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Characteristic Features of Ecology of the Pacific Saury *Cololabis saira* (Scomberesocidae, Beloniformes) in Open Waters and in the Northeast Pacific Ocean

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Abstract—The results of long-term studies of the spatial distribution, size composition, and spawning intensity of the Pacific saury *Cololabis saira* in open waters of the North Pacific Ocean and the northeastern part of the Pacific Ocean off the west coast of North America are presented. In the open waters of the Pacific Ocean, saury forms aggregations early in summer; intraseasonal changes in their distribution pattern have been identified. Migrations of Pacific saury stocks in the northeastern part of the Pacific Ocean were considered, and assumptions about their causes were made. The differences in the size composition of Pacific saury in different parts of the range are associated with the peculiarities of occurrence of favorable conditions for the formation of aggregations. Intensive spawning of Pacific saury in the northeastern part of the Pacific Ocean is observed in winter and spring, and that in open waters is observed in summer. The distribution of the early progeny of Pacific saury is associated with the systems of currents; its findings in the extreme northern regions in the 1980s are explained.

Keywords: Pacific saury *Cololabis saira*, aggregations, migration, size composition, spawning, open waters, near-American waters

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INTRODUCTION

The Pacific saury *Cololabis saira* is the only intensively harvested member of the family Scomberesocidae. From the 17th century to the present time, this species has been a valuable object of targeted fishery in the North Pacific Ocean. Modern catch of Pacific saury by all countries is 400000–600000 tons, which is 1.5–2.0 times higher than in the last decade of the 20th century. This increase is largely due to the expansion of harvested areas and the intensification of fishing (in particular, due to involvement of additional countries). The proportion of catches taken by Russia in the total catch traditionally does not exceed 20%, although there are considerable reserves for its increase (Karedin, 2001).

An in-depth scientific study of the Pacific saury started in the first half of the 20th century. In this period, the first schemes of Pacific saury migrations were drawn and the studies of the distribution of Pacific saury aggregations and the behavior of individuals were performed (Uno, 1935; Nakamura, 1937; Andriashev, 1939; Alperovich, 1940). A significant and invaluable contribution to the study of this species was made by Soviet and Russian researchers (Rumyantsev, 1947; Parin, 1960; Novikov, 1966, 1967; Serdyuk, 1967, 1970; Shuntov, 1967; Pavlychev, 1972; Sablin, 1980; Sidel'nikov, 1981; Ivanov, 1994). Their ideas on various issues of the biology and ecology of the Pacific saury have not lost their significance today. However, despite the fact that a very large number of papers were published in the second half of the XX century, including the summarizing reports (Odate, 1977; Fukushima, 1979; Sablin, 1980; Belyaev, 2003), devoted to various aspects of the biology and economic use of Pacific saury, many issues have remained unsolved. The latter include the characteristics of the population structure, the effect of various factors on the structure of populations and dynamics of abundance, as well as the prediction of abundance. Many partial issues that are of interest in terms of the economic use of this species (for example, the harvesting of its resources in the open waters of the North Pacific Ocean and the northeastern part of the Pacific Ocean) are also studied insufficiently.

From the 1960s–1980s, the Pacific Research Institute of Fisheries and Oceanography (TINRO, Vladivostok) and the Pacific Department of Fishery Survey and Research Fleet (TURNIF, Vladivostok) conducted a series of scientific surveys and prospecting operations in the open waters of the North Pacific and the northeastern part of the Pacific Ocean (off the west

Table 1. Data used in the study

Type and name of vessel	Period of work	Main content of work
FT *Ogon'*	Sept.–Nov. 1966	Prospecting
FRV *Iskatel*	Sept.–Dec. 1967	Same
FRV *Raketa*	Sept.–Nov. 1970	"
FT *Ogon'*	Aug.–Nov. 1971	Research and ichthyoplankton survey
MFFT *Korifei*	Mar.–July 1983	Prospecting
MFFT *8-432*	May–July 1983	Same
Same	June–July 1984	"
MFFT *Antiya*	June–Aug. 1984	Research and experimental work with various types of gear
MFFT *Eleninsk*	June–July 1984	Prospecting
MFFT *Parusnoe*	June–July 1985	Same
MFFT *Zavitinsk*	Mar.–July 1986	"
LFFT *Poseidon*	Mar.–June 1988	Ichthyoplankton and trawl surveys
MFFT *Eleninsk*	Apr.–June 1988	Same
LFFT *Poseidon*	June–Oct. 1989	"

Designations: FT—fishing trawler; FRV—fishing research vessel; MFFT—medium freezing fishing trawler; LFFT—large freezing fishing trawler.

coast of North America). In these studies, data on the distribution of Pacific saury and the areas of formation of aggregations, as well as the distribution of early progeny, biology, etc., were obtained. In spite of the fact that some elements of these studies were repeated later, the data obtained during this period are the most complete.

The purpose of this study is to summarize the data and describe the characteristics features of the distribution, migration, and ecology of the Pacific saury in these regions.

MATERIALS AND METHODS

In this study, we used the data obtained during scientific exploration, comprehensive surveys (Table 1), and fishing expeditions, as well as the data obtained through international scientific and technical cooperation and published data.

To analyze the distribution of Pacific saury aggregations, we used the data obtained during four scientific and prospecting cruises performed in the near-American waters (California Current waters) in autumn 1966, 1967, 1970, and 1971 and six scientific and research cruises performed in the open waters of the North Pacific in spring and summer 1983–1986. The method for searching for the areas with high concentrations of Pacific saury was based on the idea that the aggregations of schooling fish are confined to certain physical and geographical conditions (Mesyatsev, 1937) with allowance for the horizontal and vertical movements of water and its thermal state, the level of productivity, the presence of well-expressed gradients of oceanographic characteristics, etc. (Parfenovich et al., 1984). Research was performed around the clock. In the daytime, the search for saury was performed with an underwater echo sounder; in the dark, it was performed with the aid of Pacific saury lamps, spotlights, and Solnechnik-type lighting devices. Saury stocks were caught with a side saury trap or a side cone-shaped net (Sidel'nikov, 1974, 1981). Samples for length measurements and biological assays were taken from each catch. To characterize the size composition, we used the division into different size groups: small-size (individuals less than 24 cm in fork length (*FL*)), medium-size group (24–29 cm), and large-size (more than 29 cm) (Hotta, 1960; Novikov, 1960, 1967; Gong, 1984).

To analyze the distribution of eggs and larvae of Pacific saury, we used the results of three ichthyoplankton surveys that were carried out in spring and summer 1988 and in summer and autumn 1989. Icthyoplankton was harvested with an IKS-80 egg net and Maruchi-Ami and Sameoto–Jarosznsky neuston nets. Fishing operations were performed around the clock in the 0.5–0 m layer at a speed of 2 kn per 10–15 min (*Rekomendatsii* ..., 1987). In addition, we used data from ichthyoplankton surveys performed simultaneously with research in the near-American waters in the 1970s and 1980 aboard the research vessel *Tikhookeanskii*.

We performed background work, including the implementation of hydrological stations to determine the boundaries of the frontal zones, warm and cold currents and eddies and their impact on the distribution and behavior of fish and plankton stations in all cruises.

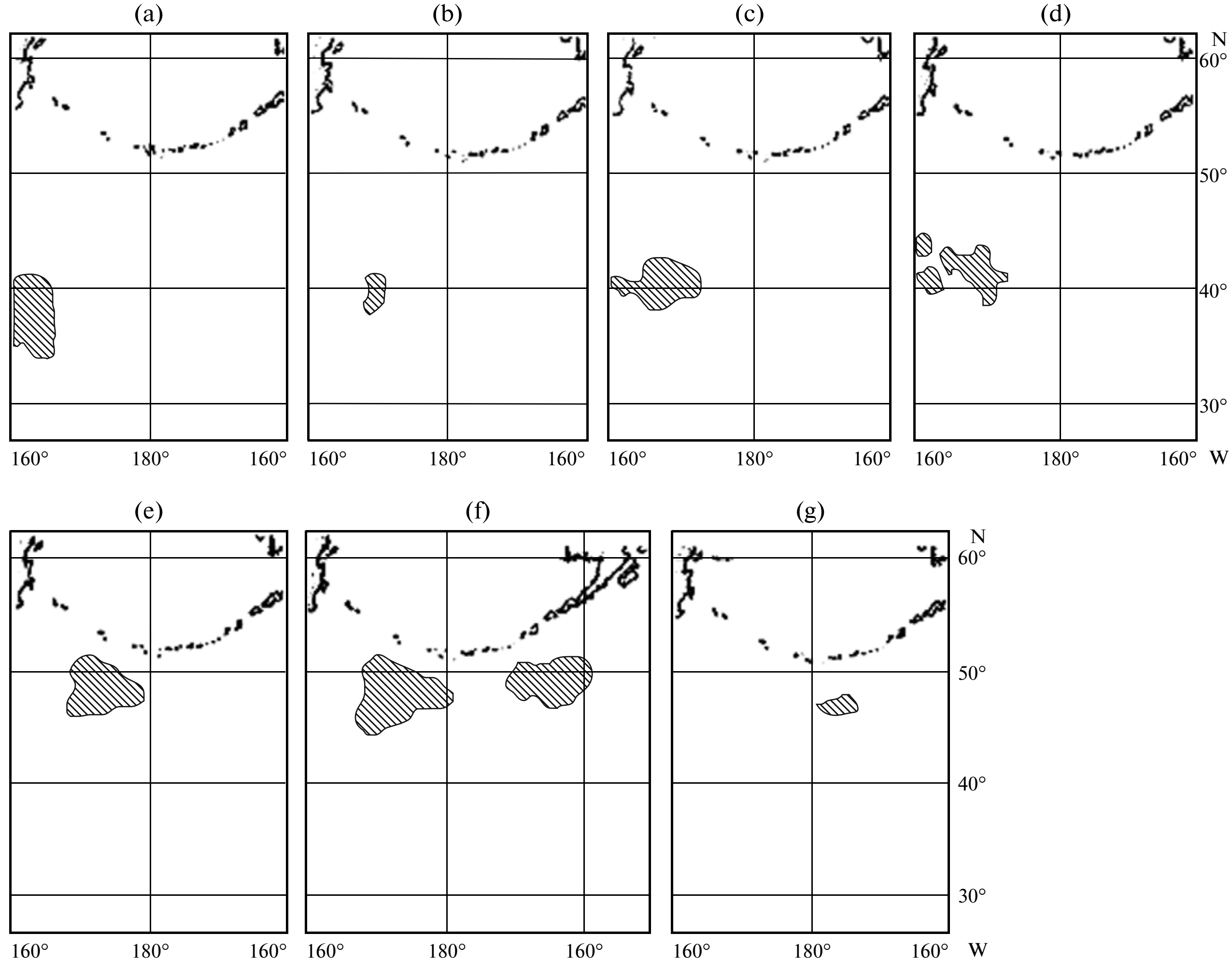

Fig. 1. Distribution of the Pacific saury *Cololabis saira* (hatched area) in the open waters of the northern part of the Pacific Ocean in the 1980s: (a) April, (b) May, (c) June, (d) July, (e) August, (f) September, and (g) October.

RESULTS

Distribution and migrations. In all years, research was performed under conditions similar by the degree of development of seasonal processes, corresponding to the summer period in the open waters and the autumn period in the near-American waters. This approach makes it possible to precisely characterize the distribution of the schools and aggregations of Pacific saury as well as their migrations in the study area at that time (the period of feeding migrations).

According to obtained results, the first schools of Pacific saury in the open waters of the North Pacific appeared in April between 33° and 40° N (Fig. 1a). At this time, schools migrated to the north and did not form large aggregations. Spatial differentiation of individuals of different sizes was observed: small- and medium-sized individuals began to migrate first, whereas the large fish were observed at that time only in the southern part of the study area.

In May, the main area of distribution of schools of Pacific saury shifted northwards (Fig. 1b). In this period, the density of schools began to increase, and by the end of the month the aggregations were already suitable for fishing. This is largely due to the migration of fish to the transformed subarctic waters, where a set of conditions required for the formation of aggregations is formed in some areas at this time. Concentrated in the upper parts of warm inflows of transformed subarctic waters, aggregations of Pacific saury did not perform noticeable migrations for a long time.

In June and July, the northern boundary of the distribution of Pacific saury aggregations was at 43°–45° N (Figs. 1c, 1d). In the second half of July, intense heating of the upper layers of the ocean led to the erosion of the frontal zone and changed the set of conditions required for the formation of aggregations. As a result, saury schools moved northwards to the subarctic waters. Despite this migration, the spatial differentiation of different size groups of Pacific saury remained.

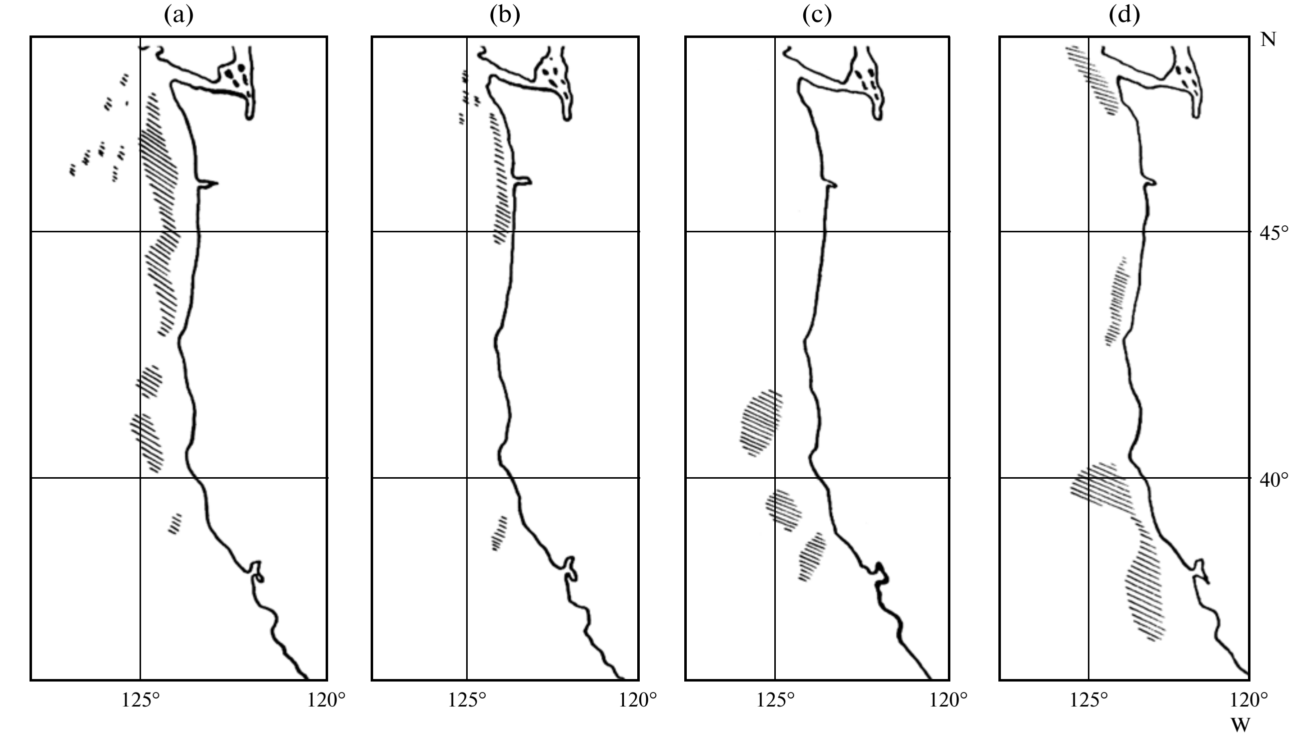

Fig. 2. Distribution of the Pacific saury *Cololabis saira* (hatched area) off the west coast of North America in autumn: (a) 1967, (b) 1969, (c) 1970, and (d) 1971.

On the basis of the earlier observations (Birman, 1958; Vigdorovich, 1967), it can be concluded that, saury is dispersed over a large area northward of 44° N, including the Pacific waters near the Aleutian Islands (Figs. 1e–1g), in the open waters of the North Pacific in August–October.

In the near-American waters, the aggregations of Pacific saury in autumn are confined to the area of divergence of the California Current and the Davidson Current (Fig. 2). Stable aggregations were formed at the end of August and disappeared in December. In the study seasons, they migrated from the north, where the major aggregations were found primarily in the coastal areas, to the south. In the course of migration, their density decreased, and the area of distribution expanded to more seaward areas.

Size composition. In April 1983, in a large area of open waters (from 33° to 37° N between 153° and 166° E), young saury (*FL* 10–14 cm) was encountered.

In May, the size composition of Pacific saury changed apparently due to the large individuals migrating from the south. The length of Pacific saury caught in the area 38°35′ N and 168°26′ E varied from 27 to 31 cm (mean, 27.9 cm).

In June, the size composition of Pacific saury in the western and eastern parts of the study area was different. For example, the catches in the area 162° E were dominated by one-size groups in all study years. In 1983, the catches of Pacific saury contained individuals with *FL* 14–32 (29.8) cm; the modal group included individuals whose size fell in the range 27–32 cm (Fig. 3a). A similar size range of Pacific saury (28–32 (29.6) cm) was observed in 1984 (Fig. 3b). In 1986, the boundaries of the size range expanded (Fig. 3c), which was accompanied by a decrease in the average body length (27.9 cm). In the area 172° E, a wider size range with several modal groups was observed in all study years. The expansion of the size range and the decrease in the average length compared to the western sector was due to the increase in the proportion of small- and medium-sized fish in catches (Figs. 3d–3f).

In July, the differences in the average length between the western and eastern sector remained, although the size composition of catches changed. In 1985, in the western sector, the size range had two distinct peaks at 23 and 30 cm; individuals with *FL* 16–32 (25.0) cm were caught (Fig. 4a). In 1986, the average size of fish increased to 27.4 cm, catches contained individuals 18–31 cm long, and the size range had three distinct peaks at 21, 25, and 29 cm (Fig. 4b). In 1984, the size composition of catches of Pacific saury in the eastern sector remained practically the same, but the proportion of large individuals and the average length of fish increased (Fig. 4c). In 1985, as in 1984, saury catches contained fish with *FL* 16–33 (22.9) cm; two modal group could be distinguished in the size range (Fig. 4d).

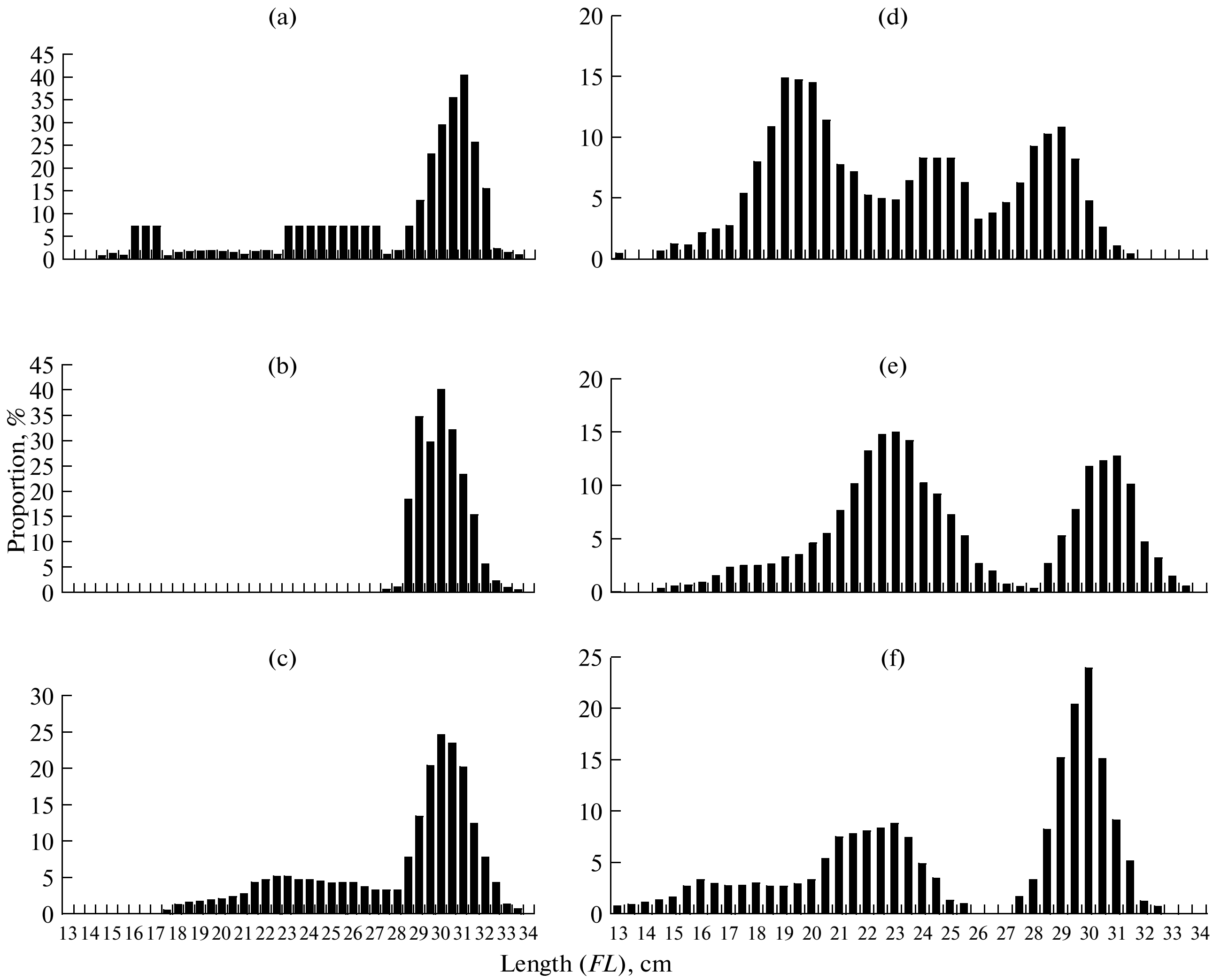

Fig. 3. Size composition of the Pacific saury *Cololabis saira* in the open waters in June in the area (a–c) 162° E and (d–f) 172° E in different years: (a) 1983 (M = 29.8 cm, n = 690), (b) 1984 (M = 29.6, n = 643), (c) 1986 (M = 27.9, n = 1000), (d) 1983 (M = 23.6, n = 400), (e) 1984 (M = 24.6, n = 2868), and (f) 1986 (M = 25.2, n = 1761).

In the near-American waters, the average size of fish in the catches in different months during the study period ranged from 21.7 to 29.6 cm (Table 2). The monthly dynamics of the average size in the catches was not expressed. In fact, the size range in the catches was represented by one modal group (small- and/or medium-sized). In August 1973, the size composition of Pacific saury in the catches was characterized by the domination of small individuals (Fig. 5). The size range was represented by one modal group, and the average length of individuals in samples did not exceed 21.7 cm. In September 1971, the proportion of small fish in the catches was lower. The size range was also represented with one modal group, but the average length of individuals in samples was greater and ranged from 21.6 to 28.3 cm in different parts of the study area. The highest proportion of medium-sized individuals (and, accordingly, the greatest average length) was observed in the samples taken in the northern parts of the study area. It should be noted that, in general, the proportion of small individuals in the near-American waters in 1960s–1970s ranged from 55 to 70% (Fig. 6a). The boundaries of the size range usually fell in the range 15–30 cm (Fig. 6b). According to the data

Table 2. Average length (*FL*, cm) of Pacific saury *Cololabis saira* in different months in 1966–1971 in the California Current area

Years	Months				
	Aug.	Sept.	Oct.	Nov.	Dec.
1966		29.6	25.5	25.2	
1967		22.6	23.9	25.1	23.1
1970		25.3	25.9	25.2	
1971	24.6	21.7	24.8		

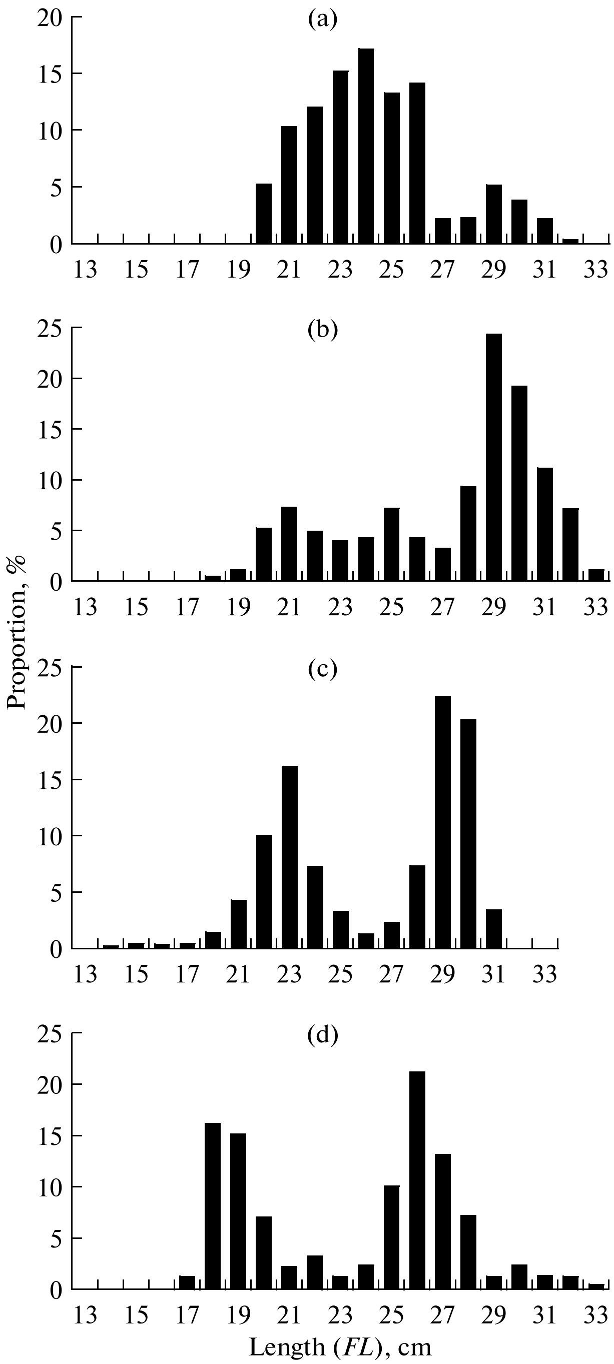

Fig. 4. Size composition of the Pacific saury *Cololabis saira* in the open waters in July in the area (a, b) 162° E and (c, d) 172° E in different years: (a) 1985 (M = 25.0 cm, n = 1500), (b) 1986 (M = 27.4, n = 200), (c) 1984 (M = 26.7, n = 1550), and (d) 1985 (M = 22.9, n = 600).

obtained during the cruise of RV *Poseidon*, which performed a trawl survey in the waters of the California Current in summer 1989, the length of Pacific saury ranged from 14 to 26 cm and the size composition of catches, as in 1970s, was dominated by the small individuals. However, in our opinion, the limited sample size (190 individuals) does not allow these results to be extrapolated to the entire California Current region.

Reproduction. In spring and summer 1988, studies were performed in the area of the subarctic front from 150°00′ E to the western coast of North America. Early progeny of Pacific saury was found throughout the study area, and the highest concentrations were reported in March near the Emperor seamount (Fig. 7a). A similar situation was observed here later. In May, the frequency of occurrence of progeny of Pacific saury in the area between 163° and 172°30′ E was more than 90%, and the average catch per net was 30 individuals (Fig. 7b), whereas the frequency of occurrence and the catches of Pacific saury larvae in the western areas were almost one order of magnitude lower.

In the summer and autumn 1989, the progeny of Pacific saury was found throughout the study area, including the Gulf of Alaska (Fig. 7c). In 1989, the maximum catches of the early progeny of Pacific saury were made at the beginning of autumn in the northeastern part of the ocean, between 155°00′ and 135°00′ W. The frequency of occurrence of progeny in this area was approximately 90%. In the area westward of the 180th meridian, including the areas of underwater ridges, the catches and frequency of occurrence of the early progeny of Pacific saury were very low. The results of the survey performed in 1989 suggests that the distribution of the early progeny of Pacific saury in the east is not limited to 135° W. The breeding of Pacific saury in the eastern areas, in the California Current waters, was confirmed by the ichthyoplankton survey conducted in September 1971. The frequency of occurrence of the early progeny of Pacific saury in the surveyed area (36°–49° N) was greater than 90%, and the highest catches were taken in the southern part of the study area.

DISCUSSION

Distribution and migration. For certain objective and subjective reasons, the methods that are currently used to identify the migratory pathways of Pacific saury include neither tagging (which shows less than 1% return) nor the genetic methods (although it was shown by these methods that individuals from the eastern areas (155°–160° E) reach the coasts of the islands of Japan in 4–6 months (Hara et al., 1982a, 1982b)) nor the identification of migration routes by remote sensing (including satellite data, which in the first phase of research gave good results). Thus, the studies of migrations of the saury today are still based on the results of research cruises and fishery statistics data.

The recently published summarized data describing the conditions of Pacific saury fishing by Taiwan (Statistics ..., 2011; Tseng et al., 2013), which performs its intensive fishing in the open waters in the past 10 years, make it possible to verify the above assumptions about the distribution and migration of Pacific

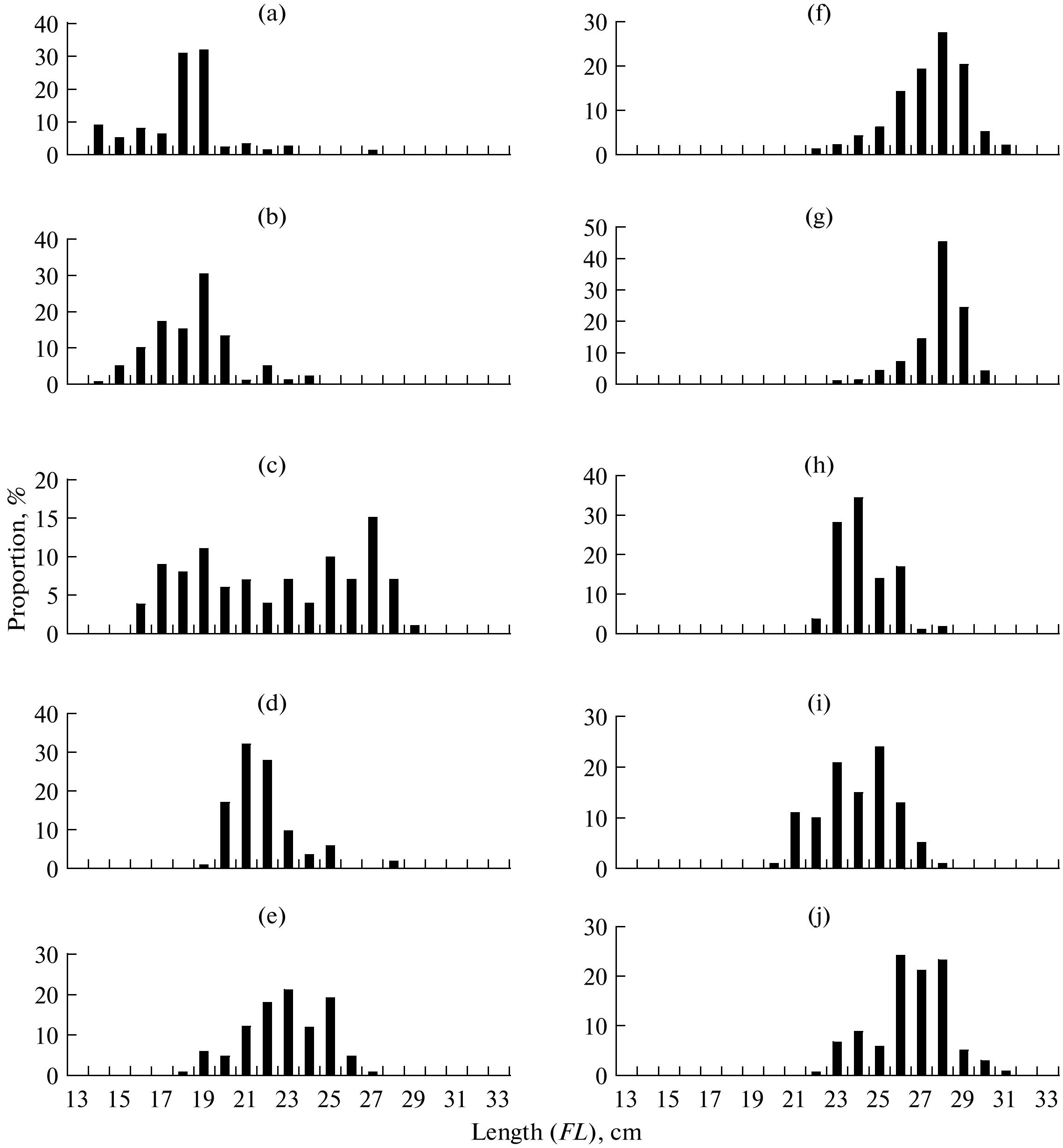

Fig. 5. Size composition of the Pacific saury *Cololabis saira* off the west coast of North America in (a–c) August 1973 and (d–j) September 1971: (a) 38°41′ N, 124°27′ W (M = 18.1 cm, n = 40); (b) 43°31′ N, 124°54′ W (M = 18.5, n = 50); (c) 42°06′ N, 125°12′ W (M = 21.7, n = 51); (d) 48°31′ N, 126° W (M = 21.6, n = 100); (e) 38°39′ N, 124°02′ W (M = 22.9, n = 100); (f) 48°57′ N, 126°16′ W (M = 27.7, n = 100); (g) 52°15′ N, 132°29′ W (M = 28.3, n = 100); (h) 47°10′ N, 125°55′ W (M = 24.2, n = 100), (i) 44°19′ N, 124°42′ W (M = 23.7, n = 100); and (j) 44°30′ N, 124°48′ W (M = 26.4, n = 100).

saury in the open waters. These data show that, firstly, the center of fishing in summer shifts to the north and northwest, and, secondly, the efficiency of fishing steadily increases from the first ten-day period of June, thus confirming the above generalized scheme of migrations of Pacific saury in the open waters.

In general, the contours of the migration routes of Pacific saury are determined by the specific features of the oceanographic regime in different parts of its range, the structure of the vortex field of the mixing zone of subtropical and subarctic waters, and the behavior patterns of individuals in the field of eddies and currents during the movement in the northern (southern) direction (Matsuadaira et al., 1956; Novikov, 1967; Fukushima, 1979; Kosaka, 2000). In the open waters, the scheme of migrations of the Pacific saury in summer is consistent with the existing scheme of development and interaction of the main currents (Kuroshio, the Kuroshio extension, and the North Pacific Current) and can be considered as part of the migration of the Pacific saury group inhabiting the northwestern part of the Pacific Ocean. For this

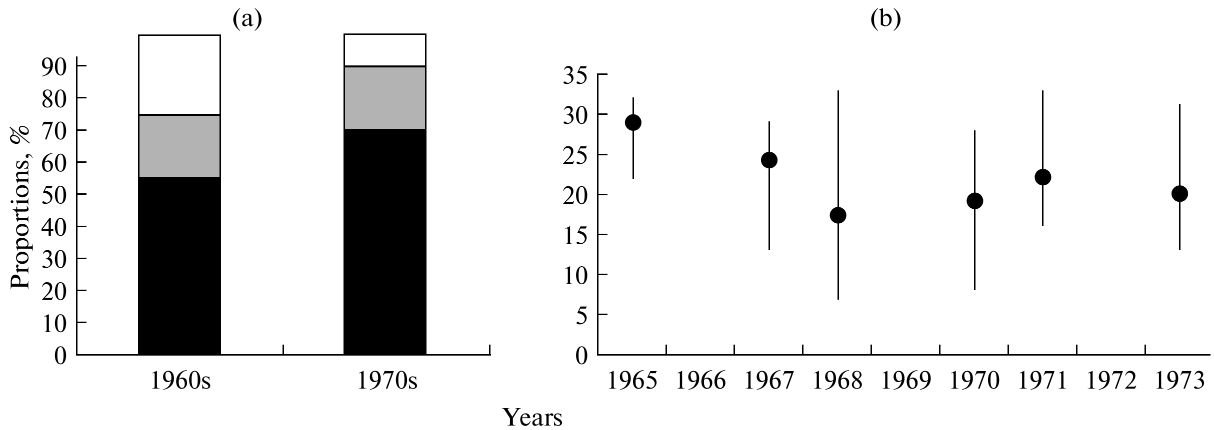

Fig. 6. (a) Ratio of different size groups of the Pacific saury *Cololabis saira* in catches in 1960s and 1970s and (b) the length of individuals in 1965–1973 off the western coast of North America. Designations: (□) large, (▒) medium-sized, (■) small, (●) mean values, and (|) limits of variation.

group, the intensity of migration and the extent of penetration of individuals to the north depend on the location and development of the branches of Kuroshio and Kuril currents. It is assumed that, in some years, the main migration routes of Pacific saury may run along the third oceanic branch of the Kuroshio Current and be included in the Western Subarctic gyre with penetration of certain saury schools to Kamchatka and their further migration to the Pacific waters of the Kuril Islands (Karedin, 1989). Indeed, recent studies have shown that the Pacific saury can penetrate by this route into the southwestern part of the Bering Sea (Glebov et al., 2010). The conclusion about the migration of Pacific saury schools from the open waters (eastward of 160° N) to the Japanese waters was also made by Suyama et al. (2012). At the same time, it cannot be ruled out that Pacific saury schools may penetrate into the waters surrounding the Aleutian Islands and the southwestern part of the Bering Sea from the east, with the Alaska Current water. These movements can be regarded as part of migrations of the American group of Pacific saury inhabiting the northeastern part of the ocean (Glebov et al., 2010). It is known that, in the near-American waters, the oceanographic situation largely depends on the redistribution of the intensity of the Alaska and California currents. The wind component, which determines the enhancement of the Alaska Subarctic Gyre and the California Current, is also of great importance (Hollowed and Wooster, 1992; Shuntov, 2001).

In the mid 1970s, abrupt climate changes occurred in the northeastern part of the ocean (Francis et al., 1988; Parrish et al., 2000). Regarding the water dynamics, they manifested themselves as changes of the intensity of the California and Alaska currents. In the 1950s, the California Current was strong, whereas the Alaska Gyre became stronger in the 1980s, which naturally affected the temperature regimen and the plankton community (Hollowed and Wooster, 1992; Kotenev, 1995; Krovnin, 1995) and the migratory routes of pelagic fish in these regions. This assumption was confirmed by the analysis of the results of studies in the waters of the Pacific Ocean surrounding the Aleutian Islands, which were performed in the 1960s (Vigdorovich, 1967). Large aggregations of immature Pacific saury were found, which consisted primarily of small and medium-sized individuals. A characteristic feature of the size composition was that, with the advance to the west, the proportion of small individuals decreased. As in the 1980s, the first half of the 1960s was characterized by an increase in the intensity of the Alaska Gyre and a decrease in the biomass of zooplankton in the California Current waters, though not as strong and durable as in the 1980s (Roemmich and McGovan, 1995).

The migrations of the Pacific saury in the waters of the California Current, which is a narrow (approximately 150 km wide) meandering stream generating eddies of opposite signs (Burkov and Pavlova, 1980; Husby and Nelson, 1982), are consistent with the existing ideas about the dynamics of water and inhomogeneity of physicochemical processes leading to the formation of local concentrations of zooplankton, including the foraging one (Feshchenko and Bocharov, 2002).

Size composition. Earlier, Kramer and Smith (1970) indicated that the average size of saury individuals in the California Current waters did not exceed 22 cm. Similar data were reported by Novikov (1972) and Sunada (1974). Thus, the majority of authors point out that only small and medium-sized individuals occur in the northeastern part of the Pacific Ocean in the waters of the California Current, although Vigdorovich (1967) and Novikov (1972) noted that this size structure in characteristic primarily of the coastal areas. Inoue and Hughes (1971), who cited unpublished data obtained at the Biological Laboratory of Honolulu, also pointed out that in the areas southward

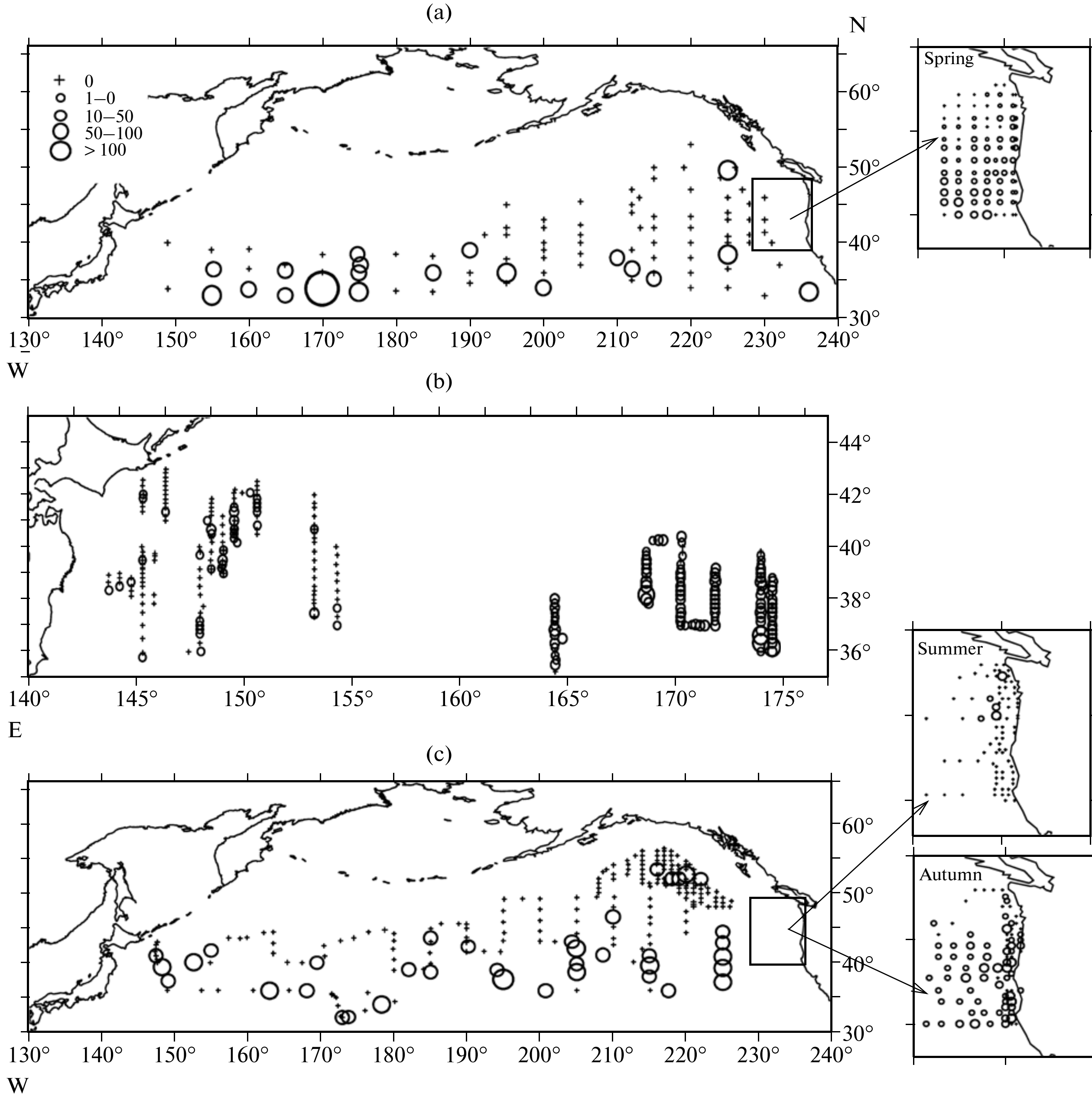

Fig. 7. Distribution of catches (ind./net) of the early progeny of the Pacific saury *Cololabis saira* in the northern part of the Pacific Ocean in (a) March–June 1988, (b) April–June 1988, and (c) June–October 1989 (by: Doyle, 1992; Baitaliuk and Davydova, 2002, amended and supplemented).

of 45° N from the American coast to 135° W, the proportion of large individuals in the catches of Pacific saury increases in autumn. The conclusion about the domination of small and medium-sized individuals in the California current can be made on the basis of more recently published data. For example, American and Japanese researchers who studied the age composition of Pacific saury off the west coast of North America (Sunada, 1974; Watanabe et al., 1988) showed that samples almost entirely consisted of the representatives of these size groups.

According to Novikov (1972), one of the main differences between the saury from the northwestern and northeastern parts of the Pacific Ocean is the size of spawners. In the Sea of Japan and in the Kuroshio Current water, sexual maturation of saury begins at *FL* of about 24 cm, and the spawners are usually at least 28–29 cm long. Similar results were obtained in the central part of the ocean. Japanese researchers (Suyama et al., 1996) showed that, in summer, individuals with $FL > 29$ cm older than 1.5 years spawn in this area. According to several authors (Novikov, 1972;

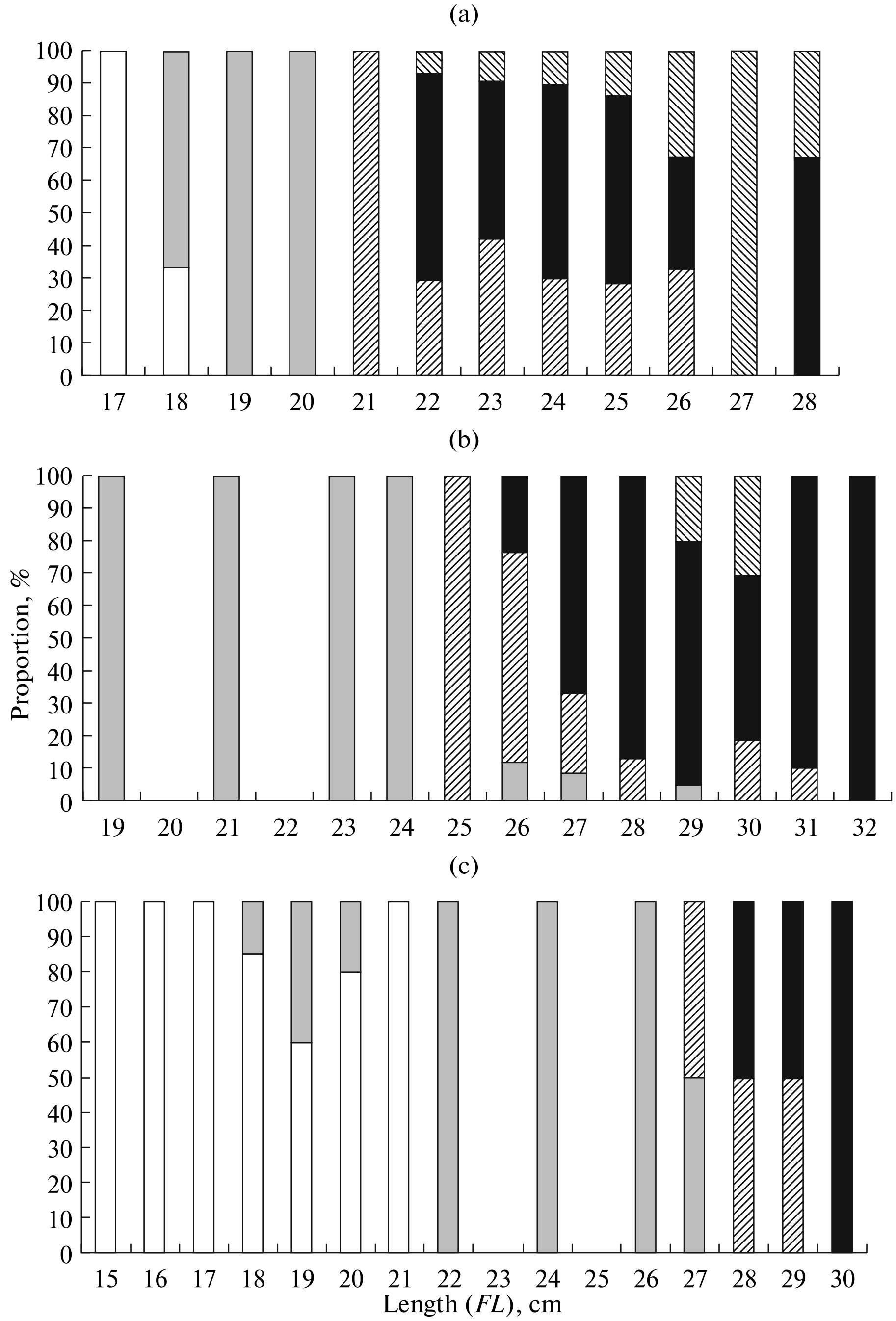

Fig. 8. Ratio of the Pacific saury *Cololabis saira* females with gonads of various stages of maturity in different size classes off the west coast of North America in (a) April and May, (b) July, and (c) August: (☐) juvenile, (☐) II, (▨) III, (■) IV, and (▧) V stage of maturity.

McGregor, 1976), the average length of spawners (IV, IV–V, and V stages of maturity) in the California Current is approximately 23 cm, and some individuals begin to spawn at *FL* of 19 cm. At the same time, on the basis of data obtained in the 1960s–1970s, it can be assumed that, similarly to the Kuroshio Current waters, the majority of individuals off the west coast of North America become sexually mature and spawn at *FL* > 22–24 cm. Figure 8 clearly shows that gonads of maturity stages IV and V are found mostly in the medium-sized and large animals. McGregor (1976) pointed to the finding off the western coast of North America of saury spawners with *FL* 19 cm; however, this is an exception rather than a rule, especially with allowance for the fact that the fish was found in the waters of the southern part of the California Peninsula, in the region where the ranges of the Pacific saury and the dwarf saury *Elassichthys adocetus* overlap (Parin, 1968; Ahlstrom and Stevens, 1976; Kovalevskaya, 1986).

Reproduction. According to an assumption of Kramer and Smith (1970), the center of the spawning area of the Pacific saury off the coast of North America is located southward of 35° N; in general, larvae and eggs of Pacific saury are found from Mexico to the Gulf of Alaska (Kovalevskaya, 1986). According to the data of the joint Soviet–American studies, which were summarized by Doyle (1992), the position of the breeding center is not constant throughout the year. From spring to summer, it shifts to the north, and in summer the spawning area occupies the extreme northern location. In winter, it is located southward of 40° N. According to the data obtained in 1967, in January–March, larvae and juveniles of Pacific saury in the California Current were encountered everywhere from 20° to 35° N; southward of 25° N, catches contained only the young saury with FL > 40 mm (Sokolovskii, 1972). Ahlstrom and Stevens (1976) pointed out that, early in spring, the maximum concentrations of larvae and eggs of Pacific saury are found southward of Cape Conception at a small distance from the coast; as the distance to the ocean increases, catches and frequency of occurrence of the early progeny of saury decrease.

On the basis of the above data, the principal scheme of seasonal migrations of the spawning areas of Pacific saury in the northeastern part of the ocean can be drawn. In winter and summer, the spawning area occupies the northern and southern positions, respectively. In the first case, the center of the spawning area is located southwestward of Cape Conception at a distance of 150–200 miles from the coast, between 29° and 31° N. During this period, the area of occurrence of the progeny of the Pacific saury in the south may overlap with the area of occurrence of the dwarf saury, whose mass spawning in the northern hemisphere is observed in winter months (Ahlstrom and Stevens, 1976; Kovalevskaya, 1986). The northern boundary of the spawning area of the Pacific saury in winter is probably located between 35° and 40° N. In summer, the spawning area is shifted to the coast. According to the survey performed in August 1980, the northern boundary of the distribution of the progeny of Pacific saury was located between 47° and 48° N; the southern boundary was located at 45° N. Therefore, the shift of the spawning area of Pacific saury in summer to the north is accompanied by a reduction in its size. In autumn and spring, the spawning area of Pacific saury occupies an intermediate position. Apparently, seasonal migrations of the spawning area of Pacific saury first northeastwards—from the seaward areas to the coast—and then back take place during the year.

The relationship between the localization of the areas with a high concentration of eggs and progeny of pelagic fish and the dynamic structures on the surface of the ocean (in particular, meanders and eddies) was noticed a long time ago. In the California region, this relationship was studied in detail using the California sardine *Sardinops caeruleus* as an example: the greatest concentrations of progeny were observed in the areas with high repeatability of eddies (Logerwell and Smith, 2001). It is known that, in this region, the vast majority of eddies are observed in the areas where the California countercurrent and the northern geostrophic countercurrent (the Davidson Current) are formed (Burkov and Pavlova, 1980; Simpson and Lynn, 1990), and their position is characterized by considerable seasonal variations (Hickey, 1989). Thus, the migrations of the areas with a high concentration of the early progeny of Pacific saury (the breeding center) are closely related to the seasonal dynamics of the location of eddies.

Here, it should be noted that, in general, the comparison of the data obtained by the American authors (Smith et al., 1970; Ahlstrom and Stevens, 1976) with the data obtained during the Soviet–American survey, which were partially summarized by Doyle (1992), shows a significant difference between the locations of the spawning areas of Pacific saury in the northeastern part of the Pacific ocean in 1950s and 1980s. In general, as compared to the period of 1951–1960, the period of 1980s was characterized by a shift of the spawning area of Pacific saury to the north and a decrease in its size. We have already mentioned the climatic changes that have occurred in the northeastern part of the Pacific Ocean and the changes in the intensity of the Alaska Gyre and the California Current in 1950s–1980s. These changes could determine the differences in the location of the spawning areas. It should be emphasized that both the detection of Pacific saury eggs in the Gulf of Alaska in 1989 and the annual detection of eggs and young progeny of Pacific saury in summer 1980 in the Gulf of Alaska (Baitaliuk and Davydova, 2002) were made during the increase in the Alaska Gyre, in the years when positive temperature anomalies of water in this area were observed (Hollowed and Wooster, 1992).

In addition to the above-mentioned causes, the location of the areas of spawning and distribution of the progeny of Pacific saury in the California region is apparently affected by the annual dynamics of hydrological conditions, which is largely determined by the extreme warming in the central and eastern parts of the equatorial region of the Pacific Ocean. El Niño that occurred in 1982–1983, was one of the strongest events in the last century. In the California Current area, this event caused a decrease in the primary production and changes in the structure of plankton communities (Hernandez-Trujillo, 1999) and ultimately led to a reduction in the number of harvested species of pelagic fish (Francis et al., 1988; McCall and Prager, 1988). From the first half of the 1980s, a reduction in the total number of eggs of Pacific saury in the California Current was observed (McCall and Prager,

Table 3. Proportion of Pacific saury *Cololabis saira* individuals with gonads of various stages of maturity in the California Current area (%)

Months	Sex	Stage of maturity				Number of fish, individuals
		II	III	IV	V	
Sept.	Males	80.5	9.3	10.2	0	108
	Females	49.0	25.0	26.0	0	92
Oct.	Males	67.0	33.0	0	0	189
	Females	7.7	63.5	28.8	0	261
Nov.	Males	26.3	38.6	34.4	0.7	134
	Females	6.0	78.5	15.5	0	116

1988), which may also be associated with adverse conditions in the spawning grounds.

As a rule, the conclusion about the terms of mass-scale spawning of fish is made on the basis of results of egg and larval surveys as well as data on the duration of embryonic development and the growth rate in early ontogeny. Data on the intensity of spawning of Pacific saury in the California area are extremely fragmentary and inconsistent; a continuous series of observations covers only the period of 1950–1966. In general, the catches of saury eggs are made from February to July; approximately as much as 90% of saury eggs are detected in this period. According to the averaged data for 1950–1959, the spawning peaked in April, although McGregor (1976) noted that, in some years, the peak of spawning is observed at the beginning of February or the end of July. In more than 50% of cases, two peaks of spawning were detected during the year. Other conclusions can be made on the basis of analysis of the data reported by Sunada (1974) for the first half of 1970s. In summer, in the California Current area, catches contained only immatures, whereas the proportion of mature individuals drastically increased in December. These results are consistent with the data obtained in the experimental study of the saury fishing in the northeastern part of the ocean in autumn 1971 (Table 3). Obviously, the proportion of fish with gonads of the III and IV stages of maturity in 1971 progressively increased from September to November.

Some ideas about the timing of spawning of Pacific saury can be provided by the analysis of the variation series of the size composition of saury progeny. According to the results of the ichthyoplankton survey in September 1971, catches were dominated by the larvae and fries with *FL* 20–40 mm. Taking the average daily gain to be 0.7 mm[1], these individuals hatch in the first half of summer (June–July). With allowance for the duration of embryonic development, these eggs were presumably spawned in late spring or early summer. Unfortunately, the lack of data does not allow us to make a final conclusion about the causes of such differences in the estimates of the spawning intensity in different months. In our opinion, similarly to the Kuroshio Current waters, the spawning of Pacific saury in the California Current waters peaks in the winter and spring months. Previously, such assumptions were made by Novikov (1972) and Sokolovskii (1972) on the basis of single ichthyoplankton surveys in the California area. The validity of this assumption is confirmed by the multiyear results of catches of the progeny of Pacific saury in this area in 1950–1966 (Fig. 9). The progeny of Pacific saury that dominated the catches in September 1971 could be produced in the open waters of the ocean and reach the California area in the flow of the North Pacific and then the California currents. This hypothesis does not contradict the earlier assumption about the existence of intense spawning in the open waters of the Pacific saury in the early summer and subsequent passive migration of the early progeny of Pacific saury in the waters of the Kuroshio Current and its extension and in the North Pacific current (Selitskaya, 1972; Kosaka, 2000; Baitaliuk and Davydova, 2002; Oozeki et al., 2009).

It should be noted that the scheme of passive transfer of the progeny of Pacific saury to the northeastern part of the ocean is much more complex than in the northwestern part. This is due not only to the existence of two large opposite currents (Alaska and California) near the western coast of North America but also to the seasonal characteristics of water dynamics—the existence of the California countercurrent and the Davidson countercurrent as well as the seasonal weakening of the California Current. As a result, in the northwestern part of the ocean, the progeny of Pacific saury is transferred primarily to the east (although part of the larvae enters the subtropical waters with the meanders of the Kuroshio Current (Sablin, 1980)), whereas the passive drift of eggs and progeny near the Pacific coast of North America proceeds in both the southern and northern directions. Note that, in different seasons, the eggs and progeny of Pacific saury in the California area are passively transferred in opposite directions: in the flow of the California Current to

[1] The average growth rate (Oozeki and Watanabe, 2000) determined under experimental conditions at temperatures close to those in the spawning grounds of saury in the northeastern part of the ocean.

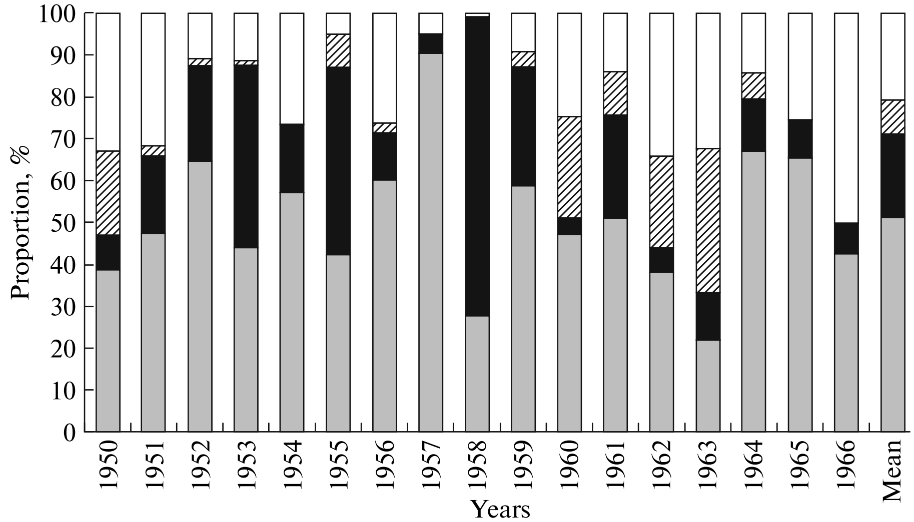

Fig. 9. Catches of the early progeny of the Pacific saury *Cololabis saira* off the west coast of North America in (☐) winter, (☐) spring, (■) summer, and (▨) autumn in 1950–1966.

the south in summer and to the north in winter, when the role of the Davidson countercurrent increases. The fact of passive westward migrations from the spawning areas can also be postulated. Ahlstrom and Stevens (1976) noted that, in spring, the frequency of occurrence of the early progeny of Pacific saury in the northeastern part of the ocean in the open waters is greater than in coastal areas and that it is more evenly distributed over the area. At the same time, the catches of progeny in the coastal areas are larger than in the open waters. The size composition is also different: the proportion of juveniles in the oceanic region is much higher. Similar features in the distribution of eggs and young progeny were observed for the northern anchovy *Engraulis mordax*. The greatest distance from the coast (300 miles) at which the eggs and larvae of this species were encountered was detected in the area of flows directed to the ocean (Stepanenko, 1972). According to O'Connell (1980, cited in Power, 1986), the total distance of the transfer of anchovy larvae in the California Current waters for 30 days may reach approximately 250 miles. In this context, data about the spatial location of areas with high concentrations of zooplankton published by Huntley et al. (1995) are of special interest. The main flow of the California Current separates the highly productive coastal waters form the low productive oceanic waters. Within these regions, there are areas with high concentrations of zooplankton that usually geographically coincide with the location of eddies of the opposite sign of rotation. Against the background of the low zooplankton biomass in the ocean compared to the coastal waters it is one order of magnitude greater in these dynamically active areas. The qualitative composition of zooplankton also changes partly due to the reduction in the proportion of small neritic species (*Paracalanus, Pseudocalanus*, and *Calanus*) and partly due to the somatic growth of juvenile planktonic organisms. Taking in to consideration that the purpose of the optimal behavioral strategy is to maximize the energy gain (Feshchenko and Bocharov, 2002), the passive drift of progeny leads to the optimization of the diet, that is, getting the most benefit with the least effort.

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