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Article in *Cahiers de Biologie Marine* · December 2020

DOI: 10.21411/CBM.A.1836C515

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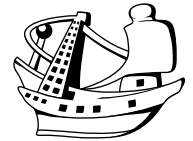
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# Morphology and scavenging behaviour of two species of the genus *Natanolana* (Crustacea: Isopoda: Cirolanidae) attacking elasmobranchs from the Tunisian coast

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**Abstract:** Between 2015 and 2018, a total of 1656 fish specimens belonging to four elasmobranch species was collected from the Tunisian coast and examined for isopods. Two species of Cirolanidae, *Natanolana borealis* and *Natanolana neglecta*, are reported for the first time from the Tunisian coast. This study presents new data on the morphology, distribution and behaviour of the two species. This is the first record of *Natanolana borealis* on *Mustelus mustelus*, *Mustelus punctulatus* and *Scyliorhinus canicula*, and of *Natanolana neglecta* on the elasmobranch *Raja clavata*. The scavenging behaviour of *N. borealis* and *N. neglecta* on elasmobranchs showed that these two species present similar behaviour. We also noted that their impact on fisheries in the first hours of infestation was negligible as the infested fish specimens did not show any external or internal damages.

**Résumé :** Morphologie et comportement de charognards de deux espèces du genre *Natanolana* (Crustacea : Isopoda : Cirolanidae) attaquant les élasmobranches des côtes tunisiennes. Entre 2015 et 2018, un total de 1656 spécimens de poissons appartenant à quatre espèces d'élasmobranches a été récolté sur la côte tunisienne et examiné pour rechercher des isopodes. Deux espèces de Cirolanidae, *Natanolana borealis* et *Natanolana neglecta*, sont signalées pour la première fois sur les côtes tunisiennes. Cette étude présente de nouvelles données sur la morphologie, la distribution et le comportement de ces deux espèces. En effet, c'est la première mention de *Natanolana borealis* sur *Mustelus mustelus*, *Mustelus punctulatus* et *Scyliorhinus canicula*. Il s'agit également de la première mention de *Natanolana neglecta* sur une espèce d'élasmobranch, *Raja clavata*. De surcroît, nous avons pu déterminer que ces deux espèces d'isopodes présentent un comportement similaire. En outre, nous avons constaté que les spécimens de poissons infestés ne présentaient aucun dommage externe ou interne, prouvant ainsi que l'impact de ces isopodes durant les premières heures d'infestation était négligeable.

**Keywords:** *Natanolana borealis* • *Natanolana neglecta* • Cirolanidae • Scavenger • Elasmobranchs • Tunisia

## Introduction

The family Cirolanidae Dana, 1852 (Crustacea: Isopoda) includes free-living, scavenging and predatory carnivorous species. Some of these species are consistent components of benthic scavenger assemblages worldwide, attacking both living and dead animals and therefore, playing an ecologically important role in the marine environments and associated food webs (Bruce, 1986; Biernbaum & Wenner, 1993; Keable, 1995). Moreover, these isopods are occasionally reported scavenging human cadavers (Nagano et al., 1963; Tiemensma et al., 2017)

Species of this family are among the most abundant isopods of shallow marine environments (Keable, 2006 and references cited therein). The family of Cirolanidae has a high species diversity with the third-largest number of species of any marine isopod family (Poore & Bruce, 2012).

Among the cirolanid isopods, *Natanolana* Bruce, 1981 is the second-largest genus with species found in all oceans other than the Arctic Ocean (Bruce, 2003). Six species of *Natanolana* are known from the North Atlantic and some localities of the Mediterranean Sea (Keable, 2006). These species are *N. caeca* (Dollfus, 1903), *N. gallica* (Hansen, 1905), *N. gracilis* (Hansen, 1890), *N. neglecta* (Hansen, 1890), *N. borealis* (Lilljeborg, 1851) and *N. imicola* (Dollfus, 1903) (Keable & Bruce, 1997). Species of this genus are known to have a significant impact on fishes with some species that attack living or trapped fish, therefore having potential commercial impacts on fisheries (Brusca et al., 1995; Mizzan, 1995).

The Mediterranean Sea has a rich diversity of elasmobranchs, with 85 reported species. Some of them have an important economic interest in many countries with a high consumption rate (Bradai et al., 2012). Consequently, in recent years, elasmobranch species, which were considered by-catch, have become the object of directed artisanal longline fisheries (Bradai et al., 2005).

However, despite the ecological and economic interest of *Natanolana* species, few studies of the diversity, morphological variation or the scavenging behaviour of these species have been carried out in the Mediterranean until now. In this work, we aimed to focus on the diversity of Cirolanidae attacking economically important elasmobranchs off Tunisian coasts in order to understand their scavenging behaviour on fish restrained on lines and their impact on these capture fish.

## Materials and Methods

This study is part of an ongoing research project that aims to investigate the diversity of ectoparasites (copepods and isopods) infesting elasmobranch fishes in Tunisian waters.

### *Sampling area and fish collection*

Between September 2015 to September 2018, 1656 line-caught fish belonging to four species of elasmobranchs (Table 1) were collected weekly from fishermen specializing in direct capture of elasmobranchs. The fish species collected were chosen for their economic interest. As this work was part of an ongoing project that aims principally to study ectoparasites that need to be alive, fish specimens were captured using longlines. These longlines are left at the bottom of the ocean in the evening for up to eight hours and then recovered. The depth range of these lines varies between 20 and 50 meters. The most frequented fishing areas are mainly located at depths of 20 to 100 meters. The sampling area includes the Bay of Bizerte (37°16'25"N-9°53'14"E), the Gulf of Tunis (37°00'0.00"N-10°29'59.99"E), the Gulf of Hammamet (36°04'60.00"N-10°44'59.99"E) and the Gulf of Gabes (34°00'0.00"N-10°30'0.00"E) (Fig. 1).

The Bay of Bizerte and the three gulfs are characterized by sandy bottoms (Masri, 1996; Ben Amor et al., 2003; Brahim & Chkioua, 2007; Brahim & Nabli, 2016).

Sampled elasmobranchs were transported directly to the laboratory in a cooler and examined the same day for the presence of isopods. Collected fish species were identified according to Fisher et al. (1987), and nomenclature used follows Froese & Pauly (2018 2019 in biblio ?).

### *Morphological identification of the collected isopods*

All body parts (skin, fins, gills, mouth, cloaca and

**Table 1.** List of elasmobranchs fish examined from Tunisian coast.

Fish species	Number of examined fishes
<i>Mustelus mustelus</i> (Linnaeus, 1758)	480
<i>Mustelus punctulatus</i> Risso, 1827	216
<i>Raja clavata</i> Linnaeus, 1758	480
<i>Scyliorhinus canicula</i> (Linnaeus, 1758)	480
<b>Total</b>	<b>1656</b>

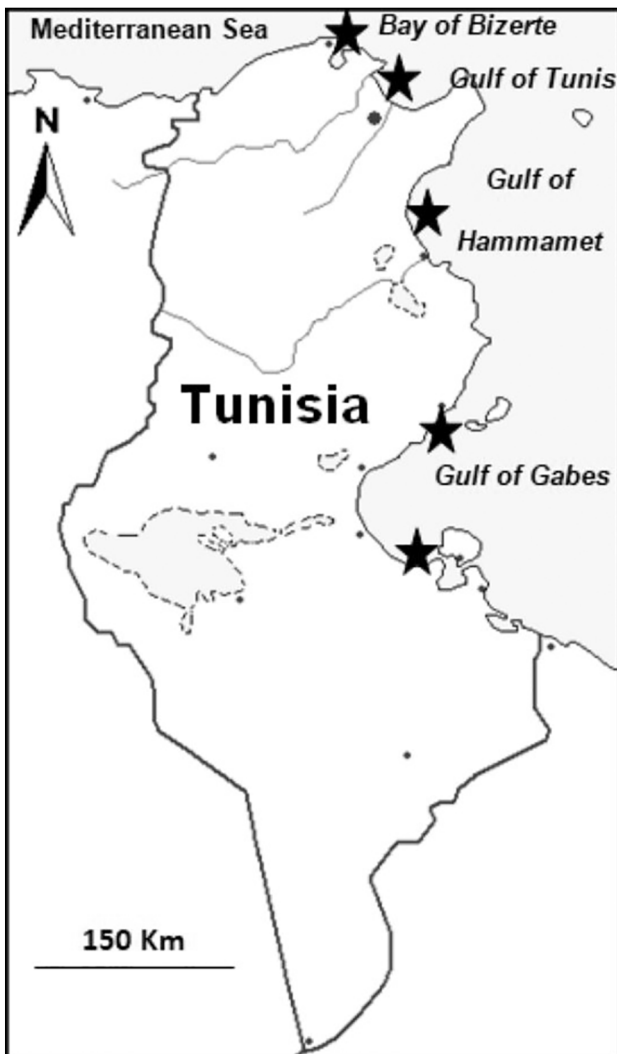


Figure 1. Sampling sites, indicated by black stars.

internal organs) of each fish specimen were carefully examined.

Some of the collected isopods (33 specimens) were removed alive from the fish and fixed in 10% formalin and then transferred in 70% ethanol to be preserved. Before being dissected, they were cleared and stained with lactic acid and then measured using an ocular micrometre. Isopods were examined to identify the different species with the aid of stereo and light microscopy [LEICA DM 1000 (CMS GmbH, Wetzlar, Germany)]. *Natatolana* species were identified using Keable & Bruce (1997) and Keable (2006).

#### Scanning electron microscopy

To check morphological characters for identification, some specimens were removed alive from the fish

and fixed in ethanol 100%, then dried using CO<sub>2</sub> in an Emitech K850 critical point dryer. After mounting, the specimens were coated with gold/palladium in a Quorum Technologies SC7640 sputter coater and examined with a Hitachi S-3400N scanning electron microscope at an acceleration voltage of 10 kV.

#### Data analyses

Rates of infestation were evaluated using relative abundance and mean intensity as defined by Margolis et al. (1982) and modified by Bush et al. (1997). **Prevalence (P)** check this correction as you give values of prevalence in your table 3 was calculated as the proportion of the number of individuals of a particular isopod species in/on a single fish species regardless of whether or not the fish specimen is infested by a given isopod and mean intensity (MI) as the total number of isopods of a particular species found in a sample divided by the number of fish specimens infested with that isopod.

## Results

From the 1656 elasmobranch specimens examined, two cirrolanid species, *Natatolana borealis* (Lilljeborg, 1851) (Fig. 2) and *Natatolana neglecta* (Hansen, 1890) (Fig. 3), were identified for the first time from Tunisia.

*N. borealis* was collected in the four different gulfs of Tunisia and was found on three fish species *Mustelus mustelus* (Linnaeus, 1758), *M. punctulatus* Risso, 1827 and *Scyliorhinus canicula* (Linnaeus, 1758), while *N. neglecta* was gathered only from *Raja clavata* Linnaeus, 1758 in the bay of Bizerte and the Gulf of Tunis (Tables 2 & 3).

#### Morphological observation

All collected specimens were of the adult stage. Indeed, we were able to collect 25 specimens (23 females and 2 males) (Table 2) of *N. borealis* and 12 specimens (females) of *N. neglecta*. The examination of these two species allowed us to identify the following morphological diagnostic characteristics:

#### *Natatolana borealis*

The interocular furrow is incomplete and does not extend across the cephalon (Fig. 2A). The lateral margins of the frontal lamina are straight. Antennae approximately 0.4 times the body length, extending to the posterior of pereonite 4 when flattened against the body (Fig. 2B). The pereonites coxal plates' furrows are developed except for coxae 2 and 3 which are

**Table 2.** Seasonal and geographic distribution of the collected Cirolanidae.

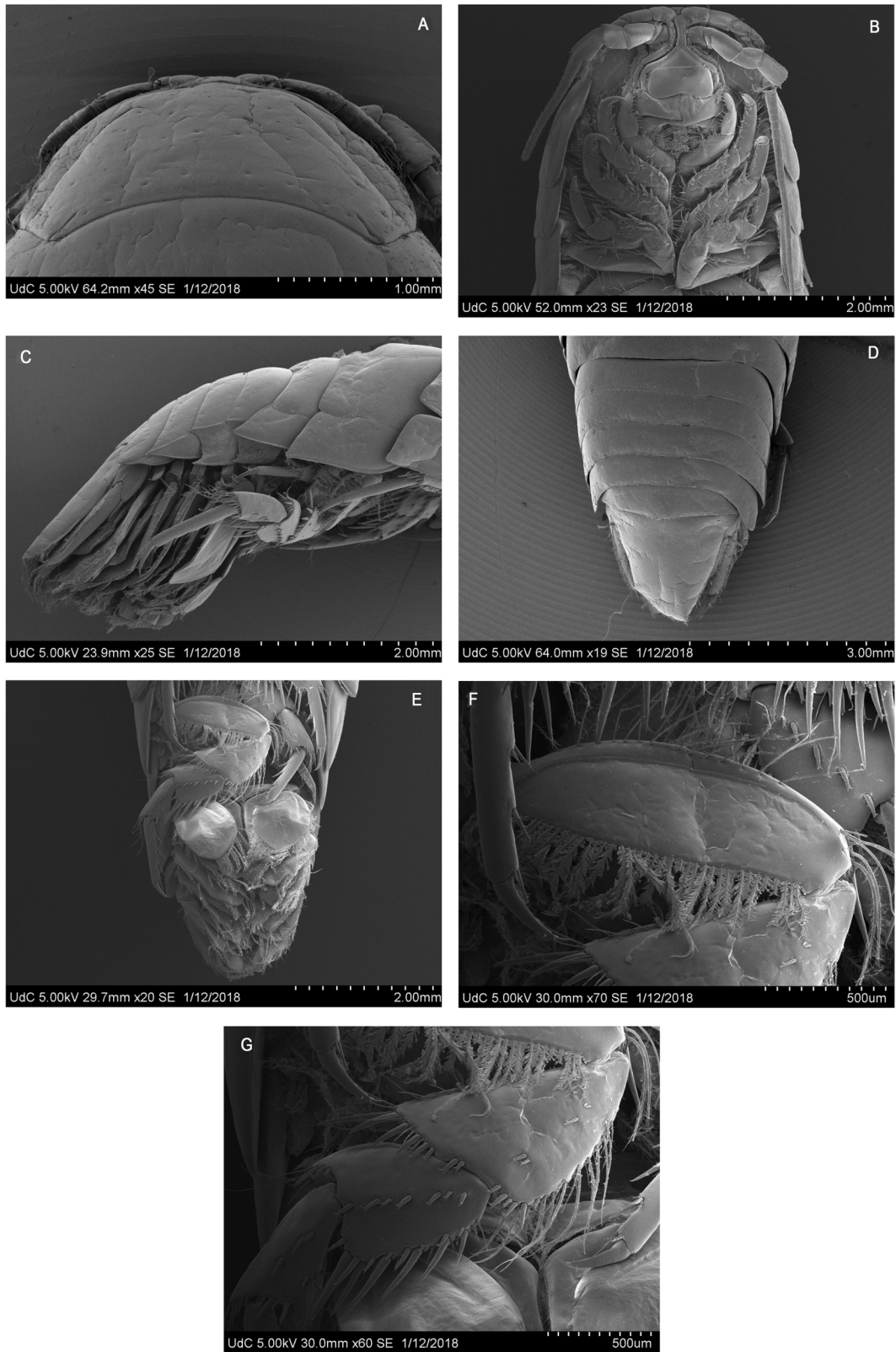
Isopod species	Localities	Number	Seasons	Sex
<i>Natanolana borealis</i>	Bay of Bizerte	4	Autumn	2 females
			Spring	1 female
			Summer	1 female
	Gulf of Tunis	6	Autumn	1female
			Winter	1 female
				1 male
			Spring	2 females
			Summer	1 female
	Gulf of Hammamet	6	Autumn	2 females
			Winter	2 females
			Spring	1 female
			Summer	1female
Gulf of Gabes	9	Autumn	1 female	
		Winter	1 female	
		Spring	3 females	
			1 male	
		Summer	2 females	
<i>Natanolana neglecta</i>	Bay of Bizerte	9	Autumn	1 female
			Winter	1 female
			Spring	4 females
			Summer	3 females
	Gulf of Tunis	3	Spring	3 females

**Table 3.** Fish species with their epidemiological characteristics, found to be infested by Cirolanidae. NEF: Number of examined fishes, NIF: Number of infested fishes, P (%): Prevalence, MI: Mean Intensity.

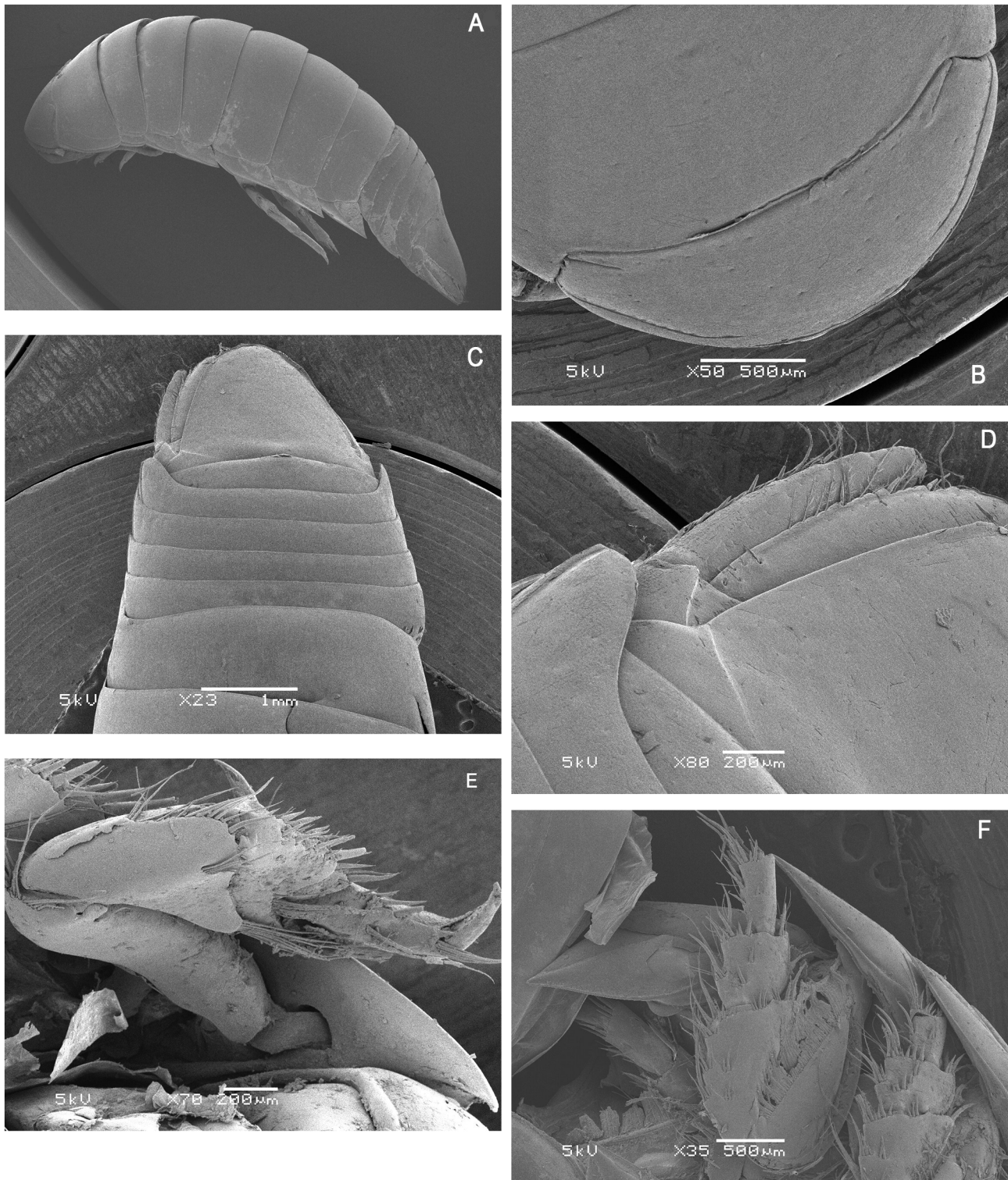
Isopods	Fish species	NEF	NIF	A	MI	Infestation site
<i>Natanolana borealis</i>	<i>Mustelus mustelus</i>	480	12	0.037	1.5	Cloacae cavity
	<i>Mustelus punctulatus</i>	216	5	0.023	1	Gills
	<i>Scyliorhinus canicula</i>	480	2	0.004	1	Cloacae cavity
<i>Natanolana neglecta</i>	<i>Raja clavata</i>	480	6	0.025	2	Nasal cavity

incomplete. Pleonite 4 posterolateral margins converge to an apex forming a broad acute point (Fig. 2C). The pleotelson is broad, its basal width measuring approximately 0.96 times its length. It does not present an anterodorsal depression. Its anterolateral margins are convex. The posterolateral margins are convex converging smoothly to a point; with 8 robust setae (Fig. 2D). Pereopod 7 has a broad basis, its width measuring 0.57 times its length; anterior and posterior margins are convex with plumose setae along the entire length of the posterior

margin (Fig. 2E & F). The distance between the anterior margin and the medial carina is less important than between the posterior margin and the medial carina (Fig. 2F). The pleopods have broader exopods than endopods. The appendix masculina (males) on pleopod 2 has a straight margin and it is slightly shorter than the endopod. Endopods lateral margins have a distinct acute projection forming a Y-shape with the apex (Fig. 2E). Uropods are characterized by shorter exopod than endopod; approximately 0.87 times the length of the endopod.



**Figure 2.** Scanning Electron Microscopy of *Natatolana borealis* (Liljeborg, 1851). **A.** Cephalon dorsal view. **B.** Cephalon and pereopod 1-4 ventral view. **C.** Pleotelson lateral view. **D.** Pleotelson dorsal view. **E.** Pleopods and 7<sup>th</sup> pereopod ventral view. **F.** 7<sup>th</sup> pereopod merus. **G.** 7<sup>th</sup> pereopod carpus and peropodus.



**Figure 3.** Scanning Electron Microscopy of *Natatolana neglecta* (Hansen, 1890). **A.** Lateral view. **B.** Cephalon dorsal view. **C.** Pleotelson and uropods dorsal view. **D.** Uropods dorsal view. **E.** 1<sup>st</sup> pereopod ventral view. **F.** 7<sup>th</sup> pereopod ventral view.

*Natanolana neglecta*

The interocular furrow is moderately developed and does not extend across the cephalon (Fig. 3B). The lateral margins of the frontal lamina are straight. Antennae approximately 0.3 times the body length, extending to the posterior of pereonite 3 when flattened against the body. All the pereonites coxal plates' furrows are strongly developed (Fig. 3A). The propodus of pereopods 2 and 3 do not have any robust setae on its anterolateral margin. Pereopod 7 has a broad basis, its width measuring 0.5 times its length; its anterior and posterior margins are convex with no plumose setae along the entire length of the posterior margin (Fig. 3F). The distance between the anterior margin and the medial carina is less important than between the posterior margin and the medial carina (Fig. 2F). The pleotelson is broad, its basal width measuring approximately 0.84 times its length. It does not present an anterodorsal depression (Fig. 3C). Its anterolateral margins are almost straight and angling posteriorly toward the midline. The posterolateral margins are straight. They are markedly angled to anterolateral margins. The lateral margins converge smoothly to a point (Fig. 3C); with 11-12 robust setae. Pleonite 4 posterolateral margins converge to an apex forming a broad acute point (Fig. 3A & C). Uropods are slightly shorter than the pleotelson (Fig. 3C). The exopod is slightly shorter than the endopod, 0.83 times the length of the endopod (Fig. 3D). The exopod margin of Pleopod 1 is rounded while its endopod margin is narrow at apex.

*Indices of the collected Cirolanidae and infestation sites*

Relative abundance (A) and mean intensity (MI) of each isopod species are reported in table 3.

Abundance is relatively low for both species studied. *N. borealis* found on three different species showed a relatively low prevalence. Its highest abundance was recorded on *M. mustelus* ( $P = 0.037$ ), while it presents the lowest abundance recorded during this survey ( $P = 0.004$ ) on *S. canicula* (Table 3).

*N. neglecta* on *R. clavata* has a relatively low abundance as well ( $P = 0.025$ ). The mean intensity of the two species was low and did not exceed 2 (Table 3).

Both species were collected from the body cavities of the different fish species (cloacae, gills and nasal cavities) (Table 3). However, during the extraction of these species, we were not able to observe any notable lesion or trauma.

**Discussion**

This survey allowed us to report the presence of two *Natanolana* species (*N. borealis* and *N. neglecta*) for the first time off the Tunisian coasts. Indeed, *N. borealis* has been recorded in the North Atlantic coasts and in the Mediterranean Sea (Kaïm-Malka, 1997; Keable & Bruce, 1997; Johansen & Brattegard, 1998). *N. neglecta* is a widespread species with records along the Atlantic coast of Europe (Rincón et al., 2014). This species distribution reaches the adjacent Atlantic coast of Africa, Spain and France (Norman, 1904; Monod, 1930; Rincón et al., 2014). However, this is the first record of these two species in the southern banks of the Mediterranean Sea. Moreover, we noted that *N. borealis* presented a larger distribution along the Tunisian coast as it was gathered from the different gulfs, while *N. neglecta* was only found in the two northern gulfs of Tunisia.

The morphological diagnostic and descriptive generic characters of these two species correspond to Keable & Bruce's (1997) key and description to the described Northern Atlantic and Mediterranean Sea species of *Natanolana*. However, the Tunisian samples of each species revealed slight morphological differences which we interpret as intraspecific variations. Indeed, the collected specimens of *N. borealis* off the Tunisian coast seem to have fewer robust setae in the merus-propodus of pereopod 1 than the specimens from Norway described by Keable & Bruce (1997) and Keable (2006). According to the present authors, the described specimens have 17 robust setae and seven slender setae on the posterior margin of the merus, the carpus has 2 robust setae on its anterior margin and the propodus have 5 robust setae on palm and a row of small slender setae extending along two-thirds of anterior margin. However, the collected specimens during this work have only seven slender setae and do not have any robust setae on the posterior margin of the merus, the carpus do not have any robust setae on its anterior margin and the propodus have 7 robust setae on palm, and no setae are observed on its anterodistal angle. Regarding *N. neglecta*, we noted the presence of robust setae on the anterolateral margin of the propodus and adjacent to the dactylus of pereopod 1 of the collected specimen during this survey. Moreover, their coxae and pleonite 4 are more acute than the type material from Naples illustrated by Keable & Bruce (1997).

These morphological variations may suggest that these two species could be cryptic species. However, to confirm this hypothesis an extensive morphological



study and a molecular characterization are needed.

Furthermore, these two isopod species have been the subject of many ecological investigations (Nilsson & Nilsson, 1981; Nilsson, 1983; Lindström & Nilsson, 1983; Wong & Moore, 1995 & 1996; Lourido et al., 2008; Revuelta et al., 2019). In fact, *N. borealis* has been reported from a wide range of bony fishes (Vader & Romppainen, 1985; Berrow, 1994; Keable & Bruce, 1997). However, reports of its presence on elasmobranchs are relatively scarce.

Previously, Bird (1981) reported this species on sharks from Atlantic coastal waters off Florida and Henderson et al. (2003) on *Lamna nasus* (Bonnaterra, 1788) in the west of Ireland waters. Therefore, we believe that it is the first record of *N. borealis* on *M. mustelus*, *M. punctulatus* and *S. canicula*.

In addition, *N. neglecta* was collected under mussels' rafts in Ría de Aldán (Spain) (Lourido et al., 2008) and on the sea turtle *Caretta caretta* (Linnaeus, 1758) on the Mediterranean coast of Spain (Revuelta et al., 2019). However, this is the first report of the presence of *N. neglecta* on any elasmobranch species.

Besides, during this survey, we noted that the two isopod species were found on different fish species yet never on the same fish; this is probably due to a slight difference of habitats of the two isopod species. Moreover, *N. borealis* presented a larger prey spectrum (three different species) while *N. neglecta* was only found on *R. clavata*. This may be explained by the fact that *N. borealis* is a cosmopolitan species which was gathered from many shark species while *N. neglecta* was never reported before on elasmobranchs.

Interestingly, we were able to notice that the two *Natanolana* species presented similar scavenging behaviour. Indeed, cirrolanid species sometimes swam in vast numbers and attack damaged fish, particularly at dusk or at night (Wong & Moore, 1995; Stepien & Brusca, 1985). However, the analysis of the different infestation indices shows that the abundance and the mean intensity of the two *Natanolana* species are relatively low; this may be explained in part by the fact that these fish specimens were very fresh during their capture without any external bleeding or damage that may attract scavengers. According to Johansen & Brattegard (1998), the search of *N. borealis* for the fish flesh is random which seems to be the case for *N. neglecta* as well. This led us to assume that these scavengers are more attracted to dead fishes than those restrained on lines. Indeed, according to Johansen & Brattegard (1998), within a short time, a piece of dead fish was almost completely covered by *N. borealis*. Moreover, it is worth considering the diet

of these two species which seem to infest teleostean fish more often than elasmobranchs.

Moreover, the two *Natanolana* species have been reported from the body cavities of fish which is consistent with our results as we found these two species on the cloacae cavity, gills and nasal cavities of their prey. However, each fish species was targeted in a precise cavity, this may be due to the morphology of these species and the accessibility for the scavenger species. Indeed, their mode of feeding on large 'targets' is to burrow into the tissue and muscle as they eat (Tiemensma et al., 2017). In one reported case they attacked and killed sharks by eating their way into the body cavity and destroying vital organs (Bird, 1981). Specimens of *N. neglecta* caused several holes in the esophagus wall of the turtle (*Caretta caretta*) and inside the skull (Revuelta et al., 2019). According to these authors, a hole found in the right eye of the turtle could be the entry route followed by the isopods, at least for the ones found in the skull and other possible points of access could be the mouth and nose.

However, during the examination of the different fish species, we did not notice any external or internal damage caused by either *N. borealis* or *N. neglecta*. Indeed, according to Stepien & Brusca (1985), fish infested by *Natanolana borealis* does not always show any external signs of damage.

This work allowed us to confirm the presence of *Natanolana* species off Tunisian coasts and on elasmobranchs. Therefore, it would be interesting to study their diversity on a larger scale (in their marine environment and on bony fish) and their morphological (phenotypic) differences from specimens of the North Atlantic. Moreover, we noted that these two species presented similar scavenging behaviour and impact.

## Acknowledgments

We are grateful to Dr. Niel L. Bruce (Queensland Museum, Brisbane, Australia) for his more than valuable help in the identification of the Cirrolanidae species and for his comments and corrections on this paper.

## References

- Ben Amor R., Brahim M. & Gueddari M. 2003. Essai d'interprétation de la dynamique sédimentaire par l'analyse granulométrique et minéralogique au large du Golfe de Gabès. *Bulletin de l'institut National des Sciences et technologies de la Mer Salammbo*, 30: 143-151.

- Berrow S. 1994. Fish predation by the marine crustaceans *Orchomene nana* and *Natanolana borealis*. *Irish Naturalists' Journal*, 24: 514.
- Biernbaum C.K. & Wenner E.L. 1993. Trapping of necrophagous crustaceans on the upper continental slope off South Carolina, U.S.A. *Journal of Crustacean Biology*, 13: 601-608. Doi: [10.2307/1548801](https://doi.org/10.2307/1548801)
- Bird P.M. 1981. The occurrence of *Cirolana borealis* (Isopoda) in the hearts of sharks from Atlantic coastal waters off Florida. *Fishery bulletin*, 79: 376-383.
- Bradaï M.N., Saidi B., Enajjar S. & Bouain A. 2005. The Gulf of Gabès: a spot for the Mediterranean elasmobranchs. In: *The Proceedings of the Workshop on Mediterranean Cartilaginous Fish with Emphasis on Southern and Eastern Mediterranean*, pp. 107-117. Turkish Marine Research Foundation: Istanbul, Turkey.
- Bradaï M.N., Saïdi B. & Enajjar S. 2012. Elasmobranchs of the Mediterranean and Black Sea: Status, Ecology and Biology. Bibliographic Analysis. In: *FAO Studies and Reviews. General Fisheries Commission for the Mediterranean*, 91: 103 pp. Rome.
- Brahim M.N. & Chkioua A. 2007. Répartitions granulométriques et minéralogiques des sédiments de surface dans le Golfe de Tunis. *Bulletin de l'institut National des Sciences et technologies de la Mer Salammô*, 34 : 167-177.
- Brahim M. & Nabli A. 2016. Dynamique sédimentaire dans le golfe de Hammamet (Centre-Est de la Tunisie). *Bulletin de l'institut National des Sciences et technologies de la Mer Salammô*, 43 : 151-161.
- Bruce N.L. 1986. Cirolanidae (Crustacea: Isopoda) of Australia. *Records of the Australian Museum*, Suppl. 6: 1-239.
- Bruce N.L. 2003. A new deep-water species of *Natanolana* (Crustacea: Isopoda: Cirolanidae) from the Chatham rise, eastern New Zealand. *Zootaxa*, 265: 1-12. Doi: [10.11646/zootaxa.265.1.1](https://doi.org/10.11646/zootaxa.265.1.1)
- Brusca R.C., Wetzer R. & France S.C. 1995. Cirolanidae (Crustacea: Isopoda: Flabellifera) of the tropical eastern Pacific. *Proceedings of the San Diego Society of Natural History*, 30: 1-96.
- Bush A.O., Lafferty K. D., Lotz J.M. Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. Revisited. *Journal of Parasitology*, 83: 575-583. Doi: [10.2307/3284227](https://doi.org/10.2307/3284227)
- Fischer W., Bauchot M.L. & Schneider M. 1987. Fiche F.A.O d'identification des espèces pour les besoins de la pêche Méditerranéenne et Mer Noire. *Zone de pêche*, 37: 761-1529.
- Froese R. & Pauly D. eds. 2019 (2018 in text ?). FishBase. [www.fishbase.org](http://www.fishbase.org)
- Henderson A.C., Flannery K. & Dunne J. 2003. Biological observations on shark species taken in commercial fisheries to the west of Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, 103B: 1-7. Doi: [10.3318/BIOE.2003.103.1.1](https://doi.org/10.3318/BIOE.2003.103.1.1)
- Johansen P.O. & Brattegard T. 1998. Observations on behaviour and distribution of *Natanolana borealis* (Lilljeborg) (Crustacea, Isopoda). *Sarsia*, 83: 347-360.
- Kaïm-Malka R.A. 1997. Biology and life cycle of *Natanolana borealis* Lilj. 1851, a scavenging isopod from the continental slope of the Mediterranean. *Deep Sea Research*, 44: 2045-2067. Doi: [10.1016/S0967-0637\(97\)00050-2](https://doi.org/10.1016/S0967-0637(97)00050-2)
- Keable S.J. 1995. Structure of the marine invertebrate scavenging guild of a tropical reef ecosystem: field studies at Lizard Island, Queensland, Australia. *Journal of Natural History*, 29: 27-45. Doi: [10.1080/00222939500770021](https://doi.org/10.1080/00222939500770021)
- Keable S.J. 2006. Taxonomic revision of *Natanolana* (Crustacea: Isopoda: Cirolanidae). *Records of the Australian Museum*, 58: 133-244.
- Keable S.J. & Bruce N.L. 1997. Redescription of the North Atlantic and Mediterranean species of *Natanolana* (Crustacea: Isopoda: Cirolanidae). *Journal of the Marine Biological Association of the United Kingdom*, 77: 655-705. Doi: [10.1017/S0025315400036134](https://doi.org/10.1017/S0025315400036134)
- Lindström M. & Nilsson H.L. 1983. Spectral and visual sensitivities of *Cirolana borealis* Liljeborg, a deep-water isopod (Crustacea: Flabellifera). *Journal of Experimental Marine Biology and Ecology*, 69: 243-256. Doi: [10.1016/0022-0981\(83\)90072-2](https://doi.org/10.1016/0022-0981(83)90072-2)
- Lourido A., Sorbe J.C. & Troncoso J.S. 2008. Inventario de los crustáceos bentónicos desedimentados infralitorales de la Ría de Aldán (Galicia, NO Península Ibérica). *Nova Acta Científica Compostelana, Biología*, 17: 149-168.
- Margolis L., Esche G.W., Holmes J.C., Kuris A.M. & Schrad G.A. 1982. The use of ecological terms in parasitology. *Parasitology*, 18: 603-607. Doi: [10.2307/3281335](https://doi.org/10.2307/3281335)
- Masri A. 1996. Etude d'impact de la dynamique sédimentaire sur la stabilité du littoral de la Baie de Bizerte. DEA, University of Tunis El Manar, Tunis, Tunisie. ?? pp.
- Mizzan L. 1995. *Cirolana neglecta* Hansen, 1890 (Crustacea, Isopoda, Cirolanidae) nelle coste del Veneziano: note su di un attacco ad una postazione di pesca. *Bollettino del Museo Civico di Storia Naturale di Verona. Botanica, Zoologia*, 44: 145-151.
- Monod T. 1930. Contribution à l'étude des "Cirolanidae". *Annales des Sciences Naturelles. Zoologie et Biologie Animale*, 13: 129-183.
- Nagano T., Kawakami K., Kajjura Y., Sakaguchi M. & Yamamoto H. 1963. Rapid destruction of submerged cadavers by tiny marine animals. *Wakayama Medical Reports*, 8: 31-39.
- Nilsson D.E. & Nilsson H.L. 1981. A crustacean compound eye adapted for low light intensities (Isopoda). *Journal of Comparative Physiology*, 143(A): 503-510. Doi: [10.1007/BF00609917](https://doi.org/10.1007/BF00609917)
- Nilsson H.L. 1983. Fine structure and convergent development of the *Cirolana* compound eye (Crustacea, Isopoda). *Zoomorphology*, 102: 165-174. Doi: [10.1007/BF00363807](https://doi.org/10.1007/BF00363807)
- Norman M.A. 1904. British Isopoda of the families Aegidae, Cirolanidae, Idoteidae, and Arcturidae. *The Annals and magazine of natural history; zoology, botany, and geology*, 7(suppl. 14): 444-448.
- Poore G.C.B. & Bruce N.L. 2012. Global Diversity of Marine Isopods (Except Asellota and Crustacean Symbionts). *PLoS One*, 7(9): e43529. Doi: [10.1371/journal.pone.0043529](https://doi.org/10.1371/journal.pone.0043529)
- Revuelta O., Domènech F., Keable S.J. & Míguez-Lozano D. 2019. First report of the scavenging isopod *Natanolana neglecta* (Crustacea: Isopoda: Cirolanidae) feeding on a sea turtle. *Mediterranean Marine Science*, 20: 297-301. Doi: [10.12681/mms.19058](https://doi.org/10.12681/mms.19058)
- Rincón B., Pérez J. & Junoy J. 2014. Description of *Natanolana neglecta* (Hansen, 1890) (Peracarida, Isopoda) from Spanish waters. *Crustaceana*, 87: 585-599. Doi: [10.1163/15685403-00003301](https://doi.org/10.1163/15685403-00003301)
- Stepien C.A. & Brusca R.C. 1985. Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. *Marine Ecology Progress Series*, 25: 91-105.

- Doi: [10.3354/meps025091](https://doi.org/10.3354/meps025091)
- Tiemensma M., Bruce N.L. & Willan R.C. 2017. Post-mortem human cadaver scavenging by marine crustaceans (Isopoda: Cirolanidae) in tropical waters. *Forensic Science, Medicine and Pathology*, 13: 515-517.  
Doi: [10.1007/s12024-017-9926-x](https://doi.org/10.1007/s12024-017-9926-x)
- Vader W. & Romppainen K. 1985. Notes on Norwegian marine Amphipoda. 10. Scavengers and fish associates. *Fauna Norvegica*, 6: 3-8.
- Wong Y.M. & Moore P.G. 1995. Biology of feeding in the scavenging isopod *Natanolana borealis* (Isopoda: Cirolanidae). *Ophelia*, 43: 181-196.  
Doi: [10.1080/00785326.1995.10429830](https://doi.org/10.1080/00785326.1995.10429830)
- Wong Y.M. & Moore P.G. 1996. Observations on the activity and life history of the scavenging isopod *Natanolana borealis* Liljeborg (Isopoda: Cirolanidae) from Loch Fyne, Scotland. *Estuarine, Coastal and Shelf Science*, 42: 247-262.  
Doi: [10.1006/ecss.1996.0018](https://doi.org/10.1006/ecss.1996.0018)