

NEW DATA ON THE DISTRIBUTION OF *Spatulodinium pseudonociluca* (NOCTILUCALES: KOFOIDINIACEAE) IN THE MEXICAN PACIFIC

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ABSTRACT. In this paper the distribution of the dinoflagellate *Spatulodinium pseudonociluca* in different areas of the Mexican Pacific is depicted based on samples gathered during 2005-2010. This species is first recorded for Bahía de los Ángeles, Loreto and Bahía de Mazatlán in the Gulf of California, and in the southwest portion of the Mexican Pacific at Bahía de Acapulco, Guerrero and Salina Cruz, Oaxaca. This species appears in the study area mainly during the winter-spring period. The mature cells of *S. pseudonociluca* range from 100-173 µm in length and 89-120 µm in width. Cell size of the gymnodinioid stages observed in Bahía de La Paz ranged from 90 to 190 µm in length.

Keywords: *Spatulodinium pseudonociluca*, Gulf of California, Noctilucales, dinoflagellates.

Nuevos datos sobre la distribución de *Spatulodinium pseudonociluca* (Noctilucaceae: Kofoidiniaceae) en el Pacífico Mexicano

RESUMEN. Se presenta la distribución del dinoflagelado *Spatulodinium pseudonociluca* en diferentes áreas del Pacífico Mexicano con base en muestras obtenidas durante el periodo 2005-2010. Esta especie se registra por primera vez para la Bahía de Los Ángeles, Loreto y Bahía de Mazatlán en el Golfo de California y en la Bahía de Acapulco, Guerrero, y Salina Cruz, Oaxaca, en la porción suroccidental del Pacífico Mexicano. En el área de estudio *S. pseudonociluca* se presenta principalmente en el periodo invierno-primavera. Las células maduras de *S. pseudonociluca* midieron 100–173 µm de largo, y 89–120 µm de ancho; los estadios gymnodinioides observados en la Bahía de La Paz midieron 90–190 µm de largo.

Palabras Clave: *Spatulodinium pseudonociluca*, Gulf of California, Noctilucaceae, dinoflagelados.

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INTRODUCTION

Taxonomy and distribution of naked dinoflagellates are scarcely studied in Mexico. Most studies on naked dinoflagellates have focused on species that form harmful blooms such as *Cochlodinium polykrikoides*, *Gymnodinium catenatum*, *Gyrodinium falcatum*, *Gyrodinium striatum* and *Karenia mikimotoi* (Cortés-Altamirano, 1987; Alonso-Rodríguez & Ochoa, 2004; Gárate-Lizárraga *et al.*, 2006; 2008; 2009). Only recent studies are concerned with the distribution of naked dinoflagellates (Gárate-Lizárraga & Verdugo-Díaz, 2007; Gárate-Lizárraga *et al.*, 2007, 2009, 2010a; 2010b). These reports were possible due to the study of living cells. Although most naked dinoflagellates are normally deformed or destroyed by sampling nets and fixative agents, some species are not totally damaged and can be identified during a routine analysis of phytoplankton (Hernández-Becerril & Bravo-Sierra, 2004; Okolodkov & Gárate-Lizárraga, 2006; Gárate-Lizárraga *et al.*, 2010a; 2010b).

The Class Noctiluiphyceae and their Order Noctilucales encompass three families of peculiar dinoflagellates: Noctilucaceae, Leptodiscaceae, and Kofoidiniaceae (Taylor, 1976; Fensome *et al.*, 1993). They differ from most others

in that the cell of the main stage of the life-cycle is diploid and its nucleus does not show a dinokaryotic organization. These cells are very large, from 1 to 2 mm in diameter, and are filled with large buoyant vacuoles. Kofoidiniaceans are characterized typically by (a) retention of both flagella and recognizable episome (with an extracellular discoid or hemispherical capsule in mature cells) and hyposome throughout their life-cycle; (b) high degree of vacuolization in mature cells, and (c) very complex life-cycle involving stages which, taken in isolation, could be (and have been) considered to represent different species (Cachon & Cachon, 1967; Fensome *et al.*, 1993).

Kofoidiniaceans are free-living marine, mainly non-photosynthetic dinoflagellates that have been poorly studied in the seas adjacent to Mexico (Gárate-Lizárraga *et al.*, 2007; 2009). According to Fensome *et al.* (1993), this family includes three genera: *Kofoidinium* Pavillard, 1928, *Spatulodinium* J. Cachon *et* M. Cachon, 1967, and *Pomatodinium* Cachon *et* Cachon-Enjume, 1966. At present the unique valid species currently belonging to *Spatulodinium* is *S. pseudonociluca* (Pouchet) J. Cachon *et* M. Cachon *ex* Loeblich Jr. *et* Loeblich III, 1969. However, Gómez *et al.* (2010), using molecu-

lar tools found a second species in the Gulf of Lyon (*Spatulodinium* sp.). Life cycle of the kofoidiniaceans based on live specimens collected from the north-western Mediterranean was investigated by Cachon and Cachon (1967). They recognized six stages, labelled 'A' to 'F'. Using molecular data, Gómez *et al.* (2010) confirmed that *Gymnodinium lebouriae* is a life stage of *S. pseudonociluca*. For the Mexican Pacific, few records of *S. pseudonociluca* have been reported (Okolodkov & Gárate-Lizárraga, 2006; Gárate-Lizárraga *et al.*, 2007; 2009). New range extensions as well as immature life stages of *S. pseudonociluca* are reported here for the first time in the Mexican Pacific region. Additionally, information about its morphology and ecology is provided.

MATERIAL AND METHODS

Samples were collected at eight sites at the Pacific coast of Mexico (Fig. 1): Bahía de La Paz, Los Cabos region, off Bahía Magdalena, Loreto (Baja California Sur), Bahía de Los Ángeles (western Baja California), Bahía de Mazatlán (southeastern Gulf of California), Bahía de Acapulco (central Mexican Pacific), and Salina Cruz (Gulf of Tehuantepec). However, this study was principally done at 2 sampling stations in Bahía de La Paz (Fig. 2). The study areas have been described recently (Alonso-Rodríguez & Ochoa, 2004; Okolodkov & Gárate-Lizárraga 2006; Gárate-Lizárraga *et al.*, 2006; 2007; 2009).

Forty two phytoplankton samples were collected at sampling station 1 (off PEMEX refin-

ery) in Bahía de La Paz (Fig. 2) from January 2009 through December 2010 with surface tows and vertical hauls from a 15-m depth with 20 µm mesh hand net. A portion of each tow was immediately fixed with Lugol acid solution and later preserved in 4% formalin. A subsample was taken for live phytoplankton observations. Additional 18 surface water samples were collected for identification and cell counting. At Station 2 (Cuenca Alfonso), nine vertical net hauls were conducted at a 60-m depth site from February through December 2010 (Fig. 2). Eight net phytoplankton samples were collected in Loreto, from February to December 2008. Ten samples were collected in Bahía de Los Angeles from February through December 2006. Nine vertical net hauls were conducted from 15-m depth to surface at Stations 3, 4, 5, 6, 7, 8, 9 and 10 in July and August 2010 in Los Cabos Region. Four samples were collected in Bahía de Mazatlán in May and June 2005. Three net samples were collected in Bahía de Acapulco in November 2009. Four net samples were collected offshore from Puerto Salina Cruz, Oaxaca during May 26 through 29, 2008. Seawater temperature was recorded at all sampling stations with a bucket thermometer. Temperature and salinity at Station 2 (Cuenca Alfonso) were recorded with a data recorder (SeaBird 19 CTD). Cell counts were made in 2-mL settling chambers under an inverted Carl Zeiss phase-contrast microscope (Germany). A compound Olympus CH2 microscope (Japan) was used to measure cells. A digital SONY Cyber-shot 8.1 MP camera was used for recording images. Other microscopic images were taken (Leica, Solms, Germany).



Figure 1. Sampling sites located at different areas from the Mexican Pacific. 1) Bahía de La Paz, 2) Los Cabos region, 3) Loreto, 4) Bahía de Los Ángeles, 5) Bahía Magdalena, 6) Bahía de Mazatlán, 7) Bahía de Acapulco, and 8) Salina Cruz.

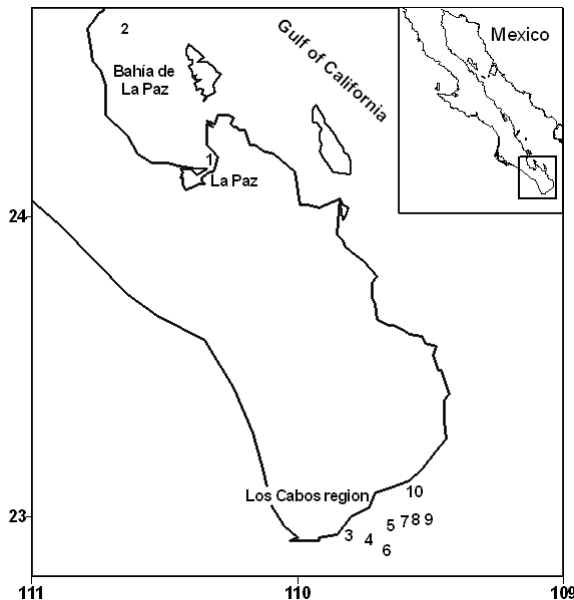


Figure 2. Sampling stations in Bahía de La Paz, and Los Cabos region, at the southern end of the Baja California Peninsula. 2) Cuenca Alfonso.

RESULTS AND DISCUSSION

Systematic account of *Spatulodinium pseudonociluca* (Pouchet 1885) J. Cachon et M. Cachon ex Loeblich Jr. et Loeblich III, 1969

Basionym: *Gymnodinium pseudonociluca* Pouchet, 1885

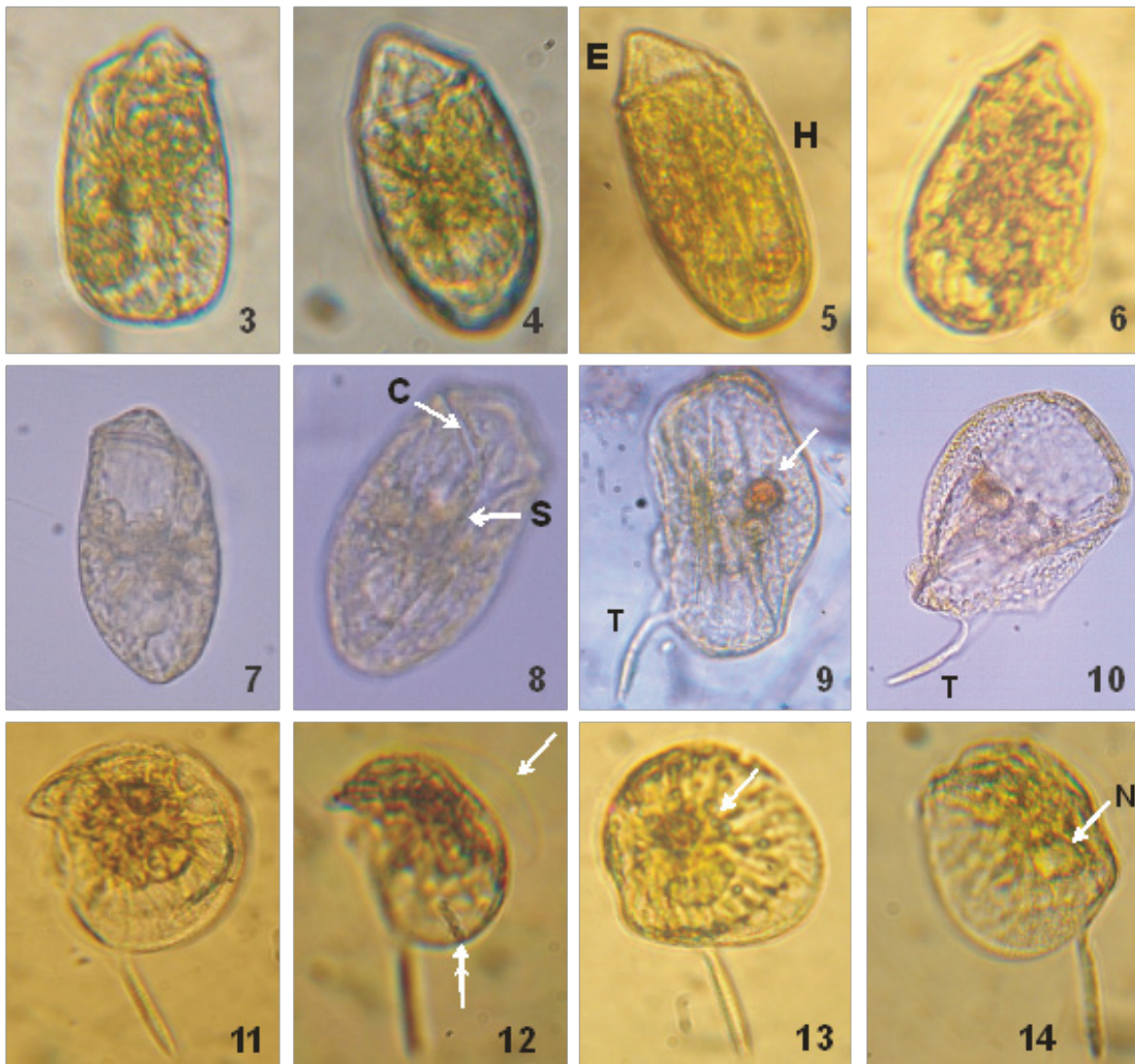
Synonyms: *Gymnodinium pyrocystis* Jørgensen, 1912; *Gymnodinium fulgens* Kofoed et Swezy 1921; *Gymnodinium conicum* Kofoed et Swezy 1921; *Gymnodinium lebouriae* Pavillard 1921.

Morphological characteristics, abundance, and cell size of *S. pseudonociluca*

The species of the family Kofoidiniaceae have been poorly studied and particularly so in Mexico, where only two genera, *Kofoidinium* and *Spatulodinium* have been reported (Okolodkov & Gárate-Lizárraga, 2006; Gárate-Lizárraga et al., 2007, 2009). The immature morphotype of *S. pseudonociluca* has the epicone, hypocone, cingulum and the sulcus well-differentiated (Figs. 3-8). Some gymnodinioid stages of *S. pseudonociluca* showed a well-developed tentacle (Figs. 9-10). Mature morphotype of *S. pseudonociluca* has a tentacle that resembles that of *Noctiluca* (Figs. 11-14). The mature cell of *S. pseudonociluca* has a subconical to round shape, deformed into a shallow cone by pushing in the left side so that the right side became somewhat convex. Ac-

cording to Pouchet (1885), the entire epicone is retractile and may almost completely disappear within the body, which is striated with radiating fibrils (Figs. 11 and 13). This species is characterized by a very small epicone and in the noctiluroid or mature stage has a long unstriated tentacle projecting at a right angle to the longitudinal axis of the body, in the sulcal region. The highly transparent extracellular hemispherical dome, known as shell or 'coque' that emerges from the epicone is shown in Fig. 12. Some mature specimens tend to be round and others are slightly oval. The nucleus is round, and appeared as a pale area in the center of the cell (Fig. 14). In some specimens it was not easy to observe the undulated flagellum. Some Lugol-fixed mature stages of *S. pseudonociluca* clearly showed the flagellum (Figs. 16, 21, 22, and 25). This species present an elongate tentacle which varied in length in the specimens observed in this study. Anterior to the tentacle, a small lip is observed (Fig. 18). In general, length of mature stage cell of *S. pseudonociluca* was 100–173 μm , and width was 89–120 μm ; gymnodinioid stages observed in Bahía de La Paz were 90–190 μm long.

Spatulodinium pseudonociluca was found in all study areas of the Mexican Pacific considered here. The species was observed from 2008 through 2010 at sampling station 1 in Bahía de La Paz. *S. pseudonociluca* was observed for the first time in 2008 during a multi-species microalgae red tide (Gárate-Lizárraga et al., 2009). In bottle samples collected in June 2008, this species reached densities from 1000 to 2000 cells L^{-1} . In November and December 2008, this species was only recorded in net samples. *S. pseudonociluca* was observed mostly from January to June 2009, with a density of 200 and 800 cells L^{-1} in May and June 2009, respectively. This species was again observed from February through July and from September through November 2010 in net phytoplankton samples. Immature life stages of *S. pseudonociluca* were observed in March, April, and May 2009 and May, July and October 2010 (Figs. 3, 4, 5, 6, and 7-8, respectively). Mature specimens of *S. pseudonociluca* were first observed in this bay during a red tide occurred in June 2008 (Figs. 11 and 12). At Cuenca Alfonso, 18 mature specimens of *S. pseudonociluca* were identified from February through August and 4 and 2 cells in November and December 2010, respectively (Figs. 15 and 16). In the Los Cabos region, 6 and 8 mature specimens of this species were identified in July and August 2010, respectively (Figs. 17 and 18). In Loreto, 2 mature specimens were observed in March 2008 and 2 in May, 2005. In Bahía de Los Angeles 5 mature cells of *S. pseudonociluca*



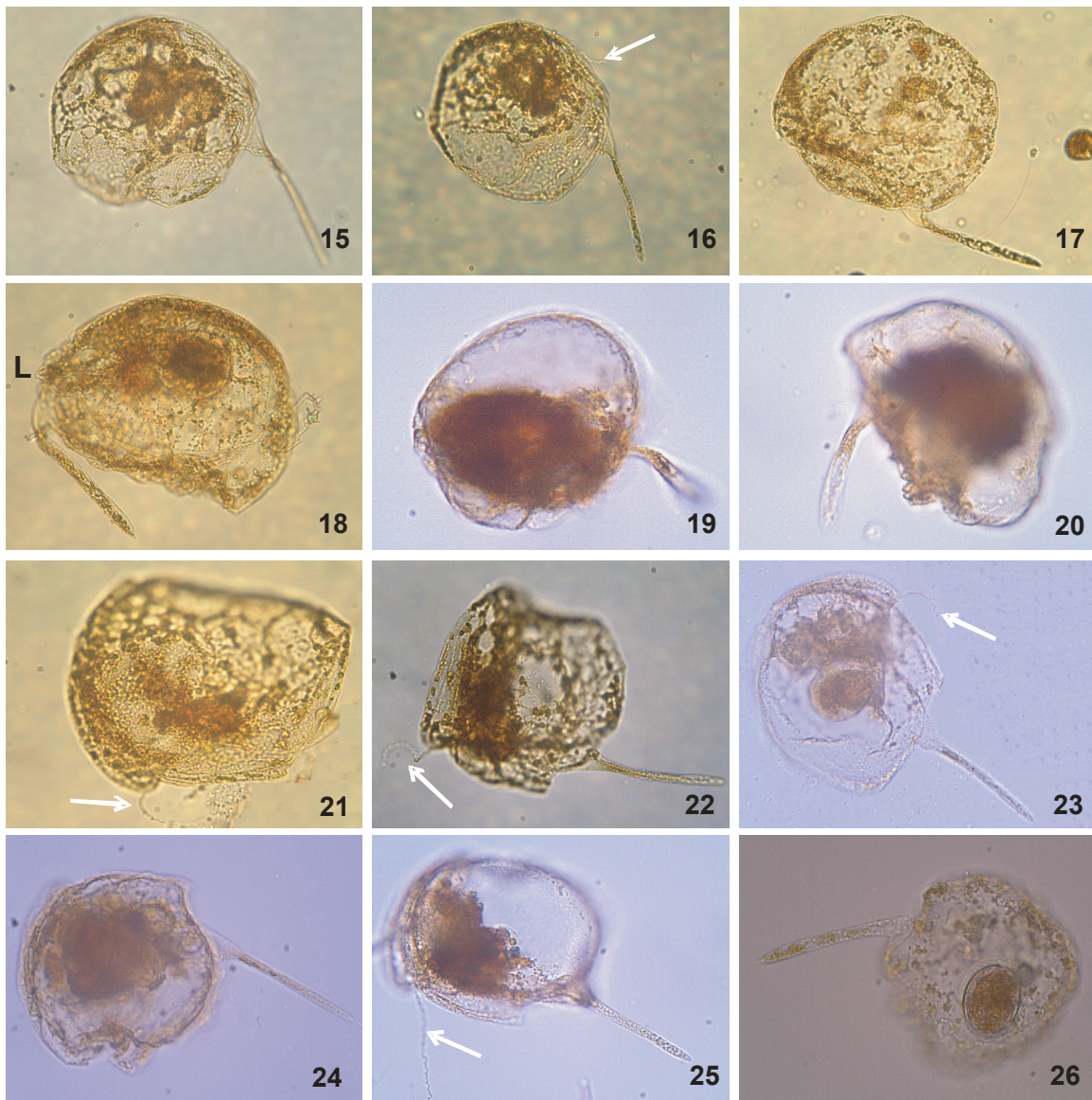
Figures 3–14. Light microscope images of *Spatulodinium pseudonociluca* found in sampling station 1 in Bahía de La Paz. Figs. 3–8 immature specimens of *S. pseudonociluca* collected on 10, February 2009, 14, March 21, 2009, January 2010, and May 21, 2010, respectively. Figs. 9–10 show specimens in gymnodinioid stages with tentacle (almost mature?). Figs. 11–12 are specimens of *S. pseudonociluca* collected in June 2008. Arrow in Fig. 12 indicates the shell or “coque”; double arrow indicates the undulate flagellum. Figs. 13 and 14 are mature specimens collected in February and June 2010. Arrow in Fig. 13 shows green inclusion around cell. Arrow in Fig. 14 indicates the nucleus of the cell. E= Epicone, H= Hipocone, C= Cingulum, S= Sulcus, and T= Tentacle.

luca were identified among samples collected in March and May 2006 (Figs. 19 and 20). In Bahía Magdalena, 10 mature specimens of *S. pseudonociluca* were identified from February through June 2009 and 2 and 4 cells in May and April 2010, respectively (Figs. 21 and 22). In Bahía de Mazatlán, 2 mature specimens were identified in May 2005 and 2 in June, 2005 (Fig. 23). In Bahía de Acapulco, 2 mature specimens were identified in November 2009 (Fig. 24). In Salina Cruz, 3 mature specimens of *S. pseudonociluca* and *Spatulodinium* sp. were identified from samples of May 2008 (Fig. 25,

and 26).

Worldwide distribution of *Spatulodinium pseudonociluca*

First reports of this species are based on the specimens described as *Gymnodinium pseudonociluca* from the coast of Brittany, south-eastern English Channel (Pouchet, 1885). Because some immature stages of *S. pseudonociluca* were identified as different species the real geographical was underestimated. Worldwide distribution of *S. pseudonociluca* is sum-



Figures 15–26. Light photomicrographs of mature specimens of *Spatulodinium pseudonociluca* from different areas from the Mexican Pacific. Figs. 15–16 show specimens of *S. pseudonociluca* collected at Cuenca Alfonso. Figs. 17–18 show specimens from Los Cabos region. L in Fig. 18 indicates a small lip of *S. pseudonociluca*. Figs. 19–20 show specimens of *S. pseudonociluca* from Bahía de los Ángeles. Figs. 21–22 show specimens of *S. pseudonociluca* from Bahía Magdalena. Fig. 23 shows a specimen of *S. pseudonociluca* found in Bahía de Mazatlán. Fig. 24 shows a specimen of *S. pseudonociluca* found in Bahía de Acapulco. Figs. 25–26 show specimens of *S. pseudonociluca* and *Spatulodinium* sp., respectively, observed in May 2008, in Salina Cruz. Arrowheads indicate the undulate flagellum in mature cells of *S. pseudonociluca*.

marized in Table 1. The new records from many disparate areas suggest that real geographical distribution has been underestimated and *S. pseudonociluca* could be cosmopolitan.

Distribution in the Mexican Pacific

Mature cells of *Spatulodinium pseudonociluca* were first reported along the west coast of the Baja California Peninsula, in Bahía Magdalena and Bahía de La Paz (Okolodkov &

Gárate-Lizárraga, 2006; Gárate-Lizárraga *et al.*, 2007; 2009). This species is here first reported for Bahía de Los Ángeles, Los Cabos region, Loreto, Bahía de Mazatlán, Bahía de Acapulco, and the Gulf of Tehuantepec. Also in this study, the presence of gymnodinioid stages of *S. pseudonociluca* in Bahía de La Paz is reported for the first time.

In general, in Bahía de La Paz, *S. pseudonociluca* occurred at temperatures

Table 1. Worldwide records of *Spatulodinium pseudonociluca*.

Reported as	Locality	References
<i>Gymnodinium pseudonociluca</i>	Brittany, France, SE English Channel	Pouchet (1885)
<i>G. lebouriae</i>	NW Mediterranean Sea	Pavillard (1921)
<i>G. pseudonociluca</i> , <i>G. fulgens</i>	Off California coast	Kofoed & Swezy (1921)
<i>G. pseudonociluca</i> , <i>G. viridis</i>	Brittany, France, SE English Channel	Lebour (1925)
<i>Spatulodinium pseudonociluca</i>	Coastal Ligurian Sea (NW Mediterranean)	Cachon & Cachon (1967)
<i>S. pseudonociluca</i>	Adriatic Sea	Bakran-Petricoli <i>et al.</i> (1998), Jasprica & Carié (2007)
<i>S. pseudonociluca</i>	NE and NW coasts of England, off Scotland	Dodge (1982)
<i>S. pseudonociluca</i>	Bulgarian waters, Black Sea	Stoyanova (1999)
<i>S. pseudonociluca</i>	Peter the Great Bay, Russia, western Sea of Japan	Konovalova & Selina (2002)
<i>S. pseudonociluca</i>	Odessa Bay, Black Sea	Terenko (2005)
<i>S. pseudonociluca</i>	Canary Islands	Gil-Rodríguez <i>et al.</i> (2003)
<i>S. pseudonociluca</i>	Off Bahía Magdalena, southern Baja California	Okolodkov & Gárate-Lizárraga (2006)
<i>S. pseudonociluca</i>	Coastal waters of Italy	Avancini <i>et al.</i> (2006)
<i>S. pseudonociluca</i>	Peru-Chile Current	Gómez & Furuya (2007)
	Equatorial Pacific Ocean	Gómez & Furuya (2007)
<i>S. pseudonociluca</i>	English Channel	Gómez & Souissi (2007)
<i>S. pseudonociluca</i>	Bahía de La Paz, Gulf of California	Gárate-Lizárraga <i>et al.</i> (2009)
<i>S. pseudonociluca</i>	Helgoland and Sylt islands (North Sea)	Hoppenrath <i>et al.</i> (2009)
<i>S. pseudonociluca</i>	Basque coast (northern Spain)	Revilla <i>et al.</i> (2009)
<i>S. pseudonociluca</i>	Costa Rica, Pacific Central America	Viquez & Hargraves (2009)
<i>S. pseudonociluca</i>	Gulf of Mexico	Steidinger <i>et al.</i> (2009)
<i>S. pseudonociluca</i>	Coast of Marseille, NW Mediterranean Sea	Gómez <i>et al.</i> (2010)
<i>S. pseudonociluca</i>	Derwent River estuary, Tasman Peninsula	Hallegraeff <i>et al.</i> (2010)
<i>S. pseudonociluca</i>	Open Mediterranean Sea	Gómez (2010)

ranging from 19 °C to 30 °C, coinciding with Gómez and Furuya (2007). Salinity was 34.25–35 psu. In Los Cabos region, the specimens were recorded in a range of temperature from 24 °C to 30 °C. At Cuenca Alfonso, temperature ranged from 21.5 °C to 29.5 °C. In Bahía Magdalena, the temperature ranged from 16 °C to 26 °C. In Bahía de Los Angeles, it ranged

from 16 °C to 26 °C. In Bahía de Acapulco, the temperature at the time of finding was 29 °C. In Salina Cruz, temperature was 25°C and salinity was 32.8–34.4 psu.

According to Gárate-Lizárraga *et al.* (2009; 2010a; 2010b), heterotrophic dinoflagellates have become an important component of phy-

toplankton during upwelling conditions in Bahía de La Paz. Heterotrophic dinoflagellates are common in marine pelagic systems and have a potentially important role as herbivores (Hansen, 1991; Jeong *et al.*, 2007). *S. pseudonociluca* was traditionally considered exclusively heterotrophic (Larsen & Sournia, 1991). Terenko (2005) observed inclusions of benthic diatoms in the cytoplasm of *S. pseudonociluca*. In this study, small unidentified cell of diatoms (not illustrated), a cell of *Prorocentrum* sp. (Fig. 26), and some other inclusions were observed in some specimens. Gómez *et al.* (2010) have shown chloroplasts in *S. pseudonociluca* using epifluorescence microscopy. In our study, some spherical green inclusions were found in both immature and mature stages (Figs. 3–10). Some red spots were found in immature stages (Fig. 9). Koike *et al.* (2005) suggest that studies of the characteristics of *Spatulodinium* plastids are necessary to improve determination of whether their chloroplasts are keptoplastids or if they derive from ancient endosymbiosis, as had occurred in other dinoflagellates. Although the genus *Spatulodinium* is considered monotypic, Gómez *et al.* (2010) found that molecular data indicate at least a second species within the genus. The specimen reported as *Spatulodinium* sp. (Gómez *et al.*, 2010; Fig. 1Q) is quite similar to findings in Salina Cruz in May 2008 (Fig. 26). The specimens of *S. pseudonociluca* found in this study showed great morphological variation and wide distribution in the Mexican Pacific. Molecular studies are needed to corroborate whether there is more than one species of the *Spatulodinium* genus. Some authors have suggested that *S. pseudonociluca* have been considered as non-indigenous plankton or introduced species for other areas (Gómez & Boicenco, 2004; Terenko, 2005; Okolodkov *et al.*, 2007). However, this species seems to be well distributed in the Mexican Pacific coastal waters, which discard at the possibility that this species could be invasive in this area. Although Lugol-fixed mature specimens of *Spatulodinium* could be easily identified, immature stages were seen in fixed samples. The use of live phytoplankton samples in this study led to find some immature stages. Live phytoplankton samples must be complementary in the study of naked dinoflagellates.

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