Promjene u ekosustavu sjevernog Jadrana uslijed invazije alohtonog rebraša Mnemiopsis leidyi

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DOKTORSKI RAD

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PROMJENE U EKOSUSTAVU SJEVERNOG JADRANA USLIJED INVAZIJE ALOHTONOG REBRAŠA *MNEMIOPSIS LEIDYI*

DOKTORSKI RAD

Mentori:
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doc. dr. sc. Paolo Paliaga

Zagreb, 2022.

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FACULTY OF SCIENCE
Department of Geology

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THE RESPONSE OF NORTHERN ADRIATIC ECOSYSTEM TO THE ALIEN COMB JELLY MNEMIOPSIS LEIDYI INVASIONS

DOCTORAL THESIS

Supervisors:
Tamara Đakovac, PhD
Paolo Paliaga, PhD

Zagreb, 2022

Ovaj doktorski rad izrađen je u sklopu Interdisciplinarnog doktorskog studija iz Oceanologije, na Geološkom odsjeku Prirodoslovno-matematičkog fakulteta, Sveučilišta u Zagrebu u Centru za istraživanje mora Instituta Ruđer Bošković, pod vodstvom dr. sc. Tamare Đakovac, više znanstvene suradnice u Centru za istraživanje mora Instituta Ruđer Bošković i doc. dr. sc. Paola Paliage, docenta na Sveučilištu Jurja Dobrile u Puli.

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Doktorski rad

PROMJENE U EKOSUSTAVU SJEVERNOG JADRANA USLIJED INVAZIJE ALOHTONOG REBRAŠA *MNEMIOPSIS LEIDYI*

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Alohtoni rebraš *Mnemiopsis leidyi* je želatinozni, invazivni organizam koji se odnedavno redovito pojavljuje u sjevernom Jadranu. U europskim morima se prvi puta pojavio u Crnom moru gdje je unesen balastnim vodama iz Atlantika i gdje je ubrzo stekao reputaciju izrazito nepoželjnog morskog organizma. Naime, uslijed masovnih pojava rebraša istrijebljen je gotovo čitav fond zooplanktona, što je, na tom području u konačnici, dovelo do kolapsa ribarstva. Kako bi se ustanovila prostorno-vremenska dinamika populacije *M. leidyi* i kakve utjecaje ostvaruju na planktonsku zajednicu i inćune (kao predstavnike planktivorne ribe) u sjevernom Jadranu, analizirani su brojni kemijski, biološki i fizikalni parametri. Rezultati pokazuju da pojave ovog zooplanktonskog organizma uvelike ovise o geostrofičkim strujanjima, dok širenje i opstanak populacije značajno ograničava dostupnost hrane i temperatura mora. Pojave *M. leidyi* uz istočnu obalu vezuju se uz topliji dio godine i rezultat su sekundarnog širenja iz zimskih utočišta na zapadnom dijelu sjevernog Jadrana, dok su maksimumi brojnosti krajem ljeta povezani s povoljnim morskim strujanjima. Nadalje, *M. leidyi* istovremeno podržavaju niže i oslabljuju više trofičke razine organizama. Duga razdoblja visoke brojnosti *M. leidyi* dovode do akumulacije labilne organske tvari koja je pogodna za mikrobnu razgradnju, te ujedno i izvor hranjivih soli. Takav disbalans u sustavu utječe na rast brojnosti pikoplanktona i njihovih predatora, heterotrofnih nanoflagelata, čime se podržava mikrobna petlja, dok visoko-efikasna i neselektivna prehrana ovog rebraša, u sprezi s drugim pritiscima na riblji fond, mijenja prostorne obrasce populacije inćuna za vrijeme mrijesta, ali i zooplanktonsku zajednicu. Kako je u cilju sprječavanja posljedica pojava *M. leidyi* važno ograničiti širenje populacije rebraša, u posljednjem je dijelu ovog rada predložena prikladna obrada balastnih voda.

(198 stranice, 2 tablice, 9 slika, 404 literaturna navoda, jezik izvornika: hrvatski)
Ključne riječi: *Mnemiopsis leidyi*, planktonska zajednica, inćuni, organska tvar, hranjive soli, suzbijanje invazija, (sjeverni) Jadran
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Doctoral thesis

CHANGES IN THE NORTHERN ADRIATIC ECOSYSTEM DUE TO THE INVASION OF THE ALIEN COMB JELLY MNEMIOPSIS LEIDYI

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Alien comb jelly *Mnemiopsis leidyi* is a gelatinous, invasive organism that is since recently is regularly appearing in the northern Adriatic. Its first appearance in the European seas was in the Black Sea, where it arrived in ballast tanks from the Atlantic and soon gained a reputation as a notorious marine invader. Large *M. leidyi* swarms depleted the entire zooplankton pool, leading to the collapse of fisheries. To depict the spatiotemporal dynamics of the *M. leidyi* populations and identify their impacts on the plankton community and anchovies (as representatives of planktivore fish) in the northern Adriatic, different chemical, biological and physical parameters were analysed. The results show that the appearance of this zooplankton organism is largely dependent on the geostrophic flow, while its spread and survival limit food availability and water column temperature. Occurrence along the eastern coast is associated with warmer seasons as a result of secondary dispersion from *M. leidyi* winter refuges in the northwest and maxima abundances in late summer with favourable sea currents. Moreover, *M. leidyi* simultaneously supports lower trophic levels while interfering with transport to the higher levels. Especially long high-abundance periods provide a large amount of organic matter, in most part labile and, thus, suitable for microbial digestion that, as follows, the release of nutrients. Furthermore, such an imbalance in the system leads to an increased abundance of picoplankton and their predator heterotrophic nanoflagellate, stimulating the microbial loop. Besides, a highly efficient and non-selective comb jelly diet, combined with other stressors on fish stocks, affects the spatial patterns of anchovy spawning areas and the zooplankton community. It is most important to limit *M. leidyi* spread to prevent adverse consequences; thus, ballast water treatments are proposed in the last part of this thesis.

(198 pages, 2 tables, 9 figures, 404 references, original in Croatian)
Keywords: *Mnemiopsis leidyi*, plankton community, anchovies, organic matter, nutrients, anchovies, invasion control, (northern) Adriatic Sea

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PROŠIRENI SAŽETAK

Posljednjih se desetljeća bilježe sve češće i intenzivnije pojave želatinoznih zooplanktonskih organizama u morskim ekosustavima diljem svijeta, koje se povezuju s klimatskim promjenama, prekomjernim izlovom ribe, eutrofikacijom, fizičkim modifikacijama prirodnih staništa i unosom alohtonih vrsta (Purcell i sur., 2007; Richardson i sur., 2009; Sola i sur., 2019; van Walraven i sur, 2015; Wright, 2019). Jedna od češćih masovnih pojava želatinoznih organizama u euroazijskim morima je bioinvazija rebraša *Mnemiopsis leidyi* (Shiganova i sur., 2019), koji se ujedno smatra jednim od najnepoželjnijih morskih invazivnih organizama (Reusch i sur., 2010). Ta je vrsta 80-ih godina prošlog stoljeća iz zapadnog Atlantika balastnim vodama unesena u Crno more (Frazier i sur., 2013) gdje je uspjela ostvariti stabilnu populaciju i odakle se, potpomognuta morskim strujama i pomorskim transportom, nastavila širiti u susjedna mora (Shiganova i sur., 2019). Masovne pojave *M. leidyi* opustošile su gotovo čitav crnomorski fond zooplanktona što je dovelo do kolapsa ribarstva prouzročivši ogromne ekonomske gubitke (Bodini i sur., 2017). *M. leidyi* se od 2016. godine redovito pojavljuje u sjevernom Jadranu (Tirelli i sur., 2021) – desetak godina nakon prve kratkotrajne pojave u Tršćanskom zaljevu (Shiganova i Malej, 2009), a uspješno održavanje njenih populacije izvan izvornih staništa pripisuje se njenom velikom reprodukcijskom kapacitetu, širokoj ekološkoj valenciji, i nizu drugih prilagodbi. Kako je u kratkom vremenu prisutnost *M. leidyi* u sjevernom Jadranu postala masovnija i učestalija od drugih, autohtonih, želatinoznih organizama poput meduza (Tirelli i sur., 2021; Violić i sur., 2022), nameće se pitanje o utjecaju na lokalni ekosustav, dok se u kontekstu invazivne prirode razmatra mogućnost suzbijanja. Ovim doktorskim radom obuhvaćeni su neki od najvažnijih bioloških aspekata bioinvazije *M. leidyi* te analizirani brojni kemijski, biološki i fizikalni parametri. Ciljevi rada su razlučiti doprinos rebraša povećanju koncentracije hranjivih soli i organske tvari, odrediti njihov utjecaj na mikrobnu zajednicu, zooplankton i ribe u sjevernom Jadranu, te naposljetku, predložiti model sprječavanja daljnjeg širenja ove vrste unaprjeđenjem obrade balastnih voda. Doktorski rad započinje uvodnim dijelom s pregledom literature i dosadašnjih saznanja iz područja, nakon kojeg slijede četiri samostalne znanstvene publikacije (IV) koje odgovaraju na postavljene hipoteze: *M. leidyi* ostvaruje stabilnu populaciju u sjevernom Jadranu (i), utječe na lokalni ekosustav (ii-iv), širenje se može obustaviti primjenom termičke obrade i deoksigenacije na brodovima (v).

U I publikaciji su prikazani rezultati četverogodišnjeg praćenja dinamike populacije *M. leidyi* od prvih pojava (2016.) ove vrste u sjeveroistočnom Jadranu (brojnost i raspodjela) i prateći

abiotički uvjeti (temperatura i salinitet). Osim toga, analizirani su uzorci zooplanktona u vodenom stupcu i u sadržaju probavila rebraša, te sonarom i mrežama locirane populacije inćuna za vrijeme mrijesta (u rujnu) i opisani fizikalni sustavi vrtloženja. II i III publikacija povezuju pojave *M. leidyi* i akumulaciju organske tvari (posebice otopljene komponente), dok je mikrobna zajednica analizirana u II publikaciji. Raspodjela prema veličini jedinki za populaciju *M. leidyi* u rovinjskom priobalju 2017. godine prikazana je u III publikaciji. Dok I i III publikacija općenito analizira pojavu *M. leidyi* uz posljedice na čitav sjeverni Jadran (regionalna skala), u II. publikaciji u fokusu su utjecaji masovnih nakupina na lokalnoj skali koji su istraživani u rovinjskom priobalju. Modeli geostrofičkih strujanja poslužili su kako bi se opisali mehanizmi transporta rebraša (I-III publikacija), odredili vjerojatni izvor njihove populacije u sjevernom Jadranu (I-III publikacija) i njihova zimska utočišta (II publikacija), te objasnilo stvaranje masovnih nakupina u priobalju (II publikacija). Posljednji rad (IV publikacija) istražuje preživljavanje svih životnih stadija rebraša izloženima nekim od klasičnih tehnika za obradu balastnih voda npr. izloženost povišenim temperaturama u oksičnim, hipoksičnim i anoksičnim uvjetima, ultrazvučnoj kavitaciji i mikrovalnom zračenju. Poseban naglasak je stavljen na primjenu termičke obrade u oksičnim i anoksičnim uvjetima iskoristivši otpadnu toplinu brodskog motora za grijanje balastnih tankova. Radovi su komentirani u raspravi, iz čega su proizašli odgovori na postavljene hipoteze.

Utvrđeno je da brojnost jedinki *M. leidyi* u sjevernom Jadranu sezonski oscilira, a prostorna raspodjela je heterogena. *M. leidyi* se uz istočnu obalu sjevernog Jadrana javlja u proljeće i prisutna je do kraja jeseni ostvarujući maksimum brojnosti krajem ljeta. Dok na zapadnom dijelu sjevernog Jadrana populacija opstaje cijele godine, uz istočnu obalu ona je ograničena nedostatkom hrane što joj onemogućuje preživljavanje u nepovoljnijim zimskim uvjetima. Dinamika pojava *M. leidyi* uvelike ovisi o geostrofičkim strujanjima. Kada se pred kraj ljeta uspostavi anticiklonalni vrtlog (središte ~ 10 NM zapadno od Rovinja), bilježe se češće i masovnije pojave rebraša. Takvi vrtložni sustavi raznose planktonske organizme od ušća rijeke Po i područja Venecijanske lagune sve do zapadne obale Istre. Potpomognuta geostrofičkim strujanjima, rasprostranjenost rebraša obuhvaća veći dio sjevernog Jadrana prostirući se jugoistočno Cresa, a daljnje širenje južnije i istočnije ograničeno je samo nedostatkom hrane. Pojave *M. leidyi* se povezuju s obiljem hranjivih tvari u vodenom stupcu. Visoke koncentracije labilne organske tvari prikladan su supstrat mikrobnoj zajednici, što doprinosi povećanju koncentracije hranjivih soli, te oblikuje piko- i nano-planktonsku zajednicu. Prehrana *M. leidyi* neselektivna je, a uz to njene se jedinke hrane neumjereno, što je uz brojne prilagodbe kojima love plijen čini izuzetno uspješnim predatorima. Dakle, *M. leidyi* uslijed neurednog hranjenja, izlučivanja tvari i odumiranja jedinki istovremeno (i) potiče mikrobnu petlju doprinosom organskoj tvari te (ii) predacijom osiromašuje fond zooplanktona, tj. hrane višim trofičkim razinama npr. ribama. Naime, organska tvar supstrat je heterotrofnim prokariotima koji uslijed njene razgradnje oslobađaju hranjive soli prikladne za umnožavanje cijanobakterija. Rast brojnosti prokariotske zajednice – plijena heterotrofnih nanoflagelata dovodi i do porasta njihove brojnosti, te je time zaokružena mikrobna petlja. Uz to, uslijed pojave *M. leidyi* zamijećeno je premještanje područja mrijesta izuzetno važne komercijalne vrste ribe – inćuna čiji je fond ionako oslabljen izloženošću brojnim drugim stresorima poput prekomjernog izlova. Kako bismo spriječili daljnje negativne posljedice širenja ove vrste na nove lokacije, predložene su različite tehnike termičke brodske obrade balastnih voda iskorištavanjem otpadne topline motora. U konačnici, odabir prikladne tehnike ovisi o dostupnoj otpadnoj toplini i tipu broda, te trajanju plovidbe.

Osim odgovora na postavljene hipoteze, treba istaknuti inovativnost kojom se u ovom radu pristupa bioinvaziji *M. leidyi*, a koja se očituje u nekoliko aspekata: poboljšanju metode prebrojavanja jedinki, korištenju fizikalnih modela za opisivanje dinamike populacija, te po prvi puta ispitivanju kvalitete izlučene organske tvari, a na kraju se predlažu konkretni koraci za suzbijanje širenja balastnim vodama. Nadalje, znanstveni se doprinos očituje i kroz sveobuhvatno inter- i multi-disciplinarno istraživanje bioinvazije *M. leidyi* od njenih početaka u sjeveroistočnom dijelu Jadranu, dajući uvid u sustavne odgovore lokalnih ekosustava. Zaključci koji su predstavljeni u radu omogućuju bolje razumijevanje razmjera utjecaja, sada već redovitih, masovnih pojava *M. leidyi* u Jadranu te mogu poslužiti i kao osnova za razvijanje predikcijskih ekoloških modela npr. onih usmjerenih na više trofičke razine kao npr. zooplankton i riblji fond, ali i kao osnova plana upravljanja invazivnim vrstama.

THESIS SUMMARY

In the last decades it has frequently reported about the overwhelming appearance of gelatinous zooplankton organisms in marine ecosystems worldwide, which are associated with eutrophication, overfishing, climate change, habitat modifications and the introduction of alien species (Purcell; et al., 2009; Sola et al., 2019; van Walraven et al., 2015; Wright, 2019). A great number of reported mass occurrences of gelatinous organisms in Eurasian seas refer to the bioinvasion of comb jelly *Mnemiopsis leidyi* (Shiganova et al., 2019), considered one of the most notorious marine invasive organisms (Reusch et al., 2010). This species was introduced into the Black Sea by ballast water from the western Atlantic in the 1980s (Frazier et al., 2013), establishing a stable population and spreading further to the neighbouring seas by currents and transport (Shiganova et al., 2019). Its mass occurrences almost depleted the entire zooplankton stock in the Black Sea, leading to the collapse of fisheries and causing substantial economic losses (Bodini et al., 2017). Since 2016, *M. leidyi* has regularly appeared in the northern Adriatic (Tirelli et al., 2021) – a decade after it first occurred in a brief episode in the Gulf of Trieste (Shiganova and Malej, 2009). The success of its population outside natural habitats can be explained by its reproductive capacity, the width of its ecological valence, and several other adaptations. Frequent reports and a high abundance of *M. leidyi* in the northern Adriatic soon exceeded those of the other indigenous gelatinous organisms, e.g. jellyfish (Tirelli et al., 2021; Violić et al., 2022), raised concerns about the impact on the local ecosystem and, because of its invasive nature, encouraged to consider the possibility of its control.

This doctoral thesis covers some of the most important aspects of *M. leidyi* bioinvasion and analyses several chemical, biological and physical parameters. This thesis aims to shed light on comb jelly's contributions to the increase of nutrient loads, impacts on the microbial community, zooplankton and fish in the northern Adriatic and proposes to limit its spread by improving the ballast water treatment techniques. The thesis starts with an introduction and follows by four independent scientific publications (I-IV) hypothesizing that *M. leidyi* established a stable population in the northern Adriatic (i), affected the local ecosystem (ii-iv) and that its further spread can be limited by an onboard thermal treatment (v). The results of four-year monitoring from *M. leidyi*'s first appearance (2016) in the northeastern Adriatic are given in publication I and demonstrate its population dynamics (abundance and distribution) and the abiotic conditions (temperature and salinity). In the same publication, zooplankton samples from the water column and ingested by *M. leidyi* are analysed together with an acoustic and trawl survey of the anchovy population during the spawning period (September) linked to

a gyre formation. The connection between *M. leidyi* mass occurrence and microbial community was analysed in publication II, and the link to the accumulation of nutrients (in particular dissolved organic carbon) is given in publications II and III. The distribution of individual comb jelly in size groups is given in publication III for the coastal waters of Rovinj in 2017. In contrast to publications I and III that analyse the consequences of *M. leidyi* occurrences to the entire northern Adriatic (regional scale), publication II is focused on the changes on a local scale associated with swarm formations in the coastal waters of Rovinj. Moreover, modelling geostrophic currents helped us describe comb jelly dispersion mechanisms (publication I-III), determine the likely source of reoccurring population in the northern Adriatic (publication I-II) and their winter refuges in the northern Adriatic (publication III), and to explain the agglomeration of individuals along the northeastern coast (publication II). The last publication (IV) shows the survival of all *M. leidyi* life stages exposed to typical ballast water treatment techniques, e.g. heating, lack of oxygen, ultrasonic cavitation and microwave radiation. Among them, the focus was on the onboard application of a thermic treatment and deoxygenation by using the engine's waste heat to heat ballast tanks. The findings (publication I-IV) were commented on, and hypotheses were tested in the Discussion section.

M. leidyi abundance in the northern Adriatic is spatially heterogeneous and oscillates seasonally. The population appears along the eastern coast of the northern Adriatic in spring and is present until the end of autumn, reaching its maximum by the late summer. The individuals are present throughout the year in the northwestern Adriatic, while in the colder on the eastern side population disappears, limited by the lack of food and unfavourable winter conditions. The dynamic of *M. leidyi* occurrences depends largely on geostrophic currents. When an anticyclonic gyre is formed by the end of summer (centre point ~ 10 NM west of Rovinj), *M. leidyi* appears more frequently and in greater numbers. Gyres usually carry planktonic organisms from the mouth of the Po River and the Venetian Lagoon all the way to the western coast of Istria. With the help of physical forces, the population during the warmer months is spread throughout most of the northern Adriatic, stretching southeast of Cres, while food shortage limits the further expansion to the south and east. *M. leidyi* occurrences are associated with high nutrient abundance in the water column. High concentrations of labile organic matter are a suitable substrate for the microbial community, resulting in increased nutrients and affecting the abundance of pico- and nanoplankton communities. In combination with several capturing prey adaptations, *M. leidyi*'s excessive and generalist feeding ensures its predatory success. Thus, *M. leidyi*'s effects are two-sided; it simultaneously stimulates the microbial loop and reduces the available food (zooplankton) for higher tropic levels (fish).

Heterotrophic prokaryotes break out the organic matter in the decomposition process releasing nutrients suitable for cyanobacteria. The increased abundance of the prokaryotic community, representing the prey for heterotrophic nanoflagellates, leads to an increase in their abundance and thus completes the microbial loop. Moreover, the dislocation of anchovy spawning areas in the northern Adriatic occurred right after the first appearances of *M. leidyi*. Many other stressors, such as overfishing, already affect this commercially important fish stock. Various thermal treatments of ballast water using the engine's waste heat have been proposed to prevent adverse effects of the spread of this species. The most suitable treatment finally depends on the available heat, ship typology, and the voyage duration.

In addition to conclusions drawn from testing the hypotheses, it is important to point out the presented novelties when studying *M. leidyi* bioinvasion. This thesis presents an upgraded method of estimating the abundance of gelatinous individuals, uses physical models to describe population dynamics, analyses the quality of excreted organic matter associated with *M. leidyi* and proposes concrete techniques to eradicate its spread to new areas by ballast water-mediated transport. Furthermore, the scientific contribution is also noticeable through a presented comprehensive interdisciplinary and multidisciplinary study of *M. leidyi* bioinvasion since its first sighting in the northeastern Adriatic, providing insights into the systematic responses of local ecosystems. Here presented conclusions provide a better understanding of the impact of regularly appearing *M. leidyi* in the Adriatic and can serve as a basis for predictive ecological models that tackle zooplankton and fish stock, but also as the basis of an invasive species management plan.

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SADRŽAJ

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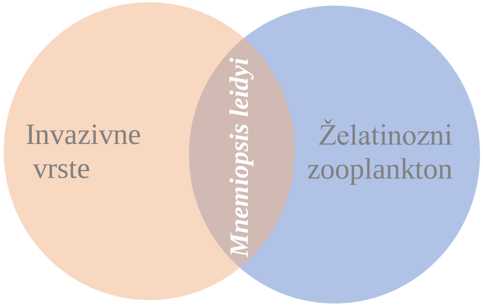
UVOD

Posljednjih godina se učestalije izvještava o iznenadnim pojavama različitih morskih želatinoznih organizama (Ordóñez i sur., 2016; Pestorić i sur., 2021) među kojima je i vrsta rebraša *Mnemiopsis leidyi*. Ova se vrsta u sjevernom Jadranu redovito pojavljuje od ljeta 2016. (Malej i sur., 2017), zapanjujućom brojnošću jedinki (Pestorić i sur., 2021) koje bi mogle predstavljati potencijalnu smetnju lokalnom ekosustavu.



Slika 1. Vennov dijagram područja istraživanja.

Prirodno stanište *M. leidyi* je zapadna obala Atlantika, dok je u ostatku svijeta ovaj rebraš alohtoni organizam (Shiganova i sur., 2019). Prema konstituciji, načinu kretanja i prehrani *M. leidyi* ubrajamo u želatinozni zooplankton (**Slika 1.**). Prirodno stanište zooplanktona je pelagijal, odnosno životna zajednica slobodnih voda. Na njega otpada 70% površine planete Zemlje pod snažnim utjecajem hidrodinamičkih procesa (Belgrano i sur., 2013). Zooplankton je fundamentalna komponenta u morskoj hranidbenoj mreži koja se nalazi na trofičkoj razini između glavnih primarnih proizvođača (fitoplankton) i viših potrošača (npr. ribe i morski sisavci) te ima ključnu ulogu u biogeokemijskom kruženju elemenata i u funkcioniranju ekosustava. Stoga bi unos i proliferacija strane vrste koja može direktno utjecati na populacije manjeg zooplanktona mogao destabilizirati ravnotežu brojnih komponenti pelagijskog sustava, naročito ako se još u obzir uzme i geomorfologija Jadrana. Radi se o poluzatvorenom moru izduženog oblika koje je u doticaju s ostatkom Sredozemlja samo u dijelu Otrantskih vrata. Takva su mora zbog velikog kontakta s kopnom i zapremnine riječnog donosa, eutrofnija i produktivnija, no istovremeno često degradirana uslijed brojnih antropogenih pritisaka (ribarstva, urbanizacije priobalja, priljeva otpadnih voda, poljoprivrede i sl.) (Carrier-Belleau i sur., 2021). Takve djelatnosti ih čine posebno ranjivima i podložnima opstanku stranih vrsta uslijed oslobođenih/ispražnjenih ekoloških niša (Leppäkoski i sur., 2009). Osim toga, i antropogene klimatske promjene posebno su izražene na regionalnoj skali poput Sredozemlja, pa su mora u ovom dijelu svijeta zbog toga izloženija promjenama u strukturi njihove pelagijske zajednice (Juza i Tintoré, 2021).

Jadransko more posjeduje geomorfološki razvedene konture obale (Pikelj i Juračić, 2013) i jasne batimetrijske zone, a prema kojima ga možemo podijeliti na sjeverni, srednji i južni dio (prosječnih dubina 43 m, 110 m i 498 m; Vrdoljak i sur., 2021). Morfološka heterogenost sustava odražava se i na heterogenost odziva na pritiske, pa i unutar Jadrana možemo identificirati područja koja su osjetljivija i podložnija na promjene. Područje sjevernog Jadrana kao najplići njegov dio, obilježen je izrazitim donosom slatke vode rijekama (Totti, 2003) i visokim stupnjem antropogenih modifikacija u priobalju (Ciadela, 2015) čime se izdvaja od ostatka bazena i čini izloženijim i osjetljivijim na promjene u morskom ekosustavu. Tome možemo pridodati i termohaline osobine koje u kombinaciji s dinamikom morskih struja mogu stvoriti vrtložne sustave koje sjeverni dio često dodatno izoliraju od ostatka Jadrana (Krajcar, 2003). Specifičnost prirodnih obrazaca u sinergiji s antropogenim pritiscima i u prošlosti su se očitovali u negativnom odzivu na ekosustav uslijed npr. cvjetanja mora (Degobbis i sur., 1999; Volf i sur., 2015) ili pojave hipoksičnih uvjeta (Kralj i sur., 2019). Masovne pojave također dodatno destabiliziraju sustav i otvaraju prostor za uspostavljanje populacija oportunističkih stranih organizama poput *M. leidyi*. Stoga i ne čudi da su prve pojave ove vrste bile zabilježene u ovom dijelu Jadrana (Shiganova i Malej, 2009). Osim toga, sjeverni dio obiluje zaljevima i uvalama (Pikelj i Juračić, 2013), upravo nalik onima koje povezujemo uz prirodna staništa *M. leidyi* (Pierson, i sur., 2021) i u kojima ta vrsta ostvaruje stabilne populacije (Condon i sur., 2010). Kada uzmemo u obzir da je upravo ovdje smješteno nekoliko većih lučkih terminala poput Rijeke, Kopra, Trsta i Venecije, koji teže daljnjem razvoju, a već sada su važna pristaništa koja ostvaruju glavninu međunarodnog pomorskog prometa u Jadranu (Kolář, 2017), ističe se važnost pomnog praćenja promjena u okolišu kao odgovora na unos nove vrste.

Strane vrste organizama

Vrste koje su slučajno ili namjerno unesene u novi ekosustav smatraju se stranim ili alohtonim vrstama (eng. non-indigenous species, NIS). One mogu općenito utjecati na kvalitetu staništa drugih organizmima, a tako i na brojne koristi koje ti organizmi pružaju ili reguliraju u ekosustavima (Gutiérrez, 2017). Kada prisustvo strane vrste negativno utječe na ostale komponente ekosustava u koji je ta vrsta pristigla, ona se smatra invazivnom (eng. invasive alien species, IAS; Riccardi, 2016). Strane vrste prema njihovom utjecaju na resurse dostupne u novom staništu, dijelimo na: (i) one koje pokazuju asimilacijsko-disimilacijske efekte pri unosu i otpuštanju tvari i energije i (ii) one koje na sustav utječu fizičkim modifikacijama i strukturama u okolišu (Gutiérrez, 2017). U slučaju morskih organizama primjer prvih je pojava *M. leidyi* u Skandinavskim vodama gdje je zbog ekstenzivne predacije u prvih pet godina od prvih pojava peterostruko smanjen broj kopepoda (plijena rebraša; Tiselius i Møller, 2017). Kako želatinozna biomasa uglavnom završava kao supstrat za mikrobnu razgradnju (Condon i sur., 2011), tijek energije konzumirane biomase usmjeren je prema dnu trofičke mreže. Primjer drugih, invazivna je vrsta školjkaša *Dreissena polymorpha*, koja gradeći kolonije mijenja sediment i utječe na zajednicu bentosa (Zaiko i sur., 2009). Globalizacija i brojne promjene u okolišu (uključujući i klimatske promjene), dovele su do toga da je pojava stranih vrsta u antropocenu postala globalna opasnost, a njene posljedice dalekosežne jer kao što i primjeri ranije pokazuju, prijete biološkoj raznolikosti (Mollot i sur., 2017), ali i gospodarstvu i ljudskom zdravlju (Early i sur., 2016). Zapanjujući doseg posljedica pojava stranih vrsta, ilustrira činjenica da predstavljaju drugu najčešću prijetnju bioraznolikosti jer ih se u posljednjih 500 godina povezuje izumiranjem većine vrsta, a posebno kralježnjaka (Bellard i sur., 2016). Uzroci pojave neke nove vrste mogu biti različiti i zavise o ljudskoj aktivnosti za koju se povezuju, a dijele se na (i) namjerne koje podrazumijevaju unos vrsta s nekim razlogom i ciljem i (ii) slučajne (Carlton i Ruiz, 2016) koji imaju i nadimak „*slijepi putnici*“. Smatra se da je porast globalnog prijevoza robe i tereta, koji je ujedno i okosnica današnjeg ekonomskog razvoja (Hulme, 2009 i 2021), a posebice njegov pomorski dio (Laeseke i sur., 2020), pokretač većine unosa stranih vrsta. Prijenos vrsta na/u brodovima možda je i najstariji način unosa alohtonih vrsta jer se prekooceanske rute održavaju stoljećima, a one unutar epikontinentalnih mora, već tisućljećima (Carlton i Ruiz, 2016). Prema nekima autorima, daljnji rast međunarodne trgovine i prijevoza dobara, ne pridonosi smanjenju širenja novih organizama. Smatra se da će vrlo brzo pritisci i štete unosa stranih vrsta nadmašiti resurse koje trenutno imamo na raspolaganju za intervencije njihovog suzbijanja, te se apelira na unaprjeđenje legislative i istraživačkih alata koji bi se trebali usredotočiti na redukciju rizika tzv. pandemije stranih vrsta (Hulme, 2021).

Koje mjere poduzeti kako bi se ograničio rizik u konačnici ovisi o dosegu i fazi u kojoj se tzv. bioinvaziju promatra. Stručna literatura nije usklađena po pitanju tijeka bioinvazija, pa ju autori opisuju različitim brojem faza čija se trajanja preklapaju (Catford i sur., 2009). U nešto novijoj literaturi navodi se kako tijek bioinvazije čine četiri osnovne faze koje prate ključne promjene u ekosustavu i, shodno tome, prate ih prikladne mjere u cilju njihovog suzbijanja (**Tablica 1**). Upravljanje invazivnim vrstama sam je po sebi izazov jer uključuje neizvjesne i višestruke ishode, ali nekad i suprotstavljene ciljeve pa proces uključuje sudionike s različitim načinom promatranja problematike (Maguire i sur., 2004). Osim toga, stručnjaci se susreću i s brojnim poteškoćama kao što su: razumijevanje, uzbuna, podrška i implementacija rješenja (Courchamp i sur., 2016).

Tablica 1. Tijek bioinvazija, pripadajuće promjene i predložene mjere suzbijanja (prilagođeno: Lewis i sur., 2016).

Faza		Pripadajući ciljevi
1.	Unos strane vrste	Prevencija, procjena rizika
2.	Uspostava populacije	Lag-faza, interakcija s lokalnim vrstama, monitoring novih kolonija, kontrola i iskorjenjivanje
3.	Širenje	Stope i obrasci širenja, monitoring, kontrola (npr. barijere, zaštićena područja za ugrožene autohtone vrste), biokontrola
4.	Utjecaji	Obnova

Unatoč postojećem znanstvenom konsenzusu da bioinvazije često negativno utječu na biološke i socio-ekonomske čimbenike (Courchamp i sur., 2016, Riccardi i sur., 2017), isti se u novije vrijeme pokušava pokolebati brojnim člancima koji umanjuju ulogu i važnost invazija u globalnim promjenama (Boltovskoy i sur., 2018;Sagoff, 2018; Tassin i sur., 2017). Kako znanost o invazijama integrira klasično istraživanje i primjenu rješenja (Courchamp i sur., 2016), poricanje posljedica pojava stranih vrsta može otežati ovo drugo i tako omesti implementaciju strategija ublažavanja ili kontrole posljedica bioinvazija (Russell i Blackburn, 2017a i b). Tome ne doprinosi ni složenost ekosustava zbog koje treba proći dosta vremena kako bi se jasno identificirali problemi, primijenile strategije suzbijanja i, naposljetku, uočila poboljšanja. Kako bi se nekakav plan upravljanja uopće adekvatno ostvario njemu prethode nužna znanstvena istraživanja koja osiguravaju vjerojatnost učinaka pojedinih odluka. Uz mnogobrojne druge pritiske na okoliš poput gomilanja otpada, iscrpljivanja prirodnih resursa, eutrofikacije, fizičkih preinaka u okolišu, emisija stakleničkih plinova, odnosno već spomenutih klimatskih promjena i sl. (EEA, 2020), i bioinvazije znatno doprinose opterećenju ekosustava. U novije vrijeme objavljena istraživanja iz domene znanosti o invazivnim vrstama, u osnovi, pokušavaju odgovoriti na ova tri pitanja: (i) kako objasniti izniman uspjeh nekih invazivnih vrsta u novom okolišu?; (ii) kako invazivne vrste utječu na lokalne zajednice?; i (iii) kako će ekosustavi izgledati u budućnosti? (Chabrerie i sur., 2019). Disciplina koja se bavi obilježjima alohtonih vrsta, njihovom sposobnosti širenja i međusobnim interakcijama kao i s djelovanjem autohtonim vrstama nadilazi sferu klasične biologije, često iziskujući interdisciplinarnost (Vaz i sur., 2016) i naziva se znanost o invazijama (eng. invasion science; Falk-Petersen i sur., 2006). Mada do danas nije razvijena usklađena shema prema kojoj bi se procijenio utjecaj bioinvazije neke vrste na lokalni ekosustav, u literaturi su ponuđeni različiti pristupi. Jedna od standardiziranih metoda je tzv. određivanje indeksa bioinvazije (eng. biopollution indeks, BPL) kojom se klasificira brojnost i rasprostranjenost jedinki te numerički opisuju (H0-4) razmjeri utjecaja na zajednicu, staništa i funkcioniranje ekosustava (Olenin i sur., 2007). Ta je metoda korištena npr. pri procjeni utjecaja pojava *M. leidyi* u Kaspijskom jezeru (H4) koji je opisan kao izuzetno velik i štetan (Pourang i sur., 2016).

Stanje u europskim morima

Kako je usvojeno da invazivne strane vrste, općenito, nanose štetu i smanjuju otpornost ekosustava, od 2014. u Europskoj Uniji je na snazi Uredba br. 1143/2014 Europskog parlamenta i Vijeća o sprječavanju i upravljanju unošenja i širenja invazivnih stranih vrsta (EU, 2014). Na taj način, osim rasta stopa bioloških invazija i broja njihovih posljedica, iz godine u godinu diljem svijeta raste i broj mjera koje pridonose ublažavanju posljedica bioinvazija (Simberloff i sur., 2013). To svakako prati i popularnost izvještaja o unosu stranih vrsta i njihovim prijetnjama, a morski ekosustavi nisu nikakva iznimka (De Poorter i sur., 2009). Zaključci nešto starijeg izvještaja o broju stranih morskih vrsta, pokazuju da je od svih europskih mora, najveći broj stranih višestaničnih životinjskih vrsta (njih 569 od ukupno 737), zabilježen upravo u Sredozemlju, što se velikim dijelom objašnjava donosom vrsta kroz Sueski kanal, zatim, razvojem marikulture, ali i dugom tradicijom Sredozemlja kao jednog od glavnih područja međunarodnog pomorskog prometa (Keller i sur, 2011). Sredozemlje je središte biološke raznolikosti s brojnim endemima, ali i mjesto gdje danas susrećemo brojne strane vrste koje prijete autohtonim zajednicama (Scorrano i sur., 2017). Do 2019. broj stranih vrsta je u europskim morima narastao na 666, a novozabilježene vrste nisu nužno povezane samo sa Sueskim transportom nego se pretpostavlja da su ovog puta klimatske promjene, koje su dovele do zagrijavanja mora odigrale bitnu ulogu i ubrzale stope širenja stranih vrsta kojima takvi novi abiotski uvjeti odgovaraju (Zenetos i Galandi, 2020). Porast broja morskih bioinvazija je između ostalog, usko povezan s intenziviranjem pomorskog prijevoza i prekooceanskog transporta robe (Riccardi, 2016).

U Hrvatskoj je do sada zabilježeno 980 stranih i kriptogenih (one nepoznatog podrijetla) vrsta od kojih se njih 101 odnosi na strane morske vrste (HAOP, 2022). Kao najčešći stvarni i potencijalni putevi unosa i širenja stranih vrsta u Republici Hrvatskoj navedeni su: (i) spontano širenje – koje kod morskih organizama može biti pasivno (morskim strujama ili uz pomoć drugih životinja, bez utroška vlastite energije) ili aktivno (kretanje snagom vlastitih mišića), te (ii) prijenos organizama koji su doputovali kao „*slijepi putnici*" (MINGOR, 2021). Nešto ranija literatura tvrdi da je povećan unos vrsta u istočni dio Jadrana prvenstveno vezan uz klimatske promjene, a u manjem, mada nezanemarivom dijelu uz druge čimbenike (Pećarević i sur., 2013). Međutim, bitno je spomenuti kako se polovica ukupnog prometa svih hrvatskih luka odnosi na Riječku luku (Pomorski promet, 2021), smještenu upravo u sjevernom dijelu Jadrana, a o čijoj podložnosti je bilo riječi nešto ranije. Direktan unos organizama, možemo u najvećoj mjeri očekivati u područjima oko većih luka, no one mogu predstavljati i ishodišta sekundarnih širenja stranih vrsta (Costello i sur., 2022). Kako bi se ta prijetnja kvalitetno ispitala najbitnije je poznavanje povezanosti lokacija i geostrofičkih strujanja. Primjer utjecaja nekog fizikalnog poremećaja koji se iz svojeg ishodišnog područja širi dalje je npr. zapadna obala Istre koja je izložena utjecajima u Venecijanskoj laguni (Supić i sur., 2002), a, pretpostavljamo i onima u Venecijanskoj luci.

Stanje morskog ekosustava, pa tako i statusa invazivnih vrsta u Republici Hrvatskoj se prati kroz: (i) akcijski program Strategije upravljanja morskim okolišem i obalnim područjem u sklopu provedbi obaveza Integralnog sustava za praćenje i procjenu stanja Sredozemnog mora i obale (IMAP IG.22/7), i (ii) Okvirne direktive o pomorskoj strategiji 2008/56/EZ (ODMS) unutar koje se jedan od deskriptora mjere stanja morskog okoliša odnosi na invazivne vrste (MINGOR, 2021). Postizanje dobrog stanja europskih mora, učinkovitija zaštita morskog okoliša i resursa o kojima ovise ekonomske i društvene aktivnosti vezane uz more u cilju je provedbe ODMS (MINGOR, 2021). Budući da više od 35% ukupnog hrvatskog teritorija čini more, očuvanje biološke raznolikosti i monitoring promjena u morskim ekosustavima od iznimne su važnosti (Pećarević i sur., 2013). Zbog toga Ministarstvo gospodarstva i održivog razvoja održava bazu pokazatelja stanja morskog okoliša, koja uključuje i podatke o prisutnim invazivnim vrstama (http://baltazar.izor.hr/azopub/bindex). Bez ulaganja u strategije za suzbijanje bioinvazija temeljene na novih znanstvenim dokazima očekuje se isključivo porast šteta kao posljedice unosa invazivnih vrsta, pa se tako u Hrvatskoj uz nekoliko monitoring projekata usmjerenih na gospodarski aspekt i ribolov, stanje obnovljivih resursa u hrvatskom teritorijalnom moru prati i kroz znanstvene ekspedicije, a to su: (i) MEDITS (Mediterranean International Bottom Trawl-Surveys) kojima se nadzire stanje pridnenih naselja, i (ii) MEDIAS (Mediterranean International Acoustic Survey) kojima se ehodetekcijom prate pučinska naselja (MINGOR, 2021).

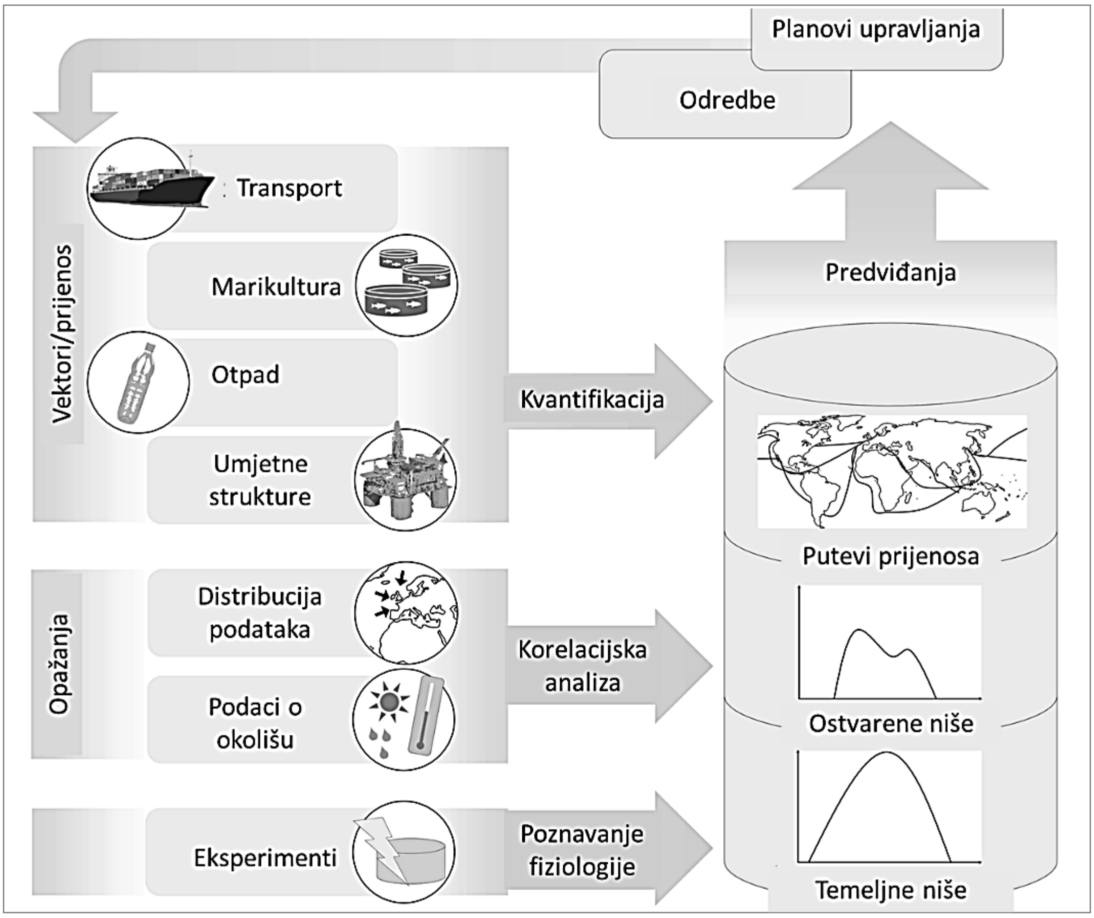
Unos stranih vrsta i mjere suzbijanja unosa

Prema Konvenciji o biološkoj raznolikosti (Convention on Biological Diversity, CBD) putevi unosa stranih vrsta dijele se na: (i) namjerni unos koji dalje dijelimo na puštanje i bijeg te (ii) nenamjerni unos u koji spadaju kontaminacija, „*slijepi putnici*“, koridori i spontano širenje (CBD, 2014). Invazivne vrste trenutno se smatraju jednom od najvećih prijetnji morskim ekosustavima diljem svijeta, a pomorska djelatnost identificirana je kao odgovor na većinu slučajnih prijenosa vrsta diljem svijeta (Miralles i sur., 2021), od čega se kao najvažniji vektor nameće transport, te s njim povezani brodarstvo i marikultura, a u novije vrijeme zabrinutost predstavljaju i plutajuće nakupine otpada te klimatske promjene (Laeseke i sur., 2020; **Slika 2.**). No čak i uz postojeće protokole (npr. CIRCABC, 2016; EU, 2014), bioinvazije danas predstavljaju jedan od najvećih izazova zaštite prirode, a čije razmjere društvo još nedovoljno razumije (Courchamp i sur., 2016) s obzirom na to da suvremeni način života omogućuje prijenos stranih vrsta.

Kada govorimo o morskom prijenosu stranih vrsta on se odvija putem (i) obraštaja oplate brodova što se uglavnom odnosi na sesilne organizme (Peters i sur., 2017) ili (ii) prijenosom odraslih organizama, njihovih juvenilnih formi, jajašaca (Gollasch i sur., 2000) ili nekih drugih životnih stadija (Di Poi i sur., 2019) u zapremi vode u balastnim tankovima. U posljednjih 70 godina na taj je način prevezeno 380 vrsta diljem svijeta (Miralles i sur., 2021).

Obraštaji su u prošlosti tretirani izuzetno toksičnim premazima koji su sadržavali tributil kositar (TBT) koji je, u međuvremenu, zabranjen Međunarodnom konvencijom o nadzoru štetnih sustava protiv obraštanja brodova iz 2001. godine od strane Međunarodne pomorske organizacije (Sousa i sur., 2018), što je ostavilo još više mogućnosti za prijenos stranih vrsta tim načinom. Neka istraživanja pokazuju izuzetnu važnost čak i malih rekreacijskih brodica u širenju stranih vrsta unutar samog Sredozemlja i apeliraju na strože lučke kontrole (Ulman i sur., 2019). Izloženost globalnom problemu obraštaja može oslikati procijenjena površina uronjenog dijela svjetske flote trgovačkih plovila koja iznosi 325 x 10^6 m^2 (Moser i sur., 2016) te očekivani trend porasta međunarodnog transporta (Hulme i sur., 2021).

Balastne vode dio su istog problema porasta globalnog transporta, a reguliraju se prema Međunarodnoj konvenciji o nadzoru i upravljanju brodskim balastnim vodama i talozima iz 2004. godine, prema kojoj je definirana maksimalna koncentracija organizama (najviše 10 organizama > 50 $\mu m\ m^{-3}$ i < 50 $\mu m\ ml^{-1}$) i gdje ih je dozvoljeno ispustiti (> 200 NM od obale, 200 m dubine) (Vorkapić i sur., 2016). Ozbiljnost ovog problema ilustrira činjenica da su transportni brodovi ukupno ispustili 21 x 10^6 t balastnih voda u 2013. godini, što je porast od 374% u odnosu na volumen ispušten 2005. (Carney i sur., 2017). Neobrađene balastne vode često su prijenosnici želatinoznih zooplanktonskih organizama, pa se smatra da su npr. pacifičke meduze *Aurelia coerulea* (Scorrano i sur., 2017) i *Cassiopea andromeda* (Schembri i sur., 2011) tako dospjele u Sredozemlje. Najpoznatiji primjer prijenosa želatinoznih organizama i balastom potpomognute bioinvazije je, svakako, unos *M. leidyi* (Frazier i sur., 2013), ali i njenog predatora *Beroe ovata* u euroazijska mora (Mamish i sur., 2020). Naime, osamdesetih godina prošloga stoljeća pojave *M. leidyi* u Crnom moru su dovele do izuzetne prirodne degradacije i kolapsa ribarstva, uz posljedicu stotine milijuna dolara financijskih gubitaka, a sustav se ni do danas nije u potpunosti oporavio (Bodini i sur., 2017).



Slika 2. Vektori određuju smjer morskih bioinvazija, ekološki modeli određuju ciljane, a laboratorijska ispitivanja temeljne niše, što može poslužiti u procjeni rizika, identifikaciji osjetljivih područja i regulativi (prilagođeno: Laeseke i sur., 2020).

Kako bi se postigle niske koncentracije organizama koje su propisane Konvencijom, nužno je ugraditi sustave za obradu balastnih voda, a alternativa preinakama na brodovima jesu sustavi za pročišćavanje u lukama (Pereira i Brinati, 2012). Do danas je izumljen i primijenjen velik broj takvih sustava koje možemo grupirati u (i) mehaničke (filtracija i ciklonsko odvajanje), (ii) fizikalne (akustična kavitacija, grijanje, deoksigenacija i UV-zračenje), te (iii) kemijske (ozon, klor, peroksid i vitamin K), no svaki od njih ima svoja ograničenja (Vorkapić i sur., 2016). Kod mehaničkih, to je uglavnom veličina postrojenja i potrošnja energije, kod akustične kavitacije oštećenje obloge broda, kod deoksigenacije preživljavanje anaerobnih organizama, kod UV-zračenja otpornost većih organizama, te kod kemijskih je mogućnost korozije i potreba za dodatnom kemijskom obradom, dok je inače neisplativu termičku obradu moguće unaprijediti iskoristivši otpadnu toplinu (Vorkapić i sur., 2016).

Od ostalih važnih načina unosa vrsta tu su još oni koji vezujemo uz marikulturu tj. na „bijeg“ pojedinih vrsta iz uzgajališta, ali i rast broja građevnih struktura podložnih obraštaju poput platformi ili vjetroelektrana, te već napomenute, klimatske promjene (Laeseke i sur., 2020) i nakupine otpada koje plutajući morima oblikuju nove ekološke zajednice (Haram i sur., 2021).

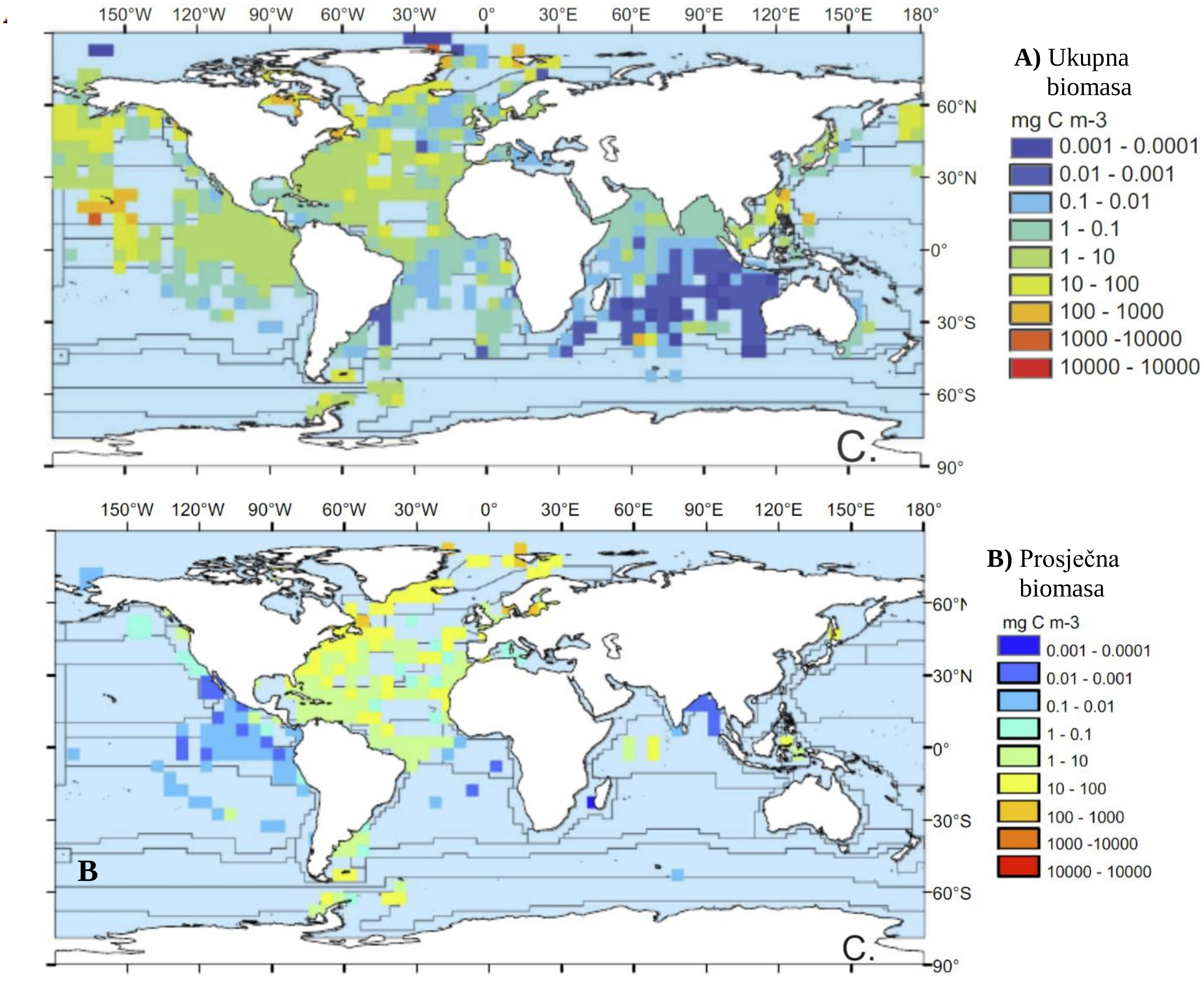
Želatinozni zooplankton

Želatinozni zooplankton je sveprisutni dio zajednice organizama morskog pelagijala u kojeg ubrajamo raznoliku skupinu organizama, od protista do svitkovaca (Chordata; Madin i Haribson, 2009), raznih veličina (< 1 mm do ~ 2 m kod meduze *Nemopilema nomurai*; Jasper i sur., 2015a). Svima njima je zajednički visoki udio vode u želatinoznom tkivu (~ 96%), a niski udio suhe tvari, npr. 0,5% ugljika (C) (Lucas i sur., 2011). Za usporedbu, većina pelagijskih organizama sadrži manji udio vode, pa tako npr. ribe sadrže ~ 70% (Akpambang, 2015), a kopepodi od 75% (Tsutomu i sur., 2006) do 85% (van der Meer i sur., 2008). Sadržaj vode također varira između pojedinih taksonomskih skupina želatinoznog zooplanktona, pa je kod organizama koji se hrane filtriranjem (plaštenjaci) ovisan o veličini tijela, što nije slučaj kod karnivora (žarnjaka i rebraša) (Jaspers i sur., 2015a).

Zbog svoje želatinozne i krhke građe, prozirnosti tijela i sporadičnih pojava, ovi se organizmi često doživljavaju enigmatskima. Međutim, unatoč tome, zbog svojih pojava koje često broje ogroman broj jedinki u stanju su znatno izmijeniti dinamiku trofičke mreže, te su važna komponenta biogeokemijskog kruženja hranjivih tvari (Lebrato i sur., 2019; Lucas i sur., 2014a; Steinberg i Saba, 2008), pa se smatra da je njihova uloga u morskim sustavima značajna (Shiganova i sur., 2004a).

Rasprostranjenost i pojave želatinoznog zooplanktona

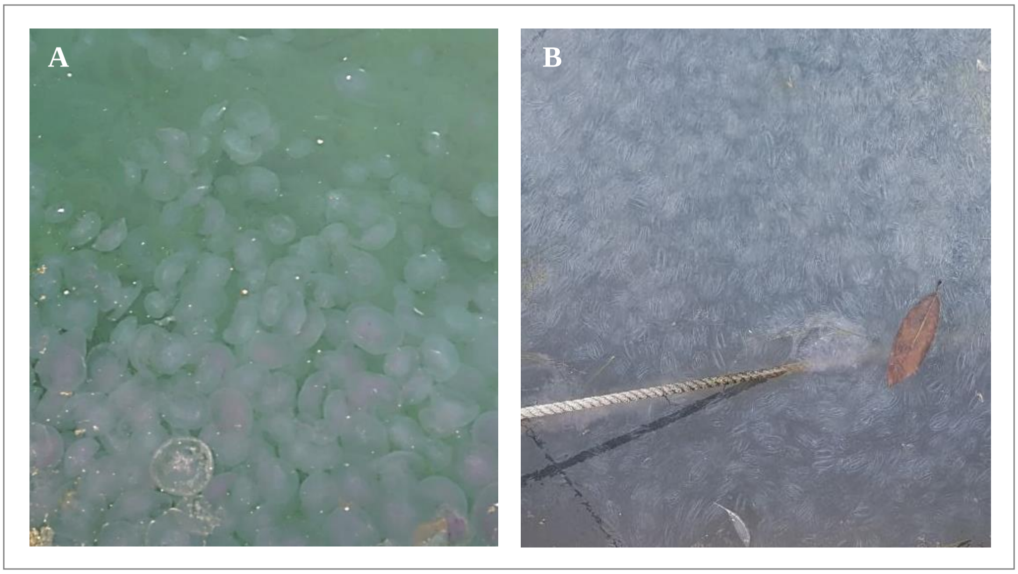
Velik broj informacija o želatinoznom zooplanktonu u posljednjih 200-tinjak godina, točnije, o njihovom prisustvu ili odsustvu, i okolišnim uvjetima za to vrijeme, pohranjen je u bazi podataka Jellyfish Database Initiative, JeDI (http://jedi.nceas.ucsb.edu) (JeDI) koja je osmišljena kao alat za istraživanje učestalosti njihovih pojava i procjenu trofičkih interakcija na lokalnoj, regionalnoj i globalnoj razini (Lucas i sur., 2014a). JeDI baza je poslužila modelima kojima je pokazano da su želatinozni zooplanktonski organizmi sveprisutni u svjetskim morima i oceanima, a biomasom najzastupljeniji u suptropskim i borealnim predjelima sjeverne hemisfere (Lucas i sur., 2014a) (**Slika 3.**). Činjenica da je ovakav oblik organizama toliko raširen u oceanima govori o izvrsnoj prilagodbi novom okolišu u kojem su fizikalni parametri relativno konstantni (Madin i Haribson, 2009). Izračunato je da njihova prosječna biomasa u svjetskim oceanima iznosi 0,53 ± 16,16 mg C m^{-3} što čini 3,83 × 10^{7} t C dostupnog heterotrofima u miješanom sloju oceana (Lucas i sur., 2014b). Mada su prisutni i u eutrofnim područjima koja nekim vrstama čak i pogoduju (Touzri i sur., 2012), u oligotrofnim područjima želatinozni zooplanktonski organizmi dominiraju brojnošću i raznovrsnošću u odnosu na zooplanktonske račiće (Crustacea), ukazujući na posebne prilagodbe života u uvjetima kada je dostupnost hrane ograničena (Madin i Haribson, 2009).



Slika 3. Obojeni dijelovi prikazuju: (A) ukupnu biomasu želatinoznog zooplanktona preko Longhurstovih zona prosječne biomase (mg C m^{-3}) i (B) prosječnu biomasu (mg C m^{-3}) preko Longhurstovih zona s pojavama rebraša (preuzeto: Lucas i sur., 2014b).

Njihova krhka građa čini ih izazovnima za uzorkovanje i uglavnom ograničava njihovo životno područje izvan zona visoke energije valova poput priobalja, ali postoje i robusnije vrste koje život provode u turbulentnijim područjima poput žarnjaka portugalske galije (*Physalia physalis*) koji živi na granici medija i može podnijeti snažne oluje (Prieto i sur., 2015) ili pak rebraša *M. leidyi* koji živi u estuarijima i izložen je snažnom utjecaju plime, oseke, i valova (Purcell i sur., 2001) te meduza *N. nomurai* i *Aurelia* sp. koje život provode uz obalu Japana i plaštenjaka *Cyclosalpa* sp. u novozelandskim priobalnim vodama (Condon i sur., 2012). U priobalju njihove pojave često završavaju nakupljanjem i propadanjem u litoralnoj zoni (Lucas i Dawson, 2014).Neke taksonomske skupine (koljena) želatinoznog zooplanktona poput žarnjaka (Cnidaria) (Baliarsingh i sur., 2020; Violić i sur., 2022), rebraša (Ctenophora) (Slesinger i sur., 2020) i plaštenjaka (Tunicata) (Pettitt-Wade i sur., 2020) posebno su zanimljive zbog svojih masovnih, ali prolaznih pojava (eng. blooms) (Sola i sur., 2019), a vjeruje se da taj fenomen prati želatinozne organizme još od njihovih početaka u kambriju (Condon i sur., 2012; Young i Hagadorn, 2020). Naime, terminom eng. *bloom and bust* opisuje se nestalni ciklus naglih pojava i propadanja želatinoznih organizama (Schnedler-Meyer i sur., 2018). Njihove epizode su obilježene visokom proliferacijom i stopama rasta od 2-3 puta većima od ostalih pelagijskih organizama (Pitt i sur., 2013).

Masovne pojave želatinoznog zooplanktona dijelimo u dvije skupine: prave (eng. true) kod kojih se proizvodnja i rast želatinozne biomase odvija na istom mjestu, i prividne (eng. apparent) kada je gomilanje želatinozne biomase na određenom području zapravo rezultat djelovanja vjetra i izmijenjenih hidrodinamičkih uvjeta (Graham i sur., 2001; Lucas i Dawson, 2014). Postojanost i trajanje epizode variraju od nekoliko tjedana, pa do čitave sezone (Oguz i sur, 2008) ovisno o skupini organizma, ali i povoljnim uvjetima za njihov opstanak (Lucas i Dawson, 2014). O pouzdanim uzrocima završetka neke epizode se malo zna, no kako su iste obično praćene masovnim propadanjem jedinki često se spominju razlozi koji su doveli do te visoke smrtnosti (Pitt i sur., 2014). Kao posljedica masovnih pojava, želatinozni organizmi se nerijetko pojavljuju i u najezdama (eng. swarms) (**Slika 4.**) što u biti prati trend njihovih sve učestalijih pojava koji je u posljednje vrijeme zabilježen diljem svijeta (Richardson i sur., 2009; Quiñones i sur., 2018; Xiao i sur., 2019), pa tako i u europskim vodama (Knutsen i sur., 2018; Prieto i sur., 2015), ali i u Jadranu (Pestorić i sur., 2012 i 2021; Tirelli i sur., 2021). O razlozima pojava se dosta raspravlja, a općenito se pokazalo da npr. u sjevernom Atlantiku raspodjela želatinoznog zooplanktona uvelike ovisi o površinskoj temperaturi mora i koncentraciji otopljenog kisika (Lucas i sur., 2014b). Proizvedena biomasa želatinoznih organizama redovito prelazi težinu od 100 kg/m^3 (Lilley i sur., 2011), ali su njihove pojave kratkog vijeka (nekoliko tjedana do mjeseci), nakon čega dolazi do kolapsa i populacije iščezavaju (Pitt i sur., 2014). I dramatični razmjeri pojava (posebno rebraša i meduza) koje su posljednjih desetljeća postale sve učestalije u morskim okolišima diljem svijeta dovode se i u vezu s već navedenim opterećenjima ekosustava npr. eutrofikacijom, prekomjernim ulovom ribe, klimatskim promjenama, namjernim ili nenamjernim unošenjem ili premještanjem alohtonih vrsta, te izmjenama u staništima (Purcell i sur., 2007; Richardson i sur., 2009; Sola i sur., 2019; van Walraven i sur, 2015; Wright, 2019).



Slika 4. Želiranje mora u rovinjskoj luci: (A) najezde meduza *Aurelia* sp. svibanj 2020. i (B) najezde rebraša *M. leidyi* rujan 2020 (autoričine fotografije nastale za vrijeme monitoringa *M. leidyi* u rovinjskom priobalju).

No neka globalna istraživanja želatinoznih organizama ističu da se ne radi tek o učestalijim pojavama nego da su one periodične te podložne značajnim oscilacijama koje prate globalne meteorološke promjene (Condon i sur., 2013). Dvojba o tome radi li se o učestalijim epizodama ili nedostatku povijesnih tragova što daje privid učestalosti, u znanstvenoj se literaturi naziva tzv. želatinoznom paradigmom (eng. jelly bloom paradigm) (Condon i sur., 2012). U medijima se fenomen aglomeracije želatinoznih organizama često ilustrira pojmom želiranjem (eng. jellification) (Bouaouina, 2014; Giggs, 2018), prikazujući tako dosege najezdi ovih naizgled fragilnih organizama, a one često znaju biti zapanjujućih razmjera brojeći i nekoliko tisuća jedinki po m^3 (Sola i sur., 2019) (**Slika 4.**).

U usporedbi s nekim drugim morskim organizmima poput riba (npr. Fortibuoni i sur., 2017; Ichinokawa i sur., 2017) koji su i u prošlosti bili od komercijalne važnosti, postoji ograničeni broj dugoročnih zapisa o prisutnosti želatinoznih organizama (Pauly i sur., 2009), koji, osim toga, često predstavljaju nehomogenu cjelinu jer ih je sve manje što se gleda u dalju prošlost, a oni najstariji se obično odnose na informacije o prilovu u mrežama (Bastian i sur., 2010 i 2011) propusnijima za manje organizme, dok se oni noviji uglavnom odnose na područje sjevernog Atlantika i Sredozemlja (Condon i sur., 2013), zbog čega određivanje frekvencija njihovih pojava i dalje predstavlja velik izazov i ostaje nepoznanica. Realno je za očekivati da će klimatske promjene, koje sa sobom nose porast temperature mora i oceana, utjecati i na ovu komponentu morskih ekosustava, tako što će pospješiti njihovo razmnožavanje i povećati im stope rasta, ali i proširiti podneblja prikladna za njihov život (Brotz i sur., 2012; Condon i sur., 2014; Lucas i Dawson, 2014; van Walraven i sur, 2015).

Praćenje i uzorkovanje želatinoznog zooplanktona

Osim zbog toga što želatinozni organizmi najčešće nisu stalno prisutni u vodenom stupcu, te njihove pojave naizgled sporadične, pomanjkanje podataka o toj skupini u usporedbi s npr. planktonskim račićima ili ribom, vjerojatno ima veze s njihovom delikatnom prirodom zbog koje se za uzorkovanja lako oštete, a tijekom monitoringa, zbog svoje prozirnosti, često previde. Klasično uzorkovanje zooplanktonske zajednice podrazumijeva povlačenje mreža (Edelist i sur., 2021; Lebrato i sur., 2012). Međutim, kod onih konusnih (npr. WP2) širina otvora kolekcijske komore može biti ograničavajući faktor za veće jedinke s obzirom na to da velik broj želatinoznih zooplanktonskih organizama svrstavamo u makrozooplankton (> 2 cm), dok mreže, kojima se standardno uzorkuju veći organizmi poput riba, mogu propuštati manje jedinke ili pak zbog povlačenja, oštetiti organizme (Condon i sur., 2012; Suchman i sur., 2012). Remsen i sur. (2004) procjenjuju da se mrežama uhvati tek trećina pelagijskih plaštenjaka i do 12x manje meduza i rebraša. Mada bi takva uzorkovanja, u teoriji, osim o brojnosti mogla nešto reći i o masi organizama, zbog njihove fragilnosti, rezultati bi bili podcijenjeni. Akustičke metode su dobra alternativa koja međutim zahtjeva i primjenu pomoćnih metoda (npr. uz mreže ili snimke) za provjeru broja i identificiranje vrsta, pa su prikladnije za prebrojavanje homogenih populacija (Alvarez Colombo i sur., 2008; Siapatis i sur., 2008). Osnovna prednost korištenja mreža je ta da su prikladne za manje organizme, a rezultati usporedivi s mnogim dugoročnim uzorkovanjima (Bashevkin i sur., 2022). O ograničenoj kvaliteti ovako prikupljenih podataka se zna već pola stoljeća, preporuke za uzorkovanja navode i poteškoće kod primjene fiksativa, te naglašavaju važnost *in situ* opažanja ronioca (Jacobs i Grand, 1978), a u novije vrijeme preporučuje se fotografiranje i/ili snimanje jedinki (Outinen i sur., 2016). Osim toga, standardnim fiksativima poput formaldehida i alkohola je teško očuvati morfologiju želatinoznih organizmima jer zbog velikog udjela mezogleje u tijelu dolazi do izobličenja organizama (Mitchell i sur., 2021). Kako formaldehid kod npr. *M. leidyi* nije prikladan jer s vremenom uzorci propadaju, danas se preporučuju novije metode poput primjene zakiseljene Lugolove otopine (Engell-Sørensen i sur., 2009) ili, posebice za očuvanje morfologije juvenilnih stadija, formaldehid uz dodatak klasičnog sredstva kojim se u kućanstvu tretiraju staklene površine čime se stvara hidrofobni film, a time uvelike unaprjeđuje očuvanje morfološkog integriteta uzoraka (Mitchell i sur., 2021).

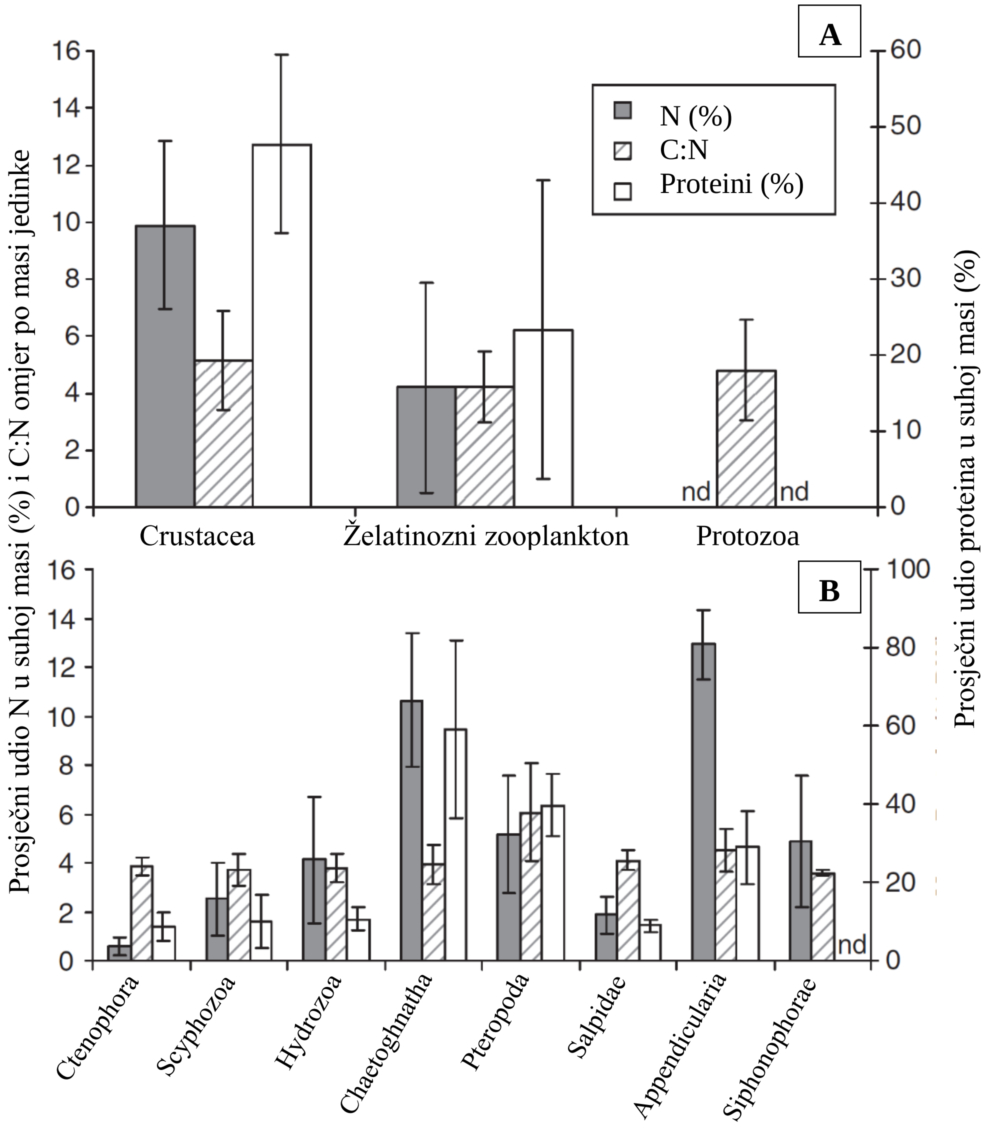
Procjene lokacija pojava, količine i kvalitete želatinozne biomase mogu se izvesti i indirektno služeći se monitoringom populacija drugih vrsta koje se njima hrane. Tako je npr. monitoring atlantske i sredozemne populacije ribe *Mola mola* poslužio u modelima trofičkog prijenosa energije za procjenu dostupne biomase želatinoznog zooplanktona (Grémillet i sur., 2017). Nalik tome, analize stabilnih izotopa predatora želatinoznih organizama (Chi i sur., 2021) i sadržaja njihovog probavila (Cardona i sur., 2012) pomogle su istaknuti često umanjenu važnost želatinoznog zooplanktona u trofičkoj mreži. Kao alternativa analizi izotopa može poslužiti i ekstrahirana DNA iz uzoraka probavila viših predatora (Lamb i sur., 2017). Ovo su u osnovi, kvalitativne metode čija je prednost da su jednako prikladne za organizme koji žive bliže površini i one koji se pojavljuju u dubljim slojevima jer je taksonomska karakterizacija potpunija, ali mogu i ukazati na neke možda zanemarene trofičke interakcije (Hays i sur., 2018). No, kada se usmjerimo na brojnost, a ne masu i sastav organizma, prebrojavanje jedinki daje zadovoljavajuće podatke. Kao alternativa mrežama, podvodne snimke koje pružaju izvrsnu podlogu za kvantifikaciju npr. nataloženih odumrlih jedinki na dnu (Lebrato i sur., 2012), a one iz zraka snimljene dronom (Hamel i sur., 2021) ili uz pomoć balona za daljinska ispitivanja pokrivaju znatno veće površine (Jo i sur., 2017), ali im nedostaje komponenta dubinske raspodjele. Prednost *in situ* opažanja je da su lako primjenjiva jer ne zahtijevaju nužno složenu opremu i mogu biti dio građanskih znanstvenih projekata (eng. citizen science), a jedan takav projekt uvevši mobilnu aplikaciju *avvistAPP* zaživio je u Jadranu (Tirelli i sur., 2021). Prednosti takve „laičke“ znanosti su da je približi pojedincu i surađuje s potencijalnim dionicima (Altobelli i sur., 2021). Kako se radi o jednostavnom prikupljanju podataka, može ih se prikupiti znatno više, pokriti veće područje i promptnije reagirati na promjene što je posebno važno kod pojava invazivnih vrsta (Tirelli i sur., 2021), a nedostatak da podaci mogu biti pristrani jer je moguće da će najveći broj njih pristizati s češće posjećivanih lokacija. Nalik tome, od velike koristi mogu biti i podaci o ulovu i prilovu ribarica (Yaragina i sur., 2021), koji imaju prednost kontinuiteta izvještavanja zbog nacionalnih strategija upravljanja morskim resursima (EU, 2013). Pristranost tih podataka se, osim u veličini i robusnosti uzorkovanih jedinki, očituje i u zabilježenim zooplanktonskim skupinama, jer je za očekivati da će organizmi čije je stanište ili niša sličnija ciljanoj ribi biti bolje pokriveni opažanjima (Yaragina i sur., 2021). S druge strane, stariji podaci o želatinoznim pojavama vrlo često su vezani uz ribarstvo (Bastian i sur., 2010 i 2011). Meduze se tradicionalno konzumiraju u Azijskim zemljama, a kako popularnost njihova ribarenja u novije vrijeme raste, proširila se na i Latinsku Ameriku, dok su se istovremeno diljem svijeta za njihovu biomasu pronašle brojne alternativne primjene, npr. u prehrani životinja, filtriranju mikroplastike ili u farmaciji (Edelist i sur., 2021), pa možemo očekivati da će u budućnosti određene vrste koje se planira eksploatirati oplemeniti baze podataka posebice o njihovim pojavama koje predstavljaju glavnu neizvjesnost ove grane ribolova. Osim toga, u cilju ribolova je dostaviti na tržište svježu i neoštećenu namjernicu (Kozačinski i sur., 2006), pa bi mnoge inovacije iz tog područja mogle poslužiti u unaprjeđenju postojećih metoda uzorkovanja npr. služeći se mrežicama s drškom i plastičnim posudama (Edelist i sur., 2021).

Želatinozni organizmi se mogu proučavati i indirektno služeći se tragovima tzv. okolišne DNA (eng. environmental DNA, eDNA) iz uzoraka morske vode (Minamoto i sur., 2017) ili sedimenata gdje mogu pružiti informacije o želatinoznom doprinosu zajednici bentosa (Ogata i sur., 2021). Osnovne prednosti ove metode su da se smatra relativno isplativom, a istovremeno daje uvid o taksonomiji i prostorno-vremenskoj raspodjeli organizama neovisno o fragilnosti organizma, a nedostaci da interpretacija rezultata ovisi o dostupnim informacijama genetskih baza (Govindarajan i sur., 2021), što u analizi nekih nedovoljno istraženih vrsta može predstavljati problem.

Kruženje hranjivih tvari

Želatinozni zooplankton bitan je izvor organske tvari u moru što implicira i njegovu važnost u kruženju ugljika, C (Condon i sur., 2011; Lucas i sur., 2014b). Osim toga (**Slika 3**.), ima i ključnu ulogu u kruženju dušika (N). Konzumacijom plijena ova skupina vrši kontrolu nad zooplanktonskim herbivorima i unosi organski N, te istovremeno kontrolira primarnu proizvodnju budući da podržava regeneraciju N i dalje potiče rast fitoplanktona. Naime, ovi organizmi otpuštaju C i N: (i) ekskrecijom koja se odvija na površini čitavog tijela (Ruppert i sur., 2004), (ii) neurednim hranjenjem (eng. sloppy feeding), (iii) fekalnim peletima i (iv) raspadanjem jedinki, što dovodi do gomilanja organske tvari koja postaje supstrat za rast mikrobne zajednice (Bronk i Steinberg, 2008). Dakle, masovne pojave želatinoznog zooplanktona povezane su sa značajnom akumulacijom otopljene organske tvari (eng. dissolved organic matter, DOM), a mikrobna zajednica razgradnjom otopljenog organskog ugljika (eng. dissolved organic carbon, DOC) i dušika (eng. dissolved organic nitrogen, DON) doprinosi povećanju koncentracija hranjivih soli, posebice ortofosfata (PO_4^{3-}) i amonijevih iona (NH_4^+) (West i sur., 2009).

U usporedbi s drugim predstavnicima zooplanktonske zajednice poput planktonskih račića, želatinozni organizmi sadrže manje N i proteina, ali okarakterizirani su s usporedivim C:N omjerom koji odgovara odnosu lipida i proteina (**Slika 5. A**). Udio proteina u želatinoznom zooplanktonu u prosjeku čini nešto manje od četvrtine udjela suhe tvari (23%), a od svih skupina, meduze i rebraši imaju najniže vrijednosti (**Slika 5. B**). Iduća skupina biokemijskih spojeva po zastupljenosti su lipidi, koji čine četvrtinu udjela proteina, dok ugljikohidrata ima oko četiri puta manje nego lipida (Clarke i sur., 1992). Većina lipida kod npr. antarktičkog želatinoznog zooplanktona je polarna te je njihov udio nešto viši (0,25-12,5% suhe biomase) od prosjeka (Nelson i sur., 2000). Količina kolesterola između pojedinih skupina se razlikuje i pokazuje npr. da su meduze uglavnom karnivori dok se rebraši hrane i fitoplanktonom (Nelson i sur., 2000).



Slika 5. Prikaz odnosa prosječnih udjela N, proteina i C:N omjera između: (A) skupine zooplanktonskih organizama i (B) predstavnicima želatinoznog zooplanktona (preuzeto i prilagođeno: Stainberg i Saba, 2008).

Kako je stehiometrija jedinke prije svega podložna dostupnosti i kvaliteti plijena, te vrijednosti u drugim uvjetima mogu odudarati od navedenih, a mogu se javiti i razlike među vrstama i unutar same vrste zbog npr. različitog udjela vode, veličine jedinki, razvojne faze, podneblja i doba godine, pa tako više vode u organizmu znači manje mišićne mase, a to znači manje proteina i N (Steinberg i Saba, 2008). Najvažniji oblik izlučenog N je anorganski produkt katabolizma proteina i aminokiselina, odnosno NH_4^+, koji je morskim organizmima energetski povoljniji za asimilaciju od ostalih oblika u višim oksidacijskim stanjima (npr. nitrat NO_2^- i nitrit NO_3^-), dok se DON izlučuje u manjem, no ipak značajnom udjelu ukupno izlučenog N (total dissolved nitrogen, TDN) (Bidigare, 1983). Ukupni doprinos NH_4^+ iz biomase želatinoznog zooplanktona smatra se značajnijim za ekosustav tek na lokalnoj razini, jer za masovnih pojava količina otpuštenog NH_4^+ može biti i po nekoliko puta veća od one koju je proizveo ostatak zooplanktona (Schneider, 1989). Stope izlučivanja NH_4^+ variraju i ovise o taksonomskoj pripadnosti (**Table 2.**), pa tako kod želatinoznih organizama mogu biti vrlo male od tek nekoliko mmol ili pak značajne od preko 40 mol N h^{-1} po jedinci. Očekivano, najniže stope, reda veličine 10^{-8} μg N h^{-1} po jedinci, zabilježene su kod najmanje veličinske frakcije organizama (Protozoa), a najveće, reda veličine 10^2, zabilježene su kod meduza (Scyphozoa), dok su najveće količine stopa izlučivanja po suhoj tvari jedinki (mg N mg$_{\text{suhe tvari}}$ h^{-1}) zabilježene za najmanje organizme (10^{-1}-10^2, Protozoa), a manje za one veće (10^{-3}-10, želatinozni zooplankton) (Steinberg i Saba, 2008).

Tablica 2. Zooplankton i stope izlučivanja NH_4^+ (prilagođeno: Bronk i Steinberg, 2008).

Taksonomske skupine predstavnika zooplanktona			Raspon stopa izlučivanja po jedinci (mmol N h^{-1})
Želatinozni zooplankton	Chaetognatha		1,7-6,7
	Ctenophora		2,5-600
	Molusca	Pterotracheoidea	160
		Pteropoda	32-200
	Chordata	Salpidae	5,8-1 200
	Cnidaria	Schyphomedusae	23-45 500
		Siphonophorae	4,2-8,3
		Hydromedusae	1,7-46
Ostali	Mikrozooplankton		66,2-1 200
	Crustacea		$1,9 \times 10^{-5}$-$1,9 \times 10^{-2}$
	Polychaetes		29-350

Ako uzmemo u obzir suhu masu organizama, stope izlučivanja NH_4^+ zooplanktonskih račića su za red veličine veće od onih kod želatinoznog zooplanktona (plaštenjaka, žarnjaka i rebraša), ali usporedive ako se odnos izrazi preko količine ukupnog C (Schneider, 1990) jer je udio C (< 10%) u želatinoznim organizmima puno niži od udjela kod račića (~ 40%) (Steinberg i Saba, 2008). I kod račića i želatinoznog zooplanktona izluči se uglavnom do 10% ukupnog N iz organizma, no kod neke vrste salpa u jednom danu mogu izlučiti i čitav postotak N iz organizma

(Ikeda i Mitchell, 1982). Izlučivanje je vezano i uz abiotičke faktore. Porastom temperature ubrzava se metabolizam čime raste koncentracija NH_4^+, ali treba uzeti u obzir i promjenu saliniteta koja obično utječe na veličinu i težinu jedinke (Steinberg i Saba, 2008). Izlučivanje organske frakcije N (DON) odnosno kombinacije uree i aminokiselina kod želatinoznih organizma iznosi 16-46% TDN (Steinberg i Saba, 2008 i literaturni navodi u radu), što je od posebne važnosti u ciklusu N jer podržavaju mikrobnu petlju. Osim direktnim izlučivanjem, želatinozni organizmi proizvode velike količine sluzi koja je također bitan izvor DON-a (Steinberg i sur., 2002), ali i DOC-a pa npr. *A. aurita* može u danu otpustiti i do 7% ugrađenog C u obliku DOC (Hansson i Norrman, 1995). Želatinozni organizmi uglavnom imaju veće stope rasta, i dnevno ugrađuju više C od ostalih zooplanktonskih skupina što vjerojatno objašnjava i velike količine N za epizoda masovnih pojava (Steinberg i Saba, 2008).

Rezervoar dostupnog ugljika u moru dogovorno se dijeli na otopljenu (DOC) i partikularnu odnosno čestičnu (eng. particulate organic carbon, POC) frakciju definiranu veličinom pora filtra (0,7 µm GF/F Whatman®) (Livanou i sur., 2017). Poznato je da želatinozni organizmi doprinose i većoj (> 0,2 mm) POC frakciji svojim fekalnim peletima i odumrlim jedinkama u procesu koji ima nadimak „*jelly-fall*" (Lebrato i sur., 2012). Ta biomasa u usporedbi s ostalim planktonom brzo tone jer se obično radi o velikim, makroplanktonskim jedinkama (Lebrato i sur., 2013). Želatinozni zooplankton se također smatra važnim rezervoarom C (eng. carbon sink) kojeg se u globalnom kruženju C često zaboravlja (Lebrato i sur., 2012 i 2013). Procjene globalne potrošnje C u literaturi znatno variraju, no unatoč tome ističu da značajan udio želatinoznog C može biti nepravedno zanemaren (Luo i sur., 2020). Vertikalni transport želatinoznog POC nejednako se distribuira po dubini, pa se procjenjuje da prema nekim modelima od ukupne godišnje biomase želatinoznih organizama $3{,}8\times10^{7}$ t C koja je stvorena u prvih 200 m vodenog stupca (Lucas i sur., 2014b) 59-72% dostigne dubinu od 500 m, 46-54% 1 000 m, 43-48% 2 000 m i 25-33% 4 500 m (Lebrato i sur., 2019). Modeliranje ciklusa C pokazalo je nešto veće vrijednosti i drugačije udjele, pa je tako procijenjeno da želatinozni organizmi u prvih 200 m dubine godišnje konzumiraju $7{,}9\text{-}13 \times 10^9$ t C u obliku fito i zooplanktona od čega se $3{,}9\text{-}5{,}8 \times 10^9$ t C ugradi u biomasu, a udio u ukupnom globalnom godišnje POC transportu do 100 m iznosi 32-40%, do 1 000 m 16-47%, dok 11-31% stigne do morskog dna (Luo i sur., 2020). Doprinos POC-u je značajan jer lokalno može premašiti godišnji priljev C do sedimenata za red veličine (Billett i sur., 2006), a samo je epizoda taloženja dovoljna da dopremi 4x više C nego u čitavoj godini (Lebrato i Jones, 2009). Ako se uzme u obzir zagrijavanje površine mora koje pogoduje rastu populacije želatinoznog zooplanktona, može se pretpostaviti da će to isto povećati vertikalni transport čestica prema dubljim slojevima, i možda pružiti neku vrstu kompenzacije ekosustavu obogaćivanjem zajednice bentosa hranjivim tvarima za očekivane gubitke u pelagijalu (Lebrato i sur., 2012). O ovoj temi u literaturi ima puno manje podataka nego o živućim organizmima, a svi zapisi se odnose na isključivo na meduze i plaštenjake (Lebrato i sur., 2012), dok npr. o rebrašima, unatoč njihovim brojnim i masovnim pojavama, nema dovoljno podataka (Fuentes i sur., 2010).

Biogeokemija frakcije DOM uključuje poznavanje triju glavnih komponenti, već spomenutih DOC i DON, ali i frakcije otopljenog organskog fosfora (dissolved organic phosphorus, DOP). Condon i sur. (2010) su pokazali da i meduze i rebraši izlučuju veće količine DOC u odnosu na DON i DOP. Kod rebraša DON je činio 21% ukupnog otopljenog dušika (total dissolved nitrogen, TDN), a DOP 34% od ukupno otopljenog fosfora (total dissolved phosphorus, TDP), a kod meduza DON 35% TDN i DOP 46% TDP. *M. leidyi* je u stanju dnevno izlučiti četvrtinu ukupnog C i nešto manje od petine TDN, dok meduza *Chrysaora quinquecirrha* izlučuje DOC i DON u Redfieldovom omjeru, ali u manjem udjelu u odnosu na ukupni sadržaj C i N u tijelu (< 0,5%). Odnos DOC:DON u DOM kod rebraša *M. leidyi* (29:1) bio je veći od Redfieldovog omjera (C:N=6,6:1) i značajno pridonio ukupnoj količini labilnog (reaktivnog) DOC-a (18-29% na dan). DOC iz oceana je najveći rezervoar reduciranog organskog C u biosferi (Hansell i sur., 2009) čije su komponente molekule različitih veličina i tipova (Pontiller i sur., 2020), zbog čega njihovo vrijeme razgradnje može varirati od minuta, pa do tisućljeća (Hansell i Carlson, 2015). Zbog svoje sposobnosti asimilacije i metabolizma DOC, bakterije imaju ključnu ulogu u regulaciji ciklusa C (Azam i sur., 1983) i razgrađuju labilni DOC vrlo brzo, do nekoliko dana (Hansell, 2013). U usporedbi s neaktivnim odnosno refraktornim dijelom ($\sim 630 \times 10^9$ t C) labilnog DOC-a u površinskim vodama je relativno malo ($< 0{,}2 \times 10^9$ t C), ali se iz njega do ugljičnog dioksida (CO_2) godišnje prevede 10x više C ($\sim 25 \times 10^9$ t C) (Hansell, 2013). To znači da i male promjene funkcionalnog dijela biote mogu imati značajan odziv u biogeokemijskom ciklusu C (Falkowski i sur., 1998). Kako prisutnost želatinoznih organizama mijenja dinamiku trofičke mreže (Shiganova i sur., 2004a) i utječe na brojnost i sastav zoo- i fito-planktona što sve može imati brojne sekundarne posljedice, čini se neopravdanim da su do prije desetak godina želatinozni organizmi uglavnom izostavljani iz simulacijskih biogeokemijskih modela funkcioniranja ekosustava (Lamb i sur., 2019).

Osim zbog doprinosa makrokonstituentima biomase (C, N, P), želatinozni organizmi predstavljaju bitnu kariku u trofičkom transportu nekih metala u tragovima. Mada se koncentracije elemenata u prosjeku ne razlikuju među taksonomskim skupinama želatinoznog zooplanktona, salpe ih nakupljaju u svom probavnom sustavu, a time i fekalnim peletima

(Romeo i sur., 1992) što nije zabilježeno kod ostalih skupina čija konzumacija ne bi trebala predstavljati rizik jer kod njih ne dolazi do bioakumulacije (Basso i sur., 2021).

Uloga želatinoznog zooplanktona u trofičkoj mreži

Želatinozni zooplankton utječe na trofičku mrežu tako što vrši *bottom-up* utjecaj na fitoplanktonsku zajednicu doprinosom hranjivih metabolita i *top-down* kontrolu hraneći se njihovim predatorima, odnosno sitnijim zooplanktonom (Pitt i sur., 2005), te je u kompeticiji za resurse (zooplankton) s višim predatorima, čijim se juvenilnim stadijima (jajašcima i ličinkama) često i hrani (Oguz i sur., 2008; Stoltenberg i sur., 2021). Utjecaj na fitoplanktonsku zajednicu je dvojak jer se predacijom zooplanktona uklanjaju njihovi predatori (Deason i Smayda, 1982), a izlučeni organski metaboliti potiču bakterijsku zajednicu koja razgradnjom proizvodi hranjive tvari i time podržava primarnu proizvodnju (Nasrollahzadeh i sur., 2008). Općenito, njihov je utjecaj na mikroorganizme značajan jer je pokazano da izlučivanjem tvari i svojim mikrobiomom mijenjaju sastav bakterijske zajednice okolne vode (Dinasquet i sur., 2012; Hao, i sur., 2019; Jaspers i sur., 2019), a i oblikuju fitoplanktonsku zajednicu (Tiselius i Møller, 2017). Utjecaj na sitnije zooplanktonske organizme nije manje bitan jer uslijed svih masovnih pojava i neselektivne ishrane mogu ukloniti značajne količine zooplanktona (Tiselius i Møller, 2017) i, vjerojatno, direktno osiromašiti fond brojnih vrsta, pa i komercijalno zanimljivih riba.

S druge strane, masovne pojave želatinoznih organizama mogu ukazivati na perturbacije u ekosustavima. Najjasniji primjeri potječu iz 1980. godine kada je duž jugozapadnih obala Afrike i u Crnom moru uslijed osiromašenja ribljeg fonda ljudskim djelovanjem i unosa obilja hranjivih soli došlo do povećanja brojnosti fitoplanktona, a time i sitnijeg zooplanktona, nakon čega je uslijedila masovna pojava želatinoznih organizama (Shannon i sur., 2009). Unatoč tome što hidrodinamika znatno utječe na kvalitetu života ovih fragilnih organizama (Graham i sur., 2001), ovi primjeri govore o tome kako im ona često i nije ograničavajući faktor. Pokazano je da želatinozni organizmi mogu preživjeti i u raslojenim, mirnijim sustavima gdje neselektivnom ishranom s lakoćom nadvladavaju kompeticijske vrste poput riba (npr. *M. leidyi*, Crno more), ali i u dinamičnijim područjima miješanja npr. eng. upwellinga (Chiaverano i sur., 2018) gdje će zbog obilja hranjivih tvari, a posljedično i planktona, također uspješno održavati svoju populaciju (Shannon i sur., 2009).

Kompleksnost interakcija s višim predatorima ilustrira i to da se neke ribe hrane želatinoznim organizmima (Dong, 2019), dok neki od njih osiguravaju opstanak juvenilnih stadija ribe i beskralježnjaka pružajući im zaštitu od predatora (Condon i sur., 2014; Pitt i sur., 2014). Mada se uvriježeno smatra da želatinozni organizmi predstavljaju tek mrtvi ogranak trofičke mreže, kemijske i biološke analize tkiva i sadržaja probavila nekih predatora su pokazale kako se mnoge od njih redovno njima hrane unatoč njihovoj niskoj energetskoj vrijednosti (Hays i sur., 2018). Uz to, nema razlike između želatinoznih i ostalih komponenti zooplanktona u potrošnji kisika (O_2) odnosno respiraciji, ako se ona izrazi u ovisnosti o količini C u biomasi (Schneider, 1992). Uzevši u obzir činjenicu da predstavljaju lako dostupan plijen koji se brzo probavlja, moguće je da je važnost njihovog doprinosa energije prema višim trofičkim razinama, umanjena (Hays i sur., 2018). Naprotiv uvriježenom da želatinozni organizmi potiču mikrobnu petlju i tako umanjuju energetski doprinos višim trofičkim razinama (Condon i sur., 2011), u oligotrofnim staništima ishrana nekih vrsta repnjaka (npr. Appendicularia, Tunicata) spona je koja nedostaje između zajednice pikoplanktona (0,2-2 μm) i viših predatora tj. riba (Llopiz i sur., 2010). Također, kod nekih je vrsta meduza zabilježena fascinantna prilagodba koja im omogućava da unosom hranjivih tvari zaobiđu ulogu mikrobne petlje. Naime, one imaju sposobnost asimilacije DOM-a direktno iz vodenog stupca (to isključuje POC i čitave stanice manjih organizama), iskoristivši hranu nižih trofičkih razina kako bi preživjeli razdoblja oskudice, a čime se može objasniti i njihovo uspješno preživljavanje i u oligotrofiji i u eutrofiji (Skikne i sur., 2009).

Veliki broj prilagodbi fiziologije i načina hranjenja poput neselektivne ishrane, neprekidne konzumacije plijena potaknute podražajima iz okoliša i mogućnošću redukcije obujma tijela, omogućio je ovoj raznovrsnoj skupini organizama uspješno preživljavanje i u područjima gdje je dostupnost hrane ograničena (Jaspers i sur., 2015a; Richardson i sur., 2009), i neke od njih učinio uspješnim invazivnim vrstama. Od mnogobrojnih opisanih pojava stranih morskih organizama, zadnjih desetljeća upravo zapanjuje broj bioinvazija vrsta želatinoznog zooplanktonskih organizama npr. meduza (Cevik i sur., 2011) i rebraša (Pestorić i sur., 2021, Verwimp i sur., 2019). Interakcije ljudi i želatinoznih organizama u obalnom području danas su sve češće (Condon i sur., 2012) te se javlja potreba za znanstveno utemeljenim strategijama upravljanja kako bi se ublažile negativne socio-ekonomske posljedice, a iskoristile potencijalne prednosti njihovih ekoloških usluga (eng. ecosystem services) (Fuentes i sur., 2018). Osim problematike pojave želatinoznih organizama i načina na koje se one očituju, danas nedostaje jedinstveni pogled na prostorno- vremenske dinamike bioinvazija što uključuje i svijest o antropogenim utjecajima (Chabrerie i sur., 2019), pa problematika bioinvazija želatinoznih organizama uz ove nepoznanice predstavlja poseban izazov brojnim istraživanjima (Verwimp i sur., 2019).

Želatinozni zooplankton i ekološki i fizikalni modeli

Promjene niza abiotičkih faktora mogu oblikovati populacije morskih organizama i djelovati na njihove interakcije u trofičkom sustavu. Razni modeli su se u posljednje vrijeme pokazali kao izuzetno koristan alat za povezivanje ekoloških odgovora na promjene okolišnih čimbenika. Mnogi od njih danas uključuju skupinu želatinoznog zooplanktona kako bi pokušali objasniti razne aspekte problematike njihovih pojava npr. prijenosa energije u trofičkom sustavu (Lebrato i sur., 2019; Luo i sur., 2020), funkcioniranje ekosustava (Ramirez-Romero i sur., 2018), prostornoj distribuciji (Bentlage i sur., 2013) i disperziji (Macías i sur., 2021), a ovdje će biti izdvojeni tek neki od važnijih i recentnijih.

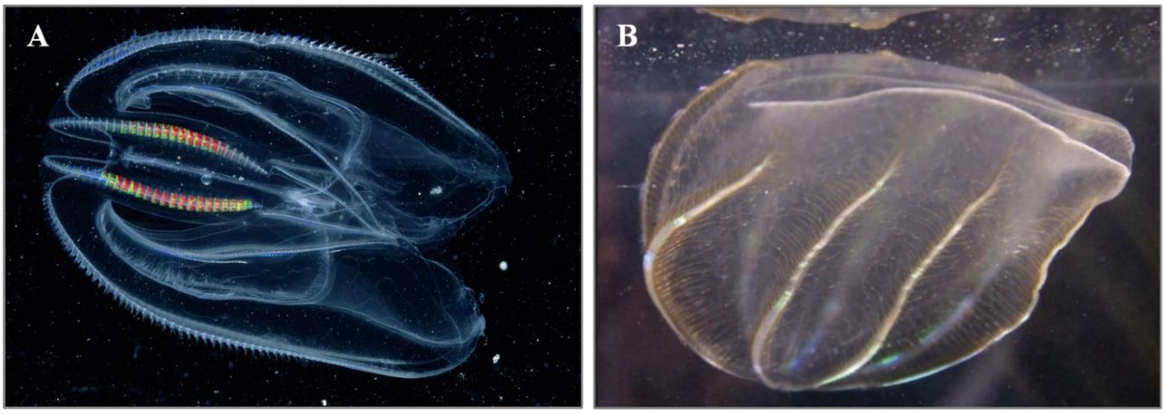
Primarni fokus ranijih modela bio je na ekosustavima temeljenih na ribolovu i upravljanju resursima jer se želatinozni organizmi hrane ribljim ličinkama i jajašcima što osiromašuje riblji fond (Pauly i sur., 2009). Među njima, najčešće su korišteni modeli Ecopath i Ecopath with Ecosim (Colléter i sur., 2015) koji prate protok energije između komponenti ekosustava (vrste ili funkcionalne skupine), pretpostavljajući da je sustav u ravnoteži, tj. da je biomasa unutar sustava konstantna. Njihov nedostatak je bio da su želatinozni organizmi ili vrlo rijetko uključivani kao dio hranidbene mreže ili su smatrani jedinstvenom skupinom zanemarivši taksonomske razlike među njima. Osim toga, u posljednjih je 30-ak godina tek nešto više od trećine objavljenih radova koji su se služili navedenim modelima, uopće vodilo računa o uključivanju želatinoznih organizama, pojedinačno ili kao dio šire zoooplanktonske zajednice (Lamb i sur., 2019). Model trofičke ravnoteže mase (eng. trophic mass-balance) koji primijenjen s ciljem kvantifikacije utjecaja ribolova, opisa strukture prehrambene mreže i funkcioniranja ekosustava sjevernog i srednjeg Jadrana 1990. godina, također je grupirao želatinozne organizme zanemarivši njihovu taksonomiju (Coll i sur., 2007). Ti modeli inače mogu biti vrlo korisni jer razmatraju želatinozne organizme uz one s viših trofičkih razina, međutim kako ovise o vrijednostima mokre mase organizma automatski obezvrjeđuju utjecaj organizama s visokim udjelom vode (Pauly i sur., 2009). Primjer uspješno implementiranog modela je analiza interakcija riba i meduza u području gdje se te skupine nadmeću za resurse (sjeverna Humboltova struja, Peru), a koja je pokazala negativni utjecaj pojava želatinoznog zooplanktona na riblji fond (Chiaverano i sur., 2018). Naime, izlov ribe podržava proliferaciju želatinoznog zooplanktona koji u kompeticiji za hranu dovodi do manjka ribe, a to dalje može utjecati na čitav ekosustav, počevši s višim trofičkim razinama jer nedostatak ribe može utjecati i na populaciju morskih ptica (Chiaverano i sur., 2018). Unatoč tome što s godinama sve veći broj takvih modela uključuje želatinozne organizme (Lamb i sur., 2019), njihova primjenjivost na iste je limitirana, a simulacije manje uspješne od onih za ostale skupine poput riba i nekih beskralježnjaka (Innes-Gold i sur., 2020).

Nasuprot tome, neki su se populacijski modeli (npr. stage-structured models) pokazali uspješnima u identifikaciji ključnih varijabli koje kontroliraju intenzitet i učestalost pojava meduza (Goldstein i Steiner, 2019) i rebraša (Salihoglu i sur., 2010) pokazujući dosljedne rezultate i uzimajući u obzir fiziološku složenost populacija. Opisivanjem dinamike složenih populacija meduza za vrijeme obilja i oskudice hrane pokazano je kako dovoljno hrane i rast temperature mogu potaknuti sazrijevanja polipa i shodno tome voditi do povećanja broja odraslih meduza (Goldstein i Steiner, 2019). Na istom principu su analizirani utjecaji temperature i ishrane na pojave i razmnožavanje *M. leidyi* (Salihoglu i sur., 2010). Uzevši u obzir varijabilnu ishranu za životnog ciklusa i temperaturni raspon 10-30 °C, pokazano je da se temperatura i oskudica hrane slično odražavaju na sve faze životnog ciklusa (npr. porast temperature uzrokuje rast, a za oskudice hrane biomasa opada), dok dovoljno hrane pogoduje sazrijevanju (Salihoglu i sur., 2010).

Od ostalih uspješno primijenjenih modela mogu se istaknuti i oni koji su usredotočeni na lokalne, ali ne i globalne pojave želatinoznih organizama. Neki od njih su npr. pojednostavljeni modeli zajednica npr. nutrient-phytoplankton-zooplankton-detritus (NPZD), koji ovise o unosu nekih količina makronutrijenata, a koriste se kako bi varijabilnost okolišnih čimbenika povezali s dinamikom pojava (Daewel i sur., 2019; Ramirez-Romero i sur., 2018; Schnedler-Meyer i sur., 2018). Na taj način je pokazano kako u umjerenom pojasu povišene temperature zimi povlače za sobom i masovne pojave meduza te dovode do pomaka trofičkog sustava iz onog u kojem prevladavaju kopepodi u sustav u kojem prevladavaju cilijati i želatinozni organizmi (Ramirez-Romero i sur., 2018). Osim toga, pojave želatinoznih organizama dovode i do istrebljenja zooplanktona što omogućuje, inače netipičnu pojavu, ljetnog fitoplanktonskog cvata (Schnedler-Meyer i sur., 2018). Na globalnoj skali, u kombinaciji s hidrodinamičkim modelima NPZD, pokazano je kako će povećana stratifikacija slojeva oceana koja nastaje uslijed globalnog zagrijavanja dovesti do smanjenja globalne biomase planktona, a posebice zooplanktona (Chust i sur., 2014). Hidrologija je iznimno bitna kada se raspravlja o dinamici zooplanktonske populacije s obzirom na to da potpomaže stvaranju njihovih tzv. prividnih pojava, a može utjecati i na horizontalnu (Graham i sur., 2001) i vertikalnu disperziju jedinki (Skliris i Djenidi, 2006). Fizikalni model prema Lagrangeu poslužio je npr. za predviđanje ulazaka potencijalno opasnih organizama poput meduze *Physalia physalis* kroz Gibraltarski tjesnac i određivanje njihovih trajektorija u Sredozemlju, te poslužio zainteresiranim stranama kao osnova za ranu uzbunu i izradu strategija upravljanja pojavama (Macías i sur., 2021). Dio drugih, puno složenijih modela se integrirano bavi problemom fizikalnih strujanja i bioloških komponenata kako bi bolje razumjeli globalno kruženje u sustavu npr. Dynamic Green Ocean Models (DGOMs), no oni do danas ne uključuju želatinozne organizme (Le Quéré i sur., 2015). U istu skupinu modela spada i globalni oceanski biogeokemijski model Plankton Type Ocean Model (PlankTOM11) koji organizme grupira u funkcionalne tipove planktonske zajednice. Model je, uključivši podatke o ekologiji želatinoznog zooplanktona (stope rasta i mortaliteta, ishrana i respiracija u ovisnosti temperaturi i biomasi), pokazao njihovu važnu globalnu ulogu u reguliranju ekosustava kroz strukturu planktonske zajednice, prostorno-vremensku dinamiku i biomasu, što je do sada bilo zanemarivano (Wright i sur., 2021). Točnije, simulacije su pokazale da je ukupna želatinozna biomasa usporediva s biomasom ostalih skupina zoo- i fitoplanktona, da njihovo uvođenje u model direktno utječe na zooplanktonske račiće, a na ostatak planktona indirektno preko trofičkih kaskada.

Invazivna vrsta rebraša – morski orah (Mnemiopsis leidyi)

Rebraši su skupina morskih beskralježnjaka koje taksonomski svrstavamo u koljeno Ctenophora koje čini dva razreda i nekoliko redova, a smatraju se sestrinskom skupinom žarnjaka (Cnidaria) (Redmond i McLysaght, 2021). Najčešći su u vodama umjerenog klimatskog područja, a najmanje ih nalazimo u polarnim krajevima (Pang i Martindale, 2008). Od pelagijskih plaštenjaka ih je lako razlikovati jer nemaju izraženi stolon u području ždrijela (Gershwin i sur., 2014), a od puno poznatijih srodnika – žarnjaka, se prvenstveno razlikuju po obliku tijela. Naime, rebraši su isključivo biradijalno simetrični organizmi, i ne posjeduju žarne stanice nego koloblaste – ljepljive stanice (Jager i Manuel, 2016). U razred Tentaculata ubrajamo vrste rebraša koje u nekoj fazi života posjeduju lovke (Cydippida, Ganeshida, Thalassocalycida, Cambojiida, Lobata, Cestida i Platyctenida), a u razred Nuda one bez njih (Beroida) (Licandro i Lindsay, 2017). Većina vrsta ubraja se u planktonske organizme, a oko trećine, uglavnom iz reda Platyctenida, nastanjuje bentos (Ryan i sur., 2016). Svi rebraši su karnivori koji love plijen, no kako se predstavnici potonjeg roda, odnosno vrste *Beroe* i *Neis*, uglavnom hrane drugim rebrašima, smatra se da su zbog prelaska na novi oblik hrane izgubili lovke (Moroz i Norekian, 2018). Na svijetu je zabilježeno oko 200 vrsta rebraša (Ryan i sur., 2016) od kojih su najviše proučavani kozmopolitski rodovi *Beroe*, *Mnemiopsis* i *Pleurobrachia* (El-Bawab, 2020). U Jadranu obitava nekoliko autohtonih vrsta rebraša: *Beroe forskalii*, *Leucothea multicornis*, *Bolinopsis vitrea* (Shiganova i Malej, 2009), *Cestum veneris* i *Pleurobrachia rhodopis* (Violić i sur., 2022), a zabilježene su i dvije strane vrste (**Slika 6.**): *B. ovata* i *M. leidyi* (Shiganova i Malej, 2009).



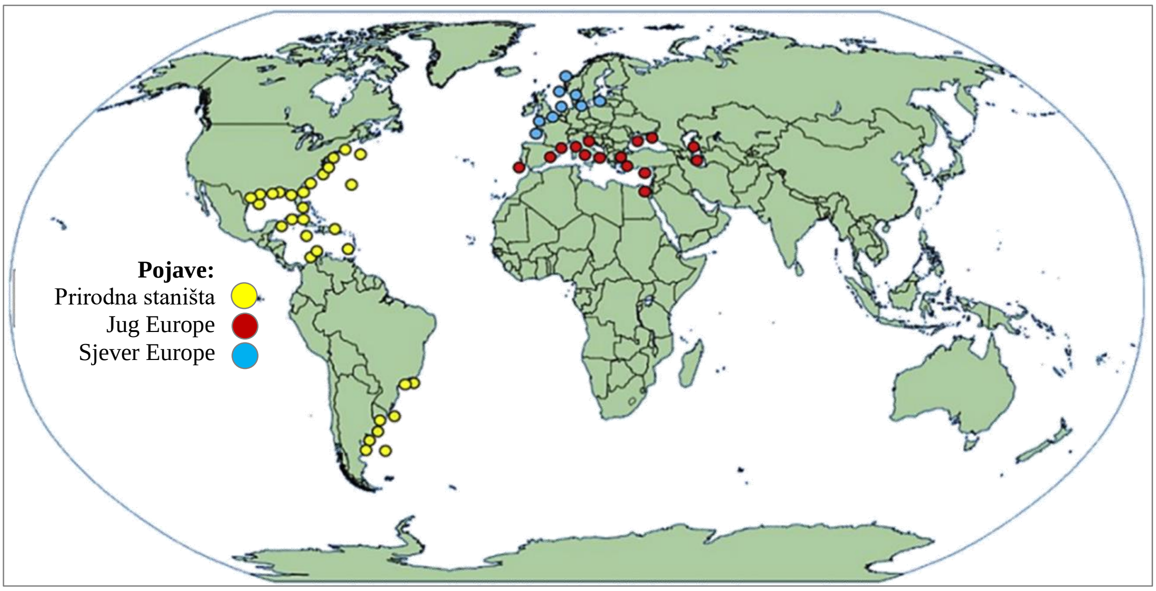
Slika 6. Strane vrste rebraša u Jadranu: (A) *M. leidyi* (Grinevetsky i sur., 2015) i (B) *Beroe ovata* (Kideys i sur., 2005).

Ova potonja – *Mnemiopsis leidyi* A. Agassiz, 1865 koja spada u red Lobata, naziva se i morski orah i posebno se ističe među invazivnim morskim vrstama te je proglašena jednom od najnepoželjnijih (eng. *one of the world's most notorious marine invaders*) (Reusch i sur., 2010) zahvativši brojna euro-azijska mora (**Slika 7**.). Njeno je širenje 80-ih godina prošlog stoljeća omogućeno netretiranim balastnim vodama brodova (Frazier i sur., 2013) koji su iz njezinog izvornog/prirodnog staništa – južne i sjeverne američke obale Atlantika (Kulhanek i sur., 2011), doplovili u Crno more. Međutim, unatoč brojnim izvještajima o zahvaćenosti europskih mora (Shiganova i sur., 2019) i, posljedično, ekonomskim gubicima u nekima od njih (Bodini i sur., 2017), *M. leidyi* do 2022. nije uvedena u tzv. Unijin popis (List of Invasive Alien Species of Union Concern) (EC, 2020), a niti u registre koje popisuju njenu prisutnost u hrvatskim vodama (npr. Boršić i sur., 2022 i https://invazivnevrste.haop.hr/) unatoč prisustvu u Jadranu (Malej i sur., 2017).

M. leidyi u europskim morima

Ekosustav Crnog mora je krajem 80-ih godina prošlog stoljeća doživio značajne perturbacije poput opadanja broja lokalne populacije meduza vrste *Aurelia aurita*, istovremene pojave invazivnog rebraša *M. leidyi*, te naposljetku, kolapsa zaliha pelagijske ribe i porasta brojnosti fitoplanktona (Shannon i sur., 2009). Mada je prekomjerni izlov bio glavni razlog kolapsa ribljeg fonda, a pojava *M. leidyi* imala tek manji utjecaj, smatra se da se daljnja proliferacija *M. leidyi* dogodila zbog dostupnosti ispražnjenih ekoloških niša koje su zauzimale pelagijske vrste riba, a omogućila ju je povećana zaliha planktona koji se pojavila uslijed eutrofikacije antropogenim utjecajima (Shannon i sur., 2009).

Uspješno uspostavljena populacija u Crnom moru postala je ishodište prvog vala bioinvazije koji se nastavio širiti, morskim strujanjima i djelomično, opet, balastnim vodama na susjedna mora, i to na: Azovsko (Studenikina i sur., 1991), Kaspijsko (Ivanov i sur., 2000), Mramorno (Shiganova, 1997), Egejsko (Shiganova i sur., 2004b), Levantinsko (Galil i sur., 2009) i zapadno Sredozemlje (Boero i sur., 2009), a 2013. je *M. leidyi* zabilježena čak i u slanom jezeru Qarun u Egiptu (Shabrawy i Dumont, 2016). U Jadranskom moru se pojavila prvi puta 2005. godine u Tršćanskom zaljevu (Shiganova i Malej, 2009).



Slika 7. Globalna rasprostranjenost *M. leidyi* (prilagođeno iz: Shiganova i sur., 2019).

Međutim do iduće je godine populacija u potpunosti iščezla što se objašnjava istovremenom pojavom još jedne strane vrste rebraša – *Beroe ovata* Bruguière, 1789, jednog od rijetkih prirodnih predatora *M. leidyi*. Ponovno se pojavila tek 2016. godine, no ovog puta u većem dijelu sjevernog Jadrana (Malej i sur., 2017). Prvi val širenja (Sredozemlje) genetski je bliži populaciji s izvorištem u Meksičkom zaljevu, dok se drugi val koji je zahvatio sjever Europe povezuje s populacijama sjeveroistočnih obala SAD-a (Reusch i sur., 2010). Drugim valom (2005.) zahvaćen je sjeverozapad Europe, tj. danske teritorijalne vode (Tendal i sur., 2007), Engleski kanal (Antajan i sur., 2014), nakon čega je *M. leidyi* pronađena na više lokacija u Baltiku (Hansson, 2006; Javidpour i sur., 2006), Sjevernom moru (Faasse i Bahya, 2006; Boersma i sur., 2007) i u norveškim vodama (Oliveira, 2007) (**Slika 7.**). Dok su jedinke iz sjevernih europskih mora i godinama nakon prvih zapisa o pojavama zadržale gotovo neizmijenjenu genetiku, u Sredozemlju se populacije razlikuju prema njihovim genetskim markerima što ukazuje na višekratne unose iste vrste i izloženost posebnim okolišnim uvjetima (Bolte i sur., 2013).

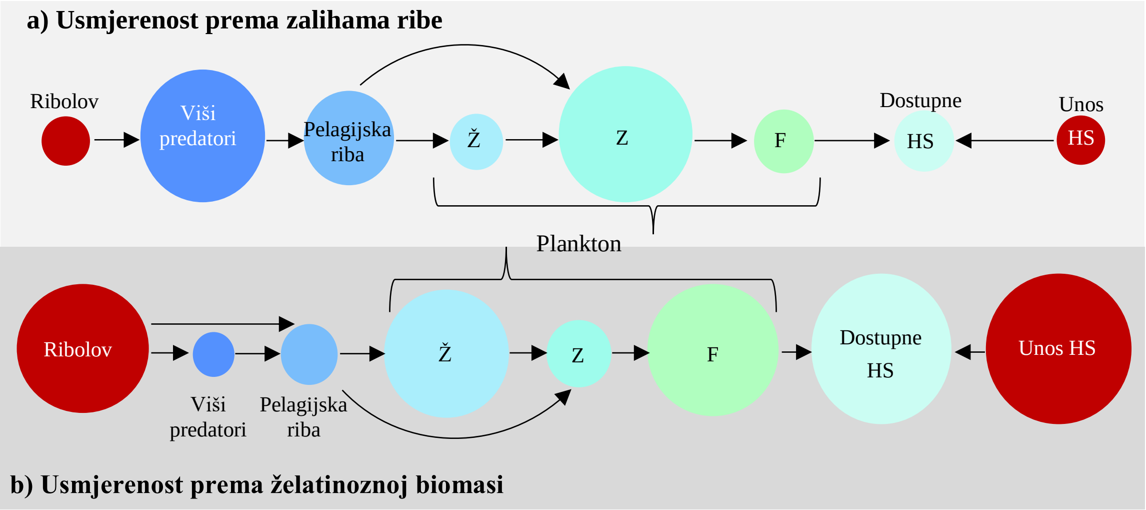
Ključ uspješnosti opstanka *M. leidyi* te njene redovite pojave, djelomično leži i u lokacijama na kojima su jedinke dospjele i gdje mogu najbolje napredovati. Obalni ekosustavi, estuariji, uvale, luke i zaljevi mjesta su najčešćih dojava o najezdama rebraša (Antajan i sur., 2014). To su ujedno i najosjetljivije lokacije koje zadnjih desetljeća zbog antropogenog utjecaja trpe razne pritiske. Brojna zagađivala, eutrofni uvjeti i izloženost kompeticijskim stranim vrstama uslijed intenzivnog pomorskog prometa, koje podnose tek dio autohtonih organizama, dovode do osiromašenja bioraznolikosti ostavljajući brojne slobodne ekološke niše (Pan i sur., 2014). Modeli su pokazali da je Crno more bilo upravo takav sustav izložen izrazito jakim perturbacijama okoliša koje su stvorile prikladnu nišu da *M. leidyi* postane dio prehrambene mreže i da dijeli resurse s lokalnom zajednicom malih pelagijskih riba (Oguz i su., 2008).

Perturbacije ekosustava

Odjek bioinvazija se očitovao različito (pozitivno ili negativno) na pojedine dijelove lokalne zajednice, i to kroz razne utjecaje od najviših (npr. ribe) do najnižih razina trofičke mreže (mikroorganizmi) (**Slika 8.**). Utjecaj na riblje vrste je dvostruk i očituje se kroz: (i) kompeticiju za resurse (hranu) (Kideys i sur., 2002) i (ii) predaciju ličinkama i jajašcima ribe (Kideys, 1994). Negativni utjecaji *M. leidyi* na komponente prehrambene mreže pelagijskih, obalnih i estuarijskih ekosustava, zabilježeni su u Crnom moru (Shiganova, 1997), Azovskom moru (Studenikina i sur., 1991) i Kaspijskom jezeru (Ivanov i sur., 2000) gdje je iscrpljena zaliha zooplanktona pridonijela i kolapsu ribarstva (Kideys i sur., 2005).

Slika 8. Pojednostavljena shema utjecaja *M. leidyi* koji se očituju na brojnost populacije i koncentracije kemijskih tvari.

Prije pojave rebraša *M. leidyi* u Crnome moru, inćuni su bili glavni konzumenti ne-želatinoznog zooplanktona (Kideys, 1994). Nakon proliferacije *M. leidyi* fond sitne plave ribe doživio je kolaps, a trofički se sustav promijenio iz onog u kojem prevladava riba u onaj u kojem je dominantan želatinozni zooplankton (Oguz i sur., 2008) (**Slika 9**.). Posljedice u Kaspijskom jezeru krajem devedesetih dovele su do uništenja populacija pelagijskih riba *Clupeonella* spp. (crnomorsko-kaspijska haringa) (Pourang i sur., 2016) npr. prepolovljenog ulova *C. cultriventris* (Fazli i Roohi, 2002), dok je 2003. proglašen moratorij u ribarstvu zbog nedostatka ribe (Kideys i sur., 2004).



Slika 9. Promjena sustava iz onog u kojem prevladava riba u onaj gdje dominira želatinozni zooplankton uslijed prekomjernog izlova ribe i eutrofikacije, npr. *M. leidyi* u Crnom moru (Ž – želatinozni, Z – zoo- i F – fitoplankton, HS – hranjive soli) (prilagođeno: d'Armengol i sur., 2017).

Sjeverni dio Jadrana, koji je ujedno i lokacija prvih pojava *M. leidyi* u Jadranskom bazenu (Malej i sur., 2017; Shiganova i Malej, 2009) važno je područje mrijesta inćuna (*Engraulis encrasicolus*) i sardina (*Sardina pilchardus*), dviju komercijalnih vrsta koje zajedno čine oko 40% ulova u Jadranu (Morello i Arneri, 2009). U pogledu bogatstva ribljeg fonda – važnog ekonomskog resursa, posljedice invazije bi mogle biti ozbiljne, ne samo iz ekološke nego i gospodarske perspektive. Sezona mrijesta inćuna u Sredozemlju se događa u toplijem razdoblju godine, od travnja do listopada (Morello i Arneri, 2009), a prema trenutnim spoznajama to je i doba godine kada je zabilježeno najviše najezda *M. leidyi* (Gambill i sur., 2015). Prema obrascu bioinvazije koja je „poharala" Crno more i od čijih posljedica se ekosustav još nije oporavio (Bodini i sur., 2017), moguće je zaključiti da bi dugoročne posljedice na ravnotežu viših trofičkih razina jednog od najproduktivnijih dijelova Sredozemlja – sjevernog Jadrana (Ben-Hamadou i sur., 2012), mogle imati značajan odjek na cijeli ekosustav.

Smatra se da su klimatske promjene u Atlantskom oceanu utjecajem na pojave *M. leidyi* i doprinijele promjenama dinamike lokalnih zajednica. Dugoročni niz podataka pokazao je da su povišene prosječne temperature utjecale na ranije pojave i duži boravak morskog oraha u njegovom prirodnom staništu (ljeto/jesen ⇨ proljeće/ljeto) (Sullivan i sur., 2001). Zamijećene promjene mogle bi imati drastične učinke na planktonsku dinamiku umanjujući šanse za opstanak jajašaca i ličinki riba čije se vrijeme mrijesta preklapa s razdobljem pojava *M. leidyi*, a koje bi predacijom zooplanktona u proljeće mogle dovesti do češćeg i brojnijeg cvata fitoplanktona ljeti.

M. leidyi intenzivnom predacijom vrši *top-down* utjecaj na trofički sustav, djelujući negativno na mezozooplankton (0,2-20 mm). Utjecaj na dinamiku zajednice zooplanktona zamijećen je osim u Crnom moru (Kideys, 1994) i u sjeverozapadnom Jadranu, gdje je ukazano na pad broja i raznolikosti zooplanktona u samo dvije godine od prve pojave *M. leidyi* (Fiori i sur., 2019). Predacija zooplanktona posljedično dovodi do obilja fitoplanktona, a primjeri toga su zabilježeni u prirodnom staništu morskog oraha (Deason i Smayda, 1982; Purcell i Decker, 2005), i u područjima zahvaćenima bioinvazijom npr. u čitavom Crnom moru (Oguz i sur., 2008) i Skandinavskim vodama, gdje su u novonastalim uvjetima posebno profitirale dijatomeje (Tiselius i Møller, 2017), što nije nužno bio slučaj i u Crnom moru (Kideys, 1994). Pojave su pogodovale i rastu brojnosti cijanobakterija (Roohi i sur., 2007), ali posljedično i promjeni sastava fitoplanktonske zajednice u kojoj je dominirao manji fitoplankton (Nasrollahzadeh i sur., 2008). Isti utjecaj na brojnost fitoplanktona potvrđen je i eksperimentalno (Shiganova i sur., 2003). Utjecaji na fitoplankton su, dakle, stimulirajući i to: (i) indirektni, uslijed uklanjanja njihovog predatora i (ii) direktni, uslijed proizvodnje hranjivih tvari potrebnih za njihov rast (Treible i sur., 2014).

M. leidyi u staništima svojim pojavama i njihovim iščezavanjem pokazuje tzv. *source-sink* dinamiku. Na sustav djeluje tako što za vrijeme masovnih nakupina *M. leidyi* koncentrira hranjive tvari u svojoj biomasi koje uslijed propadanja postaju izvorom istih (McNamara i sur., 2013a). Guste nakupine *M. leidyi*, nekada i do > 400 jedinki/m^3, mogu pokriti velika područja i postići zapanjujuće količine biomase (McNamara i sur., 2010; Sullivan i sur. 2001), poput one zabilježene 1989. u Crnom moru kada je 10^9 t biomase rebraša premašilo težinu godišnjeg ulova ribe u svijetu (Ivanov i sur., 2000; Sorokin, 2002). Udio suhe tvari varira s lokacijama i razdobljima godine, te može iznositi do 3% (McNamara i sur., 2013a) što je neznatna količina u odnosu na volumen jedinke, ali značajna zbog broja jedinki. Ogromne količine želatinozne biomase, dakle, dovode do otpuštanja značajnih količina hranjivih soli, prvenstveno, NH_4^+ i PO_4^{3-} (Treible i sur., 2014) vršeći *bottom-up* utjecaj na trofičku mrežu potičući razvoj fitoplanktonske zajednice i primarnu proizvodnju (Nasrollahzadeh i sur., 2008). Laboratorijski eksperimenti su potvrdili iznimno jak lokalni *bottom-up* učinak uslijed razgradnje biomase rebraša (Dinasquet i sur., 2012). Raspadanje proizvedene biomase uz otpuštanje hranjivih soli može lokalno doprinijeti hipoksiji (Treible i sur., 2014). Pokazalo se da biomasa varira u sastavu u ovisnosti o dostupnoj hrani, pa tako koncentracije N i P opadaju prema kraju masovnih pojava, vjerojatno zbog nestašice hrane (McNamara i sur., 2013a). Elementarni sastav odraslih jedinki može biti različit, npr. C:N može biti znatno niži (4,4) ili viši (9,9) od Redfieldovog omjera (6,6) (Treible i sur., 2014). Varijacije su vezane uz stadij u kojem se nakupine organizama nalaze, pa tako prosječni omjeri (C:N=6:1 i C:P=66:1) izmjereni za vrijeme vrhunca pojava, pred njihov kraj opadaju, a posebno se iscrpljuje P (C:N=5:1 i C:P=128:1), što ukazuje na nejednaku ulogu u izvoru hranjivih soli (McNamara i sur., 2013a). Značajan utjecaj *M. leidyi* na ciklus hranjivih soli zabilježen je u estuariju Chesapeake Bay, gdje je želatinozni zooplankton naveden kao primarni izvor recikliranih hranjivih soli, točnije izvora anorganskog N i P (Condon i sur., 2010). Međutim, druga je studija pokazala da razgradnja želatinoznih nakupina u visoko eutrofnim uvjetima ne predstavljaju značajan doprinos ekosustavima (< 1% primarne proizvodnje po danu) (Treible i sur., 2014). Isto, međutim, vjerojatno ne bi vrijedilo za sustave u kojima je dostupnost hranjivih soli ograničena, s obzirom na to da je zabilježen doprinos anorganskim hranjivim solima bio je najizraženiji za vrijeme N-limitacije (Condon i sur., 2010). K tome, pokazano je npr. da u Kaspijskom jezeru razdoblje pojave *M. leidyi* bilo je povezano porastom koncentracije hranjivih soli, a shodno tome porast brojnosti i raznovrsnosti fitoplanktona u površinskom sloju vodenog stupca (Nasrollahzadeh i sur., 2008).

M. leidyi je u stanju prilagoditi svoje fiziološke potrebe prema uvjetima u okolišu, pa tako pri nedostatku hrane, može smanjiti svoju veličinu i energetsku vrijednost, a time i količinu C u biomasi, i izlučiti ih u okoliš (Finenko i sur., 2006). Kako se u literaturi ne spominju vrste u područjima zahvaćenima bioinvazijom čiji bi plijen bila vrsta *M. leidyi,* i kako je tek u nekolicini (npr. Egejskom; Shiganova i sur., 2007, i Crnom moru; Shiganova i sur, 2001a, te danskim vodama; Shiganova i sur., 2014) pronađen njen prirodni predator *B. ovata* može se očekivati da će velika količina biomase, baš kao i kod ostalog želatinoznog zooplanktona (Condon i sur., 2011), uglavnom podržavati trofički niže razine i mikrobnu razgradnju. Naime, *M. leidyi*, može izlučiti značajne količine labilnog DOM-a češće bogatijim C nego N (npr. C:N = 25,6), koji se iznimno brzo metabolizira i tako utječe na rast i razvoj mikroorganizama (Codon i sur., 2011). Osim toga, primarna i sekundarna proizvodnja te ishrana zooplanktona se direktno očituju u količini, ali i kvaliteti otopljene organske frakcije (Fonda Umani i sur., 2007; Pettine i sur., 2001). Biokemija i reaktivnost želatinoznog DOM-a su nepoznanica i pretpostavlja se da se kao i kod ostalih sluzavih izlučevina radi o polisaharidima (Wild i sur., 2010), međutim C:N omjeri ukazuju na to da u biomasi prevladavaju proteini (Treible i sur., 2014). Većina organske tvari u jedinci zaista se odnosi na proteine (80%), za kojima slijede lipidi (10%), i ugljikohidrati (< 6,5%) među kojima dominira glikogen koji opada s nedostatkom hrane (Anninsky i sur., 2005). Kvaliteta organske tvari dostupne u morskoj vodi može se jasnije predočiti određivanjem hidrofobnosti/hidrofilnosti iste, odnosno mjerenjem tzv. površinski aktivnih tvari (eng. surface-active substances, SAS) (Croot i sur., 2007; Ćosović i Vojvodić, 1998; Sabbaghzadeh i sur., 2017). Novije studije ukazuju na značajni doprinos otopljene frakcije SAS i u prosjeku više DOC-a u sjevernom Jadranu nego u prethodnom desetljeću (Ciglenečki i sur., 2020) u koincidenciji s masovnim pojavama *M. leidyi* u tom sustavu (Malej i sur., 2017).

M. leidyi obitava u eufotskoj zoni, a do sada nisu zabilježene jasne dnevne vertikalne migracije, kakve su poznate npr. kod meduza. Međutim pokazano je da manje jedinke mogu vertikalno migrirati kako bi regulirali izloženost svjetlosti i izbjegli oštećenja uslijed prevelikog intenziteta (Haraldsson i sur., 2014). To znači da se većine želatinoznih izlučevina proizvede upravo u ovom dijelu vodenog stupca, a njegova glavnina tu se i reciklira čime doprinosi brza fotokemijska razgradnja organske tvari do jednostavnijih molekula (Carlson i Hansell, 2014). U teoriji je moguće da uslijed masovnog propadanja jedinki velike količine sluzave biomase, potonu po istom tzv. „*jelly-fall*" principu, jer su neke žive nakupine zabilježene na dubinama većim od 60 m (Costello i Mianzan, 2003), međutim u literaturi to još nije opisano. Inkubacijski eksperimenti pokazuju su dnevne stope kojima *M. leidyi* u teoriji može tonuti (400-1 500 m) sličnije onima kod žarnjaka (npr. *Pelagia noctiluca*), nego kod npr. salpa (467-1 002 m) (Stone, 2016). Kako *in situ* opažanja to još nisu potvrdila njihov pravi doprinos zajednici bentosa i dalje ostaje nepoznanica.

Mnoga istraživanja su pokazala da *M. leidyi* utječe na bakterijsku zajednicu. Condon i sur. (2011) su primijetili da DOM rebraša potiče rast broja bakterija iz skupine γ-proteobakterija koje uspiju nadvladati inače dominantne α-proteobakterije. Laboratorijski eksperimenti su pokazali da su u prisustvu *M. leidyi* najbrojnije određene skupine bakterija, točnije *Flavobacteriaceae* (Bacteroidetes) koje povezujemo sa probavnim sustavom rebraša (Dinasquet i sur., 2012). Takav zaključak otvara prostor za pitanje: jesu li rebraši prijenosnici nekih drugih stranih organizama? Mikrobiom rebraša u prirodnim staništima i onih u područjima zahvaćenima bioinvazijom se značajno razlikuje, ali je i vezan uz domaćina (Jaspers i sur., 2019), baš kao i nove skupine jednolančanih DNA-virusa koje se povezuje s *M. leidyi* (Breitbart i sur., 2015). Daljnja istraživanja u tom smjeru bi tek mogla rasvijetliti razmjere ukupnog učinka invazije rebraša.

Ključne prilagodbe M. leidyi

M. leidyi uspješno održava populacije izvan svojeg prirodnog staništa zahvaljujući svojem velikom reprodukcijskom kapacitetu, širokoj ekološkoj valenciji, ali i nizu specijaliziranih prilagodbi poput obnavljanja tkiva ili strategije lova.

Životni ciklus morskog oraha započinje jajašcem (~ 0,5 mm, Jaspers i sur., 2015a) iz kojeg se razvija karakteristična cydippid ličinka sa slobodnim lovkama (< 4 mm), a nastavlja se kroz prijelaznu fazu ličinke (4-6 mm) (Sullivan, 2010) koju obilježava prisustvo slobodnih lovki, ali i malih uški (eng. lobes) (Costello i sur., 2021), te fazom odrasle jedinke kod kojih se lovke stapaju s uškama (Waggett i Sullivan, 2006). Zbog želatinozne građe, organizam ne zadržava postojani oblik, pa određivanje veličine jedinke, npr. oralno-aboralne duljina tijela, predstavlja problem (Purcell i sur., 2001), ali procijenjeno je da odrasli primjerci mogu narasti i do 15 cm (Sullivan, 2010). Od jajašaca do reproduktivno zrele odrasle jedinke roda dovoljno je tek dva tjedna (Baker i Reeve, 1974; Costello i sur., 2012), no već su i juvenilni primjerci u stanju proizvesti vitalne gamete (Martindale, 1987). Konačni broj proizvedenih jajašaca ovisi o brojnim biotičkim čimbenicima poput veličine jedinke, dostupnosti hrane (Javidpour i sur., 2020a) i cirkadijalnom ritmu (Sasson i Ryan, 2015), te abiotičkim čimbenicima, poput osvjetljenja (Sasson i Ryan, 2015), saliniteta i temperature (Jaspers i sur., 2011; Lehtiniemi i sur., 2011). Smatra se da *M. leidyi* nastoji izbjeći srođivanje kako bi se održala zdrava populacija (Ryan i Sasson, 2015). Eksperimenti su pokazali da ova vrsta baš poput njenih dalekih srodnika divizije Bilateria, primjenjuje neku vrstu signalizacije (ispuštanje kemijskih supstanci) kako bi upravljala mrijestom među jedinkama tzv. eng. conspecific signaling (Sasson i sur., 2018).

Danas je ovaj organizam rasprostranjen u sjevernijim staništima (58° S) u usporedbi s njegovim prirodnim staništem (42° S) gdje razdoblje nedostatka hrane traje znatno duže (Hosia i Falkenhaug, 2015). Osim toga, radi se o holoplanktonskom, brzorastućem organizmu (Sullivan i Gifford, 2007). Naime, *M leidyi* ne posjeduje dio životnog ciklusa vezan uz bentos npr. u obliku jajašaca, cista ili nekih drugih specijaliziranih stadija koji bi poslužio za preživljavanje u nepovoljnim uvjetima (npr. prezimljavanje) (Hyman, 1940) te ima relativno mali kapacitet pohrane rezervi hrane (van Walraven i sur., 2014). *M leidyi* drugim prilagodbama nadilazi ove izazove, npr. radi se o dvospolcima sa sposobnošću samooplodnje koji su u stanju proizvesti na tisuće jajašaca dnevno (Baker i Reeve, 1974; Costello i sur., 2006; Jaspers i sur., 2011 i 2015a; Lehtiniemi i sur., 2011) i tako povećati svoje šanse za opstanak.

Široki raspon ekološke valencije podrazumijeva visok prag tolerancije na čitav niz abiotičkih faktora, pa su tako jedinke *M. leidyi* u stanju preživjeti niske koncentracije otopljenog kisika do čak 1 mg l^{-1} (Decker i sur., 2004; Grove i Breitburg, 2005). *M. leidyi* je eurihalina vrsta koja podnosi raspon saliniteta od 2 do 38 (Kremer, 1994) i čiju populaciju u obalnim područjima abiotički značajno ograničava samo temperatura (Costello i sur., 2006; Jaspers i sur., 2011; Kremer, 1994; Lehtiniemi i sur. 2012). Unatoč tome, radi se o vrsti koja posjeduje izuzetno široki raspon temperaturne tolerancije (0-32 °C) te možemo je nedvojbeno smatrati euritermnom vrstom (Roohi i Sajjadi, 2011). S porastom temperature raste reproduktivnost i ubrzava se razvoj ličinke (Graham i sur., 2001). Optimalna temperatura (19-23 °C) može omogućiti da jedinka proizvede i više od 8 000 jajašaca (Kideys, 1994) i dostigne dnevni maksimum od 14 000 jajašaca (Kremer, 1976). Odrasla jedinka prosječne veličine na istoj temperaturi može opstati 9 dana, no kako se bazalni metabolizam usporava na nižim temperaturama, pri 3 °C te energetske zalihe mogu biti dovoljne i za 80 dana (Javidpour i sur., 2020b). Unatoč malim šansama za preživljavanje potomstva, za vrijeme oskudice hrane započinju masovno razmnožavanje (Boero i sur., 2008; Purcell i sur., 2001) kako bi se hraneći vlastitim ličinkama prebrodili nepovoljno razdoblje (Javidpour i sur., 2020a).

Pokazano je da je predacija primarni mehanizam regulacije populacije rebraša (Kremer, 1976). U svojem prirodnom staništu *M. leidyi* je proždrljivi grabežljivac koji guta uhvaćeno na ljepljive lovke (Bumann i Puls, 1997), a brzina hranjenja proporcionalna je dostupnom plijenu (Reeve i Walter, 1978). Kako je prehrana neselektivna, plijen je šarolik i uključuje razne planktonske organizme manje od 100 µm (planule žarnjaka) do 5 mm (ličinke *M. leidyi*) (Javidpour i sur., 2009). Ličinke su u stanju hraniti se mikroplanktonom (organizmima veličine 20-200 µm) odmah nakon što se izlegnu, a ova prilagodba objašnjava se time da uklanjanjem ostalog mikroplanktona smanjuju izloženost interakcijama te rizika od oštećenja čime si povećavaju šanse za opstanak (Sullivan i Gifford, 2007). Sadržaj probavila ličinki *M. leidyi* pokazuje da se hrane sitnijim plijenom poput ranijih stadija kopepoda (kopepoditi i nauplii), ličinka poliheta, ličinka školjkaša, rotifera i njihovih jajašaca, cilijata i bičaša (flagelati), no zbog brzine probave se ne može zaključiti u kojoj se mjeri prehrana sastoji od drugih protista kao dijela mikroplanktonske zajednice (Sullivan, 2010). O predaciji ličinki se malo zna, međutim, poznato je da se odrasle hrane neumjereno, nastavljajući loviti plijen i kada je gastrovaskularna šupljina puna i istovremeno izbacujući sluzave ugruške neprobavljene hrane (Bumann i Puls, 1997; Harbison i sur., 1978). Njihovo učinkovito hranjenje rezultat je aktivnog i efikasnog pretraživanja vodenog stupca (Colin i sur., 2014) i dodatnoj prilagodbi odnosno proizvodnji blagog laminarnog strujanja kojim se usmjerava plijen ka ustima (Colin i sur., 2010). Uz to, pokazano je da jedinka u samo sat vremena može ukloniti sav zooplankton iz gotovo 2 l okolne vode (Stone, 2016), što dovodi do drastičnog osiromašenja prehrambenog fonda za ostale komponente trofičke mreže, pa tako direktnom predacijom utječe na zooplanktonske račiće (McNamara i sur., 2013b), a indirektno ribu zbog kompeticije u resursima (Purcell i sur., 2001; Reusch i sur., 2010).

Neke vrste rebraša su u stanju obnavljati svoja tkiva, pa tako za razliku od roda *Beroe* koji je evolucijski potpuno izgubio tu sposobnost, vrsta *M. leidyi* je zadržala sposobnost regeneracije i danas postala popularan modalni organizam za proučavanje zacjeljivanja rana i obnovu tkiva

(Edgar i sur., 2021; Ramon-Mateu i sur., 2019), ali i on uvelike ovisi o dostupnosti resursa (Bading i sur., 2017). Za vrijeme nedostatka hrane, jedinke ne uspijevaju obnoviti svoj organizam, dok je za izobilja proces regeneracije čitavog tijela brz i traje od 8 do 10 dana (Bading i sur., 2017). Ova prilagodba može objasniti uspjeh ove vrste i u nepovoljnim uvjetima kao što su balastni tankovi koji jedinkama mogu nanijeti brojna oštećenja.

M. leidyi je u stanju prilagoditi potrebe svog organizma uvjetima u okolišu, pa tako da u vrijeme nedostatka hrane pribjegava smanjivanju. Uz pretpostavku da jedinka gubi dnevno 1% svoje kalorične vrijednosti izračunato je da odrasla jedinka prosječne veličine (6,5 cm duga i 20 g teška) relativno brzo smanji volumen tijela za > 5x i masu ~ 50x, ali ako pretpostavimo postepenu promjenu uvjeta (sve manje hrane, postepena prilagodba nižim temperaturama pri kojima se usporava metabolizam), jedinka može preživjeti duga nepovoljna razdoblja (Finenko i sur., 2006). Drugi eksperimenti su pak pokazali da u periodu gladovanja jedinka dnevno gubi 1,2% ukupnog C u organizmu, što je za nešto više od mjesec dana dovodi do redukcije od 63% (Granhag i Hosia, 2015). Da je to najvjerojatnije jadna od strategija preživljavanja razdoblja oskudice hrane potvrđuje veličina jedinki zimi (< 2 cm) koje su uzorkovane u područjima vjerojatnih utočišta u kojima *M. leidyi* prezimljava u Sredozemlju (Berre laguna i sjeverozapadna obala Jadrana) (Delpy i sur., 2016; Fiori i sur, 2019). Ova istraživanja upućuju na to da nedostatak hrane nije limitirajući čimbenik koji bi za vrijeme prijenosa balastnim vodama uspio skratiti životni vijek jedinki.

Sve ove prilagodbe pokazuju da se radi o vrlo rezistentnoj vrsti koja bi mogla značajno ugroziti dinamiku ekosustava u Jadranu unatoč tome što su neki modeli sjeverni Jadran opisali kao prostor potencijalnog širenja *M. leidyi*, ali ne i okoliš koji će nužno podržati razvoj i proliferaciju jedinki te uspostavu stabilne populacije (Siapatis i sur., 2008). Kao što znamo, ovu vrstu redovito bilježimo u sjevernom Jadranu (Tirelli i sur., 2021) no da bi znali procijeniti posljedice pojava potrebno je poznavanje dinamike njene populacije i uvjeta u kojima se pojavljuje. Istraživanje ove vrste u Jadranu bi trebalo obuhvatiti nekoliko aspekata, a koji se nameću kao iznimno bitnima. Naime, uz rekonstruirane povijesne tragove, modeli su pokazali jasne znakove degradacije trofičkog sustava Jadrana, a oni obuhvaćaju: iscrpljene zalihe ribe, osiromašenju populaciju morskih sisavaca i, općenito, pomak trofičkog sustava prema raznolikosti na nižim trofičkim razinama i sitnijim organizmima (Lotze i sur., 2010). Ovaj scenarij, u nekoj mjeri podsjeća na situaciju koja je prethodila unosu *M. leidyi* u Crno more i, dakle, u potpunosti opravdava napore da se istraži u kojoj mjeri i na koji način pojave *M. leidyi* utječu na riblji fond i zooplankton u sjevernom Jadranu. K tome, radi se o organizmu koji se zna pojavljivati u masovnim nakupinama, koje su predstavljale poteškoće ne samo ribarima, nego funkcioniraju obalne infrastrukture poput desalinizatora (Galil i sur., 2009) i tako donijele u novi sustav velike količine organske tvari kao prikladnog supstrata za bakterijsku digestiju i razgradnju (Condon i sur., 2011). To sve naglašava važnost da se proučavanje tih pojava usmjeri upravo na utjecaje koji vrši na niže trofičke razine. U konačnici, ove bi spoznaje trebale poslužiti kako bi se utvrdila zahvaćena područja i predložile mjere da se ograničio daljnje širenje bioinvazija *M. leidyi*.

CILJEVI I HIPOTEZE ISTRAŽIVANJA

Ovaj doktorski rad objedinjuje četiri samostalne znanstvene publikacije (I-IV) u jednu cjelinu koja pokriva niže navedene ciljeve (C1-5) i pripadajuće hipoteze (H1-5).

C1 Opisati prostorno-vremenske razmjere invazije *M. leidyi* uz abiotičke uvjete u kojima uspješno uspostavlja populacije u sjevernom Jadranu (I publikacija).

C2 Povezati geostrofička strujanja i disperziju populacije *M. leidyi* uz pomoć ROMS modela (II publikacija).

C3 Istražiti utjecaj masovnih nakupina *M. leidyi* na mikrobnu zajednicu i ciklus hranjivih soli i organske tvari, odnosno, promjene kemijske ravnoteže lokalnih morskih ekosustava (II i III publikacija).

C4 Usporediti stanje ribljeg fonda (inćuna) u razdoblju prije i nakon invazije te opisati utjecaj invazije *M. leidyi* na zooplankton (I publikacija).

C5 Predložiti korake za ograničavanje daljnjeg prijenosa *M. leidyi* balastnim vodama (IV publikacija).

H1 *M. leidyi* uspostavlja stabilnu populaciju u sjevernom Jadranu.

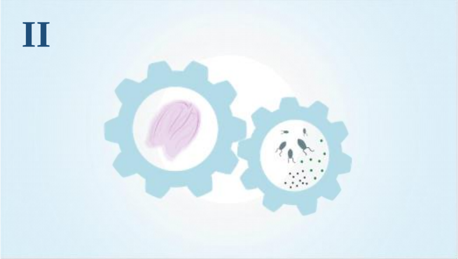
H2 Modeli geostrofičkih strujanja opisuju dinamiku širenja populacije *M. leidyi* u sjevernom Jadranu.

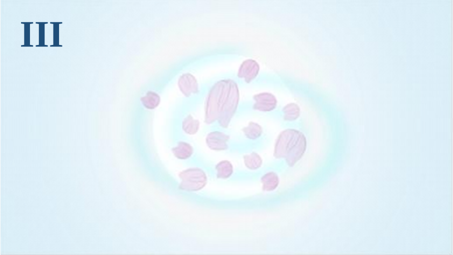
H3 Masovne nakupine *M. leidyi* mijenjaju kemijsku ravnotežu područja zahvaćenima invazijom i utječu na lokalnu mikrobnu zajednicu.

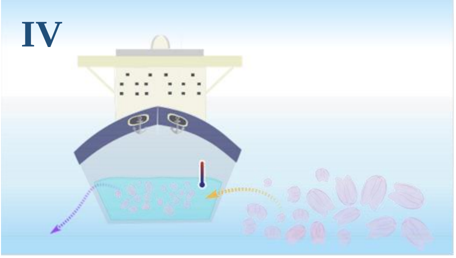
H4 Utjecaj invazije rebraša *M. leidyi* u sjevernom Jadranu se očituje na zooplankton i riblji fond.

H5 Obradom balastnih voda moguće je ograničiti širenje bioinvazije *M. leidyi*.

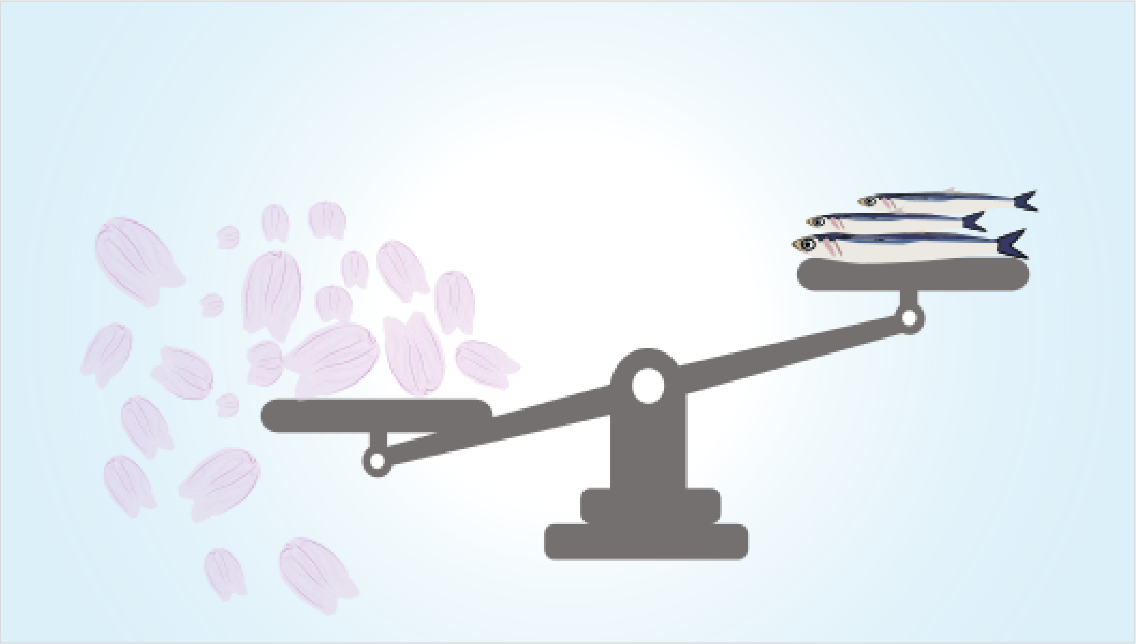
SAMOSTALNE ZNANSTVENE PUBLIKACIJE







I Publikacija



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Distribution, diet and relationships of the invasive ctenophore Mnemiopsis leidyi with anchovies and zooplankton, in the northeastern Adriatic Sea

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Contribution to the Special Issue: "MEDiterranean International Acoustic Survey (MEDIAS)"

Distribution, diet and relationships of the invasive ctenophore *Mnemiopsis leidyi* with anchovies and zooplankton, in the northeastern Adriatic Sea

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Abstract

Blooms of invasive ctenophore *Mnemiopsis leidyi* can have massive consequences on fish stocks and marine food webs. The distribution, abundance and diet of this ctenophore were investigated in the northeastern (NE) Adriatic between 2016 and 2019. The abundance of *M. leidyi* was determined daily along the coast of Rovinj (Croatia), and its spatial distribution monitored by visual census from research vessels and by pelagic trawl during acoustic surveys in September of each year. Mesozooplankton samples were collected along the western coast of Istria by vertical tows from the bottom to the surface. Spatial distribution and abundance of anchovy (*Engraulis encrasicolus*) assemblages were determined by geo-referenced hydro-acoustic sampling using a scientific echosounder. Large swarms of *M. leidyi* covering several km^2 were regularly reported between July and November extending up to 25 NM from the western coast of the Istrian peninsula and reaching maximum offshore densities of 270 individuals per m^2. The abundance of anchovy in the areas where *M. leidyi* was present evidently decreased. The content of *M. leidyi*'s digestive tract and plankton samples consisted both mainly of cladocerans, copepods, pteropods, echinodermata and bivalvia larvae. Results indicate that *M. leidyi* may accumulate and increase its abundance in the stagnant and trophically rich areas of the northern Adriatic gyres, spreading to the surrounding larger areas with currents. We assume that *M. leidyi* presence correlates with a decrease in anchovy population due to competition for food (zooplankton). Our findings support the importance of implementing an international monitoring program throughout the Adriatic Sea and demonstrate the ability of current MEDIAS surveys to detect changes in the pelagic ecosystem throughout surveyed areas.

Keywords: *Mnemiopsis leidyi*; Adriatic Sea; zooplankton; *Engraulis encrasicolus*; acoustic survey.

Introduction

Swarms of gelatinous organisms are not an unusual phenomenon in the Mediterranean (Boero, 2013). However, over the past few decades, new invasive species such as the ctenophore *Mnemiopsis leidyi* (sea walnut) have appeared in many Mediterranean basins, raising concerns about the ecological impact they may have on those systems (Shiganova *et al.,* 2019a, b). In the Adriatic Sea, *M. leidyi* made its first appearance in 2005 (Shiganova & Malej, 2009), but it failed to establish a stable population. However, the situation changed since 2016, when *M. leidyi* started appearing in large swarms every year from early summer until early winter (Malej *et al.,* 2017). In the northern Adriatic, it exhibited high fecundity and appeared in a wide range of sizes indicating favourable conditions, e.g., sufficient food to reproduce successfully, grow and agglomerate in significant numbers (Malej *et al.,* 2017).

M. leidyi is a very successful and adaptable species, which was able to survive a voyage by ballast waters in the '80s from its native habitats – the Gulf of Mexico and the eastern coast of the USA, to the other side of the Atlantic Ocean, specifically to the Black Sea (Vinogradov *et al.,* 1989). From the Black Sea, it has spread to other coastal areas (e.g., Mediterranean, Caspian and Azov

Seas) (Shiganova, 1997; Shiganova *et al.,* 2019a) showing a wide range of tolerance to different temperatures and salinities (Costello *et al.,* 2012). *M. leidyi* arrived in the Adriatic most likely through ballast waters since its appearance was not recorded in the southern part of the basin. Moreover, the molecular analysis of *M. leidyi* individuals isolated from the Adriatic, based on the Cytochrome Oxidase, indicated relation to the ones from the Black Sea (A. Baričević, pers. comm.).

The presence of this invasive organism in the Adriatic could represent a potential threat considering it is a fast reproducing, voracious carnivore that preys mainly on zooplankton (Monteleone & Duguay, 1988; Purcell *et al.,* 2001; Costello *et al.,* 2012) and has a limited number of predators (Grosholz, 2002; Marambio *et al.,* 2013). *M. leidyi* has already disrupted various food webs affecting valuable pelagic, coastal and estuarine ecosystems (Grosholz, 2002; Marambio *et al.,* 2013), especially in the Black Sea (Shiganova, 1997), the Sea of Azov (Studenikina *et al.,* 1991) and the Caspian Sea (Ivanov *et al.,* 2000). In those areas *Mnemiopsis* blooms contributed to the collapse of local fisheries, depleting the available stock of zooplankton consumed by commercial fish such as anchovy (*Engraulis encrasicolus*) additionally feeding on fish eggs and larvae (Kideys *et al.,* 2005).

Anchovy's spawning season in the Adriatic Sea (April-October) (Morello & Arneri, 2009) unfortunately coincides with the appearance of ctenophore blooms. In the Adriatic, anchovies represent one of the most relevant fish stocks, and their populations over time have been subjected to many stressors such as climate change-driven shifts in biotic factors and overfishing (Grbec *et al.,* 2002). Specific autumn and winter conditions were invoked in the explanation of Adriatic anchovy stock changes (Santojanni *et al.,* 2006; Kraus & Supić, 2011; Kraus *et al.,* 2015). Moreover, the northern Adriatic is considered a vital nursery and foraging area for anchovy and sardine (*Sardina pilchardus*), which together account for about 40% of the total marine catch in the basin (Morello & Arneri, 2009).

We hypothesize that the presence of *M. leidyi* in the NE Adriatic has affected the native ecosystem, in particular, the components that can be preyed on or outcompeted by it. The main objective of this study is to investigate the relation between the abundance and the distributions of *M. leidyi* and those of zooplankton and anchovy from 2016 to 2019 in the NE Adriatic Sea.

Materials and Methods

Study area

The study area (Fig. 1) is defined as the eastern part of the northern Adriatic Sea that consists of Croatian territorial waters and the Ecological and Fisheries Protection

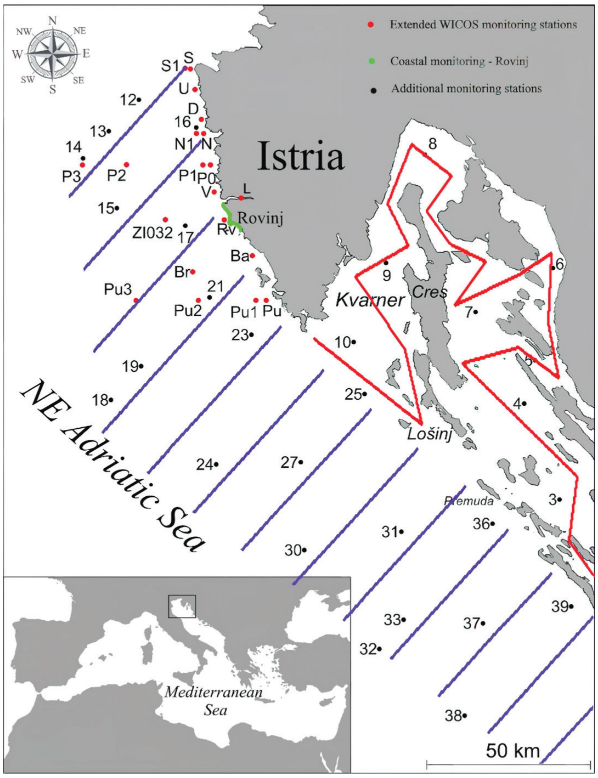

Fig. 1: The study area; red and black dots represent offshore monitoring locations, while in green stretch covers the location of the coastal monitoring; MEDIAS transects of acoustic sampling in September are marked by red lines for transects in the inner sea and blue lines for transects in the open Adriatic Sea.

Zone. Those areas have been monitored by acoustic surveys conducted in September each year (2015-2019) following MEDIAS working protocols (www.medias-project.eu). This part of the Adriatic extends to a bathymetry of approximately 80 m of depth to the south; and includes the western Istrian coastal waters and the Kvarner Bay.

Seawater temperature in the northern Adriatic shows pronounced seasonal cycles (Supić & Vilibić, 2006), fluctuating between around 10 °C (February) and 25 °C (July, August) while at the bottom temperature is around 10 °C (February) and 15 °C (in October).

The salinity seasonal cycle is highly pronounced in the surface layer only. The salinity of the lowermost layer is approximately 38 throughout the entire year, while the surface value changes depending on season and region, e.g., during winter, it is approximately 38; in the eastern part of the region, it is approximately 35; during June in the western part of the region, it is 32. The circulation in the northern Adriatic is part of the global Adriatic cyclonic gyre during the winter, while in spring, low-salinity waters start meandering toward the east. This anticyclonic meander reaches the Istrian coast in August and September (Krajcar, 2003). In general, the circulation is held to be "open" in the colder part of the year, allowing central Adriatic water to enter freely the northern Adriatic basin and "closed" in the warmer part of the year, implying that the northern Adriatic is separated from the rest of the basin with waters from the Po River spreading towards the east (e.g., Orlić *et al.,* 1992; Krajcar, 2003). However, there are winters in which waters from the Po River spread across the northern Adriatic (Supić *et al.,* 2012). The warm part of the year is generally characterised by the presence of gyres whose position and extent varies from year to year (Supić *et al.,* 2000, 2003; Orlić *et al.,* 2013; Djakovac *et al.,* 2013, 2015; Kuzmić *et al.,* 2007). An anticyclonic gyre, containing low salinity waters originating from the Po River, whose presence is indicated by the Istrian Coastal Countercurrent, frequently appears in the eastern part of the region, starting from early spring (or even earlier; the circumstances in which the gyre is formed were not yet investigated).

Mnemiopsis monitoring

Monitoring included the waters along the coast of Rovinj and a grid of 49 offshore stations along the western coast of Istria (large-scale monitoring) (Fig. 1).

The surveys were performed with the research vessels 'Vila Velebita', 'Burin', R/V 'BIOS DVA', and a private motorboat. The collected spatial distribution data were visualised using SURFER® 12 Golden Software.

In the coastal waters of Rovinj, the monitoring of *M. leidyi* was carried out from the summer of 2016 until the end of 2019 (Table 1). Ctenophora presence and abundance were surveyed daily along the coast (in a four-year period). Abundance was determined by visual census of individuals longer than 1 cm (the only observable *in situ* with a naked eye) and by scuba divers along transects parallel to the coast with the help of a cube frame of a known volume (cube dimensions: 1×1×1 m and 0.5×0.5×0.5 m) (Fig. S1) to facilitate the counting of the individuals. The average depth of the surveyed area along the coast was around 3 m. The coastal surveys were performed by determining the daily average number of ctenophores along 3 km of coastline.

The offshore monitoring was performed from the boat by visual census coupled with the WP2 plankton net which was towed (3 times) at the sea surface in stretches of 100 m for about 3 km and scuba divers. The densities of the individuals were counted per m^3 and expressed as the number of individuals per unit area (ind. m^{-2}) (Table S1, Supplementary Material).

The large-scale monitoring of the abundance and distribution of *M. leidyi* (49 stations), which covered a large portion of the northeastern (NE) Adriatic, was carried out only during September 2016, 2017, 2018 and 2019 respectively (Table 1). The stations along the western coast of Istria were disposed of two groups: the first one (20 stations) – the extended WICOS transect – included 14 stations (Pu, Pu1, Ba, Rv, V, P1, P$_0$, N, N1, D, U, S, S1, L) located at 1 NM and 2 NM from the coast and 6 stations (P2, P3, ZI032, Br, Pu2, Pu3) away from the coast (between 12 and 20 NM); the second group consisted of 29 additional stations covering the majority of the NE

Table 1. The spatial and temporal overview of sampling throughout the monitoring project, where environmental indices imply parameters describing hydrological conditions, and indicated locations correspond to those given in Figure 1.

Parameter		**Sampling period**	**Location**
M. leidyi	Abundance and distribution	September (2016-2019)	NE Adriatic (Extended WICOS and MEDIAS)
	Daily abundance	2016-2019	Rovinj coastal waters (3 km along the coast)
Zooplankton	Abundance and identification	August 2017-August 2018	WICOS and Rv station
Anchovy	Abundance and distribution	September (2015-2019)	NE Adriatic (MEDIAS)
Environmental indices	Temperature, salinity and density	September (2016-2019)	North Adriatic
	Seasonal temperature and seasonal salinity	2016-2019	Rv station

Adriatic (Fig. 1). *M. leidyi* presence and abundance were determined by visual census of individuals longer than 1 cm from the boat and by scuba divers.

The distribution of *M. leidyi* was plotted on the basis of the data collected on various days in September (1, 2, 6, 8, 28 and 29 in 2016; 4, 5, 6, 7, 13 and 21 in 2017; 10, 17, 21 and 29 in 2018, 7, 8, 9, 26, 27, 28 and 29 in 2019). Thus, the discrepancy in time intervals of sampling should be considered when analysing the data in regard to average means of current fields.

Hydrological parameters

Temperature and salinity were measured seasonally during the period 2016-2019 with multiparametric CTD (Sea Conductivity, Temperature, Depth) probe (SeaBird Electronic SBE 25) and an automated buoy system at the station Rv at 1 NM west of Rovinj (Fig. 1). The data were graphically displayed.

The atmosphere-ocean modelling system

The distribution of temperature, salinity and density in the northernmost part of the Adriatic was investigated in September of 2016, 2017, 2018 and 2019. Monthly fields of vertically averaged temperature, salinity and currents were obtained by the Regional Ocean Modelling System (ROMS) that was implemented over the Adriatic Sea at the spatial resolution of 2 km. Meteorological forcing was obtained from Weather Research and Forecasting (WRF) model run over the area at 8 km spatial resolution. Open boundary conditions at the Otranto strait were provided by the operational Adriatic REGional model (AREG) within the Adriatic Forecasting System (AFS). The climatological values for the Adriatic river run-offs were used. More details on the atmosphere-ocean modelling system can be found in Mihanović *et al.* (2018).

Zooplankton

Mesozooplankton was sampled monthly from August 2017 to August 2018 at the Rv station. At the other WICOS stations, sampling was carried out in August, September and October of 2017, and March, May and July of 2018 (Fig. 1, Table 1).

Samples were collected vertically from bottom to surface by WP2 plankton nets and preserved in 4% formaldehyde for microscopic inspection. Subsequently, the taxonomic level identification analysis was performed in a laboratory on a stereomicroscope with an 80x magnification. The results are shown as the number of individuals per cubic meter (ind. m^{-3}).

Mnemiopsis leidyi's ***diet***

Samples for *M. leidyi*'s diet analysis were taken during 2017: in August, September and October at Rv station, and in September at stations Pu and P_0. In total, 155 individuals were examined. *M. leidyi* individuals were collected by a soft mesh landing net at a depth of 0-0.5 m and immediately placed with care in glass beakers with filtered seawater (0.22 µm pore size). Individuals were then exposed for 5 min to a range of stressful conditions such as vortexing the surrounding water and prodding them with tweezers to stimulate the excretion of their stomach contents, all performed in laboratory conditions. The expelled filamentous dark substance was collected with a pipette, transferred to a falcon tube (50 mL), and preserved by adding neutralized formaldehyde to a final concentration of 2%. Finally, samples were stored at 4 °C until further analysis of the diet composition by a stereomicroscope.

Based on the numbers of prey noted in September 2017 at the stations Rv, Pu and P_0 after analyses of 95 individuals, the Similarity Percentage (SIMPER) method was used to determine which taxa contribute to the similarity of prey. For the above-mentioned multivariate analyses, the statistical package PRIMER v6 was used.

Anchovy abundance and distribution

Spatial distribution and abundance of anchovy assemblages within the study area have been determined by geo-referenced hydro-acoustic sampling (Dadić *et al.,* 2008) performed with the scientific echosounder SIMRAD EK60 operating at 38 kHz and using a split-beam transducer with 7° beam angle. The acoustic sampling equipment was installed on R/V 'BIOS DVA', and acoustic data were collected during the annual acoustic survey MEDIAS in September from 2015 to 2019 (Table 1), following common MEDIAS working protocol (MEDIAS, 2015). Nautical Area Scattering Coefficient (NASC, m^2/NM^2) data related to anchovy have been used as direct unbiased estimates of anchovy abundance. In addition to hydro-acoustic sampling performed by the echosounder SIMRAD EK60, a mid-water trawl with otter boards and small mesh size in the cod-end have been used in order to obtain information on assemblages of various pelagic organisms and characteristics (i.e. size) of different acoustic targets identified by hydro-acoustic sampling. Mid-water trawl samples were collected at trawling speed of 4 knots, with trawling duration of 30 min (i.e. along sampling trails of 2 NM).

Results

Mnemiopsis leidyi ***abundance along the coast of Rovinj and the relation to thermohaline conditions at the Rv station (2016-2019)***

Daily average *M. leidyi* abundances along the coast of Rovinj are given in Figure 2, while the monthly averages are given in Figure S2 (Supplementary Material).

M. leidyi was recorded and identified for the first

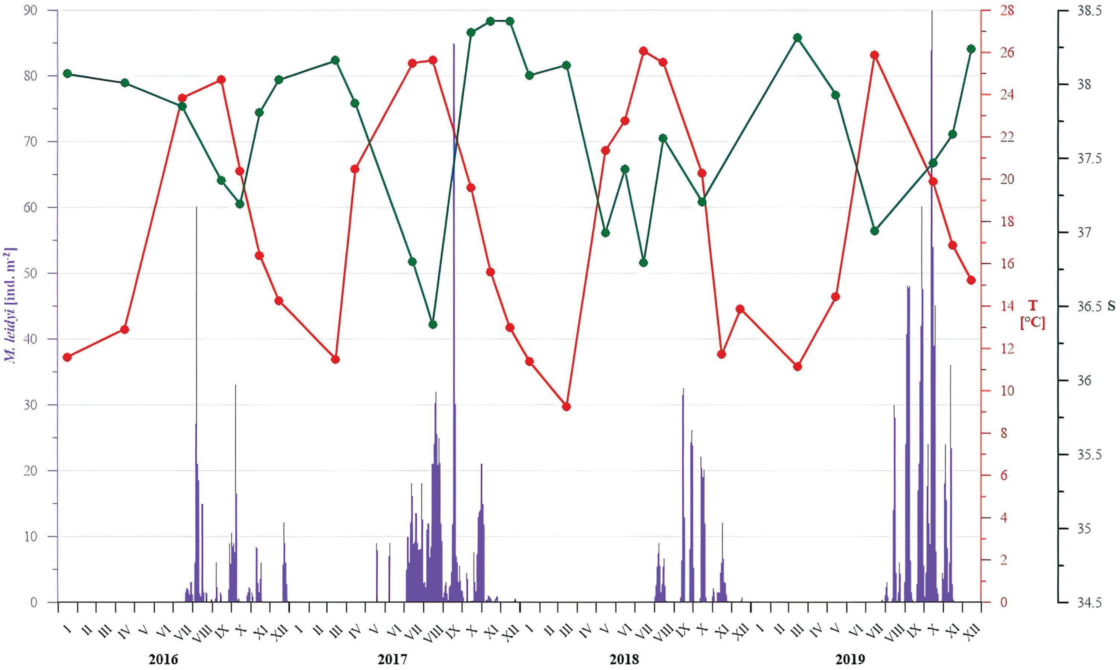

Fig. 2: Daily average abundance of *M. leidyi* (ind. m^{-2}) along the coast of Rovinj in the period from the summer of 2016 until the end of 2019 regarding the monthly sea surface temperatures (T) and salinities (S) at Rv station in the same period.

time along the coast of Rovinj at the end of July 2016 in moderate amounts (~1.5 ind. m^{-2}) (Fig.2). In the first half of August 2016, *M. leidyi* proliferated, reaching the highest average daily abundance of that year 60±45 ind. m^{-2}. This was also the month with the highest average abundance of *M. leidyi* in 2016 (5±12 ind. m^{-2}) (Fig. S2). Higher daily averages were registered again in the first half of October, reaching 33±30.9 ind. m^{-2}. After that, two minor swarming events were recorded, at the beginning of November, reaching 8.4±7.8 ind. m^{-2}, and at the end of December with 12±7.5 ind. m^{-2}.

M. leidyi was not present in the waters of Rovinj in the first three months of 2017. From the end of March until the beginning of July, records were infrequent. In contrast, from July to October 2017, individuals were present in considerable numbers almost continuously. Three distinct episodes with a significant increase in average daily abundances can be identified in Figure 2, i.e., mid-July (18±8.4 ind. m^{-2}), mid/end August (32.1±12 ind. m^{-2}), and mid/end September (84.9±60.6 ind. m^{-2}). The highest average monthly abundance in 2017 was measured in July (6.8±5.4 ind. m^{-2}) (Fig. S2). In August and September 2017, some parts of swarms confined within bays and harbours counted almost 900 ind. m^{-2} (Center for Marine Research database). During autumn, abundances were similar to those measured in July, but later, in December, records were scarce (Fig. 2).

In 2018, *M. leidyi* first appeared at the beginning of August (maximum daily average abundance 9±3 ind. m^{-2}), abundances remained low until the middle of September. Only a few episodes of relatively high daily average abundances were registered that year, i.e., 32.4±27.6 ind. m^{-2} and 26.1±22.5 ind. m^{-2} in September, 21.9±11.4 ind. m^{-2} in October and 12±4.3 ind. m^{-2} in November. Throughout December, abundances ranged between $3\cdot10^{-3}$ ind. m^{-2} and 0.6 ind. m^{-2} (Fig. 2).

In 2019, *M. leidyi* was first recorded at the end of July. In August, *M. leidyi* reached the maximum abundance of 30±25.8 ind. m^{-2}. In September and October, abundances increased, reaching the highest peak of the year in October (90±75.9 ind. m^{-2}) (Fig. 2). In the enclosed parts of bays and harbours, *M. leidyi* displayed the absolute highest abundances for the entire monitoring period (exceeding 1200 ind. m^{-2}) (Center for Marine Research database). In mid-November, the average daily abundance of *M. leidyi* reached up to 24±20.7 ind. m^{-2}, while in December, only a few individuals were detected (Fig. 2).

The data gathered over four years revealed that *M. leidyi* was present for the longest amount of time in 2017, counting 141 days in total. Populations were observed for a total of 79 days in 2016, 115 days in 2018, and 109 days in 2019. During 2018, the average daily abundances exhibited by *M. leidyi* were lower than those in other years (Fig. 2). The average monthly abundances in 2016 and 2018 never exceeded 6 ind. m^{-2}, while in 2017 and 2019 the values recorded were more than double (Fig. S2).

The oceanographic data gathered at the Rv station (1 NM west from Rovinj) allowed for a comparison of abundances of *M. leidyi* found in the coastal waters around Rovinj against sea surface temperature and salinity as shown in Figure 2. The sea temperatures follow seasonal changes which correlate with the air temperatures; whereas, salinity of the NE Adriatic is higher in the winter and generally lower in the summer/autumn due to the Po River inputs and the prevailing currents.

In July 2016, when *M. leidyi* first appeared, sea surface temperatures were above 23 °C, and surface salinities began to decline seasonally from 37.9 in July to a minimum (37.2) in October. The average monthly abundance of *M. leidyi* was the highest in August (5±12 ind. m^{-2}) when temperatures were above 24 °C (Figs. 2 & S2). In the months following, the average abundances declined until December while the sea surface temperatures were below 15 °C and salinities rose back to 38.

In 2017 salinity was relatively high in March (38.1), then decreasing in April (37.9) and May when the temperature was around 20 °C. The highest average monthly abundances that year were recorded in August and coincided with the warmest sea surface temperature (25.5 °C) and the lowest salinity (36.4) (Fig. 2). *M. leidyi* completely disappeared in December when the sea had cooled to 14.3 °C (Fig. 2).

In 2018, salinity was high in March (38.1) and decreased towards the summer. *M. leidyi* appeared later that year (in August) when the sea surface temperature was above 25 °C. The maximum monthly average was recorded in September when salinity was around 37.3, and temperatures had already descended to 20 °C (Figs. 2 & S2). In November and December, temperatures oscillated between 11 and 14 °C and *M. leidyi* was not recorded.

In March 2019, salinity was 38.3 and decreased to a minimum of 37.1 in July. The sea surface warmed somewhat later, reaching the maximum in July (25.8 °C) when *M. leidyi* was first detected. Even higher monthly averages were recorded in September and October when the sea temperatures were ~20 °C, and salinity increased to 37.5. In November, temperatures were relatively high (16.9 °C), salinity continued to increase (37.7), and *M. leidyi* remained relatively abundant (3.2±10.7 ind. m^{-2}) (Figs. 2 & S2). In December, when salinity reached 38.2 and the temperature was 15.2 °C, *M. leidyi* were not found (Fig. 2).

Abundance and distribution of **Mnemiopsis leidyi** *in September (2016-2019) in the NE Adriatic*

Data presented from daily observations of the coastal waters of Rovinj and the monthly monitoring of the NE Adriatic during 2016-2019 (Center for Marine Research, Rovinj) showed that abundance of *M. leidyi* reached the peak of its expansion from the end of August until the end of October consecutively. In September 2016, *M. leidyi* was detected in a large area extending from the coast of the Istrian peninsula towards the west (Fig. 3A). The bloom was characterised by an almost continuous presence of *M. leidyi* with an average abundance of 0.3±0.8 ind. m^{-2}. Individuals were almost completely concentrated around the sea surface. The highest abundances were detected in the vicinity of the Istrian coast (P_0 and P1, 2-4 ind. m^{-2}). In the western Kvarner Bay, only a few individuals were found.

Extending in a wide stripe from west to south of Istria, *M. leidyi* blooms reached their widest spatial extension in 2017 (Fig. 3B) with an average number of individuals (14.5± 45.8 ind. m^{-2}) which were considerably higher (~50 times) than the previous year. In 2017, numerous *M. leidyi* were registered all the way to the thermocline (15 m) at Rv, P_0, and ZI032, with high abundances (99, 133 and 225 ind. m^{-2}, respectively). The area occupied by *M. leidyi* from the south to the east was considerably larger than previously seen, reaching the western coasts of the Kvarner islands for the first time.

In the 3rd year of *M. leidyi* invasion (2018), the bloom occupied a smaller area along the western Istrian coast compared to those measured in 2017 (Fig. 3C). *M. leidyi* was once again present only significantly in surface waters, and their average abundance (0.8±1.3 ind. m^{-2}) was a bit higher (2.6 times) than in 2016 but still much lower (~18 times) than the average in 2017. The highest concentrations were detected closer to the coast, with the maximum at Rv (~6 ind. m^{-2}) and N (~3 ind. m^{-2}). In 2018 no *individuals* were observed in Kvarner Bay.

During September 2019, we recorded the maximum average swarm abundance (27.7±65.8 ind. m^{-2}). *M. leidyi* was concentrated in the south-western Istrian waters with maxima at Pu, Pu1, Ba, Rv, and 23 (270, 195, 90, 105 and 90 ind. m^{-2} respectively) (Fig. 3D), where *M. leidyi was homogeneously distributed up to 15 m of depth. At greater depths, no individuals were recorded.* Along the eastern Istrian coast and the Kvarner Bay, no individuals were detected. However, a few individuals were recorded at 31 and 36, i.e. around the islands Premuda and Škarda, where *M. leidyi* had never been reported before (Fig. 3).

Numerical hydrodynamic model

The distribution of temperature, salinity and density indicates that the northernmost part of the Adriatic was affected by warmer, less salty and lower water density of the Po River origin (Figs. 4 & S3) in all the four investigated periods (September of 2016, 2017, 2018 and 2019). Circulation, represented by monthly means of vertically averaged currents, developed in gyres of various extent. An anticyclonic gyre containing Po affected waters of lower salinity was observed in all four years. The gyre was located north to the section Po delta-Rovinj in 2016, across the same line in 2017, south to it in 2018 and between lines Po delta-Rovinj and Pesaro-tip of Istria in 2019. In 2016, 2017, and 2018 salinity in the gyre region was below 38.1 and in 2019, over that value. In 2019 salinity of northern Adriatic was affected by very high salinity waters from the south, as indicated by the position of the 38.5 isolines, found to be more north than in other investigated years, stretching across the Pesaro-tip-of Istria line. Mixing of these very high salinity waters with freshened Po waters resulted in the water of higher salinity than in other investigated years. Model representation of high salinity values in 2019 is supported by observations performed in 2019 near the tip of Istria (38.5 in summer and 38.9 in autumn; N. Supić, pers. comm.). According to transversal currents along the Pesaro-tip-of- Istria line, which was pronounced in 2016, 2018 and

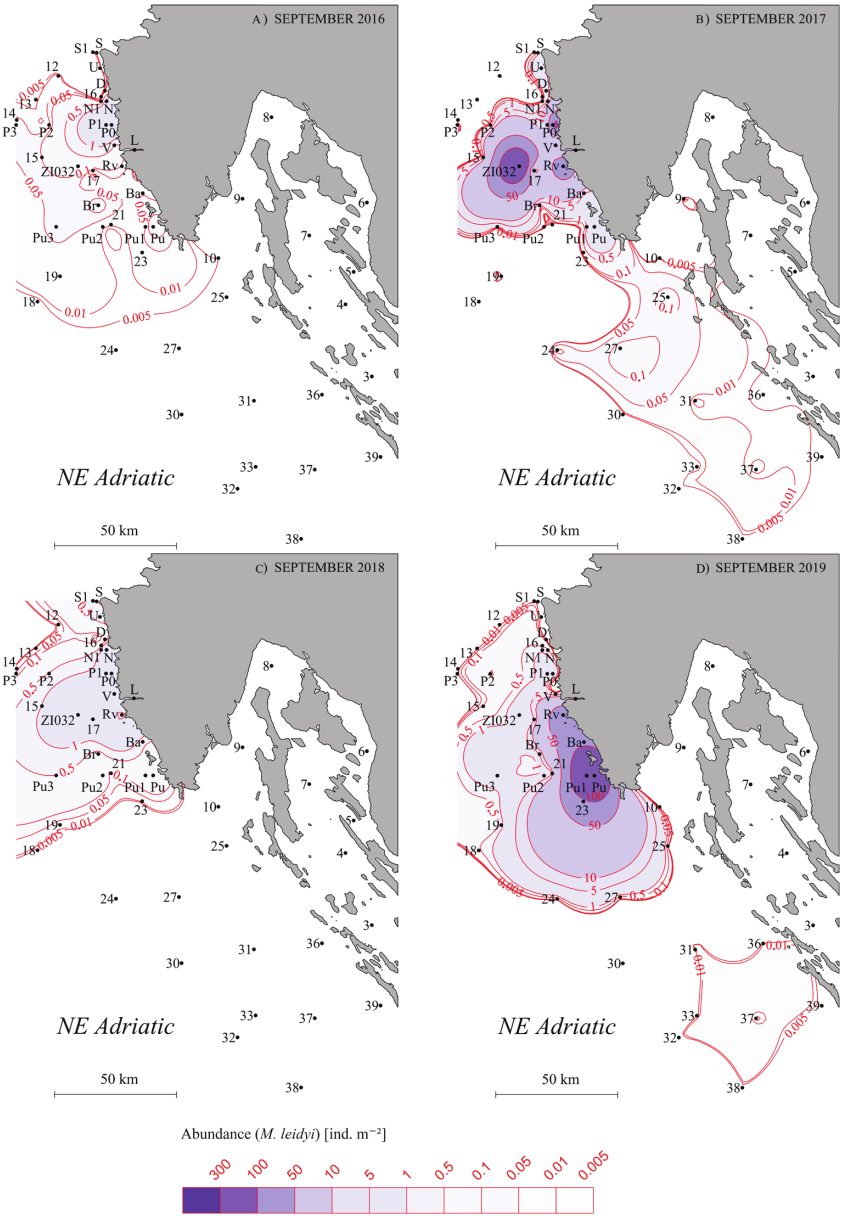

Fig. 3: Distribution and abundance of *M. leidyi* (ind. m^{-2}) in the NE Adriatic in Septembers 2016 (A), 2017 (B), 2018 (C) and 2019 (D); labels of stations are in black, while red numbers and lines refer to isolines of abundances.

2019, and not in 2017, the northern Adriatic was in these three years more isolated from the rest of the Adriatic than in 2017.

Mnemiopsis leidyi's *gut contents*

Food was found in 95 of the 155 ctenophores analysed. The amount of prey that was found in the digestive tract was relatively small, averaging between 1.2 and 2.5 zooplankton individuals per ctenophore. A total of 39 zooplankton taxa ranging from protists to fish eggs have been found in the digestive tract of *M. leidyi* (Table 2).

Annual distribution of zooplankton abundances at Rv station (Fig. S4) and along the west coast of Istria (Fig. S5) are given in the Supplementary Material.

At the Rv station, dominant prey taxa were bivalvia larvae, copepod *Temora stylifera* and cladocera *Penilia avirostris*. High contributions were annotated for calanoid copepodites, copepods (*Oithona plumifera* and *Clausocalanus furcatus*), and pteropods (*Limacina trochiformis* and *Creseis clava*), too.

At the Pu station, cladocerans, copepods, pteropods, and bivalvia larvae made up the majority of the prey. The

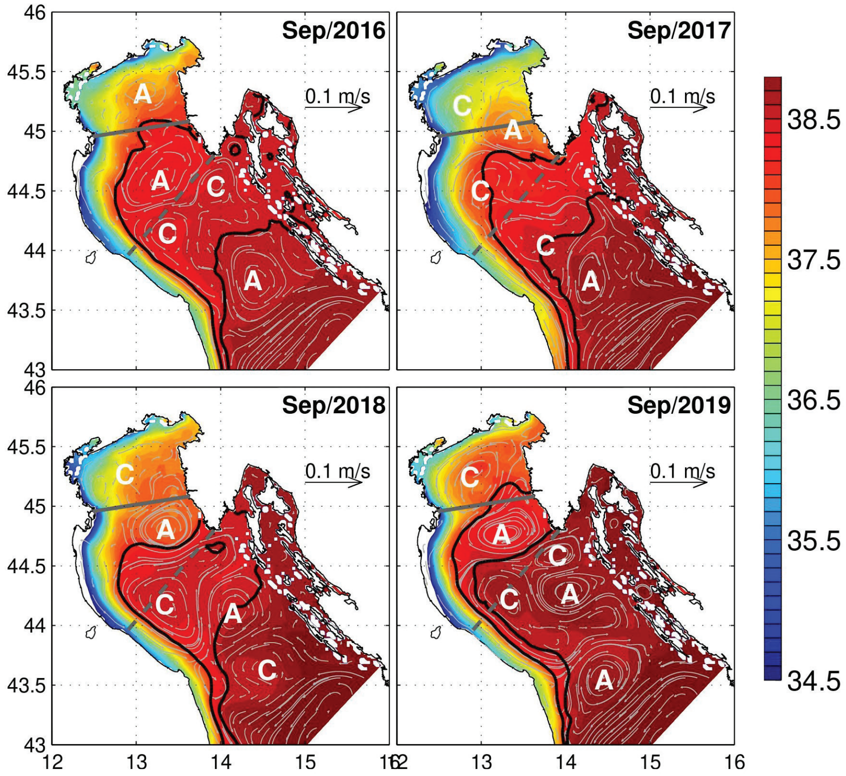

Fig. 4: Vertically averaged fields of salinity and currents in September 2016-2019, obtained by the numerical hydrodynamical model. The solid line is drawn between the Po River delta and Rovinj and dashed line between Pesaro (Italy) and the tip of Istria (Cape Kamenjak). Cyclonic gyres are marked with 'C' and anticyclonic with 'A'.

most dominant prey was the cladocera *Penilia avirostris*, followed by the copepod *Temora stylifera*. Additionally, the high contributions of other taxa included both *Evadne spinifera* and *Creseis virgula*. At the P_0 station, the dominant prey was the pteropod *Creseis clava* and bivalvia larvae.

A comparison in terms of percentages between prey specimens and abundances of zooplankton from net samples revealed noticeable differences (Table 2). Specifically, abundances of small copepods *Paracalanus parvus parvus* and *Oncaea* spp. were higher in net samples than in ctenophores gut contents. On the other hand, large copepods such as *Temora stylifera*, *Oithona plumifera* and *Clausocalanus furcatus* were dominant in the ctenophores' guts. This fact is especially relevant for pteropods which can reach a relatively large size of up to 4 mm. Moreover, prey analysis indicated that bivalve larvae prevailed in the gut contents but not in net samples. However, a similar relation was found for copepodites and cladocerans (*Evadne spinifera* and *Pseudevadne tergestina*). Based on SIMPER analysis of all zooplankton data obtained for September 2017 (n=95), ten taxa accounted for about 90% of *M. leidyi*'s prey (Table 3). Except for cladocerans, the majority of the other taxa were found to be more abundant in the gut contents rather than in net samples.

Distribution and abundance of anchovy from 2015-2019

Geo-referenced and log-transformed NASC data (Log values ranged 0-4) used as an unbiased proxy for abundance data, as shown in Figure 5 showed different patterns of anchovy distribution and abundance within the study area from 2015 to 2019.

Anchovy abundance data, collected during September 2015 acoustic survey, depicted a population whose spatial distribution showed a typical patchy pattern and occupied all parts of the study area (Fig. 5A). The following year (2016), acoustic recordings showed the absence of anchovy in the proximity of the western Istrian coast, which suggests no or very limited abundance of fish (Fig. 5B). Anchovy population in the rest of the studied area showed a patchy distribution with good coverage. A drastic change in its spatial distribution was noticed in data collected during September 2017. That year, anchovies were almost entirely absent from a large portion of the studied area (Fig. 5C). Anchovies were mostly present in the area furthest from the Istrian coast, along the mid-line, in the inner waters and further south. Data collected in September 2018 indicated a similar situation to that of 2017. Anchovy schools were again scarce in a large portion of the studied area (Fig. 5D), while the anchovies recorded alongside the mid-line of the Adriatic Sea in

Table 2. A comparison of zooplankton taxa (%) observed in *M. leidyi*'s gut contents and in net samples collected at the same time at the Rv (65 ctenophore analysed of which 27 with food), Pu (45 ctenophore analysed of which 15 with food) and P_0 (45 ctenophore analysed of which 18 with food) in September 2017. The prey is represented by the average values of the individuals found as a gut content of analysed specimens, while the "sample" as the average value of zooplankton for the water column, while '+' indicates the presence of a particular zooplankton when its share was under 1%.

	Rv prey	Rv sample	Pu prey	Pu sample	P_0 prey	P_0 sample
Prostista						
Tintinnina					1	
Foraminifera			+			
Radiolaria			1			
Hydrozoa						
Podocorynoides minima			+			
Clytia spp.			1		1	
Solmaris spp.			+			+
Muggiaea atlantica	+	+				
Ctenophora						
Cydipid larvae			+	+	+	
Cladocera						
Penilia avirostris	15	47	44	75	6	37
Evadne spinifera		4	8	2	6	+
Pseudevadne tergestina	5	2	3	2	7	1
Copepoda						
Nauplii			1	+	1	+
Copepodites	7	8	7	2	10	7
Calanus helgolandicus	+	+	+		1	+
Nannocalanus minor					+	
Paracalanus parvus	5	13	1	7	1	3
Clausocalanus arcuicornis			+	+	1	3
Clausocalanus furcatus	6	3	1	+	2	2
Pseudocalanus elongatus			1	+	1	1
Centopages kröyeri	1	+	+	+		
Temora stylifera	15	4	11	1	9	6
Acartia (Acartiura) clausi	3	+		+	+	
Oithona nana				+	1	
Oithona plumifera	7	2	1	1	1	1
Euterpina acutifrons			+	+		
Oncaeidae			1	3	4	8
Corycaeidae			1	+	+	
Pteropoda						
Limacina trochiformis	5	1				
Creseis clava	5	+	2		17	1
Creseis virgula			8	1	2	3
Appendicularia						
Oikopleura (Coecaria) longicauda	4	7	+	1	3	7
Oikopleura (Coecaria) fusiformis		+	+	2		
Chaetognatha						
Sagitta inflata			+	+		
Chaetognatha juv.		5	1	1		3
Other larvae						
Bivalvia larvae	21	+	4	1	22	16
Gastropoda larvae		+	+	+	+	
Polychaeta larvae	+	+	+	+		+
Decapoda larvae	+	1	+	+	1	+
Ophiopluteus larvae		2	2	+	1	
Fish eggs		+			+	

Table 3. Similarity of percentages (SIMPER, n=95) analysis shows species that account for the most similarity of *M. leidyi* prey between individuals collected along Istria coast during September 2017 (stations Rv, Pu and P_0).

Average similarity: 50.21	*Average abundance*	*Average similarity*	*Sim/SD*	*Share (%)*	*Cumulative (%)*
Penilia avirostris	19.89	10.01	0.86	25.01	48.58
Temora stylifera	6.72	6.12	1.43	15.31	40.32
Bivalvia larvae	6.39	5.16	0.98	12.90	53.22
Calanoida copepodites	5.06	4.90	1.40	12.25	65.47
Creseis clava	4.06	2.93	0.68	7.33	72.80
Pseudevadne tergestina	3.28	2.45	1.06	6.11	78.91
Evadne spinifera	4.06	1.96	0.87	4.90	83.18
Oikopleura (Coecaria) longicauda	1.17	0.95	0.72	2.38	86.18
Oncaeidae	1.61	0.94	0.66	2.36	88.54

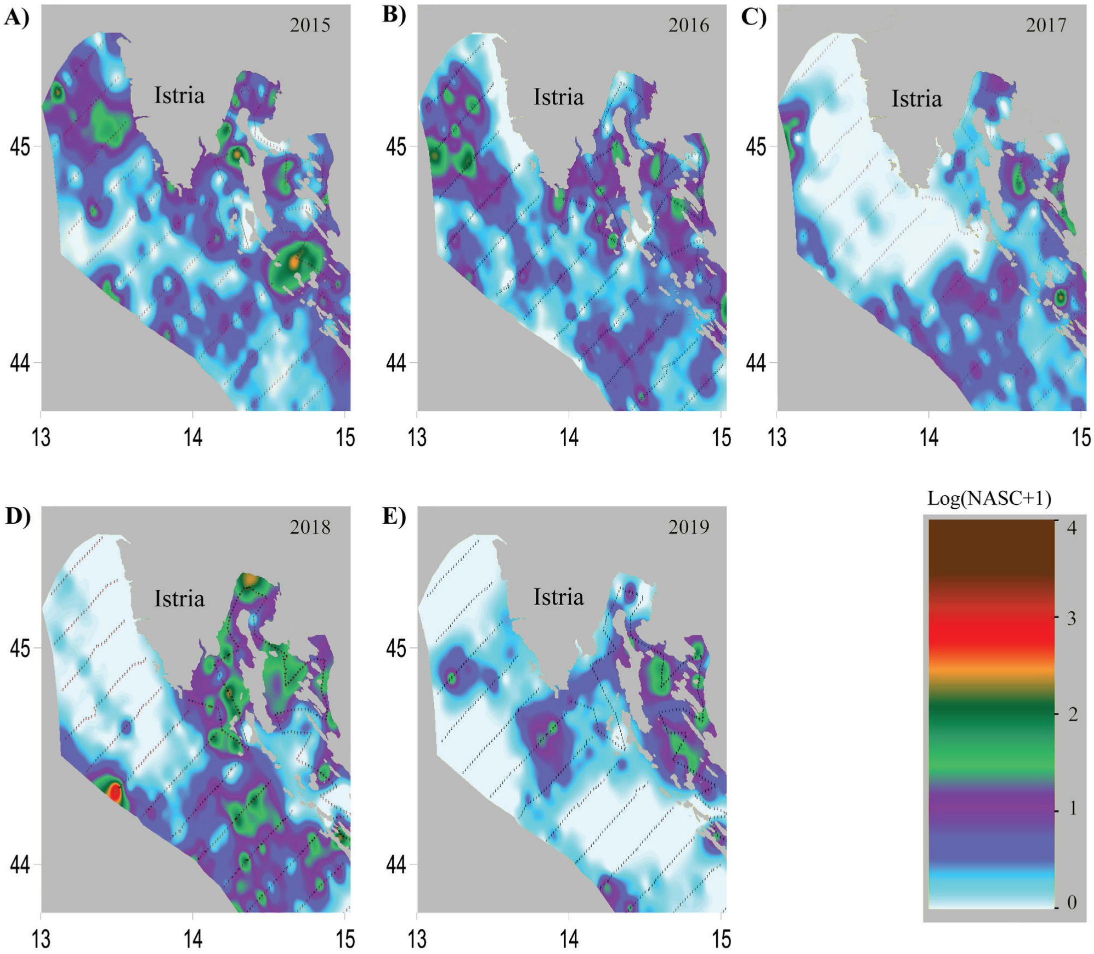

Fig. 5: Distribution and abundance of anchovy (*E. encrasicolus*) within the area covered by the acoustic survey in the NE Adriatic Sea in Septembers of following years: A) 2015, B) 2016, C) 2017, D) 2018 and E) 2019.

2018 were registered further south. The density of the anchovy in the inner waters, as well as the southern part of the studied area, was noticeably higher than the previous year. The most recent acoustic survey data collected in September 2019 showed a similar situation as in the period 2017-2018, indicating a low abundance of anchovy in the area close to western Istria shore. Some anchovy's schools were recorded in the open waters, distributed in several patches scattered throughout the northern Adriatic (Fig. 5E). The most northern part of the study area, zone along the mid-line, as well as areas further south, also showed very low anchovy abundance.

Discussion

Even though *M. leidyi* was first spotted in the northern Adriatic (Gulf of Trieste) in 2005 (Shiganova & Malej, 2009), no individuals were observed in the following decade until 2016. The introduction of *M. leidyi* into the northern Adriatic most probably occurred by ballast waters, because in the southern and middle part the basin, this species has not been observed, except for the narrower part of the port of Ploče (south-eastern Adriatic) where individuals were found in September 2017 (D. Lučić, pers. comm.) and along the Apulian Coast (south-western Adriatic) where it was reported in 2019 (Dragičević *et al.,* 2019). Temporal trends collected over the four-year-long monitoring (2016-2019) showed that in the NE Adriatic *M. leidyi* tends to appear in higher numbers during summer and autumn. Conversely, in winter and spring, there were only scarce sightings of individuals or even no records at all. In the southern part of European waters, *M. leidyi* was found in a wide range of temperatures (3-30 °C) (Shiganova *et al.,* 2019a, b), while in the northern Adriatic, this species was observed in offshore, coastal, and lagoon systems at temperature ranging from 13 °C to 29 °C and salinity from 11 and 38 (Malej *et al.,* 2017). In the NE Adriatic (2016-2019), *M. leidyi* was present in the temperature range from 14.3-25.9 °C, while the highest abundances were detected at temperatures above 19 °C. This fits within the range of favourable temperatures for *M. leidyi*'s reproduction and population growth (12-27 °C), as previously reported (Shiganova *et al.,* 2019b). In 2017 when there was a warmer spring, ctenophores appeared earlier, while in 2019, when the spring was colder and the autumn warmer, the presence and the peak abundances were shifted to later in the year. The salinity range in which *M. leidyi* can successfully grow and reproduce is rather broad, ranging from 6 to 40 (Shiganova *et al.,* 2019b). In that regard, salinities found in the NE Adriatic are within that range and show minor seasonal oscillations. Our results are consistent with existing knowledge of the Mediterranean Sea, where *M. leidyi* abundance may be limited by low temperatures (Shiganova *et al.,* 2019b), while low salinity may be a limiting factor in the North Sea and the Baltic (Jaspers *et al.,* 2011).

The spatial distribution of *M. leidyi* during their maximum expansion in September (2016-2019) indicated that they were present on a large spatial scale. The area included mainly western Istrian coastal waters, from the shore to 25 NM offshore. Previously, large masses of *M. leidyi* have occurred in ecosystems that underwent extensive modifications due to overfishing and excess nutrient loading (Bodini et al., 2018). According to Shiganova et al. (2019a, b), global warming and other environmental disturbances in the marine environment facilitate the establishment of large *M. leidyi* populations. For example, large masses of Aurelia sp. disrupted relationships in the food web in the Black Sea and facilitated later the development of stable comb jelly populations (Shiganova et al., 2019a). The northern Adriatic, as a commercially important basin with a strong fishing effort (Bastardie et al., 2017) and intensive maritime traffic (Zupančič et al., 2015), in recent decades experienced ecological crises such as eutrophication (Degobbis et al., 2000; Giani et al., 2012; Marić et al., 2012) and a frequent mass occurrence of jellyfish (Kogovšek et al., 2010).

Both the maximum and the monthly average in the coastal waters of Rovinj (15.9±19.2 ind. m^{-2}) and the spatial average in the NE Adriatic in September (2016-2019) (10.8±13 ind. m^{-2}) were moderately higher than the values measured throughout four-years of monitoring in the NW Baltic (mean monthly values ranging from 0-4.3 ind. m^{-2} and maxima, generally oscillating between 10 and 20 ind. m^{-2}) (Schaber *et al.,* 2011). The lower averages of *M. leidyi* in the NE Adriatic during 2016 and 2018 were relatively close to those measured in the Dardanelli straight in September of 1998 (2.5 ind. m^{-2}) and the NE Aegean in June (1998) (1.5-2.5 ind. m^{-2}) (Shiganova *et al.,* 2001) while the higher ones (2017 and 2019) were comparable to the data registered in 1990 in the Saronikos Gulf in the W Aegean (45-75 ind. m^{-2}) (Shiganova *et al.,* 2001) and in a high-density patch (5-100 ind. m^{-2}) in the coastal waters of Denia (Israel) in July 2009 (Fuentes *et al.,* 2010). The distribution of *M. leidyi* in the NE Adriatic was not homogeneous and was characterised by high-density patches that could surpass even 100 ind. m^{-2}, mainly located between 1 and 10 NM off the western and southern coast of Istria. This increased abundance of *M. leidyi* in coastal waters was probably associated with favourably higher nutrient concentrations, greater density of phytoplankton, chlorophyll *a* concentration, and lastly, a greater zooplankton availability in accordance with previous observations in the Black Sea (Kamburska *et al.,* 2006; Shiganova *et al.,* 2019b).

High-density *M. leidyi* agglomerates in coastal areas were surrounded by large low-density areas where the abundances were comparable to the ones registered in oligotrophic seas such as the NW Mediterranean (Offshore Ligurian, Tirrenian and Sardinian waters) where scattered individuals were detected during the summer (Boero *et al.,* 2009; Diciotti *et al.,* 2016).

Furthermore, unlike in the Baltic Sea where *M. leidyi* appeared up to 60 m depth (Schaber *et al.,* 2011), in the NE Adriatic, this ctenophore was concentrated mainly along the sea surface with only a few findings during seasonal maxima, when it reached the thermocline at about 15 m of depth. Our findings are more in line with those published by Costello & Mianzan (2003) that have reported large clusters within a meter from the sea surface. Nonetheless, it has been reported that dense agglomerates of ctenophores can move through the water column from the top, just 0.5 m above the seafloor in shallow waters (<5 m depth) to depths of 70 m, within a single day (Costello & Mianzan, 2003).

The average *M. leidyi* densities in the NE Adriatic were much lower than the ones measured in the shelf area of the NE Black Sea, ranging from 4-11 ind. m^{-3}, or. 120-330 ind. m^{-2} respectively (given the average depth of 30 m), and those measured offshore in the Black Sea of 5-13 ind. m^{-3}, i.e., 150-390 ind. m^{-2} (Kamburska *et al.,* 2006). Only the highest peak abundances reported in the NE Adriatic were comparable to the NE shelf and offshore Black Sea averages.

The differences were even more pronounced between the NE Adriatic and the eutrophic shelf waters of the NW and W Black Sea (average abundances about 62 and 55 ind. m^{-3}, or about 1860 and 1650 ind. m^{-2} respectively) (Kamburska *et al.,* 2006). Similar results were also reported for the Caspian Sea, where the average abundances of *M. leidyi* were about 63 ind. m^{-3} (~1260 ind. m^{-2}), concentrated mostly in the top 20 m from the sea surface (Rostamian *et al.,* 2012).

However, some of the highest *M. leidyi* abundances reported indicating that the upper abundances in a system might reach up to 10^{4} ind. m^{-2} surpassing the highest NE Adriatic abundances by two orders of magnitude. Such values were reported in 2001, in the central and N Caspian Sea in August and October (9103±5690 ind. m^{-2} and 5375±2145 ind. m^{-2}) (Shiganova *et al.,* 2004a) and during the most significant Black Sea outburst in the October of 1989 (~8000 ind. m^{-2}) (Shiganova, 1998).

Also, in the areas of the Black Sea where the natural predator of *M. leidyi* – *Beroe ovata* was present, the abundances (59.5±50 ind. m^{-2} inshore and 197±170 ind. m^{-2} offshore) (Shiganova *et al.,* 2004b) were well above the values found in the NE Adriatic. From the comparison with the most *M. leidyi*-impacted basins (Black and Caspian Sea), it emerges that the presence of this invasive Ctenophora in the NE Adriatic is still smaller by one-two orders of magnitude but perhaps not yet reached its full potential. In the Black Sea, *M. leidyi* was first observed at the beginning of the 1980s (Vinogradov & Tumantseva, 1993). It took several years after its initial accidental introduction to reach the extreme outbreaks of 1988-89. So far, the data on *M. leidyi* abundance and distribution in the NE Adriatic indicate that the changes between consecutive years can be substantial. There seems to be a trend of increasing *M. leidyi* overall abundance as well as affected areas becoming more widespread over the years. As noted in the Black Sea (Dumont *et al.,* 2004), the catastrophic consequences of *M. leidyi* were, in fact due to a combination of many different factors ranging from eutrophication (often exceeding chlorophyll *a* concentrations of 50 µg L^{-1} (ICPDR – ICPBS, 1999)), to overfishing. Thus, it is possible that the Adriatic, being less eutrophic (Djakovac *et al.,* 2012), might respond differently to the introduction of the invasive ctenophore *M. leidyi*.

Expectedly, in the most oligotrophic parts of the northern Adriatic, where food could be scarce, jelly combs did not thrive. Their presence remained mainly restricted to the area that extends from the north of the Cape Kamenjak to the south part of the Po River delta (Malej *et al.,* 2017; Fiori *et al.,* 2019). *M. leidyi* thrived much more in the Black Sea than it ever did in the eastern Mediterranean, possibly due to high salinity (Shiganova, 2001). Similarly, the lower salinity and eutrophic conditions of the NW Adriatic could favour *M. leidyi* blooms, while the oligotrophic conditions in the east (Kvarner Bay) (Degobbis, 1983; Vukić Lušić *et al.,* 2013) might have limited its spread.

Areas of increased *M. leidyi* concentration were located near (2016) or within the low salinity anticyclonic gyres (2017, 2018). Since gyres are considered stagnant areas in which organic matter and food can accumulate, it can be hypothesised that the growth and reproduction of *M. leidyi* took place within them. Being multiplied in gyres, the population may spread either towards the coastal zone or towards the south. In 2017, when transversal currents along the Pesaro-tip of Istria line were less pronounced than in 2016 and 2018, the population of *M. leidyi* reached the far south. In 2019 the maximal concentration of *M. leidyi* corresponded roughly to a large anticyclonic gyre between the lines Po delta-Rovinj and Pesaro-tip of Istria in an area of salinity over 38.1. We suppose that the gyre area was affected by lower salinity and food rich waters from Po, which when mixed with central Adriatic waters of especially high salinity, resulted in waters of salinity over 38.1.

M. leidyi's gut content analysis revealed a diversified diet in terms of taxonomic composition and prey size. The dominant prey taxa were representatives of summer zooplankton. Copepods were the most diverse group in the gut content. Calanidae copepods were found among the dominant prey taxa in *Mnemiopsis*' gut. According to Borme *et al.* (2009), they are the main prey for anchovy, which indicates resource competition between *M. leidyi* and *E. encrasicolus.* Literature data also confirms that planktonic shrimps, mainly copepods, are the main prey for *M. leidyi*, followed by meroplankton, eggs and juvenile fish (Purcell & Arai, 2001; Hamer *et al.,* 2011; Costello *et al.,* 2012; Tiselius & Møller, 2017). We noted that large zooplanktons (>2 mm) were more abundant in the digestive system than the surrounding sea. Examples of the "prey selectivity" of *M. leidyi* are known from other seas. The main prey in the Black Sea and French lagoons were invasive alien species of Atlantic origin, such as the copepod *Acaria (Acanthacartia) tonsa* and nauplii of barnacle *Amphibalanus improvisus* (Gubanova, 2000; Delpy *et al.,* 2012). In the Gulf of Kiel (Baltic Sea), *A. improvisus* formed 82% of the *Mnemiopsis* preys during the winter, while in September and October 52-72% of prey composition was represented by the planulae of the schyphomedusa *Aurelia aurita* (Javidpour *et al.,* 2009).

A relatively small amount of prey found in the digestive tract (1.2-2.5 ind. per ctenophore) differs from considerably higher prey quantities reported in several studies (Reeve *et al.,* 1989; Mutlu, 1999; Costello *et al.,* 2012). Nevertheless, the average zooplankton abundances measured at stations along the Istrian coast during 2017 and 2018 were lower compared to those observed in the northern Adriatic survey over the last two decades, using the same sampling method (Fonda Umani *et al.,* 2005; Camatti *et al.,* 2008; Bernardi Aubry *et al.,* 2012; Bojanić Varezić *et al.,* 2015, Vidjak *et al.,* 2019).

The northernmost part of the Adriatic Sea is characterized by shallow waters (<50 m), and it is recognized as an important ground for the development of early stages of small pelagic fish (Giannoulaki *et al.,* 2013). Since the detection of swarms of *M. leidyi*, changes in the spatial distribution of anchovy were recorded in the same area; Starting in 2016 and becoming more noticeable from 2017 onward, a decrease in abundance was observed. In 2016, the decrease was assumed to cover coastal waters along the west side of the Istrian peninsula. From 2017, the affected area spread westwards, almost to the midline of the basin, which was previously rich in anchovy schools. A similar situation continued in 2018. This effect could have appeared due to a reduction in the number of fish (heightened mortality), or more likely, due to anchovy's migration to another zone within the Adriatic basin. The overlap in timing of the appearance of *M. leidyi* swarms with the change in the distribution of anchovy indicates a possible relation between the two.

In the Black Sea, negative correlations were reported between the abundance of early development stages of summer-spawning zooplanktivorous fish species (like anchovy) and ctenophores. These correlations were also recorded in winter-spawning species, but not to the same extent (Shiganova, 1998). If an event similar to the one in the Black Sea is presumed to have happened in the Adriatic, it would potentially explain why the anchovy population (which spawns during the peak of *M. leidyi* abundance) was so affected.

The influence of *M. leidyi* swarms on the distribution of anchovy could be due to strong competition for food resources as in the Adriatic Sea *E. encrasicolus* feeds on similar zooplanktonic taxa than this ctenophore (Borme *et al.,* 2009). *M. leidyi*'s predation on fish eggs was also suspected, but in this study, we rarely found fish eggs in *Mnemiopsis*'s gut contents, probably due to the low abundance of spawning fish in the area and the consequent absence of fish eggs at sea (Table 2). Local changes in the spatial distribution of anchovy are indeed evident, but the implications on their entire stock and the ecosystem of the Adriatic Sea remain unclear. Thus, further monitoring of the Adriatic Sea is recommended.

Conclusions

The simultaneous monitoring of *M. leidyi* and anchovy in the NE Adriatic revealed that *M. leidyi*'s presence coincided with a reduction in anchovy abundance. It can be assumed that the reduction in anchovy is a consequence of competition for food with the invasive generalist feeder – *M. leidyi*.

The spatial distribution *M. leidyi*'s appearance overlapped with large seasonal anticyclonic gyres, which indicated that within those systems, conditions suitable for its proliferation could be found. Further research on *M. leidyi* within gyres of NE Adriatic is expected to unravel the roles of those systems as their nurseries and conveyors.

The crisis in fish stock that occurred in the Black Sea during the '80s, together with our findings, serves as a warning. An attentive and focused international monitoring program should be implemented in the Adriatic with the aim to understand the changes occurring in the basin and to find possible solutions to contain the problem.

Although MEDIAS surveys are designed specifically to monitor small pelagic fish stocks; these surveys could be a valuable source of information on large-scale changes in macro and mesozooplankton communities and other ecosystem's components.

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Supplementary Data

The following supplementary information is available online for the article:

Figure S1: A cube frame used for *in situ* observations (dimensions: 0.5×0.5×0.5 m).

Figure S2: Monthly average abundances of *M. leidyi* along the coast of Rovinj for months when its presence was recordes during the four-year monitoring.

Figure S3: Monthly means of vertically averaged temperatures and sigma-t values for September 2016, 2017, 2018 and 2019, obtained by the numerical hydrodinamical model. Solid line is drawn between the Po River delta and Rovinj, and dashed line between Pesaro (Italy) and the tip of Istria (Cape Kamenjak). Isolines 38.1 and 38.5 are depicted in black.

Figure S4: Annual distribution of zooplankton abundances at Rv station.

Figure S5: Zooplankton abundances (ind. m^{-3}) at stations along the western Istrian coast from Agust 2017 to July 2018.

Table S1. *M. leidyi*'s abundance (ind. m^{-3}) at the sea surface measured in September (from 2016 to 2019) at each of the stations accompanied with the depth at the location.

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Distribution, diet and relationships of the invasive ctenophore Mnemiopsis leidyi with anchovies and zooplankton, in the northeastern Adriatic Sea

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Contribution to the Special Issue: "MEDiterranean International Acoustic Survey (MEDIAS)

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Mediterranean Marine Science, 2021, 2021, 22/4, Special Issue

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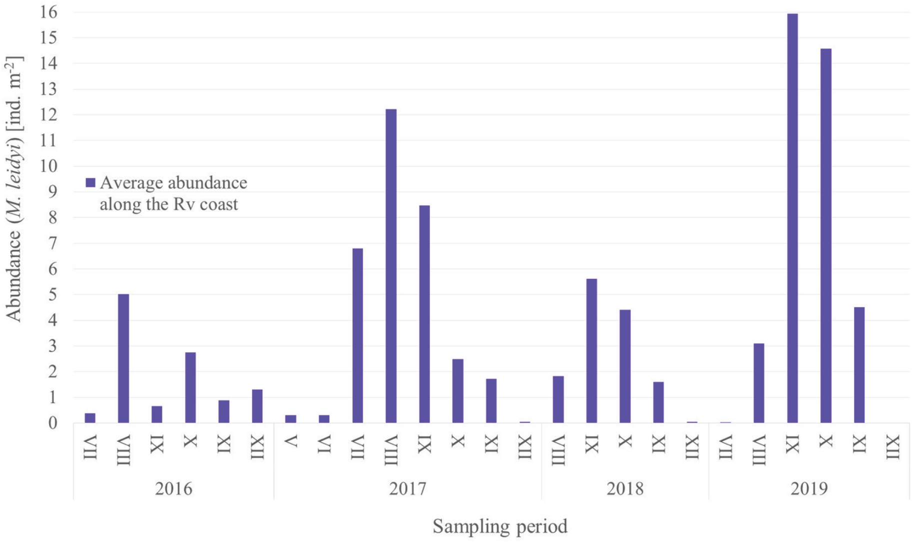

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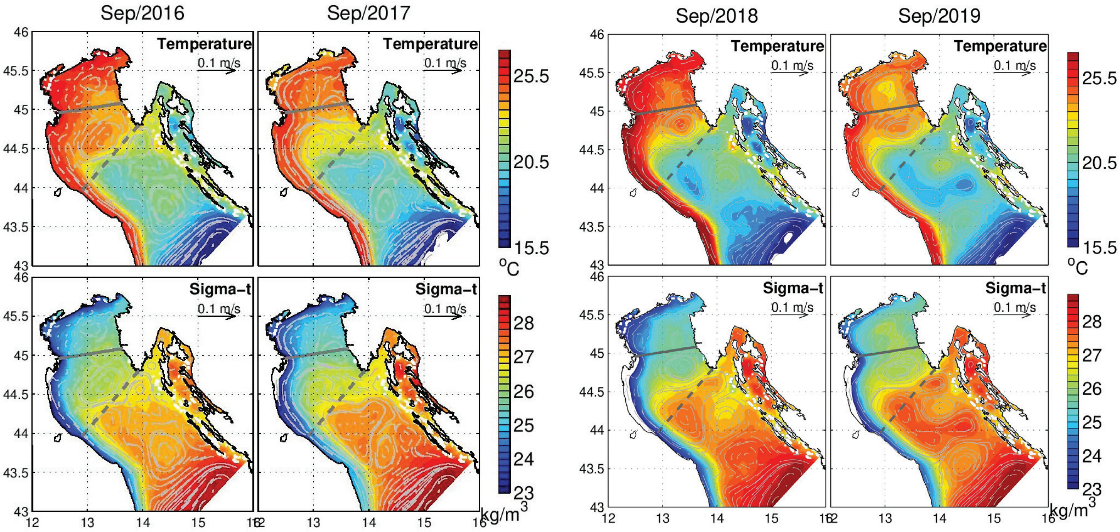

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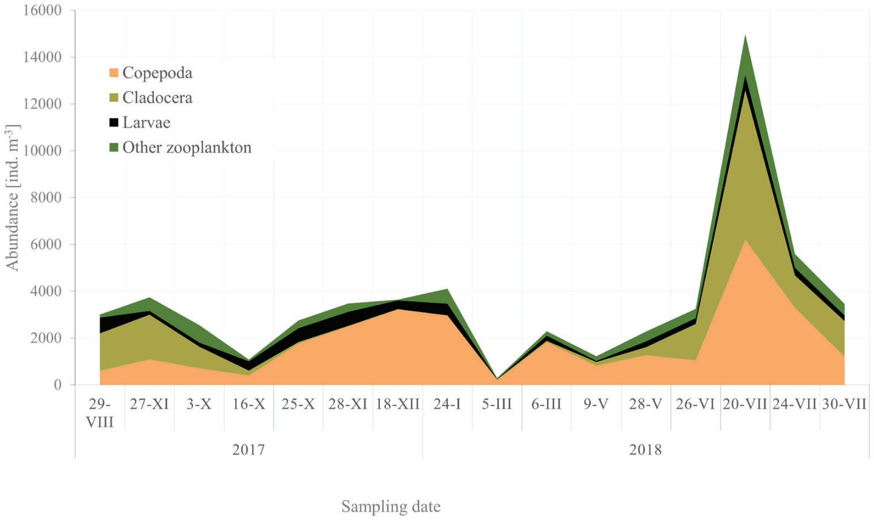

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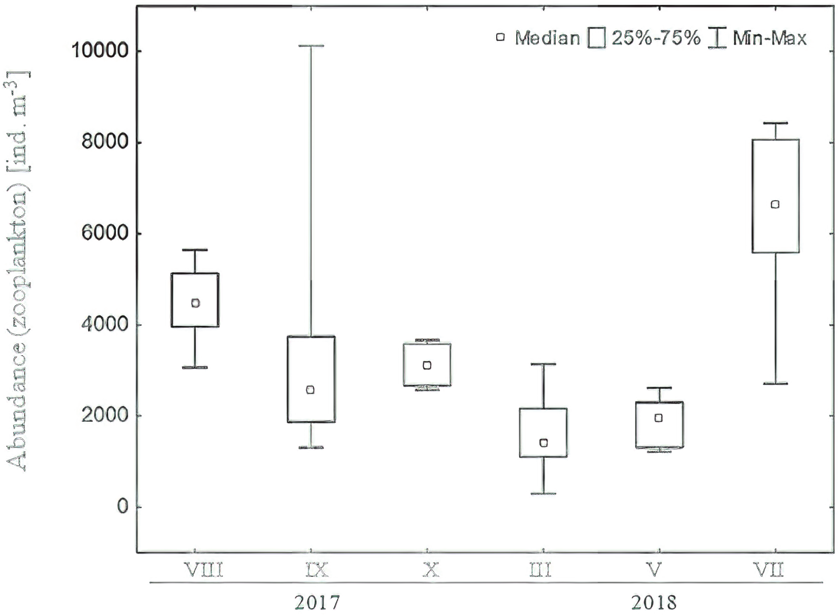

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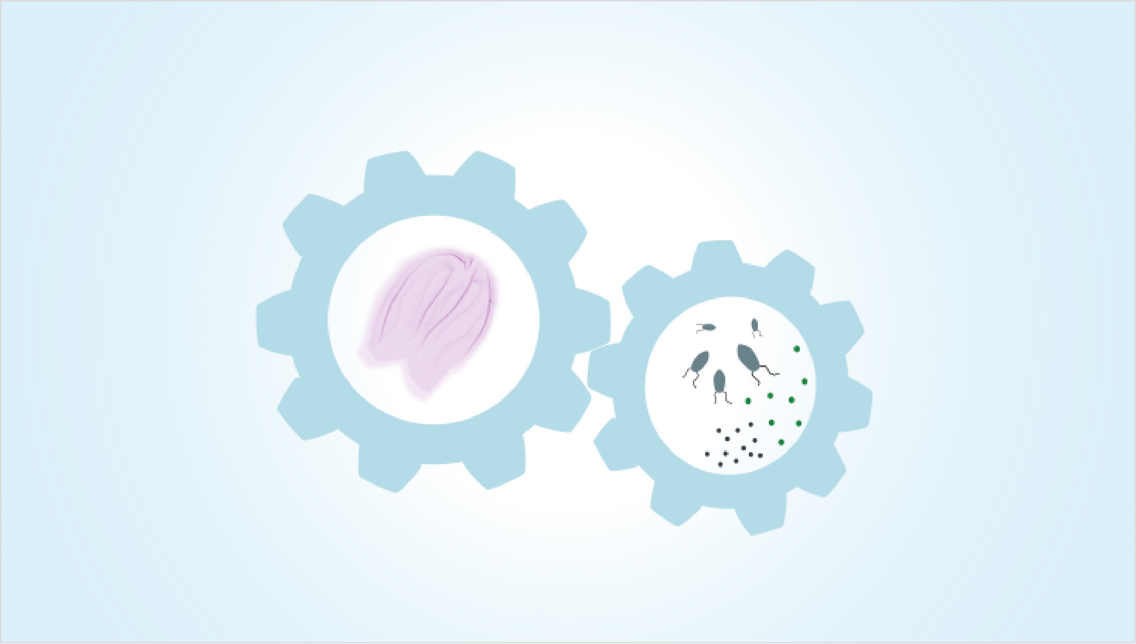
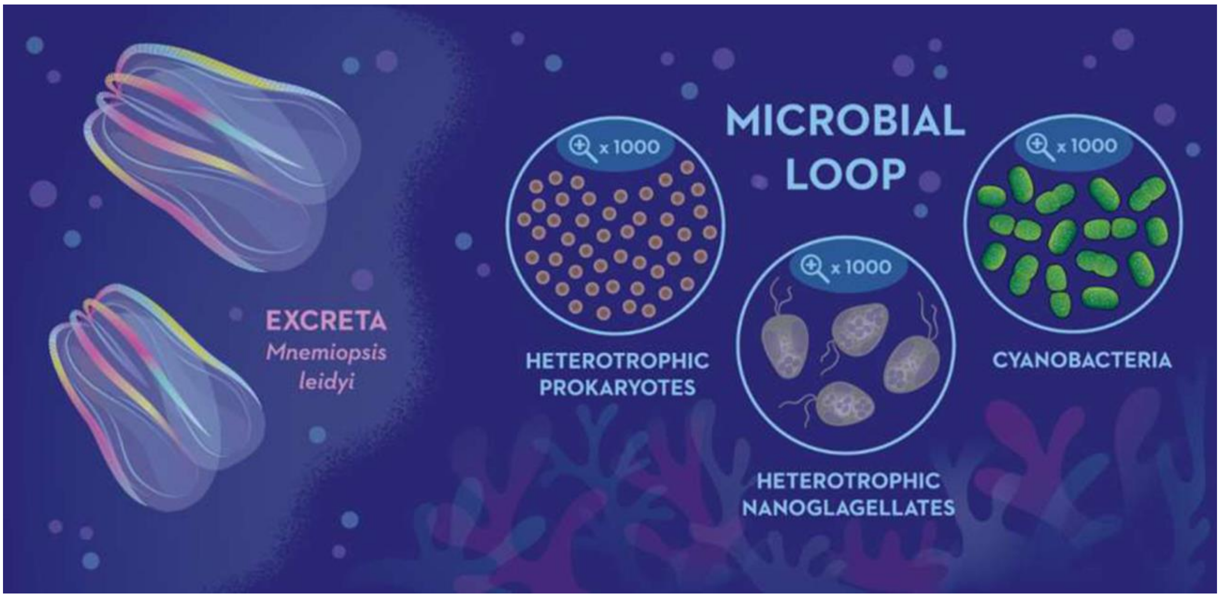
Table S1. *M. leidyi*'s abundance (ind. m^{-3}) at the sea surface measured in September (from 2016 to 2019) at each of the stations accompanied with the depth at the location. Asterisks (*) mark the locations where *M. leidyi*'s distribution extended beyond the surface layer reaching the thermocline (15 m).

Station	**Depth (m)**	Surface abundance *M. leidyi* (ind. m^{-3})			
		2016	**2017**	**2018**	**2019**
3	50	0	0	0	0
4	60	0	0	0	0
5	45	0	0	0	0
6	70	0	0	0	0
7	92	0	0	0	0
8	60	0	0	0	0
9	52	0	0.1	0	0
10	51	0.005	0.01	0.005	0
12	23	0.02	0.25	0.01	0
13	23	0.005	0	0.01	0
14	25	0.06	0	0.03	0
15	26	0.1	0.75	1	0.1
16	24	0	0.125	0.5	0.3
17	33	0	0.55	0.8	2
18	44	0	0	0	0.5
19	45	0.05	0.07	0.02	0.5
21	25	0.01	0.001	0.03	1.8
23	40	0.02	0.255	0.01	6*
24	49	0	0.14	0	0
25	51	0	0.14	0	0.02
27	49	0	0.13	0	0.1
30	55	0	0	0	0
31	60	0	0.001	0	0.01
32	63	0	0	0	0
33	59	0	0	0	0
38	62	0	0	0	0
39	50	0	0	0	0
36	50	0	0.0001	0	0.01
37	80	0	0	0	0
S	20	0.01	0.5	0.4	0
S1	30	0.005	0.1	0.8	0
U	25	0.001	4.5	0.7	0
D	25	0.03	2.8	0.1	0.05
N	25	1.5	2.9	3.1	0.6
N1	26	0.03	0.1	0.7	1
P_0	24	2	8.9*	1.4	4
P1	25	3.4	4	1	2
P2	24	0.01	0.03	0.5	0.6
P3	25	0.1	0.1	0.05	0.01
V	25	0.5	3.8	2	0.08
L	27	0.001	2.8	0.1	0.02
Rv	29	0.1	6.6*	6	7*
ZI032	35	0.2	15*	3	3
Ba	32	0.05	3.8	0.6	6*
Br	40	0.15	0.06	0.3	4
Pu	37	0.2	5.8	0.4	18*
Pu1	38	0.03	0.4	0.2	13*
Pu2	40	0.01	0.3	0.3	2.5
Pu3	42	0.06	0.1	0.5	2

II Publikacija



Graphical abstract



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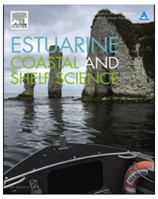

Microbial response to the presence of invasive ctenophore *Mnemiopsis leidyi* in the coastal waters of the Northeastern Adriatic

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ABSTRACT

Seasonal blooms of the invasive ctenophore *Mnemiopsis leidyi* have been recorded throughout the Adriatic Sea, affecting the ecosystem and its pelagic resources. Gelatinous organisms such as *M. leidyi* release significant quantities of excreta as labile and surface active dissolved organic carbon (DOC) that supports the microbial activity.

The effects of *M. leidyi*'s presence on heterotrophic prokaryotes (HP), cyanobacteria (CB) and heterotrophic nanoflagellates (HNF) were investigated at five locations in the coastal waters of Rovinj-Rovigno (northern Adriatic) during intensive blooms in September 2019. Additionally, circulation in the study area was examined using available current measurements and a hydrodynamic model. In September, low-pass filtered currents near the surface were mostly directed toward S-SE reaching 25 cm/s, indicating the presence of the Istrian Coastal Countercurrent (ICCC).

Ctenophores displayed a patchy spatial distribution from 0.05 to 100 *M. leidyi* individuals per m^3. When ctenophore density in the swarms surpassed 1 individual per m^3, the change in the abundances of microbial groups became evident. The lowest microbial densities and lowest concentrations of dissolved and particulate organic carbon (DOC and POC) and surface-active substances occurred in the absence of *M. leidyi,* while the highest were within the swarms.

We hypothesise that HP utilises the available DOC enhancing the remineralisation of organic matter. Finally, greater availability of HNF's prey (HP and CB) leads to an increase in their abundance.

This study illustrates how the release of surface-active DOC during intensive *M. leidyi*'s blooms can stimulate the microbial loop. The current system with the ICCC prevailing in September enables the spreading of *M. leidyi* from its hypothetic origin in an open sea gyre towards the coast. Bora wind episodes may initiate and favour this type of circulation. In these conditions, *M. leidyi* agglomerates in large numbers along the coast, enabling the accumulation of organic matter and altering the abundance of pico- and nanoplankton.

1. Introduction

The invasive ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865, has successfully established in the Adriatic Sea since 2016 (Malej et al., 2017; Budiša et al., in press). *M. leidyi*'s swarms last usually from the summer to the end of the autumn, occupying vast coastal areas in between the northwestern (NW) coast of Istria (Croatia and Slovenia) and through the Italian coast down to Ancona, mostly reaching their maximum density and extension in September (P. Paliaga, pers. comm.). Effects on both zooplankton and fish stocks in the Adriatic have been reported (Budiša et al., in press), raising concerns on the long-term consequences for the equilibria in the upper trophic levels in one of

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the most productive parts of the Mediterranean (Ben-Hamadou et al., 2012). Similar effects have been previously reported for other food webs in pelagic, coastal and estuarine ecosystems (Grosholz, 2002; Marambio et al., 2013), e.g. the Black Sea (Shiganova, 1997), the Sea of Azov (Studenikina et al., 1991) and the Caspian Sea (Ivanov et al., 2000) where *M. leidyi* depleted the zooplankton stocks and contributed to the fisheries collapse (Kideys et al., 2005).

Gelatinous zooplankton, e.g. *M. leidyi*, can also affect the lower trophic levels. Some members of this diverse group of pelagic taxa (i.e. cnidarians, ctenophores, chaetognaths and tunicates) are known to form blooms (Lucas et al., 2014; Lebrato et al., 2019; Sola et al., 2019; Luo et al., 2020). A *M. leidyi* bloom can reach enormous biomasses, i.e. 10^9 t of wet weight such as the one recorded in the Black Sea (summer-autumn 1988), exceeding even the world's annual fish landings (Ivanov et al., 2000; Sorokin, 2002).

In these events, substantial quantities of dissolved organic matter (DOM) and nutrients can be released via excretion, mucus production or body decomposition (Pitt et al., 2009; Condon et al., 2011; Hao et al., 2019; Tinta et al., 2020).

HP are the most abundant component of the marine microbial community (Azam, 1998) and the major consumers of DOM in the oceans (Williams and Gray, 1970; Azam and Hodson, 1977). Massive gelatinous organism blooms can be considered an ecosystem disturbance, and their effects on the dynamics of the microbial community are still unclear (Riemann et al., 2006; Titelman et al., 2006; Tinta et al., 2010, 2012 & 2016; Condon et al., 2011; Dinasquet et al., 2012a, b & 2013; Blanchet et al., 2015; Basso et al., 2019; Hao et al., 2019; Jaspers et al., 2019; Guy-Haim et al., 2020). In many marine systems, the majority of bacterial production is sustained by organic matter (OM) derived from primary production or phytoplankton exudates (del Giorgio and Cole, 1998; Hansell and Carlson, 2002). However, the bacterial carbon demand often exceeds the supply rates from primary production (del Giorgio and Peters, 1993; del Giorgio and Cole, 1998), and bulk organic pools contain large concentrations of refractory DOM (Hansell and Carlson, 2002). In those conditions, the DOM excreted by gelatinous zooplankton may be an important source of C, N and P for bacterioplankton. The predominant forms of DOM produced by jellyfish are labile, suggesting a tight coupling between DOM excretion and bacterioplankton production (Pitt et al., 2009; Condon et al., 2011; Hao et al., 2019; Tinta et al., 2020).

A field study by Riemann et al. (2006) found an increased bacterial activity where the biomass of jellyfish *Periphylla periphylla* (Péron & Lesueur, 1810) was the highest. *In situ* incubated jellyfish *Aurelia aurita* (Linnaeus, 1758) doubled bacterial biomass and production (Turk et al., 2008). Decaying jellyfish blooms also promote bacterial growth and biomass production (Titelman et al., 2006; Tinta et al., 2010; Blanchet, 2015; Blanchet et al., 2015). Laboratory-scale incubation experiments revealed the influence of *M. leidyi* on bacterioplankton activity and microbial community composition (Dinasquet et al., 2012a). Temporary aggregations of ctenophore locally affect bacterial growth and may significantly contribute to the spatial heterogeneity of bacterioplankton activity and community composition (Dinasquet et al., 2012a).

Relative to other marine phytoplankton, cyanobacteria (CB) have lower growth rates (Paerl and Millie, 1996). Nonetheless, it is estimated that $^1/_4$ of the ocean primary production is assigned to unicellular CB (Flombaum et al., 2013). Picocyanobacterial abundances (cells/mL) at their peak in the Adriatic are reported from 10^2-10^6 (del Negro, 2007).

HP and CB represent the main prey for heterotrophic nanoflagellates (HNF) (Caron et al., 1992). In ecosystems where CB are the dominant primary producers, e.g. oligotrophic Mediterranean waters, HNF preferably preyed on CB rather than HP (Hagström et al., 1988).

Primary and secondary production, including zooplankton grazing, directly reflects on DOM quantity and quality (Pettine et al., 2001; Fonda Umani et al., 2007). OM quality in seawater, i.e. reactivity, can be directly related to its hydrophobic and hydrophilic properties, measured under the term surface-active substances (SAS) (Ćosović and Vojvodić, 1998; Croot et al., 2007; Sabbaghzadeh et al., 2017; Ciglenečki et al., 2020).

Our work presents a field study aiming to explain the ecological effects of the invasive *M. leidyi* presence on the microbial community, dissolved organic carbon (DOC), and its surface-active substances (SAS) fraction in the Adriatic Sea. We hypothesise that dense swarms will affect the abundance of the microbial community by providing readily available OM.

Hydrographic conditions alone, especially circulation dynamics in the Adriatic coastal area, are often held responsible for favouring gelatinous zooplankton aggregations by directing population variations, especially at local scales (Graham et al., 2001). Thus, we also examined the relation with the circulation properties during the sampling period. The end of summer circulation in the Istrian coastal zone in some years is characterised by the Istrian Coastal Countercurrent (ICCC), a surface geostrophic current following the coastal line, with a pronounced southeastern (SE) component and an average speed of 7 cm/s (Supić et al., 2000). The current is a part of an anticyclonic gyre located in open waters of the NE Adriatic and filled with lower salinity waters of Po River origin (Supić et al., 2003). This gyre is assumed to be an important seasonal spawning area for *M. leidyi* and the main origin for ctenophore along the coast of Istria (Budiša et al., in press). The SE motions, especially intense in September, as observed during several years of measurements in open waters off the Istrian coast (Brana and Krajcar, 1995), are presumably a part of the same gyre. Numerical modelling results for September 2019 show that the gyre and the ICCC were also present in 2019. The possibility of *M. leidyi*'s transport from the gyre to the coast by the ICCC is also investigated here.

2. Materials and methods

2.1. Sampling

The samplings were performed on 4 and September 21, 2019 at five locations in the coastal waters of Rovinj-Rovigno (Rv), NE Adriatic (Fig. 1, Table S1) during *M. leidyi*'s annual bloom peak. Four locations represented semi-enclosed accumulation areas for ctenophore and OM in contrast to the open sea area of Bagnole. *M. leidyi* was counted, and samples were collected for biological and chemical analysis. At each location, 4 to 12 sites were sampled along a grid distributed at distances from 50 to 200 m. Additional field observations on *M. leidyi* presence in relation to prevailing currents were carried out in the summer of 2020.

Water samples were collected at 0.5 m depth because *M. leidyi* individuals were concentrated close to the surface. At every location, water temperature and salinity were measured with a pIONneer 65 probe (Radiometer analytical, Copenhagen). Moreover, the relation between the invasive ctenophore, microbial community and OM was investigated.

2.2. Abundance and distribution of *M. leidyi*, pico- and nanoplankton

At the beginning of September, ctenophores were monitored at Valdibora Bay, Monsena Bay and the Southern Harbour on the same day, while at the end of the month, locations around islands St. Ivan and Bagnole were sampled. The density (ind./m^3) was determined by visual census of specimens (length>1 cm) by scuba divers with the help of a submerged cube frame (0.5 m x 0.5 m x 0.5 m) carried along the transects of the coastline. Samples for microbial community analysis were preserved with formaldehyde (2% final concentration) and stored at 4 °C. For determining HP and HNF abundances, 2 mL of fixed samples were stained with 4.6-diamidino-2-phenylindol (DAPI, 1 μg/mL final concentration) for 10 min, and then passed through 0.2 μm black polycarbonate filters (Whatman® Nuclepore™). HP abundance was determined by epifluorescence microscopy at a magnification of 1000x (Leitz Laborlux D) according to Porter and Feig (1980). For HP count, at least 500 cells per sample were counted. From the total number of prokaryotes, the number of CB was subtracted to obtain the number of HP. The HNF abundance was determined by counting a minimum of

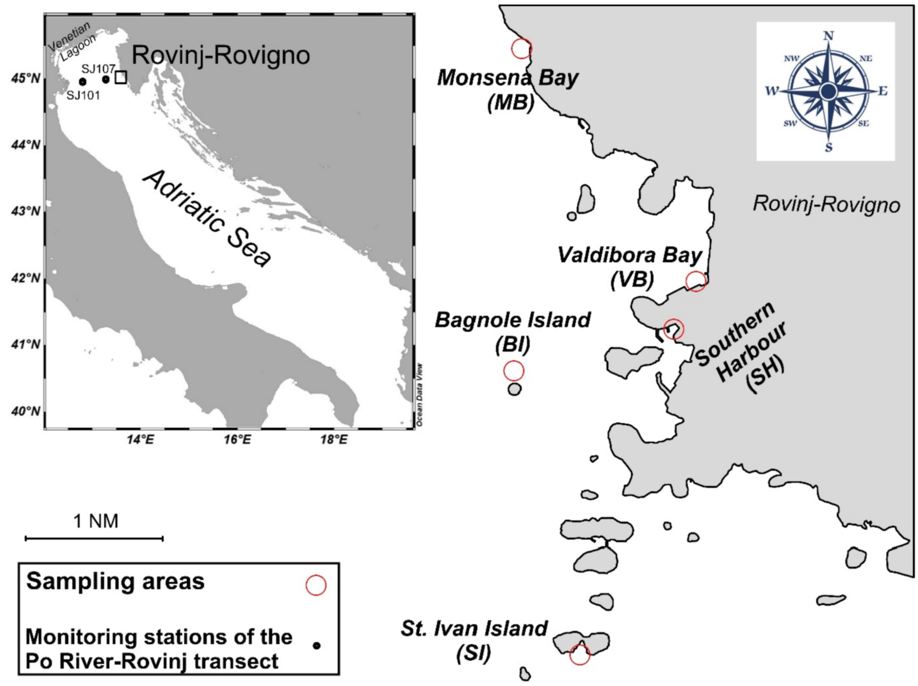

Fig. 1. Sampling locations in the coastal waters of Rv.

100 cells/sample (Sherr et al., 1993). The CB abundance was determined using green light excitation, with a minimum of 300 cells/sample counted (Takahashi et al., 1985).

Data sets were tested for normal distribution using the Shapiro-Wilk test and data homogeneity using Levene's test. For normally distributed ($p > 0.05$) homogeneous data ($p > 0.05$), One-Way ANOVA or two-tailed T-tests were performed. When logarithm transformation of data did not help attain a normal distribution, non-parametric two-tailed Mann-Whitney or Kruskal-Wallis tests were performed. For data that violated homogeneity of variances, the Games-Howell test was applied. In addition, plankton abundances were normalised and compared.

2.3. *Organic matter content measured as surface-active substance (SAS), DOC and POC*

For DOC and POC quantification, seawater was sampled in dark 1.3 L bottles and then filtered (1 L) through 0.7 μm pore size precombusted Whatman GF/F fibre filters for 4 h at 450 °C. Sub-samples of the filtrate were collected in 20 mL glass vials, preserved with 100 μL of mercury (II)-chloride (10 mg/L), closed with Teflon-lined screw caps and stored in the dark until analysis. These filtrates were used for DOC analysis. Filters were stored in liquid nitrogen (−80 °C) until TOC, i.e. POC analysis. DOC was determined by the high–temperature catalytic oxidation (HTCO) method at a TOC–VCPH instrument (Shimadzu, Japan) (Cauwet, 1994, 1999; Dafner and Wangersky, 2002; Dautović et al., 2017). The DOC measurement was performed by direct injection of the sample into a combustion furnace at a temperature of 680 °C through a sensitive Pt/silica catalyst. Organic carbon from the sample generated CO_2 that was directly measured using a non–dispersed infrared (NDIR) detector. Prior to the oxidation, the inorganic carbon was removed from the sample by acidification with HCl (~2%) to pH 2–3 and evaporation of the resulting CO_2 in the stream of pure air for 10 min. System calibration was performed with potassium hydrogen phthalate. POC was determined in filters with the calibration using glucose. A solid sample module SSM–5000A with TOC–VCPH carbon analyzer was used for measurements. Inorganic carbon was removed from samples prior to POC measurement by adding 2 mol/dm^{-3} HCl. Oxidation of organic carbon in the flow of pure oxygen at 900 °C produced CO_2 that was detected using an NDIR detector. The quantification limit was 0.228 mg/dm^3 for DOC and 7.11 $\mu g/dm^3$ for POC. The precision of DOC and POC measurements, given as the RSD, was based on the analysis of selected samples and the reference materials; RSD never exceeded 6% and 5%, respectively. Both measurement procedures were validated through the international intercalibrations as a prerequisite for accreditation achieved in 2017 (HRN EN ISO/IEC 17025:2007).

All glassware used for organic matter analyses, including sampling and sample filtration and preservation till measurements, were washed with chromic-sulphuric acid and rinsed well with organic-free Milli-Q water (Millipore) and seawater samples. SAS measurements were done by the electrochemical method a.c. voltammetry based on the measurements of the SAS adsorption effects at the surface of the hanging mercury drop as a working electrode in the seawater sample (0.55 M NaCl as the model electrolyte) (Ćosović & Vojvodić, 1982, 1998; Ciglenečki et al., 2020). Selected adsorption potential conditions (−0.6 V by Ag/AgCl electrode) and adsorption time (15–120 s) with stirring were used. Changes of the working electrode double layer reflected on the capacitance current are approximately proportional to all (dissolved and particulate) SAS in the solution. The total SAS (i.e. NF, non-filtered) is separated into particulate and dissolved fractions (SAS F, filtered) by filtering through 0.7 μm GF/F Whatman® filters. SAS content is expressed in the equivalents of the selected model OM substance of Triton-X-100 (eq. T-X-100) – a good representative of the most reactive part of the SAS in natural waters (Ćosović and Vojvodić, 1982, 1998; Ciglenečki et al., 2020 and references therein). The detection limit (LoD) for voltammetric SAS determination is 0.02 mg/L eq. T-X-100, with the limit of quantification (LoQ) of 0.05 mg/L. If SAS is normalised to DOC, then the normalised surfactant activity value, NSA = [SAS (eq. T-X-100)/DOC], can be calculated. NSA can be compared with normalised surfactant activities of different model SAS substances: Triton-X-100 (1.54), protein albumin (0.20), fulvic acid (0.17), polysaccharides dextran T-500 (0.20) and xanthan (0.04), which are representatives for surface active organic matter composition of natural samples (Ćosović and Vojvodić, 1998; Ćosović et al., 2000: Ciglenečki et al., 2018).

In addition, the Pearson's 'r' correlation coefficients were calculated (significance level, α = 0.05) for *M. leidyi* abundances and C-content.

2.4. *Current measurements*

Vertical profiles of currents were measured close to Bagnole Island (Fig. 1, Table S1). Teledyne RDI ADCP 600 kHz instrument (acoustic Doppler current profiler) was deployed at 29.5 m depth (bottom depth at the location was 31.5 m) between July 5 2019, and March 9 2020, enabling continuous high-resolution current profiling (1 m vertical resolution and 15 min sampling interval). Measurements were available at 3.4 m–27.4 m depths. Sea temperature data were collected at a depth of the instrument (29.5 m). Current data were quality checked. Data analysis included spectral analysis, low-pass filtering procedures (to exclude tidal and inertial motions and seiches) and daily averaging of current measurements in July–September 2019 period, covering the period before and during *M. leidyi* sampling.

2.5. *Numerical modelling*

The ROMS model was used for the hydrodynamic simulation of the northern Adriatic system and is described in detail in Janeković et al. (2010). The surface forcing was obtained from the ECMWF forecasts and provides 2 m air temperature, cloud fraction, 2 m relative humidity, mean sea level pressure, 10 m wind, longwave and shortwave flux, rainfall rate. The boundary forcing at the Otranto strait was obtained from the ADAM-ADRIA project results (Janeković et al., 2020) and is used as climatology in this run. The climatological river inflow data for 41 Adriatic rivers, provided by Vilibić et al. (2016), was also used in the model setup. Monthly averaged surface current fields and the results of a dispersion model coupled with the hydrodynamic model are presented in our study. The drifters in the lagrangian dispersion model were set to be purely isobaric (they follow currents but remain at the same depth) to model the behaviour of ctenophores. Starting on July 1, 2019, drifters were continuously released from the model grid point corresponding to the station SJ107 (Fig. 1) with a rate equalling 15 drifters per day (3 drifters for each of the 5 different depths: 0.2 m, 0.4 m, 0.6 m, 0.8 m, 1.0 m). Their average distribution for July, August and September 2019 is analysed and presented here.

3. Results

3.1. *Temperature and salinity*

Surface temperatures during the whole sampling period were similar at all locations (23.4 ± 1.2 °C). The water column was strongly stratified with the thermocline at 16 m depth. Surface salinities were also very similar at all the locations (37.1 ± 0.01) but were slightly higher at the end of the investigated month (37.4 ± 0.02).

3.2. *ADCP currents*

Stationary spectral analysis (Jenkins and Watts, 1968) showed that

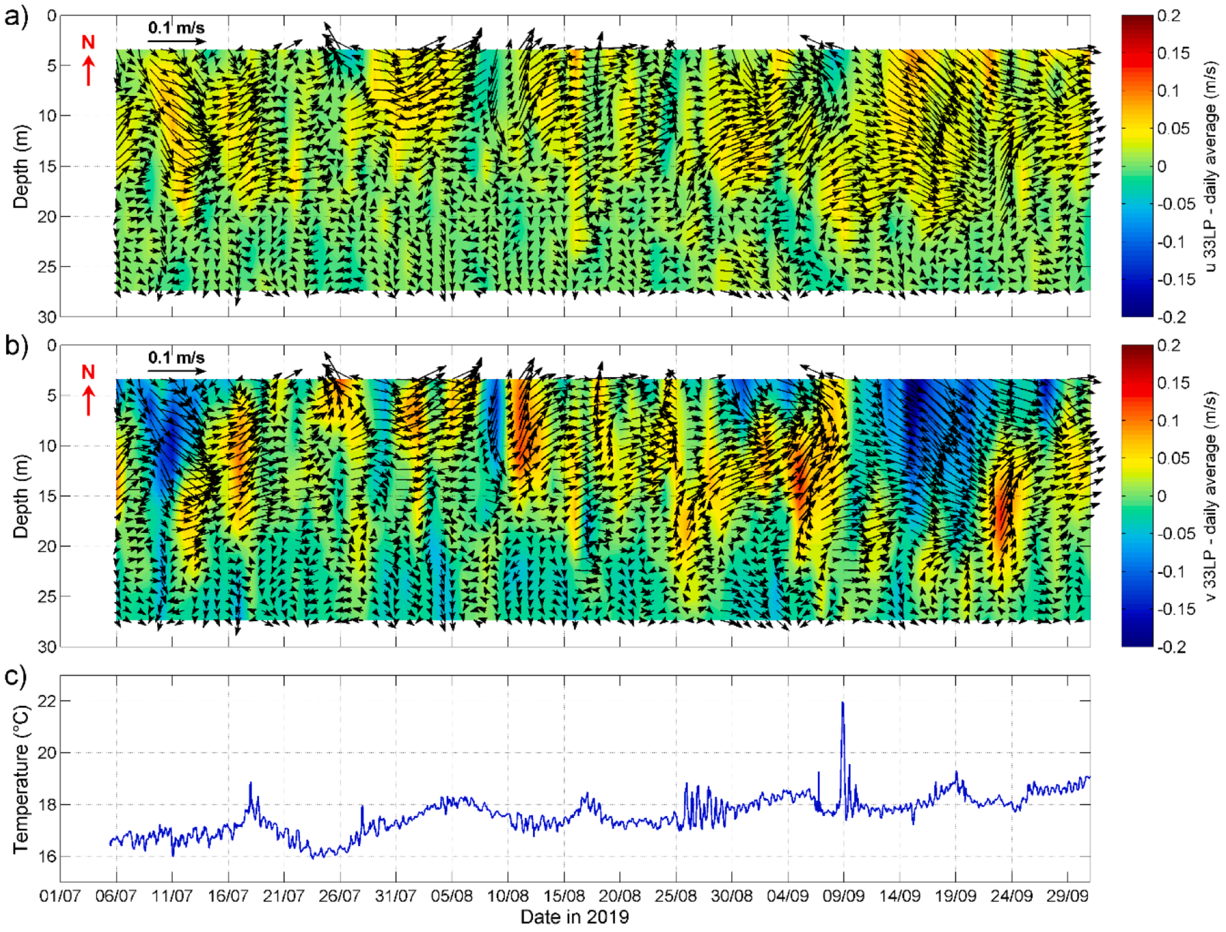

Fig. 2. a) Daily-averaged current vectors obtained by filtering original current measurements using a low-pass filter with a cut-off period of 33 h. The corresponding eastern current component is presented as a filled contour plot. b) As in a) except that the northern current component is presented as a filled contour plot. c) Near-bottom sea temperature measured every 15 min at the current meter location (sensor depth 29.5 m).

the most energetic oscillations in ADCP current data between July and September 2019 were at tidal frequencies (not shown), more specifically at diurnal (~24 h) and semi-diurnal period (~12 h). Moreover, inertial oscillations were also present, with a period of ~17 h.

Currents components were filtered using 33-h low-pass filter (e.g. Emery and Thomson, 1997) to remove higher frequency oscillations and analyse low-frequency changes in the current field. Filtered data were then averaged every 24 h. Daily-averaged current vectors obtained from such a procedure are presented in Fig. 2 at every depth between July and September 2019. Current vectors and the corresponding eastern and northern components are given in Fig. 2a and b, respectively. Additionally, original temperature data at 29.5 m depth, measured every 15 min, are shown in Fig. 2c.

Daily averaged low-pass filtered currents having S-SE direction, with speeds up to 25 cm/s, generally appeared in upper layers (0–15 m). S-SE circulation was first observed between 8 and 11 July, down to 15 m depth, with speeds reaching 12 cm/s. Another short episode with mainly E-SE currents occurred at the end of July. S-SE currents were again observed at the end of August/beginning of September in the uppermost layer (down to 8 m), with speeds reaching 10 cm/s. These S-SE motions could be attributed to the ICCC, as they are in its direction and corresponding range. In September 2019, they were more frequent and prevailed over motions with the N-NE component (typical for August). Subsurface currents were more intense than the bottom ones. From 10–21 September, they were predominantly S-SE directed down to 15–20 m depth, reaching their maximum on 15 September (~25 cm/s).

A prominent change in current direction and magnitude occurred after September 9, 2019, when near-bottom temperature swiftly rose from ~18 °C to ~22 °C, possibly due to vertical mixing induced by surface cooling episodes within a period of strong winds over the northern Adriatic. Between 6 and 9 of September 2019, the wind changed from bora (N, NE) to sirocco (SE) (Croatian Meteorological and Hydrological Service, 2019). The change in the near-bottom sea temperature was followed by a change in current direction in upper layers, from NW (8 and 9 September) to SE (10 September onwards). After this bora-sirocco episode, currents in the upper layer were mostly in the SE direction, almost till the end of the month. From 10–21 September, sub-surface and intermediate low-pass filtered currents with SE direction were occasionally very strong (up to 25 cm/s close to the surface) and observed to 20 m depth.

3.3. Modelled currents and dispersion model results

Monthly averaged modelled surface currents in July–September period indicate the presence of an anticyclonic gyre in the northeastern Adriatic (to the southwest of Rv) and a large cyclonic gyre encompassing almost the entire area north of the Po delta-Rv transect (Fig. 3). These two gyres seem to be permanent features during this period, although the anticyclonic gyre slightly shifted towards the northwest. The resulting currents in the area around station SJ107 (which is at the rim of this anticyclonic gyre) were mostly directed eastward towards the western Istrian coast.

The dispersion of passive surface drifters originating at the station SJ107 (where a high accumulation of *M. leidyi* was observed during the summer of 2017; P. Paliaga, pers. comm.) was also examined, and nondimensional drifter concentrations were the highest between SJ107 and the coast (in August) and along the western Istrian coast (in July and September; Fig. 3). These results qualitatively confirm the hypothesis that *M. leidyi* seasonally accumulated in an anticyclonic gyre to the west-southwest of Rv could be advected towards the western Istrian coast, as we observed in September 2019.

3.4. *M. leidyi* abundance

Spatial distributions of *M. leidyi* are given in Fig. 4 and supplementary material (Fig. S1). At the beginning of September, the highest average abundances were registered in Valdibora Bay (~59 ind./m^3), reaching up to 100 ind./m^3 accumulated along the SE coast and covering $1.3 \cdot 10^4$ m^2. At Monsena, abundance averaged to ~6 ind./m^3, covering $2.7 \cdot 10^4$ m^2. The maximum (12 ind./m^3) was found in the inner part due to wave transport. Northwards to the open sea, abundances dropped to zero. The lowest sampling average (~5 ind./m^3) was found in the Southern Harbour. Abundances reached up to 10 ind./m^3 and covered $1.6 \cdot 10^4$ m^2. Due to the current flow, ctenophore amassed at the SE coast. At St. Ivan, abundances averaged to 13 ind./m^3 covering $3 \cdot 10^4$ m^2. The maximum recorded on the bay's NE side decreased progressively towards the outer sea, indicating accumulation by waves and currents. Around Bagnole Island, a relatively uniform distribution of 0.05 ind./m^3 covered ~10^5 m^2. Ctenophora swarms remained approximately within the same areas for a couple of days before being redistributed to other locations.

3.5. Organic matter content measured as surface-active substance (SAS), DOC and POC

The lowest concentrations (mg/L) of DOC (1.35 ± 0.1), POC (0.112 ± 0.02), SAS NF and F (0.143 ± 0.01) were found outside of swarms, while the highest were measured in the presence of ctenophore (1.9 ± 0.64 for DOC, 1.3 ± 1.38 for POC, 0.2 ± 0.08 for SAS NF and F). Overall, DOC, POC and the total SAS (NF and F fractions) were higher in the denser swarms (Fig. S2a).

The values measured at Bagnole represented a background level (0.133 mg/L) (data not shown) for SAS concentration and were comparable to those measured where ≤1 ind./m^3 (Fig. S2b). In Fig. 4, spatial distributions of plankton abundances and C-contents are given. A coupling between an increasing density of ctenophore and higher concentrations of SAS was more pronounced at the locations Valdibora and St. Ivan, where ctenophore density surpassed 10 ind./m^3. When the abundance of *M. leidyi* per m^3 was lower than 10, OM was dominantly in the surface-active DOC form, while the POC form increased with the higher abundance of *M. leidyi* (Fig. S2). The normalised surfactant activity of analysed samples to their DOC content (NSA) indicate the presence of more hydrophobic nature of OM with NSA values around 0.1.

3.6. Microbial abundance

During all samplings, the distribution of HP, HNF and CB indicated a visible coupling between them and increased ctenophore densities. The relation with SAS appeared to a lower extent (Fig. 4 & S1). The average abundances (cells/mL) of HP, HNF and CB were the highest at Valdibora Bay ($1.2 \pm 0.3 \cdot 10^6$, $18.9 \pm 9.2 \cdot 10^3$ and $7.4 \pm 1.1 \cdot 10^4$ respectively). The average HP abundance in swarms doubled ($1.4 \cdot 10^6$ cells/mL) with respect to the outside waters ($6.9 \cdot 10^5$ cells/mL) (Fig. 5a), HNF abundances ($7 \cdot 10^3$ cells/mL) increased 3.5x in swarms ($24 \cdot 10^3$ cells/mL) (Fig. 5c), while CB increased by 40% (Fig. 5b). In Monsena Bay, abundances (cells/mL) increased by 50% ($8.12 \cdot 10^5$) for HP, 2.5x ($5.1 \cdot 10^4$) for CB and 60% ($6 \cdot 10^3$) for HNF (Fig. 5). In harbour's waters, abundances of HP CB, and HNF, increased moderately, i.e. by 40%, 80% and $^1/_3$, respectively (Fig. 5).

Later in September, the average abundances (cells/mL) of HP, CB and HNF within the swarm at St. Ivan were $14.7 \cdot 10^5$, $12 \cdot 10^4$ and $21 \cdot 10^3$, respectively. The increase in abundance of microbial groups was the most pronounced in this location, where averages rose 3x for HP, 4x for CB and 5x for HNF (Fig. 5). HP displayed a strong coupling with *M. leidyi.* Their abundances rose from outer waters ($4.8 \cdot 10^5$ cells/mL) to maximums of $1.6 \cdot 10^6$. CB and HNF (cells/mL) displayed a trend similar to HP, reaching their peak concentrations ($41.3 \cdot 10^4$ and $26.5 \cdot 10^3$, respectively) in the densest part of the swarm and decreasing substantially to $3 \cdot 10^4$, and $4 \cdot 10^3$, respectively, in the open waters. Around Bagnole Island, ctenophores abundance was very low, and microbial abundances were comparable to the values registered at the outer parts

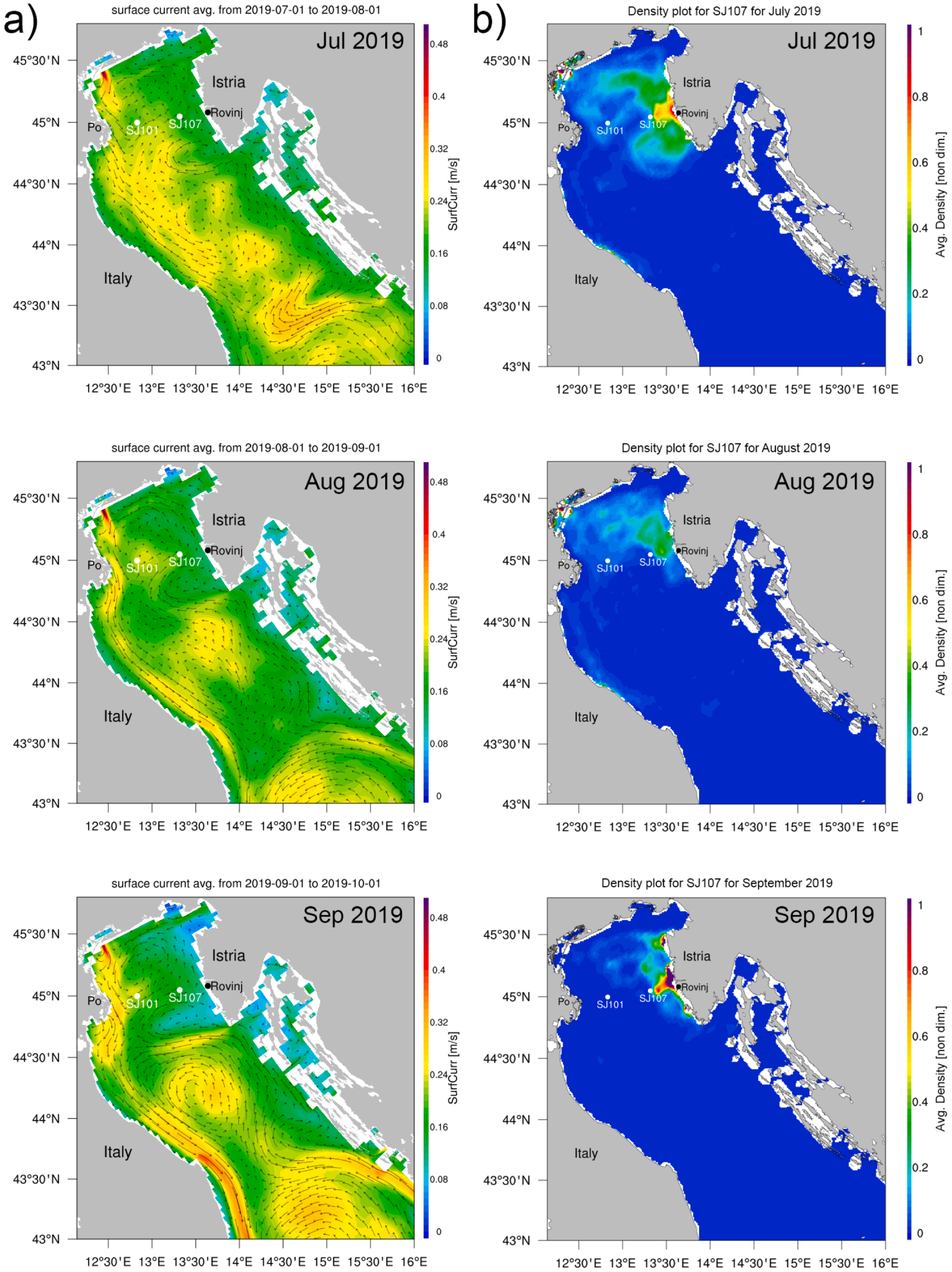

Fig. 3. a) Monthly averaged modelled surface currents for July (upper panel), August (middle panel) and September 2019 (lower panel), and b) monthly averaged density of drifters, released from 1 July 2019 in the amount of 15 drifters per day from the location corresponding to the station SJ107, for July (upper panel), August (middle panel) and September 2019 (lower panel).

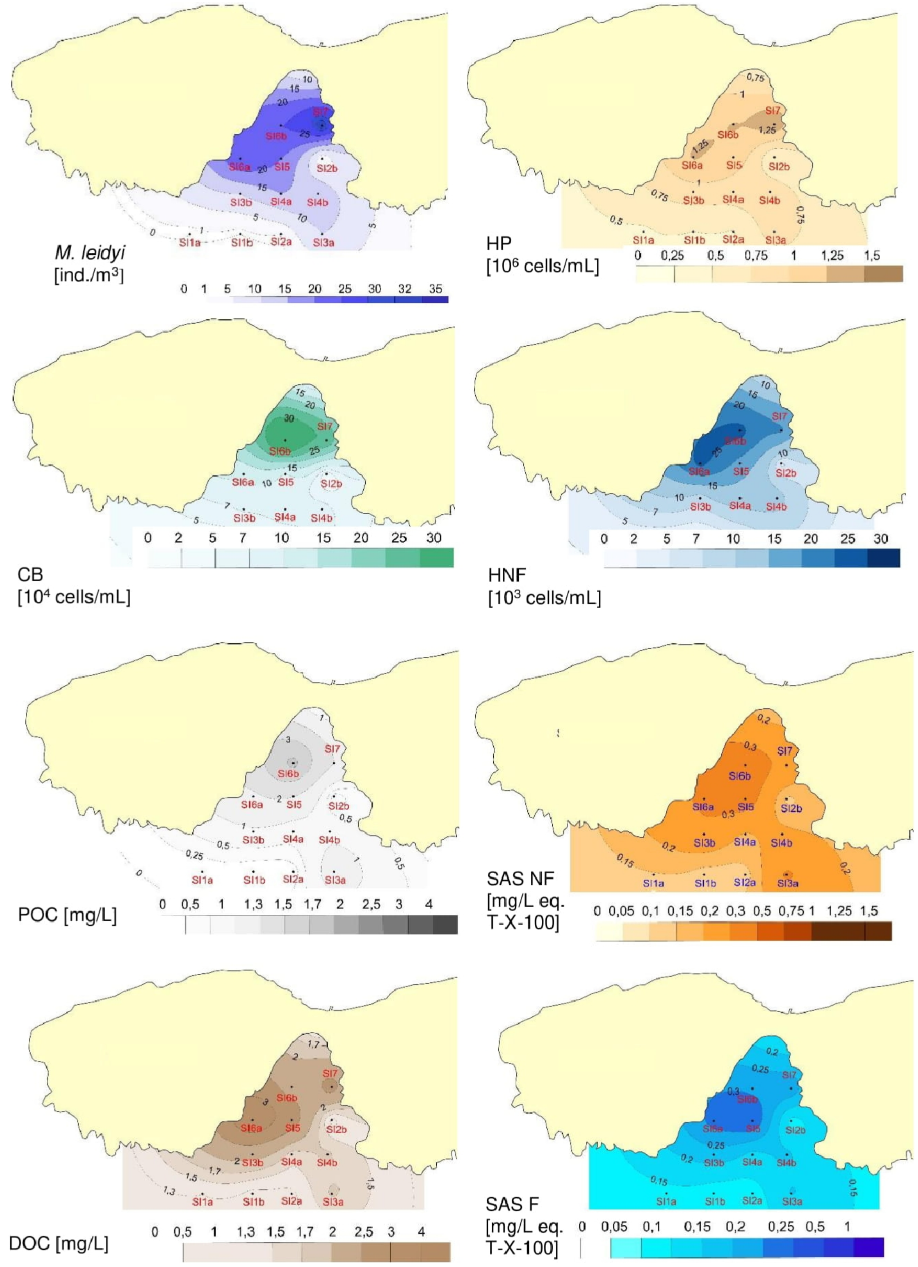

Fig. 4. Spatial distributions of plankton abundances (*M. leidyi*, HP, HNF, CB) and C-contents (DOC, POC, SAS) at St. Ivan Island.

of St. Ivan's swarm. HP varied in a narrow range (3.7–4.1·10^5 cells/mL) and averaged to ~3.8·10^5 cells/mL. CB and HNF (cells/mL), too, did not show significant variations (2.5–3.3·10^4 and 2.4–3.4·10^3, respectively). Statistical tests for differences among groups revealed significance in microbial abundances and *M. leidyi*'s presence at all the locations except at Bagnole (Table 1). Overall, statistically significant ($p < 0.01$, $N = 135$) positive correlations were obtained between *M. leidyi*, HP ($r_{HP} = 0.72$) and HNF ($r_{HNF} = 0.78$), while a weak one was found for CB ($r_{CB} = 0.35$, $N = 133$). Overall averages ctenophore abundances and POC correlated strongly ($r_{POC} = 0.88$, $p < 0.01$, $N = 16$). HNF was strongly correlated with HP, $r_{HNF \to HP} = 0.78$, and moderately with CB $r_{HNF \to CB} = 0.59$, ($p < 0.01$, $N = 133$). Picoplankton abundances also strongly correlated among themselves ($r_{HP \to CB} = 0.80$, $p < 0.01$, $N = 133$). At St. Ivan, where the best data distribution was available, swarms strongly correlated also with DOC and SAS F ($r_{DOC} = 0.89$, $r_{SAS\ F} = 0.79$, $p < 0.01$, $N = 7$) but not SAS NF. However, the latter is represented by a small data pool; thus, all the correlations should be considered just as an indication of a trend that might be confirmed in future. In addition, regression lines between the averaged, normalised plankton abundances at four potential OM accumulation areas (St. Ivan, Bagnole, Valdibora, Monsena and South Harbour) were compared (Fig. S3) and revealed linearity (R = ~0.8) up to 35 ind./m^3. In denser swarms (100 ind/m^3), microbial abundances did not follow linearity.

4. Discussion

The average concentrations of ctenophores registered at the sampling locations (0.05–59 ind./m^3) were comparable to those previously reported for September (2016–2019) for Rv coastal waters, i.e. 2.5 ± 2.1 ind./m^3 (Budiša et al., in press) except in Valdibora Bay, where abundances were higher. Ctenophore (ind./m^3) enumerated during the monitoring were comparable to those measured in other areas such as the Berre Lagoon (Mediterranean coast of France) ~2 (Marchessaux et al., 2020), 2–7 in the NW Baltic (Schaber et al., 2011), 4–11 the NE

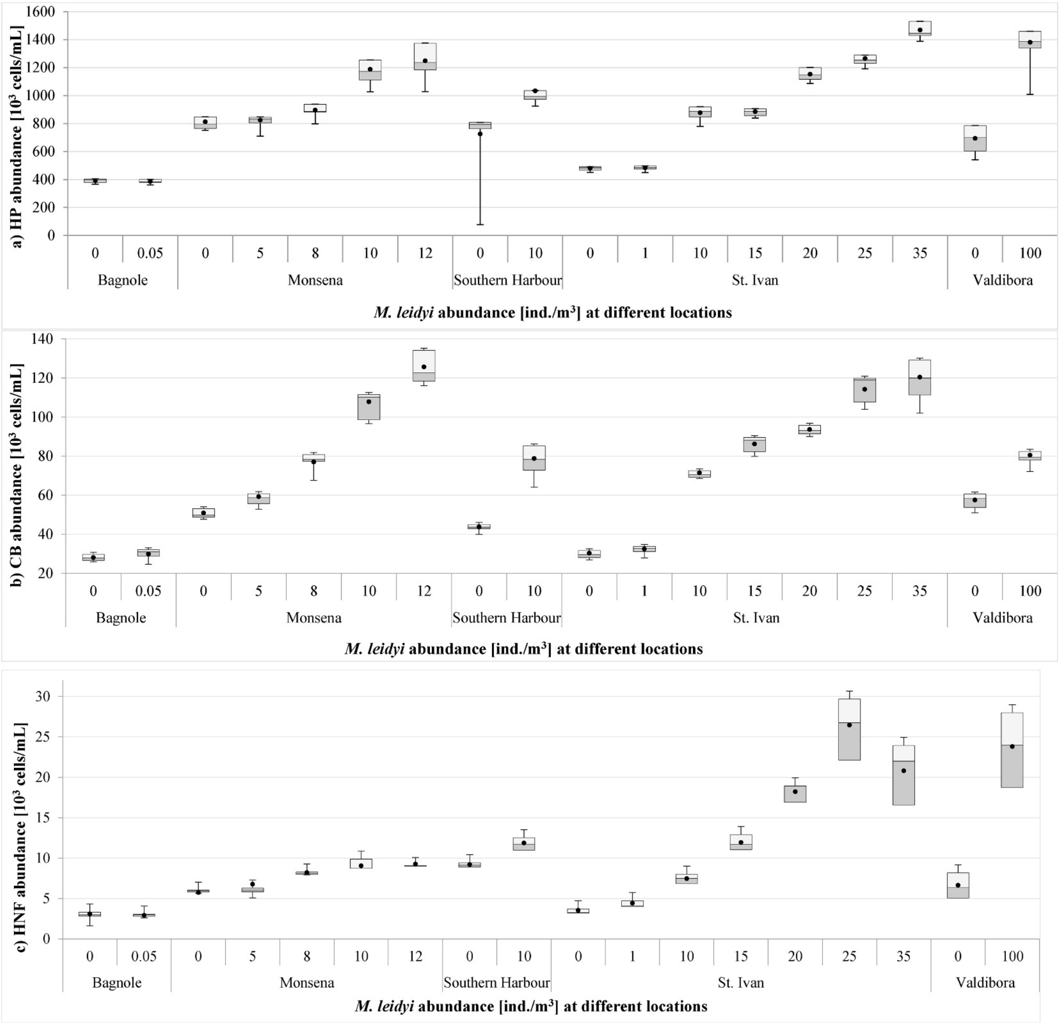

Fig. 5. The abundances of microbial community: a) HP, b) CB, and c) HNF in relation to the swarm density. The median is shown as a line inside the rectangle and the average (mean) as a dot, for each sample. The rectangle itself is an Inter-Quartile Range (IQR). The error bars represent the most extreme points, i.e. the maximum and minimum value of the group within the 1.5 IQR.

Table 1
Statistical differences between the microbial abundances in the swarms and when *M. leidyi* was absent (significance level $\alpha = 0.05$). The statistically non-significant values are marked in red. A small pool of data for the Mann-Whitney rank test allowed only for a comparison of calculated $U_{statistical}$ values with the table of critical values, and thus is marked with an asterisk (*).

	Location	Monsena Bay	Southern Harbour	Valdibora Bay	St. Ivan Island	Bagnole Island
	N (samples)	30	20	35	40	10
HP	Normal distribution	yes	No	yes	yes	yes
	Equality of variances	Homogeneous	Homogeneous	Homogeneous	Homogeneous	Homogeneous
	Difference	One way ANOVA	Mann-Whitney test	T test	One way ANOVA	T test
	p-value	$<10^{-4}$	*$U_{statistic}(0)<U_{critical}(23)$	$<10^{-4}$	$<10^{-4}$	0.72
CB	Distribution	yes (Log)	Yes	Yes	yes	yes
	Equality of variances	Homogeneous	Homogeneous	Homogeneous	Homogeneous	Homogeneous
	Difference	One way ANOVA	T test	T test	One way ANOVA	T test
	p-value	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	0.33
HNF	Distribution	no	Yes	yes (Log)	yes	Yes
	Equality of variances	Homogeneous	Nonhomogeneous	Homogeneous	Nonhomogeneous	Homogeneous
	Difference	Kruskal-Wallis	Games–Howell	T test	Games -Howell	T test
	p-value	$<10^{-4}$	$<10^{-4}$	$<10^{-4}$	0.033	0.51

Black Sea (Kamburska et al., 2006) and ~55 the western Black Sea, (Kamburska et al., 2006). The lowest concentrations measured at the swarm edges and in the open sea were close to the ones registered in oligotrophic environments, such as by the coast of Israel (0.1 ind./m^3) (Shiganova et al., 2019) and the Aegean Sea (0.3–0.5 ind./m^3) (Shiganova et al., 2001). *M. leidyi* swarms in the NE Adriatic appear in large swarms from May to November, with higher densities along the western coast of Istria and patches, covering several km^2 in the open sea (Budiša et al., in press).

In winter, *M. leidyi* is almost absent from the NE Adriatic and essentially relegated to the waters in front of and within the Italian lagoons of the NW Adriatic with a few specimens reaching the monitoring station SJ101 (Fig. 1) (CMR – Center for Marine Research database and V. Tirelli, pers. comm.). From those areas, by the end of winter and in early spring, *M. leidyi* can spread towards the NE Adriatic, as it occurred in 2017 (Ciglenečki et al., in press). *M. leidyi* increased in number within an anticyclonic gyre around the station SJ107 (Fig. 1) between May and July 2017, indicating it as an accumulation area.

The anticyclonic gyre also appeared in summer 2019 and included an area around SJ107, as observed earlier in 2017. According to the numerical model, station SJ107 was at the northern rim of the anticyclonic gyre in July–September 2019 period (Fig. 3). By hypothesizing that the gyre acts as an accumulation place for *M. leidyi*, we investigated its possible spreading paths using a lagrangian dispersion model, coupled with the results of the hydrodynamic model (Fig. 3). The results confirmed that the modelled circulation patterns could result in the advection of drifters from the gyre to the western Istrian coast. Further spreading of drifters along the coast is related to the costal dynamic. Abiotic factors, temperature and salinity that can impact the abundance of picoplankton in the northern Adriatic (Fuks et al., 2005) were similar at all the sampling stations. Therefore, the described patterns of microbial distribution in this investigation cannot be explained by those conditions.

Low-pass filtered near-surface currents with mostly S-SE direction were observed during sampling (4 and 21 September) and could be responsible for transporting *M. leidyi* along the coast (Fig. 2). The intensification of eastward transports towards the Istrian coast in relation to bora events (e.g. the one around September 6, 2019) was documented in several research papers for data collected in different time periods and based on models, satellite data and geostrophic currents computation (Kuzmić et al., 2007; Lyons et al., 2007; Kraus and Supić, 2015). Lyons et al. (2007) analysed a large number of weekly measured temperatures and salinities along the western Istrian coast with a high spatial resolution during the warm part of 2003. For most of the investigated period, geostrophic circulation implied both large cyclonic (located north of the line Po delta-Rv) and anticyclonic (positioned to the south) gyres off the Istrian coast. A similar pattern was obtained for the 2003 winter by Kuzmić et al. (2007), based on models and measurements. Changes in geostrophic circulation were found to be primarily related to changes in the thermal structure of the water column in the area, e.g. very strong eastward motions along the ‘frontal’ transect parallel to the western Istrian coast, induced by bora (September 2003), were related to the increase in average temperature in the southern part of the section, due to the formation of a deep warm water pool in open waters east of Pula (Lyons et al., 2007).

The change in current direction from NW to SE coinciding with a large temperature increase at the bottom (September 2019) may support the idea that changes in the thermal structure of the water column, reflecting on geostrophic components of the current field, were also observed directly from ADCP measurements. Finally, the intensification of eastward transports towards the western Istrian coast in September 2019 was also confirmed by the modelling results (Fig. 3).

The spatial distribution of the studied microbial components displayed a remarkably similar pattern to the swarms, indicating a coupling between them (Figs. 4 and S1). The abundances of HP, HNF and CB (cells/mL) outside the swarms (i.e. $6 \pm 2{\cdot}10^5$, $5.8 \pm 2.6{\cdot}10^3$, and $4.3 \pm 1.2{\cdot}10^3$, respectively) were close to the average, typical summer values at the sea surface of the northern Adriatic ($4.7{\cdot}10^5$-$6.3{\cdot}10^5$, $0.5{\cdot}10^3$-$1.2{\cdot}10^3$, and $40{\cdot}10^5$, respectively) (Fuks et al., 2005 & 2012). Moreover, by comparing our data to the observations for the microbial community in coastal waters of Rv registered in September (2000–2014) by the CMR database, which can be considered as a background level with an average HP of $6.9 \pm 3.4 \cdot 10^5$, HNF of $3.2 \pm 3 \cdot 10^3$ and CB of $5.5 \pm 5.4{\cdot}10^4$ cells/mL it emerges that outside the swarms, HP and HNF were very similar to the long-term averages while CB was quite smaller but not so unusual due to the high oscillations of this parameter in various years. Where ctenophore densities were ≥ 1 ind./m^3, the average HP abundance ($1.1 \pm 0.3{\cdot}10^6$ cells/mL) was around twice as high as the usual values, HNF concentration ($15 \pm 8.4{\cdot}10^3$ cells/mL) of an order of magnitude higher than the long-term maxima, and CB concentration ($8.3 \pm 2.3{\cdot}10^4$ cells/mL) close to the upper values previously registered in the basin and the long-term values in Rv (Fig. 5). Similar HP abundances were reported during phytoplankton blooms ($1.24{\cdot}10^6$ cells/mL) in the NW Adriatic, linked to the nutrient enrichment by the Po River inflow when HNF reached their annual maximum of $1.6{\cdot}10^3$ cells/mL (Fuks et al., 2012) – considerably lower than the values in swarms. Comparable HP abundances ($1.4{\cdot}10^6$ cells/mL) nearby the studied locations were reported around sewage (Paliaga et al., 2017) and industrial outfalls ($3.9{\cdot}10^6$-$5.8{\cdot}10^6$ cells/mL) (Paliaga, 2015) and during mucilage events (summers of 1999–2002) when they coincided with higher DOC and more hydrophilic nature of SAS with NSA values around 0.05 (Dautović et al., 2017; Dautović, 2019; Ciglenečki et al., 2020). Microbial abundances (cells/mL) during mucilage events averaged to $\sim 1.1{\cdot}10^6$ (from $3{\cdot}10^5$ to $3.8{\cdot}10^6$) for HP, $\sim 3.5{\cdot}10^4$ (from 10^3 to $16.6{\cdot}10^4$) for CB, and to $\sim 2.4{\cdot}10^3$ (from 10^2 to $24{\cdot}10^3$) for HNF (Fuks et al., 2005). In general, CB develop faster with increased eutrophication and due to the shifts in the N:P ratio affecting the ecosystem’s equilibrium (Stal et al., 2003). It seems that *M. leidyi*’s effects on picoplankton resemble the effects of anthropogenic organic pollution, phytoplankton blooms or mucilage events.

Ctenophores (and gelatinous organisms) release OM in the surrounding waters in different ways. One way of releasing DOC to the surrounding waters is through excretion and mucus production. In Condon et al. (2010), the estimate for *M. leidyi* is given between 0.02 and 8.86 mmol DOC (i.e. 0.24–106.4 μg C) per ind./h and increases at higher temperatures. By applying the expected higher excretion rates due to higher sea temperatures present in our research and considering an average residence time of *M. leidyi* of 48 h (as it was observed on the field) to the average abundances found in here analysed swarms, we calculated that our swarms could release between 0.026 and 0.301 mg/L of DOC. This input could only partially explain the *in situ* differences between the swarms and the surrounding waters with no Ctenophora. Within every swarm, we observed damaged and dying individuals decomposing relatively quickly. Thus, it is reasonable to assume that they have been another significant source of DOC as it is the case in other gelatinous species such as *A. aurita*, where rates of release of TOC can be by order of magnitude greater than those produced by living medusa (Hansson and Norrman, 1995; Pitt et al., 2009).

Only a part of the ingested material by *M. leidyi* is assimilated and incorporated in their biomass, while the rest is egested as faeces. This OM highly contributes to the SAS pool of DOC (Croot et al., 2007) – potentially as a significant source of utilisable substrate for HP, which is found here to be more hydrophobic OM type, with NSA around 0.1 (Ćosović et al., 2000; Ciglenečki et al., 2018, 2020). These substances contain hydrophobic (e.g. fatty acid chains, aromatic rings, or hydrocarbons) and hydrophilic functional groups (e.g. NH_2, COOH, OH, or SH) that enable the accumulation of SAS at different marine interfaces (seawater boundaries with living cells, with dispersed and particulate matter and with the atmosphere). By adsorption and desorption processes, SAS influence oceanographic properties and the structure of the natural interfaces, moderating transfer processes between different phases. Aside from zooplankton grazing, bacterial activities also contribute to the SAS pool (Kurata et al., 2016). Long-term data from the northern Adriatic demonstrated an increase in SAS concentrations, especially in its dissolved fraction (Ciglenečki et al., 2020). In part, that could be explained by recently recurring gelatinous blooms –for instance, the SAS concentration (mg/L eq. T-X-100) at the surface along the Po River-Rv transect (1989–2017) ranged from 0.015 to 0.417 (average 0.116) for SAS F, and 0.015–1.22 for SAS NF (average 0.137), being the lowest at the easternmost point – Bagnole Island (Dautović, 2019; Ciglenečki et al., 2020). There, from 1989 to 2020 averaged concentrations (mg/L eq. T-X-100) were 0.097 (in the range

0.015–0.272) for SAS F and 0.105 (in the range 0.016–0.273) for SAS NF, being lower than reported in this study (0.131–0.360 SAS NF and 0.127–0.352 SAS F). The average DOC concentration in the surface waters for 1989–2016 was 1.2 mg/L in the same area.

The total released OM by, e.g. ctenophore decomposition, may support microbial production, whilst nutrients (N, P) may support algal production (Pitt et al., 2009). Indeed, *M. leidyi*'s abundance, microbial assemblages and organic material (DOC) < 0.45 µm, e.g. living and dead cells, faecal pellets (Kharbush et al., 2020) positively correlated, pointing to enhanced microbial loop activities. The dissolved C fraction was probably readily assimilated. Expectedly, the picoplankton bloom correlated with higher abundances of its predator (HNF). Another correlation (i.e. between CB and HP) pointed to a mutual stimulus of picoplankton groups, as shown for mucilage events (Fuks et al., 2005). Up to 35 ind./m^3 a linear regression to microbial groups was noticed (Fig. S3). Higher values (100 ind./m^3) probably indicate the upper limits of the microbial response. However, further examinations of high-density swarms should be performed to prove the latter.

From late spring to the end of autumn, populations of invasive ctenophores in the northern Adriatic display substantial fluctuations in their presence (from few days to a month) (Budiša et al., in press). At the same time, maximal concentrations of DOC (up to 3.2 mg/L) overlapped with the presence of *M. leidyi* (Ciglenečki et al., in press). Previous studies showed that gelatinous zooplankton is a small DOC source compared to exudates from primary producers (Hansson and Norrman, 1995; Condon et al., 2010, 2011) but can be significant in oligotrophic environments (Guy-Haim et al., 2020) such as the northern Adriatic (Dautović et al., 2017; Ciglenečki et al., 2020) where their local abundance can be very high (Olesen et al., 1994; Benović et al., 2000). In oligotrophic ecosystems, DOM released by jellyfish is enough to sustain a high bacterial production (Turk et al., 2008). By the end of the summer in the northern Adriatic, the water column displays a strong vertical stratification and depletion of nutrients and OM in the top layer. When other sources are scarce, labile and highly reactive OM (more hydrophobic SAS) and nutrients released by the ctenophore seems to boost the growth of picoplankton that is being preyed on by HNF. The seasonal presence of *M. leidyi* in the NE Adriatic is starting to affect many components of the pelagic system that might lead to deleterious environmental alterations requiring further attentive monitoring.

5. Conclusions

The present study provides insights unravelling the effects of high densities aggregations of gelatinous zooplankton on the organic matter (SAS, DOC and POC) and the pelagic ecosystem. Intensive blooms of *M. leidyi* accumulated in the coastal waters of Rovinj-Rovigno change the content and type of OM (with more hydrophobic SAS) in the surrounding water, which exceeded SAS and DOC long-term values and caused a trophic cascade on the microbial community. The ctenophore release dissolved, highly surface-active OM that tends to be absorbed in different surfaces or interfaces or degraded by microorganisms. Moreover, OM accumulates only in bays with reduced current flow and the available C fuels the local pico- and nanoplankton microbial loop. In the open sea area with intense current dynamics, no accumulation of ctenophores, OM and microorganisms were found.

ADCP measurements of coastal currents and model results indicate that a specific circulation system of eastward transports and pronounced ICCC could advect *M. leidyi* from its hypothesized spring/summer nursery areas towards and along the coast, where their number can significantly increase. The eastward motions of *M. leidyi* could be initiated by vertical instability events, altering thermal fields and reflecting on the geostrophic component of currents.

The *M. leidyi* biomass in the Adriatic Sea is higher than any other gelatinous zooplankton so far in the basin, suggesting the need to follow its effects on the pelagic system. In addition, other long-term effects of the invasive *M. leidyi* on the whole ecosystem, the fisheries could be studied by ecosystem modelling approaches. To the best o our knowledge, this study is the first that attempted to connect and correlate *M. leidyi* and surface-active DOC.

CRediT authorship contribution statement

Paolo Paliaga: Conceptualization, Methodology, Validation, Visualization, Project administration, Writing – review & editing, Investigation. **Andrea Budiša:** Conceptualization, Project administration, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Methodology, Validation, Writing – review & editing, Investigation, Writing – original draft. **Jelena Dautović:** Investigation. **Tamara Djakovac:** Funding acquisition, Supervision, Resources, Data curation, Writing – original draft, Writing – review & editing. **Mathieu Andre Dutour-Sikirić:** Writing – review & editing, Methodology, Software, Validation, Formal analysis. **Hrvoje Mihanović:** Conceptualization, Visualization, Writing – review & editing, Writing – original draft, Methodology, Software, Validation, Formal analysis. **Nastjenjka Supić:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing, Visualization, Methodology, Software, Resources, Formal analysis, Validation, Data curation, Writing – original draft. **Igor Celić:** Methodology, Validation, Formal analysis, Writing – original draft. **Neven Iveša:** Writing – review & editing. **Moira Buršić:** Writing – original draft, Writing – review & editing. **Ivan Balković:** Writing – original draft, Writing – review & editing. **Lara Jurković:** Writing – original draft, Writing – review & editing. **Irena Ciglenečki:** Conceptualization, Funding acquisition, Project administration, Methodology, Writing – review & editing, Writing – original draft, Validation, Resources, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107459.

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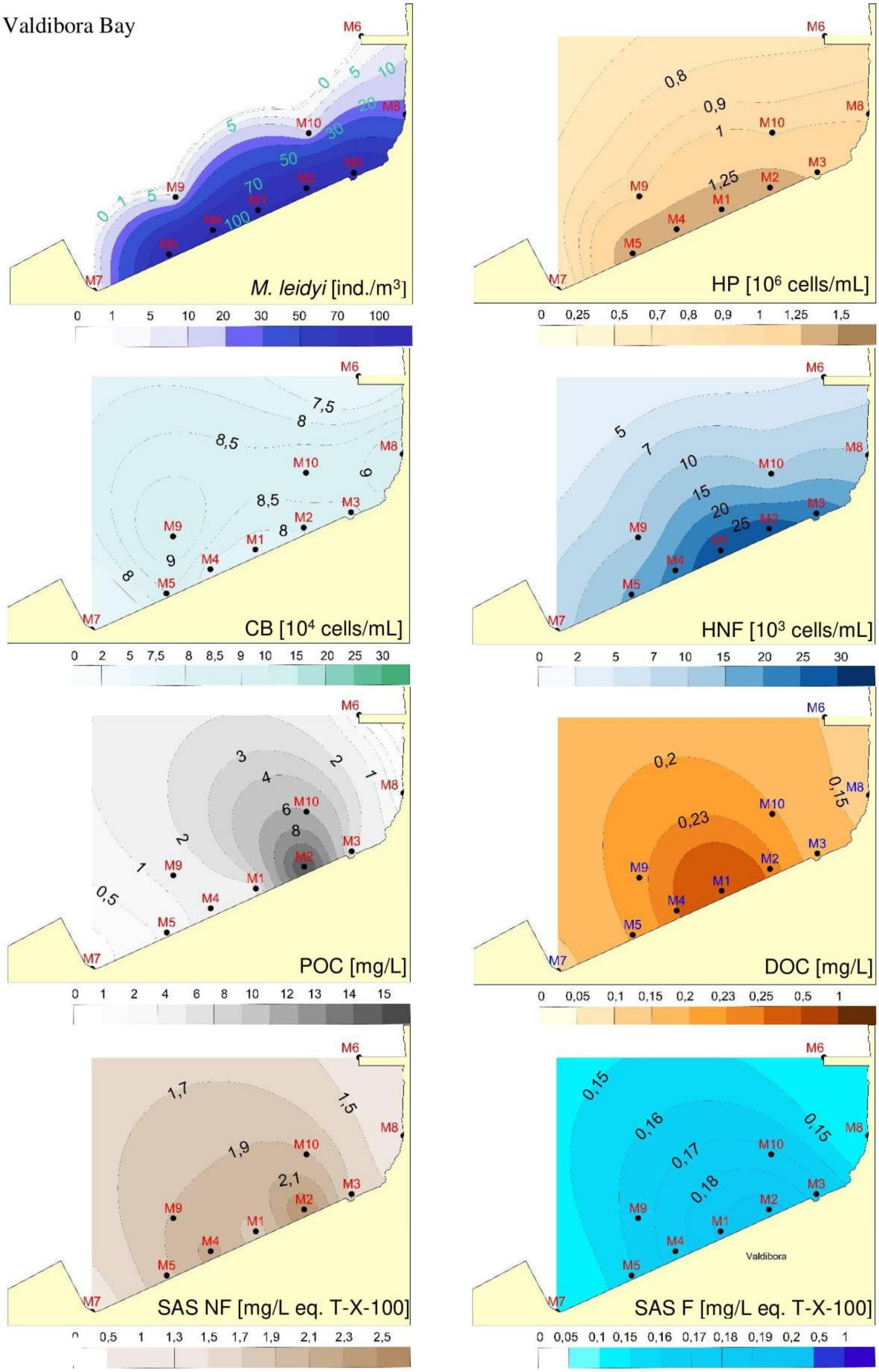
Supplementary material

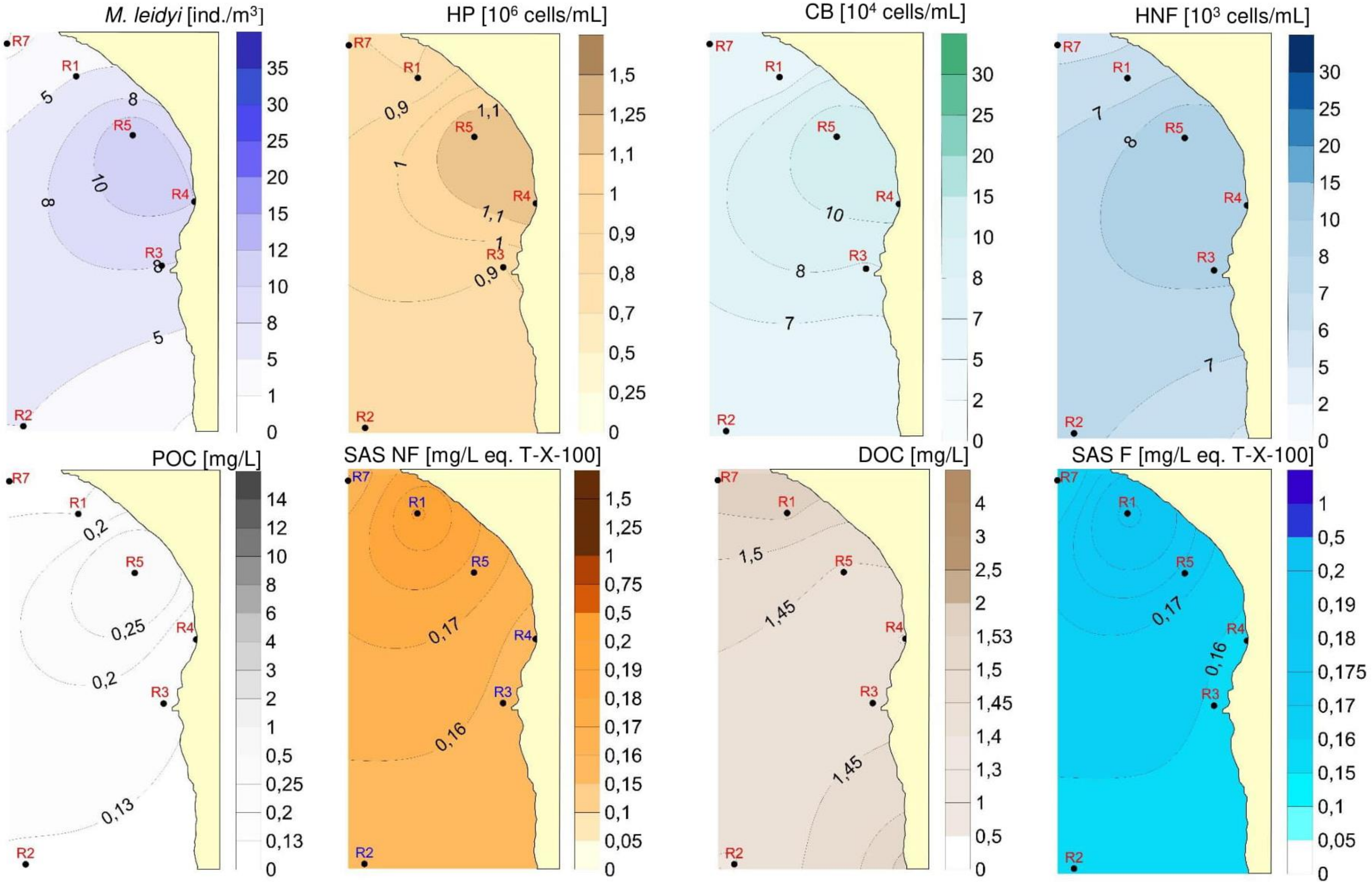
Table S1 Sampling specifications

Location	Coordinates	Sampling period
Valdibora Bay	45°05'10.0"N 13°38'19.1"E	4 September 2019
Southern Harbour	45°04'53.0"N 13°38'07.8"E	4 September 2019
Monsena Bay	45°06'42.3"N 13°36'39.4"E	4 September 2019
Bagnole Island	45°04'32.3"N 13°36'39.2"E	21 September 2019
St. Ivan Island	45°02'46.7"N 13°37'22.2"E	21 September 2019
Current meter station	45°04'44.8"N 13°36'27.9"E	July-September 2019
Station SJ107	45°02'53.9"N 13°19'0.0 "E	July-September 2019
Station SJ101	44°59'53.9"N 12°49'48"E	January-March 2017 (Ciglenečki et al., under review)

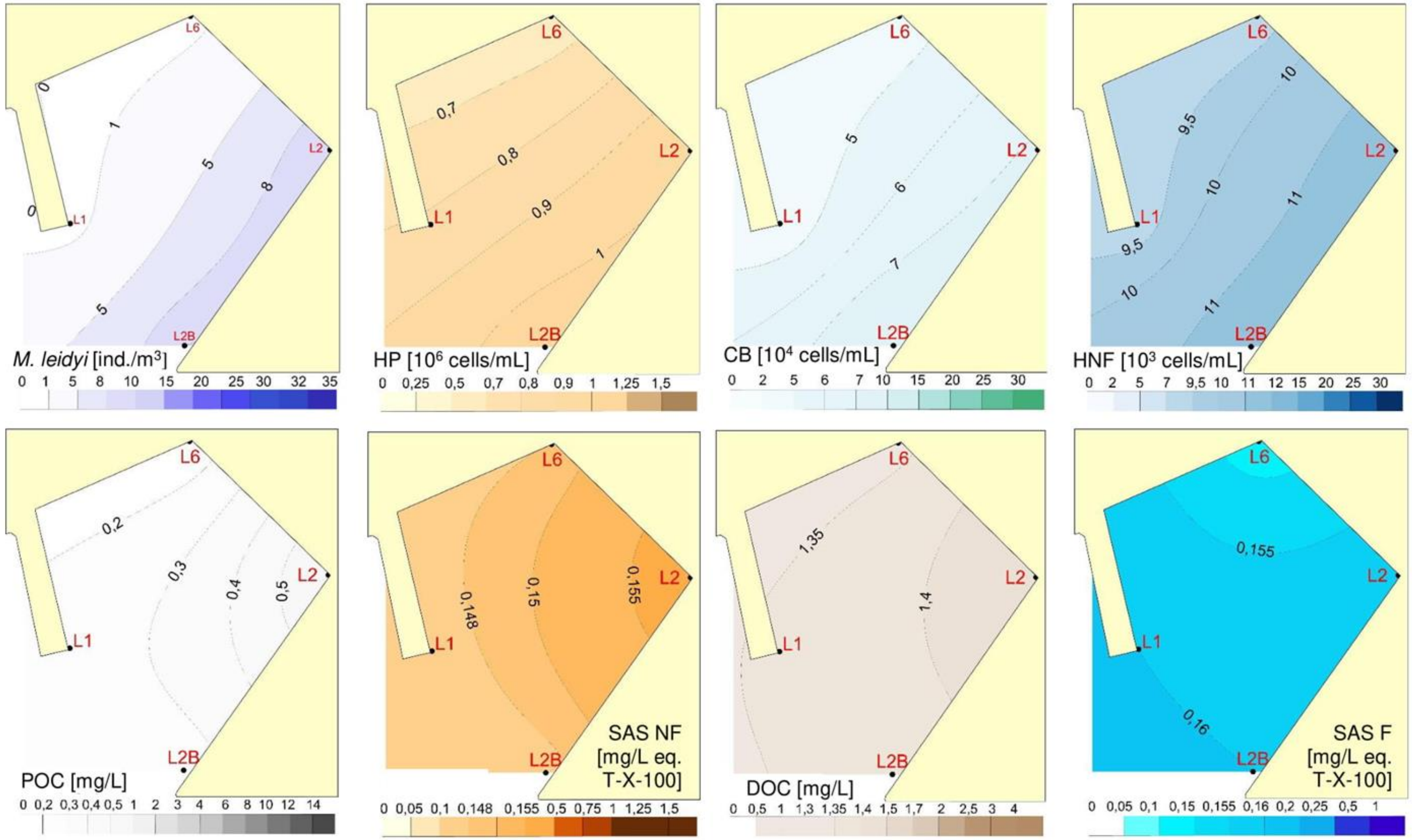
a) Valdibora Bay



b) Monsena Bay



c) Southern Harbour



d) Bagnole Island

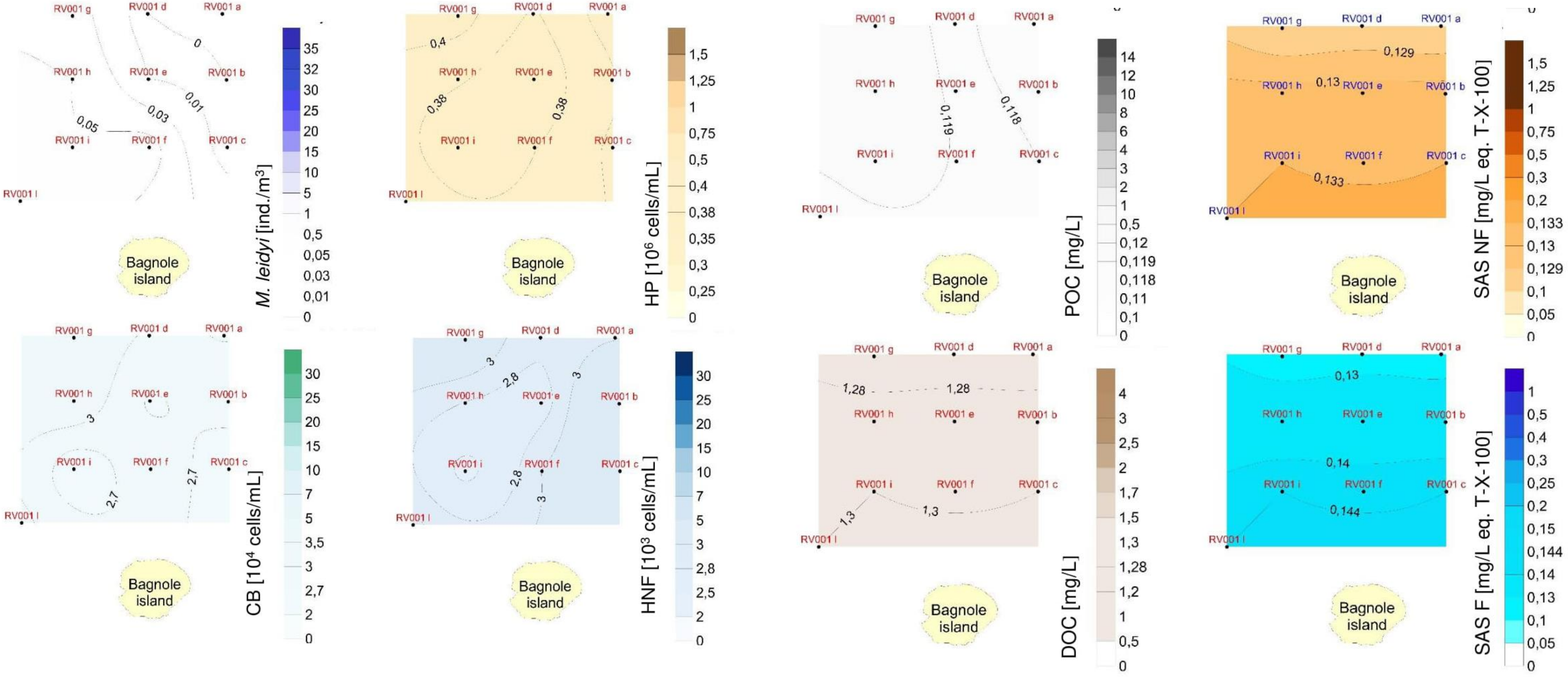


Figure S1 Spatial distributions of plankton abundances (*M. leidyi*, HP, HNF, CB) and-C contents (DOC, POC, SAS) at: a) Valdibora Bay, b) Monsena Bay, c) South Harbour and d) Bagnole Island.

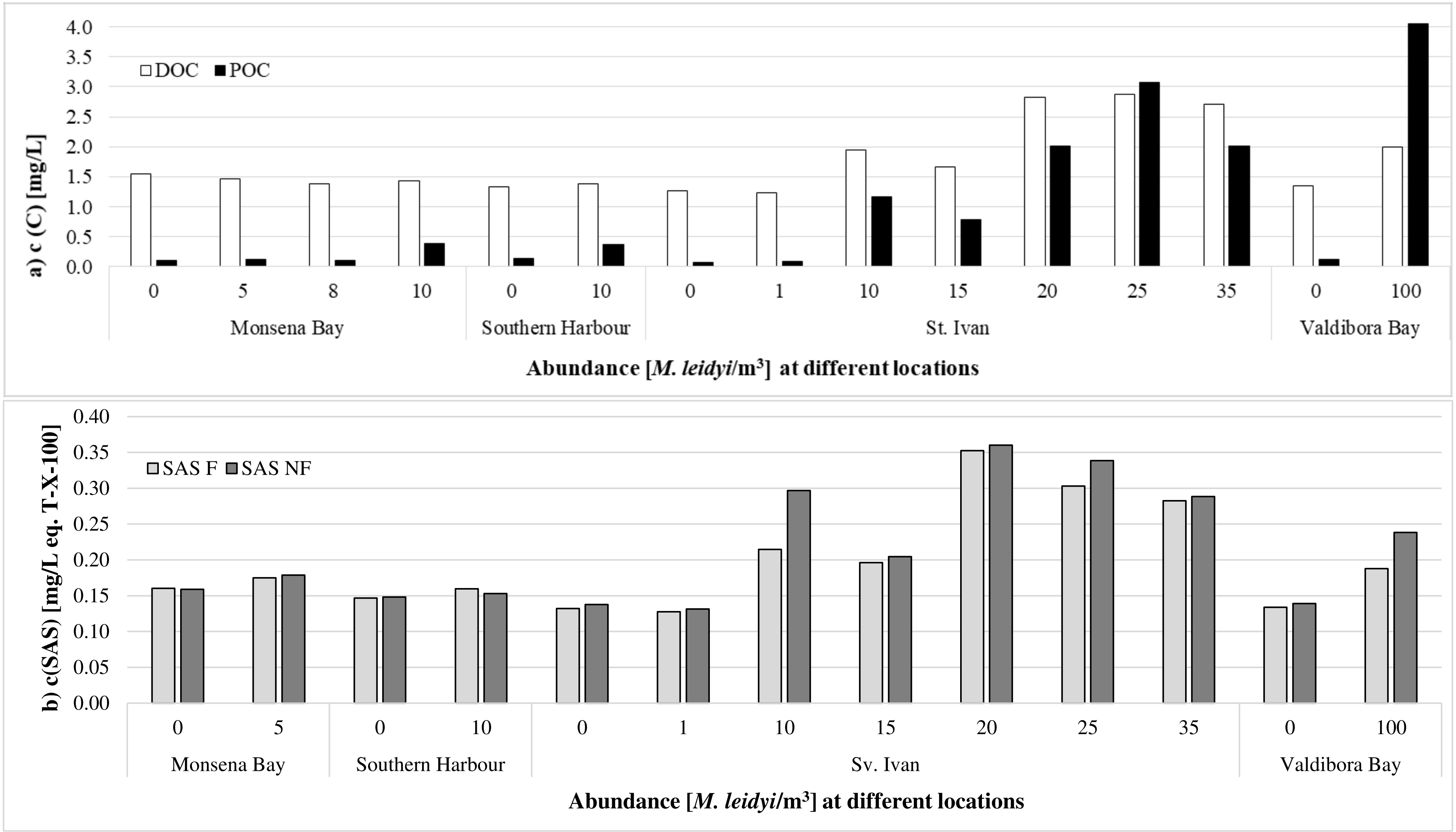


Figure S2 C-content in the seawater in relation to *M. leidyi*'s presence, measured at four potential OM accumulation areas and expressed as: a) POC and DOC, and b) SAS NF and SAS F.

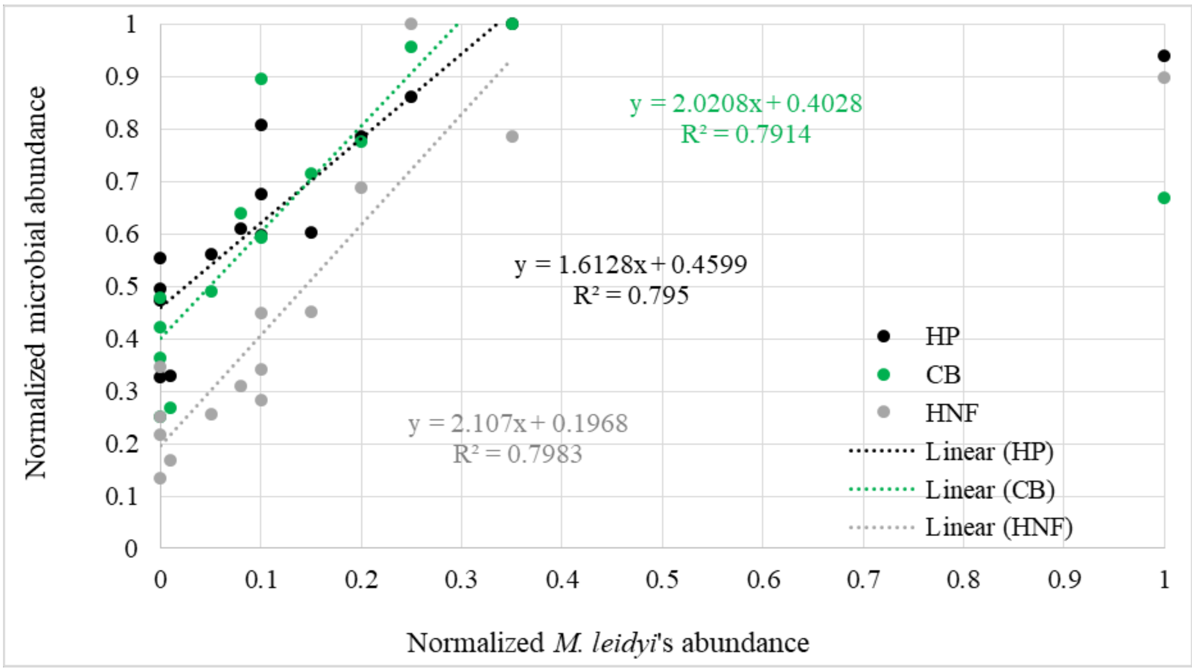
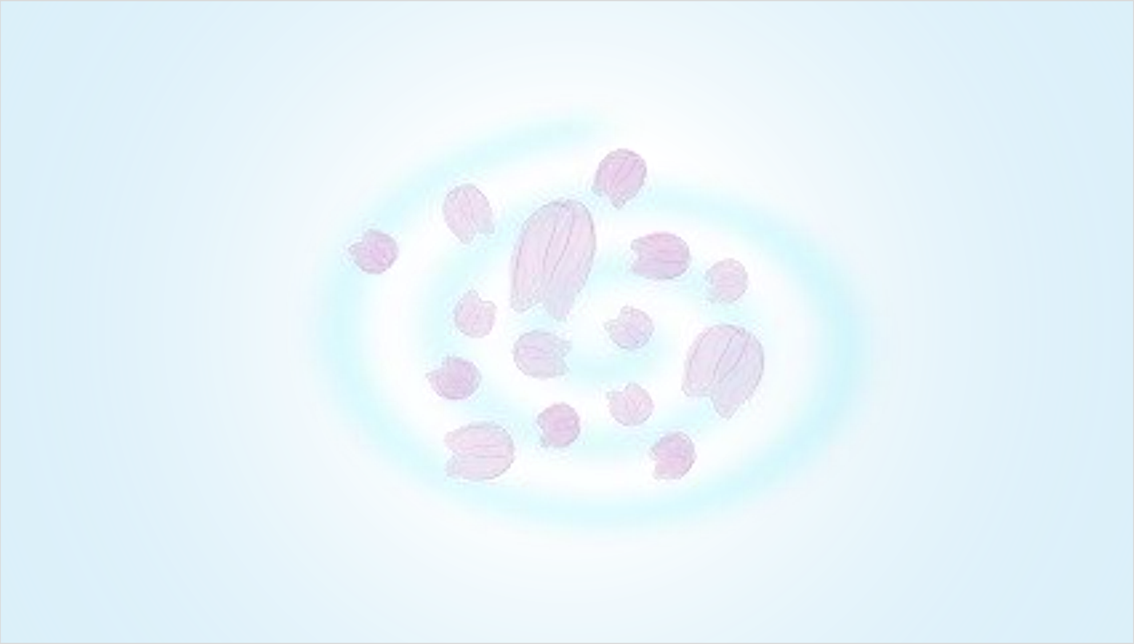


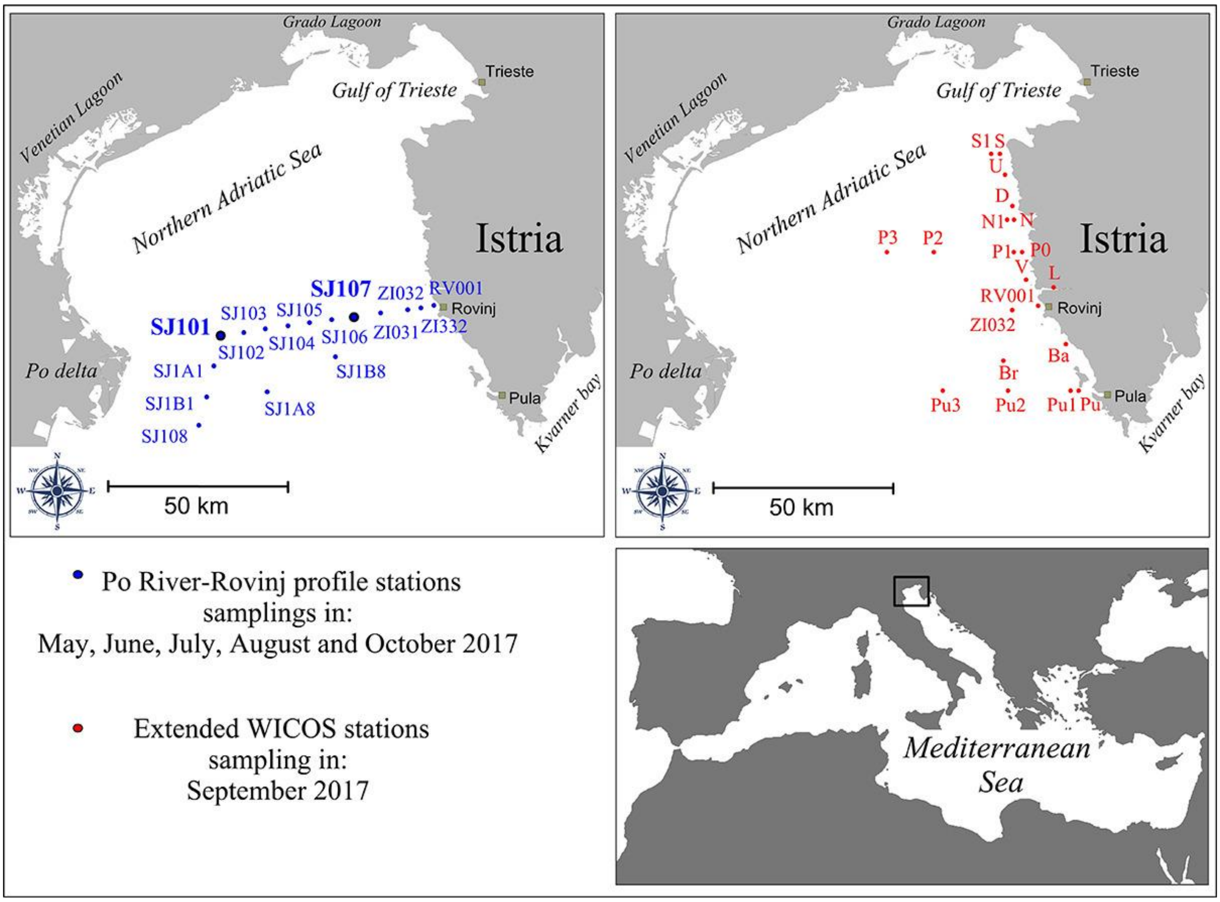
Figure S3 Regression lines between average abundances of microbial community and swarm densities at four potential OM accumulation areas.

III Publikacija



Graphical abstract

Map of the studied area and main sampling locations along the Po River-Rovinj transect (in blue, upper left panel), and additional coastal stations (extended WICOS profile, in red, upper right panel) in the northern Adriatic.



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Dissolved organic carbon accumulation during a bloom of invasive gelatinous zooplankton *Mnemiopsis leidyi* in the northern Adriatic Sea; case of the anomalous summer in 2017

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ABSTRACT

In the so-called “anomalous” summer in 2017, an increased concentration of DOC was measured in the entire water column at the station SJ107 (eastern part of the Po River delta-Rovinj transect, Graphical abstract) in the northern Adriatic (NAd). Surface DOC ranged between 1.56 and 3.10 mg l^{-1}, being 2.5 times higher than the long-term (1989–2017) average for the same area. Such enlarged concentration of DOC, typical for eutrophic lagoons or lakes and not for open waters, was most probably a consequence of an intensive bloom of *Mnemiopsis leidyi*, which was recorded with an exceptionally high population density (up to 76 ind. m^{-3}) in the same waters.

The number of jelly combs showed a decrease from the east (SJ107) to the west (SJ101) of the transect (Graphical abstract). Abundance in the central part of the transect was also quite low. Maximum of DOC corresponded with the abundance of the *M. leidyi* smallest specimens (<3 cm). At the western station of the same profile (SJ101), *M. leidyi* abundance was insignificant, and DOC concentration appeared to be controlled by seasonal changes in primary production and grazing activities. In contrast, at the eastern station (SJ107), changes in the complex food web interaction shaped the DOC quantity and quality. A large fraction of DOC at both stations was found to be reactive, significantly contributing to the organic matter pool represented by surface-active substances (SAS).

A large anticyclonic gyre which developed from April to November in 2017 in the area of SJ107, supported calm water column conditions and abundant resources of zooplankton, which could support the residence and accumulation of the invasive ctenophore *M. leidyi*. For the first time, the presence of a long-lasting gyre (duration of at least 4 months) is documented both with hydrographic measurements and by numerical modelling. Such a situation characterised by the production of highly reactive DOC leads to an extreme eutrophic episode.

A dispersion model indicated a high probability of *M. leidyi* spreading by the end of winter from the Venice Lagoon, its hypothetical winter residing area, to the Istrian coast (Croatia).

1. Introduction

Dissolved organic carbon (DOC) represents a dynamic fraction in the global carbon cycle, and it is now recognized as an important tracing factor of global change (Ciglenečki et al., 2020 and references therein). DOC, the measurable elemental organic carbon content of dissolved organic matter (DOM) (Filella, 2009) that can pass through a 0.45 μm pore size filter, plays an important role in photochemical reactions, metal complexation, and the transport of nutrients and contaminants in natural waters. A significant proportion of seawater DOC is composed of surface active substances (SAS), considered as its most reactive fraction (Ciglenečki et al., 2020 and references therein). DOC and SAS in coastal

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areas predominantly originate from biological, mostly phytoplankton production, and from terrigenous inputs. Still, some human activities can contribute as well (tourism, maritime traffic, oil rigs).

In planktonic food webs, zooplankton has an important role in nutrient cycling via its excretion of inorganic compounds, primarily in the form of ammonium (NH_4^+) and phosphate (PO_4^{3-}) (Steinberg and Saba, 2008), and by the release of DOM. Most studies on zooplankton excretion have emphasized the role of crustacean zooplankton (e.g. copepods, euphausiids); some underlined the excretion of DOM and nutrients by gelatinous zooplankton due to their high biomass during blooms (Condon et al., 2010 and references therein). Gelatinous zooplankton is referred to as a major source of recycled nutrients to dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) pools in the York River estuary, Chesapeake Bay (Condon et al., 2010). In gelatinous zooplankton, the excretion of DOM may be significantly enhanced through mucus production. The release of nutrients by gelatinous zooplankton may favour phytoplankton growth because the excretion of NH_4^+ and PO_4^{3-} occurs in ratios similar to the Redfield N:P stoichiometry (Kemp et al., 2005) and may release phytoplankton from N-limitation.

The ctenophore *Mnemiopsis leidyi* releases significant quantities of their total excretes as DOC (Hansson and Norrman, 1995). These DOC substances are classified as an important labile DOC pool, which supports and controls microbial production.

In the northern Adriatic (NAd), the first large-scale blooming of the invasive ctenophore *M. leidyi* was registered in the offshore, coastal and lagoon systems of the Istrian and Italian coasts in 2016 from July to December (Malej et al., 2017; Paliaga et al., 2019; Budiša et al., 2021). Specimens were mainly observed in the surface layer down to 5 m depth and occasionally deeper (up to 15 m). Collected adult individuals reached a total length maximum of 13.5 cm, and dense blooms were detected intermittently from mid-August to November 2016. The spatial distribution between the rest of the Mediterranean where *M. leidyi* is recorded regularly (Ghabooli et al., 2013; Shiganova et al., 2014), and the NAd, where it resides since 2016, points to its most plausible transfer by ballast waters (Malej et al., 2017; Paliaga et al., 2019; Budiša et al., 2021).

Mass occurrences of gelatinous organisms can form a true bloom, caused by the combination of favourable environmental conditions and life history events resulting in a rapid increase in population numbers (Hamner and Dawson, 2009; Kogovšek et al., 2010; Shiganova et al., 2019). On the other hand, they can also represent aggregations of individuals brought together by the physical forcing of water movements and bottom topography (Graham et al., 2001) or behavioural responses (Hamner and Dawson, 2009; Boero, 2013). However, dramatic spatial increases and temporal shifts in the occurrence of gelatinous organisms (in particular ctenophores and cnidarians) that have appeared worldwide (i.e. in many estuarine, coastal, and open-ocean ecosystems) over the past decades are discussed as a consequence of eutrophication, overfishing, climate variations, accidental introductions or translocations, increased polyp abundances, and habitat modifications (Purcell et al., 2007; Richardson et al., 2009).

Production in the NAd so far is held to be mainly dependent on the nutrient-rich freshwater outflow of the Po River delta (Degobbis et al., 2000), with phosphorus identified as the main limiting factor in organic matter (OM) growth (Ivančić et al., 2016). In some years, increased organic production leads to eutrophication and the appearance of mucilage events (e.g. Precali et al., 2005) characterised by high DOC content (Ciglenečki et al., 2003; Giani et al., 2005; Dautović et al., 2017). Gyres of cyclonic and anticyclonic cycling are known to appear in the investigated region (Supić et al., 2000, 2012; Kuzmić et al., 2007) and are attributed as locations where the accumulation of OM occurs and may lead to hypoxic and anoxic events (Orlić et al., 2013; Djakovac et al., 2015).

The year-to-year changes in primary and secondary production in the NAd have been discussed and explained by changes in the circulation as well as in the Po River discharge rates or the degree of the Po waters spreading towards the east (Djakovac et al., 2012; Marić et al., 2012; Kraus et al., 2015, 2016).

Long-term trends and changes of the oceanographic conditions and production in the NAd appear to be controlled by large scale atmospheric phenomena (e.g. Dulčić et al., 2004; Grbec et al., 2018) and by the inflow of Mediterranean waters forced by the so-called Bimodal Oscillating System (BIOS; e.g. Civitarese et al., 2010). The impact of these processes in the NAd has already been discussed (Supić et al., 2004; Peharda et al., 2018) and recently correlated with the long-term (1989–2017) OM changes (Dautović et al., 2017; Ciglenečki et al., 2020). These OM changes indicate altering episodes of eutrophication (DOC >2.44 mg l^{-1}) and oligotrophication (DOC <1.44 mg l^{-1}), embedded into an overall oligotrophication trend. At the same time, an increasing SAS trend was recorded, which points towards OM qualitative changes (Ciglenečki et al., 2020).

In this study, we focused on a remarkable DOC increase episode in the NAd recorded during a bloom of the invasive ctenophore *M. leidyi* in the water column along the Po River – Rovinj transect in 2017 (Graphical abstract). The year 2017 has been considered anomalous regarding high salinity and temperature values that vastly affected microbial activities (Beg Paklar et al., 2020). Here, analyses of DOC and particulate organic carbon (POC), including estimation of their reactivity, based on measurements of their surface-active fraction (SAS), were conducted at two stations in the NAd, representing the western (SJ101) and the eastern (SJ107) part of the region (Graphical abstract). Thus, to explain OM dynamics (its quantitative and qualitative characteristics), we have additionally considered the following oceanographic parameters: physical (temperature, salinity, density), chemical (concentration of nutrients) and biological parameters (chlorophyll-*a,* Chl *a* concentration, phytoplankton abundance and community composition, microzooplankton and mesozooplankton, including ctenophores, i.e. *M. leidyi*).

2. Materials and methods

2.1. Study site and sampling

The Adriatic Sea is a landlocked NW-SE orientated sea, connected to the Mediterranean (Ionian Sea) through the Straits of Otranto (Graphical abstract). A broad shelf in the north is also the shallowest part of the basin (average depth of 40 m) (Kourafalou, 1999; Pikelj and Juračić, 2013). During the winter, cyclonic circulation brings in warmer waters from the south. In contrast, the northernmost waters exposed to powerful, cold wind Bora (NNE/ENE) get transported southwards along the west coast (Dorman et al., 2006). In spring, low-salinity waters from the Po delta start meandering towards the east (anticyclonic meandering), reaching the Istrian coast in August and September (Krajcar, 2003). The overall circulation in the north part is considered “open“in the cold and “closed“in the warm part of the year, implying its separation from the rest of the Adriatic (e.g. Orlić et al., 1992). Sampling in this study was conducted at two stations in the NAd, representing the western (SJ101) and the eastern (SJ107) part of the region (Graphical abstract). These stations are part of the most investigated area in the transect situated between the Po River delta and the town of Rovinj.

Water samples were collected by 5 L Niskin bottles from January to October in 2017 (January 27, February 16, March 28, May 3, June 12, July 12, August 30, October 4-only SJ107) at standard depths of 0, 5, 10, 20 and around 30 m at SJ101, while station SJ107 was additionally sampled at a depth of 35 m. On February 16, samples for POC and DOC were not taken at 20 m depth; microzooplankton was not sampled, and phytoplankton was collected additionally at 5 m depth. Phytoplankton samples were collected from the depths of 0 and 10 m, as well as from 2 m above the bottom. Besides these depths, samples for microzooplankton analysis were additionally collected from 20 m. The temperature was measured with protected reversing digital thermometers

(Richter&Wiese; precision ±0.01 °C) attached to the Niskin bottles. Salinity samples were analysed in the laboratory by high precision salinometers (Beckman RS-7C and Yeo-Kal 601; precision ±0.01), using algorithms recommended by UNESC-O (1983). In addition to the collected water samples, vertical profiles of temperature, salinity and density were measured by CTD probe at stations SJ101, SJ102, SJ103, SJ104, SJ105, SJ106, SJ107, ZI031, ZI032, ZI332 and RV001. The Seabird SBE25 CTD probe (vertical resolution 8 cm; measurements frequency 8 Hz) was used in all cruises and stations, except the July cruise where the CTD probe Sontek CastAway (vertical resolution of 1 cm; measurements frequency 5 Hz) was used at all stations except RV001. Prior to further analysis, the raw data were averaged every 0.5 m along the water column. The SBE25 CTD samplers skip the surface layer of the water column, and the first measured depth is at 1 m or more. On the contrary, the CTD probe Sontek CastAway first samples refer to the 0.5 m depth.

2.2. *Chemical and biological analyses*

Nutrient concentrations (total inorganic nitrogen – TIN as the sum of nitrate-NO_3^-, nitrite-NO_2^- and ammonium-NH_4^+, and orthophosphate-PO_4^{3-}) were analysed aboard, immediately after sample collection by spectrophotometric methods widely used in oceanography (Strickland and Parsons, 1972). Ammonium was determined by a modified technique of the indophenol blue method (Ivančić and Degobbis, 1984).

Chl a concentrations were measured fluorometrically after extraction of Whatman® GF/F filters with acetone (Parsons et al., 1984).

Dissolved (DOC) and particulate (POC) organic carbon were measured by high-temperature catalytic oxidation (HTCO) method and non-dispersive infrared (NDIR) CO_2 detection using a TOC-Vcph instrument (Shimadzu, Japan). Pt on silica was used as a catalyst to determine the dissolved fraction (DOC). The combination of Pt/Si and CoO was used as a catalyst, and the analysis was performed in the solid sample module SSM-5000A to determine the particulate fraction (POC).

SAS measurements were conducted by the electrochemical method a. c. voltammetry as previously described (Ćosović and Vojvodić, 1982, 1998; Ciglenečki et al., 2020). The method is based on the measurements of the SAS adsorption effects at the surface of the hanging mercury drop as a working electrode in the seawater sample and 0.55 M NaCl used as the model electrolyte. Selected adsorption potential conditions (−0.6 V by Ag/AgCl electrode) and adsorption time (15–120 s) with stirring were used. Changes of the working electrode double layer, reflected on the capacitance current, were approximately proportional to all (dissolved and particulate) SAS in the solution. By filtration through a Whatman® GF/F filter (0.7 μm pore size), total SAS (SAS_T, non-filtered) from the original sample was separated into particulate and dissolved fractions (SAS_{diss}, filtered). Content of SAS was expressed in the equivalents of the selected model organic matter substance of Triton-X-100, which was proved to be a good representative of the most reactive part of SAS in natural waters (Ćosović and Vojvodić, 1982, 1998; Orlović-Leko et al., 2016; Ciglenečki et al., 2020 and references therein).

2.2.1. *Phytoplankton*

Samples (200 ml) for the identification and enumeration of phytoplankton cells were preserved in a neutralised formaldehyde (2% final concentration) solution. Sub-samples of 50 ml were allowed to precipitate for 24 h, and cells were counted on an inverted Zeiss Axiovert 200 microscope following the Utermöhl method (Utermohl, 1958). Cells were counted on transects or randomly selected fields. Nanophytoplankton cells (2–20 μm) were first analysed at 400× magnification. In this way, a number of small coccolithophorids, as well as individual diatom cells (e.g. members of genus *Chaetoceros*), and dinoflagellates / nanoflagellates were counted. Flagellates (<20 μm) were not identified at the species level but grouped in the following algal groups: cryptophytes, prymnesiophytes, prasinophytes, and chlorophytes. The groups that were very numerous were counted in randomly selected fields at 400× magnification. After that, microphytoplankton was counted at 200× magnification on two transects using phase contrast, followed by examining the whole chamber bottom at 100× magnification. In this way, large dinoflagellate cells were counted together with low abundance cells, which were not counted before. Very abundant cells were counted with randomly selected fields at 200× magnification. The accuracy of counting with this method is around ±10%. Counted values were converted to the number of cells per litre (cells l^{-1}) of seawater with different conversion factors. The main taxonomic references used to identify the phytoplankton were Tomas (1997) and Viličić (2002) and other relevant literature for taxonomic identification.

2.2.2. *Zooplankton*

Microzooplankton abundance was computed as a sum of non-loricate ciliates, loricate ciliates, nauplii, and copepodites. The samples were preserved with formaldehyde (3.5% final concentration) neutralised with $CaCO_3$, and sedimented for 72 h. The original volume of 5 l was reduced to 10 ml by discarding the supernatant. The organisms were counted with Olympus inverted microscope at magnifications of 100× and 400×. Mesozooplankton samples were collected by bottom-to-surface vertical tows with WP2 plankton net (diameter 80 cm) and were examined under Olympus SZX 9 stereomicroscope.

2.3. *M. leidyi sampling and analyses*

The monitoring and samplings of *M. leidyi* were carried out at the sea surface (0–1 m depth) of 16 stations (including SJ107 and SJ101) along the Po River delta-Rovinj transect (SJ1A8, SJ108, SJ1B1, SJ1A1, SJ101, SJ102, SJ103, SJ104, SJ105, SJ106, SJ107, SJ1B8, ZI031, ZI032, ZI331, and RV001) (Graphical abstract, Table S1) from May to October 2017. In September 2017, surface sampling was performed at another set of 20 stations (S1, S, U, D, N0, N1, P0, P1, P2, P3, V, RV001, Ba, Pu, Pu1, Pu2, Pu3, and ZI032) along the western Istrian coast named extended WICOS (Graphical abstract, Table S1). Stations ZI032 and RV001 are part of both transects. Sampling was performed by research vessels ‘Vila Velebita’ and a small motorboat. Water samples were collected by 5 L Niskin bottles.

Abundances of *M. leidyi* were determined by visual census from the boat, zooplankton net and skin divers at the sea surface. The collected spatial distribution data were analysed and graphically displayed using SURFER 12 Golden software.

2.3.1. *M. leidyi – biometric characteristics*

M. leidyi specimens collected from the zooplankton net were placed in pre-weighed aluminium weighting bowls (15 cm × 15 cm area). Wet mass (WM) was determined after blotting on paper, while dry mass (DM) after drying at 60 °C to constant weight (>24 h). Total length (TL) and body width (BW) were measured to the nearest 1.0 mm.

2.3.2. *M. leidyi – organic content*

Several representative specimens were selected for gravimetric analysis by loss on ignition. Selected pre-weighted samples were lyophilised for 48 h to eliminate water and then placed in weighed ceramic cups. Samples were weighted and burned for 4 h at 550 °C to determine the organic content. At this temperature, covalent carbon bonds in the organic material break and the material that remains to contain only inorganic carbon forms. Ignition was carried out in a furnace with a digital temperature display. Cups with the remaining matter were placed in a desiccator to cool before any further measurements and, lastly, weighted. As suggested by Heiri et al. (2001), the following equations were used to calculate organic matter as a loss on ignition: $LOI_{550}(°C) = [DW_{105}(°C)–DW_{550}(°C)/DW_{105}(°C)] \times 100$, where DW stands for dry weight and LOI for loss on ignition. Results were graphically displayed as the organic matter content in specimens and the water column.

2.4. Statistical analyses

2.4.1. Basic statistical analyses

Total amount in the water column of SJ101 and SJ107 for nutrients, Chl *a*, phytoplankton, zooplankton, Ctenophora, DOC, POC, SAS was computed from values obtained at 0 m (v_0), 5 m (v_5), 10 m (v_{10}), 20 m (v_{20}), 30 m (v_{30}) and 35 m (v_{35}):

$$\text{Total (SJ101)} = 2.5\ v_0 + 5\ v_5 + 7.5\ v_{10} + 10\ v_{20} + 5\ v_{30} \tag{1}$$

and

$$\text{Total (SJ107)} = 2.5\ v_0 + 5\ v_5 + 7.5\ v_{10} + 10\ v_{20} + 7.5\ v_{30} + 2.5\ v_{35}. \tag{2}$$

The average values are:

$$\text{Average (SJ101)} = \text{Total (SJ101)}/30 \tag{3}$$

and

$$\text{Average (SJ107)} = \text{Total (SJ107)}/35. \tag{4}$$

The same principle was applied to compute the total abundances of parameters (phytoplankton and zooplankton) that were sampled at fewer depths.

The above method is generally not used in computing averages of biological parameters such as, for example, zooplankton or phytoplankton abundances. Commonly, average zooplankton or phytoplankton abundance would be computed as:

$$\text{Average (SJ101)} = (v_0 + v_5 + v_{10} + v_{20} + v_{30})/5 \tag{5}$$

and

$$\text{Average (SJ107)} = (v_0 + v_5 + v_{10} + v_{20}\cdot + v_{30} + v_{35})/6. \tag{6}$$

For all parameters sampled at both 0 m and 5 m value of the 0–5 m layer was computed as ½ ($v_0 + v_5$).

2.4.2. Correlations

Similarity in yearly changes of various parameters were evaluated by computing ordinary correlation coefficients.

Principal component analysis (PCA) was used to summarise subsets of the main zooplankton groups, and environmental data for each seasonal sample at two investigated stations and was performed with Canoco (v. 5) software (Lepš and Šmilauer, 2003). Before analysis, data were log normalised.

2.4.3. Modelling

Monthly mean fields of vertically averaged currents and salinity in March–October 2017 were obtained by Regional Ocean Modelling System (ROMS). A detailed description of the model itself is given by Shchepetkin and McWilliams (2005, 2009). In the present application, the horizontal resolution was 2 km, with 20 s-levels along the vertical. Along the coastline, no-slip boundary conditions were imposed. At the open boundary, in the Otranto Strait, free surface temperature, salinity, and velocity were taken from the operational Adriatic REGional model (AREG) (Oddo et al., 2006), which is a part of the Mediterranean Forecasting System (MFS). The riverine forcing was taken from the climatology of Vilibić et al. (2016). Further details on the ocean model setup can be found in Mihanović et al. (2018).

The atmospheric component used to provide ocean model forcing is based on the National Center for Atmospheric Research (NCAR) Advanced Research WRF (ARW) model version 3.7 (Skamarock et al., 2005). In the present case, the larger model domain (parent) covers the whole Europe region with a horizontal grid spacing of 9 km inside which a 2-way nested child domain is embedded. It covers the whole Adriatic Sea region at 3 km horizontal resolution. Boundary and initial conditions for the WRF model are taken from the NCEP – GFS global model outputs at 25 km horizontal and 3 hourly spatial resolutions. Bulk parameterisation (Fairall et al., 1996) has been used for transferring surface variables into the ocean ROMS model.

The dispersion model was based on the ROMS model described in Janeković et al. (2010), following the Lagrangian approach. In particular, the same parameterisation of turbulence and transparency is used. The grid used has a 4 km resolution which is adequate here. The surface forcing is obtained from the ECMWF forecasts, while the boundary conditions at the Otranto strait (temperature, salinity, currents and water height), as well as initial state, were taken from the climatology obtained from the model runs of the ADAM-ADRIA project (Janeković et al., 2020). The river inflow was obtained from Vilibić et al. (2016). Based on the winter field observations and personal communication with Italian researchers, the Venice Lagoon is taken as a starting point for the spreading of *M. leidyi* to the Istrian coast. Three drifters were released every day of 2017 starting from 1 January in the surface layer of the area outside the Venetian Lagoon, and their density distribution in January–March was analysed. The same was done additionally for two other potential winter sources of *M. leidyi*: Trieste and Pula harbours.

The verification of the dispersion model was done using the Sea Surface Temperature (SST). Data were retrieved from the Copernicus project (https://marine.copernicus.eu/) at the 1 km resolution. The daily L4 high-resolution SST product was used (Buongiorno Nardelli et al., 2013, 2015). These are merged SST data, derived from both infrared and microwave sensors, into a single daily product that provides the best estimate of foundation SST, i.e. the SST free of diurnal warming influence and cool skin effect. Since foundation temperature represents the temperature of the upper mixed layer, this temperature should correspond to the surface layer of the ocean model and therefore is suitable for comparison with model data. This estimated foundational temperature was compared with the model temperature at 05:00 AM.

3. Results

3.1. Hydrological parameters and nutrients in 2017

The temperature in winter was around 10 °C rising over 26 °C in summer at the surface and up to around 14 °C at the bottom for both stations (Fig. 1). Surface salinity values showed pronounced seasonal cycles, ranging from 37.5 in January to 38.6 in February, followed by a decrease to 36 in July and an increase towards 38 in October at SJ107. At SJ101, after being similar to bottom values, around 38, in January and February, salinity started to decrease to 28 in June and rose again to over 36 in July and August. In the 0–5 m layer, temperature and salinity values were similar to the surface ones, except at SJ101 in June when a pool of very low saline water appeared at the very surface, presumably due to a recent freshwater spread from the Po delta.

The nutrient concentrations were mostly correlated to the oceanographic conditions. PO_4^{3-} concentrations were largely below 0.1 μmol l^{-1} at both stations, with a peak value of around 0.15 μmol l^{-1} in May at SJ107 and peaks in the surface layer of around 0.35–0.4 μmol l^{-1} in February, May and August at SJ101, but in general near the analytical limit, as usual for the orthophosphate (Fig. 1). At both stations, concentrations of TIN in the surface layer were generally higher in winter (up to over 7 μmol l^{-1} at SJ107 in January and up to 5 μmol l^{-1} in February at SJ101) than in spring and summer (around 1 μmol l^{-1} at SJ107 and between 2 μmol l^{-1} in May–June and 1 μmol l^{-1} in July–August at SJ101). These winter values were still remarkably below the averages of the western station, while at the eastern one, the differences from average were smaller and related to extremely high Po River discharge in December of 2016 (CMR, database). In the bottom layer, TIN was higher at SJ101 than at SJ107 as expected, where it was extremely low, especially in June–July when it peaked over 3 μmol l^{-1} (Fig. 1).

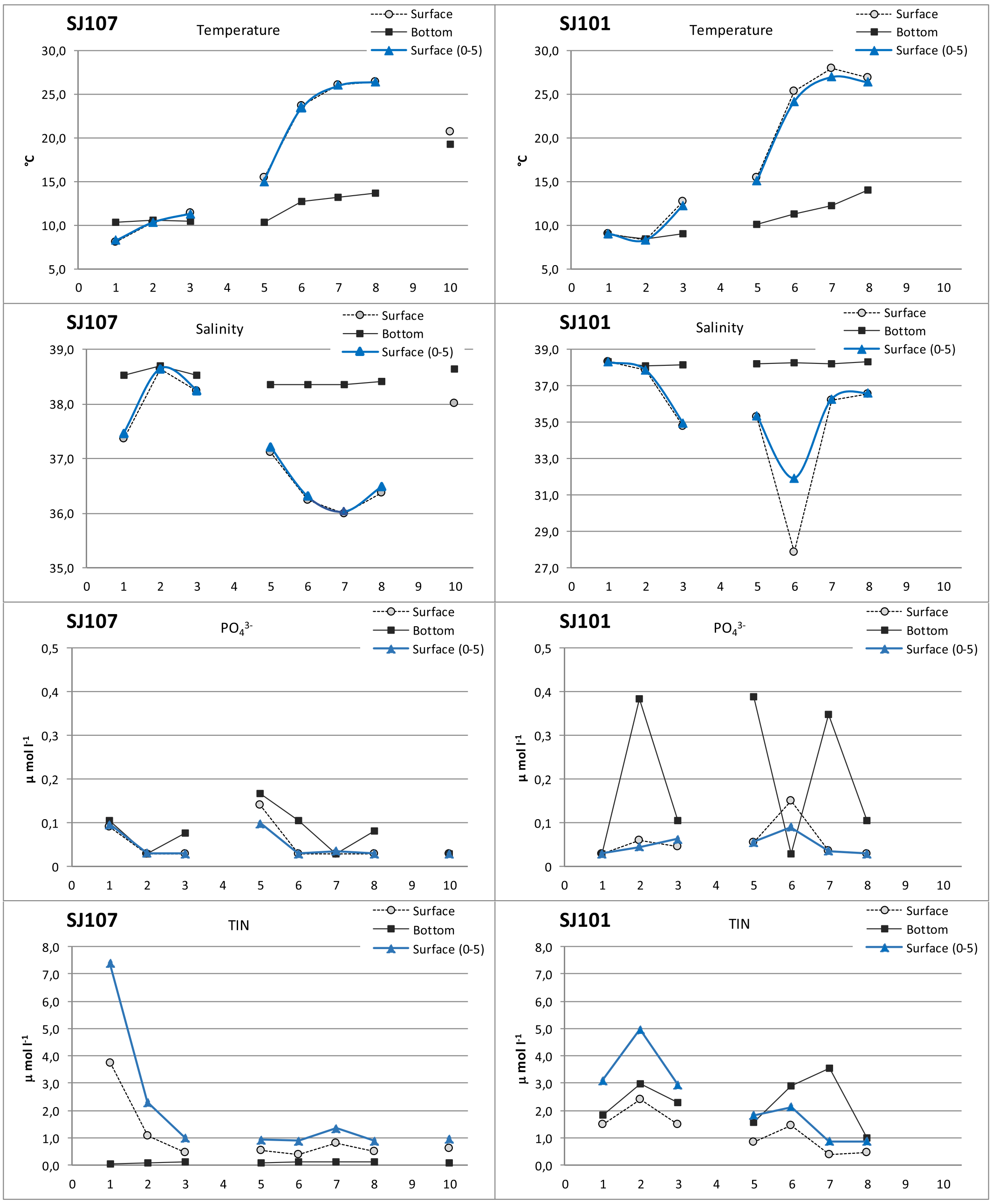

Fig. 1. Surface and bottom values of environmental parameters (temperature, salinity) and nutrients at SJ107 and SJ101 in 2017. For comparisson data for surface sampled at 0 m and surface averaged 0–5 m are shown.

3.2. Primary production

Averaged phytoplankton abundance in the water column of SJ107 ranged between 1.2 × 10^6 and 1.5 × 10^6 cells l^{-1} during all cruises except in February and June when it was low, between 0.6 × 10^6 and 0.8 × 10^6 cells l^{-1} (Fig. 2). At station SJ101, phytoplankton values were very high in March, 8.1 × 10^6 cells l^{-1}, considerably lower in February and June, between 1.8 × 10^6 and 2.2 × 10^6 cells l^{-1}, while in other months values were low, between 0.6 × 10^6 and 1 × 10^6 cells l^{-1}. There was a prominent diatom bloom composed mainly of *Chaetocerotaceae* lasting from January until April. The bloom was composed by *Chaetoceros curvisetus* and *Leptocylindrus* cf. *danicus*, with maximum abundances recorded in March at SJ101. At station SJ107, higher abundances were recorded at 10 m depth, but the diatom community was different. The most abundant species were *C. contortus, C. affinis, C. vixisibilis* and *C. socialis*, together with *Cerataulina pelagica* in this deeper layer. Most of the phytoplankton abundance was in microfraction (200–20 μm) and just some minor part in nano fraction (20–2 μm) during March at both stations. During the summer months, the community changed, and the maximal abundances of *Pseudo-nitzschia delicatissima* group and *Dactyliosolen fragilissimus*, especially in deeper layers (30 m), were recorded.

At SJ107, averaged Chl *a* concentration in the water column was in the range 0.4–0.5 μg l^{-1}, with the lowest value in June and October (0.2 μg l^{-1}) and the highest in January and August (0.7 μg l^{-1}) (Fig. 2). At SJ101, Chl *a* values were in the range 0.6–0.7 μg l^{-1}, with the lowest value in August (0.4 μg l^{-1}), while in March, values were higher (1.2 μg l^{-1}) and reached maximum for the investigated period in July, with 2.1 μg l^{-1}.

3.3. Zooplankton

At SJ107, microzooplankton abundances were very high in January,

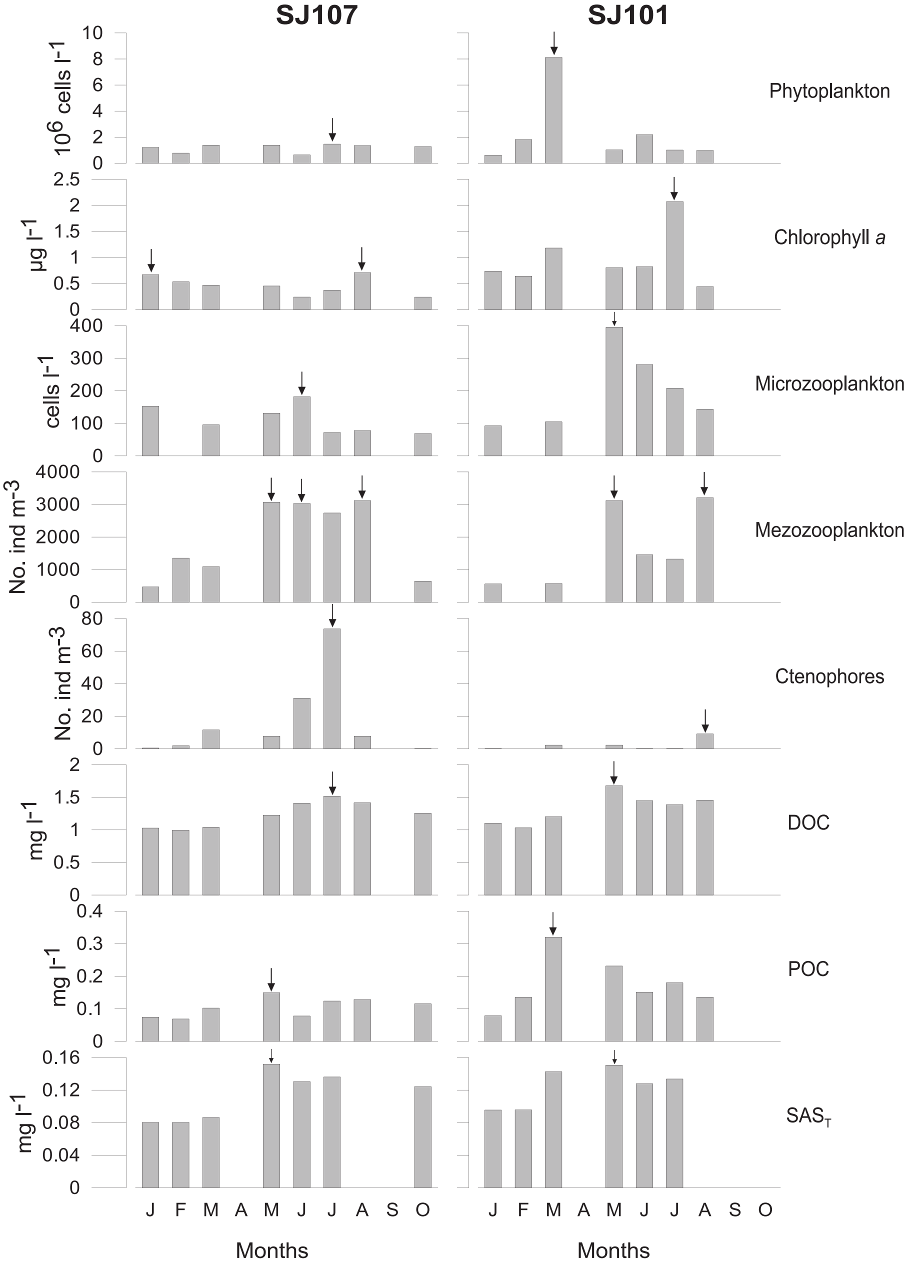

Fig. 2. Averaged water column abundances of microzooplankton, mesozooplankton, ctenophores and phytoplankton, and concentrations of chlorophyll *a* (Chl *a*), DOC, POC and SAS_T at SJ107 and SJ101 during investigated period in 2017. Maximal and close to maximal abundances/concentrations are marked by arrows.

lower in March, high (but lower than in January) in May, maximal in June, with minimal and similar values in the following months. At SJ101, winter values of microzooplankton abundances were similar and low compared to spring and summer values; maximum appeared in May, decreasing gradually later (Fig. 2).

Mesozooplankton abundances at SJ107 were similarly high, with maximum values (around 3000 ind. m^{-3}) from May to August (Fig. 2). At SJ101, similar values were observed in May and August, while lower abundances of approx. 1500 ind. m^{-3} were measured in June and July.

Ctenophores abundances were highest at SJ107 in June and July, ranging from 35 to 75 ind. m^{-3}, respectively (Fig. 2). At the western station of the same profile (SJ101), their abundance was insignificant, with maximum values around 10 ind. m^{-3} measured in August.

In Table 1, averages of microzooplankton abundances in the water column are given as computed using two different methods of averaging, by Eqs. (3)&(4) and (5)&(6). The differences between these two methods were, in most cases, below 10%. The largest values, 17% and 21%, in May and June 2017, occurred in cases when the sampled value at single depth was significantly different from values at other levels (nauplii at 0 m in May and ciliates at 20 m in June at SJ107). The first method, Eqs. (3)&(4), is more accurate as it considers different distances between sampling levels. However, results obtained by such calculation are not necessarily "more precise" as it is based on a linear approximation of changes of a parameter between sampling depths, which may not be generally true. Due to the high correlation between Avg (3&4) and Avg (5&6) of 0.98, we assume that the use of one or another set of formulae would not significantly affect our correlation analysis.

Table 1
Average values of microzooplankton abundance in the water column given for a specific date and station, as computed using Eqs. (3) and (4) (Avg 3&4) or (5) and (6) (Avg 5&6).

Date		Avg (3&4; cells l^{-1})	Avg (5&6; cells l^{-1})	Δ (cells l^{-1})	Δ (%)
27-Jan-17	SJ107	152	144	-8	-5
28-Mar-17		96	83	-13	-13
5-May-17		132	154	23	17
12-Jun-17		182	144	-38	-21
12-Jul-17		72	68	-5	-6
30-Aug-17		78	76	-2	-3
4-Oct-17		69	69	0	0
27-Jan-17	SJ101	92	85	-7	-8
28-Mar-17		105	97	-8	-7
5-May-17		395	347	-49	-12
12-Jun-17		281	303	22	8
12-Jul-17		207	181	-26	-13
30-Aug-17		143	143	0	0

Differences between computed values are given in measuring units, Δ (cells l^{-1}), and in percents, Δ (%).

3.4. Ctenophore *M. leidyi*

3.4.1. Distribution and abundance of *M. leidyi* in the surface layer along the the Po River delta-Rovinj transect and wider

In early May 2017, sporadic *M. leidyi* specimens were observed along the transect (Fig. 3 left). The average abundance of jelly combs was quite low (~4 ind. 10^4 m^{-3}). The highest abundances were observed at station SJ101 (2 ind. 10^3 m^{-3}) and the surrounding stations SJ102 and SJ1A1 (1 ind. 10^3 m^{-3}) strongly influenced by the Po River.

A slight increase in jelly comb abundance was registered at the eastern side of the NAd at stations ZI332 and ZI032 (5 ind. 10^3 m^{-3} at both stations). In the central part of the transect, Ctenophora were absent.

In June 2017 (Fig. 3 right), the average number of jelly combs on the transect was 6.5 ind. 10^3 m^{-3} which represents an increase of 16 times with respect to May. The maximum abundance of 1 ind. 10 m^{-3} was registered at station ZI032 at 10 NM west of Rovinj. In general, the number of jelly combs showed a decrease to the west, where in the area under the influence of the Po River, specimens were not detected. Also, in the central part of the transect, the jelly comb abundances were quite low (about 1 ind. 10^3 m^{-3}).

In July 2017 (Fig. 3 left), the average number of jelly combs was 1.94 ind. m^{-3}, around 300 times higher than in June and around 4800 times higher than in May. Then three main areas with increased abundances of jelly combs can be identified (Fig. 3, left): a) station SJ107 in the middle-eastern part of the NAd, with the highest abundance (6 ind./m^3); b) the easternmost part of the transect at the coast of western Istria (RV001, ZI332 and ZI032) (4–5 ind. m^{-3}) and c) the western part of the Po River influenced transect (turns at SJ101-SJ108 with 2–3 ind. m^{-3}). As in previous months, the central part of the transect, corresponding to the most open waters, had the lowest abundances concentrations or even complete absence of the adult jelly combs.

In August 2017 (Fig. 3 middle right), the average number of jelly combs was 2.04 ind. m^{-3}, similar to the average abundance in July. Then two large areas with high abundances can be identified: a) the easternmost part of the Po River – Rovinj transect (RV001-ZI032) and b) the westernmost section of the transect (SJ101-SJ108), both with abundances ranging between 3 and 5 ind. m^{-3}. This time as well, the central part of the transect showed lower jelly comb abundances, especially in the southern part (SJ1A8 and SJ1B8 with 1 and 5 ind.100 m^{-3}, respectively). The lowest abundances (0.5 ind. 1000 m^{-3}) were measured at station ZI031. During the sampling, there were no stations where jelly combs were absent.

In September (Fig. 3 bottom left), samples were collected from an additional set of 20 coastal stations (including RV001 and ZI032) along the western coast of Istria (extended WICOS, Graphical abstract). *M. leidyi* was present at all stations within 12 NM from the coast with an average abundance of 3.13 ind. m^{-3}.

In October (Fig. 3 bottom right), only the eastern part of the transect was sampled, and *M. leidyi* was detected at all stations except at SJ107. The abundances were higher close to the Istrian coast (0.1 ind./m^3) and decreased towards the west with the minimum value at SJ104 (1 ind. 1000 m^{-3}). The average abundance of jelly combs at this transect was 3.5 ind. 100 m^{-3}.

3.4.2. Size class distribution of *M. leidyi*

All the collected specimens were grouped in six size classes ranging from the smallest sizes up to 3 cm to the biggest adult specimens above 11 cm (Fig. 4).

Throughout the investigated period, the dominant size classes were altering between each other, although no significant differences between months were found $\chi^2 = 1.314$ (5, $n = 6$) using the Friedman statistic test (data not shown). In May of 2017, over 60% of the individuals ranged from 7 to 8.9 cm. Thus, the majority of sampled jelly combs belonged to the size class categorized as adult specimens (≥3 cm) while there were no records of specimen belonging to the transitional (1–3 cm) or juvenile (≤1 cm) phases of life (Kamburska et al., 2006). However, the very next month, the majority of individuals were smaller in size, thus younger specimens. More than 50% of them ranged from 3 to 4.9 cm, and about 40% of individuals were a size class above, ranging from 5 to 6.9 cm, implying that in just a month, the population was rejuvenated. This trend continued in July when almost 40% of individuals belonged to a size class under 3 cm and another 40% to the class above up to 4.9 cm. From August to October, the size variability increased, and recorded specimens belonged to every size class. The share of the smallest individuals dropped to a quarter, from about 20% in August to about 5% in October. The numbers of those up to 4.9 cm dropped from around 35% in August to about 10% in October. In the same period, a size class above counted about 20–30% of individuals up to 6.9 cm. In contrast to the smallest specimens, the larger specimens (7–8.9 cm) quadrupled in numbers, from around 10% in August to almost 40% in October. Consistently, individuals up to 10.9 cm rise from around 1% in June and July, about 10% in August, and 20% in September, to above 30% in October. Additionally, in October, we have observed a few percentages of the largest (>11 cm) specimens of the whole year.

3.4.3. Organic matter content – *M. leidyi*

The average biomass assigned to the top layer of the water column was calculated and presented in Fig. 5. The average biomass of *M. leidyi* for a wet specimen was about 22 g. During the peak of its expansion in late summer and early autumn, wet weight reached 40 g in the monitored area. The average wet weight and organic carbon content of *M. leidyi* specimens were highest in October (Fig. 5, upper and middle panel). Both distributions looked alike, starting in May with relatively high values that were not exceeded until reaching a maximum in October. The lowest values were found in July. At that time, the share of juvenile specimens (<3 cm) was the greatest, while the share of biggest adult specimens (>11 cm) was the highest in October (Fig. 4). The shares of the smallest and biggest specimens likely contributed to the shifts that happened in the biomass quantity and quality. However, total biomass, i.e., the organic content of jelly combs, did not follow the same pattern (Fig. 5, lower panel). Due to the low abundance of jelly combs in October (Fig. 5), the overall organic content in the surface layer of the water column along the Po River – Rovinj transect seemed to be rather low. The highest average concentration of organic content in the water column (>0.74 g m^{-3}), due to jelly comb presence, was registered in September and to the peak of their abundance (Figs. 3 and 5).

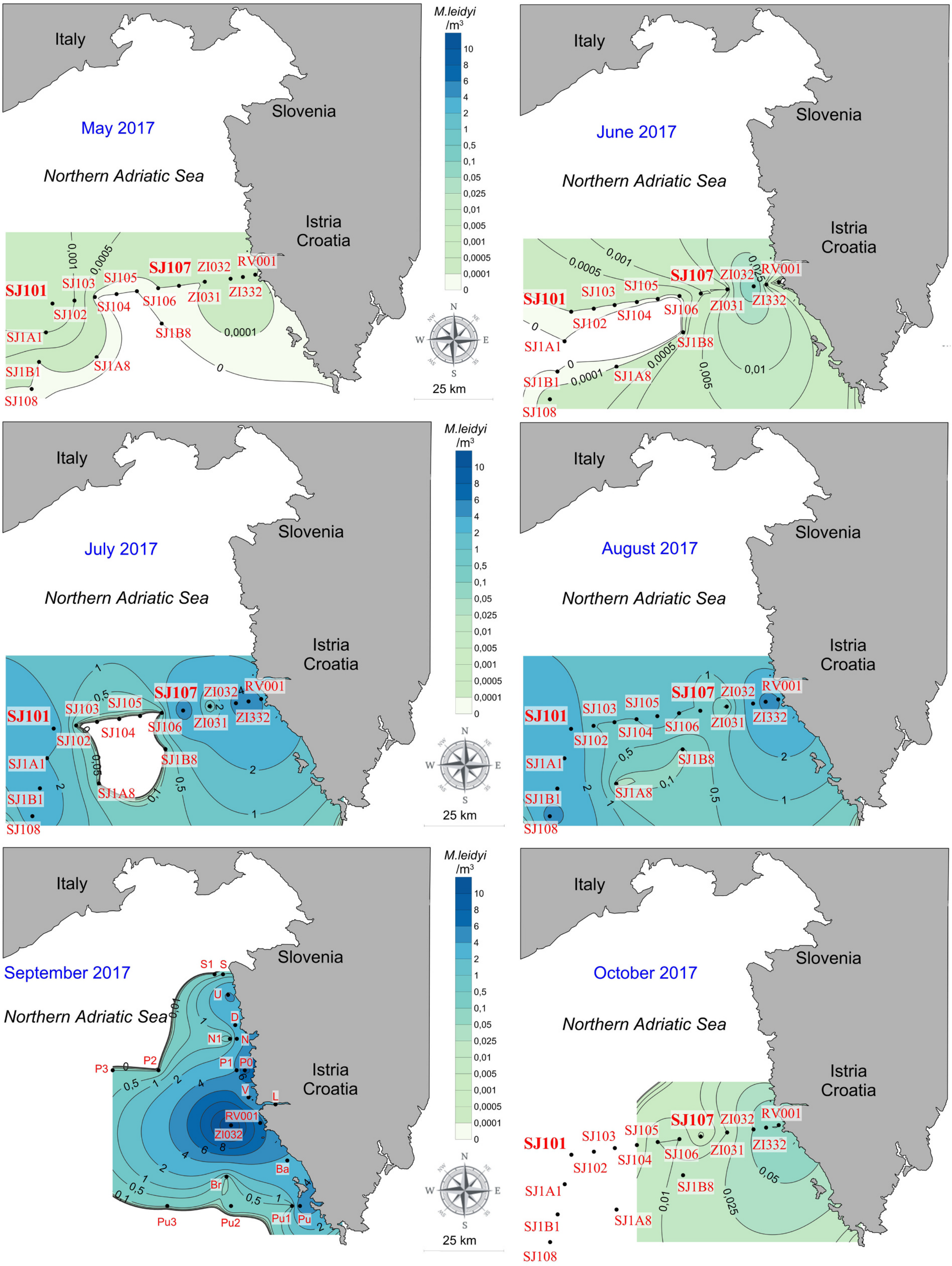

Fig. 3. Spatial distribution of the *M. leidyi* invasion in May–October 2017 along the Po River-Rovinj transect; red labels represent names of the stations, while black numbers indicate *M. leidyi* abundances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

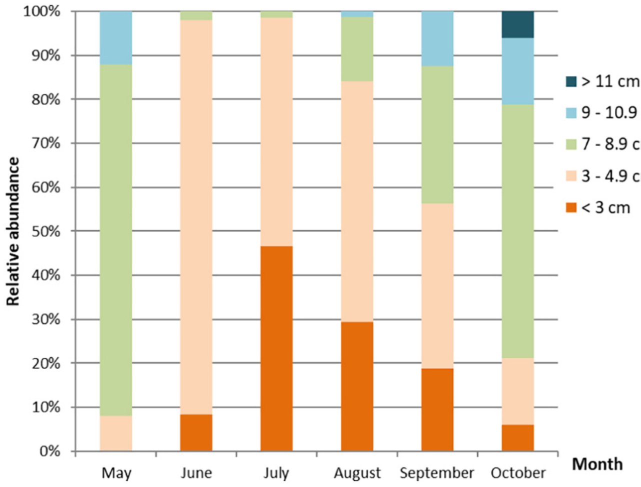

Fig. 4. Size-frequency diagram, *M. leidyi* size class (cm) shares during its invasion in the northern Adriatic in 2017. Samples were collected in coastal waters of the Rovinj city (around RV001-ZI032-ZI332, Graphical abstract).

3.5. Organic matter (DOC, POC, SAS) dynamics and concentration

During the study, in the so-called anomalous summer of 2017, an increased concentration of DOC was observed in the entire water column of SJ107, with a maximum in the surface waters (Fig. 6). The concentration of DOC ranged between 1.56 and 3.10 mg l^{-1}. For the comparison, the water column profile for DOC and POC was shown for 2016, which can be taken as a normal, average year regarding OM presence at the studied transect. The seasonal cycle of DOC and POC in the surface (0–10 m) and bottom layer of the studied stations SJ107 and SJ101 showed a general increase from winter to summer (Fig. 6). At SJ107, DOC displayed higher values during cruises in May–October, with a maximum in July, and a slight decrease in August and October. Similarly, in the same period, at station SJ101, DOC increased from lower values in winter to a maximum in June, reducing its concentration in July and August. The DOC was exceptionally high at SJ107 in July, at the surface, in waters characterised by salinity values above the long-term average (Djakovac et al., 2019). Usually, higher DOC is measured in lower salinity waters (Dautović et al., 2017). In July 2016, salinity was higher than in 2017, and the DOC concentration was relatively low (Fig. 6).

POC followed a similar pattern with the highest concentrations measured in general at the surface of SJ101. An exception is the concentration peak (0.4 mg l^{-1}) measured at the surface of SJ107 in May 2017 (Fig. 6). Maximal concentrations of POC around 0.7 mg l^{-1} were measured in March and June 2017 at SJ101. The large fraction of DOC and POC was found to be surface-active. Water column-averaged concentrations of total SAS_T, which mainly corresponds to dissolved fraction since there was a negligible difference between filtered and non-filtered samples (data not shown), were highest (0.14–0.16 mg l^{-1}) from March to July at SJ101, and from May to July and October at SJ107 (Fig. 2).

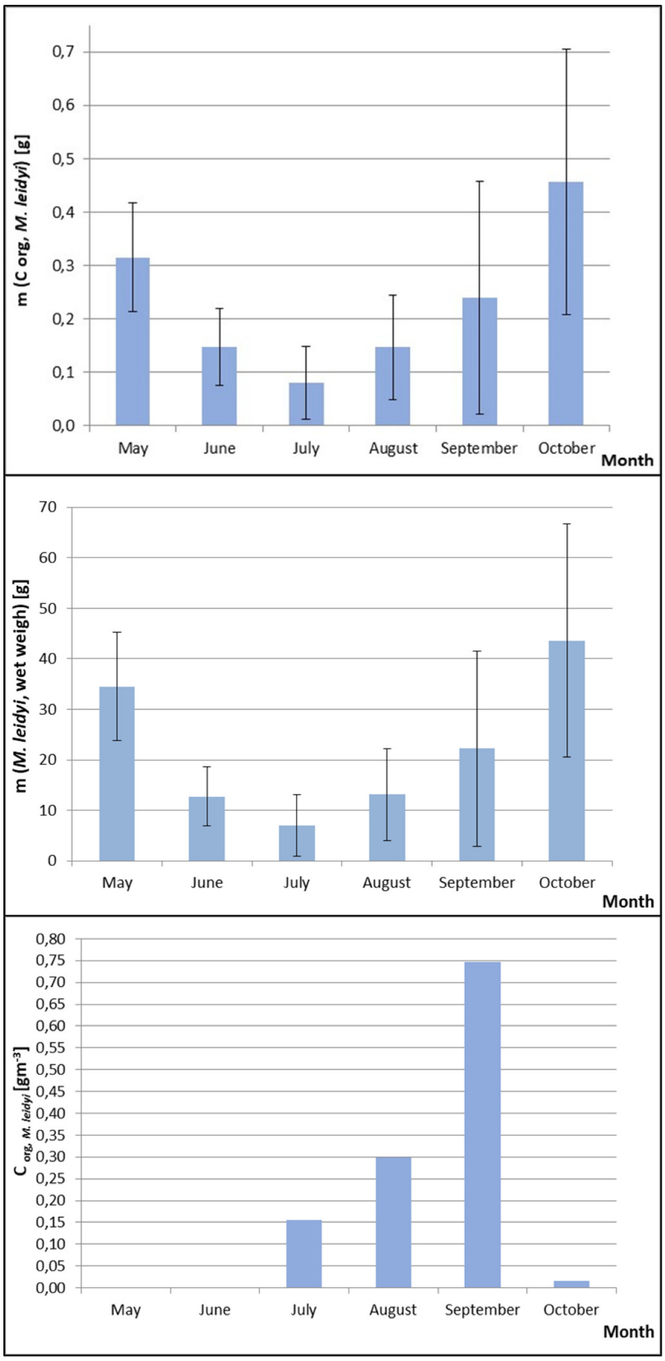

Fig. 5. Average wet weight (above) and average organic content (center) of *M. leidyi* specimens during its expansion in 2017 along the Po River – Rovinj profile and additional stations (September 2017) (Graphical abstract). Average organic content contribution (bottom) due to *M. leidyi* expansion in 2017 at studied transects. Please note that C organic content in May and June 2017 was around 0.

3.6. Statistical correlations

We calculated correlation coefficients between six-to-eight pairs of monthly values of various oceanographic parameters measured at SJ101 and SJ107 (Fig. 2; Tables S2 and S3), aiming to detect possible similarities in their seasonal cycles during the year 2017. To some extent, this type of analysis could also be performed by visual comparison between the data in Fig. 2. However, correlation coefficients used as a diagnostic tool give a quantitative measure where we have somewhat arbitrarily chosen that correlation coefficient exceeding 0.6, which points to the similarity in seasonal cycles. In a population of random numbers of six-to-eight data pairs, a correlation coefficient of 0.6 would appear by chance in less than 20% of cases. We also calculated correlation coefficients between pairs of parameters as above but taken with a relative delay of one or 2 months. Unfortunately, in this way, the number of data pairs is further reduced, so the results should be considered only as a possible indication of the delayed influence of one parameter to another.

There was no direct correlation between seasonal cycles of water-

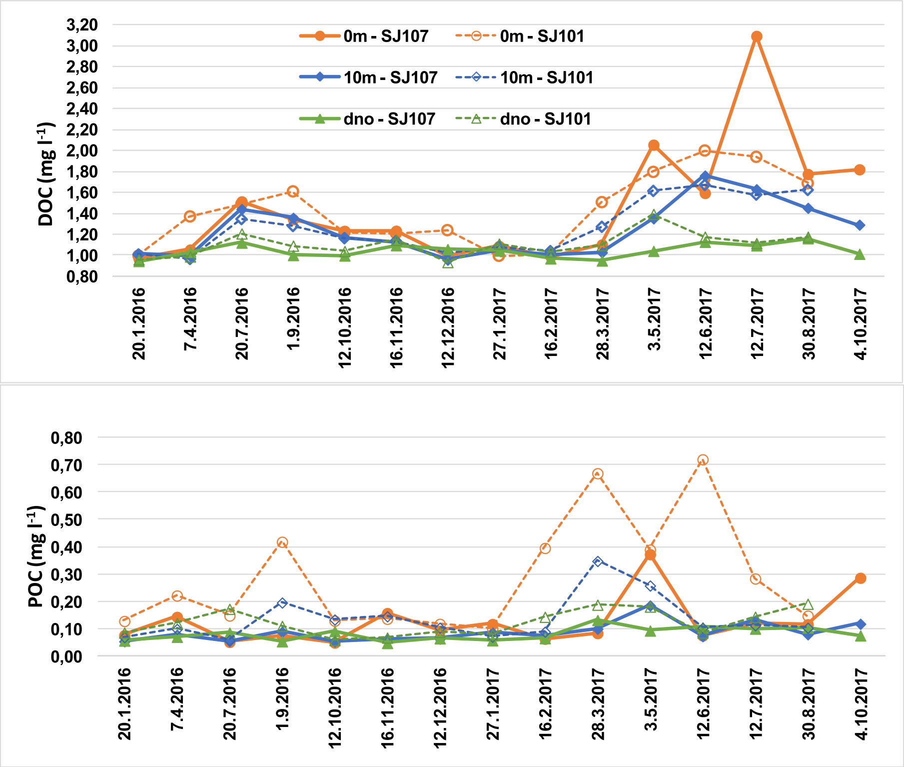

Fig. 6. DOC-POC seasonal variations at SJ107 and SJ101 in 2016 and 2017. Data for 2016 are shown for comparisson.

column averaged primary production parameters, phytoplankton and Chl *a*. Averaged values of the two parameters appeared not to be related to nutrients except maybe with a delay. In separate layers, some direct correlations were, however, obtained (at SJ107 upper layer values, 0–5 m, of PO_4^{3-} and TIN were positively related to Chl *a* in the same layer with r over 0.70; in the surface layer, 0 m, TIN was related to Chl *a* with r of 0.93; at SJ101, PO_4^{3-} was positively correlated in upper and surface layer to Chl *a* with r of 0.83). There was no direct positive correlation between the water-column average of phytoplankton and microzooplankton at SJ107 and SJ101. Introducing the delay of −2 months resulted in a positive correlation at SJ101, indicating that the rise in phytoplankton could lead to a delayed increase in zooplankton at this station. No such behaviour was indicated at SJ107.

Average phytoplankton was positively related to POC at both stations. There are indications that high phytoplankton abundances and Chl *a* concentrations reflected a delay in the rise in DOC, SAS_T and SAS_{diss} at SJ101. At SJ107, high phytoplankton abundances possibly induced a delayed rise in SAS_T and SAS_{diss}, while high Chl *a* concentrations induced a delayed reduction in DOC, SAS_T and SAS_{diss}. Interestingly, at station SJ107, a slightly lower negative correlation was recorded without delay between Chl *a* and both SAS_T and SAS_{diss}; although a slightly higher correlation was found with SAS_{diss}. At SJ101, a relatively high correlation was found between micro- or mesozooplankton with DOC and SAS, being slightly higher with a dissolved fraction (SAS_{diss}). A high positive correlation was found between Ctenophora and SAS_T ($r = 0.71$) at SJ101. At SJ107, a similar correlation was found only between mesozooplankton, while Ctenophora was positively correlated with DOC and SAS_{diss}.

Seasonal changes in ambient conditions, represented here by seasonal changes in upper 0–5 m salinity and temperature, were not related to seasonal changes in biological and chemical parameters with exceptions of mesozooplankton and DOC at SJ107 (positively related to temperature and negatively to salinity changes), and DOC and TIN at SJ101 (positively and negatively related to changes in temperature, respectively).

3.7. PCA analysis

PCA of the here studied environmental variables (Fig. 7) highly contributed to the first two principal components, indicating a strong relationship between these variables at both stations. The PCA cumulatively explained 91.06% of the variance for the station SJ101 (eigenvalue: Axis 1 = 0.7871; Axis 2 = 0.1235) (Fig. 7), and 87.44% of variance for the station SJ107 (eigenvalue: Axis 1 = 0.4943; Axis 2 = 0.3801).

The most important response variables for the first axis at station SJ101 were mesozooplankton (F = −0.992) and microzooplankton (F = −0.962). A strong inverse relationship was also found for DOC (F = −0.539) and temperature (F = −0.540). For the second axis, the most important factor was phytoplankton (F = 0.982), followed by POC (F = 0.900), salinity (F = −0.815), Chl *a* (F = 0.675) and SAS (F = 0.681).

At the station SJ107, strong negative loadings on the first axis were observed for microzooplankton (F = −0.782), ctenophore *M. leidyi* (F = −0.710) and mesozooplankton (F = 0.619). In contrast to station SJ101, none of the other parameters was found to be important at SJ107.

Overall, the abundance of the main zooplankton groups, including ctenophore, was strongly related to observed seasonal variations of other measured parameters, especially at SJ107, whereas the variability at SJ101 was also supported by phytoplankton, POC, salinity and Chl *a*, indicating higher importance of primary production at this station.

3.8. Modelling

In order to explain the development of a highly abundant population of ctenophores at SJ107 and a simultaneous negligible ctenophores number present at SJ101, in spite of a high amount of microzooplankton, the variability in circulation over the NAd was studied using the numerical hydrodynamic model supported by hydrographic measurements (Fig. 8a–c). The spreading of *M. leidyi* in the investigated area was tracked by a dispersion model (Fig. 9, and S1), which shows that tracer material released from the Venice Lagoon in winter

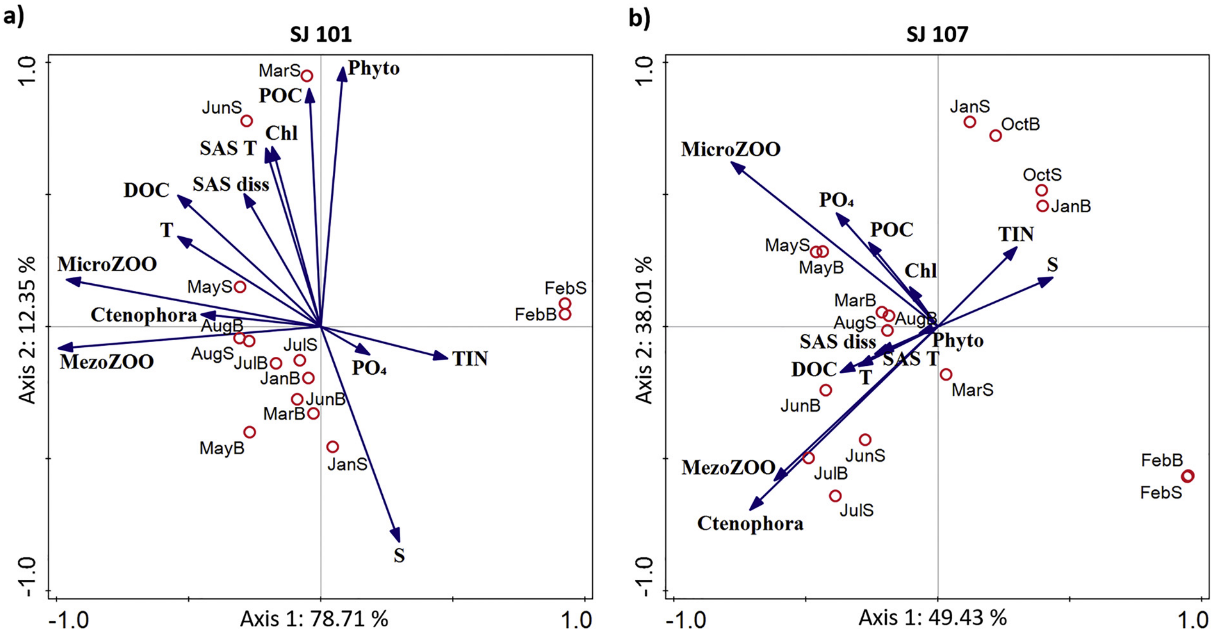

Fig. 7. Principal components analysis (PCA) of the environmental variables (arrows): microzooplankton (MicroZOO), mesozooplankton (MesoZOO), ctenophores, phytoplankton (Phyto), particulated (POC) and dissolved (DOC) organic carbon, surface active substances (SAS; non-filtered, total (T); filtered-dissolved (diss)), chlorophyll-*a* (Chl), temperature (T), salinity (S), orthophosphates (PO_4), and total inorganic nitrogen (TIN) on stations SJ101 (a) and SJ107 (b). Samples are represented as circles and labelled according to the sampling month. The capital letters stand for surface (S) and bottom (B).

(January–March) expands across the NAd, reaching the waters of SJ107. Additionally, drifters released from Pula spread to a much lower extent towards the open sea, remaining confined mainly to the western Istrian coastal belt; drifters released in front of the Trieste harbour displayed a remarkable lack of dispersion, remaining concentrated within a few miles from the origin point, while the last analysed possible source of the spreading of *M. leidyi,* Grado-Marano Lagoon, located approximately 15 NM west from the Trieste harbour, showed that drifters from this location spread mainly in a thin coastal strip along the western coast of the NAd without reaching the central or eastern parts of the NAd (all shown in Fig. S1). The quality of this dispersion model was tested using the L4 high-resolution SST estimates of foundational temperatures. Nodes that are less than 10 km from the coastlines or have an error estimate higher than 0.5 ^{o}C are excluded. Over the year 2017, this leaves 1.6 million SST estimates to compare the model output with. The mean error was −0.18 ^{o}C, the mean absolute and the root means square errors were 0.53 and 0.72 ^{o}C, respectively. The CTD measurements give 987 different values of temperature and salinity to estimate the quality of the model. For temperature the CTD gives a mean error of 0.09 ^{o}C, mean absolute error of 0.35 ^{o}C, and root means square error of 0.47 ^{o}C. For salinity, the results are less good with a mean error of 0.57, the mean absolute error of 0.69 and the root means square error of 0.77. This relatively good comparison suggests that the model is adequate for the intended purpose.

The NAd in 2017 was characterised by the inflow of very saline waters of salinity 38.5 and more. The 38.5 isoline was north to the Pesaro-tip-of-Istria line in March-May, around it in June, south to it in July–September, reaching it again in October (Fig. 8a). Changes in its position were obviously induced by changes in the Po River influence, indicating that the area under river influence gradually became larger in the warm part of the year and reduced in size in autumn (September). Cyclonic and anticyclonic gyres of various extent appeared in the region in all monthly averaged fields, being more numerous in June and October. Interestingly, in April and May the region south to the Pesaro-tip-of-Istria line was characterised by a single large-scale cyclonic gyre, while in other months, domination of a number of small-scale gyres was recorded (Fig. 8a).

Hydrodynamic modelling results indicate that the water column at SJ107 was gradually filled with low saline waters from the vicinity of the Po River delta area, which remained within an anticyclonic gyre. The gyre developed already in April and was clearly visible from May to October. On the contrary, at station SJ101, water mass dynamics seem more diverse, with an initial anticyclonic gyre changing into a cyclonic between April and May and again to the anticyclonic circulation between September and October. In March, the anticyclonic motion around the SJ101 was observed along with transversal motions, from west to east, between SJ101 and SJ107. In April, an anticyclonic gyre between SJ101 and SJ107 was clearly visible. In May and June, the anticyclonic gyre was located around SJ107, while around SJ101, a smaller cyclonic gyre seemed to develop. In July and August, the cyclonic gyre around SJ101 and an anticyclonic gyre around SJ107 were large and well developed. The anticyclonic gyre around SJ107 was very large in size, encompassing a large part of the area between the Po-River-delta-Rovinj and Pesaro-tip-of-Istria lines. That large gyre may be a feature combined with several smaller circulation areas that are not clearly visible in average fields. In September, the cyclonic gyre around SJ101 was still present, while the anticyclonic gyre around SJ107 reduced in size. The presence of an anticyclonic gyre in the eastern part of the NAd that appeared between March and May cruises, and persisted at least till August was indicated by depth of a pycnocline (or more precise: isolines of sigma-t) at the vertical section between SJ101 and RV001 (Fig. 8b). In March, the area around SJ107 was warm and of high salinity resulting in hight density in the area. In May-August, in the same area, there was a surface pool of warm, low salinity and low-density water.

Along the transect, ROMS shows lower salinity in the upper layer than it was observed, with summer months halocline being deeper than the halocline obtained by CTD measurements (Fig. 8c). This was in line with hydrological conditions in 2017 when freshwater inflow was below the climatological values (R. Precali, pers. comm.) and which were used to force the model. The temperatures in the upper layer are reasonably reconstructed, while those in the deeper layer appear somewhat higher than the observed ones. However, lowering of pycnocline around station SJ107, and particularly how it evolves in time, is generally well

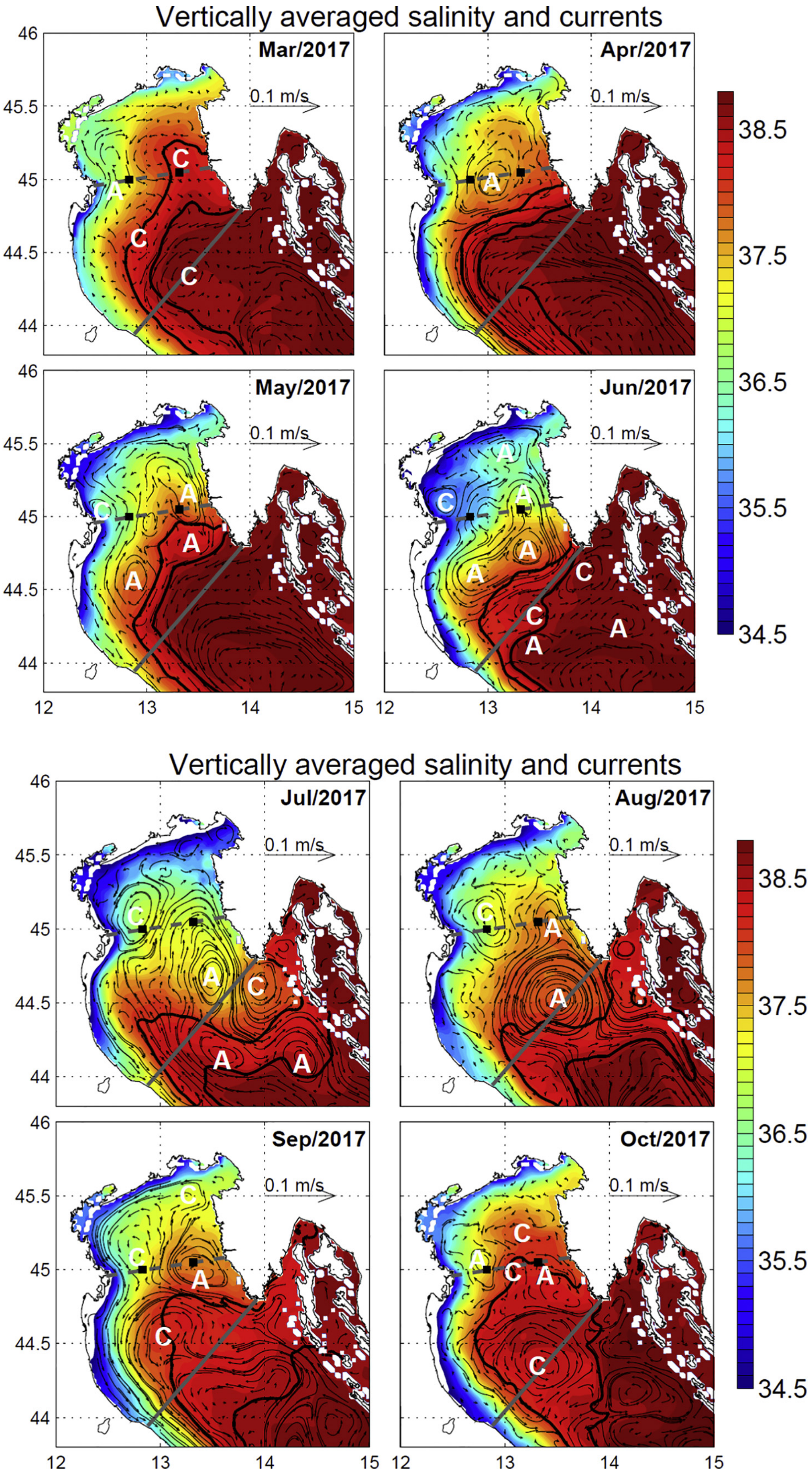

Fig. 8. (a) Vertically averaged fields of salinity and currents in March–October 2017, obtained by the numerical hydrodynamical model. The dashed line is drawn between the Po River delta and Rovinj and solid line between Pesaro (Italy) and the tip of Istria (Cape Kamenjak). Cyclonic gyres are marked with 'C' and anticyclonic with 'A'. The two thick black lines denote salinity values of 38 and 38.5.

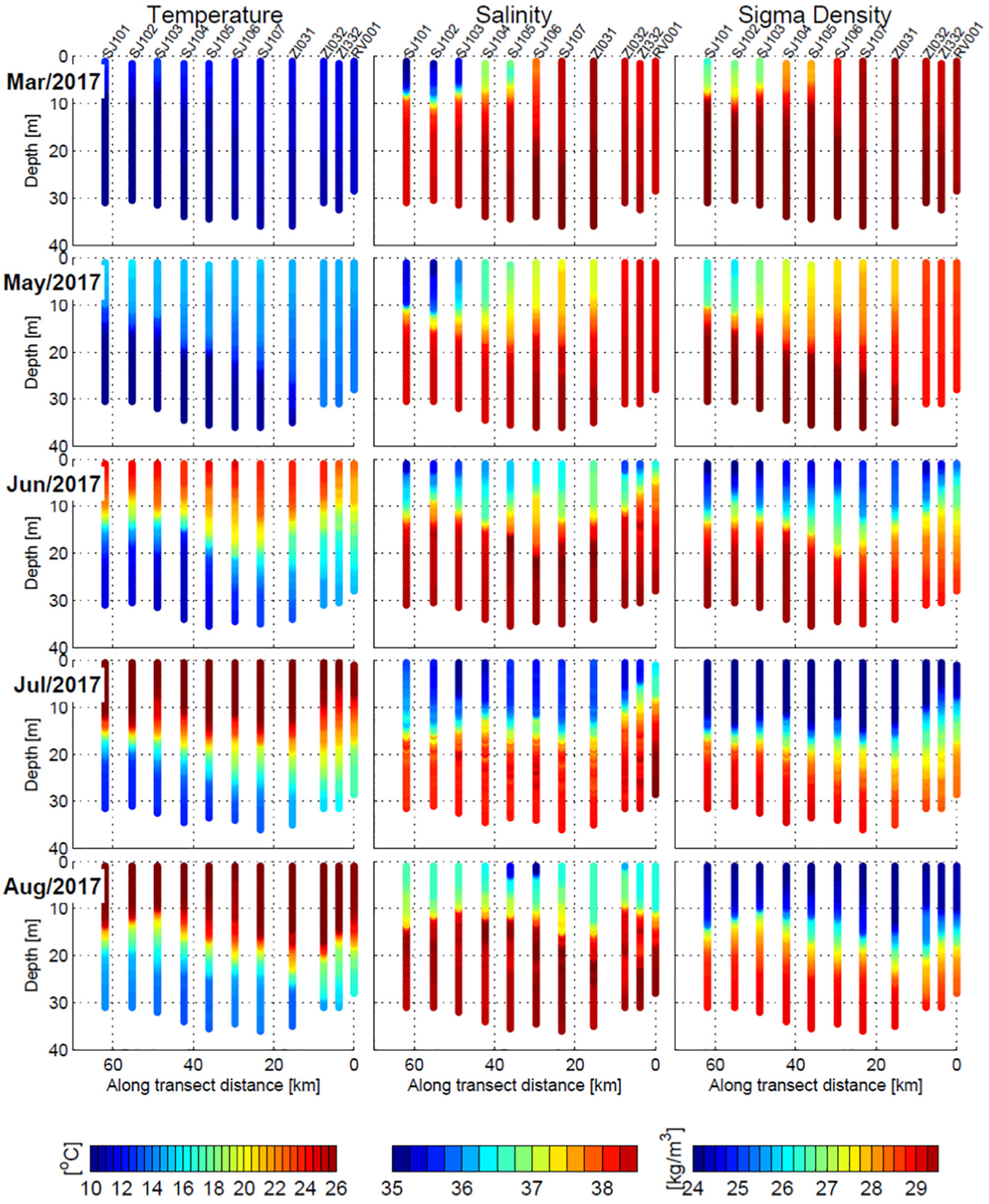

Fig. 8. (b) In situ temperature, salinity and sigma-t obtained by CTD-probe at vertical section between stations SJ101 and SJ107.

reconstructed by the model.

4. Discussion

4.1. Organic matter and zooplankton relation

Seasonal water column DOC and POC values in 2017 were very high when compared to long-term ones, being for DOC 2.5 times higher than average for the same area in the long-term period (1989–2017) (Dautović et al., 2017; Ciglenečki et al., 2020). An example of one average year regarding water column concentration of DOC and POC is 2016, for which data are shown on the same Fig. 6 for comparison. Values of DOC recorded in July 2017 at SJ107 in the surface layer were among the highest recorded in the NAd ever (3.20 mg l^{-1}). Similarly, high concentrations were recorded during the mucilage appearance (1997–2002 period) (Giani et al., 2005; Dautović et al., 2017; Ciglenečki et al., 2003, 2020). It appears that changes in DOC corresponded mainly to changes in zooplankton abundances at both stations, SJ107 and SJ101, especially when time lag between 0 and −2 months were considered. Such enlarged, and for eutrophic conditions typical concentrations of DOC for the NAd (> 2.44 mg l^{-1}), which otherwise can be considered as an oligotrophic area, are explained as a consequence of the intensive bloom of *M. leidyi* that was found in an exceptionally high population (up to 76 ind. m^{-3}) during summer months of 2017 along the Po River – Rovinj transect. At station SJ101, where the presence of *M. leidyi* was insignificant, DOC changes were dependant on the

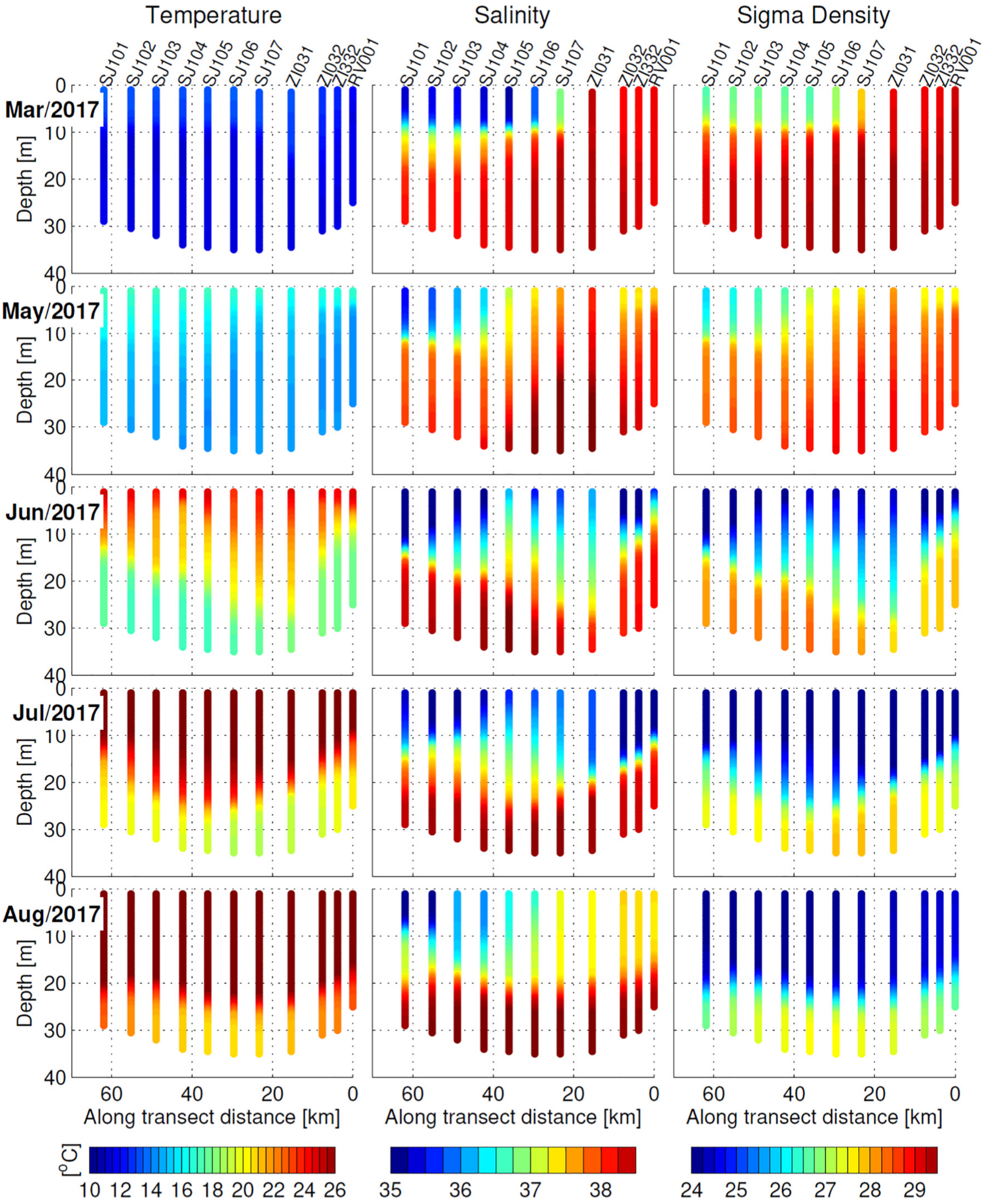

Fig. 8. (c) Temperature, salinity and sigma-t obtained by the numerical hydrodynamical model at vertical section between stations SJ101 and SJ107.

abundance of both micro- and meso-zooplankton species. However, at station SJ107, they were primarily driven by changes in total mesozooplankton abundance and an intensive bloom of the invasive ctenophore *M. leidyi*.

Values of microzooplankton observed during 2017 were generally high, implying that a large amount of OM measured in 2017 was related to microzooplankton activity. Winter (January and March) and spring (May and June, except in May of 2001 for SJ107 and 2004 for both stations) abundances of microzooplankton at SJ107 were higher than previously published for the 2000–2008 interval (Kraus et al., 2015), while the ones at SJ101 were around the median in January and higher than in most other years in March. The water column averages from our study presented in Fig. 2 should be multiplied by 30 at SJ101 and by 35 at SJ107 to obtain comparable numbers with Kraus et al. (2015) and data presented in their Fig. 5. However, yearly averages in their Fig. 6 are not suitable for comparison with data in 2017 due to an insufficient number of samplings in 2017. In July, values at SJ101 were still higher than in any other year of the 2000–2007 interval (the exception was 2008), but at SJ107, the abundance of microzooplankton was low compared to the same time period, presumably due to an increase in "grazing" following the rise in ctenophore densities. In August, when the last sampling in 2017 at station SJ101 took place, the abundance of microzooplankton was still high. At station SJ107, the abundance was close to medians of the 2000–2008 interval, while in October (last sampling at SJ107), it was lower than in any other case from the same time interval.

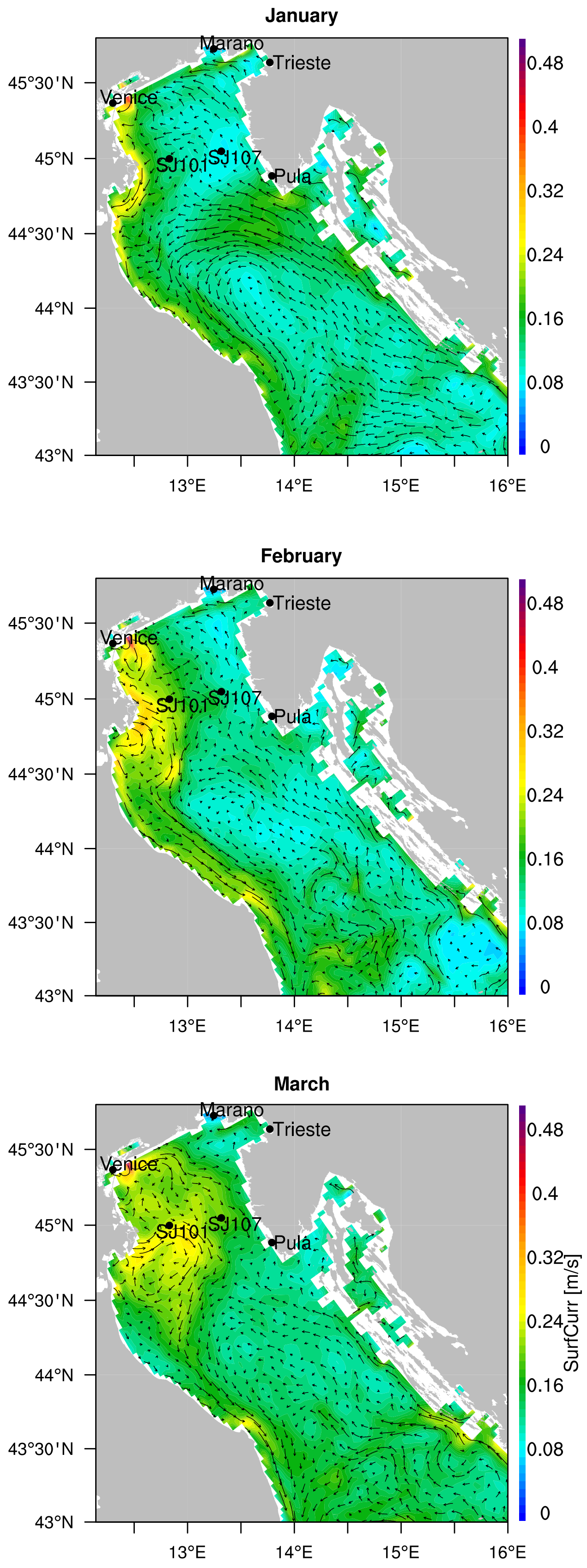

Fig. 9. Averaged current fields (SurfCurr (m/s) for January, February and March 2017) used in dispersion experiment.

Similar results, showing a generally high abundance of microzooplankton in 2017, were obtained when the water column averages were computed according to formulae (5)&(6) (see *Statistical analyses* in Section 2) compared to long-term averages computed by the same method. The most important differences refer to May at station SJ101 when the large difference between results obtained by formulae (3)&(4) and (5)&(6) was explained as a consequence of the very high abundance of zooplankton species Tintinnids concentrated at a single depth (mainly on the surface) as already reported for 2004 and 2006 (Kršinić, 2010).

In general, increased zooplankton abundance led to an increased release of DOM by the zooplankton through sloppy feeding, faecal pellet leaching and excretion processes, which play an important role in the recycling of dissolved carbon and nitrogen (Moller, 2007; Saba et al., 2011). Nitrogen and phosphorus recycling mediated by zooplankton excretion may have also enhanced bacterioplankton activity, thus stimulating mineralization processes (Valdes et al., 2018), as already reported for the Mediterranean Boughrara Lagoon (Ciglenečki et al., 2020a). In all these processes, a significant amount of OM with surface-active properties can be produced (Ćosović et al., 2000; Ciglenečki et al., 2020 and references therein; Paliaga et al., 2021), which is also proven here by correlations between mesozooplankton and ctenophore with SAS (Table S3).

SAS were measured as total and in the dissolved form, both of which contributed to POC and DOC, respectively. However, in analysed samples there were no expressed differences between these two fractions implying that the large pool of OM was in dissolved form. In natural samples depending on their hydrophobic character, almost always higher SAS were measured in unfiltered samples (Orlović-Leko et al., 2016; Ciglenečki et al., 2020). It is important to note that highly reactive colloids, which can make up to 50% of seawater DOM (Benner et al., 1992; Pettine et al., 2001) are part of the dissolved fraction and could contribute to SAS. At SJ107, high abundance of mesozooplankton during spring and summer provided an abundant food supply for the ctenophore population, which enabled it to increase substantially, reaching the highest measured densities in the period from 2016 to 2019 (Budiša et al., 2021). In addition, it is important to point out that extreme DOC value in July at SJ107 appeared when a large population of ctenophore, especially smaller specimens of *M. leidyi* (<3 cm), were found in the water column. At the same time, increased SAS concentrations that were measured in the water column (Fig. 2), point on zooplankton grazing as a significant source of SAS (Croot et al., 2007; Kurata et al., 2016).

We assume that *M. leidyi* developed at SJ107 from April to November within a large anticyclonic gyre, as confirmed by the numerical hydrodynamic model (Fig. 8a), where calm conditions favoured its reproduction and growth. The presence of an anticyclonic gyre in the north-eastern Adriatic is generally related to the appearance of geostrophic Istrian Coastal Countercurrent (ICCC), the current with a pronounced SE component in the coastal zone off Istria (Supić et al., 2000, 2002, 2003). The ICCC appears in spring-summer along with a warm, low salinity and low-density surface pool in the open north-eastern Adriatic. The pool is also characterised by the deep position of density isolines when compared to surrounding areas. The density difference between the pool area and the coastal zone induces the appearance of the ICCC. Typically, the ICCC is especially strong in August. Such pool, indicating the presence of the ICCC and the anticyclonic gyre in open waters, was also observed in 2017 (Figs. 8b and c). The idea that the pool is part of an anticyclonic gyre (based on earlier analysis of hydrographic data) is here for the first time supported by model results. Long-lasting duration of the gyre with reduced dynamics could result in hypoxia or anoxia – occasionally ocurring events, mostly in autumn, in the bottom layers (Djakovac et al., 2015). Waters of the gyre can be characterised by long time (up to 30 days in 2004) specific phytoplankton species distribution (Kraus and Supić, 2011). In addition, the presence of gyres, favouring mucilage aggregation, can support excessive production of opportunistic species inhabiting mucilages (as observed for diatoms *Cylindrotheca* *closterium* and *Thalassionema nitzschioides*; Kraus and Supić, 2015). The gyre is held to be in the time of mucilage events a place of OM accumulation (Ciglenečki et al., 2003); in 2017, due to an abundant food supply, zooplankton and ctenophores became very numerous, accumulating a large amount of organic carbon. Fast decay of the population resulted in the release of an extreme amount of DOC in the water column. A large fraction of this DOC at both stations was reactive, significantly contributing to the pool of OM with surface-active properties (SAS).

PCA analyses clearly showed that DOC is mainly controlled by microzooplankton dynamic and primary production (bottom-up control) at SJ101, while at SJ107, it appears that more complex food-web interactions operated largely under the influence of *M. leidyi*. A positive correlation attained at SJ101 implies that the rise in phytoplankton led to an increase in zooplankton with a delay. A similar positive relationship is missing at SJ107, pointing to the more complex food-web interactions affected by invasive ctenophores.

4.2. *Environmental conditions and primary production*

It appears that high saline waters in 2017 reflected in all investigated parameters, as are hydrographical conditions and nutrients, which consequently resulted in lower primary production when compared to the long-term dataset.

The temperature in Jan-May was around or below averages at both stations, at the bottom and the surface. In June–August, the surface temperature was higher than average long-term values (Supić and Vilibić, 2006), especially in June. The single measurement at SJ107 in October indicates that both surface and bottom temperature were still very high.

Bottom salinity values were high when compared to the long-term values (Supić and Vilibić, 2006) and higher at SJ107 (over 38.3 with extreme values of around 38.7 in February and October) than at SJ101 (between 38 and 38.3). Similar and higher salinities (up to 39.02) within the entire water column were recorded in the middle Adriatic as well, which along with high subsurface temperatures, were the main characteristics of the anomalous summer of 2017 (Beg Paklar et al., 2020).

During the investigated period, the correlation of nutrients with oceanographic conditions was obtained (Table S2). Nutrient concentrations were close or below the long-term average, confirming the already established theory of promoted decreasing eutrophication in the NAd (Giani et al., 2012).

During 2017, phytoplankton and Chl *a* were generally lower when compared to long-term data in the period 2000–2007, with some outstanding exceptions. Phytoplankton values were considerably lower at SJ101, whereas at SJ107, values were higher in winter and lowered in the summer period when compared to long-term values (Kraus and Supić, 2011). However, an extremely pronounced increase in March of 2017 at SJ101 and a decrease at SJ107 in February were observed in contrast to the long-term averages, with different species composition between the two stations.

Exceptionally high phytoplankton abundances observed at the station SJ101 were composed of diatoms from the genus *Chaetoceros* especially *Chaetoceros curvisetus*. Usually, NAd in the winter months is dominated by pronounced *Skeletonema marinoi* bloom (Marić Pfannkuchen et al., 2018), which is not observed in 2017. At station SJ107, higher abundances were recorded at 10 m depth, but diatom community was different. The most abundant species were *C. contortus, C. affinis, C. vixisibilis* and *C. socialis*, and *Cerataulina pelagica* in this deeper layer. Most of the phytoplankton abundance was in the microfraction (200–20 μm) and just some minor part in the nano fraction (20–2 μm) during March at both stations. In July and August, the situation was different, besides diatoms from genus *Pseudo-nitzschia,* the nanoplankton fraction was more pronounced, especially at station SJ101 in the surface layer, where they were more abundant than diatoms. In the bottom layer (around 30 m depth), diatoms were 5 times more numerous than the nanoplankton fraction. Such species composition highly affects zooplankton activities and abundances. It is shown that phytoplankton speciation in terms of different cell sizes and classes contribute differently to the NAd phytoplankton carbon content (Marić et al., 2013). Furthermore, given its different dimensions, it is likely that phytoplankton is grazed by various sizes of predators (Fonda Umani et al., 2007), consequently producing different quantity and quality of OM either by direct production or exudation and grazing activities, which can further govern different microbial activities (Fonda Umani et al., 2007; Korlević et al., 2016; Čanković et al., 2017).

Variations of Chl *a* in 2017 were characterised by considerable decreases in June and October and an increase in August at SJ107. In contrast, at SJ101, values decreased considerably in August with an exceptional increase in July. Quite expectedly, changes in the total water column abundances of phytoplankton were positively related to changes in the water column amount of POC at both stations, with a slightly higher correlation at SJ101 (Table S3).

Missing correlation between water column-averaged phytoplankton and Chl *a,* at both stations, potentially indicate constant change of phytoplankton community. Absent correlation between both nutrients and either phytoplankton or Chl *a*, based on averaged water column values, in contrast to notable correlations among the same parameters at the surface (0 m) and upper layer (0–5 m) values, indicate that primary production in surface/upper layer might be mostly bottom-up controlled, whereas deeper layer seems to be involved in more complex food-web interactions, as confirmed by PCA. Still, correlations between water column-averaged phytoplankton and nutrients with some delay in time at both stations might indicate that primary production is generally related to nutrient impact.

4.3. *Oceanographic conditions and water circulation supporting the accumulation of zooplankton and DOC*

The initial trigger of the extreme OM production during the summer of 2017 seems to originate from the winter-early spring spread of *M. leidyi* from the Venice Lagoon to the eastern part of the NAd, as indicated by the dispersion model (Fig. 9). *M. leidyi* is absent from most of the NAd in winter except for rare sightings in the westernmost part of the Po River delta-Rovinj transect (10 NM from the Italian coast; database CMR) or at SJ107 (as seen in Fig. 2). New monitoring results (V. Tirelli, pers. comm) along the Italian coast have revealed that *M. leidyi* has been found during the winter and early spring, even with low abundances, within or just outside of the Venetian and Grado-Marano Lagoons. Lagoon systems with their eutrophic waters seem to be favourable for *M. leidyi*, functioning as a refuge, as previously reported for the other Mediterranean areas such as the lagoons in the Gulf of Lyon (France) (Marchessaux and Belloni, 2021).

Our investigations also included three additional potential source areas (Trieste and Pula harbours, and Grado-Marano Lagoon, located approximately 15 NM west from the Trieste harbour) (Fig. S1), which are more eutrophic than the rest of the NAd and could receive direct discharges of ballast waters containing *M. leidyi*. However, the dispersion results indicate that the spreading of *M. leidyi* from those sites are quite limited and do not support the spreading to the open waters of the NAd. After comparing the results of the model, we can say that due to a sufficient presence of *M. leidyi* and a specific circulation system that transported waters towards the east, only the source area of the Venetian Lagoon, was able to disperse *M. leidyi* across the entire NAd. Within the large anticyclonic gyre developed from April around SJ107, the retention of plankton-rich waters favoured a substantial growth and reproduction of *M. leidyi*, linked with the unusually high accumulation of DOC.

Surface data distribution across the NAd in May-August shows the presence of *M. leidyi* in the eastern and western part of the Po River delta – Rovinj transect, in western cyclonic and eastern anticyclonic gyres, with a lower amount or absence of the species in the middle part of the section. The central area of the section between the two gyres, characterised by the continuous inflow of the central Adriatic waters, was less suitable for *M. leidyi* accumulation because of the intense dynamic. In September, due to more pronounced eastward motions in the gyre, as indicated on circulation plots, *M. leidyi* was transported from the open sea to the coastal area. Size distribution of *M. leidyi* species implies that their reproduction started in June when the gyre structure was well developed along the transect. Thus, presented results point that reproduction of *M. leidyi* is closely related to gyres.

5. Conclusion

The results documented here are in accordance with previous studies showing that: 1) circulation patterns in the NAd consist of several gyres (cyclonic/anticyclonic) that change position and extent seasonally and yearly (Supić et al., 2012); 2) gyres act as “hot spots” characterised by waters with lower salinity, which affect different prokaryotic activity (Orlić et al., 2013) and consequently govern the accumulation of nutrients and organic matter. We related here measurements and numerical hydrodynamic model to assess the extension of the gyre in time and space.

Rates of bacterial production, nitrogen regeneration and community respiration are highest at intermediate salinities in the near-rivers plume (Benner et al., 1992; Pettine et al., 2001; Mannino and Harvey, 2000). All these facts support the observed accumulation of surface-active DOC.

The NAd in 2017, as an anomalous year, was characterised by the inflow of very high salinity water, usually associated with oligotrophic conditions. The high abundance of phytoplankton recorded at the beginning of the year was the main trigger for the initial rise in zooplankton. The development of the long-lasting closed circulation gyres was especially pronounced at SJ107, favouring the accumulation of mesozooplankton and *M. leidyi*, which later, during spring and summer months by enhanced grazing activities and decay processes, led to the release of an extreme amount of DOC and SAS in the water column.

Inclusive, in line with climate change and its impact on thermohaline properties in the Adriatic, the response in geostrophic currents patterns and generally in dynamic of the region is to be expected. In this paper, the presence and long-time duration of the anticyclonic gyre around SJ107 as the main cause of OM accumulation are invoked. It is to be evaluated by further research whether such dynamic conditions are supported by expected climate changes. With the appearance of the invasive ctenophore *M. leidyi*, now residing in the NAd since 2016, and its production of highly reactive DOC, extreme eutrophic episodes in the NAd (or further south due to its spread by ballast waters, and here reported changes in the circulation system) can be more common and long-lasting. Analysis of the long-term SAS data (Ciglenečki et al., 2020) points to the same conclusion.

The parameters relevant to OM production were analysed here by correlating seasonal changes of their averaged water column values at selected stations, which enabled a better understanding of basic processes in the NAd food-web for the studied period. The lack of correlations between seasonal changes in temperature and salinity and most oceanological parameters indicates that changes in the pelagic life cycle cannot be easily interpreted in terms of seasonal heating/cooling processes but necessitate a more complex approach. In any case, basic dynamics of the NAd, including the transport of OM across the region and its retention within gyres, should be taken into consideration.

In addition, we showed that the accumulation of *M. leidyi* and DOC could be related to open sea areas and not only to coastal regions and lagoons.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2021.103599.

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Supporting information:

Dissolved organic carbon accumulation during a bloom of invasive gelatinous zooplankton *Mnemiopsis leidyi* in the northern Adriatic Sea; case of the anomalous summer in 2017

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Table S1. *M. leidyi* monitoring details

Date	Depth (m)	Station	*M. leidyi* (ind./m^3)
3.5.2017.	0-1	RV001	0.0001
		ZI332	0.0005
		ZI032	0.0005
		ZI031	0.0001
		SJ107	0.0001
		SJ106	0.0001
		SJ105	0
		SJ104	0
		SJ103	0
		SJ102	0.001
		SJ101	0.002
		SJ1A1	0.001
		SJ1B1	0.0001
		SJ108	0.0001
		SJ1A8	0.0001
		SJ1B8	0
12.6.2017.	0-1	RV001	0.0001
		ZI332	0.001
		ZI032	0.1
		ZI031	0.001
		SJ107	0.001
		SJ106	0.0001
		SJ105	0.0001
		SJ104	0.0001
		SJ103	0.0001
		SJ102	0.0001
		SJ101	0.0001
		SJ1A1	0
		SJ1B1	0
		SJ108	0.0002
		SJ1A8	0.0001
		SJ1B8	0.0001
12.7.2017.	0-1	RV001	4
		ZI332	5
		ZI032	5
		ZI031	0.0001
		SJ107	6
		SJ106	0.0003
		SJ105	0.0001

		SJ104	0.0001
		SJ103	0.0001
		SJ102	0.0001
		SJ101	3
		SJ1A1	2
		SJ1B1	3
		SJ108	3
		SJ1A8	0.0001
		SJ1B8	0.0003
30.8.2017.	0-1	RV001	4
		ZI332	5
		ZI032	3
		ZI031	0.0005
		SJ107	1
		SJ106	1
		SJ105	1,5
		SJ104	1
		SJ103	1
		SJ102	1
		SJ101	3
		SJ1A1	3
		SJ1B1	3
		SJ108	5
		SJ1A8	0.01
		SJ1B8	0.05
13-14. 9.2017.	0-1	RV001	6.6
		ZI032	15
		S	0.5
		S1	0.1
		U	4.5
		D	2.8
		N	2.9
		N1	0.1
		P0	8.9
		P1	4
		P2	0.03
		P3	0.1
		V	3.8
		L	2.8
		Ba	3.8
		Br	0.06
		Pu	5.8

		Pu1	0.4
		Pu2	0.3
		Pu3	0.1
3.10.2017.	0-1	RV001	0.1
		ZI332	0.1
		ZI032	0.05
		ZI031	0.01
		SJ107	0
		SJ106	0.01
		SJ105	0.01
		SJ104	0.001

Table S2. Correlation coefficients between total concentrations of biological and chemical (TIN, PO_4^{3-}) parameters measured in 2017 at SJ107 and SJ101, taken with 0, -1 and -2 months time lag. (Note that correlations remain the same if total amounts of parameters are averaged over the water column and then compared.) Correlation coefficients over ≥ 0.6 are in yellow and below ≤ -0.6 in light blue. They include microzooplankton (MicroZOO), mezozooplankton (MezoZOO), ctenophores (Cten), chlorophyll *a* (Chl), phytoplankton (Phyto).

		MicroZOO	MezoZOO	*Cten*	Chl	Phyto	PO_4	TIN
SJ107	Chl (0 months)	-0,05	-0,07	-0,36	-	0,25	0,28	0,56
	Chl (-1 months)	0,47	-0,72	-0,79	0,13	-0,59	-0,60	0,50
	Chl (-2 months)	-0,04	-0,91	-0,20	-0,80	-0,37	-0,16	-0,69
SJ101	Chl (0 months)	-0,01	-0,41	-0,52	-	0,15	0,54	-0,10
	Chl (-1 months)	-0,25	0,97	0,93	-0,48	-0,44	-0,39	-0,67
	Chl (-2 months)	0,97	0,66	-0,11	-0,32	-0,49	0,49	-0,26
SJ107	Phyto (0 months)	-0,77	-0,02	0,15	0,25	-	0,21	-0,16
	Phyto (-1 months)	0,47	0,42	-0,59	0,30	-0,58	0,10	0,35
	Phyto (-2 months)	0,24	-0,36	0,28	-0,88	0,13	0,32	-0,64
SJ101	Phyto (0 months)	-0,34	-0,46	-0,04	0,15	-	-0,24	0,30
	Phyto (-1 months)	-0,26	-0,63	-0,50	0,90	0,32	0,33	-0,32
	Phyto (-2 months)	0,93	0,69	-0,02	-0,42	-0,45	0,39	-0,26
SJ107	MicroZOO (0 months)	-	-0,12	-0,32	-0,33	-0,83	0,45	0,33
	MicroZOO (-1 month)	0,00	-0,45	0,65	-0,63	-0,05	-0,05	0,17
	MicroZOO (-2 months)	-0,73	-0,18	-0,15	0,73	-0,28	-0,83	0,69
SJ101	MicroZOO (0 months)	-	0,57	-0,17	-0,01	-0,34	0,57	-0,39
	MicroZOO (-1 month)	1,00	-0,76	-0,80	0,31	0,25	-0,38	-0,59
	MicroZOO (-2 months)	-0,22	0,01	0,01	0,50	-0,58	0,31	-0,55
SJ107	PO_4 (0 months)	0,52	0,05	-0,23	0,28	0,21	-	0,40
	PO_4 (-1 months)	0,94	0,09	-0,14	-0,48	-0,98	0,17	0,54
	PO_4 (-2 months	-0,27	-0,09	0,76	-0,11	0,76	-0,41	0,25
SJ101	PO_4 (0 months)	0,57	0,27	-0,24	0,54	-0,24	-	0,12
	PO_4 (-1 months)	-0,17	0,44	0,61	-0,50	0,26	-0,96	-0,59
	PO_4 (-2 months	0,16	-0,23	-0,59	0,86	-0,46	0,80	-0,15
SJ107	TIN (0 months)	0,39	-0,50	-0,26	0,56	-0,16	0,40	-
	TIN (-1 months)	-0,51	-0,76	-0,53	0,32	-0,29	-0,90	0,77
	TIN (-2 months)	0,07	-0,57	-0,27	0,06	-0,07	-0,32	-0,35
SJ101	TIN (0 months)	-0,39	-0,87	-0,64	-0,10	0,30	0,12	-
	TIN (-1 months)	-0,69	-0,66	-0,12	0,07	0,93	-0,08	0,57
	TIN (-2 months)	0,41	0,01	-0,18	-0,39	0,47	-0,08	0,54

Table S3. Correlation coefficients between concentrations of DOC, SAS$_{diss}$ (SAS filtered), SAS$_T$ (SAS non-filtered) and POC measured in 2017 at SJ107 and SJ101, and concentrations of chlorophyll *a* (Chl), abundances of phytoplankton (Phyto), microzooplankton (MicroZOO), mezozooplankton (MezoZOO), ctenophores (C*ten*) and nutrients PO$_4^{3-}$ and TIN, taken with 0, -1 and -2 months time lag. Correlation coefficinets over 0.6 are in yellow and below -0.6 light blue.

	SJ107				SJ101			
	DOC	SAS $_{diss}$	SAS$_T$	POC	DOC	SAS $_{diss}$	SAS$_T$	POC
Chl (0 montsh)	-0,34	-0,71	-0,65	-0,04	0,06	0,33	0,40	0,34
Chl (-1 month)	-0,91	-0,84	-0,88	-0,81	0,52	0,35	-0,15	-0,43
Chl (-2 months)	-0,66	-0,69	-0,72	-0,57	0,92	0,98	0,77	-0,06
Phyto (0 months)	0,16	0,14	0,22	0,75	-0,25	0,06	0,37	0,80
Phyto (-1 month)	0,06	-0,02	-0,09	-0,28	0,26	0,56	0,82	0,61
Phyto (-2 months)	-0,22	0,99	0,95	0,01	0,91	0,96	0,82	-0,04
MicroZOO (0 months)	-0,22	-0,04	-0,07	-0,58	0,89	0,87	0,60	0,16
MicroZOO (-1 month)	-0,07	-0,12	-0,16	-0,23	0,79	0,98	0,86	0,50
MicroZOO (-2 months)	0,17	-0,52	-0,57	-0,18	-0,07	-0,15	-0,86	-0,76
MezoZOO (0 montsh)	0,74	0,77	0,77	0,50	0,85	0,78	0,61	-0,06
MezoZOO (-1 month)	0,96	0,97	0,98	0,55	0,69	0,86	0,67	0,24
MezoZOO (-2 months)	0,82	0,54	0,40	0,06	-0,12	-0,18	-0,88	-0,58
Cten (0 months)	0,70	0,51	0,46	0,19	0,27	0,34	0,71	0,00
Cten (-1 months)	0,62	0,76	0,79	0,80	0,39	0,64	0,37	0,02
Cten (-2 months)	0,53	0,97	0,98	0,46	0,60	0,76	-0,03	-0,16
PO$_4$ (0 months)	-0,22	0,12	0,20	0,21	0,21	0,17	0,27	0,21
PO$_4$ (-1 months)	-0,11	0,10	0,03	-0,85	0,59	0,63	0,59	0,16
PO$_4$ (-2 months	0,08	-0,95	-0,92	-0,52	0,04	0,01	-0,77	-0,36
TIN (0 months)	-0,46	-0,59	-0,62	-0,60	-0,82	-0,87	-0,68	-0,01
TIN (-1 months)	-0,83	-0,83	-0,84	-0,57	-0,64	-0,30	0,25	0,87
TIN (-2 months)	-0,80	-0,98	-0,96	-0,74	0,20	0,33	0,94	0,75

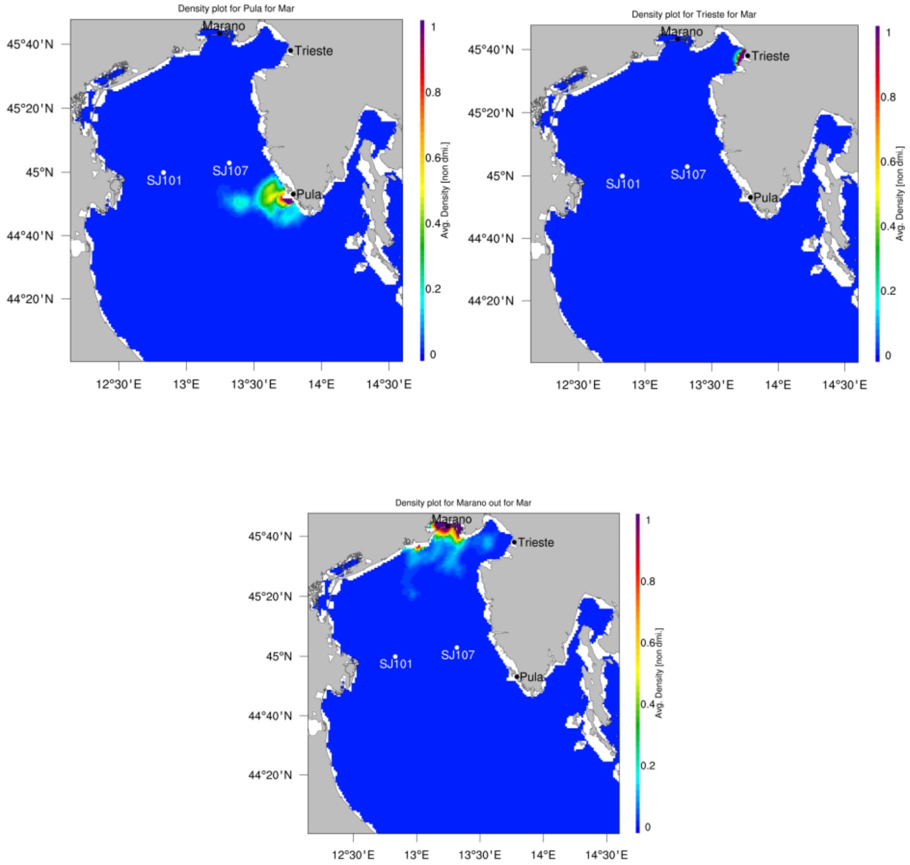

Figure S1. Density of drifters, released in amount of 3 per day from Pula (up, left) and Trieste (up, right) harbours as well as from outer part of the Grado-Marano Lagoon (down) in surface layer starting on 1 January 2017, modelled and averaged for March.

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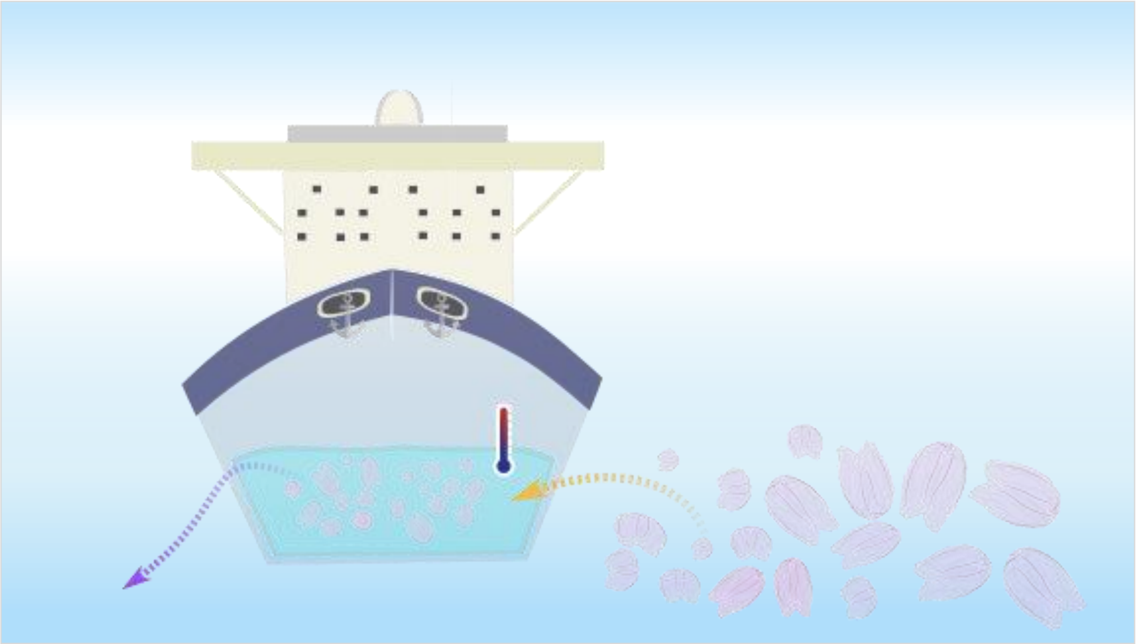

Manuscript type: Short communications

Title: Treating ballast waters to limit *Mnemiopsis leidyi* access to new habitats

Keywords: Marine invasive species · *Mnemiopsis leidyi* · ballast water treatment · *Mnemiopsis* survival · onboard thermal treatments · Adriatic Sea

Abstract

Discharging untreated ballast waters supports the spread of invasive species. The most successful ballast-water mediated biological invasion was a transatlantic transport of the ctenophore *Mnemiopsis leidyi* to many Eurasian seas, where it has significantly impacted local ecosystems. To prevent its spread to new areas, we studied the survival of different *M. leidyi* life stages exposed to several eradication techniques. We looked closely into the technical applicability of an onboard thermal treatment by calculating its duration and the required energy to perform it. The duration was considered as a sum of the time to heat ballast tanks by using the engine's waste heat for two types of ships and *M. leidyi*'s eradication. The calculated duration of the proposed treatment allowed us to estimate a minimum travel length undertaken by a specific type of ship to eliminate *M. leidyi* successfully. The travel length determines the appropriate technique and minimal requirements to eliminate *M. leidyi* successfully and, thus, can serve as a guideline to a strategic management plan. In conclusion, the proposed onboard treatment would be efficient on smaller ships and minimum distances of 200-300 km depending on the season but not on the short routes where other treatment techniques, e.g. exposure to ultrasonic cavitation or microwave radiation, should be considered.

Introduction

Nowadays, approximately two-thirds of traded goods are shipped worldwide by sea (Kumar & Hoffmann 2002), involving the transport of ~3.5 10^9 t of ballast waters annually (Endresen et al. 2004). Ballast waters ensure ships' buoyancy, stability and manoeuvrability (Werschkun et al. 2014) but can also carry organisms into new ecosystems (Carlton 1985; Williams et al. 1988). Therefore, to prevent or at least reduce the intensity of biological invasions mediated by ballast waters, their adequate management and treatment are becoming progressively urgent. One of the most successful ballast-water mediated biological invasions was the transatlantic transport of the ctenophore *Mnemiopsis leidyi* to the Eurasian seas, which significantly impacted local ecosystems.

M. leidyi is one of the world's worst invaders (Lowe et al. 2000). After arriving in the Black Sea, it dramatically increased its population and spread by currents and ballast waters to the neighbouring basins (Shiganova et al. 2019). The huge adaptability of *M. leidyi* to a vast range of environmental conditions, such as wide temperature and salinity ranges and the tolerance to low concentrations of oxygen (O_2) (Shiganova et al. 2019) coupled with exceptionally high fecundity (Reeve et al. 1989), lead to one of the most successful ballast-water mediated biological invasions.

Ballast waters also likely offered the means for the arrival of *M. leidyi* to the Adriatic Sea. The first record occurred in 2005 in the Gulf of Trieste (Shiganova & Malej 2009)—an area of intensive maritime traffic. Since 2016 *M. leidyi* has consistently appeared in the northern and western but not in the southern Adriatic—in direct contact with the rest of the Mediterranean (Budiša et al. 2021). The only exception was a brief appearance in 2017 in the Port of Ploče (south-east Adriatic) (D. Lučić pers. comm.)—a cargo port receiving ships from the northern/western Adriatic. In addition, a preliminary molecular study (A. Baričević pers. comm.) linked Adriatic populations to those in the Black Sea. In the north of the basin, seasonal *M. leidyi* booms covering tens of km^2 exert multiple effects on the pelagic ecosystem by influencing plankton communities and the carbon pool along the coast (Budiša et al. 2021; Paliaga et al. 2021).

In this context, the geomorphology of the Adriatic represents a compliance problem with the International Convention (IMO 2004) because ballast exchange allowed at ≥200 m depth and never closer than 50 NM of the land is applicable within a very limited area and could significantly slow down ship transport. Furthermore, according to Markovina et al. (2007), the Adriatic is inadequate for ballast waters exchange. Thus, it is essential to effectively treat ballast waters onboard/in harbours for transport ships in the Adriatic. Moreover, the management standards stating that <10 smaller (<50 µm) viable organisms per mL and bigger per m^3 have to be discharged (Vorkapić et al. 2016) is insufficient for such a resilient species. Therefore, to prevent the spread of *M. leidyi* within the Adriatic and other nearby seas, we considered preventive measures to eliminate it from ballast waters.

There are plenty of ballast water treatments. The primary onboard separation techniques include various physical methods, e.g., self-cleaning filter systems (pores size 40 µm), allowing smaller organisms to enter (Werschkun et al. 2014). Secondary techniques include various mechanical and chemical methods or their combination. The most common mechanical methods are ultrasound, UV-light, thermal, magnetic and electrical treatments (Vorkapić et al. 2016). Another efficient technique is deoxygenation which involves bubbling nitrogen (N_2) or other inert gases to supersede O_2 and eliminate organisms while protecting tanks against corrosion (Tamburri et al. 2002). A combination of several treatments is used most of the time (Balaji & Jaakob 2011). This research is focused primarily on thermal treatments since they offer the advantage of using the engine and backup boiler-generated waste heat (Balaji & Jaakob 2011).

To recommend an adequate treatment against *M. leidyi*, we tested the effects of temperature, microwaves, ultrasonication and deoxygenation on its survival. Moreover, we give preliminary calculations to assess the feasibility of an onboard treatment using engine coolant water.

Materials & Methods

Laboratory experiments

Intact adult *M. leidyi* (length ~7 cm) collected during blooms were placed in a 40 L pool with circulating seawater (21±0.5 °C, salinity 37) at a 12:12 h light regime.

To study *M. leidyi* survival, we performed 5 experiments (E1-5), monitoring specimens until their decay.

In E1, we used the seawater from the Adriatic during *M. leidyi* blooms. We placed 30 adult specimens into enclosed tanks (setups A1 and A2, x 100 L, in triplicates) with filtered seawater (industrial filters, pore size 0.7 µm) at 21 °C (*in situ* temperature). In A1, stagnant water and food scarcity simulated ballast water conditions and served as control. In A2, *Artemia salina* larvae (food), circulation and air bubbling were added to simulate the conditions in the sea. We considered that the specimens entered the decay stage when they started sinking and losing their structural integrity turning to a brownish gelatinous mass.

In E2, the thermal effects were studied by placing 30 adults into three open tanks (100 L) in non-filtered seawater at six selected temperatures – also applied in E3-4.

In E3, to investigate the effects of hypoxia/anoxia, we vigorously bubbled N_2 into the tanks while measuring O_2 saturation (Hanna Instruments® multiparametric probe) up to 20% saturation for hypoxia and 0% for anoxia and placing 30 adults in three 100 L enclosed tanks.

E4 was set in triplicates (N_{adult}=90), placing five specimens in 3 L buckets into an ultrasonication bath (VWR Scientific 750D).

In E5, we investigated the microwave heating effects on adults by placing a bucket (1.5 L) with filtered seawater (0.7 µm pore size Whatman™ GF/F) and five specimens into a microwave oven. We tested their survival at 100 W, 450 W and 900 W, repeating it 6x.

Finally, we applied E2-5 tests on eggs and larvae. First, we placed 10 adults into 3 L buckets containing filtered seawater (zooplankton mesh, pore size 50 µm) to reproduce. After 24 h, we returned adult specimens to the collection tank. Next, we applied to the remained water: reverse filtration (Holm-Hansen et al. 1970), centrifugation (200 rpm for 5 min), decantation, and sample concentration to 50-100 mL. Then, randomly selected intact *M. leidyi* eggs and larvae were isolated under a stereomicroscope (20-50x). Seawater was pre-filtered (zooplankton mesh, pore size 20 µm) for all eggs/larvae experiments. Each treatment was set in triplicates using 30 eggs/10 larvae produced by different adults. We incubated specimens in open Petri dishes containing 15 mL of pre-filtered seawater at selected temperatures. For deoxygenation, the specimens were incubated in 15 mL plastic test tubes containing anoxic/hypoxic pre-filtered seawater (see E3). To prevent O_2 from entering, we opened sample tubes only at the time of adults' decay. If the specimen were still viable, we extrapolated the actual time to total decay. Then the same setup was repeated to test select ultrasonication (see E4) and microwave (see E5) effects.

Technical calculations

To estimate the feasibility of *M. leidyi* thermal control, we calculated the total heating capacity for the thermal treatment of the ballast tanks comprising the term for the replacement of heat losses from the ballast tank water to the outer air and seawater and the term for heating the tank to the desired final temperature:

$$\dot{Q}_{\mathrm{tot}} = \dot{Q}_{\mathrm{r}} + \dot{Q}_{\mathrm{h}} \qquad \text{(Eq. 1).}$$

The heating capacity for the replacement of heat losses can be expressed as:

$$\dot{Q}_{\mathrm{r}} = \sum_{i=1}^{n} U_{\mathrm{i}} \cdot A_{\mathrm{i}} \cdot (T_{\mathrm{in}} - T_{\mathrm{out}}) \qquad \text{(Eq. 2),}$$

where the overall heat transfer coefficient (U-value) of the i^{th} element wall of the ballast tank is denoted by U_{i} ($\mathrm{W/m^2K}$), the corresponding heat transfer surface area is A_{i} ($\mathrm{m^2}$), and the temperature difference between internal tank water and the outer seawater is $T_{\mathrm{in}} - T_{\mathrm{out}}$ (K). The overall heat transfer coefficient is calculated from the convective heat transfer coefficients at the inner and outer tank walls, h_{in} and h_{out} ($\mathrm{W/m^2K}$), the thickness δ (m), and the thermal conductivity λ (W/mK) of the tank wall material as:

$$U_{\mathrm{i}} = \left(\frac{1}{h_{\mathrm{in}}} + \frac{\delta}{\lambda} + \frac{1}{h_{\mathrm{out}}}\right)^{-1} \qquad \text{(Eq. 3).}$$

The capacity for heating up the ballast tank water to the desired final temperature can be expressed as:

$$\dot{Q}_{\mathrm{h}} = \frac{V_{\mathrm{w}} \cdot \rho_{\mathrm{w}} \cdot c_{\mathrm{w}} \cdot (T_{\mathrm{f}} - T_{0})}{t} \qquad \text{(Eq. 4),}$$

where V_{w} ($\mathrm{m^3}$) is the water volume in the ballast tank, ρ_{w} ($\mathrm{kg/m^3}$) is the density of water and c_{w} (J/kgK) is the specific thermal capacity of water. The difference between the final and the initial ballast tank water temperatures is $T_{\mathrm{f}} - T_0$ (K); thus, the internal tank water temperature ranges from the initial to the final temperature during the thermal treatment process, $T_0 \leq T_{\mathrm{in}} \leq T_{\mathrm{f}}$. The time duration of the ballast water heating is t (s). The physical properties of water are calculated using the CoolProp library for fluids properties embedded in MSExcel.

The physical properties of water change with the temperature and thus change the heat transfer coefficients at the ballast tank walls. An iterative assumption-correction procedure was implemented to obtain the real tank wall temperatures at the inner and outer surfaces. In the first iteration step, the inner and outer tank wall temperatures are assumed and used to calculate the physical properties of water and obtain the heat transfer coefficients and the heat flow rates. These values are then used to update the tank wall temperatures until convergence between all heat flow rates is achieved. The calculation proceeds with a temperature step of 1 K, starting from the initial tank water temperature T_0 and finishing with the final tank temperature T_f. This procedure is repeated for all the tank wall surfaces.

Depending on the case, the convective heat transfer coefficients are calculated from the heat transfer correlation for natural or forced convection. The dimensionless convective heat transfer is expressed with the Nusselt number, which depends on the Grashof and Prandtl dimensionless parameters in natural convection problems and similarly on the Reynolds and Prandtl dimensionless parameters in forced convection problems:

$$Nu = \frac{h\cdot l}{\lambda} = \begin{cases} f(Gr, Pr) - \text{ natural convection} \\ f(Re, Pr) - \text{ forced convection} \end{cases} \qquad \text{(Eq. 5).}$$

These dimensionless parameters are evaluated using the following expressions:

$$\text{a)} \;\; Gr = \frac{g\cdot l^3}{(\mu/\rho)^2}\cdot\frac{\rho-\rho_\infty}{\rho} \;\; \text{; b)} \;\; Re = \frac{w\cdot l\cdot \rho}{\mu} \;\; \text{; c)} \;\; Pr = \frac{\mu\cdot c}{\lambda} \qquad \text{(Eq. 6).}$$

The symbols in the above dimensionless parameters represent g – gravitational acceleration (9.81 m/s^2), l – characteristic length (m), and w – fluid flow velocity (m/s). The fluid properties such as ρ – density (kg/m^3), μ – dynamic viscosity (Pa·s), c – specific heat capacity (J/kgK) and λ - thermal conductivity (W/mK) are evaluated at the film temperature $T_f = 0.5\cdot(T_w + T_\infty)$, which is the arithmetic mean between the wall (T_w) and the undisturbed flow temperature (T_∞). The fluid density evaluated at the temperature of the undisturbed flow is denoted by ρ_∞ (kg/m^3). Table 1 reports the heat transfer correlations adopted for evaluating the heat transfer coefficients for natural and forced convection at horizontal or vertical surfaces in contact with water or air (Cengel & Ghajar, 2020). Heat transfer coefficients for natural convection are typically low compared to forced convection. Therefore, radiation must be considered in natural convection problems involving gases, but it can be disregarded in forced convection problems.

We analysed two types of ships: *type I* with horizontal and *type II* with horizontal and vertical side tanks (Fig. S1, Supplementary material). The principal dimensions of horizontal tanks are width (D), length (L) and distance between inner and outer shell (H_1), and vertical are the height of water column (H_2), the height of air fill (H_3) and distance between inner and outer shell (B_1). The heat transfer at the surfaces of the tanks is determined from the overall heat transfer coefficients (Eq. 2-3), and convective heat transfer coefficients are evaluated from the Nusselt number correlation reported in Table 1. For instance, the overall heat transfer coefficient at the inner shell of the double bottom ballast tank (U_8) is determined from the heat transfer coefficient for external natural convection on the upper surface of a hot plate (Eq. 8.1 or 8.2) and the heat transfer coefficient for internal natural convection. In Table 1, we also listed a series of geometry assumptions for ships. The ballast tank geometry was assumed from the Technical specification for the RO-PAX ship, courtesy of Uljanik Shipyard (Pula, Croatia).

Results and Discussion

Laboratory experiments

The results from E1-5 are given in Table 2, and the images of viable and decayed stages of *M. leidyi* life are given in Fig. S2. The results from the ballast tank simulations (E1) set *M. leidyi* survival up to a month. The survival in control simulating ideal conditions (A2) exceeded 30 days, but the longest survivals in comparable conditions recorded in the Aquarium of Pula were in the range between 60 and 90 days (M. Mičić pers. comm.), in line with survival times estimated for the much colder (3 °C) Baltic Sea (Javidpour et al., 2020).

In E2, adults' survival was the longest at 21 °C. At 30 °C—specimens survived for approximately 20 days. The shortest survival occurred at 50 °C, 1.5 h for adults and larvae and 2.5 h for eggs. Monitoring larval and eggs' intact structural integrity up to 30 °C was not applicable because of hatching and maturing.

Lack of O_2 (E3) set the decay of adults within a day, and it was ~2x as fast during anoxia. Ultrasonication sets the survival within a few h, while microwave exposure even within an h. Overall, above 40 °C, adults' survival was <10 h, somewhat for larvae longer and 12 h for eggs. Eggs represented the most enduring life stage in all the treatments, but their viability was unaccounted for, defining their decay solely as a loss of structural integrity. Thus, as reported for some techniques (Osman et al. 2016), the inside damage could set the 'decay' earlier.

Of all the treatments, microwave exposure was the most efficient, especially when temperature increased rapidly, eliminating every life stage of *M. leidyi* within an h. Ultrasonication combined with temperatures >40 °C gave similar results. Moreover, introducing vigorous bubbling and water circulations seemed to shorten adults' life expectancy further. The use of microwaves or ultrasound techniques requires expensive additional onboard equipment available on the market or in a prototype stage but has not been consistently installed and employed yet. In the present research, we focus on assessing the applicability of alternative approaches in the thermic treatment of ballast waters that rely on the existing ship infrastructure and energy sources, with the addition of simple, low-tech components such as tubes and additional insulation to the ballast tanks. The objective of the thermal treatment would be to reach temperatures of >40 °C which would set the survival threshold under 10 h. or, if feasible, even at higher temperatures of 50 °C which would ensure the elimination of *M. leidyi* within 2.5 h.

Alternatively, the thermic treatment could be complemented with the addition of N_2 in order to deoxygenate the ballast waters and eliminate *M. leidyi* faster (Table 2) or with much higher energy efficiency at lower temperatures. Our data show that releasing untreated ballast waters containing *M. leidyi* within less than 20 days will likely convey live specimens to the receiving waters. In addition, if a portion of water gets exchanged during the voyage, bringing food and O_2 to the ballast tanks, even voyages lasting a couple of months might ensure *M. leidyi*'s survival.

Technical calculations

Here we consider the thermic onboard treatment for *M. leidyi*'s eradication. In Table 3, different case scenarios corresponding to different duration of thermal treatments are given. We assumed the cargo space to be empty (filled with air) and the total ballast volume to be 288 m^3 for ship *type I* and 648 m^3 in *ship type II*, according to specifications given in Table 1.

The relationship between the temperature in water tanks, heat transfer coefficients ($U_{2,7,8}$) and heat losses ($\dot{Q}_r$) for the double bottom tank surfaces shows that *U*-values increase with the ballast temperature as a consequence of increasing temperature differences between tank wall and water that intensifies natural buoyancy in the tank (e.g., *type I*/1.2 case, Fig. S3). The highest *U* is at the vertical sidewall of the double bottom tank (U_2) – a consequence of forced convection heat transfer at the external seawater side, and the lowest at the inner shell of the tank (U_2), if we assume air-filled cargo space, thus low heat transfer properties. Increases in $\dot{Q}_r$ become faster at higher tank temperatures – a consequence of larger temperature differences and higher *U*-values (Eq. 2), e.g. $\dot{Q}_r$=0.40 MW (30 °C), 0.84 MW (40 °C) and 1.39 MW (50 °C). The minimum heating capacity for thermal treatment should be sufficient to replace heat losses in ballast tanks, $\dot{Q}_{tot} = \dot{Q}_r$, (Eq. 1). When this is applied to, e.g. *type I*/case 1.2 (Fig. S4), it demonstrates initially fast heating (23.6 h to reach 49 °C) because of a surplus of heating capacity for the water heating itself ($\dot{Q}_h$) that is followed by heat losses ($\dot{Q}_r$) progressively slowing the process (additional 33 h to 50 °C). Including the time for eradication, the process becomes very long (59.1 h) and requires excessive energy (*E*) consumption (82.74 MWh). To speed up heating and reduce consumption, we need $\dot{Q}_{tot} > \dot{Q}_r$. In practice, the eradication starts already above 40 °C, and *M. leidyi* could be eliminated within 20 h, which would require 28 MWh.

The problem of heating the ballast tanks can also be approached differently by arbitrarily limiting the duration of the heating and increasing $\dot{Q}_{\mathrm{tot}}$. For instance, a process of 10 h (heating 7.5 h and eradication 2.5 h) would require 2.26 MW to compensate for heat losses (1.39 MW) and speed up the heating. In this case, E consumption (20.43 MWh) is 4x lower than previously discussed. Similarly, it can be calculated for the other cases (Table 3), e.g., the process at 45 °C requires 14% less energy (1.89 MW) but takes 14 h, increasing the total consumption (21.33 MWh) slightly. Indeed, the total consumption depends on the final temperature and speed of the heating, while energy consumption also depends on *M. leidyi* eradication. In Fig.1, $\dot{Q}_{\mathrm{tot}}$ and E are given for all the cases and show that $\dot{Q}_{\mathrm{tot}}$ increases with the increased tank-seawater temperature difference, while E depends on the eradication time. Besides, combining thermal and deoxygenation treatments would speed eradication and would reduce both $\dot{Q}_{\mathrm{tot}}$ and E. Compared to *type I*, $\dot{Q}_{\mathrm{tot}}$ and E for ship *type II* are over 2x higher due to the bigger tanks (2.25x) and greater heat losses. The lowest values for *type II* are calculated for case 3.3 ($\dot{Q}_{\mathrm{tot}} = 1.27$ MW, $E = 12.57$ MWh), and the highest for the 1.2 ($\dot{Q}_{\mathrm{tot}} = 4.78$ MW, $E = 42.28$ MWh). However, for cases 1.1, 1.2, 2.4 and 3.1, $\dot{Q}_{\mathrm{r}} > \dot{Q}_{\mathrm{tot}}$ and requires >2 MW to achieve the desired temperature.

To provide a realistic scenario and verify the feasibility of the proposed treatments, we considered $\dot{Q}_{\mathrm{tot}} = 2.0$ MW accounted from the ship-built specifications: two diesel generator sets, each with an electric capacity of 1368 kW and an emergency diesel generation set (280 kW) (Uljanik Shipyard, 2015). Out of the available 3.0 MW, ⅔ could be used for heating and the rest for other energy consumers.

In Fig. 2, the duration of treatments and E are compared and show that treatment slows as the heating time (T_{h}) increases with the tank-seawater temperature difference, e.g. for the ship *type I*, $T_{\mathrm{h}} = 9.2$ h in case 1.2 and 1.8 h in case 3.3. The consumption increases with T_{h}, e.g., for the ship *type I*, E=21.8 MWh in case 1.2 but only 5.2 MWh in case 3.3. In all cases for *type I*, the total thermal treatment time is finite, meaning that the fixed 2.0 MW exceeds $\dot{Q}_{\mathrm{r}}$. For *type II*, cases 1.1, 1.2, 2.4 and 3.1 were omitted as unfit considering parameters from Table 3, while the rest shows longer T_{h} than in *type I*.

To further check for the feasibility of an onboard thermic treatment, we considered that the heat supplied by the engines could be distributed in the form of saturated steam flowing through tubes in the ballast tanks. The estimated length of the tubes is indeed technically viable (Fig. S5).

However, even if both systems can be constructed, the treatments could only be used throughout the year for ship *type I*. The fastest treatment for the worst scenario (case 1.2) that simulates winter conditions can be concluded within 11 h or 9 h if combined with deoxygenation (case 1.4). In the best scenario simulating summer conditions, the eradication can be attained within 9 h (case 3.2) or by 7 h if combined with deoxygenation (case 3.4). Moreover, in the autumn (or spring), the fastest eradication can be achieved within 9.5 h (case 2.2) and within 8 h when combined with N_2 (case 2.4). Overall, combined treatments reduce treatments' duration from 16 to 25%. In addition, the thermal treatments are more energy-consuming than those combined (Fig. 2) as the higher temperatures shorten *M. leidyi*'s survival (Table 2). The most efficient energetically approach and the 2nd fastest is the combined treatment at 35 °C (case 2.3).

The calculated treatment times, in combination with the average cruising speed of 15 kn (Wang et al. 2007), help us estimate minimum voyage lengths where proposed treatments could be applied. For thermal treatments, the worst scenario (case 1.2) requires a distance of 318 km, and the best case is 208 km (3.2), while the combined treatment is 249 km (case 1.4), while for the best case, it would be 180 km (case 3.4). For the most likely scenarios, travelled distances should be between 222 km (case 2.4) and 263 km (case 2.2). Our results show that the proposed treatments could be applied on long-range oceanic cruises and numerous medium-range voyages, such as the ones within the Mediterranean and other epicontinental basins. Because the proposed treatments would be too long for short routes, the treatment could start earlier while the ship is docked or by prolonging the travelling. Alternatively, other treatments, such as ultrasonication or microwave radiation (Table 2), should be considered. On the other hand, accounting for the *M. leidyi*'s overwhelming large coverage in the blooming season, e.g. the whole northern Adriatic (~22-35 · 10^3 km^2) (Budiša et al. 2021), shows treatment's ineffectiveness for close-range voyages because its spread would be supported by natural forcing (Paliaga et al. 2021). Within the Adriatic, the proposed onboard treatments might be more useful for longer distances, e.g. connecting Port of Venice and Ploče (~500 km) and so preventing *M. leidyi* from settling in another enclosed and likely eutrophic area.

Unfortunately, the proposed treatments have limited applicability for larger ships (e.g. *type II*); thus, the equipment for other kinds of approaches (e.g. ultrasonication, microwave radiation) should be considered.

Conclusions

We demonstrated a preliminary attempt to evaluate the efficiency of different ballast water treatments to eradicate all life stages of the invasive comb jelly *M. leidyi*. Our laboratory experiments combined with technical estimates indicate several possible solutions which can help us set potential protection against *M. leidyi* global spreading. In brief, we proposed different treatments for different trajectories to ensure that there would be no viable specimens. This study can prove useful to management efforts to prevent adverse effects of introducing this ctenophore to new habitats. However, further research on combined techniques using thermal control and other physical treatments is needed to provide a more concrete management framework for *M. leidyi*'s eradication and successful control of its spread.

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Figures and Tables

Table 1 Ballast tank geometry and convection heat transfer correlations.

Ballast tank geometry and assumptions (see Fig. S1)			
L – length	18 m	H_3 – height of air fill	3 m
D – width	8 m	δ – tank wall thickness	25 mm
H_1 – distance between shells	2 m	λ – wall thermal conductivity (steel)	46 W/mK
H_2 – height of water fill	5 m	v – cruising speed	15 kn
Natural convection		Parameter range	Eq.
External natural convection on a vertical surface	$Nu = \left\{0.825 + \frac{0.387 \cdot Ra^{1/6}}{[1+(0.492/Pr)^{9/16}]^{8/27}}\right\}^2$	$10^4 \le Ra < 10^{13}$ $Ra = Gr \cdot Pr$	(7)
External natural convection on a horizontal surface: - Upper surface of a hot plate or lower surface of a cold plate - Lower surface of a hot plate or upper surface of a cold plate	$Nu = 0.54 \cdot Ra^{1/4}$ $Nu = 0.15 \cdot Ra^{1/3}$ $Nu = 0.27 \cdot Ra^{1/4}$	$10^4 \le Ra < 10^7$ $10^7 \le Ra < 10^{11}$ $10^5 \le Ra < 10^{11}$	(8.1) (8.2) (8.3)
Internal natural convection in a vertical rectangular enclosure (double hull side tank)	$Nu = 0.18\left(\frac{Pr}{0.2+Pr}Ra\right)^{0.29}$ $Nu = 0.22\left(\frac{Pr}{0.2+Pr}Ra\right)^{0.28}\left(\frac{H}{L}\right)^{-0.25}$	$1 \le H/B < 2$ $2 \le H/B \le 10$	(9.1) (9.2)
Internal natural convection in a horizontal rectangular enclosure (double bottom ballast tank)	$Nu = 1 + 1.44\left(1 - \frac{1708}{Ra}\right) + \left(\frac{Ra^{1/3}}{18} - 1\right)$	$Ra < 10^8$	(10)
External natural convection around a horizontal tube	$Nu = \left\{0.6 + \frac{0.387 \cdot Ra^{1/6}}{[1+(0.559/Pr)^{9/16}]^{8/27}}\right\}^2$	$Ra < 10^{12}$	(11)
Forced convection			
Laminar flow over a flat plate	$Nu = 0.664 \cdot Re^{1/2} \cdot Pr^{1/3}$	$Re < 5 \cdot 10^5$	(12.1)
Turbulent flow over a flat plate	$Nu = 0.037 \cdot Re^{4/5} \cdot Pr^{1/3}$	$5 \cdot 10^5 < Re < 10^7$	(12.2)
Film condensation inside horizontal tube	$Nu = 0.555 \cdot \frac{\lambda}{d}\left\{\frac{g \cdot \rho_l \cdot \lambda_l^3 \cdot (\rho_l - \rho_v)}{\mu_l \cdot d \cdot (T_s - T_w)}\left[\Delta h + \frac{3}{8}c_l(T_s - T_w)\right]\right\}^{\frac{1}{4}}$	$Re < 35000$	(13)
Heat radiation			
Radiative heat transfer coefficient	$h_r = \frac{\varepsilon \cdot \sigma \cdot (T_1^4 - T_2^4)}{T_1 - T_2}$	$\varepsilon = 0.8$ – surface emissivity $\sigma = 5.67 \cdot 10^{-8}$ W/m^{2}K^4 – blackbody constant	(14)

Table 2 *M. leidyi* survival thresholds (start of decay, 50% and 100% of specimen decayed) in various treatments.

Specimen decay		Adults			Larvae	Eggs
Treatment		Start	50%	100%	100%	100%
E1 (21 °C)	A1 (Stagnant)	5-7 days	11-15 days	17-22 days	[a]	[b]
	A2 (Bubbling air, food)	8-9 days	15-18 days	31-34 days	[a]	[b]
E2-Temperature	21 °C	5-7 days	10-13 days	20-22 days	[a]	[b]
	30 °C	4-6 days	10-12 days	10-20 days	[a]	[b]
	35 °C	7-10 h	14-16 h	20-22 h	24 h	24-28 h
	40 °C	5-5.5 h	6-7 h	7.5-8 h	8.5 h	11-12 h
	45 °C	1 h	2.5-3 h	4-4.5 h	5.5 h	~6.5 h
	50 °C	30 min	~70 min	85-90 min	1.5 h	2.5 h
E3-Hypoxia	21 °C	19 h	24-25 h	25-26.5 h	26.5 h	48 h
	30 °C	3.5-4.5 h	6-6.5 h	8-8.5 h	8.5 h	18 h
	35 °C	2.5-3 h	3.5-4 h	5.5-6 h	9 h	16 h
	40 °C	1.5 h	2.5-3 h	4-4.5 h	5 h	8 h
	45 °C	1.5-2 h	2-2.5 h	2.5-3 h	3 h	5.5 h
	50 °C	15 min	45-60 min	75 min	75 min	3 h
E3-Anoxia	21 °C	5 h	7-7.5 h	8-9 h	9 h	9 h
	30 °C	3.5-4.5 h	4.5- 5 h	5.5-6.2 h	6.2 h	7.5 h
	35 °C	3-3.5 h	3.5-4 h	4.2-4.7 h	4.7 h	6 h
	40 °C	2 h	2.5-3 h	3.2-3.5 h	3.5 h	3.5 h
	45 °C	1-1.5 h	1.7-2 h	2.2-2.5 h	2.5 h	2.5 h
	50 °C	15 min	25-30 min	36-45 min	45 min	50 min
E4-Sonication	21 °C	61 min	81 min	98 min	110 min	147 min
	30 °C	50 min	77 min	85 min	90 min	108 min
	35 °C	25 min	43-46 min	55 min	62 min	77 min
	40 °C	25 min	40-44 min	50 min	50 min	62 min
	45 °C	23 min	25-26 min	30 min	30 min	40 min
	50 °C	11 min	13-14 min	17 min	17 min	37 min
E5-Microwaves	100 W (0.8±0.2 °C/min)*	34-39 min (55.9-60 °C)	38-41 min (60-62.3 °C)	40-43 min (60.8-63 °C)	45 min	65 min
	450 W (2.5±0.2 °C/min)*	15 min (55.8-58.1 °C)	16-17 min (60.5-64 °C)	16-19 min (60.5- 68.1 °C)	25 min	30 min
	900 W (7.6±0.4 °C/min)*	5 min (56-60 °C)	5-6 min (58-72 °C)	6-7 min (67.5-74.3 °C)	7 min	10 min

[a] Rapid hatching of larvae occurs from 12-20 h at 20-31 °C (Baker & Reeve, 1974).

[b] It was reported that 13 days are sufficient for the development of reproducing adults from the hatching of the eggs (Baker & Reeve, 1974; Kremer & Reeve, 1989).

* Temperature increases from an initial 21 °C during the microwave treatment are given in brackets.

Table 3 Duration of ballast water treatment (thermal and thermal in combination with anoxia) in variable conditions.

Case scenario	**Treatment**	**Seawater temperature (˚C)**	**Ambient air temperature (˚C)**	**Ballast water temperature (˚C)**	**Treatment duration (h)**
1.1 Worse	Temperature	15	10	45	6.5
1.2 Worse	Temperature	15	10	50	2.5
1.3 Worse	Temperature, N_2	15	10	35	6
1.4 Worse	Temperature, N_2	15	10	45	2.5
2.1 Most likely	Temperature	20	15	45	6.5
2.2 Most likely	Temperature	20	15	50	2.5
2.3 Most likely	Temperature, N_2	20	15	35	6
2.4 Most likely	Temperature, N_2	20	15	45	2.5
3.1 Best	Temperature	25	25	45	6.5
3.2 Best	Temperature	25	25	50	2.5
3.3 Best	Temperature, N_2	25	25	35	6
3.4 Best	Temperature, N_2	25	25	45	2.5

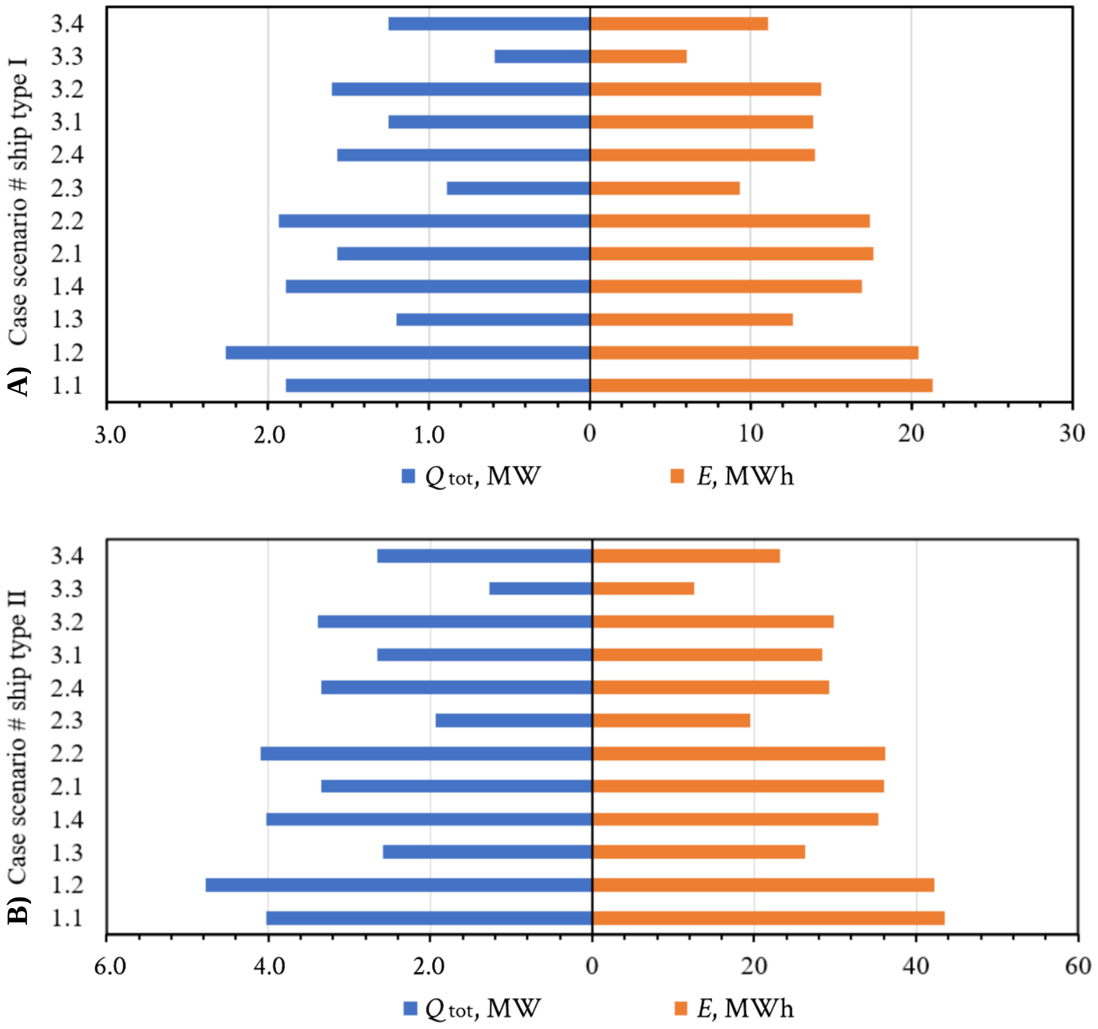

Fig. 1 Heating capacity ($\dot{Q}$) and heating energy consumption (*E*) for ballast water thermal treatment in ship A) *type I* and B) *type II* (maximum heating time 7.5 h).

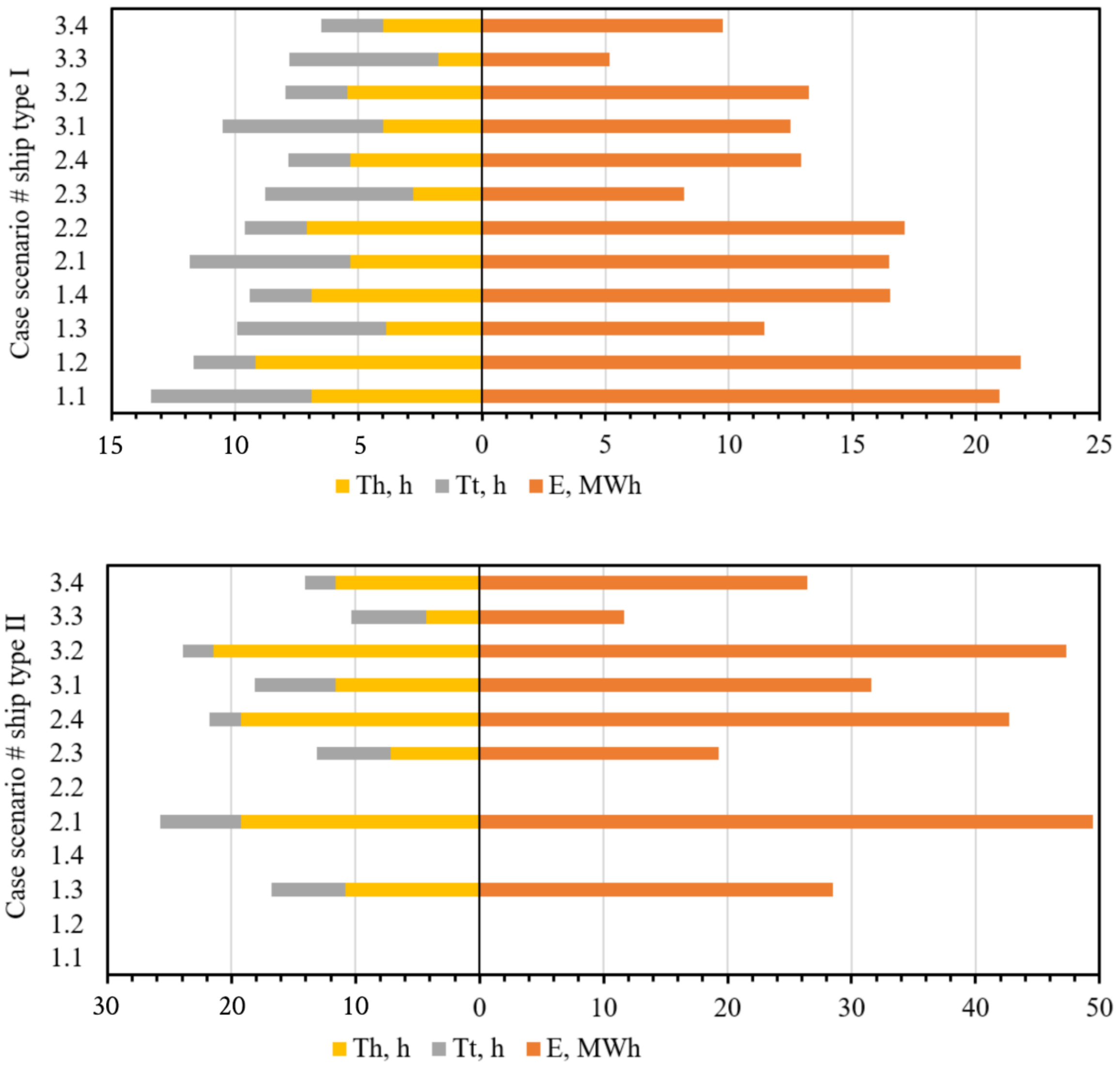

Fig. 2 Thermal treatment time; T_h – ballast heating up time, T_t - *M. leidyi*'s eradication, and heating energy consumption (*E*) for A) *type I* and B) *type II* (2.0 MW fixed heating capacity).

Supplementary material

Supplementary figures

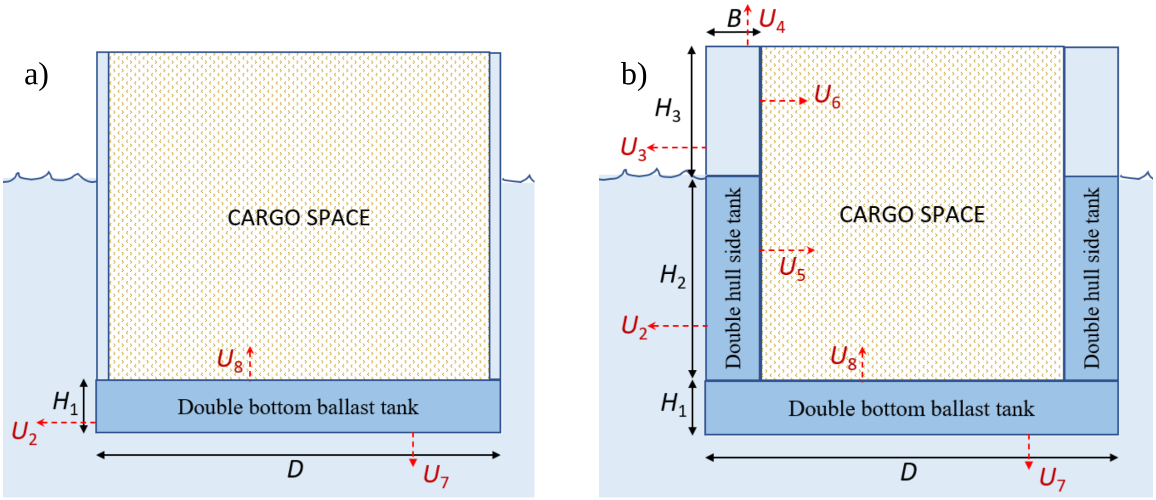

Fig. S1 Simplified cross-sections of a) *type I* ship with double bottom ballast tank (288 m^3) and b) *type II* ship with additional double hull side tanks (648 m^3).

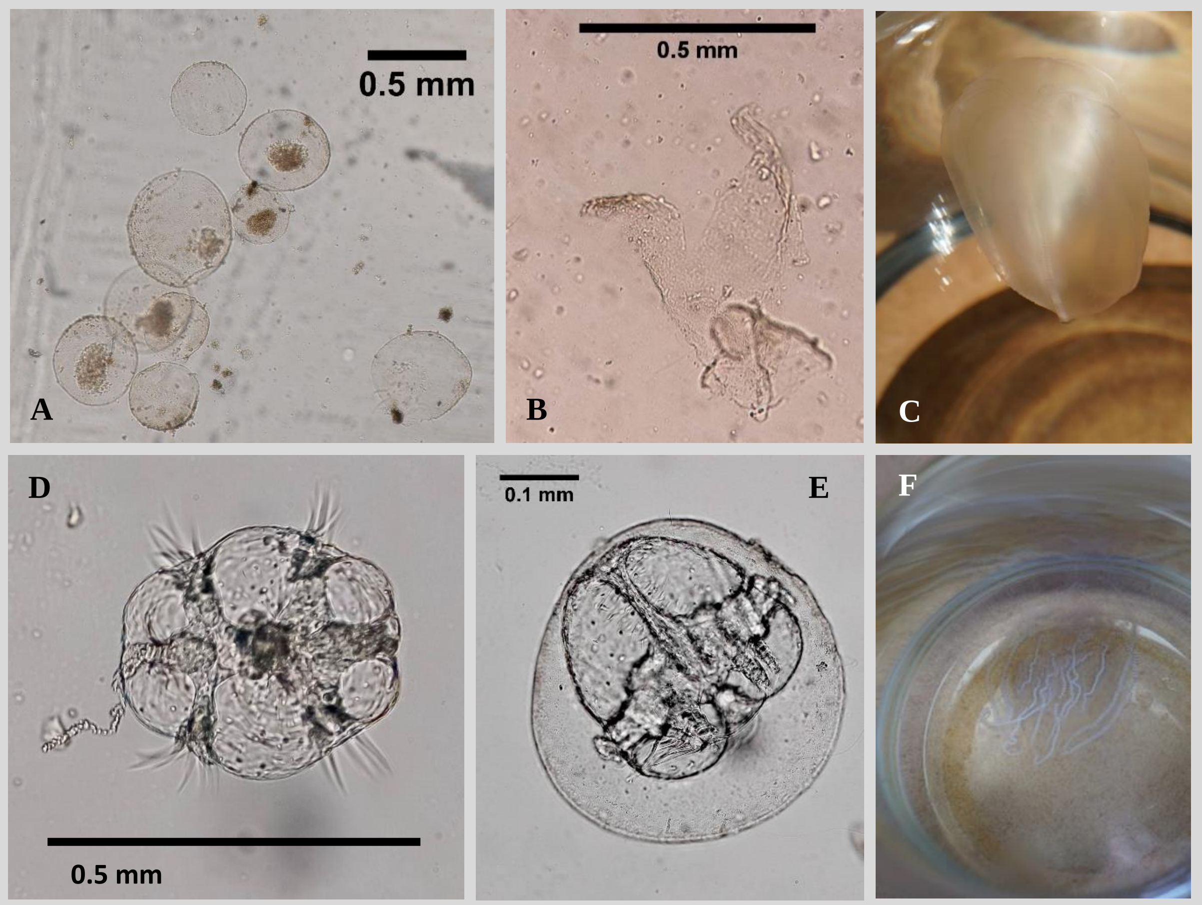

Fig. S2 Life stages of ctenophore *M. leidyi*: A – eggs under the microscope (80x), B – decayed egg under the microscope (200x), C – vial adult specimen, D – aboral view of larva under the microscope (200x), E – unhatched larvae under the microscope (200x), F – decayed adult specimen.

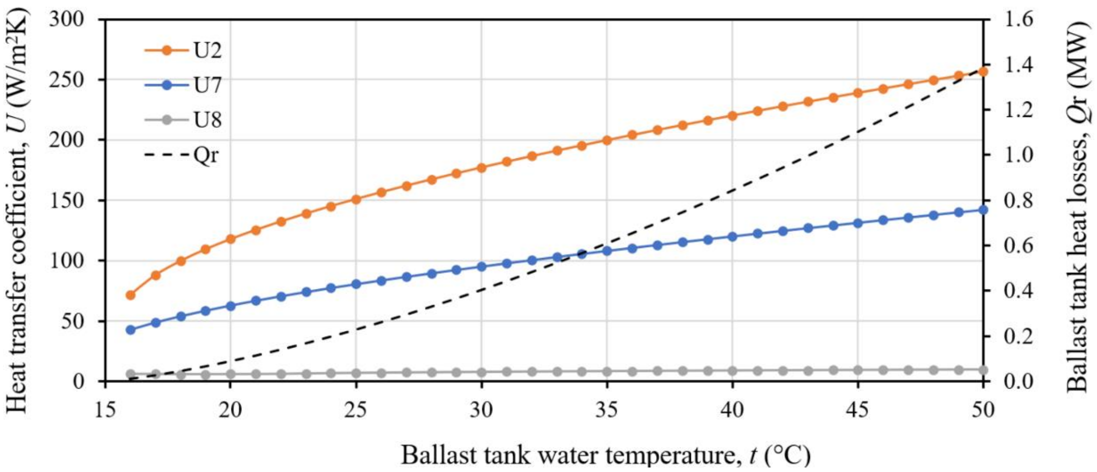

Fig. S3 Heat transfer coefficients (*U*-values) and heat losses ($\dot{Q}_\mathrm{r}$) (*type I*/case 1.2).

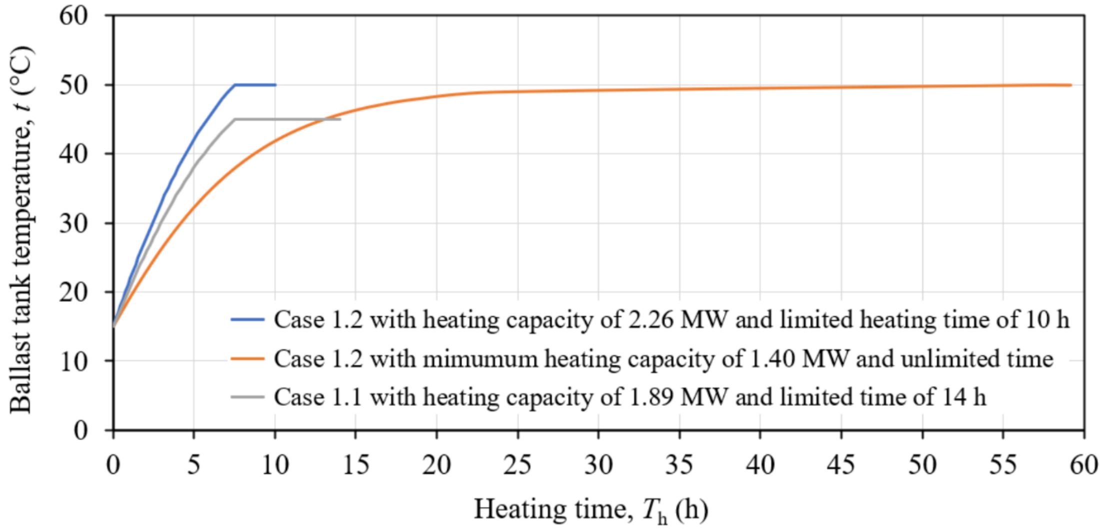

Fig.S4 Heating process for ship *type I* using a) the minimum heating capacity (case 1.2) of A) 1.40 MW and B) 2.26 MW (case 1.2), and C) 1.89 MW (case 1.1).

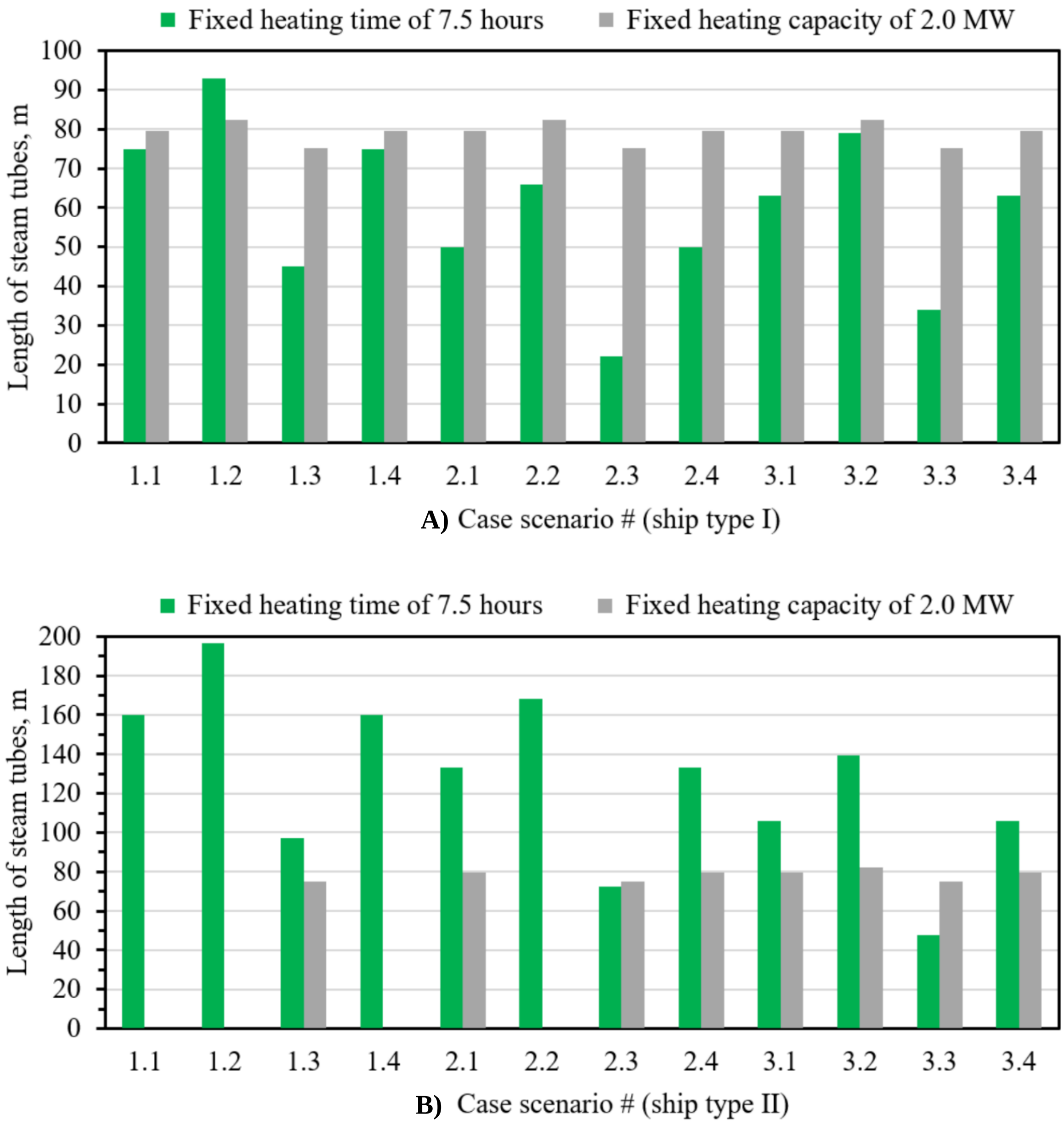

Fig. S5 Steam tube length for the heating of ballast tank water in ship *types* A) *I* and B) *II*.

Ship engines could supply the necessary heating capacity $\dot{Q}_{\mathrm{tot}}$ in the form of saturated steam (8 bar) condensing through tubes submerged into the ballast water. The steam tube length can be determined by equating the total heating capacity to the heat flow rate between steam tubes and ballast tank water

$$L_{\mathrm{tube}} = \frac{\dot{Q}_{\mathrm{r}} + \dot{Q}_{\mathrm{h}}}{U_{\mathrm{tube}} \cdot d \cdot \pi \cdot (T_{\mathrm{s}} - T_{\mathrm{w}})} \qquad \text{(Eq. S1)}$$

Heat transfer between steam and ballast water is characterised by high heat transfer coefficients (U_{tube}) due to the phase change heat transfer inside the tubes and high-temperature difference between steam and ballast water (T_{s} – T_{w}). The convection heat transfer coefficients are evaluated for film condensation inside the horizontal tube (Eq. 13) and natural convection around a horizontal tube (Eq. 11). The tube's inner and outer diameters are 50 and 56 mm, while the tube wall thermal conductivity is 50 W/mK.

From Fig. S5, the steam tube length depends on the total heating capacity necessary for ballast tank thermal treatment, which in turn depends on the ship type and total heat losses. For example, when the heating time is fixed at 7.5 h, the obtained steam tube lengths are between 22 m (case 2.3) and 93 m (case 1.2) in *ship type I* and between 48 m (case 3.3) and 197 m (case 1.2) in *ship type II*. In contrast, when the total heating capacity is limited to 2.0 MW, the steam tube length should be around 80 m in both ship types, but the thermal treatment time may become longer than 7.5 hours, as shown in Fig. 2 of the manuscript. However, in certain cases in ship *type II,* the heat losses exceed the maximum heating capacity of 2.0 MW. Thus the thermal treatment would be only possible at lower ballast tank temperatures.

RASPRAVA

Ovaj rad objedinjuje najvažnija istraživanja različitih aspekata bioinvazije rebraša *M. leidyi*, u ekosustavu sjevernog Jadrana. Postavljenim ciljevima (C1-5) nastoje se provjeriti hipoteze (H1-H5) koje povezuju pojavu bioinvazije s ustanovljenim promjenama u istraživanom području. Predstavljanje znanstvenih radova na ovaj način prvenstveno doprinosi objedinjavanju prikupljenih podataka o želatinoznim organizmima, koji inače ne predstavljaju karizmatičnu skupinu morskih organizama kao npr. neke ribe ili drugi organizmi (Mazzoldi i sur., 2019) i o čijim se ulogama u pelagijskim trofičkim mrežama puno manje zna. Osim toga, ovaj rad, pristupa inovativno problematici pojava želatinozne zooplanktonske vrste *M. leidyi* unaprjeđenjem metodologije uzorkovanja rebraša (I publikacija), primjenom fizikalnih modela za opisivanje dinamike populacije (I i II publikacija), ispitivanjem kvalitete otpuštene organske tvari (II i III publikacija), te povezanosti između ovih pojava s brojnosti mikrobne zajednice (III publikacija), ali i predlaže konkretne korake kako bi se ograničile štetne posljedice pojava (IV publikacija). U I publikaciji je prikazan *top-down* učinak na fond zooplanktona, te kompeticija za resurse s inćunima, dok je u II i III publikaciji prikazan doprinos hranjivim tvarima i mikrobnoj zajednici, ali i *bottom-up* učinak na autotrofe (cijanobakterije). U cijelosti, ovaj rad identificira asimilacijsko-disimilacijski utjecaj *M. leidyi* na lokalni ekosustav sjevernog Jadrana, predacijom, umnožavanjem populacije, i na posljetku, propadanjem jedinki. Osim inovativnog pristupa ovoj problematici, bitno je istaknuti da su metodologije primijenjene u svim publikacijama usporedive. Kao prvi primjer možemo navesti uzorkovanje rebraša. Unatoč tome što se kod uzorkovanja jedinki za potrebe laboratorijskih analiza služimo mrežama (I. publikacija) i iznimno grabilicama (IV publikacija), u ovom radu se većinom oslanjamo na prebrojavanje jedinki koje definira status populacije (njenu gustoću) i izvodi se na nekoliko načina: (i) prebrojavanjem s brodova i (ii) obale, te (iii) ronjenjem na potezu poznate duljine uz pomagalo koje obrubljuje poznati volumen (I-III publikacija). Za rovinjsko priobalje rezolucija podataka o pojavama *M. leidyi* tijekom četverogodišnjeg razdoblja (2016.-2019.) iznimno je visoka, brojnost *M. leidyi* je, naime, brojnost jedinki bilježena je dnevno (I publikacija), a u njihovo prikupljanje su bile uključene i zainteresirane stranke, npr. ribari i lokalno stanovništvo (I publikacija). Sudjelovanje zajednice i podizanje svijesti pojedinaca navode se kao ključni u prevenciji širenja stranih morskih vrsta (De Poorter i sur., 2009), ali i, na konkretnom primjeru, informiranju o posljedicama prisutnosti ove vrste. Od ostalih primjera usporedivih metodologija mogu se istaknuti: (i) određivanje brojnosti mikrobne zajednice (II publikacija), (ii) određivanje koncentracije organske tvari (II i III publikacija) i (iii) hranjivih soli (III publikacija), koje se na ovaj način mjere u sjevernom Jadranu već više od 20 godina (baza podataka Centra za istraživanje mora, IRB, te ZIMO IRB Zagreb) i time omogućavaju usporedbu stanja prije i nakon bioinvazija, te ažuriranje dugoročnih nizova prikupljenih podataka. Dio prikazanih podataka (I publikacija) prikupljen je u sklopu međunarodnog projekta MEDIAS koji se donedavno, bar u Jadranu, većinom bavio pelagijskom ribom, dok je u ovom radu stavljen u kontekst šire pelagijske zajednice i jasno pokazao kako se i uz primjenu trenutne metodologije može proširiti doseg istraživanja o promjenama u pelagijalu. Kao konačni doprinos ove cjeline, razvijen je prijedlog ublažavanja posljedica bioinvazije, koji je rezultirao kao odgovor na opažanja i analize značajne količine podataka prikazanima u I-III publikaciji.

Recentna literatura ove tematike bioinvazije uglavnom se bavi odgovorima na tri najčešća pitanja (Chabrerie i sur., 2019). U kontekstu *M. leidyi* ta pitanja mogu biti: (i) kako ova invazivna vrsta utječe na lokalne zajednice u pelagijalu i priobalju, (ii) čemu zahvaljuje iznimno uspješan opstanak u novom okolišu i (iii) kakve su dugoročne posljedice ovih bioinvazija na ekosustave. Ovaj rad se uglavnom bavi istraživanjem prvoga (I i III publikacija), dok drugo pokriva djelomično, opisujući uvjete zatečene u tom novom okolišu u kojem ova vrsta opstaje (I-IV publikacija), a trećem pridonosi novoprikupljenim podacima koji bi mogli poslužiti kao temelj modelima za predviđanje stanja ekosustava (I-III publikacija), ali i procijeniti ekonomske posljedice masovnih pojava *M. leidyi*.

Prostorno-vremenska raspodjela i intenzitet pojava u sjevernom Jadranu

Jadran je u odnosu na ostala mora i oceane relativno plitko more jer polovica njegove površine otpada na dubine > 100 m, dok je njegov najsjeverniji dio ujedno i najplići (Vrdoljak i sur., 2021). Taj se najplići dio prostire od Tršćanskog zaljeva na sjeveru, obuhvaća Kvarner te se pruža sve do sjevernih Zadarskih otoka na jugu. Vodena masa sjevernog Jadrana pod značajnim je utjecajem dotoka kopnenih voda posebno rijekom Po i, u manjem dijelu, istarskim rijekama (Sekulić, 1996). Cirkulaciju u ovom dijelu Jadrana pokreće sprega vjetra, riječnih donosa, promjene u gustoći vodenih masa i njihove izmjene s ostatkom Jadrana (Giani i sur., 2012). Zbog svojih dimenzija koje omogućuju provođenje kvalitetnijeg nadzora nad promjenama u okolišu, sjeverni je Jadran prozvan *prirodnim, živućim laboratorijem za ispitivanje promjena u sustavu* (Zuschin i Stachowitsch, 2008). Iako je čitav Jadran područje visoke biološke raznolikost, bogato endemima, i u kojem obitava gotovo polovica sredozemnih vrsta (UNEP, 2015), njegov sjeverni dio u tome ima posebnu ulogu s obzirom na to da je područje mrijesta mnogih riba (Morello i Arneri, 2009) koje podržavaju i oblikuju ekosustave diljem Sredozemlja

(UNEP-MAP-RAC/SPA, 2015). Osim zbog cirkulacije, istočni dio Jadrana prema svojim biogeokemijskim karakteristikama možemo smatrati oligotrofnim morem (Mozetič i sur., 2010), dok su uvjeti na zapadnoj strani uslijed donosa rijekom Po i razgradnjom organske tvari, eutrofniji (Giordani i sur., 1997). Uslijed izloženosti brojnim antropogenim pritiscima (UNEP, 2015), Jadran danas pokazuje znakove degradacije trofičkog sustava, a veća biološka raznolikosti bilježi se tek na nižim trofičkim razinama (Lotze i sur., 2010). Uz to, zadnjih je desetljeća sve češći unos stranih organizama (Pećarević i sur., 2013), pogotovo u sjevernom dijelu gdje su zabilježene prve pojave *M. leidyi* (Shiganova i Malej, 2009) i njihova masovna pojava desetljeće kasnije (I publikacija).

Pošto su temperatura i (u manjem dijelu) salinitet glavni abiotički faktori koji ograničavaju rasprostranjenost *M. leidyi* (Shiganova, 1998), u I publikaciji je dan pregled njihove varijabilnost za četverogodišnje razdoblje (2016.-2019.) u kojem bilježimo prve, redovite pojave *M. leidyi*. Temperaturni raspon (14-26 °C) zabilježen u površinskom sloju u vrijeme pojava bioinvazije u sjevernom Jadranu (III publikacija) je unutar granica tolerancije za ovu vrstu (0-32 °C; Purcell i sur., 2001) i blizak je optimalnim uvjetima (12-18 °C) za razvoj *M. leidyi* (Pang i Martindale, 2014), te se poklapa i s temperaturama koje su zabilježene za masovnih pojava na drugim područjima Sredozemlja (Shiganova i sur. 2001b). Na sjeveru Europe temperature su nešto niže (npr. 0-25 °C Baltičko more; Kube i sur., 2007) i teoretski mogu, duže vrijeme osiguravati reprodukcijski optimum za *M. leidyi* (230-350 dana godišnje; Collingridge i sur., 2014). Nasuprot tome, površinski sloj u sjevernom Jadranu, a posebno u njegovom priobalju, se ljeti zagrije na više od 25 °C što prelazi temperaturni optimum i teoretski bi mogao negativno utjecati na brojnost populacije. Međutim, prosječne brojnosti *M. leidyi* u Jadranu su bile 4x više (do 4 jedinke po m^2) (I publikacija) od onih u Baltiku (Schaber i sur., 2011), i bile su najsličnije onima zabilježenim u drugim dijelovima Sredozemlja, npr. u Egejskom moru (Shiganova i sur., 2001b). U usporedbi s Crnim morem, koje je nešto hladnije (raspon mjesečnih prosjeka ~ 7-25 °C; Mohamed i sur., 2022) u odnosu na Jadran (mjesečni prosjeci ~ 12-25 °C; Bonacci i sur., 2021), uključujući i njegov sjeverni dio (I publikacija), brojnost populacije u Jadranu je bila zamjetno manja (i do 10x) od one u Crnom moru (Kamburska i sur., 2006). Abiotički uvjeti u Sredozemlju ljeti (površinske temperature > 25 °C i visoki salinitet) se za razliku od onih koje nalazimo npr. u Crnom moru, općenito smatraju suboptimalnima za proliferaciju *M. leidyi* (Shiganova i sur. 2001b), ali ne i ograničavajućima kako tolerira salinitete < 2-38. Rasponi temperature (~ 9-25 °C) i saliniteta (32-38,5) (Slika 2, I publikacija; Slika 1., III publikacija) ne odstupaju od ranije izmjerenih u ovom dijelu Jadrana (Grilli i sur., 2020; Supić i sur., 2004), ali su različiti od onih zabilježenih u nekim drugim morima gdje ova strana vrsta ostvaruje stabilne populacije. Čini se da visoke temperature ljeti u sjevernom Jadranu ne utječu značajno na populaciju jer se jedinke uglavnom nalaze u površinskom sloju, a ne niže, oko termokline, gdje su temperature bliže njihovom reprodukcijskom optimumu, mada nejednake vertikalne raspodjele mogu ovisiti i o svjetlu koje im omogućava fototaksiju (Baiandina, 2020). Uz to, masovne pojave bilježimo u toplijem dijelu godine (proljeće – jesen) (I i III publikacija) baš kao i u drugim morima gdje je *M. leidyi* strana vrsta (npr. Azovsko more; Shiganova, 1998), ali i njenom prirodnom okolišu (Chesapeake zaljev, SAD; Sullivan i sur., 2001). Brojnost populacije za temperaturnih maksimuma ne opada (I publikacija), a s blagim padom temperature (ponajprije u rujnu, I.-III, publikacija), dostiže maksimum. Ljetni je longitudinalni gradijent temperature na površini zanemariv (Russo i sur., 2012), te bioinvazija zahvaća čitav sjeverni Jadran. Nasuprot tome, zimske temperature (Slika 2., I publikacija) ispod reprodukcijskog minimuma (12 °C) (Purcell i sur., 2001) uz nedostatak hrane (Slika S4., I publikacija) onemogućuju opstanak populacija uz istočnu obalu. Poznato je da i salinitet utječe na reprodukcije *M. leidyi*, pa je tako pri npr. 6 reprodukcija izuzetno niska, a od 25-33 bila najveća (Baltik; Jaspers i sur., 2011). Druga mora u kojima su masovne pojave redovite npr. Crno more i Baltik, veliki su recipijenti slatkih voda i k tome obilježeni površinskim gradijentom saliniteta (npr. Baltik 7-21; Jaspers i sur., 2011). Mada i sjeverni Jadran uvelike ovisi o slatkovodnom donosu, pretežito rijekom Po, uz istočnu obalu nema tako izraženog gradijenta (I publikacija, Slika S3), ali moguće je da je rasprostiranje istočnije u Kvarnerski zaljev, i južnije u ostatak Jadrana, ograničeno nešto višim površinskim salinitetom ljeti zbog manjeg dotoka slatke vode i veće evaporacijske površine (Ruso i sur., 2012). Jasne razlike u područjima saliniteta za 2017. pokazane su na Slici 8. (III publikacija), a za mjesec rujan u razdoblju od 2016.-2019. na Slici 4. (I publikacija). Iako se salinitet pokazao glavnim, a temperatura tek popratnim ograničavajućim faktorom rasta brojnosti *M. leidyi* u lagunama zapadnog Sredozemlja (Delpy i sur., 2016), preživljavanje populacije u istočnom dijelu sjevernog Jadrana vjerojatno je biotički uvjetovano nedostatkom hrane što je uobičajeno za oligotrofna područja (Degobbis, 1983). Slično je zabilježeno i u Egejskom moru, gdje se salinitet nije pokazao ograničavajućim faktorom unatoč tome što nadilazi 39 (Poulos i sur., 1997). Dakle, populaciju u sjevernom Jadranu abiotički ograničavaju tek niske temperature, a sezonske pojave uz istočnu obalu posljedica su tzv. periodične kolonizacije (eng. cyclic colonisation) koje kreću iz zimskih utočišta uz zapadnu obalu. A kako se disperzija odvija u mjesecima kada na istočnoj strani abiotički (temperatura) i biotički (količina hrane) čimbenici omogućuju opstanak *M. leidyi*, dolazi do uspješnog umnožavanja rebraša. Sve navedeno ilustrira činjenicu da su uvjeti u sjevernom Jadranu bili prikladni i omogućili da *M. leidyi* uspostavi stabilnu populaciju čime se potvrđuje hipoteza (H1). Dinamika populacije se, međutim (baš kao i stupanj trofije i ostalih abiotičkih i biotičkih parametara), razlikuje od zapadnog prema istočnom dijelu sjevernog Jadrana. Dok je na nekim lokacijama uz zapadnu obalu *M. leidyi* prisutna tijekom godine, populaciju uz istočnu obalu obilježava *source-sink* dinamika i upućuje na izvorište izvan tog staništa. To je obrazac koji *M. leidyi* pokazuje i u svojim prirodnim staništima, npr. na istoku SAD-a gdje se strujama iz plitke uvale Greenwich Cove, populacija u proljeće proširi do Narragansett zaljeva (Costello i sur., 2006). Pretpostavlja se da je to tipična prilagodba koju *M. leidyi* pokazuje u umjerenim područjima. I doista, iako su i longitudinalni i latitudinalni batimetrijski gradijenti za razliku od ostalog dijela Jadrana u njegovom sjevernom dijelu beznačajni (Vrdoljak i sur., 2021.), uz zapadnu obalu uslijed donosa sedimenata rijekom Po postoji više plićih dijelova u odnosu na istočnu (Lipizer i sur., 2014) vjerojatno, nalik fiziografiji prirodnih staništa *M. leidyi*.

Kako se radi o zooplanktonskom organizmu za čija su širenja vrlo bitna geostrofička strujanja, koristeći se prikupljenim hidrografskim i klimatološkim podacima, razvijeni su fizikalni modeli cirkulacije u Jadranu (I publikacija), a posebno u njegovom sjevernom dijelu (II-III publikacija). Modeli su korišteni kako bi se odredili fizikalni fenomeni koji oblikuju populaciju *M. leidyi* u sjevernom Jadranu, a to su: (i) privremena disperzijska središta u cirkulacijskim vrtlozima, (ii) strujna gibanja i (iii) stalna disperzijska središta. Prvi fizikalni fenomen koji je povezan s pojavama *M. leidyi* u sjevernom Jadranu je vrtloženje (I-II publikacija). Naime, primjena hidrodinamičkog ROMS modela (Regional Ocean Modeling System) je pokazala da je proliferacija *M. leidyi* povezana s centralnim dijelom anticiklonalnih cirkulacijskih vrtloga koji osiguravaju dovoljno resursa za napredovanje populacije (I-II publikacija). Središta vrtloga, područja su mirovanja i akumulacije, te je nakupljanje fito- (Ishikawa i sur., 2002) i zooplanktonskih populacija (Yebra i sur., 2018) u takvim tvorbama, i ranije dokazano. Povezanost *M. leidyi* i sustava vrtloženja je dodatno potvrđena u II publikaciji u kojoj je akumulacija DOC-a s višim koncentracijama (0,5-3 mg l^{-1}), povezana s prisustvom masovnih nakupina *M. leidyi* (10-100 jedinki po m^3) tijekom rujna 2019. što je odgovaralo neočekivano dugom, četveromjesečnom anticiklonalnom vrtloženju u sjevernom Jadranu. Naime, zimi je cirkulacija u sjevernom Jadranu dio otvorenog jadranskog ciklonalnog sustava, dok se tijekom toplijih mjeseci ona mijenja u zatvorenu anticiklonalnu koja djelomično izolira vodene mase sjevernog Jadrana od ostatka bazena (Krajcar, 2003). Pretpostavljajući da su vrtlozi područja nakupljanja *M. leidyi*, navedeni fizikalni modeli su nadograđeni primjenom lagrangeovskih metoda da bi se utvrdili putevi širenja populacije. Inače se povezivanje Langrangeovog modela disperzije i hidrodinamičkog modela, pokazalo uspješnim pristupom u opisivanju dinamike populacije stranog želatinoznog zooplanktona u Sredozemlju (Macías i sur., 2021). U kombinaciji sa GETM modelom (General Estuarine Transport Model), razvijen je statistički alat (Physalia-SIM) kojim se uz obalu Sredozemnog mora lako određuje vjerojatnost pojave žarnjaka portugalske galije (*Physalia physalis*) – izuzetno opasnog za ljudsko zdravlje (Macías i sur., 2021), tako da bi ovaj rad mogao dati i kvalitetnu osnovu za daljnji razvitak predikcijskih modela. Hidrodinamički modeli su uz mjerena strujanja također identificirali i drugi fenomen, tj. prisutnost jake Istarske obalne protustruje (eng. Istrian Coastal Countercurrent, ICCC; II publikacija) koja pred kraj ljeta (Krajcar, 2003) rebraše dodatno usmjerava prema istočnom priobalju potpomažući stvaranju masovnih nakupina (I publikacija). Kao treći fenomen, kombinacijom istih hidrodinamičkih i disperzivnih fizikalnih modela uspješno je locirano vjerojatno izvorište disperzije rebraša (II i III publikacija). Ovi modeli ukazuju na to da su prve pojave *M. leidyi* na istočnoj strani sjevernog Jadrana često rezultat donosa rebraša morskim strujanjima čije je izvorište zapadnije, vjerojatno u području Venecijanske lagune, s obzirom na to da se u njima upravo ta lokacija pokazala vjerojatnim ishodištem (III publikacija). U literaturi se spominje da *M. leidyi* prezimljava i obnavlja svoje populacije tako da opstaje u tzv. zimskim utočištima u kojima temperatura, inače istaknuta kao ograničavajući faktor za proliferaciju populacije u priobalju (Costello i sur., 2006), ne dostigne kritično niske vrijednosti. Salinitet također ograničava disperziju, npr. na istoku Baltika gdje su utjecaji priljeva slatkih voda značajni populacija nestaje (Jaspers i sur., 2011), ali ponovno se javlja kao rezultat cirkulacije koja se širi iz smjera Sjevernog mora (Riisgård, 2017). Unatoč tome što su zaklonjene lokacije poput Mramornog mora (Shiganova i sur, 2001), Berre (Marchessaux i sur., 2020) i Venecijanske lagune (I i II publikacija) identificirana kao utočišta za prezimljavanje, u nekim manjim zatvorenim bazenima njihova populacija redovito iščezava. Periodička kolonizacija pogodovana morskim strujanjima iz Crnog mora opisuju dinamiku populacije *M. leidyi* u najplićem svjetskom moru – Azovskom moru koje se zimi može ohladiti i ispod 4 °C što populacija ne može svladati (Shiganova i sur., 2001b). Unatoč razvijenoj morfologiji istočne obale sjevernog Jadrana koja obiluje zaljevima i estuarijima, *M. leidyi* na toj strani nije našla prikladno zimsko utočište, a razlog tome može biti njihova izloženost hladnim vjetrovima (bura) koji mogu relativno brzo ohladiti čitav vodeni stupac i do npr. 8 °C (Najdek i sur., 2020). Uz to, kako je istočnija obala, u usporedbi s područjem ušća rijeke Po, manje eutrofna, pa osim suboptimalne temperature, prehrana jedinki ne uspijeva zadovoljiti energetske potrebe za opstanak. Ukratko, modeli geostrofičkih strujanja bili su ključni kako bi se opisala dinamika populacije *M. leidyi* u sjevernom Jadranu, što podrazumijeva prostorno-vremensku pojavu i rasprostranjenost, ali i nastajanje gustih nakupina, te tako potvrdila hipoteza (H2).

Izuzetno velika brojnost i činjenica da su pojave *M. leidyi* u sjevernom Jadranu postale redovite, navode na pitanje: koja je sudbina ogromne količine proizvedene biomase i koji dio trofičke mreže od nje može imati koristi? Literatura koja istražuje bioinvazije *M. leidyi* dotiče se brojnosti (Delpy i sur., 2016), težine biomase, i čak %C u jedinkama, procjenjuje da gustoća od 1,7-7 jedinki po m^2 odgovara biomasi od 35-88 g koja sadrži oko 20-50 mg C (Mutlu, 2009), no zanemaruje direktan doprinos organskoj tvari u vodenom stupcu, a čiji je značaj ustanovljen u prirodnim staništima *M. leidyi* (Condon i sur., 2010 i 2011). Osim toga, i kvaliteta iste u kontekstu želatinoznog zooplanktona je slabo istražena, a u vezi s *M. leidyi* do sada nije bila uopće ispitivana.

U sjevernom su Jadranu zabilježene značajne promjene u dinamici organske tvari čiji najveći udio čini otopljeni dio (DOM) (III publikacija). Za vrijeme intenzivnih masovnih pojava *M. leidyi* tijekom toplijeg dijela 2017. godine u otvorenom moru su zabilježene visoke koncentracije organske tvari (POC i DOC) i to znatno više od vrijednosti izmjerenih prethodnih godina. Naime, koncentracije DOC-a su za 2,5x (III publikacija) premašile tridesetljetni prosjek (Ciglenečki i sur., 2020). Takve koncentracije bilježe se u biološki aktivnim sustavima proizvodnje i akumulacije poput priobalnih laguna Aljaske (~ 1-5 mg l^{-1}; Connolly i sur., 2021), kanadskih jezera (~ 1,2-4 mg l^{-1}; Molot, 2009) ili eutrofnih mora poput Baltika (~ 2-8 mg l^{-1}; Maciejewska i Pempkowiak, 2014) no ne i u otvorenim morima poput svjetskih oceana gdje su vrijednosti inače znatno niže (~ 0,5 mg l^{-1}; Follett i sur., 2014). Drastični rast koncentracija DOC-a može ukazivati na perturbacije ekosustava (Dautović i sur., 2017), a jedan od njih je pokazan i u inkubacijskim eksperimentima s mikroalgom *Tetraselmis striata* koji pokazuju da unos nekog organizma može značajno promijeniti strukturu i funkcioniranje mikrobne zajednice (Kim i sur., 2020). DOC koji otpušta *M. leidyi* u najvećem je dijelu labilan, dakle podoban za brzu mikrobnu razgradnju (Condon i sur., 2010). Većina DOC-a izmjerenog tijekom bioinvazije *M. leidyi* 2017. godine odnosila se na njegovu reaktivnu formu značajno doprinoseći ukupnoj organskoj tvari površinski aktivnim komponentama (SAS) (III publikacija). Tijekom prošlih desetljeća značajni porast koncentracije DOC-a u sjevernom Jadranu zabilježen je za vrijeme cvjetanja mora i pojave sluzavih agregata, nakon čega su njegove koncentracije do prvih masovnih pojava *M. leidyi* bile relativno niske (~ 1 mg l^{-1}), u skladu s oligotrofnim karakteristikama istočnog dijela sjevernog Jadrana (Dautović i sur., 2017). Da je doprinos rekordnih koncentracija otopljene organske tvari 2017. godine mogao biti vezan uz pojavu *M. leidyi* potvrđuju dodatna istraživanja koja su analizirala masovne nakupine rebraša za vrijeme maksimuma njihovih pojava u rovinjskom priobalju (II publikacija). Naime, povišene koncentracije POC-a i DOC-a pronađene su u područjima masovnog nakupljanja rebraša, gdje su potvrđene i povišene koncentracije SAS frakcije (Slike 4. i S1., II publikacija). Služeći se procjenama izlučivanja organske tvari koje *M. leidyi* pokazuje u svojem prirodnom staništu (Condon i sur., 2010), procijenjeno je da njihove nakupine u dva dana mogu na lokalnoj skali proizvesti 26-301 μg l^{-1} DOC-a (II publikacija). Osim toga, zabilježene koncentracije SAS-a (posebno iz otopljene frakcije DOC-a) u područjima nakupljanja rebraša (II publikacija) su više u odnosu na prethodna mjerenja na istom području (Ciglenečki i sur., 2020). Kako prema kemijskim karakteristikama (funkcionalnim skupinama) organsku tvar možemo podijeliti na hidrofobnu (npr. dugolančane masne kiseline, aromatski prstenovi i ugljikovodici) i hidrofilnu (npr. skupine $-NH_2$, $-COOH$, $-OH$, $-SH$), mjerenja su pokazala kako je ona u nakupinama rebraša hidrofobnija (II publikacija) te također pogodnija za bakterijsku razgradnju (Choi i sur., 2004). Ovdje predstavljeni rezultati pokazuju da masovne nakupine *M. leidyi* mogu biti privremeni izvor značajnih količina organske tvari, a uslijed njene razgradnje, i hranjivih soli, što je u suprotnosti s gotovo neznačajnim dnevnim doprinosom ukupnom DOC-u (< 1%) kojeg *M. leidyi* ostvaruje u svojim prirodnim staništima (Condon i sur., 2010). Međutim, podaci se podudaraju kad je riječ o kvaliteti organske tvari. Većina proizvedenog DOC-a u prirodnim staništima *M. leidyi* (18-29% na dan) (Condon i sur., 2010), a i u sjevernom Jadranu je bila labilna/hidrofobnija (II i III publikacija). Za razliku od oligotrofnih uvjeta uz sjeveroistočnu obalu Jadrana (Dautović i sur., 2017; Ciglenečki i sur.,2020; Penezić i sur., 2022), zaljevi istočne obale SAD-a su eutrofniji (Cuker, 2020), pa je tamo relativni doprinos rebraša zanemariv. Kako je u III publikaciji zaključeno da nejednaki doprinos ostvaruju različiti veličinski razredi jedinki, osim brojnosti, na količinu proizvedene organske tvari vjerojatno utječe i faza životnog ciklusa, npr. jajašca *M. leidyi* u veličinskom su razredu kopepoda i ličinki školjkaša te imaju istu nutritivnu vrijednost (Jaspers i sur., 2015b).

Iako nedostaju istraživanja kojima bi se pokazala direktna veza između proizvodnje organske tvari i bioinvazija *M. leidyi*, ipak je ustanovljena ona između razgradnje ogromne količine želatinozne biomase u područjima zahvaćenima bioinvazijom i porasta koncentracija hranjivih soli. Tako je u Kaspijskom jezeru primijećeno da porast koncentracije hranjivih soli u površinskom sloju korelira s razdobljem pojava *M. leidyi*, ali i utječe na promjenu kvalitete i kvantitete fitoplanktona (Nasrollahzadeh i sur., 2008). Međutim, prema III publikaciji, ako promatramo sjeverni Jadran u cjelini, tijekom 2017. povećana razgradnja organske tvari nije korelirala s porastom koncentracija hranjivih soli, te su ustanovljene koncentracije (npr. PO_4^{3-} < 0,1 μmol l^{-1}, anorganski N ~ 1-2 μmol l^{-1}) bile uobičajene ili čak nešto niže vrijednosti od prosjeka (Giani i sur., 2012) što se može pripisati i trendu tzv. oligotrofikacije ovog područja, a naročito njegovog istočnog dijela (Djakovac i sur., 2012; Ciglenečki i sur., 2020; Penezić i sur., 2022). Moguće je da je značajno sniženje koncentracija N i P prikrilo utjecaj masovnih pojava *M. leidyi.* I u ranijim je istraživanjima pokazano da su više koncentracije NH_4^+ i PO_4^{3-} povezane s pojavama *M. leidyi* značajne u odnosu na ukupne koncentracije u sustavu (Dinasquet i sur., 2012; Treible i sur., 2014), međutim treba istaknuti i to da je njihov doprinos *in situ* bio najizraženiji za N-limitacije (Condon i sur., 2010), koje u sjevernom Jadranu ne bilježimo (Degobbis i sur., 2000). No, i unatoč značajnim količinama koje su otpuštene za vrijeme pojava *M. leidyi*, količine N su bile dovoljne za samo oko 4% primarne proizvodnje (Condon i sur., 2010). Pretpostavlja se da su te niže koncentracije N posljedica njegovog povećanog unosa od strane bakterijske zajednice kako bi zadovoljila svoje unutarstanične kvote elemenata (Condon i sur., 2010). Na temelju toga, u II publikaciji, analiziran je utjecaj pojava bioinvazija *M. leidyi* na mikrobnu zajednicu. *In situ* mjerenja pokazala su pozitivnu korelaciju područja masovnih nakupina *M. leidyi* s koncentracijom heterotrofnih prokariota i cijanobakterija, ali i njihovih predatora heterotrofnih nanoflagelata (Slika 4. i 5., II publikacija). Ova međusobna ovisnost veće brojnosti bakterijske zajednice i povišenja koncentracije hranjivih soli u okolnoj vodi koja je rezultat remineralizacije već je ranije dokazana laboratorijskim eksperimentima (Dinasquet i sur., 2012). Općenito, dosadašnja istraživanja povezanosti bakterijske zajednice i pojava *M. leidyi* su nepotpuna, a međusobni rezultati se značajno razlikuju. Tako na primjer, Dinasquet i sur. (2012) u laboratorijskim eksperimentima koristeći jedinke iz Sjevernog mora navodi dominaciju bakterija *Flavobacteriaceae* (Bacteroidetes) dok Condon i sur. (2011) u eksperimentima s jedinkama iz prirodnog staništa navodi predominaciju γ-proteobakterija nad inače dominantnim α-proteobakterijama. Navedene razlike u rezultatima, dijelom se mogu objasniti činjenicom da je mikrobiom ovisan o tkivu (epidermu i gastrodermu), da se razlikuje od okolne vode, ali i da je značajno drugačiji kod organizama iz prirodnog staništa od onih iz područja bioinvazija (Jaspers i sur., 2019). O promjenjivosti prokariotske zajednice u mnogim područjima u kojima danas nalazimo *M. leidyi* se malo zna, pa bi ovaj rad mogao poslužiti kao osnova za daljnja istraživanja detaljnije strukture prokariotske zajednice u sjevernom Jadranu. Porast broja heterotrofnih prokariota mogu objasniti i izrazito povišene koncentracije dostupne organske tvari (POC i DOC, II-III publikacija) uslijed izlučivanja sluzi, neurednog hranjenja, otpuštanja fekalnih peleta i propadanjem jedinki rebraša. Razgradnjom dostupne organske tvari posljedično se otpuštaju hranjive soli koje postaju izvor hrane cijanobakterijama (II publikacija). Povezanost bakterijske razgradnje neuobičajeno velike količine organske tvari i cijanobakterijskog cvata je u sjevernom Jadranu već ranije ustanovljena za razdoblja cvjetanja mora (Fuks i sur., 2005).

Takav sastav mikrobne zajednice (omjer cijanobakterija i heterotrofnih prokariota) prikladan je plijen heterotrofnim flagelatima (Caron i sur., 1992), s tim da u oligotrofnim morima uglavnom dominiraju cijanobakterije (Hagström i sur., 1988). Dakle, na lokalnoj skali (rovinjsko priobalje) rast brojnosti prokariota, dovodi do povećane brojnosti heterotrofnih nanoflagelata (II publikacija) kojima se hrani tek nekolicina taksonomskih skupina npr. cilijati (Hansen, 1995), što znači da većina dostupne energije ostaje zarobljena na nižim razinama trofičkog sustava. Naime, literatura pokazuje da udio cilijata u prehrani mezozooplanktona (Rotifera, Cladocera, Copepoda) može biti istovremeno i beznačajan i bitan, te da je taj udio veći kada je brojnost fitoplanktona mala ili je zajednica većinom sastavljena od manjih fitoflagelata, ali u svakom slučaju, čini značajniji udio u njihovoj prehrani od heterotrofnih flagelata (Jakobsen i Hansen, 1997). Zbog toga možemo zaključiti da nakupine *M. leidyi* podržavaju mikrobnu petlju (II publikacija), i prekidaju cirkulaciju energije prema višim trofičkim razinama (II publikacija). Sve navedeno upućuje na to da masovne pojave *M. leidyi* dovode do neravnoteže u ekosustavu gdje se dodatnim doprinosom hranjivih tvari njihovim otpuštanjem mijenja kemijska ravnoteža, ali oblikuje mikrobna zajednica, čime se potvrđuje H3.

Želatinozni zooplankton u kompeticiji s ribom

Fluktuacije pojava *M. leidyi* u četverogodišnjem periodu prikazane su za rovinjsko priobalje u I publikaciji (Slika 2.) i jasno ocrtavaju njihovu sezonalnost. U osnovi, sve publikacije uključene u ovaj rad (I-IV) pozitivno odgovaraju na prvu postavljenu hipotezu (H1) pokazujući kako se *M. leidyi* u sjevernom Jadranu redovito pojavljuje, a njena se brojnost i struktura populacije mijenja ovisno o sezoni. Štoviše, bioinvazije *M. leidyi* su i prostorno (zapadna obala Istre, I publikacija) i vremenski zastupljenije od pojava bilo kojeg drugog želatinoznog zooplanktona u Jadranu, npr. masovne pojave meduza *Chrysaora hysoscella*, *Cotylorhiza tuberculata* i *Discmedusa lobata* su ograničene na manja područja poput zaljeva (Violić i sur., 2019) ili morskih jezera (Kogovšek i sur., 2012), a traju tek 2-3 mjeseca (Violić i sur., 2019). Povijesni zapisi pokazuju da se 5 vrsta želatinoznih zooplanktona (žarnjaka) u posljednjih 200 godina redovito pojavljivalo u sjevernom Jadranu, a to su: *A. aurita, C. hysoscella, C. tuberculata, R. pulmo*, i holoplanktonska vrsta *P. noctiluca* koja nije autohtona, a nijedna od njih svake godine (Kogovšek i sur., 2010). Treba napomenuti da je *Aurelia* spp. do nedavno bila najčešće zapažan želatinozni zooplankton u Jadranu, a čije se populacije periodički javljaju i iščezavaju (Kogovšek i sur., 2010), izuzev na području Mljetskih jezera gdje populacija opstaje čitave godine (Kogovšek i sur., 2012). Plaštenjaci (Boero i sur., 2013) i rebraši (Violić i sur., 2022), čije pojave se danas često spominju, u povijesnim analizama nisu zastupljene. Od značajnih pojava želatinoznog zooplanktona u sjevernom Jadranu, posebno se ističu dva razdoblja učestalijih pojava: (i) razbolje oko 1910. obilježeno periodicitetom od 8-12 godina i (ii) razdoblje nakon 1960. godina kada je učestalost pojava skraćena na manje od 8 godina (Kogovšek i sur., 2010). Od pojava želatinoznih organizama koji nisu autohtoni za sjeverni Jadran posebno se ističe ona 1970-ih i 1980-ih godina, kada su u sjevernom Jadranu prvi puta zabilježene masovne pojave meduza vrste *P. noctiluca* (Malej i Malej, 2009). Osim što su pojave *M. leidyi* prostorno rasprostranjenije i traju dulje u odnosu na ostali želatinozni zooplankton, važno se osvrnuti i na brojnost jedinki. Gustoća nakupina u sjevernom Jadranu nerijetko postiže rekordne vrijednosti od nekoliko stotina jedinki po m^3 (I publikacija) što je u rangu maksimuma za ovu vrstu, ali i među najvišim vrijednostima brojnosti makro frakcije zooplanktona uopće (isključujući juvenilne organizme). Naime, u Kaspijskom jezeru su najveće brojnosti *M. leidyi* znale prijeći i tisuću jedinki po m^3 (Roohi i sur., 2016), dok su u danskim vodama takve brojnosti zabilježene kod meduze *A. aurita* (Olsen i sur., 1994). Redovne pojave rebraša uz učestalije pojave drugog želatinoznog zooplanktona daju naslutiti da je u Jadranu, a ponajprije u njegovom sjevernom dijelu, trofička uloga ribe smanjena u korist želatinoznih organizama. Takvo što već je zamijećeno u nekim morima gdje je masovni izlov ribe opustošio ekološke niše i omogućio učestalije pojave želatinoznih organizama (Greene i sur., 2015; Lynam i sur., 2006) kao npr. i u Crnom moru uslijed unosa *M. leidyi* (d'Armengol i sur., 2017; Shiganova i sur., 2004a).

Razdoblje pojava *M. leidyi* možemo promatrati i u kontekstu njihovog utjecaja na manje planktonske frakcije (fito- i mezozooplanktonsku zajednicu). Godišnja dinamika fitoplanktona u sjevernom Jadranu slijedi sezonski ciklus i prvenstveno je vođena promjenama u donosu rijekom Po (Bernardi Aubry i sur., 2012), a može se opisati dvostrukim cvatom: (i) u proljeće i (ii) u jesen. Tijekom ljeta brojnost opada do rujna, a isto se događa pred kraj jeseni, što vodi do najnižih vrijednosti zimi (Cerino i sur., 2019). Povezanost pojava *M. leidyi* i obilja fitoplanktona je opisana u uvodnom dijelu ovog rada, dok su Delpy i sur. (2016) pokazali i indirektnu vezu s koncentracijama klorofila *a* (Chl *a*), a što u sjevernom Jadranu nije zamijećeno (Slika 7., III publikacija). U istoj publikaciji, pokazano je da je maksimum fitoplanktona bio u zapadnom dijelu sjevernog Jadrana i to u ožujku kada je brojnost rebraša bila iznimno niska (< 5 jedinki po m^3), dok je ljetni maksimum zabilježen istočnije u srpnju i poklapa se s najvećim brojnostima rebraša (Slika 2., III publikacija). Ovi maksimumi se ujedno poklapaju i s razdobljem maksimuma (svibanj-kolovoz) sitnijeg zooplanktona (mikro- i mezozoo frakcija) (Slika 2., III publikacija), plijena rebraša (I publikacija). Općenito, jaka povezanost *M. leidyi* i mezozooplanktona pokazana je u III publikaciji. Brojnost sitnijeg zooplanktona, uz određeni vremenski odmak, prati rast brojnosti fitoplanktona, a čija je kvalitativna promjena (promjena u strukturi zajednice) zabilježena već unazad 30 godina (Bernardi Aubry i sur., 2012). Kvalitativne promjene zooplanktona prikazane su u I publikaciji zaključivši da je njegova brojnost u sjeveroistočnom dijelu Jadrana niža u odnosu na desetljeće ranije. Manja brojnost i raznovrsnost zooplanktona je također zabilježena u sjeverozapadnom dijelu Jadrana nakon prvih pojava *M. leidyi*, što je izazvalo zabrinutost u pogledu odjeka tih promjena na riblji fond (Fiori i sur., 2019). Naime, uslijed pojava *M. leidyi* stradao je čitav crnomorski riblji fond, a najjače je pogođen fond inćuna (Barbier i Knowler, 2005) čija potražnja za zooplanktonom u Crnom moru ljeti iznosi oko 20% dnevne proizvodnje (Bulgakova,1996). Stoga, u ovom radu utjecaje bioinvazije na riblji fond sjevernog Jadrana, razmatramo u kontekstu utjecaja na inćune. Dislokacija mrijesta europskog inćuna (*Engraulis encrasicolus*) kojeg su zamijenile pojave *M. leidyi* (Slika 3. i 5., I publikacija), daje nam prvi uvid u posljedice masovnih pojava rebraša na riblji fond u Jadranu. Općenito se smatra se da je dostupnost hrane biotički faktor koji upravlja brojnošću jedinki odnosno gustoćom *M. leidyi* populacije, dok je prostorna raspodjela uvjetovana abiotičkim faktorima (Shiganova, 1998). Ishrana inćuna u Sredozemlju uglavnom se sastoji od kopepoda (Tudela i Palomera, 1997), dok je ona za vrijeme mrijesta u istočnom Jadranu nešto drugačija, pa tako glavninu čine ličinke desetonožaca (Decapoda), kopepodi reda Calanoia, od kojih uglavnom *Temora stylifera*, te predstavnici porodica Oncaeidae i Corycaeidae (Mustać i Hure, 2020). Za usporedbu, u uzorcima sadržaja probavila *M. leidyi* kopepodi su činili trećinu plijena (Tablica 2., I publikacija). Ličinke desetonožaca, ali i predstavnici Oncaeidae i Corycaeidae vrlo su malo zastupljeni na lokacijama mrijesta, i u sadržaju probavila *M. leidyi* (Tablica 2., I publikacija). *T. stylifera* je pak više zastupljena kao plijen *M. leidyi* (12±4%), i manje u uzorcima morske vode (3,1±2,5%) (Tablica 2., I publikacija) što može ukazivati na preferenciju plijena inćuna, ali svakako ističe kompeticiju za resurse. Fiori i sur. (2019) su nakon pojava *M. leidyi* u sjeverozapadnom Jadranu također zabilježili manju brojnost *Temora* spp., ali i jajašaca ribe. Na sjeveroistoku Jadrana najbrojniji su bili rašljoticalci (Cladocera) i ličinke školjkaša (Bivalvia) (Tablica 2., I publikacija). *Penilia avirostris* (Cladocera) činila je gotovo polovicu u vodenom stupcu, a tek petinu plijena rebraša, dok je školjkaša bilo manje (6±9%) u vodenom stupcu nego u plijenu (16±8%), što može ukazati na spretnost pojedinih vrsta da izmaknu ovom predatoru. Relativno visok udio školjkaša može se objasniti plićim, priobalnim lokacijama, pa se očekuje da bi kompozicija plijena otvorenom moru bila drugačija, kako se takve zooplanktonske zajednice značajno razlikuju (Miloslavić i sur., 2012). Usporedbom zooplanktona i inćuna prije i nakon redovitih pojava *M. leidyi* u sjevernom Jadranu (I publikacija) pozitivno je odgovoreno na hipotezu (H4) da rebraši predacijom utječu na zooplankton (*top-down*), a kompeticijom za resurse na fond inćuna, ali nije utvrđen *top-down* utjecaj na inćune predacijom juvenilnih stadija te ribe, jer je u sadržaju probavila zastupljenost ribljih jajašaca bila iznimno mala (Tablica 2., I publikacija).

Kada spominjemo inćune, njihova je nezaobilazna odlika, osim ekološke važnosti, i gospodarska vrijednost s obzirom na to da na njih otpada čak 74% ukupnog godišnjeg ulova sitne plave ribe u Jadranu (Zorica i sur., 2018b), a što čini više od 80% u hrvatskim vodama (Mustać i Hure, 2020). Osim toga, inćuni, za razliku od druge sitne pelagijske ribe poput sardina, pokazuju iznimnu prilagodljivost tipu ishrane i lokacijama na kojima se hrane (Chouvelon i sur., 2014). No, unatoč očitim prednostima u odnosu na druge vrste, njena populacija u Jadranu snosi posljedice izloženosti brojnim pritiscima. Opća komisija za ribarstvo na Sredozemlju (GFCM) posljednjih godina izvještava o padu ulova i smanjenom mrijestu inćuna u Jadranu, ali i u nekim drugim dijelovima Sredozemlja, (FAO, 2017). Sjeverni Jadran posebno je bitan u dinamici populacije inćuna s obzirom na to da se upravo ovdje odvija najveći dio mrijesta inćuna u Jadranu (Zorica i sur., 2018a), ali pri tome treba uzeti u obzir i da se ribolov u Jadranu odvija tijekom cijele godine uz primjenu razdoblja privremene obustave ribolovne aktivnosti (lovostaja) dva put godišnje: (i) ljeti na talijanskoj, a (ii) zimi na hrvatskoj strani Jadrana (FAO, 2017). Kako razdoblje mrijesta inćuna u Jadranu počinje u proljeće, a završava pred kraj ljeta, uz maksimum od travnja do srpnja (Zorica i sur., 2013), razdoblje obustave na hrvatskoj strani ne pogoduje njegovom mrijestu. Uz problem neadekvatnog režima ribolova, istovremeno, i pojave *M. leidyi* dodatno umanjuju šansu za oporavak komercijalno značajnog fonda inćuna (I publikacija). Stoga je u teoriji moguće i pritiske bioinvazija promatrati iz perspektive ekonomskih i financijskih gubitaka. Općenito, masovne pojave želatinoznih organizama izazivaju ogromne troškove u ribarstvu diljem svijeta s više aspekata (Palmieri i sur., 2014). Osim u problemima zbog nedostatka ribe, jadranski ribari se i od prije redovitih pojava *M. leidyi* suočavaju sa štetama otežalih ribarskih mreža zbog ogromnih količina raznih želatinoznih organizama (Palmieri i sur., 2014). Procijenjeno je da bi se uslijed učestalijih pojava želatinoznih organizama gospodarski gubici u godini dana samo za talijansku flotu u sjevernom Jadranu mogli popeti i do 8,2 milijuna € zbog manjka ribe, 460 000 € zbog veće potrošnje goriva, te bi na popravak oštećenih mreža bilo potrebno utrošiti još 89 000 radnih sati (Palmieri i sur., 2014).

Kako inćuni zauzimaju središnji položaj trofičkog sustava povezujući energiju proizvedenu na nižim trofičkim s organizmima na višim trofičkim razinama, ekološki modeli su pokazali kako ih možemo smatrati jednom od ključnih vrsta koja osigurava funkcioniranje jadranskog ekosustava (Coll i sur., 2007). Osim na sve navedene gospodarske gubitke, odjek pojave *M.*

leidyi može se odraziti i na niz trofičkih razina ekosustava jer inćuni predstavljaju najnižu razinu koja (za razliku od zooplanktona) samostalno prevladava velike udaljenosti i pronalazi nova područja prilagođena zahtjevima populacije (Bakun, 2006). Upravo se na ovo nadovezuje dislokacija mrijesta koja je prikazana u I publikaciji. Nedostatak ribe se trofičkim karikama prenosi na njihove predatore u morima, ali i izvan njih npr. na morske ptice (Lotze i sur., 2010). Veliki broj organizama poput morskih ptica (Luczak i sur., 2011; Okes i sur., 2009), morskih sisavaca (Piroddi i sur., 2010; Zorica i sur, 2018b), većih pelagijskih riba npr. tune (Lezama-Ochoa i sur., 2010; Zorica i sur., 2018b), i pridnenih riba npr. oslića (*Merluccius merluccius*) i romba (*Lepidorhombus whiffiagoni*s) (López-López i sur., 2012), ali i meduza (Sabates i sur., 2010), hrani se nekim od stadija životnog ciklusa inćuna. Posljedično bi i ekonomski gubici mogli porasti s obzirom na to da su neke od vrsta (npr. tuna) također od komercijalne važnosti. Nadalje, kako je predacija neselektivna, plijenom bi mogle postati (ili već jesu) i druge ribe koje se u to vrijeme mrijeste, s obzirom na to da se ukupna krivulja reproduktivnih perioda komercijalne ribe u Jadranu (Giansante i sur., 2008) podudara s pojavama *M. leidyi* (I publikacija). Osim na već spomenute inćune, reproduktivno razdoblje većine vrsta komercijalne ribe ostvaruje se od ožujka do rujna, s maksimumom u svibnju, a neke vrste poput skušovki (npr. *Euthynnus alletteratus*) (Giansante i sur., 2008) ili oslića (*Merluccius merluccius*) se u to vrijeme i mrijeste (Zorica i sur., 2021). Posljedice na riblji fond mogu se očitovati i kroz nedostatak i drugih, ne-komercijalnih vrsta riba, koje za svoj mrijest biraju zaklonjene uvale, inače mjesta akumulacije *M. leidyi* (Delpy i sur., 2016).

Što poduzeti za ograničavanje i kontrolu pojave M. leidyi?

Prilikom informiranja javnosti o štetnim posljedicama pojava raznovrsnih bioinvazija, često se postavlja pitanje na koji način iste suzbiti ili ih bar ublažiti. Morske bioinvazije posebno su izazovne samim time što se odvijaju u mediju kojeg ljudi koriste i u koji zalaze, ali ne borave toliko dugo kao i na kopnu, pa se naizgled ne doimaju relevantnima, u odnosu na kopnene bioinvazije, čiji su utjecaji očitiji jer one mogu biti prisutnije u svakodnevnom životu. Osim toga, radi se o vrsti koja je zbog svojeg izgleda i prozirnosti teže uočljiva, pa zbog toga nije na istoj vizualnoj razini s nekim drugim vrstama kada se razmatra trend istraživanja njihovih pojava. U Hrvatskoj je 2021. godine projektom „Jeste li ih vidjeli?“ popisano 8 najproblematičnijih vrsta od kojih je 6 kopnenih, a ostale dvije vezane uz slatkovodne sustave (MINGOR, 2021). Na istoj mrežnoj stranici promovirana je i mobilna aplikacija *Invazivne vrste u Hrvatskoj* koja sadrži digitalni katalog istoimenih vrsta među kojima je popisano 10 invazivnih beskralježnjaka. Od svih navedenih 4 otpadaju na morske vrste od kojih je jedna upravo *M. leidyi* – ujedno i jedina zooplanktonska vrsta. Time se potvrđuje činjenica da unatoč izuzetno visokom udjelu mora u ukupnom teritoriju Republike Hrvatske (35%) i brojnim lukama kao potencijalnim izvorima unesenih stranih organizama koje godišnje primaju stotine brodova, strane morske vrste ostaju marginalizirane čak i kada su neke od njih, poput *M. leidyi*, u ostalim dijelovima svijeta izazvale alarmantne štete i dovele do velikih financijskih gubitaka (Bodini i sur., 2017). Kako bi se dočarao doseg gospodarskih gubitaka prouzročenih pojavama *M. leidyi* mogu se uzeti u obzir utjecaji bioinvazija na crnomorski riblji fond (s naglaskom na inćune) koji su doveli do godišnjih gubitaka od 16,7 × 10^6 $ (Knowler, 2005). Općenito, invazivne vrste opterećuju gospodarstvo, a posljedice njihovog unosa na globalnoj razini opisuju sljedeće brojke. Ukupan svjetski trošak posljedica bioinvazija u svim vodenim sustavima iznosi 345 × 10^9 $ od čega većina (62%) otpada na beskralješnjake (Cuthbert i sur., 2021). Procijenjeni troškovi unosa invazivnih vrsta u razdoblju od 1960.-2020. su samo u Europi iznosili čak 140,2 × 10^9 $, odnosno 116,6 × 10^9 € (Haubrock i sur., 2021). Navedeno opterećenje gospodarskog sustava ukazuje na hitnu potrebu suzbijanja invazivnih organizama. U konkretnom slučaju bioinvazija *M. leidyi*, do danas nema pravog rješenja s obzirom na to da je ona i dalje prisutna gdje god se pojavila kada su uvjeti u novom okolišu bili prikladni za uspostavu populacije. Međutim, primjer iz Crnog mora, pokazuje da se sustav donekle uspio oporaviti, nakon moratorija na ribolov, a posebno nakon nehotičnog unosa njenog prirodnog predatora rebraša *Beroe ovata* (Oguz i sur., 2008; Shiganova i sur., 2004a). Unos novih vrsta predstavlja uvijek rizik uslijed brojnih neizvjesnosti koje prate dinamičan ekosustav morskog okoliša koji je izložen raznim pritiscima (Freer i sur., 2018), a čije je funkcioniranje vrlo teško simulirati u laboratorijskim uvjetima da bi se taj neizvjestan ishod mogao sa sigurnošću ustvrditi. Namjerno ili nenamjerno unesene nove vrste mogu biti čak i vektori drugih organizama (Guy i sur., 1998). U svakom slučaju, postoje brojni faktori koje treba odvagati ne bi li kao plan suzbijanja neke bioinvazije namjerno unijeli neki novi, ali kompetitivni strani organizmi poput *B. ovate*, s obzirom na to da su dobrobit i zahtjevnost sprovođenja plana uvođenja nove vrste prostorno i vremenski neravnomjerno raspoređene (Ewel i sur., 1999), a time i uspjeh takve odluke. Takav akcijski plan upravljanja bioinvazijom predlaže se tek onda kada je taj drugi organizam, u ovom slučaju, predator, autohtoni organizam, čijom zaštitom i obnavljanjem populacije ojačavamo lokalni ekosustav i istovremeno oslabljujemo utjecaj invazivne vrste (Giakoumi i sur., 2019). Međupovezanost morskih okoliša pod utjecajem vodenih masa potiče disperziju organizama što otežava kontrolu bioinvazija. Kako se radi o zooplanktonskoj vrsti za koju je pokazano da su geostrofička strujanja izuzetno važna s obzirom na to da potpomažu sekundarnom širenju bioinvazije s područja izvorišta (I i III publikacija) ili područja umnožavanja (II publikacija) do novih lokacija, kontrola unosa još jedne vrste za koju vrijede različiti optimalni uvjeti za opstanak i održavanje populacije, problem čini još kompleksnijim. Kako su, u osnovi, bioinvazije *M. leidyi* potaknute njenim unosom balastnim vodama, napore da se umanje posljedice bioinvazija trebalo bi promatrati iz kuta prevencije daljnjeg širenja. Mada danas postoje zakoni prema kojima se regulira ispuštanje balastnih voda poput onih propisanih Međunarodnom konvencijom o nadzoru i upravljanju brodskim balastnim vodama i talozima, ista se čine neprikladnima uzmemo li u obzir obilježja bioinvazije *M. leidyi* u Jadranu. Konvencija nalaže da se izmjena balastnih voda vrši najmanje 200 NM od najbližeg kopna, a ako je to neizvedivo onda najdalje moguće uz minimalnu udaljenosti od najbližeg kopna 50 NM i u oba slučaja na mjestima gdje je dubina mora bar 200 m (Učur, 2011). Posebne regulacije su dozvoljene ako su ovi uvjeti teško ostvarivi. U Jadranu, a posebno u njegovom sjevernom dijelu, takvih lokacija nema, s obzirom na to da se radi o plitkom moru, čiji presjek (istok-zapad) na sjeveru iznosi oko 80 NM. Konvencija također dozvoljava da se ispusti do 10 održivih organizama (≥ 50 μm) po kubiku balastnog ispusta. U konkretnom slučaju rebraša *M leidyi*, taj broj obeshrabruje jer se radi o dvospolcima s mogućnošću samooplodnje i koji su u stanju proizvesti dnevno na tisuće jajašaca. Zato je napore provođenja posebnih regulacija važno usmjeriti i na obradu balastnih voda, a kao onaj najekonomičniji u pogledu energetskog utroška, ističe se termička obrada korištenjem otpadne topline brodskog motora (Vorkapić i sur., 2016). U IV. publikaciji je istražen utjecaj temperature na održivost organizma u pojedinim stadijima životnog ciklusa *M. leidyi* (jajašce, ličinka, odrasla jedinka), a u teoriji razmatrana i energetska isplativost iskorištavanja otpadne topline da bi se balastni tankovi zagrijali na temperature od 40-50 °C na kojima je rezistentnost organizama najmanja te su procijenjene najprikladnijima za relativno brzo uklanjanje *M. leidyi* (Tablica 2.). Pokazano je da je to itekako moguće za npr. Ro-Ro tip teretnog broda koji je odabran kao predstavnik pomorskog prijevoza na kraćim relacijama unutar Jadrana, odnosno onima koji se služe tzv. Jadranskim koridorom (Mazzarino, 2003). Međutim, u obzir treba uzeti i izolaciju oplata balastnih tankova zbog značajnih gubitaka uslijed aktivne vožnje (IV. publikacija). Relacije unutar Jadrana čine se iznimno bitne, zbog toga što, kako je pokazano u I publikaciji, bioinvazija *M. leidyi* nije još uspjela zahvatiti većinu područja istočnije od Istarskog poluotoka, npr. Riječki zaljev, a niti se proširiti na područja južnije od sjeverno-kvarnerskih otoka (Cres) (Slika 3.). Kod predlaganja rješenja u cilju ograničavanja daljnjeg širenja bioinvazije *M. leidyi* imali smo na umu da je sjeverni Jadran područje intenzivnog pomorskog prometa jer se tu nalazi nekoliko bitnih terminala i luka, a to su: Venecija, Trst, Kopar i Rijeka. U najveću od njih – Venecijansku luku, godišnje uplovi oko 3500 brodova, od čega više od polovice otpada na teretnjake, a ostatak na putničke brodove (NASPA, 2019). Radi se i o jednoj od najvećih europskih luka za projektne i opće terete, ali je i jedna od glavnih luka na Jadranu po broju pretovarenih kontejnera (Environmental Unit NASPA, 2019) što ilustriraju podaci iz 2017. kada je zaprimljen teret iznosio > 25 × 10^6 t, a broj putnika više od milijun i pol (NASPA, 2019). Osim toga, postoji direktna linija putničkog prijevoza koja Veneciju povezuje s istočnim dijelom sjevernog Jadrana. Međutim, ni ostale veće luke nisu manje bitne kao središta za potencijalno širenje *M. leidyi*. Naime, izuzev Riječke luke, sve ostale su zadnjih godina izložene redovitim pojavama *M. leidyi* (Tirelli i sur., 2021), ali ona bi uslijed potencijalnog unosa *M. leidyi* mogla postati nova lokacija gdje bi ta vrsta mogla uspostaviti barem privremenu populaciju. Smatramo da je razlog što se širenje već nije nastavilo istočnije – Kvarnerom u oligotrofnijim uvjetima na tom području, a time i nedostatku hrane, što se prilično razlikuje od uvjeta koje bilježimo uz zapadnu obalu Istre (I publikacija). To ne znači da populacija u teoriji ne bi mogla opstati u zaklonjenim područjima gdje je i inače brojnost *M. leidyi* najviša (I i II publikacija). Riječka luka se već pokazala lokacijom gdje su balastnim vodama dopremljeni brojni strani organizmi (Di Poi i sur., 2019), no ne isključuje se da izloženost unosa stranih vrsta ne prijeti i drugim manjim lukama na istočnoj obali Jadrana. Podaci iz 2017. godine pokazuju i to da je u hrvatskim lukama ispušteno skoro ~ 1,8 × 10^6 m^3 od ukupno 5,3 × 10^6 m^3 balastnih voda koje su ušle u Jadran (Čović i sur., 2019). Unatoč tome što se u Riječkoj luci ispusti gotovo polovica te ukupne količine balastne vode, iznosi su i u ostalim lukama (Pula, Senj, Zadar, Šibenik, Split, Ploče i Dubrovnik) značajni, i broje se u stotinama tisuća kubika (Čović i sur. 2019). Izloženost daljnjem širenju ove vrste Jadranom potkrepljuje nekoliko zabilježenih epizoda pojava *M. leidyi* na i jugu Jadrana, točnije u luci Ploče premda ondje nije uspjela ostvariti stabilnu populaciju (Violić i sur., 2022). Osim toga, i rezultati simulacija biogeokemijskog modela Eco3M-MED u kojem je *M. leidyi* uvedena u trofički sustav Sredozemlja pokazali su da bi se potrebni uvjeti (količina i kvaliteta hrane) za održavanje njene stabilne populacije mogli naći diljem sredozemnog obalnog pojasa kao najproduktivnijeg dijela, a manje u otvorenom moru (Alekseenko i sur., 2019).

Kako bi sa sigurnošću predložili neku vrstu mjere za suzbijanje ove bioinvazije, opstanak triju stadija životnog ciklusa *M. leidyi* smo, uz izloženost temperaturi, dodatno ispitali u uvjetima hipoksije i anoksije odnosno primjenom deoksigenacije, te izloženosti ultrazvučnoj kavitaciji, ali i, odvojeno, samo na utjecaj zagrijavanja mikrovalovima. Svi oni su se pokazali učinkovitijima od isključivo termičke obrade (uklanjanje svih stadija *M. leidyi* odvija se brže), no sa sobom povlače nužna ulaganje u novu infrastrukturu broda. Drugim riječima, u IV publikaciji je pozitivno odgovoreno na hipotezu (H5) da se obradom balasta suzbija potencijalno širenje *M. leidyi*. Između ispitanih tehnika obrade balastnih voda bitno je istaknuti da je prednost kombinacije deoksigenacije uz upuhivanje dušika zaštita od korozije, dok primjena mikrovalova osigurava iznimno brzu obradu što je čini prikladnom i za najkraće rute. Duljina puta određuje odgovarajući tretman za uspješno eliminiranje *M. leidyi* i može poslužiti kao smjernica za kreiranje strateškog plana za upravljanje njenom bioinvazijom. Predložena termička obrada na brodovima (tzv. onboard), s ili bez upuhivanja N_2 prikladna je za primjenu na udaljenostima većima od 200-300 km, a što preciznije ovisi o godišnjem dobu odnosno temperaturnim i hidrografskim uvjetima (IV publikacija). Na kratkim rutama prikladnije bi bila obrada balastnih voda nekim drugim tehnikama poput izlaganja ultrazvučnoj kavitaciji ili mikrovalnom zračenju (IV publikacija). U prilog tzv. onboard obradi svakako ide to da je tretman balastnih voda neovisan o kvaliteti lučke infrastrukture, a ona je pak često ovisna o veličini luke, ali i gospodarskoj važnosti, te u različitim dijelovima svijeta nejednako razvijena (Munim i Schramm, 2018). Dakle, premda se čini da bi obrada u lukama bila jednostavnije rješenje koje ne bi iziskivalo infrastrukturne modifikacije raznih tipova brodova, iste osiguravaju minimalan rizik unosa stranih vrsta balastnim vodama neovisno o ruti koju brod prelazi i o luci u koju pristiže.

U konačnici, bitno je istaknuti da uspjeh ublažavanja posljedica ili eliminacije nekog invazivnog organizma ne ovisi samo o jednom aspektu nego o mnogo njih, koje smo već ranije spomenuli. Nedavno je predložen novi model koji se bavi problemom invazivnih vrsta, a zasnovan je na već, mada nesustavno, primjenjivanim aktivnostima, strategijama i istraživanju invazivnih vrsta u Sredozemlju (Rotter i sur., 2020). Model pristupa pojavama invazivnih organizama kao biološkom zagađenju i naziva se 8R (od eng. Recognize, Reduce, Replace, Reuse, Recycle, Recover/Restore, Remove, and Regulate), kao skraćenica ključnih koraka, a to su: (i) prepoznavanje, (ii) umanjivanje, (iii) zamjena, (iv) ponovna uporaba, (v) recikliranje, (vi) oporavak, (vii) uklanjanje i (viii) regulacija. Kad bi se takva strategija primijenila na *M. leidyi* ona bi pod (i) uključivala upravo istraživanje (kao što je prikazano u I-III publikaciji), ali i implementaciju sustava dojave. Osim ranije navedenih opcija dojave (mobilne aplikacije: *Invazivne vrste u Hrvatskoj* i *avvistAPP*) koje djeluju na nacionalnom i internacionalnom nivou, ponukani promjenama koje su ova istraživanja pokazala u sklopu projekta EcoRENA (I-III publikacija) osnovana je stranica www.rebrasi.com koja na jednom mjestu integrira nove spoznaje o ovom problemu na lokalnoj razini i omogućuje dojavu pojava. Kao drugi korak (ii), odnosno umanjivanje pojava, bila bi primjena metoda koje bi ograničile daljnje širenje *M. leidyi* što je predloženo u IV publikaciji. Treći korak (iii) je problematičniji jer se odnosi na unos drugog stranog organizma, npr. *B. ovata*, jer su se njene predatorske karakteristike pokazale kao uspješnim saveznikom u umanjivanju posljedica masovnih pojava *M. leidyi* i njihovog utjecaja na zooplankton. Međutim, kao što je već objašnjeno ranije, unošenje bilo kojeg novog organizma unosi brojne nesigurnosti kako se radi o jedinstvenoj konstelaciji tog ekosustava. Četvrti (iv) i peti (v) korak se odnosi na iskorištavanje rebraša kao gospodarskog resursa, što do sada nije dovoljno istraženo, ali predstavlja svojevrsni potencijal. Naime, brojni želatinozni organizmi se već primjenjuju kao dodaci gnojivima (Emadodin i sur., 2020) ili se iz njih ekstrahiraju vrijedne kemijske tvari (Frazão i Antunes, 2016). Oporavak bi, u kontekstu *M. leidyi* bioinvazija, mogao značiti da se područjima izloženima stalnim pojavama, ali gdje *M. leidyi* ne boravi permanentno, kao što je u I-III publikaciji pokazano uz istočnu obalu sjevernog Jadrana, posveti veća pažnja kako bi se minimalizirali antropogeni pritisci i ojačao lokalni ekosustav i tako djelomično nadomjestili gubici koji su za inćune i zooplankton pokazani u I publikaciji. Nadalje, pitanjem uklanjanja bavi se IV publikacija, dok je posljednji korak regulacija aktivnosti vezana za već spomenute mjere, npr. CBD, ODMS, Međunarodna konvencija o nadzoru i upravljanju brodskim balastnim vodama i talozima, ali i neke druge regulative, npr. EU Strategija za bioraznolikost do 2030. i EU Uredba br. 1143/2014 o invazivnim stranim vrstama (Rotter i sur., 2020). Iz priloženog se vidi da problem unosa stranih invazivnih vrsta iziskuje multidisciplinarnost pristupa (IV publikacija), ali i interdisciplinarnost u istraživanjima (I-III publikacija) koje su u ovom radu i korištene.

ZAKLJUČCI

Na osnovu provedenih istraživanja doneseni su niže navedeni zaključci.

1. *M. leidyi* svojim redovitim i masovnim pojavama te njihovim intenzitetom nadmašuje sve ostale pojave želatinoznog zooplanktona u Jadranu.

2. Dinamika pojava invazivnog rebraša *M. leidyi* u sjevernom Jadranu je sezonska. Najveće brojnosti populacija ostvaruje za vrijeme toplijeg razdoblja (proljeće ⇨ jesen) te dostiže svoj vrhunac pred kraj ljeta. Tijekom hladnijih mjeseci populacija iščezava uz istočnu obalu, što nije slučaj na zapadnoj strani.

Iako su do sada u drugim morima utvrđeni brojni čimbenici koji ograničavaju napredak populacije (npr. svjetlost i salinitet), pokazalo se da su prevladavajući ograničavajući u sjevernom Jadranu: hrana i temperatura. Nestašica hrane sprječava širenje populacije istočnije prema Kvarnerskom zaljevu i područja istočnije od Istarskog poluotoka, npr. Riječkom zaljevu, te južnije od sjeverno-kvarnerskih otoka, dok sniženjem temperature mora (posebno ispod 14 °C) opada i brojnost jedinki.

3. Istočna obala sjevernog Jadrana izložena je periodičkim, sekundarnim valovima invazije, a čije je vjerojatno izvorište u području obalnog pojasa oko Venecijanske lagune utvrđeno fizikalnim modelima.

4. Neki od fizikalnih fenomena imaju poseban značaj u oblikovanju dinamike *M. leidyi* populacije u sjevernom Jadranu, a to su: anticiklonalni sustavi vrtloženja i ICCC. Sustavi vrtloženja zone su nakupljanja organske tvari, fitoplanktona i zooplanktona, te mogu poslužiti kao područja povećanja brojnosti populacije, iz kojih se dalje jedinke šire izvan vrtloga, dok ICCC krajem ljeta pospješuje stvaranje gustih nakupina uz obalu.

5. *M. leidyi* izlučivanjem sluzi, neurednim hranjenjem i propadanjem jedinki, doprinosi stvaranju značajnih količina organske tvari od kojih je većina labilna i reaktivna frakcija DOC-a. Organska tvar prikladni je supstrat heterotrofnim prokariotima, čija brojnost raste u područjima nakupljanja jedinki *M. leidyi*. Uslijed heterotrofne razgradnje dostupne organske tvari otpuštaju se hranjive soli koje potiču umnožavanje cijanobakterija. Izobilje prokariota osigurava glavni plijen heterotrofnim nanoflagelatima, čija brojnost posljedično također raste. Dakle, narušena ravnoteža sustava uslijed pojave *M. leidyi* oblikuje piko- i nanoplanktonsku zajednicu i potiču mikrobnu petlju.

6. Neselektivna prehrana *M. leidyi* prijetnja je raznolikosti planktonskih eukariota, ali i obilju mezozooplanktona, te posljedično fondu inćuna čiji je to glavni izvor hrane. Masovne

pojave rebraša zamijenile su populaciju inćuna na područjima njihovih mrijestilišta u sjeverno-istočnom Jadranu.

7. Diljem sjevernog Jadrana, a i šire, postoje lokacije na kojima bi u teoriji, mogla opstati populacija *M. leidyi*, no do kojih se još uvijek nije proširila. Daljnje širenje populacije može se naročito ograničiti obradom balastnih voda u tankovima na brodu, i to: primjenom termičke obrade, deoksigenacije, ultrazvučne kavitacije ili mikrovalnog zračenja, koje uspješno eliminiraju sve faze životnog ciklusa *M. leidyi*. Od svih navedenih tehnika obrade, prednost ima termička jer iskorištava otpadnu toplinu koju proizvodi motor broda, a čija se efikasnost i povećava uz primjenu deoksigenacije. Ovisno o trajanju plovidbe, tipu broda i dostupnoj količini otpadne topline mogu biti prikladne različite tehnike obrade balasta ili pak njihove kombinacije.

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Internetski navodi

- Mrežni portal Informacijskog sustava MORE: http://baltazar.izor.hr/ azopub/bindex
- Baza podataka Jellyfish Database Initiative, JeDI: http://jedi.nceas.ucsb.edu
- Invazivne strane vrste, Ministarstvo Gospodarstva i održivog razvoja, Zavod za zaštitu okoliša i prirode: https://invazivnevrste.haop.hr/
- Portal projekta EcoRENA: www.rebrasi.com

ŽIVOTOPIS

Andrea Budiša je rođena 10. rujna 1986. u Puli. Osnovnu školu je završila u Rovinju, a srednju – klasičnu gimnaziju, u Pazinu. Preddiplomski studij 2011. završava na kemijskom odsjeku Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu, a 2012. primijenjenu ekologiju na Sveučilištu Singidunum u Beogradu, čime time je stječe zvanje prvostupnice kemije i diplomiranog analitičara okoliša. Dodiplomski studij završava 2015. u Essenu na Sveučilištu Duisburg-Essen u Njemačkoj i 2016. u Nijmegenu na Radboud Sveučilištu u Nizozemskoj te stječe zvanje magistra biologije. Eksperimentalni dio završnog rada izradila uz stipendiju Stichting Nijmeegs Universiteitsfonds u Brazilu u suradnji sa Sveučilištem savezne države Mato Grosso u Cáceresu, Brazil. Od 2017. godine zaposlena je na radnom mjestu asistenta u Centra za istraživanje mora Instituta Ruđer Bošković u Rovinju, te iste godine upisuje Interdisciplinarni doktorski studij iz oceanologije na Prirodoslovno-matematičkom fakultetu Sveučilišta u Zagrebu. Koautorica je: 10 znanstvenih radova, od kojih je na 3 glavni autor, 17 znanstvenih priopćenja u obliku postera ili predavanja, od kojih je na 6 glavni autor, 3 monitoring izvještaja i 6 znanstveno popularnih priopćenja.

ZNANSTVENA AKTIVNOST I PUBLIKACIJE

CROSBI PROFILE: Andrea Budiša (CROSBI Profil: 34596, MBZ: 366580)

ZNANSTVENI RADOVI

Ciglenečki, I., Paliaga, P., **Budiša, A.,** Čanković, M., Dautović, J., Djakovac, T., Dutour-Sikirić, M., Kraus, R., Kužat, N., Lučić, D., Marić Pfannkuchen, D., Njire, J., Pasarić, Z., Supić, N., 2021. Dissolved organic carbon accumulation during a bloom of invasive gelatinous zooplankton *Mnemiopsis leidyi* in the northern Adriatic Sea; case of anomalous summer in 2017. Journal of Marine Systems, 222:103599. doi:10.1016/j.jmarsys.2021.103599.

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Magić, L., Blažina, M., **Budiša**, **A.,** Konjević, L., 2017. Algae potential for combined wastewater treatment and biomass production. (poster) MOL DS R&D International Poster Day, Zagreb, Hrvatska.

Budiša, **A.,** Sobreira Oliveira Junior, E., Nauta, J., Kosten, S., 2015. Respiração em lagos de baixa latitude dominados por *Eichhornia crassipes*. (poster) 22º ConBio Congresso Biólogos do CRBio-01, Cuiaba, Mato Grosso, Brazil.

Sobreira Oliveira Junior, E., Nauta, J., van Bergen, Tamara **Budiša**, **A.,** Kosten, S., 2015, O Impacto de *Eichhornia crassipes* no fluxo ebulitivo do metano em lagos tropicais. (poster) 22º ConBio Congresso Biólogos do CRBio-01, Cuiaba, Mato Grosso, Brazil.

POPULARIZACIJA ZNANOSTI

Budiša, A., 8.11.-14.12.2021. Prezentacija: Kako se morski orah snašao u Jadranu? 130 godina Centra za istraživanje mora (CIM) u Rovinju. Rovinj, Hrvatska.

Budiša, A., 22.- 24.11.2019. Sudjelovanje, stand CIM (IRB) International Fisheries, Fishing equipment, Aquaculture, sport fishing and water sports fair CROFISH, Poreč, Hrvatska.

Paliaga, P., **Budiša, A.**, Robert Precali, R., Mirta Smodlaka, M., Marić Pfanncuchen, D., Radolović, M., 29.6.2018. Prezentacija: Hydrological systems in Croatia: Challenges and opportunities for sustainable management - Current state of the Northern Adriatic and major environmental threats, Grad Rovinj-Rovigno, Hrvatska.

Budiša, A., 20.5.2018. Prezentacija: Cijanobakterije – od prapočetaka do biotehnologije, Otvoreni Dan Instituta Ruđer Bošković (ODI), Zagreb, Hrvatska.

Budiša, A., 28.3.2018. Prezentacija: Dall'inizio della vita sulla Terra alle nuove applicazioni biotechnologiche, Conferenza Settore Giovani, Comunità degli Italiani 'Pino Budicin', Rovinj-Rovigno, Hrvatska.

Budiša, **A.**, Paliaga, P., 21.11. 2017. Prezentacija: Invazivne vrste Sjevernog Jadrana, Obilježavanje blagdana sv. Maura, Srednja škola Mate Balota, Poreč, Hrvatska.

SURADNJE I SUDJELOVANJA NA PROJEKTIMA

- Sustav praćenja i promatranja za stalnu procjenu stanja Jadranskog mora (2019.-2024.) (dr. sc. Martin A. Pfannkuchen)
- Sustavne ispitivanje stanja prijelaznih i priobalnih voda u 2021. godini na području sjevernog Jadrana (dr. sc. Tamara Đakovac)
- Sustavno ispitivanje stanja prijelaznih i priobalnih voda i voda u područjima podložnima eutrofikaciji u 2020. godini na području sjevernog Jadrana (dr. sc. Tamara Đakovac)
- Sustavno ispitivanje kakvoće prijelaznih i priobalnih voda u 2018. i 2019. godini na području sjevernog Jadrana (dr. sc. Tamara Đakovac)
- MZOS-001-0013077-0532 Bioraznolikost i održivo gospodarenje pelagičkim i demerzalnim resursima Jadrana (dr. sc. Nedo Vrgoč)

- HRZZ-IP-2016-06-4764 Ekološki odziv sjevernog Jadrana na klimatske promjene i antropogeni učinak, EcoRENA (dr.sc. Nastjenjka Supić)
- HRZZ-IP-2018-01-1717 Rogozničko morsko jezero kao model odziva ekosustava na promjene u okolišu, MARRES (dr. sc. Irena Ciglenečki-Jušić)
- HRZZ-PKP-2016-06-9081 Procjena potencijala jadranskih algi za ko-generacijsku proizvodnju biogoriva 3. generacije, A3-PICO-3G (dr. sc. Maria Blažina)

RADIONICE I ZNANSTVENO USAVRŠAVANJE

11.-14.4.2022. Srce, Radionica: Osnove programiranja (Python).

8.4.2022. Srce, Radionica: GIMP ili kako besplatno fotošopirati slike.

25.3.2022. Srce, Radionice: Inkscape ili vektorska grafika za svakoga.

10.3.2022. Radionica je organizirana kao promocija projekta „AdriAquaNet – Jačanje inovacija i održivosti u jadranskoj akvakulturi”.

16.2.2022., 9.3.2022., 11.5.2022, Laboratory Animal Science webinar series „Improving nonclinical research practices: way forward”.

7.-11.12.2021 Znanstvena škola: Sveobuhvatni pristup istraživanju antropogenih pritisaka na okoliš, Institut Ruđer Bošković, Zagreb, Hrvatska i online.

24.-27.3.2019. Završna radionica u sklopu projekta Hrvatske zaklade za znanost pod nazivom „Potencijal jadranskih mikroalgi za proizvodnju biogoriva 3. Generacija, A3-PICO-3G”, Mikroalge kao biogorivo budućnosti: Prilike i izazovi.

24.9.2018. Radionica: The Strategic Energy Technology (SET) Plan: Putting research and innovation at the heart of the Energy Union, Sveučilište u Zagrebu, Fakultet strojarstva i brodogradnje, Zagreb, Hrvatska.

21.-30.6.2018. Znanstvena škola: International School of Marine Conservation Science (isMCS) Department of Biodiversity, University of Primorska, Slovenia, Department of Wildlife and Fisheries, Oregon State University, USA, Blue World Institute of Marine Research and Conservation, Croatia, Kopar, Slovenija.

5.-7.12.2017. Radionica: Uvod u metode plinske i tekućinske kromatografije BICRO BIOCentar, Zagreb, Hrvatska

26.10.2017. Certifikat: Opus software, Tensor II FTIR spectrometer.