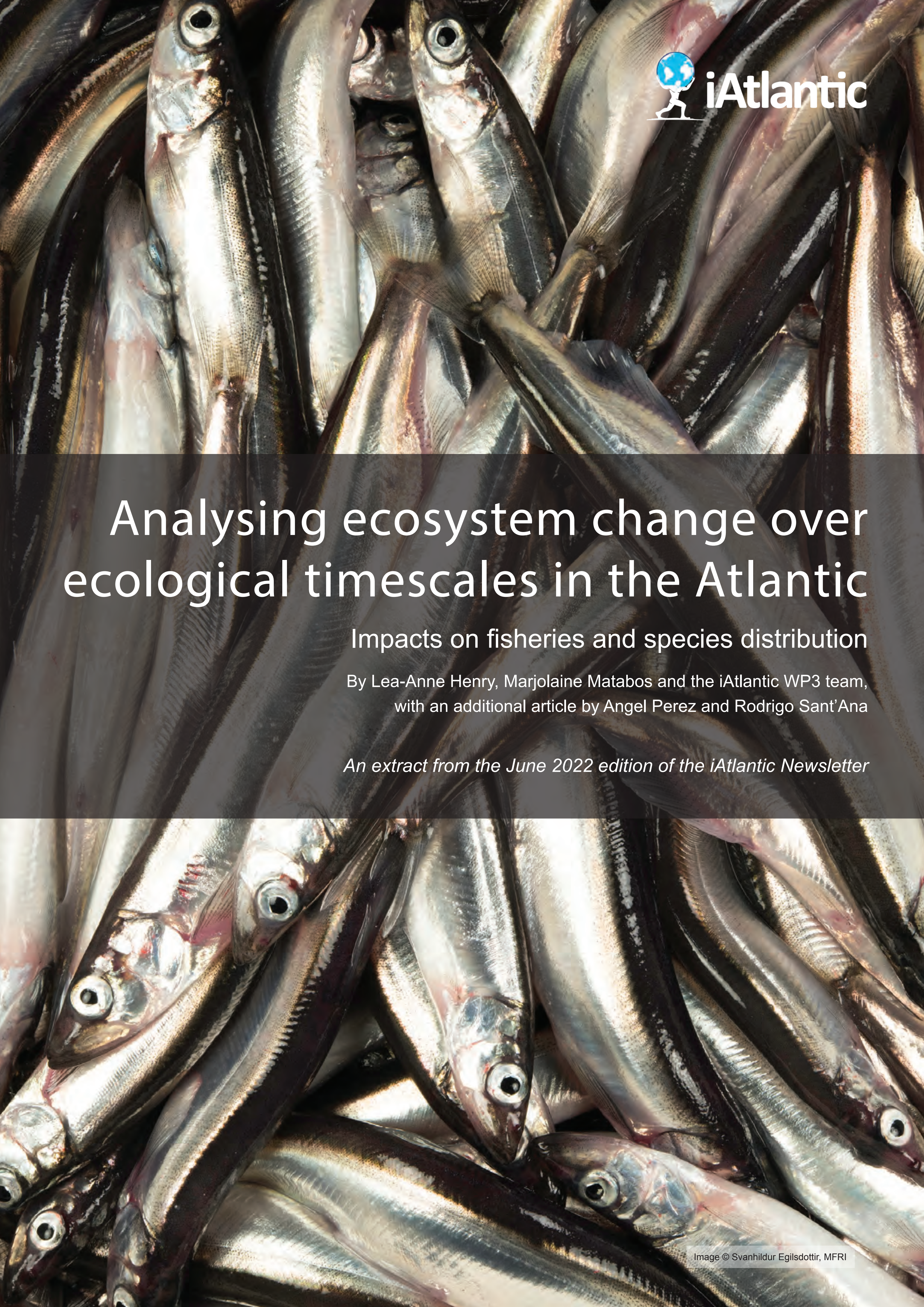

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Analysing ecosystem change over ecological timescales in the Atlantic

Impacts on fisheries and species distribution

By Lea-Anne Henry, Marjolaine Matabos and the iAtlantic WP3 team, with an additional article by Angel Perez and Rodrigo Sant'Ana

An extract from the June 2022 edition of the iAtlantic Newsletter

Within iAtlantic, a major component of our work focuses on understanding the drivers of ecosystem change at regional to ocean scales across different ecosystems. This research takes a multidisciplinary approach to investigating ecosystem stability, vulnerability, and tipping points over inter-annual to millennial timescales. With a focus on ecosystem change over the last 50 years, the iAtlantic WP3 team led by Lea-Anne Henry and Marjolaine Matabos recently completed a major analysis that reports on change over ecological timescales, and identified several cross-cutting issues for iAtlantic to consider going forward.

With increasing exploitation and industrialisation of the oceans and accelerating climate change, marine ecosystems have experienced a lot this last century. Decision-makers and wider society now recognise the urgent need for comprehensive assessments of the status, trends and tipping points of marine ecosystems. Area-based management tools for planning a sustainable blue economy include marine spatial planning, strategic environmental assessment or environmental impact assessment. These tools require us to understand the drivers of ecosystem change and to predict impacts of our plans, policies, programmes, strategies and projects under future climate change scenarios. But for deep-sea and open-ocean biomes, there is a high degree of uncertainty about how naturally variable these ecosystems are or what drives these changes. It's therefore difficult to speculate how human activities will impact ecosystems in these places; it's then even harder to predict how cumulative impacts of climate change and human activities could alter ecosystems and the services they provide.

Figure 1: The iAtlantic study areas.
For key and details see www.iatlantic.eu/our-work/study-regions

The iAtlantic project developed an entire workstream on "Understanding drivers of ecosystem change" to deliver an international and multidisciplinary effort that would improve our understanding of ecosystem stability, vulnerability and tipping points in each of the twelve iAtlantic study regions (Figure 1). But the lack of robust, long-term observations of marine species and ecosystems over the last 50 years in the deep sea and open ocean still remains a massive challenge, even in the well-studied Atlantic.

International collaborations and networking opportunities called for by the Belém and Galway Statements extended our capacity to create new time series in these realms and develop the approaches we use to understand drivers behind these changes. Most of our analyses were undertaken by early career researchers (ECRs) like Edson Cavalcante dos Santos (Figure 2) for whom such networks are critical, but it is also our ECRs that have helped to showcase new methods for analysing such complex datasets, which have revealed new trends – even in well-studied datasets.

We analysed various ecosystem compartments, from bacteria and primary producers, zooplankton to groundfish and benthic invertebrates, to whales, swordfish and sharks – many of which are of great conservation interest and value to the Atlantic socioeconomy (Figure 3).

Methods to collect and reconstruct our time series were themselves as diverse as the study regions, species and ecosystems we studied. We are extremely grateful to the many collaborators, institutes, governments and authorities for permission to make use of the facilities, the data and the many experts who advised analysts along the way. Marine observatories were instrumental to our work, including those from the European Multidisciplinary Seafloor and water column Observatory (EMSO), the Cape Verde Ocean Observatory (CVOO) and the Bermuda Atlantic Time-Series (BATS). Long-term monitoring programmes and surveys of zooplankton, cetaceans, and groundfish off study regions like Nova Scotia in eastern Canada, and the North Atlantic Sightings Surveys (NASS) off Iceland were key, as was local ecological knowledge of humpback whales in the Sargasso Sea. We relied heavily on fisheries-dependent data in our South Atlantic study regions. These were sourced from the International Commission for the Conservation of Atlantic Tunas (ICCAT) and from the University of Vale do Itajaí's (UNIVALI) monitoring of landed catches of groundfish along the Brazilian Meridional Margin. The latter dataset comes from

Figure 2: A) Scientists sent deep-sea coral samples from Canada to Brazil and the EU for geochemical analysis to study carbon sources (scale bar 1m – photo courtesy of DFO & Ellen Kenchington), including work done by B) undergraduate student Edson Cavalcante dos Santos to reconstruct coral age (photo courtesy Christian Millo). C) This international collaboration revealed the gorgonian Paragorgia arborea *underwent wide swings in food sources over its lifetime in the Davis Strait, northern Canada.*

Figure 3: International collaborations unlocked a range of time series across different species and ecosystems, e.g., A) zooplankton (photo courtesy Erica Head), B) vent mussels (photo courtesy Marjolaine Matabos), C) amphipods (photo from Horton et al. 2020), D) whitemouth croaker (photo courtesy Rodrigo Sant'Ana), E) tuna (photo courtesy Roberto Bavares & Dimas Gianuca), F) blue shark (photo courtesy Roberto Bavares & Dimas Gianuca), G) humpback whale (photo courtesy Andrew Stevenson), H) microbial mats (photo courtesy Marjolaine Matabos), and I) zoanthids (photo courtesy Marjolaine Matabos).

UNIVALI being able to support governmental requests for oceanic and deep fisheries development and management, and the licensing processes of Brazilian offshore oil and gas exploration activities.

Besides classical survey and monitoring methods, alternative approaches such as structure from motion photogrammetry, capture-recapture modelling from whale flu e photos, the use of acoustic Doppler conductivity profilers (ADCPs), and palaeoceanographic and geochemical proxies of ecosystem change over centuries to millennia were all used to reconstruct time series (Figure 4). All to say, our best efforts led to improving the understanding of what's driving ecosystem changes in each place.

The Atlantic community must continue working towards standardising and aligning ocean observations. We adopted a more fl xible 'place-based approach': this allowed existing time series to be integrated into ecosystem assessments for each iAtlantic study region. But we harmonised the approach by setting a common suite of overarching questions about drivers of change and by creating statistical workflows with common design principles to guide analyses.

Through this fl xible place-based approach, several themes emerged about ecosystem change over the last 50 years that cross-cut our study regions and the ecosystems we studied.

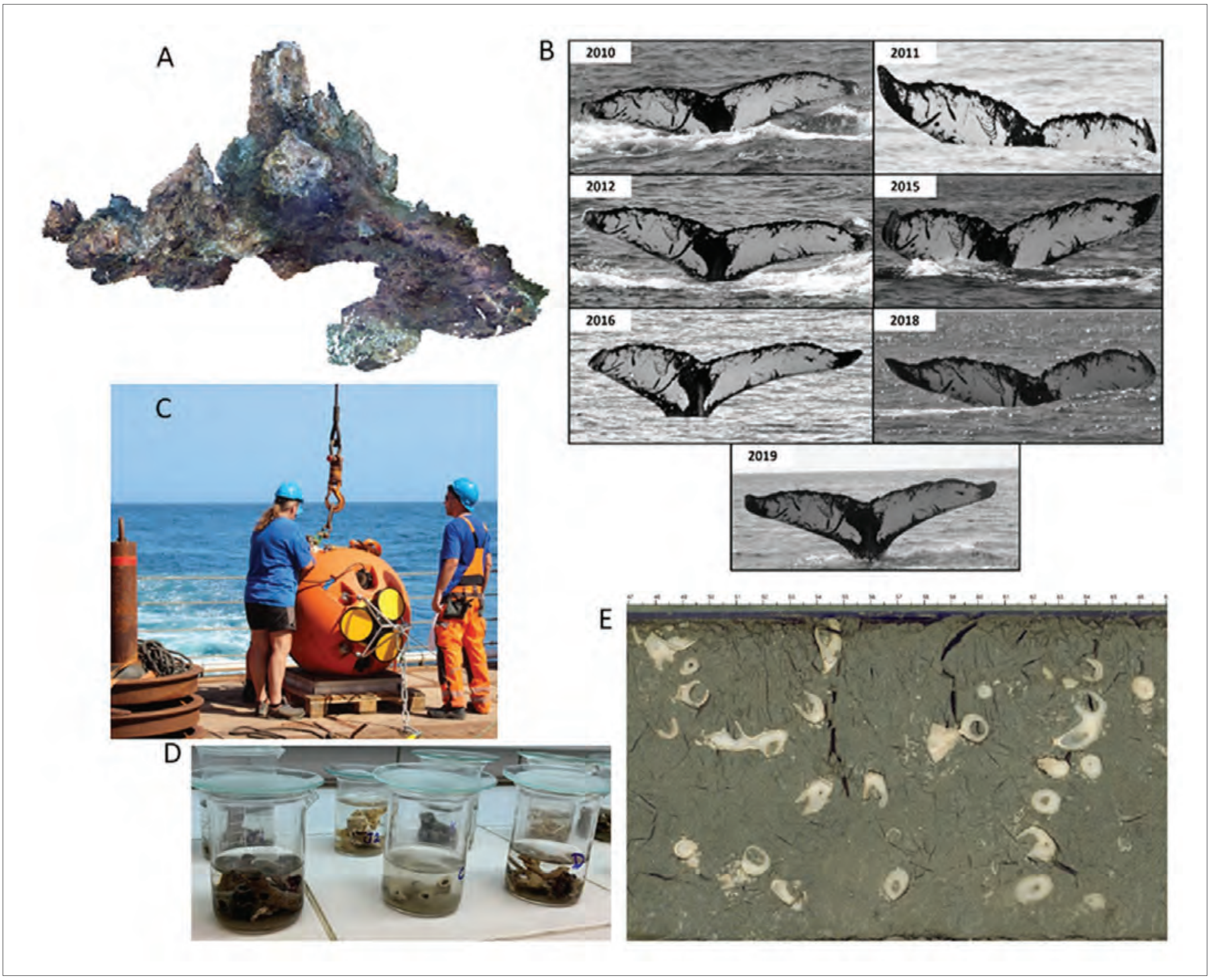

Figure 4: Reconstructing time series was made possible using structure-from-motion photogrammetry on A) hydrothermal vents (photo courtesy Marjolaine Matabos), B) capture-recapture modelling from whale flu e identific tion (photos courtesy Andrew Stevenson), C) trialling the use of ADCPs to reconstruct inter-annual changes in mesoplankton (photo courtesy Helena Hauss), D, E) reconstructing ecosystem changes from cold-water corals over decades and millennia (photos courtesy Christian Millo and Dierk Hebbeln, respectively).

Cross-cutting theme #1: Abrupt ecosystem changes in the late 1990s to early 2000s

First, we discovered statistical 'breakpoints' in our datasets, which suggest tipping points in conditions were reached in many study regions, especially around the late 1990s and early 2000s. Breakpoints are strong, significant and abrupt changes in species or ecosystems. The late 1990s and early 2000s coincided with larger-scale surface, mid- and deep-water oceanographic trends reported from the surface of the open ocean to the abyss across the Atlantic.

Some of these breakpoints involved commercially important fish stocks. This was particularly evident off Iceland. For example, in 2003 researchers from the Marine and Freshwater Research Institute (MFRI) found catches of capelin at maturity stage 6 and higher had significantly expanded their range north and westward around Iceland, indicating a large and abrupt redistribution of fish stock spawning habitat (Figure 5).

MFRI scientists also discovered capelin larval connectivity was highly sensitive to spawning habitat location: when larval particles were virtually released in a simulated model environment, the more northerly Latragrunn and Snæfellsnes release sites gradually increased connectivity to Greenland, while release sites just due west at Faxaflói hardly connected at all (Figure 6). Therefore, recent increases in juvenile capelin in Greenlandic waters may in part be explained by enhanced larval connectivity and recruitment from northwestern spawning grounds off Iceland since 2003.

Meanwhile, the late 1990s to 2000s also coincided with a significant breakpoint in the groundfish surveyed from the cooler, fresher waters to the northwest of Iceland. Here, MFRI scientists discovered Norway haddock, capelin, saithe, and haddock rapidly becoming caught in more of their survey stations after 1999, whereas the number of stations with records of other species like halibut, plaice, redfish and polar cod rapidly decreased. Besides these shifts in composition, the total beta diversity in both the northwest and southwest of Iceland both abruptly increased after 1999 (Figure 7).

Monkfish (Figure 8) are a species for which Iceland is located at the northernmost border of their habitable range. However, a weaker subpolar gyre bringing warmer and more saline water masses reached Iceland by 2000. In response, the monkfish centre of gravity moved westward, followed by a change towards the north along with increased biomass and effective area occupied. Just before or around 2010 this trend reversed again and while sea temperature remained high until 2015 (Figure 9), salinity dropped markedly around the same time as the declines in monkfish

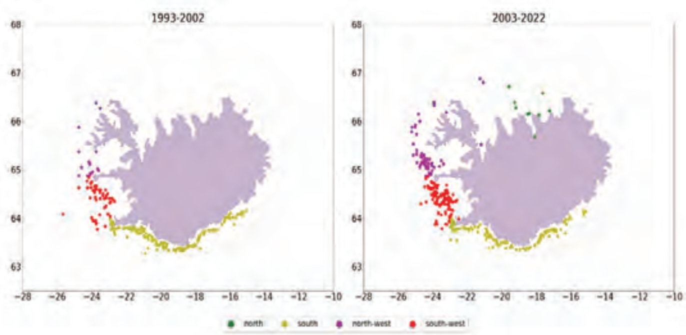

Figure 5 (above): All catch locations of capelin at maturity stage 6 and higher between 1993 and 2002 (left) and 2003 to 2019 (right). Catch locations north of 64.85° N are coloured red, those south of it in blue.

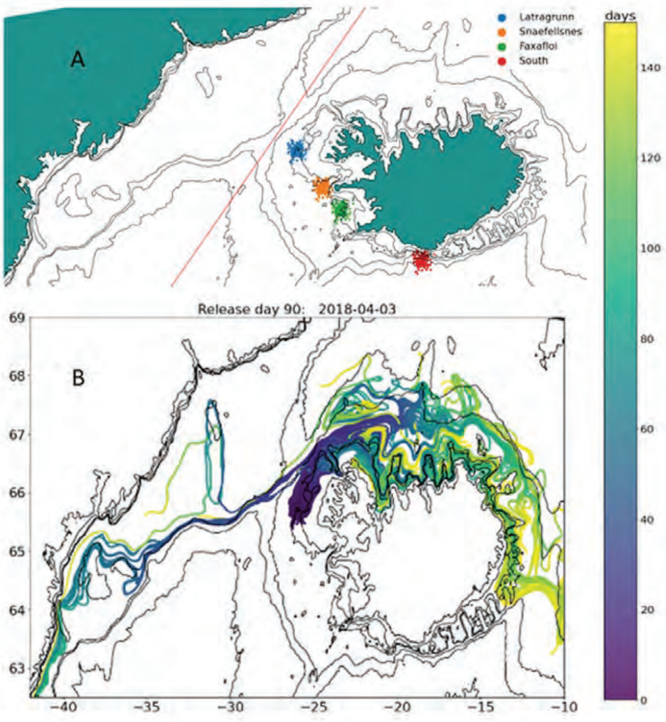

Figure 6 (right): A) Locations of four modelled particle release sites for simulated larval drift experiments. The red line separates areas for which the simulated larvae go to nursery areas in Greenland from those that remain in Icelandic waters. B) Spatial distribution patterns of larval drift trajectories released from Latragrunn over a 140-day period, with colours reflecting the age of the particles (simulated larvae) since spawning (day zero, purple) until day 140 (yellow). Shown are particles that were released at five-day intervals in 2018 between 9 March (day 65) and 3 April (day 90), assuming diurnal vertical migration.

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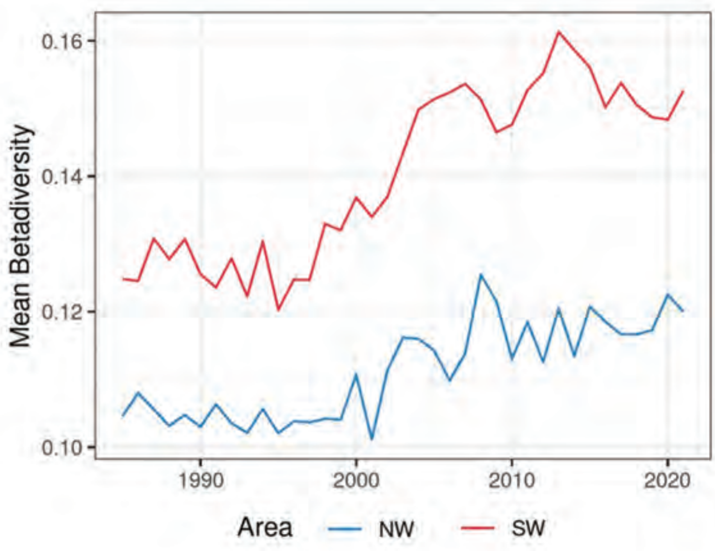

Figure 7 (left): Annual mean beta diversity per study region based on the spring Icelandic Groundfish Survey for 1985-2021 (NE area: blue line and SW: red line). Figure 8 (right): A juvenile monkfish Lophius piscatorius) approx.12 cm in length (photo courtesy of Magnús Thorlacius).

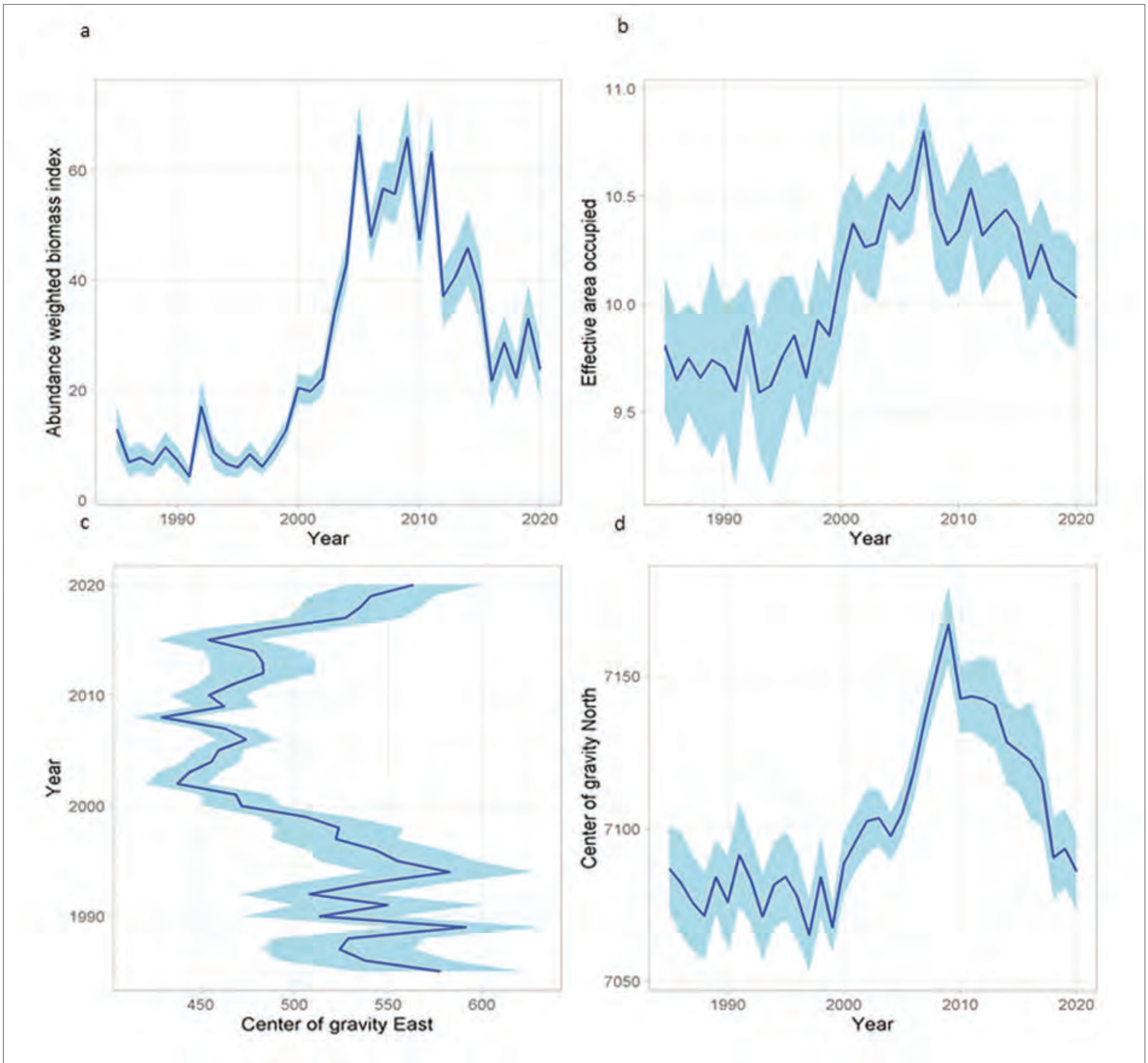

Figure 9: (a) Monkfish biomass ind x, (b) effective area occupied and (c) centre of gravity east and (d) north, estimated using the VAST package.

Cross-cutting theme #2: Tropicalisation of fauna and relationships with sea temperature

From eastern Canada to the Malvinas Current, and from Iceland to South Africa and the Walvis Ridge, species with warm-water affinities have become more abundant and many now dominate communities. While sea temperature alone may not be 100% responsible for driving these trends, iAtlantic discovered that long-term ocean warming has heralded in a new era of widespread species "tropicalisation".

In eastern Canada on Nova Scotia's continental slope, scientists at Bedford Institute of Oceanography, University of Edinburgh and Instituto Español de Oceanografía discovered that zooplankton species with warm-water affinities now characterise the community in both the spring and autumn, with cooler water taxa disappearing over time. Meanwhile on the Brazilian Meridional Margin, the Brazil-Malvinas Confluence has shifted south over the past decades due to a poleward displacement of South Atlantic wind patterns, which has produced a pronounced warming region over the wider southwest Atlantic Ocean.

Here is where scientists at UNIVALI discovered declines in catches of commercially important cooler-water species of groundfish like Argentine croaker and Brazilian codling, and a notable increase in warm water species like whitemouth croaker, stripped weakfish and grey triggerfish after 2013 (Figure 10).

Likewise, the UNIVALI team also discovered massive swings in the catches of cooler-water migratory species recorded by the International Commission for the Conservation of Atlantic Tunas (ICCAT). Large migratory pelagics important to the commercial and sport-fishing sectors, like albacore and Atlantic bluefin tuna, have also significantly declined across parts of the South Atlantic, while over time yellowfin tuna and then bigeye tuna became more dominant in catches (Figure 11). With sport fishing being so closely linked to another blue economy – marine tourism – the discovery of basin-scale thermally driven changes in such species is something multiple sectors should watch.

More detail on this research is provided in the second article extract on p10-12 of this document.

Figure 10: Commercially important fisheries stocks have seen a "tropicalisation" trend, with increased catches of warmer-water species now prevailing catches across Brazil and the wider South Atlantic. A) Argentine croaker, a cool-water species off Brazil; B) spotted pink shrimp off Brazil; C) monkfish off Brazil, a cool-water species; D) yellowfin tuna, a warm-water species. Images courtesy Roberto Bavares, Dimas Gianuca, Rodrigo Sant'Ana and Angel Perez.

Figure 11: A tropicalisation of species targeted by both the South Atlantic commercial and sport-fishing industry has occurred: in the open ocean, catches of albacore (A) have been increasingly replaced by yellowfin tuna (B) and finally by big eye tuna (C). Images courtesy Roberto Bavares and Dimas Gianuca.

Cross-cutting theme #3: Human activities and marine management are intertwined with trends

The tropicalisation trends we discovered are all strongly related to thermal regimes, but effects of fisheries pressure itself could not be entirely discounted. Nor could the effect of the International Whaling Commission (IWC) ban on commercial whaling in 1986, and marine protected area designations. Reanalysis of beaked whale sightings in the Gully MPA recorded by Dalhousie University off eastern Canada show increases over time, which Whitehead (2020) suggests could in part relate to decreases in noise after the MPA was designated in 2004. For pilot whale, striped dolphin and white-sided dolphin, a combination of shifts in overall population size, habitat suitability and anthropogenic activity levels are also likely drivers of change (Whitehead, 2020).

In the Sargasso Sea, scientists at the University of Edinburgh and Whales Bermuda reconstructed humpback whale abundance and discovered whales have been steadily increasing since 2012 (Figure 12). Although some of these changes might relate to progressive increases in primary production recorded by the Bermuda Institute of Ocean Sciences at the Bermuda Atlantic Time-Series Study (BATS), these increases are very much intertwined with larger scale population recovery post-whaling.

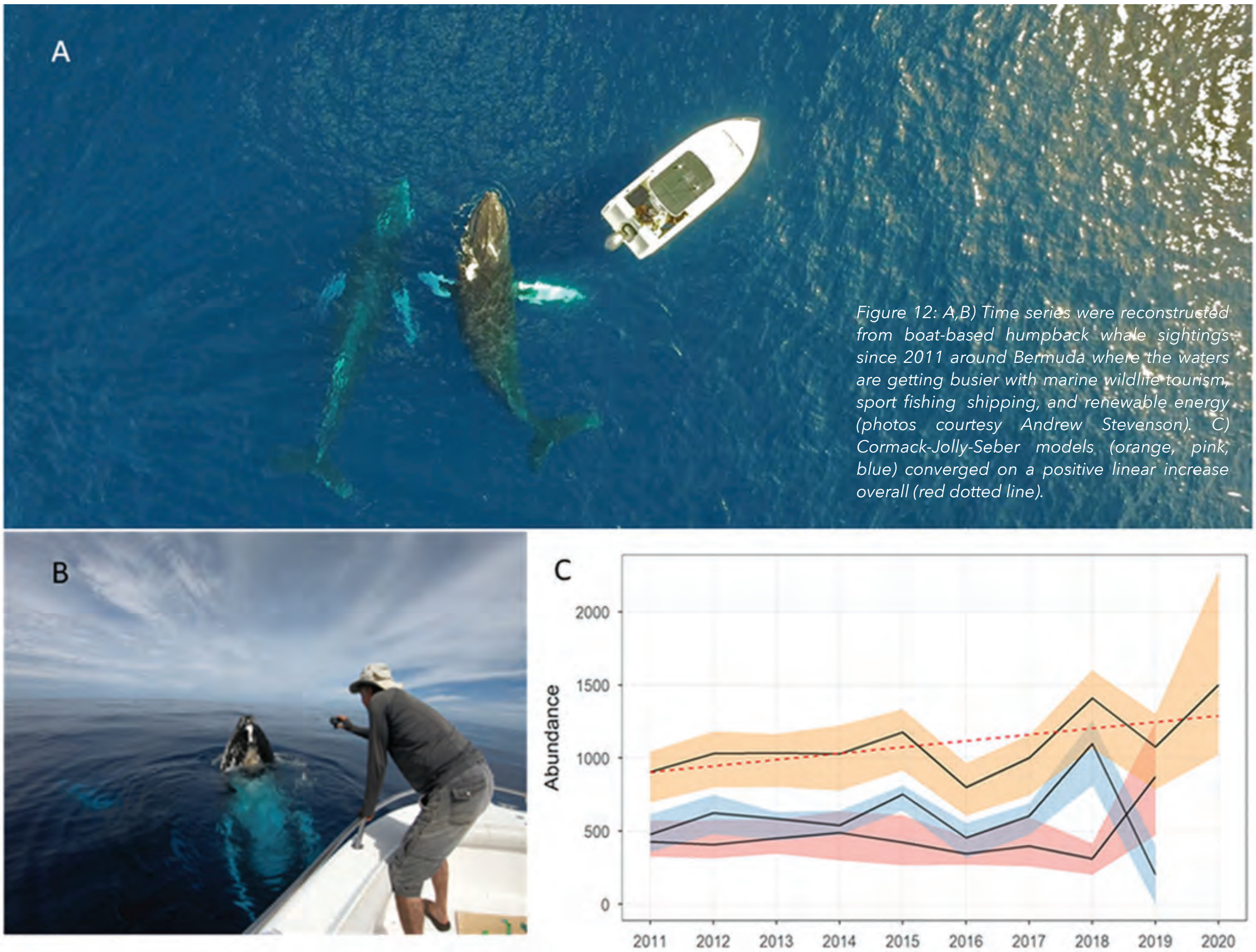

Figure 12: A,B) Time series were reconstructed from boat-based humpback whale sightings since 2011 around Bermuda where the waters are getting busier with marine wildlife tourism, sport fishing shipping, and renewable energy (photos courtesy Andrew Stevenson). C) Cormack-Jolly-Seber models (orange, pink, blue) converged on a positive linear increase overall (red dotted line).

While all of our time series analyses come with heavy caveats, our place-based approach gives managers and spatial planning authorities a better understanding of ecosystem variability and vulnerability to climate change. It provides insights into alternative states or trajectories of ecosystems in each study region, and possible drivers that could push or tip ecosystems into a new state. Notably, scientists at Ifremer discovered remarkable long-term multi-decadal stability of benthic ecosystems at the Lucky Strike hydrothermal vent on the Mid-Atlantic Ridge. Both the vent fauna and microbes varied only slightly over time, and there was little environmental variability (Figure 13).

This is strong evidence that these climax communities are highly preserved and not used to experiencing disturbances or much environmental variability. The exploitation of hydrothermal vents like Lucky Strike would have long-lasting impacts in an ecosystem characterised by such stability,

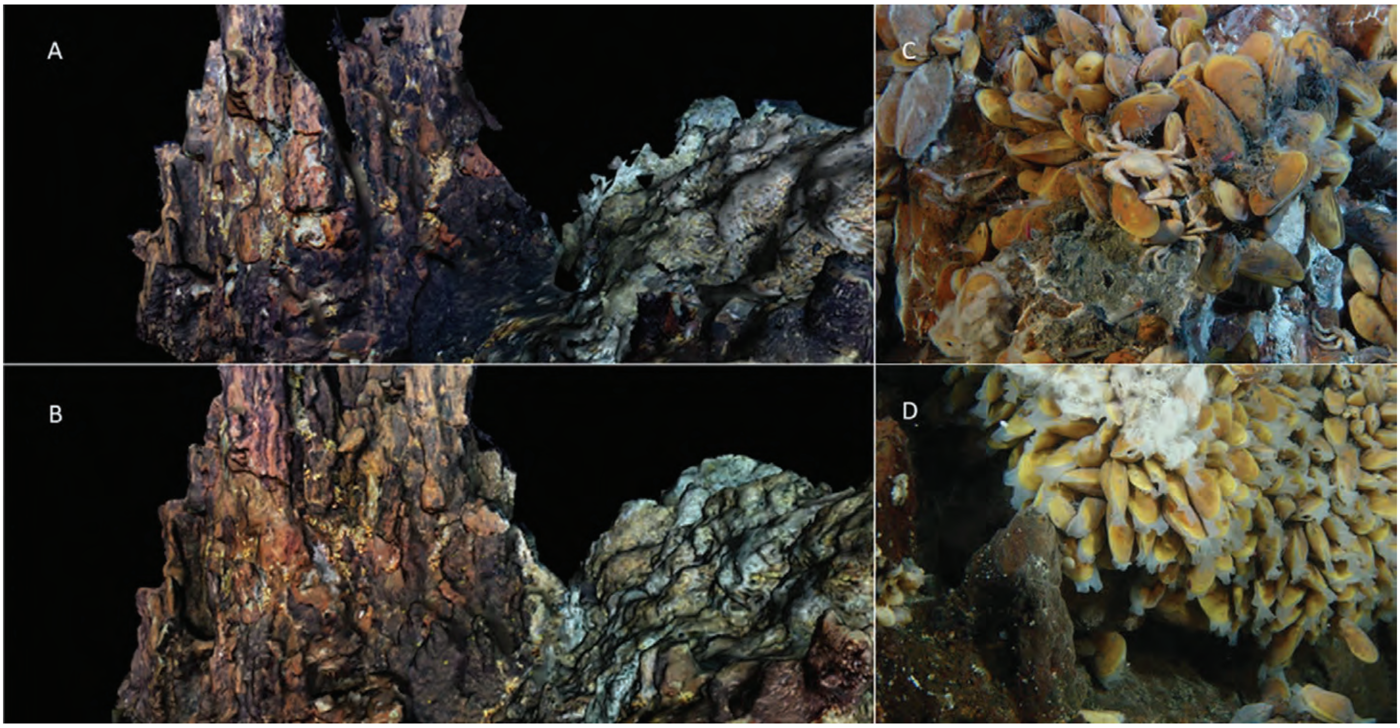

*Figure 13: A,B) Remarkable stability in the vent ecosystem at the Eiffel Tower edifice in the Lucky Strike field was recorded over time, from 2015 (image A) to 2020 (image B). C) Mussel cover (*Bathymodiolus azoricus *with a crab visitor was also stable, as was (D) white bacterial mat cover over the mussels. All photos courtesy Marjolaine Matabos.*

despite the incredibly extreme conditions of such systems, and would likely tip this ecosystem over into a significantly and likely undesirable altered state.

Next steps

Our next step in iAtlantic will take these results from the 12 study regions to drive a risk analysis, scoring the threat posed by future changes in sea temperature (T), salinity (S) and the strength of the Atlantic Meridional Overturning Circulation (AMOC). The risk analysis multiplies the likelihood of oceanographic changes in T, S and AMOC by 2070 as forecast by iAtlantic's oceanography team, using the Flexible Ocean and Climate Infrastructure Version 1 (FOCI), with the severity of ecosystem change reported by the results from this study. The risk analysis will provide decision-makers with high-level guidance about where we have the most confidence that the threats posed by changes in T, S and AMOC by 2070 are going to significantly alter ecosystems; – and therefore where we should be ramping up investments in ecosystem monitoring as we plan the blue economy so as to avoid reaching tipping points in those regions.

Noisy data, incomplete data, the lack of longer-term datasets, effects of seasonality and mesoscale oceanographic dynamics, effects of intra- and interspecific biological interactions and species phenology, and impacts of fishing fleet behaviour and management challenged all our analyses and interpretations. What needs to be done to reduce our uncertainty in place-based ecosystem assessments? Expert opinions of iAtlantic scientists involved in this study overwhelmingly noted the lack of regular and annual time series covering time periods long enough to capture oceanographic regime change at local, regional and basin scales, making it difficult to pin down specific drivers of change or tipping points. We used some alternative approaches to reconstruct time series where there were none before, and some of the more recently established datasets are going to become vital in years to come, for example local ecological records of humpback whales in Bermuda (established 2011), mesoplankton time series at the Cape Verde Ocean Observatory (established 2012). With the correct resourcing of human and infrastructure capacity underpinned by political declarations for international collaborations such as the Belém Statement and Galway Declaration, we can continue building robust time series and ensuring these are aligned with ocean observations at the correct spatial and temporal scales.

For more information on this work, please contact Lea-Anne Henry, L.Henry@ed.ac.uk

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Historical catches reveal signs of megafauna tropicalisation in 'hot spots' of the South Atlantic

By Angel Perez and Rodrigo Sant'Ana (UNIVALI)

Oceans have absorbed most of the heat increase of the atmosphere since pre-industrial times, gradually warming on average by 0.61°C. This process, however, has included large spatial variability with discrete regions warming much faster than average in the rest of ocean. These warmer regions have been called marine 'hot spots' and regarded as natural labs to understand the derived patterns of ecosystem change and anticipate adaptive actions to be taken by human societies. Over 20 marine hot spots have been identified around the world by sea surface temperature anomalies, two of them in the South Atlantic. Marine hot spots have been related to changes in complex patterns of ocean circulation, but much less is known about the consequences of rising temperatures in the related ecosystems.

In the context of the iAtlantic project, we have investigated an ocean warming-related ecological process known as "tropicalisation" of marine fauna and the extent to which it may have been operating in the SW and SE Atlantic marine hot spots. In such rapidly warming ocean regions, benthic and pelagic habitats become more suitable to tropical/subtropical megafauna species, allowing for a poleward expansion of their latitudinal distribution. The spatial extent of these changes seem to vary from species to species, but in subtropical/temperate transition regions they contribute to modific tions in megafauna assemblages, gradually becoming dominated by invading warm-water species, therefore more tropicalised. We looked for signs of these changes in catches of multispecies fisheries conducted historically off South America and South Africa. Because these catches include varying abundances of different target and non-target species over time, they could carry signs of change in the regional fish and shellfish assemblages that fishers have long elied on.

We started by analysing catches of over 29,000 multispecies demersal fishing operations conducted in the Brazilian Meridional Margin (SW Atlantic) between 2000 and 2019 and monitored at the fishing harbours of Santa Catarina, Brazil. The region (c. 20°S to 34°S) encompasses a biogeographical subtropical/warm temperate fauna transition zone highly influenced by the dynamics of the Brazil Current, a western boundary current that flows southwards along the shelf break and slope carrying generally warm tropical waters. At approximately 38°S, the Brazil Current collides with cold sub-Antarctic waters carried northwards by the Malvinas Current, forming the Brazil-Malvinas Confluence (Fig. 1). This feature contains important environmental gradients, which are also noted on shelf waters off northern Argentina, Uruguay and southern Brazil. Since its early development in the 1960s, demersal fisheries operations off southern Brazil have been sustained by megafauna communities influenced by this dynamic oceanographic scenario, economically thriving from the catch of assorted subtropical and warm-temperate fish crustaceans and cephalopod species. In the past decades, however, a poleward displacement of wind patterns over the South Atlantic has led to a southward expansion of the Brazil Current's path, and displacement of Brazil-Malvinas Confluence (0.6-0.9° latitude per decade). Under the warming conditions promoted by a stronger influence of the Brazil Current, it was expected that subtropical species would have become more common on the Brazilian Meridional Margin and therefore more abundant in multispecies commercial catches. A previous study conducted by Ignacio Gianelly, Alberto Piola and others in 2019 provided important evidence for such process taking place since the 1980's further south, at the Argentinian-Uruguayan Common Fishing Zone.

We used available global compilations of species thermal preferences to assign mean 'optimum' temperatures for each of 78 species recorded in the catches. Following a procedure first described by William Cheung, Reg Watson and Daniel Pauly in 2013, we used these optimum temperatures to calculate annual 'mean temperatures of the catches' (MTC), an index of aggregated thermal affinities of species contained in the catches. Our MTC time series showed a sharp increasing trend from 2012 onwards, significantly explained by increasing sea bottom temperatures and the transport volumes of the Brazil Current. Applying spatial and temporal community analyses we demonstrated that the MTC positive trend derived from biomass losses of cold-water species and gains of warm-water species in the catches, consistent with a general process of tropicalization of demersal megafauna off southern Brazil during the analysed period (Fig. 2). A few species had a particularly important role in this process including the Argentine croaker (*Umbrina canosai*), the Argentine hake (*Merluccius hubbsi*), the codling (*Urophycis mystacea*) and the monkfish (*Lophius gastrophysus*), all cold-water species that have become scarcer in the catches and counterbalanced by increasing catches of the warm-water whitemouth croaker (*Micropogonias furnieri*), grey triggerfish (*Balistes capriscus*), the spotted pink shrimp (*Penaeus brasiliensis*) and others. None of these are 'invading' species in the region, but subtropical species that seem to have become more available to fisheries than they used to be

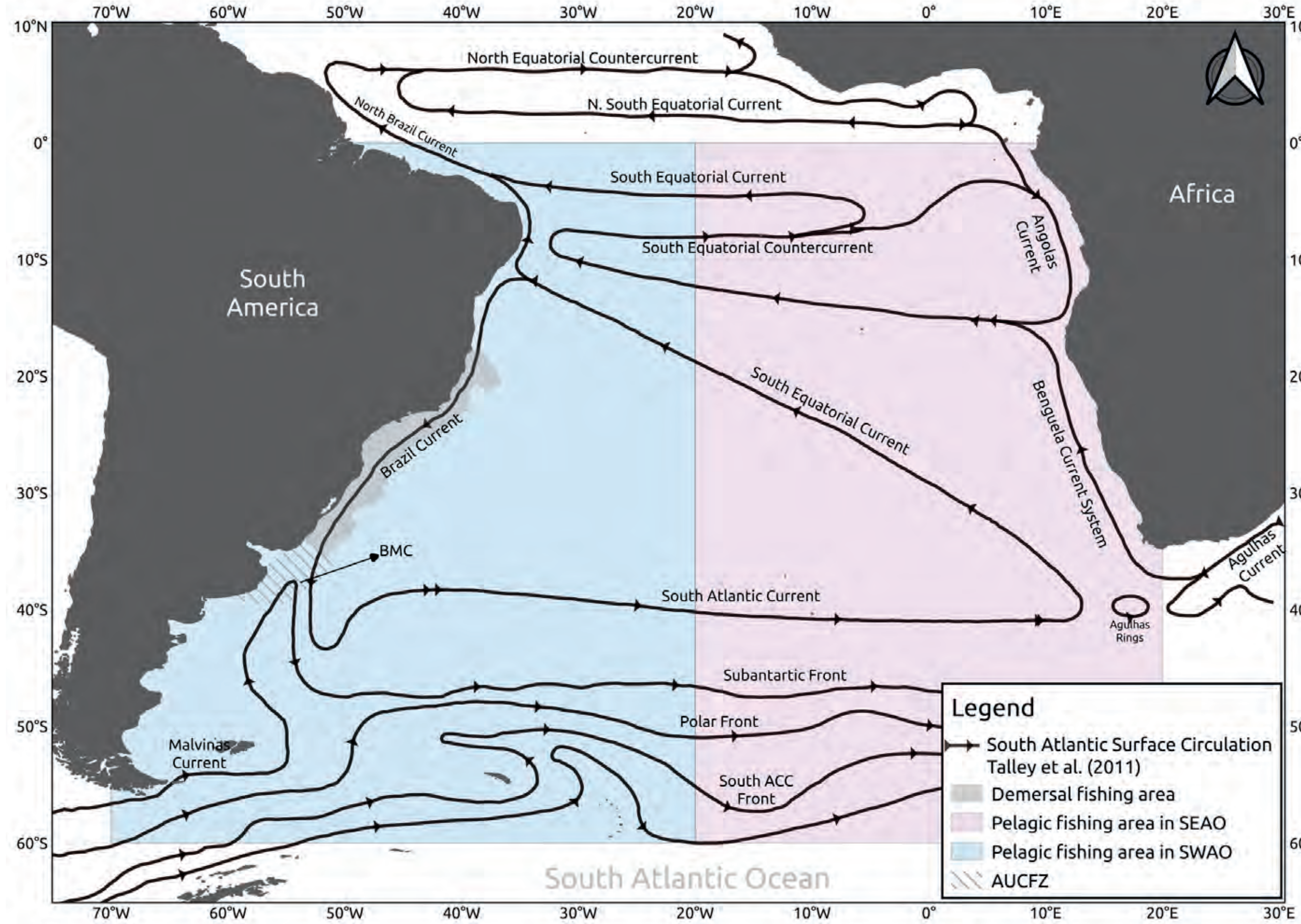

Figure 1: South Atlantic Ocean with schematic view of surface circulation. Also indicated are the study areas of demersal and pelagic fishing time series. BMC: Brazil-Malvinas Confluence; AUCFZ: Argentinian-Uruguayan Common Fishing Zone.

Similar analytical approaches have been applied to the pelagic line fisheries for sharks, tuna and tuna-like species, this time in both the SW and SE Atlantic regions. Time series of catches originated from historical records of the International Commission for the Conservation of Atlantic Tunas (ICCAT) between 1978 and 2018. Because these are highly migratory fish that can cover vast areas of the South Atlantic within the annual period, we had to consider much broader areas to compile both catches and sea surface temperatures. Yet we also found that annual MTC increased continuously on both sides of the South Atlantic during the studied period, and these trends were explained by increasing sea surface temperatures. Increasing MTC rates, however, were considerably low when compared to the ones observed in the demersal fisheries and higher in the SW Atlantic than in the SE Atlantic. It is plausible that by being so mobile and having the capability to thermo-regulate, these large pelagic predators may find mechanisms to better assimilate environmental variability than demersal species. Also, although most species present in the catches occurred in both SW and SE regions where hot spots have been delineated, the associated ocean circulation processes differ greatly as well as, potentially, the mechanistic links between warming and biological responses. We found that biomass losses of the 'cold-water' albacore (*Thunnus alalunga*) in the catches had an important role in modulating MTC on both sides of the South Atlantic, being counterbalanced by catches of species with higher affinity for warm waters, chiefly the skipjack tuna (*Katswonus pelamis*), serra spanish mackerel (*Scomberomorus brasiliensis*), swordfish (*Xyphias gladius*), bigeye tuna (*Thunnus obesus*), yellowfin tuna (*Thunnus albacares*) and king mackerel (*Scomberomorus cavalla*). We are now concentrating on modelling abundance indices of some of these species to look into temperature-related temporal variability at the population level.

After the global study published by William Cheung and partners in 2013, similar analyses of commercial catches have evidenced tropicalisation scenarios in different regions around the world. Yet often this evidence can be hindered by regional factors unrelated to climate change, including fishing economic strategies, overfishing and management actions. Efforts must be done to measure/reduce their interference. Notwithstanding this, historical catch data have proven to be an effective proxy to global climate effects on marine ecosystems regionally, with the advantage of further signalling to future changes in the economic performance of current of fishing regimes. How will the fishing industry in these areas of the South Atlantic Ocean adapt to changes in the availability of traditional and non-traditional targets? Which fishing economic strategies will no longer be viable and which ones may emerge to explore expanding stocks of subtropical species? What adaptive measures can be incorporated in fishing management regimes (both national and transnational) to attain ecological and economic objectives in the coming decades? These are critical questions that will guide further applications and improvements of these analytical approaches in the South Atlantic and other ocean regions.

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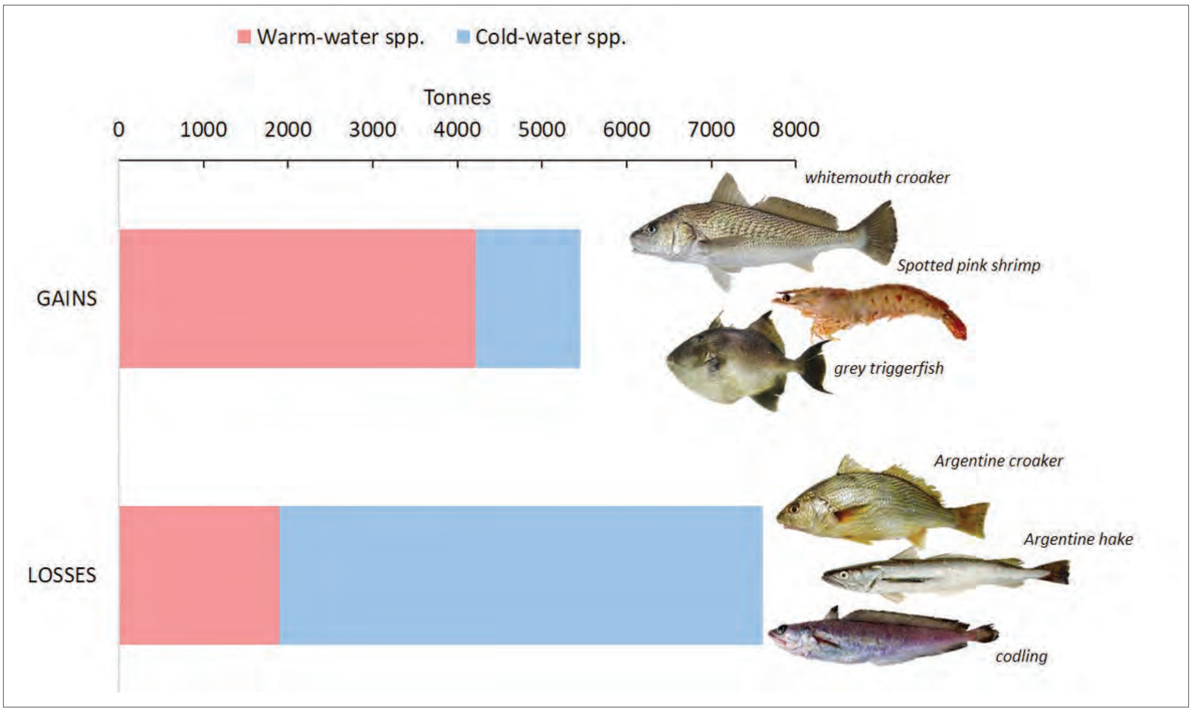

Figure 2: Average biomass gains and losses in the demersal catches in the Brazilian Meridional Margin between 2000-2002 and 2017-2019. Biomass gains and losses are dominated by warm- and cold-water species, respectively. Fish images: www.fishbase.o g, www.pt.wikipedia.org , INIDEP, www.demersais.furg.br , Luciano Fischer, FAO, https://pt.frwiki.wiki/

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This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 818123 (iAtlantic). This output reflects only the autho 's view and the European Union cannot be held responsible for any use that may be made of the information contained therein.

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INTEGRATED ASSESSMENT OF ATLANTIC MARINE ECOSYSTEMS IN SPACE AND TIME