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FISH AND JELLYFISH: USING THE ISOLATED MARINE 'LAKES' OF MLJET ISLAND, CROATIA, TO EXPLORE LARGER MARINE ECOSYSTEM COMPLEXITIES AND ECOSYSTEM-BASED MANAGEMENT APPROACHES

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ABSTRACT

The marine 'lakes' of Mljet Island, southern Croatia, provide an interesting ecological setting for investigating structure and function of marine ecosystems outside the lakes. This paper synthesizes some of the historical and on-going research projects involving the lakes, with special attention given to recent studies on the isolated lake population of the scyphozoan Aurelia sp. 5. This species appears to be geographically isolated within and evolutionarily limited to the lakes of Mljet Island. As such, we are utilizing the lakes as a tool to better understand the ecological relationship between jellyfish and a diverse community of fish species that also inhabit the lakes. We promote future studies to parameterize an ecosystem model of the lakes as a test-bed system for an ecosystem-based management approach using similar models outside the lakes.

Key words: medusae, planktivorous fishes, *Aurelia*, *Boops*, *Atherina*

PESCI E MEDUSE: UTILIZZO DEI 'LAGHI' MARINI ISOLATI DELL'ISOLA DI MLJET, CROAZIA, PER LO STUDIO DELLE COMPLESSITÀ DI UN PIÙ AMPIO ECOSISTEMA MARINO E APPROCCI PER UNA GESTIONE BASATA SUGLI ECOSISTEMI

SINTESI

I 'laghi' marini dell'isola di Mljet, Croazia meridionale, forniscono un interessante ambito ecologico per lo studio della struttura e della funzione degli ecosistemi marini esterni ai laghi. L'articolo sintetizza alcuni dei progetti di ricerca storici e attuali che coinvolgono i laghi, con una speciale attenzione rivolta a studi recenti sulle popolazioni di scifozoi Aurelia sp. 5. Tale specie risulta essere geograficamente isolata ed evolutivamente limitata ai laghi dell'isola di Mljet. I laghi vengono quindi utilizzati quali strumenti per una migliore comprensione delle relazioni ecologiche fra le meduse e diverse comunità di pesci, che pure vivono nei laghi. Gli autori incoraggiano future ricerche finalizzate a parametrizzare un modello ecosistemico dei laghi, che possa servire quale sistema sperimentale di approccio per una gestione basata sugli ecosistemi, che si avvalga pure di modelli simili esterni ai laghi.

Parole chiave: meduse, pesci planctivori, *Aurelia*, *Boops*, *Atherina*

INTRODUCTION AND BACKGROUND

Geographically isolated marine lakes and lagoons are particularly intriguing for marine scientists as they provide opportunities to understand population, community or ecosystem-level processes without compounding effects of immigration and emigration. While evolutionary biologists realize opportunities to study rates of speciation under restricted gene flow (e.g., Dawson & Hamner, 2005), community and ecosystem ecologists can investigate underlying processes that regulate population numbers and the flow of energy and nutrients within the system (Hamner *et al.*, 1982; Schneider & Behrends 1998; Malej *et al.*, 2007). Importantly, ecosystem models such as those employed to manage marine fisheries (Christensen & Walters, 2004) can be developed and refined from isolated marine lake and lagoon ecosystems. These nearly-enclosed systems act in essence as large, natural laboratories to explore fully the ecological complexities (e.g., competition and predation) of important open systems that are otherwise intractable for study.

The lakes of Mljet Island, Croatia, are particularly interesting as they contain a seemingly resident and

quasi-stable population of medusae embedded within a diverse community of nektonic, demersal and benthic organisms (Vučetić, 1961; Benović *et al.*, 2000; Peharda *et al.*, 2002). To this end, a multi-national group of marine scientists has been studying the ecology and hydrographic setting of the marine 'lakes' of northern Mljet Island, Croatia, as part of Project 'Meduza'. This paper describes this isolated marine setting, its natural history and the scientific benefit of using the Mljet lakes as model ecosystems to explore ecosystem-based management strategies beyond the lakes with special attention given to the role of jellyfish (e.g., *Aurelia* sp. 5; Dawson & Jacobs, 2001) in marine ecosystem structure and function.

GEOLOGICAL HISTORY OF MLJET ISLAND'S 'LAKES'

The geological history of the Mljet Island doline marine system is a complex result of the porous carbonate terrain, subterranean aquifers, and eustatic sea level rise over the past 10,000 years. The entirety of the Dalmatian coast is comprised of thousands of islands as a result of both tectonic lifting followed by late Pleistocene-Holocene flooding of the coastal region (Wunsam *et al.*,

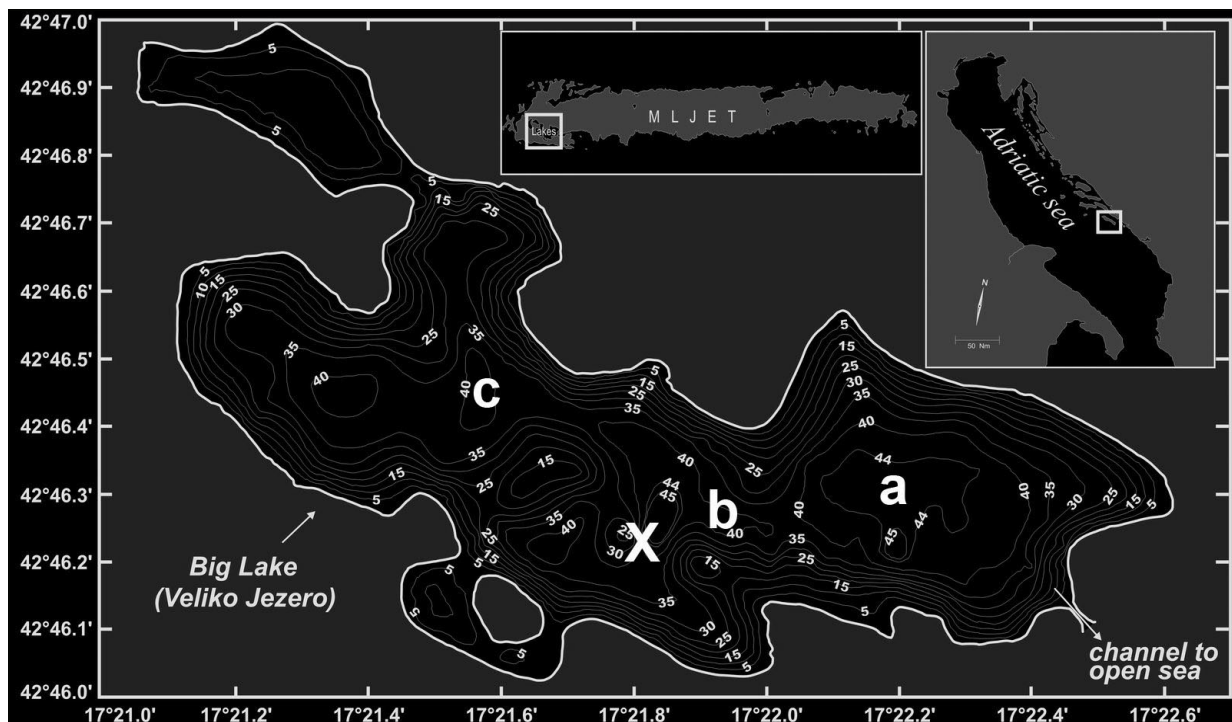


Fig. 1: Bathymetric map of Veliko Jezero on the northern end of Mljet Island, Croatia, in the southern Adriatic Sea. The two basins marked (a, b) are the location of a resident population, though medusae also make excursions into the basin labeled as (c). Location of outcroppings where polyps are located is indicated by the (x).

Sl. 1: Batimetrična karta Velikega jezera na severnem koncu otoka Mljeta, Hrvatska, južno Jadransko morje. Kotanji označeni z (a, b) sta lokaciji rezidentne populacije, čeprav se meduze pojavljajo tudi v kotanji označeni s (c). Lokacija polipov je označena z (x).

1999). Dominating the karstic landscape of the northern end of Mljet Island are several depressions. The modern expression of these depressions includes two fjord-like marine 'lakes', Malo Jezero (MJ) (Small Lake) and Veliko Jezero (VJ) (Big Lake). The term 'lake' here is a misnomer as there is connectivity of Veliko Jezero to the outer sea via the shallow and long Soline Channel (SC) (Fig. 1). It is believed that the smaller of the two lakes, Malo Jezero, with a maximum depth of ~35 m, is fed by subaquatic springs and was essentially a freshwater lake until a small channel (~ 1 m deep by 2 m wide by 29 m long) was opened in the 13th Century by resident Benedictine monks to allow small vessel passage from VJ into MJ (Wunsam *et al.*, 1999). Small daily exchange of surface water between the outer Adriatic Sea and VJ through the SC, as well as between the two lakes, is tidally driven.

Veliko Jezero is a series of three basins separated by sills (Fig. 1) that allow surface-water exchange but not deep-water exchange. The southeastern-most basin of VJ has a maximal depth of 46 m and has the most direct connection to the outer Adriatic Sea via SC through a naturally occurring passage. Exchange of water and animals including medusae between basins may occur during rare excursions into the surface layer where residual tidal or wind driven flows forces lateral advection into adjacent basins (Benović *et al.*, 2000). The historical depth of the sill into VJ was about 0.6 m, but this was increased to its current depth of ~ 2.5 m by the Yugoslav navy in the 1950s to allow deeper draft vessels into the lakes (Benović *et al.*, 2000).

RESIDENCY OF LAKE *AURELIA* SP.: RECENT INVASION OR HOLOCENE RELICT?

Using diatom assemblage and geochemical mineral analysis of cores from the Mljet lakes, Wunsam *et al.* (1999) suggested that VJ began filling with seawater via percolation about 8,400 ybp, and true seawater ingression through SC did not occur until about 5,000 ybp. Suric *et al.* (2005) dated marine encrustations on speleothems from a submarine cave north of Mljet to suggest sea level reached -3 m about 4,000 ybp. Therefore, we can reasonably place a range of at least 4,000 ybp and not greater than 5,000 ybp as the period when an open connection between VJ and the Adriatic occurred (*i.e.*, the earliest period of potential colonization by *Aurelia* sp. in the lakes).

A variety of evidence supports an emerging theory that *Aurelia* sp. 5 is a locally retained relict population from a Mediterranean cold-water phase several thousand years ago. Two key molecular studies by Dawson & Jacobs (2001) and Schroth *et al.* (2002) independently showed marked divergence from other *Aurelia* populations found in the Adriatic and Mediterranean Seas. Interestingly, Schroth *et al.* (2002) placed Mljet medusae

within a boreal clade of *Aurelia* closely related to individuals sampled from the North Atlantic, which could account for the cold-water affinity of Mljet *Aurelia*. Endemism and local adaptation of jellyfish in marine lakes is not novel and has been described previously in tropical settings like marine lakes and lagoons of Palau, western Pacific (Hamner & Haury, 1981; Hamner *et al.*, 1982; Dawson & Hamner, 2005).

Timing the establishment of *Aurelia* in the lakes is difficult, but there were two major cooling episodes in the southern Adriatic Sea during the Holocene (Sangiorgi *et al.*, 2003). Approximately 7,000 ybp, winter temperatures were decreased on average by about 2 °C, and 3,000 ybp when spring (and possibly summer) temperatures were lowered on average by about 3 °C. The former cooling predates the opening of the lakes to direct exchange, but the latter cooling period 3,000 ybp was after the opening of SC to the Adriatic Sea. We believe local retention and isolation is facilitated by medusa behavior and physiology in response to the unique local hydrography (see, Graham *et al.*, 2001 for a review) that maintains adequate thermal regime (<15 °C year-round) within the lakes (Benović *et al.*, 2000) that is reminiscent of this Holocene cold-water phase.

REGULATION OF FISH POPULATIONS IN THE MLJET LAKES

Using readily available database information (Fish-Base Project, <http://www.fishbase.org>) and historical observations by us (Onofri, *unpubl. data*), we compiled a list of 53 species and 2 genera believed to occur within the Mljet lakes (Tab. 1). This list certainly contains several transient migratory species (*e.g.*, *Sphyma mokarran* and *Scomber* spp.), but the majority tends to be either reef or seagrass (*Posidonia oceanica*) associated species. Only 5 species, *Atherina boyeri*, *Spicara maena*, *Liza aurata*, *Boops boops* and *Spondyllosoma cantharus*, are described as zooplanktivorous at the adult stage (www.fishbase.org) with the rest preying largely on zoobenthos or larger invertebrate prey with the exception of *Sarpa salpa* which is herbivorous. Of these zooplanktivores, *Atherina*, *Liza* and *Boops* have calculated trophic levels that are similar to the trophic levels calculated previously for *Aurelia* spp. elsewhere (Pauly *et al.*, 2009). This latter point is relevant to our studies because trophic overlap is a key element in discerning resource competition between jellyfish and fish.

With the exception of the transient migrants (sharks and mackerels), the lakes appear to lack higher order predatory fish populations. This is despite the apparent abundance of nocturnally schooling fish believed to be largely comprised of *Boops boops* and *Atherina boyeri* based on our own observations from video and acoustics (Alvarez Colombo *et al.*, 2009; Fig. 2). Thus, with the lack of apparent predation mortality by piscivorous

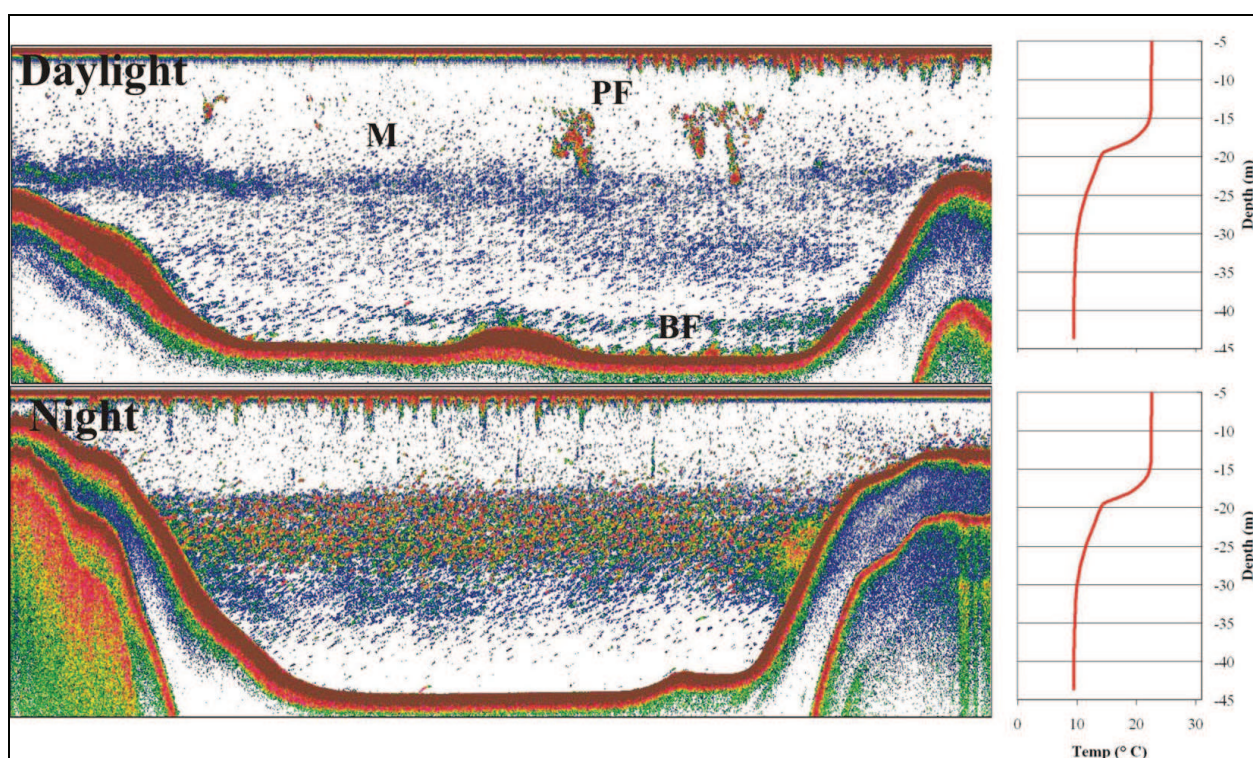


Fig. 2: Acoustic echogram of the southern-most basin in Veliko Jezero at daylight and at night. During the day, jellyfish (labeled M) exclusively occupy the sub-thermocline region, with benthic fishes (BF) below and pelagic schooling fishes (PF) above the medusa layer. At night, medusae and fish occupy the same layer in the water below the thermocline.

Sl. 2: Akustični ehogram najjužnije kotline v Velikem jezeru podnevi in ponoči. Podnevi se meduze (označene z M) nahajajo izključno pod termoklino, pod njimi se gibljejo bentoške ribe (BF), nad njimi pa pelaške ribe v jatah (PF). Ponoči se tako meduze kot ribe gibljejo v istem sloju pod termoklino.

fishes as well as a very minimal artisanal fishery in the protected lakes, we believe population regulation of fish is driven by a combination of bottom-up processes (*i.e.*, productivity) and intra- or inter-specific competition.

Very little information exists on the role of food resource competition involving fish or jellyfish (but see Purcell & Arai, 2001). We suggest inter-specific competition between fish and jellyfish is likely rare unless spatial, temporal and trophic overlap is strong. Moreover, resource partitioning within overlapping resources is likely rare as well, and the expectation is that longer-lived and slower-growing fish are competitively dominant over 'opportunistic' jellyfish unless mortality (either natural or fishing) removes enough fish to force jellyfish into a niche-occupying role. This makes the Mljet lake system particularly interesting because both jellyfish and fish, at least the likely competitors *Atherina*, *Liza*, and *Boops*, overlap in a fashion that seems to promote strong intra-specific competition (see for example Alvarez Colombo *et al.*, 2009 and our Fig. 2). Thus one of the more important continuing research areas is to collect accurate species-specific biomass and trophic information for

both jellyfish and zooplanktivorous fish to realize the extent of competitive interactions that might lead to regulation of fish and jellyfish populations.

REGULATION OF *AURELIA* SP. 5 POPULATIONS IN MLJET'S LAKES

We hypothesize that bottom-up controls are important for the regulation of jellyfish biomass whether they are driven strictly by changes in primary production, detritus delivery or through variations in competition for food resources with planktivorous fishes. We cannot ignore, however, that predation on jellyfish by fish may be an important source of top-down control of *Aurelia* sp. Interestingly, bogue (*Boops boops*) is described as a predator of jellyfish (www.fishbase.org) and we have observed directly the consumption of a tethered *Aurelia* sp. by *Boops boops* during acoustical calibrations in VJ (H. Mianzan and colleagues, *pers. comm.*). A number of examples of medusivory by fishes have been published or reviewed (*e.g.*, Mianzan *et al.*, 2001; Arai, 2005), however, it remains unclear whether such predation con-

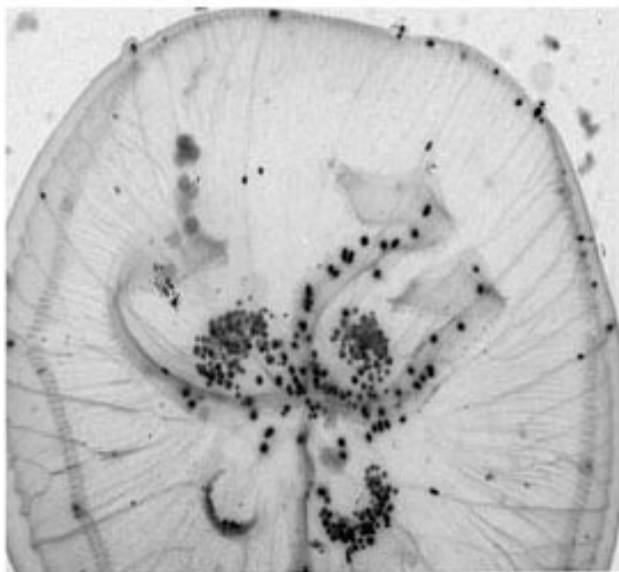


Fig. 3: Heavily parasitized *Aurelia* sp. 5 medusa from Veliko Jezero, Mljet Island. The anthozoan parasites are the numerous reflective points around the oral lobes and semi-circular gonads.

Sl. 3: Močno parazitirana meduza vrste *Aurelia* sp. 5 iz Velikega jezera, otok Mljet. Antozojski paraziti so vidni kot številne odsevne točke okoli ustnih krp in polkrožnih spolnih žlez.

tributes to top-down population regulation of jellyfish in open systems. The Mljet system will hopefully provide insight into such interactions in the future.

Another important source of regulation of *Aurelia* sp. in this system is parasitism. We previously measured parasitic loads of larval anthozoans (Fig. 3), presumably of the genus *Edwardsiella* in the tissues of *Aurelia* sp. 5 in VJ (D'Ambra & Graham, 2009). More than 50% of the population is moderately to heavily parasitized during warmer, stratified periods (Chiaverano & Graham, *unpubl. data*) and parasite loads dropping to around 25% of the population during the unstratified winter period. Chiaverano & Graham (*unpubl. data*) show that parasitism retards growth and alters morphology of *Aurelia* sp. 5 in a way that presumably changes swimming patterns and strength. The alteration of energy transfer away from somatic and reproductive tissue undoubtedly has a large but still unquantified impact on *Aurelia* sp. 5 population dynamics. While parasitic loads tend to be much lower in open marine systems, their influence on populations of jellyfish is relatively unexplored, and the Mljet system may provide insight into parasitism as a potential regulator of nuisance jellyfish blooms elsewhere.

By nature of their bipartite life-histories, the abundance of the medusa stage of *Aurelia* sp. is inextricably linked to the dynamics of the benthic polyp populations.

Thus, any inferences about population dynamics of *Aurelia* sp. 5 in the Mljet lakes must be made in the context of the polyp stage. No published accounts of polyp population dynamics are available, however our own observational work revealed polyps along a narrow band of rocky outcroppings below about 22 m along the northern rim of the southern-most basin of VJ (Fig. 1). Several observational SCUBA dives made during spring, summer and winter found active strobilation (= production of new medusae) during each of these periods. While year-round occurrence of *Aurelia* sp. 5 may be due to longevity and stability of the population, it may also be due to a constant infusion of young medusae throughout the year (Malej *et al.*, 2009). Moreover, constant production of young medusae may be a bet-hedging strategy against pulsed food supplies, thus equalizing the competitive advantage that slower growing, longer-lived fish have over time.

MLJET LAKES AS MODEL ECOSYSTEMS FOR MANAGEMENT

Ecosystem-based approaches are gaining in popularity for the management of marine fisheries (Christensen & Walters, 2004). Because these approaches rely heavily on modeling strategies, their utility for understanding whole system processes is largely limited by quality data to support their development and accuracy. While jellyfish are grossly underrepresented in published ecosystem models (Pauly *et al.*, 2009) there are a few examples demonstrating a key role for jellyfish in ecosystem functioning largely through bottom-up controls on predators (e.g., sea turtles populations) or top-down controls on zooplankton prey (Feigenbaum & Kelly, 1984; Schneider & Behrends, 1998). Inclusion of jellyfish in ecosystem models is limited largely by the lack of adequate time-series data on abundance and by the relatively poor understanding of diet and growth.

We promote the utility of the Mljet lakes system as model marine ecosystem to explore ecosystem-based management approaches using models that accurately reflect the functional role of jellyfish. Critical in the development of accurate ecosystem models are diversity of functional compartments, knowledge of diet and growth parameters, quality time-series information on populations. Also important to fisheries management is the availability of accurate fishery-independent data to support the fishery-dependent assessment of population structure.

The Mljet lakes provide a rare opportunity to develop a functional ecosystem model (e.g., with EwE) using realistic data rather than manipulated approximations. Owing to similarities of species or ecological guilds, such a model would be comparative of ecosystems outside of the lakes. To this end, the Mljet lake system offers high functional and trophic diversity of benthic, demer-

sal, nektonic and planktonic organisms suitable for model development. Interestingly, these small lakes were the subject of whole-lake nutrient enrichment experiments during the 1950s at which time inorganic phosphorus was added in an attempt to stimulate fish and shellfish production (Buljan, 1957; Puchér-Petković, 1960; Vučetić, 1957, 1966). Unfortunately there is little available quantitative information on jellyfish populations in response to increased nutrient loading, but we continue to explore available datasets for more information from these experiments.

The lakes are small and relatively contained allowing the accurate collection of system-wide data on population structure for mobile organisms (specifically fish and jellyfish) without great concern for variations due to immigration and emigration. Most of the target species are either well-represented outside the lakes with complete data on growth and diet (see www.FishBase.org), or we are currently collecting the necessary information in ongoing studies (*e.g.*, *Aurelia* sp.). And finally, owing to the

small size of the lakes and their protection from large-scale fishing, we can carefully assess an ecosystem model with fishery-independent statistics and, by working closely with Mljet residents, we can accurately determine catch statistics for the small artisanal fishery of the lakes.

In conclusion, the lakes of northern Mljet Island, Croatia, are likely unique in their temperate marine setting and geographic isolation. Because of this, we see opportunity to use the lakes as a model ecosystem to test the development and application of ecosystem-based management models with respect to the role of jellyfish as a potentially important component of marine ecosystems. In light of the potential for jellyfish populations to increase under added human stressors (coastal eutrophication, over-harvesting of fish, habitat modification and climate change), we see this opportunity as a critical step for marine scientists and fishery managers to refine their modeling tools to accurately reflect the trophic role of jellyfish at the ecosystem scale.

Tab. 1: Check list of fish species and families found in the marine lakes of Mljet Island, Croatia. Also presented are common and regional names. Information collected from the online resource www.fishbase.org includes relative importance of the species for fishing (- is not fished; + is minor fishing; ++ is moderately fished; +++ is heavily fished), whether the species is a zooplanktivorous (* indicates only early stages known to prey on zooplankton), and trophic level values where 2.0 is entirely herbivorous, 3.0 is a first order carnivore, 4.0 a second order carnivore, and so on.

Tab. 1: Seznam ribjih vrst in družin iz morskih jezer na otoku Mljetu, Hrvatska. Našteta so tudi splošna in regijska imena. Podatki, pridobljeni s spletne strani www.fishbase.org, vključujejo tudi informacijo o pomenu vrste za ribolov (- se ne lovi, + se lovi redko, ++ se lovi zmerno, +++ se veliko lovi), prehranjevanju vrste z zooplanktonom (* označuje samo zgodnje razvojne oblike, ki se hranijo z zooplanktonom) in trofičnih ravneh, in sicer 2.0 za popolnoma rastlinojede vrste, 3.0 za mesojede vrsta prvega reda, 4.0 za mesojede vrste drugega reda, itd.

Family	Scientific name	Common name	Regional name	Fishing pressure	Zooplankton feeding	Trophic level
Anguillidae	<i>Anguilla anguilla</i>	European eel	Angulja	++	N	2.3-3.5
Apogonidae	<i>Apogon imberbis</i>	Cardinal fish	Matulicic	+	N	3.9
Atherinidae	<i>Atherina boyeri</i>	Big-scale sand smelt	Brfun	++	Y	2.2-3.1
Belonidae	<i>Belone belone</i>	Garpike	Jagla	++	N	4.0-4.2
Blenniidae	<i>Parablennius</i> spp.			-	N	3.0-3.5
Carangidae	<i>Pseudocaranx dentex</i>	White trevally	Šnjurak	++	Y*	3.1-3.9
Carangidae	<i>Seriola dumerili</i>	Greater amberjack	Bilizmuša	++	N	3.7-4.5
Centracanthidae	<i>Spicara maena</i>	Blotched picarel	Cipavica	+	Y	3.0-4.2
Congridae	<i>Conger conger</i>	European conger	Grum	++	N	3.5-4.5

Family	Scientific name	Common name	Regional name	Fishing pressure	Zooplankton feeding	Trophic level
Gadidae	<i>Merlangius merlangus</i>	Whiting	Pišmolj	+++	Y*	3.2-4.5
Gadidae	<i>Trisopterus minutus</i>	Poor cod	Mol	++	N	3.2-4.0
Gobiesocidae	<i>Lepadogaster lepadogaster</i>	Shore clingfish	Priljepnjak kamenjaric	-	N	N/A
Gobiidae	<i>Gobius</i> spp.			-	N	3.0-3.5
Labridae	<i>Coris julis</i>	Mediterranean rainbow wrasse	Dundica	+	N	3.2-3.6
Labridae	<i>Labrus merula</i>	Brown wrasse	Crnac	+	N	3.2-3.5
Labridae	<i>Symphodus cinereus</i>	Grey wrasse	Hinac sivi	+	N	3.2-3.3
Labridae	<i>Symphodus doderleini</i>		Cucuruša	-	N	N/A
Labridae	<i>Symphodus mediterraneus</i>	Axillary wrasse	Podujka	+	N	3.2
Labridae	<i>Symphodus melops</i>	Corkwing wrasse	Kosirica mjesecica	+	N	3.2
Labridae	<i>Symphodus ocellatus</i>		Martinka	-	N	2.5-3.3
Labridae	<i>Symphodus roissali</i>	Five-spotted wrasse	Kosirica	+	N	3.4-3.5
Labridae	<i>Symphodus rostratus</i>		Dugonosica	-	N	3.3-3.7
Labridae	<i>Symphodus tinca</i>	East Atlantic peacock wrasse	Božjak	+	N	N/A
Mugilidae	<i>Liza aurata</i>	Golden grey mullet	Cipal zlatac	++	Y	2.2-2.9
Mullidae	<i>Mullus barbatus barbatus</i>	Red mullet	Barbun	++	N	2.7-3.6
Mullidae	<i>Mullus surmuletus</i>	Striped red mullet	Barbun	++	N	3.0-3.5
Muraenidae	<i>Muraena helena</i>	Mediterranean moray	Marina	-	N	N/A
Pomacentridae	<i>Chromis chromis</i>	Damselfish	Crnej	+	N	3.0-4.2
Sciaenidae	<i>Sciaena umbra</i>	Brown meagre	Kavala	++	N	3.8
Scombridae	<i>Scomber japonicus</i>	Chub mackerel	Lancarda	+++	Y*	2.8-4.3
Scombridae	<i>Scomber scombrus</i>	Atlantic mackerel	Bokulja	+++	Y*	3.0-4.4
Scorpaenidae	<i>Scorpaena porcus</i>	Black scorpionfish	Bodec	+	N	3.5-4.3
Scorpaenidae	<i>Scorpaena scrofa</i>	Largescaled scorpionfish	Crljenak	++	N	4.2-4.4
Serranidae	<i>Epinephelus caninus</i>	Dogtooth grouper	Kirnja zubuša	++	N	N/A
Serranidae	<i>Epinephelus costae</i>	Goldblotch grouper	Kirnja zatica	+	N	N/A

Family	Scientific name	Common name	Regional name	Fishing pressure	Zooplankton feeding	Trophic level
Serranidae	<i>Epinephelus marginatus</i>	Dusky grouper	Kirnja	+++	N	3.7-4.3
Serranidae	<i>Serranus cabrilla</i>	Comber	Giricar	+	N	3.4-4.4
Serranidae	<i>Serranus hepatus</i>	Brown comber	Cucin	+	N	3.5-3.8
Serranidae	<i>Serranus scriba</i>	Painted comber	Buruca	+	N	3.8
Soleidae	<i>Solea solea</i>	Common sole	List	+++	N	3.0-3.3
Sparidae	<i>Boops boops</i>	Bogue	Batelj	+++	Y	2.5-3.0
Sparidae	<i>Dentex dentex</i>	Common dentex	Dental	++	N	4.5
Sparidae	<i>Diplodus annularis</i>	Annular seabream	Baraj	++	N	3.1-3.4
Sparidae	<i>Diplodus puntazzo</i>	Sharpsnout seabream	Karoc	++	N	2.9
Sparidae	<i>Diplodus vulgaris</i>	Common two-banded seabream	Crnoguz	++	N	3.1-3.8
Sparidae	<i>Lithognathus mormyrus</i>	Striped seabream	Arkaj	+	N	N/A
Sparidae	<i>Oblada melanura</i>	Saddled seabream	Cešalj	++	N	3.0
Sparidae	<i>Pagellus acarne</i>	Axillary seabream	Arbun	++	N	3.3-4.4
Sparidae	<i>Pagellus erythrinus</i>	Common pandora	Arbor	++	Y*	3.2-3.8
Sparidae	<i>Sarpa salpa</i>	Salema	Salpa	++	N	2.0
Sparidae	<i>Spondyliosoma cantharus</i>	Black seabream	Grobar	++	Y	3.2-3.3
Synodontidae	<i>Synodus saurus</i>	Atlantic lizardfish	Gušter	+	N	4.5
Trachinidae	<i>Trachinus draco</i>	Greater weever	Dragan	+	N	N/A
Zeidae	<i>Zeus faber</i>	John dory	Kovač	++	Y*	3.7-4.5

RIBE IN MEDUZE: UPORABA IZOLIRANIH MORSKIH 'JEZER' NA OTOKU MLJETU, HRVAŠKA, PRI RAZISKOVANJU KOMPLEKSNOŠTI VEČJEGA MORSKEGA EKOSISTEMA IN PRISTOPOV EKOSISTEMSKEGA UPRAVLJANJA

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POVZETEK

Morski 'jezeri' na otoku Mljetu, južna Hrvaška, predstavljata zanimivo ekološko okolje za raziskovanje strukture in funkcije morskih ekosistemov zunaj samih jezer. Pričujoči članek sintetizira nekatere pretekle in sedanje raziskovalne projekte na jezerih s posebnim poudarkom na novejših študijah izolirane jezerske populacije klobučnjaške meduze *Aurelia* sp. 5. Ta vrsta je po vsej verjetnosti geografsko izolirana in evolucijsko omejena na jezeri otoka Mljeta. Kot taki jezeri predstavljata orodje za boljše razumevanje ekološkega razmerja med meduzami in raznoliko skupnostjo ribjih vrst, ki prav tako naseljujejo jezeri. Z bodočimi študijami avtorji spodbujajo k parametriziranju ekosistemskega modela jezer kot preizkusnega sistema za pristop ekosistemskega upravljanja ter uporabo podobnih modelov zunaj samih jezer.

Ključne besede: meduze, planktivore ribe, *Aurelia*, *Boops*, *Atherina*

REFERENCES

Alvarez Colombo, G., A. Benović, A. Malej, D. Lučić, T. Makovec, V. Onofri, M. Acha, A. Madirolas & H. Mianzan (2009): Acoustic survey of a jellyfish-dominated ecosystem (Mljet Island, Croatia). *Hydrobiologia*, 616, 99–111.

Arai, M. N. (2005): Predation on pelagic coelenterates: a review. *J. Mar. Biol. Assoc. U.K.*, 85, 523–536.

Benović, A., D. Lučić, V. Onofri, M. Peharda, M. Carić, N. Jasprica & S. Bobanović-Colić (2000): Ecological characteristics of the Mljet Island seawater lakes (South Adriatic Sea) with special reference to their resident populations of medusae. *Sci. Mar.*, 64, 197–206.

Buljan, M. (1957): Report on the results obtained by a new method of fertilization experimented in the marine bay "Mljetska Jezera". *Acta Adriat.*, 6, 1–44.

Christensen, V. & C. J. Walters (2004): Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.*, 172, 109–139.

D'Ambra, I. & W. H. Graham (2009): Early developmental sequence of an anthozoan parasite of the jellyfish *Aurelia* sp. 5 in an isolated marine lake (Mljet, Croatia). *Annales, Ser. Hist. Nat. (This volume)*

Dawson, M. N. & W. M. Hamner (2005): Rapid evolutionary radiation of marine zooplankton in peripheral environments. *Proc. Natl. Acad. Sci.*, 102, 9235–9240.

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

Dawson, M. N., L. E. Martin & L. K. Penland (2001): Jellyfish swarms, tourists, and the Christ-child. *Hydrobiologia*, 451, 131–144.

- Feigenbaum, D. & M. Kelly (1984):** Changes in the lower Chesapeake Bay food chain in presence of the sea nettle *Chrysaora quinquecirrha* (Scyphomedusa). *Mar. Ecol. Prog. Ser.*, 19, 39–47.
- Graham, W. M., F. Pages & W. M. Hamner (2001):** A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, 451, 199–212.
- Hamner, W. M. & L. R. Haury (1981):** Long-distance horizontal migrations of zooplankton (Scyphomedusae: *Mastigias*). *Limnol. Oceanogr.*, 26, 414–423.
- Hamner, W. M., R. W. Gilmer & P. P. Hamner (1982):** The physical, chemical and biological characteristics of a stratified, saline, sulfide lake in Palau. *Limnol. Oceanogr.*, 27, 896–909.
- Malej, A., V. Turk, D. Lučić & A. Benović (2007):** Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea). *Mar. Biol.*, 151, 824–841.
- Malej, A., V. Turk, T. Kogovšek, T. Makovec, V. Onofri, L. Chiaverano, T. Tinta & D. Lučić (2009):** *Aurelia* sp. 5 (Scyphozoa) population in the Mljet Lake (southern Adriatic): trophic interactions and link to microbial food web. *Annales, Ser. Hist. Nat. (This volume)*
- Mianzan, H., M. Pajaro, G. Alvarez Colombo & A. Madirolas (2001):** Feeding on survival-food: gelatinous plankton as a source of food for anchovies. *Hydrobiologia*, 451, 45–53.
- Pauly, D., W. Graham, S. Libralato, L. Morissette & M. L. D. Palomares (2009):** Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia*, 616, 67–85.
- Peharda, M., M. Hrs-Brenko, V. Onofri, D. Lučić & A. Benović (2002):** A visual census of bivalve distributions in the saltwater lake Malo jezero (Mljet National Park, South Adriatic Sea). *Acta Adriat.*, 43, 65–75.
- Puchér-Petković, T. (1960):** Effet de la fertilisation artificielle sur le phytoplancton de la région de Mljet. *Acta Adriat.*, 6, 1–19.
- Purcell, J. E. & M. N. Arai (2001):** Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia*, 451, 27–44.
- Sangiorgi, F., L. Capotondi, N. Nebout, L. Vigliotti, H. Brinkhuis, S. Giunta, A. F. Lotter, C. Morigi, A. Negri & G.-J. Reichert (2003):** Holocene seasonal sea-surface temperature variations in the southern Adriatic Sea inferred from a multiproxy approach. *J. Quat. Sci.*, 18, 723–732.
- Schneider, G. & G. Behrends (1998):** Top-down control in a neritic plankton system by *Aurelia aurita* medusae – a summary. *Ophelia*, 48, 71–82.
- Schroth, W., G. Jarms, B. Streit & B. Schierwater (2002):** Speciation and phylogeography in the cosmopolitan marine moon jelly, *Aurelia* sp. *BMC Evol. Biol.*, 2, 1–10.
- Surić, M., M. Jauracić, N. Horvatincić & I. K. Bronić (2005):** Late Pleistocene-Holocene sea-level rise and the pattern of coastal karst inundation: records from submerged speleothems along the Eastern Adriatic Coast (Croatia). *Mar. Geol.*, 214, 163–175.
- Vučetić, T. (1957):** Zooplankton investigations in the sea water lakes "Malo Jezero" and "Veliko Jezero" on the island of Mljet (1952–1953). *Acta Adriat.*, 6, 1–51.
- Vučetić, T. (1961):** Vertical distribution of zooplankton in the bay Veliko Jezero on the island of Mljet. *Acta Adriat.*, 6, 1–20.
- Vučetić, T. (1966):** Quantitative ecology investigations of the zooplankton during the fertilization experiments in the bay Veliko Jezero (I. Mljet). *Acta Adriat.*, 6, 1–29.
- Wunsam, S., R. Schmidt & J. Muller (1999):** Holocene lake development of two Dalmatian lagoons (Malo and Veliko Jezero, Isle of Mljet) in respect to changes in Adriatic sea level and climate. *Palaeogeogr.*, 146, 251–281.