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Review Article

Assessing causal links in fish stock–recruitment relationships

Maud Pierre[1]*, Tristan Rouyer[2], Sylvain Bonhommeau[3], and J. M. Fromentin[2]

[1]*Irstea, UR EABX, 50 Avenue de Verdun, 33612 Cestas Cedex, France*
[2]*Ifremer Station de Sète, UMR MARBEC, Avenue Jean Monnet, CS 30171, 34203 Sète Cedex, France*
[3]*Ifremer, Délégation de l'Océan Indien, Rue Jean Bertho, BP 6097822, Le Port Cedex, La Réunion, France*

**Corresponding author: tel: +33 (0)5 57 89 08 25; e-mail: maud.pierre@irstea.fr.*

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Understanding whether recruitment fluctuations in fish stock arise from stochastic forcing (e.g. environmental variations) rather than deterministic forces (e.g. intrinsic dynamics) is a long standing question with important applied consequences for fisheries ecology. In particular, the relationship between recruitment, spawning stock biomass and environmental factors is still poorly understood, even though this aspect is crucial for fisheries management. Fisheries data are often short, but arise from complex dynamical systems with a high degree of stochastic forcing, which are difficult to capture through classic modelling approaches. In the present study, recent statistical approaches based on the approximation of the attractors of dynamical systems are applied on a large dataset of time series to assess (i) the directionality of potential causal relationships between recruitment and spawning stock biomass and potential influence of sea-surface temperature on recruitment and (ii) their performance to forecast recruitment. Our study shows that (i) whereas spawning stock biomass and sea surface temperature influence the recruitment to a lesser extent, recruitment causes also parental stock size and (ii) that non-linear forecasting methods performed well for the short-term predictions of recruitment time series. Our results underline that the complex and stochastic nature of the processes characterizing recruitment are unlikely to be captured by classical stock–recruitment relationships, but that non-linear forecasting methods provide interesting perspectives in that respect.

Keywords: causality, forecasting models, marine fish populations, non-linear dynamics, time series analysis.

Introduction

Understanding the relationship between recruitment (i.e. the number of new individuals to enter the fishery, constituting the arrival of a new age class in the stock) and spawning biomass is one of the most challenging topics in fisheries ecology, which have key applied consequences for the management of exploited fish populations (Walters and Martell, 2004). For instance, the fishing mortality that produces the maximum sustainable yield (i.e. Fmsy) estimates mostly depend upon fish stock productivity, which in turn depend on the shape of stock–recruitment relationships (steepness). A substantial number of stock–recruitment models exist, which often involve density dependence mechanisms between the offspring and the parental stock size and can also include environmental effects (Shepherd and Cushing, 1980; Köster *et al.*, 2003). However, stock–recruitment models rarely display a good fit to the data and generally have minimal forecasting power (Sakuramoto, 2005; Cury *et al.*, 2014; Szuwalski *et al.*, 2015). This is partly due to the lack of accurate proxy for the stocks reproductive potential (Marteinsdottir and Begg, 2002) or the imprecision on the estimates of spawning biomass and recruitment (McGarvey and Kinloch, 2001) or the difficulty of including appropriate processes reflecting the environmental effects on recruitment within these relationships (Ottersen and Sundby, 1995; Sparholt, 1996; Ottersen and Loeng, 2000). In addition, autocorrelation in time series can obscure stock–recruitment relationship parameters (Walters, 1985; Hilborn and Walters, 1992; Myers and Barrowman, 1995).

This study aims at exploring potential relationship between recruitment (R) and spawning-stock biomass (SSB) and potential influence of sea-surface temperature (SST) on recruitment by assessing causal relationships between them. Analysing causality between two variables is complicated as it is often confused with (linear) correlations, even though correlation does not necessarily imply causality (Sugihara *et al.*, 2012). A correlation can be detected between two variables although there is no causal link between them. Indeed, if these two variables are driven by a third one, the correlation between them while seeming "real" is actually spurious. In the case of stock recruitment relationships, establishing causal links can be complicated by the likely non-linear nature of processes and strong influence of environmental stochasticity, which can be further blurred by the fact that most stock–recruitment data are estimated from models over relatively short time-periods.

Ecological time series can be viewed as an outcome of complex dynamical systems, that transcribe the evolution of the dynamical behaviour over time (Sugihara, 1994; Perretti *et al.*, 2015). In recent years, flexible non-linear and non-parametric techniques have been used to analyse this type of data (Sugihara *et al.*, 2012; Glaser *et al.*, 2014; Clark *et al.*, 2015). The techniques employed allow analysing complex dynamical systems through their approximation obtained from the time series (Takens' theorem, Takens' (1981)). Here, a selection of these non-linear equation-free techniques were applied on a large dataset of time series from various fish stocks to investigate (i) if any causal links between recruitment, SSB and SST could be identified and (ii) whether accurate short-term recruitment forecasts can be obtained using these statistical techniques.

Material and methods

Data

Because this study aims at investigating generic aspects of stock–recruitment relationships, the dataset had to include as long time series as possible for a broad range of species. Two databases were used. The RAM Legacy Stock Assessment Database (Ricard *et al.*, 2012) and a data compilation built from stock assessment reports from the International Council for the Exploration of the Sea (ICES) and from the Northwest Atlantic Fisheries Organization (Rouyer, 2008). The first database contained both spawning biomass and recruitment time series for 295 stocks, whose length ranged between 6 and 132 years. The second database contained recruitment, spawning biomass and SST time series for 25 stocks, whose length ranged between 17 and 100 years depending on the stock. The time series resulting from models integrating a stock–recruitment relationship were not used. The two databases had 15 stocks in common. For these stocks, the data from the second database were chosen because it contained SST information.

Before the analysis, data were normalized (i.e. the mean was subtracted and they were divided by their standard deviation) and recruitment time series were lagged so that years corresponded to age 0 fish. The minimum length for the time series to be included in the analysis was fixed to 40 consecutive years, as done in previous works (Glaser *et al.*, 2011; Rouyer *et al.*, 2014). After selection, the final dataset included 53 fish stocks whose time series displayed an average length of 50 years. SST time series were available for 17 stocks. The main characteristics (i.e. species name, geographical area, time series length, etc.) for the whole data set used in this study can be found in Supplementary Table S1.

Non-linear forecasting methods

State space approximation by simplex

Ecological time series are considered as a product of dynamical systems (Sugihara, 1994). In this study, non-linear forecasting techniques applied on dynamical system were used. The approaches used are briefly described herein, but fully detailed explanations can be found in Sugihara and May (1990), Sugihara (1994), and Sugihara *et al.* (2012).

A system is characterized as dynamical when its states evolve over time (i.e. the value of at least one of the driving variables that structures the system changes at each time step). The trajectory of its states (i.e. the attractor) spreads out into the space composed by all possible states which can be taken by the dynamical system. Each axis of the state space describes one driving variable of the dynamical system. Thus, states with comparable values for each driving variables are neighbours on the attractor. An approximation of the attractor can be obtained from lagged versions of a reduced set of observed variables. An univariate attractor approximation from a single time series X is composed of a library of embedded vectors (or states) as follows: X_t, $\{x_t, x_{t-\tau,} x_{t-2\tau,}, \ldots, x_{t-(E-1)\tau}\}$ (Takens' Theorem, Takens, 1981). When two variables belonging to the same dynamical system are available, it is also possible to reconstruct a composite attractor approximation (Multivariate State Space Reconstruction; Sauer *et al.*, 1991; Deyle *et al.*, 2011, 2013) as follows: X_t, Y_t, $\{x_t, x_{t-\tau,} x_{t-2\tau,}, \ldots, x_{t-(E-1)\tau}, y_t\}$. Within an attractor approximation, states with similar dynamical profile during a period of length E are neighbours. For instance, on the attractor approximation from the recruitment time series only, states characterized by E consecutive years of high recruitment values are close (Figure 1a). On the attractor approximation based on the recruitment and the SSB time series, states characterized by high recruitment values during the period from time t till time $t-(E-1)$ combined with a high SSB at time t are close (Figure 1b). In both cases, the embedding dimension (E, i.e. the number of time steps) and the time lag (τ) have to be determined. Due to the relatively short length of time series, the parameter τ was fixed at 1. The nearest neighbours algorithm named Simplex projection applied on the different time series was used to identify the best embedding dimension (E) (Sugihara and May, 1990). The main idea being that the appropriate embedding dimension of an examined variable is set equal to the minimal number of neighbouring vectors (i.e. the simplex) in the state-space needed to obtain the best prediction of the original time series. A cross-validation procedure was applied to determine the best embedding dimension. The first half of the embedded vectors was used to approximate the attractor of the dynamical system. Whereas the second half was used to compute goodness of fit between observed and predicted values.

The embedding dimension value selected is important as too small a dimension may generate an artificial refolding (i.e. considering that points are close whereas they are actually distant) (Landini *et al.*, 2002) whereas too high a dimension adds uncertainty (Deyle *et al.*, 2013), which would ultimately affect the accuracy of the attractor approximation. In order to have enough vectors to use for forecasting, the range of embedding dimensions tested was arbitrarily set from 2 to the quarter of the size of the time series considered. From this range, the embedding dimension was selected by assessing the simplex performance on the basis of the forecasting skill.

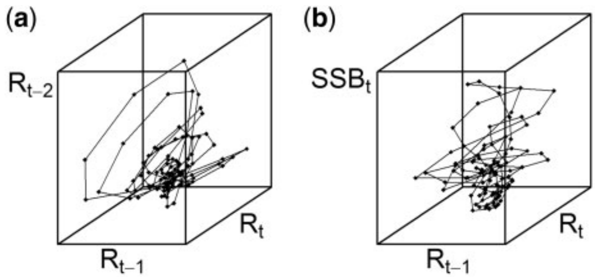

Figure 1. State space approximation for a three-dimensional attractor. (a) Univariate attractor approximation based on the recruitment (R) time series of the Chilipepper rockfish (Sebastes goodie) from the Southern Pacific Coast only. Each point is a time-lagged coordinate vector ⟨R(t), R(t-1), R(t-2) ⟩; (b) Multivariate (or Composite) attractor approximation based on both recruitment (R) and SSB time series of the Pacific herring (Clupea pallasii) from the west coast of Vancouver Island. Each point is a time-lagged coordinate vector ⟨R(t), R(t-1), SSB(t) ⟩.

Convergent cross mapping to detect causal link

Once the embedding dimension was set, the cross-map procedure was applied (see Sugihara *et al*., 2012 for details). The principle of cross-mapping is to measure the concordance between the local neighbourhoods of two attractor approximations. If one variable x influences another variable y, their attractor approximations should converge towards similar trajectories. Thus, the simplex of each embedded vector should be the same in both attractors. So, reliable estimations for the variable x can be obtained using the simplex of each embedded vector determined from the variable y. Recruitment estimate for a given year can thus be obtained as follows. Years having similar dynamical profile than the year of interest are identified in the attractor approximation of SSB. Then, the recruitment estimate is computed as a weighted average of the recruitment observations for these years. If recruitment estimates are comparable to recruitment observations, then dynamical information for recruitment is encoded in spawning stock size, meaning that recruitment influences the parental stock size.

The accuracy of an attractor approximation increases with the number of historical data points available. If causation links two variables, the denser their attractor approximations, the closer estimates should be to observations. The reduction of the gap between the state-space vectors from the two variables of interest, called convergence, is the proof of causation. Looking at the increase in forecast performance with extra information allows to assess whether variables are causally linked.

To assess the convergence, cross-mapping was applied for different library sizes (L; number of embedded vectors used to approximate the attractor). The values of forecasting skill (i.e. the accuracy of estimates to observed values) were plotted against the library size to follow the evolution of the prediction error obtained by cross-mapping with the increase in information. A causal relationship was considered meaningful only if the predictability was significantly improving with library size. To quantify the statistical significance of the average trend, a General Linear Mixed Model (GLMM) was applied including each stock as a random effect, which allows to include variability for both intercept and slope coefficient for each stock. In order to respect the conditions of use of a linear model, the relationship between the predictability and the library size was linearized applying a logarithmic transformation on the response variable. However, using only a parametric model was insufficient for looking at convergence (Clark *et al*., 2015). Because GLMM does not give information about the significance of the slope for each random effect, a Mann-Kendall test for monotonic trend (Mann, 1945) was applied for each stock to detect a potential lack of causation. The correlation coefficient returned by the test gave an indication on the trend: a positive value indicated an increasing trend whereas a negative value indicated a decreasing trend. Stocks characterized by a significant correlation coefficient lower than −0.95 displayed a causal link.

S-map to forecast

Recruitment forecasts were obtained using S-map method (Sugihara, 1994). The basic principle of the S-map procedure is similar to the Simplex method excepted that it does not only account for the $E + 1$ nearest neighbours (or the simplex) but for all the library embedded vectors. In the S-map procedure, the weighting function includes a tuning parameter $\theta \geq 0$ which corresponds to the extent of the weighting used for neighbour vectors in the state-space approximation (Sugihara, 1994). When θ is equal to zero, identical weights are assigned to all embedded vectors, which is equivalent to a linear model [autoregressive model (AR) of order E – AR($\boldsymbol{E}$)] that characterized auto-correlated red noise; whereas a high value of θ indicates that more weight is given to neighbouring vectors compared with remote vectors in the attractor, which reveals non-linearity. Values between 0 and 1 by steps of 0.01 were explored for θ. Again, the value of θ—the best model—was chosen based on the forecasting skill. To assess whether recruitment forecasts could be improved from the dynamical system encoded in time series and from the covariates, the S-map method was applied on univariate or composite attractors. S-map recruitment forecasts applied on multivariate attractor were done incorporating the SSB and/or incorporating the SST to the recruitment univariate attractor.

Forecast performance

The comparison between observed and estimated values was done through the Mean Absolute Scaled Error (MASE) measure (Hyndman and Koehler, 2006). The MASE, which is not scale-dependent and applies equal weights to each error, was used to evaluate the model performance:

$$\mathrm{MASE} = \frac{\sum_{t=1}^{n} |e_t|}{\frac{n}{n-1}\sum_{i=2}^{n} |Y_i - Y_{i-1}|},$$

where Y_t is the value of time series Y at time t, $\hat{Y}_t$ is its forecast and $e_t = Y_t - \hat{Y}_t$ is the forecast error. The MASE corresponds to the ratio between the effective forecasts error and the naïve forecasts error (i.e. the last observed value in the time series is used as the forecast of the present value). The MASE measure has thus the advantage to be easy to interpret as a value lower than 1 indicates that forecasts obtained with the method of interest give better results than naïve forecasts. A null MASE indicates perfect forecasts with the method of interest (i.e. forecasts are equal to

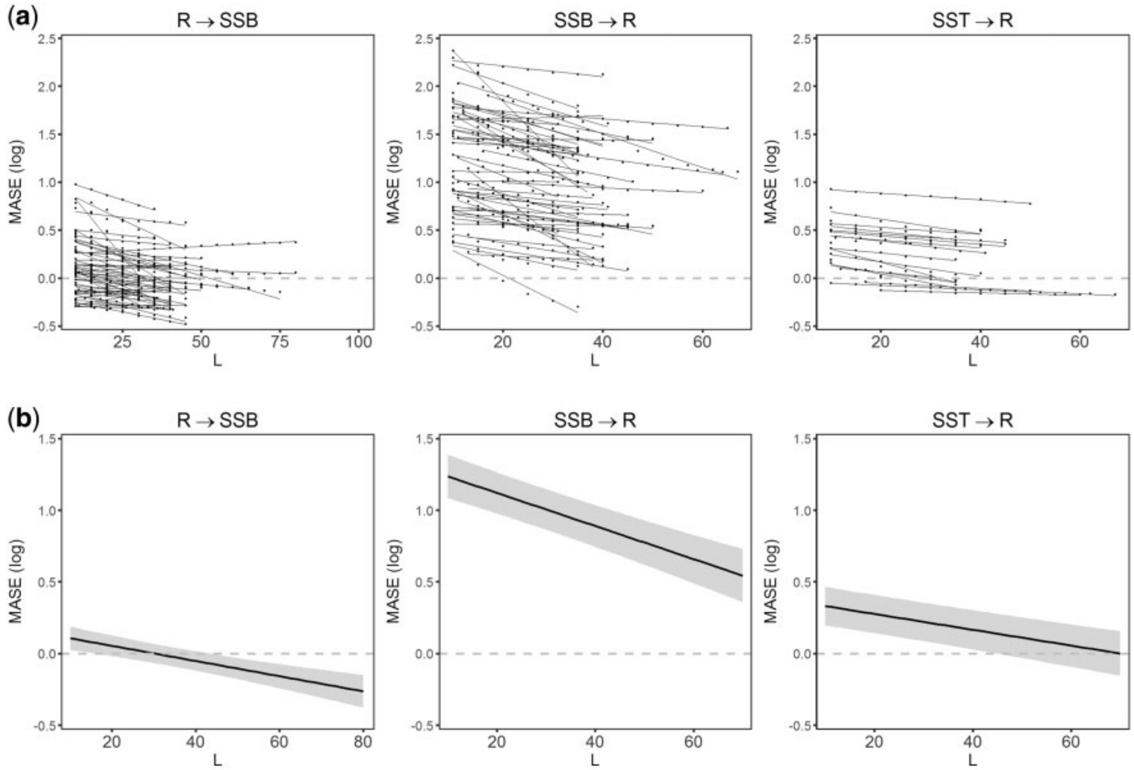

Figure 2. Detecting causation between recruitment (R) and SSB and between recruitment (R) and SST using convergent CCM. Results are presented for R→SSB causation (on the left), for SSB→R causation (on the middle) and for SST→R causation (on the right). The behaviour of the MASE (i.e. the performance of cross-map estimates) with extra information was analysed with a GLMMs. A significant decrease in MASE with the length of the time series (L) indicates the existence of a causal link (i.e. convergence). The results of GLMMs are presented in two ways. (a) In detail, indicating the causation for each stock. The black points are observations whereas grey lines represent estimated curves. (b) On the whole, indicating the global causation trend. The solid line is the average estimated curve and the grey zone represents the 95% confidence bands. This shows that a bidirectional causal link between recruitment and spawning biomass is detected and that recruitment is also forced by temperature.

observations). Furthermore, it is a useful metric to compare forecast accuracy across several time series as it is independent of the data scale.

In this work, the MASE value was used as follows. First, the MASE metric was used to determine the embedding dimension *E*. For each stock, the embedding dimension associated to the smallest MASE value was selected. Second, the MASE was used to assess causal links: a statistically significant decreasing in MASE with extra information was interpreted as the presence of causation. Finally, it was used to characterise the forecasting performance: a MASE value lower than 1 indicated good recruitment prediction ability.

In this study, conventions for the notation of causation between recruitment (R) and SSB and between recruitment (R) and SST are as follows: SSB causes R is referred as SSB→R and conversely R→SSB means that R causes SSB. Finally, the influence of SST on R is referred as SST→R. A significant decreasing in MASE is a proof of causation.

The forecasting analysis has been applied on four different attractors: the univariate attractor based on recruitment data only, the composite attractor R-SSB with recruitment and SSB data, the composite attractor R-SST with recruitment and SST data and the composite attractor R-SSB-SST with recruitment, SSB and SST data. MASE values lower than 1 indicate good predictive ability for recruitment, and the lower, the better.

Results

Causation analysis

Our causation analysis using convergent cross mapping (CCM) method demonstrates the existence of both R→SSB and SSB→R causal links, but also the presence of a SST→R causal link. Indeed, a decrease in MASE with library size was found for the three causal links tested for the majority of stocks (Figure 2a). Consequently, GLMM average curves modelling the three causations exhibit a significant decreasing trend with library size (cf. Table 1 and Figure 2b). So a bidirectional causal link between SSB and recruitment was detected and SST influenced recruitment as well. However, even if at least one causal link was found for 85% of the stocks, the three causations were not present for all stocks (Figure 3).

The most common causation was the SSB→R (found for more than 70% of the stocks) and more than half of the stocks were concerned by the R→SSB causation (Figure 3a). A bidirectional causal links between recruitment and SSB was found for more than 40% of stocks.

The influence of temperature on recruitment was found for the majority of stocks (Figure 3b). On the 17 stocks having SST data available, 10 of them displayed a SST→R causal link. The simultaneous influence of temperature and SSB on the recruitment were found for about 40% of the 17 stocks.

A complete set of figures for the CCM analysis for each stock can be found in the Supplementary Material.

Table 1. Modelling the causation trend.

		Fixed effects			Random effects	
		Estimates	SE	*p*-value	*SD*	Corr
R→SSB	Intercept	0.16	0.05	<0.01	0.35	−0.71
	L	−5.28e-03	1.02e-03	<0.01	0.01	–
SSB→R	Intercept	1.35	0.08	<0.01	0.61	−0.50
	L	−0.01	1.48e-03	<0.01	0.01	–
SST→R	Intercept	0.39	0.07	<0.01	0.29	−0.21
	L	−5.51e-03	8.03e-04	<0.01	3.19e-03	–

GLMM results obtained for each causal link R→SSB, SSB→R and SST→R with each stock as random effect. The relationship between the logarithmic MASE values obtained by CCM and the library size (*L*) was modelled by regression. A significant negative slope (i.e. *L* estimates) indicates the presence of causation.

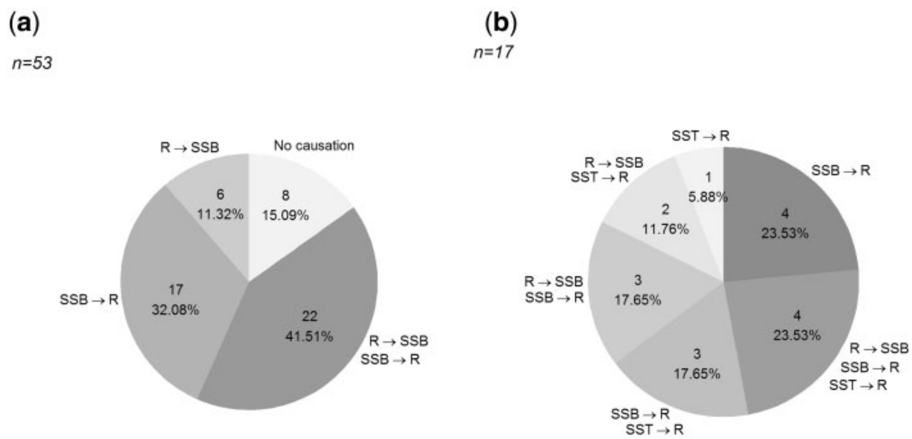

Figure 3. Presence of each causal link detected between recruitment (R) and SSB and between recruitment and SST. R→SSB suggests that recruitment influences parental stock size and vice versa; and SST→R indicates that temperature influences recruitment. (a) Proportion of each type of causation detected for all the 53 stocks. (b) Proportion of each type of causation detected for the 17 stocks having SST information available. These two plots show that the 3 causations are detected and that SSB→R is the most prevalent causation.

Forecasts

Good ability to predict recruitment was obtained using the S-map method. Most of stocks displayed a non-linear behaviour (i.e. no auto-correlated red noise) as their θ values were above 0 (Figure 4a). For the majority of stocks, good ability to predict recruitment was obtained using the S-map method based on the univariate attractor R (only using recruitment data) (Figure 4b). The more variables were used to approximate the attractor (i.e. two variables for composite attractors R-SSB or R-SST and three variables for the composite attractor R-SSB-SST), the less the proportion of stocks obtaining good recruitment prediction ability was found (Figure 4b). Whatever the attractor approximation, a good recruitment prediction ability using the S-map method was obtained for more than half of the 53 stocks (Figure 4c): 30 stocks (more than 56% of the stocks) obtained a MASE value lower than 1, among which 13 had the available information on SST.

Using parental stock size or SST information was not useful to forecast the recruitment with S-map. Considering all 53 stocks, including SSB information into the attractor approximation did not significantly improve the ability to predict the recruitment [Wilcoxon test, alpha risk fixed at 5%: $\mathbf{W} = 530$, *p*-value= 0.10; median MASE improvement and 95% $CI = -0.11$ (-0.59; 0.01)]. Two stocks out of 17 obtained best recruitment predictive ability based on the composite attractor R-SST and only one stock obtained best recruitment predictive ability based on the composite attractor R-SSB-SST (cf. Figure 4c and Supplementary Figures and Tables).

The presence of a causal link did not improve the ability to predict the recruitment. The improvement in recruitment prediction ability when integrating the SSB into the attractor approximation was not significantly different for stocks displaying a SSB→R causal relationship compared with stocks without SSB→R causal link [Mann-Whitney two-sided test, alpha risk fixed at 5%: $\mathbf{U} = 198$, *p*-value = 0.13; difference in medians and 95% $CI = -0.16$ (-0.61; 0.03); Figure 5a]. Furthermore, the MASE gain including SSB to forecast recruitment for the stocks displaying SSB→R causation was not signicantly different from 0 (Mann-Whitney two-sided test, alpha risk fixed at 5%: $\mathbf{U} = 441$, *p*-value = 0.49; difference in medians and 95% $CI = 0.07$ (-0.05; 0.44)]. In the same way, the improvement in recruitment prediction ability when integrating the SST into the attractor approximation was not significantly different for stocks displaying a SST→R causal relationship compared with stocks without SST→R causal link [Mann-Whitney two-sided test, alpha risk fixed at 5%: $\mathbf{U} = 52$, *p*-value = 0.11; difference in medians and 95% $CI = 0.10$ (-0.04; 0.59); Figure 5b]. Moreover, including SST to forecast recruitment for the stocks displaying SST→R causation caused a significant loss in ability to forecast recruitment [Mann-Whitney two-sided test, alpha risk fixed at

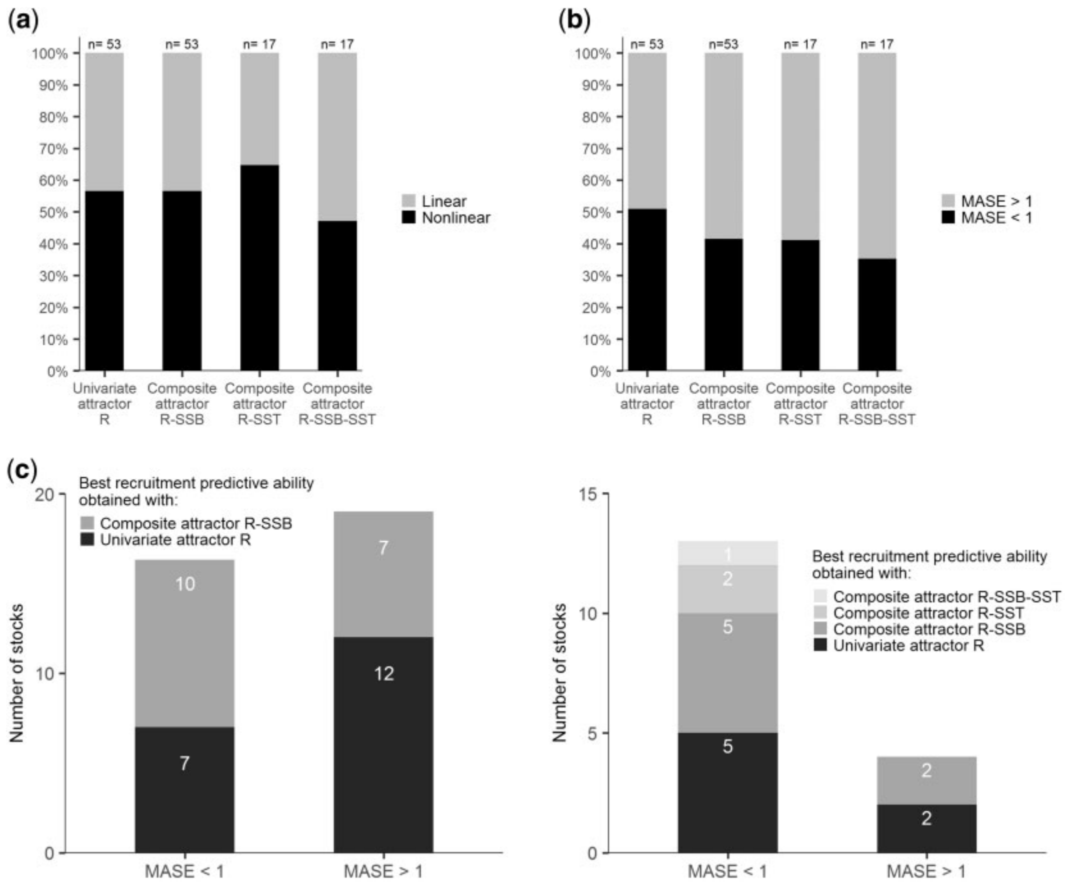

Figure 4. Recruitment predictive ability obtained by S-map applied on different attractor approximations. The univariate attractor approximation is based on recruitment (R) data only whereas composite attractor are approximated using at least two variables. The number of stocks concerned by the univariate attractor R approximation and the composite attractor R-SSB approximation (using both recruitment and SSB data) is 53. The number of stocks concerned by the composite attractor R-SST (using both recruitment and SST data) and the composite attractor R-SSB-SST (using recruitment, SSB and SST data) is 17. (a) Proportion of non-linear dynamics for the different attractor approximations used to obtain S-map recruitment forecasts. This shows that non-linear dynamics are mainly detected. (b) Proportion of stocks obtaining good predictive ability for the recruitment with S-map method (i.e. MASE $<$ 1) based on each univariate or composite attractor approximations. The more variables were used to approximate the attractor, the less the proportion of stocks obtaining good recruitment prediction ability was found. (c) Repartition of each attractor approximation obtaining the best recruitment predictive ability (i.e. the smallest MASE) for the 36 stocks having no SST information available (plot on the left) and for the 17 stocks having SST information available (plot on the right). S-map performs to forecast recruitment because good recruitment predictive abilities (i.e. MASE $<$ 1) are obtained for more than half of the 53 stocks and best recruitment forecasts are mainly obtained using recruitment data only (i.e. based on the univariate attractor R).

5%: $\mathbf{U} = 53$, p-value = 5.86e-3; difference in medians and 95% $CI = 0.32$ (0.06; 5.39)].

Discussion

In an ecosystem approach to fisheries perspective, a step forward in our understanding of stock–recruitment relationships would consist in establishing the relative importance of deterministic and stochastic forces on recruitment (Szuwalski *et al.*, 2015). This would improve our understanding of the stock–recruitment relationship and in turn our ability to forecast fish-stock productivity. For this purpose, two forecasting techniques based on dynamical systems were applied in this article.

Even if the arbitrary constraint to select time series with a minimum of 40 consecutive annual values reduced the number of stocks studied, preserving as long time series as possible is an important aspect because the techniques used here rely on estimating the embedding dimension. As in Cury *et al.* (2014), the dynamical systems generating recruitment time series were found complex and mostly stochastic processes. Non-linear dynamics were identified for most marine species stocks, which is in accordance with previous works (Dixon *et al.*, 1999; Royer and Fromentin, 2006; Glaser *et al.*, 2011). The use of non-linear model-free forecasting techniques rather than deterministic methods for recruitment forecasts seems therefore appropriate, as advocated in several studies (Sugihara *et al.*, 2012; Deyle *et al.*, 2013; Glaser *et al.*, 2014).

The results of our analysis suggested that the underlying process of recruitment is multi-factorial. The evidence of causal relationships in a number of stocks between an intrinsic (SSB) and/or an extrinsic (SST) variable on recruitment has been

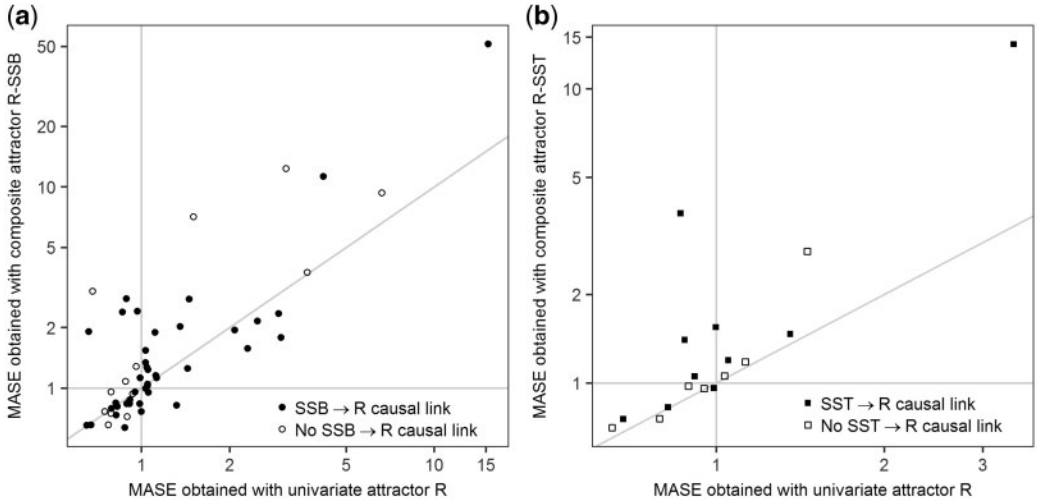

Figure 5. Improvement of the ability to predict the recruitment (i.e. MASE) using composite attractor approximation. A MASE value lower than 1 indicates that forecasts obtained with the method of interest give better results than naïve forecasts. (a) Comparison of the predictive abilities for recruitment obtained applying S-map on the univariate attractor R (i.e. using recruitment data only) with those obtained based on composite attractor R-SSB (i.e. using both recruitment and SSB data). The black dots represent the 39 stocks displaying a SSB→R causal link whereas the white dots represent the 14 stocks displaying no SSB→R causal link. (b) Comparison of the predictive abilities for recruitment obtained applying S-map on the univariate attractor R with those obtained based on composite attractor R-SST (i.e. using both recruitment and SST data). The black squares represent the 10 stocks displaying a SST→R causal link whereas the white squares represent the 7 stocks displaying no SST→R causal link. Stocks below the bisectors obtained best recruitment predictive ability based on composite attractor than based on univariate attractor R and vice versa. These two graphs show that using the composite attractor does not necessarily improve recruitment forecasts and that the presence of a causal link does not help to forecast recruitment.

demonstrated. Information about recruitment was also found in parental biomass for more than half of the stocks. This was a rather expected result as over years, recruitment spreads through age-classes and eventually contributes to the SSB (Bjørnstad *et al.*, 2004). Footprint of spawning biomass was also detected in most recruitment time series. Such results differ greatly from other recent work using other methodology (Cury *et al.*, 2014). This could be due to the complexity of the non-linear nature of the link between SSB and recruitment, whose shape might not be the same across all stocks.

Potential density-independent control found also support for most of the stocks in our analysis. This result suggests that density-independent processes, such as stochastic environmental control, might be an important aspect of the interplay between deterministic and stochastic forces governing recruitment fluctuations (Bjørnstad and Grenfell, 2001). This aspect and the stock-specific processes involved in recruitment might partly explain why general stock–recruitment relationships do not clearly emerge through meta-analyses.

However, the detected causal links were found to be weak and therefore to have little influence on the predictability of recruitment in accordance with Cury *et al.* (2014) and Szuwalski *et al.* (2015). The presence of causal relationships between an intrinsic (i.e. SSB) and/or an extrinsic (i.e. SST) variable on recruitment led to improved recruitment predictive ability obtained by S-map in only a few stocks. Indeed, S-map succeeded in forecasting the recruitment for more than half of the stocks and recruitment forecasts similar to observations were mostly obtained using recruitment data only. Thus, S-map appeared as a robust tool as it only required recruitment data to provide accurate recruitment forecasts.

The use of non-linear and non-parametric forecasting techniques provided a useful tool to test for potential environmental drivers of recruitment which could then be used to eventually improve our ability to understand changes in fish stock productivity. Including external factors will improve fisheries management only if the effect of the driving factors is well known (Punt *et al.*, 2014). SST was the only environmental factor tested in this work. Although SST is not likely the main driver governing recruitment success for all stocks (Hjort, 1914; Cushing and Dickson, 1976; Cushing, 1990), it would be interesting to test the predominant environmental drivers emerging from the literature for each stock. Furthermore, sudden and unexpected shifts in a population could be explained by networks of interacting species (Travis *et al.*, 2014). Between two interacting species, the fluctuations of one can affect the fluctuation of the other. Abiotic interactions influencing recruitment of each stock, such as predator-prey relationship, could be then explored in order to improve fisheries management.

Non-linear forecasting technics have a great potential for unravelling underlying processes in fisheries ecology. The non-correlative nature of the technique used in the manuscript allowed eliminating spurious effects between recruitment and the environment which could arise due to the interplay between environmental noise and population dynamics (Rouyer *et al.*, 2012). The convergence cross-mapping method can help identifying sources of recruitment variability, and thus help to improve our knowledge of dynamical processes underlying recruitment variability. In addition, S-map provides good recruitment forecasts and also allows to include judiciously chosen driving variables. The use of these methods to predict next years recruitment is a real interesting perspective for stock assessment, as it provides a model-free and empirical approach to estimate fish-stock productivity, a key parameter in fish-stock assessment (Houde, 2008).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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