ABSTRACT

Bioluminescence is produced by a broad range of organisms for defense, predation or communication purposes. Southern elephant seal (SES) vision is adapted to low-intensity light with a peak sensitivity, matching the wavelength emitted by myctophid species, one of the main preys of female SES. A total of 11 satellite-tracked female SESs were equipped with a time-depth-light 3D accelerometer (TDR10-X) to assess whether bioluminescence could be used by SESs to locate their prey. Firstly, we demonstrated experimentally that the TDR10-X light sensor was sensitive enough to detect natural bioluminescence; however, we highlighted a low-distance detection of the sensor. Then, we linked the number of prey capture attempts (PCAs), assessed from accelerometer data, with the number of detected bioluminescence events. PCA was positively related to bioluminescence, which provides strong support that bioluminescence is involved in predator–prey interactions for these species. However, the limitations of the sensor did not allow us to discern whether bioluminescence (i) provided remote indication of the biological richness of the area to SES, (ii) was emitted as a mechanic reaction or (iii) was emitted as a defense mechanism in response to SES behavior.

INTRODUCTION

Bioluminescence is defined by the production and emission of light by a living organism (1). In the vast majority of bioluminescent marine organisms, the spectral range of bioluminescence is limited to blue/green wavelengths, centered around 470 to 500 nm (2). Due to sophisticated control mechanisms to produce precise patterns of light emission (flashes and glows), it is commonly assumed that bioluminescence increases the emitter’s fitness in at least three critical ways: (i) it is essential as a defense against predators (defensive function); (ii) it is used in food acquisition by means of, for example, a lure or built-in headlights (offensive function); and (iii) it allows to attract a mate by means of species-specific spatial or temporal patterns of light emission (matching function) (1,3). The defensive function, the most common use of bioluminescence, takes many forms such as startling, sacrificial lure or counter illumination (i.e. the silhouette of an animal seen by a predator coming from under is concealed by the ventral bioluminescence of same color, intensity and angular distribution of the residual ambient light). However, bioluminescence emitted by an organism can also be “diverted” by others organisms not targeted by the emissions; in that case, the beneficiary of the emissions might not be the emitter (e.g. a visual predator taking advantage of the bioluminescence emitted by the prey to catch it).

The presumed functions of the light emission are generally deduced from morphological and physiological characteristics observed ex situ rather than from in situ studies or observations (4). As an example, the defensive function based on counter illumination has been mainly investigated during ex situ experiments, where the ability of organisms to adjust their light ventral characteristics to match light characteristics of artificially manipulated light fields has been highlighted (5–8). Behavioral experiments on the role of the bioluminescence exist, such as those demonstrating that dinoflagellate bioluminescence reduces grazing by copepods by attracting top predators (5,9,10). However, they remain extremely rare probably because the direct observation of bioluminescence in situ still represents a challenge for scientists. The use of remote-operated vehicles, submersibles or video profilers constitutes a valuable opportunity to explore the deep ocean. These instruments reveal the existence of new luminescent organisms. They also reveal the vertical distribution of bioluminescent organisms within the water column as well as the spatial variation in bioluminescence activity (11–13). However, in the vast majority of cases, due to the size and noise generated by the equipment, they remain of limited value to properly investigate natural behaviors or interactions between the organisms. In the last decades, studies deploying irradiance time-depth recorders on marine predators were able to sample the luminescent field to which these animals were exposed (14,15). The use of such devices represents then an interesting alternative to observe bioluminescence in situ and to better understand the interspecific interactions based on bioluminescence.

Southern elephant seal (SES hereafter), Mirounga leonina, spends 10 months per year feeding at sea and come back ashore only to breed in October, or to molt in January. When foraging at sea, SES travels large distances and dives almost continuously, performing on average 60 dives per day. They dive in the
mesopelagic zone to about 600 m depth where they encounter bioluminescence (15). Nitrogen stable isotope analyses revealed that bioluminescent myctophids were one of the most dominant components of the diet of females SES from Kerguelen Islands (16). Bioluminescent myctophids are extremely abundant in the mesopelagic zone, their peak eye sensitivity ranges from 450 to 480 nm (2), and their maximal wavelength emission ranges from 450 to 480 nm depending on the species (17–19), suggesting a wavelength range overlap in the spectral eye sensitivity and bioluminescence. The bioluminescence functions of these fish are not completely understood but dimorphism (sex- and species-specific lateral photophores distribution) is in favor of sexual and species recognition, while the ventral distribution of photophores, meanwhile, supports the countershading use of light for camouflage purposes (4,20). Myctophid otoliths from the following species—Electrona antarctica, Electrona carlsbergi and Gymnocephalus nicholsi—were found in abundance in stomachs of SES from the Kerguelen sector (21) and elsewhere (22). One critical question is how these predators locate their prey in the deep dark ocean, as SESs do not echolocate as cetaceans (23). To date, this question remains unresolved; however, there is some evidence that elephant seals could partly rely on vision to locate their prey in deep waters (15,24). Pinnipeds in general and elephant seals, especially, have some evolved visual abilities (25,26). They have large eyes composed by a retina with a deep sea rhodopsin exhibiting a maximum sensitivity around 470–490 nm (24).

Based on this information, SES should be able to use bioluminescence emission from Myctophids to forage on them. Previous study showed that the foraging intensity of SESs during their dives was positively related to the number of bioluminescence events detected in dives (15). This result could suggest that (i) bioluminescence may provide indications of the biological richness of the area, and therefore indirect clues of prey occurrence. This bioluminescence might be detected and used by SESs to locate their prey. Alternatively or additionally, bioluminescence might be emitted (ii) as a mechanic reaction to SES movement, just as an indirect consequence of its movement (i.e. in response to pressure wave associated with a moving object in the water (12,27)) or (iii) as a defense mechanism to an approaching predator. In particular, it is assumed that a bright flash at close range is produced to startle and/or divert predators, causing them to hesitate as in a form of predator intimidation (the startle effect) (1).

In this previous study, the bioluminescence events were detected from head-mounted light sensors on SES female looking backward. Indeed, these light sensors were initially deployed to address other questions such as the assessment of phytoplankton concentration by measuring light attenuation (28,29). The backward orientation of the light sensor prevented investigating whether the bioluminescence events were occurring prior or after the animal passage and therefore would act as an attractor of the SES or were the consequence of its passage. In addition, bioluminescence events were detected as discontinuities/ anomalies into the light signal recorded by a photodiode integrated into classical irradiance time-depth recorder tags, (TDR tags, Wildlife Computers) deployed on SES (15). However, neither calibration of that photodiode nor validation of the correspondence between light anomalies and real bioluminescence events was performed in the previous study. Finally, the foraging intensity of SES was estimated in this previous study by the diving behavior of the animal, which provides only qualitative proxies of the foraging activity at a dive scale (15) and hence avoided the temporal identification of the foraging in a dive.

In that context, the aim of this study was to complement the previous one and in particular to address the question as to whether bioluminescence can be used by SESs as a guide to locate their prey. To address that question, we first tested under experimental conditions the ability of the photodiode integrated into the TDR tags from Wildlife Computers to detect bioluminescence. Then, we investigated the quantitative and chronological link between forward bioluminescence and prey capture attempts (PCAs hereafter), a continuous and quantitative proxy of the foraging activity along dives, detected from the processing of acceleration signal on head-mounted accelerometers (30–34).

MATERIALS AND METHODS

Experimental design for testing the light sensor

The photodiode integrated into classical irradiance time-depth recorder tags (TDR tags, Wildlife Computers) was a Hamamatsu silicon S2387 equipped with a blue window transmittance filter. It was built to measure changes in light under very low light conditions, the light level being measured as an irradiance at a wavelength of 550 nm with a logarithmic range from 5 × 10^{-12} W cm^{-2} to 5 × 10^{-2} W cm^{-2} represented by raw values from 10 to 250. Considering that all TDR tags include the same photodiode, we only used one device (one TDR10-X) in the experimental phase. The tag was programmed to sample the light level every one-second.

Spectral sensitivity. The spectral sensitivity of the photodiode was assessed using a 100 W halogen cold light source (Euromex LE 5210) and a monochromator (Oriel—Analytis).

The tag was immersed in a few centimeters of seawater (~10–12°C) in a black container. The light source was used to emit a directed white light to the monochromator, while the monochromator was used to transmit a mechanically selectable wavelength of the white light to the tag. The monochromator inlet and outlet apertures of light were fixed to 5 mm. During that experiment, the photodiode was exposed to increasing wavelengths ranging from 360 nm to 660 nm by a 10 nm step every 20 s.

Detection angle. Tag shape and/or epoxy coverage may impact viewing angle of the photodiode, once integrated into the tag, both on the x– (Fig. 1) or on the y-axis (Fig. 1).

This experiment was intended in assessing the angle of view of the photodiode once integrated into the tag, both on the x– (Fig. 1) or on the y-axis (Fig. 1).

To do this, once the tag put in a few centimeters of seawater, the two axes (i.e. x and y Fig. 1) were tested using 19 incidence angles going from 90° to 90° measured against the z-axis (Fig. 1) with 10° step increments. A 465 nm blue-light-emitting diode (i.e. LED) was chosen with an intensity of 700 million of relative light units (i.e. RLU) for the light emission, which corresponds to 1.2 × 10^{-7} W cm^{-2}. For each tested angle, the tag was initially put in

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presented previously. Finally, the last sensor samples and archives at 16 Hz the acceleration of the animal on three axes: longitudinal, vertical (heave) and lateral (roll) axes.

Each TDR10-X tag was firstly glued to the Splash-10 tag. These associations were then glued using quick-setting epoxy (Araldite AW 2101, Ciba) on the head of the 11 seals to measure the light in front of animals with the x-axis of the tag oriented from the left to the right of the animal and the y-axis of the tag oriented from the top to the bottom of the animal (Fig. 2). Upon returning from their post-breeding foraging trip after 65 to 80 days, females were localized on land via the Argos system and recaptured and the electronic devices were recovered.

**Data processing—detection of dives and nighttime separation.** Dives of the 11 animals were analyzed from the time-depth records (from TDR10-X tags) using a custom-written MATLAB (version 7.0.1) code (available on request). For this, each dive was defined as an excursion over a 15 m depth (33). Then, each detected dive was divided into three distinct phases based on a cubic polynomial function fitted on the time-depth records. The descent and ascent phases were defined when the fitted value of vertical speed (dz/dt) exceeded 0.75 m s⁻¹. The bottom phase was defined as the period between the end of the descent and the beginning of the ascent phases. Finally, each dive was associated with a day or night period. Day period was here considered to encompass the day but also the dawn and the dusk. To do so, we calculated the elevation of the sun (degrees) at the location and the time where the dives occurred (using the package “maptools” (R 2.10.1), function “solarpos”). If the elevation of the sun was lower than −6°, the dive was considered as a night dive and otherwise the dive was considered as a day dive.

**Detection of bioluminescence events.** Considering that the ambient light reaches nearly constant low values at depths of 550 m during the day (including dawn and dusk in this study), and 250 m at night (15), any sudden increase in the ambient light level at depths deeper than these limits can be considered as a bioluminescent event around the SES. For this reason, bioluminescent events were only detected from the light signals recorded by the TDR10-X tags at depths deeper than the thresholds aforementioned. To do so, we used a custom-written MATLAB code (version 7.0.1; code available on request). This code used the “findpeaks” function, and we considered a true bioluminescence event only when the threshold height difference between a peak and

![Figure 2. Deployment of a TDR10-X on a female SES. The association of the TDR10-X and the Splash-10 tag was glued on the head of the seal to measure the light in front of animals with the x-axis of the tag oriented from the left to the right of the animal and the y-axis of the tag oriented from the top to the bottom of the animal.](image-url)
its previous neighboring values was higher than the precision threshold obtained in the experimental part.

Data processing—detection of prey encounter events. Acceleration data from the 11 individuals were processed according to (32) and (36) (custom-written MATLAB code—available on request). The procedure has been described in detail in (33). Briefly, acceleration records from the TDR10-X tags were first filtered on the three axes to remove "noises" in the signals induced by swimming movement. For each axis, significant peaks in acceleration were then detected when standard deviation of acceleration values within a "5 s" moving window was over a certain threshold. Such a threshold was determined for each axis and each animal using a clustering method where the number of clusters was predefined to 2 (function "kmeans"—tool box statistics—MATLAB). Only peaks above threshold simultaneously detected on the three axes were considered as a PCA.

Statistical analyses. Statistical analyses were carried out at the dive scale. For this reason, the number of PCA and the number of bioluminescence events were counted for each dive. Only dives for which depth exceeded the depth thresholds for the day and night period were kept into analyses. Considering that foraging is mainly related to the bottom phase of a dive (30,37–40), only bioluminescence events and PCA detected at the bottom phase of dives and deeper the depth thresholds aforementioned were included in the analyses. Knowing that the bottom time and the depth of a dive are linked to the foraging activity of animals (15,41), these variables were also taken into account. For this analysis, bottom time was calculated as the time of the bottom exceeding the depth thresholds. For this analysis, we used generalized linear mixed model (nlme package in R 2.10.1, function glmmPQL). Due to the fact that the bioluminescence events were detected differently during the day and the night (i.e. depth threshold of 250 m for night dives and 550 for day dives), two models were performed: one for the day and one for the night. Individuals were included as random factors, and we accounted for the temporal correlation in our data using an autoregressive variance–covariance matrix (corAR1). The complete models were built as such: Number of PCA Bottom time + Depth + Number of bioluminescence event, random = 1 | ID, correlation = corAR1 (1). The best models for night and day were selected using stepwise likelihood ratio tests.

In parallel to that, statistical analyses were also performed at the bioluminescence event scale. To this end, each bioluminescence event was isolated per dive and the time difference (in seconds) between each of them and the closest PCA was calculated.

RESULTS

Experimental tests of the light sensor

The maximum spectral sensitivity of the photodiode integrated into the TDR10-X tag was found to be 465 nm with a half band width of 50 nm (Fig. 3).

The repeated measures under constant light conditions were found to be constant and equal to 2 in raw values (i.e. $4 \cdot 10^{-15}$ W cm$^{-2}$). The angular detection ranges of the photodiode were found to be from $-40^\circ$ to $50^\circ$ on the $x$-axis (total angular detection range equal to $90^\circ$) and from $-50$ to $90^\circ$ on the $y$-axis (total angular detection range equal to $140^\circ$) (Fig. 4).

The maximum detection distance of the photodiode to detect a blue bright light source (i.e. a 465 nm blue LED with an intensity of $1.2 \cdot 10^{-7}$ W cm$^{-2}$) was found to be 290 cm (Fig. 5).

Finally, the photodiode integrated into the TDR10-X tag was able to detect real bioluminescence events represented by series of flashes and glows from different brittle stars mechanically...
stimulated three times in front of the tag immersed in aquarium (Fig. 6).

**DISCUSSION**

A light sensor adapted to the study of the bioluminescence

In this study, we experimentally showed that the photodiode integrated into the TDR10-X has the ability to detect events of light emitted by bioluminescent organisms. This result strongly supports the idea that this sensor is able to record *in situ* bioluminescence. We showed then that the sensor sensitivity ranges from 400 to 490 nm, with a maximal sensitivity to 465 nm and a half band width between 420 and 490 nm. Numerous pelagic taxa such as dinoflagellates, jellyfishes, krill, crustaceans, squids and fishes emit bioluminescence mostly within this wavelength window (1,2). Consequently, equipping SES with such a light sensor could provide important information on the horizontal and vertical distribution of bioluminescence within the Southern Ocean. Among all of these bioluminescent organisms, we are particularly interested in Myctophids, known to represent one of the major prey items of SES from Kerguelen Islands (16), with the most common myctophids species in their diet being *Gymnoscopelus nicholsi*, *Electrona antarctica* and *Electrona calsbergi* (21,22). Assuming from literature that myctophids emit light with maximal wavelengths ranging from 450 to 480 nm (17–19), the photodiode we used has the ability to detect bioluminescence emissions from these Myctophids species.

Despite the fact that the photodiode allows the *in situ* observation of a large range of bioluminescence events, this sensor is not specific enough to be able to distinguish between different sources (i.e. organisms) of bioluminescence. Moreover, the low sampling frequency of the sensor (respectively, 1 Hz) and limited detection range (<3 m) are likely to induce an undersampling of bioluminescence events such as very short (fast flashes) and low-energy ones.

At the bioluminescence event scale. Considering the maximum distance detection of the photodiode, estimated at 290 cm in the experimental part and the mean speed of an SES estimated to be approximately 1 m/s, only the differences under 3 s were conserved. This represents 37% of the detected bioluminescence events, which is much higher than expected just by chance ($W = 121, \, P<0.001$). Among these events, 69% occurred simultaneously to a PCA, 19% of them took place prior to a PCA and 12% of them took place after a PCA.

### Table 1. Descriptive statistics of the elephant seal tracks.

<table>
<thead>
<tr>
<th>Individual ID</th>
<th>Date of deployment</th>
<th>Duration (days)</th>
<th>Duration of TDR10-X (days)</th>
<th>Number of dives</th>
<th>Number of analyzed dives</th>
<th>Number of analyzed dives with at least one PCA</th>
<th>Number of dives with at least one bioluminescence event</th>
<th>Total number of detected PCA</th>
<th>Total number of bioluminescence events</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010–18</td>
<td>26.10.2010</td>
<td>60</td>
<td>60</td>
<td>3361</td>
<td>2479</td>
<td>2053</td>
<td>510</td>
<td>8841</td>
<td>717</td>
</tr>
<tr>
<td>2010–19</td>
<td>31.10.2010</td>
<td>80</td>
<td>80</td>
<td>4123</td>
<td>2258</td>
<td>1018</td>
<td>227</td>
<td>4144</td>
<td>240</td>
</tr>
<tr>
<td>2010–21</td>
<td>18.11.2010</td>
<td>73</td>
<td>73</td>
<td>4515</td>
<td>2170</td>
<td>1776</td>
<td>401</td>
<td>10487</td>
<td>466</td>
</tr>
<tr>
<td>2011–16</td>
<td>26.10.2011</td>
<td>87</td>
<td>10</td>
<td>653</td>
<td>426</td>
<td>367</td>
<td>34</td>
<td>1900</td>
<td>75</td>
</tr>
<tr>
<td>2011–27</td>
<td>30.10.2011</td>
<td>79</td>
<td>14</td>
<td>1229</td>
<td>753</td>
<td>500</td>
<td>73</td>
<td>1684</td>
<td>150</td>
</tr>
<tr>
<td>2013–1</td>
<td>28.10.2013</td>
<td>75</td>
<td>25</td>
<td>1724</td>
<td>1359</td>
<td>1185</td>
<td>87</td>
<td>796</td>
<td>195</td>
</tr>
<tr>
<td>2013–3</td>
<td>29.10.2013</td>
<td>81</td>
<td>23</td>
<td>1583</td>
<td>1175</td>
<td>1038</td>
<td>78</td>
<td>7207</td>
<td>164</td>
</tr>
<tr>
<td>2013–4</td>
<td>29.10.2013</td>
<td>64</td>
<td>18</td>
<td>1256</td>
<td>798</td>
<td>485</td>
<td>62</td>
<td>2285</td>
<td>238</td>
</tr>
<tr>
<td>2013–6</td>
<td>29.10.2013</td>
<td>72</td>
<td>16</td>
<td>1284</td>
<td>863</td>
<td>663</td>
<td>106</td>
<td>3666</td>
<td>221</td>
</tr>
<tr>
<td>2013–7</td>
<td>30.10.2013</td>
<td>63</td>
<td>26</td>
<td>1816</td>
<td>1403</td>
<td>1149</td>
<td>78</td>
<td>4590</td>
<td>140</td>
</tr>
</tbody>
</table>
which could be the most common ones. Consequently, our results should be considered at least as an underestimation of all bioluminescent events encountered by SES.

This leads us to discuss the nature of the current detected events. It is important to note that bioluminescence can be of two sorts. While fast flashes (<2 s) are used generally for communication (i.e. intraspecific and sex identification) or to startle potential predators, glow emissions (>2 s) are classically used to attract prey or to mask the fish silhouette from predators underneath (counter illumination) (1,42,43). Despite the fact that these two types of bioluminescence events are not characterized by specific intensities, it is often observed, and principally due to their functions, that the fast flashes are bright, while the glows are characterized by a low intensity (1,42,43). Because of the capabilities of the photodiode and especially the frequency of the measurement, we believe that the vast majority of the glows met by SES with a wavelength into the sensor detection range are detected by the photodiode, while the flashes are likely to be significantly undersampled because of their low duration (<2 s). Therefore, future research should use a higher sampling rate with more sensitive photodiodes or photomultipliers as performed in (44).

Our results showed a positive relationship between bioluminescence and foraging activity of SES both during day and night. These new results confirm those previously obtained on the qualitative relationship between the foraging intensity, estimated from the diving behavior of SES, and the bioluminescence (15). But these new results highlight also a quantitative relationship between bioluminescence and PCA. Our initial hypothesis was based on the idea that the detected bioluminescence events were those of Myctophids hunted by SES. However, SESs from Ker-guelen area are known to forage also on other types of prey such as cephalopods (21,45) including some bioluminescent species. Thus, considering the large number of bioluminescence sources which can be detected by the light sensor, we cannot exclude that bioluminescent events recorded by the sensor and linked to PCA might be emitted by other SES prey such as cephalopods or even from organisms not hunted by SES but living in the same ecological niche as SES prey.

This quantitative relationship between bioluminescence and PCA leads to a new stage to understand more precisely the inter-species interactions using bioluminescence. However, it is important to note that nothing leads us to rule whether (i) SES intentionally moves to feed toward areas exhibiting high levels of bioluminescence or (ii) bioluminescent organisms emit bioluminescence as a mechanic reaction to the SES motion activity or (iii) bioluminescent organisms emit bioluminescence as a defense mechanism to an approaching predator. The fact that bioluminescence was detected frontward is in line with the possibility that bioluminescence would preexist in the area before its passage. However, the limited capacities of the photodiode and principally its restricted detection distance of 290 cm do not allow us to address correctly this issue. Without information from the bioluminescent area beyond three meters, we are not able to distinguish between these three assumptions. To answer this question, further

Table 2. Results of models of the variation of PCA according to bottom time, maximum depth and the number of bioluminescence events both for night- and daytime periods.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Night dives</th>
<th>Day, dawn and dusk dives</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.33E+00</td>
<td>8.70E-01</td>
</tr>
<tr>
<td>Bottom Time</td>
<td>-1.17E-01</td>
<td>3.40E-01</td>
</tr>
<tr>
<td>Maximum depth</td>
<td>-2.50E-01</td>
<td>-1.10E-01</td>
</tr>
<tr>
<td>Number of bioluminescence events</td>
<td>4.80E-02</td>
<td>3.00E-02</td>
</tr>
</tbody>
</table>

Figure 7. Number of bioluminescence events detected in the bottom of a dive in function of the number of PCA per bottom. Graph A represents this relationship in day period, and the graph B represents this relationship during the night.

Bioluminescence cause or reaction of the SES foraging activity?

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research is needed using new loggers allowing the three-dimen-
sional reconstruction of the SES trajectory during dives in combi-
nation with new highly sensitive light sensors (allowing an
improved distance detection and higher sampling rate) and
accelerometers. Furthermore, highly sensitive cameras triggered by
bioluminescence flashes could characterize the type of biolumines-
cent organisms. The objectives of this further work might be stud-
ying the succession of the three following phenomena: changes in
direction, bioluminescence events and PCA. Such work would
move forward in the understanding of a possible use of biolumi-
nescence in the foraging behavior of the predator.

Despite the fact that the limited detection distance and sampling
rate of the photodiode prevent us to obtain a full description of bio-
oluminescent events, the new results bring new insights. Indeed, a
total of 37% of the bioluminescence events occurred within 3-s of
a PCA, which is much higher than expected just by chance and
which suggests a functional link between bioluminescence and
predation of SES. Furthermore, the vast majority of them (69%)
were detected exactly at the same time as a PCA, which is in line
with the fact that bioluminescence could be a mechanistic reaction
of the predator activity. Nevertheless, 19% of them preceded a PCA,
which signifies that bioluminescence was present before the begin-
ning of the foraging activity and hence could be used as an attrac-
tive event for the SES. However, it is noteworthy that PCA
occurred also during dive in the absence of detected biolumines-
cence events (Fig. 7). As already mentioned, the photodiode could
miss some bioluminescence events in the case where they were
outside the detection range or the viewing angles of the sensor or
even if they were too short in duration. It is also possible that not
all SES prey is bioluminescent, as we mentioned previously, and
would explain why PCA could be detected without biolumines-
cence. At this stage, to determine whether bioluminescence is used
by SES to detect their prey or is emitted as mechanism response or
as a defense behavior in response to the SES passage remains a chal-
lenge, and it is rather likely that both three assumptions are true.

Bioluminescence is a common feature of the marine environ-
ment. It constitutes the only source of light at deep depth and for
moonless nights. Therefore, deep diving mammals are likely to
key on bioluminescence organisms when searching for prey.
Despite the fact that our study was focused on a possible role of
the vision in foraging activity of SES, it is possible that SESs
depend on other sensory channels to locate their prey. Pinnipeds,
which do not echolocate, have to rely on other senses to detect
and locate their prey. For instance, they are known to rely on the
tactile sense of their innervated facial vibrissae or whiskers for
underwater orientation and foraging by detecting vibration fields
produced by moving prey (46). Audition is another likely candidate
to locate prey fields. Indeed, elephant seals have very good
hearing abilities and detect sounds better under water than in air
(47). With all these possibilities, it is likely that SESs rely on
hierarchical and multisensorial channels such as hearing, vision
and tactile senses to detect and locate their preys. Hearing is
likely to be used at larger scale than vision and the vibrissae
vibrations detection, which may only be efficient at short ranges.

CONCLUSION

In this study, we chronologically investigated the detected biolu-
minescence events with the foraging ones. We showed that the
bioluminescence was positively related to PCA, which comforted
the previous results. Theoretically, it could have been possible to
determine whether the detection of bioluminescence takes place
before or after the foraging. However, the measurement range of
the photodiode is being limited to less than 3 m around the mov-
ing animal, and this did not allow to investigate whether the bio-
oluminescence was present long before the foraging. Nevertheless,
we managed to determine the chronology of the events within a
period of 3 s. These results remain promising but they highlight
the need to develop more powerful and sensitive bioluminescence
devices in order to be able to accurately report on the relationships
existing between bioluminescence and organisms in situ.

Acknowledgements—The authors would like to thank the IPEV logistical
staff as well as all the colleagues and volunteers for their work in the
field, with the special acknowledgment of the invaluable field
contribution of N. El Ksabi and G. Bessigneur.

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