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Resolving Hjort's Dilemma

How Is Recruitment Related to Spawning Stock Biomass in Marine Fish?

By Philippe M. Cury, Jean-Marc Fromentin, Sarah Figuet, and Sylvain Bonhommeau

ABSTRACT. The relationship between spawning fish abundance and the number of offspring, the so-called stock-recruitment relationship, is crucial for fisheries management and conservation measures. Using the most comprehensive data set ever assembled, we quantify this relationship for 211 fish stocks worldwide, revealing a global pattern with a pervasive asymptotic shape that shows increasing recruitment reaching an upper limit for values around half to two-thirds of parental biomass. This corroborates previous theoretical and modeling results. However, parental biomass is a predictor for only 5% to 15% of the variance in recruitment, demonstrating the weak predictive power of the stock-recruitment relationship in marine fish populations. Thus, there is a need to move rapidly toward models that integrate environmental conditions and species interactions in fisheries stock assessment and management, as suggested by Johan Hjort 100 years ago.

INTRODUCTION

Sudden collapses and slow recoveries of exploited marine fish populations indicate a lack of understanding of the resilience of these highly fecund vertebrates (Neubauer et al., 2013). The relationship between parental stock size and subsequent recruitment of marine fish is fundamental to the management of exploited fish populations (Walters and Martell, 2004). Stock-recruitment relationships (SR) are widely used by international organizations and national fishery management agencies to define optimal spawning stock sizes and maximum sustainable yields and to estimate exploited fish populations' responses to different management actions (Hilborn and Stokes, 2010). SR models assume that the number of offspring of teleost fishes (a group of ray-finned fishes that include most of the best-known commercial and sport fishes) increases with parental stock up to a point where it plateaus or perhaps decreases due to density-dependent processes (e.g., competition and/or cannibalism) resulting from habitat and/or food limitation (e.g., Hixon and Carr, 1997). Consequently, SR models are mostly deterministic and do not integrate density-independent factors, such as environmental variations.

Indeed, ever since Johan Hjort's (1914) seminal work, there has been a continuing debate about the relative importance of the density-dependent versus density-independent factors in the renewal and resilience of marine fish populations (Houde, 2008). Several studies have found that marine fish recruitment is predominantly environmentally driven because fish larvae production is related to favorable abiotic (e.g., temperature and currents) and biotic (prey and predators) conditions, which are conceptualized using the popular "match-mismatch" hypothesis (Cushing, 1990; Durant et al., 2005). Review of overfished stocks reveals that severe reduction in parental stock size results in low production of offspring (Keith and Hutchings, 2012). Thus, the renewal of marine fish populations could be primarily environmentally driven and, secondarily, dependent on parental stock size (Szuwalski et al., 2014). Combined effects have been emphasized, as overexploitation increases instability in fish dynamics and truncates population demography, which translates into higher vulnerability to environmental changes (Hsieh et al., 2006; Anderson et al., 2008). The SR relationship is thus still widely debated, and recent studies have utilized the RAM Legacy Stock Assessment Database (Ricard et al., 2012) to re-examine relationships (Szuwalski et al., 2014) and sometimes to question its existence (Vert-pre et al., 2006).

FORM AND STRENGTH OF STOCK-RECRUITMENT RELATIONSHIPS

Using the updated long-term data sets from the RAM Legacy Stock Assessment Database (Ricard et al., 2012) and the International Council for the Exploration of the Sea (ICES) stock assessment database (Supplementary Table 1), we quantified the strength of the SR relationship through a meta-analysis of 211 time series of fish stock abundance and recruitment data from around the world. This constitutes the most comprehensive data set ever analyzed, with inclusion of 7,326 years of recruitment and spawning stock biomass data collected from 117 geographic locations (Figure 1, left panel). The biomass and recruitment data were mostly derived from virtual population analysis, statistical age- or length-structured assessments, or direct estimates based on scientific surveys (Supplementary Table 1). Three groups drawn from the 90 fish species considered were pooled according to habitat characteristics, as defined in FishBase (http://www.fishbase.org): (1) demersal species (e.g., cod, hake, flat fish, groupers), (2) small pelagic species (e.g., sardine, anchovy, herring), and (3) large pelagic species (e.g., tuna, marlin, yellowtail). Data were standardized by dividing the recruitment and spawning biomass of each stock by its maximum observed value. We lagged the recruitment data to match the stock size for the birth year of recruits using the recruitment age provided in the RAM Legacy database. Supplementary Table 1 indicates the main characteristics (species name, area, number of years, etc.) for the whole data set used in the present analysis.

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We investigated the empirical SR relationships using generalized additive models (GAM; Hastie and Tibshirani, 1990). GAMs allow nonlinear modeling, making no a priori assumptions about the forms of relationships while avoiding some statistical difficulties in fitting deterministic functions (Wood, 2011). GAMs are fitted to the stock and recruitment data using the packages *gam* and *mgcv* of the R software. We fit GAMs to the global data set as well as to data aggregated by habitat and by family to investigate whether the SR relationship varies systematically. The smoothing parameter for each GAM is automatically calculated within the *mgcv* package. We calculated the percentage of variance explained by the model as

$$\textit{\% variance explained} = 1 - \frac{SS_{res}}{SS_{tot}},$$

where SS_{res} is the sum of the square of the residuals, and SS_{tot} is the total sum of the square.

For all species or groups of species, recruitment was related to spawning stock biomass in a nonlinear manner (Figure 1, middle panel). For all species combined, and different assemblages of species, the general asymptotic shape of the relationships, depicted by the GAM, first increases and then reaches an asymptote or decreases slightly; the threshold value occurs at about half to two-thirds of spawning stock biomass, that is, 60% for all species combined (model confidence interval [CI] at 95% = ±0.79%), and 54% (CI = ±0.82%), 59% (CI = ±1.15%),

and 67% (CI = ±0.44%) for large pelagics, demersal fishes, and small pelagics, respectively (Figure 1, middle panel). Although the forms of the SR relationship and estimated reference points are consistent among groups of species, the variance explained by these empirical models remains very low: 8.8%, 5%, 9.6%, and 15.4% for all species, demersal fishes, large pelagics, and small pelagics, respectively (Figure 1, right panel).

COMPARISON BETWEEN EXPECTED LOW/HIGH RECRUITMENT WHEN STOCK IS LOW/HIGH

Putting aside the low variance explained, the stock-recruitment relationship implies that recruitment is low at low spawning
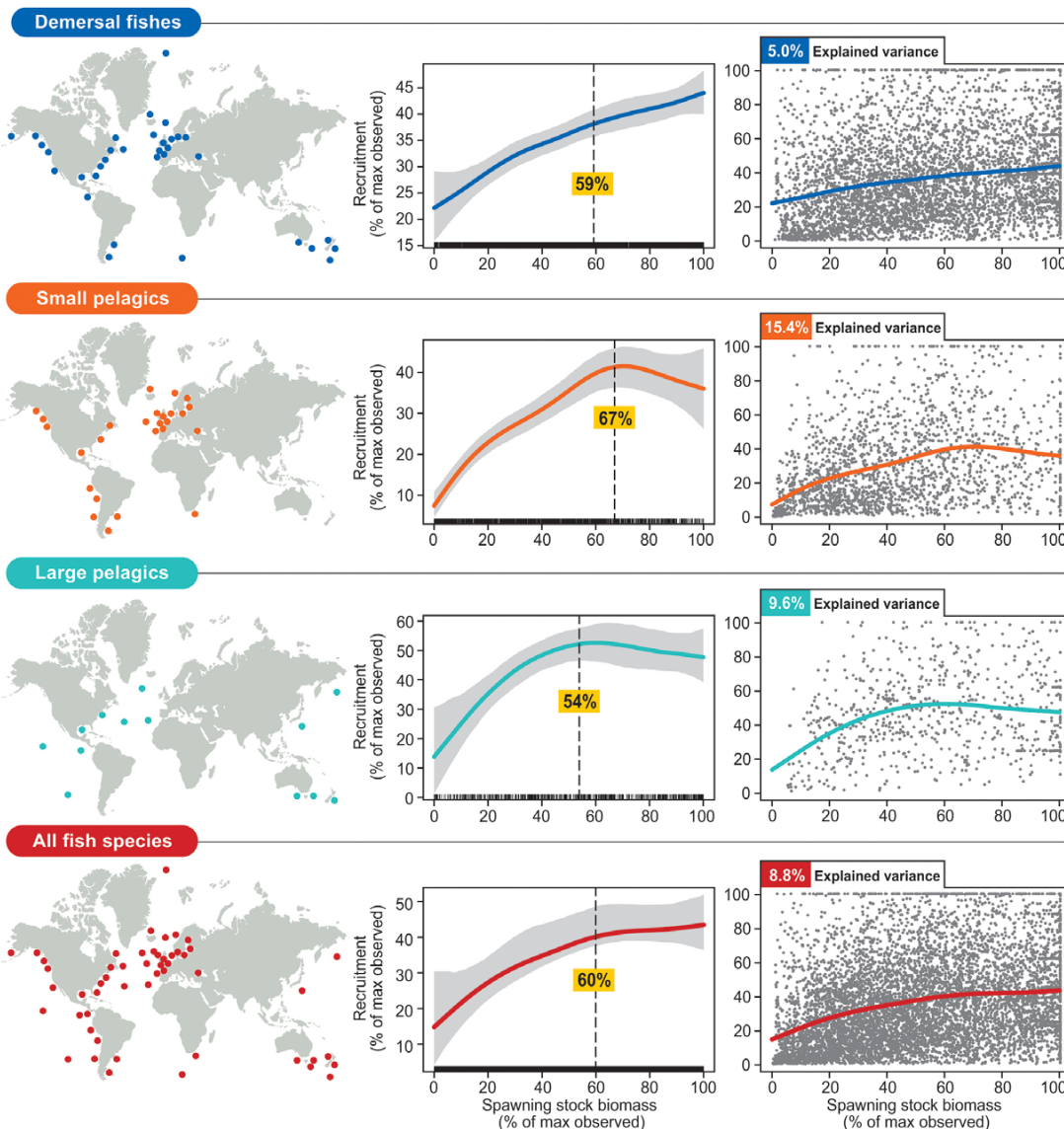

FIGURE 1. Relationships between adult fish and offspring in marine fish species. (left panel) Maps of the distributions of stock-recruitment (SR) relationship data for demersal, small pelagic, large pelagic, and all fish species. (center panel) Relationships between normalized recruitment and normalized spawning stock biomass investigated by a generalized additive model (GAM; solid colored lines). The gray areas represent the 95% confidence interval of the fitted GAM, and the thresholds in the nonlinear relationship (black dashed vertical line) were detected using a change-point analysis. (right panel) Similar plots as in the center panel but representing each data point from all the time series, with the explained variance from the fitted GAM ranging from 5% to 15.4%

biomass and higher at larger spawning biomass (Myers and Barrowman, 1996). To examine this observation further, we compared, for each stock, the distribution of the percentage of times where recruitment (R) is low/high when stock biomass (S) is low/high with a random distribution (Figure 2). As recruitment time series are often auto-correlated, to generate a random recruitment time series that accounts for auto-correlation, we used the surrogate approach (Rouyer et al., 2008) to generate simulated recruitment time series displaying variance and autocorrelation structure similar to those of the original time series. For each recruitment time series, we thus tested, using the Kolmogorov-Smirnov test, the distribution of the percentage of times where R is low/high when S is low/high against the empirical distribution generated by 1,000 surrogates of that time series. The results show that low/high R is significantly associated with low/high S more often than a random process (Figure 2). However, low R is associated with low S for only 29% of cases (random process predicts 20%), and high R is associated with high S for 25% of cases (random process predicts 20%). In general, recruitment is thus lower at low spawning biomass and higher at large spawning biomass, but the percentages are only slightly higher than expected at random, which confirms the weakness of the SR relationship in driving population dynamics of marine species.

MODELING THE STOCK-RECRUITMENT RELATIONSHIPS

Last, we fit to the global data and habitat subset data sets the two theoretical models for the stock recruitment relationship: the Beverton and Holt model (Beverton and Holt, 1957) and the Ricker model (Ricker, 1954). These model formulations are:

$$R = \frac{a.SSB}{1 + b.SSB}$$

for the Beverton-Holt model, where R is recruitment, SSB is spawning stock biomass, and a and b are estimated parameters, and

$$R = a.SSB.e^{-b.SSB}$$

for the Ricker model.

As for the GAMs, we estimated the percentage of variance explained and selected the "best" model using the Akaike Information Criterion (AIC; Akaike, 1974). The "best model" is the Beverton and Holt model for the global data set and for demersal and small pelagic species (Figures 3 and 4 and Table 1). The Ricker model has a better fit for the large pelagic species (Figure 3 and Table 1). Similar results are obtained for major groups of species regarding the form of the SR and the appropriate type of model (Figure 4). Among the different deterministic SR models, the Beverton-Holt SR type relationship (Beverton and Holt, 1957), widely used by international fisheries organizations, appears to be the best fitted parametric model (Figures 3 and 4). Nonetheless, the Beverton-Holt SR type also explained a low percentage of the variance between spawning stock biomass and offspring (8.3% for the global data set).

DISCUSSION: IMPLICATIONS FOR MANAGEMENT OF AN ELUSIVE RELATIONSHIP BETWEEN ADULT MARINE FISH AND OFFSPRING

These results demonstrate that marine fish recruitment is not totally stochastic and depends, up to some point, on parental stock size. However, this relationship is typically weak and may not be particularly useful for management purposes. This result may appear surprising, as density dependence is known to be a key driver in vertebrate population dynamics (Begon et al., 2006). However, reproductive strategies of marine bony fish differ greatly from those of other vertebrates. Although mammals and birds give birth to one (e.g., albatross, gorilla) to 20 (e.g., partridge) offspring per reproductive event, marine female bony fish generally produce between 15,000 (e.g., anchovy, herring) to 45,000,000 (e.g., tuna) very small (~ 1 mm diameter) eggs in the marine environment (Cury and Pauly, 2000). As opposed to bird and mammal eggs, bony fish eggs are externally fertilized,
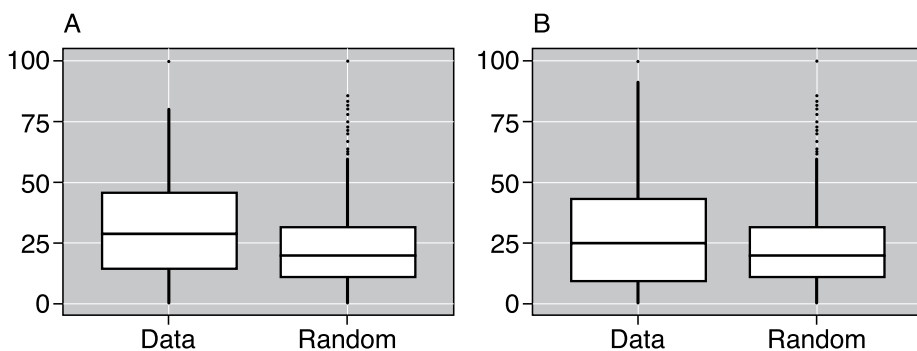

FIGURE 2. Percentage of times where low (A) or high (B) recruitment is associated with low or high spawning stock biomass (left boxplot). This percentage is compared to random distribution of recruitment (right boxplot). "Low" recruitment (R) or spawning stock biomass (SSB) are assumed to be lower when R or SSB is lower than the 20% quantile. "High" recruitment (R) or spawning stock biomass (SSB) are assumed to be higher when R or SSB is greater than the 80% quantile.

TABLE 1. Akaike Information Criterion (AIC; Akaike, 1974) for the two parametric models (Beverton and Holt, 1957; Ricker, 1954). The bold numbers are the lowest AIC values, indicating better fit.

Data	Beverton and Holt model	Ricker model
Global dataset	**133.5**	253.5
Demersal species subset	**249.3**	377.3
Small pelagic species subset	**−212.0**	−203.4
Large pelagic species subset	−77.8	**−87.5**

and hatching generally happens without parental care after an incubation period of less than a few days. Fish larvae are typically pelagic, with a yolk sac and relatively undeveloped body form, but the mortality is massive and the great majority (> 99%) die during the first week of life (the so-called "critical period," as discussed by Hjort, 1914, 1926). So, while mammals and birds (and some cartilaginous fish-like large pelagic sharks) invest in the quality of a few offspring, the great majority of bony fish mainly invest in the quantity, resulting in larval survival being mostly determined by physical and biological environmental variations. Hjort recognized this, but due to lack of data over a century ago, he was unable to demonstrate the substantial weakness in the stock-recruitment relationship.

We thus confirm Hjort's primary assumption that recruitment in marine fish is a complex and mostly stochastic process that is not primarily driven by parental stock size. To some extent, this demonstrates that using deterministic SR models to forecast future recruitment in fisheries management applications is likely to be inappropriate. The SR relationship was derived in the 1950s from a mathematical formulation for fish populations (Beverton and Holt, 1957), with the wish that future research effort in fisheries science would be carried out to collect data and to calibrate SR models (Fréon et al., 1993; Houde, 2009). Recent synthetic studies confirm the weakness of this relationship for marine bony fish (Szuwalski et al., 2014), advocating for better integration of ecosystem considerations into management (Travis et al., 2014). Paradoxically, many national and international fisheries organizations still consider SR models to be the cornerstone of fish stock assessment and fisheries management, particularly for Europe (e.g., ICES) and for the high seas (e.g., regional fisheries management organizations).

Therefore, a century after Hjort's seminal work, it is clearly time to integrate environmental factors and biotic interactions into fisheries management (Travis et al., 2014). Recently developed, novel, nonlinear and nonparametric approaches have been shown to be more powerful in predicting complex system, such as marine fish recruitment (Sugihara et al., 2012; Deyle et al., 2013; Glaser et al., 2013). Moreover, recent studies appear promising in evaluating species interactions in order to set minimal population size required to sustain ecosystem interactions (e.g., Cury et al., 2011; Pikitch et al., 2014). Full appreciation of the nature, strength, complexity, and outcomes of species interactions and environmental effects will enhance management of marine fish stocks, individually and globally. 🔁

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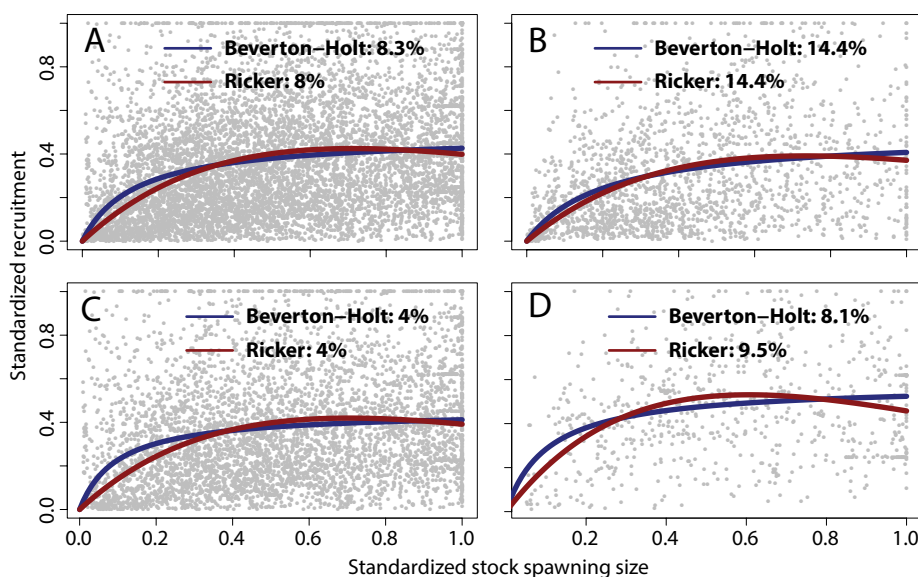

FIGURE 3. Fit of the Beverton-Holt (blue line) and the Ricker (red line) parametric models to the (A) global, (B) demersal, (C) small pelagics, and (D) large pelagics data sets. The percentage of variance explained by each model is indicated in the legend box.
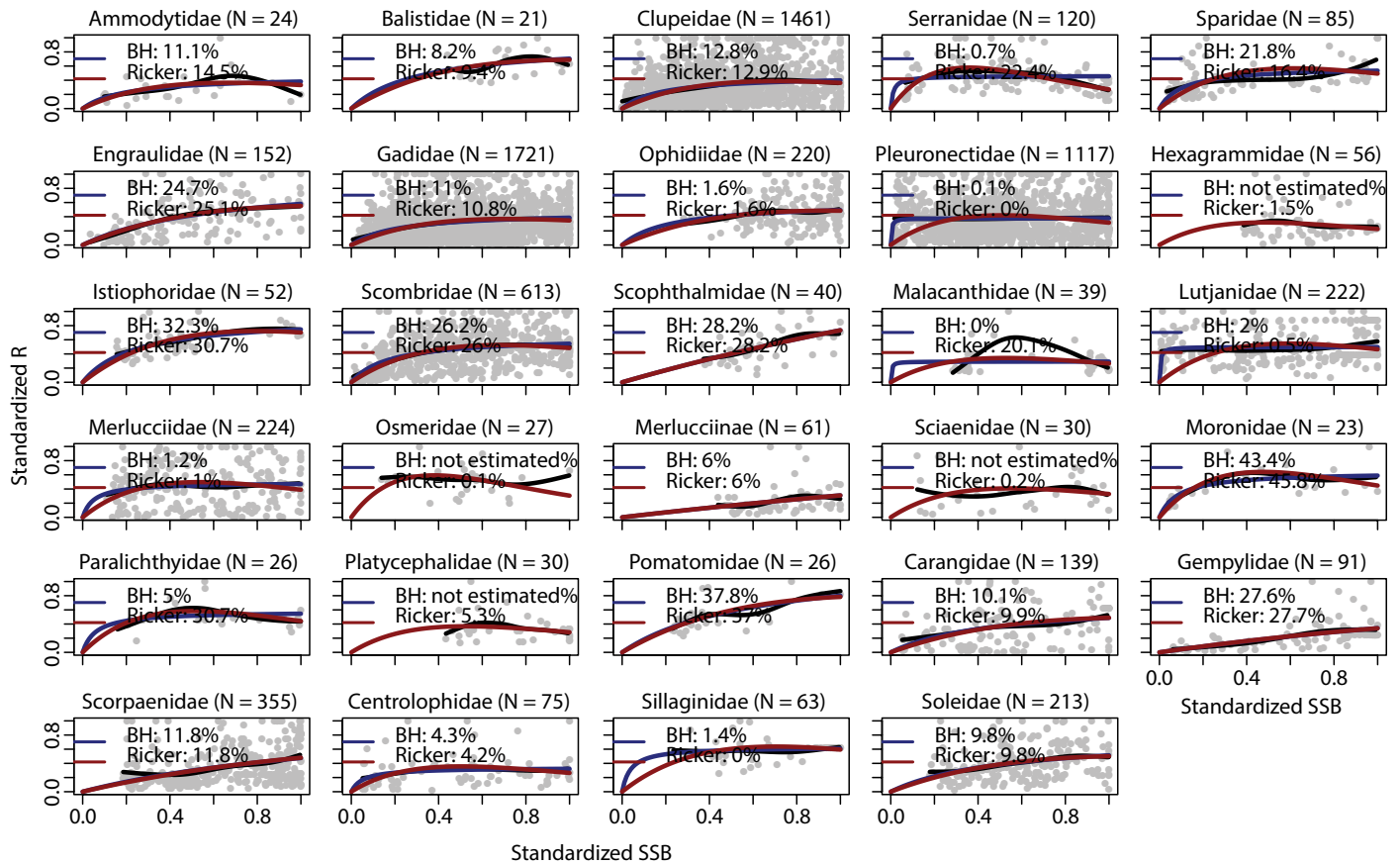
FIGURE 4. Fits of the Generalized Additive Model (black lines) and the Beverton-Holt (blue lines) and Ricker (red lines) parametric models for each family of marine species available in the global data sets. The percentage of variance explained by each model is indicated in the legend box.

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