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Resource competition and fisher behaviour mediate the effect of effort reduction strategies in brown shrimp (*Crangon crangon*) fishery in the North Sea

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Abstract

The fishery for brown shrimp (*Crangon crangon*) is one of the most valuable fisheries in the North Sea. There are concerns about the effects of this fishery on the ecosystem, especially since it takes place predominantly within Natura 2000 areas. The fishery potentially disturbs foraging seabirds and the seafloor ecosystem and produces substantial amounts of non-target bycatch. Furthermore, brown shrimp are an important food web component, both as predators and as food. There is societal pressure to reduce the shrimp fishing intensity. We study two qualitatively different approaches by which the maximum fishing effort can be limited: either by reducing the weekly allowed fishing time or by reducing the number of vessels. To do so, we combine an individual-based fleet model and a mechanistic, individual-based model of the shrimp stock. We show that a moderate fishing effort reduction can increase landings, but simultaneously yields higher bycatch of undersized shrimp. This is caused by stronger resource competition among shrimp at lower fishing mortality. The effort reduction also changes the seasonal pattern in shrimp growth as well as in the fishery. At fleet level, as well as for the shrimp stock, differences between the two scenarios are small. However, at vessel level, a reduced number of vessels leads to increased effort and landings for the remaining vessels. Our model accounts for both the ecological complexity of the stock as well as elements of the behaviour of the fishers The dynamic interplay between the two shapes the outcome of our study, and accounting for this level of complexity is essential when fishery management seeks to balance ecological and economic outcomes.

Keywords fisheries management, physiologically structured population model, individual-based fleet model, density dependence, life history, bottom trawling

Introduction

The fishery for brown shrimp (*Crangon crangon*) is an important fishery along the southeastern coast of the North Sea and is one of the most valuable in the North Sea (Baer et al. 2017). Following a period of sustained increases in landings beginning in the 1960s, annual total landings from all countries have remained relatively stable at approximately 25 000–30 000 tonnes since the mid-1990s, but have decreased in the last few years (ICES 2025). The fleet consists of 400–500 active trawlers, mostly of Dutch, German, Danish, and Belgian origin. Despite its high value there is no formal stock management for brown shrimp. However, most of the fleet is MSC certified since 2017 and required to follow the MSC management plan (Marine Stewardship Council 2023). In addition, there are some regulations self-enforced by national producer organizations, such as an upper limit to weekly fishing time, a minimum landing size, and a minimum mesh size.

The bottom-contacting trawls used by shrimp fishers cause substantial seafloor disturbance, as well as bycatch of undersized shrimp, other benthic invertebrate species and fish (Depestele et al. 2014, Rijnsdorp et al. 2020). It has been suggested that the bycatch of small fish in the shrimp fishery negatively affects the recruitment of commercial fish stocks (Revill et al. 1999). These effects have led to concerns about the environmental sustainability of the fishery (see e.g. Seas at Risk et al. 2024), in particular because the fishery occurs predominantly inside Natura 2000 protected areas (Baer et al. 2017, Hintzen 2021). As a result, the shrimp fishery is under strong pressure to operate sustainably and not to jeopardize the Natura 2000 policy objectives. The historical lack of management, the management required as part of the existing MSC certification and the legal obligation for nature conservation pose a challenge for the fishers as well as the responsible government bodies.

In addition to the physical disturbance of the gears and the bycatch mortality, the removal of shrimp also has potential indirect effects through the food web in which shrimp play an important role. Such effects become more relevant with the increasing policy focus on ecosystem-based management. Brown shrimp are opportunistic feeders on a wide variety of prey, including fish (Siegenthaler et al. 2019). Predation by shrimp can limit

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the settlement of bivalve larvae (Beukema 1992, Beukema et al. 1998, Beukema and Dekker 2005) and affects the settlement behaviour of flatfish larvae (Wennhage and Gibson 1998). Shrimp are also prey for a variety of fish species, in particular whiting (*Merlangius merlangus*) and cod (*Gadus morhua*) (Kuhl and Kuipers 1978, Berghahn, 1996, Welleman and Daan 2001, Temming and Hufnagl 2015). Although it is unclear to what extent the productivity of fish populations depends on brown shrimp, they can make up a substantial part of the diet of small and juvenile fish (Daan 1973, Hislop et al. 1991, Poiesz et al. 2024). The important role of shrimp in the food web implies that a reduction of the shrimp stock through large-scale fishery may affect the dynamics of the larger ecosystem, including North Sea gadoid stocks and commercially harvested shellfish stocks.

One way to safeguard the ecological role of brown shrimp and limit the environmental impact of the fishery is to reduce fishing intensity, but this can be achieved in various ways. Here, we compare two qualitatively different ways to do so, either by limiting the weekly fishing time for all vessels or by reducing the total number of vessels. Both have real-world relevance, as limitation of fishing time is part of the MSC management plan (Marine Stewardship Council 2023) and both the Dutch and German governments have proposed buy-out schemes to reduce the number of vessels (Anonymous 2024, van Oostenbrugge and Salz 2024). We study the similarities and differences between these reduction scenarios with regards to shrimp growth and population dynamics, as well as (the timing of) realized fishing effort, landings, undersized shrimp bycatch and landings per unit effort (LPUEs). The results are discussed in relation to their consequences for the stock, the fishery, as well as its potential food web effects.

To study the different effects of these two ways to reduce fishing intensity, it is essential to include some of the complexity of the fishing process. Classical work on the ecological effects of fisheries has often simplified fisheries as a constant mortality rate or constant quota (e.g. Beddington and May 1977), but in practice fishing intensity is dynamic, and depends not only on the quota or fishing capacity, but on many other practical, economic and social factors (Schadeberg et al. 2021, Letschert et al. 2023). To understand the net effect of management measures on a fishery, the stock it exploits, as well as indirect effects of the fishery on the marine ecosystem, it is essential to include this dynamic interaction between the stock and the fishery (Salas and Gaertner 2004). We do this by combining a semi-spatial physiology-based population model of the North Sea shrimp stock with an individual-based model of the shrimp fishing fleet. The shrimp population model captures the ecological and physiological complexity of the shrimp stock, including individual energetics, food-dependent growth, development and reproduction, as well as local resource competition. The individual-based fleet model is designed to capture important elements of the dynamic decisions of individual fishers, such as when and where to fish or to give up, but in highly simplified form. The combination of fishing mortality as the outcome of a dynamic behavioural decision process by the fishers and a mechanistic population model is an important novelty of this study. This combination uniquely allows us to study the interplay between ecology and the decision-making process of fishers.

Our results demonstrate that this social–ecological system is shaped by the interplay between fisher behaviour and shrimp ecology, meaning that policy changes affecting fishers may trigger unintended consequences through their dynamic interactions with the ecosystem.

Methods

Model overview

The developed model consists of two components, a model of shrimp individual-level processes and population dynamics, combined with an individual-based model of the fishing fleet for shrimp. The shrimp population model is based on the well-developed framework of mechanistic, physiologically structured population models (PSPMs), which have been used successfully to link theory, experiments and observations (De Roos and Persson 2013). Spatially implicit versions of such models already exist (e.g. van Kooten et al. 2004), and the framework has been used extensively to study the population dynamical consequences of harvesting using a predefined fishing mortality rate (e.g. van Kooten et al. 2007, Croll et al. 2023). Here, we link the shrimp model to an individual-based fleet model in which fishing mortality is an outcome of the dynamic decision-making process of fishers.

Our model is largely deterministic, which allows us to directly couple observed model outcomes to assumptions about the ecology of shrimp and fleet behaviour. There is a long tradition of using deterministic PSPMs in this way (De Roos and Persson 2013, and references therein). The model code used to generate the results, as well as all code to generate the figures presented in this study is publicly available at https://doi.org/10.5281/zenodo.18709920. The model runs within the Escalator Boxcar Train software, more information about which is available from https://staff.fnwi.uva.nl/a.m.deroos/EBT/Software/index.html. The individual-based fleet model used here is similar to an agent-based model (Grimm et al. 2005) in the sense that we simulate individual vessels explicitly, but we use only limited differentiation among vessels. The spatial configuration, equations, parameters and the scenarios we study are summarized in Tables 1–4. Further description of the model, following the ODD protocol approach (Grimm et al. 2010), is included in the Supplementary Material. Throughout this study, we use the terms 'effort' and 'fishing effort' as shorthand for the time spent at sea, which is appropriate because we assume all fishers use the same gear, for the same fraction of the time at sea, and fish at the same speed.

Spatial setup

The total area along the Belgian, Dutch, German, and Danish coast where shrimp fishing occurs was divided into nine distinct areas (Fig. 1). These areas are an abstraction on the basis of a spatial data analysis of Dutch shrimp fishery, structured interviews with fishers and fishery representatives, and the distribution of national boundaries and important home- and landing ports along the southeastern North Sea coast (Steenbergen et al. 2015). The naming of the areas is simplified, e.g. a smaller part of the 'Dutch delta' also consists of Belgian waters, and the 'Sylt' area consists of waters further from the Danish and German coast with fishing effort concentrated in the vicinity of the Outer Sylt Reef. Areas differ in size, and area-specific temperature curves

Table 1. Environmental properties of areas used to divide the shrimp populations and fishing fleets in the model

Number	Name	Abbreviation	Surface area (ha)	Temperature (K) parameters			
				Amplitude	Centre	Offset	Width
1	Dutch delta	NL_Delta	341 853	7.5	136.0	284.0	182.4
2	Dutch west coast	NL_West	287 707	7.3	139.9	284.0	182.4
3	Dutch north coast	NL_North	410 669	7.0	140.5	283.6	182.4
4	Dutch Wadden Sea	NL_Wadden	258 918	8.2	119.3	283.5	182.5
5	German north coast	DE_North	281 659	7.6	136.8	282.9	182.5
6	German/Danish Wadden Sea	DE_Wadden	583 055	8.7	121.6	283.1	182.5
7	German west coast	DE_West	587 597	6.9	144.7	282.5	182.4
8	Sylt	DE_Sylt	608 027	6.7	146.8	282.5	182.4
9	Danish west coast	DK_West	283 107	6.9	144.7	282.5	182.4

were used to scale physiological rates of the modelled shrimp stock (Table 1). Each area was further divided into a shallow and a deep habitat of equal size, as an abstraction of existing size-dependent habitat suitability for shrimp. The model contains a single shrimp larvae pool to which all reproducing shrimp individuals from all areas contribute. From this larvae pool, shrimp larvae are divided over the shallow habitat of the nine areas in proportion to the size of the areas. Shrimp migrate to the deep habitat when reaching a certain length and shrimp fishing is assumed to only occur in these deep waters. This set-up is a simplification of shrimp shifting to deeper waters as they grow, and movement being predominantly perpendicular to the coast (Hufnagl et al. 2014)

Effort data comparison

Model outcomes were compared with data of the Dutch shrimp fishing fleet from four areas consisting of Dutch waters (the 'Dutch delta' also covering Belgian waters). Fishing effort and landings data were analysed using VMS and logbook datasets collected by The Netherlands Enterprise Agency (Rijksdienst voor Ondernemend Nederland, RVO), and compiled following data-processing procedures described in Hintzen et al. (2013).

Fleet model

An individual-based approach was used to model the fishing fleet. Based on a combination of data analysis (VMS) and consultation of representatives of the Dutch shrimp fishery through interviews, the fleet has been divided into 'local' and 'mobile' vessels (Steenbergen et al. 2015). The first (and largest) group consists of 360 local vessels, which are bound to a specific area (40 vessels per area) and fish only in that area. The mobile group consists of 140 vessels that may fish in any of the nine areas. This number approximates the number of large vessels in the fleet, which make up about half the total Dutch shrimp fleet (Steenbergen et al. 2015). They choose where to fish at the start of each week. For each mobile fisher, we calculate its expected landings in each location for the coming week, based on area LPUEs from the previous week and the fishing time it would have at that location. This fishing time depends on the maximum allowed fishing time per week, but is reduced by the time lost steaming from each vessel's current location to any potential new location. For simplicity, no home port is assumed for the mobile vessels. We assume that each movement 'step' incurs a loss of a half-day fishing time (Supplementary Table A1). If far-away locations would have a negative fishing time it is set to zero. 95% of the time, mobile fishers relocate using stochastic profit maximization using these expected landings, and 5% of the time, each vessel picks a random location. This can result in fishers ending up in unfavourable locations.

The fleet operates on a weekly basis, where each vessel is assumed to start fishing on Monday and to stop on Friday (in the baseline scenario). In addition, a vessel can decide to stop fishing for the remainder of the week if Monday's landings (after 12 hours of fishing) is below a certain threshold LPUE. The local fishers are assumed to give up more easily, i.e. they have a higher threshold LPUE value below which they stop fishing. Furthermore, half of the fleet does not fish for shrimp between December and February, reflecting a combination of the availability of more profitable activities (fishing for sole or Norway lobster), and the prevalence of bad weather in these months, preventing vessels from fishing (ICES 2015, Steenbergen et al. 2015). In this period, we set to zero the effort of a fixed half of the mobile vessels as well as the local vessels in each location.

Per area, the realized effort of all vessels is summed, resulting in the total realized fishing effort (in days) in area j, denoted by Z_j (Table 2). We assume that each fishing day consists of, on average, 12 hours of fishing, at 3 knots, with two 9 m wide trawls. Hence, one fishing day equals ~120 ha of fished surface (parameter $area_F$; Table 3). The imposed fishing mortality for a shrimp in a certain area is then the result of the summed effort multiplied with the trawled surface area, and the net selectivity based on shrimp size, as measured for a typical Dutch shrimp trawl (Table 2, eq. 18). We use an increasing size-dependent relative gear selectivity as measured for the shrimp trawls used in the Dutch fleet (Santos et al. 2018, Table 2, eq. 17), and assume catchability equals size selectivity.

Table 2. Variables, equations and functions for the shrimp population, individual physiology and the resources. Index i denotes an individual shrimp cohort, index j denotes one of nine model areas, and index k denotes the deep or shallow habitat within an area

#	Variables	Equation	Unit
	Total number of cohorts	D	–
	Set of cohorts in habitat *k* of area *j*	$d_{k,j}$	–
	Number of individuals in cohort *i*	N_i for $i \in \{1, D\}$	#
	Volume of individuals in cohort *i*	V_i	cm^3
	Energy reserves of individuals in cohort *i*	E_i	J
	Energy reserve density of individuals in cohort *i*	$[E]_i = \frac{E_i}{V_i}$	$J\ cm^{-3}$
	Reproductive energy of individuals in cohort *i*	$E_{r,i}$	J
	Resource density in habitat *k* of area *j*	$R_{k,j}$	$J\ m^{-2}$
	Total fishing effort in area *j*	Z_j	d
	Brown shrimp dynamics		
1	Growth in individual volume of individuals in cohort *i*	$\frac{dV_i}{dt} = \frac{\kappa P_{E,i} - M_i}{[E_G]}$	$cm^3\ d^{-1}$
2	Energy dynamics of individuals in cohort *i*	$\frac{dE_i}{dt} = \varepsilon I_i - P_{E,i}$	$J\ d^{-1}$
3	Dynamics of individual reproductive energy of individuals in cohort *i*	$\frac{dE_{r,i}}{dt} = (1-\kappa)P_{E,i} - P_{R,i}$	$J\ d^{-1}$
4	Dynamics of number of individuals in cohort *i*	$\frac{dN_i}{dt} = -(\mu_n + \mu_s + \mu_f)N_i$	$\#\ d^{-1}$
	Resource dynamics		
5	Resource dynamics in habitat *k* of area *j* (for $L_i > L_S$)	$\frac{dR_{k,j}}{dt} = r(f_\tau K - R_{k,j}) - R_{k,j}(\frac{\sum_{i \in d_{k,j}} N_i a_m S_i A_{\tau,j}}{area_j})$	$J\ m^{-2}\ d^{-1}$
	Brown shrimp functions		
6	Maximum intake of individuals in cohort *i*	$I_{m,i} = \{\dot{p}_{Xm}\}V_i^{2/3}$	$J\ d^{-1}$
7	Search time of individuals in cohort *i*	$S_i = \begin{cases} 1/(1 + K_W\ a_m/I_{m,i}) \text{ if } L_i < L_S \\ 1/(1 + R_{k,j}\ a_m/I_{m,i}) \text{ if } L_i \geq L_S \end{cases}$	–
8	Resource ingestion of individuals in cohort *i*	$I_i = \begin{cases} A_\tau a_m K_W S_i \text{ if } L_i < L_S \\ A_\tau a_m R_{k,j} S_i \text{ if } L_i \geq L_S \end{cases}$	$J\ d^{-1}$
9	Maintenance of individuals in cohort *i*	$M_i = A_\tau [P_M] V_i$	$J\ d^{-1}$
10	Energy utilization	$P_{E,i} = \frac{[E]_i}{\kappa\ [E]_i + [E_G]}(\frac{\varepsilon\ \{\dot{p}_{Xm}\}[E_G]V_i^{2/3}}{[E_m]} + M_i)$	$J\ d^{-1}$
11	Development and maintenance of maturity	$P_{R,i} = \begin{cases} \frac{V_i\ (1-\kappa)}{\kappa}[\dot{p}_M] \text{ if } V_i \leq V_P \\ \frac{V_P\ (1-\kappa)}{\kappa}[\dot{p}_M] \text{ if } V_i > V_P \end{cases}$	$J\ d^{-1}$
12	Total larvae numbers	$N_L = S_L \frac{\sum_{i=1}^{D} E_{r,i} N_i}{E_L + [E_G]V_L}$ for $V_i > V_P$	#
13	Initial number of larvae in area *j*	$N_{L,j} = N_L \frac{area_j}{\sum_{m=1}^{9} area_m}$	#
14	Natural mortality	$\mu_n = \mu_b + \alpha V_i^{-\beta}$	d^{-1}
15	Starvation mortality	$\mu_s = \begin{cases} 0 \text{ if } \frac{V_i}{V_m} \geq S_t \\ S_r(\frac{S_t}{V_i/V_m} - 1) \text{ if } \frac{V_i}{V_m} < S_t \end{cases}$	d^{-1}
16	Individual length	$L_i = V_i^{1/3}/\delta$	cm
17	Net selectivity (the fraction of individuals in cohort *i* of length L_i which dies in a single trawl pass)	$\Omega(L_i) = \frac{1}{1+e^{(\frac{L_{50} - L_i/10}{0.5 S_R})}}$	-
18	Fishing mortality	$\mu_f = -\ln(1 - \Omega(L_i))\frac{\frac{Z_j}{7} area_F}{area_j}$	d^{-1}
19	Ambient temperature on day τ in area *j*	$T_{\tau,j} = amp_j \sin(\pi \frac{(\tau - center_{r_j})}{width_{h_j}}) + offset_j$	K
20	Arrhenius scaling at day τ in area *j*	$A_{\tau,j} = e^{\frac{T_A}{T_{ref}} - \frac{T_A}{T_{\tau,j}}} \frac{(1 + e^{\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}} + e^{-\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}})}{(1 + e^{\frac{T_{AL}}{T_\tau} - \frac{T_{AL}}{T_L}} + e^{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{\tau,j}}})}$	–
	Resource functions		
21	Seasonality effect on resource productivity	$f_\tau = amp_r \sin(\pi \frac{(\tau - center_{r_r})}{width_{h_r}}) + offset_r$	–

Table 3. Model parameters, values, units, and references used.

Parameter	Symbol	Value	Unit	Reference
Individuals				
Maximum search rate	a_m	1.5	$m^2\ d^{-1}$	Andresen and van der Meer (2010)
Max. surface-area specific ingestion rate	$\{\dot{p}_{Xm}\}$	58.9	$J\ cm^{-2}\ d^{-1}$	Campos et al. (2009)
Volume-specific maintenance rate	$[\dot{p}_M]$	15.9	$J\ cm^{-3}\ d^{-1}$	Campos et al. (2009)
Cost of growth	$[E_G]$	1800	$J\ cm^{-3}$	This study
Maximum energy density	$[E_m]$	851	$J\ cm^{-3}$	Campos et al. (2009)
Length at settlement	L_S	0.5	cm	This study
Egg energy content	E_L	0.413	J	Campos et al. (2009)
Volume larva	V_L	0.000 0416	cm^3	Urzua et al. (2012)
Volume movement	V_M	0.15	cm^3	
Volume maturation	V_P	0.261	cm^3	Campos et al. (2009)
Shape coefficient	δ	0.213	–	Campos et al. (2009)
Kappa	κ	0.8	–	Campos et al. (2009)
Conversion efficiency	ε	0.8	--	This study
Starvation mortality rate	S_r	1.0	d^{-1}	This study
Starvation threshold	S_t	0.5	–	This study
Egg survival	S_L	0.2	–	This study
Background mortality rate	μ_b	0.006	d^{-1}	Temming and Hufnagl (2015)
Size-dependent mortality constant	α	0.003	$cm^{3\beta}\ d^{-1}$	This study
Size-dependent mortality exponent	β	0.35	–	This study
Arrhenius temperature	T_A	9000	K	Campos et al. (2009)
Optimum temperature	T_{ref}	283	K	–
Lower boundary of tolerance range	T_L	273	K	–
Upper boundary of tolerance range	T_H	303	K	Campos et al. (2009)
Rate of decrease at lower boundary	T_{AL}	6 700 000	K	Campos et al. (2009)
Rate of decrease at upper boundary	T_{AH}	49 368	K	Campos et al. (2009)
Resource				
Carrying capacity	K	3000	$J\ m^{-2}$	This study
Regrowth rate	r	0.04	d^{-1}	This study
Amplitude	amp_r	0.7291	–	This study
Centre	$center_r$	273.45	–	This study
Width	$width_r$	−181.5	–	This study
Offset	$offset_r$	0.9944	–	This study
Pelagic resource	K_W	10^9	$J\ m^{-2}$	–
Fishing				
50% net selectivity	L_{50}	44.9	mm	Santos et al. (2018)
Net selectivity selection range	S_R	9.3	mm	Santos et al. (2018)
Commercial size	L_c	5.0	cm	ICES (2015)
Day surface	$area_F$	1.26×10^6	m^2	Polet (2000)
Number of local vessels per area	–	40	#	This study
Number of mobile vessels	–	140	#	This study
Giving up threshold local vessels	–	50	kg	This study
Giving up threshold mobile vessels	–	25	kg	This study
Maximum fishing time per week per vessel	–	4.5	d	This study
Fishing hours per day	–	12	h	This study

Shrimp population model

The shrimp population model is simulated using the Escalator Boxcar Train method to numerically track the shrimp and resource populations in all areas (de Roos et al. 1992). This method divides the shrimp stock into cohorts of individuals that hatch at the same time and settle in the same location. The cohort approach assumes that individuals in the same cohort experience identical development throughout their life. The number of shrimp within a cohort diminishes over time from background, fishing and potential starvation mortality. The individual-level processes describing shrimp food consumption, growth and energy allocation to reproduction are based on the Dynamic Energy Budget model for brown shrimp derived by Campos et al. (2009). Equations to describe energetics are all functions of the body volume of an individual (van der Meer 2006, Table 2). A fraction κ of assimilated energy intake

Table 4. Scenario overview used in the model.

Scenario name	Effort per vessel per week (d)	Maximum annual effort per vessel (d)	Total number of vessels	Number of local vessels per area	Number of mobile vessels	Max. fleet effort (d)	Approximate effort reduction (%)
4.5D_500V	4.5	234	500	40	140	117 000	0
4.0D_500V	4.0	208	500	40	140	104 000	12
3.5D_500V	3.5	182	500	40	140	91 000	22
2.5D_500V	2.5	130	500	40	140	65 000	44
1.5D_500V	1.5	78	500	40	140	39 000	67
4.5D_437V	4.5	234	437	35	122	102 258	12
4.5D_388V	4.5	234	388	31	109	90 792	22
4.5D_276V	4.5	234	276	22	78	64 584	44
4.5D_167V	4.5	234	167	14	41	39 078	67

is allocated to volumetric growth and maintenance (Table 2, van der Meer 2006, Kooijman 2009, eq. 1 and 2). The cost of growth given by Campos et al. (2009) was reduced to match experimentally and empirically obtained growth curves (Hufnagl and Temming 2011a, 2011b). The remaining fraction of assimilated energy (1-κ) is used for development of maturity and reproduction (van der Meer 2006, Table 2, eq. 3). Energy invested into maturity accounts for both development and maintenance of reproductive organs and tissues (Kooijman 2009). Intake and maintenance are temperature dependent (Table 2, eq. 8 and 9) following Campos et al. (2009), with area-specific temperature curves. The temperature curves were obtained by fitting a sine function through daily average, area specific bottom temperatures from a hydrodynamic model (Delft3D model, Deltares, Los et al. 2008). Comparison of an experimentally determined handling time (Andresen and van der Meer 2010) and maximum ingestion rate based on gut capacity (Campos et al. 2009) indicates that gut capacity is a stronger limiting factor in the acquisition of food. Hence, we assume that digestion limits resource consumption (Table 2, eq. 7 and 8). Based on a 12-hour activity span and the data presented in Andresen and van der Meer (2010) a search rate of 1.5 m^2 d^{-1} was determined. Food consumption is modelled as a saturating function using the maximum intake rate scaled with food encounter rate (Table 2, eq. 8). Other shrimp parameters (Table 3) were taken from Campos et al. (2009).

Temming and Damm (2002) find two peaks in egg presence in brown shrimp along the German coast, in early June and mid-November. We model reproduction as an abstraction of this pattern, with reproduction occurring twice per year, coinciding with these observed peaks (on day 167, mid-June and day 320, mid-November). The number of larvae produced is determined by summing the reproductive energy from all adult individuals in all cohorts, and dividing by the energetic content of an egg plus the energetic cost of creating the corresponding volume (Table 2, eq. 12). The reproductive energy of all contributing individuals is subsequently reset to 0. The total number of larvae is then distributed over the nine areas proportional to the size of each area, resulting in an equal larval density across all areas. Once assigned to an area, shrimp cohorts do not move. We assume larvae to hatch at a length of ∼0.15 mm, and to feed on pelagic resources (which are assumed to be highly available) until they reach length of settlement of $L_s = 0.5$ cm, at which they settle on the sea floor in the shallow regions and begin feeding on the benthic resource. Larvae suffer from background mortality during both the pelagic and the benthic phase. This background mortality has a size-dependent component which exponentially decreases with increasing body size. A baseline mortality is applied to larger sizes, which is based on estimates of natural mortality for larger shrimp (Table 2, eq. 14, Temming and Hufnagl 2015). Upon reaching volume V_M, corresponding to a length of ∼2.5 cm, individuals move from the shallow to the deep habitat, as larger shrimp are found in deeper waters (Janssen and Kuipers 1980). In each of the deep habitats, fishing mortality is applied according to the length-dependent net selectivity (Table 2, eq. 17, using parameters for a diamond-mesh 25 mm cod-end, table S3 in Santos et al. 2018), using the effort of the vessels operating in that location. Fishing mortality is thus an emergent result of the fishing effort and the size distribution of the shrimp population.

When food is scarce, shrimp individuals can compensate by 'shrinking' in volume. However, when a threshold value for body condition (the ratio of individual volume to maximum volume) is reached, starvation mortality occurs proportional to the volume deficit (Table 2, eq. 15).

Resources

Each shallow and deep habitat of each area has its own resource, which follows semi-chemostat dynamics in absence of shrimp foraging (Table 2, eq. 5). Maximum resource density is the same between areas and follows a sine function with a one-year period and an average level of 3000 J m^{-2}, based on Wadden Sea benthos density (Beukema 1976) and caloric content of species or species groups (Brey et al. 1988, Table 2, eq. 21). Because only an unknown fraction of resource productivity is suitable and available as food for brown shrimp, while the rest is, e.g. buried deeply in the sediment or too well-defended (e.g. larger shellfish), the resource renewal rate used is well below that reported for total secondary production (Beukema 1976). Resource renewal rate was adjusted to match the reported density estimate of large brown shrimp of 0.56 g m^{-2} (Tulp et al. 2016) based on the Dutch and German Demersal Young Fish Survey (ICES 2024c). This resulted in a resource renewal rate of 0.04, which corresponded to a maximum shrimp biomass of 20 776 tonnes across all model areas, or a biomass density of 0.57 g m^{-2}. The caloric food density in each area determines

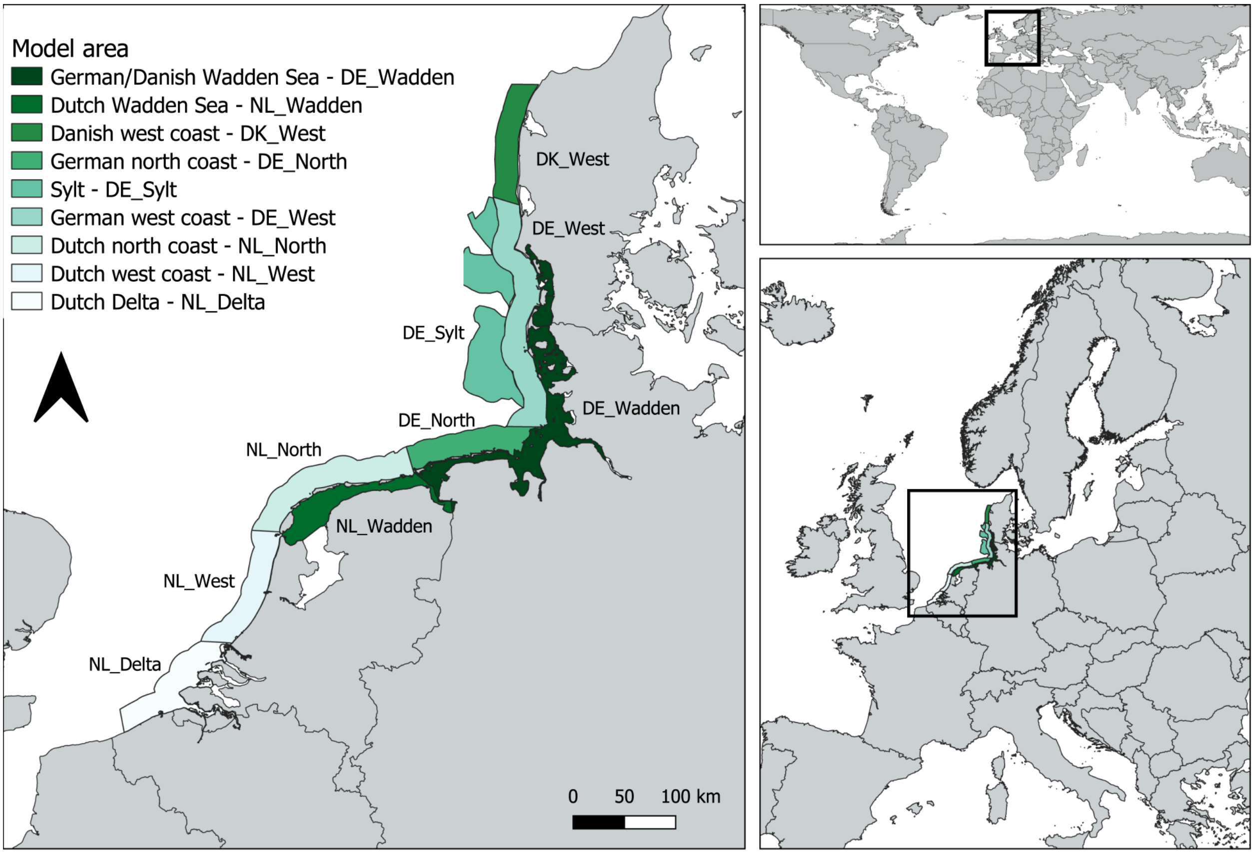

Figure 1. Model areas and their position along the European coastline. Right-hand graphs illustrate the position of the model area in relation to Europe and the world.

the growth rate of shrimp in that area, and the sum of all food consumption by shrimp determines the rate at which the food abundance declines (Table 2, eq. 5).

Scenarios

The different scenarios either involved a reduction of the maximum number of fishing days per week (hour reduction scenarios), or the number of vessels (fleet reduction scenarios, Table 4). In the baseline scenario, all 500 vessels (360 local and 140 mobile) were allowed to fish at maximum for 4.5 days per week. Note that maximum fishing time per week only sets an upper limit to the effort of each vessel, while the realized effort also depends on Monday's landings and the associated decision of fishers whether or not to continue fishing for the remainder of the week. In the hour reduction scenarios, the maximum fishing time was decreased to 4.0, 3.5, 2.5, and 1.5 days per week, corresponding to a reduction of maximum effort by respectively 12%, 22%, 44% and 67%. In the fleet reduction scenarios, all vessels were allowed to operate 4.5 days per week, but each fleet segment (each location-specific group and the mobile vessels) was reduced by the same percentages as used for the hour reduction scenarios. This resulted in a total number of vessels of 437 (−12%), 388 (−22%), 276 (−44%) and 167 (−67%) for the different fleet reduction scenarios.

Simulations

Dynamics of the coupled shrimp and fisher models were simulated for 20 years, of which the first 10 years were discarded to avoid dependence on initial conditions. Overall, model dynamics converged to an annually repeating attractor well within the first couple of years. Furthermore, to account for random differences between individual runs, 20 replicate simulations were performed for each scenario. Differences between simulations arise from the partly stochastic decisions of mobile fishers in area selection. Inspection of model output showed only minor differences between individual replicate simulations (Supplementary Figure S 1). Nonetheless, all presented results were derived from model output that was averaged across 20 replicate simulations. Simulation results are expressed as the following quantities: effort—the number of 24-hour intervals spent at sea; discards—weight of shrimp below marketable length caught per week; landings—weight of shrimp at or above marketable length; LPUE—landings divided by effort; discard fraction—discards divided by landings plus discards; shrimp biomass—weight of shrimp in the sea (total, below or above marketable length); resource biomass—shrimp food energetic value per surface area; shrimp age—time since hatching; shrimp length (or size)—individual body length of shrimp; cohort abundance—the number of shrimp in a cohort, i.e. hatched at the same time. These quantities are presented either for the entire fleet, for the local or mobile fleet segments or per location (with a distinction between shallow and deep habitats for shrimp biomass and resource abundance), either as totals or averaged per vessel. Post processing analysis of model results was performed in R (R Core Team 2024) at vessel, fleet and shrimp population level.

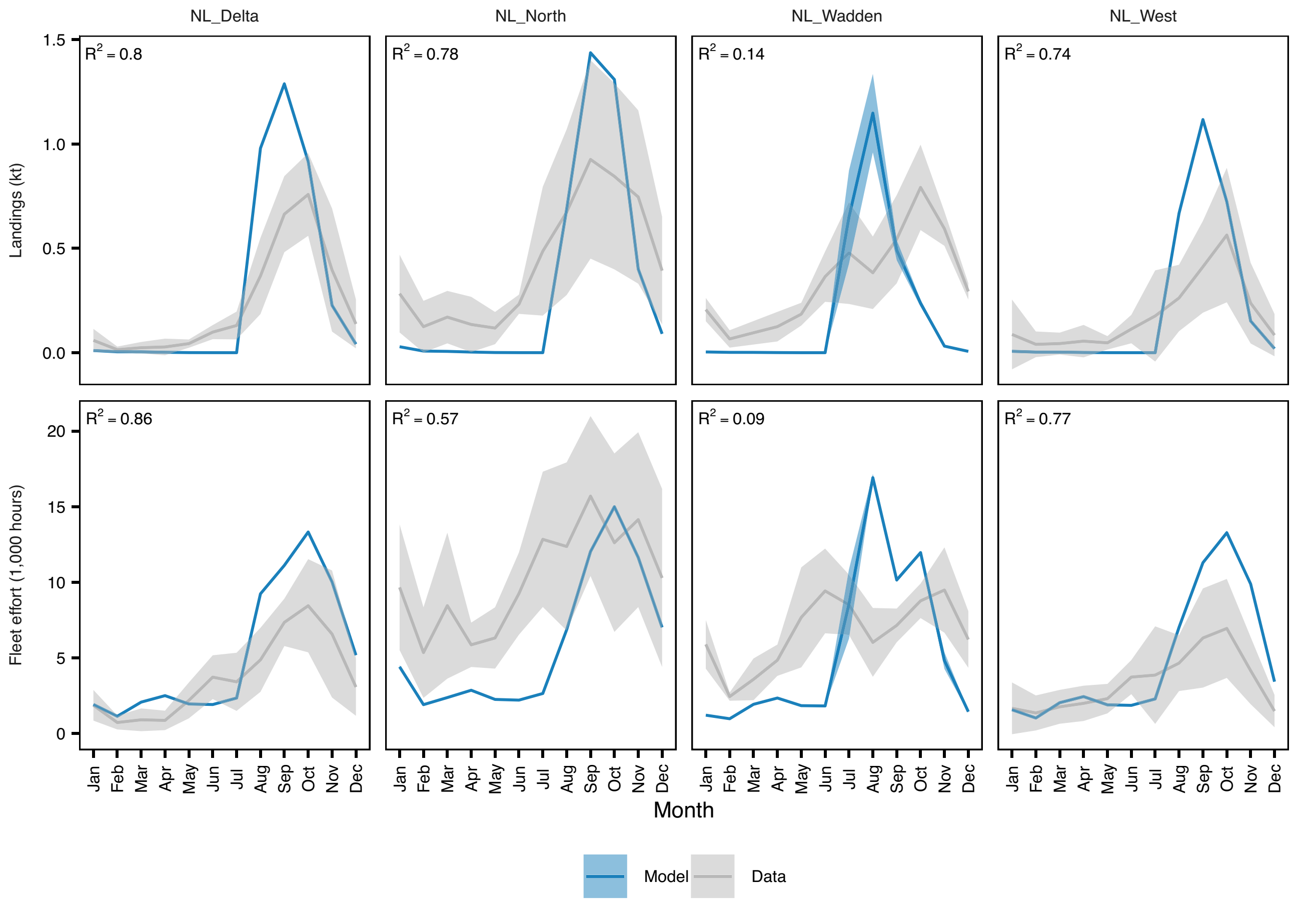

Figure 2. Comparison between model output (dark lines and shading) and data (light lines and shading) of landings per month (metric kilo tonnes, upper panel) and monthly fleet effort (1000 hours, lower panel) for the four Dutch areas (Beier et al. 2023b); see Table 1 for area definitions). Model output is derived from the baseline scenario '4.5D_500V', with a maximum of 4.5 fishing days per week. Modelled effort was calculated by assuming a single fishing day consists of 12 fishing hours. Lines represent monthly mean values of the Dutch shrimp fishing fleet calculated over the period 2016–2022. Shadings indicate standard deviations.

Sensitivity analysis

To study the robustness of our results we repeated the fishing time and hour reduction scenarios varying three key parameters. To assess sensitivity to resource productivity, we increased and decreased the resource carrying capacity by 20% to 3600 J m^{-2} and 2400 J m^{-2}, respectively. To vary the strength of the fisher's response to stock dynamics, we have halved (25 kg for the local and 12.5 for mobile vessels) and doubled (100 kg for local and 50 kg for mobile vessels) the 'giving up on Monday' LPUE threshold. To test assumptions regarding shrimp life history, we studied a model version where shrimp reproduce four instead of two times per year, on day 75 and 228, the middle of March and August, in addition to day 167, and 320, the middle of June and November.

Results

Data comparison

Modelled landings from the total fishing area equal 34 536 tonnes per year for the entire fleet (500 vessels), compared to the reported average annual landings of 27 832 tonnes (95% conf.int. 21 939–33 725 tonnes) for the period 2016–2022 for the Dutch, German, Danish, and Belgian shrimp fisheries (ICES 2025). For the baseline scenario (4.5D_500 V; Table 4) modelled monthly landings of shrimps of commercial size (>5 cm) and modelled fleet effort (hours) in four out of the nine areas compare well with data from the Dutch shrimp fishery, both in terms of absolute numbers and their seasonal pattern (Fig. 2). The model output shows stronger seasonal variation in both landings and effort compared to the data in four of the different areas (Beier et al. 2023a), in which observed landings and effort are spread more evenly throughout the year. This difference arises because our model assumes a limited number of distinct cohorts (two cohortsper year in each of nine areas) consisting of identical individuals (size, maturity, and reproductive capabilities). There is no variation among individuals within a single cohort. This creates a sudden increase in landings and effort when all individuals in a cohort reach commercial size simultaneously. In reality, reproduction and settlement of shrimp larvae will occur throughout the year and, together with environmental stochasticity and developmental variation within a cohort, result in landings that are distributed more evenly throughout the year.

Effect of hour reductions

Limiting the maximum number of fishing days per week leads to changes in the annual sum of landings, discards and effort (blue bars in Fig. 3), as well as their seasonal pattern (Fig. 4). Reducing the maximum number of fishing days from 4.5 days to either 4 (scenario 4.0D_500 V; 12% effort reduction) or 3.5 days per week (scenario 3.5D_500 V; 22% effort reduction) increases annual landings to, respectively, 41 357 or 48 919 tonnes per year (Supplementary Table A2). Because total fleet effort decreases and the number of vessels remains constant in the hour reduction scenarios, landings per effort and landings per vessel also increase. Further reducing maximum fishing effort to 2.5 days (scenario 2.5D_500 V, 44% effort reduction) or 1.5 days (1.5D_500 V, 67% effort reduction) per week leads to a decrease in both total landings and landings per vessel compared to the baseline scenario, while landings per effort for these scenarios are approximately equal to baseline. Total discards of undersized shrimp (<5 cm) initially increase with an increasing reduction of maximum fishing effort but decline again for a reduction of 67%. When expressed as fraction of the total catch (landings plus discards), the amount of discards of undersized shrimp stays constant at approximately 17% when maximum effort is reduced by 12, and sharply increases to around 43%–47% for highest reduction levels (Fig. 3 and Supplementary Table A2).

Effect of fleet reduction

Reducing the number of fishing vessels leads to the same effect on annual landings, discards and realized effort of the entire fleet, when expressed as a function of the relative reduction in maximum effort (orange bars in Fig. 3). However, both landings per vessel and effort per vessel increase with lower number of vessels and are still higher than baseline levels for the highest fleet reduction scenario (4.5D_167 V) that leads to a 67% decrease in maximum effort. The higher effort per vessel for scenarios with fewer vessels indicates that they are able to fish profitably for a longer period before the shrimp cohort is depleted.

Seasonal effect

In the baseline scenario (4.5D_500 V), both biomass of commercial-sized shrimp and weekly landings summed across model areas stay low during the first 30 weeks of the year, increase from week 30 onwards, peak during weeks 35 to 40 and then decline again (Fig. 4). The onset of the increase in landings and commercial shrimp biomass differs between areas, with landings and biomass in the Wadden Sea model areas (NL_Wadden & DE_Wadden) increasing before all other areas (Supplementary Fig. S2). Total fishing effort increases concurrently with the increase in total landings, and remains high as landings and commercial biomass decline, until the 50% winter effort reduction takes effect in week 50. The catch of undersized shrimp (discards) peaks around week 30, approximately 5 weeks before the peak in landings.

Reducing the maximum number of fishing hours by 12% or 22% postpones the peak in landings and commercial shrimp biomass by, respectively, 3 and 7 weeks. The height of the landings peak also increases (Fig. 4). With 22% effort reduction, the maximum weekly landings increase by 43% from 2 749 tonnes in week 37 (scenario 4.5D_500 V) to 3939 tonnes in week 42 in the 3.5D_500 V scenario. Discards change in a similar way, although the effect on the maximum weekly discards is even larger. At the 22% lower maximum effort, landings are still high when the 50% winter closure of the fisheries takes effect and landings continue to decline into the new year. A further reduction of maximum effort to 2.5 or 1.5 days per week leads the peak of commercial biomass occurring during the modelled 50% closure of the shrimp fisheries in winter (Supplementary Fig. S3). Because the active fleet is smaller during this period, exploitation is less intense, and the landings are distributed more homogenously throughout the year.

Cohort dynamics

In the baseline scenario (4.5D_500 V), the summer cohort is dominant over the winter cohort in terms of initial abundance and biomass (Figs 5 and 6). The winter cohort grows more rapidly and reaches commercial size after 289 days, versus after 414 days for the summer cohort. Both summer and winter cohort reach commercial size around the same time of year, at day of year 218 and 246 for summer and winter cohort, respectively. At commercial size, the summer cohort is still numerically dominant and the autumn peak in landings in the baseline scenario is therefore mainly taken from the cohort that hatched in the summer of the preceding year. Both cohorts grow to a maximum length of 8 cm, although the winter cohort grows faster and reaches 95% of this length at an earlier age.

Reduction of maximum fishing effort changes cohort dynamics and leads to slower growth, reduced maximum length, increased survival and higher maximum age (Figs 5 and 6). Figure 6 shows that maximum length is reduced from ∼8 to ∼6.5 cm at the lowest fishing intensity (max. 1.5 days per week). Shrimp also grow slower and take longer to reach both commercial size (5 cm) and 95% of their maximum length, despite the reduction in maximum length. Consequently, the day of the year at reaching commercial size is postponed. Decreasing maximum fishing effort also changes the dominance of the summer cohort in terms of biomass and abundance. At a maximum fishing effort of 3.5 days per week (22% effort reduction) or less, the winter cohort has a higher biomass at onset (initiation of the cohort) and at reaching commercial size (Fig. 6) than the summer cohort.

We show only the effect of reducing the maximum weekly fishing time, but results are strongly similar for changes in the number of vessels (at corresponding maximum effort reduction). Changes in growth patterns result from increased competition for food at lower fishing effort. Reduced fishing mortality, either through hour or vessel reduction, increases survival of shrimps and leads to an overall increase in shrimp biomass and decrease in resource biomass (Supplementary Fig. S3). Because shrimp growth is food-dependent, the reduction in resources leads to stagnation of growth at high reductions of maximum effort (Fig. 5). The growth reduction also affects the timing of recruitment of shrimp to commercial size, which, in turn, affects the timing of the peak in realized effort and landings of the shrimp fisheries.

Effect of vessel type

Because mobile vessels lose fishing time from moving between areas, the effort and landings realized by local vessels during the most profitable fishing times exceeds that of mobile vessel (Supplementary Fig. S4). However, mobile vessels can select the best

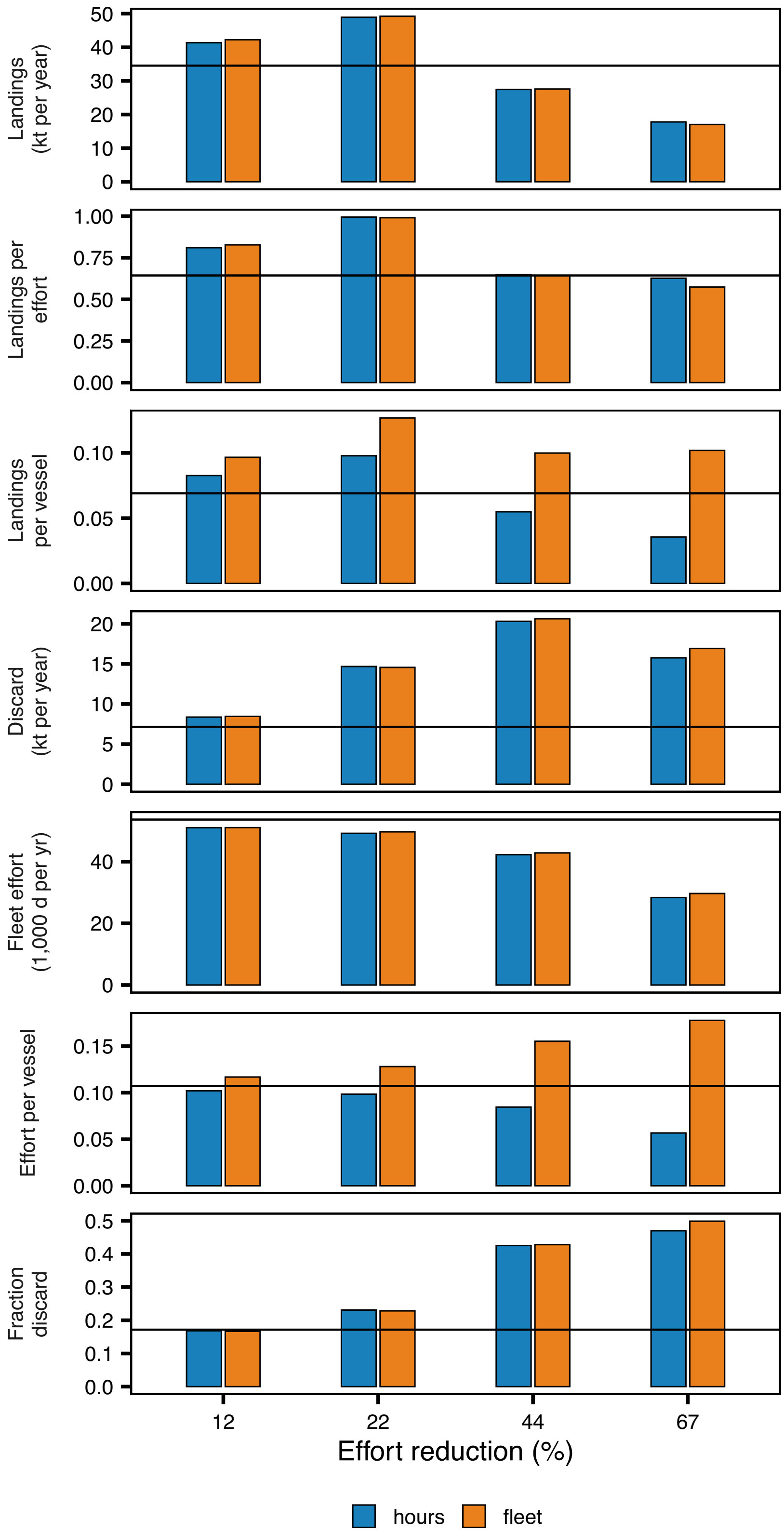

Figure 3. Annual sum over all vessels and areas of landings of commercial-sized shrimp (>5 cm), discards of undersized shrimp (<5 cm), fleet effort, and the derived statistics landings per effort and landings per vessel, effort per vessel, and fraction of undersized shrimp in total catch (landings plus discards). Different scenarios are plotted as a function of the relative reduction in maximum annual effort compared to the baseline scenario ('4.5D_500V'), with comparable hour and fleet reduction scenarios shown as pairs (Table 4). The horizonal black line indicates the baseline scenario ('4.5D_500V').

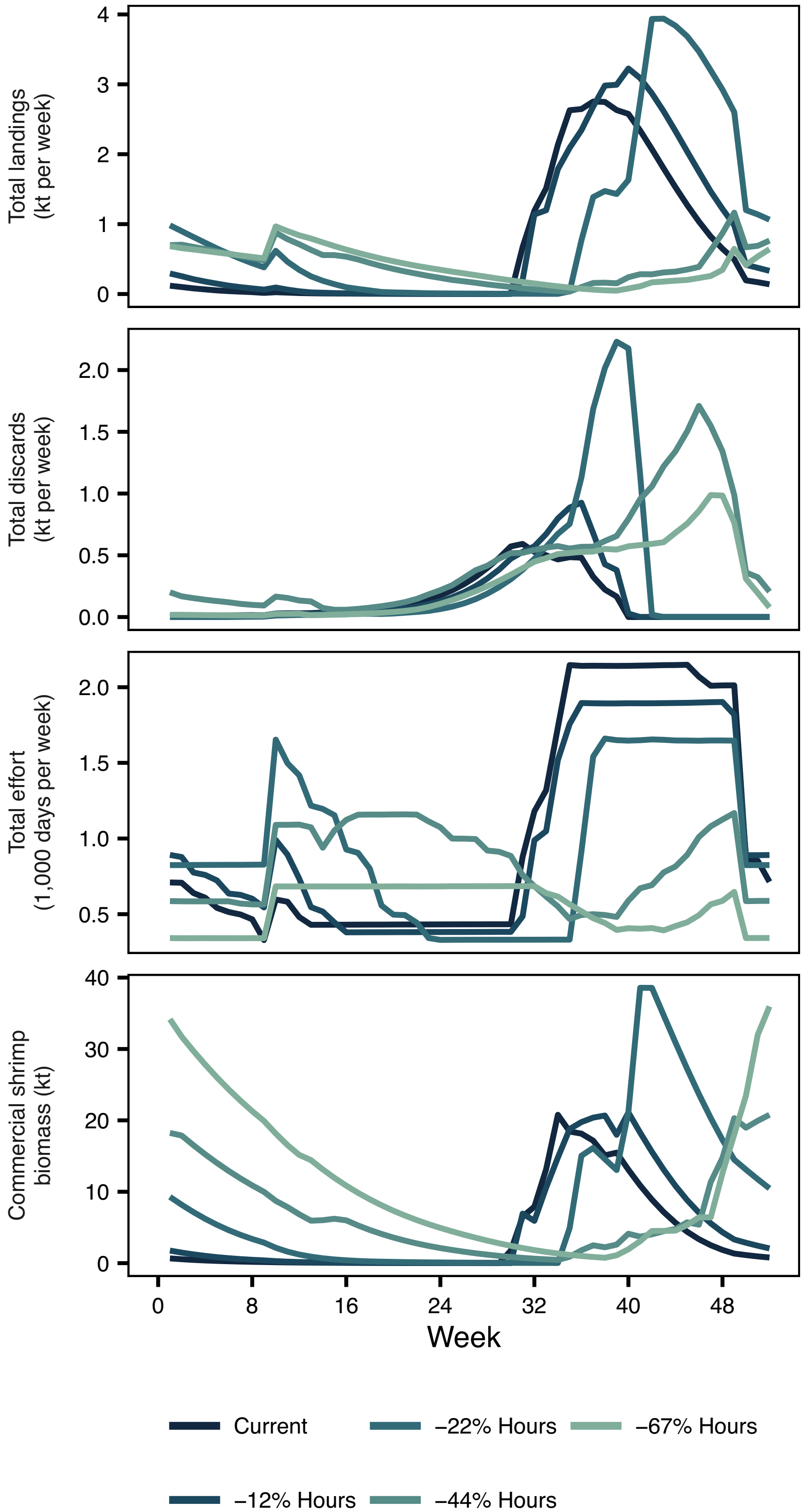

Figure 4. Landings of shrimp of commercial size (metric kilo tonnes per week), discards of undersized shrimp (metric kilo tonnes per week), fleet effort (1000 days per week) and biomass of shrimp of commercial size (metric kilo tonnes) for the entire modelled fleet (500 vessels). Coloured lines indicate scenarios that differ in maximum number of fishing days per week (Table 4).

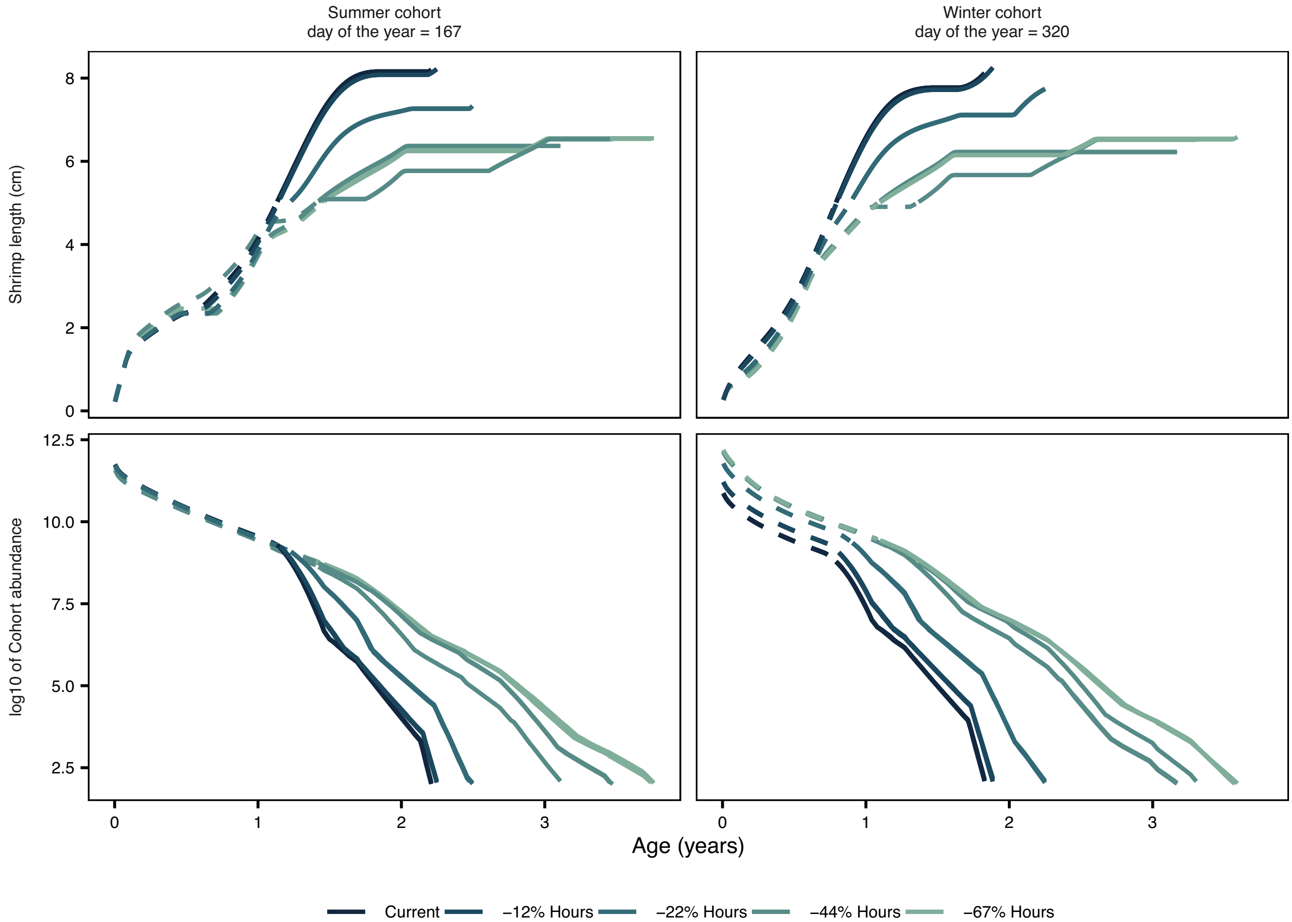

Figure 5. Scatter plot of abundance (bottom panels, log scale) and length (upper panels) of shrimp cohorts hatched in summer (day of the year 167; left) and winter (day of the year 320; right) in the Dutch Delta area (NL_Delta), as a function of cohort age (years). Cohorts from scenarios that impose hour reductions are shown in different colours (Table 4). For scenario 2.5D_500 V (44% hour reduction) there are two abundance and growth curves that alternate between years (a 2-year cycle). Solid lines correspond to shrimps of commercial size, while dashed lines are shrimps below commercial size.

area for fishing during the remainder of the year and realize higher effort and landings right before the onset of the peak in landings. Despite these subtle differences in landings and effort between mobile and local vessels, the LPUE of both vessel types are very similar. Changing the maximum number of fishing days or the number of vessels does not induce any differences in the LPUE between vessel types.

Sensitivity analysis

Increasing or decreasing the resource productivity in our model by 20% had only quantitative effects on the results (Supplementary Figure S5). The same is true when doubling or halving the threshold landings below which the fishers 'give up on Monday' (Supplementary Figure S6). A version of our model with two additional reproduction opportunities per year shows that while the general shrimp stock dynamics remain driven by the annual seasonality, large changes occur in the annual patterns of fishing effort, landings and the discards (Supplementary Figure S7). Total landings and effort now peak in spring and earlier summer, while discards peak right before and right after the peak in landings. In addition, yearly landings are much lower in the model version with four reproductive opportunities as we did not attempt to recalibrate this model version to match modelled landings against those observed.

Discussion

We developed an PSPM of the brown shrimp stock in the North Sea, coupled to an individual-based model for the fishery. The general patterns in our model output correspond to those found in data, even though we have not formally calibrated the model. To inform potential management measures to protect the shrimp stock from ongoing growth overfishing (Temming and Hufnagl 2015), we studied the effects of reduced maximum fishing effort on the brown shrimp stock in the southeastern North Sea, either by reducing the fleet size or by imposing a shorter maximum weekly fishing time. For corresponding magnitudes of the reduction, we find similar effects on realized fleet effort, landings, undersized discards, stock size and shrimp growth of these two modes of reduction. The effects we find are driven by the feedback between the fishery and the stock dynamics, emphasizing the value of this type of model to study management scenarios.

The smallest maximum effort reductions we simulate (by 12% and 22%) lead to a substantial increase in fleet landings and

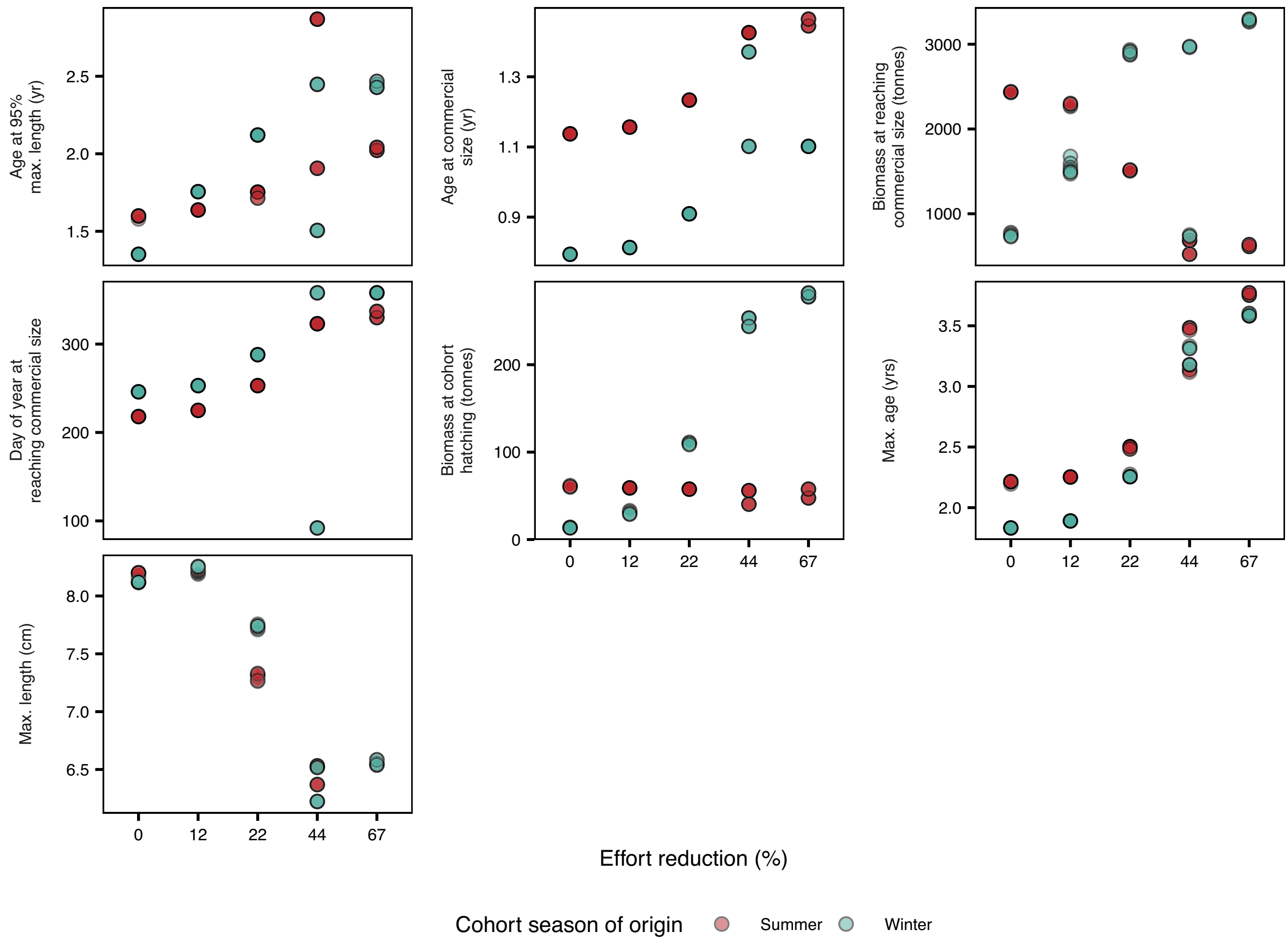

Figure 6. Summary statistics of the summer and winter cohorts as a function of effort reduction for the hour reduction scenarios in the Dutch Delta area (NL_Delta). At 44% effort reduction there are multiple points per cohort type, because cohort dynamics alternate between years. Statistics from other areas show highly similar patterns with only minor quantitative deviations.

efficiency (LPUE). This effect is consistent with recovery from growth overfishing: the reduced mortality allows the shrimp to reach larger size before being harvested, leading to higher availability of harvestable biomass (Allen 1953). For stronger reductions (44% and 67%), the fleet landings are reduced compared to the current situation. This result is in agreement with classical fisheries theory (Beverton and Holt 1957), where strongly reduced fishing mortality means individuals are likely to die from natural mortality before being harvested.

For all magnitudes of reduction we observe a strong increase in discards of undersized shrimp. Reduced fishing leads to higher shrimp abundance, which leads to lower per capita resource availability and thus slower individual growth. As a consequence, there is more temporal overlap between cohorts of marketable and discard-sized shrimp. Another effect of reduced harvesting capacity is that it takes longer to deplete a marketable cohort. Together, higher overlap and a wider harvesting interval cause the higher discards at reduced fishing.

A further consequence of the reduced growth in all reduced fishing scenarios is that the peak in shrimp fishing, which occurs when the large shrimp cohort reaches harvestable size, shifts to a later date in the year, or even to the early spring of the following year. In other words, we observe that a management regulation to curb fishing effort induced a shift in the life-history of the target species, which in turn changes not only landings and discards, but also the seasonal pattern in exploitation. This result highlights the strength of our modelling approach, where the dynamics of the stock as well as the fishery are modelled in sufficient complexity. Seasonal LPUE for Dutch and German vessels indicate that substantial seasonal variability in LPUE (a proxy for large shrimp abundance) exists among years (Supplementary Figure S8). Although this is not a formal model-data comparison, it indicates that a shift in the timing of marketable shrimp abundance, which our model predicts for reduced effort, does historically occur (compare Fig. 4 and Supplementary Fig. S8). Further analysis of the relationship between this variability and the preceding timing and intensity of fishing mortality is an important subject of further study.

Despite similarity of results between the two modes of reduction on the fleet level, the results differ strongly for individual vessels. For the maximum weekly fishing time reduction, both the effort per vessel and the landings per vessel closely follow the fleet-level pattern. A reduction in the number of vessels shows a different pattern: the greater the fleet size reduction, the more each remaining vessel fishes, while landings per vessel peak and then stabilize at a high level. This difference between the two modes of effort reduction for individual vessels is visible because we use an individual-based fleet model. In other models of high mechanistic ecological complexity, fisheries are often implemented as a simple constant additional mortality (e.g. van Kooten et al. 2007, 2010, Croll et al. 2023). Here, it is driven by the modelled decision framework which, though still highly simplified, results in more fishing by each remaining vessel when the fleet becomes smaller, because remaining vessels keep fishing as long as landings are above the giving-up threshold. This allows a reduced number of vessels to compensate for some of the capacity lost through the fleet reduction.

Our model includes local fishers as well as fishers operating throughout the available spatial domain, based on where landings are best. In our model results, landings, effort, and discards by mobile and local fishers are similar because the dynamics of the shrimp stock are highly synchronized across the areas, so that moving to other areas is rarely profitable. Effort and landings of local and mobile fishers will likely differ under other scenarios, particularly those where the dynamics of the shrimp are less synchronous. We based the distinction between local and mobile fishers on interviews with Dutch shrimp fishery representatives (Steenbergen et al. 2015). Our classification conforms to a recent statistical analysis of the spatial distribution of German shrimp fishers (Orey et al. 2024). In reality, fisher decisions of where and when to fish are much more complex. Fishers rarely have the perfect knowledge we assume, as they tend to share information on landings with friends but shield it from competitors. Furthermore, their decisions depend on the characteristics of their vessel, weather forecasts, their financial situation, the price of shrimp, as well as the behaviour of other fishers (Schadeberg et al. 2021, Letschert et al. 2023). Increasing the level of differentiation in the modelled fleet could reveal which strategies or fisher types profit from particular management regulations. This could also highlight how differences in vessel characteristics and behaviour among countries determine efficacy of management. This is a relevant further application of our model, but beyond the scope of the current work. The strength of the dynamic response of fishers to the shrimp stock is determined largely by the 'giving up on Monday' threshold values, which were chosen to roughly match model behaviour to observed mean number of days at sea (Steenbergen et al. 2015). However, significant changes to their values affect our results mostly in a quantitative sense, with the qualitative patterns showing robustness (Supplementary Figure S6).

The change in the seasonal pattern of shrimp fishing resulting from slower shrimp growth could directly affect other ecosystem components. The coastal areas where the shrimp trawlers operate are also important habitat for benthic invertebrates and juvenile demersal fish species (Heessen et al. 2015), which often use the area seasonally. Shrimp trawling causes substantial bycatch of these species (Beier et al. 2023a). A major shift in the timing of the fishery which our model results show, would likely also change the amount of bycatch per unit fishing effort as well as the species composition of the bycatch. Similarly, many of the areas used by the fishery are important seasonal feeding and resting grounds for (often highly protected; Dias et al. 2019) migrating seabirds, which are often disturbed by the presence of fishing vessels. Both for bycatch and seabird disturbance, a shift in the timing of fishing could dampen, negate or even reverse the effect of reduced annual fishing effort.

Both the shift in the timing of the fishery as well as the change in shrimp growth in response to fishing can furthermore have important ramifications in a food web context. Brown shrimp are important predators as well as prey. Although opportunistic feeders, there is evidence that larger shrimp focus on different and generally larger food items (Pihl and Rosenberg 1984, Oh et al. 2001). Fishing-induced changes in shrimp distribution and dynamics could affect abundances and seasonal patterns in shrimp prey dynamics. For example, there is evidence that the recruitment success of bivalve species in the Wadden Sea is in part determined by the relative timing of bivalve spatfall and the arrival of brown shrimp of suitable size to consume the larvae (Beukema and Dekker 2014). The timing of this arrival has been attributed to temperature, but our work suggests that fishery-induced changes in shrimp growth also affect the timing and hence could also play an important role in bivalve recruitment success. Bivalves are important food for many bird species, so that shrimp fisheries could indirectly have wider food web effects. Experiments also indicate that settlement of flatfish larvae, another potential prey item for larger brown shrimp, is negatively affected by their presence (Wennhage and Gibson 1998). This means that changes in shrimp growth could also affect the recruitment success of (commercially important) flatfish stocks.

Brown shrimp are also important prey species, in particular, for cod (*Gadus morhua*) and whiting (*Merlangius merlangus)*. With the advent of shrimp fishing since the 1970s, fishing mortality (of larger shrimp) has replaced natural mortality of (mainly smaller) shrimp in the southeastern North Sea and it is hypothesized that the expansion of the shrimp fishery has been facilitated by the fishing-induced reduction in cod and whiting abundance (Temming and Hufnagl 2015). However, cod and whiting mostly target small shrimp, below marketable size (Hislop et al. 1991, Welleman and Daan 2001). In our model, more consumption by predators would 'thin out' the small shrimp, leading to faster growth, higher production of large, marketable shrimp, and potentially higher shrimp landings. The theoretical foundations of this 'emergent facilitation' between predators and fishers are well-understood (de Roos et al. 2007, 2008, Huss et al. 2014). In our model we have not included mortality from fish predation, because cod and whiting abundance has long been very low (ICES 2024a, 2024b). However, whiting has recovered since 2013 and it is conceivable that whiting predation has increased to such an extent that the shrimp stock is no longer limited by competition among small individuals. A reduction of fishing effort to reduce growth overfishing would then simply lead to more food for whiting, rather than higher landings. In support of this conjecture, we found that in our simulations, the link between shrimp growth rate and fishing effort disappears when we increased the mortality of small shrimp (results not shown).

Our model is largely deterministic. The only stochasticity is in the decision where the mobile fleet vessels fish each week. The determinism helps to keep the model analysis tractable. The small difference between the stochastic model realizations suggests that the model is not extremely sensitive to stochasticity in the fishery process, but we have not further tested this. There are indications that fisher decision making depends on individual history (Schadeberg et al. 2021), which could cause stochastic differences to lead to diverging strategies among fishers. While beyond the scope here, this is an important and interesting subject for further study. In the deterministic shrimp model, all shrimp of the same age and location are identical throughout life. As a consequence, all shrimp of equal age in a patch reach commercial size simultaneously, which leads to a sharp peak in landings. In the data, the pattern is similar, but the transition is more gradual because many sources of stochasticity make the dynamics in nature more gradual. In general, the dynamics of PSPMs are remarkably robust to environmental stochasticity (van Kooten et al. 2004), although the effect of other sources of divergence (e.g. genetic diversity within the shrimp stock) remain untested.

The equilibrium dynamics of PSPMs are similar between models with pulsed and continuous reproduction, including the effects of size-dependent mortality. This is because food-dependent growth and the ontogenetic scaling of intake and energetics together lead to converging growth trajectories of similar-sized individuals, so that discrete size groups emerge even if they are not enforced by pulsed reproduction (van Kooten et al. 2007). A model variant with four rather than two reproduction pulses per year confirms the robustness of the shrimp stock dynamics, but shows that it strongly alters the fishing, catches and discards, which requires further scrutiny, especially when using our model for policy advice. The main driver of dynamics in PSPMs is the direction of 'ontogenetic asymmetry' (de Roos and Persson 2013), which is determined by the size-scaling of biomass production and mortality rates. Our fishing scenarios directly affect the balance of mortality between large and small shrimp, and large changes in the relative productivity of the shallow and deep habitats (or underlying parameters) would affect the outcomes of these scenarios, but the parameter values determining relative productivity are measured estimates (Campos et al. 2009), making them unlikely to be very different from the values used. Our sensitivity analysis shows that even substantial changes in overall resource productivity have only quantitative effects. In our model, we find that landings mostly consist of shrimp hatched the previous summer. This is consistent with Campos et al. (2009), but contradicts the result of growth experiments (Hufnagl and Temming 2011a), which suggest that the bulk of the autumn landings come from the previous winter cohort. However, these experiments were conducted under *ad libitum* feeding. Lower realized feeding rates could lead to slower growth in the field, more in line with our model results and those of Campos et al. (2009).

We assume redistribution of larval shrimp across the entire spatial domain, but do not include mixing or migration later in life. There is evidence of migration and directed larval transport along the North Sea coast (Daewel et al. 2011, Respondek et al. 2022), but we have assumed that for our large spatial patches, the relative contribution of migration to the patch-level stock is minor. The effects of a more realistic stock connectivity structure would be a relevant further study, particularly because it would connect the local fisheries.

The socio-economic impact likely differs between the two modes of effort reduction we have studied (Beier et al. 2023b, Steenbergen et al. 2015). Limiting the allowable fishing time is easier to implement than reducing fleet capacity through a decommissioning program. It is a uniformly applicable rule that implies a level playing field among fishers, and could potentially increase profits through higher market prices. The downside is that it reduces the profitability of the entire sector at once, with the risk that all shrimp fishing becomes economically inviable. A targeted vessel buyout program could provide more secure long-term economic prospects for remaining fishers and potentially reduce the need for further management restrictions such as real-time closures, but requires significant governmental commitment, financial resources, and policy prioritization. Such decommissioning of the shrimp fleet may also impact the fishing industry as a whole, and indirectly the processing industry as well as the fishing communities In the Netherlands, a first buyout scheme has led to the decommissioning of 19 vessels from the Wadden sea fleet. The buyout led to an increased effort as well as landings per remaining vessel (Hamon et al. 2023), but this apparent agreement with our model results is confounded by many other factors. Fixed maximum effort reductions can also be implemented as part of a more complex management. Steenbergen et al. (2015) explored the effect of a harvest control rule (HCR): a set of rules limiting maximum fishing time when LPUE are low. While the efficacy of an HCR depends on the chosen trigger values, their results suggest that the benefits of reduced fishing, which we show here, could also be obtained as part of a dynamic effort limitation strategy. Since that publication, an HCR has been implemented as part of the fisheries' MSC certification (Marine Stewardship Council 2023), but has been triggered only rarely. An important further development of our model would be to strengthen the socio-economic mechanisms such as shrimp price dynamics and fishing cost. This would allow for further studies of the dynamic interplay between fishery economics, fisher behaviour and stock dynamics underlying the net effects of potential management of the brown shrimp fishery.

Although many integrated ecological–economic fisheries models exist, there is an underrepresentation of models where landings are modelled on the level of individual fishers rather than aggregated on target species or fleet level (Nielsen et al. 2017). Our model implements vessel-level landings and discards, and our results show the relevance of contrasting fleet- and vessel-level effects of management measures. Our work highlights the importance of modelling both the life history of the target species as well as the fishery in sufficient detail and plasticity, as our results are the combined effects of density-mediated changes in shrimp growth, resulting from changed fishing mortality, which in turn changes the timing of fishing effort and shrimp landings, thus completing the feedback cycle. Models to study social–ecological systems such as fisheries should take into account this dynamic interplay between the ecological dynamics of the target stock and the behaviour of the fishers. While these models are complex and results can be less intuitive, we see a great risk of mismanagement when this complexity is not taken into account, in particular when management includes ecosystem-level objectives.

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Author contributions

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Supplementary material

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflicts of interest

None declared.

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Data availability

No new data were generated or analysed in support of this research.

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