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DIVERSITY AND VARIABILITY OF THE COPEPOD BEHAVIOUR IN ENVIRONMENTAL GRADIENTS: AN OVERVIEW

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The overview is based on results of long-term experimental studies of the authors and literature data, and applies to copepod species from plankton of the Black Sea, the Mediterranean Sea and the Atlantic Ocean. The work has incorporated the analysis of diversity and variability of the locomotory acts under the impact of abiotic factors: light, temperature, salinity, and the turbulent diffusion. Variability of locomotory activity depending on intensity, orientation (for the scalar factors), from a various combination of the environmental factors is shown. One of the mechanisms of a preferred conditions selection and phenomenon of a polymodality of copepod distribution in gradient conditions of environment is analyzed on an example of *Acartia clausi* behaviour in a vertical salinity gradient. It is emphasized**,** that intra- and inter-species variability of selection behaviour provides more effective utilization of environmental resources, promotes reduction of competition between species and, as a consequence, supports a high degree of species diversity in pelagic ecosystems.

Key words: diversity, copepod behaviour, light, temperature, salinity, turbulent diffusion

Обзор основан на литературных данных и результатах многолетних экспериментальных исследований авторов на разных видах планктонных копепод из Черного и Средиземного морей и Атлантического океана. Работа включает анализ разнообразия и изменчивости локомоторных актов копепод под влиянием абиотических факторов: света, температуры, солености и турбулентного перемешивания. Показана изменчивость двигательной активности в зависимости от интенсивности, направленности (для скалярных факторов) и различного сочетания факторов среды. На примере поведения *Acartia clausi* в вертикальном градиенте солености анализируются один из механизмов выбора предпочитаемых условий и явление полимодальности распределения копепод в градиентных условиях среды. Подчеркивается, что меж- и внутривидовая вариабельность поведения выбора обеспечивает более эффективное использование ресурсов среды, способствует ослаблению конкуренции между видами и, в конечном счете, поддерживает высокую степень видового разнообразия пелагических экосистем.

Ключевые слова: разнообразие, поведение копепод, свет, температура, соленость, турбулентная диффузия

Biodiversity Convention defined "biodiversity" as the variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems, as well as the other ecological complexes these organisms belong to. The term also includes the inter-species diversity, the intra-species diversity and the diversity between the ecosystems [3]. Behaviour has its own specific role among the adaptations preserving species diversity. As a display of vital activity, the behaviour reflects the integral property of organisms. The variability of behavioral patterns allows organisms to get adapted to environmental conditions and provides an opportunity for growth, development and reproduction for individuals and populations.

Copepods are known to be a key taxonomic group in marine plankton communities due to contribution into the abundance, biomass, and species diversity. The variability of copepod behaviour could be analyzed at different levels of structural organization, from the elementary locomotory acts to the complexes and cycles of the behaviour [38]. The behavioral patterns could be traced through the study of an organism motion in space and time. Hence, for the quantitative assessments and comparisons of behavioral acts one should appeal to the spatial-temporal parameters; such as the extension of behavioral acts in space, the duration, frequency, and direction of these acts.

Analyzing the influence of the environmental factors on the structure of pelagic plankton communities, we will consider the abiotic factors, which form the vertical stratification of the upper layer of the ocean. This layer acts as the biotope for many copepod species.

The stratified waters of the ocean accomodate a greater variety of copepod species, if compared with the less stratified ones [5]. The heterogeneity of abiotic factors and the interaction of these factors create an unique microlayered structure of biotopes, with a huge amount of accessible ecological niches. This interferes with the competitive replacement of species and in many ways defines a phenomenon of the coexistence of allied species in a pelagic ocean [30].

Influence of abiotic factors. In late 80s, an important role of the behaviour in the feeding and microdistribution of copepods was understood [39]. Active selection of environmental gradients was acknowledged as one of the basic patterns of the copepod behaviour.

We will consider the light intensity, temperature, salinity and turbulent diffusion as the major factors determining the layered-mosaic structure of the pelagic biotopes.

Light. A peculiar role of light is associated with its impact on the synchronization of biological rhythms [36]. The periodic forms of the copepod behaviour could be exemplified by their diel vertical migrations in which the light factor could play the major role in the upward and downward shifts of a depth preferred by the populations [13, 37, 56]. Diel rhythms of photopreference do also impact on spatial and temporal distribution of organisms [23].

Light could have also a kinetic impact on the behavioral acts of copepods similarly to the temperature and salinity. Locomotory and feeding activity of some coastal species of copepods, is given in the Table 1 [61], in which the variability of behavioral patterns was summarized for the light changes spanning two orders of magnitudes.

Our experiments with *Acartia clausi* Giesbreht in different light conditions have shown, that the frequency of locomotions did not depend on the light intensity ranging from 10 - 15 to 2 - 3×10^3 lux [52]. Changes of locomotory activity usually resulted in spatial redirection of motion, when the site of the illumination source (i. e. the aquarium side) was changed (Tab. 2).

Table 1. Fraction of total observed time when mouthparts were moving, feeding bout length and jump frequency at low (1,7 mE m $^{-2}$ s $^{-1}$) and high (220 mE m $^{-2}$ s $^{-1}$) light levels [61]

Таблица 1. Относительное время движения ротовыми конечностями, длительность пищевых скольжений и частота скачков при низкой (1,7 mE m $^{-2}$ s $^{-1}$) и высокой (220 mE m $^{-2}$ s $^{-1}$) освещенности [61]

Species	Light level	n	Mouthparts moving, % of total time, ± SD	Feeding bout length, s ± SD	Jump frequency, min^{-1} ± SD
Paracalanus parvus	high	3	47 ± 17	2.0 ± 1.4	0.3 ± 0.5
	low	3	48 ± 15	1.2 ±.0.6	0.9 ± 0.8
Pseudocalanus elongatus	high	2	55 ± 21	9.1 ± 8.3	4.0
	low	2	84 ± 0	18 ± 0.6	0
Temora longicornis	high	3	99 ± 0	9.1 ± 1.2	6.6 ± 2.1
	low	2	99 ± 0	8.7 ± 0.7	6.4 ± 0.9
Centropages typicus	high	3	58 ± 6	4.0 ± 0.3	0.8 ± 0.3
	low	2	42 ± 2	1.9 ± 0.5	2.7 ± 1.8
Centropages hamatus	high	2	41 ± 4	0.6 ± 0.1	0
	low	2	27 ± 1	0.4 ± 0.0	14 ± 7.5
Acartia clausi	high	3	0	-	54 ± 24
	low	3	0.6 ± 1.1	-	19 ± 11

Table 2. Some motion parameters of *Acartia clausi* at different modes of illumination

Таблица 2. Параметры локомоторной активности *Acartia clausi* при разных режимах освещения

Behavioral parameters	Conditions:	
	Top light, t=20-23°C, n = 21	Lateral light, t = 17-18°C, n =11
Jump length, cm	0.25 ± 0.1	0.41 ± 0.2 (P = 0.95)
Jump frequency, min^{-1}	38.1 ± 9.4	23.3 ± 5.3
Pause frequency, min^{-1}	25.3 ± 3.9	-
Pause length, s	2.2 ± 0.4	2.6 ± 0.5
NGDR (net-to-gross displacement ratios)	Female: 0.19 ± 0.11 Male: 0.20 ± 0.10 Total: 0.19 ± 0.10	Female: 0.59 ± 0.20 (P=0.99) Male: 0.85 ± 0.06 Total: 0.71 ± 0.20
Travel speed, cm min^{-1}	9.7 ± 5.7	9.6 ± 5.2
Net speed in the basic direction, cm min^{-1}	1.5 ± 0.7	6.1 ± 2.0

The behavioral response was mostly pronounced at the top illumination mode, when a combination of several factors is applied (like light–temperature gradient, or light–salinity gradient). And the positive photoreaction dominated, if the light source was down sideways. Thus, light could play the role of the focusing factor [31].

It should be taken into account however, that motivation of the behaviour could change to an opposite one in experiments with infringed combination of natural factors and gradients. In natural conditions, copepods do not sense spatial limitations, while in the experiments the escape reactions can dominate, due to the limitation. For instance, there is a sharp increase of the straightforwardness in the motion of *A. clausi* under lateral illumination mode versus the top illumination (Tab. 2).

In the table, the NGDR factor estimates the straightforwardness of the motion, i. e. a tendency of the organisms to hold in a certain zone [8]. For instance, low NGDR with the top uniform illumination, implies a complex (nonlinear) trajectories of locomotion. Infringed combination of natural factors, stimulating escape reactions could also strengthen the photopositive responses of copepods [55]. In this case, one could expect the link between adequacy of experimental conditions and intensity of escape reactions.

The light implements an important alarm function. Light flashes induced by the organisms could be perceived by copepods as a signal alarming the presence of predators. Escape (photofobic) reactions of copepods at bioluminescent flares [8, 10, 11] and short-term shadows [8, 9] could be attributed to the category of behavioral responses, in which the light impacts similarly. The variability of photofobic reactions might be attributed to the factors influencing the survival. In our experiments with *A. clausi* placed in the vertical gradient of salinity ranged from 14,5 to 25 ‰ and accompanied by a sharp increase of light, copepods were actively moving towards the deep layers. After 10 to 20 minutes however, an initial distribution of the individuals has been restored [52]. Similar reaction to light could be channeled through a passive descending to deep layers, as it was noted for *A. tonza* [56, 57]. Obviously, the above listed photoreactions are the adaptive ones, in terms of their essence. They were rather directed to escape a danger than to retain the organism in the preferred light conditions.

The light factor chiefly impacts the formation of the copepod schools. Hamner and Carleton [17] have found out that, schooling of copepods could be initiated by a certain light level. The integrity of swarms and their size is due to a visual contact of individuals [62]. Schooling of litoral copepods is associated with a patchy distribution of light and shadows (for example, in mangrove cays). The formation of swarms results from the combination of phototactic and klinocinetic patterns [12], although a simple spot light source could initiate the school formation of many copepod species in experiments [28].

Salinity. Sharp increase of the salinity usually results in active motion of the plankton animals towards the surface [19, 21] while the decline of the salinity causes an opposite effect. In the downward motion, the locomotory activity increases (if compared to the normal one) or, if the descent takes place in a passive (motionless) phase, the motion might be regulated by negative buoyancy [18, 26, 32, 40]. When salinity changes, the direction of motion can be controlled by a geo- and phototactic reactions [15, 27].

An ability to overcome a sharp halocline at the vertical migrations is the species-specific feature depending upon the tolerance to the salinity range [26]. This ability also depends upon the food conditions the individuals grew up in. The poor food conditions expand the tolerant salinity range while when food is easily available, this range gets narrowed [34].

Response of zooplankton organisms to halocline is based on the tolerance to the salinity gradients [4, 18, 26]. Quantitative parameters of copepod motion exhibit minimal changes in the preferred zone of the salinity gradient.

Similar trend in the jerk frequency was revealed for *A. clausi* [51, 52] (Fig.1).

In the experiments, a theoretically expected distribution of *A. clausi* in a salinity gradient coincided well with the distribution in a horizontally stepped gradient of salinity (Tab. 3).

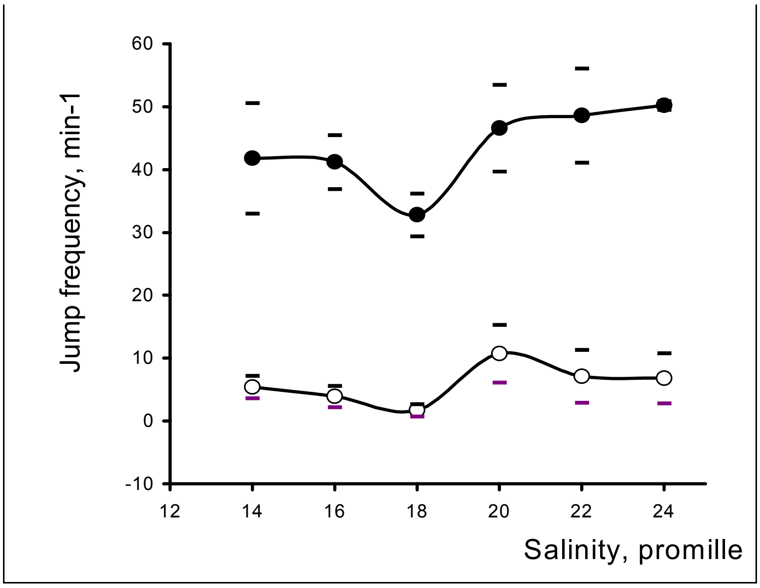

Fig. 1. Changes of the jerk (upper curve) and big jerk frequencies of *Acartia clausi* as a function of the salinity

Рис. 1. Частота скачков (вверху) и "больших скачков" (внизу) у *Acartia clausi* при разной солености

Table 3. Locomotory activity and distribution of *Acartia clausi* in the experiments with the salinity gradient

Таблица 3. Двигательная активность и распределение *Acartia clausi* в градиенте солености

Salinity ‰	Jerk frequency, min^{-1} ± SD	Big jerk frequency, min^{-1} ± SD	Mean length, cm ± SD		Mean calculated rates (cm min^{-1}) by:			Copepod distribution in salinity gradient, %	
			jerk	big jerk	jerks	big jerks	sum	prospective	really
14	41.8 ± 8.8	5.4 ± 1.8	0.4 ± 0	1.2 ± 0.1	14.6	6.5	21.1	16.9	16.7
16	41.2 ± 4.3	3.9 ± 1.7	0.4 ± 0	1.2 ± 0.1	14.9	4.7	19.6	18.2	16.7
18	32.8 ± 3.4	1.7 ± 1.0	0.4 ± 0	1.2 ± 0.1	12.4	2.0	14.4	24.8	23.3
20	46.6 ± 6.9	10.7 ± 4.6	0.4 ± 0	1.2 ± 0.1	14.4	12.8	27.2	13.1	23.3
22	48.6 ± 7.5	7.1 ± 4.2	0.4 ± 0	1.2 ± 0.1	16.6	8.5	25.1	14.2	13.3
24	50.2 ± 0.7	6.8 ± 4.0	0.4 ± 0	1.2 ± 0.1	17.4	8.2	25.6	14.0	6.7

However, the above unimodal distribution of copepods characterizes only general patterns of their behaviour in the environmental gradients. It does not reflect the fine scale distribution in the microlayers.

For a number of freshwater zooplankton species, it was shown, that the distribution of individuals in the gradients of temperature, oxygen, food suspension and pH used to be a polymodal one, associated with changes of motion [47, 48]. On the basis of this data, the hypothesis of a multicoherent ecological niche was developed [49]. It was aimed to explain a phenomenon of coexistence of a large number of species in stratified pelagic ecosystems.

Working with the copepod *A. clausi,* we analyzed the distribution and behaviour in a vertical gradient of salinity [52, 53]. It was shown, that changes of the motion were in a wide range of the salinity, including the preferred and escaped ranges. As well, a tendency of the reduction of motion has taken place, when salinity increased within the preferred gradient zone. Thus, the same changes of the copepod locomotions were monitored in various ranges of the salinity change.

The selection of optimal ranges has taken place in a certain spatial zones of the salinity gradient. A high activity of locomotions (lasting about one minute) was noticed in the initial phase. At this stage, copepods quickly escape the zone where salinity was beyond the limit of species tolerance. These motions were accompanied by the orientation of the locomotory acts in a vertical direction. At the end of an initial phase and the beginning of intermediate one, when initial schooling in "non-escaped" zones of the gradient occurred, the distribution was usually a unimodal one (i.e. the same as in the case with a horizontal salinity gradient). The maximum of preference was noted in a wide zone (15 - 20 ‰), with the peak at 17 - 18 ‰. The peak of the preferred salinity was at 10 - 11 ‰ causing transition of the normal distribution to the bimodal one. In a subsequent 15 to 30 minutes, the distribution stabilized and has been accompanied by some expansion of the selected salinity range. Besides that, a polymodal type of the distribution was noticed (Fig. 2). The trajectories of motion have partly changed, due to greater nonlinearity of motion.

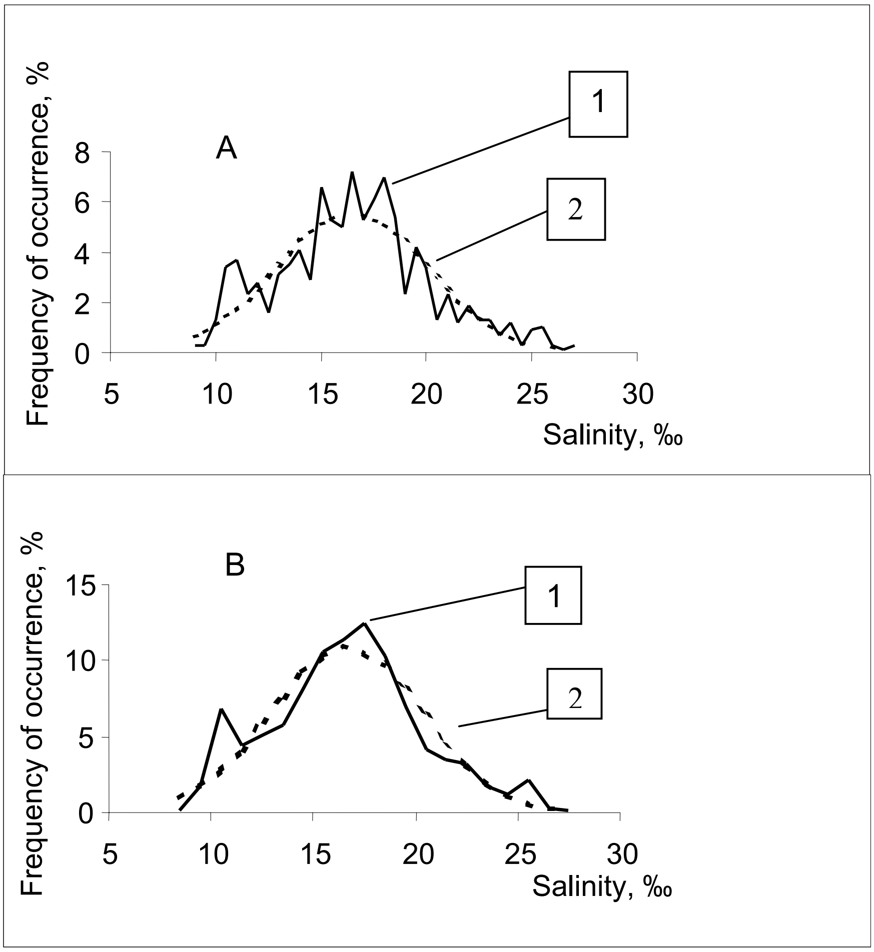

Fig. 2. Averaged frequency of occurrence (1) and a theoretical curve for the normal distribution (2) of *Acartia clausi* in the salinity gradient. A – class interval = 0.5 ‰. B – class interval = 1.0 ‰

Рис. 2. Средняя частота встречаемости (1) и теоретическая кривая нормального распределения (2) особей *Acartia clausi* в градиенте солености. A – классовый интервал = 0.5 ‰. B – классовый интервал = 1.0 ‰

It should be noted, that modal levels of preferred salinity (i. e., maxima of occurrence) were demonstrated by same individuals visiting steady gradient zones more often.

This is essentially important, since it confirms an objective pattern of a polymodal distribution and, probably, its essence: a search for an optimal conditions for individuals.

Intervals between neighboring modal salinities, characterizing the "density of packing" of the preferred zones, are usually less at the center of the distribution profile and increase in the peripheral zones (Fig. 3).

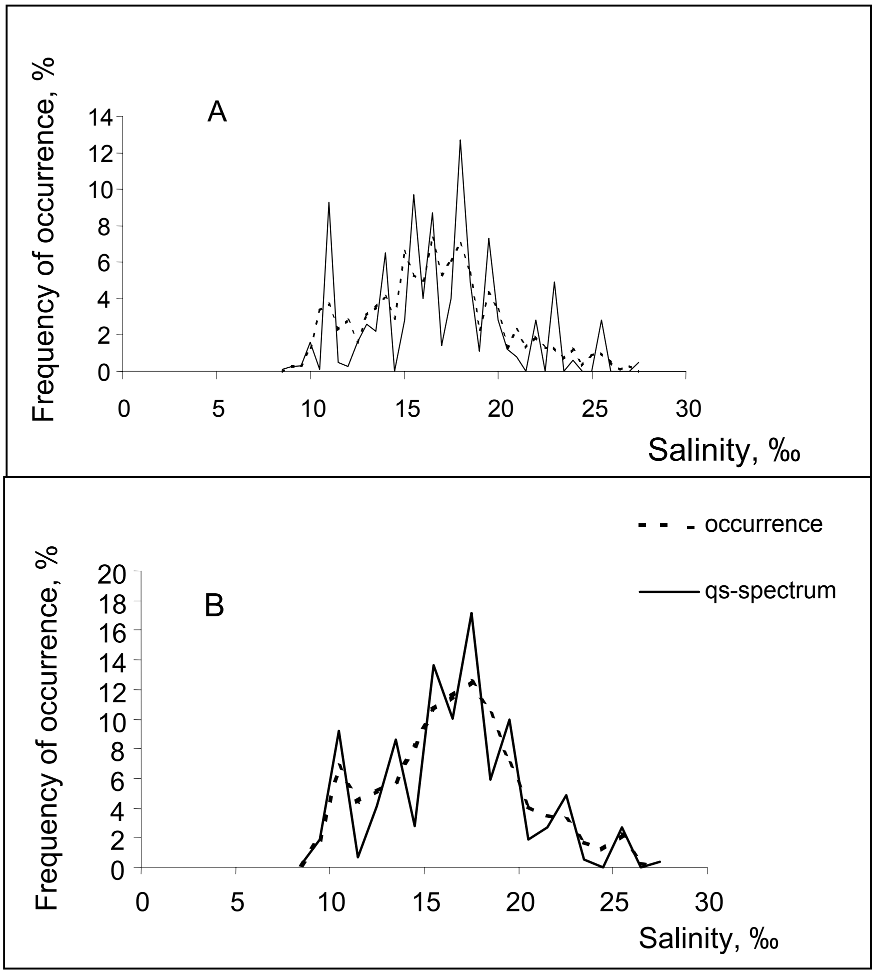

Fig. 3. Average frequency of occurrence (1) and qs-spectrum (2) for the *Acartia clausi* distribution in the salinity gradient. A – class interval = 0.5 ‰. B – class interval = 1.0 ‰

Рис. 3. Средняя частота встречаемости особей (1) и qs-спектры распределения (2) *Acartia clausi* в градиенте солености. A – классовый интервал = 0.5 ‰. B – классовый интервал = 1.0 ‰

The relation of the periphery width and its size might be associated with an increase of inter-specific competition in the optimal range and its decrease in peripheral zones. The divergence and alternation of modal values of factors was observed for 10 freshwater crustacean species [49]. The division of vital resources in time or space is widely used by nature, to avoid competitive replacement. Replacing species, the number of ecological niches accessible in one space can be multiplied.

Thus, *polymodal distribution can serve as a special form of adaptation of the plankton communities:*

- *to a comprehensive use of the environment resources;*
- *to the reduction of inter- and intra-specific competition;*

- *to support of a high degree of ecosystem diversity.*

Polymodal distribution could be achieved through the same mechanisms of motion in combination with variability of the individual requirements of optimal conditions of the environment.

Temperature. An importance of the temperature for the plankton is determined by the poikilotherm nature of the plankton animals in which biochemical, physiological and behavioral processes chiefly depend on temperature.

The behavioral response to changes of temperature is supposed to be the fastest one at the temporal scale of adaptive responses. This allows us to use direct visual observations on locomotory activity in experiments.

Vilenkin [63] reported some basic types of locomotory activity of marine organisms to respond the temperature change (Fig. 4).

The first type of the response curve (Fig. 4 A) could be attributed to the case, when the activity distinctly exceeds the spontaneous one. For copepods, similar type of the curve was reported for the frequency of the mouthpart beats of *Temora longicornis* [16]. For *Calanus finmarchicus*, the form of the curve corresponded to the "B" type (Fig. 4 B) [59]. The motion of the ostracod *Conchoecia atlantica* has been changing in the same way [42].

The type of the curve shown in the Figure 4 C (with the maximum of locomotory activity in the preferred zone) might be interpreted as an escape off a negative environment influences. For copepods, such type of changes was not clearly reported. Perhaps, the decrease of the locomotory activity of *Calanus glacialis* in an increasing temperature gradient might be attributed to this type of response [20]. It was also reported for a jelly-fish species [4, 7, 51].

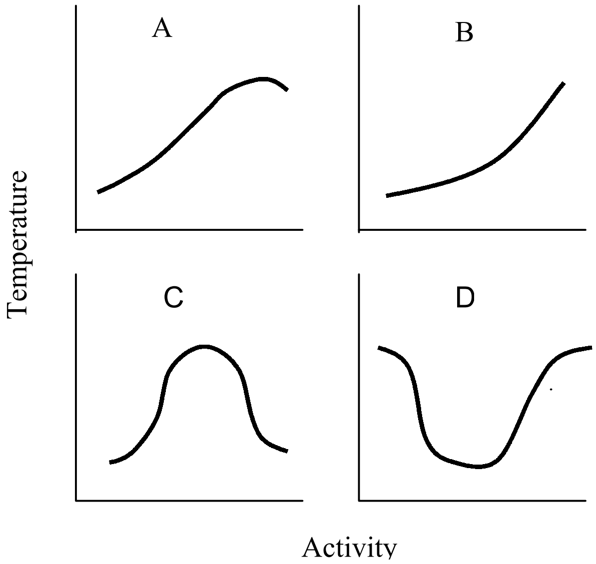

Fig. 4. Basic types of locomotory activity of marine animals as a response to the temperature changes. A: Moderately high level of activity capable of being supported for a long time. B, C: Routine level of activity; the selection of the preferred temperature requires the oriented motion. D: Routine level of activity; the selection of the preferred temperature does not require the oriented motion [63]

Рис. 4. Температурная зависимость двигательной активности – основные типы. А – умеренно высокий уровень активности, способный поддерживаться длительное время. В, С – рутинный уровень активности; выбор предпочитаемых температур предполагает ориентированное движение. D - рутинный уровень активности; выбор предпочитаемых температур не требует ориентированного движения [63]

A similar curve was reported for *A. clausi* [52, 54] (Fig. 5 a). It was recorded in "sharp" experiments when the fast (behavioral) response was exhibited. With a longer acclimation, the locomotory activity of *A. clausi* changed proportionally to temperature (Fig. 5 b) [52], which reflected a general pattern of the relationship between metabolic processes and temperature for poikiloterm organisms.

The 4-th type of the curve exemplifies absence of necessity in a strictly directed motion: the aggregation in the optimum is achieved through the change of the motion speed.

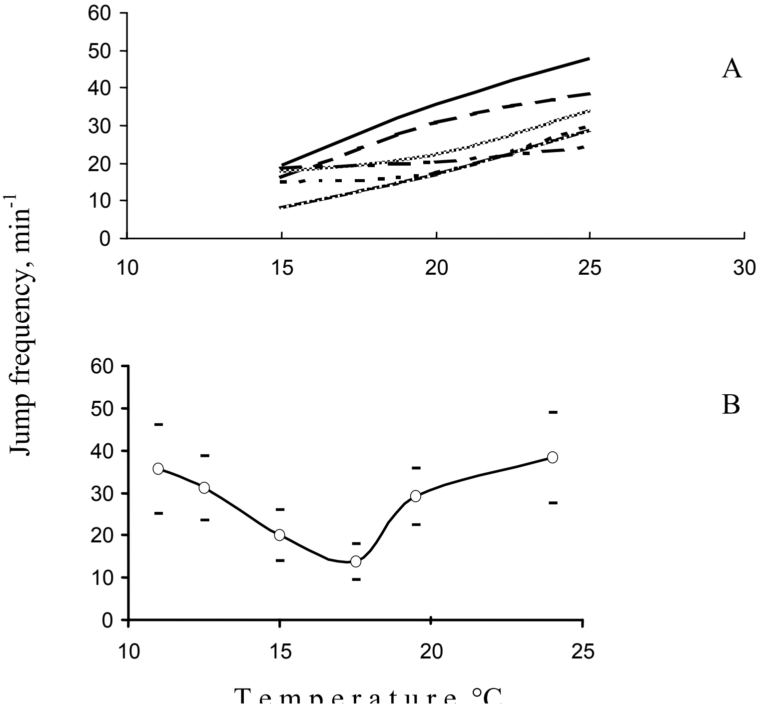

Fig. 5. The relationship between temperature and jerk frequency for *Acartia clausi.* A: with acclimation to the temperature (15°, 20°, and 25° C). B: no acclimation (11°, 12,5°, 15°, 17,5° and 19° C)

Рис. 5. Влияние температуры на частоту скачков *Acartia clausi.* A: при акклимации к каждой из температур (15°, 20° и 25° C). B: без акклимации (11°, 12,5°, 15°, 17,5° и 19° C)

Variability of the copepod behavioral responses to temperature also includes the cases when the locomotory activity does not respond to the temperature factor, as it was observed for *C. finmarchicus, C. hyperboreus,* and *Metridia longa* [20].

It is also important, (from the view point of a variety of behavioral responses) that temperature-dependent locotomory activity is not strictly associated with the type of thermal reception and taxa. Even for fishes, the focused and chaotic motions were observed. In the case of "primitive" ciliates, the response can include hierarchically higher elements of orientation [60].

Turbulent diffusion. A typical feature of the pelagic biotopes is the mobility of water. Therefore, the turbulent diffusion, which impacts the feeding and growth rates of copepods was in the focus of research in the past decade [6, 58, 62, 65]. Initial studies were gradually influenced by the work of Rothschild and Osborn [41] who hypothesized that the turbulence should increase the frequency of interactions between copepods and their food particles (the phytoplankton cells). In the above study, as well as in the other ones [65] a “turbulent resolving” model of the “predator-prey” interactions based on the Navier-Stoks equations has been developed.

According to the model, the frequency of the predator-prey interactions supposed to be higher in the case of the turbulent environment in which the predators moving with a constant speed and direction could search much greater space. The first version of the model assumed that predators and preys move though a lifeless objects in the three-dimensional space, where the behavioral phenomena have been reflected by the following formula: "contact = feeding". In the later version of the model, Osborn [36] faced a necessity to update too simple way of presentation of behavioral phenomena, in order to approach a quantitative conclusions. The experiments testing the Rothschild-Osborn hypothesis have shown, that the influence of the small-scale turbulent diffusion on copepod feeding is much more diverse, than it was thought before. It does not always results in an increase of the consumption rate and depends on many variables: concentration of food objects, their mobility, escape reactions, and size. For instance, the turbulence with a speed of dissipation 0,05 - 0,15 cm^2s^{-3} (which is a moderately intensive level) did not result in an increase of a flow of food particles at suspension feeding mode of *Centropages hamatus*. Its influence on the efficiency of feeding was negative at high concentration of phytoplankton [33]. This was due to the deformation of the flow field of food particles created by manipulatory activity of copepods consuming phytoplankton cells and due to increase of the frequency of escape reactions [14].

An increase of the length of jerks in a turbulent environment, if compared with the non-turbulent one, was also shown for *A. clausi* in our experiments (Fig. 6).

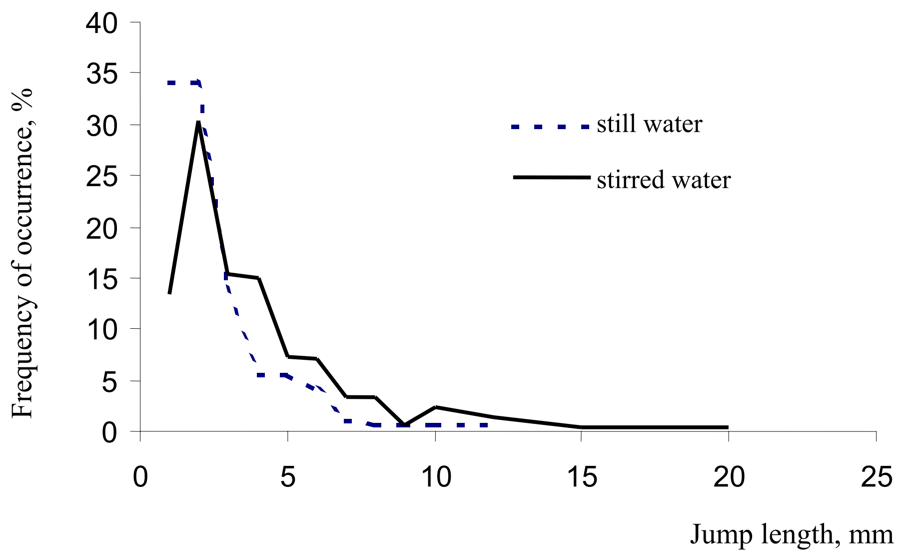

Fig. 6. Distribution of *Acartia clausi* jerk length in a still and stirred water. Mean jerk length: in still water - 0.23 sm, mean jerk length in stirred water - 0.37 sm

Рис. 6. Распределение длин скачков *Acartia clausi* в спокойной и “турбулентной” воде. Средняя длина скачка: в спокойной воде – 0.23 см, в “турбулентной” воде – 0.37см

The same copepod species could react differently to the turbulence depending on the behavioral mode of feeding. For instance, the consumption of food was four times higher for *Acartia tonsa* consuming ciliates at a low level of turbulence (10^{-2} - 10^{-3} $cm^2 s^{-3}$) in comparison to the non-turbulent environment.

For herbivores, a weak turbulence did not influence the feeding rate [43, 46]. The authors emphasized, that for *A. tonsa,* the negative effect of the turbulence occurred at the intensity higher than the usual one. The influence of turbulent diffusion results in a shift of the selectivity towards large mobile preys in the mixed food cultures, when the opportunity to select preys is enforced [24, 46].

In terms of types of feeding behaviour, turbulence has a minimal impact on suspension feeders while the most impacted ones are the ambush predators (like *Acartia* and the *Cyclopoida* species).

In this classification, actively moving (cruising) predators have an intermediate position [25]. The interaction of turbulence and the copepod behaviour, strengthening food consumption, do also results in an increase of the growth rates [1, 2, 45] and the metabolism resulting in a fast ontogenetic development [2, 44]. It could lead to increase of the phytoplankton biomass, reduction of zooplankton biomass, and accelerated recycling of nutrients on the ecosystem level [2]. Taking into account a reverse relationship between the plankton biomass and species diversity [3, 29, 30], one could propose that a moderate turbulence should favor the maintenance of high zooplankton biodiversity.

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