

**Biological structure of the ocean  
and the general patterns in the  
spatial-temporary distribution of  
the integral characteristics of  
pelagic macrofauna of the  
northwestern Pacific**



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# Investigated part of the North-western Pacific

The waters of an area of 6 mln.km<sup>2</sup>




20000 pelagic trawl stations, 882 one-degree trapezia, 48 standard areas of averaging of biostatistical information, and the surveyed sectors of 4 water bodies

## Time period

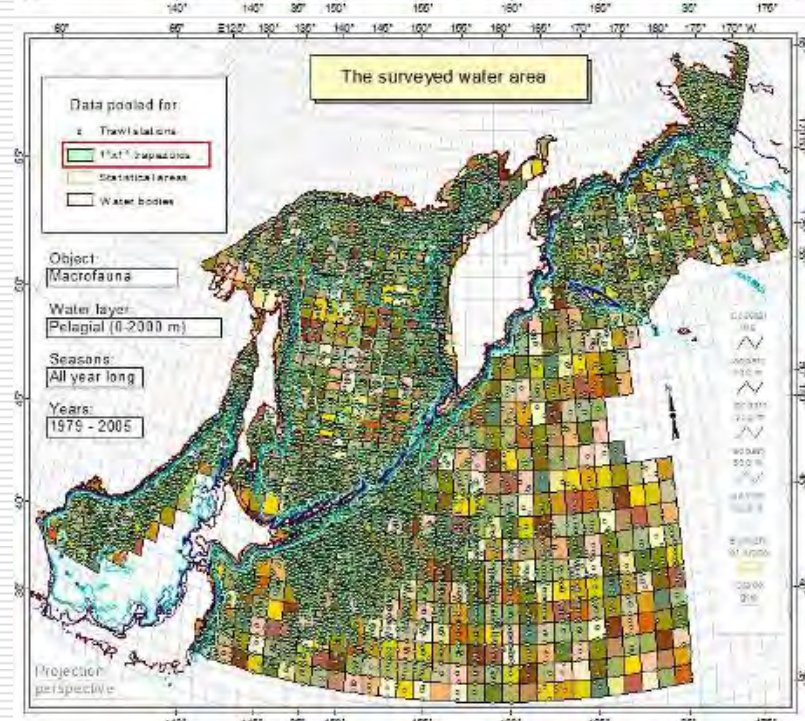
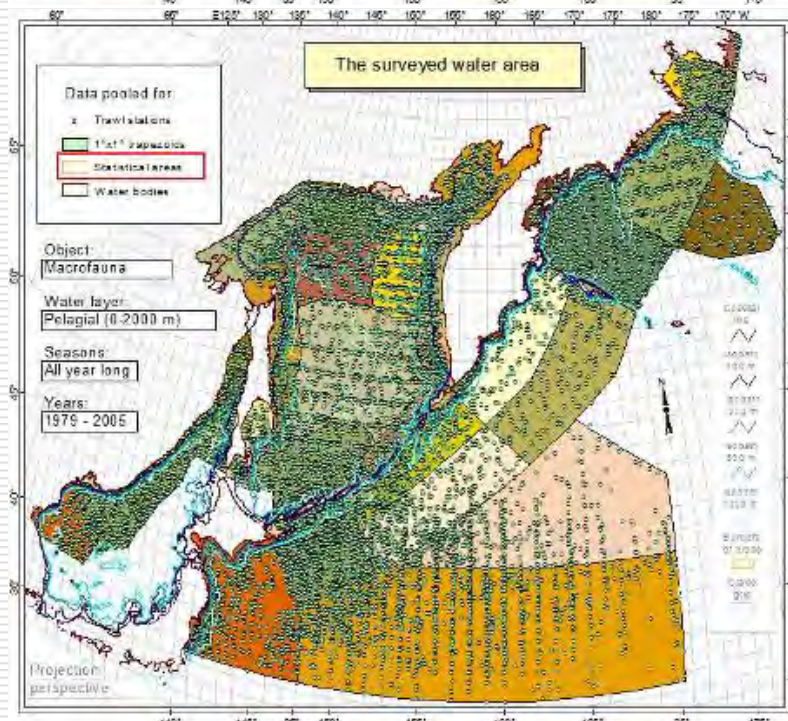
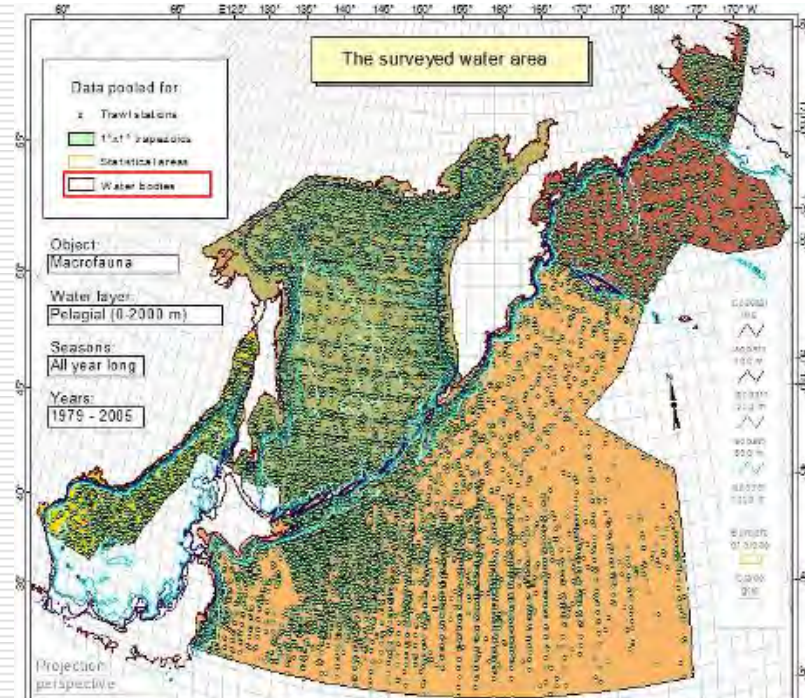
- 1979-1990 – Sardine and pollack epoch of fish abundance
- 1991-1995 – Transition period of sharp abundance reduction
- 1996-2005 – The period of low level and new growth of fish capacity

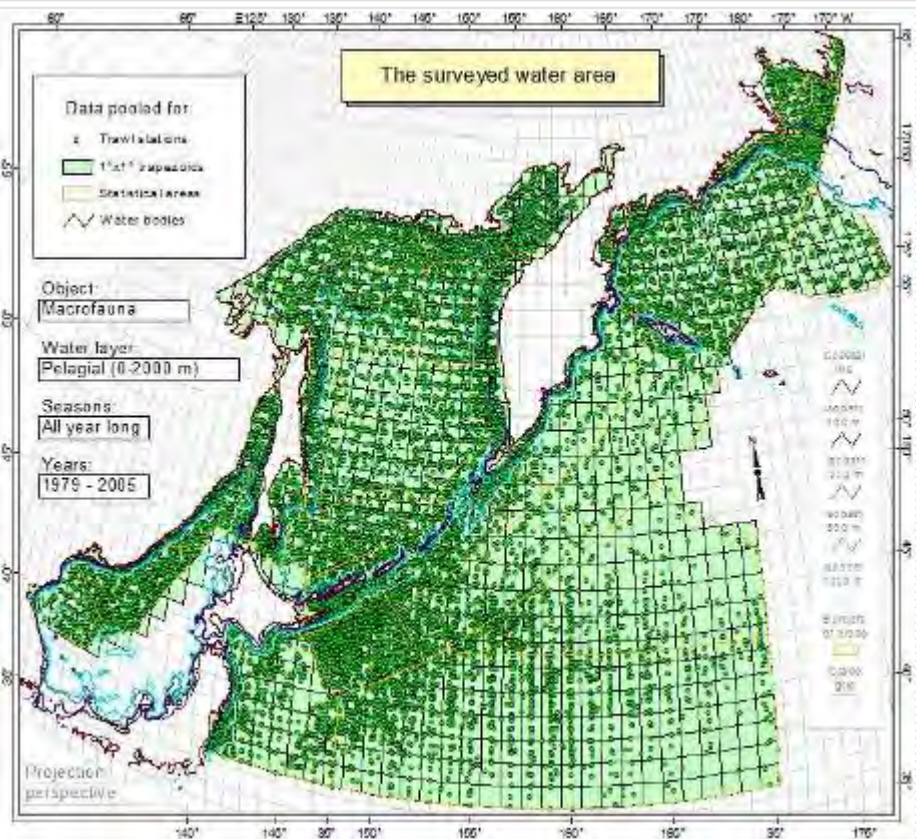
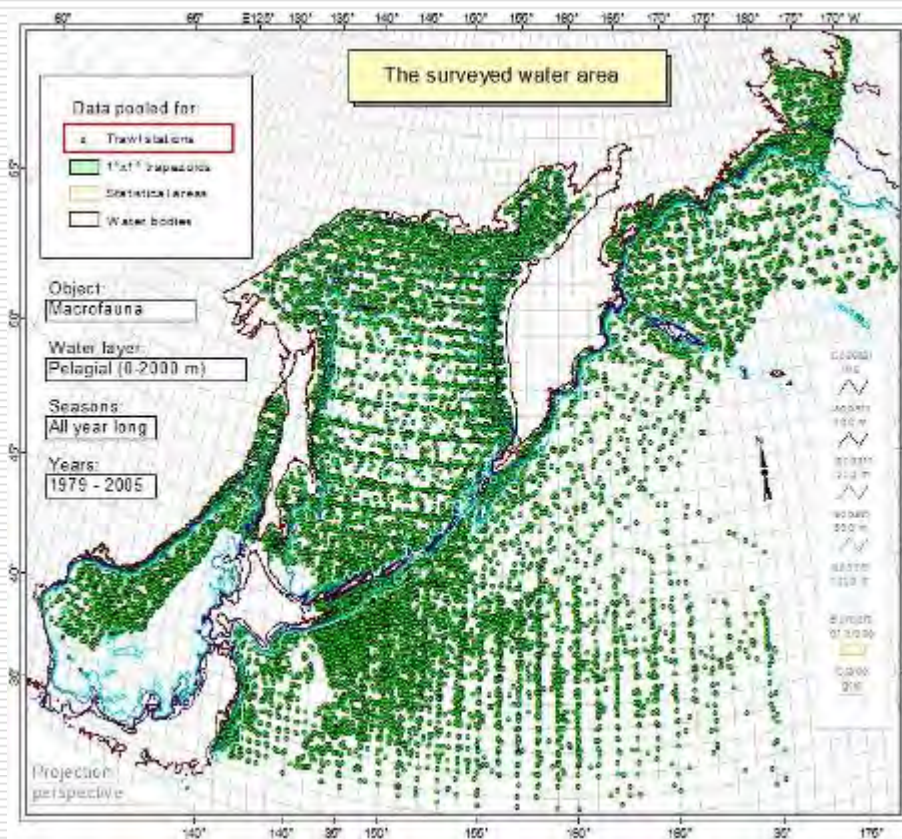
**Macrofauna - all organisms which are caught in a trawl with a fine mesh (10-12 mm) insert 12-15 m in length in the rear of the cod end**

## Composition of the studied fauna (number of species)

Biotope group	Ecological forms	Taxonomic groups	
 Population of the pelagic zone (814)	Nekton (780)	Vertebrates (672)	Mammals, birds and reptiles (0)
			Fishes and cyclostomata (672)
		Invertebrate (142)	Cephalopods (71)
	Crustaceans (37)		
	Jellyfish (24)		
	Ctenophora (2)		
Plankton (34)		Others (8)	

Note: The group “cephalopods” includes squids, cuttlefish, and pelagic octopus; the “crustaceans” are shrimp and prawn; the “others” are pteropods, nudibranchs, pyrosoms, salps, and cyclomaria.

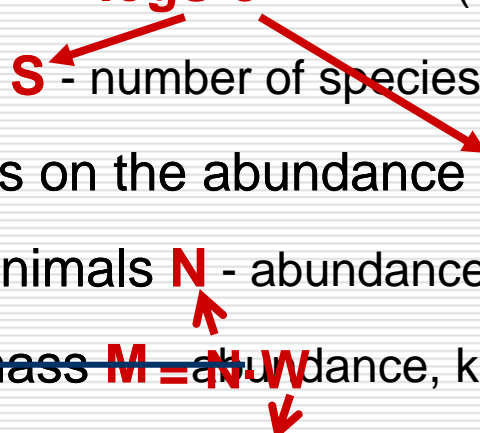




## Subject of investigation

### The integral properties of macrofauna:

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- 1) ~~species diversity  $H = -\sum_{i=1}^S p_i \log p_i$~~  Shannon's index (Shannon, 1948), bit/ind.
  - 2) species richness  $S$  - number of species
  - 3) species evenness on the abundance  $J$  - Pielou's index (Pielou, 1966)
  - 4) total number of animals  $N$  - abundance, ind./km<sup>2</sup>
  - 5) ~~their overall biomass  $M = N \cdot W$~~  abundance, kg/km<sup>2</sup>
  - 6) average individual weight  $W$  - size of an animal, kg/ind.
- 

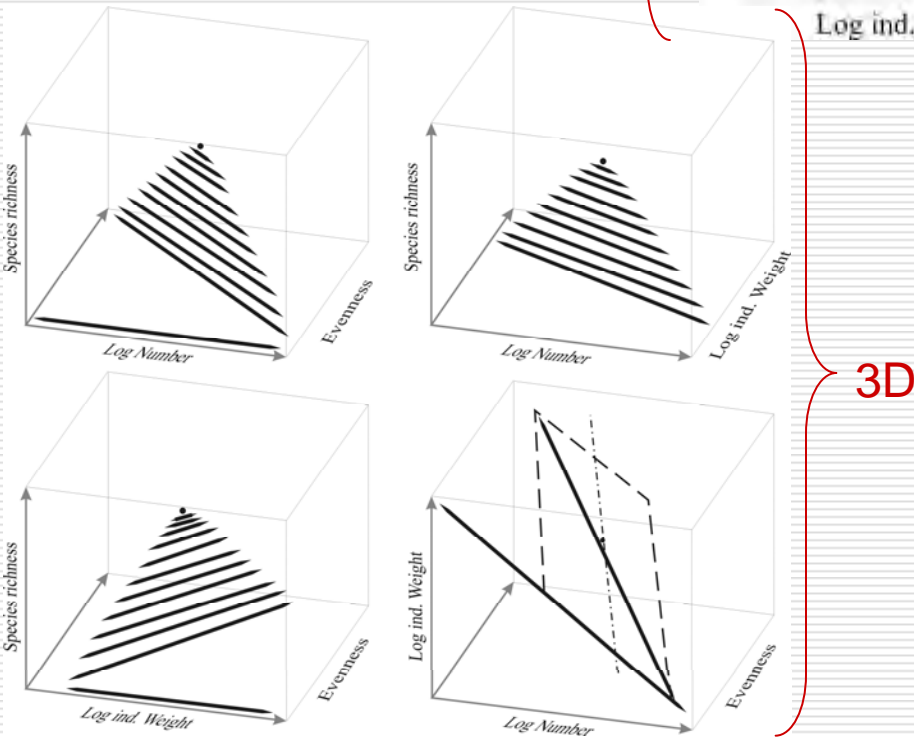
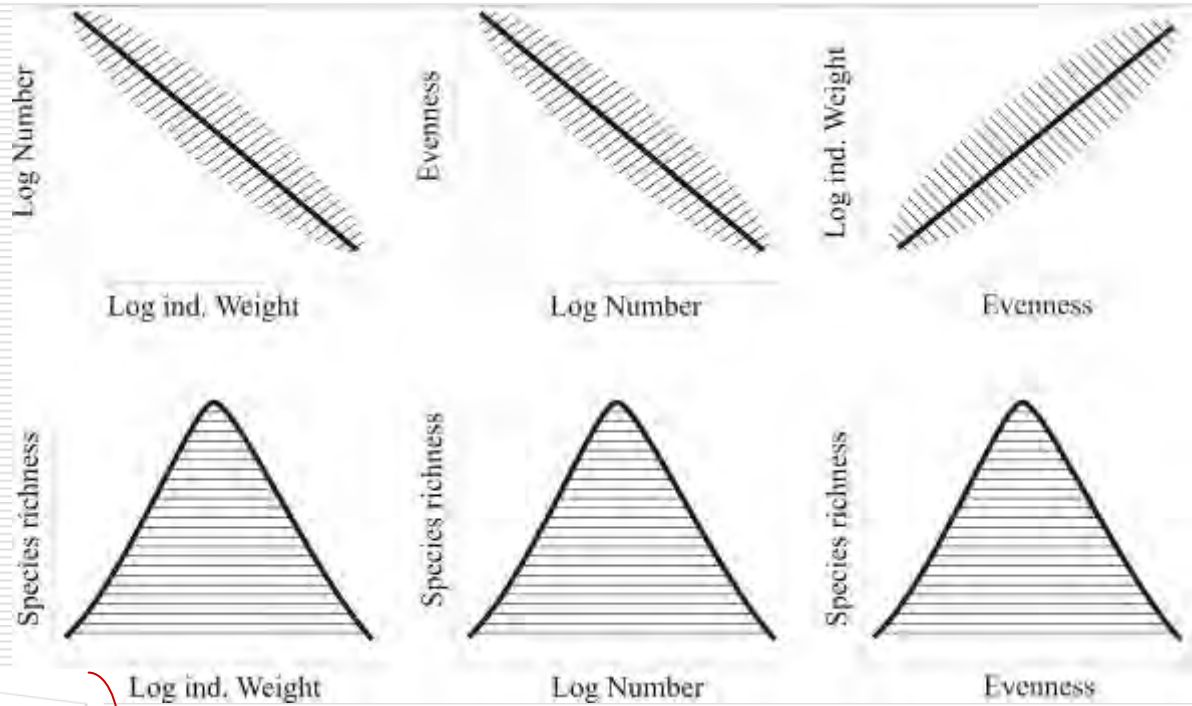
*It turned out that with any method of sampling and pooling of data all these characteristics are interrelated in a special way – neither of them varies in space and time independently of the others (Volvenko, 2009)*

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# 4D virtual space

(with  $\text{Log}N$ ,  $\text{Log}W$ ,  $J$  and  $S$  as coordinate axes)

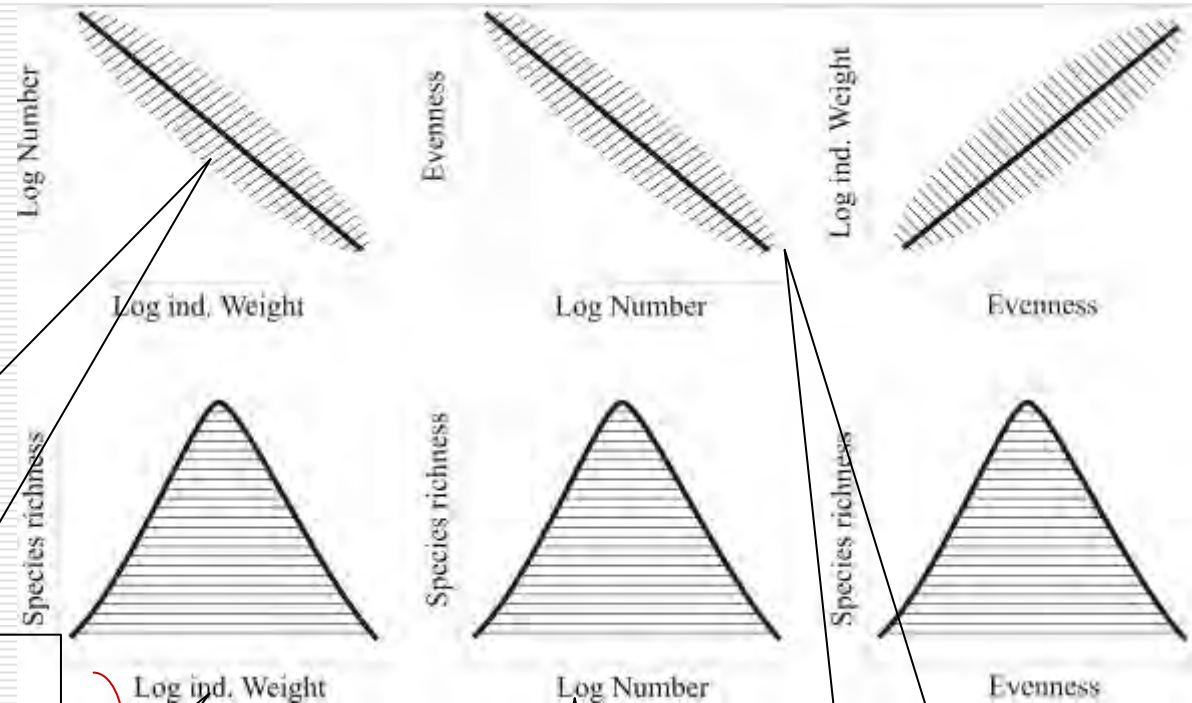
visually represented by six plane projections - 2D graphs or by four 3D space projections



# 4D virtual space

(with  $\text{Log}N$ ,  $\text{Log}W$ ,  $J$  and  $S$  as coordinate axes)

visually represented by six plane projections - 2D graphs or by four 3D space projections



2D

3D

The population density of animals is inversely proportional to its size or body weight (Mohr, 1940; Damuth, 1981, 1987; Peters, 1983; Peters, Raelson, 1984; Blackburn et al., 1993; Currie, Fritz, 1993; Blackburn, Lawton, 1994; Strayer, 1994; Cyr et al., 1997a, b; Navarette, Menge, 1997; Enquist et al., 1998; Volvenko, 2009)

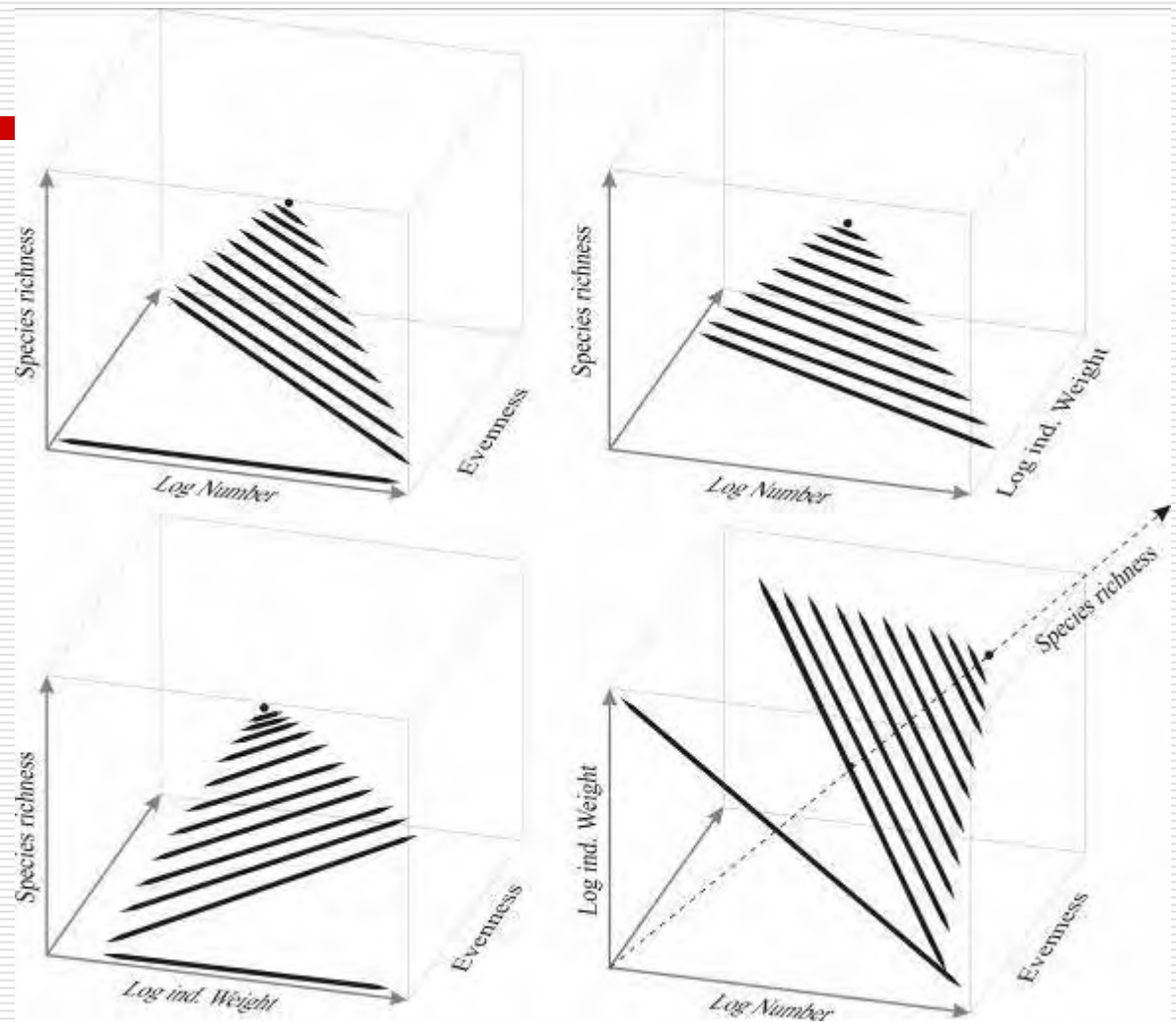
The species richness is maximum for average size classes (Hutchinson, MacArthur, 1959; Stanley, 1973; May, 1978, 1986, 1988; Brown et al., 1993; Blackburn, Gaston, 1994a, b; Brown, 1995; Greenwood et al., 1996; Siemann et al., 1996; Navarette, Menge, 1997; Fa, Fa, 2002; Volvenko, 2008, 2009)

The species richness is maximum for average abundance value (Preston, 1948; Williams, 1953; Whittaker, 1965; May, 1975; Sugihara, 1980; Greenwood et al., 1996; Volvenko, 2008, 2009)

The evenness of the species distribution is in negative correlation with abundance (Fujita et al., 1993; Drobner et al., 1998; Колпаков, 2003; Buzas, Hayek, 2005; Bock et al., 2007; Volvenko, 2009)

## 3D projections of 4D virtual space

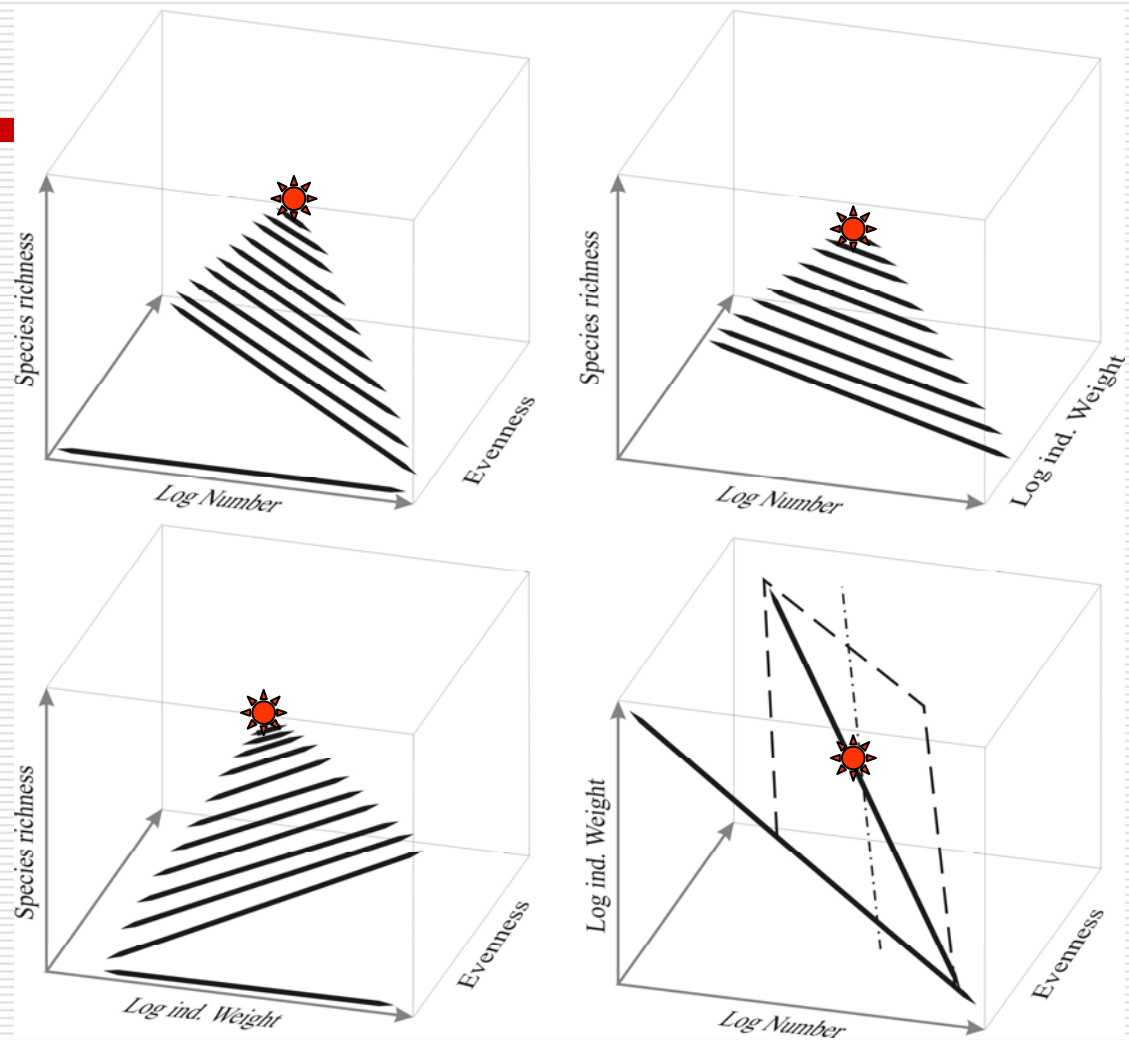
This is the variables  
intercorrelation  
structure



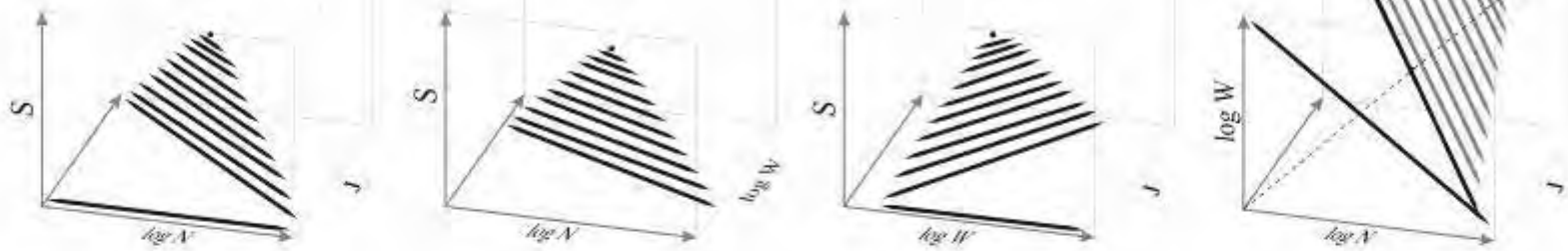


## 3D projections of 4D virtual space

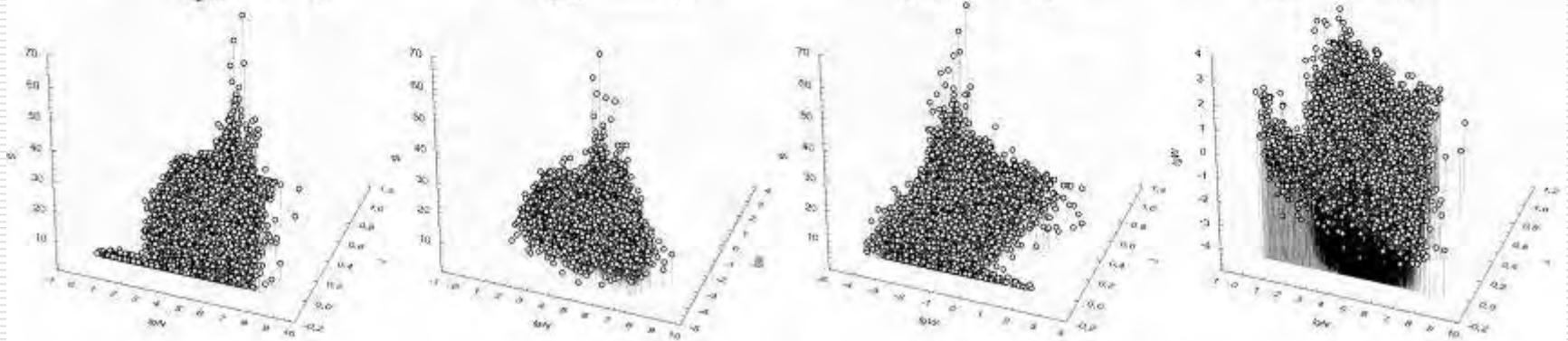
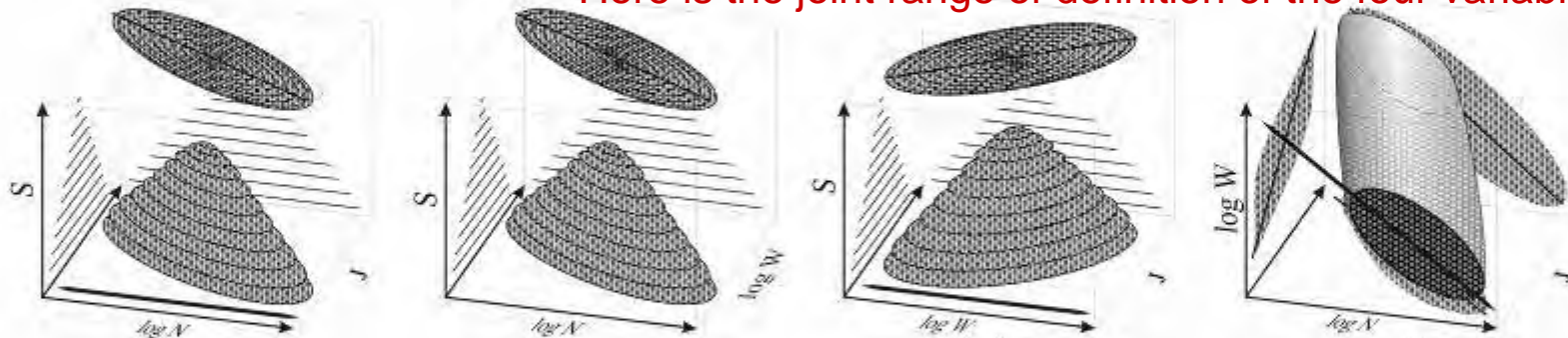
This is the variables  
intercorrelation  
structure



This is the variables intercorrelation structure



Here is the joint range of definition of the four variables

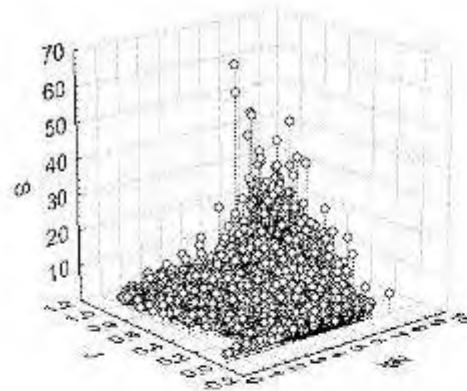


The points, which correspond to certain measurements, are placed not only on the lines, but form a cloud along the segments

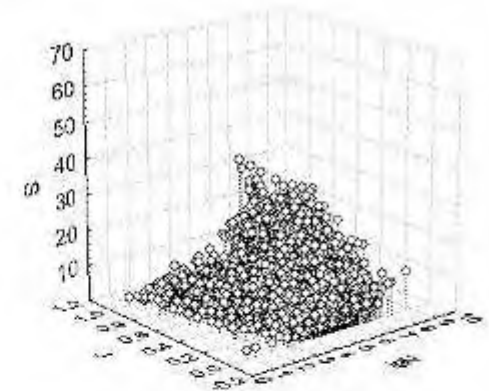
## 3D distributions describing interrelation between logN, J, and S of pelagic macrofauna in northwestern Pacific:

for the different water bodies, seasons, long-term periods, water layers, samples collected over various depths, and on various distances from the shoreline

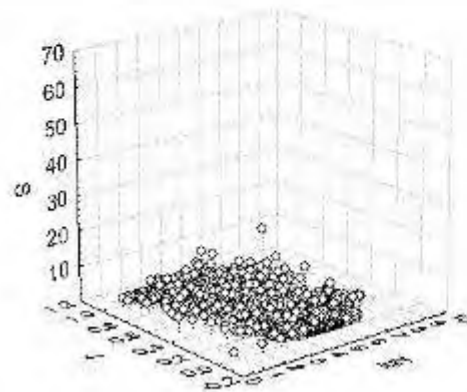
Each point on the graphs corresponds to one sample (a trawl station)



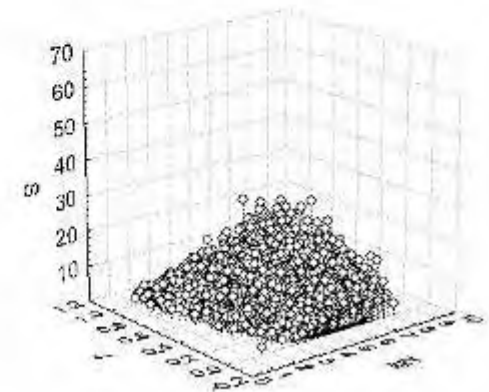
Ocean waters



Bering sea



Japan (East) sea

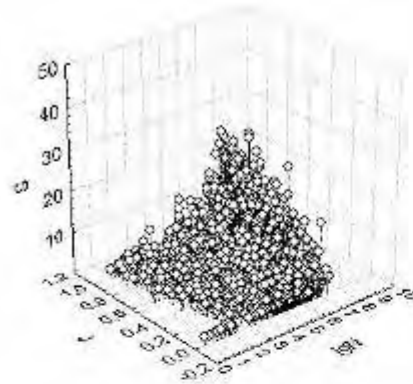


Okhotsk sea

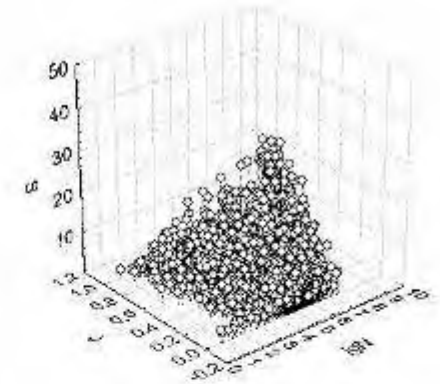
## 3D distributions describing interrelation between $\log N$ , $J$ , and $S$ of pelagic macrofauna in northwestern Pacific:

for the different water bodies, seasons, long-term periods, water layers, samples collected over various depths, and on various distances from the shoreline

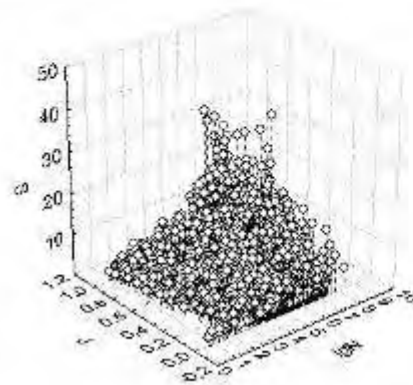
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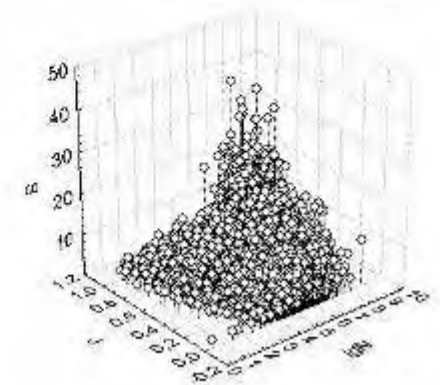
Winter



Spring



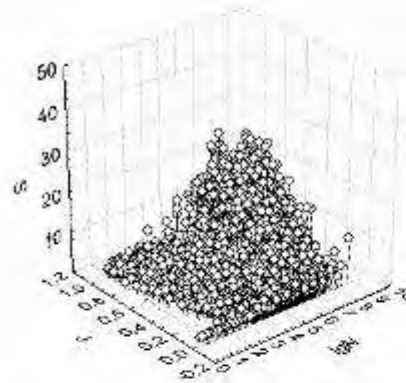
Summer



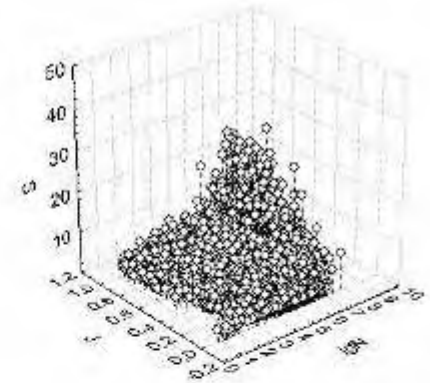
Autumn

## 3D distributions describing interrelation between logN, J, and S of pelagic macrofauna in northwestern Pacific:

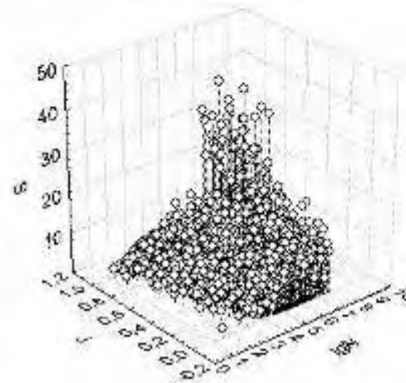
for the different water bodies, seasons, long-term periods, water layers, samples collected over various depths, and on various distances from the shoreline



1979-1990



1991-1995



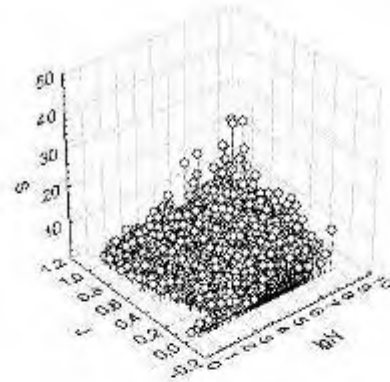
1996-2005

Each point on the graphs corresponds to one sample (a trawl station)

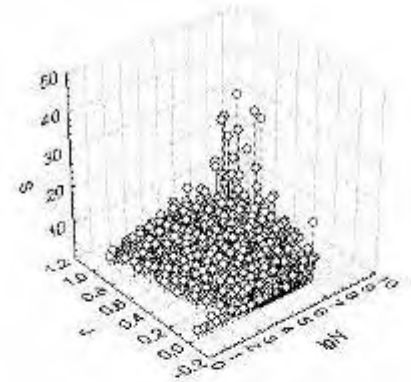
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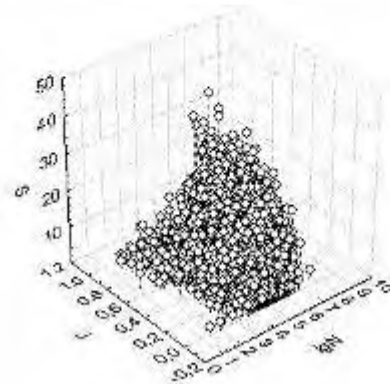
Each point on the graphs corresponds to one sample (a trawl station)



0-50 m



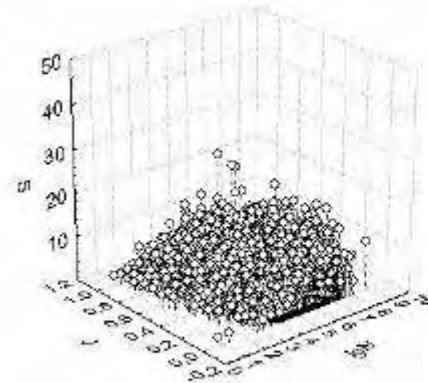
50-200 m



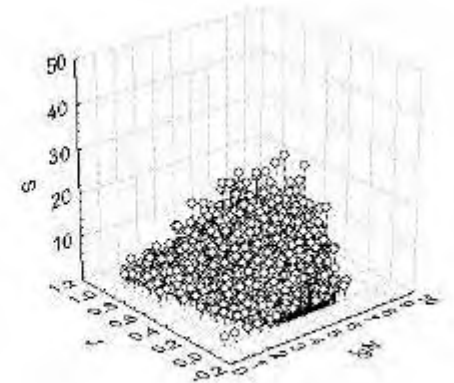
> 200 m

## 3D distributions describing interrelation between logN, J, and S of pelagic macrofauna in northwestern Pacific:

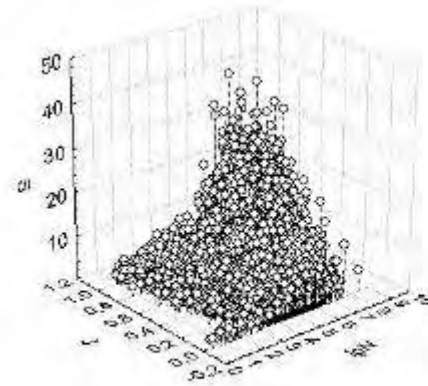
for the different water bodies, seasons, long-term periods, water layers, samples collected over various depths, and on various distances from the shoreline



0-200 m



200-1000 m



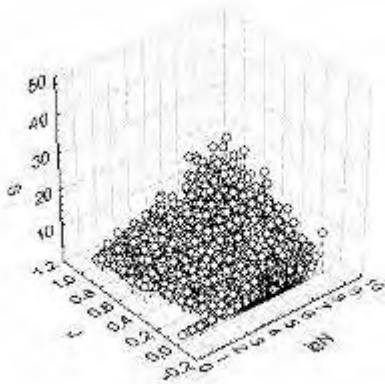
> 1000 m

Each point on the graphs corresponds to one sample (a trawl station)

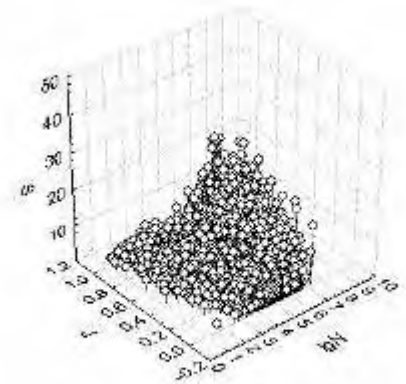
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for the different water bodies, seasons, long-term periods, water layers, samples collected over various depths, and on various distances from the shoreline

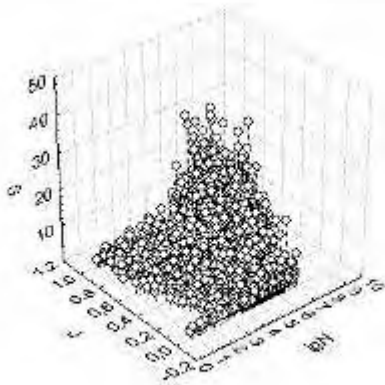
Each point on the graphs corresponds to one sample (a trawl station)



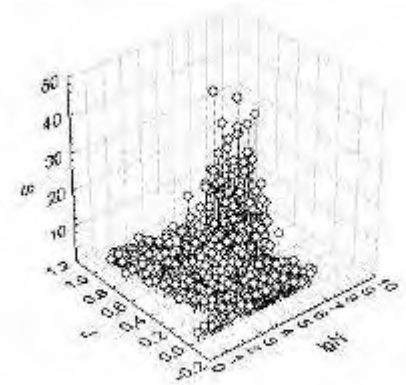
0-100 km



100-200 km



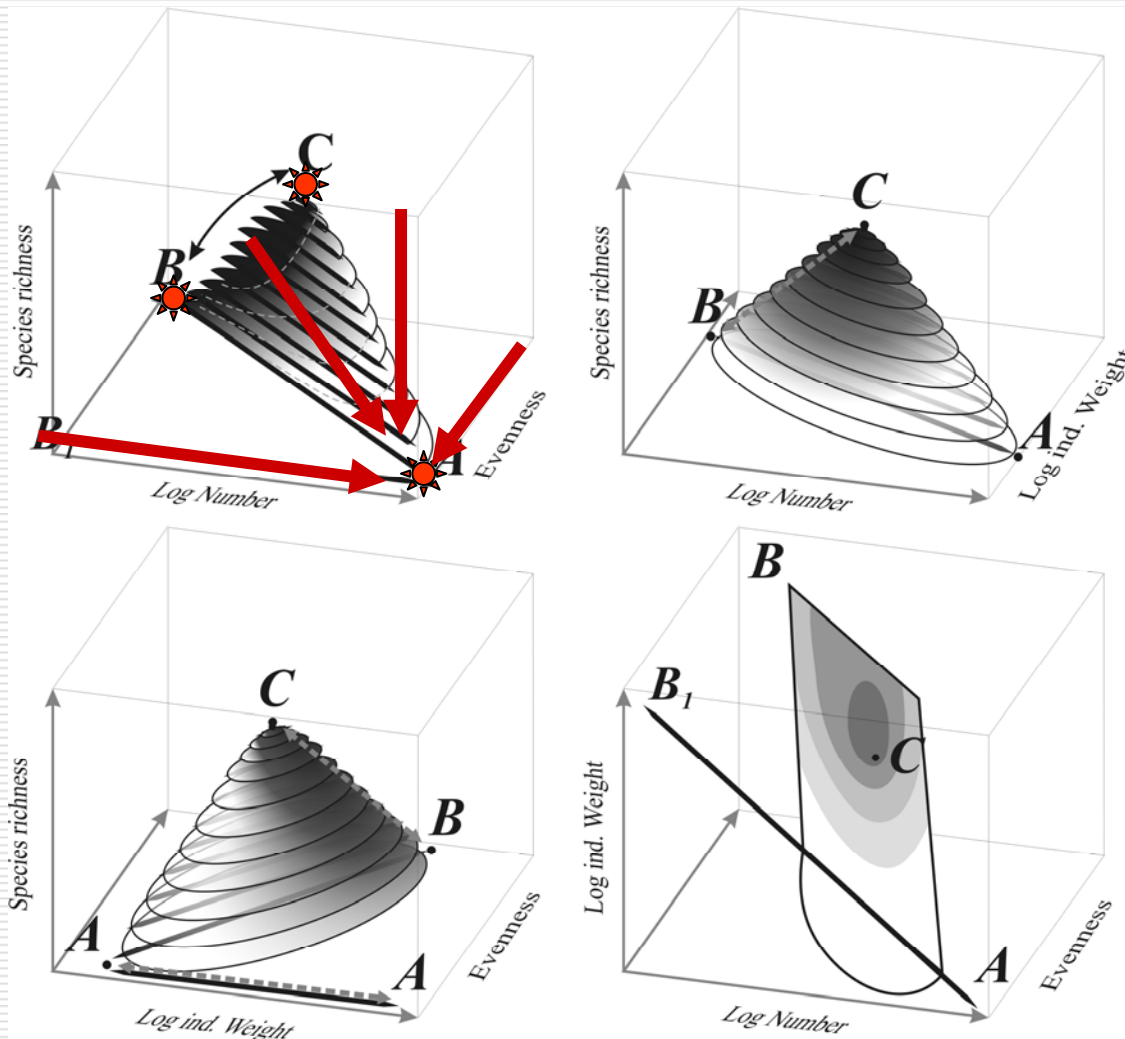
200-500 km



> 500 km



## Four 3D projections of mutual interrelations for integral parameters of pelagic macrofauna

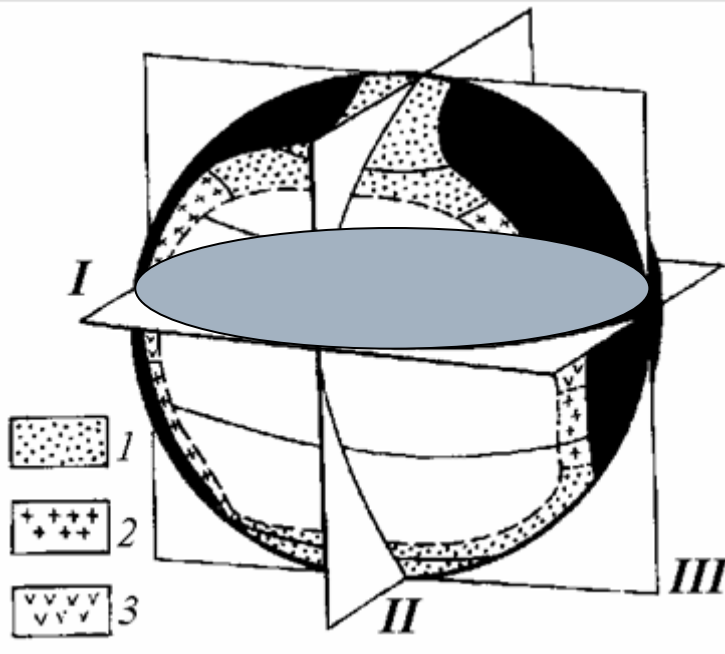


The letters A-C here mark the points which describe extreme states of biocenotic system, typical for some its positions in real space and time.

The first and last figures are given in section for display of their internal structure.

The color intensity shows the change in diversity H (decrease from dark to light)

**Biological structure of the ocean** (Zenkevich, 1948; Bogorov, 1959, 1970; Bogorov, Zenkevich, 1966)

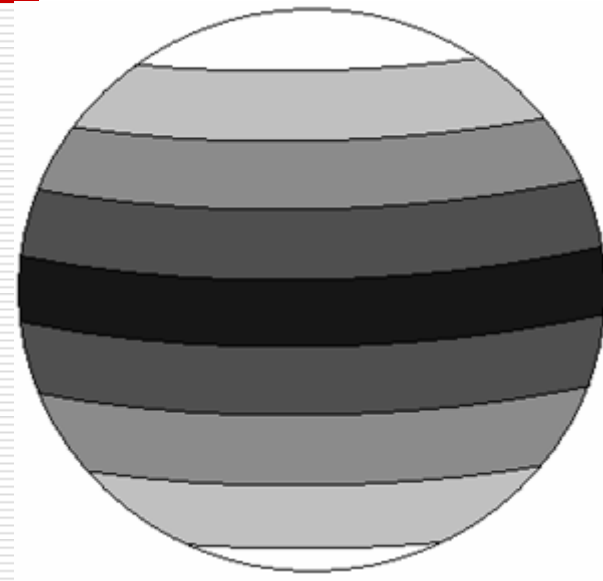
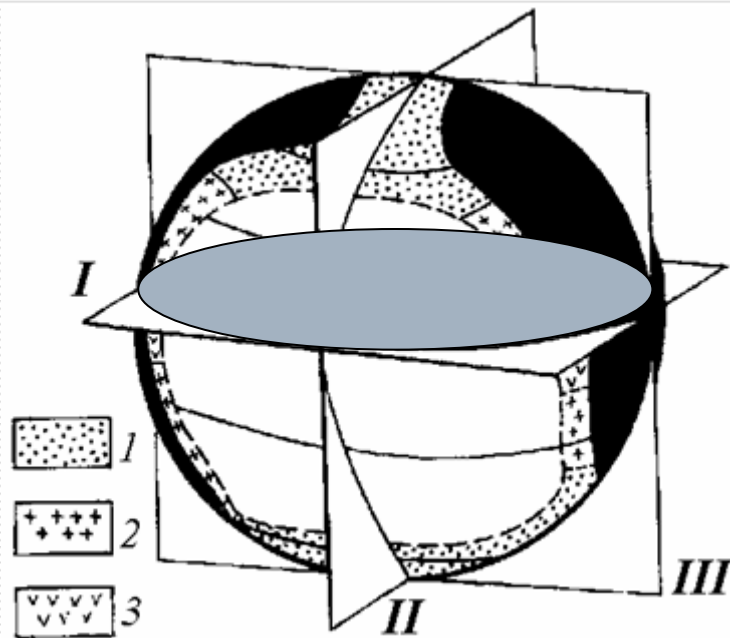


**Symmetry planes** from  
(Zenkevich, 1948):

*I* – equatorial, *II* & *III* – meridional

Zones: 1 – polar, 2 – temperate, 3  
- equatorial

**Biological structure of the ocean** (Zenkevich, 1948; Bogorov, 1959, 1970; Bogorov, Zenkevich, 1966)



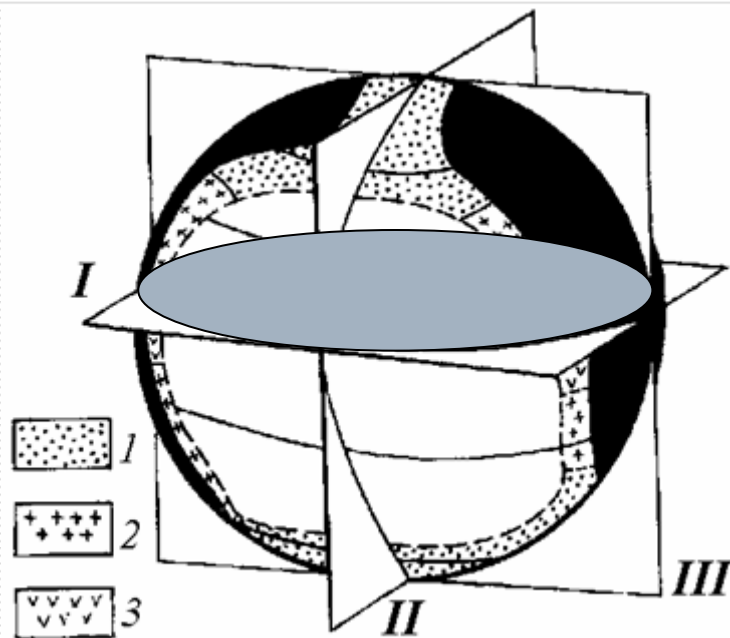
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*I* – equatorial, *II* & *III* – meridional

Zones: 1 – polar, 2 – temperate, 3  
- equatorial

Solar energy, species richness *S*  
(Humboldt-Wallace's law)

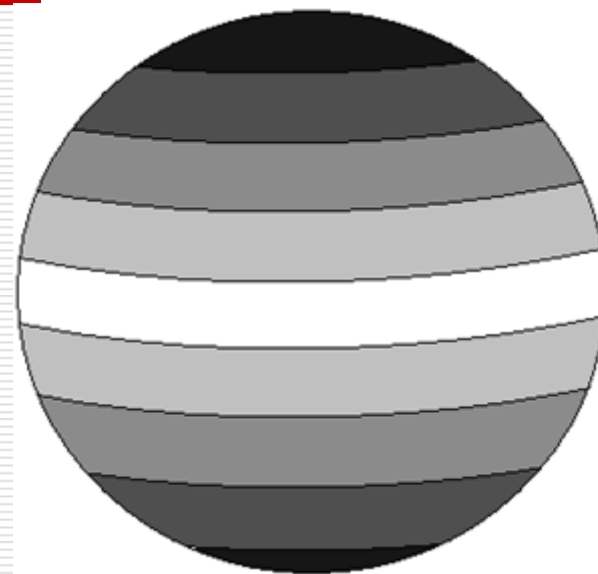
**Biological structure of the ocean** (Zenkevich, 1948; Bogorov, 1959, 1970; Bogorov, Zenkevich, 1966)



**Symmetry planes** from  
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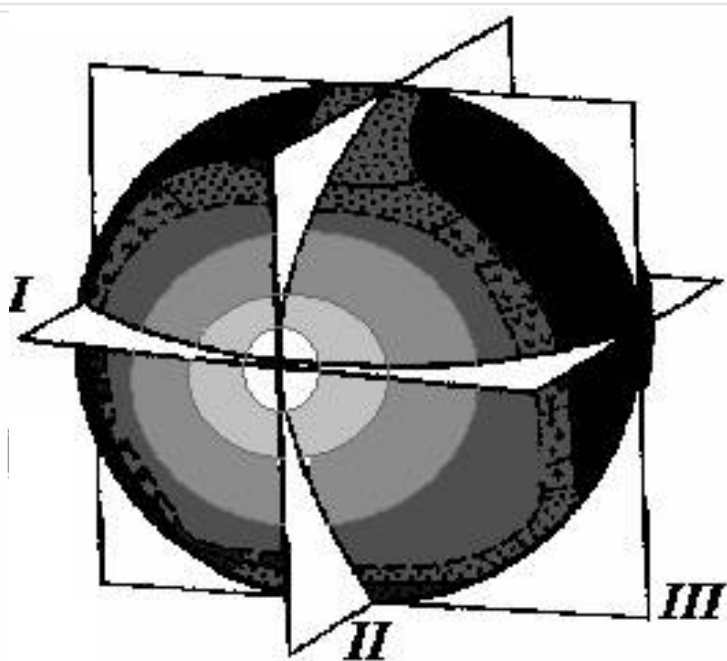
*I* – equatorial, *II* & *III* – meridional

Zones: 1 – polar, 2 – temperate, 3  
- equatorial



The average size of the animals *W*  
(Bergman's rule)

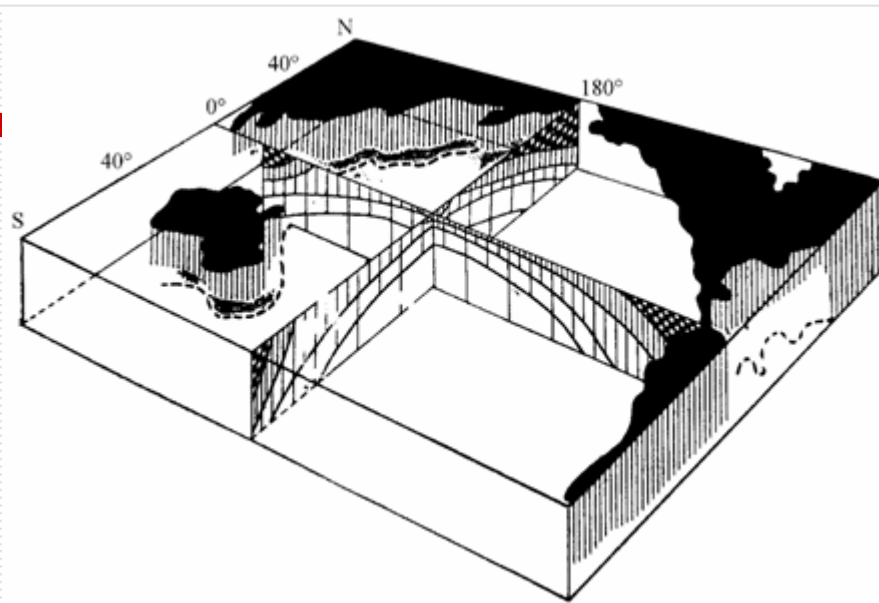
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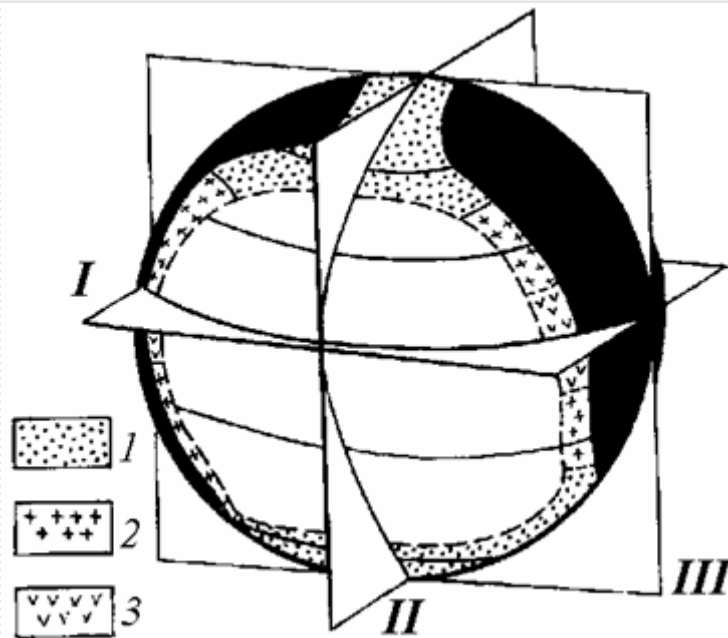
Zones: 1 – polar, 2 – temperate, 3 – equatorial



**Pacific symmetry planes** from (Bogorov, 1970)

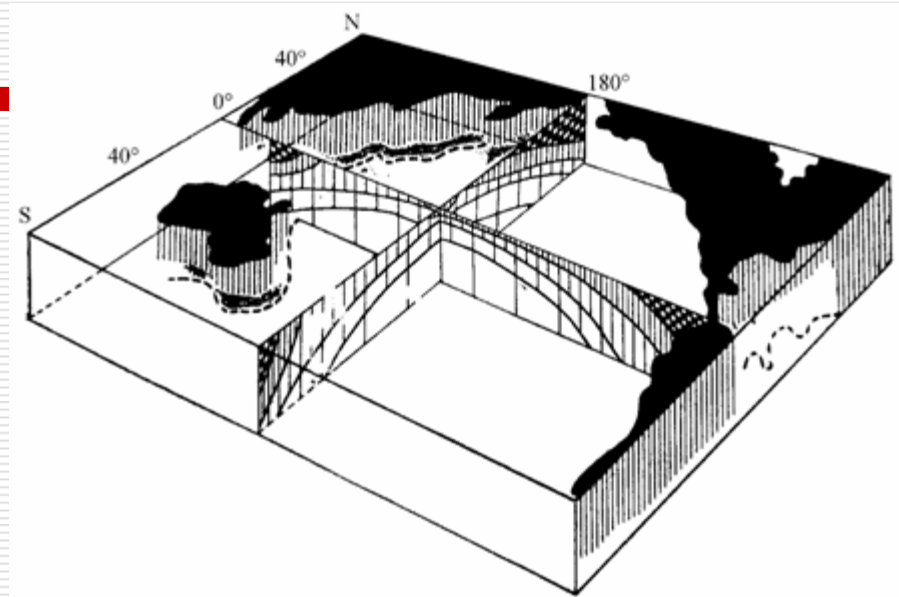
By shading density the symmetry of waters productivity is shown

**Biological structure of the ocean** (Zenkevich, 1948; Bogorov, 1959, 1970; Bogorov, Zenkevich, 1966)



**Symmetry planes** from (Zenkevich, 1948):

*I* – equatorial, *II* & *III* – meridional  
Zones: 1 – polar, 2 – temperate, 3 – equatorial

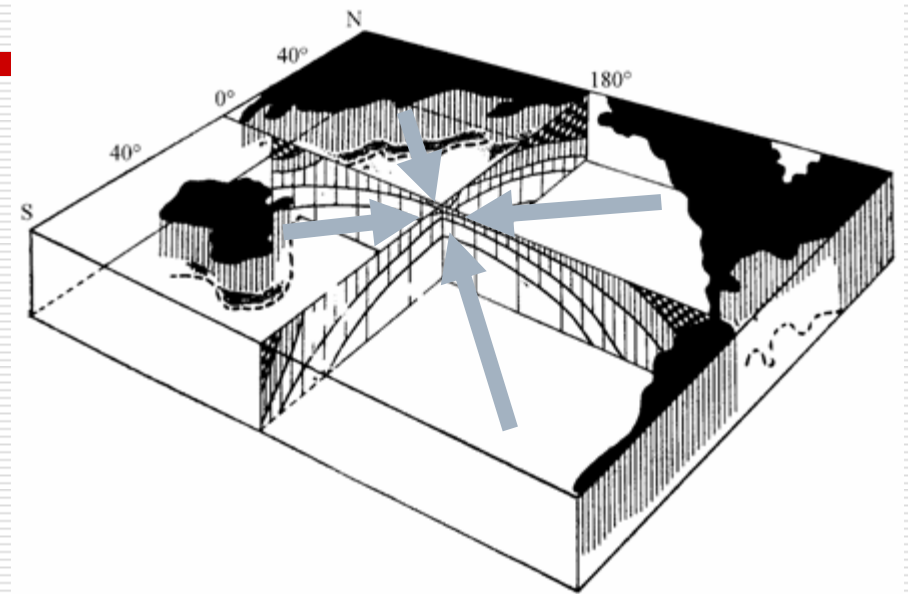


**Pacific symmetry planes** from (Bogorov, 1970)

By shading density the symmetry of waters productivity is shown

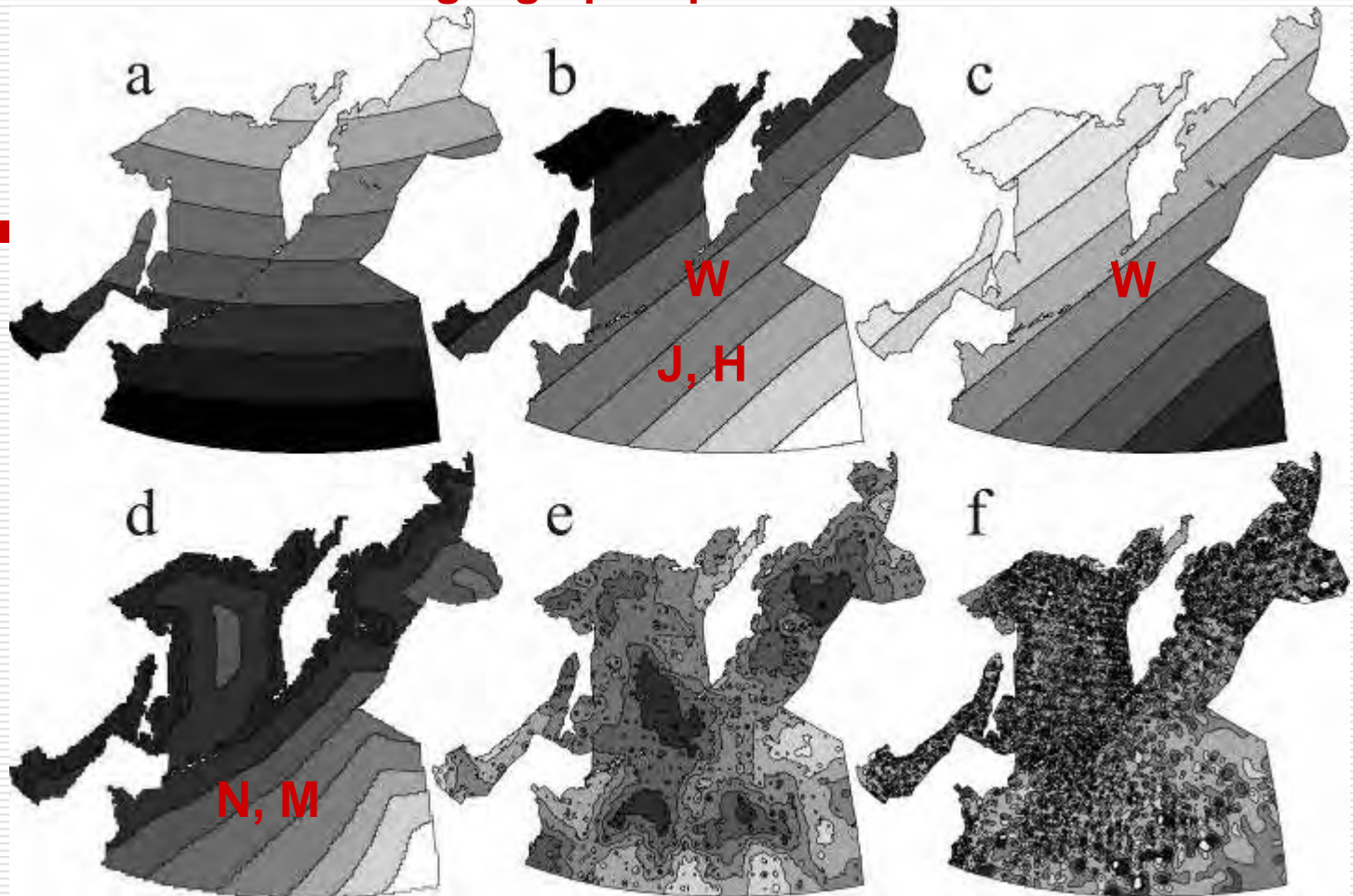
## Biological structure of the ocean (Zenkevich, 1948; Bogorov, 1959, 1970; Bogorov, Zenkevich, 1966)

It is well known that neritic and shelf regions are characterized by higher rates of primary production, biomasses of phyto- and zooplankton, benthos, fish and seabirds (Bogorov, Zenkevich, 1966; Bogorov, 1967, 1970; Moiseev, 1969, 1977; Koblents-Mishke et al., 1970; Zenkevich et al., 1971; Shuntov, 1972; Vinogradov, 1977)



The arrows indicate the direction of productivity reduction from the periphery to the center of the ocean

## Examples of hierarchical levels for geographic patterns:

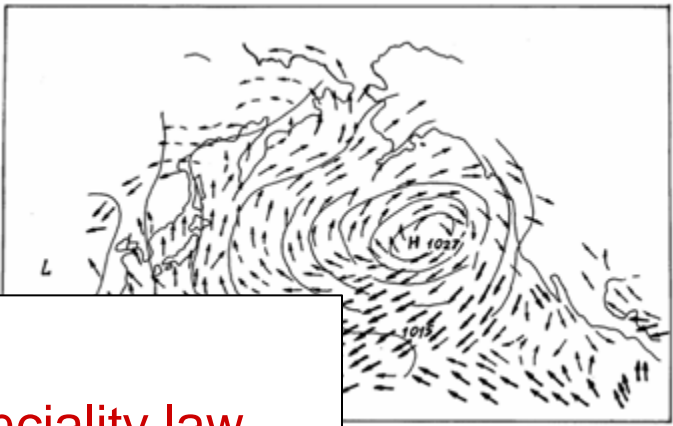
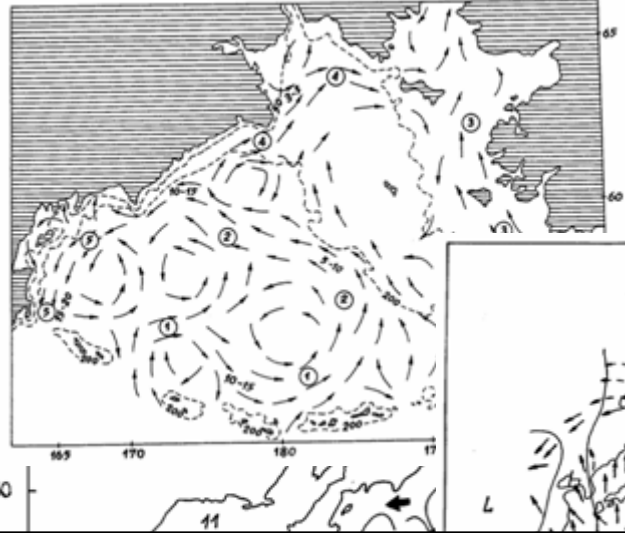
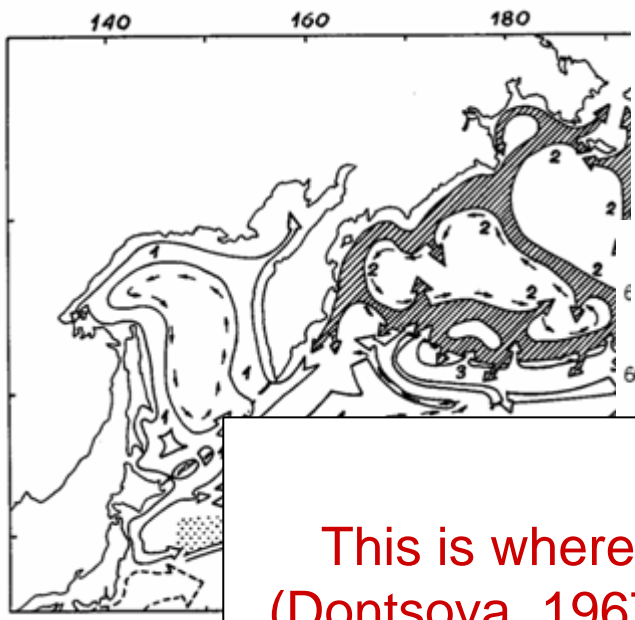


a) - latitudinal zonation on a global level, b) c) - circumcontinental zonation on the global level, d) - circumcontinental zonation on a regional scale, e) - the local level, where zonation is not observed, f) - sublocal level at which hardly differ or do not see any pattern

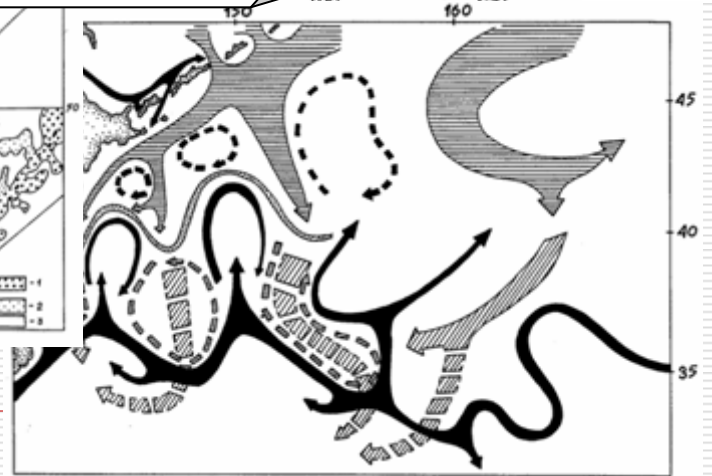
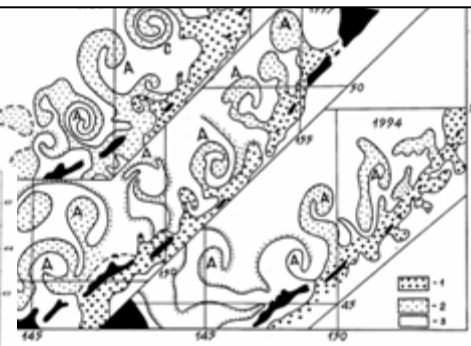
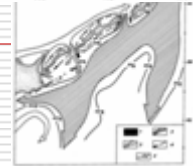
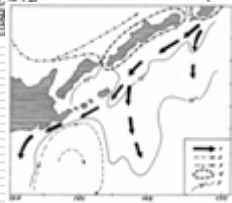
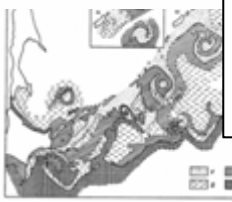


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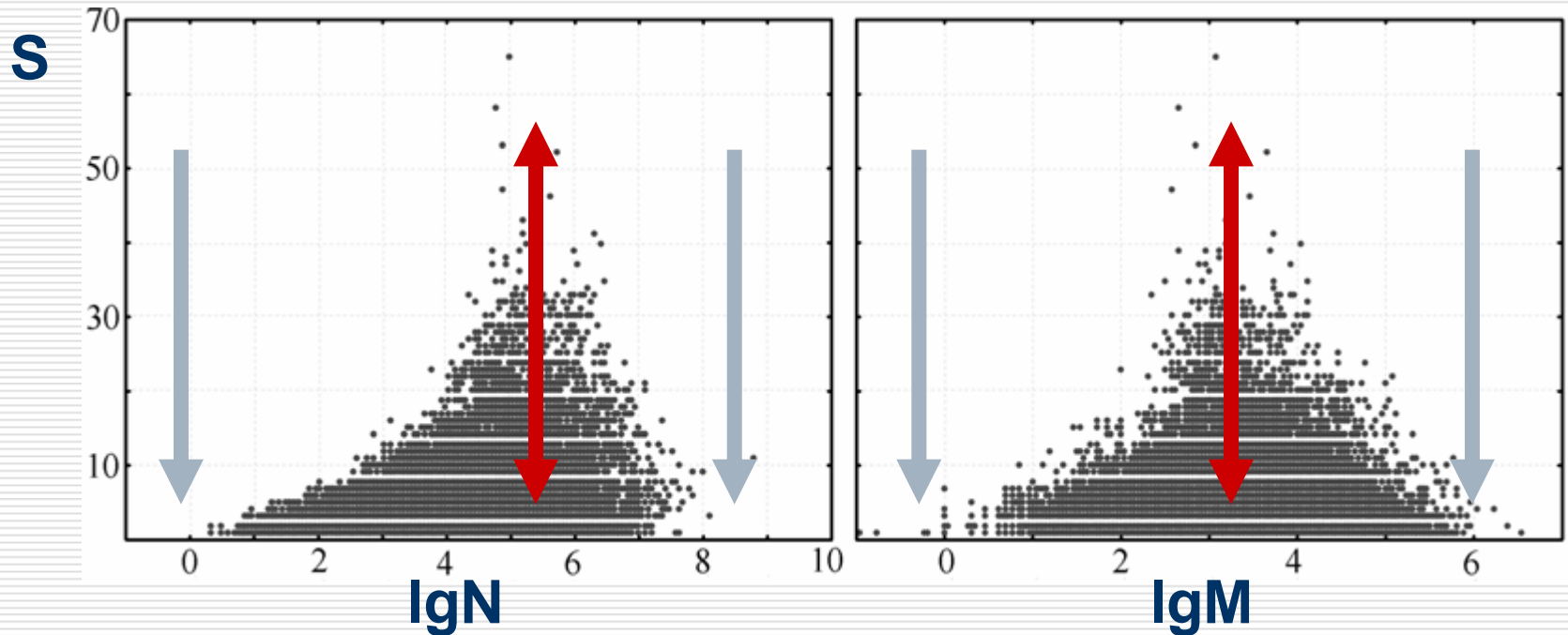
The absence of any latitudinal zonality display in the region is conditioned by the fact that meridional, and not latitudinal, air and water mass transport prevail here, unlike in southern regions. Collision and interaction between northern and southern, cold and warm waters creates a number of local whirlpools, fluid fronts, eddies



This is where Neustruev's provinciality law (Dontsova, 1967; Volvenko, 2009) proves itself



The reason for the absence of circum-continental zonality of species richness ( $S$ ) display in the region:



**S** is connected with **N** and **M** so that **the species richness cannot be high either by high population density, or by a low one, either in shore, or far in the ocean**

The average abundance is necessary but insufficient condition for maximization of  $S$

# Ecosystem = Biocenosis + Biotope

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Add abiotic  
↑  
factors

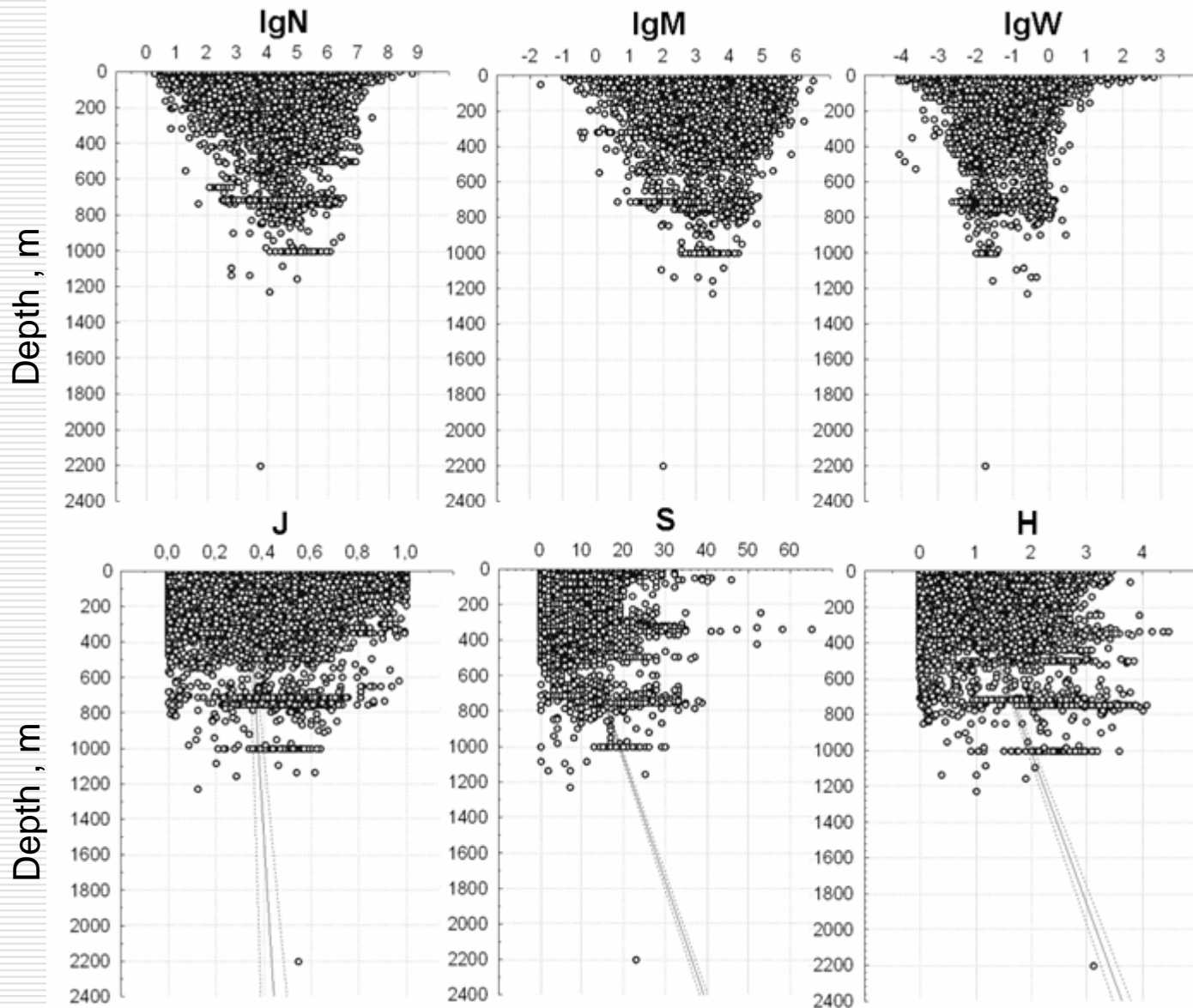
- Ecosystem level
- Biogeographic level
- Biocenotic level

## The supplement to Zenkevich-Bogorov's concept of biological structure of the ocean

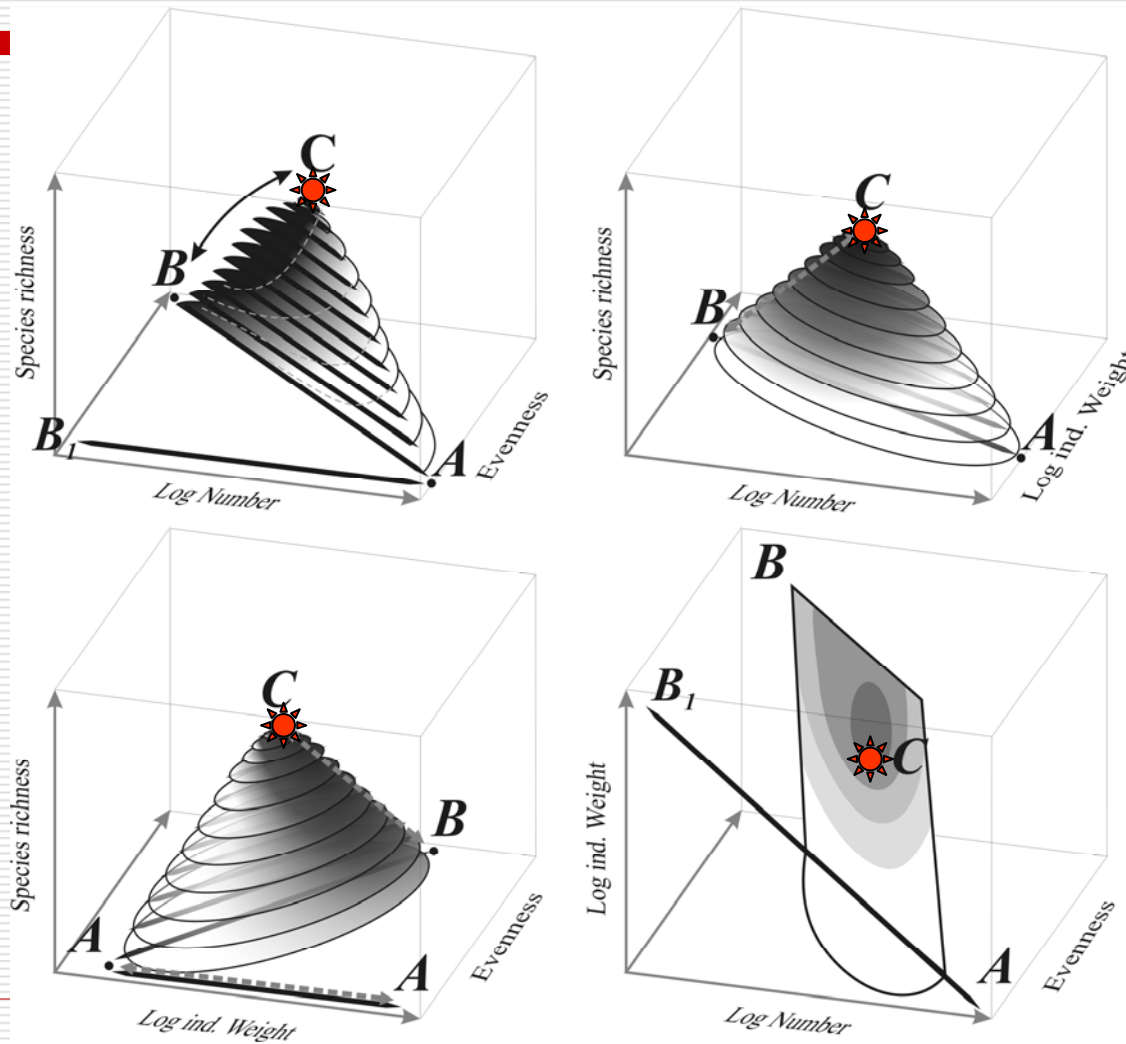
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In the directions from the ocean center to the periphery, the environment stability declines, while the water exchange intensity increases, whereby the environment ecologic capacity grows up. Accordingly, the primary production and biogeochemical cycle intensity as a whole increases, as well as animal's number, biomass and variations of their size, numerical and weighting prevalence of few dominant species over the others. At the same time, species diversity decreases.

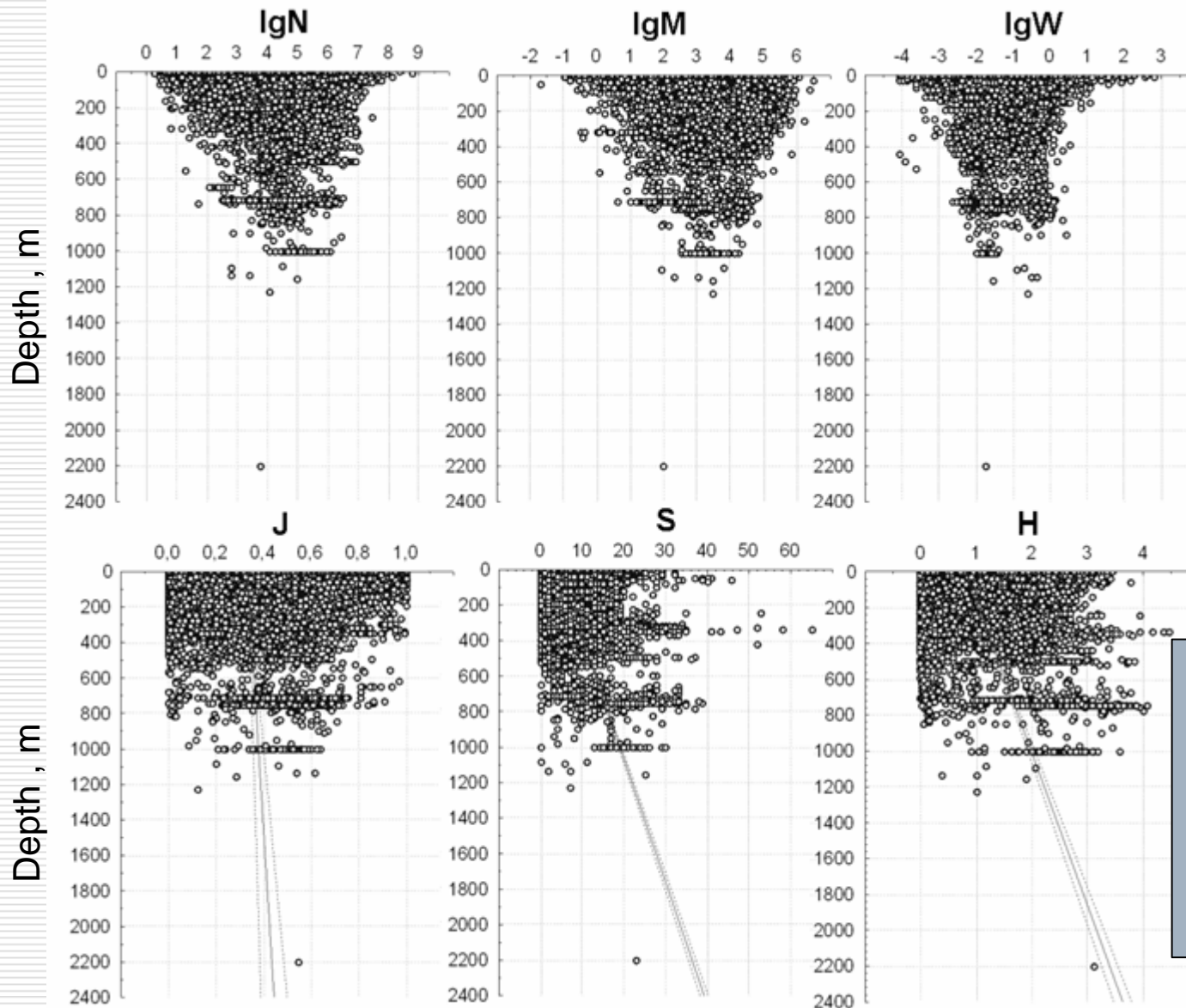
# The vertical distribution of integral characteristics



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The depth increase corresponds to the movement from the poles to the tropics (Whittaker, 1970)



## The supplement to the concept of biological structure of the ocean with taking into account the vertical axes of the spatial variability

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The environment conditions stability decreases and the water exchange intensity increases in the depth to surface direction, the same as by moving from the equator to the high latitudes and from the ocean center to its periphery. The environment ecologic capacity and intensity of the biogeochemical cycle as a whole increase. As the depth decreases, the primary production, variability of the population density and size of animals, numerical and weighting prevalence of few dominants over the others increase respectively, while species richness and diversity decrease

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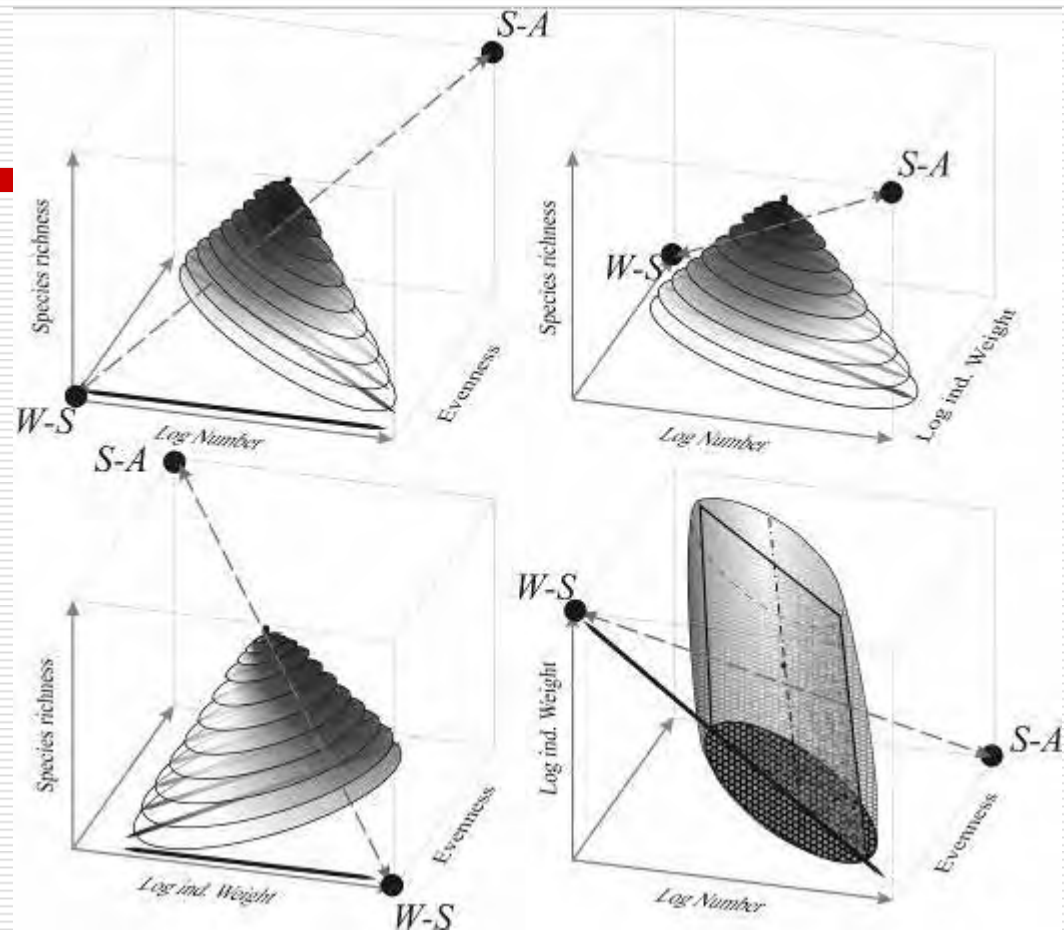
In the **seasonal dynamics** of integral characteristics, one could trace the following tendencies

The winter-spring period is characterized by S, J and H reduction, as well as reduction of hydrobionts abundance and increase of their W

The summer-autumn period is characterized by opposite transformations

W-S – winter-spring period

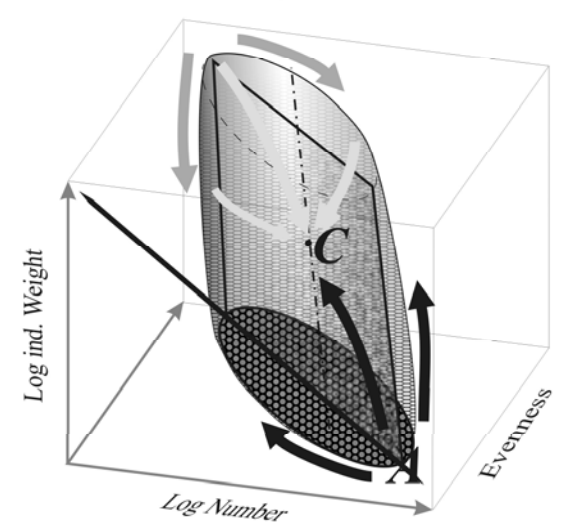
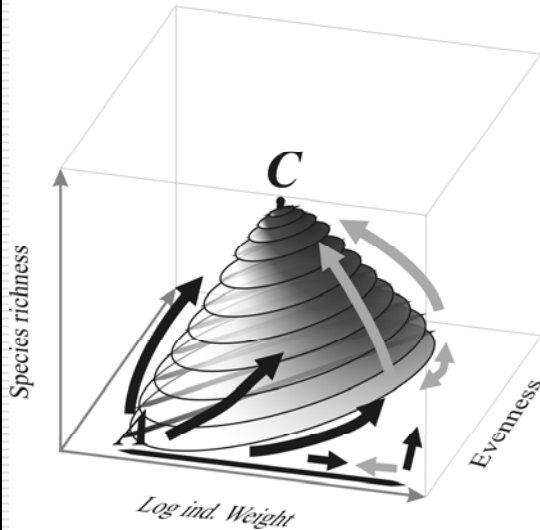
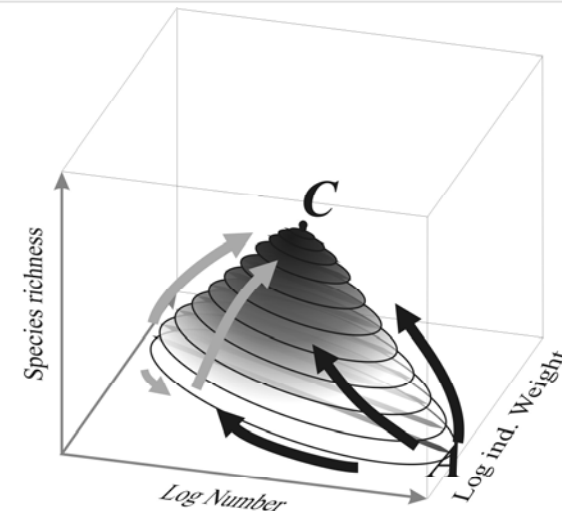
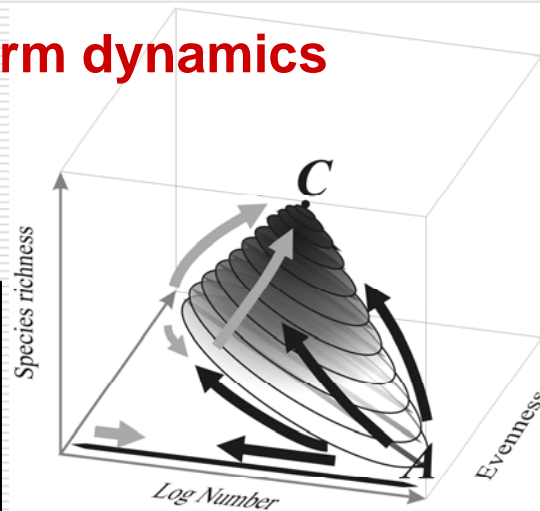
S-A – summer-autumn period



Two extreme points, situated in the opposite sections of each coordinates system, correspond to the directionality of such changes in all analyzed spaces of integral characteristics

## The tendencies of long-term dynamics of all analyzed indices of the system

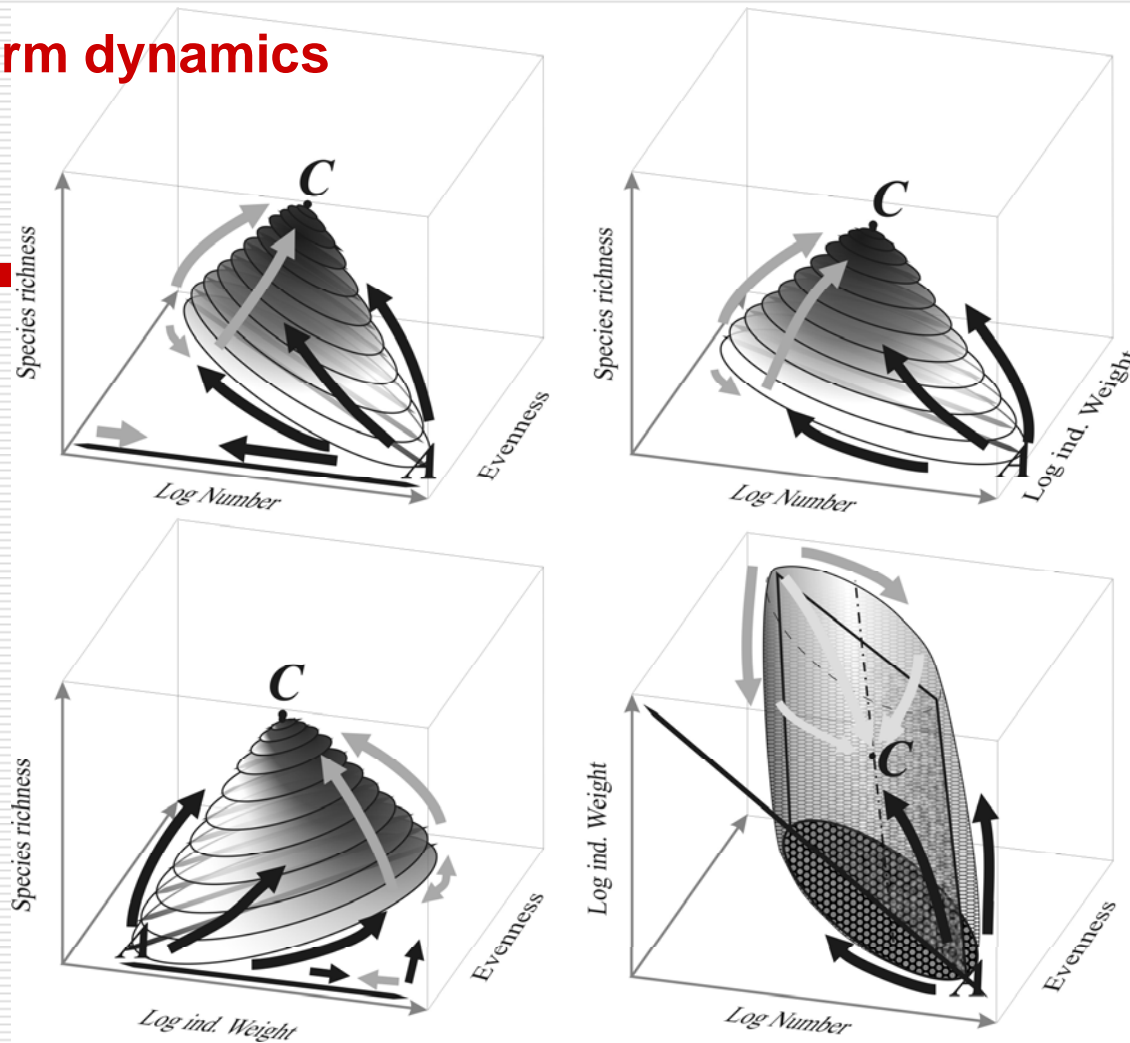
It has previously been shown that dynamic water exchange and high water productivity correspond to point A, while weak water exchange, abiotic conditions stability and low primary production correspond to point C. It totally conforms to the hypothesis (Shuntov, 1986, 1998, 2001, Shuntov et al., 1998; Volvenko, Titiayeva, 1999; Volvenko, 2004) that large-scale biocoenotic alterations in the northwestern Pacific are connected with the ratio of the shelf and oceanic water landscape areas



The centrifugal tendency from point A corresponds to the reduction of dominants abundance, while the centripetal tendency to point C corresponds to the growth of small mesopelagic species share

## The tendencies of long-term dynamics of all analyzed indices of the system

Dark arrows show the transition from the "epoch of high abundance" (1980s) to the "stage of the resources reduction" (1991-1995), and light arrows – the following transition to the "epoch of lowered productivity" (1996-2005). The extreme states of the system discussed before (talking about spatial variability) are marked by the letters A and C

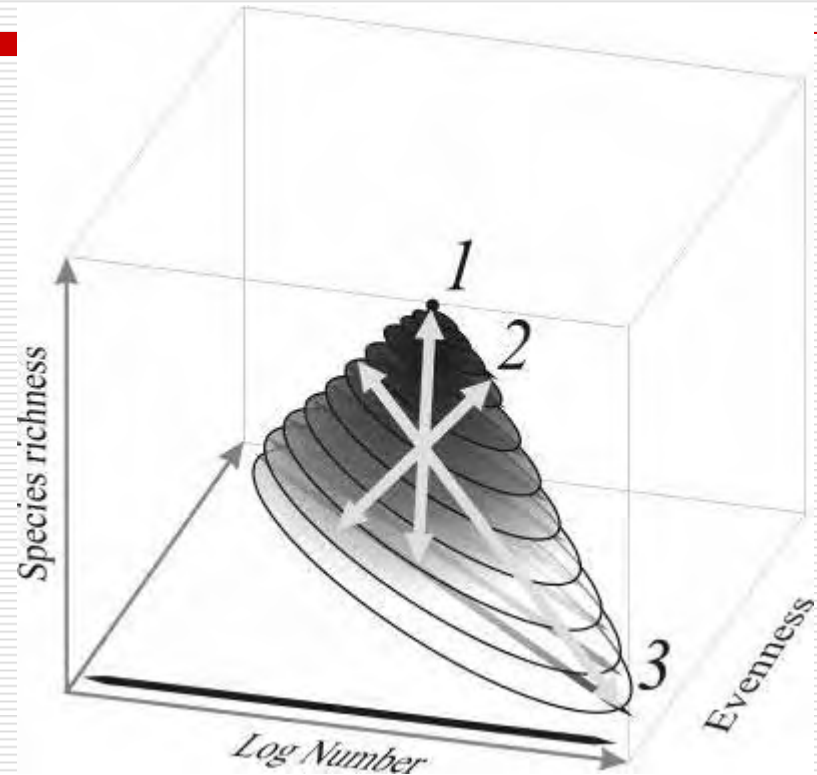


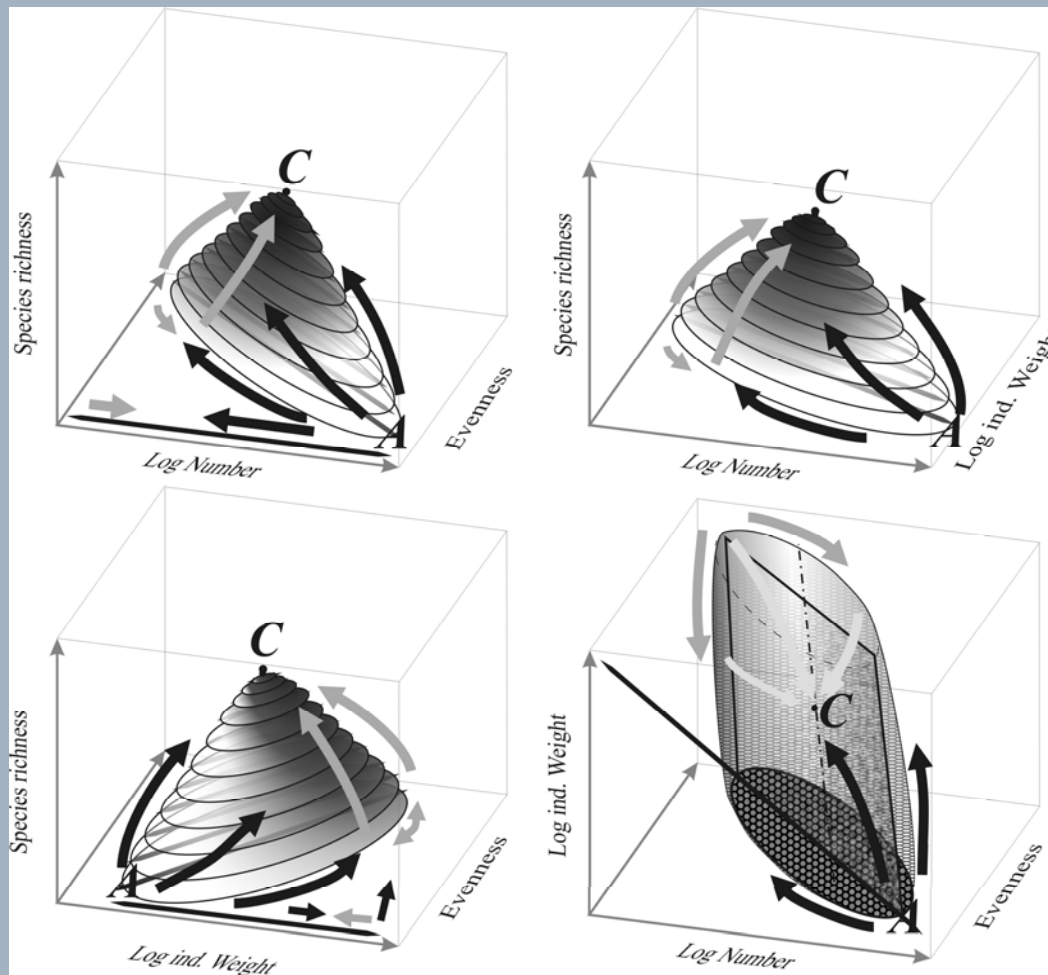
Accordingly, there are alternative groups of species, some of which are favored by shelf landscapes predomination, while the others are favored by oceanic landscapes predomination

Depending on the system state, position in space and time, the points density is redistributed within the mount

Three vectors  
of integral characteristics  
temporary variability.

Directions of:  
1 – daily,  
2 – seasonal,  
3 - long-term changes



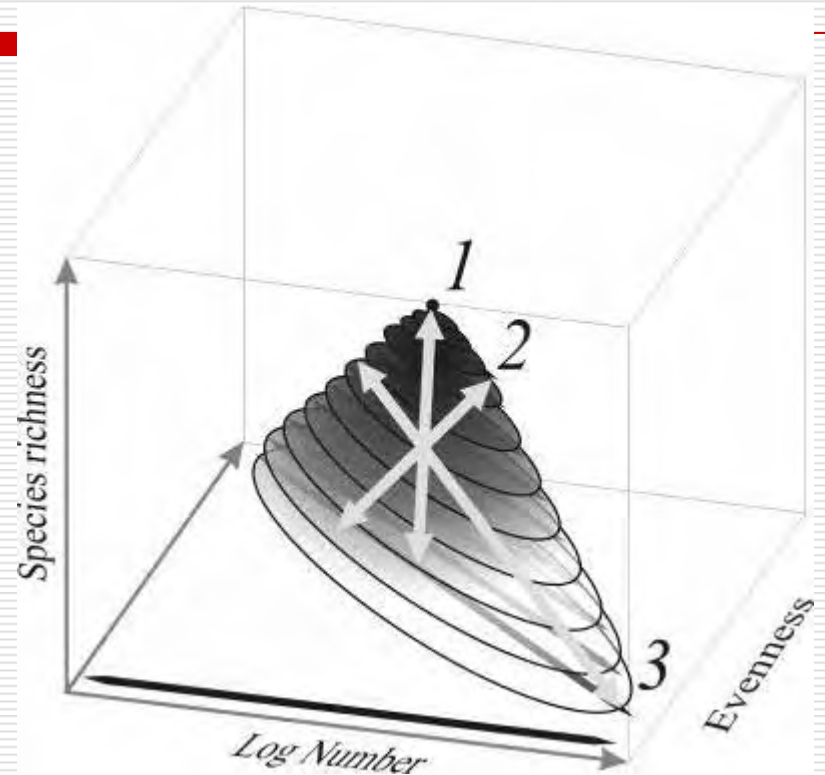


The reason for plurannual ecosystem alteration during the analyzed period of time (1979-2005) generally consists in the change of water exchange regime, which caused the shift to the oceanic water landscapes predomination over the shelf ones. Such biotopic transformations caused the shift of biocoenotic equilibrium to the correspondent group of species predomination

Depending on the system state, position in space and time, the points density is redistributed within the mount

Three vectors  
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Neither point can leave its boundaries, because it is drawn to the rigid interrelations carcass. This “skeleton” is formed by small number of relatively simple regularities. By no means are all of them purely biological

The semibiological (hydrological-biogeographic, bio- and physical-chemical, thermodynamic, ethological) regularities:

- *Environment ecological capacity is directly proportional to the water exchange intensity (consequence of the fact that in the places of intense circulation, the food capacity of the water increases and the negative influence of density factor decreases – the more dynamic the water exchange is, the more intense are the substance flows: the inflow of the substances, consumed by hydrobionts and the outflow of the substances, excreted by them)*

The metabiological fundamental magnitude relation:

- $M=N \cdot W$
- $H=J \cdot \text{Log}S$
- $S$  cannot be higher than  $N$
- if  $S$  is constant, the lower limit of  $J$  decreases as  $N$  grows
- if  $N$  is constant, the lowest possible  $J$  will increase as  $S$  grows, until  $S$  is equal to the given  $N$



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➤ *The concentration density is inversely proportionate to the average individual weight of the animals (consequence of the constancy of total metabolism to substance and energy flows ratio)*

➤ *The evenness is inversely proportionate to the hydrobionts concentration density (consequence of the fact that individuals, similar in species, size, biological state, are inclined to form thick single-species aggregations – schools, swarms, etc.)*

## The analyzed schemes allow to:

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- Vividly prove the postulate that the main principles of life organization in the pelagial are common for the whole World Ocean, but their displays are different in different parts of it
- Underline the interrelation and unity of the origin of two types of spatial regularities: "horizontal" – geographical and "vertical" – chorologic
- Connect the spatial variability with time plurannual variability of the system according to the complex of its integral characteristics, and both of them with such ecosystem parameters as environmental conditions stability and water exchange dynamics, which determine the ecologic capacity of biotope, and, consequently, biologic production and general intensity of biogeochemical cycle

## The analyzed schemes allow to:

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The reasons for large-scale plurannual changes in pelagic cenosis abundance, composition and structure are not in the rise of temperature, but in water exchange regime shift