Fishing destabilizes the biomass flow in the marine size spectrum

M.-J. Rochet[1, *] and E. Benoît[2]

[1] Ifremer, Rue de l'île d'Yeu, BP 21105, 44311, Nantes cedex 3, France
[2] Laboratoire de Mathématiques, Université de la Rochelle, Avenue Michel Crépeau, 17042 La Rochelle, France

*: Corresponding author : M.-J. Rochet, email address : mjrochet@ifremer.fr

Abstract:

Fishing impacts on marine food webs are predicted by simulations of a size spectrum community model. In this model, predation is determined by predator and prey size and abundance, and drives predator growth and prey mortality. Fishing amplifies temporal oscillations in the biomass flow. Oscillations appear at lower fishing intensity and have wider amplitude when fishing is selective (removes a narrow size range) and/or when large fish are targeted, than when fishing is more balanced (catching a larger size range) or when small fish are targeted. A novel index of size diversity is developed, and is shown to be sensitive to both fishing intensity and selectivity. To avoid unstable food web dynamics with potential harmful consequences for fisheries, limiting both fishing intensity and selectivity might be an appropriate exploitation strategy.

Keywords: size spectrum, ecosystem approach to fisheries management, biodiversity, fishing selectivity, community stability

1. Introduction

Fishing magnifies fluctuations in fish stock abundances, because age-truncated populations have more variable dynamics (Anderson *et al.* 2008). Selective harvesting of old individuals alters the basic dynamics of exploited populations and favours booms and busts that can ultimately lead to stock collapses. This might also apply to higher organization levels. If selective removals destabilize population dynamics, could they affect the stability of community trophic dynamics? Fishing indeed is selective at the community level: valuable species are preferentially targeted; many of these species are large-sized; within species large size-classes are usually preferred and minimum size limits are often used as management tools (Pascoe 1997). Although most fisheries catch various amounts of unwanted size classes or species (Alverson *et al.* 1994; Kelleher 2005), still any fishing gear is selective because catch composition is different from that of the fish population, or community, in the area where the gear is used (Wileman *et al.* 1996): many animals escape owing to their size or behaviour. There is a general belief that more selective is better (e.g., Pikitch *et al.* 2004; Worm *et al.* 2009), and gear technologists generally see their goal as 'perfect gear selectivity' (Broadhurst 2008).

However, attention has recently been drawn on the idea that selective fishing might alter biodiversity and ecosystem functioning (Zhou *et al.* 2010). Evidence accumulates that, because not all sizes are targeted, fishing affects the size-structure of communities, both directly by removing large fish (Rice & Gislason 1996) and indirectly by increasing the abundance of smaller fish released from predation (Dulvy *et al.* 2004; Blanchard *et al.* 2005; Daan *et al.* 2005). Not only is selective fishing ecologically disruptive; unselective fishing might be economically beneficial. *E.g.* in prawn fisheries, the removal and discarding of small fish that are prawn predators or competitors likely increases prawn production (Zhou 2008). Within species it is now well established that size-selective fishing creates an evolutionary selective pressure that drives generally counter-productive genetic changes in populations (Stokes *et al.* 1993; Law 2007); for example, targeting large individuals induces evolution towards smaller sizes and slower growth (Conover & Munch 2002).

Size is recognized as a key feature in marine ecological processes and, because fishing is size-selective, the size distribution of marine populations and assemblages is often used to monitor fishing impacts at various organization levels (Shin *et al.* 2005). In particular, the 'size-spectrum theory' has been developed for marine ecosystems (Silvert & Platt 1978; Kerr & Dickie 2001; Benoît & Rochet 2004; Andersen & Beyer 2006). This class of models describes the ecological processes underlying the biomass size spectrum, the distribution of biomass across body size classes, where each individual is defined by size regardless of species. When the energy transfer is governed by size-dependent predation, which determines prey mortality and predator growth, unfished size spectra have two classes of dynamics depending on assumed prey size preferences: either a steady state (also called stable spectrum hereafter), or an oscillatory solution in which waves move over time along the size spectrum from small to large body size (Law *et al.* 2009). The question is, how does fishing affect these dynamics? The shape of the size spectrum is known to be sensitive to fishing intensity (Gislason & Rice 1998; Shin & Cury 2004). Intuitively selective fishing might generate gaps that would disturb the biomass flow and potentially favour oscillatory dynamics, creating temporal variations in biomass and catch. Clearly both fishing intensity and selectivity interact to determine the impact of fishing on size spectrum dynamics.

Here we use Benoît & Rochet (2004) model to predict how various fishing intensities and selectivities affect the marine food web. Measures of fishing impacts include indices of both the spectrum shape and temporal variations. We first recall the main assumptions of the Benoît & Rochet (2004) model, slightly modified to account for recruitment depending on the reproductive biomass in the ecosystem. We then introduce a series of fishing scenarios, and various

measures of fishing effects. We present simulation results and discuss the consequences of our findings for fisheries management at an ecosystem scale.

2. Methods

(a) A size spectrum model

As in the Benoît & Rochet (2004) model, we assume that predation is the force driving growth and mortality and that size determines all processes. Here size is measured by body-weight w log-transformed to $x = \log w/w_0$ (see all variable and parameter definitions in Table 1). The probability φ of a predation event after encounter of two individuals with log-weight x and y only

depends on the ratio of their weights $q = y - x$. Here we use $\varphi(q) = \begin{cases} e^n \left(\dfrac{q}{q_0} \right)^n e^{-nq/q_0} & \text{if} \quad q \geq 0 \\ 0 & \text{if} \quad q \leq 0 \end{cases}$,

a positive, dome-shaped function that peaks at q_0; the larger n the sharper the peak. Encounter rate is determined by the volume searched by the predator, an allometric function of predator weight $Ae^{\alpha y}$ where A and α are constant. Any predation event generates prey mortality and predator growth with constant growth efficiency K. In summary, as in Benoît & Rochet (2004) the dynamics of fish density is given by

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x} \left[KAe^{\alpha x} \int_{-\infty}^{+\infty} e^{-q} \varphi(q) u(x-q,t) u(x,t) \mathrm{d}q \right] - Ae^{\alpha x} \int_{-\infty}^{+\infty} e^{\alpha q} \varphi(q) u(x+q,t) u(x,t) \mathrm{d}q \quad \text{(equation 1)}$$

There exists a unique slope λ such that $u(x) = u_0 e^{\lambda x}$ is a stationary solution of equation 1, the linear size spectrum. The model is defined for x varying from $-\infty$ to $+\infty$. In simulations x varies on a bounded interval $[x_{min}, x_{max}]$ and boundary conditions need to be specified. First, energy is input to the system by a size structured plankton population with size $[x_{Pmin}, x_{min}]$. Fish eat plankton with the weight-ratio dependent predation probability φ; predation events generate predator growth but no prey mortality. Second, a population of "sea monsters" with size $[x_{max}, x_{Mmax}]$ exerts predation on large fish. Sea monsters mimic both intrinsic mortality due to senescence (Reznick *et al.* 2002), and extrinsic mortality. The latter is caused by large predators whose growth and mortality differ from those of fish and are therefore not included in the spectrum dynamics, *e.g.* marine mammals. This mortality prevents biomass accumulation in large sizes and improves the stability and regularity of the size spectrum. Predation events by sea monsters have probability φ again. For the sake of parsimony, both the plankton and sea monster populations are time-invariant, independent of the size spectrum u, and set as a linear size-spectrum with slope λ. Third, to calculate the lower boundary condition $u(x_{min})$, the recruitment of fish at minimum size x_{min} is assumed to depend on the number of fish above a

constant reproduction size x_{mat} according to $R = \int_{x_{mat}}^{+\infty} \gamma e^{\beta x} u(x,t) \mathrm{d}x$ where γ and β are parameters of

a weight-fecundity relationship. In this model energy devoted to reproduction is constant, and density-dependence in recruitment is described by the predation exerted by larger fish on recruits.

(b) Fishing selectivity

For a target species, size-selectivity of a gear is described by its selection curve, that is, the probability that an individual with a given length be caught by that gear. Traditionally, selection curves are taken as sigmoid functions, with the probability of being caught monotonically

increasing with size up to 1 so that large fish present in the area will certainly be caught (Wileman *et al.* 1996). However, the assumption that all large fish are caught is related to the design of most trawl selectivity experiments using small mesh covers over codends, twin or trouser trawls, that cannot account for the presence of larger, uncaught fish in the area. But recent comparisons of catches by several types of gears have shown that trawls do not catch large animals that are taken in the same area by other gears like gillnets, hooks or traps; this applies to various species of fish (e.g., Huse *et al.* 1999; Huse *et al.* 2000; Lauth *et al.* 2004) and crustaceans (e.g., Bellchambers & de Lestang 2005), or to the fish community (Olin *et al.* 2009). Fish behaviour greatly influences catchability and some species are able to avoid the gear (Engås 1994; Lorance & Trenkel 2006); for those swimming away from mobile gears, probability of escape is positively related to swimming speed, that is, to body size (Engås 1994). Beside trawls and other towed gears, dome-shaped selection curves are relevant for other gears such as gill-nets, or hooks (Millar & Fryer 1999). At the community level, a dome-shaped selection curve might be representative of the multi-species catches relative to video estimates of total abundance (Wells *et al.* 2008). Thus, we used a dome-shaped, gaussian fishing mortality:

$$\mu_f = a \exp\left(-\frac{s^2\left(x-x_f\right)^2}{2}\right) \text{(equation 2)},$$

where selectivity is described by two parameters, x_f catch modal size, or target size, and s inverse width of the selection curve, or fishing selectivity *stricto sensu*. Larger s values imply narrower selection curves that is, more selective fishing. The traditional view of improving selectivity by increasing mesh size to let smaller fish escape (Beverton & Holt 1957) could imply either increasing target size x_f, or increasing selectivity *stricto sensu s*, or both. Parameter a is a fishing mortality multiplier.

(c) Indices of fishing effects
Many solutions of equation 1 do not converge to a stable spectrum, but oscillate in time. Therefore measures of fishing effects cannot be taken at any particular time and need to be summarized over some time period after the system reached a stationary limit, either steady or oscillatory (below: over years 130 to 150). To detect fishing effects on the size spectrum including disturbances of the biomass flow, we calculated the range of total biomass in the system and total catch, and their median.

To describe spectrum regularity, we developed a measure of size diversity. To take account of size classes being ordered, an index including some measure of distance like the taxonomic diversity indices of Clarke and Warwick (1998) is required. We sought a non-linear distance metric, that would be zero for animals the same size, small when size difference is low, and reach a maximum 1 when size difference increases – two animals with a weight ratio of 10 would be approximately as distant as when the weight ratio is 5. We used a 'V-shaped' distance $d(x,y) = 1 - \exp(-|y - x|/\delta)$ between two log-weights x and y, where δ determines the 'V' width (figure S-1a of the electronic supplementary material). As d is a function of $y - x$, two fish with a given weight ratio have a similar distance, irrespective of their individual weight. Size diversity is then the expected size-distance between two random biomass units,

$$\Sigma = \frac{\int_{x_0}^{x_1}\int_{x_0}^{x_1} d\left(x, y\right)u\left(x\right)\exp(x)u\left(y\right)\exp(y)dxdy}{\int_{x_0}^{x_1}\int_{x_0}^{x_1} u\left(x\right)\exp(x)u\left(y\right)\exp(y)dxdy}$$

where $u(x)$dx is the number of individuals with size in $[x,x+dx]$. In this definition the denominator is set so that the index is 1 when all individuals are distant by $d(x,y)=1$. Using the distance between two biomass units rather than two individuals by multiplying by $\exp(x)$ and $\exp(y)$ gives

more weight to larger individuals. The diversity of a linear biomass spectrum increases as δ decreases, and peaks when the spectrum slope is −1 (figure S-1b). Peaks or gaps in the size spectrum lower its diversity. Below size diversity is calculated over the fish size range from $x_0 = 0$ to $x_1 = 4 \ln 10$.

(d) Numerical simulations

Parameters for the predation dynamics were set to the reference values used in Benoît & Rochet (2004) (table 1). Preliminary simulations showed that this choice of parameters led to sustained oscillations over time with low amplitude in the unfished spectrum. This is consistent with the findings of Law *et al.* (2009) who concluded that a Hopf bifurcation from a steady state to oscillatory solution occurs at values of volume searched (parameter *A*) lower than the one used here. A wide range of fishing scenarios was explored. Fishing selectivity varied from unselective fishing $s = 0.25$ where the typical weight ratio of a large to a small fish caught is close to $\exp(1/s) = 55$, to selective fishing $s = 4$ where this ratio is 1.28. Target sizes span from 100 g (as forage fish targeted by industrial fisheries for fish meal, or small crustaceans such as prawn) to 10 kg (a large size in modern fisheries). Actual fishing gears such as hooks, gillnets and large-mesh trawls would have a 2 to 50 kg target size with a selectivity parameter *s* between 0.5 and 1.5; small mesh trawls (*e.g.* used to catch small crustaceans) target 20 to 200 g sizes with a low selectivity $s \approx 0.5$; traps have a higher selectivity ($s \approx 1.5$) and their target size depends on the target species. All these are educated guesses based on references cited in the 'fishing selectivity' section rather than true estimates; data at the community level are lacking. Highly selective fishing $s = 4$ would describe an ideally selective fishing gear and does probably not reflect any existing gear. As for fishing intensity, parameter *a* was set so that applying the resulting fishing mortality rate to a so far unexploited ecosystem would yield a total reference catch C_0 spanning the range $0.00125 – 0.08$ g·m^{-3}. The simulated catch varied as a result of the spectrum dynamics and was lower than C_0, encompassing realistic values of total catch taken from actual ecosystems, estimated between 0.002 and 0.02 g·m^{-3} (table 2). We explored the phase-portrait in the fishing intensity-selectivity space for two target sizes.

To guard against numerical artefacts, three simulation methods were used. The classical Euler and Runge-Kutta methods approximate the dynamic system $du/dt = A(u)$ by the discrete system $u(t+dt) = u(t) + A_d(u(t))dt$ with a time step *dt*, where A_d is *A* discretized into fixed steps *dx*, starting from a given initial value. Third, we used the method of characteristics, which consists in following the evolution of cohorts. This method is more adapted to the structure of the ecological problem, as the step *dx* varies with log-weight *x*. Similar results were found with the three methods using various integration steps (from $dx = 0.02 \cdot \ln(10)$ to $0.05 \cdot \ln(10)$ and from $dt = 0.2/360$ to $2/360$). Results converged towards identical solutions as step lengths were reduced (Figure S-2). All figures shown were obtained with the characteristics method unless otherwise specified. The influence of the choice of boundary conditions was also examined by increasing the maximum size of fish x_{max} from $6 \ln(10)$ to $9 \ln(10)$; the spectrum dynamics were not qualitatively affected.

(e) Model variants

The size spectrum model of equation 1 is an idealized food web where size determines all processes and food availability is linearly reflected in growth. The lack of diversity in processes and of density-dependence might generate non-realistic instability. To investigate the impact of fishing on more stable spectra, we simulated a restricted set of fishing scenarios on size spectra stabilized by either of two ways. First, we included starvation mortality, for at low food density, growth does not just slow down: some fish die. The starvation mortality rate was $\mu_s = \mu_0 \exp(\theta(g_{st} - g) / g_{st})$ where μ_0 and θ are coefficients, *g* is assimilated food and

$g_{st} = \kappa \exp(px)$ is energy required for standard metabolism. θ was chosen large such that $\mu_s \sim 0$ when food is sufficient, and increases steeply when food becomes scarce. Second, as a proxy to growth diversity among individuals, we added a diffusion term $\sigma_d \partial^2 u / \partial x^2$ to equation 1. This mimics diversity in growth whereby two fish the same size eating the same ration have log-normally distributed growth rates, and stabilizes the size spectrum (Benoît & Rochet 2004). The diffusion coefficient σ_d was chosen just sufficient to stabilize the unfished size spectrum. In a third model variant, we acknowledge that equation 1 is a first order approximation of a more realistic model with jump-growth (Datta *et al.* 2010). Simulations including the second-order term showed no significant difference with the first-order approximation, because the size ratio between prey and predator is small enough.

3. Results

Without fishing, the size-spectrum oscillated lightly within a wavy shaped contour (figure 1a). This spectrum was not linear as in Benoît and Rochet (2004) model because of the discontinuity at minimum fish size x_{min} between the plankton and the fish spectra. This discontinuity occurs because we did not force recruitment parameters to be consistent with the plankton spectrum density. Our purpose was not to obtain a linear spectrum and we rather selected the 'most realistic' parameters; wavy size spectra are commonly observed when size classes are small enough (e.g., Pope & Knights 1982; Rice & Gislason 1996). Fishing mortality destabilized the spectrum – wave amplitude increased. Selectively targeting small sizes created a step at the target size and decreased wave period in larger sizes (figure 1b); when large sizes were targeted unselectively, waves with sharper peaks propagated both top-down and bottom-up (figure 1c); when large sizes were targeted selectively, waves increased again in amplitude and became less regular (figure 1d). High, selective fishing depleted biomass at the target size; as a consequence, predators feeding on this size range grew very slowly, and their biomass accumulated, which still amplified the depletion at the target size; similarly biomass accumulated in size ranges normally preyed upon by the target size. The biomass flow, choked with these accumulations, became oscillatory. These oscillations were sustained as shown by the time-series of summary indices (figure 2): total biomass oscillated with low amplitude and a simple pattern with no fishing (figure 2a); when small fish were targeted selectively (figure 2b and 2c), the time period was shorter, the oscillations were wider, and total catch peaked sharply; when large fish were targeted selectively, biomass had wider and less regular oscillations (figure 2d), catch showed the widest oscillations from very low values to high and steep peaks (figure 2e), and size diversity showed a complex oscillatory pattern (figure 2f).

Fishing lightly with low selectivity and targeting small sizes (left area in figure 3a) did not destabilize the spectrum much: minimum, average and maximum biomass were almost the same. When fishing intensity was increased with high selectivity ($s > 1$), oscillations amplitude increased. Oscillations widened at lower fishing intensity when fishing was more selective (top area in figure 3a). Fishing with high intensity and low selectivity was unsustainable and left no fish in the system (bottom right corner in figure 3a). When a large size was targeted, biomass oscillations appeared at lower fishing intensity and selectivity, and their amplitude at a given combination of fishing selectivity and intensity was higher, except at highest fishing intensity where both amplitude and biomass in the system decreased (figure 3b).

Maximum catch could be very large when fishing selectively, especially when large sizes were targeted (figure 4b). However, in that case minimum catch was almost zero (figure 4b), and median catch was low (figure 4a), because the high catches only happened on isolated peaks (figure 2c). Catch range was much smaller and median catch higher when fishing unselectively, especially when small fish was targeted (figure 4a,b). Maximum size diversity was insensitive to

fishing selectivity (figure 4d), but minimum and median size diversity were lower when large sizes were targeted (figure 4c,d).

Starvation mortality moderately stabilized the unfished spectrum, which oscillated within a narrower contour (not shown). Under all combinations of fishing selectivity and intensity, oscillations were less wide and there was slightly less biomass in the stabilized spectrum than without starvation mortality (figure 5a,b). Diffusion was stabilizing as well, and resulted in a stable spectrum with no or moderate fishing (minimum and maximum biomass superimposed on figure 5c). Oscillations were less wide in the stabilized spectrum than without diffusion (figure 5a,c). The effects of fishing selectivity on spectrum dynamics were qualitatively similar, whether or not the spectrum was stabilized by either mechanism (not shown).

4. Discussion

(a) Which fishing attributes destabilize the size spectrum?

Strong, non-selective fishing can eliminate the biomass from the ecosystem, while a low fishing intensity has low impact, irrespective of selectivity. All other combinations of fishing selectivity and intensity destabilize the size spectrum, that is, amplify temporal oscillations in the biomass flow. When fishing is selective and/or when large fish are targeted, oscillations appear at lower intensity; for a given intensity, oscillations have wider amplitude.

Size spectrum models can be unstable when all processes are determined by size only. Silvert & Platt (1980) showed that owing to the non-linear feedback, a wave-like instability that would damp at infinite time was created by *e.g.* a perturbation in plankton input. Law *et al.* (2009) found a Hopf bifurcation in unexploited size spectra, depending on the parameters of the feeding regime. Here we started with parameters yielding a slightly wavy size spectrum with no fishing, and showed that fishing-induced waves amplify these oscillatory dynamics. More realistic models show that various processes stabilize size spectra in the real world. A diffusion term mimicking variability in food assimilation efficiency, or a non-predation mortality term, improve the stability of the linear size spectrum (Benoît & Rochet 2004). A more explicit modelling of biodiversity with life histories (growth and reproduction) determined by asymptotic size leads to stable size spectra (Andersen & Pedersen 2010). Dynamic interactions between benthic and pelagic size spectra also improve the food web stability and resilience (Blanchard *et al.* 2010). However, our simulations show that fishing generates oscillations even in more realistic spectra stabilized by either diffusion or starvation mortality. Thus, the result that fishing destabilizes the trophic flow in size-based food webs might be quite general.

Whether actual size spectra exhibit oscillations over time is difficult to examine, because many observations are published averaged across years, or summarized by slopes or other statistics which overlook oscillations. However, a few publications show time series of survey-based demersal fish biomass size spectra that suggest oscillations with a period from a few years on Georges Bank (Murawski & Idoine 1992) to a decade on Scotian Shelf (Duplisea *et al.* 1997). This is also suggested by groundfish trawl surveys in French waters, which exhibit oscillations of various amplitude with periods of five to ten years: peaks move along the size-axis over time (figure S-3). A systematic analysis of size spectra time series with appropriate tools is required to ascertain these visual results.

(b) Is size diversity affected by fishing?

The size diversity index is sensitive to both fishing intensity and selectivity, especially when large fish are targeted. High fishing intensity or selectivity generate waves; in addition, selective fishing creates gaps in the size spectrum; both lower the size-diversity index. This result is consistent with the results of a size-spectrum model with distinct life histories determined by asymptotic size (Andersen & Pedersen 2010). With this model, exploiting limited, either large or

small, size ranges generated gaps in the exploited range and stable peaks and valleys in the adjacent sizes, thus would lower the size diversity index; this effect was stronger when fishing intensity was higher.

As size is related to many life history traits and largely determines ecological role in trophic chains (Shin *et al.* 2005), size diversity provides a proxy for functional diversity. Our results imply that both fishing intensity and selectivity affect biodiversity components of conservation interest.

(c) Consequences for fisheries management

Sustained oscillations in the size spectrum result in oscillations in the catch that can be wide when fishing is selective, especially when large fish are targeted. This has potential ecological and economic consequences. Biomass oscillations are hazardous because unstable dynamics increase the risk of change in ecosystem state and dynamics. For example, oscillations might increase system sensitivity to environmental variability – the co-occurrence of low or very high biomass and unfavourable environmental conditions increasing the probability of collapses. Catch oscillations are not desirable economically and socially as stable landings will favour stable profits and employment. Stabilizing fisheries has long been taken as a management objective (e.g., Horwood *et al.* 1990), and *e.g.* in the European Union relative stability is one of the basic principles of the Common Fisheries Policy (Morin 2000).

However, a high variability is observed in European landings, especially when fishing mortality is high (Patterson & Résimont 2007). This variability could be due to unstable fish stocks, or unstable food web dynamics, or the interplay of both. Without waiting for the investigations necessary to determine the main factor of variability, actions to stabilize either of those dynamics could be taken to stabilize landings. The results of our simulations suggest that, rather than just reducing fishing pressure as usually advised (e.g., Hall 1999; Patterson & Résimont 2007; Worm *et al.* 2009), it might be wise to reduce fishing selectivity at the same time. The idea that exploitation should be balanced across trophic levels to maintain the ecosystem trophic structure has already been put forward (Bundy *et al.* 2005). Actually fishing the size spectrum less selectively protects both large species (Myers & Worm 2005) and large individuals within species, which would also reduce the destabilizing effect of fishing on stock dynamics (Anderson *et al.* 2008). Regulations to prevent the capture of small fish, either minimum landing size or mesh size regulations, have long proven less beneficial than generally expected (Halliday & Pinhorn 2002). Our results suggest that this is because the expected benefit was wrong to start with. Of course catching and discarding small fish is sacrificing their future growth, a waste both ecologically (Christensen 1995) and economically (Pascoe 1997). Developing bycatch utilisation (Clucas 1997; Nunoo *et al.* 2009) or using a wide diversity of gears each targeting different ecosystem components (Misund *et al.* 2002) might be better ways forward than striving to avoid catching small-sized individuals and/or species.

Acknowledgements

References

Alverson, D. L., Freeberg, M. H., Murawski, S. A. & Pope, J. G. 1994 A global assessment of bycatch and discards, pp. 233. Rome, Italy: UN/FAO.

Andersen, K. H. & Beyer, J. E. 2006 Asymptotic size determines species abundance in the marine size spectrum. *Am. Nat.* **168**, 54-61.

Andersen, K. H. & Pedersen, M. 2010 Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. Lond. B* **277**, 795–802.

Anderson, C. N., Hsieh, C.-H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M. & Sugihara, G. 2008 Why fishing magnifies fluctuations in fish abundance. *Nature* **452**, 835-839.

Bellchambers, L. M. & de Lestang, S. 2005 Selectivity of different gear types for sampling the blue swimmer crab, *Portunus pelagicus* L. *Fish. Res.* **73**, 21-27.

Benoît, E. & Rochet, M. J. 2004 A continuous model of biomass size spectra governed by predation, and the effects of fishing on them. *J. Theor. Biol.* **226**, 9-21.

Beverton, R. J. H. & Holt, S. J. 1957 *On the dynamics of exploited fish populations*. Fishery Investigations, Series II. London: Her Majesty's Stationery Office.

Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A. & Kell, L. T. 2005 Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES J. Mar. Sci.* **62**, 405-411.

Blanchard, J. L., Law, R., Castle, M. D. & Jennings, S. 2010 Coupled energy pathways and the resilience of size-structured food webs. *Theor. Ecol.* **doi:10.1007/s12080-010-0078-9**.

Broadhurst, M. K. 2008 Working laterally towards perfect selectivity in fishing gears. *American Fisheries Society Symposium* **49**, 1303-1309.

Bundy, A., Fanning, P. & Zwanenburg, K. C. T. 2005 Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES J. Mar. Sci.* **62**, 503-510.

Christensen, S. 1995 Potential bioeconomic impact of reduced mortality of codend escapees of the shrimp fishery in the Davis Strait. *ICES J. Mar. Sci.* **52**, 843-851.

Clarke, K. R. & Warwick, R. M. 1998 A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* **35**, 523-531.

Clucas, I. 1997 *A study of the options for utilization of bycatch and discards from marine capture fisheries*. FAO Fish. Circ. Rome: FAO.

Conover, D. O. & Munch, S. B. 2002 Sustaining fisheries yield over evolutionary time scales. *Science* **297**, 94-96.

Daan, N., Gislason, H., Pope, J. G. & Rice, J. 2005 Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES J. Mar. Sci.* **62**, 177-188.

Datta, S., Delius, G. W. & Law, R. 2010 A jump-growth model for predator-prey dynamics: derivation and application to marine ecosystems. *Bull. Math. Biol.* **72**, 1361-1382.

Dulvy, N. K., Polunin, N. V. C., Mill, A. C. & Graham, N. A. J. 2004 Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can. J. Fish. Aquat. Sci.* **61**, 466-475.

Duplisea, D. E., Kerr, S. R. & Dickie, L. M. 1997 Demersal fish biomass size spectra on the Scotian Shelf, Canada: species replacement at the shelfwide scale. *Can. J. Fish. Aquat. Sci.* **54**, 1725-1735.

Engås, A. 1994 The effects of trawl performance and fish behaviour on the catching efficiency of demersal sampling trawls. In *Marine fish behaviour in capture and abundance estimation* (ed. A. a. O. Fernö, S.,), pp. 45-68. Oxford: Fishing News Books.

Gislason, H. & Rice, J. 1998 Modelling the response of size and diversity spectra of fish assemblages to changes in exploitation. *ICES J. Mar. Sci.* **55**, 362-370.

Hall, S. J. 1999 *The effect of fishing on marine ecosystems and communities*. Fish Biology and Aquatic Resources Series. Oxford: Blackwell.

Halliday, R. G. & Pinhorn, A. T. 2002 A review of the scientific and technical bases for policies on the capture of small fish in North Atlantic groundfish fisheries. *Fish. Res.* **57**, 211-222.

Horwood, J. W., Jacobs, O. L. R. & Ballance, D. J. 1990 A feed-back control law to stabilize fisheries. *J. Cons. int. Explor. Mer* **47**, 57-64.

Huse, I., Gundersen, A. C. & Nedreaas, K. H. 1999 Relative selectivity of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) by trawls, longlines and gillnets. *Fish. Res.* **44**, 75-93.

Huse, I., Løkkeborg, S. & Soldal, A. V. 2000 Relative selectivity in trawl, longline and gillnet fisheries for cod and haddock. *ICES J. Mar. Sci.* **57**, 1271-1282.

Kelleher, K. 2005 Discards in the world's marine fisheries: an update, pp. 131. Rome, Italy: FAO.

Kerr, S. R. & Dickie, L. M. 2001 *The biomass spectrum. A predator-prey theory of aquatic production*. Complexity in ecological systems series. New York: Columbia University Press.

Lauth, R. R., Ianelli, J. & Wakefield, W. W. 2004 Estimating the size selectivity and catching efficiency of a survey bottom trawl for thornyheads, *Sebastolobus spp.* using a towed video camera sled. *Fish. Res.* **70**, 27-37.

Law, R. 2007 Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.* **335**, 271-277.

Law, R., Plank, M. J., James, A. & Blanchard, J. L. 2009 Size-spectra dynamics from stochastic predation and growth of individuals. *Ecology* **90**, 802-811.

Lorance, P. & Trenkel, V. 2006 Variability in natural behaviour, and observed reactions to an ROV, by mid-slope fish species. *J. Exp. Mar. Biol. Ecol.* **332** 106–119.

Millar, R. B. & Fryer, R. J. 1999 Estimating the size-selection curves of towed gears, traps, nets and hooks. *Rev. Fish Biol. Fish.* **9**, 89-116.

Misund, O. A., Kolding, J. & Fréon, P. 2002 Fish capture devices in industrial and artisanal fisheries and their influence on management. In *Handbook of Fish Biology and Fisheries. Volume 2: Fisheries* (ed. P. J. B. Hart & J. D. Reynolds), pp. 13-36. Oxford, UK: Blackwell Publishing.

Morin, M. 2000 The fisheries resources in the European Union. The distribution of TACs: principle of relative stability and quota-hopping. *Mar. Policy* **24**, 265-273.

Murawski, S. A. & Idoine, J. S. 1992 Multispecies size composition: a conservative property of exploited fishery systems? *J. Northw. Atl. Fish. Sci.* **14**, 79-85.

Myers, R. A. & Worm, B. 2005 Extinction, survival or recovery of large predatory fishes. *Proceedings of the Royal society London B* **360**, 13-20.

Nunoo, F. K. E., Boateng, J. O., Ahulu, A. M., Agyekum, K. A. & Sumaila, U. R. 2009 When trash fish is treasure: The case of Ghana in West Africa. *Fish. Res.* **96**, 167-172.

Olin, M., Malinen, T. & Ruuhijärvi, J. 2009 Gillnet catch in estimating the density and structure of fish community—Comparison of gillnet and trawl samples in a eutrophic lake. *Fish. Res.* **96**, 88-94.

Pascoe, S. 1997 Bycatch management and the economics of discarding, pp. 137. Rome, Italy: UN/FAO.

Patterson, K. & Résimont, M. 2007 Change and stability in landings: the responses of fisheries to scientific advice and TACs. *ICES J. Mar. Sci.* **64**, 714-717.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. J. 1998 Fishing down marine food webs. *Science* **279**, 860-863.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P. K., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J. G. & Sainsbury, K. J. 2004 Ecosystem-based fishery management. *Science* **305**, 346-347.

Pope, J. G. & Knights, B. J. 1982 Comparison of length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank. In *Multispecies approaches to fisheries management advice*, vol. 59 (ed. M. C. Mercer), pp. 116-118: Can. Spec. Publ. Fish. Aquat. Sci.

Reznick, D., Ghalambor, C. & Nunney, L. 2002 The evolution of senescence in fish. *Mechanisms of Ageing and Development* **123**, 773-789.

Rice, J. & Gislason, H. 1996 Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J. Mar. Sci.* **53**, 1214-1225.

Rochet, M. J., Cornillon, P. A., Sabatier, R. & Pontier, D. 2000 Comparative analysis of phylogenetic and fishing effects in life history patterns of Teleost fishes. *Oikos* **91**, 255-270.

Shin, Y.-J. & Cury, P. 2004 Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can. J. Fish. Aquat. Sci.* **61**, 414-431.

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J. & Gislason, H. 2005 Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* **62**, 384-396.

Silvert, W. & Platt, T. 1978 Energy flux in the pelagic ecosystem: a time-dependent equation. *Limnol. Oceanogr.* **23**, 813-816.

Silvert, W. & Platt, T. 1980 Dynamic energy flow model of the particle size distribution in pelagic ecosystems. In *Evolution and ecology of zooplancton communities* (ed. W. C. Kerfoot), pp. 754-763. Hanover, NH: University Press of New England.

Sparholt, H. 1990 An estimate of the total biomass of fish in the North sea. *J. Cons. int. Explor. Mer* **46**, 200-210.

Stokes, T. K., McGlade, J. M. & Law, R. (ed.) 1993 *The exploitation of evolving resources.* Lect. Notes Biomath. Berlin: Springer-Verlag.

Wells, R. J. D., Boswell, K. M., Cowan Jr., J. H. & Patterson, W. F. 2008 Size selectivity of sampling gears targeting red snapper in the northern Gulf of Mexico. *Fish. Res.* **89**, 294-299.

Wileman, D. A., Ferro, R. S. T., Fonteyne, R. & Millar, R. B. (ed.) 1996 *Manual of methods of measuring the selectivity of towed fishing gears.* ICES Cooperative Research Report. Copenhagen: ICES.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A., Ricard, D., Rosenberg, A. A., Watson, R. & Zeller, D. 2009 Rebuilding global fisheries. *Science* **325**, 578-585.

Zhou, S. 2008 Fishery by-catch and discards: a positive perspective from ecosystem-based fishery management. *Fish Fish.* **9**, 308-315.

Zhou, S., Smith, A. D. M., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., Bulman, C., Bayliss, P. & Sainsbury, K. 2010 Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proc. Natl Acad. Sci. USA* **107**, 9485-9488.

Tables

Table 1. Definition of the model variables and parameters

Variable / parameter	Definition	Unit	Reference value
w	Weight of a fish	g	
x	Logarithm of w/w_0 with $w_0 = 1$g		
t	Time	year = yr	
$u(x,t)$	Number of fish at time t by unit volume, by unit of x	m^{-3}	
$\varphi(q)$	Probability of predation when a predator size x meets a prey size $x - q$		
α	Exponent of weight in volume water searched	—	0.82*
A	Volume searched by unit weight	$m^3\ yr^{-1}$	640*
e^{q_0}	Modal ratio of predator to prey size	—	100*
n	An inverse measure of the width of the predator-prey size-ratio distribution	—	5*
K	Growth efficiency	—	0.2*
x_{min}	Minimum size of fish		$-3\ln(10)$
x_{max}	Maximum size of fish		$6\ln(10)$
x_{mat}	Log weight at first reproduction		$2.7\ln(10)$ [†] (500g)
γ	Number of eggs spawned by unit weight	yr^{-1}	100[†]
β	Exponent of fecundity-weight relationship	—	1.2[†]
	Plankton spectrum	m^{-3}	$0.01\exp(-1.05x)$*
	Sea monster spectrum	m^{-3}	$0.01\exp(-1.05x)$*
	Initial fish spectrum		$0.01\exp(-1.05x)$*
$\mu_f(x)$	Fishing mortality rate	yr^{-1}	
C_0	Total catch from unexploited spectrum	$g\ m^{-3}\ yr^{-1}$	0.01 (Table 2)
a	Fishing mortality multiplier	yr^{-1}	
s	Selectivity of fishing: inverse width of the selection curve		1.44
w_0	Reference weight for size	g	1
$x_f = \log_{10}(w_f/w_0)$	Modal size of the selection curve		$2\ln(10)$
δ	Size difference for which the distance in the size diversity index is $1 - 1/e$		$2\ln(10)$
μ_s	Starvation mortality rate	yr^{-1}	
μ_0	Starvation mortality rate when food supply is just sufficient ($g = g_{st}$)	yr^{-1}	0.1
θ	Coefficient of starvation mortality rate	—	5
κ	Coefficient for standard metabolism	yr^{-1}	4[‡]
p	Exponent of standard metabolism	—	3/4[‡]
σ_d	Diffusion coefficient	yr^{-1}	0.1

* (Benoît & Rochet 2004)

[†] (Rochet *et al.* 2000)
[‡] (Andersen & Pedersen 2010)

Table 2. Estimated total catch and surface area from exploited marine ecosystems. Catch per unit volume is approximated assuming that most fishing effort is deployed in a 200 m layer near surface, except for Baltic Sea which is shallower, thus we used total volume.

Area	Total catch (10^6 tonnes yr^{-1})	Area (10^6 km²) or volume	Catch / water volume (10^{-3} g/m^3 yr^{-1})
Mediterranean	1-2[*]	2.5[‡]	2-4
North-West Atlantic	2-5[*]	6.3[‡]	2-4
North-East Atlantic	6-12[*]	14.4[‡]	2-4
North Sea	2.7[†]	0.58[†]	23
Baltic Sea	0.5[†]	21.7 10^3 km^{3}[#]	23

[*](Pauly *et al.* 1998)
[†](Sparholt 1990)
[‡]http://www.fao.org/fishery/area/search/fr
[#]http://www.marbef.org/wiki/Baltic_Sea
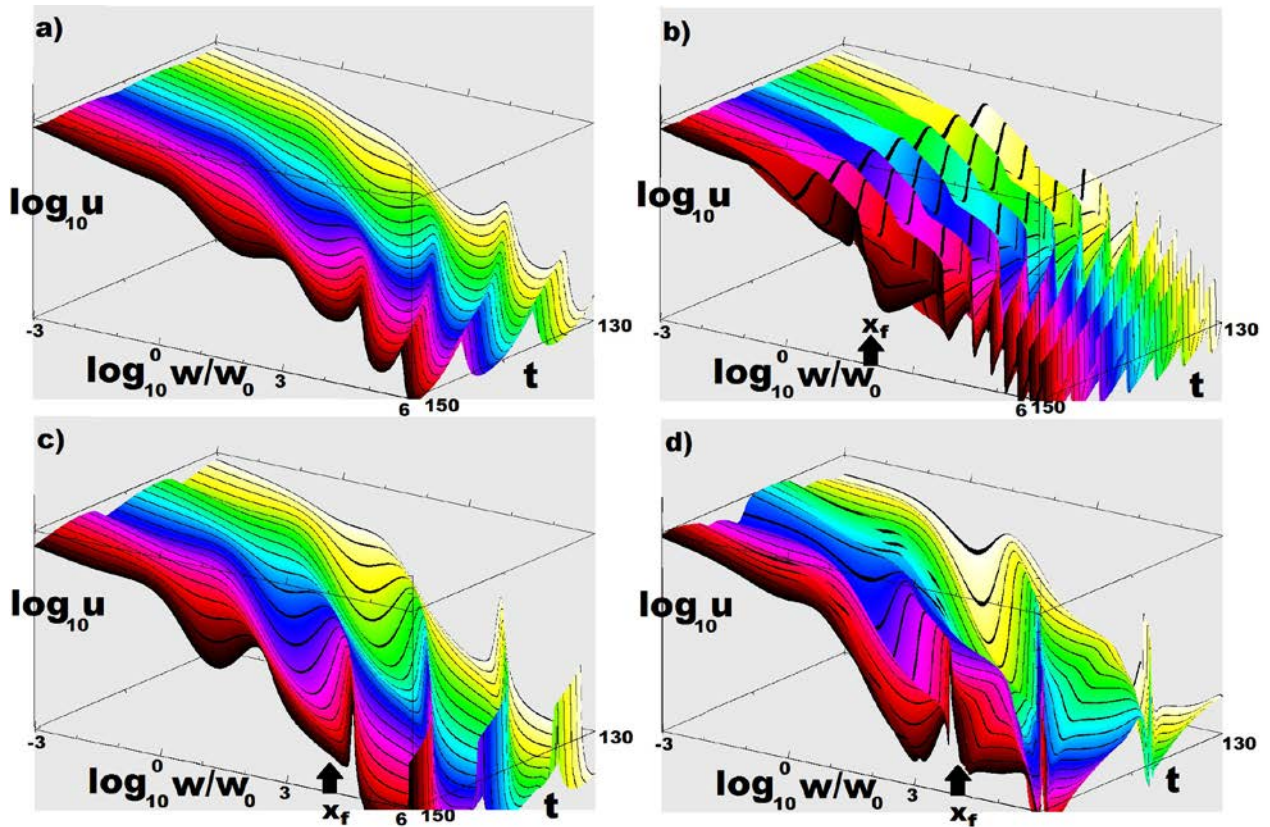
Figures

Figure 1: Examples of simulated size spectra (parameters from Table 1) over years 130 to 150. a) no fishing; b) selectively fishing small fish ($s = 4$, $\log_{10}(w_f/w_0) = 2$, $C_0 = 0.01$); c) non-selectively targeting large fish ($s = 0.25$, $\log_{10}(w_f/w_0) = 4$, $C_0 = 0.01$); d) selectively fishing large fish ($s = 4$, $\log_{10}(w_f/w_0) = 4$, $C_0 = 0.01$). Colors vary from yellow to black from year 130 to year 150. Arrows show the size targeted by fishing.
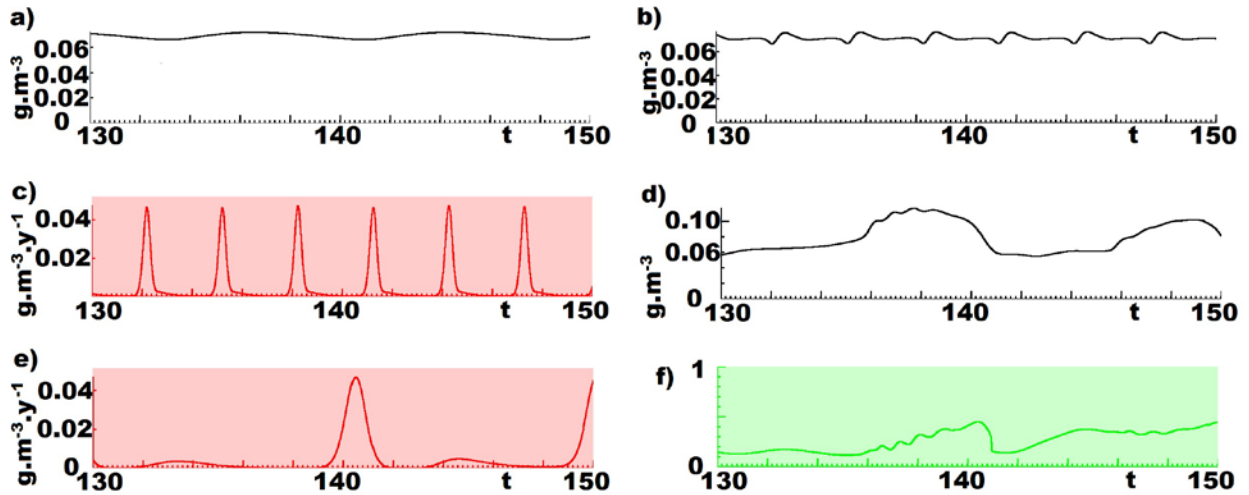
Figure 2. Examples of simulated time series of normalized biomass, catch and size diversity (parameters from Table 1) over years 130 to 150. a) Total biomass with no fishing; b) Total biomass and c) total catch with selectively fishing small fish ($s = 4$, $\log_{10}(w_f/w_0) = 2$, $C_0 = 0.01$); d) total biomass, e) total catch, and f) size diversity with selectively fishing large fish ($s = 4$, $\log_{10}(w_f/w_0) = 4$, $C_0 = 0.01$).
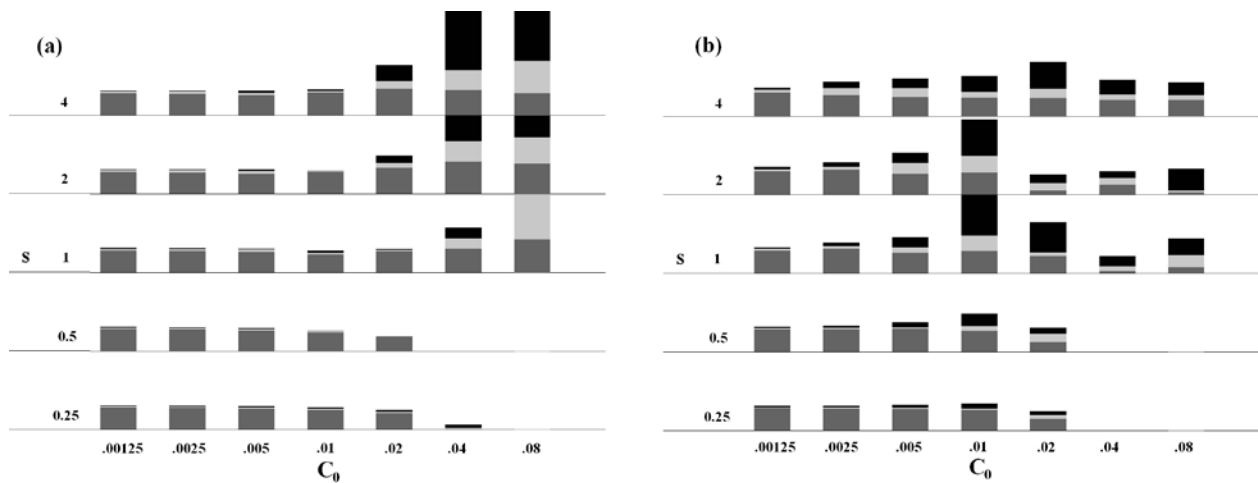

Figure 3: Summary of biomass variations as a function of fishing selectivity and intensity when target size is $\log_{10}(w_f/w_0) = 2$ (a) or $\log_{10}(w_f/w_0) = 4$ (b). The x-axis spans fishing intensity measured by expected catch C_0 that is, the catch that would be produced by applying the fishing effort to the unfished spectrum (C_0 is used to calculate the fishing mortality multiplier a). The y-axis spans fishing selectivity s. Each bar shows: minimum (dark gray), median (light gray), and maximum (black) biomass (over simulated years 130 to 150). Median biomass ≈ 0.07 $g.m^{-3}$ for $C_0 = 0.00125$. Empty cells correspond to total extinction of biomass in the system.
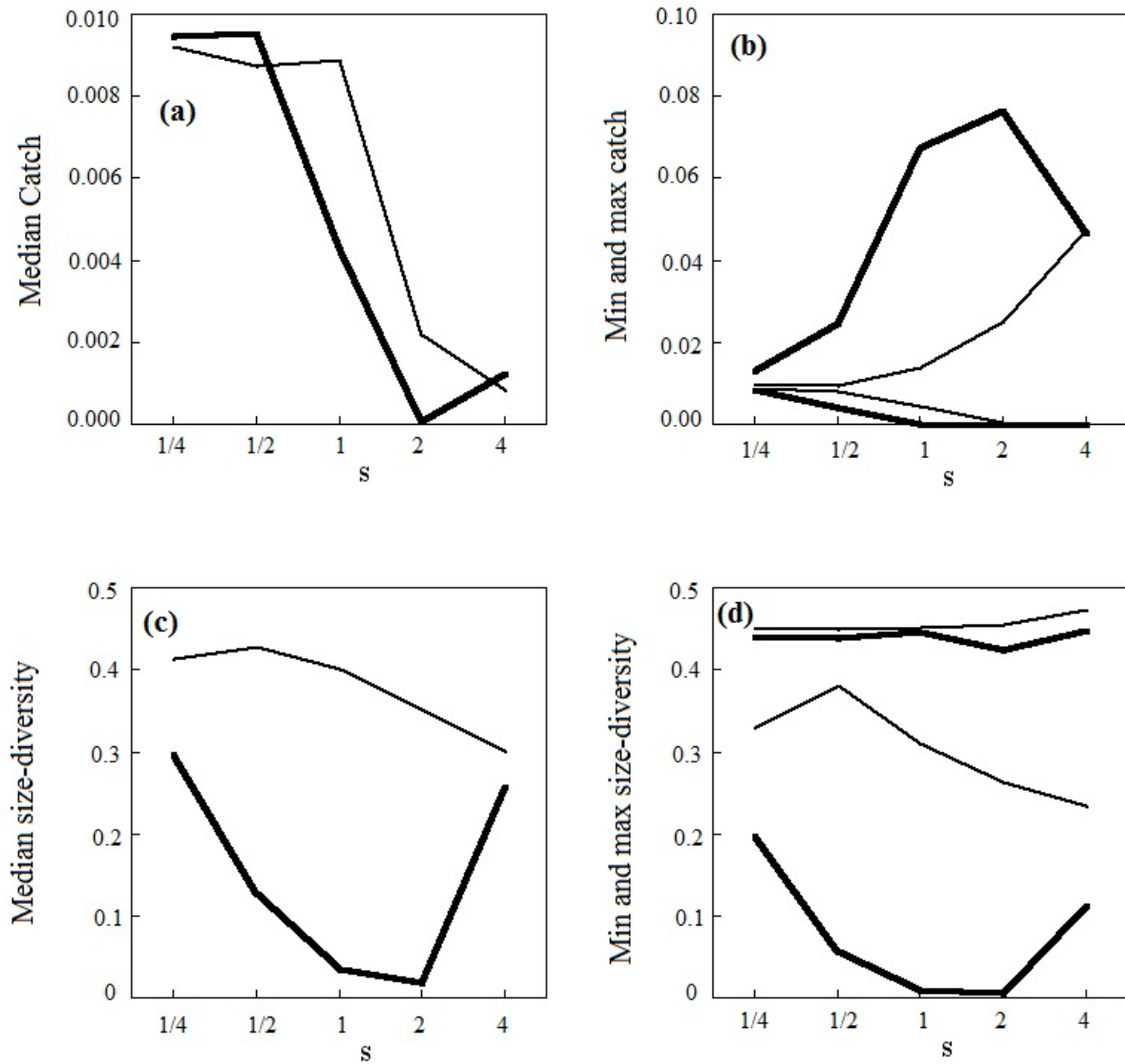
Figure 4. Community metrics as a function of fishing selectivity when targeting small ($\log_{10}(w_f/w_0) = 2$, thin lines) or large ($\log_{10}(w_f/w_0) = 4$, bold lines) fish with moderate fishing intensity ($C_0 = 0.01$), over years 130 to 150. a) median catch, b) minimum and maximum catch, c) median size diversity, d) minimum and maximum size diversity.
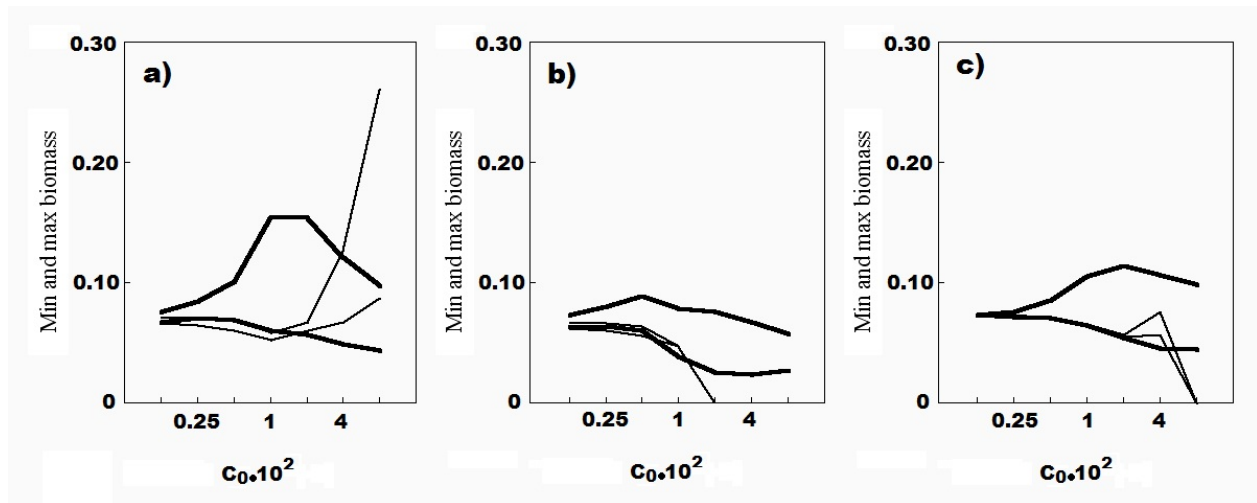
Figure 5. The effects of stabilizing spectrum dynamics on biomass amplitude: minimum and maximum biomass as a function of fishing intensity when targeting small ($\log_{10}(w_f/w_0) = 2$, thin lines) or large ($\log_{10}(w_f/w_0) = 4$, bold lines) fish with moderate fishing selectivity ($s = 1$), over years 130 to 150 (Euler method). a) non-stabilized spectrum, b) spectrum with starvation mortality, c) spectrum with diffusion.