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Effects of experience and risk of predation on the foraging behaviour of the South-eastern Pacific muricid *Concholepas concholepas* (Mollusca: Gastropoda)

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Summary

1. Different size classes of the muricid *Concholepas concholepas* (Bruguière)(small and medium subadult specimens inhabiting mainly the high- and mid-intertidal, and large adult ones inhabiting mainly the subtidal) were assessed for handling times and diet selection by offering them three different sizes of the high-intertidal mussel *Perumytilus purpuratus* (Lamarck).

2. The effect of experience on the foraging efficiency of the different size classes of the muricid was tested by comparing the handling times of specimens starved after collection from the field with those of specimens subjected to starvation after having been exclusively fed with this mussel.

3. Experienced predators showed a consistent reduction in handling time with corresponding increase in prey profitability, although this varied in magnitude in the nine distinct predator/prey size combinations. As a consequence, foraging experience changed the profitability ranking of different classes of prey.

4. Prey-size preferences changed with foraging experience in accordance with the associated variations in prey profitabilities. Particularly, the number of attacks per unit time and the average weight of the mussels consumed by the different size classes of *C. concholepas* increased with experience, while the total time devoted to foraging decreased slightly.

5. The exposure of experienced *C. concholepas* to effluent from a higher-order predator, the subtidal asteroid *Meyenaster gelatinosus* (Meyen), induced the muricid to reduce the time devoted to foraging. This reduction in foraging time was achieved differently, according to the size of the forager: small individuals reverted to their initial preference for smaller mussels, while medium and large individuals reduced the number of attacks. Both effects lowered the rate of food intake, which must be seen as a cost of reducing risk of predation.

Key-words: behavioural trade-off, diet selection, foraging behaviour, handling time, predation risk, prey profitability.

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Introduction

Theoretical and experimental investigations have progressively relaxed the energy maximization premise underlying the original approach to optimal foraging theories (Stephens & Krebs 1986; Schoener 1987). In particular, the effects of different internal and external environmental factors on foraging behaviour have received increasing attention (for reviews see Hughes 1987; Houston 1993; Sih 1993). Hughes (1979) introduced learning into a model of foraging optimization and showed that experience of the prey can induce the predator to change its diet following variations in prey profitability. Concerning gastropod predators, the reduction of handling times by experience, and its effect on diet selection, have been experimentally demonstrated by Hughes & Dunkin (1984) in the intertidal muricid predator *Nucella lapillus*. Moreover, dietary conditioning has been shown to influence prey selectivity in *Nucella* spp. (Hughes & Dunkin 1984; Palmer 1984; West 1986; Hughes & Burrows 1991).

Also receiving increasing attention in studies of foraging behaviour, is the risk of predation associated with specific foraging activities or choices (Lima & Dill 1990). Both experimental and theoretical studies have shown how the presence of predators can affect the decision-making processes of foragers (for reviews see Godin 1990; Sih 1993). In particular, Palmer (1990) and, more recently, Vadas, Burrows & Hughes (1994) examined changes in the foraging activity of *N. lapillus* in relation to the perceived risk of predation.

Concholepas concholepas is a muricid gastropod present along the south-eastern Pacific rocky shores, from southern Chile to central Peru (Castilla 1982, 1983), where it is exploited by artisanal fishermen (Castilla & Jerez 1986). A comprehensive review of the literature on this species, commonly known in Chile as 'loco', was published by Castilla (1988). This predator is considered to play a crucial role in structuring the intertidal rocky shore communities, and has been recognized as a 'key-stone' species (Castilla & Paine 1987). *C. concholepas* shows a size-related variation in zonation (Castilla, Guisado & Cancino 1979; Guisado & Castilla 1983); settlement of larvae occurs mainly in the high–mid rocky intertidal from where individuals move progressively down to the sublittoral with age, but a fraction of adults move back periodically toward shallower waters for capsule deposition (Duran & Castilla 1989).

Field observations (Castilla *et al.* 1979) have shown that juvenile locos feed mostly on the mussel *Perumytilus purpuratus* and on barnacles of the genus *Balanus*; subadult locos similarly feed on barnacles and also on the tunicate *Pyura chilensis*. On the other hand, the diet of subtidal adult locos includes mainly *Balanus* spp., *P. chilensis* and, to a lesser degree, *Mytilus edulis* (Du Bois, Castilla & Cacciolatto 1980). Mendez & Cancino (1990) showed, under laboratory conditions, the existence of relative preferences by postmetamorphic locos (peristomial length smaller than 20 mm) for mussels and barnacles. Castilla *et al.* (1979) and Castilla & Guisado (1979) demonstrated a positive correlation between preferred prey size and locos size (15–66 mm in peristomial length) when feeding upon *Perumytilus purpuratus*. However, experimental studies on the effects of experience on the foraging behaviour of locos are lacking.

The complete range of potential predators of *C. concholepas* has been reviewed by Castilla & Cancino (1979); in particular, data on predation by the subtidal sea star *Meyenaster gelatinosus* are given by Dayton *et al.* (1977) and Castilla *et al.* (1994). Nevertheless, the effect of the presence of potential predators on decision-making processes of foraging locos has never been investigated.

The present laboratory study aimed to address these gaps in the knowledge of the behavioural ecology of this important key-stone species, by assessing the effects of experience with specific prey types, and of the presence of a higher-order predator, on *C. concholepas* foraging behaviour. The study, however, goes beyond the specific interest for the behavioural ecology of *C. concholepas*: despite an increase in theoretical studies on dynamic optimization of foraging, empirical data on the trade-off between energy maximization and reduction of predation risk are still scant, especially regarding invertebrate species (Sih 1993).

Methods

The study was conducted at Las Cruces (33°30′S, 71°38′W), on the central Chilean coast, at the Estacion Costera de Investigaciones Marina (ECIM) of the Pontificia Universidad Católica de Chile. Experiments were conducted during two study periods: November 1994 to February 1995, and December 1995 to March 1996, respectively. Experimental tanks were placed in the outdoor laboratory of the ECIM, under natural light. Sea water, continuously pumped from the sea, flowed through each tank and was aerated.

EXPERIMENTAL ANIMALS

The predator

Three size classes of *C. concholepas* were collected from the rocky shore around ECIM: small (S), with a peristomial length (pl) of 30–40 mm; medium (M), $55 \leqslant \text{pl} \leqslant 65$ mm; and large (L), $98 \leqslant \text{pl} \leqslant 110$ mm. S and M specimens were collected intertidally, and L individuals subtidally (about 10–15 m below sea level). Except for the locos offered to the sea stars as prey, all individuals used in the experiments were eventually released at the collection sites.

The prey

To measure handling times and test prey selectivity, we offered locos individuals of the mussel *Perumytilus purpuratus*, a species commonly found in the high and mid-intertidal of south-eastern Pacific rocky shores. Alvarado & Castilla (1996) showed that in the Las Cruces area the size-frequency distribution of this species is bimodal, corresponding to small specimens (< 10 mm in length) and adults (22–28 mm). Different sized mussels were collected weekly at the high–mid-intertidal level, north of ECIM, and maintained in aquaria of the same type as those used for experimental locos. The size of individual mussels was measured as the maximum length of valves (mlv), using a Vernier caliper to 1 mm precision (after Guiñez 1996). Three non-overlapping size classes were chosen: (I) $20 \leqslant \text{mlv} \leqslant 23$ mm; (II) $26 \leqslant \text{mlv} \leqslant 27$ mm; and (III) $30 \leqslant \text{mlv} \leqslant 33$ mm. The average dry flesh weight of *P. purpuratus* in each size class was estimated from a weight–length regression provided by Guiñez (1996): 43 μg for class I, 91 μg for class II, and 153 μg for class III. According to Alvarado & Castilla (1996), our class II is the most frequent among natural populations, while class I and III are relatively less frequent.

Although no quantitative assessment of natural encounter rates between *C. concholepas* and *P. purpuratus* is available, the size-specific variation in zonation pattern of locos (Castilla *et al.* 1979; Guisado & Castilla 1983) suggests that encounter rates should decrease as locos become older and larger. In particular, large adult locos, inhabiting the subtidal, can be assumed to have had no recent encounters with mussels. On the other hand, the partial zonal overlap of S and M locos with *P. purpuratus* indicates the possibility of recent encounters, as has indeed been recorded in the field (Castilla *et al.* 1979).

The higher-order predator

The sea star *Meyenaster gelatinosus* (Echinodermata: Asteroidea) is commonly found on hard substrata from 2 to 3 m below sea level (maximum density at a depth of 10–15 m), along the south-eastern Pacific. Individuals of the sea star, with a mean radius length of 250–300 mm, were collected from the subtidal, north of ECIM area. Preliminary observations showed that the introduction of sea stars in a tank containing locos of different sizes produces clear avoidance behaviours: withdrawing and crawling to the air–water interface or rapidly raising and twisting the shell on the foot when contact with the sea star occurs. Dayton *et al.* (1977) noted a clamping down response of *C. concholepas* when *M. gelatinosus* was introduced into a tide pool where locos were present.

HANDLING TIME ASSESSMENT

Handling times (HT, min) were measured for inexperienced control (naive) and experienced locos: the control group ($n = 30$) comprised individuals freshly collected in the field; the experienced group ($n = 30$) consisted of locos fed with *P. purpuratus* for 30 days before observations began. Both groups were starved for a week before testing. Since *C. concholepas* is active mainly at night (authors' personal observation), both groups were subjected to an inverted day–night cycle, to enable observations on foraging behaviour during the experimenter's day, made under the illumination of red light. Individual handling times of *C. concholepas* were determined by recording, to the nearest 10 min, the time elapsing between first tactile contact with the mussel and release of the opened, empty valves. Thus, handling time included the time spent in forcing and opening the valves, together with ingestion time.

A total of 180 observations were made, 10 for each combination of predator–prey size of experienced and inexperienced locos. Locos of each size class (S, M, L) were each offerred three mussels (class I, II, III) in random sequence during successive sessions. Handling times of experienced and inexperienced locos were compared, for each forager size class preying upon each mussel class, by the Mann–Whitney test (Siegel & Castellan 1989). Since energy per unit dry flesh weight (DFW) of different sizes of mussel can be considered constant, average profitability (P) of a mussel of class m for a loco of class c was computed as $P_{m,c} = DFW_m/\text{average } HT_{m,c}$, where DFW_m is the dry flesh weight of a mussel of class m.

PREY SELECTION TESTS

Soon after collection from the shore, 84 locos (27 small, 29 medium and 28 large) were placed individually in 80 × 50 × 30 cm plastic aquaria, supplied with a steady flow of running sea water, which was continuously aerated. Tests on the three classes were conducted from December 1994 to February 1995 and replicated during January to February 1996. All the experiments were carried out at ambient light and temperature. Water temperature was almost constant throughout experiments (15 °C ± 3 °C). Individual aquaria were cleaned weekly to avoid bacterial and algal growth and sediment accumulation.

Effect of experience

Locos were starved for about 10 days and then, during a period of 30–35 days, each specimen was offered a cluster of nine mussels, three of each size class (I–III). Each individual's tank was inspected daily (mid-morning) and the number of consumed prey items of each class was recorded. The mussels were considered consumed by the predator when found with open empty valves. Mussels very rarely died for reasons other than predation, and such cases were easily recognizable. As a precaution, however, mortality rate not due to predation was assessed by observing two groups of mussels of the three experimental size classes maintained in aquaria similar to the experimental ones but lacking locos. These control observations showed that the mortality rate of mussels not due to predation was negligible over the experimental period.

Constant availability of prey was maintained throughout the experiment by daily replacement of consumed prey, using matching size classes. The number of mussels of different size classes (I–III) consumed by each loco was recorded daily. Numbers of prey eaten within each 10-day period following the first attack were pooled. Differences in the following measurements between the first and the third 10-day period were assessed using the Wilcoxon test for paired data (Siegel & Castellan 1989):

1. TPN: total number of mussels eaten;
2. TPW: total dry flesh weight (μg) of eaten mussels;

3. APW: average dry flesh weight (μg) of eaten mussels.

Using mean handling times (HT) specific to each combination of prey/predator size, and to inexperienced and experienced locos, we obtained the additional measure:

4. THT: total time devoted to predation (min), computed as $\Sigma(n_m.\mathrm{HT}_m)$, where n_m is the number of mussels of each class predated during each 10-day period, and HT_m is the average handling time of a given class of predators (inexperienced for the first period, and experienced for the third period) on the *m*-th size class of prey.

Effect of exposure to a higher-order predator

Locos of each size class, having been fed for at least 30 days with *P. purpuratus,* were randomly assigned to two groups, an experimental group ($n = 10$ for each class) exposed to the scent of *M. gelatinosus*, and a control group ($n = 10$ for each class) not exposed to the scent of *M. gelatinosus*. Control locos were placed in tanks as in the previous tests. For the experimental group, a second tank containing one sea star was connected to each tank containing a loco so that sea water continuously flowed from the sea star to the loco. To amplify odours potentially signalling risk, at three-days intervals we placed a freshly collected loco with each sea star, on the assumption that olfactory cues emanating from a loco under attack will alert conspecifics (Dayton *et al.* 1977).

During these experiments locos were offered clusters of mussels according to the same procedure used in the previous experiment, and foraging data were recorded accordingly. The total duration of the higher-predator tests was 20 days (late February to mid-March 1996), but only the last 10 days were considered, to allow time for locos to settle down in the tanks. The Mann–Whitney test (Siegel & Castellan 1989) was used to compare foraging parameters (TPN, TPW, APW, THT) of experimental and control locos.

Results

VARIATION OF HANDLING TIME AND PREY PROFITABILITY WITH EXPERIENCE

The average handling times of locos of the three size classes preying upon mussels of different size are shown in Fig. 1a. Inexperienced S individuals showed a threefold increase in HT when preying upon class II–III mussels, in comparison to the average HT observed with class I mussels. Inexperienced M and L locos showed a more modest increase in average HT when preying upon class I–III mussels.

HT was generally less in experienced than in inexperienced locos. This difference was statistically significant (Mann–Whitney test) for S locos preying on class II, for M locos preying on classes I, II and III, and for L locos preying on classes I and III. As a consequence, the average profitability of prey (μg min^{-1}) was greater for experienced than for inexperienced locos (Fig. 1b). This effect was particularly evident for M and L locos preying upon class III mussels.

VARIATION OF FOOD INTAKE AND DIET SELECTION WITH EXPERIENCE

The total number of mussels consumed by each loco size class (TPN) and the total weight of ingested prey (TPW) increased between the first and third 10-day period after the first attack on *P. purpuratus* (Table 1).

A definite shift in relative preference for prey of different sizes occurred between the two test periods. Figure 2 shows the average number of mussels of different sizes eaten during the first and the third 10-day period by the locos of the different size classes. Study of this figure suggests that: the relative preference of S locos shifted from class I to class II mussels; of M locos from class I to class III, and of L locos from class II to class III. In order to test the significance of these shifts in terms of flesh yield, we computed the individual average prey weight (APW) for each period (Fig. 3). The APW of S locos increased from 79·1 μg ($\pm$ 18·0) to 95·4 μg ($\pm$ 22·4) between the first and third period, respectively, ($Z = 3{\cdot}89$; $P < 0{\cdot}001$); the APW of M specimens increased from 85·0 μg ($\pm$ 22·5) to 114·5 μg ($\pm$ 18·0) ($Z = 4{\cdot}29$; $P < 0{\cdot}001$); the APW of L specimens increased from 101·6 μg ($\pm$ 19·3) to 125·6 μg ($\pm$ 14·4) ($Z = 4{\cdot}50$; $P < 0{\cdot}001$).

By using the average handling times of different size classes of inexperienced and experienced locos preying upon mussels of different sizes and taking into account the number of prey of different sizes eaten by each loco, it was possible to estimate the variation in total time devoted to handling prey (THT) between the first and the third 10-day periods. The estimated THT of the third period was slightly lower than that estimated for the first period in all the classes: THT per day of S specimens varied from 244 min ($\pm$ 118) to 219 min ($\pm$ 102) ($Z = 1{\cdot}17$; $P = 0{\cdot}244$); THT per day of M specimens decreased from 150 min ($\pm$ 99) to 103 min ($\pm$ 42) ($Z = 2{\cdot}16$; $P = 0{\cdot}031$); THT per day of L locos varied from 157 min ($\pm$ 126) to 133 min ($\pm$ 63) ($Z = 0{\cdot}99$; $P = 0{\cdot}319$).

EFFECTS OF THE EXPOSURE TO THE HIGHER-ORDER PREDATOR

The total number of prey ingested was consistently lower in locos exposed to *M. gelatinosus*, in comparison to control specimens, but the difference was significant only for M and L individuals. For control and experimental S individuals the average TPN was 3·30 ($\pm$ 1·57) and 2·40 ($\pm$ 1·58), respectively, (Z =

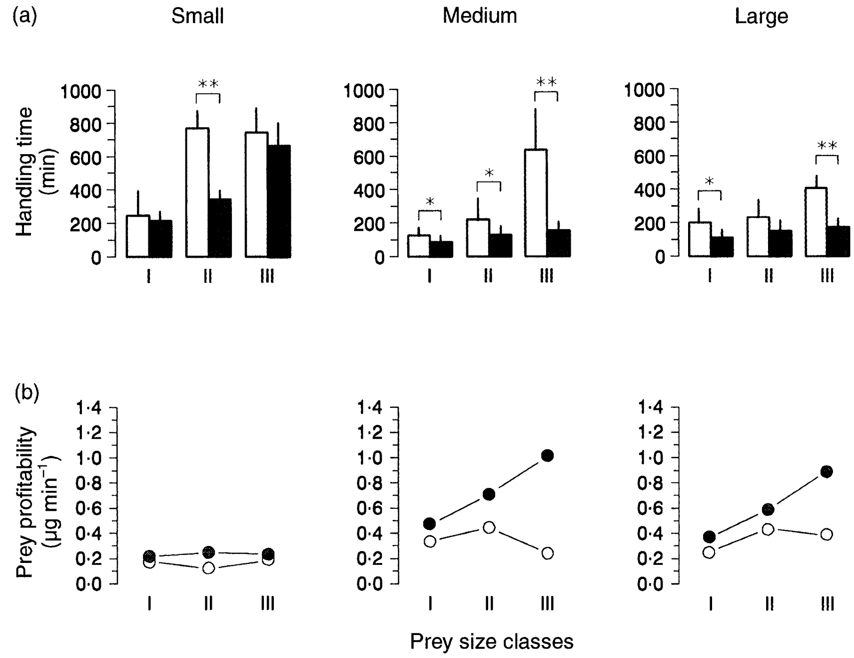

Fig. 1. (a) Average handling time (bars) and standard deviation (vertical segments) of different sizes classes of *C. concholepas* (Small, Medium, Large) preying upon *P. purpuratus* of different size (I, II, III). □, inexperienced specimens; ■, experienced specimens. Sample size is $n = 10$ for each locos–mussels size combination. Results of Mann–Whitney test (two-tailed) are given: $*P < 0{\cdot}05$; $**P < 0{\cdot}01$. (b) Average profitability of mussels of different size for inexperienced (○) and experienced (●) locos of different sizes. The method to compute the prey profitability is explained in the text.

Table 1. Total number (TPN) and total weight (TPW) of prey consumed during the first and the third 10-day periods of the prey selection experiments. Average values ± (standard deviation) are indicated for each size class of predators. The statistics (Z) and the probability (*P*) of rejecting the null hypothesis for the comparison between the first and the third period is also given (Wilcoxon test for paired data)

	1st period	3rd period	Wilcoxon test
S locos ($n = 27$)			
TPN (n)	4·48 ± (1·81)	5·63 ± (2·13)	$Z = 1{\cdot}96$; $P = 0{\cdot}048$
TPW (μg)	367·9 ± (188·4)	534·9 ± (243·6)	$Z = 3{\cdot}19$; $P < 0{\cdot}01$
M locos ($n = 29$)			
TPN (n)	5·3 ± (3·1)	7·9 ± (3·5),	$Z = 3{\cdot}25$; $P = 0{\cdot}001$
TPW (μg)	473·0 ± (296·2)	887·4 ± (350·9)	$Z = 4{\cdot}08$; $P < 0{\cdot}001$
L locos ($n = 28$)			
TPN (n)	5·6 ± (4·8)	8·4 ± (4·1)	$Z = 2{\cdot}95$; $P < 0{\cdot}001$
TPW (μg)	584·3 ± (470·5)	1028·2 ± (455·9)	$Z = 3{\cdot}80$; $P < 0{\cdot}001$

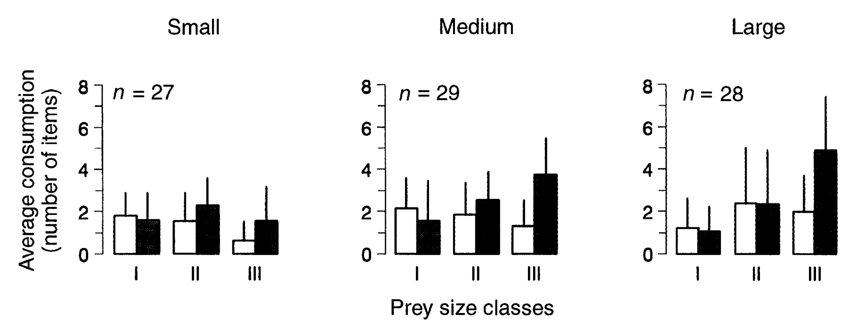

Fig. 2. Average number (bars) and standard deviation (vertical segments) of mussels of different classes (I, II, III) consumed by *C. concholepas* of different sizes (Small, Medium, Large), during the first (□) and the third (■) 10-day period following the first attack. *n*, sample size.

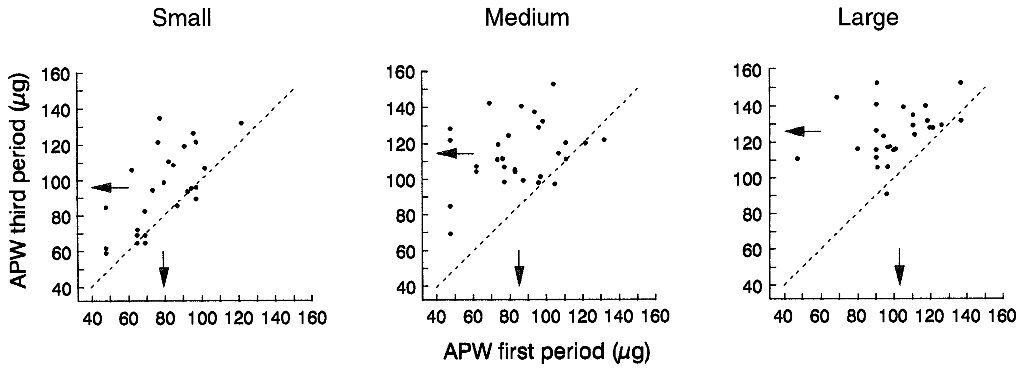

Fig. 3. Dry flesh weight of *P. purpuratus* ingested by *C. concholepas* during the first (abscissa) and third 10-day period (ordinate), following the first attack. Each dot represents the average weight of the mussels consumed by a single loco. Dashed line, invariance expectation. Arrows show the second-order mean value.

–1·36; $P = 0{\cdot}173$); in M locos the average TPN was 4·10 ($\pm$ 1·59) and 2·20 ($\pm$ 1·13), respectively, ($Z = -2{\cdot}50$; $0{\cdot}01 < P < 0{\cdot}05$); in L locos the values were 9·64 ($\pm$ 2·84) and 6·40 ($\pm$ 2·87), respectively, ($Z = -2{\cdot}35$; $0{\cdot}01 < P < 0{\cdot}05$).

On the other hand, only S locos showed a consistent reduction in average prey weight (APW) when exposed to the sea star: from 122·1 μg ($\pm$ 37·1) in controls to 79·3 μg ($\pm$ 36·2) in experimentals ($Z = -2{\cdot}19$; $0{\cdot}01 < P < 0{\cdot}05$). For medium and large locos there was no effect: for M locos the reduction of APW from 129·1 μg ($\pm$ 18·0) to 108·0 μg ($\pm$ 22·6) was not significant ($Z = -1{\cdot}53$; $P = 0{\cdot}127$); the APW of control and exposed L locos was very similar: 129·7 μg ($\pm$ 14·3) and 128·1 μg ($\pm$ 19·9), respectively, ($Z = -0{\cdot}04$; $P = 0{\cdot}97$).

These size-related effects on TPN and APW result in a reduction in food intake rate for all locos size classes when exposed to the sea star (abscissa in Fig. 4). Average TPW ($\pm$ SD) of control and exposed S locos during the 10-days test was 405·2 μg ($\pm$ 201·7) and 180·6 mg ($\pm$ 115·1), respectively, (Mann–Whitney two-tailed $Z = -2{\cdot}69$; $P < 0{\cdot}01$); for M locos the values were 514·7 μg ($\pm$ 180·5) and 246·9 μg ($\pm$ 14·35), respectively, ($Z = -2{\cdot}77$; $P < 0{\cdot}01$); in L locos the values were 1236·7 μg ($\pm$ 346·6) and 818·9 μg ($\pm$ 402·2), respectively, ($Z = -2{\cdot}29$; $0{\cdot}01 < P < 0{\cdot}05$). Based on average size-specific HT values of experienced locos, a reduction in the average TPW following exposure to the sea star is translated into a reduction in the average time spent in foraging (ordinate in Fig. 4): in the case of S locos this is from 170 min day^{-1} to 78 min day^{-1}, from 56 min day^{-1} to 29 min day^{-1} for M locos, and from 150 min day^{-1} to 103 min day^{-1} for L ones (significance levels are the same as those relative to TPW comparisons).

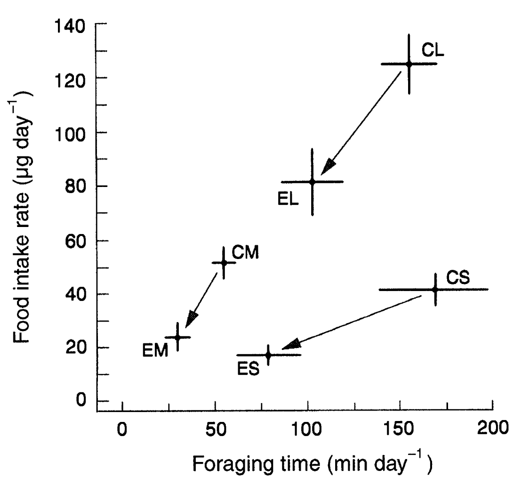

Fig. 4. Daily average of food intake rate (ordinate) and daily estimated time devoted to foraging (abscissa) by experienced *C. concholepas* unexposed (C) and exposed (E) to the sea star *M. gelatinosus*. S, M, L correspond to small, medium and large locos, respectively. Vertical and horizontal segments represent standard error.

Discussion

Differences in handling times between size classes of inexperienced locos are probably due to size-related functional constraints. The general reduction seen in handling times and the consequent increase in prey profitabilities with increasing exposure to the prey, observed in all the classes of *C. concholepas*, accords with similar findings for other predatory gastropods (Morgan 1972 in Hughes 1979; Edwards & Huebner 1977; Hughes & Dunkin 1984). We believe that this effect was due to increased experience with the prey and not simply to acclimatization to the laboratory conditions, because both inexperienced and experienced groups were treated similarly before testing. The particular component of the handling process which was specifically improved by experience is, however, unknown. Mendez & Cancino (1990) reported that locos with a peristomial length greater than 18 mm prey on mussels by forcing the valves apart with the anterior portion of the foot. Hence the experience on *P. purpuratus* may have specifically enhanced this capacity.

The average increase in profitability of classes I–III mussels for S locos (by a factor of 1·4) was less than that for M and L locos (× 2·2 and × 1·8, respectively) and may be due to stronger functional constraints acting on the smaller locos, limiting the effect of experience. It is interesting that the largest increase in profitability following experience corresponded to class II mussels for S locos (× 2·3) and to class III for M and L ones (× 4·3 and × 2·3, respectively). In the latter two cases, this resulted in a shift in size-related ranking of prey profitability, with class III mussels becoming clearly the most profitable for experienced predators. This observation strongly supports Hughes' (1980) prediction that changes in prey value, due to learning by the predator, are likely to transpose the rank preferences of different prey types which are not too dissimilar in value.

As a result of experience, the three size classes of predator changed their prey preferences in accordance with the independently observed variation in prey profitability. Thus, after feeding on *P. purpuratus* each size class of predators showed a preference for the most profitable class of mussels, in agreement with the predictions of classical models based on energy maximization (Stephens & Krebs 1986) and similar to reports for other muricids (Hughes & Dunkin 1984; Palmer 1984).

The benefit of actively selecting more profitable prey and increasing the attack rate, is an increase in food intake per unit time, by a factor of 1·5, 1·9 and 1·8 in S, M and L locos, respectively. This increase in foraging efficiency was obtained despite a slight decrease in the time spent foraging from the first to the third period. This latter finding strongly suggests that the observed effects were due to an improvement of foraging skills resulting from experience with the prey, rather than simply to acclimatization to the laboratory conditions.

Intertidal locos (S and M classes) remain within shelters when inactive (authors' personal observations), moving out only for the purpose of foraging. Hence, total foraging time represents the time when locos are at risk to predation, and this may be expected to be traded-off against foraging efficiency (Godin 1990; Lima & Dill 1990). Interestingly, the data in the present study reveal different responses to the higher-order predator, depending on the loco's size: S specimens reduced slightly their attack rate, but markedly shifted their preference towards smaller prey. M and L specimens, on the other hand, did not significantly alter their relative preference for different size classes of prey, but instead reduced their overall attack rate. This difference can be explained by considering the handling times of different size classes of experienced locos preying upon different-sized mussels: the S locos, for which—due to functional constraints—handling larger mussels remains time-consuming, even after prolonged experience, reduced the time spent foraging by selecting prey requiring a lower handling time. In contrast, the other two size classes of locos, for which experience reduced the differences in handling times for different-sized prey, reduced their overall attack rate. These differences in prey selection and attack rate produced a size-related effect in terms of exposure to the higher-order predator which probably reflects a different vulnerability of the different size classes of locos. Thus, the estimated time devoted to foraging was reduced under risk of sea star predation by a factor of 0·54, 0·49 and 0·34 in S, M and L locos, respectively. The cost of reducing predation risk, evaluated as the corresponding reduction of food intake per unit time, amounts to factors of 0·55, 0·52, 0·34 in S, M and L specimens, respectively.

In conclusion, this study shows that *C. concholepas*, when free from external constraints and well acquainted with a given prey, adopts an energy maximization strategy based on improving the handling efficiency and on selecting prey of different sizes according to their relative profitability. However, when risk of mortality associated with foraging increases, locos switch to a time minimization strategy, which is obtained through different mechanisms by different-sized foragers.

More generally, this study provides specific evidence on how experience and risk of predation affect the dietary decisions of a forager, and confirms the validity, under particular circumstances, of the energy maximization premise underlying the original approach to the study of optimal diets (Schoener 1987), but also stresses the need for dynamic, state-dependent methods in the study of foraging behaviour (Burrows & Hughes 1991; Houston 1993).

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