



Overfishing of marine resources: some lessons from the assessment of demersal stocks off Mauritania

B. Meissa^{1,2} and D. Gascuel^{2*}

¹Institut Mauritanien de Recherches Océanographiques et des Pêches (IMROP), BP: 22, Nouadhibou, Mauritania

²Université Européenne de Bretagne, Agrocampus Ouest, UMR985 Ecologie et santé des écosystèmes, 65 rue de Saint Brieuc, CS 84215, 35042 Rennes cedex, France

*Corresponding author: e-mail: didier.gascuel@agrocampus-ouest.fr

Meissa, B., and Gascuel, D. Overfishing of marine resources: some lessons from the assessment of demersal stocks off Mauritania.

– ICES Journal of Marine Science, doi: 10.1093/icesjms/fsu144.

Received 29 April 2014; revised 28 July 2014; accepted 31 July 2014.

The recent, rapid development of fishing in Mauritania offers a good case study for a comparative approach of the resilience of the species exploited there, in the face of increasing fishing pressure. First, we assessed the health of 22 demersal stocks with differing ecological requirements, demographic strategies, and states of exploitation. A dynamic production model was fitted in a framework of Bayesian statistics to abundance indices estimated from scientific trawl surveys or commercial catch per unit efforts. We show that 12 of the 22 stocks assessed are overexploited and 3 are fully exploited. The combined assessment of all 22 stocks demonstrates an overall overexploitation, with total demersal biomass decreasing by ~75% since 1982 and fishing effort 30% higher than that at maximum sustained yield (40% higher for finfish). Second, relations between states of stocks and life history traits were analysed. The stocks of large and vulnerable species currently undergo the highest fishing pressure and are those that are the most overexploited. At the scale of the community represented by the stocks considered, surveys-based indicators of the mean intrinsic vulnerability, the mean maximum length, and the mean trophic level exhibit a significant decrease from 1990 to 2010. Changes observed in catch-based indicators depend on fishing strategies and are impacted by the recent development of the small-scale fishery. But indicators expressed as a function of a multiplier of fishing effort or fishing mortality clearly decrease, thus confirming that the intensification of exploitation leads to communities dominated by smaller species and lower trophic levels. We conclude that large and high trophic level species, such as white grouper, meagre, guitarfish, and smooth-hound, are markers of ecosystem health and should be considered as sentinel species.

Keywords: Bayesian approach, ecosystem health, ecosystem indicators, fisheries management, fishing down the marine foodweb, sentinel species, surplus production model, Western Africa.

Introduction

The resilience of exploited marine species especially depends on their intrinsic capacity to react to increasing fishing pressures. In general, large slow-growing species with a later age at maturity are more vulnerable to fishing, exhibiting a larger decrease in abundance for a given fishing pressure (Gislason, 2003; Reynolds *et al.*, 2005). Many empirical studies using abundance data of exploited fish populations have shown a significant correlation between the rate of decline and life history traits (Jennings *et al.*, 1998; Dulvy *et al.*, 2004; Reynolds *et al.*, 2005). Thus, lacking the data necessary to apply conventional methods for estimating stock size of most species of exploited fish, researchers have used biological and ecological life history traits to indirectly measure the potential impact

of fishing on marine resources and identify the most vulnerable species (Jennings *et al.*, 1998; Cheung *et al.*, 2005, 2007). In particular, Cheung *et al.* (2005) define an index of the intrinsic extinction vulnerability of marine species to fishing. This index is estimated from life history traits and ecological characteristics of these species. Most studies in this domain use comparative approaches and meta-analyses that aim to identify the main eco-biological factors that determine the vulnerability of exploited stocks to fishing (Myers and Mertz, 1998). Using hierarchical Bayesian models, Zhou *et al.* (2012) identified natural mortality as the parameter with the highest impact on the biological reference points used to manage fishing. Jennings *et al.* (1998) revealed a significant relation between the maximum length of species and their abundance

by considering phylogenetic relationships between stocks, even if length is strongly influenced by fishing (Daan *et al.*, 2005).

Based on commercial catches, Pauly *et al.* (1998) revealed changes in the trophic structures of fish communities caused by fishing; they attribute this phenomena of “fishing down the marine food web” to a higher vulnerability of high trophic levels. The role of trophic levels in the resilience of exploited marine populations has since become the subject of many debates. The use of the mean trophic level of catches as an indicator of exploitation, in particular, has been questioned by several studies (Caddy *et al.*, 1998; Rochet and Trenkel, 2003; Branch *et al.*, 2010). Essington *et al.* (2006) show that changes in fishing strategy may explain the decrease in the mean trophic level of catches without observing an equivalent decrease in the ecosystem itself; this is called “fishing through the marine food web”. More generally, Branch *et al.* (2010) disagree that these changes occur globally, thus questioning whether species of high trophic level are the most vulnerable. Many studies based on data from scientific surveys, however, have shown that changes in trophic structure affect not only catches but also the underlying ecosystem, thus confirming the existence of “fishing down the marine food web”. In Western Africa, a significant decrease in the biomass of high trophic levels and a relative increase in low trophic levels have been observed off the coasts of Senegal and Guinea (Laurans *et al.*, 2004) and Mauritania (Gascuel *et al.*, 2007a).

Western Africa, particularly Mauritania, is a good case study for studying the impact of fishing on resources and ecosystems, identifying factors influencing species resilience, and analysing larger ecosystem changes such as “fishing down the marine food web”. This region is experiencing rapid development of fishing. In Mauritania, the main fishing resources, notably coastal demersal fish, were little exploited until the end of the 1960s (Josse and García, 1986; Garibaldi and Grainger, 2004; Gascuel *et al.*, 2007b). Fishing effort has greatly increased during the last few decades (Chavance, 2004), which has led to a severe decrease in biomass and serious signs of overexploitation of demersal resources (Christensen *et al.*, 2004; Gascuel *et al.*, 2007a; Meissa *et al.*, 2013). There is thus a strong contrast in the series of data available. Naturally, not all species are affected in the same way or have the same response to increasing fishing pressure (Labrosse *et al.*, 2010), and thus, there is a contrast among species. However, the situation of most stocks remains poorly known, stock assessments until now having focused only on small pelagic species and a small number of demersal species from targeted catches. From this viewpoint, identifying the most vulnerable species, based on their life history traits, is a key step to improve fisheries management.

This study thus aims to quantify the impact of fishing on the demersal resources of Mauritania and analyse the factors that influence the resilience of stocks to fishing effects, via a comparative-ecology approach applied to 22 taxa. Our objectives are: (i) to establish the very first diagnosis of the health of demersal resources in Mauritania, (ii) to identify sentinel species which should be considered in priority for fisheries management, due to their intrinsic vulnerability, and (iii) to characterize the fishing impact not only at the stock level but also at the scale of the demersal community. First, the response of the stocks to fishing pressure was analysed. Using delta-generalized linear model (GLM), abundance indices were estimated from scientific trawl surveys performed on the Mauritanian continental shelf since 1982. A dynamic production model was fitted to these data in a Bayesian statistics framework; it reveals the impact of fishing of stock abundance. Second, we

sought to identify the factors that explain the variability in resilience of stocks. The parameters of the response function of the stocks to the increasing fishing pressure were thus compared with eco-biological parameters using multivariate analyses and statistical tests of relations between indicators of stock state and eco-biological parameters (demographics, intrinsic vulnerability index, trophic level, habitat, etc.). Finally, changes induced by fishing at the scale of the demersal community were investigated using ecosystem indicators.

Material and methods

Species selection and data used

The species were selected according to two criteria: their commercial importance and the availability of reliable information about their abundance and catches, in particular their taxonomic identification. The choice of species was then refined to cover as much as possible the large diversity of their demographic strategies and eco-biological characteristics. For three genera, determination down to species level is uncertain in catch data, but survey data show that one species is dominating the genus. Thus, assessments were performed at the genus level. These three were tonguesole (*Cynoglossus* spp., dominated by *Cynoglossus canariensis* and also including *Cynoglossus senegalensis*), croakers (dominated by *Pseudotolithus senegalensis* and also including *Pseudotolithus typus*), and sea catfish (dominated by *Carlarius heudolotii* and also including *Arius* spp. such as *Arius parkii*). In all, 22 demersal taxa were selected, which represent ~60% of the demersal catches currently made in Mauritania. Fitting population's models to data related to genus, and not to species, may be controversial. Thus, sensitivity analyses of the overall diagnosis were also conducted, excluding the tree taxa defined at the genus level.

Three databases managed by the Mauritanian Institute of Oceanographic and Fisheries Research (IMROP) were used:

- (i) All scientific demersal surveys performed along the Mauritanian continental shelf from 1982 to 2010, totalling 5532 trawls in 65 surveys. Only surveys covering the whole continental shelf, from 5 to 200 m depth, were considered here. Each observation corresponds to one trawl, dragged at a speed of 3.2 nautical knots, for a standard duration of 30 min and with a 40 mm mesh-size in the cod and a 17 m horizontal opening on average. Since fishing gear was modified in 1989, correction coefficients estimated by Gascuel *et al.* (2007a) were applied to data gathered before that date.
- (ii) Logbooks of national and foreign industrial fishing since 1990, which provide catch data aggregated by commercial categories. These data were disaggregated into species using profiles of species composition by license type estimated from data from the fisheries observation programme (see details on the sampling scheme and methods in Labrosse *et al.*, 2010 and Meissa *et al.*, 2013).
- (iii) A small-scale fishing database covering 1994–2010. Catches from 1990 to 1993 were estimated from the number of pirogues per year and the mean catch per pirogue from 1994 to 1996 (Gascuel *et al.*, 2007b). Given the small number of pirogues during this period, related catches are relatively low.

Catches before 1990 are available in the scientific literature for two species: octopus (*Octopus vulgaris*) since 1982 and white grouper (*Epinephelus aeneus*) since 1985.

Abundance index

Annual abundance indices were estimated over the 1982–2010 period, by linear modelling of scientific survey data for all taxa regularly fished during these surveys. Due to the large number of null values in surveys data (ca. 40–90%), a delta-GLM zero-inflated model was used (Stefansson, 1996; Meissa *et al.*, 2008, 2013). This delta-GLM model combines the following two submodels:

1. A presence–absence submodel, which estimates the probability that each taxon will be present during each trawl. The GLM based on assuming a binomial distribution is expressed as follows:

$$\begin{aligned} z_{t,j,k,l} &= \text{logit}(p_{t,j,k,l}) \\ \text{with } z_{t,j,k,l} &= \mu_0 + \varphi_t + \beta_j + \pi_l, \end{aligned} \quad (1)$$

where $p_{t,j,k,l}$ is the expected probability of presence for year t , region j (north, central, and south), bathymetric strata k (0–30, 30–80, 80–200, and 200–400 m), and season l (cold: January–May, hot: August–October, and the two inter-seasons); ϕ_t , β_j , and π_l are the related statistical effects and μ_0 is the constant of the model.

The prediction of the probability of presence was obtained via inverse transformation of the natural logit function:

$$\hat{p}_{t,j,k,l} = \frac{e^{\hat{z}_{t,j,k,l}}}{1 + e^{\hat{z}_{t,j,k,l}}}. \quad (2)$$

2. A linear submodel on log-transformed data, to analyse non-null values (i.e. non null densities per trawls). This model accounts for the factors year, region, bathymetric strata, and season, predicting the related non-null density $\hat{D}_{t,j,k,l}$.

Annual abundance indices (A_t) were calculated by averaging the product of the probability of species presence and the predicted density for non-null observations:

$$A_t = \text{Mean}_{j,k,l}(\hat{p}_{t,j,k,l} \times \hat{D}_{t,j,k,l}). \quad (3)$$

This index was then smoothed using second-order local polynomial regression to decrease the interannual variability due to sampling effects (Cleveland, 1979). All calculations were performed using the R platform (R development Core Team, 2008).

For six species for which the demersal trawl used during scientific surveys is not adapted, abundance indices were derived from commercial fishing data. In that case, a linear model accounting for the factors year, season, and region was fitted to catch per unit effort (cpue), using cpue of the small-scale fishery targeting fish in the Banc d'Arguin zone for meagre (*Argyrosomus regius*) and for two species of mullet (*Mugil capurrii* and *Mugil cephalus*) (data available since 1995), and cpue of the industrial shrimp and cephalopod fishery for two shrimp species (*Parapenaeus longirostris* and *Farfantepaeus notialis*) and European squid (*Loligo vulgaris*). According to previous sensitivity analyses (Gascuel and Menard, 1997; Meissa *et al.*, 2013), commercial cpue were preliminarily corrected assuming that the mean fishing power of vessels is increasing by 3% per year. This increase is linked to the modernization of the Mauritanian fleets throughout the years, especially associated with the construction of aluminium pirogues and with the increase in

engines power, for both the artisanal and industrial fisheries (Labrosse *et al.*, 2010). A sensitivity analysis was also conducted, excluding these six species from the global analysis of the status of the Mauritanian demersal resources.

Stock-assessment model

Stock assessments were performed by adjusting a biomass-production model (Fox, 1970) in a Bayesian framework. The Bayesian stochastic process calculates the biomass of year $t + 1$ from that of year t , with a process error around the biomass-production function estimated as:

$$B_{t+1} = (B_t + g(B_t) - Y_t) \times e^{\varepsilon_t}, \quad (4)$$

where Y_t is the catch observed in year t , e^{ε_t} the multiplicative log-normal process error, with $\varepsilon_t \sim N(0, s_p^2)$, and $g(B_t)$ the biological production function of the stock. Note that implicitly Equation (4), which was commonly used in several papers (e.g. McAllister and Kirkwood, 1998; Ono *et al.*, 2012), implies that observation errors associated with catches are assumed to be negligible compared with the process error.

According to preliminary analyses (see Meissa *et al.*, 2013), the production function $g(B_t)$ was assumed to follow the model of Fox:

$$g(B_t) = r \times B_t \times \left(1 - \frac{\ln(B_t)}{\ln(K)}\right), \quad (5)$$

where r is the intrinsic growth rate of the stock (expressed in year⁻¹) and K its carrying capacity.

The observations (abundance indices) are related to the biomass by considering a lognormal observation uncertainty:

$$A_t = q \times B_t \times e^{\varepsilon'_t}, \quad (6)$$

where q is the catchability and $e^{\varepsilon'_t}$ the observation error, with $\varepsilon'_t \sim N(0, s_o^2)$.

To ensure that all parameters can be estimated, further hypotheses were formulated. First, the ratio of the process to observation error variances needs to be specified. There are no data which could be used to set the baseline values for the extent of observation and process error, but previous works showed that inferences in state–space models are seldom sensitive to the value used for this ratio, unless it strongly favours observation or process error (Kimura *et al.*, 1996; Schnute and Kronlund, 2002; Punt, 2003). Therefore, in the absence of any particular information, a ratio equal to 1 was used as a default choice (i.e. $s_p^2 = s_o^2 = s^2$).

Second, in the framework of Bayesian adjustment, constraints on parameter values of the Fox model were introduced as prior probabilities. In agreement with preliminary sensitivity tests and results obtained by Meissa *et al.* (2013), a constraint was placed on initial biomass B_0 (for the first year of the series) by assuming that the prior of the ratio B_0/K had a weakly informative normal distribution between 0 and 1, centred on 0.5. Such a value is consistent with the fact that industrial demersal fisheries developed since the 1960s, with large catch over the 1970s (Josse and Garcia, 1986; Gascuel *et al.*, 2007b). An informative lognormal prior distribution was assumed for r , while the other parameters (K , q , and σ^2) were assumed to have uniform prior distributions with large bounds (i.e. weakly informative priors). The mean values of the prior distribution of r (Table 1) were estimated with the interactive calculation tool in FishBase (www.fishbase.org; Froese and Pauly, 2012). This

Table 1. Taxa analysed and their eco-biological parameters.

No.	Scientific name	Common name	TL	K_{vb}	L_{max}	L_{inf}	Q/B	P/B	T_m	T_{max}	r	M	W_{inf}	V
1	<i>Epinephelus aeneus</i>	White grouper	4.0	0.23	120.0	100.0	4.0	0.6	3.9	19.3	0.40	0.25	25.00	52
2	<i>Dicentrarchus punctatus</i>	Spotted sea bass	3.9	0.16	70.0	40.0	3.3	0.6	4.1	19.1	0.44	0.27	15.12	43
3	<i>Psettodes belcheri</i>	Spottail spiny turbot	4.1	0.29	80.0	83.0	4.3	0.6	2.2	9.9	0.76	0.46	5.64	44
4	<i>Cynoglossus</i> spp.	Tonguesole	3.6	0.25	62.0	64.0	11.6	0.7	3.5	15.5	0.86	0.44	2.42	45
5	<i>Dentex canariensis</i>	Canary dentex	3.6	0.15	74.0	85.0	8.3	0.7	2.2	19.1	0.46	0.28	13.70	60
6	<i>Plectorhinchus mediterraneus</i>	Rubberlip grunt	3.5	0.18	80.0	63.7	10.6	0.8	3.6	15.9	0.56	0.34	4.12	54
7	<i>Arius</i> spp.	Sea catfish	4.0	0.16	79.0	64.9	11.6	0.6	4.6	18.0	0.51	0.31	1.98	54
8	<i>Pseudotolithus</i> spp.	Croaker	3.8	0.26	114.0	60.3	9.0	0.7	2.8	11.0	0.76	0.46	5.31	40
9	<i>Pagellus bellottii</i>	Red pandora	3.6	0.24	42.0	37.1	7.0	0.7	2.9	11.8	0.80	0.49	0.96	49
10	<i>Pagrus caeruleostictus</i>	Bluespotted sea bream	3.8	0.24	90.0	41.2	6.4	0.7	2.9	11.9	0.76	0.47	1.64	47
11	<i>Pseudupeneus prayensis</i>	Goatfish or red mullet	3.2	0.53	55.0	31.7	8.0	0.9	1.4	5.4	1.48	0.91	0.58	30
12	<i>Umbrina canariensis</i>	Canary drum	3.4	0.26	80.0	57.2	3.5	0.8	2.6	11.0	0.76	0.46	2.40	44
13	<i>Argyrosomus regius</i>	Meagre	4.3	0.09	230.0	210.0	2.4	0.5	6.2	32.2	0.24	0.15	39.40	79
14	<i>Mugil capurrii</i>	Leaping African mullet	2.0	0.34	74.0	70.3	12.3	2.0	3.6	8.5	0.88	0.54	1.13	52
15	<i>Mugil cephalus</i>	Flathead mullet	2.1	0.39	100.0	74.0	12.3	1.9	3.0	7.4	0.94	0.59	2.05	42
16	<i>Mustelus mustelus</i>	Smooth-hound	3.8	0.09	200.0	175.0	2.9	0.7	7.1	36.2	0.26	0.16	24.30	74
17	<i>Rhinobatos rhinobatos</i>	Guitarfish	4.1	0.15	147.0	149.0	3.0	0.6	3.9	19.3	0.38	0.23	10.48	75
18	<i>Octopus vulgaris</i>	Common octopus	3.6	0.72	40.0	30.0	4.7	1.4	0.8	1.5	1.90	1.20	10.00	78
19	<i>Loligo vulgaris</i>	European squid	4.1	0.89	82.0	78.1	4.0	1.2	0.8	1.5	2.11	1.20	1.50	19
20	<i>Sepia officinalis</i>	Common cuttlefish	3.6	0.74	30.0	28.6	4.0	1.2	0.8	1.5	1.96	1.20	2.00	30
21	<i>Parapenaeus longirostris</i>	Deep-water rose shrimp	2.3	0.83	3.9	3.7	12.0	2.4	0.4	3.0	3.78	1.80	0.06	10
22	<i>Farfantepenaeus notialis</i>	Pink shrimp	2.3	1.60	4.9	4.0	12.0	2.4	0.5	1.6	4.00	1.60	0.08	10

Trophic level TL, von Bertalanffy growth coefficient K_{vb} (in year⁻¹), maximum length L_{max} (cm), asymptotic length L_{inf} (cm), consumption rate Q/B, productivity rate P/B, age of first maturity T_m (year), maximum age T_{max} (year), intrinsic growth rate r (prior value), natural mortality M (year⁻¹), asymptotic weight W_{inf} (kg), vulnerability index V (lengths for cephalopods and crustaceans are those of their mantles and carapaces, respectively).

calculation was based on the empirical equation of Ricker (1975) expressing r as a function of F_{msy} ($r = 2 \cdot F_{msy}$), the latter predicted by a model of relative yield-per-recruit by Beverton and Holt (1957) based on the growth parameters.

The curve of equilibrium catch corresponding to the parameters of the dynamic model was drawn from the joint posterior distribution of its r and K parameters (for more details, see Ono *et al.*, 2012, and Meissa *et al.*, 2013). The parameters for fishing mortality are calculated a posteriori:

- (i) fishing mortality at the current fishing level: $F_{cur} = Ye_{cur}/Be_{cur}$,
- (ii) fishing mortality at MSY: $F_{msy} = MSY/B_{msy}$,

where Ye and Be are catch and biomass at equilibrium, respectively.

Bayesian posterior distributions of all model parameters and unknown variables (e.g. biomass time-series) were approximated via Monte-Carlo Markov-Chain (MCMC) methods using the open-source OpenBUGS[®] software (Thomas *et al.*, 2006). Three independent MCMC chains with dispersed initialization points were used. The first 100 000 iterations of each chain were discarded. After this “burn-in” period, inferences were derived from a sample of $3 \times 400\,000$ iterations. One out of ten iterations was kept to reduce MCMC sampling autocorrelation. To check convergence of MCMC sampling, the Gelman–Rubin test was applied to all posterior sampling (R ratio 1.05 for all variables), as implemented in the Coda package of R (Brooks and Gelman, 1998). Goodness-of-fit was assessed using the coefficient of determination R^2 between predicted and observed biomass. The R code used is provided in Supplementary data.

Exploitation indicators and eco-biological life history parameters

Many exploitation indicators, derived from estimates of abundance indices and results of exploited-stock assessments, were considered:

the slope of abundance over time (Slope, in percentage of interannual variation), obtained by adjusting an exponential model to the series of abundance intervals available; the parameters q , B_0/K , r , and K of the biomass-production model (median posterior estimates); fishing mortality at MSY (F_{msy}); current fishing mortality (F_{cur}); multiplier of fishing effort for any year t ($mE_t = F_t/F_{ref}$), with a value set to 1 for the mean effort of the last 3 years; a multiplier of fishing effort at MSY ($mE_{msy} = F_{msy}/F_{ref}$); the ratio of current biomass observed to that at the beginning of the study period (B_{cur}/B_{start}); and the current level of stock depletion, equal to the ratio of current biomass at equilibrium to that of virgin biomass (i.e. without fishing mortality; Be_{cur}/K). In addition, taxa were classified by fishing effort at MSY (mE_{msy}), defining stocks that were overexploited ($mE_{msy} \leq 0.9$), fully exploited ($0.9 < mE_{msy} < 1.1$), or underexploited ($mE_{msy} \geq 1.1$).

Also, 12 life history traits were selected: the von Bertalanffy growth coefficient (K_{vb}), asymptotic length (L_{inf}), maximum length (L_{max}), maximum age (T_{max}), age at first maturity (T_m), trophic level (TL), intrinsic growth rate (r , estimated with the method presented above), natural mortality (M), consumption rate (Q/B), production rate (P/B), asymptotic weight (W_{inf}), and the intrinsic vulnerability to fishing (V) of Cheung *et al.* (2005). The latter was extracted from the FishBase and SeaLifeBase databases; it comes from a classification algorithm based on fuzzy set theory that combines several ecological characteristics and life history traits of species to estimate their vulnerability to extinction between 0 (no extinction risk) and 100 (certain extinction). The production rate was calculated for fish from empirical equations of Gascuel *et al.* (2008) [$P/B = 2.31 \cdot TL^{-1.71} \cdot \exp(0.053\theta)$, with θ the mean water temperature = 20°C]. Other parameters used in this study (Table 1) came from the Mauritanian zone when they were available (biological database of IMROP and Ecopath model from Guénette *et al.*, 2014). Otherwise, information came from adjacent zones (Northwest African subregion). Values from FishBase

or SeaLifeBase were used as a last resort in the absence of estimates from the subregion.

Comparative analysis of resilience factors

Principal component analysis (PCA) was used to study relations between exploitation indicators and parameters representing life history traits. Two R packages were used (Factominer and ade4, available at <http://factominer.free.fr/> and <http://pbil.univ-lyon1.fr/ade4/>, respectively). In a first PCA (called “stock PCA”), exploitation indicators were considered as covariables (used to estimate factorial axes), while life history traits were considered as supplementary variables. Reciprocally, life history traits were used as covariables and exploitation indicators as supplementary variables, in a second analysis (called “ecology PCA”). Variables were normalized so that the analysis would give the same weight to all individuals and variables.

Given the PCA results, three indicators of life history traits (the vulnerability index V , maximum length L_{\max} , and trophic level TL) were targeted for specific analyses:

- (i) Calculation of correlations between indicators and the three main exploitation parameters: mortality at MSY F_{msy} (defining a potential of exploitation intensity), the effort multiplier mE_{msy} (indicating the current state of over- or underexploitation), and the current level of stock depletion Be_{cur}/K .
- (ii) Calculation of ecosystem indicators of the mean vulnerability index (MV), the mean maximum length (MML), and the mean trophic level (MTL) within catches and within the ecosystem (represented by the biomass of the 22 taxa) and analysis of their change from 1990 to 2010.
- (iii) Use predictions of the surplus production models to express these indicators (MV, MML, and MTL) either as a function of the fishing effort multiplier (i.e. compared with the current effort) or as a function of fishing mortality (i.e. for the same fishing pressure applied to all stocks).

To investigate how the list of taxa included in the calculation may affect ecosystem indicators, sensitivity analyses were conducted using Jackknife test (Quenouille, 1949), where indicators are recalculated excluding taxa one after the other. Results are included in Supplementary data and briefly summarized hereafter.

Results

Stock abundance and assessment

The delta-GLM model provided a significant fit to data from scientific surveys, revealing changes in abundance during the 1982–2010 period. When cpue data were also considered, abundance of 15 of the 22 taxa decreased over time (Figure 1). The mean decrease over the study period exceeded 5% per year for seven taxa: flathead mullet (−13.0%), meagre (−10.8%), spottail spiny turbot (*Psettodes belcheri*, −10.0%), canary drum (*Umbrina canariensis*, −8.3%), European squid (−8.3%), white grouper (−7.2%), and octopus (−5.5%). The decrease was also strong, especially at the beginning of the period, for the sharks and rays (*Mustelus mustelus* and *Rhinobatos rhinobatos*). No significant increase in abundance was observed, and the other stocks showed fluctuating or relatively stable abundances during the period. For a few species, particularly cephalopods, an increase in biomass was observed from 2005 to 2010.

From 1982 to 2010, catches of the 22 taxa fluctuated without a noticeable trend between 50 and 90 000 t year^{−1} (Figure 2a). Total

demersal biomass decreased from an extrapolated 1.1 million t in 1982 to 280 000 t in 2005, a decrease of ~75% (Figure 2b). For the 16 taxa whose abundance is estimated from surveys, the decrease over the 1982–2005 period reached 78%. Since 2005, total biomass stabilized, reaching 320 000 t in 2010. The mean exploitation rate (Y/B) changed from just over 6% in 1982 to nearly 20% in recent years; that is, a threefold increase in overall fishing pressure on these 22 taxa.

The biomass-production model fit well abundance indices estimated from scientific surveys and commercial cpue, with coefficients of determination from 52 to 96% (Table 2). In addition, the model satisfactorily represented the functional relation between stock abundance and fishing effort, following the decreasing exponential curve of a Fox model for 19 of the 22 taxa (Supplementary Figure S1). In such cases, correlations between observed values and values predicted at equilibrium are significant (Table 2). In contrast, for three species (rubberlip grunt, croaker, and leaping African mullet) whose abundance varied little during the period, the lack of contrast in the data led to low-confidence fits.

According to the value of the multiplier of fishing effort at MSY (mE_{msy}), among the 22 taxa, 12 (55%) were overexploited, 3 (14%) were fully exploited, and 7 (32%) were underexploited in 2010 (Table 2; Supplementary Figure S2). The taxa overexploited by fishing were those whose abundance decreased the most during the period (in decreasing order of magnitude: *Umbrina canariensis*, *E. aeneus*, *Pseudotolithus* spp., *M. mustelus*, *Argyrosomus regius*, *Mugil cephalus*, *L. vulgaris*, *Pagelus bellottii*, *O. vulgaris*, *P. belcheri*, *Dentex canariensis*, and *Pagrus caeruleostictus*). In comparison, the abundance of fully exploited species fluctuated during the period (*Arius* spp., *R. rhinobatos*, and *Sepia officinalis*). Among the underexploited species were the two shrimp species (*Farfantepenaeus notialis* and *P. longirostris*) and the fish whose abundance did not significantly decrease in the scientific-survey data (*Plectorhinchus mediterraneus*, *Dicentrarchus punctatus*, *Pseudupeneus prayensis*, *Cynoglossus* spp., and *M. capurrii*).

Combined assessment of the 22 taxa indicates overall overexploitation of demersal stocks, with current fishing effort that exceeds that at MSY by around 30% (Figure 2c). For all taxa together, the MSY was estimated at 72 000 t, while the catch at equilibrium corresponding to current effort is 69 300 t (i.e. a loss of 4% of total catch). For fish alone, the excess effort is >40%, with an overall fishing effort at MSY (mE_{msy}) estimated at 0.59 and a catch loss of 12% (24 000 and 27 000 t for combined catch and combined MSY, respectively). Also, the mean total catch over the last 3 years was 66 000 t, close to the equilibrium value. Finally, the models indicated that equilibrium biomasses corresponding to the current effort represent 25% of virgin biomass for all 22 taxa (Figure 2d) and <20% for fish alone, with values varying from 11 to 78% among taxa (Table 2).

In addition, global results on the state of the Mauritanian demersal resources appeared little sensitive to methodological choices related to the selection of taxa. Excluding either the three stocks assessed at the genus level or the six stocks whose abundance was estimated based on commercial cpue does not modify the diagnosis of overexploitation (with excess in fishing effort compared with the F_{msy} target equal to 31 and 26%, and biomass depletion equal to 76 and 72%, respectively; Supplementary Table S1).

Stock state and resilience factors

Whether for “stock PCA” (with exploitation indicators as covariables) or “ecology PCA” (with life history traits as covariables);

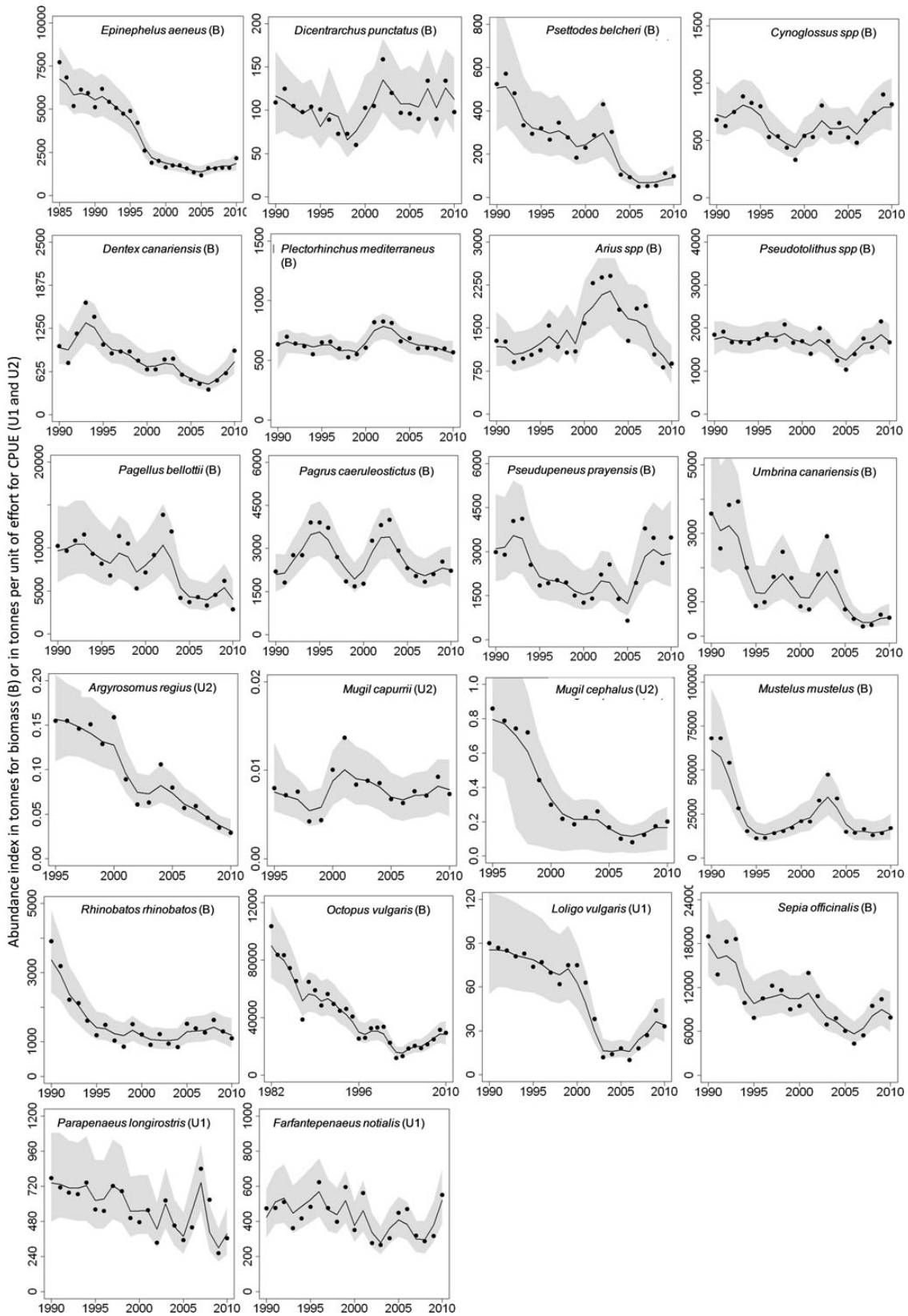


Figure 1. Fit of abundance indices of the biomass-production model of Fox (1970) in a Bayesian statistics framework for the 22 taxa (time-series B refer to abundance indices from trawl surveys; time-series U1 and U2 refer to cpue from industrial and artisanal fisheries, respectively).

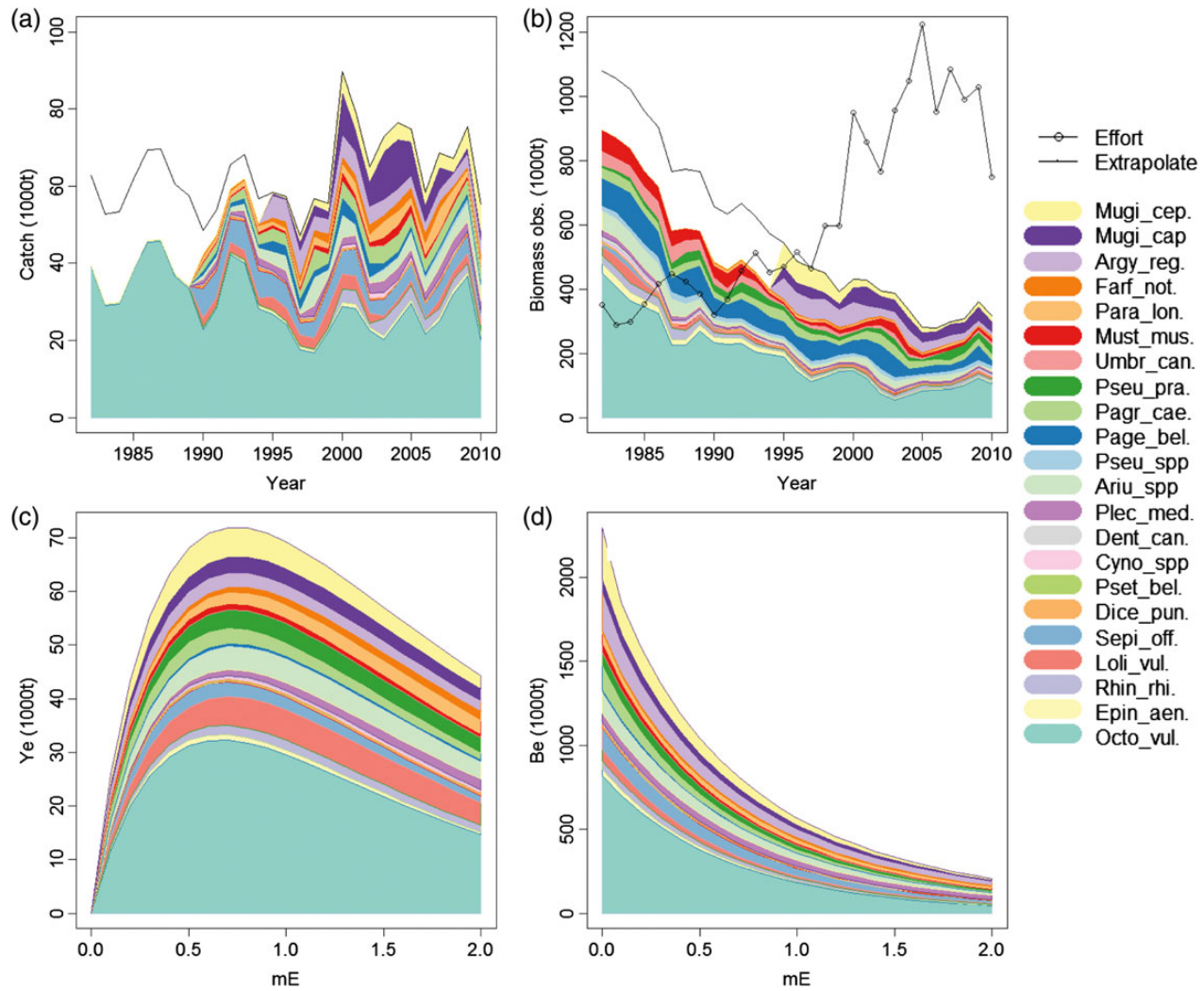


Figure 2. Combined assessment of 22 taxa: (a) catch, (b) biomass and total fishing effort, (c) production at equilibrium, and (d) biomass at equilibrium (Note that for some taxa, catch and biomass have been extrapolated over the starting period (assuming constant values), for graphical representation. These extrapolated data are not used in the fit of the surplus production model).

Supplementary Figure S3), the first two factorial axes explain ~78% of the total inertia of the data; consequently, only these two axes were kept (Figure 3). In “stock PCA”, the axis 1 is highly correlated with the multiplier of fishing effort at MSY (mE_{msy}), separating over-exploited taxa (negative values on the axis representing low mE_{msy}) from underexploited taxa (positive values). The variable mE_{msy} is correlated with the indicators of biomass depletion Slope, Be_{cur}/K , and B_{cur}/B_{start} , which increasing as fishing impact decreases (underexploited stocks), and mortality at MSY (F_{msy}), which is highest for species able to withstand high fishing pressure and which are currently underexploited. Axis 2 is built from mortality at MSY (F_{msy}) and mortality from current fishing (F_{cur}). The factorial plot of individuals separated the taxa most impacted by fishing from those less impacted (axis 1) and taxa heavily fished from those less targeted (axis 2). Taxa were distributed among all four quadrants of the plot, which indicates different stock states in response to similar fishing pressure. High overexploitation was observed in taxa with high fishing mortality (e.g. European squid) but also in vulnerable taxa with relatively low current mortalities (e.g. canary drum, white grouper, meagre). In contrast, underexploited taxa

were either subject to low current fishing mortality (e.g. tonguesole) or intrinsically more robust, with high F_{msy} (e.g. shrimps).

Axis 2 can thus be interpreted as an axis of taxon sensitivity that is independent of its current state of exploitation. It is correlated with life-history-trait parameters and separates, in particular, taxa with rapid turnover (variables r , M , K_{vb} , and P/B) from taxa with high vulnerability index (V) and high longevity (T_{max} , T_m). In contrast, axis 1 is more directly related to the current level of overexploitation, which seems a characteristic of taxa with large individuals (L_{inf} , L_{max} , W_{inf}) and of high trophic level (TL). The “ecology PCA” confirms this interpretation, with high correlations between F_{msy} and rapid turnover and between trophic level and the current level of stock depletion (Supplementary Figure S3). Four species, the meagre, the white grouper, the smooth-hound, and the guitarfish, can be considered as delicate species, with simultaneously large lengths, high trophic levels, low turn-overs or productivities, and high indices of intrinsic vulnerability.

The exploitation indicators F_{msy} and mE_{msy} are significantly correlated with the eco-biological factors maximum length (L_{max}) and vulnerability index (V ; Figure 4). Logically, large or vulnerable

Table 2. Exploitation indicators calculated from predictions of the stock-assessment model (median posterior estimate).

No.	Scientific name	r. post.	K	B ₀ /K	mE _{msy}	F _{msy}	F _{cur}	B _{cur} /B _{st}	Slope	MSY	B _e _{cur} /K	B _{cur} /K	R ² dyn.	R ² fun.
1	<i>Epinephelus aeneus</i>	0.62	25 320	0.51	0.55	0.07	0.11	0.24	-7.2	1 025	0.16	0.13	0.92	0.93
2	<i>Dicentrarchus punctatus</i>	2.22	14 630	0.69	2.69	0.28	0.10	0.82	-0.2	235	0.78	0.65	0.56	0.31
3	<i>Psettoodes belcheri</i>	0.64	12 040	0.39	0.69	0.06	0.09	0.13	-10.0	341	0.16	0.06	0.85	0.73
4	<i>Cynoglossus</i> spp.	1.16	24 960	0.92	1.55	0.07	0.04	1.05	-0.1	580	0.54	0.98	0.78	0.26
5	<i>Dentex canariensis</i>	0.99	7 400	0.80	0.52	0.11	0.21	0.48	-4.2	364	0.25	0.48	0.94	0.26
6	<i>Plectorhinchus mediterraneus</i>	1.65	12 750	0.50	2.01	0.18	0.09	0.88	0.0	2 302	0.78	0.39	0.78	0.07
7	<i>Arius</i> spp.	1.23	28 130	0.54	1.08	0.12	0.11	0.73	0.8	3 123	0.38	0.39	0.69	0.96
8	<i>Pseudotolithus</i> spp.	0.58	19 540	0.59	0.57	0.08	0.14	0.89	-0.6	476	0.11	0.71	0.66	0.10
9	<i>Pagellus bellottii</i>	1.15	100 200	0.67	0.68	0.10	0.18	0.58	-4.7	3 263	0.19	0.38	0.78	0.24
10	<i>Pagrus caeruleostictus</i>	1.33	63 830	0.21	0.89	0.12	0.13	1.01	-0.8	3 654	0.32	0.21	0.85	0.39
11	<i>Pseudupeneus prayensis</i>	1.06	529	0.59	1.42	0.18	0.13	0.96	-1.2	26	0.40	0.55	0.78	0.30
12	<i>Umbrina canariensis</i>	0.50	43 910	0.59	0.49	0.07	0.14	0.13	-8.3	379	0.12	0.49	0.88	0.46
13	<i>Argyrosomus regius</i>	0.63	332 200	0.57	0.48	0.06	0.13	0.28	-10.8	4 820	0.14	0.18	0.94	0.55
14	<i>Mugil capurrii</i>	1.32	82 040	0.96	1.22	0.13	0.11	1.08	0.3	6 808	0.56	1.34	0.90	0.08
15	<i>Mugil cephalus</i>	1.0	178 500	0.35	0.65	0.09	0.14	0.16	-13.0	4 149	0.21	0.06	0.96	0.90
16	<i>Mustelus mustelus</i>	0.60	50 650	0.79	0.57	0.08	0.14	0.28	-4.0	1 300	0.14	0.25	0.92	0.60
17	<i>Rhinobatos rhinobatos</i>	1.14	37 570	0.85	1.00	0.12	0.12	0.42	-3.8	1 856	0.37	0.21	0.92	0.77
18	<i>Octopus vulgaris</i>	2.05	696 900	0.53	0.69	0.15	0.23	0.34	-5.5	36 750	0.23	0.18	0.92	0.86
19	<i>Loligo vulgaris</i>	2.27	47 120	0.51	0.46	0.21	0.45	0.42	-8.3	3 209	0.19	0.21	0.92	0.42
20	<i>Sepia officinalis</i>	1.45	84 500	0.57	1.02	0.12	0.12	0.43	-4.3	5 777	0.37	0.13	0.75	0.36
21	<i>Parapenaeus longirostris</i>	2.97	32 220	0.63	2.68	0.29	0.10	0.54	-2.7	3 182	0.63	0.33	0.66	0.21
22	<i>Farfantepenaeus notialis</i>	4.05	9 900	0.51	2.56	0.28	0.11	0.76	-1.7	1 796	0.75	0.35	0.52	0.20

Intrinsic growth rate r (posterior estimate in year⁻¹), carrying capacity (in tonnes), ratio of initial biomass B_0/K , fishing effort multiplier at MSY mE_{msy} , fishing mortality at MSY F_{msy} , current fishing mortality F_{cur} , ratio of the current biomass over the starting biomass (i.e. at the beginning of the study period) B_{cur}/B_{st} , slope of the trend in the stock biomass (in % per year), maximum sustainable yield MSY (in tonnes), current biomass at equilibrium over the carrying capacity $B_{e,cur}/K$, current biomass observed over the carrying capacity B_{cur}/K , coefficient of determination for the dynamic biomass-production Fox model fitted to abundance indices R^2_{dyn} (Figure 1), coefficient of determination for the functional relationship between biomass at equilibrium (derived from the Fox model) and the abundance indices R^2_{fun} (see Supplementary Figure S1).

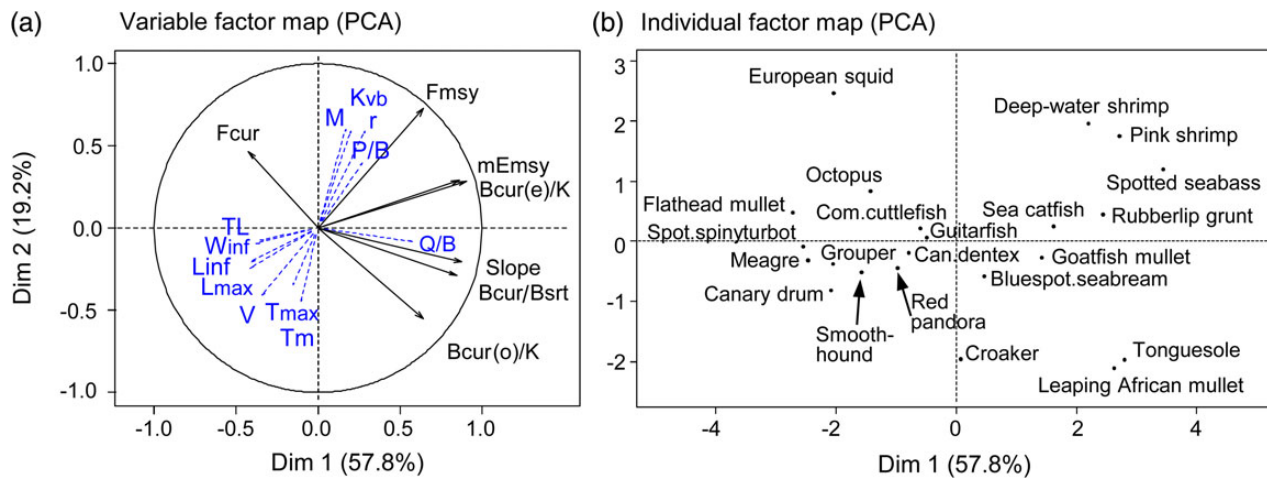


Figure 3. Factorial plots of (a) variables and (b) individuals (taxa) for the “stock” PCA.

taxa have low F_{msy} mortality levels. They are also the taxa the most overexploited at present and consequently those whose biomass has been the most impacted by fishing, compared with virgin biomass. The exploitation indicators, however, are not significantly correlated with trophic level (TL), due to mullet stocks, which have low trophic levels and are overexploited. Without these two species, trophic level is significantly ($p < 0.05$) correlated with the three exploitation indicators. Grouping the stocks by exploitation state (Figure 4, bottom) confirms that the overexploited taxa are on average larger, more vulnerable, and of higher trophic level.

Ecosystem indicators

The mean vulnerability index MV and the mean maximum length MML computed for biomass significantly decreased over the 1990–2010 period (Figure 5a). In particular, the strong decrease observed in the MML indicator (from 91 to 74 cm for all taxa, and from 122 to 96 cm for fish only) revealed changes in demersal species assemblage. Jackknife test shows that these changes are especially related to the drastic decline observed in the abundance of meagre (see Supplementary Table S2). The mean trophic index MTL did not change significantly over the study period. This is mainly due to

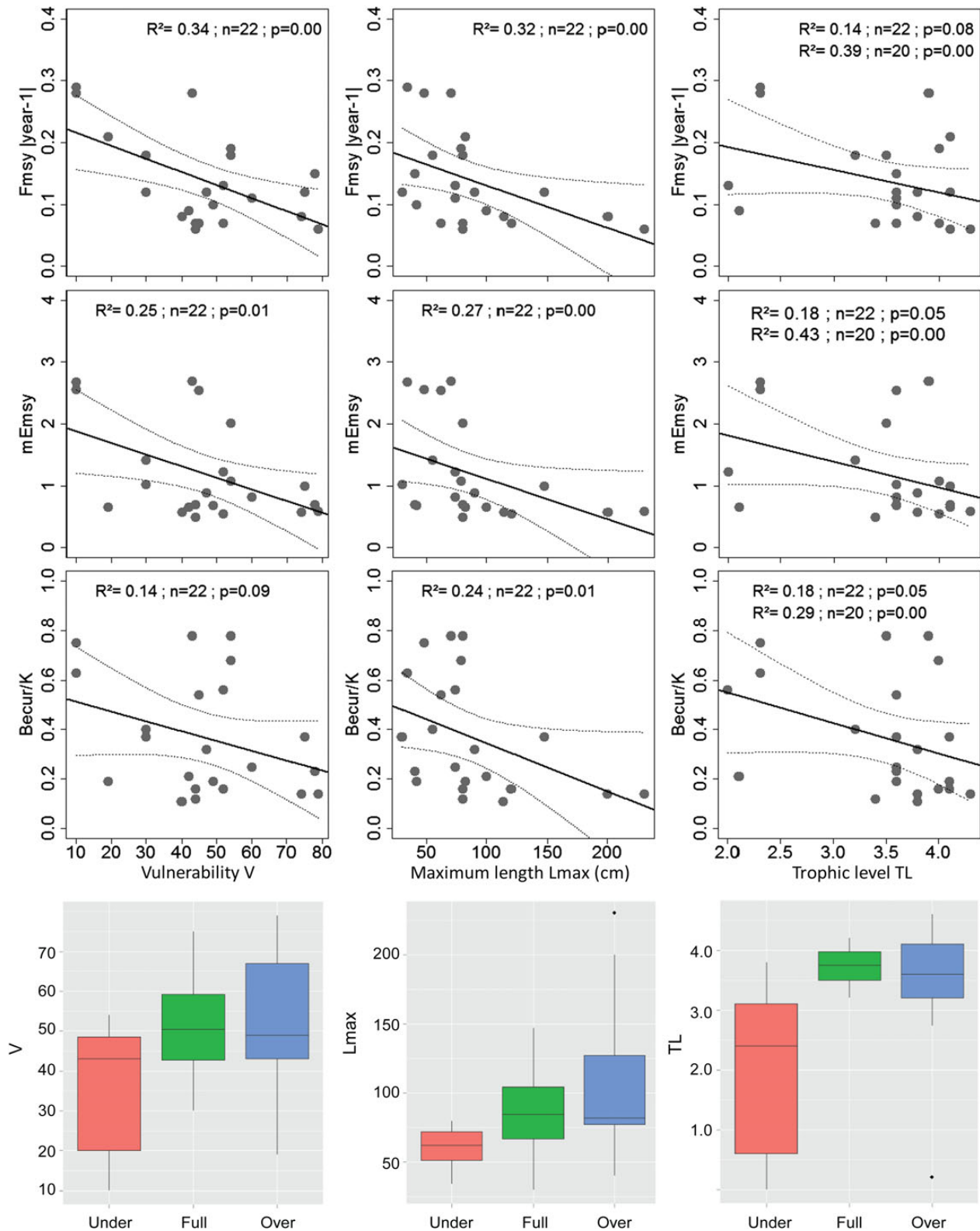


Figure 4. Relationships between exploitation indicators and eco-biological life history parameters. On the three top rows, exploitation indicators (fishing mortality at MSY F_{msy} , effort multiplier at MSY mE_{msy} , and ratio of the current biomass over the carrying capacity B_{cur}/K) are expressed as function of the species vulnerability index V (left column), the species maximum length L_{max} (middle column), and the species trophic level TL (right column). On the bottom row, the three eco-biological parameters are presented according to the exploitation state of stocks (mE_{msy} divided into three classes: under, full, and overexploited).

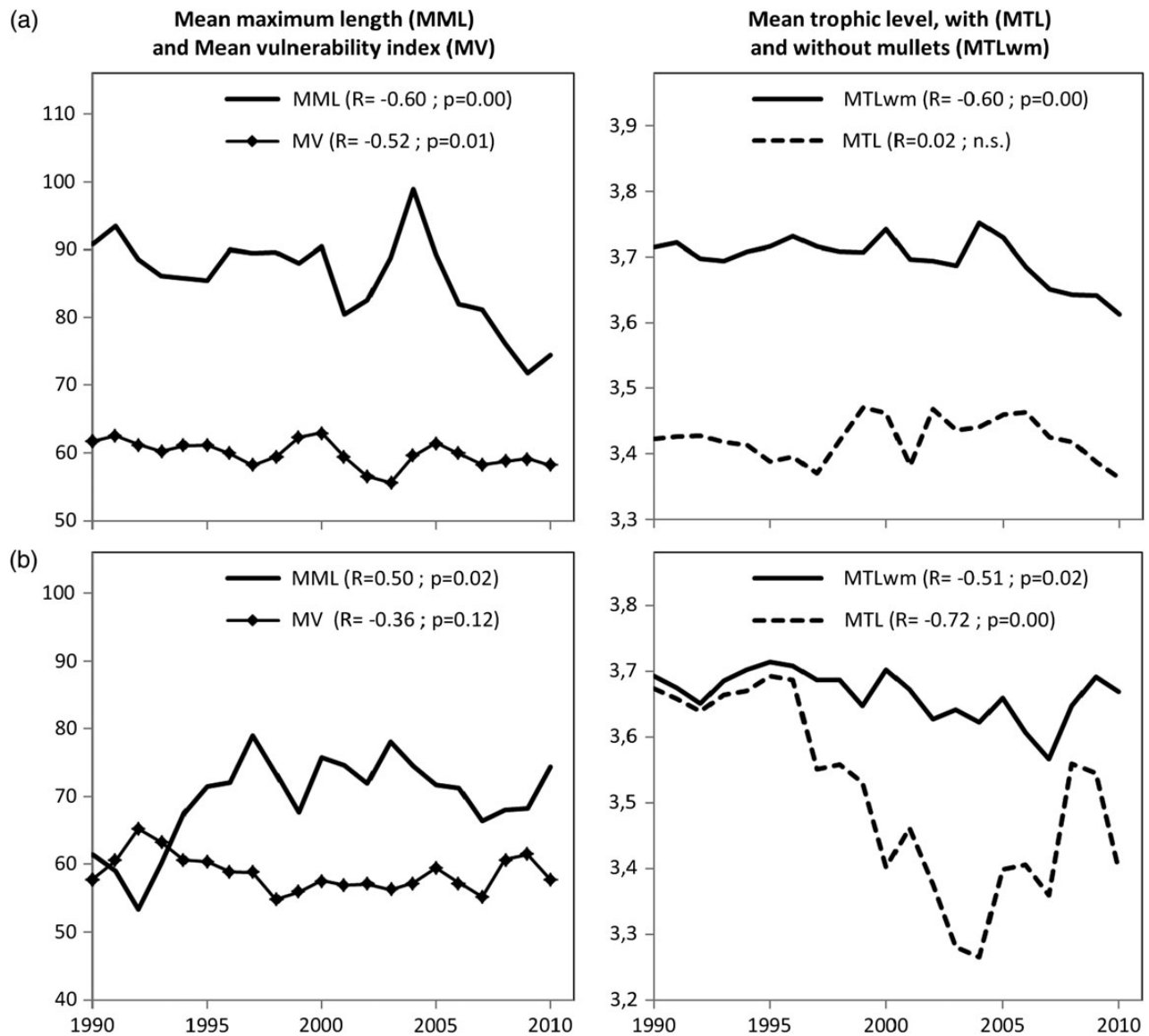


Figure 5. Trends over the study period of ecosystem indicators: (a) for ecosystem biomass; and (b) for catches. [Mean maximum length MML in cm, mean vulnerability index MV, and mean trophic level MTL; 22 taxa considered; biomass were computed based on abundance indices from scientific survey and commercial cpues, using $B = A/q$ according to Equation (6).]

the sharp reduction in abundance of the flathead mullet, a coastal and very low trophic level species. Thus, without mullets, the mean trophic level of biomass did slightly but significantly decrease within the considered community (MTLwm from 3.7 to 3.6).

Ecosystem indicators based on catches exhibit contrasted trends, due to changes which have occurred over the study period in the species targeted by the various fisheries (Figure 5b). The mean maximum length of catches increased, mainly because the fishing pressure on large fish such as white grouper, guitarfish, flathead mullet, and croakers, increased, at the same time the small-scale fishery developed. In contrast, the mean trophic level of catch decreased (MTL from 3.7 to <3.3 in 2004 and ~3.4 in 2010), mainly due to increasing catch for mullets, but also for shrimps.

Changes in ecosystem indices expressed as a function of a multiplier of fishing effort, are marked, confirming changes in the species composition of demersal communities induced by fishing

(Figure 6a). Compared with the virgin state, the current situation represents a decrease of 5.8 points for the mean vulnerability of biomass within the ecosystem (MV_{Be} from 62.8 to 57.0), related to the higher decrease in the abundance of vulnerable species. The mean maximum length decreased by 23.5 cm compared with the virgin state (MML_{Be} from 93.5 to 70.0 cm), while the mean trophic level decreased by 0.16 TL (MTL_{Be} from 3.53 to 3.37). This change also influenced catches, with a significant decrease in the three indices. The decrease is even stronger when the indices are calculated for fish alone (17 taxa), with decreases compared with the virgin state of 5.9 points, 34 cm, and 0.21 TL for MV_{Be} , MML_{Be} , and MTL_{Be} , respectively. Logically, these decreases would decrease even further if fishing effort were to increase (i.e. for the multipliers $mE > 1$).

Changes in the three indices as a function of fishing mortality show the impact of exploitation from a more theoretical viewpoint

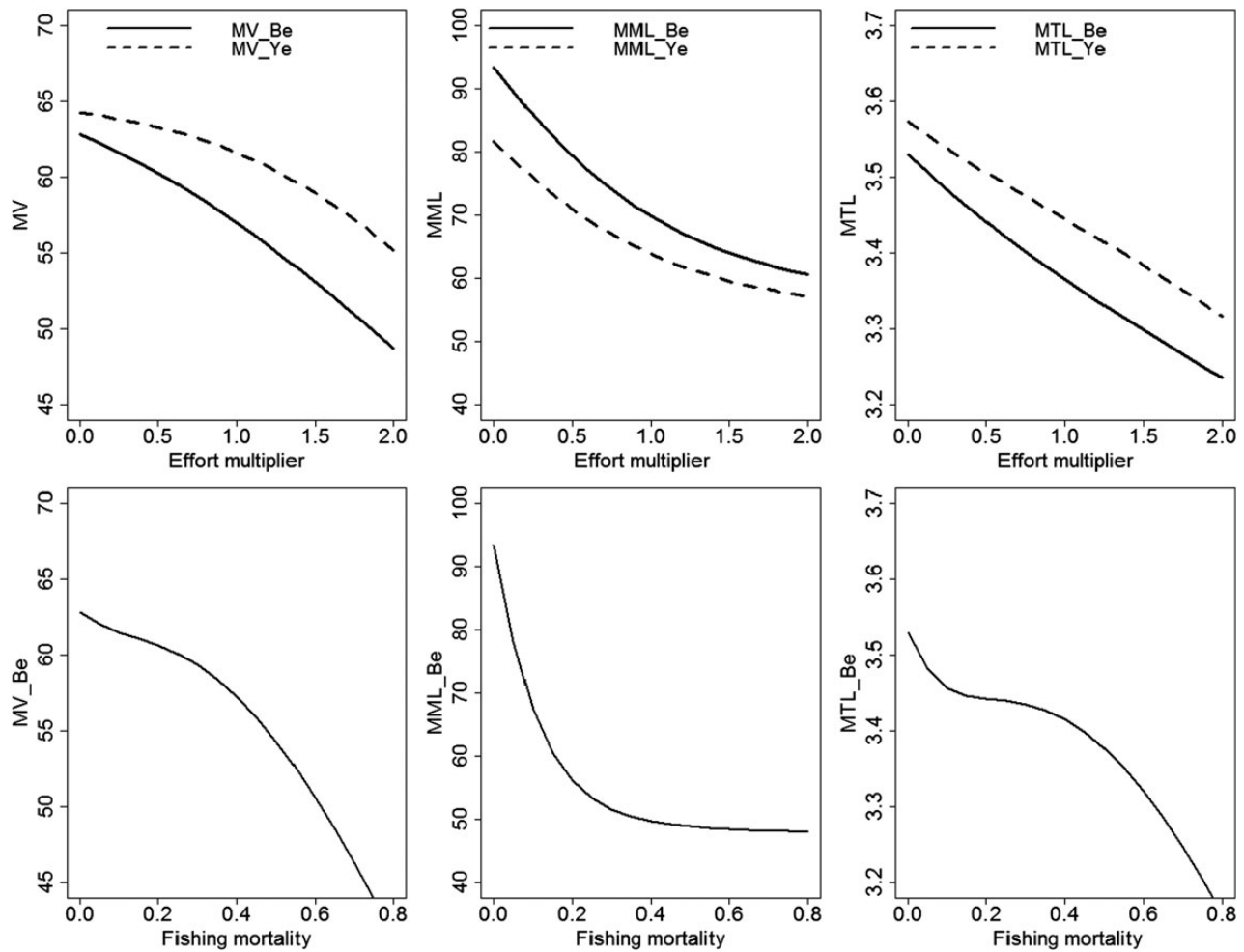


Figure 6. Relationships between the ecosystem indicators and: (a) the fishing effort; and (b) the fishing mortality. (Mean vulnerability index MV, mean maximum length MML, and mean trophic level MTL; predictions at equilibrium derived from the production model.)

(Figure 6b). The same mortality applied to all taxa would thus lead to significant decreases in the indices, in catches as well as within the ecosystem (because $Ye = F \times Be$, the two types of indices are equal here). Compared with the virgin state, for a fishing mortality of 0.3 year^{-1} applied to all 22 taxa, MV would decrease from 63 to 59, MML from 93 to 51 cm, and MTL from 3.53 to 3.44.

Discussion

An overall overexploitation of Mauritanian demersal resources

The stock assessments we performed represent $\sim 60\%$ of current Mauritanian demersal catches. The dynamic production model we used includes four parameters (B_0 , r , K , and q , in addition to the common error σ^2) and correlations between parameters may lead to high uncertainty in the parameter estimates and model forecasts (Gascuel and Menard, 1997). To ensure identifiability of parameters, a Bayesian framework was used, based on informative priors. Assessment results show that two-thirds of demersal stocks exploited in Mauritania are either overexploited or fully exploited. Overexploitation seems especially high for the fish, with current biomass reduced to 20% of that at the virgin state and current fishing effort that should be reduced by a mean of 40% to reach

that at $MSY (mE_{msy})$. These results confirm and refine partial assessments performed in Mauritania or at the subregional scale, particularly the strong decrease in abundance of demersal resources (Chavance *et al.*, 2004; Christensen *et al.*, 2004; Gascuel *et al.*, 2004, 2007a), overall plateauing of catches despite increase fishing effort (Gascuel *et al.*, 2007b; Labrosse *et al.*, 2010) and the assessment of overexploitation already determined for a few species (Chassot *et al.*, 2010; FAO-Cecaf, 2012; Meissa *et al.*, 2013).

Industrial demersal fisheries started to develop in Mauritania during the 1960s. Since that period, total demersal landings (including unreported bycatch) were estimated to fluctuate around $160\,000 \text{ t year}^{-1}$ (Gascuel *et al.*, 2007b). At the same time, the fishing effort strongly increased, the number of industrial trawlers growing from around 150 in the early 1980s to 300–350 in the late 1990s/early 2000s. The number of artisanal pirogues jumped from 500 in the 1980s to more than 4000 in the most recent years, with the sharpest increase observed during the 1990s. For certain particularly targeted species, such as white grouper, flathead mullet, or octopus, the overexploitation may be long standing, while the opposite is true for species such as spotted sea bass, tonguesole, and rubberlip grunt, which seem to have been exploited more recently. This asynchronous history among stocks exploitation explains why some catch-based ecosystem indicators exhibit

unexpected trends over the study period, with, for instance, an increase in the mean maximum length. In other words, changes which have occurred in the fishing strategies, especially with the development of the small-scale fishery, may mask or counterbalance changes occurring within the ecosystem. Results related to the mean trophic level MTL demonstrate that both a *Fishing through the foodweb* process and a *Fishing down the foodweb* process occurred, with a strong decrease in catch-based MTL partially due to the intensification of mullets and shrimps fisheries, and a slight decrease in survey-based MTL. However, taking into account a larger set of species, Gascuel *et al.* (2007a) showed a more pronounced decrease in survey-based MTL from >3.7 to <3.5 from 1982 to 2006.

Model predictions confirm a highly degraded community structure compared with the virgin state. The mean maximum length MML of the main taxa exploited decreased by 23.5 cm and that of the fish alone by 34 cm, due mainly to the high overexploitation of large species such as white grouper, meagre, and smooth-hound. At the same time, the mean vulnerability index MV and the mean trophic level MTL of the communities studied decreased. It is likely that these values underestimate the true decreases, mainly because of the decline in large species of sciaenid, which were overexploited in the 1970s and 1980s (Josse and Garcia, 1986) and are no longer included in the selection we studied.

Naturally, fishing does not affect all stocks in the same way, and certain stocks remain underexploited today. This is particularly true for rapid-turnover species such as shrimp but also for fish such as spotted sea bass, tonguesole, and rubberlip grunt. These three species largely escape industrial fishing due to their coastal distribution and are targeted mainly by small-scale dugouts to supply local markets. In contrast, octopus and cuttlefish stocks, considered resilient to fishing, are overexploited. Since the 1960s, these species have been the main resources targeted by national (industrial or small scale) and foreign demersal fishing. In a way, they are victims of their high commercial values. Their resiliency, however, allows them to rebuild their abundance rapidly if fishing effort decreases and to withstand long-term overexploitation. The excess effort exerted on octopus has been estimated at $\sim 30\%$ in all assessments of this species for the past two decades (FAO-CNROP, 1999).

Since 2005, overall fishing effort appears to be decreasing. This change is related to the withdrawal of a part of the European shrimp and cephalopod fleets, retirement of some very old Mauritanian trawlers, and extension of seasonal closures of octopus fishing. The decrease in fishing pressure seems to have stabilized total biomass due to increased abundance of a few species, especially cephalopods. This increase remains limited, however, and does not reverse the overall overexploitation of these resources. On the other hand, recent changes suggest that the overall overexploitation was even stronger a few years ago, with a fishing effort exceeding the mE_{msy} target by 40% for all taxa together and by 50% for fish alone.

Resilience factor of exploited taxa and ecosystem indicators

Analysis of relations between exploitation parameters and life history traits shows that fishing generally impacts more the taxa that are long-lived and large, with slow turnovers and high trophic levels. In particular, maximum length (L_{max}) appears to be an influential indicator determining taxon resilience, in the same way as the index of intrinsic vulnerability proposed by Cheung *et al.* (2005). In general, species of high trophic level also

appear more impacted by exploitation. These are often the most delicate species due to their slower turnover (Pauly *et al.*, 1998; Gascuel and Pauly, 2009). In contrast, species of low trophic level usually have a rapid turnover, which renders them more resistant to fishing; this is particularly true for shrimp.

This rule has significant exceptions, however, especially for herbivorous fish such as mullets, which have low trophic levels but low turnover, and cephalopods, which are short-lived with rapid turnover but have relatively high trophic levels. There is also no simple relation between the commercial value of species and their length or trophic level. Thus, the most targeted species are obviously not chosen based on ecological criteria. In addition, certain smaller taxa (e.g. shrimp) or taxa of low trophic level (e.g. mullets) experienced recent decreases in abundance as high as those of larger predatory species, while in contrast, predators such as sea catfish had their abundance fluctuate without a strong trend during the period.

In a general matter, such complex relations explain why ecosystem changes expected from theory are not always observed in real case studies. Comparable results have been observed in other case studies characterized by increasing ecosystem overexploitation but little or unexpected change in ecosystem indicators. For example, Branch *et al.* (2010) observed plateauing of the mean trophic level for biomasses of the Canary Island ecosystem from 1982 to 2010. They also observed negative correlations between indicators of trophic level based on catches and those based on biomasses in the system. They thus concluded, in contrast to previous studies, that the mean trophic level from landings is an unreliable indicator of ecosystem health.

The results obtained here shed light on this controversy. On the one hand, they confirm that ecosystem changes observed using catch-based indicators may differ from real changes occurring within ecosystem, especially in a context of developing fisheries and changing strategies of fishing. In our case, a negative correlation was observed between surveys-based and catch-based indicators for the mean maximum length only, while only the slope of the decreasing trend differed for the mean trophic level. Such discrepancies clearly highlight that changes in ecosystems can be better analysed using fisheries-independent data, and especially surveys data, when they exist. In contrast, in many ecosystems, even if this is not the case in Mauritania, catch or landings data cover a long period in the past, and include both pelagics and demersals, allowing for a long term and broader analysis compared with scientific surveys (Pauly *et al.*, 2013; Gascuel *et al.*, 2014). Shannon *et al.* (2014) showed that indicators derived from ecosystem models can also be very useful, providing an even wider view on the whole ecosystem.

On the other hand, even if temporal changes in the indicators are erratic or difficult to interpret, including for survey-based indicators, their theoretical change as a function of a multiplier of effort or fishing mortality is clear. Our results demonstrate that, compared with the virgin state, exploitation leads to a significant decrease in the mean maximum length and in the mean trophic level, for catches and for biomass within the ecosystem as well. "Fishing down the marine food web" does not imply that species of high trophic level are exploited first. It means that these species tend to be less resilient and thus inevitably impacted more by a given exploitation. In contrast, the indices can only change little over time because the study period does not cover the beginning of the exploitation, the stock are not all exploited synchronously, and natural variability hides some of the theoretical changes.

Conclusion

Until recently, demersal resources of Mauritania remained relatively little exploited, especially in coastal zones. Scientific monitoring begun in the early 1980s allows the change that occurred during part of the period of fishery development to be analysed. Paradoxically, except for a few species of interest (particularly to European fleets), most of the stocks had not been assessed until recently. This analysis helps to fill in this gap and shows that the situation has passed from moderate exploitation to marked overexploitation in a few decades. It also reveals the changes that have occurred in the structure of the exploited communities, today dominated by smaller species and those of lower trophic level.

Here as elsewhere, ecosystem management is necessary. However, it faces the challenge of making a system of high-quality observation and expertise operational in a country facing many economic difficulties. It seems particularly difficult to monitor all components of the ecosystem, especially due to the high biodiversity of landings. More than elsewhere, simple approaches based on robust indicators are required. They must lead to monitoring exploitation indicators, especially trends in biomass changes, by first targeting the highly vulnerable species.

From this viewpoint, it seems essential to pass from a fisheries management based until now mostly on monitoring a few species, especially octopus and shrimp, to one also monitoring changes in certain demersal fish. Priority should be given to large species and those of high trophic level, such as white grouper, meagre, guitarfish, and smooth-hound. Beyond their specific importance for fisheries, particularly small scale, these species can be considered markers of ecosystem health. This study shows the utility of considering them as sentinel species.

Supplementary data

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

Acknowledgements

The present study was supported by the Mauritanian Institute IMROP and by the Service for Cooperation and Cultural Activities (SCAC) of the Embassy of France in Mauritania. The authors acknowledge scientists and technicians from IMROP who contributed to the collection of data used and two anonymous referees for their helpful comments on the manuscript.

References

- Beverton, R., and Holt, S. J. 1957. *On the Dynamic of Exploited Fish Populations*. Chapman and Hall, London.
- Branch, T. A., Watson, R., Fulton, E. A., Jennings, S., McGilliard, C. R., Pablico, G. T., Ricard, D., *et al.* 2010. The trophic fingerprint of marine fisheries. *Nature*, 468: 431–435.
- Brooks, S. P., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7: 434.
- Caddy, J. F., Csirke, J., Garcia, S. M., and Grainger, R. J. R. 1998. How pervasive is “fishing down marine food webs”? *Science*, 282: 1383–1383.
- Chassot, E., Balguerias, E., Guitton, J., Jouffre, D., Tfeil, B., and Gascuel, D. 2010. Diagnostic de l'état du stock de poulpe (*Octopus vulgaris*) mauritanien: synthèse et nouvelles évaluations par approche globale. In *Evaluation des ressources et aménagement des pêcheries de la ZEE Mauritanienne*, pp. 95–116. Ed. by P. Labrosse, K. Brahim, M.O. Taleb Sidi, and D. Gascuel. Actes du sixième Groupe de travail

- de l'IMROP, Nouadhibou, Mauritanie, décembre 2006 Document Technique n°5, IMROP éditions [ISSN 199-2728].
- Chavance, P. 2004. Towards reconstructing half a century of change in west African fisheries. In *Marine Fisheries, Ecosystems, and Societies in West Africa: Half a Century of Change* [Pêcheries maritimes, écosystèmes et sociétés en Afrique de l'Ouest: un demi-siècle de changement], pp. 113–130. Ed. by P. Chavance, M. Bah, D. Gascuel, M. Vakily, and D. Pauly. Actes du Symposium international Dakar, Juin 2002, Luxembourg Office des publications officielles des Communautés Européennes, XXXVI, Collection des rapports de recherche halieutique ACP-UE n° 15, 530 pp.
- Chavance, P., Bah, M., Gascuel, D., Vakily, M., and Pauly, D. 2004. *Marine Fisheries, Ecosystems, and Societies in West Africa: Half a Century of Change* [Pêcheries maritimes, écosystèmes et sociétés en Afrique de l'Ouest: un demi-siècle de changement]. Actes du Symposium international Dakar, Juin 2002, Luxembourg Office des publications officielles des Communautés Européennes, XXXVI, Collection des rapports de recherche halieutique ACP-UE n° 15. 532 pp., ISBN 92-894-7480-7, 530 pp.
- Cheung, W., Pitcher, T. J., and Pauly, D. 2005. A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation*, 124: 97–111.
- Cheung, W., Watson, R., Morato, T., Pitcher, T., and Pauly, D. 2007. Intrinsic vulnerability in the global fish catch. *Marine Ecological Progress Series*, 333: 1–12.
- Christensen, V., Amorin, P. A., Diallo, I., Diouf, T., Guénette, S., Heymans, J. J., Mendy, A. N., *et al.* 2004. Trends in biomass off Northwest Africa, 1960–2000. In *Marine Fisheries, Ecosystems, and Societies in West Africa: Half a Century of Change* [Pêcheries maritimes, écosystèmes et sociétés en Afrique de l'Ouest: un demi-siècle de changement], pp. 377–386. Ed. by P. Chavance, M. Ba, D. Gascuel, J. M. Vakily, and D. Pauly. Actes du Symposium international DAKAR Juin 2002, Office des publications officielles des communautés Européennes, XXXVI, collection des rapports de recherche halieutique ACP-UE 15.
- Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association*, 74: 829–836.
- Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science*, 62: 177–188.
- Dulvy, N. K., Ellis, J. R., Goodwin, N. B., Grant, A., Reynolds, J. D., and Jennings, S. 2004. Methods of assessing extinction risk in marine fishes. *Fish and Fisheries*, 5: 255–276.
- Essington, T. E., Beaudreau, A. H., and Wiedenmann, J. 2006. Fishing through marine food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 103: 3171–3175.
- FAO-Cecaf. 2012. Report of the FAO/CECAF Working Group on the Assessment of Demersal Resources—Subgroup South, Freetown, Sierra Leone, 9–18 October 2008. CECAF/ECAF Series No. 11/73. Rome, 311p.
- FAO-CNROP. 1999. Rapport du 4ième groupe de travail du CNROP: évaluation des stocks et aménagement des pêcheries de la ZEE mauritanienne (Nouadhibou, 7–13 décembre 1998). Copace-Pace Sér. 99/64. 180 pp.
- Fox, W. W. 1970. An exponential surplus-yield model for optimizing exploited fish populations. *Transaction of the American Fisheries Society*, 99: 80–88.
- Froese, R., and Pauly, D. 2012. FishBase. World Wide Web Electronic Publication Version 06/2012.
- Garibaldi, L., and Grainger, R. 2004. Chronicles of catches from marine fisheries in the eastern central Atlantic for 1950–2000. In *Marine Fisheries, Ecosystems, and Societies in West Africa: Half a Century of Change* [Pêcheries maritimes, écosystèmes et sociétés en Afrique de l'Ouest: un demi-siècle de changement]. Ed. by P. Chavance, M. Bah, D. Gascuel, M. Vakily, and D. Pauly. Actes du Symposium international Dakar, Juin 2002, Luxembourg Office des publications officielles des Communautés Européennes,

- XXXVI, Collection des rapports de recherche halieutique ACP-UE n° 15. 530 pp.
- Gascuel, D., Coll, M., Fox, C., Guénette, S., Guitton, J., Kenny, A., Knittweis, L., *et al.* 2014. Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. *Fish and Fisheries*, doi: 10.1111/faf.12090.
- Gascuel, D., Labrosse, P., Meissa, B., Taleb Sidi, M. O., and Guenette, S. 2007a. Decline of demersal resources in North-West Africa: an analysis of Mauritanian trawl-survey data over the past 25 years. *African Journal of Marine Science*, 29: 331–345
- Gascuel, D., Laurans, M., Sidibé, A., and Barry, M. D. 2004. Diagnostic comparatif de l'état des stocks et évolutions d'abondance des ressources démersales dans les pays de la CSRP. *In* Marine Fisheries, Ecosystems, and Societies in West Africa: Half a Century of Change [Pêcheries maritimes, écosystèmes et sociétés en Afrique de l'Ouest: un demi-siècle de changement], pp. 205–222. Ed. by P. Chavance, M. Bah, D. Gascuel, M. Vakily, and D. Pauly. Actes du Symposium international Dakar, Juin 2002, Luxembourg Office des publications officielles des Communautés Européennes, XXXVI, Collection des rapports de recherche halieutique ACP-UE n° 15. 530 pp.
- Gascuel, D., and Menard, F. 1997. Assessment of a multispecies fishery in Senegal, using production models and diversity indices. *Aquatic Living Resources*, 10: 281–288.
- Gascuel, D., Morissette, L., Palomares, D., and Christensen, V. 2008. Trophic flow kinetics in marine ecosystems: toward a theoretical approach to ecosystem functioning. *Ecological Modelling*, 217: 33–47.
- Gascuel, D., and Pauly, D. 2009. EcoTroph: modelling marine ecosystem functioning and impact of fishing. *Ecological Modelling*, 220: 2885–2898.
- Gascuel, D., Zeller, D., Taleb Sidi, M. O., and Pauly, D. 2007b. Reconstructed catches in the Mauritanian EEZ. *In* Reconstruction of Marine Fisheries Catches for Key Countries and Regions (1950–2005). Ed. by D. Zeller, and D. Pauly. Fisheries Centre Research Reports, University of British Columbia (Canada), 15: 105–119.
- Gislason, H. 2003. The effects of fishing on non-target species and ecosystem structure and function. Food & Agricultural Organization of the United Nations, Rome.
- Guénette, S., Meissa, B., and Gascuel, D. 2014. Assessing the contribution of marine protected areas to the trophic functioning of ecosystems: a model for the Banc d'Arguin and the Mauritanian shelf. *PLoS ONE* 9: e94742.
- Jennings, S., Reynolds, J. D., and Mills, S. C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London, Series B*, 265: 333–339.
- Josse, E., and Garcia, S. M. 1986. Description et évaluation des ressources halieutiques de la ZEE mauritanienne, rapport du groupe de travail CNROP-FAO-Orstom (16–27 Septembre 1985, Nouadhibou). *Copace-Pace Sér.* 86/37, 300 pp.
- Kimura, D. K., Balsiger, J. W., and Ito, D. H. 1996. Kalman filtering the delay-difference equation: practical approaches and simulations. *Fishery Bulletin US*, 94: 678–691
- Labrosse, P., Brahim, K., Taleb Sidi, M. O., and Gascuel, D. (Eds) 2010. Evaluation des ressources et aménagement des pêcheries de la ZEE Mauritanienne. Actes du sixième Groupe de travail de l'IMROP, Nouadhibou, Mauritanie, décembre 2006. Document Technique n°5, IMROP éditions [ISSN 1992–2728]. 267 pp.
- Laurans, M., Gascuel, D., Chassot, E., and Thiam, D. 2004. Changes in the trophic structure of fish demersal communities in West Africa in the three last decades. *Aquatic Living Resources*, 17: 163–174.
- McAllister, M. K., and Kirkwood, G. P. 1998. Bayesian stock assessment: a review and example application using the logistic model. *ICES Journal of Marine Science*, 55: 1031–1060.
- Meissa, B., Gascuel, D., and Rivot, E. 2013. Assessing stocks in data-poor African fisheries: a case study on the white grouper (*Epinephelus aeneus*) of Mauritania. *African Journal of Marine Science*, 35: 253–267.
- Meissa, B., Rivot, E., and Gascuel, D. 2008. Analysis of CPUE data series through Generalized Linear Models and Delta method to derive annual series of abundance indices Application to the Mauritanian demersal fishery. Scientific report European project ISTAM, Deliverable D.3.2, AgrocampusOuest, Rennes. 13 pp.
- Myers, R. A., and Mertz, G. 1998. The limits of exploitation: a precautionary approach. *Ecological Applications*, 8: S165.
- Ono, K., Punt, A. E., and Rivot, E. 2012. Model performance analysis for Bayesian biomass dynamics models using bias, precision and reliability metrics. *Fisheries Research*, 125–126: 173–183.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, 279: 860–863.
- Pauly, D., Hilborn, R., and Branch, T. A. 2013. Does catch reflect abundance? *Nature*, 494: 303–306.
- Punt, A. E. 2003. Extending production models to include process error in the population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 1217–1228.
- Quenouille, M. 1949. Approximate tests of correlation in time series. *Journal of the Royal Statistical Society, Series B*, 11: 18–84.
- R Development Core Team. 2008. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>.
- Reynolds, J. D., Dulvy, N. K., Goodwin, N. B., and Hutchings, J. A. 2005. Biology of extinction risk in marine fishes. *Proceeding of the Royal Society of London, Series B*, 272: 2337–2344.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, 191: 1–382.
- Rochet, M. J., and Trenkel, V. M. 2003. Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 86–99.
- Schnute, J. T., and Kronlund, A. R. 2002. Estimating salmon stock–recruitment relationships from catches and escapement data. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 433–449.
- Shannon, L., Coll, M., Bundy, A., Gascuel, D., and Heymans, J. J. 2014. Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecological Progress Series*, 412: doi: 10.3354/meps10821.
- Stefánsson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES Journal of Marine Science*, 53: 577–588.
- Thomas, A., O'Hara, B., and Sturtz, S. 2006. Making BUGS open. *Journal of Statistical Software*, 6: 12–17.
- Zhou, S., Yin, S., Thorson, J. T., Smith, A. D. M., Fuller, M., and Walters, C. J. 2012. Linking fishing mortality reference points to life history traits: an empirical study. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 1292–1301.

Handling editor: Shijie Zhou