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Potential for long-distance dispersal of *Euphausia crystallorophias* in fast current jets

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Abstract The euphausiid *Euphausia crystallorophias* Holt and Tattersall, 1906 is considered to be a neritic species. It has been found in greatest abundance along the Antarctic continental margins, often in association with regions of pack ice. Although *E. crystallorophias* has been observed at some islands to the west of the Antarctic Peninsula, the species has not previously been reported from islands of the maritime- or sub-Antarctic further north. During an oceanographic transect in November 1997 from South Georgia to the South Sandwich Islands, acoustic observations revealed a dense, discrete pelagic target at 50 m. The target was fished and was found to be an aggregation of small *E. crystallorophias*. The fishing location (54.48°S; 30.61°W) was >1500 km from the Antarctic continent, and >250 km from the nearest land, in water of several thousands of metres depth – clearly a non-neritic environment. Examination of hydrographic data revealed that the *E. crystallorophias* swarm had been located within a fast-flowing band of water that had characteristics of water found near the Antarctic Peninsula. This band was ≃150 km wide, and had a speed ranging from 9 to 22 km d^{-1} in a north-easterly direction. The possible origins of this *E. crystallorophias* swarm are explored in the light of the eddy-dominated current patterns prevalent in the Weddell–Scotia Confluence region, and with reference to published growth-rate estimates for the species. We discuss the potential for long-distance dispersal of *E. crystallorophias* and other neritic species in fast current jets, and examine how such oceanographic features could facilitate long-distance dispersal, colonization, and gene flow.

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Introduction

The ice krill *Euphausia crystallorophias* Holt and Tattersall, 1906 is considered to be a neritic species. It has been found in greatest abundance on-shelf along the Antarctic continental margins (John 1936; Fischer and Hureau 1985), often in association with regions of pack ice. In such areas *E. crystallorophias* is of considerable ecological importance (e.g. Thomas and Green 1988). Although the species has also been observed at some islands to the west of the Antarctic Peninsula (e.g. Deception Island: Brierley 1999), it has not been reported from the more northerly maritime- or sub-Antarctic regions (e.g. Hardy and Gunther 1935; Ward et al. 1990).

During sampling along a transect from South Georgia to the South Sandwich Islands (Fig. 1), however, we caught *Euphausia crystallorophias* at a location >1500 km from the Antarctic continent and >250 km from the nearest land, in water of several thousands of metres depth – clearly a non-neritic environment.

Here, we show how a high-velocity current jet may have transported a *Euphausia crystallorophias* swarm well beyond the species' normal geographic range, and examine the possible rôle of such oceanographic features in the dispersal of Antarctic marine organisms generally, and as mediators of long-distance colonisation, recruitment, and gene flow.

Materials and methods

During November and December 1997, the British Antarctic Survey carried out a "Gene Flow" cruise aboard R.R.S. "James Clark Ross" in the Scotia Sea with the objective of sampling fish and zooplankton species from widespread locations for genetic analyses (North et al. 1998). On transect, a fully calibrated (Brierley et al. 1998) Simrad EK500 scientific echo-sounder (operating at 38, 120 and 200 kHz) was run continuously, and the acoustic display was often the primary cue for biological sampling. Simultaneously, a 150 kHz hull-mounted acoustic Doppler current profiler (ADCP; RD Instruments) was used to collect current velocity data underway. The ADCP was configured to record data in 2 min ensembles

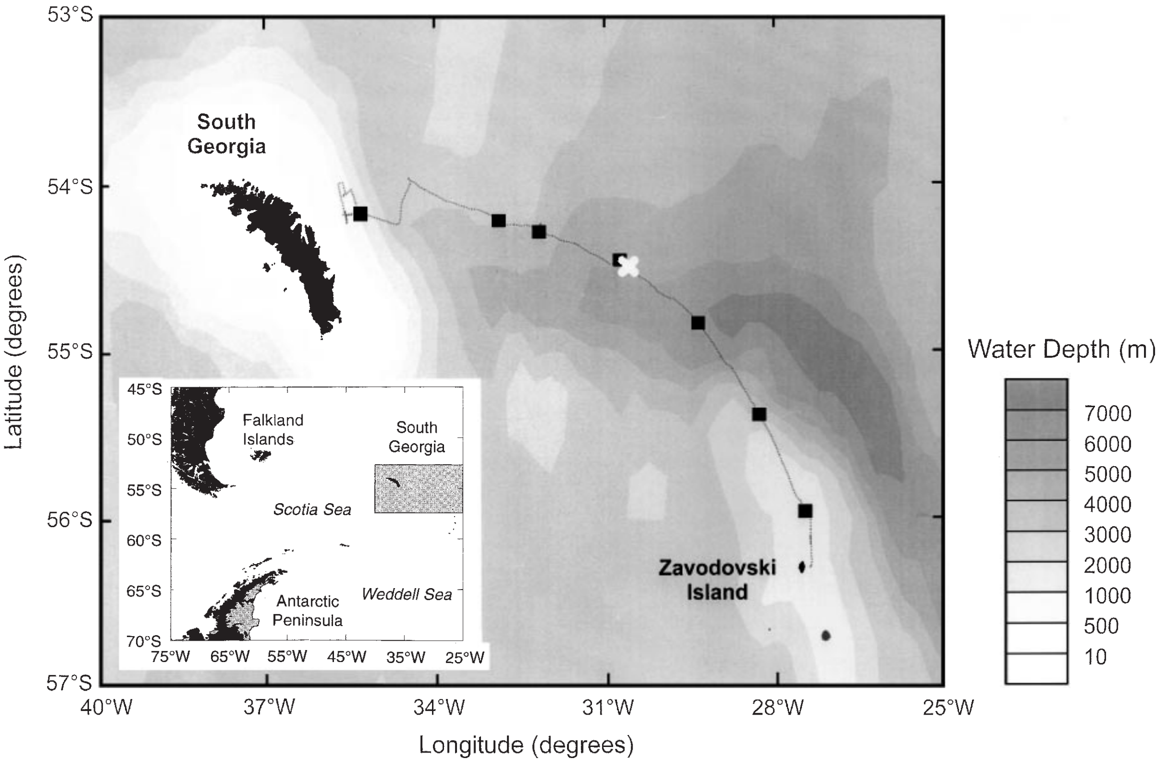


Fig. 1 Cruise track of RRS "James Clark Ross" from South Georgia to South Sandwich Islands, showing water depth, fishing location (*white cross*) and CTD stations (■)

from 64 × 8 m bins. ADCP data were corrected for gyrocompass error using an Ashtec 3DF GPS system (Griffiths 1994), and then for misalignment angle and scaling factor (Pollard and Read 1989). Conductivity–temperature–depth (CTD) casts (Neil Brown Mk IIIb) were carried out at $\simeq$50 nautical-mile intervals throughout the cruise. CTD temperature and pressure sensors had previously been calibrated by Ocean Scientific International (4 July to 6 August 1997), and the conductivity sensor was calibrated against in situ salinity samples using Ocean Scientific International standard seawater (Batch P120). In addition, an XBT probe (T5, Sippican Ocean Systems) was deployed between each CTD station to provide additional temperature-profile information, usually down to 1200 m. The XBT system comprised a PC running Sippican MK 9 Data Acquisition System software (Version 5.2) interfaced to a MK 9 Digital XBT System deck unit.

Results

On 25 November, almost mid-way between South Georgia and Zavodovski (the northernmost island in the South Sandwich chain: Fig. 1) and 1 h after a CTD cast, a dense, discrete target was detected by the echo sounder in the upper 50 m (Fig. 2). The target was fished with an 8 m^2 rectangular mid-water trawl (RMT8: Roe and Shale 1979). Examination of the catch revealed that the acoustic target comprised small, mostly immature *Euphausia crystallorophias* (from a random sub-sample of 100 individuals, mean total length to the nearest mm below = 22 ± 4 mm SD). The sub-sample length-frequency distribution is shown in Fig. 3.

The modal difference in mean volume backscattering strength between 38 and 120 kHz ($\Delta \mathrm{mvbs} = \mathrm{mvbs}_{120\ \mathrm{kHz}} - \mathrm{mvbs}_{38\ \mathrm{kHz}}$) of 14 dB was characteristic of euphausiids of this size, and dense, discrete acoustic targets with spherical cross-section and clearly defined edges are typical of *Euphausia crystallorophias* (S. Nicol and T. Pauly personal communication 1998) rather than the Antarctic krill *E. superba*.

Fig. 4 shows the upper 300 m of the hydrographic section from South Georgia to Zavodovski Island. At $\simeq$32°W, there is a front in potential temperature, salinity and resulting potential density, where cold high-salinity and thus high-density water is brought to the surface. Fig. 4D shows the northern component of the acoustic Doppler current-profiler data, and a strong current jet flowing northwards can be seen associated with the front. East of the front, the water velocity decreases, but is still directed northwards. The *Euphausia crystallorophias* swarm was located at the edge of the frontal current. This jet is $\simeq$150 km wide, and the range of velocities indicate a transport rate of between 9 and 22 km d^{-1} in a north-easterly direction.

Discussion

The fishing location (54.48°S; 30.61°W) at which the *Euphausia crystallorophias* swarm was sampled was clearly non-neritic, and was therefore outside the usually accepted distribution range of the species. Our underway oceanographic observations, however, allow us to associate this sample with a specific water body rather

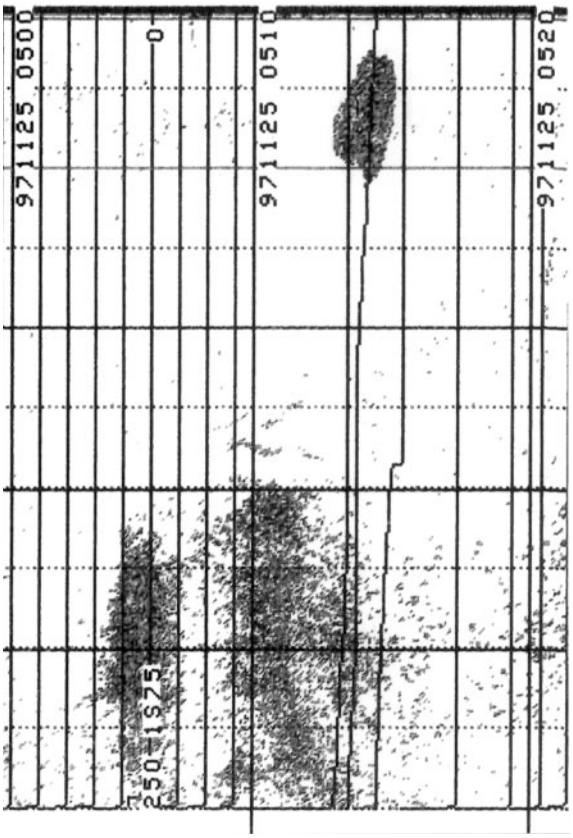


Fig. 2 *Euphausia crystallorophias*. Echo chart at 38 kHz with dense, spherical target fished (*horizontal lines* 50 m depth intervals from surface). At nominal towing speed of 2 knots, 10 min time intervals = distance travelled of ≃600 m

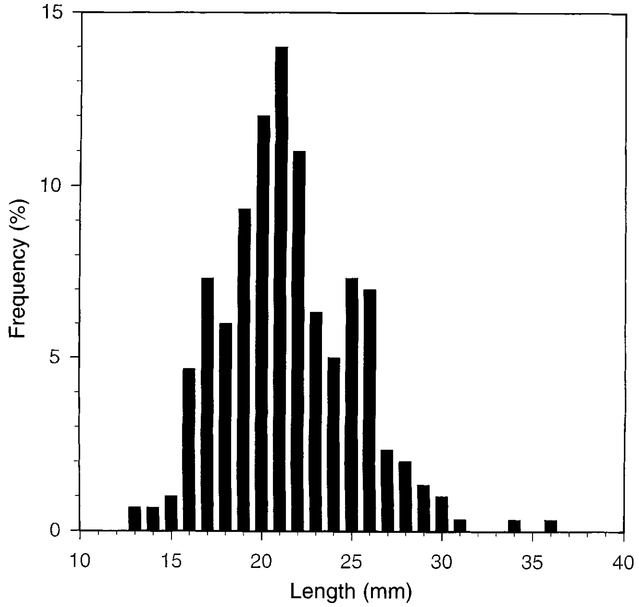


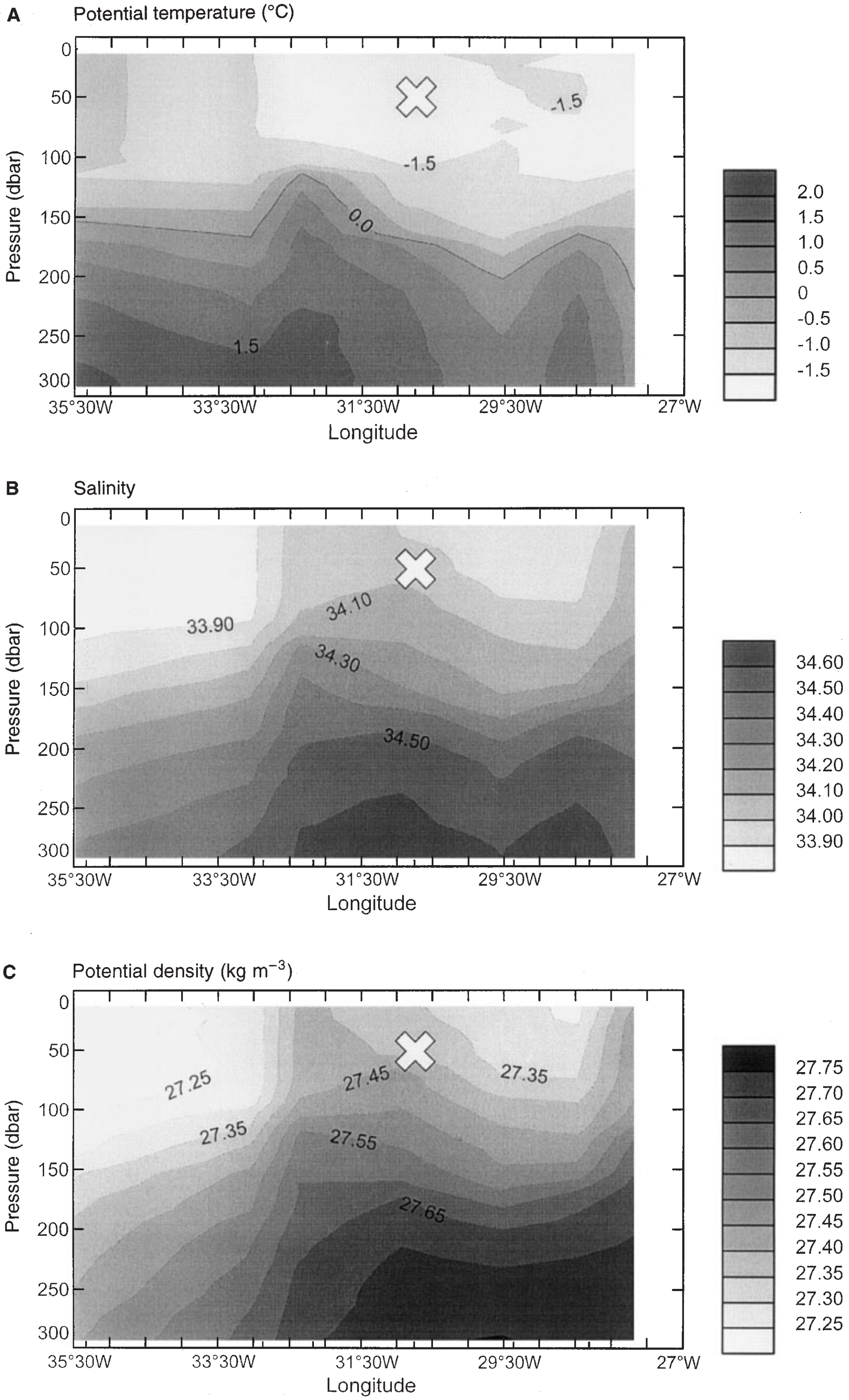
Fig. 3 *Euphausia crystallorophias*. Length-frequency histogram for random sub-sample of 100 individuals fished from dense, spherical aggregation in Fig. 2

than simply with a geographical location. On the basis of potential temperature and salinity properties, we have identified the front with which the swarm was associated as being indicative of the Weddell Scotia Confluence. Using a large CTD data set collected on World Ocean Circulation Experiment (WOCE), Leg A23, Locarnini et al. (1995) noted that this front was present to the south of South Georgia. Furthermore, our oceanographic observations suggest that the *E. crystallorophias* swarm was within a fast-moving jet of water with characteristics of the Antarctic Peninsula region. It is possible, therefore, that the *E. crystallorophias* we observed had become entrained in this jet in the vicinity of the Peninsula and had been transported north-east in it. Such transport, albeit on a smaller scale, may have been observed previously. Hosie (1991), for example, found a limited number of *E. crystallorophias* individuals to the north of the continental shelf off Mawson in Prydz Bay, where previous observations had shown a strong north-westerly water flow to exist (Hodgkinson et al. 1988).

Growth rates for *Euphausia crystallorophias* reported by Brinton and Townsend (1991) and Pakhomov and Perissinotto (1996) suggest that the individuals we sampled were aged 2+ yr and older. Spawning in *E. crystallorophias* peaks during November and December (Harrington and Thomas 1987; Makarov and Menshenina 1992) and it seems likely therefore that the individuals we sampled were spawned in late 1995 and before. *E. crystallorophias* abundance is high in the Gerlache and Bransfield Straits (Pakhomov and Perissinotto 1996), and indeed we also caught *E. crystallorophias* off the shelf to the west of the Antarctic Peninsula later during the present cruise. Given documented current patterns (Hofmann et al. 1996), either of these regions are possible locations at which the *E. crystallorophias* swarm could have become entrained in the jet. Furthermore, given the speed of the jet, it is probable that these individuals became entrained within it after they had completed larval development (Kirkwood 1996), possibly as recently as only three months previously. Although transport of larvae in currents is a recognised dispersal mechanism (but see Todd et al. 1998), dispersal of nektonic adult stages is less well accepted.

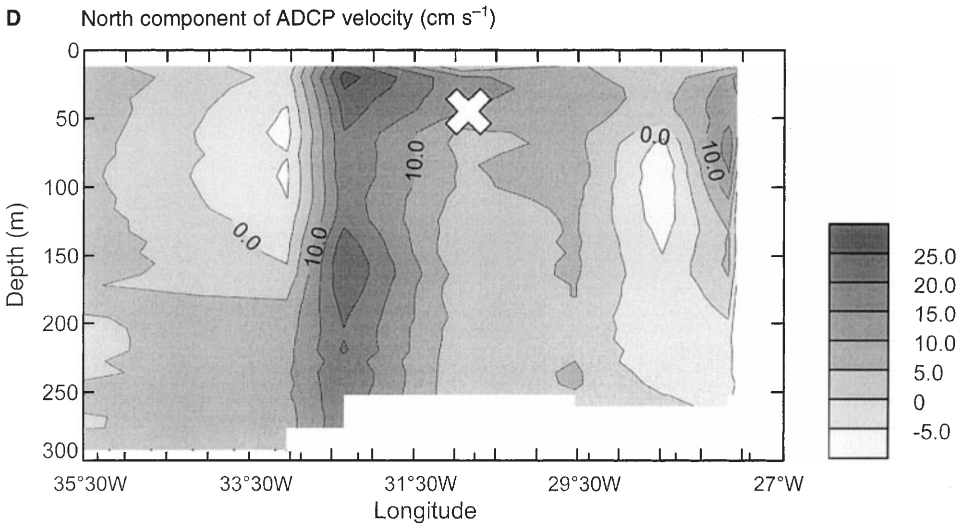
Kuhl and Schneppenheim (1986) have argued that since *Euphausia crystallorophias* is a neritic species with a more restricted distribution than *E. superba*, it would be reasonable to expect that geographically remote *E. crystallorophias* populations would exist in reproductive isolation. Their genetic analyses, however, suggested that, like *E. superba* (see Fevolden and Schneppenheim 1989), *E. crystallorophias* exists as a single interbreeding population. Noting that *E. crystallorophias* inhabited shelf waters only, Pakhomov and Perissinotto (1996) argued that the genetic exchange required to maintain such genetic homogeneity must be mediated by larval dispersal. Hosie (1991) has suggested that the Antarctic Coastal Current may facilitate dispersal of some *E. crystallorophias* larvae along the coast of Antarctica away from

Fig. 4 *Euphausia crystallorophias*. Hydrographic section from South Georgia to Zavodovski Island. Potential density is referenced to 0 dbar. (*Small ticks on x-axes* CTD station positions; *longer ticks on x-axes* degrees longitude; *white cross* RMT fishing location; *ADCP* acoustic Doppler current profiler)



Prydz Bay, and larvae of *E. crystallorophias* have also been caught from oceanic locations in the Weddell Sea (Hempel and Hempel 1982). *E. crystallorophias* eggs are neutrally buoyant (Ikeda 1986), and dispersal of eggs by surface currents offers a further possible mechanism for population mixing. Our own observations here of *E. crystallorophias* adults far from recognised spawning areas suggests that dispersal and subsequent genetic exchange may also be mediated by transport of adult stages in current jets. The individuals we obtained were mostly

Fig. 4 (continued)



immature. Their sizes however (Fig. 2), suggest that they may have reached maturity later in the 1997/1998 season (Brinton and Townsend 1991), and the swarm we encountered may thus have had the potential of establishing a founder population if the current had carried it to a favourable location, perhaps the South Sandwich Islands.

How often such dispersal events occur to *Euphausia crystallorophias* swarms is unknown, although given the persistent nature of eddy-dominated transport in the Weddell Scotia Confluence region (Foster and Middleton 1984) they may be frequent. Alternately, our observation may be of a rare event arising primarily from the atypical far-northern extent of ice in the 1997/1998 season (we encountered sea ice from the first CTD station shown at top left of Fig. 1 onward to Zavadovski: the specific name "*crystallorophias*" refers to the fact that the species is associated closely with ice: Holt and Tattersall 1906). Ocean currents have though been implicated as dispersive agents for other Antarctic species. For example, the neritic copepod *Drepanopus forcipatus* is common on-shelf at South Georgia (Atkinson and Peck 1990), and Hulsemann (1985) has suggested that the species there is distinct from the South American continental-shelf species. Atkinson and Peck (1990), however, found *D. forcipatus* off-shelf on a number of occasions, and relatively fast surface currents may facilitate dispersion. *E. superba* is an Antarctic species, but isolated aggregations have been observed beyond the Antarctic Polar Front as far north as Chilean fjords (El-Sayed and George 1984). Genetic evidence suggests that larval phases of the benthic nemertean worm *Parbolasia corrugatus* may recruit to the South Orkneys from more than one location (Rogers et al. 1998), and the ommastrephid squid *Martialia hyadesi* has on occasion been reported from the Patagonian Shelf prior to anomalous oceanographic conditions (Gonzalez et al. 1997): it is possible that population subdivision within this species may result (Brierley et al. 1993). The centric diatom *Coscinodiscus bouvet* is a typically neritic species that has also on occasion been found widespread across the Scotia Sea: advection from the Bransfield Strait has been implicated as a factor behind these observations in oceanic locations (Priddle and Thomas 1989).

Traditionally, biological sampling has recorded distribution of species relative to fixed geographic coordinates. Mackintosh (1972) recognised the importance of water masses as habitats for Antarctic krill and was amongst the first to relate species' distribution in the Southern Ocean to the dynamic oceanographic regime. With the advancement of underway oceanographic sampling technology, biologists would be prudent to consider species' distributions with reference to this information, rather than within restrictive latitudinal and longitudinal bounds.

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