Research Article

Acoustic observations of the vertical distribution and latitudinal range of small pelagic fish schools in the Midriff Islands Region, Gulf of California, Mexico

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ABSTRACT. Within the Gulf of California, the Midriff Islands Region (MIR) is characterized by mixing conditions of water masses that lead to high primary productivity, which fosters the presence of sardines, anchovies, and their predators. Using acoustic tools, we analyzed the presence and characteristics of schools detected in three surveys carried out in late spring of 2012 and 2013 and early summer of 2014. We sought to relate changes in the geographical distribution of schools with Sea Surface Temperature (SST) and Net Primary Productivity (NPP). The largest number of schools was observed in 2012, coinciding with the highest and most extensive NPP, while the following years were associated with lower NPP coupled with a lower number of detections. During the study period, the Ballenas-Salsipuedes Channel and its area of influence showed the lowest SST and higher NPP even toward the summer as compared to the rest of the MIR, favoring the presence of fish schools and supporting the importance of this site as a feeding center for these species. As for their vertical distribution, it was found that during the day schools reach greater depths, while during the night these are concentrated in surface waters. However, no differences in size, density, or other characteristics were detected either between periods or between years. Finally, we found a high proportion of schools during the night (61%), which departs from the typical nocturnal dispersal behavior described for similar species in other areas.

Keywords: schools, vertical distribution, fisheries acoustics, small pelagic fish, Gulf of California.

INTRODUCTION

The Gulf of California (GC) is a semi-enclosed sea that displays high diversity and abundance of marine life, which support various industrial and small-scale fisheries (Álvarez-Borrego, 2010). Its high biological productivity is attributed to three main fertilization mechanisms: wind-induced upwelling events, tidal mixing, and exchange of water masses between the GC and the Pacific Ocean. The coastal areas with the highest biological productivity are those subjected to strong tidal mixing (Case & Cody, 1983; Álvarez-Borrego & Lara-Lara, 1991; Cudney-Bueno *et al*., 2009).

According to its oceanographic features, the Gulf of California can be divided into various regions. Lavín & Marinone (2003) have established six areas, including the so-called archipelago zone or Midriff Islands Region (MIR) (Fig. 1), characterized by several narrow channels and plains which reach maximum depths ranging from 300 to 1600 m. The presence of large islands such as Ángel de la Guarda and Tiburón, which gives its name to this area, produce the mixing of water masses as a result of extensive and strong tides caused by the compression of water flowing through narrow areas. In turn, these lead to the intensification of tidal currents, giving rise to turbulence so intense that subsurface water masses can be observed at the surface (Lavín & Marinone, 2003; Álvarez-Borrego, 2010).

Studies of the concentration of photosynthetic pigments on the sea surface have shown that, unlike the other GC regions, high values are maintained around the Midriff Islands due to the combination of low temperatures and high surface concentration of dissolved inorganic carbon and nutrients (Álvarez-Borrego, 2002; Escalante *et al*., 2013). This high prima-

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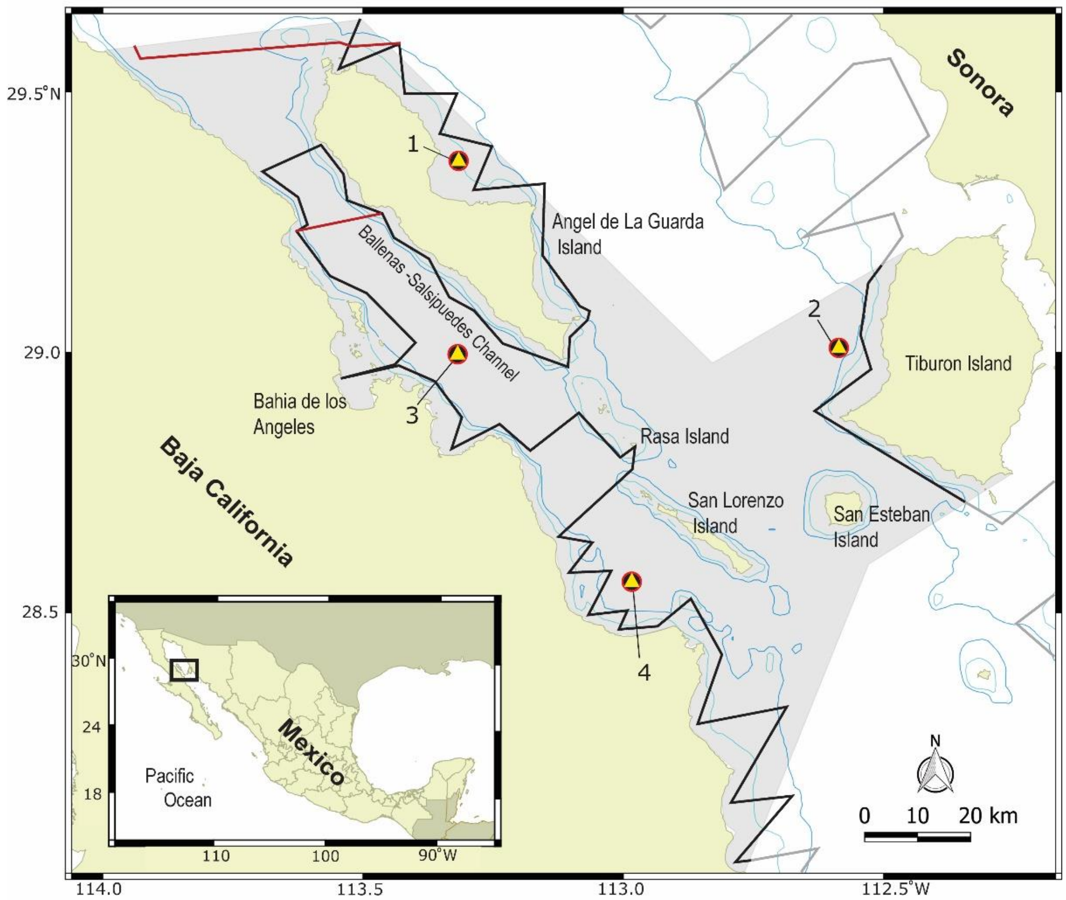

Figure 1. Midriff Islands Region in the Gulf of California (shaded area), with the generalized survey design used in the three years inside of MIR (black line) with some modifications in 2014 due to logistics (red line). The yellow triangles indicate the locations where the time series of Sea Surface Temperature and Net Primary Productivity were extracted. 1: East coast of Ángel de la Guarda Island; 2: West coast of Tiburón Island; 3: Central region of Ballenas-Salsipuedes Channel; 4: San Rafael Bay.

ry productivity is maintained throughout the year, favoring large numbers of sardines, anchovies, seabirds and marine mammals (Tershy *et al*., 1991; Álvarez-Borrego, 2010).

Several species of sardines and anchovies are caught in the small pelagic fishery in the Gulf of California, and the high fishing volumes recorded have made this the most important fishery resource in Mexico in recent decades (Nevárez-Martínez *et al*., 2006; Martínez-Zavala *et al*., 2010). The Pacific sardine, *Sardinops sagax*, is the main species caught, representing over 70% of landings, although other species such as northern anchovy (*Engraulis mordax*), Pacific thread herring (*Opisthonema libertate*, *O. bulleri* and *O. medirastre*), chub mackerel (*Scomber japonicus*), Pacific anchoveta (*Cetengraulis mysticetus*), round herring (*Etrumeus teres*), and Pacific jack mackerel (*Trachurus symmetricus*) can also be fishing targets (Ponce-Díaz & Lluch-Belda, 1990).

Some authors stress the importance of the MIR for the GC small pelagics, in particular for S. *sagax*, since this area is considered as its dispersal center (Nevárez-Martínez *et al*., 2006; Martínez-Zavala *et al*., 2010). It has been suggested that the migration of sardine schools into this area is associated with the rise in seawater temperature in late spring, in particular at the Ballenas-Salsipuedes Channel (Sokolov, 1974; Cisneros-Mata *et al*., 1987) where the average annual water temperature is relatively lower than in the rest of the GC.

The spatial distribution of small pelagic fish within the GC has been documented mainly using fishery data; this information provides no details on the vertical distribution of schools in the water column or on the aggregation and dispersal dynamics. Therefore, in the present work, we use acoustic tools and methods to analyze the presence and characteristics of small pelagic fish schools in the MIR in late spring and early summer for three consecutive years. The geographical distribution of the schools detected is described, discussing their possible relationship with sea surface temperature and net primary production. Besides, the presence of many schools during nighttime is reported.

MATERIALS AND METHODS

The study was carried out in the Midriff Islands Region of the Gulf of California (Fig. 1), which is located between ~28ºN and ~29.5ºN (Lavín & Marinone, 2003).

Environmental data acquisition

Sea surface temperature (SST) and net primary production (NPP) data were analyzed from satellite images for the period 2012-2014. SST (ºC) data were obtained from the NASA web page OceanColorWeb (https://oceancolor.gsfc.nasa.gov/). Specifically, eight-day averaged nighttime images with 4×4 km spatial resolution derived from MODIS-Aqua remote sensing reflectance data were used.

The net primary production (mg C m^{-2} d^{-1}) data were downloaded from the University of Oregon web page Ocean Productivity (http://www.science.oregonstate.edu/ocean.productivity/index.php), with the same temporal resolution as SST but with a 9×9 km spatial resolution. NPP is calculated using the vertical generalized production model (VGPM) of Behrenfeld & Falkowsky (1997), which, in addition to chlorophyll concentration, combines other variables such as daylight irradiance over a 24 h cycle, depth of the euphotic zone, and rate of maximum inorganic carbon fixation per unit of phytoplankton biomass.

SST and NPP time series were obtained and plotted for four sites within the study area: 1) eastern margin of Ángel de la Guarda Island, 2) Tiburón Island west coast, 3) central part of the Ballenas-Salsipuedes Channel and 4) vicinity of San Rafael Bay, in order to explore the seasonal behavior of both variables (Fig. 1).

Also, to depict the prevailing environmental conditions and their spatial distribution during surveys, maps of SST and NPP in the MIR were produced by averaging the weekly images matching the periods of acoustic data acquisition mentioned below. On the other hand, given the proposed relationship between annual small pelagics fishery catches in the GC and the anomalous sea warming (Lluch-Belda *et al*., 1986), the Oceanic Niño Index (ONI, http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) was reviewed to confirm that the years of observation do not coincide with any anomaly in the Pacific Ocean that could lead to unusual results.

Acoustic data acquisition

Data from three acoustic surveys focused on small pelagic fish carried out in late spring 2012 (May 16-26), and 2013 (May 4-18) and early summer 2014 (June 22 to July 1) were analyzed. The survey design followed the specifications of the International Council for the Exploration of the Sea (Simmonds & McLennan, 2005). Parallel transects were drawn perpendicular to the coastline in the eastern margin of the GC, covering depths down to the 200 m isobaths, approximately; in the western margin, where the continental shelf is narrow, the transects followed a zig-zag pattern (Fig. 1). The surveys were conducted onboard the research vessel "BIP XI" of Mexico's National Fisheries Institute (INAPESCA), which has a Simrad EK60 scientific echosounder with a hull-mounted 38 kHz transducer (ES38-12, 12° circular beamwidth). Before each survey, the echo sounder was calibrated with a 38.1 mm diameter tungsten carbide sphere according to the standard procedures described in Simmonds & MacLennan (2005). The navigation speed was 8 knots (kn); the ping rate was variable, depending on the bottom depth (<50 m = 0.25 s; 50-100 m = 0.5 s; 100-150 m = 0.75 s; 150-200 m = 1 s; >200 m = 2 s). The pulse duration was 512 m s^{-1}, and the transmission power was 1000 W.

We sought to maintain a similar sampling effort in all years. Each day, the prospection started at 6:00 PM and lasted until 3:00 AM the next day, although frequently lasted until 6:00 AM and occasionally started before 6:00 PM in order to record acoustic data during twilight. An average of three fishing hauls was carried out every night using a mid-water trawl (16 m horizontal and 12 m vertical opening; mesh size of 19 mm at the codend). When putative small pelagic fish schools were observed, hauls were done in the opposite direction of the prospection (at 3 kn during 30 min) targeting the detected schools. The species composition was obtained from a sample of each haul.

Digital echograms were stored in the echosounder manufacturer raw data format and later converted to HAC files (ICES, 2005) for processing with the Movies+ software (Berger *et al*., 2005). When needed, the detected bottom depth was corrected manually to prevent errors in the detection algorithm that would lead to an over- or underestimation of the acoustic energy in the water column. Acoustic school data were obtained (from now on referred to as schools) using the shoal echo-integration tool of Movies+. Based on previously defined size and energy thresholds, a set of detections with vertical and horizontal continuity across the water column are accepted as a school by the recognition algorithm (Diner *et al*., 2003). Thresholds were initially set, based on the acoustic and morphological properties of small pelagic fish schools from other regions, to get a proper delimitation of the echo traces as reported in the literature (Reid, 2000; Petitgas *et al*., 2003; Zwolinski *et al*., 2007). As different conditions prevailed in this case, however, the thresholds were modified to obtain adequate shoal recognition and delimitation (Table 1).

Each recognized school was validated visually to avoid counting non-fish groups (*e.g.*, zooplankton swarms or zooplankton scattering layers).

In order to determine the time of the day when schools were detected, the times of sunrise and sunset were calculated, as well as the nautical twilight, according to the mean position of the vessel in each day using an algorithm from the U.S. National Oceanic and Atmospheric Administration (NOAA). This additional information was later used to explore possible differences in the characteristics of schools between day and night. Before comparing school descriptors, normality was tested, and the Mann-Whitney test was done accordingly.

Finally, the potential relationship between the number of schools detected and environmental conditions was also investigated. To this end, we obtained the SST and NPP values temporally and spatially associated with the schools detected. From the histogram of values obtained, two class intervals were defined for each variable, and the number of schools in each combination was counted. Using the number of schools as a response variable and SST and NPP classes as predictive variables, generalized linear models (GLM) were applied using the Poisson distribution and its canonical link function (log). Satellite images, maps, and statistical analyzes were performed in the R programming language environment (R Core Team, 2017).

Table 1. Threshold values used for the recognition of schools in Movies+.

Settings	Min value	Max value
Recognition threshold (dB)	-55	0
σ_{ag} (m^2)	0.006	100
Height (m)	1	300
Length (m)	3	926
Area (m^2)	5	500,000
Density (dB)	-50	0
Queue threshold (dB)	-20	-17

RESULTS

The SST time series in the four sites selected in the study area showed similar behavior in the three years, with higher temperatures in summer (~30°C) *vs*. winter (~15°C) (Fig. 2a). In general, SST is slightly lower at the Ballenas-Salsipuedes Channel and San Rafael Bay, relative to sites close to the islands; differences became more pronounced in the summer. Figure 2 also shows the acoustic sampling periods for the three surveys, revealing that these occurred at different times in the annual cycle, leading to different temperature conditions in each.

Concerning primary production, there is a high variability within and between the four sites selected, so that a seasonality process is less evident. However, the three years analyzed showed peak values during the first half of the year, toward the spring, and to a lesser extent in the autumn of the years 2013 and 2014. In general, the sites in the Ballenas-Salsipuedes Channel show higher productivity values relative to those in the vicinity of the islands (Fig. 2b).

The spatial distribution of SST in May and June, averaged over 15-day periods, show a very similar pattern across the three years studied. The lowest temperatures were recorded in the Ballenas-Salsipuedes Channel and its area of influence and between Ángel de la Guarda and Tiburón Islands. SST raises steadily in both the northern and southern portions of the Gulf of California, mainly off the coast of Sonora; in the Ballenas-Salsipuedes Channel, however, SST remains relatively low (maps not shown). Figure 3a (upper panel) shows SST maps only for the 15 day periods matching the three campaigns analyzed. Taken together, the pattern previously described can be recognized; the differences between the three maps are mainly due to the periods of acoustic data acquisition in each year.

Concerning the spatial distribution of NPP, maximum values were observed around Tiburón and Ángel de la Guarda islands, as well as in the Ballenas-Salsipuedes Channel, mainly in May, while it was low in the second half of June in virtually the entire area. Productivity was higher and more widespread spatially and temporally in 2012, contrary to 2014 when high values were observed during the first half of May only (maps not shown). As in the case of SST, Figure 3b shows the NPP maps for the periods matching the surveys, highlighting the different productivity conditions in each. The highest values of the three-year period were recorded in 2012 mainly in the Ballenas-Salsipuedes Channel; to the south, on the coast of the Baja California Peninsula. High NPP values were also recorded between the islands and the coast of Sonora, both south and north of Tiburón Island in this year; in 2013, relatively lower values were observed, restricted to the coast of the Baja California Peninsula, south of the Ballenas-Salsipuedes Channel; finally, in 2014 NPP was low in almost the entire area.

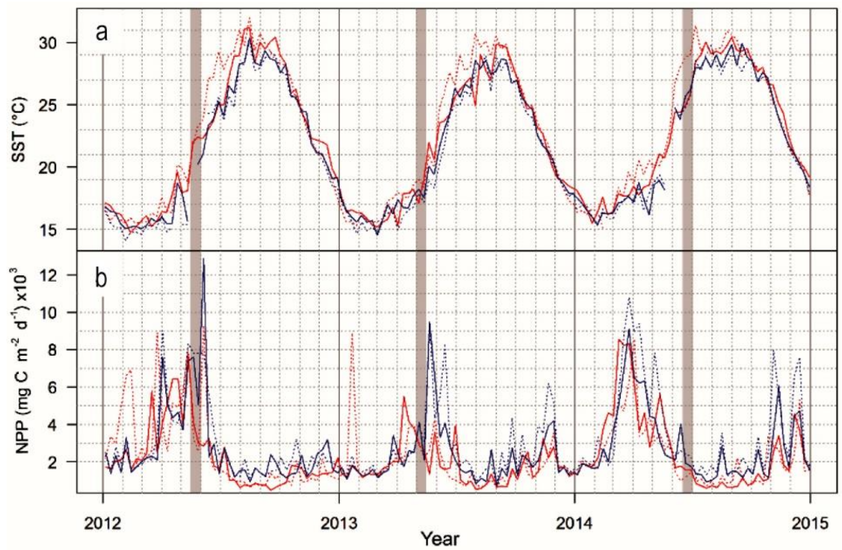

Figure 2. Time series (average values of 8 days) of a) sea surface temperature and b) net primary production at four sites in the Midriff Islands Region (Fig. 1). Eastern coast of Ángel de la Guarda Island: continuous red line; Western coast of Tiburón Island: dotted red line; Central region of the Ballenas-Salsipuedes Channel: continuous blue line; San Rafael Bay: dotted blue line. The vertical stripes in gray indicate the periods of acoustic sampling.

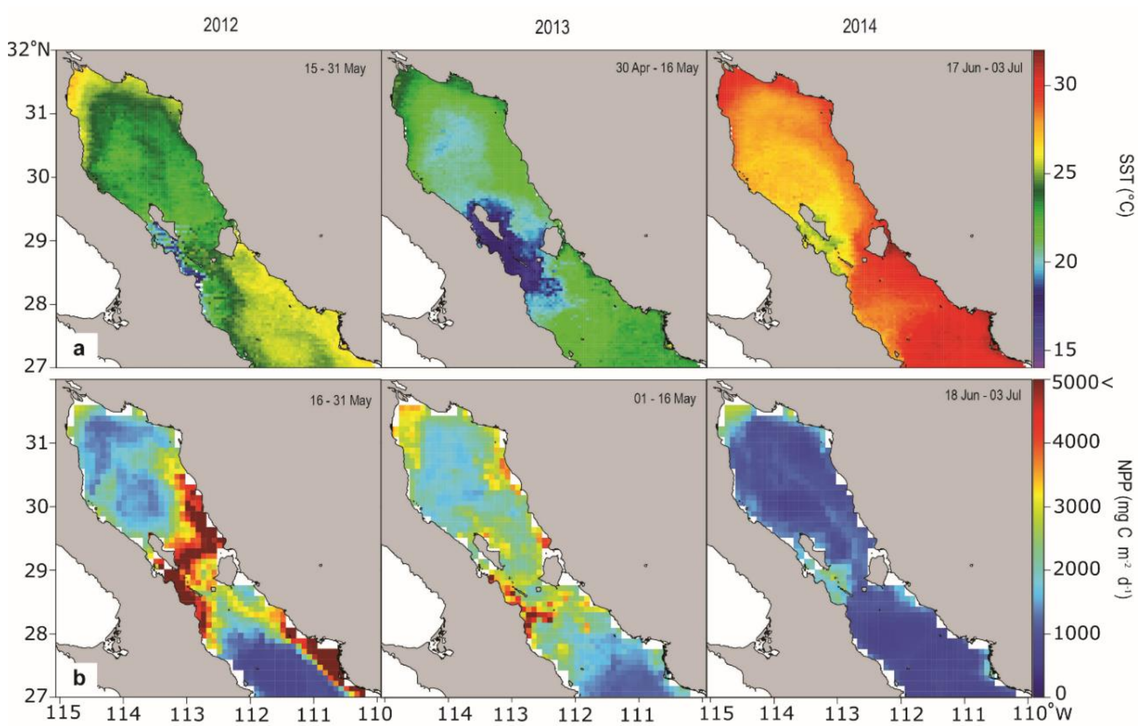

Figure 3. Satellite images of a) sea surface temperature and b) net primary production in the northern Gulf of California. The averaged periods (15 days) correspond to the acoustic surveys dates of each year. For comparison purposes, NPP values above 5000 mg C m^{-2} d^{-1} were regrouped into a single class.

Acoustic data

The sampling effort, in terms of the number of hours surveyed in the study area, was similar for the three years (86, 84 and 73 h, respectively). However, the number of schools observed differed between years: from 355 schools detected in the three campaigns, 67.3% (239) were observed in 2012, 30.1% (107) in 2013, and only 2.5% (9) in 2014. Similarly, the geographic distribution of schools differed between years, with a broad distribution in 2012 and 2013 and

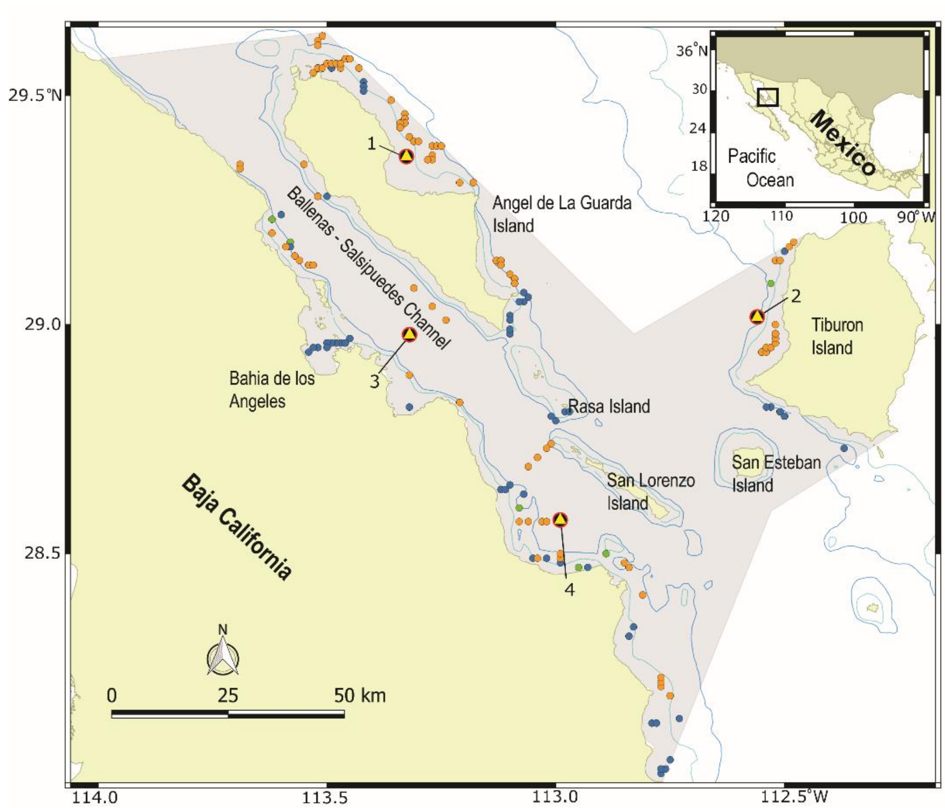

Figure 4. Midriff Islands Region in the Gulf of California (shaded area), showing the occurrence sites of schools for the years 2012 (orange points), 2013 (blue points) and 2014 (green points). The yellow triangles indicate the locations where the time series of Sea Surface Temperature and Net Primary Productivity were extracted. 1: East coast of Ángel de la Guarda Island, 2: West coast of Tiburón Island, 3: Central region of Ballenas-Salsipuedes Channel, 4: San Rafael Bay.

the most restricted one in 2014. In the first survey, schools were observed on the eastern coast of Ángel de la Guardia Island, the western coast of Tiburón Island, the Ballenas-Salsipuedes Channel, San Rafael Bay, and southward. The following year, with less than half of the schools detected in 2012, a similar distribution was recorded, with some schools south of Tiburón Island up to the southern margin of MIR in the coast of Baja California. Finally, in 2014, the little detections observed were located almost exclusively in the Ballenas-Salsipuedes Channel to San Rafael Bay, with only one located west of Tiburón Island (Fig. 4).

Considering the time of the day where schools were observed, the majority were recorded during the nighttime (61%), followed by the daytime (31%), and only 8% during twilight. In 2012 the twilight moments in the region lasted 57 min (dawn: nautical twilight beginning 04:45, civil twilight ending 05:42; dusk: civil twilight beginning 19:19, nautical twilight ending 20:16), in 2013 it lasted 56 min (dawn: beginning 04:45, ending 05:42; dusk: beginning 19:19, ending 20:16), and in 2014 it lasted 59 min (dawn: beginning 04:37, ending 05:36; dusk: beginning 19:36, ending 20:36). It is for the short twilight duration than those observed during the dawn were clustered together with those of the daytime, while schools spotted in the dusk were included in the nighttime period. Figure 5 shows the vertical distribution of schools (geometric center depth) by year and period.

There were no apparent differences in school depth between years. However, the comparison of daytime *vs* nighttime reveals that most of the detections are distributed closer to the surface (<40 m) during the night, while their vertical distribution was broader (up to 80 m) during the day, especially in 2012. Also interesting is that the few 2014 detections occurred during the night, and most were restricted to approximately 25 m depth.

The average values and corresponding standard errors for three school descriptors are shown by year and period of the day in Table 2. However, given the departures from normality exhibited by these descriptors, the statistical test reported is based on ranks. The comparison of schools regarding size (school area) by

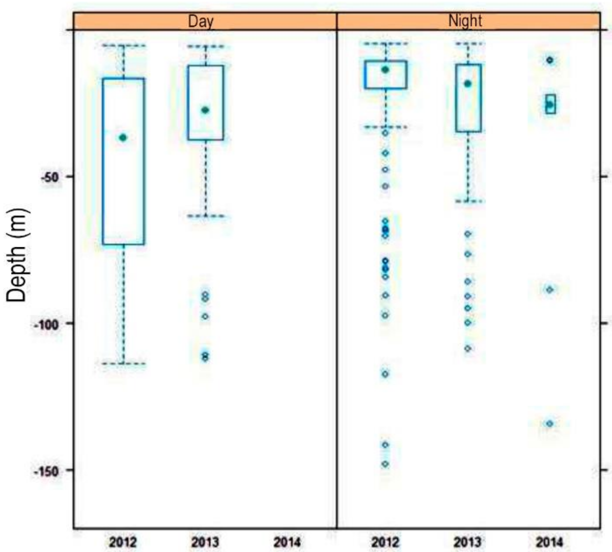

Figure 5. Boxplots of detected schools vertical distribution (geometric center depth) during 2012-2014. The symbol inside the boxes indicates the median; the boxes include 50% of the observations (quartiles 0.25 and 0.75), and the whiskers extend to observations that are less than 1.5 times the interquartile distance.

year revealed slight differences for the day schools between 2012 and 2013 (Mann-Whitney U = 2043, P = 0.00506). When comparing the acoustic energy (volume backscattering strength, S_v), no significant differences were found.

The results of the geographical distribution of schools suggest a relationship between the number of schools recorded and environmental variables since the largest number of schools was observed during 2012, the year with the highest net primary production and the broadest geographic distribution (Fig. 3), with values ranging between 7000 and 12000 mg C m^{-2} d^{-1} in the MIR (Fig. 2). In 2013, a year that recorded less than 50% of the schools observed in 2012, productivity was lower, with values between 3000 and 9000 mg C m^{-2} d^{-1} concentrated in some portions of the area of influence of the Ballenas-Salsipuedes Channel, near the coast of Baja California (Fig. 3). SST values in the four MIR selected sites were lower (17-20°C) in the first half of May 2013 *versus* the second half of May 2012 (20-24°C). The lowest NPP values in the MIR selected sites were recorded in 2014, with only nine schools detected and maximum values between 1000 and 4000 mg C m^{-2} d^{-1}, while the SST values in the sites showed values above 25°C. As previously mentioned the few schools observed in 2014 were restricted to the area with lower SST in the Ballenas-Salsipuedes Channel, observed only during nighttime hours and vertically further down from the surface relative to the previous two years.

The results of the GLMs to test for the relationship between location and number of schools observed during each year with NPP and SST were inconclusive. On the one hand, the model of independence between the year, SST category (sst1: >16.5 and ≤21°C; sst2: >21 and ≤29.5°C), and NPP category (npp1: >1300 and ≤3500 mg C m^{-2} d^{-1}; npp2: >3500 and ≤11000 mg C m^{-2} d^{-1}) was rejected (residual deviance = 245.35, d.f. = 7, $P = 4.12\times10^{-59}$), suggesting the existence of some kind of association between these variables. On the other hand, however, the model built including the interactions between pairs of variables (the interaction between the three variables was excluded given the analysis of deviance of the saturated model) showed three significant interactions (year: sst, P-val = 2.2×10^{-16}; year: npp, P-val = 6.107×10^{-9}; sst: npp, P-val = 0.0001954), although the standard errors associated with them were very high.

DISCUSSION

The observation of the Oceanic Niño Index (ONI) (NOAA, 2017) highlights that from July 2010 to February 2012 a very strong La Niña event took place, followed in 2015 by a El Niño event (from November to May 2016). During the period covered by this study, however, both positive and negative anomalies were below 0.5°C. On the other hand, it has been documented that these anomalous events do not significantly affect either temperature or primary production in the Gulf of California, especially in its northern portion, which usually responds with a lag of between three to six months (Escalante *et al*., 2013). Given such gap, a potential influence of La Niña 2010-2012 would be expected on the MIR conditions; however, the signal of this cooling event is not evident in the time series in (Fig. 2). Therefore, it is considered that the acoustic observations during this study do not reflect any alterations related to anomalous events.

The annual SST pattern observed in the MIR is cyclical, with a marked seasonal variation, typical of subtropical zones. In the case of NPP, although any periodicity is less apparent, a certain degree of correlation with temperature is apparent, as the lowest productivity was observed during summer and the peak when the temperature is at its lowest or either increasing or decreasing. It has been reported that the lowest mean SST occurs in this region due to the intense mixing of water masses associated with tidal dynamics, in particular in the Ballenas-Salsipuedes Channel (Martínez-Díaz de León *et al*., 2006).

The tidal dynamics produces an upward flow of enriched cold subsurface water, which subsequently promoted the highest mean chlorophyll and primary pro-

Table 2. Average values and standard errors (in parenthesis) for three descriptors (school area; school S_v; geometric center depth) of small pelagic fish schools by year and period of the day.

	2012				2013				2014			
	Day (n = 65)		Night (n = 174)		Day (n = 48)		Night (n = 59)		Day (n = 0)		Night (n = 9)	
Area (m^2)	514.4	(91.7)	439.46	(35.55)	195.84	(27.48)	725.21	(162.07)	--	(--)	268.26	(150.15)
S_v (dB)	-40.56	(0.53)	-40.17	(0.27)	-37.58	(0.72)	-40.64	(0.61)	--	(--)	-36.25	(2.45)
Depth (m)	45.03	(3.79)	21.47	(1.77)	32.36	(3.97)	31.96	(4.75)	--	(--)	41.33	(13.97)

ductivity levels in the GC (Millan-Nuñez & Yentsch, 2000; Escalante *et al*., 2013). However, oceanographic studies in the area have reported that the enriched subsurface water gradually disappears in the summer, as a result of two main factors. The sinking of this water mass and the intrusion of Equatorial surface water, which favors the rise in temperature, reduces the supply of nutrients, hence lowering primary production (Escalante *et al*., 2013; Hernández-Ayón *et al*., 2013). The former explains the highest SST and the lowest NPP values observed in 2014 when the sampling took place in early summer (whereas in the others occurred in late spring of 2012 and 2013). It is worth noting, however, that in the Ballenas-Salsipuedes Channel the lowest temperatures were recorded even at this time of the year, as well as higher primary productivity relative to the rest of the area (Figs. 2-3).

These features lead the Ballenas-Salsipuedes Channel to be regarded as a biological activity center (BAC), in the GC (Lluch-Cota & Arias-Arechiga, 2000). The term BAC has been proposed to refer to areas in the eastern continental margins of highly productive systems, noticeable for the existence of sardine and anchovy fisheries, such as the California, Humboldt and Benguela currents, among others, where biological activity is particularly high.

It seems to be linked to coastal characteristics and tends to show little seasonal variation in production levels, providing a significant fraction to total primary production at the various trophic levels (Lluch-Belda *et al*., 2000). In some production-based regionalizations of the GC (*e.g.*, Lluch-Cota & Arias-Arechiga, 2000), the Ballenas-Salsipuedes Channel and its area of influence are almost exclusively recognized as a small region where biological production levels are higher than in the rest of the adjacent system. Other authors support the importance of this channel for the concentration of various species of mammals and birds (Tershy *et al*., 1991; Breese & Tershy, 1993; Enríquez-Andrade *et al*., 2005).

In this environmental context, it is worth noticing that this channel showed a constant presence of small pelagic fish schools throughout the three surveys analyzed in this work. As mentioned above, the largest number of schools recorded in 2012 coincided with the highest and geographically broadest primary production levels. In 2013, although the distribution of schools was similar, most were concentrated in an area that showed the highest production values (Fig. 3). Finally, in 2014, when in the GC the productivity was at its lowest and coupled with the highest temperature, the scarce schools observed mainly occurred in an area (San Rafael Bay), which showed higher productivity values and lower temperatures relative to the rest of the MIR.

The net primary production represents the amount of carbon fixed by photosynthesis that is available for the first heterotrophic level (Behrenfeld & Falkowsky, 1997), being, therefore, an indicator of food availability at the base of the marine food chain. As such, it is a factor that favors the presence of small pelagic fish, many of which feed by filtration or selecting individual prey items (*e.g*., copepods) (Durbin, 1979) and are always in search of plankton aggregations distributed as patches. In the case of phytoplankton, these patches are related to the physical processes that govern nutrient availability, while zooplankton aggregations are commonly related to the phytoplankton concentrations upon which they feed (Lalli & Parsons, 1997). It has been proposed that several species of sardines and anchovies are omnivores, although it has been determined that the primary source of carbon incorporated into these fish is supplied by zooplankton (Van der Lingen *et al*., 2009).

Sea temperature can also influence the habitat preference of small pelagic fish. Studies on the thermal behavior, of different subpopulations of *S. sagax* in the northeast Pacific Ocean, point to different thermal limits and physiological capabilities that, in conjunct-tion with other factors, may promote latitudinal movements of large fish schools (Martínez-Porchas, 2012). Several authors have discussed the relationship between capture of small pelagic fish schools and seawater temperature. Although it is crucial in determining the favorable or unfavorable conditions for primary producers, this relationship is typically weaker and less significant than the one between small pelagic fish and chlorophyll concentrations (Lluch-Belda *et al*., 1986, 1992; Butler *et al*., 1993; Lynn, 2003; Emmett *et al*., 2005; Lanz *et al*., 2009; Demer *et al*., 2012).

It is highly likely that feeding is the core biological process governing the presence of small pelagic fish in the MIR, particularly in the Ballenas-Salsipuedes Channel. It has been reported that in summer, based on the high-fat content observed in the viscera, coupled with poor gonadal development in individuals collected from the area (Sokolov & Wong-Ríos, 1973). Sardine schools in the MIR display a marked increase in feeding intensity suggesting the existence of a fattening period, mainly in the area around the Tiburón and Ángel de la Guarda islands. Also, the reproductive peak of this species in the GC takes place in the winter (Nevárez-Martínez, 2006). Studies on ichthyoplankton have reported a low abundance of small pelagic fish larvae in this area during the summer (Sánchez-Velasco *et al*., 2009; Inda-Díaz *et al*., 2010).

It has been hypothesized that under conditions of decreased upwelling in the coastal areas of the GC, small pelagic species such as *S. sagax* recurrently use the MIR, restricting their habitat to that area in the summer during periods of low population abundance, which suggests the existence of a resident population in this region (Lluch-Belda *et al*., 1986; Nevárez-Martínez, 2000). In this sense, Lluch-Belda *et al*. (1986) documented the capture of large numbers of juveniles of *S. sagax* in the MIR during summer.

In general, the information from the fishery shows that the abundances of small pelagic species decline toward the end of the summer, leading to lower catches throughout the Gulf of California. For example, although catches of *S. sagax* are maintained during this period, it has been suggested that this species displays low population abundance at that time (Nevárez-Martínez, 2000; Lanz *et al*., 2009), that could explain the small number of schools recorded in the early summer of 2014, when temperatures were higher, and productivity decreased.

In schooling fish, the size of the group is proportional to population density, since it depends on the encounter rate of individuals or groups already formed (Bakun, 1996; Rangeley & Kramer, 1998). The above would lead to understanding besides being present in lower numbers that schools in the MIR during the adverse conditions in the summer would also be of a smaller size. Considering the school area as *a proxy* of size, the schools in 2012 were significantly bigger than those in 2013 (daytime) (Table 2) according to the Mann-Withney test. However, the comparison of acoustic energy (S_v) of the groups revealed no differences either between years or between periods of the day, although some of the denser and smaller schools over the three-year period were observed in 2014. Swartzman (1991) mentions that in periods of low abundance, the few existing schools may be more prone to predator attacks; this would lead to an increase in their defensive strategies, which in turn modifies their structure. When predation leads to extreme stress levels, the distance between individual fish drops rapidly to a minimum, especially at the periphery of the group, but also inside the school, forming dense and compact structures (Fréon *et al*., 1992). In particular in the Ballenas-Salsipuedes Channel during the summer, it is known that the high abundance of some predators of small pelagic fish, such as birds and cetaceans, responds to the high prey abundance due to the migration of sardine schools (*S. sagax* and *Opistonema* spp.) into the area (Tershy *et al*., 1991, 1993).

About the time of the day when schools were observed and their vertical distribution, it is worth noting that almost twice the number of detections was observed in the nighttime, mostly in shallow water (less than 25 m). In daylight hours, a wider vertical distribution also occurred. In the literature, there is a consensus that during the day individuals of these species clusters together, and is located at greater depths in the water column. During the evening, they migrate toward the surface and disperse in shallow waters in search of food at night (Fréon & Misund, 1999).

This generalized schooling behavior of small pelagic fish has facilitated their capture with purse seines, which necessarily require schools of sufficient size to make fishing operations profitable. In the case of the European sardine and mackerel, fishing operations are carried out during daylight hours in the summer (Fréon & Misund, 1999). In contrast, in Mexico, and in particular in the GC, the sardine fleet operates during nighttime hours for 22 to 26 days around the new moon (Nevárez-Martínez *et al*., 2015), suggesting that the school structure is maintained even at night. Our results show a high number of nighttime schools, including the few detections of 2014 that were observed during this period of the day. Zwolinski *et al*. (2007) also recorded nighttime European sardine schools off the coast of Portugal, mentioning that these could be formed in response to predation or any other factor similar to those that occur during daylight hours. Schooling would provide, among other advantages, a greater vigilance in the presence of predators and better defense if attacked (Scalabrin & Massé, 1993; Petitgas & Levenez, 1996). The data analyzed in this work, however, are insufficient to make inferences in this regard. Given the close relationship between schooling behavior and the fishery, it is paramount to broaden our knowledge about the mechanisms that affect it, as well as the biological influence of the MIR on adjacent areas. It requires further in-depth observations of the characteristics of schools in this and other regions of the Gulf of California, as well as of the catch dynamics of the commercial fleet.

CONCLUSIONS

The geographical distribution of the small pelagic fish schools observed here supports the importance of the Ballenas-Salsipuedes Channel within the MIR as a sheltered area or feeding center for these species, supported by the relatively lower temperatures and higher net primary production recorded in this area. Larger sample size could help to establish a statistically significant relationship between the number of schools detected and environmental conditions. The higher proportion of schools detected during the nighttime *vs* daytime, coupled with the similar size and density throughout the day, differs from the typical behavior described for similar species in other areas, which perform vertical migrations to the surface during the night and then disperse, losing the school structure.

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