

Global effects of moon phase on nocturnal acoustic scattering layers

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ABSTRACT: The impact of moon phase on the global nocturnal vertical distribution of acoustic scattering layers (SLs) in the upper 200 m was studied during the Malaspina expedition that circumnavigated the world. We assessed the nocturnal weighted mean depths and the vertical extension of the SL (the range between the upper 25th percentile and lower 75th percentile of the backscatter) and used a generalized additive model to reveal the relationship between the nocturnal vertical distribution of the SL and moon phase, as well as other environmental factors. Moon phase significantly affected the SL distribution on a global scale, in contrast to other factors such as dissolved oxygen, temperature and fluorescence, which each correlated with nocturnal SL distribution during the large geographic coverage. Full moon caused a deepening effect on the nocturnal SL. Contrary to expectations, the shallowest distribution was not observed during the darkest nights (new moon) and there was no difference in vertical distribution between new moon and intermediate moon phases. We conclude that the trend of deepening SL during approximately full moon (bright nights) is a global phenomenon related to anti-predator behavior.

KEY WORDS: Moon phase · Diel vertical migration · Acoustics · Predator avoidance

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INTRODUCTION

Pelagic organisms adjust their behavior in relation to nocturnal light levels as the trade-offs between risk of predation and foraging opportunity vary (Kampa & Boden 1954, Kampa 1970, Gliwicz 1986, Benoit-Bird et al. 2009a, Prihartato et al. 2015). Moonlight is a dominant source of nocturnal light and may affect vertically migrating species (Kampa 1970, Alldredge & King 1980, Luecke & Wurtsbaugh 1993, Benoit-Bird et al. 2009a,b). Behavioral responses to moonlight may be particularly pronounced in oligotrophic, clear waters in regions with little cloud cover (Dodson 1990, Hernández-León et al. 2001).

The anti-predation window theory suggests that planktivorous fish exploit periods with limited light intensities to forage on food-enriched surface layers, while avoiding visually searching piscivorous fish (Clark & Levy 1988, Rosland & Giske 1994,

Scheuerell & Schindler 2003). As the light intensity decreases at night, foraging ability of piscivorous fish is hampered by reduced reaction distance and extended searching time (Aksnes & Utne 1997, Staby et al. 2013). Other organisms may forage in the upper water column while the predation risks are reduced (Iwasa 1982, Clark & Levy 1988, Dypvik & Kaartvedt 2013, Staby et al. 2013), although nights may also become too dark for foraging for planktivores detecting their prey by sight (Giske & Aksnes 1992).

Mesopelagic acoustic scattering layers (SLs) comprising organisms carrying out diel vertical migration (DVM) are ubiquitous in the oceans (Marshall 1951, Barham 1966, Gjøsæter & Kawaguchi 1980, Irigoien et al. 2014). Light intensity has been established as a cue for mesopelagic animals to perform DVM (Kampa & Boden 1954, Roe 1984, Frank & Widder 1997). Mesopelagic fish may follow fixed thresholds of light intensity called isolumines (Baliño & Aksnes

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1993), or be associated with ranges of light intensities (Staby & Aksnes 2011). Migrations may also possibly be initiated by the rate of change in the light intensity, as shown in the case of mesopelagic krill (Ringelberg 1995).

Monthly patterns in mortality and population structure among zooplankton have been related to the state of the moon (Hernández-León et al. 2001, 2010). In such cases, recurrent monthly declines and increases in zooplankton standing stock were explained by high predation rate at new moon when mesopelagic fish migrated all the way to the surface, and low mortality of zooplankton on moonlit nights, when mesopelagic fish were assumed to avoid the upper layers where zooplankton reside, minimizing their own predation risk (Hernández-León et al. 2001, 2010). Moonlight is hypothesized to have global effects on diel migrating mesopelagic fish (Hernández-León 2008), yet no large-scale, global study has been carried out to date.

During the Malaspina expedition analyses were made of how nocturnal SLs in different environmental settings behave in the different light regimes following varying lunar cycles. Klevjer et al. (2016) analyzed the DVM patterns along the cruise track and showed that diel migrating mesopelagic organisms contribute considerably to the nocturnal backscatter in upper waters. This concurs with other studies (e.g. Escobar-Flores et al. 2013). Irigoien et al. (2014) concluded that the majority of the mesopelagic backscatter recorded during the Malaspina expedition originated from fish. This assumption is in accordance with many other studies of mesopelagic SLs (e.g. Kloser et al. 2009, Olivar et al. 2012), although other taxa will also contribute to the backscatter (e.g. Barham 1966). Here we use the acoustic data from the Malaspina expedition to analyze whether the moon phase has a global effect on nocturnal vertical distributions and thereby DVM. We hypothesize that in this large-scale exercise, global effects of moon phase (interpreted in terms of moonlight) will override other potential significant factors known to be important for the vertical distribution and DVM of mesopelagic fish (and other taxa). This includes varying taxonomic and ontogenetic composition of the SLs (Linkowski 1996), cloud cover (Boden & Kampa 1967, Baliño & Aksnes 1993), distribution of food (Shreeve et al. 2009, Dypvik et al. 2012), presence of predators (Kaartvedt et al. 2012), water clarity (Kaartvedt et al. 1996, Widder & Frank 2001, Frank & Widder 2002), temperature (Wurtsbaugh & Neverman 1988, Giske & Aksnes 1992) and oxygen level (Torres et al. 1979, Childress & Seibel 1998).

We aimed to address 3 hypotheses: (1) moonlight effect on the distribution of nocturnal SLs in upper waters is a worldwide phenomenon; (2) moonlight during the brightest phase (full moon) hampers migrations to upper layers due to increased danger of predation, so that diel migrating organisms deepen their nocturnal distribution; and (3) the shallowest distribution occurs during the darkest nights (new moon).

MATERIALS AND METHODS

Data were collected during the Malaspina expedition on board R/V 'Hespérides' (www.expedicionmalaspina.es) that circumnavigated the world in tropical and subtropical waters from 14 December 2010 to 15 July 2011. Acoustic records that encompassed nearly 8 lunar cycles and covered more than 32000 miles of ship track were recorded (Fig. 1). A Simrad EK60 echo sounder operating at 38 kHz was used to collect the data. The taxonomic composition of the organisms responsible for the backscatter along the path of this circumnavigation voyage is not known. However, organisms with air inclusions make stronger echoes, and organisms smaller than the acoustic wavelength of ~3.9 cm at 38 kHz will normally be relatively weak acoustic targets at this frequency (MacLennan & Simmonds 1992), so Irigoien et al. (2014) concluded that most of the backscatter was made up of fish. Swimbladder resonance may increase acoustic backscatter from small mesopelagic fish and other organisms with air bubbles, yet resonance effects at 38 kHz seem to be most prevalent at day depth (Kloser et al. 2009). Regardless, we do not believe this is an important factor in the comparison on vertical distributions relative to moon phase in the upper 200 m at night.

The acoustic data were cleaned of noise in several steps. Prior to import into the large scale surveying system (LSSS) software (Korneliussen et al. 2009) for post-processing, the data were subjected to a series of filters to remove bad data, as outlined in Irigoien et al. (2014). Thereafter, a moving average sliding window was applied to smooth the data. Finally, additional visual examination of echograms was performed to ensure that bubbles and bottom effects did not affect the echoes. This procedure was performed using the LSSS software. Noise was particularly prominent in the nocturnal data due to periodic interference from the ship's navigation system at night and such obviously corrupted data were deleted from the analyses. The procedures outlined above left 106

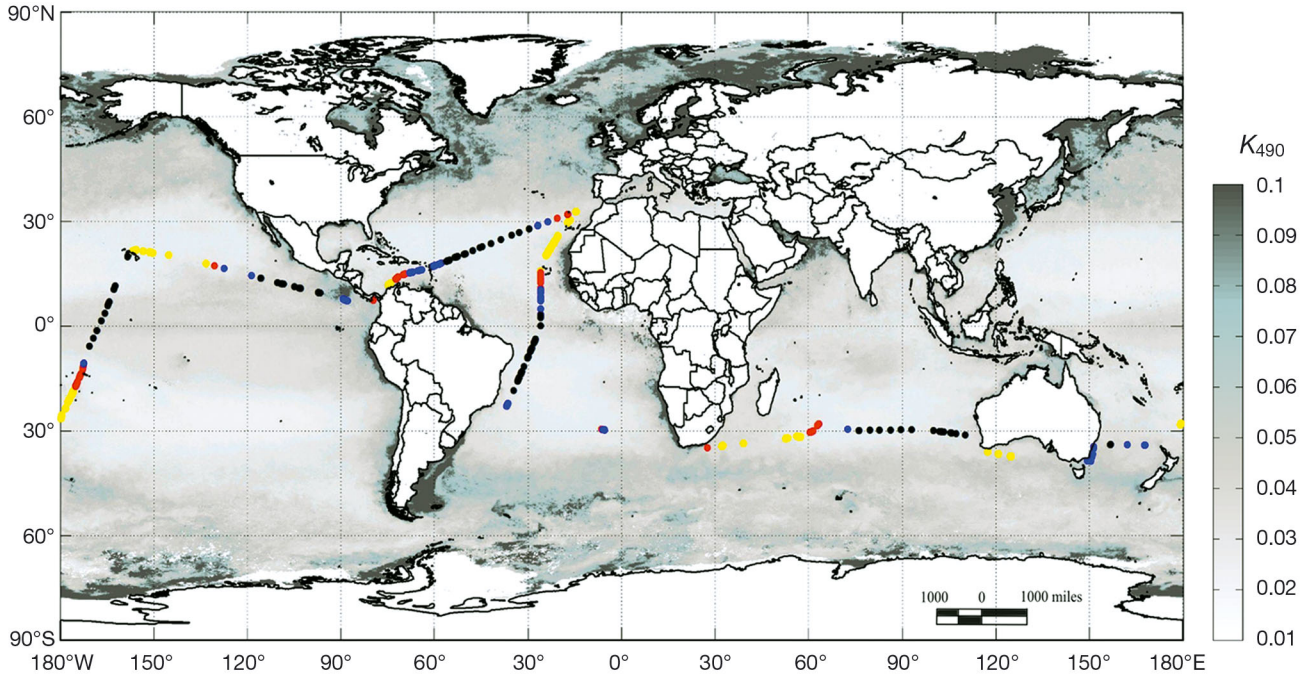


Fig. 1. Cruise track with color symbols referring to moon phase (C_1 : black; C_2 : blue; C_3 : red; C_4 : yellow). Background shading shows 6 mo average of the attenuation coefficient irradiance at 490 nm (K_{490}), as retrieved from the Aqua MODIS level 3 satellite at 4 km resolution, with darker color depicting water with increased K_{490}

nights of cleaned data usable for the acoustic analyses out of a total of 206 d sailing time. For exporting purposes, data were integrated at 2 min per 2 m depth for the upper 200 m water column, apart from the upper 15 m (the acoustic dead zone and near field). This depth range was selected as it basically encompasses the nocturnal distribution of the diel migrating mesopelagic organisms (Klevjer et al. 2016). The extracted nautical area scattering coefficient S_A ($\text{m}^2 \text{ nmi}^{-2}$) was used as an estimate of acoustic biomass (Knudsen 1990).

In this study, only nocturnal acoustic data were used, here defined as data from 2 h after sunset until 2 h before sunrise at local time. Information on the sunrise and sunset along with the moon phase (percentage illuminated phase of the moon) was obtained from <http://aa.usno.navy.mil/data/>. Night length according to these criteria roughly varied between 6 and 8 h throughout the cruise.

SL density center estimated as weighted mean depth (WMD) was calculated for each night, t , hence $\text{WMD}(t)$ is a value of S_A at each integrated depth multiplied by depth index, d_i , and divided by the total S_A for the respective date, where i refers to the depth layer corresponding to the d_i :

$$\text{WMD}(t) = \frac{\sum_i S_A(t, i) d_i}{\sum_i S_A(t, i)} \quad (1)$$

We categorized moon phase into 4 different groups: C_1 (moon phase 0–25%; 47 d), C_2 (moon phase 25.1–50%; 21 d), C_3 (moon phase 50.1–75%; 13 d) and C_4 (moon phase 75.1–100%; 27 d). Analysis of variance (ANOVA) with Tukey's post hoc test was applied to WMD averaged across each moon phase in order to reveal which of the categories distributed more deeply or shallowly.

Moon phase was also analyzed as a variable per night, assessing the WMD and the vertical extension of the SL. The daily vertical extension of the SL was calculated by estimating the daily upper limit at the 25th percentile (P25) and the lower limit at the 75th percentile (P75) of S_A . Each of these characteristics of SL depth (P25, WMD and P75) were tested against daily means of environmental parameters for the upper 200 m using generalized additive model (GAM) regressions (Hastie & Tibshirani 1990, Swartzman 1997). GAM is a non-parametric method with the ability to analyze the relationship between response and predictor variables without limiting the form of the relationships. Specifically, we fit a GAM model as follows:

$$\text{WMD}(t) = f_1[\text{WMD}(t-1)] + f_2[\text{temperature}(t)] + f_3[\text{dissolved oxygen}(t)] + f_4[\text{fluorescence}(t)] + f_5[\text{turbidity}(t)] + f_6[\text{salinity}(t)] + f_7[\text{moon phase}(t)] + e(t)$$

where $f_1, \dots, f_7$ are nonparametric functions, WMD($t-1$) is used to account for temporal autocorrelation

and $e(t)$ is an independent and identically distributed normal error term with mean zero and constant variance. We fitted the same GAM model to P25 and P75.

We used the *mgcv* package (version 1.7-28) of the R program (Wood 2006) with cubic smoothing spline functions (Hastie & Tibshirani 1990). In order to better visualize the GAM result, we multiplied the depth index by -1 so that the effects on the SL visualized shallowing trends as positive and deepening trends as negative.

Environmental parameters were measured daily (data from 92 d used in this study) using a CTD for temperature and salinity (Catalá et al. 2015), the instrument package also being equipped with turbidimeter, oxygen sensor and fluorometer. For 3 of the 92 d, high turbidity values were considered as outliers, and for the analyses these were substituted with averages based on the previous and subsequent measurements. CTD stations were mainly from day-time, whereas the acoustic data were from night, but space–time lags between measurements are negligible on the large spatial scales presented here. Data

were imported into MATLAB for visualization. A global coverage of water clarity was also presented in the form of downwelling attenuation coefficient irradiance at 490 nm (K_{490}) retrieved from the Aqua MODIS using monthly averages and 4 km spatial resolution (<http://oceancolor.gsfc.nasa.gov>).

RESULTS

Water properties

Sea surface temperatures varied from 18.1 to 29.3°C throughout the voyage. The depth of the thermocline ranged from ~20 to 140 m, with temperatures at ~20°C often delineating the mixed layer depth. Surface salinity varied between 33.4 and 37.6, with high salinity detected at the edge of the Gulf of Panama (mid-June to July). In general, turbidity values were below 0.1 NTU (nephelometer turbidity units), with values for the upper 200 m being 0.031 ± 0.008 (mean $\pm$ SD). This was also shown by the surface K_{490} of the Aqua MODIS satellite over 6 mo

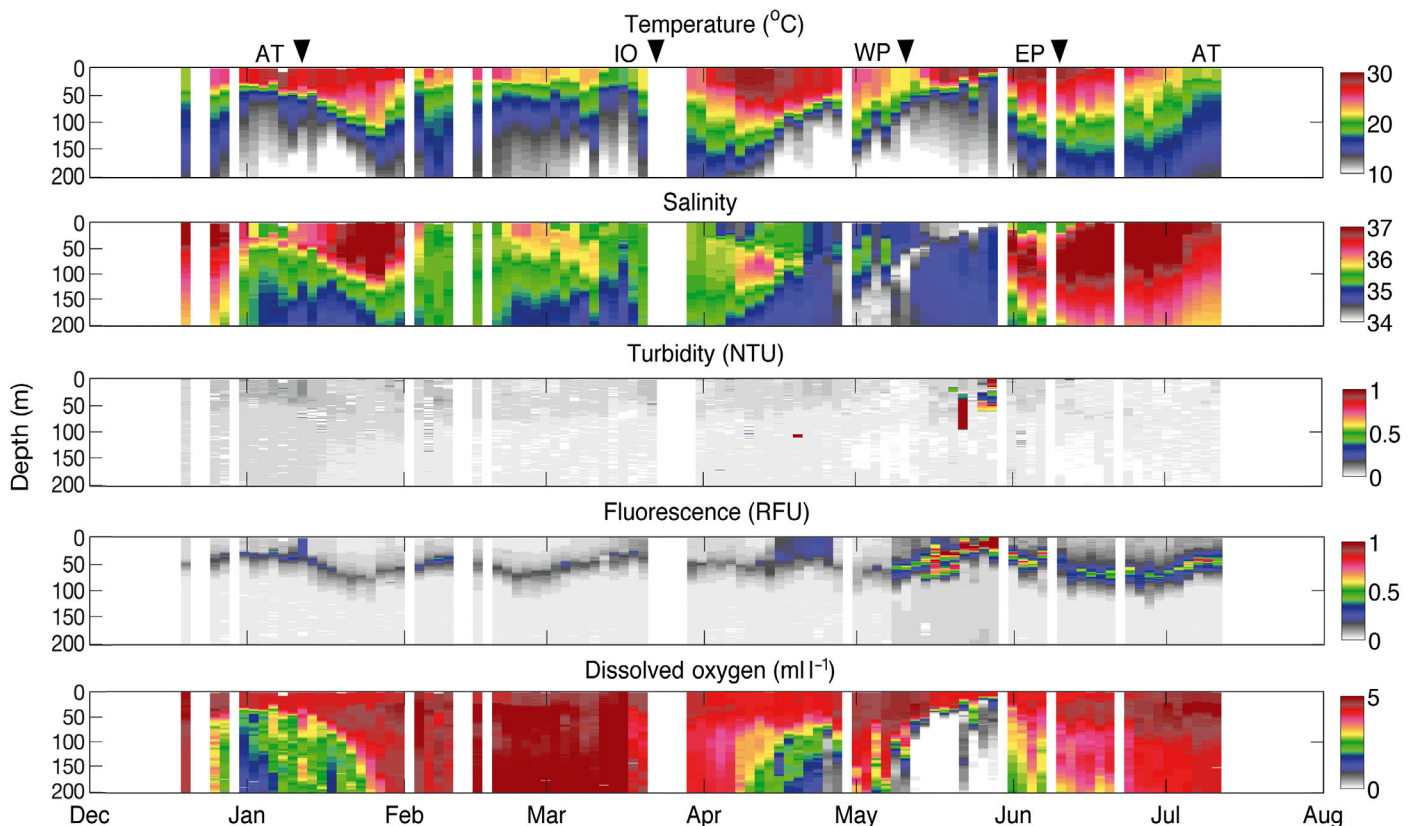


Fig. 2. Hydrography along the cruise track showing temperature, salinity, fluorescence, turbidity and dissolved oxygen. Color scale with red illustrating the highest and white the lowest value. Blanks represent gaps between measurements. (▼) Borders between geographical regions); AT: Atlantic Ocean; IO: Indian Ocean; WP: western Pacific; EP: eastern Pacific

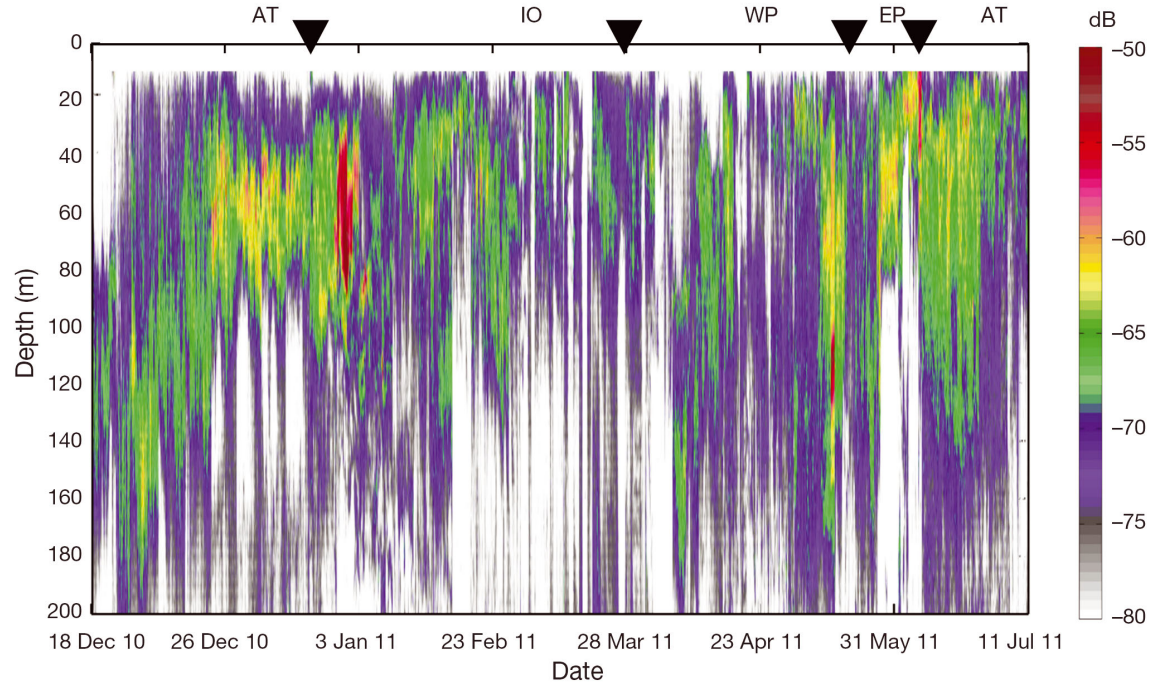


Fig. 3. Nocturnal echogram for the upper 200 m along the cruise track. There are no data for the upper 10 m. (▼) Borders between geographical regions; AT: Atlantic Ocean; IO: Indian Ocean; WP: western Pacific; EP: eastern Pacific. Nights without records are not included, so the x-axis does not represent a realistic temporal/geographic scale. Color scale refers to acoustic backscatter (dB), with red as strongest and white as weakest values

period of the cruise, with an average K_{490} at near surface of $0.15 \text{ m}^{-1} \pm 0.64$ (Fig. 1). Fluorescence values for the upper 200 m were 0.075 ± 0.049 relative units. Fluorescence generally peaked between depths of 25 and ~90 m. The maximum recorded value was 3.55 (Fig. 2). There was a distinct oxygen minimum zone ($<1 \text{ ml l}^{-1} \text{ O}_2$) near 50 to 200 m in the eastern Pacific Ocean (May to June; Fig. 2).

Acoustic analyses and GAM model of SL and environmental factors

The WMD of the nocturnal SL for the upper 200 m varied from the shallowest at ~31 m to the deepest at ~130 m. The average nocturnal WMD for the whole cruise was 74.7 m, with 95 % CI at 43.8 to 108.6 m (Figs. 3 & 4).

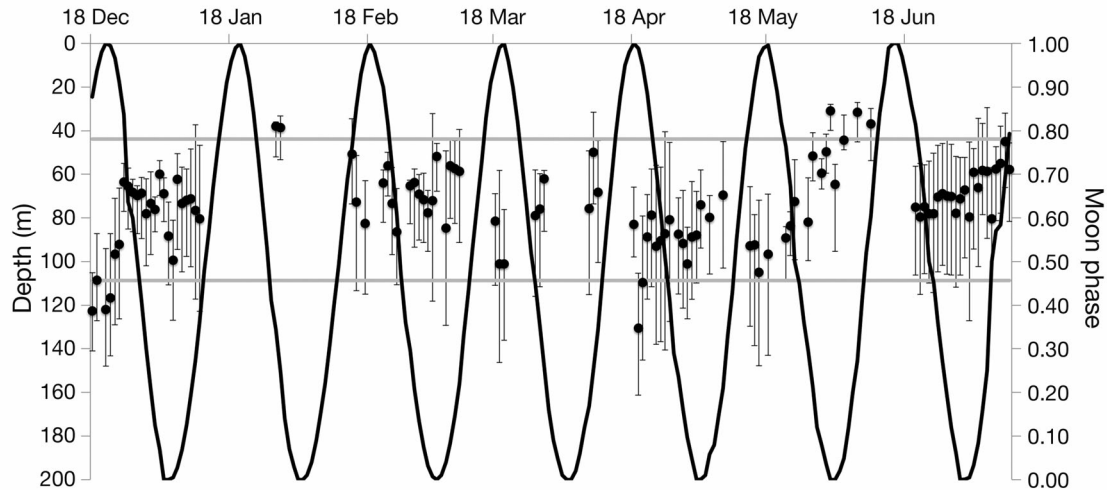


Fig. 4. Daily averages of statistics representing the vertical distribution of the scattering layer (SL) in relation to lunar illumination: WMD (weighted mean depth; ●), with the 25th percentile (P25) and 75th percentile (P75) given as whiskers. Right-hand y-axis refers to moon phase (continuous line). Gray horizontal lines border the 95 % CI for the whole study period

Table 1. Results of generalized additive model (GAM) regression for the effect of environmental factors on the scattering layer (SL) parameters. Values are degrees of freedom with p-values in parentheses. P25: 25th percentile; WMD: weighted mean depth; P75: 75th percentile. **Bold:** significantly different at $p < 0.05$

SL parameters	Environmental factors					
	Moon phase	Dissolved oxygen	Temperature	Salinity	Turbidity	Fluorescence
P25	8.525 (<0.0001)	4.593 (0.003)	0 (0.384)	8.330 (0.002)	5.048 (0.0001)	4.992 (<0.0001)
WMD	6.723 (<0.0001)	5.768 (<0.0001)	3.157 (0.004)	1.363 (0.018)	6.269 (<0.0001)	1.282 (0.001)
P75	4.049 (0.046)	0 (0.440)	0.955 (0.0002)	0 (0.511)	0.069 (0.290)	0.942 (0.0001)

Moon phase had significant effects on the WMD ($p < 0.0001$), the P25 ($p < 0.0001$) and the P75 ($p = 0.046$) (Table 1). In general, a deeper distribution of the SL (negative effect) occurred when the values were 0.75 to 1 (full moon) (Fig. 5). The acoustic results from the 4 moon phase categories suggested that the deepest occurred at C_4 (Fig. 6), although for the 4 periods (C_1 , C_2 , C_3 , C_4) the mean depths were not significantly different from each other (ANOVA with post hoc Tukey). Most of the backscatter was confined to ~40 to 80 m during the dark periods (C_1 , C_2 and C_3), whereas during brighter nights (C_4), SLs were dispersed more deeply at ~40 to 140 m (Fig. 6).

The distribution of the SL also was significantly related to environmental factors other than the moon phases (Table 1). Temperature significantly affected WMD and P75 (Table 1), becoming deeper in warmer waters (Fig. 5). The GAM model expected the SL depths to be shallower with integrated dissolved oxygen values of less than $\sim 3 \text{ ml l}^{-1}$ (Fig. 5). The nocturnal SLs also shallowed with increasing fluorescence. This was particularly evident for the lower part of the SL, with P75 moving $\sim 50 \text{ m}$ toward the surface with increasing values (Fig. 5). The distribution of WMD and P25 was significantly related to turbidity (Table 1), yet there was no consistent association with depth along the cruise track (Fig. 5). Correspondingly, it appeared

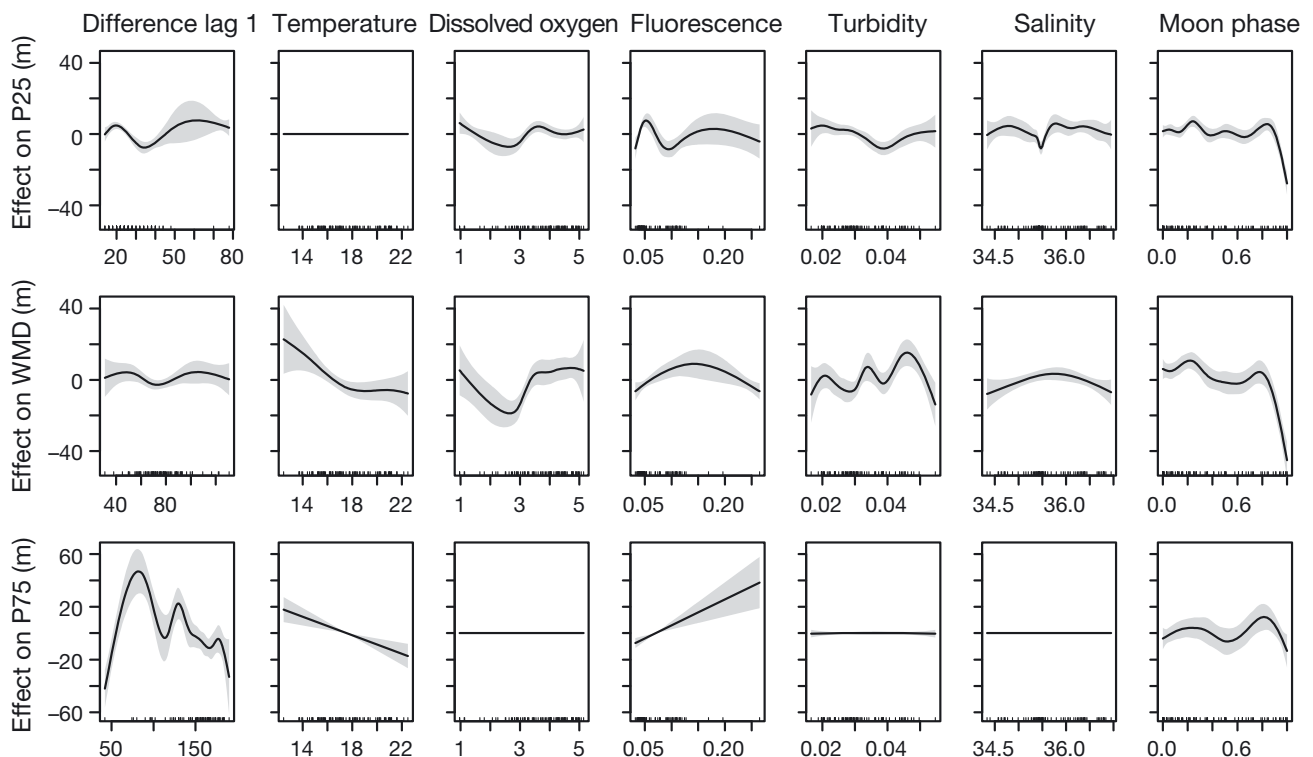


Fig. 5. Generalized additive model (GAM) showing the effect on the statistics representing the vertical distribution of the SL (P25, WMD and P75). Difference lag 1 refers to the effect of the respective parameters in the GAM model if lagged by day. The y-axis represents the effect of the spline functions on the statistics (m). Shaded gray areas indicate 95% CI. Note that the y-axis scale differs for P75. Tick marks on the x-axis refer to observed data points

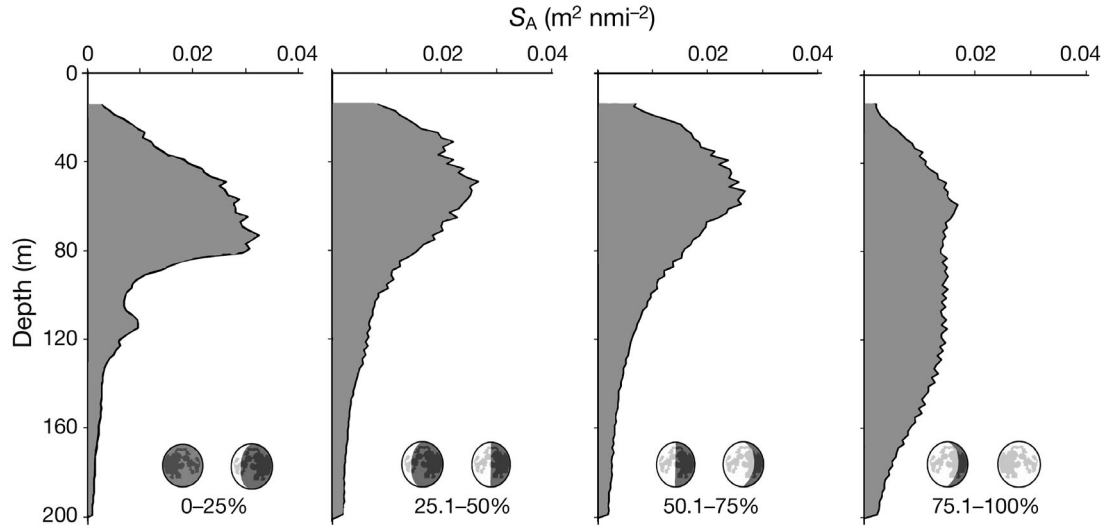


Fig. 6. Vertical strata of SL calculated based on the nautical area scattering coefficient (S_A) for different moon phase categories. No data for upper 10 m

that salinity did not have any consistent effect on the SL (Fig. 5), even though significant relations appeared in the analyses (Table 1, Fig. 5).

The residuals from GAM fits to the SL (P25, WMD and P75) were analyzed in Fig. 7. Plots of scaled

Pearson residuals (first column) did not reveal any abnormal patterns. Normal quantile–quantile plots of the residuals (second column) suggest that the assumption of normality is reasonable. Plots of the residuals' autocorrelation functions with 95 % confi-

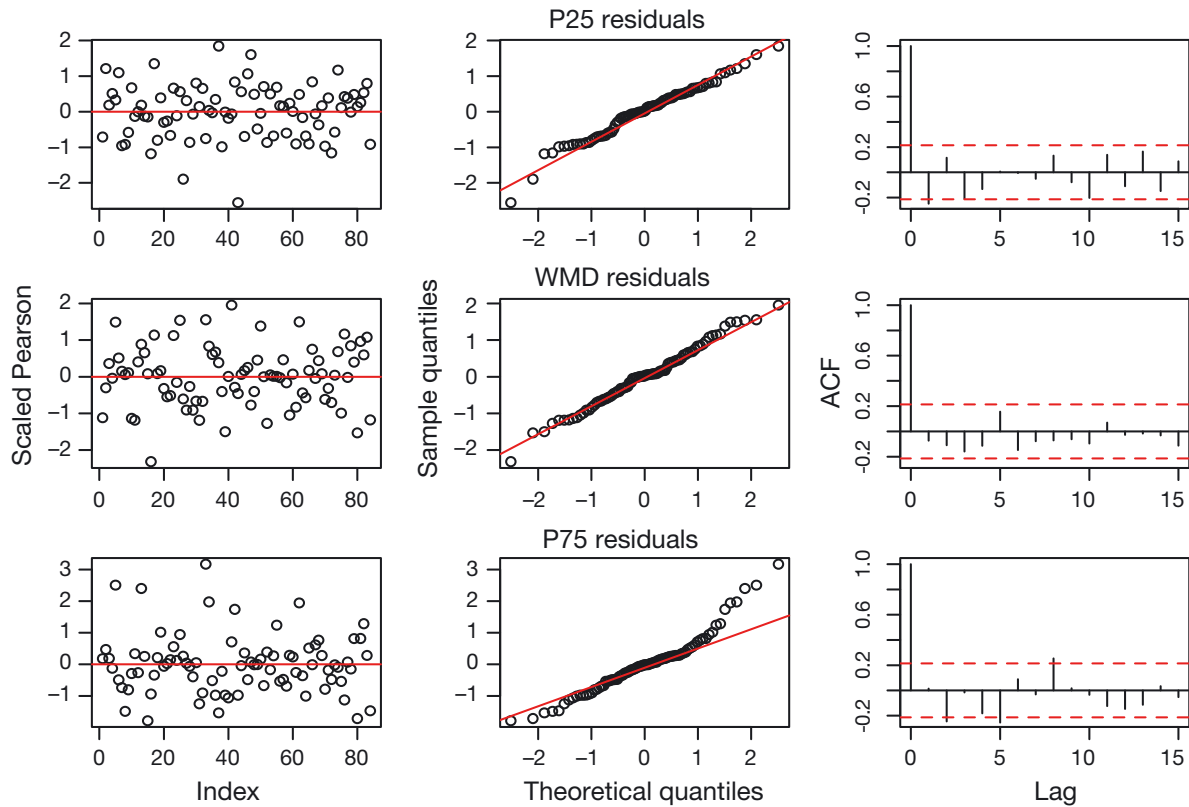


Fig. 7. Residuals from GAM fits to the SL (P25, WMD and P75). Plot of scaled Pearson residuals (first column); normal quantile–quantile plot of residuals (second column); residuals autocorrelation function (ACF) plot with 95 % CI (third column)

dence bounds (third column) show that no temporal autocorrelation remains. Therefore we conclude that these model fits are adequate.

DISCUSSION

Here we present the first study of the effect of moon phase on the distribution of nocturnal SL in the tropical and subtropical ocean worldwide, documenting consistent effects on the habitat choice of the vertical migrants. We could not identify the species constituting the SL, since no trawling was carried out during the cruise. However, the backscatter was likely mainly caused by diel migrating mesopelagic fish (cf. Irigoien et al. 2014). This concurs with a multitude of studies from throughout the world's oceans concluding that mesopelagic SLs at 38 kHz echo are dominated by mesopelagic fish, as follows: Arabian Sea (Gjøsæter 1984, Kinzer et al. 1993), Red Sea (Dallpadado & Gjøsæter 1987, Klevjer et al. 2012, Dypvik & Kaartvedt 2013), Japan Sea (Sweatt & Forward 1985), Hawaiian waters (Clarke 1978), Northeastern Atlantic Ocean (Roe 1984), Tasman Sea (Kloser et al. 2009) and the Mediterranean Sea (Olivar et al. 2012), although the relative contribution to nocturnal backscatter in upper layers remains to be established.

The GAM showed that moon phase significantly affected the nocturnal SL (P25, WMD and P75), particularly in causing a deeper distribution when moon phase was above 0.75 (Fig. 5). The pattern was consistent throughout the voyage, even though the data were collected on a large geographic scale, encompassing regions characterized by different environmental conditions, which each independently correlated to some extent with the vertical distribution. Also consistent along the cruise track was the similarity of the vertical distribution in the darker, yet still variable periods, with respect to moonlight (C_1 , C_2 and C_3 ; Fig. 6). Similar results appear from a long-term acoustic study in the northern Arabian Sea, where Wang et al. (2014) found what they call a critical light intensity at ~65% of full moonlight, above which diel migrating mesopelagic SLs stayed deeper. Therefore, a step function, and not a linear relation, between vertical distribution and moonlight is suggested in both cases. This deviates from studies suggesting the shallowest distribution occurs during the new moon (Hernández-León 2008, Benoit-Bird et al. 2009a).

A relatively deep nocturnal distribution during full moon is most likely explained in terms of predator avoidance. This explanation is in accordance with

several previous studies addressing different taxa in various pelagic environments (Gliwicz 1986, Luecke & Wurtsbaugh 1993, Tarling et al. 1999). Hernández-León et al. (2001) concluded that oceanic mesozooplankton biomass and abundance peaked at full moon, as planktivorous mesopelagic fish then avoided the upper layers at night to reduce vulnerability to piscivores, thereby alleviating predation pressure on the plankton. Benoit-Bird et al. (2009b) concluded that a predator–prey relationship between dolphins and mesopelagic fish in Hawaiian waters was synchronized to the lunar cycle, with dolphins diving deeper to forage on the mesopelagic fish during full moon in contrast to shallow foraging depth during new moon. Similar behavior was also observed for other mesopelagic fish predators, when during full moon they had to search for mesopelagic fish more deeply than during other lunar phases; for example, cod (Giske et al. 1990), octopus (Villanueva 1993) and seabirds (Connan et al. 2007).

While a deeper nocturnal distribution during full moon was in accordance with our initial hypothesis, we did not find the shallowest distribution during the darkest night at new moon, as we had initially expected. Examples of another, seemingly counter-intuitive, response to moonlight are the Myctophidae *Hygophum macrochir* and *Hygophum taaningi*, which apparently ceased their migration during new moon and rather stayed at 400 m depth (Linkowski 1996).

We suggest that limited moonlight would provide sufficient light to forage on zooplankton-enriched surface layer at night, with sufficiently reduced mortality risk during most phases of the moon. Such trade-offs between visual foraging and predator avoidance would be in accordance with the anti-predator window theory (Clark & Levy 1988, Rosland & Giske 1994, Scheuerell & Schindler 2003). The presence of shallow anti-predation windows for mesopelagic fish foraging in upper layers has mostly been related to short periods of intermediate light at dusk and dawn (Staby et al. 2013), but also to less dark summer nights at high latitudes (Kaartvedt et al. 1998, Prihartato et al. 2015). These studies have focused on the more shallow-living components of the mesopelagic fauna (the pearlside *Maurolicus muelleri*). The deeper-living myctophids that prevail among mesopelagic fish in the world's ocean (Catul et al. 2011) have more dark-adapted vision (cf. Warrant & Locket 2004), with other trade-offs between foraging and predator avoidance. Clear oligotrophic oceanic waters likely provide appropriate anti-predation windows throughout the night for dark-

adapted fishes (cf. Dypvik & Kaartvedt 2013), possibly enhancing nocturnal foraging opportunities compared to more productive regions. Note, however, that although we here assume that most of the backscatter is related to diel migrating fish, the distributions of other organisms also relate to nocturnal light. For example, results from nights with lunar eclipse suggest that krill may immediately respond to sudden changes in the light level (Tarling et al. 1999). The trade-off between foraging and predator avoidance would be different for organisms not searching for prey by sight (most invertebrate predators), as only vulnerability to visual predators, and not own foraging success, would increase during full moon.

Reduced nocturnal light related to overcast nights versus clear nights may affect the relationship, as mesopelagic fish are known to move to shallower depths with the presence of clouds in daytime (Baliño & Aksnes 1993). We have not analyzed weather data along the cruise track, yet overcast versus clear nights would likely mainly have the effect of including noise in the data set. Benoit-Bird et al. (2009a) found that lunar phase per se actually accounted for more of the variability in migration of a SL at the shelf than variation in nocturnal surface irradiance. They suggested that moonlight might be a cue for an endogenous lunar rhythm in the process of diel migration rather than a direct cause.

Among other environmental factors, reduced dissolved oxygen correlated with a shallower distribution. Oxygen plays a vital role for the habitat selection of migrating animals, particularly in regions with oxygen minimum zones (oxygen values $<1.4 \text{ ml l}^{-1}$) (Childress & Seibel 1998). Regions of hypoxic waters, particularly in the marked oxygen minimum zones of the eastern tropical Pacific (Gilly et al. 2013), will affect the vertical extension of DVM (Longhurst 1967, Stramma et al. 2008, Bianchi et al. 2013). This clearly relates to daytime depth, but may cascade into nocturnal distributions as well, and Irigoien et al. (2014) recorded shallower nocturnal distributions in regions of hypoxic waters than elsewhere.

Fluorescence values may be used as a proxy for productivity. There was limited variation in the depth of the fluorescence maximum throughout the survey (Fig. 2), with mean values at $67.7 \pm 11.82 \text{ m}$, while absolute fluorescence values varied considerably. In particular, the deeper part of the SL was consistently related to fluorescence values, suggesting some causative relation to the shallower distribution of the mesopelagic fish in regions with high fluorescence. Increased fluorescence values in the surface may

reflect increased food abundance for zooplankton, in turn causing the migrating mesopelagic fish to stay near surface. Increased fluorescence will also cause increased shading, affecting the nocturnal light conditions. We cannot distinguish between these 2 possibilities.

Previous studies on mesopelagic fish document shallower daytime distribution with increasing turbidity, ascribed to shading (Kaartvedt et al. 1996, Widder & Frank 2001, Frank & Widder 2002). While the GAM analyses gave significant relations between the SL and turbidity, no such consistent trend appeared in our data.

The nocturnal SL during the cruise was confined to depths above the thermocline except for approximately full moon (bright nights). The deeper part of the SL (WMD and P75) became significantly deeper with increasing temperature. Temperature is known to play a role in nocturnal habitat selection for diel migrating fish (Wurtsbaugh & Neverman 1988), and nocturnal habitat selection to speed up metabolism in warmer waters has also been suggested for mesopelagic fish (Giske & Aksnes 1992). However, we cannot conclude whether the correlation with temperature and the SL in our data relates to the temperature per se, or rather reflects another water mass signature. One possibility is the effect of warm and clearer oligotrophic water masses.

In conclusion, regardless of the many factors that can affect the nocturnal vertical distribution of diel migrating organisms, the full moon caused a deepening effect on the nocturnal SL worldwide. The relation to moonlight was not linear, but rather appeared to be a step function, with predator avoidance during full moon as the main effect.

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