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BEYOND SALTY REINS – MODELING BENTHIC SPECIES' SPATIAL RESPONSE TO THEIR PHYSICAL ENVIRONMENT IN THE POMERANIAN BAY (SOUTHERN BALTIC SEA)

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Abstract

The brackish water environment of the Baltic Sea is dominated by a strong gradient of salinity and along with salinity the benthic diversity decreases – salinity is regarded as the master factor regulating benthic diversity in brackish habitats. In this scheme, consistently small patches of comparatively higher or lower benthic diversity do emerge in areas where either environmental or an-thropogenic impacts on the benthic habitat change drastically over short spatial distances. Hence, spatial diversity of ecological factors creates diversity among benthic colonization and community structures. We show through a logistic modeling approach the possibility to predict thereby induced benthic colonization areas and community structures inside the broad scheme of a brackish water habitat. This study bases upon quantitative macrozoobenthic abundance data collected over a period of 4 years. It clearly demonstrates the need to analyze species' relationships in gradient systems such as the Baltic Sea and provides a tool to predict natural and anthropogenic forced changes in species distribution.

Key words: Baltic Sea, Pomeranian Bay, macrozoobenthos, ecological modeling, environmental factors, multivariate analysis, species' response curves

INTRODUCTION

Across the Baltic Sea, a long and strong gradient of salinity stretches over a distance of about 1100 km, steadily decreasing from the Skagerrak and Kattegat in the West (about 25-30 psu) over the Belt Sea (about 10-25 psu) and Baltic Proper (about 5-10 psu) up to the Baltic's most northerly and north-easterly parts, the Finnish and Bothnian Gulfs (about 0-5 psu) – and with salinity as dispersion barrier for marine species, the benthic diversity as well decreases. Hence, the factor salinity is regarded as the master factor regulating benthic diversity in brackish habitats (Zettler et al. 2007). On the whole, it seems to explain on a large spatial scale benthic diversity

patterns examined in the Baltic Sea as well as in other brackish habitats all over the world. However, inside this general picture of decline in diversity, consistently small scale patches of comparatively higher or lower benthic diversity do emerge namely in areas where either the environmental "texture" (e.g. the sea bottom structure), other environmental factors (e.g. sediment type) or anthropogenic impacts (e.g. man-made pollution) influencing the benthic habitat change drastically over short spatial or temporal distances. Thus, spatial and temporal diversity in ecological factors can create diversity among benthic colonization and community structures. Due to the variability of species in terms of habitat selection, reciprocal effects between species' distribution and environmental factors manifest in patterns, visible in their abundances or assemblages (Keitt et al. 2002, Fortin et al. 2005). Always, benthologists have dreamt of possibilities to forecast such patterns and structures – modern comforts now at hand via computer-aided statistical model development. providing us with a useful tool to relate ecological features to environmental factors. Through validation and modification, it can even reveal the underlying mechanisms responsible for the structure and organization of communities (Austin 1987). However, an exploratory statistical description of the prevailing ecological structure based on observations always is a necessity – not only to examine and understand the structure and dynamics of benthic biotic/environmental interactions and processes but to evaluate and model natural and anthropogenic influences and effects on ecological systems (Bourget and Fortin 1995, Legendre and Legendre 1998). Furthermore, in-depth knowledge is indispensible regarding the autecology of the species for the interpretation of the found relationships (Sachs 1997). On this account, we described patterns in the distribution of benthic organisms and determined the parameters causing such patterns via a multivariate statistical approach, thus establishing a statistical link between benthic infauna distribution and environmental factor patterns for the German part of the Pomeranian Bay in a preliminary study (Glockzin and Zettler 2008). There, we already announced the possibility of "[...] modeling species response curves on the basis of this study, using an appropriate model [...] and using the found equations in a GIS-based approach shall enable us to create a two-dimensional ecological model of the Pomeranian Bay and to predict species assemblages [...] by two-dimensional morphological, geological or hydrological data sets". On this account, we utilize in this present study species' response towards responsible environmental key factors to model spatial distributions for selected benthic species via a binomial logistic regression approach (Trush et al. 2003) in a GIS based environment (ArcGIS, ESRI Inc.).

STUDY AREA, MATERIALS AND METHODS

Proper choice of a spatial scale for our investigation was important – to bring into focus the prevailing biotic-abiotic interactions and to diminish or even eliminate the influence of an all-dominating factor like salinity in brackish habitats (Fig. 1). Therefore, we chose the Pomeranian Bay as an adequate "test site" for the methods used in this study. This work bases upon environmental and quantitative macrozoo-



environmental factor near-bottom salinity in the Pomeranian Bight (study area). Numbers and isolines indicate the water depth (e.g. -20-20 m Fig. 1. Left: spatial distribution of the environmental factor near-bottom salinity in the Baltic Sea. Right: spatial distribution of the water depth)



Fig. 2. Study area and distribution of the 191 sampling stations, filled circles indicate stations with a full set of data available for all six abiotic variables. Sampled stations per year: 2003 (53 stations), 2004 (78 stations), 2005 (30 stations), 2006 (30 stations)



Fig. 3. Environmental framework prevailing in the study area and inter-factor relationships derived from path model analysis with partial correlations (Legendre and Legendre 1998). The dotted line indicates a two-way connection added due to causal interpretation

benthic abundance data collected at 191 stations in the German part of the Pomeranian Bay (Southern Baltic Sea) over a period of 4 years (2003-2006, Fig. 2). A detailed description of the study area, sampling procedures, sample analysis as well as factor and species exclusion/choice would go beyond the scope of this paper and can be found in Glockzin and Zettler (2008). In order to evaluate existing coherencies among environmental parameters, and to assess the primary descriptor predicting all other environmental variables in the Pomeranian Bay, a partial correlation analysis (path analysis) according to the methods described in (Legendre and Legendre 1998) was already conducted in Glockzin and Zettler (2008). Figure 3 illustrates the underlying interactions among environmental factors prevailing in the Pomeranian Bight. Taking a closer look on the prevailing environmental conditions in the study area is indispensible to understand the physical framework of the Bight and to illuminate the later described selection of environmental factors for the modeling approach. Due to prevailing wind, wave conditions and saline water inflows from deeper areas of the Bay and fresh water from the coastal river runoff no homogeneous near bottom salinity zonation develops. Deeper areas of the southern Baltic as Sassnitzrinne, Arkona and Bornholm Basin are the main accumulation areas for fine particles with input of high organic material from the Pomeranian Bay (Kuhrts et al. 2006). This explains the apparent correlation between salinity and organic content, i.e. with increasing water depths and equally rising salinity, the content of organic carbon in the sediment also increases. With increasing amounts of fine particles at the sea bottom, permeability of the sediment in turn decreases rapidly because of the blocking of the interstice (Forster et al. 2003). Due to the glacifluviatile and glaciaeolian genesis of the Bay, median grain size and sorting are merely modified by hydrography, but not created. To highlight the physical and physiographical control of water depth on most of the environmental conditions prevailing in the Pomeranian Bay, a detailed bathymetric structure for the study area is also given in Figure 2. The species' response towards this environmental framework was modeled in terms of probability of occurrence via a generalized linear modeling approach (GLM), using species binomial data (abundance data reduced to presence/absence) in logistic regression with corresponding (logit) link functions (Guisan et al. 1999, Thrush et al. 2003, Gogina et al. 2010) available in STATISTICA 6 (StatSoft Inc.). Therefore, a biotic matrix of three exemplary species (Bathyporeia pilosa, Tubificoides benedii and *Hediste diversicolor*) and an abiotic matrix of six environmental parameters (water depth, salinity, median grain size, organic content, permeability and sorting), estimated for 78 out of 191 sampling stations, were used. For the six environmental factors, measuring units together with lower and upper boundaries are given (Tab. 1). Water depth influences through its physical and physiographical forcing almost all other environmental parameters in the study area, it can act as a "proxy", a type of integral parameter combining the effects of various available (measured) or unavailable (not measured or incapable of measurement) habitat features. But its influence can be spatially inhomogeneous or simply superimposed by other factors and therefore warp the outcome of the analysis. With almost all other factors being strongly dependant on it and keeping in mind a certain susceptibility of models to such redundancy; we only examined it in the model building procedure but excluded it as

Table

Factor range	Unit
4.4-35	[m]
5.7-15.4	[psu]
80-348	[µm]
0.12-9.31	[%]
0.29-1.40	[no unit]
0.4-4.5	$[10^{-5} \text{ cm s}^{-1}]$
	4.4-35 5.7-15.4 80-348 0.12-9.31 0.29-1.40

Measuring units together with lower and upper boundaries for the six environmental factors used in the modelling approach

a factor from further analysis. Regarding the aforementioned physical behavior of salinity, this factor was also excluded. Thus, for model and habitat map building we regarded species probabilities of occurrence calculated as functions of only four factors (organic content, median grain size, sorting and permeability). To find the best combination from the set of single-factor models we considered the philosophy described in Burnham and Anderson (2004). Here, consideration of maximum likelihood as a possible approach to model selection uncertainty is discussed. Hence, the predictor set with the highest amount of likelihood by means of maximum likelihood scores was selected as the set of factors for further analysis. For each factor and taxon combination, estimates of significance from Wald statistic (STATISTICA) were used to estimate the single model significance, with a significance level defined at 0.05. Then, the single-factor model for each species that explained most of the observed variability and fit best to the data was selected. The same maximum likelihood scores, but calculated for the single predictors, were used in further analysis as scaled weights in weighted overlay of probability maps to create habitat suitability maps. The habitat suitability maps were generated with the ArcView spatial analyst (raster calculator), implemented in the Geographic Information System ArcGIS (ESRI Inc.). The factor weights for each species and predictor were scaled, assigning a value of "1" to the factor with the highest maximum likelihood score (Tab. 2). The underlying mechanism of the whole modeling approach is given in Figure 4.

Table 2

Species	Bathyporeia pilosa	Tubificoides benedii	Hediste diversicolor
Organic content	1.00	1.00	1.00
Median grain size	0.78	0.39	0.46
Sorting	0.77	0.65	0.20
Permeability	0.70	0.72	0.62

Scaled weights used in GIS for a weighted overlay for three species and four factors



Fig. 4. Flowchart of the modeling approach to model spatial distributions for three selected benthic species and six environmental factors via species' response towards responsible environmental key factors a binomial logistic regression approach in a GIS based environment (ArcGIS, ESRI Inc.)

RESULTS

Figure 5 shows the probability of species occurrence as well as data points and fitted logit curves for three species and each of the four environmental factors used for the generation of probability maps. They explained best the variability of the benthic fauna distribution and were used in the last step of weighted overlay procedure. Here, the organic content of the sediment shows the most dramatic effect on Bathyporeia pilosa. The response curve estimated for this species indicates almost no chance of finding it in sediments with organic content exceeding 0.5%. In contrast, Tubificoides benedii seems to benefit strongly from organic enriched sediments. For this species, sediments with too low organic content (< 0.5%) seem to be neglected or even avoided. Yet, Hediste diversicolor does not discriminate too much between sediments with different organic content. Though its probability of occurrence decreases with a rising organic load, it can occur over the whole range of this factor. Good sorted sediments (i.e. with low values of sorting) appear to favor the occurrence of *B. pilosa* to the point of vanishing where sediments are poorly sorted, whereas such sediments seem to advantage T. benedii and H. diversicolor. Occurrence of these species can be suppressed strongly but not entirely by this factor for they can most probably exist over its entire range. A different picture can be seen for the probability of occurrence regarding the factor permeability. Here, a rising probability of occurrence of B. pilosa and H. diversicolor seems to be associated strongly with a rising permeability of sediments, whereas the likelihood of occurrence of *T. benedii* falls close to zero at sediments more permeable than 2.5×10^{-5} cm s⁻¹. In any case, permeability below 0.3×10^{-5} cm s⁻¹ seems to be an exclusion criterion for H. diversicolor, B. pilosa and T. benedii are both affected by median grain size – but with opposing trends. While the probability of occurrence of *B. pilosa* rises with decreasing grain size it is almost exactly the other way round with T. benedii. The occurrence of *H. diversicolor* seems to be almost unaffected by sediments median grain size. Though probability of occurrence drops to low values all three species can occur with the utmost probability over the whole factor range in the study area. Four habitat suitability maps, derived from the weighted overlay of probability maps calculated via species probability of occurrence, corresponding to four single environmental factors (Fig. 5), are shown in Figure 6. Additionally to modeled probability surfaces, sampled species abundance is given for evaluation of modeling success in each map. For *B. pilosa*, two different maps were created: Figure 6 (upper left) shows the modeling result for all four environmental factors; Figure 6 (upper right) illustrates the spatial probability for this species when only organic content of sediments was used as predictor. In both cases, the high probability of species occurrence covers the shallow areas of the German Part of the Bay to the extend of certain water depths, the Oder Bank, and a small area between Greifswalder Bodden Sill and Oder Bank, and it is very unlikely to observe *B. pilosa* in the Greifswalder Bod-

den Sill itself. Figure 6 (lower left) shows the modeled probability-of-occurrencesurface of *T. benedii*. As for this map, this species mostly occurs in the deeper parts of the Pomeranian Bay along the North-South axis of the Pomeranian Bay and in areas around the Greifswalder Bodden Sill. The probability-of-occurrence surface of







Fig. 6. Four maps for three species, derived from the weighted overlay of probability maps calculated via species probability of occurrence, corresponding to four single environmental factors (Fig. 5). Habitat suitability map for: *B. pilosa* vs. four environmental factors (upper left), *B. pilosa* vs. organic content of sediment only (upper right), *T. benedii* vs. four environmental factors (lower left), *H. diversicolor* vs. four environmental factors (lower right)

the third species, *H. diversicolor*, is shown in Figure 6 (lower right). Almost all areas of the Bay can be inhabited by *H. diversicolor* with high probability, except for the deeper parts along the Sassnitzrinne up to the Arkona Basin.

DISCUSSION

The present study was the first attempt towards a benthic – abiotic interaction model using a complex data set of recent investigations in the German part of the Pomeranian Bay. Such model allows making predictions on how and to what extent natural or anthropogenic influences affect benthic community assemblages not only in the Pomeranian Bay but in other areas of the Baltic Sea (e.g. Gogina et al. 2010). It can be a useful tool in marine ecosystem management (habitat mapping, e.g. Pavlikakis and Tsihrintzis 2000) and environment conservation planning (e.g. to plan the length of a pipeline in marine habitats etc.). However, an exploratory statistical description of the prevailing ecological structure based on in-situ observations is always an indispensible first step (Bourget and Fortin 1995). As in this study, the extraction of patterns of benthic community distributions using large-scale studies is characterized by a large number of data points randomly sampled over long distances and in irregular spatial intervals.

Modeling species spatial distribution via logistic regression and logit function from such data can be regarded as a legacy from plant ecology (e.g. Guisan et al. 1999). Few applications of the method are known in marine science, especially for the Baltic Sea, to date. For example, though not in the Baltic itself, Thrush et al. (2003) investigated response of species to a single environmental factor (sediment mud content) and Ysebaert et al. (2002) performed a comprehensive study, using salinity, depth, flow parameters, median grain size and mud content as predictors. For the regions where distribution is strongly and directly coupled to physiochemical processes statistical models are capable of satisfactorily predicting species distributions (Ellis et al. 2006). To assess the correctness of such calculated biotic – abiotic dependencies, not only geographical and ecological discrimination of species is necessary (Meissner et al. 2008), but also the in-depth knowledge of autecology of the species is indispensible. This expert knowledge stems from different sources: study, utilization of physiological experiments on (benthic) species, observation, (benthic) habitat monitoring as well as experience; it has to be at hand in the first place and cannot be simply deduced from statistics (Sachs 1997). Not till then, statistically modeled descriptions of species distribution patterns can be explained by causality as per ecological behavior of species, e.g. their habitat selection and colonization or the "response type" towards their physical environment (e.g. stenoecious, euryoecious etc.). The question that arises here is whether the modeled results for the three species used in our study mirror their autecology and thus legitimate the use of our modeling approach? B. pilosa, a coast-dwelling, sandlicking amphipod which grazes diatoms off the surface of sand grains (Nicolaisen and Kanneworff 1969, Sundbäck and Persson 1981) inhabits all sea-bottom elevations of post-glacial origin in the Pomeranian Bay (see Fig. 6, upper left and right). They consist of well sorted fine

sand, deposited and sorted here by postglacial aeolian processes. Wind and wave energy induce currents strong enough to vent these fine grained sediments and to keep them organic-poor through abrasion. This scheme fits perfectly well the described autecology of this species as an inhabitant of good sorted, well oxygenated and organic-depleted sediments (e.g. Speybroeck et al. 2008). In sharp contrast, the euryoecious and meso- to euryhaline deposit feeder T. benedii is most abundant in sediments rich in nutrients and organic carbon which form a trail along the North-South axis of the Pomeranian Bay, formed by the deposition of sedimented fine material, discharged by the Oder River in great amounts (ca. 39 kt year-1 total nitrogen, ca. 3.1 kt year-1 total phosphorus, Pastuszak et al. 2005). For this opportunistic oligochaete, mass reproductions in areas with high accumulation rates of organic carbon in sediments are known (Diaz 1984). Such sediments are distributed from the Oder River mouth up to the northwest and along the submerged ancient riverbed of the Oder, the Sassnitzrinne, all the way to the Arkona Basin. The preference of T. benedii for impermeable silty sediments seems to originate from his apparent tolerance of hydrogen sulphide occurrence and oxygen deficiency. It can penetrate sediments up to a depth of about 10 cm. It is often typified as well adapted to rapid environmental fluctuations and harsh conditions in estuaries. This advantage makes T. benedii one of the most successful inhabitants of ecologically stressed benthic environments with the aforementioned appropriate environmental conditions (Giere et al. 1999, Giere 2006). This oligochaete can also dominate coastal areas with fine sediments highly enriched in organic matter (Dubilier et al. 1994). The environmental preferences of *B. pilosa* and *T. benedii* are very special and this is clearly illustrated by the fact that both habitat suitability maps appear like blanked out by one another. This could be caused by the fact that B. pilosa can be regarded as stenoecious to organic content of sediment, causing a "yes or no" response of this species towards this environmental parameter, limiting the possible habitat that can be colonized by this species (Fig. 5, upper left and Fig. 6, upper left). In this respect, B. pilosa and T. benedii seem to represent some kind of "ecological antagonists" whereas H. diversicolor can be regarded as a kind of "cosmopolite". This endobenthic euryoecious and oligohaline polychaete settles as well in lotic as in lenitic sediments with salinity minima given as 5 psu. Of all the species inhabiting the Pomeranian Bay, it has the widest diet range. H. diversicolor can survive as a predatory carnivore as well as a scavenger, grazer and suspension feeder. H. diversicolor can penetrate the sediment up to depths of about 30 cm (Zettler et al. 1994). This species colonizes the Pomeranian Bay apparently homogenously and, vice versa to *B. pilosa* and T. benedii, completely independent from depth. Food quality or at least food availability due to high sedimentation and resulting accumulation rates of organic material can lead to a discrimination of benthic species over depth (O'Brien et al. 2003, Pearson and Rosenberg 1978). Such accumulation of organic material occurs throughout the year in the Pomeranian Bay and causes shifts in macrobenthic community assemblages, and thus is not necessarily a result of eutrophication (Zettler et al. 2006). It seems more likely that such community shifts are typical for estuarine ecosystems, caused by physical abrasion, accumulation or biological decomposition of aforementioned organic enrichments. This might be, together with other major

environmental parameters, most likely the cause of a periodically occurring "bouncing" of benthic zonation borders (Pazdro et al. 2001, O'Brien et al. 2003). The colonization success of such opportunistic species as T. benedii or H. diversi*color* can locally be explained by their sheer surviving and reproduction abilities in the extreme environmental conditions prevailing in some areas of the Pomeranian Bight, e.g. sulphidic sediments or temporarily existing oxygen deficiency zones through upwelling from deeper areas (Kube et al. 1996). On a larger (time)scale it might be due to the relatively young "ecological age" of the present Baltic Sea ecosystem (about 8 000 years), resulting in still ongoing primary succession processes, leaving numerous ecological niches available for such species (Bonsdorff 2006). Modeling species response works best with species showing a clear and recognizable optimum in the factor range examined. Nevertheless, such models can even mirror tendencies of opportunistic species without the full factor range of the ecological niche of a species. This applies for instance to H. diversicolor: a clear and sharply defined optimum was never found in our modeled response curves. For such species, modeling results reveal the best of available conditions in contrast to their optima. The best results are obtained for species with a response towards a factor that equals a "jump function", as is the case for the response of *B. pilosa* to organic content (Fig. 5, upper left). Here the "speed of response" is the all-dominant term regarding the modeling results. All other factor responses are simply too slow and therefore is ruled out. With such a reaction to a factor change, modeling the probability of occurrence for this factor alone can give satisfactorily results (Fig. 6, upper left and right). A factor combination with "slower" terms of the weighted overlay equation can at best compliment the picture but in the last resort can even lead to diffused results. A further inaccuracy might be the use of data sampled temporally differently. But that is not necessarily a bad thing. As was pointed out by Praca et al. (2008), the use of temporally heterogeneous data can confound the effect of interannual variation in species occurrence and environmental conditions - though one has to accept a noise floor increase in the analysis (own investigations). However, it should be mentioned that, as for all statistical methods, the inference about model selection uncertainty is conditional on both data and the full set of a priori models considered (Burnham and Anderson 2004). To derive acceptable ecological species response curves with logistic regression, Coudun and Gégout (2006) suggest a general minimum value of 50 occurrences per species and factor. This assumption was met for every species – factor combination used in our modeling approach. High variance in species distribution is not always due to sampling errors or random "noise" but rather the mechanistic consequence of shifts between limiting resources or other effects and factors (e.g. intra- and inter-species competition, predation, mortality or dispersal). The abundance of species may be very low, even under favorable conditions if, for some reason, the number of propagule is very low or species never even reach a given area. This natural phenomenon of species failing to colonize all areas where it could potentially thrive may explain some inconsistencies between the predicted high probability of species occurrence and its factual absence according to observations (Huston 2002). Under optimal conditions, species might reach maximal reproduction rates and maximal abundances, but macrobenthic survey often shows an entirely different reality: species and communities are distributed rather patchily and often the relatively smooth structure of abiotic gradients and other characteristics can increase statistical uncertainty and blur the picture. For a detailed overview and reflection *inter alia* on our method and alternatives used in marine modeling of species response see also Guisan and Zimmermann (2000), Muñoz and Felicisimo (2004), Guisan and Thuiller (2005), Guisan et al. (2006), Wisz and Guisan (2009) and Gogina et al. (2010). However, our objectives were to attempt a general description of species habitats and to investigate the predictive ability of the modeling technique at the selected spatial scale. Confirming the postulates of Ysebaert et al. (2002), Thrush et al. (2003), and Ellis et al. (2006), we have found that logistic regression in combination with a weighted overlay approach is a useful and relatively transparent approach to predict the response of species occurrence as a function of various environmental conditions.

CONCLUSIONS

Often, salinity is regarded as the one and only primary descriptor in brackish estuarine ecosystems. Considering the fact that all species examined (this study, Glockzin and Zettler 2008) are regarded as euryhaline and that the salinity does not vary strongly in the center of the Pomeranian Bay, the apparent influence of salinity as the main predictor on the benthic assemblage becomes insignificant under certain scale. As already pointed out, the prevailing environmental parameters in the study area, such as salinity, organic content, sorting or permeability, seem to be controlled primarily by water depth; it could even be described as a "master factor" and most likely, through its impact on all other factors, it is mainly responsible for the spatial zonation of benthic species, not only in the Pomeranian Bay but other marine habitats as well (e.g. Kube et al. 1996, Bonsdorff et al. 2003, O'Brien et al. 2003, Kröncke et al. 2004, Warzocha 1995, Zettler et al. 2006, Glockzin and Zettler 2008, Gogina et al. 2010). Our study clearly demonstrates the possibility to model species' relationships in gradient systems such as the Baltic Sea where their patterns of distribution are strongly and directly coupled to abiotic processes. By using species' response towards responsible environmental key factors to model spatial distributions for selected benthic species via a binomial logistic regression approach, we propagate an easy-to-use tool to assess natural and anthropogenic forced changes in benthic species distribution patterns. Thinking through the consequences and possibilities of these methods and doing the necessary enhancements, e.g. by coupling species ecological functions (e.g. filtration rates, bioturbation modes, e.g. Forster and Zettler 2004) to our model, we might even be able to assess an ecosystems functioning – and the loss of it. Bearing in mind the currently experienced impact of natural (e.g. via climate change) or anthropogenic forced changes (e.g. by pipeline building or dredge fishing) on the Baltic Sea ecosystem – never has the need for such a tool been more urgent than nowadays.

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