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By B. G. Ivanov

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BIOLOGY OF THE NORTHERN SHRIMP (PANDALUS BOREALIS Kr.) IN THE BERING SEA AND THE GULF OF ALASKA /392*

B.G. Ivanov

The northern shrimp (chilim**) (Pandalus borealis Kr.) is an important commercial commodity for a number of European countries, USA and Japan. Shrimp fishing is also being successfully developed in the USSR. The catch of this species in the Atlantic has consisted, in the last few years, of 20-25.5 thousand tons, and in the Pacific, about 25 thousand tons. In 1965 the Soviet fishing fleet caught approximately 2.7 thousand tons of shrimps, and in 1966, 10.7 thousand tons (primarily in the Gulf of Alaska).

Many studies have been devoted to the biology of this very important commercial product, and P. borealis is, at the present time, one of the better know species. The interest

*Translator's note: Number in the margin refers to the page number of original text.

**Translator's note: Chinese common name.

in this species is stimulated not only by its commercial importance, but by the fact that P. borealis is one of the most common and numerous of invertebrate species in the Atlantic, from the North Sea to Spitsbergen and Iceland and along the shores of Newfoundland and Greenland, and in the Pacific Ocean, from the Japan Sea and British Columbia to the Bering Sea. The study of the biology and distribution of this species is extremely important for the establishment of zoogeographic and biocoenotic patterns.

P. borealis was described in 1838 (Kroyer, 1838), and until the end of the nineteenth century, this species was of interest only to zoologists. It was not until after the work of Hjort and Petersen, who used a special small-meshed trawl, that there was proof of its commercial potential, in the fiords of Gul'mar, Larvik and Langesund. In 1898, commercial shrimp fishery commenced in southern Norway and Sweden. The development of the industry required exploratory work and research into the biology of P. borealis, which led to the discovery of new commercial banks (Wollebaek, 1903, 1908). However, until 1929, the study of the biology of this species could not become fully successful. It was only after the discovery of the existence of proterandrous hermaphroditism in the shrimps of the family Pandalidae, the sharpest and most characteristic feature of their biology, that the study of P. borealis and other representatives of this family began to forge ahead rapidly. This discovery belongs to A. Berkeley (1929, 1930) who published the first data on the biology of P. borealis (and other species) off the shores of British Columbia and who first described the complete development of the larvae of this species (as indicated by M. Lebour, 1930, the larvae of P. borealis described by Sars (1930), were found to be actually the larvae of Caridion gordoni). After the discovery of the existence of proterandrous hermaphroditism in the pandalids, the knowledge of the biology of P. borealis expanded rapidly. Though the first data on the histology of the gonads and the gametogenesis were produced by A. Berkeley (1930) (utilizing P. danae as the example), Jagersten (1936) supplemented her imformation and was the first to isolate from the ordinary females which have undergone sex reversal and who first deposit eggs at the age of 2.5 years, fast-growing females which already deposit eggs at the age of 1.5 years, Jagersten divided the latter into "primary" and "secondary". The ordinary females, which undergo their change in sex at the age of 2 years and which function in the capacity of males at the age of 1.5 years, retain their male sex openings on the coxopodites of the fifth pair of /393 pereiopods, for their entire life. Primary females, which are encountered much more rarely than ordinary females, never function in the capacity of males, and their development takes place so rapidly that their external male sexual characteristics are never formed. These females do not have male sex openings.

In secondry females, encountered even more rarely than primary females, development in the male direction at first predominates over the female. They display a number of male characteristics and the male sex openings or their traces, are retained by them for their whole life, as they are in ordinary females.

Jagersten (1936) described the pattern of the growth and the sexual development of the northern shrimp of Gul'mar Fiord (Sweden). Hjort and Ruud (1938) made a detailed survey of the development of the fishery of P. borealis in European waters, described the fishery areas and examined pertinent aspects of their biology. They also threw light on the growth and the sexual development of the shrimps of southern Norway. In 1946 Poulsen published data on the Danish northern shrimp fishery and his own observations on the biology of this species in the Skagerrak. His results proved to be very similar to those of Hjort and Ruud.

All the studies mentioned concerned the biology of the northern shrimp inhabiting areas close to the southern boundaries of its range (the southern coast of Norway, Sweden, Skagerrak, British Columbia). For this reason, P. borealis appeared to be a species with relatively constant basic biological characteristics (rate of growth, sexual development, time of egg laying and the hatching of larvae and so on). In all these areas, P. borealis matured and participated in reproduction in the capacity of the male at the age of 1.5 years, and in the following reproductive season, the great majority of the individuals functioned in the capacity of females and deposited eggs for their first time. Only an insignificant number of the shrimps would have already deposited eggs by the age of 1.5 years, or conversally, remained males into the third year. Relatively small also were the variations in the times of transferring eggs to the pleopods and in the times of the hatching of larvae. However, the remarks of various authors (Stephensen, 1935; Hofsten, 1916; Dons, 1915; Kiaer, 1903) on the finding of females with eggs and on the sizes of shrimps in the waters of Greenland, Spitsbergen and northern Norway, provided a basis to consider that, in northern regions, the growth and the times of the laying of eggs and the hatching of the larvae were different than in the south.

In 1941, Z.G. Palenichko (1941) demonstrated that, in the waters of the central part of the Barents Sea, there was a significant change in the times of egg deposition and in the hatching of larvae, and in the other features of the biology of the northern shrimp, by comparison with those of the southern regions. The materials available to Z.G. Palenichko were limited. For this reason, a number of her conclusions on growth, sexual development and the times of the hatching of eggs are found to be in need of refinement and correction in the light of later data. However, the sections dealing with the distribution of P. borealis in the Barents Sea and on the distribution of various size groups, continues to attract considerable interest. Unfortunately, her work remains unknown to authors abroad.

Rasmussen (1942, 1945, 1947, 1953) was the one who most clearly demonstrated the plasticity and variability of the basic indicies of the biology of P. borealis. It was only after his work that it became clear that the time of the onset of sexual maturity and the change in the sex of P. borealis varies within extremely wide limits, depending primarily on thermal conditions in the locale inhabited by the shrimps. Relative to this, the populations of the northern regions are observed to have a much slower growth rate and rate of development of sexual maturity, than the populations of the southern, warmer regions, Rasmussen indicated, that even within the limits of the same fiord, the shrimps of /394
different generations can grow at completely different rates, depending on the hydrological peculiarities of a particular year, though he was unable to illustrate this with extended hydrological data, and did not show which period appeared to be critical in the determination of the rate of growth of the population.

Due to the variability in the biology of P. borealis, the need arose, in order to obtain the accurate biological data required by the shrimp fishing industry, to carry out research work throughout the entire range, or at least, in all the areas in which shrimp fishery was being carried out. The biology of this species along the coasts of western Greenland was elucidated in the work of Horsted and Smidt (1956). These authors also first demonstrated the influence of temperature, not only on the rate of growth and maturation, but also on the reserve stocks and on the fluctuation of the numbers of shrimps in the various regions of Greenland (Horsted and Smidt, 1956, 1965). Under the conditions off Greenland, where P. borealis exists at close to a limiting temperature, near the northern boundary of its range, the smallest fluctuations in temperature might constitute a vast influence on the shrimp population. Considerable attention was also devoted to the influence of fisheries on the reserve stock. As a result, very interesting data were published on the relationship between the temperature at the time of hatching of the larvae and the yield of the corresponding generation (Dow, 1963, 1964).

Allen (1959) studied the life cycle of the northern shrimp in the North Sea, off the shores of Northumberland, that is, at the southern boundary of its range, where this species exists at higher temperatures. It was found that the percentage of primary females here was considerably higher than in Norway. Besides this, he supplemented the data of Berkeley and Jagersten on gametogenesis and the changes of the external sexual appendages throughout the course of development, and summarized data on growth and development. After the work of Allen, the biology of the northern shrimp in the Atlantic was seen to have been completely studied throughout the whole extent of its range, from the north to the south. However, the interest in this subject has not flagged, and apparently, will not flag for a long time yet. The interest in the northern shrimp is maintained, primarily, as was the case earlier. by the continuing development of the fishery. In latter years it has been shown how intensive fishing affects the size composition of the population (Jensen, 1965), and how, in isolated fiords, it can even disrupt the stock (Sigurdsson and Hallgrimsson, 1965). This listing of basic studies of the biology of P. borealis would not be complete without note being taken of the work of Carlisle (1959a, b and c), which was devoted to the study of the hormonal control over the sex transformation of the shrimps.

The foregoing short review of the main studies on the biology of the northern shrimp represents an inumeration of the successes of European researchers. Quite different were the facts of the matter in the Pacific Ocean where, after the brilliant work of Berkeley (1930), a long pause ensued. Shrimp fishery was only weakly developed in the

Pacific Ocean basin, though trawl fishing (beam-trawls) had commenced in Puget Sound, apparently, even earlier than in European waters (Smith, 1937). The northern shrimp was not present in great numbers along the shores of Japan and the Soviet Union, and the attention of researchers was attracted by other species (Kubo, 1951; Jgarashi, 1951; Aoto, 1952). Along the coats of Canada and south-eastern Alaska (Hynes, 1929) the shrimp fishery was small in scale. The exploratory work of American authors led to the discovery of many rich commercial banks and afforded considerable aid to the developing fishery. However, the papers published by these authors contained practically no information on the biology of the northern shrimp in the new regions of the Gulf of Alaska (Greenwood, 1958, 1959; Johnson, 1959; Shaefers and Smith, 1954; Wathne and Johnson, 1961; Alverson, 1962; Roncholt, 1963; Rathjen and Jesaki, 1966). The interest /395
in the northern shrimp was once more renewed in connection with the development of fisheries in the Bering Sea and the Gulf of Alaska and the work of the Bering Sea Scientific and Fisheries Expedition of the Pacific Scientific Research Institute of Fisheries and Oceanography and the All-Union Scientific Research Institute of Fisheries and Oceanography.

In 1963 and 1964 we published the first preliminary data on the life cycle of the northern shrimp of the western part of the Gulf of Alaska and the Bering Sea (Ivanov, 1963, 1964,b), collected during the cruises of SRT-4454 (April-May, 1961) RT "Adler" (August, 1962) and SRTR "Krym" (December, 1962-February, 1963).

Utilized for the present study were materials obtained in previous voyages, and additional new materials, collected in the western part of the Gulf of Alaska (islands of Kodiak and the island of Sanak) and the Berling Sea, off the Pribiloff Islands, during the cruise of SRT "Baksan", from 13 July to 29 September, 1963 and SRT "Kal'mar" from 1 March to 1 June, 1965. Besides the author, the collection of biological and hydrological data was engaged in by the following co-workers of the Far-Eastern Scientific and Fisheries Long-Range Exploration; O.A. Petrov, Yu.I Lemza, S.R. Filipas, G.I. Krovetskii, the Moscow State Pedagogical Institute student S.G. Karapetyan, M.V. Kuchin, V. Bessarab, N. Koval'chuk and V. Golovko. The author is sincerely grateful to them for their assistance in the work.

The methadology of the work and the fishing equipment employed was the same as that of the previous cruises (Ivanov, 1963, 1964 a, b). Taken as the basic measurement was the length of the carapace from the posterior edge of the orbit of the eye to the posterior edge of the lateral side of the carapace, as was done by Horsted and Smidt (1965) and Allen (1959). For conversion to overall length we employed the coefficients developed in the preceding work (Ivanov, 1946 b).

REPRODUCTION PERIODS

As indicated by Rasmussen (1953), Horsted and Smidt (1956) and Allen (1959), the reproduction periods of P. borealis vary considerably in the various parts of their range. In the northern regions the period of the incubation of the eggs is longer, relative to which, this longer period is due both to the earlier deposition of the eggs and as a result of the later hatching of the larvae. Off Northumberland, at the southern boundary of the range of P. borealis, hatching takes place between the 10th. of March and the 16th. of April, and the deposition of the eggs takes place between the 10th. of October and the 1st. of December, while off Spitsbergen, near the northern boundary of the range, the laying of the eggs takes place from the beginning of July to the end of October, that is, over a period of almost three months, and the hatching of the larvae commences at the end of April, reaches its maximum in May, and ends in June, that is extending 2-2.5 months. Thus, in the more southerly and warm part of the range, the period of egg-carrying lasts for 4.5 months, and in the colder parts, about 9 months.

In the Pacific Ocean, where the southern boundary of the range of the northern shrimp passes along Peter the Great Bay and the island of Hokkaido in Asia, and through the Columbia River on the American coast, and the northern boundary is located in the Chukotsk Sea, it is natural to expect that in the western part of the Gulf of Alaska and in the Bering Sea, the periods of egg laying and the hatching of the larvae will be intermediate between the corresponding periods off Northumberland and Spitsbergen.

We did not carry out any collections during the period of egg laying in the Gulf of Alaska, but, from the state of the gonads in the shrimps during the period of our observations and the overall thermal regime in the region of the islands of Shumagin and Kodiak, it may be assumed, that the deposition of the eggs among the northern shrimps takes place from September to November. It is likely, that this process proceeds most intensively from the end of September to the beginning of October.

Work was twice carried out in the Gulf of Alaska /396 in spring and therefor it is possible to give more accurate data on the hatching of the larvae. In 1961 the number of observations was small, but in 1965, during the cruise of SRT "Kal'mar", we were able to accomplish a considerably greater volume of work than in 1961. The data on the process of the hatching of larvae in the Gulf of Alaska in 1961 and

1965 are presented on Table 1. From the information given in this Table it can be seen, that in the western part of the Gulf of Alaska, the hatching of larvae commences at the beginning of March, becomes more intensive in April, and ends, evidently, towards the middle of May. Despite the poverty of data for 1961, it can be seen nonetheless, that in 1961 the hatching of larvae began somewhat earlier and did not proceed as rapidly as in 1965, when practically all the females were freed of their eggs within one month (April).

Table 1 Relationship of egg-carrying females and females freed of eggs in the Gulf of Alaska (islands of Shumagin - island of Kodiak) in various observational periods

Date	Number of females with eggs	Number of females freed of eggs	Percentage of females freed of eggs in the overall number of females
2-10/IV 1961	26	12	32
10-20/IV 1961	9	13	59
20/IV-1/V 1961	38	75	67
1-10/III 1965	362(21)	7	2(7.6)
2-4/IV 1965	279 (4)	6	2.5(3.6)
30/IV 1965	--	--	--
11/V 1965	79(60)	667	89(97.5)

Remarks: In the second column the figure in brackets indicates the number of females in which the hatching of larvae had already commenced, that is, females with eggs remaining. In the fourth column the figure in brackets indicates the percentage of females freed of eggs and with eggs remaining, in the overall number of females.

In the Bering Sea, in the region of the Pribiloff Islands, the deposition of the eggs commences, most likely, at the end of July and the beginning of August. According to our observations, the maximum intensity is reached in the second half of August and the beginning of September, and ends in October. Data on the laying of eggs, for the fall of 1962 and for 1963 are presented in Table 2.

Table 2 Relationship of females with eggs on pleopods to females with eggs held internally in the Bering Sea during various periods of observation

Region	Date	Number of females with eggs internally	Number of females with eggs	Percentage of spawning females
Pribiloff	18-29/VIII 1962	666	352	35
	10-20/VIII 1963	207	90	30
	28-31/VIII 1963	34	135	80
	1/IX-7/IX 1963	5	73	94
Anadyr	10/IX 1963	27	13	32.5

From Table 2 it can be seen that in 1963, the hatching /39/
of larvae took place somewhat earlier than in 1962, and that with respect to the population of P. borealis inhabiting the Anadyr region, the deposition of eggs took place somewhat later by comparison with this process in the shrimps of the Pribiloff area. It is likely that in the Anadyr region, the

most intensive egg laying period occurs in September. The hatching of larvae occurs, evidently, in April and the beginning of May. After the 20th. May, 1965, we encountered only isolated females which had not yet freed themselves of their eggs. Thus, the laying of eggs in the Bering Sea takes place approximately one month earlier than in the western part of the Gulf of Alaska. The hatching of the larvae in the Bering Sea on the other hand, occurs later than in the Gulf of Alasks, but the difference consists of approximately two weeks. Thus, the egg-carrying period of the northern shrimp in the western part of the Gulf of Alaska consists, on the average, of 6.5 months, and in the Bering Sea, 7.5-8 months, counting from the end of the egg-laying period to the completion of the hatching of larvae. Inasmuch as the process of egg deposition and the hatching of larvae is fairly extended, the period, in the course of which females with eggs may be encountered (from the beginning of deposition of eggs to the completion of the hatching of larvae), is found to be significantly greater than the period of egg-carrying, in the Gulf of Alaska, 8.5, and in the Bering Sea, 9.5-10 months.

Despite the fact that females with eggs may be encountered throughout the greater part of the year, we cannot agree with the opinion of Z.G. Palenichko (1941), that "the reproductive period of the species in the north loses its seasonal character and becomes a year-round matter". Such a conclusion was made, basically, as a result, as it would appear to us, of erroneous data on the times of larvae hatching (January-August). It would appear that Kuznetsov (1964) demonstrated more correct periods during which the hatching of the larvae of P. borealis takes place in the Bering Sea, April-May. Z.G. Palenichko (1941) indicates, that it is precisely during these months that the discovery in quantity of shrimp larvae in the plankton occurs, but considering that the first two larval stages remain near the bottom, it is erroneous to assume that the finding of larvae in quantity is related to the later stages of development and that their hatching occurs much earlier, Kuznetsov (1964) did not however, examine the data of Palenichko (1941) and did not utilize other basic studies of the biology of the shrimps, published up to 1961, the year of his death. In his sample he had only 166 females with eggs, and the time at which the collection was made was not indicated. For this reason, his indication to the effect that the deposition of the eggs of P. borealis in the Bering Sea commence only from November is not likely to be correct. As indicated by Z.G. Palenichko (1941), the first females with recently laid eggs occur as early as June, and the deposition of eggs continues right through to October. It is likely that this process is most intensive in the period July to August.

Table 3

Reproductive periods of P. borealis in various areas

Area	Beginning of egg deposit	Maximum intensity of egg deposit	End of egg deposit	Duration of egg deposit	Beginning of larvae hatching	Maximum intensity of hatching	End of hatching	Duration of hatching period	Duration of egg carrying	Period of encountering females with eggs	Author
Northumberland	10/X	X–XI*	1/XII	2.2–3	10/III	III–IV	16/IV	1.2	4.5	6.2	Allen, 1959
Oslo fiord	1/X	XI*	15/XII	2.5	1/III	IV*	15/V	2.5	5	7.5*	Hjort and Ruud, 1930; Rasmussen, 1953
Skagerrak	1/X	X*	15/XI	1.5	1/III	IV*	15/IV	1.5	5	6.5*	Agersten, 1936; Rasmussen, 1953
Vigra Fiord	15/IX	X*	30/X	1.5	1/III	IV*	15/IV	1.5	5.5	7*	Rasmussen, 1953
Brands Fiord	15/X	XI*	15/XII	2	1/III	IV*	15/IV–1/V	1.5–2	5	6.5*	Rasmussen, 1953
Mist Fiord	≈15/XI	XI*	≈1/XII	≈1.5	≈1/IV	IV*	30/V	2	6	6.5*	Rasmussen, 1953
Ofoten Fiord	≈1/XI	XI*	1/XII	2	---	---	---	---	---	---	Rasmussen, 1953
Eids Fiord	≈1/XI	XI*	15/XI–1/XII	1.5–2	≈1/IV	---	---	---	---	---	Rasmussen, 1953
Bals Fiord	1/VII	VIII–IX*	≈1/XI	4	---	---	---	---	---	---	Rasmussen, 1953
Jan-Mayen	≈VI*	VII*	---	---	---	V*	≈1/VI	---	9*	11*	Rasmussen, 1953
Iceland	---	IX–X	---	---	---	III–IV	---	---	6	---	Sigurdsson and Hallgrimson, 1965
Barents Sea	VI	VIII*	X	3.5*	---	IV–V	---	---	8–8.5*	11*	Palenichko, 1941; Kuznetsov, 1964
Western Greeland	End VI	VIII	IX	3*	III	IV	V	2.5*	8–9	10.5–11*	Horsted and Smith, 1959
Spitsbergen	VII	VIII	IX	3	IV	V	VI	2.5	9	11*	Rasmussen, 1953
British Columbia	15/XI	XI*	---	---	III	End III–Beg. IV	IV	2*	5	---	Berkeley, 1930; Butler, 1964
North-western part of Gulf of Alaska	1/IX*	IX–X	1/XI*	2*	1/III	IV	15/V	2.5	6.5	8.5	Author's data
Pribiloff region of the Bering Sea	20/VII	VIII–IX	1/X	2.1/3	---	IV	20/V	---	8.5	10	Author's data

Remark: Asterisk denotes data which is assumed on the basis of the times of the beginning and end of spawning as indicated by authors.

Thus, though females with eggs on their pleopods may indeed be encountered over a period of 11 months of the year in the Bering Sea (Table 3), a break of at least one month occurs between the laying of the eggs and the hatching of larvae. Utilizing the corrected data of Palenichko (1941) and Kuznetsov (1964) and the materials of Rasmussen (1953), Horsted and Smith (1956), Allen (1959) and Berkeley (1930), we present a generalized table of reproductive periods for **P.** borealis in the area under study, and supplement, with our data, the picture developed by Allen (1959), which illustrates the relationship between the basic processes of reproduction and the mean temperature in the areas inhabited by shrimps (Fig. 1).

According to our data, differences in the periods of the basic reproductive processes exist not only between the various populations, but also in the same population between different size groups, and it follows, between age groups of the females. On the basis of the Bering Sea samples, it can be considered that the smaller females deposit their eggs earlier than the large females. This can be seen from the fact that, during the egg-laying season, the percentage of females with eggs already deposited, among the small females (with a carapace length of up to 27 mm), is higher than among the large females (Table 4). An exception is afforded by the very small and rarely encountered females /399 (with a carapace length of 20-23 mm), among which no individuals with eggs were to be found. It is probable that these individuals grow quickly, deposit their eggs one year earlier than other shrimps of the same age and that their oocytes mature only towards the second half of the spawning period.

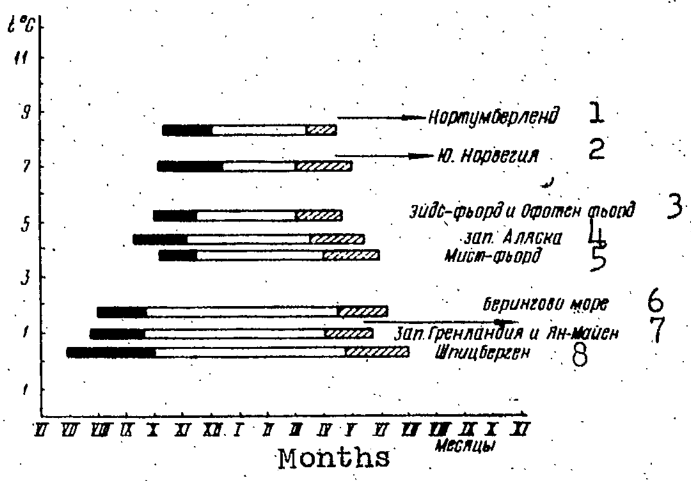


Fig. 1. Relationship between the main reproductive processes and the mean temperature in places inhabited by shrimp.
Black - period of the hatching of larvae;
Shaded - period of spawning.
White - incubation period.
Arrows indicate the duration of larval development.

1.- Northumberland
2.- Southern Norway
3.- Eids Fiord and Ofoten Fiord
4.- Gulf of Alaska
5.- Mist Fiord
6.- Bering Sea
7.- West. Greenland and Jan-Mayen
8.- Spitsbergen

The number of observations of the process of the hatching of larvae among the population off the Pribiloff Islands is not great. In the spring of 1965 we were able to carry out work in this area only after 20th. May, when the hatching of larvae in the case of most of the shrimps had already ended, and only a few of the females had the remains of eggs left on their pleopods. Nevertheless, despite the limited data, it is notable that among the small females, the percentage of individuals with the remains of eggs on their pleopods was higher than among the larger (see Fig. 4). Thus, in the Bering Sea, the small females normally deposit their eggs earlier, but spawn later, than the large females.

In the western part of the Gulf of Alaska, individuals with eggs or the remains of live eggs were similarly encountered more often among the small females, at the end of the period of larvae hatching (the end of April to May). In this connection it must not be forgotten, of course, that the understanding of "small" and "large" females is relative; the shrimps of one and the same size may be considered as small in one region and large in another. Despite the fact that we did not carry out any work during the period of the hatching out of the larvae of the northern shrimp in the Gulf of Alaska, it can be considered that the same phenomenon is also to be observed here, following the laying of the eggs and the hatching of the larvae, as in the Bering Sea. It is likely that the same characteristic is to be observed in the Atlantic.

The influence of the thermal condition of the shrimp /400 habitat on the progress of the basic biological processes reflects itself most clearly in the examination of the growth and the sexual development of shrimps of different populations.

Table 4. Relationship of females with eggs and without eggs at the beginning of the spawning period in the Bering Sea, by size groups

Period of observation	Length of carapace	Size of females by length of carapace in mm													
		20	21	22	23	24	25	26	27	28	29	30	31	32	33
14-19 August, 1962	Females without eggs	--	2	--	2	7	19	46	91	100	70	30	10	3	0
	Females with eggs	--	0	--	0	3	27	66	92	59	31	5	2	0	1
	Total of females	--	2	--	2	10	46	112	183	159	101	35	12	3	1
	Percentage of females with eggs in the overall number	--	0	--	0	30	59	59	50	37	31	14	17	0	100
10-20 August, 1963	Females without eggs	1	--	--	1	1	7	24	42	40	42	27	15	3	--
		0	--	--	1	1	4	16	34	25	9	1	2	0	--
	Total of females	1	--	--	2	2	11	40	76	65	51	28	17	3	--
	Percentage of females with eggs in the overall number	0	--	--	50	50	36	64	45	39	17	4	12	0	--
28 August to 1 September, 1963	Females without eggs	--	--	--	--	1	1	3	10	16	10	7	2	1	--
	Females with eggs	--	--	--	--	0	8	26	39	35	22	20	1	0	--
	Total of females	--	--	--	--	1	9	29	49	51	32	27	3	1	--
	Percentage of females with eggs in the overall number	--	--	--	--	0	89	90	80	69	69	74	33	0	--

GROWTH AND MATURATION OF SHRIMPS IN THE WESTERN PART OF THE GULF OF ALASKA

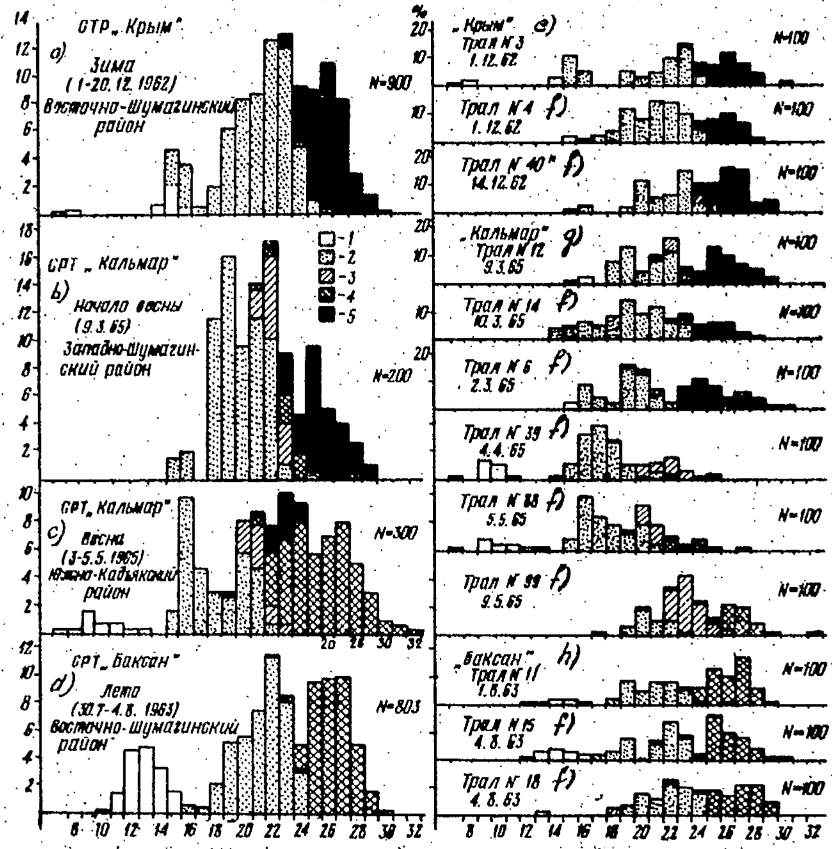
The last, VI, stage of the larvae of the northern shrimp is approximately 17 mm in length (Berkeley, 1930).

Close to the southern boundary of the range, the larval development is completed in approximately three months after hatching, and the first young individuals, with an average length of 31 mm, become caught in trawls off the shores of southern Norway as early as the middle of July (Rasmussen, 1953). At the beginning of August, off the shores of Northumberland, the shrimp of the year average 35 mm length (Allen, 1959). Such small individuals are encountered in trawl catches in only very small numbers, since most of them slip out of the trawl, and besides this, the young shrimp normally remains separated from the adults and occupies lower depths than the adults, where trawling is more difficult. The joining up of the young with the adult population normally occurs in the winter-spring period, after 9 to 10 months, and off Northumberland in as little as 7 months, after hatching (Hjort and Ruud, 1938; Rasmussen, 1953; Allen, 1959).

Similarly in the western part of the Gulf of Alaska, /401
it was in winter and spring that we encountered smaller shrimps, that is, it can be considered that here also, the

joining up of the young with the adults takes place in the winter-spring period, 8-9 months after the hatching of the larvae. To the east of the islands of Shumagin, the former size group of shrimps considered, in December, 1962, of individuals of 35-42 mm length (the length of the carapace - 7-10.5 mm). These shrimps came into the world in the spring of 1962.

The growth and development of the shrimps can be followed in the observations of December, 1962, August, 1963 and March-May, 1965, Observations were not carried out in 1964, and for other years, data was obtained only for certain seasons. For this reason, in order to establish an overall picture of the growth of the shrimps of the 1962 generation in the course of 1.5 - 2 years, we were obliged to apply data on the growth of other generations, estimating that the growth of different generations would not differ greatly in their early years. Proceeding from this, it can be assumed that in April, that is, at the age of 12 months, the shrimps of the 1962 generation would have a length of from 33 to 56 mm (length of the carapace l_c - 7-12 mm), with an average of 44 mm (l_c = 9.5 mm). In May, no significant increase in the length of the shrimps takes place, and the average length in the first size group /402
consists of 46 mm (l_c + 9.7 mm) (see Fig. 2).



*Sex determinations not carried out.

Fig. 2. Size composition of shrimps in the different observational periods, in the western part of the Gulf of Alaska. The left part presents the average curves; the right, the typical graphs of the size composition by individual trawls.
1 - young; 2 - males; 3 - individuals in the process of sex change; 4 - females without eggs; 5 - females with eggs.

a) STR "Krym"
Winter
(1-20.12.1962)
Eastern Shumagin region.

b) SRT "Kal'mar"
Early spring
(9.3.1965)
Western Shumagin region

c) SRT "Kal'mar"
Spring
(3-5.5.1965)
South Kodiak region.

d) SRT "Baksan"
Summer
(30.7.-4.8.1963)
Eastern Shumagin region

e) "Krym"
Trawl No. 3.

f) Trawl No.

g) "Kal'mar"
Trawl No. 12.

h) "Baksan"
Trawl No. 11.

During a summer of rapid growth, the length increases considerably and in August, at the age of 16 months, the average measurement of the shrimps consists of 62 mm (l_c = 13.5 mm). The more rapidly growing shrimps of this age may already take part in reproduction in the capacity of males, and have a length of 74-79 mm. However, their numbers are small, constituting only 3-4% of the overall number of the individuals of this age group.

In December, at the age of 20 months, the mean length of the shrimps increases to 72 mm (l_c = 15.5 mm), and the majority, in accordance with the character of the endopodite of the first pair of pleopods, must be identified as females. in March, at the age of 23 months, the average length of the shrimps consists of 74 mm (l_c = 16 mm), and in May, 77-78 mm (l_c = 16.5). In August, when the shrimps attain the age of 28 months, their average length increases to approximately 88 mm (lc = 19.5 mm), and in September-October. they begin to take part in reproduction in the capacity of males. In August, 1963, there were practically no females or individuals in the process of transformation among the shrimps of the 28 month age group. Thus, it can be considered that, in the western part of the Gulf of Alaska, primary and secondary females do not occur.

As has already been stated, no observations of the growth of the 1962 generation were carried out in 1964.

Utilizing the data of December 1962, it can be considered that towards December, that is, at the age of 32 months, the length of the shrimps would not increase greatly, and would be in the order of 90 mm (l_c = 19.7 mm). In March-April, the length increases to 95 mm (l_c = 19-21 mm), and in August, at the age of 40 months, the average length of the shrimps would be 100 mm (l_c = 22 mm), judging by the August diagram for 1963 (SRT "Baksan"). In these diagrams, the generation of 1960 corresponds to the shrimps with the carapace length of 22 mm. The greater part of the shrimps of this generation remained male at the age of 3.5 years, as can be seen from Fig. 2. Females constituted about 3% of the corresponding age group and their average length was 105 mm (l_c = 23 mm). However, it appears from the spring diagrams for 1965, that among the individuals of the 1962 generation, at the age of 3.5 years, there should be considerably more females than among the individuals of the 1960 generations. Unfortunately, due to the lack of observations in August-September, 1965, it is not possible to estimate the proportion of females during the egg-laying period of the 3.5 year old shrimps, from the number of individuals undergoing transformation during the spring, since many more shrimps would undergo sex transformation during the summer. In many of the diagrams of the size composition, the females display two peaks, generated by shrimps with carapace lengths of 25 and 27 mm. This is evidence of the fact that the majority of the shrimps of the western part of the Gulf of Alaska undergo sex transformation in spring, at the age of 4 years, and deposit eggs for the first time at the age of 4.5 years, when their length is 112 mm (l_c = 25 mm). At this age almost all the shrimps become females. The second peak is formed, evidently, by females which take part in reproduction for the second time. Their average length is 120 mm (l_c = 27 mm).

Thus, it can be said, that the age of 1.5 years, the shrimps are still sexually immature, and they first take part in reproduction in the capacity of males at the age of 2.5 years. In the next egg-laying season, in September-October, that is, at the age of 3.5 years, the greater part of the shrimps function as males a second time, but part of the animals now become females. The change of sex of the northern shrimp in the area under study, occurs in the main, in four years, and the majority of the shrimps first deposit eggs at the age of 4.5 years. Apparently, the females of the northern shrimp take part in reproduction, and it follows, produce off spring two /403
times. The life span of the shrimps of the western part of the Gulf of Alaska consists, probably, of about 6-6.5 years. Older individuals, with a length of 130 mm (l_c = 29 mm), are encountered quite rarely. The growth of the northern shrimp in the western part of the Gulf of Alaska is

illustrated in Fig. 3 and Table 5. The rate of the sexual maturation of the northern shrimp of the western part of the Gulf of Alaska is most like that of the shrimps of northern Norway (Mist Fiord, Bals Fiord), inhabiting regions from 67°N to 70°N.

In the Pacific Ocean, the most detailed biological study of the northern shrimp has taken place with respect to the southern shores of British Columbia (Berkely, 1930); Butler, 1964). In this region the shrimps of the 1.5 year category are all males, and about half of them (47%), are even primary and secondary females. At 2.5 years, all the shrimps become female (butler, 1964). Thus, the sexual development of the northern shrimp on the shores of British Columbia takes place more rapidly than off Northumberland. No detailed studies are available on the life cycle of the northern shrimp inhabiting the area along the coast of Alaska. Our previous studies (Ivanov, 1963, 1964b), did not take place during spawning, a time when the age and

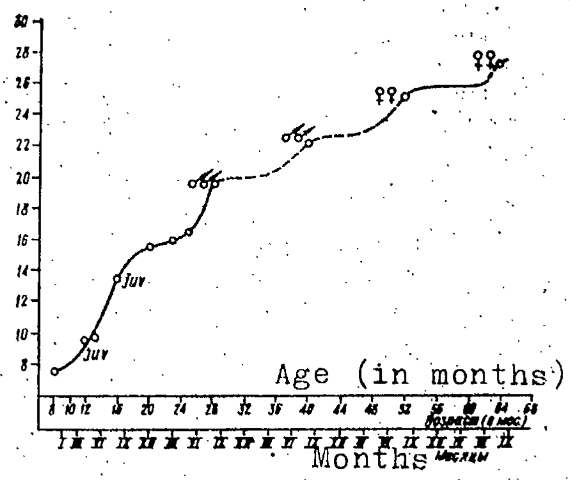


Fig. 3. Growth of the northern shrimp in the western part of the Gulf of Alaska.

sex groups are most clearly expressed. For this reason, our data on the rate of the maturation of the shrimps were found to be over-estimated. In accordance with American researchers, the change in the sex of the north- /404
ern shrimp, in the southern part of the Gulf of Alaska in the region of Petersburg, Wrangell and Oak Bay, takes place in the third year, and in the northern part of the Gulf, off the city of Homer, at the age of 4 years (Anon, 1965b),

Utilizing the data of the present study, those of Butler (1964) and the data of American researchers (Anon, 1956b), the life cycle of the northern shrimp can be approximately envisaged for all the regions off the coast, from British Columbia to the islands of Shumagin (see Fig.6). We see, that with movement north along the coast of North America, from British Columbia to the Kenai Peninsula, the shrimps mature later than in the southern regions, that is, the same tendency is observed as in European waters, and which was brought out well in the results of the work of Rasmussen (1953), Horsted and Smidt (1956) and Allen (1959). Howeverm this tendency is not displayed in the western part of the Gulf, and the sexual development of the shrimps off the islands of Shumagin, evidently, differs little from the development of the shrimps in the northern part of the Gulf.

Table 5. Growth and maturation of shrimp in the western part of the Gulf of Alaska

Date	Approx. age, months	Number of shrimp	Male juvenile		Males		Females		Overall mean length, mm
			%	Mean length, mm	%	Mean length, mm	%	Mean length, mm	
December, 1962	8	14	100	42	--	--	--	--	42
April, 1965	12	22	100	44	--	--	--	--	44
May, 1965	13	14	100	46	--	--	--	--	46
August, 1963	16	134	100	62	--	--	--	--	62
December, 1962	20	80	100	72	--	--	--	--	72
March, 1965	23	95	100	74	--	--	--	--	74
May, 1965	25	99	100	78	--	--	--	--	78
August, 1965	28	105	100	88	--	--	--	--	88
December, 1962	32	125	100	90	--	--	--	--	90
March, 1965	35	327	84.5	89	15	97	0.5	99	90
April, 1965	36	225	69	90	28	95	3	92	92
August, 1963	40	235	96	100	1	108	3	105	100
December, 1962	44	307	90.7	100	1	108	8.5	108	101
August, 1963	52	137	8	108	2	109	90	113	112
August, 1963	64	164	--	--	--	--	100	120	120

Despite the fact that the islands of Shumagin are located south of Petersburg and Wrangell, where the change in sex takes place in the third year, the northern shrimp of the Shumagin region ordinarily changes sex at the age of 4 years, as is the case in the northern part of the Gulf, that is, almost 5° more northerly than the islands of Shumagin. In the shrimps of the Norwegian fiords, located 4-5° of latitude apart from each other, the differences in the biology are easily distinguishable.

Thus, a feature of the populations of shrimp, inhabiting the shelf of the western part of the Gulf of Alaska, is the relative similarity between them in terms of the rate of growth, maturation, egg deposition and spawning. This peculiarity, it seems to us, may be explained by the direction of the warm current passing along the continental slope of the shelf of the Gulf of Alaska, and the changes in temperature along this current. As is well known, the warm Alaska Current moves north along the shores of British Columbia and south-eastern Alaska, and then turns to the west and south-west, along the whole coast of Alaska, right through to the Aleutian Islands. The temperature of the main stream of the Alaska Current, as well as its branches, which pass out on to the shelf, decreases as a measure of the movement of the stream to the north, west and south-west (Plakhotnik, 1964).

In the south-eastern part of the Gulf of Alaska, where the current moves along the shore in a northerly direction, as is the case off Northumberland, the decrease in the temperature of the water along the direction of the movement of the stream is accompanied by an overall cooling, related to the movement to the north. As a result of this, the basic biological processes are retarded with movement to the north, along the shores of British Columbia and eastern Alaska, as is the case in Europe. However, after this, as the Alaska Current reaches the northern part of the Gulf and turns to the south-west, the loss of heat due to the movement of the stream among surrounding colder waters, is compensated for to some extent by the overall warming associated with movement to the south.

The thermal conditions in which the shrimps exist in the western part of the Gulf, apparently not only do not become more severe with distance to the north, but may even be milder. As a result of this, the environmental conditions of the shrimps, and therefor their basic biological characteristics, are relatively the same, over a vast distance (about 500 miles), from the island of Sanak to the Kenai Peninsula. The biology of the northern shrimp off the island of Kodiak still remains practically unstudied. It is possible, that in this region, situated to the north of the islands of Shumagin, the maturation of the shrimps takes place in even more early periods, than in the Shumagin Gulf.

Rasmussen (1942, 1953), who was the first to demonstrate the geographical variability in the growth and sexual development of the northern shrimp, also showed that itself, the geographic position does not determine the rate of growth and the maturation of the shrimps, and that the determining factor in this respect is the thermal regime. Thus, in the fiords which have shallows at their entrance which hinder the entry into them of warm, deep Atlantic waters, the populations of shrimps grow and develop relatively slowly, regardless of the geographic position of the fiord. However, such exceptions are related to small, isolated fiords, and do not hold true for large areas of the coast, as this can be seen in the Gulf of Alaska.

GROWTH AND MATURATION OF THE NORTHERN SHRIMP IN THE BERING SEA

In the Bering Sea, the smallest individuals among the northern shrimps, encountered in August of 1962 and 1963, were 35-50 mm in length, that is, their length was the same as that of the shrimps of the first size group off Spitsbergen and Jan Mayen (Rasmussen, 1953). However, while in the latter regions they constituted an isolated size group, in the Bering Sea these small individuals were to be found only in the very left part of the size group, with a length of carapace of from 7 to 14 mm, and with an average length of 61 mm (l_c = 12.54 mm). The average length of our first size group (61 mm) is very similar to the average length of the northern shrimp of the second size group off Spitsbergen and Jan Mayen (60.5 and 73 mm respectively), the age of which Rasmussen determines as approximately 2.5 years. However, despite this similarity, we cannot consider that our first group and the second size group off Spitsbergen is of one and the same age, that is, 2.5 years.

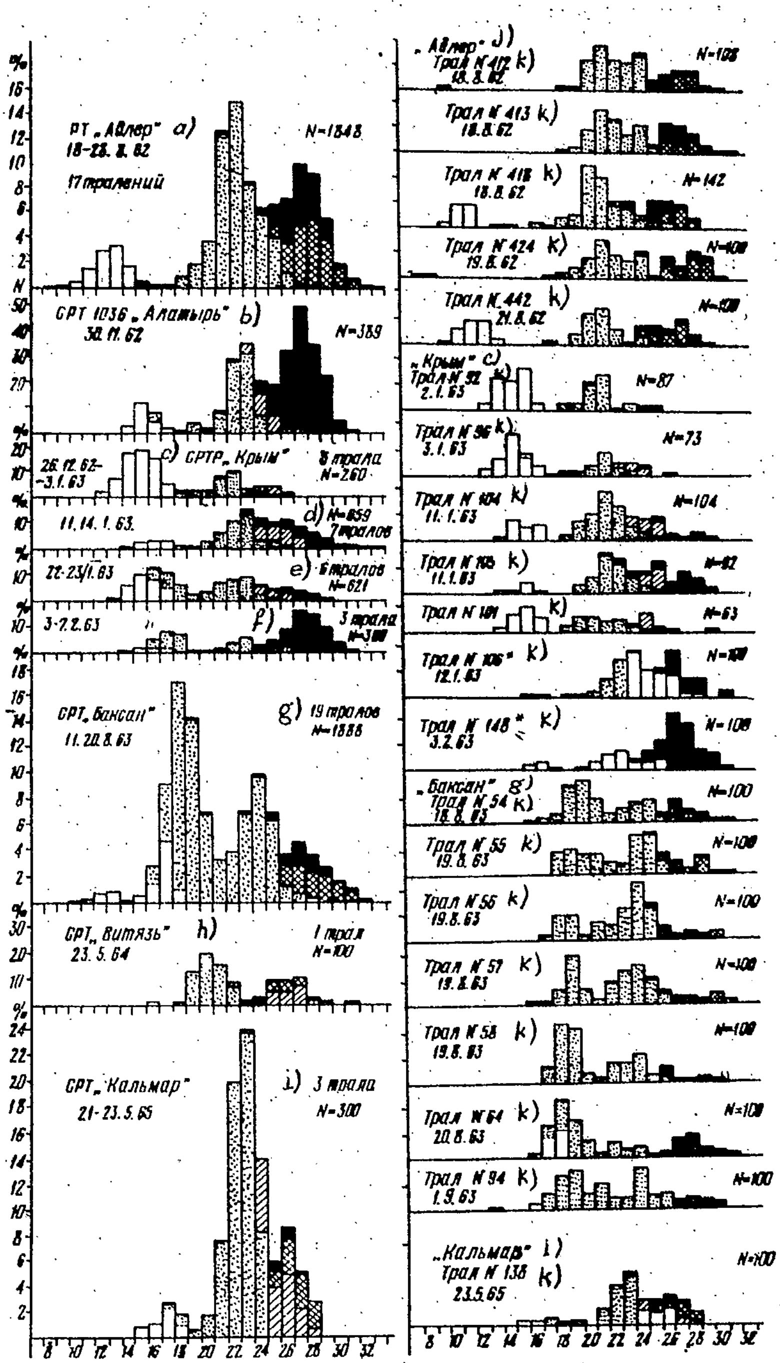
We consider that the shrimps of the first size group, with an average length of 61 mm, is 16 months of age in August, that is, were hatched in April of the preciding year. If subsequent studies lead to a discovery of a size group of smaller shrimps, we must introduce a correction of one year in all our future considerations.

In comparing the measurements of shrimps, constituting the second size group in August, 1962 and 1963, the substantive differences are very notable (Fig. 4). In August of 1962 the average length of the shrimps of the second size group was 102 mm (l_c = 21.6 mm), and in 1963, 88 mm (l_c = 18.3 mm), that is, considerably smaller than in 1962. If it is taken that in both cases the shrimps of the second size group are 28 months of age, and if it is considered that these large differences in size are due to variations in the rate of growth of different generations, then it would be found that the generation of 1960 grows more rapidly than the shrimps of the Gulf of Alaska, which at the age of 28 months have an average length of 88 mm (l_c = 19 mm). In view of the fact that the thermal regime in the Bering Sea is considerably more severe than in the

Gulf of Alaska, this result cannot be considered satisfactory.

Much more correct, in our view, is the other explanation; namely that in August of 1962, in the size diagrams, there is an almost total lack of shrimps of the 1960 generations, that is, the second size group in August 1962 consisted of individuals of the generation of 1959, which were of the age of 3 years, 4 months. The 1960 generation was probably very low in yield. This was also reflected in the diagrams of August 1963, which lacked peaks corresponding to the generation of 1960, which in August of 1963 would have been approximately 100-105 mm (l_c = 21-22 mm) in length.

The third size group in August, 1962 and 1963 consisted of individuals approximately 112-118 mm (l_c = 24-25 mm) in length. The age of the shrimps of this group was 4 years, 4 months. In 1962, the shrimps of this group are to be observed only on some of the diagrams, and they /407
generate a peak only in 8 samples out of the 17 taken by us for measurement. This occurs, probably, as a result of the fact that the yield of the generation of 1958 was not large, though not as small as that of the 1960 generation. The individuals of the fourth size group, in August of 1962 and 1963, averaged 125 mm in length



a) RT "Adler"
17 trawls

b) SRT 1036 "Alatyr'"

c) SRTR "Krym"
3 trawls

d) 7 trawls

e) 6 trawls

f) 3 trawls

g) SRT "Baksan"
19 trawls

h) SRT "Vityaz"
1 trawl

i) SRT "Kal'mar"
3 trawls

j) "Adler"

k) Trawl No.

Fig. 4. Size composition of the northern shrimp in subsequent periods of observation. The distribution of the diagrams and the legends are the same as in Fig. 2.

(l_c = 27 mm). This group consisted almost exclusively of females, the approximate age of which was 5 years, 4 months. By virtue of their size the shrimps of this group are more valuable and, in the catches, their weight, of course, constitutes a much important consideration than their numbers. In 1963, the females in the catch constituted a considerably smaller percentage than in 1962. While in August of 1962, females with a carapace length of 27 mm (age 5 years, 4 months), in 14 samples out of 17, formed peaks of not less than 10% on the curve of the size composition, in August of 1963, this peak was observed only in two samples out of 36. If it is taken into account that in August of 1963, this size group was represented by the low-yield generation of 1958, which in the preceding year of 1962 showed up poorly in the August diagram of the size composition, then such a large difference in the percentage composition of females in two consecutive years would afford us no surprise. However, one should not forget the growing Japanese fishing effort, the results of which is the removal primarily of the large individuals, that is, females.

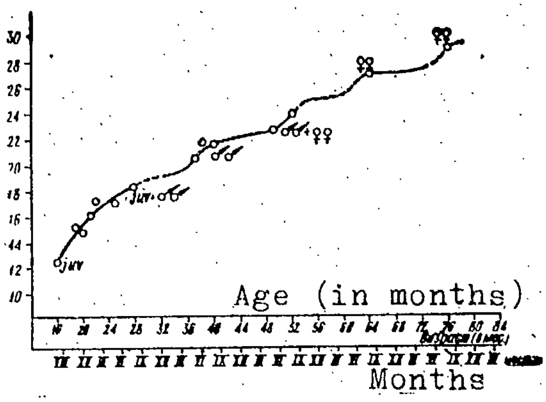


Fig. 5. Growth of the northern shrimp in the Pribiloff region of the Bering Sea.

Shrimps of more than 6 years of age did not display sharp size group, either in 1962 or in 1963, a fact which is explained by the infrequent moulting and slow growth of older individuals. The mortality of shrimps after the hatching of larvae is, apparently, very high, since females with a carapace of over 29 mm in length are encountered extremely rarely and their proportion among all the females is very small. Inasmuch as shrimps of the age of 5.5 years were relatively few in numbers in the fall of 1963, the proportion of large females of over 135 mm in length (l_c = more than 29.5 mm) and which would be, evidently, 6.5 years of age, was higher in the overall number of females than in the fall of 1962. These large females are evidently the remnants of the generation of 1957.

A fuller picture of the growth and development of shrimps, utilizing our results of observations in the Bering Sea of August, 1962, December-February, 1962-1963 and May, 1965, and the collections kindly carried out at our request by SRT "Alatyr'" in November, 1962 and SRT "Vityaz" in May-June, 1964, is presented in Table 6. The growth of the shrimps of the Pribiloff region is shown in Fig. 5.

Summarizing the results of our observations, it can be considered that the northern shrimp of the Pribiloff region, at the age of 1.5 years (l_c = 12-13 mm), remains

immature and does not take part in propogation. At the age of 2.5 years, the shrimps have an average carapage length of about 18-19 mm. Part of the shrimps of this age, which in August have sperm ducts full of sperm, would, for the first time, take part in reproduction, in the capacity of males. However, part of the shrimps remains sexually immature. Even amongst individuals, which by the character of the endopodite of the first pair of pleopods should be regarded /408
as males, individuals were encountered in August with empty sperm ducts, and it is doubtful that they could participate in reproduction. At the age of 3.5 years (l_c = 22 mm), all the shrimps become males, while a very insignificant number (less than 1%), may even become females. At 4.5 years (l_c = 24-25 mm), the majority of the shrimps function once more in the capacity of males, and only at the age of 5.5 years does the main mass of the shrimps undergo sex change, and in the fall, at the age of 5.5 years, lay eggs for the first time. Very few females live to the age of 6.5 years. Among them are many "steriles", that is, individuals whose oocytes do not mature in time for the next spawning season and who miss laying eggs during the reproductive season (Ivanov, 1946b). Rasmussen (1953) earlier pointed to a similar phenomenon off Spitsbergen and Jan Mayen.

Thus, in the Pribiloff region, the maturation of /409
the northern shrimp takes place approximately one year

Table 6. Growth and maturation of the northern shrimp of the Pribiloff region

Date	Age months	No. of shrimp	Juveniles		Females	
			%	Average length, mm	%	Average length, mm
August, 1962	16	197	100	(61 12,5)***	--	--
November, 1962	19*	30	100	74	--	--
December, 1962	20	171	100	72(14.8)	--	--
January, 1963	21	390	73	74(16.2)	27	82
February, 1963	22	73	25	78	75	85
May, 1965	25	23	70	82	30	87
August, 1963	28	1710	15	83(18.27)	85	89
May, 1964**	37	72	--	--	92	95
June, 1964**	38	106	--	--	96	102
August, 1962	40	626	--	--	99.2	102
May, 1965	49	201	--	--	87	105
August, 1963	52	772	--	--	96.8	111
August, 1963	64	--	--	--	--	--
August, 1963	76	--	--	--	--	--
August, 1963	88	--	--	--	--	--

Table 6 (Cont'd)

	Transitional		Females		Overall average, mm
	%	Average length, mm	%	Average length, mm	
August, 1962	--	--			61
November, 1962	--	--			74
December, 1962	--	--			72(14.8)
January, 1963	--	--			79(16.2)
February, 1963	--	--			84(17.3)
May, 1965	--	--			83(17.7)
August, 1963	0.001	89	0.01	94	88(18.27)
May, 1964**	6.6	105	1.4	103	97(20.54)
June, 1964**	4	109	--	--	103(21.9)
August, 1962	0.16	108	0.65	104	102(21.61)
May, 1965	13	114	--	--	106(22.6)
August, 1963	--	--	3.2	116(24.7)	112(23.86)
August, 1963	--	--	100	≈125	≈125(27)
August, 1963	--	--	100	≈135	≈135(29)
August, 1963	--	--	100	≈145	≈145(31)

*"Alatyr'", without small-mesh liner.
**"Vityaz'", without small-mesh liner.
*** Figure in brackets is length of carapace (l_c).

later in the western part of the Gulf of Alaska.

The growth and development of the shrimps of the Pribiloff region are most similar to these processes in the shrimps of Jan Mayen, Spitsbergen (Rasmussen, 1953) and Greenland (Horsted and Smidt, 1956).

A schematic representation of the life cycle of P. borealis throughout its whole range, according to the literature and our data, is presented in Fig. 6.

If the picture presented by us, of the growth of the shrimps of the Pribiloff region is correct, and if we /410 were able to present all the age groups of shrimps on a diagram of the size composition, that is, shrimps of the ages 1.5, 2.5, 3.5, 4.5 and 5.5 years, the peaks of the curves would occur approximately at 12-13, 18-19, 21-22, 24-25 and 27 mm. By the size and constancy of the peaks, it is likely that judgements can be made on the yield of the corresponding generations, with the exception of the generation which corresponds to the shrimps of the first age group, which is not easily caught up in the trawls.

It follows then, that having some understanding of the growth of the shrimps, and knowing what size groups make up the main part of the catches of the commercial fishing fleet, it is possible to forecast fishery conditions for 2-3 years ahead. Particulary reliable

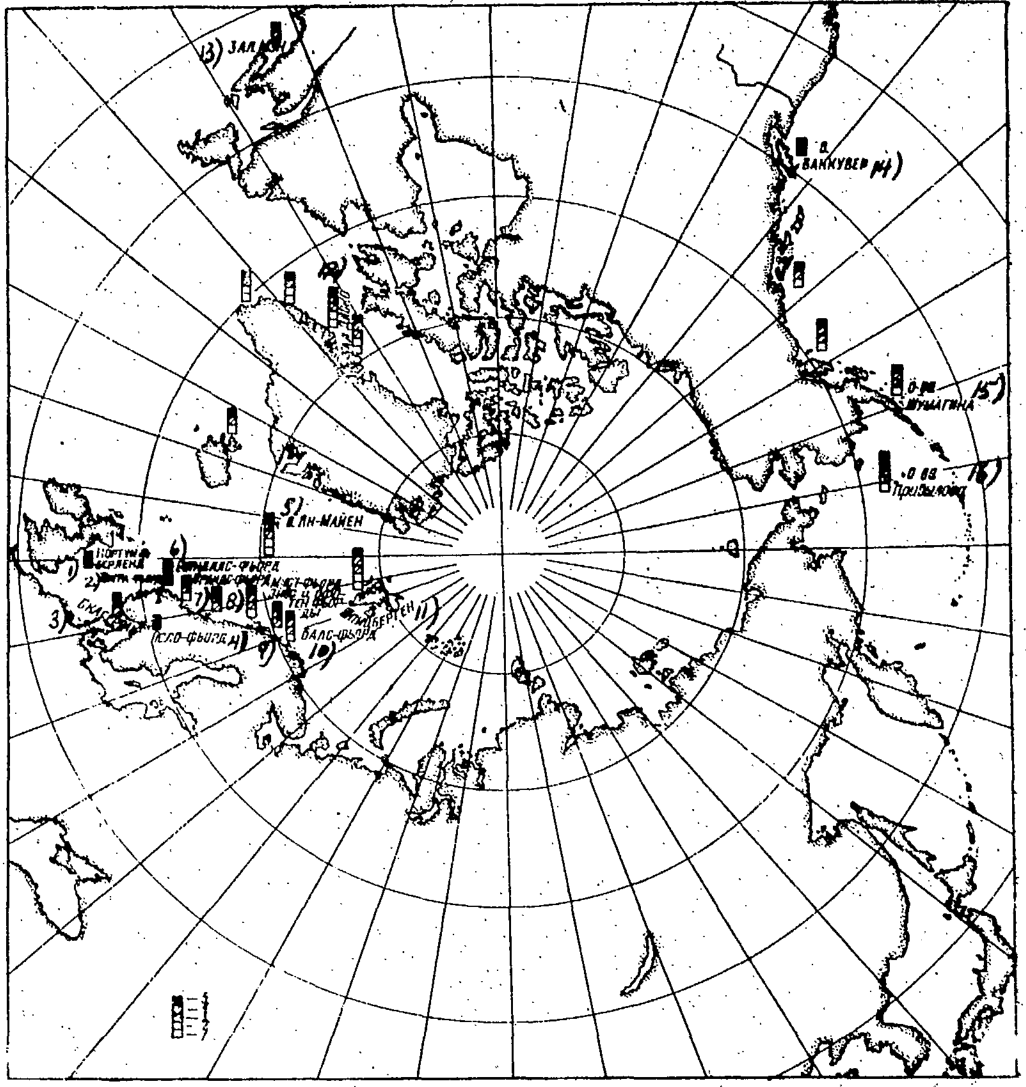


Fig. 6. Life cycle of the northern shrimp in various parts of its range, in accordance with our own data and the literature. Figures to the left/sic/ of the columns indicate the approximate age during the period of reproduction. White squares - young; shaded - males; black - females.

1) Northumberland
2) Vigra Fiord
3) Skagerrak
4) Oslo Fiord
5) Jan Mayen
6) Sunndals* Fiord
7) Brands Fiord
8) Mist Fiord
9) Eids* and Ofoten Fiord
10) Bals Fiord
11) Spitsbergen
12) Disko Bay
13) Men* Bay
14) Vancouver
15) Shumagin Islands
16) Prigiloff Islands

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* Translator's note: Text type illegible or place otherwise not completely identified.

predictions can be made of the approximate size composition of the shrimps in the coming year, from the data of the current year. Thus, from the diagrams of the size composition for August, 1963, it was possible to expect that in 1964, shrimps with an average carapace length of about 22 mm and 27 mm would predominate in the catches, that is, the picture that would be observed would be similar to that of 1962. The diagrams of the size composition for May, 1965 confirm this expectation (see Fig. 4).

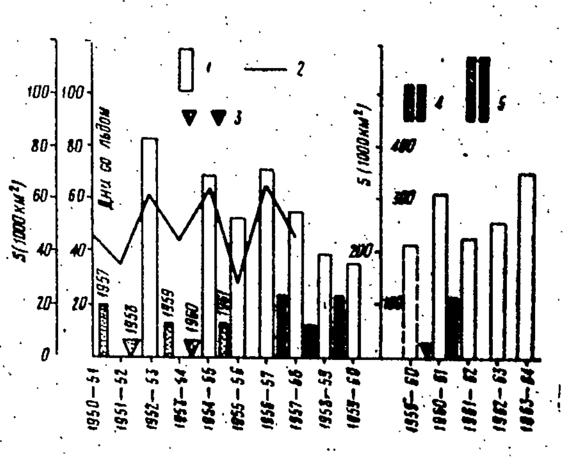
From the diagrams of the size composition for August 1962 and 1963 it is possible to draw the conclusion, that the generation of 1960 was extremely low in yield and was practically absent from the diagrams. The 1959 generation was strong, the 1958 generation was low in yield, and the 1957 generation was good. The generation of 1961 was, apparently, also a good one. Proceeding from this, the fishing conditions in five years after the spawning of a generation could be characterized in this way: 1962 - good, 1963 - below normal, 1964 - good, 1965 - poor, 1966 - good. Relative to this, we have in mind the relationship of the various size groups, but not the sizes of the catches, which, because of the intensity of fisheries, may decrease regardless of the favorability of the size composition.

RELATIONSHIP BETWEEN THE YIELD OF A GENERATION AND HYDROLOGICAL CONDITIONS

Unfortunately, regular, long-term observations of the average temperature of the water in the bottom layers of the Pribiloff region are lacking. It seems to us that, according to the character of the winter in the Bering Sea, an approximate estimate may be made of the thermal regime in the shrimp habitats in the corresponding year. In the Bering Sea, accumulations of shrimps are normally to be found at a depth of not more than 120 m (Ivanov, 1964a,b); the purely thermal convection in the Bering Sea off the Pribiloff Islands, penetrates to 50 to 100 m (Bulgakov, 1965). In icy winters, when the Pribiloff region is covered with ice, the temperature at the bottom, apparently, decreases considerably, regardless of the flow of warm deep waters. This is confirmed by our observations of May, 1965 in SRT "Kal'mar", when, following the cold winter of 1964-65, the temperature at the bottom in the region of the shrimp accumulation was below 0°C, and our only commercial catch was taken at a bottom temperature of 0.7°C. Thus, judging by the occurrence of ice in the south-western part of the Bering Sea, the winter of 1956/57 was severe, 1957/58 moderate, 1958/59 mild, and 1959/60 mild (Kryndin, 1964). Information on the occurrence of ice in the Bering Sea in subsequent years was kindly forwarded by the chief of the Marine Division of the Hydro-

Meteorological Centre of the USSR, A.I. Karakash. According to his data it could be considered that the winter of 1960/61 was severe, 1961/62 mild, 1962/63 moderate, According to our observations in SRTR "Krym", the winter of 1962/63, with respect to the bottom layers, was mild (Ivanov, 1964b).

In comparing the yields of the generations 1957-1961, on which we have direct observations, with the available data on the occurrence of ice (Fig. 7), attention is attracted to the fact that the extremely low-yield generation of 1960 was spawned prior to the icy winter of 1960/61, that is, the shrimps of the 1960 class were subjected to a /411



1 - area, covered with ice;
2 - days with ice;
3 - low-yield generation;
4 - generation of average yield;
5 - good-yield generation (shaded-assumed yield of parent generations; black-observed generations.

Fig. 7. Relationship of the yield of a generation of shrimp to the severity of winter and the yield of the parent stock. Left part of the graph - data on the iciness of the western part of the Bering Sea and on the number iced-over days according to Kryndin (1964). The right part of the graph - data on the severity of the whole Bering Sea (personal communication of A.I. Karakash):

severe winter in the first year of their life. It is natural to suppose that the yield of a generation is determined by the character of the first winter in the lives of the shrimps. Inasmuch as the nature of the winters in the Bering Sea has been noted in a long series of observations (Kryndin, 1964), if we proceed from the supposition, and utilize the data compiled over the years on the iciness of the winters in the Bering Sea (Kryndin, 1964), we are able to make an approximate determination of the strength of the generation of the preceding year, even without direct observations, on the grounds that a generation preceding an icy (severe) winter will produce a low yield, and preceding a mild winter, a good yield.

Thus also, it is possible to make an evaluation of the numerical strength of the parental stock of the generations under study, considering that the number of females with eggs, and it follows, the quantity of larvae, depend on the strength of the generation of shrimps spawned 6 years prior to the hatching of the larvae (see Fig. 7). In making the forecast, it is arbitrarily accepted that all the spawning shrimps, during the fall egg-laying period, were 5.5 years of age, and that in the following spring, at the time of the hatching of larvae, they were 6 years of age. The relationship between the yield of the 1957-1961 generation, the yield of their parental classes and the character of the winters during the first year of the lives of shrimps of the generations under study, is demonstrated in Table 7.

As it can be seen from Table 7, our assumption with respect to the fact that the character of the winter determines the strength of the shrimp generation, spawned during the preceding winter, affords an explanation of the yield of the generations of 1957-61. Thus, the extreme poverty, the virtual absence, of the generation of 1960, is explained by the simultaneous effect of two unfavorable factors, a severe winter during the course of the first year of life of the shrimps and the low numerical strength of the parental stock. The numerical strength of the parental stock apparently exerts an influence on the numerical strength of the offspring. In this way, despite the mild winter of 1959-1960, the generation of 1958 produced a lower than normal yield, as a result of the low numerical strength of the parental stock. The strongest generations apparently turn out to be those which are spawned by a /412
numerically strong parental stock, and which experienced, during the first year of their life, either a mild (such as the generation of 1959) or, at least, a moderate winter (such as the generation of 1957). We do not possess data on a generation produced by a numerically strong parental stock but which had been subjected to a severe winter in

Table 7. Relationship between the yield of a generation, the character of the winter during the course of the first year of life and the probable yield of the parental stock

Generation	Year of birth of parental stock	Character of winter in first year of life of parental stock	Probable yield of parental generation	Character of the winter in the first year of life of a given generation	Yield of the generation
1957	1951	Mild	Good	Moderate	Good
1959	1952	Severe	Poor	Mild	Below normal
1959	1953	Moderate	Average	Mild	Good
1960	1954	Severe	Poor	Severe	Extremely poor
1961	1955	Moderate	Average or heavy	Mild	Good

the first winter of life. It is likely that its yield would not be high, though not as low as that of the generation of 1960.

Thus, it can be assumed that the yield of a generation of shrimps in the Pribiloff region is determined by the character of the winter which is experienced by the shrimps in the first year of their life, and the numerical strength of the producers, that is, the parental stock. Inasmuch as the shrimps of the Pribiloff region live in the open sea, and in the event of a deterioration of the hydrological conditions may retreat into warmer waters nearer the continental slope, no loss of the entire population of shrimps takes place, as is sometimes the case in isolated fiords of Greenland. However, the character of the winter has a strong effect on the yield of individual generations in the Pribiloff region.

It will be appreciated that our observations were not large in numbers. It is likely that the yield of a generation is affected by such factors as the food supply of the larvae, the coincidence of massive spawning and the blooming of phytoplankton, and abundance of plankto-phagous fish which may feed on the larvae, and others. We regard the results of our work as a preliminary outline for future study, confirmation and correction; as an out-line which may assist in selecting the future direction in the study of shrimps.

Up to now we have been examining only the natural factors influencing the strength of various generations. However, proceeding from our preliminary data on the fact that the numerical strength of the parental stock has an effect on the yield of the offspring, it can be assumed that intensive fishery, removing a large proportion of the females, could disrupt the shrimp stock. In such an event, due to the slowness of the growth and maturation of the shrimps in the Bering Sea and the Gulf of Alaska, several years would be required for the restoration of the stock.

The fishing industry has a different influence on the various populations of shrimps, which depends on conditions in their habitats. In Norwegian and Greenland fiords, where the area of the trawl banks is not large by comparison with the region inhabited by the shrimps, no serious symptoms of overfishing are evident despite the intensive fishing that has taken place over the course of many years, since the catch of shrimps on the trawling banks is compensated for by the movement of shrimps from adjacent areas which are not suitable for trawling. The ice cover in Greenland also affords good protection to the shrimps from fishing activities during the period of egg-carrying and spawning (Rasmussen, 1965; Smidt, 1965).

In isolated bays, where the larger part of the population is concentrated, apparently, on areas with a /413 smooth bottom, fishery activities may lead to overfishing, such as that which has already occurred in the fiords of Iceland (Sigurdsson and Hallgrimsson, 1965). With respect to populations which are located in the sea and at some distance from shore, such as in the Skagerrak and off Northumberland, as well as in the accumulations off the islands of Shumagin and the island of Kodiak, apparently the larger part of the shrimp, with the exception of the young, live on bottoms which are suitable for trawling, and are readily caught up by the fishing fleet. The catch in the Skagerrak has increased in recent years only as a result of increasing effort. The trawl catch had decreased, which obliged fishing enterprises to increase the dimensions of their trawls, and their has been a decrease also in the dimensions of the shrimps (Jensen, 1965). In 1965, the catch in Norway and Sweden decreased.

Taking into account that the productivity of the shrimp banks in the Skagerrak is higher than in the western part of the Gulf of Alaska, since the northern shrimp off the shores of southern Norway grows and develops much faster than the shrimps in our study areas in the Gulf, it should be considered that the accumulation of shrimps off the islands of Shumagin and Kodiak are more sensitive to fishing activity, than the accumulations off southern Norway. This is true also with respect to the Pribiloff accumulation. Due to the distance of this accumulation from the shore, in the Bering Sea, young and adult shrimp often inhabit the same areas.

In connection with the fact that the smooth bottom of the eastern part of the Bering Sea permits the conduct of fisheries throughout the entire shrimp habitat, and since the young shrimp do not apparently, have natural retreats, it is particularly important, in this area, to avoid the incidental catching of small individuals. In the Bering Sea, the shrimps grow and mature even more slowly than in the western part of the Gulf of Alaska, while the yield of a generation is subject to strong fluctuations depending on the hydrological character of different years. All this demands a careful approach to the shrimp stock of the Pribiloff region.

The state of the shrimp stock in the Pribiloff region is currently generating serious concern. This concern is linked to the sharp decrease of the Japanese catch in this region, which is illustrated by the following figures (Sakai, 1967): 1961 - 10.2; 1962 - 21.0; 1963 - 31.6; 1964 - 20.9; 1965 - 8.8; 1966 - 2.9 thousand tons. In the spring of 1965 we became convinced that the stock of shrimps in the Pribiloff region had seriously decreased, by comparison with 1962 and 1963. In the vicinity of the island of St. Paul, where in 1962 and 1963 the catch was about 3 centner/hour, in 1965, it did not exceed a few kilograms. This decrease in the catch can only be explained by overfishing. The protection of the shrimp stocks of this region is becoming a very real problem.

As distinct from the situation in the crab fishery, it is possible to recommend, for the shrimp fishery, that males should be predominantly taken, since, in the first place, the males are considerably smaller than the females, and secondly, the males of proterandrous hermaphrodites ultimately become females. Thus, in taking males, we disrupt the future stock of females. However, in taking females, it is necessary, it would appear to us, to give them an opportunity to leave offspring, that is, it is essential to cease fishing at least 1.5-2 months prior to the hatching of the larvae. May-August in the Bering Sea, or May-September in the Gulf of Alaska constitute periods when the female shrimps do not have eggs on their pleopods, and from this point of view, this period is the most favorable for fishery.

As indicated by Jensen (1965), trawls possess considerable selectivity with respect to shrimp. In the Skagerrak the dimensions of the shrimps (in mm), 50% of which are caught in the trawls and 50% of which slip through the mesh, exceed the dimensions of the mesh by 3.3 times. /414
In accordance with the Swedish-Norwegian Convention of 1952, the minimum mesh in the cod-end of the trawl in the Skagerrak-Kattegat was established at 17 mm, knot to knot, or 30 mm by standard measurement (Jensen, 1965; Rasmussen, 1965). In the Bering Sea and the Gulf of Alaska, the shrimp is larger and has different body proportions than in Norwegian waters. For this reason, the dimension of the mesh of shrimp trawls in the Northern Pacific should, evidently, be larger than in the Skagerrak. Special research in this direction has thus far not been carries out, but it can be assumed that the mesh dimensions of the cod-end must be not less than 20 mm, knot to knot. Besides this, it would be desirable to ban fisheries in those areas where observations are made of a large admixture of individuals below commercial size, even those cases when the proportion of shrimps of commercial sice would ensure reasonable catches. The determination of the maximum allowable incidental catch of small shrimps demands special study.

Thus, we consider the primary measure for the protection of shrimp stocks, in the first stage, to be the establishment of closed seasons for fishery: in the Bering Sea, from February to the middle of May, and in the western part of the Gulf of Alaska, from January to the middle of May, that is, 1.5-2 months prior to the commencement of spawning, and also for the entire spawning period.

CONCLUSIONS

1. In the western part of the Gulf of Alaska, the northern shrimp deposits its eggs in September-October, and the larvae hatch, in the main, in April. In the Bering Sea, the deposition of eggs takes place in August-beginning of September, that is, approximately one month earlier, while the hatching of the larvae occurs in April-beginning of May, approximately 0.5 months later, than in the Gulf of Alaska.

2. In the western part of the Gulf of Alaska the northern shrimp, at the age of 1.5 years, is still sexually immature, and first takes part in reproduction in the capacity of a male at the age of 2.5 years. The change of sex in the majority of the individuals takes place at the age of 4 years, and the shrimps first deposit eggs at the age of 4.5 years.

3. In the waters from the island of Sanak to the Kenai Peninsula, the main features of the biology of the northern shrimp are, apparently, quite similar, despite the fact that the Kenai Peninsula is situated considerably further north than Sanak. This similarity is explained by the fact, evidently, that the warm current along the western part of the Gulf of Alaska flows from north to south. For this reason, the thermal conditions of the shrimp habitat in the western part of the Gulf of Alaska do not become more severe by virtue of the more northerly location, and the process of growth and maturation is not retarded, as it is off the shores of Norway and in the eastern part of the Gulf of Alaska.

4. In the Bering Sea the shrimps often remain sexually immature up to the age of 2.5 years, and many first take part in reproduction in the capacity of males at the age of 3.5 years. At the age of 4.5 years, a majority of the shrimps functions in the capacity of males for the second time. The change of sex occurs, in the main, at the age of 5 years, and the first deposition of eggs, at the age of 5.5 years.

5. From the diagrams of the size composition, it is possible to make judgements of the yield of a generation and to make approximate forecasts of the size composition of catches for 2-3 years ahead.

6. By way of a working hypothesis, the assumption emerges with respect to the fact that the yield of a generation depends on the character of the first winter in the life of the shrimps, and on the numerical strength of the parental stock.

7. We consider the basic measures for the regulation of fishery to be the establishment of closed seasons for fishery (especially for the period of the hatching of the larvae), the establishment of a minimum mesh size for the trawls and the establishment of a maximum allowable incidental catch of individuals that are of less than commercial size.

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