Defining and mapping functional groups for fishes and invertebrates in the Scotian Shelf Bioregion

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ABSTRACT

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The Government of Canada has committed to creating a national network of marine protected areas (MPAs) that will protect at least 10% of coastal and marine areas by 2020. The Scotian Shelf Bioregion is one of five bioregions in Canada currently developing an MPA network. An important design principle in the development of an MPA network is "ecological representation", *i.e.*, including areas with relatively intact, naturally functioning examples of a broad variety of habitat types and species. One way to explore ecological representation is by using functional groups as a key representation component. Functional groups are considered to be a collection of species that perform a similar ecological function, regardless of taxonomy. DFO is taking into account various spatial and temporal patterns of species, including functional groups, in the design of the Scotian Shelf Bioregion MPA network. The purpose of this report is to categorize and map fish and invertebrate functional groups in the Scotian Shelf Bioregion for use in the design of this MPA network and other oceans planning and management applications. Here, fish and invertebrate species recorded during DFO's Maritime Region Summer Ecosystem survey were described and categorized into fifteen main groups based on size, habitat, and feeding guild. Spatiotemporal patterns of each of these groups are mapped and can be used to identify priority conservation areas for MPA network planning and design.

RÉSUMÉ

Le Canada s'est engagé à établir un réseau national d'aires marines protégées (AMP) afin de protéger au moins 10 % de ses zones côtières et marines d'ici 2020. La biorégion de la plate-forme néo-écossaise est l'une des cinq biorégions au Canada qui élaborent actuellement un réseau d'AMP. La « représentation écologique » est un important principe de conception dans le cadre de l'élaboration d'un réseau d'AMP, *c'est-à-dire* qu'elle inclut des zones relativement intactes et naturellement fonctionnelles qui regroupent une vaste gamme de types d'habitat et d'espèces. Les groupes fonctionnels peuvent être un moyen essentiel de parvenir à la représentation écologique. On considère ces groupes comme un ensemble d'espèces qui remplissent la même fonction écologique, peu importe la taxonomie. Dans le cadre de la conception du réseau d'AMP de la biorégion de la plate-forme néo-écossaise, Pêches et Océans Canada (MPO) tient compte de divers modèles spatiaux et temporels propres aux espèces, y compris des groupes fonctionnels. Le présent rapport a pour but de catégoriser et de cartographier les groupes fonctionnels de poissons et d'invertébrés dans la biorégion de la plate-forme néo-écossaise aux fins d'utilisation dans la conception de ce réseau d'AMP et d'autres applications de planification et de gestion des océans. Ici, les espèces de poissons et d'invertébrés enregistrées pendant les relevés estivaux de l'écosystème de la région des Maritimes ont été décrites et classées en quinze principaux groupes en fonction de leur taille, de leur habitat et de leur régime alimentaire. On a cartographié les tendances spatiotemporelles de chacun de ces groupes. Elles peuvent être utilisées pour définir les zones de conservation prioritaires pour la planification et la conception du réseau d'AMP.

INTRODUCTION

Canada has committed to establishing a network of marine protected areas (MPAs) through domestic legislation and policy (*e.g.*, *Oceans Act*, National Framework for Canada's Network of MPAs), and international agreements (*e.g.*, Convention on Biological Diversity) (Government of Canada 2011). Under the *Oceans Act*, Fisheries and Oceans Canada (DFO) is responsible for leading the development and implementation of a network of MPAs on behalf of the Government of Canada. The vision for Canada's national network of marine protected areas is for an "An ecologically comprehensive, resilient, and representative national network of marine protected areas that protects the biological diversity and health of the marine environment for present and future generations" (Government of Canada 2011). In developing this MPA network, Canada will join a suite of other countries that have already designated MPA networks (*e.g.*, Australia, New Zealand, The Bahamas) in an effort to protect marine biodiversity, ecosystem functioning and special natural features, and the social and economic values and ecosystem services they provide (Government of Canada 2011). The Scotian Shelf Bioregion has been identified as one of five priority bioregions across Canada for MPA network development over the next five years, and is the focus area for this report.

MPA networks are generally expected to include "ecological representation" or areas with relatively intact, naturally functioning examples of the full range of ecosystem and habitat types (Government of Canada 2011). This type of consideration is now possible in MPA network design with the availability of long-term datasets and improved scientific understanding of the characteristics that influence marine biodiversity and ecosystem functioning. This is especially true for the Scotian Shelf, much of which has been systematically sampled and studied for decades. DFO has explored many characteristics of the Scotian Shelf, including species diversity, productivity, uniqueness/rarity, vulnerability, naturalness, and key species (Government of Canada 2011).

Spatial and temporal patterns of the species composition and relative abundance of various functional groups, which are considered to be a collection of species that perform a similar ecological function, regardless of taxonomy (Bellwood et al. 2004), have also been explored (Shackell and Frank 2007; Shackell et al. 2012). The focus of these studies was largely to evaluate the impacts of fishery-induced declines of commercially targeted groups (*e.g.*, groundfish) on such patterns. This is well aligned with an ecosystem-based approach to management; it is largely accepted that maintaining functional diversity and redundancy is imperative to preserve ecosystem function and improve the chances of recovery from intervening disturbances (McCann 2000; Micheli and Halpern 2005; Shackell and Frank 2007; Cadotte 2011). Functional diversity describes the trait variation or dispersion in an assemblage (Cadotte 2011), and is considered to be a similarly important factor in management and conservation as species richness (Cadotte 2011; Stuart-Smith et al. 2013; Rice et al. 2013). Functional redundancy describes the availability of multiple species within each functional group such that compensation is possible in the case that one species is extirpated or depleted; in effect, there are enough species per functional group to ensure that the function is maintained despite species-specific perturbations (McCann 2000; Fonseca and Ganade 2001). It has been shown that increased functional redundancy – or the 'portfolio effect' – contributes to increased resilience (Bellwood et al. 2004) and recovery (Micheli and Halpern 2005) of marine fish communities, even if the stabilizing effect can be attributed solely to the Law of Large Numbers (Rice et al.

2013). Similarly, when multiple species of a functional group are disturbed, like the effect that extensive bottom trawling had on the benthic fish complex of the Scotian Shelf, the entire ecosystem can be restructured such that one functional group may replace another (Shackell and Frank 2007; Bundy et al. 2009; Frank et al. 2011). Therefore, the spatial and temporal patterns of functional groups, and their within-group richness, can be dynamic.

The Scotian Shelf is a heavily exploited marine ecosystem that has experienced numerous population collapses as a result of complex anthropogenic and environmental interactions (Choi et al. 2004; Bundy 2005; Frank et al. 2005; Zwanenburg et al. 2006). These collapses involved some of the region's most common species, which resulted in large absolute losses of species and ecosystem biomass, thereby disrupting ecosystem structure, functioning and services (Bundy 2005; Bundy and Fanning 2005; Gaston and Fuller 2007). In this case, the biomass of large-bodied benthic fishes, primarily cod, but also pollock, haddock, hake, cusk, redfish, plaice, flounder, thorny skate and winter skate, substantially decreased, and the biomass of planktivorous forage fishes (*e.g.*, herring, capelin, sand lance) and macroinvertebrates (*e.g.*, northern snow crab, northern shrimp) greatly increased (Bundy 2005; Frank et al. 2005). As such, the spatial distribution and species composition of functional groups have changed through time on the Scotian Shelf. These changes warrant investigation and consideration in the design of the Scotian Shelf MPA network.

In order to further explore the spatial and temporal trends in functional diversity and redundancy on the Scotian Shelf, a generalized method to assign species to functional groups was required. In the literature, how species are grouped into their functional roles has varied greatly and has depended on the goals and scope of the investigation. For example, in the Celtic Sea predatory fish community, a comprehensive approach using eleven functional traits (including body size and diet) yielded eleven functional groups from 33 species (Reecht et al. 2013). On the other hand, in the Ligurian Sea, more than 50 species were grouped into three functional groups based on diet and predators alone (Britten et al. 2014). Around the Channel Islands in California, 49 species of marine plants, invertebrates and fishes were placed into 12 functional groups, one group of which had only one species (Micheli and Halpern 2005). On the Scotian Shelf and northeast US shelf, various traits that focus on diet (*e.g.*, trophic guild, trophic level), habitat preferences, and body size have been used to assign some species, mostly commercially important, to functional groups (Garrison and Link 2000; Bundy 2005; Shackell and Frank 2007; Shackell et al. 2012), but there has been no standardized categorization across all species.

In this report, functional groups from the DFO Summer Ecosystem research vessel trawl survey (RV Survey) are categorized and mapped to further explore functional diversity and redundancy for inclusion into the MPA network design for the Scotian Shelf Bioregion. Further, overlay analyses were conducted to highlight the importance of areas across functional groups, that is, hotspots of functional group diversity. To accomplish this, all fish and invertebrate species recorded in the RV Survey were systematically described based on body size, habitat, and feeding guild. Using these main descriptions, species were then combined into groups (*e.g.*, size + habitat + feeding guild) and mapped by fishing era. Because fish and invertebrates have been systematically recorded on different time scales (*i.e.*, fish since 1970, invertebrates since 2007), harvested at different rates over different time periods, have different catchabilities by the trawl gear, and have different life history characteristics that determine their vulnerability and resilience to external disturbances (*e.g.*, fishing, climate change), fish and invertebrates were treated separately in the analyses.

METHODS AND MATERIALS

DATA

Standardized fishery-independent bottom trawl research surveys have been conducted by Fisheries and Oceans Canada (DFO) on the Scotian Shelf each summer since 1970. The survey has a stratified random design, with strata (strata 434-509, which includes surveys from adjacent Gulf of St Lawrence, and Georges Bank Strata 5Z1-5Z9) defined by depth range and geographic locations (for further details see Doubleday 1981; Simon and Comeau 1994; Figures 1- 3). The research vessel and trawl gear were changed after 1981 from the AT Cameron vessel fishing with a Yankee 36 trawl to the Lady Hammond then the Alfred Needler fishing vessel, both using a Western IIA trawl. Catch rates for a limited number of species were adjusted to account for these changes based on the conversion factors estimated by Fanning (1985). The net was towed for approximately 30 minutes at a speed of 3.5 knots. All catch rates were standardised to a tow distance of 1.75 nautical miles. Invertebrate biomass in the survey catch has been recorded since 1999 (Tremblay et al. 2007), however, invertebrate species have only been reliably identified since 2007 (D. Clark, Fisheries and Oceans Canada, pers. comm.). For finfish, the sampling protocols were rigorous throughout the survey duration. Within each set, the total number and weight of all finfish species were measured as well as the individual length and weights of a sample of each species (up to ~300 individuals). Therefore, in this analysis, 8 years of invertebrate data (2007-2014) and 45 years of fish data were used (1970-2014).

Prior to analysis and following Ward-Paige and Bundy (2015), the data were examined to remove records with insufficient taxonomic resolution and/or rare occurrences. Where possible, survey data resolved to the species level were used. In addition, cases with no specific species records but with a higher taxonomic record (*i.e.,* to the genus level) were also retained. Data were then extracted from this dataset where species were observed in more than 5 survey sets or were recorded in 2 or more years. This dataset was then separated into invertebrates and fish. For invertebrates, records collected before 2007 were discarded. For fish, the data were split into the five fishing eras partially defined by Horsman and Shackell (2009): era 1, 1970 – 1977 (when foreign fleets fished Canadian waters); era 2, 1978 – 1985 (domestic stock recovery following 200 mile Exclusive Economic Zone implementation and prior to domestic fishery being fully developed); era 3, 1986 – 1993 (fully established domestic fleets with cold eastern Scotian Shelf waters, fish stocks decline in growth and some collapse); era 4, 1994 – 2006 (several groundfish species collapse and show signs of non-recovery); and era 5, 2007 – 2014 (years when both fish and invertebrate data are available; a new addition since Horsman and Shackell's [2009] work). A complete fish dataset across all eras was also included (see Table 1 for summary). See Tables 2 and 3 for the complete list of species included and details on values used to define groups.

FUNCTIONAL GROUP DEFINITIONS

Following from a literature review of traits, environmental gradients and species interactions used to define various fish and invertebrate species' ecological roles, three main defining traits were used to describe and group fish and invertebrate species. These included: i) length, grouped into small (<31 cm), medium (30-80 cm) and large (>80cm) based on maximum length reported for adult stages, or colonial/non-colonial for certain invertebrate groups; ii) habitat, where the species lives, grouped into benthic (infauna, bottom dwelling and bentho-pelagic) or pelagic (living in the water column and not associated with the bottom); and iii) feeding guild, based on predominate prey type and included mainly piscivore, mainly benthivore, mainly planktivore and mainly zoopiscivore, and for invertebrates included benthivore, zoopiscivore, filter feeder, and detritivore. See Tables 2 and 3 for the groups, total biomass, traits and species membership. As well, to explore spatiotemporal trends in hotspots, fish groups were further separated into each of 5 fishing eras (Table 1) and mapped separately.

MAPPING PROCEDURE

Similar mapping procedures to those described in Horsman and Shackell (2009) were followed. For each functional group, the observed weight per tow (biomass) was interpolated across the sampled area using inverse distance weighting (IDW) interpolation. This method provides an interpolation that uses a weighted distance average that is constrained by the maximum and minimum values set by the data. Prior to interpolation, the data points for each functional group within each era were divided into two groupings ('east' and 'west') using the NAFO divide between 4VW and 4X. This was done to eliminate the bias of higher biomass of functional groups in 4X. The 4VW and 4X data points within each era were thus interpolated separately, to ensure that important areas for these groups in both the eastern portion of the region (often referred to as 4VW in this report) and the western portion of the region (often referred to as 4X in this report) were represented in the output.

The interpolation was performed in ArcGIS® (version 10.1) Spatial Analyst. To create the interpolated surface, we used the IDW settings used by Horsman and Shackell (2009) with a cell size of 0.026177, a power of 2, and a fixed search with radius of 0.15 degrees (~14-15 km for the study area) that constrains the interpolation to the areas with data. These settings were specified by DFO Oceans for consistency between other data layers.

For the fish functional groups, following Horsman and Shackell's (2009) approach, the interpolated surfaces for each era were reclassified into ten equal-area classes (deciles), using Quantile Breaks (ArcGIS® version 10.1), and ranked from 1-10. To create a summed map for all eras, the ranked surfaces from each era were summed to create a surface with varying ranks of 1-50. This was done to approximate the importance of the area for each functional group over time. E.g., for a given functional group, if an area ranked 10 in each time period, its summed rank would be 50, indicating that higher relative biomass had consistently been found in that area, regardless of changes in abundance. As there was only one time period for the invertebrate functional groups, only the initial reclassified decile surface was used and no invertebrate summed rank maps were created.

Overlay analyses were also done to show the importance of areas across functional groups, that is, hotspots of functional group diversity. The reclassified surfaces (deciles; described above) were added using Raster Calculator (ArcGIS® version 10.1). This was done for all fish functional groups for each era and for all eras combined, for all invertebrate functional groups, and for both fish and invertebrate groups combined (era 5 only).

RESULTS

In total, 185 species were included in the analyses, 72 invertebrates and 113 fish species, which were classified into 9 fish and 6 invertebrate functional groups. Three species were excluded because they were too dissimilar to other species and did not fit into a group: (i) sea lamprey (*Petromyzon marinus*), a parasite which feeds off a host's blood, body fluids and flesh; (ii) Atlantic hagfish (*Myxine glutinosa*), which feeds off dead and dying fish, and (iii) short-fin squid (*Illex illecebrosus*), which feeds on fish and squid, like other fish and invertebrate species, but was the only piscivorous invertebrate, and whose presence on the Scotian Shelf is highly variable.

MAP INTERPRETATION

In the 6-panel maps showing distribution of biomass for each functional group in each era and in all eras combined (e.g., Figure 4), dark blue represents areas where no species of that functional group were observed, light blue shows 1-20% of values by area (i.e. bottom two deciles), and red represents 80-100% of values (i.e. top two deciles). In the summed rank maps for each fish functional group (e.g., Figure 5), and for all of the overlay maps (e.g., Figure 22), there are no zero values. Therefore, dark blue represents 1-20% of values by area and red represents 80-100% of values. It is important to note that since 4X and 4VW values were interpolated separately for each functional group, biomass classes should be interpreted relatively within 4X and 4VW for each map.

NAFO Divisions and place names referred to in the text are provided in Figures 1 and 2 respectively.

Fish

Piscivores

For small and medium benthic piscivorous fish (Figure 4), hotspots across all eras were consistently concentrated in the middle Shelf (i.e. the eastern half of 4X and western half of 4W), mainly on Middle and Sable Island Banks, with wide coverage on Banquereau and Eastern Shoal as well. Hotspots that appeared often but with less consistency across eras included Emerald Basin, LaHave Basin, Browns Bank, and a few smaller hotspots along the western Shelf edge and in the Bay of Fundy. The western portion of the region in era 5 did not resemble other eras, and had a lower biomass overall with only one prominent hotspot just south of Grand Manan Island. The map of all eras combined showed that the greatest concentrations of biomass overall occurred in 4VW on Sable Island Bank and Banquereau. It also highlighted the complete absence of hotspots for this group anywhere north of Banquereau. The summed rank map for this functional group (Figure 5) showed that the highest biomass persistence in 4VW was on Banquereau and on much of the middle Shelf (mainly Sable Island and Middle Banks, and Emerald Basin). In 4X, persistent hotspots occurred on Emerald Basin, the south western edge of Browns Bank, north of Yarmouth and the outer reaches the Bay of Fundy on the Nova Scotia side.

Hotspots for large benthic piscivorous fish were fairly spread out across the region (Figure 6). Some of the more consistent concentrations throughout all eras occurred along the northeastern portion of the eastern Scotian Shelf and in the Gulf of Maine and outer Bay of Fundy. Occurrence of areas in the top 20% (red areas) appeared to be highest in era 1, and decreased over time to be the lowest in era 5. Era 5 had noticeably fewer hotspots overall compared to other eras, particularly from the 4X/4VW divide to the Georges Basin, and in the Bay of Fundy.

The map of all eras showed that in 4VW, hotspots were fairly small and scattered with some concentration along the edge of the Laurentian Channel and at the top of the Gully, but in 4X a large concentration of high biomass occurred in the Gulf of Maine, mostly in the shallower areas but also spanning into Jordan Basin. This pattern was also reflected in the summed rank map for this functional group (Figure 7). The summed rank map also highlighted that the areas to the north and south of Sable Island were consistently absent of hotspots in all eras, as was LaHave Bank and other areas along the outer Shelf in 4W and the eastern half of 4X.

For pelagic piscivorous fish (all sizes, Figure 8), all eras had very low biomass compared to the other fish functional groups, with a much more limited distribution. Only a few sites had any recorded biomass in eras 1-3. In era 1, the only two sites with any records were in the Northeastern Channel and inner Bay of Fundy. In eras 2 and 3 a few more locations were recorded, mainly along the Laurentian Channel and the Shelf edge. This group was recorded more frequently in eras 4 and 5 with most locations following the Shelf edge, but some were also recorded in the inner Bay of Fundy, around/north of Sable Island, and on Canso and French Banks. The map of all eras showed that overall, the highest biomass occurred along the outer Shelf edge and along the New Brunswick side of the Bay of Fundy, and the majority of the region had no records for this group. The summed rank map (Figure 9) showed patterns similar to era 4, though there were few areas of high biomass persistence (red) due to the lower occurrences in eras 1-3.

Benthivores

Figures 10-15 show the results for benthic benthivorous fish. For small benthic benthivores (Figure 10), hotspots were scattered across the Shelf in all eras. In the east, the most consistent hotspots occurred in Sydney Bight and on St. Anns, Canso and Misaine Banks. In the west the hotspots were more scattered but most consistently occurred in the outer portion of the Bay of Fundy near Brier Island, and around Browns, Baccaro, Roseway and LaHave Banks. Era 3 showed particularly high biomass following the coast of Cape Breton south along outer Chedabucto Bay to just south of Canso. In eras 4 and 5 this group was more widely distributed across the Shelf, with less overall area where no fish were observed. The summed rank map (Figure 11) showed areas of highest biomass persistence in Sydney Bight, Misaine, Roseway, LaHave and Baccaro Banks, Roseway Basin, and the outer portion of the Bay of Fundy along the Nova Scotia side.

For medium sized benthic benthivores (Figure 12), eras 1 and 2 showed fairly similar quantity and distribution of hotspots. Many hotspots were small and scattered in these two eras, with some consistency throughout the Bay of Fundy and within the northeastern portion of the Shelf. In eras 3 and 4, hotspots tended to be less scattered and more concentrated in certain areas, and the lack of hotspots in middle Shelf (i.e., eastern 4X and western 4W) was more pronounced. The highest concentrations in 4VW occurred in Sydney Bight, along the Northeastern Shelf edge, in the area between Misaine Bank and Banquereau, in the upper reaches of the Gully, and on Sable Island and Western Banks. In 4X the main concentrations occurred on Browns Bank, the inshore areas off of Yarmouth and Brier Island, and the entire inner Bay of Fundy. Era 5 showed somewhat similar distribution patterns but lower biomass, particularly in the entire middle Shelf. When all eras were combined, hotspots in the east were less prominent and biomass was more spread out. In the west, hotspots very clearly appeared in a swath from the western part of Browns Bank along the nearshore areas of Nova Scotia, all the way into the Bay of Fundy. The summed rank map (Figure 13) showed that persistence of biomass reflected a similar pattern to the distribution of biomass in eras 3 and 4.

The distribution of large benthic benthivores (Figure 14) was fairly similar across all eras with the exception of eras 1 and 2, which had higher biomass on Banquereau and Eastern Shoal (4Vsc) compared to eras 3, 4 and 5. The map of all eras showed very similar distribution of hotspots to the summed rank map (Figure 15). These hotspots occurred along the southern edge of Banquereau, on Sable Island, Western, LaHave, Roseway, Baccaro and Browns Banks, and the nearshore area off of Yarmouth around to Brier Island.

Planktivores

For pelagic planktivorous fish (all sizes, Figure 16), hotspots were dotted fairly sparsely across the Shelf in the first three eras, with large spatial absences on the eastern Shelf (with the exception of era 2 which had a larger concentration of hotspots around Emerald Basin). In the west, eras 1-3 showed consistent hotspots along the Fundian Channel and in various locations throughout the Bay of Fundy. The distribution of planktivores was more widespread in eras 4 and 5 with a greater concentration in 4W (excluding the area near the Shelf edge) as well as some scattered hotspots on the eastern end of the Shelf (particularly on Misaine and Artimon Banks). The summed rank map (Figure 17) showed the highest biomass persistence in 4W (excluding the Shelf edge). There were also smaller, isolated hotspots in Sydney Bight, Banquereau, along the Fundian Channel, off of Yarmouth, and nearshore patches in the mid Bay of Fundy.

Zoopiscivores

Benthic zoopiscivores (all sizes, Figure 18) had wide, but mostly sparse coverage across the region; much of the area with recorded biomass fell within the bottom two deciles (1-20th percentile). The pattern of hotspots remained fairly consistent across all five eras. The entire edge of the northeastern Shelf along the Laurentian Channel showed up consistently in all eras, and other more prominent hotspots occurred along the nearshore edge of the middle Shelf (i.e., 4W and eastern 4X) and in the far west portion of the region between Georges and Grand Manan Basins. The map of all eras reflected these same patterns. Patterns of high biomass persistence for this group were fairly concentrated, as seen in the summed rank map (Figure 19). Hotspots were concentrated along the Northeastern Shelf edge, along the northern edges of Emerald, LaHave and Roseway Basins, and within the basins and deeper areas in the Gulf of Maine. A few other isolated hotspots occurred on other parts of the Shelf edge and in the upper reaches of the Gully.

There were very few areas with high biomass for pelagic zoopiscivores (all sizes, Figure 20). Hotspots in eras 1-3 were concentrated mainly in the middle Shelf. The majority of these small hotspots occurred in and around LaHave and Emerald Basins, with a scattering on Baccaro, Middle and Sable Island Banks. The hotspots for these eras in the far west part of the region had little consistency. In eras 4 and 5 this group was found to be more widely distributed across the Shelf, yet there were fewer hotspots, particularly in the entire eastern portion of the Shelf. The distribution of these small, isolated hotspots for these two eras did not appear to be aligned, with the exception of the nearshore area off of Yarmouth. The map of all eras highlighted that overall biomass was concentrated in a few areas and density was very low throughout most of the region (bottom two deciles). The summed rank map (Figure 21) showed that very few areas had persistently high biomass for this group. The majority of these areas fell within the middle Shelf and in a small nearshore area off of Yarmouth.

Invertebrates

Benthivores

Records of small benthic benthivorous invertebrates were recorded throughout the entire region, though hotspots were concentrated in only a few areas (Figure 22). The concentration of hotspots in the east focused around Misaine, Canso, and Middle, and French Banks, and the area just north of Sable Island. These hotspots extended close to shore and cut across the outer portions of Chedabucto Bay. There was low biomass and no hotspots anywhere west of French Bank to the 4X/4VW divide. In the west, the hotspots were mainly concentrated throughout the outer portions of the Bay of Fundy, and often reached close to shore. Some smaller hotspots could also be seen just north of Roseway Bank and in Roseway Basin.

Medium sized benthic benthivorous invertebrates followed similar distribution patterns as the small benthic benthivores and also had very few concentrations in the middle Shelf (Figure 23). In the east, most of the hotspots were in a large grouping around Sable Island, Middle, French, Canso, Banquereau and Misaine Banks. Other prominent hotspots occurred in Sydney Bight and along the Shelf edge by Emerald and Western Banks. Hotspots in the west concentrated around the perimeter of the Bay of Fundy and around Grand Manan, the nearshore area off of Yarmouth, and on Browns Bank.

Zoopiscivores

Zoopiscivorous invertebrates (all sizes, Figure 24) had a restricted distribution with only a few, scattered hotspots. In the east the hotspots occurred on St. Anns Bank and in Sydney Bight. In the west the hotspots occurred in LaHave Basin, on Browns Bank, a few scattered areas off of Southwest Nova Scotia, on Grand Manan Banks, and in the mid-to-outer portion of the Bay of Fundy. Much of 4VW had no observed biomass.

Filter Feeders

Invertebrates in the filter feeding, benthic, colonial group were found almost exclusively in 4V (Figure 25) and had almost no records of biomass in 4W. In 4V, the majority of hotspots occurred around Aritmon Bank and Banquereau, the nearshore areas between Misaine Bank and the Cape Breton coast, and a spot just off the most northerly tip of Cape Breton. In the west there was only one small hotspot on the eastern edge of the Northeast Channel.

For invertebrates in the filter feeding, benthic, non-colonial group (Figure 26), there were records across most of the region, and hotspots were found in small pockets across 4X and 4VW. In the east, the largest hotspots occurred around Emerald Basin and on Misaine Bank, with lesser concentrations on Western, Banquereau, and St. Anns Banks. In the west, the largest hotspots occurred just to the east of LaHave Bank, and on Browns Bank. There were a couple smaller hotspots just off of Yarmouth and in the inner Bay of Fundy.

Detritivores

Invertebrates that are detritivores (Figure 27) were recorded throughout much of the region in the bottom two deciles (1-20th percentile), but with very few hotspots. Some small areas with higher biomass in the east were on Banquereau, Middle, and Sable Island Banks. In the west, hotspots were located on LaHave, Roseway, and Browns Banks, a nearshore area directly south of St. Margarets Bay, and a nearshore area off of Southwest New Brunswick.

Hotspots of Functional Group Diversity - Overlays

Fish Functional Group Overlay

The overlay of all fish functional groups (Figure 28) showed that the areas where fish functional group diversity was most consistently recorded (and most consistently absent) were very comparable across all five eras, and similar patterns were seen in the map combining all eras. Though red areas (top two deciles) could be found across much of the region, higher concentrations occurred in a few keys locations. These locations in 4VW included the entire northeastern edge of the Shelf, the area between Misaine Bank and Banquereau, the upper reaches of the Gully, and much of 4W. In 4X, the largest concentration was consistently found in shallow waters from Digby Neck to Yarmouth, and other persistent hotspots included the upper reaches of the Bay of Fundy and the western part of Browns Bank also had prominent hotspots.

There were two main areas of the Scotian Shelf that had consistently low biomass of fish functional groups and therefore low diversity: the eastern portion of 4X, i.e., the area between Brown's Bank and Emerald Bank including LaHave Bank (in some eras, this area extended from the inshore to the offshore), and areas to the east and north of the Gully.

Invertebrate Functional Group Overlay

The overlay of all invertebrate functional groups (Figure 29) showed large, distinct areas where high invertebrate diversity was consistently recorded. In 4VW, the eastern portion of the Shelf had the highest concentrations of diversity hotspots, whereas the western half of 4W had almost none. In the east, areas in the top two deciles (81-100th percentile) concentrated on the eastern half of Sable Island Bank, on Middle, Banquereau, Misaine and Artimon Banks, in Sydney Bight and on St. Anns Bank. In 4X, the largest concentration occurred throughout the entire Bay of Fundy. Other noticeable concentrations in 4X occurred on Grand Manan Banks, in waters off of Yarmouth, and on Browns and Roseway Banks.

Fish and Invertebrate Functional Group Overlays

The overlay of all fish and invertebrate groups in era 5 (Figure 30) showed some similar patterns to the invertebrate overlay (particularly in 4X), though the hotspots were more fragmented. In 4VW, areas with the most consistent records of biomass often occurred in between and around the edges of major banks. These hotpots could be seen in Sydney Bight, on Artimon Bank, around the edges of Banquereau, on Sable Island Bank (mainly the northern edge), and on Western Bank. In 4X, most of the Bay of Fundy had consistent records of biomass, as did Grand Manan and Browns Banks and the shallower areas off of Southwest Nova Scotia. With the exception of western Browns Bank, much of the eastern half of 4X was absent of hotspots. Note that the two areas noted above with low fish functional group diversity (eastern 4X and areas to the east and north of the Gully) also had low overall diversity.

DISCUSSION

Some general spatiotemporal patterns were observed in the distribution of functional group hotspots on the Scotian Shelf. No sites were consistently hotspots across all groups, but the Bay of Fundy and the major banks of the Scotian Shelf (Browns, Emerald, Middle, Western, Sable Island, LaHave, Misaine, Banquereau, and St. Anns), the Eastern Shoal and the Shelf edge were frequently identified as hotspots for many groups. Despite a large and varied distribution of hotspots across the Scotian Shelf, within and between fish and invertebrate functional groups, clear areas were identified with low biomass and diversity. This is important to note for spatial planning since protecting these areas may not contribute much protection for fish or invertebrate diversity or production.

There was a clear shift in the distribution of fish functional group hotspots over time: for many groups they remained fairly constant throughout the first three fishing eras, but in the later eras hotspots became more concentrated in a few areas. For example, large benthic piscivores and large benthic benthivores were fairly spread out across the Shelf in eras 1-3, but, as their abundance decreased, they became more concentrated in a few areas of the western and middle Shelf in eras 4 and 5. This is consistent with the literature where studies have shown that these groups, which are dominated by depleted species like cod and haddock, decreased in abundance and biomass, which resulted in decreased spatial ranges (Garrison and Link 2000; Shackell and Frank 2007) and replacement with other groups (Bundy 2005).

We also found evidence of space partitioning between small and large fish. Looking at the functional groups where size was a differentiating factor, both the small benthic benthivores and small/medium benthic piscivores concentrated in the eastern Shelf and in the middle and offshore eastern Shelf, respectively. Whereas the large benthic benthivores concentrated on the southwestern and middle Shelf areas, and large benthic piscivores concentrated in the Bay of Fundy and the inshore western Shelf. Where sizes were differentiated for invertebrates, this size partitioning also occurred and hotspots of the small benthic invertebrate benthivores were also mostly on the eastern Shelf, similar to the fish. These findings also seem to agree with the literature where studies have found spatial partitioning based on size and decreased overlap between functional groups in populations that have been depleted (Garrison and Link 2000).

Synoptic views of marine ecosystems are hard to achieve and this analysis is no exception. We relied on fishery independent bottom trawl research surveys of the Scotian shelf as our data source for describing priority areas for the conservation of functional groups. The Survey data provide widespread coverage spatially and temporally, but nonetheless do have some limitations: (i) The survey bounds do not cover the population bounds for all species and therefore only represent the relative hotspots within the survey footprint, rather than the absolute hotspots for the species. For example, for the group of pelagic fish that are mainly planktivores (all sizes, Figures 16 and 17), it is important to note that there were large inshore herring populations (herring represents 73% of this group; Power et al. 2006) that were not captured in the trawl survey. (ii) Some species are not well sampled by the RV Survey, which was originally designed to catch groundfish. Pelagic species, for example, are generally located higher in the water column above the trawl net; therefore their catchability by trawl gear will be minimal. This is especially true for large pelagic piscivores such as tunas and swordfish which were not included in this analysis. Similarly, the survey may not adequately catch all species within functional groups, particularly for groups where species of various sizes were combined, such as the pelagic piscivore and pelagic planktivore groups that include small, medium and large-sized fish (Table 3). (iii) The RV survey is only conducted during the summer months over the whole Scotian Shelf, and therefore gives a summer snapshot of the spatiotemporal distributions. Some of these gaps may be filled by including other data sources, especially ones that run in alternate seasons, sample other parts of the water column, or target different sizes or taxa, into a similar analysis that describes spatial patterns of these functional groups.

DFO's primary goal for MPA networks is "To provide long-term protection of marine biodiversity, ecosystem function and special natural features" (Government of Canada 2011). To help meet this goal, we suggest prioritizing areas with high functional diversity, that is, areas that are important across multiple groups, and at least a portion of the hotspots represented by every functional group. Protecting areas of high functional diversity will help to maintain biodiversity and ecosystem functioning. As well, we suggest prioritizing the hotspots for groups that are dominated by a few species that are particularly vulnerable to perturbations (*e.g.*, fishing or climate change), such as the large benthic benthivores that have been heavily targeted and depleted (Bundy 2005; Shackell and Frank 2007; Shackell et al. 2012). Since many of the groups identified in this study are dominated by only a few species, and with many newly developing fisheries in the areas, care is needed to ensure functional groups are preserved to maintain and restore resilience and integrity of the ecosystem.

REFERENCES

Bellwood, D.R., Hughes, T.P., Folke, C., and Nystrom, M. 2004. Confronting the coral reef crisis. Nature, 429: 827-833.

Britten, G.L., Dowd, M., Minto, C., Ferretti, F., Boero, F., and Lotze, H.K. 2014. Predator decline leads to decreased stability in a coastal fish community. Ecol. Lett. 17(12): 1518-1525.

Bundy, A. 2005. Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s. Can. J. Fish. Aquat. Sci. 62: 1453-1473.

Bundy, A., and Fanning, LP. 2005. Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada. Can. J. Fish. Aquat. Sci. 62: 1474-1489.

Cadotte, M.W. 2011. The new diversity: management gains through insights into the functional diversity of communities. J. App. Ecol. 48: 1067-1069.

Choi, J.S., Frank, K.T., Leggett, W.C., and Drinkwater, K. 2004. Transition to an alternate state in a continental shelf ecosystem. Can. J. Fish. Aquat. Sci. 61: 505–510.

Doubleday, W.G. 1981. Studies No. 2, Manual on groundfish surveys in the Northwest Atlantic (NAFO Scientific Council Studies, 1981).

Fanning, L.P. 1985. Intercalibration of research vessel survey results obtained by different vessels. CAFSAC Res. Doc. 85/3: 43 p.

Fonseca, C. R., and Ganade, G. 2001. Species functional redundancy, random extinctions and the stability of ecosystems. J. Ecol. 89(1): 118-125.

Frank, K.T., Petrie, B., Choi, J.S., and Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308: 1621-1623.

Frank, K.T., Petrie, B., Fisher, J.A.D., and Leggett, W.C. 2011. Transient dynamics of an altered large marine ecosystem. Nature, 477: 86-89.

Garrison, L.P., and Link, J.S. 2000. Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. ICES Journal of Marine Science, 57: 723-730.

Gaston, K.J., and Fuller, R.A. 2007. Commonness, population depletion and conservation biology. Trends Ecol. Evol. 23(1): 14-19.

Government of Canada. 2010. Spotlight on Marine Protected Areas in Canada. Fisheries and Oceans Canada. Ottawa. 24 pp.

Government of Canada. 2011. National Framework for Canada's Network of Marine Protected Areas. Fisheries and Oceans Canada, Ottawa. 31 pp.

Horsman, T.L., and Shackell, N.L. 2009. Atlas of important habitat for key fish species of the Scotian Shelf, Canada. Can. Tech. Rep. Fish. Aquat. Sci. 2835: viii + 82 p.

McCann, K.S. 2000. The diversity–stability debate. Nature, 405(6783): 228-233.

Micheli, F., and Halpern, B.S. 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett, 8: 391-400.

Power, M., K.J. Clark, F.J. Fife, D. Knox, G.D. Melvin, R.L. Stephenson and L.M. Annis. 2006. 2006 Evaluation of 4VWX Herring CSAS. 2006/049.

Reecht, Y., Rochet, M.J., Trenkel, V.M., Jennings, S., and Pinnegar, J.K. 2013. Use of morphological characteristics to define functional groups of predatory fishes in the Celtic Sea. J. Fish. Biol. 83: 355-377.

Rice, J., Daan, N., Gislason, H., and Pope, J. 2013. Does functional redundancy stabilize fish communities? ICES J. Mar. Sci. 70(4): 734-742.

Shackell, N.L., and Frank, K.T. 2007. Compensation in exploited marine fish communities on the Scotian Shelf, Canada. Mar. Ecol. Prog. Ser. 336: 235-247.

Shackell, N.L., Bundy, A., Nye, J.A., and Link, J.S. 2012. Common large-scale responses to climate and fishing across Northwest Atlantic ecosystems. ICES J. Mar. Sci. 70(4): 755-767.

Simon, J.E., and Comeau, P.A. 1994. Summer Distribution and Abundance Trends of Species Caught on the Scotian Shelf 1970-92, by the Research Vessel Groundfish Survey. Can. Tech. Rep. Fish. Aquat. Sci. 1953: x+145 p.

Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoldi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M.A., Willis, T.J., and Edgar, G.J. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature, 501: 539-541.

Tremblay, M.J., Black, G.A.P., and Branton, R.M. 2007. The distribution of common decapod crustaceans and other invertebrates recorded in annual ecosystem surveys of the Scotian Shelf 1999-2006. Can. Tech. Rep. Fish. Aquat. Sci. 2762: iii + 74 p.

Ward-Paige, C.A., and Bundy, A. 2015. Mapping biodiversity on the Scotian Shelf. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/006: v + 90 p.

Zwanenburg, K.C.T., Bundy, A., Strain, P., Bowen, W.D., Breeze, H., Campana, S.E., Hannah, C., Head, E. and Gordon, D. 2006. Implications of ecosystem dynamics for the integrated management of the Eastern Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2652: xiii + 91 p.

TABLES

Table 1. Summary of number of sets in each of the data layers created in this study.

Time period (by fishing era)	Fish (1970-2014)	Invertebrates (2007-2014)
Era 1: 1970-1977	1145	NA
Era 2: 1978-1985	1181	NA
Era 3: 1986-1993	1516	NA
Era 4: 1994-2006	2487	NA
Era 5: 2007-2014	1315	1315
Complete	7644	NA

Table 2. Total biomass in kilograms from all tows for each functional group in each fishing era (average annual biomass in brackets).

Group	Era 1 (1970-77)	Era 2 (1978-85)	Era 3 (1986-93)	Era 4 (1994-2006)	Era 5 (2007-14)	Era All (1970-2014)
1. Fish: Piscivore, Benthic, Small + Medium	12904 (1613)	21379 (2672)	23080 (2885)	29916 (2301)	22676 (2835)	109955 (2443)
2. Fish: Piscivore, Benthic, Large	63285 (7911)	118950 (14869)	152925 (19116)	160829 (12371)	60825 (7603)	556814 (12374)
3. Fish: Piscivore, Pelagic, Small + Medium + Large	1 (0.13)	1 (0.13)	2 (0.25)	58 (4.5)	43 (5.4)	105 (2.3)
4. Fish: Benthivore, Benthic, Small	4 (0.5)	5 (0.63)	18 (2.3)	122 (9.4)	28 (3.5)	176 (3.9)
5. Fish: Benthivore, Benthic, Medium	4454 (557)	3709 (464)	5450 (681)	9996 (769)	6929 (866)	30538 (679)
6. Fish: Benthivore, Benthic, Large	33394 (4174)	59078 (7385)	58329 (7291)	97866 (7528)	41411 (5176)	290078 (6446)
7. Fish: Planktivore, Pelagic, Small + Medium + Large	2637 (330)	2964 (371)	7912 (989)	40541 (3119)	17449 (2181)	71503 (1589)
8. Fish: Zoopiscivore, Benthic, Small + Medium + Large	35801 (4475)	31887 (3985)	51091 (6386)	81227 (6248)	72862 (9108)	272868 (6064)
9. Fish: Zoopiscivore, Pelagic, Small + Medium + Large	213 (27)	617 (77)	2725 (340)	2516 (194)	710 (89)	6781 (151)
10. Invertebrate: Benthivore, Benthic, Small	NA	NA	NA	NA	9231 (1154)	NA
11. Invertebrate: Benthivore, Benthic, Medium	NA	NA	NA	NA	8126 (1016)	NA
12. Invertebrate: Zoopiscivore, Small + Medium + Large	NA	NA	NA	NA	23 (2.9)	NA
13 Invertebrate: Filter feeder, Benthic, Colonial	NA	NA	NA	NA	67 (8.4)	NA
14. Invertebrate: Filter feeder, Benthic, Non-colonial	NA	NA	NA	NA	854 (107)	NA
15. Invertebrate: Detritivore	NA	NA	NA	NA	1853 (232)	NA

Table 3. List of species and traits used to define membership in each group. Size: 1 = small, 2 = medium, 3 = large; Habitat: 1 = benthic (in, on, or just above substrate), 2 = pelagic (in water column); Feeding guild: 1 = mainly piscivore, 2 = mainly benthivore, 3 = mainly planktivore, 4 = mainly zoopiscivore, 5 = filter feeder, 6 = detritivore. The percent of total group biomass for all time periods is also included, which shows the species that makes the majority of the biomass in each group and therefore influential for the spatial patterns of hotspots.

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
Fish: Piscivore, Benthic, Small + Medium							
	14	Silver hake	*Merluccius bilinearis*	2	1	1	53.3
	19	Off-shore hake	*Merluccius albidus*	2	1	1	0.6
	42	Yellowtail flounder	*Limanda ferruginea*	2	1	1	29.2
	118	Greenland cod	*Gadus ogac*	2	1	1	0.0
	143	Brill/windowpane	*Scophthalmus aquosus*	2	1	1	0.1
	149	Longnose greeneye	*Parasudis truculenta*	1	1	1	0.0
	300	Longhorn sculpin	*Myoxocephalus octodecemspinosus*	2	1	1	10.9
	320	Sea raven	*Hemitripterus americanus*	2	1	1	5.9
Fish: Piscivore, Benthic, Large							
	10	Cod (Atlantic)	*Gadus morhua*	3	1	1	27.0
	12	White hake	*Urophycis tenuis*	3	1	1	7.4
	15	Cusk	*Brosme brosme*	3	1	1	0.9
	16	Pollock	*Pollachius virens*	3	1	1	17.0
	30	Halibut (atlantic)	*Hippoglossus hippoglossus*	3	1	1	1.5
	31	Turbot, greenland halibut	*Reinhardtius hippoglossoides*	3	1	1	0.9
	40	American plaice	*Hippoglossoides platessoides*	3	1	1	7.3
	141	Summer flounder	*Paralichthys dentatus*	3	1	1	0.0
	200	Barndoor skate	*Dipturus laevis*	3	1	1	0.2
	204	Winter skate	*Leucoraja ocellata*	3	1	1	1.9
	216	Atlantic torpedo	*Torpedo nobiliana*	3	1	1	0.0
	220	Spiny dogfish	*Squalus acanthias*	3	1	1	34.4

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	400	Monkfish, goosefish, angler	*Lophius americanus*	3	1	1	1.6
	704	Amer. John dory	*Zenopsis ocellata*	3	1	1	0.0
Fish: Piscivore, Pelagic, Small + Medium							
	63	Rainbow smelt	*Smerus mordax mordax*	2	2	1	1.3
	159	Boa dragonfish	*Stomias boa*	1	2	1	60.6
	169	Viperfish	*Chauliodus sloani*	2	2	1	9.1
	712	White barracudina	*Notolepis rissoi kroyeri*	1	2	1	29.0
Fish: Benthivore, Benthic, Small							
	44	Gulf stream flounder	*Citharichthys arctifrons*	1	1	2	5.5
	302	Arctic staghorn sculpin	*Gymnocanthus tricuspis*	1	1	2	2.5
	303	Grubby (little)	*Myoxocephalus aeneus*	1	1	2	0.6
	304	Moustache (mailed) sculpin	*Triglops murrayi*	1	1	2	52.3
	306	Arctic hookear sculpin	*Artediellus uncinatus*	1	1	2	1.2
	307	Polar sculpin	*Cottunculus microps*	1	1	2	2.9
	313	Twohorn sculpin	*Icelus bicornis*	1	1	2	0.1
	314	Spatulate sculpin	*Icelus spatula*	1	1	2	0.5
	316	Arctic sculpin	*Myoxocephalus scorpioides*	1	1	2	0.1
	331	Armored sea robin	*Peristedion miniatum*	1	1	2	0.3
	340	Alligatorfish	*Aspidophoroides monopterygius*	1	1	2	7.2
	341	Arctic alligatorfish	*Uleina olrikii*	1	1	2	0.0
	350	Atlantic sea poacher	*Leptagonus decagonus*	1	1	2	9.3
	502	Atlantic spiny lumpsucker	*Eumicrotremus spinosus*	1	1	2	11.7
	503	Atlantic seasnail	*Liparis atlanticus*	1	1	2	0.9
	505	Seasnail, gelatinous	*Liparis fabricii*	1	1	2	0.2
	508	Inquiline seasnail	*Liparis inquilinus*	1	1	2	0.0
	520	Sea tadpole	*Careproctus reinhardi*	1	1	2	0.1

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	603	Wolf eelpout	*Lycenchelys verrilli*	1	1	2	1.7
	617	Common wolf eel	*Lycenchelys paxillus*	1	1	2	0.0
	621	Rock gunnel (eel)	*Pholis gunnellus*	1	1	2	0.2
	626	4-Line snake blenny	*Eumesogrammus praecisus*	1	1	2	0.7
	637	Spotfin dragonet	*Callionymus agassizi*	1	1	2	0.3
	816	Tongue fish	*Symphurus pterospilotus*	1	1	2	0.1
	880	Hookear sculpin, Atlantic	*Artediellus atlanticus*	1	1	2	1.8
Fish: Benthivore, Benthic, Medium							
	17	Tomcod (Atlantic)	*Microgadus tomcod*	2	1	2	0.1
	41	Witch flounder	*Glyptocephalus cynoglossus*	2	1	2	35.6
	43	Winter flounder	*Pseudopleuronectes americanus*	2	1	2	43.1
	111	Spotted hake	*Urophycis regia*	2	1	2	0.0
	114	Fourbeard rockling	*Enchelyopus cimbrius*	2	1	2	0.2
	115	Threebeard rockling	*Gaidropsarus ensis*	2	1	2	0.0
	122	Cunner	*Tautogolabrus adspersus*	2	1	2	0.2
	123	Rosefish (black belly)	*Helicolenus dactylopterus*	2	1	2	3.2
	142	Fourspot flounder	*Paralichthys oblongus*	2	1	2	0.2
	156	Short-nose greeneye	*Chlorophthalmus agassizi*	2	1	2	0.0
	202	Smooth skate	*Malacoraja senta*	2	1	2	5.8
	203	Little skate	*Leucoraja erinacea*	2	1	2	8.3
	301	Shorthorn sculpin	*Myoxocephalus scorpius*	2	1	2	0.1
	308	Pallid sculpin	*Cottunculus thompsoni*	2	1	2	0.0
	410	Marlin-spike grenadier	*Nezumia bairdii*	2	1	2	0.7
	412	Roughnose grenadier	*Trachyrhynchus murrayi*	2	1	2	0.0
	512	Seasnail, dusky	*Liparis gibbus*	2	1	2	0.0

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	616	Fish doctor	*Gymnelis viridis*	2	1	2	0.0
	620	Laval's eelpout	*Lycodes lavalaei*	2	1	2	0.1
	622	Snakeblenny	*Lumpenus lumpretaeformis*	2	1	2	0.2
	631	Slender eelblenny	*Lumpenus fabricii*	2	1	2	0.0
	647	Checker eelpout (vahl)	*Lycodes vahlii*	2	1	2	2.1
	742	Atlantic batfish	*Dibranchus atlanticus*	2	1	2	0.0
Fish: Benthivore, Benthic, Large							
	11	Haddock	*Melanogrammus aeglefinus*	3	1	2	87.2
	50	Striped Atlantic wolffish	*Anarhichas lupus*	3	1	2	2.9
	51	Spotted wolffish	*Anarhichas minor*	3	1	2	0.0
	52	Northern wolffish	*Anarhichas denticulatus*	3	1	2	0.1
	201	Thorny skate	*Amblyraja radiata*	3	1	2	8.9
	221	Black dogfish	*Centroscyllium fabricii*	3	1	2	0.3
	411	Roughhead grenadier	*Macrourus berglax*	3	1	2	0.0
	604	Slender snipe eel	*Nemichthys scolopaceus*	3	1	2	0.0
	630	Wrymouth	*Cryptacanthodes maculatus*	3	1	2	0.0
	640	Ocean pout (common)	*Zoarces americanus*	3	1	2	0.6
	743	Amer barrelfish	*Hyperoglyphe perciformis*	3	1	2	0.0
Fish: Planktivore, Pelagic, Small + Medium + Large							
	60	Herring (Atlantic)	*Clupea harengus*	2	2	3	72.7
	61	Shad American	*Alosa sapidissima*	2	2	3	1.7
	62	Alewife	*Alosa pseudoharengus*	2	2	3	2.3
	160	Argentine (Atlantic)	*Argentina silus*	2	2	3	9.8
	163	Lanternfish, horned	*Ceratoscopelus maderensis*	3	2	3	0.0
	165	Blueback herring	*Alosa aestivalis*	2	2	3	0.0

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	610	Northern sand lance	*Ammodytes dubius*	1	2	3	13.5
	625	Radiated shanny	*Ulvaria subbifurcata*	1	2	3	0.0
	720	Atlantic saury, needlefish	*Scomberesox saurus*	2	2	3	0.0
	771	Beardfish	*Polymixia lowei*	1	2	3	0.0
Fish: Zoopiscivore, Benthic, Small + Medium + Large							
	13	Squirrel or red hake	*Urophycis chuss*	2	1	4	1.0
	23	Redfish unseparated	*Sebastes sp.*	2	1	4	97.6
	112	Longfin hake	*Phycis chesteri*	2	1	4	0.7
	409	American straptail grenadier	*Malacocephalus occidentalis*	2	1	4	0.0
	414	Rock grenadier (roundnose)	*Coryphaenoides rupestris*	3	1	4	0.4
	501	Lumpfish	*Cyclopterus lumpus*	2	1	4	0.2
	595	Red dory	*Cyttus roseus*	2	1	4	0.0
	602	Gray’s cutthroat eel	*Synaphobranchus kaupi*	3	1	4	0.1
	623	Daubed shanny	*Leptoclinus maculates*	1	1	4	0.0
	641	Arctic eelpout	*Lycodes reticulatus*	2	1	4	0.0
	714	Frostfish	*Benthodesmus elongates simonyi*	3	1	4	0.0
	744	Stout beard fish	*Polymixia nobilis*	2	1	4	0.0
Fish: Zoopiscivore, Pelagic, Small + Medium + Large							
	64	Capelin	*Mallotus villosus*	1	2	4	38.2
	70	Mackerel (Atlantic)	*Scomber scombrus*	2	2	4	59.0
	158	Muller’s pearlsides	*Maurolicus muelleri*	1	2	4	0.0
	646	Atlantic soft pout	*Melanostigma atlanticum*	1	2	4	0.0
	701	Butterfish	*Peprilus triacanthus*	1	2	4	2.7
	711	Short barracudina	*Paralepis atlantica*	2	2	4	0.1
Invertebrate: Benthivore, Benthic, Small							
	2211	Pandalus borealis	*Pandalus borealis*	1	1	2	53.1
	2212	Pandalus montagui	*Pandalus montagui*	1	1	2	17.3

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	2213	Pandalus propinquus	*Pandalus propinquus*	1	1	2	0.0
	2221	P. multidentata	*Pasiphaea multidentata*	1	1	2	0.5
	2312	Lebbeus polaris	*Lebbeus polaris*	1	1	2	0.0
	2313	S. liljeborgii	*Spirontocaris liljeborgii*	1	1	2	0.0
	2316	S. spinus	*Spirontocaris spinus*	1	1	2	0.0
	2319	L. groenlandicus	*Lebbeus groenlandicus*	1	1	2	0.0
	2411	Argis dentata	*Argis dentata*	1	1	2	0.8
	2414	S. boreas	*Sclerocrangon boreas*	1	1	2	0.1
	2415	P. norvegicus	*Pontophilus norvegicus*	1	1	2	0.0
	2417	C. septemspinosa	*Crangon septemspinosa*	1	1	2	0.0
	2420	Sabinea sp.	*Sabinea sp.*	1	1	2	0.0
	2511	Jonah crab	*Cancer borealis*	1	1	2	1.9
	2513	Atlantic rock crab	*Cancer irroratus*	1	1	2	3.5
	2519	Spider crab (NS)	*Majidae F.*	1	1	2	0.0
	2521	Hyas coarctatus	*Hyas coarctatus*	1	1	2	0.6
	2523	Northern stone crab	*Lithodes maja*	1	1	2	1.1
	2527	Toad crab	*Hyas araneus*	1	1	2	0.5
	2532	Deep sea red crab	*Geryon quinquedens*	1	1	2	0.9
	2541	Axius serratus	*Axius serratus*	1	1	2	0.0
	2555	Munida iris	*Munida iris*	1	1	2	0.0
	2559	Hermit crabs	*Paguridae F.*	1	1	2	0.3
	3200	Sea mouse	*Aphrodita hastata*	1	1	2	0.1
	3501	L. squamatus	*Lepidonotus squamatus*	1	1	2	0.0
	4211	Wave whelk, common edible	*Buccinum undatum*	1	1	2	0.1
	4221	Moonshell	*Lunatia heros*	1	1	2	0.1
	5100	Sea spider	*Pycnogonida sp.*	1	1	2	0.0
	6113	L. polaris	*Leptasterias polaris*	1	1	2	2.5
	6117	H. phrygiana	*Hippasteria phrygiana*	1	1	2	2.0
	6119	Blood star	*Henricia sanguinolenta*	1	1	2	0.1
	6125	Pteraster militaris	*Pteraster militaris*	1	1	2	0.0

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	6411	S. droebachiensis	*Strongylocentrotus droebachiensis*	1	1	2	13.7
	6413	Heart urchin	*Brisaster fragilis*	1	1	2	0.2
	6421	Purple sea urchin	*Arabacia punctulata*	1	1	2	0.0
	6511	E. parma	*Echinarachnius parma*	1	1	2	0.2
	8346	Pseudarchaster parelli	*Pseudarchaster parelli*	1	1	2	0.0
	8347	Psilaster andromeda	*Psilaster andromeda*	1	1	2	0.2
Invertebrate: Benthivore, Benthic, Medium							
	2525	Spiny crab	*Lithodes/Neolithodes*	2	1	2	0.0
	2526	Snow crab (queen)	*Chionoecetes opilio*	2	1	2	23.9
	2528	Spiny spider crab	*Neolithodes grimaldi*	2	1	2	0.0
	2550	American lobster	*Homarus americanus*	2	1	2	67.1
	6101	Ceremaster granularis	*Ceremaster graularis*	2	1	2	0.1
	6111	Purple starfish	*Asterias vulgaris*	2	1	2	4.8
	6121	Purple sunstar	*Solaster endeca*	2	1	2	2.4
	6123	Sun star	*Solaster papposus*	2	1	2	1.7
Invertebrate: Zoopiscivore, Small + Medium + Large							
	4512	Long-finned squid	*Loligo pealei*	1	2	4	47.9
	4536	Sepiolidae F.	*Sepiolodae f.*	1	1	4	10.7
	8520	Jellyfish	*Pelagia noctiluca*	1	2	4	41.4
Invertebrate: Filter feeder, Benthic, Colonial							
	8322	P. resedaeformis	*Primnoa resedaeformis*	4	1	5	0.5
	8323	Paragorgia arborea	*Paragorgia arborea*	4	1	5	94.1
	8324	Sea cauliflower	*Duva multiflora*	4	1	5	1.8
	8325	Gold-banded/Bamboo coral	*Keratoisis ornata*	4	1	5	3.1
	8326	Acanthogorgia armata	*Acanthogorgiana armata*	4	1	5	0.3
	8329	Acanella arbuscula	*Acanellana arbuscula*	4	1	5	0.1
	8330	Radicipes gracilis	*Radicipes gracilis*	4	1	5	0.2
Invertebrate: Filter feeder, Benthic, Non-colonial							
	1823	Sea potato	*Boltenia sp.*	1	1	5	13.0

Group	Code	Name	Latin name	Size	Habitat	Feeding guild	% of group biomass (all time periods)
	4304	Ocean quahaug	*Arctica islandica*	1	1	5	0.1
	4312	Bank clam	*Cyrtodaria siliqua*	1	1	5	0.2
	4317	Bar, surf clam	*Spisula solidissima*	1	1	5	0.4
	4321	Sea scallop	*Placopecten magellanicus*	1	1	5	41.9
	4322	Iceland scallop	*Chlamys islandicus*	1	1	5	10.9
	4331	Common mussels	*Mytilus edulis*	1	1	5	1.2
	4332	Horse mussels	*Modiolus modiolus*	2	1	5	1.1
	8335	Cup coral	*Flabellum sp.*	1	1	5	0.4
	8356	Sponge	*Rhizaxinella sp.*	1	1	5	1.0
	8601	Russian hats	*Vazellana pourtalesi*	1	1	5	30.0
Invertebrate: Detritivore							
	6115	Mud star	Ctenodiscus crispatus	1	1	6	3.0
	6201	Ophiacantha abyssicola	*Ophiacanthana abyssicola*	1	1	6	0.0
	6211	Daisy	*Ophiopholis aculeata*	1	1	6	0.0
	6213	Ophiura sarsi	*Ophiura sarsi*	1	1	6	0.3
	6611_6600	Sea cucumbers + Cucumaria frondosa	*Holothuroidea c. + Cucumaria frondosa*	2	1	6	96.7

FIGURES

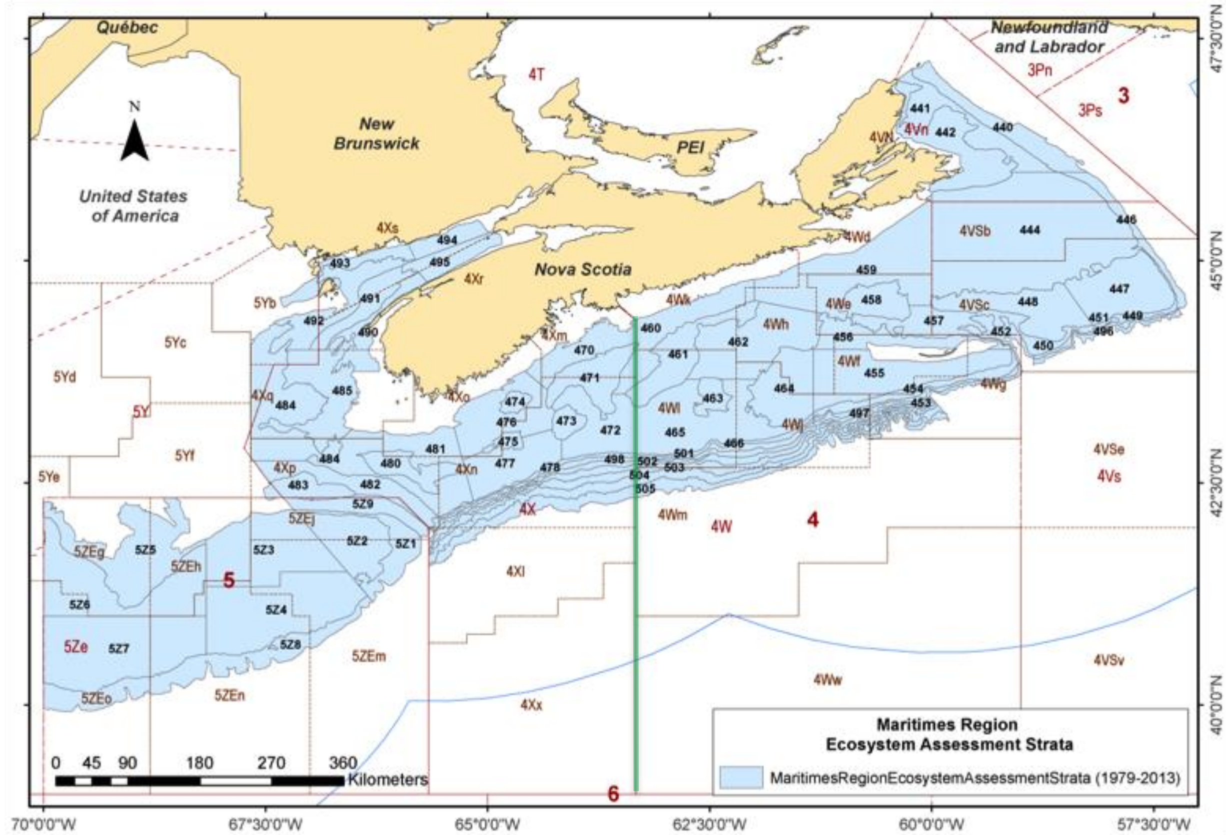

Figure 1. Research vessel survey strata in study area, which includes the Bay of Fundy, Atlantic Coast around Nova Scotia and the Offshore Scotian Shelf. Green line highlights the divide between the western portion of the study area (4X) and the eastern portion (4VW).

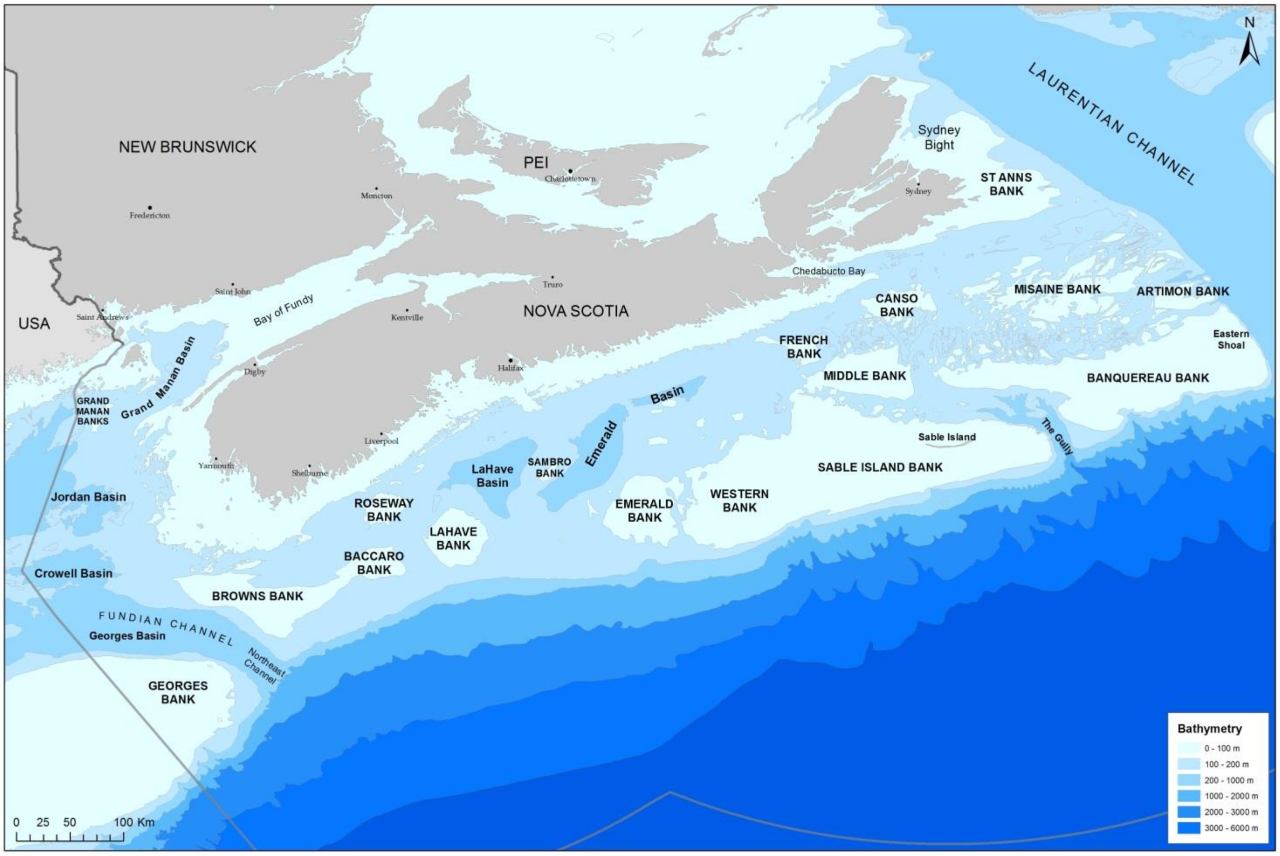

Figure 2. Map of the Scotian Shelf showing the location of the major banks and basins.

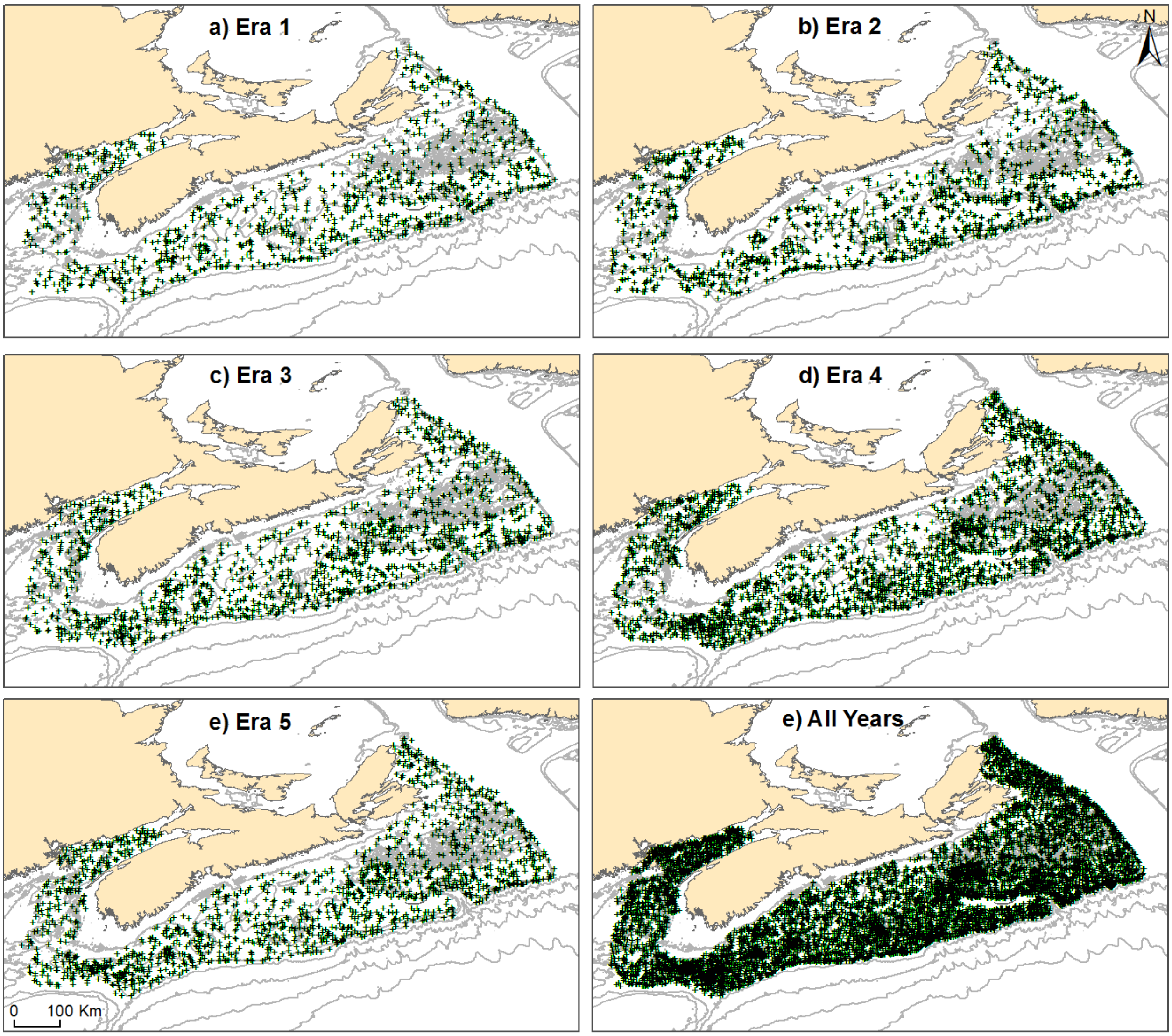

Figure 3. Research vessel survey footprint for each era and all eras combined.

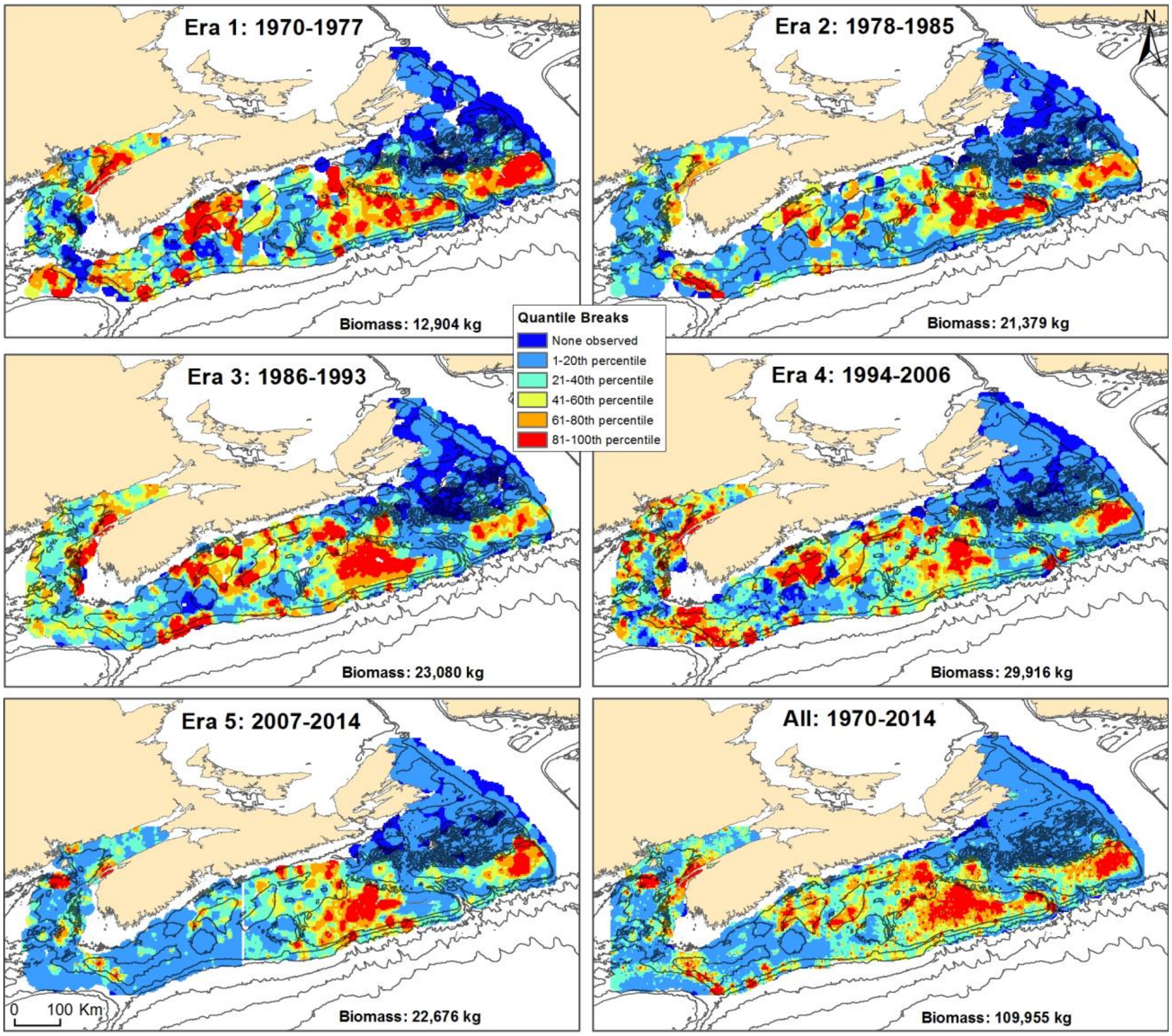

Figure 4. Fish: Piscivores, benthic, small and medium. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

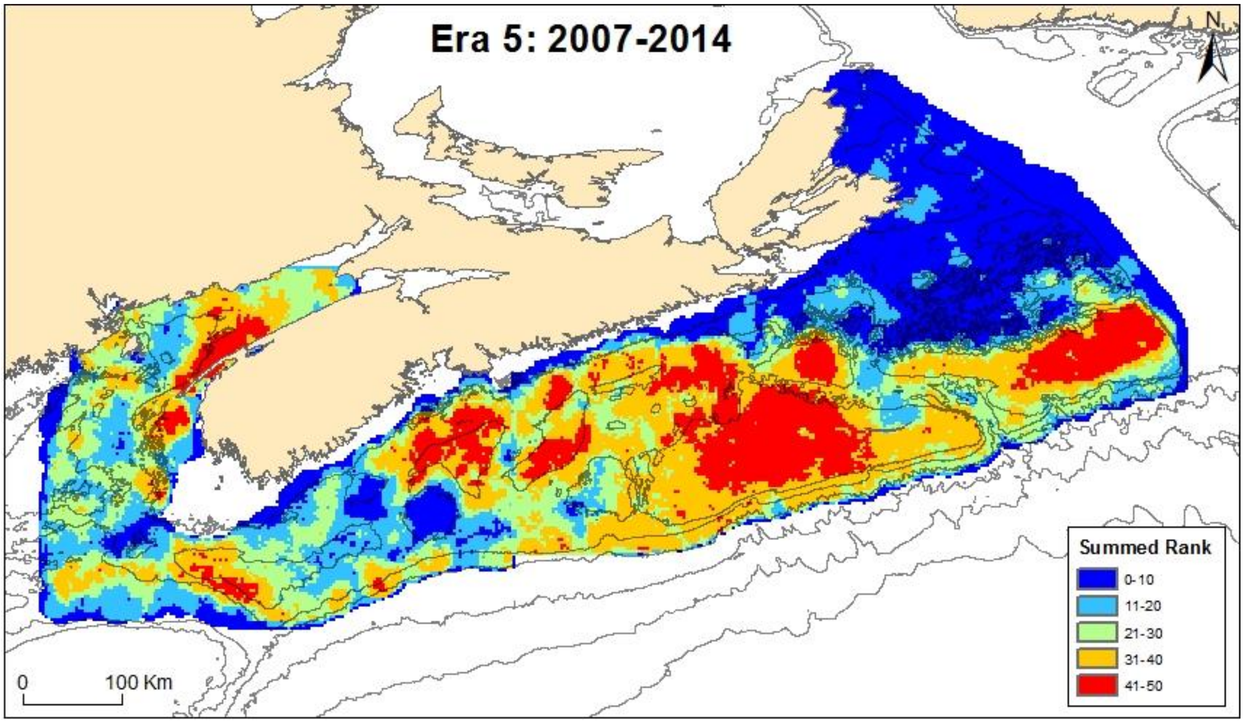

Figure 5. Fish: Piscivores, benthic, small and medium. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

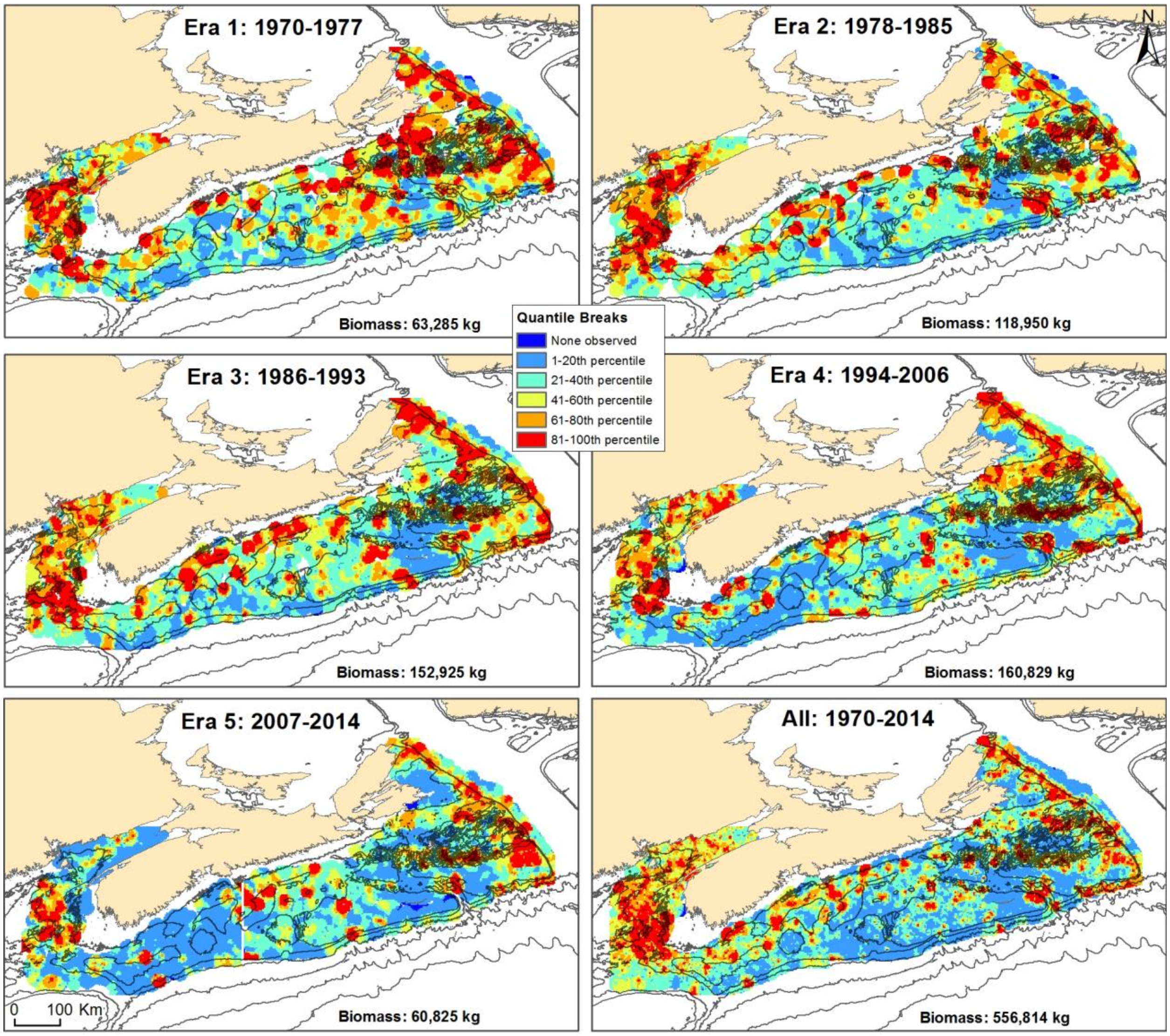

Figure 6. Fish: Piscivores, benthic, large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

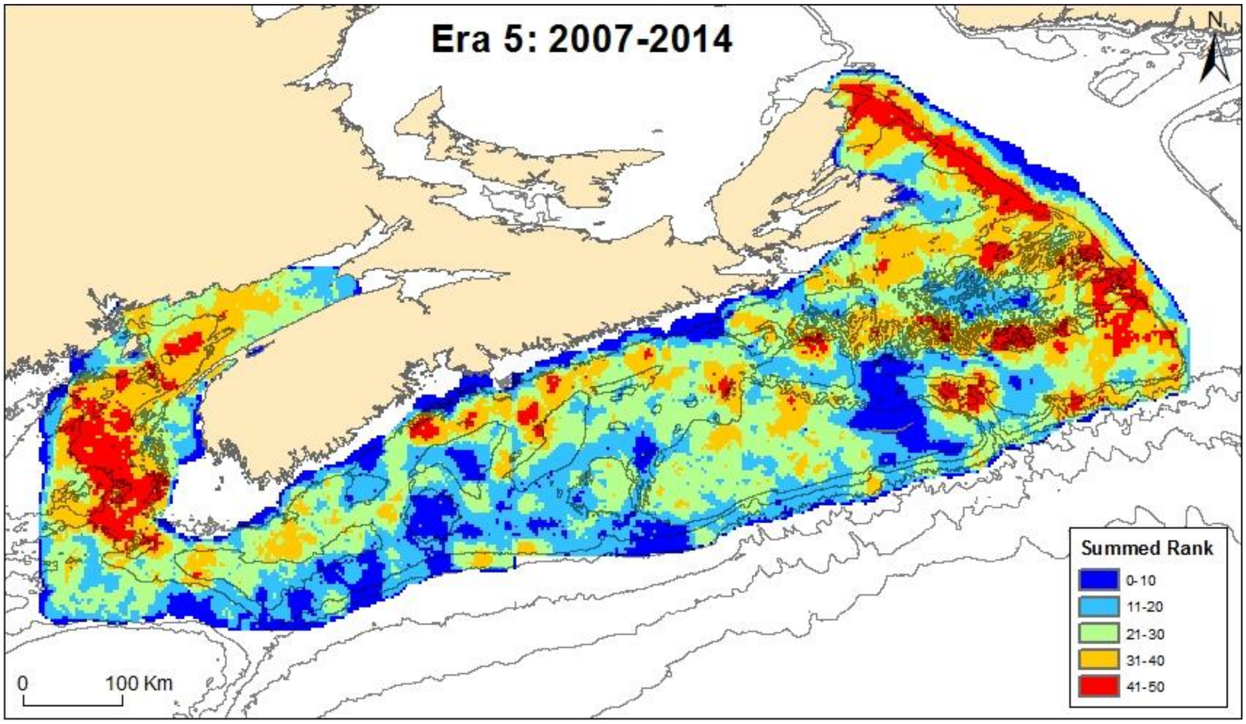

Figure 7. Fish: Piscivores, benthic, large. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

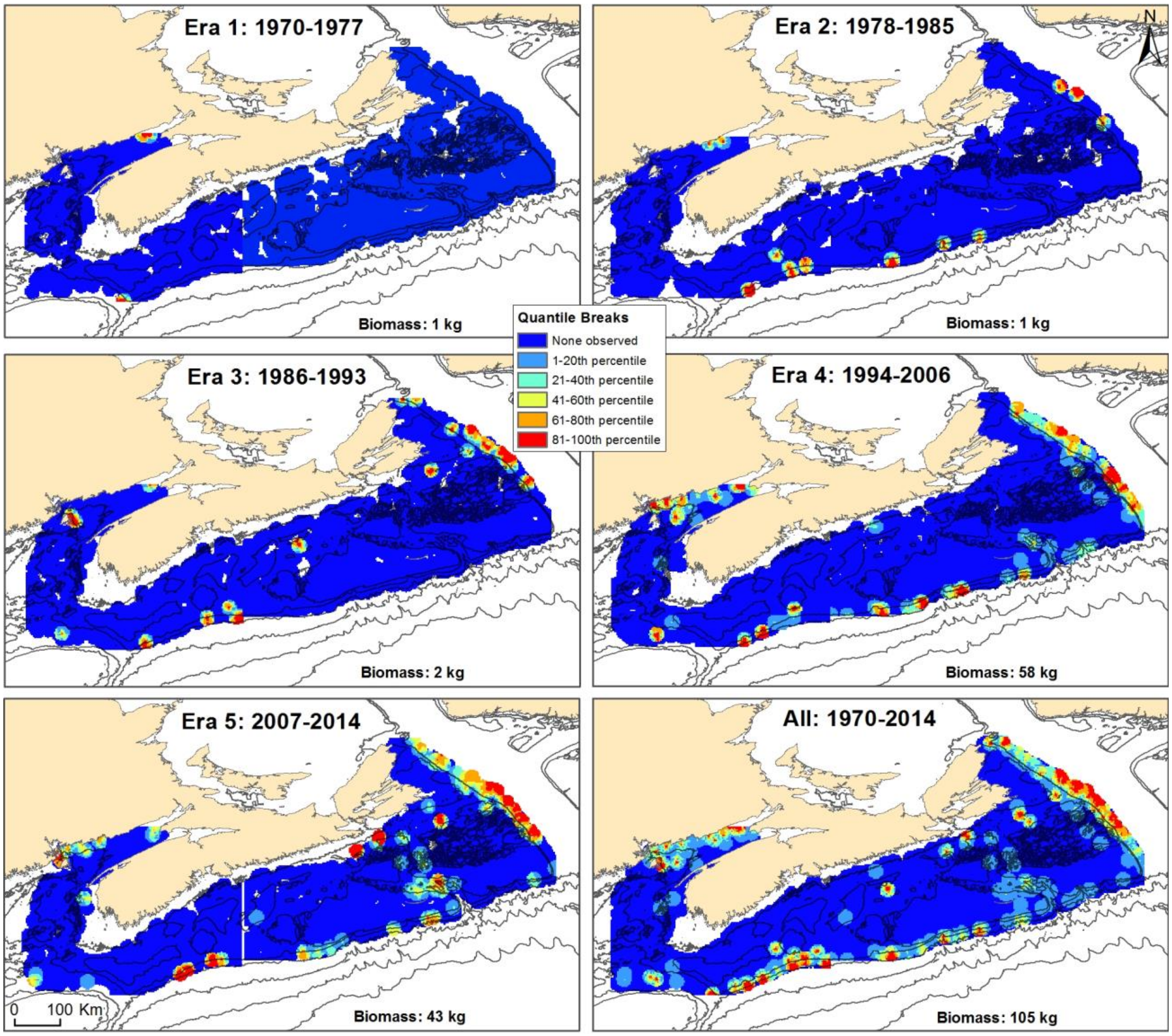

Figure 8. Fish: Piscivores, pelagic, small, medium and large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

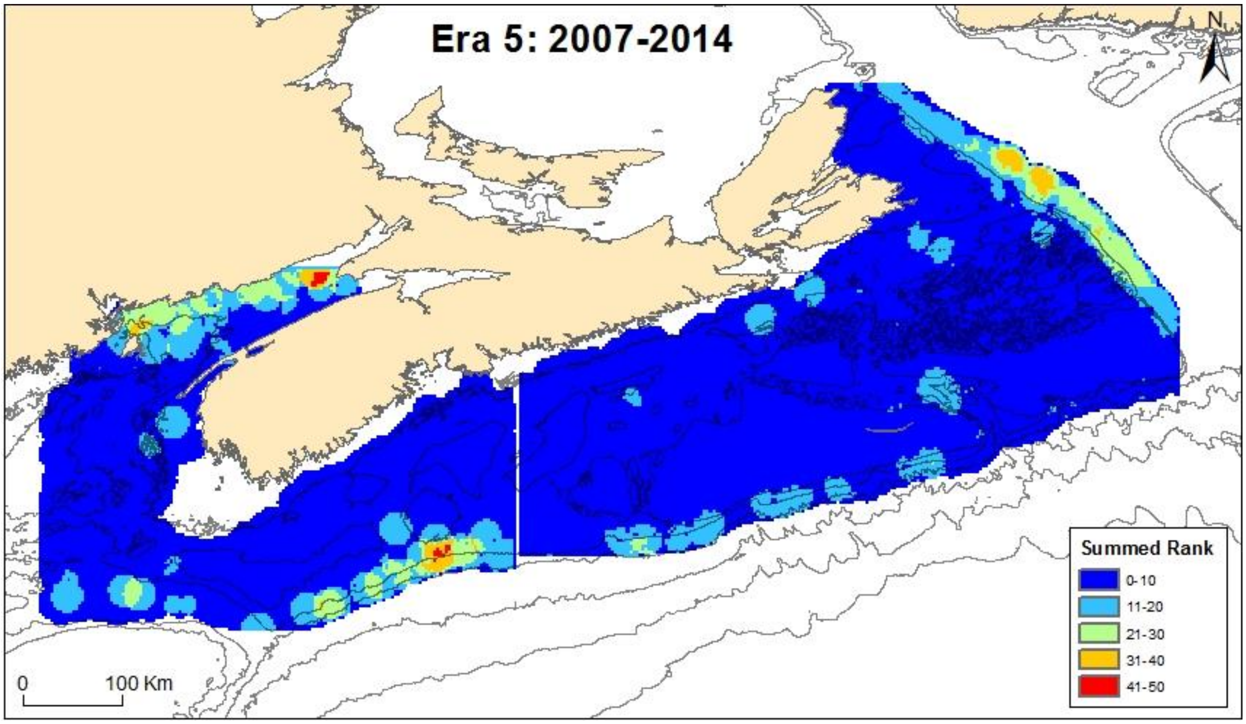

Figure 9. Fish: Piscivores, pelagic, small, medium and large. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

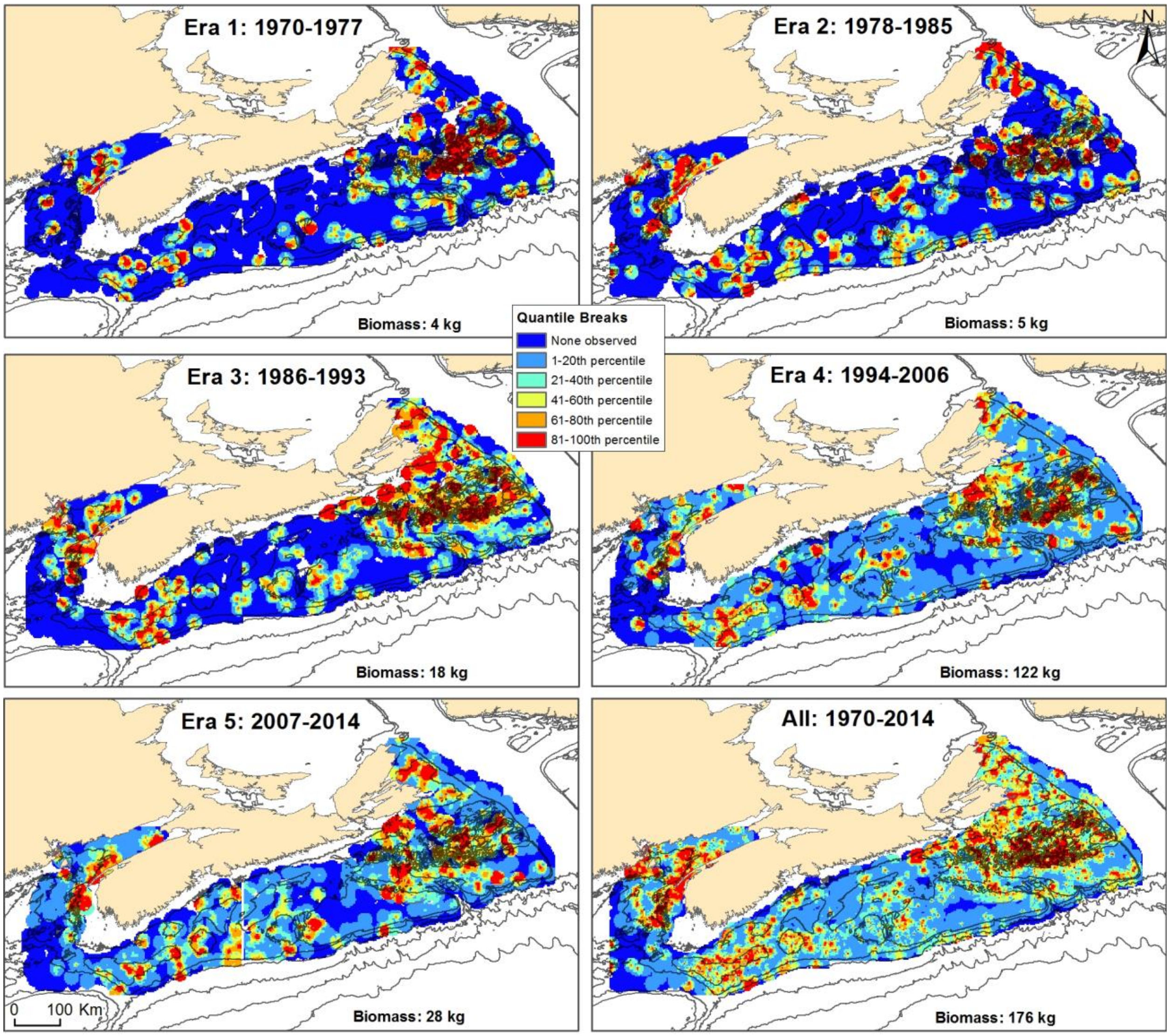

Figure 10. Fish: Benthivores, benthic, small. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

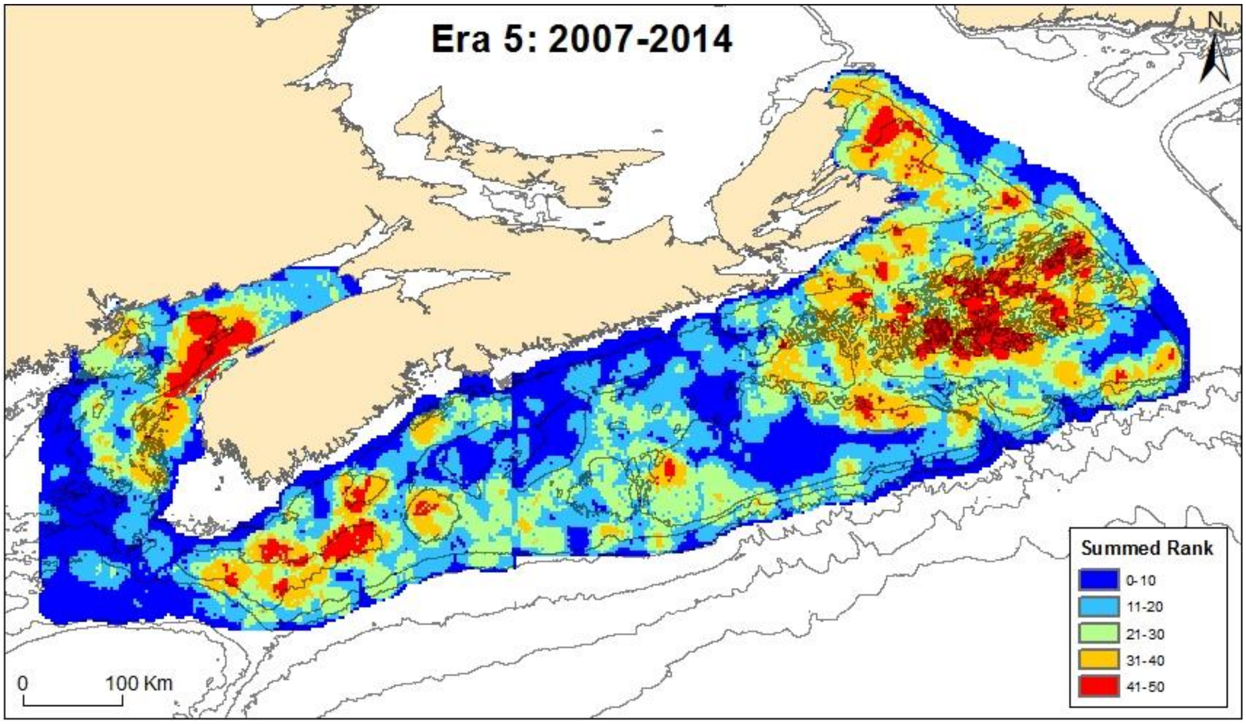

Figure 11. Fish: Benthivores, benthic, small. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

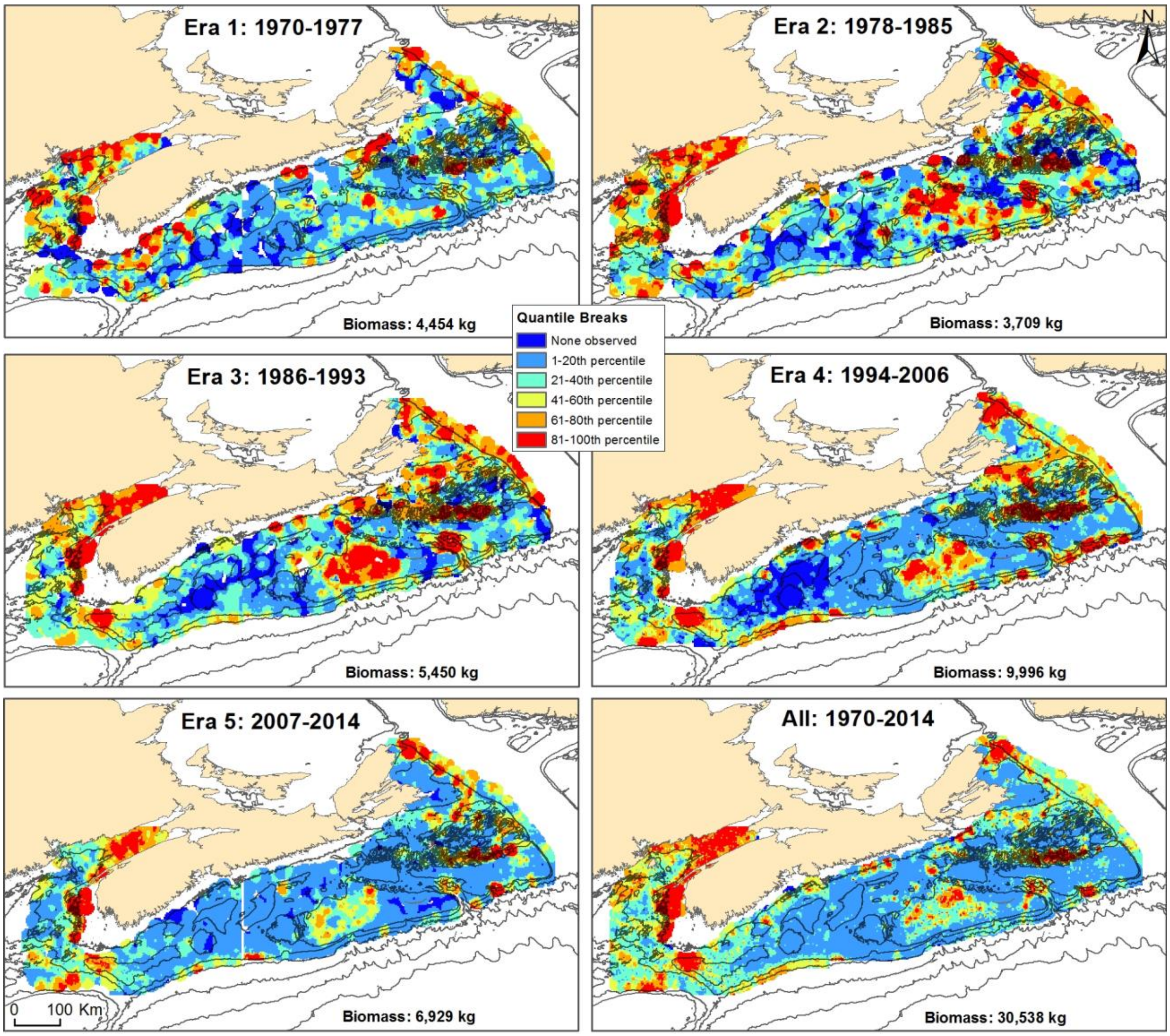

Figure 12. Fish: Benthivores, benthic, medium. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

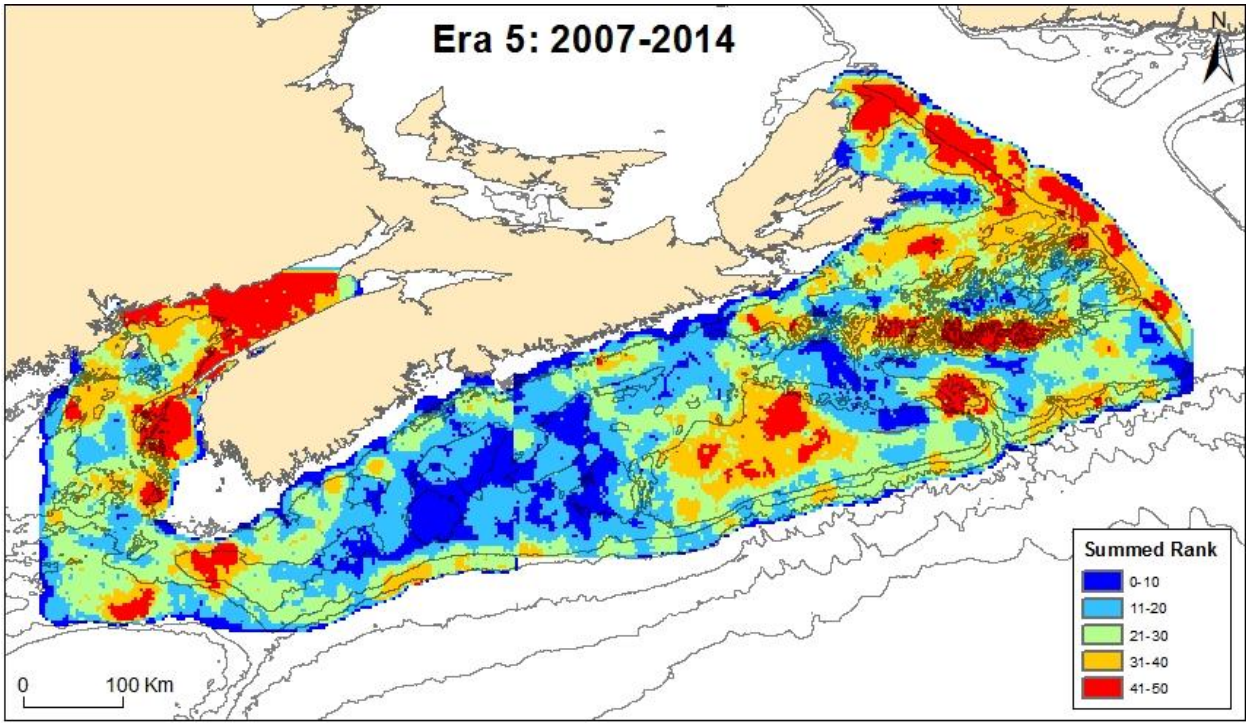

Figure 13. Fish: Benthivores, benthic, medium. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

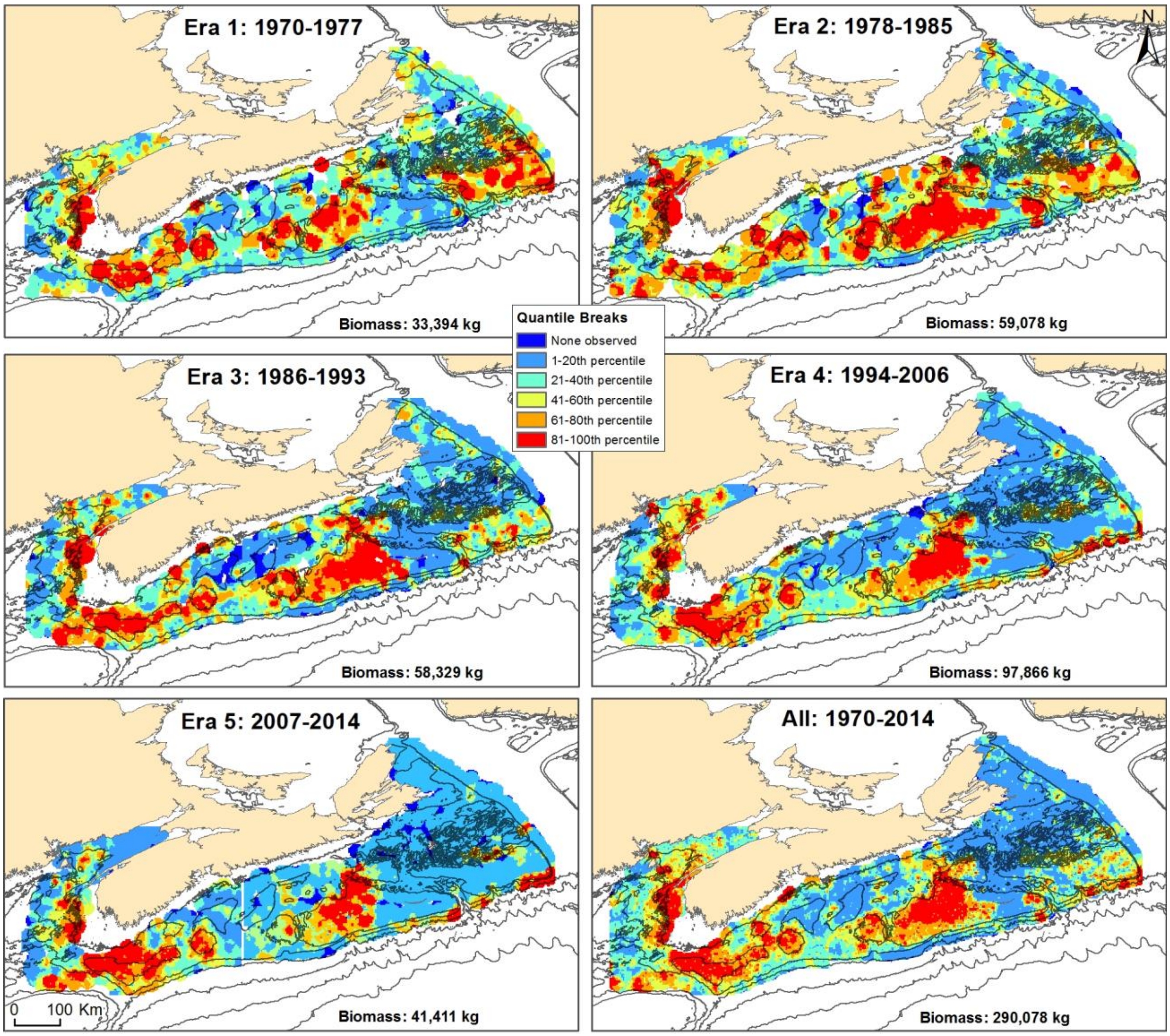

Figure 14. Fish: Benthivores, benthic, large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

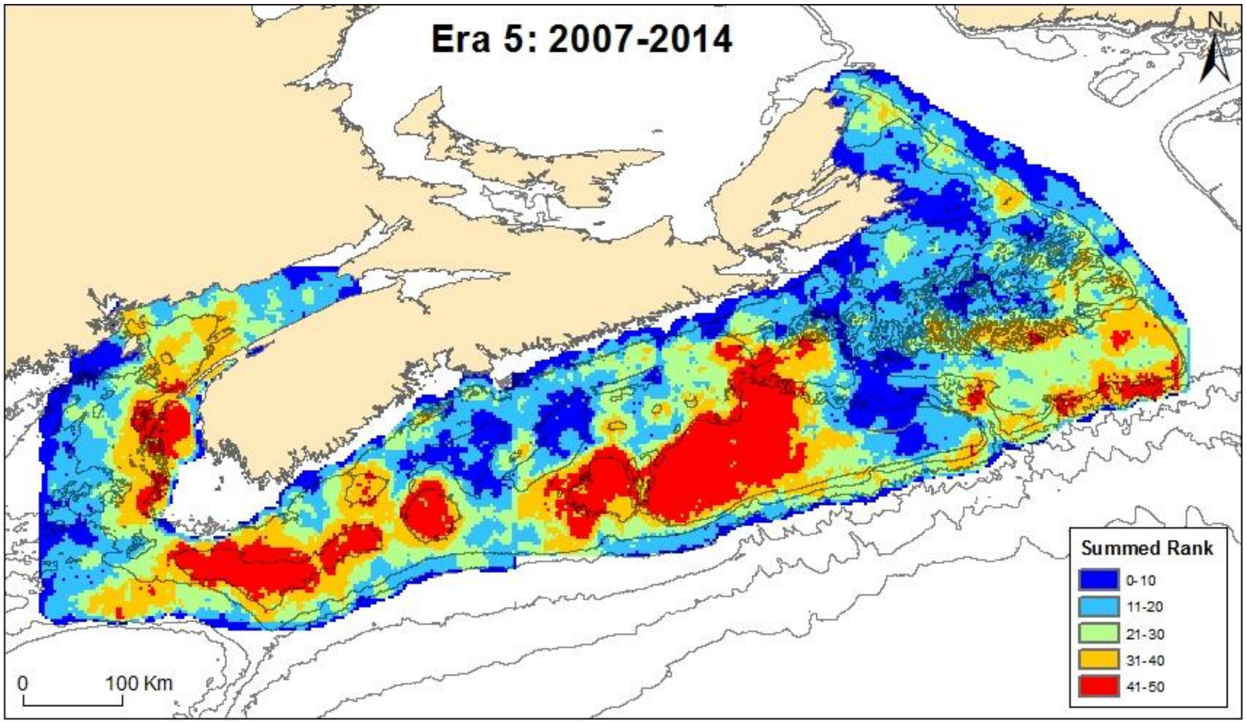

Figure 15. Fish: Benthivores, benthic, large. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

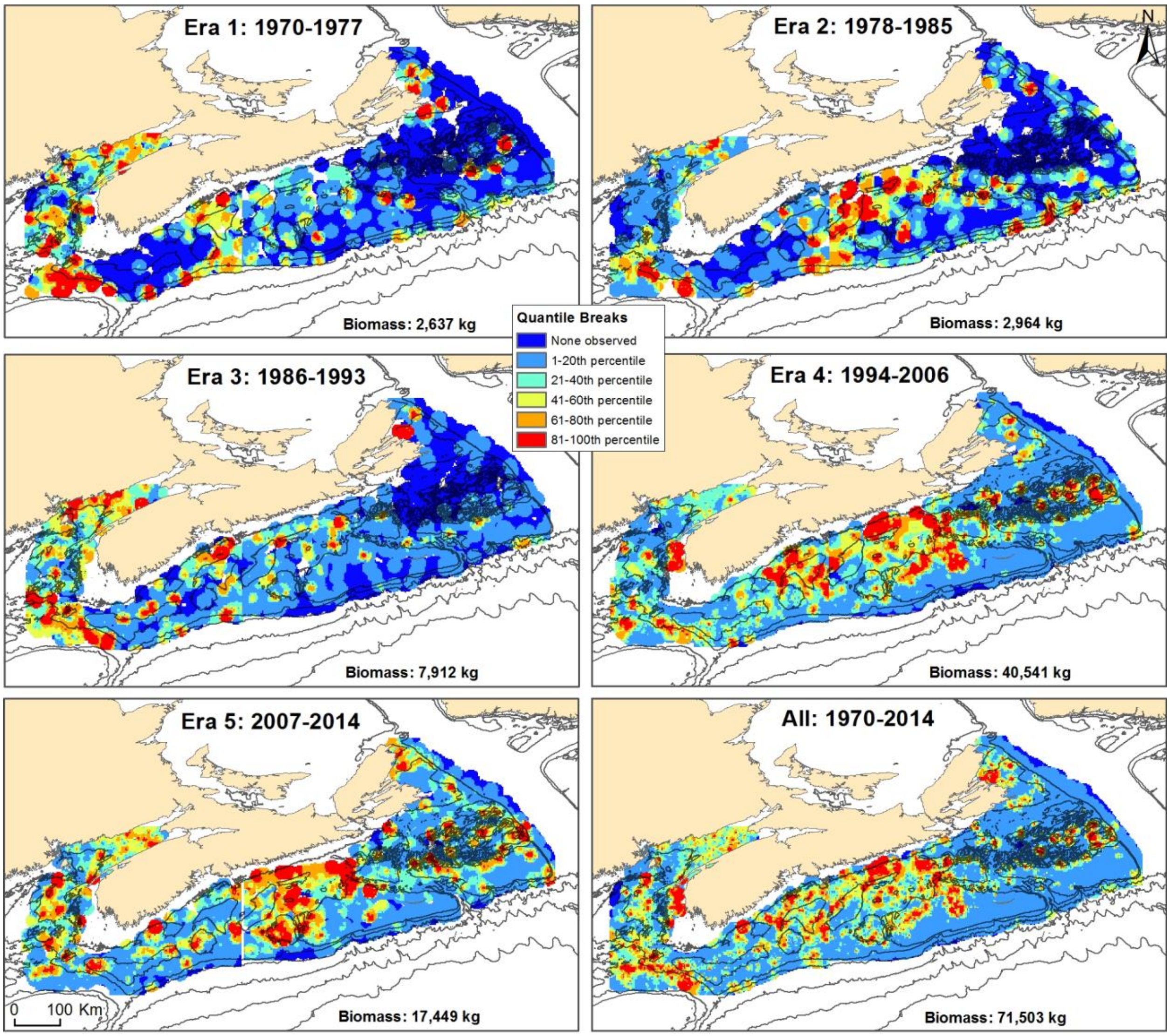

Figure 16. Fish: Planktivores, pelagic, small, medium and large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

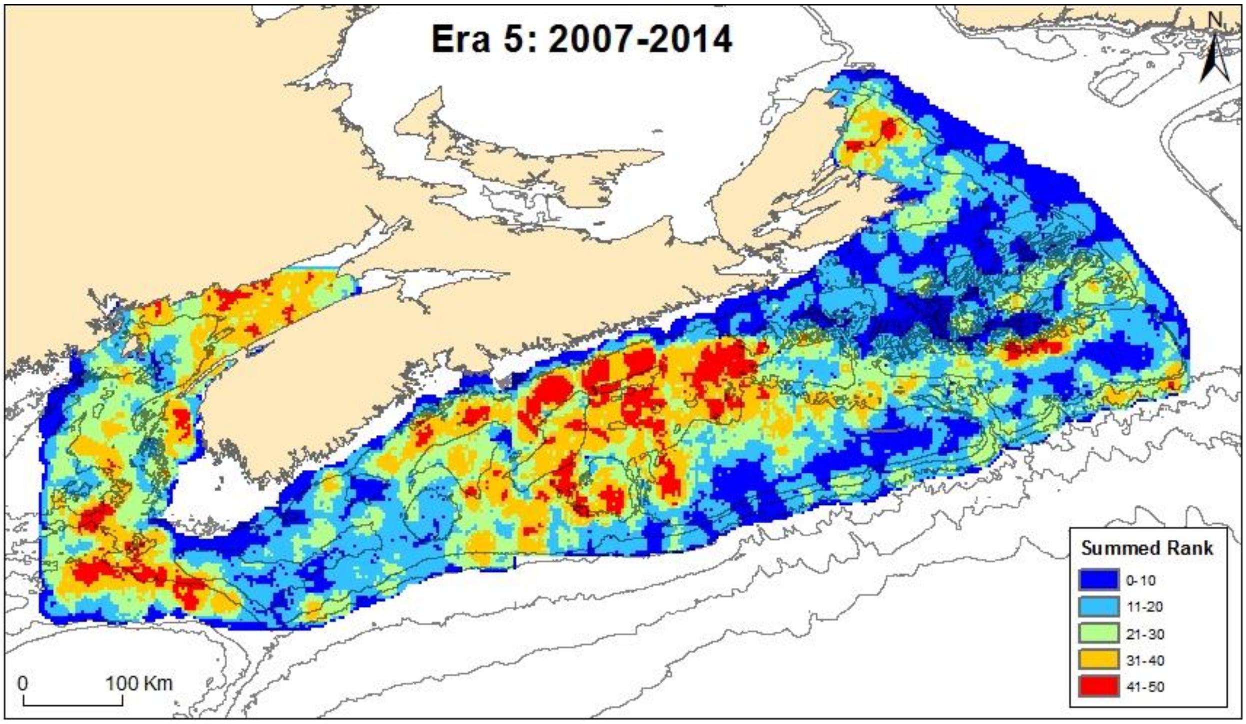

Figure 17. Fish: Planktivores, pelagic, small, medium and large. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

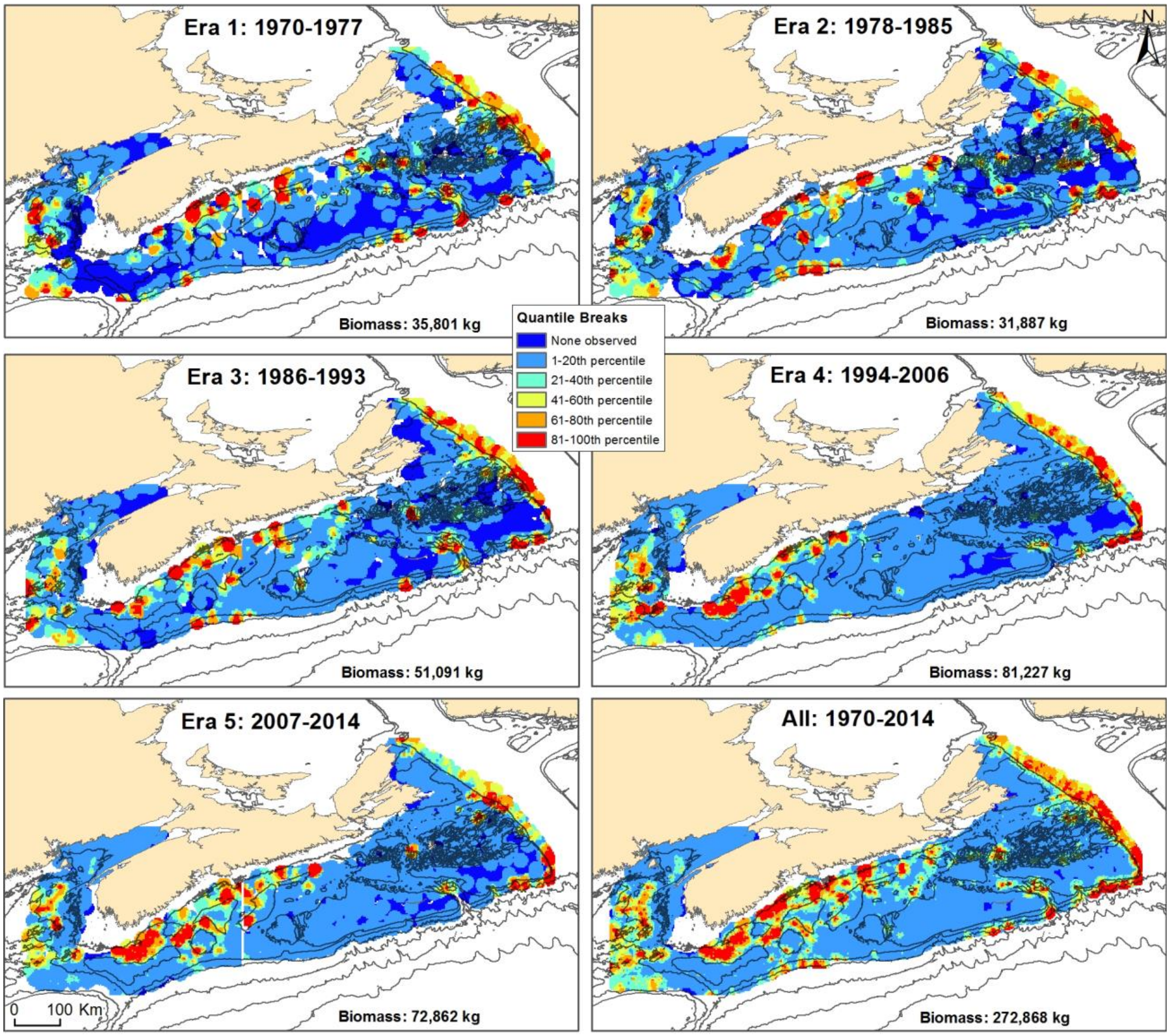

Figure 18. Fish: Zoopiscivores, benthic, small, medium and large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

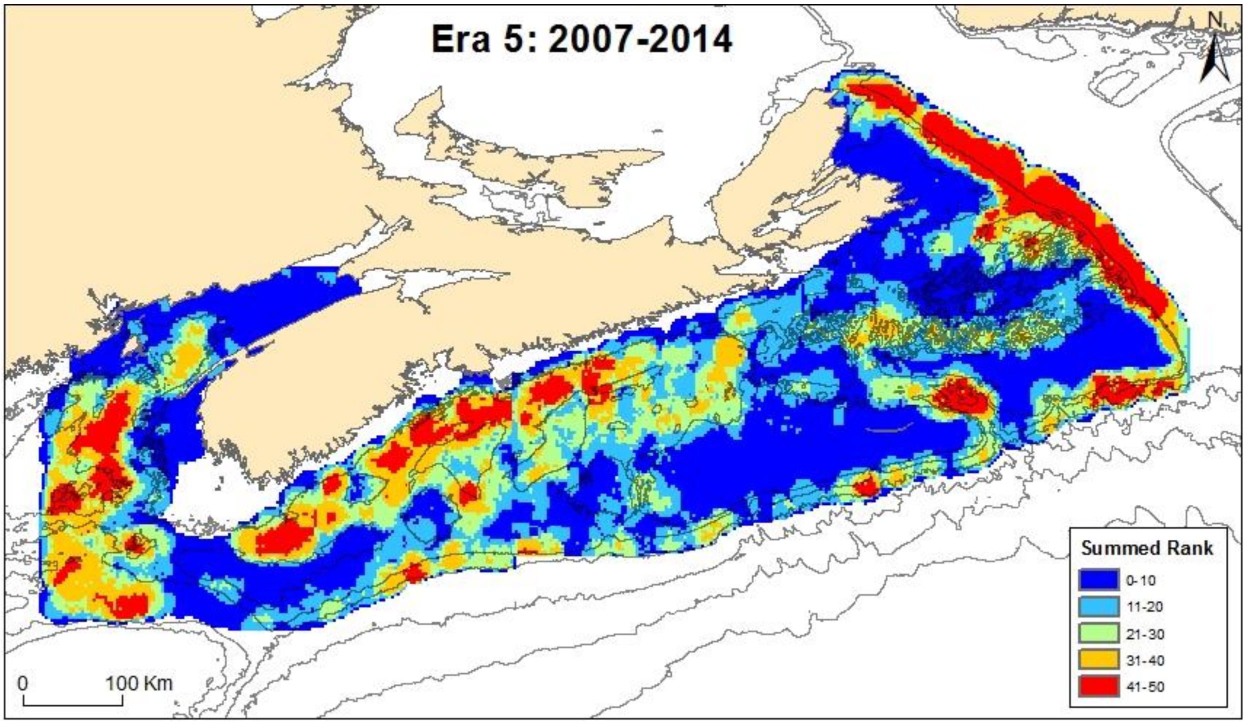

Figure 19. Fish: Zoopiscivores, benthic, small, medium and large. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

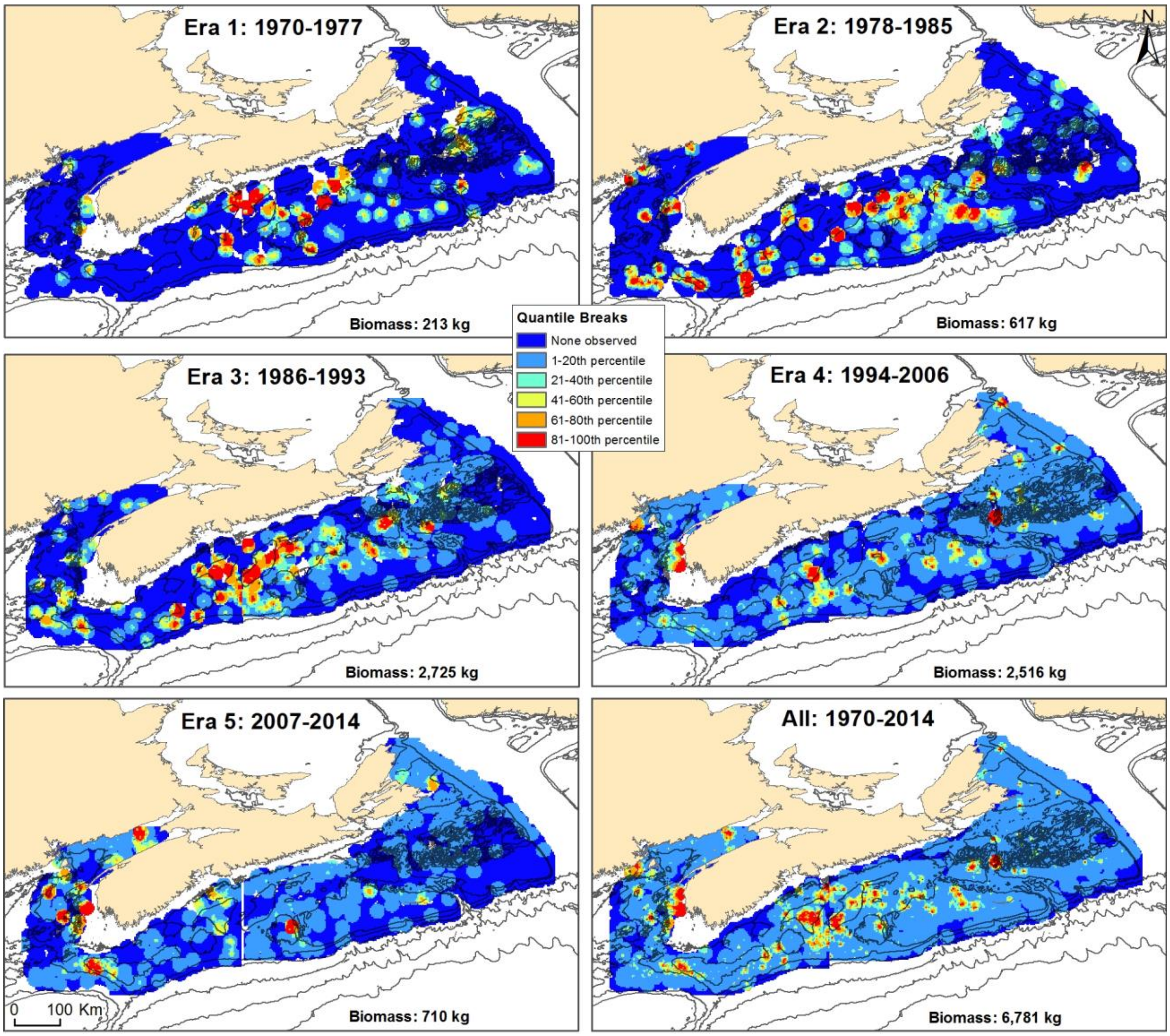

Figure 20. Fish: Zoopiscivores, pelagic, small, medium and large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area for each fishing era, and for all eras combined.

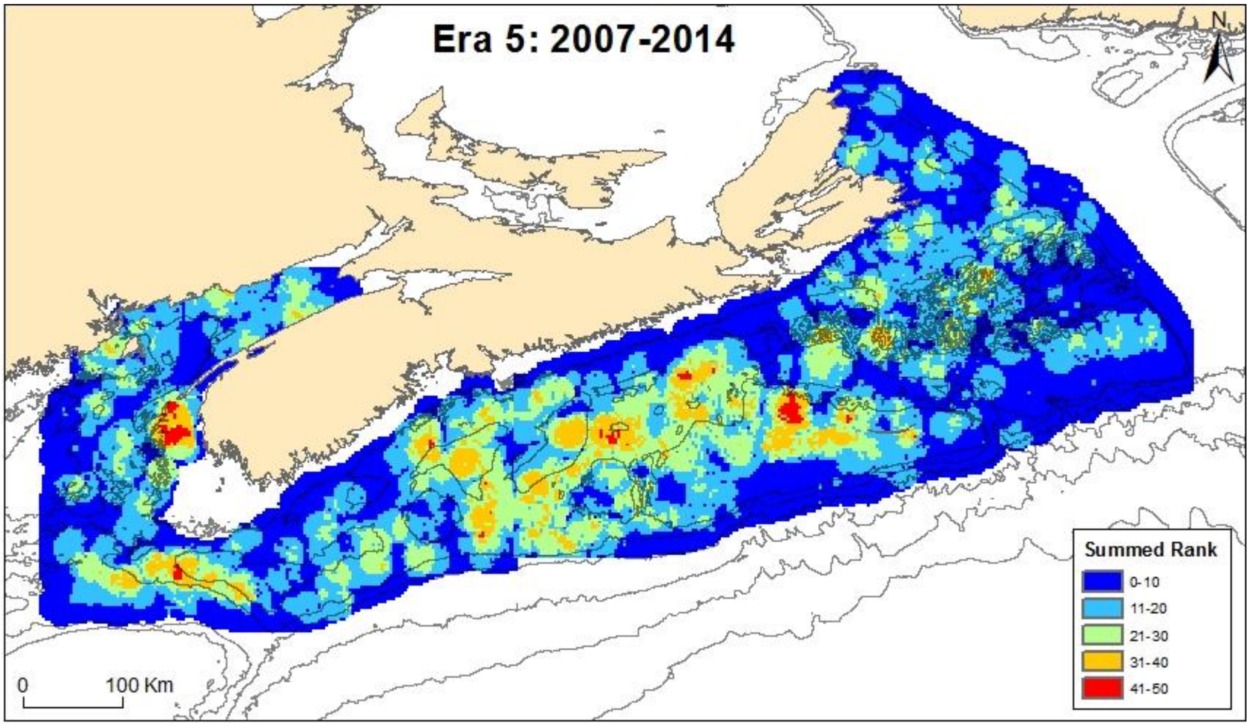

Figure 21. Fish: Zoopiscivores, pelagic, small, medium and large. Summed rank map showing persistence of observed biomass (weight per tow) over all fishing eras.

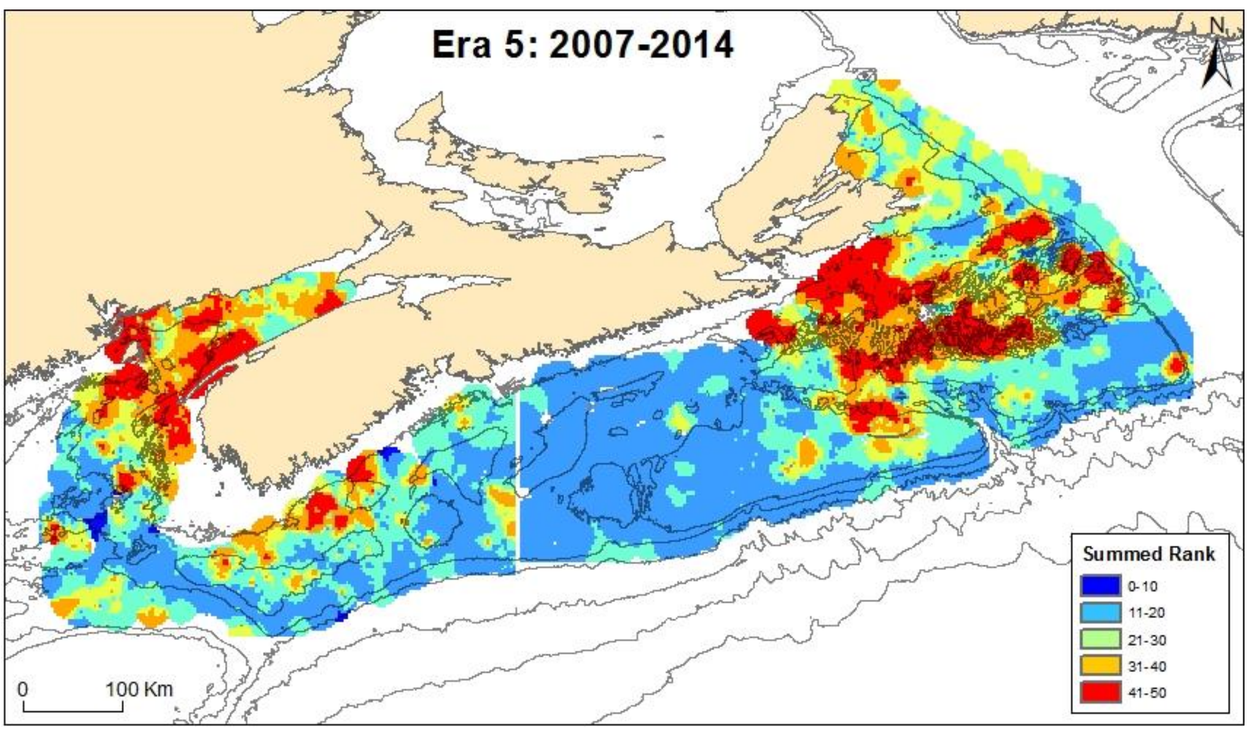

Figure 22. Invertebrate: Benthivores, benthic, small. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area.

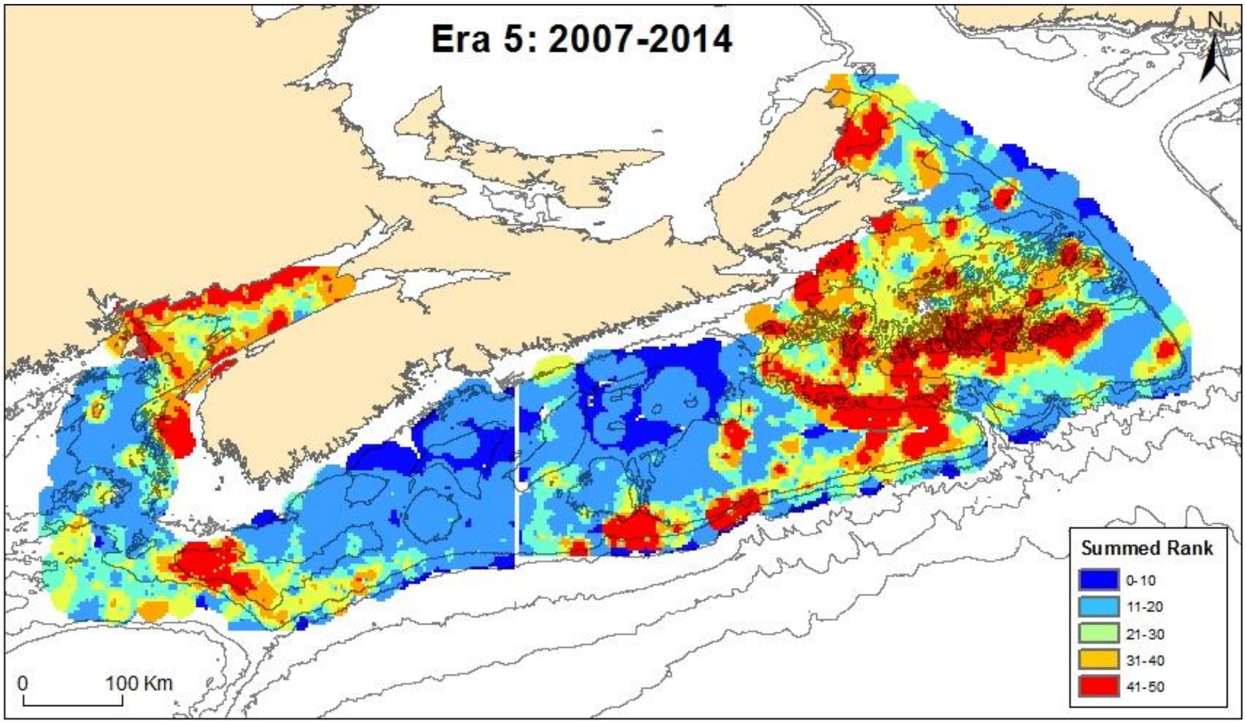

Figure 23. Invertebrate: Benthivores, benthic, medium. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area. a

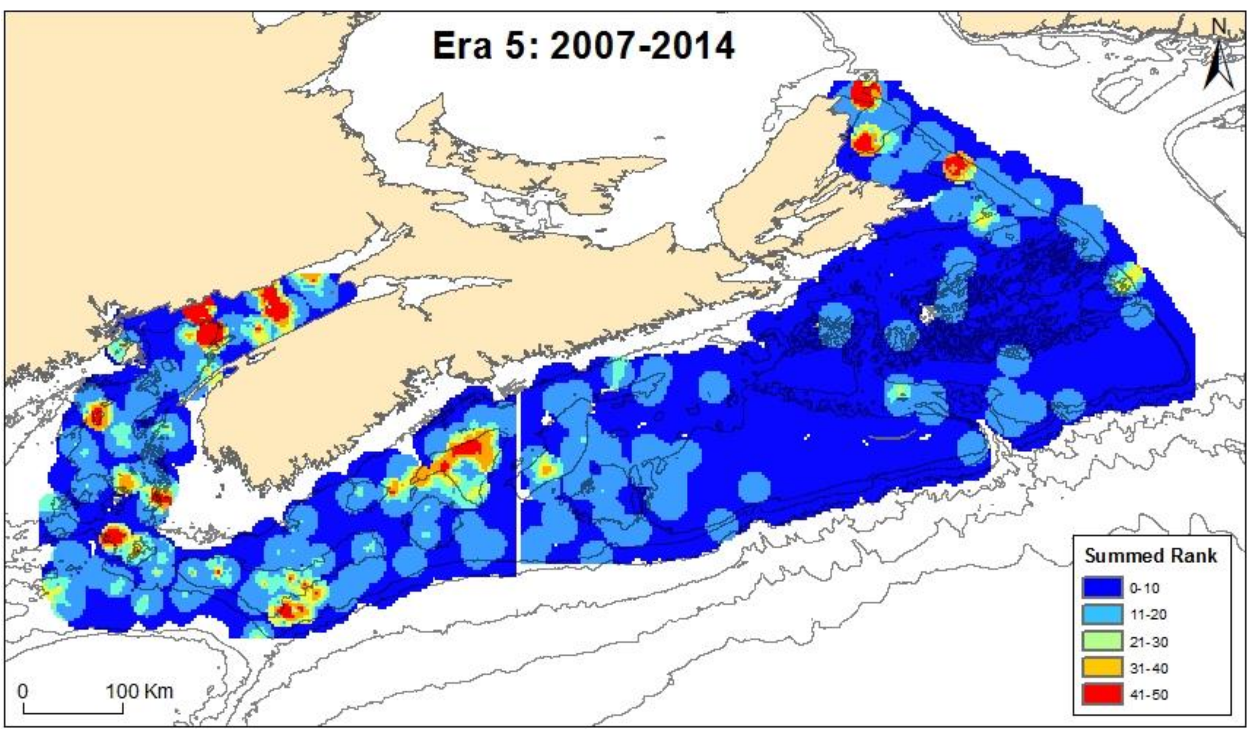

Figure 24. Invertebrate: Zoopiscivores, small, medium and large. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area.

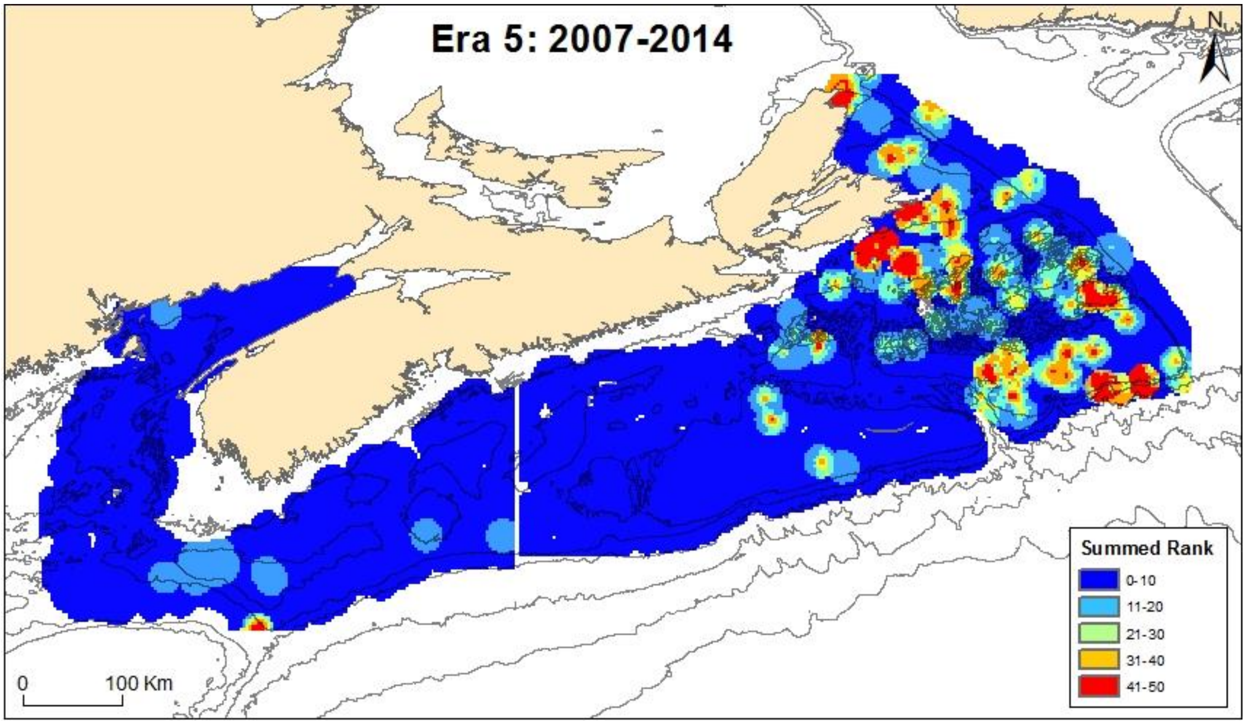

Figure 25. Invertebrate: Filter feeders, benthic, colonial. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area.

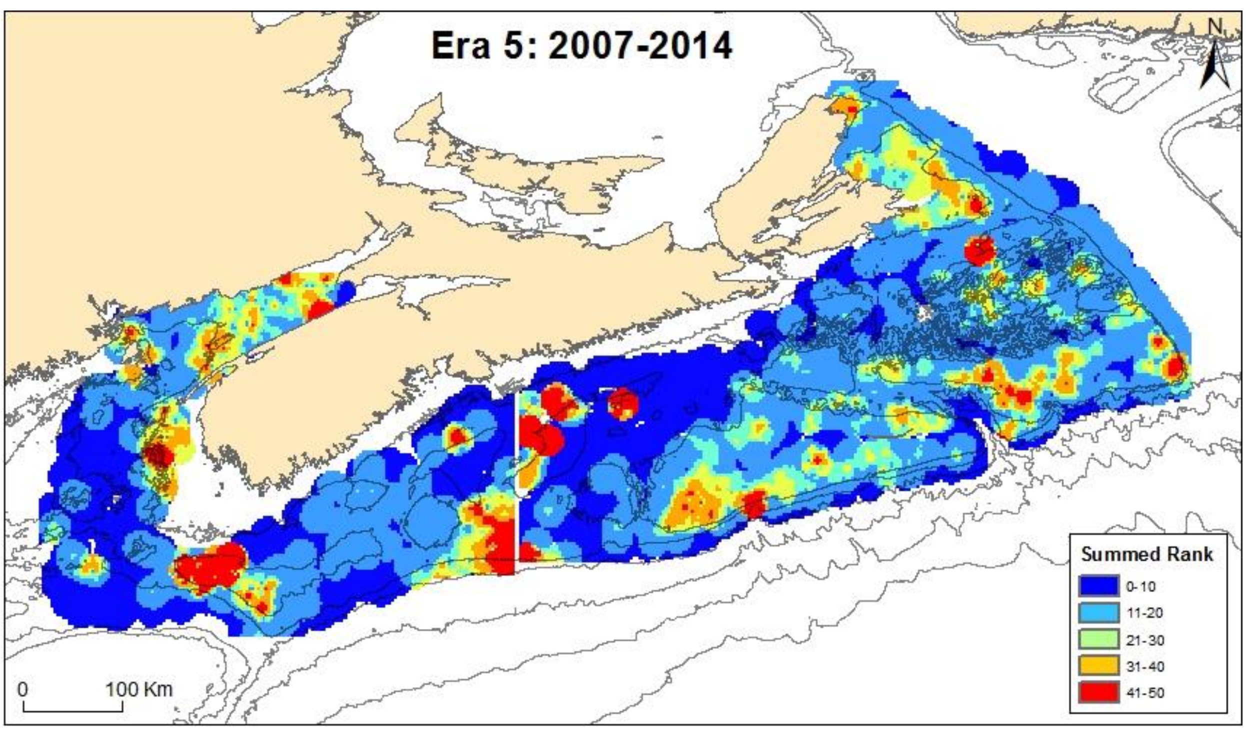

Figure 26. Invertebrate: Filter feeders, benthic, non-colonial. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area.

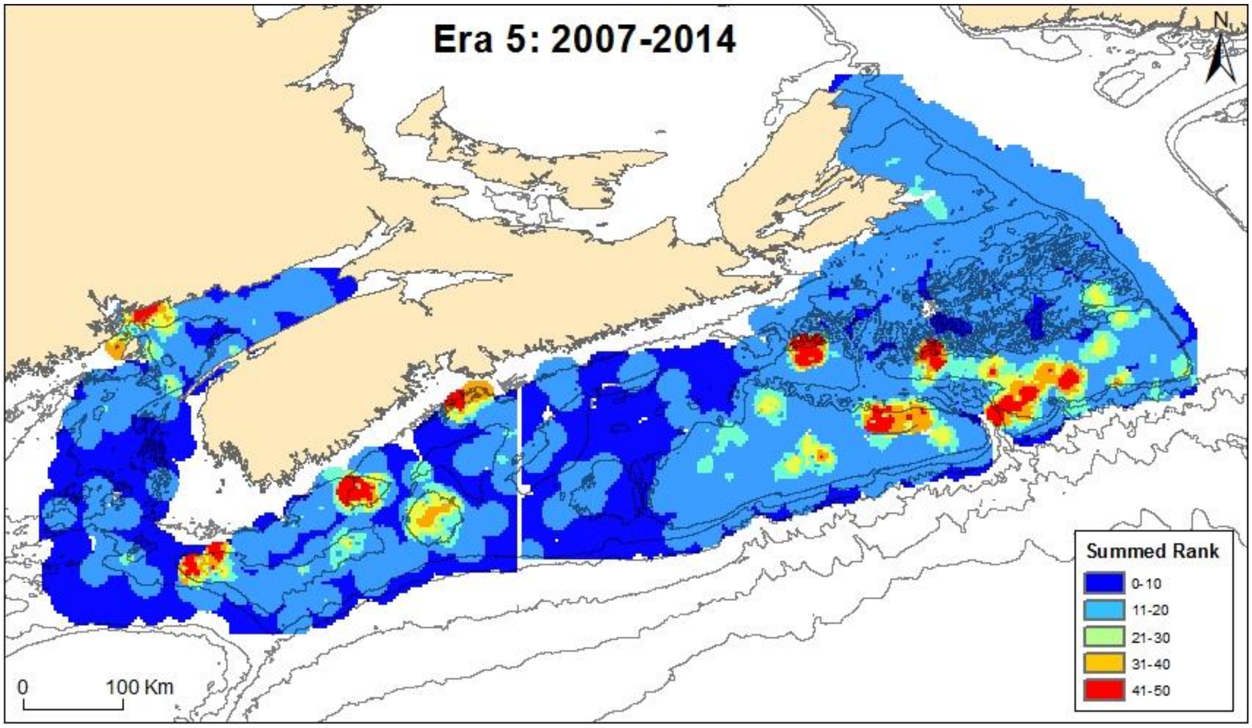

Figure 27. Invertebrate: Detritivores. Shown is an IDW interpolation of observed biomass (weight per tow) divided into 20% classes by area.

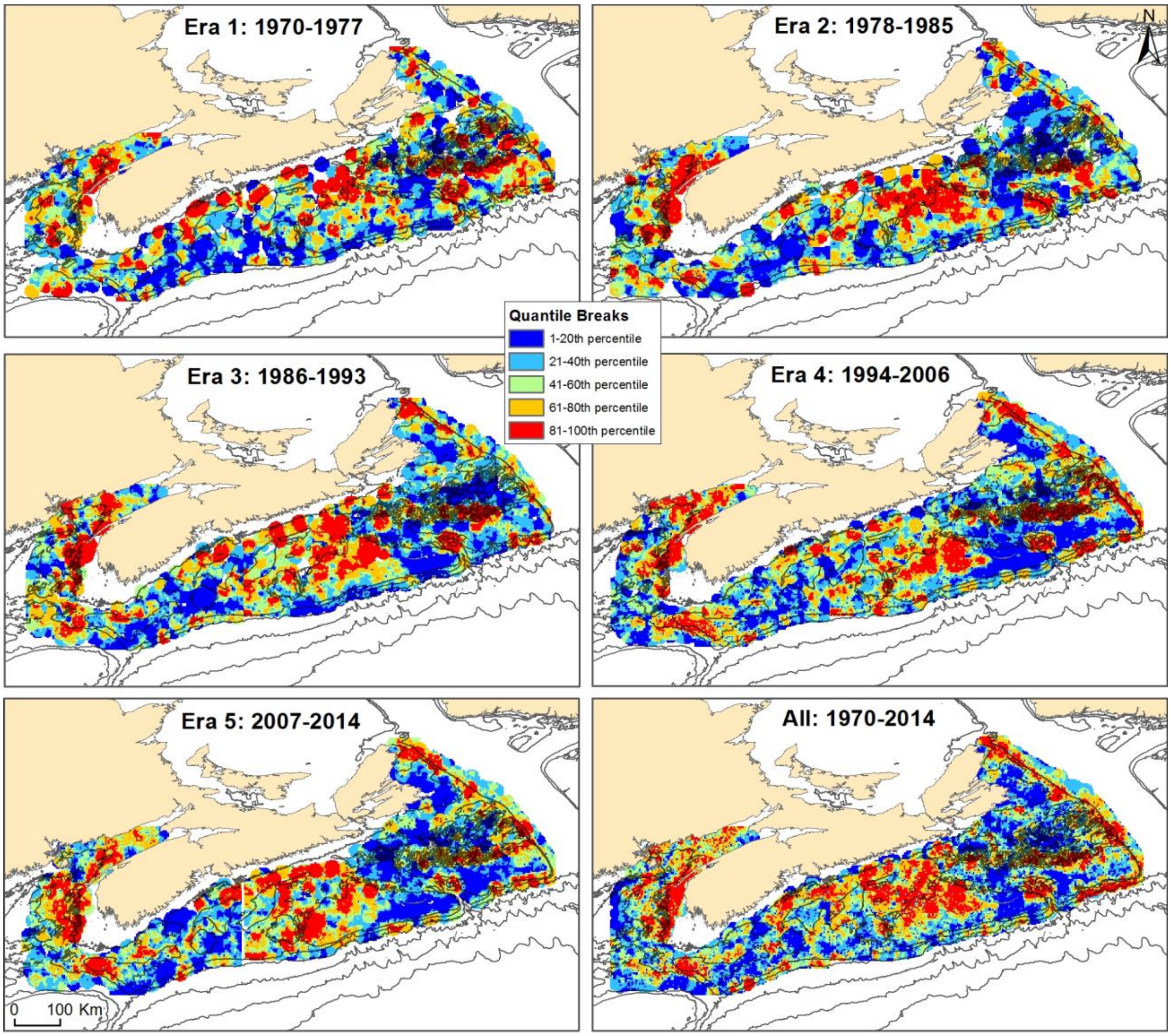

Figure 28. Overlay of all fish functional groups by era, and for all eras combined.

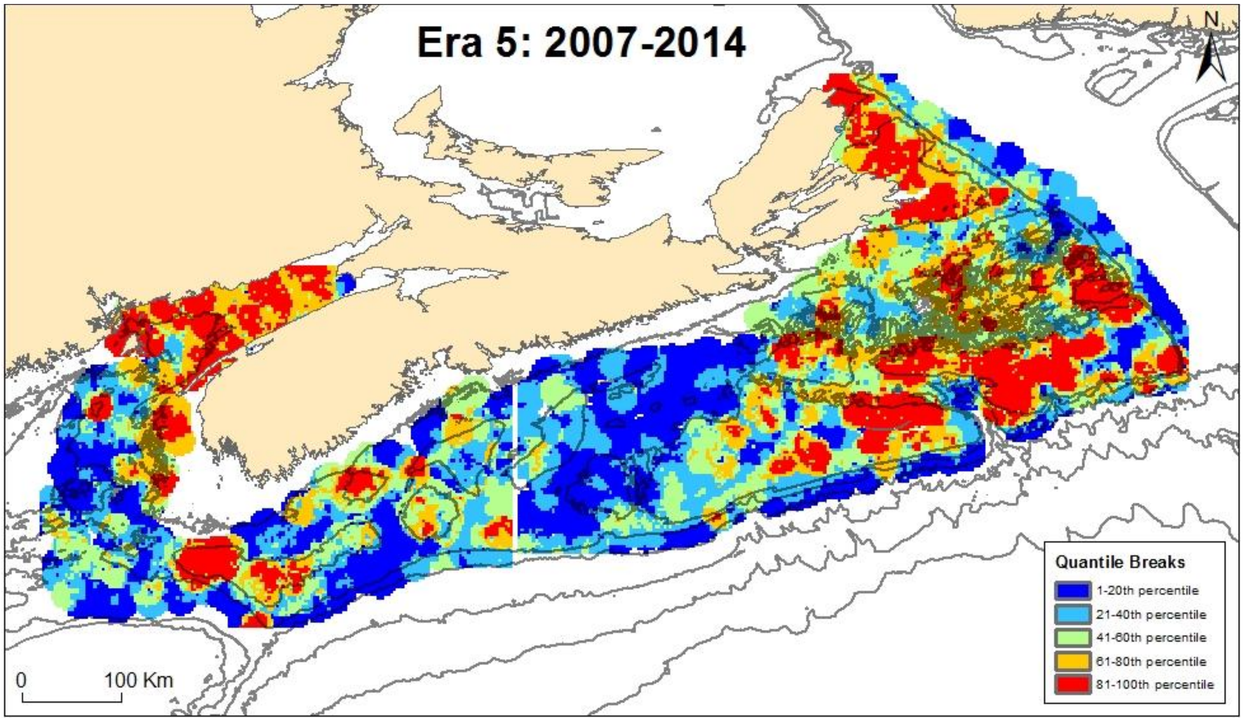

Figure 29. Overlay of all invertebrate functional groups.

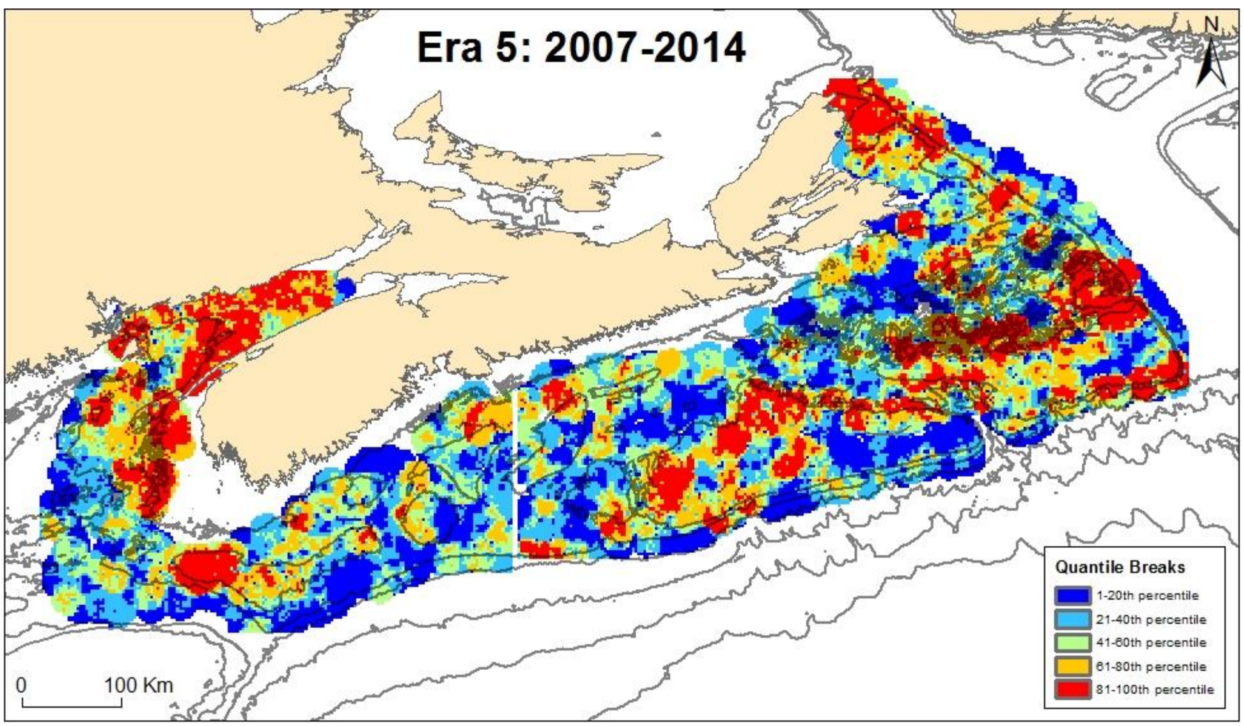

Figure 30. Overlay of fish functional groups (era 5 only) and all invertebrate functional groups.