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COASTAL LAGOON ECOSYSTEMS

Sea urchin–seagrasses interactions: trophic links in a benthic ecosystem from a coastal lagoon

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Abstract Seagrasses could constitute a major component of lagunal ecosystems. Generally, in seagrass beds, consumer control is strong. In coastal lagoons, where seagrass beds are particularly extensive, there is only scarce data on seagrass herbivory. In Mediterranean coastal lagoons, *Paracentrotus lividus* populations are extensive and consume *Cymodocea nodosa* beds. In this study, we monitored a *P. lividus* population during 18 months in order to analyse changes in population density and structure. On the basis of results of previous studies (i.e. biomass, density, production and nutrition parameters), we assessed the importance of *P. lividus* with respect to *C. nodosa* herbivory in a Mediterranean coastal lagoon. The results show that this sea urchin, when its density is low, is estimated to consume about 0.6–18.9% of the seagrass production. However, active movement of consumers among adjacent habitats influences nutrient fluxes. During sea urchin migration, when densities of 10–98 ind. m^{-2} were observed, the consumption rates in sea urchin feeding fronts temporarily exceeded seagrass production rates. The overgrazing of the *C. nodosa* results in patches where leaves of this plant are completely consumed, and this phenomenon may explain a part of interannual variations in the distribution pattern of this species.

Keywords Seagrass · Herbivory · Sea urchin · Food web grazing · Feeding fronts · Overgrazing

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Introduction

Coastal lagoons are among the most productive ecosystems worldwide and represent important nursery and feeding zones for many trophic groups such as invertebrates, fishes and birds, as well as rich fishery grounds (Barnes, 1980; Kjerfve, 1994). This high production is supported, inter alia, by high-nutrient inputs or from internal recycling and several types of primary producers.

Generally, coastal lagoons can be distinguished by the dominant primary producer (phytoplankton, algal mats and benthic macrophytes), although terrestrial plants are also potentially available to consumers (Knoppers, 1994). The dominance of a single type of primary producer depends on the interaction of numerous environmental factors (e.g. hydrology and nutrients). For numerous coastal lagoons, aquatic

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macrophytes, in particular the aquatic Magnoliophyta, constitute a major component of lagunal ecosystems (e.g. Sfriso & Ghetti, 1998; Duarte et al., 2002; Sfriso et al., 2003). These plants are of particular interest in view of their ecological (Tamisier & Boudouresque, 1994) and economic roles (Pearce & Crivelli, 1994; Skinner & Zalewski, 1995). They also contribute to sedimentary balance (Skinner & Zalewski, 1995).

Among the 60 seagrasses described worldwide (Kuo & den Hartog, 2001), only a few are major components of Mediterranean lagoon ecosystems (e.g. *Cymodocea nodosa* (Ucria) Ascherson, Zostera: *Zostera marina* L. and *Zostera noltii* Horneman; Sfriso & Ghetti, 1998; Agostini et al., 2003). The distribution of seagrasses is influenced by various environmental parameters, such as hydrodynamic conditions, nature of the substrate, light (Peralta et al., 2002), temperature (Pérez-Lloréns & Niell, 1993; Marbà et al., 1996), salinity (Wortmann et al., 1997), nutrient concentrations in the water column (Orth, 1977) and/or in the sediment (Viaroli et al., 1993) but also by herbivory. Controls of herbivory and decomposition are important in understanding the trophic transfer, recycling and storage of carbon and nutrients in seagrass ecosystems (Cebrian & Lartigues, 2004; Holmer & Marbà, 2010).

The relative importance of herbivory on seagrasses is still controversial. The currently prevailing premise of food web theory is that the ingestion of living seagrass biomass is infrequent and virtually without consequences for the demography of these plants and their impact on biogeochemical cycling (see Heck & Valentine, 2006, for a review). However, studies during the last two decades have clearly shown that a number of herbivorous species can ingest large amounts of aboveground seagrass biomass (Valentine & Heck, 1991). Therefore, the complex interactions between these rooted macrophytes and their consumers are important in regulating the dynamics of seagrass meadows. Only a few marine species are able to feed directly on vascular plants and digest them. This group includes some species of vertebrates, such as sirenids, birds, sea turtles and fishes, and also invertebrates, generally sea urchins, crustaceans and some molluscs (Heck & Valentine, 2006). In the absence of dominant mega-grazers (e.g. sirenians or turtles in tropical areas, waterfowl in temperate areas), sea urchins are one of the most common seagrass macro-grazers in contemporary seagrass systems (Eklöf et al., 2008).

In fact, the estimation of grazing intensity in seagrass food webs has generally been made in open sea ecosystems, and little attention has been focused on seagrass grazing and trophic transfer pathways in coastal lagoon food webs. In coastal lagoons, when inlets connecting lagoons to the open sea are large enough to allow inflow of seawater and thus higher salinity levels, seagrasses are the main primary producer, and echinoderms and sea urchins, in particular, are strongly represented.

The aim of this article is to estimate the extent of seagrass grazing by a sea urchin species and trophic links between these two trophic levels in a benthic coastal lagoon ecosystem. Therefore, we have analysed the population dynamics of *Paracentrotus lividus* Lamarck in a *C. nodosa* meadow during 18 months in order to determine the population structure and density variability in a Mediterranean coastal lagoon with low-anthropogenic pressure. These data in combination with earlier published data on sea urchins ingestion rates, and the biomasses and primary production seagrasses (Fernandez & Caltagirone, 1998; Fernandez & Boudouresque, 2000; Agostini et al., 2003; Pasqualini et al., 2006), collectively allowed us to quantify the interactions between plants and herbivores by calculating the percentage of seagrass production consumed by sea urchins. These results contribute to our understanding of the importance of sea urchins with regard to seagrass dynamics in these ecosystems.

Materials and methods

Study site

The study was carried out in the Urbino lagoon situated in Corsica (France, Mediterranean Sea) on the east coast of the island (42°03′N; 9°28′E). The Urbino lagoon belongs to the *Conservatoire du littoral* since 2007. The *Conservatoire du Littoral* is a public administrative body with responsibility for conducting appropriate land-use policies for the protection of threatened natural areas. The Urbino lagoon is of tectonic origin with an area of 760 ha and a maximum depth of 9.2 m (Table 1; Orsoni et al., 2001). There is a small opening leading to the sea in this lagoon, and some water exchanges occur between the two environments (less than 6% of the total volume of the

Table 1 General characteristics of the Urbino lagoon, Mediterranean Sea (from Pasqualini et al., 2006)

Abiotic parameters	
Surface area (ha)	760
Maximum depth (m)	9.2
Mean depth (m)	5
Volume (millions of m^3)	33
Catchment area (km^2)	31
Temperature (°C)	9–29
Salinity (‰)	26–44
Human pressure sources	
Catchment area (ha)	245
Industrial and touristic activities in the catchment area	None
Agricultural activities in the catchment area	Orchards, vineyards (only in parts)
Activities at the 'lido'	None
Fishing and aquaculture	Limited fishing Aquaculture: 150 t $year^{-1}$ of fish; 40 t $year^{-1}$ of shellfish

lagoon per month; Clanzig, 1992). This euryhaline lagoon (Table 1; Sacchi, 1985) is characterized by the high degree of homogeneity of its water mass (except at the river outlets, in the north-west sector). The bottom consists of silt, rich in organic matter, sand and terrigenous or shelly sediments (Pasqualini et al., 2006). This lagoon is subject to low levels of human pressure (agricultural activities in the catchment area; Table 1). The Urbino lagoon was mainly used for aquaculture until 2002 (Table 1).

Species

Sea urchin populations

Paracentrotus lividus is a widespread species on Atlantic and Mediterranean coasts, and it plays a determining role in the development of benthic macrophyte communities (Verlaque, 1987). This species is the most abundant echinoid species in Mediterranean littoral communities. The sea urchin is a herbivore (Boudouresque & Verlaque, 2001) but can also consume animal food (Fernandez & Caltagirone, 1998). In Mediterranean coastal ecosystems, *P. lividus* is known to cause overexploitation of seagrasses (Verlaque, 1987) particularly in *Posidonia oceanica* (Lineaus) Delile beds. Although this is a stenohaline species, it also occurs in coastal lagoons (Allain, 1975; Fernandez & Boudouresque, 1997).

Paracentrotus lividus occurs, in variable densities, in four habitats of the Urbino lagoon, i.e., pebble bottom, seagrass beds, silt and sand sediment habitats (Fig. 1), and represents an important store of materials and energy within this lagoonal environment (Fernandez, 1998). For this study, the sea urchin populations in seagrass meadows were monitored during 18 months in order to analyse population fluctuations and, subsequently, to study the trophic links between the sea urchin population and the seagrasses.

For population fluctuations, 100 quadrats of 1 m^2 along a fixed permanent transect was censused in seagrass bed to assess density fluctuations of the populations and size variability. This transect is perpendicular to the coastline and running from 0.1 to 1.7 m depth. A single transect was chosen as two transects have been monitored at the beginning of the study (3 month). After, these 3-month data analysis show no variations between the two transects in terms of urchins densities and urchin size (*t* tests, $P > 0.05$); there is also no variation in terms of frequencies (χ^2 test, $P > 0.05$). Moreover, authors also studying sea urchin population structure have used only for one habitat (Turon et al., 1995). All the specimens present in this transect were counted and measured at approximately the same time (11:00–13:00 h) during daylight every month (between 50 and 350 urchins per month). For counts, rhizomes were closely examined. All sea urchins occurring within the transect were measured using a calliper rule with a precision of 1 mm (ambitus diameter without the spines). Population structure was analysed with a size class interval of 0.3 cm, already used for this species (Fenaux et al., 1987). Variations in the demographic structure, as a function of sampling, were analysed using the χ^2 test (Zar, 1999); variations of mean size and mean density were analysed using ANOVA or Kruskal–Wallis test. Different cohorts were identified using the Bhattacharya (1967) method. Bhattacharya's method is a modal progression analysis technique that does not require an estimate of the number of components included in the observed distribution (Bhattacharya, 1967). These analyses were performed using FISAT II v.1.0 package (FAO–ICLARM software).

For the analysis of trophic links between sea urchin and seagrass, we used also studies already published on diet and nutrition (ingestion rate) of the sea urchin

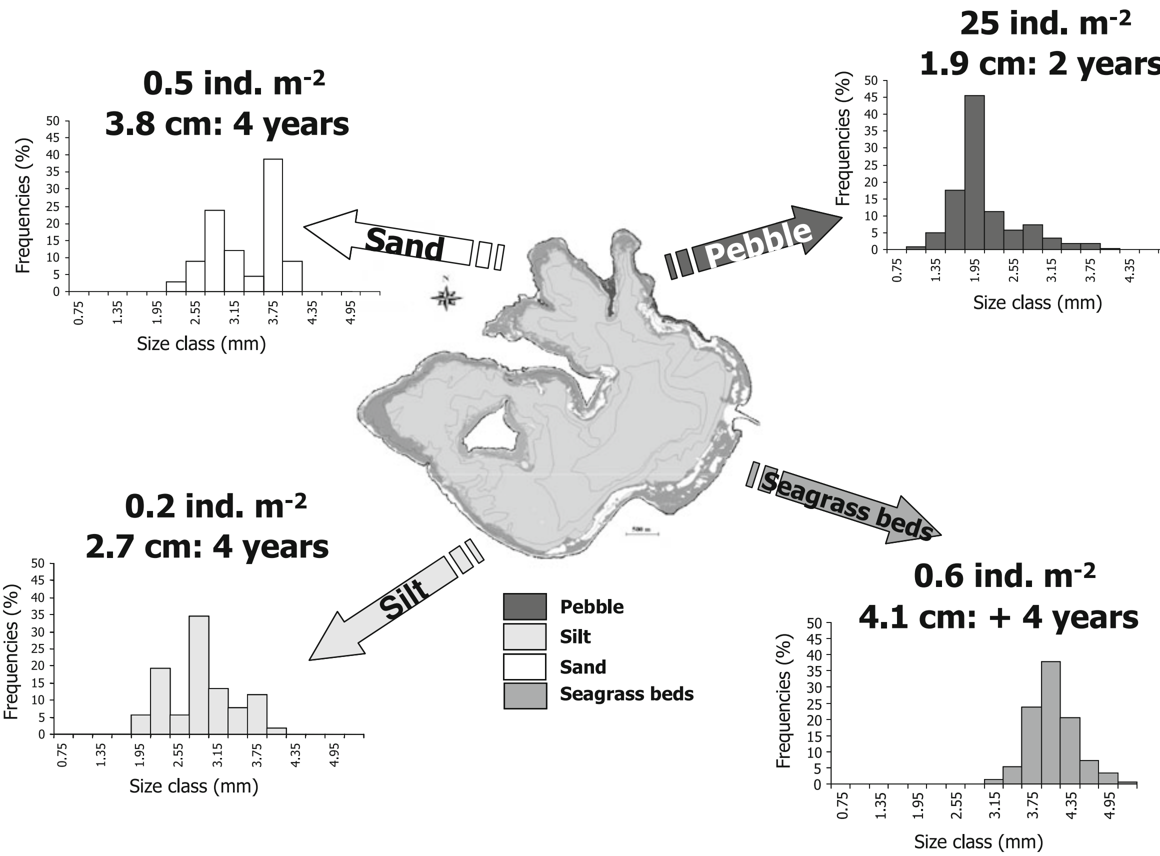


Fig. 1 Distribution of benthic communities and bottom types (central map) and population structure (size frequency distribution) measured in the four habitats of Urbino lagoon (Corsica, Mediterranean). Data on mean densities, mean size and age estimation for each habitat are also presented (from Fernandez et al., 2006 modified)

from Urbino lagoon (Fernandez & Caltagirone, 1998; Fernandez & Boudouresque, 2000). In the study on diet published by Fernandez & Caltagirone (1998), gut contents of sea urchins living in seagrass beds were analysed in order to quantify the composition of the natural diet of *P. lividus* in meadows of Urbino lagoon. In the study on nutrition published by Fernandez & Boudouresque (2000), ingestion rates of sea urchins from Urbino lagoon were measured monthly in aquaria. Over a 3-day period, a given amount of food was provided every 24 h. The feed not ingested at the end of 24 h was collected, freeze dried and weighed. Individual ingestion rates (for 10 individuals) were calculated as being the difference between the provided food biomass and the biomass not ingested (dry weight). Similarly, the water content and dissolution rate of food were studied. These parameters provided a basis for an assessment of food biomass losses and were used to correct the daily ingestion rates. Ingestion was calculated in terms of wet weight and dry weight.

Cymodocea nodosa meadows

Cymodocea nodosa is a common seagrass species in the Mediterranean Sea and the North-Atlantic coast of Africa, including the Canary Islands (Den Hartog, 1970), which shows a wide depth distribution range from the intertidal (Vermaat et al., 1993) to depths of 33–35 m (Canals & Ballesteros, 1997). It can be found on a wide range of substrata too, from coarse sand to muddy sediments (Pavón-Salas et al., 2000), and forms extensive meadows in shallow, sheltered places such as lagoons (Terrados & Ros, 1992; Ribera et al., 1997; Agostini et al., 2003). The general plant morphology was described under the name *Phucagrostis major* Cavolini (Bornet, 1864). Most of the knowledge on the seasonality of biomass, growth and primary production of *C. nodosa* is already available (e.g. Terrados & Ros, 1992; Vermaat et al., 1993; Pérez & Romero, 1994; Sfriso & Ghetti, 1998; Guidetti et al., 2002).

Seagrass bed characteristics (cartography, spatio-temporal changes, biomasses and primary production) were also studied by our team in Urbino lagoon, during the same period as the sea urchin population, and the results have already been published (Pasqualini et al., 1997; Agostini et al., 2003; Fernandez et al., 2006; Pasqualini et al., 2006).

To map the habitats, computer image processing based on aerial photographs was used. The method employed for the digitized photograph analysis, using MULTISCOPE software (version 2.4, Matra Cap System and Information®), was the same as that used by Pasqualini et al. (1997). This technique combines a high level of precision and rapid processing (Pasqualini et al., 1997).

Spatio-temporal changes and biomass of the seagrasses were analysed by Pasqualini et al. (2006) using the same transect as for sea urchins and over the same period. The markers (metal rods) were positioned along the outer limit of a meadow (marked survey area) or within a stand along a precise axis (transect; Pasqualini et al., 2006). The aim was to record accurately the existing meadows and bottom types that occur in order to develop an accurate map (precision 20 cm). For biomass determination, five cores were extracted randomly from the meadow using a thin-walled, serrated, stainless steel core tube (15 cm diameter) inserted to a depth of 30 cm (i.e. maximum root length). Leaves, rhizomes and roots were separated and dried at 75 °C to constant weight to determine the dry weight of each fraction.

Leaf production was carried out by Agostini et al. (2003) from July 1998 to July 1999 in situ (using four permanent quadrats of 40 cm × 40 cm each, situated near the transect used for sea urchin and seagrass spatio-temporal changes), using the Zieman method (Zieman, 1974; Pérez & Romero, 1994). Seasonal leaf net production (g DW m^{-2}) was calculated as the mean leaf production per shoot multiplied by the mean shoot density of the respective season.

Sea urchins–seagrasses trophic link

On the basis of all these data obtained on sea urchins (density, size, ingestion rate) and seagrasses (biomass, primary production), interactions between plants and herbivores have been quantified by calculating the percentage of seagrass production consumed (per month and during an annual cycle) by the sea urchins. In our study, this percentage is defined as the fraction of production of seagrass consumed by sea urchin: consumption/production × 100. This parameter was calculated for each month using mean urchin density, mean urchin size and mean ingestion rate but also for several months on sea urchin fronts with high density. For the latter calculation, the percentage of seagrass production consumed by sea urchin may exceed 100%, indicating overgrazing of the meadow.

Results

Sea urchin populations

Paracentrotus lividus populations occur in the four habitat types of the lagoon (i) pebble bottom, (ii) sand area, (iii) silt areas and (iv) seagrass beds (Fig. 1). In the latter habitat, the results obtained in this study show a relative low density (Fig. 2). Statistical analysis revealed that densities varied significantly during the 18-month sampling periods (Kruskal–Wallis test, $W = 38.2$; $P < 0.001$). The densities were quite similar from June 1998 to June 1999 (around 0.8 ind. m^{-2}) and increased during the last 3 months of the study (2–3 ind. m^{-2}; SNK test, $P < 0.05$; Fig. 2). With a more detailed analysis, we have also

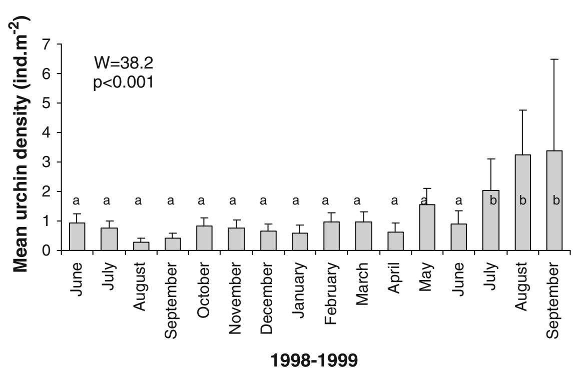


Fig. 2 Mean and confidence interval values for sea urchin density (for the 100 m^2) transect in Urbino lagoon from June 1998 to September 1999. Results of Kruskal–Wallis tests (*W*- and *P*-values) and post-hoc tests for temporal variations are also presented. Values not differing by 5% are denoted with the same letter

observed a pattern of variability along the transect. The first part of the transect (0–0.7 m depth) presented a very low density, and most of the surface explored were without sea urchins. The second part of the transect (0.7–1.7 m depth) presented a higher density with a more homogeneous distribution pattern (Fig. 3). The data also show that very high densities occurred from March to September 1999 at the end of the transect; the density in these zones varied from 9 to 66 ind. m^2 (mean densities; Fig. 4). In addition to these density variations, we also found changes in the size of the sea urchins (Kruskal–Wallis test, $W = 272.5$, $P < 0.001$; Fig. 5). Overall, mean size was quite stable from June 1998 to March 1999 (around 34 mm) and then decreased until September 1999 (around 25 mm). The population structure of sea urchins in Urbino seagrass beds varied significantly from month to month (Fig. 3; χ^2 tests, $P < 0.001$). All cohort sizes, calculated using the Bhattacharya method, do not occur every month. Moreover, the number of individuals for each cohort varies by month. Three major changes can be noted:

(i) From June to October 1998, only adult sea urchins were observed in the seagrass beds with 2 or 3 cohorts with a mean size of around 30–35, 40–45 and +50 mm (Fig. 3).

(ii) From October 1998 until March 1999, a small cohort (mean size 15 mm) occurred in low quantities (Fig. 3). During this period, the oldest sea urchin (>40 mm) disappeared.

(iii) From April 1999 to September 1999, the mean size of the small cohort increased (from 15 to 20 mm) and the density of these small individuals greatly increased.

Finally, during the last period, the sea urchin presented aggregations composed of high densities of sea urchins (mean density: 9–66 ind. m^{-2}; Fig. 4 and maximum density of 98 ind. m^{-2}).

Cymodocea nodosa meadows

In Urbino lagoon, seagrass beds form a quasi-continuous belt on the periphery of the lagoon that can reach 300 m width (Fig. 1). *C. nodosa* presents high densities depending on depth (from 509 to 1,471 shoots m^{-2}; Pasqualini et al., 2006) and high-aboveground biomass (mean: 88 g DW m^{-2} with variations from 11 to 185 g DW m^{-2}; Fig. 6; Pasqualini et al., 2006). The

Fig. 3 Sea urchin density measured along the transect (mean for 5 m^2 and confidence interval) from June 1998 to September 1999 (on the left of the figure) and population structure (size frequency distribution in total number of individuals per size class observed on the transect for each date) measured during the same period. The characteristics of the different cohorts identified using the Bhattacharya method are presented at top of each histogram (*grey point* for mean size and *black line* for the standard deviation in mm)

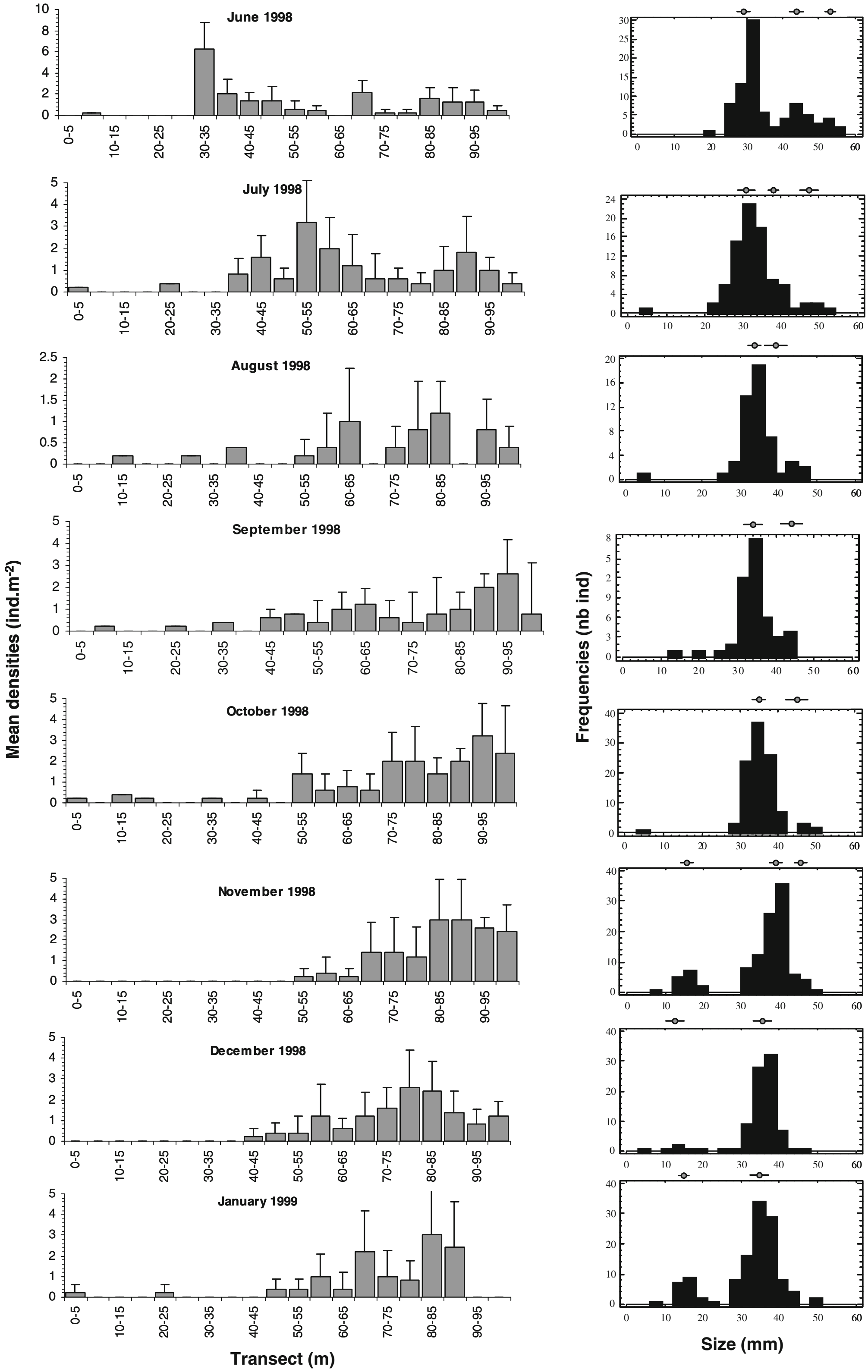
aboveground productivity in Urbino lagoon was high with a mean of 5.8 g DW m^{-2} day^{-1} with variations from 1.5 to 17.8 g DW m^{-2} day^{-1} (Fig. 7; Agostini et al., 2003). Primary production of *C. nodosa* for the Urbino lagoon was estimated at 2470 g C m^{-2} $year^{-1}$ by Agostini et al. (2003). These values have been used to assess the sea urchin–seagrasses trophic link.

Sea urchin–seagrasses trophic link

The nutritional parameters and growth of *P. lividus* from Urbino lagoon have been studied showing an ingestion rate ranging from 93 mg DW $ind.^{-1}$ day^{-1} for smaller sea urchins to 330 mg DW $ind.^{-1}$ day^{-1} for the larger ones depending on the month (Fig. 8; Fernandez & Boudouresque, 2000). The production rate varied from 3.8 g DW $ind.^{-1}$ $year^{-1}$ for the smaller urchins to 5.9 g DW $ind.^{-1}$ $year^{-1}$ for the larger ones (Fernandez & Boudouresque, 2000). The estimated percentage of leaf production consumed by sea urchin varied from 0.6 to 18.9% according to the month (Fig. 9).

Discussion

Urbino lagoon contains large populations of *P. lividus* (Fernandez & Caltagirone, 1990; Fernandez et al., 2006). Population living in seagrass bed showed a relative low density but with temporal variability. Particularly, very high densities of sea urchins were observed from March to September 1999 in the deeper zone of the transect. During several months, a dense aggregation of sea urchins occurred in the seagrass bed. These aggregations are often called "sea urchin feeding fronts" (Eklöf et al., 2008). Variations in densities were accompanied by changes in population structure with the arrival of young sea urchins in the seagrass meadow particularly during the second part of this study. These sea urchins were localised at the


June 1998
July 1998
August 1998
September 1998
October 1998
November 1998
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January 1999
Mean densities (ind.m-2)
Transect (m)
Frequencies (nb ind)
Size (mm)

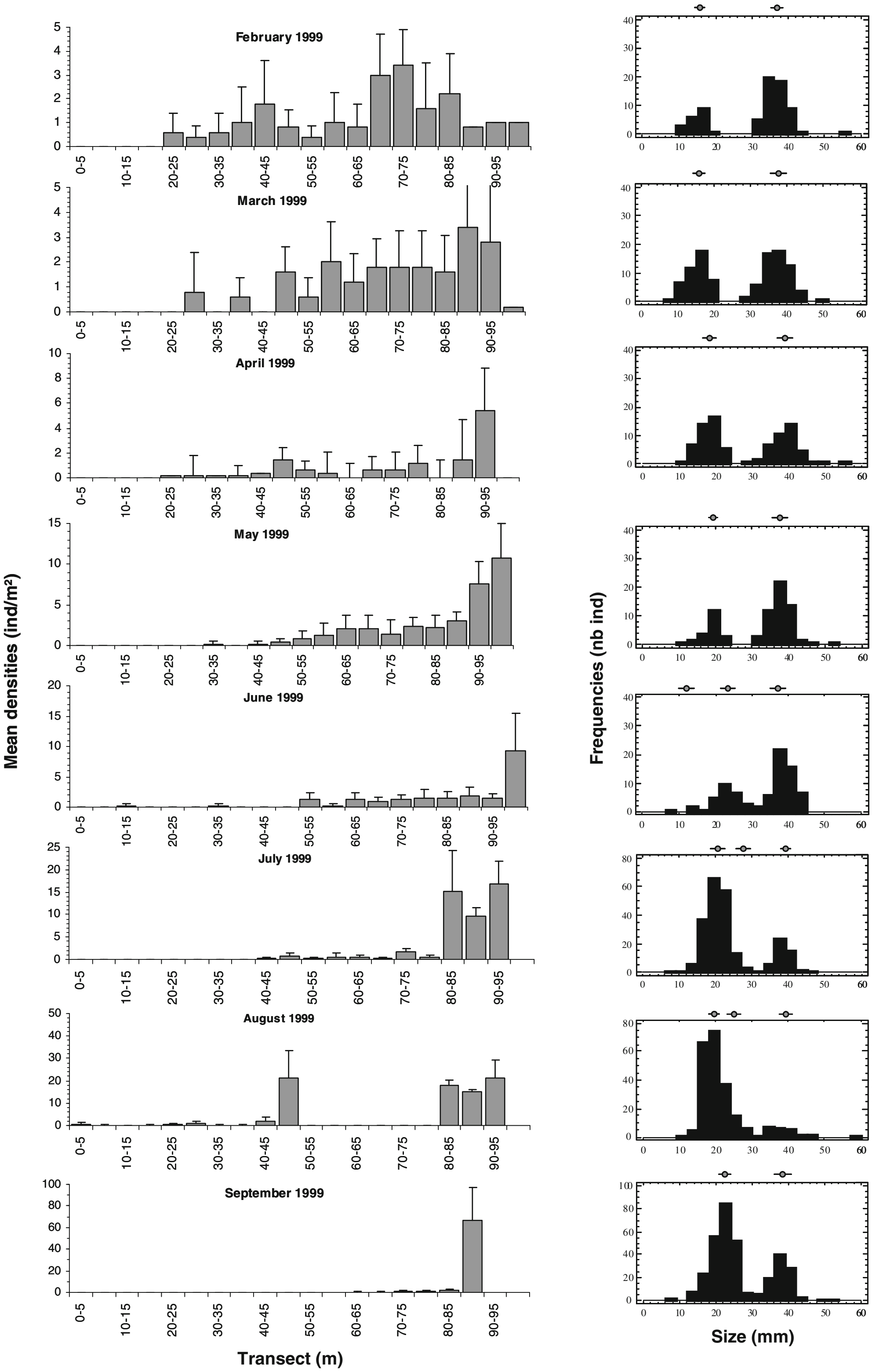

Fig. 3 continued

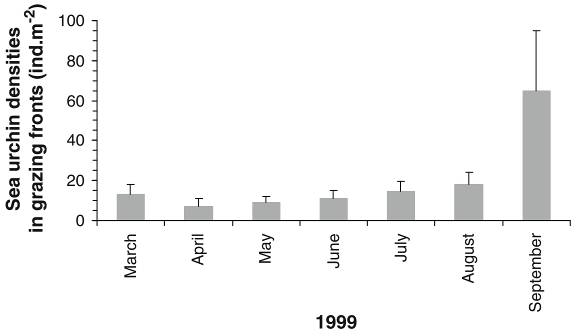

Fig. 4 Sea urchin densities in grazing fronts (mean and confidence interval; ind. m^{-2})

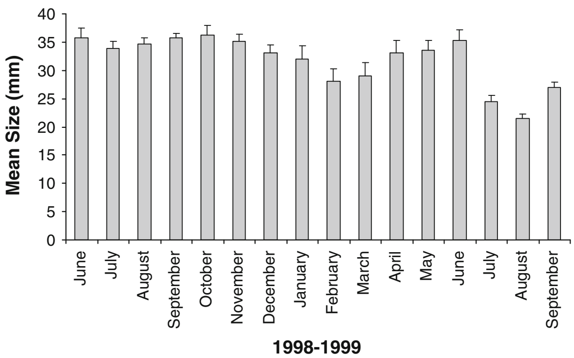

Fig. 5 Mean size of sea urchin from June 1998 to September 1999 (and confidence interval in mm)

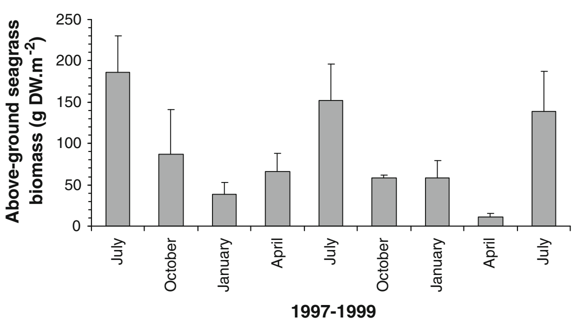

Fig. 6 Annual variations of mean aboveground biomass of *C. nodosa* (from Pasqualini et al., 2006 modified)

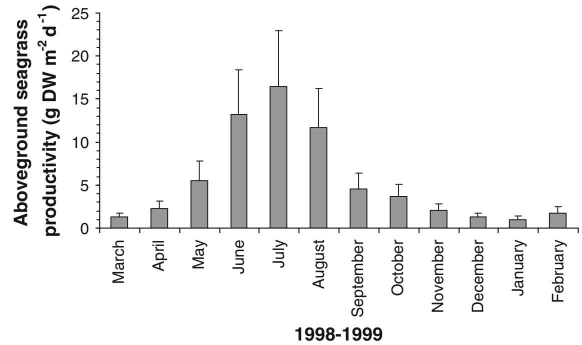

Fig. 7 Annual variation of mean aboveground primary production of *C. nodosa* shoots (from Agostini et al., 2003 modified)

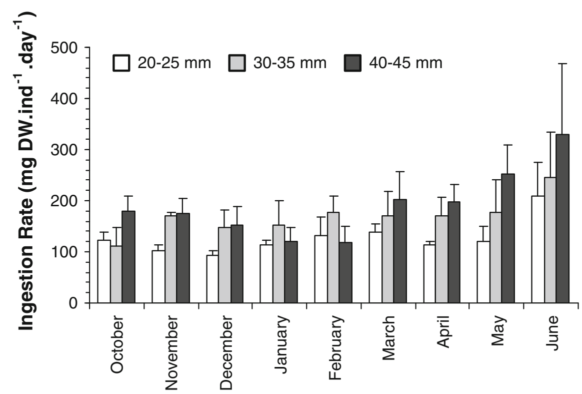

Fig. 8 Mean ingestion rates of sea urchins from October to June (expressed in terms of dry weight) for three class sizes: 20–25, 30–35 and 40–45 mm (from Fernandez & Boudouresque, 2000 modified)

limit between the seagrass and sand habitat and would appear to herald the arrival of a wave of migration. These data confirm the existence of migration events of sea urchins in this lagoon that have been suggested earlier (Fernandez et al., 2001). Sea urchin migration occurred from the pebble area (recruitment area, high sea urchin density and overgrazing facies) towards areas comprising *C. nodosa* seagrass beds (growth areas, low density and abundant preferred food; Fernandez et al., 2001). Thus, the sea urchins migrate in order to seek out new food resources (Kitching & Ebling, 1961; Mattison et al., 1977). Sea urchin fronts were observed in this coastal lagoon a decade earlier (Fernandez & Caltagirone, 1990), albeit with lesser densities (10–30 ind. m^{-2}) and have not been reported since. This kind of aggregation has already been observed for several species of sea urchins (Dean et al., 1984; Maciá & Lirman, 1999; Alcoverro & Mariani, 2002; Gagnon et al., 2004). These sea urchin aggregations, because representing such high densities, are often destructive for the meadow (Abraham, 2007).

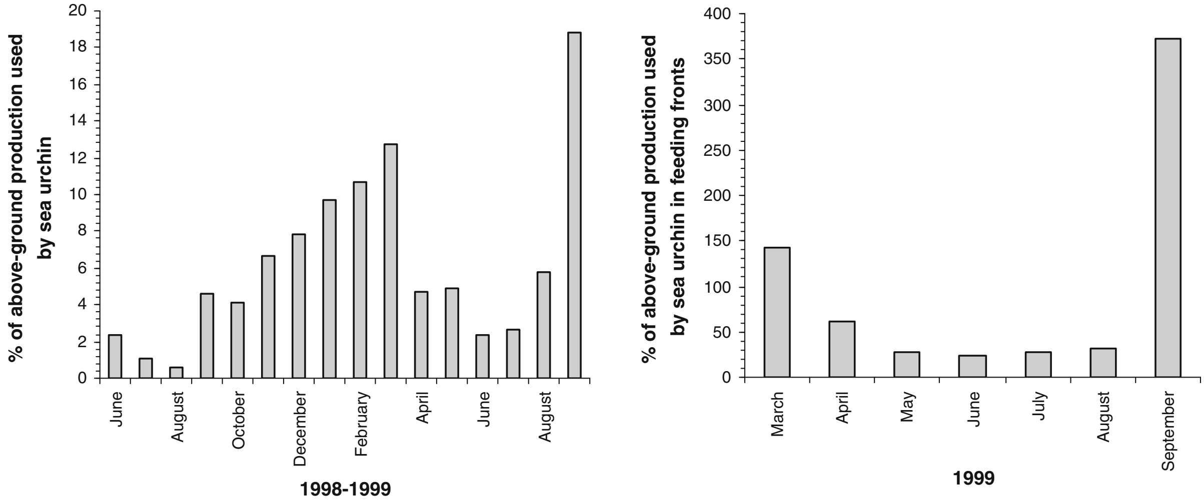

Fig. 9 Estimation of leaf removal by sea urchin as a percentage of leaf production. *On the left*: urchin density, size obtained for the whole of the transect each month was used for this estimation. *On the right*: data obtained only on sea urchin feeding fronts was used

Concerning seagrass beds, they are generally present in the shallower part of the lagoon (between the surface and 4 m depth), representing a surface area of about 20.7% of the lagoon (Ferrat et al., 2003; Pasqualini et al., 2006). However, inter-annual fluctuations (decline or increase) in the surface area covered by seagrasses have been observed in this lagoon (Fernandez et al., 2006) due to the fast growth rate (Caye & Meinesz, 1985) and year-to-year variations in space occupation (Scarton et al., 1995; Vidondo et al., 1997). Even if three species of seagrass have been recorded in the Urbino lagoon (*C. nodosa*, *Z. noltii* and *Ruppia cirrhosa*), monospecific meadows are mostly made up of *C. nodosa*. This species is particularly well developed with densities, biomass and production higher in Urbino lagoon than in other lagoons (Terrados & Ros, 1992; Rismondo et al., 1997; Agostini et al., 2003).

In Urbino lagoon, sea urchins living in seagrass beds consumed mostly *C. nodosa* aboveground biomass: in particular, leaves and, to a lesser degree, sheaths and litter (Fernandez & Caltagirone, 1998). *C. nodosa* provides an abundant supply of food to sea urchins as among the seagrasses, this species is known to be a preferred food source for *P. lividus* (Traer, 1980). Thus, this area is favourable for sea urchin growth (Fernandez & Caltagirone, 1998; Fernandez et al., 2006). The exceptionally comprehensive set of data comprising simultaneous data of seagrass and sea urchins in Urbino lagoon enables us to accurately estimate the trophic link between these two trophic levels. This estimation for an annual cycle is around 1.4% (when the calculation is made with usual urchin densities and size). Therefore, when density is usual, *P. lividus* is assumed to consume a small part of the *C. nodosa* production in the coastal lagoon. But when sea urchin densities are around 10–30 ind. m^{-2} (Fernandez & Caltagirone, 1990), consumption reaches 100% of the *C. nodosa* production. Finally, in the front aggregations observed during this study, herbivory largely exceeded the seagrass production with a biomass ingested exceeding 500 g m^{-2} (which corresponds to an estimate percentage of leaf production consumed by sea urchin approaching 370%), causing overgrazing and seagrass regression. In this case, the seagrass regression rate may reach several metres each month. However, it could be noted that seagrass recovery seems to be quite rapid in this coastal lagoon (10 months; personal observation) as observed for other regression episode due to salinity drop (Fernandez et al., 2006).

Even though *C. nodosa* is clearly preferred to *P. oceanica* by *P. lividus* (Traer, 1980; Cebrian & Duarte, 1998), there have been few studies on the impact of grazing on the former seagrass. Nevertheless, Cebrian et al. (1996) underline the trophic importance of *C. nodosa* as a food resource for herbivores. The consumption of *C. nodosa* by grazing could vary according to these authors from 0.1 to 42.5% of leaf production lost by herbivory. During periods with relative low-sea urchin density, the Urbino seagrass population suffered only modest losses of leaf production as in most of the sites studied in Spain by Cebrian et al. (1996).

Our study also shows overgrazing phenomena during a few months. Overgrazing events on seagrasses have generally been observed in coastal waters (Eklöf et al., 2008) and have not been accurately described in coastal lagoons. The observations have been made in tropical zones and are generally based on *Lytechinus variegatus* in America (Zimmerman & Livingston, 1976; Peterson et al., 2002) or *Tripneustes gratilla* in Africa (Alcoverro & Mariani, 2002). In the Mediterranean, it has been described that *P. lividus* overgrazed *P. oceanica* in several documented cases (Kirkman & Young, 1981; Verlaque & Nedelec, 1983; Shepherd, 1987). Our study has highlighted the first observation of overgrazing in *C. nodosa* meadow. Potential causes of overgrazing have been identified or investigated in very few cases (Eklöf et al., 2008). The major causes mentioned by the authors were divided into three categories: (1) top-down (loss of predation), (2) bottom-up (nutrient enrichment) and (3) "side-in" (e.g. temperature). From the present study, it seems clear that the cause of overgrazing is the arrival by migration of large numbers of sea urchins.

Conclusion

The results obtained over a period of more than 10 years on urchin and seagrass populations in Urbino lagoon show that grazing by the sea urchin *P. lividus* can be substantial on coastal lagoon *C. nodosa* meadows. However, urchin grazing appears to be highly variable in both space and time. Most of the time, sea urchin densities are low in seagrass meadows and *P. lividus* grazing is minor with a low-leaf production removal. However, during migration events, when urchin densities are high, grazing could greatly exceed seagrass leaf production and also stock, thus causing a clear decline in shoot biomass. The complete loss of seagrass biomass observed could probably have an impact on the seagrass community and might generate a loss of seagrass-associated ecosystem services. In the short term, sea urchin–seagrass interaction is controlled by sea urchin abundance fluctuations and migration events.

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