Effect of age, injury, and predator odors on settlement and shelter selection by lobster *Homarus americanus* postlarvae*

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ABSTRACT: The effects of endogenous and exogenous factors on settlement and habitat selection behaviours of *Homarus americanus* postlarvae were studied under controlled conditions in the laboratory. Light level within shelters, a primary cue used in microhabitat selection by settling lobsters, was manipulated to create 4 microhabitats of different quality (= level of illumination). Preliminary experiments indicated that, when offered separately, low light intensity shelters induced more postlarvae to settle and seek a shelter than microhabitats presenting higher light levels. Choice experiments (all types of shelter offered simultaneously) were designed to test whether (1) delayed settlement, (2) injuries at metamorphosis (loss of one or both chelipeds), and (3) metabolites of the fish predator *Tautogolabrus adspersus*, influenced settlement rate and selectivity of competent lobsters. Postlarvae settled more quickly and sheltered less selectively as they aged. Similarly, postlarvae released in seawater previously conditioned by *T. adspersus* tended to exhibit a higher settlement rate and lower degree of selectivity than when tested in control (unconditioned) water. Lobsters which had lost both chelipeds at metamorphosis exhibited a reduced settlement rate compared to normal postlarvae or postlarvae with a single chela. Severely injured postlarvae also appeared less selective than normal or slightly injured postlarvae. Implications of these results for further habitat choice experiments are discussed.

INTRODUCTION

Most benthic marine invertebrates have a complex life cycle including a pelagic dispersal phase which can extend from a few minutes in some species to several months in others (Thorson 1950, Mileikovsky 1971, Scheltema 1986). By the end of this planktonic period, behaviourally competent larvae (*sensu* Coon et al. 1990, Fitt et al. 1990) typically settle in response to appropriate environmental stimuli characteristically associated with their preferred juvenile habitat (see reviews by Chia & Rice 1978, Burke 1983, Crisp 1984, Morse 1985, Hadfield & Miller 1987, Svane & Young 1989). In the absence of a suitable site for settlement (Birkeland et al. 1971, Highsmith 1982, Young 1989,

O'Connor 1991), or under conditions unfavorable to subsequent survival and growth (e.g. in the presence of a dominant competitor, Grosberg 1981, Young & Chia 1981, Petersen 1984), many species can prolong their planktonic life, thus demonstrating an important degree of selectivity for the substratum. Whereas environmental cues involved in the settlement process of benthic marine invertebrates have received considerable attention, there is little understanding of how endogenous and exogenous factors affect habitat choice behaviour of larvae (i.e. responses to environmental cues) during this process.

Age of competent larvae has been recognized as one of the potential endogenous factors influencing their ability to discriminate among habitats of different quality at settlement. For instance, Knight-Jones (1953) observed that larvae of the polychaete *Spirorbis borealis* exhibited a lower degree of selectivity when settling after an artificially prolonged pelagic phase, a

result further reported for mollusc (Coon et al. 1990), barnacle (Rittschof et al. 1984), and echinoderm larvae (Highsmith 1982). Other intrinsic (e.g. physical condition of larvae) and extrinsic factors (e.g. presence of predators or competitors) may also modify larval responses to settlement cues. To date, however, few attempts have been made to test their importance experimentally. The present study investigates the effect of age, presence of injuries, and odors emitted by predators on the behavioural responses of the American lobster *Homarus americanus* postlarvae to a single cue (light intensity within shelters) at settlement.

Homarus americanus passes through 3 planktonic larval stages before metamorphosing and settling as a postlarva (Charmantier et al. 1991). Although behavioural competence is reached shortly after metamorphosis (Botero & Atema 1982), evidence of considerable flexibility in the timing of settlement has been reported, both in the field (Cobb et al. 1989) and in the laboratory (Cobb 1968, Botero & Atema 1982). Lobsters settle preferentially and more quickly on hard heterogeneous bottoms than on soft, featureless substrata (Botero & Atema 1982). We suggested that light intensity within shelters could be the primary cue involved in microhabitat selection by settling lobsters (Boudreau et al. 1990), postlarvae strongly preferring opaque to transparent shelters. In the present study, this factor was manipulated to create 4 microhabitats of different quality (level of illumination). Experiments were specifically designed to test whether settlement rate and selectivity of competent *H. americanus* are affected when postlarvae (1) settle during the dark phase of the light cycle (i.e. when the light cue is unavailable), (2) postpone their settlement; (3) are injured (i.e. when they have lost one or both chelipeds at metamorphosis); and (4) settle in water conditioned by fish predators (cunner *Tautogolabrus adspersus*) compared to an unconditioned control.

MATERIALS AND METHODS

Homarus americanus postlarvae were reared in the facilities of the Maurice-Lamontagne Institute (Department of Fisheries and Oceans, Mont-Joli, Québec, Canada) as described in Boudreau et al. (1991). Nineteen ovigerous females (from Iles-de-la-Madeleine, Gulf of St. Lawrence, Canada) were held individually in running seawater and fed a daily ration of mussels *Mytilus edulis* or northern shrimp *Pandalus borealis*. The females' tanks were maintained at constant temperature, ranging from 11 to 19 °C, to spread hatchings over a 2 mo period. Larvae of the same age ($\Delta t \leq 24$ h) were reared together in 60 l kreisel tanks (initial

density <40 ind. l^{-1}) and fed once daily ad libitum a highly concentrated suspension of newly-hatched brine shrimp nauplii *Artemia franciscana*. To provide a continuous larval supply during the experiments, the kreisel tanks were kept at different temperatures (from 13 to 20 °C), using thermoregulated heating rods ($\Delta T \pm 0.5$ °C). Both ovigerous females and larvae were maintained under an artificial (12L:12D) light cycle with simulated periods of dawn and dusk.

General experimental procedure. All experiments were carried out using rectangular low profile shelters (cavity of 0.5 cm height × 1 cm width × 4.5 cm length) similar to those described in Boudreau et al. (1990, Fig. 1C). Previous observations have shown that shelters of this size cannot accommodate more than 1 postlarva at one time. Since the light level within shelters is an important cue in microhabitat selection for settling lobsters (Boudreau et al. 1990), this factor was manipulated to create a gradient in shelter quality. Four types of microhabitat, corresponding to shelters offering different light intensities (measured with a Biospherical quantum meter), were obtained (Fig. 1a). High and low light intensity shelters were made of transparent and opaque Plexiglas, respectively. Shelters with intermediate levels of illumination were obtained by painting the outside of transparent shelters to the desired level of opacity using a dark felt-tip pen. This procedure did not substantially alter the quality of the visible light spectrum (400 to 700 nm) transmitted by the different shelters (measured with a Shimadzu DUAL-wavelength/double-beam spectrophotometer, Model UV-3000) (Fig. 1b). Painting was carefully calibrated to create a light intensity gradient as linear as possible from black to transparent shelters (Fig. 1a). The 4 types of shelter were rinsed for 48 h in running seawater prior to experimentation to enhance attractiveness.

The shelters tested were randomly placed in a 4 × 6 matrix on the bottom of a 54 l aquarium (60 × 30 × 30 cm) which had previously been covered by a layer of coarse sand, 2 cm thick (grain size ≤ 1.12 mm). The sand was collected in the intertidal zone on the south shore of the Lower St. Lawrence Estuary near Sainte-Flavie (Québec, Canada). Such a soft substratum is unsuitable for lobster burrowing (Botero & Atema 1982), but was found to promote settlement when offered in conjunction with structural shelters (Boudreau pers. obs.). At the beginning of the experiments, a fixed number of light- and temperature-adapted postlarvae were released haphazardly at the surface of the aquarium and a period of 5 or 48 h was allowed for settlement (see below). The number of swimming postlarvae (non-settled individuals) was recorded regularly during this period. Temperature and salinity in the test conditions were 17.3 ± 1.2 °C and 28 ± 1 ‰
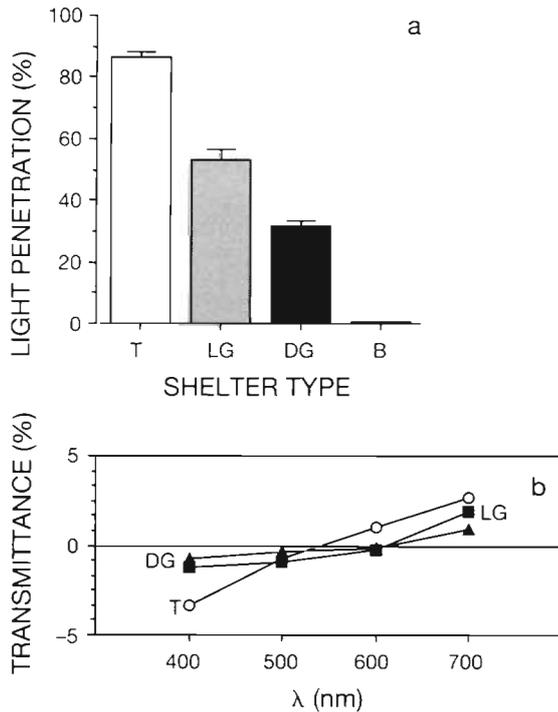
Fig. 1. Characteristics of the 4 types of shelter used in experiments. (a) Light penetration as a proportion of the ambient light intensity (mean ± SD, n = 10). (b) Percentage of transmittance (deviation from the mean transmittance of a given shelter type) in the visible light spectrum. B = black, DG = dark gray, LG = light gray, T = transparent shelter

(mean ± SD, n = 60 and n = 23), respectively. Postlarvae reared at lower temperatures were gradually acclimated ($\Delta T \leq 2\,°C\ d^{-1}$) to the experimental temperature prior to testing. Lobsters used were uninjured and at least 4 d old since moulting to the fourth stage (except where otherwise stated: see 'Degree of selectivity of postlarvae'). All the experiments were conducted in 5 µm filtered and sterilized standing water under a 12L:12D cycle. Ambient light intensity on the bottom of the experimental tanks was $22.35 \pm 0.26\ \mu E\ m^{-2}\ s^{-1}$ during the day (mean ± SD, n = 10). The corresponding light intensities within the different shelters were as follows: Transparent (T): 19.27 ± 0.44; Light Gray (LG): 11.89 ± 0.41; Dark Gray (DG): 7.02 ± 0.42; Black (B): $0.13 \pm 0.05\ \mu E\ m^{-2}\ s^{-1}$ (mean ± SD, n = 10). Postlarvae were used only once and were not fed during the experiments. Each experimental treatment was replicated 4 times (= 4 aquaria) at the same time of day, to control for any possible effects of an endogenous activity rhythm. Statistical analyses were conducted on SAS (SAS Institute 1989).

Shelter quality. The effectiveness of the different shelters in inducing settlement and sheltering behaviour of competent postlarvae was used as a relative measure of microhabitat quality. This index was deter-

mined by offering each type of shelter separately to postlarvae. Thirty 8-d-old postlarvae were released per replicate at the start of the experiment (total no. used = 480). The number of swimming, sheltered (> 3/4 body length in shelter), and benthic unsheltered postlarvae was then recorded once every 4 h during 2 d. Night counts were carried out using a red light (see Boudreau et al. 1990). To avoid disturbances during the experiment, the number of sheltered postlarvae was obtained by subtracting swimming and benthic unsheltered postlarvae from the total number of individuals initially introduced to the aquarium. This method was reliable since mortality during the experiment was low (4.2 ± 1.2 %; mean ± SE, n = 16) and did not differ significantly among treatments (1-way ANOVA on arcsine transformed data, $F = 0.76$, df = 3,12, p = 0.54).

The influence of shelter type on postlarval settlement and shelter occupancy was tested using repeated measures ANOVAs (2-way split-plot factorial design; Kirk 1982), with shelter type and time as main effects. Specific contrasts and multiple comparisons (SNK test, $\alpha = 0.05$) were used to analyze further any significant interactions or treatments, respectively (Kirk 1982). The multisample circularity assumption underlying repeated measures ANOVAs was verified using a sphericity test. When the circularity was rejected ($\alpha = 0.05$), the probability of making a type I error (p) was adjusted according to the Greenhouse-Geisser's coefficient (Kirk 1982). Data were arcsine transformed to satisfy assumptions of normality and homoscedasticity as determined by stem-and-leaf diagrams and cumulative probability plots of residuals, and Cochran's C-tests, respectively (Kirk 1982). Untransformed data are presented in figures.

Degree of selectivity of postlarvae. Four experiments, using the same general design, were carried out to determine the influence of different factors likely to affect the degree of selectivity of settling lobster postlarvae (Table 1). Six shelters of each of the 4 types were offered simultaneously to postlarvae and a period of 5 h was allowed for settlement and microhabitat selection. In order to follow the settlement rate, the number of swimming postlarvae was recorded at 15 min intervals during the first hour and at 30 min intervals thereafter. At the end of the experiment, postlarvae in shelters were individually counted and removed. To ensure each type of shelter was limiting, 15 postlarvae were used per replicate (for a ratio of 2.5 postlarvae per type of shelter). All experiments were carried out during the daylight portion of the light cycle, except for Expt 1 where a part was conducted during the dark phase (see Table 1). Red fluorescent lights (wavelengths between 600 and 700 nm) were then used to minimize light disturbance (Boudreau et al. 1991). Age treatments in Expt 2 were obtained by

Table 1. Summary of experiments carried out on factors influencing the degree of selectivity of *Homarus americanus* postlarvae at settlement (n = 4 replicates). Age of postlarvae in days since moult to the fourth stage

	Expt 1	Expt 2	Expt 3	Expt 4
Factor tested	Light phase	Age of postlarvae	Degree of injury	Odors emitted by a fish predator
Treatment levels	Light, Dark	4, 8, 12, 16	Postlarvae with 2, 1, 0 cheliped(s)	Control (unconditioned), predator-treated water
Age of postlarvae	5	4, 8, 12, 16	12	8
Total no. of postlarvae	120	240	180	120

keeping postlarvae in the rearing tanks for periods of various durations (4 to 16 d after the moult to stage IV). Injured postlarvae used in Expt 3 were haphazardly chosen among those that had lost one or both chelipeds at metamorphosis (based on daily observations). Finally, predator-conditioned water used in Expt 4 was obtained by maintaining 3 cunners *Tautogolabrus adspersus* for 24 h in a closed 54 l aquarium (= 1 replicate).

The proportion of swimming postlarvae was analyzed as a function of treatment (e.g. light phase; see Table 1) and time with repeated measures ANOVAs (2-factor split-plot design; Kirk 1982). The effects of the different treatments on shelter selection at the end of the experiments were tested using 2-way fixed-factor ANOVAs with shelter type and specific treatment (see Table 1) as main effects. Interactions were examined with unplanned pairwise comparisons (LSD test) with the level of significance (α) adjusted for the Bonferroni inequality (Kirk 1982). Where appropriate, significant treatment effects were analyzed using the SNK procedure ($\alpha = 0.05$). For all statistical tests, data were arcsine transformed to fulfill conditions of normality and homogeneity of variances. Untransformed data are used in the figures. No mortality occurred during the experiments.

RESULTS

Shelter quality

In the absence of choice (each type of shelter offered separately), low light intensity shelters induced a significantly higher proportion (mean ± SE, n = 48) of postlarvae to settle than shelters allowing greater light penetration (Table 2a, Fig. 2a; B: 84.4 ± 1.2 > DG: 79.7 ± 1.2 > LG: 74.2 ± 1.4 > T: 71.2 ± 1.6 %; SNK test). Shelter

type also influenced the proportion of sheltered postlarvae but only during the light phase of the day/night cycle (Table 2b, Fig. 2b; B: 69.6 ± 2.7, DG: 57.1 ± 3.2, LG: 49.0 ± 2.1, T: 42.7 ± 2.8 %; mean ± SE, n = 24). During dark periods, all types of microhabitat tended to be equally colonized, particularly on the second night (Table 2b, Fig. 2b). In contrast, shelter type had no significant effect on the proportion of postlarvae settling in open areas (Table 2c, Fig. 2c). The percentage of swimming, sheltered, and benthic unsheltered postlarvae varied significantly with time, major changes being observed during the transitional periods between light and dark phases (Table 2, Fig. 2).

Table 2. *Homarus americanus.* Split-plot factorial ANOVAs of the effect of shelter type on settlement of postlarvae (n = 4 replicates). The proportion of (a) swimming, (b) sheltered, and (c) benthic unsheltered postlarvae was monitored at 4 h intervals during 48 h. When the circularity assumption was rejected (sphericity test, Kirk 1982), the p-value was adjusted according to the Greenhouse-Geisser's coefficient. Interaction in (b) was analyzed using specific contrasts testing the effect of shelter type for day and night periods separately

| Source of variation	df	MS	F-ratio	p > F
(a) Swimming postlarvae				
Shelter type	3	0.2525	6.10	0.0092
Time	11	0.0701	11.68	0.0001
Shelter × Time	33	0.0066	1.10	0.3863
Replicate (Shelter)	12	0.0414		
Time × Replicate (Shelter)	132	0.0060		
(b) Sheltered postlarvae				
Shelter type	3	0.3994	2.47	0.1119
Time	11	0.0459	7.06	0.0001
Shelter × Time	33	0.0102	1.57	0.0385
Shelter during the day	3	0.3667	4.36	0.0269
Shelter during the night	3	0.0875	1.04	0.4100
Replicate (Shelter)	12	0.1617		
Time × Replicate (Shelter)	132	0.0065		
Error for specific contrasts	12	0.0841		
(c) Benthic unsheltered postlarvae				
Shelter type	3	0.0621	0.29	0.8318
Time	11	0.0277	4.62	0.0001
Shelter × Time	33	0.0057	0.95	0.5552
Replicate (Shelter)	12	0.2140		
Time × Replicate (Shelter)	132	0.0060		
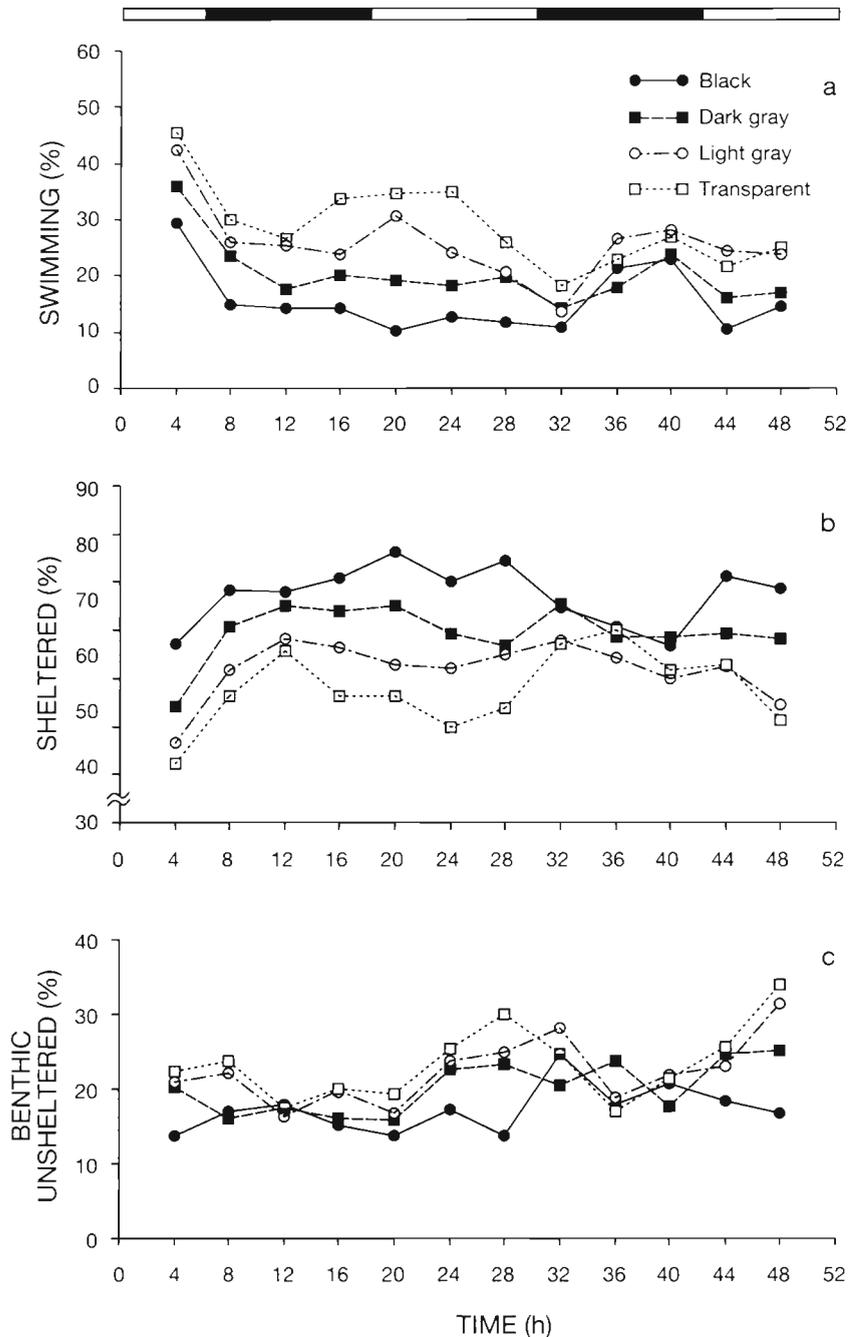
Fig. 2. *Homarus americanus*. Mean proportion of (a) swimming, (b) sheltered, and (c) benthic unsheltered postlarvae in relation to the type of shelter offered (n = 4 replicates). Error bars were omitted for more clarity. Black bars over the graphs represent the dark phase

Influence of light conditions

Light phase apparently had no detectable effect on the settlement rate of lobster postlarvae since there was no significant interaction between light phase and time in the ANOVA (Table 3a, Fig. 3a). The proportion

of swimming postlarvae was not significantly affected by the light regime (light: 40.6 ± 2.1 %, dark: 46.5 ± 2.5 %; mean ± SE, n = 48) but the percentage of swimming post-larvae declined consistently during the experimental period, both in light and dark conditions (Table 3a, Fig. 3a). On average, about 73 % of postlarvae had settled by the end of the experiment (Fig. 3a).

The mean proportion of shelters occupied at the end of the experiment did not differ significantly under light and dark conditions (27.1 ± 7.4 and 28.1 ± 5.8 %, respectively) but was strongly affected by shelter type (Table 4a, Fig. 3b). Overall, based on the percentage of occupancy (mean ± SE, n = 8), black shelters were preferred to the 3 other types, dark gray shelters were selected preferentially to light gray and transparent shelters, while the latter 2 categories did not differ significantly (B: 64.6 ± 5.8 > DG: 27.1 ± 4.4 > LG: 10.4 ± 4.4 = T: 8.3 ± 4.4 %; SNK test). Selected pairwise comparisons revealed, however, that this pattern was more representative of the preferences of postlarvae during the light period (Table 4b, Fig. 3b). During the dark phase, the only significant differences observed were between dark shelters and shelters presenting higher light penetration (light gray and transparent shelters), other pairwise comparisons being statistically non-significant (Table 4b, Fig. 3b).

Influence of age of postlarvae

The proportion of swimming post-larvae was influenced by both main factors (postlarval age and time) and their interaction (Table 3b). The interaction effect was primarily attributable to higher settlement rate of 4-d-old postlarvae in the first hour of the experiment compared to that of older individuals (Fig. 4a). The percentage of swimming postlarvae (mean ± SE, n = 48) was inversely related to the age of postlarvae (Fig. 4a; 4 d: 49.3 ± 2.5 > 8 d: 33.7 ± 1.6 > 12 d: 25.7 ± 1.8 > 16 d: 14.0 ± 1.8 %; SNK test). The

Table 3. *Homarus americanus*. Split-plot factorial ANOVAs testing the effects of (a) light phase, (b) age of postlarvae, (c) degree of injury of post-larvae, and (d) odors emitted by fish predators, on settlement of postlarvae. The p-values were adjusted according to the Greenhouse-Geisser's coefficient. See Figs. 3a to 6a for mean ± SE values per level of treatment

Source of variation	df	MS	F-ratio	p > F
(a) Experiment 1				
Light phase	1	0.0936	0.86	0.3895
Time	11	0.1453	20.18	0.0001
Phase × Time	11	0.0043	0.60	0.6427
Replicate (Phase)	6	0.1088		
Time × Replicate (Phase)	66	0.0072		
(b) Experiment 2				
Age	3	1.7431	14.60	0.0003
Time	11	0.2438	30.86	0.0001
Age × Time	33	0.0188	2.38	0.0187
Replicate (Age)	12	0.1194		
Time × Replicate (Age)	132	0.0079		
(c) Experiment 3				
Degree of injury	2	0.3968	3.01	0.0998
Time	11	0.0528	12.00	0.0001
Injury × Time	22	0.0099	2.25	0.0585
Replicate (Injury)	9	0.1318		
Time × Replicate (Injury)	99	0.0044		
(d) Experiment 4				
Water conditioning	1	0.6635	3.89	0.0960
Time	11	0.0559	7.35	0.0013
Water × Time	11	0.0073	0.96	0.4417
Replicate (Water)	6	0.1705		
Time × Replicate (Water)	66	0.0076		

tion of dark gray, light gray and transparent shelters when black shelters were limited (Table 5b, Fig. 4b). Apparently, shelters unsuitable for younger postlarvae seemed acceptable to older individuals. As a result, the overall percentage of shelter occupied (mean ± SE, n = 16) increased significantly with age of postlarvae (Table 5a, Fig. 4b; 4 d: 31.2 ± 10.5 = 8 d: 35.4 ± 8.8 < 12 d: 43.7 ± 10.4 < 16 d: 53.1 ± 8.5 %; SNK test).

Influence of degree of injury

Lobsters which had lost both chelipeds at metamorphosis exhibited a reduced settlement rate compared to normal individuals and those with 1 chela (Fig. 5a), although this difference was non-significant (see interaction term in Table 3c). After 5 h, the proportion of the 'no cheliped' swimming postlarvae was significantly higher than for the 2 other levels of treatment (Fig. 5a; LSD test, p = 0.0001). In contrast, the loss of only 1 cheliped at metamorphosis did not seem to affect the settlement rate of lobster postlarvae when compared to control condition (i.e. normal postlarvae) (Fig. 5a).

overall mean proportion of settled postlarvae was 81 % at the end of the experimental period.

Shelter selection was also strongly influenced by the age of postlarvae (see interaction term in Table 5a, Fig. 4b). Young postlarvae (4 d old) preferred shelters characterized by lower levels of illumination (mainly black shelters) and prolonged their planktonic phase rather than sheltering in suboptimal (high light intensity) microhabitats (Fig. 4a, b). In contrast, older postlarvae (16 d old) occupied a significantly higher propor-

The habitat selection behaviour of settling lobsters was also modified when postlarvae were severely injured during metamorphosis (Fig. 5b) but results were not statistically significant (interaction term in Table 6a). Normal and slightly injured postlarvae preferred black to dark gray shelters, and dark gray to light gray and transparent shelters (Table 6b). In comparison, postlarvae without chelipeds appeared much less selective and did not discriminate between shelters of neighbouring levels of illumination (Table 6b,
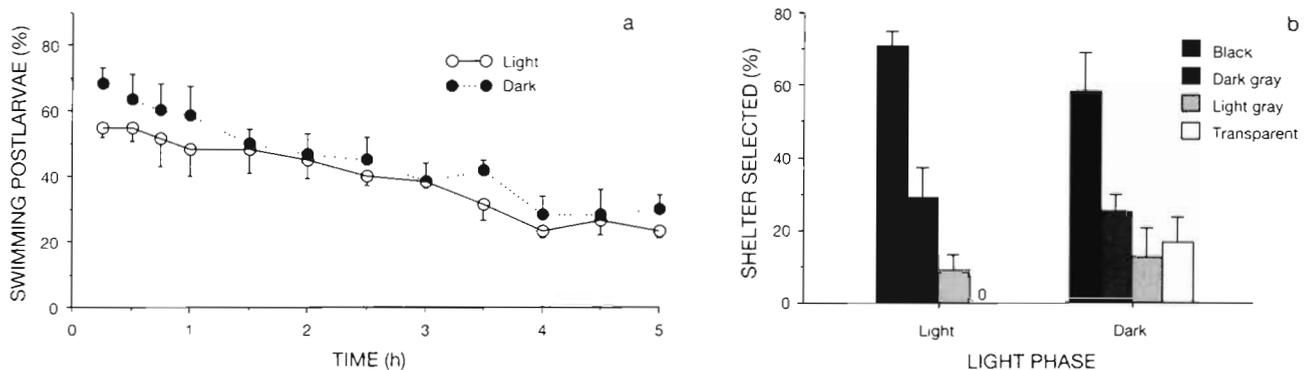

Fig. 3. *Homarus americanus*. (a) Settlement and (b) shelter selection by postlarvae in relation to light conditions during the experiment. Each point in (a) indicates the mean ± SE for 4 replicate aquaria. Data in (b) represent the proportion (mean ± SE, n = 4 replicates) of shelters of each type occupied by a postlarva at the end of the experiment. Twenty-four shelters (6 of each type) were offered simultaneously to postlarvae. 0 indicates that no shelter of this type was selected by postlarvae

Table 4. *Homarus americanus*. (a) Two-way ANOVA testing the effect of light phase and shelter type on shelter occupancy. (b) Interaction was examined with unplanned pairwise comparisons (LSD test) with the level of significance (α) adjusted for the Bonferroni inequality (Kirk 1982). Dashed lines underscore shelter types that do not significantly differ for a given light condition (see Fig. 3b for means ± SE). Shelter types as in Fig. 1

(a) ANOVA

Source of variation	df	MS	*F*-ratio	p > *F*
Light phase	1	0.0295	0.72	0.4044
Shelter type	3	0.9713	23.69	0.0001
Phase × Shelter	3	0.0922	2.25	0.1084
Residual	24	0.0410		

(b) Interaction

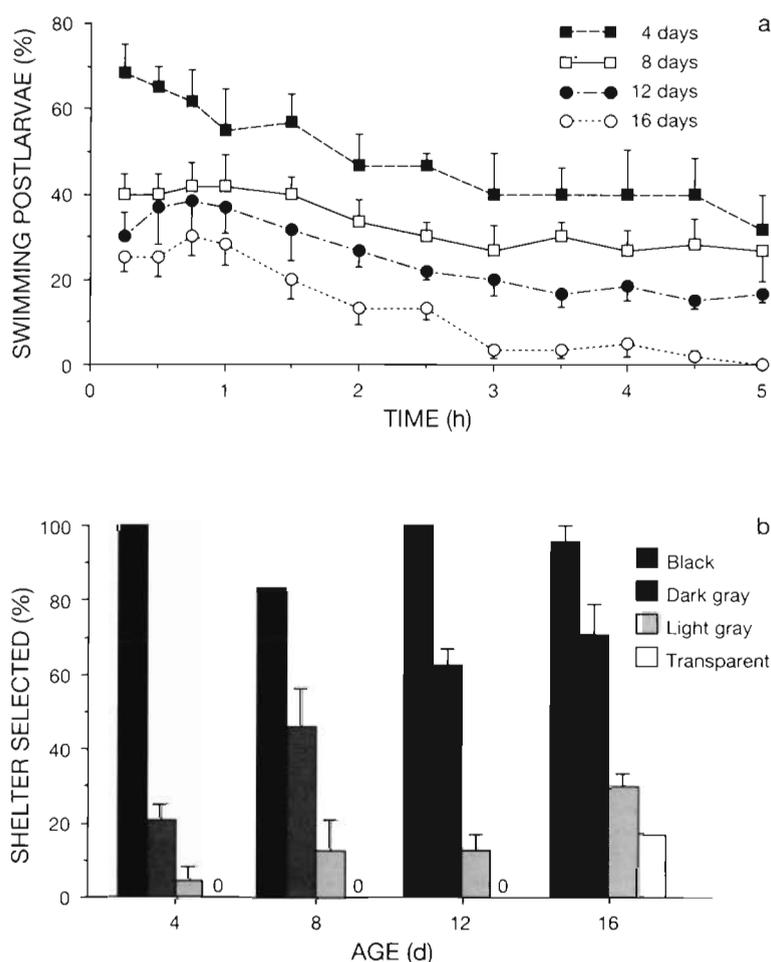| Light condition		Shelter type		
Light	B	DG	LG	T
Dark	B	DG	LG	T

Fig. 4. *Homarus americanus*. (a) Settlement and (b) shelter selection by postlarvae in relation to age since metamorphosis (i.e. moult to the fourth stage). Data presentation (mean ± SE, n = 4) as in Fig. 3

Fig. 5b) Moreover, severely injured postlarvae were the only ones selecting transparent shelters (Fig. 5b). In summary, postlarvae lacking chelipeds selected fewer black and dark gray shelters and more light gray and transparent shelters than normal postlarvae or postlarvae with a single chela (Fig. 5b).

Influence of odors emitted by fish predators

The proportion of swimming postlarvae (mean ± SE, n = 48) was lower in water conditioned by metabolites of the fish predator *Tautogolabrus adspersus* than in control (unconditioned) water (22.9 ± 1.9 and 37.5 ± 2.0 %, respectively; Fig. 6a). However, this difference was not statistically significant (Table 3d). Conversely, the mean proportion of postlarvae observed in open areas on the bottom was significantly higher when postlarvae settled in water conditioned by *T. adspersus* (16.1 ± 1.1 and 7.4 ± 1.0 %, respectively; 2-factor split-plot ANOVA; Water conditioning: $F = 5.65$, $df = 1,6$, $p = 0.05$; Time: $F = 1.21$, $df = 11,66$, $p = 0.33$; Interaction: $F = 0.61$, $df = 11,66$, $p = 0.63$; Fig. 7). The percentage of swimming postlarvae decreased consistently with time (Fig. 6a) but did not vary significantly with water condition (interaction term in Table 3d). On average, 83 % of postlarvae settled by the end of the 5 h experimental period (Fig. 6a).

The overall proportion of shelters occupied (mean ± SE, n = 16) was not significantly influenced by water condition (control: 40.6 ± 10.3, predator-treated: 42.7 ± 9.4 %; Table 7a). As in the previous experiments, black shelters were preferred to dark gray shelters, and dark gray shelters were selected preferentially to light gray and transparent ones (B: 97.9 ± 2.1 > DG: 47.9 ± 7.3 > LG: 12.5 ± 4.2 = T: 8.3 ± 4.4 %; mean ± SE, n = 8; SNK test; Fig. 6b). When shelter effects were examined within each water condition, however, the selectivity of lobster postlarvae appeared to be higher in control than in predator-treated water (Table 7b, Fig. 6b). In particular, 16.7 ± 6.8 % of transparent shelters were occupied when postlarvae were released in water conditioned by predators.

Table 5. *Homarus americanus*. (a) Two-way ANOVA examining the effect of age of postlarvae and shelter type on shelter occupancy. (b) Interaction was analyzed using unplanned pairwise comparisons (LSD test) with the level of significance (α) adjusted for the Bonferroni inequality (Kirk 1982). Dashed lines underscore age treatments that do not significantly differ for a given shelter type (see Fig. 4b for mean ± SE values)

(a) ANOVA

Source of variation	df	MS	*F*-ratio	p > *F*
Age of postlarvae	3	0.3973	18.92	0.0001
Shelter type	3	5.6089	267.09	0.0001
Age × Shelter	9	0.1036	4.93	0.0001
Residual	48	0.0210		

(b) Interaction

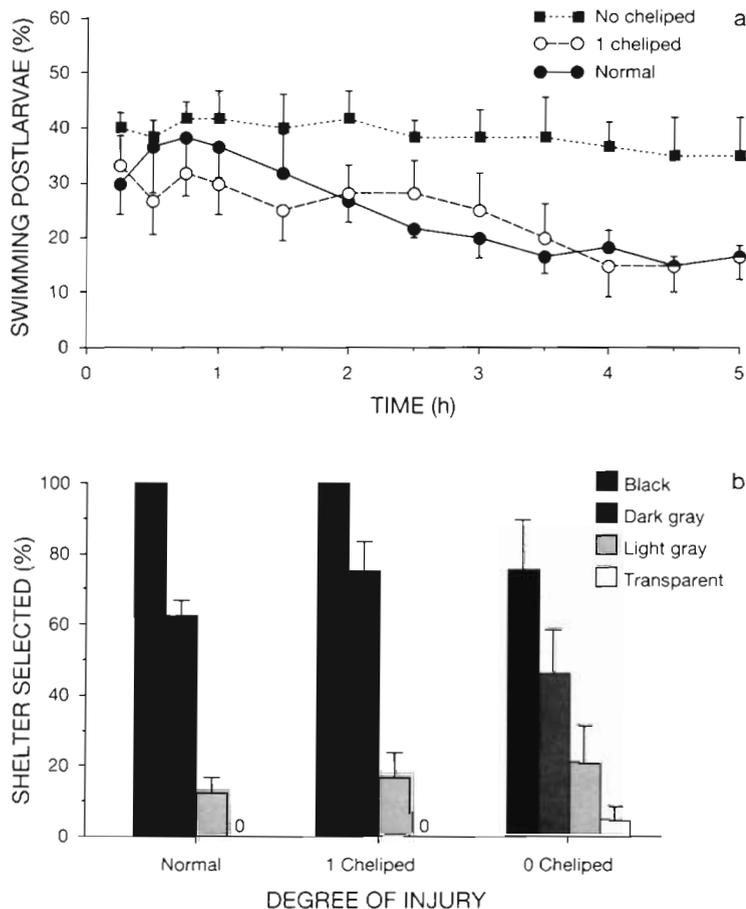| Shelter type	Age of postlarvae (d)			
Black	4	12	16	8
Dark gray	4	8	12	16
Light gray	4	8	12	16
Transparent	4	8	12	16

Fig. 5. *Homarus americanus*. (a) Settlement and (b) shelter selection by postlarvae suffering from different degrees of injury. Data presentation (mean ± SE, n = 4) as in Fig. 3

DISCUSSION

Establishing a range of microhabitat quality was essential to the conduct of experiments on factors influencing the degree of selectivity of settling *Homarus americanus* postlarvae. This prerequisite condition was verified by submitting postlarvae to one type of shelter at the time. Based on previous observation that settling lobsters significantly preferred opaque to transparent shelters in choice experiments (Boudreau et al. 1990), we predicted that low light intensity shelters would be more efficient in inducing settlement and sheltering behaviour of competent postlarvae than shelters characterized by higher levels of illumination. Results (Table 2, Fig. 2) indicate that the average proportion of postlarvae settling during the experimental period (48 h) was negatively correlated to the relative amount of ambient light penetrating into the shelters (Pearson product-moment correlation, r = −0.98), suggesting a strong linear relationship between settlement intensity and the quality of shelters offered to postlarvae. This result is consistent with earlier observations by Botero & Atema (1982) and Cobb et al. (1989) who reported that the onset of settlement is substratum-dependent in lobsters. In the presence of an appropriate substratum, postlarvae have been found competent to settle as early as 1 d (Botero & Atema 1982) or 2 d (Cobb et al. 1989) after metamorphosis, whereas postlarvae could prolong their planktonic life over 2 wk when a suitable substratum for settlement was lacking (Botero & Atema 1982). Analogous results have been obtained with other crustacean megalopae (Christy 1989, Jensen 1991, O'Connor 1991). In addition to promoting settlement, low light intensity microhabitats also induced a higher proportion of postlarvae to seek shelter, especially during the day (Table 2b), substantiating the prediction that the level of light within a shelter would be responsible for the difference in microhabitat quality.

If shelters differed only in quality on the basis of their transparency, one might expect the different types of shelter to be equally colonized when postlarvae settled under dark rather than light conditions.

Table 6. *Homarus americanus*. (a) Two-way ANOVA testing the effect of the degree of injury and shelter type on shelter occupancy. (b) Interaction was analyzed using unplanned pairwise comparisons (LSD test) with the level of significance (α) adjusted for the Bonferroni inequality (Kirk 1982). Dashed lines underscore shelter types that do not significantly differ for a given degree of injury (see Fig. 5b for mean ± SE values). Shelter types as in Fig. 1

(a) ANOVA

Source of variation	df	MS	F-ratio	p > F
Degree of injury	2	0.1019	2.34	0.1109
Shelter type	3	4.4638	102.38	0.0001
Injury × Shelter	6	0.0981	2.25	0.0601
Residual	36	0.0436		

(b) Interaction

Degree of injury	Shelter type			
Normal	B	DG	LG	T
1 cheliped	B	DG	LG	T
0 cheliped	B	DG	LG	T

Fig. 6. *Homarus americanus*. (a) Settlement and (b) shelter selection by post-larvae released in filtered and sterilized seawater (control), and in water conditioned by fish predators (treated). Data presentation (mean ± SE, n = 4) as in Fig. 3

Selected pairwise comparisons revealed that the discrimination capacities of post-larvae were indeed strongly reduced in darkness. Nevertheless, even in dark conditions, postlarvae preferentially colonized black as compared to light gray and transparent shelters (Table 4b, Fig. 3b). This suggests that part of the light spectrum emitted by red fluorescent lamps used during the dark phase of the light-dark cycle may be detectable by postlarvae, thus allowing them to distinguish between shelters presenting extreme levels of illumination. In agreement with our previous observations (Boudreau et al. 1990, Boudreau et al. 1992), light phase apparently had no effect on the number of settling postlarvae, supporting the hypothesis that negative phototaxis is not a primary mechanism initiating settlement in lobsters (Boudreau et al. 1992). This result should be interpreted with caution, however, because of the potential effect of experimental red light conditions discussed above.

Within the temporal window used in the present study, time required for settlement in *Homarus americanus* decreased with age of postlarvae. Similarly, Crisp & Meadows (1963) have shown that cypris of *Semibalanus balanoides* settled more rapidly in response to a standard stimulus (barnacle extract) if settlement was delayed, a phenomenon also observed in other invertebrate larvae (Birkeland et al. 1971, Pechenik & Cerulli 1991). Two different mechanisms can be invoked to explain higher settlement rates in older lobster postlarvae. First, it could simply reflect an increase with age in the average proportion of individuals competent to settle. Such a possibility is not supported, however, by the results of Botero & Atema (1982), who observed that 100 % of 1-d-old postlarvae had settled on 'rock garden' after 36 h, suggesting that behavioural competence is fully achieved in lobsters 4 d after metamorphosis, the lower age limit used in our study. Second, higher settlement rates in older postlarvae could denote decreasing selectivity for the substratum with increasing age. Analysis of shelter occupancy strongly supports this hypothesis. Postlarvae aged 4 d exhibited a clear preference for shelters of better quality (i.e. black shelters) and delayed
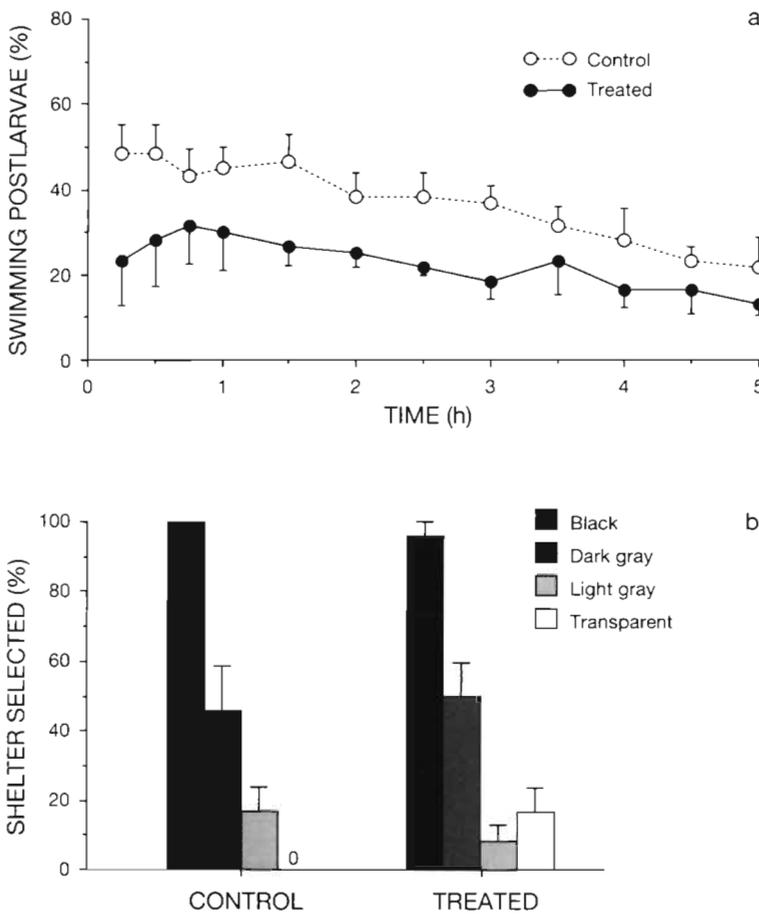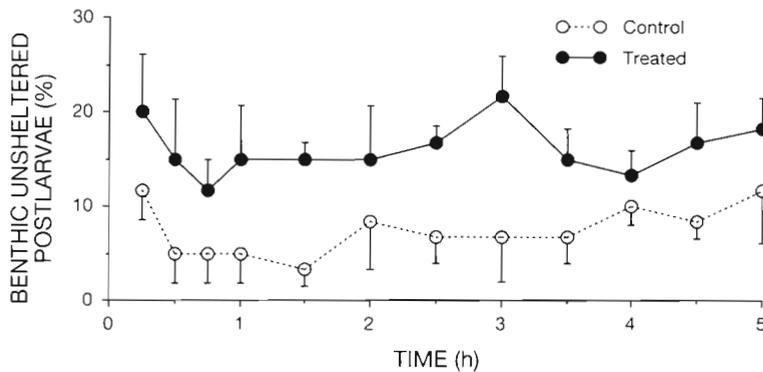
Fig. 7. *Homarus americanus*. Temporal variation in the proportion of benthic unsheltered postlarvae (mean ± SE, n = 4) in relation to water conditioning. Control (unconditioned) water was tested against predator-treated water

Table 7. *Homarus americanus*. (a) Two-way ANOVA of the effect of water conditioning and shelter type on shelter occupancy. Water conditioned by predators (*Tautogolabrus adspersus*) was tested against control (unconditioned) water. (b) Interaction was analyzed using unplanned pairwise comparisons (LSD test) with the level of significance (α) adjusted for the Bonferroni inequality (Kirk 1982). Dashed lines underscore shelter types that do not significantly differ for a given water condition (see Fig. 6b for mean ± SE). Shelter types as in Fig. 1

(a) ANOVA

Source of variation	df	MS	F-ratio	p > F
Water conditioning	1	0.0100	0.23	0.6361
Shelter type	3	2.9658	68.18	0.0001
Water × Shelter	3	0.1091	2.51	0.0829
Residual	24	0.0435		

(b) Interaction

Water conditioning		Shelter type		
Control	B	DG	LG	T
Treated	B	DG	T	LG

peared less selective than normal or slightly injured postlarvae (Fig. 5). Differential competitive ability cannot be invoked here since lobsters tested in one tank were all of the same level of injury. These results suggest that in the field, chances may be higher for postlarvae without chelipeds to be preyed upon by planktonic predators without gaining the benefits presumably attributable to additional searching time (e.g. the location of more suitable benthic microhabitats). The actual proportion of lobsters losing either one or both chelipeds at metamorphosis is still unknown for natural populations. Consequently, the potential importance of these results remains to be determined.

Settling lobsters are sensitive to odors emitted by cunners *Tautogolabrus adspersus* (Boudreau, Bourget & Simard unpubl.). In the present study, postlarvae released in seawater previously conditioned by this predator fish (see Wahle & Steneck 1992 for field evidence) tended to settle more quickly and less selectively than their counterparts tested in control situations (Fig. 6). The proportion of benthic unsheltered postlarvae was also higher in predator-treated water (Fig. 7), suggesting that additional settlers were not sheltered but rather distributed in open areas on the bottom. For prey organisms such as early benthic lobsters, a common tactic to reduce predation risk by visually hunting predators is restricting the frequency of movement (Johns & Mann 1987, but see Williams & Brown 1991 for examples in other taxa). A major cost associated with such 'freezing behaviour' would be a lower foraging efficiency (Williams & Brown 1991). For settling lobsters in particular, this antipredator strategy could also increase the average time required to find a shelter (Johns & Mann 1987) and reduce their ability to make the best possible choice (this study).

An often implicit assumption in field studies on settlement of marine benthic invertebrates has been that behavioural responses of competent larvae to environmental cues are stereotyped. The present experiments on *Homarus americanus* indicate that the degree of selectivity of settling lobsters for microhabitats of different quality can be strongly affected by a variety of endogenous and exogenous factors. These factors are potentially confounding in habitat selection experiments and should be adequately controlled to ensure the validity of the conclusions.

settlement rather than sheltering in marginal microhabitats (Table 5, Fig. 4). In contrast, postlarvae tested after an artificially prolonged pelagic phase occupied a higher proportion of suboptimal shelters (i.e. light gray and transparent shelters). Pechenik (1990) suggests that the potential costs associated with an extended planktonic phase could be responsible for the evolution of the age-dependent selection behaviour (i.e. reduced selectivity with age) observed in many marine invertebrate species. Unfortunately, due to the difficulty of determining these costs for the entire process of settlement, including water column events, only post-settlement effects have been considered (see Pechenik & Cerulli 1991, and references therein) and the question remains partly resolved.

Postlarval lobsters which were severely injured at metamorphosis exhibited lower settlement and ap-

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