmental regimes. This issue of
41 whether or not recruitment and subsequent production is coupled to stock size is highly
42 relevant to management. Here we apply Empirical Dynamical Modeling (EDM) to a
43 global database of 185 fish populations to address the questions of whether or not
44 variation in recruitment is a) predictable and b) coupled to stock size. We find that a
45 substantial fraction of recruitment variation is predictable using only the observed
46 history of fluctuations (~40% on average). In addition, although recruitment is often
47 coupled to stock size (107 out of 185 stocks), stock size alone explains very little of the
48 variation in recruitment; In ~90% of the stocks analyzed, EDM forecasts have
49 substantially lower prediction error than models based solely on stock size. We find that
50 predictability varies across taxa and improves with the number of generations that have
51 been sampled. In light of these results, we suggest that EDM will be of greatest use in
52 managing relatively short-lived species.

53

54 Key Words: , Empirical Dynamical Modeling, Gaussian process regression,
55 Recruitment, Time-delay embedding.

56

57 1. Introduction

58 2. Methods

59 2.1 Database selection

60 2.2 Convergent Cross-mapping

61 2.3 Gaussian process-EDM

62 3. Results

63 4. Discussion

64

65

66 **1. Introduction**

67 The relative importance of environmental and intrinsic controls on population growth has
68 been a source of controversy in ecology since the beginning (Howard & Fisk, 1911;
69 Adrewartha & Birch, 1954; Nicholson, 1954, etc). Like many dichotomies in ecology,
70 this battle has dissipated in the middle ground where both factors appear relevant (e.g.
71 Milne, 1962; Orians, 1962; Dixon et al., 1999). Nevertheless, predicting changes in
72 abundance remains an important goal in applied ecology, where models separating
73 intrinsic and extrinsic dynamics form the foundation for conservation and management
74 decisions for threatened and harvested species.

75 Like their terrestrial counterparts, fisheries oceanographers grapple with the balance of
76 intrinsic dynamics and environmental drivers. The number of new fish recruiting to a
77 population may vary over an order-of-magnitude from one year to another, with serious

78 consequences for fisheries management and food security (Glantz, 2005). For much of
79 the last century, fisheries oceanographers have attempted to solve this ‘recruitment
80 problem.’ Since the seminal work of Hjort (1914, 1926), numerous factors influencing
81 recruitment have been identified.

82 During early life stages, fish growth is dominated by environmental conditions, while
83 mortality rates are extremely high and size-dependent (Bailey & Houde, 1989; Perez &
84 Munch, 2010). Early growth and survival are also influenced by oceanographic
85 conditions such as turbulence (Rosthchild & Osborn, 1988; MacKenzie, 2000),
86 stratification (e.g. Lasker, 1975; Jenkins et al., 2010), and larval transport (e.g. Checkley
87 et al., 1988; Epifanio et al., 1989), as well as temperature, salinity, and dissolved
88 oxygen concentrations (e.g. Koster et al., 2005). Biotic factors such as food availability
89 (Cushing, 1990; Bergenius et al., 2002), predator abundance (Bailey & Houde, 1989),
90 competition (Holbrook & Schmidt, 2002), the age composition of the population
91 (Marteinsdottir & Thorarinsson, 1998; Shelton et al., 2012), and maternal effects
92 (Green, 2008; Berkeley et al., 2004) also contribute to variation in egg production,
93 growth, and early survival.

94 Despite the substantial increase in our *understanding* of recruitment ecology, we are not
95 much closer to *predicting* recruitment. Most recruitment – environment correlations
96 become non-significant within a few years of their publication (Myers 1998). As a
97 consequence, contemporary fisheries management rarely makes use of environmental
98 drivers or other ecosystem indicators when setting harvest rates (Skern-Mauritzen et al.,
99 2016). Rather, simple models are used to relate current reproductive output, often
100 indexed by some measure of population biomass, to the production of juveniles
101 recruiting to the population. These ‘stock-recruitment’ models typically explain very little
102 of the observed variation in recruitment (Cury, 2014; Lowerre-Barbieri et al., 2017);
103 deviations up to an order of magnitude are considered as the norm and generally
104 attributed to environmental stochasticity and/or measurement error. Nevertheless, the
105 parameters of these models are often critical in setting benchmarks for fisheries
106 management (Mangel et al., 2013).

107 In light of the complexity of processes governing recruitment and the apparent
108 dominance of environmental stochasticity, several authors have claimed that prediction
109 using fisheries models is unattainable (Schindler & Hilborn, 2015; Glaser et al., 2014)
110 and solving the 'recruitment problem' is impossible (Ottersen et al., 2014; Lowerre-
111 Barbieri et al., 2017). In addition, several recent analyses suggest that the productivity
112 of fish populations is independent of population size; rather, seemingly discrete changes
113 in productivity are interpreted as environmental regimes leading to the conclusion that
114 very little of the observed variation in fished populations results from intrinsic dynamics
115 (Vert-Pre et al., 2013; Szuwalski et al., 2015). If this is the case, then fishing – which
116 clearly affects current population size – can have very little influence on the long-term
117 dynamics of harvested populations. Moreover, since fisheries management attempts to
118 maximize production by manipulating fishing effort, the question of whether or not
119 population size and recruitment are causally coupled is highly relevant (Pierre et al.,
120 2017). But how best to predict recruitment and identify its causal drivers in the face of
121 considerable empirical complexity is unclear.

122 We hypothesize that a substantial fraction of the apparent indeterminism in recruitment,
123 often attributed to environmental stochasticity, arises from collapsing complex
124 recruitment dynamics into low dimensional indices. Takens' theorem of time-delay
125 embedding (Takens, 1981) and its generalizations (Sauer et al., 1991; Stark et al.,
126 2003) offer a way around this problem. Time-delay embedding uses lags of observed
127 variables to construct synthetic axes that account for unobserved variables. e.g. time
128 lags of abundance for a focal species can be used to implicitly account for variations in
129 the abundance of other, unmeasured, species with which it interacts. This is particularly
130 effective at reconstructing low dimensional dynamics. But extrinsic drivers, like the
131 weather, typically emerge from very high dimensional systems. Since the number of
132 dimensions we can resolve with time-lags is limited by the time series length (Cheng &
133 Tong, 1994), we expect extrinsic forcing to be sufficiently high dimensional as to appear
134 essentially stochastic. In light of this we operationally define any dynamics that can be
135 recaptured with a low dimensional embedding as 'intrinsic.'

136 In ecology, Takens' theorem was initially used to uncover low dimensional chaos
137 (Schaffer, 1984) and distinguish observational noise from nonlinear dynamics (Sugihara
138 et al., 1990; Sugihara & May, 1990; Sugihara, 1994). Because these methods allow us
139 to make inferences about dynamics directly from time series, they are currently referred
140 to as empirical dynamical modeling (EDM). Here, we apply EDM to a global dataset of
141 stock assessments to address several fundamental questions on the relationship
142 between current population biomass and recruits.

143 Pierre et al. (2017) recently addressed the question of whether stock biomass and
144 recruitment are causally coupled, by applying convergent cross-mapping (CCM,
145 Sugihara et al., 2012) to 53 time-series of stock and recruits. They found that although
146 stock size and recruitment were often coupled, stock size did not contribute much to
147 prediction accuracy. In addition, they showed that nonlinear forecasting using S-map
148 (Sugihara, 1994) typically produced predictions that were better than chance. This
149 analysis is an important first step, but leaves open several questions including How
150 much of the variation in recruitment can be explained using time-delay embedding?
151 How well do EDM predictions compare with those of existing models? and What factors
152 influence differences in the degree of predictability among stocks?

153 To address these questions, we expanded the number of stocks analyzed from 53 to
154 185. From this larger data set, we reconsider the question of whether biomass and
155 recruits are causally coupled using convergent cross mapping (Sugihara et al., 2012).
156 Next, using Gaussian process EDM (Munch et al., 2017), we explicitly quantify what
157 fraction of the observed variation in recruitment can be explained by intrinsic dynamics.
158 We then benchmark our predictions against several commonly used models. Finally, we
159 evaluate the importance of life history and assessment method in determining the
160 results.

161

162 **2. Methods**

163 2.1 Database selection

164 Ransom Myers and colleagues assembled a global database of stock sizes and
165 recruitment estimates for over 600 fish populations, representing 100 species from
166 marine and freshwater environments (Myers et al., 1995a,b hereafter referred to as the
167 RAM database). The database also tracks the methods used in estimation, the site or
168 management area the data represent, and life history parameters for each population.
169 Recruitment in this database refers to the abundance of a cohort as it enters the fishery.
170 More details on the database are provided in (Myers et al., 1995b; Myers & Barrowman,
171 1996)

172 All populations with at least 20 years of both stock size and recruitment data were
173 included in our analysis, representing 185 populations from 49 species, spanning 8
174 Orders. First, we determined how much of the intrinsic variation in recruitment is
175 accounted for by stock biomass. Second, we evaluated how the predictability of
176 recruitment varies with the life histories of the species analyzed. Third, we tested
177 whether the intrinsic dynamics we recover can be adequately described with a linear
178 model. Several recent studies have cautioned against treating assessment model
179 outputs as data in meta-analyses (Brooks & Deroba, 2015). Fortunately, the RAM
180 database includes estimates obtained using a variety of tools, ranging from direct
181 observations of juveniles in surveys to statistical catch-at-age models. And so, fourth,
182 we evaluated how our results vary across several coarse categories of estimation
183 methods that differ in their structural assumptions. For all comparisons, we used leave-
184 one-out cross validation to approximate out-of-sample prediction.

185 2.2 Convergent cross-mapping

186 EDM is based on ‘attractor reconstruction’ using time-delay embedding (Takens, 1981).
187 The fundamental idea is that for an M dimensional system that converges to a d-
188 dimensional attractor, we can reconstruct the attractor from a single time series of
189 observations, say y_t , $t=1, \dots, T$. This is done using lags of y (at time step τ) as surrogate
190 coordinates, i.e. $\mathbf{y}_t = \{y_t, y_{t-\tau}, \dots, y_{t-E\tau}\}$. Provided that the embedding dimension, E, is
191 greater than 2 (Takens, 1981) and T is sufficiently large, the collection of delay
192 coordinate vectors, $\{\mathbf{y}_{E+1}, \dots, \mathbf{y}_T\}$ reconstructs (i.e. ‘embeds’) the attractor.

193 Since Takens' theorem holds generically for any observable from the M dimensional
194 system, alternate reconstructions using different observables share a common attractor.
195 Convergent cross mapping (Sugihara et al., 2012) exploits this to identify whether two
196 variables are causally coupled. Specifically, if x and y share a common attractor, then
197 we expect contemporaneous values x to map to nearby points on the attractor
198 reconstructed with y, and vice versa. CCM has been used to identify drivers of climate
199 change (vanNes et al., 2015), flu outbreaks (Deyle et al., 2016), and gene expression
200 (Ma et al., 2014). Here, we applied CCM to test whether recruitment is causally driven
201 by the size of the adult population (indexed by stock biomass) and how this changes
202 across different methods for estimating recruitment. To do so, we estimated the
203 predictive capacity of the stock biomass time series on the recruits' time series (ρ_{original}).
204 We then tested the significance of the causal relationship detected by CCM by
205 generating 100 surrogate shuffles of the recruits' time series and calculating the
206 predictive capacity of the original stock biomass time series on each of them ($\rho_{\text{surrogate}}$).
207 A relationship was considered significant when ρ_{original} was higher than the 95th
208 percentile of the distribution of $\rho_{\text{surrogate}}$ values ($P < 0.05$).

209 2.3 Gaussian process EDM

210 Although CCM provides a robust approach to testing for causal coupling, it does not
211 address the question about the relative importance of intrinsic and extrinsic dynamics.
212 To address this question, we operationally define any dynamics that can be recaptured
213 with a low dimensional embedding as 'intrinsic' and use time-delay embedding to make
214 predictions of recruitment. Doing so involves estimating the map from past states to the
215 future using lag-coordinates, i.e. $y_t = f(y_{t-1}, \dots, y_{t-E})$. This map may be inferred using
216 any of a variety of function approximation tools including polynomials (e.g. Ellner &
217 Turchin, 1995), local linear regression (Sugihara, 1994), support vector machines (e.g.
218 Mukherjee et al., 1997), and neural networks (e.g. Bakker et al., 2006). Here, we used
219 Gaussian process regression (Rasmussen & Williams, 2006; Munch et al., 2016) to
220 estimate the map from the past to the future and quantify the intrinsic component of
221 recruitment dynamics (defined below). The GP approach extends the EDM toolkit by
222 allowing automatic lag selection, incorporating information from multiple sources using

223 hierarchical modeling, and allowing for non-stationary dynamics (Munch et al., 2016).
224 Gaussian process regression has been used in population modeling to estimate the
225 form of density dependence (Munch et al., 2005), test for the presence of Allee effects
226 (Sugeno & Munch, 2013), and as a tool to assess model misspecification (Thorson et
227 al., 2014).

228 Traditional stock-recruitment (SR) models assume that recruitment is some function of
229 the current population (i.e. stock) biomass, written as $R_t = \alpha S_t g(S_t)$ where R is
230 recruitment, S is stock size, and α is the maximum rate of reproduction (Myers 1995a).
231 The function $g(S)$ accounts for density-dependence. This model is typically fit on a log
232 scale where it is re-written as $\ln[R_t/S_t] = \ln[\alpha] + \ln[g(S_t)] + \varepsilon_t$, $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$. Letting
233 $y_t = \ln[R_t/S_t]$, a natural extension of this model in an EDM framework is to write

$$234 \quad y_t = f(S_t, \dots, S_{t-E}, y_{t-1}, \dots, y_{t-E}) + \varepsilon_t$$

235 where f is the unknown mapping from the past states of the system to the present and
236 E is the embedding dimension. An obvious alternative would be to use EDM to
237 estimate a model of the form $R_t = f(S_t, \dots, S_{t-E}, R_{t-1}, \dots, R_{t-E})$. Although we do not show
238 the results for this alternative, they are qualitatively identical to those presented below.

239 To simplify notation, let $\mathbf{x}_t = \{S_t, \dots, S_{t-E}, y_{t-1}, \dots, y_{t-E}\}$ represent the ‘current’ state in
240 delay-coordinates. We used GP regression with a tensor-product kernel to fit a model
241 of the form $y_t = f(\mathbf{x}_t) + \varepsilon_t$, $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$ for $t \in \{E + 1, \dots, T\}$. Specifically, we set
242 $\text{Cov}[f(\mathbf{x}_t), f(\mathbf{x}_s)] = \tau^2 \prod_{i=1}^{E_{\max}} \exp(-\phi_i |\{\mathbf{x}_t\}_i - \{\mathbf{x}_s\}_i|^2 / r_i)$ where the factor $r_i =$
243 $\max_t \{\mathbf{x}_t\}_i - \min_t \{\mathbf{x}_t\}_i$ scales the i^{th} distance to stay in $[0, 1]$ and the length-scale
244 parameters, ϕ_i , control the ‘wiggleness’ of f in the i^{th} direction. The product is taken
245 over all lags from 1 to the maximum embedding dimension, E_{\max} . In light of the relatively
246 short time series available in the RAM database, we set the maximum E for S and y to 5
247 so that $E_{\max}=11$.

248 Previous analyses based on S-map (e.g. Deyle et al., 2014; Pierre et al., 2017) use a
249 fixed lag for each coordinate. Specifically, the time step was set to one and all lags up
250 to E are included in the model. Importantly, not all lags are equally important to the

251 dynamics and the best embedding may involve several lags with uneven spacing to
252 account for effects on different time scales (see e.g. Judd & Mees, 1998). A trivial
253 ecological example would be delayed density dependence, $n_t = n_{t-1}f(n_{t-\tau})$ in which
254 the next population size is a function of the previous population size and the population
255 size τ years ago. A reconstruction that includes all lags up to τ , i.e. $\{n_{t-1}, n_{t-2}, \dots, n_{t-\tau}\}$,
256 is perfectly acceptable under Takens, but clearly includes lags that are unnecessary
257 ($n_{t-2}, \dots, n_{t-\tau-1}$). Thus, rather than conduct an exhaustive search, we used automatic
258 relevance determination (Neal, 1996), to select lags and identify a parsimonious model.
259 Specifically, we used a penalty function to shrink ϕ_i toward zero which automatically
260 selects relevant lags (Munch et al., 2016). Further details on GP implementation are
261 provided in the Supplement (Appendix 2). Rasmussen & Williams (2006) is an excellent
262 source for additional background on GP modeling.

263 We apply this method to all 185 time-series to quantify the intrinsic predictability of
264 recruitment. Specifically, if V_{EDM} is the mean squared out-of-sample prediction error for
265 y and V_Y is variance in y , $\pi_{EDM} = 1 - V_{EDM} / V_Y$ is the predictable fraction of variation.
266 Note that π_{EDM} is not restricted to $[0, 1]$, *a priori*, because it is estimated out-of-sample;
267 V_{EDM} could be greater than V_Y if the predictions are biased or out of phase. In this
268 case, $\pi_{EDM} < 0$ would indicate that the model is worse than using the sample mean to
269 make a prediction.

270 We next determined how much of the explainable variation in recruitment is driven by
271 stock biomass. The natural comparison here would be to use a GP with the current
272 stock size as the sole input (e.g. Munch et al., 2005; Sugeno & Munch, 2013).
273 However, most readers will be unfamiliar with this method, so we also determined how
274 much of the variation in recruitment could be explained by three commonly used stock-
275 recruit models: Ricker, Beverton-Holt, and Schnute (See Appendix S3 for model
276 definitions and fitting methods). To determine whether the apparent predictability of
277 recruitment can be explained as autocorrelated noise, we also fit autoregressive models
278 using the same inputs provided to the GP.

279 Finally, we addressed whether the predictability of recruitment varies across Orders and
280 estimation methods. Because we are quantifying predictability in terms of mean-
281 squared errors we tested these effects using generalized linear models with a gamma
282 likelihood.

283

284 **RESULTS**

285 In keeping with earlier results by Pierre et al. (2017), we find that causal coupling
286 between stock and recruitment is fairly common (Fig 1). CCM identified significant
287 causal coupling between stock size and recruits for 107 of the 185 time series tested
288 (Fig. 1). In addition, we find compelling evidence for intrinsic dynamics in recruitment.
289 The GP EDM approach explains 39% of the variation on average with an interquartile
290 range of (20%, 54%).

291 The fishes we analyzed have diverse life histories, ranging from the relatively short lived
292 Salmoniformes and Clupeiformes to the much longer lived Pleuronectiformes and
293 Scorpaeniformes. It is therefore not surprising that the relative performance of EDM
294 varies significantly among taxa (likelihood ratio comparing prediction error among
295 orders: 39.6, $df = 7$, $p < 0.0001$). From this cross-taxon comparison, it appears that our
296 prediction error tends to increase with the generation time, as indexed by the ages at
297 recruitment and maturation (Figure 2, A-C) and decrease with the ratio of the time
298 series length to generation time.

299 In the GP-EDM framework, the effective embedding dimension is determined by the
300 number of lags for which the inverse length-scale parameter is above a threshold (of
301 say, 0.1, Munch et al., 2016). Although E_{\max} was set to 11, the effective E was 4 or less
302 in 96% of the populations (177/185). In addition, $E > 1$ in 76% (140/185) of populations.
303 These values for E are consistent with previous estimates for ecological time series
304 (Glaser et al., 2014). Importantly, in 84% of the cases where the embedding dimension
305 was greater than 1, it is the previous history of recruitment, not stock size that is most
306 relevant. This observation is consistent with the results of Pierre et al. (2017) as well
307 as empirical evidence that recruitment is controlled by factors affecting the early life

308 history. But most importantly, it suggests that these early-life dynamics are not
309 unpredictable.

310 Since the RAM database aggregates stock and recruitment estimates generated with a
311 wide range of analytical tools, it is important to determine whether the results depend on
312 the method used. To summarize results, we aggregated these methods into four
313 coarse categories: biomass dynamic models (BDM, $n=62$), statistical catch at age
314 models (SCA, $n=4$), sequential population analyses (SPA, $n=101$), and surveys (SUR,
315 $n=18$). For BDM and SCA outputs, CCM identified significant coupling between stock
316 and recruits in 58% of the time series, with some variability across methods: 71% for
317 BDM, 0% for SCA, 53% for SPA, and 50% for SUR. Interestingly, recruitment estimates
318 from surveys and sequential population analyses are significantly more predictable than
319 estimates derived from biomass dynamic and statistical catch at age models (Figure 2D,
320 log-likelihood ratio 13.5, $df=3$, $p=0.003$).

321 Thus far, we have found that recruitment is frequently coupled to stock size and that
322 intrinsic dynamics contribute substantially to variation in recruitment. Next, we evaluated
323 how much of the variation in recruitment could be explained solely in terms of current
324 population biomass. To do so, we compared predictions from the GP EDM to four
325 stock-recruit models (i.e. a GP with current stock size as the only input as well as three
326 commonly used parametric SR models). EDM outperformed these single-input SR
327 models for at least 83% of the populations analyzed, explaining an additional 25% of the
328 variance on average (Table 2, Figure 3).

329 Two additional calculations help clarify how much of the predictable variation is missed
330 by these single-input models. First, we can ask how often the fitted model is actually
331 worse than using the series mean to make an out-of-sample prediction. While this rarely
332 happens for GP EDM (4%, Table 1 column U), it is much more common for the single-
333 input models (35-40%, Table 2). Another way to characterize the results is in terms of
334 the fraction of the variation explained by a stock-recruit model relative to that explained
335 by EDM, i.e. π_{SR}/π_{EDM} . Summarizing in terms of the median (interquartile range), the
336 best SR model (Schnute) typically accounted for 26% (0%, 72%) of the intrinsic

337 variation explained with EDM. Results for the other models were quite similar, Beverton-
338 Holt: 20%(0%, 68%), Ricker: 22% (0%,64%), GP: 20% (0%, 63%).

339 Since EDM is making use of more inputs than any of the 1-d models, we next compared
340 EDM to linear autoregressive models that used the same collection of inputs. EDM
341 produced lower predictions errors 96% of the time. However, the out of sample error for
342 the AR model was quite large because many of the time series are relatively short. To
343 compensate for this, we introduced a regularizing penalty on the regression coefficients
344 analogous to the automatic relevance determination approach used in the GP
345 (Appendices 2 and 3). Although the regularized AR model performed much better out
346 of sample, EDM still explained an additional 36% of the variation on average. Since
347 both EDM and the AR use the same input data, we conclude that predictability of
348 recruitment under EDM is not due to simply using more explanatory variables; both the
349 additional dimensions and nonlinearity are essential.

350

351 **DISCUSSION**

352 Predictable, intrinsic dynamics account for roughly 40% of the observed variation in
353 recruitment. This result is not surprising – rather it is consistent with many previous
354 experimental studies that have demonstrated effects of food availability, competition,
355 predation, and maternal effects, etc. What is surprising -and considerably more
356 important - is that in the absence of detailed data on these mechanisms, we can use
357 GP-EDM to make short term predictions about recruitment. This result, based on 185
358 series supports and generalizes earlier analyses based on a S-map (Pierre et al., 2017).
359 Of course, when additional driving variables are known they can be readily incorporated
360 into this framework (Dixon et al., 1999; Deyle et al., 2013; Ye et al., 2015). Since
361 prediction skill increases with the number of generations sampled, we expect these
362 methods to be of greatest use for relatively short-lived fishes (see also Giron-Nava et
363 al., 2017).

364 In keeping with previous applications of time-delay embedding, our implementation of
365 GP-EDM implicitly assumed temporally uncorrelated errors. However, previous meta-

366 analyses found that recruitment deviations are typically autocorrelated, with an average
367 value of ~ 0.45 (Thorson et al., 2014) which suggests that accounting for serial
368 correlation within GP-EDM might be relevant. Indeed, a fully general approach to
369 embedding stochastic dynamics would include moving average terms for the residuals
370 (Stark et al., 2003). To assess the importance of this for modeling recruitment, we
371 calculated autocorrelation coefficients for the residuals in all 185 time series. In contrast
372 with earlier work, we found that lag-1 autocorrelation in residuals was quite small; the
373 median was 0.04 and 79% of series had correlation coefficients less than 0.25 in
374 absolute value. Fewer than 10% were significant ($p < 0.05$ using a Durbin-Watson test,
375 Durbin & Watson, 1971). Although we view including serial autocorrelation in GP-EDM
376 as an important task for the future, we doubt that doing so would affect the results
377 reported here.

378 Brooks & Deroba (2015) have cautioned against using assessment model outputs as
379 data in meta-analyses. Fortunately, the RAM database includes estimates that vary
380 considerably in their structural assumptions ranging from survey data to statistical catch
381 at age models. The CCM results were largely independent of the methods used to
382 estimate recruitment. Moreover, estimates of recruitment from surveys and sequential
383 population analyses are actually *more* predictable using GP-EDM than estimates
384 derived from other models. Based on this, we conclude that the predictability of
385 recruitment is not an artifact of modeling assessment model output.

386 CCM identified significant coupling between stock and recruitment for the majority of
387 populations in the database. This is particularly noteworthy in light of several decades of
388 speculation on the existence of a stock-recruit relationship (Ottersen et al., 2014;
389 Rothschild, 2000; Strong 1986) and recent analyses suggesting that productivity is
390 independent of population size (Vert-Pre et al., 2013; Szuwalski et al., 2015). Despite
391 this, our results are broadly consistent with these previous studies in that current
392 population size, though coupled to recruitment, does not by itself account for a large
393 fraction of the intrinsic dynamics (see also Pierre et al., 2017). Other factors are clearly
394 important.

395 In many species, distinct productivity ‘regimes’ are apparent within which fluctuations
396 appear random (Vert-Pre et al., 2014; Munch & Kottas, 2009). These regimes are, quite
397 reasonably, interpreted as being driven by shifts in broad-scale environmental drivers.
398 Significant forcing by environmental regimes would seem to contradict our inference of
399 intrinsic dynamics. It is therefore worthwhile to think about how we might reconcile
400 intrinsic dynamics with the appearance of productivity regimes. A simple, if somewhat
401 abstract, example is illustrative.

402 Consider the case where local dynamics exhibit an Allee effect but are supplemented by
403 immigrants from outside the focal area which subsequently compete with residents.
404 Specifically, we may think of the map $\{ x_{n+1} = x_n \exp[r(x_n - a)(1 - x_n/K)] +$
405 $R_n \exp[-\mu x_n]$, where x_n is population size, r is growth rate, K is the carrying capacity
406 and a is the Allee effect threshold below which residents go extinct in the absence of
407 immigration. The second term represents the supply of immigrants with
408 $\log [R_n] \sim N(m, \sigma)$ and resident-dependent mortality, μ . The resulting population size
409 oscillates between two regimes within which dynamics appear ‘noisy’ (see Appendix 5,
410 figure S2 for details). A piecewise constant ‘regime’ model explains ~75% of the
411 variance, which probably seems like a lot. However, the piece-wise constant model
412 foregoes any attempt to learn the within-regime dynamics. In contrast, given 30 data
413 points, short term predictions for this system using GP-EDM are almost perfect ($R^2 =$
414 0.98). We do not mean to suggest that recruitment follows this particular model; many
415 models exhibit such dynamics. Rather, we suggest that the appearance of productivity
416 regimes that seem independent of stock biomass is not inconsistent with intrinsic
417 nonlinear dynamics that may be highly predictable.

418 The conventional perspective in fisheries is that deviations from the stock-recruitment
419 model represent noise that is outside the bailiwick of both modeling and management.
420 An implicit corollary is that fishing affects recruitment solely through changes in stock
421 size. However, we’ve shown that these recruitment deviations are predictable using
422 EDM; they are clearly not ‘noise.’ Other mechanisms including species interactions,
423 migration, contemporary evolution, and environmental forcing are likely at play.
424 Differentiating between these mechanisms has important operational consequences: If

425 recruitment fluctuations are driven by interactions between several species that we are
426 currently managing, maternal effects, or contemporary evolution, then harvesting will
427 surely influence recruitment beyond what is captured by changes in stock size. For
428 example, Olsen et al. (2010) demonstrated that the shape of the stock-recruit curve
429 changes with food availability in North Sea cod (*Gadus morhua*). Consequently,
430 management actions that impact food availability, e.g. harvesting a forage species or a
431 competitor, could lead to changes in cod productivity at a given stock size. It is not
432 difficult to imagine many other mechanisms through which harvesting one species can
433 influence recruitment in another. In this context, CCM may be extremely useful in
434 determining which potential mechanisms are active (Sugihara et al., 2012).

435 On the other hand, if recruitment fluctuations are driven by the environment, then there
436 is not much that management can do other than leave precautionary margins for
437 uncertainty-- as is the standard practice (Walters & Collie, 1988). In this context, EDM
438 may also be extremely useful by improving predictions of environment-driven
439 fluctuations in recruitment (e.g. Ye et al., 2015). Ultimately, however, our long-term goal
440 must be to develop multi-species management strategies that allow for complex
441 interactions among different life stages of interacting species. Ideally, these should be
442 robust to our uncertainty in how ecosystems function. Extending the EDM toolkit to
443 produce robust harvest policies in multispecies systems in an important next step.

444

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448

449

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629

630 Table 1. Variance explained, summarized by Order. N is the number of time series
631 within each order. Two additional Orders were excluded from this summary because
632 they each had one time series. Mean is the average fraction of variance explained,
633 calculated as 1 minus the prediction variance / total variance. 25th and 75th give the
634 quartiles of the variance explained across the time series. P indicates the fraction of
635 series for which the out-of-sample prediction error exceeded the variance.

Order	N	Mean	25th	75th	P
Clupeiformes	29	0.45	0.31	0.60	0.00
Gadiformes	50	0.41	0.21	0.57	0.03
Perciformes	12	0.51	0.35	0.60	0.00
Pleuronectiformes	12	0.43	0.08	0.74	0.02
Salmoniformes	73	0.32	0.14	0.46	0.00
Scorpaeniformes	7	0.41	0.12	0.67	0.17
Overall	185	0.39	0.20	0.54	0.04

636

637

638 Table 2. Variance explained by alternative approaches. The variance explained is
 639 calculated as 1 minus the prediction variance / total variance. Values less than 0
 640 indicate that the out-of-sample prediction error exceeds the variance. 25th and 75th give
 641 the quartiles of the variance explained across the time series. P indicates the fraction of
 642 series for which the out-of-sample prediction error exceeded the variance.

Model	Mean	25 th	75 th	P
Beverton-Holt	0.11	-0.05	0.17	0.39
Ricker	0.04	-0.12	0.12	0.40
Schnute	0.12	-0.05	0.17	0.40
GP-SR	0.08	-0.01	0.06	0.35
AR	-1.70	-3.58	0.19	0.70
AR(reg)	-0.07	-0.40	0.29	0.50

643

644 Figure Captions

645 Figure 1. Fraction of series for which recruitment was shown to be causally driven by the size of the adult
 646 population (indexed by stock biomass) across methods used to estimate recruitment. BDM – Biomass
 647 dynamic models (n = 62), SCA – Statistical catch at age models (n = 4), SPA – Sequential population
 648 analyses (n = 101), SUR – direct survey estimates (n = 18).

649

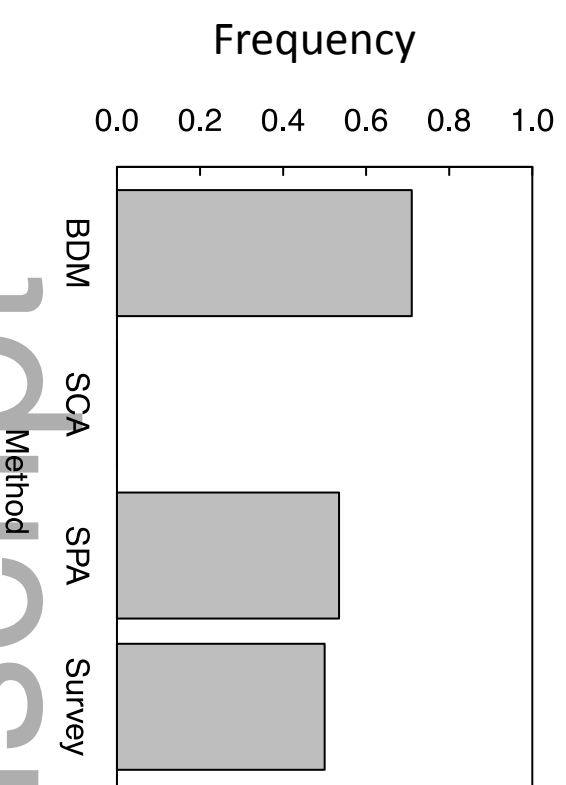
650 Figure 2. Intrinsic variation in recruitment by Order and estimation method. A-C. The vertical axis in each
 651 plot is the fraction of out-of-sample variation in recruitment predicted by EDM, i.e. π_{EDM} as defined in the
 652 Methods. Circles in each plot indicate means aggregated by Order: Clupeiformes (cyan), Gadiformes
 653 (red), Perciformes (yellow), Pleuronectiforms (magenta), Salmoniformes (blue), and Scorpaeniformes
 654 (black). The error bars indicate +/- 1 s.e. The average fraction of explained variation for each Order is
 655 plotted against: A. the age at maturation, B. the age at recruitment to the fishery, and C. the number of
 656 generations sampled, as indexed by the length of the time series divided by the age at maturation. D.
 657 Apparent changes in predictability across methods used to estimate recruitment. BDM – Biomass
 658 dynamic models, SCA – Statistical catch at age models, SPA – Sequential population analyses, SUR –
 659 direct survey estimates.

660

661 Figure 3. Predictability using intrinsic dynamics compared to models that use only current biomass (A,B)
662 or linear dynamics (C). In each panel the axes indicate the scaled mean-square error (i.e. the variance in
663 predictions estimated by leave-one-out cross validation divided by the total variance in y). The horizontal
664 and vertical lines at 1 indicate the scaled mean-square error (SMSE) using only the sample mean for
665 prediction. The diagonal is the 1:1 line. The horizontal axis in each panel is the prediction error using
666 EDM and the vertical axes are for A) the Beverton-Holt SR model, B) the GP SR model, and C) the
667 regularized AR model. Colored points indicate results for each population in the database, colored
668 according to Order. Note that 16 populations with AR SMSE >1.5 have been dropped from panel C.

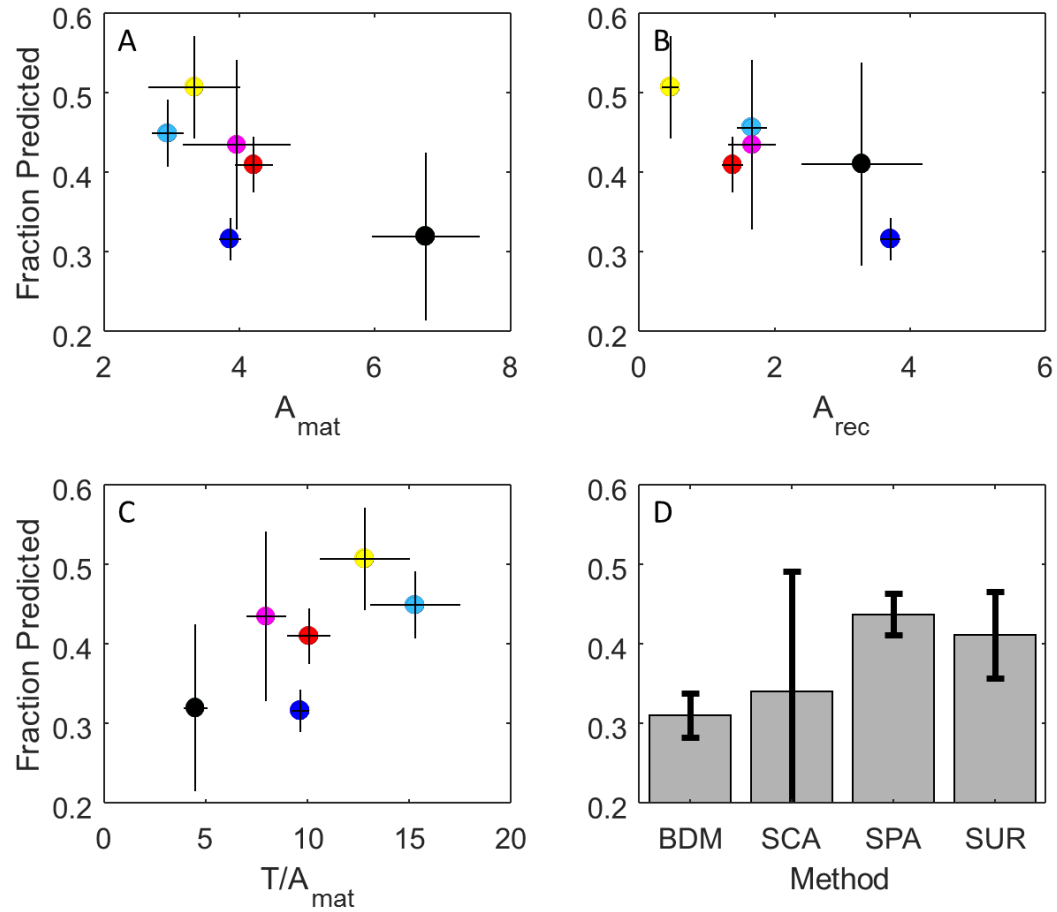
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Figure 1



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Figure 2



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Figure 3

