DAVID DROLET

CAUSES PROXIMALES ET ULTIMES DU COMPORTEMENT CRYPTIQUE DE L'OPHIURE *Ophiopholis aculeata*

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Résumé

J'ai étudié les causes proximales et ultimes du comportement cryptique (tendance à se cacher) de l'ophiure *Ophiopholis aculeata*. Le comportement est dû à une forte tendance à éviter la lumière blanche et à une préférence pour les environnements complexes. L'exposition au rayonnement ultraviolet n'influence pas directement le comportement de l'ophiure alors que l'exposition à la lumière blanche influence grandement la tendance des ophiures à utiliser les refuges. L'utilisation des crevasses réduit le risque de prédation par l'oursin vert *Strongylocentrotus droebachiensis*, mais augmente la vulnérabilité à l'étoile de mer *Asterias vulgaris*. Ces résultats suggèrent que l'ophiure fait face à un compromis dans l'utilisation des refuges dû à l'effet inverse de la complexité de l'habitat sur le risque de prédation par deux prédateurs majeurs. La présence de prédateurs modifie l'intensité du comportement cryptique de l'ophiure de façon adaptative. Le contact avec un oursin pousse les ophiures à se cacher plus profondément dans les crevasses alors qu'une menace sévère venant de l'étoile fait sortir les ophiures des crevasses. Ces résultats suggèrent que la valeur adaptative du comportement cryptique de l'ophiure est en lien avec l'évitement de la prédation et non à l'évitement des stress environementaux.

Abstract

I studied the proximate and ultimate causes of the cryptic behavior of the ophiuroid *Ophiopholis aculeata*. This behavior is caused by a strong tendency to avoid white light and a preference for complex habitats. Exposure to ultraviolet radiation did not influence the behavior of ophiuroids, whereas white light strongly influenced the extent to which ophiuroids used refuge. Use of refuges reduced threat of predation by the green sea urchin *Strongylocentrotus droebachiensis*, but increased vulnerability to the sea star *Asterias vulgaris*. These results suggest that the ophiuroid faces a trade-off related to the inverse effect of habitat complexity on predation risk by two major predators. The presence of predators modified the tendency of ophiuroids to use crevices in an adaptive way. Contact with an urchin caused the ophiuroid to retract deeper in crevices whereas ophiuroids left crevices following a threatening contact with a sea star. These results suggest that the adaptive value of the cryptic behavior in this ophiuroid is linked to predator avoidance and not to avoidance of environmental stress.

Avant-propos

Je tiens premièrement à remercier mon directeur John Himmelman pour m'avoir fait confiance lors des trois années que j'ai passées au sein de son laboratoire, tant comme assistant que comme étudiant gradué. Je remercie sincérement mon co-directeur Rémy Rochette pour avoir accepté de s'embarquer dans l'aventure de mon projet de maîtrise. Merci à Myriam Barbeau pour avoir vérifié certaines analyses statistiques et pour avoir fourni une version non publié d'un manuscrit. Ce projet n'aurait jamais été possible sans l'aide incommensurable des nombreux assistants avec qui j'ai passé des centaines d'heures dans l'eau glacée: Catherine, Damien, François, Isabelle, Marc, Myles, Pierre et Simon-Pierre. Je remercie de façon particulière Clément Dumont pour ses conseils et son support. Les articles présentés dans ce mémoire ont été grandement améliorés par les commentaires de plusieurs collègues et amis.

Ce mémoire comporte deux chapitres rédigés en anglais sous forme d'articles scientifiques qui on été acceptés pour publication:

Chapitre 1. Drolet, D., Himmelman, J.H. and Rochette, R. Trade-off in the use of refuges by the ophiuroid *Ophiopholis aculeata* related to contrasting effects of substratum complexity on the risk of predation from two predators. *Marine Ecology Progress Series*

Chapitre 2. Drolet, D., Himmelman, J.H. and Rochette, R.. Effect of light and substratum complexity on microhabitat selection and activity of the ophiuroid *Ophiopholis aculeata. Journal of Experimental Marine Biology and Ecology*

J'ai planifié (sous la supervision de mes directeurs) et exécuté toutes les expériences décrites dans le mémoire. J'ai rédigé les deux articles et j'ai effectué toutes les analyses présentées. Par la suite, les manuscrits ont été grandement améliorés par les commentaires de mes superviseurs.

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Introduction générale

Les animaux reçoivent de l'information à propos de leur environnement sous la forme de stimuli biotiques et abiotiques. La réponse d'un organisme à ces stimulations est critique à sa survie et à son succès reproducteur. Par exemple un animal qui choisit un habitat va évaluer une variété de facteurs l'informant des risques et des gains potentiels, et choisira théoriquement l'habitat ayant le plus fabile ratio coûts/bénéfices. La complexité structurale est une propriété caractéristique à chaque habitat, définie comme l'abondance de structures physiques (Bell et al., 1991). Plusieurs caractéristiques physiques et biologiques varient en fonction de la complexité des habitats. De façon générale, la complexité de l'habitat offre une protection contre la prédation et les stress environnementaux. Conséquemment plusieurs espèces vont préférer les habitats complexes.

Les ophiures (Echinodermata; Ophiuroidea) sont présentes dans toutes les mers du monde; leur distribution s'étend de l'équateur aux pôles et de la zone intertidale aux abysses. Dans quelques habitats, les populations d'ophiures atteignent des densités très élevées et constituent l'espèce macro-benthique dominante (Allain, 1974; Aronson and Sues, 1987; Warner, 1971). Les bancs d'ophiures qui se nourissent sur des particules en suspension dans la colonne d'eau constituent un lien important dans les réseaux trophiques en transférant une grande quantité d'énergie de l'environnement pélagique vers le benthos (Loo et al., 1996). Les ophiures font partie de la diète de plusieurs types de prédateurs, dont les poissons (Keats et al., 1987; Packer et al., 1994; Witman and Sebens, 1992), les crustacés décapodes (Carter and Steel, 1982; Wurzian, 1977) et les étoiles de mer (Brun, 1972; Gaymer et al, 2001a; b). Malgré leur ubiquité et leur importance dans les réseaux trophiques, relativement peu d'études se sont intéressées à l'écologie des ophiures, et plusieurs lacunes sont présentes dans la littérature, en particulier en écologie comportementale. Une connaissance plus approfondie des facteurs influençant leur comportement est essentielle à une meilleure compréhension de la dynamique des communautés infralittorales benthiques. L'expérimentation avec ces organismes est compliquée par leur fragilité et leur sensibilité à plusieurs facteurs. De plus, leur taille relativement petite et leur grande manoeuvrabilité rendent certaines techniques expérimentales traditionnelles à l'écologie benthique (e.g. utilisation de cages, marquage-recapture) difficiles à appliquer. Afin d'améliorer la compréhension des intéractions entre ces organismes et leur environement, il est impératif de développer des nouvelles techniques manipulatives tant sur le terrain qu'en laboratoire.

Dans la communauté benthique infralittorale des Îles Mingan, l'ophiure *Ophiopholis aculeata* forme des populations très denses sur les murs verticaux. Elles vivent habituellement avec leur disque central caché dans les anfractuosités de la roche-mère et au travers des algues corallines. Généralement, certains bras sont étendus dans la colonne d'eau pour se nourrir sur des particules en suspension. Les individus exposés (disque hors d'une crevasse) sont peu communs. Les prédateurs principaux d'*O. aculeata* sont l'oursin *Strongylocentrotus droebachiensis* (cette étude) et l'étoile de mer *Asterias vulgaris* (Gaymer et al., 2001a; b) et les autres prédateurs connus sont le crabe araignée *Hyas araneus* (Bérubé, 1988), la loquette d'Amérique *Macrozoarces americanus* (Thomas, 1989) et l'étoile de mer *Crossaster papposus* (Himmelman, 1991). De plus, des observations sur le terrain et en laboratoire portent à croire que la lumière et la complexité structurale ont une grande influence sur le comportement des ophiures.

L'objectif principal de ce mémoire est d'élucider les causes proximales et ultimes du comportement cryptique de l'ophiure *Ophiopholis aculeata* dans les Îles Mingan. J'ai évalué l'effet proximal de l'intensité lumineuse, de la complexité structurale et de la présence de prédateurs sur la tendance des ophiures à utiliser des refuges. Par la suite, j'ai investigué les causes ultimes (valeur adaptative) du comportement cryptique de l'ophiure en relation avec l'évitement de la prédation et des stress environementaux.

CHAPITRE 1

Trade-off in the use of refuges by the ophiuroid Ophio*pholis aculeata* related to contrasting effects of substratum complexity on the risk of predation from two major predators

RÉSUMÉ

Nous avons évalué l'effet de la complexité structurale du substrat sur la vulnérabilité de l'ophiure *Ophiopholis aculeata* à deux prédateurs majeurs, l'étoile de mer *Asterias vulgaris* et l'oursin vert *Strongylocentrotus droebachiensis* et nous avons examiné les réponses comportementales de l'ophiure à ces deux prédateurs. Sur le terrain et en laboratoire, l'utilisation des refuges par l'ophiure a tendu à réduire la prédation par les oursins. La réponse des ophiures au contact avec un oursin est de se cacher plus profondément dans les crevasses. À l'inverse, en laboratoire, la vulnérabilité de l'ophiure à l'étoile de mer était plus grande sur un substrat complexe. En laboratoire, l'ophiure a peu réagi au contact avec avec le bout du bras ou le sillon ambulacraire d'*A. vulgaris*, mais est rapidement sortie des crevasses après un contact avec l'estomac de l'étoile. Sur le terrain, la densité d'ophiures dans des aires circulaires de 20 cm de diamètre placées autour d'étoiles (en alimentation ou pas) était similaire à celle observée dans des zones où il n'y avait pas d'étoiles. Par contre, plus d'ophiures avaient leur disque exposé (hors d'une crevasse) à proximité d'une étoile et moins d'ophiures se trouvaient directement sous les étoiles que dans les zones sans étoile. Ces deux effets étaient plus prononcés quand l'étoile était en alimentation. L'ophiure montre un comportement de sensibilté au risque ajusté aux deux prédateurs. Elle fuit les crevasses en dessous des étoiles lorsqu'elle est touchée par l'estomac et bouge de seulement quelques centimètres. Le délai de réponse à l'étoile peut augmenter la probabilité de capture par l'étoile, mais réduit le temps passé en milieu ouvert où elle est plus vulnérable aux oursins.

ABSTRACT

We investigated the effect of substratum complexity on the vulnerability of the ophiuroid *Ophiopholis aculeata* to its two main predators, the sea star *Asterias vulgaris* and the urchin *Strongylocentrotus droebachiensis* and further examined behavioral responses of ophiuroids to these predators. Field and laboratory experiments showed that the use of crevices by ophiuroids tended to reduce predation by urchins. The ophiuroid's response to contact with the urchin was to retract deeper into crevices. In contrast, in the laboratory, the ophiuroid's vulnerability to the sea star was higher on complex substrata. In the laboratory, ophiuroids reacted weakly to contact with the arm tip or ambulacral groove of *A. vulgaris*, but immediately fled refuges when there was contact with the sea star's stomach. In the field, the density of ophiuroids in 20-cm diameter circular plots placed around sea stars (both feeding and non-feeding) was similar to that in areas without sea stars. However, the estimated density of ophiuroids directly under sea stars was less than in areas without sea stars, and exposed ophiuroids (with the disk outside a crevice) were more abundant near *A. vulgaris* than in areas without sea stars: both differences were greater when the sea star was feeding. Ophiuroids display risk sensitivity adjusted to the two predators. They mainly flee crevices under a sea star when there is contact with sea star's stomach but only move a few centimeters. A last-moment departure should increase the probability of capture by sea stars, but reduces time spent on open surfaces where they are vulnerable to urchin attacks.

INTRODUCTION

The structural complexity of habitats can affect aquatic communities by influencing recruitment (Lemire and Bourget, 1996; Walters and Wethey, 1996), distribution patterns (Steger, 1987; Moran and Reaka, 1988) and species diversity (Eklov, 1997). Use of complex habitats can also decrease exposure to environmental stress (Gosselin and Chia, 1995; Jones and Boulding, 1999). Many studies showed that refuges associated with macrophytes (e.g. Johns and Mann, 1987; Russo, 1987; Diehl, 1988; Nelson and Bonsdorff, 1990; Kenyon et al., 1995; Moksnes et al., 1998; Stunz and Minello, 2001), corals (e.g. Beukers and Jones, 1997; Nemeth, 1998) and bottom materials (e.g. Coull and Wells, 1983; Sponaugle and Lawton, 1990; Wahle and Steneck, 1992; Stunz and Minello, 2001; Wong and Barbeau, 2003) can reduce rates of predation. Structural components can either make the prey less visible (Main, 1987) or enhance escape probability by slowing the movement of predators (Ryer, 1988; Bartholomew et al., 2000) and permitting prey to stay out of reach of predators (Main, 1987). The use of refuges is a good mean of avoiding fast-moving visual predators and can also reduce predation by slow-moving predators that locate prey using chemodetection (Levitan and Genovese, 1989; Arsenault and Himmelman, 1996; Wong and Barbeau, 2003). As a general rule, habitat complexity reduces predation but systems with ambush predators are an exception; in these cases habitat complexity may not affect, or even increase, mortality from predation as structural components reduce the capacity of prey to detect predators (James and Heck, 1994; Walsh, 1995; Flynn and Ritz, 1999).

In addition to causing death, predators may also modify the behavior of their prey. Energetic costs are associated with behavioral responses, either directly when costly escape responses are deployed (Brokordt et al., 2003) or indirectly when foraging is reduced in situations of risk (Fraser and Gilliam, 1987; Bishop and Brown, 1992; Vadas et al., 1994; Behrens Yamada et al., 1998). To minimize such costs, prey often show threat-sensitivity and adjust the intensity of their responses to the level of predatory threat (Helfman, 1989; Legault and Himmelman, 1993). Prey species should adjust anti-predator behaviors to minimize the ratio of costs (direct and indirect) and benefits (e.g. foraging or mating), thus maximizing fitness (Lima and Dill, 1990).

Ophiuroids are preyed upon by many organisms, including fishes (Keats et al., 1987; Witman and Sebens, 1992; Packer et al., 1994), decapod crustaceans (Wurzian, 1977; Carter and Steel, 1982) and asteroids (Brun, 1972; Gaymer et al., 2001a; b). They avoid encounter with predators by responding to chemical exudates from the predators (Feder and Arvidsson, 1967) or injured conspecifics (Rosenberg and Selander, 2000) and by hiding in refuges (Hendler, 1984; Witman, 1985). Once there has been contact with a predator, ophiuroids can avoid being eaten by using active flight (Feder and Arvidsson, 1967; Skold, 1998), arm autotomy (Wilkie, 1978), protective secretions (Fontaine, 1964) and bioluminescence (which may function as aposematic coloration; Grober, 1988a; b; Deheyn et al., 2000). Cryptic ophiuroids may also retreat deeper into refuges to stay out of reach of the predator (Solan and Battle, 2003)

In the subtidal community of the Mingan Islands in the northern Gulf of St. Lawrence (eastern Canada), the brittle star *Ophiopholis aculeata* occurs in dense populations (up to 1700 ind m^{-2}) on vertical walls, particularly in zones with strong tidal currents (Gaymer et al., 2001a). Most individuals keep their central disc tucked into crevices in rock and coralline algae, and the arms are often extended to feed on suspended particles (see LaBarbera, 1978). The green sea urchin *Strongylocentrotus droebachiensis* (this study) and the sea star *Asterias vulgaris* (Gaymer et al., 2001a; b) are the main predators of *O. aculeata* in this region, and other reported predators are the spider crab *Hyas araneus* (Bérubé, 1989), the ocean pout *Macrozoarces americanus* (Thomas, 1988) and the sunstar *Crossaster papposus* (Himmelman, 1991). Two other important predators of ophiuroids in the western North Atlantic, the lobster *Homarus americanus* (Carter and Steel, 1982; Witman, 1985) and the cunner *Tautogolabrus adspersus* (J.H.H., pers. obs.; Witman and Sebens, 1992), are absent in the Mingan Islands, probably due to the cold summer conditions caused by persistent upwelling.

Although most *Ophiopholis aculeata* are cryptic, we have observed individuals outside of crevices (central disc exposed) in the vicinity of the sea star *Asterias vulgaris* and at times they even crawl over the aboral surface of the sea star. This usually occurs when the sea star is feeding. The presence of *A. vulgaris* does not seem to cause ophiuroids to flee, as they often extend their arms to feed within centimeters of, and even when underneath, the sea star (D.D. pers. obs.). Since in the same region (Mingan Islands), Rochette et al. (1995) and Rochette and Himmelman (1996) observed that the whelk (*Buccinum undatum*) will at times approach its major predator (in this case the asteroid *Leptasterias polaris*) to kleptoparasitize (steal) food, we thought that *O. aculeata* might similarly be steeling food from *A. vulgaris*. However, preliminary studies did not indicate that ophiuroids approach feeding *A. vulgaris*, or that ophiuroids gain food from feeding sea stars (D.D., unpublished data). Studies by Gaymer et al. (2001a) on prey selection of *A. vulgaris* show that *O. aculeata* is never consumed when ophiuroids are provided in glass aquaria (where there are no crevices), whereas sea stars readily eat ophiuroids that are tied to substratum. They speculated that the high predation rate in the field (*O. aculeata* accounts for > 80 % of diet of *A. vulgaris* on vertical walls) was a consequence of the cryptic behavior of ophiuroids that allowed the sea star to corner them in crevices. If this is so, exposed ophiuroids near sea stars may represent fleeing individuals: the ophiuroids would be leaving crevices to avoid being captured. This would be contrary to the general rule that habitat complexity decreases prey vulnerability.

The main purpose of our study was to elucidate the apparently strange interaction between the ophiuroid *Ophiopholis aculeata* and the sea star *Asterias vulgaris* in the Mingan Islands. We first quantified the effect of sea star presence and activity (feeding and non-feeding) on the micro-distribution of ophiuroids. Secondly, we tested the counterintuitive proposal that refuge use and substratum complexity increase sea star predation on ophiuroids. We started by performing a tethering experiment in the field to evaluate the effect of substratum complexity on the vulnerability of ophiuroids to the sea star. To our surprise, we found that the urchin *Strongylocentrotus droebachiensis* was the main predator at our study site. We therefore included both sea stars and urchins in subsequent laboratory experiments investigating the effect of substratum complexity on the vulnerability of ophiuroids to predators. Finally, we compared the tendency of ophiuroids to use refuges following simulated attacks by sea stars and urchins and linked responses of ophiuroids to the nature of the threat that predators present.

METHODS

Our study was conducted between June and August 2003 at Pointe-Enragée, in the Mingan Islands, northern Gulf of St. Lawrence, eastern Canada (50°13.6"N, 63°41.12"W). The site is an abrupt rocky cliff extending from 0 to 6 m in depth at the northern end, and from 10 to 20 m at the southern end. The wall is interrupted by narrow horizontal ledges at several locations. The cliff provided a highly complex substratum, there being abundant pits in the calcareous rock and irregularities created by encrusting coralline algae (*Lithothamnion* sp. and *Clathromorphum* sp.).

The laboratory experiments were conducted in a wet laboratory at Havre Saint-Pierre, located 3 km from the field site, using animals collected at Pointe-Enragée by SCUBA diving. The experiments were run in tanks with flowing sea water pumped from 10 m in depth (except when otherwise mentioned). Experimental animals were usually collected 1-4 days prior to being studied and were never collected more than 7 days in advance.

Reaction of ophiuroids to *Asterias vulgaris* in the field

To determine the impact of *Asterias vulgaris* on the distribution of ophiuroids, we quantified ophiuroid densities in 0.03 m^2 circular areas (20 cm in diameter) placed around haphazardly-selected feeding (N = 19) and non-feeding (N = 39) sea stars (only sea stars with five intact arms were studied) and also in areas where there were no sea star within a 50-cm radius (N = 21). These measurements were made on vertical walls in zones where ophiuroid densities were relatively homogenous. We applied a one-factor ANOVA to total ophiuroid densities in the circular plots with (1) non-feeding sea stars, (2) feeding sea stars and (3) without sea stars. As the preliminary analysis showed no effect of sea star presence on the density of ophiuroids in the area surrounding sea stars, we refined the observation scale by analyzing the number of ophiuroids found under the sea stars. We compared the number of ophiuroids found under each sea star (counted as we slowly lifted the sea star from the substratum) with the value expected in an area the size of the same sea star if ophiuroids were evenly distributed at the density recorded in the 20-cm diameter plot. This value was calculated by multiplying the number of ophiuroids in the circular plot by the proportion of the area covered by the sea star. The area covered by each sea star was estimated from the relation of area to radius, as previously determined from measurements of 50 sea stars (area = $1.08x^2 - 1.21x + 14.59$, where x is radius, $r^2 = 0.93$; the area of these sea stars was measured from digital images using the image analysis software Sigma Scan Pro 5.0). For both non-feeding and feeding sea stars, we used paired t tests to compare observed and expected value. Also, we performed a t test on the deviations from expected values to evaluate if reaction of ophiuroids was different to non-feeding and feeding sea stars.

In the above sampling of 20-cm diameter plots we also quantified the number of ophiuroids which did not have their central disk in a crevice. As the variances of these data were not homogeneous, we applied a Kruskal-Wallis H test to analyze the density of exposed ophiuroids in the three sampling conditions (i.e., feeding sea stars, non-feeding sea stars, and absence of sea stars) and we followed with Tukey HSD post-hoc tests on the rank-transformed data.

Effect of substratum complexity on predation in the field

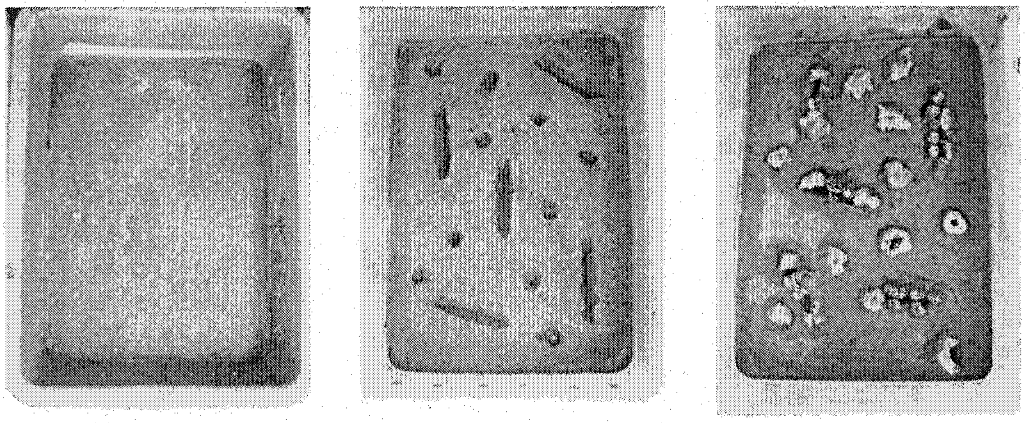
We performed experiments in the field with tethered ophiuroids to identify the major predators of ophiuroids and also to evaluate the effect of substratum complexity on vulnerability to predation. Ophiuroids were tethered to 28-cm diameter concrete plates that we set out horizontally on the ledges that interrupted the vertical wall. The surface of plates was either smooth or complex. The complex plates (which were made to mimic the natural complexity of the wall) had two 6-8 cm long crevices (1 cm wide) and three 1.5 cm diameter holes (the holes and crevices were ~ 1 cm deep), all crevices and holes were partly covered by pieces of coralline algae glued in place using marine epoxy. Each trial began by tethering one ophiuroid to a bolt in the center of a plate using a 10-cm long monofilament thread (8-pound test). The thread was passed through the mouth and central disc of the ophiuroid [technique adapted from Witman (1985) and Aronson (1987)] and a 5-mm piece of rubber was attached at the end of the thread (on the aboral face of the ophiuroid) to keep it from pulling back through the disc. We returned 6 h later to quantify predation. The experiment was run in four blocks (each during a different day on a different portion of the wall) and in total we ran 30 replicates for each of the two substratum types. In parallel, we ran 12 control trials in which predators were excluded by placing a cage over the plates with tethered ophiuroids. We used a semi-quantitative index to quantify predation in each trial, with 0 assigned to intact ophiuroids, 1 to ophiuroids with one arm damaged, 2 to individuals with two or more arms damaged, 3 to individuals with the disk damaged and 4 to dead individuals. We analyzed the data using a mixed-model two-factor ANOVA with Block (experimental period) as the random factor and Treatment (smooth, complex and caged) as the fixed factor. We followed with multiple comparisons on the fixed factor using Tukey HSD test. In all but one of the attacks (out of 32), the predator was identified because it was still feeding when we returned after 6 h. The one case in which the predator was not observed (the ophiuroid and the rubber at the end of the thread had disappeared) was excluded from the analysis. At the end of the experiment, we sampled the experimental area (the horizontal ledges that interrupted the vertical walls) with 25 randomly placed 0.25-m^2 quadrats to quantify the density of the predators present.

Effect of substratum complexity on predation in the laboratory

We performed separate laboratory experiments to quantify the predation rates of *Asterias vulgaris* and *Strongylocentrotus droebachiensis* on ophiuroids under different levels of substratum complexity. The trials were run in plastic tanks (45 x 33 x 5 cm) with concrete bottoms with either low (smooth concrete), medium (five crevices and ten holes, mimicking pitted calcareous rock) or high (five crevices and ten holes partly covered with pieces of coralline algae, mimicking the substratum found on vertical walls) complexity (Fig. 1.1). Prior to each trial we placed 20 ophiuroids (6-13 mm in disk diameter) in the tank and allowed them to acclimate for at least 2 h. We began the trial by adding the predators (3 sea stars or 5 sea urchins) and then made observations at 10-14 h intervals (twice daily) over a week to quantify predation. The experiments with sea stars and urchins were both run in three blocks (time periods) with 6 replicates of each level of substratum complexity per block. The sea stars measured 4-9 cm in radius and had been starved for a week in a 230 l pool prior to the trials, and the urchins measured 3-6 cm in test diameter and had been starved in 20 l buckets for at least two days prior to the trials. We quantified predation by counting the number of ophiuroids that were eaten for each one-week trial. In some cases, the outcome of an attack was not clear, as the sea star had not begun to digest the ophiuroid or the urchin had no more than one of the ophiuroid's arms in its mouth. These events were considered as partial attacks and were scored as 0.5. The dependant variable measured for each tank was the sum of all ophiuroids that were killed (a score of 1.0 per death) plus those that were not killed but suffered attacks (a score of 0.5 per partial attack). All ophiuroids that were attacked were removed from the tanks. For each predator, the intensity of predation was analyzed using a mixed-model ANOVA with Block (period of the trial) as a random factor and Substratum complexity as a fixed factor. The data for the sea star trials were log (x +1)-transformed to homogenize variances. Post-hoc comparisons were made with Tukey HSD tests when a significant effect of substratum complexity was detected.

Reaction of ophiuroids to simulated attacks in the laboratory

We made laboratory trials examining the reaction of ophiuroids to the two predators and different levels of predatory threat. We quantified responses in 15.5-cm diameter circular tank (with no inflow), which had a concrete bottom with one artificial refuge (a 1.5-cm diameter hole, 1 cm deep, partly covered with a piece of coralline algae). We first placed an ophiuroid in the tank and allowed it to crawl into the refuge. Two minutes after the ophiuroid stopped moving in the refuge, we exposed it to one of five 2-min treatments: (1) touched with a harmless object (a 7-mm diameter plastic pipe), as a procedural control, (2) touched with the podia and spines of a large urchin, (3) touched with the arm tip of a sea star (mimicking an approaching asteroid), (4) touched with active podia along the



Low Medium High

Substratum complexity

Figure 1.1. Picture of tanks used in the laboratory experiments investigating the effect of substratum complexity on predation showing substrata of low, medium and high complexity.

ambulacral groove of a sea star (to stimulate an attack), and (5) touched with a piece (mean mass 0.84 g, SD = 0.19, N = 4) of sea star stomach (to simulate an advanced attack). As we wanted to minimize the number of sea stars sacrificed, the tests each day were performed with the stomach of one sea star. We made 75 trials (15 for each stimulus) in a randomized order.

Using digital photos and the image analysis software Sigma Scan Pro 5.0, we calculated the total area of each ophiuroid and also the area exposed (outside the hole) before and after the 2-min treatment. The bottom of the tank was painted in white to facilitate the analyses of the digital photos. Then for each trial we calculated the change in the proportion of the ophiuroid exposed resulting from the stimulation. A positive value meant that the ophiuroid tended to leave the crevice and a negative value that ophiuroid retreated into the crevice. We analyzed the changes in exposure resulting from the different stimulations using a Kruskal-Wallis H test, as variances could not be made homogeneous, and followed with two-tailed Dunnett tests on the rank transformed data to compare the effect of each treatment with the procedural control.

RESULTS

Reaction of ophiuroids to *Asterias vulgaris* in the field

Our sampling of areas without sea stars indicated that the density of ophiuroids on the vertical wall was 1460 ind. m^{-2}, similar to the density reported by Gaymer et al. (2001a) for vertical walls elsewhere in the Mingan Islands. The densities observed in 20-cm diameter circular plots placed around feeding and non-feeding asteroids were virtually the same as in areas without sea stars (Fig. 1.2A). Thus, at this spatial scale there was no evidence that the presence of sea stars (whether feeding or not) influenced the density of ophiuroids.

For both feeding and non feeding sea stars, our counts of the number of ophiuroids directly under the body of sea stars was significantly lower than the expected number in an area the size of the sea star if ophiuroids were evenly distributed at the density recorded in the 20-cm diameter plots ($t = 8.16$, $df = 18$, $p < 0.0001$ for feeding sea stars; $t = 5.84$, $df = 38$, $p < 0.0001$ for non feeding sea stars; Fig. 1.2B). Also, ophiuroids avoided the oral face of feeding sea stars more than that of non-feeding sea stars, as the deviation from expected values was greater for feeding than non-feeding sea stars ($t = 2.97$, $df = 56$, $p = 0.004$; Fig. 1.2B).

The counts of exposed ophiuroids in the 20-cm diameter plots showed that only 0.3 % (4.5 ind. m^{-2} ; SD = 11.4) were exposed in areas without sea stars. In contrast, densities of exposed ophiuroids increased 8-fold in the proximity of non-feeding *Asterias vulgaris* and 15-fold in the proximity of feeding sea stars (Fig. 1.3). A Kruskal-Wallis test indicated that exposed ophiuroid densities varied with sea star presence and activity ($H_{2,79} = 22.53$, $p < 0.0001$) and Tukey test showed that all means were significantly different ($p < 0.02$ for all comparisons).

Effect of substratum complexity on predation in the field

Surprisingly, we only observed urchins attacking tethered ophiuroids, even though sea stars were relatively abundant and Gaymer et al. (2001ab) observed that ophiuroids are the preferred prey of *Asterias vulgaris* in the zone below shallow water mussel beds. The interaction between Block and Treatment (caged control, smooth substratum and complex substratum) was found to be non-significant ($F_{6, 59} = 1.34$, $p = 0.25$) and was pooled with the error term as suggested by Winer et al. (1991). Predation intensity varied among the four experimental periods ($F_{3, 65} = 3.32$, $p = 0.03$). The predation index also differed among the different treatments ($F_{2, 65} = 8.00$, $p < 0.001$). Tukey HSD multiple comparisons showed that predation index in the caged controls was marginally smaller than on complex substratum ($p = 0.06$) and was smaller than on smooth substratum ($p < 0.001$; Fig. 1.4). In fact, all 12 ophiuroids in the caged controls showed no damage indicating that the tethers had no short term effect on their survival. Although predation index tended to be smaller on complex than on smooth substrata, no significant difference was found ($p = 0.09$; Fig. 1.4).

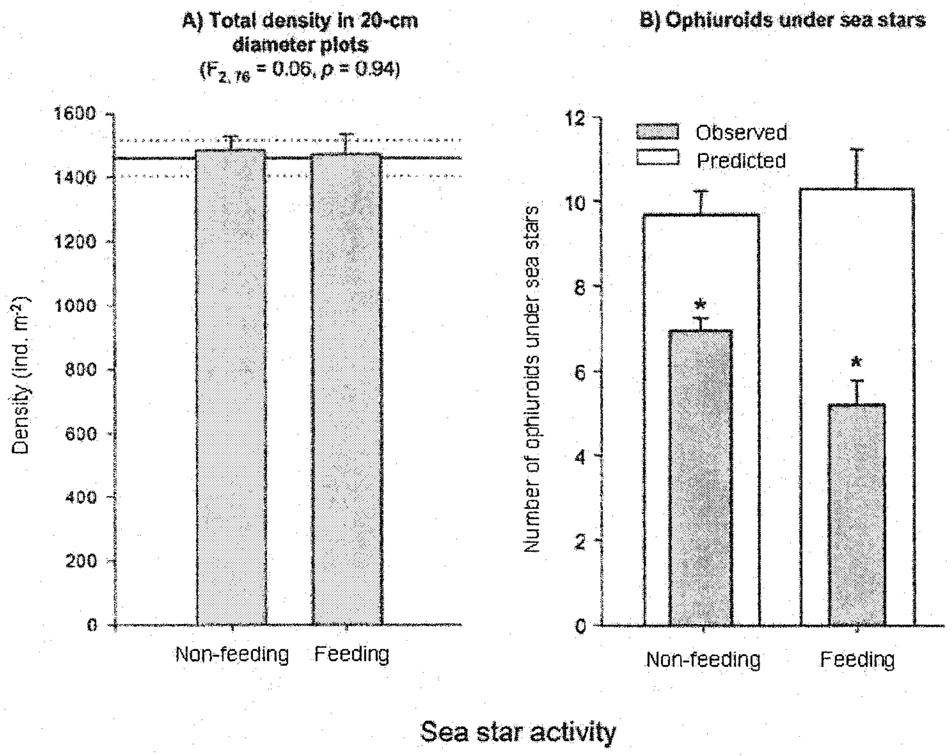


Figure 1.2. A) Field measurements of mean (+SE) density of *Ophiopholis aculeata* in proximity of non-feeding and feeding *Asterias vulgaris* compared with background densities (mean [solid line] ± SE [dashed lines]). B) Mean (+SE) number of ophiuroids found under non-feeding and feeding sea stars compared to values predicted if ophiuroid were evenly distributed in the 20-cm diameter plot. An asterisk indicates that a column is significantly different from the expected value and the difference between number observed and predicted value was greater when sea stars were feeding.

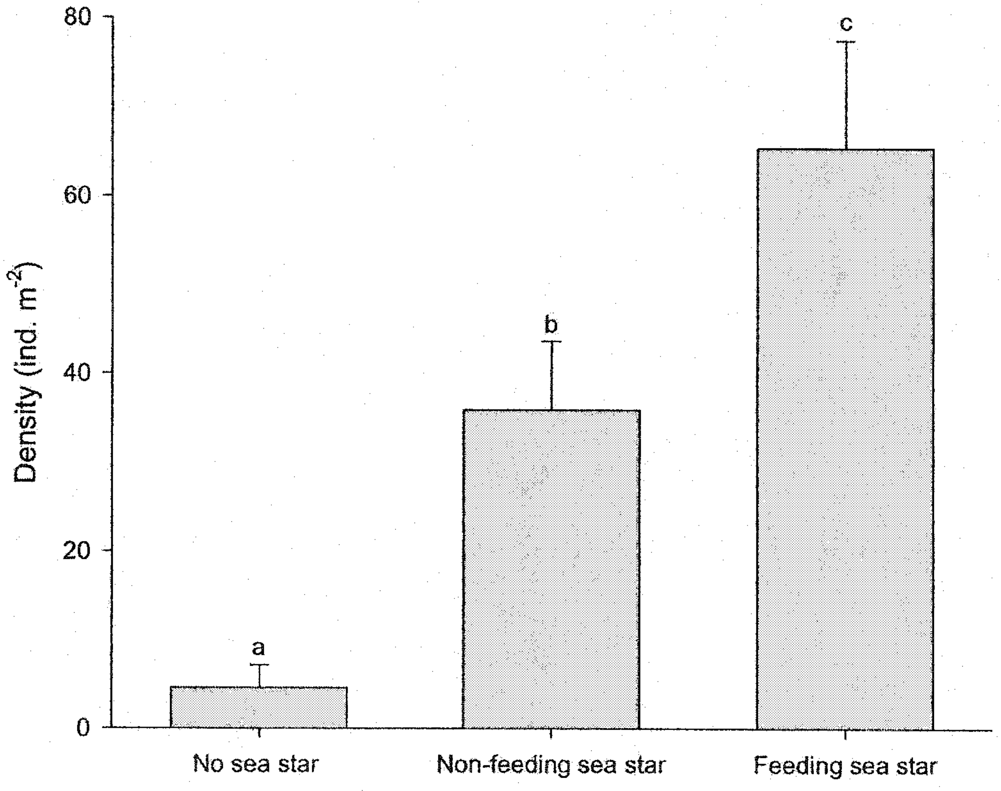


Figure 1.3. Mean (+SE) density of exposed *Ophiopholis aculeata* in 20-cm diameter circular areas where there were no *Asterias vulgaris* and in proximity of non-feeding and feeding sea stars. Columns not sharing a common letter are significantly different (Tukey HSD test on the rank-transformed data, $p < 0.02$ for all comparisons).

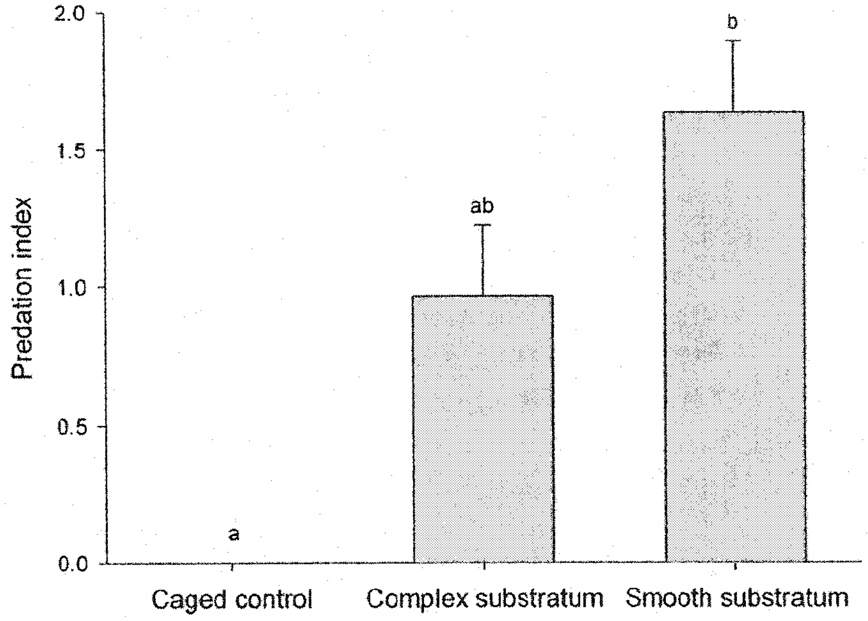


Figure 1.4. Mean (+SE) predation index for *Ophiopholis aculeata* tethered in the field on smooth and complex substrata and in cages (controls). Columns not sharing a common letter are significantly different (Tukey HSD test).

Predator densities at the experimental site were 109.4 (SD = 44.0) urchins $m^{-2}$and 3.0 (SD = 2.9) sea stars m^{-2}.

Effect of substratum complexity on predation in the laboratory

When substratum complexity was low (smooth concrete) the ophiuroids tended to aggregate along the side and in the corners of the tanks. Their behavior was similar on medium substratum complexity except that a few ophuroids were found in holes and crevices. Ophiuroid behavior was strikingly different when substratum complexity was high. Almost all individuals had their central disc hidden in a hole or crevice although some arms were extended in the water column to feed. This is the usual position of ophiuroids in the field.

The full-model ANOVA applied to the log-transformed predation index for the sea stars showed no interaction between Block (period of the trial) and Substratum complexity ($F_{4, 45}$= 0.21, $p = 0.93$). Thus, we used the pooled interaction and error terms to calculate F-ratios for the effects of Block and Substratum complexity, as suggested by Winer et al. (1991). The partial model revealed an effect of both Block ($F_{2, 49}$= 9.23, $p = 0.0004$) and Substratum complexity ($F_{2, 49}$= 7.56, $p = 0.001$). The Block effect was probably because water temperature increased gradually from trial to trial and the feeding of *Asterias vulgaris* increases with temperature (Gaymer et al. 2002). Tukey tests showed that the predation index was higher on the most complex substratum than on the two less complex substrata ($p < 0.01$ for both comparisons). The predation index did not differ between low and medium substratum complexity ($p = 0.84$; Fig. 1.5).

We again pooled the interaction and error terms when we analyzed the urchin predation data as the interaction term in the full model was non-significant ($F_{4, 45}$= 1.35, p = 0.27). The partial model revealed no effect of Block ($F_{2, 49}$= 0.74, $p = 0.48$) and a weak

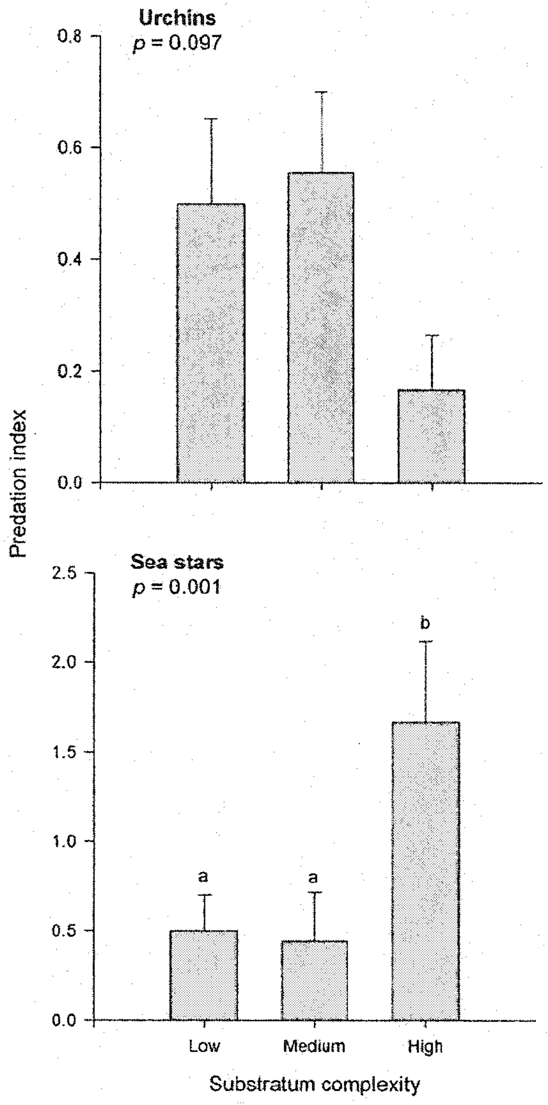


Figure 1.5. Mean (+SE) predation index on *Ophiopholis aculeata* in laboratory predation experiments with the urchin *Strongylocentrotus droebachiensis* and the sea star *Asterias vulgaris* on substrata of low, medium and high complexity. P-values are for the substratum complexity factor of the partial mixed model ANOVA with the interaction term pooled with the error term. Predation indices for sea stars were log-transformed prior to analysis and back-transformed for presentation. In the lower graph, columns not sharing a common letter are significantly different (Tukey HSD).

effect of Substratum complexity ($F_{2,\ 49} = 2.44$, $p = 0.098$). The pattern of predation rates observed on the different substrata was strikingly different from that observed for sea stars. Predation intensity was similar at low and medium substratum complexity and was 3 times lower at high substratum complexity (Fig. 1.5).

Reaction of ophiuroids to simulated attacks in the laboratory

The tendency of ophiuroids to hide in a crevice in response to different predatory and non predatory stimuli varied markedly (Kruskal-Wallis $H_{4,\ 69} = 40.04$, $p < 0.0001$; Fig. 1.6). Ophiuroids retracted deeper into refuges when touched with an urchin than when touched with a plastic pipe in the control treatment (Dunnett, $p = 0.02$). In contrast, the response to being touched by the arm tip or ambulacral groove of the sea star (representing low levels of threat) was similar to the response in the control treatment (Dunnett, $p = 0.87$ and 0.84, respectively). There was a great increase in exposure when touched with the stomach of the sea star (Dunnett, $p < 0.0001$). In fact, 93 % of the ophiuroids tested completely left their refuge and the mean departure time was 31 s.

DISCUSSION

Our predation experiments in both the field and laboratory indicated that substratum complexity tended to offer the ophiuroid *Ophiopholis aculeata* with protection from predation by the urchin *Strongylocentrotus droebachiensis* (Figs. 1.4, 1.5). Although no significant effect of substratum complexity was found in either of the experiments, they both yielded similar results. In both cases predation by urchins was less intense on the more complex substratum and in both cases the effect approached statistical significance ($p \approx 0.1$), thus we are confident that these tendencies represent a true effect. For practical reasons, the densities of ophiuroids and urchins in the laboratory experiment were lower than in the field (>10 times lower for ophiuroids and 3 times lower for urchins). It is likely that natural densities would increase encounter rates, and consequently enhance the effect of substratum complexity on the mortality risk of ophiuroids. The ophiuroid retracted into refuges in response to contact with the urchin (Fig. 1.6). This escape response, and the use

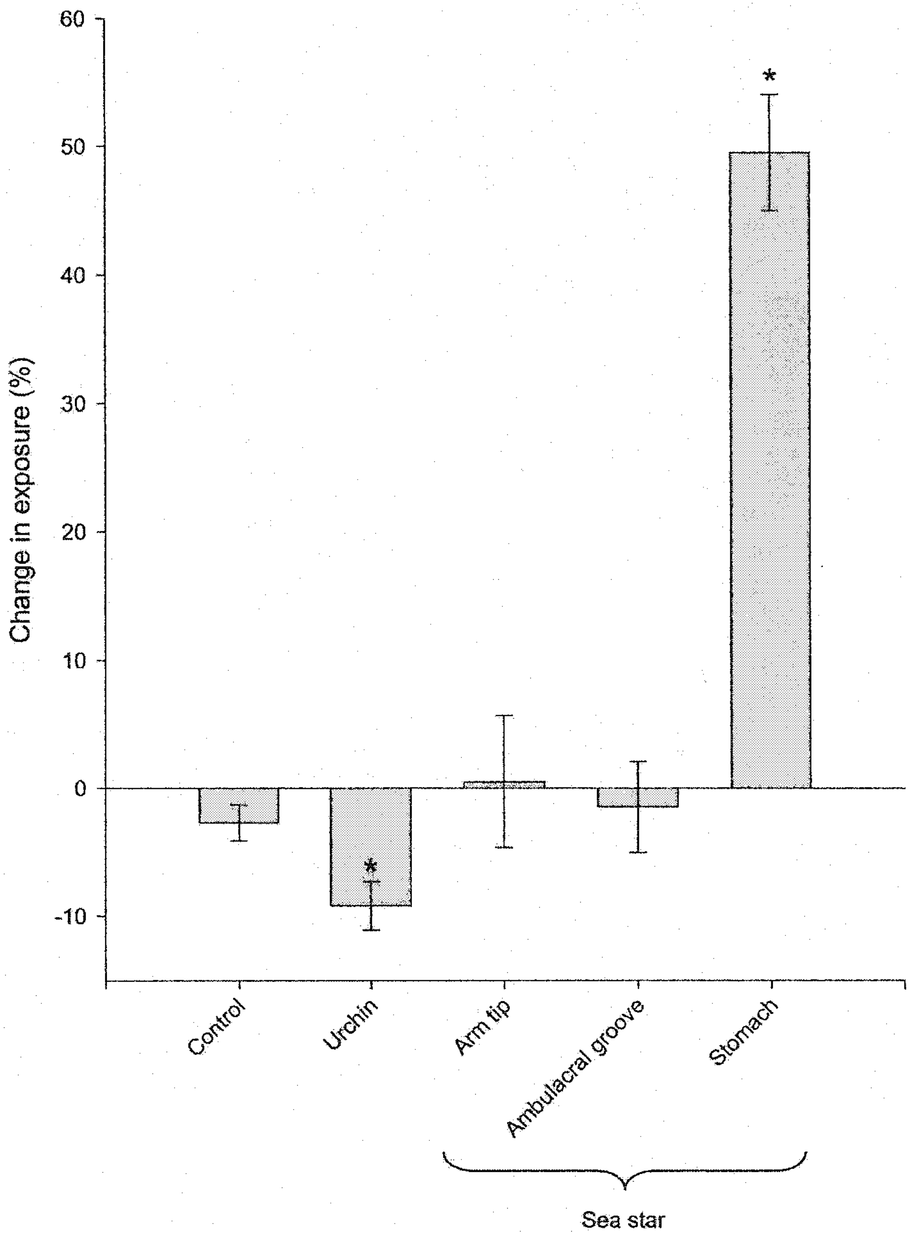


Figure 6. Mean (+SE) change in body exposure of ophiuroids following simulated attacks by urchins and different threats posed by sea stars. An asterisk indicates a significant difference from the procedural control (Dunnett Test on the rank transformed data).

of crevices in itself, should distance the ophiuroid from the urchin's feeding apparatus. Our observations of the interaction between the ophiuroid and the urchin corroborate the hypothesis that habitat complexity provides protection from predation (see references in introduction). Algae are the main food of sea urchins and their intensive grazing limits the distribution of most fleshy macroalgae (Himmelman et al., 1983). However, the urchin also consumes animals when available and accessible (Himmelman and Steel, 1971; Briscoe and Sebens, 1988). Our experiments show that *S. droebachiensis* feeds on ophiuroids, as noted in one early report by Blegvad (1914; cited in Lawrence, 1975). In fact, ophiuroids appear to be a common food item of urchins on vertical walls in the Mingan Islands as ophiuroids were found in the guts of 26 % of urchins (N = 53) collected at Pointe-Enragée in August 2002 (D. D. unpublished data).

In contrast with urchins, predation by sea stars on ophiuroids increased with substratum complexity (Fig 1.5). Although contrary to the general rule that substratum complexity decreases vulnerability to predators, these results make sense if we consider the biology of the organisms involved. *Asterias vulgaris* moves slowly and can easily be outrun by the ophiuroid on smooth substratum (Gaymer et al., 2001a). However, substratum complexity may interfere with the displacement of ophiuroids, but does not appear to reduce the movement of the sea star, at least with the arrangement of structural components used in our experiments which was meant to mimic the substratum at our field site (i.e., pitted calcareous rock covered by encrusting coralline algae). The soft body of the sea star likely allows it to block the departure of an ophiuroid from a crevice and then the sea star's stomach is everted to digest the ophiuroid in its crevice. Following encounter, prey escape probability is usually enhanced in complex habitats, as structural components may reduce either the predator's maneuverability or access to prey (Ryer, 1988; Bartholomew et al., 2000). This does not appear to be the case with interactions between *O. aculeata* and *A. vulgaris*. The sea star's access to the ophiuroid is not reduced by substratum complexity, as the sea star can readily evert its stomach into crevices. Also, the movement of the sea star does not seem to be limited by the degree of substratum complexity provided by the pitted calcareous rock and nodules of coralline algae. On the contrary, it appears that ophiuroids can be trapped in crevices in calcareous rock and coralline algae. Batholomew et al. (2000)

proposed that the ratio of spacing of structural components in a habitat to the width of a predator can be used as a predictor of predation rates. However, our results suggest that predation rates may be more accurately predicted by considering the relative effect of structural complexity on displacement of both predator and prey. We predict that habitat complexity should increase predation when the movement of the prey is more limited by structural components than that of the predator.

Tethering experiments are criticized because experimental artifacts may differ between treatments. For example, using tethering to evaluate predation rates in different habitats is often biased if predator guilds vary with habitat (Peterson and Black, 1994; Haywood et al., 2003) as tethering artifacts can vary for different predators (Barbeau and Scheibling, 1994). Our trials were not subjected to this bias, as we placed the artificial substrata in the same habitat at a single location. Also, only urchins were observed attacking tethered ophiuroids. We cannot exclude the possibility that the tethers restricted the movement of ophiuroids more on one substratum than another, or that they facilitated attacks by one predator (e.g. the urchin) more than by other predators. Thus, we cannot definitively conclude that predation by urchins is more important than predation by sea stars although our results strongly suggest that it is the case.

In the laboratory, ophiuroids displayed strong threat-sensitivity to *Asterias vulgaris*. They reacted little to the arm tip and ambulacral groove, which represented low and medium levels of threat respectively, but they showed a violent reaction to the sea star's stomach (Fig. 1.6). Since ophiuroids in crevices are at greater risk of being preyed upon by the sea star, fleeing from crevices may reduce the probability of capture following encounter with *A. vulgaris*. It was shown that many prey species of sea stars react to the presence of their predator through the detection of asterosaponins (molecules exuded by many sea star species) (Harvey et al., 1987) and these molecules are most concentrated in stomach tissues (Garneau et al., 1989). The strong response to the stomach of *A. vulgaris* might be due to the high concentration of asterosaponins in the stomach. Concentrations exuded by arm tips and ambulacral grooves appear to be too low to elicit flight, although it is also possible that ophiuroids discriminate chemicals present in different tissues.

We first became interested in the interaction between *Ophiopholis aculeata* and *Asterias vulgaris* after observing ophiuroids on the top of the sea star. This was surprising given that the ophiuroid is the main prey of *A. vulgaris* in this community. Our initial hypothesis was that the ophiuroid might approach the feeding sea star to kleptoparasitize food. Our sampling in 20-cm circular areas showed that the density of the ophiuroid did not change with the presence or absence of the sea star, or with whether the sea star was feeding or not (Fig. 1.2A). This suggests that ophiuroids do not move toward sea stars. Our sampling of ophiuroids directly under the body of the sea star revealed that densities were less than on equivalent surfaces without sea stars, and further that densities were less under feeding than non feeding sea stars (Fig. 1.2B). The reduction of the number of ophiuroids under feeding sea stars is probably a consequence of the fleeing of ophiuroids that came into contact with the stomach, as observed in the laboratory simulations. However, the explanation for the reduction under non feeding sea stars is unclear as ophiuroids in the laboratory did not react to contact with the arm tip and ambulacral groove of *A. vulgaris*. Possibly the duration of the laboratory stimulations (2 min) was too short to elicit a reaction. In parallel, we documented a strong increase in densities of exposed individuals in proximity of *A. vulgaris* in comparison to areas without sea stars, and exposed ophiuroids were most abundant near feeding sea stars (Fig. 1.3). The exposed individuals probably represented fleeing individuals, as the escape response of ophiuroids to the sea star in the laboratory was to flee from crevices. These observations suggest that ophiuroids do react to their sea star predator, although only by moving a few centimeters. A proportion of these fleeing ophiuroids likely climbs onto the aboral surface of the sea stars, which should be a low risk location. Thus, the peculiar observation of ophiuroids on top of sea stars does not represent individuals drawn to sea stars for feeding opportunities, but rather ophiuroids fleeing to escape being eaten.

The strong threat-sensitivity of *Ophiopholis aculeata* to its sea star predator (not fleeing until the last moment) probably represents a trade-off between predation risk from the sea star and other predators. Although delayed departure from crevices probably increases the capture probability by the sea star, it minimizes time spent on open surfaces, where the ophiuroid is vulnerable to urchins and perhaps other predators. These behavioral responses to the two predators should minimize the overall probability of mortality. This hypothesis needs to be tested using experiments with combinations of both predators. We predict that presence of *Asterias vulgaris* will indirectly increase the predation efficiency of urchins by increasing the number of exposed ophiuroids. Studies are also needed to investigate changes in the behavior of the ophiuroid in warmer North Atlantic areas where other ophiuroid predators, notably fish and decapod crustaceans, are abundant (Witman, 1985; Witman and Sebens, 1992).

CHAPITRE 2

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

RÉSUMÉ

Nous avons évalué l'effet de l'intensité lumineuse et de la complexité du substrat sur les préférences d'habitat et la vitesse de déplacement de l'ophiure *Ophiopholis aculeata*. L'ophiure préfère fortement une faible intensité lumineuse et dans une moindre mesure un substrat complexe. De plus, la vitesse de déplacement a augmenté avec une augmentation de l'intensité lumineuse et a diminué avec la complexité du substrat (les ophiures étaient virtuellement immobiles sur un substrat complexe et ombragé). Sur le terrain, la densité d'ophiures exposées (avec le disque en dehors d'une crevasse) était toujours faible, indépendamment de l'intensité du rayonnement solaire. Par contre, leur activité d'alimentation était inversément corrélée avec l'intensité lumineuse, puisque le nombre de bras étendus était faible au soleil, intermédiaire à l'ombre et maximum la nuit. Une expérience sur le terrain a montré que la réponse à la lumière n'était pas modifiée quand les rayons UV étaient éliminés avec un filtre, et une expérience de laboratoire a montré que la lumière blanche seule peut produire un patron d'activité similaire à celui observé sur le terrain. *O. aculeata* réduit probablement son activité d'alimentation lorsque l'intensité lumineuse est élevée pour réduire l'exposition aux prédateurs visuels qui chassent plus efficacement à la lumière. Par contre, les prédateurs visuels sont rares dans notre aire d'étude. Nous émettons l'hypothèse que la dispersion larvaire à grande échelle d'*O. aculeata* (à cause d'un long développement planctonique) empêche les ophiures de s'adapter aux prédateurs locaux. La réponse à la lumière reflèterait donc une adaptation aux prédateurs visuels présents dans d'autres régions.

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. 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.

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, 1977; 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 (chapter 1), but the arms are extended to various degrees. *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* (chapter 1) 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 (chapter 1). 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 *Ophiopholis aculeata*. We first evaluated 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.

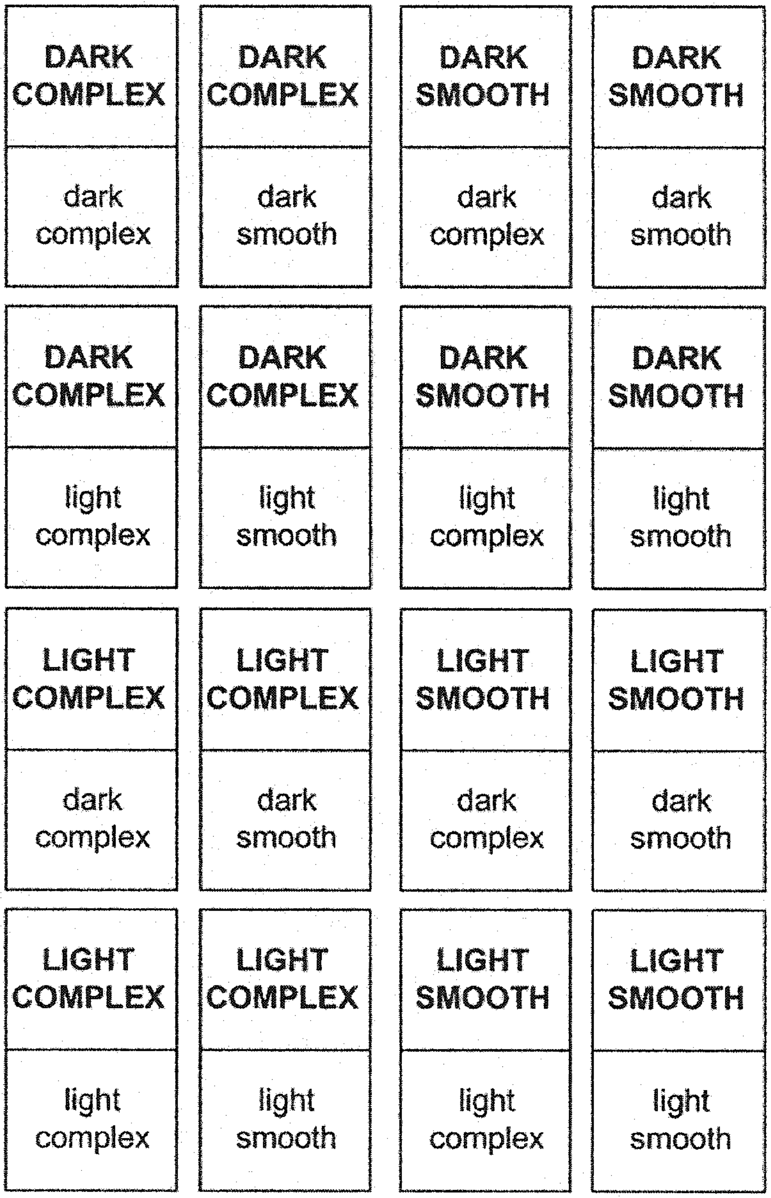
METHODS

Our field studies were conducted between June and August 2003 on a population of *Ophiopholis 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}; chapter 1).

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.

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 x 24 x 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. 2.1). 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. 2.1), each of which was replicated six times in a random order with one replicate of each treatment per day of trial.



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

Figure 2.1. 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.

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, SD = 2.15, N = 960) on a line across the center of the tank and then after 10 min recorded the proportion that chose the targeted side (uppercase letters in Fig. 2.1). Ophiuroids that did not leave the centerline (2-cm in width) were excluded from the analysis.

We analyzed the data using a fixed 4 x 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 targeted 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.

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 x 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 x 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, SD = 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 six treatments was replicated ten 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 Results), 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.

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 sub-sites, each in a different period. At each sub-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.

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 x 15 x 6 cm) that were covered with a 30 x 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, SD = 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).

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 x 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.

RESULTS

Effect of light and structural complexity on micro habitat selection

The experiment in which we recorded the responses of *Ophiopholis aculeata* to all combinations of four levels of the factor light and four levels of the factor substratum complexity (Fig. 2.1) 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. 2.2). 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. 2.2). 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. 2.2), although this latter difference was not significant. Thus, our data indicated a preference for complex substratum.

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 moved in the arenas ($F_{2,54} = 85.9$ for Light intensity and $F_{1,\ 54} = 79.1$ 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. 2.3).

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 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 2.1, Fig. 2.4). In contrast, the density of extended arms varied markedly with

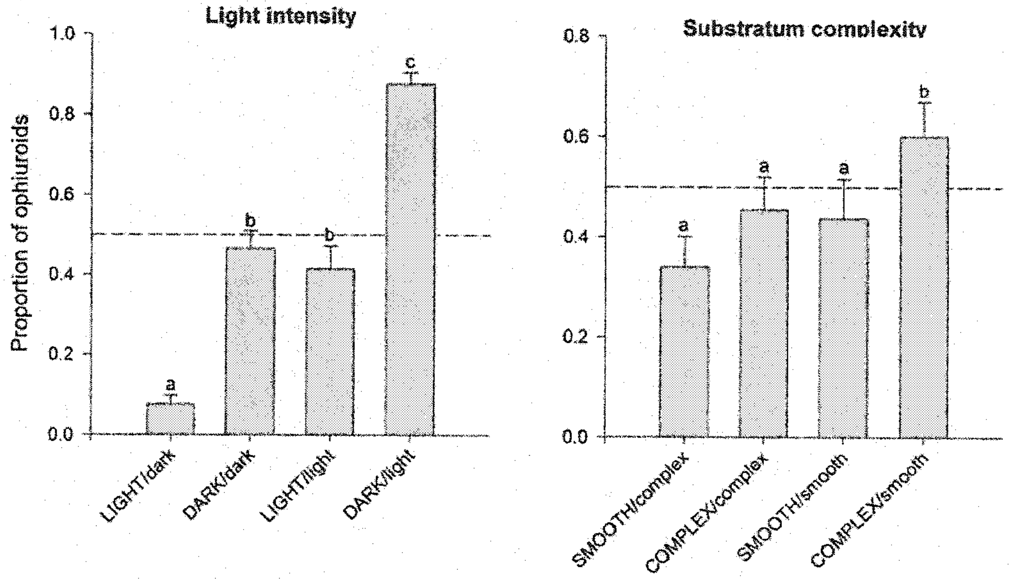


Figure 2.2. Proportion of ophiuroids that choose a pre-selected side of the tank having different levels of light intensity and substratum complexity in the multifactor choice experiment. Uppercase letters denote the condition present on the half of the tank where preference of ophuiroids was evaluated and lowercase letters, the condition on the other half. Error bars show standard error and columns not sharing a common letter are significantly different (Tukey HSD). Dashed line represents the 1:1 distribution representing non preference.

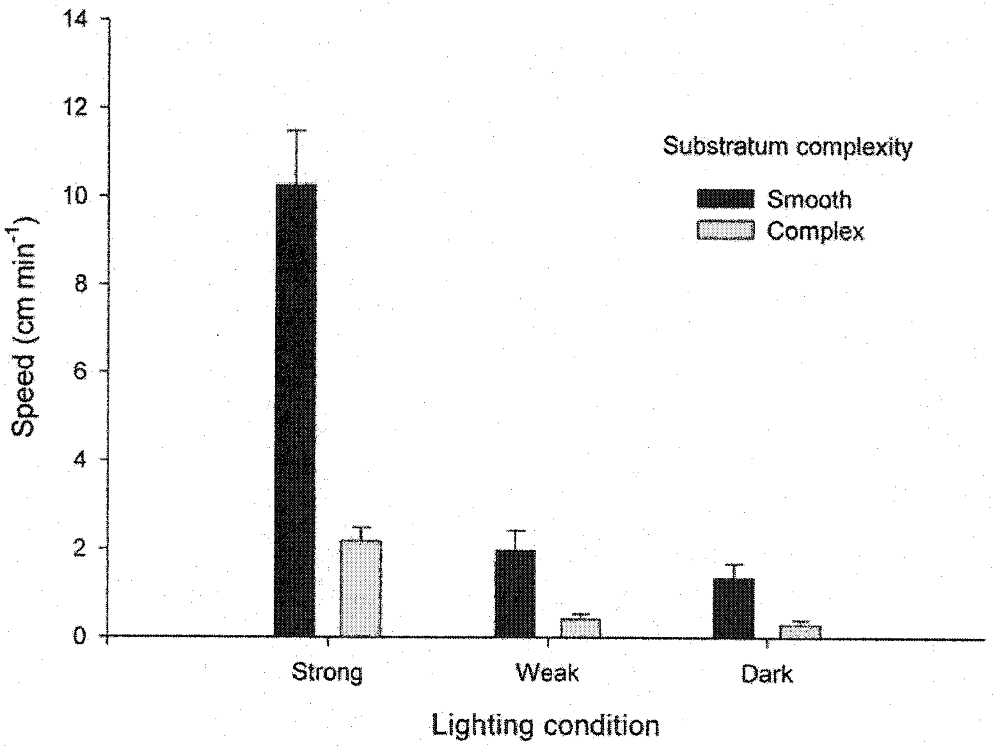


Figure 2.3. Mean (+SE) displacement speed of ophiuroids exposed to different combinations of light intensity and substratum complexity in the laboratory. Under all light intensities speed was significantly higher on smooth substratum and for both substrata speed was higher under strong light than under weak light or in the dark. Raw data are presented but analyses were performed on the log-transformed data.

Table 2.1. Nested ANOVA table of the number of exposed ophiuroids and the number of extended arms (square root-transformed data) under different light intensities in the field.

			Exposed ophiuroids			Extended arms		
Factor	d.f.	Denom.	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 x Site LS_{ij}	4	$LT(S)_{ik(i)}$	0.040	1.67	0.23	10.8	3.87	0.033
Light x 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		

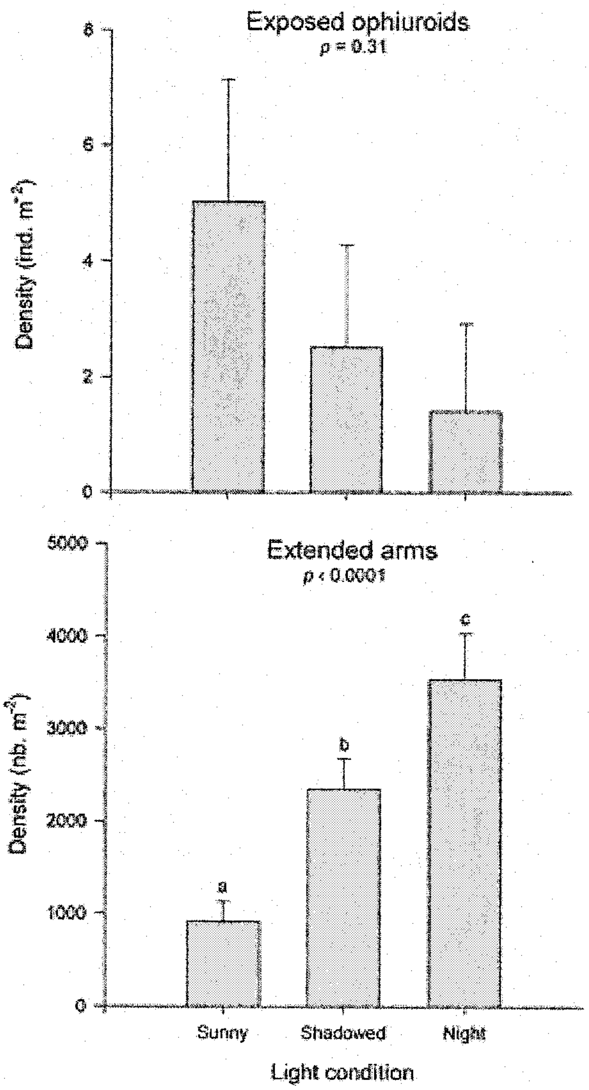


Figure 2.4. Effect of solar radiation intensity on the density of exposed ophiuroids and suspension feeding arms in the field. P-values are from the light factor of the ANOVA. Error bars show standard error and columns not sharing a common letter are significantly different (Tukey HSD). Densities of extended arms were square-root transformed prior to analysis.

Sites, Transects and Time of day (Table 2.1). The density was least in sunlight, increased by >2-fold in shadow and by almost 4-fold in darkness (Fig. 2.4; all means were significantly different). The effect of light varied among Site (Table 2.1) probably because of variations in irradiance on the different days of the study. The effect of light also varied with transects within sites (Table 2.1), as the effect of light was greater at one transect at the first site.

Effect of UV radiation

The field experiment exploring the response of *Ophiopholis 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 2.2). At the two depths, there tended to be a weak effect of Block (Table 2.2) 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 cages without UV filter (Fig. 2.5).

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 their body was exposed ($F_{2,\ 57}$= 17.4, $p < 0.0001$). During the 10-min trials, ophiuroids became more 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. 2.5, 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. 2.5, all means were significantly different).

Table 2.2. ANOVA table of the number of suspension feeding arms per ophiuroid in the UV effect field experiment at 3 and 7 m in depth.

	3 m				7 m			
Factor	d.f.	MS	F	*p*	d.f.	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		

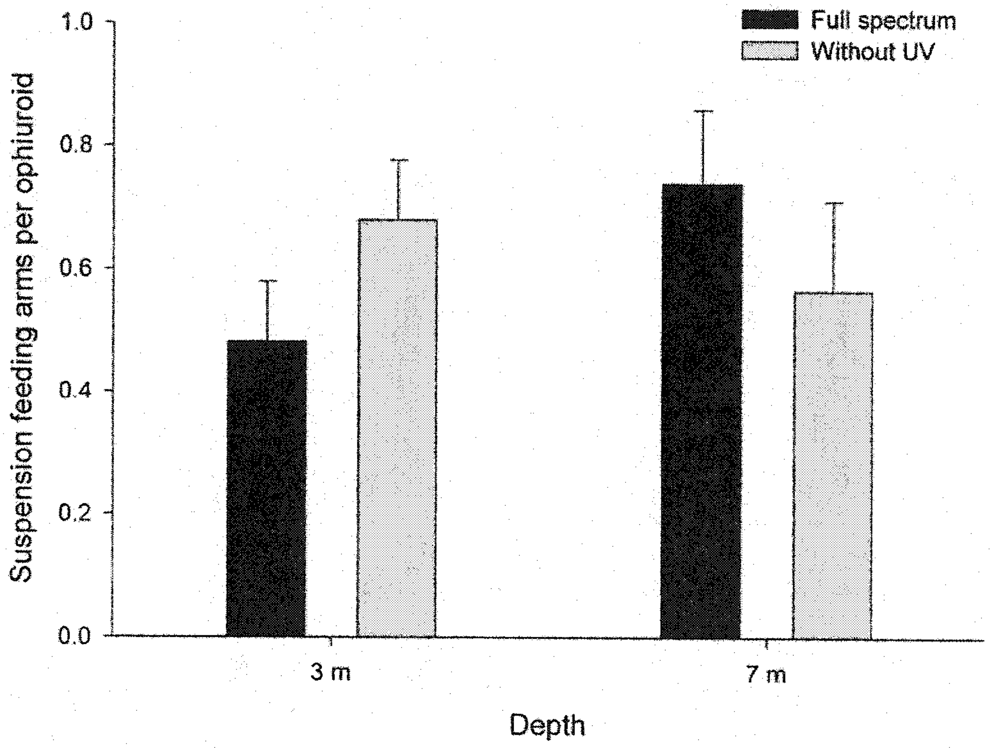


Figure 2.5. Effect of UV radiation and depth on the number of suspension-feeding arms per ophiuroids. No significant effect of UV light (presence or absence) was detected by the analysis.

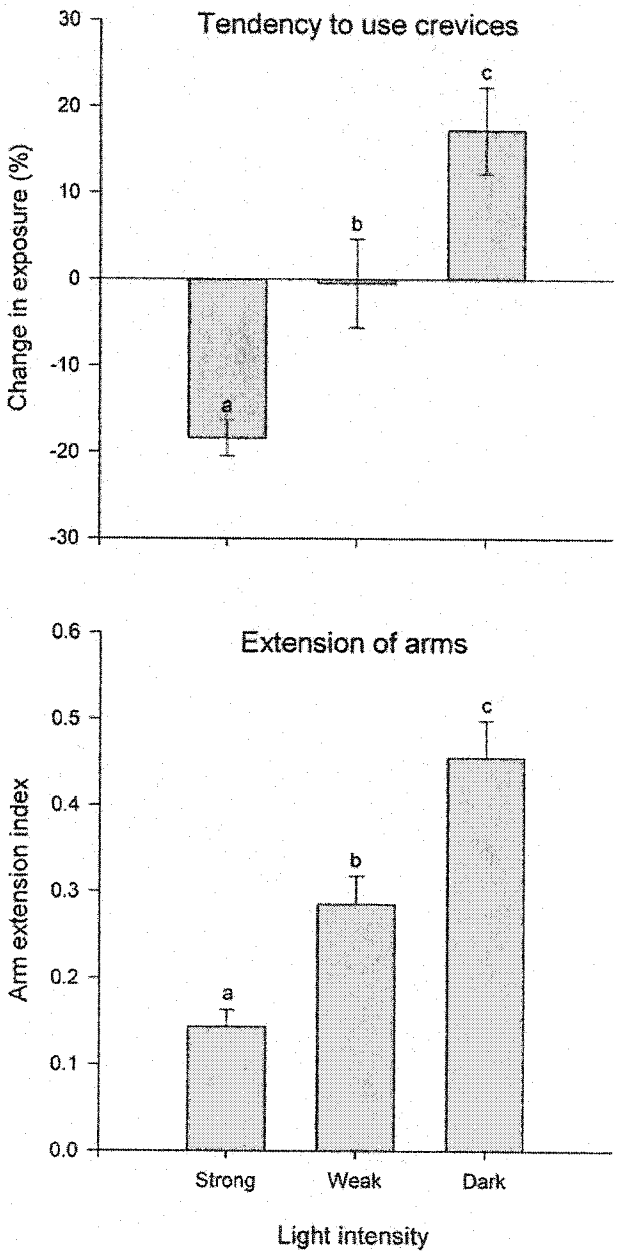


Figure 2.6. Effect of white light intensity on the suspension-feeding activity and tendency to use refuge of ophiuroids in the laboratory. Error bars show standard error and columns not sharing a common letter are significantly different (Tukey HSD).

DISCUSSION

The ophiuroid *Ophiopholis 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. 2.2). *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. 2.3). Thus, on complex substratum ophiuroids were virtually immobile at low light intensities (preferred conditions; less than 0.2 cm min^{-1}) and moved more rapidly when exposed to strong light (Fig. 2.3). We similarly observed an increased displacement speed with increasing light on smooth substratum, but the change was more pronounced (Fig. 2.3). 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. 2.4), 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. 2.4). 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 *Strongylocentrotus 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. 2.5), suggesting that UV light plays a minor role, or no role, in modulating 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. 2.6) and the pattern related to the intensity of white light was remarkably similar to that observed in the field (Figs. 2.4 and 2.6). 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 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-dependant feeding pattern of *O. aculeata* in the Mingan Islands is not obvious since their main predators, the urchin *S. droebachiensis* and the asteroid *Asterias 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 (chapter 1). 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 an 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.

Conclusion générale

Les résultats de cette recherche montrent que plusieurs facteurs vont influencer le comportement cryptique de l'ophiure *Ophiopholis aculeata* et que ce comportement a des conséquences écologiques importantes. L'utilisation de refuges offre une protection contre la prédation par les oursins, mais augmente le risque de prédation par l'étoile de mer. Par contre, les résultats des expériences portant sur l'effet de la complexité du substrat sur la vulnérabilité des ophiures face aux différents prédateurs doivent être interprétés avec une certaine prudence. En effet, les substrats complexes ont été construits avec des morceaux d'algue coralline et il est difficile de séparer les effets de la complexité du substrat et de l'ajout d'un nouvel élément dans les bassins. Toutefois, les bassins ont été conçus pour mimer un environnement naturel et les résultats des expériences représentent probablement ce qui se passe en situation naturelle. En réponse à l'effet contrastant de la complexité du substrat sur le risque de prédation face aux différents prédateurs, l'ophiure adopte des stratégies différentes face aux deux prédateurs. Elle se cache plus profondément dans les crevasses suite à un contact avec l'oursin pour rester hors d'atteinte du prédateur. L'ophiure ne réagit pas au contact avec le bras ou le sillon ambulacraire de l'étoile, mais quitte rapidement les crevasses (où le risque de prédation est plus élevé) lorsqu'elle est touchée par l'estomac du prédateur. Ce comportement sensible au risque posé par l'étoile laisse croire que l'ophiure fait face à un compromis dans l'utilisation des crevasses relié à l'effet contrastant de la complexité du substrat sur le risque de prédation par les deux prédateurs. Le délai de réponse face à l'étoile augmente probablement la probabilité de capture par l'étoile, mais réduit le temps passé en milieu ouvert où le risque de prédation par l'oursin est plus élevé. Le système ophiures-oursins-étoiles serait un bon modèle pour l'étude des interactions d'ordre supérieur et les modifications d'interaction. L'activité des étoiles augmente le nombre d'ophiures hors d'une crevasse ce qui pourrait augmenter la vulnérabilité aux oursins. On peut donc s'attendre à observer une interaction de second ordre dans laquelle l'effet des étoiles et des oursins sur les populations d'ophiures est non additif.

Le comportement cryptique de l'ophiure est dû à une forte tendance à éviter la lumière blanche et à une préférence pour les environnements complexes. L'intensité de lumière blanche influence le degré d'exposition des ophiures par une modification du nombre de bras sortant des crevasses. L'intensité de l'alimentation est inversement corrélée à l'intensité lumineuse tant sur le terrain qu'en laboratoire. Les ophiures ne semblent pas se cacher pour éviter les dommages dus à l'exposition au rayonnement ultraviolet. Il est possible que le patron d'activité d'alimentation inverse à la quantité de lumière des ophiures soit une adaptation pour réduire le risque de prédation par les prédateurs visuels. Toutefois les prédateurs visuels sont rares dans les Îles Mingan et les prédateurs principaux (oursins et étoiles) ne sont pas affectés par l'intensité lumineuse. Ceci porte à croire que le fort potentiel de dispersion du stade larvaire pélagique des ophiures ne leur permet pas de s'adapter aux prédateurs locaux. Des études de structure génétique des populations d'ophiures dans le Golfe du Saint-Laurent seraient requises pour tester les postulats de cette hypothèse. Par la suite, des expériences de prédation en transplantation réciproque entre des populations d'ophiures de différentes origines sont requises pour tester l'hypothèse. Selon l'hypothèse de l'inaptitude des ophiures des Îles Mingan à s'adapter à la pression de prédation locale, on s'attendrait à ne pas observer de différences dues à l'origine des ophiures sur leur comportement et leur vulnérabilité à la prédation.

La plupart des méthodes utilisées dans cette étude sont nouvelles et fournissent des outils qui peuvent être utilisés pour l'étude du comportement de toutes les ophiures. Malgré les difficultés inhérentes à l'expérimentation avec les ophiures, cette étude a démontré qu'il est possible de développer des techniques efficaces. Les ophiures en laboratoire montrent des comportements très similaires à ce qui est observé sur le terrain. Toutefois, afin d'obtenir des comportements naturels, il est important d'utiliser des ophiures collectées récemment et de maintenir les ophiures dans des bassins avec une importante circulation d'eau. Une captivité prolongée modifie le comportement des ophiures et réduit conséquemment le potentiel d'inférence des expériences de laboratoire. L'utilisation des cages sur le terrain est difficile à cause de la grande manoeuvrabilité des ophiures. Les cages doivent être construites avec un grillage fin (moins de 5 mm) et des efforts considérables doivent être déployés pour boucher la moindre ouverture. De plus, afin de permettre des études plus détaillées de déplacement sur le terrain, il est impératif de développer une technique de marquage des individus. Une possibilité serait d'utiliser des marqueurs fluorescents qui se fixent aux structures calcaires (e.g. calcéine ou tétracycline).

Les résultats présentés dans ce mémoire sont novateurs en plusieurs points et constituent une des études les plus approfondies sur le comportement des ophiures en général. De plus l'expérience de prédation en laboratoire avec les étoiles de mer a généré des résultats contraires à la 'règle' voulant que le risque de prédation diminue avec une augmentation de la complexité de l'habitat. Ces résultats ont permis de mettre en évidence certains mécanismes qui ont mené à une compréhension plus approfondie de l'effet de la structure de l'habitat sur les interactions entre les proies et les prédateurs.

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