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Non-trophic interactions amplify kelp harvest-induced biomass oscillations and biomass changes in a kelp forest ecological network model

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ABSTRACT: Kelp forests are important marine ecosystems providing habitat for numerous species. Despite over 50 yr of mechanical harvesting in the Northeast Atlantic, the indirect impacts of kelp harvesting and associated habitat loss on faunal species within kelp forests remain poorly understood. We investigated the consequences of kelp harvesting by developing an allometric trophic network model for a subtidal Northeast Atlantic kelp forest (dominated by *Laminaria hyperborea*). Additionally, we designed a novel mechanistic model to explore the non-trophic interactions between kelp and age-class 0 Atlantic cod *Gadus morhua* and between kelp and European lobster *Homarus gammarus*, specifically focusing on the increased survival benefits provided by the kelp habitat. Simulations were conducted over a 50 yr period, incorporating harvesting cycles of 2, 5, and 9 yr, as well as low and high harvesting intensities. Our findings reveal the complex dynamics resulting from kelp harvesting. The recovery of kelp biomass was observed with 5 and 9 yr harvesting cycles, whereas a decline was observed with a 2 yr cycle. Furthermore, the non-trophic interactions facilitated a higher pre-harvest biomass for both European lobster and Atlantic cod compared to scenarios without this interaction. These results highlight the multitrophic effects of kelp harvesting and emphasize that the recovery of kelp-associated species may not necessarily align with kelp recovery, depending on harvesting intensity and recovery periods. Importantly, our study contributes to a better understanding of the ecological consequences of kelp harvesting and underscores the need for sustainable management practices to mitigate habitat loss in kelp ecosystems.

KEY WORDS: Kelp harvesting · Allometric trophic network · *Laminaria* spp. · Atlantic cod · European lobster · Food web · Habitat complexity · Northeast Atlantic

1. INTRODUCTION

Kelp forests are highly productive and diverse underwater ecosystems found in temperate coastal waters worldwide (Mann 1973). In the Northeast Atlantic, kelp forests provide many ecosystem services. For example, they protect coastlines through reduced wave action (Løvås & Tørum 2001) and offer habitat

for various species, including commercially important ones such as European lobster *Homarus gammarus* and Atlantic cod *Gadus morhua* (Schoenrock et al. 2021). Kelp harvesting in the Northeast Atlantic has been carried out mechanically since the 1950s to meet the needs of biotechnology, food production, and pharmaceuticals (Smale et al. 2013, Araújo et al. 2021). However, kelp forests are declining in one-

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third of their ecoregions globally due to various factors (Krumhansl et al. 2016), including ocean acidification, large storms, overfishing, and kelp harvesting, which threatens the resilience of these ecosystems (Steneck et al. 2002, Connell & Russell 2010, Lorentsen et al. 2010, Byrnes et al. 2011). Few comprehensive studies exist on the ecosystem-scale effects of kelp harvesting (but see Lorentsen et al. 2010, Christensen-Dalsgaard et al. 2020, Norderhaug et al. 2020a).

Kelps are large brown algae, mostly in the order Laminariales, that inhabit rocky shores in temperate regions. Kelp thalli consist of 3 parts: the holdfast, the stipe, and the lamina (or blade). Kelps are ecosystem engineers that modify and create habitat structure for many organisms with their 3-dimensional form (Miller et al. 2018), and they alter physical factors such as light availability and waterflow in coastal waters (Dayton 1985). The ability of kelps to attach to a hard substratum with their holdfast facilitates kelp dominance on rocky coastlines (Mann 1982). Kelp-derived carbon is important for nearshore ecosystems and can be a carbon source for marine animals such as filter feeders (Fredriksen 2003, Miller & Page 2012, Schoenrock et al. 2021) and mobile invertebrate fauna (e.g. mesograzers; Koenigs et al. 2015), which are important in transporting kelp-carbon to higher trophic levels; large quantities of kelp are also exported from the ecosystem by detachment and drifting (Norderhaug & Christie 2011). Kelp forests are nurseries for juvenile fish and invertebrates, and important feeding grounds for fish and vertebrates (Norderhaug et al. 2005, Lorentsen et al. 2010).

Wild kelp harvesting has ecological implications for both the kelp and the other species in the ecosystem, with increased mechanical harvesting causing great concern regarding over-exploitation and the sustainability of the use of these natural resources (Mac Monagail et al. 2017). In the Northeast Atlantic, mechanical harvesting takes place mostly in Norway, France, and Ireland, where the growing demand for seaweed resources is pushing towards increased mechanical harvesting (Werner & Kraan 2004). Approximately 230 000 t of wild Laminariales are harvested each year, with Norway accounting for 157 000 t, France 40 000 t, and Ireland 30 000 t (Araújo et al. 2019, 2021). Kelp forests have been harvested mechanically for over 50 yr, and a 5 yr cycle of harvesting (1 yr of harvesting followed by 4 yr of recovery) is generally considered sustainable (Vea & Ask 2011). While the biomass of kelp can recover within the 4 yr recovery time, the average age and size of kelp individuals, and the density of kelp recruits (new kelp

individuals) remain below pre-harvesting levels (Steen et al. 2016). Additionally, kelp epiphyte density and diversity remain below pre-harvesting levels after 4 yr of recovery (Steen et al. 2016), and this microhabitat is home to a diversity of mesofauna (Norderhaug et al. 2002). The abundance of small fish can decrease due to kelp harvesting, suggesting potential ecosystem-wide consequences (Lorentsen et al. 2010). While our study does not directly investigate the effects of kelp harvesting on the behaviour of birds, it is worth noting that on the coast of Norway, the foraging effort of great cormorants *Phalacrocorax carbo* is higher in harvested kelp forests compared to pristine kelp forests (Lorentsen et al. 2010, Norderhaug et al. 2020a). The effect of kelp harvesting can, however, be species- or behaviour-specific, as kelp harvesting does not alter the diving activity of European shags *P. aristotelis* (Christensen-Dalsgaard et al. 2020).

In ecological networks, species can have both trophic (energy transfer from one species to another) and non-trophic (non-consumptive) interactions. Habitat complexity is known to increase prey survival, and the survival is likely linked to species-specific predator-prey behaviours (Scharf et al. 2006). Kelp forest habitats can facilitate competitive dominance of sessile invertebrates in giant kelp *Macrocystis pyrifera* forests (Arkema et al. 2009), and a wide range of macrofaunal species may colonize *Laminaria hyperborea* alongside epiphyte communities (Schoenrock et al. 2021). In an experiment, artificial kelp was exposed for short time periods in kelp forests, and within 2 to 7 d of exposure, a significant number of kelp forest fauna colonized the artificial kelp, demonstrating high mobility (Norderhaug et al. 2002). In Atlantic cod juveniles, the mortality rate varied based on habitat complexity, with sand habitats, cobble surfaces, and sponge habitats exhibiting 93.4, 66.8, and 32.2% mortality rates, respectively; juvenile cod are known to prefer more complex areas as their habitat (Lindholm et al. 1999, Elliott et al. 2016). Similarly, the survival of juvenile lemon damselfish *Pomacentrus moluccensis* depends on coral reef habitat complexity and predator density; reefs with high-complexity coral and abundant predators supported the same number of damselfish as high-complexity reefs with no resident predators, but on low-complexity reefs with resident predators, the abundance of juvenile damselfish was significantly lower than on low-complexity reefs with no predators (Beukers & Jones 1998). This effect could be analogous to the effect that kelp harvesting will have on the complexity of seafloor habitats in temperate

reefs, and therefore the effect of kelp harvesting at the ecosystem scale.

Here, we used an allometric trophic network (ATN) model to study the effects of kelp harvesting on the wider kelp forest ecosystem including kelp consumers and higher trophic levels. We extended the ATN model to include a non-trophic interaction with kelp for 2 commercially important species: juvenile (0 yr old) Atlantic cod and European lobster. Northeast Atlantic kelp forests are essential habitats for Atlantic cod and European lobster (Bertocci et al. 2015), and these fisheries species provide a great opportunity to study the non-trophic interactions between kelp forests and species at higher trophic levels. Our research was particularly motivated by the potentially significant, yet poorly understood, ecosystem-wide consequences of kelp harvesting (see data for one region in Norderhaug et al. 2020a). We address the following questions with the models: (1) How well does kelp recover after harvesting with varying harvesting intensities and recovery period lengths? (2) How does kelp harvesting affect the abundance of kelp-consumer species (trophic interaction)? and (3) How does kelp harvesting affect the abundance of Atlantic cod and European lobster that utilise kelp for habitat (non-trophic interaction)?

2. MATERIALS AND METHODS

2.1. Overview

To study the effects of kelp harvesting at the ecosystem scale, data on Northeast Atlantic kelp forest species and their feeding interactions were collected from the literature (Table S1 in the Supplement at www.int-res.com/articles/suppl/m722p019_supp.pdf), and an ATN model was used to simulate different kelp-harvesting scenarios. The focus was on non-trophic interactions between kelp and 2 commercially important species: Atlantic cod and European lobster. Cod and lobster have non-trophic interactions with kelp through the survival benefit that the habitat kelp provides (kelp cover) and are connected to kelp via trophic interactions of other species in the ecological network. In total, the ecological network consisted of 43 species or taxonomic groups (Table S1), in which the fish species were further divided into 5 age classes that were represented by distinct nodes (Table S2). Consequently, the nodes representing guilds in the ecological network totalled 123 and were interconnected through 1300 feeding links (trophic interactions). Additionally, we incorpo-

rated 2 non-trophic interactions involving kelp: one with age-class 0 Atlantic cod and the other with European lobster. Kelp harvesting was simulated with a 'low harvesting intensity' (~20% reduction in biomass, corresponding approximately to the historical average of annual harvesting estimates in Norway and France in 2004: Werner & Kraan 2004; and to a more recent estimate of 26% loss of kelp canopy at one trawled station: Norderhaug et al. 2020b) and a 'high harvesting intensity' (~80% reduction in biomass, representing a hypothetical extreme case), and harvesting cycles of 2, 5, and 9 yr.

2.2. Northeast Atlantic kelp forest ecological network

The ecological network was used to describe the trophic interactions between the Northeast Atlantic kelp forest species as well as the non-trophic interactions between kelp and Atlantic cod and between kelp and European lobster (Fig. 1). To construct the kelp forest ecological network, a list of invertebrate and fish species from the kelp forests of the west coast of Ireland was used (Schoenrock et al. 2021). Common Northeast Atlantic phytoplankton and zooplankton species for the ecological network model were collected from the literature (Kennington & Rowlands 2006, Hinder et al. 2012, Oksman et al. 2019). The invertebrate and fish species list utilised for the Northeast Atlantic kelp forest ecological network model included abundance ranks of Superabundant, Abundant, Common, Frequent, Occasional, and Rare (SACFOR; Hiscock 1996) for the species. In choosing the species for the ecological network model, we focused on invertebrates (within the phyla Mollusca, Crustacea, Echinodermata, and Actiniaria) with SACFOR abundances of Superabundant, Abundant, and Common, while including all abundance levels for fish species (Schoenrock et al. 2021). The rationale behind this criterion was to prioritize the inclusion of species that are more prevalent or ecologically significant within the kelp forest ecosystem. Superabundant, Abundant, and Common invertebrate species are likely to have stronger interactions and contribute more significantly to the overall network dynamics. In contrast, including all abundance levels for fish species was necessary to capture the complexity of fish interactions within the ecological network.

The final species/group list included dissolved organic carbon (DOC), particulate organic carbon (POC), kelp, phytoplankton, zooplankton, inverte-

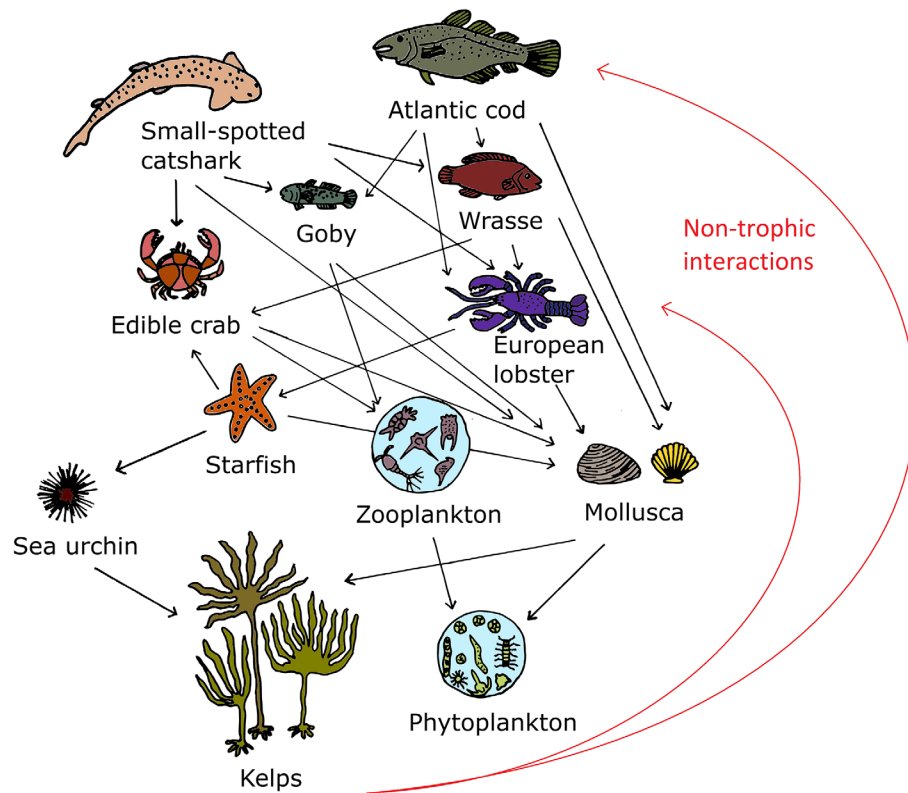


Fig. 1. Simplified Northeast Atlantic kelp forest ecological network model used in this study. The black arrows represent the trophic interactions (feeding links) between the species or groups in the ecological network, and the red arrows represent the non-trophic interactions between kelp and Atlantic cod *Gadus morhua* and between kelp and European lobster *Homarus gammarus*

brate, and fish taxa (Table 1; for detailed fish information, see Table S2). Some of the key parameters of the ATN model were determined based on the body masses (in μg of carbon) of individuals within each guild, M_i , which were either directly obtained from the literature or calculated based on published information (Table S1). Common prey items for each species were found in the literature (Table S1). Fish species were separated by age into age classes of 0, 1, 2, 3, and 4+ yr olds, which allows the model to account for age-related changes in body size, metabolic rates, maturity, and trophic links (changes in prey choice).

To estimate the biomass of an individual kelp, M_K , the fresh weight of a 4 yr old *Laminaria hyperborea* was used (Steen et al. 2016, M. Pedersen pers. comm.). The dry weight was calculated with known water content in fresh weight (Rajauria et al. 2021) as follows:

$$\text{dry weight} = \text{fresh weight} \times 0.15 \quad (1)$$

and the carbon content from the dry weight was calculated based on Sjøtun et al. (1996) with the equation:

$$M_K = \text{dry weight} \times 0.29 \quad (2)$$

To describe the phytoplankton groups in the model, diatoms (Oksman et al. 2019) and dinoflagellates (Hinder et al. 2012) were used as representative species. Both groups were divided into 3 size groups (small, medium, and large) based on carbon content values. The carbon content of small (924 pg C), medium (2311 pg C), and large (7798 pg C) diatoms were estimated from the carbon content values of *Thalassiosira gravida*, *Thalassiothrix longissima*, and *Rhizosolenia hebetata* f. *semispina*, respectively, which were extracted from a global diatom database (Leblanc et al. 2012). The carbon content of dinoflagellates is based on abundance data from Hinder et al. (2012), so that *Ceratium lineatum* was the representative species for small (<2000 pg C) dinoflagellates, the average of *C. furca*, *C. fusus*, *C. tripos*, *C. macroceros*, and *C. longipes* was used for medium-sized (2000–7400 pg C) dinoflagellates, and *Protoperidium curtipes* was used as the representative species for large (>7400 pg C) dinoflagellates. The carbon content for these species was extracted from <http://nordicmicroalgae.org>. An average carbon con-

Table 1. Species or groups (guilds) included in the Northeast Atlantic kelp forest ecological network model. Body masses and prey items are listed (using the Table ID numbers) for kelp, phytoplankton, zooplankton, and invertebrates. For information on fish species, see Table S2. DOC: dissolved organic carbon; POC: particulate organic carbon; na: not applicable

Table ID	Species/group (guilds)	Body mass ($\mu\text{g C}$)	Prey items (links)
1	DOC	na	na
2	POC	na	na
3	<i>Laminaria hyperborea</i>	2.08×10^7	na
4	Diatom small	9.24×10^{-4}	na
5	Diatom medium	2.31×10^{-3}	na
6	Diatom large	7.80×10^{-3}	na
7	Dinoflagellate small	1.83×10^{-3}	na
8	Dinoflagellate medium	5.78×10^{-3}	na
9	Dinoflagellate large	9.21×10^{-3}	na
10	Copepoda small	6.37×10^1	4–9
11	Copepoda medium	2.53×10^3	4–9
12	Copepoda large	1.03×10^4	4–9
13	Decapoda larvae	4.14×10^1	4–12
14	Euphausiacea	1.60×10^1	4–12
15	<i>Palaemon serratus</i>	7.88×10^4	10–14, 16, 17
16	<i>Actinia equina</i>	3.62×10^4	10–14, 17, 21, 22
17	Mollusca	9.46×10^4	3–9, 16
18	Asteroidea	1.79×10^6	17, 19
19	Echinoderms	1.45×10^6	2, 3
20	<i>Cancer pagurus</i>	1.14×10^7	10–13, 17, 21–23
21	<i>Carcinus maenas</i>	3.83×10^6	10–13, 15, 17, 20, 22
22	<i>Pagurus bernhardus</i>	1.46×10^6	4–15, 17, 20, 21
23	<i>Homarus gammarus</i>	1.52×10^8	10–13, 17–22
24	<i>Ctenolabrus rupestris</i>		
25	<i>Centrolabrus exoletus</i>		
26	<i>Symphodus melops</i>		
27	<i>Labrus mixtus</i>		
28	<i>Labrus bergylta</i>		
29	<i>Pholis gunnellus</i>		
30	<i>Platichthys flesus</i>		
31	<i>Taurulus bubalis</i>		
32	<i>Gobiusculus flavescens</i>		
33	<i>Pomatoschistus</i> spp.		
34	<i>Thorogobius ephippiatus</i>		
35	<i>Gobius niger</i>		
36	<i>Gobius paganellus</i>		
37	<i>Lipophrys pholis</i>		
38	<i>Callionymus lyra</i>		
39	<i>Ammodytes tobianus</i>		
40	<i>Ciliata mustela</i>		
41	<i>Pollachius pollachius</i>		
42	<i>Gadus morhua</i>		
43	<i>Scyliorhinus canicular</i>		

tent from different-sized cells was used if more than one size was recorded for the species.

The data for the zooplankton species used in this study were acquired from Kennington & Rowlands (2006), where zooplankton species and groups were listed by abundance percentages. Zooplankton groups with abundance composition of more than 5% were chosen for the ecological network model, and from those groups, species with abundance composition of

more than 1% of all zooplankton were taken into consideration and their individual carbon content was found in the literature or calculated based on Lindley et al. (1997). The carbon content of small (<1369 $\mu\text{g C}$) copepods was based on *Calanus helgolandicus* and *Centropages hamatus* (Williams & Robins 1982, Conley & Turner 1985); carbon content of medium-sized (1369–3743 $\mu\text{g C}$) copepods was based on *Pseudocalanus elongatus*, *Acartia clausi*, and *Calanus finmarchicus* (Lindley et al. 1997, Swailethorp et al. 2011); and carbon content of large (>3743 $\mu\text{g C}$) copepods was based on *Temora longicornis* (Lindley et al. 1997). To represent decapod larvae, the larvae of *Inachus dorsettensis* were used as a representative species for the guild (megalopa stage; Anger 1988), and the Euphausiacea larval representative species was *Nyctiphanes couchi* (Lindley et al. 1997, 1999).

The individual carbon content and the prey species for 9 species or groups of invertebrates were used in the model: *Palaemon serratus*, *Actinia equina*, *Cancer pagurus*, *Carcinus maenas*, *Pagurus bernhardus*, and *H. gammarus* (Lowndes & Panikkar 1941, Davenport 1972, Dawirs 1981, Zoutendyk & Bickerton 1988, Anger et al. 1998, Naczka et al. 2004, Kiørboe 2013, Madeira et al. 2015, Zotti et al. 2016, Yatkin et al. 2017, <https://www.glaucus.org.uk/Lobster.htm>), and the groups Mollusca, Asteroidea, and Echinodermata. The molluscan carbon content was averaged from *Calliostoma zizyphinum* and *Hinia reticulata* (Robinson et al. 2010, Mitra et al. 2015, Pereira et al. 2018), for Asteroidea the representative species was *Asterias rubens* (Nauen 1978,

Lebrato et al. 2010, Robinson et al. 2010), and for echinoderms the representative species was *Echinus esculentus* (Mol et al. 2008, Lebrato et al. 2010, Robinson et al. 2010) based on species abundance from Schoenrock et al. (2021) and the available literature.

Literature searches were conducted for all 20 species of fish common in kelp ecosystem surveys (Schoenrock et al. 2021) to get an estimate of their average lengths and prey species for the different

age classes (Table S2). As information about the lengths of 0 yr old fish was not available, they were assumed to be the average of 1 cm and the average length of 1 yr old fish. The weight of fishes in different size classes were estimated based on the length using the length–weight equation (Ricker 1975):

$$W = a \times L^b \quad (3)$$

where W = fresh weight (g) and L = length (cm). The coefficients a and b in the equation for each fish species were found in the literature and using <https://fishbase.org> (see Table S2). The dry weight was calculated based on the fresh weight following Murray & Burt (2001):

$$\text{dry weight} = \text{fresh weight} \times 0.2 \quad (4)$$

and from that, the carbon content for fish guild i was calculated based on Blaxter (1989) with the equation:

$$M_i = \text{dry weight} \times 0.53 \quad (5)$$

Thus, the carbon content of fish in this study is roughly 10% of the fresh weight.

2.3. ATN model

The ATN model was introduced by Brose et al. (2006) and further developed by Kuparinen et al. (2016) and Bland et al. (2019) to include fish life-history structure. The ATN model is based on the metabolic theory of ecology, which states that most biological activities are determined by metabolic rates (Brown et al. 2004). Here, the model was parametrized for subtidal Northeast Atlantic kelp forests dominated by *L. hyperborea*. The constructed ecological network contained 123 guilds and 1300 links in total. A non-trophic interaction was added to the model to explore the survival benefits of the protection provided by the kelp habitat to age-class 0 Atlantic cod and European lobster.

The ATN model is based on ordinary differential equations that describe the rates of change in carbon densities (hereafter 'biomass') in the ecological network. The model shows how biomass is transferred between the different species or groups of functionally similar species or fish age classes (commonly referred to as 'guilds') in the ecological network through consumer–resource interactions. The biomass is expressed in units of micrograms of carbon per cubic meter of water ($\mu\text{g C m}^{-3}$). The equations

for the biomass dynamics during the growth season for producers (Eq. 6), non-fish consumers (Eq. 7), particulate organic carbon (POC) (Eq. 8), and dissolved organic carbon (DOC) (Eq. 9) are based on Brose et al. (2006), Boit et al. (2012), and Kuparinen et al. (2016):

$$\dot{B}_i = \overbrace{\frac{\text{gain from producer growth}}{r_i B_i G_i(\mathbf{B})(1-s_i)}} - \sum_j \overbrace{\frac{\text{loss to consumer } j}{x_j Y_{ji} B_j F_{ji}(\mathbf{B})}} \quad (6)$$

$$\dot{B}_i = - \overbrace{\frac{\text{maintenance loss}}{f_m x_i B_i}} + \overbrace{\frac{\text{gain from resources } (j)}{f_a x_i B_i \sum_j Y_{ij} F_{ij}(\mathbf{B})}} - \sum_j \overbrace{\frac{\text{loss to consumer } j}{x_j Y_{ji} B_j F_{ji}(\mathbf{B})}} \quad (7)$$

$$\dot{B}_{\text{POC}} = \sum_i \left[\sum_j \overbrace{\frac{\text{ingestion of resource } j \text{ by consumer } i}{x_i Y_{ij} B_j F_{ij}(\mathbf{B})}} \overbrace{\frac{\text{egestion}}{(1-e_{ij})}} \right] \quad (8)$$

$$+ \sum_i \overbrace{\frac{\text{exudation by producer } i}{r_i B_i G_i(\mathbf{B}) s_i}} - \sum_j \overbrace{\frac{\text{loss to detritore } j}{x_j Y_{ji} B_j F_{ji}(\mathbf{B})}} - \gamma B_{\text{POC}}$$

$$\dot{B}_{\text{DOC}} = \gamma B_{\text{POC}} \quad (9)$$

In the equations, \mathbf{B} is the vector of all biomasses, B_i is the biomass of guild i , and \dot{B}_i is its derivative with respect to time. The daily intrinsic growth rate, r_i of producer guild i is calculated based on allometric scaling (Boit et al. 2012):

$$r_i = \left(\frac{M_i}{M_4} \right)^{-0.15} d^{-1} \quad (10)$$

where M_4 is the body mass of the reference producer (Alg1). $G_i(\mathbf{B}) = 1 - K^{-1}[\sum_{j=\text{producers}} c_{ij} B_j]$ is the limiting factor in the producers' logistic growth model, which includes interspecific, $c_{ij} = 1$, and intraspecific, $c_{ii} = 2$, producer competition coefficients (Uusi-Heikkilä et al. 2018), and carrying capacity coefficient K of phytoplankton (see Section 2.5 for details on parametrization). The fraction of newly created producer biomass lost to exudation $s_i = 0.2$ (Boit et al. 2012). The daily mass-specific metabolic rate, x_i , of consumer or fish guild i is obtained using the following allometric scaling equation (Boit et al. 2012):

$$x_i = a \left(\frac{M_i}{M_4} \right)^{-A} d^{-1} \quad (11)$$

For consumer guilds, the allometric scaling parameter $a = 0.314$ (Brose et al. 2006) and the allometric scaling exponent $A = 0.15$ (De Castro & Gaedke 2008), and for fish guilds, $a = 0.88$ (Brose et al. 2006) and $A = 0.11$ (Killen et al. 2007, 2010). The maximum consumption rate scaling factor $y_{ij} = 8$ for inverte-

brate consumer guild j feeding on guild j , and $y_{ij} = 4$ for fish guild i (Brose et al. 2006). The assimilation efficiency $e_{ij} = 0.45$ when j is a producer or detritus guild, and $e_{ij} = 0.85$ when j is a consumer or fish guild, and it describes the fraction of ingested biomass that is assimilated. The maintenance respiration coefficient $f_m = 0.1$ (Boit et al. 2012), and the fraction of assimilated carbon used for the production of consumer biomass $f_a = 0.4$ (Boit et al. 2012). The daily per capita dissolution rate of POC to DOC was set to $\gamma = 0.1 \text{ d}^{-1}$. The normalized functional response of consumers, based on the commonly used Holling type III–Beddington–DeAngelis hybrid response is:

$$F_{ij}(\mathbf{B}(t)) = \frac{\omega_{ij} B_j(t)^q}{B0_{ij}^q + d_{ij} B0_{ij}^q B_i(t) + \sum_k \omega_{ik} B_k(t)^q} \quad (12)$$

where the prey preference parameter:

$$\omega_{ij} = \begin{cases} (\text{no. of resource guilds } j \text{ of guild } i)^{-1}, & \text{if } i \text{ eats } j \\ 0, & \text{otherwise} \end{cases} \quad (13)$$

and $q = 1.2$ is the parameter controlling the form of the functional response (Boit et al. 2012). The half-saturation density, $B0_{ij}$ and the intraspecific feeding interference parameter, d_{ij} , depend on the types of consumer guild i and its resource guild j and are determined using the algorithm presented by Bland et al. (2019) with the exceptions that for invertebrates $d_{ij} = 0.01 \text{ m}^3 \mu\text{g C}^{-1}$, age-class 0 fish are treated as invertebrates, and additionally, for detritivores $B0_{ij} = 150\,000 \mu\text{g C m}^{-3}$ and $d_{ij} = 0.01 \text{ m}^3 \mu\text{g C}^{-1}$. Furthermore, we made it more difficult for 2 omnivores, namely *C. maenas* and *P. bernhardus*, to eat algae by increasing $B0_{ij}$ to $50\,000 \mu\text{g C m}^{-3}$ for those feeding interactions, to avoid too great a proportion of the energy gains of these 2 omnivores coming from plant-based sources.

Fish species were divided into 5 age classes. The dynamics of age-classes 0 and 1 are governed by the same equation (Eq. 7) that is used for the consumers, but adult fish (i.e. age-classes 2, 3, and 4+) also allocate a portion of their biomass to reproduction according to the following equation based on Uusi-Heikkilä et al. (2022):

$$\dot{B}_i^+ = \begin{cases} P_i I_i \cdot \frac{g_i^2}{2I_i}, & g_i < I_i \\ P_i I_i \cdot (g_i - \frac{1}{2}I_i), & g_i \geq I_i \end{cases} \quad (14)$$

where \dot{B}_i^+ denotes the rate of biomass allocation to reproduction by adult fish guild i during the growth

season, the consumption gains $g_i = f_a x_i B_i \sum_j y_{ij} F_{ij}(\mathbf{B})$ and the maintenance losses $l_i = f_m x_i B_i$ determine the biomass allocation enforcing impaired reproduction when the consumption gains are less than the maintenance losses. The proportion of mature biomass in adult fish guild i is denoted by P_i , and I_i is a parameter controlling how much energy is invested into reproduction. The proportions of mature biomass in age-classes 2, 3, and 4+ are assumed to be 5, 50, and 95 %, respectively, for all fish species, and the reproductive investment parameter values were set to 10, 15, and 20 %, respectively. To form the equation for the adult fish (Eq. 15), the reproduction term (Eq. 14) is subtracted from the right-hand side of the consumer equation (Eq. 7) as follows:

$$\dot{B}_i = - \overbrace{f_m x_i B_i}^{\text{maintenance loss}} + \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\mathbf{B})}^{\text{gain from resources } (j)} - \overbrace{\sum_j \frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}^{\text{loss to consumer } j} - \dot{B}_i^+ \quad (15)$$

After the growth season of year Y , the accumulated biomass allocated to reproduction $B_{Y,i}^+(t^{\text{end}})$ contributes to the initial biomass of age-class 0 for the next growth season. The equation for the initial biomass of age-class 0 fish in year $Y + 1$ is the sum of biomasses allocated to reproduction by all adult fish classes of the species:

$$B_{Y+1,i}(0) = \sum_{a=2}^4 B_{Y,i+a}^+(t^{\text{end}}) \quad (16)$$

The initial biomasses of age-classes 1, 2, and 3 for the year $Y + 1$ are the biomasses of the previous age classes at the end of the growth season of year Y :

$$B_{Y+1,i}(0) = B_{Y,i-1}(t^{\text{end}}) \quad (17)$$

Age-class 4+ consists of fish of age 4 yr and older, and the initial biomass for age-class 4+ for the year $Y + 1$ is the sum of the biomasses of the previous age class (3 yr olds) and age-class 4+ at the end of the growth season of year Y :

$$B_{Y+1,i}(0) = B_{Y,i}(t^{\text{end}}) + B_{Y,i-1}(t^{\text{end}}) \quad (18)$$

For the non-fish guilds, the initial biomass for the year $Y + 1$ is their biomass at the end of the growth season of year Y . The length of the growth season was set to $t^{\text{end}} = 90 \text{ d}$.

To investigate the non-trophic impact of reduced habitat resulting from kelp harvesting on Atlantic cod and European lobster, we implemented the non-

trophic interaction within the ATN framework mechanistically. As a practical strategy to aid in mathematical modelling, we partitioned the species that rely on kelp habitat for cover into 2 subpopulations: protected and unprotected subpopulations. The biomasses of the protected and unprotected subpopulations of guild i are denoted by B_i^p and B_i^u , respectively, and the total biomass of guild i is $B_i = B_i^p + B_i^u$. The kelp biomass is divided into kelp in the unoccupied (available) state, B_K^0 , and kelp being occupied (unavailable) by species i , B_K^i , such that the total kelp biomass is $B_K = B_K^0 + \sum_i B_K^i$.

We assumed that for every biomass unit of species i protected by the kelp, λ_i units of kelp biomass are required (see Section 2.4 for details on parametrization). Furthermore, any biomass unit of kelp can be only used by one species at a time, meaning there is no overlap between the kelp users. The transfer of unprotected biomass of species i to unoccupied kelp occurs at a daily per capita rate of $\alpha_i = 10^{-5} \text{ m}^3 (\mu\text{g C})^{-1} \text{ d}^{-1}$. This transfer process effectively provides protection to the majority of the biomass within a span of 2 d, aligning with the colonization rates observed in experimental studies on kelp fauna (Norderhaug et al. 2002). On the population level, the biomass transfer from the unprotected subpopulation to the protected subpopulation of species i occurs at rate $\alpha_i B_i^u B_K^0$, which is directly proportional to the biomasses of the unoccupied kelp and the unprotected subpopulation of species i . In terms of kelp dynamics, this means that the rate at which kelp becomes occupied by species i is $\alpha_i \lambda_i B_i^u B_K^0$. Finally, during the years when kelp is being harvested, the harvesting occurs at per capita rate h . The harvesting rate h was parametrized for 2 scenarios, namely, 'high harvesting intensity' ($h = 0.0222 \text{ d}^{-1}$) and 'low harvesting intensity' ($h = 0.0033 \text{ d}^{-1}$), such that high-intensity harvesting leads to approximately 80% decrease and low-intensity harvesting leads to a 20% decrease in the kelp biomass at the end of the growth season compared to the pre-harvesting stable state.

The ordinary differential equations for the biomasses of the 0 yr old Atlantic cod and the European lobster in the unprotected and protected subpopulations are obtained by extending Eq. (7) to include the non-trophic interaction with kelp by introducing additional terms for the transfer of biomass between the 2 subpopulations, and by excluding the term for the biomass loss by predation from the equations of the protected subpopulations:

$$\begin{aligned} \dot{B}_i^u = & - \overbrace{f_m x_i B_i^u}^{\text{maintenance loss}} + \overbrace{\sum_j f_a x_i y_{ij} B_i^u F_{ij}(\mathbf{B})}^{\text{gain from resources (j)}} \\ & - \overbrace{\sum_j \frac{x_i y_{ji} B_j F_{ji}^u(\mathbf{B})}{e_{ji}}}_{\text{loss to consumer j}} - \overbrace{\alpha_i B_i^u B_K^0}_{\text{moving to kelp cover}} \\ & + \lambda_i^{-1} \overbrace{\left(h B_K^i + \frac{B_K^i}{B_K} \sum_j \frac{x_j y_{jK} B_j F_{jK}(\mathbf{B})}{e_{jK}} \right)}_{\text{moving away from cover due to kelp harvesting or consumption}} \end{aligned} \quad (19)$$

$$\begin{aligned} \dot{B}_i^p = & - \overbrace{f_m x_i B_i^p}^{\text{maintenance loss}} + \overbrace{\sum_j f_a x_i y_{ij} B_i^p F_{ij}(\mathbf{B})}^{\text{gain from resources (j)}} + \overbrace{\alpha_i B_i^u B_K^0}_{\text{moving to kelp cover}} \\ & - \lambda_i^{-1} \overbrace{\left(h B_K^i + \frac{B_K^i}{B_K} \sum_j \frac{x_j y_{jK} B_j F_{jK}(\mathbf{B})}{e_{jK}} \right)}_{\text{moving away from cover due to kelp harvesting or consumption}} \end{aligned} \quad (20)$$

Here, the superscript u in the functional response F_{ji}^u is used to emphasize that only the unprotected subpopulation of the prey is considered in the functional response between the predator and its prey, and the subscript K is used to indicate the biomass of kelp or any process or parameter related to kelp.

The dynamic equations for kelp biomass are similarly divided into 2 parts to include these non-trophic interactions. Note that the maintenance losses and resource gains of cod and lobster occupying kelp also cause changes in the amount of occupied and unoccupied kelp due to the shrinking or growing of the protected individuals' body sizes. In terms of kelp biomass changes, these gains and losses are scaled by the corresponding species' kelp utilisation multiplier λ_i . That is, whenever the biomass of the protected subpopulation of species i changes for reasons other than the movement of individuals to or from the kelp cover, the amount of change in the unoccupied and occupied kelp biomasses equals the protected subpopulation's biomass change multiplied by λ_i . This leads to the following equations for the kelp biomass dynamics:

$$\begin{aligned} \dot{B}_K^0 = & - \overbrace{\sum_i \lambda_i \alpha_i B_i^u B_K^0}_{\text{kelp becomes unavailable}} + \overbrace{\sum_i \lambda_i f_m x_i B_i^p}_{\text{kelp users' maintenance losses}} \\ & - \overbrace{\sum_i \left[\sum_j \lambda_i f_a x_i y_{ij} B_i^p F_{ij}(\mathbf{B}) \right]}_{\text{kelp bound up due to resource gains}} \\ & + \overbrace{I_K B_K(t) \left(1 - \frac{B_K(t)}{K_K} \right) (1 - s_K)}_{\text{gain from kelp growth}} - \overbrace{\sum_j \frac{B_K^0 x_j y_{jK} B_j F_{jK}(\mathbf{B})}{B_K e_{jK}}}_{\text{loss to consumer j}} - \overbrace{h B_K^0}_{\text{kelp harvesting}} \end{aligned} \quad (21)$$

$$\begin{aligned}
\dot{B}_K^i = & \overbrace{\lambda_i \alpha_i B_i^u B_K^0}^{\text{kelp becomes unavailable}} - \overbrace{\lambda_i f_m x_i B_i^p}^{\text{kelp user's maintenance losses}} \\
& + \overbrace{\sum_j \lambda_i f_a x_i y_{ij} B_i^p F_{ij}(\mathbf{B})}^{\text{kelp bound up due to resource gains}} \\
& - \overbrace{\sum_j \frac{B_K^i x_j y_{jK} B_j F_{jK}(\mathbf{B})}{e_{jK}}}_{\text{loss to consumer } j} - \overbrace{h B_K^i}_{\text{kelp harvesting}}
\end{aligned} \quad (22)$$

where r_K , K_K , and $s_K = 0.2$ are the allometrically scaled intrinsic growth rate (Eq. 10), carrying capacity (see Section 2.5), and the fraction of exudation for kelp, respectively.

Note that since the aim here is to investigate the impact of the survival benefits provided by being protected by kelp, we assumed that the protected subpopulations of age-class 0 cod and lobster gain full protection from predation, such that only the unprotected biomass is prone to predation (visible to predators). However, the above model is readily extendable to situations where kelp offers only partial protection. In this case, we would add the corresponding term for the loss to consumers in Eq. (20) of the protected biomass, similarly to Eq. (19), multiplied by a probability of being captured while protected by the kelp. Also, note that new kelp growth always enters the unoccupied state, whereas losses due to consumption or harvesting occur for both the unoccupied and occupied biomasses.

The functional response for unprotected 0 yr old Atlantic cod and European lobster is as follows:

$$\begin{aligned}
F_{ij}^u(\mathbf{B}(t)) = & \frac{\omega_{ij} B_j^u(t)^q}{B_0^{q_{ij}} + d_{ij} B_0^{q_{ij}} B_i(t) + (\omega_{ijc} B_{jc}^u(t)^q + \omega_{ijL} B_{jL}^u(t)^q + \sum_{k \notin \{j_C, j_L\}} \omega_{ik} B_k(t)^q)} \quad (23)
\end{aligned}$$

where j_C and j_L are used to denote the indices of 0 yr old Atlantic cod and European lobster, respectively. Finally, we assumed that at the end of each year, the cod and lobster that were occupying the kelp move away so that all kelp biomass is again unoccupied at the beginning of the next year.

2.4. Estimation of the kelp utilisation multiplier

In the model equations, λ_i expresses how many biomass units of kelp are required to provide cover for 1 biomass unit of guild i . For example, $\lambda = 1$ would mean that 1 unit of kelp biomass is required to cover 1 unit of biomass of the species seeking protection. Knowing exactly how much kelp is required for pro-

tection is difficult. However, we can estimate the relative kelp requirement between European lobster and 0 yr old Atlantic cod by comparing how their bodies' physical proportions scale with weight (body mass). We achieved this by using random close packing (RCP) for spheres to determine how many 0 yr old cod fit into the space of 1 average-sized lobster. The RCP is an empirical tool used to characterise the maximum volume fraction of solid objects obtained when they are packed randomly (Scott & Kilgour 1969). For spheres, the fraction is 0.64, which means that the packing efficiency is 64%. The body mass ratio between lobster and 0 yr old cod is 104.4. Calculating from that value and using RCP for spheres, we found that the same biomass takes approximately 1.5 times more space in 0 yr old cod than in lobster. Therefore, we estimated $\lambda_{j_L} = 2$ for European lobster and $\lambda_{j_C} = 3$ for 0 yr old Atlantic cod to represent how much kelp they need to gain habitat protection. The chosen λ -values provide protection for most of the biomass of lobster and 0 yr old cod. If the values were much smaller, even a small amount of kelp would provide protection for the whole biomass of the species and the effect of kelp harvesting would not influence the biomass as a habitat effect, and if the values were much bigger, the protection would not cover any biomass and the effect of the kelp cover would be lost.

2.5. Simulation design and carrying capacity estimation

Six different kelp-harvesting scenarios were simulated. First, a 200 yr burn-in period was run to find an ecologically stable state for the ecological network. This was then followed by a 50 yr period of kelp harvesting during which the kelp biomass was harvested with low and high harvesting intensity. The low harvesting intensity is based on the actual harvest rates (Werner & Kraan 2004), and the high harvesting intensity was chosen to exemplify increased harvest or potential devastation of kelp communities *in situ* (via natural disturbance or otherwise). The kelp was harvested in cycles occurring every 2, 5, or 9 yr, each of which consisted of 1 yr of harvesting followed by a recovery period of 1, 4, or 8 yr, respectively. After the 50 yr period of kelp harvesting was finished, the simulations were continued for another 50 yr. All simulations were run on MATLAB Version 9.4 R2018a, and the differential equations were solved using MATLAB's 'ode23' differential equation solver.

An estimate of the carrying capacity of a north-east Atlantic kelp forest is needed for the model, but data on kelp forest carrying capacity is lacking. A $1\,000\,000\ \mu\text{g C m}^{-3}$ carrying capacity was chosen for both kelp (K_K) and phytoplankton (K) for the simulations, which was based on similar work in Lake Constance where the annual phytoplankton productivity is estimated to be $300\ \text{g C m}^{-2}$ (Tilzer & Beese 1988) and where the ATN model carrying capacity for phytoplankton was set to $540\,000\ \text{g C m}^{-3}$ (Boit et al. 2012). Carrying capacity in the model is not the same as annual net primary productivity, which is estimated to be $166\text{--}738\ \text{g C m}^{-2}$ for kelp forests (Smale et al. 2020) and $73\ \text{g C m}^{-2}$ for phytoplankton (Skogen et al. 2007). Since the kelp forest net primary productivity in the Northeast Atlantic is estimated to be higher than in Lake Constance, we chose a higher carrying capacity for both kelp and phytoplankton.

3. RESULTS

We quantify the changes in the biomasses as the relative difference between pre-harvesting equilibrium state and the biomass during the 50 yr harvesting period. We are mostly interested in the differences between the highest and the lowest kelp biomass levels during the harvesting period, or in the biomass levels at the end of the harvesting period in those situations where the biomass oscillations between the highest and lowest biomass levels after the harvest were negligible. The non-trophic interaction

is included in all the results, except for the European lobster and the Atlantic cod, where the results also include the exploration of kelp harvest without the non-trophic interaction in the model.

3.1. Kelp biomass

Harvesting of kelp caused periodic oscillations in its biomass. The biomass of kelp recovered after each harvest at both harvesting intensities when the harvesting cycle was 5 or 9 yr, but not when the harvesting cycle was 2 yr (Fig. 2). At low harvesting intensity, kelp biomass recovered above the pre-harvest level when the harvesting cycle was 5 or 9 yr, and slightly below the pre-harvest level when the harvesting cycle was 2 yr (Fig. 2). At high harvesting intensity, the kelp recovered to approximately 30% below the pre-harvest level with the 2 yr harvesting cycle, and to approximately 15% above the pre-harvest level with the 5 and 9 yr harvesting cycles (Fig. 2).

3.2. Kelp consumers

The responses of kelp consumers, namely, Mollusca and Echinodermata, to kelp harvesting varied. Biomass of Mollusca trended with oscillations in kelp biomass and recovered above the pre-harvest biomass level with a 5 and 9 yr harvesting cycle at both the low and the high harvesting intensity (Fig. 3a). In the 2 yr harvesting cycle, the biomass of Mollusca failed to recover at both harvesting intensities; with

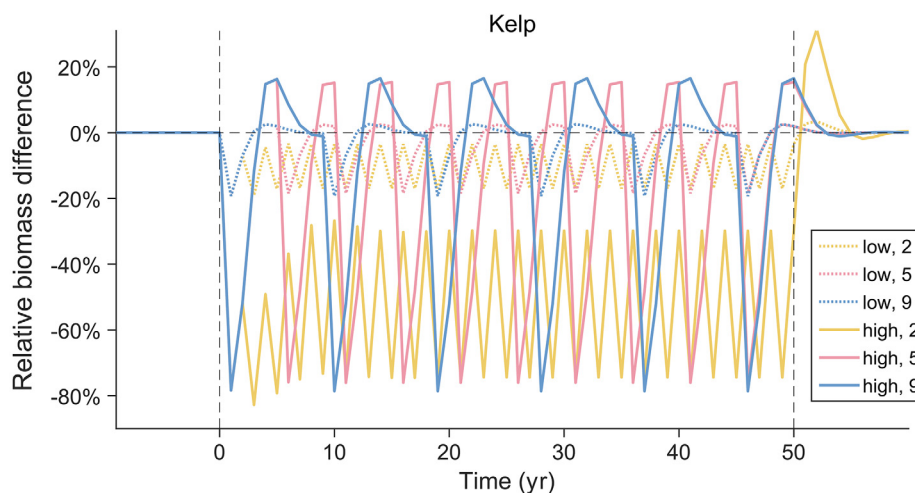


Fig. 2. Relative difference in kelp biomass at the end of the growth season of each year with respect to the pre-harvesting equilibrium state at low (dotted lines) and high (solid lines) harvesting intensities and 2, 5, and 9 yr harvesting cycles. The harvesting period of 50 yr is denoted with the vertical dashed black lines, and the pre-harvesting equilibrium state is shown as a reference using a horizontal dashed line at 0%

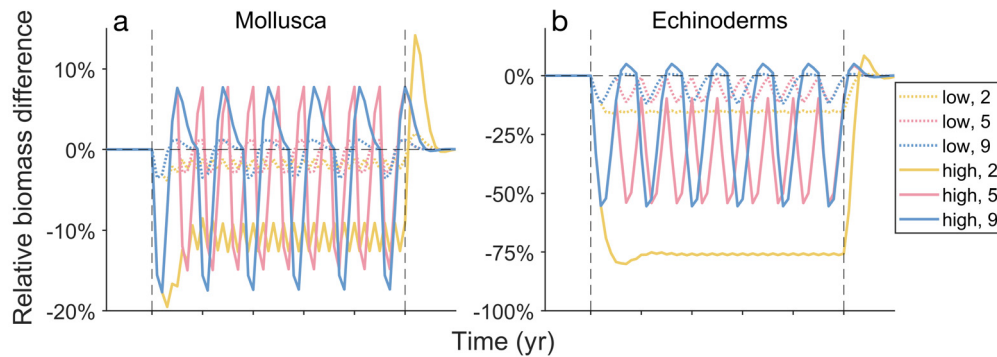


Fig. 3. Effect of kelp harvesting on the biomass of invertebrate consumers feeding on kelp with low (dotted lines) and high (solid lines) kelp-harvesting intensities in 2, 5, and 9 yr harvesting cycles: (a) Mollusca, (b) echinoderms. The figure shows the relative difference in biomass with respect to the pre-harvesting equilibrium state of the model including the non-trophic effect. The biomass difference of each year is the biomass difference at the end of the growth season. The harvesting period of 50 yr is denoted with the vertical dashed black lines, and the pre-harvesting equilibrium state is shown as a reference using a horizontal dashed line at 0%. (Note that the vertical axis scale varies between the subplots)

low harvesting intensity, the biomass was approximately 2% lower compared to the biomass level before harvesting, and with high harvesting intensity, the biomass was approximately 9% lower. Similarly, the biomass of echinoderms followed the kelp biomass oscillations (Fig. 3b). At both kelp-harvesting intensities, the biomass of echinoderms failed to recover when the harvesting cycle was 2 yr. At low harvesting intensity, the echinoderm biomass stayed at approximately 15% below the pre-harvest level, and at high harvesting intensity, it stayed at approximately 75% below the pre-harvest level. In a 5 yr harvesting cycle and low harvesting intensity, the biomass of echinoderms declined to approximately 10% below the pre-harvest level and recovered to the pre-harvest level after each harvest, while high harvesting intensity led to a decrease to approximately 50% below and a recovery to approximately 10% below the pre-harvest biomass level. In a 9 yr harvesting cycle, the biomass of echinoderms declined to approximately 10% below the pre-harvest level at low harvesting intensity, and 50% below the pre-harvest level at high harvesting intensity, and after the harvest, the biomass of echinoderms recovered to approximately the pre-harvest level at low harvesting intensity and to 5% above the pre-harvest level at high harvesting intensity.

3.3. European lobster

For lobster, we explored the effect of kelp harvesting with and without the non-trophic interaction. For the sake of simplicity and figure legibility, the effect of kelp harvest on lobster without the non-trophic interaction is presented for the 5 yr cycle only. When

the non-trophic interaction was not modelled, the pre-harvesting biomass level of lobster was approximately 95% less compared to the scenario with the non-trophic interaction (Fig. 4). As a result, without the survival benefits included in the model, the effect of kelp harvesting on lobster was negligible. When the non-trophic interaction was modelled, however, kelp harvesting had a marked effect on lobster biomass by the end of the 50 yr harvesting period. At low harvesting intensity and 2, 5, and 9 yr harvesting cycles, the biomass declined to 15, 6, and 4% below the pre-harvest level, respectively (Fig. 4). At high harvesting intensity, the corresponding values were 74, 42, and 35% below the pre-harvest level.

3.4. Atlantic cod

Similar to European lobster, we explored the effect of kelp harvesting on cod with and without the non-trophic interaction in the model. When the non-trophic interaction was not included in the model, the pre-harvesting biomass of cod was markedly less compared to the scenario with the non-trophic interaction, so that for 0, 1, 2, 3, and 4+ yr old cod, the biomass level was approximately 23, 21, 14, 11, and 6.4% below the pre-harvest level with the non-trophic interaction (Fig. 5). When kelp was harvested at low intensity, no marked decline in cod biomass was observed, and the average increase in the magnitude of the relative biomass difference compared to the pre-harvest level with the non-trophic interaction was 0.01, 0.27, 0.31, 0.41, and 0.67% for 0, 1, 2, 3, and 4+ yr old cod, respectively. When kelp was harvested at high intensity, however, there was on average an increase of 0.09, 1.67, 1.87, 2.48, and

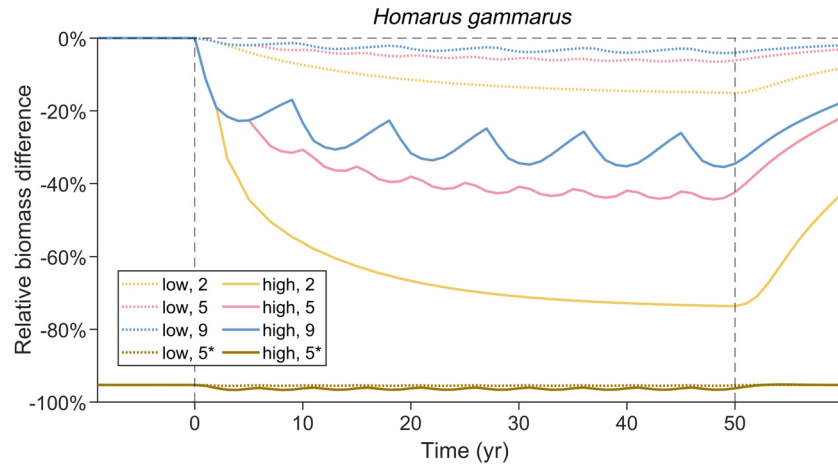


Fig. 4. Effect of kelp harvesting on European lobster *Homarus gammarus* biomass with low (dotted line) and high (solid line) kelp-harvesting intensities in 2, 5, and 9 yr harvesting cycles. The effect of excluding the non-trophic interaction of kelp cover is explored with the lines marked with *, where the harvesting cycle is 5 yr. Other details as in Fig. 3

4.05%, respectively, in the magnitude of the relative biomass difference (Fig. 5).

When the non-trophic interaction was included in the model, the low-intensity harvest caused an average relative decrease in biomass compared to the pre-harvest level for 0, 1, 2, 3, and 4+ yr old cod of 0.08, 0.74, 0.78, 1.01, and 1.59% with the 2 yr harvesting cycle; 0.03, 0.30, 0.31, 0.41, and 0.64% with the 5 yr harvesting cycle; and 0.02, 0.19, 0.20, 0.26, and 0.37% with the 9 yr cycle. The high-intensity harvest caused markedly greater changes in the cod biomasses with the relative decrease in the biomass compared to the pre-harvest level being 0.72, 4.64, 4.79, 6.06, and 9.36% for the 2 yr harvesting cycle; 0.50, 2.09, 2.08, 2.59, and 3.94% for the 5 yr harvesting cycle; and 0.41, 1.35, 1.31, 1.66, and 2.09% for the 9 yr harvesting cycle (Fig. 5). In addition to the

change in average biomass, kelp harvesting also caused oscillations in the cod age class biomasses. While the magnitude of the decline was negatively correlated with the length of the harvesting cycle and positively correlated with age class, the amplitude of the oscillation had a positive correlation with the length of the harvesting cycle and a negative correlation with age class (Fig. 5).

3.5. Sensitivity analysis on carrying capacities

During the process of model parametrization, we observed that the carrying capacity parameters for kelp (K_K) and phytoplankton (K) in their respective logistic growth models had a significant impact on the magnitude of the relative changes in species bio-

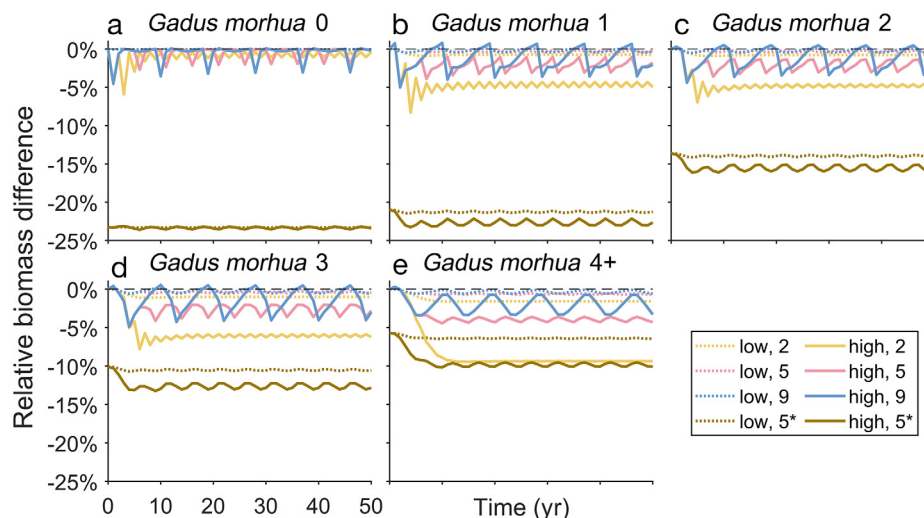


Fig. 5. Effect of kelp harvesting on Atlantic cod *Gadus morhua* for age classes (a) 0, (b) 1, (c) 2, (d) 3, and (e) 4+ yr in low (dotted line) and high (solid line) kelp harvesting intensities in 2, 5, and 9 yr harvesting cycles. Other details as in Fig. 4

masses within the ecological network. As there is great uncertainty about these parameters, we studied how varying these parameter values affects the results compared to the baseline scenario where $K_K = K = 1\,000\,000\ \mu\text{g C m}^{-3}$. A lower $K = 200\,000\ \mu\text{g C m}^{-3}$ resulted in larger and a higher $K = 5\,000\,000\ \mu\text{g C m}^{-3}$ resulted in smaller relative changes in the species' biomasses when K_K was unchanged. On the other hand, a lower $K_K = 200\,000\ \mu\text{g C m}^{-3}$ resulted in smaller and a higher $K_K = 5\,000\,000\ \mu\text{g C m}^{-3}$ resulted in higher relative changes in the species' biomasses when K was unchanged.

4. DISCUSSION

In this study, we demonstrate how kelp harvesting on a 5 yr cycle, which is commonly believed to be good practice for kelp recovery, can have significant ecosystem-wide effects at different trophic levels in the kelp forest ecosystem. While the kelp biomass recovered in our 5 and 9 yr cycle models, the analysis revealed how certain species in the ecosystem failed to recover to their pre-harvesting levels in line with earlier studies (Vea & Ask 2011, Steen et al. 2016, Norderhaug et al. 2020a). This raises concerns about the poorly understood multitrophic and non-trophic ecosystem effects of kelp harvesting.

The non-trophic interaction (i.e. kelp providing protection from predators) between kelp and age-class 0 Atlantic cod or European lobster increased their pre-harvest biomass level compared to a scenario without the non-trophic interaction, indicating that the carrying capacity of these species in kelp forests is greater than previously understood. When kelp was harvested, the non-trophic interaction caused a larger drop in the biomasses of European lobster and Atlantic cod compared to the scenario without the non-trophic interaction, because the kelp harvest caused a loss of habitat for lobster and cod. Lobster biomass did not recover to the pre-harvesting level in any of the scenarios with the non-trophic interaction, potentially because it was impacted via both trophic and non-trophic interactions, which supports studies showing that complex habitats, such as kelp forests, can increase the survival of species (Beukers & Jones 1998, Lindholm et al. 1999, Norderhaug et al. 2020a). These results demonstrate the importance of non-trophic interactions when studying the ecosystem-wide effects of anthropogenic stressors.

It is well documented that harvesting of higher trophic levels, such as by fishing, can cause or amplify

biomass oscillations in ecosystems (Steneck et al. 2004, Kuparinen et al. 2016, Norderhaug et al. 2021, Uusi-Heikkilä et al. 2022). However, it is important to acknowledge the fundamental difference in effects between centuries of overfishing on vulnerable stocks with specific life histories and the harvesting of kelp, which is a resilient primary producer that is harvested at relatively low levels compared to fishing practices. While centuries of overfishing have been extensively discussed in classic papers by Jackson et al. (2001) and Steneck et al. (2004), our study focuses on the impacts of kelp harvesting, specifically demonstrating that it can lead to similar effects with cascading impacts on the entire ecological network (see Norderhaug et al. 2020a for an *in situ* study). Oscillations in the biomass of populations in the ecological network may destabilise the ecosystem and erode its resilience (Scheffer et al. 2001), and can also be caused by resource limitation, competition, or predation (Kuno 1987). Further, population oscillations can have evolutionary effects depending on the wavelength and amplitude of the oscillation and can drive changes in the life history traits of the species (Ahti et al. 2022). The introduction of the non-trophic interaction of the habitat effect of kelp cover for age-class 0 Atlantic cod and European lobster amplified the biomass oscillations of these 2 species. Considering non-trophic interactions can thus be important to better understand changes observed in ecosystems.

The species feeding directly on kelp had different responses to kelp harvesting, but the biomass oscillations caused by kelp harvesting on kelp biomass were propagated through the trophic links in the ecological network. At high-intensity harvest, the biomass of Mollusca recovered during the 5 and 9 yr cycles of kelp harvesting. This is facilitated by the fact that Mollusca had other food resources in the diet in addition to kelp. Additionally, Mollusca had many predator species in the ecological network, some of which decreased in biomass during the harvesting period, which in part facilitated the recovery of the biomass of Mollusca when the predation pressure was lower during the harvesting period. At high-intensity harvest, the biomass of echinoderms declined during the 2 and 5 yr cycles but recovered when the harvesting cycle was 9 yr. Of the kelp consumers, echinoderms were the most dependent on kelp in this model, having feeding links only to kelp and POC. *Echinus esculentus* is known to rarely feed on live kelp, but certainly has impacts on recovering kelp communities in Norway, especially the sub-canopy epiphytes common on *Laminaria hyperborea* stipes (Bekkby et al. 2015).

The kelp-harvesting intensities investigated in this study resulted in approximately 20 and 80% reductions in kelp biomass for the low and high intensities, respectively. Historical estimates from 2004 indicated that kelp biomass removal annually amounted to 10–15% of the total standing stock in Norway and 30% in France (Werner & Kraan 2004). More recent research from 2020 estimated a loss of about 26% of the total kelp canopy at the scale of a trawled station (at a scale of hundreds of metres; Norderhaug et al. 2020b). While the low harvest intensity in the present study may appear unrealistically high when applied to the entire ecosystem, it could potentially reflect conditions at smaller scales. It is important to note, however, that significant species migration to neighbouring areas might occur, which could lead to an overestimation of the effects of kelp removal in our results. Nonetheless, our primary objective is to comprehend and model the underlying mechanisms driving these dynamics. Conversely, the high harvesting intensity was employed to investigate a hypothetical extreme scenario. As observed in other systems, such as high harvest in *Lessonia trabeculata* forests (Bularz et al. 2022), our study demonstrated that the high harvesting intensity induced more pronounced changes in species biomass compared to the low intensity. Additionally, it is worth noting that natural removal of kelp from the ecosystem, as documented by Norderhaug & Christie (2011), can significantly augment the local impact of kelp harvesting efforts. This effect may exceed the mechanistic removal rates reported. For instance, in our study, a 5 yr harvesting cycle with high intensity led to a biomass reduction of over 40% in the European lobster population compared to the pre-harvesting levels, signifying a substantial shift in the population structure. Considering localized kelp removal rates of 80%, a level not currently sanctioned in any EU country, there could be profound repercussions for species dwelling within kelp forest ecosystems. It is important to highlight that our model did not encompass other factors contributing to biomass loss, such as human exploitation of additional species within the ecosystem. Consequently, the realized impact on species residing in kelp forest habitats could be even more substantial than what our model predicts.

As with all modelling studies, the present work has some limitations. Here, the kelp biomass was simulated based on data from a 4 yr old kelp (*L. hyperborea*), and no kelp age-structure was included in the model. However, the growth rate and fecundity of *L. hyperborea* vary with age (Kain & Jones 1975, Sjøtun & Fredriksen 1995), and site-specific factors

such as latitude, wave exposure level, and depth also influence kelp forest primary and secondary production, growth, and recovery. The age structure of kelp populations can play a significant role in shaping trophic and non-trophic interactions within the ecosystem. Older kelp individuals may exhibit greater non-trophic interactions, such as providing physical structure and habitat complexity, influencing nutrient cycling, and acting as substrate for epiphytic communities, whereas young kelp individuals are often more tender and palatable compared to mature individuals, which can make them more susceptible to herbivory. While our current model did not explicitly incorporate these age-related dynamics, future iterations of the model should consider the age structure of kelp populations and its implications for trophic and non-trophic interactions. By incorporating these factors, we can gain a more comprehensive understanding of the long-term effects of kelp harvesting, considering the potential variations in trophic dynamics, herbivory patterns, non-trophic interactions, and overall ecosystem functioning among different age classes. Furthermore, including a spatial component that captures the influence of site-specific factors would allow for a more robust assessment of the regional and local variations in kelp ecosystem dynamics. This holistic approach, considering both temporal and spatial dimensions, will enhance our understanding of how kelp biomass responds to harvesting activities and how the effects propagate through the ecosystem (as observed by Steen et al. 2016 and Gouraguine et al. 2021).

Although our study primarily focused on the survival benefits provided by the kelp habitat to cod and European lobster, it is essential to acknowledge the intricate ecological dynamics within the kelp ecosystem (defined by Kain 1979, Christie et al. 2003, 2009, Schoenrock et al. 2021, among others). The interactions between kelp, epiphytes, invertebrates, urchins, and trawling play a vital role in shaping the overall health and sustainability of kelp habitats. The availability of micro-habitats, the predation dynamics between prey animals living among the small epiphytic algae on kelp stipes and kelp-associated fish, and the recovery of epiphytic algae on newly grown canopy kelps are factors of significant importance (Christie et al. 2003, 2009). Future research and ATN model development should aim to explore these relationships further to gain a comprehensive understanding of kelp ecosystem dynamics and inform effective conservation strategies.

In addition to the novel non-trophic interaction, our model also considers competition between primary

producers, specifically different species of algae, as they compete for shared resources. While our study has focused on these specific non-trophic interactions, it is important to acknowledge that other non-trophic interactions may also play a role in our study system. These may include mutualistic relationships, symbiotic associations, and other forms of interspecies interactions within the kelp forest ecosystem. Although not explicitly modelled in our current study, future investigations into these additional non-trophic interactions will contribute to a more comprehensive understanding of the ecological dynamics and the potential implications of kelp harvesting within the broader ecosystem.

The decision to include invertebrate species with SACFOR classes of Superabundant, Abundant, and Common in our ecological network model may have introduced some bias. The selection of these species was based on their ecological significance and their potential interactions within the kelp forest ecosystem (see Schoenrock et al. 2021). By focusing on these abundant species, we aimed to capture the dominant ecological processes and dynamics within the network. However, it is important to note that the exclusion of less abundant species may overlook certain ecological interactions and their potential influence on the overall network structure and functioning. Future studies could explore the effects of including less abundant species to further refine the model and investigate potential biases introduced by the selection criteria.

Here, we extended the ATN modelling framework by developing a novel mechanistic model for non-trophic interactions between kelp and Atlantic cod or European lobster in the form of survival benefits provided by the kelp habitat. Our mechanistic approach offers notable benefits to earlier modelling investigations into the role of non-trophic interactions in ecological networks. Most earlier network studies focused on community composition, fluxes of energy from primary producers up to consumers (Thompson et al. 2012, Kéfi et al. 2016, Miele et al. 2019), and even multiple networks simultaneously in an agroecosystem (Pocock et al. 2012). What these studies are lacking, however, is the mechanistic underpinning in the individual behaviour of their study systems. Our model architecture is specifically designed to realistically incorporate the non-trophic interactions of individuals in kelp habitat. We not only extended the ATN model to account for kelp biomass available for refuges, but we further developed a highly advanced within-population substructure for each population of kelp habitat users. Our mechanistic modelling approach was particularly characterised by temporal

subpopulation dynamics, in which we divided the biomass of each kelp-utilising species into those that either occupy kelp for protection or that are unprotected and prone to predation. This approach, coupled with detailed species-specific rates of moving to kelp cover and kelp utilisation efficiencies (i.e. how many units of kelp biomass are required for protection by 1 unit of a given species), enabled us to gain novel insight and more specific predictions from enhanced ecological realism. Admittedly, due to the novelty factor, many of these newly introduced parameter values were based on rough estimates due to lack of empirical data. Although these challenges in parametrizations may overestimate the role of non-trophic kelp interactions, our findings nevertheless provide useful qualitative insight.

Although we developed the model for the survival benefits solely for Atlantic cod and European lobster, the model can be readily extended for an arbitrary number of species known to benefit from the kelp habitat. Moreover, the developed model for the survival benefits of habitat can also easily be applied to other systems, such as coral reefs in marine systems or trees or other flora in terrestrial systems to study questions related to degradation of coral reefs or the sustainability of land use or forestry. However, it must be noted that currently, before empirical validation, this model should be used for theoretical exploration of ecosystem dynamics and mechanisms only, and not as a basis for decision making.

Overall, the results of this study showed that not all species in the kelp forest ecosystem recovered within the commonly used 5 yr kelp-harvesting cycle, which validates the concern over multitrophic effects of kelp harvesting previously raised by Lorentsen et al. (2010), Steen et al. (2016), Christensen-Dalsgaard et al. (2020), and Norderhaug et al. (2020a). We also found that periodic kelp harvesting can induce biomass oscillations in other species in the ecological network through trophic links, and the oscillations can be amplified by non-trophic interactions with kelp cover. Kelp forest ecosystems harbour vast numbers of species, including commercially important fisheries species, and the need to manage kelp harvesting sustainably from an ecosystem perspective is crucial for ensuring the existence of the species-rich kelp forests in the future.

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