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Journal of Experimental Marine Biology and Ecology
313 (2004) 139–154

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

www.elsevier.com/locate/jembe

Effect of light and substratum complexity on microhabitat selection and activity of the ophiuroid *Ophiopholis aculeata*

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Received 25 April 2004; received in revised form 27 June 2004; accepted 5 August 2004

Abstract

We evaluated the effect of light intensity and substratum complexity on habitat preference and displacement speed of the ophiuroid *Ophiopholis aculeata*. The ophiuroid strongly preferred reduced light and to a lesser extent complex substrata. Further, displacement speed increased with light intensity and decreased with substratum complexity (ophiuroids were virtually immobile on darkened complex substrata). In the field, the density of exposed ophiuroids, with the disk out of a crevice, was always low, irrespective of the intensity of solar radiation. However, the extent to which they extended their arms (to feed) was inversely related to light intensity, as the number of suspension-feeding arms was low under direct sunlight, intermediate under indirect light and high at night. Field observations showed that the response to light was not modified when UV radiation was eliminated with a filter, and a laboratory experiment showed that white light intensity alone produced patterns similar to those observed in the field. *O. aculeata* may reduce arm extension with increasing light intensity to reduce the threat of visual predators, whose foraging efficiency increases with light intensity. However, visual predators are rare in our study site. We hypothesize that the large-scale larval dispersion of *O.*

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doi:10.1016/j.jembe.2004.08.004

aculeata (due to the long pelagic phase) prevents ophiuroids from adapting to local conditions so that its response to light reflects adaptation to visual predators in other locations.

Keywords: Cryptic behavior; Light; Ophiuroid; Microhabitat selection; *Ophiopholis aculeata*; Ultraviolet radiation

1. Introduction

Many marine organisms exhibit cryptic behaviors which lead to their use of habitats providing shelter. Cryptic animals often evaluate microhabitat quality by assessing structural complexity (Main, 1987; Wahle and Steneck, 1992; Kenyon et al., 1997; Jones and Boulding, 1999) and light intensity (Barbeau et al., 2004). Structural complexity can provide refuges from environmental stress (Gosselin and Chia, 1995; Jones and Boulding, 1999) and predation (Johns and Mann, 1987; Russo, 1987; Diehl, 1988; Nelson and Bonsdorff, 1990; Kenyon et al., 1995; Moksnes et al., 1998; Stunz and Minello, 2001), and the use of weakly illuminated habitats can reduce predation pressure as visual predators forage less efficiently under low light conditions (Diehl, 1988; James and Heck, 1994; Petersen and Gadomski, 1994; Kenyon et al., 1995). An alternative (or complementary) hypothesis for the evolution of cryptic behaviors by marine invertebrates is the avoidance of ultraviolet radiation, which has often been shown to cause severe damage to larval stages (Adams and Shick, 2001; Lesser and Barry, 2003) and adults (Bingham and Reyns, 1999; Bingham and Reitzel, 2000). In response, organisms have evolved physiological (Adams and Shick, 2001), mechanical (Karentz and Gast, 1993) and behavioral (Adams, 2001) adaptations to limit damage from UV light.

Ophiuroids are usually cryptic, living in burrows (Zimmerman et al., 1988; Gielazyn et al., 1999), crevices or under loose material (Sloan, 1979; Hendler, 1984; Sides and Woodley, 1985), and also they show a strong tendency to avoid light (Cowles, 1910; Hendler, 1984). The potential predators of ophiuroids are many and include fishes (Keats et al., 1987; Witman and Sebens, 1992; Packer et al., 1994), decapod crustaceans (Wurzian, 1976; Carter and Steel, 1982) and sea stars (Brun, 1972; Gaymer et al., 2001a,b). Cryptic behaviors and use of complex habitat have been shown to reduce predation on ophiuroids (Witman, 1985). In addition, Johnsen and Kier (1998) show that ophiuroids can be severely damaged by exposure to ultraviolet radiation and cryptic behaviors might reduce such damages.

In the subtidal community of the Mingan Islands in the northern Gulf of St. Lawrence, eastern Canada, the daisy brittle star, *Ophiopholis aculeata*, occurs in dense populations on vertical walls, particularly in zones of strong tidal currents (Gaymer et al., 2001a). This ophiuroid usually keeps its central disc hidden under rocks, in crevices and among coralline algae; exposed individuals being rare (Drolet et al., in press), but the arms are extended to various degrees. However, an exception occurs when individuals leave crevices and raise their central disc above the bottom to spawn (Litvinova, 1981). Over several years, we observed highly synchronized mass spawnings of *O. aculeata* in the Mingan Islands, in which most individuals were out of their crevices during a short period of gamete release (J.H.H., unpublished data). *O. aculeata* is mainly a suspension feeder (Warner, 1982). Its extended arms, with mucous-covered tube feet, capture suspended particles, and then the tube feet transfer a bolus of particles from the arm tips towards the mouth (LaBarbera, 1978). The main predators of *O. aculeata* in the Mingan Islands are the green sea urchin, *Strongylocentrotus droebachiensis* (Drolet et al., in press), and the sea star, *Asterias vulgaris* (Gaymer et al., 2001a,b), and we previously showed that refuge use by ophiuroids reduces the risk of predation by the urchin, but increases vulnerability to the sea star (Drolet et al., in press). Other potential predators in this region are the spider crab *Hyas araneus* (Bérubé, 1989), the zoarcid fish *Macrozoarces americanus* (Thomas, 1988) and the sunstar *Crossaster papposus* (Himmelman, 1991). Two other reported predators of ophiuroids along the western North Atlantic are the lobster *Homarus americanus* (Carter and Steel, 1982; Witman, 1985) and the cunner *Tautogolabrus adspersus* (Witman and Sebens, 1992), but these predators are absent in the Mingan Islands, probably due to the cold conditions caused by upwelling.

The main objective of this study was to assess the importance of substratum structural complexity and light intensity on micro-habitat selection and feeding behavior of the ophiuroid *O. aculeata*. We first ran laboratory experiments to evaluate microhabitat preferences in relation with substratum complexity and light intensity and also the effect of both factors on displacement speed. We then conducted field observations at different times of the day to assess the behavior of ophiuroids under varying light conditions in nature. Finally, to provide further insight on the adaptive value of light avoidance of *O. aculeata*, we quantified behavior when we used filters to remove UV light in the field and examined the reaction to white light in the laboratory.

2. Methods

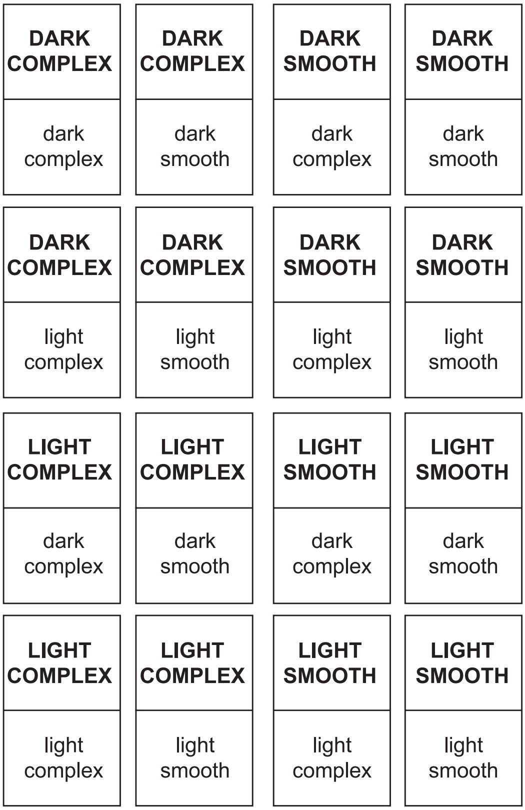
Our field studies were conducted between June and August 2003 on a population of *O. aculeata* on a vertical wall at Pointe-Enragée in the Mingan Islands, northern Gulf of St. Lawrence, eastern Canada (50°13.6″N, 63°41.12″W). The substratum on the wall was highly complex, being composed of pitted calcareous rock covered with encrusting coralline algae (*Lithothamnion* sp. and *Clathromorphum* sp.) and supported a high density of ophiuroids (~1460 ind. m^{-2}; Drolet et al., in press).

The laboratory experiments were conducted in a wet laboratory at Havre Saint-Pierre, located 3 km from the field site, using ophiuroids collected at Pointe-Enragée by SCUBA diving. The experiments were run in tanks with flowing seawater pumped from 10 m in depth. All experimental animals were used only once and within 4 days of being collected.

2.1. Effect of light and structural complexity on microhabitat selection

To evaluate the effect of light intensity and substratum complexity on microhabitat preferences of the ophiuroid, we used the multifactor choice experiment developed by Barbeau et al. (2004). The trials were run in 38×24×5-cm plastic tanks (with concrete bottoms) that were separated into two halves, each with a particular light intensity (light or dark) and substratum complexity (smooth or complex). Preference of ophiuroids for every combination of light intensity and substratum complexity on one half of the tank was evaluated with all possible combinations of the same two factors on the other half of the tank (Fig. 1). Thus, the experimental design included four levels of the factor light and four levels of the factor substratum complexity for a total of 16 treatment combinations (Fig. 1), each of which was replicated six times.

The trials were conducted in a dark room illuminated by fluorescent lights. The light intensity reaching the ophiuroids was either ambient lighting (2.55 μmol photon cm^{-2} s^{-1}) or darkened by covering the tanks with an opaque plastic plate (0.04 μmol photon cm^{-2} s^{-1}). The substratum was either smooth (smooth concrete) or complex (a grid of vertical straws implanted in the concrete, 6 mm diameter and 2 cm high, spaced by 2.5 cm). No shadow was created by the combination of straws and fluorescent lighting. We began each trial by placing 10 ophiuroids (mean disc diameter=9.14 mm, S.D.=2.15, N=960) on a line across the center of the tank and then after 10 min recorded the proportion that chose each side of the tank. Ophiuroids that did not leave the centerline (2 cm in width) were excluded from the analysis.



DARK COMPLEX dark complex	**DARK COMPLEX** dark smooth	**DARK SMOOTH** dark complex	**DARK SMOOTH** dark smooth
DARK COMPLEX light complex	**DARK COMPLEX** light smooth	**DARK SMOOTH** light complex	**DARK SMOOTH** light smooth
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LIGHT COMPLEX light complex	**LIGHT COMPLEX** light smooth	**LIGHT SMOOTH** light complex	**LIGHT SMOOTH** light smooth

Fig. 1. The combinations of light intensity and substratum complexity used in the multifactor choice experiment. Bold uppercase letters denote the side of the tank for which measurements of preferences of ophiuroids was made for each combination.

We analyzed the data using a fixed 4×4 factorial ANOVA with four levels of light (DARK/dark, DARK/light, LIGHT/dark and LIGHT/light; capital letters denote the condition present on the half of the tank where preference was evaluated and lowercase letters the condition on the other half of the tank) and four levels of substratum complexity (COMPLEX/complex, COMPLEX/smooth, SMOOTH/complex and SMOOTH/smooth). We applied the ANOVA to the raw data, as no transformation succeeded in making the variances homogeneous because of the presence of a few extreme values. The results of the ANOVA should be robust (even though the assumption of homogeneous variance was not respected) because of the relatively large sample size, large number of treatments and balanced design (Underwood, 1997). We interpreted significant effects using Tukey HSD multiple comparisons.

2.2. Effect of light and substratum complexity on displacement speed

We performed a laboratory experiment to investigate the combined effect of light intensity (white light) and substratum complexity on the activity and displacement of ophiuroids. The experiment involved a 3×2 factorial design with three levels of light (strong, weak and dark) and two levels of complexity (smooth and complex) and the order of treatments was determined at random. The experimental arenas were 50×50-cm concrete plates, with either a smooth surface or a grid work (2-cm spacing) of 4-mm diameter plastic straws implanted vertically into the concrete. The straws were cut off at 2 cm about the surface. The experiment was carried out in a dark room illuminated by two fluorescent bulbs suspended 1.5 m above the arenas. In the strong-light treatment, ophiuroids were exposed to ambient lighting (2.59 μmol photon cm^{-2} s^{-1}). In the weak light treatment, a 1-m^2 opaque plastic sheet was placed 15 cm above the arena (0.04 μmol photon cm^{-2} s^{-1}). Finally, the dark treatment was run with the lights off. No shadow was created by the combination of straws and fluorescent lighting. Each trial was initiated by placing an ophiuroid (8–11 mm in disk diameter, mean=9.35 mm, S.D.=1.87) in the center of the plate and then we measured the distance the ophiuroid had moved after 5 min. In cases where the ophiuroid left the plate in <5 min, we recorded the distance covered and time taken to reach the edge of the plate. Each of the 6 treatments was replicated 10 times. We analyzed the data by applying a fixed two-way factorial ANOVA to the log-transformed speeds. As the interaction between the two factors was significant (see Section 3), we compared the log-transformed speeds between the different levels of light intensity for both substrata separately using Tukey HSD tests. We used *t*-tests to compare log-transformed speeds between the two levels of substratum complexity for each light intensity separately.

2.3. Effect of natural light in the field

We compared the behavior of ophiuroids on the vertical wall at Pointe-Enragée under three contrasting light conditions, in direct sunlight in the morning (sunny days), in indirect light (shadow) in the afternoon and in darkness at night. The wall faced eastward and thus received direct light in the morning and was in shadow in the afternoon. The behaviors quantified were the number of exposed ophiuroids (with the central disk out of a crevice) and the number of extended arms. Extended arms were likely capturing food particles as the podia were almost always extended (see LaBarbera, 1978). We performed the measurements at three sites, each in a different period. At each site, we installed three 4-m long transects, at 2–3 m in depth. We chose this depth to increase the differences in light intensity between the three periods of the day. For each transect, we recorded the behaviors in 0.07-m^2 circular areas (15 cm in diameter) placed at five randomly chosen positions for each light intensity (chosen from 15 predetermined positions at 25-cm intervals along the transects). The irradiance, as estimated with a Li-Cor light meter, was about 335 μmol photon cm^{-2} s^{-1} in direct sunlight, 14 μmol photon cm^{-2} s^{-1} in shadow and 0 μmol photon cm^{-2} s^{-1} at night.

We analyzed the densities of exposed individuals and extended arms using three-way mixed-model ANOVAs with two random factors, site and transect (nested in site), and the fixed factor time of day. The proper terms for F calculations were determined using the method suggested by Underwood (1997). Numbers of extended arms were square root transformed prior to analysis. When significant fixed effects were detected, we followed with Tukey HSD post-hoc tests.

2.4. *Effect of UV radiation*

To test whether exposure to ultraviolet radiation affects the tendency of ophiuroids to use refuges, we compared the number of extended arms in the field under two conditions, (1) exposed to solar radiation and (2) exposed to solar radiation but with ultraviolet wave lengths removed with a filter. The ophiuroids studied were held in wire mesh boxes (15×15×6 cm) that were covered with a 30×30-cm transparent plastic plate that either did (UF-5 plexiglass®) or did not (GS plexiglass®) filter out UV wavelengths. The bottom of each box was covered with pieces of coralline algae to provide refuges. These experimental units were attached at random positions along a metal rail that was permanently installed at each of two depths, 3 and 7 m. Each trial was begun by placing 10 ophiuroids in a box in the evening, 12–18 h prior to making the measurements the next morning. All measurements were made during sunny mornings. As some ophiuroids escaped from the cages (mean number of escapes per cage=1.9, S.D.=2.1), we divided the number of suspension feeding arms by the number of ophiuroids present. The experiment was repeated on four dates (blocks) and we made three replicates of each treatment per block. On one date, we could not estimate variance at 7 m in depth as water motion turned over two cages of the same treatment. To overcome this problem, we analyzed the data for the two depths separately (thus 4 blocks at 3 m and 3 blocks at 7 m). We analyzed the number of extended arms per ophiuroid using a two way mixed-model ANOVA with the random factor block (date) and the fixed factor light (with and without UV). At both depths, the interaction between block and light was not significant (p>0.25) so the interaction term was pooled with the error term as suggested by Winer et al. (1991).

2.5. *Effect of light in the laboratory*

We further ran laboratory experiments to evaluate the effect of the intensity of white light on the tendency of ophiuroids to use crevices and to extend their arms. We quantified the response of ophiuroids to three levels of irradiance within the range of conditions recorded in the field, (1) strong light (280 μmol photon cm^{-2} s^{-1}; 120 W light bulb at a distance of 20 cm), weak light (4.45 μmol photon cm^{-2} s^{-1}; a 15 W light bulb at a distance of 20 cm) and (3) darkness (~0 μmol photon cm^{-2} s^{-1}). The trials were run on a 15.5-cm diameter circular concrete plate on which there was a 1.5-cm diameter hole (1 cm deep) at the center of the plate. The hole was partly covered with a piece of coralline algae glued with marine epoxy. In each trial, we first placed an ophiuroid in the center of the plate under weak light (see below) and allowed it to crawl into the refuge. Two minutes after the ophiuroid was in the crevice and not moving, we changed the light intensity (except for weak light treatment) and then after 10 min we quantified the behavior of the ophiuroid. To stimulate feeding activity (which involve extending arms) and to avoid variation in temperature caused by the different lighting conditions, the plate was placed in a 50×35-cm flow tank with a current velocity of 3–4 cm s^{-1} (estimated using methylene blue dye). All experimental ophiuroids had five complete or nearly completely regenerated arms.

We estimated the tendency of ophiuroids to use crevices by quantifying the change in the proportion of the body that was exposed during the 10-min trial. We used a digital camera to record the area exposed (outside the hole) before and after the 10-min treatment and also the total area of each ophiuroid when removed from the crevice. The areas were calculated using the image analysis software Sigma Scan Pro 5.0. A positive value meant that the ophiuroid tended to leave the crevice over the course of the 10-min experimental period and a negative value that it retreated into the crevice. The bottom of the tank was painted white to facilitate the analyses of the digital photos. We also quantified an index of the degree to which the ophiuroids had their arms raised at the end of the 10-min period. As *O. aculeata* captures suspended particles using its podia (LaBarbera, 1978), the extent to which an arm is raised (which provides an estimate of the number of podia extended to feed) should reflect feeding activity. For all ophiuroid tested, we ranked the position of each of its arms using six categories (0=arm retracted in the crevice, 1=arm exposed but flat on the substratum, 2=<25% of the arm extended in the water, 3=between 25% and 50% of the arm extended, 4=50–75% of the arm extended, 5=75–100% of the arm extended) and then calculated the index as the sum or the scores divided by 25, the maximum score possible (all arms >75% raised). A few individuals that left the crevice during the trial were not included in this analysis. Each treatment (the three light intensities) was replicated 20 times in a random order. We used a one-way ANOVA to analyze both the change in exposure and arm extension index and followed with post-hoc comparisons using Tukey HSD tests.

3. Results

3.1. Effect of light and structural complexity on microhabitat selection

The experiment in which we recorded the responses of *O. aculeata* to all combinations of four levels of the factor light and four levels of the factor substratum complexity (Fig. 1) showed that both light intensity and substratum complexity influenced habitat choices ($F_{3,80}$=84.96 and 9.19, respectively, p<0.0001) but the effect of light was more pronounced. The interaction term was not significant ($F_{9,80}$=1.07, p=0.40), the response to one factor was not affected by the level of the other. Thus, we conducted post-hoc tests for light and substratum complexity separately.

When light intensity was the same on both sides of the tank (LIGHT/light or DARK/dark treatments), the distribution of the ophiuroids in the two halves of the experimental tanks was close to 1:1 (Fig. 2). In contrast, fewer ophiuroids chose the lighted side of the tank when in combination with a dark side (LIGHT/dark treatments), and more chose the dark side when the other side of the tank was lighted (DARK/light treatments). Thus, ophiuroids preferred lower light intensity.

When substratum complexity was the same on both sides of the tank (SMOOTH/smooth and COMPLEX/complex treatments), the distribution of the ophiuroids in the two halves of the experimental tanks was again close to 1:1 (Fig. 2). In contrast, we found that significantly more ophiuroids chose the complex side of the tank when the other side was smooth (COMPLEX/smooth treatments), and fewer ophiuroids tended to chose the smooth side when in combination with a complex side (SMOOTH/complex treatment; Fig. 2), although this latter difference was not significant. Thus, our data indicated a preference for complex substratum.

3.2. Effect of light and substratum complexity on displacement speed

The laboratory experiment on the combined effects of light intensity and substratum complexity showed that both factors strongly affected the speed at which the ophiuroids

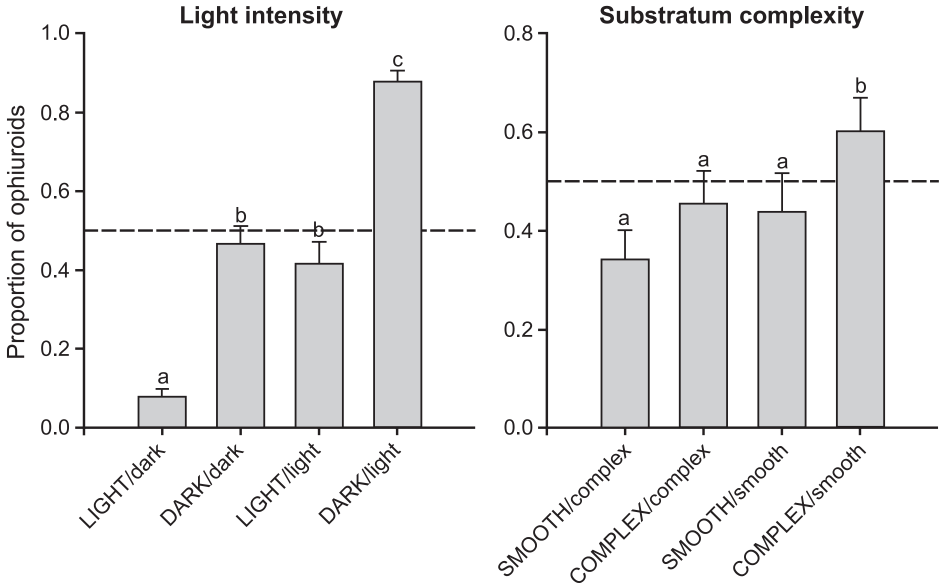

Fig. 2. Proportion of ophiuroids that choose a pre-selected side of the tank having different levels of light intensity and substratum complexity in the multifactor choice experiment. Uppercase letters denote the condition present on the half of the tank where preference of ophuiroids was evaluated and lowercase letters, the condition on the other half. Error bars show standard errors and columns not sharing a common letter are significantly different (Tukey HSD). Dashed line represents the 1:1 distribution representing no preference.

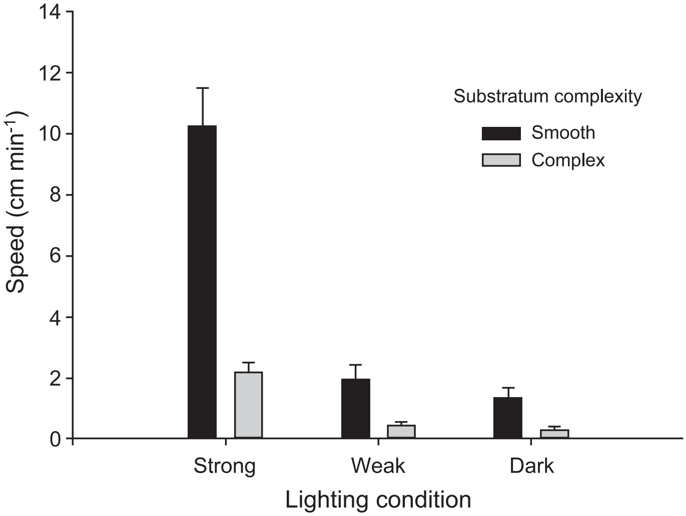

Fig. 3. Mean (+S.E.) displacement speed of ophiuroids exposed to different combinations of light intensities and substratum complexity in the laboratory. Under all light intensity, speed was significantly higher on smooth substratum and for both substrata speed was higher under strong light than under weak light or in the dark. Raw data are presented but analyses were performed on the log-transformed data.

moved in the arenas ($F_{2,54}$=85.9 for light intensity and $F_{2,54}$=79.1 for substratum complexity: p<0.0001 for both effects). Also, the interaction between the two factors was significant ($F_{2,54}$=5.9, p=0.005). On both substratum types, speed was markedly greater in strong light than in weak light and darkness, but the difference was more pronounced on smooth than complex substratum. At all light intensities, speed was lower on complex than smooth substratum (Fig. 3).

3.3. Effect of light in the field

Our studies of the behavior of ophiuroids on the vertical wall at Pointe-Enragée under three contrasting light conditions (in direct sunlight, in shadow and at night) showed that

Table 1
Nested ANOVA table of the number of exposed ophiuroids and the number extended arms (square root-transformed data) under different light intensities in the field

Factor	*df*	Denom.	Exposed ophiuroids			Extended arms		
			MS	*F*	*p*	MS	*F*	*p*
Light L_i	2	LS_{ij}	0.055	1.38	0.35	186.3	17.24	0.011
Site S_j	2	$T(S)_{k(i)}$	0.052	0.80	0.49	80.3	20.39	0.002
Transect (site) $T(S)_{k(i)}$	6	Error	0.064	1.17	0.33	3.9	3.38	0.004
Light×site LS_{ij}	4	$LT(S)_{ik(i)}$	0.040	1.67	0.23	10.8	3.87	0.033
Light×transect (site) $LT(S)_{ik(i)}$	11	Error	0.023	0.43	0.94	2.8	2.39	0.012
Error	102		0.055			1.2		

density of exposed ophiuroids (disk outside a crevice) was always extremely low (<5 ind. m^{-2}, representing <0.3% of the population) irrespective of site, transect and time of day (Table 1, Fig. 4). In contrast, the density of extended arms varied markedly with site, transect and time of day (Table 1). The density was least in sunlight, increased by >2-fold in shadow and by almost 4-fold in darkness (Fig. 4; all means were significantly different). The effect of light varied among sites (Table 1) probably because of variations in irradiance on the different days of the study. The effect of light also varied among transects within sites (Table 1), as the effect of light was greater at one transect at the first site.

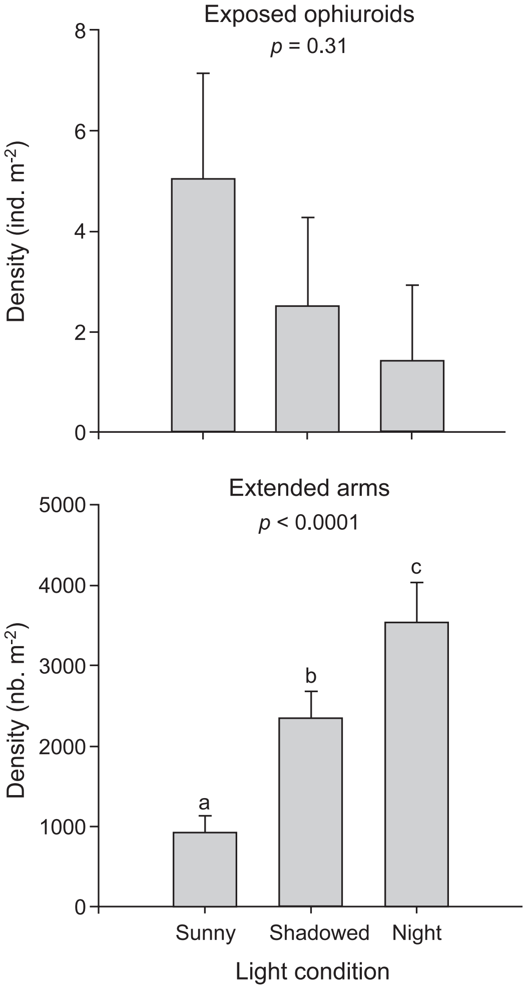

Fig. 4. Effect of solar radiation intensity on the density of exposed ophiuroids and suspension feeding arms in the field. P-values are from the light factor of the ANOVA. Error bars show standard error and columns not sharing a common letter are significantly different (Tukey HSD). Density of suspension-feeding arms were square-root transformed prior to analysis.

Table 2
ANOVA table of the number of suspension feeding arms per ophiuroid in the UV effect field experiment at 3 and 7 m in depth

Factor	3 m				7 m			
	df	MS	*F*	*p*	*df*	MS	*F*	*p*
Light	1	0.31	2.55	0.13	1	0.34	0.54	0.47
Block	3	0.32	2.87	0.06	2	0.06	3.19	0.07
Error	19	0.12			14	0.11		

3.4. Effect of UV radiation

The field experiment exploring the response of *O. aculeata* to UV radiation showed that removing ultraviolet radiation with plastic filters had no effect on the number of extended arms at either depth (3 and 7 m; Table 2). At the two depths, there tended to be a weak effect of block (Table 2) probably due to variations in solar radiation on the different days when measurements were made. The only indication of a possible effect of UV radiation was a slight increase in the number of extended arms under UV filters at 3 m, in comparison to control cages without UV filter (Fig. 5).

3.5. Effect of light in the laboratory

The study in which we recorded the responses of the ophiuroid to changes in light intensity (white light) showed a strong effect of light on the extent to which the body was exposed ($F_{2,57}$=17.4, p<0.0001). During the 10-min trials, ophiuroids became more

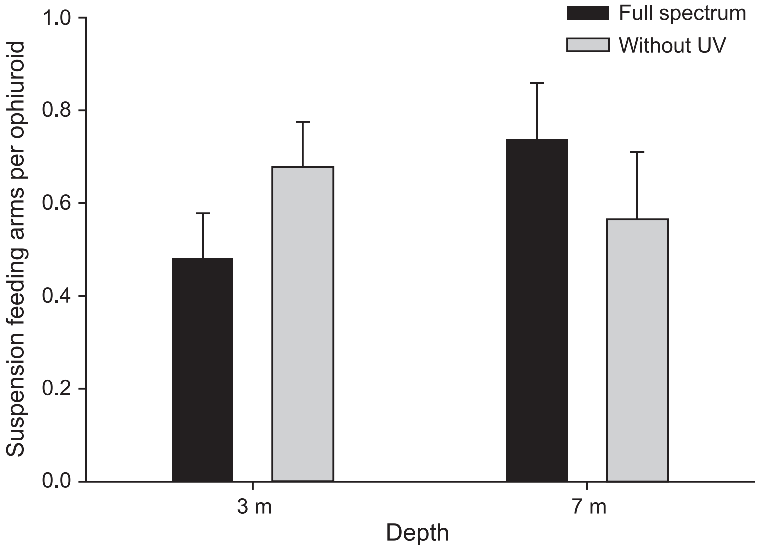

Fig. 5. Effect of UV radiation and depth on the number of suspension-feeding arms per ophiuroids. No significant effect of UV light (presence or absence) was detected by the analysis.

exposed with the change from weak light to darkness, and less exposed with the change from weak light to strong light, whereas no change occurred in the treatment where light intensity remained weak (Fig. 6, all means were significantly different). A one-way ANOVA applied to the index of arm extension of ophiuroids in the same trials also showed a strong effect of light intensity ($F_{2,51}$=25.1, p<0.0001). The index was greatest in darkness, less in weak light and least in strong light (Fig. 6, all means were significantly different).

4. Discussion

The ophiuroid *O. aculeata* in the Mingan Islands, like many other ophiuroids, is a very cryptic animal. On the vertical walls, ophiuroids keep their central disk tucked in anfractuosities but often extend arms to feed. The multifactor choice experiment investigating the effect of light intensity and substratum complexity on microhabitat preferences showed that the ophiuroid's cryptic behavior is a consequence of strong preferences for weakly illuminated microhabitats and to a lesser extent for complex substrata (Fig. 2). *O. aculeata*, as many other ophiuroids, shows negative phototactic and positive stereotactic (attracted to solid objects) behaviors (Cowles, 1910; Hendler, 1984). In the field, *O. aculeata* is usually found hidden in a refuge, so that displacement likely represents a search for a suitable microhabitat. In the study of the effect of light intensity and substratum complexity on the displacement of *O. aculeata*, speed varied inversely with the degree to which the test habitat was preferred (Fig. 3). Thus, on complex substratum, ophiuroids were virtually immobile at low light intensities (preferred conditions, <0.2 cm min^{-1}) and moved more rapidly when exposed to strong light (Fig. 3). We similarly observed an increase displacement speed with increasing light on smooth substratum, and the change was more pronounced (Fig. 3). The very strong fleeing response of ophiuroids when placed on well-lighted smooth substratum suggests that the animal senses vulnerability in this situation.

In the field, few *O. aculeata* occur out of crevices (the disc exposed) even in the darkness of night (Fig. 4), and this contrasts with ophiuroid species in warmer waters that often leave crevices at night (Sides and Woodley, 1985). Nevertheless, the feeding activity of *O. aculeata*, as indicated by the numbers of extended arms, was inversely related to the intensity of solar radiation, decreasing from direct sunlight to shadow and also from shadow to darkness (Fig. 4). A plausible explanation for the observed light-dependant feeding pattern was the avoidance of ultraviolet radiation; as the retraction of arms deeper into crevices during periods of exposure to direct sunlight would prevent UV damage. A UV-dependant covering behavior has previously been reported for the urchin *S. droebachiensis* (Adams, 2001). However, our field trials using UV filters failed to show that UV light reduced the tendency of the ophiuroids to extend arms (Fig. 5), suggesting that UV light plays a minor role, or no role, in modulating the cryptic behavior of *O. aculeata*. One possibility is that lack of a response of *O. aculeata* to UV light is because its survival is not affected by UV radiation due to the turbidity in the regions where it is found. Alternatively, ophiuroids may be protected from UV radiation merely by responding to white light, since the intensity of white light is likely a good predictor of

UV radiation. Further experiments testing the vulnerability of *O. aculeata* to UV-induced damage and sensitivity to UV radiation in the laboratory are needed to resolve this issue.

Our laboratory trials with white light revealed that increases in light intensity lead to decreased extension of arms and vice versa (Fig. 6) and the pattern related to the intensity of white light was remarkably similar to that observed in the field (Figs. 4 and 6). This suggests that the intensity of white light is a major determinant of the light-dependent feeding pattern. We also show that proportion of the body of ophiuroids that is exposed

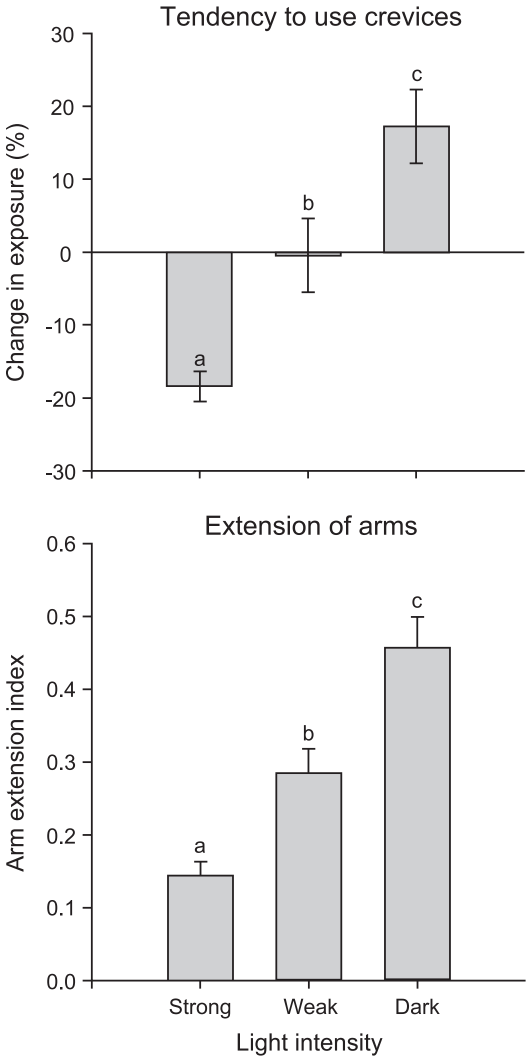

Fig. 6. Effect of white light intensity on the tendency to use crevices and on the suspension-feeding activity of ophiuroids in the laboratory. Error bars show standard error and columns not sharing a common letter are significantly different (Tukey HSD).

decreases with light intensity. The changes in exposure are mainly due to retraction or extension of the arms as the disc was almost always maintained deep in the crevice. It is tempting to suggest that a trade-off exists between feeding and predation risk as extending arms to feed increases exposure to visual predators for which foraging efficiency likely increases with increasing light as reported for several predators (Diehl, 1988; James and Heck, 1994; Petersen and Gadomski, 1994; Kenyon et al., 1995). Retraction of arms in response to light is likely effective in reducing predation from visual predators. However, the adaptive value of the light-dependent feeding pattern of *O. aculeata* in the Mingan Islands is not obvious since their main predators, the urchin *S. droebachiensis* and the asteroid *A. vulgaris* locate prey using odors rather than vision (Zafiriou, 1972; Zafiriou et al., 1972; Garnick, 1978; Mann et al., 1984). In addition, ophiuroids are more vulnerable to sea star predation (*A. vulgaris*) inside crevices than on open surfaces (Drolet et al., in press). The important fish and decapod crustaceans predators of *O. aculeata* in other areas are rare in the Mingan Islands, probably because of persistent cold summer temperatures related to upwelling. We hypothesize that the reaction of *O. aculeata* to light in the Mingan Island does represent an evolved adaptation to visual predators, but that individuals in the region have not adjusted to local conditions because the long-lived pelagic larval stage causes high genetic exchange with nearby populations where visual predators are important.

Acknowledgements

We are grateful to D. Aeillo, I. Deschênes, S.-P. Gingras, P. Grondin, M. Nadon, F. Praira, M. Thompson and C. Vallières who assisted with the field and laboratory work. Special thanks to C. Dumont for many good suggestions and to M.A. Barbeau for statistical advice and for providing an unpublished version of a manuscript. This research was financed by a NSERC operating grant to JHH and DD received financial support from Québec-Océan. **[SS]**

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