Received: 17 June 2024 | Accepted: 25 October 2024

DOI: 10.1111/2041-210X.14465

Methods in Ecology and Evolution

APPLICATION

FEISTY Fortran library and R package to integrate fish and fisheries with biogeochemical models

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Funding information
HORIZON EUROPE Digital, Industry and Space, Grant/Award Number: 101081273; National Oceanic and Atmospheric Administration, Grant/Award Number: NA20OAR4310438, NA20OAR4310441 and NA20OAR4310442; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 101024886; HORIZON EUROPE Food, Bioeconomy, Natural Resources, Agriculture and Environment, Grant/Award Number: 101083922; Danmarks Frie Forskningsfond, Grant/Award Number: 1026-00198B

Handling Editor: Clive Trueman

Abstract

1. The FishErIes Size and functional TYpe model (FEISTY) is a mechanistic ecosystem model that fully integrates ecosystem structure across trophic levels through functional types.
2. We present an R package that enables users to run simulations ranging from a 0D chemostat to full global scales. The library is written in Fortran90 with an R interface and provides a web application for visual exploration.
3. We present and compare results from four core configurations across a range of depths, productivity and fishing levels, and we assess the convergence of solutions as the number of size classes is increased.
4. The model has historically been coupled to biogeochemical models of mesozooplankton and detritus production, but it can also be applied in a stand-alone version. We demonstrate the library to set up and simulate fish communities under varying productivity of mesozooplankton and benthos, and top-down forcing from fishing.
5. We outline three strategies for coupling FEISTY with biogeochemical model output and discuss future directions and open issues.

KEYWORDS
climate change, fish community, fisheries, marine ecosystem model, physiologically structured populations

1 | INTRODUCTION

Fish communities in the world's oceans are under threat from fisheries and climate change. Understanding the impact of these threats requires an understanding of how fish stocks interact with fisheries, with other fish stocks and with the environment including physics, biogeochemistry and lower trophic levels.

The representation of fish communities in current biogeochemical models is generally limited to a non-linear mortality closure term that mimics the effects of predation by all higher trophic-level

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organisms. Analogously, most fish community models have a very primitive representation of primary or secondary production or do not have a structure that makes them amenable to inclusion in a biogeochemical model framework, for example no respect of mass balancing. Often, fish models are regionally constrained with detailed representation of the specific fish species in a given community. This makes it difficult to generalize the models globally. Food webs of specific species provide the degree of detail needed for regional fisheries applications, but the high empirical nature of the frameworks poses challenges when they are projected outside their calibration envelope in future environments.

The FishErles Size and functional TYpe model (FEISTY) framework is designed to be mechanistic, simple and fast, generally applicable globally, and compatible with biogeochemical model principles. The fundamental FEISTY model has been documented in Petrik et al. (2019) and van Denderen et al. (2021), respectively. It is based on ordinary differential equations and careful accounting of mass balancing. The model structures the fish community around functional types (aka. functional groups or guilds) based on traits instead of representing specific species. This simplification, together with the mechanistic basis, allows for projections into novel environments, for example climate change projections.

Here, we describe a reference implementation of four set-ups of FEISTY with differences in parameterization and structure. The core library is written in FORTRAN90, which makes for a very computationally efficient model that may be linked directly into biogeochemical model frameworks. We provide an R front-end with a web-based graphical user interface that allows the simulation of scenarios of secondary production, fisheries pressure and temperature. We compare set-up solutions across a range of productivity levels, depths and fishing levels, and we assess solution convergence as the number of size classes in increased. The model is designed to be coupled to biogeochemical models and we discuss different coupling approaches for future applications.

2 | METHODS

Here we provided a brief overview of FEISTY. For full details, including equations and parameters, please access the vignettes in R after installing the package:

browseVignettes("FEISTY").

FEISTY is similar to other size-based fish models (Andersen, 2019; Scott et al., 2014) by representing the processes of competition and predator–prey interactions that emerge from larger fish feeding on smaller fish that share the same habitat. In contrast to most fish food web models, it abstains from representing specific species in favour of grouping species into functional types, that is small and large pelagic fishes, demersal fish, mesopelagic fish and midwater predators. The description removes the requirement of having a species-specific representation of density dependence between spawning biomass and recruitment, the traditional 'stock-recruitment' relationship used in fisheries science (Hilborn & Walters, 2013, Chap. 7), which was a hindrance to properly representing the influence of the secondary production on the fish community. Loss processes, for example resource competition and mortality, that affect the larval and juvenile stages are here explicitly represented instead of imposing an external carrying capacity on each functional type.

All processes in FEISTY are described at the level of an individual fish that is defined by its body size (mass) m and is affected by temperature. The core is a mechanistic description of the individual's energy budget (Figure 1a). Prey are consumed based on encounter rates, consumed food is assimilated and respired, and the remaining available energy $\nu(m)$ is divided between growth and reproduction according to the maturity of the fish.

Individual-level processes are scaled to the population level of each functional type. A functional type is characterized chiefly by its maximum (asymptotic) mass M and its vertical feeding habitat (Figure 1b,c). Fish are spawned at their offspring size (1 mg) and use their available energy to grow through each size class i. Somatic growth leads to a flux of biomass between size classes J_i. Mature fish allocate energy to reproduction and that defines the flux of new offspring that is routed back to the smallest size (Figure 1b).

The main governing equation is a discretization of the McKendric-von Foerster equation for mass balanced growth (de Roos et al., 2008). The equation describes the change of biomass in a size class due to the flux between neighbouring size classes and the accumulation and loss of biomass due to somatic growth, reproduction and mortality:

$$\frac{dB_i}{dt} = J_i - J_{i+1} + \left(\nu_i - \rho_i - \mu_i\right)B_i, \tag{1}$$

with B_i being the biomass (units of biomass per area) in the ith size class, J_i and J_{i+1} are the fluxes of biomass in and out of the size class i (units of biomass per area per time), ρ_i is the biomass-specific reproduction rate (units of per time), and μ_i is the biomass-specific mortality rate (units of per time). ν_i represents the biomass-specific energy acquired from predation on the resources or fish (units of per time) after accounting for basal metabolism, which is used for increasing the biomass and for reproduction ρ_i in the adult size classes. Fish interact with other size-classes through predation following the principle that big fish eat smaller fish in a shared habitat, such that the feeding preference (dimensionless) between a predator size class i and a prey size class j (including mesozooplankton and benthic resource) is

$$\theta_{i,j} = \theta_{\text{size}\,i,j}\ \theta_{\text{vertical}\,i,j}, \tag{2}$$

where, θ_{size} represents the size-based feeding preference and θ_{vertical} represents the vertical overlap between the predator and prey (Figure 1c).

Predation fuels growth and reproduction of the predator while also imposing predation mortality on the prey. These feeding interactions, together with the bioenergetic model, define fluxes in and out of size class i, J_i and J_{i+1}, the available energy for growth and reproduction ν_i, the reproduction rate ρ_i, and the mortality μ_i in Equation (1).

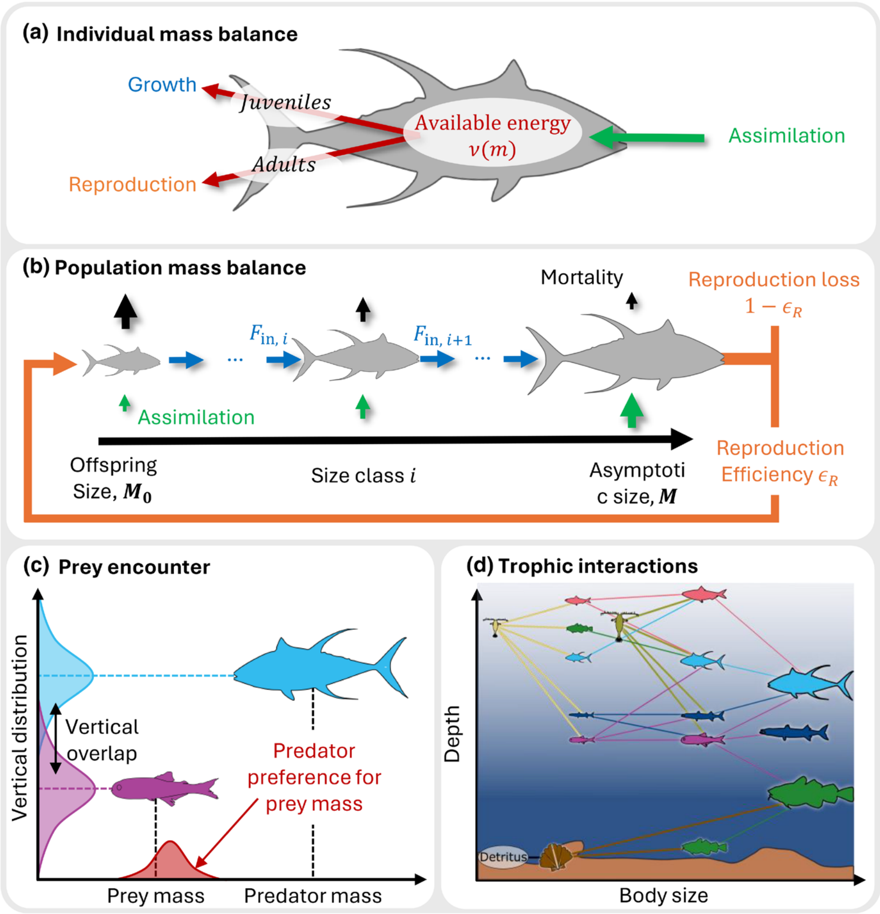

FIGURE 1 Sketch of the FEISTY framework. (a) Individual mass balanced allocation of energy of a fish. (b) Population mass balance of a fish functional type. (c) An example of a prey encounter between two functional types where a large fish (blue) eats a smaller prey (purple) when their vertical distributions overlap. (d) Schematic representation of trophic interactions between functional types emerging from the size and vertical interactions. The full model encompasses three resources: Small and large mesozooplankton (sand colour), a benthic resource (brown) and five functional types: Small and large pelagics (pink and cyan), demersal fish (green), mesopelagic fish (purple) and midwater predators (blue).

The current FEISTY implementation includes four set-ups that define which fish functional types are present and how they predate upon one another (Table 1). Two 'Basic' set-ups contain just three functional types: small and large pelagic fish species and demersal species (Petrik et al., 2019). Two 'Vertical' set-ups augment the model with two additional functional types, mesopelagic fish and mid-water predators, and further automates the calculation of the interaction between the functional types based on their vertical overlap (van Denderen et al., 2021). Versions '2' of the Basic and Vertical set-ups modify the published set-ups with notable parameter updates and structural changes: fish mature at a more realistic larger size (at 0.25 times the asymptotic mass), the number of size classes is flexible, and fishing is size-dependent. The set-ups generally handle temperature by taking the mean temperature in the different vertical habitats of each functional type. Which set-up to use depends upon the application.

3 | THE FEISTY R PACKAGE

The FEISTY R package can be installed from GitHub in R:

```
remotes::install_url("https://github.com/Kenhasteandersen/FEISTY/
archive/refs/tags/v1.0.0.tar.gz")
library(FEISTY)
```

An alternative is to get the source code archived on Zenodo and install the package manually (Zhao et al., 2024).

The package uses R as a front-end to the FEISTY Fortran library which provides the right hand side of the central differential equations (Equation 1). The package includes a Shiny application that allows rapid testing and quick visualizations for the four built-in set-ups: webFEISTY(). Setting up a model, running a simulation and plotting the result can be as simple as (further code examples are given in the vignettes):

```
parameters = setupVertical2()
sim = simulateFEISTY( p=parameters )
plot( sim )
```

The simulation structure sim contains the simulation results and can be used for plotting (Figure 2) or analysis functions (see the help page for simulateFEISTY()). This example simulates a productive shelf break at 800 m depth with the 'Vertical2' configuration. A distinct vertical structure is evident, characterized by epipelagics, mesopelagics and demersal fish. Mesopelagic fish are preyed upon by larger pelagics as well as demersal fish and, as a result, the fish food web is coupled through cross-habitat feeding dynamics (Figure 2e).

Moving from a shelf across a shelf break towards the deep ocean illustrates how the food web changes according to the productivity

TABLE 1 Description of the current four FEISTY set-ups.

	Basic	Basic2	Vertical	Vertical2
Functional types				
Pelagic + demersal	Yes	Yes	Yes	Yes
Meso + midwater	No	No	Yes	Yes
Prey preference				
Size[a]	Manual	log-Gaussian	Error-function	log-Gaussian
Vertical	Manual	Manual	Distribution	Distribution
Others				
No. of stages[b]	2 and 3	Flexible	4 and 6	Flexible
Temperature input	Epipelagic, bottom	Epipelagic, bottom	Full water column	Epipelagic, mesopelagic, bottom
Maturation size	0.002*M*	0.25*M*	0.002*M*	0.25*M*
Fishing	Constant	Size selective	None	Size selective
Validation	Sea Around Us catches[c]	Indirectly[d]	EcoPath comparison	Indirectly[d]
Usage	When no. of state variables is limiting	If only 3 types are needed		For general applications

[a] Size preferences are manually assigned or calculated using size-preference functions (i.e. log-normal distribution or the error-function).

[b] Flexible stages are in multiples of 2 or 3, up to 18 or 27; see also Figures S3 and S4.

[c] Zeller and Pauly (2015); see Petrik et al. (2019).

[d] The set-ups which are not directly validated by catches (setupBasic) or EcoPath models (setupVertical) are validated indirectly by comparing their outputs of total biomass to the validated set-ups; see Figure 5c; Figures S1 and S2.

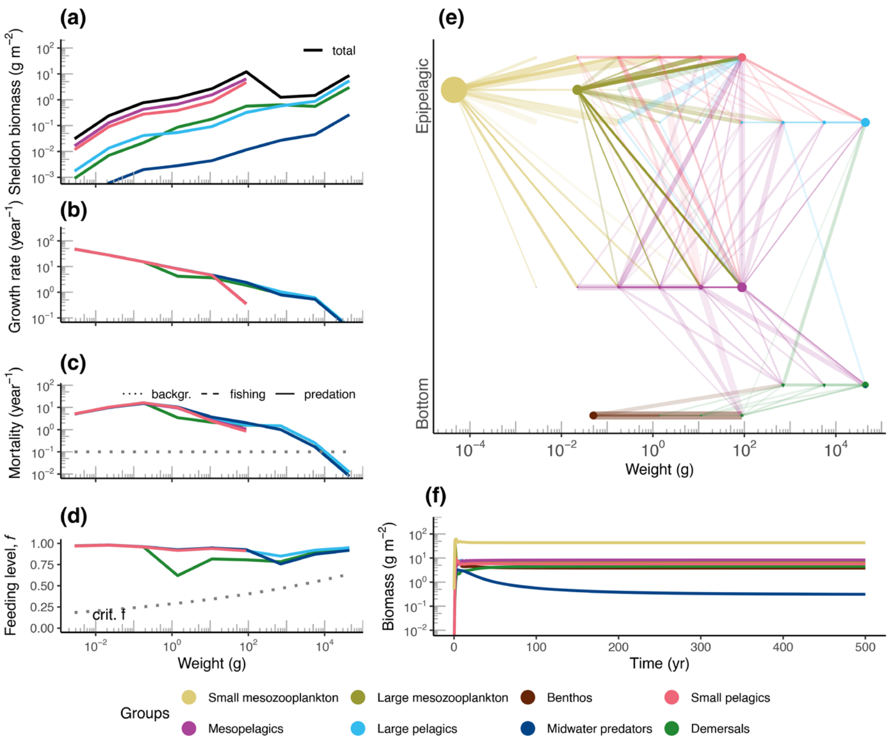

FIGURE 2 Main FEISTY outputs using the Vertical2 set-up with a seafloor depth of 800 m, a mesozooplankton productivity of 80 g WW m^{-2} year^{-1}, and no fishing. (a) Normalized 'Sheldon' biomass spectrum (g m^{-2}; see Box V in Andersen and Visser (2023)), (b) growth rate (energy invested in growth, year^{-1}), (c) total mortality μ (year^{-1}) and (d) feeding level f (consumption relative to maximum consumption, dimensionless), with the dotted line showing metabolic requirements (critical feeding level). (e) Illustration of the food web. Circle areas scale with the biomass of each size class, while line width, representing the feeding flux level between prey and predator, scales with the cube root of the feeding flux. (f) Convergence of the total biomass of each functional type. These plots are provided in the Shiny app webFEISTY().

and water depth (Figure 3). On the shallow shelf, the food web is dominated by small pelagic and large demersal fish. The large pelagic fish are out-competed by the demersal fish that has a rich benthic food source available in addition to the small pelagic fish. Moving across the shelf opens the niche for large pelagic fish at the expense of large demersal fish, which now have fewer resources available. Further offshore, the deeper water opens the niche for small mesopelagic fish and mid-water predators. In the deep ocean, the productivity is generally low and the food web is dominated by small pelagic and mesopelagic fish. Using the output of mesozooplankton production and detritus flux from an Earth system model extends the predictions to the global scale (Figure 4).

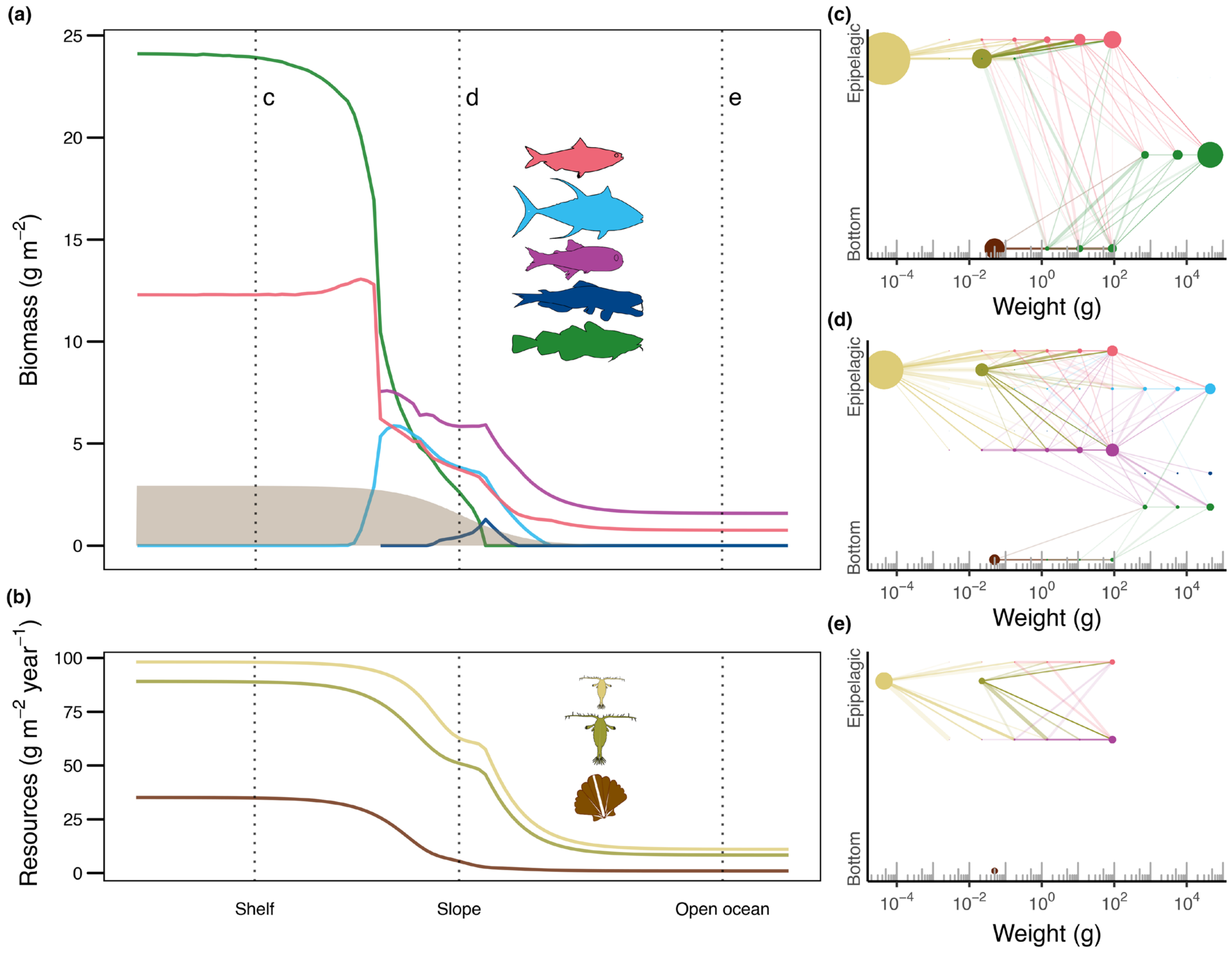

FIGURE 3 Model output across a shelf break of (a) fish functional types and (b) resource productivity. The shelf break ranges 70–3000 m depth and is depicted in (a) as grey shading. (c–e) show the food webs at depths 75, 1500 and 3000 m, as indicated by the dotted lines in panel (a). Line type legends as in Figure 2.

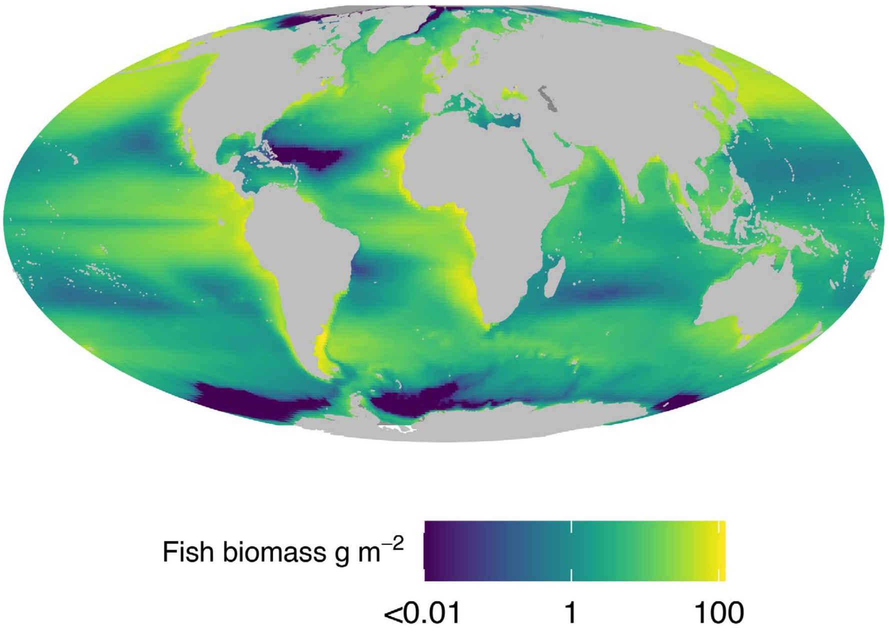

FIGURE 4 Output of a global run of setupVertical2. The model run used estimates of mesozooplankton and the flux of detritus to the benthos from the COBALT biogeochemistry model from a climatology representative of the early 1990s of the GFDL ESM2.6 (Stock et al., 2017). All resource groups are modelled with semi-chemostat dynamics.

FEISTY has been validated by comparing the output of potential fisheries catch to historical global catches (Petrik et al. (2019) for setupBasic), and the food web structure of the ecosystems has been validated with published EcoPath models (van Denderen et al. (2021) for setupVertical). All four configurations create comparable cross-shelf gradients in fish biomass when run across the same shelf-slope-open ocean gradient as in Figure 3, though biomasses in the setupBasic and setupBasic2 configurations are greater than those in setupVertical and setupVertical2 (Figure 5). Comparison of configuration behaviours in shallow and deep waters across a range of zooplankton productivity (Figures S1 and S2) reveals some differences between the set-ups. With setupBasic, which features the coarsest resolution of size and functional types, exhibits more abrupt shifts in the prominence of different functional types with changing productivity than the other configurations, and includes multiple stable states at high mesozooplankton productivities. This is not surprising as physiological structured models are well known to produce multiple stable states (de Roos & Persson, 2013). However, we have only been able to identify multiple stable states in setupBasic, which is special by having only three stages. In the other set-ups with more stages, we have been unable to find multiple stable states.

Analysis of setupBasic2 solutions as a function of the number of stages included shows fairly rapid convergence when more than six stages are included, though relatively minor discrepancies remained in more productive systems (Supporting Information B). Similar results are found for setupVertical2.

Finally, we show realistic responses of biomass and yield to fishing pressure setupVertical2. Small pelagics, for example, sustained high yields despite fishing rates of ≈3 year^{-1}, while large pelagics are much less resilient (Supporting Information C). Configurations such as setupBasic and setupVertical, which featured small maturation sizes, proved to be unrealistically resilient to fishing.

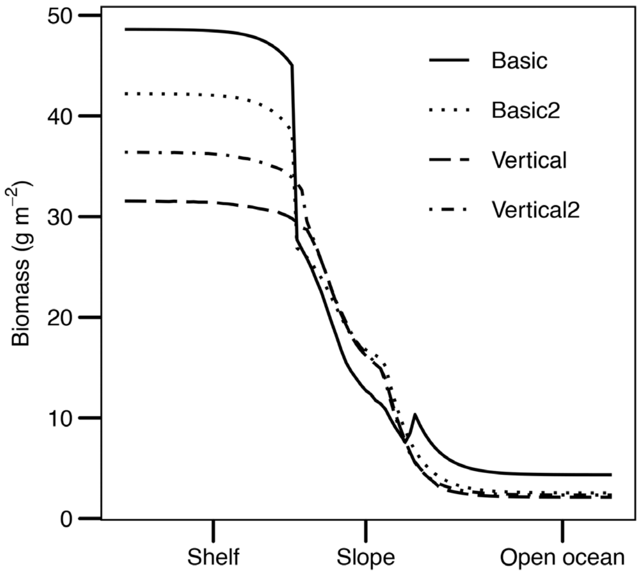

FIGURE 5 Comparison of total biomass from all four set-ups across the same shelf break scenario gradient as in Figure 3.

4 | DISCUSSION

We have demonstrated the FEISTY framework across a shelf break and globally, and compared the four different configurations. We generally recommend the 'Vertical2' or the 'Basic2' set-ups to get realistic responses to fishing. However, if the number of state variables are limiting we recommend the 'Basic' set-up.

4.1 | Coupling with lower trophic levels

FEISTY relies on three resources: small and large mesozooplankton (small 0.2–2 mm ESD, large 2–20 mm ESD) and benthic biomass. Mesozooplankton biomass and production are input directly from the output of biogeochemical models, while benthic biomass is derived from the flux of detritus to the seafloor (because very few models have explicit benthic groups). FEISTY can be forced with a single mesozooplankton group (e.g. Heneghan et al., 2021; Tittensor et al., 2021) by adjusting the feeding preferences (see the vignettes). Coupling with the biophysical forcing can be accomplished in three ways: fully two-way (online), production-constrained one-way (offline) and with resources as a semi-chemostat (offline).

Fully two-way is the ideal solution where FEISTY is implemented in the biogeochemical model with fish size classes and functional types as additional state variables. Here, FEISTY and biogeochemical models are resolved simultaneously by the differential equation solver at each time step. The fish community grazes directly on mesozooplankton and provides mortality that replaces part or all of the non-linear closure term in the biogeochemical model (e.g. Kearney et al., 2012). While this coupling is straightforward in principle there are two considerations. First, FEISTY requires at least nine state variables (eight size classes for fishes and one for benthos in setupBasic), which can impose computational constraints. Second, one needs to make assumptions on how and where the fish feed. In terms of the vertical structure: do fish inhabit individual layers, or do they move between layers? The setupVerticals indicate a vertical structure, but only coarsely (pelagic, mesopelagic, benthic). Do the fish in the pelagic feed on the average concentration of zooplankton, or on the maximum concentration? Additionally, the absence of horizontal movement implies that fish roam the entire area of a grid cell, but do not interact with neighbouring grid cells. While this assumption may hold for small pelagic and demersal fishes in a coarse global grid (e.g. 1°), it likely does not for large pelagic fish that make large feeding and spawning migrations, nor would it be valid for higher resolution spatial domains (e.g. <10 km). Future implementations of vertical and/or horizontal movement require decisions about which size classes and functional types experience advection and diffusion, and which do directional motions and how. Any application of movement should ultimately rely on behavioural rules, either as fitness taxis (Watson et al., 2015) or an explicit game (Frølich & Thygesen, 2022; Pinti et al., 2021).

The production-constrained coupling is an offline (one-way) coupling, which constrains the production in the fish community with the production of the mesozooplankton (Petrik et al., 2019). At a given timespan, fish encounter mesozooplankton biomass (time-averaged data), but consumption rates of mesozooplankton are constrained to not exceed predation mortality loss rates in the biogeochemical model (usually the quadratic closure term). Constraining the model by the mesozooplankton production is necessary to ensure approximate mass balancing—essentially that fish do not eat more zooplankton than is produced by the biogeochemical model. The production-constrained coupling requires that both mesozooplankton biomass and mesozooplankton predation rates are available. The benthic biomass is driven by the flux of detritus (particulate organic matter) to the seafloor minus the losses from predation by the fish, and may be limited by an upper cap. The production-constrained coupling provides estimates of fish biomass and production that are consistent with the biogeochemical models that are often carefully tuned to observations of chlorophyll, net primary production and plankton biomass.

Last, all resource groups can be modelled with semi-chemostat dynamics. Here, FEISTY is augmented with explicit models of mesozooplankton and benthos, each determined by a turnover rate r and maximum biomass density $R_{\max}$. With this coupling, the resource production from the biogeochemical model (from the quadratic mortality term) defines the production $rR_{\max}$ and the production rate is fixed (default 1/year). For small mesozooplankton, we assume that the maximum production $rR_{\max}$ of small mesozooplankton equals their loss to higher predators from the biogeochemical model as small mesozooplankton are mainly eaten by fish larvae and not effectively controlled by them in FEISTY. Large mesozooplankton are more strongly controlled by fish. Using the biogeochemical model output on large mesozooplankton, we estimate maximum production $rR_{\max}$ by considering temperature-specific ratios between loss to fish predators and maximum production. These ratios were found through simulations in FEISTY (van Denderen et al., 2021, supplement. 2). All examples presented here are made with the semi-chemostat formulation of resources.

4.2 | Applications

FEISTY has applications in biogeochemical, ecological, fisheries and climate change research. Early publications demonstrated how contemporary bottom-up drivers (mesozooplankton and benthos productivities) structure fish communities across the global ocean, resulting in regional differences in dominance and pelagic-benthic coupling (Petrik et al., 2019; van Denderen et al., 2021). Given this understanding, FEISTY has been used to project fish biomass under climate change scenarios (Petrik et al., 2020; Tittensor et al., 2021) and was included in an ensemble of marine ecosystem models that informed the latest report by the Intergovernmental Panel on Climate Change (Cooley et al., 2022). The influence of top-down forcing, that is fishing, is another useful application. Global simulations of the effects of past fishing efforts and future fishing scenarios are underway through Phase 3 of the Fisheries and Ecosystem Model Intercomparison Project (Blanchard et al., 2024). Yet there are many more studies of fishing impacts to be explored from purely theoretical to regionally specific approaches. FEISTY can also be applied to assess the consequences of other anthropogenic actions on the marine environment, such as the bioaccumulation and biomagnification of persistent organic pollutants in marine food webs (Wu & Zhang, 2023). Implementing the fully two-way coupling would allow for examinations of the role of the fish community on nutrient cycling and the biological carbon pump (Dupont et al., 2023; Pinti et al., 2023), both directly via exudation and indirectly through predation on mesozooplankton. The two-way implementation would also allow biogeochemical models to partly replace the non-linear mortality on mesozooplankton with an explicit representation of predation by higher trophic levels, either to directly estimate all components of the marine food web or to better constrain plankton parameterizations (see section 'Coupling with lower trophic levels'). Finally, FEISTY could be applied to species-specific models whereby the fishes represented as functional types act as resources and/or predators for the species of interest.

Integration of biogeochemical and fish community models holds immense potential for advancing our understanding of marine ecosystems and their responses to environmental changes. FEISTY, with its compatibility with biogeochemical model principles, offers a versatile framework for exploring interactions in fish communities in different environmental scenarios. While further developments and refinements are warranted, the applications of FEISTY have a high potential for assessing the impacts of fishing and climate change on fish biogeochemical fluxes.

AUTHOR CONTRIBUTIONS

Ken H. Andersen, Colleen M. Petrik, P. Daniël van Denderen and Charles A. Stock conceived the idea and designed methodology; Yixin Zhao, Ken H. Andersen, Daniel Ottmann, Rémy Denéchère, P. Daniël van Denderen and Karline Soetaert wrote the Fortran and R codes; Daniel Ottmann, Yixin Zhao, Rémy Denéchère, Jonathan E. Falciani and P. Daniël van Denderen made the visualizations; Ken H. Andersen led the writing of the manuscript. All authors contributed critically to model development, the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Jessica Luo for discussions and advice and Yi-Cheng Teng for providing suggestions and comments through an internal review. This work was funded by the EU grants 101083922 (OceanICU), 101024886 (DemFish) and 101081273 (NECCTON), by the Independent Research Fund Denmark 'Future Oceans' 1026-00198B, and by NOAA CPO MAPP NA20OAR4310438, NA20OAR4310441 and NA20OAR4310442.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14465.

DATA AVAILABILITY STATEMENT

The FEISTY package has been archived on Zenodo: https://doi.org/10.5281/zenodo.14036082 (Zhao et al., 2024). Data and scripts to generate the figures in this manuscript are on GitHub: https://github.com/Kenhasteandersen/FEISTY_model_paper. The development version of the FEISTY package is available on GitHub: https://github.com/Kenhasteandersen/FEISTY.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information: Supporting information section A to C.

How to cite this article: Zhao, Y., van Denderen, P. D., Denéchère, R., Falciani, J. E., Jacobsen, N. S., Konstantinopoulos, T., Ottmann, D., Petrik, C. M., Soetaert, K., Stock, C. A., & Andersen, K. H. (2025). FEISTY Fortran library and R package to integrate fish and fisheries with biogeochemical models. *Methods in Ecology and Evolution*, *16*, 40–48. https://doi.org/10.1111/2041-210X.14465