

Moon jellyfish, *Aurelia aurita*, in the Gulf of Gdansk: threatening predator or not?

Dominika Brulińska^{1)*}, Michał Olenycz¹⁾²⁾, Marcelina Ziółkowska¹⁾, Stella Mudrak-Cegiołka³⁾ and Maciej Wołowicz¹⁾

¹⁾ Department of Marine Ecosystem Functioning, Institute of Oceanography, University of Gdansk, Al. Marszałka Piłsudskiego 46, PL-81-378 Gdynia, Poland (*corresponding author's e-mail: dominika.brulinska@ug.edu.pl)

²⁾ Department of Ecology, Maritime Institute in Gdańsk, ul. Długi Targ 41/42, PL-80-830 Gdańsk, Poland

³⁾ Department of Marine Plankton Research, Institute of Oceanography, University of Gdansk, Al. Marszałka Piłsudskiego 46, PL-81-378 Gdynia, Poland

Received 6 Jan. 2015, final version received 20 Jan. 2016, accepted 30 Oct. 2015

Brulińska D., Olenycz M., Ziółkowska M., Mudrak-Cegiołka S. & Wołowicz M. 2016: Moon jellyfish, *Aurelia aurita*, in the Gulf of Gdansk: threatening predator or not? *Boreal Env. Res.* 21: 528–540.

The seasonal population dynamics and feeding preferences of the moon jellyfish, *Aurelia aurita*, in the Gulf of Gdansk (southern Baltic Sea) were investigated. Medusae were present in the water column from June to November, with maximum occurrence in August and September. The medusa bell diameter and weight increased during the study period reached maximum values in October. The relationship between bell diameter and wet weight was strong. No ephyrae were observed during the study period. Gastric content analysis revealed that the medusae fed mainly on copepods and cladocerans. Rotifers that dominated the water column throughout the study period were not found in the jellyfish guts, but the stable isotope signature indicated that they could have been a significant source of derived carbon. Low numbers of plankton prey and the lack of fish larvae in *A. aurita* guts suggest that the jellyfish is of minor relevance as a predator and competitor in the Gulf of Gdansk.

Introduction

Jellyfish occur in great abundance in many marine coastal waters, and this is a natural phenomenon in such ecosystems (Graham *et al.* 2001). More frequent blooms are, however, reported worldwide (Boero *et al.* 2008). Observations suggest that mass jellyfish outbreaks are caused by overfishing, eutrophication, climate change, translocations, and habitat modification (Richardson *et al.* 2009). The mass occurrence of medusae is of commercial consequence since

jellyfish cause problems for fisheries by clogging trawl nets, competing for prey, preying on fish, blocking water intakes to power plant cooling systems, killing fish species reared in aquaculture, and reducing the attractiveness of seaside resorts for tourists (Möller 1980, Mills 2001, Lynam *et al.* 2006, Purcell *et al.* 2007, Baumann and Schernewski 2010).

Species of the genera *Aurelia* have a global distribution and often form aggregations (Purcell 2003). One of the most extensively studied species is the moon jellyfish, *Aurelia aurita*

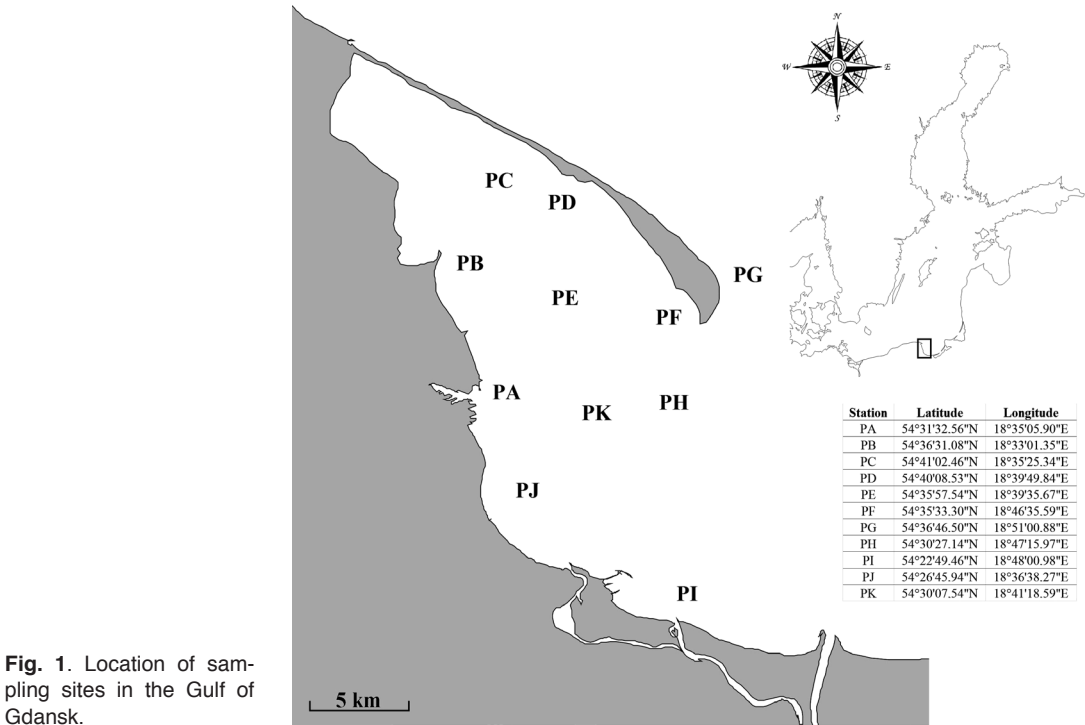


Fig. 1. Location of sampling sites in the Gulf of Gdansk.

(Scyphozoa), which is widespread in coastal waters between 40°S and 70°N (Möller 1980). The moon jellyfish is a predator that feeds on a wide variety of planktonic organisms such as fish larvae, ciliates, diatoms, rotifers, copepods, cladocerans, and barnacle larvae (reviewed in Arai 1997). It can affect the structure of plankton communities, and reduce standing fish stocks by competing with planktivorous fish for zooplankton prey and by preying on fish larvae (Möller 1980, Schneider 1989, Bamstedt *et al.* 2001, Barz *et al.* 2006). Finally, it can also modify the food web structure.

The moon jellyfish occurs in the Baltic Sea (Barz and Hirche 2005), and is the dominant scyphomedusa species in the Gulf of Gdansk (southern Baltic Sea) that is an important tourism and fishing region of Poland (Schernewski and Schiewer 2002). In the biological context, it is a diverse ecosystem providing nursery grounds for many species of commercial and non-commercial fishes (Lizińska 2002). Although *A. aurita* is common in the Polish fisheries zone of the Baltic Sea (Janas and Witek 1993), there are no data on the size (bell diameter), weight, or diet of

the medusae or their significance in the pelagic food web. Therefore, the aim of this study was to investigate the population size of *A. aurita* in the Gulf of Gdansk and to determine their prey structure to define their role in the regulation of the mesozooplankton community in this area. The role of the moon jellyfish in the food web and as a zooplankton predator are also discussed.

Material and methods

Sampling and analysis of medusae gut content

Aurelia aurita and mesozooplankton samples were collected every two weeks: during the first and the third weeks of a month from April to December 2008 at 11 sites located in the Gulf of Gdansk (Fig. 1). Oblique hauls with a plankton net (0.75 m diameter, 100 μ m mesh size) equipped with a flow meter were conducted from the r/v *Oceanograf 2* owned by the Institute of Oceanography at the University of Gdansk. Surface water salinity and temperature measure-

ments were taken concurrently with a WTW Multiline P4 analyser equipped with the Tetra-Con 352 probe.

All medusae examined were blotted, then measured (bell diameter) on board the vessel, and then dissected to collect prey organisms from the canals, stomachs, and gastric pouches. Zooplankton prey was preserved in 4% formaldehyde, and later analyzed in the laboratory under a Nikon SMZ800 zoom stereomicroscope. The organisms were counted and identified to the genus or species. The medusae were frozen, and later weighed in the laboratory.

Mesozooplankton sampling and analysis

Mesozooplankton samples were collected simultaneously with the medusae, preserved in 4% formaldehyde, and analysed in the laboratory under a stereomicroscope. The organisms were identified to the genus or species.

Stable isotope analysis

Pelagic food web components such as suspended organic matter, phytoplankton, zooplankton, jellyfish, and planktivorous fish were sampled in August 2011 to assess the trophic position of jellyfish in the pelagic food web structure by means of determining their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ contents. Additionally, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of zooplankton, jellyfish and fish samples were used to assess the assimilation of different sources by *Aurelia aurita* by using Isotopic Mixing Model (see section 'Isotopic mixing model').

Suspended particulate organic matter samples were obtained by filtering sea water through grade GF/F Whatman glass microfiber filters immediately after sampling. The samples were

kept frozen until analysis. Pelagic food web components were collected vertically with two WP2 nets, phytoplankton (25–100 μm size) was collected with nets with 25 μm mesh and 57 cm diameter, while mesozooplankton, jellyfish and fish (200–500 μm size) were sampled with nets with 200 μm mesh and a diameter of 57 cm. The plankton was then sieved gently through 1 mm mesh (mesozooplankton) and 125 μm mesh (micro-zooplankton) to remove larger, free-floating items. Sampling was repeated several times to collect sufficient quantities for stable isotope analysis. The plankton collected was then placed separately in water collected *in situ*, transported to laboratory, and left overnight to clear their guts. After this, the phytoplankton and mesozooplankton samples were fractionated through 25–100 μm and 200–500 μm sieves using the modified method by Rolf and Elmgren (2000). This method is based on a vacuum set of polyethylene bottles with different mesh sized sieves and facilitates segregating planktonic fractions by size (Table 1). To ensure that samples of all zooplankton types were well separated and dead organisms were not analysed, the light trapping method was used. In a dark room, each segregated fraction was placed at one end of a long container, and then a light source was placed at the opposite end of the container. After 15 minutes, live zooplankton that swam towards the light was collected, while dead individuals remained in the second, dark part of a container. This separation method relies on the positive phototaxis of some zooplankton orders (cladocerans and copepods). After separation, mesozooplankton was filtered through Whatman GF/C and stored in vials. Subsamples of each zooplankton fraction were preserved in formaldehyde and taxonomically analysed. The remaining parts of the samples were stored at $-20\text{ }^\circ\text{C}$ until stable isotope analysis. Afterwards

Table 1. Classification of plankton by size.

Symbol	Size (μm)	Collected plankton type
zoo200–500	200–500	zooplankton
zoo100–200	100–200	zooplankton
zoo50–100/phyto50–100	50–100	phytoplankton/zooplankton
phyto25–50	25–50	phytoplankton

phytoplankton fractions were filtered through Whatman GF/C filters, washed by Milli-Q water and stored at -20°C .

After that all plankton fractions, jellyfish and fish (muscle) were ground to a fine powder using a Mixer Mill mm 200 homogenizer.

The stable isotope ratio of C and N was measured using an Isoprime Micromass IRMS-EA (MicroMass CHN analyser coupled with MICROMASS mass spectrometer) that provides simultaneous data on carbon and nitrogen content. Isotope composition was expressed as standard δ (‰) according to the following formula:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 10^3$$

where $R_{\text{sample}} = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon, $R_{\text{sample}} = {}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen, and R_{standard} is the value of the reference material (Vienna PDB for carbon and N_2 for nitrogen). Replicate analyses of standards allowed calculating analytical error (SD) of the overall procedure that was $\pm 0.1\%$ for carbon and $\pm 0.2\%$ for nitrogen.

Isotopic mixing model

The jellyfish diet composition was determined with the SIAR Bayesian mixing model in the R environment (ver. 4.0; Parnell *et al.* 2010). The SIAR model estimates probability distributions of multiple source contributions to a mixture while accounting for the observed variability in source and mixture isotopic signatures, dietary isotopic fractionation, and elemental concentration. Our single model used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of potential food sources (50–100, 100–200, and 200–500 zooplankton fractions) that constitute the prey of moon jellyfish. We used the trophic enrichment factor (TEF) $0.4\% \pm 0.17\%$ for $\delta^{13}\text{C}$ and $2.3\% \pm 0.28\%$ for $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen 2001, McCutchan *et al.* 2003).

Statistical analysis

Because of the non-normal distribution (Shapiro-Wilk's test for goodness of fit) and non-homogeneous variances (Bartlett's test) in the data, a non-parametric approach was used in the statistical

analysis. Kruskal-Wallis one-way ANOVA was used to compare jellyfish size (bell diameter, wet weight) and prey composition among sampling sites and sampling periods, as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among food web components.

Selectivity of *A. aurita* for prey taxa was estimated using Pearre's selectivity index calculated on pooled data (Wintzer *et al.* 2011). Differences between species composition in jellyfish guts and water were evaluated with a χ^2 -test.

Data analyses were performed in STATISTICA ver. 10.

Results

Environmental conditions

The mean (\pm SD) surface water temperature at the beginning of June was $13.5 \pm 0.4^{\circ}\text{C}$, the maximum of 20.5°C was reached in beginning of August, and the minimum (8.3°C) was recorded in the second part of November (Fig. 2).

At the PI site situated near the Vistula River mouth salinity fluctuated between 3.0 and 5.1 PSU (mean \pm SD = 3.6 ± 0.5 PSU). At all the remaining sites, salinity fluctuated between 5.5 PSU (PK site) and 7.1 PSU (PG site) with an average (\pm SD) of 6.5 ± 0.2 PSU.

Jellyfish abundance and growth

A total of 2769 *A. aurita* medusae were collected at 11 stations in the Gulf of Gdansk.

The first medusae occurred in June and were present in the water column until November. Jellyfish abundance varied among sampling periods (Fig. 2). The highest numbers were observed in August (mean \pm SD = 1.01 ± 0.05 indiv. m^{-3}) and September (1.02 ± 0.02 indiv. m^{-3}), after which they decreased, and the lowest numbers were recorded in mid-November (0.12 ± 0.02 indiv. m^{-3}). At all the station except PI, the mean \pm SD number of moon jellyfish was 260 ± 20 indiv.; at PI much lower numbers were observed (152 indiv.).

At each sampling site, bell diameter and wet weight were statistically different among sampling periods (Table 2). They also differed among

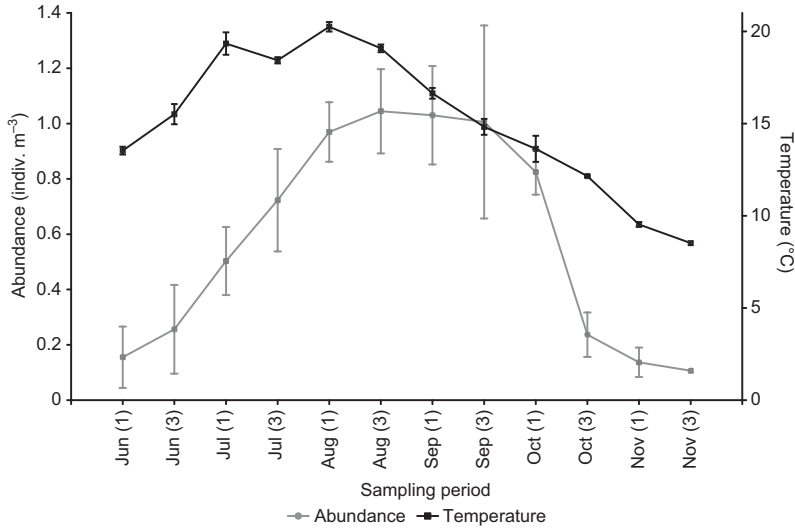


Fig. 2. Abundance (\pm SD) of *A. aurita* and temperatures (\pm SD) in the Gulf of Gdansk during the study period in 2008; 1 = first week of the month, 3 = third week of the month.

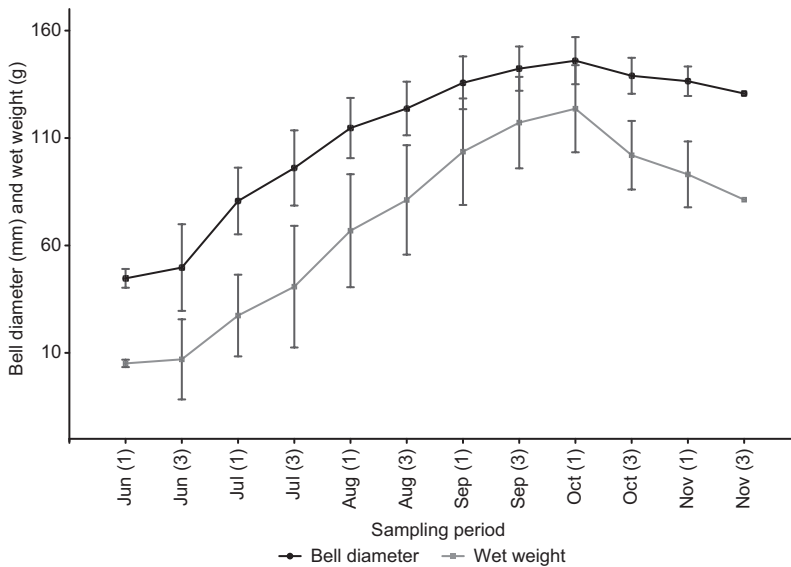


Fig. 3. Mean (\pm SD) bell diameter and wet weight of *A. aurita* at all sites in subsequent sampling periods; 1 = first week of the month, 3 = third week of the month.

the different sites from July to October (Table 2). *Aurelia aurita* bell diameter and wet weight changed in a similar manner: they increased from July to the beginning of October (Fig. 3), and then decreased. The maximum diameter was 146 mm at the beginning of October. The greatest bell diameter increase was observed at the beginning of July at PF, PG, PH, PI, and PK (4.3, 41.9, 45.5, 35.4, and 44.3 mm per 2 weeks, respectively); in mid-July at PD, PE, and PK (27.0, 26.5, and 44.3 mm per 2 weeks, respectively); and at the beginning of August at PA,

PB, and PC (25.6, 38.8, and 25.0 mm per 2 weeks, respectively). The relationship between the wet weight and the length (bell diameter) of *A. aurita* was expressed as $WW = 0.0002L^{2.7108}$ ($r^2 = 0.9843$, $n = 2769$) (Fig. 4).

Mesozooplankton and meroplankton abundance

Mesozooplankton was most abundant at the beginning of July (Fig. 5). During each month,

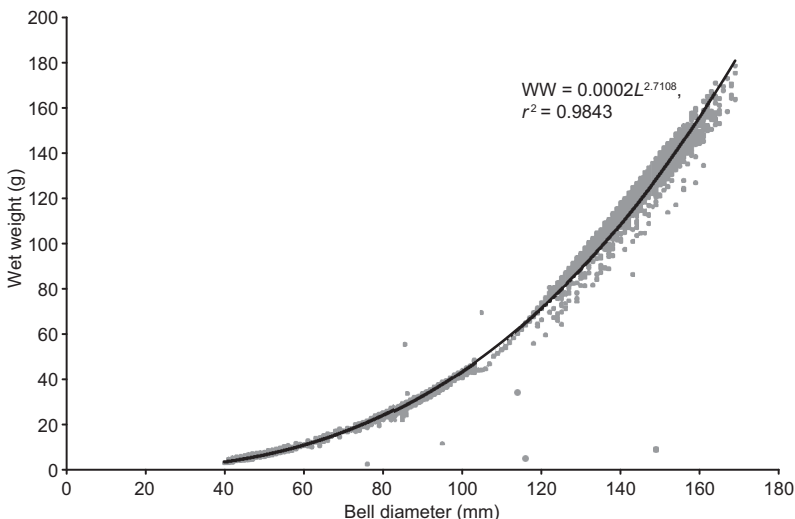


Fig. 4. Relationship between bell diameter and wet weight of *A. aurita* from the Gulf of Gdansk.

Table 2. Comparisons (Kruskal-Wallis one-way ANOVA) of jellyfish bell diameter (mm) and wet weight (g) among different sampling periods at the same sampling site, and among different sampling sites in the same sampling period. Differences are considered significant at $p < 0.05$; n = number of analysed jellyfish, H = Kruskal-Wallis test value. 1 = first week of the month, 3 = third week of the month.

	df	n	Bell diameter		Wet weight	
			H	p	H	p
Same sampling site different periods						
PA	11	265	219.6678	< 0.0001	213.5766	< 0.0001
PB	9	261	155.9129	< 0.0001	148.0691	< 0.0001
PC	8	215	165.8471	< 0.0001	163.4178	< 0.0001
PD	9	257	195.7739	< 0.0001	197.1931	< 0.0001
PE	9	269	186.1824	< 0.0001	185.8046	< 0.0001
PF	11	280	212.2003	< 0.0001	212.2374	< 0.0001
PG	11	271	175.3713	< 0.0001	175.1459	< 0.0001
PH	10	291	204.1691	< 0.0001	203.7936	< 0.0001
PI	6	152	85.1461	< 0.0001	82.9982	< 0.0001
PJ	9	248	178.8550	< 0.0001	178.0452	< 0.0001
PK	9	260	125.1869	< 0.0001	124.9339	< 0.0001
Same sampling period different sites						
Jun (1)	5	35	8.65625	0.1236	4.81528	0.4388
Jun (3)	5	106	15.66397	0.1097	10.76534	0.3761
Jul (1)	10	208	65.62313	< 0.0001	69.46098	< 0.0001
Jul (3)	10	299	35.03578	0.0001	37.85321	< 0.0001
Aug (1)	10	401	43.28040	< 0.0001	42.76312	< 0.0001
Aug (3)	10	432	61.79925	< 0.0001	60.59442	< 0.0001
Sep (1)	10	426	31.05980	0.0006	30.21098	0.0008
Sep (3)	10	416	26.76519	0.0028	27.72742	0.0020
Oct (1)	9	309	23.43911	0.0053	26.09139	0.0020
Oct (3)	9	89	35.06158	0.0001	33.00787	0.0001
Nov (1)	6	37	8.45084	0.2069	7.17415	0.3050
Nov (3)	2	11	0.15152	0.9270	1.61364	0.4463

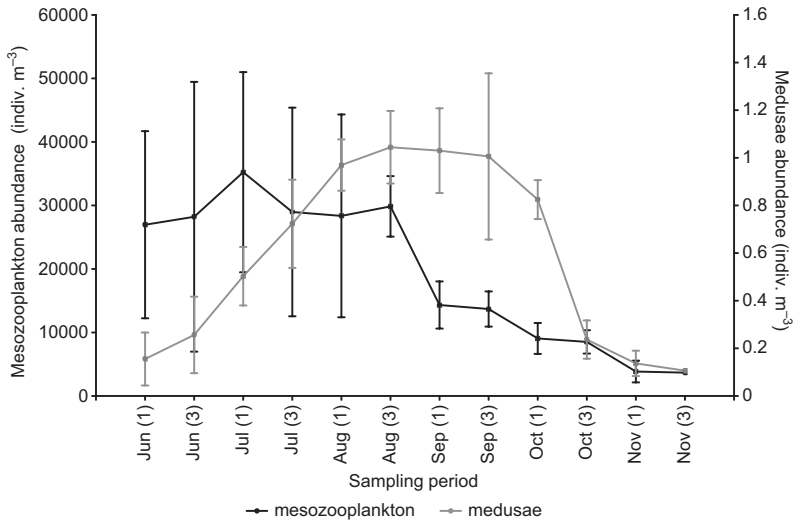


Fig. 5. Mesozooplankton and *A. aurita* abundance (\pm SD) in the Gulf of Gdansk in the subsequent months of 2008; 1 = first week of the month, 3 = third week of the month.

it was dominated by Rotifera (Fig. 6, top). *Keratella quadrata* was the most abundant rotifer, with the maximum density in July (22 497 indiv. m⁻³). Cladocera were observed from June to October and were dominated by *Podon* spp. (48%–93% of all Cladocera, or 38–1175 indiv. m⁻³). Copepoda reached the maximum density in the third week of August (5639 indiv. m⁻³) and were dominated by *Acartia* spp. (84% of all Copepoda, or 4761 indiv. m⁻³).

Meroplankton was represented by Bivalvia, Gastropoda, Cirripedia, and Polychaeta larvae. Gastropoda larvae dominated between June and November (from 68 to 1154 indiv. m⁻³) except for August when Bivalvia larvae were most abundant (832 indiv. m⁻³).

Diet composition according to gut content analysis

The diet of *A. aurita* consisted mainly of two components: Cladocera and Copepoda (Fig. 6, bottom). Cladocera dominated in the gut contents in June (58%), October (91%), and November (100%). Four Copepoda taxa were identified: *Acartia* spp., *Temora longicornis*, *Centropages hamatus*, *Pseudocalanus elongatus*. *Acartia* spp. was consumed most frequently (82%) with an average of 42 specimens per medusa, while *P. elongatus* was the least frequent (0.04%) part of the diet. Cladocera were represented by *Podon*

spp., *Bosmina coregoni maritima*, and *Evadne nordmanii*. *Bosmina coregoni maritima* was most frequently consumed (44%) at an average of 29 specimens per medusa, followed by *Podon* spp. (42%). Bivalvia larvae were recorded in the jellyfish guts between mid-June and mid-October, but they were the least abundant and represented less than 1% of the diet. No ichthyoplankton was found in the *A. aurita* diet. The composition of the moon jellyfish prey did not differ among sites in the same sampling period [Kruskal-Wallis one-way ANOVA: $H = 10.000$, $df = 10$, $p > 0.05$ for June (3), July (1, 3), August (1, 3), September (1, 3); $df = 10$, $p > 0.05$, $H = 0.000$ for June (1), October (1, 3), November (1, 3)].

The selectivity (C) values for *A. aurita* were always positive but very low, i.e. close to 0 (Table 3). The highest values were recorded for Cladocera, *Bosmina coregoni maritima* and the lowest for Bivalvia larvae. Of the 14 taxa available *A. aurita* consumed only eight.

Jellyfish and zooplankton isotope signatures and the moon jellyfish diet

The mean (\pm SD) value of $\delta^{13}\text{C}$ in *A. aurita* was $-25.58\text{‰} \pm 0.34\text{‰}$ and there was no statistical differences among individuals. There was little separation, $< 1\%$, in the $\delta^{13}\text{C}$ zooplankton fraction and no statistical differences among fractions were found in terms of $\delta^{13}\text{C}$ values;

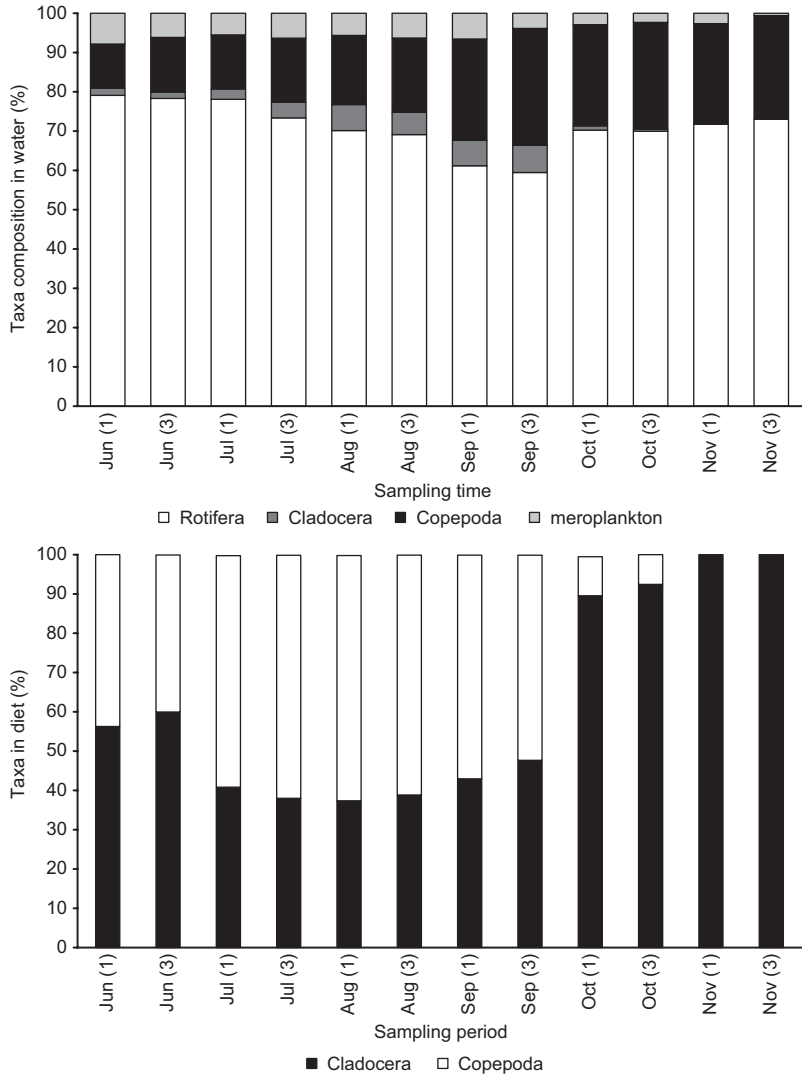


Fig. 6. Taxonomic composition of mesozooplankton in water (top) and in diet composition of *A. aurita* (bottom) in the Gulf of Gdansk in 2008.

nevertheless, the smallest value was found for the 50–100 fraction ($-24.64‰ \pm 0.77‰$), while the highest was for the 100–200 fraction ($-24.24‰ \pm 1.09‰$) (Table 4). The SIAR mixing model indicated that the majority of

carbon (mean = 56%) was derived from the 100–200 zooplankton fraction, which is represented mainly by Copepoda and Rotifera. Furthermore, the model estimated that the medusae received 33% of their carbon from the smaller

Table 3. *Aurelia aurita* prey selectivity (Pearre’s selectivity index, *C*), and differences between species composition in jellyfish guts and water (χ^2 -test) * significant at $p < 0.05$.

	<i>Acartia</i> spp.	<i>Temora longicornis</i>	<i>Centropages hamatus</i>	<i>Pseudocalanus elongatus</i>	<i>Podon</i> spp.	<i>Bosmina coregoni maritima</i>	<i>Evadne nordmanni</i>	Bivalvia larvae
<i>C</i>	0.057*	0.013*	0.009*	0.027*	0.096*	0.139*	0.090*	0.008*
χ^2	63.813	3.142	1.422	13.793	179.366	376.117	157.966	1.159

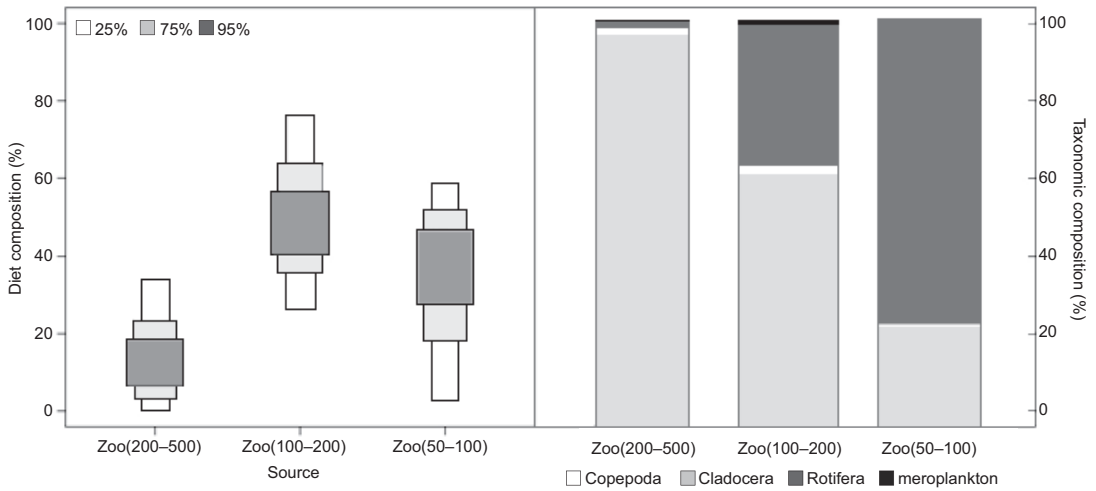


Fig. 7. (a) Bayesian mixing model (SIAR) results of estimated diet composition (boxes explain 95%, 75% and 25% of credible intervals) of *A. aurita* in summer 2011, and (b) taxonomic composition of zooplankton in summer 2011.

fraction of the zooplankton (50–100) comprised mainly Rotifera (75.5%) and Copepoda (24.5%). The rest of the carbon (11%) was probably derived from the largest fraction which is represented almost entirely by Copepoda (Fig. 7). SIAR did not confirm that Cladocera was an important food source for *A. aurita*.

Position of *A. aurita* in pelagial food web structure of Gulf of Gdansk

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differed among food web components such as sediment suspended matter, phytoplankton, zooplankton, jellyfish, and fish (Kruskal-Wallis one-way ANOVA: $H = 9.848$,

$df = 8$, $p < 0.01$ for $\delta^{13}\text{C}$; $H = 7.552$, $df = 8$, $p < 0.01$ for $\delta^{15}\text{N}$). The $\delta^{13}\text{C}$ values ranged between $-25.56\text{‰} \pm 0.74\text{‰}$ for the suspended particulate organic matter (SPOM) and $-20.43\text{‰} \pm 1.28\text{‰}$ for *Gasterosteus aculeatus*; $\delta^{15}\text{N}$ varied between $5.76\text{‰} \pm 1.57\text{‰}$ for SPOM and $11.53\text{‰} \pm 0.75\text{‰}$ for *Gasterosteus aculeatus*.

Jellyfish had less $\delta^{15}\text{N}$ and more $\delta^{13}\text{C}$ than did the other benthic-pelagic predators. This suggests that *A. aurita* is one of the significant consumers of zooplankton. Since the standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were also very low, this could indicate that *A. aurita* consumed only one type of food: zooplankton (Fig. 8). The isotopic fractionation for nitrogen between *A. aurita* and the most consumable fraction of zoo-

Table 4. Summary of the isotopic values, and carbon and nitrogen concentrations (% of dry weight) of food web components; nd = no data, n = number of samples. Values are means \pm SDs. SPOM = suspended particulate organic matter

	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N
SPOM	12	-25.56 ± 0.74	5.76 ± 1.57	nd	nd
Phytoplankton (25–50)	7	-23.64 ± 0.85	5.79 ± 1.65	21.62 ± 1.76	3.09 ± 0.64
Phytoplankton (50–100)	7	-23.84 ± 0.73	6.39 ± 1.32	22.56 ± 7.81	3.68 ± 1.67
Zooplankton (50–100)	5	-24.64 ± 0.79	9.57 ± 1.53	12.53 ± 8.80	3.14 ± 2.21
Zooplankton (100–200)	5	-24.24 ± 1.10	8.26 ± 1.17	22.64 ± 16.57	4.19 ± 2.92
Zooplankton (200–500)	8	-24.31 ± 1.23	10.25 ± 1.20	35.18 ± 5.33	8.79 ± 1.36
<i>Aurelia aurita</i>	8	-23.58 ± 0.35	11.02 ± 0.25	18.15 ± 9.50	4.48 ± 2.48
<i>Pungitius pungitius</i>	3	-22.07 ± 0.99	11.51 ± 0.33	38.83 ± 7.38	8.00 ± 2.59
<i>Gasterosteus aculeatus</i>	4	-20.43 ± 1.28	11.53 ± 0.75	29.22 ± 3.94	8.03 ± 1.14

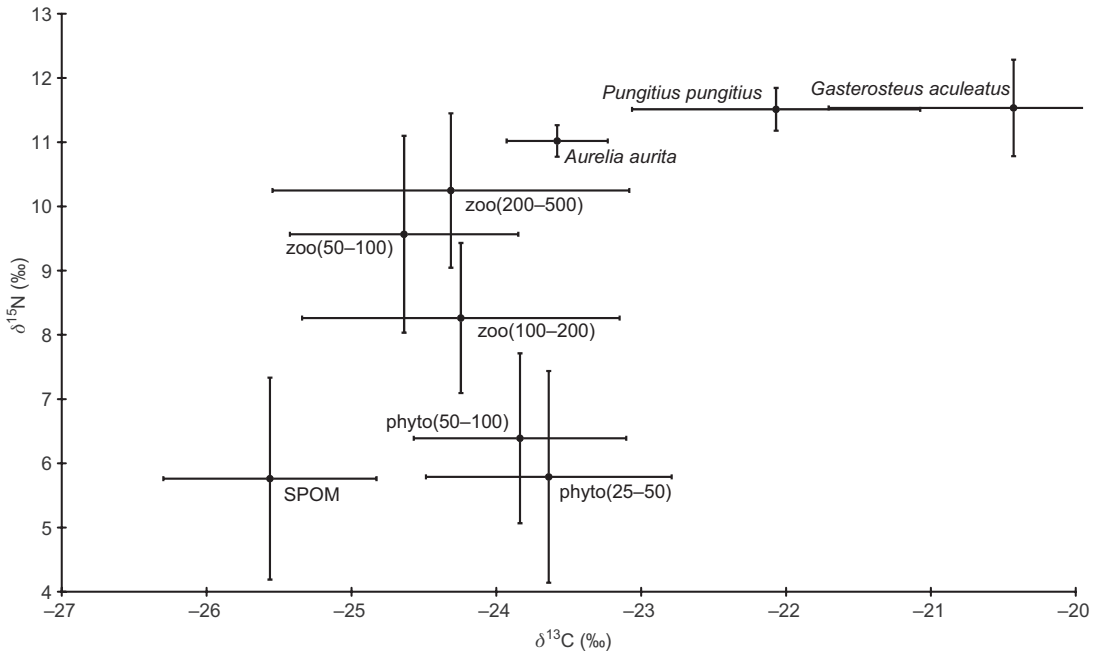


Fig. 8. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with standard deviations of suspended organic matter (SPOM), phytoplankton fractions (phyto25–50, phyto50–100), zooplankton fractions (zoo50–100, zoo100–200, zoo200–500), and consumers (jellyfish, *A. aurita*, and selected benthopelagic fishes: *P. pungitius* and *G. aculeatus*) in summer 2011.

plankton was 2.76‰ which falls precisely within the ranges of estimates of the trophic enrichment factor (McCutchan *et al.* 2003, Vander Zanden and Rasmussen 2001).

Discussion

Two species of Scyphozoa are found in the Gulf of Gdansk: *Cyanea capillata* and the dominant *A. aurita* (Janas and Witek 1993). Our studies showed that *A. aurita* was present in the Gulf of Gdansk from June to November 2008, and mass occurrence was observed in August and September. Similar observations were made in the Bornholm Basin (Barz and Hirche 2005), but we recorded about 500 times higher abundances of medusae during the bloom. Janas and Witek (1993), who studied the occurrence of medusae in the Polish fisheries zone in 1983–1991, observed *A. aurita* for a longer period — from July to January (with maximum numbers between August and November) — but the densities were lower. Since moon jellyfish in the Gulf of Gdansk are transported from the

western Baltic Sea (Janas and Witek 1993), we assume that the strong currents in 2008 might have delivered their greater numbers. We also observed the lowest densities of medusae at the station (PI) situated near the river mouth indicating that low salinity is a limiting factor for jellyfish proliferation. The abundance of moon jellyfish is usually $< 1 \text{ indiv. m}^{-3}$ (Lo and Chen 2008), but higher abundances have also been reported: e.g. $3.22 \pm 0.8 \text{ indiv. m}^{-3}$ [mean \pm SD] in Sihwa Lake in Japan (Han *et al.* 2012), $14.8 \pm 0.8 \text{ indiv. m}^{-3}$ in Skive Fjord, Denmark (Riisgård *et al.* 2012), 1–14 indiv. m^{-2} in the Black Sea (Multu 2001), and 300 indiv. m^{-2} in the Kertinge Nor Fjord in Denmark (Olsen *et al.* 1994). Abundances similar to or lower than found by us have been observed in Kiel Bight, Germany [14–23 indiv. 100 m^{-3} , Schneider (1989); 0.2–16 indiv. 100 m^{-3} , Schneider and Behrends (1994)], in Honjo District, Japan [0.55 indiv. m^{-3} , Han *et al.* (2009)], and in the Bornholm Basin in the central Baltic Sea [2.3 indiv. 100 m^{-3} , Barz and Hirche 2005].

From the moment the medusae appear, their diameter and weight increased rapidly suggest-

ing sufficient food availability. The maximum average diameter and wet weight were recorded at the beginning of October. Subsequently, the wet weight started to decrease, which is a natural process observed after the release of gametes (Möller 1980). Janas and Witek (1993) also observed the maximum weight of moon jellyfish in October. Nevertheless, we found about 1.4 times heavier medusae. Our observations do not support the conclusion of Schneider and Behrends (1994) that smaller and lighter medusae are abundant, while larger and heavier individuals occur at lower densities.

During our investigation no ephyrae were found, which indicates that *A. aurita* does not reproduce successfully in the Gulf of Gdansk. This confirms the assumption of Janas and Witek (1993) regarding medusae drifting from the western part of the Baltic Sea into the Polish coastal waters.

In many reservoirs, zooplankton limitation is caused by gelatinous zooplankton predation (Schneider 1989, Olsen 1995). Nonetheless, the small numbers of plankton prey in the diet of *A. aurita* suggest that it did not regulate the mesozooplankton community in the Gulf of Gdansk. Similar was reported for the Bornholm Basin (Barz and Hirche 2005). Sullivan *et al.* (1994), Multu (2001), and Uye and Shimauchi (2005) also described higher prey densities in the gut of moon jellyfish. Ishii and Tanaka (2001) assumed that the stomach content of the medusae reflects the zooplankton composition in the seawater. Our observations do not confirm this conclusion. Cladocera, Copepoda, and Rotifera are the main zooplankton components in the Gulf of Gdansk (Bielecka *et al.* 2000). Rotifera were most abundant throughout the study period, *Keratella* being the dominant genus. Copepoda and Rotifera were present throughout the study period, and *Acartia* spp. was the dominant taxa in the zooplankton community. Similar zooplankton structure was described by Bielecka *et al.* (2000) and Józefczuk *et al.* (2003). The taxonomic composition of the diet reflected the available food items only partially, and we observed low prey selection. Han *et al.* (2009) also states that moon jellyfish fed on mesozooplankton largely non-selectively. Interestingly, rotifers were the most abundant in seawater, but they were not identi-

fied in the guts of the medusae during our investigation, which suggests that *A. aurita* digest them quickly. The results of the stable isotope mixing model confirmed that *A. aurita* receives a significant percentage of carbon from this group of zooplankton. The diet of *A. aurita* from the Gulf of Gdansk comprised predominantly copepods and cladocerans, which was found by Schneider and Behrends (1994), Barz and Hirche (2005), Han *et al.* (2009), and by Purcell (2003) in *Aurelia labiata*. Stable isotope analysis did not confirm cladocerans to be an important food source, because of the lack of this group in the mesozooplankton fractions. This might have been caused by the absence of cladocerans in the ambient seawater during the sampling period. Interestingly, gut content and isotope analyses can be valuable methods for filling in the data gap in the *A. aurita* diet, but they must be performed simultaneously. Similarly to Hansson (2006), we observed the selection of large prey (cladocerans and copepods over larvae) by *A. aurita*. Our data confirmed that the majority of carbon is derived from the medium fraction of mesozooplankton which can indicate prey size selectivity. No fish larvae were found either in the water column or in the guts of the moon jellyfish.

In view of the above, studies of the moon jellyfish in the Gulf of Gdansk should be continued. It is widely acknowledged that factors such as climate change, eutrophication, hard substrate supplementation, and the lack of predators such as fish (e.g., *Mola mola*) or turtles (e.g., *Derموchelys coriacea*) can contribute to the mass occurrence of *A. aurita*. Our observations reveal that *A. aurita* is on the third trophic level with other benthic-pelagic consumers, and it probably belongs to the top pelagic predators in the southern Baltic Sea. Therefore, increased numbers of medusae in the future could potentially modify the food web in this area through its control of zooplankton abundance.

Acknowledgments: This work was supported by the Polish Ministry of Science and Higher Education [N N304 142636; NN304 162 237]. We are grateful to Adam Sokołowski from the Department of Marine Ecosystem Functioning, University of Gdansk and Pierre Richard from University of La Rochelle for assistance during stable isotope analysis. Jennifer Zielińska proofread the paper.

References

- Arai M.N. 1997. *Functional biology of Scyphozoa*. Chapman & Hall, London.
- Bamstedt U., Wild B. & Martinussen M.B. 2001. Significance of food type for growth of ephyrae *Aurelia aurita* (scyphozoan). *Mar. Biol.* 139: 641–650.
- Barz K., Hinrichsen H.-H. & Hirche H.-J. 2006. Scyphozoa in the Bornholm Basin (central Baltic Sea) — the role of advection. *J. Marine Syst.* 60: 167–176.
- Barz K. & Hirche H.-J. 2005. Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). *Mar. Biol.* 147: 465–476.
- Baumann S. & Schernewski G. 2012. Occurrence and public perception of jellyfish along the German Baltic coastline. *J. Coast. Conservat.* 16: 555–566.
- Bielecka L., Gaj M., Mudrak S. & Żmijewska M.I. 2000. The seasonal and short-term variability of zooplankton taxonomic composition in the shallow coastal area of the Gulf of Gdańsk. *Oceanol. St.* XXIX: 57–76.
- Boero F., Bouillon J., Gravili C., Miglietta M.P., Parsons T. & Piraino S. 2008. Gelatinous plankton: irregularities rule the world (sometimes). *Mar. Ecol. Prog. Ser.* 356: 299–310.
- Graham W.M., Pagès F. & Hamner W.M. 2001. A physical context for gelatinous zooplankton aggregation: a review. *Hydrobiologia* 451: 199–212.
- Han C.-H., Chae J., Jin J. & Yoon W. 2012. Estimation of the minimum food requirement using the respiration rate of medusa of *Aurelia aurita* in Sihwa Lake. *Ocean Sci.* 47: 155–160.
- Han C.-H., Kawahara M. & Uye S.-I. 2009. Seasonal variations in the trophic relationship between the scyphomedusa *Aurelia aurita* s.l. and mesozooplankton in a eutrophic brackish-water lake, Japan. *Plank. Benth. Res.* 4: 14–22.
- Hansson L.J. 2006. A method for in situ estimation of prey selectivity and predation rate in large plankton, exemplified with the jellyfish *Aurelia aurita* (L.). *J. Exp. Mar. Biol. Ecol.* 328: 113–126.
- Ishii H. & Tanaka F. 2001. Food and feeding of *Aurelia aurita* in Tokyo Bay with n analysis of stomach contents and a measurement of digestion times. *Hydrobiologia* 451: 311–20.
- Janas U. & Witek Z. 1993. The occurrence of medusae in the southern Baltic and their importance in the ecosystem, with special emphasis on *Aurelia aurita*. *Oceanologia* 34: 69–84.
- Józefczuk A., Guzera E. & Bielecka L. 2003. Short-term and seasonal variability of mesozooplankton at two coastal stations (Gdynia, Sopot) in the shallow water zone of the Gulf of Gdańsk. *Oceanologia* 45: 317–336.
- Lizińska A. 2002. Seasonal and daily distribution of commercial and non-commercial fish in shallow inshore waters of the Gulf of Gdańsk. *Oceanol. St.* XXXI: 31–42.
- Lo W.T. & Chen I.L. 2008. Population succession and feeding of Scyphomedusae, *Aurelia aurita*, in a eutrophic tropical lagoon in Taiwan. *Estuarine, Coast. Shelf Sci.* 76: 227–238.
- Lynam C.P., Gibbons M.J., Axelsen B.E., Sparks C.A.J., Coetzee J., Heywood B.G., Andrew S. & Brierley A.S. 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Curr. Biol.* 16: R492–R493.
- McCutchan J.H.J., Lewis W.M., Kendall C. & McGrath C.C. 2003. Variation in trophic shift for stable isotope ratio of carbon, nitrogen and sulfur. *Oikos* 102: 378–390.
- Mills C.E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451: 55–68.
- Möller H. 1980. Population dynamics of *Aurelia aurita* medusa in Kiel Bight, Germany (FRG). *Mar. Biol.* 60: 123–128.
- Multu E. 2001. Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. *Mar. Biol.* 138: 329–339.
- Olsen N.J. 1995. Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. *Mar. Ecol. Prog. Ser.* 124: 63–72.
- Olsen N.J., Frandsen K. & Riisgård H.U. 1994. Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. *Mar. Ecol. Prog. Ser.* 105: 9–18.
- Parnell A.C., Inger R., Bearhop S. & Jackson A.L. 2010. Source partitioning using stable isotope: coping with too much variation. *PLoS ONE* 5: e9672. doi:10.1371/journal.pone.0009672.
- Purcell J.E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 246: 137–152.
- Purcell J.E., Uye S.-I. & Lo W.-T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Prog. Ser.* 350: 153–174.
- Richardson A.J., Bakun A., Hays G.C. & Gibbons M.J. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* 24: 312–322.
- Riisgård H.U., Madsen C.V., Barth-Jensen C. & Purcell J.E. 2012. Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). *Aq. Inv.* 7: 147–162.
- Rolff C. & Elmgren R. 2000. Use of riverine organic matter in plankton food webs of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 197: 81–101.
- Schernewski G. & Schiewer U. 2002. *Baltic coastal ecosystems — structure, function and coastal zone management*. Springer, Berlin.
- Schneider G. 1989. The common jellyfish *Aurelia aurita*: standing stock, excretion and nutrient regeneration in the Kiel Bight, Western Baltic. *Mar. Biol.* 100: 507–514.
- Schneider G. & Behrends G. 1994. Population dynamics and the trophic role of *Aurelia aurita* medusa in the Kiel Bight and western Baltic. *ICES J. Mar. Sci.* 51: 359–367.
- Sullivan B.K., Garcia J.R. & Klein-MacPhee G. 1994. Prey selection by the scyphomedusan predator *Aurelia aurita*. *Mar. Biol.* 121: 335–341.

- Uye S. & Shimauchi H. 2005. Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the inland sea of Japan. *J. Plankton Res.* 27: 237–248.
- Wintzer A.P., Meek M.H. & Moyle P.B. 2011. Trophic ecology of two non-native hydrozoan medusa in the upper San Francisco Estuary. *Mar. Freshwater Res.* 62: 952–961.
- Vander Zanden M.J. & Rasmussen J.B. 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol. Oceanogr.* 46: 2061–2066.