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## Sublethal foot-predation on Donacidae (Mollusca: Bivalvia)

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### Abstract

The incidence of foot nipping was studied on the *Donax* spp. of the littoral of Málaga (Southern Spain, 2875 specimens collected from February 1990 to January 1991) and of Ré island (French Atlantic coast, 262 specimens of *Donax vittatus* (Da Costa, 1778) collected in May 1996). In Málaga, *Donax trunculus* L., 1758 was the species most regularly nipped (18% of individuals), with peaks in summer (25% in August and 48% in September) and winter (34% in December). In Ré island, 27% of the specimens showed a nipped foot.

Logistic regression shows that in *D. trunculus* length is the variable that most influences the probability of foot nipping, followed by weight and chlorophyll *a*. However, the difference in length between damaged and undamaged individuals was not significant (U-Mann–Whitney test). The size class frequency and the values of Ivlev's index show that the small size classes were avoided, while for the other size classes predation remained balanced throughout the year. Therefore, the avoidance of the small size classes makes length the most influential variable. The logistic regression indicated a coefficient  $B = -0.03$  for weight. This implies a slightly negative influence on the probability of foot nipping. However, without the data of September, there is a positive correlation ( $r = 0.76$ ,  $p < 0.01$ ) between the monthly percentages of predation and the flesh dry weight of a standard individual (25 mm long). The peak in September could be due to the recruitment peak of bivalves, which may have attracted more predators to the area, and/or to the recruitment of predators such as crabs to the swash zone. Logistic regression and test of comparison of percentages indicate that there was not any influence of the sex of an animal on the probability of foot nipping. Only in February was a significantly higher percentage ( $p < 0.05$ ) of females nipped (44.44%) than the total of females in the sample (20.20%).

The biomass (as flesh dry weight) of *D. trunculus* lost by foot nipping amounts to more than 20% in most of the size classes. There was an increase from the small sizes to the largest ones, in which it reaches 37%, with a positive correlation ( $r = 0.84$ ;  $p < 0.005$ ) between size class and loss of biomass. Possible predators responsible for the foot nipping are crabs. Crab species usually found together with the donacids were *Portumnus latipes* (Pennant, 1777) *Liocarcinus vernalis* (Risso, 1816) and *Atelecyclus undecimdentatus* (Herbst, 1783). In aquarium experiments, they demonstrated an ability to nip the foot of clams. *Portumnus latipes* was the most active foot nipper, but left alive all the damaged clams. Therefore, we conclude that crabs are the most likely foot-nipping predators in the field. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** Sublethal foot predation; Donacidae; Mollusca; Bivalvia; Crabs

### 1. Introduction

Predation is often considered to be the most

important cause of mortality in bivalves (Dame, 1996; Nakaoka, 1996; Van der Veer et al., 1998). However, the predation is not always lethal. Sublethal predation results in the loss of siphons by 'nipping', 'cropping' and 'browsing' predators, mainly fish (Edwards and Steel, 1968; Trevallion et al., 1970;

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Gilbert and Suchow, 1977; De Vlas, 1979, 1985; Brewer and Willan, 1985; Peterson and Quammen, 1982; Ansell et al., 1999) and occasionally birds (Ens and Zwarts, 1980) and crustaceans (De Vlas, 1985).

Although bivalves are able to regenerate their siphons, such regeneration takes place at the expense of somatic growth (Peterson and Quammen, 1982; Coen and Heck, 1991; Bonsdorff et al., 1995) and of the development of gonads (Trevallion et al., 1970; Trevallion, 1971). Amputation of the siphon has another negative consequence for deposit feeding bivalves: they are forced to live closer to the sediment surface, and this increases the risk of predation by birds (Zwarts, 1986; Zwarts and Wanink, 1989). Besides, this partial predation by siphon-cropping predators reduces deposit feeding in bivalves (e.g. *Macoma balthica*), and they switch to suspension feeding (Peterson and Skilleter, 1994). However, if the amputation of siphon tissue in *Macoma balthica* is made in the presence of another suspension-feeding species (*Rangia cuneata*), the deposit-feeding activity is maintained (Skilleter and Peterson, 1994). Therefore, there is an interaction between interspecific competition and siphon cropping.

Among the extant molluscivorous animals reported by Vermeij (1987, 1993), the crustaceans — mainly crabs and lobsters — are one of the most important groups preying on bivalves, because of their high mobility and specialised claws (chela) and mandibles. Moreover, they are able to capture both epibenthic and infaunal bivalves (Seed, 1993). A detailed list on the methods by which crustaceans penetrate the bivalve shell is given by Lau (1987). Nine methods are considered: (1) swallowing whole; (2) chipping–biting; (3) wedging; (4) prying; (5) crushing; (6) chipping–peeling; (7) boring; (8) tubercular peeling; and (9) shearing. On the other hand, a number of shell features such as larger size, thicker shell, ability to close tightly, more inflated shape with a steep ventral margin and deeper burial in the sediment, increase the resistance of molluscs to crab predation (Boulding, 1984).

Donacids are the dominant bivalves of many tropical to temperate exposed beaches, particularly in highly productive areas, where they are able to develop and maintain large populations (Ansell, 1983), and where they are preyed on by a wide variety

of animals. Loesch (1957) gives a list of 12 predators of *Donax* for the beaches of the Gulf of Mexico (Texas), which includes other invertebrates (mainly gastropods, polychaetes and crustaceans), fish, birds and mammals. Most of the predation is lethal, because the clams are swallowed whole or opened (by crushing, edge chipped, etc., see Smith, 1975) to remove the soft parts. However, siphon cropping by birds such as the sanderling (*Crocethia alba*) on *D. serra* (McLachlan et al., 1980; Hodgson, 1982), and by fish such as juvenile flatfishes on *D. vittatus* in Scottish beaches (Ansell et al., 1999) is also frequent.

The laboratory experiments of Ansell et al. (1999) show that when individuals with siphons nipped by flatfishes are re-attacked before successfully reburying, the predation can again be directed at the siphon, or at the foot as it extends in the initial probing movements of reburial. Ansell and Gibson (1990) report the presence of parts of the foot of *D. vittatus* in flatfish stomachs from St Andrews, which provides evidence that similar attacks occur in the natural population. Vermeij (1993) indicates that some tropical wrasses and temperate dogfishes grab and bite off the exposed foot of crawling snails. However, an evaluation of the impact of this type of predation on the individuals (such as percentage of weight) or on the population through time was not given.

In the littoral of Málaga (Southern Spain), the five European species of Donacidae (Mollusca, Bivalvia) live sympatrically in the same beaches. These are *Donax trunculus* L., 1758 (Atlantic and Mediterranean), *Donax vittatus* (Da Costa, 1778) (Atlantic), *Donax venustus* Poli, 1775 (Mediterranean), *Donax semistriatus* Poli, 1775 (Mediterranean), and *Capsella variegata* (Gmelin, 1791) (Atlantic and Mediterranean) (Salas-Casanova, 1987). During a yearlong study on the reproduction of these clams, we detected appreciable levels of foot predation by nipping. This was also observed on *Donax vittatus* from the French Atlantic coast (Ré island) (Gofas, pers. obs., 1996). All the foot-nipped specimens were collected live and showed some signs of recovery and healing.

This paper evaluates the incidence of foot predation in the donacids from these locations (particularly in the littoral of Málaga, where monthly samples were available), studies the relationship between predation and size, sex or biomass of clams, and points out possible predators.

## 2. Material and methods

A total of 2875 specimens of the *Donax* species collected on the littoral between Fuengirola and Benalmádena (province of Málaga, 36°34.8'N, 4°32.6'W) were analysed from February 1990 to January 1991 to study the variation in flesh dry weight. We considered separately as 'intermediate morphotypes', specimens with intermediate shell characteristics between *D. venustus* and *D. semistriatus*, whose taxonomy has been debated (Tirado and Salas, 1999). Additionally, 262 specimens of *D. vittatus* were collected in May 1996 near low tide level at Ré island, Atlantic coast of France (Anse du Martray, 46°11.9'N, 01°28.0'W), during a workshop of the University of La Rochelle, organised by Prof. J. Tardy. These specimens were examined in order to check the existence of foot predation.

The samples from Málaga were collected monthly, using a dredge with a toothed aperture and 1.5 cm mesh. The samples were taken parallel to the shore at two depths: (a) between 1 and 3 m, with sediment of medium-grained sand with stones, for *D. trunculus* and (b) at 5 m depth in a fine-grained sand bottom, for *D. vittatus*, *D. venustus*, *D. semistriatus* and the intermediate morphotypes. The sample of *D. vittatus* from Ré island was collected using a hand dredge with 5 mm mesh, at a depth of 1 m below the low water of neap tide, in fine-grained sand.

In Málaga, traces of foot nipping on the specimens were observed in all the species during the analysis of biomass variation (Tirado and Salas, 1998, 1999). A temporal study of the foot nipping in relation to biological or environmental parameters was limited to *D. trunculus*, which is the species most often affected.

The variables considered for a possible relationship with the incidence of predation on *D. trunculus* were size (expressed as antero-posterior length of shell), biomass (flesh dry weight), sex (male, female, or inactive without differentiated gonads), and some environmental factors (seawater surface temperature and chlorophyll *a* concentration).

For biomass (flesh dry weight), we considered all the damaged and undamaged individuals and the data of a standard individual (25 mm), over the year of study. The soft parts were removed, placed in a drying stove at 100°C for 24 h and weighed to the nearest milligram. The estimation of the standard individual

is based on a regression of flesh dry weight versus length for each month for undamaged specimens only: the logarithmic transformation of Ricker's function  $W = aL^b$  (Ricker, 1975), where  $W$  is the weight,  $L$ , the length,  $a$ , the ordinate at origin and  $b$  is the slope. The data of flesh dry weight of the nipped individuals were then obtained in order to evaluate the loss of biomass due to foot predation.

The environmental factors (chlorophyll *a* and surface seawater temperature) analysed in relation with the sexual cycle of *Donax* spp. were also checked against the data of foot-nipping predation. Samples of surface water (2 dm<sup>3</sup>) were taken monthly, pigment analyses were carried out following the recommendations of Lorenzen and Jeffrey (1980), and concentrations of chlorophyll *a* were calculated using the trichromatic equations of Jeffrey and Humphrey (1975).

All the variables considered were included in a logistic regression (SPSS.10), in order to assess the relationship between these variables and the probability of foot-nipping predation in the population of *D. trunculus*. We tested the significance of the difference between damaged and undamaged individuals for the variable with the highest score in the logistic regression (Student's *t* or U-Mann–Whitney test).

A Kolmogorov–Smirnov test was used to check the distribution of the data, and we accordingly applied a Kendal (*t*) or Pearson (*r*) rank correlation to analyse the monthly relationships between the environmental factors or flesh dry weight of a standard individual and percentage of foot nipping.

We also investigated a possible relationship between the percentage of foot nipping and the reproductive cycle in *D. trunculus*, that is to say, if there was more predation on clams with filled gonads (active stage or with residual gametes), which could be expected to be less mobile; or if there was a preference for a particular sex. For this, in addition to including the sex in the logistic regression, we performed tests of comparison of percentages (Lamotte, 1976) to analyse whether the monthly percentages of sex (with active, coloured gonads) and gonadal developing stages (males and females — active individuals, and undifferentiated — inactive individuals) were different in the whole sample and in the sub-sample with foot-nipped individuals.

The relationship between percentage of predation

Table 1

Annual percentages of predation (%Pr) by species and sex. Inter. Morph. = Intermediate morphotypes between *D. venustus* and *D. semistriatus*. Ft = Number of females; Fp = Number of females with foot nipped; Mt = Number of males; Mp = Number of males with foot nipped; It = Number of individuals without differentiation of gonads; Ip = Number of individuals without differentiation of gonads and with foot nipped; Nt = Number of individuals over the year; Np = Number of individuals with foot nipped over the year

Species	Ft	Fp	%Pr	Mt	Mp	%Pr	It	Ip	%Pr	Nt	Np	%Pr
<i>D. trunculus</i>	365	64	17.5	425	79	18.5	492	92	18.7	1282	235	18.3
<i>D. venustus</i>	246	25	10.2	216	27	12.5	77	5	6.5	539	57	10.6
<i>D. semistriatus</i>	63	1	1.6	77	5	6.5	25	1	4	165	7	4.2
<i>D. vittatus</i>	130	10	7.7	115	9	7.8	42	5	11.9	287	24	8.4
Inter. Morph.	271	10	3.7	242	3	2.1	86	2	2.3	599	15	2.5

and size (length) of *D. trunculus* was analysed by logistic regression, and by histograms of size class frequency, in which 17 size classes between 16 and 33 mm length (1 mm range) were considered separately for the whole sample and for nipped individuals. Ivlev's index of selectivity (Krebs, 1989) was applied to each size class to test if there was preference for one or several size classes. According to this index, selectivity varies from  $-1.0$  to  $+1.0$ , with values between 0 and  $+1.0$  indicating preference, values between 0 and  $-1.0$  indicating avoidance, and 0 indicating a random choice.

The amount of biomass lost by predation in *D. trunculus* is difficult to distinguish from that related to the reproductive cycle because of the amplitude and asynchrony of the sexual cycle in Málaga (Tirado and Salas, 1998), which implies, during most of the year, different weights for individuals of a particular size in relation with their stage of sexual cycle. Therefore, we used only the data of December, in which the gonads are not active and many specimens are in the cytotoxic (or resting) stage (Tirado and Salas, 1998). Flesh dry weight was regressed against size class separately for specimens with and without their foot nipped. The difference in biomass was estimated for each size class by subtracting the average of flesh dry weight of damaged individuals from that of undamaged individuals. The differences in weight can be considered to be due to consumption by predators, at least during December.

Observations in the laboratory were carried out only to test the ability of different species of crabs — which are possible foot predators — to nip the foot of *D. trunculus*, the most attacked species. A total of 152 individuals, and the associated crabs, were dredged on 15 March 1999. The crabs captured

were: *Atelecyclus undecimdentatus* (Herbst, 1783), (one specimen; Fig. 1A), *Portumnus latipes* (Pennant, 1777) (five specimens; Fig. 1C) and *Liocarcinus vernalis* (Risso, 1816) (five specimens; Fig. 1E). In the laboratory, the bivalves were anaesthetised with  $MgCl_2$  (6% in seawater) to check whether their feet were intact; after recovery, they were put back in seawater. An aquarium of 60 (length)  $\times$  30 (height)  $\times$  30 cm (high) was divided into three parts with two glass panes, with a layer of ca. 10 cm of medium grained sand collected in the *D. trunculus* zone and ca. 20 cm of seawater in each compartment. The crabs and the *Donax* were placed in the compartments (53 *Donax* with 5 *Liocarcinus*, 52 *Donax* with 5 *Portumnus* and 45 *Donax* with 1 *Atelecyclus*), and left until 25 March. During the ten days of observation, the seawater of each compartment was oxygenated and renewed completely every two days, but no food was added. The predation, mortality of bivalves and mortality of crabs were recorded. Nakaoka (1996) distinguishes three categories of effects on bivalves: (1) alive, (2) preyed on (broken shell; unbroken empty shell), and (3) mortality due to other causes (unbroken shell with soft parts remaining). We added another category: (4) surviving but foot nipped.

### 3. Results

#### 3.1. Incidence of predation

The total incidence of foot nipping by species and sex, in the littoral of Málaga, throughout the year is shown in Table 1. *D. trunculus* was the most attacked species, with 18.3% of the specimens captured, followed by *D. venustus* and *D. vittatus* with 10.6

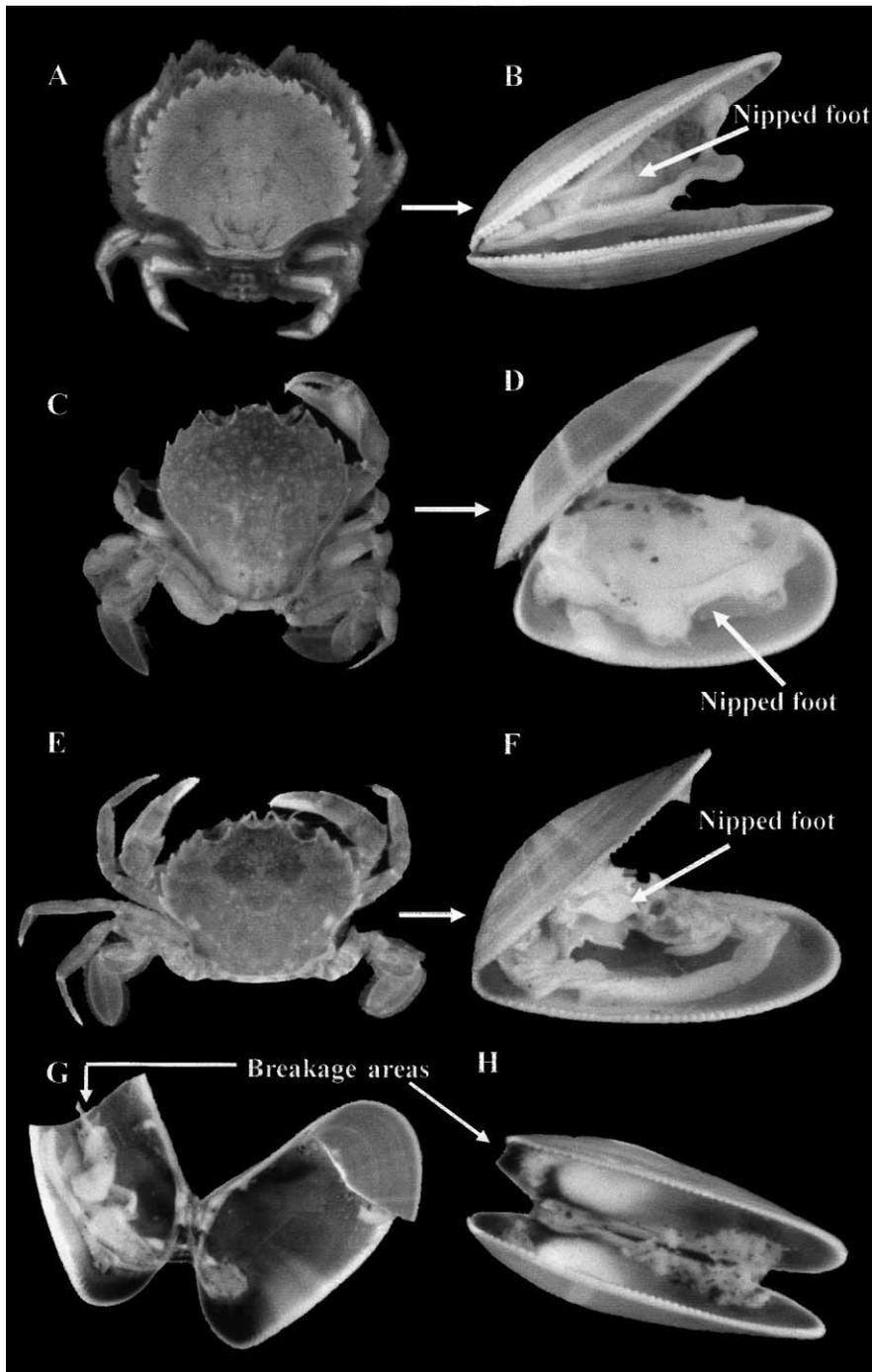


Fig. 1. Crab species and specimens of *D. trunculus* observed in the aquaria. (A) *Atelecyclus undecimdentatus* (width of carapace = 49.6 mm). (B) Specimen of *D. trunculus* (length of valve = 30 mm) with foot nipped by *A. undecimdentatus*. (C) *Portumnus latipes* (width of carapace = 19.7 mm). (D) Specimen of *D. trunculus* (length of valve = 25.1 mm) with foot nipped by *P. latipes*. (E) *Liocarcinus vernalis* (width of carapace = 17.4 mm). (F) Specimen of *D. trunculus* (length of valve = 26.1 mm) with foot nipped by *L. vernalis*. (G) Specimen of *D. trunculus* (length of valve = 26 mm) eaten by *L. vernalis* with breakage of the shell. (H) Specimen of *D. trunculus* (length of valve = 29.6 mm) eaten by *L. vernalis*; the small breakage of posterior side of the shell is made to introduce the chelae for cutting the posterior adductor muscle.

Table 2

Monthly percentages of foot nipping on Donacidae. Nt = Number of individuals; Np = Number of individuals with foot nipped; %Pr = Monthly percentage of foot nipping for each species; *Donax* spp. = All the individuals of different species together to see the incidence of foot nipping in the group

Months	<i>D. trunculus</i>			<i>D. venustus</i>			<i>D. semistriatus</i>			<i>D. vittatus</i>			Inter. Morph.			<i>Donax</i> spp.		
	Nt	Np	%Pr	Nt	Np	%Pr	Nt	Np	%Pr	Nt	Np	%Pr	Nt	Np	%Pr	Nt	Np	%Pr
F	99	19	19.2	5	0	0.0	32	0	0.0	0	0	0.0	87	0	0.0	223	19	8.5
M	201	6	3.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	201	6	3.0
A	101	16	15.8	77	14	18.2	7	0	0.0	14	2	14.3	46	0	0.0	245	32	13.1
M	100	16	16.0	50	1	2.0	15	0	0.0	19	1	5.3	70	3	4.3	254	21	8.3
J	97	13	13.4	50	6	12.0	10	1	10	15	0	0.0	48	5	10.4	220	25	11.4
J	99	11	11.1	132	15	11.4	3	0	0.0	8	1	12.5	7	0	0.0	249	27	10.8
A	96	24	25.0	11	0	0.0	36	0	0.0	59	4	6.8	64	0	0.0	266	28	10.5
S	95	46	48.4	18	2	11.1	20	0	0.0	49	3	6.1	55	0	0.0	237	51	21.5
O	99	19	19.2	38	2	5.3	15	4	26.7	36	3	8.3	63	0	0.0	251	28	11.2
N	98	17	17.3	44	4	9.1	11	2	18.2	30	3	10.0	34	2	5.9	217	28	12.9
D	97	33	34.0	57	6	10.5	9	0	0.0	21	2	9.5	75	5	6.7	259	46	17.8
J	100	15	15.0	57	7	12.3	7	0	0.0	36	5	13.9	50	0	0.0	250	27	10.8

and 8.4%, respectively, of the specimens collected. *D. semistriatus* with low densities showed only 4.2% of foot nipping. Interestingly, the intermediate morphotypes (IM), with high numbers of individuals collected, were the least foot nipped (2.5%).

The temporal distribution of nipping is shown in Table 2. Again, *D. trunculus* is the species most regularly nipped during the year, with peaks of predation in summer (25% in August and 48% in September) and winter (34% in December) (Table 2). *D. venustus* and *D. vittatus* were also nipped during most of the year (Table 2), but the monthly percentages in both species were lower than in *D. trunculus*. *D. semistriatus* and intermediate morphotypes were attacked only in three or four months, respectively (Table 2). Analysis of all donacids together (Table 2: *Donax* spp.) showed foot nipping in all months with percentages

ranging from 3% (March) to 21.5% (September), and most of these monthly percentages higher than 10%.

Among the 262 specimens of *D. vittatus* from the French Atlantic coast, there were 70 individuals with a nipped foot (Fig. 2B–E), which represent 27% of the sample. Fig. 2A shows an intact specimen with extended foot for comparison with the following. The specimens of Fig. 2B and C are different but show similar foot nipping; in Fig. 2B, one valve has been removed to better display the foot, and Fig. 2C shows the breakage of the shell. Fig. 2D displays an individual of *D. vittatus* in which the foot was nipped when poking out of the shell. There the edges of the mantle on both sides are intact, in contrast to the foot-nipped specimen of Fig. 2E, in which it is possible to appreciate that the shell has been slightly broken on the anterior side, and the mantle edges damaged.

Table 3

*Donax trunculus*. Data of the variables obtained in the logistic regression. B = Coefficient; S.E. = Standard error; Wald = Wald test; d.f. = degree of freedom; Sig. = Signification level; exp(B) = Confidence interval of B; FDW = Flesh dry weight; Chl a = Chlorophyll a; A = constant

	B	S.E.	Wald	d.f.	Sig.	exp(B)
Length	3.16	0.40	63.86	1	0.0005	23.580
FDW	-0.03	0.00	84.45	1	0.0005	0.967
Chl a	-0.356	0.066	28.71	1	0.0005	0.700
A	-5.971	0.74	64.65	1	0.0005	0.003

### 3.2. Temporal analysis of predation on *Donax trunculus*

The result of the logistic regression (Table 3) shows that length is the variable that most influences the probability of foot-nipping predation ( $B = 3.16$ ;  $\exp(B) = 3.58$ ), followed by weight ( $B = -0.03$ ;  $\exp(B) = 0.967$ ), and chlorophyll a ( $B = -0.36$ ;  $\exp(B) = 0.70$ ). The other variables included in the logistic regression (temperature of seawater and sex)

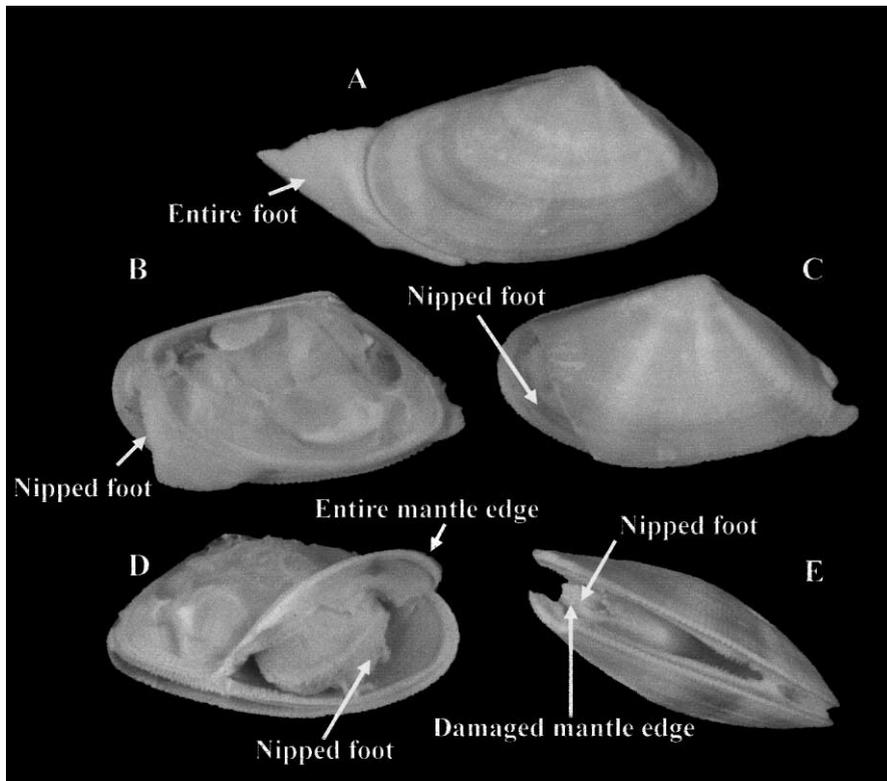


Fig. 2. *Donax vittatus* from Ré Island (Atlantic French coast). (A) Specimen with entire foot (length of valve = 29.2 mm). (B) Specimen with foot nipped showing the breakage of the shell (length of valve = 22.1 mm). (C) Specimen with foot nipped (valve and mantle removed to disclose the foot) (length of valve = 24.4 mm). (D) Specimen with foot preyed on without damage of the mantle (length of valve = 26.2 mm). (E) Foot nipped specimens with breakage of the anterior part of the shell and damage of the edges of the mantle (length of valve = 27.4 mm).

(Fig. 3) did not show any influence on the probability that *D. trunculus* was foot nipped.

To test whether the difference in length between damaged and undamaged individuals was significant,

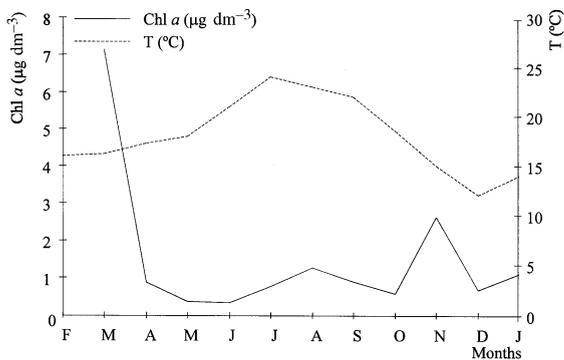


Fig. 3. Temperatures and chlorophyll *a* concentrations in seawater.

we applied the U-Mann–Whitney test, because the undamaged sample did not show a normal distribution. The result of the test (U-Mann–Whitney = 112,005.5;  $p < 0.05$ ) indicated no significant difference.

The values of Ivlev’s index, for each monthly size class and for the size classes pooled over the year, are indicated in Table 4. This indicates that only the small sizes are avoided throughout the year (−1); for the other size classes predation remained balanced throughout the year; most of the values were near 0 (random) (Fig. 4). Some sizes were more selected in some months (positive values), but avoided (negative values) in other ones.

We found no correlation between the flesh dry weight of a standard individual (25 mm long) (Fig. 5) and the monthly percentage of foot nipping. However, if we do not take into account the data for

Table 4

*Donax trunculus*. Monthly values of Ivlev's index by size class. Total = Ivlev's index values by size class over the year. According to values of Ivlev's index: [+1, 0 (preference); 0 (random); 0, -1 (avoidance)]

Mean size classes	F	M	A	M	J	J	A	S	O	N	D	J	Total
16.5		-1.00							-1.00		-1.00	-1.00	-1.00
17.5	-1.00	-1.00	-1.00						-1.00	-1.00	-1.00	-1.00	-1.00
18.5		-1.00	-1.00	0.40	-1.00	-1.00	0.22	-1.00	-1.00	0.27	0.01	0.39	0.23
19.5		-1.00	-1.00	0.40	-1.00	-1.00	0.22	-1.00	-1.00	0.27	0.01	0.39	0.23
20.5	-1.00	-1.00	0.29	-1.00	0.35	-0.04	-0.21	0.14	-0.24	-0.24	0.15	-0.17	0.15
21.5	-0.09	-1.00	-0.22	-1.00	0.21	0.39	-0.12	-0.40	0.05	-1.00	-0.08	0.06	-0.11
22.5	-1.00	0.52	0.23	-0.01	-0.34	-0.13	0.17	0.15	0.41	0.18	-0.16	-0.58	0.06
23.5	-1.00	-1.00	-0.11	-0.26	-0.27	-0.21	-0.32	0.03	0.08	-0.16	0.32	-0.11	-0.05
24.5	-0.17	-1.00	0.62	0.40	-1.00	0.67	0.25	0.03	-0.18	0.49	-1.00	0.06	0.19
25.5	0.30	-1.00	0.12	0.49	0.19	-1.00	0.13	0.09	0.34	-0.35	-0.22	-1.00	0.09
26.5	-0.23	-1.00	0.23	0.08	-1.00	0.21	-1.00	-1.00	-1.00	-0.16	-0.02	0.39	-0.28
27.5	0.00	-1.00	0.03	-0.01	0.27	-1.00	-1.00	-1.00	0.69	0.11	0.07	-1.00	-0.14
28.5	0.11	0.55	-1.00	-1.00	-1.00	-1.00			-1.00	-1.00	0.40	0.70	-0.14
29.5	0.33	-1.00	-1.00	-0.15	0.27	-1.00	-1.00	-1.00			0.49	0.70	-0.19
30.5	0.00	0.81	-0.11	0.08	-1.00	-1.00	-1.00	0.36	-1.00	0.27		-1.00	-0.05
31.5	0.67	-1.00	0.36	-1.00	-1.00	-1.00	0.32	0.18					0.12
32.5		-1.00	0.12	-1.00	0.55	-1.00	0.59	-1.00	-1.00	-1.00			-0.30

September, the month in which the peak of recruitment of bivalves occurs in the studied area (Tirado and Salas, 1999, and pers. obs.), there is a positive correlation ( $r = 0.76$ ,  $p < 0.01$ ) between both variables.

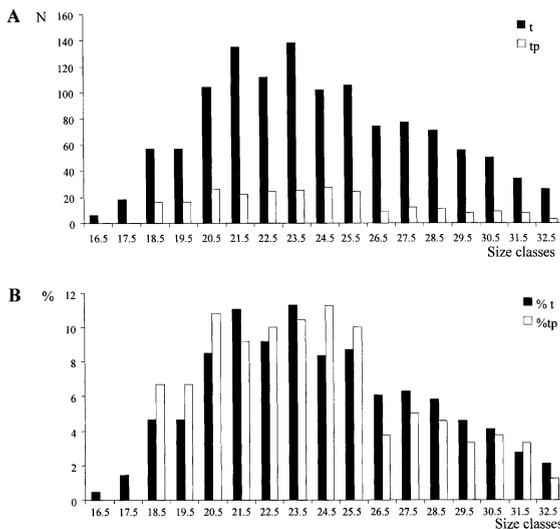


Fig. 4. Histograms of size class frequencies of *D. trunculus* over the year of study for damaged individuals (white) and for whole sample (black). Seventeen size classes (1 mm range) between 16 and 33 mm long were established. (A) Absolute frequencies; (B) Relative frequencies.

The test of comparison of percentages shows that only in the sample of February is the percentage of foot-nipped females (44%) significantly higher ( $p < 0.05$ ) than that in the total sample (20%). The significant difference between non-active individuals (13%) and active ones (31%) ( $p < 0.05$ ) in February is actually biased by the proportion of females. Therefore, we conclude that there is no relationship between the stage of gonadal development and the percentage of foot nipping. This is corroborated by the logistic regression test, in which the sex did not show any influence on the probability of foot nipping.

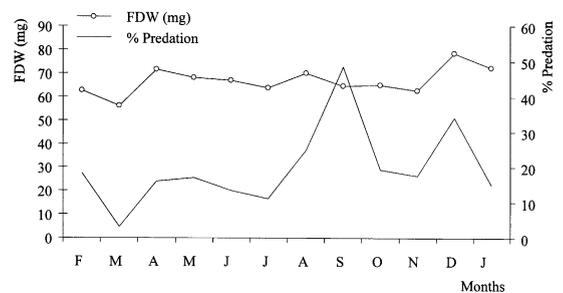


Fig. 5. Monthly percentages of foot nipping in *D. trunculus* during the year of study and flesh dry weight (biomass) variation in a standard individual of *D. trunculus* (25 mm long) during the year of study.

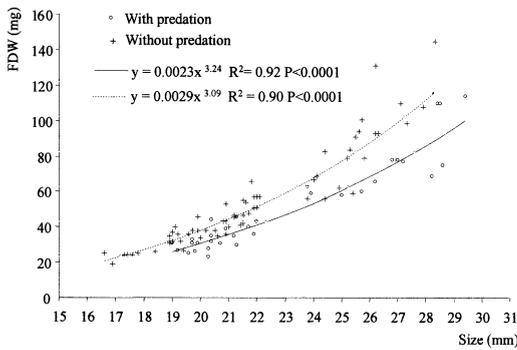


Fig. 6. Relationship between size and flesh dry weight for entire and foot nipped specimens of *D. trunculus* in December. Regression equations and their significance ( $p < 0.0001$ ) are given.

We did not find any correlation between the environmental variables (Fig. 3) and the monthly percentage of foot-nipping predation.

The data for December on flesh dry weight/size of individuals with and without predation are presented in Fig. 6. The foot-nipped clams generally have less biomass than the others. Table 5 shows the average weight by size class, eliminating the size classes in which there is only one nipped or only one intact specimen. The difference in biomass can be considered to be due to predation. The percentages of biomass lost by foot nipping generally reach more

Table 5

*Donax trunculus*. Loss of biomass due to foot nipping by size classes in December (resting reproductive stage). FDW = Average flesh dry weight of individuals with entire foot. FDWp = Average flesh dry weight of individuals with foot nipped. FDWL = Loss of flesh dry weight due to foot nipping. %Predation = Percentage of flesh dry weight of the average undamaged individual (FDW) lost by foot nipping. Size classes in which there is only one intact individual, or only one foot-nipped individual, have been omitted

Size classes	FDW (mg)	FDWp (mg)	FDWL (mg)	% Predation
18.5	32.17	31.00	1.17	3.63
19.5	36.33	28.83	7.50	20.64
20.5	40.86	33.14	7.71	18.88
21.5	49.50	37.40	12.10	24.44
22.5	55.00	43.00	12.00	21.82
25.5	83.86	59.00	24.86	29.64
26.5	98.75	72.00	26.75	27.09
27.5	105.67	77.50	28.17	26.66
28.5	145.00	91.00	54.00	37.24

Table 6

Effects of crabs on *D. trunculus* in aquaria. The specimens remaining alive at the end of the observations were opened to detect any possible damage of the foot (*Donax trunculus* Linnaeus, 1758)

Date	Crabs dead	Alive	Predated	Dead	Foot nipped
<i>Liocarcinus vernalis</i> (Risso, 1816)					
16/03/99		52	1		
17/03/99		51	1		
18/03/99	1	51			
19/03/99		48	2		1
21/03/99		43	2	3	
22/03/99	1	40	2		1
23/03/99		33	2	5	
24/03/99	1				
25/03/99		28		2	3
Total	3	28	10	10	5
<i>Portunus latipes</i> (Pennant, 1777)					
16/03/99	1	51			1
17/03/99		50		1	
18/03/99	1	50			
19/03/99		50			
21/03/99		48		2	
22/03/99		46		2	
23/03/99		44		2	
24/03/99	1	42		2	
25/03/99		34		1	7
Total	3	34	0	10	8
<i>Atelecyclus undecimdentatus</i> (Herbst, 1783)					
16/03/99		45			
17/03/99					
18/03/99		43			1
19/03/99		43			
21/03/99		42		1	
22/03/99		39		3	
23/03/99		34		2	2
24/03/99		33	1		
25/03/99		31	2		
Total		31	3	6	3

than 20%, and up to 37% in the largest size class. There is a positive correlation ( $r = 0.84$ ;  $p < 0.005$ ) between the size of the clam and the percentage of body loss by foot nipping.

### 3.3. Laboratory observations on crabs

The monitoring of predation on *D. trunculus* by decapods is shown in Table 6. The specimens remaining alive at the end of the observations were opened to detect any possible damage of the foot. Each of the

three species of crabs is capable of nipping the foot of *Donax* (Fig. 1); however, *Portunus latipes* (Fig. 1C) nipped more individuals. Of the eight nipped (Fig. 1D), seven were alive at the end of the experiment. *Liocarcinus vernalis* (Fig. 1E) nipped five, of which three were alive at the end of the experiment, while the other two were so damaged (with valves slightly open) that we removed them before they died and contaminated the water (Fig. 1F). *Portunus latipes* did not eat any clam entirely during the ten days of observation. In contrast, *L. vernalis*, ate ten specimens (Fig. 1G and H), preyed on by different mechanisms in addition to nipping: breakage of the anterior part of the shell (Fig. 1G), or slight breakage the posterior end of the shell, to introduce the chelae and to tear off or cut the posterior adductor muscle (Fig. 1H). *Atelecyclus undecimdentatus* (Fig. 1A) nipped three individuals, all very damaged with the valves slightly open (Fig. 1B). The specimen of *A. undecimdentatus* was a female with eggs, which usually eat less, but after a week it ate three specimens (Table 6). All the clams (damaged and undamaged) were able to bury themselves. Interestingly, the clams were often seen with their siphons extended, but these were not attacked by the crabs, nor did the clams retract the siphons when the crabs approached.

Several crabs of both portunid species died, presumably as a result of the continuous aggressions between them, sometimes involving the loss of claws (Fig. 1C). Mortality of *D. trunculus* was also observed in the three compartments, (Table 6). Possible causes are the stress of capture and transport, insufficient food, aggressions of the crabs, etc., but a similar number died in each compartment.

## 4. Discussion

### 4.1. Incidence of predation

There are few studies on the incidence of non-lethal or sub-lethal predation on bivalve populations, and such data always deal with the cropping or nipping of siphons. We could not find previous reports on the extent of damage caused by foot-nipping predators to the bivalve population in the field or in the laboratory.

Trevallion (1971) estimated from the study of stomach contents of flatfishes (0-group plaice) that

each specimen of *Tellina* lost a part of its siphons at least once during the summer in Firemore Bay. De Vlas (pers. obs., 2000) has estimated that an individual of *Macoma balthica* suffers three attacks on its siphons per day. Coen and Heck (1991) studied the incidence of siphon nipping in different habitats (sea grasses and sand) and localities; they found that the frequency of damaged siphons in field population of the venerid clam *Mercenaria mercenaria* (L.), in sea-grasses and adjacent sand areas, ranges from 4–11% in Massachusetts to 15–20% and 15–25% in Alabama/Florida and New Jersey, respectively. According to Ansell et al. (1999), between 2.5 and 18% of *D. vittatus* from a natural population of West Sands beach, St Andrews on the Scottish East coast, showed damages to the siphons caused by non-lethal predation by juvenile flatfishes. Predation of part of the siphon in the *Donax* spp. from the littoral of Málaga examined during this study was very rare (only one individual in some months).

The annual data of foot nipping on *Donax* populations obtained in the field in this study (Table 1) are in a similar range as the above siphon predation. However, if we take into account the monthly data for *D. trunculus* (Table 2), the percentages of foot-nipped individuals in September (48%) and December (34%) are higher than those of nipped siphons.

These data cannot be taken as the actual percentages of foot predation in the natural population, because specimens lacking part of the foot are expected to be less efficient in burying themselves than specimens with an intact foot, and therefore more easily collected with the dredge. However, the observations in the laboratory have demonstrated the ability of the foot-nipped clams to bury, because in the compartment of *Portunus latipes* (the ‘best nipper’) all the clams (with and without foot) were buried. Although we have no means of estimating this bias, we consider it to be the same throughout the year. Thus, the monthly variation of the percentages of foot nipping (Table 2, Fig. 5) is representative of the predatory activity over the year and its relationship with environmental or biotic factors.

The percentage of foot predation of *D. vittatus* from the French Atlantic coast (27%) is higher than that observed in May for the same species in Málaga (5%) (Table 2), and also higher than the percentage of siphon cropping by flatfishes in Scottish beaches

for this species (Ansell et al., 1999). Nevertheless, the percentages of foot nipping for *D. vittatus* in Ré Island are comparable to those observed in Málaga for *D. trunculus*. It is noteworthy that both populations are found within the depth interval where wave action is considerable, i.e. where the clams are continuously disturbed and need to bury themselves actively with their foot. Therefore, the *Donax* spp. which live in the surf zone are the fastest, taking just over one second to bury themselves completely (Vermeij, 1993). This does not apply to the populations of donacids living deeper, nor to most other bivalves living outside the surf zone. Thus, frequent exposure of the foot is interpreted as the factor which makes donacids of the surf zone particularly prone to foot nipping by crabs or fishes. The loss of part of the foot seems to be non-lethal for most donacids (such as those nipped by *P. latipes* in the laboratory), but some of the foot-nipped clams (such as those damaged by *L. depurator* and particularly by *A. undecimdentatus*) were severely damaged or died. It is difficult to know how many clams die in the field after being foot nipped, but even if they survive, they are more prone to predation because they have more difficulty burying themselves quickly after the disturbance caused by the waves in the surf zone. In this sense we could consider this type of predation to be sub-lethal.

#### 4.2. Regulating factors for predation

According to Ansell (1992) and Ansell et al. (1999) predation by flatfishes on *D. vittatus* in Scottish beaches is higher in summer, in correlation with the increases of temperature and peaks of recruitment of predators such as crabs or fishes. Freire and González-Gurriarán (1995) found that the predation of *Necora puber* on molluscs from mussel raft-culture areas in the Ría de Arousa (north-west Spain) increases in summer. However *Liocarcinus vernalis* from the same areas preys more in autumn and winter, which is the season of mussel reproduction and harvesting (Freire, 1996).

In the littoral of Málaga, we do observe an increase of foot predation (Fig. 5) from March to September, a period of rising temperature (Fig. 3), but the peak of predation in December coincides with a decrease of temperature. In fact, there is no correlation between percentage of foot nipping and seawater temperature,

and the logistic regression did not show any influence of this variable on the probability of foot nipping.

The peaks of predation do not accompany the clam's reproductive cycle either because in December the clams are in the resting period (cytolytic or pre-active stages) (Tirado and Salas, 1998), but nevertheless the percentage of foot-nipped individuals is high. Moreover, according to the logistic regression (Table 3) and the test of comparison of percentages, the sex did not interfere with the probability of foot nipping. Only in February were females more often selected.

The weight has a coefficient of  $-0.03$  ( $\exp(B) = 0.967$ ) in the logistic regression (Table 3), indicating a slightly negative influence on the probability of foot nipping. However, the monthly values of biomass of a standard individual coincide with the monthly percentage of foot nipping (Fig. 5), with strong decreases of both biomass and predation in March and strong increases in December. The peak of predation in September is peculiar, and coincides with a peak of recruitment of bivalves in the area studied (Tirado and Salas, 1999; pers. obs.), which probably attracts more predators. According to Ansell (1992), in the Scottish beaches there is in summer a recruitment of predators such as crustaceans and fishes which increases the incidence of predation. Sorbe (pers. comm.) has also observed in Hendaya beach (Bay of Biscay) a recruitment of portunids in the surf zone during summer. There is probably also a higher density of predators in Málaga in summer, but unfortunately no data are available. If we do not take into account September, there is a positive correlation ( $r = 0.76$ ,  $p < 0.01$ ) between the percentage of predation and flesh dry weight of the standard individual. The peak of foot-nipping predation in December is difficult to explain; the increase of biomass in the population is a possible cause. This means that if the biomass of most of the population is high (increases in the standard individual) there are more medium-sized individuals with a relatively large foot available for nipping. However, according to the logistic regression, the predators did not choose the heavier individuals (the heavier the specimens, the less probability of being nipped), possibly because they are the largest ones and thus buried deeper than the medium-sized ones.

According to the size class frequency (Fig. 4), and to Ivlev's index (Table 4), only the small size classes are avoided by the predator, while apparently any of

the remaining size classes are selected throughout the year. The avoidance of the small size classes makes length the most important variable in the logistic regression (Table 3). However, there was no significant difference between the lengths of damaged and undamaged individuals. This, together with the data of Ivlev's index, could mean that predators attack whatever size is available above a particular threshold, probably according to their own sizes.

Surprisingly, chlorophyll *a* was the third variable implied, with a value of coefficient ( $B = -0.36$   $\exp(B) = 0.70$ ) in the logistic regression (Table 3), but it has a negative influence on the probability of foot nipping, as has weight. This environmental variable was inversely correlated with the monthly changes in flesh dry weight/length in *D. venustus* and *D. semistriatus* (Tirado and Salas, 1999) explaining 42 and 79%, respectively, of the monthly changes. However, in *D. trunculus*, chlorophyll *a* is not correlated with the monthly changes in flesh dry weight, nor with the standard individual.

#### 4.3. Loss of biomass

The literature data on the amount of flesh dry weight removed in sublethal predation on bivalves regard only siphon cropping. According to Zwarts and Wanink (1989) the relative weights of the siphons from different species show a significant increase with burying depth: ca. 1–2% in *Cerastoderma*; ca. 4% in *Macoma*; ca. 5–9% in *Scrobicularia*. According to P. Edelaar (pers. comm., 2000) in *Mya arenaria* it is ca. 35%. If the amount of siphon nipped is under 15% (between 0 and 6 mg in *Scrobicularia plana*) the energetic cost is low, but if the weight removed is over 50%, (between 13 and 19 mg in *Scrobicularia plana*) the survival of the animal is low, and the regeneration in survivors is made at the expense of somatic growth (Hodgson, 1982; Zwarts, 1986). We could not find previous reports on the amount of weight removed by foot nipping; the data obtained in the natural population of *D. trunculus* from the littoral of Málaga in December (Table 5, Fig. 6) indicate that this type of predation removes more flesh dry weight (between 1.17 mg in small sizes to 54 mg in the largest size) than siphon cropping. The flesh dry weight removed is ca. 3.5–37% of body dry weight (Table 5), but in most size classes it is above 20%. A positive correlation

( $r = 0.84$ ;  $p < 0.005$ ) between size and the percentages of body loss by foot nipping indicates that the biomass removed increases with size. These data together with the high percentages of individuals of *D. trunculus* collected with a nipped foot (Tables 1 and 2) imply a considerable loss of biomass in the sandy shore donacids. The actual amount is probably higher, considering that some recovery takes place, because the foot-nipped individuals collected during this study were alive and some signs of healing and recovery were observed in all of them.

#### 4.4. Which are the predators?

In their experiment, Ansell et al. (1999) have considered only flatfishes as possible foot-nipping predators, but in the Málaga sites studied for *D. trunculus*, the bottom at 1–3 m depth consisted of medium sand mixed with stones, and crustaceans (*Liocarcinus vernalis* and *Portunus latipes*) were the principal predators captured with the clams. Flatfishes were rarely caught, although the dredge was adequate to capture them. Crab predation is not a novel observation, but it is usually associated with the crushing of shells; our aquarium observations demonstrated the ability of *Portunus* to snap at the foot without visibly damaging the shell. The shells of foot-nipped donacids studied from the littoral of Málaga did not usually show signs of breakage.

*D. venustus*, *D. semistriatus* and *D. vittatus* were sampled at about 5 m depth in a bottom of fine sand. There we found the above crabs but also flatfishes of the genera *Arnoglossus*, *Bothus* and *Buglossidium*. However, we have not analysed the stomach contents of these flatfishes.

For *D. vittatus* in Ré Island, the possible predators are again decapods. Particularly the portunids (*Carcinus maenas*, *Portunus latipes*, *Liocarcinus vernalis*) were very abundant in the shallow subtidal zone (P. Noel, pers. comm. 1999), and thus are likely foot-nipping predators probably together with the flatfishes, for which no data are available. According to Ansell (1992), tissue remains of *D. vittatus* from Scottish beaches have also been found in the stomachs of the portunid crabs *Liocarcinus holsatus* (Fabricius) and *Carcinus maenas* (L.).

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