Gallagher, C.A., Chimienti, M., **Grimm, V.**, Nabe-Nielsen, J. (2022):
Energy-mediated responses to changing prey size and distribution in marine top predator movements and population dynamics
J. Anim. Ecol. **91** (1), 241 - 254

http://dx.doi.org/10.1111/1365-2656.13627

Journal of Animal Ecology

CARA GALLAGHER (Orcid ID : 0000-0001-7094-1752)
DR VOLKER GRIMM (Orcid ID : 0000-0002-3221-9512)
DR JACOB NABE-NIELSEN (Orcid ID : 0000-0002-0716-9525)

Article type : Research Article

Handling Editor: Elise Zipkin

section: Conservation ecology

Title: Energy-mediated responses to changing prey size and distribution in marine top predator movements and population dynamics

Names:

Cara A. Gallagher[1,2], Marianna Chimienti[1,3], Volker Grimm[2,4], and Jacob Nabe-Nielsen[1]

Affiliations:

[1]Aarhus University, Department of Ecoscience, Frederiksborgvej 399, PO Box 358, DK-4000 Roskilde, Denmark

[2]University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany

[3]Centre d'Etudes Biologiques de Chizé, 405 Route de Prissé la Charrière, 79360 Villiers-en-Bois, France

[4]Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, Permoserstraße 15, 04318 Leipzig, Germany

Article type: Research Article

Corresponding author:
Cara A. Gallagher
Email: cgallagher@bios.au.dk
Address: Am Mühlenberg 3, 14476 Potsdam, Germany

Abstract:

1. Climate change is modifying the structure of marine ecosystems, including that of fish communities. Alterations in abiotic and biotic conditions can decrease fish size and change community spatial arrangement, ultimately impacting predator species which rely on these communities. To conserve predators and understand drivers of observed changes in their population dynamics, we must advance our understanding of how shifting environmental conditions can impact populations by limiting food available to individuals.
2. To investigate impacts of changing fish size and spatial aggregation on a top predator population, we applied an existing agent-based model parameterized for harbor porpoises (*Phocoena phocoena*) which represents animal energetics and movements in high detail. We used this framework to quantify impacts of shifting prey size and spatial aggregation on porpoise movement, space use, energetics, and population dynamics.
3. Simulated individuals were more likely to switch from area-restricted search to transit behavior with increasing prey size, particularly when starving, due to elevated resource competition. In simulations with highly aggregated prey, higher prey encounter rates counteracted resource competition, resulting in no impacts of prey size on movement behavior.
4. Reduced energy intake with decreasing prey size and aggregation level caused population decline. A 15% decrease in fish length, for example, resulted in total population collapse. Increasing prey consumption rates by 42.8 ± 4.5% could offset population declines, however this increase was 21.3 ± 12.7% higher than needed to account for changes in total energy availability alone. This suggests that animals in realistic seascapes require

additional energy to locate smaller prey which should be considered when assessing impacts of decreased energy availability.

5. Changes in prey size and aggregation influenced movements and population dynamics of simulated harbor porpoises, revealing that climate-induced changes in prey structure, not only prey abundance, may threaten predator populations. We demonstrate how a population model with realistic animal movements and process-based energetics can be used to investigate population consequences of shifting food availability, such as those mediated by climate change, and provide a mechanistic explanation for how changes in prey structure can impact energetics, behavior, and ultimately viability of predator populations.

Keywords:

Agent-based model, climate change effects, energy budgets, harbor porpoise, hidden Markov modelling, marine mammal, physiological ecology, predictive ecology

Introduction:

Climate change is rapidly modifying marine ecosystems through numerous and complex mechanisms (Poloczanska et al., 2013; Saba et al., 2015). Changes in abiotic ocean properties, such as circulation, upwelling strength, temperature, and oxygen saturation, can alter the abundance and distribution of primary producers (Amorim et al., 2017; Embling et al., 2012; Hoegh-Guldberg & Bruno, 2010). This can trigger responses in higher trophic levels, including changes in body size and spatial distribution of fish (Harley et al., 2006; Hoegh-Guldberg & Bruno, 2010). Such changes in fish size and distribution can affect the very organization of marine ecosystems and ultimately impact top predators. To conserve predator species in a changing ocean, potential population-level impacts of climate change-induced prey alterations should be assessed.

Though mechanisms responsible for fish size changes with ocean warming are hotly debated, they are likely related to nutritional, physiological (e.g., oxygen limitation), or adaptive (e.g., shortened development time with increased predation) mechanisms (Sheridan & Bickford, 2011; Verberk et al., 2020). Size reductions in fish species have been documented both on individual species (Clausen et al., 2018) and community-wide scales (Beukhof et al., 2019). These changes strongly affect the energy content of individual fish, which is directly related to mass and exponentially related to length (Silva et al., 2013; Temming & Herrmann, 2003). As declines in fish size are unlikely to lead to increased abundance (Audzijonyte et al., 2013, 2020), such changes can have huge energetic implications for predators. However, the population effects of prey size changes are still largely unknown and may be complicated by interactions with other environmental drivers, such as prey distribution.

Climate change impacts on ocean circulation and upwelling can influence the spatial heterogeneity, or patchiness, of plankton (Brun et al., 2016; Harley et al., 2006). This will likely influence the distribution of species which depend on plankton (Bertrand et al., 2014; McInnes et al., 2017; Woodsona & Litvinb, 2015). Alterations in prey spatial arrangement can affect how often predators encounter food resources, requiring altered movement and foraging behavior to maintain energy balance (Bailleul et al., 2013). Many marine predator species depend on finding high density food patches to meet their energetic needs (Benoit-Bird et al., 2013; Goldbogen et al., 2011, 2015). Small-scale prey patch characteristics determine how predators exploit their food supplies and have been used to predict space use patterns (e.g., Benoit-Bird et al. 2013). Despite uncertainty in predictions of climate change impacts on oceanic spatial heterogeneity, patchiness is a key driver of marine predator-prey relationships and altered prey distribution may have serious consequences for the persistence of top predator populations.

To conserve predator species, potentially interacting impacts of changing climatic-induced conditions, such as reduced prey size and altered patchiness, on their populations must be understood. Marine top predators, such as cetaceans, function as climate sentinels (Hazen et al., 2019), reflecting changes in lower trophic level dynamics while exerting top-down control on these groups. Species with high energetic demands may be especially sensitive to changes in their environments and prey resources. Harbor porpoises are a cetacean species with elevated metabolic requirements (Rojano-Donãte et al., 2018) which exhibit exceptionally high foraging rates

(Wisniewska et al., 2016). The dependence of harbor porpoises on high quality and accessible prey puts them at high risk when conditions change (Wisniewska et al., 2016), though their high capture success and generalist diet may also make them resilient to short term foraging losses (Booth, 2020; Goldbogen et al., 2019). While impacts of alterations in prey availability on porpoise survival has been discussed (e.g., MacLeod et al. 2007, Wisniewska et al. 2016), the implications of changing prey size and spatial distribution on their populations have yet to be assessed.

Integrated models which consider effects of changing resource conditions on species, such as agent-based models (ABMs), can be used to predict population-level impacts of individual responses to changing environments (Nabe-Nielsen et al., 2018). Individual-level representation and the integration of energy budgets into ABMs allows for modelled organisms to intake and use energy at rates consistent with their age, status, activity levels, and experienced environmental conditions, and to adaptively adjust their behavior to perceived changes (Chimienti et al., 2020; Railsback & Harvey, 2020; Sibly et al., 2013). The advantage of using ABMs where movements and energetics are modelled mechanistically is that population dynamics emerge from individual-level behavioral and physiological processes (Railsback & Grimm, 2019). Additionally, landscapes in ABMs can be represented explicitly, allowing for realistic patch dynamics. While empirical data linking environmental change to population responses are difficult to acquire, the bottom-up approach of energy budget ABMs makes them well-suited and powerful tools for predicting population-level impacts of environmental alterations (Stillman et al., 2015).

Here we apply an ABM of harbor porpoise energetics and movements to theoretical scenarios of two potential responses to climate change in marine ecosystems: altered length and spatial aggregation of prey resources. The ABM has been rigorously developed and tested using empirical data for this species (Gallagher et al., 2021; Nabe-Nielsen et al., 2018). By implementing the model in theoretical, yet realistic, seascapes, we control for tested impacts and assess the two drivers in tandem to investigate isolated and interacting effects. We hypothesized that decreasing fish length and aggregation will result in deviations in individual movement and space use behavior resulting from decreased foraging success. We additionally hypothesized that reduced prey length and aggregation will trigger population decline due to decreased available energy and higher potential foraging efficiency in aggregated prey patches. While it may be intuitive to assume population decline in response to reduced prey size and aggregation, it is not clear which of the two changes matters more, how they interact, or how fast decline occurs.

Additionally, as porpoises are capable of very high foraging rates and may compensate for reduced prey size by increasing prey capture rates, we explored how increased intake rates and fish abundance could prevent population decline and compared results to estimates based purely on changes in available energy. Our results provide valuable insight on how individual movement behavior and energetics can be impacted by climate-related environmental changes in prey structure, and ultimately impact viability of porpoise populations.

Materials and methods:

Model description

We implemented an existing model of porpoise movements and energetics for predicting spatiotemporal effects of environmental change on population dynamics (Gallagher et al., 2021). Model seascapes and prey characteristics were modified for this application (details below and in Appendix S1 Section 7.3). In the following we present a summary description of the model. The accompanying TRACE document (Grimm et al., 2014) in the Supporting Information (Appendix S1) includes a detailed model description following the ODD protocol (Grimm et al., 2006, 2020) and presents additional evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose. As this was a model-based study, no field work permissions or animal ethics permits were required.

Two entity types are represented: female porpoises and grid cells. Porpoises are represented as "super-individuals" (Scheffer et al., 1995), hereafter "individuals", which represent 100 female porpoises characterized by realistic movements and energetics. All key life phases are represented including birth, maturation, reproduction, and death. Individual energetics depend on age, reproductive status, environment, body condition, and activity level. Porpoises ingest prey from their environment, then expend assimilated energy on metabolic costs in order of importance to survival (Gallagher, Grimm, et al., 2021; Sibly et al., 2013): maintenance, thermoregulation, locomotion, reproduction, and growth and storage. If assimilated energy is insufficient to cover costs, energy stored as blubber can be mobilized. However, if blubber stores are low, individuals instead sacrifice reproduction and growth to maintain survival. Though alternative energy allocations strategies exist and can yield differing predictions (Pirotta et al., 2020), we selected this strategy as it allows animals to prioritize their own survival and potential future reproductive events over current reproduction and growth when experiencing low foraging success. Animals die when their body condition drops, they can no longer cover vital metabolic processes, i.e., maintenance and thermoregulation, or they reach a maximum age. By linking reproduction and mortality to foraging success, population dynamics emerge from individual interactions with their environment, characterized by food availability and abiotic conditions (e.g., temperature and salinity).

Animal movements are driven by their energetic status and occur on both fine- and large-scales. When using fine-scale movements, animals follow correlated random walks to encounter new food cells and spatial memory to return to locations where they have previously encountered food. Animals with decreasing storage levels for three consecutive days switch to large-scale movements to move to regions with potentially high food levels (Nabe-Nielsen et al., 2014).

The model environment is composed of grid cells with dynamic food levels. After prey is consumed, food levels increase logistically in daily steps until reaching their maximum value. In this study, maximum food levels remain constant throughout the year, though environmental physical properties vary seasonally. These properties directly impact porpoise energetics by altering their thermoregulation and locomotion costs and potential prey consumption rates. Water temperature, salinity, and additional thermophysical properties were incorporated as monthly averages for the inner Danish waters (see Appendix S1 Section 7.3).

Changing prey spatial aggregation levels

Theoretical seascapes with varying prey spatial aggregation levels were created to assess the impact of prey distribution on porpoise space use, movements, energetics, and population dynamics. Each seascape covered a 240×400 km region containing 600×1000 grid cells of 400×400 m^2 each and wrapped on all sides, allowing for continuous movement. Seascapes were divided into cells with (1.6%) and without (98.4%) food, as in Nabe-Nielsen et al., (2014). Maps were generated as random gaussian fields using the *nlm_gaussianfield* function in the “NLMR” package (Sciaini et al., 2018) in R statistical software (R Core Team, 2020). Three maps were created with spatial autocorrelation extents of 0.8, 4.8, and 8.8 km, hereafter referred to as “low”, “moderate”, and “high” spatial aggregation level, respectively (seed value of 100). Cells with the highest 1.6% of values in the gaussian field maps were classified as containing food using the *util_classify* function in the “landscapetools” package (Sciaini et al., 2018). Relative prey density in each food cell was extracted using the "raster" package function *extract* (Hijmans, 2020) (Fig. 1). The number, size, and distance between food patches, defined as clusters of grid cells containing food which touch on any of their eight sides, were calculated for each seascape (Table 1) using the "landscapemetrics" package (Hesselbarth et al., 2019).

Total fish abundance was calibrated by varying fish abundance between 2,000,000 to 2,500,000 individual fish using increments of 50,000, with the objective of ensuring a stable population size of 200 harbor porpoises (as in Gallagher et al. 2021). Ten replicates were run for each level and the average population size during simulations years 10-20 was measured to assess fit. The parameterization with 2,400,000 fish resulted in the best fit with an equilibrium population size of 199 ± 8.6 (mean ± SD) porpoises (Appendix S1 Fig. 7.1). To ensure model outputs could be assessed as relative changes between model scenarios, a fish length of 16.6 cm and moderate spatial aggregation level were maintained in calibration runs.

Changing prey size

To isolate impacts of community-wide changes in prey size, we developed scenarios where fish length changed over the simulation. The baseline value of 16.6 cm corresponded to the average fish length reported for porpoises in Sveegaard et al., (2012). This value was then either decreased or increased in model scenarios by an amount corresponding to the decrease in community fish length reported for the period 1985–1995 by Beukhof et al. (2019) (data extracted using automeris.io/WebPlotDigitizer). Fish lengths were the same in all food patches throughout the seascape. Possible final fish lengths tested were 14.1, 15.35, 16.6 (no change), 17.85, and 19.1 cm. In model scenarios fish lengths were linearly interpolated from the base length of 16.6 cm to their final length value; see 'Scenario specifications' for details.

To estimate the energy contained in individual fish, lengths were converted to weight using the average of the weight-length parameters found for important porpoise prey species (in >5% of porpoises) in Andreasen et al. (2017) (Appendix S1 Table 7.8). Total energy contained per fish was calculated using the mass and average energy content of these species.

Changing climatic conditions

To consider potential changes in water temperature and salinity occurring with future climate change, scenarios were constructed covering three potential outcomes: no, median, and maximal changes. Climate projections from the SSP5-8.5 scenario in the MPI-ESM1.2-LR model generated as part of Coupled Model Intercomparison Project Phase 6 (CMIP6) (Wieners et al., 2019) were obtained for the study region to establish potential decadal changes in average sea surface temperature and salinity for each 10-year period between 2021-2100. The median and maximum values found were used to modify temperature and salinity values but did not affect seasonal variability in these environmental conditions.

Scenario specifications

For simulations in each of the three seascapes, a 10-year burn-in period was used where all parameters maintained their default values. Following burn-in, fish length and mass and water temperature and salinity were interpolated in daily increments until reaching their final value at the end of the 10-year scenario period (20 simulation years in total) (Fig. 2).

All possible combinations of final fish length and spatial aggregation level were run to investigate relative impacts of and possible interactions between these environmental changes. We ran ten simulations for each combination as this number of replicates resulted in low variance (SD <5% of mean) in population size in calibration runs. Outputs for individual energetics (energy use, energy intake, body mass, and storage levels), population size, and space use were recorded weekly, while vital rates (reproduction and mortality) were recorded annually. Individual energetics and mortality metrics were recorded per age class (for energetics: calves, juveniles, non-lactating adults, and lactating adults; and for mortality: abortions, calves, juveniles, and adults), while reproduction was recorded as the number of calves born and weaned. As a measure of space use, the unique food cell encounter rate was used to represent the ability of animals to find and exploit different food cells and was defined as the number of unique cells containing food encountered by porpoises per week. To assess changes in movement behavior between scenarios, the x and y coordinate positions of ten randomly selected individuals were tracked hourly in simulation year 14 for five replicates (a total of 50 tracked individuals).

As porpoises can greatly increase their ingestion rates following periods of reduced energy intake (Kastelein et al., 2019), it is possible that individuals in environments with smaller fish would increase their foraging rates to meet their energetic needs (Booth, 2020; Hoekendijk et al., 2018). Catching more fish, however, requires that animals locate more prey within the same timeframe. To test the ability of porpoises to compensate for decreasing fish length, we additionally ran simulations where both porpoise potential ingestion rates and fish total abundance increased with decreasing fish mass. These simulations were run for all spatial aggregation levels using the minimum final fish length of 14.1 cm. Ingestion rates were modified by increasing animals' potential energy intake per timestep (see Appendix S1 Section 2). Both fish abundance and potential energy intake were increased by 0, 25, 50, 75, and 100% by the end of the scenario, with ten replicates run for each combination of these values. Population abundance and daily consumption rates were recorded as outputs.

Analysis of model outputs

Model outputs were processed and analyzed in R version 4.0.0 (R Core Team, 2020). Energetics, space use, and population vital rates were analyzed for each prey length, spatial aggregation, and climate change level tested. Total population size in each of the scenarios was averaged and presented as time series.

Behavioral classification analysis of the movement outputs was done using a hidden Markov model (HMM), where outputs were analyzed using the R package "momentuHMM" (McClintock, 2017; McClintock & Michelot, 2018). All animals were recorded as having survived or died by the end of simulation year 14. This simulation year was selected as population declines occurring after year 14 in scenarios with low prey size did not allow for tracking an adequate number of individuals. Only the last month of movement data recorded per individual was used in fitting the HMM; this was either the last month of the tracking period for individuals which survived, or the last month of life for individuals which died. We focused on this last month as it was thought that behavioral differences may be particularly evident in starving animals. Location data where animals passed from one side of the map to the other due to seascape continuous boundaries were filtered out and replaced with NAs to remove unrealistic step lengths and keep the time series regular and continuous. Models were run considering step lengths and turning angles as data streams to estimate two behavioral states (state 1 and state 2), indicating general area-restricted search and transit movement patterns (Langrock et al., 2012). Step lengths were modelled using a *Gamma* distribution and turning angles using a *von Mises* distribution (McClintock & Michelot, 2018). Alternative models were tested by varying starting parameters for step length and turning angle distributions. In addition to behavioral classification, the model computed a transition matrix indicating the probability of switching between the two behavioral states. To test the effect of different covariates on behavioral state switching probability, spatial aggregation level, final fish length (as a categorical variable), and animal fate ("*survived*", "*died*") during the tested period were added using the *formula* argument. Parameter selection was done using log-likelihood and the best model structure was assessed using Akaike's information criterion (Patterson et al., 2017). Behavioral state switching probabilities were extracted as a function of the selected covariates. Activity budgets for individual animals were calculated as the proportion of time spent in each behavioral state per day.

Results:

Impacts on movements and space use

The weekly unique food cell encounter rate increased with increasing seascape aggregation (Fig. 3a). Animals encountered 23.7 ± 5.2, 16.8 ± 3.5, and 5.9 ± 0.4 unique food cells per week for high, moderate, and low spatial aggregation levels, respectively, when fish length was held constant (results are described using mean ± SD unless otherwise stated). Seasonality was observed in food encounter rates due to seasonal fluctuations in environmental conditions (Fig. 2) and energy balance (Gallagher et al. 2021), with fewer unique food cells encountered in March-May and more in September-November (Fig. 3b). The number of food encounters increased and became more variable with decreasing fish length (Fig. 3c).

The HMM including all three covariates (prey aggregation, prey length, and animal fate) produced the lowest AIC value and was selected as the best performing model (Appendix S1 Section 7.3). Behavioral state 1, area-restricted search, was characterized by relatively short step lengths (0.786 ± 0.548 km) and highly variable turning angles (-0.0018 ± 1.6760 radians). Animals in state 2, transit, took longer steps (3.446 ± 0.826 km) and maintained high directional persistence (0.0001 ± 0.2055 radians) (Appendix S1 Section 7.3). Surviving individuals displayed a lower probability of switching from area-restricted search to transit than those that died (Fig 4a), which was exhibited in their individual activity budgets (Fig. 4b). Fish length alterations substantially impacted the probability of switching between area-restricted search and transit (Fig 4a), with decreases in fish length accompanied by decreased probability of state switching, except in the lowest fish length class. Increasing aggregation level did not considerably affect state transition probabilities (Appendix S1 Table 7.12).

Impacts on individual energetics and population dynamics

Energy intake, expenditure, body size, and storage level generally increased with increasing fish length and spatial aggregation level (Fig. 5a & b, Appendix Figs. 7.3-7.5a & b), with overall stronger impacts observed for changing prey size than aggregation level (Fig. 5b *vs* 5a). One exception was seen for calves, whose energy use decreased with increasing fish length, while their storage levels and body sizes increased. Additionally, for non-lactating adults, energy use and body masses were, on average, higher in simulations with small prey (14.1 cm) than in those with larger prey (15.35 cm), while their energy intake remained fairly constant at higher final fish lengths. Changing sea surface temperature and salinity had no detectible impacts on any of these measurements (Fig. 5c, Appendix Figs. 7.3-7.5c).

Increasing spatial aggregation led to increases in both the number of born and weaned calves and number of deaths, while reproduction increased and mortality decreased with increasing prey size (Appendix Figs.7.6-7.7a & b). Here aggregation level was observed to result in stronger impacts when compared to changing prey size. Vital rates were also unaffected by changes in climate conditions (Appendix Figs. 7.6-7.7c).

As expected, decreasing fish length caused substantial population declines. The population went extinct in year 16 in simulations with the most extreme decreases in fish length (year 16.5, 16.6, 16.6 for low, moderate, and high aggregation levels, respectively). Increasing fish length increased population size but impacts were lesser than those for length decreases (Appendix Fig. 7.8), e.g., in the final simulation year when spatial aggregation was moderate, a 7.5% fish length increase resulted in a 19.2% population size increase, while decreasing fish length by 7.5% reduced population size by 94.6%. Increasingly aggregated seascapes resulted in larger populations (Fig. 5). When fish length remained constant (16.6 cm) population sizes of 106.4 ± 18.8 and 282.8 ± 35.1 were found for seascapes with low and high spatial aggregation levels, respectively. Population size was again unimpacted by changing temperature and salinity (Appendix Fig. 7.8).

Testing the ability of animals to compensate for shrinking prey resources

When testing if effects of decreasing fish length on population abundance could be counterbalanced by increased potential ingestion rate and fish abundance, we found that increases in both factors were required to counteract decline (Fig. 7). For all aggregation levels, increases in potential ingestion rates between 50–100% resulted in comparable population abundances, while values below 50% led to population collapse. As spatial aggregation level increased, lesser increases in fish abundance were needed to maintain baseline population size in seascapes with small fish (Fig 7 and Appendix S1 Fig. 7.10), with 75%, 50%, and 25% abundance increases required for low, moderate, and high spatial aggregation levels, respectively. Increases above these values resulted in population growth beyond baseline levels.

Increasing potential ingestion rates by 50% and prey abundance by the required increases for each spatial aggregation level stated above, increased average daily ingestion rates by 45.3 ± 5.3%, 42.8 ± 3.9%, and 40.3 ± 2.85% for low, moderate, and high spatial aggregation levels, respectively (Appendix Fig. 7.11).

Discussion:

To conserve wildlife populations inhabiting changing environments we must understand linkages between trophic levels, which drive patterns in population abundances and distributions. Here we used a rigorously tested agent-based model to demonstrate how impacts of environmental change on individual behavior and population viability can be quantified after accounting for such links. We investigated how changes in fish size and spatial aggregation impact top predator behavior and population size, further highlighting the potential of marine predator species as indicators of ecosystem change (Moore, 2008). Our results demonstrate that when considering spatially-explicit seascapes and mechanistic and adaptive movements, the complex, energy-mediated responses to shifting environmental conditions can be measured.

Modifications in prey size and spatial aggregation were found to impact predator movements and space use, with exaggerated responses occurring in animals which ultimately died. As movement patterns can be driven by changes in animal energetic status (Chimienti et al., 2020; Nathan et al., 2008), it was expected that starving animals would deviate considerably in their behavior from surviving individuals. Starving animals had a higher probability of switching from area-restricted search to transit to seek out patches with higher energy profitability. Higher rates of transit found with increasing fish length contrasted with expectations that animals would maintain a higher body condition in seascapes with larger and more energy-rich fish. However, in simulations where fish length increased, the porpoise population grew while prey abundance remained static, effectively elevating rates of resource competition by decreasing relative accessibility of individual prey items. The unique food cell encounter rate decreased with increasing fish length, resulting in average energy intake and storage levels plateauing with higher fish lengths, while energy use and body masses of juvenile and adult porpoises continued to increase. This effectively decreased porpoise energy balance in seascapes with larger fish and, consequently, individuals were more likely to switch to transit movements to seek out new food patches. However, contrasting increases in transit behavior between scenarios with final fish lengths of 14.1 and 15.35 cm highlight that competition may not be the only factor influencing changing behavior; insufficient energy availability may outweigh alleviation of competition as prey size decreases. While changing aggregation levels altered population size, no noticeable differences were observed in state switching behavior due to higher food encounter rates occurring with increased aggregation level.

Population decline was predicted with decreasing prey spatial aggregation level and length. Animals' ability to readily encounter prey occurring in aggregated patches can increase foraging efficiency (Benoit-Bird et al., 2013, 2020; Goldbogen et al., 2011), which can offset mortality and increase reproductive success. Our results suggest that population growth with increased prey aggregation is, indeed, mediated through increased prey encounter and intake rates which led to increased body mass and reproductive success. In nature, animals may additionally offset prey shifts by altering their diet or distributions (Nøttestad et al., 2015; Van Baalen et al., 2001), factors that were not considered in this study.

Even small changes in fish size largely impacted total energy availability owing to the exponential relationship between fish length and mass, with a 15.1% decrease in fish length resulting in a 38.3% drop in available energy. This drop triggered population collapse in all scenarios, even with simulated length decreases corresponding to empirically documented relative reductions in community fish length (Beukhof et al., 2019). Reduced energy availability with smaller fish size led to decreased rates of energy intake, reduced body mass and stores, decreased reproduction, and increased mortality, ultimately inducing population decline.

A real-world population collapse as predicted by these scenarios, is however unlikely, as, in the North Sea, fish length reductions have occurred (Baudron et al., 2014) without any concurrent indication of porpoise population decline (Hammond et al., 2021). Harbor porpoises are highly flexible and efficient predators, making them capable of elevating their foraging rates when facing decreasing prey size (Booth, 2020; Goldbogen et al., 2019). Our results suggest that increasing individual consumption rates could offset population decline, though this only occurred when coupled with increased fish abundance. However, increases in overall abundance are unlikely to occur considering observed decreases in spawning stock biomass and recruitment with elevated temperatures for important porpoise prey species (Capuzzo et al., 2018; Clausen et al., 2018), and global predictions of biomass decline for marine species with climate change (Boyce et al., 2020). Additionally, while elevated prey capture rates needed to offset population decline of 42.8 ± 4.5% were well within observed porpoise ingestion rates (Wisniewska et al., 2016), these increases were 21.3 ± 12.7% greater than would be predicted by change in prey mass and energy content alone, suggesting that animals moving in realistic seascapes incur additional costs which should be considered when assessing the impacts of changing energy availability on populations.

While our results found no detectible impacts of climate change, we emphasize that these findings represent only direct effects of changing temperature and salinity on the modelled porpoise energy budget. Though these conditions directly influence energetic calculations, it should be considered that total changes for even the most extreme scenario were well within the seasonal variation experienced by porpoises (Fig. 2), making any population-level impacts undetectable. Additional impacts of climate change not considered here, such as distribution shifts, habitat loss, temporal mismatches with prey, and reduced fertility and health, may threaten cetacean populations (van Weelden et al., 2021).

Several simplifying assumptions were made in model development to isolate the impacts of tested alterations in prey structure on porpoise populations. The success of individuals in this study, particularly in highly aggregated seascapes, was linked to their knowledge of the regions where food levels were potentially high. These remained constant in simulations but likely shift temporally in nature. Though animals may be able to use oceanographic cues to locate profitable food patches (Cox et al. 2018), the profitability of remembered regions may shift in time (Abrahms et al. 2019). In densely aggregated seascapes, the shifting of profitable regions may have greater impacts on individual success and population dynamics due to large distances between patches. Process-based models, such as the one used here, can be used to investigate the potential mechanisms employed by animals to track their prey resources (Merkle et al., 2019). Further implementations in this direction would be feasible for testing alternative behavioral processes in changing environments and quantifying their impacts on foraging success and fitness.

In this study, fish were represented as resources rather than individual agents. We did this to isolate impacts of community-wide average length decreases for important prey species, which required controlling for changes in community structure. Additionally, no energy density variation with size, preferential fish selection, or interactions amongst fish were included in the model. While these assumptions were made to isolate the link between the prey and predator populations, in making them, some potentially important interactions occurring in response to the same tested drivers within lower trophic level species may be missed. Changes in fish mortality, fecundity, growth, and recruitment can occur with body mass (Audzijonyte et al., 2013; Beukhof et al., 2019; Capuzzo et al., 2018), potentially altering the fish community and impacting top predators. Furthermore, processes like changes in prey size can impact fish body length (Ljungström et al., 2020). Additional mechanisms, when established, could be implemented using our framework to assess climate change impacts throughout various food web levels.

Species which rely on the biodiversity of fish communities are increasingly threatened by changes in fish community structure and dynamics due to worsening climate change (Saba et al., 2015). Though challenging to demonstrate empirically, simulation studies have observed ties between prey patchiness and individual foraging and reproductive success (Bailleul et al., 2013; Massardier-Galatà et al., 2017). Our results build on these findings by quantifying impacts of potential climate-induced changes in fish community structure on both fine-scale individual behavior and energetics and population viability of a top predator. By using energy to link individual responses to population dynamics, the model presented here offers a robust approach to predicting impacts of environmental modifications on consumer populations. These predictions are made more reliably through the model's dependance on realistic underlying mechanisms and emergent properties. Moreover, the use of systematic statistical techniques for the analysis of model outputs, such as HMMs commonly applied in the movement ecology field (Langrock et al., 2012), highlights potential for standardized quantification and interpretation of behavioral changes of modelled individuals in the more widely accessible statistical language, facilitating communication of simulation model outputs (e.g., Fig. 3 in Horn et al., 2016). The benefit of using a HMM approach lies in the ability to communicate and extract statistics from movement behavior of modelled animals in a way that enables direct comparison with empirical movement analyses, using e.g., pattern-oriented modelling (Gallagher et al., 2021).

While the model has been rigorously developed and parameterized specifically for harbor porpoises, which makes direct transferal to other species challenging, its core principles are universal and widely applicable to other species for investigating the population impacts of environmental change. Additionally, the model structure facilitates the inclusion of additional stressors for the assessment of cumulative impacts (e.g., Galic et al. 2018), such as by investigating the combined impacts of climate change in the presence of direct anthropogenic disturbance (e.g., noise, pollution, direct takes) (National Academies of Sciences, Engineering, and Medicine, 2017). By considering the energy dynamics which link trophic levels, our model findings provide a mechanistic demonstration of how changes in prey structure can impact predator populations, contributing to our understanding of these systems and improving our ability to predict population viability under environmental change.

Acknowledgements:

This study was a part of CAG's PhD project at the Graduate School of Science and Technology, Aarhus University funded by the Danish Centre for Environment and Energy. We would like to thank the GenomeDK cluster team for allowing us access to their cluster, which allowed for speedy simulations. This study is part of the DEPONS project (www.depons.au.dk) funded by the offshore wind developers: Vattenfall, Forewind, ENECO Luchterduinen, Ørsted, and Scottish Power Renewables. We thank two anonymous reviewers and editors for their feedback which greatly improved the manuscript.

Conflict of interest:

The authors declare no conflict of interest.

Author contributions:

CAG conceived the study, implemented the model, analyzed model outputs, and lead manuscript writing; MC assisted with developing and analyzing the outputs of the HMM; All authors contributed to manuscript conceptualization, design, and development and gave final approval for publication.

Data availability statement:

Full model code, associated run files, input data, and scripts used to produce article figures have been deposited in the Dryad Digital Depository (doi:10.5061/dryad.5tb2rbp54; Gallagher et al. 2021).

References:

Amorim, P., Perán, A. D., Pham, C. K., Juliano, M., Cardigos, F., Tempera, F., et al. (2017). Overview of the ocean climatology and its variability in the Azores region of the North Atlantic including environmental characteristics at the seabed. *Frontiers in Marine Science*, *4*(MAR), 1–16. https://doi.org/10.3389/fmars.2017.00056

Andreasen, H., Ross, S. D., Siebert, U., Andersen, N. G., Ronnenberg, K., & Gilles, A. (2017). Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. *Marine Mammal Science*, *33*(4), 1053–1079. https://doi.org/10.1111/mms.12421

Audzijonyte, A., Kuparinen, A., Gorton, R., & Fulton, E. A. (2013). Ecological consequences of body size decline in harvested fish species: Positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, *9*(2), 20121103. https://doi.org/10.1098/rsbl.2012.1103

Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., et al. (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology and Evolution*, *4*(6), 809–814. https://doi.org/10.1038/s41559-020-1171-0

Bailleul, F., Grimm, V., Chion, C., & Hammill, M. (2013). Modeling implications of food resource aggregation on animal migration phenology. *Ecology and Evolution*, *3*(8), 2535–2546. https://doi.org/10.1002/ece3.656

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, *20*(4), 1023–1031. https://doi.org/10.1111/gcb.12514

Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., et al. (2013). Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. *PLoS ONE*, *8*(1), e53348. https://doi.org/10.1371/journal.pone.0053348

Benoit-Bird, K. J., Southall, B. L., Moline, M. A., Claridge, D. E., Dunn, C. A., Dolan, K. A., et al. (2020). Critical threshold identified in the functional relationship between beaked whales and their prey. *Marine Ecology Progress Series*, *654*, 1–16. https://doi.org/10.3354/meps13521

Bertrand, A., Grados, D., Colas, F., Bertrand, S., Capet, X., Chaigneau, A., et al. (2014). Broad impacts of fine-scale dynamics on seascape structure from zooplankton to seabirds. *Nature*

Communications, *5*, 5239. https://doi.org/10.1038/ncomms6239

Beukhof, E., Dencker, T. S., Pecuchet, L., & Lindegren, M. (2019). Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. *Marine Ecology Progress Series*, *610*, 205–222. https://doi.org/10.3354/meps12826

Booth, C. G. (2020). Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance. *Marine Mammal Science*, *36*(1), 195–208. https://doi.org/10.1111/mms.12632

Boyce, D. G., Lotze, H. K., Tittensor, D. P., Carozza, D. A., & Worm, B. (2020). Future ocean biomass losses may widen socioeconomic equity gaps. *Nature Communications 2020 11:1*, *11*, 2235. https://doi.org/10.1038/s41467-020-15708-9

Brun, P., Kiørboe, T., Licandro, P., & Payne, M. R. (2016). The predictive skill of species distribution models for plankton in a changing climate. *Global Change Biology*, *22*(9), 3170–3181. https://doi.org/10.1111/gcb.13274

Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., et al. (2018). A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, *24*(1), e352–e364. https://doi.org/10.1111/gcb.13916

Chimienti, M., Desforges, J. P., Beumer, L. T., Nabe-Nielsen, J., van Beest, F. M., & Schmidt, N. M. (2020). Energetics as common currency for integrating high resolution activity patterns into dynamic energy budget-individual based models. *Ecological Modelling*, *434*, 109250. https://doi.org/10.1016/j.ecolmodel.2020.109250

Clausen, L. W., Rindorf, A., van Deurs, M., Dickey-Collas, M., & Hintzen, N. T. (2018). Shifts in North Sea forage fish productivity and potential fisheries yield. *Journal of Applied Ecology*, *55*(3), 1092–1101. https://doi.org/10.1111/1365-2664.13038

Embling, C. B., Illian, J., Armstrong, E., van der Kooij, J., Sharples, J., Camphuysen, K. C. J., et al. (2012). Investigating fine-scale spatio-temporal predator-prey patterns in dynamic marine ecosystems: A functional data analysis approach. *Journal of Applied Ecology*, *49*(2), 481–492. https://doi.org/10.1111/j.1365-2664.2012.02114.x

Galic, N., Sullivan, L. L., Grimm, V., & Forbes, V. E. (2018). When things don't add up: quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters*, *21*(4), 568–577. https://doi.org/10.1111/ele.12923

Gallagher, C. A., Chimienti, M., Grimm, V., & Nabe-Nielsen, J. (2021). Data from: Energy-mediated responses to changing prey size and distribution in marine top predator movements and population dynamics, Dryad, Dataset, https://doi.org/10.5061/dryad.5tb2rbp54.

Gallagher, C. A., Chudzinska, M., Larsen-Gray, A., Pollock, C. J., Sells, S. N., White, P. J. C., et al. (2021). From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. *Biological Reviews*, *96*, 1868–1888. https://doi.org/10.1111/brv.12729

Gallagher, C. A., Grimm, V., Kyhn, L. A., Kinze, C. C., & Nabe-Nielsen, J. (2021). Movement and seasonal energetics mediate vulnerability to disturbance in marine mammal populations. *The American Naturalist*, *197*(3), 296–311. https://doi.org/10.1086/712798

Goldbogen, J. A., Cade, D. E., Wisniewska, D. M., Potvin, J., Segre, P. S., Savoca, M. S., et al. (2019). Why whales are big but not bigger: Physiological drivers and ecological limits in the age of ocean giants. *Science*, *366*(6471), 1367–1372. https://doi.org/10.1126/science.aax9044

Goldbogen, J. A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N. D., Schorr, G., et al. (2011). Mechanics, hydrodynamics and energetics of blue whale lunge feeding: Efficiency dependence on krill density. *Journal of Experimental Biology*, *214*(1), 131–146. https://doi.org/10.1242/jeb.054726

Goldbogen, J. A., Hazen, E. L., Friedlaender, A. S., Calambokidis, J., DeRuiter, S. L., Stimpert, A. K., et al. (2015). Prey density and distribution drive the three-dimensional foraging strategies of the largest filter feeder. *Functional Ecology*, *29*(7), 951–961. https://doi.org/10.1111/1365-2435.12395

Grimm, V., Augusiak, J., Focks, A., Frank, B. M., Gabsi, F., Johnston, A. S. A., et al. (2014). Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACE. *Ecological Modelling*, *280*, 129–139. https://doi.org/10.1016/j.ecolmodel.2014.01.018

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., et al. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, *198*(1–2), 115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., DeAngelis, D. L., et al. (2020). The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism. *Journal of Artificial Societies and Social Simulation*, *23*(2), 7. https://doi.org/10.18564/jasss.4259

Hammond, P. S., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., et al. (2021).

Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys (Issue June). https://synergy.st-andrews.ac.uk/scans3/files/2017/05/SCANS-III-design-based-estimates-2017-05-12-final-revised.pdf

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., et al. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters*, *9*(2), 228–241. https://doi.org/10.1111/j.1461-0248.2005.00871.x

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., et al. (2019). Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecology and the Environment*, *17*(10), 565–574. https://doi.org/10.1002/fee.2125

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, *42*(10), 1648–1657. https://doi.org/10.1111/ecog.04617

Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling* (R package version 3.1-5). https://cran.r-project.org/package=raster

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The Impact of Climate Change on the World's Marine Ecosystems. *Science*, *328*, 1523–1528. https://doi.org/10.1016/s0262-4079(10)61509-6

Hoekendijk, J. P. A., Spitz, J., Read, A. J., Leopold, M. F., & Fontaine, M. C. (2018). Resilience of harbor porpoises to anthropogenic disturbance: Must they really feed continuously? *Marine Mammal Science*, *34*(1), 258–264. https://doi.org/10.1111/mms.12446

Horn, J., Becher, M. A., Kennedy, P. J., Osborne, J. L., & Grimm, V. (2016). Multiple stressors: using the honeybee model BEEHAVE to explore how spatial and temporal forage stress affects colony resilience. *Oikos*, *125*(7), 1001–1016. https://doi.org/10.1111/OIK.02636

Kastelein, R. A., Helder-Hoek, L., Booth, C., Jennings, N., & Leopold, M. (2019). High levels of food intake in harbor porpoises (*Phocoena phocoena*): Insight into recovery from disturbance. *Aquatic Mammals*, *45*(4), 380–388. https://doi.org/10.1578/AM.45.4.2019.380

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. *Ecology*, *93*(11), 2336–2342. https://doi.org/10.1890/11-2241.1

Ljungström, G., Claireaux, M., Fiksen, Ø., & Jørgensen, C. (2020). Body size adaptions under climate change: zooplankton community more important than temperature or food abundance in model of a zooplanktivorous fish. *Marine Ecology Progress Series*, *636*, 1–18. https://doi.org/10.3354/MEPS13241

MacLeod, C. D., Santos, M. B., Reid, R. J., Scott, B. E., & Pierce, G. J. (2007). Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? *Biology Letters*, *3*(2), 185–188. https://doi.org/10.1098/rsbl.2006.0588

Massardier-Galatà, L., Morinay, J., Bailleul, F., Wajnberg, E., Guinet, C., & Coquillard, P. (2017). Breeding success of a marine central place forager in the context of climate change: A modeling approach. *PLoS ONE*, *12*(3), 1–24. https://doi.org/10.1371/journal.pone.0173797

McClintock, B. T. (2017). Incorporating Telemetry Error into Hidden Markov Models of Animal Movement Using Multiple Imputation. *Journal of Agricultural, Biological, and Environmental Statistics*, *22*(3), 249–269. https://doi.org/10.1007/s13253-017-0285-6

McClintock, B. T., & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, *9*(6), 1518–1530. https://doi.org/10.1111/2041-210X.12995

McInnes, A. M., Ryan, P. G., Lacerda, M., Deshayes, J., Goschen, W. S., & Pichegru, L. (2017). Small pelagic fish responses to fine-scale oceanographic conditions: Implications for the endangered African penguin. *Marine Ecology Progress Series*, *569*, 187–203. https://doi.org/10.3354/meps12089

Merkle, J. A., Sawyer, H., Monteith, K. L., Dwinnell, S. P. H., Fralick, G. L., & Kauffman, M. J. (2019). Spatial memory shapes migration and its benefits: evidence from a large herbivore. *Ecology Letters*, *22*(11), 1797–1805. https://doi.org/10.1111/ele.13362

Moore, S. E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, *89*(3), 534–540. https://doi.org/10.1644/07-MAMM-S-312R1.1

Nabe-Nielsen, J., Sibly, R. M., Tougaard, J., Teilmann, J., & Sveegaard, S. (2014). Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling*, *272*, 242–251. https://doi.org/10.1016/j.ecolmodel.2013.09.025

Nabe-Nielsen, J., van Beest, F. M., Grimm, V., Sibly, R. M., Teilmann, J., & Thompson, P. M. (2018). Predicting the impacts of anthropogenic disturbances on marine populations. *Conservation Letters*, *11*(5), 1–8. https://doi.org/10.1111/conl.12563

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., et al. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the*

National Academy of Sciences of the United States of America, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

National Academies of Sciences, Engineering, and Medicine. (2017). *Approaches to understanding the cumulative effects of stressors on marine mammals*. National Academies Press. https://doi.org/doi.org/10.17226/23479

Nøttestad, L., Krafft, B. A., Anthonypillai, V., Bernasconi, M., Langård, L., Mørk, H. L., et al. (2015). Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey. *Frontiers in Ecology and Evolution*, *2*, 83. https://doi.org/10.3389/fevo.2014.00083

Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., & King, R. (2017). Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *AStA Advances in Statistical Analysis*, *101*(4), 399–438. https://doi.org/10.1007/s10182-017-0302-7

Pirotta, E., Hin, V., Mangel, M., New, L., Costa, D. P., de Roos, A. M., et al. (2020). Propensity for risk in reproductive strategy affects susceptibility to anthropogenic disturbance. *American Naturalist*, *196*(4), E71–E87. https://doi.org/10.1086/710150

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., et al. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919–925. https://doi.org/10.1038/nclimate1958

R Core Team. (2020). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. http://www.r-project.org/

Railsback, S. F., & Grimm, V. (2019). *Agent-Based and Individual-Based Modeling: A Practical Introduction.* (2nd ed.). Princeton University Press.

Railsback, S. F., & Harvey, B. C. (2020). *Modeling Populations of Adaptive Individuals*. Princeton University Press.

Rojano-Donãte, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., et al. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*(23), jeb185827. https://doi.org/10.1242/jeb.185827

Saba, V. S., Griffies, S. M., Anderson, W. G., Winton, M., Alexander, M. A., Delworth, T. L., et al. (2015). Enhanced warming of the Northwest Atlantic Ocean under climate change. *Journal of Geophysical Research: Oceans*, *120*, 1–15. https://doi.org/10.1002/2015JC011346.Received

Scheffer, M., Baveco, J. M., DeAngelis, D. L., Rose, K. A., & van Nes, E. H. (1995). Super-individuals a simple solution for modelling large populations on an individual basis. *Ecological Modelling*, *80*(2–3), 161–170. https://doi.org/10.1016/0304-3800(94)00055-M

Sciaini, M., Fritsch, M., Scherer, C., & Simpkins, C. E. (2018). NLMR and landscapetools: An integrated environment for simulating and modifying neutral landscape models in R. *Methods in Ecology and Evolution*, *9*(11), 2240–2248. https://doi.org/10.1111/2041-210X.13076

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Sibly, R. M., Grimm, V., Martin, B. T., Johnston, A. S. A., Kulakowska, K., Topping, C. J., et al. (2013). Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods in Ecology and Evolution*, *4*(2), 151–161. https://doi.org/10.1111/2041-210x.12002

Silva, J. F., Ellis, J. R., & Ayers, R. A. (2013). Length-weight relationships of marine fish collected from around the British Isles. *Science Series Technical Report, Cefas Lowestoft*, *150*(150), 109pp.

Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *BioScience*, *65*(2), 140–150. https://doi.org/10.1093/biosci/biu192

Sveegaard, S., Andreasen, H., Mouritsen, K. N., Jeppesen, J. P., Teilmann, J., & Kinze, C. C. (2012). Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea. *Marine Biology*, *159*(5), 1029–1037. https://doi.org/10.1007/s00227-012-1883-z

Temming, A., & Herrmann, J. P. (2003). Gastric evacuation in cod. Prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. *Fisheries Research*, *63*(1), 21–41. https://doi.org/10.1016/S0165-7836(03)00041-9

Van Baalen, M., Křivan, V., Van Rijn, P. C. J., & Sabelis, M. W. (2001). Alternative food, switching predators, and the persistence of predator-prey systems. *American Naturalist*, *157*(5), 512–524. https://doi.org/10.1086/319933

van Weelden, C., Towers, J. R., & Bosker, T. (2021). Impacts of climate change on cetacean distribution, habitat and migration. *Climate Change Ecology*, *1*, 100009. https://doi.org/10.1016/J.ECOCHG.2021.100009

Verberk, W. C. E. E., Atkinson, D., Natan Hoefnagel, K., Hirst, A. G., & Horne, C. R. (2020).

Shrinking body sizes in response to warming: explanations for the temperature-size rule with special emphasis on the role of oxygen. *Biological Reviews*, *96*, 247–268. https://doi.org/10.1111/brv.12653

Wieners, K.-H., Giorgetta, M., Jungclaus, J., Reick, C., Esch, M., Bittner, M., et al. (2019). *MPI-M MPI-ESM1.2-LR model output prepared for CMIP6 ScenarioMIP ssp585*. Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.6705

Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Donãte, L., Shearer, J., Sveegaard, S., et al. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, *26*(11), 1441–1446. https://doi.org/10.1016/j.cub.2016.03.069

Woodsona, C. B., & Litvinb, S. Y. (2015). Ocean fronts drive marine fishery production and biogeochemical cycling. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(6), 1710–1715. https://doi.org/10.1073/pnas.1417143112

Tables:

Table 1. Food patch characteristics of the theoretical seascapes. Patches were defined as clusters of grid cells containing food that touch on any of their eight sides.

Spatial aggregation level	Number of patches	Average (± SD) patch size [ha]	Maximum patch size [ha]	Average (± SD) distance between patches [km]
Low	5136	29.9 ± 30.6	528	1.8 ± 1.1
Medium	1481	104 ± 388	7984	1.7 ± 2.0
High	1124	137 ± 649	12960	1.5 ± 1.9

Figures:

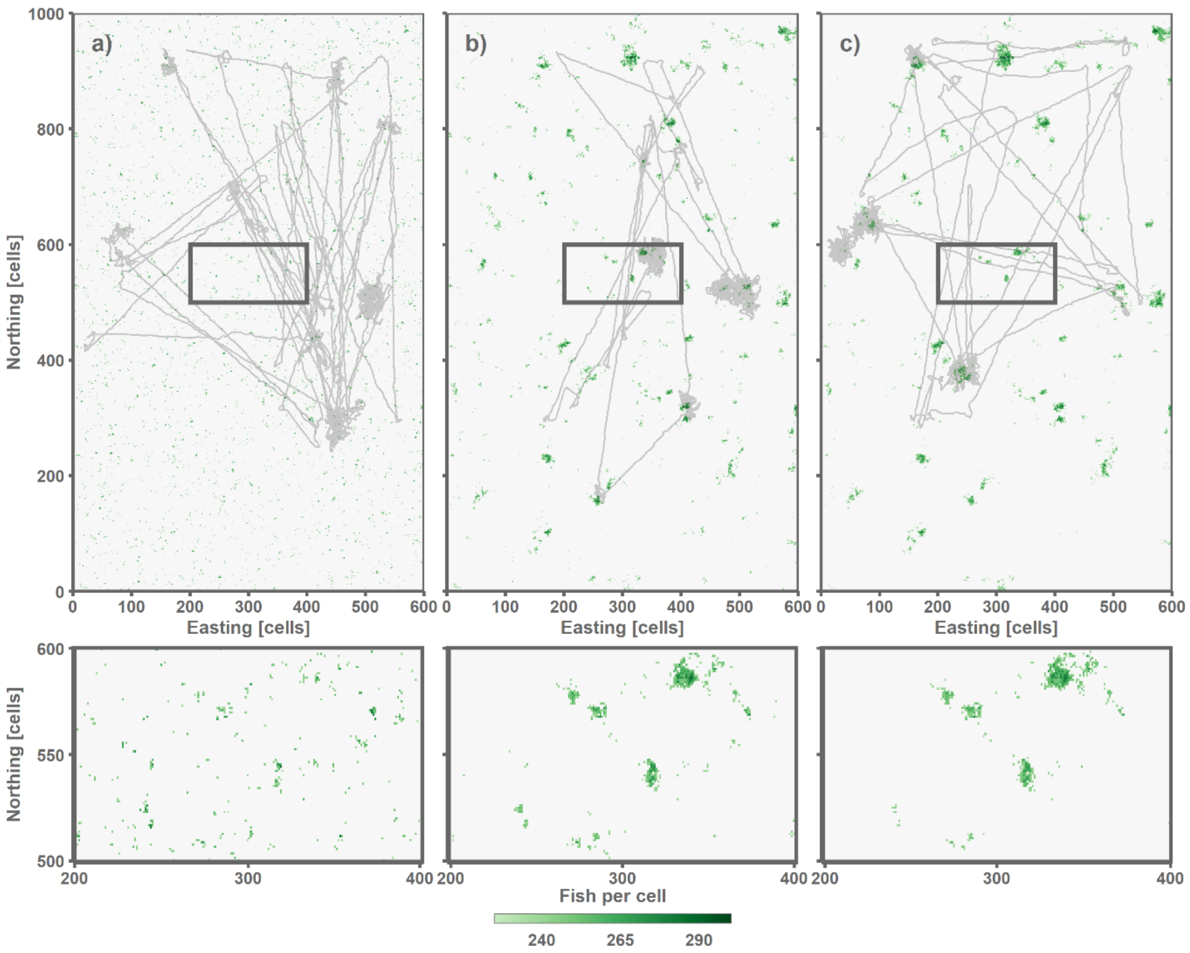

Figure 1. Simulated seascapes with (a) low, (b) moderate, and (c) high aggregation levels. Top panels depict entire seascapes, while bottom panels show zoomed-in regions (denoted by a rectangle in top map). A representative track from a single individual over 360 days is displayed in grey for each aggregation level. All seascapes contain 2,400,000 individual fish. Fish are only contained in the green grid cells and relative amounts are visualized using the color gradient.

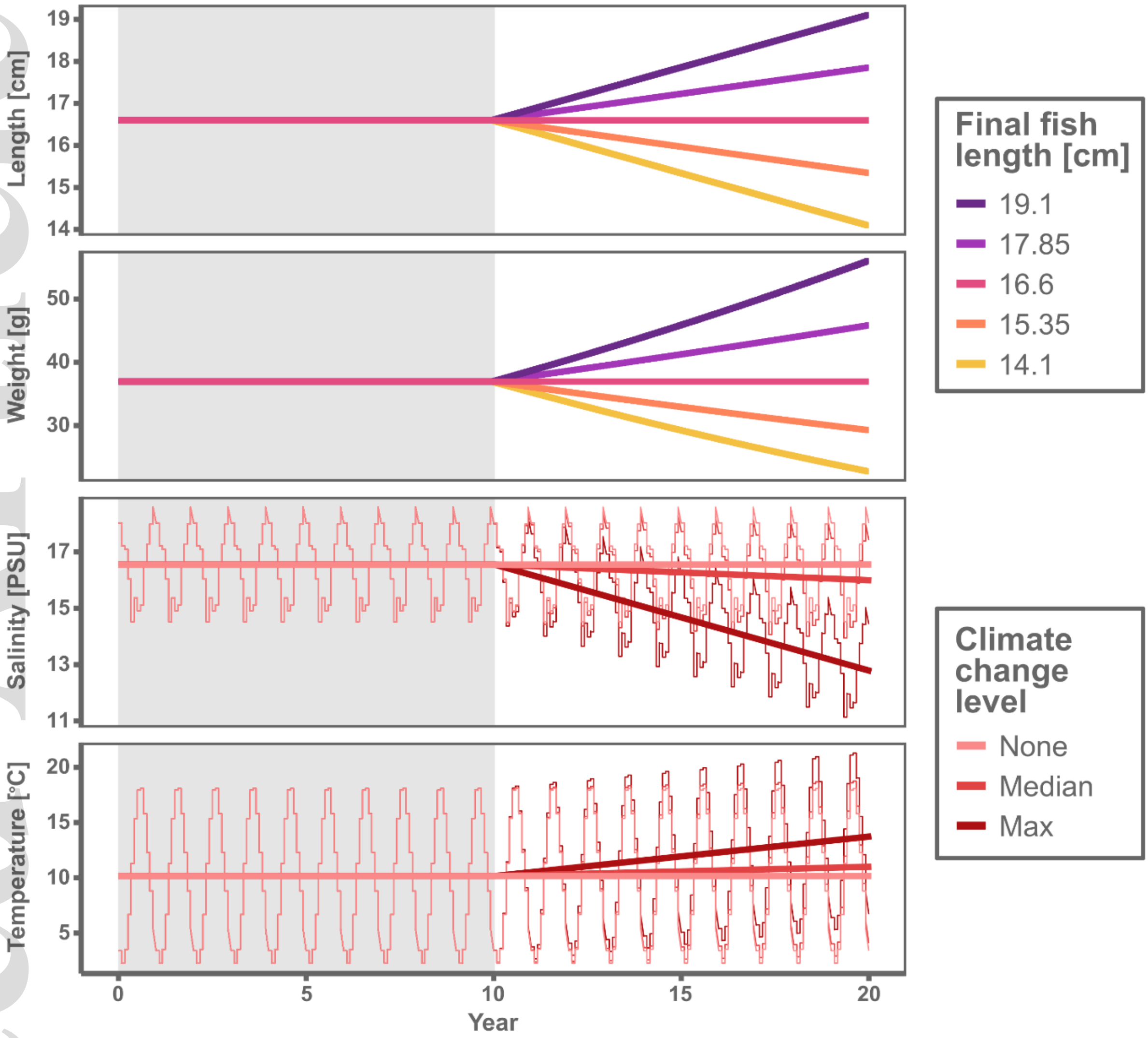

Figure 2. Example runs showing changes in fish length (cm) and weight (g) and water salinity (PSU) and temperature (°C) occurring over the 20-year simulation period. Values of the conditions are shown as they change over the simulation period for all five final fish lengths (14.1, 15.35, 16.6, 17.85, and 19.1 cm) and three climate change levels (none, median, and high). In temperature and salinity panels, seasonal fluctuations in conditions are shown in thin fluctuating lines, while average change is overlaid in bold. Grey region denotes burn-in period.

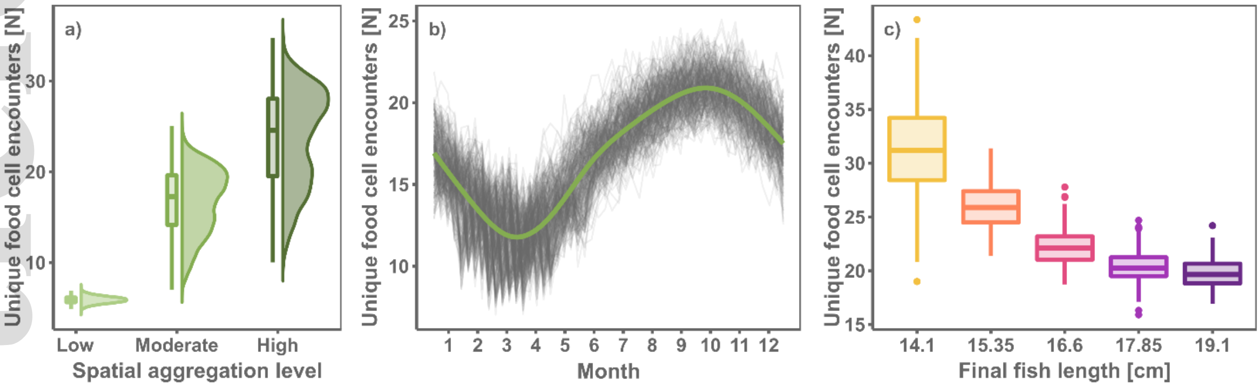

Figure 3. Changes in space use, represented by the average weekly unique food cell encounter rate, for each (a) seascape spatial aggregation level, (b) month of the year, and (c) final fish length. In (a) results are shown for simulations where fish length remained at 16.6 cm. In (b) 100 individual years are shown in grey (average in green) from simulations with moderate spatial aggregation and a final fish length of 16.6 cm. In (c) outputs are shown for January of simulation year 15 when seascape spatial aggregation was high.

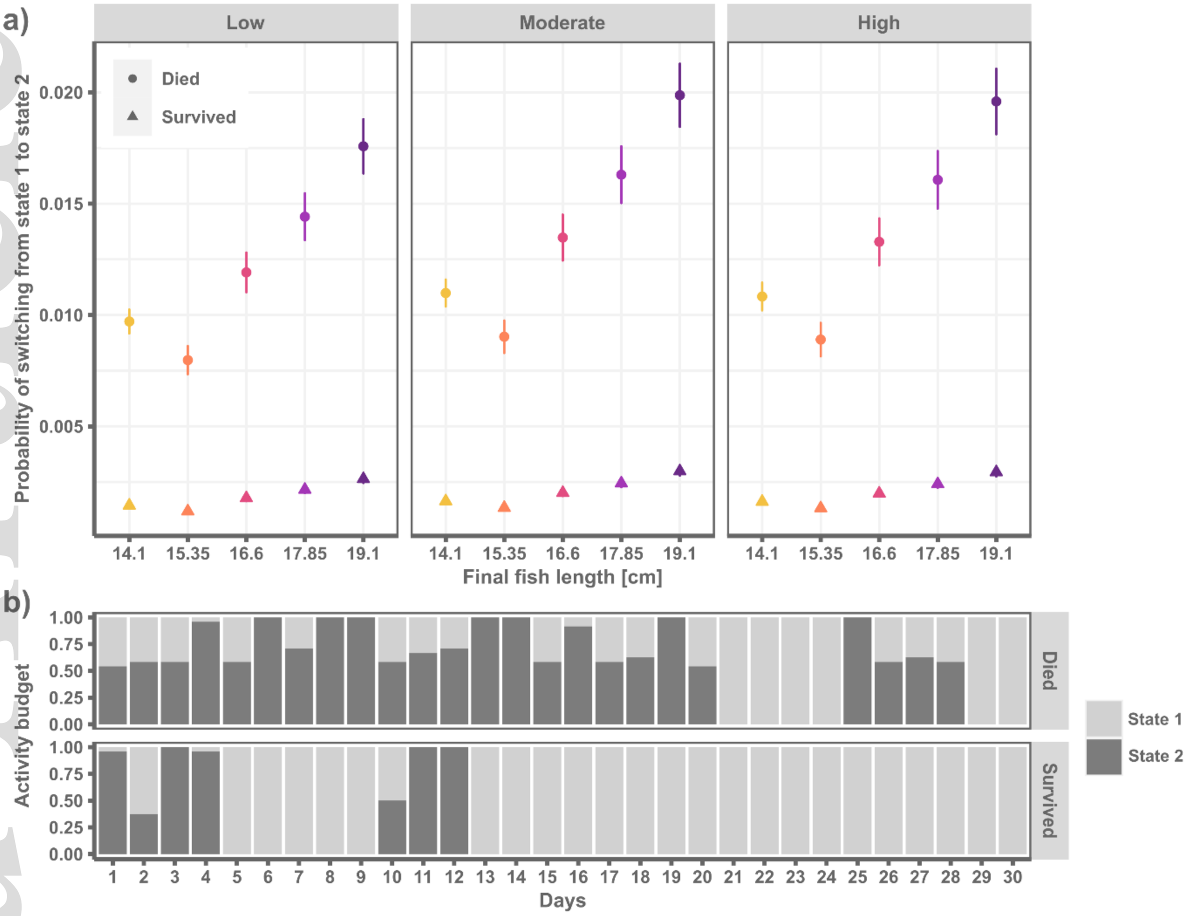

Figure 4. Behavioral classification results from the hidden Markov model. (a) Whether individuals in simulations survived or died and the scenario final fish length impacted the predicted probability of transitioning from behavioral state 1 (area-restricted search) to state 2 (transit). (b) The increase in state switching was observed in the daily activity budgets of individuals that survived and died (two individuals shown as examples).

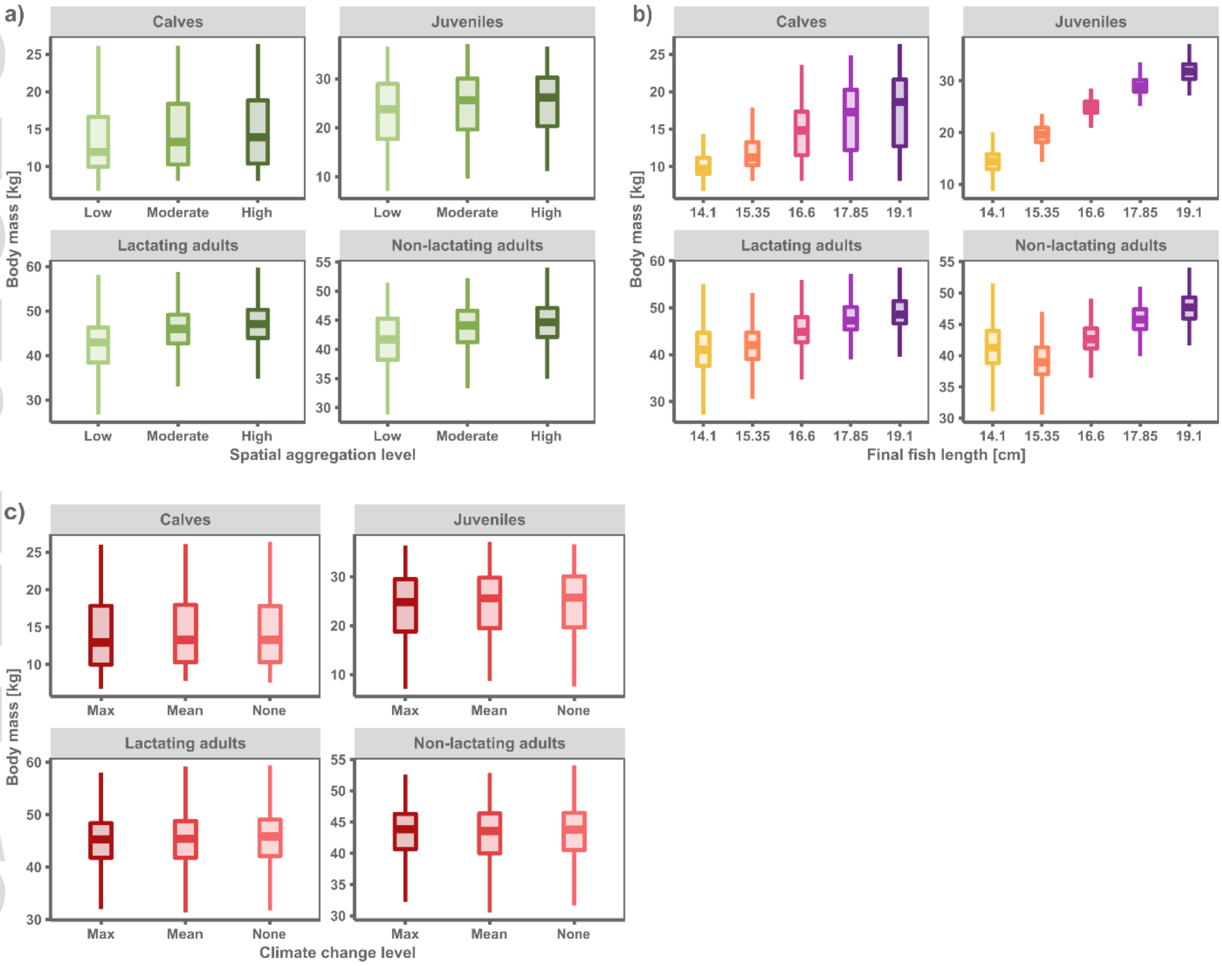

Figure 5. Impacts of changing (a) spatial aggregation level, (b) fish length, and (c) climate change on individual total body mass (kg). Results were collected as weekly averages over the ten-year simulation period for four age classes: calves (nursing offspring), juveniles (weaned animals younger than the age of maturity), lactating adults, and non-lactating adults. The boxplot horizontal line denotes the median, while upper and lower hinges represent the 25th and 75th percentiles, respectively. Results for additional energetics metrics are summarized in Appendix S1 Section 7.3.4.2.

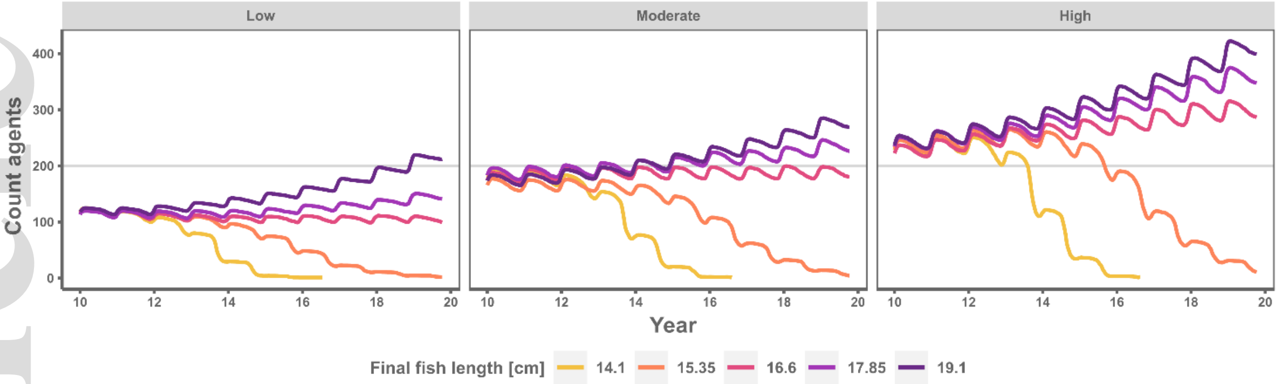

Figure 6. Population impacts of changing fish length and aggregation level. The average number of simulated porpoises for ten simulation replicates was assessed in each scenario. Panels are shown for each prey aggregation level and color denotes the final fish length (cm). Results for additional population dynamics metrics are summarized in Appendix S1 Section 7.3.4.2.

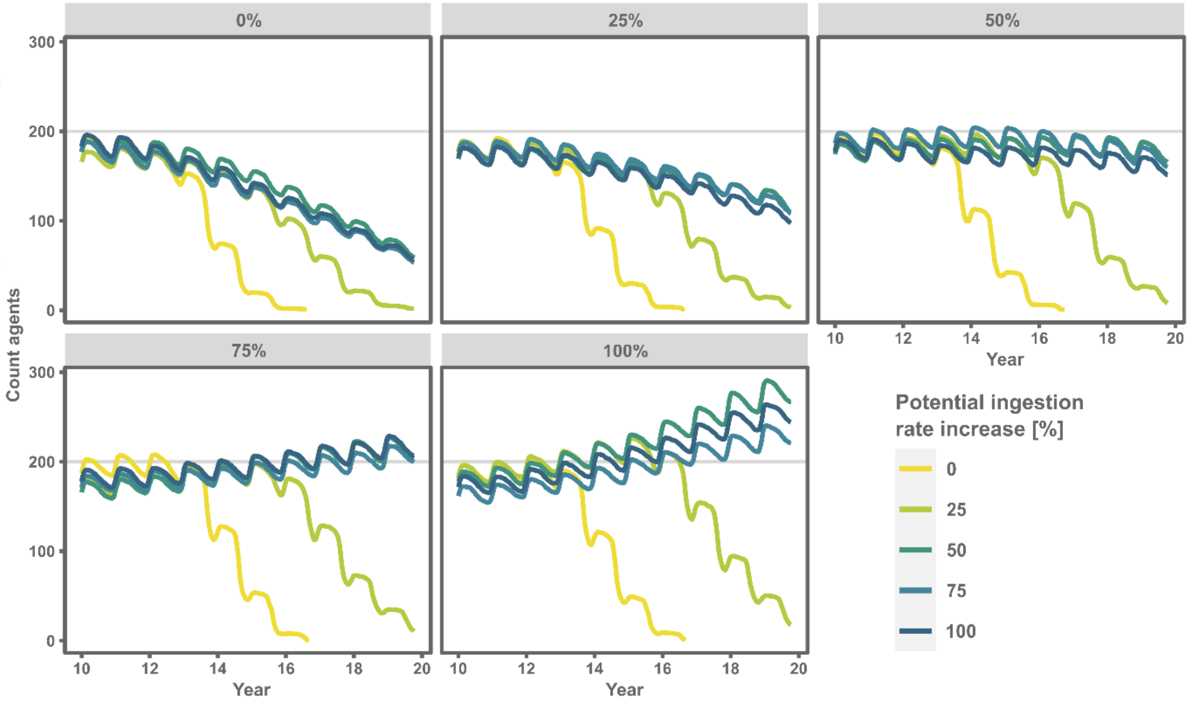

Figure 7. Impacts of alterations in potential ingestion rate and total fish abundance on porpoise population size. Percent increases in fish abundance are shown in panels and potential ingestion rates are denoted using color. All simulations used a final fish length of 14.1 cm. Results are for a seascape with moderate spatial aggregation, for low and high spatial aggregation level results see Appendix S1 Section 7.3.4.3.