

The Effect of Temporal Changes and Environmental Trophic Condition on the Isotopic Composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of *Atherina boyeri* (Risso, 1810) and *Gobius niger* (L., 1758) in a Mediterranean Coastal Lagoon (Lake of Sabaudia): Implications for Food Web Structure

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Keywords: *Atherina boyeri*, *Gobius niger*, stable isotope, coastal lagoon, MED.

Abstract. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of organic matter sources and consumers were employed to analyse trophic differentiation between a benthic consumer, *Gobius niger* (L., 1758) (Pisces, Osteichthyes), and a pelagic consumer, *Atherina boyeri* (Risso, 1810) (Pisces, Osteichthyes) in a Mediterranean coastal lagoon (Lake of Sabaudia) in winter and summer 1999. Trophic differences between the two species throughout the two sampling periods were related to the environmental trophic condition (i. e. nutrient and phytopigment concentrations). Although these two fish have different habitats, they both exploited benthic organisms, above all in summer. When the nutrient and phytopigment concentrations were higher (summer), the most abundant benthic organisms were the main food sources for both species. In winter *A. boyeri* apparently shifted its feeding preferences to include zooplankton, confirming its opportunistic feeding strategy. Particulate organic matter and algae seemed to play the main trophic role in the food web structure. Benthic invertebrates used both sources, while zooplankton seemed to rely exclusively on the particulate fraction. The overlapping and very depleted signatures of sedimentary and particulate organic matter highlights a strong link between sediments and water column, rarely observed in other aquatic ecosystems using stable isotopes. Such a finding further substantiates the importance of particulate organic matter as a food source in the study area.

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Problem

One of the main interests in the ecology of fish species is the analysis of feeding strategies and food partitioning. Assigning trophic niches within fish communities in coastal environments and, in particular, lagoons can be difficult because of the elevated level of omnivory and the marked degree of overlap in the diets of consumers (Livingston, 1982). Temporal differences in diets, usually due to environmental heterogeneity in time (Dill, 1983), can further complicate the discrimination of feeding habits and strategies.

In order to resolve such ecological complexity, stable isotope ratios have been extensively analysed to establish food web structure and trophic relationships between marine organisms (Michener & Schell, 1994). However, few stable isotope studies have been carried out to investigate processes in coastal lagoons (Cooper, 1989; Hsieh *et al.*, 2000; Mazzola *et al.*, 2001). In particular, few data exist concerning common Mediterranean species such as the sand smelt, *Atherina boyeri* (Risso, 1810), and the black goby, *Gobius niger* (L., 1758).

These species occupy two different niches. *G. niger* is an epibenthic species inhabiting estuaries and low-salinity coastal lagoons (Vesey & Langford, 1985), while *A. boyeri* is an inshore pelagic fish which generally spends most of its life cycle in lagoons, migrating through the mouths to the open sea in winter (Bamber *et al.*, 1985; Henderson *et al.*, 1988). Despite the differences observed in their respective ecological habitats, it has been suggested (Scilipoti, 1998) that in a shallow environment their feeding preferences may partially overlap as a function of the seasonal trophic background.

In order to investigate this hypothesis and gain a better understanding of the feeding strategies of *A. boyeri* and *G. niger* in a Mediterranean coastal lagoon (Lake of Sabaudia, Tyrrhenian Sea), we analysed their stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) and those of the main organic matter sources and consumers. These species were chosen because they are among the most abundant in the lagoon (Vizzini, pers. comm.). The carbon isotope ratio of an animal reflects that of the organic source plus a slight enrichment (about 1‰), while nitrogen undergoes a greater fractionation (about 3.5‰) (Michener & Schell, 1994). These ratios thus provide an indication of the trophic level of consumers.

The main aims of this study were to analyse i) the effect of temporal changes and environmental trophic condition (i. e. nutrient and phytopigment concentrations) on the isotopic composition of *A. boyeri* and *G. niger*, ii) their relative feeding strategies and lastly, iii) the food web leading to *A. boyeri* and *G. niger* in the Lake of Sabaudia (Tyrrhenian Sea, Mediterranean).

Material and Methods

Study area

The Lake of Sabaudia (13°2'E, 41°20'N; 390 ha; 4 m average depth) is a brackish basin (salinity about 33) in central Italy, separated from the Tyrrhenian Sea by a long sand spit. Wind action and weak tidal currents determine a low water exchange through the two mouths (Perdicaro, 1985). The high nutrient and chlorophyll *a* concentrations classify the lake as eutrophic (Perdicaro, 1984). The main vegetal producers are macroalgae

Table 1. Temporal changes in the environmental trophic condition expressed as dissolved inorganic nitrogen (DIN; as the sum of nitrates, nitrites and ammonium), dissolved inorganic phosphorus (DIP) and phytopigment concentrations (mean \pm SD) in the Lake of Sabaudia, according to Perdicaro (1984).

	winter	summer
DIN ($\mu\text{g-at l}^{-1}$)	19.8 \pm 3.4	29.3 \pm 5.4
DIP ($\mu\text{g-at l}^{-1}$)	1.7 \pm 0.8	6.8 \pm 4.8
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	8.9 \pm 3.2	61.0 \pm 7.6
Phaeopigments ($\mu\text{g l}^{-1}$)	5.4 \pm 4.6	8.2 \pm 5.3

(*Chaetomorpha* spp., *Ulva* spp., *Enteromorpha* spp.), while *Cymodocea nodosa* and *Ruppia maritima* form sparse meadows.

Sample collection

Sampling was carried out during the winter (January) and summer (July) of 1999 in the shallow southern area of the Lake of Sabaudia (about 1 m average depth). We chose these two periods to represent different trophic conditions in the study site, as expressed by nutrient and phytopigment concentration (Tab. 1). Samples of algae, halophytes and seagrasses were collected by hand. Sediment samples, collected using handle corers, were analysed to measure the carbon and nitrogen isotope ratios in the sedimentary organic matter (SOM). Seawater samples were filtered through precombusted fibreglass filters (Whatman GF/F) (450 °C, 4 h) for the isotopic analysis of particulate organic matter (POM). Vagile fauna was caught by means of a hand-towed net (mesh size: 400 μm). A hand-towed trawl net (mesh size: 3 mm) was used to catch adults of *A. boyeri* and *G. niger*.

Sample preparation and isotopic analysis

Seagrass leaves were scraped to remove the epiphytic organisms, and the vegetal portion of these was pooled under a stereo-binocular microscope. The biomass of autotrophic epiphyte organisms was very low in the winter season, and no sample was obtained. Invertebrates were sorted under a stereo-binocular microscope. White muscle tissue from the dorsal portion of the fish was dissected. All samples were obtained by pooling a different number of individuals (about 5 for vegetal samples, about 10 for fish and more than 100 for invertebrates) to reduce intra-individual variability. Samples were acidified in 2N HCl, rinsed in distilled water, dried at 60 °C for at least 24 h and ground. In the current literature, the necessity to acidify samples to remove carbonates is rather controversial. Some authors (e. g. Bunn *et al.*, 1995) suggest that this process, which provides a more accurate measure of $\delta^{13}\text{C}$ values, may affect the $\delta^{15}\text{N}$. While acidification is still a widely used procedure, it is not well understood how and to what extent it affects the isotopic composition of species.

The isotopic analyses were performed using a Finnigan Delta-S isotope ratio mass spectrometer. Isotopic values were expressed in parts per thousand as deviations from standards (Peedee belemnite limestone for $\delta^{13}\text{C}$ and nitrogen in air for $\delta^{15}\text{N}$):

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3, \text{ where } R = {}^{13}\text{C}/{}^{12}\text{C} \text{ or } {}^{15}\text{N}/{}^{14}\text{N}.$$

Experimental precision based on the SD of replicates of internal standards was 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Data analyses

Temporal differences between winter and summer in the isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of each taxon were tested with a t-test (Sokal & Rohlf, 1995) on the data presented in Table 2 using STATISTICA (StatSoft, Inc.) statistical package.

Table 2. Significance levels of the t-test to evaluate temporal differences between winter and summer isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; ‰) of organic matter sources and consumers in the Lake of Sabaudia. [* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; Ns = non-significant difference ($P > 0.05$)]. n = number of replicates; POM = particulate organic matter; SOM = sedimentary organic matter.

taxa	$\delta^{13}\text{C}$						$\delta^{15}\text{N}$							
	winter			summer			winter			summer				
	mean	\pm S.D.	n	mean	\pm S.D.	n	P	mean	\pm S.D.	n	mean	\pm S.D.	n	P
Halophytes	-26.8	0.7	2	-25.6	0.5	2	Ns	5.5	0.1	2	5.0	0.1	2	*
<i>C. nodosa</i>	-7.5	0.6	4	-7.0	0.9	4	Ns	6.4	1.7	4	6.8	1.1	4	Ns
POM	-21.7	0.9	4	-18.2	0.2	4	***	4.8	0.2	4	7.1	2.3	4	Ns
SOM	-22.7	2.0	4	-23.6	1.7	4	Ns	8.4	0.8	4	5.5	0.8	4	**
<i>C. linum</i>	-17.4	1.4	4	-16.3	0.5	4	Ns	6.3	0.2	4	6.7	0.9	4	Ns
Amphipoda	-19.4	1.6	4	-16.4	0.8	4	**	7.2	1.5	4	8.2	1.1	4	Ns
Calanoida	-22.8	1.8	4	-19.8	0.3	4	**	7.0	2.2	4	10.0	0.4	4	*
Harpacticoida	-18.5	2.9	4	-16.3	1.9	4	Ns	7.5	0.5	4	8.2	0.3	4	*
<i>A. boyeri</i>	-17.4	1.1	6	-14.8	0.5	6	***	12.8	0.2	6	13.5	0.3	6	***
<i>G. niger</i>	-15.3	0.4	6	-15.0	1.1	6	Ns	13.8	0.4	6	14.3	0.6	6	Ns

The hypothesis that the isotopic compositions of *A. boyeri* and *G. niger* were different as a function of the different environmental trophic condition during the year (i.e. nutrient and phytopigment concentrations that are low in winter and high in summer) was tested using ANOVA (a mixed design; Underwood, 1997). Two factors were treated as fixed and orthogonal: species (*A. boyeri* and *G. niger* = 2 levels; SPECIES) and trophic condition (low [winter] and high [summer] = 2 levels; TROPH). Times (two for each trophic state) were treated as random (2 levels; TIME) and nested in TROPH. Three replicates were randomly effected in each time. Heterogeneity of variances was tested using Cochran's test prior to analysis of variance and appropriate means compared using Student-Newman-Keuls (SNK) tests (Underwood, 1997). The GMAV (1997) statistical package (University of Sydney, AU) was used to perform ANOVA.

Results

$\delta^{13}\text{C}$ showed a wide variation in the organic matter sources (ranging from about -26‰ in halophytes to about -7‰ in seagrass) throughout the sampling periods. Algae (*C. linum* and epiphytes) showed intermediate values (about -16‰), while POM and SOM had more depleted values (about -20 and -23‰ , respectively) (Fig. 1). $\delta^{15}\text{N}$ in organic sources showed values that differed by not more than about 3‰ (minimum in halophytes with about 5‰ , maximum in SOM with about 8‰). Organic matter sources showed marginal temporal differences in their isotopic composition, with a general enrichment in summer (except in SOM) compared to winter for $\delta^{13}\text{C}$, while no well-defined trend was observed for $\delta^{15}\text{N}$ (Fig. 1).

Only POM presented significant differences in the ^{13}C content between the two periods ($p < 0.001$, $n = 4$), whereas both halophytes and SOM were significantly different for $\delta^{15}\text{N}$ ($p < 0.05$, $n = 2$ and $p < 0.01$, $n = 4$, respectively) (Tab. 2).

As regards invertebrates, Amphipoda, Calanoida and Harpacticoida showed a clear trend towards more $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enriched values from winter to summer. These differences were significant in Amphipoda ($p < 0.01$, $n = 4$) and Calanoida ($p < 0.01$,

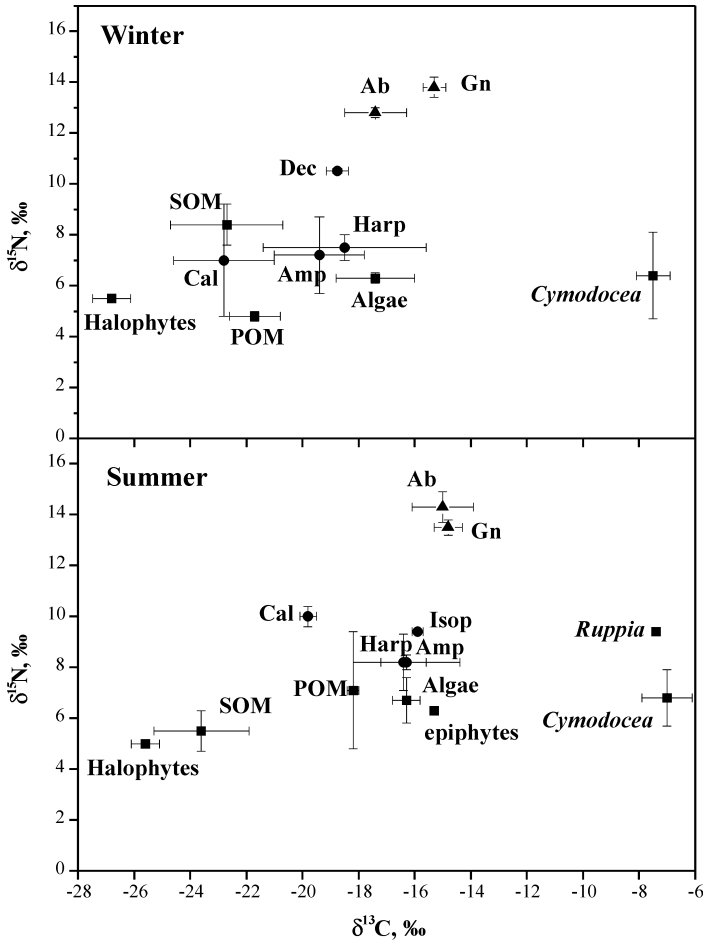


Fig. 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of main organic matter sources (■), invertebrates (●) and fish (▲) from the Lake of Sabaudia, expressed as parts per mil (‰). Ab: *A. boyeri*, Amp: Amphipoda, Cal: Calanoida, Dec: Decapoda larvae, Harp: Harpacticoida, Isop: Isopoda, Gn: *G. niger*, POM: Particulate Organic Matter, SOM: Sedimentary Organic Matter.

$n = 4$) for $\delta^{13}\text{C}$ and in Calanoida ($p < 0.05$, $n = 4$) and Harpacticoida ($p < 0.05$, $n = 4$) for $\delta^{15}\text{N}$ (Tab. 2).

In *A. boyeri* (S. L. = 75.1 ± 2.0 mm in winter and S. L. = 79.2 ± 1.8 mm in summer) the carbon ($p < 0.001$, $n = 6$) and nitrogen ($p < 0.001$, $n = 6$) isotopic composition changed significantly between the two periods, with the same pattern as observed for autotrophic sources and invertebrates (Tab. 2). Conversely, temporal differences were not evident in *G. niger* (S. L. = 95.1 ± 3.5 mm in winter and S. L. = 102.7 ± 2.3 mm in summer) ($p > 0.05$, $n = 6$), which showed closer values in the two sampling periods (winter: $\delta^{13}\text{C} = -15.3$ ‰ and $\delta^{15}\text{N} = 13.8$ ‰; summer: $\delta^{13}\text{C} = -15.0$ ‰ and $\delta^{15}\text{N} = 14.3$ ‰).

Looking at differences in the isotopic composition of the two fish species, in summer *A. boyeri* and *G. niger* had matching isotopic compositions ($\delta^{13}\text{C} = -14.8$ ‰ and

Table 3. Analysis of Variance on all measured variables. See text for acronyms and for explanation of experimental design adopted. [* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; Ns = non-significant difference ($P \geq 0.05$)].

sources of variation	Df	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		MS	F	P	MS	F	P
Species = SPECIES	1	12.0	13.6	Ns	5.2	12.9	Ns
Trophic status = TROPH	1	16.7	14.0	Ns	0.7	1.0	Ns
Time = TIME (TROPH)	2	1.2	2.6	Ns	0.7	7.0	**
SPECIES x TROPH	1	22.4	25.4	*	0.6	1.5	Ns
SPECIES x TIME (TROPH)	2	0.9	1.9	Ns	0.4	3.9	*
RESIDUAL	16	0.5			0.1		
Cochran's C				Ns			Ns

–15.0‰; $\delta^{15}\text{N}$ = 13.5‰ and 14.3‰, respectively), while in winter *A. boyeri* maintained a similar ^{15}N content (12.8‰) to that of *G. niger* (13.8‰), but showed a more depleted $\delta^{13}\text{C}$ value (–17.4‰ v. –15.3‰) (Fig. 1).

ANOVA highlighted that the $\delta^{13}\text{C}$ values of the two fish species were significantly different. The isotopic composition of both species varied as a function of environmental trophic condition (see significance of interactions in Table 3). ANOVA did not show differences for the tested hypothesis for $\delta^{15}\text{N}$ (Tab. 3).

Discussion

Temporal variations in the isotopic composition of *A. boyeri* and *G. niger* and their relative feeding strategies

This study attempts a contextual analysis of the isotopic composition and food web structure of two common coastal fish, *G. niger* and *A. boyeri*, in the Lake of Sabaudia.

The enriched carbon isotope ratios of *G. niger* indicate a diet based exclusively on benthic organic matter (France, 1995a). Moreover, *G. niger* seemed to feed on benthic prey (viz. Amphipoda, Harpacticoida and Isopoda) throughout the sampling periods, as its $\delta^{13}\text{C}$ signatures (average about –15.5‰) were always closer to those of benthic invertebrates (average about –17.0‰) than to other organic sources. However, the elevated ^{15}N content of the black goby (14‰) cannot be explained by the exclusive consumption of the above-mentioned food resources. If its food preferences were only based on benthic invertebrates (average $\delta^{15}\text{N}$ about 8.5‰), we would expect *G. niger* to show a $\delta^{15}\text{N}$ value of about 12‰, as a consequence of the nitrogen fractionation process from dietary source to consumer (+3.5‰; Michener & Schell, 1994). Such a discrepancy may be explained by the additional predation by *G. niger* on juvenile fish (belonging to a higher trophic level than invertebrates and, consequently, showing more enriched $\delta^{15}\text{N}$ values) not sampled in this study and/or by the consumption of detritus and faecal pellets (i.e. re-arranged organic matter). During decomposition, organic matter generally undergoes an increase in ^{15}N content (Curran *et al.*, 1995). Such findings and hypotheses are consistent with literature data obtained from stomach content

analyses, which indicate that *G. niger* is a benthic feeder on mainly Crustacea, Polychaeta and small fish (Vesey & Langford, 1985; Fernández *et al.*, 1995). Our results are also consistent with the observed behaviour in *G. niger* as an epi- and cryptobenthic fish living on muddy and sandy bottoms and vegetated areas (Vesey & Langford, 1985). In addition, the ingestion of ^{15}N rich detritus and faecal pellets may explain the enriched $\delta^{15}\text{N}$ isotopic composition of benthic predators in other Mediterranean areas (Pinnegar & Polunin, 2000).

When examining temporal differences, isotopic data show that *G. niger* from the Lake of Sabaudia exhibited no temporal variability. This suggests the consumption of food resources with the same isotopic composition throughout the year, or the integration of $\delta^{13}\text{C}$ composition from different prey.

The situation was different in *A. boyeri*: its nitrogen and carbon isotopic composition differed significantly in the two sampling periods. Sand smelt showed enriched isotopic signatures in summer ($\delta^{13}\text{C} = -14.8\text{‰}$; $\delta^{15}\text{N} = 13.5\text{‰}$), suggesting a preference for benthic resources ($\delta^{13}\text{C} = -16.1\text{‰}$; $\delta^{15}\text{N} = 8.5\text{‰}$) that were more abundant in late spring-early summer in the study area (Costa *et al.*, 1985–86). In contrast, the more depleted isotopic composition in winter ($\delta^{13}\text{C} = -17.4\text{‰}$; $\delta^{15}\text{N} = 12.8\text{‰}$) may reflect a slight shift in benthic prey toward more negative values ($\delta^{13}\text{C} = -19.0\text{‰}$; $\delta^{15}\text{N} = 7.3\text{‰}$), or indicate the exploitation of planktonic resources [e.g. Calanoida ($\delta^{13}\text{C} = -22.8\text{‰}$; $\delta^{15}\text{N} = 7.0\text{‰}$) and Decapoda larvae ($\delta^{13}\text{C} = -18.8\text{‰}$; $\delta^{15}\text{N} = 10.5\text{‰}$)]. In late summer the higher temperature and salinity and a lower oxygen and water exchange cause zoobenthos abundance to decrease (Costa *et al.*, 1985–86). As *A. boyeri* is known to vary its diet as a function of resource availability (Castel *et al.*, 1977; Trabelsi *et al.*, 1994), we accept the second hypothesis substantiating an opportunistic feeding habit for this species. The turnover rate in fish tissue varies with growth rate and metabolic activity, and these processes therefore play a key role in the analysis of seasonal variations of carbon and nitrogen stable isotope ratios. Hesslein *et al.* (1993) monitored changes in stable isotope ratios (carbon, nitrogen and sulphur) in broad whitefish (*Coregonus nasus*) in response to changes in the isotopic composition of their food. The authors concluded that in this slow-growing fish, changes in isotopic composition appear after one year or more. In contrast, *A. boyeri* is a small fish with rapid growth and a short lifespan. Although laboratory studies have never been carried out on its turnover rate, we hypothesize that isotopic composition changes fairly quickly in response to changes in the isotopic composition of its diet. Hence, the observed temporal shift in $\delta^{13}\text{C}$ may reflect changes in diet occurring some months before sampling. *A. boyeri* appears to be a benthivore in spring-summer and also a zooplanktivore in autumn-winter.

Temporal differences in the isotopic composition can also reflect anthropogenic and terrestrial-derived inputs. Such inputs are not negligible in coastal lagoons and often undergo seasonal variations due to agricultural and tourism pressures. Although we have no data on the quantity of anthropogenic inputs in the study site, they potentially influence the isotopic composition of plants and animals. A general trend towards more depleted $\delta^{13}\text{C}$ and more enriched $\delta^{15}\text{N}$ values in winter than in summer has been observed in several taxa. McClelland & Valiela (1998) also observed this in estuaries subjected to anthropogenic loads: natural food webs were altered by allochthonous organic matter.

The fact that *A. boyeri* and *G. niger* occupy different spatial niches – pelagic and benthic, respectively – suggests that they depend on the corresponding trophic resources.

Our experimental design highlighted that trophic condition (high or low nutrient and phytopigment concentration) can play an important role in the isotopic composition of these fish. Although *G. niger* did not temporally change its isotopic composition, its $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed from those of *A. boyeri*. Whereas *G. niger* fed exclusively on benthic prey (Harpacticoida and Amphipoda) under the two environmental trophic conditions, *A. boyeri* seemed to exploit both planktonic (Calanoida and Decapoda larvae) and benthic (Amphipoda and Harpacticoida) invertebrate prey. Consequently, although the two fish species occupy different habitats in the Lake of Sabaudia, both exploited benthic resources, above all in summer. This is probably due to the different trophic roles the sand smelt plays in the two periods, exploiting sources belonging to different trophic compartments as a function of their availability.

Food web leading to *A. boyeri* and *G. niger*

The isotopic picture provided in the present study allows us to identify the trophic links between invertebrates (benthic and planktonic) and organic matter sources and to infer the web structure.

Accordingly, zooplankton (average $\delta^{13}\text{C} = -21\text{‰}$; $\delta^{15}\text{N} = 9.2\text{‰}$) feeds on particulate organic matter (average $\delta^{13}\text{C} = -20.6\text{‰}$; $\delta^{15}\text{N} = 6\text{‰}$), while benthic invertebrates (average $\delta^{13}\text{C} = -17.3\text{‰}$; $\delta^{15}\text{N} = 8.1\text{‰}$) have a diet based on algae (average $\delta^{13}\text{C} = -16.3\text{‰}$; $\delta^{15}\text{N} = 6.4\text{‰}$) and particulate organic matter. As *G. niger* fed on benthos and *A. boyeri* fed on both plankton and benthos, algae and POM should represent the ultimate food sources for both species and are likely to be the trophic wheel-drives in the Lake of Sabaudia.

As in other Mediterranean coastal systems (Mazzola *et al.*, 2001), POM isotopic composition was strongly influenced by phytoplankton; it may represent the main trophic reservoir at the study site such that its temporal changes are reflected in both planktonic and benthonic resources. The matching isotopic values of POM and SOM thus suggest a strong link between pelagic and benthic compartments at the base of the trophic web. This fact further corroborates the importance of suspended organic matter and the direct exploitation by benthic consumers of pelagic primary production, which reaches the bottom before being grazed. Such a condition is reflected in the upper trophic levels, particularly in opportunistic consumers (i. e. *A. boyeri*) able to feed on available resources.

Similar findings, however, may contradict the general idea of a decoupling between pelagic and benthic consumers (France, 1995a; 1995b) observed in many aquatic ecosystems and revealed by means of stable isotope analyses. Further investigation is needed to resolve and better understand trophic relationships in lagoons.

Acknowledgements

We thank Dr. Robert Michener (Stable Isotope Laboratory, Boston University) for the isotopic analyses and Dr. Andrea Savona for help in sample collection and analysis. This project was supported by funds from the Ministero dell'Università e della Ricerca Scientifica e Tecnologica (MURST, 40%) (Italy).

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