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Effects of predation risk on survival, behaviour and morphological traits of small juveniles of *Concholepas concholepas* (loco)

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ABSTRACT: In marine systems, water-borne chemical cues may induce anti-predator responses that influence not only performance and survival of the prey, but also population dynamics and species interaction. The early life stages of marine species with complex life-cycles settle into unpredictable habitats, and therefore may be expected to exploit reliable chemical cues emanating from both prey and predators in order to promote plastic responses to the local conditions. We compared the behavioural responses, survival and growth of early ontogenetic stages of *Concholepas concholepas* exposed to the risk of predation by natural predators that commonly co-occur with it in the intertidal: the crabs *Homalaspis plana* and *Acanthocyclus hassleri* and the asteroid *Heliaster helianthus*. Y-maze experiments indicated that *C. concholepas* use water-borne cues both to detect prey and deploy strong anti-predator behaviour. Our results indicate lower survival rates of small specimens of *C. concholepas* when they were maintained in the direct presence of predators rather than under control conditions. Similar results and growth inhibition were found with *C. concholepas* exposed to seawater in which the predators had been maintained. Quantification of feeding activity and shell thickness in response to predation risk indicated lower prey consumption and thicker shells when *C. concholepas* were exposed to crab odours compared to control conditions. Our results suggest that this behavioural receptiveness to water-borne cues may be responsible, in part, for the early plasticity of species with complex life-cycles such *C. concholepas* under natural conditions, facilitating predator avoidance and thus enhancing survival.

KEY WORDS: Escaping behaviour · Foraging · Growth · Survival · Water-borne cues · Risk-sensitive

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INTRODUCTION

Predator-prey interactions play an important role in structuring marine communities (Paine 1966, Menge & Lubchenco 1981). Prey selection, predator detection and avoidance are essential responses for the survival of any species. However, due to the complexities of trophic relationships in ecological systems, their adaptive role is not well understood. Prey may respond to predators or damaged conspecifics by changing physiological, morphological and behavioural responses (Harvell 1984, 1990, Appleton & Palmer 1988, Palmer 1990). During early life stages, meroplanktonic marine species with complex life-cycles disperse and settle into uncertain benthic habitats, where they must find prey and

confront local predators. Many of these responses are induced by cues or odours emanating from predators or prey (Lindquist 2002). In general terms, scent and odours emanating from attacked or consumed prey provide the necessary 'alarm cue' about predation risk, and several studies have demonstrated that prey can discriminate among risks from different predators and attack strategies (Bourdeau 2009). Studies focused on anti-predatory behaviour also report that prey can resolve predator risk due to chemical 'labels' in the predator diet (Jacobsen & Stabell 2004). Therefore, there is a complex interaction between cues emanating from predators and prey (conspecific and heterospecific), and both can induce an adequate behavioural response in a prey species to minimize predation risk (e.g. Alexander & Covich 1991).

The ability of benthic marine invertebrates to respond to odour cues is widely documented (Castilla 1972, Díaz et al. 1999, Chiussi et al. 2001), and should be more important in aquatic gastropods that lack visual systems capable of resolving the details of complex natural seascapes. The predatory marine gastropod *Concholepas concholepas* is an important component of the intertidal and subtidal communities along the Pacific coast of South America (Castilla 1979). In intertidal habitats, the presence of early settlers and juveniles of *C. concholepas* is restricted to microhabitats dominated by their potential prey such as mussels and barnacles (Guisado & Castilla 1983, Moreno et al. 1993, Manríquez et al. 2009). In these habitats, crabs and starfish are among the potential predators to which *C. concholepas* are exposed during their early ontogeny. The intertidal predatory crabs *Acanthocyclus hassleri*, *A. gayi*, *Homalaspis plana* and the asteroid *Heliaster helianthus* are commonly found, together with settlers and juveniles of *C. concholepas*, inhabiting intertidal and shallow subtidal microhabitats (Paine et al. 1985, Navarrete & Castilla 1988, 1990, Navarrete & Manzur 2008). Similarly, they coexist with *Perumytilus purpuratus* mussel beds and stands of the barnacles *Balanus laevis* and *Notobalanus flosculus*, which are common prey items consumed by *C. concholepas* (Manríquez et al. 2009). Therefore, in this particular habitat, the behavioural responses of *C. concholepas* to chemical cues emanating from predators and prey may play an important role in detecting both the appropriate food and the presence of predation risk during their early ontogeny.

The potential effect of these cues in modifying the performance and survival of small settlers of *Concholepas concholepas* has been the subject of few stud-

ies (Manríquez et al. 2009). Although the presence of prey and predators can determine the temporal and spatial distribution of early settlers of *C. concholepas* in nature, little information regarding this topic is available. For instance, the exposure of *C. concholepas* to effluent from a higher-order predator, the subtidal asteroid *Meyenaster gelatinosus*, alters their foraging behaviour: juveniles exhibited a reduction in foraging time by switching their attention to smaller mussels, and larger specimens exposed to effluent from the same asteroid reduced the number of attacks on mussels (Serra et al. 1997). The 3-way ecological system involving prey (mussels and barnacles), a keystone predator (*C. concholepas*), and 2 predators (crabs and asteroid) suggests that settlers of *C. concholepas* may show a positive response to their prey and a negative response to predators inhibiting their settlement behaviour. The former is supported by the fact that under laboratory conditions, prey such as small barnacles and mussels induce settlement and metamorphosis in this species (DiSalvo & Carriker 1994, Manríquez et al. 2004). Moreover, under natural and laboratory conditions, *C. concholepas* forages at night and away from refuges (Castilla & Guisado 1979, Dubois et al. 1980), which suggests that foraging in this species is concentrated in periods where there is a low risk of predation by visual predators. Furthermore, recent evidence suggests that shell colouration in early settlers and juveniles of *C. concholepas* is determined by the colour of the consumed prey, which, in turn, is an effective mechanism to reduce visual predation by crabs (Manríquez et al. 2009).

Although knowledge of the ecological process influencing post-settlement performance is vital for an understanding of marine invertebrates with complex life-cycles (Gosselin & Chia 1995), information concerning the behavioural responses of early benthic stages of *Concholepas concholepas* after settlement is almost absent. In aquatic organisms, the response to chemical cues mediates many critical life processes with ecological consequences, such as prey detection, predator avoidance, reproduction and benthic settlement (Lindquist 2002, Webster & Weissburg 2009, Bourdeau 2010). Under laboratory conditions, we tested: (1) if juveniles of *C. concholepas* respond differently to odours of different prey; (2) if these responses to prey are modified in the presence or absence of predator odours; (3) if the presence of predators has negative effects on survival, shell thickness and growth of *C. concholepas*; and (4) if this response has a negative effect on the feeding activity of *C. concholepas*.

MATERIALS AND METHODS

Early settlers (<0.5 cm peristomal length [PL, i.e. the maximum length at the peristomal margin of the shell aperture]) and small juveniles (0.6–1.5 cm PL) of *Concholepas concholepas* were collected from 3 different rocky shores along the Chilean coast: Antofagasta (23° 30′ S, northern Chile), Las Cruces (32° 43′ S, central Chile) and Calfuco (39° 46′ S, southern Chile). Since most studies of *C. concholepas* use PL as a measure of body length (Castilla & Guisado 1979, DiSalvo & Carriker 1994, Manríquez et al. 2004, Manríquez et al. 2009), in the present study we chose this measure as opposed to any other. The crabs *Homalaspis plana* and *Acanthocyclus hassleri* were collected from the rocky shore at Calfuco. Specimens of *Heliaster helianthus* were collected from El Tabo (33° 27′ S, central Chile). All experiments were conducted between 2005 and 2010 in laboratories at the Estación Costera de Investigaciones Marinas (ECIM) Marine Reserve at Las Cruces and at the Laboratorio Costero de Recursos Acuáticos de Calfuco (LARAC) at the coast of Valdivia.

Expt 1. Prey odour and *Concholepas concholepas* displacement

At ECIM, we conducted prey choice experiments in a flow-through system glass Y-maze (Fig. 1a) to inves-
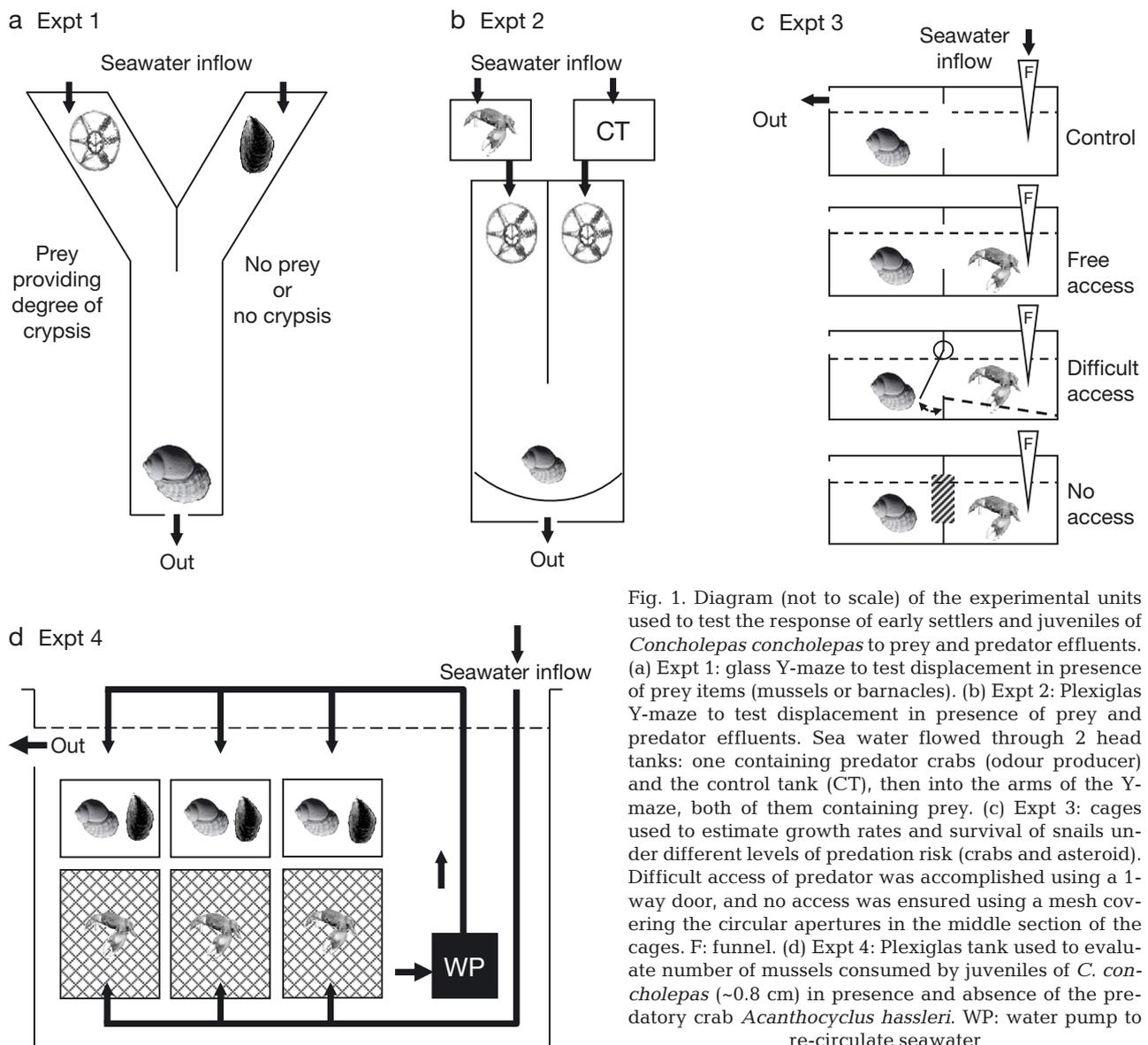

Fig. 1. Diagram (not to scale) of the experimental units used to test the response of early settlers and juveniles of *Concholepas concholepas* to prey and predator effluents. (a) Expt 1: glass Y-maze to test displacement in presence of prey items (mussels or barnacles). (b) Expt 2: Plexiglas Y-maze to test displacement in presence of prey and predator effluents. Sea water flowed through 2 head tanks: one containing predator crabs (odour producer) and the control tank (CT), then into the arms of the Y-maze, both of them containing prey. (c) Expt 3: cages used to estimate growth rates and survival of snails under different levels of predation risk (crabs and asteroid). Difficult access of predator was accomplished using a 1-way door, and no access was ensured using a mesh covering the circular apertures in the middle section of the cages. F: funnel. (d) Expt 4: Plexiglas tank used to evaluate number of mussels consumed by juveniles of *C. concholepas* (~0.8 cm) in presence and absence of the predatory crab *Acanthocyclus hassleri*. WP: water pump to re-circulate seawater

tigate whether the displacement of both early settlers and juveniles of *Concholepas concholepas* was modified by the presence of their prey items. The left and right Y-maze arms were 0.33 m long, 0.15 m wide and 0.15 m deep. Filtered (10 µm) seawater from an open system flowed into the arms at a constant rate of 0.6 l min^{-1}. Water flowing into the arms of the Y-maze dropped ~1 cm to the surface of the water to avoid unwanted vibration cues. We included trials to evaluate whether the displacement of the specimens was preferentially directed toward prey items common in the diet of *C. concholepas*: mussels and barnacles. These prey also provide background colour crypsis for early settlers of *C. concholepas* of light, dark and mixed shell colour (Manríquez et al. 2009). The prey were provided in the form of small rocks heavily encrusted with barnacles (light-coloured habitat), mussels (dark-coloured habitat), or a mixed microhabitat with both prey. A second group of experiments was conducted with *C. concholepas* from the same size categories (above) but cultured from competent larvae collected in the field (see Manríquez & Castilla 2011), metamorphosed and raised in the laboratory with mussels *Perumytilus purpuratus*, barnacles *Notochthamalus*

scabrosus or a mix of the 2, to obtain snails with light, dark or mixed-coloured shells as described by Manríquez et al. (2009). Based on the shell colouration of *C. concholepas* and the degree of crypsis provided by the offered prey in the Y-maze, we identified 8 experimental treatments (Table 1). In each treatment, the test specimens of *C. concholepas* were given the choice of 2 streams of seawater that differed only in that one flowed through an aquarium with the matching-coloured prey, while the other flowed through either an aquarium with the non-matching-coloured prey or nothing (control) (see Table 1). Before the experiments, the snails were placed for 1 d inside cages made of plastic (300 µm mesh), maintained in running seawater and deprived of food. After this period, the test snails were placed at the starting position (Fig. 1a) inside the cages for an acclimatisation period of 2 h. At the beginning of the trials, the prey items were placed inside cages constructed of 0.2 cm mesh near the seawater inlet (Fig. 1a). Three trials were conducted with 12 replicate snails at night when *C. concholepas* would normally be foraging. To avoid perturbations associated with the light regime, trials were conducted in darkness and observations

Table 1. *Concholepas concholepas*. Expt 1. Number of individuals (n) of post-metamorphic laboratory-reared larvae and field-collected juveniles occurring in Y-maze arms containing prey providing cryptic (n_c) or noncryptic (n_{nc}) background conditions. Snails were collected from intertidal habitats and raised under laboratory conditions. Snails of 3 distinctive shell colour patterns (light, dark, mix) were each allowed to select the prey provided in the extremes of the Y-maze. Prey offered: B = barnacles; M = mussels; B+M = both taxa; C = control, no prey offered. p = 2-tail binomial probability testing if the snail occurrence in any Y-maze arm was higher or lower than expected by chance (p = 0.5) in N independent trials. Significant high occurrences in **bold**. Body lengths (mean ± SD): post-metamorphic larvae, laboratory-reared = 2.79 ± 0.24 mm, field-collected = 3.11 ± 0.24 mm; juveniles, laboratory-reared = 14.72 ± 2.84 mm, field-collected = 15.47 ± 2.78 mm. For snails with mixed shell colour, the prey offered in the corresponding Y-maze arms did not provide cryptic or noncryptic conditions in the strict sense

Stage Shell colour	Prey in Y-maze arms Cryptic	Non-cryptic	Occurrence of *Concholepas concholepas* Laboratory-reared					Field-collected				
			N	n_c	%	n_{nc}	%	p	N	n_c	%	n_{nc}	%	p
Post-metamorphic larvae														
Light	B	C	32	**27**	84	5	14	0.0021	34	**30**	88	4	11	<0.0001
	B	M	32	**30**	94	2	6	<0.0001	34	**33**	97	1	3	<0.0001
Dark	M	C	33	**30**	91	3	8	<0.0001	35	**34**	97	1	3	<0.0001
	M	B	35	**35**	100	1	3	<0.0001	36	**34**	94	2	6	<0.0001
	B+M	C	35	**30**	86	5	14	<0.0001	34	**33**	97	1	3	<0.0001
	B+M	B	36	19	53	17	47	0.7358	35	**28**	80	7	19	0.0005
	B+M	M	34	18	53	16	44	0.8641	35	**32**	91	3	8	<0.0001
	B	M	35	19	54	16	44	0.7358	33	**27**	82	6	17	0.0003
Juveniles														
Light	B	C	35	**33**	94	2	6	<0.0001	34	**28**	82	6	17	0.0002
	B	M	33	**25**	76	8	22	0.0045	35	**27**	77	8	22	0.0019
Dark	M	C	35	**31**	89	4	11	<0.0001	35	**33**	94	2	6	<0.0001
	M	B	36	**36**	100	0	0	<0.0001	34	**33**	97	1	3	<0.0001
	B+M	C	35	**30**	86	5	14	<0.0001	33	**33**	100	0	0	<0.0001
	B+M	B	34	**28**	82	6	17	0.0002	36	**33**	92	3	8	<0.0001
	B+M	M	36	4	11	**32**	89	<0.0001	35	3	9	**32**	89	<0.0001
	B	M	33	9	27	**24**	67	0.0135	31	9	29	**22**	61	0.0295

made with a dim red light at regular intervals until the experimental snails reached their final position in the Y-maze. We used an exact binomial calculation to estimate the 2-tail probability that the snail occurrence in any of the Y-maze arms was higher or lower than expected by chance (p = 0.5) in N independent trials (Zar 1984). Snails showing no responses were not included in the test. In general, in 89–100% of the trials, the snails showed positive responses (N ≥ 32) (Table 1).

Expt 2. Predator odours and *Concholepas concholepas* displacement

To test the behavioural responses of *Concholepas concholepas* to chemical cues released from predators, we conducted 5 experiments at LARAC, each consisting of 4 Y-mazes and 2 head tanks (Fig. 1b). The head tanks measured 0.35 × 0.25 × 0.25 m and held ~15 l of seawater when filled to the outflow 5 cm from the top. The Y-mazes measured 1.3 × 0.25 × 0.15 m, and contained ~30 l when filled to the outflow 10 cm from the top. A Plexiglas panel measuring 0.6 × 10.5 m divided half the length of the Y-maze into 2 equal arms (Fig. 1b). To prevent light perturbations, the Y-mazes were completely opaque. Seawater from an open system flowed into the head tanks and then into the arms of the Y-mazes. Water flow into the head tank was 0.6 l min⁻¹. To prevent the transference of acoustic cues though the water, the water from the head was delivered by a 1.5 cm diameter PVC tube to a height of 10 cm above the water surface of the Y-mazes. Two small holes made at the treatment end of the cover furnished with plastic funnels delivered the seawater from the pipes into each arm of the Y-mazes (Fig. 1b). Three trials using combinations of *C. concholepas* predators and prey were run using this experimental set-up: (1) the crab *Homalaspis plana* and small rocks encrusted with barnacles, (2) the crab *Acanthocyclus hassleri* and the mussel *Perumytilus purpuratus* and (3) the asteroid *Heliaster helianthus*. To prevent variability in snail responses due to the quantity of prey available, groups of 400 similar-sized mussels and rocks with ~200 barnacles were used in the experiments. To maintain the position of the mussels close to the inflow, the mussels were placed inside plastic cages constructed of 0.2 cm mesh that did not obstruct the flow of their odour. When predatory crabs were used, in each trial, 6 crabs were allocated individually to plastic mesh cages in one of the head tanks. Mesh cages were used to avoid potential fighting between

the odour-producing crabs. The other head tank was without crabs and served as a control treatment. The crabs and asteroid were fed with mussels (either *Semimytilus algosus* or *P. purpuratus*) and removed from the rearing aquarium 12 h before the experiments to prevent contamination of the test Y-mazes with chemicals released by the mussels. The test snails were deprived of food for 1 d before the experiments, and to achieve acclimatisation, the small *C. concholepas* were maintained in the outflow area (Fig. 1b) for ~2 h prior to the start of the experimental run. To prevent *C. concholepas* using the corners of the Y-mazes as refuges, a semicircular Plexiglas panel with circular apertures covered with 0.2 cm plastic mesh was used (Fig. 1b). After the acclimatization period, the test snails were removed from the cages in the outflow and gently placed in the start area of the Y-maze. A black Plexiglas panel placed on top the Y-maze was used to prevent the snails escaping. Water flow into the head tank was 0.6 l min⁻¹, and to prevent the transference of acoustic cues though the water, the water from the head tank was delivered by a 1.5 cm diameter PVC tube to a height of 10 cm above the water surface of the Y-mazes. Two small holes made at the treatment end of the cover furnished with plastic funnels delivered the seawater from the pipes into each arm of the Y-mazes (Fig. 1b). Each experimental run or trial was conducted with small early post-metamorphic larvae and small juveniles of *C. concholepas* (n = 36) of ~0.5 and 4.0 cm PL respectively. Before the experiments, all post-metamorphic individuals were fed with a mixed diet consisting of barnacles and mussels in the absence of predators. Therefore, all the early post-metamorphic individuals were prey experienced and predator inexperienced. Trials were conducted at night, and the final position of the test specimens of *C. concholepas* in the Y-maze was recorded between 10:00 and 11:00 h the following morning. Dark-coloured and light-coloured juvenile individuals were collected from intertidal barnacle and mussel microhabitats in Calfuco, where the presence of predatory crabs has been recorded. Therefore, all the juveniles were theoretically predator experienced. The results were analysed using 2-tailed binomial tests as described above.

Expt 3. Predator odour and *Concholepas concholepas* survival and growth

To assess the effect of the predator presence (i.e. crabs or asteroid) on survival and growth, 4 or 5

specimens of *Concholepas concholepas* were assigned individually to plastic rearing boxes. All rearing boxes were provided with a Plexiglas wall 0.4 cm thick, dividing them into 2 equal halves (Fig. 1c). A PVC tube with a valve placed above the experimental boxes delivered seawater (Fig. 1c). A plastic funnel glued into the top of each box facilitated the delivery of the seawater. The specially designed plastic boxes and water delivery system permitted a net water circulation from one section to the other. Each Plexiglas wall had a circular aperture, 5 cm in diameter, which permitted water flow between the 2 sections. In Treatment 1 (free access), this aperture was kept open, allowing the free movement of the experimental individuals between sections. In Treatment 2 (difficult access), a flap suspended over the aperture permitted the predator to move from one section to the other, but prevented the snail from leaving its section. In Treatments 1 and 2, a rigid plastic net raised the base of the predator section level with the aperture to facilitate access to the other section. In Treatment 3 (no access), 2 PVC rings of 1 cm width were glued to each side of the aperture to support 2 mesh screens, 600 μm and 0.8 cm, to prevent the free movement of the predators and snails between the 2 sections. In the control boxes, the snails were maintained without a predator. Using these boxes, we conducted 3 different experiments in a laboratory at LARAC, using *Homalaspis plana* (Expt 3a) *Acanthocyclus hassleri* (Expt 3b) and *Heliaster helianthus* (Expt 3c) as predators and lasting 15, 15 and 22 wk respectively. During the experiments, small rocks encrusted with barnacles (Expt 3a), and groups of the mussel *Perumytilus purpuratus* (Expts 3b,c) were used as prey for the experimental snails and predators. In all the experiments, the predators were located in the box sections to which the seawater was delivered. The seawater then flowed out of the snails' section via a 1.5 cm aperture 4 cm above the base of the box. However, the outflow apertures were covered with a 600 μm mesh to prevent the snails from crawling out of the boxes. At weekly intervals, *C. concholepas* survival, size and weight were recorded and dead prey replaced with fresh prey. A 1-way ANOVA was used to test for the differences in mean PL at the beginning of the experiments. Analysis of covariance was used to compare growth rates estimated as the slope of the regression model (PL = $a + b$ [week]), and least square mean estimation was used to compare the adjusted PL at the mean covariate value (weeks) (SAS Institute 1996).

Expt 4. Predator odour and *Concholepas concholepas* feeding activities

To assess the effect of predation risk on prey consumption by *Concholepas concholepas*, 2 groups of 8 snails were held individually inside specially designed plastic cages (0.3 l) covered with 600 μm mesh to allow free movement of seawater. Each group of cages was assigned to 1 of 2 contrasting treatments inside 30 l Plexiglas tanks (Fig. 1d). Water was circulated by a PVC tube and pump from the bottom of each tank, where the odour-producing crabs were located. An outflow was placed 20 cm above the base of each tank. In Treatment 1, 4 plastic cages bearing an individual snail were placed on top of 9 plastic cages containing 9 specimens of *Acanthocyclus hassleri*. In Treatment 2, 4 plastic cages with an individual snail were placed on top of plastic cages without crabs. In the control treatment, cages containing only mussels were placed on top of the plastic cages without crabs to evaluate natural mortality in the absence of *C. concholepas*. In the treatments and in the control, all plastic cages contained the mussel *Perumytilus purpuratus* (n = 100). During the experiment the crabs (Treatment 1) were fed with the same species of mussel provided ad libitum. The experiment lasted 30 wk. In this experiment, mussel sizes presented as prey were increased as the mean PL of the snail increased during the experimental period. The *C. concholepas* were measured and weighed at weekly intervals, and dead and lost mussels were replaced with fresh ones 3 times a week to maintain a constant prey concentration throughout the experiment. Therefore, consumption rate was evaluated as the proportion of dead mussels. Dead mussels were assigned to 1 of the 2 potential attack methods characteristic of post-metamorphic and small *C. concholepas*: drilling (noting the drilled valve and valve zone) and the gape insertion method. Analysis of variance was used to test for treatment effects on the measured snail and prey traits. At the end of the experiment, *C. concholepas* size and weight were compared between treatments. Also, index of thickness was computed as shell thickness (measured with a digital calliper at 8 points along the growing edge) divided by the PL.

To assess feeding times, we conducted an additional experiment with juvenile *Concholepas concholepas* (~0.5 cm) collected from rocky intertidal platforms dominated by the mussel *Perumytilus purpuratus* in Las Cruces. Therefore, all experimental specimens were considered to be experienced in handling mussels. Once in the laboratory, the specimens were maintained in running seawater and fed ad libitum

with the mussel *P. purpuratu*s. However, before measurement, individual snails were removed sequentially from the rearing tanks and deprived of food for 3 d to standardize hunger levels. Then they were assigned individually to small glass Petri dishes filled with seawater, and an individual *P. purpuratus* (ranging from 0.3 to 0.4 cm in length) was offered to each of the snails. In this experiment, the attack phase (drilling) and the eating phase were observed and timed, with observations made with the aid of a stereomicroscope. Following published protocols (Hughes & Dunkin 1984, Rovero et al. 1999), mussel valves were differentiated as left or right and then divided into 4 quadrants to assess the drilling site (Fig. 4a). The experiment was run until 5 attacks per valve zone had been observed and timed. To assess whether boring location was associated with shell thickness, it was measured for 40 mussels in 3 shell fragments of each quadrant with the aid of a stereomicroscope fitted with an eyepiece graticule. All measurements were conducted on mussels with sizes ranging from 0.3 to 0.4 cm, like those used in the experiment designed to assess the preference for drilling site.

RESULTS

Expt 1. Prey odour and *Concholepas concholepas* displacement

In general, the percentage of post-metamorphic larvae and juvenile of *Concholepas concholepas* moving toward the prey items conferring crypticity was significantly higher than those moving to the control or noncryptic items (Table 1). Similar results were found for post-metamorphic individuals either reared from competent larvae or collected from the field. The only exception to this trend was found when mixed-coloured laboratory-reared post-metamorphic larvae were used (Table 1). These specimens did not significantly choose either the cryptic or noncryptic arm of the Y-maze. However, mixed-coloured field-collected post-metamorphic individuals were significantly attracted towards the maze arm in which barnacles and mussels were presented together (Table 1). A similar pattern of occurrences was shown by juvenile *C. concholepas*, however, when snails with mixed-coloured shells were exposed to a mix of barnacles and mussels they tended to choose the contrary arm containing only mussels (Table 1).

Expt 2. Predator effluent and displacement

Post-metamorphic larvae and juveniles of *Concholepas concholepas* avoided the maze arm receiving water from the head tank containing the crabs *Homalaspis plana* and *Acanthocyclus hassleri* (Table 2) However, juvenile snails with mixed-coloured shells did not exhibit a significant preference for either arm of the maze (Table 2).

Expt 3. Predator odour and *Concholepas concholepas* survival and growth

At the start of the 3 experiments, there were no significant differences in the mean PL of the individual *Concholepas concholepas* among the treatments

Table 2. *Concholepas concholepas*. Expt 2. Number of individuals (n) of post-metamorphic larvae and juvenile selecting a Y-maze arm containing prey that provide cryptic (n_c) background conditions and the same prey with the presence of predators (n_{c+p}). Snails with 3 distinctive shell colour patterns were allowed to select the prey offered in the corresponding Y-maze arm (B = barnacles; M = mussels) and in the presence of predators (crabs *Homalaspis plana* and *Acantocyclus hassleri* and asteroid *Heliaster helianthus*). p = 2-tail binomial probability testing if the snail occurrence in any Y-maze arm was higher or lower than expected by chance (p = 0.5) in N independent trials. Significant high occurrences in **bold**. Body lengths (mean ± SD): post metamorphic larvae = 4.41 ± 1.04 mm; juveniles = 11.08 ± 3.84 mm. For snails with mixed shell colour, the prey offered in the corresponding Y-maze arms did not provide cryptic or noncryptic conditions in the strict sense

Stage Shell colour	Cryptic arm	Cryptic arm + Predator effluent	——— Occurrence of *Concholepas concholepas* ———					
			N	n_c	%	n_{c+p}	%	p (N = n_c)
Post-metamorphic larvae								
Light	B	B + *H. plana*	29	**23**	79	6	21	0.0023
Dark	M	M + *A. hassleri*	21	**21**	100	0	0	<0.0001
Juveniles								
Light	B	B + *H. plana*	22	**19**	86	3	14	0.0009
Dark	M	M + *A. hassleri*	25	**18**	72	7	28	0.0433
Mixed	M	M + *H. helianthus*	72	41	57	31	43	0.2887

(Table 3). However, for those individuals that managed to survive throughout the entire experiment, on average, the control snails were significantly larger than those exposed to predator odours and predator attacks (Fig. 2a–c, Table 3). In the experiments with free access of the predator crabs *Acanthocyclus hassleri* and *Homalaspis plana*, all individuals of *C. concholepas* were attacked and consumed, evidenced by the presence of shell fragments within the first few days of the experiments. No mortality was found in the control treatment without crabs or the asteroid *H. helianthus* (Fig. 2d,f). With the option of passing through the flap to reach the snails, all crabs overcame the obstacle and consumed the snails (Fig. 2d,e). However, *H. plana* displayed more aptitude than *A. hassleri* for overcoming the obstacle (Fig. 2d,e, Table 3). This was clearly evidenced by the high survival rates of *C. concholepas* reared with *A. hassleri* in comparison to those reared with *H. plana* (Fig. 2d,e). In Treatments 1 and 2, the remains of all dead *C. concholepas* were found, and they clearly revealed that the cause of death was attack by crab. Surprisingly, when the crabs' access to the other section of the experimental chamber was prevented (Treatment 3), *C. concholepas* mortality was also recorded. Moreover, our observations determined that in this treatment, *C. concholepas* remained

motionless in the rearing boxes, away from the crabs and without obvious attempts to consume prey. Thus, only 1 and 2 snails were able to survive the entire experimental period with *A. hassleri* and *H. plana* respectively, with average life expectancies of ~12 wk (Fig. 2d,e). In this treatment, dead *C. concholepas* did not show signs of crab attack, which confirms the inability of the crabs to pass through the sealed openings. In the experiments with the asteroid *H. helianthus*, regardless if they were allowed to have free access to the snails, only 1 snail survived the entire experimental period (Fig. 2f). Presence of both species of predatory crabs and the asteroid during the experiments had a negative effect on *C. concholepas* size (ANOVA) (Fig. 2, Table 3), with significantly higher growth rates achieved by *C. concholepas* in the absence of crabs (ANCOVA, least square means test) (Table 3).

Expt 4. Predator odour and *Concholepas concholepas* feeding activities

Initial sizes and weights of *Concholepas concholepas* were not significantly different among snails (ANOVA) (Table 4). No mortality occurred in the control lacking crabs. Mortality of *C. concholepas*

Table 3. *Concholepas concholepas*. Expt 3. Initial peristomal length (PL) and growth rate estimates for snails reared with different prey and under different levels of predation risk (predator access). One-way ANOVAs with Tukey tests as a post-hoc comparison were used to test for differences in initial PL among treatments. Growth rates were estimated as the slope of the regression model: PL = $a + b$ (week). Analysis of covariance was used to test for differences in slopes among treatments, and least square mean estimation was used to compare the adjusted PL at the mean value of the covariate (weeks) (see 'Materials and methods' for further details). F-ratio and p are shown beneath the corresponding test and experiment in brackets; similar superscripts connect homogeneous mean values among treatments; n = sample size

Prey offered	Predator	Predator access		*Concholepas concholepas*				
				Initial PL (mm)	Growth rate (mm wk^{-1})		Least square means	
			n	Mean ± SD	Mean ± SE	p	PL ± SE	p
Expt 3a								
Perumytilus purpuratus	*Acanthocyclus hassleri*	Control	4	5.950[a] ± 0.290	0.971 ± 0.012	<0.001	12.582[a] ± 0.100	<0.001
		Free	4	5.330[a] ± 1.040	–		–	
		Difficult	4	4.560[a] ± 0.970	0.525 ± 0.044	<0.001	7.797[b] ± 0.115	<0.001
		No	4	6.080[a] ± 0.310	0.586 ± 0.019	<0.001	10.387[c] ± 0.100	<0.001
				($F_{3,11}$ = 2.65; p = 0.120)	($F_{2,39}$ = 107.8; p < 0.001)			
Expt 3b								
Barnacles	*Homalaspis plana*	Control	4	3.557[a] ± 0.067	0.634 ± 0.022	<0.001	8.346[a] ± 0.098	<0.001
		Free	4	4.453[a] ± 0.720	–		–	
		Difficult	4	3.853[a] ± 0.377	–		–	
		No	4	3.977[a] ± 0.556	0.386 ± 0.020	<0.001	6.796[b] ± 0.098	<0.001
				($F_{3,11}$ = 1.71; p = 0.241)	($F_{1,31}$ = 107.8; p < 0.001)			
Expt 3c								
P. purpuratus	*Heliaster helianthus*	Control	4	4.368[a] ± 0.511	0.367 ± 0.014	<0.001	8.192[a] ± 0.059	<0.001
		Free	4	4.413[a] ± 0.723	0.210 ± 0.008	<0.001	6.432[b] ± 0.059	<0.001
		No	4	4.565[a] ± 0.579	0.210 ± 0.007	<0.001	6.507[b] ± 0.059	<0.001
				($F_{2,11}$ = 0.11; p = 0.893)	($F_{2,57}$ = 107.8; p < 0.001)			

was only recorded in the treatment containing the crab predator *Acanthocyclus hassleri*. In this treatment, 3 of 4 specimens managed to survive throughout the entire experimental period. Snails reared without crab effluents showed significantly higher growth rates, measured as weekly increases in shell length, than those reared with crab effluents (ANCOVA) (Fig. 3, Table 4). At the end of the experiment, the shell thickness indices (means ± SD), measured on the outermost growing edge of *C. concholepas* reared with and without predatory crabs, were 0.07 ± 0.01 and 0.05 ± 0.01 respectively, which

were significantly different from one another ($F_{1, 54}$ = 14.79; p < 0.05).

On average, significantly more mussels were consumed by *Concholepas concholepas* in the absence of crabs than in the control treatment without crab effluents (Table 5). Similar differences were found when the mussels were consumed by either drilling or by the gap-insertion strategy. No significant differences were found in the average number of mussels lost from the rearing cages between treatments (Table 5). On average, the feeding times displayed by *C. concholepas* in drilling quadrants 1 and 2 along
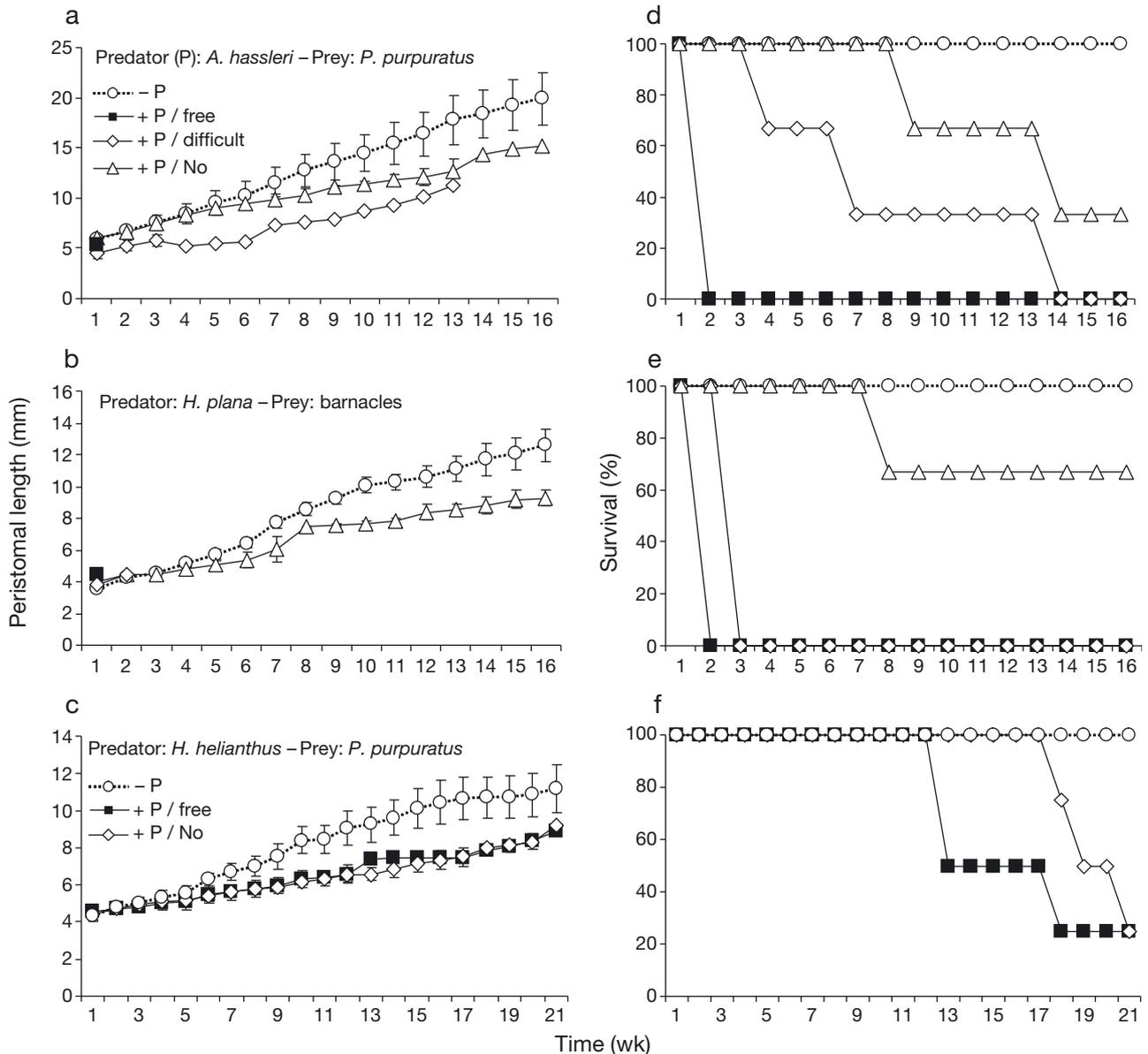
Fig. 2. *Concholepas concholepas*. Expt 3. Changes in the peristomal length (mean ± SD) and survival of settlers as a function of rearing time under different levels of predation risk (predator access) from crabs *Acanthocyclus hassleri* (a,d), *Homalaspis plana* (b,e) or the asteroid *Heliaster helianthus* (c,f), while fed on mussels (a,d;c,f) or barnacles (b,e)

the ligament or hinge zone of the mussels valves were significantly higher than those in quadrants 3 and 4 (fully nested ANOVA [quadrant within valve]: $F_{6,32} = 10.07$, p < 0.0001) (Fig. 4a). Valve zones which presented shorter feeding times were preferentially attacked compared to those which present extended feeding times (Fig. 4b) and this pattern of drilling sites on the shells of the consumed mussels was independent of the presence of predators ($\chi^2 = 3.606$; df = 5; p = 0.607) (Fig. 4b). Shell thicknesses were not significantly different among valves; however, within each valve shell, the preferentially attacked quadrants were significantly thinner than the less attacked quadrants (fully nested ANOVA [quadrant within valve]: $F_{6,312} = 90.57$, p < 0.0001) (Fig. 4c). In summary, the least attacked zones of the mussel valves were associated with higher handling times, which were in turn strongly influenced by shell thickness.

DISCUSSION

Our results show that *Concholepas concholepas* shows displacement orientated by cues emanating from prey and predators, which is in agreement with
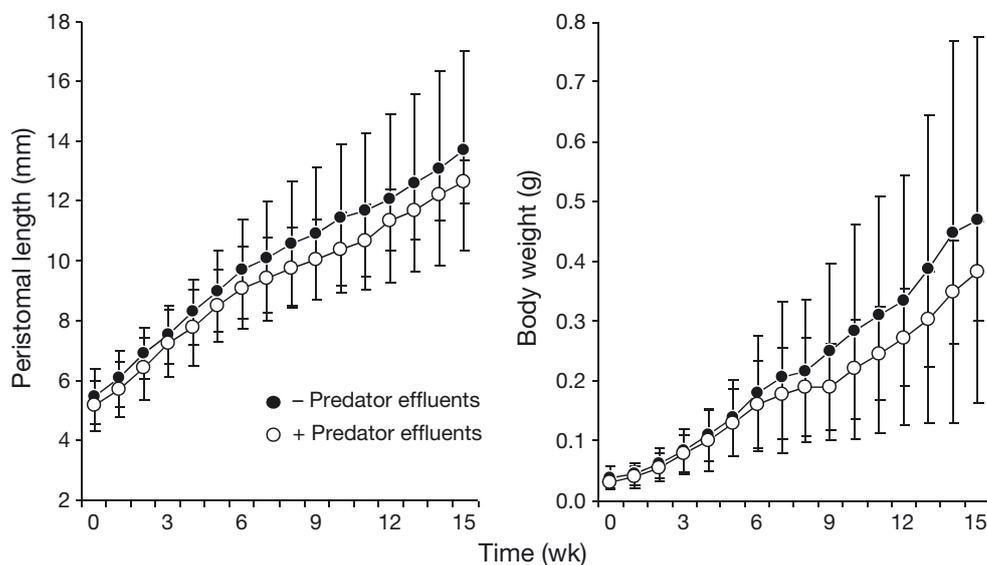
Fig. 3. *Concholepas concholepas*. Expt 4. Changes in peristomal length and weight (mean ± SD) as a function of time, recorded in early settlers reared under laboratory conditions and fed ad libitum with a mono diet of the mussel *Perumytilus purpuratus* and under presence or absence of the crab predator *Acanthocyclus hassleri* effluents in the rearing cage

Table 4. *Concholepas concholepas*. Expt 4. Initial body size measurements and growth rate estimates for *Concholepas concholepas* reared with mussels and under presence and absence of crab predator effluents (*Acanthoyclus hassleri*) during 30 sampling dates at weekly intervals. One-way ANOVA was used to test for differences in initial peristomal length (PL) and weight (W) between treatments. Growth rates were estimated as the slope of the regression model: PL or W = $a + b$ (week). Analysis of covariance was used to test for differences in slopes between treatments and least square mean estimation was used to compare the adjusted PL or W at the mean value of the covariate (weeks) (see 'Materials and methods' for further details). *F*-ratio and p are shown beneath the corresponding test in brackets; similar superscripts connect homogeneous mean values between treatments; n = sample size

| Body size variable | | Initial | | Growth rate | | | Least square means | |
Treatments	n	Mean ± SD	Variable wk^{-1} ± SE		p		Variable ± SE	p
Peristomal length (mm)								
– predator effluent	4	5.38^a ± 0.77	0.528 ± 0.018		<0.0001		9.940^a ± 0.085	<0.0001
+ predator effluent	4	5.23^a ± 0.99	0.479 ± 0.018		<0.0001		9.244^b ± 0.083	<0.0001
		($F_{1.6} = 0.28$; p = 0.615)	($F_{1,28} = 3.70$; p = 0.0647)					
Bodyweight (g)								
– predator effluent	4	0.035^a ± 0.011	0.029 ± 0.001		<0.0001		0.223^a ± 0.004	<0.0001
+ predator effluent	4	0.035^a ± 0.020	0.023 ± 0.001		<0.0001		0.183^b ± 0.004	<0.0001
		($F_{1.6} = 0.46$; p = 0.524)	($F_{1,28} = 24.58$; p < 0.001)					

studies showing the importance of chemoreception in gastropods (Croll 1983). Post-metamorphic larvae and juveniles of *C. concholepas* move toward prey items and avoid displacement toward predators. Since the large Y-maze used in the experiments was 1.3 m long and the smallest experimental snails were between 0.5 and 1.0 cm PL, our results suggest that *C. concholepas* is able to detect prey and predator odours emanating from a distance of ~100–200 body lengths. The effect of predatory crab effluent as a signal of predation risk has been described for other gastropods (Marko & Palmer 1991, Vadas et al. 1994, McCarthy & Fisher 2000). Moreover, our results suggest a negative effect of the presence of crabs and asteroid on growth and feeding activity, which is supported by lower prey consumption in treatments with the predator than in the control. This agrees with studies showing the negative effects of waterborne cues released from the predators (Palmer 1990, Côté & Jelnikar 1999). Our results are also supported by morphological studies suggesting an important role for the osphradium in food detection and escape reaction during the early ontogeny of *C. concholepas* (Huaquin & Garrido 2000).

A large variety of aquatic and terrestrial animals are directed to their prey by olfactory cues (Castilla 1972, Atema et al. 1988). In the sea, chemical information might serve as a fundamental source of sensory information linking a variety of interacting organisms (Dodson et al. 1994, Zimmer & Butman 2000), such as predators and prey. Our study was conducted under laboratory conditions with a unidirectional water flow regime, which is less turbulent than the natural water movement that occurs in the environment. Water turbulence and mixing estab-

Table 5. *Concholepas concholepas* feeding on *Perumytilus purpuratus*. Expt 4. Number of mussels (mean ± SD, n = 4) attacked using gap insertion or drilling methods, total of consumed (sum of drilled and gap inserted mussels) under presence and absence of crabs effluents. Lost mussels may result from displacement away from the experimental cages. Mean values obtained by averaging across 30 sampling dates at weekly intervals. Comparison of mussel and snail mean traits was done by using 1-way ANOVA. Significant p-values are shown in **bold**

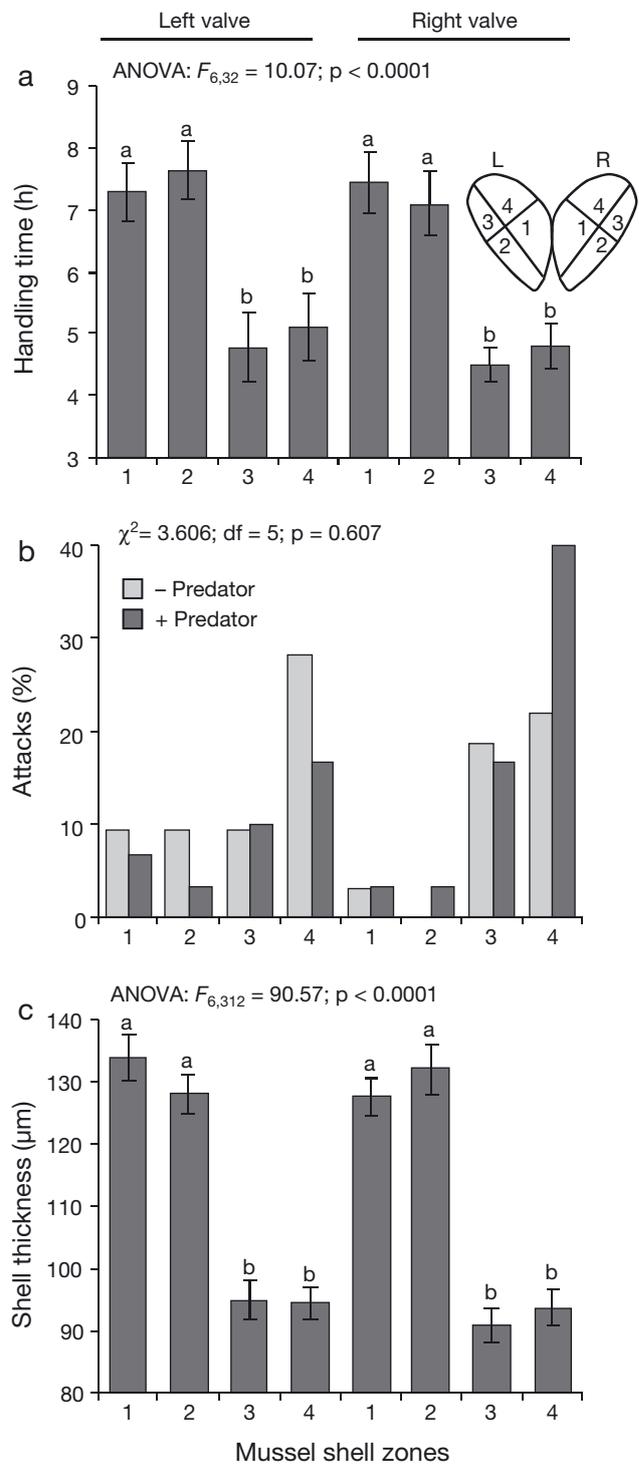| Kind of attack | Number of consumed mussels by treatment | | 1-way ANOVA | |
	+ crabs	– crabs	$F_{1,6}$	p
Drilled	2.50 ± 1.7	7.25 ± 2.75	8.53	**0.027**
Gap inserted	134.3 ± 21.9	181 ± 13.34	13.21	**0.011**
Total	136.8 ± 20.3	184 ± 19.85	11.09	**0.016**
Lost	30.8 ± 5.9	33.8 ± 6.2	0.50	0.507

Fig. 4. *Concholepas concholepas* feeding on *Perumytilus purpuratus*. Expt 4. (a) Prey handling time (the sum of boring and eating time; mean ± SD) used by early settlers in perforating different attack zones of the mussel shell in the absence of predators, (b) percentage of mussels attacked in the corresponding zone under predator presence or absence, (c) shell thickness (mean ± SE) for shell zone. In (a) and (c), means with the same letter did not differ significantly

lishes the odorant field occurring around large organisms (>10 mm) inhabiting benthic environments. It is well known that turbulent flows may affect the ability of an organism to detect chemical cues (Webster & Weissburg 2009), because they dilute the concentration of water-borne cues (Webster et al. 2003). However, slow-moving predatory gastropods such as *Concholepas concholepas* can track prey odours in fast turbulent water (Ferner & Weissburg 2005). We are aware that under laboratory conditions, using unidirectional water flow reduces the dispersion of odour cues in the water, which may impose limitations on the interpretation of the results. However, behavioural patterns found in our study in response to prey and predator cues under unidirectional flow were similar to those reported in other studies on chemoreception in gastropods.

The influence of recent ingestive conditioning on food choices in marine gastropods is well documented (Wood 1968, Hall et al. 1982). In predatory gastropods, digestive conditioning and the use of chemical cues to detect their prey has been suggested as equivalent to searching-image formation in visual predators (Hughes & Croy 1993). Therefore, the gastropods' chemotactic detection of prey and the displacement of both field-collected and laboratory-reared snails to a specific prey under laboratory conditions are likely to be affected by the type and amount of prey eaten prior to the tests. In our study, deviations from expected displacements to prey conferring cryptic camouflage were found in field-collected and laboratory-reared *Concholepas concholepas* with mixed shell colour. These snails exhibited significant displacement toward the maze arm with a single prey instead of the maze arm conferring camouflage (light and dark prey offered simultaneously) (Table 1). This suggests that the preference for a specific prey in *C. concholepas* might sometimes override the preference for crypticity.

Displacement of *Concholepas concholepas* in the direction of their prey supports evidence showing that their pattern of shell colouration during their early benthic ontogeny is modulated by the prey colouration and allows cryptic camouflage against crab predators such as *Acanthocyclus hassleri* and *A. gayi* (Manríquez et al. 2009). This highlights the importance of chemical recognition and cryptic behaviour in the early benthic performance of *C. concholepas* in nature. The present study moves a step further by detecting significant effects of crab effluents on growth rates and the amount of consumed prey. Moreover, significantly more mussels were consumed through drilled holes when the crab effluent was absent. This suggests that in *C. concholepas*, feeding behaviour can be modified by the presence of predators, favouring a strategy that reduces the rate of predator encounters or the vulnerability to attack.

In the wild, *Concholepas concholepas* shells bear scars mainly concentrated on the outermost edge of the shell, evidence of attacks by crabs that the snail has survived (P. H. Manríquez pers. obs). This is supported by our observations of *A. hassleri* attacking the outermost edge of the shell (present study). In our study, *C. concholeapas* reared in the presence of restrained crabs tended to remain motionless and not to feed, which may well explain their lower survival rates compared to those reared in the absence of crabs (control group), who fed normally. Therefore, our findings of significantly thicker shells at the growing edges of *C. concholepas* exposed to predators, compared to those not exposed to crab effluent, suggests a predator-inducible trait that may reduce crab predation success. This agrees with other studies showing that shell thickness is a morphological trait that reduces predation success in marine rocky intertidal gastropods (Hughes & Dunkin 1984, Appleton & Palmer 1988, Palmer 1990, Trussell 1996) and other groups such as mussels (Leonard et al. 1999, Smith & Jennings 2000, Caro & Castilla 2004). In our study, *C. concholepas* foraging strategy was similar in the presence and absence of predators, with drilling sites concentrated in the thinnest sites of both the mussel shells. This suggest that ability to detect predator effluents and predation risk in *C. concholepas* is not counterbalanced by the display of more efficient foraging strategies, focused, for instance, on attacks mainly directed to thinner areas of the mussels shell, whereby reduced handling times are achieved. Moreover, in our experiments, mussels were replaced at a high frequency, thus the potential confounding effect associated with mussel shell thickening in the presence of top predators can be ignored.

In studies of community structure in which predator-prey interactions are involved, avoidance behaviour can be an important component of the activities of many marine invertebrates (Trussell et al. 2003). Because anti-predatory responses involve an energetic cost (Covich et al. 1994), it would be advantageous for the prey to respond according to the level of risk experienced. The capacity for regulating avoidance behaviour in response to perception of predation risk has been described in other gastropods (Marko & Palmer 1991, Yamada et al. 1998). Therefore, high or low concentrations of predator

cues could correspond to high or low risk signals indicating whether a predator is close by or not. The avoidance of chemical cues released from predatory crabs could be a learned response. However, it is unlikely that many specimens of *Concholepas concholepas* would survive a crab attack and retain that experience with a tendency to escape from chemical cues in the future, or that snails can observe a crab attacking another snail and then associate cues from that predator with predator risk (Geller 1982). Since our study showed both predator escape and prey detection behaviour in experienced and inexperienced *C. concholepas*, we suggest that heritable traits could be involved. Therefore, our results suggest that feeding behaviour in the early ontogeny of *C. concholepas* has evolved as a strategy to reduce predation risk through minimizing handling times and maximizing attacks in the most vulnerable prey zones. Through this strategy, this species increases its survival opportunities and achieves larger body sizes, resulting in a successful strategy of escape-by-size from predators.

Predator effects on prey dynamics are commonly studied by measuring changes in prey abundance attributed to consumption by predators (Peckarsky et al. 2008). Our study, involving the 3-tier linkage of a top predator (*Heliaster helianthus*), a keystone predator (*Concholepas concholepas*) and prey items such as mussels *Perumytilus purpuratus* and barnacles *Notochthamalus scabrosus*, suggests the need to incorporate changes in prey traits or non-consumptive effects (NCE) (Lima 1998) of predators in order to better understand their coexistence. The importance of considering NCE in predator-prey interactions is highlighted in the literature as an important force that can affect the magnitude, rate or scale of prey responses to predators (Peckarsky et al. 2008). Prey traits described in the present study such as shell thickening and avoidance displacement might affect predator-prey interactions and regulate their coexistence in nature. In rocky intertidal habitats, the predatory crabs *Acanthocyclus hassleri* and *A. gayi* feed on small *C. concholepas* (Manríquez et al. 2009) and mussels. This illustrates a situation where the results of interactions between predator and prey might not simply be determined by the population or community dynamics, but modified, or rather determined, by NCE mediated by predation risk cues. Thus our study suggests that predation risk might play an important role in the coexistence of interacting species, and highlights the importance of incorporating behavioural and predator-induced traits into experimental studies of predator-prey interactions.

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