Differential variability in time and space of numbers in suspension and deposit feeding benthic species in a tidal flat area

Marine zoobenthos
Fluctuations
Distribution patterns
Food supply

Zoobenthos marin
Fluctuations
Types de distribution
Apports nutritionnels

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ABSTRACT

Evidence from a tidal flat ecosystem in the Dutch Wadden Sea is presented, substantiating a hypothesis formulated by Levinton (1972) and stating that both the food supply and the numbers of suspension feeding marine zoobenthic species fluctuate more heavily, spatially as well as temporally, than those of deposit feeders. During the year and also from day-to-day, concentrations of chlorophyll-*a* and particulate organic matter fluctuated more heavily in the water above tidal flats than in the top layer of the bottom. From year to year, the numbers of suspension feeding species (as the bivalves *Mytilus edulis*, *Mya arenaria* and *Cerastoderma edule*) fluctuated more heavily than those of deposit feeding species (as *Arenicola marina*, *Heteromastus filiformis*, *Scoloplos armiger* and *Nereis diversicolor*). Also from place to place, the numbers of suspension feeding species were more variable than those of deposit feeders. For the 10 major species of the macrozoobenthos living on the tidal flats, the 2 coefficients of variation for variability in time and space were significantly correlated, with high values for both coefficients in the polychaete *Lanice conchilega* and in the above mentioned bivalves, and low values in the bivalve *Macoma balthica* and in the above polychaetes.

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RÉSUMÉ

Différences de variabilité numérique dans l'espace et dans le temps entre des espèces suspensivores et déposivores des sédiments de la Mer de Wadden

Les résultats quantitatifs concernant l'écosystème de la mer de Wadden hollandaise ont permis d'apporter des preuves à l'appui de l'hypothèse émise en 1972 par Levinton. selon laquelle la nourriture et les abondances des espèces benthiques suspensivores fluctuent plus fortement dans l'espace et dans le temps que celles des espèces déposivores.

Au cours de l'année comme de jour en jour, les concentrations en chlorophylle et en matière organique particulaire varient en effet plus fortement dans l'eau que dans la couche superficielle du sédiment. D'année en année, les abondances de suspensivores (*Mytilus edulis*, *Mya arenaria* et *Cerastoderma edule*) présentent des fluctuations plus grandes que celles de déposivores tels que *Arenicola marina*, *Heteromastus filiformis*, *Scoloplos armiger* et *Nereis diversicolor*. En outre, les abondances des suspensivores varient dans l'espace avec une plus grande amplitude que celle des déposivores. Pour les 10 espèces dominantes du macrozoobenthos vivant dans la zone intertidale, les deux coefficients de variation (temps et espace) sont corrélés de façon significative. Ils présentent des valeurs élevées pour *Lanice conchilega* et pour les bivalves suspensivores, contre de plus faibles valeurs pour *Macoma balthica* et les autres polychètes.

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INTRODUCTION

Levinton (1972) developed a hypothesis stating that the size of populations of suspension feeding marine benthic species should fluctuate widely in numbers both over time and from place to place, whereas numbers in deposit feeders living in the same area should be relatively constant, temporally and spatially. These differences between the two groups would be connected with the relative constancy of their respective food supplies, being unpredictable and heavily fluctuating for suspension feeders and relatively constant for deposit feeders.

Several testable questions arise from this hypothesis. Firstly : is the food supply of suspension feeders really more variable than that of deposit feeders living in the same community ? Secondly : are the numerical densities of the various suspension feeding species fluctuating more heavily than those of the deposit feeding species living in the same area ? Thirdly : are the densities of suspension feeding species varying more from place to place, *i.e.* are suspension feeders distributed more patchily (less evenly) than deposit feeders in the same area ? Fourthly : when these questions can be answered positively for a particular ecosystem, what would be the direct relation (if any) between the varying food supply and the patterns of temporal and spatial variation in numbers of animals ?

Answers to the above questions will be presented from data gathered in a tidal flat area in the westernmost part of the Dutch Wadden Sea. The first author sampled the macrozoobenthos during 14 years at 15 places, the co-authors sampled year-round the phytoplankton, microphytobenthos and organic matter in the tidal inlet and on and above the tidal flats.

MATERIAL AND METHODS

Food supply in the water and in the top layer of the bottom was expressed in concentrations of functional chlorophyll-*a*. Samples were taken about fortnightly to monthly during 1974 to 1980 from the surface water in the Marsdiep tidal inlet and from the top 1 cm of the bottom on a nearby tidal flat (*see* Cadée, Hegeman, 1974 ; 1979). During 1978 and 1979 samples were taken at a similar frequency at 3 stations on the tidal flats of Balgzand, both from the water at about $2\frac{1}{2}$ cm above the bottom and from the top 1 to 2 mm of the sediment.

Macrobenthic animals were sampled quantitatively during 1969 to 1982 inclusive, at least annually at 15 places (12 transects of 1 km plus 3 squares of 900 m^2) scattered over Balgzand, a 50 km^2 tidal flat area in the westernmost part of the Dutch Wadden Sea (Fig. 1). In the following, only samples taken in the late-winter/early-spring period are used. In addition, data will be used from a single sampling of 99 transects of 1 km scattered all over the 1 300 km^2 of tidal flats of the entire Dutch Wadden Sea, sampled in late-summer/early-autumn of 1970-1974. Details on locations, sampling procedure, sieving (a 1 mm sieve was used), sorting and counting can be found in earlier papers (Beukema, 1974 ; 1976).

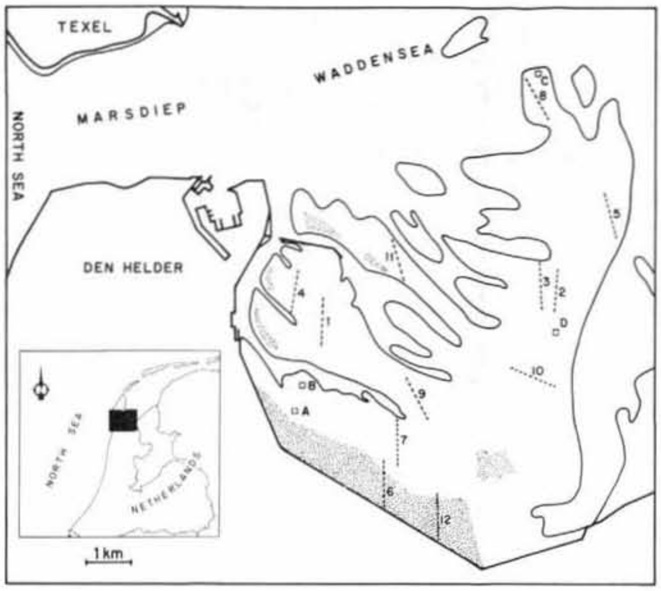

Figure 1

Map of the tidal flat area called Balgzand, situated in the westernmost part of the Netherlands part of the Wadden Sea, showing the locations of the sampling places. Food supply was measured on Balgzand near A, B and D and in the Marsdiep area at the coast of the Texel island. The macrobenthos was sampled at 3 squares (A, B and C) and along 12 transects (1-12). The approximate borders of the tidal flats at LLWS are shown. Most of the flats are below MTL, only the shaded parts are above. Mean tidal range is 140 cm. The sediment is silty along the mainland coast, becoming gradually sandier (to almost pure fine sand) at increasing distance from the coast.

Variability is expressed in the coefficient of variation of a series of observations, *i.e.* 100 times the standard deviation (s) divided by the mean (m). To avoid too low values of m, at which the quotient 100 s/m cannot be used as a measure for variability (*see* below), the present study is limited to data on common species only.

RESULTS

Variability of food supply

During year-long observations, fluctuations observed in the chlorophyll-*a* content were about 100-fold in the water (from about 1 to more than 100 $\mu g.l^{-1}$) and about 20-fold in the top-layer of the bottom (from 5 to 120 $\mu g.g^{-1}$), with the lowest values in winter and the highest in spring and early summer. The variability as expressed in the coefficient of variation was generally 2 to 3 times (on an average 138/59 = 2.3 times) higher in the water than in the bottom (Table 1). This was so both in the Balgzand area, where only the top millimeters of the bottom were sampled as in the Marsdiep area, where a 1 cm layer was used. In 9 out of 10 possible comparisons the variability of chlorophyll-*a* concentrations was significantly higher in the water than in the bottom. As the 1 odd pair of values also represented the smallest difference, it is highly improbable ($p < 0.01$, Wilcoxon matched-pairs signed-ranks test) that the greater values for the coefficient of variation were merely by chance observed for the greater part in the water samples.

Table 1

Annual values for mean concentrations and matching coefficients of variation for chlorophyll-a and particulate organic matter both in the water in $\mu g.l^{-1}$ for chlorophyll and $mgC.l^{-1}$ for organic matter and in the top layer of the sediment in $\mu g.g^{-1}$ for chlorophyll and $mgC.g^{-1}$ for organic matter, in 2 areas (B = Balgzand with stations A, B and D and M = Marsdiep, see Fig. 1). n = number of observations. + and ++ denote level of statistical significance of the difference in variability (F-test for variances, 0.05 and 0.01, respectively).

Place/year	n	Mean content water	Mean content sediment	Coeff. variation water	Coeff. variation sediment	Sign.
Chlorophyll						
B-A/79	8	40	53	182	64	+
B-B/78	10	17	15	114	68	+
B-B/79	16	25	24	129	70	+
B-D/78-9	12	26	20	102	48	++
M/74	16	4	5	140	53	+
M/75	13	6	4	179	34	++
M/76	14	5	7	100	108	
M/78	12	8	7	161	45	++
M/79	13	18	9	178	54	++
M/80	13	13	11	93	49	++
Average				138	59	
Organic matter						
B-A/79	7	9	5	157	25	++
B-B/79	18	4	3	71	32	++
B-D/78-79	7	3	2	32	28	
M/79	13	2	2	67	39	
Average				82	31	

Within series of observations of 3 to 5 successive days, fluctuations of chlorophyll-*a* content in the water could be about 20-fold (the mean coefficient of variation for 11 such series amounted to 52) and in the bottom about 10-fold, with a mean coefficient of variation for 9 such series amounting to 36. Thus much of the above total variability was already present at a day-to-day time scale. Again, the variability in the water was on an average higher than in the top-layer of the bottom.

Less observations are available for organic matter contents. As in chlorophyll, they indicate a greater variability in the water samples (Table 1). Again the coefficients of variation were on an average 2 to 3 times higher for the water samples as compared to the bottom samples.

The content of chlorophyll-*a* will be a better measure for food supply than that of particulate organic matter, because much of the organic matter will consist of indigestable material of low food value.

Temporal variation in the numbers of animals

Out of the nearly 50 macrozoobenthic species found on the tidal flats of Balgzand, results on only the 10 most important ones will be dealt with, viz. those with a high (on an average more than 1 %) contribution to total biomass. They are listed as the top-10 species in Beukema (1976). Together they account for a mean of 95 % of the total macrozoobenthic biomass of the tidal flats, both on Balgzand and in the whole Dutch Wadden Sea.

Among these 10 species, 3 are typical suspension feeders, viz. the bivalves *Mytilus edulis* L., *Cerastoderma (Cardium) edule* (L.) and *Mya arenaria* L. Most polychaetes are typical deposit feeders, viz. *Arenicola marina* (L.), *Heteromastus filiformis* (Clap.), *Scoloplos armiger* (OFM) and *Nereis diversicolor* OFM (Wolff, 1973), though part of these species will be able to supplement their ration by filtration, as has been observed in *Arenicola* by Krüger (1971) and in *Nereis* by Goerke (1971). In the remaining species the predominant way of feeding appears to be a matter of dispute. *Nephtys hombergii* Sav. appears to be both a predator (Clark, 1962) and a deposit feeder. In *Macoma balthica* (L.) both suspension and deposit feeding is important (De Wilde, 1975). Also in *Lanice conchilega* (Pall.) both feeding types are used (Ziegelmeier, 1952).

These 10 species differ strongly in the degree of their year-to-year variability (Fig. 2 *a*, Table 2). The numbers of *Arenicola* were very constant, having a coefficient of variation that is an order of magnitude lower than that of *Lanice*, the species fluctuating most heavily. Note that the typical suspension feeders rank high in Table 2, *i.e.* their numbers varied stronger from year to year than those of the typical deposit feeders. Also Figure 1 *a* shows that — over the whole range of values for mean density — the values for the standard deviation were higher for the 3 suspension feeders (plus *Lanice*) than for the 5 deposit feeders (plus *Macoma*).

Spatial variation in the numbers of animals

In all species the density ($n.m^{-2}$) varied from place to place, but the degree of patchiness differed. At the spatial scales studied, all species were distributed less evenly than randomly, as in all cases the values of the variances exceeded those of the means (Fig. 2 *b*). Some species were highly aggregated and generally formed distinctive banks or clusters, as in *Mytilus*, *Lanice* and *Cerastoderma*, ranking high for variability in space in Table 2.

Deviations from random distributions — and more generally the degree of clustering — can be detected and quantified only at sufficiently high numbers of individuals per sample. As the mean number per sample becomes smaller, the quotients s^2/m and s/m approach the value of 1 (*e.g.* Ursin, 1960 : Fig. 88-91). This is true also for the animals living on the tidal flats of the Wadden Sea (own observations). Therefore, values for the coefficient of variation should be compared only at roughly the same values of the mean. Figure 2 *b* allows such comparisons for our data, showing that very low numbers per sample did not occur (as a consequence of the intentional choice of abundant species) and that the mean densities of the suspension feeders were not consistently higher (or lower) than those of the deposit feeders. Note that the values for the standard deviations in the suspension feeders are higher than those in the deposit feeders over the whole range of mean numbers per sample. An analysis of variance showed this difference to be statistically significant ($p < 0.05$).

Spatial variability was studied at 3 scales, viz. for the whole Wadden Sea (with distances between adjacent sampling places amounting to several kilometres to tens of kilometres, *see* Beukema, 1976), for the Balgzand area (with distances of less than 1 to about 5 km, *see* Fig. 1) and within transects (subsamples per 100 m).

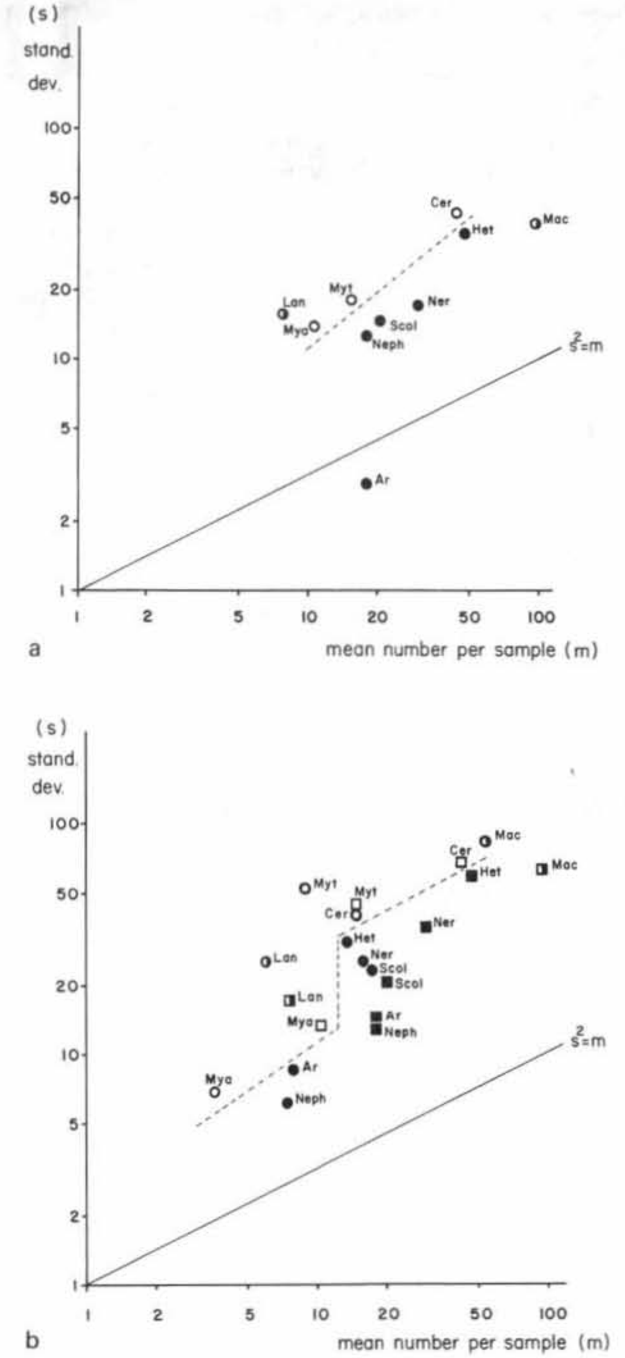

Figure 2

The relationship (on a log scale) between the means (m) and the standard deviations (s) of series of samples of 10 species of macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. The species are indicated by the first characters of their name (compare Table 2) and by a symbol defining their feeding type as follows : open (○ □) for suspension feeders, full (● ■) for deposit feeders and half-full (◑ ◧) for species using both types of feeding.

a) *Temporal variation from 14 annual estimates of the size of the total population on Balgzand (index used : mean number per 0.9 m^2 obtained from sampling at 15 places) ;*

b) *Spatial variation at 2 scales, viz. at Balgzand (squares, long-term averages from 15 places) and over the whole Dutch Wadden Sea (circles, 99 places sampled once).*

The full lines indicate the relation $s^2 = m$ (i.e. $\log s = \frac{1}{2} \log m$), the broken lines separate the points for the suspension feeders (open) and the deposit feeders (full).

As one would expect from the smaller change of environmental conditions with shorter distances, the smaller scales generally yielded the lower coefficients of variation in the various individual species (Table 2). The order of the species, however, remained nearly unchanged at the 3 spatial scales. The correlations between the rank numbers in the last 3 columns of Table 2 are high ($r = 0.8$ to 0.9) and statistically significant ($p < 0.02$ to < 0.01, Spearman rank correlation test). This would mean that the size of the clusters generally will not have exceeded $\frac{1}{2}$ to 1 km, as indeed was true at visual inspection.

Note in Table 2 that the typical suspension feeders rank relatively high not only in temporal but also in spatial variation. Their mean rank number is 3 for variability in time and 3 to 4 for variability in space. The typical deposit feeders, at the other hand, rank relatively low both for variability in time (mean : 7) as for variability in space (mean : 6 to 7). The rank numbers in the first column of Table 2 (for variability in time) are significantly correlated with those included in each of the following 3 columns (for variability in space at the 3 scales) with values of r ranging from 0.7 to 0.9 and $p < 0.05$ to < 0.01 (Spearman test). Thus a relatively high variability in numbers from year to year generally goes with a relatively high variability in density from place to place (when these places are at least some hundreds of meters apart).

DISCUSSION

Levinton's hypothesis is substantially corroborated. In the Wadden Sea, the food supply for suspension feeding benthos as compared to that for deposit feeders indeed is more variable at various time scales (seasons and days). The annual numbers of suspension feeding species on the tidal flats indeed varied more strongly than those of deposit feeding species. Also the variation from place to place (at scales from several 100 m to several km) was greater in suspension feeders than in deposit feeders. The most important point yet to discuss is : what mechanisms govern the fluctuations in time and the variability in space and has the observed difference in variability of food supply anything to do with the variabilities in the numbers of the animal species.

All of the species dealt with produce annually thousands of eggs per adult female and thus will have a high potential for annual variability in numbers. Reduced variability is to be expected in species showing some kind of feed-back mechanism to regulate their numbers. In the species investigated in the Wadden Sea in this respect, only *Arenicola* and *Macoma* showed clear evidence for the existence of such mechanisms (Beukema, De Vlas, 1979; Beukema, 1982.) Variation in recruitment was particularly high in the typical suspension feeders *Mytilus*, *Cerastoderma* and *Mya* (Beukema, 1982). The presence of a clear regulatory mechanism only in the 2 species (*Arenicola* and *Macoma*) that rank lowest for temporal variation (Table 2) indicates that the operation of such a mechanism is a prerequisite for low year-to-year variation in numbers.

Distribution patterns in the species dealt with will arise mainly from settlement of metamorphosing larvae or older stages that have been washed out or prolonged their pelagic way of life. An interplay of physical forces

Table 2

Temporal and spatial variability of the 10 major macrozoobenthic species living on the tidal flats of the Wadden Sea, listed in order of decreasing year-to-year variability. The figures shown are coefficients of variation and between brackets rank numbers. First column : variability in time of the size of the total Balgzand populations, sampled during 14 successive years. Next columns : variability in space on different scales, viz. Wadden Sea (99 transects, sampled once), Balgzand (15 places, 14-year means), and along individual transects (10 subsamples, 3 transects, 3 years).

Species	Feeding type	Variability in time	Variability in space: Wadden Sea	Balgzand	transects
Lanice conchilega	sus + dep	203(1)	413(2)	188(1)	127(3)
Mya arenaria	sus	128(2)	184(5)	78(7)	142(2)
Mytilus edulis	sus	117(3)	562(1)	164(2)	235(1)
Cerastoderma edule	sus	96(4)	266(3)	116(3)	103(5)
Heteromastus filiformis	dep	74(5)	224(4)	110(4)	120(4)
Scoloplos armiger	dep	72(6)	132(8)	81(6)	72(7)
Nephtys hombergii	prd + dep	70(7)	82(10)	65(9)	58(8)
Nereis diversicolor	dep	56(8)	159(6)	94(5)	89(6)
Macoma balthica	sus + dep	39(9)	151(7)	47(10)	44(10)
Arenicola marina	dep	16(10)	106(9)	73(8)	58(9)

(water movements from tides and wind) and behavioral mechanisms (accepting or rejecting of the substrates encountered) will shape the distribution pattern of settled animals. Settlement of small animals that cannot firmly attach will be limited to areas with low current speeds, as they would be washed out at higher speeds (*e.g.* Baggerman, 1953, for *Cerastoderma*). Thus in many species initial distribution will be limited to specific areas, where they accumulate, leaving other areas barren or only sparsely populated and thus generating a high coefficient of spatial variation. Such specific areas with high densities of young animals on tidal flats have been observed for *Arenicola* (Farke *et al.*, 1979) and *Macoma* (Beukema *et al.*, 1978).

Nevertheless, exactly these 2 species were found to be relatively evenly distributed over the tidal flats (Table 2).

The explanation of this seeming contradiction is the phenomenon of redistribution observed in these 2 species after a stay of $\frac{1}{2}$ to 1 year in the nursery and having grown up there to about $\frac{1}{4}$ to $\frac{1}{2}$ of the adult size. In winter high numbers of these young animals can be found suspended in the tidal streams and transported over long distances. In both species this mass transport results in a spreading out (Beukema, 1973 ; Beukema, De Vlas, 1979 ; Beukema *et al.*, 1978). Thus, as in temporal variation, a low spatial variability appears to be attained only by a special mechanism. The one other species, *Mytilus*, known to redistribute itself on a large scale, some time after initial settlement, makes special demands to its new settling place, viz. niches in solid substrates (Verwey, 1952). Such places are rare on tidal flats and are in fact almost limited to existing mussel beds. Consequently, redistribution in *Mytilus* promotes clustering. A similar aggregating mechanism appears to operate in *Lanice*, in which species young animals have been observed to settle preferably on the tubes of the adults (Ansell, pers. comm.). Indeed, both *Mytilus* and *Lanice* are situated at the other extreme in the order of increasing variability in space (Table 2).

In conclusion, at least the extremes (to either side) of temporal and spatial variability appear to be caused by special mechanisms that have no direct connection to the type of food source. However, mechanisms to reduce high densities (over vast areas or as clusters) will be needed more in deposit feeders than in suspension feeders. Deposit feeders depend on a limited (though relatively constant) food supply that is renewed only slowly by local production and deposition. Suspension feeders living at the bottom in shallow seas, at the other hand, experience a continuous and rapid (though erratic) renewal of food produced elsewhere and transported by water movements. Therefore, suspension feeders can permit themselves high local densities and deposit feeders cannot. Competition for food generally will be more severe at the limited food supply of deposit feeders than in the situation of suspension feeders. More generally, deposit feeders will be food-limited more frequently than suspension feeders and will be more often of the type of equilibrium or K-selected species as contrasted to suspension feeders being more of the type of opportunistic or r-selected species. The mechanisms reducing temporal or spatial variability then can be regarded as part of an adaptive strategy that will have evolved in marine benthos more often in taxa taking their food mainly from the bottom than in those feeding primarily from suspended material.

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