EARLY DEVELOPMENTAL SEQUENCE OF AN ANTHOZOAN PARASITE OF THE JELLYFISH *AURELIA* SP. 5 IN AN ISOLATED MARINE LAKE (MLJET, CROATIA)

Isabella D'AMBRA & William M. GRAHAM
Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island AL 36528, USA
E-mail: mikidambra@hotmail.com

ABSTRACT

Gelatinous zooplankton, including planktonic cnidarians, ctenophores and tunicates, share a common population dynamic of boom-bust 'bloom' cycles. Most research tends to emphasize bloom formation, and considerably less attention is paid to factors that ultimately regulate the magnitude, extent and duration of the bloom. Among these are physiological tolerances (i.e., seasonality), food-limitation, predation, and the poorly-understood role of parasitism. We have discovered in the nearly-enclosed marine 'lakes' of Mljet Island (Croatia) an interesting host-parasite association between a quasi-stable year-round population of the scyphomedusa Aurelia sp. 5 and the early and larval parasitic stages of an anthozoan. In this paper we describe the rapid (~72 hr) sequence of early development in this anthozoan. While the species-level identity of the anthozoan remains uncertain, we still provide the first description of the entire sequence of the early developmental stages for parasitic anthozoans. Our ultimate aim is to understand the basic ecology of this host-parasite relationship to further determine whether parasitism is an important factor in Aurelia sp. 5 population regulation in the Mljet lakes ecosystem.

Key words: scyphomedusae, population regulation, *Peachia, Halcampa, Edwardsiella*

SEQUENZA INIZIALE DI SVILUPPO DI UN ANTOZOO PARASSITA DELLA MEDUSA *AURELIA* SP. 5 IN UN LAGO MARINO ISOLATO (MLJET, CROAZIA)

SINTESI

Lo zooplankton gelatinoso (inclusi cnidari, ctenofori e tunicati planctonici) condivide una comune dinamica ciclica con aumenti e ricadute della popolazione. Molte ricerche tendono ad enfatizzare la formazione delle cosiddette fioriture, e quindi meno attenzione viene prestata ai fattori che in definitiva regolano la magnitudine, l'estensione e la durata della fioritura. Fra tali fattori spiccano tolleranze fisiologiche (stagionalità), limitazione alimentare, predazione ed il mal compreso ruolo del parassitismo. Gli autori hanno scoperto nei semi-chiusi "laghi" marini dell'isola di Mljet (Croazia) un'interessante associazione ospite-parassita, fra una quasi stabile popolazione di scifomedusa Aurelia sp. 5, presente tutto l'anno, ed una fase di sviluppo iniziale ed una fase larvale parassitica di un antozoo. Nell'articolo viene descritta la rapida sequenza (~72 ore) della fase iniziale di sviluppo di tale antozoo. Benché l'identificazione a livello di specie dell'antozoo resti ancora incerta, viene comunque fornita una prima descrizione dell'intera sequenza delle fasi iniziali di sviluppo di antozoi parassiti. Lo scopo finale della ricerca è quello di capire l'ecologia di base della relazione ospite-parassita, al fine di accertare se il parassitismo sia effettivamente un fattore importante nella regolazione della popolazione di Aurelia sp. 5 nell'ecosistema dei laghi di Mljet.

Parole chiave: scyphomedusae, regolazione della popolazione, *Peachia, Halcampa, Edwardsiella*

INTRODUCTION

Macro-parasitism is one of the greatest, if not the greatest, sources of morbidity in multi-cellular eukaryotic populations (Anderson & May, 1978). Our general knowledge of parasitism in the sea is far more limited in comparison to terrestrial systems, but parasitism nevertheless may be equally important in regulating host populations of marine species. Thus it would be truly beneficial to understand the nature of parasitism as a source of morbidity leading to reduced fecundity or survival in populations of nuisance blooms of gelatinous zooplankton such as medusae.

The association between gelatinous zooplankton (hydromedusae, scyphomedusae, ctenophores, and pelagic tunicates) and ectoparasitic crustaceans such as amphipods has been studied in detail (Laval, 1980; Buecher et al., 2001; Gasca & Haddock, 2004). The ecto- and endoparasitic association between gelatinous zooplankton and anthozoan sea anemones has been reported numerous times in the literature (Müller, 1860; Haddon, 1886–87; McIntosh, 1887; Haddon, 1888; Badham, 1917; Blackburn, 1948; Nyholm, 1949; Spaulding, 1972; 1974; Crowell, 1976; McDermott et al., 1982; Bumann & Puls, 1996), but ecological studies are lacking (Arai, 1997). There is the additional uncertainty regarding the taxonomy of parasitic anthozoans because the phenomenon usually involves the anthozoan larval and juvenile stages, which remain poorly described, highly variable or entirely unknown (Spaulding, 1972; 1974; Shick, 1991; Fautin, 2002). Very few successful attempts have been made to culture parasitic larvae to recognizable adults (Spaulding, 1972; 1974; Crowell, 1976).

As shown in Table 1, the larval forms of the genera *Peachia* spp. and *Edwardsiella* spp. are the most commonly reported parasites of hydromedusae, scyphomedusae and ctenophores (Müller, 1860; Haddon, 1886-87; McIntosh, 1887; Badham, 1917; Blackburn, 1948; Spaulding, 1972; Crowell, 1976; McDermott et al., 1982; Bu-

mann & Puls, 1996). *Edwardsia lineata* reported by Bumann & Puls (1996) is synonymous with *Edwardsiella lineata* (Verrill in Baird, 1873). *Halcampa chrysanthellum* reported by Haddon (1886-87) is recognized as *H. duodecimcirrata* (M.Sars, 1851), but the genus *Halcampa* spp. has been rarely mentioned as a parasite on jellyfish. *Philomedusa vogtii* cited by Müller (1860) is likely a misidentification by that author as the species has not been observed since.

As part of the large multinational "Meduza" research program investigating the ecology of gelatinous zooplankton in the southern Adriatic Sea region, we initiated an observational study on the reproductive patterns of the resident scyphomedusa, *Aurelia* sp. 5 (Dawson & Jacobs, 2001). This species, described ecologically elsewhere (Benović et al., 2000; Malej et al., 2007; Alvarez Colombo et al., 2009; Graham et al., 2009) is the dominant macroplanktonic organism in the semi-enclosed 'lakes' of northern Mljet Island (refer to Graham et al., 2009, for a detailed description). This population of *Aurelia* sp. has likely been isolated for several thousand years in the small marine lakes ecosystem of Mljet Island and recent investigations by us (Graham et al., 2009) and others (Malej et al., 2007) point to a quasi-stable year-round population of medusae that may be regulated largely by a combination of bottom-up trophic processes and reduced productivity induced by parasitism (Graham et al., 2009; L. Chiaverano & W. Graham, umpubl. data).

During initial field studies in summer 2002, we observed very heavy infections (~50%) of *Aurelia* sp. 5 by a presumed, yet unidentified, anthozoan species. Information regarding identification, developmental patterns and ecological significance of larval anthozoan infections of medusae, in general, is poor, so we have attempted to shed light on this association by describingthe the early developmental stages of the anthozoan likely responsible for at least a portion of *Aurelia* sp. 5 population regulation in this ecosystem.

Tab. 1: Compilation of anthozoan species described as parasites of specific gelatinous zooplankton.
Tab.1: Seznam koralnjaških vrst, opisanih v vlogi parazitov specifičnega želatinoznega zooplanktona.

Host	Anthozoan	Reference
Olindias sp., *Chrysaora* sp.	*Philomedusa vogtii* Müller, 1860	Müller, 1860
Leptomedusae	*Halcampa duodecimcirrata* (M. Sars, 1851) (reported as *Halcampa chrysanthellum)*	Haddon, 1886–87
Thaumantias sp.	*Peachia* sp.	McIntosh, 1887
Catostylus mosaicus (Quoy and Gaimard, 1824) (reported as *Crambessa mosaicus)*	*Peachia hilli* Wilsmore, 1911	Badham, 1917
Cyanea capillata (L.) var. *marginata* von Lendenfeld, 1844	*Peachia clava* (Quoy and Gaimard, 1833)	Blackburn, 1948
Phialidium gregarium (A. Agassiz, 1862)	*Peachia quinquecapitata* McMurrich, 1913	Spaulding, 1972
Mnemiopsis leidyi (A. Agassiz, 1965)	*Edwardsiella lineata* (Verrill in Baird, 1873)	Crowell, 1976
Cyanea capillata (Linnaeus, 1758)	*Peachia parasitica* (L. Agassiz, 1859)	McDermott et al., 1982
Mnemiopsis leidyi (A. Agassiz, 1965)	*Edwardsiella lineata* (Verrill in Baird, 1873) (reported as *Edwardsia lineata)*	Bumann & Puls, 1996

MATERIALS AND METHODS

Sampling and observations

All specimens of *Aurelia* sp. 5 medusae were collected in Veliko Jezero by SCUBA divers during July 2003 and May 2004. No more than three medusae, captured by gentle handling, were placed in a given plastic bag and quickly transported to the laboratory usually within 30 min. A total of 15 medusae were examined each year. Individual medusae were measured, photographed and then manipulated with clean glass pipettes to detach parasites from the subumbrellar surfaces and transfer them to multi-chambered petri dishes (chamber volume 15 ml). Each chamber was filled with 'lake' water filtered at 30 μm from the medusa collection sites. No more than five larvae were placed in a chamber. With the exception of observation points, larvae were maintained at 18°C in the dark.

Microscopic observations and digital photographs with scale reference were made twice each day, usually early morning and late afternoon. During the observation period, handling was minimal and limited to observations and photography only. No feeding occurred, though development clearly proceeded. There was no need to provide a substrate or to make additional water changes.

RESULTS

Parasite developmental progression and distribution within *Aurelia* sp. 5 are qualitatively linked. Moreover, presence of infection in *Aurelia* sp. 5 (Fig. 1) is con-
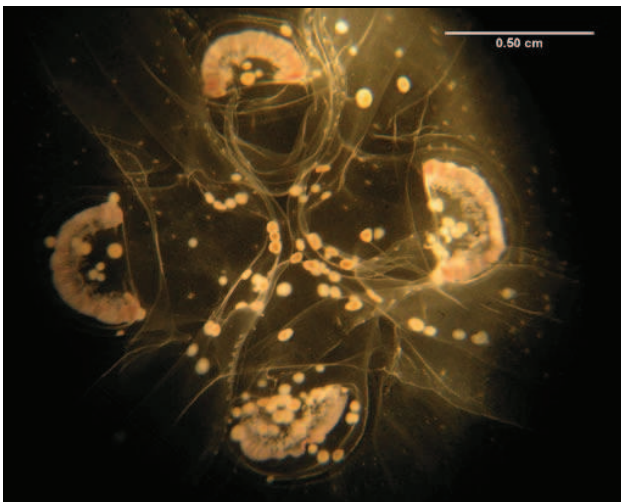

Fig. 1: Gastric cavity of *Aurelia* **sp. 5 infected by the anthozoan larvae in Veliko Jezero (Mljet, Croatia).**
Sl. 1: Prebavna votlina primerka vrste *Aurelia* **sp. 5, okužena z ličinkami koralnjaka v Velikem jezeru (Mljet, Hrvaška).**

spicuous as the large (500–600μm) and orange anthozoan zygotes and blastulae are about three times the size of white *Aurelia* sp. 5 ova and developing planulae (~180μm). Earliest parasite developmental stages found only in the gastric pouches of *Aurelia* sp. 5 are zygotes (recently fertilized and showing no evidence of mitotic divisions; Fig. 2a). The development from zygote (assumed to be time 0 hr) to larva was complete in about 72 hr after the beginning of the observation; a synopsis of the timing of each phase is shown in Table 2. The zygote is surrounded by a thin, transparent gelatinous membrane and has a granulated cytoplasm (Fig. 2a). Cleavage was visible after about 12 hr of initial observation of this earliest stage (*i.e.*, not after fertilization; Fig. 2b–c) and leading to the development of the blastula within 18 h (not shown). Gastrulation occurred around 32–36 hr through invagination (Fig. 2d). The transition from gastrula to larva is complete in about 24–36 hr. Larvae (72 h after the beginning of observations; Fig. 2e-f) migrated from the gastrovascular cavity of the medusae to colonize the sub-umbrella, ultimately burrowing either into the epithelial layer or into the radial canals. No larvae older than represented in Figure 2f were observed in any medusa collected.

Tab. 2: Timing of the early developmental stages of the anthozoan parasite on *Aurelia* ***sp. 5 in Mljet 'lakes' (Croatia).***
Tab. 2: Časovni razpored zgodnjih razvojnih faz koralnjaškega parazita na vrsti *Aurelia* ***sp. 5 v Mljetskih 'jezerih' (Hrvaška).***

Developmental stage	Time (hr)
Zygote	0
Cleavage	12
Blastula	18
Gastrula	32–36
Larva	72

DISCUSSION

Our observations on the early developmental sequence of this anthozoan parasite shed light on the ecological processes surrounding this interesting host-parasite relationship. That most of the earlier developmental stages (*i.e.*, fertilized eggs, developing zygotes and blastulas) are located in the medusa gastric cavities indicates that infection occurs shortly after egg fertilization. It also suggests that infection occurs via feeding processes by the *Aurelia*. In other words, recently fertilized anthozoan eggs or individual gametes are broadcast into the water column where medusae subsequently ingest them. This was previously theorized as the mode of infection of the hydromedusa *Phialidium gregarium* by the parasitic anthozoan *Peachia quinquecapitata* (Spaulding, 1972). By presumably avoiding digestion within the gastric pou-
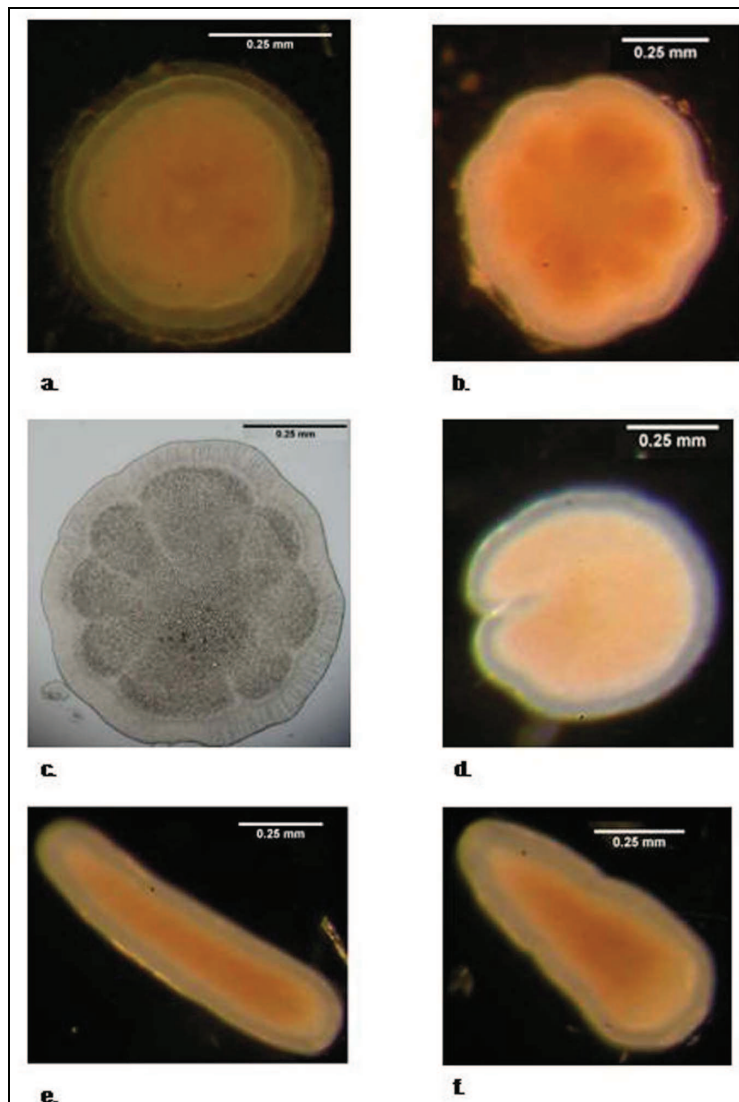
*Fig. 2: Developmental stages of the anthozoan parasitizing Aurelia **sp. 5 in Mljet 'lakes' (Croatia): a = fertilized egg; b, c = cleavage; d = gastrula; e = non contracted larva; f = contracted larva. Scale bars indicate size changes.***

*Sl. 2: Razvojne faze koralnjaka, ki paratizira vrsto Aurelia **sp. 5 v Mljetskih 'jezerih' (Hrvaška): a = oplojeno jajčece; b, c = cepitev; d = gastrula; e = neskrčena ličinka; f = skrčena ličinka. Merilo prikazuje spremembe v velikosti.***

ches, development proceeds through gastrulation and larval development with most of the later larval stages located in the radial canals of *Aurelia* sp. 5. We can only assume that recruitment of the larval stages back to the still-undescribed adult population occurs after the later-staged larvae emerge from the medusa. Over the course of dozens of dives in all seasons, we have never observed parasites further developed than shown in Figure 2f.

This is the first description of the entire sequence of the early developmental stages of a parasitic anthozoan and, to our knowledge, just the second for all anthozoans since the work of Nyholm (1949). Cnidarians, in general, manifest high developmental variability (Shick, 1991; Fautin, 2002), and developmental stages described by Nyholm (1949) for *Halcampa duodecimcirrata* (M. Sars, 1851) and by Spaulding (1972, 1974) for *Peachia quinquecapitata* McMurrich (1913) were particularly useful in our attempt to identify basic characteristics of parasitic actiniarian larvae. It is, however, unfortunate that identification below the family level is impossible due to lack of taxonomic information in the recent literature. Moreover, our limited time of about two weeks at the remote field location prohibited the rearing of these larval stages to an identifiable adult stage.

This list of potential candidate genera is limited to *Peachia*, *Halcampa*, and *Edwardsiella*, with the two former genera of most interest as they are widely described as "medusophilous" (Tab. 1). Since we never ob-

served the spiny macrovilli described by Spaulding (1972, 1974) for the eggs of *Peachia quinquecapitata*, we quickly ruled out *Peachia*. A higher level of similarity was instead found with the developmental stages described by Nyholm (1949) for *Halcampa duodecimcirrata*, even though this description was made on free-living developmental stages. One significant structural difference between our parasitic larvae and that of Nyholm's (1949) description is the presence of a thick jelly coat surrounding all the developmental stages.

Recently, however, a molecular genetic analysis on the developing parasites suggested a 16S rRNA region most closely, but not exactly, matching *Edwardsiella* sp. (L. Chiaverano & K. Bayha, *unpubl. data*). Both *Halcampa* sp. and *Peachia* sp. were included in the GenBank reference library, so we are reasonably confident that the Mljet *Aurelia* sp. 5 parasite is neither of these species. Placement within the Edwardsiidae would be an interesting finding as the only ecological descriptions of parasitism are with ctenophores (Crowell, 1976; Bumann & Puls, 1996) and not with cnidarian medusae. Moreover, parasitism has only been reported for post-larval stages of *Edwardsiella* sp., but never for the larval stages (Daly, 2002b; Reitzel *et al.*, 2006). Recent systematic revision of Edwardsiidae (Daly, 2002a) reveals a clustering of all the "medusophilous" genera within the Order Actiniaria, Suborder Nyantheae, Tribe Athenaria.

As a further complication, *Edwardsiella*, *Halcampa* or *Peachia* have not been reported in the checklist of the Anthozoan of Mljet fauna (Kružić, 2002). Rather, the only Athenarian species found close to Veliko Jezero was *Halcampoides purpurea* (Studer, 1879) from outside the lakes (Kružić, 2002). Molecular evidence, however, does not support identification as *Halcampoides* (L. Chiaverano & K. Bayha, *unpubl. data*), and we believe the adult stages simply have not been found due to the lack of effort to survey these small, cryptic anemones in the

Mljet lakes. Including the three described parasite genera mentioned above, there are 48 genera in 10 families, and it may well be that parasitic associations are taxonomically far more common than we previously believed. The accurate identification of the Mljet *Aurelia* sp. 5 parasite may remain unknown until reference DNA is collected and made accessible for comparison with our samples.

We continue to seek a better understanding of the ecology of this parasitic relationship in the Mljet 'lakes'. Parasitism has been documented over repeated trips to the Mljet 'lakes' over 5 years and during three seasons (spring, summer and winter), thus the association appears to be fixed in this system. While the anthozoan parasitism itself is not novel, the magnitude of infection across the *Aurelia* sp. 5 population (as much as 50% of the medusae), extent of infection with individual medusae (see Fig. 1 as an example) and persistence over time, give us a tantalizing picture of jellyfish population regulation by parasites rather than by food-limitation or macro-predation. Therefore, we continue to push for a complete understanding of this particular host-parasite relationship with the hope that it will ultimately reveal underlying ecology applicable to jellyfish population dynamics well beyond the boundaries of this remote and isolated marine lake ecosystem.

ACKNOWLEDGEMENTS

ZGODNJA RAZVOJNA SEKVENCA KORALNJAŠKEGA PARAZITA NA MEDUZI VRSTE *AURELIA* SP. 5 V IZOLIRANEM MORSKEM JEZERU (MLJET, HRVAŠKA)

Isabella D'AMBRA & William M. GRAHAM
Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island AL 36528, USA
E-mail: mikidambra@hotmail.com

POVZETEK

Za populacije želatinoznega zooplanktona, vključno s planktonskimi ožigalkarji, rebračami in plaščarji, je značilna ciklična dinamika izbruhov in upadanj masovnega pojavljanja. Večina raziskav se osredotoča na formiranje tega pojava, precej manj pozornosti pa se namenja dejavnikom, ki regulirajo obseg in trajanje masovnega pojavljanja. Sem vključujemo fiziološke tolerance (npr. sezonskost), omejeno količino hrane, predacijo in slabo razumljeno vlogo parazitizma. V skoraj zaprtih morskih 'jezerih' na otoku Mljetu (Hrvaška) smo odkrili zanimivo razmerje gostitelj-parazit, in sicer med kvazistabilno, skozi vse leto prisotno populacijo klobučnjakov Aurelia sp. 5 ter koralnjakov v zgodnji razvojni fazi in parazitski fazi ličinke. V pričujočem članku je opisana hitra (~72 ur) sekvenca zgodnjega razvoja tega koralnjaka. Čeprav še vedno ni popolnoma jasna identiteta koralnjaka na ravni vrste, je tu

prvič opisana celotna sekvenca zgodnje razvojne faze parazitskih koralnjakov. Naš poglavitni cilj je razumeti osnovno ekologijo tega razmerja gostitelj-parazit ter dalje oceniti, ali je parazitizem pomemben dejavnik regulacije populacije vrste Aurelia *sp. 5 v ekosistemu Mljetskih jezer.*

Ključne besede: skifomeduze, regulacija populacije, *Peachia, Halcampa, Edwardsiella*

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.

Anderson, R. M. & R. M. May (1978): Regulation and stability of host-parasite population interactions. I. Regulatory processes. J. Anim. Ecol., 47, 219–247.

Arai, M. N. (1997): A Functional Biology of Scyphozoa. Chapman & Hall, London, 315 p.

Badham, C. (1917): On a larval Actinian parasitic in a Rhizostome. Q. J. Microsc. Sci., s2–62, 221–229.

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 population of medusae. Sci. Mar., 64, 197–206.

Blackburn, M. (1948): Notes on some parasitic actinian larvae, and one of their host medusae in Australian waters. J. Counc. Sci. Ind. Res., 81, 183–189.

Buecher, E., C. Sparks, A. Brierley, H. Boyer & M. Gibbons (2001): Biometry and size distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum*. J. Plankton Res., 23, 1073–1080.

Bumann, D. & G. Puls (1996): Infestation with larvae of the sea aemone *Edwardsia lineata* affects nutrition and growth of the ctenophore *Mnemiopsis leidyi*. Parasitology, 113, 123–128.

Crowell, S. (1976): An Edwardsiid larva parasite in *Mnemiopsis*. In: Mackie, G. O. (ed.): Coelenterate Ecology and Behavior. Plenum Press, New York, pp. 247–250.

Daly, M. (2002a): A systematic revision of Edwardsiidae (Cnidaria, Anthozoa). Inv. Biol., 121, 212–225.

Daly, M. (2002b): Taxonomy, anatomy and histology of the lined sea anemone, *Edwardsiella lineata* (Verrill, 1873) (Cnidaria: Anthozoa: Edwardsiidae). Proc. Biol. Soc. Wash., 115, 868–877.

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

Fautin, D. G. (2002): Reproduction of Cnidaria. Can. J. Zool., 80, 1735–1754.

Gasca, R. & S. H. D. Haddock (2004): Association between gelatinous zooplankton and hyperiid amphipods (Crustacea: Peracarida) in the Gulf of California. Hydrobiologia, 530, 531:529–535.

Graham, W. M., L. M. 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)*

Haddon, A. C. (1886-87): Note on the arrangement of the mesentheries in the parasitic larva of *Halcampa chrysanthellum* (Peach). Sci. Proc. R. Dublin Soc., V, 473–481.

Haddon, A. C. (1888): On larval Actiniae parasitic on Hydromedusae at St. Andrew's. Ann. Mag. Natur. Hist., 2, 256–259.

Kružić, P. (2002): Marine fauna of the Mljet National Park (Adriatic Sea, Croatia). 1. Anthozoa. Nat. Croat., 11, 265–292.

Laval, P. (1980): Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. Oceanogr. Mar. Biol. Annu. Rev., 18, 11–56.

Malej, A., V. Turk, D. Lučić & A. Benović (2007): Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet lakes, Adriatic Sea). Mar. Biol., 151, 827–841.

McDermott, J. J., P. L. Zubkoff & A. L. Lin (1982): The occurrence of the anemone *Peachia parasitica* as a symbiont in the scyphozoan *Cyanea capillata* in the lower Chesapeake Bay. Estuaries, 5, 319–321.

McIntosh, W. C. (1887): The commensalistic habits of larval forms of *Peachia*. Ann. Mag. Natur. Hist., 20, 101–102.

Müller, F. (1860): On *Philomedusa vogtii* a parasite on medusae. Ann. Mag. Natur. Hist., 6, 432–436.

Nyholm, K.-G. (1949): The development and dispersal of athenaria actinia with special reference to *Halcampa duodecimcirrata* M. Sars. Zool. Bidrag Fran Uppsala, 27, 465–505.

Reitzel, A. M., J. C. Sullivan & J. R. Finnerty (2006): Qualitative shift to indirect development in the parasitic sea anemone *Edwardsiella lineata*. Integr. Comp. Biol., 46, 827–837.

Shick, J. M. (1991): A Functional Biology of Sea Anemones. Chapman & Hall, London, 395 p.

Spaulding, J. G. (1972): The life cycle of *Peachia quinquecapitata* an anemone parasitic on medusae during its larval development. Biol. Bull., 143, 440–453.

Spaulding, J. G. (1974): Embryonic and larval development in sea anemones (Anthozoa: Actiniaria). Am. Zool., 14, 511–520.