NOTE

Abundant mesopelagic fauna at oceanic high latitudes

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ABSTRACT: The presence of a dense layer of organisms in the mesopelagic zone is a ubiquitous feature of the world oceans, and these organisms may constitute a major component of marine biomass worldwide. Many mesopelagic organisms perform light-dependent diel vertical migration. It has been hypothesised that extreme light regimes encountered at high latitudes may disturb these migration patterns and thereby limit the northern expansion of mesopelagic fauna into the Arctic. Using hydroacoustic data collected during 4 surveys conducted in the open Norwegian Sea during the summer season, we evaluated if the key features of mesopelagic fauna reported worldwide (high density and diel vertical migration) are also observed in the high latitudes of the Northeast Atlantic. The results confirm that the high-latitude Northeast Atlantic hosts a high density of mesopelagic fauna which performs daily migration patterns similar to those reported in other regions. They also support the limiting effect of photoperiod on its potential biomass. These results stress the need for thorough studies on the abundance, biodiversity and trophic ecology of the mesopelagic fauna in this region.

KEY WORDS: Arctic · High latitudes · Hydroacoustics · Mesopelagic · Norwegian Sea · Sub-Arctic

INTRODUCTION

The presence of a dense layer of animals between 200 and 1000 m is a ubiquitous feature of the world oceans. Although most fisheries operate on continental shelves and slopes, where biological productivity is greater, the biomass of fish and invertebrates in the mesopelagic layer may vastly exceed world catches. Early estimates of the global biomass of mesopelagic fish suggested a billion metric tonnes (Gjøsæter & Kawaguchi 1980). However, these were based on midwater trawling, which underestimates biomass substantially (Kaartvedt et al. 2012). Recent estimates are on the order of 10 billion metric tonnes (Irigoien et al. 2014), i.e. a hundred times more than present annual global fish landings. This estimate does not include the biomass of animal groups other than fish in the mesopelagic zone. Uncertainty in mesopelagic fish biomass estimates from hydroacoustic studies remains colossal (Davison et al. 2015), but right or wrong, these biomass estimates show that a major component of the ocean ecosystems has not yet been significantly studied. Mesopelagic organisms are characterised by vertical distribution patterns, and most of the mesopelagic fauna performs light-dependent diel vertical migration (DVM) (Watanabe et al. 1999, Angel & Pugh 2000, Kaartvedt 2008). Even though this is a remarkable feature of mesopelagic organisms, species-specific patterns remain largely unknown (Brodeur & Yamamura 2005). The possible extension of boreal species into the Arctic basin following warming conditions in the ocean has been hypothesised for some commercial species (Hollowed et al. 2013, Wisz et al. 2015). However, the light regime specific to regions beyond the Arctic Circle may prevent mesopelagic species from migrating further north, since summer continuous light and winter continuous darkness disturb light-dependent vertical migration of mesopelagic species (Kaartvedt 2008). Many mesopelagic species perform DVM into the

epipelagic layer in their quest for food before migrating down several hundred meters to their daytime depths, and light has been found to be a controlling factor for migrators who optimise feeding while minimising visibility to predators (Salvanes 2004). Few investigations of the mesopelagic fauna have been conducted in high latitudes in comparison to mid- and tropical latitudes, and considerable knowledge gaps remain regarding biomass and DVM patterns of the mesopelagic fauna in oceanic high latitudes. To date, high-latitude field studies have predominantly been conducted in fjords, and they have shown that migrating organisms comprise high biomasses of mesopelagic fish (Giske et al. 1990, Baliño & Aksnes 1993) or krill (Onsrud & Kaartvedt 1998). There is comparatively little information about the distribution and abundance of the mesopelagic fauna in the open ocean at high latitudes, and it is assumed that the extreme light regime may be unfavourable to many mesopelagic species, in particular those performing DVM. The goal of the present study is to evaluate if the key features of mesopelagic fauna (high abundance and DVM) are also observed in the high latitudes of the Northeast Atlantic and to determine

whether a dense mesopelagic layer can be observed under the extreme summer light regime in this region. For this purpose, we analysed hydroacoustic data collected during 4 surveys conducted in the open Norwegian Sea during the summer season.

MATERIALS AND METHODS

Data acquisition

Hydroacoustic data were collected during 4 cruises conducted in the Norwegian Sea and to the west of Svalbard during summer, covering in total more than 7700 nautical miles (Fig. 1). In August 2008, the F/V 'Atlantic Star' (Norway) and the F/V 'Osveyskoe' (Russia) jointly surveyed the Norwegian Sea. The joint survey was initiated by the North East Atlantic Fisheries Commission and coordinated by ICES with the aim of monitoring the distribution and abundance of beaked redfish *Sebastes mentella* primarily inhabiting the mesopelagic zone (ICES 2008). In August 2009, the Norwegian survey was repeated by the F/V 'Atlantic Star'. In May 2014, the R/V 'Helmer Hansen' conducted a cruise to the northwest of Svalbard as part of the Carbon Bridge project (University of Tromsø, Norway). During each cruise, fisheries hydroacoustic measurements were made using a 38 kHz hull-mounted SIMRAD EK 60 echosounder. The ping rate was adjusted to allow registrations down to depths of 750 to 1000 m, and the calibration was done following a standard protocol (Foote et al. 1987).

Echogram interpretation

The surface backscattering strength (s_A) was used to quantify the acoustic energy in the deep scattering layer (DSL) (Simmonds & MacLennan 2005). Acoustic energy was allocated to 3 distinct categories. The first 2 categories correspond to biological signals above and within the DSL. This delimitation, which relies on a biological rather than a strict bathymetric approach, was complemented by bathymetric constraints. The DSL was considered to be mesopelagic when it was located between 200 and 800 m depth, and the biological signal that registered out-
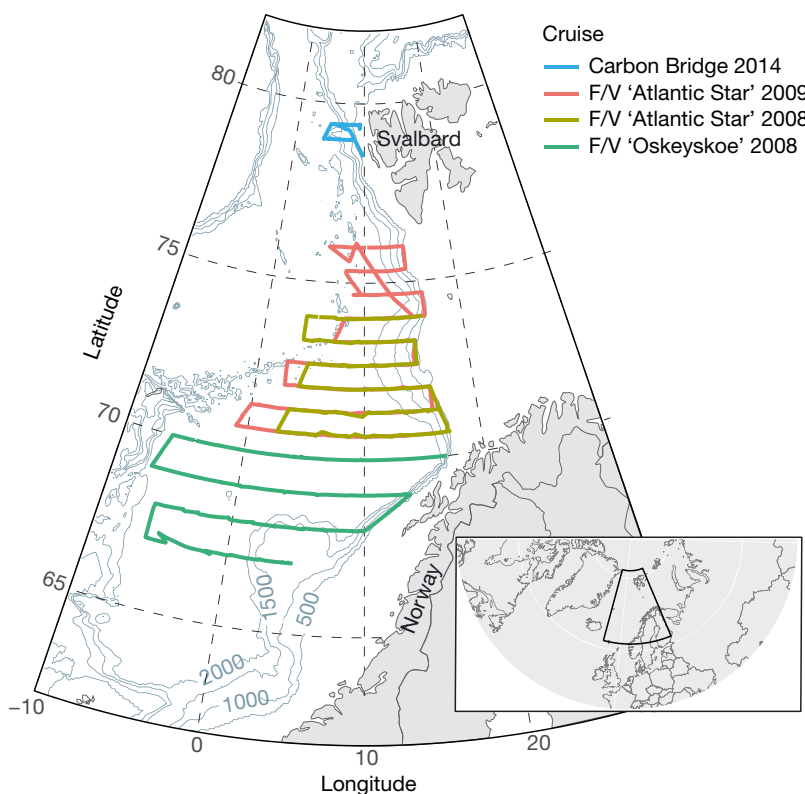

Fig. 1. Locations of the hydroacoustic transects registered during 4 cruises in the Norwegian Sea and to the west of Svalbard during the summer between 2008 and 2014. The inset indicates the location of the study area in the North Atlantic Ocean

side the DSL was assigned to the epipelagic layer when it was shallower than 400 m. Data acquisition is limited to a maximal depth of 800 m, below which instrumental noise becomes too dominant. The third category corresponds to the non-biological signal induced by e.g. instrumental noise, surface bubbles or a false bottom echo. A volume backscattering strength (s_V) threshold level of −82 dB was applied for all registrations. Data were analysed using the software Large Scale Survey System (Korneliussen et al. 2006). An illustration of echogram interpretation is shown in Fig. 2.

Vertical migration depth

The upper envelope of the DSL was used as a proxy for vertical migration depth. Daily changes in the depth of the upper envelope reflect DVM patterns for migrating organisms, while these are little influenced by the mean residence depth of non-migrating organisms. This upper envelope depth was defined using the 12.5th s_A percentile and corresponds to the depth where 12.5% of s_A is located above and 87.5% is located below. An illustration of the changes in the depth of the upper envelope of the DSL is shown in Fig. 3b.

Solar elevation and photoperiod

Solar elevation angle, in degrees, was computed with the solar position algorithm by Reda & Andreas (2008). The solar elevation is zero when the sun is at the horizon. It is positive when the sun is above the horizon (+90 = zenith) and negative when it is below (−90 = nadir).

To characterise day–night cycles, the following photoperiod coefficient was computed:

$$r_{dn} = (h_d − h_n)/24 \qquad (1)$$

where h_d is the number of hours when the sun is above the horizon, and h_n is the number of hours when the sun is below the horizon. The index value varies between −1 (full night) and +1 (full day). Solar elevation and photoperiod were computed to
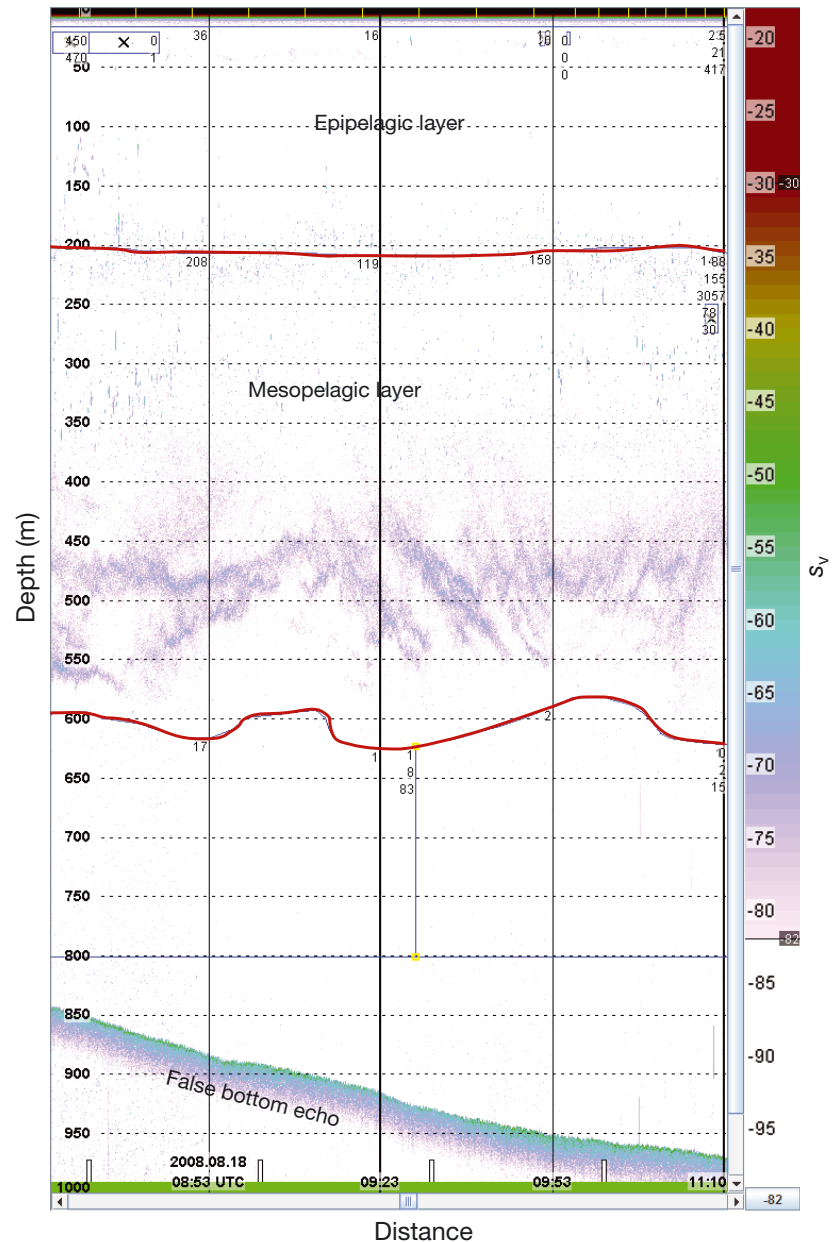

Fig. 2. Hydroacoustic registrations (echograms) during the F/V 'Atlantic Star' cruise in the central Norwegian Sea in 2008 over a distance of 2 nautical miles and from the surface down to 1000 m depth. Intensity of reflected energy per unit volume (volume backscattering strength, s_V) is indicated by the colour scale. Red lines display the upper and lower limits of the deep scattering layer

characterise the light regime for every nautical mile. An illustration of solar elevation is shown in Fig. 3a.

Epipelagic versus mesopelagic

Acoustic energies were compared in the epi- and mesopelagic layers by calculating the ratio of the
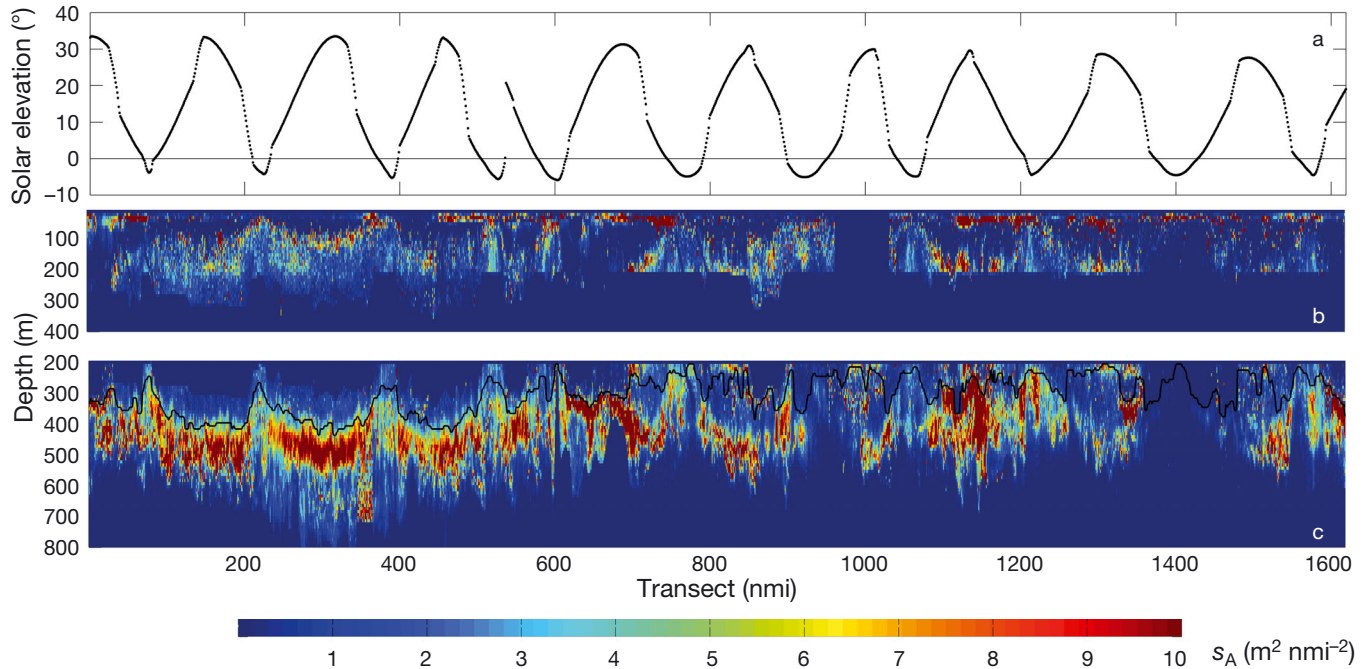
Fig. 3. (a) Solar elevation angle, (b) surface backscattering strength (s_A) allocated to the epipelagic layer and (c) s_A allocated to the mesopelagic layer during the F/V 'Atlantic Star' survey in 2008. The thin dark line in the mesopelagic transect (c) signals the upper 12.5th percentile of s_A for every nautical mile and is used as a proxy for the upper limit of the deep scattering layer

average s_A in each layer for each cruise. An illustration of acoustic energy in the epi- and mesopelagic layers is shown in Fig. 3b,c.

Depth versus solar elevation

To assess the possible link between light regime and migrating behaviour of mesopelagic organisms, the vertical migration depth was plotted against solar elevation. Under the standard DVM hypothesis, it is expected that the upper limit of the DSL should deepen with increasing solar elevation.

Acoustic energy versus photoperiod

The acoustic energy in the mesopelagic layer was plotted against the photoperiod coefficient to illustrate the possible influence of the day–night cycle on the abundance of mesopelagic fauna. Under the photoperiod constraint hypothesis (Kaartvedt 2008) and assuming that variations in s_A reflect variations in biomass, it is expected that s_A should decline as the photoperiod index approaches extreme values (i.e. full day or full night).

Numerical analyses were conducted using the software Matlab.

RESULTS

There was generally more acoustic energy in the mesopelagic than in the epipelagic layer. This was observed in all surveys (Table 1). Whilst the mean hydroacoustic energy in the epipelagic layer can be highly variable and does not seem to follow any clear geographical pattern, the energy in the mesopelagic layer appears to decrease with increasing latitude. There was 3.5 times more acoustic energy recorded at low latitudes (F/V 'Osveyskoe' cruise) than at the highest (Carbon Bridge cruise).

Following the expected DVM patterns, the upper limit of the mesopelagic layer deepened as solar elevation increased (Fig. 4). This is particularly evident for solar elevations between −20 and 10°, which correspond to crepuscular periods. For greater solar elevations (between 10 and 40°), a deepening of the mesopelagic layer was also observed but with lower amplitude.

There does not appear to be a clear relationship between the mean acoustic energy recorded in the mesopelagic layer and the photoperiod (Fig. 5). However, it appears that the maximum recorded acoustic energy in the surveys declined as the photoperiod index increased towards extreme (i.e. full daylight) values. This can be indicative of the photoperiod being a limiting factor for mesopelagic biomass.

Table 1. Average acoustic energy per square nautical mile (surface backscattering strength, in m^2 nmi^{-2}) recorded in the epi- and mesopelagic layers during 4 surveys in the Norwegian Sea and the ratio between these averages

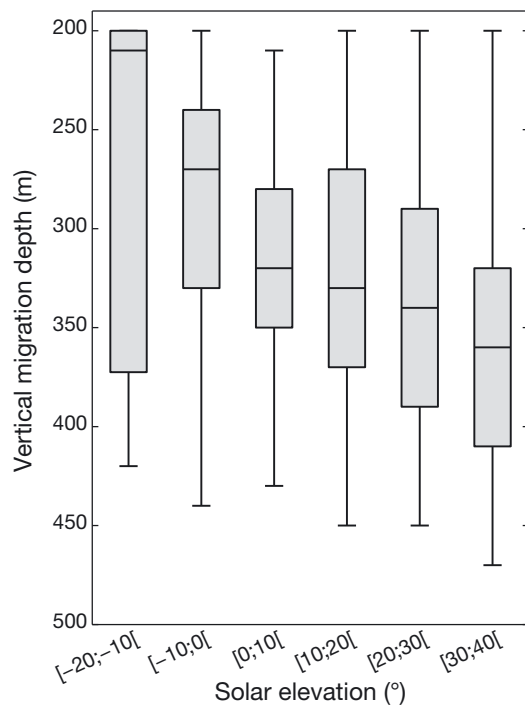| Survey	Carbon Bridge	F/V 'Osveyskoe'	F/V 'Atlantic Star' 2009	F/V 'Atlantic Star' 2008
Epipelagic	18	87	71	116
Mesopelagic	61	215	140	133
Ratio (mesopelagic:epipelagic)	3.4	2.5	2.0	1.2

Fig. 4. Depth of the upper limit of the deep scattering layer as a function of solar elevation. Central lines in the boxplots correspond to median depth, box extremities correspond to 1st and 3rd quartiles and whiskers extend to the most extreme data points

Fig. 5. Backscattered energy per unit area (surface backscattering strength, s_A) as a function of the day:night ratio; a ratio of 1 is when the sun is 24 h above the horizon, and a ratio of zero is when the sun is 12 h above and 12 h below the horizon. Central lines in the boxplots correspond to median depth, box extremities correspond to 1st and 3rd quartiles and whiskers extend to the most extreme data points

DISCUSSION AND CONCLUSIONS

The measured acoustic energy in the Norwegian Sea suggests the presence of a dense layer of mesopelagic fauna in oceanic high latitudes. Although there was no dedicated sampling to quantify the species composition, biomass and abundance, the high levels of acoustic energy recorded suggest that the biomass in the mesopelagic layer may exceed that of the epipelagic layer, a pattern similar to that reported for tropical and subtropical waters by Gjøsæter & Kawaguchi (1980) and Irigoien et al. (2014).

Changes in the depth of the upper limit of the DSL, coupled with solar elevation, confirm the hypothesis of light-driven DVM patterns. This is in agreement with previously re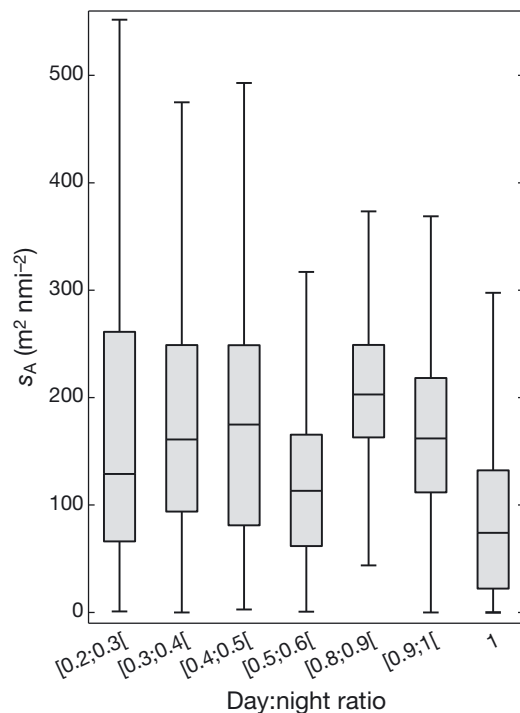ported patterns for mesopelagic fishes in the Norwegian Sea (Salvanes 2004), for other micronekton taxa in the Northeast Atlantic (Angel & Pugh 2000) and for myctophid fishes in the western North Pacific (Watanabe et al. 1999). However, these migratory behaviours may only concern a fraction of the mesopelagic fauna, and the distinction between migration types (i.e. midwater migrant, semi-migrant and passive migrant; Brodeur & Yamamura 2005) was not possible given the available data. Although the present analysis restricts the analysis of DVM patterns to waters deeper than 200 m, it is noticeable (Fig. 3b,c) that the DSL is predominantly located at mesopelagic depth also at night and seldom penetrates the epipelagic zone, in contrast to what is observed in other areas of the world ocean.

The mean acoustic energy of the mesopelagic fauna does not appear to be directly linked to the photoperiod. However, extreme high s_A values appear to decrease as the light regime tends towards a full day period. This suggests that while the actual abundance of mesopelagic fauna may be controlled by numerous factors other than photoperiod, the maximum attainable abundance could be constrained by the photoperiod. This is in agreement with the photoperiod constraint hypothesis introduced by Kaartvedt (2008). It entails that anticipated effects of ocean warming on the expansion of marine fauna distribution towards Arctic regions (e.g. Cheung et al. 2009) may be countered by the extreme Arctic light regime, which will preclude some of the mesopelagic fauna from migrating northwards.

Aside from the major mesopelagic fish species frequently encountered in the Norwegian Sea such as *Maurolicus mülleri*, *Benthosema glaciale*, *Arctozenus risso* and *Argentina silus*, the biodiversity of this layer remains largely unknown, and mesopelagic invertebrates such as some euphausiids, decapods, copepods and gelatinous plankton could well represent a more important part of the biodiversity than is commonly acknowledged (Melle et al. 2004). Considerable knowledge gaps still remain regarding trophic interactions within the mesopelagic layer as well as between the mesopelagic layer and shallower and deeper waters (Sutton 2013). The present findings suggest the existence of a dense mesopelagic layer in oceanic high latitudes and call for accurate estimates of the abundance of the mesopelagic fauna in oceanic high latitudes. They also stress the need for thorough studies on the biodiversity of the mesopelagic fauna in this region.

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