

Unseen but Connected: Exploring How Connectivity Informs the Ecosystem Approach to Fisheries Management in the Northwest Atlantic Fisheries Organization

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Abstract

Connectivity, a key property of marine ecosystems operating over various spatial scales, relies on movements of organisms, nutrients and energy. Those can be active, involving directed migration, or passive, the latter relying on transport by physical mechanisms that transport organisms, including gametes and larvae. Dispersal drives population dynamics and community structure, hence is an essential component to consider in an Ecosystem Approach to Fisheries Management (EAFM). In the Northwest Atlantic Fisheries Organization (NAFO), connectivity has been considered in a number of different contexts and applications. The distribution ranges of major marine fish species, a product of their dispersal, amongst other aspects, helped to inform the establishment of Bioregions, Ecosystem Production Units, and Ecoregions – nested spatial scales identified as relevant to the development of ecosystem summaries and management plans. For sessile and sedentary benthic species, such as the corals and sponges identified as Vulnerable Marine Ecosystem (VME) indicators, connectivity within and among high-density habitats is key to habitat formation and continuation. In such species, connectivity is governed by larval transport, predominantly by bottom currents. Recently, NAFO has used 3-D Lagrangian particle tracking models to identify connectivity networks of both the closed areas and identified VME habitats, in support of an EAFM. Here, an overview of how NAFO has incorporated information on connectivity into its decision-making processes is provided.

Key words: connectivity, vulnerable marine ecosystems, NAFO, EAFM

Introduction

Species' distributions underpin an Ecosystem Approach to Fisheries Management (EAFM) and spatial connectivity, defined as the movement of adults, gametes or larvae across space (Hanski, 1998; Tischendorf and Fahrig, 2000), is an important property of marine ecosystems that influences species' distributions (Wang *et al.*, 2021), as well as community composition (Costello and Chaudhary, 2017; Monteiro *et al.*, 2017), nutrient transport (Palter *et al.*, 2010; Fripiat *et al.*, 2021), and ultimately the productivity (McClain *et al.*, 2004; Doddridge and Marshall, 2018), dynamics (Watson *et al.*, 2012), resistance/resilience (Carr *et al.*, 2017) and restoration (McRae *et al.*, 2012) of ecosystems. It does so through exchange and subsidies of organisms, nutrients, and energy within and across population boundaries (Spanowicz and Jaeger, 2019), while driving population dynamics and community structure (Lundberg and Moberg, 2003; Pineda *et al.*, 2007), and thus is an essential component to consider in an EAFM (Shanks *et al.*, 2003).

Mediated through both active and passive biological and environmental processes, connectivity is influenced by

(among others) currents, bathymetric features, internal waves and tides, boundary layers and the thermo-haloclines between water masses, which can affect vertical movement of organisms (Crooks and Sanjayan, 2006; Pineda *et al.*, 2007). Those physical factors may not entirely constrain movements of active, nektonic animals but does influence their distributions (Dahms and Killen, 2023), while the dispersal trajectories of those sessile and sedentary species which rely on larval transport can be primarily determined by physical processes (Cowen and Sponaugle, 2009).

The importance of connectivity in the maintenance of healthy and productive marine ecosystems has been recognized in international policy, both under the auspices of protecting biodiversity and for sustainable use of the oceans. The Convention on Biological Diversity (CBD) introduced connectivity as a property of marine protected area (MPA) network design under Aichi Biodiversity Target 11 (CBD COP 10 Decision X/2). This property has been retained in the 2022 Kunming-Montreal Global Biodiversity Framework (GBF) adopted by CBD COP 15 under Target 3 (CBD Decision 15/4). The CBD guidance notes for Target 3 provide the following definition:

“Well-connected – In order for protected areas and OECMs [Other Effective Area-Based Conservation Measures] to be effective, they should be connected through corridors as well as integrated into wider landscapes, seascapes and the ocean. This is an essential element of creating effective systems or networks of protected and conserved areas that can meet sustained in situ conservation outcomes and cope with stresses and disturbances, including from the impacts of climate change.”¹.

The GBF identifies the Protected Area Connectedness Index (PARC-Connectedness) and ProtConn (Protected Connected Index) as component indicators for Target 3. The PARC index measures the extent to which protected areas are functionally connected to one another and to other areas of intact natural ecosystems². It was developed for terrestrial ecosystems but has analogues in the marine environment (Kenchington *et al.*, 2018). The ProtConn index measures the percentage of land covered by protected and connected lands (Saura *et al.*, 2018). It was developed for reporting on Aichi Target 11 but has been retained for the GBF. The Protected Area Isolation Index (PAI) which measures how connected each of the world's protected areas (PAs) are, focuses on the movement of terrestrial animals between habitats (Brennan *et al.*, 2022) and is considered a complimentary indicator to Target 3.

Connectivity has also been introduced into the United Nations Sustainable Fisheries resolutions, first appearing in 2022 in the General Assembly Resolution A/Res/77/118³ in relation to both Vulnerable Marine Ecosystems (VMEs) (paragraph 212) and fish stocks (paragraph 216). With respect to VMEs, the resolutions call for regional fisheries management organizations, such as the Northwest Atlantic Fisheries Organization (NAFO):

“...to identify and overcome barriers to the implementation of the relevant paragraphs of General Assembly resolutions 64/72, 66/68 and 71/123 such as data availability, especially with regard to baseline data and the spatial distribution and connectivity of vulnerable marine ecosystems...”.

While connectivity in the deep-sea can be difficult to measure empirically, NAFO Scientific Council has responded to this call by developing biophysical models to elucidate the connectivity networks of VMEs and of the closed areas within its Regulatory Area. In this contribution, I provide an overview of how NAFO has

incorporated information on connectivity into its decision-making process. Whenever relevant, I go beyond a recount of the facts and share my perspectives on the provision of scientific advice on this topic.

The Ecosystem Approach to Fisheries Management in NAFO and the Role of Connectivity

In NAFO, connectivity has been considered, directly or indirectly, in a number of different spatial contexts and applications (Table 1). The spatial structure of physical and biological features, including the distribution ranges of major fish stocks, helped to inform the establishment of three nested spatial scales, Bioregion, Ecosystem Production Unit (EPU), and Ecoregion, that were identified as relevant to the development of ecosystem summaries and management plans (Pepin *et al.*, 2014; NAFO, 2014). They serve as a framework supporting implementation of an EAFM (Koen-Alonso *et al.*, 2019). The NAFO Working Group on the Ecosystem Approach to Fisheries Management (WG-EAFM) (now the ‘Working Group on Ecosystem Science and Assessment’, WG-ESA) considered this issue at its first meeting in June of 2008, under its first two Terms of Reference:

ToR 1: To identify regional ecosystems in the NAFO Convention Area, and

ToR 2: To make an inventory of current knowledge on the components of each regional ecosystem (NAFO, 2008).

A spatially and temporally extensive set of observations of bathymetric, oceanographic and biotic variables was analyzed to identify regions and subregions of biophysical similarity/dissimilarity or Bioregions (NAFO, 2008; Zwanenburg *et al.*, 2010; Pepin *et al.*, 2010; Pepin *et al.*, 2014). Each Bioregion is composed of one or more EPUs. Those do not represent closed systems, but they generally correspond to the distributions of particular, major groundfish stocks, while having a coherent fish community structure internally (Koen-Alonso *et al.*, 2019). Within an EPU, geographical areas with consistent physical and biological characteristics are defined as Ecoregions. It is within this spatial scale that more precisely defined habitats (such as VME habitats) can be identified. Subsequently, EPUs and Ecoregions have been used by NAFO Scientific Council while generating ecosystem-science advice (NAFO, 2015b; Koen-Alonso *et al.*, 2019). They have been paralleled in Canada, the adjacent coastal state, using similar methods (DFO, 2009). In hindsight, it might have been better to apply the term Ecoregion to the larger spatial scale Bioregion, to be consistent with its use elsewhere, such as in the International Council for the Exploration of the Sea (ICES) where an ecoregion is a spatial unit used to synthesize evidence for ecosystem-based management (ICES, 2004). These regions share

¹ <https://www.cbd.int/gbf/targets/3#:~:text=Well%2Dconnected%20%E2%80%93%20In%20order%20for,to%20occur%20within%20their%20boundaries> Accessed 8/14/2025.

² <https://geobon.org/ebvs/indicators/protected-area-representatives-connectedness-indices/> Accessed 10/12/2025.

³ <https://docs.un.org/en/A/RES/77/118> Accessed 8/14/2025.

Table 1. Chronological development of the incorporation of information on connectivity into the science advice for NAFO.

Year	Benchmarks for the Use of Connectivity-Related Data in NAFO	Reference
2008	Delineation of ecoregions at three nested scales	NAFO (2008)
2010	Indices of biomass, abundance and biomass/abundance (BA) ratio were used to describe the changes in the fish community in two functional sub-units of the Newfoundland and Labrador Shelves Bioregion.	NAFO (2010)
	Elaboration of the overall EAFM framework described as a three-tiered, hierarchical one. The first tier defines fishery production potential at the EPU level, taking into account environmental conditions and ecosystem state.	NAFO (2010)
2011	“Roadmap for the development of and ecosystem approach to fisheries (EAF) for NAFO” introduced. Subsequent reports focus on developing and implementing the “Roadmap to EAF” which includes identification of VMEs.	NAFO (2011)
2012	First mention of connectivity in relation to recovery of sponge grounds from bottom-contact fishing.	NAFO (2012)
2013	Connectivity first raised in the assessment of areas closures for the protection of sea pen Vulnerable Marine Ecosystems (VMEs), for example: “the lack of protection for the entire eastern part of their distribution is of concern for the long term sustainability of these VME given the lack of knowledge of recruitment processes and connectivity “, “the areas between 13 and 14 should be linked for sustaining connectivity in this system”, “the system of sea pen VMEs on Flemish Cap”.	NAFO (2013)
	WG-ESA notes that “the closed areas should be viewed as connected systems”.	NAFO (2013)
2015	“Index of Risk of VME fragmentation”, the proportion of discrete VME without protection, introduced for the assessment of Significant Adverse Impacts (SAI) of bottom-contact fishing (sensu FAO, 2009). This risk was incorporated into “Overall SAI risk scores” for sponge, sea pen and large gorgonian VME in the NAFO Regulatory Area (NRA).	NAFO (2015b)
	ToRs for WG-ESA updated and include: Spatial Considerations. ToR 2. In support of the Roadmap, develop research and summarize new findings on the spatial structure and organization of marine ecosystems, with emphasis on connectivity, exchanges and flows among ecosystem units in the NAFO Convention Area.	NAFO (2015b)
2018	Connectivity agreed to be a part of the re-assessment of VME closures in 2020: “Consideration of the connectivity of VMEs through links between propagule/larval transportation and VME distribution/location... should be included. This will highlight the importance of certain VME closed areas in supporting larval dispersal and recruitment between other VME closed areas of the same type...”	NAFO (2018)
	First assessment of connectivity among closed areas within the fishing footprint in the NRA.	Kenchington <i>et al.</i> (2018); NAFO (2018)
	Agent-based modeling of sea pens introduced for understanding the level of connectivity and dependence among the distinct aggregations that exist on the seascape.	NAFO (2018)
2019	“Projected Connectivity Among Closures” added to the assessment of SAI to be applied to the reassessment of bottom fisheries in 2021. Connectivity is defined as the “physical links between two or more areas; an area is considered to have redundancy when two or more other areas connect to it. These properties relate to the ability of populations to persist.”.	NAFO (2019); Wang <i>et al.</i> (2019)
	Connectivity discussed as a part of the re-assessment of VME closures and included in the identification of High Priority Areas for Management Action.	NAFO (2019)
2020	VME Closure Connectivity Index developed based on enhanced model developments and connectivity characteristics for each of the areas closed to protect large gorgonian corals, sea pens and sponges in the NRA, including outputs from 3D forward- and backward-tracking biophysical models using yearly and seasonally averaged oceanographic models.	NAFO (2020); Wang <i>et al.</i> (2020)
	“Importance as a Larval Source for other Closed Areas” introduced to the review of the closed areas in addition to retention and redundancy.	NAFO (2020)
	Agent-based modeling of sea pens identified that, in the absence of fishing, recovery of an area could take place in 50 years. Also that, under current fishing scenarios, sea pen connectivity might be compromised, leading to longer recovery times. In the case of the NAFO closures, recovery time could exceed 100 years.	NAFO (2020)
	Proposed management actions prioritized based on connectivity. The lowest priority for management action is for ‘Sink’ areas that have ‘Moderate’ to ‘Strong’ Redundancy, on the basis that such areas likely receive larvae from other closed areas to retain their local populations. Other scenarios are discussed.	NAFO (2020)
	Isolation/Proximity Index as a measure of VME fragmentation introduced.	NAFO (2020)
	Work of WG-ESA on connectivity discussed in the context of Other Effective Area-Based Conservation Measures (OECMs).	NAFO (2020)
2021	Application of Isolation/Proximity Indices to Large-sized sponge VMEs	NAFO (2021a)
2022	Connectivity among VMEs evaluated using particle tracking models applied to the seven VME indicator taxa (Large-size sponges, Sea pens, Large and Small gorgonian corals, Black corals, Sea squirts and Erect bryozoans).	NAFO (2022a)
2024	Publication of simulations of VME habitat loss on connectivity networks for each of the VME indicator taxa.	Wang <i>et al.</i> (2024)
2025	When the six sponge areas in the NRA were submitted to the World Protected Area database as OECMs, they were considered to be ecologically connected based on connectivity analyses conducted in WG-ESA.	https://www.nafo.int/Fisheries/OECMs [Accessed 8/14/2025]

similar oceanographic conditions, habitats, and biological communities, as do the NAFO Bioregions. Further, Fisheries and Oceans Canada (DFO, 2016) uses the term ‘Biological Facies’, to refer to a fine-scale unit used to represent specific biological habitat types, such as a VME habitat, which would nest well within the EPU.

Genetic Population Structure

Genetic studies can reveal that wide-ranging species (e.g., Atlantic cod (*Gadus morhua*)) are composed of a number of smaller, locally adapted populations. Without this knowledge, high fishing pressure might extirpate one population, reducing the overall genetic diversity and stability of the species, even if the overall harvest remains high. Genetic markers can be useful tools for understanding the stock structure of fish populations, revealing patterns of connectivity and differentiation that inform both delineation of EPUs and the management of fisheries more generally (Begg *et al.*, 1999). Gene flow, defined as the movement of genes from one population to another through the migration of individual organisms that subsequently reproduce in their new population, influences fish stock structure, with high gene flow leading to less genetic differentiation and potentially a single genetic stock, while restricted gene flow can lead to distinct stocks (Cano *et al.*, 2008; Hellberg 2009). Mating may occur in discrete areas (spawning grounds), sometimes associated with natal homing (e.g., Atlantic cod: Bonanomi *et al.*, 2016) which can result in genetically distinct populations (e.g., Ruzzante *et al.*, 2006). Genetic analyses have helped to determine stock structure in a number of species occurring in the NAFO area, including northern shrimp (e.g., Jorde *et al.*, 2015), Atlantic cod (e.g., Ruzzante *et al.*, 1999), Greenland halibut (e.g., Estévez-Barcia *et al.*, 2025), redfish (e.g., Roques *et al.*, 2002), and capelin (e.g., Kenchington *et al.*, 2015).

There are few population genetic studies of VME indicator species in the NAFO Convention Area, and none within the fishing footprint of the NAFO Regulatory Area (NRA). This is in part due to limited opportunities to conduct appropriate sampling at depth, which ideally involves collection of numerous individuals using a remotely operated vehicle (ROV) from a number of putative populations over the full range of the species’ distribution. Particle tracking models which identify connectivity networks (see below), as well as species distribution models which identify suitable habitat (e.g., Murillo *et al.*, 2024; Murillo *et al.*, 2025), can help to identify appropriate sampling locations within large geographic settings. Nevertheless, population genetics of the deep-sea glass sponge, *Vazella pourtalesii*, a VME indicator taxon (NAFO, 2025) which occurs in the broader NAFO Convention Area and was sampled with a ROV, has revealed patterns of genetic diversity, structure, and connectivity (Patova *et al.*, 2025). Further, studies of the deep-sea coral genus *Paramuricea*, captured in

the NAFO Convention Area with bottom trawls, gillnets and longlines, indicated distinct, diverse genetic structure across its range to the Gulf of Mexico, and cryptic species in waters off Newfoundland and Labrador (Radice *et al.*, 2016); the latter being crucial information for the assessment of connectivity in this genus.

Connectivity and Vulnerable Marine Ecosystems

As part of an EAFM, the protection of VMEs from significant adverse impacts (SAI) of bottom-contact fishing gear is required under the UN Sustainable Fisheries resolutions. In this context, VMEs are NAFO Ecoregions with physical and biological characteristics that render them especially vulnerable. The International Guidelines for the Management of Deep-sea Fisheries in the High Seas of the Food and Agriculture Organization of the United Nations (FAO, 2009) provide a suite of characteristics for the selection of VME indicator species which can serve to define and delineate such Ecoregions (NAFO, 2015a). NAFO Scientific Council has applied those Guidelines to data on over 500 trawl-caught benthic invertebrate taxa (Murillo *et al.*, 2011) and identified nine functional groups of VME indicators, all of which form habitats of mixed species composition, viz.: Large-size Sponges, Sea Pens, Large Gorgonian Corals, Small Gorgonian Corals, Black Corals, Erect Bryozoans, Sea Squirts, Sea Lilies (Crinoids) and Tube-dwelling Anemones (NAFO, 2025). In Ecoregions where these structure-forming VME indicators occur in large concentrations (NAFO, 2019; Kenchington *et al.*, 2025), ecological processes may be highly dependent on the dominant taxa (e.g., Pham *et al.*, 2019; Murillo *et al.*, 2020a; Murillo *et al.*, 2020b; Stratmann *et al.*, 2024).

Once the VME indicators were identified, NAFO Scientific Council used a kernel density analysis and areal expansion technique to identify VME Ecoregions for each of seven functional groups of VME indicators for which data were available (Kenchington *et al.*, 2019; Kenchington *et al.*, 2025). Sea Lilies and Tube-dwelling Anemones were not evaluated. These VME Ecoregions were used to inform a series of spatial closures where bottom-contact fishing gears are prohibited (NAFO, 2025).

Connectivity issues among VME Ecoregions were first discussed by WG-EAFM at its 2012 meeting in the context of SAI on VMEs, where it was stated that connectivity amongst the sponge grounds will influence recovery dynamics (Table 1; NAFO, 2012). The following year, the Fisheries Commission requested science advice regarding sea pen closures on the Flemish Cap. WG-ESA described the sea pens as “a system of sea pen VME”, and it was noted that “the lack of protection for the entire eastern part of their distribution [was] of concern for the long term sustainability of these VME given the lack of knowledge of recruitment processes and connectivity” (NAFO, 2013). By 2015, NAFO had incorporated aspects

of habitat configuration (arrangement of the VMEs in space), as part of its assessment of SAI, in an “Index of Risk of VME fragmentation” defined as the “Proportion of discrete VME without protection” (NAFO, 2015b). This is the inverse of the ProtConn indicator under the GBF. Recognizing the importance of connectivity to the structure and functioning of marine ecosystems, WG-ESA proposed an update and revision of its long-term ToRs to incorporate connectivity, accordingly (Table 1):

ToR 1. Update on identification and mapping of sensitive species and habitats in the NAFO area. In support of the Roadmap develop research and summarize new findings on the spatial structure and organisation of marine ecosystems with an emphasis on connectivity, exchanges and flows among ecosystem units in the NAFO Convention Area (NAFO, 2016).

This change to the WG-ESA ToRs stimulated primary research on connectivity (Table 1), and in 2018 work was presented to WG-ESA detailing an assessment of connectivity among closed areas within the fishing footprint of the NRA (Kenchington *et al.*, 2018; NAFO, 2018). An agent-based modelling approach was also explored as a means to study the impacts of commercial fishing on sea pens (NAFO, 2018).

A metric of habitat configuration that incorporates habitat area and nearest neighbour distances (PX; Gustafson and Parker, 1994) was applied to the distributions of each VME previously identified by kernel density analyses, and to the configuration of the spatial closures. Lagrangian particle tracking models were used to estimate connection distances among VMEs and among closed areas. Such modeling approaches being the most practical means of assessing connectivity of benthic invertebrate VME indicators in the deep sea, where the remoteness of the region makes other approaches, such as population genetics, impractical (see above). Initially the models were 2-D, allowing only horizontal movement (NAFO, 2018; Kenchington *et al.*, 2019), and to address this deficiency, model larvae were released at different vertical positions within the water column to track their dispersal. However, by 2021, more realistic connections among the closed areas and among the VMEs were evaluated based on connectivity modeling using 3-D Lagrangian particle tracking models which included vertical movement and were run in both forward and hindcast directions (Wang *et al.*, 2021, 2024; NAFO, 2021a). These models allowed the model larvae to passively move through the water column. Although different modeling scenarios can be run to compensate for a lack of knowledge of spawning times, larval duration and behaviour of VME indicator taxa, further information on the reproductive biology of these taxa would enable more precise models to be performed (see Kenchington *et al.* (2018) for knowledge

gaps and compensatory modeling). The particle tracking trajectories resulting from these modeling scenarios identify the connectivity networks among VME habitats, including source-sink relationships, and complement species distribution models to quantify probabilities of recruitment to areas of predicted presence (*e.g.*, Wang *et al.*, 2022).

Based on this body of work, different ways of capturing the information on the connectivity network design were presented in the form of connectivity indices (NAFO, 2020). Connectivity and habitat configuration were subsequently incorporated into the assessment and recommendations for closed area protection of the VMEs (NAFO, 2021a). Meanwhile, WG-ESA defined connectivity and connectivity networks in the context of their work on VMEs as:

“physical links between two or more areas; an area is considered to have redundancy when two or more other areas connect to it. These properties relate to the ability of populations to persist” (NAFO, 2020).

Most recently, simulated removal of single VME habitats was modeled. Very considerable differences were found amongst those areas in their effects on network configuration, as measured by the change in PX resulting from their deletions (Gustafson and Parker, 1994, NAFO, 2022a). PX is an index of habitat configuration that incorporates habitat area and nearest neighbour distances, and is similar to the GBF indicator PARC, which measures the extent to which protected areas are functionally connected to one another. Removal of many VMEs, 28 of the 84, had little effect on the PX (declines of < 0.05%) but, in each of the seven VME indicator functional groups, there was at least one VME habitat that, when removed, reduced the index by more than 45% and, in some cases, by more than 85% (NAFO, 2022a; Wang *et al.*, 2024). While PX cannot capture every important aspect of network configuration, it is clear that some VMEs are much more important to achievement of overall conservation goals than are others.

In preparing for the 2027 NAFO review of the placement and effectiveness of the areas closed to bottom fishing to protect VMEs, WG-ESA agreed to consider the work done on connectivity since the last review and to consider the best way to incorporate those results into the assessment of SAI. It was noted that there are many VMEs that are not protected by area closures. For those VME connectivity networks that are only partially protected, the unprotected VMEs could be important sources of recruitment inside the closed areas, and loss or diminishment of such unprotected VMEs could undermine NAFO efforts to effectively protect VMEs through implementation of spatial closures, and hence the implementation of an EAFM (NAFO, 2024).

In going forward, NAFO could frame its connectivity indices using the terminology of the GBF Target 3 indicators (*i.e.*, PARC-Connectedness and ProtConn) when applicable, so as to parlay its work into broader global assessments.

Uptake of Science Advice on Connectivity of VMEs by Managers

Despite the importance of connectivity for the protection of VMEs being first raised by WG-EAFM in 2012 (Table 1), it was over a decade later that clear evidence of consideration of connectivity became apparent in management actions (NAFO, 2022b). The research undertaken by WG-ESA in 2020 emphasized the importance of connectivity networks for the protection of VMEs with an emphasis on sea pen connectivity (NAFO, 2020). Subsequently, in 2021, the NAFO ‘Working Group on the Ecosystem Approach Framework to Fisheries Management’ (WG-EAFFM) specifically mentioned the objective of improving connectivity for sea pens and black corals in recommending area closures to the NAFO Commission:

Extension to Area Closures 8 and 9 (linking with Area Closures 8, 9 and 12), to provide a more continuous closure to protect sea pens and black coral (Areas 8a and 9a) and improve connectivity; (NAFO, 2021b).

Further, connectivity is one of the criteria for evaluating closed areas as Other Effective Area-Based Conservation Measures (OECMs). The connectivity work undertaken by the NAFO Scientific Council informed the grouping of separate area closures to protect Large-Sized Sponge in their OECM evaluations (Table 1). With connectivity indices now established, and the subject prominent in international policy, it is hoped that connectivity will play an increased role in decision making in the 2027 review of closed areas to protect VMEs in the NRA.

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