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# In Situ Manipulation of Vertically Migrating Gelatinous Zooplankton Using Nighttime Blue-Water Scuba in the South-Central Adriatic Sea

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# *IN SITU* MANIPULATION OF VERTICALLY MIGRATING GELATINOUS ZOOPLANKTON USING NIGHTTIME BLUE-WATER SCUBA IN THE SOUTH-CENTRAL ADRIATIC SEA

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## *ABSTRACT*

*Technological advances in undersea exploration* (e.g.*, tethered cameras, remotely operated vehicles [ROVs], Autonomous Underwater Vehicles [AUVs] and manned submersibles) have opened new windows into diversity and distribution of fragile gelatinous organisms in the vast mesopelagic realm (~300 m – 1,000 m deep). While extraordinary in expanding our view of its richness, mesopelagic exploration remains largely a 'look but don't touch' environment and this limits our ability to understand these animals through physical manipulation relevant to the finer scales of the individual organism. We have been conducting a series of in situ observations and manipulations using blue-water SCUBA during the night at a 1,200 m station centrally located in the southern Adriatic Sea. We report here on a suite of vertically migrating gelatinous animals, including the narcomedusa* Solmissus albescens *and the physonect siphonophores* Forskalia formosa *and* Agalma elegans*, whose ranges extend to the mesopelagic realm during the day, but reach SCUBA diving depths during the night. Our in situ approach combined with proximity to shore exploits the natural vertical migratory behavior of some mesopelagic species, and we therefore add to the widening spectrum of methods needed to evaluate these ecologically important yet difficult to study organisms.*

**Key words:** vertical migration, *in situ*, behavior, hydrodynamics, Adriatic Sea, night-time SCUBA

# UTILIZZO DI IMMERSIONI NOTTURNE IN ACQUE APERTE IN ADRIATICO MERIDIONALE PER ESPERIMENTI *IN SITU* CON ZOOPLANCTON GELATINOSO MIGRANTE VERTICALMENTE

*SINTESI*

*Progressi tecnologici nelle esplorazioni subacquee (quali videocamere collegate ai PC, veicoli guidati a distanza [ROVs], veicoli subaquei autonomi [AUVs] e sommergibili con equipaggio) hanno aperto nuove finestre nella diversità e nella distribuzione dei fragili organismi gelatinosi nel vasto regno mesopelagico (~300 m – 1.000 m di profondità). La ricerca ha portato a straordinarie scoperte inerenti la ricchezza del regno mesopelagico, ma l'esplorazione è rimasta ai livelli di "guardare ma non toccare", il che limita la nostra capacità di comprendere questi animali attraverso la manipolazione fisica, adattata alla sensibilità di ogni singolo organismo. Gli autori hanno condotto una serie di osservazioni e manipolazioni* in situ*, durante immersioni notturne in acque aperte, in una stazione dell'Adriatico meridionale che altrimenti raggiunge i 1200 m di profondità. L'articolo riporta le osservazioni su animali gelatinosi migranti verticalmente, quali la narcomedusa* Solmissus albescens *ed i sifonofori* Forskalia formosa *e* Agalma elegans*, che si trattengono nel regno mesopelagico durante il giorno, ma che risalgono a profondità accessibili in immersione durante la notte. L'approccio* in situ*, unito alla vicinanza della costa, hanno permesso di evidenziare la migrazione verticale naturale di alcune specie mesopelagiche. Tale metodo va quindi ad aggiungersi all'ampio spettro di metodi utilizzati per la valutazione di tali organismi ecologicamente importanti e difficili da studiare.*

**Parole chiave:** migrazione verticale, *in situ*, comportamento, idrodinamismo, mare Adriatico, immersioni notturne SCUBA

## INTRODUCTION

Gelatinous zooplankton is an important member of many marine planktonic communities, including mid- and deep-water oceanic regions. The widespread presence of this phylogenetically diverse assemblage has been documented by blue-water SCUBA techniques as well as by both manned and remotely operated vehicles (reviewed in Robison, 2004). A substantial portion of pelagic biomass maybe incorporated into the bodies of these organisms and their interactions are complex enough that they have been labeled the "jelly web" (Robison, 2004).

Although the gelatinous component of the plankton is ecologically important, much of the research on oceanic gelatinous zooplankton has been descriptive in nature due to the historically poor documentation of this group's presence in oceanic systems. Consequently, much of this work has focused on discoveries of new species, establishment of systematic and phylogenetic relationships, patterns of distribution and abundance and behavioral observations (Madin, 1988; Mills & Goy, 1988; Sørnes *et al.*, 2008). Although key aspects of their physiological ecology have been described, such as the tendency for a variety of gelatinous zooplankton to largely maintain metabolic rate with depth (Thuesen & Childress, 1994; Childress, 1995), detailed experimental manipulations with gelatinous species from below the epipelagic zone have been limited due to physical vulnerability (Dennis, 2003; Haddock, 2004; Osborn & Barber, 2004) and often unexpected physiological responses to shipboard handling (Bailey *et al.*, 1994). Consequently, deeper water species neither transport well nor survive adequately during controlled experimentation. Much more is known about more accessible epipelagic species that are also physically vulnerable but within the depth range of SCUBA (Dabiri *et al.*; 2005; Rakow & Graham, 2006). This presents a dilemma for research on mesopelagic and bathypelagic species – these are obviously ecologically important species but we are unable to study them as we do other oceanic animals due to their inaccessibility. Here we provide a summary of three years' work in what we consider a rare circumstance where predictable nocturnal migrations of largely mesopelagic gelatinous organisms occur at SCUBA depths (upper 25 m) in the south-central Adriatic Sea.

## METHODS

The sampling location where we routinely encountered mesopelagic organisms at the surface at night was at the 1200 m deep station in oligotrophic waters of the south-central Adriatic Sea (42°11′ N, 17°42′ E) (Fig. 1), regularly visited by the 30 m Croatian oceanographic research vessel 'Naše more'. Only eight scuba dives were made during May–June in 2002, 2003 and 2005, specifically for the collection of video footage of mesopelagic animals; ship –time at night was devoted primarily to more traditional sampling techniques. All dives were timed to start just prior to maximum ascent of the vertical migrators (22:30–00:30 local time). Moon light is generally an important variable when investigating nocturnal species, but lunar phase could not be considered when scheduling cruises; details of lunar phase during our dives are provided in Table 1.

***Tab. 1: Summary of nighttime blue-water dives showing the starting time of each dive and the lunar phase on that date. Dive number is the same for figure 2.***
***Tab. 1: Seznam nočnih potopov v velikih globinah, z začetnim časom vsakega potopa in lunino fazo na tisti dan. Številke potopov ustrezajo tistim na sliki 2.***

| Dive No. | Date | Time (Local) | Lunar phase |
|---|---|---|---|
| 1 | 2 Jun 2002 | 22:30 | 1/4 (waning) |
| 2 | 4 Jun 2002 | 22:30 | 1/5 (waning) |
| 3 | 23 Jul 2003 | 23:30 | 1/5 (waning) |
| 4 | 24 Jul 2003 | 00:10 | 1/6 (waning) |
| 5 | 27 Jul 2003 | 00:20 | 1/10 (waning) |
| 6 | 28 Jul 2003 | 00:10 | New Moon |
| 7 | 25 May 2005 | 23:20 | 7/8 (waning) |
| 8 | 26 May 2005 | 23:00 | 7/8 (waning) |

### Night-time blue-water SCUBA and video collection

A variety of designs and gear exist for the use of specialized blue-water SCUBA (Hamner *et al.*, 1975; Heine, 1986; Haddock & Heine, 2005). These designs were all created with the intention of daylight operations when diver visibility was of primary concern. However, when blue-water SCUBA is used at night, there is a unique set of challenges for the divers (Haddock & Heine, 2005). Specifically, our dives were intended to maximize duration and clear video coverage, and so we used high intensity video lights on each dive. This necessarily entailed loss of darkened conditions favored by many species. In order to minimize the effect of our bright lights, individual divers (or diver pairs during manipulation studies) remained separated at the fully extended tether distance of 10 m. Additionally, working divers attempted to stay on opposite sides of the main down-line to avoid tether cross-over and re-sampling of organisms. Because working at full-tether distance from the safety diver poses additional risks of inadvertent sinking below maximum intended operating depth, we set the central trapeze at no deeper than 15 m on the main down-line. Due to remoteness of the fieldwork and narrow temporal window of vertical migrations, only one dive was conducted each night.

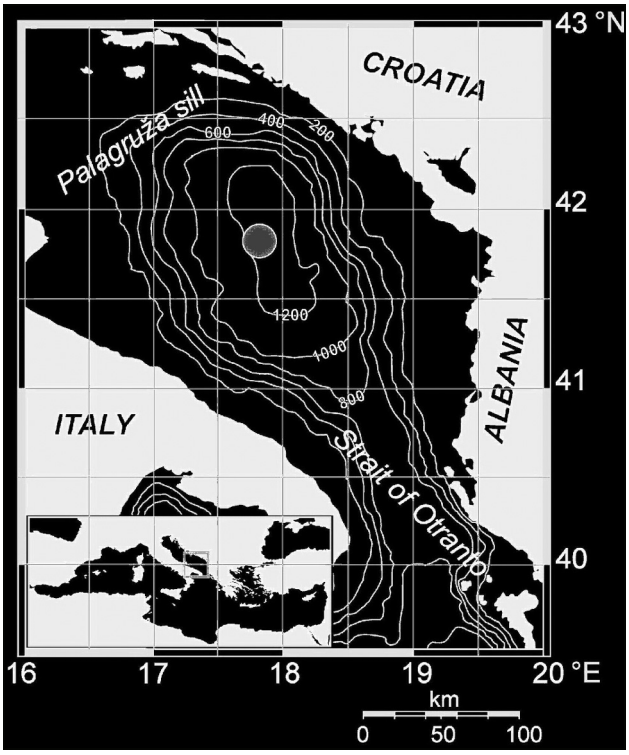


***Fig. 1: Map of the study site showing the 1,200 m station in the south-central Adriatic Sea.***
***Sl. 1: Karta obravnavanega območja z označeno postajo na 1200 m globine v južnem delu srednjega Jadranskega morja.***

During the eight dives, individual working divers used a digital video camera (Sony DCX-950, NTSC miniDV format) in a waterproof housing (Light and Motion, Inc.). Two high-intensity lights (Sun Ray HID, Light and Motion, Inc.) were turned on only while filming. Video lights were turned off to re-acclimate light sensitive animals around the divers if it was felt that lights were either attracting or distracting too many animals. We specifically targeted soft-bodied and gelatinous animals, though crustaceans and fish were common on each dive (Tab. 2). The durations of individual video sequences were limited by the length of time a tethered diver could remain with the target, and video sequences typically ranged from only a few seconds to about one minute.

All footage was reviewed in the laboratory. Individual sequences showing clearly identifiable morphologies and behaviors were isolated and archived in a video library at the Dauphin Island Sea Lab. When necessary, identification was aided by consulting taxonomic experts (as in the case of the physonect siphonophores).

***Tab. 2: List of gelatinous zooplankton taxa observed and overall contribution by frequency of individual observation. Taxon number is for reference with figure 2. Identifications were made to species level unless otherwise indicated as 'unknown'.***
***Tab. 2: Seznam obravnavanih vrst želatinoznega planktona in splošni prispevek s frekvenco posameznih opažanj. Zaporedne številke vrste ustrezajo tistim na sliki 2. Identifikacije so bile narejene na ravni vrste, sicer je uporabljena oznaka 'neznano'.***

| Taxon # | Name | Contribution (%) |
|---|---|---|
| 1 | *Solmissus albescens* | 39.9 |
| 2 | *Geryonia proboscidalis* | 3.5 |
| 3 | *Pelagia noctiluca* | k1.6 |
| 4 | *Aurelia* sp. | 0.4 |
| 5 | *Amphinema* sp. | 0.6 |
| 6 | Hydromedusa (unknown, small) | 1.4 |
| 7 | *Nanomia bijuga* | 4.5 |
| 8 | *Agalma elegans* | 3.8 |
| 9 | *Forskalia formosa* | 6.6 |
| 10 | *Athorybia rosacea* | 0.4 |
| 11 | *Hippopodius hippopus* | 1.0 |
| 12 | Dyphiid siphonophore (unknown) | 7.6 |
| 13 | *Salpa maxima* (solitary) | 5.8 |
| 14 | *Salpa maxima* (chain) | 8.2 |
| 15 | Salp (unknown) | 0.7 |
| 16 | *Pyrosoma atlanticum* | 1.4 |
| 17 | Doliolid (unknown) | 3.1 |
| 18 | *Sagitta lyra* | 4.5 |
| 19 | *Phylloroe* sp. | 2.5 |
| 20 | Gymnosome pteropod | 0.7 |
| 21 | Pseudothecosome pteropod | 0.6 |
| 22 | Pteropod (unknown thecate) | 0.7 |
| 23 | Tomopterid polychaet (unknown) | 0.7 |

## RESULTS AND DISCUSSION

Although we only made eight night dives at this location, we nonetheless documented 23 recognizable taxonomic taxa from video (Tab. 2). Eleven of these were identifiable to species and at least one identifiable to genus. Diversity within the planktonic community was dominated by cnidarians (medusae and siphonophores = 71.2% of all observations) and pelagic tunicates (salps, doliolids and pyrosomes = 19.1% of all observations) (Tab. 2). Among the cnidarians, frequency of observation was dominated by the vertically migratory hydromedusa *Solmissus albescens* (40% of all observations). In fact *S. albescens* was highly predictable at this location as it occurred on 7 of the 8 dives (Fig. 2). Mills *et al.* (1996) accumulated a species list consisting of 35 taxa during 26 ROV dives in the northwestern Mediter-

***Tab. 3: Most frequently observed gelatinous zooplankton species and their reported depth distributions. Species that have a reported mesopelagic distribution are indicated with an (*). Note that approximately 2/3 of the species commonly found in surface waters at night have previously been characterized as possessing mesopelagic distributions.***
***Tab. 3: Najpogosteje opažene vrste želatinoznega planktona in njihova globinska distribucija. Vrste z zabeleženo mezopelaško distribucijo so označene z (*). Približno 2/3 vrst, ki jih ponoči ponavadi najdemo v površinskih vodah, je bilo predhodno uvrščenih pod vrste z mezopelaško distribucijo.***

| Taxa list | Reported vertical distribution | Location | Reference |
|---|---|---|---|
| *Solmissus albescens** | 560–25 m | NW Med | Laval *et al.*, 1989; Andersen *et al.*, 1992 |
| | 1,000-surface | S Adriatic | Batistić *et al.*, 2004; Benović *et al.*, 2005 |
| *Salpa maxima** | surface | SW Atlantic | Sigl, 1912; Amaral *et al.*, 1997 |
| | >300m-surface | W Med | Franqueville, 1971 (and refs therein) |
| *Forskalia formosa** | ~600 m | W Med | Mills *et al.*, 1996 |
| *Sagitta lyra** | >600 m-surface | S Adriatic | Batistić *et al.*, 2004 |
| *Nanomia bijuga** | surface | W Med | Mills *et al.*, 1996 |
| | 10–800 m | E Pacific | Robison *et al.*, 1998 |
| *Geryonia proboscidalis* | surface | S Adriatic | Benović *et al.*, 2005 |
| *Agalma elegans** | 600–300 m | W Med | Mills *et al.*, 1996; Franqueville, 1970, 1971 |
| *Pyrosoma atlanticum** | 700–75 m | NW Med | Andersen *et al.*, 1992 |
| *Hippopodius hippopus** | >100 m-surface | S Adriatic, Med | Mills *et al.*, 1996; Batistić *et al.*, 2004 |
| | 400 m | W Med | Franqueville, 1970, 1971 |
| *Pelagia noctiluca** | surface | W Med | Mills *et al.*, 1996 |
| | 1,400 m-surface | W Med | Franqueville, 1970, 1971 |

ranean Sea. However, the difference between our observation list and theirs is likely due to greater observation durations using ROV technology.

Ten species of gelatinous zooplankton accounted for more than 80% of all observations (Tab. 3). Nine of these species are documented as having a mesopelagic distribution. Therefore we consider their presence in the upper 25 m during our dives as a consequence of a nocturnal vertical migration as no large gelatinous plankton was observed during any preliminary daytime SCUBA dives during the first year of the study at the very same location.

Previous studies demonstrated that a diverse community of both crustacean and gelatinous zooplankton commonly occur at this particular location (Benović *et al.*, 2005; Lučić *et al.,* 2005). Yet, their presence at the very near surface remains an enigma due to low production rates and plankton standing stocks in the south-central Adriatic. Our taxonomic information along with that of Benović *et al.* (2005) and Lučić *et al.* (2005) suggests seasonal shifts in the migrating community from the spring siphonophore-rich community to the summer salp-rich community. The narcomedusa *S. albescens* was consistently common through both seasons. *S. albescens* appears to be an important predator on both siphonophores and salps as we routinely observed *S. albescens* returning to depth with guts filled with both prey types. Similar interactions between mesopelagic dwellers have been characterized as a 'jelly web' where predator-prey interactions within the gelatinous zooplankton community partitions material flow away from

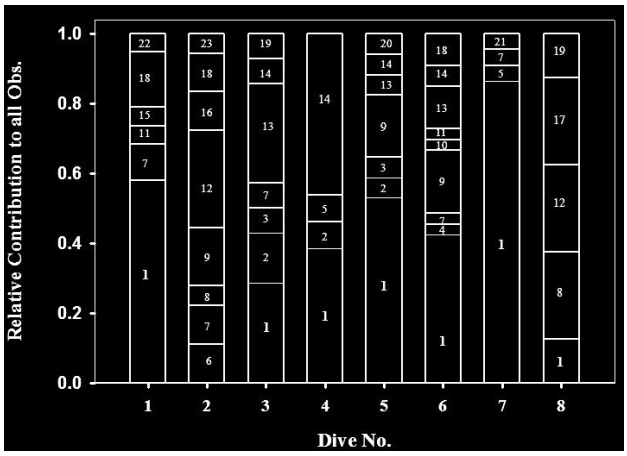


***Fig. 2: Frequency of taxa observations during eight night-time blue-water dives. Dive number is the same as in Table 1. Numbers within each stacked plot indicate taxa as referenced in Table 2.***
***Sl. 2: Frekvenca opazovanj tekom osmih nočnih potopov v velikih globinah. Številka potopa je ista kot v Tabeli 1. Številke znotraj vsakega dela stolpca ustrezajo vrsti, navedeni v Tabeli 2.***

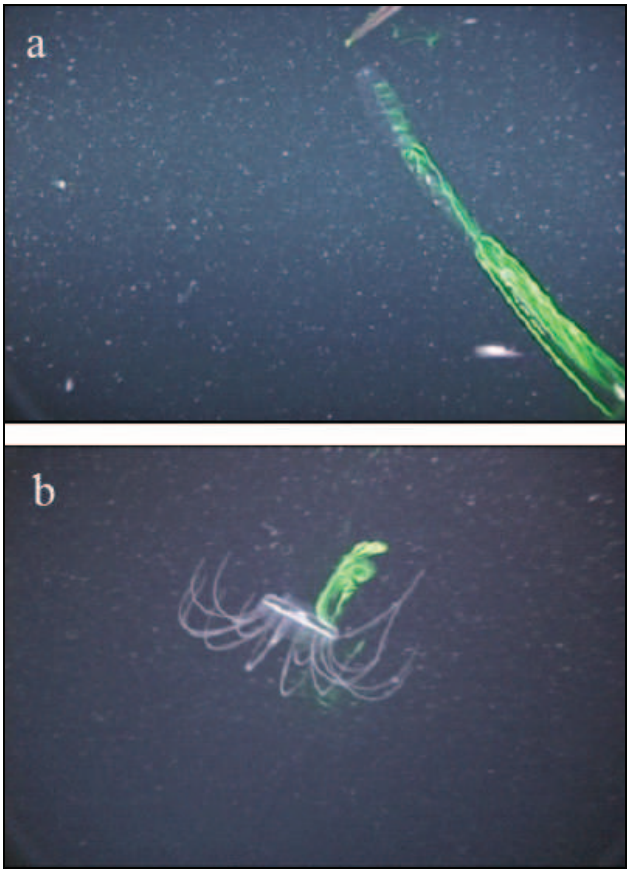


***Fig. 3: Two examples of nighttime bluewater SCUBA manipulations of mesopelagic gelatinous zooplankton, (a)*** *Agalma elegans* ***and (b)*** *Solmissus albescens.* ***Wakes and vortices are visible via manual dye injection at the upstream swimming path (the diver's pipet tip is visible in the top panel).***
***Sl. 3: Dva primera obravnave mezopelagičnega želatinoznega planktona, (a)*** *Agalma elegans* ***in (b)*** *Solmissus albescens,* ***tekom nočnih potopov v velikih globinah. Turbulence in vrtinci so vidni zaradi brizga barve v zgornji del plavalne poti (vrh potapljačeve pipete je viden na zgornji sliki).***

non-gelatinous organisms (Robison, 2004). In the present work, we documented these same mesopelagic predator-prey interactions in the south-central Adriatic Sea at depths approachable by SCUBA divers. The site is particularly valuable because the high-amplitude of the vertically migrating community is rare, if not unique, in its proximity to the shore.

**A natural laboratory for manipulative investigations**

Nocturnal vertical migration of otherwise mesopelagic species provided us with an opportunity to engage in direct manipulation of mesopelagic animals via SCUBA. Owing to the tactile and perceptional abilities of trained blue-water SCUBA divers, these types of manipulations are difficult or impossible with other 'remote' technologies such as cameras, ROVs, AUVs and submersibles. Previous studies of the swimming behavior of epipelagic medusae have demonstrated that divers can control and make detailed examination of swimming wakes to better understand unusual propulsive mechanisms (*e.g.* Dabiri *et al.*, 2005). Similarly, SCUBA access to mesopelagic species has allowed us to manipulate conditions that permit visualization and analysis of the wakes of mesopelagic species such as *Solmissus albescens* (Colin *et al.*, 2006; Fig. 3a). Furthermore, current efforts are underway with a variety of siphonophores, medusae and salps (the authors, *unpubl. data*; see Fig. 3) using these *in situ* methods and other manipulations adapted from laboratory hydrodynamic studies (*e.g.* Katija & Dabiri, 2008). The combination of new quantitative *in situ* approaches and access to mesopelagic species provides us the opportunity to examine the functional ecology of these gelatinous species at levels of quantification and direct manipulation that have not been previously possible. Consequently, this approach provides another tool among a growing list (Haddock, 2004; Robison, 2004) that enables researchers to evaluate these demonstrably important gelatinous animals which have been largely inaccessible for quantitative research.

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# UPORABA NOČNIH POTOPOV V ODPRTIH VODAH JUŽNEGA JADRANA ZA *IN SITU* POSKUSE Z VERTIKALNO MIGRIRAJOČIM ŽELATINOZNIM PLANKTONOM

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*POVZETEK*

*Tehnološki napredek v podvodnem raziskovanju (npr. fotoaparati in kamere z računalniško povezavo, vozila na daljinsko upravljanje (ROV), avtonomna podvodna vozila (AUV) in mini podmornice s posadko) je omogočil nov vpogled v diverziteto in razširjenost občutljivih želatinoznih organizmov v obsežnem mezopelagičnem pasu (~300-1000 m globoko). Raziskovanje mezopelagičnega območja nam je sicer izjemno razširilo pogled na bogastvo tega okolja, vendar v glavnem ostaja v okvirih opazovanja brez fizičnega dotika, kar omejuje našo zmožnost razumevanja teh živali s pomočjo fizične obravnave, ki bi ustrezala občutljivosti posameznega organizma. Opravljena je bila vrsta nočnih* in situ *opazovanj in obravnav s SCUBA potopi v globinah, in sicer na postaji z globino 1200 m v južnem Jadranskem morju. Obravnavana je bila skupina vertikalno migrirajočih želatinoznih živali, vključno z narkomeduzo* Solmissus albescens *in cevkači iz reda Physonectae* Forskalia formosa *ter* Agalma elegans*, katerih razpon sega od mezopelagičnega območja čez dan do globin, dosegljivih s SCUBA potapljanjem ponoči. Z* in situ *pristopom, kombiniranim z bližino obale, smo lahko sledili naravnemu vertikalnemu migriranju nekaterih mezopelagičnih vrst ter s tem prispevali v vedno širši spekter metod za evalvacijo teh ekološko pomembnih organizmov, ki pa jih je tako težko proučevati.*

**Ključne besede**: vertikalna migracija, *in situ*, vedenje, hidrodinamika, Jadransko morje, nočno potapljanje SCUBA

REFERENCES

**Amaral, W. J. A., M. A. Montu & I. M. Gloeden (1997):** Salpidae (Thaliacea) in the continental sheld of southern Brazil: composition, distribution and abundance (Summer, 1990). Atlantica, Rio Grande, 19, 31–50.

**Andersen, V., J. Sardou & P. Nival (1992):** The diel migrations and vertical distributions of zooplankton and micro nekton in the Northwestern Mediterranean Sea. 2. Siphonophores, hydromedusae and pyrosomids. J. Plankton Res., 14, 1155–1169.

**Bailey, T. G., J. J. Torres, M. J. Youngbluth & G. P. Owen (1994):** Effect of decompression on mesopelagic gelatinous zooplankton: a comparison of in situ and shipboard measurements of metabolism. Mar. Ecol. Prog. Ser., 113, 13–27.

**Batistić, M., F. Kršinić, N. Jasprica, M. Carić, D. Viličić & D. Lučić (2004):** Gelatinous invertebrate zooplankton of the South Adriatic: species composition and vertical distribution. J. Plankton Res., 26, 459–474.

**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.

**Childress, J. J. (1995):** Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends Ecol. Evol., 10, 30–36.

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

**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.

**Dennis, C. (2003):** Close encounters of the jelly kind. Nature, 426, 12–14

**Franqueville, C. (1970):** Etude comparative de macroplancton profond en Mediteranee nord-occidentale par plangees en soucoupe SP 350, et peches au chalut pelagique. Mar. Biol., 5, 172–179.

**Franqueville, C. (1971):** Macroplancton profond (Invertebres) de la Mediterranee nord-occidentale. Tethys, 3, 11–56.

**Haddock, S. H. D. (2004):** A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. Hydrobiologia, 530/531, 549–556.

**Haddock, S. H. D. & J. N. Heine (2005):** Scientific blue-water diving. La Jolla, California.

**Hamner, W. M., L. P. Madin, A. L. Alldredge, R. W. Gilmer & P. P. Hamner (1975):** Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behavior. Limnol. Oceanogr., 20, 907–917.

**Heine, J. N. (1986):** Blue Water Diving Guidelines. California Sea Grant College Program. NOAA, Department of Commerce, 46 p.

**Katija, K. & J. O. Dabiri (2008):** *In situ* field measurements of aquatic animal fluid interactions using a Self-Contained Underwater Velocimetry Apparatus (SCUVA). Limnol. Oceanogr. Methods, 6, 162–171.

**Laval, P., J.-C. Braconnot, C. Carré, J. Goy, P. Morand & C. E. Mills (1989):** Small-scale distribution of macroplankton and micronekton in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible *Cyana*. J. Plankton Res., 11, 665–685.

**Lučić, D., A. Benović, M. Batistić, J. Njire & V. Onofri (2005):** Calycophorae (Siphonophora) in the open waters of the central and south Adriatic Sea during spring 2002. J. Mar. Biol. Assoc. UK, 85, 495–501.

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

**Mills, C. E. & J. Goy (1988):** *In situ* observations of the behavior of mesopelagic *Solmissus* narcomedusae (Cnidaria, Hydrozoa). Bull. Mar. Sci., 43, 739–751.

**Mills, C. E., P. R. Pugh, G. R. Harbison & S. H. D. Haddock (1996):** Medusae, siphonophores and ctenophores of the Alboran Sea, south western Mediterranean. Sci. Mar., 60, 145–163.

**Osborn, T. & R. T. Barber (2004):** Why are large, delicate, gelatinous organisms so successful in the ocean's interior? In: Seuront, L. & P. Strutton (eds.): Handbook of Scaling Methods in Aquatic Ecology. CRC Press, Boca Raton, FL, pp. 329–332.

**Rakow, K. C. & W. M. Graham (2006):** Orientation and swimming mechanics by the scyphomedusae *Aurelia* sp. in shear flow. Limnol. Oceanogr., 51, 1097–1106.

**Robison, B. H. (2004):** Deep pelagic biology. J. Exp. Mar. Biol. Ecol., 300, 253–272.

**Robison, B. H., K. R. Reisenbichler, R. E. Sherlock, J. M. B. Silguero & F. P. Chavez (1998):** Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. Deep-Sea Res. II, 45, 1741–1751.

**Sigl, M. A. (1912):** Adriatische Thaliacenfauna. Akadamie der Wissenschaften in Wien, Methem-nature Klasse.

**Sørnes, T. A., A. Hosia, U. Båmstedt & D. L. Aksnes (2008):** Swimming and feeding in *Periphylla periphylla* (Scyphozoa, Coronatae). Mar. Biol., 153, 653–659.

**Thuesen, E. V. & J. C. Childress (1994):** Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. Biol. Bull., 187, 84–98.