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Abundance and distribution of flying fishes (Exocoetidae) and flying squids (Ommastrephidae) in the Eastern Atlantic Ocean based on a large-scale visual survey

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ABSTRACT: Flying fishes (Teleostei: Exocoetidae) and flying squids (Cephalopoda: Ommastrephidae) are key components of tropical and subtropical epipelagic ecosystems, but information about their ecology, abundance and global distribution is still scant. Here we present some notes on the occurrence of flying fishes and flying squids in the Eastern Atlantic Ocean along a large-scale visual transect between 31°S and 53° N. The density of airborne specimens startled by the passage of the ship was used as a proxy of their abundance. The number of flying individuals was estimated using visual census, and individual densities were computed according to a fixed-width strip transect protocol. During the survey, 119 vessel-based transects were performed during March and April 2017, for a total surveyed length of 1540.8 km. Flying squids were observed only in a narrow latitudinal band between 17.5° and 26.1° S. Flying fish abundance, on the other hand, varied significantly along the ship's route. Maximum densities occurred between 3° and 15° S. Flying fish abundance markedly decreased around the equator and then increased again towards 8–10° N. No flying fishes were seen north of 19° N, with the only exception of 4 individuals sighted near the Strait of Gibraltar (35–36° N). No attempt was made to identify fishes or squids down to the genus or species level; however, the observed variations in size class distribution suggest a certain degree of habitat segregation between different species or life stages. Sea surface temperature was the best descriptive variable explaining the distribution of flying fishes in the area surveyed. Further work is needed to better understand the environmental factors governing the distribution of these important, but seldom surveyed, organisms.

KEY WORDS: Flying fish · Epipelagic ecosystem · Flying squid · Fish abundance · Visual census

1. INTRODUCTION

Flying fishes (family Exocoetidae) are epipelagic, subtropical to tropical species found worldwide. Adults are of variable size (10–40 cm length) and broadly divided in 2 categories: '2-wingers' (e.g. *Exocoetus* spp.) and '4-wingers' (e.g. *Cypsilurus* spp.) (Bruun 1935, Davenport 1994). The family is represented by 71 species, grouped into 7 to 8 genera (Froese & Pauly 2019), making it one of the most species-rich epipelagic fish lineages (Lewallen et al. 2018). Flying fishes are an important source of food and income for many countries around the world from the Caribbean to the South Pacific (Lewis et al. 1962, Mahon et al. 1986, Dalzell 1993, Oxenford et al. 1993, Huang & Ou 2012). Examples include coastal waters off northeast Brazil, where the fourwing flying fish *Hirundichthys affinis* is a major artisanal fishery resource (Oliveira et al. 2015); Barbados, where flying fishes compose up to 65% of the total fish catch (CRFM 2014); and the Phil-

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ippines, where flying fishes compose up to 84% of the annual catch of small-scale gillnet fisheries (Emperua et al. 2017).

Squids in the family Ommastrephidae (collectively known as 'flying squids') and some species in the families Onychoteuthidae and Loliginidae also exhibit gliding, or 'flying', behavior, most likely to evade predators (Murata 1988, Azuma 2007, Muramatsu et al. 2013, O'Dor et al. 2013). Reports of this behavior date back to 1892, and the numbers of leaping specimens can range from solitary individuals to schools of hundreds (Maciá et al. 2004). The ommastrephids comprise commercially important species such as the neon flying squid *Ommastrephes bartramii*, the Humboldt flying squid *Dosidicus gigas* and the Japanese and European flying squids (*Todarodes* spp.), although it is unclear if all these species can actually exhibit airborne jet-propulsion. Many of these species are also intensively harvested for human consumption (Bower & Ichii 2005, Roper et al. 2010), with ommastrephids together accounting for more than 70% of the world's cephalopod catch (FAO 2005).

Flying fishes and flying squids are essential components of pelagic food webs, serving both as predators (Lewis et al. 1962, Gorelova 1980, Markaida & Sosa-Nishizaki 2003, Watanabe et al. 2004, Van Noord et al. 2013) and prey for many large predatory fish (mainly Istiophoriformes, Carangiformes and several species of Scombriformes), pelagic seabirds and marine mammals (Parin 1960, Oxenford & Hunte 1999, Mori et al. 2001, Wu et al. 2006, Rudershausen et al. 2010), thus playing a key role in the functioning of many tropical food webs around the world. However, owing to their unique predator avoidance behavior and mobility, the abundance and spatial distribution of these organisms are difficult to measure directly, and options for fishery-independent surveys are limited (Oxenford 1994, Churnside et al. 2017).

The distribution of flying fishes has been studied using various methods, including net sampling (Khokiattiwong et al. 2000, Pitman et al. 2002, Casazza et al. 2005, C. Chang et al. 2012, Randall et al. 2015, S. Chang et al. 2022), acoustic surveys (Brehmer et al. 2007) or tagging studies (Mulloney 1961, Lewis 1964, Oxenford et al. 1994). Visual census techniques have also been successfully applied (Breder 1929, Plomley 1968, Parin 1981, 1983, Fréon 1992). Most research, however, has focused on the Caribbean and the Pacific; little is known about the distribution of flying fishes in the eastern Atlantic region. While the distribution patterns of the commercially important ommastrephid squids have been thoroughly studied (Jereb & Roper 2010), there have been few reports of the flying behavior of squids. Here we present the results of a survey on the abundance of flying fishes and flying squids in the Eastern Atlantic Ocean using a visual census technique, which is likely the most widely used non-invasive method for studying animal populations in both terrestrial and aquatic ecology (Thresher & Gunn 1986, Yoo et al. 2003, Murphy & Jenkins 2010, Pierucci & Còzar 2015). This information will increase our knowledge of the ecology and geographical distribution of these 2 groups of nekton in the Eastern Atlantic region.

2. MATERIALS AND METHODS

The visual survey took place in the Eastern Atlantic Ocean between 31° S and 53° N during a research cruise from Cape Town (South Africa) to Bremerhaven (Germany) during 23 March to 10 April 2017 (see Fig. 2). Flying fishes and flying squids flushed by the passage of the RV 'Akademik Tryoshnikov' were counted during regular navigation of the ship at a mean ± SD speed of 13.9 ± 1.9 knots (min. 11.2 kts; max. 15.2 kts). The number of airborne individuals, i.e. the number of flying fishes and flying squids startled by the passage of the ship, was used as a proxy of their local abundance, assuming that the proportion of individuals taking to the air at the approach of the vessel was constant throughout the survey. All observations were made in parallel by 2 observers who scanned the sea surface from the forecastle deck of the ship at about 8.5 m above sea level (Fig. 1). Due to the large size of the bow, visual observations were limited to one side of the vessel, chosen according to sun glare and wind direction (we preferentially chose the windward side as recommended by Ryan 2013).

Observations were conducted during daylight hours while the ship was underway and weather conditions were good (Beaufort sea state < 4). During each hour, observations were conducted for 30 min followed by a 30 min break. No major storms were encountered during the survey, and during the 19 d cruise, 119 transects were sampled (generally 6–7 per day).

The total survey length was 1540.8 km (mean ± SD transect length = 12.95 ± 1.11 km). The total observation period was 59.3 h. GPS start and stop position, ship heading, speed and surveyed distance were recorded using a hand-held GPS. At the start of each transect, wind speed, wind direction and sea state were recorded from the ship's weather station. Seawater environmental parameters were obtained from the Aqualine Ferrybox system that was connected to the ship's underway seawater supply and recorded

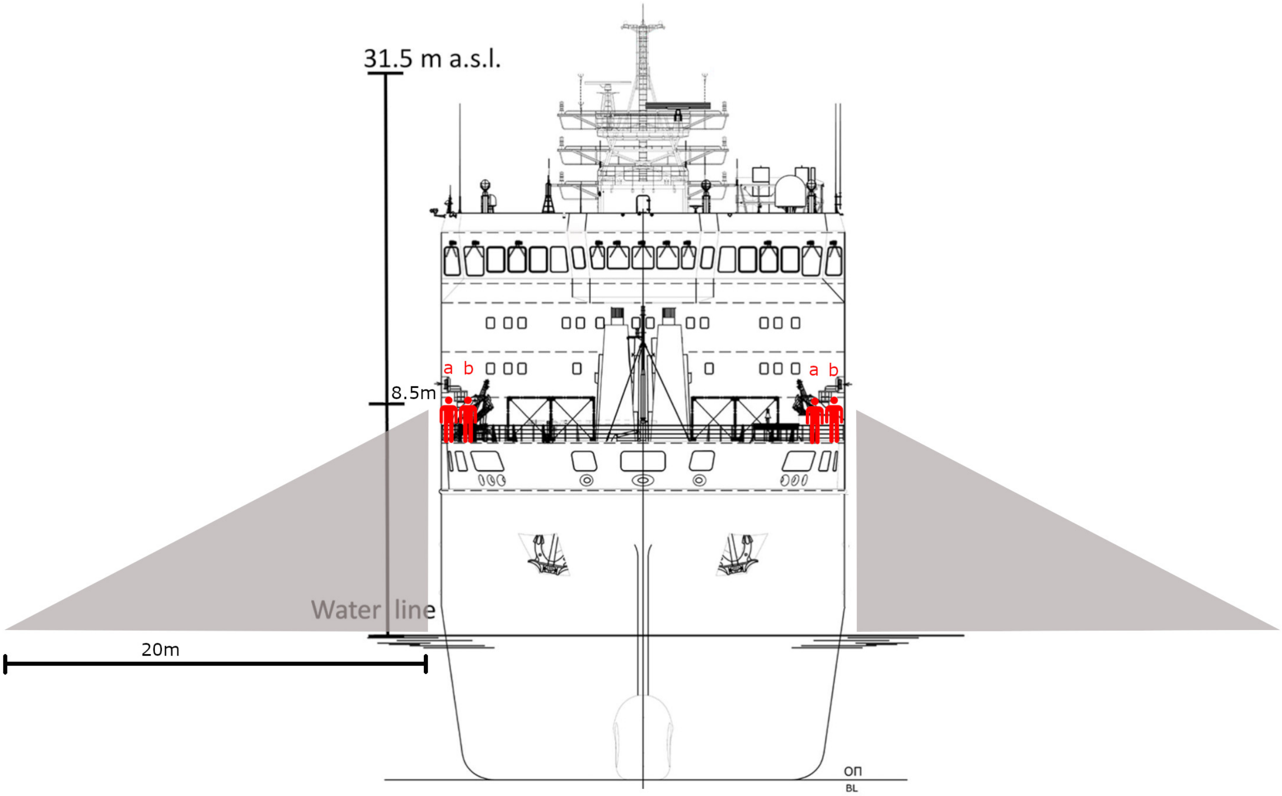

Fig. 1. The RV 'Akademik Tryoshnikov'. The left and right positions of the 2 observers (labeled a and b) are indicated in red (drawing modified by the authors). Adjusted vessel plans provided by the Arctic and Antarctic Research Institute (AARI)

environmental data at 1 min intervals (see Haumann et al. 2020 for more details). Data were then extracted and averaged across each transect. Chlorophyll *a* concentrations were recorded as $\mu g\ l^{-1}$ (calculation done in UniLux; https://aquaticsensors.com/wp-content/uploads/2022/02/1432_UniLux_2pp_V3_artwork_V2.pdf); O_2 concentrations as $\mu mol\ kg^{-1}$; sea surface temperature (SST) as °C; and salinity concentrations as PSU.

Flying fishes and squids were counted individually when numbers were small (<15), but larger groups (which reached up to 200 individuals) were estimated using photographic records. The sizes of flying fishes were visually estimated, and all individuals were allocated to 1 of 4 length categories: small (<5 cm), medium (5–10 cm), large (10–20 cm) and extra-large (>20 cm). Flying squids were always sighted in large groups of individuals of the same size (around 15–20 cm total length), so no attempt was made to classify them according to size. No attempt was made to identify the fishes or the squids to genus or species level, given the difficulty of distinguishing morphological traits during short flight times and the lack of evident external differences between many species (Parin 1981, 1983).

The abundance of flying fishes and flying squids was estimated using a standard strip-transect technique, which involves counting the number of targets detected within a pre-determined strip, outside of which the observed targets are not recorded. A fixed-width strip of 20 m was selected for this survey, as this width ensured optimal detection probability according to our observing conditions (see Fig. 1 for more details). The results were then expressed as a simple index of abundance (Eberhardt 1978). Fish and squid counts were converted into density values (D) by dividing the total number of sighted individuals by the effective area surveyed in each transect, using the following equation:

$$D_i = \frac{n_i}{W \times L_i} \quad (1)$$

where n is the number of individuals counted in transect i, L is the length of transect i, and W is the fixed strip width (20 m). The density of flying fishes and flying squids was computed for all transects and expressed in numbers of ind. km^{-2}.

Spatial and statistical analyses were performed with the R software v. 4.2 (R Core Team 2020) 'leaflet' (Graul 2016) and 'tidyverse' packages (Wickham et al. 2019). Non-normal distribution of the data was evaluated by the Shapiro-Wilk test. Spearman's non-parametric correlation coefficient was used to test significant correlations (i.e. wind speed, salinity, temperature). The significance level was set at $\alpha = 0.05$. The data collected simultaneously by the 2 observers were compared using the Mann-Whitney test for equal medians, and no statistical difference was found ($p = 0.8387$). In addition, the 2 sets of data were highly correlated ($r = 0.9255$, $p < 0.0001$, permutation $p = 0.0001$, $n = 119$); therefore, final density values were computed by averaging both counts performed simultaneously by the 2 observers during all transects.

3. RESULTS

In total, 6187 flying fishes and 494 flying squids were counted during the survey. Flying squids were sighted exclusively in 12 transects located between 26° and 17.5° S. No squids were sighted north of 17° S (Figs. 2b & 3). Squids were often observed taking off in schools of ~10–20 individuals. In the transects where squids were observed, the mean ± SD density was 138.6 ± 172.4 ind. km^{-2}. Flying squid densities ranged between 1.9 and 459.2 ind. km^{-2}, with maximum densities peaking around 20–21° S (Figs. 2b & 3).

Flying fishes were sighted in 56.3% of the transects (67 of 119), with densities ranging between 1.8 and 1741.4 ind. km^{-2} and a mean ± SD fish density of 194.3 ± 381.9 ind. km^{-2} along the entire ship route (median density = 8.95 ind. km^{-2}). Isolated flying individuals started to be sighted soon after departure from Cape Town at about 30° S (Figs. 2a, 4 & 5). Densities markedly increased in tropical waters, reaching maximum observed densities between 15° and 3° S. Flying fish abundance decreased around the equator between 1° S and 5° N (with SST >29°C), and then increased again between 8° and 10° N (Figs. 2a, 4a & 5). No flying fishes were seen north of 19° N, except for 4 individuals sighted around 35–36° N near the Strait of Gibraltar.

Most flying fishes (81.1%) were medium-sized (5–10 cm), 9.7% were large, 8.8% were small, and only 25 individuals (0.4% of the total) were extra-large (>20 cm). Small fishes were more common at higher latitudes in the southern hemisphere (Figs. 4b & 5), while bigger fishes were generally sighted at lower latitudes and most abundant between 9° and 10° N (Figs. 4b & 5).

The abundance of flying fishes was positively correlated with SST ($r_s = 0.782$, $p = 1.58 \times 10^{23}$) and negatively correlated with oxygen levels ($r_s = -0.79$, $p = 3.55 \times 10^{24}$), which is unsurprising given the almost perfect collinearity between these 2 environmental variables. The highest fish densities occurred at SSTs between 25 and 30°C and surface oxygen concentrations between 247.4 and 237.5 µmol kg^{-1}. No significant correlation was found between the observed fish abundance and wind speed, salinity or chlorophyll *a* concentrations. Flying squids occurred in a relatively narrow latitudinal band with SSTs between 21 and 24°C.

4. DISCUSSION

Surveying the abundance of highly mobile epipelagic organisms such as flying fishes is challenging, and options for fishery-independent surveys are limited (Oxenford 1994, Churnside et al. 2017). Shipboard counts have been used as an index of flying-fish abundance since the early 1930s (e.g. Breder 1929, Plomley 1968), and more recently, they have been used to study the foraging habitats of seabirds and regional differences in ocean productivity (e.g. Jaquemet et al. 2005, Weber et al. 2021). Using the number of airborne individuals as an index of flying fish abundance, however, assumes that the proportion of individuals that takes to the air as an anti-predator response at the approach of a survey vessel is constant for that vessel (Oxenford et al. 1995a). This was assumed in all previous surveys of flying fish abundance (e.g. Zuyev & Nikol'skiy 1981, Nesterov & Bazanov 1986, Khokiattiwong et al. 2000). However, as noted by previous authors, the proportion of flying fishes taking to the air can be largely influenced by the vessel size, type, speed and engine revolutions (Zuyev & Nikol'skiy 1981, Fréon 1992), as well as by the direction of the vessel in relation to wave and wind direction (Breder 1929, Hubbs 1933, Ryan 2013). Flying behavior is much less studied in the squids, and factors affecting the likelihood of flying, inter-species differences in flying and the relation between number of flying squid and abundance in a given area are not well known.

It is thus important to keep in mind that the number of organisms sighted during a ship-board visual survey is only indicative of the real density values since this method is based on some simplifying assumptions. For example, 2 fundamental assumptions are that (1) the detection probability within the transect width is 100%, and that (2) all individuals present in a given area will be flushed by the passage of the ship. Regarding the first assumption, a strip-width of 20 m

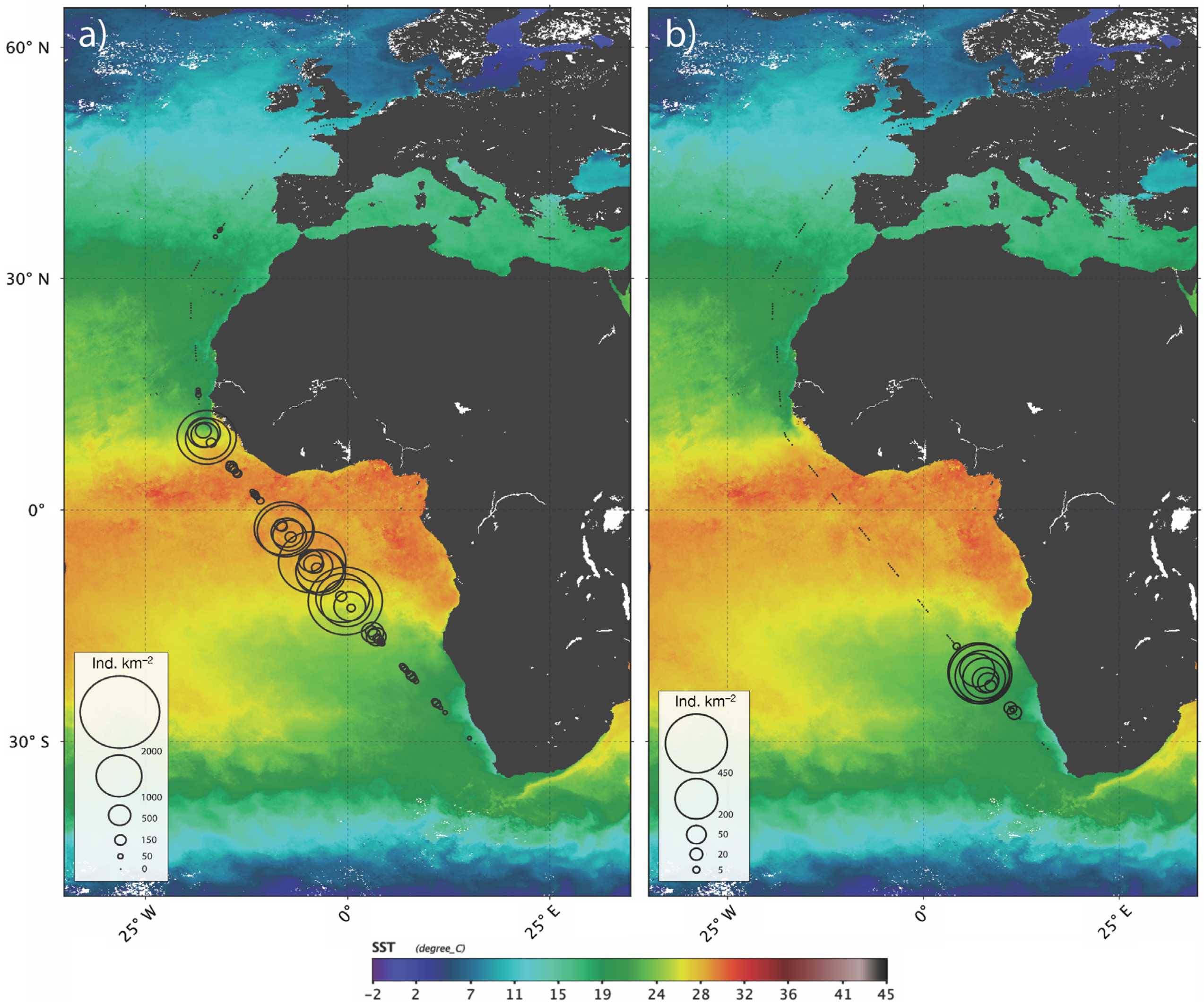

Fig. 2. Eastern Atlantic Ocean, showing the density distribution of (a) flying fishes and (b) flying squids expressed as ind. km^{-2} overlaid on Aqua MODIS SST 32 d (22 March to 22 April 2017) composite image (11µ daytime; 9 km spatial resolution) processed using SeaDAS 7.5 software. The size of the circles is proportional to the observed fish or squid density on a logarithmic scale

was selected for this survey, as this was considered to offer the best viewing conditions according to our elevation above the sea, ship speed and observation conditions encountered during the survey (Vighi et al. 2022). During the survey, we also empirically observed that fish/squid outside of this strip were not disturbed by the passage of the vessel and did not generally become airborne as the ship approached. Regarding the second assumption, several individuals within the strip width were seen escaping the ship underwater without exhibiting flying behavior. Previous authors estimated that roughly 20–25% of the actual number of flying fishes present in a given area become airborne when a ship approaches (Zuyev & Nikol'skiy 1981, Parin 1983). Thus, our estimated densities are highly conservative and should be considered as an underestimation of the real density values.

Morphological similarities among species and fast aerial gliding movements make flying fishes extremely difficult to identify *in situ* during visual observational surveys (Parin 1983). Species identification can be further complicated if a large number of species co-occur, the taxonomic differences among species are uncertain, some species remain undescribed, juveniles do not resemble the adults, and no reliable field identification guides are available (Oxenford et al. 1995a, Shakhovskoy & Parin 2019, 2022, Gladston et al. 2020). For all of these reasons, we made no attempt to identify leaping specimens down to the genus or species level, although it could be assumed that most of the smallest individuals

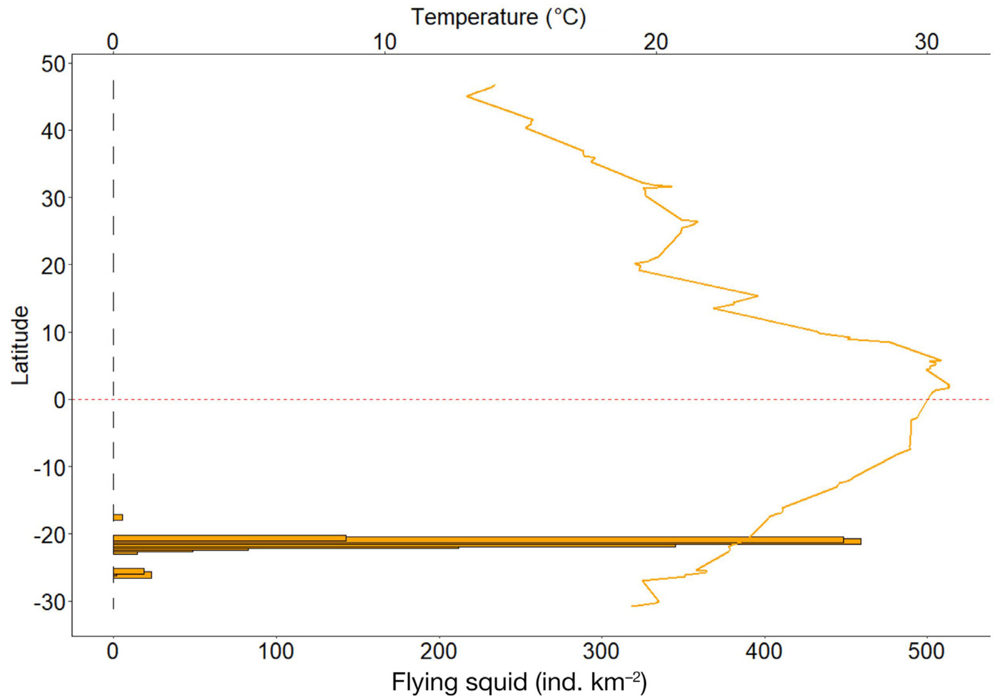

Fig. 3. Abundance of flying squids (orange bars) as a function of latitude (°) expressed in number of sighted ind. km^{-2} over the entire dataset. Overlaid sea surface temperature values (°C) were recorded by the Aqualine Ferrybox system connected to the ship's underway seawater supply which recorded environmental data at 1 min intervals, averaged across the duration of each transect (see Haumann et al. 2020 for more details). The horizontal dashed line corresponds to the equator

(< 10 cm) were juveniles, while larger fish were adults belonging to various species (Davenport 1990, Oxenford et al. 1995b,). In this regard, the observed differences in size-class distribution (Figs. 4b & 5) are likely due to inter-specific habitat differences (Shakhovskoy 2018) or to spatial segregation between life stages or developmental conditions (Oxenford et al. 1995b, Randall et al. 2015).

Minor morphological differences between some species mean that increased scrutiny or photographic techniques are required for accurate flying fish identification (Parin 1996, 1999, Parin & Belyanina 1998, 2002a,b, Parin & Shakhovskoy 2000). It is therefore prudent to always complement visual surveys with other approaches such as drift net, night-lighting or dip-net sampling, to better assess species-specific differences in the relative abundance and distribution patterns. In addition, visual census techniques are highly subjective, and fish counts always depend on a number of factors, including visibility conditions, observer fatigue and experience level. Future improvements to reduce subjectivity in fish counts could consider applying camera-based systems and/or innovative remote sensing methods (Churnside et al. 2017) such as those recently applied to the automated detection of floating litter using optical data and artificial intelligence techniques (e.g. de Vries et al. 2021).

The distribution and abundance of epipelagic organisms are partly determined by oceanographic conditions (Shakhovskoy 2018), although in a smaller-scale survey performed in the Caribbean Sea, a lack of correlation between flying fish abundance and surface water characteristics was previously reported (Oxenford et al. 1995a). In contrast, Churnside et al. (2017) reported that in the northern Gulf of Mexico, flying fishes were found most often off the continental shelf in warm water with low chlorophyll concentrations. Our survey spanned a much larger latitudinal gradient and our results are in general agreement with many other studies, showing that sea surface temperature is the best descriptive variable to explain the global distribution of flying fishes (Khokiattiwong et al. 2000, Randall et al. 2015, Churnside et al. 2017, Lewallen et al. 2018, Palo et al. 2019) and flying squids such as *Ommastrephes bartramii* (Chen et al. 2007, 2010, Yu et al. 2015, 2019, Wang et al. 2023). Our data clearly show that the number of flying fishes sighted in the Eastern Atlantic Ocean was highest where the SST was 25–30°C (Figs. 2a & 4a), which is consistent with their known habitat preferences (Shakhovskoy 2018, Weber et al. 2021). Whether or not the projected changes in SST and chlorophyll patterns will have an influence on the habitat range and global distribution of flying fishes

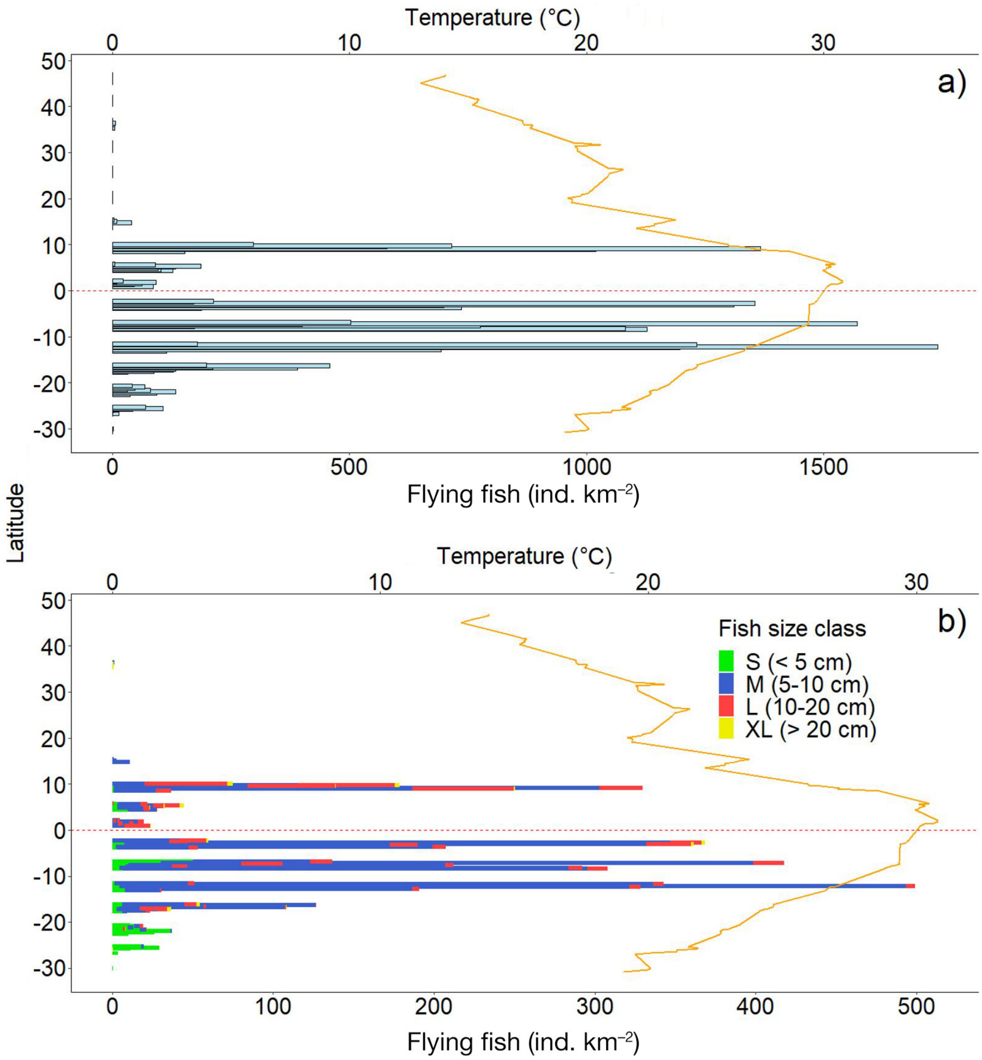

Fig. 4. (a) Abundance of flying fishes (blue bars) as a function of latitude (°) expressed in number of sighted ind. km^{-2} over the entire dataset. Overlaid sea surface temperature values (°C) were recorded by the Aqualine Ferrybox system connected to the ship's underway seawater supply which recorded environmental data at 1 min intervals, averaged across the duration of each transect (see Haumann et al. 2020 for more details). (b) Relative abundance of the 4 size classes of flying fishes (S: small; M: medium; L: large; XL: extra-large) as a function of latitude (°) expressed as the number of sighted ind. km^{-2}. In both panels, the horizontal red dashed line corresponds to the equator

is currently unknown (Komatsu et al. 2014, Lewallen et al. 2018).

Flying fishes have been recently found to ingest substantial concentrations of microplastics in the eastern Pacific (Van Noord et al. 2013, Gove et al. 2019). It has also been suggested that they can be used as indicators of trophic transfer of microplastics to higher trophic levels like tuna (e.g. Chagnon et al. 2018, Abidin et al. 2021), especially in areas where their distribution overlaps with areas of high plastic concentration. Microplastics are now ubiquitous in oceanic ecosystems, including the eastern Atlantic Ocean (Kanhai et al. 2017, Suaria et al. 2020, 2023), and ingestion by pelagic species is common and widespread (Savoca et al. 2021). It is unclear, however, if ingested plastics or microfibers are retained and bioaccumulate within the food chain or if they can affect organism survival. In addition, flying fishes typically spawn on floating material such as *Sargassum* seaweed (Breder 1938, Hall 1956, Vijayaraghavan 1973, Kovalevskaya 1982, Lao 1989, Oxenford et al. 1993, Parin & Lakshminaraiana 1993, Andrianov & Lakshminaraina 1994). Within this context, the increase in floating plastics in the world's oceans might represent a potential increase in the availability of spawning substrata for flying fishes, whose ecological consequences are currently unknown (Hunte et al. 1995).

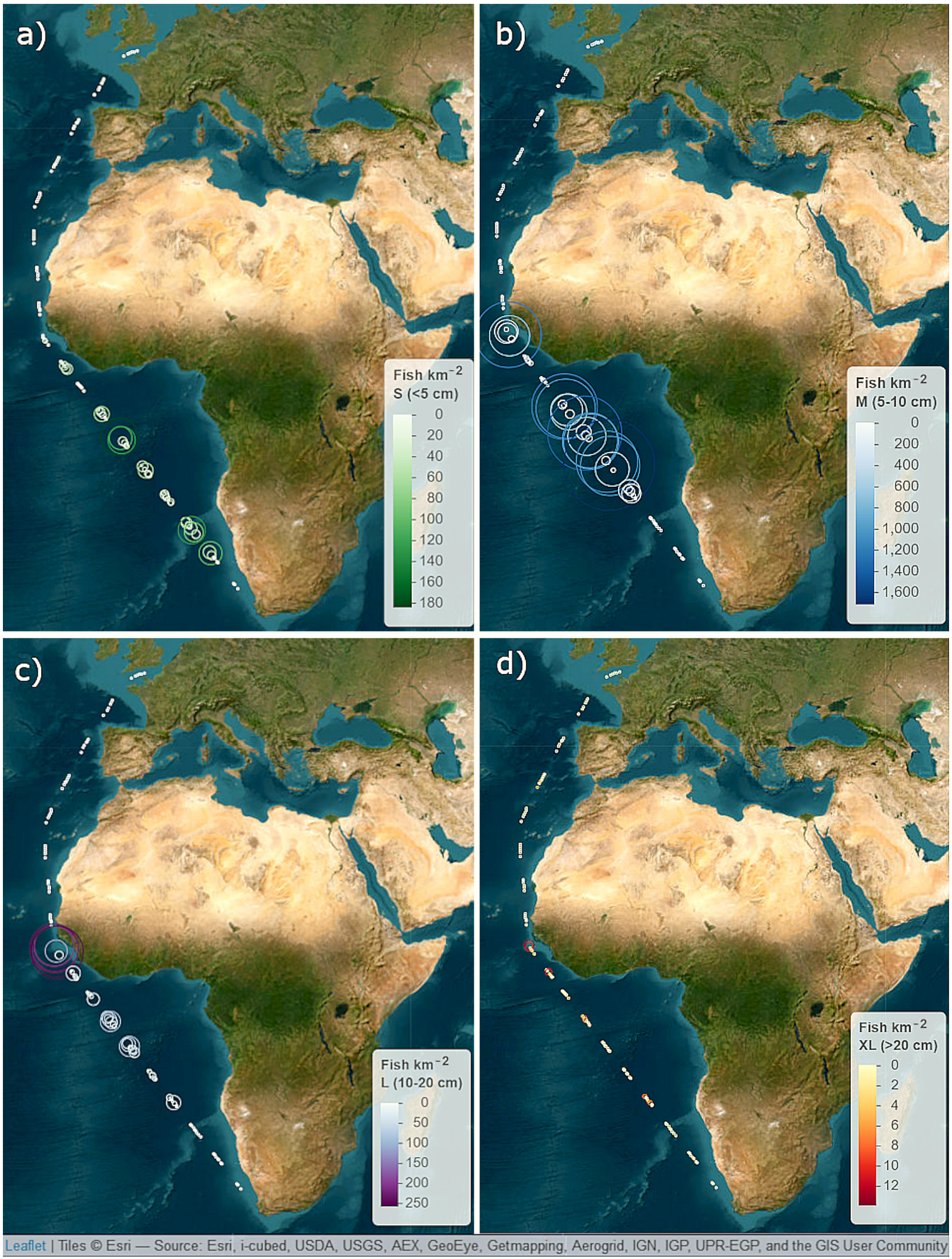

Fig. 5. Eastern Atlantic Ocean showing the observed density and distribution of (a) small (<5 cm), (b) medium (5–10 cm), (c) large (10–20 cm) and (d) extra-large (>20 cm) flying fishes expressed as the number of sighted ind. km^{-2}. The sizes and the colors of the circles are proportional to the observed fish density on a logarithmic scale

Flying fishes are a central mid-trophic component of tropical epipelagic food webs. They also represent a major fishery resource for many countries around the world. Wild populations are exploited not only for local consumption but also as bait for long-line fishing and for their eggs, which are marketed as a local delicacy in many Asian markets (S. Chang et al. 2012). Nevertheless, flying fish stocks are still data deficient, and clear knowledge about their ecology and global distribution is currently missing. Some examples of stock depletion have been recently documented in Indonesia, where flying fish landings dropped dramatically in recent years (Syahailatua 2006, Najamuddin et al. 2020). This indicates an urgent need for further investigations and proper sustainable management actions. Eco-label companies such as the Marine Stewardship Council (MSC) could have an interest in these species, potentially playing a role in the future sustainable exploitation of these resources (Pierucci et al. 2022).

To our knowledge, very few studies have reported on flying fish distributions in the Eastern Atlantic Ocean and even fewer data are available about the occurrence of flying squids in this area (Maciá et al. 2004). Ommastrephids are relatively well-studied due to their economic importance as a fishery resource. For example, Roper et al. (2010) reported the occurrence of several species of ommastrephid squids in our study area; however, since we could not identify squids down to species or genus level, it is currently unclear which squid species can actually exhibit the flying behavior we observed during our survey. In addition, the flying behavior has been much less studied in squids than in flying fishes, and the factors affecting the likelihood of a flying squid taking off, and how this is related to the actual squid abundance in a given area, are basically unknown.

Although many factors can influence the number of flying organisms counted from a research vessel (Parin 1983), shipboard observations of flying individuals flushed by a ship's passage remain one of the best non-invasive and low-cost methods to assess the abundance and distribution of these elusive species. In this paper, we provided novel information about the occurrence of flying fishes and flying squids in the Eastern Atlantic region. However, ecological components that may be relevant to explain the distribution of these organisms were not investigated in our manuscript and will need to be addressed by future studies. Expanding our baseline with larger and more detailed data sets on the spatiotemporal variability in flying fish distribution will provide critical information that can be used to further improve our understanding of population dynamics and food web interactions in the high seas.

Data availability. All data on which this manuscript is based are made available in the Supplement at www.int-res.com/articles/suppl/m725p045_supp.xlsx. Further enquiries or data requests should be directed to the corresponding author.

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