Do climate and fishing influence size-based indicators of Celtic Sea fish community structure?

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Ecosystem-based management requires the development of indicators that allow anthropogenic impacts to be detected against the background of natural variation. Size-based community metrics are potentially useful indicators because of their theoretical foundation and practical utility. Temporal and spatial patterns in size-based community metrics for Celtic Sea fish are described and calculated using data from the English groundfish survey of the area (1987−2003). The results reveal that the size structure of the community has changed over time, and that a decrease in the relative abundance of larger fish was accompanied by an increase in smaller fish (4−25 g). Temporal analyses of the effects of fishing and climate variation suggest that fishing generally has had a stronger effect on size structure than changes in temperature. Therefore, size-based metrics respond clearly to the effects of fishing even in variable environments, reflecting the ubiquity of size-based processes in defining community structure and responses to mortality. Spatial analyses were inconclusive, probably owing to the limited area for which fishing effort, temperature, and survey data were all available.

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Introduction

While the ecosystem approach to fisheries management is now being pursued worldwide (Garcia and Cochrane, 2005), it has proven challenging to identify suitable metrics of communities and ecosystems that are both quantifiable and theoretically defensible (Rice, 2000, 2003; Rochet and Trenkel, 2003; Trenkel and Rochet, 2003). Size-based approaches have such a theoretical foundation and also great practical utility for detecting the effects of exploitation upon fish communities (Shin et al., 2005). Analyses of size spectra in particular have been suggested as a powerful method, because the slope changes over time in a manner consistent with exploitation-mediated changes in community structure (Pope et al., 1988; Murawski and Idoine, 1992; Bianchi et al., 2000; Zwanenburg, 2000). However, the interaction between, and relative importance of,

environmental effects and exploitation on size spectra is difficult to quantify, and both factors may lead to changes in size structure. In addition, gear type, season, and the spatial extent of surveys produce significant differences in size-based metrics across given time-series (Trenkel et al., 2004; Daan et al., 2005).

For size-based metrics to be meaningful indicators in a management context, they should allow for discrimination between impacts of different forcing factors acting upon community structure, such as exploitation, pollution, and climate variation and change. Large-scale commercial fisheries expanded comparatively recently in the Celtic Sea and, unusually, their development was paralleled by the implementation of fishery monitoring and survey programmes (Pinnegar et al., 2002). The temperature and plankton community in the area is strongly influenced by decade-scale shifts in the North Atlantic Oscillation

(Beaugrand *et al.*, 2000, 2002). Consequently, the Celtic Sea represents an ideal system for studying the influences of exploitation and climate on fish community structure (Pinnegar *et al.*, 2002).

Here, we examine temporal and spatial patterns in three commonly used size-based metrics (average weight of an individual; average maximum size, L_{max}; and size spectrum slope; Rice and Gislason, 1996; Duplisea *et al.*, 1997; Jennings *et al.*, 1999; Bianchi *et al.*, 2000; Rochet and Trenkel, 2003) of the Celtic Sea fish community, and relate them to measures of fishing effort and sea temperature (as a proxy for climate variability).

Methods

Data sources

Size-abundance data by species from the annual CEFAS Celtic Sea groundfish surveys (Warnes and Jones, 1995) were used to calculate size-based metrics. Only locations sampled with the standard Portuguese high-headline trawl in >90% of years for the temporal analyses, and in all years for the spatial analyses, were used. The resultant time-series spanned 1987−2003 for 47 and 39 stations, respectively.

Winter and summer sea surface temperatures (SST; mean values January−March and June−August) for each year were obtained from http://www.cdc.noaa.gov/coads/. Gridded spatial data (1° longitude by 0.5° latitude) for SST and near-bottom temperature (NBT) for winter and summer were obtained from the ICES database.

Multispecies fishing mortality indices (F) were calculated as the biomass-weighted mean F for (i) all species assessed, and (ii) demersal species only (cf. Daan *et al.*, 2005; F obtained from ICES, 2003b−d). Spatial fisheries surveillance data (obtained from the UK Department of Environment, Food and Rural Affairs) were standardized for sightings effort (aircraft visits per ICES rectangle per unit time).

Size-based metrics

Average weight of an individual fish in the catch was calculated as the sum of the catch weights divided by the total number of fish caught (Zwanenburg, 2000). Average maximum length of the fish in the community (L_{max}) was calculated as in Jennings *et al.* (1999) and ICES (2003a).

The original data were standardized catch numbers by length category. Individual lengths were transformed to weights using species-specific length−weight regression coefficients, where possible (Bedford *et al.*, 1986; Dorel, 1986; Coull *et al.*, 1989); otherwise, a standard equation was used ($W = 0.01L^3$). Size spectra were standardized to remove the correlation between slope and intercept by subtracting the mean from the independent variable (Trenkel and Rochet, 2003). As our interest focused on

that part of the spectrum that could be approximated by a linear slope, only body-mass classes above a threshold mass of 4 g were included in the analysis. Slopes and intercepts of the normalized $\log_2$ biomass (y-axis) against the midpoints of $\log_2$ body-mass classes (x-axis) for each year were estimated by linear regression.

All metrics were calculated for all species caught and for demersal species only, and analyses were carried out separately for each group.

Analyses

Positive or negative trends in the size-based metrics and log-abundance over time were evaluated by comparing the rank correlation statistic for each time-series (Spearman's correlation coefficient, r_s). To test for relative effects of F and temperature, multiple linear regression was used. All variables were normalized (subtracting the mean and dividing by the standard deviation) before analysis to ensure that each series had a mean of zero and comparable variance. For each size-based metric (y-variable) and each pair of x-variables (F; and each temperature series of winter and summer SST with 0-, 1-, and 2-year lags, to allow for delayed effects of environmental change on biological processes), a combination of forward and backward selection (ANOVA, F-test) of the following models was used:

$$y = \beta_0 + \epsilon \tag{1}$$

$$y = \beta_0 + \beta_1 x_1 + \epsilon \tag{2}$$

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \epsilon \tag{3}$$

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \epsilon \tag{4}$$

Variance inflation factor (VIF) was used to evaluate the degree of collinearity. All pairs of x-variables had a VIF < 2, implying a negligible collinearity effect on the regression parameters (Fox, 1997).

Spatial analyses of size-based metrics were restricted to biomass spectrum slopes for all fish in the community. Survey data were pooled over time, and linear fits to normalized $\log_2$ biomass against $\log_2$ body mass were made for each station sampled over the period 1987−2003. Spatial maps of winter and summer SST and near-bottom temperature (NBT), and standardized sightings of fishing vessels (as a proxy for fishing effort), were produced by kriging (in the R package "spatial"; Venables and Ripley, 2002). Pearson's correlation coefficients between each of the predicted kriged surfaces (at the survey stations) and slopes were calculated after taking account of spatial autocorrelation, using software provided by Legendre (2000). With the
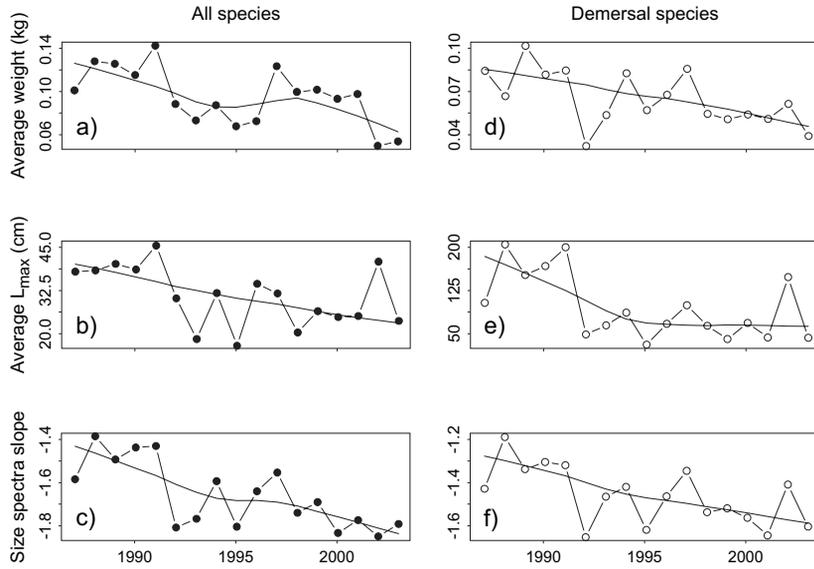
Figure 1. Time-series plots of average weight (top), average L_{max} (middle), and size spectrum slope (bottom) for all species combined (left) and demersal species separately (right) in the Celtic Sea (line fits are LOESS local smoother for visualization purposes only).

exception of the latter, all analyses were carried out using R version 2.0.0.

Results

Trends over time (Figure 1) in average weight ($r_s = -0.57$, $p < 0.05$), average L_{max} ($r_s = -0.45$, $p < 0.1$), and slopes ($r_s = -0.69$, $p < 0.01$) for all fish caught were all negative. However, all patterns exhibited a "dip" during the years 1993−1996. Metrics based on demersal fish only exhibited similar declines in average weight ($r_s = -0.54$, $p < 0.05$), L_{max} ($r_s = -0.59$, $p < 0.05$), and slopes ($r_s = 0.53$, $p < 0.05$). Winter SST increased significantly (Figure 2a; $r_s = 0.50$, $p < 0.05$), whereas summer SST exhibited similar interannual variation but the temporal trend was not significant ($p > 0.1$). The F for all commercially exploited stocks increased significantly over the period ($r_s = 0.74$, $p < 0.01$), but it appeared to be levelling off in recent years; demersal F also increased significantly ($r_s = 0.76$, $p < 0.005$), particularly after 1994, and was less than total F (Figure 2b).

Relative biomass of $\log_2$ weight classes revealed an increase in small fish (all categories <100 g) over time, which was accompanied by a reduction in large fish (all categories >100 g; Figure 3). However, only the increases in the three categories below 25 g and the declines in two of the larger ones (100−121 g; 144−169 g) were significant ($p < 0.05$).

Linear regression of each normalized y against each single explanatory x-variable revealed significant negative relationships between all species F and average L_{max} ($r^2 = 0.44$, $p < 0.001$) as well as F and slope ($r^2 = 0.33$,

$p < 0.05$). For demersal fish, the relationships were similar, but weaker (L_{max}, $r^2 = 0.21$, $p < 0.1$; slope, $r^2 = 0.20$, $p < 0.1$). Weak negative relationships between slope and 2-year lagged winter SST (all species, $r^2 = 0.18$, $p < 0.1$; demersal species, $r^2 = 0.21$, $p < 0.1$) and between L_{max}
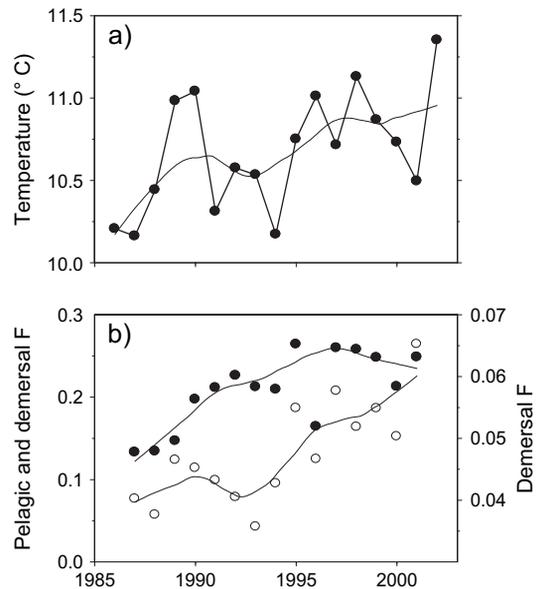
Figure 2. Time-series of (a) mean winter (January−March) sea surface temperature averaged over the entire Celtic Sea, and (b) multispecies F (weighted by biomass) over time for all species combined (solid circles) and demersal species (open circles) separately (line fits are LOESS local smoother for visualization purposes only).
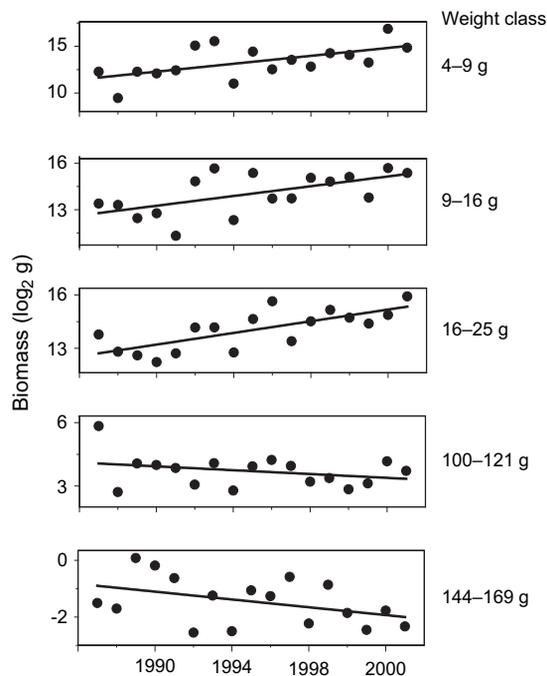
Figure 3. Relative biomass of selected weight classes for all species caught in the Celtic Sea groundfish surveys during 1987−2003. Solid lines are temporal trends fitted by linear regression.

and summer SST (demersal species, $r^2 = 0.21$, $p < 0.1$) were also detected. When the temperature series were restricted to the years for which F estimates were available, the relationships were no longer significant. Serial auto-correlation was not present in any of the variables, so should not have affected significance levels.

For the whole community sampled by the survey trawl, F had a stronger effect on mean L_{max} and slope than temperature. For mean L_{max}, adding winter (1-year lag) and summer (2-year lag) SST series to the model increased the residual variance explained from 44% (F only) to 60% and 72%, respectively. ANOVA results from the multiple regression models showed that for each combination of SST and F, when F was the first variable, addition of F alone led to the best improvement over a null model (1) when the y-variable was slope (all species). This was also the case for L_{max}, except when winter SST (1-year lag; $p < 0.1$) or summer SST (2-year lag; $p < 0.01$) was added. However, the interaction terms were not significant.

Although F did not explain a significant amount of the variance in average weight (all species), addition of F with winter SST (1-year lag, with interaction term) or summer SST (2-year lag) did. Addition of F with winter SST (1-year lag) and an interaction term led to a marginally significant improvement over the null model, because of the weak significance of the interaction alone ($p < 0.1$). Similarly, a model including F and summer SST (2-year lag) was

marginally better than the null model ($p < 0.1$) when F alone was not significant ($p > 0.1$), but the interaction term was not significant. Adding temperature first did not affect these results. There were two cases, however, where adding temperature as the first x-variable and F as the second resulted in F no longer being a significant term (and vice versa). These were the combinations of slope and winter SST (2-year lag) for all species and demersal species only. The reduction in the residual sums of squares (RSS) was greater when F was the explanatory variable (32%) rather than SST (21%) for all species, whereas SST reduced RSS by 27% and F by 20% for demersal species alone. For all other models, when SST was added as the first variable to predict a y-variable that had strong F effects, F was still significant as a second variable.

Fitting biomass spectra spatially (by sampling station) revealed that the steepest slopes were located in the eastern and western (along the shelf edge) parts of the Celtic Sea (Figure 4). After correcting for spatial autocorrelation, there were no significant correlations between slopes and any of the predicted (kriged) values at the stations for the spatial temperature series. A proxy for thermal stratification (the difference between predicted SST and NBT at each station) in winter and summer was not significantly correlated with slopes. Also, slope was not significantly correlated with fishing intensity for positions that fell within the limited range of the UK surveillance area (Figure 5).

Discussion

Patterns in size-based metrics are evident both spatially and temporally. Declines observed over time in mean weight, mean L_{max}, and slopes (all species) are associated with a reduction in the abundance of large fish and an increase in small fish. For the whole community sampled by the survey trawl, F had a stronger effect on mean L_{max} and slope than temperature. Although F did not explain a significant amount of the variance in average weight, addition of F with winter SST (1-year lag, with interaction term) or summer SST (2-year lag) did. For the demersal component of the fish community, F had a weaker effect on the size-based metrics, possibly reflecting the lower demersal species F and the partial sampling of interacting pelagic and demersal communities. In general, the results for the whole community demonstrate that fishing has a relatively large and consistent impact on size-based metrics. Even in the Celtic Sea, where environmental forcing is unusually strong (Southward *et al.*, 1988), fishing effects on size-based metrics can be disentangled from environmental effects.

Changes in F and temperature will affect the size structure of communities on a range of time scales. Changes in F reflect the direct effects of mortality, but our analyses provide evidence for longer-term indirect effects, because the biomass of fish in small size classes increased with F, consistent with studies of the response of size spectra to fishing in the North Sea (Daan *et al.*, 2005)
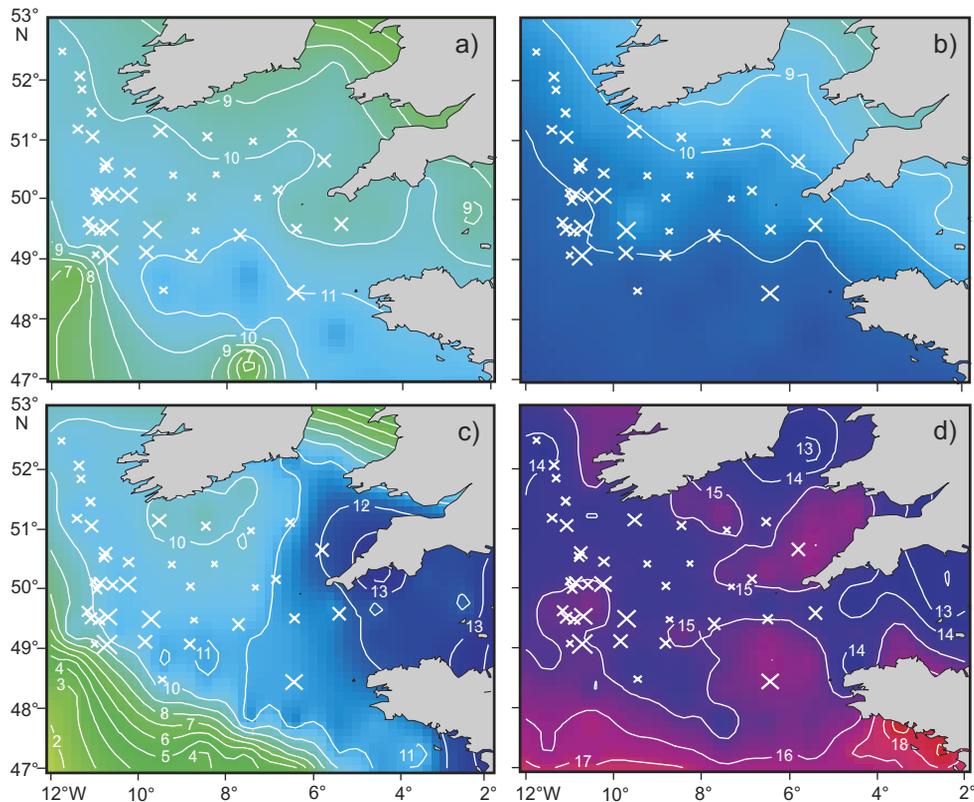
Figure 4. Slopes of biomass spectra mapped by station for pooled data, 1987−2003 (symbol size proportional to absolute value of slope; smallest symbol = −0.9; largest symbol = −2.1) in relation to (a) mean winter NBT, (b) mean winter SST, (c) mean summer NBT, and (d) mean summer SST (contours are kriged surfaces).

and Fiji (Dulvy *et al.*, 2004). Changes in temperature at a given sampling location may lead to changes in the size structure because of (i) immigration and/or emigration of species with different temperature preferences, (ii) temperature effects on the life history of resident species, and (iii) indirect effects on biological processes that support the fish community. These effects on size structure may emerge on a range of time scales, and moreover, different size classes may be affected on different time scales. For example, good recruitment of an abundant species as a consequence of improved conditions for larval survival may affect the size spectrum within 1 year, whereas the effects of temperature on asymptotic body size may not be manifest for several years. Therefore, any attempt to link changes in size-based metrics to changes in temperature assuming an instantaneous response or a fixed lag is a crude one, but this is unavoidable given the lack of detailed information on biological responses of all species and size classes to temperature. Moreover, it is questionable whether the temporal and spatial scales over which the explanatory variables were tested best reflect the effects of fishing and temperature: spatial data on fishing intensity were incomplete, and the annual set of spatial temperature data were not entirely adequate.

Because our sampling stations are fixed in space, changes in metrics attributable to the environment may represent a change in the community present at the station (owing to environmental effects on distribution) or an effect on the dynamics of the populations constituting the community. Distributional changes in response to climate are well known in the Celtic Sea. Southward *et al.* (1988) reported shifts in the distribution of pilchard (*Sardina pilchardus*; a warm-water species) and herring (*Clupea harengus*; a cold-water species) over the past 400 years, corresponding to long-term temperature fluctuations. Lagged responses to climate may also be driven by conditions affecting growth, survival, and food availability during early life history, including temperature and timing of algal blooms (Planque and Frédou, 1999; O'Brien *et al.*, 2000; Platt *et al.*, 2003), or other processes directly related to the North Atlantic Oscillation (Dippner, 1997; Attrill and Power, 2002). Determining whether and how these changes should result in altered size structure still needs to be addressed.

The body size distribution of animals in foodwebs reflects patterns of energy use and acquisition, so the slopes of size spectra are remarkably constant in many ecosystems (Boudreau and Dickie, 1992). Although temperature will
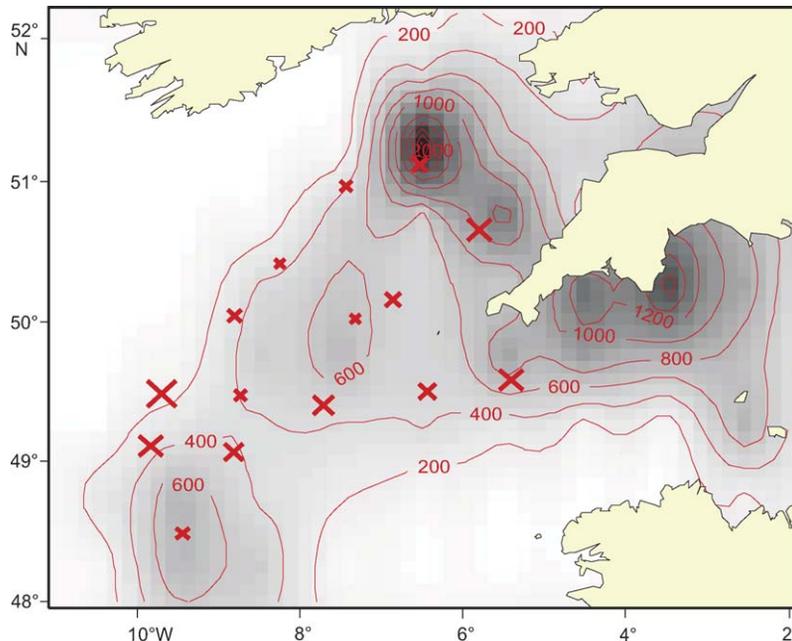
Figure 5. Slopes of biomass spectra (as in Figure 4, but excluding stations outside the area for which UK vessel sightings data were available) in relation to standardized sightings of UK fishing vessels in the Celtic Sea (pooled data for the years 1985−2002; contours are kriged surfaces; dark, highest levels; white, no data).

have a marked effect on biomass turnover and energy flux in the system, the slope is an emergent property that is largely temperature-independent (Brown *et al.*, 2004). This implies that the slopes of time-averaged size spectra for the entire foodweb are sensitive to size-selective mortality rather than to temperature, and should be reliable indicators of fishing impacts at the scale of the foodweb. In practice, however, trawls sample specific assemblages within the foodweb, and the size compositions of the samples reflect (i) gear selectivity, (ii) spatial distribution of individuals, (iii) short-term dynamics of populations, as well as (iv) part of the underlying structure of the foodweb. Theoretical understanding of the responses of size-based metrics to fishing is based primarily on changes in the underlying structure of the foodweb (iv) owing to effects of size-selective mortality, but these effects are increasingly more difficult to resolve at progressively smaller spatial and temporal scales because the environment affects factors (i)−(iii). This may explain the failure of size-based metrics to provide an effective indicator of fishing effects at small spatial and temporal scales (such as an ICES rectangle), even though they may be reliable indicators of fishing effects at larger scales (Piet and Jennings, 2005).

Acknowledgements

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