

Durinskia yucatanensis sp. nov. (Peridinales: Kryptoperidiniaceae), a new planktonic dinoflagellate species, and its habitat in coastal Yucatan waters, Gulf of Mexico

Durinskia yucatanensis sp. nov. (Peridinales: Kryptoperidiniaceae), una nueva especie de dinoflagelado planctónico, y su hábitat en aguas costeras de Yucatán, Golfo de México

Yuri B. Okolodkov^{1*}, Victor A. Cervantes-Urieta², Ana C. Aguilar-Trujillo³, Fany del C. Merino-Virgilio³, Giuliana Cruz-Trejo³, Dora A. Huerta-Quintanilla⁴, Karen A. Steidinger⁵, Ismael Gárate-Lizárraga⁶, Lorena M. Durán-Riveroll^{7,8} and Jorge A. Herrera-Silveira³

Recibido: 19 de junio de 2023.

Aceptado: 02 de octubre de 2023.

Publicado: abril de 2024.

¹ Universidad Veracruzana, Instituto de Ciencias Marinas y Pesquerías (ICIMAP-UV), Laboratorio de Botánica Marina y Planctología. Calle Mar Mediterráneo 314, Fracc. Costa Verde, Boca del Río, Veracruz, 94294, Mexico

² Programa de Doctorado en Recursos Naturales y Ecología, Facultad de Ecología Marina, Universidad Autónoma de Guerrero (UAGro). Av. Gran Vía Tropical 20, Fracc. Las Playas, Acapulco, Guerrero, 39390, Mexico

³ Centro de Investigación y Estudios Avanzados – Instituto Politécnico Nacional (CINVESTAV-IPN), Unidad Mérida, Departamento de Recursos del Mar. Carretera Antigua a Progreso km 6, Col. Gonzalo de Guerrero, Mérida, Yucatán, 97310, Mexico

⁴ Centro de Investigación y Estudios Avanzados – Instituto Politécnico Nacional (CINVESTAV-IPN), Unidad Mérida, Departamento de Física Aplicada, Laboratorio Nacional para el Estudio de Nano y Biomateriales. Carretera Antigua a Progreso km 6, Col. Gonzalo de Guerrero, Mérida, Yucatán, 97310, Mexico

⁵ Fish & Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 100 8th Ave SE, St. Petersburg, Florida, 33701, USA

⁶ Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas (IPN-CICIMAR), Departamento de Plancton y Ecología Marina. Av. Instituto Politécnico Nacional s/n, Apdo. Postal 592, La Paz, Baja California Sur, 23096, Mexico

⁷ CONACYT - Departamento de Biotecnología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Carr. Tijuana-Ensenada 3918, Zona Playitas, Ensenada, Baja California, 22860, Mexico

⁸ Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung (AWI), Department of Ecological Chemistry, Am Handelshafen 12, 27570, Bremerhaven, Germany

*Corresponding author:

Yuri B. Okolodkov: yuriokolodkov@yahoo.com

To quote as:

Okolodkov, Y. B., V. A. Cervantes-Urieta, A. C. Aguilar-Trujillo, F. del C. Merino-Virgilio, G. Cruz-Trejo, D. A. Huerta-Quintanilla, K. A. Steidinger, I. Gárate-Lizárraga, L. M. Durán-Riveroll & J. A. Herrera-Silveira. 2024. *Durinskia yucatanensis* sp. nov. (Peridinales: Kryptoperidiniaceae), a new planktonic dinoflagellate species, and its habitat in coastal Yucatan waters, Gulf of Mexico. *Hidrobiológica* 34 (1): 1-12.

DOI:10.24275/LSHU4081

ABSTRACT

Background: In the coastal waters of the northern Yucatan Peninsula, in the southeastern Gulf of Mexico, numerous pelagic algal blooms have been recorded in the 21st century. In August 2010, an unknown small-sized Peridinales species caused an intense bloom in the Sisal marina. In subsequent years, it was occasionally found at other sites along the Yucatan coast. **Goals:** The main objective of the present study was to name this dinoflagellate as a new species and determine its ecological preferences. **Methods:** Phytoplankton blooms were monitored from August 2011 to September 2014. Fixed cells of the studied species were examined in a JEOL JSM-7600F scanning electron microscope. Its ecological preferences were evaluated using multivariate permutational analysis and generalized additive models (GAM). **Results:** The name *Durinskia yucatanensis* (Dinophyceae: Peridinales) with the thecal plate formula $Po\ X\ 4' 2a\ 6'' 5c\ 4s(?)\ 5''' 2'''$ is proposed for a previously recorded Kryptoperidiniaceae species from the northern Yucatan coastal waters. Dissolved inorganic nitrogen positively correlated with cell abundances for both the exposed coast and marinas, especially in July-August, characterized by high water temperature (31-32 °C). Chlorophyll-*a* was the only parameter that presented significant spatio-temporal variability among years, months, and sampling sites. The GAM showed that temperature and salinity can predict changes in abundance in different study zones (exposed coast and marinas). The highest values were observed in the Progreso-Chicxulub area along the exposed coast in 2011 and only at Dzilam in marinas during all studied years. **Conclusions:** The species appears to prefer eutrophic conditions typical for marinas along the northern coast of Yucatan.

Keywords: autecology, new species, phytoplankton, scanning electron microscopy, thecal morphology.

RESUMEN

Antecedentes: En las aguas costeras del norte de la península de Yucatán, en el sureste del Golfo de México, numerosos florecimientos pelágicos de microalgas se han registrado en el siglo 21. En agosto de 2010, una especie pequeña y desconocida de Peridinales causó un florecimiento intenso en el puerto de abrigo de Sisal. En los años siguientes, se encontró ocasionalmente en otros sitios a lo largo de la costa de Yucatán. **Objetivo:** Nombrar a este dinoflagelado como una especie nueva para la ciencia y determinar sus preferencias ecológicas. **Métodos:** Los florecimientos de fitoplancton fueron monitoreados desde agosto de 2011 hasta septiembre de 2014. Las células se examinaron en un microscopio electrónico de barrido JEOL JSM-7600F. Sus preferencias ecológicas se evaluaron mediante análisis permutacional multivariante y modelos aditivos generalizados (GAM). **Resultados:** El nombre *Durinskia yucatanensis* (Dinophyceae:

¹ We dedicate this article to the memory of our colleague and friend, mentor and co-author Karen A. Steidinger (8 September 1938 – 11 June 2023).

Peridinales), cuya fórmula de placa teical $Po\ X\ 4' 2a\ 6''\ 5c\ 4s(?)\ 5''\ 2''''$, se propone para una especie de Kryptoperidiniaceae previamente registrada de las aguas costeras del norte de Yucatán. El nitrógeno inorgánico disuelto se correlacionó positivamente con la abundancia de células, tanto para la costa expuesta como para los puertos deportivos, especialmente en julio-agosto, caracterizados por una alta temperatura del agua (31–32 °C). La clorofila-*a* fue el único parámetro que presentó variabilidad espacio-temporal significativa entre años, meses y sitios de muestreo. Los GAM demostraron que la temperatura y la salinidad pueden predecir cambios en la abundancia en diferentes zonas de estudio (costa expuesta y puertos deportivos). Los valores más altos se observaron en el área de Progreso-Chicxulub a lo largo de la costa expuesta en 2011 y solo en Dzilam en marinas durante todos los años estudiados. **Conclusiones:** La especie parece preferir las condiciones eutróficas típicas de los puertos deportivos a lo largo de la costa norte de Yucatán.

Palabras clave: autecología, fitoplancton, microscopía electrónica de barrido, morfología teical, nueva especie.

INTRODUCTION

The northern Yucatan Peninsula is characterized by shallow waters at the seaside, extended sandy beaches, and mangroves. In some places, subaquatic vegetation is abundant and dominated by seagrasses (*Thalassia testudinum* Banks ex König, *Syringodium filiforme* Kützinger, and *Halodule wrightii* Ascherson) and green algae mainly of the genera *Caulerpa* J. V. Lamouroux, *Udotea* J. V. Lamouroux, *Halimeda* J. V. Lamouroux, *Penicillus* Lamarck, *Batophora* J. Agardh, and *Avrainvillea* Decaisne (Aguilar-Trujillo *et al.*, 2014, 2017; Okolodkov *et al.*, 2014). Along the coast, there are several marinas (Sisal, Chuburná, Uaymitún, Telchac, Dzilam and El Cuyo) and natural lagoons such as Chuburná and Río Lagartos, the latter with two fishing villages, San Felipe and Río Lagartos, on the shore. The marinas are subjected to anthropogenic influence, primarily fishery activities, and to accumulation of decomposing mangrove residues on the bottom. Some of these sites, such as Chuburná and Dzilam, are characterized by nutrient-rich underground water (Álvarez-Góngora & Herrera-Silveira, 2006; Morales-Ojeda *et al.*, 2010; Murgulet *et al.*, 2020) that discharges into the lagoon and the sea near the coast. There are no rivers along the Yucatan coast. These features are the marine part of a ring of cenotes (sinkholes with groundwater), better known as small continental water bodies in the Yucatan Peninsula, formed along the outer edge of the Chicxulub crater, produced by a meteorite collision during the Cretaceous about 65 million years ago (Connors *et al.*, 1996; Pope *et al.*, 1996). Groundwater discharges causes minor salinity variations. Three meteorological seasons can be distinguished: a dry season from March to early June; a rainy season from June to October; and the “nortes” (northerly winds) season with short periods of storms and strong winds coming from the north from November to February (Herrera-Silveira, 1993).

In August 2010, an unknown small-sized Peridinales species caused an intense bloom in the Sisal marina. In subsequent years, it was occasionally found at other sites along the Yucatan coast. It was assigned to the family Kryptoperidiniaceae, a monophyletic group of dinoflagellates known as “dinotoms” (due to the presence of plastids derived from diatoms), although a second (eukaryotic) nucleus was not observed, thus sharing its thecal features with both *Kryptoperidinium*

Lindemann (until now a monotypic genus; Tillmann *et al.*, 2023) and *Durinskia* Carty et Cox (Okolodkov *et al.*, 2020). By comparing both morphological and ecological characteristics, it was concluded that this species was different from all known *Kryptoperidinium* and *Durinskia* species, as well as from the other genera (*Blixaea* Gottschling, *Dinothrix* Pascher, *Galeidinium* M. Tamura et T. Horiguchi and *Unruhadinium* Gottschling) of the same family. However, no preference was given to either of these taxa in identifying the genus, and a name was not given to the new species then. The main objective of the present study was to reveal its ecological preferences. In addition, a name has now been assigned to this species for further reference.

MATERIAL AND METHODS

Phytoplankton blooms were monitored from 13 August 2011 to 8 September 2014 (Fig. 1). Samples were collected with a 2-liter Van Dorn bottle and fixed with acidic Lugol's solution. Nutrient concentrations (ammonium [NH₄], nitrates [NO₃], nitrites [NO₂], orthophosphates [PO₄], silicates [SiO₄] and urea [CH₄N₂O]) were determined according to spectrophotometric techniques (Strickland & Parsons, 1972). Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO₃, NO₂, and NH₄ concentrations. Surface water temperature (SWT), salinity, and dissolved oxygen (DO) were measured using a YSI Professional Plus multiparameter meter (Yellow Springs, Ohio, USA). Chlorophyll-*a* (chl-*a*) was determined by the extraction of pigments using a 90% acetone solution followed by spectrophotometric determination and recalculation formula (Jeffrey & Humphrey, 1975; Parsons *et al.*, 1984).

Cells were counted in a 1-mL Sedgwick-Rafter chamber on an Olympus CK2 inverted microscope (Olympus Optical Co., Ltd., Japan) equipped with an LCAch N 40x/0.55 PhP objective. Fixed specimens were also examined in a JEOL JSM-7600F (JEOL, Ltd., Tokyo, Japan) scanning electron microscope (SEM) at a working distance of 15 mm, a voltage of 5.0 kV and a low secondary electron detector (LEI) after a preliminary wash in distilled water followed by dehydration in a series of ethanol solutions of increasing concentration (30, 50, 70, 90, and 100%). Specimens were then air dried on 0.5” aluminum mounts and sputter-coated with gold-palladium using a Polaron SC7640 High-Resolution Sputter Coater (Quorum Technologies, Newhaven, SXE, UK).

Permutational multivariate analysis of variance (PERMANOVA) and Euclidian distance analyses were applied to determine any significant differences among physicochemical variables: SWT (°C), salinity, DO (mg L⁻¹), phosphates (µM), silicates (µM), urea (µM), chl-*a* (mg m⁻³) and DIN (µM). Years (2011, 2012, 2013, and 2014) and months were used as fixed factors for each zone (exposed coast and marinas) (Anderson, 2014). PERMANOVA was also applied to evaluate spatio-temporal differences in cell abundances (cell L⁻¹) of this new *Durinskia* species among sampling sites and months, using the same fixed factors, the Bray-Curtis similarity distance, and Adonis function of the vegan R package (Oksanen *et al.*, 2013). Similarly, spatio-temporal variation of cell abundances was visualized using a bubble chart and ggplot2 function (Lee *et al.*, 2020).

To reveal relationships between the response variable (cell abundance) and the explanatory variables (physicochemical factors) (Wood, 2006; Zuur *et al.*, 2007), generalized additive models (GAM) with a negative binomial distribution and a log link function were used to adjust the data on cell density for the effect of the physicochemical variables.

The models were constructed for each year (2011 to 2014) and zone (exposed coast and marinas) using gam function in the mgcv2 package, suggesting smooth effects of each explanatory variable on the response variable (the *Durinskia* sp. cell abundance). Previously, to avoid multicollinearity of the explanatory variables, the Pearson correlation was estimated, excluding the highly ($r \geq 60\%$) correlated variables for each constructed model. In addition, the Akaike information criterion was used to choose the best-adjusted model (Symonds & Moussalli, 2011). All analyses were performed using R (R Core Team, 2022) and RStudio (RStudio Team, 2015).

RESULTS

Taxonomy

Morphological description of the species has been previously published (Okolodkov *et al.*, 2020). It was not assigned to any genus of the family Kryptoperidiniaceae; however, as stated, by comparing both morphological and ecological characteristics, our species is different from all known *Kryptoperidinium* and *Durinskia* species in having a larger 1a plate compared to plate 2a (Fig. 2E). Morphological differences between our species and the genus *Kryptoperidinium* (Table 1) allowed us to assign the species to the genus *Durinskia*. Herein, additional SEM micrographs are given to complement the previously published description, accompanied by SEM and light microscope images.

Phylum Dinoflagellata (Bütschli) Fensome, Taylor, Norris, Sarjeant, Wharton et Williams, 1993

Subphylum Dinokaryota Fensome, Taylor, Sarjeant, Wharton et Williams, 1993

Class Dinophyceae Pascher, 1914

Subclass Peridiniphyceidae Fensome, Taylor, Sarjeant, Wharton et Williams, 1993

Order Peridinales Haeckel, 1894

Suborder Peridiniineae Poche, 1913

Family Kryptoperidiniaceae Lindemann, 1926

Genus *Durinskia* Carty et Cox, 1986

Durinskia yucatanensis Okolodkov, Steidinger et Gárate-Lizárraga *sp. nov.*

Figs. 3-7 in Okolodkov *et al.*, 2020 and Figs. 2-3 herein.

Description: Published in: Okolodkov *et al.*, 2020 (A Kryptoperidiniaceae species (Dinophyceae: Peridinales) blooming in coastal Yucatan waters, Gulf of Mexico. Protistology 14(2): 58–69, 7 figs, 1 table 1; as Kryptoperidiniaceae species).

Affinities: Out of the six to seven *Durinskia* species that have been described so far, this species is morphologically (in cell size and thecal morphology) closer to *Durinskia kwazulunatalensis* N. Yamada, Sym et Horiguchi (Yamada *et al.*, 2017), described from a marine coastal environment in South Africa. The latter is 18.4–27.4 μm long, with the median, descending, and displaced approximately by its own width, the 1a and 2a plates of almost the same size, the suture between them approximately central on the dorsal side of the epitheca, a trapezoidal 3" plate and a pentagonal 4" plate.

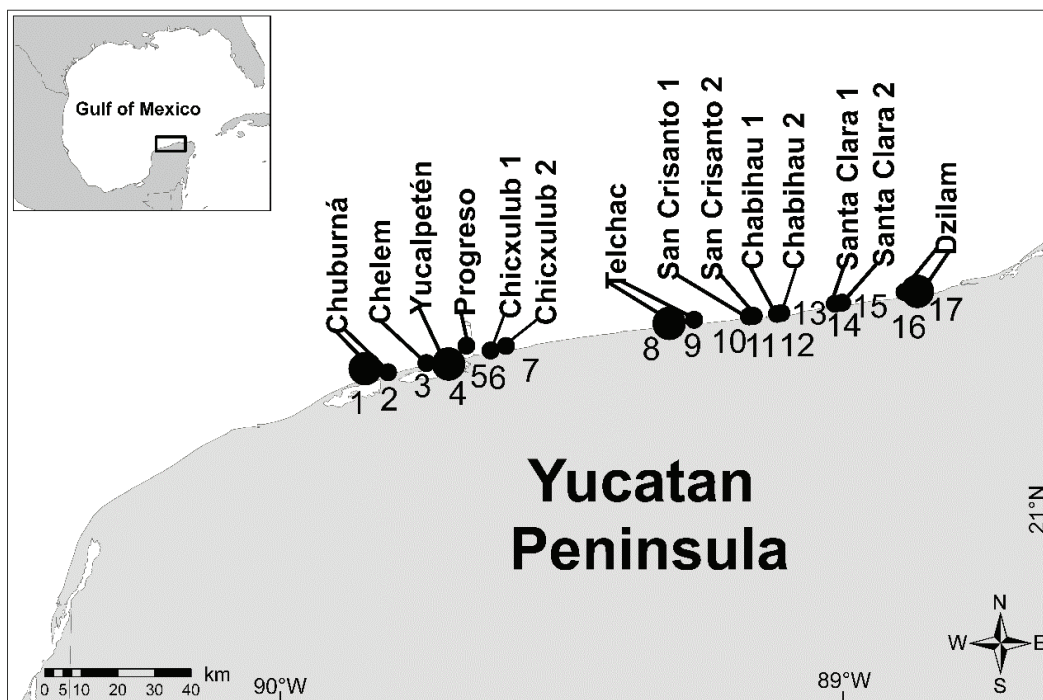


Figure 1. Sampling sites along the northern Yucatan Peninsula coast in 2011–2014. Small circles indicate stations near exposed coasts, and large circles indicate stations inside semi-enclosed marinas.

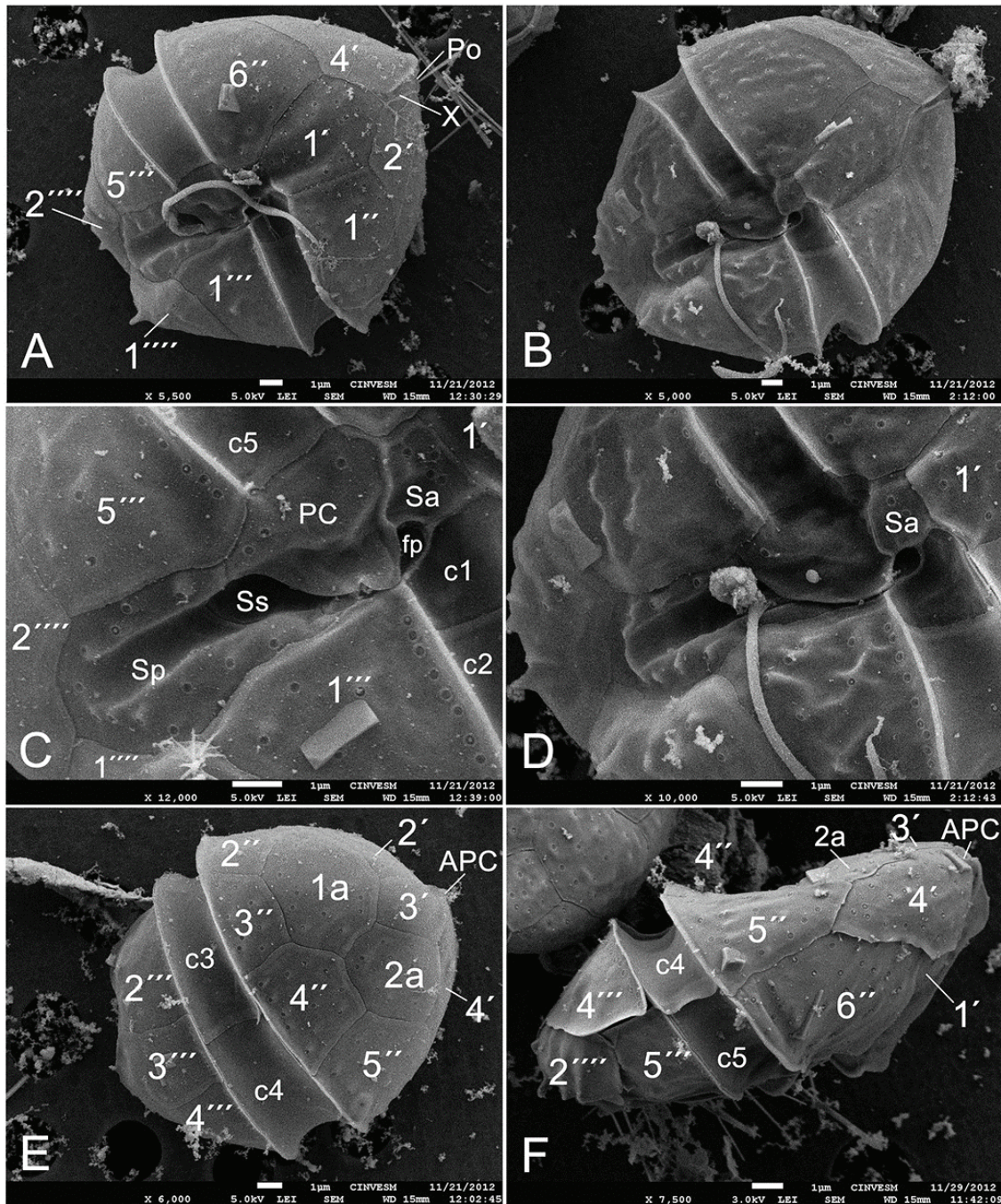


Figure 2. *Durinskia yucatanensis* under SEM: A and B – cells in ventral view; C and D – the sulcal area in ventral view; E – dorsal view; F – left-side view. Symbols for thecal plates: 1'-4' – the apical plates; 1''-6'' – the precingular plates; 1a and 2a – the anterior intercalary plates; 1'''-5''' – the postcingular plates; 1'''' and 2'''' – the posterior plates; APC – the apical pore complex; c1-c5 – the cingular plates; fp – the flagellar pore; PC – the pore cover plate; Po – the pore plate; Sa – the anterior sulcal plate; Sd – the right sulcal plate; Sp – the posterior sulcal plate; x – the canal plate. Scale bar: 1 μ m.

Holotype: Figure 6a in Okolodkov *et al.* (2020: 64) obtained from a formalin-fixed net sample from the station (st.) 1 taken on 18 August 2010, leg. Yuri B. Okolodkov. The sample is deposited in the collection of liquid samples of phytoplankton and benthic microalgae in the La-

boratory of Marine Botany and Planktology at the Institute for Marine Sciences and Fisheries, University of Veracruz (Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana (ICIMAP-UV), Boca del Río, Veracruz, Mexico).

Table 1. Comparison of *Durinskia yucatanensis* (present study) with *Kryptoperidinium triquetrum* (based on Saburova *et al.*, 2012 – *Durinskia* spp., and Tillmann *et al.*, 2023 – *K. triquetrum*).

Morphological features	<i>D. yucatanensis</i>	<i>K. triquetrum</i>
Cell length	12.5–23.7 µm	15–50 µm
Thecal pores	sparsely, irregularly located	densely located, often arranged in rows on some dorsal epithecal plates
Epitheca	slightly larger than hypotheca (up to 1.5 times)	equal to hypotheca
Plate formula	Po X 4' 2a 6" 5c 4s(?) 5''' 2'''	Po X 4' 2a 7" 5c 7s 5''' 2'''
Plate 1'	slightly asymmetrical, extended longitudinally, not subdivided	strongly asymmetrical, extended obliquely, from the apex toward the right side, subdivided into 1' a and 1' p
Precingulars	6"	7" (the 7" plate is L- or boot- shaped, very narrow)
Precingulars 1"-5"	1" and 5" are the highest	of similar height
Anterior intercalaries	1a > 2a	1a < 2a
Cingulum path	submedian (closer to the antapex), descending, displaced ¾-1 girdle width	median, circular, disconnected ventrally by plate 1' p
Plate PC*	present	absent

*Note: plate PC is probably a modified plate Sd.

Type locality: Sisal marina (21°9'40.22" N, 90°2'42.71" W), the northern coast of the Yucatan Peninsula, State of Yucatan, Mexico.

Habitat: Coastal marine, planktonic.

Etymology: The epithet *yucatanensis* refers to the Yucatan Peninsula.

Ecology

Our species was usually found at marine salinities between 32 and 40, at water temperatures between 28 °C and 33 °C, characteristic of late summer (August–September), in a wide range of macronutrient concentrations (Table 2). However, during the period 2011–2014, at the distance of 1–7 km from the coastline, in shallow waters with site depths of 1.2–6.1 m, the species was found with an abundance of 2.7×10^4 – 8.0×10^4 cells L⁻¹. Based on the bloom observed in August 2010 (with up to 3.75×10^7 cells L⁻¹), it appears to prefer eutrophic conditions that are typical for marinas along the northern coast of Yucatan.

The PERMANOVA analysis revealed significant differences between years and, months and sampling sites (Table 2). All physicochemical variables, except phosphates, showed a seasonal pattern, particularly between months and years. Orthophosphates showed a multi-year pattern (PERMANOVA, $P=0.03$; Table 2). The mean annual temperatures differed significantly between the two zones: 29.1 ± 1.84 °C along

the exposed coast and 27.92 ± 1.9 °C in the marinas (PERMANOVA; $P=0.001$). In the exposed coastal zone, the highest temperatures (33.3 °C at st. 15 and 16) and salinity values (37.56–39.37) were measured in July–August, and the minimum temperature (23 °C) was registered in March for all four years; the minimal temperature (~22.7 °C) along the exposed coast was also observed in March. The highest DO concentrations (>10 mg L⁻¹) and salinity (39.93) were observed in marinas in 2014, in particular, in August–October at st. 7, 8, 2, 3, and 5). The highest concentrations of orthophosphates (10.61 µM L⁻¹, June 2011), urea (19.48 µM L⁻¹, June 2011), and silicates (95 µM L⁻¹, March 2014) along the exposed coast were measured in spring-early summer.

The highest DIN concentrations were measured along the exposed coast in January 2012, especially at st. 2 to 14 (23.49 a 72.49 µM L⁻¹), with annual peaks up to >40 µM L⁻¹ in marinas (in June 2011, April 2012, May 2013 and March 2014). Chl-*a* was the only parameter that presented the most significant spatio-temporal variability between years, months and sampling sites ($P=0.001$). The maximal value (131.67 mg m⁻³) in marinas was measured in February 2012 when the highest DIN concentration (57.85 µM L⁻¹) occurred. Along the exposed coast, the highest chl-*a* value (34.06 mg m⁻³) occurred in 2012, while the mean annual value for the other three years was 21.83 mg m⁻³ (September 2011, October 2013, and January 2014; Fig. 4).

Table 2. Permutational multivariate analysis of variance (PERMANOVA) for the cell abundances of *Durinskia yucatanensis* transformed using Log+1 and the Bray-Curtis distance. Models for the different fixed factors, years, months, sampling sites and zones.

	Years		Months		Sites		Zone		Interaction
	Pseu.F	P	Pseu.F	P	Pseu.F	P	Pseu.F	P	
Abundance of <i>D. yucatanensis</i> (cells L ⁻¹)	12.12	0.001***	3.96	0.001***	3.16	0.001***	21.74	0.001***	Years-zones Years-months***

Significance codes: <0.001***, 0.001**, 0.01*, 0.05*.

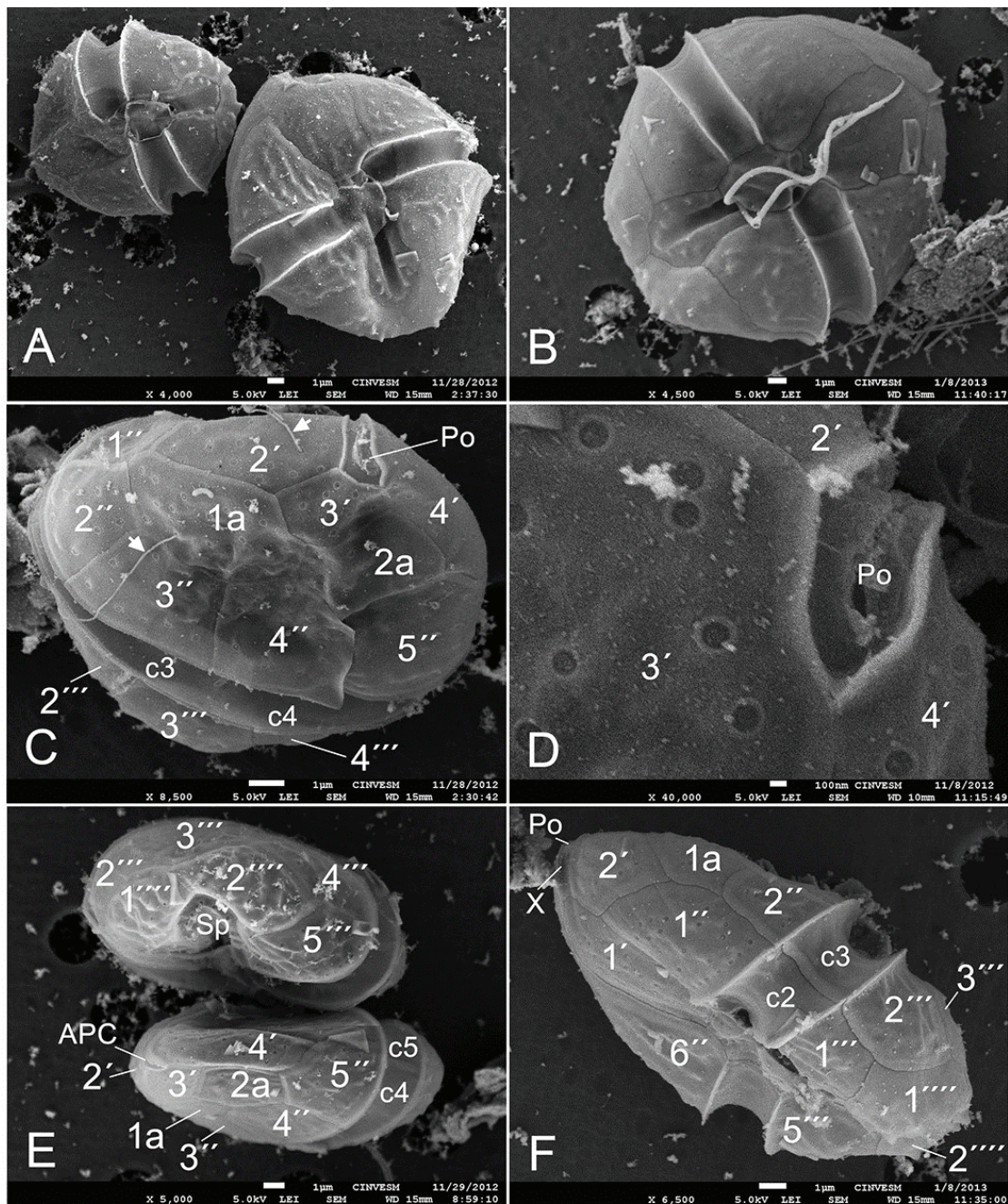


Figure 3. *Durinskia yucatanensis* under SEM: A and B – cells in ventral view; C – cell in apical-dorsal view; D – the apex with adjacent plates in apical-dorsal view; E – cells in antapical (above) and apical views (below); F – cell in left-side view. For symbols, see Fig. 2. Scale bar: 1 µm.

Cell abundance of *D. yucatanensis* changed during the study period. A temporal pattern between months was found (PERMANOVA, $P=0.001$, Table 3). In 2011, 2012, and 2014, along the exposed coast, the highest abundances were observed in September 2011 (up to 4.6×10^6 cells L^{-1} , mean 7.0×10^5 cells L^{-1}), November 2012 (up to 2.8×10^6 , mean 7.0×10^5 cells L^{-1}) and November 2014 (up to 4.1×10^5 , mean 2.1×10^5 cells L^{-1}), in particular at st. 1 to 8 and 14 to 16 (Fig. 5). The

seasonal pattern of the cell abundance of *D. yucatanensis* was similar between 2011 and 2012 when the species was found between June and November 2011 and between May and November 2012 (Fig. 5). In comparison to those years, 2013 and 2014 were different. In 2013 the species was frequent between January and July, and in 2014 during a much shorter period, from August to October. In addition, the number of species observations was much fewer in 2014 than in previous years.

As for the spatial distribution of the cell abundances of *D. yucatanensis*, the highest values were observed at st. 5, 6, and 7 (the Progreso-Chicxulub area) along the exposed coast in 2011, and only at st. 17 (Dzilam) during all studied years in marinas (Fig. 5). In marinas, the maximum cell abundances were observed in August 2012 and February 2014 (5.1×10^6 and 3.0×10^7 cells L^{-1}). In 2011, the maximum abun-

dance occurred in July (2.2×10^6 , mean 6.4×10^5 cells L^{-1}) and in May 2013 (4.9×10^6 , mean 8.2×10^5 cells L^{-1}) (Fig. 6, Table 4). DIN showed a positive correlation with cell abundances for both the exposed coast and marinas, especially in July-August, characterized by high water temperature ($31-32^\circ C$) (Table 2, Fig. 6).

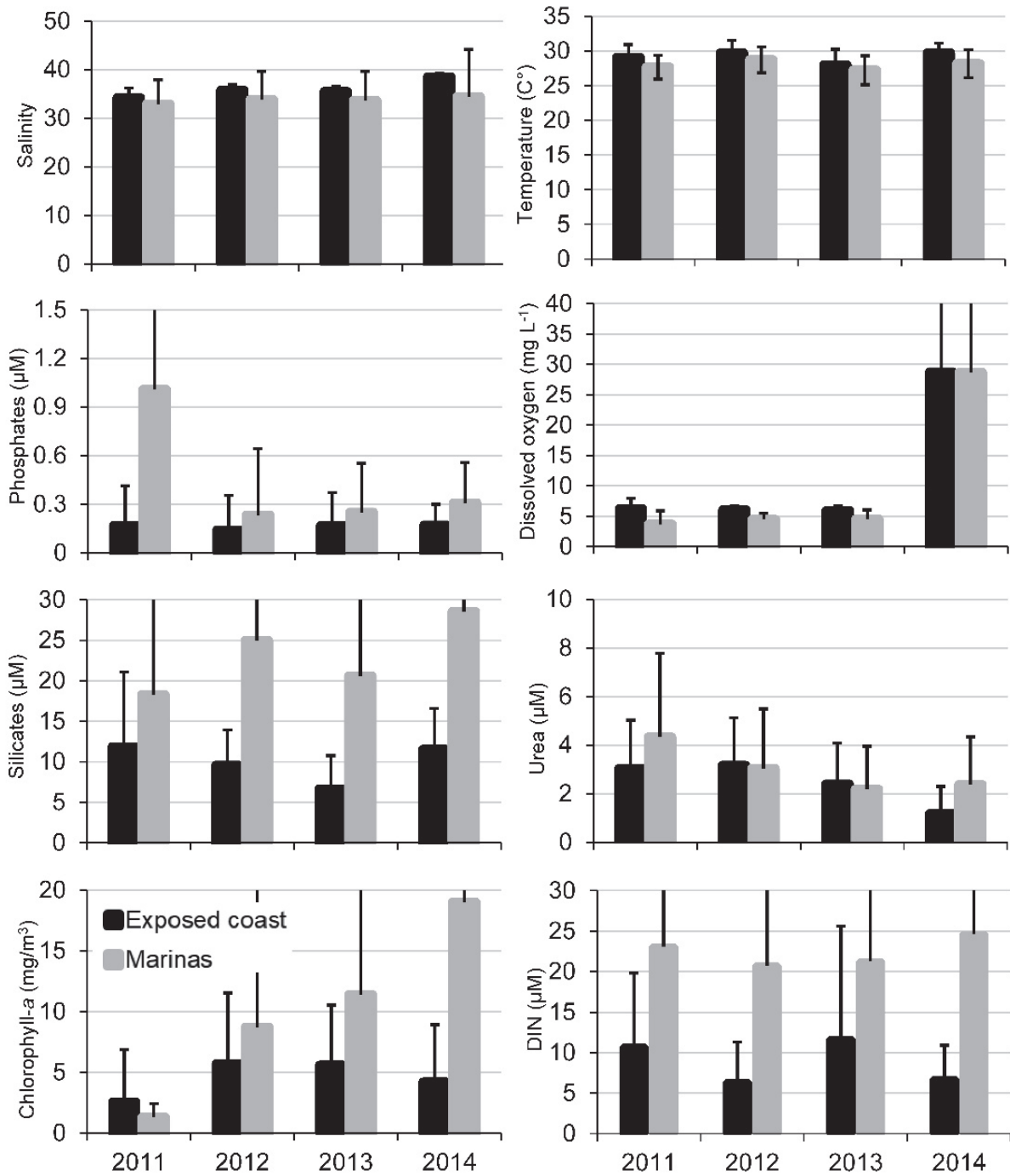


Figure 4. Annual mean values of physicochemical variables (mean ± SD) along the northern Yucatan coast in 2011-2014.

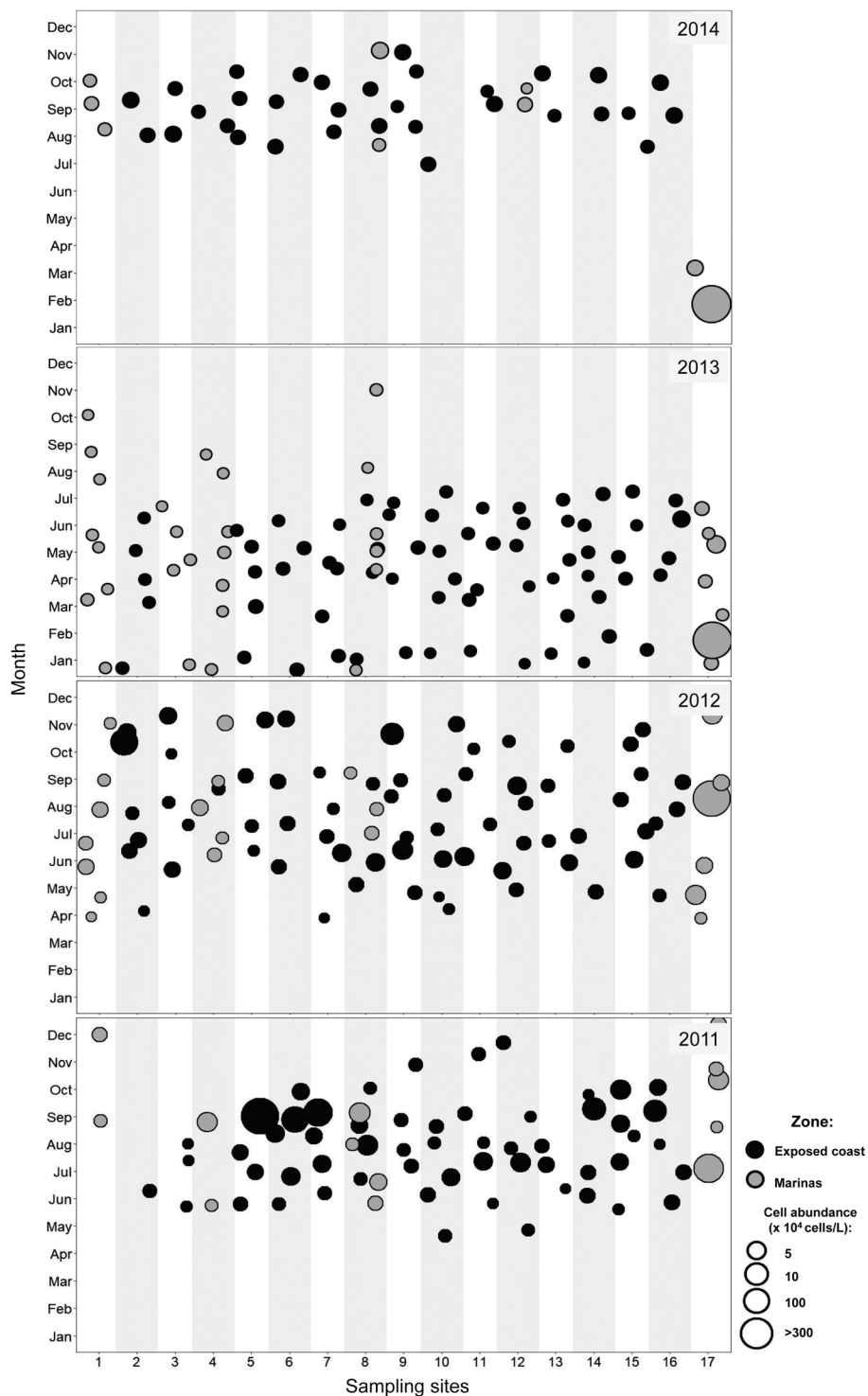


Figure 5. Spatio-temporal variation in the cell abundance of *Durinskia yucatanensis* along the northern Yucatan coast in 2011–2014. The size of the circles is proportional to the cell abundances expressed in $\times 10^4$ cells L^{-1} . The ordinate axis indicates the monthly scale, the abscissa axis indicates sampling stations (1 – Celestún, 2 – Chuburná, 3 – Chelem, 4 – Punta Bass, 5 – Progreso, 6 – Chicxulub 1, 7 – Chicxulub 2, 8 – Uaymitún, 9 – Telchac, 10 – San Crisanto 1, 11 – San Crisanto 2, 12 – Chabihau 1, 13 – Chabihau 2, 14 – Santa Clara 1, 15 – Santa Clara 2, 16 – Dzilam, 17 – San Felipe). Different segments of the graph indicate the years of sampling (2011-2014).

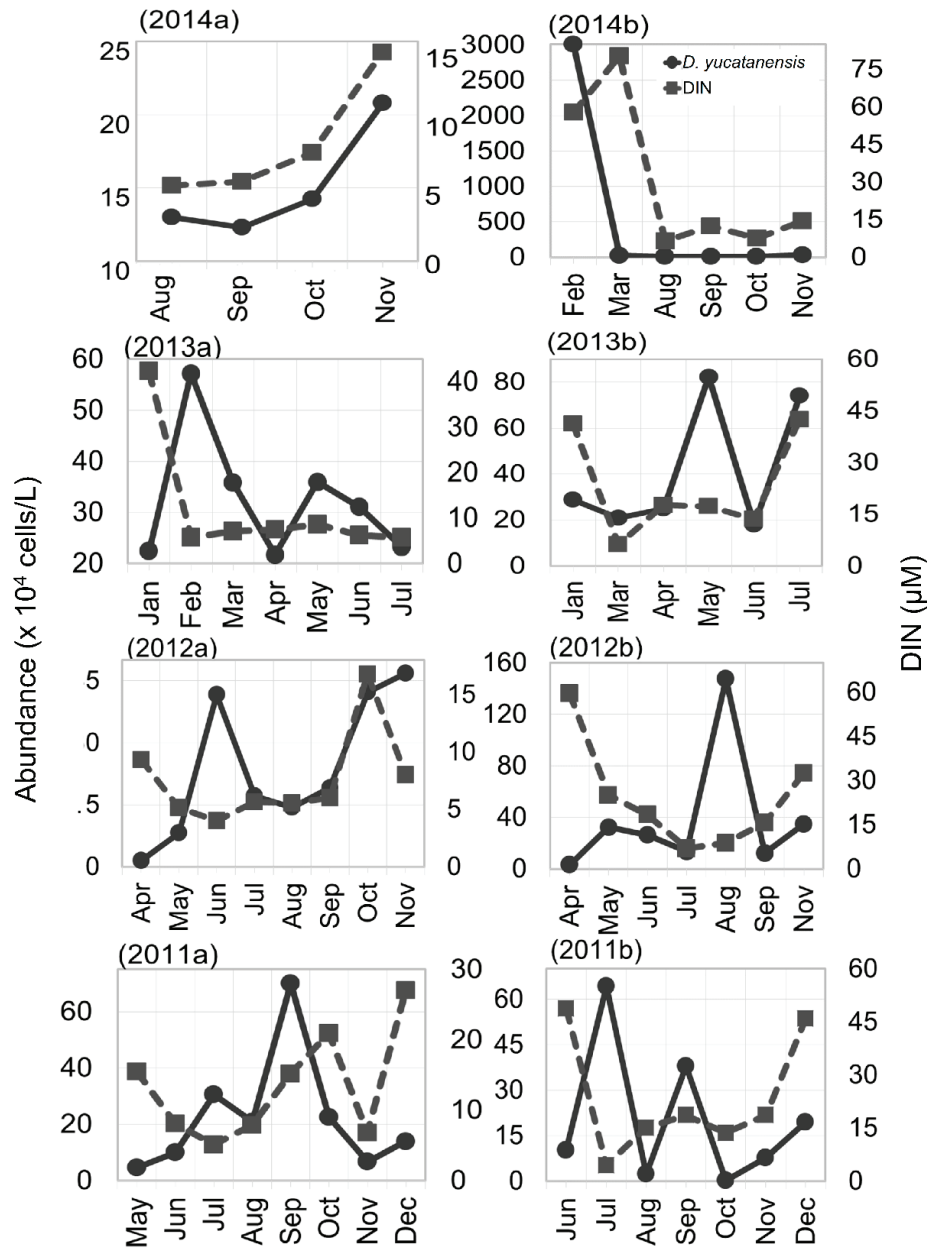


Figure 6. Annual mean cell abundances of *Durinskia yucatanensis* in relation to dissolved inorganic nitrogen (DIN) along the northern Yucatan coast in 2011–2014. The letters added to the years in the parentheses indicate exposed coasts (a) and marinas (b).

DISCUSSION

The species was placed into the family Kryptoperidiniaceae (Okolodkov *et al.*, 2020) despite the absence of the second (eukaryotic) nucleus that originated from a tertiary endosymbiont derived from a diatom (Dodge, 1971; McEwan & Keeling, 2004; for additional references, see Satta *et al.*, 2020 and Tillmann *et al.*, 2023) and characteristic of the Kryptoperidiniaceae, and it was classified according to Fensome *et al.* (1993) and Kretschmann *et al.* (2018). It is noteworthy that the isolate of *Kryptoperidinium triquetrum* (Ehrenberg) Tillmann, Gottschling, Elbrächter, Kusber et Hoppenrath (= *Kryptoperidinium foliaceum* Lindemann)

that caused a bloom event in South Carolina, USA, was mononucleate (Kempton *et al.*, 2002); the authors suggested a more transient endosymbiotic association than previously considered. Similar observations of the species were made from the Baltic Sea (Gottschling *et al.*, 2019). This species has caused recurrent blooms in southern Chile: 18% of the 220 registered bloom events that occurred from 1956 to 2021 (Barria *et al.*, 2022). The Kryptoperidiniaceae blooms appear to be spreading along the Latin American coasts. Yamada *et al.* (2019) performed a comparative study of the nuclear dynamics in three *Durinskia* species. They found that *D. capensis* Pienaar, H. Sakai et T. Horiguchi

in culture keeps its captured diatoms temporarily, only for two months. The authors also suggest the unique nuclear dynamics of converting kleptoplasts to permanent plastids in *D. kwazulunatalensis*. In all cases, the host dinoflagellates control the diatom karyokinesis.

The highest silicate concentrations (96.46–97.22 $\mu\text{mol L}^{-1}$) found in Sisal marina and at 50 m from the coast in 2010 and 2011 are most likely derived from terrestrial environments. In this case, chl-*a* reflects the sum of the total phytoplankton biomass (mainly diatoms), extracellular chlorophyll, and undigested microalgae in fecal pellets of planktonic invertebrates (mainly crustaceans), rather than the biomass of the blooming species.

The GAM model analysis showed that the temperature ($P=0.01$) and salinity ($P=0.01$) could help to explain the changes in cell abundance (up to 60.7% of the total explained deviation), in particular, along the

exposed coast (in 2011, 2013 and 2014) and in marinas (in 2011 and 2012) compared to changes in DIN and urea ($P<0.001$; Table 4). Similarly, models of the field data obtained from two Mediterranean coastal shallow lagoons in Sardinia, Italy, revealed a significant role of rainfall and DIN in the occurrence and blooms of *Kryptoperidinium* sp. (Satta et al., 2020). Cell abundances of *D. yucatanensis* were directly proportional to an increase in temperature, especially when above 30 °C, particularly during 2013 along the exposed coast and 2012 in marinas (Fig. 7: 2013a and 2012b). The GAM model applied to the exposed coast in 2012 and 2013 showed the capacity of adaptation of the species to a wide range of salinities (Fig. 7: 2012a and 2013a). In 2013, in marinas, the increase in cell abundance was significantly related to phosphates ($P<0.001$; Table 4). Similarly, the major urea and DIN concentrations resulted in predicted increases in cell abundance, particularly in 2014 (Fig. 5, 6 and 7).

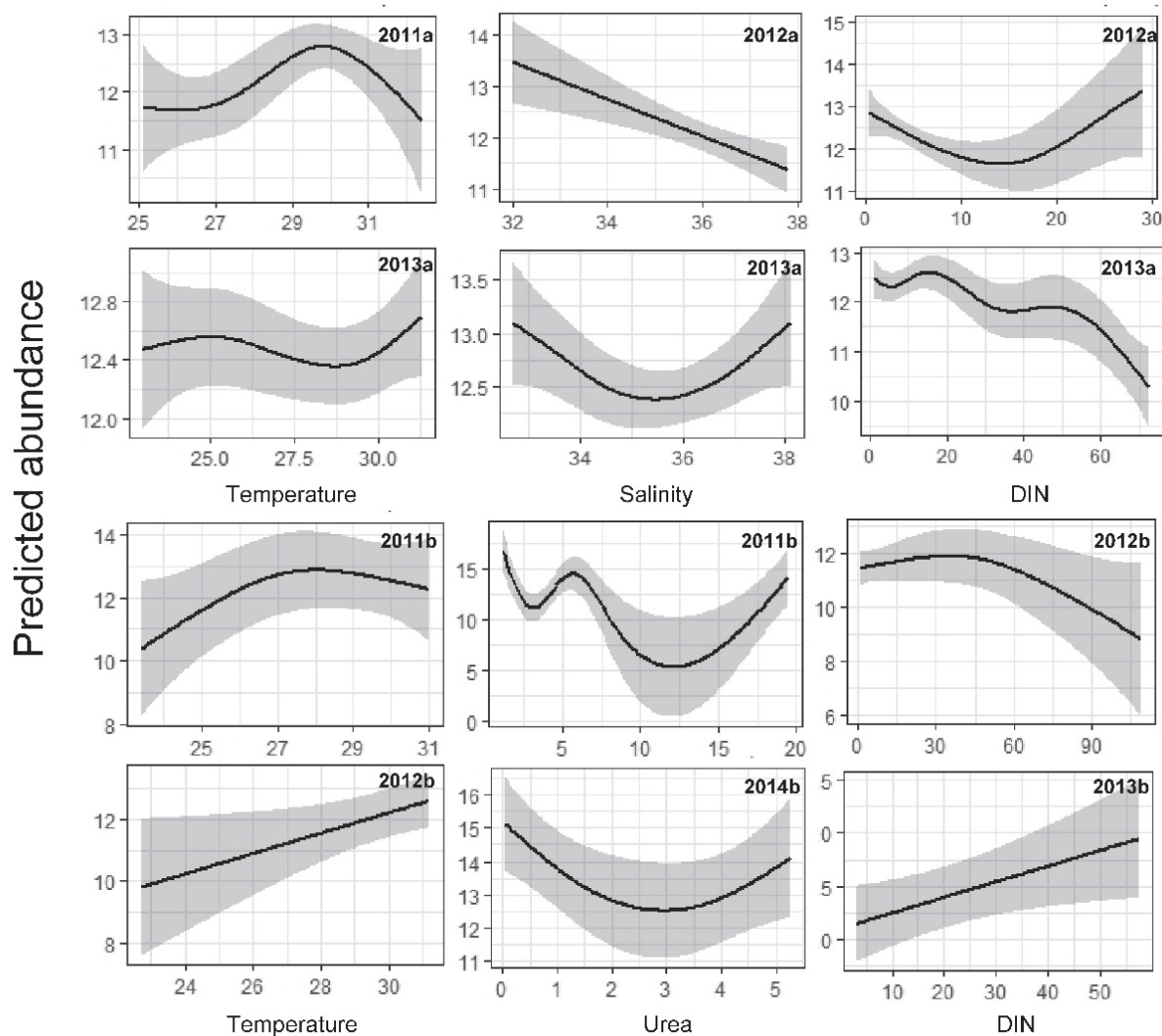


Figure 7. Generalized additive models (GAM) describing the cell abundance response of *Durinskia yucatanensis* to physicochemical variables: salinity, temperature (°C), urea and DIN (μM), during different years (2011–2014) along the northern Yucatan coast (a – exposed coasts, b - marinas). Bold lines represent GAM smoothed mean ratios, and shaded areas are 95% confidence intervals.

Table 3. Summary of the best adjusted generalized additive models and total explained deviation.

Zones/Years	Minimal adjusted model	Explained deviation (%)
Exposed coast		
2011	Cell abundance ~ Temperature ⁺ + Salinity + Phosphates ^{***}	28.9
2012	Cell abundance ~ Salinity ^{***} + Phosphates + Silicates ⁺ + DIN ⁺	23.0
2013	Cell abundance ~ Temperature + Salinity ⁺ + Urea ⁺ + Chlorophyll- <i>a</i> ^{***} + DIN ^{***}	60.7
2014	Cell abundance ~ Temperature + DO ⁺ + Silicates ⁺ + Urea + Chlorophyll- <i>a</i>	49.8
Marinas		
2011	Cell abundance ~ Temperature + Urea ^{***} + Chlorophyll- <i>a</i> ^{***}	73.7
2012	Cell abundance ~ Temperature ⁺ + DO + Phosphates ^{**} + DIN	64.1
2013	Cell abundance ~ Phosphates ^{***} + DIN ⁺	74.1
2014	Cell abundance ~ Urea ⁺ + DIN ^{***}	90.8

Significance codes: <0.001^{***}, 0.001^{**}, 0.01^{*}, 0.05^{*}.

CONCLUSIONS

Durinskia yucatanensis is a marine planktonic dinoflagellate. It differs from other known *Durinskia* species by a larger 1a plate compared to plate 2a. As for the cell size and thecal morphology, it is closer to *D. kwazulunatalensis*. It prefers semi-enclosed coastal environments characterized by more stagnant water and increased concentrations of macronutrients. Its cell abundance spatio-temporal distribution pattern along the northern Yucatan coast may change over the years; however, it prefers higher summer temperatures during the rainy season and is also common in autumn before the northerly wind season.

ACKNOWLEDGMENTS

We are grateful to Francisco F. Pedroche (Universidad Autónoma Metropolitana – Lerma, Mexico City, Mexico) for giving us advice about nomenclature, Kenneth N. Mertens (IFREMER; Station de Biologie Marine, Concarneau, France) for providing relevant literature, Natalia A. Okolodkova (Mexico City, Mexico) for preparing the plates of micrographs and to Marcia M. Gowing (Seattle, WA, USA) for improving the English style. We are grateful to anonymous reviewers for their critical comments that improved the manuscript. Financial support to the FOMIX CONACYT-Yucatán project “Análisis de las causas, dispersión y consecuencias ambientales de la marea roja en Yucatán” (No. 108897; 2009–2012) given to JAHS, the FOMIX CONACYT-Yucatán (No. 108160) and CONACYT LAB-2009-01 (No. 123913) projects of the Laboratorio Nacional de Nano y Biomateriales (CINVESTAV-IPN, Mérida) given to Patricia Quintana-Owen is much appreciated. IGL was supported by SIP-20220515 and SIP-20230144 (Secretaría de Investigación y Posgrado del IPN), and he is a COFAA (Comisión de Operación y Fomento de Actividades Académicas) fellow.

REFERENCES

- AGUILAR-TRUJILLO, A. C., Y. B. OKOLODKOV, J. A. HERRERA-SILVEIRA, F. DEL C. MERINO-VIRGILIO & C. GALICIA-GARCÍA. 2017. Taxocoenosis of epibenthic dinoflagellates in the coastal waters of the northern Yucatan Peninsula before and after the harmful algal bloom event in 2011–2012. *Marine Pollution Bulletin* 119: 396-406. DOI:10.1016/j.marpolbul.2017.02.074
- AGUILAR-TRUJILLO, A. C., Y. B. OKOLODKOV, F. DEL C. MERINO-VIRGILIO, I. OSORIO-MORENO & J. A. HERRERA-SILVEIRA. 2014. Variación espacial de dinoflagelados bentónicos/epifíticos en aguas costeras del norte de Yucatán (agosto de 2011). In: Botello, A. V., J. Rendón von Osten, J. A. Benítez & G. Gold-Bouchot (Eds.). *Golfo de México. Contaminación, impacto ambiental, diagnóstico y tendencias*. 3a ed. UAC, UNAM-ICMYL, CINVESTAV-Unidad Mérida, Mérida, Yucatán, México, pp. 147-160.
- ÁLVAREZ-GÓNGORA, C. & J. A. HERRERA-SILVEIRA. 2006. Variations of phytoplankton community structure related to water quality trends in a tropical karstic coastal zone. *Marine Pollution Bulletin* 52: 48-60. DOI: 10.1016/j.marpolbul.2005.08.006
- ANDERSON, M. J. 2014. Permutational multivariate analysis of variance (PERMANOVA). In: Wiley *StatsRef: Statistics reference online*. John Wiley & Sons, Ltd., Massey University, Auckland, New Zealand. 15 p. DOI: 10.1002/9781118445112.stat07841
- BARRÍA, C., P. VÁSQUEZ-CALDERÓN, C. LIZAMA, P. HERRERA, A. CANTO, P. CONEJEROS, O. BELTRAMI, B. A. SUÁREZ-ISLA, D. CARRASCO, I. RUBILAR, L. GUZMÁN, L. RENÉ DURÁN & D. OLIVA. 2022. Spatial temporal expansion of harmful algal blooms in Chile: A review of 65 years records. *Journal of Marine Science and Engineering* 10, 1868. DOI: 10.3390/jmse10121868
- CONNORS, M., A. R. HILDEBRAND, M. PILKINGTON, C. ORTIZ-ALEMAN, R. E. CHAVEZ, J. URRUTIA-FUCUGAUCHI, E. GRANEL-CASTRO, A. CAMARA-ZI, J. VÁSQUEZ & J. F. HALPENNY. 1996. Yucatán karst features and the size of Chicxulub crater. *Geophysical Journal International* 127: F11-F14. DOI:10.1111/j.1365-246X.1996.tb04066.x
- DODGE, J. D. 1971. A dinoflagellate with both a mesocaryotic and a eukaryotic nucleus. I. Fine structure of the nuclei. *Protoplasma*, 73, 145-157.
- FENSOME, R. A., F. J. R. TAYLOR, G. NORRIS, W. A. S. SARJEANT, D. I. WHARTON & G. L. WILLIAMS. 1993. A classification of living and fossil dinoflagellates. *Micropaleontology Special Publication Number 7*. Sheridan Press, Hanover, PA, USA. viii + 351 p.
- GOTTSCHLING, M., U. TILLMANN, M. ELBRÄCHTER, W.-H. KUSBER & M. HOPPENRATH. 2019. *Glenodinium triquetrum* Ehrenb. is a species of *Heterocapsa* F. Stein but of *Kryptoperidinium* Er. Lindem. (*Kryptoperidinium*, Peridinales). *Phytotaxa*, 391 (2), 155-158. DOI: 10.11646/phytotaxa.391.2.11

- HERRERA-SILVEIRA, J. A. 1993. Ecología de los productores primarios en la laguna de Celestún, México. Patrones de variación espacial y temporal. Tesis de Doctorado. Universitat de Barcelona, Barcelona, España. 233 p.
- JEFFREY, S. W. & G. F. HUMPHREY. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen* 167: 191-194. DOI:10.1016/S0015-3796(17)30778-3
- KEMPTON, J. W., J. WOLNY, T. TENGS, P. RIZZO, R. MORRIS, J. TUNNELL, P. SCOTT, K. STEIDINGER, S. N. HYMEL & A. J. LEWITUS. 2002. *Kryptoperidinium foliaceum* blooms in South Carolina: a multi-analytical approach to identification. *Harmful Algae* 1, 383-392. DOI:10.1016/S1568-9883(02)00051-3
- KRETSCHMANN, J., A. ŽERDONER ČALASAN & M. GOTTSCHLING. 2018. Molecular phylogenetics of dinophytes harboring diatoms as endosymbionts (Kryptoperidiniaceae, Peridinales), with evolutionary interpretations and a focus on the identity of *Durinskia oculata* from Prague. *Molecular Phylogenetics and Evolution* 118: 392-402. DOI:10.1016/j.ympev.2017.10.011
- LEE, L. K., Z. F. LIM, H. GU, L. L. CHAN, R. W. LITAKER, P. A. TESTER, C. P. LEAW & P. T. LIM. 2020. Effects of substratum and depth on benthic harmful dinoflagellate assemblages. *Scientific Reports* 10 (1): 1-14. DOI:10.1038/s41598-020-68136-6
- MCEWAN, M. L. & P. J. KEELING. 2004. HSP90, tubulin and actin are retained in the tertiary endosymbiont genome of *Kryptoperidinium foliaceum*. *Journal of Eukaryotic Microbiology* 51 (6), 651-659. DOI: 10.1111/j.1550-7408.2004.tb00604.x
- MORALES-OJEDA, S. M., J. A. HERRERA-SILVEIRA & J. MONTERO. 2010. Terrestrial and oceanic influence on spatial hydrochemistry and trophic status in subtropical marine near-shore waters. *Water Research* 44 (20): 5949-5964. DOI:10.1016/j.watres.2010.07.046
- MURGULET, D., A. R. DOUGLAS, J. A. HERRERA-SILVEIRA, I. A. MARIÑO-TAPIA & A. VALLE-LEVINSON. 2020. Submarine groundwater discharge along the northern coast of the Yucatán Peninsula. In: Land, L., Kromhout, C. & M. J. Byle (Eds.). *Proceedings of the 16th Multidisciplinary Conference on Sinkholes and the Engineering and Environmental Impacts of Karst National Cave and Karst Research Institute Symposium 8* [web format]. KIP Talks and Conferences 81. Digital Commons @ University of South Florida, Florida, USA: 206-219. Available online at: https://digitalcommons.usf.edu/kip_talks/81 (accessed: 14 August 2022).
- OKOLODKOV, Y. B., F. DEL C. MERINO-VIRGILIO, J. A. AKÉ-CASTILLO, A. C. AGUILAR-TRUJILLO, S. ESPINOSA-MATÍAS & J. A. HERRERA-SILVEIRA. 2014. Seasonal changes in epiphytic dinoflagellate assemblages near the northern coast of Yucatan Peninsula, Gulf of Mexico. *Acta Botanica Mexicana* 107: 121-151. DOI:10.21829/abm107.2014.204
- OKOLODKOV, Y. B., F. DEL C. MERINO-VIRGILIO, D. A. HUERTA-QUINTANILLA, I. GÁRATE-LIZÁRRAGA, K. A. STEIDINGER, A. C. AGUILAR-TRUJILLO, J. A. HERRERA-SILVEIRA, S. ESPINOSA-MATÍAS & A. MARTÍNEZ-MENA. 2020. A Kryptoperidiniaceae species (Dinophyceae: Peridinales) blooming in coastal Yucatan waters, Gulf of Mexico. *Protistology* 14 (2): 58-69. DOI: 10.21685/1680-0826-2020-14-2-2
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS & H. WAGNER. 2013. *Vegan: Community Ecology Package*, version 2.0-7. R Package.
- PARSONS, T. R., Y. MAITA & C. M. LALLI. 1984. *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt. 173 p.
- POPE, K. O., A. C. OCAMPO, G. L. KINSLAND & R. SMITH. 1996. Surface expression of the Chicxulub crater. *Geology* 24 (6): 527-530. DOI:10.1130/0091-7613(1996)024<0527:SEOTCC>2.3.CO;2
- R CORE TEAM. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at: <https://www.R-project.org/> (accessed: 15 May 2022).
- R STUDIO TEAM. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA, USA. Available online at: <http://www.rstudio.com> (accessed: 15 May 2022).
- SABUROVA, M., N. CHOMÉRAT, & M. HOPPENRATH. 2012. Morphology and SSU rDNA phylogeny of *Durinskia agilis* (Kofoid & Swezy) comb. nov. (Peridinales, Dinophyceae), a thecate, marine, sand-dwelling dinoflagellate formerly classified within *Gymnodinium*. *Phycologia* 51 (3): 287-302. DOI: 10.2216/10-22.1
- SATTA, C. T., S. PULINA, A. RENÉ, B. M. PADDEDA, T. CADDEO, N. FOIS & A. LUGLIÉ. 2020. Ecological, morphological and molecular characterization of *Kryptoperidinium* sp. (Dinophyceae) from two Mediterranean coastal shallow lagoons. *Harmful Algae* 97: 101855. DOI: 10.1016/j.hal.2020.101855
- STRICKLAND, J. D. H. & T. R. PARSONS. 1972. *A practical handbook of seawater analysis*. 2nd ed. Fisheries Research of Canada, Bulletin 167, Ottawa, Canada. 310 p.
- SYMONDS, M. R. & A. MOUSSALLI. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65 (1): 13-21. DOI: 10.1007/s00265-010-1037-6
- TILLMANN, U., S. WIETKAMP, J. KRETSCHMANN, J. CHACÓN & M. GOTTSCHLING. 2023. Spatial fragmentation in the distribution of diatom endosymbionts from the taxonomically clarified dinophyte *Kryptoperidinium triquetrum* (= *Kryptoperidinium foliaceum*, Peridinales). *Scientific Reports* 13: 8593. DOI:10.1038/s41598-023-32949-y
- WOOD, S. N. 2006. *Generalized Additive Models: An introduction with R*. 1st ed. Chapman and Hall/CRC Texts in Statistical Science, Boca Raton, FL, USA. 391 p.
- YAMADA, N., J. J. BOLTON, R. TROBAJO, D. G. MANN, P. DĄBEK, A. WITKOWSKI, R. ONUMA, T. HORIGUCHI, & P. G. KROTH. 2019. Discovery of a kleptoplastic 'dinotom' dinoflagellate and the unique nuclear dynamics of converting kleptoplasts to permanent plastids. *Scientific Reports* 9: 10474. DOI:10.1038/s-41598-019-46852-y
- YAMADA, N., S. D. SYM, & T. HORIGUCHI. 2017. Identification of highly divergent diatom-derived chloroplasts in dinoflagellates, including a description of *Durinskia kwazulunatalensis* sp. nov. (Peridinales, Dinophyceae). *Molecular Biology and Evolution* 34 (6): 1335-1351. DOI: 10.1093/molbev/msx054
- ZUUR, A. F., E. N. IENO & G. M. SMITH. 2007. *Analysing ecological data*. Springer, New York, NY, USA. 672 p.