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PROJECT MEDUZA IN THE CONTEXT OF ITS HISTORICAL TIME

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ABSTRACT

In 2001, the National Science Foundation, in union with the Croatian and Slovenian science ministries, provided initial support for the international collaboration that has become the Meduza project. The program was started with the goal of international collaboration. The scientists involved in the project were glad to oblige because we wanted to work together. Our initial objective was simple – use this international collaboration to develop exciting scientific research involving medusae in Southern Adriatic waters. During the subsequent eight years we collaborated on six joint summer research trips. This international collaboration has been of great importance personally and professionally to all of the investigators and institutions involved in the project, but we now ask what objective difference has the project made scientifically? We approach that question by comparing what we thought we might accomplish at the project's outset to how we now view research on gelatinous zooplankton because of research in the Meduza project. Work outside the program also has affected our views but we describe here research produced through the project that has contributed substantially to broadening our perspectives in three major areas of investigation: modes of propulsion, mechanics of predation, and trophic significance of medusae.

Key words: Meduza project, propulsion, distribution, hydrodynamics, foraging, trophic roles

PROGETTO MEDUZA NEL CONTESTO DEL SUO SVILUPPO STORICO

SINTESI

La Fondazione Nazionale di Scienze (National Science Foundation) degli USA ed i Ministeri per la Scienza croato e sloveno hanno approvato, nel 2001, la collaborazione internazionale che ha poi portato al progetto Meduza. Il programma è stato avviato allo scopo di sviluppare la collaborazione internazionale. Gli scienziati coinvolti nel progetto hanno accolto positivamente l'obbligo, in quanto desiderosi di lavorare assieme. L'obiettivo iniziale era semplice – usare la collaborazione internazionale per sviluppare la ricerca scientifica incentrata sulle meduse dell'Adriatico meridionale. Durante gli otto anni successivi, i ricercatori hanno collaborato durante sei crociere estive congiunte. Tale collaborazione internazionale si è rivelata di grande importanza personale e professionale per tutti i ricercatori e per tutte le istituzioni coinvolte nel progetto, ma resta da evidenziare quale sia stato il contributo scientifico di tale collaborazione. A tale scopo i ricercatori hanno confrontato gli obiettivi che si erano posti all'avvio del progetto con la loro visione attuale della ricerca dello zooplancton gelatinoso. Il loro punto di vista è stato influenzato anche dal lavoro svolto all'esterno del progetto, ma nell'articolo vengono presentate le ricerche svolte nell'ambito del progetto Meduza, che hanno ampliato le loro prospettive in tre maggiori aree di ricerca: modalità di propulsione, meccanismi di predazione e significato trofico delle meduse.

Parole chiave: progetto Meduza, propulsione, distribuzione, idrodinamica, alimentazione, ruoli trofici

INTRODUCTION

Project Meduza began as a collaborative effort that focused on understanding the biology and ecology of medusae. The first research planning took place in 2001. A culminating symposium that produced the series of manuscripts in this volume occurred in May, 2009. The eight intervening years involved six joint field seasons, with a host of researchers and students working together and with ship crew, local citizens and government agencies, a variety of scientific papers that have been published already, and presentations of results at a range of different scientific conferences. These have all been valuable scientific and social products of the collaborative process. But what about our initial research goal? Has collaborative work increased our knowledge of the ecological roles played by medusae?

One way to respond to that question is to compare the state of knowledge about medusae at the outset of Project Meduza with what is known now at the time of our 2009 symposium. It is important to remember that the work in Project Meduza did not occur in isolation but in the context of progress within the larger field of zooplankton studies. We sought to expand what was known, using the unique environmental advantages found in the Mljet lakes and the oligotrophic southern Adriatic Sea. Some of the details of that process have already been published, some will follow in reports gathered for this volume, and others will be published in the months and years to come. But for our present consideration, we examine the views on medusan ecology that dominated our initial planning for Project Meduza. We view these issues as falling within three major areas: swimming propulsion, predation and other interspecific interactions within the planktonic community. This discussion is biased by the origin of the manuscript from the perspective of investigators from the USA. However, it is clear that all our other collaborators influenced the process of exploration in unexpected ways and we hope these connections will be apparent.

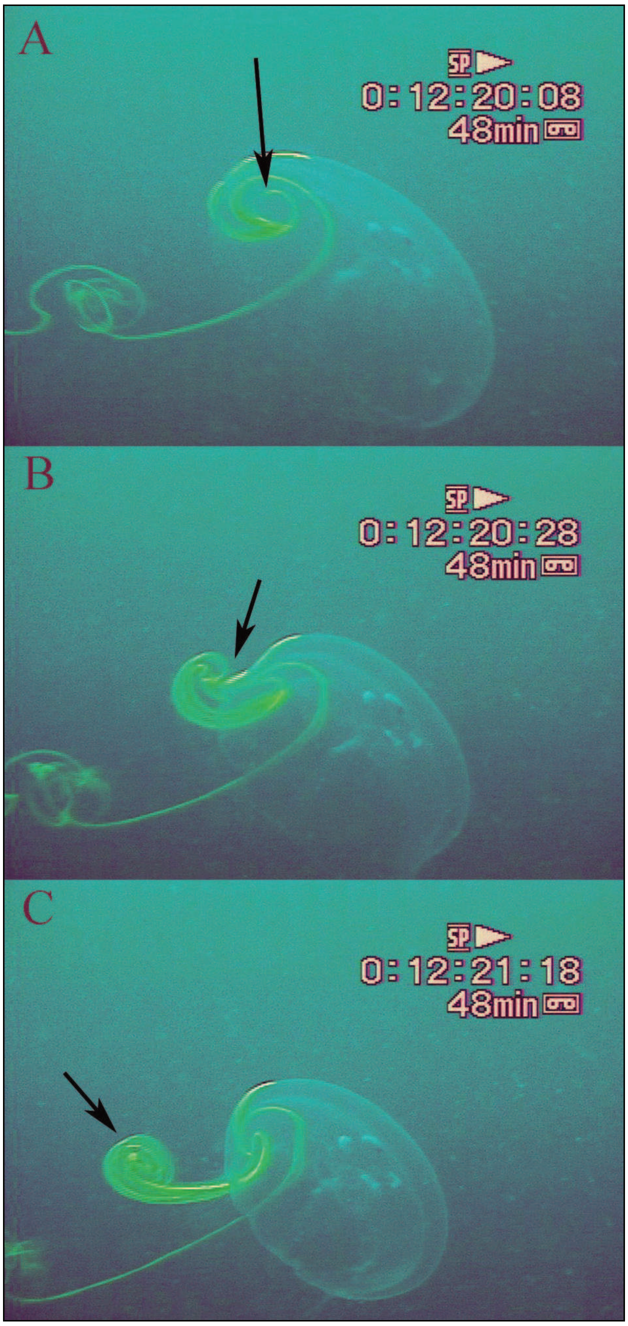

Fig. 1: Vortice ring formation during swimming by *Aurelia aurita,* ***a rowing propelled scyphomedusae. (A) Relaxation phase during which the formation of the stopping vortex is visible inside the bell. (B) Start of contraction phase during which the starting vortex is forming from fluid originating both inside and outside the bell. (C) End of contraction phase with the starting vortex superstructure trailing in the wake (The vortex from the previous pulse is visible just behind it). Arrows indicate the described vortices.***

Sl. 1: Prikaz vrtinčnega obroča, ki nastane med plavanjem skifomeduze *Aurelia aurita.* ***(A) Faza sproščanja, v klobuku viden ustavljajoči vrtinec. (B) Začetek faze krčenja, vrtinec se oblikuje iz tekočine, ki prihaja z zunanje in notranje strani klobuka. (C) Konec faze krčenja, vrtinec se razvije v vrtinčno sled. (Vrtinec, ki ga je oblikoval zadnji impulz, je viden za njim.) Puščice kažejo na opisane vrtince.***

PROPULSION AND FEEDING

Medusae are stated to be jet-propelled swimmers (Brusca & Brusca, 2003; Pechenik, 2005). A number of important correlates follow from this assumption. For example, jet propulsion is an energetically inefficient and costly propulsive mode, so jet propelled species typically have high energetic costs for swimming (Vogel, 1994). For that reason, medusae usually do not swim continuously, but alternate rest periods with bursts of activity (*e.g.* Mills, 1981). Presumably differences in prey selection would depend primarily on the type and positioning of tentacles (Madin, 1988) as well as the types of nematocysts found on the tentacles (Purcell & Mills, 1988). These were the widely accepted concepts in 2001 when Project Meduza began. Many are still widely accepted in 2009.

Do these perceptions accurately reflect reality? There were some reports in the literature that many common medusae swam continuously and, rather than waiting in ambush for prey, used feeding currents to entrain prey to their capture surfaces (Costello & Colin, 1994, 1995). These concepts were present in the medusan literature and even included in some authoritative texts at the start of Project Meduza (*e.g.* Arai, 1997), but those observations still had not been incorporated into major invertebrate zoology textbooks (cited above). Part of the significance of the issue of capture mechanics was that it broadened the consideration of prey selection by continuous swimmers, such as scyphomedusae, from capture surfaces and nematocysts to include predator-prey encounter processes. The vulnerability of prey to medusan feeding currents – and hence prey escape behavior – then became crucial for understanding prey selection by such medusae. However, this re-framing of medusae prey capture mechanisms lacked a full hydrodynamic model of the interaction between fluid motions used for propulsion compared to those used for feeding. The earliest attempts at describing oblate medusan flow patterns resulted in forcing them into conventional jet propulsion models (*e.g.* Costello & Colin, 1994, 1995) that were inadequate descriptions of swimming (Colin & Costello, 2002). The absence of a more detailed description of propulsive mechanics by oblate medusae hindered acceptance of the concept that medusae may have more than one mode of swimming propulsion. In fact, with-

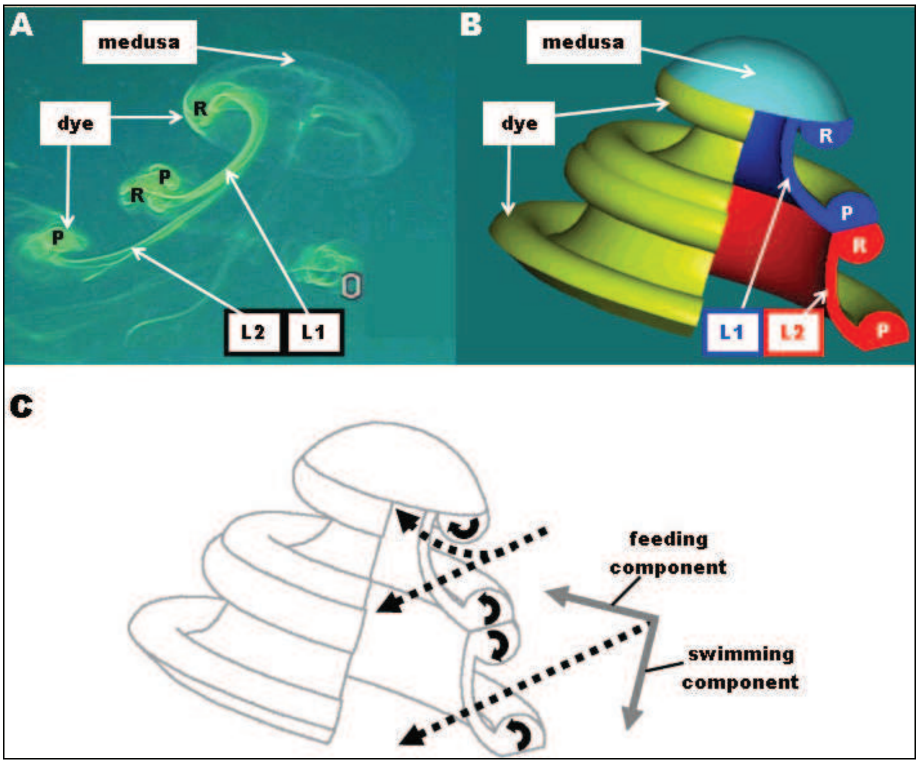

Fig. 2: (Right) Kinematics of the starting, stopping and co-joined lateral vortex structures. (A) Image of medusa vortex wake. (B) Corresponding schematic of medusa vortex wake: P – power stroke starting vortex ring; R – recovery stroke stopping vortex ring; L1/L2 – adjacent lateral vortex superstructures; (C) Flow paths in vortex wake. Solid arrows indicate directions of vortex rotation; broken arrows, flow induced by vortex rotation (from Dabiri *et al.*, ***2005).***

Sl. 2: (desno) Kinematika začetnega, končnega in veznega bočnega vrtinca. (A) Slika vrtinčne sledi meduze. (B) Shematični prikaz vrtinčne sledi meduze: P – potisk, ki sproži vrtinec; R – povratni gib, ki zaustavi vrtinec; L1/L2 – struktura veznega bočnega vrtinca. (C) Pretok v vrtinčni sledi. Polne puščice prikazujejo smer rotacije vrtinca; prekinjene puščice pa tok, ki ga povzroča rotacija (po Dabiri *et al.*, ***2005).***

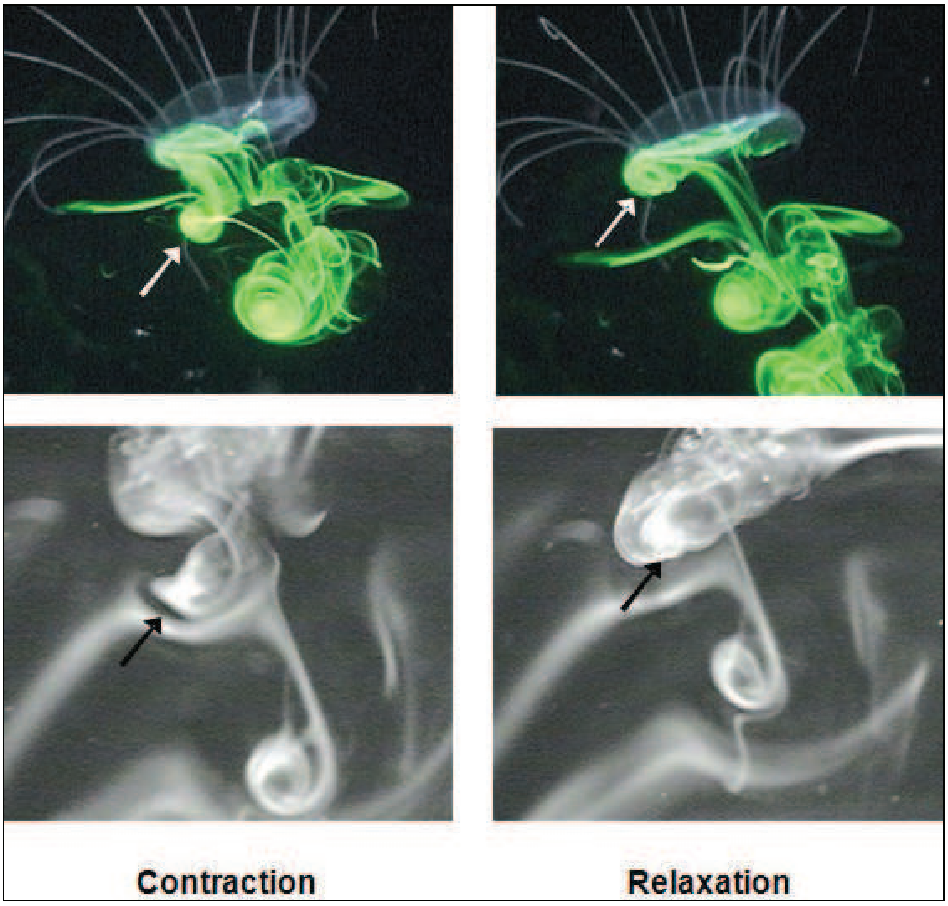

Fig. 3:** Solmissus albescens **and** Nausithoë punctata. **Flow generated by (A, B)** S. albescens **and (C, D)** N. punctata* ***during contraction (left-hand photos) and relaxation (right-hand photos) phases of the swimming cycle. Arrows point to the starting vortices in left-hand and to stopping vortices in right-hand photos (from Colin** *et al.*, **2006).

Sl. 3:** Solmissus albescens **in** Nausithoë punctata. **Tok, ki ga povzročata (A, B)** S. albescens **in (C, D)** N. punctata* ***med fazo krčenja (fotografije levo) in sproščanja (fotografije desno) znotraj plavalnega cikla. Puščice kažejo na začetne vrtince na fotografijah levo in končne vrtince na fotografijah desno (po Colin** *et al.*, **2006).

out an adequate mechanical model, some investigators entirely rejected alternatives to classical jet propulsion by medusae (*e.g.* McHenry & Jed, 2003).

The resident population of *Aurelia aurita* sp. 5 (Dawson & Jacobs, 2001) in the marine lake of Mljet Island (Big Lake, Southern Adriatic) provided the stage for a series of *in situ* flow visualization experiments that finally resolved the relationship between flow and feeding interactions for oblate rowing medusae. Aided by high water clarity and ideal SCUBA diving conditions, divers were able to precisely locate visible dyes within flows generated by medusae (Fig. 1). These methods avoided laboratory wall artifacts generated within aquariums and provided a broad mechanistic model for starting-stopping vortex interactions (Fig. 2) that we now know underlie the high propulsive efficiency and food gathering capabilities of oblate scyphomedusae (Dabiri *et al.*, 2005). Further, the hydrodynamic patterns found for *A. aurita* were demonstrated to be a useful model for species that were oblate rowers but maintained tentacles orientation towards the aboral surface (termed upstream rowers, Fig. 3).

These descriptions therefore expanded the picture of medusan propulsive and feeding interactions (Costello *et al.*, 2008) that existed before Project Meduza. This mechanical understanding served as a basis for further ecological work demonstrating unexpected links between *A. aurita*, zooplankton and the microbial communities at Mljet (Turk *et al.*, 2008) because it explained prey ingestion in terms of water processing rather than solely nematocyst activation. Both processes are necessary components of medusan predation; neither alone is sufficient to explain observed patterns.

PREDATION

Although some medusae harbor zooxanthellae as part of a mutualistic symbiosis (*e.g.* the genera *Cassiopea* and *Linuche*), medusae more typically prey upon other metazoans. However, oligotrophic open sea systems can present nutritional challenges for medusae because metazoan prey are often scarce. Yet, surprisingly, a number of small hydrozoan species successfully persist in these environments (Gili *et al.*, 1987; Benović *et al.*, 2005; Lučić *et al.*, 2009) (Fig 4). By examining the gut contents of the trachymedusa *Aglaura hemistoma*, we found that these small medusae consume a variety of protists in addition to metazoans (Fig. 5). The protistan prey are invisible in preserved specimens because most of them disintegrate in fixatives such as formaldehyde. *A. hemistoma* is cosmopolitan and found in oligotrophic surface waters in several oceans and its vertical distribution patterns in the southern Adriatic Sea probably reflect its feeding ecology throughout oceanic surface waters. In those clear waters, the ability to utilize a wide range of prey appears to have been advantageous.

Subsequently, research with other small hydromedusae has shown this type of omnivory to be relatively rare because the prey handling component of the feeding process limits consumption rates (Regula *et al.*, 2009). However, *A. hemistoma* compensates for this potential disadvantage with extremely rapid prey handling capabilities (Colin *et al.*, 2005). Other coastal hydromedusae do not appear to be similarly capable. An important consequence of research with *A. hemistoma* was an increased awareness of the possibility of medusan omnivory and an expansion of the range of alternatives considered for hydromedusan feeding.

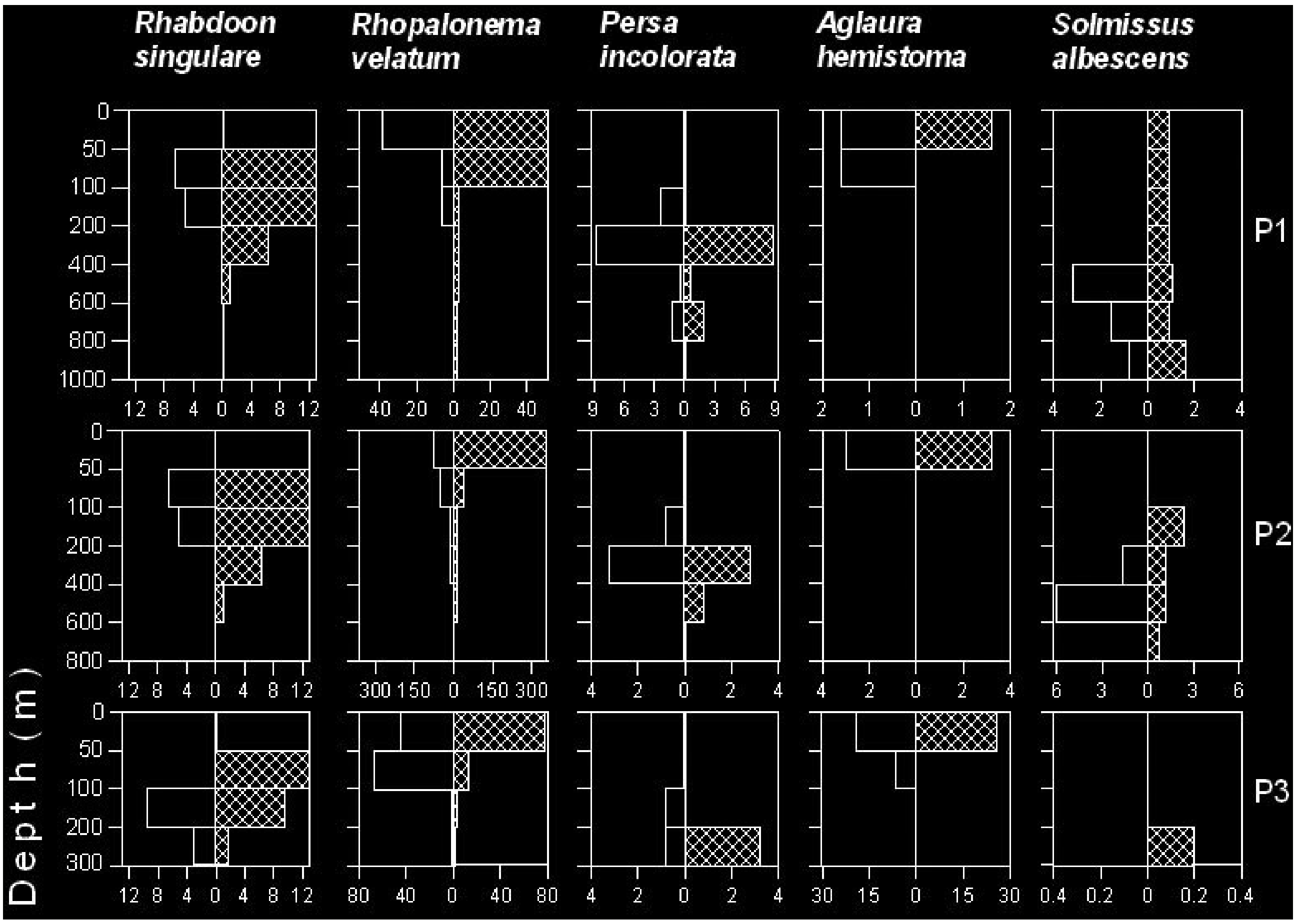

Fig. 4: Day–night vertical distribution of dominant medusae species (number of individuals 10 m^{-3}) in the middle and south Adriatic. Open bars, day samples; hatched bars, night samples (from Benović* et al., *2005).
Sl. 4: Dnevno-nočna vertikalna razporeditev dominantne vrste meduz (število osebkov 10 m^{-3}) v srednjem in južnem Atlantiku. Beli stolpci, dnevni vzorci; vzorčasti stolpci, nočni vzorci (po Benović* et al., *2005).

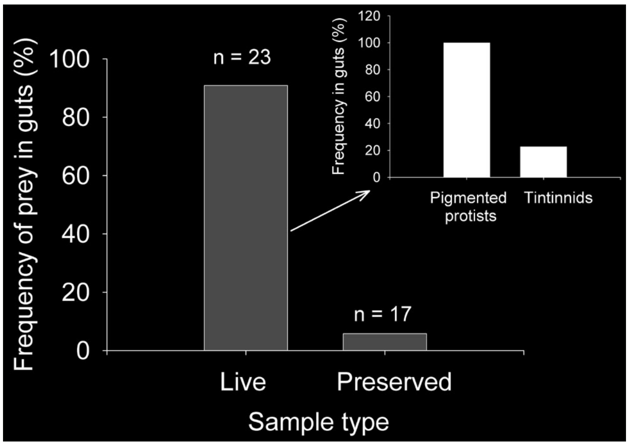

Fig. 5: Gut contents of the trachymedusa** Aglaura hemistoma. **(A) Frequency of gut contents in live and preserved (5% formaldehyde solution)** A. hemistoma **from the same date and site in the Adriatic Sea. (B) Frequency of guts of live** A. hemistoma **examined within 0.5 h of collection containing particular prey types (from Colin** et al., **2005).
Sl. 5: Vsebnost črevesa trahimeduze** Aglaura hemistoma. **(A) Frekvenca pojavljanja plena v črevesih živih in konzerviranih (5% raztopina formaldehida)** A. hemistoma, **ulovljenih istega dne in z istega mesta v Jadranskem morju. (B) Frekvenca pojavljanja posameznih skupin plena v črevesih živih trahimeduz** A. hemistoma, **pregledanih v roku pol ure od ulova (po Colin** et al., **2005).

TROPHIC ROLES

Perception of the trophic roles played by medusae has been dominated by their predatory impacts, generally on metazoan prey. But is it really that simple? Project Meduza broadened this conversation about one of the most studied medusae, *Aurelia aurita*.sp. 5. In the big lake of Mljet, *A. aurita* does not impact just the mesozooplankton it consumes, but also the microzooplankton, and ultimately, the microbial community influenced by *A. aurita*'s prey (Fig. 6). Hence, the predatory impact of *A. aurita* cascades downward through the planktonic community. But is their impact only top-down? Do they interact with higher levels of the community such as fish? One advantage of an enclosed system such as the big lake of Mljet is that members of the community are not advected throughout coastal or oceanic areas too large to sample comprehensively.

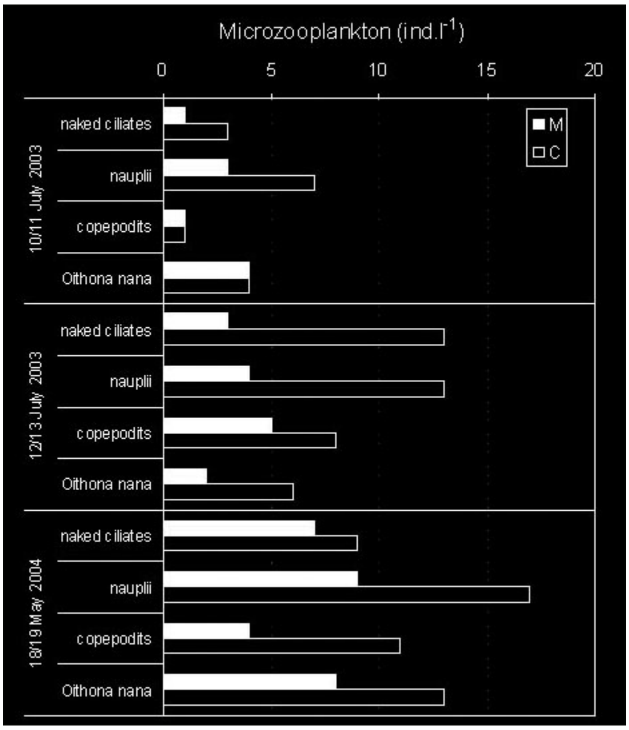

Fig. 6: Abundance of dominant microzooplankton taxa in enclosures with the presence (M – dark shaded bars) and absence (C – clear bars) of** Aurelia aurita **at the end of in situ incubation in July 2003 and May 2004 (from Turk** et al., **2008).
Sl. 6: Številčnost dominantnih mikrozooplanktonskih vrst s prisotnostjo (M – temni stolpci) in odsotnostjo (C – svetli stolpci)** Aurelia aurita **na koncu in situ inkubacije julija 2003 in maja 2004 (po Turk** et al., **2008).

The high temporal and spatial resolution of acoustical methods has allowed documentation of the rhythmic diurnal vertical migrations of both fish and scyphomedusae in an enclosed lake environment (Fig. 7). The precise nature of what drives these vertical migration patterns now needs resolution. However, the observation of these variations is the beginning of understanding the interplay between members of the lake community. Direct observation of fish-size bite marks in *A. aurita*'s exumbrellar surfaces (Graham *et al.*, 2009) suggest that fish predation may drive the downward nocturnal migration of *A. aurita* in the lake. If so, then *A. aurita*'s role as prey may become as interesting as that of predator. In this, as with the other major areas discussed here, the role of Project Meduza has served to broaden the understanding of medusae in planktonic systems.

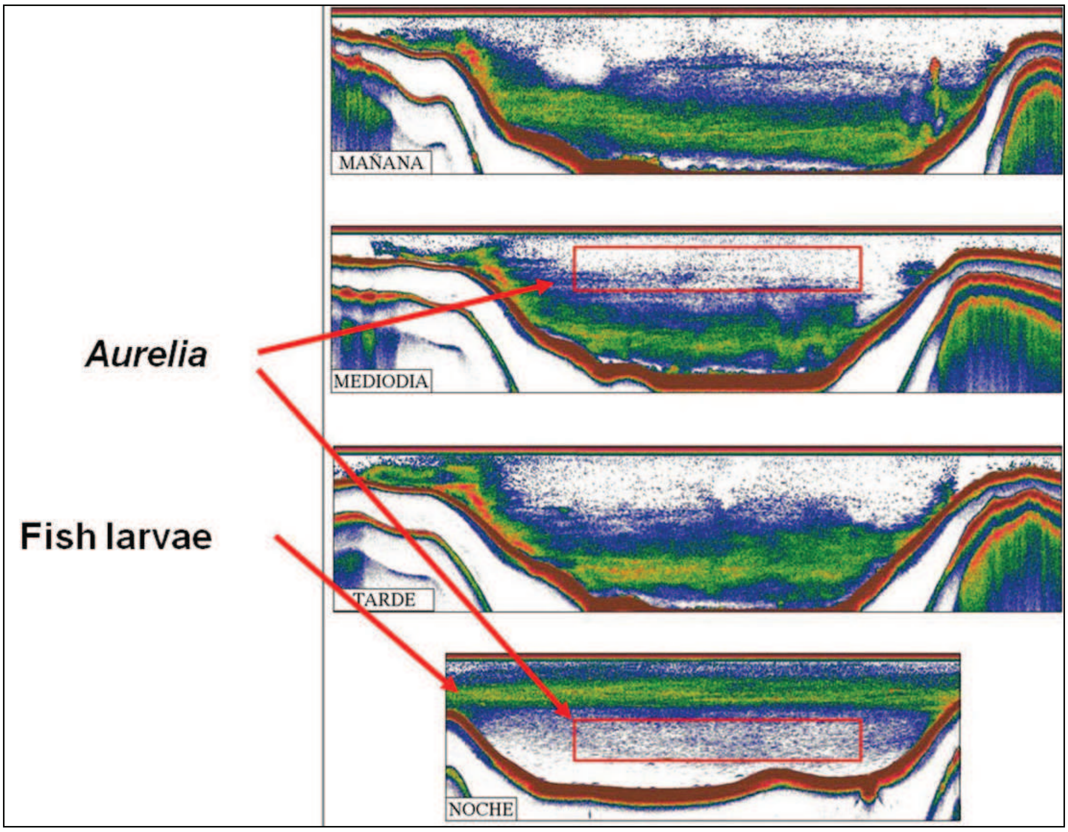

Fig. 7: Acoustic record of inverse depth relationships between fish larvae and the medusa *Aurelia aurita* ***in the big lake, Mljet Island, Croatia (Mianzan*** *et al.*, ***unpubl. data).***
Sl. 7: Akustični posnetek obratnega globinskega sorazmerja med ribjimi ličinkami in meduzo *Aurelia aurita* ***v velikem jezeru, otok Mljet, Hrvaška (Mianzan*** *et al.*, ***neobjavljeno).***

SUMMARY

The results described here and in the following reports from other Meduza participants demonstrate that scientific discovery is a powerful means of building international community.

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PROJEKT MEDUZA V KONTEKSTU ZGODOVINSKEGA RAZVOJA

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POVZETEK

Leta 2001 je Nacionalna znanstvena fundacija (National Science Foundation) iz ZDA v povezavi s hrvaškim in slovenskim ministrstvom za znanost podprla mednarodno sodelovanje, ki se je razvilo v Projekt Meduza. Vključeni raziskovalci, ki so se na pobudo z veseljem odzvali, so imeli preprost osnovni cilj – s skupnim delom razviti znanstveno raziskovanje meduz v vodah južnega Jadranskega morja. V naslednjih osmih letih je bilo izvedenih šest skupnih poletnih raziskovalnih ekskurzij. Čeprav je bilo to mednarodno sodelovanje tako na osebni kot tudi profesionalni ravni za vse raziskovalce ter vključene inštitucije zelo pomembno, se vendarle moramo vprašati, kaj je prineslo v znanstvenem smislu. Odgovora na to vprašanje so se avtorji lotili s primerjavo začrtanih ciljev na samem začetku dela ter tem, kako po izvedenem projektu vidijo raziskovanje želatinoznega zooplanktona. Na njihova stališča je seveda vplivalo tudi delo izven projekta, a v pričujočem članku predstavljajo raziskave v okviru projekta, ki so bistveno razširile njihove poglede na tri glavna raziskovalna področja: načini premikanja, plenjenje in prehrambeni pomen meduz.

Ključne besede: projekt Meduza, gibanje, porazdelitev, hidrodinamika, prehranjevanje, prehrambene vloge

REFERENCES

Arai, M. N. (1997): A functional biology of Scyphozoa. Chapman & Hall, London, 316 p.

Benović, A., D. Lučić, V. Onofri, M. Batistić & J. Njire (2005): Bathymetric distribution of medusae in the open waters of the Middle and South Adriatic Sea during spring 2002. J. Plankton Res., 27, 79–89.

Brusca, R. & G. Brusca (2003): Invertebrates, 2nd ed. Sinauer, Sunderland, MA, 936 p.

Colin, S. P. & J. H. Costello (2002): Morphology, swimming performance and propulsive mode of six co-occurring hydromedusae. J. Exp. Biol., 203, 427–437.

Colin, S. P., J. H. Costello, W. M. Graham & J. Higgins (2005): Omnivory by the small cosmopolitan hydromedusa *Aglaura hemistoma*. Limnol. Oceanogr., 50, 1264–1268.

Colin, S. P., J. H. Costello & H. Kordula (2006): Upstream foraging by medusae. Mar. Ecol. Prog. Ser., 327, 143–155.

Costello, J. H. & S. P. Colin (1994): Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. Mar. Biol., 121, 327–334.

Costello, J. H. & S. P. Colin (1995): Flow and feeding by swimming scyphomedusae. Mar. Biol., 124, 399–406.

Costello, J. H., S. P. Colin & J. O. Dabiri (2008): Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences Invert. Biol., 127, 265–290.

Dabiri, J. O., S. P. Colin, J. H. Costello & M. Gharib (2005): Flow patterns generated by oblate medusan jellyfish: field measurements and laboratory analyses. J. Exp. Biol., 208, 1257–1265.

Dawson, M. N. & D. K. Jacobs (2001): Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biol. Bull., 200, 92–96.

Gili, J. M., F. Pagés & F. Vives (1987): Distribution and ecology of a population of planktonic cnidarians in the Western Mediterranean. In: Bouillon, J., F. Boero, F. Cicogna & P. F. S. Cornelius (eds.): Modern trends in the systematics, ecology and evolution of hydroids and hydromedusae. Oxford University Press, Oxford, pp. 157–170.

Graham, W. M., L. Chiaverano, I. D'Ambra, H. Mianzan, G. Alvarez Colombo, M. Acha, A. Malej, J. H. Costello, V. Onofri & A. Benović (2009): Fish and jellyfish: Using the isolated marine 'lakes' of Mljet Island, Croatia, to explore larger marine ecosystem complexities and ecosystem-based management approaches. Annales, Ser. Hist. Nat. *(This volume)*

Lučić, D., A. Benović, M. Morović, M. Batistić & I. Onofri (2009): Diel vertical migration of medusae in the open Southern Adriatic Sea over a short time period (July 2003). Mar. Ecol., 30, 16–32.

Madin, L. P. (1988): Feeding behavior of tentaculate predators: in situ observations and a conceptual model. Bull. Mar. Sci., 43, 413–429.

McHenry, M. J. & J. Jed (2003): The ontogenetic scaling of hydrodynamics and swimming performance in jellyfish *(Aurelia aurita)*. J. Exp. Biol., 206, 4125–4137.

Mills, C. E. (1981): Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. Mar. Biol., 64, 185–189.

Pechenick, J. A. (2005): Biology of the Invertebrates, 5th ed. McGraw Hill, New York, 590 p.

Purcell, J. E. & C. E. Mills (1988): The correlation of nematocyst types to diets in pelagic Hydrozoa. In: Hessinger, D. A. & H. M. Lenhoff (eds.): The biology of nematocysts. Academic Press, San Diego, pp. 463–485.

Regula, C., S. P. Colin, J. H. Costello & H. Kordula (2009): Mechanisms of prey selection in ambushing hydromedusae. Mar. Ecol. Prog. Ser., 374, 135–144.

Turk, V., D. Lučić, V. Flander-Putrle, & A. Malej (2008): Feeding of *Aurelia* sp (Scyphozoa) and links to the microbial food web. Mar. Ecol., 29, 495–505.

Vogel, S. (1994): Life in moving fluids. Princeton University Press, Princeton NJ, 467 p.