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A wolf in sheep's clothing: carnivory in dominant sea urchins in the Mediterranean

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ABSTRACT: *Arbacia lixula* and *Paracentrotus lividus* are the dominant sea urchins in the Mediterranean sublittoral, where they are key structuring species due to their grazing activity. It has been commonly accepted that competition between both species is minimized by specializing in different algal foods. *A. lixula* is considered to feed mainly on encrusting coralline algae, while *P. lividus* prefers fleshy macroalgae. We used stable isotope analysis to test if these species occupy different trophic positions at 3 locations in the western Mediterranean and one in Macaronesia. Our results show unambiguously that *A. lixula* always occupies a higher trophic level than *P. lividus*, with a δ^{15}N comparable in some locations to strict carnivores such as *Actinia schmidti* or *Marthasterias glacialis*. A temporal monitoring at one locality showed that this signature of a higher trophic level is consistent throughout the year. These results are incompatible with the current belief of an herbivorous diet for *A. lixula* and suggest that it must be considered an omnivore tending to carnivory in Mediterranean ecosystems, feeding at least partially on sessile animals such as Cirripedia, Hydrozoa or Bryozoa. A parallel analysis of gut contents showed a predominance of vegetal items in both species, although *A. lixula* consistently had a higher abundance of animal components than *P. lividus.* Our results challenge the validity of using gut content observations alone for characterizing the trophic behaviour of omnivorous marine invertebrates that feed on a variety of food sources with different digestibility.

KEY WORDS: *Arbacia lixula* · *Paracentrotus lividus* · Trophic relationships · Benthic community · Stable isotope analysis.

INTRODUCTION

The edible common sea urchin *Paracentrotus lividus* (Lamarck, 1816) and the black sea urchin *Arbacia lixula* (Linnaeus, 1758) are the 2 dominant echinoid species in shallow rocky bottoms in the Mediterranean, where they coexist (Palacín et al. 1998b, Benedetti-Cecchi et al. 1998). Their grazing activity is commonly considered to greatly influence benthic communities (Sala et al. 1998, Palacín et al. 1998a, Bulleri et al. 1999). Their coexistence has raised questions regarding how these 2 abundant species interact and, specifically, whether and how they partition resources (Bulleri et al. 1999, Chiantore et al. 2008, Privitera et al. 2008). The currently prevalent view is that they are competitors for algal foods, although this putative competition seems alleviated by a selective preference of *P. lividus* for erect seaweeds, while *A. lixula* tends to feed more on encrusting coralline algae (Kempf 1962, Régis 1978, Verlaque & Nédelec 1983, Frantzis et al. 1988, Bulleri et al. 1999, Boudouresque & Verlaque 2001, Privitera et al. 2008).

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This herbivorous behaviour described in *Arbacia lixula* is, however, in sharp contrast with other species in the genus *Arbacia,* where omnivorous or unambiguously carnivorous diets have been reported. North American *A. punctulata* feeds on sessile invertebrate species, sand dollars and other *Arbacia* individuals, as well as some algae (Harvey 1956, Karlson 1978, Cobb & Lawrence 2005). The diet of South Atlantic *A. dufresnei* is mainly carnivorous (Penchaszadeh 1979, Penchaszadeh & Lawrence 1999). The Pacific *A. spatuligera* showed preference for animal food over common species of algae from its habitat (Silva et al. 2004). Moreover, some observations indicate omnivorous or carnivorous behaviour of *A. lixula* outside the Mediterranean (Marques 1984, Oliveira 1991, Tavares & Borzone 2005).

The crucial importance of sea urchins in shaping benthic ecosystems (Lawrence 1975) has been demonstrated by many ecological experiments along the Mediterranean coasts (e.g. Benedetti-Cecchi & Cinelli 1995, Sala & Zabala 1996, Benedetti-Cecchi et al. 1998, Palacín et al. 1998a, Bulleri et al. 1999, Guidetti et al. 2004, Bonaviri et al. 2011). The underlying premise in these experiments is that sea urchins are predominantly herbivorous and that their effects are mainly due to their grazing on benthic algae. In particular, population outbreaks of both *Arbacia lixula* and *Paracentrotus lividus* are able to create barrens in rocky substrates (Verlaque 1987, Hereu 2004), affecting both productivity and diversity of benthic assemblages (Bulleri et al. 2002, Privitera et al. 2008). The feeding behaviour and the herbivorous nature of *P. lividus* have been repeatedly assessed; however, much less information is available about the ecological role played by *A. lixula* in Mediterranean ecosystems. In fact, Privitera et al. (2008) demonstrated that both species occupy different trophic niches in resource-limited (barren) areas, again in the sense that *A. lixula* feeds mainly on encrusting corallines while *P. lividus* feeds on non-encrusting macrophytes. A knowledge gap persists about the effective diet of *A. lixula*; however information on this is essential for designing and interpreting ecological studies. Filling this gap seems necessary not only for basic research, but also for management purposes (e.g. of marine reserves or local fisheries).

We used a combination of stable isotope analysis and gut content examination to assess the diet and establish the trophic position of *Arbacia lixula* and *Paracentrotus lividus* coexisting in western Mediterranean rocky bottoms.

MATERIALS AND METHODS

Study sites and sampling procedures

Gut contents and isotopic signatures of both sea urchin species were explored both temporally, performing a year-round follow-up at a single site, and spatially, sampling at 2 additional western Mediterranean sites at a single time point. We also sampled a non-Mediterranean site for reference information. This design aimed at establishing the robustness of the patterns found.

The temporal sampling was performed at Tossa de Mar (NE Spain, 41° 43.2′ N, 2° 56.4′ E, Fig. 1) from December 2008 to December 2009. This location is fully described elsewhere (Ballesteros 1988, 1989, 1992, 1993) and is characterized by gently sloping rocks extending from the surface to 12 m depth, with a rich algal cover and almost devoid of barren zones. We sampled between 2 and 6 m depth, where the dominant communities are the *Corallina elongata* community (Ballesteros 1988) in zones with high hydrodynamism and the *Stypocaulon scoparium* community (Ballesteros 1993) in zones with moderate to low hydrodynamism. Sea urchin densities during the sampling period (mean ± SD) were 0.6 ± 0.8 and 5.7 ± 4.7 adult ind. m^{-2}, for *Arbacia lixula* and *Paracentrotus lividus* respectively, measured at a depth of 3 m following the transect method as in Turon et al. (1995).

Ten *Arbacia lixula* and 10 *Paracentrotus lividus* individuals were collected every 2 mo by scuba diving. Only adults with test diameter >35 mm in *A. lixula* and >40 mm in *P. lividus* were sampled. The 2-monthly sampling periodicity seems adequate to

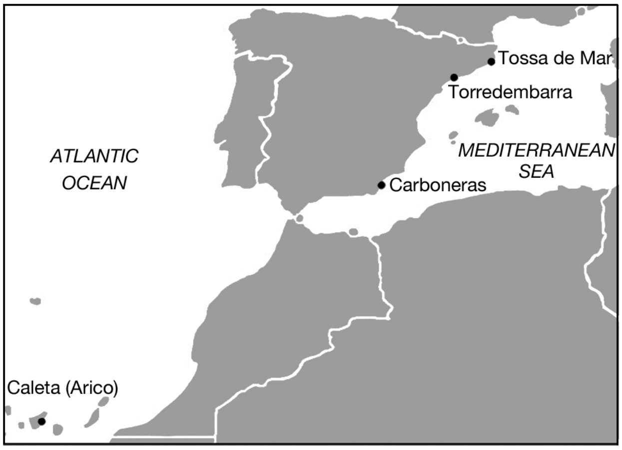

Fig. 1. Sampling locations for 2 Mediterranean sea urchin species, *Arbacia lixula* and *Paracentrotus lividus*

detect possible diet shifts (Tieszen et al. 1983, Hobson & Clark 1992). Samples of the dominant taxa from the 3 macroalgal divisions (Phaeophyta: *Stypocaulon scoparium*, *Dictyota dichotoma* and *Padina pavonica*; Chorophyta: *Codium vermilara* and *Flabellia petiolata*; Rhodophyta: *Corallina elongata, Sphaerococcus coronopifolius, Peyssonnelia* spp. and *Lithophyllum incrustans*) were collected at the same times. In addition, other invertebrates were also sampled throughout the year, including herbivores (*Patella* sp., *Amphitoe* sp.), detritivores (*Ophiothrix fragilis, Echinaster sepositus*), suspension feeders (*Balanus* spp.) and carnivores (*Actinia schmidti, Marthasterias glacialis, Ophioderma longicauda*), in order to characterize the different levels of the local trophic web. All samples were frozen (−20 °C) shortly after collection for later analysis.

For comparison, additional sampling was carried out at 2 other locations, ca. 200 and 900 km distant from Tossa de Mar, in December 2009. Although densities were not quantified, both sea urchin species were present at these localities (again with dominance of *Paracentrotus lividus*) with largely overlapping depth distributions. These sampling points were Torredembarra, (NE Spain, 41° 7.9′ N, 1° 23.7′ E) and Carboneras (SE Spain, 36° 59.6′ N, 1° 53.4′ W) (Fig. 1). The site at Torredembarra is characterized by a shallow rocky habitat (0 to 3 m depth), surrounded by a sandy bottom. The macroalgal assemblages are poorly developed, and the main primary producer is *Jania rubens,* with scarce presence of other algae such as *Corallina elongata* or *Dictyota dichotoma*. The Carboneras site is a shallow rocky habitat (0 to 4 m depth) with a denser algal cover, where the dominant producers are *Jania rubens*, *Stypocaulon scoparium* and *Peyssonnelia* spp., with a well-developed *Posidonia oceanica* meadow located nearby. At these 2 sites, samples were obtained only of the 2 echinoids and of representative algal species, following the same procedures as above. Thus, 3 communities with quite different characteristics were sampled in this study, representing some of the diversity of Mediterranean shallow habitats where *Arbacia lixula* and *P. lividus* can coexist.

Finally, samples of sea urchins (of the same sizes detailed above) for stable isotope analysis were collected at 1 Atlantic site in November 2009. This was Caleta, located near Arico, SE Tenerife, Canary Islands (28° 6.1′ N, 16° 28.7′ W, Fig. 1), where samples were collected between 0 and 3 m depth. In this location rock boulders dominate at shallow depths, with a poorly developed algal community including sparse patches of *Caulerpa webbiana* and *Lobophora variegata.* While *Arbacia lixula* and *Paracentrotus lividus* are known to broadly share spatial niches at the Canary Islands (Tuya et al. 2007), in this locality, the former was only found in vertical walls, while the latter was located under the stones at the bottom.

Stable isotope analyses

Muscles of the Aristotle's lantern of all collected sea urchins were used to perform isotopic analyses, and some of the same individuals were used for gut analyses (see next section). Algae were sampled by slicing several pieces of different parts of the thalli after carefully scraping epibionts off their surface. For faunal specimens, we sliced a small portion of a specified part of the body (the foot for *Patella* sp., an arm for Ophiuroidea and Asteroidea and the body column for *Actinia schmidti*), while the whole body of amphipods and cirripeds (excluding the shell) was used.

Before isotopic analyses, samples were rinsed in distilled water, freeze-dried and ground to a fine powder. Isotopically lighter lipids may influence carbon isotope ratios in animal tissues (Attwood & Peterson 1989, Hobson & Welch 1992), so 5 samples of each species were reanalyzed after lipid removal by chloroform-methanol 2:1 extraction (Folch et al. 1957). Passing & Bablok (1983) regression did not show any significant differences in the $\delta^{13}C$ for any species (data not shown), probably due to low lipid content in the sampled tissues. Thus, values of untreated samples were used thereafter. Carbonate rich samples (Corallinaceae, *Padina pavonica,* Ophiuroidea, Asteroidea) were rinsed several times with HCl 0.1 M to remove inorganic carbonates (Tomas et al. 2006). As HCl treatment has been reported to alter the $\delta^{15}N$ values (Bunn et al. 1995), samples including calcareous elements were split into 2 subsamples, one analyzed after acid treatment for $\delta^{13}C$ and the other, untreated, for $\delta^{15}N$.

Aliquots of 0.3 or 1 mg of dried powder from faunal or algal samples, respectively, were placed into tin capsules and crimped for combustion. Samples were oxidized in a Flash EA1112 furnace coupled to a Delta C stable isotope mass spectrometer through a Conflo III interface (Thermo-Finnigan). Isotope ratios are expressed as δ values in parts per thousand (‰) according to the equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X (‰) is ^{13}C or ^{15}N, and R is the ratio of corresponding element ($^{13}C/^{12}C$ or $^{15}N/^{14}N$), in sample or standard. The standard values were Pee Dee Belemnite for ^{13}C and atmospheric nitrogen for

^{15}N. IAEA standards were inserted every 12 samples for calibration. Replicate assays of standards indicated measurement errors of ±0.1‰ and ±0.2‰ for carbon and nitrogen, respectively.

Trophic levels were calculated according to the equation of Hobson & Welch (1992): $TL = 1 + (N_m - N_b) / TE$. Where TL is the trophic level of the species, N_m is the mean $\delta^{15}N$ value of the species, N_b is the average basis $\delta^{15}N$ value of producers (baseline) and TE is the trophic enrichment factor in the ecosystem. A constant TE factor of 3‰, commonly accepted for aquatic benthic ecosystems involving invertebrates (Vander Zanden & Rasmussen 2001, Jaschinski et al. 2008, Wan et al. 2010), was used. The baseline for $\delta^{15}N$ was estimated averaging the values obtained for the different algal species analyzed, except in the Atlantic site, where we did not collect algae. In this case, we assigned *Paracentrotus lividus* a value of TL = 2 (strict herbivore) and used it as a baseline for calculating the TL of *Arbacia lixula*.

Gut content analyses

The gut contents of sea urchins of both species collected at Tossa de Mar in June and December, and at the other 2 Mediterranean locations in December, were analyzed. Sea urchins (from 5 to 10 individuals per species and locality, and for two different months in the case of Tossa de Mar) were dissected and the total gut contents of each specimen were examined under a binocular microscope after disaggregation of the pellets. Some small calcareous remnants were collected and examined under a scanning electron microscope. Algal fragments were identified to genus level, while faunal items were classified into the following taxonomic groups: Foraminifera, Porifera, Hydrozoa, Polychaeta, Gastropoda, Bivalvia, Bryozoa, Cirripedia, Ostracoda, Copepoda, Amphipoda/Isopoda, Decapoda and 'other'. Echinoid fragments, which were present in the gut of some specimens, were not included in the analysis, since we cannot assure that they were not an artifact resulting from sample manipulation.

The frequency of occurrence of each food item in a species (FO_i) was calculated as the fraction of individuals having ingested this item (Pillay 1952, Hyslop 1980). The volumetric occupation of ingested items was assessed by quantifying 25 squares of a Petri dish with a 5 mm grid. The surface occupied by the items present in each square was semiquantitatively estimated using a scale from 1 to 5, and the occupation indices of all items were calculated for every sea urchin individual, dividing the sum of the semiquantitative scores assigned to a given food item by the total sum of the scores for all measured squares. The volumetric index of each food item in a species (V_i) was then obtained as the mean value of all individuals. A feeding index (FI_i) reflecting the relative importance of each food item in the diet of each species at a given location, was calculated following Lauzanne (1975), as $FI_i = FO_i \times V_i$ and then standardized as a percentage of the sum of the feeding indices for all items.

The relative contribution of animal and vegetal matter in the gut contents was quantified by addition of the standardized feeding indices of all items of either animal or vegetal origin (cumulative feeding indices). These indices summarize the carnivorous or herbivorous character of the diet, as inferred from gut contents.

Statistical analyses

Two-way ANOVA with species as fixed factor and month as random factor was performed to assess temporal variation of isotopic signatures of both sea urchin species at Tossa de Mar throughout the year. Two-way ANOVA with species as fixed factor and locality as random factor was used to compare the signatures and the calculated trophic levels of both sea urchin species at the sampled localities. We also used 2-way ANOVA with species (fixed) and locality (random) as factors to formally analyze differences in the cumulative animal feeding indices. In mixed models, the expected mean square for the fixed factor (species in our case) includes the variance component for the interaction term. Thus the fixed factor tests for the effect of species over and above the variation due to the interaction and the residual. It is therefore interpretable even in the presence of significant interaction (Quinn & Keough 2002). Notwithstanding, when interaction was significant, we performed separate *t*-tests with Bonferroni correction (unbalanced data prevented us from using other multiple comparison tests) at each locality to check that the effect was consistent across sites.

The assumptions of normality and homoscedasticity of the variables were checked with the Kolmogorov-Smirnov and Cochran tests, respectively. In some cases the data did not comply with these assumptions, and rank transformed data were used instead (detailed in Results). In 2 instances this transformation did not solve the lack of homoscedasticity (detailed in Results), but we performed the analysis anyway as rank transformation is robust to deviations from assumptions of parametric procedures (Conover & Iman 1981, Potvin & Roff 1993). All analyses were performed with STATISTICA 6.1 software.

RESULTS

Stable isotope analyses

At Tossa de Mar, the annual average of δ^{15}N values found for *Arbacia lixula* (8.2‰) was comparable to those of typical carnivores such as *Actinia schmidti* or *Marthasterias glacialis* (Table 1, Fig. 2). In contrast, herbivorous grazers and detritivores had lower δ^{15}N values (between 4.6‰ for the amphipod *Amphitoe* sp. and 5.3‰ for *Echinaster sepositus*) while *Paracentrotus lividus* showed a slightly higher value of 5.9‰, possibly indicating a higher intake of animal items than its more strictly herbivorous counterparts. Seaweeds, as expected, showed lower δ^{15}N values, ranging from 1.9‰ for *Flabellia petiolata* to 4.2‰ for *Sphaerococcus coronopifolius*, while the most abundant species were within the range of 3 to 3.5‰. The mean value for all algae, used as the baseline for calculating consumers' trophic levels at Tossa de Mar, was 3.13‰.

When analyzed on a temporal basis (Fig. 3), δ^{15}N values in *Arbacia lixula* were significantly higher than in *Paracentrotus lividus* (species factor, $p < 0.001$, Table 2), while time and the interaction were not significant (Table 2), indicating that the difference in trophic levels is not subject to temporal variation. The mean difference was 2.3‰. Likewise, δ^{13}C values showed a high degree of individual variability (Fig. 3), but overall they were also significantly higher (by ca. 0.7‰) for *A. lixula* than for *P. lividus* (species factor, $p < 0.001$, Table 2, Fig. 3), again suggesting a higher trophic level for *A. lixula* (the trophic enrichment factor for carbon in marine coastal trophic webs is ca. 0.8‰ according to France & Peters 1997). No clear temporal trend was apparent for δ^{13}C values (time and interaction not significant, Table 2).

Table 1. Isotopic signatures (mean ± SD) and derived trophic levels (TL = 1 for primary producers) of invertebrate species in the Mediterranean sublittoral, based on results of 2-monthly sampling at Tossa de Mar, NE Spain. Sea urchin species are shown in **bold**

Species	n	Trophic level	δ^{15}N (‰)	δ^{13}C (‰)
Actinia schmidti	5	2.7	8.3 ± 0.6	−19.8 ± 0.7
Arbacia lixula	**72**	**2.7**	**8.2 ± 0.5**	**−18.3 ± 1.1**
Ophioderma longicauda	5	2.5	7.6 ± 0.9	−17.5 ± 0.9
Marthasterias glacialis	5	2.4	7.5 ± 0.4	−15.8 ± 1.0
Balanus spp.	5	2.2	6.8 ± 0.3	−19.4 ± 0.3
Paracentrotus lividus	**71**	**1.9**	**5.9 ± 0.4**	**−19.0 ± 0.9**
Echinaster sepositus	5	1.7	5.3 ± 0.4	−15.6 ± 0.3
Ophiothrix fragilis	4	1.7	5.2 ± 0.7	−20.4 ± 1.0
Patella sp.	5	1.6	5.1 ± 0.4	−17.0 ± 0.6
Amphitoe sp.	4	1.5	4.6 ± 0.7	−22.1 ± 1.2

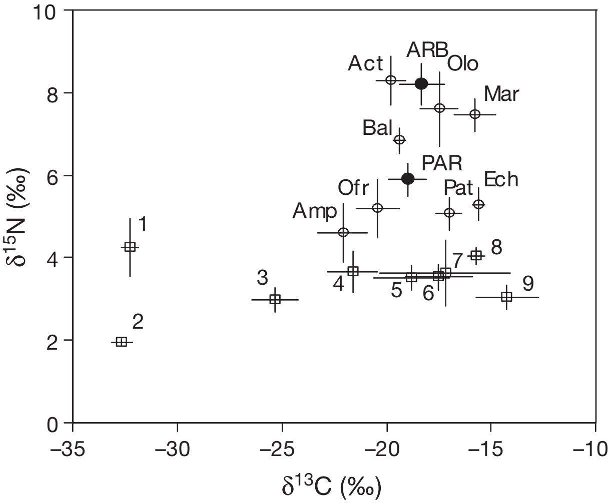

Fig. 2. Plot of δ^{15}N and δ^{13}C isotopic signatures (mean ± SD) of sublittoral species examined during 2-monthly sampling at Tossa de Mar (NE Spain): (●) sea urchin species; (○) other consumers; (□) producers. Metazoa: Act = *Actinia schmidti*, ARB = *Arbacia lixula*, Olo = *Ophioderma longicauda*, Mar = *Marthasterias glacialis*, Bal = *Balanus* spp., PAR = *Paracentrotus lividus*, Ech = *Echinaster sepositus*, Ofr = *Ophiothrix fragilis*, Pat = *Patella* sp., Amp = *Amphitoe* sp. Algae: 1 = *Sphaerococcus coronopifolius*, 2 = *Flabellia petiolata*, 3 = *Stypocaulon scoparius*, 4 = *Corallina elongata*, 5 = *Dictyota dichotoma*, 6 = *Codium vermilara*, 7 = *Peyssonnelia* spp. 8 = *Lithophyllum incrustans*, 9 = *Padina pavonica*

In the 2 additional Mediterranean locations, as well as in the Atlantic one, δ^{15}N values obtained from *Arbacia lixula* exceeded those from *Paracentrotus lividus*, as did the estimated trophic levels (Table 3). This suggests that the tendency towards a more omnivorous or carnivorous diet of *A. lixula* is probably widespread throughout its distribution range. A 2-way ANOVA of δ^{15}N values revealed a significant effect of species (fixed) and locality (random), as well as a significant interaction term (Table 4), suggesting different adaptations of sea urchin species in different conditions (see below). Separate analyses (*t*-tests with Bonferroni correction) at fixed levels of the locality factor revealed that the differences in δ^{15}N values between sea urchin species were significant (all $p < 0.01$) at all sites. Likewise, the analysis of trophic level between species and localities revealed a significant effect of species and a significant interaction between species and locality (Table 4); the

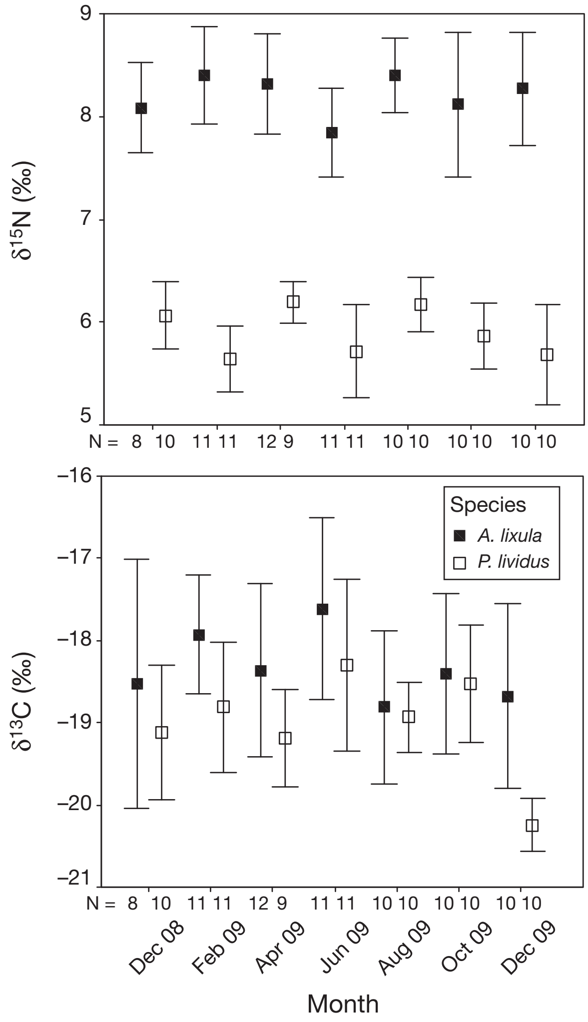

Fig. 3. *Arbacia lixula* and *Paracentrotus lividus.* Isotopic signatures of 2 sea urchin species at Tossa de Mar (NE Spain) as a function of time. Means ± SD are displayed for every sampled month. The number of individuals analyzed for each observation was from 8 to 12

Table 2. *Arbacia lixula* and *Paracentrotus lividus.* Factorial 2-way ANOVA to assess significant differences in isotopic signatures between species (fixed factor) and sampling times (random factor). Data for $\delta^{13}C$ was rank-transformed as variance was not homogeneous. Significant p-values in **bold**

Variable	Effect	df	MS	*F*	p
$\delta^{15}N$	Species (S)	1	187.663	493.66	**<0.001**
	Time (T)	6	0.632	1.66	0.28
	S × T	6	0.381	2.00	0.07
	Error	129	0.190		
$\delta^{13}C$	Species (S)	1	30481.07	15.82	**<0.001**
	Time (T)	6	6005.13	3.11	0.10
	S × T	6	1929.10	1.50	0.18
	Error	129	1282.21		

Table 3. *Arbacia lixula* and *Paracentrotus lividus.* Calculated trophic levels based on ^{15}N signatures for the 2 sea urchin species and values for seaweeds (baseline) from 4 sample locations, means ± SD. ^{13}C signatures are also shown for both sea urchin species. na: data not available

Species	n	Trophic level	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Tossa				
A. lixula	72	2.7 ± 0.17	8.2 ± 0.5	−18.3 ± 1.1
P. lividus	71	1.9 ± 0.13	5.9 ± 0.4	−19.0 ± 0.9
Seaweeds	37	1.0	3.1 ± 0.7	
Torredembarra				
A. lixula	10	3.0 ± 0.17	10.6 ± 0.5	−17.2 ± 0.6
P. lividus	9	2.7 ± 0.12	9.6 ± 0.4	−17.9 ± 0.5
Seaweeds	12	1.0	4.6 ± 0.7	
Carboneras				
A. lixula	9	2.7 ± 0.16	10.4 ± 0.5	−11.8 ± 0.6
P. lividus	10	2.1 ± 0.19	8.5 ± 0.6	−16.7 ± 0.7
Seaweeds	18	1.0	5.3 ± 0.5	
Tenerife				
A. lixula	10	3.0 ± 0.12	10.7 ± 0.4	−11.2 ± 0.7
P. lividus	7	2.0 ± 0.14	7.5 ± 0.4	−17.8 ± 0.4
Seaweeds		na	na	

Table 4. *Arbacia lixula* and *Paracentrotus lividus.* Factorial 2-way ANOVA to assess significant differences in the isotopic signatures and calculated trophic levels between species (fixed factor) at the 4 sampled locations (random factor). Data for $\delta^{13}C$ was rank-transformed as variance was not homogeneous. Significant p-values in **bold**

Variable	Effect	df	MS	*F*	p
$\delta^{15}N$	Species (S)	1	98.355	31.27	**0.01**
	Location (L)	3	87.491	22.04	**0.01**
	S × L	3	3.970	18.42	**<0.001**
	Error	190	0.216		
$\delta^{13}C$	Species (S)	1	35884.07	20.27	**0.007**
	Location (L)	3	84754.14	46.79	**0.005**
	S × L	3	1811.29	1.11	0.34
	Error	190	1624.53		
Trophic level	Species (S)	1	10.928	31.268	**0.01**
	Location (L)	3	1.667	3.779	0.15
	S × L	3	0.441	18.418	**<0.001**
	Error	190	0.024		

inter-specific differences were again significant in all localities (*t*-tests with Bonferroni correction, all $p < 0.01$). The significant interaction term is probably due to the plasticity that can be observed in the derived trophic levels of both species among the different localities and ecosystems. Thus, where algal cover was dense, as happened in Tossa de Mar and Carboneras, *P. lividus* showed a trophic level of around 2, compatible with a mainly herbivorous diet, whereas *A. lixula* showed trophic levels of around

2.7, corresponding to a predominantly carnivorous omnivore. In contrast, where algal resources were scarce (as in Torredembarra) both sea urchins tended to increase their animal intake, raising their δ^{15}N values and trophic levels. Our results showed a trophic level of 2.7 for *P. lividus* at Torredembarra, whereas *A. lixula* had a level of 3.0 (which would correspond to a strict carnivore) in this location. In Tenerife, as algal samples were not available for isotopic analysis, a baseline value for producers cannot be used, but the difference between δ^{15}N values of the 2 sea urchins was the biggest of all locations sampled, and corresponded to exactly one trophic level.

The δ^{13}C signatures at the additional localities revealed, as in Tossa de Mar, a higher enrichment in *Arbacia lixula* (Table 3). For this variable, no significant interaction between species and locality was found, while the single factors were highly significant (Table 4), highlighting the higher δ^{13}C value in *A. lixula* as well as a noticeable spatial heterogeneity in isotopic signature. The increase in δ^{13}C in *A. lixula* relative to *Paracentrotus lividus* in Torredembarra was similar to that in Tossa, but it was much higher at the other 2 localities (Carboneras and Tenerife, Table 3), suggesting a different carbon source for both sea urchins in these localities.

Gut content analyses

Gut content analyses in Tossa de Mar (Table 5) revealed a higher abundance of animal items in *Arbacia lixula* than in *Paracentrotus lividus*. In addition, the ingested material of *P. lividus* showed remarkable temporal differences. Thus, *Dictyota* and *Dasycladus*, the most frequent algal items found in June, did not appear in the gut contents of samples collected in December, when *Corallina* abundance increased. In contrast, the gut contents of *A. lixula* showed very little seasonal changes, being dominated by small filamentous algae such as *Cladophora* and *Polysiphonia*, and crushed fragments of encrust-

Table 5. *Arbacia lixula* and *Paracentrotus lividus.* Standardized feeding indices (only the 12 highest values shown, means ± SD) for major food items, as derived from gut content analysis of 2 sea urchin species at 3 Mediterranean locations. Given the prominent seasonal changes in the algal assemblages, feeding indices have been calculated separately for June and December at the site where sampling was performed over time (Tossa de Mar). Animal items are shown in **bold**

A. lixula		*P. lividus*		*A. lixula*		*P. lividus*	
Tossa de Mar				**Torredembarra**			
June: n = 6		n = 6		December: n = 5		n = 5	
Cladophora	19.4 ± 9.4	*Dictyota*	40.0 ± 21.6	**Cirripedia**	55.5 ± 12.8	*Jania*	64.9 ± 5.5
Polysiphonia	19.1 ± 9.4	*Dasycladus*	22.3 ± 10.0	**Hydrozoa**	23.3 ± 6.9	*Corallina*	8.8 ± 3.0
Lithophyllum	17.3 ± 8.3	*Stypocaulon*	11.9 ± 9.8	*Polysiphonia*	8.9 ± 4.7	*Posidonia*	8.4 ± 3.9
Bryozoa	8.1 ± 12.7	*Polysiphonia*	7.1 ± 6.1	**Porifera**	8.5 ± 4.7	**Bryozoa**	5.7 ± 4.3
Hydrozoa	7.6 ± 4.9	*Ceramium*	5.3 ± 4.7	*Cladophora*	1.3 ± 1.9	*Polysiphonia*	3.0 ± 3.0
Cirripedia	5.6 ± 6.2	**Bryozoa**	3.0 ± 3.1	**Bivalvia**	0.8 ± 1.1	*Codium*	2.1 ± 1.4
Polychaeta	5.2 ± 2.4	*Corallina*	3.0 ± 3.6	*Ceramium*	0.7 ± 0.6	*Stypocaulon*	1.9 ± 1.5
Stypocaulon	4.5 ± 4.5	*Cladophora*	1.7 ± 2.5	*Stypocaulon*	0.3 ± 0.4	*Cladophora*	1.6 ± 1.2
Foraminifera	3.6 ± 2.6	*Jania*	1.4 ± 1.9	**Gastropoda**	0.2 ± 0.4	**Hydrozoa**	1.6 ± 1.3
Dictyota	2.5 ± 3.3	*Colpomenia*	1.3 ± 1.8	**Polychaeta**	0.2 ± 0.4	Other seaweed	0.6 ± 1.1
Ostracoda	2.3 ± 2.7	Other seaweed	1.2 ± 0.9	**Bryozoa**	0.2 ± 0.3	*Peyssonnelia*	0.6 ± 0.6
Porifera	1.1 ± 1.1	*Sphaerococcus*	0.8 ± 1.4	**Other metazoa**	0.1 ± 0.2	*Padina*	0.2 ± 0.3
				Carboneras			
December: n = 9		n = 5		December: n = 7		n = 10	
Lithophyllum	19.6 ± 13.6	*Corallina*	52.2 ± 7.1	*Jania*	34.1 ± 26.3	*Jania*	59.9 ± 10.6
Polysiphonia	17.1 ± 10.6	*Stypocaulon*	21.2 ± 5.3	*Lithophyllum*	21.2 ± 23.6	*Posidonia*	11.6 ± 5.8
Hydrozoa	14.9 ± 10..9	*Peyssonnelia*	9.6 ± 6.1	*Cladophora*	17.2 ± 14.0	*Peyssonnelia*	11.0 ± 11.0
Cirripedia	11.6 ± 6.1	*Jania*	7.3 ± 5.4	**Porifera**	8.3 ± 8.8	*Cladophora*	5.0 ± 4.3
Cladophora	9.3 ± 7.9	*Cladophora*	3.0 ± 2.2	*Stypocaulon*	5.8 ± 7.0	*Stypocaulon*	4.1 ± 6.0
Polychaeta	8.3 ± 6.8	*Polysiphonia*	1.7 ± 2.2	*Ceramium*	4.0 ± 5.9	*Flabellia*	3.3 ± 2.2
Foraminifera	3.7 ± 1.4	*Cystoseira*	1.3 ± 1.6	*Polysiphonia*	2.2 ± 3.4	Other seaweed	2.6 ± 5.7
Jania	3.2 ± 2.4	**Porifera**	1.0 ± 1.0	*Peyssonnelia*	1.9 ± 3.2	*Lithophyllum*	1.6 ± 2.4
Corallina	2.8 ± 3.6	**Polychaeta**	0.8 ± 0.8	Other seaweed	1.6 ± 3.2	*Padina*	0.7 ± 0.8
Porifera	2.0 ± 2.5	*Lithophyllum*	0.8 ± 0.9	**Foraminifera**	1.4 ± 1.9	*Corallina*	0.1 ± 0.2
Bryozoa	2.0 ± 2.0	**Hydrozoa**	0.3 ± 0.3	*Corallina*	0.9 ± 2.0	**Polychaeta**	0.1 ± 0.1
Stypocaulon	1.6 ± 3.8	*Halimeda*	0.2 ± 0.4	**Hydrozoa**	0.5 ± 1.1	**Porifera**	0.0 ± 0.1

ing corallines (*Lithophyllum* spp.). Sessile invertebrate species such as hydrozoans, cirripeds and polychaetes were also commonly found throughout the year. These 6 items, with the addition of bryozoans in June, constituted the main components of *A. lixula* gut contents, with little variation between seasons.

At the 2 other Mediterranean localities analyzed, the results of the gut content analysis confirmed the higher prevalence of animal items in the diet of *Arbacia lixula* relative to *Paracentrotus lividus*, although with strong variability, probably associated with changes in benthic algal cover. Thus, at Torredembarra , where algae were less abundant, some animal items appeared frequently in *P. lividus* guts, such as the bryozoan *Schizoporella errata*, which was common in this habitat. Conversely, in Carboneras, a location with a well developed algal cover, the relative amount of animal remnants in the gut of both sea urchins was the least of all localities sampled. Remarkably, cirripeds were absent from this location, and *Jania rubens* appeared as the main food source for both sea urchin species.

The cumulative feeding indices in the 3 localities showed that the diet of *Arbacia lixula* has a significantly higher animal component than that of *Paracentrotus lividus* (Fig. 4, Table 6). The locality factor was also highly significant, reflecting the marked spatial heterogeneity, but no significant interaction was detected. Whereas for *P. lividus* gut contents were always dominated by the algal fraction, that of *A. lixula* displayed a much higher variability in the relative contribution of animal and vegetal matter among the different localities, ranging from a predominantly animal component in Torredembarra to a dominance of vegetal diet in Carboneras (Fig. 4).

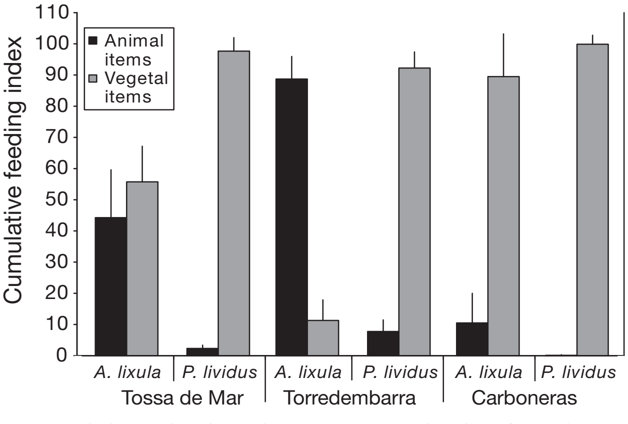

Fig. 4. *Arbacia lixula* and *Paracentrotus lividus.* Cumulative feeding indices (mean + SD) for animal and vegetal food items, derived from gut content analyses of 2 sea urchin species collected in December at 3 Mediterranean locations

Table 6. *Arbacia lixula* and *Paracentrotus lividus.* Factorial 2-way ANOVA to assess significant differences in the cumulative animal feeding index (calculated as the rank transformed sum of standardized feeding indices of animal items), between the 2 sea urchin species (fixed factor) and location (random factor). Significant p-values in **bold**

Variable	Effect	df	MS	*F*	p
Cumulative	Species (S)	1	2799.113	450.15	**0.002**
animal	Location (L)	2	917.827	149.62	**0.007**
feeding	S × L	2	6.135	0.60	0.55
index	Error	35	10.220		

DISCUSSION

Our results show that *Arbacia lixula* occupies a higher trophic level than *Paracentrotus lividus*, as shown by its consistently higher δ^{15}N across the sampled localities. The estimated trophic levels indicate that *A. lixula* is an omnivore tending to carnivory, while *P. lividus* is predominantly a herbivore that can become an omnivore in some instances. The (at least partial) carnivory in *A. lixula* is further supported by the analyses of gut contents, which reveal a consistently higher proportion of animal food items ingested in *A. lixula* as compared to *P. lividus*. However, gut content analyses alone do not reveal the full extent of the trophic gap between the 2 species, since vegetal components are dominant in most situations analyzed (except for *A. lixula* in Torredembarra). Finally, the results for δ^{13}C are consistent with those of δ^{15}N, indicating an overall enrichment of the signature of *A. lixula* with respect to *P. lividus*. The results for carbon, however, should be taken with caution as this isotope is best suited to detect differences in sources of food rather than trophic levels (Cardona et al. 2007). This implies that the role of *A. lixula* in the shallow subtidal in the Mediterranean should be, at least in part, re-evaluated. Specifically, the putative strong competition for food should be carefully re-examined.

The suitability of stable isotope analysis, and specifically δ^{15}N, for identifying trophic levels in marine ecosystems has been clearly established (e.g. Cherel et al. 2008). Much closer to the scope of the present study, this tool has revealed differences in the trophic levels of sympatric sea urchins (Vanderklift et al. 2006). These authors found that 2 littoral Australian echinoids previously thought to be herbivorous (*Phyllacanthus irregularis* and *Centrostephanus tenuispinus*) actually had an omnivorous behaviour tending towards carnivory. The differences in δ^{15}N between *Arbacia lixula* and *Paracentrotus lividus* that we report here, based on a wide temporal and geographical scale, are comparable to those found between both Australian purportedly herbivorous species and *Heliocidaris erythrogramma*, which proved to be a true strict herbivore.

In previous studies, animal items had been reported in the gut contents of both Mediterranean sea urchins (Maggiore et al. 1987, Privitera et al. 2008, Chiantore et al. 2008), but were mostly disregarded as anecdotal or accidental captures, which may be true for *Paracentrotus lividus* but is certainly not for *Arbacia lixula*. The long-held misconception about the herbivory of *A. lixula* may stem from several causes, but mainly from the fact that most primary information on this issue came from studies of gut contents, which target ingested, rather than assimilated, food. While it is true that the ecological impact of the feeding activity of an organism (in this case, *A. lixula*) may depend mostly on what is ingested, rather than on what is assimilated, gut content analysis can introduce some biases on our perception of an animal diet if used alone. Gut content analyses cannot be dismissed, though, as they provide the only direct taxonomical information about what the sea urchins ingest and, in combination with stable isotope analyses, can shed light on important aspects of their feeding strategy.

In addition, if diverse kinds of foodstuff have differential digestibility, results can be biased towards less digestible material. It is remarkable in this sense that most faunal items found in the gut of *Paracentrotus lividus* are nearly intact and easily identifiable, probably reflecting the reduced ability of this species to assimilate animal material. The opposite is true for *Arbacia lixula*, which seems to digest animal tissues completely. Conversely, undigested filamentous algae, even the most delicate ones, are regularly found intact in the guts of *A. lixula*. In a study on *A. lixula* from Brazil, Oliveira (1991) found that 50 % of the algae present in its faecal pellets survived digestion and were able to grow when cultured, in contrast to algae egested by herbivorous sea urchins such as *Lytechinus variegatus* or *Echinometra lucunter*.

Another reason for the misconception about *Arbacia lixula* herbivory is suggested by the fact that the gut contents of *A. lixula* that we examined consisted largely of small crushed pieces of pinkish-grey carbonates, which can be easily interpreted as fragments of calcareous algae. However, using scanning electron microscopy, we have unambiguously identified many of these pieces as fragments of shells of the common western Mediterranean barnacle *Balanus perforatus*. Thus, we must consider the possibility that cirriped shell remnants may have been mistaken for encrusting corallines in some studies which were carried out under the undisputed paradigm of an herbivorous *A. lixula*.

The finding that *Arbacia lixula* is an omnivore tending to carnivory may shed light on unexpected results of some ecological experiments. For example, the removal of *Paracentrotus lividus* had no effect and did not trigger an increase of the population of *A. lixula* (Gianguzza et al. 2006), as would be expected if inter-specific competition occurred between both species. Artificially reducing or increasing the density of *A. lixula* in selected patches had no effect on the percent cover of encrusting corallines (Benedetti-Cecchi et al. 1998, Bulleri et al. 1999), but the removal of *A. lixula* produced an increase in the density of *Balanus perforatus* and a decrease in the density of limpets (Bulleri et al. 1999), opposite to what would be expected if *A. lixula* was an herbivorous consumer of filamentous algae and trophic competitor of *Patella* sp.

Finally, our results add some information about the putative competition between the 2 most abundant Mediterranean sea urchins. Densities of *Paracentrotus lividus* in the NW Mediterranean are on average 10× higher (Palacín et al. 1998b) than those of *Arbacia lixula*. This fact challenges the idea that the 2 species engage in strong competitive interactions. Alternatively, at least, it suggests that *P. lividus* is able to outcompete *A. lixula*, whose shift to a different diet may help to avoid exclusion. However, both species can locally coexist at high densities (Guidetti et al. 2004, Tuya et al. 2007), and *A. lixula* is the dominant sea urchin in some communities (Benedetti-Cecchi et al. 1998). Furthermore, the 2 species segregate spatially in some cases (Kempf 1962, Chelazzi et al. 1997, Bulleri et al. 1999), as happens in our Atlantic location, where *A. lixula* is restricted to vertical walls. Thus, interference competition between these species is likely to occur in many places. Agonistic interactions (as those reported by Shulman 1990) have never been observed between them, so exploitative competition seems more likely, and feeding flexibility can be an important mechanism to alleviate its effects. On the other hand, it has to be emphasized that factors other than direct trophic competition, such as resistance to hydrodynamism (Tuya et al. 2007), resistance to predation (Guidetti 2006) or presence of predators which could modulate sea urchin behaviour (Freeman 2006) could also be involved in shaping the distribution and abundance of these 2 sea urchin species.

Few studies have addressed the possibly different foraging behaviour of these sea urchins species. Apparently, *Arbacia lixula* shows a higher mobility than *Paracentrotus lividus* in barren zones (Bonaviri et al. 2011), so that a wider area can be impacted by its grazing activity. The strong Aristotle's lantern that allows *A. lixula* to scrape the substrate for searching its prey, and the fact that this species tends to be more abundant than *P. lividus* in barren zones which offer relatively few algal food resources in comparison to animal prey (Guidetti & Dulcic 2007), could be better explained in the light of its tendency to carnivory.

Studies comparing feeding strategies between these species in communities with dominance of *Arbacia lixula* are necessary to ascertain the trophic position of both species under competitive pressures different from those found in the present study. Interestingly, at high densities, *A. lixula* may be expected to limit the abundance of its prey populations, and so it can compete with carnivores such as asteroids. Thus, the omnivory and feeding plasticity of *A. lixula* adds complexity to models of community structure, including possible trophic loops and increased connectivity between species (Camus et al. 2008).

In conclusion, the finding that *Arbacia lixula* is an omnivore tending to carnivory has important implications for the dynamics of shallow water communities in the Mediterranean, as it suggests not only a reduced competition for food with the coexisting echinoid *Paracentrotus lividus*, but also opens up new perspectives on biotic interactions in these communities. Given the important functional role of these echinoid species in shaping sublittoral assemblages, and the fact that one of them (*P. lividus*) sustains heavy fisheries in some areas, the results presented here should be taken into consideration both in basic studies of ecosystem functioning and in applied issues of environmental and fisheries management.

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