

Parasites alter behavior, reproductive output, and growth patterns of *Aurelia* medusae in a marine lake

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ABSTRACT: Parasites are known to induce phenotypic modifications in their hosts through direct competition for resources, which can negatively affect host fitness. Although parasite-induced phenotypic variation has been studied extensively in terrestrial and freshwater taxa, this phenomenon remains comparatively under-studied in marine pelagic invertebrates, such as ecologically important jellyfish. Here we studied the parasite–host relationship between *Edwardsiella* sp. anemone larvae (parasite) and medusae of *Aurelia* sp. 5 (host) in an isolated marine lake (Veliko Jezero) in Croatia. During 3 different seasons, we quantified differences in the vertical position in the water column, morphology, and egg production between parasitized and unparasitized medusae. Our results revealed that medusa behavior, morphology, and fecundity can be significantly affected by parasitism. Infected medusae were more abundant higher in the water-column where water was warmer, while unparasitized individuals displayed the opposite pattern. In addition, host somatic growth, gonad size, and egg production were negatively affected by parasitism, suggesting an ultimate negative effect on medusa fecundity. Parasitized individuals, however, developed relatively longer manubria and produced larger eggs than unparasitized counterparts, indicating a compensatory response to increase capture surface and reproductive effort. This study demonstrates the extent of parasite-induced phenotypic variation in jellyfish as well as the role of parasites in potential regulation of jellyfish population size.

KEY WORDS: Parasitism · Plasticity · Jellyfish · *Edwardsiella* · Mljet

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INTRODUCTION

Parasites are ubiquitous in nature; however, it was not until 2 decades ago that efforts were made to understand their ecological function in ecosystems (Marcogliese & Cone 1997). Now, ecologists and evolutionary biologists recognize that parasites account for a substantial portion of total biomass in an ecosystem (Kuris et al. 2008) and play an important role in determining structure in animal communities by affecting interactions among species (Horwitz & Wilcox 2005, Hudson et al. 2006, Wood et al. 2007). In effect, through direct competition for host resources, parasites can induce phenotypic changes in their host with negative consequences on host fitness

(Agrawal 2001, Lefèvre et al. 2009), including reduced growth rates (Krist 2000, Bize et al. 2003), modified behavior to maximize exposure to infection (Moore 2002), and increased costs of reproduction or decreased fecundity due to energy drain and/or size constraints (Moller 1993, Charmantier et al. 2004). However, in some cases, hosts exhibit compensatory or plastic responses to overcome the negative effects of parasitism (Lefèvre et al. 2009), including compensatory growth (Metcalf & Monaghan 2001, Bize et al. 2003), early maturation (Minchella & Loverde 1981), and increases in reproductive effort (Forbes 1993).

Parasite-induced phenotypic variation has been studied in a variety of terrestrial and freshwater hosts; however, the effects on the phenotype of

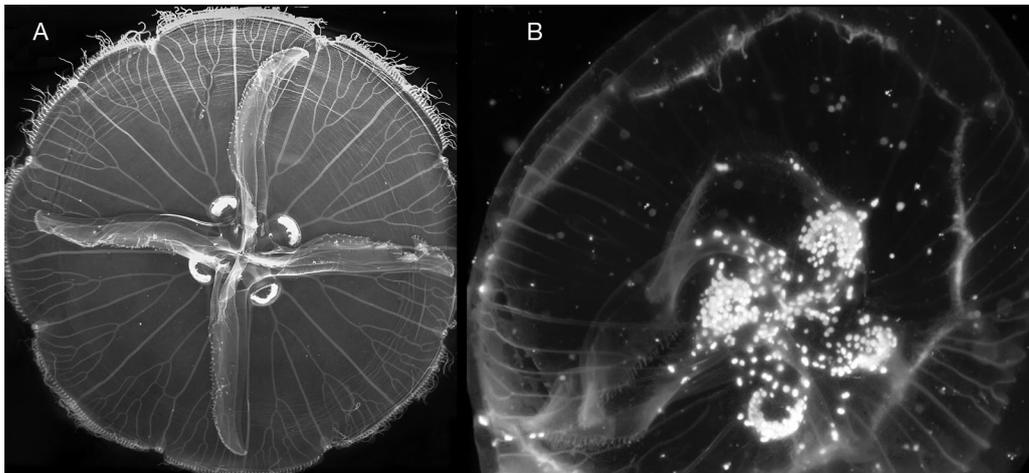


Fig. 1. *Aurelia* sp. 5 medusae from Veliko Jezero (A) unparasitized and (B) parasitized individuals. Note the parasitic larvae of the anemone *Edwardsiella* sp. (reflecting dots in the right photograph) concentrated mainly inside the gastric pouches of its host

marine pelagic invertebrate hosts, particularly those ecological and socio-economically important taxa, such as jellyfish (i.e. medusae and ctenophores), are almost unknown. Currently, jellyfish, and especially their population dynamics, are receiving special attention in coastal marine ecosystems worldwide (Condon et al. 2012, 2013). Interest has grown in population increases in response to climatic fluctuations, over-harvesting of fisheries, pollution, eutrophication and hypoxia, introduction of exotic species, habitat modification, or a combination of such factors (reviewed in Purcell 2012). When abundant, jellyfish interfere directly with human enterprise, negatively affecting fishing by clogging nets (Nagata et al. 2009, Dong et al. 2010), aquaculture by causing fish death within pens (Doyle et al. 2008, Delannoy et al. 2011), power generation and desalination by clogging intake screens (Daryanabard & Dawson 2008), and especially tourism by stinging swimmers (Fenner et al. 1996, 2010). However, despite the socio-economic impacts of mass occurrences of jellyfish, little is known about potential biological regulation/control of jellyfish population size.

Parasites are not uncommon to jellyfish (Arai 1997, 2005), thus they are purposed regulators of jellyfish blooms (Bumann & Puls 1996, Reitzel et al. 2007). However, little research effort has been made in this area perhaps because instances and magnitude of parasitism are difficult to study in natural populations. Most research involving jellyfish and their parasites has previously focused on parasite taxonomy and development (Spaulding 1972, McDermott et al. 1982, Dittrich 1988, Pages 2000, Martorelli 2001); a few

studies have addressed the ecological impact of the association (Towanda & Thuesen 2006, Reitzel et al. 2007, Riascos et al. 2012), and one study has assessed the effects of parasites on morphology and reproduction of the host and how these may lead to reduced fitness (Bumann & Puls 1996). Thus, a critical gap exists in information on the impact parasites exert on natural jellyfish populations through induced effects on the jellyfish phenotype (e.g. morphology, reproduction, behavior), which is linked to individual performance and ultimately to ecological and evolutionary processes (Ruiz 1991, Koehl 1996, Lefèvre et al. 2009).

A host–parasite relationship between the moon jellyfish *Aurelia* sp. 5 (host) and larvae of the anemone *Edwardsiella* sp. was recently discovered in the marine ‘lake’ Veliko Jezero (‘big lake’, hereafter VJ) on the island of Mljet, Croatia (Fig. 1; D’Ambra & Graham 2009), which provided an opportunity to address the effects of parasitism on the phenotype of jellyfish hosts in a natural setting (Graham et al. 2009). The moon jellyfish *Aurelia* sp. 5 (Cnidaria: Scyphozoa) appears to be endemic to this lake (referred as such although there is a shallow connection leading to the Adriatic Sea; see below), since phylogenetic studies indicate the *Aurelia* sp. 5 is genetically different at the molecular level from all other *Aurelia* species (Dawson & Jacobs 2001, Schroth et al. 2002). In this lake, about half of *Aurelia* sp. 5 medusae can be infected with *Edwardsiella* sp. larvae (D’Ambra & Graham 2009; Fig. 1), which are known to parasitize mainly ctenophores (Bumann & Puls 1996, Selander et al. 2009). Therefore, this anemone–medusae relationship is of particular interest because it represents

an excellent model for quantifying the effect of parasitism on the phenotype of jellyfish, with potential subsequent effects on medusa fitness and population size. Therefore, we compared behavior, morphology, and fecundity between parasitized and unparasitized *Aurelia* sp. 5 medusae. We also measured the prevalence and intensity of infection in medusa during 3 seasons. The specific objectives of this study were: (1) to evaluate the dynamics of parasitism in VJ by studying prevalence and intensity of infection and (2) to assess potential parasite-induced effects on the phenotype of medusae, in terms of behavior (i.e. position in the water column), morphology (i.e. size and shape), and fecundity (i.e. egg counts).

MATERIALS AND METHODS

Study site

VJ has a surface area of 1.45 km², a maximum depth of 46 m and it is connected to the Adriatic Sea through a ~1 km long, 10 m wide, and 2.5 m deep channel, which supplies a small turnover of surface waters. It is hypothesized that VJ initially filled with seawater during a sea level rise between 4200 and 7000 yr ago (Benović et al. 2000, Graham et al. 2009). Descriptive details of the physical characteristics of VJ are provided elsewhere (Benović et al. 2000, Malej et al. 2007, 2009). Water is well-mixed during winter (<10°C), while stratification develops in spring and a strong thermocline is formed by early summer in the layers between 12 and 20 m. Strong

thermal stratification remains until the beginning of fall (Benović et al. 2000). Thus, from spring to later summer, surface (above the opening sill depth) temperatures range from 23 to 30°C, while below the thermocline (below sill depth) water temperatures remain between 9 and 15°C. Salinity varies from 36.3 to 38.6 psu in the surface mixed layer, but stays relatively constant (37.5 to 38.5 psu) below sill depth throughout the year (Benović et al. 2000).

Prevalence of infection

The distribution of infected and uninfected medusae relative to depth and by season was recorded by SCUBA divers. A series of vertical transects were carried out at a single sampling site in VJ (Fig. 2) by a team of 2 to 4 SCUBA divers during 3 seasons in different field years. Each vertical transect consisted of counting the number of infected and uninfected medusae for 20 min at a series of pre-determined depths (Fig. 2). Observations were recorded at 10 m (just above the thermocline), 15 m (at the thermocline), 20 m (just below the thermocline), 25 m (below the thermocline), and 30 m depth (deeper layers), during summer 2003 and spring 2004 (except at 25 m). In winter 2006, due to the absence of a thermocline in VJ, observations were recorded at 15 m and 30 m depths. A total of 4 vertical transects (2 during summer and one each during spring and winter) were carried out close to local noon. Prevalence, i.e. the percentage of individuals infected from total medusa counts, was recorded at each depth. Seasonal prevalence was then calculated by averaging parasite prevalence recorded at all depths within a season. Temperature profiles in VJ were carried out in summer, spring, and winter using a CTD.

Medusa collection

Aurelia sp. 5 medusae were collected in VJ during summer 2003 (n = 76), spring 2004 (n = 51), and winter 2006 (n = 62). All individuals were sampled by SCUBA from 15 to 25 m depth at one sampling site (Fig. 2). Medusae were collected by hand, placed in separate sealable plastic bags, brought to surface, and then transferred to a laboratory located on Mljet.

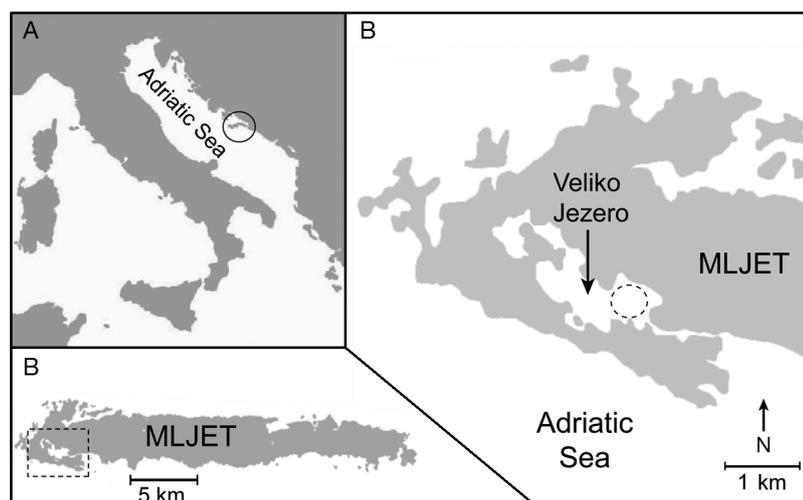


Fig. 2. Study area: (A) location of Mljet Island, Croatia (circled) in the Southern Adriatic; (B) location of marine lakes (dashed rectangle) on Mljet Island; (C) location of the collection site in Veliko Jezero (dashed circle)

Intensity of infection

Medusae were placed exumbrella surface down on a flat, transparent tray illuminated from underneath. High resolution digital images were then taken of each medusa to quantify the number of parasites per individual and to record a series of morphological features (described below). Collecting bags were carefully checked for detached parasites since the number of parasites per medusae could be influenced by manipulation. The total number of parasites per infected medusa, given by the sum of loose parasites and imaged parasites, was then averaged across infected individuals within seasons and used as a proxy of intensity of infection (Bush et al. 1997).

Morphological features

Calipers (± 0.01 mm) were used to measure bell diameter and oral arm width, halfway along their length (Fig. 3). A thickness probe scribed at 1 mm intervals was used to measure medusa height (bell + manubrium) at the center of the mouth. After excising the oral arms and manubrium, the thickness probe was reinserted through the center of the bell to measure bell height. Manubrium length (Fig. 3) was then calculated by subtracting bell height from medusa height. Both bell height and manubrium length were divided by bell diameter to obtain fineness ratio and manubrium ratio, respectively. All measurements were recorded on live medusae within 2 h after collection.

Other morphological features were obtained from digital images in the laboratory by using the software ImagePro Plus[®]. We determined manubrium width (distance between the base of 2 opposite oral arms), oral arm length, distal and proximal gastric distances (distance between the most distal and the most proximate points of opposite gastric cavities indicated by the edges of gonadal or gastric tissue, respectively), and rhopalar and non-rhopalar indentations (distance from a line drawn tangentially across adjacent velar lobes to the ring canal at rhopalar and non-rhopalar positions, respectively; Fig. 3). These features were then also divided by bell diameter to obtain a ratio. Gonad size, defined as the length between the edges of gonadal tissue within a gastric cavity (Fig. 3), was calculated by subtracting proximal gastric distance from the distal gastric distance and dividing the resulting length by 2. The gonad ratio was then obtained by dividing gonad size by bell diameter. This feature provided information about the size of gonads

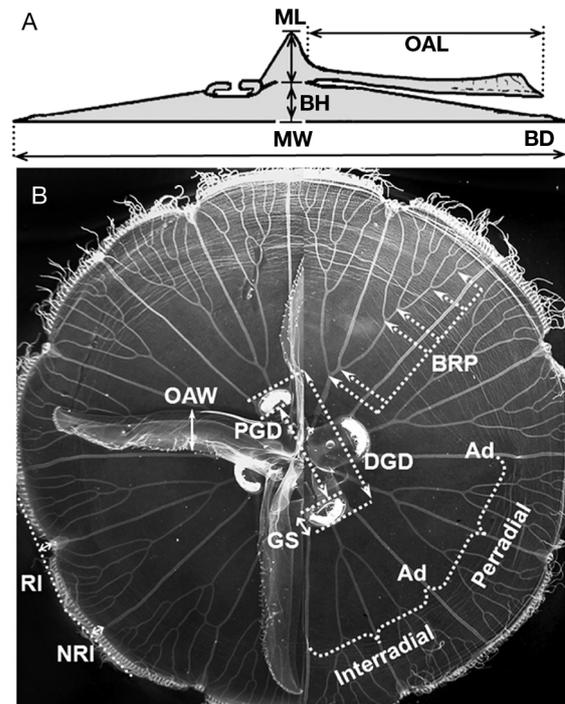


Fig. 3. (A) Cross-sectional view and (B) photo (exumbrella facing down) of an *Aurelia* sp. 5 medusa showing continuous and meristic morphological features measured in this study. BD: bell diameter; BH: bell height; ML: manubrium length; MW: manubrium width; GS: gonad size; OAW: oral arm width; OAL: oral arm length; DGD: distal gastric distance; PDG: proximal gastric distance; RI: rhopalar indentation; NRI: non-rhopalar indentation (all in mm); and BRP: maximum number of branching points. Ad: adradial canals

in proportion to the bell diameter. The branching points of the gastrovascular system were used as a proxy for relative age as in Miyake et al. (1997), who demonstrated that the number of branching points increase with time, independently of environmental conditions. For consensus, we recorded the maximum number of branching points within the perradial area (between 2 adradial canals; Fig. 3).

Oocyte number and size

Oocyte number was quantified from 16 female medusae (8 uninfected and 8 parasitized) of comparable sizes (bell diameter: 80 to 117 mm; $t(14) = 0.19$, $p > 0.05$) collected in spring 2004. Oocyte size was determined from the same individuals collected in spring 2004 and 13 individuals (7 uninfected and 6 parasitized) of similar size (bell diameter: 78 to 101 mm; $t(11) = 0.21$, $p > 0.05$) collected in winter 2006. Gonadal tissue from 2 (out of 4) randomly chosen gastric pouches was excised completely using a Pasteur pipette

and placed on a glass microscope slide. All oocytes in the excised tissue were then counted using microscopy (40 \times). Digital images were taken and used to measure the Feret diameter of oocytes (Lucas & Lawes 1998) using ImagePro Plus[®] software. Since jellyfish gonads usually carry oocytes in various states of development (Eckelbarger & Larson 1988, Lucas & Lawes 1998), we measured only mature oocytes to account for the effect of developmental state in oocyte size. Mature oocytes can be easily recognized by their larger size and pale appearance, which contrasts with the smaller size and darker coloration of immature oocytes (Lucas & Lawes 1998). We measured between 30 and 50 mature oocytes per medusa.

Statistical analyses

Before statistical analyses, prevalence of infection was square-root transformed, while intensity was log transformed. Bell diameter was also log transformed. Normality and homocedasticity were tested by Kolmogorov-Smirnov and Levene's tests, respectively. Differences in prevalence and intensity among seasons were tested using a 1-way ANOVA and Tukey tests for multiple comparisons. Pearson correlations were used to test the potential association of prevalence with depth and temperature, as well as between intensity of infection and bell diameter, within seasons. The effect of parasitism on medusa morphology was first tested by one 2 \times 2 MANOVA per season, with 'age' (i.e. number of branching points) and 'condition' (infested versus uninfested) as main fixed factors. This analysis included bell diameter (log transformed) and 10 morphological features as ratios of bell diameter. Subsequent univariate 2-way ANOVAs and post-hoc Tukey tests were performed for all features. The effect of parasitism on oocyte number was tested with an ANCOVA, with 'condition' as the main factor and 'bell diameter' as covariate. Since mature oocyte diameter did not correlate significantly with medusa size (Pearson correlation: $r < 0.1$, $p > 0.05$), a Student's *t*-test was used to compare mature oocyte size between infected and uninfested individuals within seasons.

RESULTS

Vertical distribution of prevalence

During stratified periods in VJ (spring and summer), parasite prevalence correlated negatively with

depth (summer: $n = 126$; $r = -0.82$, $p < 0.001$; spring: $n = 88$; $r = -0.70$, $p < 0.001$) and consequently correlated positively with water temperature (both seasons: $r = 0.78$, $p < 0.001$; Fig. 4). In winter, when the water column is mixed, prevalence did not correlate significantly with depth ($n = 68$; $r = 0.09$, $p > 0.2$; Fig. 4). Maximum parasite prevalence was observed at the top of the thermocline (10 m depth) in both summer (61% infected, 27°C) and spring (31% infected, 19°C; Fig. 4). As depth increased (and temperature decreased), prevalence steadily decreased and reached its minimum value in layers below the thermocline at 25 m depth in summer (33%, 12°C) and 20 m depth in spring (5%, 11°C), with a slight increase observed in deeper layers (Fig. 4).

Temporal variation in prevalence and intensity of infection

Mean prevalence and intensity of infection varied among seasons (prevalence: $F_{2,8} = 7.14$, $p = 0.02$; intensity: $F_{2,82} = 12.6$, $p = 0.001$; Fig. 5A,B). Both parameters were significantly higher in summer 2003 (prevalence: $43 \pm 4\%$; intensity: $76 \pm 8\%$) than in spring 2004 (prevalence: $24 \pm 6\%$; intensity: $44 \pm 16\%$) and winter 2006 (prevalence: $18 \pm 5\%$; intensity: $37 \pm 12\%$). No significant differences were

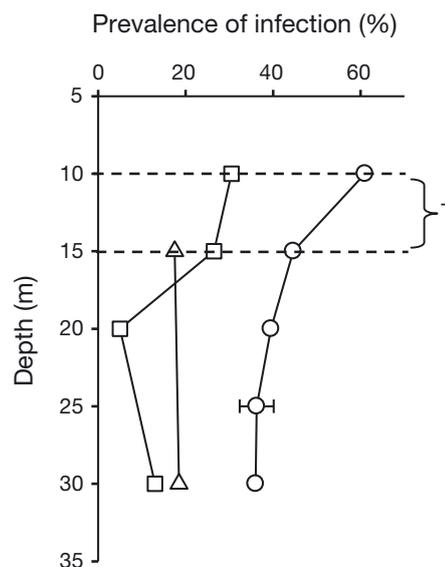


Fig. 4. Vertical distribution of prevalence of infection (%) by *Edwardsiella* sp. in *Aurelia* sp. 5 population from Veliko Jezero in (O) summer 2003, (□) spring 2004 and (Δ) winter 2006. Dashed lines represent the top and bottom of the thermocline (T) during summer 2003 and spring 2004. Note there is no thermocline in the lake during winter months. Horizontal bars represent SE

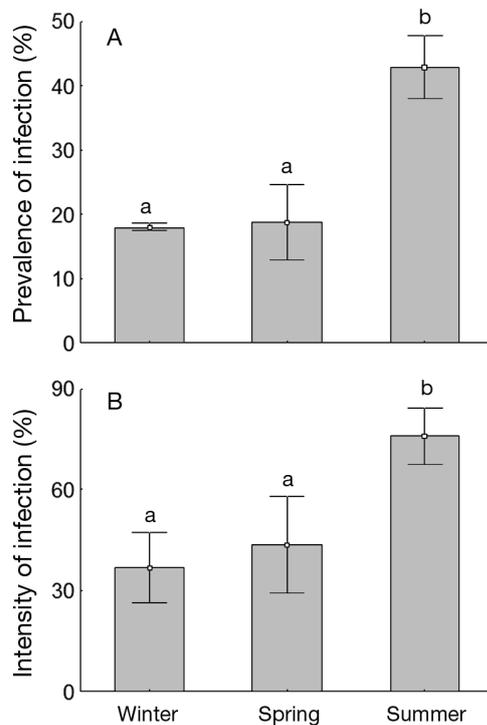


Fig. 5. Mean \pm SE (A) prevalence and (B) intensity of infection by *Edwardsiella* sp. in *Aurelia* sp. 5 medusae from Veliko Jezero in summer 2003, spring 2004, and winter 2006. Means with different letters are significantly different (post-hoc Tukey test: $p < 0.05$)

detected in prevalence and intensity between spring 2004 and winter 2006 (Tukey's $p > 0.05$; Fig. 5A,B). In addition, no significant correlations were detected between intensity of infection and bell diameter in any season (summer 2003: $r = -0.04$; spring 2004: $r = -0.13$; winter 2006: $r = -0.15$; $p > 0.1$ in all cases).

Effect of parasites on medusa size and shape

MANOVA detected significant main effects ('age' and 'condition'), as well as interaction effects ('age \times condition'), in all seasons (Table 1). Therefore, both main factors were included in subsequent univariate analyses. Two-way ANOVAs detected significant effects of parasitism in 4 morphological features including bell diameter (i.e. size), bell height (finesness ratio), manubrium length (manubrium ratio) and gonad size (gonad ratio) (Table 2).

Bell diameter of both infected and uninfected *Aurelia* sp. 5 medusae increased significantly as medusae aged in summer (Table 2, Fig. 6). However, parasitized individuals had a significantly smaller bell diameter than unparasitized counterparts at any

given branching point (Tukey's $p < 0.05$; Fig. 6). In spring and winter the bell diameter of unparasitized medusa increased with the number of branching points (Table 2, Fig. 6), while it did not show a significant increase in parasitized individuals as they aged (Table 2, Fig. 6). Infected medusae were smaller than uninfected counterparts at 6 branching points (Tukey's $p < 0.05$), while bell diameter did not differ between infected and uninfected individuals with 4 and 5 branching points (Tukey's $p > 0.05$; Fig. 6).

The finesness ratio of uninfected medusae increased significantly with age (Tukey's $p < 0.01$; Table 2, Fig. 6), while it significantly decreased in infected medusae as they aged in summer (Tukey's $p < 0.05$; Fig. 6). In spring, the finesness ratio remained constant as both parasitized and healthy medusae aged, while in winter this feature significantly increased only in uninfected individuals (Tukey's $p > 0.05$; Fig. 6). No significant differences in finesness ratio were detected between uninfected and infected medusae in both spring and winter at any given branching point (Tukey's $p > 0.05$; Fig. 6).

The manubrium ratio remained constant in all seasons as both infected and healthy medusae aged (Tukey's $p > 0.05$; Fig. 6). However, parasitized medusae showed a significantly higher manubrium ratio than uninfected individuals at any given branching point in summer (Tukey's $p < 0.01$; Table 2, Fig. 6). No significant differences in manubrium ratio were detected between healthy and parasitized medusae during spring and winter at any given branching point (Table 2, Fig. 6).

The gonad ratio of *Aurelia* sp. 5 medusae was significantly affected by parasitism only during spring

Table 1. Summary of 2-way MANOVA used to test the effect of age (number of branching points) and condition (infected versus uninfected) on the morphology of *Aurelia* sp. 5 medusae from Veliko Jezero during 3 seasons. $p < 0.001$ for all cases

Season	Effect	Wilks' Lambda	F	df Effect	df Error
Summer 2003	Age	0.17	7.38	22	128
	Condition	0.16	8.42	11	64
	Age \times Condition	0.09	28.92	22	128
Spring 2004	Age	0.06	46.34	11	40
	Condition	0.14	41.53	11	40
	Age \times Condition	0.19	7.57	11	40
Winter 2006	Age	0.28	5.98	22	98
	Condition	0.09	22.93	11	49
	Age \times Condition	0.27	6.16	22	98

Table 2. Summary of 2-way ANOVA used to test the effect of age (number of branching points) and condition (infected versus uninfected) on the morphology of *Aurelia* sp. 5 medusae from Veliko Jezero during 3 seasons. Of 11 morphological features analyzed, 4 were significantly different between infected and uninfected individuals (i.e. significant condition or interaction effect) during at least 1 season. All morphological features were converted to ratios of bell diameter before the analysis. NS: non-significant

Feature	Effect	Summer 2003				Spring 2004				Winter 2006			
		df	MS	F	p	df	MS	F	p	df	MS	F	p
Bell diameter	Age	2	0.51	7.95	<0.001	1	0.10	1.96	NS	2	0.12	2.49	NS
	Condition	1	1.64	25.60	<0.001	1	0.05	1.02	NS	1	0.10	2.11	NS
	Age × Condition	2	0.01	0.08	NS	1	0.44	8.73	<0.01	2	0.54	10.90	<0.01
	Error	71	0.06		NS	48	0.05			57	0.05		
Bell height	Age	2	0.00	0.45	NS	1	0.00	2.30	NS	2	0.00	0.08	NS
	Condition	1	0.00	1.70	NS	1	0.00	1.06	NS	1	0.00	0.19	NS
	Age × Condition	2	0.00	9.92	<0.01	1	0.00	0.03	NS	2	0.00	6.38	<0.01
	Error	71	0.00			48	0.00		NS	57	0.00		
Manubrium length	Age	2	0.01	0.57	NS	1	0.00	0.12	NS	2	0.00	0.04	NS
	Condition	1	0.00	75.10	<0.001	1	0.00	1.37	NS	1	0.00	0.79	NS
	Age × Condition	2	0.00	0.05	NS	1	0.00	1.37	NS	2	0.00	1.21	NS
	Error	71	0.00		NS	48	0.00		NS	57	0.00		NS
Manubrium width	Age	2	0.00	1.21	NS	1	0.00	0.18	NS	2	0.00	0.24	NS
	Condition	1	0.00	2.93	NS	1	0.00	0.29	NS	1	0.00	2.36	NS
	Age × Condition	2	0.00	0.77	NS	1	0.00	0.22	NS	2	0.00	0.94	NS
	Error	71	0.00			46	0.00			52	0.00		
Gonad size	Age	2	0.00	9.16	<0.001	1	0.00	0.84	NS	2	0.00	2.16	NS
	Condition	1	0.00	0.59	NS	1	0.00	1.53	NS	1	0.00	0.84	NS
	Age × Condition	2	0.00	3.35	0.04	1	0.00	7.86	<0.001	2	0.00	0.92	NS
	Error	71	0.00			46	0.00			52	0.00		
Oral arm length	Age	2	0.00	0.26	NS	1	0.01	6.56	0.02	2	0.01	2.59	NS
	Condition	1	0.01	1.48	NS	1	0.00	0.35	NS	1	0.00	0.93	NS
	Age × Condition	2	0.00	0.55	NS	1	0.00	2.26	NS	2	0.00	0.66	NS
	Error	71	0.00			48	0.00			57	0.00		
Oral arm width	Age	2	0.00	0.52	NS	1	0.90	82.33	<0.001	2	0.00	0.87	NS
	Condition	1	0.00	1.89	NS	1	0.03	2.79	NS	1	0.00	1.78	NS
	Age × Condition	2	0.00	1.59	NS	1	0.02	1.38	NS	2	0.00	0.02	NS
	Error	71	0.00			48	0.01			57	0.00		
Proximal gastric distance	Age	2	0.01	5.55	0.02	1	0.29	79.67	<0.001	2	0.00	0.37	NS
	Condition	1	0.00	0.29	NS	1	0.01	2.09	NS	1	0.00	3.65	NS
	Age × Condition	2	0.00	2.32	NS	1	0.01	2.31	NS	2	0.00	0.04	NS
	Error	71	0.00			48	0.00			57	0.00		
Distal gastric distance	Age	2	0.00	1.01	NS	1	29.56	97.96	<0.001	2	0.00	0.05	NS
	Condition	1	0.00	0.28	NS	1	0.71	2.34	NS	1	0.00	2.15	NS
	Age × Condition	2	0.01	1.68	NS	1	0.40	1.32	NS	2	0.00	0.07	NS
	Error	71	0.00			48	0.30			57	0.00		
Rhopalar indentation	Age	2	0.00	7.93	0.01	1	0.04	120.20	<0.001	2	0.00	0.14	NS
	Condition	1	0.00	0.49	NS	1	0.00	1.51	NS	1	0.00	3.32	NS
	Age × Condition	2	0.00	2.23	NS	1	0.00	1.99	NS	2	0.00	0.18	NS
	Error	71	0.00			48	0.00			57	0.00		
Non-rhopalar indentation	Age	2	0.00	16.98	<0.001	1	0.00	27.92	<0.001	2	0.00	4.84	0.01
	Condition	1	0.00	1.57	NS	1	0.00	0.43	NS	1	0.00	3.99	NS
	Age × Condition	2	0.00	2.00	NS	1	0.00	0.05	NS	2	0.00	2.54	NS
	Error	71	0.00			48	0.00			57	0.00		

and winter (Table 2, Fig. 6). During these seasons, the gonad ratio remained constant as infected individuals aged (Tukey's $p > 0.05$; Fig. 6), but it increased significantly with age in uninfected medusae (Tukey's $p < 0.01$; Fig. 6). Thus, uninfected medusae had pro-

portionally larger gonads than their infected counterparts at 6 branching points (Tukey's $p < 0.05$), while no significant differences were detected between infected and uninfected individuals with 4 and 5 branching points (Tukey's $p > 0.05$; Fig. 6).

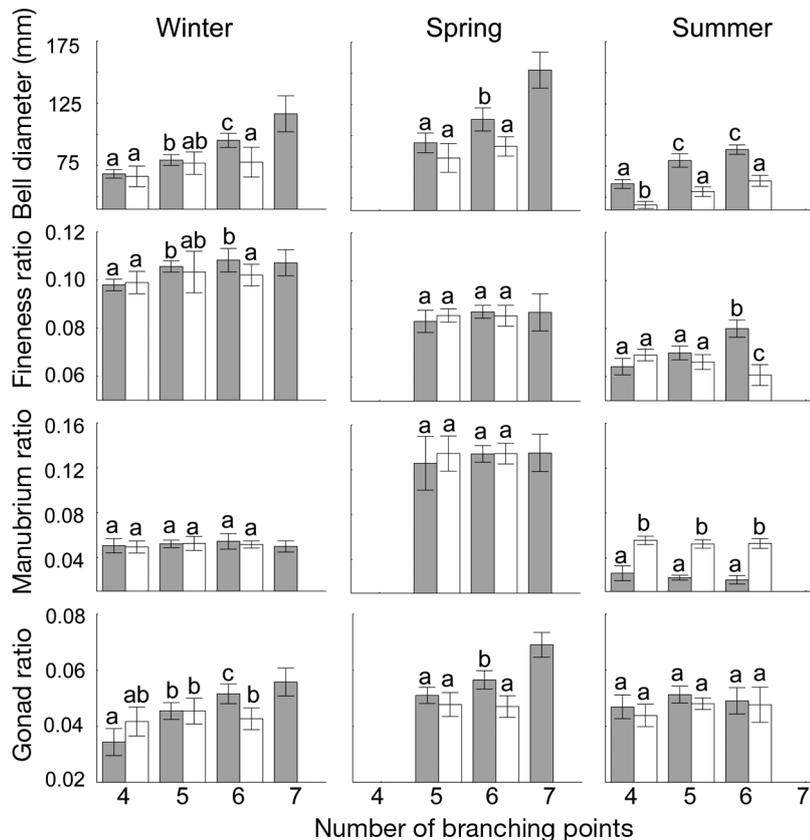


Fig. 6. Morphological features versus age (i.e. number of branching points) in parasitized (open bars) and unparasitized (solid bars) *Aurelia* sp. 5 medusae collected in Veliko Jezero during summer 2003, spring 2004 and winter 2006. Different letters above bars indicate significant differences in mean values determined by post-hoc Tukey tests ($p < 0.05$). Comparisons were performed within seasons. Data are mean \pm SE

Oocyte number and size

Parasitism had a significant effect on the number of oocytes produced by female *Aurelia* sp. 5 medusae collected in spring 2004. The ANCOVA revealed that parasitized medusae produced significantly fewer oocytes than uninfected individuals (ANCOVA: $F_{1,15} = 10.6$, $p < 0.01$; Fig. 7). In addition, the size of mature oocytes was significantly larger in infected individuals than in uninfected counterparts collected in both spring ($t(730) = 3.99$, $p < 0.05$) and winter ($t(533) = 4.05$, $p < 0.05$; Fig. 8).

DISCUSSION

The results of this study demonstrated that infection by *Edwardsiella* sp. larvae induced seasonal-specific phenotypic alterations in *Aurelia* sp. 5 medusae from

VJ. These traits included altered position in the water column, slower somatic and gonad growth, thinner umbrellas, longer manubria, and production of fewer, larger eggs.

The vertical distribution of prevalence (i.e. percentage of host population infected) of infection by *Edwardsiella* larvae on *Aurelia* sp. 5 medusae in VJ varied significantly with depth only during warm, stratified periods (summer and spring). In winter, when the temperature is uniform throughout the water column (Benović et al. 2000), parasite prevalence did not change with depth (Fig. 5). However, in summer and spring, parasitized medusae were proportionally more abundant above and within the thermocline than below it, while healthy individuals showed the opposite pattern (Fig. 5). These observations suggest a difference in behavior between infected and uninfected medusae. Previous studies have shown that during the daytime in summer, spring, and fall *Aurelia* sp. 5 medusae are found in swarms of very high numbers of individuals that spread vertically from slightly above the thermocline (10 to 12 m depth) to deep layers (30 m) and concentrate mostly (~50% of the population) within the sub-thermocline layer (20 m) (Malej et al.

2007, 2009, Alvarez Colombo et al. 2009). Although parasite-induced behavior has been documented for numerous taxa (Moore 2002, Thomas et al. 2005 and references therein), to our knowledge, this is the first report of such phenomenon in jellyfish.

Infected *Aurelia* sp. 5 medusae may be able to increase their daily energy intake and compensate for the effects of parasitism by spending more time foraging within and slightly above the thermocline layers in VJ. Food availability has been previously shown to be significantly higher at the thermocline than in the sub-thermocline and deeper layers in summer, spring and fall (Malej et al. 2007, 2009). Since parasites can impose large nutritive demands upon their hosts through direct competition for resources, parasitized individuals are likely to have higher energy requirements than their healthy counterparts (Coop & Holmes 1996, Metcalfe & Monaghan 2001, Lefèvre et al. 2009). Several studies

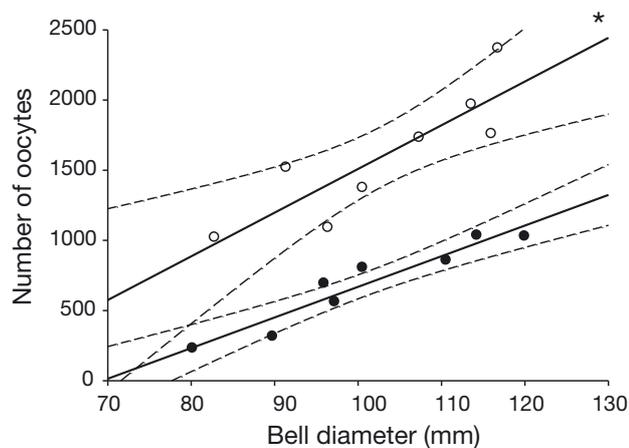


Fig. 7. Linear relationships (solid lines) between number of oocytes and bell diameter in (●) parasitized and (○) unparasitized *Aurelia* sp. 5 medusae from Veliko Jezero in spring 2004. The asterisk denotes a significant effect of parasitism on the relationship (ANCOVA: $p < 0.05$). Dashed lines indicate 95% confidence level

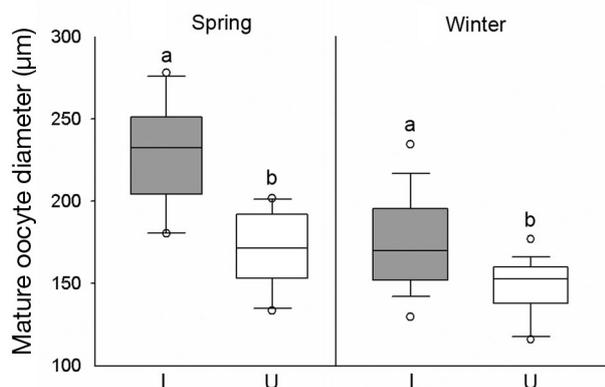


Fig. 8. Mature oocyte size of infected (I) and uninfected (U) female *Aurelia* sp. 5 medusae from Veliko Jezero, collected in spring 2004 and winter 2006. Significant differences in mature oocyte diameter between infected and uninfected individuals per seasons are indicated by different letters (t -test: $p > 0.05$). The horizontal line in each box represents the median. Boxes represent the 25th to 75th percentiles, and whiskers indicate range. Small circles are outliers

have shown that infected hosts must have higher forage rates to compensate for energy loss, which may translate to an altered habitat (or microhabitat) selection (Poulin 1995 and references therein). A similar behavior has been reported in parasitized fish, which maximize their foraging rate to obtain the same nutritional state as unparasitized individuals (Barber & Huntingford 1996, Barber et al. 2000).

Parasite prevalence and intensity (i.e. mean number of parasites per host) varied among seasons, with the highest values observed in summer. Previous studies have shown that *Edwardsiella* larvae typi-

cally infect ctenophores during summer and fall (Reitzel et al. 2007), but they are almost absent during winter. In addition, parasitic larvae of the genus *Peachia* are also found infecting medusae during summer (McDermott et al. 1982, Riascos et al. 2012). Considering *Aurelia* sp. 5 medusae in VJ occur in large numbers throughout the year (Benović et al. 2000, Malej et al. 2007, 2009), the differences observed in both prevalence and intensity of infection among seasons likely reflects the natural dynamics of parasitism in VJ. However, since we assessed prevalence and intensity in different years, our results should be interpreted with caution. Although the seasons included in this study were representative of 'typical years' based on water temperature and salinity (Kogovšek et al. 2012, Miloslavi et al. 2014), potential inter annual differences in host and parasite population size and prey availability (Malej et al. 2009), among others, could have affected the *Edwardsiella*–*Aurelia* relationship in VJ. Further research will be needed to fully understand the host–parasite dynamics in this system.

Infection by anthozoan larvae in VJ also induced morphological changes in *Aurelia* sp. 5 medusae. The results showed that parasitized medusae reached significantly smaller bell diameters than uninfected individuals in all seasons (Fig. 6). Infected medusae also developed thinner umbrellas (i.e. lower fineness ratio; Fig. 6) than their uninfected counterparts during summer, when intensity of infection was high. These findings suggest that parasitism has a negative effect on somatic growth rates of medusae during development, likely as a direct consequence of parasite-induced energy depletion. In addition, parasitized *Aurelia* sp. 5 medusae were unable to increase their fineness ratio as they aged in any given season, which contrasted with the pattern observed in uninfected individuals in most seasons (Fig. 6). This observation suggests that the energy required to sustaining growth in bell diameter and in bell height simultaneously may be too high for infected medusae. Previous studies found that the ctenophore *Mnemiopsis leidyi* exhibited significantly higher growth rates and reached larger size than their counterparts infected by larvae of the anemone *Edwardsiella lineata*, and such differences were attributed to parasites feeding upon food previously ingested or pre-digested by their ctenophore hosts (Bumann & Puls 1996, Reitzel et al. 2007). Similarly, *Edwardsiella* sp. larvae settle predominantly inside the gastric cavities (i.e. stomachs) of *Aurelia* sp. 5 medusae (Fig. 1), and this strategic location can give them direct access to food previously ingested by their hosts.

Not all morphological features of *Aurelia* sp. 5 medusae were negatively affected by parasitism. When intensity of infection was high (summer 2003), infected individuals unexpectedly developed proportionally longer manubria (i.e. higher manubrium ratios) than their healthy counterparts at any given age. In *Aurelia*, the manubrium is a pyramid-like, downward projection of the sub-umbrella considered to be a feeding structure (the mouth sits atop; Arai 1997). To feed, *Aurelia* spp. medusae generate flow currents that allow fluid from outside the bell to entrain the sub-umbrellar area, one of the primary body surfaces involved in prey capture (Heeger & Moller 1987, Costello & Colin 1994, Dabiri et al. 2005). Therefore, by lengthening their manubria infected medusae may be able to increase their sub-umbrellar surface area and potentially maximize their 'capture' area. Similarly, in echinoderms, the Aristotle's lantern, a feeding structure, becomes bigger and larger compared to the overall body size as a plastic adaptive response to low nutrient conditions (Ebert 1996). Therefore, a lengthened manubrium in parasitized *Aurelia* sp. 5 medusae may be interpreted as a plastic response that allows medusae to enhance their daily ration by increasing feeding capacity to compensate for the extra nutritional demands imposed by parasitism.

Reproductive growth of *Aurelia* sp. 5 medusae was also affected by parasitism. Infected medusae developed significantly smaller gonads than their healthy counterparts, not only because they reached significantly smaller bell diameters (Fig. 6), but also due to a negative effect of parasitism directly on gonad growth (Fig. 6). These findings suggest that parasites can diminish the amount of assimilated energy that *Aurelia* sp. 5 medusae would 'normally' invest into both somatic and reproductive growth by competing for resources, potentially translating in negative effects on reproductive capacity (i.e. fecundity), and subsequently on fitness. In *Aurelia* spp., fecundity relates not only to body size (and gonad size), but also to nutritional status (Lucas 2001). Life-history evolution theory states that females will produce many small offspring (*r* strategy) under favorable conditions (e.g. abundant food) and few large offspring (*k* strategy) when conditions are poor (e.g. food limitation) (Stearns 1992, Roff 2002). Our results from female medusae collected in spring 2004 and winter 2006 showed that parasitized individuals produced significantly fewer (Fig. 7), larger eggs (Fig. 8) than uninfected counterparts. These findings suggest potential different reproductive strategies between

infected (*k* strategy) and uninfected (*r* strategy) individuals, perhaps as a result of a parasite-induced poor nutritional state. Lucas & Lawes (1998) showed that *Aurelia aurita* produced few, large planula larvae under food limitation, and many small larvae when food was abundant.

Infected *Aurelia* sp. 5 medusae analyzed in this study produced fewer eggs (i.e. lower fecundity) than uninfected individuals; thus, the energy invested per egg was probably higher than that invested by their unparasitized counterparts. Larger eggs possibly result in production of planula larvae of greater quality (Schneider 1988), and suggests an increase in reproductive effort over somatic growth (Forbes 1993). Since fecundity can only be increased at the expense of offspring size (Jennings et al. 2001), when energy is invested into producing many offspring, resources available for each offspring will be limited (Timi et al. 2005), generating a trade-off between offspring size and offspring number (Guisande et al. 1996, Christians 2000, Brown 2003). Studies on marine invertebrates showed that the amount of organic material in the egg increases with egg size (McEdward & Chia 1991, Pernet & Jaeckel 2004). This mechanism is thought to be an adaptive strategy to maximize reproductive success (i.e. fitness) and to increase offspring survival under unfavorable conditions (e.g. parasitism; Roff 2002).

This work shows that a substantial fraction of *Aurelia* sp. 5 population (~20 to 50%) is infected by *Edwardsiella* sp. larvae throughout the year. Parasitism had significant effects on medusa behavior, morphology, and reproduction. These findings highlight not only the extent of phenotypic change induced by parasites in jellyfish, but also the strategies that jellyfish can generate to cope with parasitism. Although some parasite-induced phenotypic alterations could be interpreted as compensatory, plastic responses from the host to alleviate negative effects of parasitism (e.g. foraging activity, manubrium growth, increased egg size), parasites had overall negative effects on somatic growth, gonad growth, and egg production. These effects likely translate to a parasite-induced reduced fecundity, which can potentially have negative effects on larva production, recruitment, and subsequently on medusa population size. Thus, it is likely that parasites ultimately control/regulate population size of *Aurelia* sp. 5 medusae in VJ. These findings highlight the potential crucial role of parasites as biological controls/regulators of medusa population size in ecosystems worldwide.

Acknowledgements. This paper is dedicated to the memory of our colleagues and dear friends Dr. Adam Benović and Dr. Hermes Mianzán. We thank all members of the 'Croatian Team' and 'Slovenian Team' for their valuable support and assistance in the field, especially to Zeljko Bace, Marko Zari, Vladimir 'Vlado' Onofri, Ivona Onofri, Pavica Sršen, Alenka Malej, and Tihomir Markovec. We deeply appreciate the help of Keith Bayha in the identification of the Actinian parasite via molecular analysis. We also thank Sean Colin, Hermes Mianzán, Laura Linn, Mary-Elizabeth Miller, John Higgins III, and Heather Fletcher for their help in the collection of specimens. We are also grateful to the Mljet National Park authorities for the hospitality during field work. This study was funded by the US National Science Foundation OCE-0623508, OCE-0727587 to J.H.C., and OCE-0425311 to W.M.G.

LITERATURE CITED

- Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–326
- Alvarez Colombo G, Benović A, Malej A, Lučić D and others (2009) Acoustic survey of a jellyfish-dominated ecosystem (Mljet island, Croatia). *Hydrobiologia* 616:99–111
- Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London
- Arai MN (2005) Predation on pelagic coelenterates: a review. *J Mar Biol Assoc UK* 85:523–536
- Barber I, Huntingford FA (1996) Parasite infection alters schooling behavior: deviant positioning of helminth-infected minnows in conspecific groups. *Proc R Soc B* 263:1095–1102
- Barber I, Hoare DJ, Krause J (2000) The effects of parasites on fish behaviour: an evolutionary perspective and review. *Rev Fish Biol Fish* 10:131–165
- Benović A, Lučić D, Onofri V, Peharda M, Carić M, Jasprica N, Bobanović-Čolić S (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
- Bize P, Roulin A, Bersier L, Pfluger D, Richner H (2003) Parasitism and developmental plasticity in Alpine swift nestlings. *J Anim Ecol* 72:633–639
- Brown CA (2003) Offspring size-number trade-offs in scorpions: an empirical test of the van Noordwijk and de Jong model. *Evolution* 57:2184–2190
- Bumann D, Puls G (1996) Infestation with larvae of the sea anemone *Edwardsia lineata* affects nutrition and growth of the ctenophore *Mnemiopsis leidyi*. *Parasitology* 113:123–128
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997). Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitology* 83:575–583.
- Charmantier A, Kruuk LE, Lambrechts MM (2004) Parasitism reduces the potential for evolution in a wild bird population. *Evolution* 58:203–206
- Christians JK (2000) Trade-offs between egg size and number in waterfowl: an interspecific test of the van Noordwijk and de Jong model. *Funct Ecol* 14:497–501
- Condon RH, Graham WM, Duarte CM, Pitt KA and others (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. *Bioscience* 62:160–169
- Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *P Natl Acad Sci USA* 110:1000–1005
- Coop RL, Holmes PH (1996) Nutrition and parasite interaction. *Int J Parasitol* 26:951–962
- Costello JH, Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Mar Biol* 121:327–334
- D'Ambra I, Graham WM (2009) Early developmental sequence of an anthozoan parasite of the jellyfish *Aurelia* sp.5 in an isolated marine lake (Mljet, Croatia). *Ann Ser Hist Nat* 19:59–64
- Dabiri JO, Colin SP, Costello JH, Gharib M (2005) Flow patterns generated by oblate medusan jellyfish: field measurements and laboratory analyses. *J Exp Biol* 208:1257–1265
- Daryanabard R, Dawson MN (2008) Jellyfish blooms: *Crambionella orsini* (Scyphozoa: Rhizostomeae) in the Gulf of Oman, Iran, 2002–2003. *J Mar Biol Assoc UK* 88:477–483
- Dawson MN, Jacobs DK (2001) Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria: Scyphozoa). *Biol Bull* 200:92–96
- Delannoy CM, Houghton JD, Fleming NE, Ferguson HW (2011) Mauve stingers (*Pelagia noctiluca*) as carriers of the bacterial fish pathogen *Tenacibaculum maritimum*. *Aquaculture* 311:255–257
- Dittrich B (1988) Studies on the life cycle and reproduction of the parasitic amphipod *Hyperia galba* in the North Sea. *Helgol Meeresunters* 42:79–98
- Dong Z, Liu D, Keesing JK (2010) Jellyfish blooms in China: dominant species, causes and consequences. *Mar Pollut Bull* 60:954–963
- Doyle TK, De Haas H, Cotton D, Dorschel B and others (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *J Plankton Res* 30:963–968
- Ebert TA (1996) Adaptive aspects of phenotypic plasticity in echinoderms. *Oceanol Acta* 19:347–355
- Eckelbarger KJ, Larson RL (1988) Ovarian morphology and oogenesis in *Aurelia aurita* (Scyphozoa: Semaestomae): ultrastructural evidence of heterosynthetic yolk formation in a primitive metazoan. *Mar Biol* 100:103–115
- Fenner P, Williamson J, Burnett J (1996) Clinical aspects of envenomation by marine animals. *Toxicol* 34:0041-0101
- Fenner PJ, Lippmann J, Gershwin LA (2010) Fatal and non-fatal severe jellyfish stings in Thai waters. *J Travel Med* 17:133–138
- Forbes MRL (1993) Parasitism and host reproductive effort. *Oikos* 67:444–450
- Graham WM, Chiaverano L, D'Ambra I, Mianzán H and others (2009) Fish and jellyfish: using the isolated marine 'lakes' of Mljet Island, Croatia, to explore larger marine ecosystem complexities and ecosystem-based management approaches. *Ann Ser Hist Nat* 19:39–48
- Guisande C, Sanchez J, Maneiro I, Miranda A (1996) Trade-off between offspring number and offspring size in the marine copepod *Euterpina acitifrons* at different food concentrations. *Mar Ecol Prog Ser* 143:37–44
- Heeger T, Moller H (1987) Ultrastructural observations on prey capture and digestion in the scyphomedusa *Aurelia aurita*. *Mar Biol* 96:391–400
- Horwitz P, Wilcox BA (2005) Parasites, ecosystems and sustainability: an ecological and complex systems perspective. *Int J Parasitol* 35:725–732
- Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? *Trends Ecol Evol* 21:381–385

- Jennings S, Kaiser MJ, Reynolds JD (2001) Marine fisheries ecology. Blackwell Science, Oxford
- Koehl MAR (1996) When does morphology matter? *Annu Rev Ecol Syst* 27:501–542
- Kogovšek T, Molinero JC, Lučić D, Onofri I and others (2012) Interannual size changes of adult *Aurelia* sp. 5 medusae stage in the Marine Protected Area of Mljet Island South Adriatic. *Acta Adriat* 53:233–242
- Krist AC (2000) Effect of the digenean parasite *Proterometra macrostoma* on host morphology in the freshwater snail *Elimia livescens*. *J Parasitol* 86:262–267
- Kuris AM, Hechinger RF, Shaw JC, Whitney KL and others (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454: 515–518
- Lefèvre T, Lebarbenchon C, Gauthier-Clerc M, Missé D, Poulin R, Thomas F (2009) The ecological significance of manipulative parasites. *Trends Ecol Evol* 24:41–48
- Lucas CH (2001) Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 451:229–246
- Lucas CH, Lawes S (1998) Sexual reproduction of the scyphomedusa *Aurelia aurita* in relation to temperature and variable food supply. *Mar Biol* 131:629–638
- Malej A, Turk V, Lučić D, Benović A (2007) Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea). *Mar Biol* 151:827–841
- Malej A, Turk V, Kogovšek T, Makovec T and others (2009) *Aurelia* sp. 5 (Scyphozoa) population in the Mljet lake (the southern Adriatic): trophic interactions and link to microbial food web. *Ann Ser Hist Nat* 19:49–58
- Marcogliese DJ, Cone DK (1997) Food webs: a plea for parasites. *Trends Ecol Evol* 12:320–325
- Martorelli SR (2001) Digenea parasites of jellyfish and ctenophores of the southern Atlantic. *Hydrobiologia* 451: 305–310
- McDermott JJ, Zubkoff PL, Lin AL (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
- McEdward LR, Chia FS (1991) Size and energy content of eggs from echinoderms with pelagic lecithotrophic development. *J Exp Mar Biol Ecol* 147:95–102
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260
- Miloslavić M, Tinta T, Molinero JC, Kogovšek T and others (2014) Mljet Lake (South Adriatic Sea) as a natural laboratory for assessing warming effects on plankton. In: 2nd Int Ocean Res Conf, Barcelona, 16–21 Nov 2014. Program and abstracts. UNESCO IOC, Paris, p 88
- Minchella DJ, Loverde PT (1981) A cost of increased early reproductive effort in the snail *Biomphalaria glabrata*. *Am Nat* 118:876–881
- Miyake H, Iwao K, Kakinuma Y (1997) Life history and environment of *Aurelia aurita*. *South Pacific Studies* 17: 273–285
- Moller AP (1993) Ectoparasites increase the cost of reproduction in their hosts. *J Anim Ecol* 62:309–322
- Moore J (2002) Parasites and the behaviour of animals. Oxford University Press, Cary, NC
- Nagata RM, Haddad MA, Nogueira M Jr (2009) The nuisance of medusae (Cnidaria, Medusozoa) to shrimp trawls in central part of southern Brazilian Bight, from the perspective of artisanal fishermen. *Panam J Aquat Sci* 4:312–325
- Pernet B, Jaeckel WB (2004) Size and organic content of eggs of marine annelids, and the underestimation of egg energy content by dichromate oxidation. *Biol Bull* 207: 67–71
- Poulin R (1995) 'Adaptive' changes in the behavior of parasitized animals: a critical review. *Int J Parasitol* 25: 1371–1383
- Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Annu Rev Mar Sci* 4:209–235
- Reitzel AM, Sullivan JC, Brown BK, Chin DW and others (2007) Ecological and developmental dynamics of a host-parasite system involving a sea anemone and two ctenophores. *J Parasitol* 93:1392–1402
- Riascos JM, Vergara M, Fajardo J, Villegas V, Pacheco AS (2012) The role of hyperiid parasites as a trophic link between jellyfish and fishes. *J Fish Biol* 81:1686–1695
- Roff DA (2002) The evolution of life histories: theory and analysis. Chapman & Hall, New York, NY
- Ruiz GM (1991) Consequences of parasitism to marine invertebrates: host evolution? *Am Zool* 31:831–839
- Schneider G (1988) Chemical composition and biomass parameters of the common jellyfish *Aurelia aurita* (In German with English Abstract). *Helgol Meeresunters* 42: 319–327
- Schroth W, Jarms G, Streit B, Schierwater B (2002) Speciation and phylogeography in the cosmopolitan marine moon jelly, *Aurelia* sp. *BMC Evol Biol* 2:1
- Selander E, Moller L, Sundberg P, Tiselius P (2009) Parasitic anemone infects the invasive ctenophore *Mnemiopsis leidyi* in the North East Atlantic. *Biol Invasions* 12: 1003–1009
- Spaulding JG (1972) The life cycle of *Peachia quinquecapitata*, and anemone parasitic on medusae during its larval development. *Biol Bull* 143:440–453
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Thomas F, Adamo S, Moore J (2005) Parasitic manipulation: where are we and where should we go? *Behav Processes* 68:185–199
- Timi JT, Lanfranchi AL, Poulin R (2005) Is there a trade-off between fecundity and egg volume in the parasitic copepod *Lernanthropus cynoscolica*? *Parasitol Res* 95:1–4
- Towanda T, Thuesen EV (2006) Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. *Mar Ecol Prog Ser* 315:221–236
- Wood CL, Byers JE, Cottingham KL, Altman I, Donahue MJ, Blakeslee AMH (2007) Parasites alter community structure. *Proc Natl Acad Sci USA* 104:9335–9339