A macroecological perspective on the fluctuations of exploited fish populations

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ABSTRACT: The natural variability of fish populations is increased by exploitation, but the specific mechanisms driving this variability are still debated. We propose a macroscopic approach combining the size–density relationship and Taylor’s law to predict the temporal variance of exploited and unexploited fish populations. Using information from 11 years of fishery-independent abundance surveys, we showed that the body-size dependence of the variance of exploited (targeted) and unexploited (non-targeted or bycatch) fish populations can be accurately predicted. Targeted fish populations showed a variability that was 2 orders of magnitude greater than that of non-targeted fish populations. Such variability was explained solely by the higher relative abundance of the former, regardless of their specific trophic position, while aggregated community fluctuation was lower in a high trophic position group. This study showed the usefulness of the macroscopic approach to predict fish variability and fishing effect in the whole community. This approach is complementary to other modeling strategies and seems to be useful in tackling the problem of variability in population fluctuations of exploited fish, particularly in cases where specific details of the interacting species are lacking.

KEY WORDS: Macroecology · Fish community fluctuations · Species abundance · Taylor’s law · Variance–mass allometry

1. INTRODUCTION

Understanding the variability of natural populations is relevant because it allows prediction of the probabilities of extinction, blooms of noxious algal species, pest outbreaks, and fishery collapses (Anderson et al. 2017). Fisheries are among the last remaining large-scale economic activities based on capturing natural populations, and fisheries science has a long tradition of developing models and methods to predict and project potential harvests in the following years (e.g. Quinn & Deriso 1999). When harvesting natural populations, the effects of population dynamics, environmental variability, species interactions, and fishing mortality combine to generate complex ecological dynamics (Anderson et al. 2008, Sugihara et al. 2011, Cohen et al. 2012a). There is consensus on the destabilizing effect of harvesting on fish dynamics (Aubone 2004, Anderson et al. 2008, Botsford et al. 2014).

Multiple modeling strategies to understand and predict exploited fish dynamics range from simple, but dynamically complex, single-population logistic models (May 1973), to end-to-end models with a de-
etailed description of the growth and biophysical interactions of every species (Shin & Cury 2004, Travers et al. 2007, Fulton 2010). However, a consensus on the specific mechanisms driving fish variability is missing. The macroscopic approach seeks to find general relationships underpinning the state of a system without including detailed information on the interacting agents (Maurer 1999, Jennings & Mackinson 2003, Marquet 2005). This approach is complementary to other modeling strategies and seems to be useful in tackling the problem of variability in exploited fish fluctuations because, in many exploited ecosystems, detailed and updated information about the interacting population dynamics is usually lacking.

Two general patterns in ecology link population abundance and variability with body size. Firstly, the local size−density relationship (SDR) states that abundance \( N; \text{ind. area}^{-1} \) is related to body size (mass, \( M; \text{g ind.}^{-1} \)) via a power law of the form: \( N = aM^b \) \((a > 0; \ b < 0)\) (White et al. 2007). Secondly, Taylor’s law (TL) states that the variance in the population abundance \( \text{Var}[N] \) is related to the average population abundance \( \text{E}[N] \) via a power law \( \text{Var}[N] = c\text{E}[N]^d \); \( d ~ 2)\) (Taylor 1961), where \( a, b, c \) and \( d \) are statistical parameters (powers and pre-powers). Recently, variance−mass allometry (VMA) combined these 2 power laws to theoretically predict an explicit relationship between variance and body size \( \text{Var}[N] = e\text{E}[N]^f \), where the exponent \( f \) and pre-power \( e \) are a combination of SDR and TL parameters \( (f = bd, \ e = ca^d) \) (Marquet 2005, Cohen et al. 2012b). This relationship has been evaluated empirically in a spatial context for oak trees, among life forms in a lake ecosystem (Cohen et al. 2012b, Lagrue et al. 2015), and in the spatial form for felids (Anile & Devillard 2020). VMA was suggested as a useful indicator to evaluate human-induced disturbance and to explore community effects of fishing in a model simulation (Cohen et al. 2012a), but empirical evaluation of the temporal formulation of the VMA, i.e. when population variances are estimated across time, is lacking. The lack of detailed and lengthy data on exploited and un-exploited (control) populations found in the same ecosystem makes it generally difficult to evaluate the relationship between population variance and body size (Anderson et al. 2008).

Characterization of variability patterns in exploited and unexploited fish populations will provide an important empirical evaluation of the VMA macroecological hypothesis, and open an avenue to explore fish fluctuations in data-poor fisheries. We used SDR, TL, and the temporal version of the VMA to explore patterns in co-occurring exploited and un-exploited fish species in a large estuary in South America (see Fig. 1). The SDR and TL estimated from fisheries-independent surveys of 66 species conducted over 11 years allowed us to generate a theoretical prediction on the power scaling and pre-power of the VMA. We contrasted predicted values with the empirically fitted VMA and showed an accurate prediction to the first and second decimal place in the intercept and slope, respectively. We suggest that macroscopic patterns are useful for understanding natural fish fluctuations in natural ecosystems.

2. MATERIALS AND METHODS

2.1. Sampling and species abundance estimation

The Río de la Plata estuarine system comprises 35000 km² of estuarine waters in the Uruguayan and the northernmost part of the Argentinian coasts (Fig. 1). The area is characterized by vertical density gradients modulated by wind force and freshwater discharge (Jaureguizar et al. 2003). Bottom water temperatures can be divided into a warm period (December−March), with a mean value of 20°C, and a cold period (June−September), with values from 10 to 12°C. Data comprised relative abundance (ind. nautical mile [n mile]−2) of fish species of the middle section of the Río de la Plata (~5000 n mile2) collected from multispecies fisheries-independent bottom trawl surveys conducted each winter by the National Institute for Fisheries Research and Development (INIDEP, 2003).
The time series spans 1993 to 2004 and includes 429 sampling stations, monitored with the use of the swept area method (Sparre & Venema 1997). No sampling field trip was made in 2003 due to lack of funding from the government.

At each sampling location, the number of individuals of each species was obtained by counting all individuals in the catch or by extrapolating the number of individuals in a sample to the total catch of the species. Fish densities (individuals per unit area) were calculated for each fishing set using the standard swept area method.

Trawls lasted ~15 min each at a speed of 4 knots. The fishing gear used was an Engel-type bottom-trawl with a stretched mesh size of 120 mm. Only daytime sampling was conducted (from 07:30 to 19:30 h). Further details of the sampling design can be found in Jaureguizar et al. (2006).

2.2. Data analysis

The SDR was constructed using the temporal abundance average \( (N; \text{ind. n mile}^{-2}) \) and the maximum adult size \( (M; \text{g}) \) of all recorded species. The SDR pattern remained unchanged when using the average size or maximum adult size. The parameters were estimated using linear least squares regression with log_{10}-transformed variables. The exploitation status was a binary covariable representing whether the species was targeted by the industrial fleet (i.e. exploited) or non-targeted (i.e. not exploited or bycatch) and coded as 0 and 1, respectively. We assumed that fishing mortality in non-target species is low and therefore considered them to be unexploited. The trophic position was a continuous covariable whose values were gathered from literature reviews on stomach content and ecosystem modeling (Lercari et al. 2015). We classified species according to their lifestyle (pelagic/demersal) and habitat use (marine/estuarine/freshwater). Labels resulting from this classification were then used as covariables when fitting SDR models.

A temporal version of TL was fitted for the whole community. Each species’ average temporal abundance \( (E[N]) \) and its variance \( (\text{Var}[N]) \) were log_{10}-transformed, and a linear model was fitted by least squares regression. The exploitation status and trophic position were included as covariables, and their interaction was also tested. The VMA relationship was fitted to the log_{10}-transformed variance and body mass \( (M) \) using the exploitation status and the trophic position as covariables. For each relationship, the best model was chosen based on Akaike’s information criterion (AIC). When AIC was similar (>2 units) among competing models, by parsimony, the simplest model was chosen following Burnham & Anderson (2002). A sensitivity analysis was conducted to compare the performance of AIC and AIC corrected for small sample size, but no differences in model selection were found between criteria. We compared theoretical predictions on the VMA generated by combining exponents from the SDR and TL (Table 1) with the observed value fitted to empirical data on body size and variability (empirical VMA).

2.3. Community fluctuations

The temporal abundance fluctuation of each species \( (i) \) was calculated for each year \( (t) \) as \( r_i = \log_{10}(N_{it+1}/N_{it}) \). In addition, community fluctuations were aggregated across species with a high trophic position (TP \( \geq 3.5 \)) and a low trophic position (TP \( < 3.5 \)) (Segura et al. 2017). In a stationary community, community fluctuations are expected to follow a Laplace distribution, with an average of zero, a higher variance for low trophic position species, and low variance for high trophic position species (Segura et al. 2017). Laplace distributions were fitted to observations using the ‘VGAM’ package (Yee 2010). The symmetry of the distribution was tested using the Miao, Gel, and Gastwirth test (Miao et al. 2006), which was implemented in the ‘lawstat’ package. We also compared the AIC of a symmetric Laplace distribution and a 3-parameter asymmetric Laplace distribution implemented in the ‘ald’ package (Galarza & Lachos 2018). All statistical analyses and simulations were conducted in R (version 3.2.3) (R Core Team 2015) under Linux-gnu.

<table>
<thead>
<tr>
<th></th>
<th>Observed</th>
<th>Theoretical prediction</th>
<th>Empirical fit</th>
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</thead>
<tbody>
<tr>
<td>Slopes</td>
<td>( b )</td>
<td>( d )</td>
<td>( f = bd )</td>
</tr>
<tr>
<td>All species</td>
<td>−0.77</td>
<td>2.11</td>
<td>−1.61</td>
</tr>
<tr>
<td>Intercept</td>
<td>( a )</td>
<td>( c )</td>
<td>( e = cd )</td>
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<tr>
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</tr>
<tr>
<td>Unexploited</td>
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<td>−0.38</td>
<td>9.51</td>
</tr>
</tbody>
</table>

Table 1. Exploited fish populations were ca. 1 order of magnitude more abundant and almost 2 orders of magnitude more variable than unexploited fish populations. Theoretical predictions on the variance–mass allometry (VMA; \( i \) and \( e \), respectively) were generated by combining fitted parameters from the size–density relationship \( (b, a) \) and Taylor’s law \( (d, c) \). Theoretical predictions showed excellent congruence with empirical fit of the VMA (see Fig. 2C).
3. RESULTS

The analyzed species in the Río de la Plata Estuary encompassed 3 orders of magnitude in size, from small herrings (~8 g) to large sharks (~100 kg). Exploited species showed larger fluctuations than did unexploited counterparts, and the variability tended to decrease for large-sized organisms (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m665p177_supp.pdf). Population collapses were larger than population outbursts, which is consistent with previously registered patterns of larval assemblages and adult animal populations (Anderson et al. 2008, 2017). The body size and trophic position of exploited and unexploited species showed similar patterns to California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval assemblages evaluated previously (Anderson et al. 2008; see Fig. S2 for details).

The SDR presented a common negative slope \( b = -0.77; R^2 = 0.27; N = 66; p < 0.01 \) for exploited and unexploited species (Fig. 2A, Table 1). However, at a given size, targeted species were ca. 1 order of magnitude more abundant than their non-targeted counterparts (Table 1). Lifestyle (demersal or pelagic) and habitat preference (marine/estuarine/freshwater) were not selected as covariates in the SDR (\( \Delta AIC > 5 \)), while the best model including body size and targeted status showed residuals consistent with normality, homoscedasticity, and absence of trends (Fig. S3). Fitted parameters from competing models and associated descriptive statistics are provided in Tables S1−S3.

The relationship between mean and variance (TL) of the fish populations showed almost perfect linearity \( R^2 = 0.96; N = 66; p < 0.01 \), with no differences in slopes or intercepts between targeted and non-targeted species (Fig. 2B, Table 1). The slope showed no
statistical differences with the null expected value of 2 (t-test; p > 0.05, N = 66). A significant negative relationship between variance and body mass was found with a common slope and different intercepts for targeted and non-targeted species (Fig. 2C). The former species were almost 2 orders of magnitude more variable than were the latter at a given size (Table 1). The theoretical predictions of the slope and intercept of the VMA agreed closely with the statistical fits to empirical data to the first and second decimal place (Table 1). Residual analysis of the VMA model suggests that the linear model is adequate (Fig. S4). The similarity between predicted and fitted values suggest that the variability in exploited fish populations can be predicted accurately by combining 2 fundamental ecological scaling laws, namely the SDR and TL.

The effect of these scaling relationships on the community fluctuation distribution was estimated by aggregating species into 2 groups: low trophic position (TP < 3.5) and high trophic position (TP ≥ 3.5). Community fluctuations followed a symmetric Laplace distribution for both groups (MGG test; p > 0.1). The variance of the whole community fluctuation was significantly smaller for the high trophic position group ($\sigma^2 = 2.86$) than the low trophic position group ($\sigma^2 = 4.12$; Fig. 3). This result was expected since trophic position and body size are correlated, which implies that larger species tend to show reduced fluctuations, as reported previously (Segura et al. 2017). However, the average of the community fluctuations tended to depart from zero towards negative values for high trophic position species, which implies a net reduction in the abundance of large-sized species (Fig. 3).

4. DISCUSSION

Theoretical predictions of fish fluctuations from macroscopic scaling laws agreed well with the observations. The results suggest that fishing exploitation harvests species that are relatively more abundant, and therefore have larger variability. Most fish fluctuation patterns are similar to those found previously for the CalCOFI ichthyoplankton larval assemblages (Anderson et al. 2008), suggesting that these patterns are general and independent of the life stage being evaluated (e.g. larvae, juveniles, adults). This macroscopic perspective reveals the effect of the relatively large variability observed in exploited fish populations due to their inherently higher abundances. However, fish species with larger body sizes tended towards negative average community fluctuations in population density, which may be a symptom of over-exploitation.

Detailed and more complex models to analyze fish fluctuations rely on the availability of population parameters (e.g. growth rate, spawning rate) or the density of larval stages (Botsford et al. 2014). However, in most fisheries worldwide, such detailed knowledge about exploited populations is lacking, especially in tropical areas and the Southern Hemisphere (Wiff et al. 2018). Therefore, the community-level patterns used here (SDR, TL, VMA) provide a simple and straightforward way to analyze fluctuations in fish density in cases where knowledge of the species’ biological and population attributes is fragmentary.

Results generated under an extensive modeling approach, using a stage-specific model whose parameters were derived from metabolic size-dependent scaling (Cohen et al. 2012a), agreed with our empirical findings based on SDR, TL, and VMA relationships in exploited fish populations. Therefore, the results of the macroscopic theory should be considered as the first empirical confirmation for the exploited populations described by Cohen et al. (2012a). Regarding unexploited populations, the VMA was re-
cently confirmed in different aquatic species (Lagru et al. 2015) and in a spatial version for felids (Anile & Devilllard 2020). Therefore, our results contribute to the establishment of a general framework to study fluctuations in animal populations, regardless of their exploitation status. Our approach calls for an integrated evaluation of the effect of harvesting on the whole community, from which specific residual deviations might be evaluated (Jennings & Mackinson 2003, Rochet & Benoit 2012).

From a theoretical standpoint, fluctuations in fish populations should be mostly determined by population renewal and variations in cohort-specific mortality. Population renewal, usually treated as a stock–recruitment relationship in fish populations, is determined by density-dependent and density-independent processes. Fishing exploitation affects the density-dependent component of the renewal process by selecting older and larger individuals, producing changes in the population structure (known as the age truncation effect) (Zhou et al. 2010). The reduction of age classes as a consequence of fishing exploitation has been associated with recruitment fluctuations (Marteinsdottir & Thrarinsson 1998, Anderson et al. 2008) and variation in the spawning intensity and spawning period in relation to individual body size (Kjesbu et al. 1996). On the other hand, fish are also affected by a density-independent component which contributes to the variation in fish populations (Bakun 1996) as has been mostly observed in small pelagic fishes. This group is usually represented by few age classes showing a large variability in abundance that is highly driven by density-independent components (e.g. river discharge, El Niño–Southern Oscillation, upwelling) that determine survival in early stages and affect egg quality in future generations (Cury & Roy 1989). Our macroscopic approach, without the need for specific details, was able to integrate and reproduce the patterns generated by density-dependent and density-independent mechanisms along a continuous gradient, from the smallest to the largest organisms in the food web. Testing this framework in multiple ecosystems with different characteristics would allow researchers to evaluate the generality of our results.

Modern fisheries management is based on projecting abundances under different management strategies defined by biological reference points or thresholds for sustainable exploitation. On these projections, the variability in abundance is key to assess the accuracy and associated risk of implementing a management strategy. Variability in abundance is usually incorporated by adding a coefficient of variation in the stock–recruitment relationship (e.g. Canales et al. 2020, van Deurs et al. 2021) or by projecting stochastic recruitment time series under different climatic regimes (e.g. Szuwalski & Punt 2013). In this context, the proposed macroscopic approach can serve as a rapid method to assess population variability based only on body size, which can help to propose quantitative guidelines for benchmark scenarios when projecting population abundances for managing exploited populations. Ignoring population variability may produce inaccurate and biased recommendations for management purposes (van Deurs et al. 2021), resulting in over- or under-exploitation of a given fish stock. The acknowledgment of all sources of uncertainty, including intrinsic sources of population variability in abundance projections, will aid decision-makers in assessing the risk of implementing a management strategy in the context of sustainable exploitation.

It should be emphasized that the proposed macroscopic approach is not expected to work for species that are rare but generate high economic profit (e.g. invertebrates and shellfish; Sethi et al. 2010). For some of these species (e.g. oysters), their natural abundance is low due to their body size; thus even moderate exploitation efforts driven by high profits could lead to extinction (Sethi et al. 2010). The focus on economic profit of the industrial fisheries requires extracting large amounts of biomass, which is possible by targeting fish species that are relatively more abundant at a given body size. The fact that large-sized high trophic position species tended towards more negative community fluctuations suggests a pronounced effect of this fishing strategy in this size class. The higher vulnerability of low-abundance, high-trophic position organisms and their prevalent role in ecosystem dynamics suggest that large-scale fishery exploitation could further erode the stability of aquatic ecosystems.

Data accessibility. Data are available upon request from the National Institute for Fisheries Research and Development, INIDEP, Argentina (www.inidep.edu.ar/).

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