INTRODUCTION

Sustainable management of populations impacted by harvesting and climate change

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ABSTRACT: The sustainable use of natural resources is critical for addressing the global challenges of today. Strategies for sustainable harvesting need to consider not only harvested species, but also other non-harvested species interacting with them in the same ecosystem. In addition, environmental variation needs to be considered, with climate change currently being one of the main sources of this variation. Understanding the consequences of complex interactions between different drivers and processes affecting dynamics of species and ecosystems across spatial scales requires large-scale integrative research projects. The Norwegian research initiative "Sustainable management of renewable resources in a changing environment: an integrated approach across ecosystems" (SUSTAIN) was launched to fill knowledge gaps related to the sustainable management of populations and ecosystems experiencing climate change. SUSTAIN investigated terrestrial, marine and freshwater ecosystems in boreal and Arctic regions, using both theoretical developments and empirical analyses of long-term data. This Climate Research Special contains both synthesis articles and original research exemplifying some of the approaches used in SUSTAIN. In this introduction we highlight 4 key topics addressed by SUSTAIN: (i) population structure, (ii) interactions between species, (iii) spatial processes, and (iv) adaptive management. These topics are fundamental to the understanding of harvested species from an ecosystem perspective, and to ecosystem-based management approaches, which we are striving to work towards.

KEY WORDS: Sustainable harvesting · Yield · Population synchrony · Strategic foresight protocol

1. CHALLENGES

Sustainable use of natural resources is critical for addressing the global challenges of today, not least because exploitation of nature has put humanity in a critical situation due to severe degradation of ecosystems (IPBES 2019). Several of the UN Sustainable Development Goals (SDG), such as SDG2 (zero hunger) or SDG6 (clean water and sanitation), directly depend on well-functioning ecosystems (SDG14: life below water; SDG15: life on land) and their services (Blicharska et al. 2019). Harvesting of natural resources in ways that are sustainable both for the affected species and their ecosystems is therefore a win-win goal for both nature and humans. However, harvesting of species fluctuating in environments that are also systematically changing at unprecedented rates, presents particular challenges for sus-

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tainable management and for maintaining ecosystem functions.

In stable environments, maintaining sustainable harvesting of individual species requires different strategies than those maximizing the yield (Beddington & May 1977, May et al. 1978, Lande et al. 1995, 1997). Ecosystem-based management has been promoted as the most relevant framework to account for interactions among species and the harvesting of multiple species (Levin et al. 2009, Katsanevakis et al. 2011, Lee et al. 2022 in this Special). Climate change has become a main source of environmental variability, and this poses challenges, as it shifts species and ecosystems beyond known regimes of stochastic fluctuations in the environment (novel climate) and species-interactions (novel ecosystems). Although these topics have received considerable attention in the literature, there are few integrative studies and large knowledge gaps remain. Understanding the consequences of complex interactions between different drivers and processes affecting dynamics of species and ecosystems across spatial scales requires large-scale integrative research projects.

The Norwegian research initiative "Sustainable management of renewable resources in a changing environment: an integrated approach across ecosystems" (SUSTAIN) was launched to fill knowledge gaps related to the sustainable management of populations and ecosystems that experience climate change — with a particular emphasis on interacting factors such as population structure and species interactions. SUSTAIN investigated terrestrial, marine and freshwater ecosystems in boreal and Arctic regions (Fig. 1), and was organized around seven case studies within these 3 main ecosystems, including: (1) semi-domestic reindeer in alpine and sub-arctic ecosystems, (2) reindeer, rock ptarmigan and arctic fox in high-arctic tundra, (3) willow ptarmigan in sub-arctic and low-arctic tundra, (4) increasing red fox populations in a tundra ecosystem, (5) moose and small game in boreal forests, (6) fish stocks in the Mjøsa lake, and (7) fish stocks in the Barents Sea. The work included both theoretical developments and empirical analyses of long-term data. This Climate Research Special contains both synthesis articles of the overall work done within SUSTAIN and original research articles that exemplify some of the approaches that were employed.

In this introduction we highlight 4 key topics addressed by SUSTAIN, and also emphasized in the articles included in this Climate Research Special: (i) population structure, (ii) interactions between species, (iii) spatial processes, and (iv) adaptive management. These topics are fundamental to the understanding of harvested species from an ecosystem perspective, and to developing ecosystem-based management approaches.

2. POPULATION STRUCTURE

Population structure, such as age, size and sex structure, plays an important role in determining how harvesting influences population dynamics (Sæther et al. 2001). Different segments of a population (e.g. different gender, age classes) often experience different risks of being harvested (Markussen et al. 2018, 2019, Stubberud et al. 2019). Such biased or selective harvesting is often intentional (e.g. harvest of individuals of specific age or size; Kuparinen & Festa-Bianchet 2017, Nater et al. 2020, Peeters et al. 2022 in this Special), but can also be an unintentional consequence of the way harvesting is carried out (e.g. when harvest is concentrated in areas used by certain types of individuals; Ofstad et al. 2020). Herfindal et al. (2022a in this Special) illustrate how biased harvesting causes fluctuations in the population structure from an individual-based long-term study of an island moose population.

Effects of environmental variation and change on individuals within the population are also known to differ among groups of individuals (Coulson 2001, Sæther et al. 2013, Bleu et al. 2015). Such environmental effects on population dynamics may be delayed when important mediators such as body condition link to weather in one season/year and to e.g. reproduction the next season/year (Herfindal et al. 2015, Henden et al. 2022 in this Special, Nater et al. 2022 in this Special). Thus, the overall impact of environmental variation on population dynamics depends on how sensitive different classes of individuals are to impacts of both harvesting and environmental changes. In some cases, harvesting targets those individuals that are also being most impacted by climate change; in other cases, selective harvesting biases population structure towards individuals that are more sensitive to environmental variation (Berkeley et al. 2004, Rouyer et al. 2011). Explicit consideration of such effects is crucial to avoid unwanted population responses due to harvesting (Gamelon et al. 2019, Lee et al. 2022). In this context, the application of state-of-the art analytical techniques is essential for studies that consider how population structure and life history adaptations affect the resilience of species both to harvesting and to environmental change (e.g. Stubberud et al. 2022 in this Special).
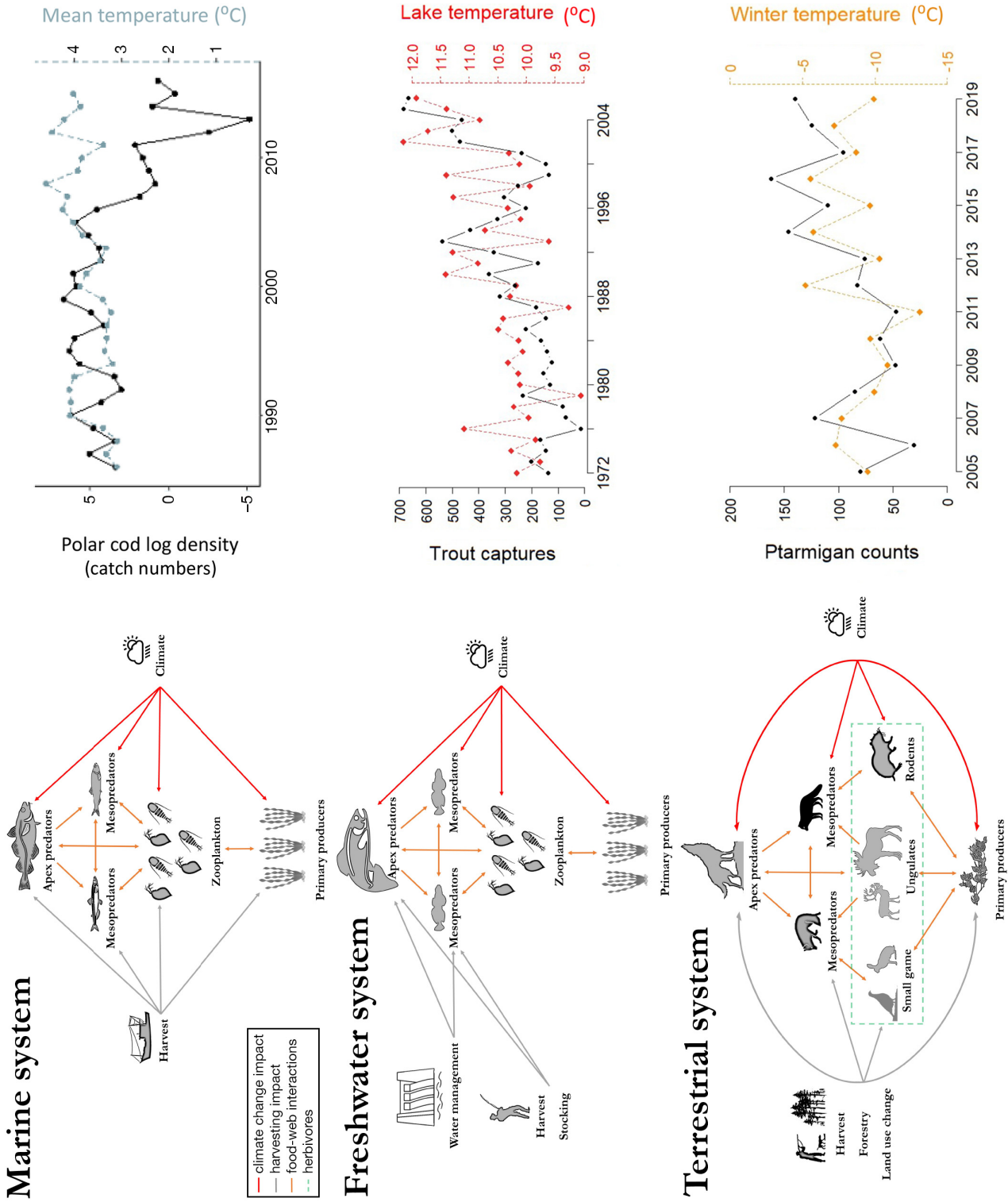
Fig. 1. Case studies in marine, freshwater, and terrestrial ecosystems studied by the Norwegian research initiative "Sustainable management of renewable resources in a changing environment: an integrated approach across ecosystems" (SUSTAIN). The figure illustrates the importance of considering not only the harvested species, but also other interacting species in the ecosystems to understand responses to harvesting pressures. In addition, both harvested and other interacting species may be affected by climatic changes, as the time-series examples illustrate. To sustainably manage harvested species, it is, hence, necessary to account for not only the harvesting pressure, but also for other interacting species and the fact that the whole ecosystem might be affected by climate change

3. INTERACTIONS BETWEEN SPECIES

Natural systems consist of many species that interact with each other in complex ways. Thus, the population dynamics and responses to harvesting and environmental change of one species depend on the dynamics and responses of other species within the ecosystem (Anderwald et al. 2015, Gamelon et al. 2020). This interdependence calls for a multi-species or ecosystem approach to manage harvesting (Levin et al. 2009). Single species harvesting quotas can have serious and detrimental consequences in systems of interacting species, in particular when more than one species is harvested simultaneously (Legović et al. 2010). In fact, in some cases annual yields can be optimized when different types of harvesting strategies are used on different species. Bellier et al. (2021) found that applying proportional harvesting to a prey species and proportional threshold harvesting to its predator gave optimal results when species-specific responses to the environment were accounted for. We know that climate warming can change species interactions and restructure food webs (Bartley et al. 2019, Pecuchet et al. 2020, Tanentzap et al. 2020), making these effects even more complex. Mellard et al. (2022 in this Special), who provide a synthesis of SUSTAIN studies on Arctic harvested species, conclude that adding the food web dimension to predicting changes in harvested population sizes may or may not improve near-term predictions (see also Henden et al. 2020, Marolla et al. 2021). This may be due to data limitation, for instance, leading to inadequate approximations of species interaction in the prediction models. Moreover, multi-driver impacts on complex communities — composed of many interacting species with divergent phenologies — represent a challenge for both establishing causality and making predictions (Moe et al. 2022 in this Special).

4. SPATIAL PROCESSES

Spatial processes involving movement of individuals among localities (e.g. migration and dispersal), along with geographical covariation in the environment, are important for both population dynamics and harvesting yield. Thus, these have been key topics addressed in the SUSTAIN project (Herfindal et al. 2022b in this Special, Melsom et al. 2022 in this Special). The influence of harvesting on population synchrony (see Herfindal et al. 2022c in this Special, Lee et al. 2022) is one spatial process which has only recently received more attention. Shared environ-mental fluctuations, for instance in weather, are known to cause synchronized population dynamics, sometimes over large areas (Moran 1953, Koenig 2002, Walter et al. 2017). Such patterns of spatial synchrony are expected to change as the climate warms (Hansen et al. 2019). Since the spatial scaling of environmental variation is different in marine, limnic and terrestrial systems (Herfindal et al. 2022b,c), climate change-induced changes in population synchrony may also differ among these environments.

Increased population synchrony enhances the global extinction risk (Heino et al. 1997, Earn et al. 2000). However, even if species within a given area and system are experiencing the same environmental conditions, they do not necessarily show the same degree of population synchrony. Differences in the degree of spatial synchrony in population fluctuations are related to dispersal (Lande et al. 1999), life history strategy (Marquez et al. 2019), interspecific interactions (Lee et al. 2020), age structure (Marquez et al. 2021) and sensitivity to environmental variables (Hansen et al. 2019, Herfindal et al. 2020). In addition, the choice of harvesting strategy can strongly influence the patterns of synchronized fluctuations in the size of populations separated in space, sometimes increasing (Engen et al. 2018a,b, Jarillo et al. 2018) and sometimes reducing it (Engen et al. 2018a). Furthermore, population synchrony is influenced by species interactions, and harvest effects on one species can influence the population synchrony of interacting species (Jarillo et al. 2018, 2020), even if they are not harvested (Jarillo et al. 2018). Reviewing different harvest strategies, Lee & Sæther (2022 in this Special) suggest that proportional threshold harvesting may be a good starting point for adapting harvesting strategies in the context of populations and ecosystems subjected to climate change.

5. ADAPTIVE MANAGEMENT

Adaptive management will become increasingly important as climate change causes regime shifts in many ecosystems (Walters 2007). SUSTAIN case studies have dealt with several essential elements of adaptive management, such as strategies for implementing and estimating the effects of management interventions (Marolla et al. 2021, Henden et al. 2022, Nater et al. 2022, Peeters et al. 2022), adapting harvesting strategies to a changing climate (Gamelon et al. 2019, Lee & Sæther 2022, Lee et al. 2022) and the important dialogue between researchers, managers and other stakeholders (Henden et al. 2020,

Mellard et al. 2022). With respect to the latter point, SUSTAIN implemented a Strategic Foresight Protocol (Cook et al. 2014) in its case studies and Hamel et al. (2022 in this Special) summarize the experiences with this protocol. Experience with the Strategic Foresight Protocol demonstrates that the success of such an endeavor depends on the willingness of the people involved, which in turn depends on their availability and opportunities to meet on common ground (both geographically and otherwise). In addition, building social capital among all directly involved participants from the beginning of the process is essential for building the trust needed to ensure an effective functioning among social groups with different interests and values, as has been the case with SUSTAIN. In the most successful cases (e.g. Henden et al. 2020), such a structured way of interacting with stakeholders has had significant influences on the research, and increased the likelihood that SUSTAIN's science will be helpful to the management of species and ecosystems subjected to climate change.

6. THE BROADER CONTRIBUTION OF SUSTAIN

The integrated approach of SUSTAIN clearly shows that management strategies for exploited species must take the expected climatic changes into account. SUSTAIN has, through its comparisons across ecosystems, identified some general points that should be included in developing such sustainable management principles. First, it is necessary to disentangle the effects of harvest from the effects of variation in environmental conditions on population dynamics. Climate change complicates this, requiring more detailed analyses and even better data than previously collected to reduce unintended negative consequences of harvesting, such as population collapse or increased variability in annual yields. Second, alterations of the geographical distribution of exploited species, e.g. caused by changes in climate, can influence species interactions and population fluctuations over large areas. The results from SUSTAIN clearly indicate that an ecosystem-based management strategy must include a spatial perspective that also incorporates non-harvested species. Finally, because future management plans for exploited species must respond to potential environmental changes, adaptive management is key. This approach requires stronger interactions between managers, end-users, and researchers. The Strategic Foresight Protocol used in SUSTAIN illustrates one way to formalize such interactions.

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