

Why the size structure of marine communities can require decades to recover from fishing

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Supplement. This supplement details (1) the model structure, dynamics and underlying key assumptions for the PDMM (Population-Dynamical Matching Model) variant used in the main text; (2) the methodology used to parameterise the model; (3) details of how the 5 indicators used in the main text are calculated for the model community used; and (4) example recovery trajectories for 4 of the 5 indicators used, including power-law fits.

MODEL STRUCTURE AND DYNAMICS — FURTHER DETAILS

The Population-Dynamical Matching Model (PDMM) generates large model communities using an iterative process representing the natural assembly of complex ecological communities. For the PDMM variant used in the main text, the iterative assembly process is the same as that for the PDMM variant used in Rossberg et al. (2008), except for four differences: (1) only one community is modelled, as opposed to a metacommunity of 4 communities connected by migration; (2) more than 2 new species can appear in a modelled community in one iteration; (3) all trait values of model species are now constrained within defined boundaries (described in more detail below); and (4) a new formula for the functional response is used, incorporating a recent theory of prey-switching (described in more detail below). Hereafter, a summary of the iterative assembly process is given, followed by descriptions of details regarding the determination of trait values for newly invading species and the population dynamics of each model species. Throughout, there is particular focus on parts that differ from the PDMM variant used in Rossberg et al. (2008). Fig. S1 schematically illustrates the iterative assembly process, and Table S1 lists definitions for all model parameters used (Table S1 also gives the values derived for each parameter, and hence is found below after the section on ‘Model Parameterisation’).

Starting with an empty community, the first step in the iterative process is determination of the types (producer or consumer) and trait values of a small number of new species to be added to the community. The number of species added is $pS + 1$ rounded down to the nearest integer, where S is the number of species currently in the community and p is a constant. When there are no extant producer species, the type of an invading species is automatically set to be a producer, because consumers can never invade in this case.

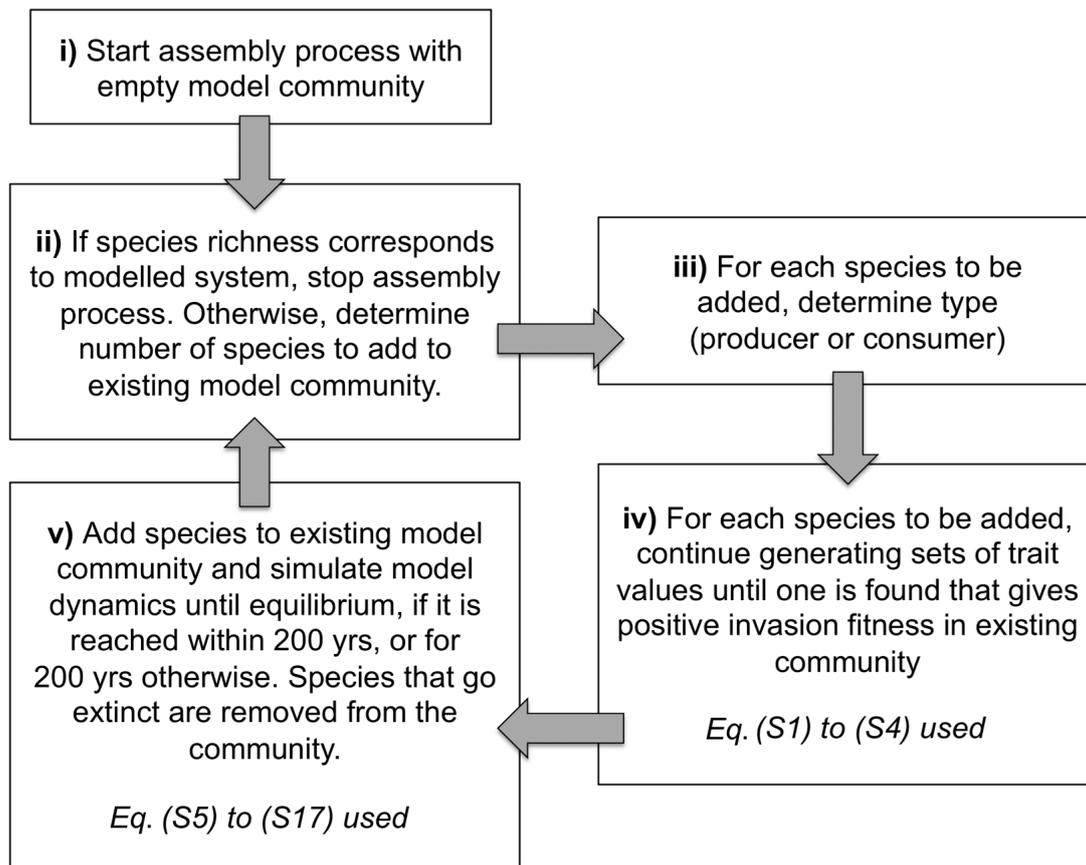


Fig S1. Schematic representation of the process by which the Population-Dynamical Matching Model (PDMM) generates a model community. Starting with an empty model community in Step i), an iterative loop, Steps ii)-v), is run repeatedly until the model community has species richness corresponding to the modelled system

Otherwise, the type of an invading species is determined by deciding at random with equal probability if it will be a producer or a consumer. Then, to determine the trait values of the invading species, an extant species of the same type is chosen at random and its traits modified, as described below, until one with a positive invasion fitness (Metz 2008) in the current community is found. This method of determining the trait values of invading species gives rise to phylogenetic correlations of traits, which have been empirically found to be important in structuring food-webs (Cattin et al. 2004, Bersier & Kehrlı 2008, Naisbit et al. 2012). If there are no extant species of the same type as the invading species, then the body mass of the invading species is set to a default value and its other trait values are determined randomly, as described below.

After the types and trait values for all invading species have been determined, the set of invading species is then added to the community and population dynamics are simulated until the community reaches a dynamic equilibrium, where all populations have attained an equilibrium state. A heuristic algorithm is used at each time-step to determine whether this is the case, whereby, at a particular time-step, a species is taken to have reached an equilibrium if the natural logarithm of its population biomass has changed by <0.01 in the last third of the time-series simulated. In the uncommon situations where an equilibrium for the community cannot be detected after 200 yr of simulation time, the simulation is stopped at this point. Species that go extinct (species with population biomass smaller than maturation body mass, M_{mat} , or with an exponentially decaying population biomass) are removed from the model. An iteration ends after this simulation of the model dynamics. Once all iterations have been completed, if the final model community is not at a dynamic equilibrium, then model dynamics are simulated until one is reached.

Determination of Trait Values for New Species

For a new (invading) model species k , let \vec{F}_k , \vec{G}_k and \vec{V}_k be the vectors of foraging, (producer) competition and vulnerability traits respectively. The length of each vector, i.e. the number of quantitative traits it represents, is D . Contrary to the PDMM variant used by Rossberg et al. (2008), the value of each foraging, competition and vulnerability trait is now constrained such that it falls within a hypersphere of dimension D and radius r_F , r_G or r_V respectively. [A hypersphere is a sphere generalised to higher dimensions; specifically, a hypersphere of dimension $D \geq 4$ and radius R is the set of vectors (x_1, x_2, \dots, x_D) satisfying $x_1^2 + x_2^2 + \dots + x_D^2 = R^2$.] Constraining the trait values to within hyperspheres effectively constrains the volume of trophic niche space, and hence the maximum number of species that can coexist in the model.

If there are no extant species of the same type as species k , then each trait vector is sampled from an even distribution of all trait vectors lying within the corresponding hypersphere. Otherwise, the trait values of species k are determined by mutating the trait values of a randomly chosen extant producer or consumer species i . The trait vectors for species k are given by:

$$\vec{F}_k = \vec{F}_i + \mu_F \vec{\xi} \quad (\text{S1})$$

$$\vec{G}_k = \vec{G}_i + \mu_G \vec{\xi} \quad (\text{S2})$$

and

$$\vec{V}_k = \vec{V}_i + \mu_V \vec{\xi} + \vec{V}_0 \quad (\text{S3})$$

where $\vec{\xi}$ represents a vector of random numbers that are independently sampled from a standard normal distribution, and μ_F , μ_G and μ_V determine the rates of change of the foraging, competition and vulnerability trait vectors, respectively. The vector \vec{V}_0 has as its first entry $s/2$ for producers and $-s/2$ for consumers, and all other entries equal to zero; the parameter s quantifies the separation of producers and consumers in their vulnerability traits (Rossberg et al. 2008). If the new trait value given by Eq. (S1), (S2) or (S3) falls outside the hypersphere with radius r_F , r_G or r_V , respectively (centred at 0 or, for vulnerability traits, at \vec{V}_0), then it is reflected back in at the surface of the hypersphere — for hypothetical neutral evolution, this leads to even distributions of traits in the hyperspheres.

If there are no extant species of the same type as species k , then the maturation body mass of the new species, $M_{\text{mat},k}$, is set to the default value of 10^{-10} kg when species k is a producer and the default value of 10^{-7} kg when species k is a consumer. The default maturation body mass for consumers is the default value for producers multiplied by the preferred predator-prey M_{mat} ratio, $\eta_c = 10^3$ (see section on ‘Model Parameterisation’ below). Otherwise, if an extant species of the same type as k exists, then $M_{\text{mat},k}$ is obtained by mutating the maturation body mass of the selected ancestral species i , $M_{\text{mat},i}$, according to:

$$M_{\text{mat},k} = d^{\xi} M_{\text{mat},i} \quad (\text{S4})$$

where ξ is a random number sampled from a standard normal distribution, so that $\log_e^2(d)$ becomes the variance of $\log_e(M_{\text{mat},k})$ in one time-step (Rossberg et al. 2008). If $M_{\text{mat},k}$ is outside the range $[M_{\text{min}}, M_{\text{max}}]$, then the loss rate of the new species (see Eqs. S8 & S9 below) is increased by over an order of magnitude, which makes this species unviable.

Equations for Population Dynamics of Model Species

For a PDMM community with S species, which are indexed such that the S_p producer species come first, the equation describing the population biomass dynamics of a producer species i is:

$$\frac{dB_i}{dt} = \sigma_i \exp\left(-\sum_{j=1}^{S_p} d_{ij} B_j\right) B_i - \sum_{j=S_p+1}^S f_{ij} B_j - l_i B_i \quad (S5)$$

where σ_i is the maximum population growth rate, d_{ij} is the competition coefficient for producer species i and j , f_{ij} is the functional response for prey species i and consumer species j , and l_i is the loss rate due to processes other than consumption. d_{ij} is a function of M_{mat} and the competition traits of species i and j ; f_{ij} is a function of M_{mat} , the vulnerability traits of species i and the foraging traits of species j . The explicit forms of d_{ij} and f_{ij} are given in Eqs. (S11) & (S13) below.

The equation describing the population biomass dynamics of a consumer species i is:

$$\frac{dB_i}{dt} = \varepsilon \sum_{j=1}^S f_{ji} B_j - \sum_{j=S_p+1}^S f_{ij} B_j - l_i B_i \quad (S6)$$

where ε is the assimilation efficiency.

The maximum growth rate in Eq. (S5) and the loss rates in Eqs. (S5) & (S6) follow allometric scaling laws:

$$\sigma_i = C_\sigma M_{\text{mat},i}^{\xi_\sigma} \quad (S7)$$

$$l_{i,p} = C_{lp} M_{\text{mat},i}^{\xi_{lp}} \quad (S8)$$

and

$$l_{i,c} = C_{lc} M_{\text{mat},i}^{\xi_{lc}} \quad (S9)$$

where $l_{i,p}$ and $l_{i,c}$ are the loss rates, l_i , for producer and consumer species, respectively. An additional parameter determining the population dynamics of consumer species i is its maximum growth rate, $r_{i,\text{max}}$. This is used to derive its handling time (Rossberg et al. 2008; see Eq. S15 for the explicit form of handling time), which is used in the formula for the functional response f_{ij} (see Eq. S13). $r_{i,\text{max}}$ also follows an allometric scaling law:

$$r_{i,\text{max}} = C_{r,\text{max}} M_{\text{mat},i}^{\xi_{r,\text{max}}} \quad (S10)$$

To model the physiological constraints that limit the maturation body sizes of organisms to lie above M_{min} , the loss rate is increased by $(\sigma_i - l_{i,p})\nu$ for producers and $(r_{i,\text{max}} - l_{i,c})\nu$ for consumers, where $\nu = 1/[(M_{\text{mat}}/M_{\text{min}}) - 1]$. For the empirically-derived value of $M_{\text{min}} = 10^{-15}$ kg (see next section on ‘Model Parameterisation’), ν is very small (≤ 0.0101) if $M_{\text{mat}} \geq 10^{-13}$ kg, so that the increase in the loss rate is negligible for all but the smallest species.

The explicit form of the producer competition coefficients d_{ij} is:

$$d_{ij} = d_{ij} \exp\left(-\frac{|\vec{G}_i - \vec{G}_j|^2}{2w_p^2}\right) \quad (\text{S11})$$

where the exponential term represents the niche overlap between the two producer species i and j , \vec{G} is the competition trait vector and w_p is the producer niche width (Rossberg et al. 2008). In addition,

$$d_{ij} = \sigma_j \frac{\log_e(\sigma_j/l_{j,p})}{GPP_{\max} A} \quad (\text{S12})$$

where GPP_{\max} is the maximum gross primary production of a producer species in monoculture and A is the model area (Rossberg et al. 2008).

The formula for functional responses f_{ij} differs from that used by Rossberg et al. (2008). It is designed to give a more natural representation of prey-switching while preserving the ‘‘common sense condition’’ of Arditi & Michalski (1995) and Berryman et al. (1995): if a resource population is split into 2 populations with identical traits, then all dynamics are invariant (remain the same). This new form incorporates a theory of predator switching between multiple prey species (van Leeuwen et al. 2013) and is given by:

$$f_{ij} = \frac{a_j c_{ij} B_i \sum_{k=1}^S s_{ik} c_{kj} B_k}{\sum_{k=1}^S c_{kj} B_k \left(1 + a_j T_j \sum_{m=1}^S s_{km} c_{mj} B_m\right)} \quad (\text{S13})$$

where a_j is the attack rate for consumer species j , T_j is the handling time for consumer species j , s_{ij} is the similarity between two prey species i and j with respect to prey switching, and c_{ij} is the trophic interaction coefficient for prey species i and consumer species j . Specifically, we used:

$$a_j = \frac{g l_{j,c}}{A} \quad (\text{S14})$$

where g is the aggressivity of consumer species,

$$T_j = \frac{\varepsilon}{r_{j,\max} + l_{j,c}} \quad (\text{S15})$$

as in Rossberg et al. (2008), and

$$s_{ij} = \exp\left(-\frac{|\vec{V}_i - \vec{V}_j|^2}{2w_s^2}\right) \quad (\text{S16})$$

where w_s is the switching similarity width, controlling the degree of prey switching. Unlike in the model variant of Rossberg et al. (2008), in Eq. (S14), the aggressivity g is fixed for all species following the model of Andersen & Pedersen (2010). This does not fundamentally change the model assembly procedure as the consumers still have different growth rates by virtue of their different traits, and accelerates model assembly.

The explicit form of c_{ij} has the same dependence on trophic traits as that given in the original formulation by Rossberg et al. (2008), but with a modified dependence on the predator-prey M_{mat} ratio. It is given by:

$$c_{ij} = \exp\left(-\frac{|\vec{F}_j - \vec{V}_i|^2}{2w_c^2}\right) \left[\left(\frac{M_{\text{mat},j}}{M_{\text{mat},i}}\right)\left(\frac{1}{\eta_c}\right)\right]^{-\alpha_c} \quad \text{for } \frac{M_{\text{mat},j}}{M_{\text{mat},i}} > \eta_c \quad (\text{S17a})$$

and

$$c_{ij} = \exp\left(-\frac{|\vec{F}_j - \vec{V}_i|^2}{2w_c^2}\right) \left[\left(\frac{M_{\text{mat},j}}{M_{\text{mat},i}}\right)\left(\frac{1}{\eta_c}\right)\right]^{\beta_c} \quad \text{for } \frac{M_{\text{mat},j}}{M_{\text{mat},i}} \leq \eta_c \quad (\text{S17b})$$

where w_c is the consumer niche width and η_c is the preferred predator-prey M_{mat} ratio. α_c and β_c are exponents that determine how quickly the interaction strength c_{ij} decreases when the predator-prey M_{mat} ratio increases above and decreases below η_c respectively.

The functional response, Eq. (S13), can be derived by distinguishing for a predator species j , as in Holling's (1959) 'disk equation', those individuals that are currently handling prey and those that are actively foraging. However, differing from Holling, the propensity of the predator to consume prey k after having previously consumed prey m is scaled by a dimensionless factor s_{km} satisfying $s_{km} = s_{mk}$. Let B_{0k} be the biomass of predators belonging to species j that are not handling any prey and whose previous prey was species k , and let B_{km} be the biomass of predators belonging to species j that are handling prey species k and whose previous prey was species m . Then, following van Leeuwen et al. (2007, 2013), assuming that birth and death processes for the predator are slow compared to handling, since a predator handles many prey between births and deaths, gives:

$$\frac{dB_{0k}}{dt} = \sum_{m=1}^S \left(-a_j c_{mj} s_{mk} B_m B_{0k} + \frac{B_{km}}{T_j} \right) \quad (\text{S18a})$$

$$\frac{dB_{km}}{dt} = -\frac{B_{km}}{T_j} + a_j c_{kj} s_{km} B_k B_{0m} \quad (\text{S18b})$$

Assuming that these biomass components of predator species j are at equilibrium, so that we can set the right-hand sides in Eqs. (S18a,b) to 0, solving Eq. (S18b) for B_{km} and substituting into Eq. (S18a) gives:

$$\sum_{m=1}^S \left(-a_j c_{mj} s_{mk} B_m B_{0k} + a_j c_{kj} s_{km} B_k B_{0m} \right) = 0 \quad (\text{S19})$$

Eq. (S19) gives rise to a set of S equations with S unknowns B_{01}, \dots, B_{0S} . This system can be solved to give $B_{0m} = \lambda c_{mj} B_m$, where λ is a constant. The total biomass of predator species j is, using Eq. (S18b):

$$\sum_{k=1}^S \left(B_{0k} + \sum_{m=1}^S B_{km} \right) = \sum_{k=1}^S \left(B_{0k} + a_j T_j \sum_{m=1}^S s_{km} c_{kj} B_k B_{0m} \right) \quad (\text{S20})$$

whereas the biomass of prey species i consumed by attacking individuals of predator species j is

$$B_i \sum_{k=1}^S a_j c_{ij} s_{ik} B_{0k} \quad (\text{S21})$$

The functional response f_{ij} is the mean consumption rate of species j on species i , which is the expression in Eq. (S21) divided by the expression in Eq. (S20). This is equivalent to Eq. (S13).

MODEL PARAMETERISATION — FURTHER DETAILS

To fully specify the model, the rationale underlying the quantification of all model parameters is now described. After an explanation of the rationale for quantifying the parameter p , the detailed rationale for quantifying parameters related to the trait values of new species is given. This is followed by a discussion of the quantification of parameters related to population dynamics. The final part of this section shows how some of the model parameters can be changed to scale the biomass for each species in a PDMM community, such that results in the main text can be taken to be biomass-invariant.

Table S1 summarises the values used for all model parameters, together with data sources used for parameterisation. Methodologically, the parameterisation largely follows Rossberg et al. (2008), but a number of new data sources are used to achieve parameterisation of the model for a temperate marine shelf community. Wherever possible, data from the Northeast Atlantic is used.

Number of Invading Species

The parameter p , which determines the number of newly invading species per iteration, is chosen to be 0.01, as motivated by the need to ensure that model assembly is sufficiently quick while generally avoiding interactions between invading species.

Quantification of Parameters Used in Determination of Trait Values for New Species

The length of the trait vectors, D , is chosen to be 5, following Rossberg et al. (2008). In addition, the minimum maturation body mass, M_{\min} is taken to be 10^{-15} kg, which is the lowest body mass found for marine phytoplankton from Beardall et al. (2009), assuming that $1 \mu\text{m}^3$ is equivalent to 10^{-15} kg (Fenchel & Finlay 1983). The maximum maturation body mass, M_{\max} , is taken to be $10^{2.54}$ kg (347 kg), which is the highest maturation body mass calculated for fish species from the Celtic-Biscay Shelf and North Sea. These maturation body masses are calculated by applying length-weight conversion parameters from FishBase (Froese & Pauly 2010) to maturation lengths for all fish species in the two regions. The lists of all fish species for the two regions are produced using the ‘Information by Ecosystem’ tool and ‘All fishes’ option at www.fishbase.org (Froese & Pauly 2010).

For the other parameters used to determine trait values of new species, no directly measured empirical values are available. Thus, these parameters are adjusted freely to values (see Table S1) that give desirable model communities with properties resembling those for a temperate marine shelf community in the Northeast Atlantic (properties as described in ‘Model validation’ in the main text). In particular, the radius of the hypersphere constraining the values of the foraging traits, r_F , is fixed at a high value relative to the radius of the hypersphere constraining the values of the vulnerability traits, r_V (100 compared to 3.81). This means that the range of foraging traits of viable consumer species is limited and controlled by the range of vulnerability traits of viable resource species.

Quantification of Parameters Used in Equations for Population Dynamics of Model Species

In the dynamic equation for model consumer species, Eq. (S6), the assimilation efficiency, ε , is set to 0.6. This is the average of the 2 typical values for herbivores and carnivores taken from Hendriks (2007), derived by considering a range of invertebrates and vertebrates, including aquatic invertebrates and bony fish (Hendriks 1999).

The prefactors and exponents for the allometric scaling laws, Eq. (S7) to Eq. (S10), influencing population dynamics via Eqs. (S5) & (S6), are quantified as follows. For the scaling law used for the maximum population growth rate of producers, σ_i , the prefactor C_σ and exponent ζ_σ are set according to the empirical power-law of Niklas & Enquist (2001) for producers, including phytoplankton. For the scaling law used for the loss rate of producers, $l_{i,p}$, the prefactor C_{lp} is set to the empirical value found by Brown et al. (2004) for unicellular eukaryotes and the exponent ζ_{lp} is set to the theoretically derived, but empirically supported, value of $-1/4$ for biological organisms in general (Brown et al. 2004). Similarly, for the scaling law used for the loss rate of consumers, $l_{i,c}$, the prefactor C_{lc} is set to the average of the 2 empirical values found by Brown et al. (2004) for fish and invertebrates, and the exponent is again set to $-1/4$ (Brown et al. 2004). For the scaling law used for the maximum growth rate of consumers, $r_{i,max}$, the prefactor $C_{r,max}$ is difficult to quantify because in studies such as Hendriks (2007) and those used by Savage et al. (2004), the growth of organisms under conditions of maximum growth (no predators and a food supply that is not limiting) is not considered, or an approximation for $C_{r,max}$ is used that could lead to heavy underestimates for iteroparous species (May 1976) such as many marine fish and invertebrate species. In light of this uncertainty, $C_{r,max}$ is simply set to be a multiple of the prefactor for the loss rate, C_{lc} , with the constant of proportionality chosen such that model consumer species can be generated with an M_{mat} range corresponding to that spanned by marine invertebrates and fish. The corresponding exponent $\zeta_{r,max}$ is set to the theoretically derived value of $-1/4$ (Savage et al. 2004). The precise values chosen for all prefactors and exponents are given in Table S1.

The parameters controlling the producer competition coefficients d_{ij} , given in Eq. (S11), are quantified as follows. Firstly, the producer niche width, w_p , is set freely in the absence of appropriate empirical data (as in Rossberg et al. 2008) to the value 1.32, which gives desirable model communities with properties resembling those for a temperate marine shelf community in the Northeast Atlantic (properties as described in ‘Model validation’ in the main text). Secondly, the maximum GPP of a single producer species, GPP_{max} , is determined using primary production values from the Sea Around Us Project (2010) and the conversion relationship $1 \text{ g C} = 1/0.07 \text{ g wet weight}$ (Peters 1983). Using this data, the primary production of the North Sea is calculated as $5.81 \text{ kg m}^{-2} \text{ yr}^{-1}$ and that for the Celtic-Biscay Shelf is calculated as $4.99 \text{ kg m}^{-2} \text{ yr}^{-1}$. Thus, GPP_{max} is set to a value, $0.131 \text{ kg m}^{-2} \text{ yr}^{-1}$, that is below these 2 upper bounds and which gives producer species in the M_{mat} range for phytoplankton. Thirdly, the model area A is set to $5 \times 10^{10} \text{ m}^2$, which is the area of the Celtic Sea as calculated using ICES rectangles (ICES 1977) and Vincenty’s formulae (Vincenty 1975). However, as shown in the next section on Scaling Biomasses, model results can be taken to be invariant over a wide range of values of A spanning an order of magnitude.

Next, the parameters in the consumer functional response, Eq. (S13), are quantified. Firstly, as for w_p , the switching similarity width and the consumer niche width, w_s and w_c respectively, are set freely in the absence of appropriate empirical data to a value of 0.75. Similarly, the aggressivity for consumer species, g , is set freely in the absence of empirical data to $10^{5.51} \text{ kg}^{-1} \text{ m}^2$. These choices give desirable model communities with properties

resembling those for a temperate marine shelf community in the Northeast Atlantic. Secondly, the preferred predator-prey M_{mat} ratio, η_c , is set to 10^3 following the analysis of Jennings et al. (2002) for a benthic fish and invertebrate community from the North Sea. Thirdly, the exponent that determines how quickly the interaction strength c_{ij} decreases when the predator-prey M_{mat} ratio increases above η_c , α_c (see Eq. S17a), is set to 0.05. This means that c_{ij} declines with an exponent of -0.05 above η_c (Fig. S2). Lastly, the exponent that determines how quickly the interaction strength c_{ij} decreases when the predator-prey M_{mat} ratio decreases below η_c , β_c (see Eq. S17b), is set to 0.25. This means that c_{ij} also decays below η_c , but quickly with an exponent of 0.25 (Fig. S2). These values of α_c and β_c are chosen to model the broad population-level predator-prey size windows resulting from the wide range of body sizes covered by typical marine organisms (Rossberg 2012, Section IX.C). For example, the larvae of cod (*Gadus morhua*) are about 0.4 cm long (Folkvord 2005) and feed on plankton (Mackinson & Daskalov 2008) that have small maturation body masses below about 10^{-8} kg (Beardall et al. 2009, Barnes et al. 2011); however, adult cod can grow to over 100 cm in length (Froese & Pauly 2010) and feed on fish that have maturation body masses above 10^{-1} kg, such as whiting (*Merlangius merlangus*) (diet of cod given by Mackinson & Daskalov [2008] and maturation body masses derived using data from FishBase [Froese & Pauly 2010], as described above). Thus, for cod, which has a maturation body mass of about 1 kg (derived using data from FishBase [Froese & Pauly 2010], as described above), the predator-prey mass ratio window spans more than 7 orders of magnitude. The window used in the PDMM decays exponentially below the preferred predator-prey ratio η_c , which means that a consumer's diet can contain species with larger maturation body masses, representing consumption of these larger species at early life-history stages. For example, small pelagic fish such as herring can feed upon the larvae of their larger predators (Walters & Kitchell 2001, Fauchald 2010). Thus, the wide predator-prey windows used in the PDMM capture competition between small and large species for food, as well as predation of small species on large species.

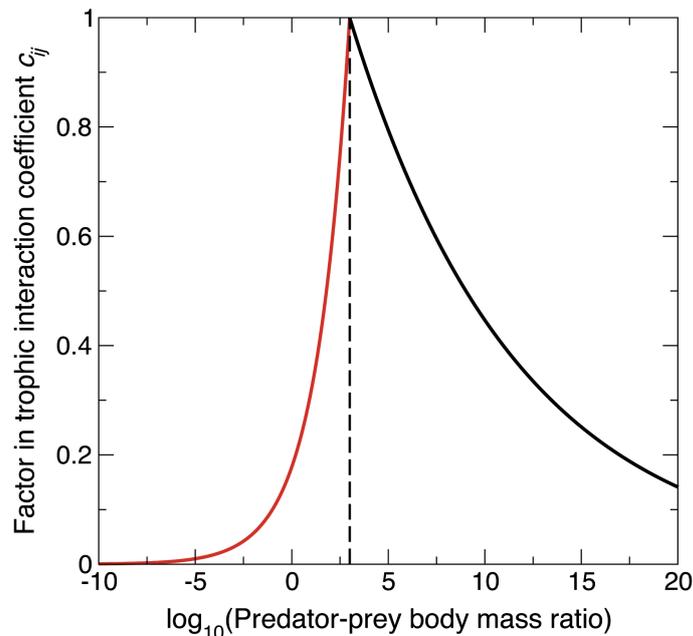


Fig. S2. Body-size dependence of the non-exponential factor in the model trophic interaction coefficient c_{ij} , for prey species with a smaller (black line; Eq. S17a) and larger (red line; Eq. S17b) maturation body mass than that corresponding to the preferred predator-prey M_{mat} ratio (dashed vertical line)

Scaling Biomasses of Modelled Populations

One of the PDMM parameters is the area modelled, A (see Table S1). It is easily verified from Eqs. (S5) to (S17) that, ignoring extinctions, model dynamics remain invariant when changing the value of A and scaling the population biomasses accordingly by a constant factor. Thus, changing A can only affect model dynamics by changing extinction times. However, for the large areas we consider, the biomass extinction threshold for each species is typically small relative to the biomass of any species in the model community, such that model dynamics should change by little with A (for example, species that take longer to go extinct when A is increased are expected to change model dynamics by little because their biomasses generally remain relatively small during the extended period). Therefore, changing A is expected to have little effect on model dynamics, and hence model assembly.

Nonetheless, we test the effects of using a range of A values covering the area of the Celtic Sea (approx. $5 \times 10^{10} \text{ m}^2$; calculated using ICES rectangles (ICES 1977) and Vincenty's formulae from Vincenty 1975) to an area greater than that of the North Sea (approx. $7 \times 10^{11} \text{ m}^2$; Sea Around Us Project 2010). Values for the other parameters are taken from Table S1, except for the radii of the hyperspheres for the foraging, competition and vulnerability traits (r_F, r_G, r_V); the parameters determining the variability of these traits (μ_F, μ_G, μ_V); and the producer-consumer separation (s). These seven parameters are multiplied by a factor of 2/3, such that the possible range of values that each foraging, competition and vulnerability trait can take is smaller, resulting in fewer model species and smaller model communities. Using these parameter values in the PDMM assembly procedure gave a model shelf community that grew in species richness, at similar rates over the range of A considered (Fig. S3). For each of the six A values tested, model assembly was run until about 24000 species were added to the existing community by invasion. At this point, it was clear that increasing A did not produce a systematic trend in the species richness trajectories. Thus, only one value of A was used to produce simulation results in the main text, the smallest value (Table S1). Note that the set of parameters used to draw the black line in Fig. S3, with the smallest value of A , was also used to generate the small model community used for Fig. 9 in the main text.

There is a second scaling transformation that leaves model dynamics essentially unchanged. Ignoring extinctions, from Eqs. (S5) to (S17), increasing the maximum GPP of a single producer species, GPP_{\max} , and decreasing the aggressivity, g , by a constant factor X has the same effect as increasing A by the factor X , except that now both biomass density and biomass of each species increases by X . Thus, as for changing A , changing GPP_{\max} and g in this way can only affect model dynamics by changing extinction times. However, as for changing A , model dynamics should change by little when rescaling GPP_{\max} and g , because the biomass extinction threshold for each species is typically small relative to the biomass of any species in the model community. GPP_{\max} can be varied up to $5.81 \text{ kg m}^{-2} \text{ yr}^{-1}$ (see details of its parameterisation in the section on 'Model Parameterisation' above; Sea Around Us Project 2010) and g can be varied in the absence of empirical data for its parameterisation. Thus, for the model community used in the main text, the biomass of each species can be scaled up or down by varying A or GPP_{\max} and g , with little effect on model dynamics. Therefore, our results can be taken to hold if the biomass and/or biomass density of each species is scaled by a factor X , because model dynamics can be taken to be largely invariant in these cases.

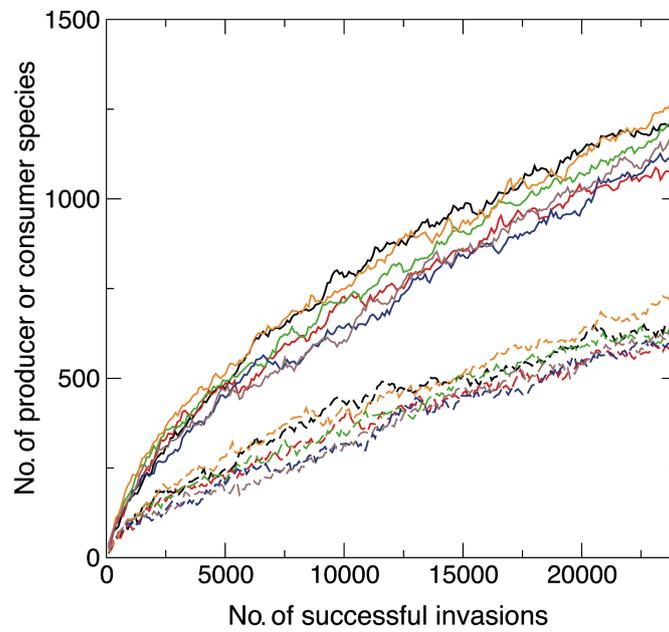


Fig. S3. Model assembly trajectories for parameter sets (see text in Supplementary Material for details) with different areas A , showing how the number of producer and consumer species (solid and dashed lines respectively) change with the number of species added to/invading the community. The black, red, green, blue, orange and brown lines represent increasing values of A being used: $5 \times 10^{10} \text{ m}^2$, $1 \times 10^{11} \text{ m}^2$, $2.5 \times 10^{11} \text{ m}^2$, $5 \times 10^{11} \text{ m}^2$, $7.5 \times 10^{11} \text{ m}^2$ and $1 \times 10^{12} \text{ m}^2$ respectively

Table S1. List of parameters in the Population-Dynamical Matching Model (PDMM) together with their definitions and values, and any data sources used for quantification

Parameter	Definition	Value	Data source(s)
Species invasion parameters			
d	Determines the amount by which M_{mat} for an existing species varies when determining M_{mat} for a new invading species. The new value of $\log_e(M_{\text{mat}})$ is the old value plus a random normal variable with mean 0 and standard deviation $\log_e(d)$.	4	
D	Niche space dimension	5	Rossberg et al. (2008)
M_{min}	Minimum M_{mat} that a model species can take.	10^{-15} kg	Fenchel & Finlay (1983), Beardall et al. (2009)
M_{max}	Maximum M_{mat} that a model species can take.	$10^{2.54}$ kg	Froese & Pauly (2010)
p	$pS + 1$ rounded down to the nearest integer is the number of species invading at each iteration.	0.01	
$r_{\text{F}}, r_{\text{G}}, r_{\text{V}}$	Radii of hyperspheres for the foraging traits (r_{F}), producer competition traits (r_{G}) and vulnerability traits (r_{V}).	100, 6.42, 3.81	
s	Producer-consumer trait separation	1.91	

μ_F, μ_G, μ_V	Determines the amount by which each of the foraging, competition and vulnerability trait values for an existing species varies when determining values for a new invading species. A new trait value is given by the old value plus a random normal variable with mean 0 and standard deviation μ_F (foraging traits), μ_G (competition traits) or μ_V (vulnerability traits).	1.2, 1.5, 1.05	
<hr/>			
Model dynamics parameters			
A	Area modelled	$5 \times 10^{10} \text{ m}^2$	Vincenty (1975), ICES (1977)
g	Aggressivity	$10^{5.51} \text{ kg}^{-1} \text{ m}^2$	
C_{lc}	Prefactor for $l_{i,c}$	$0.298 \text{ kg}^{1/4} \text{ yr}^{-1}$	Brown et al. (2004)
C_{lp}	Prefactor for $l_{i,p}$	$0.161 \text{ kg}^{1/4} \text{ yr}^{-1}$	Brown et al. (2004)
$C_{r_{\max}}$	Prefactor for $r_{\max,i}$	$5C_{lc}$	
C_σ	Prefactor for σ_i	$0.531 \text{ kg}^{1/4} \text{ yr}^{-1}$	Niklas & Enquist (2001)
GPP_{\max}	Maximum GPP of a single producer species	$0.131 \text{ kg m}^{-2} \text{ yr}^{-1}$	Peters (1983), Sea Around Us Project (2010)
w_c	Niche width for consumers	0.75	
w_p	Niche width for producers	1.32	

w_s	Switching similarity width	0.75	
α_c	Small prey exponent	0.05	
β_c	Big prey exponent	0.25	
η_c	Preferred predator-prey M_{mat} ratio	10^3	Jennings et al. (2002)
ε	Assimilation efficiency for consumers	0.6	Hendriks (2007)
ξ_{lc}	Allometric exponent for $l_{i,c}$	-0.25	Brown et al. (2004)
ξ_{lp}	Allometric exponent for $l_{i,p}$	-0.25	Brown et al. (2004)
$\xi_{r_{\text{max}}}$	Allometric exponent for $r_{\text{max},i}$	-0.25	Savage et al. (2004)
ξ_{σ}	Allometric exponent for σ_i	-0.25	Niklas & Enquist (2001)

Calculation of Five Indicators for Model Community

The model Large Fish Indicator (LFI), using a 50 cm large fish length threshold, is calculated following Shephard et al. (2012). First, for each model fish species, the maturation body mass, M_{mat} , is converted to a corresponding L_{max} using the empirical equation (working in cm and kg) $\log_{10}(L_{\text{max}}) = 0.385 \times \log_{10}(M_{\text{mat}}) + 1.88$ ($r^2 = 0.640$; Fig. S4a). This equation was derived by performing a reduced major axis (RMA) regression on 91 pairs of $\log_{10}(M_{\text{mat}})$ and $\log_{10}(L_{\text{max}})$ values for 91 fish species from the West Coast Groundfish Survey (WCGFS) for the Celtic Sea. A RMA regression was used to account for uncertainty in both M_{mat} and L_{max} ; this is an improvement over the linear regression used in Shephard et al. (2012), which only accounted for uncertainty in L_{max} .

Second, for each model fish species with $L_{\text{max}} > 50$ cm, the proportion of total species biomass due to individuals above 50 cm, α , is derived using the empirical equation $\alpha = 2.55 \times \log_{10}(L_{\text{max}}) - 4.32$ ($r^2 = 0.461$; Fig. S4b), with the value of α capped at 1, as required. This equation was derived by performing a RMA regression on 38 pairs of α and $\log_{10}(L_{\text{max}})$ values for 38 fish species from the WCGFS. This is an improvement over the non-linear regression used in Shephard et al. (2012), which only accounts for uncertainty in α . By definition, $\alpha = 0$ for model fish species with $L_{\text{max}} \leq 50$ cm. The model LFI is then easily calculated as the sum of the products of biomass and α for all model fish species divided by the biomass of all model fish species.

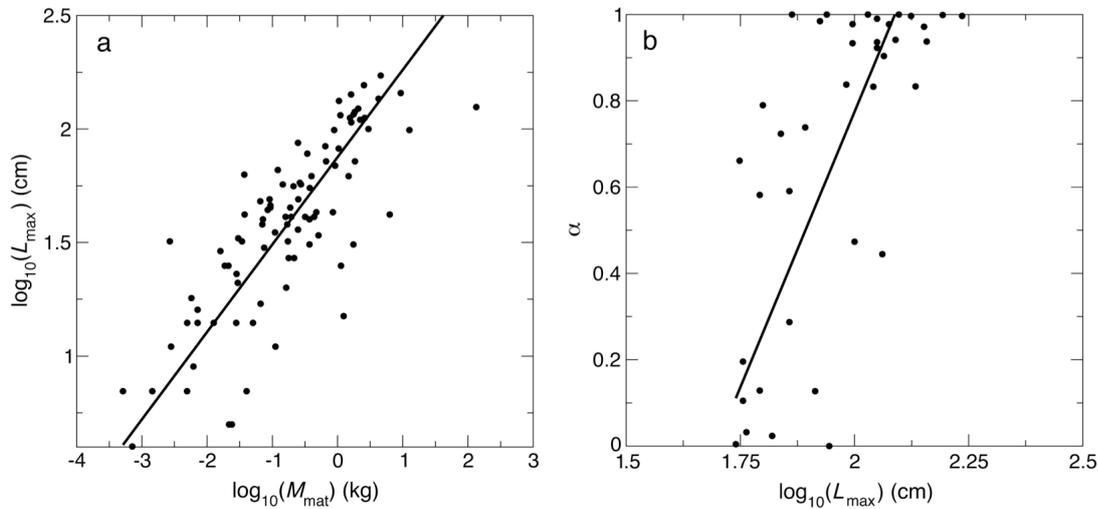


Fig. S4. (a) Relationship between maximum length, L_{max} , and maturation body mass, M_{mat} , derived using RMA regression (solid line) on data for 91 fish species from the West Coast Groundfish Survey (WCGFS) (filled circles). (b) Relationship between proportion of species biomass due to individuals above 50 cm, α , and L_{max} , derived using RMA regression (solid line) on data for 38 species from the WCGFS (filled circles). See text for equations and goodness of fits

The model Large Species Indicator (LSI), using an 85 cm large fish species maximum length threshold, is calculated following Shephard et al. (2012). First, the 85 cm L_{\max} threshold is converted to an M_{mat} threshold of 1.38 kg using the empirical equation relating M_{mat} and L_{\max} above (see also Fig. S4a). The model LSI is then simply the sum of the biomass of all model fish species with $M_{\text{mat}} > 1.38$ kg divided by the biomass of all model fish species.

The model biomass-weighted mean maximum length of fish species (\bar{L}_{\max}) is calculated by first converting M_{mat} for each model fish species to the corresponding L_{\max} , using the empirical equation relating M_{mat} and L_{\max} above (see also Fig. S4a). The model \bar{L}_{\max} is then calculated as the biomass-weighted mean of all these L_{\max} values.

To calculate the model biomass-weighted mean maturation length of fish species (\bar{L}_{mat}), L_{\max} for each model fish species is first converted to a corresponding L_{∞} using the empirical equation (working in cm) $\log_{10}(L_{\infty}) = 0.9841 \times \log_{10}(L_{\max}) + 0.044$ ($n = 551$, $r^2 = 0.959$; Froese & Binohlan 2000). Subsequently, L_{∞} for each model fish species is converted to a corresponding L_{mat} using the empirical equation (working in cm) $\log_{10}(L_{\text{mat}}) = 0.8979 \times \log_{10}(L_{\infty}) - 0.0782$ ($n = 467$, $r^2 = 0.888$; Froese & Binohlan 2000). Both these equations were derived from hundreds of recorded pairs of values of the regressed variables (Froese & Binohlan 2000). The model \bar{L}_{mat} is then calculated as the biomass-weighted mean of all these L_{mat} values.

The total fish biomass density (B_{tot}) is calculated simply by summing up the biomasses of all model fish species, working in kg, and then dividing by the modelled area A (Table S1).

RECOVERY TRAJECTORIES — FURTHER EXAMPLES

Fig. S5a–d shows recovery trajectories for the LFI, the biomass-weighted mean maximum length of fish species (\bar{L}_{\max}), the biomass-weighted mean maturation length of fish species (\bar{L}_{mat}) and the total fish biomass density (B_{tot}), respectively, after non-selective fishing for 25 yr at harvesting rates $H = 0.1, 0.2, 0.3, 0.4$ and 0.5 yr^{-1} . Power-law saturating functions fitted to the recovery trajectories (as described in main text), are also shown. These give extremely good fits, with R^2 ranging from 0.927 to 0.998. The saturating shape means that recovery becomes increasingly slow, resulting in slow recovery times to near equilibrium — usually multiple decades. Moreover, the common shape of the recovery trajectories for all indicators facilitates prediction for management. As for the LSI, for all indicators, R^2 was lowest for $H = 0.5 \text{ yr}^{-1}$, but was nonetheless high and close to R^2 for the smaller H values. In addition, this trend was not found when considering selective fishing for 25 or 50 yr. Thus, there is no evidence of its general importance.

As described in the main text, recovery times to near equilibrium for B_{tot} were typically longer than that for both \bar{L}_{\max} and \bar{L}_{mat} , which in turn were usually longer than that for both the LSI and LFI. Longer recovery times are reflected by trajectories that take longer to saturate (Fig. S5).

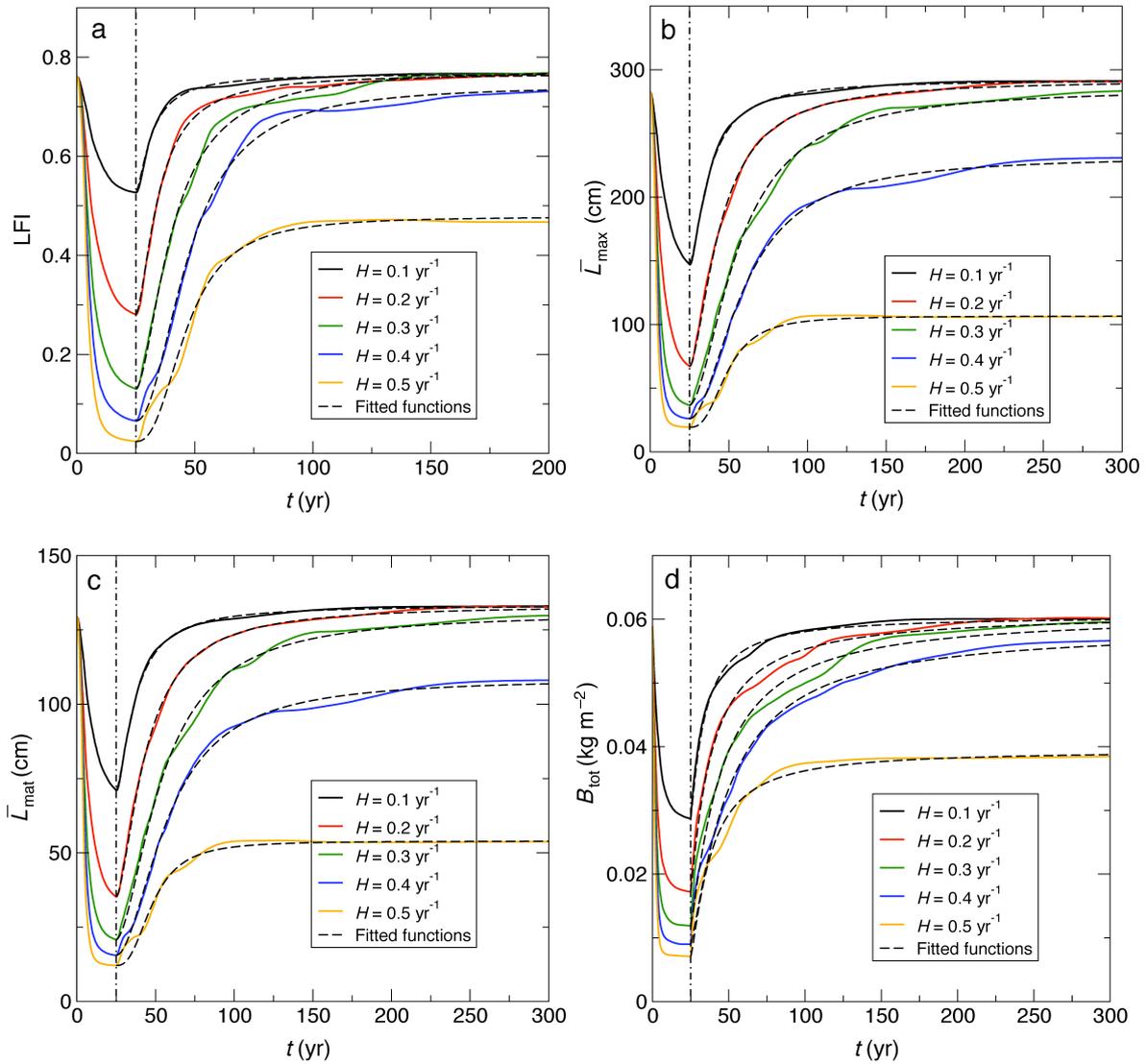


Fig S5. Recovery trajectories across different harvesting rates H for (a) LFI, (b) \bar{L}_{\max} , (c) \bar{L}_{mat} and (d) B_{tot} , after non-selective fishing for 25 yr. For each trajectory, a power-law function is fitted according to Eq. (1) in the main text. The semi-dashed vertical lines represent the time when fishing stops

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