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RESEARCH ARTICLE

Direct and indirect trophic interactions of *Aurelia* sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea)

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Abstract The pattern of diel vertical migration and the trophic interactions of moon jelly (*Aurelia* sp.) were investigated in the sea lakes of Mljet Island (Adriatic Sea) where this scyphomedusa is present throughout the year. Water column characteristics, plankton and in situ behaviour of *Aurelia* were followed over several 24-h cycles (6–8 times during each cycle) from the surface to the bottom (44 m). *Aurelia* exhibited a consistent pattern of diel vertical migration. Most of the time *Aurelia* were located at the bottom of the thermocline layer at temperatures lower than 19°C. *Aurelia* migrated towards the surface at dusk when the majority was found within the thermocline or just above it. During the night the medusae sank into the deepest layers below 25 m. The main medusa food items inferred from stomach contents were small adult copepods like *Oithona nana* and *Paracalanus parvus* and copepodites of small calanoids and cyclopids. In addition, in situ feeding experiments indicated high clearance rates for nauplii and naked ciliates and clear response of bacterial populations pointing to indirect cascade effects of *Aurelia* on microbial in addition to classical food web.

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Introduction

In many areas worldwide there is strong evidence for changes in plankton communities, over recent decades (Hays et al. 2005), an increase in the frequency and intensity of jellyfish outbreaks is among most evident (Purcell et al. 2001; Dumont et al. 2004). Some studies have indicated a correlation between high jellyfish abundance and increased eutrophication (Papathanasiou et al. 1987) but Purcell et al. (1999) argued that the connections between jellyfish population size and eutrophication are difficult to make because of the lack of appropriate historical data. Arai (2001) concluded that increases in coelenterates could rarely be unequivocally linked to eutrophication. Long-term fluctuations in jellyfish abundance have been associated with climatic changes (Brodeur et al. 1999; Mills 2001; Molinero et al. 2005), which, in turn, mediated trophic regime shifts (Lynam et al. 2004). The decline of fish competitors due to over-fishing has also been suggested as factor favouring jellyfish and contributing to regime shift (Daskalov 2002; Sommer et al. 2002). When very numerous, jellyfish play an important trophic role (Mills 1995; CIESM 2001), if massive occurrences persist, ecosystem structure and functioning may change (Kideys 2002). Dramatic changes in zooplankton and a strong decline of the pelagic fishery have been attributed to predation and competition by pelagic coelenterates (Hay et al. 1990; Niermann 2004), although the significance of such interactions to either fish or jellyfish populations is still poorly understood (Purcell and Arai 2001).

Most studies of the trophic interactions of jellyfish and their impact concentrated on mesozooplankton. Despite some evidence of jellyfish preying on micro-

zooplankton (Stoecker et al. 1987; Sullivan et al. 1994; Fukuda and Naganuma 2001) little is known about the cascading impact of jellyfish predation on the microbial food web, via indirect trophic linkages. Laboratory and in situ studies have demonstrated the influence of grazers of different size fractions (nano, micro and mesozooplankton) on the microbial food web (Azam et al. 1983; Calbet and Landry 1999). The heterotrophic part of the microbial food web appears to contain several trophic levels, representing a link to higher animals (Sherr and Sherr 1988; Wikner and Hagström 1988; Turk and Hagström 1997). Larger protists, copepods and other planktonic grazers are known to be the main predators on nanoflagellates, and these, in turn, are dominant bacteriovores (Stoecker and Capuzzo 1990; Verity 1991; Deibel and Lee 1992). Recent studies have described the ingestion of bacteria by the naupliar and juvenile copepodite stages of small copepod species, Cladocera, and pelagic tunicates (Turner et al. 1988; Deibel and Lee 1992; Bedo et al. 1993), which in turn may represent food items for jellyfish (Omori et al. 1995; Purcell and Sturdevant 2001; Barz and Hirche 2005). In any case, direct or indirect trophic interactions are likely to be central for understanding changes in jellyfish abundance as well as their effects on the marine ecosystem.

Among macroscopic jellyfish that recurrently appear in great densities, *Aurelia* is the most widespread. It forms large aggregations particularly in enclosed seas such as the Black Sea, the Baltic and the Seto Inland Sea, in protected coastal waters i.e. bays, fjords, estuaries and enclosed water bodies (Möller 1980; Hay et al. 1990; Hamner et al. 1994; Schneider and Behrends 1994; Omori et al. 1995; Ishii and Båmstedt 1998; CIESM 2001; Fukuda and Naganuma 2001; Kideys and Romanova 2001; Mutlu 2001; Xian et al. 2005). Swarms of *Aurelia* are more common in shallow cold and temperate regions with lower salinities; however, aggregations were also observed in warm to tropical euhaline waters (Hamner et al. 1982; Papathanassiou et al 1987; Avian and Rottini 1994; Dawson and Martin 2001). Despite many field and laboratory studies there are still controversies regarding the prey and feeding of *Aurelia* (Sullivan et al. 1994; Graham and Kroutil 2001) and consequently their effects on the plankton food web. Behavioural characteristics like the presence/absence of migration behaviour can also be expected to have important consequences for trophic interactions in environments where this species forms dense aggregations. There is evidence from field and laboratory results that *Aurelia* is flexible in its migration patterns (Mackie et al. 1981; Hamner et al. 1982, 1994), undertaking diurnal vertical migrations, no vertical migration and/or horizontal migrations in relation to sun orientation.

Our study of *Aurelia*'s vertical migration, feeding and the cascading effects of *Aurelia* predation were carried out in the Mediterranean euhaline enclosed water body, where dense swarms were observed (Benović et al. 2000). A seawater lake situated on the southern Adriatic island of Mljet has been part of a national park for more than 40 years; hosts a large *Aurelia* population with medusae presents throughout the year and thus provides an excellent study site without direct human impact. In particular, our study concentrates on *Aurelia* vertical migration in a stratified water column and the impact on microbial plankton that has been ignored in past studies of jellyfish trophic interactions.

Materials and methods

Study area

Veliko Jezero (Big Lake), a submerged karstic valley, is situated on the north-western side of Mljet, an offshore south Adriatic island that extends in a NW–SE direction (Fig. 1). Big Lake (BL) has a surface area of 1.45 km^2 and a maximum depth of 46 m. Exchange between this enclosed marine lake and open Adriatic waters is established through a 1 km long, 10 m wide channel that has been artificially deepened to a depth of about 3.8 m (Ridžanović and Šimunović 1995). The whole north-western part of the island of Mljet including BL has been protected as a national park since 1960.

The environmental and biological characteristics of BL are mainly defined by lake bathymetry and restricted communication with the open sea through the channel. Tides are weak with a tidal range of <25 cm. The waters of BL are generally calm since BL is surrounded by shores with inclinations of 12°–32° towards the south and west, and 32°–55° towards north and east (Bognar and Čurić 1995). During the summer months a strong thermocline at a depth of around 12–20 m influences hydrographical, chemical and biological parameters (Vučetić 1957; Kršinić 1995). The water mass below this layer is characterized by stable conditions with low temperatures (10–12°C) and high salinity (37.5–38.5 psu) throughout the year. Higher values of nutrients and nanophytoplankton were measured in this layer compared to the surface (Benović et al. 2000). During late summer maximal surface temperatures are around 26°C but may reach 28°C.

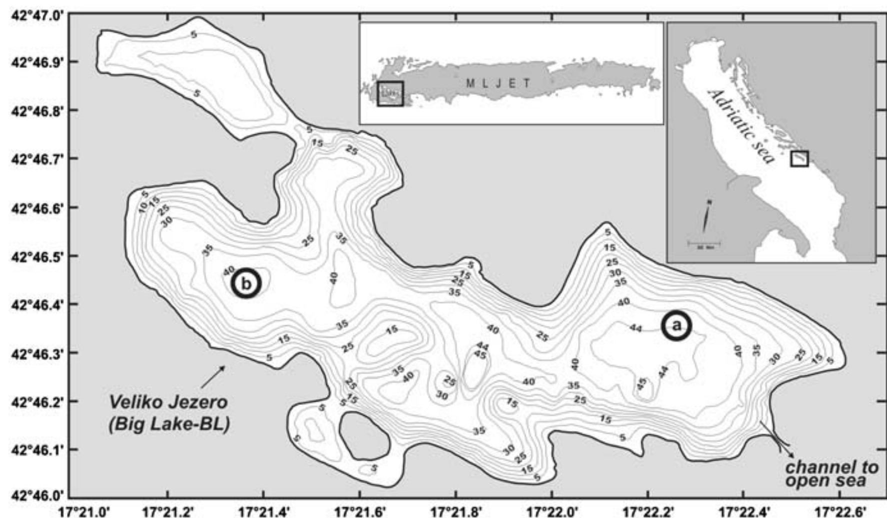

Fig. 1 Location of study sites (**a**, **b**), bathymetry of Big Lake and the geographic position of the Island Mljet in the southern Adriatic Sea

The salinity of the surface layer is also more variable (36.3–38.6 psu) compared to deeper layers. Phytoplankton structure and density are similar to that in neighbouring open Adriatic waters with a maximal abundance of microphytoplankton and nanophytoplankton of around 4.0×10^4 and 4.5×10^6 l^{-1}, respectively (Jasprica et al. 1995). Jasprica (pers. comm.) identified 78 microphytoplankton species in lake, which is comparable to 83 species he found in neighbouring open Adriatic waters. In contrast, zooplankton in BL are characterised by lower abundances and a remarkably reduced number of species compared to neighbouring open Adriatic waters. For example: 22 species of copepods were found in BL versus 53 species at a location about 300 m from the opening of the Lake's channel to open Adriatic waters. Abundances assessed using zooplankton net with 250-µm meshes was not that different (max. 581 in lake vs. 879 ind. m^{-3} outside, Lučić et al. 1995). Among copepods *Oithona nana* is the dominant species in BL with an annual average contribution to total mesozooplankton of 43% followed by *Paracalanus parvus* (26%) and *Oithona similis* (21%). Other Copepods (*Calanus helgolandicus, Acartia clausi, Isias clavipes, Diaixis pygmaea*) contributed less than 5% of total copepod abundance (Lučić, unpubl. data). *Oithona nana* dominates the surface and thermocline layers while *Calanus helgolandicus, Diaixis pygmaea* and *Oithona similis* are found in the deeper layer (>20 m). Other zooplankton groups that have been recorded in significant numbers throughout the year in BL are *Oikopleura dioica*, *Sagita setosa*, as well as Bivalvia and Gastropoda larvae. Copepod nauplia and ciliates are dominant microzooplankton groups that are most abundant in the surface 10 m (Kršinić 1995). An important component of the BL zooplankton that is absent in open Adriatic waters around offshore Mljet island, is the jellyfish *Aurelia*. This jellyfish is present in the shallow northern Adriatic and some semi-enclosed bays along eastern Adriatic. It has traditionally been termed *A. aurita* although molecular criteria used in recent studies questioned this designation (Schroth et al. 2002; Dawson 2003); therefore we prefer to use *Aurelia sp*. Abundance of *Aurelia* in BL may reach 10 ind. m^{-3} and up to a few hundred in swarms (Benović et al. 2000).

Environmental parameters, vertical distribution and stomach content of *Aurelia sp.*

The water column structure, plankton characteristics and vertical distribution of *Aurelia*, were studied in 2003 (4–18 July) and 2004 (16–23 May) in the two deepest areas of BL (Fig. 1, open circles a, b). The vertical distribution of temperature, salinity, and fluorescence were determined using a CTD fine-scale probe (University of Western Australia and a Sea-Tech inc. fluorometer). The vertical distribution of *Aurelia* was estimated using a Sony DCR-VX200E video camera enclosed in an underwater housing (Ikellite) equipped with two 100 W lights and a depth gauge. The dimension of the imaged area of the video camera was assessed according to Youngbluth and Båmstedt (2001) and was 2.3 m^2. The camera was lowered at a speed of about 2 m min^{-1} until the bottom was visible. The depth of occurrence of medusae was recorded and the abundance of *Aurelia* was estimated in the laboratory. We used digital video playback and "frame by frame" mode to estimate *Aurelia* abundance and orientation. Afterwards medusae abundances were pooled in four separate layers according to CTD depth

profiles: above thermocline, within thermocline, below thermocline and deep layer (below 25 m). In addition, the mean vertical position (MVP), i.e. weighted mean depth (Schabetsberger et al. 2000) of the *Aurelia* population in the water column was calculated using the method of Pearre (1973):

$$\mathrm{MVP} = \sum n_i d_i / \sum n_i$$

where

n_i is the total number of *Aurelia* recorded over a depth range i (2 m), and

d_i is the mid-point of depth range i.

We also recorded radial orientation of medusae in the plane of image: medusae with aboral surface straight up and angled up (i.e. animals were swimming upwards either straight up or under an angle) were assigned to category up, individuals swimming straight down or angled down (aboral surface straight down and angled down) were assigned to category down, to last category horizontal were assigned individuals swimming in horizontal plane. Additional information on *Aurelia*'s vertical distribution was provided by divers who quantified the number of medusae in their field of view as none, rare, dense, and very dense. Medusae bell diameters were measured for *Aurelia* collected by divers during five video recordings. Individuals were spread flat on a glass plate and the bell diameter was recorded to the nearest 1 mm. *Aurelia* were collected individually by divers for stomach content analysis. Freshly collected animals were brought aboard the research boat where they were dissected immediately. Stomach, canals and gastric pouches we examined for prey organisms which were identified to genus or species level.

Aurelia feeding experiments

We carried out five in situ feeding experiments: 8 July, 10–11 July, 12–13 July 2003 and 18–19 May, 22 May 2004. *Aurelia* feeding experiments were carried out in large enclosures made of clear acrylic plastic with a volume of 110 l, and additionally, in polycarbonate enclosures with a volume of 8 l, which were all incubated in situ (Fig. 2). The natural plankton assemblage at ambient concentration was the food source for the enclosed *Aurelia*. On the basis of CTD and video camera casts we selected incubation depths for the large and small enclosures: the former were incubated within the thermocline layer (14 m in 2003, and 12 m in 2004) and the latter in the surface layer (5 m) and below the thermocline layers (25 m). Experiments in small enclosures were carried out only during 2003. Since no light/dark difference in the feeding rate was found (Bailey and Batty 1983) and in accordance with our observations of *Aurelia* migration towards the surface layers at dusk, we decided to start feeding experiments between 7 and 8 p.m.

Two large enclosures were lowered open (the top and bottom were removable) to a pre-selected depth where the bottoms were then sealed. Both enclosures thus contained plankton at that depth. Divers collected medusae individually close to the incubation depth and placed them gently in one enclosure while the second served as control and contained the natural plankton assemblage without medusae. After putting 15 *Aurelia* in one enclosure the tops of both were also sealed. In addition, plankton was pumped from 5 and 25 m depths into four 8 l Nalgene bottles; into two of these we added 1 *Aurelia* while two served as controls. These experimental bottles, one with *Aurelia* and one control, were incubated at depths above the thermocline (5 m) and below the thermocline (25 m) (see Fig. 2 for the experimental set-up schema and underwater photo of the large enclosures). Feeding experiments lasted for 6–7 h and changes in the abundance of the enclosed plankton assemblage were compared. Bell diameter of *Aurelia* used in feeding experiments varied between 7.5 and 10.1 (8.4 ± 0.7) cm for July 2003 experiments and 6.2 and 12.6 (9.2 ± 2.1) cm for May 2004 experiments. After recovering *Aurelia*, samples were taken for bacteria (50 ml), phytoplankton (1 l), and microzooplankton (5 l) from all enclosures. In addition, mesozooplankton samples were collected from the two large enclosures filtering all remaining water, after other samples were withdrawn, through 125 μm mesh. Clearance (F) for specific taxa was calculated (Båmstedt et al. 2000) from the equation:

$$F = \ln[(C_0/C_t)] \times V/t \times n$$

where

C_0 and C_t = number of prey organisms at time 0 and t, respectively,

t = incubation time (hours),

V = volume of the experimental bottle,

n = number of medusae.

Plankton collection and analyses

Plankton samples were collected at the beginning of each feeding experiment. Samples of phytoplankton, bacterioplankton, and microzooplankton were taken with a 5-l Niskin bottle at several depths according to the physical structure of the water column: above the thermocline (0.5, 5 m), in the middle of the thermo-

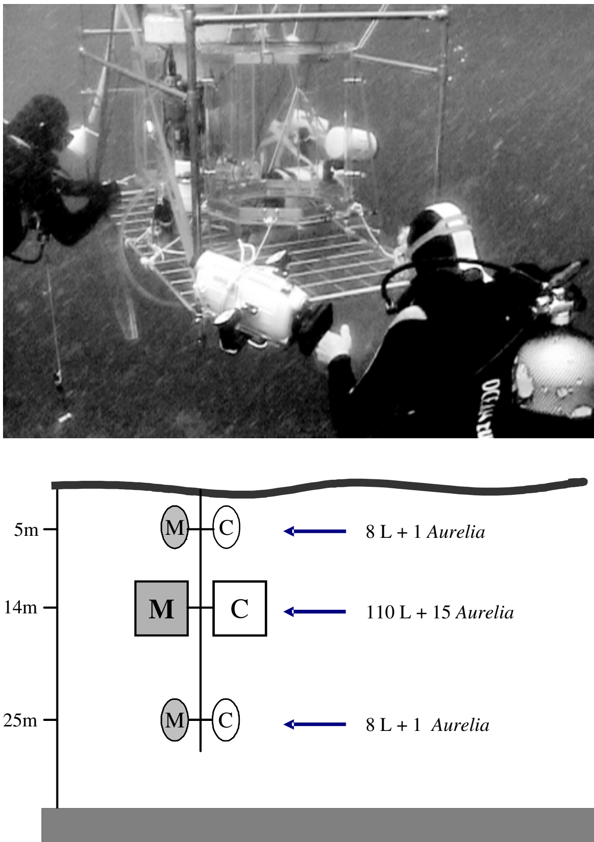

Fig. 2 The experimental set-up for in situ feeding experiments with *Aurelia*: an underwater photo of a large (110 l) enclosure (*top*) and a schematic presentation (*bottom*) of all enclosures. *Squares* on the schema indicate 110 l enclosures incubated at thermocline depth while *circles* represent 8 l nalgene bottles incubated above (5 m) and below (25 m) the thermocline. Enclosures marked with *M* contained 15 medusae (large enclosures) or 1 *Aurelia* (nalgene bottles); *C* indicates enclosures containing natural plankton assemblages only

cline layer (14 and 10 m in July 2003 and May 2004, respectively) and below the thermocline (25 m). Mesozooplankton were collected by vertical tows (a Nansen net equipped with a closing system, 125 µm mesh, 54 cm diameter) at depth intervals of 40–20, 19–10, 9–0 m as rough approximations of below thermocline, thermocline and above thermocline layers.

Formaldehyde-fixed samples of microzooplankton and mesozooplankton were analysed according to standard procedures (Postel et al. 2000). Seawater samples for heterotrophic bacteria counts were fixed with formalin (2% final concentration) and stained with 4′6-diamidino-2-phenylindole (DAPI) then filtered on 0.2 µm black polycarbonate filters (Poretics) (Porter and Feig 1980). Bacterial abundance was converted into carbon biomass using 19.8 fg C $cell^{-1}$ as the conversion factor (Lee et al. 1987). Autofluorescent cyanobacteria were counted in green excitation light (Takahashi et al. 1985). Bacterial protein synthesis rates were measured using ^{3}H-leucine by applying the centrifugation method described by Smith and Azam (1992). For each determination, three replicates containing seawater only were incubated with ^{3}H-leucine (final concentration 20 nM) for 2 h. Incubation was stopped by adding concentrated trichloracetic acid (TCA) to a final concentration of 5%. In addition, two replicates were treated with TCA (final concentration of 5%) before the addition of ^{3}H-leucine, and served as blanks. After incubation, all samples were centrifuged, aspirated, washed, and, after the addition of a scintillation cocktail (Ultima Gold, Packard), were counted in a scintillation counter (TR2500, Packard). Incorporation rates of ^{3}H-leucine were converted to bacterial carbon production according to Simon and Azam (1989).

Feeding of *Oithona nana* on radio labelled bacteria

Feeding experiments and stomach content analyses indicated adults and copepodites of *Oithona nana* as important food items of *Aurelia*. Expanding upon this, during experiment in 2004 we tested the possibility of a direct trophic loop between these small copepods and bacteria using a radiolabeled culture of the natural bacterial assemblage from the lake to feed *Oithona nana*.

The work procedure was similar to that used by Turk and Hagström (1997) and described in detail by Båmstedt et al. (2000). The detailed experimental schema is shown in Fig. 3. The culture of bacteria for radiolabeling was prepared with 340 ml of seawater from BL filtered through 0.6 µm filters (Poretics membrane filters, Osmonics) to remove all bacteriovores. Bacteria were inoculated with ^{3}H-thymidine (specific activity 82 Ci $mmol^{-1}$) and then incubated in the dark at room temperature for 24 h. When the concentration of bacteria reached a density of approx. $10 \times 10^{8}\ l^{-1}$ the culture was divided into five subsamples and inoculated with 15 individuals of *Oithona nana* in 50 ml tubes (sterile Brand tubes). Replicate samples of the labelled bacteria were taken for initial measurement of isotope activity (expressed as disintegrations per minute, dpm). *Oithona nana* was isolated from natural plankton samples by the filtration of seawater through a plankton net with a 1 mm mesh size to remove larger organisms. In the filtrate, *Oithona nana* were picked out individually under a stereomicroscope (Olympus SZX9) and washed in prefiltered seawater (through 0.22 µm) three times successively. They were starved in particle and organism free seawater (0.22 µm filtered seawater) for 2 h before the

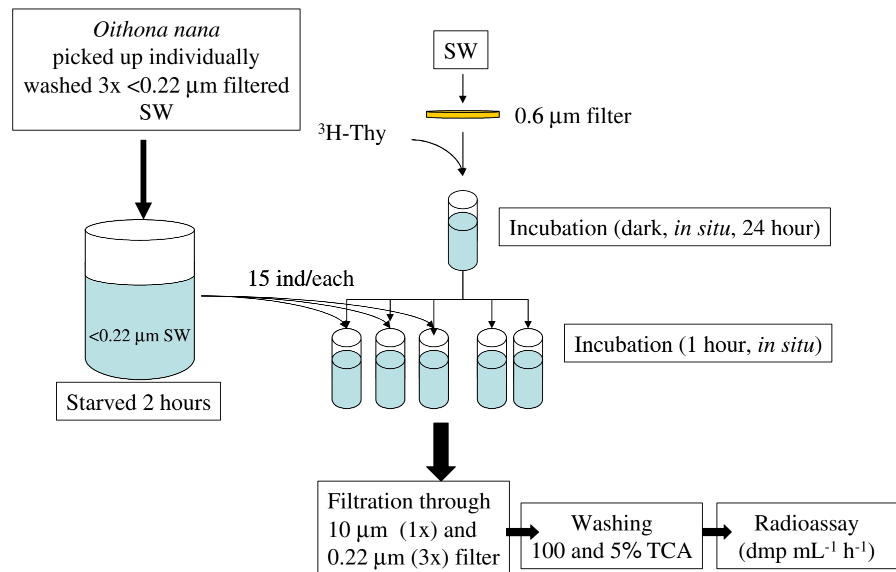

Fig. 3 Schema of the experimental set-up showing procedures used for the *Oithona nana* feeding experiment with radiolabeled bacteria

experiment with the labelled bacteria. Fifteen individuals of *Oithona nana* were added to each tube containing labelled bacteria in triplicates, and incubated for 1 h in situ (in the sea at 2 m depth). As a blank, two subsamples (50 ml) with bacteria only were incubated under the same conditions and for the same incubation time. Subsamples were taken at the beginning and at the end of the incubation period for bacterial counts and isotope activity analysis. Seawater (5 ml) from each incubated tube was filtered through 0.22 µm pore size Poretics filters in triplicates. Each filter was well washed three times with trichloracetic acid (TCA) to a final concentration of 100%. After incubation, *Oithona nana* was collected on 10 µm Poretics filters rinsed abundantly three times with filtered seawater to wash off any remaining label and finally washed three times with 100% TCA. The number of individuals trapped on the filter was controlled under the stereomicroscope. In the laboratory, after addition of scintillation cocktail (Ultima Gold, Packard), samples were counted in a scintillation counter (TR2500, Packard) and the results expressed as dpm (disintegrations per minute).

Results

Environmental conditions and plankton vertical distribution

During both periods of our study the water column was stratified with the thermocline depth between the 10–15 and 9–14 m in July 2003 and May 2004, respectively. Surface temperatures were above 25°C in July 2003 and about 20°C in May 2004 while bottom temperatures were close to 10°C in both years (Fig. 4). In May 2004 a slight halocline was also noticeable at the same depth as the thermocline, while in July 2004 salinity was rather homogeneous throughout the water column.

Phytoplankton biomass was low in the layer above the thermocline as indicated by fluorescence. With decreasing temperature oxygen concentrations increased with depth but in the deep layers oxygen diminished. In July 2003 the average concentration of chlorophyll *a* in the surface layer (5 m) was 0.15 (0.1–0.42) µg Chl *a* l^{-1}, at the thermocline layer 0.31 (0.24–0.5) µg Chl *a* l^{-1} and below the thermocline layer (25 m) 0.23 (0.1–0.35) µg Chl *a* l^{-1}. Similar chlorophyll *a* concentrations but with slightly higher values in the above thermocline layer were also measured in 2004 (0.1–0.5 µg Chl *a* l^{-1}, Flander Putrle, unpubl. data). The abundance of cyanobacteria varied from 1.9 to 4.6×10^7 l^{-1} with the maximal values within the thermocline.

The abundance of heterotrophic bacteria varied between 5.3 and 8.9×10^8 cells l^{-1}, showing a slight increase with the depth in July 2003. The abundance was slightly lower in May 2004 with highest values (6.9×10^8 cells l^{-1}) in the surface layer (Fig. 5, top). Bacterial carbon production measured by the ^{3}H-leucine method varied from 0.3 to 2.8 µg C l^{-1} d^{-1} and was the lowest in deep layers in both years (Fig. 5, bottom).

Both, microzooplankton and mesozooplankton were more abundant in the upper water column (above and within the thermocline layers) either in July 2003 (Fig. 6, top) or May 2004 (Fig. 6, bottom). Microzooplankton was dominated by small nauplii and naked ciliates (Fig. 6, lines); both were more abundant in July

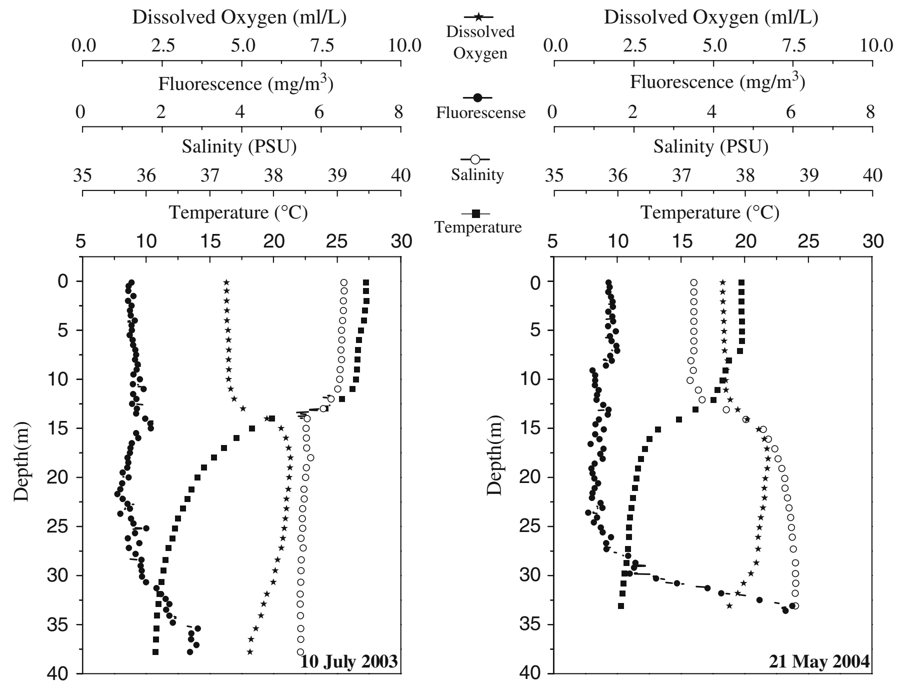

Fig. 4 Typical temperature (*solid square*), salinity (*open circle*), dissolved oxygen (*star*) and fluorescence (*solid circle*) profiles during experimental periods in July 2003 (*left*) and May 2004 (*right*)

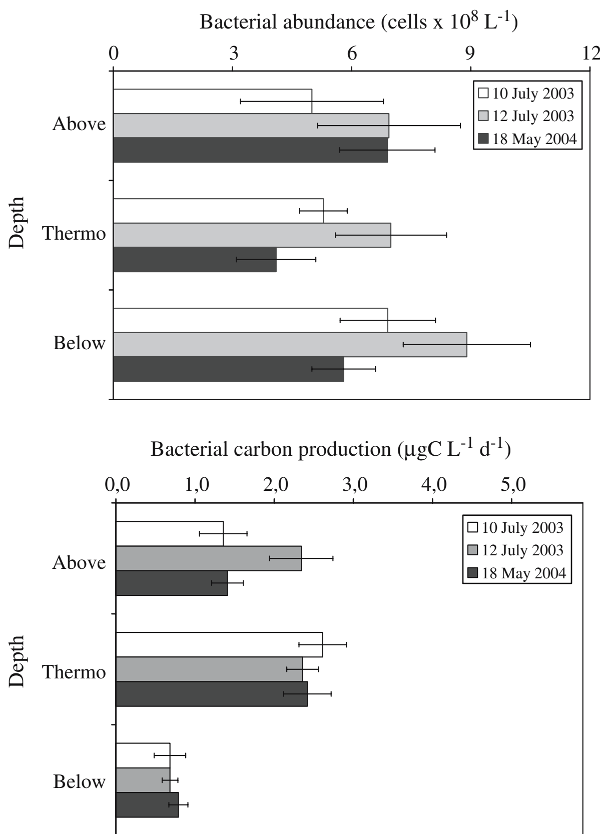

Fig. 5 Heterotrophic bacterial abundance (*top*) and bacterial carbon production (*bottom*) in the water column in layers above, within and below the thermocline at the beginning of the feeding experiments in July 2003 and May 2004

compared to May. The most abundant mesozooplankton organisms, particularly in the upper part of the water column were two small copepods (adults and copepodites, since 125 µm mesh was used for sampling) *Oithona nana* and *Paracalanus parvus* (Fig. 6, bars), the former being most numerous within thermocline layer in July and the latter within the same layer in May. In the surface layer, the pteropod *Limacina trochiformis* was also moderately abundant, while in the layer below 20 m *Oithona similis* was numerous.

Vertical distribution of *Aurelia*

An overview of CTD casts and video profiles at different hours during both experimental periods (2003, 2004) is given in Table 1. The total number of *Aurelia* recorded per profile was highest at dusk and lowest during the night but variability was high and indicated some horizontal dispersion over the diel cycle. Additional semi-quantitative data from divers' observations were obtained for the surface 25 m: four dives at dusk, and four dives during the day. During our observations medusae were swimming continuously with only a few exceptions.

The results obtained in 2003 (July) and 2004 (May) differed slightly although a general pattern was clear. During the night all medusae were located in deep layers below 20 m and the mean population depth

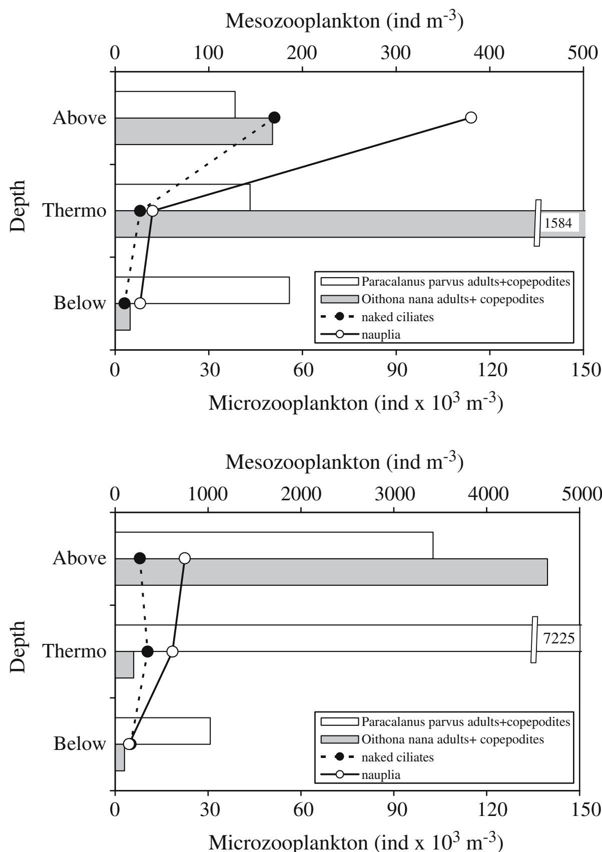

Fig. 6 Abundance of the dominant mesozooplankton (*Paracalanus parvus* adults + copepodites, *white bars*; *Oithona nana* adults + copepodites, *grey bars*) and microzooplankton (*naked ciliates*, *dashed line*, *solid circles*; *nauplia*, *solid line*, *open circles*) organisms in layers above (9 m-surface), within (19–10 m) and below (40–20 m) the thermocline at the beginning of the feeding experiments on 12 July 2003 (*top*) and 18 May 2004 (*bottom*)

Table 1 Overview of video profiles and CTD/fluorescence casts at different times of the day (local time) at two deep locations in Big Lake (a and b, see Fig. 1)

Time (hours)	Number of casts		Number of medusae per profile (mean ± SE)	Measurements of medusae size
	CTD	Video		
Early morning (04 30–0730)	6	4	28 ± 5	
Day (0730–1730)	10	7	27 ± 20	+
Dusk (1730–2130)	8	8	50 ± 46	+
Night (2130–0430)	5	5	11 ± 7	
Total	29	24		

(MVP) of *Aurelia* for all night recordings in both years was 28.6 ± 4.5 m. However, MVP was shallower in May (25.7 ± 3.3 m) compared to July (33.2 ± 2.0 m, Table 2). Orientation of *Aurelia* during the night recordings was variable without a clear prevailing direction. As with the night observations, daytime

Table 2 Mean vertical position (MVP = depth in m) of the *Aurelia* population (mean ± SE) in the water column at different times of the day during July 2003 and May 2004

Time (hours)	Depth	
	July 2003	May 2004
Early morning (0430–0730)	19.3 ± 0.9	No data
Day (0730–1730)	22.5 ± 0.5	16.0 ± 0.5
Dusk (1730–2030)	13.5 ± 0.5	12.4 ± 1.0
Night (2030–0430)	33.2 ± 2.0	25.7 ± 3.3

MVP in May were also at shallower depths, while at dusk MVP was similar for both years (Table 2). The proportion of the *Aurelia* population recorded in different layers over the diel cycle for the July 2003 observations is shown in Fig. 7. The peak in medusa abundance occurred in the sub-thermocline layer most of the time (44 ± 5% at dusk, 55 ± 10% during day and 56 ± 8% early morning) but a larger proportion of *Aurelia* were recorded in the thermocline layer at dusk and at that time only did *Aurelia* also appear in the above thermocline layer.

In both years a very clear migration of *Aurelia* towards the surface was registered at dusk with the large part of the *Aurelia* population located within the thermocline layer and a significant part recorded at depths shallower than 10 m. On two occasions in May 2004 we observed a swarming of *Aurelia* at the very surface for a short period. No such surface swarming of medusae was observed in July 2003 when surface temperatures exceeded 26°C. We followed one surfacing of *Aurelia* from 1730 to 2015 hours (local time) on 21 May 2004 when sunset was at about 1930 hours (the location where medusae surfaced was in shadow after this time), with repeated video recordings of vertical profiles from the surface to the bottom. At 1730 hours we recorded a total 150 *Aurelia* distributed from above the thermocline (18 individuals), within the thermocline (60 individuals) and just below the thermocline at a depth of 14–18 m (66 individuals). Only 6 animals were seen deeper than 22 m. Individuals within and above the thermocline layer were predominantly oriented upwards (64%); for about 28%, orientation was not clear from the video since the *Aurelia* were so numerous. The remaining 8% were oriented horizontally. Individuals in deeper layers were oriented upwards, downwards and horizontally in similar proportions. At 1830 hours about 70% of the medusae were recorded in the surface 15 m and all were oriented upwards; they surfaced shortly to form a surface swarm at about 1850–1900 hours. About 1 h later no *Aurelia* were observed shallower than 10 m and the highest density was at 12–14 m (bottom of the

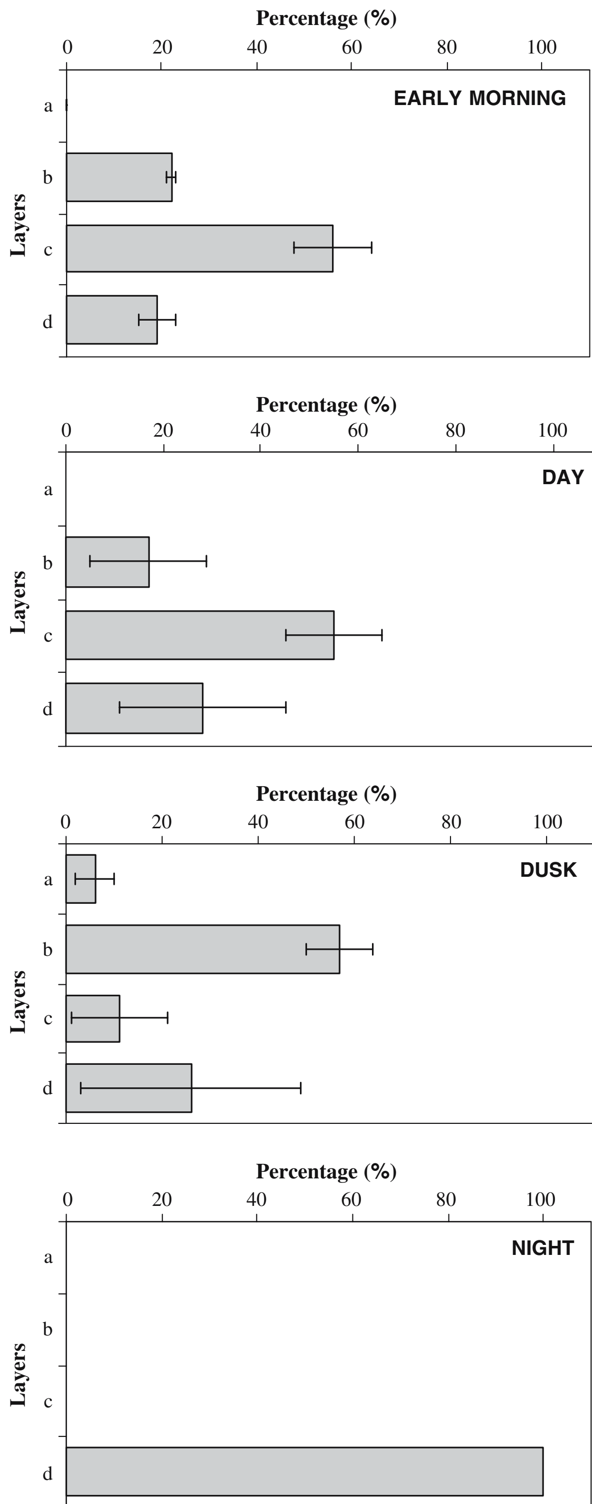

Fig. 7 Vertical position of the *Aurelia* population at different times over the diel cycle during July 2003 layers: **a** above the thermocline layer, **b** the thermocline layer, **c** below the thermocline layer, **d** the deep layer (>25 m). Error bars represent standard deviation

thermocline). Also, a significantly smaller total number (44) of *Aurelia* per profile was observed indicating that there was also some horizontal displacement of medusae. Divers observed this event from 1850 to 2010 hours and were located at 5 and 10 m depths. At 1855 hours, in a dense patch at a depth of 5 m, 77% of *Aurelia* were oriented upwards; at 1930 hours, at the same depth (5 m), essentially all individuals were observed to be oriented downwards. At a depth of 10 m more than 60% were oriented downwards between 1940 and 2010 hours. These data indicate rather rapid upward and downward swimming and migration greater than 10 m in 1 h.

In addition to the described event we collected eight data sets (video recordings) on vertical distribution and orientation of *Aurelia* between 1730–2130 hours. In both years *Aurelia* were most numerous in the layers within and above the thermocline (72 ± 19%) and the remaining medusae were observed just below the thermocline (15–16 m). More animals were recorded in the layers closer to the surface in May when temperatures in the upper 10 m were slightly less than 20°C, than in July when we measured temperatures over 26°C in surface 10 m (Fig. 4).

Feeding of *Aurelia*

The average size (bell diameter) of *Aurelia* analysed for gut content and used in enclosure feeding experiments was 7.4 ± 2.6 cm (n = 86) in 2003 and 9.9 ± 2.3 (n = 42) in 2004.

Gut content analyses of *Aurelia* indicated 27 ± 6 prey items per medusa (bell diameter from 4.9 to 11.4 cm). The dominant prey were small copepods (*Paracalanus parvus*, *Oithona nana*) and copepodites that on average constituted 72% of food items; among these *Paracalanus parvus* adults and copepodites contributed 24%, *Oithona nana* adults and copepodites accounted for 21% and unidentified copepodites were 27% followed by the larvae of Gastropoda, Bivalvia, Cirripedia (17%) nauplii (8%) and Appendicularia (2%). Other prey items (less than 1%) included Cladocera and *Limacina*.

In situ feeding experiments using plankton at natural densities also indicated high clearance rates for small calanoid and cyclopoid copepods, copepodites and nauplii (Table 3; Fig. 8, top). In addition, naked ciliates were found to be an important prey of *Aurelia*. Clearance rates were the highest for *Oithona nana*, adults and copepodites, followed by nauplii and by

Table 3 Average clearance rates (ml ind^{-1} h^{-1}) of *Aurelia* preying on natural plankton during enclosure experiments in 2003 and 2004 (mean ± SE)

Depth of incubation	Above	Thermocline	Below
	ml ind^{-1} h^{-1}	ml ind^{-1} h^{-1}	ml ind^{-1} h^{-1}
Temperature (°C)	26.3	17–18	12.2
Nauplia	541	102 ± 13	23
Paracalanus parvus [a]	309	70 ± 11	46
Oithona nana[b]	79	147 ± 32	–
Naked ciliates	396	47 ± 12	12

Three enclosure experiments were carried out in the thermocline layer and one in the layers above and below the thermocline

[a] *Paracalanus parvus* adults + copepodites

[b] *Oithona nana* adults + copepodites

Paracalanus parvus adults and copepodites, naked ciliates were also important prey items. Feeding data obtained for surface (5 m) and deep (25 m) layers are merely indicative because only the experiment done on 12 July 2003 included additional enclosures at depths of 5 and 25 m. Nevertheless, results point to strong temperature dependence but may also reflect a higher natural density of zooplankton, particularly of nauplia and ciliates in the surface layer. Neither stomach content analysis nor feeding experiments indicated any non-migrating organisms that are found in deeper layers, like the copepods *Diaixis pygmoea*, *Oithona similis, Calanus helgolandicus* (Lučić, pers. obs.), as prey items of *Aurelia*.

In addition to the direct effect on micro- and mesozooplankton prey, *Aurelia* also had an important indirect impact on microbial plankton as evidenced by cyanobacteria and heterotrophic bacterial biomass, as well as heterotrophic bacterial production during the enclosure experiments (Fig. 8, middle, bottom). At the end of incubations cyanobacteria and heterotrophic bacteria abundances were steadily lower in enclosures without jellyfish i.e. with micro- and mesozooplankton only (control, Fig. 8). The difference between control and enclosures containing jellyfish was the largest in treatments incubated in the thermocline layer (Table 4). Moreover, bacterial carbon production rates were invariably lower in enclosures without *Aurelia* (Fig. 8, bottom), as were P/B ratios (Table 4). These results suggest an indirect, yet consistent, trophic linkage at the base of the food webs either through consumption of bacteriovores or by release of DOM.

Microscopic observations of large clumps of bacteria in the Mljet lake (Turk pers. obs.) prompted us to test the possibility that one important prey for *Aurelia*, the small cyclopoid *Oithona nana* (about 0.5–0.7 mm body length), could ingest bacterioplankton clumps and thus reduce the number of trophic levels between bacteria

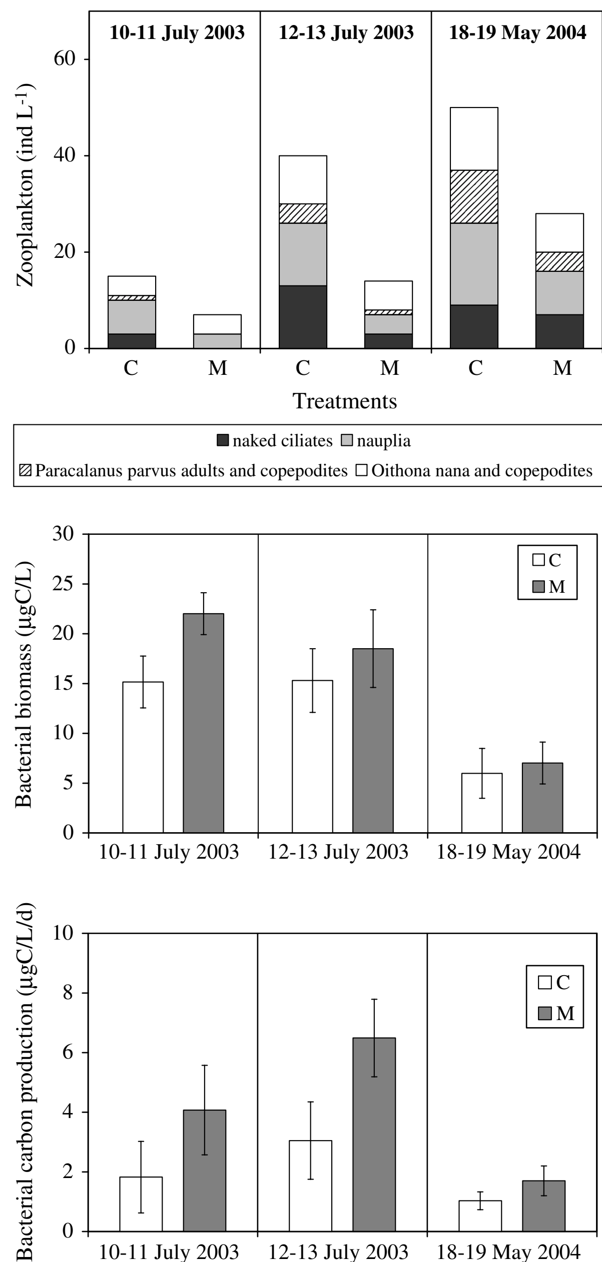

Fig. 8 Abundance of dominant micro- and mesozooplankton organisms (*top*), heterotrophic bacterial biomass (*middle*) and production (*bottom*) in large enclosures with (*M* dark shaded bars) and without (*C* clear bars) *Aurelia* at the end of incubations (*error bars* indicate SE of three replicate measurements)

and medusae. Radiolabeled bacteria were offered to *Oithona* at levels comparable to natural abundances (8×10^5 ml^{-1}) in the lake. When counting bacteria incubated for 24 h with labelled ^{3}H-thymidine that were subsequently used in feeding experiments with *Oithona nana* (abundance at t_0, Table 5 and Fig. 9) we observed that bacteria formed large chains. Fifteen *Oithona nana* were incubated in 50 ml tubes containing on average $8.5 \pm 4.6 \times 10^5$ radiolabeled bacterial cells ml^{-1}, which

Table 4 Aurelia feeding experiments: Heterotrophic bacterial abundance and biomass, bacterial carbon production (BCP), P/B ratio and cyanobacteria abundance in enclosures incubated at different depths (above, within and below the thermocline layer) during 12–13 July 2003 and 18–19 May 2004 (*C* treatment with no jellyfish; *M* treatment with jellyfish)

Date	Layer	Treatment	Bacteria		BCP	P/B	Cyanobacteria
			Cells × 10^8 l^{-1}	μgC l^{-1}	μgC l^{-1}day^{-1}		Cells × 10^7 l^{-1}
July 2003	Above	C	8.2	16.3	5.4	0.33	3.6
		M	8.6	16.9	8.0	0.47	4.3
	Thermo	C	7.7	15.3	3.1	0.20	3.2
		M	9.3	18.5	6.5	0.35	3.6
	Below	C	4.7	9.3	0.9	0.10	3.8
		M	5.9	11.7	1.6	0.14	4.6
May 2004	Thermo	C	3.0	6.0	1.0	0.17	
		M	3.5	7.0	1.7	0.24	

Table 5 Heterotrophic bacterial abundance during the *Oithona nana* grazing experiment with radiolabeled bacteria: (±SE) at the beginning (t_0) and after 1 h (t_1) of incubation (control, treatment with radiolabel bacteria only; Bacteria + *Oithona nana*, treatment with *Oithona nana* and radiolabeled bacteria)

Time/treatment	Bacterial abundance (cells × 10^5 ml^{-1})	
	Control	Bacteria + *Oithona nana*
Start (t_0)	8.55 (±4.6)	8.55 (±4.6)
End (t_1)	7.82 (±2.3)	4.70 (±3.7)
No counts	9	9

was equivalent to 25.1 ± 3.2 dpm ml^{-1}. After 1 h incubation bacterial abundance decreased by 3.4 ± 0.8 × 10^5 ml^{-1} compared to control (Table 5) indicating measurable ingestion. Since no other bacterial grazers could pass through the 0.6-μm filters we may assume that *Oithona* grazed bacteria. Ingestion of radiolabeled bacteria was also confirmed by radioactivity measured in *Oithona* (Fig. 9). These very preliminary data indicate that *Oithona nana* might be able to consume clumped bacteria.

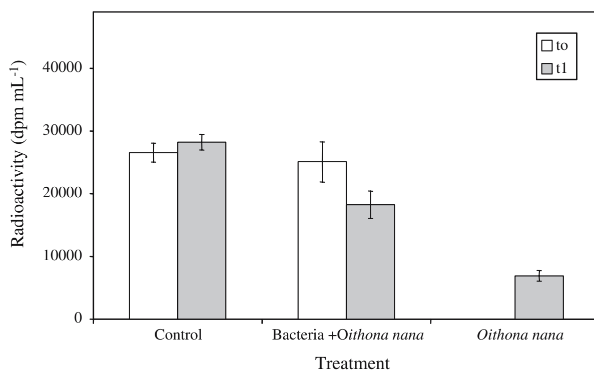

Fig. 9 *Oithona nana* grazing experiment with radiolabeled bacteria: radioactivity (dpm ml^{-1}) before (t_0, clear bars) and after 1 h of incubation (t_1, *grey bars*) for three treatments—control with bacteria only, bacteria and *Oithona nana, Oithona nana* only

Discussion

In contrast to most coastal areas where *Aurelia* medusae appear seasonally, in the Mljet lakes they occur throughout the year (Onofri pers. comm.). Moreover, being located within a protected national park where human activities are very limited makes the Mljet lakes very suitable for ecological studies. Our study concentrated on the spring-summer season, which is the typical season for *Aurelia* medusae outbursts in many other marine environments. *Aurelia* is one of the most studied scyphomedusa due to its widespread distribution, seasonally high abundances and consequent important ecological role. It is known to be an opportunistic predator feeding on zooplankton of a wide taxonomic and size range. Costello et al. (1998) classified *Aurelia* as a cruising predator entraining fluid during both bell contraction and relaxation (Dabiri et al. 2005). Prey capture success and ingestion depends on the relative sizes of medusa and prey, prey escape behaviour, as well as environmental factors such as temperature and prey availability (Sullivan et al. 1994; Olesen 1995; Schuman and Sullivan 2000; Graham and Kroutil 2001). Like other jellyfish, *Aurelia* is traditionally considered an important predator/competitor within a classical trophic chain (Purcell and Sturdevant 2001). A few studies indicate that this jellyfish may consume ciliates (Stoecker et al. 1987; Omori et al. 1995) and suggest a closer link to the microbial food web (Hansson and Norrman 1995; Fukuda and Naganuma 2001). A structuring impact of vertically migrating medusa *Periphylla periphylla* on microbial activity and composition was also observed by Riemann et al. (2005) in a Norwegian fjord dominated by this jellyfish.

Our data (gut content and in situ feeding experiments) indicate that *Aurelia* preyed upon adults and copepodites of small calanoids and cyclopoids, nauplii and naked ciliates, which were typically most abundant

within and/or above the thermocline layer. It is difficult to compare our results on clearance rates with other similar studies because experimental conditions differ; however, obtained values are in the lower range of published estimates. This may be explained by oligotrophic nature of Mljet lakes but may partly be also due to depletion of prey during 6–7 h incubation. Larger calanoids or other zooplankton located in deep layers (>25 m) was not consumed although our vertical distribution analysis (Fig. 5) showed that practically the whole *Aurelia* population stayed in the deep layer over night. *Aurelia* were recorded at shallower depths in the early morning and during the day with the mean vertical position of the population in the sub-thermocline layer.

Similar vertical distribution was found by Mutlu (2001) who studied *Aurelia* in the inshore and offshore waters of the southern part of the Black sea: *Aurelia* was generally confined to depths up to 20–40 m, avoided warm surface waters (25–26°C) but were found within cold intermediate water at about 50 m towards midnight. Our results, video recordings and divers' observations, indicate that *Aurelia* start to migrate towards the surface well before sunset, i.e. between 1700 and 1800 hours (local time) and the majority stayed in the upper layers (above and within the thermocline) until dark. After 2300 hours the main body of *Aurelia* population was in layers below 25 m in both years. All monitored vertical displacements, i.e., ascents and descents, were the result of active swimming.

Papathanassiou et al. (1987) also observed diel vertical migration in the stratified water column in Saronikos Gulf, Greece. *Aurelia* were recorded at shallower depths in late afternoon and early morning but the authors ascribed the sinking of medusae to inactivation of bell pulsation. In contrast, we believe that swimming upwards and downwards enables *Aurelia* to prey actively when passing through the thermocline and the above-thermocline layers where nauplii and ciliates aggregate at dusk. During daylight hours we found the peak of *Aurelia* concentration in the sub-thermocline and, to lesser extent, thermocline layers, where small copepods and copepodites *Paracalanus parvus* and *Oithona nana*, were the most numerous. Such vertical distribution over the diel cycle would enable *Aurelia* to use available food resources most efficiently. When located in the deep layers at night *Aurelia* were also observed to be active. However, neither gut content nor feeding experiments indicated ingestion of larger copepods that dominated the deep (>25 m) layer. It is not clear why *Aurelia* would migrate to deeper layers overnight although residing in cold water may provide a metabolic advantage (Hays 2003). A number of factors may influence the migratory behaviour of zooplankton (Ohman 1990), among which, in particular light (Mackie et al. 1981; Hamner et al. 1994; Schuyler and Sullivan 1997), temperature conditions (Sparks et al. 2005) and increased reproduction success (Hamner et al. 1994) or a combination of factors seem to be important for jellyfish. Observed patterns of *Aurelia* migration behaviour in Mljet lakes indicates that, besides changes in light levels, other factors may be important. Predator avoidance did not seem to be a likely factor in the Mljet lakes since no obvious *Aurelia* predators were identified; optimal foraging behaviour (Graham et al. 2001) would thus be more probable.

The observed vertical migration also has important implications for *Aurelia* impact on the water column food web. *Aurelia* impact on the classical plankton food web has been well documented in the past and seems to be important also in the Mljet lakes. Predatory pressure by *Aurelia* is a likely explanation for the drastically reduced number of copepods in the lakes compared to the open Adriatic a short distance (300 m) from the lake channel. Moreover, we propose that *Aurelia* might have important effects on the microbial food web preying on naked ciliates as well as nauplii and copepodites. These results indicating microzooplankton as an additional food source to mesozooplankton are further supported by measurements of stable isotope ratios of carbon and nitrogen of *Aurelia*, mesozooplankton and microzooplankton which imply that *Aurelia* preyed upon both micro- and mesozooplankton (Malej et al. 2006).

It has been demonstrated that the nauplii and copepodites of several small copepods are capable of bacterivory (Turner and Tester 1992; Roff et al. 1995). Further, jellyfish could stimulate bacterial production and growth by providing a supplementary source of DOC (Hansson and Normann 1995). In addition, our preliminary experiment with radiolabeled bacteria indicates that the small cyclopoid copepod *Oithona nana* might also be able to ingest clumped bacteria reducing the number of trophic levels from bacteria to jellyfish. This finding is particularly relevant in the stratified water column and where small-sized food resources may be dominant.

In conclusion, our results, obtained during feeding experiments, elicited clear responses of bacterial populations indicative of indirect cascade effects of *Aurelia* on 'microbial', in addition to, 'classical' food webs. The observed impacts are very likely to be found in other stratified and/or oligotrophic environments where *Aurelia* is seasonally abundant.

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