



ELSEVIER

Journal of Experimental Marine Biology and Ecology 325 (2005) 27–34

**Journal of  
EXPERIMENTAL  
MARINE BIOLOGY  
AND ECOLOGY**

www.elsevier.com/locate/jembe

# Trophic facilitation by the oystercatcher *Haematopus palliatus* Temminick on the scavenger snail *Buccinanops globulosum* Kiener in a Patagonian bay

Pedro Daleo<sup>a,b,\*</sup>, Mauricio Escapa<sup>b,c</sup>, Juan Pablo Isacch<sup>a,b</sup>,  
Pablo Ribeiro<sup>a,b</sup>, Oscar Iribarne<sup>a,b</sup>

<sup>a</sup>Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, Funes 3250, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina

<sup>b</sup>Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

<sup>c</sup>Instituto Argentino de Oceanografía (IADO), Argentina

Received 25 August 2004; received in revised form 4 April 2005; accepted 7 April 2005

## Abstract

This study investigated the role of the American oystercatcher (*Haematopus palliatus*) as a resource subsidizer for the scavenger snail *Buccinanops globulosum* in a northern Patagonian bay (40°45'S, 64°56'W, San Antonio Bay, Argentina). The most frequent food item for the snails was dead crabs *Cyrtograpsus angulatus* Dana, and the snails preferred this item. In the field, most dead crabs (78%) resulted from oystercatcher predation. Field densities of dead crabs were within the 95% confidence limits of the estimated densities produced by oystercatcher foraging activity, suggesting that a large proportion of carrion available for snails is a byproduct of oystercatcher predation. Dead crabs with injuries were more rapidly detected and consumed by snails, probably because injuries produced by oystercatchers increase leakage of body fluids and facilitate penetration of the proboscis of the snails. Our results suggest that oystercatcher predation subsidize this scavenger snail by increasing availability of food, decreasing variability in their provision and facilitating their consumption.

© 2005 Elsevier B.V. All rights reserved.

**Keywords:** Oystercatcher; Scavengers; Snails; Source subsidizer; Trophic facilitation

## 1. Introduction

Trophic facilitation is a common phenomenon in food-webs (Wilmers et al., 2003a). Most studies on trophic facilitation focus on the capacity of a predatory species to increase the availability of prey to another predatory species (Korpimäki et al., 1996;

\* Corresponding author. Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, Funes 3250, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina. Tel.: +54 223 475 3150.

E-mail address: pdaleo@mdp.edu.ar (P. Daleo).

de Goeij et al., 2001). However, much less is known about the potential for predators to subsidize scavenger species by supplying them with carrion. In natural environments, predation is probably the most significant source of corpses that are at least partially available as carrion and scavengers have the ability to take nutritional benefits from this carrion (Britton and Morton, 1994). Recent studies have shown that top predators can have strong positive effects on scavenger species by increasing the availability of carrion and affecting its physical and temporal distribution (Rochette et al., 1995; Wilmers et al., 2003a,b).

On intertidal sand-flats, corpses of resident and nonresident organisms are rapidly detected and consumed by scavengers such as nassariid gastropods (Morton and Jones, 2003). However, carrion that is available to intertidal and marine scavengers is ephemeral and unpredictable (Britton and Morton, 1994). Thus, carrion availability may limit (Britton and Morton, 1994) snail growth (McKillup and McKillup, 1997), reproduction (McKillup and Butler, 1979; Rochette et al., 2001) and, eventually, population size (Rochette et al., 1995; Morton and Chan, 1999).

*Buccinanops globulosum* is an intertidal nassariid gastropod endemic to the SW Atlantic and distributed from La Plata River (Samborombon Bay; 36°22'S, 56°45'W) to Southern Patagonia (53°S, 68°W, Argentina; Pastorino, 1993). Along this coastline, American Oystercatchers (*Haematopus palliatus*) forage on the intertidal grapsid crab *Cyrtograpsus angulatus*, mainly consuming the eggs of ovigerous females and occasionally consuming viscera of males (Bachmann and Martinez, 1999). This is a relatively large crab (up to 60 mm carapace width) that is distributed from southern Brazil to the southern tip of South America (Iribarne et al., 2003). In order to consume crab eggs, oystercatchers stab the center of the pleon with their bill, thus killing the crabs and leaving a characteristic mark on the corpse (Bachmann and Martinez, 1999). Because the body of the crab is not consumed by oystercatchers (Bachmann and Martinez, 1999), this activity generates carrion for other consumers (e.g., birds such as the Chimango caracara *Milvago chimango*; Biondi et al., 2005.). Per capita feeding rate of *H. palliatus* on crabs can reach values of 60 crab h<sup>-1</sup> (Bachmann, 1995). Because of this high rate of carrion production, and the type of injuries made on

the exoskeleton of the crab, we hypothesized that the feeding habit of *H. palliatus* can increase the food availability to *B. globulosum*.

The objective of this work was to evaluate the importance of carrion produced by *H. palliatus* on *B. globulosum* diet, and to determine whether the partial processing of crabs by *H. palliatus* facilitates food detection and consumption by *B. globulosum*.

## 2. Methods

### 2.1. Study site

Field experiments and observations were performed in San Antonio Bay, Argentina (40°45'S, 64°56'W) from September 2003 to March 2004. This is an 80 km<sup>2</sup> embayment located at northern Patagonia, affected by a semidiurnal tidal regime (up to 9 m tidal amplitude) and characterized by extensive intertidal flats (see Iribarne, 1990), which are surrounded by marshes dominated by *Spartina alterniflora*. This area is an important conservation site being part of the Western Hemisphere Shorebird Reserve Network International (WHSRNI) given their importance as stopover site for Neotropical migratory shorebirds (González et al., 1996).

### 2.2. Snail feeding, food availability and source

The importance of oystercatchers as source subsidizers may depend on the feeding habits of the snails. To evaluate the type of carrion used by *B. globulosum*, 50 transects (40 m long, 4 m width) were sampled along the intertidal zone during low tide. In each transect, clusters of *B. globulosum* (Nassariids snails usually form feeding aggregations; see Ansell, 2001) were detected and the carrion being consumed was identified. To evaluate if *B. globulosum* prefer particular types of carrion, a field experiment was performed. In this experiment, 20 dead individuals of the 5 dominant intertidal invertebrate species (the small mussel *Brachidontes rodriguezii* (d'Orbigny), the burrowing crab *Chasmagnathus granulatus* Dana, the mud crab *Cyrtograpsus angulatus*, the chiton *Chaetopleura isabellei* (d'Orbigny) and the limpet *Fissurella radiosa tixierae* (Metivier) that are potentially available as car-

rion (P. Daleo, personal observation) were randomly deployed (minimal distance between items (dead individuals)=50 m) along the intertidal during the ebbing tide. The presence or absence of snails was determined after 20 min. The null hypothesis of no preference for any type of carrion was analyzed using  $\chi^2$  test (Zar, 1999).

To determine the proportion of carrion available to *B. globulosum* that is produced as a result of predation by *H. palliatus*, the number of dead crabs with and without oystercatcher injuries was determined in 28 sampling units (quadrants of 2 × 2 m) that were randomly taken along the low intertidal during low tide. In addition, to determine whether the number of dead crabs is constant among different tidal cycles, 145 samples of 2 × 2 m were randomly taken along the intertidal over 9 consecutive days in December (2nd to 10th 2003) and January (23rd to 31st 2004). The number of dead crabs was determined in each sample. The null hypothesis of no difference in the number of dead crabs between days was analyzed with one-way ANOVA (Zar, 1999).

### 2.3. Estimation of carrion production by oystercatchers

Carrion production was estimated indirectly, by estimating the density and feeding rate of oystercatchers. The density of oystercatchers was estimated as follows: 174 transects (100 m long, 10 m wide) were performed along the low intertidal during multiple low tides. The number of oystercatchers in each transect was counted. To estimate feeding rate, 50 focal observations (telescope 18 × 36; total observation time=277.92 min) of oystercatchers were performed during the study period (at least 50 m apart from the observed area, each bird was observed for 5–10 min) and, the duration of observation and the number of crabs consumed was recorded. Then, to estimate carrion production, the frequency distribution of mean densities of dead crabs was generated by bootstrapping (1000 iteration, 28 oystercatcher density data and 28 oystercatcher foraging rate data). Carrion production (density of dead crabs) was then estimated as oystercatcher density \* foraging rate \* 6 h of foraging time (6 h of uncovered intertidal).

### 2.4. Food detection by snails

Food detection by snails may not only depend on the prey type, but also on the presence of injuries (Evans et al., 1996). Injuries produced as a result of oystercatcher predation may increase the leakage of body fluids. To evaluate whether the presence of injuries influences the time it takes for snails to arrive to a crab corpse, 100 individuals of *C. angulatus* were collected. Crabs were frozen at  $-4$  °C and, after 1 day, defrosted. Injuries similar to those produced by oystercatcher (circular perforation on the pleon, ~5 mm diameter) were made in 50 of the collected crabs. The remaining 50 crabs were maintained with the exoskeleton intact. Dead crabs were randomly located in the low intertidal. The period of time (seconds) between crab deployment and the arrival of the first snail to the crab was recorded. The null hypothesis of no differences in the time that snails arrive to crabs with and without injuries was analyzed with a *t*-test (Zar, 1999). Although freezing and subsequent thawing can generate carapace damages and increase the leakage of body fluids, the fact that this process is done to all treatments may not affect the comparisons.

The injuries produced by oystercatchers may also increase the number of snails that can detect the corpse. The same experimental design was used to evaluate whether there are differences in the number of snails that detect crabs with and without injuries. The number of snails feeding on crabs was determined at two separate times: 5 and 10 min after crab deployment (15 per treatment). The null hypotheses of no differences in the number of snails feeding on crabs with and without injuries for both times were analyzed with *t*-test (Zar, 1999).

### 2.5. Food consumption by snails

The presence of injuries in the exoskeleton of crabs can facilitate the consumption of corpses by snails because the soft parts may be more accessible to their proboscis. A field experiment was performed to evaluate if there are differences in the rate at which crabs with and without injuries are consumed. Four groups of 30 dead crabs were formed (all groups had similar carapace size distribution and sex ratios) and each group was assigned to one of four treatments

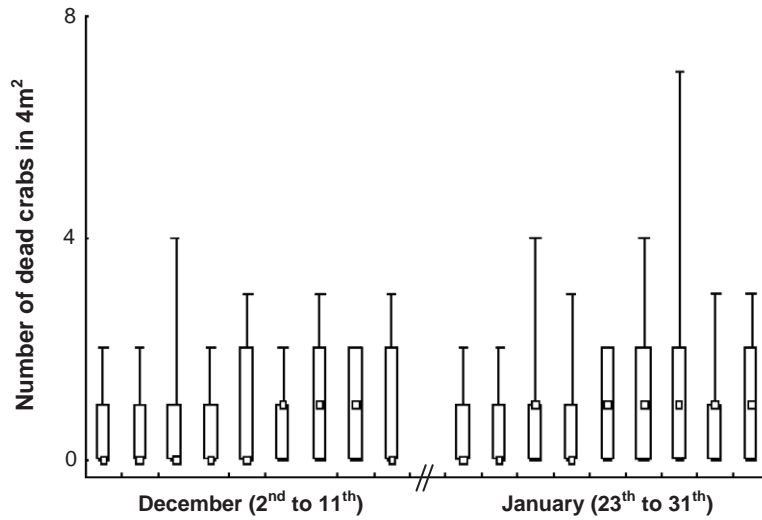


Fig. 1. Number of dead crabs within  $2 \times 2$  m sampling units. Here and thereafter limits of the boxes represent 25th and 75th percentiles, lines represent 1st and 99th percentiles, and points inside boxes represent medians.

that were conducted in the low intertidal: (1) Crab with injuries (circular perforation on the pleon,  $\sim 5$  mm diameter, similar to those produced by oystercatchers) allowing *B. globulosum* to feed for 20 min; (2) Crab without injuries allowing *B. globulosum* to feed for 20 min; (3) Crab with injuries deployed for 20 min with removal of *B. globulosum* before feeding; and (4) Crab without injuries, deployed for 20 min with removal of *B. globulosum* before feeding. Treatments (3) and (4) were designed to detect if differences in dry weight were only due to snail

feeding. These crabs were recovered after the experimental trial and their dry weight (dried at  $70^\circ\text{C}$  for 48 h) and carapace width were measured (carapace width was measured because size of crabs may affect the rate of consumption and the proportion of mass that can be consumed). The null hypothesis of no difference in dry weight between treatments was analyzed with ANCOVA (Zar, 1999) with carapace width as covariate. Because crabs of all treatments were deployed in a relatively small area, snail activities were very high and there were no apparent

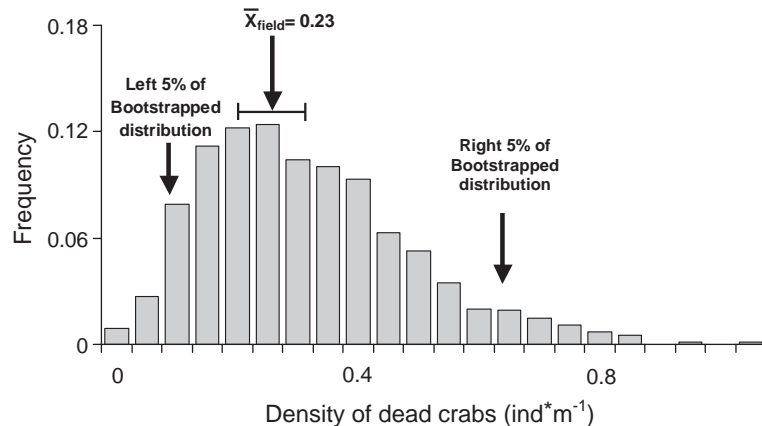


Fig. 2. Frequency distribution of mean density of dead crabs, calculated by bootstrapping the product of oystercatcher densities and foraging rates data.

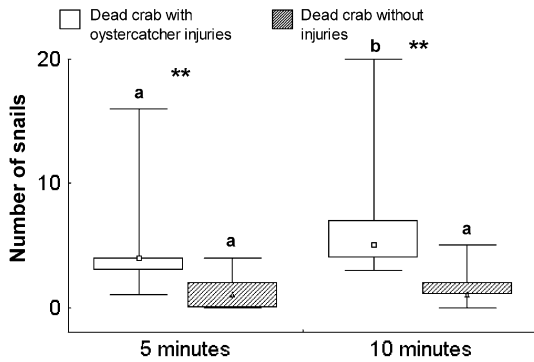


Fig. 3. Number of *Buccinanops globulosum* feeding on dead crabs with and without injuries after 5 and 10 min of depletion. The symbol \*\* represent significant differences ( $P < 0.01$ ) between treatments for the same time and different letters represent significant differences between times for the same treatment.

differences in the number of snails per crab in treatments (1) and (2).

### 3. Results

#### 3.1. Snail feeding, food availability and source

In 75% of the feeding clusters sampled ( $n = 43$ ), the carrion was the crab, *Cyrtograpsus angulatus*. In the preference experiment, after 20 min, *Buccinanops globulosum* was present on all ( $n = 20$ ) crabs of both species (*Chasmagnathus granulatus* and *C. angulatus*), in 80% of small mussels (*Brachidontes rodri-*

*guezi*), 45% of the limpets (*Fissurella radiosa tixierae*) and none on the chitons (*Chaetopleura isabellei*). There was a significant preference for crushed crabs (Chi-square,  $\chi^2 = 64.18$ ,  $df = 4$ ,  $P < 0.001$ ). The density of dead crabs was  $0.7$  (S.D. =  $0.53$ ) corpses  $m^{-2}$  and the number of crabs with oystercatcher injuries was higher than the number of dead crabs without injuries ( $\bar{x}_{injuries} = 0.53$ , S.D. =  $0.38$  vs.  $\bar{x}_{without} = 0.16$ , S.D. =  $0.25$ ;  $t_{dependent} = 5.41$ ,  $df = 27$ ,  $P < 0.001$ ), corresponding to 78% of the total. There was no difference in the density of dead crab between days (ANOVA,  $F_{17,252} = 0.65$ ,  $P > 0.8$ ; Fig. 1).

#### 3.2. Estimation of carrion production by oystercatchers

The density of *Haematopus palliatus* averaged 11 (S.D. = 32) individuals  $ha^{-1}$ . Its feeding rate was  $58.65$  crab  $h^{-1}$  (95% confident limits: 46.87–70.43). The observed frequency of dead crabs with oystercatcher injuries using the day sequences data ( $\bar{x} = 0.23$  crabs  $m^{-2} day^{-1}$ ) was within the 95% confidence limits of the frequency distribution of the mean number of dead crabs generated by bootstrapping ( $0.263$  crabs  $m^{-2} day^{-1}$ , 95% confident limits: 0.064–0.631; Fig. 2).

#### 3.3. Food detection by snails

The period between crab deployment and arrival of the first snail was shorter in dead crabs with injuries compared to those without injuries ( $\bar{x}_{injuries} = 95.08$

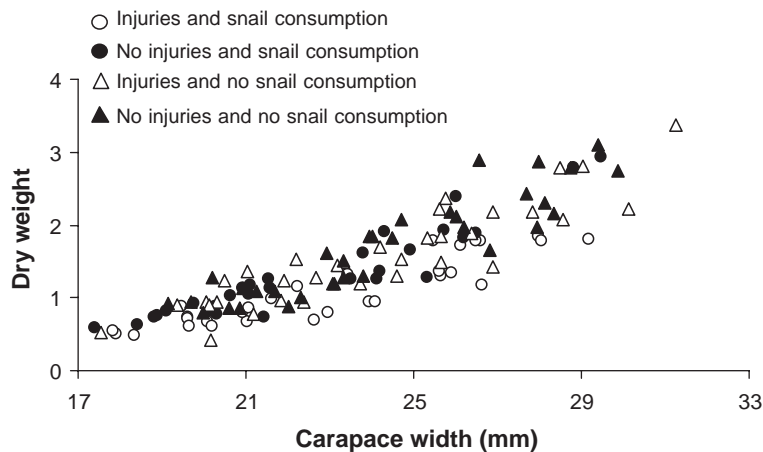


Fig. 4. Dry weight of crabs of different treatments in relation to their carapace width.

(72.6);  $\bar{x}_{\text{without}}=511.02$  (309.84); log transformed data,  $t=10.22$ ,  $df=98$ ,  $P<0.001$ ).

The number of snails feeding on individual crabs was higher for crabs with oystercatcher injuries than for crabs without injuries at both times (5 min:  $t=3.524$ ,  $df=28$ ,  $P<0.005$  and 10 min:  $t=3.326$ ,  $df=28$ ,  $P<0.005$ ; Fig. 4). The number of snails feeding on crabs with oystercatcher injuries was higher at 10 min than at 5 min after deployment ( $t_{\text{paired}}=3.326$ ,  $df=14$ ,  $P<0.005$ ; Fig. 3), but there was no difference in the number of snails on crabs without injuries between 5 and 10 min after deployment ( $t_{\text{paired}}=2$ ,  $df=14$ ,  $P>0.05$ ; Fig. 3).

While feeding on crabs with oystercatcher injuries, 96% of the snails reached the soft parts by introducing their proboscides through the injuries, whereas 4% did not reach the soft parts. On crabs without injuries, only 41.5% of the snails reached the soft parts by introducing their proboscis through the mouth parts (29.0%) or through the articulations of autotomized legs (12.5%). The rest of the snails on uninjured crabs (58.5%) were not able to reach the soft parts.

### 3.4. Food consumption by snails

The dry weight of crabs after snail feeding differed among treatments (ANCOVA,  $F_{3,115}=14.296$ ,  $P<0.001$ ; Fig. 4). It was lower in crabs with injuries than in crabs without injuries (i.e., treatment 1 < treatment 2, LSD post ANCOVA). The dry weight of crabs consumed by snails (either injured or not) was lower than those of the crabs not consumed by snails (i.e. treatment 1 < treatment 3 and treatment 2 < treatment 4, LSD post ANCOVA).

## 4. Discussion

Our results show that a large proportion of the diet of the intertidal snail *Buccinanops globulosum* is composed of carcasses of the dominant intertidal crab species, *Cyrtograpsus angulatus* and *Chasmagnathus granulatus* (Iribarne et al., 2003), which are supplied by oystercatcher predation on eggs of these crab species. In addition, *B. globulosum* preferred dead crabs over other food items. The large proportion of dead crabs in the intertidal showing evidence of *H.*

*palliatus* predation suggests that most crab corpses resulted from *H. palliatus* predation. In fact, the densities of dead crabs observed in the field are within the 95% confidence limits of the estimated rates of carrion production due to oystercatcher foraging. Britton and Morton (1994) proposed that a great proportion of produced corpses are the result of predation and partial consumption, because death as a natural consequence of aging is unlikely. Indeed our results suggest that in this Patagonian bay the main source of corpses is due to oystercatcher predation.

One of the main disadvantages of scavenger organisms is that carrion is usually unpredictable (Britton and Morton, 1994) or highly variable over time (Wilmer et al., 2003a). However, in our case densities of crab corpses were consistent over different low tides and along time. Thus, predation of crabs by oystercatchers may not only increase carrion levels but also make it more predictable. Oviparous females of *C. angulatus* were present during the entire study period, and there is evidence they are present throughout the year at this site (T. Luppi, personal communication). In addition, oystercatchers forage not only upon oviparous females of *C. angulatus* but also upon males of this species and individuals of *C. granulatus*, consuming mainly their viscera and, as upon females, leaving the rest of the body (Bachmann and Martinez, 1999). Thus, because birds are present year round and do not seem to be changes in their diets (P. Daleo, personal observation), all evidence suggests that oystercatcher production of corpses may be stable year round.

Dead crabs with injuries, like those produced by the oystercatcher, were detected more rapidly and by more individuals than those without injuries. The injuries may increase the amount of body fluids leaking from the corpse and thus increase chemical cues for this nassariid species (Morton and Jones, 2003). Dead crabs with injuries were also more rapidly consumed. The presence of holes in the exoskeleton facilitates penetration of the proboscis making soft tissues more accessible. A large detection capacity and rapid consumption rate are common features of nassariid species (Morton, 1990) and allow them to outcompete other scavengers (Morton and Yuen, 2000). Very efficient detection capacity and a rapid consumption rate are also seen in *B. globulosum*, and this feature may allow them to detect and consume dead crabs faster than other species capable of con-



suming carrion (crabs of the species *C. granulatus* and *C. angulatus* are facultative scavengers and consumed dead crabs; P. Daleo, personal observation).

Several studies have shown that the activities of benthic predators and bioturbators can rapidly attract scavenger organisms (Oliver et al., 1985; Evans et al., 1996), and nassariid gastropods are reported to aggregate in the vicinity of invertebrate predators feeding on bivalves and stealing prey fragments (Rochette et al., 1995, 2001). However, the importance of predators as carrion makers and thus their effect on scavenger organisms as another form of trophic facilitation has only recently been noted (Wilmers et al., 2003a). The availability of carrion usually influences nassariid snails and, increases in food supply affect their fecundity, growth and population density (McKillup and Butler, 1979; Rochette et al., 1995; McKillup and McKillup, 1997; Morton and Chan, 1999). In some cases, large biomasses of nassariid species are supported by their associations with predators that increase food supplies (Rochette et al., 1995). Although we have not tested the hypothesis, a predator that increases levels of carrion and facilitate its consumption may positively affect scavenger species by increasing survival and reproduction. Our results strongly suggest that oystercatchers have a substantial effect on this nassariid species by increasing availability of carrion.

## Acknowledgements

We thank the staff of the Instituto de Biología Marina y Pesca “Alte. Storni” (San Antonio Oeste), particularly to Dr. M. Narvarte, for facilitating the use of their facilities. This article benefited from the critical reading of Julie C. Ellis and two anonymous referees. This project was partially supported by Universidad Nacional de Mar del Plata, CONICET and Fundación Antorchas (Grant 13900-13; all granted to O.I.). P.D., M.E., J.P.I. and P.D.R. were supported by fellowships from CONICET (Argentina). [AU]

## References

- Ansell, A.D., 2001. Dynamics of aggregations of a gastropod predator/scavenger on a New Zealand harbor beach. *J. Molluscan Stud.* 67, 329–341.
- Bachmann, S., 1995. Ecología alimentaria del Ostrero Pardo (*Haematopus palliatus*) en la Albufera Mar Chiquita. Licenciature thesis, Universidad Nacional de Mar del Plata, Argentina. 41 pp.
- Bachmann, S., Martinez, M., 1999. Feeding tactics of the American oystercatcher (*Haematopus palliatus*) on Mar Chiquita coastal lagoon, Argentina. *Ornitol. Neotrop.* 10, 81–84.
- Biondi, L.M., Bo, M.S., Favero, M., 2005. Dieta del Chimango (*Milvago chimango*) durante el período reproductivo en el sudeste de la provincia de Buenos Aires, Argentina. *Ornitol. Neotrop.* 16, 31–42.
- Britton, J.C., Morton, B., 1994. Marine carrion and scavengers. *Oceanogr. Mar. Biol.: Ann. Rev.* 32, 369–434.
- de Goeij, P., Luttikhuisen, C.L., van der Meer, J., Piersma, T., 2001. Facilitation on an intertidal mudflat: the effect of siphon nipping by flatfish on burying depth of the bivalve *Macoma balthica*. *Oecologia* 126, 500–506.
- Evans, P.L., Kaiser, M.J., Hughes, R.N., 1996. Behaviour and energetics of whelks, *Buccinum undatum* (L.), feeding on animals killed by beam trawling. *J. Exp. Mar. Biol. Ecol.* 197, 51–62.
- González, P.M., Piersma, T., Verkuil, Y., 1996. Food, feeding, and refuelling of Red Knots during northward migration at San Antonio Oeste, Rio Negro, Argentina. *J. Field Ornithol.* 67, 575–591.
- Iribarne, O.O., 1990. Use of shelter by the small Patagonian octopus *Octopus tehuelchus*: availability, selection and effects on fecundity. *Mar. Ecol. Prog. Ser.* 66, 251–258.
- Iribarne, O., Martinetto, P., Schwindt, E., Botto, F., Bortolus, A., Garcia Borboroglu, P., 2003. Evidences of habitat displacement between two common soft-bottom SW Atlantic intertidal crabs. *J. Exp. Mar. Biol. Ecol.* 296, 167–182.
- Korpimäki, E., Koivunen, V., Hakkarainen, H., 1996. Microhabitat use and behavior of voles under weasel and raptor predation risk: predator facilitation? *Behav. Ecol.* 7, 30–34.
- McKillup, S.C., Butler, A.J., 1979. Modification of egg production and packaging in response of food availability by *Nassarius pauperatus*. *Oecologia* 43, 222–231.
- McKillup, S.C., McKillup, R.V., 1997. The effect of supplemental feeding on the growth of an intertidal scavenger. *Mar. Ecol. Prog. Ser.* 148, 109–114.
- Morton, B., 1990. The physiology and feeding behaviour of two marine scavenging gastropods in Hong Kong: the subtidal *Babylonia lutosa* (Lamarck) and the intertidal *Nassarius festivus* (Powys). *J. Molluscan Stud.* 56, 275–288.
- Morton, B., Chan, K., 1999. Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gasteropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. *J. Exp. Mar. Biol. Ecol.* 240, 213–228.
- Morton, B., Jones, D.S., 2003. The dietary preferences of a suite of carrion-scavenging gastropods (Nassariidae, Buccinidae) in Princess Royal Harbour, Albany, Western Australia. *J. Molluscan Stud.* 69, 151–156.
- Morton, B., Yuen, W.Y., 2000. The feeding behaviour and competition for carrion between two sympatric scavengers on a sandy shore in Hong Kong: the gastropod, *Nassarius festivus* (Powys)

- and the hermit crab, *Diogenes edwardsii* (De Haan). J. Exp. Mar. Biol. Ecol. 246, 1–29.
- Oliver, J.S., Kvitek, R.G., Slattery, P.N., 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. J. Exp. Mar. Biol. Ecol. 91, 233–246.
- Pastorino, G., 1993. The taxonomic status of *Buccinanops* d'Orbigny, 1841 (Gasteropoda: Nassariidae). Veliger 36, 160–165.
- Rochette, R., Morissette, S., Himmelman, J.H., 1995. A flexible response to a major predator provides the whelk *Buccinum undatum* L. with nutritional gains. J. Exp. Mar. Biol. Ecol. 185, 167–180.
- Rochette, R., Tétreault, F., Himmelman, J.H., 2001. Aggregation of whelks, *Buccinum undatum*, near feeding predators: the role of reproductive requirements. Anim. Behav. 61, 31–41.
- Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003a. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. J. Anim. Ecol. 72, 909–916.
- Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W., Getz, W.M., 2003b. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in greater Yellowstone. Ecol. Lett. 6, 996–1003.
- Zar, J.H., 1999. Biostatistical Analysis, 4th edition. Prentice Hall, Englewood Cliffs, NJ.