

## AURELIA SP. 5 (SCYPHOZOA) POPULATION IN THE MLJET LAKE (THE SOUTHERN ADRIATIC): TROPHIC INTERACTIONS AND LINK TO MICROBIAL FOOD WEB

*Alenka MALEJ, Valentina TURK, Tjaša KOGOVSŠEK & Tihomir MAKOVEC*  
Marine Biology Station, National Institute of Biology, SI-6330 Piran, Fornače 41, Slovenia  
E-mail: malej@mbss.org

*Vladimir ONOFRI*  
University of Dubrovnik, Institute for Marine and Coastal Research, HR-20000 Dubrovnik, Damjana Jude 12, Croatia

*Luciano CHIAVERANO*  
Dauphin Island Sea Lab, University of South Alabama, 101 Bienville Blvd., Dauphin Island AL 36528, USA

*Tinkara TINTA & Vesna FLANDER-PUTRLE*  
Marine Biology Station, National Institute of Biology, SI-6330 Piran, Fornače 41, Slovenia

*Davor LUČIĆ*  
University of Dubrovnik, Institute for Marine and Coastal Research, HR-20000 Dubrovnik, Damjana Jude 12, Croatia

### ABSTRACT

*Vertical distribution, population structure and chemical composition of a population of the scyphomedusan Aurelia sp. 5 were studied in the Mediterranean euhaline lake on Mljet Island (Veliko jezero, the Southern Adriatic) where dense aggregations have been observed throughout the year. A majority of Aurelia were located in a layer below the thermocline with temperatures 13–19 °C over most of the day during summer, whereas in October the population was shallower. The medusae migrated towards the surface at dusk but rarely crossed the thermocline. Elemental analysis of Aurelia revealed low dry weight specific carbon, nitrogen and phosphorus content ranging from 0.9–1.7%, 0.2–0.5% and 0.02–0.06%, respectively. In addition to the direct predatory impact on micro- and mesozooplankton, a clear positive response of heterotrophic bacteria to the presence of live and dead Aurelia was observed.*

**Key words:** *Aurelia*, vertical distribution, C, N, P contents, microbial plankton, Adriatic Sea

### POPOLAZIONE DI AURELIA SP. 5 (SCYPHOZOA) NEL LAGO DI MLJET (ADRIATICO MERIDIONALE): INTERAZIONI TROFICHE E LEGAME CON LA RETE ALIMENTARE MICROBICA

#### SINTESI

*Gli autori presentano la distribuzione verticale, la composizione chimica e la struttura della popolazione di scifomeduse Aurelia sp. 5, studiata nel lago Mediterraneo eualino sull'isola di Mljet (Veliko jezero, Adriatico meridionale), dove dense aggregazioni sono state osservate nel corso dell'anno. Durante il periodo estivo, la maggioranza degli individui di Aurelia era situata, per gran parte della giornata, nello strato sottostante il termoclino, con temperature fra i 13 e i 19 °C, mentre in ottobre la popolazione si trovava in acque più superficiali. Le meduse migravano verso la superficie all'imbrunire, ma raramente oltrepassavano il termoclino. L'analisi elementare di Aurelia ha rivelato un basso peso secco specifico in contenuti di carbonio, azoto e fosforo, variando rispettivamente fra 0,9–1,7%, 0,2–0,5% e 0,02–0,06%. A prescindere dall'impatto diretto di predazione su micro- e mesozooplankton, è stata registrata una chiara risposta positiva dei batteri eterotrofi alla presenza di esemplari di Aurelia vivi e morti.*

**Parole chiave:** *Aurelia*, distribuzione verticale, contenuti C, N, P, plancton microbico, mare Adriatico

## INTRODUCTION

The classical linear planktonic food chain that described transfer of material from dissolved nutrients through phytoplankton to herbivorous and carnivorous mesozooplankton was changed radically by the discovery of the 'microbial loop' more than two decades ago (Azam *et al.*, 1983). At the opposite end of the marine planktonic size-spectrum, more recently we have also modified our understanding of the importance, trophic position and ecosystem role of jellyfish. Traditionally, jellyfish were viewed as a single functional group (Pauly *et al.*, 2009) largely unpalatable to consumers due to high water content, nematocysts and toxins (*e.g.*, Shanks & Graham, 1988), and thus significant for organic matter cycling only as 'top' predators. However, recent discovery of diverse feeding modes (Costello *et al.*, 2008), widespread and frequently massive presence (Purcell *et al.*, 2007), and the fact that even some large marine animals such as sunfish (*Mola mola*) and leatherback turtles (*Dermochelys coriacea*) prey on jellyfish (Houghton *et al.*, 2006), has changed our perception of jellyfish as a dead-end in food webs. Jellyfish were conventionally viewed as voracious predators feeding mainly on mesozooplankton and competing for food with pelagic fish (Purcell & Sturdevant, 2001).

An important factor for the assessment of an organism's trophic position is its biochemical composition, and it is likely that differences in composition will affect their biogeochemical role. Recently, the role of jellyfish in elemental cycling has been reviewed (Pitt *et al.*, 2009) with special attention to the accumulation and release of inorganic and organic carbon, nitrogen and phosphorus. Excretion of dissolved organic matter as a nutrient source for bacterioplankton was also discussed, although it was stressed that very few data were available. A study on the linkage between jellyfish and microbes was carried out in a jellyfish (*Periphylla periphylla*) dominated fjord, where it was found that the layer of maximal jellyfish biomass coincided with elevated total organic carbon, bacterial production and ectoenzymatic activities (Riemann *et al.*, 2006). Another study conducted in this fjord found the microbial community clearly responding to dead jellyfish in different ways; some morphotypes proliferated while others were inhibited by jellyfish tissue (Titelman *et al.*, 2006).

The moon jellyfish *Aurelia* spp. is a cosmopolitan genus but molecular criteria used in recent evolutionary studies indicate that it includes numerous cryptic species (Dawson, 2003). *Aurelia* can form large aggregations, particularly in enclosed seas (the Adriatic, Baltic, Black, Seto Inland, Wadden seas) and in protected coastal waters such as fjords, bays, estuaries and marine lakes where it often attains very high biomass (Lucas, 2001). In many cases *Aurelia* has significant impact on plankton communities, and its structuring effect on mesozooplankton has

been demonstrated in several coastal environments (Olesen, 1995; Omori *et al.*, 1995; Lucas *et al.*, 1997; Schneider & Behrends, 1998; Barz & Hirche, 2005).

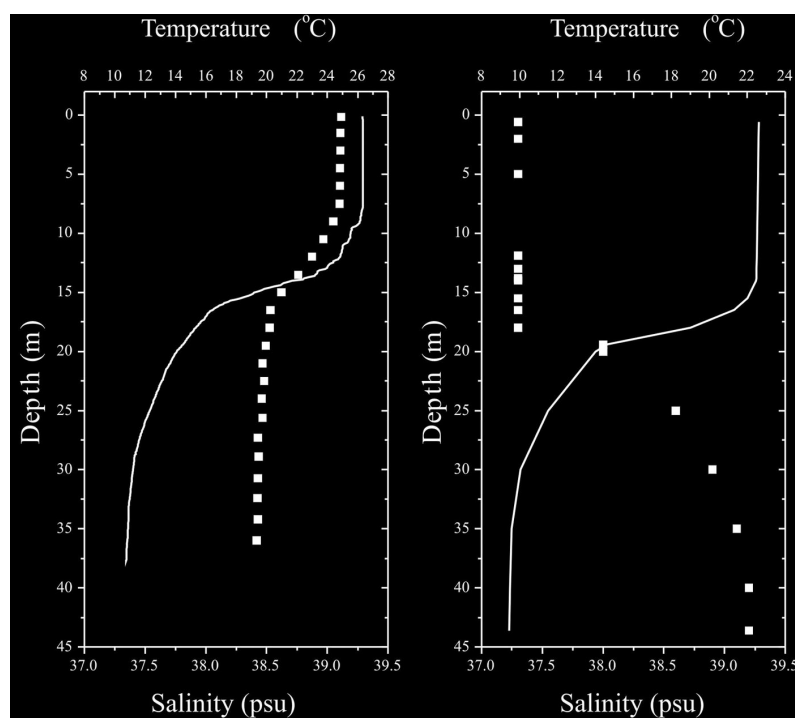
Several studies have also linked jellyfish to the microbial loop via direct consumption of ciliates (Stoecker *et al.*, 1987; Båmstedt, 1990; Omori *et al.*, 1995). High clearance rates for nauplii and naked ciliates were found by Malej *et al.* (2007) who pointed to indirect cascading effects of *Aurelia* on the microbial loop in addition to its impact on the entire food web. A more direct connection with bacterioplankton which may use DOC released by *Aurelia aurita* was suggested by Hansson & Norrman (1995).

Our study on the *Aurelia* sp. 5 population and its links to the microbial food web was carried out in a Mediterranean euhaline lake, where dense aggregations have been observed throughout the year (Benović *et al.*, 2000). Genus *Aurelia* is present in the shallow northern Adriatic and in some semi-enclosed bays and lagoons along the eastern and western Adriatic. It has traditionally been termed *A. aurita* although molecular criteria used in recent studies questioned this designation (Schroth *et al.*, 2002; Dawson, 2003); following these authors we use *Aurelia* sp. 5 for the Mljet lake population.

Large (110 L) and small (8 L) mesocosm experiments were used to study the influence of *Aurelia* sp. 5 on microbial biomass and production (Turk *et al.*, 2008) and the response of the native bacterial community to biomass originating from dead *Aurelia* (Tinta *et al.*, submitted). We report here on the vertical position, seasonal size structure, and elemental composition (C, N, P) of *Aurelia* and discuss these data in relation to microbial plankton.

## MATERIAL AND METHODS

Our study was conducted in a euhaline marine 'lake' located on the north-western side of Mljet, an offshore south Adriatic island. Veliko jezero (Big Lake – BL, see Fig. 1 in Graham *et al.*, 2009) is a submerged karstic depression that was flooded during Holocene sea-level rise (Wunsam *et al.*, 1999). Exchange between this small lake (surface area about 1.45 km<sup>2</sup>) and the open Adriatic is through a 1 km long and 10 m wide channel that was artificially deepened to about 2.8 m (Ridžanović & Šimunović, 1995). Weak tides (< 25 cm tidal range) restrict water exchange with the open sea through the channel. The lake bathymetry has two main depressions (depths > 40 m) separated by a sill (depth < 15 m), which affect the environmental and biological characteristics of the lake. During summer, a strong thermocline separates the 12–20 m deep upper layer from deeper waters where temperature is rather stable throughout the year (9–12 °C). Maximal surface temperatures may reach 26–28 °C. Small salinity differences between the surface layer (36.3–38.6 psu) and deeper layer (37.5–38.6 psu) also exist (Fig. 1).



**Fig. 1:** Temperature (solid line) and salinity (solid square) profiles in July 2003 (left) and October 2006 (right).  
**Sl. 1:** Temperatura (polna črta) in slanost (polni kvadrati) julija 2003 (levo) in oktobra 2006 (desno).

The water column characteristics and *Aurelia* vertical distribution were studied in the two deepest areas of BL (Fig. 1, Graham *et al.*, 2009). A CTD fine-scale probe (Microstructure Profiler MSS90, Sea & Sun Technology GmbH) was used to determine temperature and salinity, and vertical distribution of *Aurelia* was assessed using a Sony DCR-VX200E video camera in an Ikellite underwater housing.

*Aurelia* were collected either with a zooplankton net (WP2, 200  $\mu\text{m}$  mesh) or manually by divers during following periods: 4–18 July 2003, 16–23 May 2004, 20–21 July 2005, 6–10 March 2006, 3–6 October 2006, 6–16 May 2008, 14–23 May 2009. For bell diameter measurements, medusae were spread flat on a glass plate and the diameter was recorded to the nearest 1 mm. *Aurelia* were stored individually in bags for elemental analysis and kept deep-frozen ( $-30\text{ }^{\circ}\text{C}$ ). Samples were freeze-dried and chemically analysed using a CHN elemental analyzer (CarloErba). Phosphorous was estimated after digestion of samples with  $\text{K}_2\text{S}_2\text{O}_8$  in an autoclave and subsequent colorimetric detection of phosphate produced (Grasshoff *et al.*, 1983).

The concentration of Chlorophyll *a* in the water samples was determined using the reverse-phase HPLC (High Performance Liquid Chromatography) method (Mantoura & Llewellyn 1983; Barlow *et al.*, 1993) and by absorbance at 440 nm using a UV/Vis spectrophotometric detector (Spectra Physics, Model UV2000).

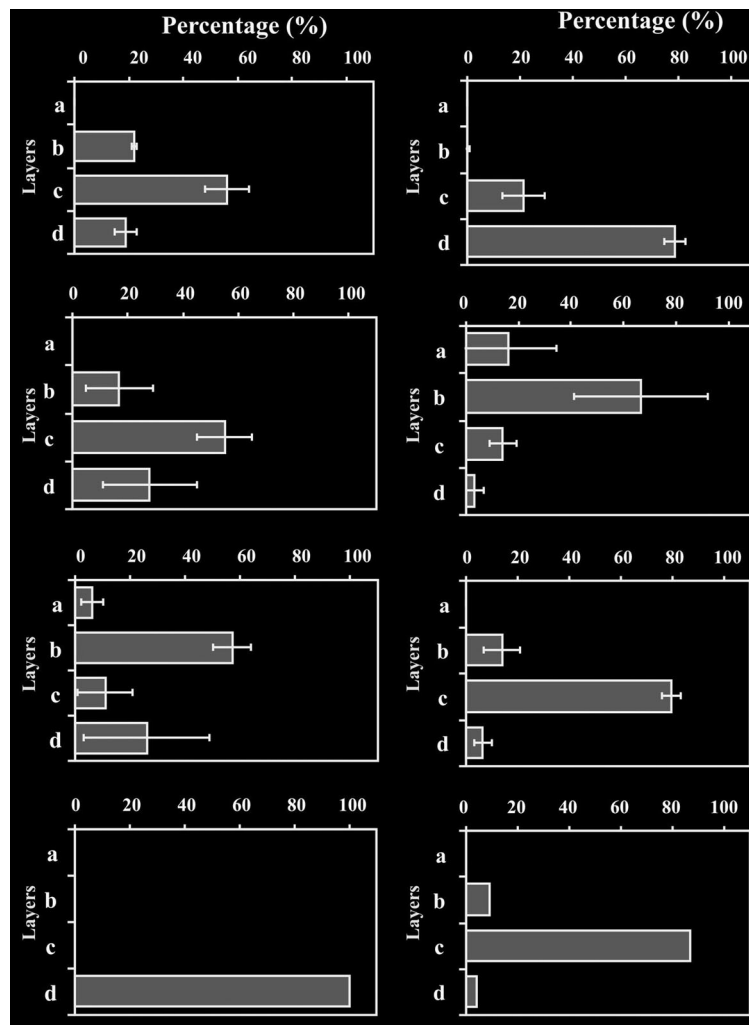
Bacterial abundance and production were deter-

mined using standard procedures of staining formalin-fixed samples with DAPI (Porter & Feig, 1980) and bacterial protein synthesis using  $^3\text{H}$ -Leucine (Smith & Azam, 1992); methodology used is described in detail in Turk *et al.* (2008).

## RESULTS AND DISCUSSION

### Vertical distribution

Vertical distribution of *Aurelia* was followed over several diel cycles in the deepest parts of the lake ( $> 40\text{ m}$ ). There was a clear difference in vertical position of *Aurelia* population over the diel cycle in October, particularly when compared to months when surface temperatures were  $> 26\text{ }^{\circ}\text{C}$  (Fig. 2). In summer during the day, most *Aurelia* were below the thermocline in a layer with temperatures of  $13\text{--}19\text{ }^{\circ}\text{C}$ . They migrated towards the surface at dusk but rarely crossed the thermocline. In October, the population was located shallower during daylight, occupying mostly the thermocline layer with similar temperatures as during summer (see Fig. 1 for temperature and salinity profiles). The water column was still thermally stratified in October although temperature differences between surface and 20 m depth were significantly smaller (about  $8\text{ }^{\circ}\text{C}$ ) than in July (about  $16\text{ }^{\circ}\text{C}$ ). At night most medusae were below the thermocline. *Aurelia* were very rarely observed in surface layers ( $< 5\text{ m}$ ; temperatures higher than  $20\text{ }^{\circ}\text{C}$ ) during any season.



**Fig. 2:** Vertical position of *Aurelia* population over the diel cycle in July 2003 (left) and October 2006 (right) in different layers: a – above the thermocline layer, b – the thermocline layer, c – below the thermocline layer, d – deep layer (> 25 m). Times of the day (local hour): early morning (04:30–7:30), day (7:30–17:30), dusk (17:30–20:30), night (20:30–04:30).

**Sl. 2:** Vertikalna razporeditev populacije *Aurelia* v dnevno-nočnem ciklusu julija 2003 (levo) in oktobra 2006 (desno) po slojih: a – sloj nad termoklino, b – termoklinski sloj, c – sloj pod termoklino, d – globoki sloj (> 25 m). Ure (lokalni čas): zgodnje jutro (04:30–7:30), dan (7:30–17:30), večer (17:30–20:30), noč (20:30–04:30).

Short-term (< 60 min) surface swarming was observed on rare occasions during periods of very calm weather during summer and autumn. We did not determine vertical distribution of *Aurelia* population during winter (February–March), but divers that collected jellyfish for bell diameter and elemental analysis reported aggregations between 15 and 5 m.

#### Population characteristics

Medusae from BL were sampled in all seasons but more frequently during the warmer part of the year. In other temperate marine systems with *Aurelia* popula-

tions, medusae tend to show seasonality with winter-spring recruitment of ephyrae, spring growth, followed by summer accumulation of medusae biomass and eventual disappearance from the water column in autumn (Lucas, 2001). However, *Aurelia* in BL do not show distinct seasonal dynamics. Medusae are present year-round, and from our data we could not see a clear seasonal recruitment and growth (Fig. 2). Presumably, there is an extended recruitment period of new medusae from benthic scyphopolyp in this lake. Bell diameter varied from 2.8 cm in May (2009) to 18.8 cm in July (2006) with the largest average and median diameter in October. However, large year-to-year variability of me-

**Tab. 1: Mean size and weight of measured jellyfish (*Aurelia*) during 2003–2009.**

**Tab. 1: Srednje vrednosti premera klobuka in mokre mase izmerjenih meduz (*Aurelia*) v obdobju 2003–2009.**

	Bell diameter (cm)	Wet weight (g)
Average	8.4	42.3
SD	2.9	46.7
Median	8.2	25.0
Min	2.8	10.0
Max	18.5	380.0
N	379	379

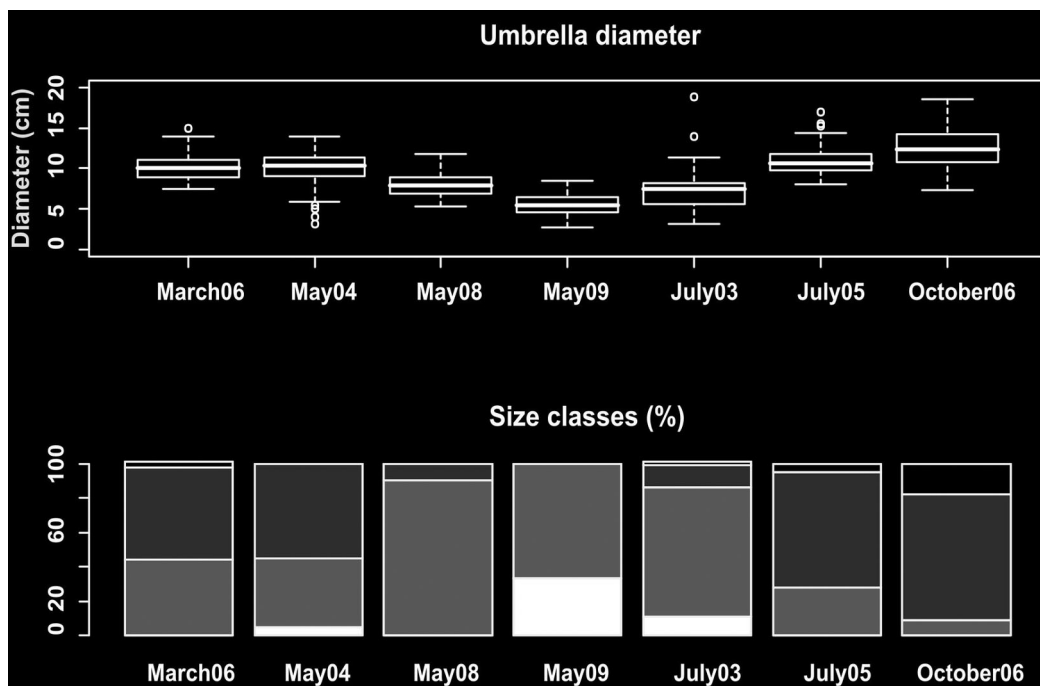
dusae size in the same period was also found (Fig. 3) and May samples (collected in three years: 2004, 2008, and 2009) clearly illustrate this divergence. Mean wet weight (Tab. 1) of *Aurelia* individuals was rather low and showed a seasonal pattern that matched bell diameter, with slightly higher values in July compared to March and May and with maximum weight in October.

Elemental analysis of *Aurelia* reveals low dry weight specific carbon and nitrogen content (Fig. 4) ranging from 0.9 to 1.7% and 0.2 and 0.5% for carbon and nitrogen, respectively, and rather low C/N atomic ratios

(3.9–4.9). Similarly, phosphorus content of *Aurelia* was low with an overall average of 0.04% of dry weight. These contents are comparable to other gelatinous plankton but lower than some other Scyphomedusae (Larson, 1986; Malej et al., 1993) as well as *Aurelia* from the northern Adriatic (Malej et al., 2006). Proteins represent the largest organic fraction consistent with low atomic C/N ratio ( $4.3 \pm 0.21$ ). Some seasonal differences were observed with significantly higher organic contents in samples collected in October ( $p < 0.01$ ).

***Aurelia*-associated organic mass in BL**

The average October 2006 values of DW (3% of wet weight), carbon (1.3% of DW), nitrogen (0.3% of DW) and phosphorous (0.04% of DW) contents were applied to abundance estimates of *Aurelia* based on acoustic surveys done during the same period (Alvarez Colombo et al., 2009) to calculate total *Aurelia*-associated mass in the BL (Tab. 2). Taking into account the BL volume, these values translate to average *Aurelia* wet mass of  $19.63 \text{ g m}^{-3}$  and organic carbon, nitrogen and phosphorus biomass of  $7.9 \text{ mg C m}^{-3}$ ,  $1.8 \text{ mg N m}^{-3}$ , and  $0.2 \text{ mg P m}^{-3}$ , respectively. Since *Aurelia* C, N, P contents and mean size were higher in October compared to other months we may consider these estimates as upper biomass levels.



**Fig. 3: *Aurelia* median bell diameter (top) and size-frequency distribution (bottom) in different months. Bell diameter (cm): black < 5; dark grey 5–9.9; light grey 10–14.9; white: > 15 cm.**

**Sl. 3: *Aurelia*: – premer klobuka (mediana, zgoraj) in frekvenčna distribucija (spodaj) v različnih mesecih. Premer klobuka (cm): črno < 5; temno sivo 5–9.9; svetlo sivo 10–14.9; belo: > 15 cm.**

**Tab. 2: Carbon, nitrogen and phosphorus biomass of *Aurelia* population in the Big Lake (BL) during October 2006 (\* from Alvarez Colombo et al., 2009).**

**Tab. 2: Biomasa populacije *Aurelia* v Velikem jezeru (BL), izražena kot mokra masa, ogljik, dušik in fosfor (\* po Alvarez Colombo et al., 2009).**

Abundance*		4,238,602
Wet mass	per lake	745,993 kg
	per m <sup>3</sup>	19.63 g m <sup>-3</sup>
C <sub>biomass</sub>	per lake	291 kg
	per m <sup>3</sup>	7.9 mg C m <sup>-3</sup>
N <sub>biomass</sub>	per lake	67 kg
	per m <sup>3</sup>	1.8 mg N m <sup>-3</sup>
P <sub>biomass</sub>	per lake	8.9 kg
	per m <sup>3</sup>	0.2 mg P m <sup>-3</sup>

### Top-down control and *Aurelia* as a source of nutrients

Gut content analyses and *in situ* enclosure experiments indicated small copepods, copepodites (*Paracalanus parvus*, *Oithona nana*) and nauplii, followed by naked ciliates, which are the most important prey of *Aurelia*. Other prey items (mollusc larvae, cirripedia nauplii, *Limacina*) were seasonally abundant in guts. Malej et al. (2007) speculated that this top-down control of the food web is responsible for lower zooplankton abundance and reduced number of species in Mljet's Veliko jezero compared to the neighbouring open Adriatic waters.

In addition to the direct predatory impact on micro- and mesozooplankton, a clear response of heterotrophic bacteria (Turk et al., 2008) to the presence of *Aurelia* in mesocosm experiments was also observed as an increase of bacterial biomass (average 1.8 µg C L<sup>-1</sup>) and production (average 1.8 µg C L<sup>-1</sup> d<sup>-1</sup>). Microbial plankton dynamics in the BL are not well-understood, and few data exist on abundance and production of microorganisms in this system. Most of our analyses were conducted during the warm stratified period when it is expected that abundance and production of autotrophic and heterotrophic microbial plankton are higher than during the cooler periods of the year. The highest chlorophyll *a* concentrations were found in the thermocline layer and were between 233–423 ng L<sup>-1</sup> in July 2003 (Fig. 5, right). During the same period, numbers of heterotrophic bacteria varied between 5.0 and 8.9 × 10<sup>8</sup> cells L<sup>-1</sup>, with elevated abundance above and below the thermocline layer (Fig. 4, left). In contrast to abundance, bacterial growth tended to be higher at the thermocline layer with an average value of 2.7 µg C L<sup>-1</sup> d<sup>-1</sup>, compared to 2.4 µg C L<sup>-1</sup> d<sup>-1</sup> and 0.5 µg C L<sup>-1</sup> d<sup>-1</sup>, above and below the

thermocline, respectively (Fig. 4, middle). These results of bacterial abundance and production rates differ only slightly from those found in the more eutrophic Gulf of Trieste and are consistently higher than in the southern Adriatic waters (Tab. 3).

*Aurelia* could be a substantial source of nutrients for bacteria in the BL where average phytoplankton biomass is nearly an order of magnitude lower (Carić & Jasprica, 1995) than in the Gulf of Trieste (Turk et al., 2007). Applying the weight normalized carbon release rate of 0.012 mg C g<sup>-1</sup> wet weight/d (Hanson & Norman, 1995) to data on *Aurelia* in BL during October suggests the whole BL *Aurelia* population releases 8.9 kg C d<sup>-1</sup>. Applying nitrogen (ammonium) and phosphorus (phosphate) excretion rates by *Aurelia* determined by Shi-mauchi & Uye (2007) we estimate 2.3 kg N d<sup>-1</sup> and 0.26 kg P d<sup>-1</sup> was released across the whole lake in October. These values indicate that *Aurelia* released about 3%, 3.4%, and 2.9% of its carbon, nitrogen and phosphorus biomass daily. These values do appear comparatively

**Tab. 3: Comparison of data for bacterial abundance and bacterial carbon production for different areas in the Adriatic Sea.**

**Tab. 3: Primerjava bakterijske abundance in produkcije v različnih območjih Jadranskega morja.**

Area	Abundance (× 10 <sup>8</sup> cells l <sup>-1</sup> )	Bacterial carbon production (µg C l <sup>-1</sup> d <sup>-1</sup> )	Reference
Mljet, Veliko jezero	4.7–8.9	0.68–4.3	This work
Southern Adriatic	1.31–1.61	0.24–4.80	Corinaldesi et al., 2003
Middle Adriatic Sea	8.8±0.06	17.19±1.99	Šolić & Krstulović, 1994
Middle Adriatic Sea	2.0–10		Šestanović et al., 2004
Northern Adriatic	1.0–60		Fuks et al., 2005
Gulf of Trieste	4.4–17	0.5–16.0	Turk and Hagström, 1994; Turk et al., 2001
Gulf of Trieste	0.06–18.5	9.6–55.2	Pugnetti et al., 2005

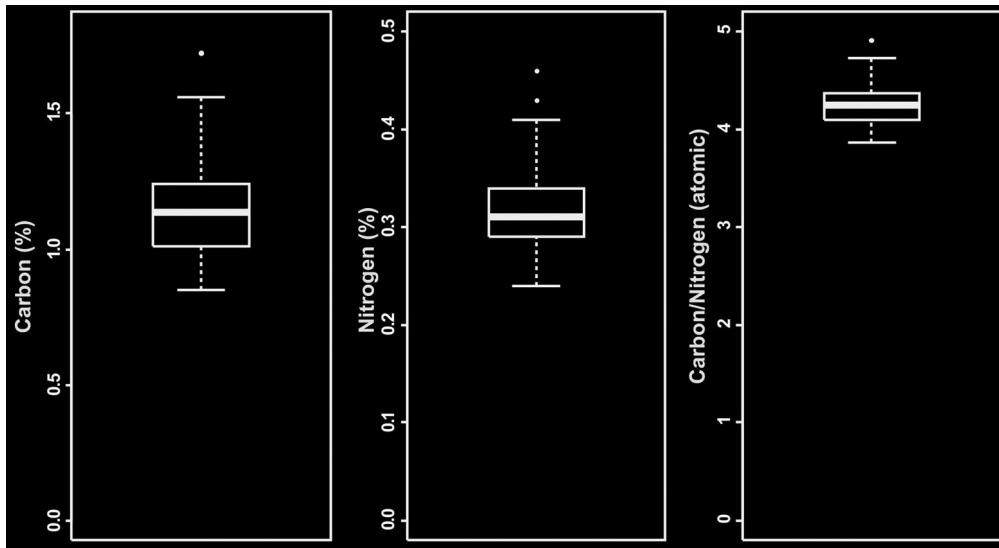


Fig. 4: *Aurelia* carbon and nitrogen contents (as % of dry weight) and atomic C/N ratio.

Sl. 4: *Aurelia* – vsebnost ogljika in dušika (% suhe mase) in atomsko C/N razmerje.

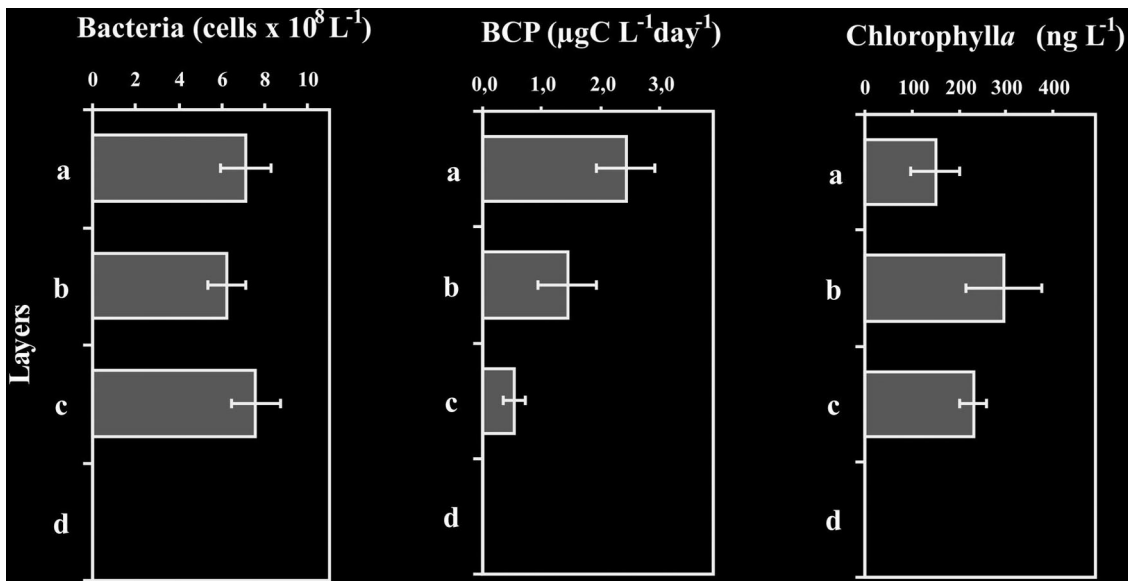


Fig 5: Vertical distribution of an average bacterial number (left), bacterial carbon production (middle) and chlorophyll a concentrations (left) in July 2003 in different layers: a – above the thermocline layer, b – the thermocline layer, c – below the thermocline layer, d – deep layer (> 25 m).

Sl. 5: Vertikalna razporeditev povprečnega števila bakterij (levo), bakterijske produkcije (sredina) in koncentracij klorofila a (levo) v juliju 2003 v različnih slojih: a –sloj nad termoklino, b – termoklinski sloj, c – sloj pod termoklino, d – globoki sloj (> 25 m).

high and should be considered as very preliminary since we do not have direct excretion measurements. Moreover, Shimauchi & Uye (2007) carried out excretion experiments at temperatures that were higher than favoured by Mljet *Aurelia* population, as inferred from their prevailing vertical distribution.

Dead *Aurelia* are likely to be an important nutrient source for bacteria in the lake. Enclosure experiments investigating degradation rates of *Aurelia* homogenates from the Mljet Lake show a more rapid response of the lake's bacterial community when compared to the Gulf of Trieste (Tinta *et al.*, submitted). In addition to different measured response times, changes in community com-

position also diverged in the two ecosystems. The addition of jellyfish tissue did not trigger large changes in the Mljet Lake bacterial community; however, it resulted in changes in the Gulf of Trieste communities, as determined by genetic fingerprinting. In conclusion, we found out that the lake's bacterial community is well adapted to utilize this type of substrate. *Aurelia* provide significant nutrient sources for bacterioplankton in addition to direct predatory pressure on meso- and microzooplankton and indirect cascading effect on microbial plankton.

#### ACKNOWLEDGMENT

This research was financed by the Ministry of Higher Education, Science and Technology of the R Slovenia (P1-0237), and bilateral cooperation with the Ministry of Science, Education and Sport of the Croatia. We also acknowledge the support of the US National Science Foundation (OCE-0116236). We are grateful to the Mljet National Park authorities for the hospitality during field work. We are grateful to anonymous reviewers for their critical and valuable comments on the manuscript.

## POPULACIJA VRSTE *AURELIA* SP. 5 (SCYPHOZOA) V MLJETSKEM JEZERU (JUŽNO JADRANSKO MORJE): TROFIČNE INTERAKCIJE IN POVEZAVA Z MIKROBNIM PREHRAMBENIM SPLETOM

*Alenka MALEJ, Valentina TURK, Tjaša KOGOVŠEK & Tihomir MAKOVEC*  
Morska biološka postaja, Nacionalni inštitut za biologijo, SI-6330 Piran, Fornače 41  
E-mail: malej@mbss.org

*Vladimir ONOFRI*

University of Dubrovnik, Institute for Marine and Coastal Research, HR-20000 Dubrovnik, Damjana Jude 12, Croatia

*Luciano CHIAVERANO*

Dauphin Island Sea Lab, University of South Alabama, 101 Bienville Blvd., Dauphin Island AL 36528, USA

*Tinkara TINTA & Vesna FLANDER-PUTRLE*

Morska biološka postaja, Nacionalni inštitut za biologijo, SI-6330 Piran, Fornače 41

*Davor LUČIĆ*

University of Dubrovnik, Institute for Marine and Coastal Research, HR-20000 Dubrovnik, Damjana Jude 12, Croatia

#### POVZETEK

Študija vertikalne distribucije, strukture in kemijske sestave populacije skifomeduz *Aurelia* sp. 5 je bila narejena v sredozemskem slanem jezeru na otoku Mljetu (Veliko jezero, južni Jadran), kjer se skozi vse leto pojavljajo goste združbe teh organizmov. Večina meduz se je poleti skozi večji del dneva nahajala v sloju pod termoklino 13–19 °C, medtem ko je bila populacija oktobra v plitvejši vodi. Meduze so se proti gladini pomikale zvečer, a zelo redko prečkale termoklino. Elementna analiza meduz je v suhi masi pokazala nizko specifično vsebnost ogljika, dušika in fosforja od 0,9–1,7%, 0,2–0,5% in 0,02–0,06% za ogljik, dušik in fosfor. Poleg neposrednega plenilskega vpliva na mikro- in mezozooplankton so raziskovalci zabeležili tudi jasen pozitiven odziv heterotrofnih bakterij na prisotnost živih in mrtvih *Aurelia*.

**Ključne besede:** *Aurelia*, vertikalna distribucija, vsebnost ogljika (C), dušika (N) in fosforja (P), mikrobní plankton, Jadransko morje.



## REFERENCES

- Alvarez Colombo, G., A. Benović, A. Malej, D. Lučić, T. Makovec, V. Onofri, M. Acha, A. Madriolas & H. Mianzan (2009):** Acoustic survey of a jellyfish-dominated ecosystem (Mljet Island, Croatia). *Hydrobiologia*, 616, 99–111.
- Azam, F., T. Fenchel, J. G. Field, L. A. Meyer-Reil & F. Thingstad (1983):** The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.*, 10, 257–263.
- Båmstedt, U. (1990):** Trophodynamics of the scyphomedusae *Aurelia aurita*. Predation rate in relation to abundance, size and type of prey organism. *J. Plankton Res.*, 12, 215–229.
- Barlow, R. G., R. F. C. Mantoura, M. A. Gough & T. W. Fileman (1993):** Pigment signatures of the phytoplankton composition in the northeastern Atlantic during the 1990 spring bloom. *Deep-Sea Res.*, 40, 459–477.
- Barz, K. & H.-J. Hirche (2005):** Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). *Mar. Biol.*, 147, 465–476.
- Benović, A., D. Lučić, V. Onofri, M. Peharda, M. Carić, N. Jasprica & S. Bobanović-Čolić (2000):** Ecological characteristics of the Mljet Island seawater lakes (Southern Adriatic Sea) with special reference to their resident populations of medusae. *Sci. Mar.*, 64, 197–206.
- Carić, M. & N. Jasprica (1995):** Koncentracije hranljivih soli i klorofila a u Velikom jezeru u razdoblju stratifikacije (1990) In: Durbešić, P. & A. Benović (eds.): Natural characteristics and social valuation of the Mljet Island. Croatian Ecological Society, Zagreb, pp. 55–70. (*In Croatian*)
- Corinaldesi, S., E. Crevatin, P. Del Negro, M. Marini, A. Rosso, S. Fonda Umani & R. Danovaro (2003):** Large-scale distribution of virioplankton in the Adriatic Sea: testing the trophic state control hypothesis. *Appl. Environ. Microbiol.*, 69, 2664–2673.
- Costello, J. H., S. P. Colin & J. O. Dabiri (2008):** Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences. *Invertebr. Biol.*, 127(3), 265–290.
- Dawson, M. N. (2003):** Macro-morphological variation among cryptic species of the moon jellyfish, *Aurelia* (Cnidaria, Scyphozoa). *Mar. Biol.*, 143, 369–380.
- Fuks, D., J. Radić, T. Radić, M. Najdek, M. Blažina, D. Degobbi & N. Smodlaka (2005):** Relationships between heterotrophic bacteria and cyanobacteria in the northern Adriatic in relation to the mucilage phenomenon. *Sci. Total Environ.*, 353, 178–188.
- Graham, W. M., L. Chiaverano, I. D'Ambra, H. Mianzan, G. Alvarez Colombo, M. Acha, A. Malej, J. H. Costello, V. Onofri & A. Benović (2009):** Fish and jellyfish: Using the isolated marine 'lakes' of Mljet Island, Croatia, to explore larger marine ecosystem complexities and ecosystem-based management approaches. *Annales, Ser. Hist. Nat. (This volume)*
- Grasshoff, K., M. Ehrhardt & K. Kremling (1983):** Methods of Sea Water Analysis. Second, Revised and Extended Edition, Verlag Chemie, Weinheim, 419 p.
- Hansson, L. J. & B. Norrman (1995):** Release of dissolved organic carbon (DOC) by the scyphozoan jellyfish *Aurelia aurita* and its potential influence on the production of planktonic bacteria. *Mar. Biol.*, 121, 527–532.
- Houghton, J. D. R., T. K. Doyle, M. W. Wilson, J. Davenport & G. C. Hays (2006):** Jellyfish aggregations and leatherback turtle foraging patterns in a temperate environment. *Ecology*, 87, 1967–1972.
- Larson, R. J. (1986):** Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *J. Exp. Mar. Biol. Ecol.*, 99, 107–120.
- Lucas, C. H. (2001):** Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia*, 451, 229–246.
- Lucas, C. H., A. G. Hirst & J. A. Williams (1997):** Plankton dynamics and *Aurelia aurita* production from two contrasting ecosystems: causes and consequences. *Estuar. Coast. Shelf Sci.*, 45, 209–219.
- Malej, A., J. Faganeli & J. Pezdič (1993):** Stable isotope and biochemical fractionation in the marine pelagic food chain: the jellyfish *Pelagia noctiluca* and net zooplankton. *Mar. Biol.*, 116, 565–570.
- Malej, A., B. Čermelj, S. Lojen & Č. Miloš (2006):** Elemental and stable isotope composition of bloom-forming Scyphomedusae from the Adriatic Sea. Abstract book. ASLO Summer Meeting, Victoria, British Columbia (Canada), 4–9 June 2006, pp. 76
- Malej, A., V. Turk, D. Lučić & A. Benović (2007):** Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea). *Mar. Biol.*, 151, 827–841.
- Mantoura, R. F. C. & C. A. Llewellyn (1983):** The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. *Anal. Chim. Acta*, 151, 297–314.
- Olesen, N. J. (1995):** Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. *Mar. Ecol. Prog. Ser.*, 124, 63–72.
- Omori, M., H. Ishii & A. Fujinaga (1995):** Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on zooplankton community of Tokyo Bay. *ICES J. Mar. Sci.*, 52, 597–603.
- Pauly, D., W. Graham, S. Libralato, L. Morissette & M. L. Deng Palomares (2009):** Jellyfish in ecosystems, on line databases, and ecosystem models. *Hydrobiologia*, 616, 67–85.

- Pitt, K., D. T. Welsh & R. H. Condon (2009):** Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. *Hydrobiologia*, 616, 133–149.
- Porter, K. G. & Y. S. Feig (1980):** The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, 25, 943–948.
- Purcell, J. E. & M. V. Sturdevant (2001):** Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.*, 210, 67–83.
- Pugnetti, A., M. Armeni, E. Camatti, E. Crevatin, A. Dell'Anno, P. Del Negro, A. Milandri, G. Socal, S. Fonda Umani & R. Danovaro (2005):** Imbalance between phytoplankton production and bacterial carbon demand in relation to mucilage formation in the Northern Adriatic Sea. *Sci. Total Environ.*, 353, 162–177.
- Purcell, J. E., S.-I. Uye & W.-T. Lo (2007):** Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Prog. Ser.*, 350, 153–174.
- Ridžanović, J. & V. Šimunović (1995):** Geographical characteristics of the island Mljet. In: Durbešić, P. & A. Benović (eds.): Natural characteristics and social valuation of the Mljet Island. Croatian Ecological Society, Zagreb, pp. 55–70. (*In Croatian*)
- Riemann, L., J. Titelman & U. Båmstedt (2006):** Links between jellyfish and microbes in a jellyfish dominated fjord. *Mar. Ecol. Prog. Ser.*, 325, 29–42.
- Schneider, G. & G. Behrends (1998):** Top-down control in a neritic plankton system by *Aurelia aurita* medusae – a summary. *Ophelia*, 48, 71–82.
- Schroth, W. G., Jarms, B., Streit & B. Schierwater (2002):** Speciation and phylogeography in the cosmopolitan moon jelly, *Aurelia* sp. *BioMed Cent. Evol. Biol.*, 2, 1–10.
- Shanks, A. L. & W. M. Graham (1988):** Chemical defense in a scyphomedusa. *Mar. Ecol. Prog. Ser.*, 45, 81–86.
- Shimauchi, H. & S.-I. Uye (2007):** Excretion and Respiration Rates of the Scyphomedusa *Aurelia aurita* from the Inland Sea of Japan. *J. Oceanogr.*, 63, 27–34.
- Smith, D. C. & F. Azam (1992):** A simple, economic method for measuring bacterial protein synthesis rates in seawater using  $^3\text{H}$ -Leucine. *Mar. Microb. Food Webs*, 6, 107–114.
- Stoecker, D. K., A. E. Michaels & L. H. Davis (1987):** Grazing by jellyfish, *Aurelia aurita*, on microplankton. *J. Plankton Res.*, 9, 901–915.
- Šestanović, S., M. Šolić, N. Krstulović & Ž. Ninčević (2004):** Seasonal and vertical distribution of planktonic bacteria and heterotrophic nanoflagellates in the middle Adriatic Sea. *Helgoland Mar. Res.*, 58, 83–92.
- Šolić, M. & N. Krstulović (1994):** Role of predation controlling bacterial and heterotrophic nanoflagellate standing stocks in the coastal Adriatic sea: seasonal patterns. *Mar. Ecol. Prog. Ser.*, 114, 219–235.
- Titelman, J., L. Riemann, T. A. Sørnes, T. Nilsen, P. Griekspoor & U. Båmstedt (2006):** Turnover of dead jellyfish: stimulation and retardation of microbial activity. *Mar. Ecol. Prog. Ser.*, 325, 43–58.
- Tinta, T., A. Malej & V. Turk:** Degradation of the Adriatic medusa *Aurelia* sp. by native bacteria, *Hydrobiologia*. (*Submitted*)
- Turk, V. & A. Hagström (1997):** Seasonal distribution of nanoflagellates and bacteriivory in the Gulf of Trieste (Northern Adriatic). *Period. Biol.*, 99, 205–208.
- Turk, V., P. Mozetič & A. Malej (2001):** Seasonal variability in phytoplankton and bacterioplankton distribution in the semi-enclosed temperate Gulf (Gulf of Trieste, Adriatic Sea). *Annales, Ser. Hist. Nat.*, 11(1), 53–64.
- Turk, V., P. Mozetič & A. Malej (2007):** Overview of eutrophication-related events and other irregular episodes in Slovenian Sea (Gulf of Trieste, Adriatic sea). *Annales, Ser. Hist. Nat.*, 17(2), 197–216.
- Turk, V., D. Lučić, V. Flander Putrle & A. Malej (2008):** Feeding of *Aurelia* sp. and links to the microbial food web. *Mar. Ecol.*, 29, 495–505.
- Wunsam, S., R. Schmidt & J. Müller (1999):** Holocene lake development of two Dalmatian lagoons (Malo and Veliko Jezero, Isle of Mljet) in respect to changes in Adriatic sea-level rise and climate. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 146, 251–281.