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

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Abstract

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

KEYWORDS

empirical dynamical modelling, gaussian process regression, recruitment, time-delay embedding

1 | INTRODUCTION

The relative importance of environmental and intrinsic controls on population growth has been a source of controversy in ecology since the beginning (Andrewartha & Birch, 1954; Howard & Fiske, 1911; Nicholson, 1954; etc). Like many dichotomies in ecology, this battle has dissipated in the middle ground where both factors appear relevant (e.g. Dixon, Milicich, & Sugihara, 1999; Milne, 1962; Orians, 1962). Nevertheless, predicting changes in abundance remains an important goal in applied ecology, where models that separate intrinsic and extrinsic dynamics form the foundation for conservation and management decisions for threatened and harvested species.

Like their terrestrial counterparts, fisheries oceanographers grapple with the balance of intrinsic dynamics and environmental

drivers. The number of new fish recruiting to a population may vary over an order of magnitude from year to year, with serious consequences for fisheries management and food security (Glantz, 2005). For much of the last century, fisheries oceanographers have attempted to solve this “recruitment problem.” Since the seminal work of Hjort (1914, 1926), numerous factors influencing recruitment have been identified.

During early life stages, fish growth is dominated by environmental conditions, while mortality rates are extremely high and size-dependent (Bailey & Houde, 1989; Perez & Munch, 2010). Early growth and survival are also influenced by oceanographic conditions such as turbulence (MacKenzie, 2000; Rothschild & Osborn, 1988), stratification (e.g. Jenkins, Conron, & Morison, 2010; Lasker, 1975) and larval transport (e.g. Checkley, Raman, Maillet, & Mason, 1988;

Epifanio, Masse, & Garvine, 1989), as well as temperature, salinity and dissolved oxygen concentrations (e.g. Köster et al., 2005). Biotic factors such as food availability (Bergenius, Meekan, Robertson, & McCormick, 2002; Cushing, 1990), predator abundance (Bailey & Houde, 1989), competition (Holbrook & Schmitt, 2002), the age composition of the population (Marteinsdottir & Thorarinnsson, 1998; Shelton, Munch, Keith, & Mangel, 2012) and maternal effects (Berkeley, Chapman, & Sogard, 2004; Green, 2008) also contribute to variation in egg production, growth and early survival.

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

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

We hypothesize that a substantial fraction of the apparent indeterminism in recruitment, often attributed to environmental stochasticity, arises from collapsing complex recruitment dynamics into low-dimensional indices. Takens’ theorem of time-delay embedding (Takens, 1981) and its generalizations (Sauer, Yorke, & Casdagli, 1991; Stark, Broomhead, Davies, & Huke, 2003) offer a way around this problem. Time-delay embedding uses lags of observed variables

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to construct synthetic axes that account for unobserved variables. For example, time lags of abundance for a focal species can be used to implicitly account for variations in the abundance of other, unmeasured, species with which it interacts. This is particularly effective at reconstructing low-dimensional dynamics. But extrinsic drivers, like the weather, typically emerge from very-high-dimensional systems. As the number of dimensions we can resolve with time lags is limited by the time-series length (Cheng & Tong, 1994), we expect extrinsic forcing to be sufficiently high-dimensional as to appear essentially stochastic. In the light of this, we operationally define any dynamics that can be recaptured with a low-dimensional embedding as “intrinsic.”

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

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

To address these questions, we expanded the number of stocks analysed from 53 to 185. From this larger data set, we reconsider the question of whether biomass and recruits are causally coupled using convergent cross-mapping (Sugihara et al., 2012). Next, using

Gaussian process–EDM (Munch, Poynor, & Arriaza, 2017), we explicitly quantify what fraction of the observed variation in recruitment can be explained by intrinsic dynamics. We then benchmark our predictions against several commonly used models. At last, we evaluate the importance of life history and assessment method in determining the results.

2 | METHODS

2.1 | Database selection

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

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

2.2 | Convergent cross-mapping

Empirical dynamical modelling is based on “attractor reconstruction” using time-delay embedding (Takens, 1981). The fundamental idea is that for an M -dimensional system that converges to a d -dimensional attractor, we can reconstruct the attractor from a single time series of observations, say y_t , $t = 1, \dots, T$. This is done using lags of y (at time step τ) as surrogate coordinates, that is, $\mathbf{y}_t = \{y_t, y_{t-\tau}, \dots, y_{t-E\tau}\}$. Provided that the embedding dimension, E , is $>2M$ (Takens, 1981) and T is sufficiently large, the collection of delay coordinate vectors, $\{\mathbf{y}_{E+1}, \dots, \mathbf{y}_T\}$ reconstructs (i.e. “embeds”) the attractor.

As Takens’ theorem holds generically for any observable from the M -dimensional system, alternate reconstructions using different observables share a common attractor. Convergent cross-mapping

(Sugihara et al., 2012) exploits this to identify whether two variables are causally coupled. In particular, if x and y share a common attractor, then we expect contemporaneous values x to map to nearby points on the attractor reconstructed with y , and vice versa. CCM has been used to identify drivers of climate change (Van Nes et al., 2015), flu outbreaks (Deyle, Maher, Hernandez, Basu, & Sugihara, 2016) and gene expression (Ma, Aihara, & Chen, 2014). Here, we applied CCM to test whether recruitment is causally driven by the size of the adult population (indexed by stock biomass) and how this changes across different methods for estimating recruitment. To do so, we estimated the predictive capacity of the stock biomass time series on the recruits’ time series (ρ_{original}). We then tested the significance of the causal relationship detected by CCM by generating 100 surrogate shuffles of the recruits’ time series and calculating the predictive capacity of the original stock biomass time series on each of them ($\rho_{\text{surrogate}}$). A relationship was considered significant when ρ_{original} was higher than the 95th percentile of the distribution of $\rho_{\text{surrogate}}$ values ($p < 0.05$).

2.3 | Gaussian process–EDM

Although CCM provides a robust approach to testing for causal coupling, it does not address the question about the relative importance of intrinsic and extrinsic dynamics. To address this question, we operationally define any dynamics that can be recaptured with a low-dimensional embedding as “intrinsic” and use time-delay embedding to make predictions of recruitment. Doing so involves estimating the map from past states to the future using lag coordinates, that is, $y_t = f(y_{t-1}, \dots, y_{t-E})$. This map may be inferred using any of a variety of function approximation tools including polynomials (e.g. Ellner & Turchin, 1995), local linear regression (Sugihara, 1994), support vector machines (e.g. Mukherjee, Osuna, & Girosi, 1997) and neural networks (e.g. Bakker, Schouten, Giles, Takens, & Van Den Bleek, 2006). Here, we used Gaussian process regression (Munch et al., 2017; Rasmussen & Williams, 2006) to estimate the map from the past to the future and quantify the intrinsic component of recruitment dynamics (defined below). The GP approach extends the EDM toolkit by allowing automatic lag selection, incorporating information from multiple sources using hierarchical modelling and allowing for nonstationary dynamics (Munch et al., 2017). Gaussian process regression has been used in population modelling to estimate the form of density dependence (Munch, Kottas, & Mangel, 2005), test for the presence of Allee effects (Sugeno & Munch, 2013a,b) and to assess model misspecification (Thorson, Ono, & Munch, 2014).

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

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

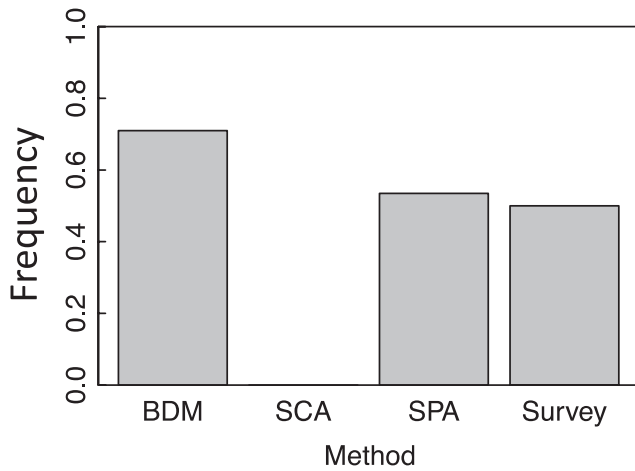


FIGURE 1 Fraction of series for which recruitment was shown to be causally driven by the size of the adult population (indexed by stock biomass) across methods used to estimate recruitment. BDM: biomass dynamic models ($n = 62$); SCA, statistical catch-at-age models ($n = 4$); SPA: sequential population analyses ($n = 101$); SUR, direct survey estimates ($n = 18$)

where f is the unknown mapping from the past states of the system to the present and E is the embedding dimension. An obvious alternative would be to use EDM to 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 the results for this alternative, they are qualitatively identical to those presented below.

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 delay coordinates. We used GP regression with a tensor product kernel to fit a model of the form $y_t = f(\mathbf{x}_t) + \varepsilon_t$, $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$ for $t \in \{E+1, \dots, T\}$. In particular, we set $\text{Cov}[f(\mathbf{x}_t), f(\mathbf{x}_s)] = \tau^2 \prod_{i=1}^{E_{\max}} \exp(-\phi_i |\mathbf{x}_t|_i - |\mathbf{x}_s|_i|^2 / r_i)$ where the factor $r_i = \max_i \{\mathbf{x}_i\} - \min_i \{\mathbf{x}_i\}$ scales the i th distance to stay in $[0,1]$ and the length-scale parameters, ϕ_i , control the “wiggleness” of f in the i th direction. The product is taken over all lags from 1 to the maximum embedding dimension, E_{\max} . In the light of the relatively short time series available in the RAM database, we set the maximum E for S and y to 5 so that $E_{\max} = 11$.

Previous analyses based on S-map (e.g. Deyle et al., 2013; Pierre et al., 2017) use a fixed lag for each coordinate. In particular, the time step was set to one and all lags up to E are included in the model. But, not all lags are equally important to the dynamics and the best embedding may involve several lags with uneven spacing to account for effects on different time scales (see e.g. Judd & Mees, 1998). A trivial ecological example would be delayed density dependence, $n_t = n_{t-1} f(n_{t-\tau})$, in which the next population size is a function of the previous population size and the population size τ years ago. A reconstruction that includes all lags up to τ , that is $\{n_{t-1}, n_{t-2}, \dots, n_{t-\tau}\}$, is perfectly acceptable under Takens, but clearly includes lags that are unnecessary ($n_{t-2}, \dots, n_{t-\tau-1}$). Thus, rather than conducting an exhaustive search, we used automatic relevance determination (Neal, 1996) to select lags and identify a parsimonious model. In particular, we used a penalty function to shrink ϕ_i towards zero, which automatically selects relevant lags (Munch et al., 2017). Further details

on GP implementation are provided in the Supporting Information (Appendix S2). The text by Rasmussen and Williams (2006) is an excellent source for additional background on GP modelling.

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

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

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

3 | RESULTS

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

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

In the GP-EDM framework, the effective embedding dimension is determined by the number of lags for which the inverse length-scale parameter is above a threshold (of say, 0.1, Munch et al., 2017). Although E_{\max} was set to 11, the effective E was 4 or

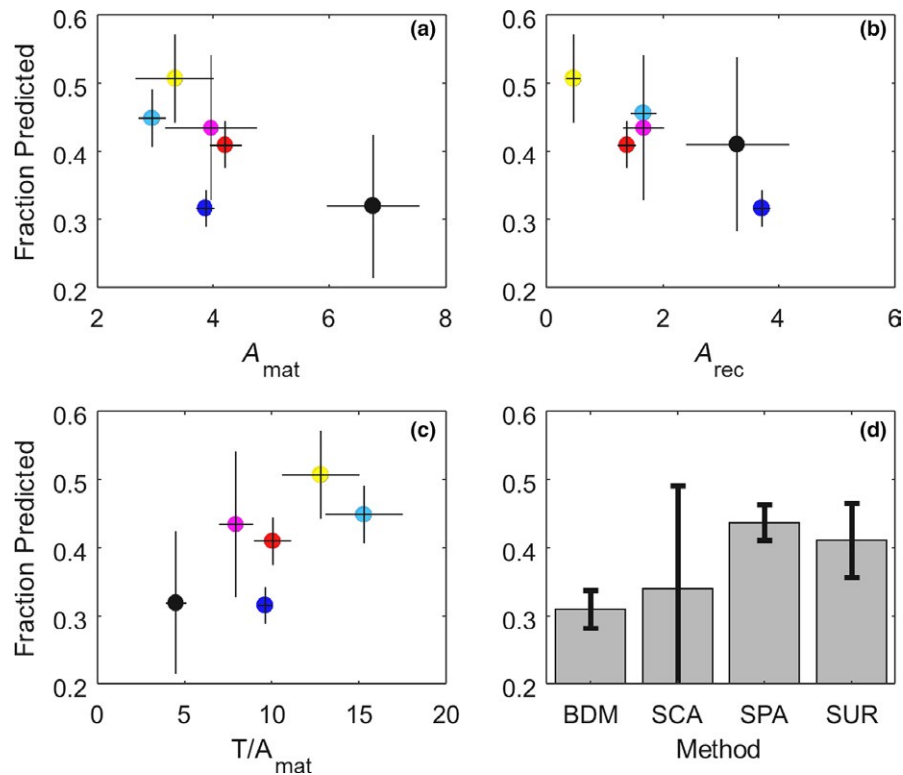


FIGURE 2 Intrinsic variation in recruitment by Order and estimation method. (a–c) The vertical axis in each plot is the fraction of out-of-sample variation in recruitment predicted by EDM, that is π_{EDM} as defined in Methods. Circles in each plot indicate means aggregated by Order: Clupeiformes (cyan), Gadiformes (red), Perciformes (yellow), Pleuronectiformes (magenta), Salmoniformes (blue), and Scorpaeniformes (black). The error bars indicate ± 1 SE. The average fraction of explained variation for each Order is plotted against: (a) the age at maturation, (b) the age at recruitment to the fishery and (c) the number of generations sampled, as indexed by the length of the time series divided by the age at maturation. (d) Apparent changes in predictability across methods used to estimate recruitment. BDM, biomass dynamic models; SCA, statistical catch-at-age models; SPA, sequential population analyses; SUR, direct survey estimates

less in 96% of the populations (177/185). In addition, E is >1 in 76% (140/185) of populations. These values for E are consistent with previous estimates for ecological time series (Glaser et al., 2014). It is important that in 84% of the cases where the embedding dimension was >1 , it is the previous history of recruitment, not stock size, that is most relevant. This observation is consistent with the results of Pierre et al. (2017) as well as empirical evidence that recruitment is controlled by factors affecting the early life history. But most important, it suggests that these early-life dynamics are not unpredictable.

As the RAM database aggregates stock and recruitment estimates generated with a wide range of analytical tools, it is important to determine whether the results depend on the method used. To summarize results, we aggregated these methods into four coarse categories: biomass dynamic models (BDM, $n = 62$), statistical catch-at-age models (SCA, $n = 4$), sequential population analyses (SPA, $n = 101$) and surveys (SUR, $n = 18$). For BDM and SCA outputs, CCM identified significant coupling between stock and recruits in 58% of the time series, with some variability across methods: 71% for BDM, 0% for SCA, 53% for SPA and 50% for SUR. It is interesting that recruitment estimates from surveys and sequential population analyses are significantly more predictable than estimates derived from biomass dynamic and statistical

catch-at-age models (Figure 2d, log-likelihood ratio 13.5, $df = 3$, $p = 0.003$).

Thus far, we have found that recruitment is frequently coupled to stock size and that intrinsic dynamics contribute substantially to variation in recruitment. Next, we evaluated how much of the variation in recruitment could be explained solely in terms of current population biomass. To do so, we compared predictions from the GP-EDM to four stock-recruitment models (i.e. a GP with current stock size as the only input as well as three commonly used parametric SR models). EDM outperformed these single-input SR models for at least 83% of the populations analysed, explaining an additional 25% of the variance on average (Table 2, Figure 3). Results for Ricker and Schnute models are plotted in Figure S1.

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

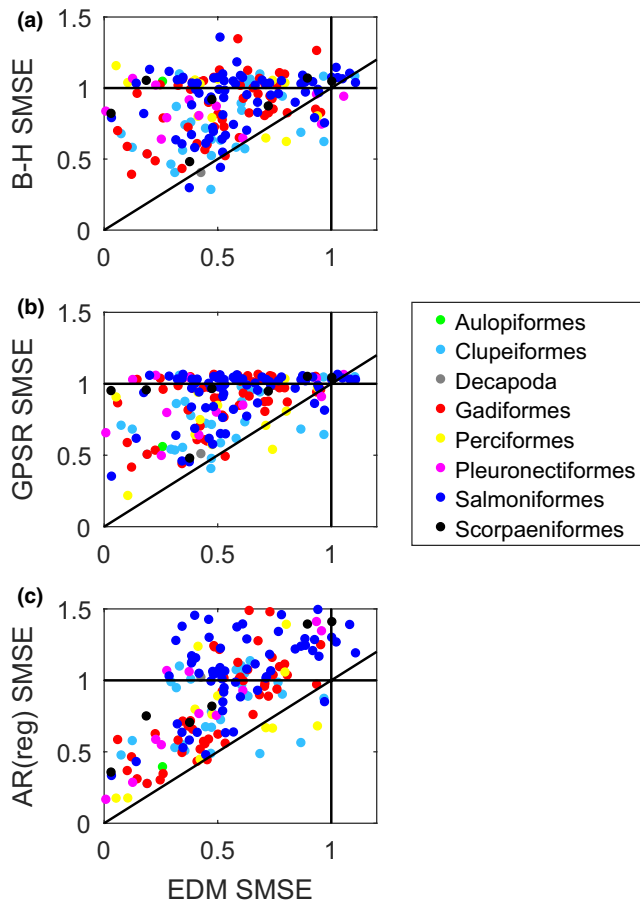


FIGURE 3 Predictability using intrinsic dynamics compared to models that use only current biomass (a, b) or linear dynamics (c). In each panel, the axes indicate the scaled mean-square error (i.e. the variance in predictions estimated by leave-one-out cross-validation divided by the total variance in y). The horizontal and vertical lines at 1 indicate the scaled mean-square error (SMSE) using only the sample mean for prediction. The diagonal is the 1:1 line. The horizontal axis in each panel is the prediction error using EDM, and the vertical axes are for (a) the Beverton–Holt SR model, (b) the GP-SR model and (c) the regularized AR model. Coloured points indicate results for each population in the database, coloured according to Order. Note that 16 populations with AR SMSE >1.5 have been dropped from Panel (c)

26% (0%, 72%) of the intrinsic variation explained with EDM. Results for the other models were quite similar, Beverton–Holt: 20% (0%, 68%), Ricker: 22% (0%, 64%), GP: 20% (0%, 63%).

As EDM is making use of more inputs than any of the 1-d models, we next compared EDM to linear autoregressive models that used the same collection of inputs. EDM produced lower prediction errors 96% of the time. However, the out-of-sample error for the AR model was quite large because many of the time series are relatively short. To compensate for this, we introduced a regularizing penalty on the regression coefficients analogous to the automatic relevance determination approach used in the GP (Supporting Information Appendices S2 and S3). Although the regularized AR model performed much better out of sample, EDM still explained an additional

TABLE 1 Variance explained, summarized by Order. N is the number of time series within each order. Two additional Orders were excluded from this summary because they each had one time series. Mean is the average fraction of variance explained, calculated as 1 minus the prediction variance/total variance; 25th and 75th give the quartiles of the variance explained across the time series. p indicates the fraction of 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

TABLE 2 Variance explained by alternative approaches. The variance explained is calculated as 1 minus the prediction variance/total variance. Values <0 indicate that the out-of-sample prediction error exceeds the variance; 25th and 75th give the quartiles of the variance explained across the time series. p indicates the fraction of series for which the out-of-sample prediction error exceeded the variance

Model	Mean	25th	75th	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

36% of the variation on average. As both EDM and the AR use the same input data, we conclude that predictability of recruitment under EDM is not due to simply using more explanatory variables; both the additional dimensions and nonlinearity are essential.

4 | DISCUSSION

Predictable, intrinsic dynamics account for roughly 40% of the observed variation in recruitment. This result is not surprising—rather it is consistent with many previous experimental studies that have demonstrated effects of food availability, competition, predation, and maternal effects, etc. What is surprising—and considerably more important—is that in the absence of detailed data on these mechanisms, we can use GP-EDM to make short-term predictions about recruitment. This result based on 185 series supports and generalizes earlier analyses based on an S-map (Pierre et al., 2017). Of course, when additional driving variables are known they can be readily incorporated into this framework (Deyle et al., 2013; Dixon et al.,

1999; Ye et al., 2015). As prediction skill increases with the number of generations sampled, we expect these methods to be of greatest use for relatively short-lived fishes (see also Giron-Nava et al., 2017).

In keeping with previous applications of time-delay embedding, our implementation of GP-EDM implicitly assumed temporally uncorrelated errors. However, previous meta-analyses found that recruitment deviations are typically autocorrelated, with an average value of ~ 0.45 (Thorson, Jensen, & Zipkin, 2014), which suggests that accounting for serial correlation within GP-EDM might be relevant. Indeed, a fully general approach to embedding stochastic dynamics would include moving average terms for the residuals (Stark et al., 2003). To assess the importance of this for modelling recruitment, we calculated autocorrelation coefficients for the residuals in all 185 time series. In contrast with earlier work, we found that lag-1 autocorrelation in residuals was quite small; the median was 0.04, and 79% of series had correlation coefficients < 0.25 in absolute value. Fewer than 10% were significant ($p < 0.05$ using a Durbin-Watson test, Durbin & Watson, 1971). Although we view including serial autocorrelation in GP-EDM as an important task for the future, we doubt that doing so would affect the results reported here.

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

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

In many species, distinct productivity “regimes” are apparent within which fluctuations appear random (Munch & Kottas, 2009; Vert-Pre et al., 2013). These regimes are, quite reasonably, interpreted as being driven by shifts in broad-scale environmental drivers. Significant forcing by environmental regimes would seem to contradict our inference of intrinsic dynamics. It is therefore worthwhile to think about how we might reconcile intrinsic dynamics with the appearance of productivity regimes. A simple, if somewhat abstract, example is illustrative.

Consider the case where local dynamics exhibit an Allee effect but are supplemented by immigrants from outside the focal area which subsequently compete with residents. In particular,

we may think of the map $\{x_{n+1} = x_n \exp[r(x_n - \alpha)(1 - x_n/K)] + R_n \exp[-\mu x_n]\}$, where x_n is population size, r is growth rate, K is the carrying capacity, and α is the Allee effect threshold below which residents go extinct in the absence of immigration. The second term represents the supply of immigrants with $\log[R_n] \sim N(m, \sigma)$ and resident-dependent mortality, μ . The resulting population size oscillates between two regimes within which dynamics appear “noisy” (see Supporting Information Appendix S5, Figure S2 for details). A piecewise constant “regime” model explains $\sim 75\%$ of the variance, which probably seems like a lot. However, the piecewise constant model foregoes any attempt to learn the within-regime dynamics. In contrast, given 30 data points, short-term predictions for this system using GP-EDM are almost perfect ($R^2 = 0.98$). We do not mean to suggest that recruitment follows this particular model; many models exhibit such dynamics (see Figure S3). Rather, we suggest that the appearance of productivity regimes that seem independent of stock biomass is not inconsistent with intrinsic nonlinear dynamics that may be highly predictable.

The conventional perspective in fisheries is that deviations from the stock-recruitment model represent noise that is outside the bailiwick of both modelling and management. An implicit corollary is that fishing affects recruitment solely through changes in stock size. However, we have shown that these recruitment deviations are predictable using EDM; they are clearly not “noise.” Other mechanisms including species interactions, migration, contemporary evolution and environmental forcing are likely at play. Differentiating between these mechanisms has important operational consequences: If recruitment fluctuations are driven by interactions between several species that we are currently managing, maternal effects or contemporary evolution, then harvesting will surely influence recruitment beyond what is captured by changes in stock size. For example, Olsen et al. (2010) demonstrated that the shape of the stock-recruitment curve changes with food availability in North Sea cod (*Gadus morhua*). Therefore, management actions that impact food availability, for example harvesting a forage species or a competitor, could lead to changes in cod productivity at a given stock size. It is not difficult to imagine many other mechanisms through which harvesting one species can influence recruitment in another. In this context, CCM may be extremely useful in determining which potential mechanisms are active (Sugihara et al., 2012).

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

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