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Expansion of hagfish fisheries in Atlantic Canada and worldwide

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ABSTRACT

Over the past 60 years, low-trophic level fisheries have greatly expanded in terms of landings, target species, and the number of countries fishing, and are now prominent around the world. Hagfish (family Myxinidae) have been commercially fished in Asia since the 1940s where their skin is used as leather and their meat for human or animal consumption. Since the 1980s, the animals have been increasingly exploited on a global scale. Using landings and effort data supplied by government agencies and extracted from published literature, as well as government reports and assessments, we analyzed spatial and temporal patterns in hagfish fisheries in Atlantic Canada and worldwide. Exploitation patterns have been driven by the Asian market; after local hagfish stocks were depleted in the 1980s, fisheries expanded sequentially to the West and East coasts of North America and into New Zealand. In addition to strong spatial expansion, our results reveal some serial depletion patterns around the world, as previously documented in sea urchin and sea cucumber fisheries. In Atlantic Canada, the hagfish fishery has strongly expanded over the past 20 years with a 24-fold increase in both annual landings and fishing effort and a 10-fold increase in the number of NAFO units fished. The spatial expansion has been accompanied by some serial depletion of individual regions. Overall, hagfish fisheries around the world have not been very sustainable over the past 70 years. Given the poor knowledge of hagfish populations and their response to fishing, coupled with limited stock assessments and fisheries regulations, it is doubtful that current hagfish fisheries are more sustainable.

1. Introduction

Global fisheries have experienced major changes in the late 20th and early 21st century: while finfish catches peaked in the 1980s and have declined or remained stable since the early 1990s, catches of lower trophic levels (TL 2–3), particularly invertebrate species (e.g. echinoderms, bivalves, gastropods and crustaceans) and forage fish (e.g. anchovy, sardine, herring, mackerel and capelin) have continued to increase (Pauly et al., 2002; FAO, 2010; Anderson et al., 2011a; Smith et al., 2011). During 1950–2004, the number of countries reporting landings of invertebrates to the Food and Agriculture Organization (FAO) increased 1.5-fold, reported landings increased 6-fold (from 2 to 12 million mt), and the mean number of invertebrate taxa fished per country doubled (Anderson et al., 2011a). Unfortunately, knowledge about populations or stocks of many emerging, low-trophic level target species is often limited, which can hamper efficient management and conservation (Anderson et al., 2008). Thus, an increasing proportion of invertebrate fisheries have been estimated as overexploited (Anderson et al., 2011a).

Several low-trophic level species have substantial market value, which drives the expansion of their commercial exploitation locally and on a global scale (Berkes et al., 2006; Anderson et al., 2011a,b). If local resources cannot meet the ongoing or growing demand, fisheries expand spatially (Berkes et al., 2006). In some cases, this coincides with a serial depletion, whereby the fisheries closest to the market are depleted first and successively replaced by fisheries farther away. Such spatial expansion and serial depletion have been described for sea urchins and sea cucumbers driven by demand in Asian markets (Berkes et al., 2006; Anderson et al., 2011b), and historically for oysters in North America and Australia (Kirby, 2004). In this paper, we investigate whether recent trends in fisheries for hagfish, another increasingly valued low-trophic level species highly prized for its leather, follow similar patterns of spatial expansion and serial depletion in Atlantic Canada and worldwide.

Hagfish are benthic, eel-like organisms found in temperate marine regions worldwide, including the Gulfs of Mexico and Panama (Nelson, 2006). They are classified as basal vertebrates, or

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craniates, making them the closest ancestor to the vertebrate line (Nelson, 2006). Currently, there are 76 described species of hagfish (Knapp et al., 2011; www.iucnredlist.org), including 2 recently discovered ones (Fernholm and Mincarone, 2010; Kuo et al., 2010) and at least 4 awaiting formal description (Martini and Beulig, 2013). Of these, nine species are listed under one of the International Union for the Conservation of Nature's (IUCN) Red List Categories as Critically Endangered (1), Endangered (2) and Vulnerable (6), and 30 are listed as Data Deficient. Hagfish are extensive burrowers; with their eel-like form and mucous secreting glands, they are perfectly adapted for life in sandy and silty substrata (Martini, 1998). This life style, however, makes accurate abundance estimates difficult to obtain (Martini, 1998).

Traditionally, hagfish were fished in Asia (e.g. Japan and Korea) for food and as bait (Gorbman et al., 1990; Honma, 1998; Martini and Flescher, 2002). A large expansion in the Japanese fishery during the 1940s, when other fish stocks were being exhausted (Honma, 1998), and in Korea into the 1980s (NEFSC, 2003). Since the 1980s, fisheries for hagfish also developed in other parts of the world (NEFSC, 2003). Currently, hagfish are highly prized for their skins as a source of leather, but also for their meat as food for humans and animals, and their slime in cleaning agent production (Gorbman et al., 1990; NEFSC, 2003). Processing of hagfish skins takes place almost exclusively in South Korea, where hagfish are received alive, iced or frozen (Gorbman et al., 1990). Between 1997 and 2001, 'eelskin', believed to be primarily hagfish skins, comprised 91% of fish leather imports to the United States (US) (Grey et al., 2006). Commercial hagfish fisheries use baited traps, traditionally woven from bamboo, but now largely plastic, which are deployed for 25–50 h (Gorbman et al., 1990). Grant (2006) found that significantly larger individuals were caught at greater depth, and smaller escape holes resulted in greater retention of juveniles. As a management strategy, Barss (1993) suggested gear restrictions and seasonal limits.

The goal of this study was to evaluate whether current trends in hagfish fisheries show similar patterns of spatial expansion and serial depletion as observed in sea urchin and sea cucumber fisheries. First, we compiled all available landings and effort data and other information on hagfish fisheries from around the world and compared their temporal and spatial trends. Then, we analyzed how the expanding hagfish fishery in Atlantic Canada has changed over time with regard to geographic extent, fishing effort, landings and catch per unit effort (CPUE). Together, our analyses provide a comprehensive overview on current trends of hagfish fisheries in Atlantic Canada and worldwide.

2. Materials and methods

2.1. Data sources

Fisheries landings and effort data, as well as information on fisheries regulations and management, were obtained from applicable government agencies and extracted from published scientific articles, as well as government reports and regional or national fisheries assessments as available. We also contacted regional fisheries biologists to obtain information on hagfish fisheries in different parts of the world. Our aim was to obtain available data for recorded fishing effort, annual landings, including peak and minimum landings, and start and end dates of the individual fisheries around the world. Data reporting for regional fisheries was inconsistent; in many cases only annual landings data were available, whereas some fisheries reported landings per day. We were able to compare annual landings, as well as start and end dates of fisheries for all regions, whereas in Atlantic Canada, we were able to also analyze fishing effort and catch-per-unit-effort (CPUE).

The global FAO database on reported fisheries catches does not have detailed records on hagfishes. Thus, all available data were obtained from regional and national marine fisheries organizations, along with the few published articles on hagfish fisheries in Japan, Canada, the US and New Zealand (Table 1). In Canada, data were subdivided by region (Atlantic Canada and British Columbia) and in the US by states (see below), due to the countries' large geographic size, distinct fisheries management approaches, and different data reporting. To double-check the data, we compared the numbers taken from databases with those in published articles wherever possible. For consistency, we used 2010 as the cut-off date.

For Atlantic Canada, data were obtained from the Canadian Department of Fisheries and Oceans (DFO, Commercial Data Division Request) and included: date, Northwest Atlantic Fisheries Organization (NAFO) fishing unit, catch per day (kg/day), the number of days fished and gear type if available. No published scientific articles covered the entire Atlantic region or individual provinces. However, Grant (2006) confirmed and outlined the timeline of the fishery in Newfoundland, which was also detailed in DFO (2012). Gear type was not analyzed because in many cases that information was not available. The Atlantic Canada fishery generally uses baited traps; however some changes may have occurred in trap design (e.g. size of trap, number and size of escape holes) over time. For British Columbia, a published review of the fishery (Leask and Beamish, 1999) cited annual landings data that varied slightly from the Pacific DFO database (http://www.pac.dfo-mpo.gc.ca/stats/comm/summ-somm/index-eng.htm). To remain consistent, we used the DFO data when there were irregularities between datasets.

The US landings data were compiled by state from the National Marine Fisheries Service (NMFS) database (http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html) and were limited to catch per year. Any other US landings referred to in published articles were also taken from the NMFS database. One exception was the Californian fishery where the NMFS data did not exactly match those from the California Department of Fisheries and Game (CDFG, http://www.dfg.ca.gov/marine/fishing.asp#Commercial), although overall trends were the same. Again, to remain consistent, we used the data provided by NMFS on all occasions except during years of no reported catch; in such cases we used the CDFG data for that year if they had reported landings.

Data for New Zealand were provided by the New Zealand Ministry of Primary Resources (MPI) official reporting system (http://www.fish.govt.nz/en-nz/default.htm) and included annual landings data. Catch data for the Japanese fishery was limited to the landings data reported by Gorbman et al. (1990), which was provided by the Izumozaki Cooperative Fisheries Association (a commercial fishery on the western coast of Japan) and did not include landings for the entire country. These data were also limited by the start date of data recording; the earliest date of reporting was 1962.

We could not find hagfish landings for Korea, but did obtain a general description of the hagfish fishery development (NEFSC, 2003). We could also not find data on hagfish fisheries in any other country around the world, so we contacted fisheries experts in Australia and Europe, including the United Kingdom, Ireland, France, Germany, Norway, Denmark and Sweden, as well as a specialist on worldwide hagfish fisheries (Frederic Martini, personal communication 2011). However, there appear to be no other reported commercial hagfish fisheries at this point.

2.2. Global trends in hagfish fisheries

To derive spatial and temporal patterns in hagfish fisheries around the world, we compared trends in available landings

Table 1
Sources of hagfish landings and fisheries regulations and the different regulatory measures employed in each region as of 2010 or last reporting: F = state of the fishery, LB = logbook required, P = number of permits issued, T = maximum number of traps permitted per license, B = bycatch permitted. Y = yes, N = no, ? = unknown, NMFS = US National Marine Fisheries Service, DFO = Canadian Department of Fisheries and Oceans.

Fishery	Sources: regulations	Sources: landings	F	LB	P	T	B
Japan	Gorbman et al. (1990)	Gorbman et al. (1990)	Open access	?	?	?	?
California	T. Tanaka, California Department of Fish and Game (CDFG)	NMFS, CDFG	Open access	N	Unlimited; General trap permit	200 bucket traps or 500 Korean traps	N
Washington	L. Wargo, Washington Department of Fish and Wildlife (WDFW)	NMFS, WDFW	Trial	Y	20	Max 100	N
Oregon	T. Buell, Oregon Department of Fish and Wildlife (ODFW)	NMFS	Developmental	Y	25	Max 200	N
British Columbia	Leask and Beamish (1999) and Benson et al. (2001)	DFO, Leask and Beamish, 1999	Experimental, exploratory	Y	11	2000–3500 Korean traps	N
Atlantic Canada	Grant (2006) and DFO (2009)	DFO	Commercial, experimental, exploratory	Y	9	200–500	N
Maine	S. McNamara, NMFS; H. Bray, Maine Department of Marine Resources (DMR)	NMFS	Open access	N	Unlimited	Unlimited	Y
Massachusetts	S. McNamara, NMFS	NMFS	Open access	N	Unlimited	Unlimited	Y
New Hampshire	S. McNamara, NMFS	NMFS	Open access	N	Unlimited	Unlimited	Y
New Zealand	J. Oliver, New Zealand Ministry of Primary Resources (MPI)	MPI	Open access	N; but reporting forms	Unlimited; General commercial fishing permit	Unlimited	Y; but depends on species

records across regions and over time. We tested for spatial expansion patterns by comparing the best available estimates of start dates of all regional and national fisheries and geographically tracking these start dates over time with respect to the original market in Asia. Since a real start date for the Japanese hagfish fishery was lacking, we used 1940 as the start date because the hagfish fishery strongly expanded during World War II (Honma, 1998). For Korea, we could not find a start date and only included this region in the descriptive part of this analysis. Next, we evaluated whether spatial expansion was accompanied by serial depletion, by checking whether the peak and decline of one fishery was followed sequentially by the peaks and declines of other fisheries. We also analyzed whether the "time to peak", which is the time from the start to the peak of a fishery, progressively decreased over time, as reported for sea cucumber fisheries (Anderson et al., 2011b). To do so, we recorded the date of the largest annual landings and compared the time-to-peak relative to the start date across all fisheries using linear regression. When a fishery was still expanding and had not peaked yet, we used the last year of recorded landings as the peak year, knowing that this is a minimum estimate.

To gain more information on the management strategies adopted by different countries for their respective hagfish fisheries, we compiled as much information as possible on access to the fishery, whether permits and logbooks were required and whether there were restrictions on the number of traps and bycatch.

2.3. Temporal and spatial trends in Atlantic Canada

To determine temporal trends in the hagfish fishery in Atlantic Canada, we analyzed total annual landings (in metric tonnes, mt), fishing effort and CPUE. Given the lack of other consistent effort data across all NAFO areas, such as duration of fishing trips, number of traps or number of boats, we used the number of days fished per year as the metric for fishing effort. CPUE was then calculated as the average landings per day in a given year. Because several fishers could fish for hagfish at any given day, the total number of fished days per year could exceed 365 days. In some instances, multi-day trips had reported all catch on one landing day, which would have inflated the catch-per-day estimate. In DFO's data base this was dealt with by splitting the overall catch into equal portions for each day fished; however, in a few cases we ran into highly inflated catch-per-day estimates and had to cross-check with DFO to insure we had accurate data. The same issue may have occurred in less obvious catch-per-day estimates, indicating that more effort needs to be placed on standardized data reporting.

Spatial trends in the hagfish fishery were assessed using landings records for each NAFO fishing unit provided by DFO. We calculated the number of NAFO fishing units being fished each year and at the start of each decade, and mapped the spatial expansion of the fishery over time. To test whether the spatial expansion was associated with signs of serial depletion, we checked whether a peak and decline in catches or CPUE in one NAFO area (e.g. 4X) was followed by an increase in another area. We repeated this within selected NAFO areas to also compare catches and CPUE among subareas (e.g. 4XU, 4XO).

3. Results

3.1. Data sources

Overall, data on hagfish fisheries are scarce and not recorded in detail at the FAO. Regional fishery experts in the United Kingdom, Ireland, France, Germany, Norway, Sweden, and Denmark were contacted regarding any hagfish fisheries in different parts of the Northeast Atlantic and from Australia regarding fisheries in their respective regions. None of the fishery experts reported either commercial or experimental hagfish fisheries in their respective regions. In total we found 12 regions that had commercial hagfish fisheries: Japan, Korea, California, Oregon, Washington, British Columbia, Atlantic Canada, Massachusetts, Maine, New Hampshire, Connecticut and New Zealand. However, we could not find landings data for Korea, and Connecticut reported only 70 pounds in the year 2001 and was therefore excluded from further analysis (Table 1). There have been reports that fishery scientists in other regions with no commercial hagfish fishery have been approached with the prospect of opening a fishery, so far to no avail (Bo Fernholm, personal communication, 2011).

3.2. Global trends in hagfish fisheries

Trends in individual regional fisheries display a high level of variability (Fig. 1). Although traditional fisheries for hagfish have occurred in several parts of Asia (Korea, Japan), the earliest commercial hagfish fishery began in Japan, where it strongly expanded during World War II (Gorbman et al., 1990; Honma, 1998). Recorded landings of part of the country are available since 1962, with highest landings at the start of the time series. Following the drastic decline of the Japanese fishery towards the late 1980s, and the collapse of the Korean fishery in the early 1990s (NEFSC, 2003), nine other regional fisheries emerged in North America and New Zealand supplying the Asian market with hagfish. Of the eight North American fisheries, only Atlantic Canada and Oregon have shown continuous increases in landings for more than a decade. The fisheries in California, British Columbia and Maine peaked very sharply with either very low or no landings in the following years. In Washington and New Zealand, the fisheries have recently had sharp increases in landings with the highest values in 2010. The Massachusetts fishery peaked in 2000, with much lower landings afterwards, and there was only one year of fishing reported in New Hampshire (Fig. 1).

Comparing the landings trends and the start, peak and end dates across regions, global hagfish fisheries have exhibited spatial expansion and some serial depletion patterns (Figs. 2 and 3). Based on start dates, the fishery first expanded from Japan eastward to the West coast of North America in the 1980s and the East coast in the 1990s, and more recently southward to New Zealand in 2001 (Fig. 2). Following the decline of the Japanese fishery, another four fisheries (Korea, British Columbia, Massachusetts and New Hampshire) have either collapsed or been shut down as of 2010 indicating some serial depletion (Fig. 3A). Of the remaining six, which had landings reported in 2010, two had already peaked within 8 years of starting (California, Maine) while the remaining four fisheries continued to expand with highest landings reported in 2010. We note, however, that landings in New Zealand have declined since 2010, which was the peak year, Oregon so far reported peak landings in 2011 and Washington in 2012, and only in Atlantic Canada landings continue to increase (Hugues Benoit, personal communication 2014). There was limited evidence for a shortening of the time-to-peak (Fig. 3B, linear regression: $p > 0.1$, $R^2 = 0.23$). However, the time-to-peak for Japan represents a minimum estimate (likely starting much earlier than 1940) which would strengthen the pattern, and the start date of the Korean commercial fishery which peaked sometime in the mid-1980s is unknown. New Zealand peaked in 2010, Oregon in 2011, and Washington in 2012, all supporting the shown pattern. Only Atlantic Canada has been active for more than 20 years, with no evidence of a peak in the fishery as of 2014 (Fig. 1; Hugues Benoit, personal communication); thus, a larger time-to-peak estimate for Atlantic Canada would weaken the shown pattern (Fig. 3A).

Several of the hagfish fisheries had some management strategies put in place, yet the realized approaches varied widely (Table 1). Little is known about the Japanese and Korean fisheries; there were few landings records kept in English and even less information on monitoring and regulations (Gorbman et al., 1990). In other regions, some governing agencies have opted for more stringent regulations with relatively low numbers of permits and traps per boat, such as Washington, Oregon, and Atlantic Canada (Table 1). In Oregon, for example, there is a harvest guideline of 1.6 million pounds (725.75 mt) that, if exceeded, requires public consultation (Troy Buell, personal communication 2012). Other regions have adopted

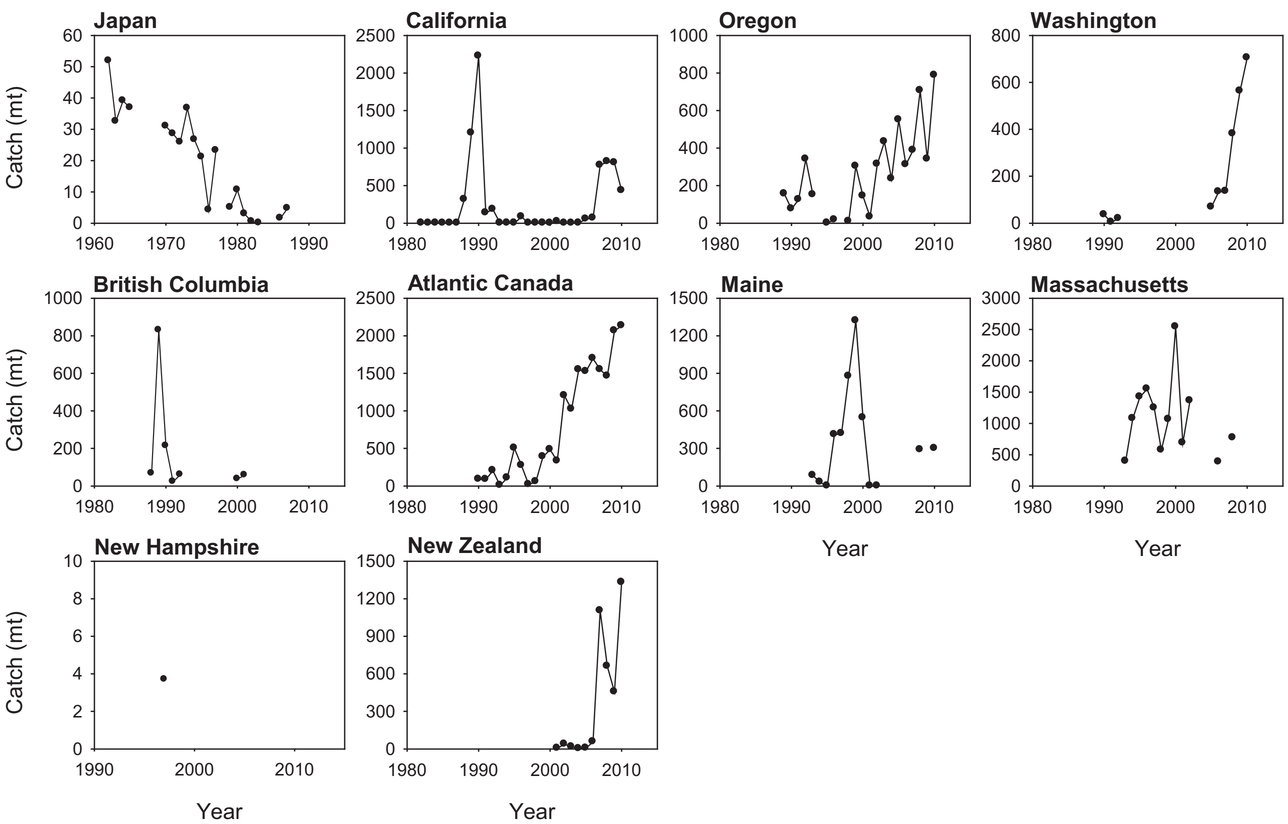

Fig. 1. Trends in reported annual hagfish landings by region. Note that data for Japan only represent landings of a part of the country (Gorbman et al., 1990). The fishery in Maine continued until 2010 but the number of boats was too small to allow the landings data to be accessible to the public for some years; New Hampshire reported landings for 1 year only (data sources are listed in Table 1 and Section 2.1).

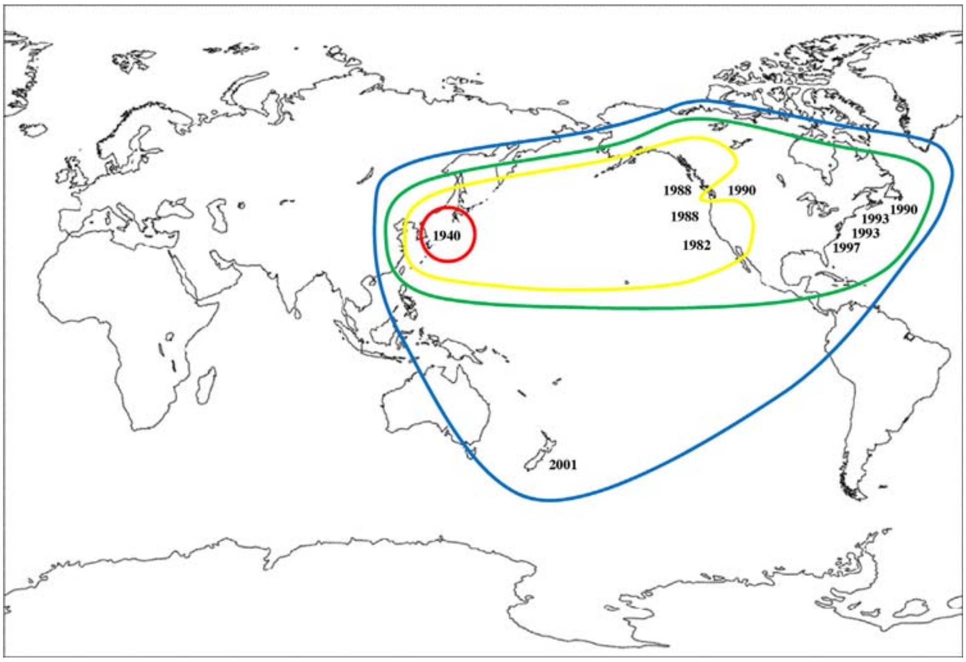

Fig. 2. Spatial expansion of hagfish fisheries worldwide. The commercial fishery originated in Japan and strongly expanded during World War II (1940s). After its decline, the fishery expanded to the West coast of North America in the 1980s, to the East coast of North America in the 1990s, and to New Zealand in 2001.

a very hands-off management plan with open access and little restrictions, such as California, Maine, Massachusetts, and New Zealand (Table 1), that will have to deal with problems as they arise as opposed to being proactive. Recently, however, the New Zealand MPI decided to move hagfish onto their Quota Management System effective October 2014 (Jennifer Oliver, personal communication, 2014). In the Northeast US, recommendations for managing the Atlantic hagfish fishery have been made (NEFSC, 2003) and a management plan will be introduced in the future (Scott McNamara, personal communication, 2014).

3.3. Temporal and spatial trends in Atlantic Canada

The hagfish fishery in Atlantic Canada has grown steadily since 1990 with total landings increasing from less than 100 mt to >2000 mt in 2010. During the same time, fishing effort increased

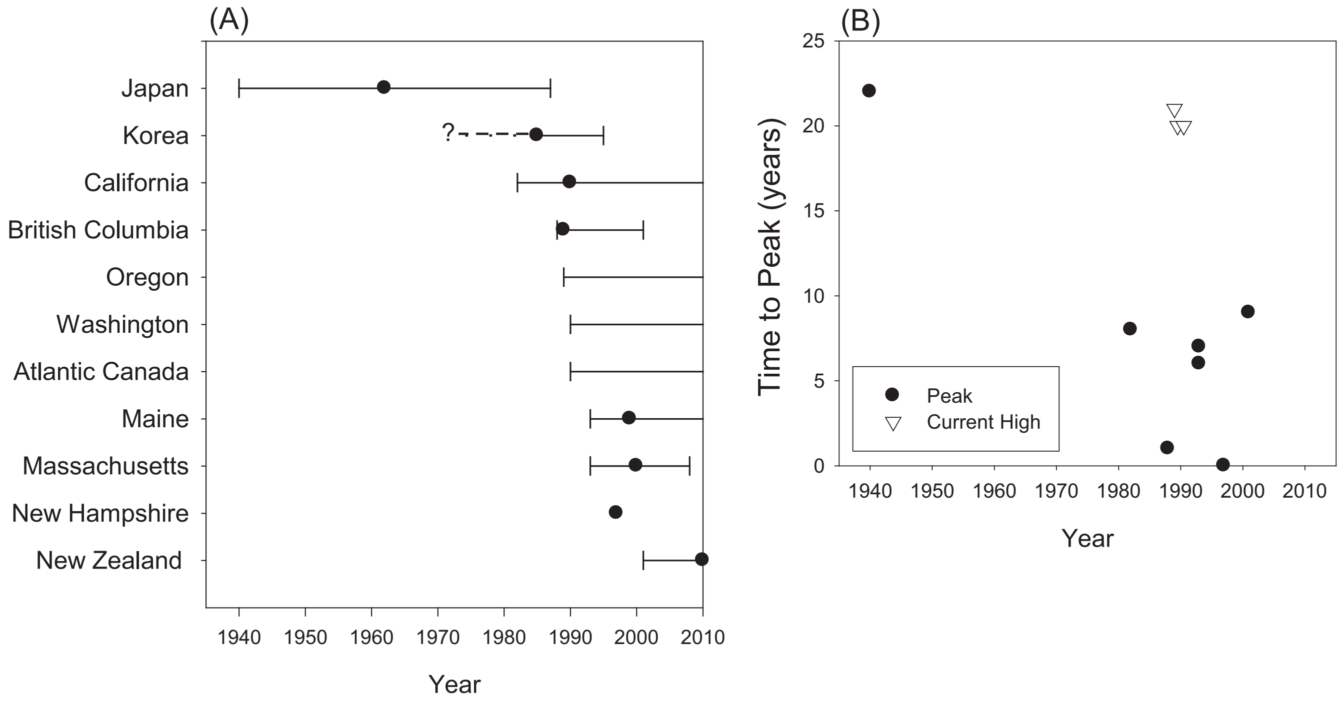

Fig. 3. Temporal patterns of hagfish fisheries worldwide. (A) Timeline of fisheries indicating the start date (left error bar), peak annual landings (black circles) and either end date (right error bar) or fisheries still continuing as of 2010 (data sources are listed in Table 1 and Section 2.1). The start date for Korea is unknown, and peak and end dates were derived from the literature. (B) Time-to-peak (years) of individual fisheries relative to their start date with those that have already peaked (black circle) or are at a current high (white triangle).

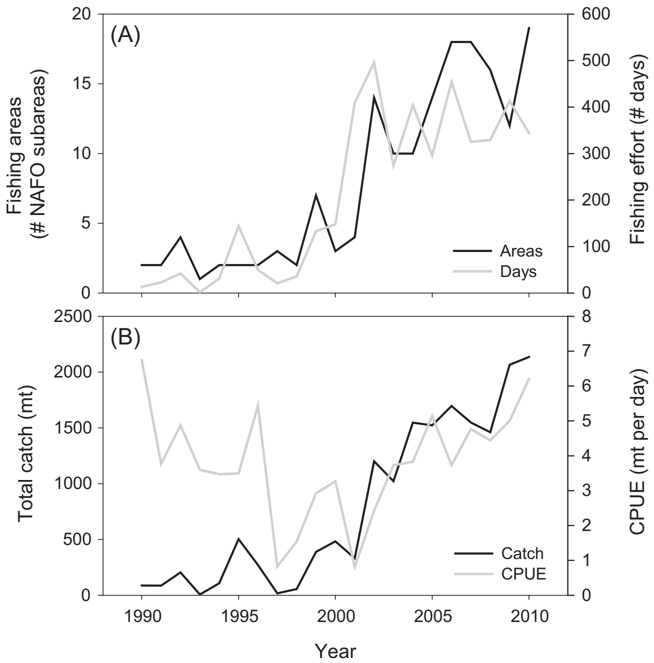

Fig. 4. Trends in the hagfish fishery in Atlantic Canada: (A) Fishing effort (number of days fished) and the number of NAFO subareas fished; (B) Total catch (mt) and CPUE (mt/day).

from less than 15 to >300 days fished per year and the number of NAFO subareas fished increased from 2 in 1990 to 19 in 2010 (Fig. 4). Fig. 5 further illustrates the strong spatial expansion of the hagfish fishery across main NAFO areas by decade. However, there appear to be two periods: before 2001, total catch, effort and areas fished remained at a lower level, whereas all metrics strongly increased afterwards and either stayed on a higher level (effort, areas fished) or continued to increase (total catch). Thus, the higher level of catch after 2001 has been achieved by higher fishing effort and fishing a larger area. Interestingly, CPUE shows a very high initial value followed by a fluctuating but overall strong decline until about 1998 and again 2001 after which CPUE steadily increased to almost initial values in 2010 (Fig. 4B). The CPUE decline coincides with the first period when catches came from a restricted number of fishing areas and with low effort, whereas the increase after 2001 coincides with a strong spatial expansion and increase in days fished.

To further investigate whether the spatial expansion was associated with serial depletion, we evaluated trends in catch, effort and CPUE across individual NAFO areas (Fig. 6) as well as subareas within 4X (Figure A.1) and 4W (Figure A.2). From 1990 to 1999, almost all catch came from area 4X, specifically 4XU and to a lesser extent 4XO. The CPUE trends for 4X as well as for 4XU and 4XO during this time show a decline. With the expansion of the fishery from 2000 onwards, a continuous amount of the catch came from 4X (Fig. 6), albeit only little from 4XU and instead larger amounts from 4XM, 4XN and 4XO (Figures A.1). Moreover, a large amount of the overall catch since 2000 came from NAFO area 4W, with some additional amounts from 3P, 3O and 5Z (Fig. 6). Within 4W, most catch came from 4WK but after 2005 this shifted to 4WH (Figure A.2). CPUE trends for individual NAFO areas or subareas did not show any strong trends from 2000 to 2010. Overall, all graphs indicate that patterns in catch closely match patterns in effort, and that after 2000 the increase in overall catch is largely achieved through an addition of effort in new areas. In summary, during the first decade of the hagfish fishery there was some depletion in 4X, particularly in 4XO and 4XU. However, after 2000 the fishery strongly expanded and sequentially added catch from new NAFO areas and subareas with so far no sign of depletion.

Supplementary Figures A.1 and A.2 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2014.06.011.

4. Discussion

Over the past 60 years, low-trophic level fisheries have strongly increased in terms of landings and effort on a regional and global scale (Berkes et al., 2006; Anderson et al., 2011a; Smith et al., 2011). Yet the growing exploitation has also caused an increase in the number of depleted or collapsed fisheries and has spurred the spatial expansion and serial depletion of some species around the world (Berkes et al., 2006; Anderson et al., 2011a,b). Our results demonstrate that hagfish fisheries, on a global scale and in Atlantic Canada, also show strong spatial expansion and some

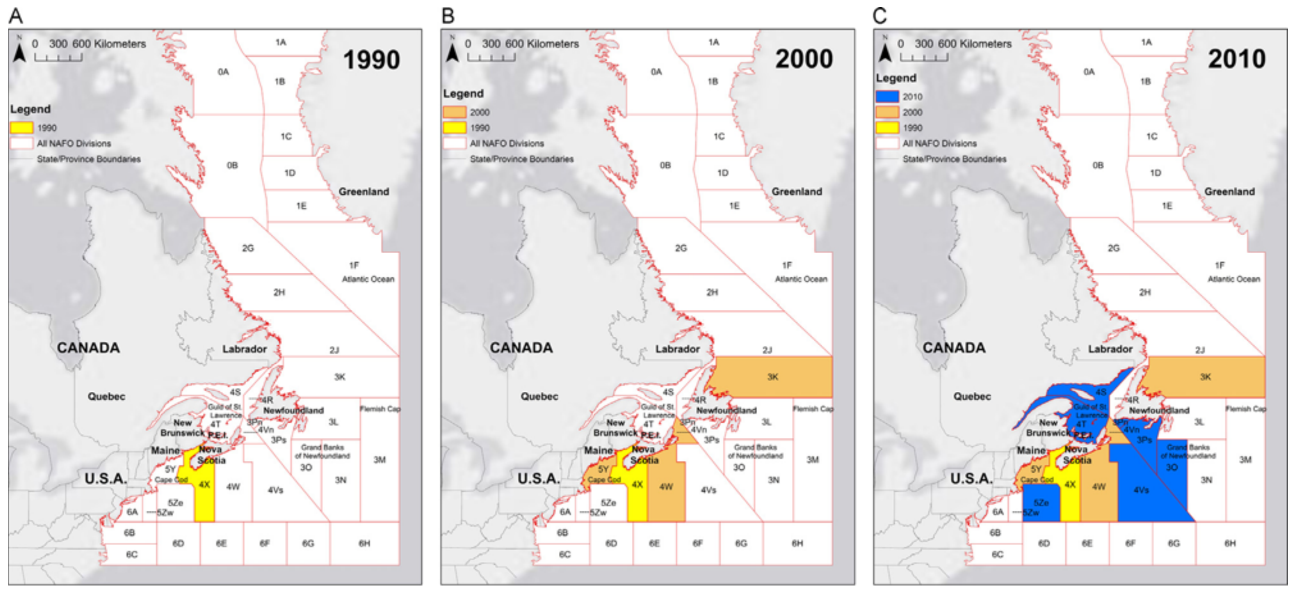

Fig. 5. Spatial expansion of hagfish fisheries in Atlantic Canada. Shown are all NAFO fishing units fished for hagfish in 1990 (A) and added units by 2000 (B) and by 2010 (C).

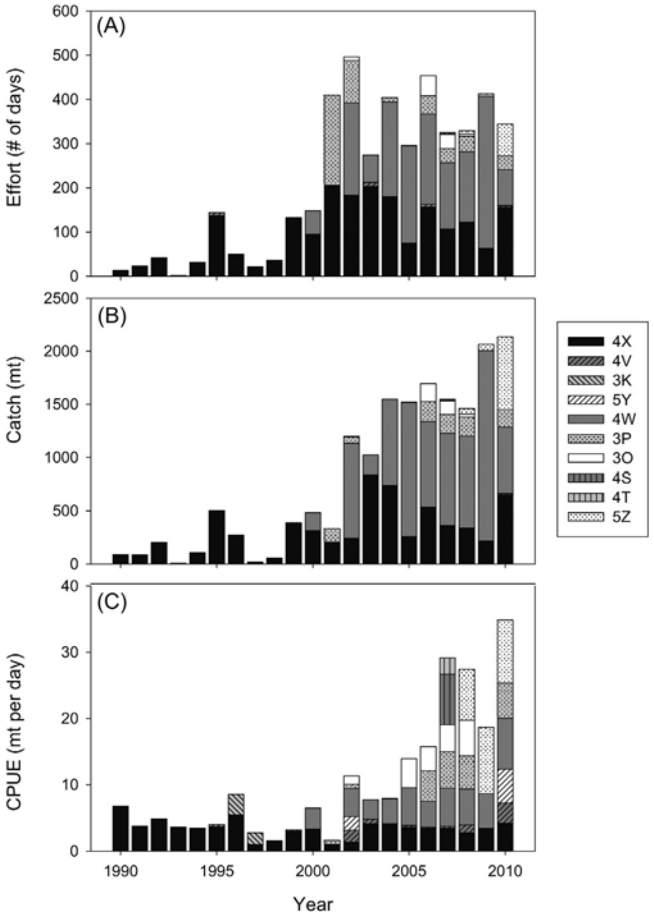

Fig. 6. Hagfish fishery in Atlantic Canada by NAFO fishing unit: (A) fishing effort (number of days fished); (B) total catch (mt); and (C) CPUE (mt/day).

serial depletion patterns similar to other emerging low-trophic level fisheries, though some patterns are less pronounced.

4.1. Global exploitation patterns

The commercial fishery for hagfish began in Japan, where it strongly expanded during World War II with peak catches around 1962, followed by a strong decline towards the late 1980s (Gorbman et al., 1990; Honma, 1998). In Korea, hagfish fisheries had grown towards the mid- to late-1980s, with about 1000 vessels employed, 100 shore-side processing plants and exported hagfish leather products worth $80 million, yet overfishing caused a collapse of the Korean hagfish fishery by the early 1990s (Martini and Flescher, 2002; NEFSC, 2003). Subsequent global exploitation patterns have been driven by the Asian market (Gorbman et al., 1990; Honma, 1998), similar to global fisheries for sea urchins and sea cucumbers. When Japanese and Korean hagfish stocks were depleted, the fishery expanded first on the West and later the East coasts of North America in 1982 and 1990, respectively, followed by New Zealand in 2001. While some fisheries have already peaked and declined (e.g. Japan, Korea, California, British Columbia, Maine, and Massachusetts), others continued to increase until 2010, which was our cut-off date. More recent official landings data indicate, however, that New Zealand peaked in 2010, Oregon in 2011, and Washington in 2012, while Atlantic Canada continues to expand. These patterns reveal that hagfish fisheries have exhibited spatial expansion, as well as some serial depletion patterns around the world. On a regional scale, the hagfish fishery in Atlantic Canada has also strongly expanded spatially, as well as in terms of the amount of hagfish landed and the fishing effort employed. A similar pattern of spatial expansion and local depletion has been reported for hagfish in the Gulf of Maine (NEFSC, 2003).

Spatial expansion and serial exploitation patterns have been previously documented in other emerging low-trophic level fisheries globally (Berkes et al., 2006; Anderson et al., 2011b), as well as historically for oysters along the coasts of North America and Australia (Kirby, 2004). Typically, in serial exploitation, new fisheries are opened in sequence to replace declining or collapsed harvests in existing fisheries, resulting in a constant supply of the product in demand (Berkes et al., 2006; Anderson et al., 2011b). In comparison, spatial expansion occurs if fisheries expand over an increasing spatial area, thereby increasing landings and supply to an often highly valuable market (Berkes et al., 2006; Anderson et al., 2011b). Such spatial expansion has generally occurred in marine fisheries worldwide (Swartz et al., 2010). Bioeconomic models state that the cost of fishing is directly proportional to the distance from the market (Merino et al., 2011), making fishing more economically viable for fisheries closer to the market. In the case of the hagfish fishery, the limiting factor is the supply of highly valued skins for the leather industry (Honma, 1998). Individual regional fisheries appeared to be unable to supply an adequate amount of hagfish to meet the growing Asian demand; thus, the fishery expanded spatially to other regions, allowing multiple fisheries to persist at once. Although some regional fisheries have declined or shut down, such as Japan, British Columbia, Massachusetts and Maine, others continue to exist. This evidence suggests partial serial depletion.

The lack of stronger serial exploitation patterns may be a result of the relatively small number of hagfish fisheries that are currently present on a global scale, and the limited and often low-quality data available. For example, Anderson et al. (2011b) analyzed sea cucumber fisheries data for 37 countries and regions, compared to only 12 past and present regional hagfish fisheries in our study. It is also possible that the global expansion of the hagfish fishery is in relatively early stages. Hagfish are present in almost all oceans in suitable soft-bottom habitat, in seemingly large numbers (Martini, 1998). Thus, the potential for continued global expansion of the hagfish fishery may be vast, as there seem to be many unexploited stocks.

With the exception of the Japanese, Korean and New Zealand fisheries, the only other existing hagfish fisheries have been located in North America. This is potentially driven by the large commercial fishing fleets already in place in North America which, due to depleted or restrictively managed groundfish stocks, are looking for new target species, such as many invertebrates (Anderson et al., 2008, 2011a, 2011b). Since opening in 1993, the size of boats fishing hagfish in Massachusetts has dramatically increased, with the majority of boats weighing 51–500 tonnes in 2002 (NEFSC, 2003). The greater yield brought in by larger vessels may drive down the per-unit cost, thereby driving smaller fishing vessels out of the market. There are likely other fishing fleets worldwide that have the capacity to fish for hagfish but have not tried yet or were not allowed. For example, requests to open a hagfish fishery in the Baltic Sea have so far been declined (Bo Fernholm, personal communication, 2011). Another explanation for the strong expansion of hagfish, sea cucumber and sea urchin fisheries across North America may be that it is home to a large Asian population, which might constitute a connection to the Asian market place.

In addition to spatial expansion and serial exploitation, Anderson et al. (2011b) also revealed a pattern in global sea cucumber fisheries whereby the more recent the fishery started, the less amount of time it took for the fishery to peak in landings. The decreasing time-to-peak in sea cucumbers fisheries is likely caused by strong growth in demand along with the exploitation of increasingly smaller stocks (Anderson et al., 2011b). Due to the limited number of hagfish fisheries worldwide, and some with still increasing annual landings, we found only limited evidence for a decrease in this time-to-peak across fisheries and over time. In terms of overall length of the fishery from start to end, the Japanese fishery exhibited the longest lifecycle, followed by decreasing lengths in British Columbia, Massachusetts and New Hampshire, which all ceased to have any reported landings in recent years. Overall, landings for hagfish in individual regions have fluctuated greatly, yet total global catch increased over time, a trait the industry shares with the sea cucumber fishery (Anderson et al., 2011b). What the hagfish fishery has not yet exhibited is an increase in the number of fisheries located in small and developing nations, as observed in the sea cucumber fisheries (Anderson et al., 2011b).

4.2. Hagfish fishery in Atlantic Canada

In Atlantic Canada, the hagfish fishery started in 1990 and has since increased 24-fold, both in terms of overall landings and effort. During its 20-year history, the fishery has spatially expanded from 1 to 10 NAFO fishing areas and from 2 to 19 NAFO subareas, respectively. This augmentation of the fishery began in NAFO unit 4X near Southern Nova Scotia, and then expanded towards the Gulf of Maine, Newfoundland and the Gulf of St. Lawrence, including eastward towards the edges of the Scotian Shelf (Fig. 5). However, during the first decade of the hagfish fishery, fishing mainly stayed within 4X, particularly 4XO and 4XU, but there was a strong decline in the CPUE. In contrast, after 2000 the fishery expanded and sequentially added more catch from new NAFO areas and subareas with no sign of depletion thus far.

The trends in hagfish fisheries are similar to those exhibited by other low-trophic level fisheries throughout Atlantic Canada. Since the 1980s, there has been a steep decline in the established finfish fisheries (Anderson et al., 2008) and many fishers moved to target lower-trophic level species, such as Northern shrimp (*Pandalus borealis*), sea urchins (*Strongylocentrotus droebachiensis*), sea cucumbers (*Cucumaria frondosa*), several species of crabs, as well as rockweed (*Ascophyllum nodosum*); all of which have seen an increase in catch since the 1980s or 1990s (Anderson et al., 2008). Some evidence suggests that low-trophic level species have increased in abundance in response to a release from predation; for example, the increasing abundance of shrimp on the Scotian Shelf during the 1990s has been linked to the depletion of groundfish stocks (Worm and Myers, 2003). The recent increase in many other low-trophic level fisheries in Atlantic Canada and worldwide may in part be explained by a similar release from predation that allowed their abundances to increase (Anderson et al., 2008; Boudreau and Worm, 2010), making them more viable target species for commercial fisheries.

Several low-trophic level species, however, have not been targeted commercially before and represent new fisheries with often limited knowledge on populations, stocks and their response to fishing, which can hamper effective management (Perry et al., 1999; Anderson et al., 2008). For example, sea cucumber catches in both Atlantic and Pacific Canada have strongly increased since the mid-to-late 1980s, displaying strong boom and bust patterns as observed for other sea cucumber fisheries around the world (Anderson et al., 2011b). Several other low-trophic level fisheries in Atlantic Canada also show high variability, and some have reached a peak and show a recent decline, indicating that more restrictive management is required (Anderson et al., 2008). Since many invertebrate species have high commercial value (in 2011, invertebrate fisheries in Canada were valued at over half a billion dollars; DFO, 2012) and represent an important new source of income for many fishers (Anderson et al., 2008, 2011a), sustainable management of these fisheries is critical, which includes the need for proper stock assessments based on good population and life-history information.

4.3. Regulations and management

The Japanese hagfish fishery was seemingly unregulated for its entire history (Gorbman et al., 1990). Given the timing of the fishery, during and following World War II, this was not unusual (Wilen, 2000). The most prominent factors limiting regulations during this time were the lack of comprehensive property rights for fisheries lying outside the control of coastal nations (Anderson, 1977) and explicit evidence that fisheries needed to be actively managed (Wilen, 2000). For the other hagfish fisheries, some regulations have been implemented to limit the number of licences available and number of traps per boat (Table 1). Within Atlantic Canada, the hagfish fishery has taken a variety of forms over time and in different locations ranging from small scale experimental permits to full commercial access (Grant, 2006; DFO, 2009). Logbooks are required, no bycatch is permitted and effort is regulated by the maximum number of traps per boat (DFO Maritimes Region: 500 traps for exploratory and commercial licence holders and 200 traps for experimental licence holders; DFO Newfoundland and Labrador Region: 200 traps) and the number of permits issued (7 permits in DFO Maritimes Region and 2 permits in DFO Newfoundland and Labrador Region as of 2007; DFO, 2009). In practice, the number of traps per boat has been much lower (typically up to 180 in the Maritimes and 150 in Newfoundland; DFO, 2009). One issue we encountered, however, was inconsistent data reporting, such as the catch-per-day in Atlantic Canada, which limits proper assessment of the development of a fishery assessment and consequently its management.

The catch trends observed in the regional hagfish fisheries worldwide were highly variable. If we assume that commercial fisheries are profit driven, then the limited regulations imposed on the hagfish fishery could cause a boom and bust trend, similar to that observed in sea urchins and sea cucumbers. The aggregate value of all invertebrate fisheries has been increasing since the early 1980s (Perry et al., 1999), thereby increasing the pressure on lower trophic level species. Sethi et al. (2010) found that when an assemblage of shellfish and invertebrates (species at low-trophic levels) is compared to higher trophic level species, it is the low-trophic level species which receive the highest price and revenue. Despite their high value, regulation and management of many invertebrate fisheries is minimal to non-existent and there are an increasing number of collapsed invertebrate fisheries (Anderson et al., 2011a).

Even though landings for four regional hagfish fisheries have increased until 2010, an equal number of regional fisheries closed down as of 2010. Another two, California and Maine, both peaked early on in the fishery and recently had much lower landings (Fig. 1). Rationale for closing the hagfish fisheries has ranged from overfishing in Japan (Gorbman et al., 1990; Honma, 1998) and a collapse in Korea (NEFSC, 2003) to lack of interest from the market in British Columbia (Benson et al., 2001). Korean hagfish harvesters were reported fishing in Japanese waters (Gorbman et al., 1990), which may have aided in the decline of Japanese hagfish stocks (Fig. 1). Anderson et al. (2011b) cited overfishing and population declines as the reason behind the decrease seen in many of the sea cucumber fisheries. Decreases in landings can be driven by a variety of other factors; natural causes such as recruitment failures on a large scale and human driven economic and regulatory impacts can have similar effects on the fisheries (Shepherd et al., 1998).

4.4. Conservation efforts

Of the 76 described species of hagfish, 30 are categorized as data deficient and 9 are listed under one of the IUCN's Red List

Categories: Critically Endangered (1), Endangered (2) or Vulnerable (6) (Knapp et al., 2011). The 9 IUCN Red Listed species are endemic to a region or a country, most are listed as threatened by bycatch and habitat degradation and only one, *Myxine garmani*, which is listed as vulnerable, is directly targeted by a fishery (Knapp et al., 2011). The one listed critically endangered species is *Eptatretus octatrema*, a very rare species endemic to a region that is less than 100 km^2 in South Africa (Knapp et al., 2011). It can be argued that the ecological requirements of hagfish, such as a propensity for burrowing (Martini, 1998), make them difficult to survey, hampering population assessments and thus conservation efforts. The Convention on International Trade in Endangered Species (CITES, www.cites.org) regulates international trade of species, but does not list hagfish under any of its appendices. Designation of species occurs at a meeting every 2–3 years; an ineffective means of conservation when fisheries expand quickly as seen in sea urchin and sea cucumber fisheries. This is exemplified in the Egyptian sea cucumber fishery which grew so rapidly that it was shut down after only 2 years of fishing (Anderson et al., 2011b).

4.5. Population and ecosystem consequences

At present, it is difficult to determine the impacts of the fisheries on hagfish stocks, since information on population size, biomass, distribution, individual growth rates, recruitment rates, and longevity is largely lacking (Martini and Beulig, 2013). Reductions in abundance have been recorded in Japan, as the fishery seemingly collapsed due to overfishing (Gorbman et al., 1990). Trawl surveys in the Gulf of Maine saw a decrease in the number of hagfish prior to 1990; yet as the commercial hagfish fishery opened there was an increase in the number of hagfish observed (NEFSC, 2003). However, landings per unit effort showed a decline from 1994–2002 to 50% of 1994 levels in the Gulf of Maine (NEFSC, 2003) and there was a period of declining CPUE in Atlantic Canada (Fig. 4b). Because abundance estimates of hagfish may be difficult to obtain (Martini, 1998) non-traditional methods of stock assessment, such as habitat or potential carrying capacity estimates, may be necessary to monitor their populations (Powell et al., 2005; DFO, 2012; Tallman et al., 2012). For example, Powell et al. (2005) suggest quantifying reproductive steroid concentrations to determine reproductive periods of hagfish, during which they could then be protected. Existing data indicate that the reproductive potential of hagfish is very low (Martini and Beulig, 2013) and that hagfish have a limited tolerance to changes in temperature and salinity (Martini, 1998). Thus, they are not likely to survive being discarded as bycatch or having escaped from traps as they are hauled to the surface (Martini et al., 1997).

Hagfish play an important role in nutrient cycling in benthic ecosystems (Martini, 1998). They can be highly abundant on the seafloor both in numbers and biomass, are a prey source for many marine mammals and predatory invertebrates, and prey upon some benthic invertebrates along with dead and decaying carcasses (Martini, 1998). By turning over the substrate hagfish help maintain ecosystem health in regions of intense commercial fishing, whereby huge amounts of bycatch are discarded and sink to the seafloor (Martini, 1998). St Martin (2001) cites a New England fisher who reported a decrease in flounders caught after hagfish harvesters had moved into the area. He suggests that the removal of hagfish alters the benthic ecosystem in such a way that it can no longer support some fishes (St Martin, 2001). This example demonstrates the chain reaction that might occur in an ecosystem when one vital piece is removed. Overall, the sustainability of the hagfish fishery is difficult to assess or manage as much of the population and ecosystem knowledge of these species and their response to fishing are still unknown (Powell et al., 2005).

5. Conclusion

Since the 1980s, the hagfish fishery spatially expanded from its original market in Asia to include both the West and East coasts of North America and New Zealand. While some regional fisheries continued to expand until 2010, others have already peaked and declined indicating some serial depletion. There was strong variability in the regulatory measures for individual fisheries, almost no stock assessments and inconsistent data reporting. In Atlantic Canada, the hagfish fishery also showed strong spatial expansion and increase in landings and effort over time with only few signs of depletion. Given the global distribution of hagfish, the fishery has the potential to further expand if there is continued demand for the product, but proper population assessments and monitoring as well as spatial and effort regulations should be in place to ensure sustainability.

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References

Anderson, L., 1977. Economic Impacts of Extended Fisheries Jurisdiction. Ann Arbor Science Publishers, Ann Arbor, MI.
Anderson, S.C., Flemming, J.M., Watson, R., Lotze, H.K., 2011a. Rapid global expansion of invertebrate fisheries: trends, drivers and ecosystem effects. PLoS ONE 6, 1–9.
Anderson, S.C., Flemming, J.M., Watson, R., Lotze, H.K., 2011b. Serial exploitation of global sea cucumber fisheries. Fish Fish. 12, 317–339.
Anderson, S., Lotze, H.K., Shackell, N., 2008. Evaluating the knowledge base for expanding low-trophic-level fisheries in Atlantic Canada. Can. J. Fish. Aquat. Sci. 65, 2553–2571.
Barss, W.H., 1993. Pacific hagfish, *Eptatretus stouti*, and black hagfish, *E. deani*: the Oregon fishery and port sampling observations, 1988–92. Mar. Fish. Rev. 55, 19–30.
Benson, A.J., Neville, C.M., McFarlane, G.A., 2001. An update for the British Columbia experimental fishery for Pacific hagfish (*Eptatretus stouti*). Can. Stock Assess. Sec. Res., 1–25, Doc. 2001/149.
Berkes, F., Hughes, T.P., Steneck, R.S., Wilson, J.A., Bellwood, D.R., Crona, B., Folke, C., Gunderson, L.H., Leslie, H.M., Norberg, J., Nystrom, M., Olsson, P., Osterblom, H., Scheffer, M., Worm, B., 2006. Globalization, roving bandits, and marine resources. Science 331, 1557–1558.
Boudreau, S.A., Worm, B., 2010. Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys. Mar. Ecol. Prog. Ser. 403, 181–191.
Department of Fisheries and Oceans (DFO), 2009. Proceedings of a Workshop on Canadian Science and Management Strategies for Atlantic Hagfish, DFO Can. Sci. Advis. Sec. Proceed. Ser. 2009/009.
Department of Fisheries and Oceans (DFO), 2012. National Advisory Process for Technical Expertise in Stock Assessment Workshop on Stock Assessment Methods for Data Poor Species in Canada, 11–12 May 2010, DFO Can. Sci. Advis. Sec. Proceed. Ser. 2011/063.
FAO, 2010. The State of World Fisheries and Aquaculture 2009. Technical report. Food and Agriculture Organization of the United Nations, Rome, Italy.
Fernholm, B., Mincarone, M.M., 2010. A new species of hagfish (Myxinidae: *Eptatretus*) from Papua New Guinea. J. Fish. Biol. 77, 998–1005.
Gorbman, A., Kobayashi, H., Honma, Y., Matsuyama, M., 1990. The hagfishery of Japan. Fisheries 15, 12–18.
Grant, S.M., 2006. An exploratory fishing survey and biological resource assessment of Atlantic hagfish (*Myxine glutinosa*) occurring on the southwest slope of the Newfoundland Grand Bank. J. Northw. Atl. Fish. Sci. 36, 91–110.
Grey, M., Blais, A.-M., Hunt, B., Vincent, A.C.J., 2006. The USA's international trade in fish leather, from a conservation perspective. Environ. Conserv. 33, 100–108.
Honma, Y., 1998. Asian hagfishes and their fisheries biology. In: Jorgensen, M., Lomholt, J.P., Weber, R.E., Malte, H. (Eds.), The Biology of Hagfishes. Chapman and Hall, London, pp. 45–56.
Kirby, M.X., 2004. Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. Proc. Natl. Acad. Sci. U.S.A. 101, 13096–13099.
Knapp, L., Mincarone, M.M., Harwell, H., Polidoro, B., Sanciangco, J., Carpenter, K., 2011. Conservation status of the world's hagfish species and the loss of phylogenetic diversity and ecosystem function. Aquat. Conserv. Mar. Freshw. Ecosyst. 21, 401–411.

Kuo, C.-H., Lee, S.-C., Mok, H.-K., 2010. A new species of hagfish *Eptatretus rubicundus* (Myxinidae: Myxiniformes) from Taiwan, with reference to its phylogenetic position based on its mitochondrial DNA sequence. Zool. Stud. 49, 855–864.
Leask, K.D., Beamish, R.J., 1999. Review of the fisheries and biology of the Pacific hagfish (*Eptatreus stoutii*) in British Columbia, with recommendations for biological sampling in a developmental fishery. Can. Stock Assess. Sec. Res., 1–47, Doc. 99/205.
Martini, F.H., 1998. The ecology of hagfishes. In: Jorgensen, M., Lomholt, J.P., Weber, R.E., Malte, H. (Eds.), The Biology of Hagfishes. Chapman and Hall, London, pp. 57–77.
Martini, F.H., Beulig, A., 2013. Morphometics and gonadal development of the hagfish *Eptatretus cirrhatus* in New Zealand. PLoS ONE 8 (11), e78740, http://dx.doi.org/10.1371/journal.pone.0078740.
Martini, F.H., Heiser, J.B., Lesser, M.P., 1997. A population profile for Atlantic hagfish, *Myxine glutinosa* (L.), in the Gulf of Maine. Part I: Morphometrics and reproductive state. Fish. Bull. 95, 311–320.
Martini, F.H., Flescher, D., 2002. Hagfishes, Order Myxiniformes. In: Collette, B.B., Klein-MacPhee, G. (Eds.), Bigelow and Schroeder's Fishes of the Gulf of Maine. , third ed. Smithsonian Institution Press, Washington, pp. 9–16.
Merino, G., Barange, M., Rodwell, L., Mullon, C., 2011. Modelling the sequential geographical exploitation and potential collapse of marine fisheries through economic globalization, climate change and management alternatives. Sci. Mar. 75, 779–790.
Northeast Fisheries Science Center (NEFSC), 2003. Report of the 37th Northeast Regional Stock Assessment Workshop (37th SAW): Stock Assessment Review Committee (SARC) Consensus Summary of Assessments. National Marine Fisheries Service, Northeast Fisheries Science Center Ref. Doc. 03-16, Woods Hole, MA.
Nelson, J.S., 2006. Fishes of the World, fourth ed. Wiley and Sons, Edmonton.
Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689–695.
Perry, R.I., Walters, C.J., Boutillier, J.A., 1999. A framework for providing scientific advice for the management of new and developing invertebrate fisheries. Rev. Fish Biol. Fish. 9, 125–150.
Powell, M.L., Kavanaugh, S.I., Sower, S.A., 2005. Current knowledge of hagfish reproduction: implications for fisheries management. Integr. Comp. Biol. 45, 158–165.
Sethi, S.A., Branch, T.A., Watson, R., 2010. Global fishery development patterns are driven profit but not trophic level. Proc. Natl. Acad. Sci. U.S.A. 107, 12163–12167.
Shepherd, S., Turrubiates-Morales, J., Hall, K., 1998. Decline of the abalone fishery at La Natividad, Mexico: overfishing or climate change? J. Shellfish. Res. 17, 839–846.
Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L.J., Shin, Y.-J., Tam, J., 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science 333, 1147–1150.
St Martin, K., 2001. Making space for community resource management in fisheries. Ann. Ass. Am. Geogr. 91, 122–142.
Swartz, F., Sala, E., Tracey, S., Watson, R., Pauly, D., 2010. The spatial expansion and ecological footprint of fisheries (1950 to present). PLoS ONE 5, e15143.
Tallman, R., Cadigan, N., Cass, A., Duplisea, D., Healey, B., Trzcinski, K., Wade, E., 2012. Techniques for the provision of advice in information-poor situations. DFO Can. Sci. Advis. Sec. Res., Doc. 2011/106.
Wilen, J.E., 2000. Renewable resource economists and policy: what differences have we made? J. Environ. Econ. Manage. 39, 306–327.
Worm, B., Myers, R.A., 2003. Meta-analysis of cod-shrimp interactions reveals top-down control on oceanic food webs. Ecology 84, 162–173.