

METABOLIC STRATEGY IN PELAGIC SQUID OF GENUS
STHENOTEUTHIS (OMMASTREPHIDAE) AS THE BASIS
OF HIGH ABUNDANCE AND PRODUCTIVITY:
AN OVERVIEW OF THE SOVIET INVESTIGATIONS

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ABSTRACT

The long-term investigations of nektonic squid *Sthenoteuthis pteropus* and *Sthenoteuthis oualaniensis* (between 1978 and 1990) have revealed some special features in a metabolism of these animals. These are: (1) rate of energy expenditure is very high (coefficient 'a' in equation $Q = aW^k$ is from 3.1 to 4.7 at 26° to 30°C (more than that of other fast swimming animals); (2) hepatopancreatic index is about 4% wet body weight, twice that of actively swimming fishes; (3) protein is the main substrate for energy metabolism; (4) the polyenoic fatty acid 22:6w3 in phospholipids of squid muscle is 42.6 to 45.7% of fatty acids (more than in the most active marine animals); (5) the large proportion of anaerobic metabolism of nitrogenous substances in energy metabolism enables the squid to inhabit zones of very low oxygen concentration.

Recently a hypothesis about alternative metabolic strategies of biological progress in marine animals was put forward by Shulman and Love (1999). The first strategy suggests that the animals maximize their energy and substance metabolism to maintain high abundance and expansion of species ranges. The second strategy is characterized by extreme specialization. These strategies have been studied in detail in fishes. As was shown, the representatives of the first 'extensive' strategy have a high level of energy catabolism, ensuring large activity: appropriate biochemical processes and transport structures allow them to carry out such metabolism.

There is no doubt that squid also have this strategy in contrast to the representatives of another group of cephalopods - octopuses. Peculiarities of squid metabolism are described in many papers (Okutani, 1962; Kao, 1970; La Roe, 1971; Young, 1975; Bidder, 1976; Hurley, 1976; Soichi, 1977; Bellman, 1978; Spratt, 1978; O'Dor et al., 1979, 1985, 1994; Suyama and Kabayashi, 1980; Macy, 1980; Hirtle et al., 1981; O'Dor, 1982; Hanlon et al., 1983; De Mont and O'Dor, 1984; Webber and O'Dor, 1985, 1986; O'Dor and Webber, 1986; O'Dor and Wells, 1987; Hoeger et al., 1987; Boucher-Rodoni and Mangold, 1989; Segawa, 1991, 1995; Seibel et al., 1997; Poertner and Zeilinski, 1998; etc.).

The researchers of the Institute of Biology of the Southern Seas (Academy of Science of Ukraine) in Sevastopol work at the same problem on two squid species, abundant in the tropical pelagic zone; *Sthenoteuthis pteropus* (Steenstrup, 1885) from the Atlantic and *Sthenoteuthis oualaniensis* (Lesson, 1830) from the Indian Ocean (Shchepkin et al., 1981; Shulman and Nigmatullin, 1981; Shulman and Yakovleva, 1981; Shulman, 1982; Shulman et al., 1984, 1992; Abolmasova, 1984, 1985; Abolmasova and Belokopytin, 1987; Abolmasova and Stolbov, 1991; Abolmasova et al., 1990a,b; Stolbov, 1988; Chesalin et al., 1992; Yuneva et al., 1994).

The purpose of the present view is to elucidate the main features of squid metabolism, on the basis of these and literature data, which ensure their biological progress, and to

show an originality of some unique metabolic features, distinguishing the squid from other animals and even other cephalopods.

The long-term investigations on squid were carried out from 1978 to 1990 in expedition cruises, mainly on RV PROFESSOR VODYANITSKY. The details of material and methods have been given in the papers (Shchepkin et al., 1981; Shulman and Nigmatullin, 1981; Abolmasova, 1985; Chesalin et al., 1992; Yuneva et al., 1994). The parameters studied were: (1) energy and nitrogen metabolism of squid; (2) total chemical composition and its dynamics; (3) lipid and fatty acid composition; (4) changes of metabolism during experimental starvation.

In this paper we consider the following special features of genus *Sthenoteuthis* metabolism:

- rate of energy expenditure
- substrates of catabolism
- elements of the energy balance
- adaptations to low oxygen conditions
- metabolic strategies of adaptations

RATE OF ENERGY EXPENDITURE

Squid have one of the highest rates of energy metabolism among marine animals. At the same time among squid, a very high rate of metabolism is characteristic of the genus *Sthenoteuthis*. It is linked, first of all, to the active life of these pelagic animals, and secondly, to the high temperature of their habitat. According to our calculations, value of the coefficient 'a' in the equation $Q = aW^k$ (Vinberg, 1956), which determines the rate of oxygen consumption (Q) per unit body weight (W) for squid is 1.3–1.9 times higher than in squid such as *Onichoteuthis banksii*, 5.2–7.6 times higher in comparison with octopuses and 41–130 times higher than gastropods and bivalves (Table 1). Coefficient 'a' in

Table 1. Coefficients of equation $Q = aW^k$ at environmental temperature (a) and calculated to 20°C (A)* in some marine molluscs and fishes (ml O₂ g⁻¹ h⁻¹).

Species	T, °C **	a	k	A	Authors
Molluscs					
<i>Sthenoteuthis oualaniensis</i>	29–30	4.71	0.75	2.18	Abolmasova, 1985
<i>Sthenoteuthis pteropus</i>	26–28	3.11	0.80	1.76	Abolmasova, 1984
<i>Onichoteuthis banksii</i>	28	2.45	0.84	1.28	Abolmasova, 1978
<i>Octopus</i> sp.	24–27	0.62	0.68	0.41	Abolmasova, 1978
<i>Rapana thomasiana</i>	17.5	0.037	0.78	0.04	Muravskaya and Galkina, 1979
<i>Mytilus galloprovincialis</i>	23	0.076	0.90	0.06	Finenko et al., 1990
Fishes					
<i>Exocoetus volitans</i>	28–29	1.10	0.75	0.55	Lipskaya, 1974
<i>Coryphaena hippurus</i>	27–29	1.39	0.91	0.73	Lipskaya, 1974
<i>Epinephelus</i> sp.	26–30	0.24	0.83	0.12	Lipskaya, 1974
<i>Engraulis encrasicolus</i>	20	0.97	0.80	0.97	Belokopytin, 1993
<i>Trachurus mediterraneus</i>	20	0.70	0.80	0.70	Belokopytin, 1993
<i>Spicara smaris</i>	20	0.39	0.73	0.39	Belokopytin, 1993
<i>Gadus merlangus</i>	9	0.10	0.90	0.25	Belokopytin, 1993

* According to Vinberg (1983)

** Environmental temperature

Table 2. Coefficients 'a' of equation $Q = aW^k$ at standard and active metabolism in some squid species ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$).

Species	Weight, g		a	T°C	Authors
<i>Sthenoteuthis oualaniensis</i>	20–750	standard	1.39	29–30	Shulman et al., 1984
		active	3.33	29–30	
<i>Sthenoteuthis pteropus</i>	20–300	standard	1.83	26–28	Abolmasova and Belokopytin, 1987
		active	6.69	26–28	
<i>Illex illecebrosus</i>	200–550	standard	0.08	15	Webber and O'Dor, 1985
		active	4.17	15	
<i>Todarodes sagittatus</i>	100	active	2.07	19	Abolmasova, 1978
<i>Loligo pealei</i>	50–100	standard	1.30	20	Macy, 1980
		active	1.65	20	
<i>Loligo opalescens</i>	0.6–40	standard	0.09	20	Hurley, 1976
		active	0.39	20	

squid is higher than in fast swimming tropical fishes such as swordfish, dolphin fish and flying fish, and much higher than in moderately mobile tropical and Black Sea fish species. As coefficients 'k' are close for most species in Table 1 (0.7–0.8), rates of energy expenditure for whole individuals of these species are similar in pattern to coefficient 'a'.

It is known that the metabolic rate relates to swimming speed and temperature (Prosser, 1979). The active metabolic rates for squid *S. pteropus* with mantle length (ML) from 11 to 25 cm at swimming speeds of 1, 1.5 and 2 length per second (L sec^{-1}) increase from 1.4–2.2, 1.7–3.3 and 2.0–4.9 times, respectively (Abolmasova and Belokopytin, 1987). Our data are similar to the literature ones on oxygen consumption for the standard and active metabolism in different squid species (Table 2). Other authors also pointed out that the high metabolic rates of squid considerably exceed those of fish, based on investigations of oxygen consumption (O'Dor, 1982; O'Dor et al., 1994; Webber and O'Dor, 1985; Seibel et al., 1997), ATP (Arai and Saito, 1961), hemocyanin content (Zammit, 1978) and intermediate metabolism (Storey and Storey, 1978).

Pelagic fish, the main competitors of the squid, have lower levels of energy metabolism, but are more effective swimmers. It is known that the energy cost of swimming at critical speeds of squid *Illex illecebrosus* is nearly five times higher than in salmon *Oncorhynchus nerka* (O'Dor and Webber, 1986; Webber and O'Dor, 1986). The squid use jet-propelled swimming, which is less effective in comparison with sustainable oscillatory swimming of fishes (Alexander, 1975). Obviously, the success in competitive struggle and squid's ability to capture fish prey and evade fish predators depend on burst swimming and the manoeuvrability with high acceleration in any direction (O'Dor, 1982). They also have special protective mechanisms, such as ink ejection for disorientation of the predator.

SUBSTRATES OF ENERGY AND SUBSTANCE CATABOLISM

Because squid energy requirements are much higher than in fish, they have developed mechanisms for their maintenance. It is known that fast swimming animals (notably fish) attain high levels of energy metabolism by developing red and white muscle structures and using highly calorific 'fuel' during swimming (Webb, 1971). Muscle weight (mantle and arms) of pelagic squid of the genus *Sthenoteuthis* reaches 60–65% of body weight.

Similar values are characteristic of active fish, such as bonito and trout (65 and 57%, respectively), whereas less active fish (porgy, carp) have muscle weight less than 50% (Belokopytin, 1993).

Features of chemical composition of mantle, fins, arms and tentacles of squid include a high content of protein (approximately 17–22% of wet weight), low content of lipids (1–3%) and very low glycogen content (0.1%) (Ertel, 1970; Suryanarayanan and Alexander, 1971; Suryanarayanan et al., 1973; Shchepkin et al., 1981). These parts of the body carry out the main movement functions. Mantle muscles are almost constantly contracting, providing fast jet-swimming; fins play the role of a rudder and act as the engine while slow moving; the tentacles can be immediately extended and contracted to capture and retain prey. The dry, lipid-free matter of these tissues is approximately 85–90% protein, contraction of which provides most of the intensive motor forces (Shulman et al., 1984).

The liver (or more correctly hepatopancreas) attracts special attention. The role of the liver in the total metabolism of squid (as well as molluscs in general) seems to be especially important. The liver differs from other tissues with higher contents of the basic biochemical substances (protein, lipids and glycogen). Thus, the liver of *S. oualaniensis* contains 1.5–2 times more dry matter, 2 times more glycogen, 1.2–1.4 times more protein, and 3.6–7.5 times more lipids, than muscular tissues (Schepkin et al., 1981). The weight of the liver in *Sthenoteuthis* is more than 4% of total body mass (Fig. 1A) (Shulman and Nigmatullin, 1981; Chesalin et al., 1992) and it can be much higher in some other species such as *Todorodes sagittatus* (10 to 16%) (Dvinin and Konstantinov, 1979; Wiborg, 1980). At the same time the weight of the liver in fast swimming fish, for example mackerel, does not exceed 1.0–2.5% (Vinogradova, 1957; Shulman and Love, 1999). However, comparable to squid among the fish are the so-called white ones (Gadidae, Gobiidae, Scorpaenidae) and also sharks; their liver weight also attains 4 to 10% or more of body mass (Vinogradova, 1957; Shatunovsky, 1980; Love, 1980). The main energy and substance reserves are concentrated in the liver of these fish. The role of the liver in metabolism is peculiarly important for fish with burst swimming, when the fast mobilization of energy substrates for locomotion is necessary. Obviously, similar factors are the reason for high functional activity of squid liver, which also plays an important role in storing some substances. It is shown that the reserve substances of the liver can easily be mobilized in starvation (Shulman and Nigmatullin, 1981). Other researchers, studying food digestion by squid, also specified the important role of squid liver, as a 'reserve depot' (Bidder, 1976; Boucaud-Camou, 1971; Boucher-Rodoni and Mangold, 1977).

However, chemical composition of the livers of the white fish and the squid is different. The liver of white fish and sharks is the depot for lipids (Vinogradova, 1957; Shatunovsky, 1980; Love, 1980), and glycogen (Plisetskaya, 1975). On the contrary, the liver of squid reserves a significant amount of proteins, moderate quantities of lipids and very low glycogen content (Fig. 1B) (Shchepkin et al., 1981; Abolmasova et al., 1990a; Hayashi, 1996). Amounts of these components indirectly indicate the substrates for energy and substance metabolism.

It is known for various groups of animals (mammals, birds, fish, crustaceans, insects) that their sustained movement is provided by the aerobic utilization of neutral lipids (triacylglycerols, fatty acids). Whereas slow movement is provided by aerobic use of proteins (and amino acids), and burst movement by anaerobic use of glycogen (and glucose) (Hochachka and Somero, 1973). Thus, primary utilization of lipids in energy metabolism is a characteristic of actively swimming fish species, and proteins of inactive

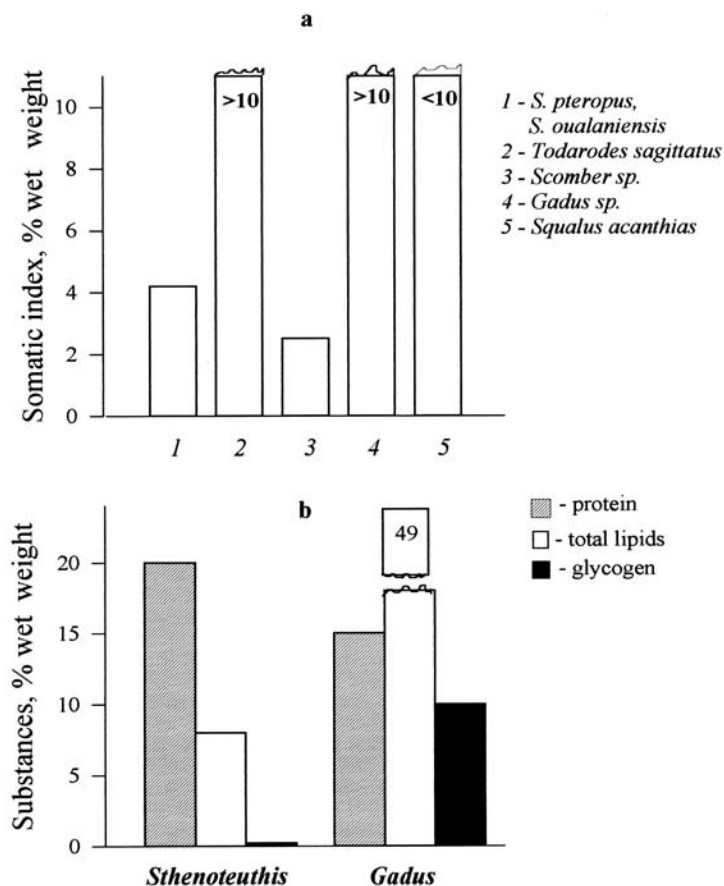


Figure 1. Hepatopancreas of squid and livers of fish: somatic index (a) and proximate chemical composition (b). From: Shulman and Nigmatullin, 1981; Dvinin and Konstantinov, 1979; Vinogradova, 1957; Shchepkin, 1981; Chesalin et al., 1992.

ones (Fischer, 1970; Shulman and Love, 1999). However, squid during their evolution have developed quite another pathway for structural-functional maintenance of high levels of metabolism. Perhaps their unique type of active swimming indirectly promoted this.

Squid of the genus *Sthenoteuthis* take primary place among animals using proteins and free amino acids to maintain a high functional activity (Shulman et al., 1984). Actively swimming fish with similar levels of natural mobility use triacylglycerols as the main sources of energy. To define the quantitative contribution of various substrates to energy metabolism of *Sthenoteuthis* squid, research on the following parameters were carried out: ammonia quotient (AQ), that is, the ratio between oxygen consumption and nitrogen excretion (O:N); variability of the reserves in the livers during experimental starvation. These parameters were studied on whole organisms (Shulman and Nigmatullin, 1981; Shulman et al., 1992a, 1993). Stroganov (1956) originally introduced AQ coefficient into hydrobiological studies. When $AQ > 30$, lipid-carbohydrate substrates dominate energy metabolism, when values range from 20 to 30, a mixture of protein and non-protein sub-

Table 3. The ratio between oxygen consumption and nitrogen excretion (O:N) and percentage of protein in energy metabolism of some marine animals.

Species	O:N	Share of protein (%)	Part in metabolism (%)		Authors
			aerobic	anaerobic	
<i>Sthenoteuthis pteropus</i>	3.3	100	50.8	49.2	Shulman et al., 1992a
<i>Sthenoteuthis oualaniensis</i>	6.9	100	67.2	22.8	Shulman et al., 1992a
<i>Mytilus galloprovincialis</i>	23.2	36.4	100	0	Muravskaya, 1966
<i>Calanus euxinus</i>	20.0	48.0	100	0	Svetlichny et al., 1998
<i>Trachurus mediterraneus ponticus</i>	77.8	12.7	100	0	Stolbov et al., 1995

strates are used, and an AQ < 20 indicates that protein is the main source of energy. An AQ value of 8.67 corresponds to 100% of the oxygen having been utilized by protein, and, with values less than this, a proportion of the protein is catabolized anaerobically. The values of AQ for *Sthenoteuthis* squid are very low (3.3–6.9), indicating the sole use of protein in energy metabolism (Table 3). Mussels and crustaceans have a mixed type of energy source (AQ about 20), while fish have AQ ten times higher than squid, mostly using lipids in energy metabolism.

The experiments on squid starvation in aquaria show the liver to be a reserve store for protein (Shulman and Nigmatullin, 1981; Shulman, 1982). During a 20 h starvation period, the hepatopancreatic index of *S. oualaniensis* decreased to less than half (from 4.1 to 1.8): in this case the main decrease was in proteins (Fig. 2A,B). The main portion of protein was lost during the first 5 h of starvation, demonstrating the fast activation of reserve protein in the squid liver under adverse conditions. We also showed that the reserve store of proteins play an important role in the processes of gametogenesis (Chesalin et al., 1992): the protein content of the hepatopancreas decreased markedly in females and males during maturation (Fig. 3). Thus, a characteristic property of squid metabolism is not only the increased reserve capacity of the liver, but also in its specific content of reserve substances. Also, close correlation between protein content (approximately estimated by de-fatted dry matter) and dry matter content of the squid body was noted (Fig. 4) that is absent in fish (Nikolsky and Shulman, 1980). Other authors have also pointed out the high intensity of protein metabolism of different squid species (Campbell and Bishop, 1970; Hochachka et al., 1973; Storey and Storey, 1978; O'Dor and Well, 1987).

What is the reason for this unique peculiarity of energy metabolism in squid? Probably, molluscs (unlike plankton crustaceans and fish) are unable to utilize highly calorific lipid substances. Instead, they have maximally developed the ability to utilize protein, which is characteristic of the lowest invertebrates with slow motility (Shulman et al., 1984, 1993). It has been observed that fish with moderate mobility also use protein as the main energy substrate, but fast-swimming ones never do (Shulman, 1974; Stolbov et al., 1995; Shulman and Love, 1999).

Besides, very low values of the AQ show that a considerable amount of the protein substrates (20 to 50%) are used anaerobically in the energy metabolism of squid (see Table 3). This may be explained as 'overfeeding', or surplus food consumption by squid (mainly proteins as in myctophids and fry of their own species). The consumed oxygen is insufficient for the oxidation of this food. This is an example of a peculiar functional hypoxia connected, not with oxygen deficiency in the external environment, but with the necessity to utilize 'endogenous' oxygen, which is formed during catabolism of reserve substances and probably from tissue destruction (Shulman et al., 1993). A similar phe-

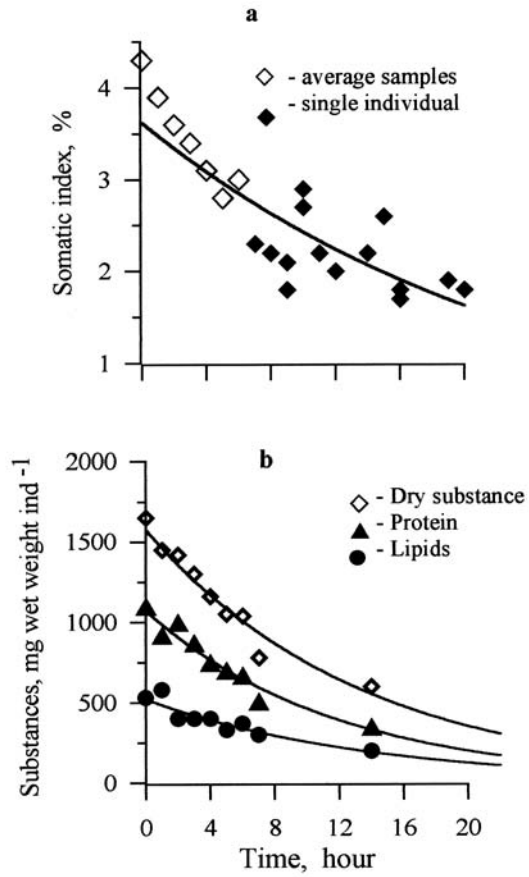


Figure 2. *Sthenoteuthis oualaniensis*. Decrease in somatic index (a) and substances content (b) in hepatopancreas during experimental starvation. From: Shulman and Nigmatullin, 1981; Shulman, 1982.

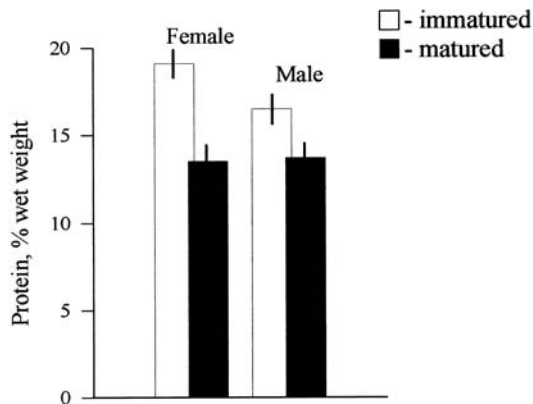


Figure 3. *Sthenoteuthis pteropus*. Decrease in protein content in hepatopancreas during maturation. From: Chesalin et al., 1992.

Table 4. 22:6 ω 3 fatty acid content (% of total fatty acids) in phospholipid of different marine animals.

Animal	Species	22:6 ω 3, %	Authors
Molluscs			
Squids	<i>Sthenoteuthis pteropus</i>	44.0	Yuneva et al., 1994
	<i>Illex illecebrosus</i>	40.7	Jangaard and Ackman, 1965
Cuttlefish	<i>Heteroteuthis dispar</i>	32.0	Culkin and Morris, 1970
Octopus	<i>Eledonela pygmaea</i>	22.8	Culkin and Morris, 1970
Pecten	<i>Pecten maximus</i>	8.4	Ackman, 1982
Mussel	<i>Mytilus edulis</i>	3.2	Ackman, 1982
Oyster	<i>Ostrea edulis</i>	2.3	Ackman, 1982
Crustacean			
Copepoda	<i>Calanus euxinus</i>	39.8	Yuneva et al., 1998
Euphausida	<i>Stylocheiron abbreviatum</i>	29.2	Yuneva et al., 1992
Fishes			
Anchovy	<i>Engraulis encrasicolus</i>	34.6	Yuneva, 1990
Horse mackerel	<i>Trachurus mediterraneus ponticus</i>	40.0	Yuneva et al., 1991

nomenon was noted for some predatory fish just after hunting (Sukumaran and Kutty, 1977). Apparently, the phenomenon can be specific to many predators, but until now has not been paid enough attention. In any case, squid have a powerful mechanism to use protein and amino acids in anaerobic metabolism for providing high functional activity based on the same mechanism as in some other marine invertebrates (Hochachka and Mustafa, 1972; Hochachka et al., 1973; Hochachka, 1994).

Also it is necessary to pay attention to the significance of carbohydrate substrates (glycogen and glucose) in the energy metabolism of the squid. It is known that fish use glycogen as 'starting fuel' in burst swimming (Black et al., 1961; Morozova et al., 1978). There is also information that squid use glycogen for burst swimming during hunting or evading predators (Hochachka et al., 1975). The liver of squid hardly stores glycogen at all

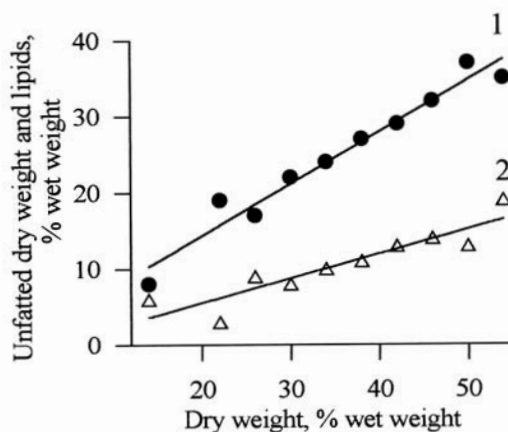


Figure 4. *Sthenoteuthis pteropus*. The relationships between dry weight content and unfatted dry weight (1) and lipids (2) (% of BW) in hepatopancreas squids. (Tropical zones of the Indian Ocean, RV PROFESSOR VODYANITSKY, July–August, 1978) From: Nikolsky and Shulman, 1980.

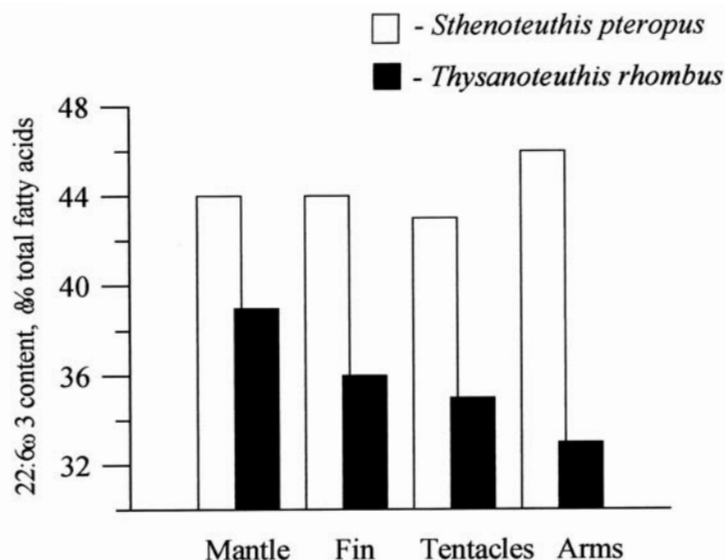


Figure 5. Percentage of 22:6ω3 fatty acid in phospholipids of the different parts of the squid body. From: Yuneva et al., 1994.

(Shchepkin et al., 1981), perhaps because jet swimming does not allow accumulation in appreciable quantities.

In studying major chemical components of squid, the main attention has been to proteins, but lipids have been 'in shadow'. Neutral (reserve) lipids play a subordinate energy role in squid, probably being used mostly in reproductive processes. But the significance of polar lipids (phospholipids) in vital functions of squid (as well as animals in general) is extremely important. Phospholipids are a principal component of cellular and subcellular membranes, as bilayers. The content of phospholipids in total lipids of tissues and organs in *S. pteropus* is 20 to 30% (Yuneva et al., 1994) and in *S. oualaniensis* is even higher, 36-51% (Shchepkin et al., 1981). High contents of sphingomyelin, phosphatidyl serine and phosphoinositol were shown in phospholipids of *S. pteropus* tissues (Yuneva et al., 1994). High content of polyunsaturated fatty acids (PUFA) in phospholipids of muscle attract special attention. First of all, the most unsaturated in the w3 series is docosahexaenoic acid 22:6w3 (Table 4, Fig. 5). The content of this fatty acid in phospholipids of fin, mantle, tentacles and arms is 44 to 45%. Hayashi (1996) also showed high content of 22:6 w3 in muscles of different squid species. Earlier it was concluded that, in marine animals, 22:6w3 fatty acid plays a cardinal role in providing the high functional activity and adaptive plasticity of membranes, tissues and the whole organism (Shulman and Yakovleva, 1983; Shulman and Yuneva, 1990; Yuneva et al., 1998). There is also a close correlation between the content of this acid in bodies of fish and plankton crustaceans and their motility. The content of 22:6w3 in squid muscle is considerably higher than in cuttlefish or octopods, not to mention bivalve molluscs. Significantly, in *S. pteropus* it is higher than in another less motile species from tropical Atlantic *Thysanoteuthis rhombus*. Such high 22:6w3 content in squid muscle, even in comparison with fast swimming fish and vertically migrating copepods, is evidence of extremely high functional activity (in this case, mobility) of squid.

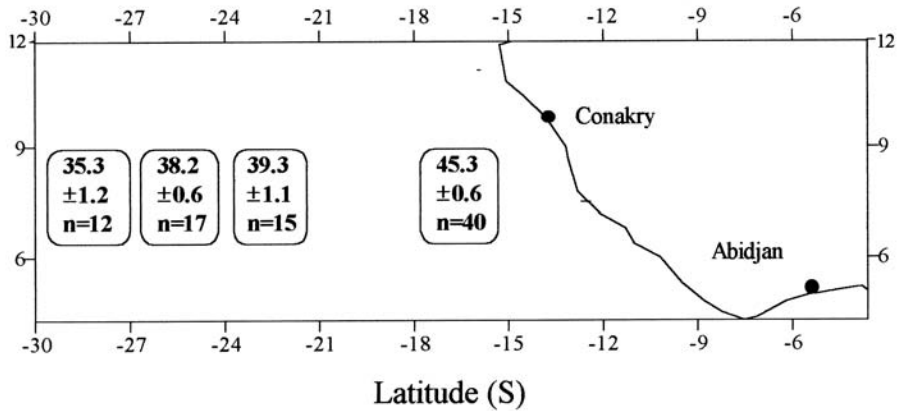


Figure 6. *Sthenoteuthis pteropus*. Dry weight content (% of BW) in hepatopancreas (transection of Conakry, RV "Mikhail Lomonosov", July 1988).

Contents of reserves are connected to conditions of feeding and reflect the food supply of animals. This is demonstrated by spatial-temporary variability of dry matter in the squid *Sthenoteuthis* liver in areas that differ in biological productivity (Shulman et al., 1992b). Also it is possible to use dry weight (consisting almost completely of proteins and lipids) as an index of squid food supply in field conditions. Thus, it was shown that liver dry weight of *S. pteropus* decreases in the direction from the African coast to the open ocean (Fig. 6) (Abolmasova et al., 1990 b). The dry weight of squid liver near the Guinea shelf (59.5%) was higher than in the Caribbean Sea (48%), and in the Amazon-River region (41.5%) (Abolmasova et al., 1990 a). *S. oualaniensis* from the Indian Ocean has the highest liver dry weight (44.8%) in the Southern Hemisphere (from 10 to 20° S). This is followed by Bengal Bay at 39.1% and the sector between the African Horn and India (36.6–37.6%). The lowest was in the Red Sea (35.3%) (Shulman and Yakovleva, 1981). Probably all these data even without information on the fodder base, indicate the status of the overall food supply in the regions investigated.

ELEMENTS OF THE ENERGY BALANCE

The majority of pelagic squid, including the genus *Sthenoteuthis*, have a high growth rate, short life span and high fecundity. Thus, taking into account a very high-energy metabolism, it is interesting to estimate total food consumption and overall energy budget for these squid.

Estimations of food consumption by squid have been carried out by various methods. Some results are shown in the Table 5. The calculations of daily food intake by adult *S. oualaniensis* (15–24 cm ML), based on the reduction of their liver weight during starvation, have shown that it attains values of 9 to 12% wet body weight (Shulman and Nigmatullin, 1981). Many calculations for different size age groups of the *Sthenoteuthis* squid were made using field data on daily dynamics of stomach content and experimental data on rate of food digestion (Nikolsky and Chesalin, 1983; Chesalin, 1988, 1994a,b, 1996). The values of intake vary from 27.8% for juveniles to 2.9–4.0% for large adult squid. From data on nitrogen, excretion of the daily intake of *S. oualaniensis* (300 g BW,

Table 5. Daily increments and food rations (% body weight) of some squids species.

Species	Weight, g	T, °C	Growth increments	Rations	Authors
<i>Sthenoteuthis oulaniensis</i>	90–350	26–29	-	12.0–9.0	Shulman and Nigmatullin, 1981
<i>Sthenoteuthis oulaniensis</i>	300	26–29	-	6.5	Shulman et al., 1984
<i>Sthenoteuthis oulaniensis</i>	20–700	26–29	-	19.2–7.4	Abolmasova et al., 1990
<i>Sthenoteuthis oulaniensis</i>	20–100	26–29	-	16.8	Chesalin, 1994
<i>Sthenoteuthis oulaniensis</i>	100–500	26–29	-	7.2	Chesalin, 1994
<i>Sthenoteuthis oulaniensis</i>	1,000–6,500	26–29	-	5.4	Chesalin, 1994
<i>Sthenoteuthis pteropus</i>	300	26–28	-	8.6–6.7	Shulman et al., 1984
<i>Sthenoteuthis pteropus</i>	100–700	26–28	-	10.5–4.5	Shulman et al., 1984
<i>Sthenoteuthis pteropus</i>	1–700	26–28	-	45.7–7.5	Abolmasova et al., 1990
<i>Sthenoteuthis pteropus</i>	5–20	26–28	-	27.8	Chesalin, 1994
<i>Sthenoteuthis pteropus</i>	20–100	26–28	-	13.4	Chesalin, 1994
<i>Sthenoteuthis pteropus</i>	100–1000	26–28	-	6.9	Chesalin, 1994
<i>Sthenoteuthis pteropus</i>	1000–5000	26–28	-	4.0	Chesalin, 1994
<i>Loligo plei</i>	12–285	18–23	1.9	18.0–10.0	Hanlon et al., 1983
<i>Loligo pealei</i>	28–235	15–23	1.4	11.0	Hanlon et al., 1983
<i>Loligo pealei</i>	75	15	-	9.3	Macy, 1980
<i>Loligo opalescens</i>	1–100	15–20	5.5–0.6	-	Hurley, 1976
<i>Loligo opalescens</i>	108–232	20	-	14.9	Yang et al., 1983
<i>Illex illecebrosus</i>	100–300	7–15	1.9–1.2	10.0	Hirtle et al., 1981
<i>Illex illecebrosus</i>	169	7	-	8.8	Hirtle et al., 1981
<i>Illex illecebrosus</i>	10–290	7–15	3.0–0.9	-	O'Dor et al., 1979
<i>Illex illecebrosus</i>	142	7–17	1.9–1.0	6.7–3.6	O'Dor et al., 1979
<i>Illex illecebrosus</i>	230	15	-	6.7	Kao, 1970
<i>Illex illecebrosus</i>	100–280	10–15	-	5.8	Vinogradov and Noskov, 1979
<i>Todarodes pacificus</i>	30–35	15–27	-	25–20	Mikulich and Kozak, 1971
<i>Dosidicus gigas</i>	0.5–30	25–30	22–17	-	Arkhipkin and Murzov, 1986
<i>Dosidicus gigas</i>	30–300	25–30	3.8–3.6	-	Arkhipkin and Murzov, 1986
<i>Dosidicus gigas</i>	300–950	25–30	2.8–2.5	-	Arkhipkin and Murzov, 1986
<i>Dosidicus gigas</i>	950–3500	25–30	2.5–2.2	-	Arkhipkin and Murzov, 1986
<i>Dosidicus gigas</i>	300–500	25–30	-	9.0–7.2	Bazanov, 1986
<i>Dosidicus gigas</i>	1000–1500	25–30	-	5.5–4.2	Bazanov, 1986

20 cm ML) was estimated as 6.5%, and for *S. pteropus* of same sizes - 6.7% (Shulman et al., 1984). The data on oxygen consumption (Abolmasova, 1985; Belokopytin, 1982), weight increments (Zuyev et al., 1985) and food assimilability, accepted as 95% (La Roe, 1971; Boletzky, 1974; O'Dor et al., 1979), have allowed the calculation of food assimilation, daily food consumption and coefficients of utilization of the consumed food for growth. The daily ration was calculated: for *S. pteropus* (1–700 g) from 45.7 to 7.5% (mean 14.5%); and for *S. oualaniensis* (20–700 g) 19.2–7.4% (mean 11.4%) (Abolmasova et al., 1990a). The coefficients of utilization of energy consumed (K_1) and assimilated (K_2) food for growth (Ivlev, 1939) for *S. pteropus* were 10.2–37.2% and 10.8–39.0%, for *S. oualaniensis* 7.2–34.1% and 7.6–34.9%, respectively*. The energy balance was estimated from the equation:

$$C = Q + P + F,$$

where F is energy of unassimilated food. The energy balance for squid of 300 g BW were calculated according Abolmasova et al. (1990a) as:

$$25.20 = 3.10 + 20.84 + 1.26 \text{ (} S. \text{ pteropus)}$$

$$26.11 = 2.63 + 22.46 + 1.30 \text{ (} S. \text{ oualaniensis)}.$$

The average daily rations for these specimens of both species have made about 9% wet body weight.

It should be noted that the data on energy expenditure for formation generative and other released products (for example, ink and mucus) were not included in these balance calculation, therefore values of food consumption (daily ration) should be even higher. Also after publication of these calculations, new data on growth increments of the squid genus *Sthenoteuthis*, based on the analysis of recording structures (statoliths, gladii) were obtained (Arkhipkin, 1989; Arkhipkin and Mikheev, 1992; Bizikov, 1991, 1996). They have shown that these squid have short life spans of about 1 yr, whereas earlier results of the analysis of size structure estimated their life span as 2 yrs (Zuyev et al., 1985). Thus, the expenditure on the substance metabolism, food assimilation and food consumption should be higher.

Doubtless, the correct estimations of the energy balance for the squid of genus *Sthenoteuthis* is a very difficult task. Their behavior and distributions change significantly during ontogeny, and they have a complicated intraspecific structure. *S. oualaniensis* has at least three intraspecific forms: dwarf early-maturing equatorial (adult females 9–15 cm ML); middle-sized late-maturing tropical (adult females 16–30 cm ML) and giant Arabian (adult females 27–62 cm ML) (Chesalin, 1994b). Nevertheless, even the rough estimations of the energy balance of squid are very important, because they are an approach to defining their quantitative role in communities.

The results of all research show very high food rations for squid to maintain their active mode of life. The daily food rations of the adult squid are estimated on the average from 8 to 10% body weight, while it is known that the daily rations for most adult pelagic fish are on average 1–5% wet body weight.

* $K_1 = P/C$ and $K_2 = P/P+Q$, where C is energy of consumed food; Q is expenditures on energy metabolism; P is expenditure on growth. All values are represented in kcal ind⁻¹ day⁻¹.

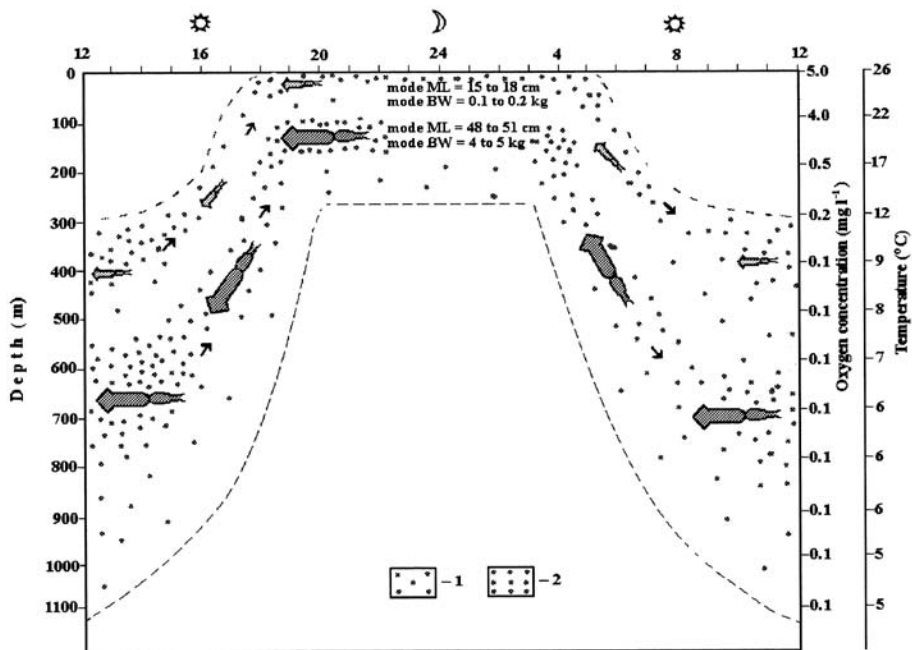


Figure 7. *Sthenoteuthis oualaniensis*. Pattern of vertical distribution of middle-sized and giant forms in the Arabian Sea. Concentration of individuals: 1 – low density, 2 – high density.

ADAPTATIONS TO LOW OXYGEN CONDITIONS

Despite of very high levels of the energy metabolism and oxygen requirements, the squid have developed special metabolic mechanisms, promoting their living in zones with low oxygen content (hypoxia). Earlier, it was assumed, that *Sthenoteuthis* squid cannot exist at oxygen concentration lower than 40%, which would limit their distribution top to the 200 m (Zuyev et al., 1985). However, using submersibles in 1986 the extensive aggregations of large *S. oualaniensis* in depths to 350 m were found in the Arabian Sea (Gutsal, 1989; Zuyev and Gutsal, 1989).

Giant form *S. oualaniensis* inhabit in depths of 550–800 m (maximal 1100 m) in daytime and migrate to the gradient layer (approximately 50–150 m) for feeding during the night (Fig. 7). At the same time the middle-sized *S. oualaniensis* lives in the epipelagial at depth set about 300–400 m during daytime and ascend to the surface at night.

Oxygen concentration at the depth 300 to 400 m does not exceed $0.1\text{--}0.2\text{ mg L}^{-1}$ (2–4% of saturation) and a water temperature of $9\text{--}12^{\circ}\text{C}$; at depth of 250–150 m are 0.2 to 0.5 mg L^{-1} (4–10% of saturation), at $12\text{--}17^{\circ}\text{C}$, and only between 150 and 100 m in the gradient layer do oxygen concentrations vary from 0.5 to 4 mg L^{-1} , at $17\text{--}22^{\circ}\text{C}$. It is remarkable that squid which live most of the time in the hypoxic zone are considerably bigger than upper layer squid. For instance, females of *S. oualaniensis* caught in the surface at night had modal sizes 15–18 cm ML and 0.1–0.2 kg BW (maximal 32 cm and 0.9 kg). Females caught at the same time in the depth about 100 m amount to modal sizes 48 to 51 cm ML, and 3.9 to 4.8 kg BW (maximal 62 cm and 8.9 kg). Thus, body weights of the *S.*

oualaniensis giant form exceed the weight of the middle-sized form almost in 50–100 fold!

The *Sthenoteuthis* squid are not unique inhabitants of the hypoxic zone; also in this zone live abundant marine animals such as copepods, salps and small mesopelagic fish (myctophids, gonostomatids, etc.) (Kukharev et al., 1988). It is possible that these animals have special mechanisms allowing them to live in these conditions.

Until now glycogen was considered as the main biochemical substrate, for marine animals under hypoxic conditions (Brandt, 1951; Blazka, 1958; Hochachka and Somero, 1973; Goromosova and Shapiro, 1984; Lushchak, 1994). But, this mechanism was discovered in bottom animals (gastropods, bivalves, sessile and free-swimming crustaceans, and sluggish fish), which have high glycogen content in tissues. On the contrary, the glycogen content of tissues of active pelagic animals, especially squid, is extremely low.

Recently, it has been shown that one of the most important mechanism of adaptations, which provides normal existence of planktonic crustaceans and fish in oxygen deficiency may be anaerobic utilization of protein in energy metabolism. These data are supported by physiological research on whole organism (Douglas et al., 1976; Schmidt-Nielsen, 1975; Shulman et al., 1993; Svetlichny et al., 1998), as well as subcellular and molecular studies (Hochachka et al., 1973; Savina, 1992). It was noted above that squid in normoxic conditions during overfeeding utilize considerable part of protein in energy metabolism anaerobically. Consequently, this suggests that these animals have powerful mechanisms, which could resist hypoxia. Thus, they can inhabit depth of the Arabian Sea almost without oxygen.

The role of 'protector' from hypoxia is transferred from glycogen to protein. The 'deep' squid caught in the Arabian Sea have a distinct smell of ammonia, the main terminal product of protein catabolism in most marine animals. There is evidence of its high ammonia concentration in tissues. Its rate of excretion from organisms is the indicator of the intensity of this process.

Hypoxic zones (with oxygen concentration $0.1\text{--}0.2\text{ mg L}^{-1}$) occur rather often in the World Ocean especially in its tropical parts, occupying a thick layer of water, from 200 to 800 m (Douglas et al., 1976; Lalli and Parsons, 1997). Therefore it is possible to assume that in such sites the new populations of *Sthenoteuthis* squid can be found that are adapted to existence in such conditions.

It is remarkable that squid of the giant form of *S. oualaniensis* not only have adapted to live in hypoxic conditions, but essentially have increased the growth rate and biomass there. Obviously, it is connected to a 'redistribution' of consumed energy: reduction of expenditure on energy metabolism and an increase of expenditure on growth. Presumably, 'deep' squid have lower expenditures on aerobic respiration and are less active than 'surface' squid. Anaerobic metabolism gives 12–15 times less energy, than aerobic. However, it is necessary to take into account the temperature factor. Obviously, the energy expenditures of the giant form of *S. oualaniensis* at lower temperatures will be lower than for the middle-sized squid. The observations from submersibles show that large squid do not form schools and their behavior is rather quiet, they 'hover' in the water and occasionally make pendular motions to catch prey (mainly, myctophids).

The values of increments in length and weight in 'deep hypoxic' squid of the giant form, evaluated by gladii analysis (Bizikov, 1991, 1993) are much higher, than for middle-sized forms, living in normoxic conditions, but the life span of both forms is about 1 yr. Thus, the giant Arabian form has much higher efficiency in the usage of consumed food

energy for growth than middle-sized tropical form. Besides this, giant squid possible eat more. According to our preliminary estimations the coefficient of utilization of energy from assimilated food for growth (K_2) for the giant form can reach 60%.

The marvelous phenomena of giant weight and size of these animals from the hypoxic zone is the result of an energy balance change in squid from expenditure for metabolism to utilization for growth and maturation. It has resulted in the formation of large squid aggregations in hypoxic zones that can be of present special interest for fishery.

METABOLIC STRATEGIES OF ADAPTATIONS

What are the special features of metabolic strategies of squid genus *Sthenoteuthis* that provide their biological progress? Characterizing conditions of the squid habitat we already mentioned some abiotic (temperature, oxygen concentration) and biotic (food base) factors which are important for their adaptations.

Temperature is one of the main determining factors of vital functions, influencing the level of energy metabolism, the rate of substance and energy consumption, and the intensity of production processes. Most *Sthenoteuthis* are active pelagic animals, which constantly live in the tropical zone at high water temperature (to 30°C), and therefore, have a very high level of energy metabolism and, according to these high food requirements. Obviously, to constantly maintain high metabolism in the rather poor biomass areas of the open ocean is very difficult for the squid. Therefore these squid have adapted to diel vertical migrations; they rises to the surface (with the temperature 25–30°C) for active feeding at the night, and descend in the depth (where temperature are on 10 to 15°C lower) to rest during daytime. The rate of the active energy metabolism is reduced 3–4 times, and, there is a change of assimilated energy benefiting to the increase the efficiency of growth and maturation. The squid not only optimize the energy expenditures and energy balance, but also avoid the pressure from daytime predators.

The high natural mobility of squid, and their physiological features have determined: the high levels of oxygen consumption and, accordingly, high levels of energy metabolism, utilization of protein as the main substrate for energy metabolism; the fatty acid composition of muscles and liver including the prevalence of the most polyunsaturated 22:6w3 fatty acids in phospholipids, high muscle weight; high efficiency in use of food for metabolism (at low efficiency of swimming), high productivity over all.

The original abiotic factor of the environment, that exerted the most influence on the metabolic adaptation of *Sthenoteuthis* and their intraspecific differentiation, was hypoxia. Squid have appeared that are capable of living in conditions of extreme oxygen deficiency, passing on anaerobic utilization of proteins and their breakdown products, free amino acids. Some have adapted to live in gradient layer with sharp changes of many environmental parameters (temperature, density, salinity, oxygen content, etc.).

The difference of level of metabolic activity of squid reflects the difference of the level of food consumption, which depends on such biotic environmental factors as the state of food base. Some squid have adapted to migrations to the water surface in night, where one of their main food objects is flying fish, while others, such as giant Arabian form, have adapted to eat in the so-called sound-scattering layer (SSL), where many mesopelagic fish (myctophids, gonostomatids, etc.) concentrate. Thus, the squid have mastered the most productive surface and gradient water layers and they are divided on two intraspecific groupings (forms). The formation of new populations and complicated in-

traspecific structures of *Sthenoteuthis* provide an example of the process of sympatric speciation, which is very difficult to study on other marine animals.

So, the squid of genus *Sthenoteuthis* due to high functional activity and metabolic plasticity have evolved the strategy of maximal utilization of food base resulting in a wide expansion of species ranges: geographically, worldwide in tropical zone and vertically, epi- and mesopelagial. It is known, that the large squid have little internal energy limits for their distribution (O'Dor, 1988). The *Sthenoteuthis* squid along with other active predators, such as tunas, dolphin fish, and small sharks are widely distributed and occupied all tropical zones of the World Ocean. They successfully compete with predatory fish and, due to high abundance and high food consumption, have practically filled a niche of middle-sized and in some places of large nektonic predators (the apex trophic levels).

CONCLUSION

Summarizing the results of investigations carried out on squid with two vicariant species *S. pteropus* from the Atlantic and *S. oualaniensis* from the Indian Ocean, it can be considered that these animals have a range of unique special features of metabolism. They are: (1) very high level of energy expenditures and substance catabolism as well (according to nitrogen excretion) in comparison with other animals; (2) an obvious nutritious reserve (mainly protein) function in the hepatopancreas (liver); (3) utilization of protein as the main biochemical substrate in energy metabolism; (4) significant anaerobic protein utilization in energy metabolism during intensive food consumption; (5) very high content of the most unsaturated 22:6w3 fatty acid (especially in phospholipids) in the muscles; (6) providing squid' habitant under changeable oxygen and temperature regimes; and (7) increased rate of growth in deficient oxygen environments, due to high efficiency of food utilization.

The metabolic strategy of the squid genus *Sthenoteuthis* consists of maximal intensification of their energy and substance metabolism, utilizing for this purpose the appropriate biochemical substrates, especial functional organization of cellular and tissue structures. All this provides biological progress for these animals, their high abundance and the domination in pelagial of the tropical zone of the World Ocean.

There is still much more to be learned from the study of the physiology and biochemistry of squid, with even strange species promising discoveries concerning wonderful new properties of their metabolism and biology.

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