

CESTUM VENERIS LESUEUR, 1813 (CTENOPHORA) – A RARE GUEST IN THE NORTHERN ADRIATIC SEA

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ABSTRACT

We report the occurrence of the ctenophore *Cestum veneris* Lesueur, 1813 in the Gulf of Trieste (northern Adriatic Sea). Three individuals were found in March 2022, representing the first documented record in the scientific literature in more than 130 years. They were observed and photographed in the sea, and two specimens were brought to the Piran Aquarium, where their behaviour was observed. Historical and recent literature on the occurrence of this species in the Adriatic Sea was reviewed. The occurrence in the Gulf of Trieste is likely related to the transport of *C. veneris* with the currents, and therefore we present simulation results for the period January-February. Despite the relatively rare detections near the coast, this species is probably widespread in the offshore waters of the central and southern Adriatic.

Key words: winter gelatinous plankton, Ctenophora, distribution, Gulf of Trieste

CESTUM VENERIS LESUEUR, 1813 (CTENOPHORA) – OSPITE RARO NELL'ADRIATICO SETTENTRIONALE

SINTESI

Gli autori segnalano la presenza dello ctenoforo *Cestum veneris* Lesueur, 1813 nel Golfo di Trieste (mare Adriatico settentrionale). A marzo 2022 sono stati avvistati tre esemplari, che rappresentano il primo ritrovamento documentato dopo oltre 130 anni. Osservati e fotografati prima in mare, due esemplari sono stati portati all'Acquario di Pirano, dove è stato seguito il loro comportamento. È stata esaminata la letteratura storica e recente sulla presenza di questa specie nel mare Adriatico. Gli avvistamenti nel Golfo di Trieste sono probabilmente legati al trasporto di *C. veneris* con le correnti, e nell'articolo vengono presentati i risultati della simulazione per il periodo gennaio - febbraio. Nonostante i rilevamenti relativamente rari in prossimità della costa, questa specie è probabilmente diffusa nel mare aperto dell'Adriatico centro-meridionale.

Parole chiave: plancton gelatinoso invernale, Ctenophora, distribuzione, Golfo di Trieste

INTRODUCTION

Plankton in the northern Adriatic, including the Gulf of Trieste, is affected in winter and early spring not only by the well-mixed and cold water, but also by the greater influx of water from the south (Zavatarelli & Pinardi, 2003), which brings some otherwise rare species to this northernmost part of the Adriatic (Fonda Umani et al., 1992). These dynamics also affect the structure of the gelatinous plankton community. According to Miloš & Malej (2005), the cold-water group of gelatinous mesozooplankton was more diverse and less abundant, while some organisms originating from the deep southern waters of the Adriatic, such as the siphonophore *Vogtia pentacantha*, were occasionally observed. The most common winter-spring macrojellyfish in the northern Adriatic included the syphozoans *Aurelia solida*, *Rhizostoma pulmo*, the hydrozoan *Aequorea forskalea*, and the ctenophore *Leucothea multicornis*, while *Cestum veneris* was observed in the central and southern Adriatic and only in a few years in the northern Adriatic (Pestorić et al., 2021).

C. veneris is a tentaculate ctenophore species that lives circumglobally in temperate, subtropical and tropical seas (Mayer, 1912; GBIF, 2019). It is considered epipelagic (Harbison et al., 1978), but has also been observed in the mesopelagic zone (Lindsay et al., 2015; Hidaka et al., 2021).

Péron and Lesueur, who found this gelatinous species in coastal waters near Nice, France, on 12 May, 1809, named it after the magical girdle of Aphrodite - Ceste de Venus - and assigned this beautiful new ctenophore *C. veneris* with a distinctly elongated and transversely compressed body to the beroids (Lesueur, 1813). However, they had only one specimen available for examination. Lesueur reported in the same note (1813) that this organism, unknown to him and his collaborator Péron, was occasionally observed in large numbers in the harbour of Villefranche, where it

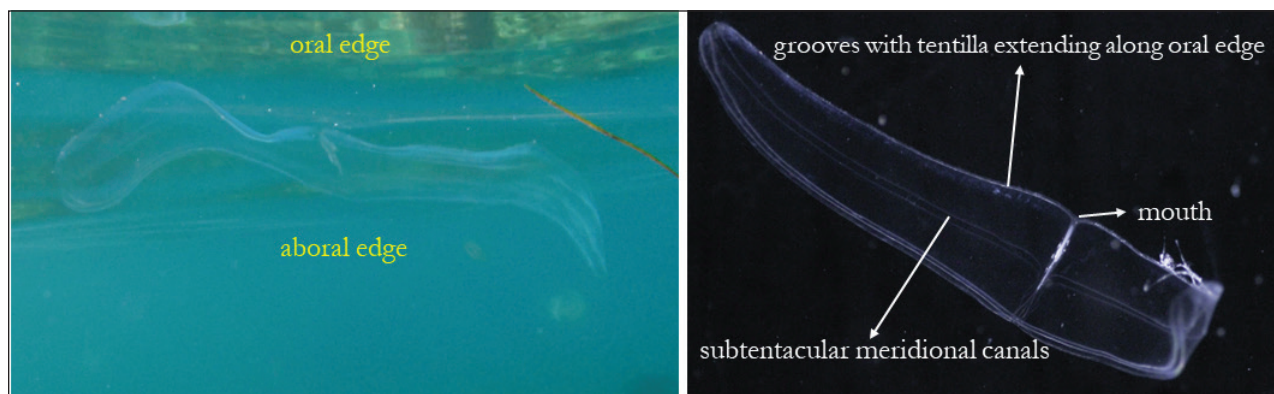
was called by fishermen ‘sabres de mer’ (a sea saber, a kind of curved sword used especially by pirates). Later Gegenbaur (1856) created the order Cestida and the family Cestidae, which today includes two monotypic genera: *Cestum veneris* Lesueur 1813 and *Velamen parallelum* Krumbach 1925.

In our contribution, we reviewed the historical and current literature on the occurrence of *C. veneris* in the Adriatic Sea. The recent discovery of this organism in the Gulf of Trieste, the first documented after 138 years (Graeffe, 1884), prompted us to describe its distribution and discuss some ecological characteristics of this beautiful ctenophore. We also present modelling results of the winter circulation, which likely support the entry of planktonic organisms of more southern origin into the northern Adriatic and the Gulf of Trieste.

MATERIAL AND METHODS

In total, three specimens of *C. veneris* were observed, two on 2 March and one on 3 March 2022 near the coast of Piran, Gulf of Trieste. The first observed specimen was not visible from the surface, but was accidentally felt by hand while taking underwater photos. During the capture, a part of the animal broke off, so the ctenophore was immediately released after inspection. At the same time, another specimen was observed 20 m away and collected undamaged. The next day, a third specimen was found at the same location and was also collected. The sea temperature was 8°C, salinity 38.6 and the sea surface near the shore was calm with almost no waves.

Two captured specimens were brought to the Piran Aquarium, but the specimen collected on March 2 began to disintegrate very quickly. The specimen caught on March 3 was immediately transferred to the 325 litres kreisel tank with a water temperature of 13°C and salinity of 38. It was fed freshly hatched *Artemia* nauplii. Photos and videos were taken, but the quality



**Fig. 1: Photo of *Cestum veneris* in the sea (left) and in the aquarium (right).
Sl. 1: Fotografija *Cestum veneris* v morju (levo) in v akvariju (desno).**

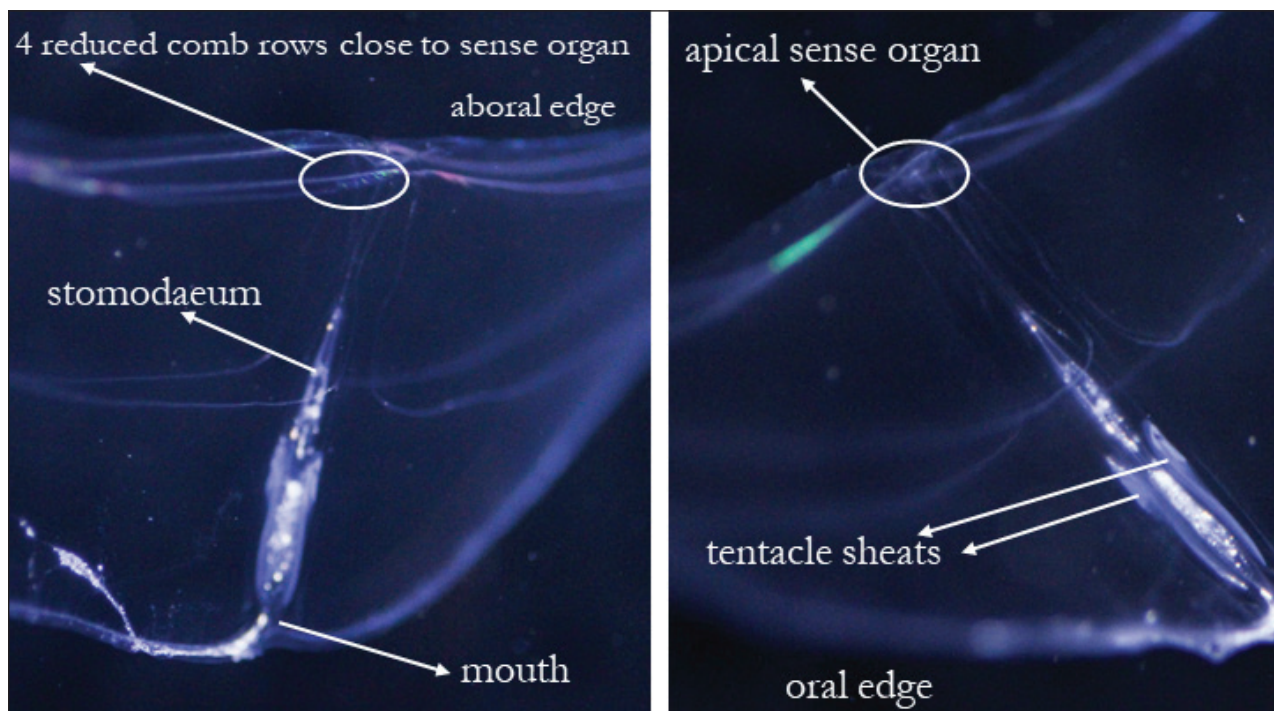


Fig. 2: Characteristics of the central part of *Cestum veneris*.
Sl. 2: Značilnosti osrednjega dela *Cestum veneris*.

was not very good due to the great transparency and rapid movements of the *C. veneris*.

We reviewed the available published sources on ctenophores in the Adriatic Sea in the last 150 years since the first description of *C. veneris*. With regard to the ecology of this species, we also consulted other published sources. The global distribution of *C. veneris* shown in Fig. 2 is from the Global Biodiversity Information Facility database (GBIF, 2019).

The CROCO ocean model (Coastal and Regional Ocean COMMunity model, formerly known as ROMS_AGRIF; www.croco-ocean.org) was used to simulate the Adriatic circulation during the 2000-2018 period. The model configuration was similar to the one used in Vodopivec *et al.* (2017), but with horizontal resolution reduced to 4 km and new atmospheric forcing provided by ERA5 (Hersbach *et al.*, 2020). Barotropic currents and free surface were averaged over the entire simulation period for January and February to provide an overview of the general circulation during the months when the *Cestum veneris* was likely transported from the central to the northern Adriatic.

RESULTS AND DISCUSSION

In the current classification, *C. veneris* is listed as a single species of the genus, belonging to the family Cestidae along with another monotypic genus *Velamen* Krumbach 1925 (Mills, 1998 - present):

Phylum Ctenophora
 Class Tentaculata
 Order Cestida Gegenbaur 1856
 Family Cestidae Gegenbaur 1856
 Genus *Cestum* Gegenbaur 1856
 Species *Cestum veneris* Lesueur 1813

C. veneris is characterised by a transparent, ribbon-shaped body, flattened in the tentacular axis while the lobular axis is elongated (Fig. 1). Adults can reach a height of about 8 cm and a length up to nearly 1,5 m but usually less than 80 cm. In contrast to those in g. *Velamen*, where subtentacular meridional canals arise directly without bending, in *Cestum* they arise from the stomodaeum then bend outward and run along the midline of the body. Substomodaeal comb rows are greatly elongated, while four subtentacular ones are rudimentary on aboral edge close to the sense organ (Fig. 2). On both sides of the mouth, grooves with tentilla extend along the entire oral margin of the body. Gonads run in continuous line under substomodaeal meridional canals.

All Ctenophora are carnivorous and their feeding mode is related to their morphology: they forage with tentacles, lobes, or feed by engulfing the prey (Haddock, 2007). *C. veneris* search for prey hovering or gliding horizontally with the oral edge leading (Matsumoto & Harbison, 1993) and tentilla stream aborally like curtains. After a few meters, *Cestum*

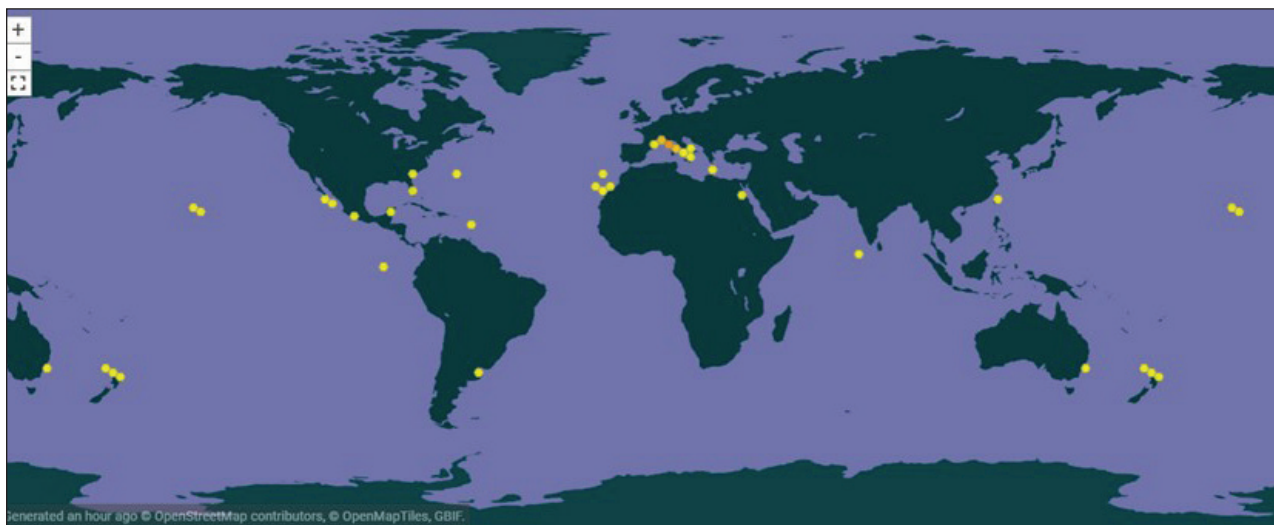


Fig. 3: Global distribution of *Cestum veneris* (<https://www.gbif.org/species/2501198>).
Sl. 3: Globalna razširjenost rebrače *Cestum veneris* (<https://www.gbif.org/species/2501198>).

move vertically and reverse swimming direction. Tentillae with sticky colloblasts attach to prey such as small copepods and then contract. Prey items are transferred to the oral groove and moved toward the mouth using cilia (Matsumoto & Harbison, 1993). Besides comb-row hovering or gliding, *Cestum* can also swim by muscular body undulations (Ceccaldi, 1972).

***Cestum veneris* distribution**

Cestum veneris is probably one of the most fragile ctenophores. Therefore, it is not surprising that we cannot catch them with conventional nets, which have been most commonly used in plankton surveys in the past. This characteristic, therefore, has a major impact on assessing *C. veneris* distribution and abundance. Nevertheless, researchers in the past have described the distribution of this species based on observations either from the coast or during research cruises. Their distribution was studied in particular during the 'first golden age of gelata research', from the late 19th to the early 20th century (Haddock, 2004), when many new species of Ctenophora were described, (Chun, 1878; Bigelow, 1904; Mayer, 1912). The development of autonomous diving, remote sensing, and new *in situ* observation techniques improved the collection of data on delicate gelatinous organisms. In addition, citizen science has enabled the collection of large amounts of data over broad areas and long periods of time. The availability of photographs and video clips facilitated the recognition of observed organisms by experts. Today, platforms such as Mer et littoral - European Marine Life or Global Biodiversity Information Facility provide information on the distribution of many marine species, including *C. veneris* (Fig. 3).

There are relatively few published data on ctenophores in the Adriatic Sea (Pestorić *et al.*, 2021). The rare records of ctenophores are usually not the result of systematic studies of these gelatinous organisms but are rather based on incidental observations such as ours. Some evidence come from published regular plankton observations for those species that are better preserved and later from the establishment of citizen science programs. The non-native *Mnemiopsis leidyi* is more systematically studied and is therefore a rare exception due to its significant impact on the ecosystem (Malej *et al.*, 2017; Budiša *et al.*, 2021).

The first record of *C. veneris* from the Adriatic Sea dates back to the 19th century when Graeffe (1884) reported rare, occasional observations of single specimens in the Gulf of Trieste. Krumbach (1911) found four specimens near Rovinj in mid-December 1910; two were about 10 cm and two about 25 cm long. In the southern Adriatic, Babić (1913) reported one small specimen observed near the island of Mljet in March 1912 and three larger specimens (about 50 cm) near Komiža (island of Vis). These few observations suggest that *C. veneris* was rare in the Adriatic, but Benović & Lučić (2001) described massive strandings and swarms near the island of Korčula and Dubrovnik after strong southerly winds. For more information on temporal and spatial distribution of *C. veneris* in the Adriatic, see Pestorić *et al.* (2021) and Violić *et al.* (2022). It was described as common in the central and southern Adriatic in winter and formed blooms in some years (1999, 2013). In the northern Adriatic, only few individuals were recorded in 2015-2017 period, while none were observed in the Gulf of Trieste (Pestorić *et al.*, 2021). Also, in the checklist of Ctenophora in the Italian seas (Mills, 2008), *C. veneris* was listed only for the central

and southern Adriatic. In the Mediterranean (Gulf of Naples), blooms of *C. veneris* were reported by Chun (1878) between December and May. Harbison *et al.* (1978), presenting the distribution and natural history of oceanic ctenophores of the North Atlantic, reported that *C. veneris* was the most abundant ctenophore species, and its density exceeded 1 per m³ at some stations.

Being an oceanic species, it is not surprising that it is so rare in the shallow northern Adriatic and Gulf of Trieste. Our observation of *C. veneris* in March 2022 is the first from the Gulf of Trieste (Fig. 2) since the report of Graeffe (1884). All three observed specimens were in shallow water, had a rectilinear posture, and swam just below the sea surface. They were swimming by bending, which resembled a wave moving from one side of their body to the other. The undulation started on the side of their body where the movement was directed and ran over to the other side like a wave. They could swim in either direction by changing sides at the beginning of the bend. Similar behaviour of individuals up to 80 cm in length was observed in diving by Ceccaldi (1972), who also noticed curling (rolling upon itself) in captivity and attributed this behaviour to stress.

Our observations in the aquarium agree with those of Ceccaldi (1972). Immediately after release into the kreisel tank, the *Cestum* curled up and remained in this shape for some time. Then it slowly stretched and moved in the same manner as it had previously been observed in the sea. In the following hours it was mostly fully stretched and moved with the circular flow of the water. A continuous movement of the cilia was observed. *Cestum* also ate newly hatched *Artemia* nauplii offered as food, as individual nauplii were observed in the stomach in the following hours (Fig. 2). During this time, it moved effortlessly and remained undamaged. The length was roughly estimated at 40 to 50 cm, measured by the size of the container in which they were held.

The rare sporadic records in the northern Adriatic and the Gulf of Trieste (Graeffe, 1884; Krumbach, 1911; Pestorić *et al.*, 2021; this article) during winter are likely due to the transport of *C. veneris* with the currents. This assumption is supported by the modeled barotropic currents for January and February, shown in Figure 4. The northward current along the eastern Adriatic coast is clearly visible. It passes the Kvarner Bay (KV) and splits into two branches at the southern tip of the Istrian peninsula (IS). The stronger branch veers westward and crosses the basin, while the weaker branch travels further north towards the Gulf of Trieste (GT).

The presence of *C. veneris* in the Gulf of Trieste in March 2022 could be caused by a bora (strong NE wind) event lasting several days, which occurred

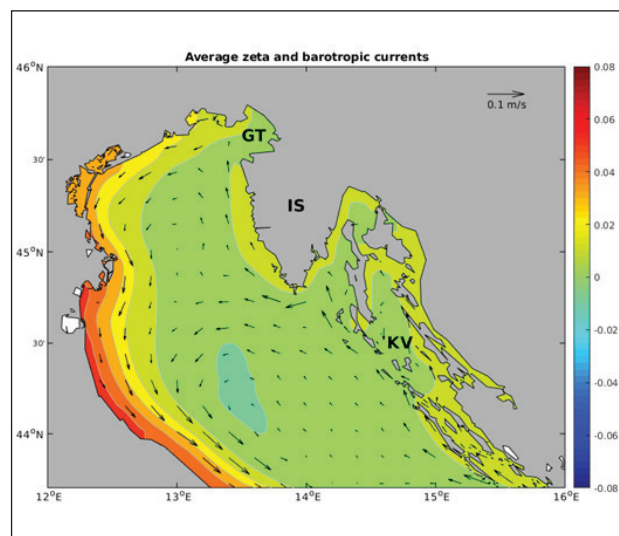


Fig. 4: Average January and February barotropic currents and free surface for the 2000-2018 period (model results). The arrow top-right represents current speed of 0.1 m/s, the colour scale is in meters. Arrows are plotted for every fourth grid cell. GT – Gulf of Trieste, IS – Istrian peninsula, KV – Kvarner Bay.

Sl. 4: Povprečni barotropni tokovi in prosta gladina v januarju in februarju za obdobje 2000-2018 (modelski rezultati). Puščica v desnem zgornjem kotu slike predstavlja tok s hitrostjo 0.1 m/s. Barvna skala je v metrih. Puščice so narisane za vsako četrto točko modelske mreže. GT – Tržaški zaliv, IS – Istra, KV – Kvarner.

shortly before its discovery. A study of topographic control of wind-driven circulation has shown that the bora induces a compensating current on the southeastern side of the Gulf of Trieste (Malačič *et al.*, 2012 - Figure 7). The leeward current (flowing into the gulf) is present almost throughout the entire water column, except for a few meters below the surface, where the current is windward. The inflowing north-eastward current could be responsible for the transport of the *C. veneris* individuals into the Gulf of Trieste.

In summary, despite the relatively rare finds near the Adriatic coasts, especially in the shallow northernmost area, this species is probably widespread in the offshore waters of the central and southern Adriatic.

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CESTUM VENERIS LESUEUR, 1813 (CTENOPHORA) – REDEK GOST V SEVERNEM JADRANU

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POVZETEK

Avtorji poročajo o redkem pojavu rebrače venerin pas (*Cestum veneris* Leseuer, 1813) v Tržaškem zalivu (severni Jadran). Trije osebki venerinega pasu so bili opaženi marca 2022, kar je prva v znanstveni literaturi dokumentirana najdba po več kot 130 letih. Osebkje smo opazovali in fotografirali v morju, dva pa prenesli tudi v Akvarij Piran, kjer smo opazovali obnašanje. Pregledali smo historično in novejšo literaturo o pojavljanju te vrste rebrač v Jadranskem morju. Pojav venerinega pasu v Tržaškem zalivu povezujemo z vnosom oz. transportom vodnih mas iz južnejših delov. Na osnovi nekaterih objav za Jadransko in Sredozemsko morje ter opazovanj v severnem Atlantiku sklepamo, da je ta vrsta, kljub ne ravno pogostim opažanjem v priobalnih vodah, dokaj običajna v odprtih vodah srednjega in južnega Jadrana.

Ključne besede: zimski želatinozni plankton, Ctenophora, razširjenost, Tržaški zaliv

REFERENCES

- Babić, K. (1913):** Planktonički celenterati iz Jadranskog mora. Rad JAZU Zagreb, 55, 186-202.
- Benović, A. & D. Lučić (2001):** Jellyfish outbreaks: natural cycles or stress response effects. CIESM Workshop Series, 14, 59-62.
- Bigelow (1904):** Medusae from the Maldive Islands. Bull. Museum Comp. Zool., 39, 245-269
- Budiša, A., P. Paliaga, T. Juretić, D. Lučić, N. Supić, Z. Pasarić, T. Djakovac, M. Mladinić, V. Dadić & V. Tičina (2021):** Distribution, diet and relationships of the invasive ctenophore *Mnemiopsis leidyi* with anchovies and zooplankton, in the northeastern Adriatic Sea. Mediterranean Marine Science, 22(4), 827-842.
- Ceccaldi H.J. (1972):** Observations biologiques de *Cestus veneris*. Tethys, 4, 707-710.
- Chun, C. (1878):** Die im Golf von Neapel erscheinenden Rippenquallen. Mittheilungen. a.d. Zoologischen Station zu Neapel, 1, 180-217.
- Fonda Umani, S., P. Franco, E. Ghirardelli & A. Malej (1992):** Outline of oceanography and the plankton of the Adriatic Sea. In: Marine Eutrophication and Population Dynamics (Eds. Colombo et al), Olsen & Olsen, Fredesborg, 347-365.
- GBIF Secretariat (2019):** GBIF Backbone Taxonomy. European-marine-life.org/06/cestum-veneris.php, Downloaded on 29 March 2022.
- Gamulin, T. (1979):** Zooplankton of the eastern Adriatic Sea. Prir. Istr. JAZU, 43, 177-270 (in Croatian).
- Gegenbaur, C. (1856):** Studien über Organisation und Systematik der Ctenophores. Archiv für Naturgeschichte, 2(1), 163-205.
- Graeffe, E. (1884):** Uebersicht der Seethierfauna des Golfes von Triest. III. Coelenteraten. Arbeit. Zool. Inst. Wien, Bd. 5, 333-362.
- Gueroun, S.K.M, S. Schäfer, F. Gizzi, S. Álvarez, J.G. Monteiro, C. Andrade & J. Canning-Clode (2021):** Planktonic Ctenophora of the Madeira Archipelago (Northeastern Atlantic). Zootaxa, 5081(3), 433-443.
- Haddock, S.H.D. (2004):** A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. Hydrobiologia, 530/531, 549-556.
- Haddock, S.H.D. (2007):** Comparative feeding behaviour of planktonic ctenophores. Integrative and Comparative Biology, 47(6), 847-853. <https://doi.org/10.1093/icb/icm088>.
- Harbison, G.R., L.P. Madin & N.R. Swanberg (1978):** On the natural history and distribution of oceanic ctenophores. Deep-Sea Research, 25(3), 233-256.
- Hersbach, H., B. Bell, P. Berrisford, S. Hirahara, A. Horányi, J. Muñoz-Sabater et al. (2020):** The ERA5 global reanalysis. Quarterly Journal of the Royal Meteorological Society, 146(730), 1999-2049.
- Hidaka, M., J. Nishikawa & D.J. Lindsay (2021):** Gelatinous zooplankton community around a hydrothermally active deep-sea caldera: Results from ROV video records. Plankton and Benthos Research, 16(1), 40-58. <https://doi.org/10.3800/pbr.16.40>.
- Krumbach, T. (1911):** Notizen über die Fauna der Adria bei Rovigno. IV. Die Ctenophorenfauna von Rovigno nach den Novemberstürmen 1910. Zool. Anz., 37, 315-319.
- Lesueur, C.A. (1813):** Mémoire sur quelques nouvelles espèces d'animaux mollusques et radiaires recueillis dans la Méditerranée près de Nice. Nouveau Bulletin des Sciences, par la Société Philomatique de Paris, 3(69), 281-285.
- Lindsay, D.J., M. Umetsu, M. Grossmann, H. Miyake & H. Yamamoto (2015):** The gelatinous macroplankton community at the Hatoma Knoll hydrothermal vent. In: Ishibashi, J., Okino, K. & Sunamura, M. (Eds.), Subseafloor Biosphere Linked to Hydrothermal Systems: TAIGA Concept. Springer, Tokyo, pp. 639-666.
- Malačić, V., B. Petelin & M. Vodopivec (2012):** Topographic control of wind-driven circulation in the northern Adriatic. Journal of Geophysical Research: Oceans, 117(C6).
- Malej, A., V. Tirelli, P. Paliaga, M. Vodopivec, A. Goruppi, S. Ancona, M. Benzi, N. Bettoso, E. Camatti, M. Ercolessi, C.R. Ferrari & T. Shiganova (2017):** *Mnemiopsis leidyi* in the northern Adriatic: here to stay? J. Sea Res., 124, 10-16.
- Matsumoto, G.I. & G.R. Harbison (1993):** *In situ* observations of foraging, feeding, and escape behavior in three orders of oceanic ctenophores: Lobata, Cestida, and Beroida. Marine Biology, 117, 279-287.
- Mayer, A.G. (1912):** Ctenophores of the Atlantic coast of North America. Carnegie Institution, Washington, 58 pp. <https://doi.org/10.5962/bhl.title.5968>.
- Mer et Littoral - European Marine Life: <https://www.european-marine-life.org/06/cestum-veneris.php>**, Downloaded, 31 March 2022
- Mills, C.E. (1998-present):** Phylum Ctenophora: list of all valid species names. Electronic internet document. *Cestum veneris* Lesueur, 1813. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106363> on 2022-04-03.
- Mills, C.E. (2008):** Ctenophora. Checklist of Fauna Italiana. Biol. Mar. Mediterr., 15 (suppl.), 102-104.
- Miloš, Č. & A. Malej (2005):** Gelatinous plankton assemblages in temperate coastal waters – seasonal variations (Gulf of Trieste, Adriatic Sea). Annales, Ser. Hist. Nat., 15(1), 11-20.

Pestorić, B., D. Lučić, N. Bojanić, M. Vodopivec, T. Kogovšek, I. Violić, P. Paliaga & A. Malej (2021): Scyphomedusae and Ctenophora of the Eastern Adriatic: Historical Overview and New Data. *Diversity*, 13, 186.

Purcell, J.E. (2012): Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations. *Annu. Rev. Mar. Sci.*, 4, 209-235.

Rossi, L. (1971): Guida a cnidari e ctenofori della fauna italiana. *Quad. Civ. Staz. Idrob. Milano*, 2, 91-95.

Violić, I., D. Lučić, N. Bojanić, B. Pestorić, B. Gangai Zovko, I. Onofri & M. Hure (2022): Long-term Monitoring of Carnivorous Macrozooplankton Dubrovnik-Neretva County. *Naše more*, 69(1), 22-29.

Vodopivec, M., Á.J. Peliz & A. Malej (2017): Offshore marine constructions as propagators of moon jellyfish dispersal. *Environmental Research Letters*, 12(8), 084003.

Zavatarelli, M. & N. Pinardi (2003): The Adriatic Sea modelling system: a nested approach. *Annales Geophysicae*, 21(1), 345-364.