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Introduction

Contribution to the Symposium Section: '*Shellfish - Resources and Invaders of the North*'

Cold-water shellfish as harvestable resources and important ecosystem players

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The symposium, *Shellfish—Resources and Invaders of the North*, took place 5–7 November 2019 in Tromsø, Norway. Approximately 110 participants presented and discussed 60 talks and 25 posters. Of these, ten articles are published in this symposium issue. The goal of this symposium was to discuss the role of shellfish, both as harvestable resources and as important ecosystem players in northern hemisphere cold marine environments. To provide perspective for the symposium, the development of four major crustacean fisheries (northern shrimp, snow crab, *Homarus*, Norway lobster) are reviewed. Our review showed that landings of all these fisheries are still in a state of flux due to inherent population dynamics, fishing, and climate change. The talks and posters covered a broad range of state-of-the-art bioecological knowledge and present challenges in the assessment and management of the most ecologically and/or commercially important cold-water shellfish species belonging to the phyla Arthropoda, Mollusca, and Echinodermata. Various alternative harvesting and management techniques were presented along with perspectives for shellfish aquaculture. Methods and models for stock assessment were thoroughly covered as well as the ecological role of shellfish, their population dynamics, new insights into their biology and genetics, and their changing distribution and significance as invasive species.

Keywords: climate change, ecosystem impacts, fishery, harvesting methods, invasive species, natural history, population dynamics, resource management, shellfish, stock assessment

Introduction

Shellfish is the popular name for a wide range of aquatic invertebrates that, for the most part, support their body structures with an exoskeleton or "shell" (exceptions include octopuses, squid, and most sea cucumbers). They include various species of crustaceans, molluscs, and echinoderms. Shellfish are ecologically and commercially important components of marine ecosystems. Some are "ecosystem engineers" that create, maintain, change, or destroy habitats (Jones *et al.*, 1994, 1997). Some clams and mussels aggregate into beds or reefs, modifying the nature and complexity of the substrate to form habitats for other species (Ysebaert *et al.*, 2019); various crab species, such as snow crab (*Chionoecetes opilio*) and the king crabs (*Paralithodes* spp.), may play important roles in structuring the benthic community through predation and perturbation of sediment (Oug *et al.*, 2011, 2018; Boudreau and Worm, 2012); green sea urchin

(*Strongylocentrotus droebachiensis*) through destructive grazing transforms thick kelp forests to barren grounds (Fagerli *et al.*, 2013; Filbee-Dexter and Scheibling, 2014).

Other shellfish serve as important prey resources for higher trophic levels. For instance, krill (*Euphausia* spp.) are the dominant prey of numerous marine mammals such as blue whale (*Balaenoptera musculus*), different species of right whales (*Eubalaena* spp.), fin whale (Balaenoptera *physalus*) and sei whale (*Balaenoptera borealis*; Pauly *et al.*, 1998). Bivalves and gastropods are important prey species for walrus (Sheffield and Grebmeier, 2009); bivalves are also central in the diet of seabirds like eider ducks (Merkel *et al.*, 2006). Northern shrimp (*Pandalus borealis*) is an important part of the diet of a number of fish species (Parsons, 2005), such as Atlantic cod (*Gadus morhua*; Hvingel and Kingsley, 2006; Holt *et al.*, 2020), Pacific cod (Albers and Anderson, 1985), redfish (*Sebastes* spp.), skates (*Rajidae* spp.) (Parsons, 2005 and references therein), and Greenland halibut (*Reinhardtius hippoglossoides*; Chumakov and Podrazhanskaya, 1986).

Shellfish species also provide high-value, high-quality food sources for humans and thereby support major commercial fisheries in cool temperate, boreal and arctic seas (see next section). In 2018, invertebrates accounted for 12.5 million t (14.8%) of the total global capture fisheries production [84.4 million t; FAO (Food and Agriculture Organization), 2020]. Among invertebrates, crustaceans comprised 6.0 million t (48.0%), molluscs 6.0 million t (47.7%), and other invertebrates (e.g. sea cucumbers, sea urchins) 0.5 million t (4.3%). In Arctic to cool temperate waters, particularly important crustacean fisheries include northern shrimp, snow crab, and American (*Homarus americanus*) and Norway lobster (*Nephrops norvegicus*) [Otto and Jamieson, 2001; Penn *et al.*, 2018; FAO (Food and Agriculture Organization), 2020; Gardner *et al.*, 2020].

For all of these reasons, there is a strong interest in shellfish, their population dynamics, and their management in the North Pacific, North Atlantic, and Arctic Oceans. This interest is heightened under climate change, which is already causing native cold-water species to move northward and/or deeper and stressing them at the southern limits of their distribution (Pinsky *et al.*, 2013; Hiddink *et al.*, 2015; Reygondeau, 2019). Some species are shifting into the Low or High Arctic. For instance, the snow crab has expanded its distribution from the eastern Bering Sea into the northern Bering Sea (Zacher *et al.*, 2020) and Chukchi and Beaufort Seas (Feder *et al.* 2005; Bluhm *et al.*, 2009; Divine *et al.*, 2019), where its biomass has been increasing. Northern shrimp are now fished further north off West Greenland—recently fishing has taken place in Melville Bay between 74–76°N (Burmeister and Rigét, 2019). In the Barents Sea, northern shrimp are now found further to the northeast than they were previously (Hvingel and Thangstad, 2019) and the edible crab (*Cancer pagurus*), whose northern boundary stood half-way up the Norwegian west coast, has now extended its distribution to North Cape in northern Norway (Bakke *et al.*, 2018). Concomitantly, major reductions in resource availability for some of the largest shellfish fisheries, like those for northern shrimp and snow crab in the Northwest (NW) Atlantic (see next section), have become a big challenge for fishing-dependent communities. Impacts of these declines on fishing communities have been significant, with cascading economic effects on onshore businesses and municipal revenues used to fund economic (e.g. roads, sewer, water) and social infrastructure (e.g. hospitals, schools; Carruthers *et al.*, 2019).

In addition to changes in distribution and abundance of native invertebrates under climate change, Arctic and subarctic marine ecosystems are subject to invasions by invertebrate species that may lead to unwanted ecosystem effects, as well as new fishing opportunities. An important case study in this regard is the red king crab (*Paralithodes camtschaticus*), which was successfully introduced into the Barents Sea after multiple attempts over 2-3 decades (Orlov and Ivanov, 1978; Hvingel *et al.*, 2012; Windsland *et al.*, 2014). The growing red king crab stock created bycatch issues in the coastal gillnet fisheries (Sundet and Hjelset, 2002) and resulted in concerns about their ecological effects through, for example predation on bottom fauna (Oug *et al.*, 2018). On the other hand, red king crab also provided for a valuable new commercial fishery (Sundet, 2014). Shellfish, including commercially important species, are strong candidates for further natural or human-mediated expansion into or within the Arctic under various projected climate scenarios (e.g. Cheung *et al.*, 2009; Goldsmit *et al.*, 2020). In addition to the impact of these non-indigenous invertebrates, invasion and/or range expansion into Arctic waters by predatory fish species may affect benthic invertebrates through changes in food web structure, including strengthening connectivity between pelagic and benthic compartments of these ecosystems (Kortsch *et al.*, 2015).

Ongoing effects of climate change, and concerns for sensitive species and habitats, raise questions about how best to sustainably harvest shellfish resources from northern waters while minimizing potential negative ecosystem effects. Many shellfish are harvested using traps (pots) and trawls that have differential effects on target species, non-target species, and habitats. Research into new gear technologies is needed to optimize the trade-offs between commercial harvest and adverse effects on species and ecosystems. There is also a need to develop management strategies that provide for sustainability, despite data limitations and changing environments. Thus, the prime motivation for organizing a symposium to discuss the role of cold-water shellfish, both as harvestable resources and as key ecosystem players, was their increasing importance as target species in the capture fisheries of the northern hemisphere over the last 50 years.

The development of fisheries for cold-water shellfish

None of the cold-water shellfish fisheries can compete in volume landed with those of the finfish fisheries for gadoids or pelagic species, such as herring or mackerel. However, when compared by landed value, the difference is much smaller and shellfish fisheries rise to central importance to the national or regional economies in some areas like Alaska, West Greenland, and Atlantic Canada. The four most economically important shellfish species in northern cold temperate and arctic regions are the northern shrimp, snow crab, American lobster, and Norway lobster. These fisheries have undergone a conspicuous development over the last 40–50-year period and are still highly variable due to environmental change and fishing pressure.

Northern shrimp

Northern shrimp is the primary northern hemisphere cold-water shellfish resource. Large fisheries for northern shrimp were established in the Northeast (NE) Pacific and across the North Atlantic during the 1960s (Figure 1). In the North Atlantic, catches increased continuously for >40 years until the early 2000s when an abrupt decline commenced. To a large extent, the increase in the shrimp fisheries was a part of a major change in the composition of species within the marine ecosystem of the NW Atlantic. In the late 1980s, many of the groundfish stocks, in particular cod (*Gadus morhua*), declined to historically low levels (Buch *et al.*, 1994; Myers *et al.*, 1996) while shrimp abundance increased substantially (Lilly *et al.*, 2000; Hvingel, 2006).

The recent decline in world shrimp catches was caused by a decline in shrimp abundance in the NW Atlantic: shrimp stocks started to decline first in their southernmost areas of distribution, like the Gulf of Maine (Figure 2a), and shortly after the international Flemish Cap and Northwest Atlantic Fisheries Organization (NAFO) Div. 3LNO fisheries were closed (NAFO 2015). Quotas were also reduced dramatically further north in Atlantic Canadian waters. Although in some areas, like the Gulf of St. Lawrence, the overall decline can be attributed, at least partly, to predation by a booming redfish stock (Bourdages *et al.*, 2020), the mechanisms behind the decline are not fully understood, but temperature increase and concomitant ecosystem changes are believed to be the main drivers (Wieland and Siegstad, 2012; Jónsdóttir *et al.*, 2013; Richards *et al.*, 2016). Whether this wave of declines in shrimp stocks will continue into Baffin Bay and affect the large fishery off West Greenland remains to be seen.

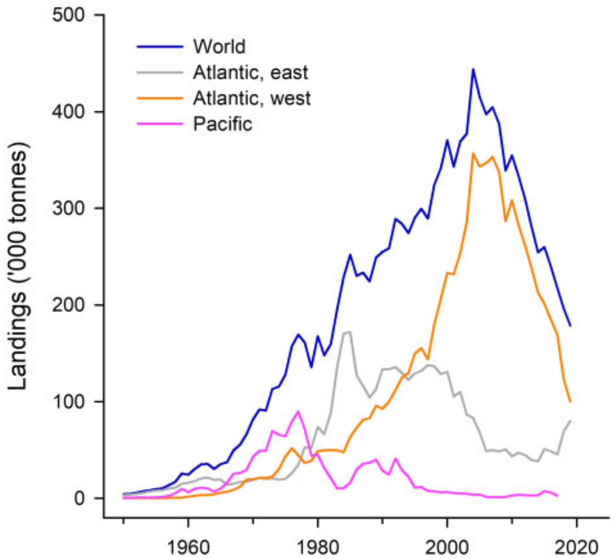

Figure 1. World landings of northern shrimp, *Pandalus borealis* (source: FAO statistics up to 2018 and extended by information from assessment reports and expert knowledge).

Meanwhile, in the NE Atlantic, a recent period of reduced shrimp catches, in the Barents Sea primarily due to economics rather than low stock size, is now transitioning into a sizeable increase (Figure 1). The smaller fishery in the North Sea-Skagerrak area at the southernmost limit of the distribution area is, however, being affected by lower stock size (Figure 2b) following a period of reduced recruitment [ICES (International Council for the Exploration of the Sea), 2020].

In the NE Pacific, a large northern shrimp fishery developed in the Gulf of Alaska in the 1960s and collapsed in the late 1970s and early 1980s. Anderson and Piatt (1999) attributed plummeting catches to recruitment failure and increased groundfish predation owing to warmer temperatures and other ecosystem changes associated with a major regime shift in climate in the late 1970s. A community reorganization ensued, including a decline in species like shrimp and capelin (*Mallotus villosus*), and increases in predatory species like walleye pollock (*Gadus chalcogrammus*) and many species of flatfish. Fisheries for northern shrimp in the NE Pacific have failed to recover as ocean conditions have tended to remain warm and many groundfish stocks have generally remained at high abundance. In many ways, the fisheries of the Gulf of Alaska and Bering Sea showed similar

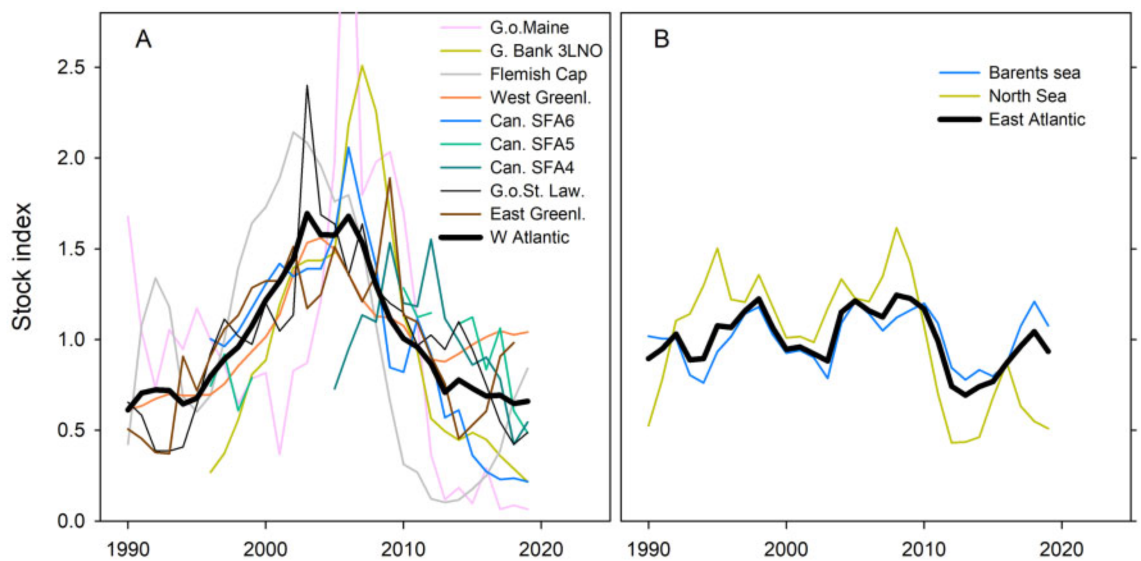

Figure 2. Stock size dynamics of the most important management units of northern shrimp (*Pandalus borealis*) in the NW (a) and NE (b) Atlantic. Values are indices of stock size, scaled to the mean of their time series. The overall indices for the NW and NE Atlantic are the mean of the individual series weighted by the productivity of the stock (i.e. the average annual catch taken from the stock during the period monitored) (data sources: various assessment reports and working documents from ICES, NAFO, DFO, and the Atlantic States Marine Fisheries Commission).

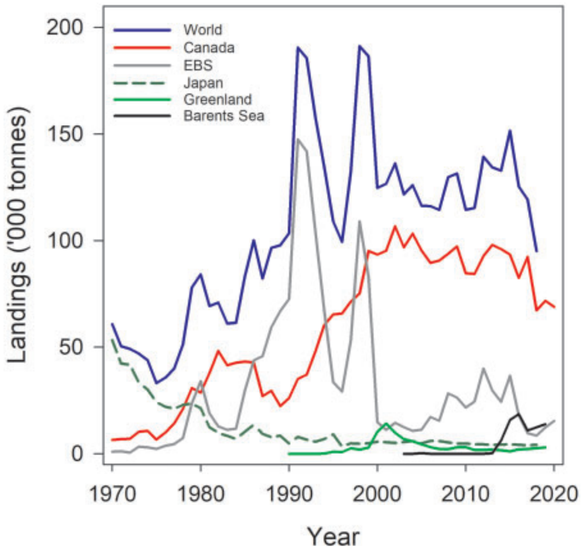

Figure 3. World landings of snow crab, *Chionoecetes opilio*, and contributions from domestic Japanese fisheries, EBS (EBS = domestic United States + Japan until 1981), Canadian Atlantic coast, Greenland, and Barents Sea (Russia and Norway). Some additional landings of *C. opilio* occur in the Japan Sea (by Korea), the Okhotsk Sea, and the West Bering Sea but are not reported or are confounded with landings of other *Chionoecetes* species in the FAO statistics database (source: FAO statistics; Kon, 1996; the 2019 and 2020 preliminary data are from NMFS, Alaska Department of Fish and Game or Canadian databases or assessment reports).

boom and bust sequences as described for the NW Atlantic, however, the precipitous decline happened 25 years earlier in the Pacific (Figure 1). On the contrary, Orensanz *et al.* (1998) considered overfishing as having been more of a determining factor in the decline of the Gulf of Alaska shrimp resource. As there was no shrimp stock assessment, and there were little controls on commercial harvest at that time, it seems likely that fishing was complicit in the decline of northern shrimp stocks that were experiencing reduced productivity associated with the shift in climate regime.

Snow crab

Snow crab has been fished in the Sea of Japan at least since the 18th century. Commercial domestic landings by Japan peaked at 29 000–30 000 t in 1967–1970 (Kon, 1996) and then declined continuously to <6000 t annually since 1996 (Figure 3). In the 1950s, Japanese snow crab fishing expanded into the eastern Bering Sea (EBS) and substantial amounts were landed until the US Magnuson-Stevens Fishery Conservation and Management Act resulted in a ban on foreign fishing in the early 1980s.

Domestic snow crab fisheries in the EBS and along Canada's Atlantic coast started to develop in the late 1960s. In the EBS, there were two sharp spikes (>100 000 t) in landings centred on 1991–1992 and 1998 that were followed by a pronounced decline (Figure 3) and the stock was declared overfished after the 1999 post-season trawl survey due to the mature biomass falling below the minimum stock size. Since then, the landings have varied but always remained ≤40 000 t (Figure 3) and the stock is considered rebuilt. Climate has and continues to play a large role in the distribution and productivity of snow crab in the EBS and is expected to do so in the future (e.g. Orensanz *et al.*, 2004; Murphy, 2020; Szuwalski *et al.*, 2020). In Canada, the snow crab fishery expanded spatially (along the coast and offshore) until the late 1990s to become the world's most important, with average annual landings of 94 200 t over the period 1999–2015 that have since declined by 26% to 69 400 t in 2018–2020 (Figure 3). However, this overall picture masks a more severe 49% decline of the predominant Newfoundland–Labrador annual landings from an average of 54 600 t in 1999–2009 to 27 800 t in 2018–2020 [DFO (Department of Fisheries and Oceans Canada), 2019a; D. Mullowney, Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans (DFO), St. John's, Newfoundland, pers. comm.]. Habitat warming and contraction were identified as the most likely factors driving the decline (Mullowney *et al.*, 2014)—as in the case of the recent collapse of Canada's most southerly snow crab stock in SW Nova Scotia (Zisserson and Cook, 2017)—and were probably compounded more recently by overfishing (Mullowney and Baker, 2020). The decline in Newfoundland–Labrador landings was somewhat offset by generally increasing (although oscillating) landings in the Gulf of St. Lawrence and on the Scotian Shelf, but landings there were lower in the last 3 years due to a recruitment lull that is currently, or soon expected to be, reversed (DFO (Department of Fisheries and Oceans Canada), 2019b, 2020a, b). Retreating north in face of warming may not be an easy option for Canadian snow crab, as the southerly flowing Labrador current is not favourable to poleward larval dispersal along Canada's northeast coast (e.g. Le Corre *et al.*, 2019).

Snow crab harvesting in the Arctic is more recent. Exploratory fishing for indigenous snow crab along the west coast of Greenland started in the early 1990s and commercial landings peaked at 10 000–14 000 t in 2000–2002 but then declined and have been at or below 3000 t since 2006 (Figure 3). The recent invasion of the Barents Sea by snow crab—first observed there in 1996—and the subsequent westward expansion of the species (Agnalt *et al.*, 2011) has created opportunity for a new fishery by Russia and Norway that started in 2013 (Figure 3). The 2012 discovery and subsequent spreading of snow crab in the adjacent Kara Sea to the east (Zimina, 2014; Zalota *et al.*, 2019) suggests that the species is still expanding spatially in the Arctic.

American and European lobster

Commercial fisheries for American lobster were initiated in the 1800s in both the United States and Canada, with total landings rising steeply from the mid-1880s to peaks of about 52 000 t in the late 1880s through the 1890s. Total landings then declined to a low of ∼15 000 t in the mid-1920s and then gradually increased to reach and remain around 30 000 t through the 1950s, 1960s, and 1970s (Ennis, 1986). Starting in the early 1980s total annual landings again began to increase and reached unprecedented levels in 2016–2018, averaging 161 500 t (Figure 4a). Multiple factors, of varying importance depending on region, may have contributed to this latest increase. Initially, these include improved fishing gear technology, spatial fishery expansion and predator release due to the collapse of groundfish, and subsequently climate warming and possibly a rising nutritional subsidy in the form of lobster bait (Drinkwater *et al.*, 1996; Grabowski *et al.*, 2010; Steneck and Wahle, 2013; Le Bris *et al.*, 2018; and see below). In addition, starting in the 1990s, conservation measures aiming to increase egg/larval production (and hence settlement

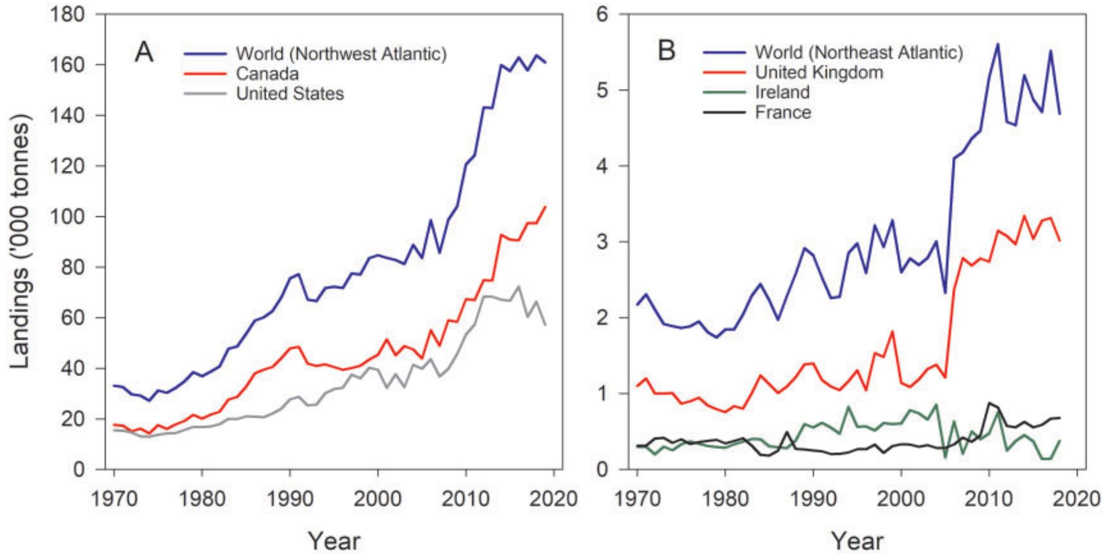

Figure 4. World landings of American lobster, *Homarus americanus* (a), and of European lobster, *H. gammarus* (b), and shares of the countries contributing most to these world landings from 1970 to 2018 or 2019 (preliminary). Note that the sudden upward shift in UK landings in 2006 is likely due to implementation of the Registration of Buyers and Sellers legislation, which increased reporting [ICES (International Council for the Exploration of the Sea), 2016] (source: FAO statistics extended to 2019 for *H. americanus* based on assessment reports or NMFS and Canadian databases).

intensity) were implemented or strengthened in many northerly fishing areas, notably increases in minimum legal size, imposition of a maximum legal size, and v-notching.

The direction and magnitude of change of Canadian and US American lobster landings were largely coherent from 1970 to the early 2010s, but they have increasingly diverged since 2013 (Figure 4a). Canadian landings continued to increase while US landings peaked in 2012–2016 and then declined. This pattern reflects the collapse of American lobster populations in southern New England—the warmest part of the American lobster's range—and the peaking of landings in northern New England and growing productivity in Canadian waters. For example, landings in the north Gulf of St. Lawrence—the most northerly and coldest part of the American lobster's range—have more than quadrupled since 2013 [DFO (Department of Fisheries and Oceans Canada), 2019c].

European lobster has been fished commercially at least since the 17th century (Sundelöf *et al.*, 2013) and landings in the late 1800s and early to mid-1990s in some countries were 1–2 or even more orders of magnitude greater than they have been in the last 5 decades (Dow, 1980; Browne *et al.*, 2001; Sundelöf *et al.*, 2013). Since 1970, annual total landings of European lobster are currently about 30 times less than those of American lobster (Figure 4). On the other hand, total landings of European lobster like those of American lobster have been increasing since the mid-1970s (Figure 4). However, the severely depleted state of European lobster, notably in Scandinavia (e.g. Agnalt *et al.*, 1999), and deficient and spatially inconsistent management measures, may hinder rebuilding of its metapopulation even under favourable environmental conditions.

Norway lobster

Norway lobster (*N. norvegicus*) has been fished in the NE Atlantic for decades, mainly by trawling. However, creeling (trapping) has gained in importance especially in shallower coastal areas with a higher minimum legal size (Ungfors *et al.*, 2013) because there are discard mortality and bottom disturbance issues with trawling (e.g. Raveau *et al.*, 2012; Skold *et al.*, 2018) and creeling may be more profitable (Leocádio *et al.*, 2012). World reported landings of Norway lobster increased to above 60 000 t in 1985. The sudden increase to 70 400 t in 2006 (Figure 5a) is partly due to a new landings registration system in the United Kingdom and Ireland that reduced under-reporting [ICES (International Council for the Exploration of the Sea), 2016]. From 2007, the world landings declined.

Time series of *N. norvegicus* landings are strongly positively correlated ($p < 0.001$) among the main fishing countries in the northern NE Atlantic (United Kingdom, Ireland, Denmark, Sweden), except Iceland, and generally trending upward (Figure 5; Ungfors *et al.*, 2013). Iceland is at the northern limit of the distribution of *N. norvegicus* and landings in 2018 were at their lowest level since 1970 due to poor recruitment since 2005 (Eiríksson and Jónasson, 2018). The temporal landings pattern for the main *N. norvegicus* fishing countries in the southern NE Atlantic (France, Spain) is the reverse (Figure 5), as noted previously by Ungfors *et al.* (2013). A recent meta-analysis found that this same general spatiotemporal pattern was reflected in biomass indices for *N. norvegicus* and demonstrated that fishing mortality was overall much higher in the southern than in the northern NE Atlantic (Vasilakopoulos and Maravelias, 2016). The role of temperature in shaping these patterns, rather than other factors, such as top-down predator control, fishing mortality, and nutritional subsidy via discards, is not yet clear (Ungfors *et al.*, 2013). However, very cold water may impair reproduction and lead to recruitment failure in Iceland (Eiríksson and Jónasson, 2018) and conversely warm water limits the distribution and abundance of *N. norvegicus* in the Mediterranean Sea (Sbrana *et al.*, 2020).

The symposium

There is no doubt that interest in the retreat, or natural and human-mediated expansion, of boreal species to more northerly habitats under climate change, and in the challenges and

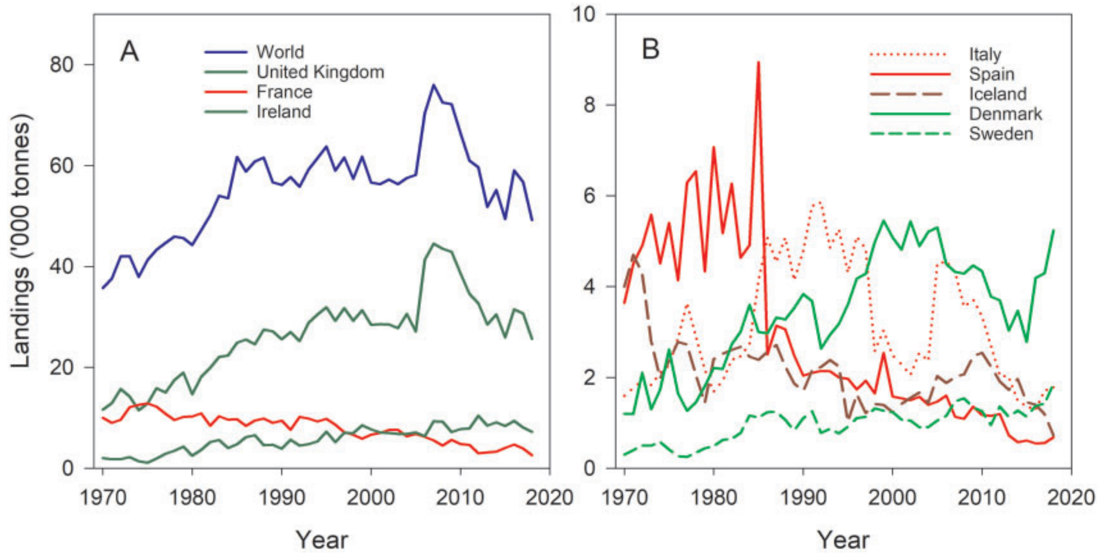

Figure 5. World landings of Norway lobster, *Nephrops norvegicus*, and shares of the three countries contributing most to these world landings from 1970 to 2018 (a). Landings of *N. norvegicus* from the five next most important contributing countries (b). Green lines represent countries with landings trending upward and red lines indicate the reverse trend (source: FAO statistics).

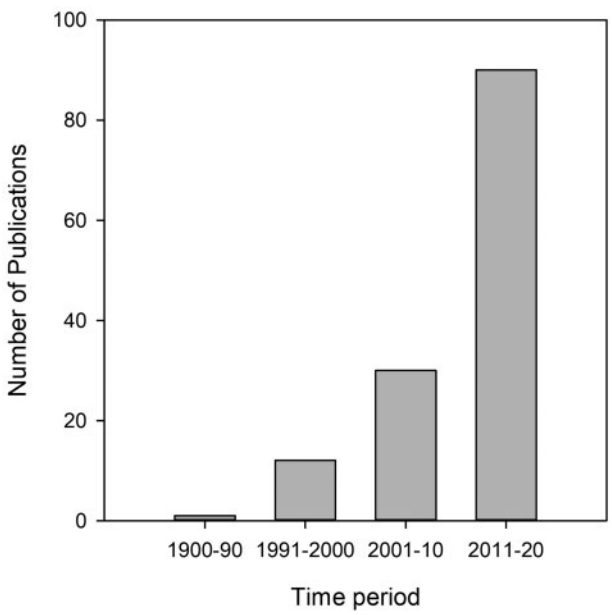

Figure 6. Number of primary publications addressing "arctic", changes in distribution of marine life, and consequent impacts on ecosystem, fisheries, or ocean health from Web of Science v.5.35, Core Collection, all years (1900–2020); search performed 23 August 2020 (further details in Supplementary material S3).

opportunities these range shifts pose to ecosystems, industry and management, has been growing. This is illustrated by the exponential growth in scientific contributions within this theme in recent decades (Figure 6). The symposium—held 5–7 November 2019 in Tromsø, Norway—addressed this through four sessions, titled "Shellfish in new and changing environments", "Managing shellfish fisheries", "New ways of harvesting shellfish", and "Assessment and population dynamics of shellfish". Approximately 110 participants from 12 countries presented and discussed 60 talks and 25 posters within these sessions (list of authors and abstracts in Supplementary materials S1 and S2). Of these presentations, ten are published as articles in this symposium issue.

In the symposium keynote address, Gordon Kruse spoke about snow crab in the EBS and US Arctic as a case study owing to its global importance as a harvestable cold-water shellfish resource in both the North Pacific and North Atlantic Oceans and marginal seas of the Arctic Ocean. It is also a well-studied species that was the subject of 18 oral presentations and seven posters at the symposium. Gordon Kruse discussed the northward shift in this subarctic species owing to warming of the EBS and commensurate increases in their abundance in the US portions of the Chukchi and Beaufort Seas. He noted that snow crabs are challenged by the effects of temperature on their reproductive biology, ontogenetic migration patterns in a changing thermal landscape and dynamic predator-prey associations, and by ocean acidification. He concluded that climate change appears to have mostly negative effects on snow crab population dynamics and that these changes pose major challenges to stock assessment and fishery management as former estimates of stock productivity and fishery management units no longer hold.

Session 1: shellfish in new and changing environments

This was the largest of the four sessions with 20 talks on a wide range of species and topics. Keynote speaker, Richard Wahle (University of Maine, USA), talked about American lobster as a poster child for the impacts of environmental change on coastal ecosystems and economies. In southern New England, mass mortality and disease induced by summer heat stress and hypoxia have led to widespread collapse of the region's fishery. However, lobster have increased in abundance to the north in the Gulf of Maine, benefiting from the positive effects of ocean warming in this cooler part of the species' range and the widespread depletion of predatory groundfish, such as Atlantic cod (Wahle *et al.*, 2020). This triggered an unprecedented boom in lobster production (Figure 4a) that has contributed to elevate the lobster to its current status as the most valuable single-species fishery in the United States and Canada. However, lobster landings in the Gulf of Maine appear to have peaked or started to decline and surveys of young-of-the-year along the New England coast predict a further pronounced downturn in the next decade (Oppenheim *et al.*, 2019). One contributed talk focused on the decline of American lobster in southern New England and future prospects for the species and its fishery in this region (Pugh and Glenn, Supplementary material S2).

The thrust of the contributed talks in this session was the changing distribution and abundance of boreal shellfish species in response to climate change and the impacts on ecosystems and fisheries (nine talks). The recent invasion of Iceland by rock crab *Cancer irroratus* leading to displacement of indigenous brachyurans is one interesting case (Gíslason *et al.*, 2020). Two talks focused on trophic relationships of the non-indigenous snow crab in the Barents Sea, one as an important predator of diverse benthic taxa (Zakharov *et al.*, 2020) and one as a prey of Atlantic cod (Holt *et al.*, 2020). The establishment and spread of the Pacific oyster (*Crassostrea gigas*) in Scandinavia, and the ensuing ecosystem impacts and commercial opportunity for harvest and control of this species, were addressed in two presentations (Freitas *et al.* and Laugen *et al.*, Supplementary material S2). The blue mussel (*Mytilus edulis*) was presented as a clear case of a substantial northerly shift in distribution on both sides of the Atlantic (Strohmeier *et al.*, Supplementary material S2). Two presentations exemplified how modelling can be used to predict distribution of shellfish under climate change: one on non-indigenous bivalves assessed future harvest opportunities through the use of habitat suitability from species distribution models (Therriault *et al.*, Supplementary material S2); the other one reported on changes in spatial patterns of snow crab larval connectivity in the EBS from an individual based model (Stockhausen *et al.*, Supplementary material S2).

Several other talks addressed early (larvae) or later (benthic) life history characteristics of indigenous cold-water species of commercial interest or of non-indigenous species in their new northern habitats, and the implications of these traits for sustainable harvest or further range expansion. Finally, one talk reported on the effects of temperature on growth and moulting of snow crab (Sainte-Marie *et al.*, 2020) and another one considered temperature effects on genes regulating growth and moulting of red king crab (Andersen *et al.*, Supplementary material S2). This represents important information for understanding productivity of these resources in their native and new habitats.

Session 2: managing shellfish fisheries

There were 16 talks in the session "Managing shellfish fisheries", which began with two keynote presentations. Jahn Petter Johnsen (Norwegian College of Fishery Science, UiT, The Arctic University of Norway) talked about how to govern ungovernable objects. Until the establishment of the Norwegian exclusive economic zone (200 nm) in 1977, the resources in Norwegian waters were in principle ungovernable, but with the new framework, peoples' activities could be regulated in effective ways. Through this change, industry became a partner in governance. Over time both the ability to govern, and the willingness to be governed, increased. In the second keynote Elisabeth Sørdahl on behalf of Vidar Landmark (Ministry of Trade, Industry and Fisheries, Norway) spoke about the four main elements of the Norwegian national fisheries management: research, regulatory measures, enforcement and sanctions. She pointed out that catch capacity is regulated to enhance efficiency and profitability for the fishing fleet, and technical measures and quotas coupled with strict enforcement measures are used to ensure sustainability. She stressed that good knowledge and scientific advice is the key to good fisheries management and highlighted the Norwegian management of the introduced red king crab both as a resource and an ecological threat as an example of such successful management.

Red king crab was also the subject of several other presentations. One gave an overview of the relatively new fishery for this species and its management, highlighting an eastward shift in the distribution of this stock (Sokolov and Bakanev, Supplementary material S2). Another, Stesko and Bakanev (2020), addressed the associated management issues as this change in the distribution has led to increased overlap with the traditional bottom-trawl fisheries resulting in bycatch problems. Some presentations looked at different approaches to crab stock management and their implications for the sustainability of the resource, two of them with particular focus on bioeconomic trade-offs in the Barents Sea red king crab fisheries (Fernandez *et al.* and Kaiser *et al.*, Supplementary material S2).

Snow crab in the Barents Sea is not just a new resource but may also have effects on the ecosystem. One presentation applied ecosystem modelling to evaluate ecosystem effects of the crab invasion, different management strategies and how and where the species can spread and settle in the Barents Sea in the future (Hansen *et al.*, Supplementary material S2). Another presentation dealt with how access to this new fishery could be regulated (Nøstvold and Voldnes, Supplementary material S2) and yet another presentation considered the problems of ghost fishing by abandoned traps following changes in stock management procedures (Eliassen *et al.*, Supplementary material S2). Mullowney and Baker (2020) addressed the challenges involved in the management of the fishery on a snow crab stock that is also impacted by changes in ocean climate. When the environmentally forced reduction in productivity is not fully compensated for by a reduction in catches, exploitation rates increase and successive changes take place like declines in size-at-terminal moult in males, which may impact mating dynamics and also the behaviour of the harvesters.

Management questions in scallop and Norway lobster fisheries were also addressed. One talk addressed the Islandic scallop (*Chlamys islandica*) fishery in the Russian portion of the Barents Sea, where the stock was severely overfished, and the fishery has been closed since 2018 (Manushin *et al.*, Supplementary material S2). It was suggested that young scallops experienced high discard mortality associated with the use of automatic catch processing, and concerns were expressed about impacts on scallops of heavy dredges that result in injuries and gill clogging by suspended sediment. In addition, the invasive red king crab may have contributed to the scallop decline as stomach analysis revealed that crabs fed on scallop fishing waste, damaged scallops, and young scallops with thin shells. Proposed solutions include reduction of fishing mortality, use of hand-sorting only, and spatial management (rotational fishing areas). Another talk reported on the use of genetics to evaluate the spatial management of a Norway lobster fishery in the "Norwegian Deep, Skagerrak and Kattegat" region (Westgaard *et al.*, Supplementary material S2). This region is divided into two management units: Skagerrak/Kattegat area and the Norwegian Deep, which are managed separately with quotas established by ICES. The study suggested no population genetic differentiation among lobsters from the two management units. Although separate area management is not supported by the microsatellite analysis, it was recognized that other reasons can be invoked to manage areas separately. Catches, fishing pressure, monitoring, and regulation differ among the two management areas.

Session 3: new ways of harvesting shellfish

The session "New ways of harvesting shellfish", was comprised of nine talks including a keynote by Bradley Stevens (University of Maryland Eastern Shore, USA) (Stevens, 2020). He discussed benefits and disadvantages of traps (pots) as fishing gear. He pointed out that little research has been conducted on the response of target species to traps or the impacts of trap fishing. He further noted that trap impacts fall into three categories: direct impacts on target populations, impacts on non-target populations including pelagic fish used as bait and marine mammals at risk of entanglement, and impacts on environment or habitat. After reviewing their effects, he concluded that the future of trap fisheries will depend on investment in research on new ways to reduce their negative impacts on benthic and pelagic resources.

Other presentations in this session addressed issues related to snow crab fisheries such as alternative baits fabricated from the waste stream from seal (*Pagophilus groenlandicus*) and minke whale (*Balaenoptera acutorostrata*) capture (Araya-Schmidt *et al.*, Supplementary material S2), and the potential of light and sound to enhance crab catch rates (Donovan *et al.*, Supplementary material S2). A scheme for quantifying the welfare of crabs after capture was presented and seen as a tool in the sorting of crabs for processing, live holding, export or slaughtering (Voldnes and Nøstvold, Supplementary material S2). The importance of product quality for a profitable industry was also pointed out in other presentations, e.g. one looked at how different processing methods and freezing affect the quality of snow crab leg clusters (Lorentzen *et al.*, Supplementary material S2).

The red king crab caught in Norwegian waters is to a large extent exported live right after capture: one presentation dealt with live holding of crabs onshore as a tool to even out seasonal variations in quality and enhance the control of the export industry for this product (Lian *et al.*, Supplementary material S2). Live holding and transport were also the theme of a presentation focusing on shrimp caught in a trap fishery (Larssen *et al.*, Supplementary material S2).

Session 4: assessment and population dynamics of shellfish

The session on "Assessment and population dynamics of shellfish" included 16 talks. The keynote address was delivered by Cody Szuwalski [National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center, USA]. He spoke about his experiences in conducting stock assessments of crab resources in the EBS, USA. He pointed out that one of the key challenges faced in assessing Bering Sea crab is estimating reference points because no clear stock-recruit relationships exist, and population dynamics appear to have changed over time. He described several case studies and provided an overview of an open-source assessment platform designed to streamline the stock assessment process (General Model for Assessing Crustacean Stocks, https://seacode.github.io/gmacs/).

Several talks in this session described surveys used to assess shellfish resources, including dredge/video surveys of sea urchins (Thorarinsdottir, Supplementary material S2), multi-species dive surveys at selected index sites (Bureau and Lochead, Supplementary material S2), and the use of a bio-sampler (cod) to estimate the abundance of the invading snow crab in the Barents Sea (Hvingel, Holt *et al.*, Supplementary material S2). Mesquita *et al.* (2020) used "bycatch data" from scientific surveys, one directed at scallops and one at groundfish, to provide a first-time description of the spatial distribution and population dynamics of the data-poor stocks of brown crab around Scotland. The methods described have potential use also for other data-poor stocks. A Norway lobster stock index based on trawl survey data in Skagerrak and Norwegian Deep using advanced modelling techniques was presented (Hvingel, Søvik *et al.*, Supplementary material S2); in another presentation on the same species, the use of fishery data in a newly started trap fishery was investigated (Kleiven *et al.*, Supplementary material S2).

Four talks focused on assessment and advisory questions related to shrimp, ranging from the development of reference points (Zhang *et al.*, Supplementary material S2), the use of no-take zones in fisheries (Zimmerman *et al.*, Supplementary material S2), management of small fjord populations, to an evaluation of the assessment framework used for the largest stock of northern shrimp off West Greenland over a 20-year period (Hvingel, Burmeister *et al.*, Supplementary material S2). An assessment procedure for red king crab off northern Norway that was able to estimate stock density in areas with no data collection was presented along with potential future distribution of this introduced species (Hvingel, Nilssen *et al.*, Supplementary material S2). Distributional aspects were also the theme of a presentation about the great scallop *Pecten maximus*; recruitment appears to have improved in the northernmost areas following a period of warming (Grefsrud *et al.*, Supplementary material S2). Finally, generalized additive models were used to analyse European lobster *Homarus gammarus* moult increment data collected from the Adriatic Sea to northern Norway (Coleman *et al.*, 2020). Latitude was a significant predictor of moult increment, but with low explanatory power. The largest growth increments were observed in the centre of this species' range, with smaller moult increments at southern and northern latitudes, suggesting an optimum temperature for growth.

Conclusion

Important fishery resources such as northern shrimp, American lobster, and snow crab are declining in the southern part of the native range and generally increasing in the north; the multifaceted factors involved are increasingly well understood. Modelling holds promise for projecting future distributions and harvest opportunities. However, adjusting fishing intensity in the context of environmental change (and highly variable population distributions and dynamics) is a great challenge, whether for indigenous or non-indigenous species, and particularly at the current extremes of their range. Fishing and climate may affect not only distribution and abundance but also the species traits that make a resource desirable (e.g. size-at-terminal moult in snow crab). Ecosystem approaches to management are needed because of the interactions of many shellfish with top predators including other major resources (groundfish) or endangered species. Such approaches, in conjunction with bioeconomic considerations, are increasingly required both to maximize harvest revenues and to optimally manage invading species.

The environmental cost of fishing, for instance impact on habitats, bycatch, bait species and the risk of ghost fishing, is also gaining increased attention. Methods for the quantification of impacts, as well as the engineering of better/low impact fishing methods, are being developed to provide new tools for fisheries management. In addition, the development of new fishing practices also seeks to enhance the value of harvested resources itself, e.g. through live-hold and live-export, as well as best processing practices for highest quality end-products. Shellfish, in many instances already being a high-value product, are for that reason at the forefront of this development.

Extirpating invasive/introduced species of commercial interest and attempting to counter or delay climate change effects through ecosystem engineering does not seem to be a viable option with greenhouses gases still increasing and given the harvest opportunity these species provide to communities that are losing other sources of income. In the case of the red king crab, even an unregulated fishery on this high-value species has not been able to stop its spread along the Norwegian coast.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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