Specific features of distribution in the World Ocean of some flying fishes of the genera *Exocoetus*, *Hirundichthys* and *Cypselurus* (Exocoetidae)

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Abstract

The paper describes distribution (both seasonal and the average long-term) of the species and subspecies of the three previously taxonomically studied by the author groups of flying fishes: genus *Exocoetus*, subgenus *Hirundichthys* s.str. and *Cypselurus* "*poecilopterus*" species group. Species distribution is compared with oceanographic features (temperature, salinity, water masses, currents, biological productivity). The cases of joint occurrence of species in one sample are analyzed. It is shown that allopatric (and parapatric) species from different groups have different patterns of area partition. In the case of flying fishes of the genus *Exocoetus*, the main factor determining the boundaries between species is circulation of surface waters, among the representatives of the subgenus *Hirundichthys* – it is the distance from coasts, and in the *"poecilopterus"* group – it is the salinity. The boundaries between the ranges of species of the genus *Exocoetus* pass mainly along the boundaries of ocean currents, in the species of the subgenus *Hirundichthys* - along the boundary between the far-neritic and oceanic zones, and in the "*poecilopterus*" group - according to isohaline of ~ 35 ‰. Sympatric species are supposed to have different mechanisms to reduce the interspecies competition: in the genus *Exocoetus*, there is a division into few-raker and many-raker species, while for the species of the subgenus *Hirundichthys* it was noticed an alternate use of the Arabian Sea basin and spatial separation of fishes having similar sizes.

Keywords: Exocoetidae, Area partition, Surface circulation, Sea surface temperature, Sea surface salinity, Subtropical convergence.

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Introduction

Flying fishes are the most characteristic representatives of fish communities of the epipelagic ocean. They occupy a unique position in the ecosystem of the tropical open ocean being the only mass planktivors permanently inhabiting the surface layers of the epipelagic zone, and, in turn being an important component in the diet of predatory fishes, squids, seabirds, and dolphins (Parin 1970). The vertical distribution of flying fishes has been studied in detail by a number of authors (Tsukahara et al. 1957; Shiokawa 1967; Zuev and Nikolskiy 1980; Nesterov and Bazanov 1986). According to their data, flying fishes do not descend deeper than 18 meters and the overwhelming majority (80-95%) is confined to a narrow surface layer to a depth of 1-3 meters. However, spawning of flying fishes was sometimes observed at a depth of 20 meters (see Imai 1959; Oxenford 2007). A lifespan of flying fishes usually does not exceed one year, and only a few, the largest, individuals survive up to 2 years age (Grudtsev et al. 1986; Alekseev et al. 1989; Campana et al. 1993; Oxenford 1994; Chang et al. 2012b). Some species of flying fishes spawn in coastal waters and require a large amount of bottom or floating substrate for eggs laying; others can breed in the open ocean using a small amount of drifting objects that is present there; finally, some species do not need drifting objects for reproduction at all (Kovalevskaya 1982). As it will be shown below, some of these features of flying fishes biology leave an imprint on their geographical distribution.

The upper epipelagic zone of the ocean is a very dynamic and homogeneous environment, and finding those invisible boundaries which separate sister (and ecologically similar) species of flying fishes is of great interest. One of such boundaries is the sea surface temperature (SST): a division into tropical and subtropical species has occurred in many groups of flying fishes (for example, *Cheilopogon melanurus* – *Ch. heterurus*, see Parin and Belyanina 2000). Another example is division into neritic (or nerito-oceanic) and oceanic species (e.g. *Prognichthys occidentalis* and *P. gibbifrons* - *P. glaphyrae*, see Parin 1999). It will be shown here that these examples do not exhaust the variety of area partition patterns in species of flying fishes.

Previously performed taxonomic revisions of three groups of flying fishes (Parin and Shakhovskoy 2000;

Shakhovskoy and Parin 2010, 2013a, 2013b) allowed to make species identification for all available collections and to draw up maps of geographical distribution of species and subspecies (both for long-term period and by seasons of year). The resulting areas of distribution were compared with certain oceanographic characteristics (temperature, salinity, surface circulation, water masses and biological productivity). Some features of distribution of the three flying fishes groups were previously briefly outlined (Shakhovskoy 2014a, b). This article develops the ideas set forth in these papers in more details.

Material and Methods

Flying fishes collected in numerous research cruises of the Shirshov Institute of Oceanology (IORAS) were mainly used in the present work. Specimens from a number of Russian and foreign museums and institutes were used as well: AtlantNIRO, Institute of Biology of Southern Seas, Zoological Museum of Moscow State University, Zoological Institute of RAS, Zoological Museum of Copenhagen (ZMUC), National Museum of Natural History (USNM), Natural History Museum of Los Angeles (LACMNH), Scripps Institute of Oceanography (SIO), Australian Museum (AMS), Museum of Western Australia (WAM) and several others.

For preparation of distribution maps, taxonomic identification of all specimens of flying fishes of *Exocoetus*, *Hirundichthys* s.str and *C. "poecilopterus"* group from the collection of IORAS and a number of foreign collections was done to the lowest possible taxon (several thousands of fishes). Data from the personal scientific archive of N.V. Parin on morphology of numerous specimens of flying fishes having studied by him during visits to scientific institutions in Russia and abroad in the 60s - 90s of the past century have also been used (several thousands of fishes). A total of 5571 samples have been identified (see Fig. S1), including 2010 samples from the personal archive of N.V. Parin. The study material is mainly the same as for maps in our previous works (Parin and Shakhovskoy 2000; Shakhovskoy and Parin 2010, 2013a, 2013b).

To prepare maps, fishes were divided into 2 size groups: up to 100 mm SL, attributed in this work to the planktonic life-form, and more than 100 mm SL, regarded as nekton. This division is rather subjective, since there is no information in the literature available on the size of flying fishes at which the transition to the nektonic stage takes place. However according to Dudnik (1975), individuals of the saury (a species closely related to flying fishes) whose length exceeded 100 mm, were generally more mobile than smaller ones. Their swimming speed in the light zone was approaching the swimming speed of sexually mature individuals, which this author interpreted as their transition to nektonic stage. According to Parin (1968), the minimum length of a nektonic fish with a fully developed ability to active swimming may, apparently, be in the range from 15 to 20-30 cm. Thus, the standard length (SL) 100 mm (which roughly corresponds to total length (TL) of about 130 mm), which is accepted in the present work as a transitionary between planktonic and nektonic life-forms of flying fishes, is about midway between the estimates of Dudnik (1975), and Parin (1968). Given the pronounced ability of flying fishes for active swimming and gliding flight, such an assessment seems to be quite realistic. However, this issue requires organizing and conducting special experiments.

When preparing maps of seasonal distribution of species, seasons for the northern hemisphere have always been used: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). The same seasons (unless expressly stated otherwise) have always been used in the text of the work.

In the present study, only juvenile and adult fishes were used, and larval stages were not studied (see works of Kovalevskaya (1972, 1978, 1980, 1982) for data on early life history stages of species under consideration). Flying fishes used in the work were collected over a period of more than a hundred years (from the late 19th to the early 21st century), but the bulk of material was collected in oceanographic expeditions carried out from 1950 to 1990. In the vast majority of cases, flying fishes were caught by a dip net at night light stations. Since the used fishing gear (dip net) is not strictly quantitative, the quantitative distribution of species of flying fishes is not

addressed in this paper and the density of signs on distribution maps may reflect not the abundance of flying fishes but merely the frequency of sampling in a given area. Each sign on the maps represents one sample (or several closely located samples), regardless of the number of fishes caught in it. The material studied mainly includes (although not limited to) the material used in the previous works of the author (Parin and Shakhovskoy 2000; Shakhovskoy and Parin 2010, 2013a, 2013b).

I intentionally refused to use literature data and data from databases of the Internet due to a large number of misidentifications of flying fish species, relying only on material studied. I hope that this resulted in, in spite of some decrease in the amount of data and geographic coverage, a gain in the accuracy of species identification and, as a result, a greater correspondence of the resulting maps to the actual ranges of species as they exist in nature, which is very important when comparing maps with fields of oceanographic characteristics. Thus, the maps given in this paper are not composite and cannot be considered as showing distribution of species with maximal fullness.

The maps of species and subspecies distribution were compared with several oceanographic parameters: temperature (according to Locarnini et al. 2010), salinity (according to Antonov et al. 2010), surface circulation and water masses (according to Burkov et al. 1973; Stepanov 1983; Neiman et al. 1997; Dubravin 2013; Reid 1989, 1994, 1997, 2003; Peterson and Stramma 1991; data of satellite altimetry (http://www.aviso.altimetry. fr/las/) averaged for the period of 1993-2017 were also used) and biological productivity (according to Bogorov et al. 1968; Dubravin 2013). The works of Bogorov et al. (1968), Burkov et al. (1973), Stepanov (1983) and Neiman et al. (1997) were based mainly on those Soviet oceanographic expeditions in which flying fishes used in the present work were collected too. The other works were based mainly on oceanographic expeditions which did not collected flying fishes used here, but their data were obtained within much the same time frame (or broadly overlapping with) as for collecting of flying fishes used in the present work. Only the AVISO data were obtained later than the bulk of our material. But they are used here because of their high spatial resolution.

When plotting diagrams of dependence of the flying fishes distribution upon temperature and salinity, monthly average data of World Ocean Atlas 2009 were mainly used (Locarnini et al. 2010; Antonov et al. 2010). Temperature and salinity data were taken from the WOA 2009 maps for each sample (except for rare cases when temperature and salinity at the place of capture were specified in the label data) and plotted according to the frequency of occurrence (in %) for the intervals of 1°C and 0.5‰ or 0.2‰. It should be noted, however, that the temperature and salinity at any particular time of the capture may differ from the average monthly data. Therefore, the plots obtained in the work should be considered only as an approximate description of the environmental requirements of different species.

Since I had at my disposal extensive data (collected for the period of more than a century) concerning the samples in which species under consideration were caught, but there were no data on samples in which they were absent (gathering this information would have required incredible efforts and very long time), I had to abandon the use of the correlation coefficient and be content only with a visual comparison of the obtained distribution ranges with the maps of oceanographic characteristics fields. Maps have been drawn up using Golden Software Surfer 9; plots and diagrams were generated with Microsoft Excel.

Abbreviations used: NWPO, NWAO - north-western part of the Pacific (Atlantic) Ocean; SEPO (SWPO), south-eastern (south-western) part of the Pacific Ocean; SEC, South Equatorial Current; SSTC, NSTC - southern (northern) subtropical convergence; SL - Standard length; SST - sea surface temperature; SSS - sea surface salinity.
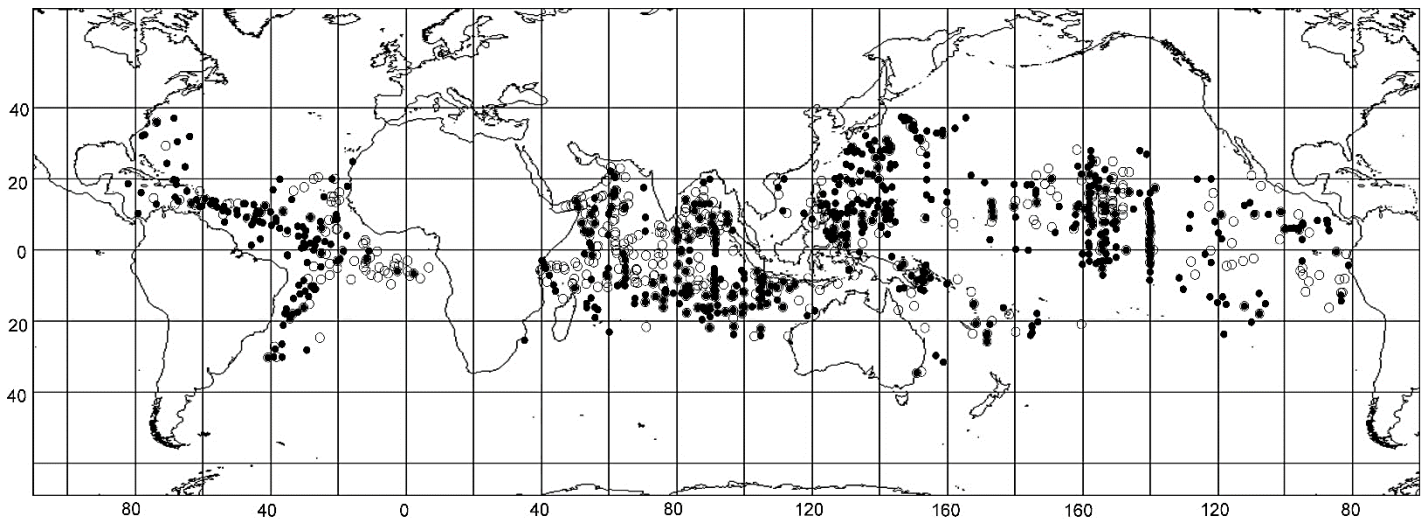
Figure 1. Distribution of flying fish *Exocoetus volitans*. Darkened signs - fishes with SL≤100 mm.

Results and Discussion

Flying fishes of the genus *Exocoetus*

Distribution of flying fishes of the genus *Exocoetus* was detailed by Parin and Shakhovskoy (2000). However, they used summary maps which included data from the literature sources in addition to their original data. This could be a potential source of errors. Only distribution maps based on original species identifications are used here.

Exocoetus volitans is a circum-tropical species widely distributed in the tropical waters of all the oceans (Parin and Shakhovskoy 2000; see also Fig. 1). This species occurs at a temperatures ranging between 20.5 and 29.5°C, usually 24-28°C (Parin 1962; Grudtsev et al. 1986). According to our data (see Fig. S2): range 19.0-30.0°C, mean 27.05±0.045, SD 1.474. Juveniles of *E. volitans* occur throughout the species distribution region, indicating that the spawning and foraging areas generally coincide. Juveniles are found during all seasons, which may be the result of year-round spawning.

Exocoetus monocirrhus inhabits warm waters of the Indian and Pacific oceans (Parin and Shakhovskoy 2000; see also Fig. 2). This species is found at SST of 22-30°C, usually 23.5-29.5°C (Parin 1962). According to our data (see Fig. S2): range 19.2-30.0°C, mean 27.47±0.065, SD 1.832. The geographical distribution of *E. monocirrhus* in these oceans is mainly similar to the one of *E. volitans*. However, this species has a somewhat more northern position of the range boundary in the open waters of the southern hemisphere. *Exocoetus monocirrhus* penetrates along the coast of South Africa in the Atlantic Ocean (the Bay of St. Helena). One specimen of *E. monocirrhus* was reported to be present even in the waters of the western Atlantic (Brazil). It's the lectotype of *E. georgianus* Valenciennes 89 mm SL (Valenciennes 1847). However, the label data of this specimen are apparently erroneous (Parin and Shakhovskoy 2000). It should be noted here that Indo-Pacific flying fishes have been found repeatedly in the waters of the southern Atlantic (see, for example, Parin 1999) and, in my opinion, it would be a mistake to regard all these findings as mislabeling. Apparently, there is a theoretical possibility of penetration of flying fishes juveniles from the Indian Ocean into the Atlantic with anticyclonic eddies. Such eddies (their existence is up to 4-10 years, the speed of propagation about 5-12 cm/s) are periodically generated by the Agulhas Current and they cross the southern subtropical gyre and reach the Brazilian Current (see Peterson and Stramma 1991; Guerra et al. 2018). However, the velocity of these eddies is too low to deliver such a small juvenile of *E. monocirrhus* from the Indian Ocean to the coast of Brazil, given the rapid growth and short life span of flying fishes.
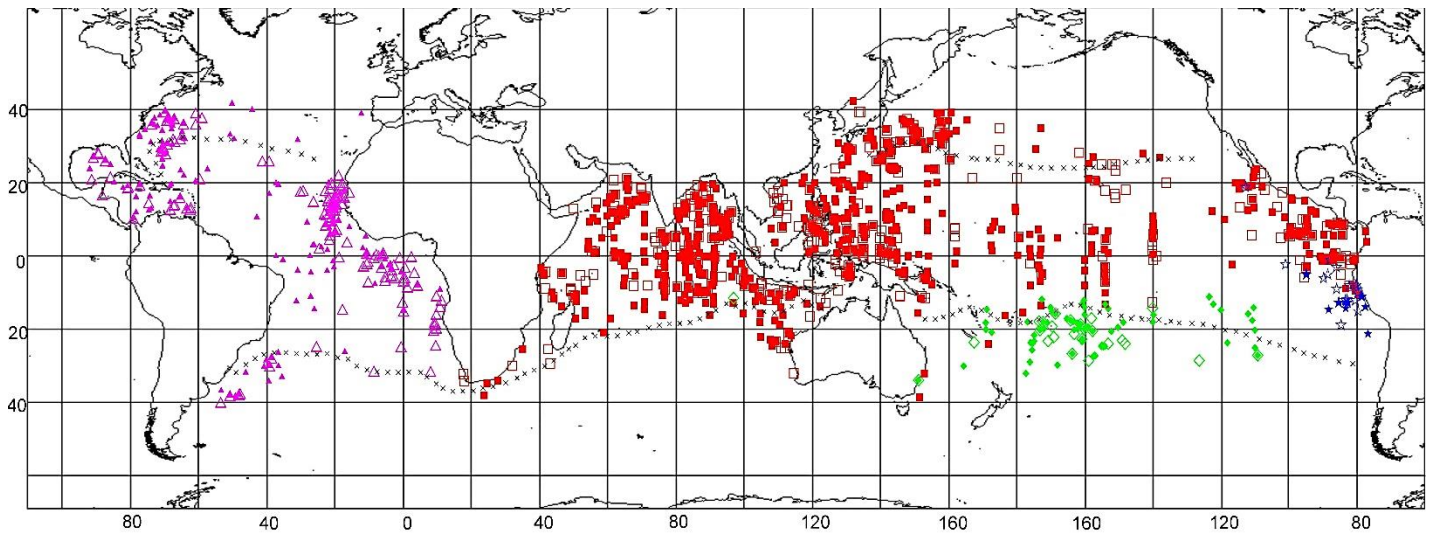
Figure 2. Distribution of flying fishes *Exocoetus monocirrhus* (□), *E. obtusirostris* (△), *E. gibbosus* (◇) and *E. peruvianus* (☆). Darkened signs - fishes with SL≤100 mm, the crosses indicate annual mean position of subtropical convergence according to Burkov et al. (1977).

Exocoetus obtusirostris is an endemic of the Atlantic Ocean (Parin and Shakhovskoy, 2000; see also Fig. 2). In the western part of the ocean this species occurs between 46°N and 40°S; in the eastern part - between 30°N and 30°S. The species is found in waters with SST of 18-29°C, usually 20-27°C (Grudtsev et al. 1986; Parin and Shakhovskoy 2000). According to our data (see Fig. S2): range 15.3-29.5°C, mean 25.0±0.148, SD 2.381. According to the data of the present study, this species is almost entirely absent from the western tropical Atlantic; only its larvae or juveniles carried away by the North and South Equatorial currents are sporadically found here (Fig. 2).

The range of *E. gibbosus* is confined to the waters of the Pacific Ocean southern subtropical gyre where it occurs from the coastal waters of Australia near Sydney to 101°W between 10°S and 32°S (Parin and Shakhovskoy 2000; see also Fig. 2). This species occurs in waters with SST of 21-27.5°C (Parin 1962; Kovalevskaya 1980). According to our data (see Fig. S2): range 20.0-29.1°C, mean 25.8±0.198, SD 1.963. The discovery of *E. gibbosus* in the southern Indian Ocean (see Shakhovskoy 2011)[1] indicates that a native population of this species in the southern subtropical gyre of this ocean may also exist. However, an occasional migration of single fishes from the Pacific or their drift on early life history stages with the South Equatorial Current through Torres Strait is also possible, since the currents of this region (see Rochford 1977; Wolanski et al. 2013) can facilitate this.

Exocoetus peruvianus occurs only in the area of the southeastern Pacific Ocean between the equator and the southern tropic (Parin and Shakhovskoy 2000; see also Fig. 2), where it inhabits waters with the SST of 18-23°C (Parin 1970; Kovalevskaya 1980). According to our data (see Fig. S2): range 19.7-26.5°C, mean 24.1±0.375, SD 1.948. In addition I have identified as *E. peruvianus* one specimen 180 mm SL with the following label data: "USNM 144865, Mexico: vicinity of Revilla Gigedo Ids, 4.01.1934". This specimen has features characteristic of *E. peruvianus* and differs from *E. monocirrhus* in the following: higher number of vertebrae, lighter coloration (dark gray) of pectoral fins and larger postero-lateral outgrowth of cleithrum (see Fig. 3). The meristic and morphometric characters of this specimen (see Parin and Shakhovskoy 2000 for the methodology of measurements) are given below:

Dorsal fin rays 14, anal fin rays 13, pectoral fin rays I 14, predorsal scales 19, transverse scales 7, gill rakers

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[1] In the scientific archive of N.V. Parin, I have found a record about one more specimen SL 38 mm identified by him as *E. obtusirostris* (label data: AMS I.18085-001, Indian Ocean, 1857). This specimen may be in fact *E. gibbosus*. However I have not got an opportunity to study it personally.
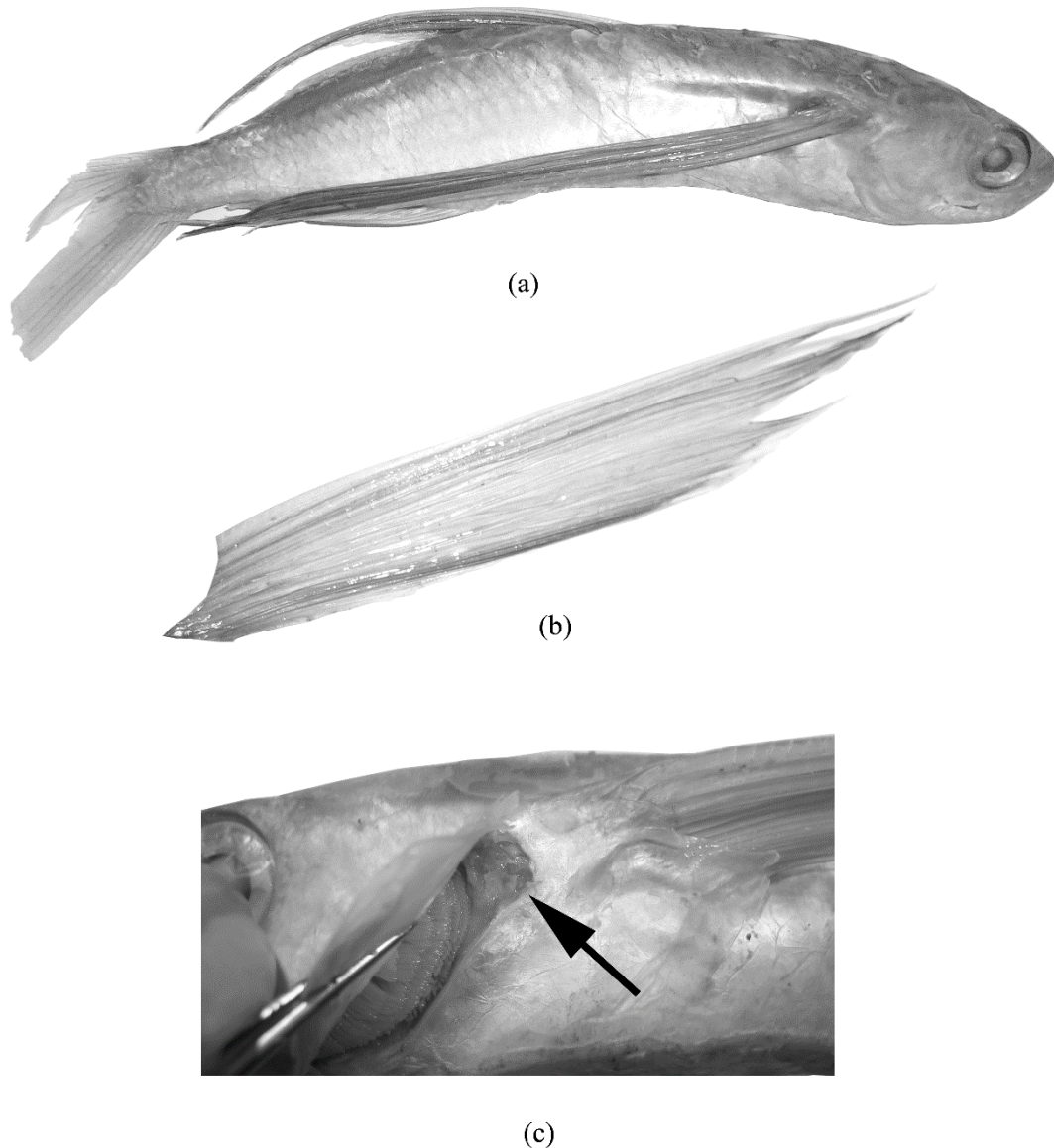
(a)

(b)

(c)

Figure 3. *Exocoetus peruvianus* (USNM 144865, SL 180 mm): (a) side view of the fish, (b) pectoral fin spanned (top view), and (c) posterolateral process of cleithrum (marked with arrow).

28, vertebrae (urostyle included) 44 (26 precaudal + 18 caudal). Measurements in % of SL: preanal distance 66.6, predorsal distance 70.2, prepelvic distance 42.8, distance from the posterior edge of head to the pelvic fin origin 17.9, distance from the pelvic fin origin to the origin of caudal fin lower lobe 53.9, head length 24.5, postorbital distance 12.9, eye horizontal diameter 6.6, snout length 4.3, width of bony interorbital space 9.0, head depth near the posterior eye edge 15.0, the greatest head depth 17.3, the greatest body depth before the vertical through the end of pectoral fin base 17.6, the greatest body depth behind this vertical 19.4, the lowest depth of caudal peduncle 7.3, dorsocaudal distance 27.8, length of pectoral fin 76.1, length of the first pectoral fin ray 51.1, length of pelvic fin 13.0, length of dorsal fin base 21.8, length of anal fin base 23.2, height of the largest dorsal fin ray 11.5, height of the largest anal fin ray 11.5, body width above the bases of pectoral fins 15.0. Separate, very small teeth are present only in the upper jaw. Palatine teeth are absent.

A comparison of this specimen with representatives of *E. peruvianus* from the SEPO (see Parin and Shakhovskoy 2000) shows no significant differences. Only a slightly larger predorsal distance (70.2 vs. 65.3-69.0) should be noted. Apparently, this specimen is an accidental migrant into the northeastern Pacific (unless,
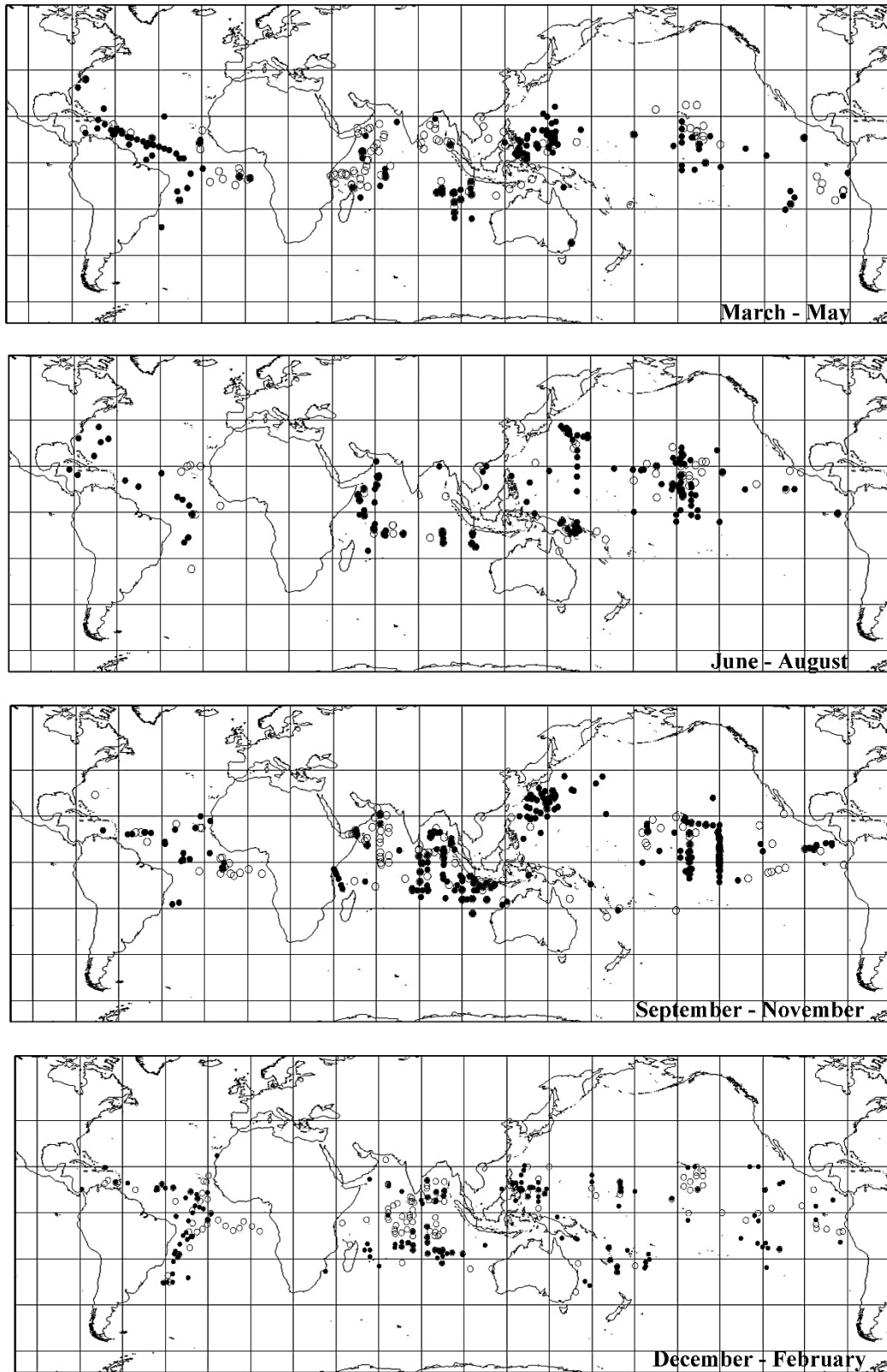
Figure 4. Distribution of *Exocoetus volitans* in different seasons. Darkened signs - fishes with SL≤100 mm.
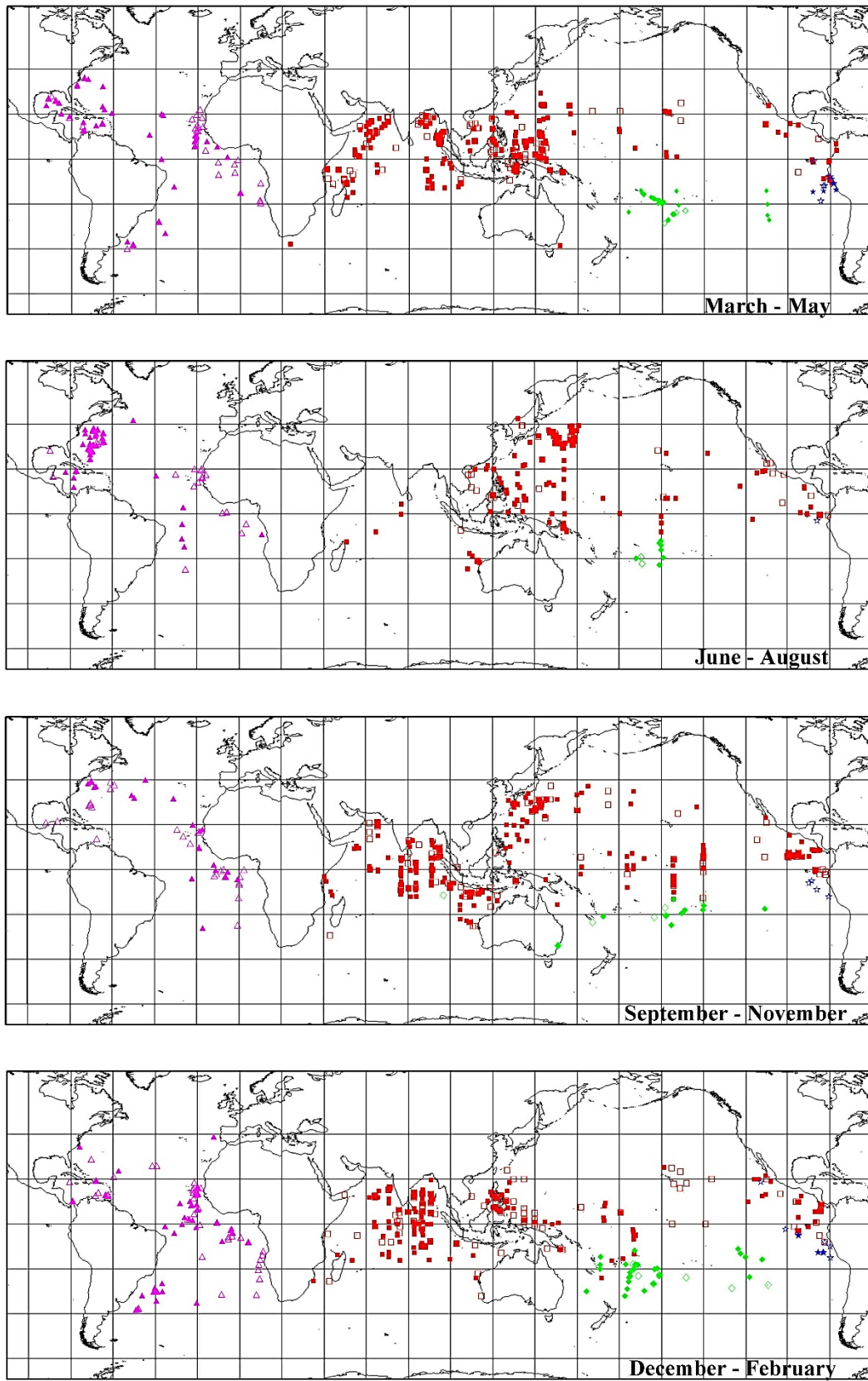
Figure 5. Distribution of flying fishes *Exocoetus monocirrhus*, *E. obtusirostris*, *E. gibbosus* and *E. peruvianus* in different seasons. Legend is the same as for Figure 2.

of course, there was an erroneous labeling) and the existence of a still unknown self-sustained population of *E. peruvianus* seems highly unlikely in such a well-studied region.

Analysis of our data on seasonal distribution of species of the genus *Exocoetus* (see Figs. 4-5) reveals a number of interesting points. First of all, it is almost complete absence of *E. monocirrhus* throughout the vast areas of open Indian Ocean in the summer (there are only 3 samples with juveniles), although *E. volitans* (as well as *H. speculiger*, see below) is presented here in fairly large quantities. There is no data on captures of *E. monocirrhus* at this time of year available in the literature. For example, Balasubrachmanyan et al. (1967b) collected 1172 specimens of larvae, juveniles and adult of *E. volitans* in the eastern part of the Bay of Bengal in June and early July, but no specimens of *E. monocirrhus*. It is possible that such absence is the result of a one-year life cycle of *E. monocirrhus* (like in other representatives of the genus, see above) and dying of the majority of adults after the spawning season. In this case, such absence may represent an interval between successive spawning cohorts, which, for example, was noted for *H. affinis* (a species with one-year life cycle) from July to November in the eastern Caribbean (Oxenford et al. 1993). Also interesting is a spring migration of *E. volitans* and *E. monocirrhus* (as well as *H. speculiger* and *H. indicus*, see below) from the central Indian Ocean, where they are mainly concentrated in winter, to the eastern and western coasts. Future studies will show whether this phenomenon is the result of small number of samples available, or it reflects some common features of life cycles of these species.

According to our data, *E. volitans* and *E. monocirrhus* in the NWPO region spread far north with the waters of the Kuroshio Current during the warm season, but are absent in the waters of Japan during the cold one (winter and spring). However, based on published data, these species approach the coast of Japan as early as in the spring (Abe 1955, 1957; Imai 1959). Juveniles of *E. peruvianus* from our samples were caught only during warm season (winter and spring of the northern hemisphere), which may indicate the seasonal nature of spawning of this species (although this may also be a consequence of small number of samples available).

Our data (see Fig. 1) fully confirm the conclusions of Parin (1962) and Kovalevskaya (1978, 1980) regarding the absence of *E. volitans* in the warmest equatorial waters of the western Pacific. In the Indian Ocean, this species also avoids waters with higher temperature. *Exocoetus monocirrhus* does occur here, apparently being more eurythermic species (see Fig. S2). However, it is found here infrequently and, primarily, as juveniles.

Contrary to the data of Kovalevskaya (1980), who noted an almost complete absence of *E. volitans* larvae and juveniles in the Arabian Sea, our data shows that juveniles of this species were collected in the Arabian Sea during all seasons. The smallest juveniles, about 20-40 cm in length, were collected only during spring-summer months, while during autumn-winter period - the larger juveniles of about 70-100 mm SL predominated. Juveniles of *E. volitans* are probably carried away into the Arabian Sea by currents (mainly the Somali Current during the southwestern monsoon) from nearby spawning areas, grow there until maturity is reached, and then leave those waters for reproduction. Why does not this species reproduce here? Kovalevskaya (1980) supposed that high sea surface salinity (SSS) may be the reason for that. However this hypothesis is somewhat contradicted by the fact that *E. volitans* spawns in waters with even higher salinity in the Atlantic.

Flying fishes of the subgenus *Hirundichthys* s.str.

Hirundichthys speculiger is a circum-tropical species, widespread in warm waters of all oceans. This species is found mainly in the waters of the open ocean: it has been collected in surface waters mainly over depths ranging from 2000 to 6000 m, with the average depth is 4423 m (Shakhovskoy and Parin 2013a; see also Fig. 6). *Hirundichthys speculiger* occurs in waters with SST of 19.0-29.5°C, usually 25.0-28.5°C (Parin 1967; Kovalevskaya 1980, 1982; Grudtsev 1987). According to our data (see Fig. S3): range 19.2-29.9°C, mean 27.1±0.059, SD 1.569. Our data support the conclusions of previous authors (Parin 1960b; Kovalevskaya 1980)
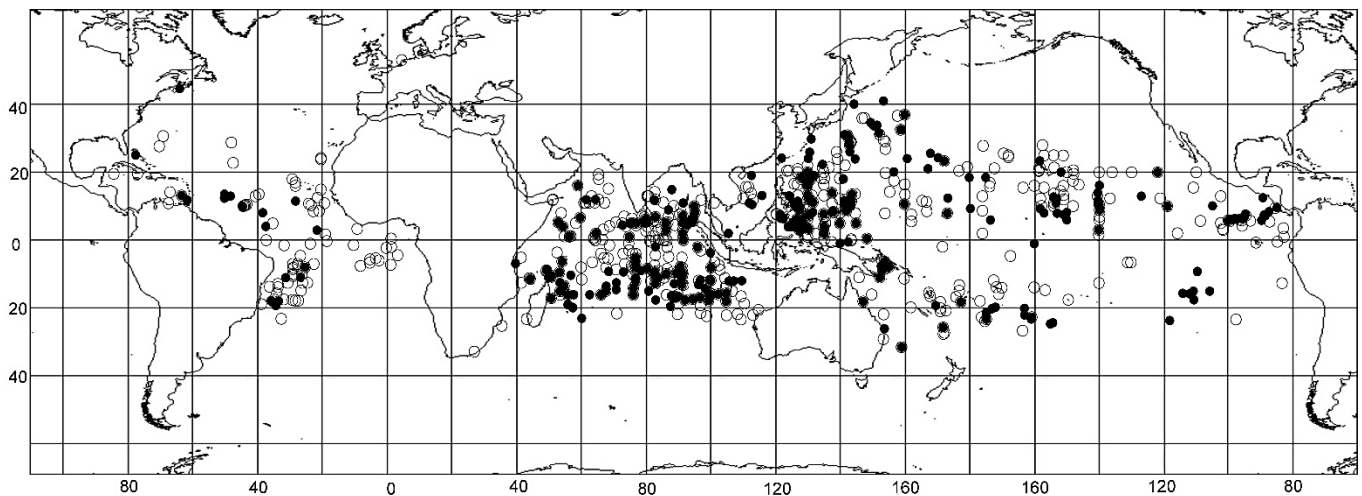
Figure 6. Distribution of flying fish *Hirundichthys speculiger*. Darkened signs - fishes with SL≤100 mm.

that the area of *H. speculiger* in the western and central parts of the Pacific Ocean is disrupted by 12-20 degrees and can be referred in this region to the antiequatorial type (Fig. 6).

Juveniles of *H. speculiger* were caught almost throughout the entire distribution range of the species (except for the Gulf of Guinea and the southeastern Pacific), which may indicate almost complete coincidence of the spawning and foraging areas, and in all seasons (Fig. 7), which may indicate year-round spawning (in the Atlantic there is only one capture in summer, but this may be due to the insufficient number of samples).

Hirundichthys indicus is widely distributed in the tropical Indian Ocean, usually found in the open ocean (Shakhovskoy and Parin 2013a; see also Fig. 8). According to our data (see Fig. S3) this species occurs in waters with SST 24.0-29.7°C, mean 28.1±0.069, SD 0.769. This species prefers higher temperature than *H. speculiger* and is nearly absent in areas where the annual mean SST falls below 26°. *Hirundichthys indicus*, apparently, does not inhabit the Red Sea, the Persian Gulf and the waters of the western coast of Australia. Also this species probably does not enter the eastern part of the Arabian Sea and the northern part of the Bay of Bengal. Juveniles of *H. indicus* were very rarely collected in the central Indian Ocean between 70°E and 90°E (Fig. 8). This fact may be the indirect evidence that although *H. indicus* is an open ocean species, its spawning, unlike *H. speculiger*, is confined to more neritic waters. Juveniles of *H. indicus* were collected in all seasons, which possibly indicates the year-round spawning (Shakhovskoy and Parin 2013a, see also Fig. 9).

This species is represented by two subspecies. *Hirundichthys indicus indicus* is distributed in the waters of the western and central Indian Ocean from the west coast of Africa to the meridian of 96°E and from 15°S to the northern part of the Arabian Sea, the southern part of the Bay of Bengal and the Andaman Sea. *Hirundichthys indicus orientalis* is distributed in the eastern Indian Ocean from the meridian of 100° E to the Timor Sea. Early stages of development can probably be drifted away westward up to 90°E by the South Equatorial Current. Specimens of this subspecies were collected only in the spring, summer and, mainly, autumn, and none were captured in winter (see Fig. 9).

Hirundichthys oxycephalus is distributed in the northern Indian Ocean (to the north of the equator) and in the western Pacific Ocean (Fig. 10). This species, unlike *H. speculiger* and *H. indicus*, usually does not move far from the waters above the shelf and slope (depths at the places of capture from 30 to 9022 meters, usually from 1000 to 4500 m, average depth 3319 m) and thus belongs to the nerito-oceanic group of flying fishes (see Shakhovskoy and Parin 2013b). *Hirundichthys oxycephalus* inhabits mainly waters with SST of 23-30°C (Parin 1960a, 1960b; Chen 1987). According to our data (see Fig. S3): range 18.0-30.0°C, mean 27.8±0.094, SD 1.613.

This species is polytypic and includes 3 subspecies (see Shakhovskoy and Parin 2013b). *Hirundichthys*
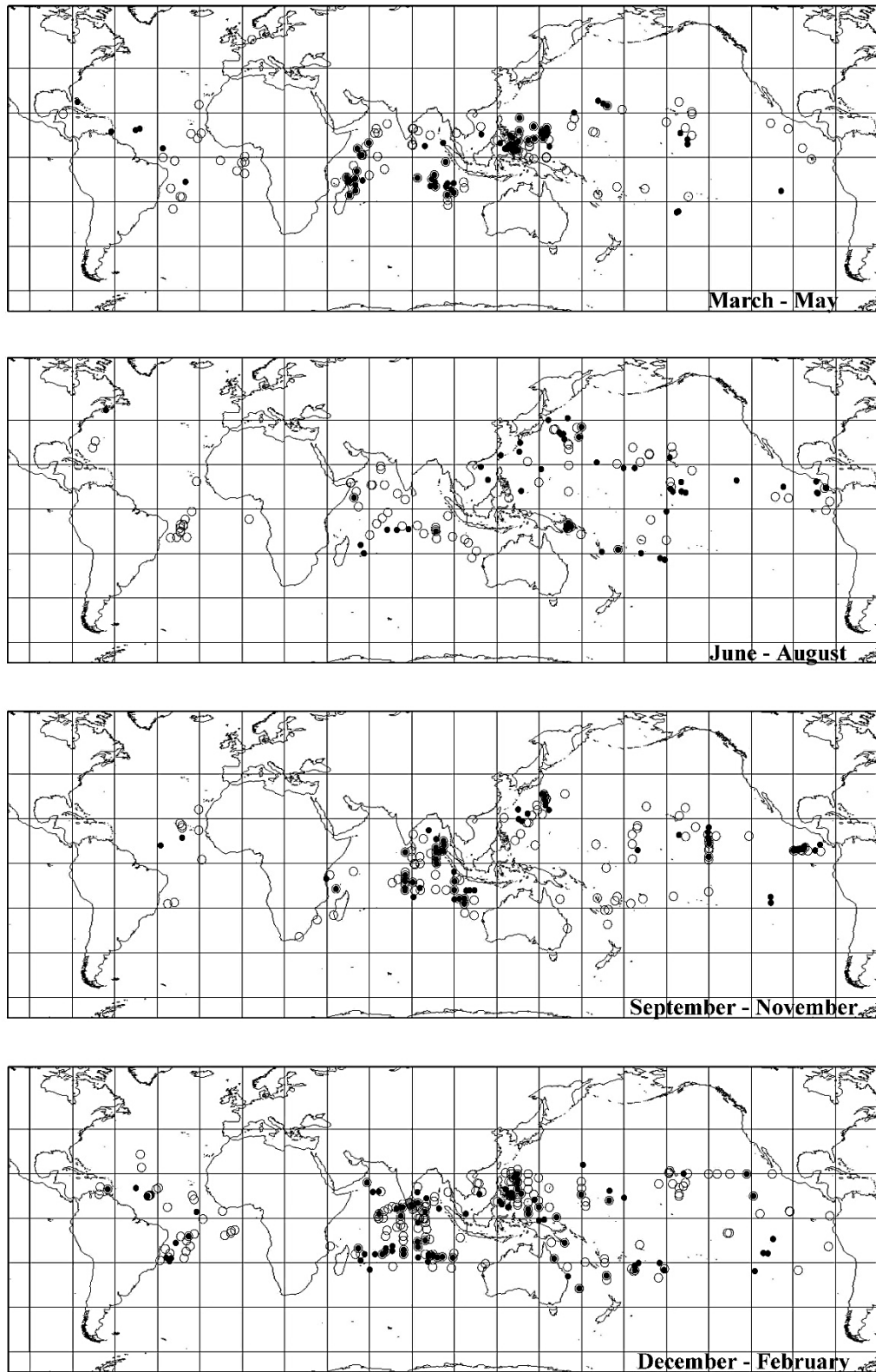
Figure 7. Distribution of flying fish *Hirundichthys speculiger* in different seasons. Darkened signs - fishes with SL≤100 mm.

oxycephalus oxycephalus is distributed in the waters of Indonesia east of 100°E, in the South China Sea, East China Sea and Sea of Japan; in the waters of the western Pacific Ocean near the Ryukyu, Kyushu and Honshu Islands and in the adjacent waters of the Kuroshio Current up to 160°E; in the waters of the north-western and eastern coasts of Australia and in the western Polynesia. *Hirundichthys oxycephalus oxycephalus* reaches the
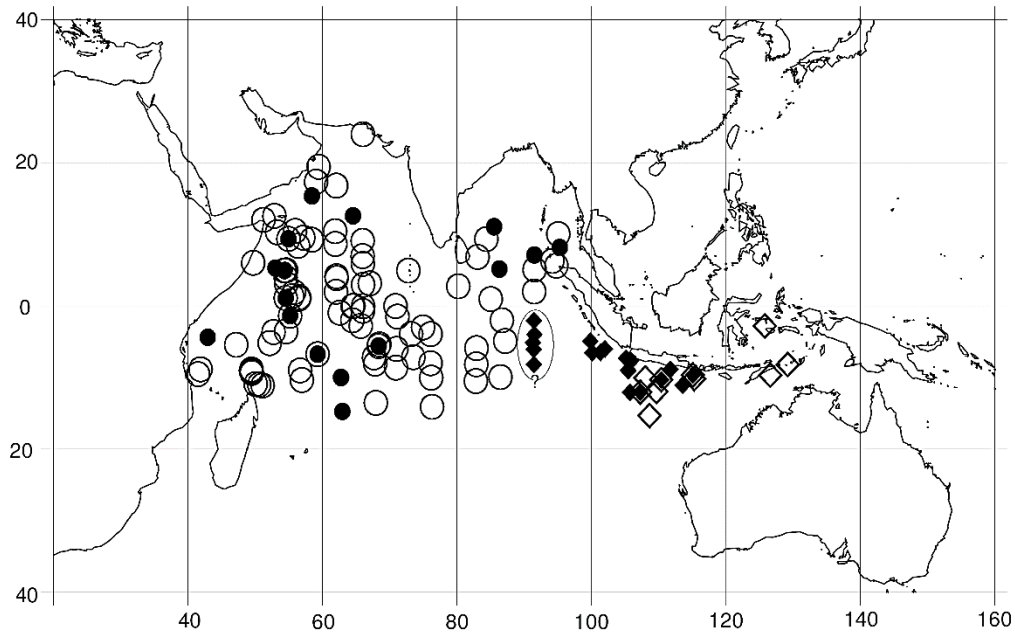
Figure 8. Distribution of flying fish *Hirundichthys indicus*: ○ - *H. indicus indicus*, ◊ - *H. indicus orientalis*. Darkened signs - fishes with SL≤100 mm. Based on Shakhovskoy and Parin (2013a) (with additions).

waters of Russia (Peter the Great Bay). Thus, in the IORAS collection (№03347), I found a juvenile of this subspecies 107 mm SL (see Fig. 11a) with the following label data: "Sea of Japan, Gulf of Slavyanka, North Inlet, August 10, 1985, depth 0.5 m, temperature 23.5°C, collector V.M. Shpak". This finding is the fourth for the waters of Russia (the first three ones are reported in the works of Kharin and Saveliev (2011) and Saveliev et al. (2015) and the first one according to the date of capture.

Hirundichthys oxycephalus coromandelensis is distributed from the coast of Somalia to the northern coast of Sumatra: in the Andaman Sea, Bay of Bengal, Arabian Sea and the adjoining waters of the Indian Ocean to the north of the equator (extreme southern location: 1°00'N, 55°00'E). Randall (1995) indicated presence of *H. oxycephalus* in the coastal waters of Oman. One specimen (Fig. 11b) of this subspecies is probably caught in the eastern part of the Mediterranean Sea (see Shakhovskoy and Parin 2013b).The third subspecies, *H. oxycephalus frereensis*, is known by the only specimen captured in waters of Indonesia (Cape Frere, Goodenough Bay).

Hirundichthys affinis is common in the western and eastern Atlantic Ocean (Fig. 10). This species prefers mainly the waters above the shelf and slope, but it is also often found in the waters of open ocean (the species was usually collected over the depths from 1000 to 5500 m, an average of 3279 m), and it can be referred to the group of nerito-oceanic fishes (Shakhovskoy and Parin 2013b). According to Grudtsev (1987), *H. affinis* occurs in the waters with SST of 20.0-29.2°C, preferring temperatures of 25-27°C. According to our data (see Fig. S3): range 19.0-29.5°C, mean 26.4±0.166, SD 1.727.

In the western Atlantic the species is found from 38°N to 21°S. In the eastern Atlantic from 25°N to 17°S. Juveniles under 100 mm SL from the collections studied were caught in all the seasons of year and throughout the area of adult fish distribution, except for the waters of the Southern Hemisphere, suggesting year-round spawning in the tropical ocean and extending it to more northern areas in the western Atlantic at warm season. However, spawning of this species undoubtedly takes place in the southern hemisphere as well, since its larvae and juveniles have also been found there (see Poll 1953; Monteiro et al. 1998; De Castro et al. 2008).
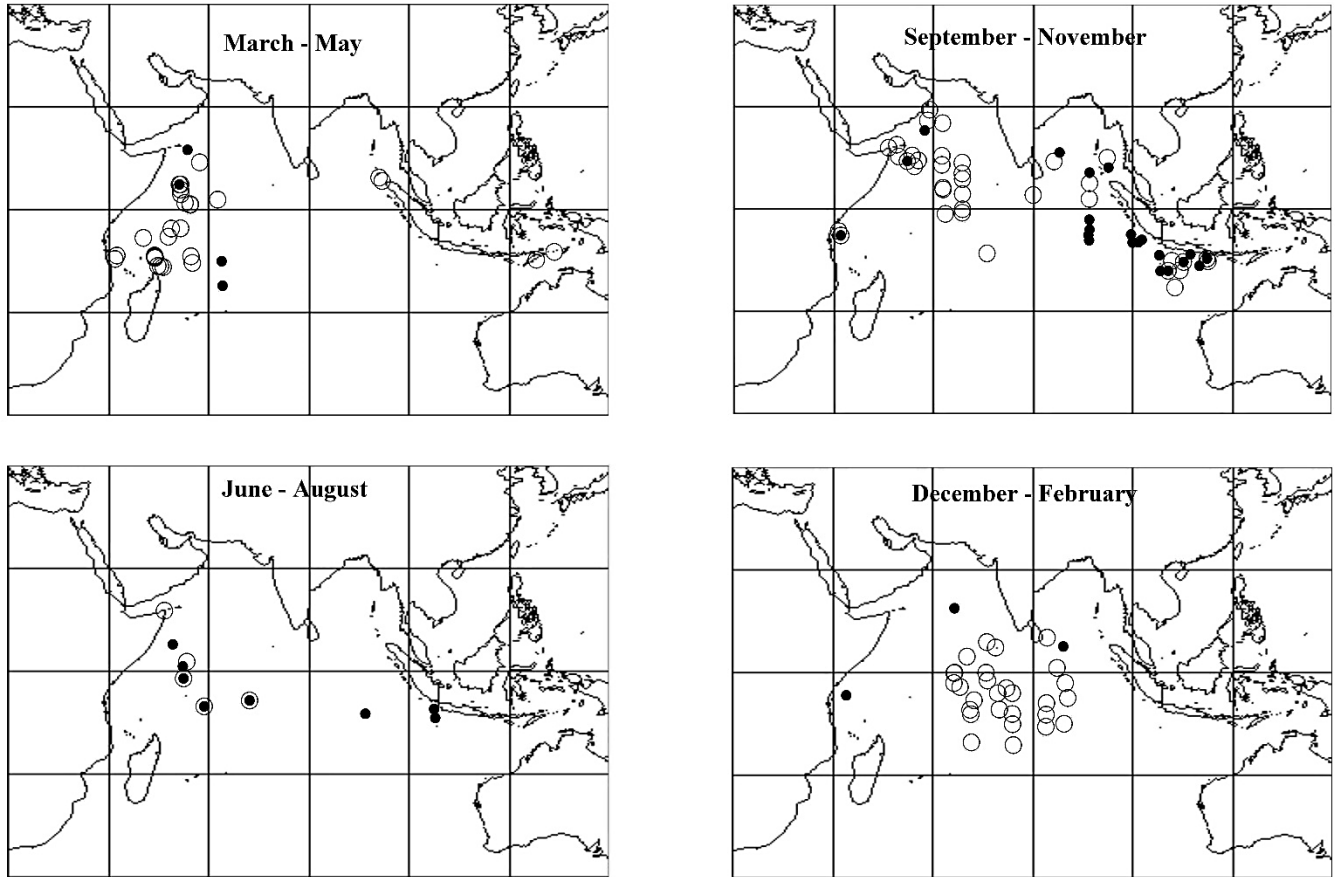
Figure 9. Distribution of flying fish *Hirundichthys indicus* in different seasons. Darkened signs - fishes with SL≤100 mm.
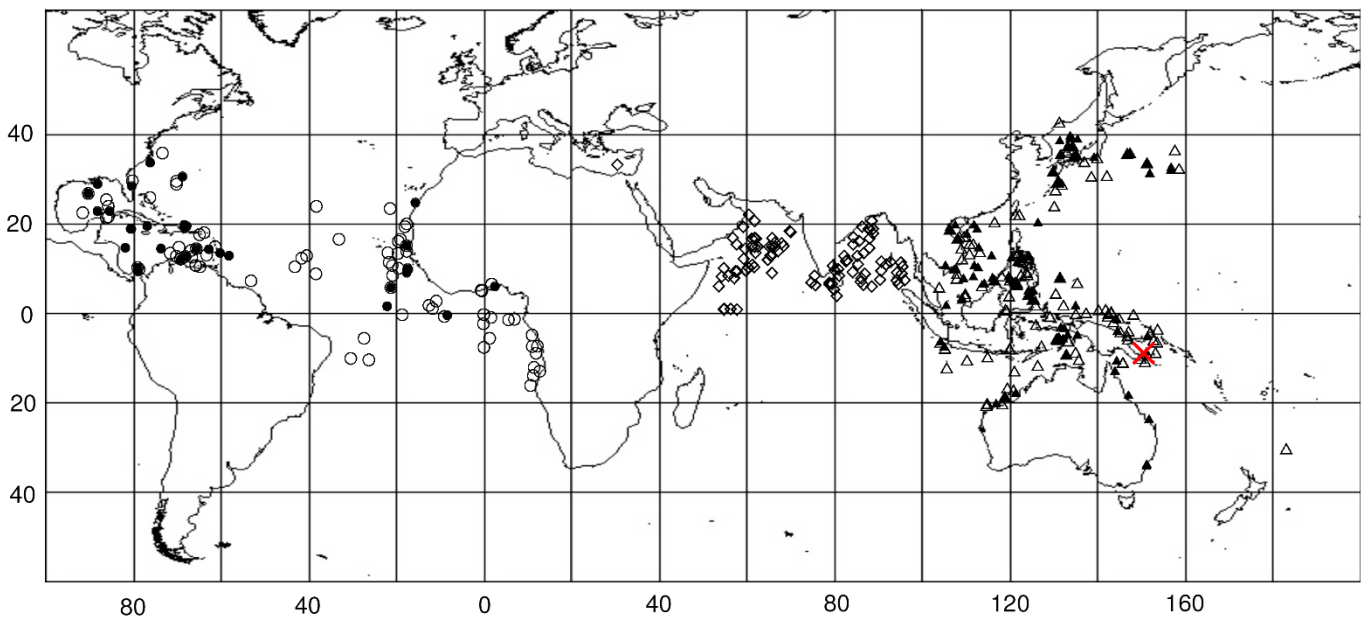

Figure 10. Distribution of flying fishes *Hirundichthys affinis* (○) and *H. oxycephalus* (Δ - *H. oxycephalus oxycephalus;* ◊ - *H. oxycephalus coromandelensis;* x - *H. oxycephalus frereensis*). Darkened signs - fishes with SL≤100 mm.
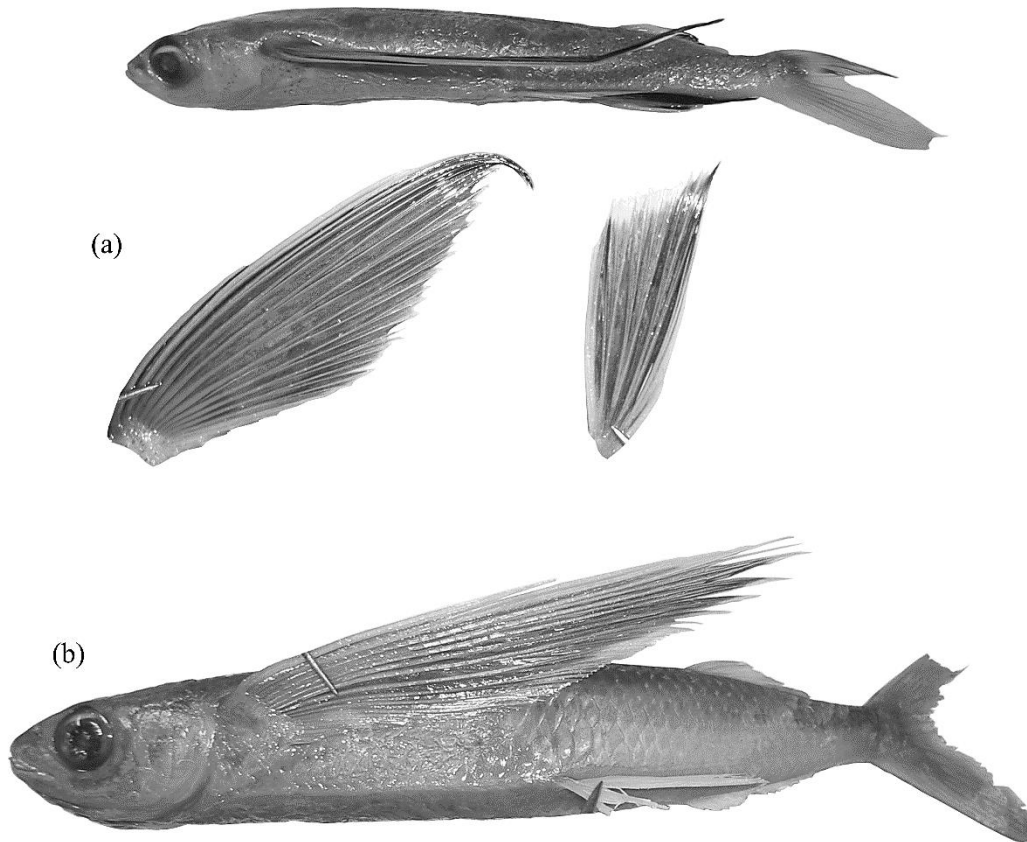
Figure 11. Flying fish *Hirundichthys oxycephalus*. (a) *H. oxycephalus oxycephalus* SL 107 mm (IORAS collection, No. 03347, Sea of Japan, Gulf of Slavyanka, North Inlet, 10.08.1985): side view of the fish, pectoral and pelvic fins; (b) *H. oxycephalus coromandelensis* SL 166 mm (IORAS collection, No. 03165, R/V "Academic Petrovsky", cruise 9, Mediterranean Sea, en route from Port Said to Piraeus, January 1980).

Analyses of the distribution maps of the subgenus Hirundichthys species by seasons (see Figs. 7, 9, 12) reveals a number of interesting features. In the western Pacific significant migrations to higher latitudes are noted during the summer in the corresponding hemisphere. In the NWPO *H. oxycephalus* reaches the Russian waters of the Peter the Great Bay and *H. speculiger* - the Kurile Islands (see Saveliev et al. 2015). According to our data, in winter and spring *H. speculiger* does not occur in the NWPO to the north of 22°N, while in summer it extends north up to 40°N. However, based on published information (Imai 1954; Abe 1956), this species appears in the southern waters of Japan in spring. In the northeastern Pacific Ocean, such seasonal migrations are not observed. In the southern hemisphere, except for Australian waters, it is not possible to trace a seasonal variability in distribution due to small amount of data.

Like *H. speculiger*, *H. oxycephalus* was found in the waters of Japan north of 22°N only during summer and autumn and in the northern part of the South China Sea only during summer. Juveniles of *H. oxycephalus oxycephalus* less than 100 mm SL were captured in all seasons and throughout nearly the entire area of adult distribution (see Fig. 12), which suggests year-round spawning in the tropical ocean region, which spreads during the warm season of the corresponding hemisphere over subtropical areas (Japan, the east coast of Australia) as well. At the same time, juveniles of *H. oxycephalus coromandelensis* were absent in our samples. This fact allows, following Kovalevskaya (1972), to assume that the early development of this subspecies takes place in the coastal zone.

In the Indian Ocean, an almost complete absence of all species of the subgenus (as well as the studied species of *Exocoetus* and *Cypselurus*) in the Bengal Bay during the summer period particularly interesting. However, it is most likely being the result of a small number of summer samples available for this study, since there are
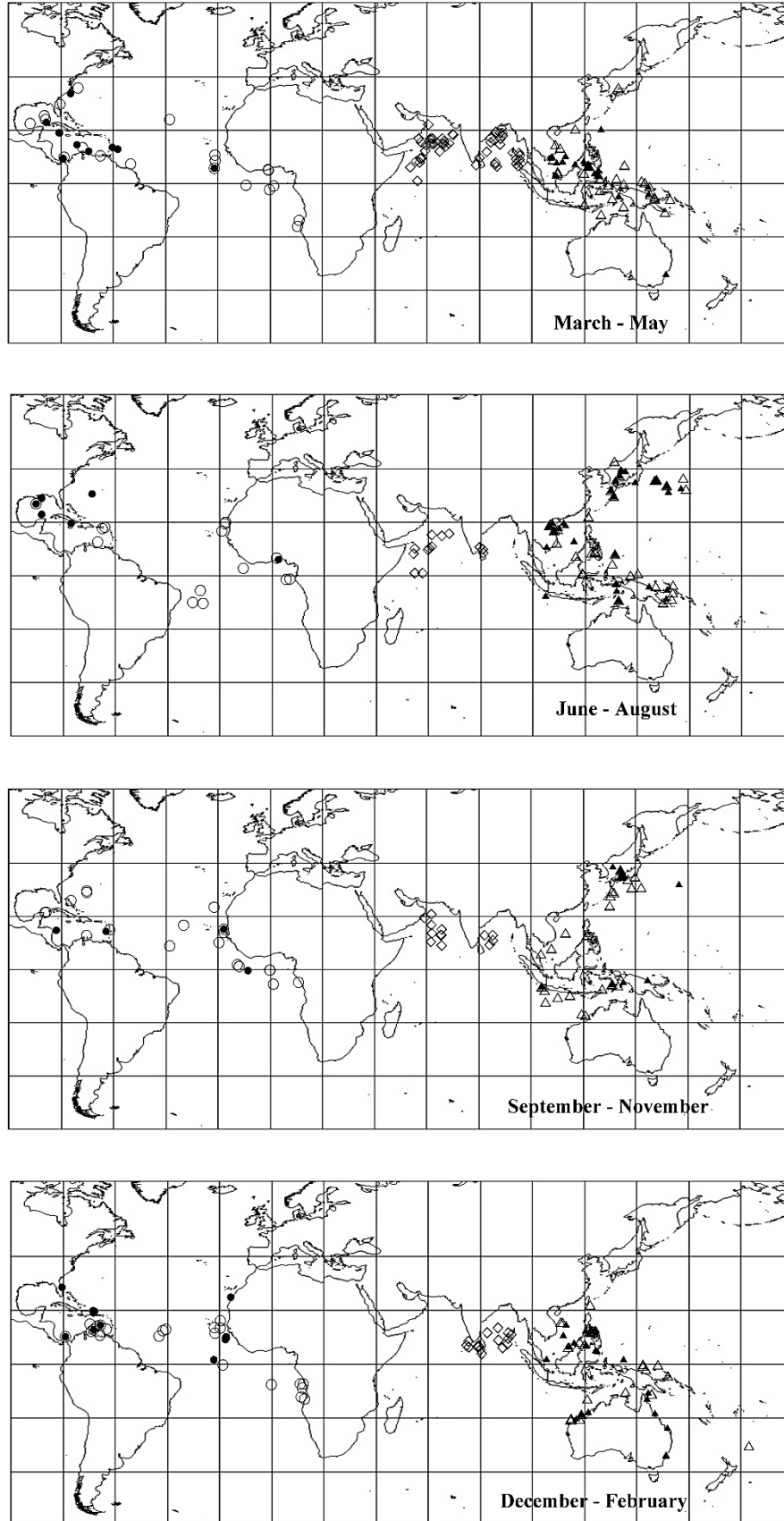
Figure 12. Distribution of flying fishes *Hirundichthys affinis* and *H. oxycephalus* in different seasons. Legend is the same as for Fig. 10.

H. speculiger ■   *H. indicus* ■   *H. oxycephalus* ■   *H. affinis* ■
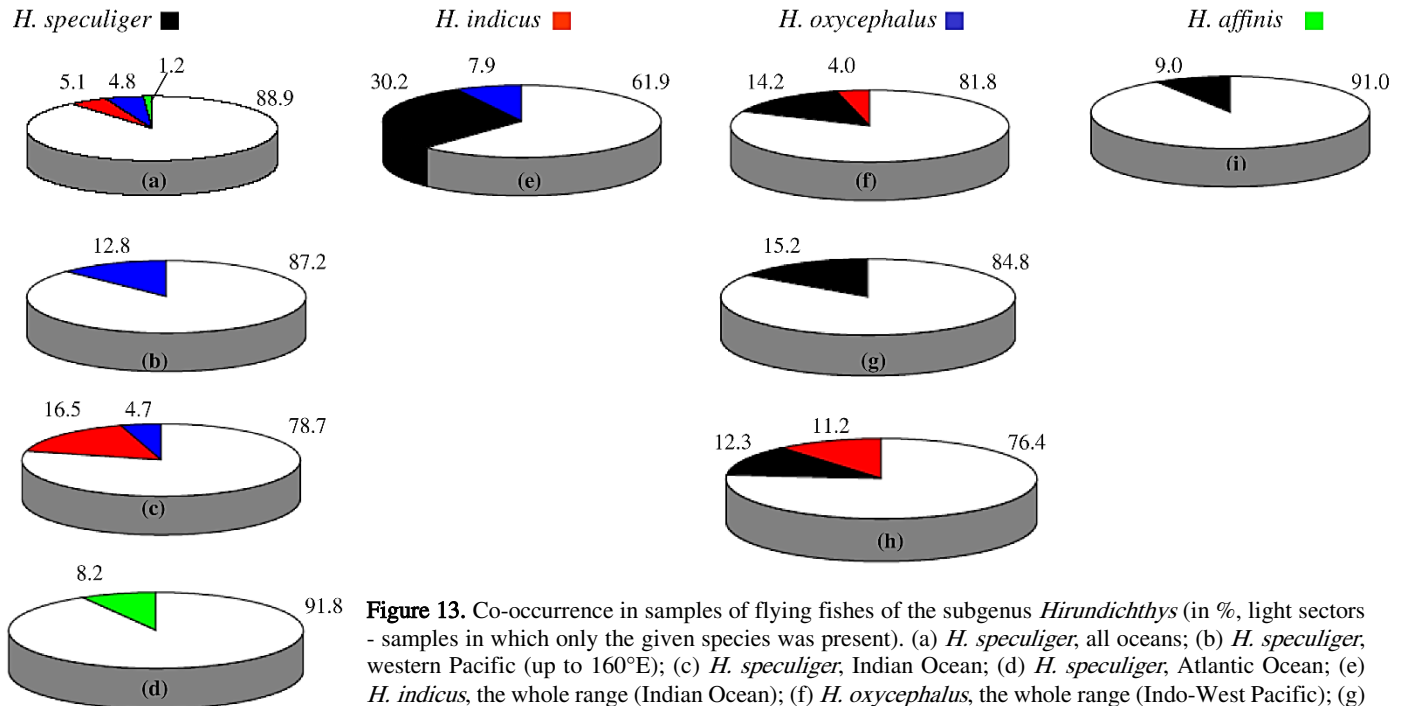

Figure 13. Co-occurrence in samples of flying fishes of the subgenus *Hirundichthys* (in %, light sectors - samples in which only the given species was present). (a) *H. speculiger*, all oceans; (b) *H. speculiger*, western Pacific (up to 160°E); (c) *H. speculiger*, Indian Ocean; (d) *H. speculiger*, Atlantic Ocean; (e) *H. indicus*, the whole range (Indian Ocean); (f) *H. oxycephalus*, the whole range (Indo-West Pacific); (g) *H. oxycephalus*, western Pacific; (h) *H. oxycephalus*, Indian Ocean; (i) *H. affinis*, the whole range (Atlantic Ocean).

reports of numerous summer captures in the area (Balasubrachmanyan et al. 1967a, 1967b). Migration of *H. indicus* from the central Indian Ocean (where this species is represented, mainly by adolescent individuals, only in winter) closer to neritic areas in other seasons should also be noted.

The ranges of *H. indicus* and *H. speculiger* largely overlap with each other in the Indian Ocean (but the range of *H. speculiger* extends somewhat further to south, and this species is nearly absent in the eastern Indian Ocean where *H. indicus orientalis* dwells). Despite the coincidence of the ranges, these two species were rarely captured together in the same sample (see Fig. 13). This may be the result of an alternate use of the same areas by these species. Thus, *H. speculiger* is completely absent in the Arabian Sea and adjacent waters up to 2-3°S from September to the end of January, and *H. indicus,* on the contrary, is most abundant here in autumn, and nearly absent (except for the area of Somalia coast) in spring and summer when *H. speculiger* occurs here again. Apparently, such separation may be a mechanism for reducing interspecific competition for food. Although there is no data on feeding habits of *H. indicus*, it can be assumed that they have similar diets because these species have approximately the same number of gill rakers (see Shakhovskoy and Parin 2013a).

Early life history stages of *H. speculiger* were absent in the Arabian Sea in all seasons (Kovalevskaya 1980; our data). Thus, this extensive and productive area is probably used only as feeding ground. Apparently, the seasonal occurrence of *H. speculiger* in the Arabian Sea may be the result of fluctuations of biological productivity caused by monsoon transformation of surface circulation: during the southwestern monsoon, when the Somali Current is directed to the north and the biological productivity is increased as a result of the development of the Somali and Arabian upwellings (see Neiman et al. 1997), *H. speculiger* enters the Arabian Sea. In autumn and winter, the circulation under influence of the northeast monsoon transforms and becomes more closed, and the biological productivity is reduced. However, this relation with the monsoon circulation seems to be indirect because, according to our data, *H. speculiger* disappears from the Arabian Sea in September, when the summer Somali Current is still quite developed, and appears again in February, when the surface

circulation is not yet transformed into the summer type[2].

It can be assumed that the appearance of *H. speculiger* in the Arabian Sea is associated with an increased biological productivity here in spring and summer. However, it is hardly possible to explain the disappearance of this species only by biological productivity. The Arabian Sea is one of the most highly productive areas of the Indian Ocean (Parin 1989), and the concentration of food here is quite high, despite a slight decrease, in autumn-winter period too. For example, according to Dubinets et al. (1989), the biomass of zooplankton in autumn-winter period (the period of the northeast monsoon) decreases compared to spring-summer (the period of the south-western monsoon) from 120 mg/l to 90 mg/l in the open Arabian Sea. Another possible explanation for the disappearance of *H. speculiger* may be migration of mature fishes to other areas for spawning.

An additional mechanism for reducing the competition between *H. speculiger* and *H. indicus* may be the spatio-temporal separation of their representatives of similar sizes. Such fishes should maximally compete for food resources. Thus, fishes of these two species collected together in the same sample usually differed in size: 63.1% of such samples contained large specimens of one species with small specimens of another. Their lengths were overlapping or the size difference was small (below 20 mm) only in 36.9% of samples. Interestingly, in sympatric species of the genus *Exocoetus*, which have appreciable differences in the number of gill rakers, in only 31.2% of samples the sizes of fishes from different species differed greatly, i.e. 2 times more rarely. Perhaps, such size differences may be the result of difference in spawning times between these two species. Thus, in the western Indian Ocean, large specimens of *H. indicus* were collected in one sample with small specimens of *H. speculiger* in spring, and the opposite pattern was observed in summer, autumn and winter.

Hirundichthys oxycephalus coromandelensis was collected in the Arabian Sea in all seasons, with the exception of winter, when it was practically absent (Fig. 12). Although there are a few samples available (especially in the northeastern part of the sea), the migration of *H. oxycephalus* from the western coasts (where it mostly occurs in spring and summer) to the central part of the sea (in autumn) and further to the southeast shores (in winter) may be suggested. Such migration could be explained by the fact that in spring and summer, during the southwestern monsoon, the most favorable feeding conditions (as a result of the development of upwelling) are formed near the western shores, and in winter, during the northeast monsoon, near the eastern ones.

Flying fishes of the *Cypselurus "poecilopterus"* species group.

The group includes 3 neritic species which are usually found around oceanic islands: Indo-West Pacific *C. poecilopterus*, central Pacific *C. simus*, and eastern Pacific *C. callopterus* (Shakhovskoy and Parin 2010; see also Figs. 14 and 15).

Cypselurus poecilopterus has the most extensive distribution among representatives of the "*poecilopterus*" species group and more often than other species occurs far from neritic waters. It is found in waters with SST of 24-29°C (Parin 1960a; Chen 1987). According to our data (see Fig. S4): range 21.5-30.0°C, mean 27.9±0.094, SD 1.332. In the Indian Ocean, this species occurs in the north from 16°N in the Arabian Sea (SL 191 mm, IORAS 03397, R/V "Vityaz" 31, Sta 4722, 13.04.1960, 16°10'N, 60°45'E) and 14°N in the Bay of Bengal (4 specimens SL 71-86 mm, IORAS 03429, R/V "Vityaz" 33, Sta 4927, 28.01.1961, 14°11'N, 82°53'E) up to the Mascarene Islands (4 specimens SL 33-74 mm, IORAS 03437, R/V "Vityaz" 36, Sta 5322, 18.12.1964, 18°58'S, 56°05'E)[3] and the west coast of Australia (SL 49 mm, IORAS 03438, R/V "Vityaz" 35, Sta 5185, 27.07.1962, 24°34'S, 108°20'E) in the south. This species occurs in the Gulf of Aden, but is absent in the Persian Gulf and

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[2] According to Neiman et al. (1997), the summer period lasts from May to September, and the winter period from December to February; the spring and autumn transition periods, when transformation of circulation from one type to another takes place, are 2 months long both.

[3] One specimen of *C. poecilopterus* about 200 mm long was captured in the vicinity of Rodriguez Island (Elaine Heemstra, personal communication).
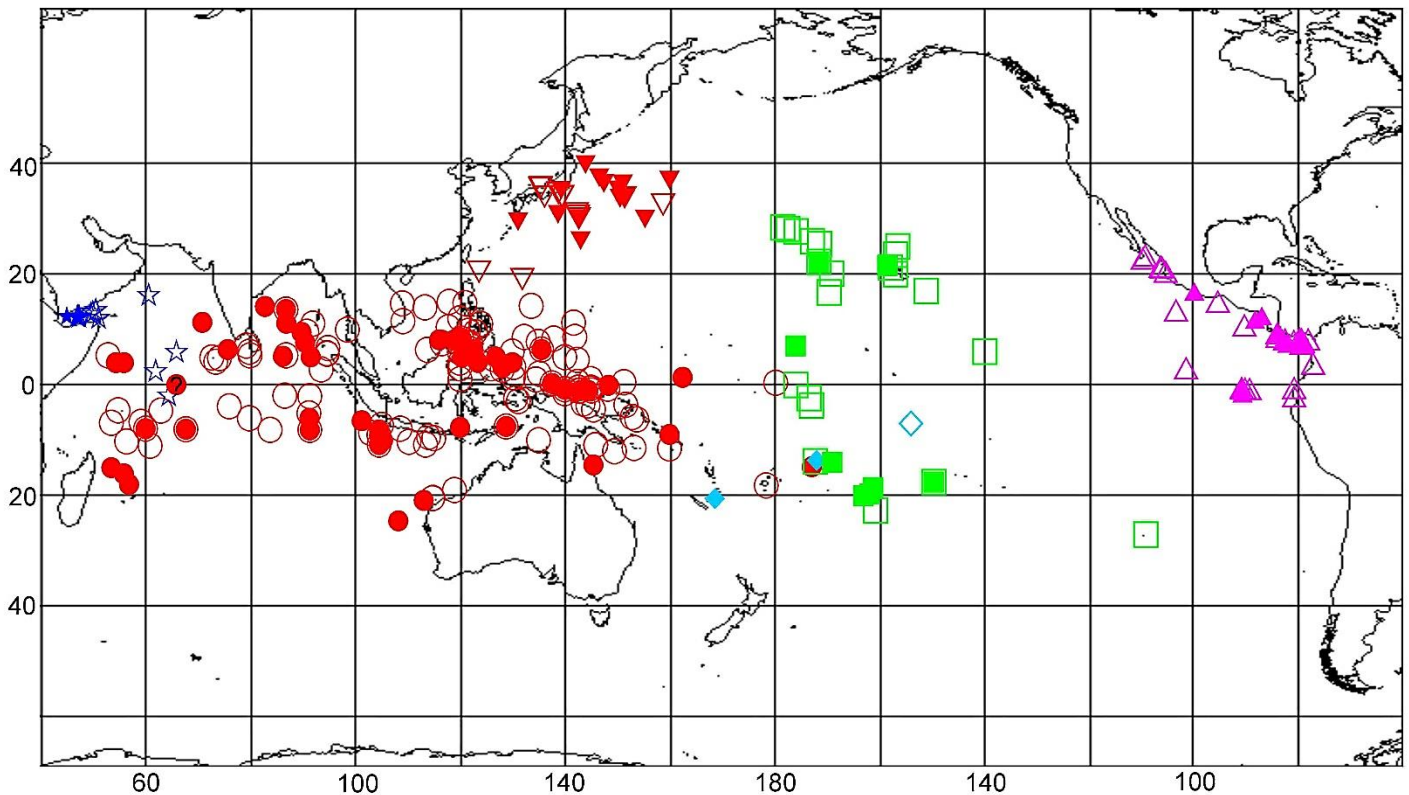
Figure 14. Distribution of flying fishes of "*poecilopterus*" species group. *C. poecilopterus* (○ - typical form, ▽ - Japanese subspecies, ☆ - Arabian subspecies); *C. simus* (□); *C. callopterus* (△); putative hybrids of *C. poecilopterus* x *C. simus* (◇). Darkened signs are fishes with SL ≤100 mm.

the Gulf of Oman as well as in the Red Sea. In the Pacific Ocean *C. poecilopterus* is found in the waters of Indonesia, Philippine, northern Australia (southward up to Lizard Island: SL 39.5 mm, AMS I. 24973-004), New Guinea, western Polynesia (SL 31 mm, IORAS 03439, R/V "Vityaz" 26, Sta 3812, 9.12.1957, 14°49'S, 172°56'W) and Japan (including the Kuroshio Current zone up to 160°E). To the north this species is distributed to Hokkaido (SL 77 mm, IORAS 03440, R/V "Vityaz" 46, Sta 6162, 15.08.1969, 39°50'N, 144°00'E). Two populations of *C. poecilopterus* - of the Arabian Sea and of the waters of Japan - differ from other populations in a number of characters (see Shakhovskoy and Parin 2010) and ecological features (see below) and, in my opinion, deserve a rank of subspecies[4]. However description of these subspecies will be made in a separate work.

Cypselurus simus is distributed in the central Pacific between 30°N and 25-27°S from 180°W (SL 270 mm, BPBM 34377, Kure; SL 180 mm, IORAS 03441, R/V "Vityaz" 43, Sta 5943, 6.02.1968, 13°51'S, 172°13'W) up to 140ºW in the north (SL 160 mm, IORAS 03442, R/V "Vityaz" 34, Sta 5082, 16-17.09.1961, 5°58'N, 139°57'W) and up to the Easter Island in the south (SL 219 mm, BPBM 39415). This species occurs mainly in the neritic zone near oceanic islands (Fig. 14). According to our data (see Fig. S4), it occurs in waters with SST 22.0-29.0°C (mean 26.2±0.356, SD 2.016).

Cypselurus callopterus is distributed in the eastern Pacific Ocean from Mexico (SL 195 mm, SIO 63-1073) to Ecuador and adjacent islands (SL 257 mm, R/V "Anton Bruun" 18B, Sta 774-775, 11.09.1966, 2°29'-1°03'S,

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[4] A subspecies, in my opinion, is such a population (or a group of populations) of a species that is partially (or completely) reproductively isolated (or has recently been isolated) from other populations of the species and has acquired, as a result of this isolation, certain morphological (genetic, biochemical, etc.) differences great enough for a taxonomic isolation at this level but not sufficient (taking into account the existing species differences in the group studied) for describing it as a new species.
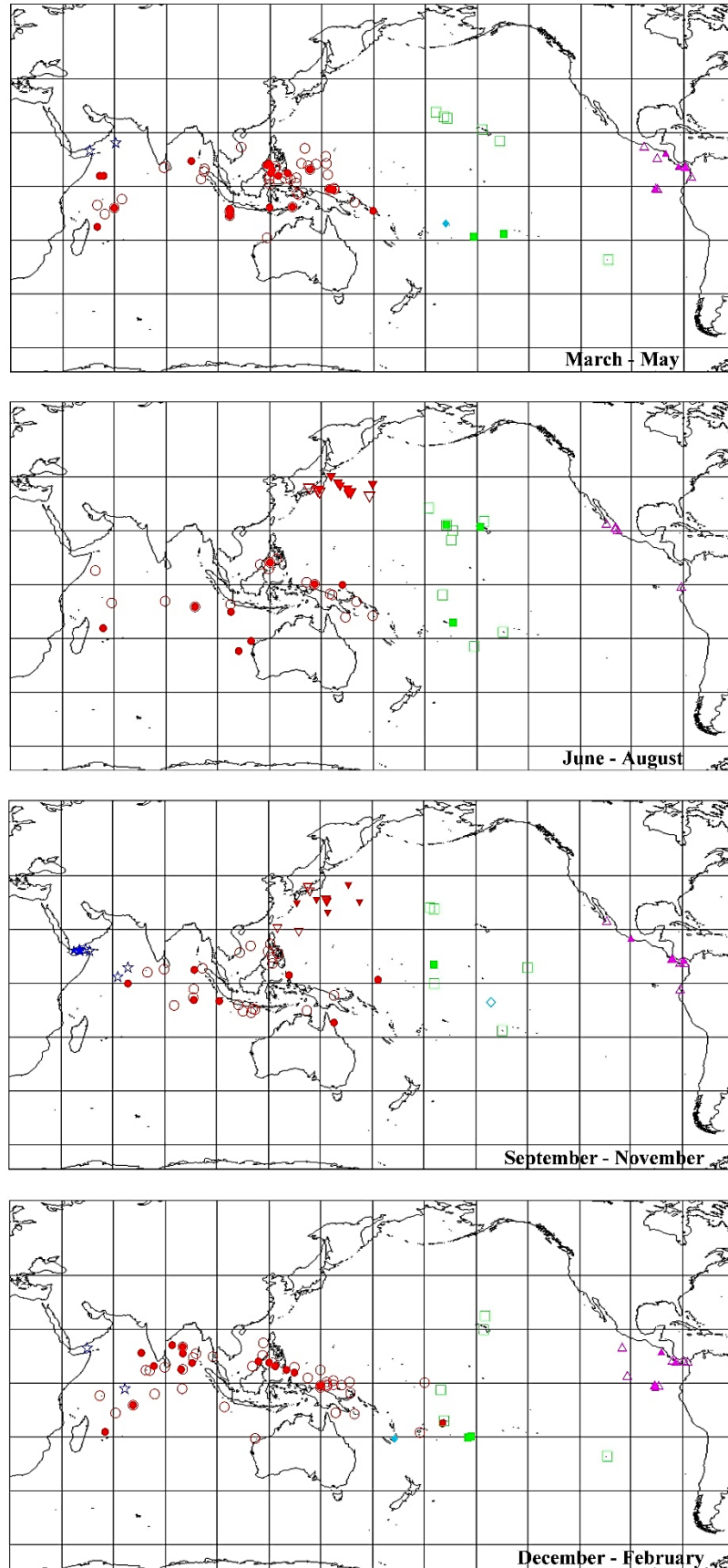
Figure 15. Distribution of flying fishes of the "*poecilopterus*" species group in different seasons. Legend is the same as for Fig. 14.

80°59'W). According to our data (see Fig. S4) this species occurs in waters with SST 21.0-30.0°C (mean 26.9±0.340, SD 2.040).

Juveniles of *C. poecilopterus* (with SL up to 100 mm) are generally distributed in the same areas as larger fishes. However there is a gap of about 20º latitude between ranges of juveniles from western Pacific and Japan populations, which, along with the morphological distinctiveness of the population from the waters of Japan (see Shakhovskoy and Parin 2010), suggests the possibility of its reproductive isolation from other populations. Previously published data support this idea. For example, Chen (1987) could not find larvae and juveniles of this species south of 20°N. According to Chang et al. (2012a), mature individuals of this species were found only in the northern waters of Taiwan, and immature specimens in the southern waters, which makes these authors suppose migration to more northern areas for spawning.

There are no *C. poecilopterus* from the waters of Mariana and Marshall Islands in our material. However, Parin (1960b) reported captures of *C. poecilopterus* in these areas, although captures of *C. poecilopterus* in the vicinity of the Gilbert, Samoa, Fiji and Tonga islands reported by this author may in fact represent another species - *C. simus*.

The areas of *C. poecilopterus* and *C. simus* contact in western Polynesia around 170-180°W (although these species have never been captured together in the same sample), and several individuals of presumably hybrid nature (having intermediate characters) have been found near this boundary region (Fig. 14). Juveniles of *C. poecilopterus* and *C. simus* were found in all seasons, which may be indicative of year-round spawning. The only exceptions here are two populations (subspecies) of *C. poecilopterus*: in Japanese population, juveniles were caught only in summer and autumn, and in Arabian one - only in autumn. This indicates seasonality of spawning, although for the Arabian population it may be a consequence of small number of samples available. The absence of *C. callopterus* juveniles in summer can also be a consequence of scanty data.

Distribution of flying fishes in relation to oceanographic factors

A comparison of the distribution of flying fishes with oceanographic characteristics showed a lack of similarity between the areas configuration, on one hand, and the distribution of biological productivity and water masses, on the other. This is not surprising, since water masses are usually outlined by the presence of extrema in the distribution of temperature and salinity by depth for the entire surface zone of the ocean (up to a depth of 100-200 m). For flying fishes, which are confined in their distribution mainly to the thin surface layer of the ocean up to depths of 2-3 m (see above), the presence of such extrema is not of a great importance. The biological productivity, influencing, of course, the quantitative distribution of flying fish (see Parin 1967), does not appreciably affect the ranges of species. At the same time, there is a similarity in the distribution of flying fishes with fields of SST, SSS and surface currents.

The range of *E. volitans*, as in most of nektonic fish species (see Parin 1968; Beklemishev et al. 1977), is limited mainly by water temperature and roughly corresponds to the position of 25°C isotherm (and does not cross the isotherm of 20°C) (see Locarnini et al. 2010). The absence of this species in the region of the Pacific Ocean thermal equator, previously noted by Parin and Kovalevskaya and confirmed by our data (see above), indicates that this species avoids the most heated waters as well. In considering the seasonal distribution of *E. volitans*, the similarity of the species range boundaries to the seasonal fluctuation of the 25°C isotherm (see Locarnini et al. 2010) becomes conspicuous. The range of this species expands in the warm season of the corresponding hemisphere and narrows in the cold one.

The ranges of other species of the genus appear to be determined mainly by circulation of surface waters, and the sea surface temperature is an important factor only in the colder periphery of the species areas. The influence of currents on distribution of fishes of this genus was earlier considered in the work of Parin (1962).

Noting that the warm-water part of the range of *E. obtusirostris* (= *E. gibbosus*) in the central Pacific lies within the temperature range similar to that of *E. monocirrhus* (whereas these species are extremely rarely found jointly), he suggested that the boundary between their areas coincides with the southern boundary of the SEC. Our data confirm his conclusions.

Exocoetus gibbosus is found in the waters of the southern subtropical gyre of the Pacific (and, presumably, the Indian) Ocean mainly south of SSTC and *E. monocirrhus* – mainly north of SSTC (see Fig. 2, S5). Thus this dynamic front seems to be the boundary between the ranges of these two species. *Exocoetus peruvianus* occurs in the waters of the southern tropical cyclonic gyre of the Pacific Ocean. *Exocoetus obtusirostris* inhabits Atlantic in the southern and northern subtropical gyres (also mainly south (north) of the convergence), as well as in the southern and northern tropical cyclonic gyres[5].

If we compare the maps of species distribution and the maps of dynamic topography of the ocean surface (see Burkov et al. 1973; Reid 1989, 1994, 1997, 2003; AVISO website), the following hypothesis can be proposed (see Figures 16, S5 and S6): *E. gibbosus* inhabits the waters south of SSTC, where an eastern transport predominates, and only in the area east of about 120°E, where the zonal currents is replaced by the meridional ones, its juveniles are carried away north of the convergence. *Exocoetus monocirrhus*, on the other hand, lives in the Southern Pacific in areas where a western transport prevails (i.e., in the waters of SEC) and crosses convergence only with warm meridional currents flowing southward[6]: with the East Australian Current and a current revealed by Australian oceanographers (see Rochford 1977) which is a branch of SEC directed to the south-west and flowing between New Caledonia and Norfolk Island. This flow is most developed in February-April - the same time when *E. monocirrhus* was found here (4 specimens SL 37-54 mm, CHG 55-61, 16°12'S, 176°44'E, 22.02.1962; SL 77 mm, CHG 55-47, 24°02'S, 171°45'E, 12.02.1962). All other cases of SSTC crossing by both species (see Fig. 2, and S5) can probably be explained by the seasonal and interannual variability of its position relative to the annual mean one shown by Burkov et al. (1973). This variability (seasonal and with 3-4-year periodicity associated probably with the ENSO cycle) was revealed by Morris et al. (1996) on a meridional transect from New Zealand to Hawaii: the convergence zone may shift here by several degrees from its annual mean position adjacent to Fiji (18°S) moving closer to the equator in April-May. Stramma and Lutjeharms (1997) also noted the seasonal movement of the South Indian Current northward in winter of southern hemisphere and southward in summer on a transect in the area of 65°E. *Exocoetus monocirrhus* is more rarely found in the waters of SEC in spring-summer than in autumn-winter time, and it does not spread far southward then. Also, according to Kovalevskaya (1980), the early stages of development of this species in the Pacific were collected in the waters of SEC only in the autumn-winter period.

Similarly, in the southern Indian Ocean *E. monocirrhus* does not expand south of the SSTC. An exception is the eastern region, where due to the difference in levels of the Pacific and Indian oceans oceanographic conditions unique for eastern margins of oceans exist. Warm waters pumped by SEC penetrate through the Indonesian straits (the Indonesian Throughflow) and are further distributed in the Indian Ocean with the SEC, Eastern Gyral Current and Leeuwin Current (Pearce and Cresswell 1985; Schott and McCreary 2001; Domingues et al. 2007). As it was previously shown (Domingues et al. 2007; Aguiar-González et al. 2016), the Eastern Gyral Current is in fact a recirculation of SEC and transports to the west coast of Australia waters that are of tropical rather than subtropical origin, which, apparently, explains presence of *E. monocirrhus* juveniles here. Like many tropical species of animals (see, for example, Pearce and Cresswell 1985; Sutton and Beckley

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[5] For description of these gyres see Stepanov (1974, 1983), Mittelstaedt (1991). The tropical cyclonic gyres are also well pronounced in altimeter-derived dynamic topography (see AVISO website).

[6] These narrow meridional currents may be not reflected on maps of dynamic topography of ocean surface due to a large averaging scale.
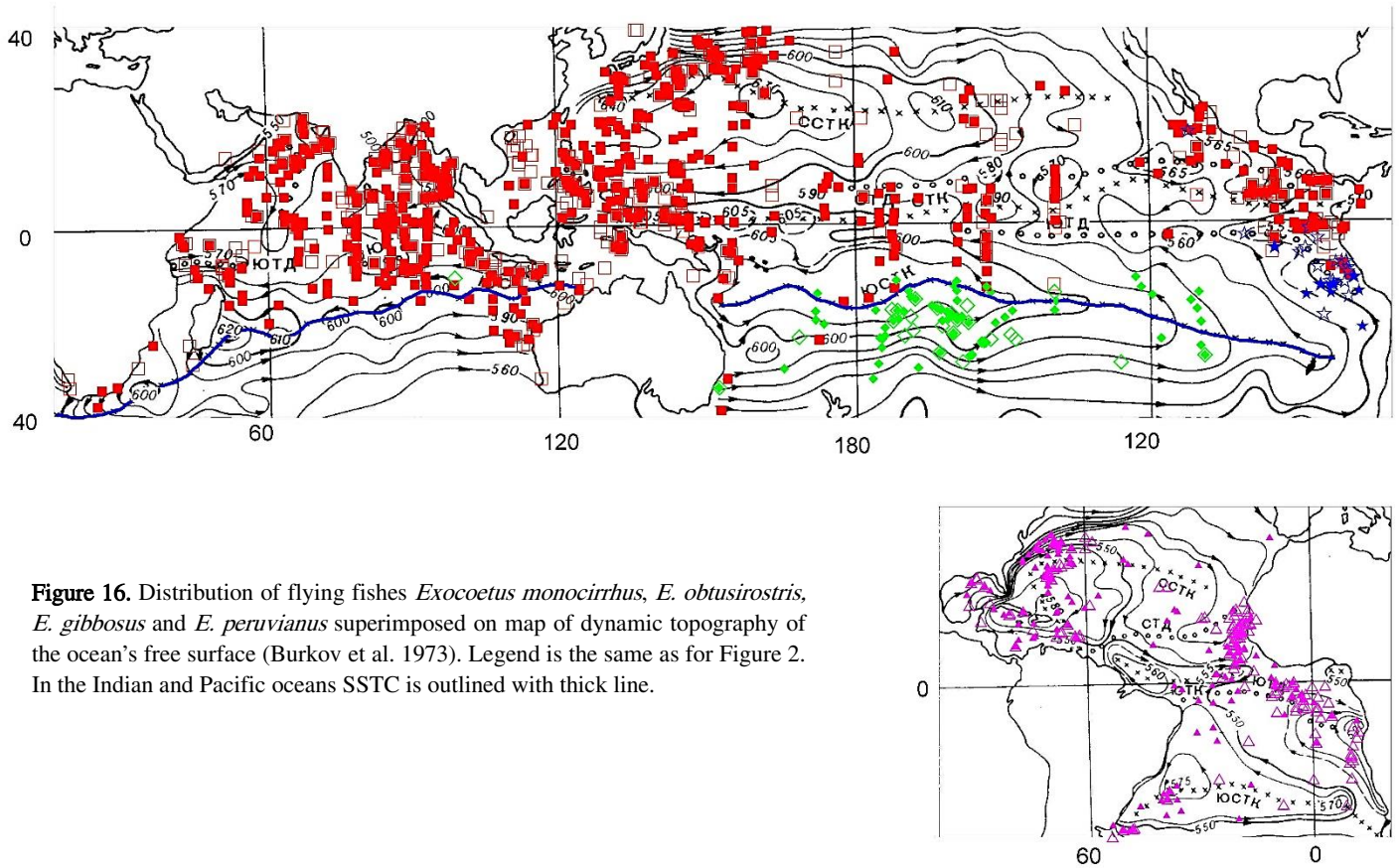
Figure 16. Distribution of flying fishes *Exocoetus monocirrhus*, *E. obtusirostris*, *E. gibbosus* and *E. peruvianus* superimposed on map of dynamic topography of the ocean's free surface (Burkov et al. 1973). Legend is the same as for Figure 2. In the Indian and Pacific oceans SSTC is outlined with thick line.

2016), *E. monocirrhus* (both juveniles and adults) spreads with the Leeuwin Current far to the south.

The flow rate of Leeuwin Current has interannual fluctuations associated mainly with the ENSO cycle (Deng et al. 2008). Due to particularly large water level difference between the western Pacific and the eastern Indian Ocean, occurring in some years, there is a phenomenon named the "marine heat wave" in this region (Pearce and Feng 2013). During La Niña events, a portion of warm water pumped by the trade winds and entered the eastern part of the Indian Ocean is transported far to the south along the Australian coast, which is accompanied by an abnormally high water temperature. Apparently the warm wave has an impact on distribution of *E. monocirrhus*: the most southern finding of this species from our collections (SL 178 and 194 mm, FRSKU No. 1122614 and 112618, 32°00'S, 114°47'E, 22.12.1987) falls on the year when the strong La Niña event was noted (see Wang and Fiedler 2006). In the northern Pacific Ocean, NSTC does not limit distribution of *E. monocirrhus* (see Fig. 2). Distribution range of this species in this region is very similar to one of *E. volitans* and probably SST is the main limiting factor for both species here.

Exocoetus peruvianus occurs in the waters of southern tropical cyclonic gyre of the Pacific where *E. monocirrhus* penetrates only with the warm El Niño Current (or Peru-Chilean Current according to nomenclature of Stepanov (1974, 1983)). Santander (1976) reports that this current is a southern branch of Cromwell Current and its manifestations are most pronounced to the north of 9°S. Although the upwelling of deep waters is mainly observed year-round, it is usually less intensive from December to February. In these months, warm waters spread southward along the Peruvian coast usually up to 5°S, but some years they spread even further to the south, raising the sea surface temperature by 7°C.

The pattern of *E. peruvianus* and *E. monocirrhus* distribution in the eastern Pacific changes quite dynamically depending on season: the boundary between the ranges of both species shifts southward to about 10°S in warm

season, and in cold period makes the opposite movement to 1-2°S. The El Niño and La Niña events probably influence the distribution of these two species. Thus, the southernmost records (up to 10°S) of *E. monocirrhus* in the SEPO fall on the El Niño years, while in the La Niña years this species was not observed south of 2°S even in warm season. In contrast, *E. peruvianus* was not found north of 8°S in the El Niño years, but a penetration into the waters of the Galapagos Islands during the warm season was noted in the La Niña years.

Distribution patterns of *E. obtusirostris*, on the one hand, and of *E. gibbosus* and *E. peruvianus*, on the other, are very similar. *Exocoetus obtusirostris* is found in the Atlantic Ocean mainly in tropical cyclonic gyres and in subtropical gyres, also mainly to the north (south) of the northern (southern) subtropical convergence. In the western Atlantic, *E. obtusirostris* very rarely (almost exclusively in juvenile stages) occurs in the zone of the Equatorial currents and in the zone of western boundary currents (within tropics) – Guiana Current and Brazil Current. *Exocoetus volitans*, on the contrary, is the most numerous here. Earlier, Bruun (1935), John (1976), Lopez and John (1988) and Monteiro et al. (1998) have obtained a very similar picture of these species distribution in the tropical Atlantic. It can be assumed that *E. obtusirostris* has 4 populations (or groups of populations), one in each of the gyres, which can be largely reproductively isolated. However, the small latitudinal extent of the Atlantic in comparison with the Pacific Ocean seems to facilitate the exchange of genes between these populations and does not allow them to separate. This matter requires special study, like, for example, one carried out by Lewallen, Bohonak et al. (2017). These authors compared *E. gibbosus* and *E. peruvianus* using genetic markers (Cytb, Rag2) and found that they did not differ. However, the specimens (Voucher No. ROM-79289, 1.73°S 85.45°W; Voucher No. ROM-92584, 3.60°S 97.13°W), identified by Lewallen and co-authors as *E. gibbosus*, were caught in the area where according to our data only *E. peruvianus* occurs. And I do identified these specimens as *E. peruvianus* basing on their photos kindly provided by Drs. R. Winterbottom and E. Holm (Royal Ontario Museum).

The above-described isolation by currents is very effective (see Fig. 17): *E. monocirrhus* was collected together with *E. gibbosus* only in one sample (both species in juvenile stage; R/V "Vityaz", Cruise 34, Sta. 5110, 15.10.1961, 13°06'S, 154°00'W), and with *E. peruvianus* - only in 2 samples, one of which is represented only by juveniles (R/V "A. Bruun", Cruise 14, Sta. 572, 15.03.1966, 10°30'S, 79°40'W; R/V "Academic Kurchatov", Cruise 34, Sta. 3565, 10.02.1982, 8°01'S, 82°30'W). Both these samples were obtained in the years when the El Niño event was observed (see Wang and Fiedler 2006), with the water temperature in the area of Sta. 3565 being 25.8°C. At the same time, since the plots of dependence of these species distribution upon temperature and salinity, although differ, but overlap quite significantly (see Fig. S2), the differences in requirements of these species as to the temperature and salinity of surface waters cannot be the cause of their allopatric distribution.

The area of *E. obtusirostris* corresponds quite well to the area of planktonic peripheral species (Beklemishev et al. 1977: Fig. 13). The distribution of *E. gibbosus* in the southern Pacific is very similar to a fairly widespread type of areas of zooplankton species, named by Beklemishev et al. (1977) "central", and by Reid et al. (1978) "subtropical" (the range of *E. gibbosus* is rather exactly coincides with the areas of *Euphausia brevis* and, especially, *E. gibba*, given in the work of these authors). The dependence of distribution on a system of surface currents, hypothesized here for *E. gibbosus*, *E. peruvianus* and *E. obtusirostris,* is very common for planktonic species and quite unexpected for representatives of the nekton life form, since it is believed that the range of nektonic fish is mainly determined by temperature conditions, and the boundaries of areas generally correspond to the position of the isotherms (Parin 1968; Beklemishev et al. 1977).

Exocoetus obtusirostris, *E. monocirrhus*, *E. gibbosus*, and *E. peruvianus* seem to occupy similar ecological niches and compete for food (the number of gill rakers in these species is approximately the same), therefore
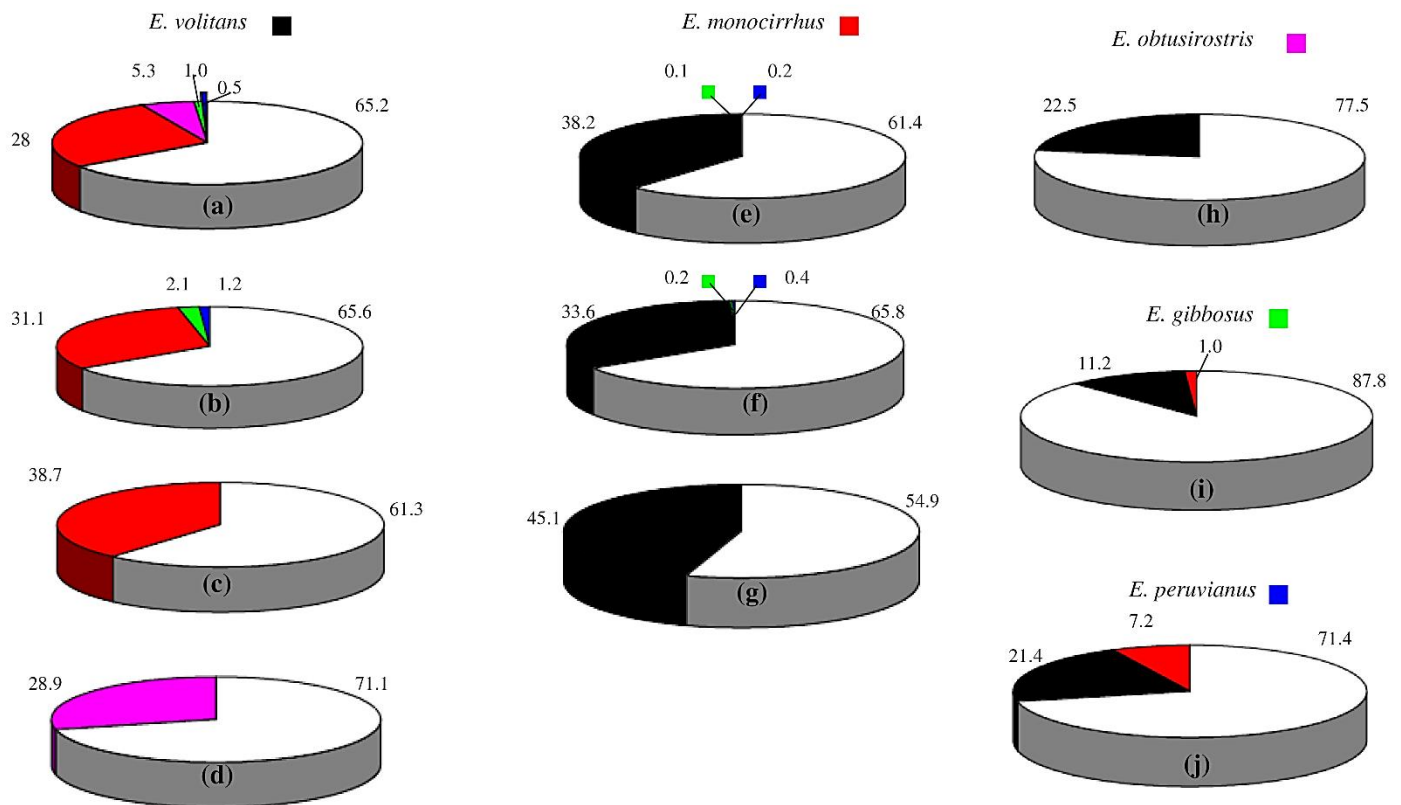
Figure 17. Co-occurrence in samples of flying fishes of the genus *Exocoetus* (in %, light sectors - samples in which only the given species was present). (a) *E. volitans*, all the range; (b) *E. volitans*, Pacific Ocean; (c) *E. volitans*, Indian Ocean; (d) *E. volitans*, Atlantic Ocean; (e) *E. monocirrhus*, the entire range (Indo-Pacific); (f) *E. monocirrhus*, Pacific Ocean; (g) *E. monocirrhus*, Indian Ocean; (h) *E. obtusirostris*, the whole range (Atlantic Ocean); (i) *E. gibbosus*, the whole range (west-central Pacific); (j) *E. peruvianus*, the whole range (southeastern Pacific).

their areas are almost completely disjunct (allopatric or parapatric). *Exocoetus volitans* has more gill rakers and is smaller, which may reduces its competition for food. As a result, its range is sympatric with the ranges of the above species. *Exocoetus volitans* differs somewhat from other representatives of the genus by preferred food items (see Lipskaya 1987; Gorelova and Grudtsev 1987; Van Noord et al. 2013). This species was collected together with *E. monocirrhus, E. obtusirostris, E. peruvianus* and *E. gibbosus* in 38.2, 22.5, 21.4 and 11.2% of the samples, respectively. Thus, *E. volitans* is captured more frequently with *E. monocirrhus* than with any other species, which is probably due to the more thermophilic nature of these two species. In contrast to the subgenus *Hirundichthys*, where fishes of different species captured together differed mainly in size, in the genus *Exocoetus* fishes of different species caught in the same sample were mostly represented by similar size groups (see above).

Distribution of flying fishes of the subgenus *Hirundichthys* is probably determined mainly by SST and remoteness from the neritic zone. All species of the subgenus belong to the group of tropical fish and are distributed almost exclusively within waters limited by the isotherm of annual mean temperature of 20°C. There is a fairly clear division into nerito-oceanic and oceanic species within the subgenus. Thus, *H. affinis* and *H. oxycephalus*, two very closely related species, inhabit the neritic and far-neretic waters of the Atlantic and Indo-West Pacific. For reproduction, these species approach shelf zones in search of a floating substrate for egg laying. *Hirundichthys speculiger* and *H. indicus* inhabited open ocean waters, and thus the ranges of these two pair of species are quite greatly isolated.

The range of *H. speculiger* is extremely similar to the range of *E. volitans* and, like in the latter, it is apparently

determined by the SST: the boundaries well correspond to the annual mean 20ºC isotherm, and usually do not cross the 25ºC isotherm. This species is also absent in the region of the thermal equator (as was previously noted by Parin (1960b) and Kovalevskaya (1980)) and extremely rare in the region of the Indonesian seas. When considering seasonal distribution of *H. speculiger*, one can see a correspondence of the range boundary to the position of 25ºC isotherm, and this species very rarely occurs in waters with SST below 25ºC (see Fig. S3). The distribution of *H. indicus* is apparently affected by SST as well. But this species is more thermophilic, and the boundaries of its range do not cross the annual mean 26ºC isotherm.

Our data on the distribution of *H. affinis* and *H. oxycephalus* suggests that they are nerito-oceanic species (although some fishes are caught far from shores in the open ocean). In their distribution, these species are confined to coasts of large land masses and marginal seas and are extremely rare around the oceanic islands. This may be due to the lack of large volumes of river runoff here, which is probably a requirement for reproduction of these species characterized by mass spawning and laying eggs on drifting objects (see Shakhovskoy and Parin 2013b). These species are rarely found in one sample together with the oceanic species of the subgenus (see Fig. 13).

There are no considerable differences between species of the subgenus in the temperature and salinity of habitats (see Fig. S3). Some difference in salinity of habitat between *H. affinis* and other species is resulted from the higher salinity of the tropical Atlantic. If we compare the ranges of nerito-oceanic and oceanic species of the subgenus with the scheme of zoogeographical zoning of the World Ocean for plankton animals (Beklemishev et al. 1977), it can be seen that the area boundaries of the nerito-oceanic species correspond well to the boundaries of far-neritic species of plankton. This can apparently be explained by two factors: the need for returning to coasts for reproduction and the short life cycle of these fishes. After hatching, larvae of *H. affinis* and *H. oxycephalus* are carried far away from the spawning areas by currents, including the open ocean. Having reached the size of transition to the nekton stage, they could have spread widely in the open ocean. But the need to return to the coasts for spawning in the nearest future and completion of the life cycle seems to prevent extensive colonization of the open ocean by these non-oceanic species. Oceanic species (*H. indicus* and *H. speculiger*) were able to do this, probably due to some traits of their reproductive biology. Eggs of *H. speculiger* (eggs of *H. indicus* are still undescribed) have shorter and fewer in number filaments than eggs of two nerito-oceanic species (see Shakhovskoy and Parin 2013a, 2013b for details). It can be assumed that fishes of these oceanic species spawn in pairs or in small groups (although their spawning has not yet been described) and do not form such huge spawning aggregations as nerito-oceanic species, and therefore are not so dependent on the presence of large amount of drifting objects brought from the land, being content with a small amount that is always present in the open ocean.

Distribution of species and local populations of the "*poecilopterus*" species group is apparently determined by a combination of three main factors: SSS, proximity to shallow water (continental shelf and, mainly, oceanic islands) and SST. All species in this group do not spread beyond the tropical region of the World Ocean singled out by Parin (1968) on the basis of the ichthyogeographical zoning of the epipelagial, and only one aberrant population (Japanese subspecies) of *C. poecilopterus* has colonized the waters of the subtropical region in the northwestern Pacific, where its representatives penetrate during warm season. They apparently occur in waters near Taiwan during winter season.

Besides SST, the distribution of flying fishes of "*poecilopterus*" group is apparently influenced by two more factors of primary importance: SSS and distance from the coast. The boundaries of species and subspecies ranges in general correspond well to isohaline 35.0 ‰ (see Fig. 18). *C. poecilopterus* (except for the Arabian population) and *C. callopterus* occur in waters with a decreased salinity. The Arabian population (subspecies) of *C. poecilopterus*, in contrast, lives in waters with an increased salinity. *Cypselurus simus* also lives mainly in
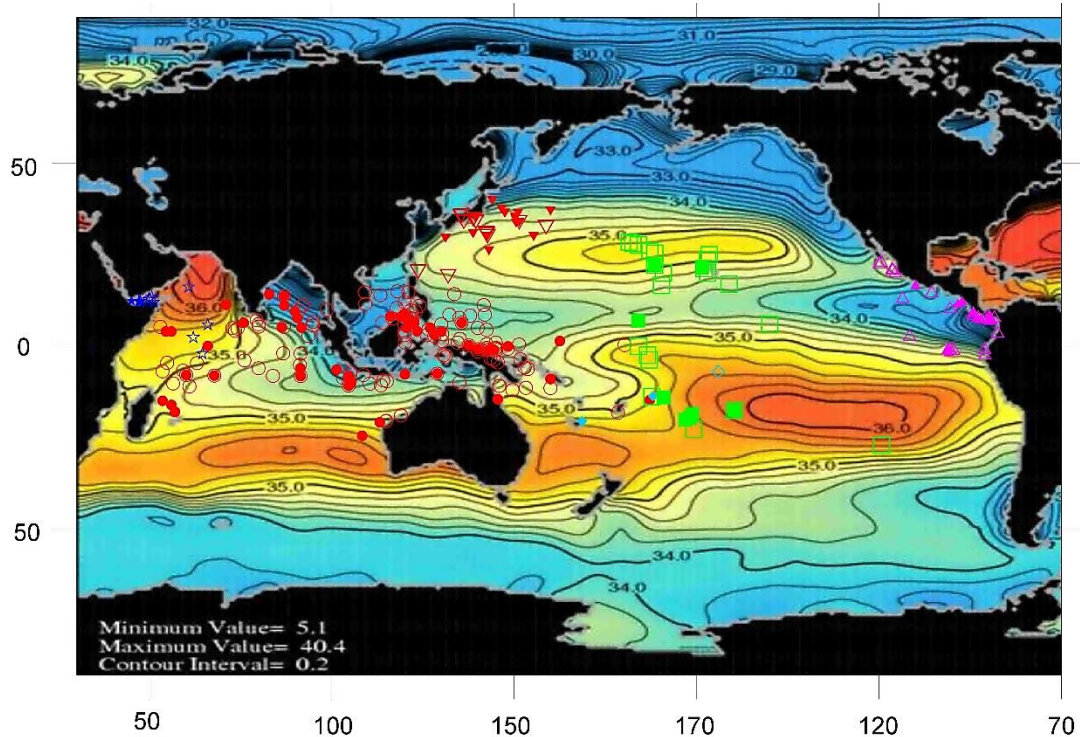
Figure 18. Distribution of flying fishes of "*poecilopterus*" species group superimposed on map of annual mean sea surface salinity (according to Antonov et al. 2010). See Figure 14 for the legend.

waters with SSS above 35‰ and, apparently, is nearly absent in waters of the North Equatorial Counter Current where the salinity is low. Probably it is exactly this zone that isolates local populations of *C. simus* from the northern and southern Pacific and makes gene flow difficult. The difference of these populations in number of vertebrae (see Shakhovskoy and Parin 2010) may be the result of such isolation. *Cypselurus poecilopterus* and *C. callopterus* probably could not colonize this zone with SSS suitable for them due to its remoteness from coasts.

When considering the distribution by seasons, it is noteworthy that neither *C. poecilopterus* in the waters of Africa, western Australia and eastern Australia, nor *C. callopterus* in the Peruvian region expand to higher latitudes in warm season, whereas many tropical species of flying fishes in these regions do so. It is likely that an increased salinity in these areas may be the reason for it, since in the northern hemisphere (in the region of Japan and California), where SSS is not so high, these species significantly expand their area in warm season (see Fig. 15).

In the western Indian Ocean, where seasonal changes in salinity under the influence of reversing of monsoon circulation are observed (see Neiman et al. 1997[7]), the corresponding migrations are noted. The typical form of *C. poecilopterus* approaches the western part of Arabian Sea in spring and summer with the low-salinity waters of the Somali Current, and it penetrates into the eastern part of Arabian Sea in winter with the waters of northern branch of the Winter Monsoon Current. On the contrary, the Arabian subspecies of *C. poecilopterus* propagates to the equator at about 60-65°E with high-salinity waters of the Shtokman Current during the autumn-winter period. According to Kantha et al. (2008: Fig. 9), from 1993 to 2004, an increase in the salinity of surface waters was noted in this region (0° 65°E) exactly in the autumn and winter months (except in February).

On the plots of dependence of distribution of species and subspecies of the group upon SST and SSS (Fig.

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[7]It should be noted, however, that the winter circulation system in the northern Indian Ocean given by several authors (Schott and McCreary 2001; Shankar et al. 2002) differs somewhat from that of Neiman and co-authors.

S4), the divergence in salinity of habitat is clearly evident. There are no considerable differences in temperature, and the curves overlap greatly; whereas two groups of taxa are clearly distinguishable in the salinity curve, with the approximate boundary between them being 35 ‰. However it should be noted that according to Lewallen, van Wijnen et al. (2017) SSS is not among the main factors defining habitat of *C. callopterus*.

If we compare distribution of the species of "*poecilopterus*" group and distribution (see Parin et al. 1980) of species of the closest to flying fishes family Hemiramphidae (halfbeaks), then the similarity of their ranges is striking. Thus, in the genus *Hemiramphus*, the range of *H. lutkei* is extremely similar (with the only difference that this species is absent in the Arabian Sea) to the range of *C. poecilopterus*, *H. depauperatus* - to *C. simus*, and *H. saltator* - to *C. callopterus*. Apparently, these two groups of species are ecological analogues. In the genus *Hyporhamphus*, the ranges of *Hy. balinensis* and *Hy. dussumieri* are very similar to that of *C. poecilopterus* (differing only in the absence of the both species in the waters of Japan and in the Arabian Sea, as well as in the presence of the first species in the Red Sea) and the range of *Hy. acutus* - to that of *C. simus*. Moreover, in the latter species the isolation by waters of the North Equatorial Counter Current might be the cause of the formation of 2 subspecies: *Hy. acutus acutus* and *Hy. acutus pacificus*. In the genus *Oxyporhamphus*, the distribution of O. *convexus bruuni* is similar to that of the Arabian subspecies of *C. poecilopterus*, and the distribution of O. *convexus convexus* – to that of the typical form of *C. poecilopterus*.

The aforementioned similarity of the ranges of flying fishes and halfbeaks may be caused by extreme similarity in the requirements for environmental factors in these species. Thus, if the hypothesis presented here is correct, then, the same as in the species of "*poecilopterus*" group two main factors might define the distribution of the above-mentioned species of halfbeaks: SSS and distance from coasts. In another family closely related to flying fishes, the garfishes (Belonidae), such a pattern of distribution is not found, and most marine species of garfishes are widespread (see Cressey and Collette 1970).

Conclusion

As early as in the beginning of the last century Schott (1912, 1926, cited according to Bruun 1935), who was studying the distribution of flying fishes taking off out of the water during passage of vessel, came to the conclusion that their range was determined by SST. Other researchers subsequently came to the same conclusion (Bruun 1935; Parin 1962, 1967, 1968, 1970; Shuntov 1973; Ovchinnikov and Nesterov 1986; Chen 1987; Lewallen, van Wijnen et al. 2017). According to Parin (1967, 1970), all flying fishes are stenothermic and more or less thermophilic, and most of the species do not occur in the waters with SST below 23°C (usually at 26°C and above). These species constitute a tropical group of flying fishes. Only a few species adapted to life in subtropical waters with SST of 18-20°C and below, which penetrate in summer even into warm temperate regions. To this group, which can be named subtropical, only about 10% of all species of flying fishes (Exocoetidae) belong.

Our data, in general, confirm the conclusions of the above-mentioned authors. Poleward distribution in the World Ocean of all the groups of flying fishes studied is limited primarily by SST. The limits of their ranges vary by seasons, and especially in the areas of western boundary currents, as well as of the Peru Current (where the El Niño and La Niña phenomena also affect) and the Benguela Current. The ranges of species practically does not cross the isotherms of 20°C (*E. obtusirostris*, *E. gibbosus*, *E. peruvianus*, *E. monocirrhus*, *E. volitans*, *C. simus*, *H. speculiger;* the last 4 species, however, are more thermophilic than the three first and occur mainly at a temperature of 25°C and above) or 25°C (*H. oxycephalus*, *H. affinis*, *H. indicus*, *C. poecilopterus*, *C. callopterus*) (see Figs. S2, S3, S4). However, the specialization and colonization of ocean within each of the three studied groups have probably been occurring in different ways, and boundaries between ranges of species are determined by absolutely different factors. Circulation of surface waters is most important for *Exocoetus*,

distance from the neritic zone for *Hirundichthys* and SSS for the "*poecilopterus*" species group.

The vast majority of species and subspecies in the studied groups of flying fishes have an allopatric (or parapatric) distribution, which can indicate a strong interspecific competition. And there are only few cases of sympatric areas of some species. In such cases, however, there may be mechanisms for reducing the interspecific competition: in *Exocoetus* species there is a division into many-raker and few-raker species, accompanied by divergence in food items, and in species of *Hirundichthys* – an alternate use of the same water areas by sympatric species as well as a spatiotemporal isolation of their uniform-sized stages of development.

Of course, the present paper does not state that the distribution of any flying fish species is determined solely by the aforementioned environmental factors. There is no point in denying that a distribution of any species of fish (and not only fish) is determined by the combined action of a variety of factors. Any factor (for example: concentrations of NO_3 and O_2, turbidity of water), reaching a certain critical value, begins to exert a depressing effect, limiting distribution of a species. An example of such a local factor for flying fishes is the increased turbidity of the water in the area affected by the Amazon River discharge. Apparently, it is the increased turbidity that may be responsible for the absence of many species of flying fishes in this area (see maps in Parin et al., 2018). However, most such factors have only a local effect on distribution of flying fishes. At the same time, the factors identified in the present study have, as the author supposes, a global significance, determining to a large degree the configuration of species ranges. However, all the hypotheses set forth in this work require a thorough checking by field studies and experiments.

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Appendix 1: Supplementary Materials
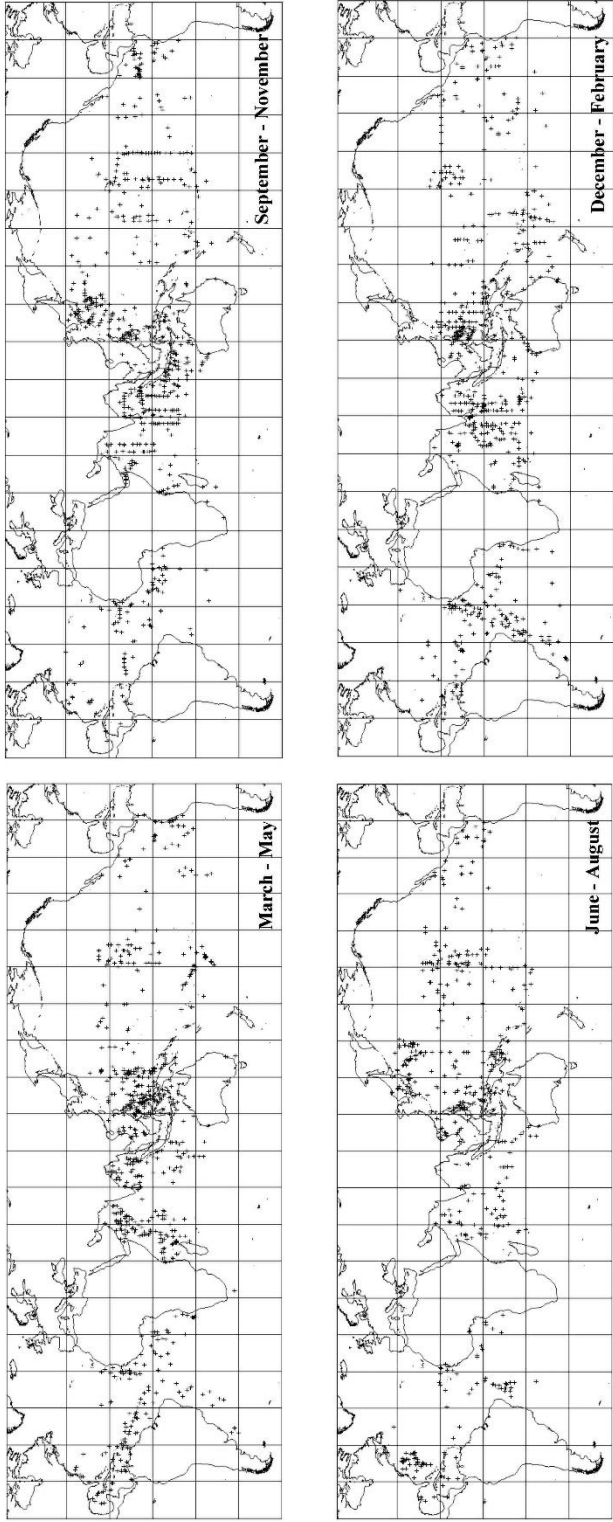
**Figure S1.** Coordinates of captures of flying fishes used in the work (+). Only those samples are shown for which the date of capture is known.
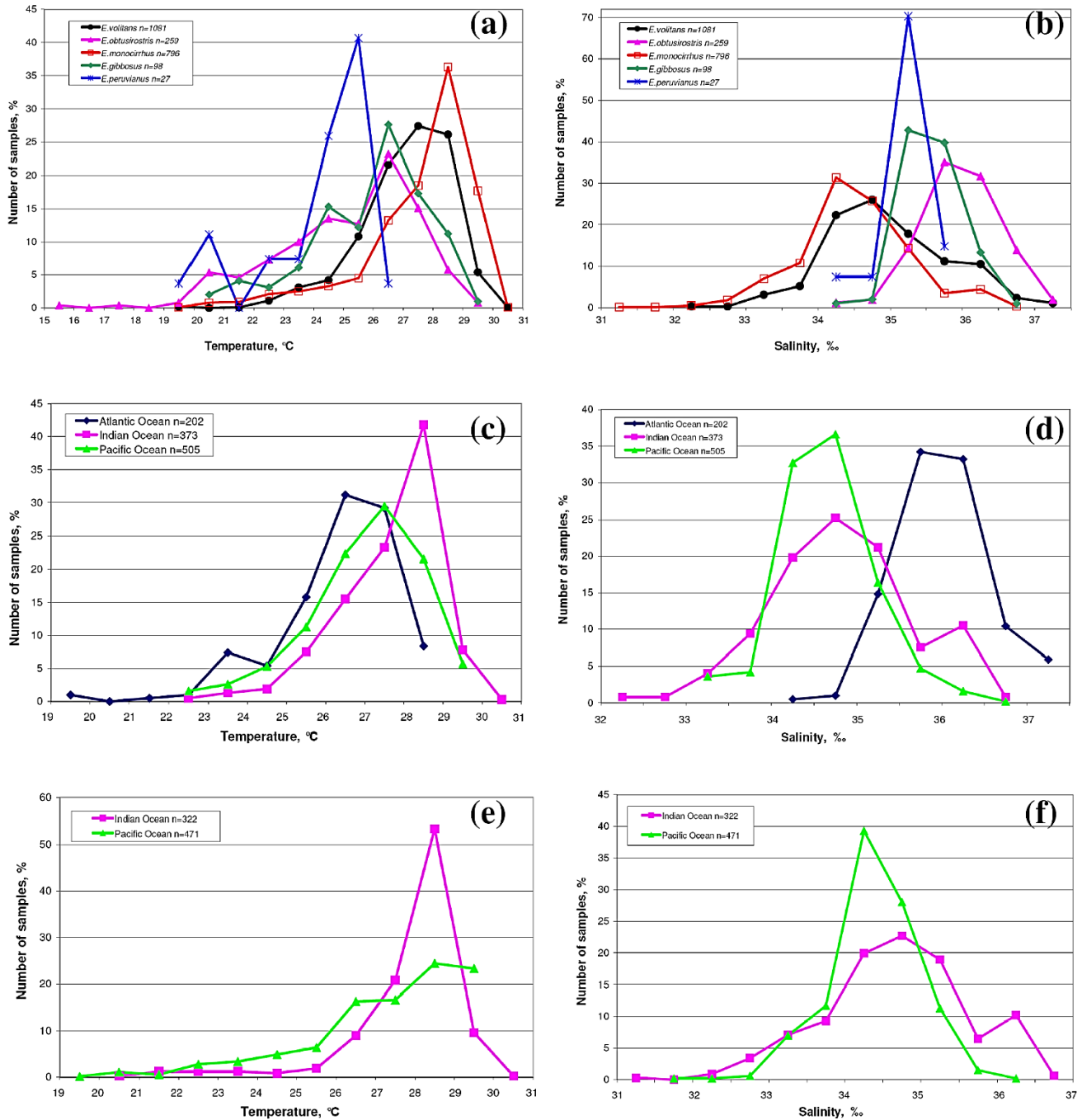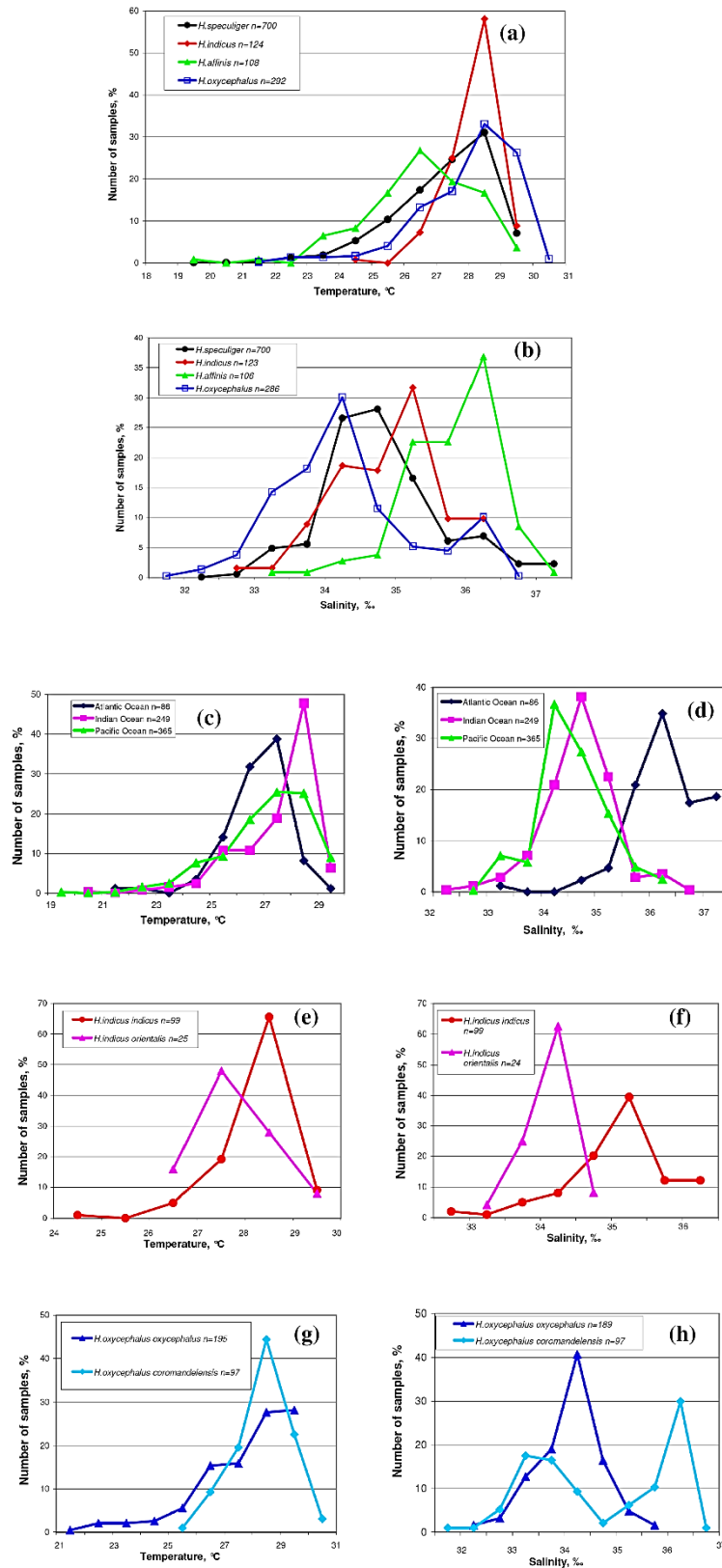
Figure S2. Distribution of flying fishes of the genus *Exocoetus* in relation to temperature and salinity of surface waters. (a) all species and all regions, temperature; (b) all species and all regions, salinity; (c) *E. volitans*, temperature; (d) *E. volitans*, salinity; (e) *E. monocirrhus*, temperature; (f) *E. monocirrhus*, salinity; (g) Atlantic Ocean, temperature; (h) Atlantic Ocean, salinity; (i) Indian Ocean, temperature; (j) Indian Ocean, salinity; (k) Pacific Ocean, temperature; (l) Pacific Ocean, salinity.
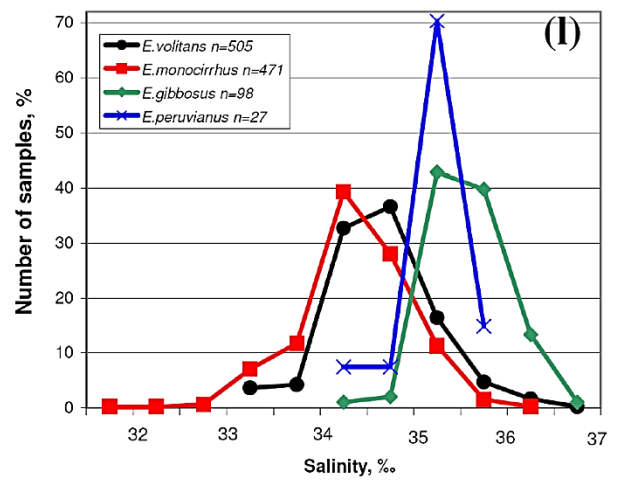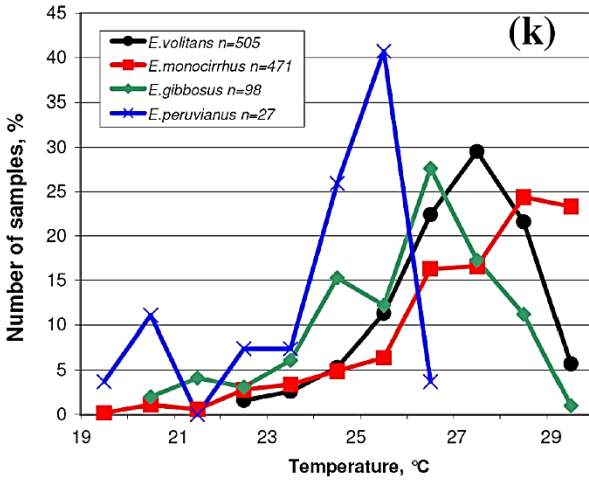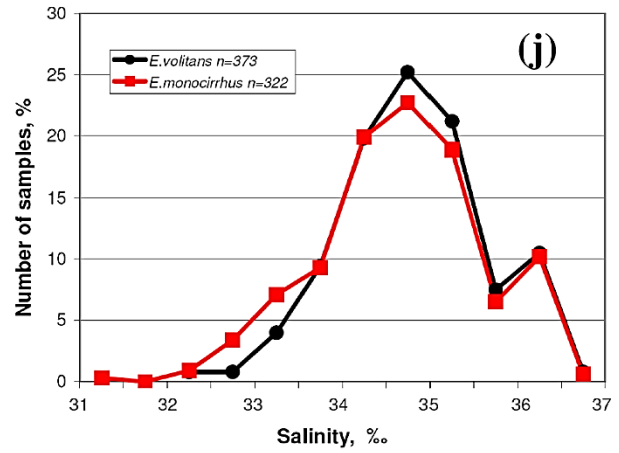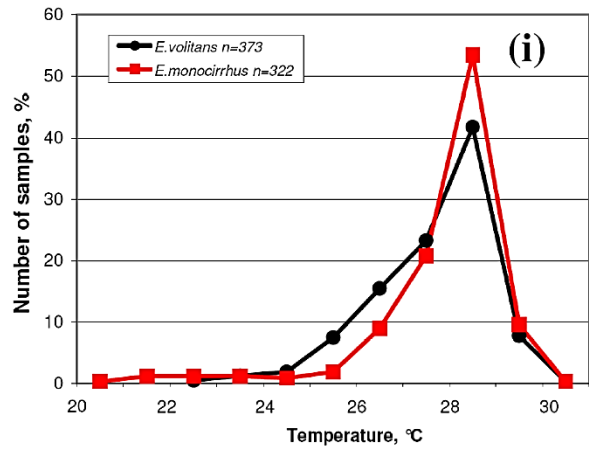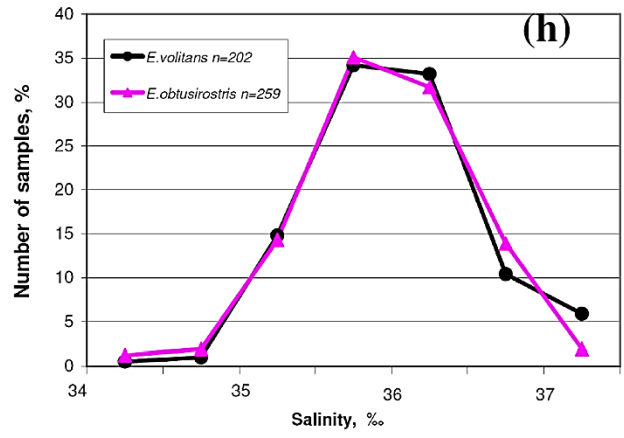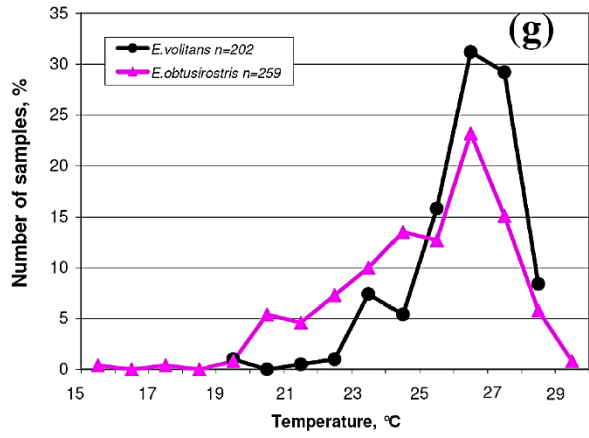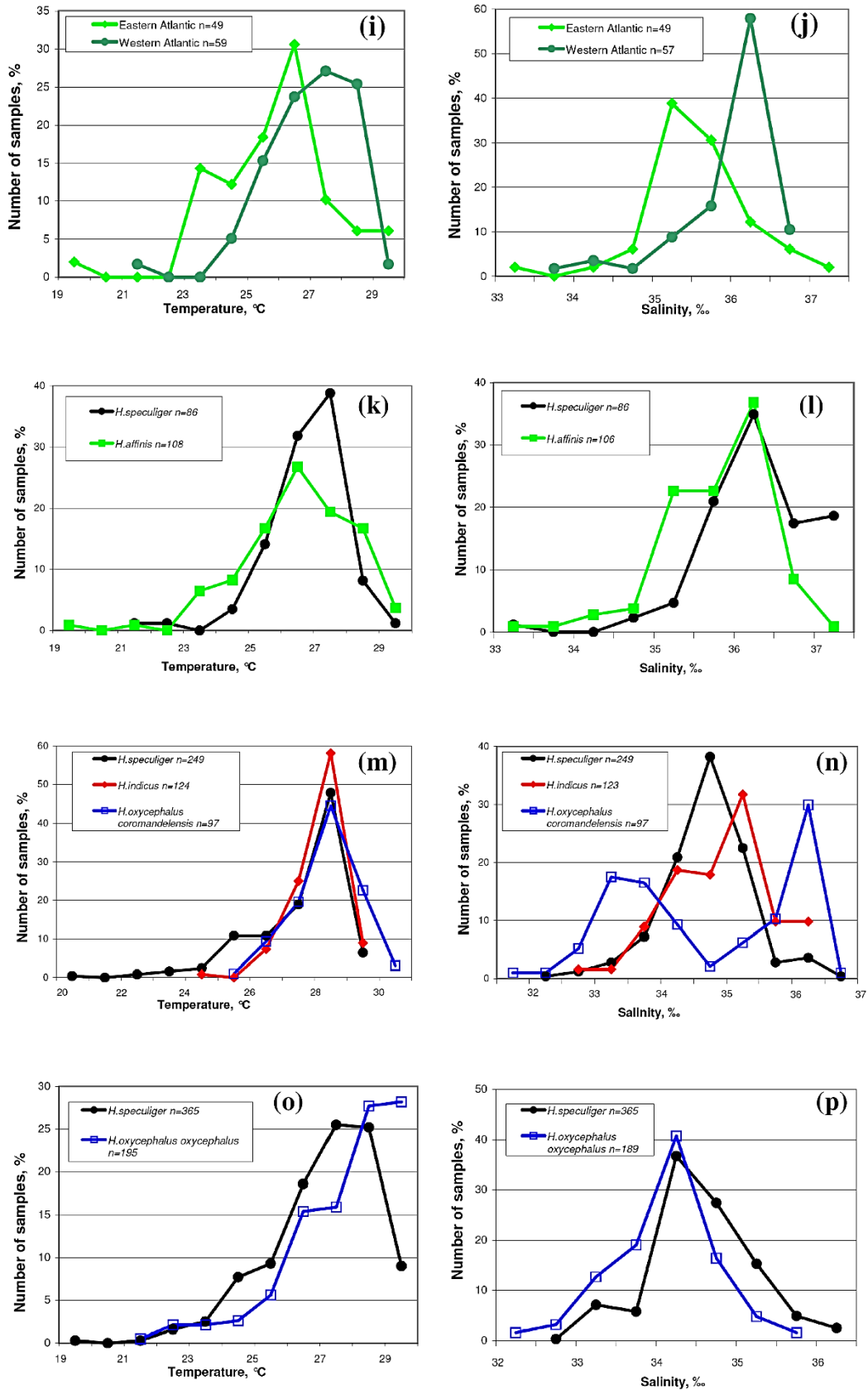
Figure S2. Continuation.

Figure S3. Distribution of flying fishes of the subgenus *Hirundichthys* in relation to temperature and salinity of surface waters. (a) all species and all regions, temperature; (b) all species and all regions, salinity; (c) *H. speculiger*, temperature; (d) *H. speculiger*, salinity; (e) *H. indicus*, temperature; (f) *H. indicus*, salinity; (g) *H. oxycephalus*, temperature; (h) *H. oxycephalus*, salinity; (i) *H. affinis*, temperature; (j) *H. affinis*, salinity; (k) Atlantic Ocean, temperature; (l) Atlantic Ocean, salinity; (m) Indian Ocean, temperature; (n) Indian Ocean, salinity; (o) Pacific Ocean, temperature; (p) Pacific Ocean, salinity.
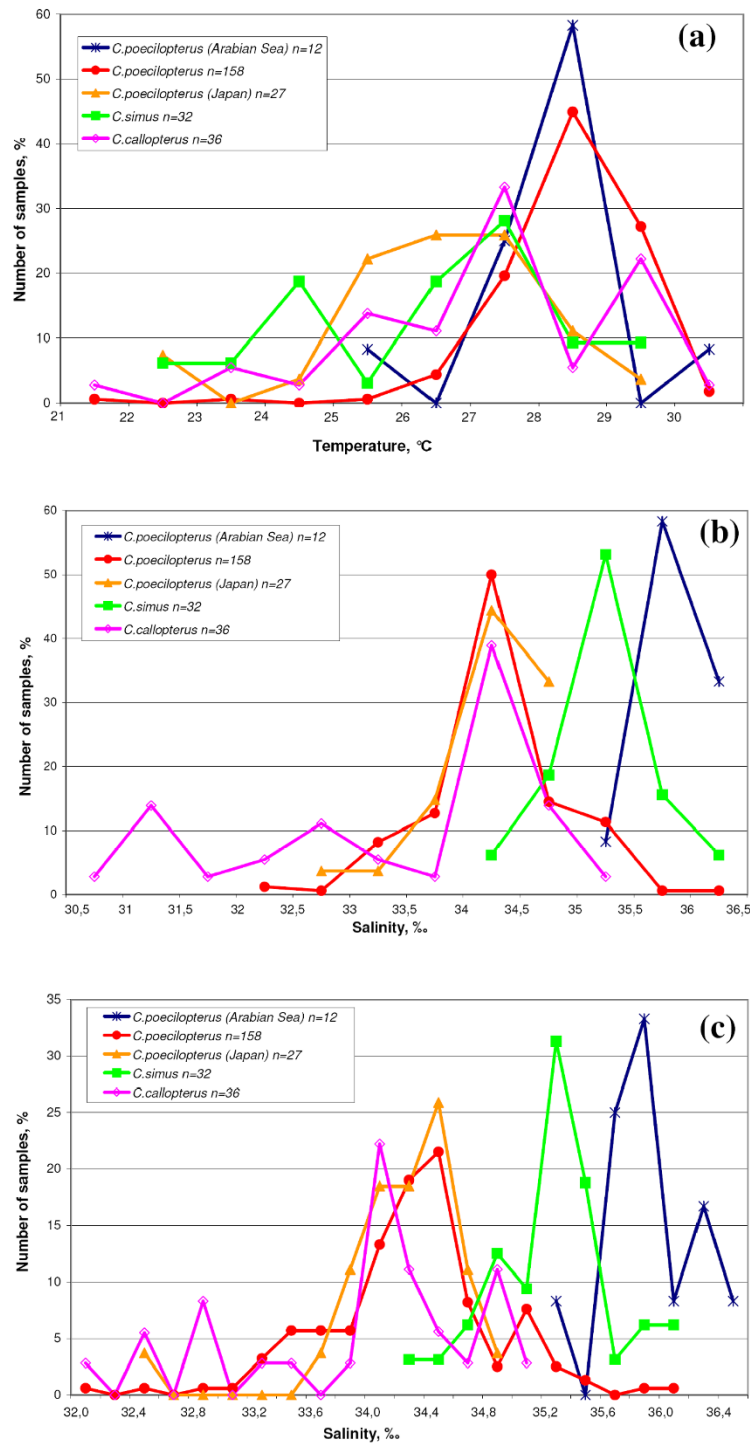
Figure S3. Continuation.

Figure S4. Distribution of flying fishes of the "*poecilopterus*" species group in relation to temperature and salinity of surface waters. (a) - all species and all regions, temperature; (b) - all species and all regions, salinity; (c) - the same as (b), but the scale interval is 0.2 ‰ (values less than 32 ‰ are not shown).
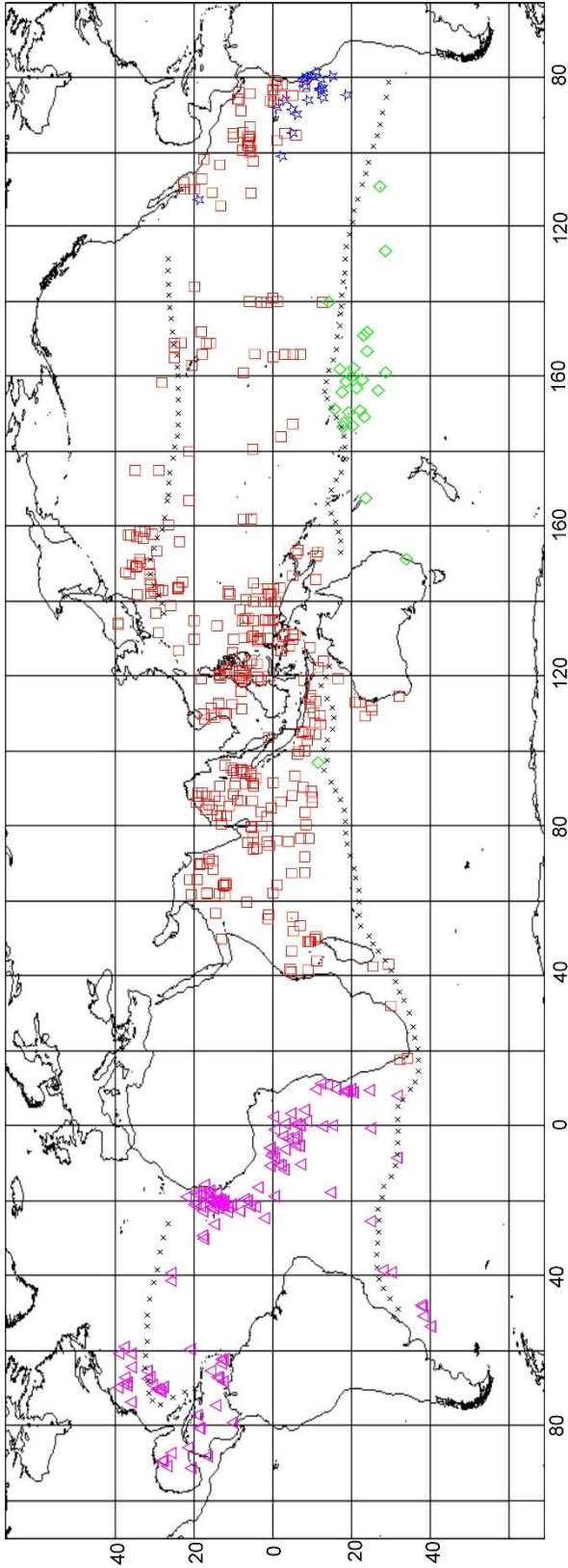
Figure S5. Distribution of flying fishes (*SL* above 100 mm) *Exocoetus monocirrhus*, *E. obtusirostris*, *E. gibbosus* and *E. peruvianus*. Legend is the same as for Figure 2.
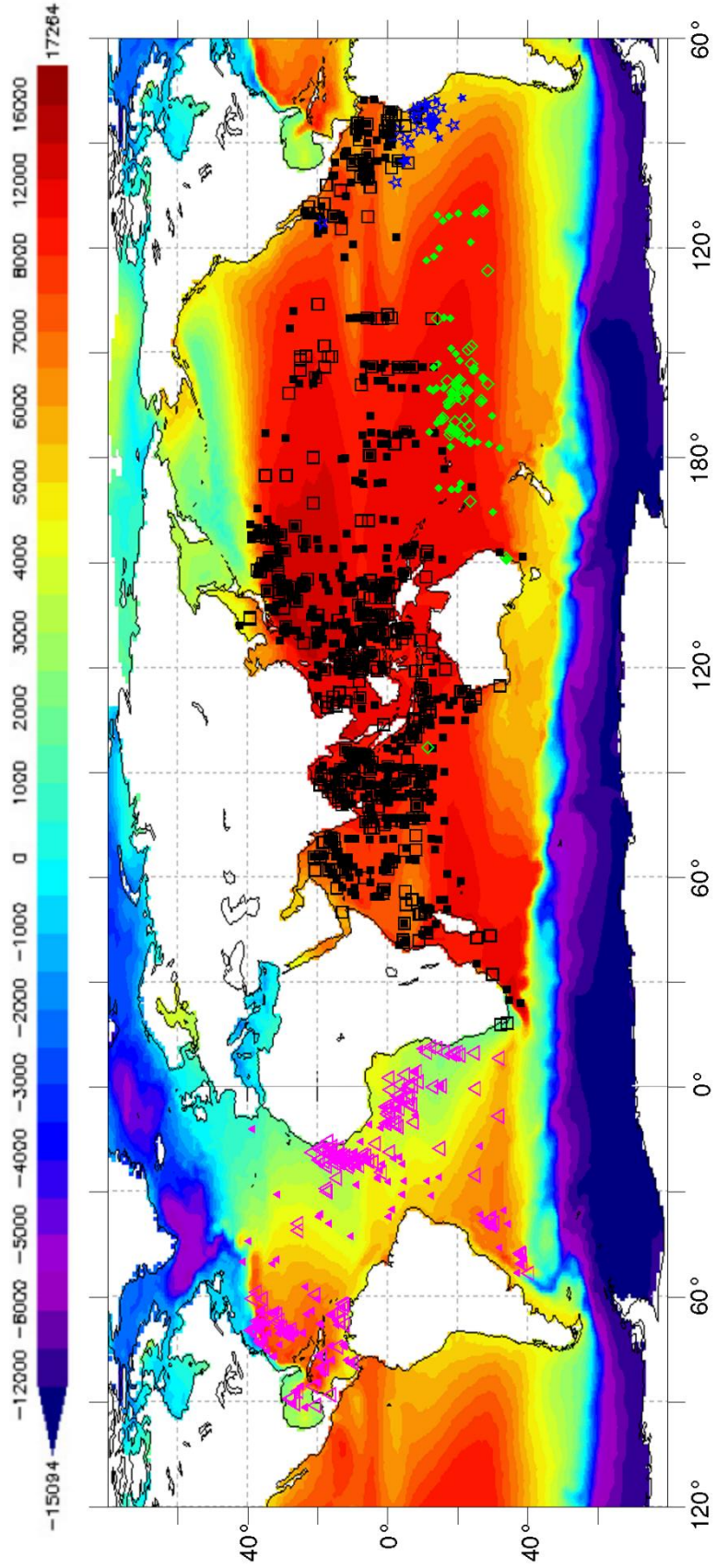
Figure S6. Distribution of flying fishes *Exocoetus monocirrhus*, *E. obtusirostris*, *E. gibbosus* and *E. peruvianus* superimposed on map of annual mean dynamic topography of sea surface for 1993-2017 (http://www.aviso.altimetry.fr/las/). Legend is the same as for Figure 2.