How many sea scallops are there and why does it matter?

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Oceanic conditions along the Atlantic Coast of North America are changing rapidly. Surface water temperatures in the Gulf of Maine have increased faster than 99% of the global oceans, and major infrastructure projects, including the largest windfarm in the world, are under development along this seaboard. In Canada and the US, the Atlantic sea scallop (*Placopecten magellanicus*) supports lucrative fisheries, which were originally founded on an extensive scientific framework focusing on stock assessment. The sea scallop is an ideal sentinel species, as it is highly sensitive to changes in marine conditions. We used a drop camera system to estimate the number and size of scallops, as well as the distribution of their reproductive potential, over 70,000 km^2 of the continental shelf in 2016–2018, an area that nearly covers the entire range of this species. In total, we estimated that there were 34 billion individual scallops (95% confidence limits: 22–46 billion) within the species' range. In this paper, we examine the role of the sea scallop as a baseline sentinel species that can be used to measure the impacts of environmental change and anthropogenic developments.

Climate change is permeating every aspect of science. Ocean warming and acidification are increasing rapidly along the Atlantic Coast of North America, with marked impacts on marine communities. Over the past decade, sea-surface temperatures in the Gulf of Maine have risen faster than in 99% of the global ocean, due primarily to a northward shift in the Gulf Stream and alterations in the Atlantic Multidecadal and Pacific Decadal oscillations (Pershing *et al.* 2015). Of 82 fish and invertebrate species inhabiting the waters of the Northeast continental shelf, half are categorized as being highly or very highly vulnerable to anthropogenic climate change and natural decadal climatic variability, with diadromous fish and benthic invertebrate species being the most sensitive (Hare *et al.* 2016). In marine systems, climate change has been associated with changes to seven factors (namely, ocean surface temperature, pH, and salinity; surface air temperature; precipitation; currents; and sea-level rise); likewise, climate vulnerability has been defined as variations in the abundance and productivity of marine species due to changing conditions, and the degree of their vulnerability to change has been measured by 12 biological traits (Table 2 in Hare *et al.* [2016]). Most species have a high potential for distribution change (Pereira *et al.* 2010), thereby impacting the human fishing communities they support.

Given the current pace of global environmental change, quantifying changes in species abundance is crucial for assessing ecosystem impacts (Rosenberg *et al.* 2019). Yet estimates of the number of individuals of a particular species over its entire range are rare, with the exception of imperiled plants and animals. The "Endangered" designation of the International Union for Conservation of Nature requires a population to have declined by 50–70%, cover a total geographic area less than 5000 km^2, have fewer than 2500 adults, have restricted subpopulations smaller than 250 adults, or be pending extinction within 20 years (IUCN 2019). The focus on species extinctions underestimates the extent of biotic change, as the decline of still common species or in aggregate across large species assemblages is rarely quantified (Dirzo *et al.* 2014; Ceballos *et al.* 2017). A recent example of this is the unexpected discovery that 29% of the North American avifauna has been lost since 1970 (~3 billion birds in 48 years; Rosenberg *et al.* 2019).

The marine environment complicates estimating the abundance of organisms. Species counts are available for a handful of endangered or threatened marine mammals (eg 409 North Atlantic right whales [*Eubalaena glacialis*] were observed in 2018) (NOAA 2020), but assessments of most fishes and invertebrates are based on biomass rather than abundance. Biomass

In a nutshell:

- Estimates of the number of individuals of an abundant marine species are both unusual and scarce
- A drop camera system was used to approximate the number and size of Atlantic sea scallops (*Placopecten magellanicus*) over an area that encompassed virtually the species' entire range
- Photographic quadrats allow for estimation of the sea scallop's spatial distribution at scales ranging from centimeters to thousands of kilometers, as well as its habitat productivity
- The sea scallop is an ideal sentinel species to track ocean health and climate-change impacts

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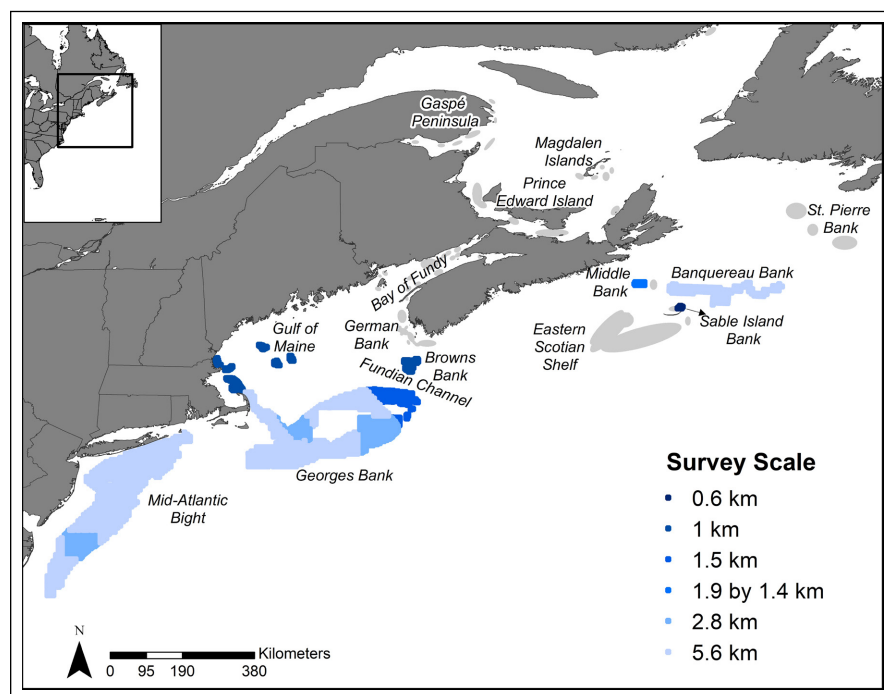
Figure 1. The range of the Atlantic sea scallop (*Placopecten magellanicus*), including areas sampled by our drop camera survey area (various shades of blue) and areas where scallops exist but were not surveyed (light gray). The survey scale refers to the size of the sampling grid, with the distance between each station presented in kilometers. Station latitudes and longitudes are listed in WebTable 1.

variations in sea level and temperature signaled changes in the composition and distribution of the species over geological time (Shaw 2014). Expected variations due to global climate change will probably strongly influence the distribution of sea scallops as they are sensitive to acidification and changes in seawater temperature (Cooley *et al*. 2015).

Global warming, ocean acidification, and other anthropogenic stressors (eg offshore energy, commerce) are rapidly transforming the coastal oceans, and were emphasized in the recommendation for reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act (Miller *et al.* 2018). For a dataset to be used as a baseline study for quantifying the effects of these changes, it must be able to address fundamental questions of marine population dynamics, including (modified from Sinclair [1988]): what is the population richness (the number of populations within a species), where are the component populations of a particular species distributed, what is the absolute abundance of the individual populations, and what are the temporal fluctuations in abundance of the individual populations? Our survey of the Atlantic sea scallop was designed to answer these questions by measuring scallop abundance and distribution from the scale of centimeters to thousands of kilometers over the species' entire range. In 2017, we surveyed the continental shelf using a drop camera system (composed of a digital still camera and lights on a metal frame) measuring the number of scallops, their size, and their distribution, supplemented by surveys of other areas conducted in 2016 and 2018. After quantifying the Atlantic sea scallop's absolute abundance, habitat, and distribution of reproductive potential, we discuss these data in the context of a baseline against which the effects of environmental change and other anthropogenic impacts may be assessed.

■ Methods

Observations of scallops were made using a drop camera survey with a centric systematic sampling design (Bethoney and Stokesbury 2018). At each survey station, a steel sampling pyramid outfitted with cameras and other equipment was lowered from a research vessel to the sea floor four times, based on the assumption that the minimal commercial density of sea scallops is about one scallop per 10 m² (Figure 1; Stokesbury 2002). The survey was conducted from May to October in 2017, with additional areas surveyed in 2016 and 2018. In total, 22,592 quadrat samples were collected at 5648 stations (that is, 5648 stations × 4 quadrats per station = 22,592 quadrats overall; Table 1).

dampens the extent of change in population abundance due to the length–weight relationship, as 50 small animals may weigh the same as one large animal. An exception among fisheries organisms assessed by biomass is the Atlantic sea scallop (*Placopecten magellanicus*), which ranges from Newfoundland to Virginia; because this species is sedentary and lives on the surface of the sea floor, direct measures of abundance can be made via optical surveys. As such, it is a marine organism for which the number of individuals across virtually the species' entire range can be quantified. Furthermore, quadrat counts allow for abundance estimates without the need to construct complex stock assessment models.

Scallops (Order Pectinida) have had a tumultuous existence over the past 245 million years, bearing witness to numerous transformations in ocean conditions and surviving two mass extinctions. Scallop fossils occur in the Clearwater Formation (outside Fort McMurray, Alberta, Canada) as far back as the early Cretaceous period (112–110 million years before present [bp]) when the ancient Bearpaw Sea extended over 1.7 million km² of what is now central North America (Serb 2016). More recently, the Laurentide Ice Sheet covered much of northern North America (2.6 million years bp) and shaped the sediment deposits of the Atlantic continental shelf. In the Late Pleistocene, *P magellanicus* was repeatedly forced off of and allowed to reestablish on the continental shelf several times by fluctuations in sea level due to the advance and retreat of continental glaciers (D Bailey pers comm). As seen in the fossil record, subsequent

Table 1. Sample area (km²), mean abundance of Atlantic sea scallops (millions), and lower and upper 95% confidence limits (LCL and UCL, respectively) for each of the major aggregations, as well as the area (km²) associated with the number of scallops in a quadrat representing potential reproductive output

| Region | Stations | Survey area (km²) | Scallops (1 × 10⁶) | | | Scallops per quadrat (area km²) | | |
			95% LCL	Abundance	95% UCL	0	1–2	>2
Northern grounds	645	4851	470	634	798	4280	392	180
Gulf of Maine	889	889	97	124	151	591	235	63
Georges Bank	2614	29,447	14,272	24,316	34,360	17,951	6771	4725
Mid-Atlantic	1500	32,783	7017	9084	11,150	17,663	11,486	3634
Total	**5648**	**67,970**	**21,856**	**34,158**	**46,459**	**40,485**	**18,884**	**8602**

One of three types of cameras was mounted on each sampling pyramid when collecting the quadrat sample: namely, a Kongsberg OE14-408 digital still camera (dimension of photographed area: 1.7 m²; image resolution: 0.41 mm per pixel), an Imperx Bobcat digital still camera (dimension of photographed area: 2.3 m²; image resolution: 0.29 mm per pixel), or a GoPro Hero 5 (dimension of photographed area: 1.4 m²; image resolution: 0.86 mm per pixel) (Figure 2). Water depth and temperature, time, date, latitude and longitude, number of live scallops, and scallop shell height were recorded for each image. Macroinvertebrates and fish were identified to species when possible, and substrate type was also recorded (Bethoney and Stokesbury 2018).

Mean density (± standard error) of scallops within each region (Figure 2) was calculated using equations for a two-stage sampling design with a random starting point (Cochran 1977; Bethoney and Stokesbury 2018). For density calculations, quadrat size was increased based on the average scallop shell height to adjust for partially visible scallops counted along the edge of the image (O'Keefe *et al.* 2010). The absolute number of scallops was calculated by multiplying scallop density by the total area surveyed. The total number of individuals and associated 95% confidence limits (CL) were calculated by summing scallop abundance in each area (Bethoney and Stokesbury 2018).

The spatial distribution of scallop reproductive potential was plotted using ArcGIS version 10.6 (ESRI; Redlands, CA). The quadrat image technique enables examining scallops on the scale of centimeters; at that scale, scallops group together to form clumps (Stokesbury and Himmelman 1993). The productivity of sampled areas was ranked by the presence or absence of scallops observed in each quadrat image: 0 scallops for low productivity, 1–2 scallops for medium productivity, and 3 or more scallops for high productivity. Our sampling represented a snapshot in time; over our 20-year time-series of the US resource, areas that at one time did not have scallops could potentially support high densities at a later date if a recruitment event were to occur (Bethoney *et al.* 2016).

◼ Results

We estimated that there were approximately 34 billion (3.4 × 10¹⁰, 95% CL: 22–46 billion) individual scallops covering 27,000 km² of the ~68,000 km² surveyed (Table 1). Scallop counts ranged from 1 to 363 per quadrat and from 1 to 1083 per station. Covering 43% of the total area sampled, Georges Bank was the most densely populated region in the sea scallop's range, accounting for 71% of total scallop abundance (Table 1; Figure 3). The Mid-Atlantic, which covered 48% of the area sampled, was found to contain 27% of total scallop abundance. Aggregations north of the Fundian Channel were grouped together (Figure 1; included Banquereau Bank, Middle Bank, Sable Island Bank, and Browns Bank); collectively termed the "Northern grounds", they covered about 7% of the survey area, and contained approximately 2% of total scallop abundance. The Gulf of Maine covered 1.3% of the survey area and contained 0.4% of total scallop abundance. Water depths ranged from an average of 54–94 m, and bottom water temperatures ranged from an average of 8.0–20.1°C, varying with the time of the survey, but overall becoming progressively cooler as one traveled farther north.

Mean scallop shell height was 83.9 mm (standard deviation [SD] = 23.33, n = 24,589) in Georges Bank, 83.3 mm (SD = 25.81, n = 5474) in the Mid-Atlantic, 69.0 mm (SD = 38.40, n = 4176) in the Northern grounds, and 88.8 mm (SD = 37.35, n = 1021) in the Gulf of Maine. Large recruiting year-classes created bimodal size distributions in each area, with the exception of Georges Bank.

Survey areas were determined by fishing history and current harvesting efforts, but we found that 60% of the area included in our survey contained few scallops (Table 1; Figures 1 and 3). Georges Bank contained the largest amount of high productivity, covering 4725 km² and making up 16.0% of the Georges Bank surveyed area, while medium productivity covered 23.0% (Table 1; Figure 3). The Mid-Atlantic had 11.1% high productivity and 35.0% medium productivity,
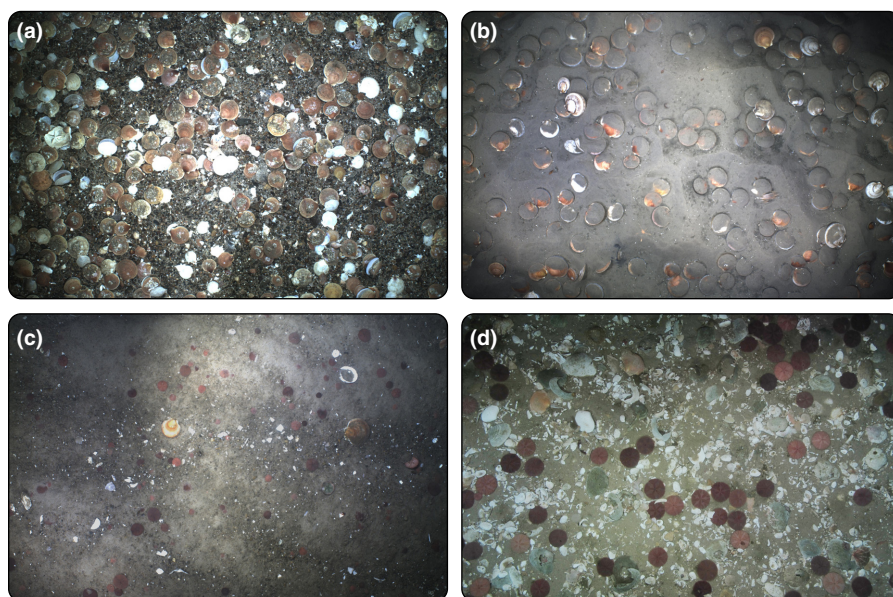
Figure 2. Digital still quadrat samples from each of the four regions included in our survey: (a) Georges Bank, (b) the Mid-Atlantic, (c) the Gulf of Maine, and (d) the Northern grounds off Nova Scotia. Photos in panels (a–c) were taken with an Imperx Bobcat digital still camera; photo in panel (d) was taken with a Kongsberg OE14-408 digital still camera. Images from US waters can be observed at http://bit.ly/scallopsurvey.

which was greater than any other area and covered 11,000 km². In the Northern grounds, only 3.7% of the area had high productivity, whereas 8.1% of the area was of medium productivity. In the Gulf of Maine, 7.1% of the area had high productivity and 26.4% had medium productivity.

■ Discussion

Along the Atlantic coast of North America, there is a high degree of climate variability, which is projected to increase in the future as a result of climate change. The current range of the Atlantic sea scallop covers much of the area that will be affected by future climate change, from subarctic to sub-tropical waters. Furthermore, the proposed development of 18,000 megawatts of offshore wind energy (with 1800 turbines in US waters alone) and tidal power in the Bay of Fundy will lead to changes in the offshore marine environment (S McClellan; US Offshore Wind Conference, Boston, MA; 10 Jun 2019). As such, the estimates of Atlantic sea scallop abundance and distribution presented here represent data that could be used to evaluate the impacts of future change.

Population richness of marine invertebrates and fishes with larval phases that are subject to drift is difficult to determine, as the location of the spawning adults and the settling juveniles may differ. Sinclair *et al.* (1985) suggested that 19 discrete sea scallop populations exist based on evidence from sustained fishing activity, but our results indicate that sea scallop population richness is less clearly spatially defined, with large areas of high productivity in the Mid-Atlantic and Georges Bank potentially producing zygotes. This estimate is based on the spatial distribution of scallops on the scale of centimeters. Sea scallops are gonochoristic (either male or female) broadcast spawners (eggs and sperm are released into the water column where fertilization occurs), and their larvae remain in the water column for ~30 days (Caddy 1989); moreover, scallops can swim short distances, especially at adolescent sizes (<75 mm shell height; Manuel and Dadswell 1991). Scallops form clumps of three or more individuals located within 1–2 m of each other, and there is therefore at least a 75% chance that a member of the opposite sex will be within the clump, assuming a 1:1 ratio of males to females (Stokesbury and Himmelman 1993). Our quadrat size was roughly the size of one of these clumps. This clumped distribution, with its short distances between individuals, results in minimal gamete dilution during broadcast spawning; fertilization success is considerably reduced over distances exceeding 1 m to the nearest neighbor (Claereboudt 1999; Smith and Rago 2004; Bayer *et al.* 2016). Bayer *et al.* (2018), however, found that higher densities did not necessarily increase fertilization success, and suggested that the formation of a clump leads to the production of high numbers of zygotes. Sea scallops become sexually mature when they reach a size of about 75 mm shell height, and produce about 50 million eggs annually (Parsons *et al.* 1992). Ring sizes for scallop dredging (the bag of the dredge is made of steel rings) in Canada and the US are 88.9 mm and 102.5 mm, respectively; the minimum ring catch size helps to ensure at least one spawning event per adult. The bimodal size distribution (first mode was roughly associated with 2–3 years of age) observed in three of the regions and periodic extreme recruitments, such as the event dominating Georges Bank (Bethoney *et al.* 2016), suggest that the present abundance has a high reproductive potential.

Determining the distribution of component populations of a species requires examination of the species' entire range. We surveyed 68,000 km² of the continental shelf, focusing on sea scallop fishing grounds. Productive sea scallop habitat covered 27,000 km² within the survey area. There are several scallop grounds that we were unable to sample in the northern portion of the range. The largest of these was in the Bay of Fundy, which supports a strong nearshore fishery totaling 10,434 metric tons (mt) of scallop meat biomass that in 2017 produced a harvest of 1425 mt (DFO 2018). Scallops are distributed in small beds along the length of the Atlantic Canada coastline, with densities varying between 0.1 and 1.0 scallops per square meter (MacDonald and Bajdik 1992; Stokesbury and Himmelman 1993). A 2017 survey conducted by the Government of France for the purpose of examining scallop aggregations around the islands of Saint Pierre and Miquelon (a self-governing territorial overseas collectivity of France in the St Lawrence Seaway)
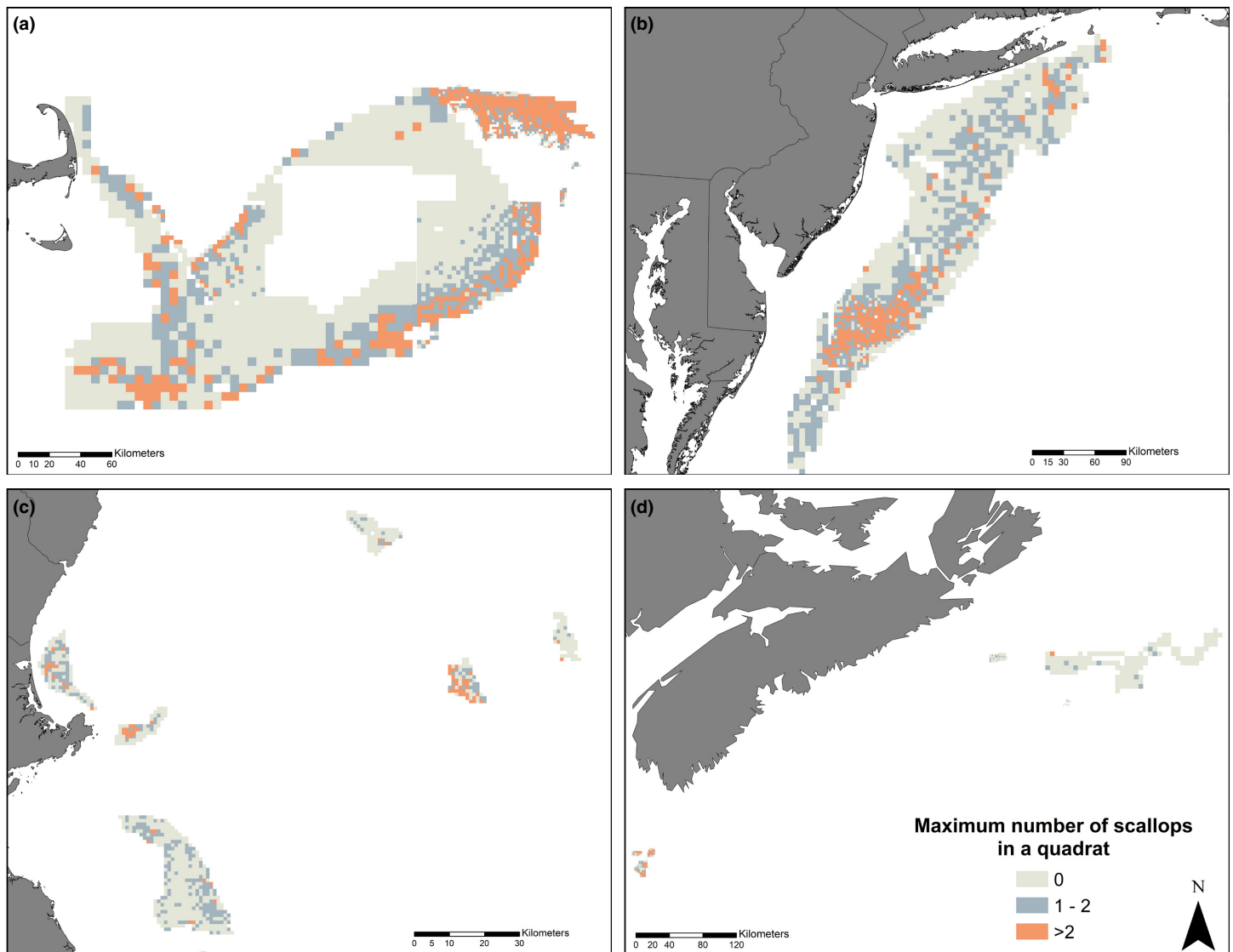
Figure 3. Areal extent (km²) associated with the number of scallops in a quadrat representing potential reproductive output, based on assumptions of fine-scale aggregation to increase fertilization success: (a) Georges Bank, (b) the Mid-Atlantic, (c) the Gulf of Maine, and (d) the Northern grounds off Nova Scotia.

found very few scallops (Foucher 2018). These aggregations are persistent and have been documented since the early 1900s (Caddy 1989), but are relatively small and fall within the 95% CL estimated for the total abundance.

Determining the overall abundance of individual populations is challenging due to the difficulty of simply defining the boundaries of a population. A population is a group of inter-breeding individuals that exist in three dimensions (latitude, longitude, and time) and that are reproductively isolated from other groups (Taylor and Taylor 1977). Modeled recruitment patterns for scallop populations in Georges Bank and the Mid-Atlantic indicated that each is a self-sustaining aggregation (Davies *et al*. 2015; Munroe *et al*. 2018). Aggregations in the Northern grounds and the Gulf of Maine may be reproductively isolated, but recruitment patterns and extreme recruitment events extending across all available scallop habitat suggest that these areas may be seeded by larval clouds

emanating from highly reproductive aggregations (Bethoney *et al*. 2016). Based on DNA sequencing, there seems to be a northern and a southern grouping of sea scallops, with water temperature variation influencing population structure (Van Wyngaarden *et al*. 2017; Lehnert *et al*. 2018). According to these genetic studies, our surveys described the entire southern population of scallops with the exception of those in the Bay of Fundy.

Atlantic sea scallops have persevered for several millennia despite numerous fluctuations in marine conditions, and are a prime candidate for sentinel species designation, as they are long-lived (+16 years) and their distribution, growth, and physical condition are all highly sensitive to oceanic conditions. Moreover, scallops are abundant and support a vibrant, valuable fishery, one that recognizes the need for scallop-related science, which helps to ensure continuance of funding for year-to-year monitoring of changes in scallop populations. Such data collection, though focusing on sea scallops, also

contributes information about associated marine macroinvertebrate and benthic fish fauna and habitat, and forms the structure of a baseline dataset from which changes in oceanic conditions can be detected and quantitatively measured. In light of various anthropogenic threats across the species' range, the development of a baseline of population abundance – such as that provided here – will hopefully mark the beginning of a more holistic program to regularly assess the health of Atlantic sea scallop populations, including measuring such characteristics as meat quality and shell-height-to-meat-weight condition, as well as conducting isotopic analyses of shells to estimate growth. Such a program would allow for the scientific examination, through hypothesis-driven and statistically rigorous experimentation, of the extent and ramifications of changing marine conditions along the Atlantic coast of North America.

■ Acknowledgements

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■ Supporting Information

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Frontiers**EcoPics**

Superb advantage from carrion-associated arthropods?

Carcasses of adult African elephants (*Loxodonta africana*), as well as those of juveniles and subadults under certain conditions, often persist long enough to allow members of the blowfly family (Calliphoridae) to complete their life cycle en masse before the tissues are fully consumed and the skeletons disarticulated. The presence of tens of thousands of blowflies and other carrion-associated arthropods attracts species that are typically unaffiliated with carrion, such as the superb starlings (*Lamprotornis superbus*) shown here.

This relationship may be more functionally important than it first appears. Each year, the availability of elephant carrion peaks during dry seasons, which bookend the wet seasons when superb starlings breed.

The amount of seasonal rainfall influences insect population size, which in turn impacts the fitness of superb starlings (Rubenstein 2015; doi.org/10.1017/CBO9781107338357.012). Elephant carcasses may serve as reliable resource hotspots for superb starlings foraging during dry seasons. Given the persistence of carcasses and the presence of their accompanying arthropods, these hotspots may remain valuable to the starlings into the early portion of their breeding seasons.

Although the arthropod-rich elephant carcasses likely provide fitness benefits to superb starlings and other insectivorous birds, these sites are not without peril. Predators (including Verreaux's eagle-owl [*Bubo lacteus*]) are also attracted by the concentration of prey at carcasses. Carrion ecology is a burgeoning field, and an improved, comprehensive understanding of the effects of carcasses within ecosystems is needed.

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doi:10.1002/fee.2271