UNIVERSITÉ DU QUÉBEC À RIMOUSKI

Caractérisation de la dynamique de la prédation du pétoncle géant (*Placopecten magellanicus*) juvénile à court terme après un ensemencement à grande échelle au large des îles de la Madeleine, Québec

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AVANT-PROPOS

L'ensemencement de pétoncles juvéniles sur le fond marin a débuté au Japon dans les années 1940, afin de rétablir les gisements naturels aux niveaux existants avant la surpêche. Pour y parvenir, les Japonais ont développé au fil des ans diverses approches et techniques qui, aujourd'hui, portent fruit. Des taux de retour à la pêche aussi élevés que 60 % y sont rapportés et le Japon demeure toujours le chef de file mondial pour ce type d'élevage.

L'enthousiasme japonais pour la pectiniculture a atteint le Québec au début des années 1990. Une vingtaine de pétoncliers des Îles-de-la-Madeleine ont alors accepté de s'associer à un projet d'ensemencement du pétoncle géant, en se basant en bonne partie sur le modèle japonais, afin de restaurer les gisements naturels et assurer une stabilité des débarquements. Dix ans plus tard, la compagnie Pétoncles 2000 a été créée, visant des ensemencements annuels de plusieurs millions de pétoncles juvéniles. Les premiers résultats d'ensemencements à grande échelle ont alors été récoltés et les taux de retour, en deçà des prévisions, ont remis en question la rentabilité de cette approche de production. Parmi les divers facteurs pouvant occasionner les pertes en pétoncles d'élevages, ceux associés à la prédation ont été jugés déterminants. L'entreprise a donc demandé au centre de recherche en aquaculture des Îles-de-la-Madeleine d'évaluer l'importance de l'impact de la prédation sur les semis de pétoncles.

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RÉSUMÉ

La prédation est un élément important dans la dynamique des populations et des communautés. Les bivalves marins sont particulièrement vulnérables à la prédation au stade juvénile ce qui complique la gestion des espèces à intérêt commercial pour les pêcheries et l'aquaculture. Les travaux sur l'élevage du pétoncle géant (*Placopecten magellanicus*) par l'ensemencement de fonds marins dans l'est du Canada ont d'ailleurs obtenu dans le passé des résultats mitigés qui ont souvent été associés au problème de prédation.

Cette thèse visait donc à caractériser la dynamique de la prédation des pétoncles juvéniles à court terme à la suite d'ensemencements à grande échelle réalisés au large des îles de la Madeleine, Québec. L'accès à un gisement naturel de pétoncles géants fermé à la pêche a également permis de récolter des informations sur la dynamique de la prédation des pétoncles juvéniles dans un contexte sans ensemencement et sur une échelle saisonnière.

Les travaux de terrain ont été menés de 2003 à 2005 et 2007. Les assemblages de prédateurs ont été étudiés avec une caméra sous-marine montée sur traîneau ou trépied tandis que le potentiel de prédation des pétoncles juvéniles a été estimé à l'aide d'un procédé d'attachement adapté pour le travail en eau profonde (>30 m). Des travaux en laboratoire réalisés en 2005 ont également permis de documenter les taux de prédation et le comportement des principaux prédateurs benthiques envers les pétoncles juvéniles. Les données de laboratoire ont ensuite été utilisées dans un modèle de prédation assumant une action indépendante des prédateurs multiples. Les valeurs de prédation estimées ont été comparées aux valeurs observées afin de détecter les possibles interactions prédateur-prédateur.

À la suite d'un ensemencement, les inventaires ont révélé que les pétoncles juvéniles étaient distribués par agrégats, et qu'après quelques semaines, la densité initiale des pétoncles ensemencés avait déjà diminué de près de 10 fois. Du côté des prédateurs, les ensemencements n'ont pas révélé de réponse d'agrégation des principales espèces d'étoiles de mer (*Asterias vulgaris*, *Leptasterias polaris* et *Crossaster papposus*) et de crabes

(*Cancer irroratus* et *Hyas araneus*), mais plutôt une réponse fonctionnelle en relation à l'augmentation de la densité de proies. Le potentiel de prédation observé a atteint jusqu'à 10 % par jour. Ces données de prédation se sont avérées assez près de celles estimées par le modèle et suggèrent une action indépendante des prédateurs. La prédation n'a toutefois pas permis d'expliquer toutes les pertes en pétoncles juvéniles estimées sur les sites ensemencés. Il semble donc que la dispersion des pétoncles ensemencés jouerait également un rôle déterminant.

Dans les sites non ensemencés, l'assemblage des prédateurs au large des îles de la Madeleine et leur potentiel de prédation n'a pas semblé suivre de variation saisonnière importante. Cette étude et celle portant sur les ensemencements ont cependant révélé que les principales variations se situaient sur une échelle spatiale, et essentiellement au dernier niveau d'échantillonnage. Ainsi, dans le futur, la récolte de données plus précises sur la distribution spatiale des prédateurs et des pétoncles ensemencés en lien avec la dynamique de la prédation et de la dispersion devrait permettre de mieux conseiller l'industrie dans le développement d'une stratégie optimale d'ensemencement.

Mots clés: bivalve, aquaculture, crabe, étoile de mer, prédateur multiple, agrégation, modélisation

ABSTRACT

Predation is an important factor affecting the population and community dynamics. Marine bivalves are particularly vulnerable to predation at juvenile stage which also complicates the management of species with commercial interest to fisheries and aquaculture. Indeed, earlier studies on sea scallops (*Placopecten magellanicus*) seeding on the seabed in eastern Canada have obtained mitigated results that were related to predation problems.

The goal of this thesis was to characterize the short term predation dynamics of juvenile sea scallops following a large-scale seeding trial off the Îles de la Madeleine, Québec. A natural scallop bed closed to fishing was also selected to collect information on the predation dynamics of juvenile scallops in a non-seeded situation and on a seasonal scale.

Field studies were conducted from 2003 to 2005 and in 2007. The benthic predators' community was studied using a video camera system mounted on a sleigh or a pyramid. The predation potential was estimated on juvenile scallops using a tethering approach adapted for a deep water (>30 m) environment. A laboratory study was also performed in 2005 to collect data on the predation rates and behaviours of the main benthic predators of juvenile scallops. These data were thereafter used in a predation model that estimates multiple predation effects of tethered scallops with independent predation impact. The estimated data were compared with observed predation potential to detect eventual predator-predator interactions.

Shortly after seeding, the distribution of juvenile scallops on the seabed was observed clumped and, after few weeks, the initial seeded scallop density dropped 10 times. Meanwhile, scallop seeding did not induce an aggregative response by the main predators such as sea stars (*Asterias vulgaris*, *Leptasterias polaris* and *Crossaster papposus*) and crabs (*Cancer irroratus* and *Hyas araneus*). However, predators tended to have a functional response to increased scallop density. Predation assays estimated scallop mortality as much as 10% per day. These observed predation potential values were closely related with predicted predation from the model which suggested that predator species act

independently from each other. Besides, predation explains only partly the juvenile scallop losses observed on seeded site. Thus, dispersal of scallops following seeding may also be an important factor influencing the seeding success.

In non-seeded sites off the Îles de la Madeleine, the predators' community and their predation potential varied little on a seasonal scale. However, this study, as well as the study on scallop seeding, showed that variations were mainly on a spatial scale, and essentially at the last sampling level. Thus, in the future, additional information on the spatial distribution of predators and seeded scallops in relation with predation dynamic and scallop dispersal should allowed a better understanding of the system. This will also refine the industry guidelines for the development of an optimal seeding strategy.

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INTRODUCTION GÉNÉRALE

1.1. Concept de la prédation

La prédation est l'issue d'une interaction entre deux espèces, dont l'une appelée « prédateur », capture et s'alimente d'une autre appelée « proie » (Morin 2011). Elle représente donc un processus important dans la dynamique des populations et des communautés (Taylor 1984; Sih et al. 1998). L'activité de prédation peut être décrite comme un cycle séquentiel de comportements divisé en actions de localisation, poursuite, attaque, capture et consommation de la proie (Holling 1966; O'Brien 1979; Barbeau & Scheibling 1994a). L'aboutissement d'une interaction prédateur-proie dépend donc des taux de rencontre entre le prédateur et la proie et de la probabilité pour la proie d'être consommée après la rencontre (par ex. Riessen et al. 1984; Osenberg & Mittelbach 1989; Barbeau & Caswell 1999). À cet effet, les proies ont développé différentes stratégies pour réduire leur risque de prédation (Sih 1987; Seitz et al. 2001) comme la fuite ou une morphologie particulière rendant plus ardue la manipulation par le prédateur (par ex. Feder 1967; Legault & Himmelman 1993; Smee & Weissburg 2006).

Les comportements de prédation sont également modulés par divers processus écologiques. En particulier, la densité des proies peut faire intervenir deux types de réponses de la part des prédateurs : une réponse fonctionnelle, qui correspond à la relation entre la densité de la proie et le taux de consommation du prédateur, et une réponse numérique, qui signifie une relation entre la densité de la proie et celle des prédateurs (Hassell et al. 1976; Taylor 1984). La présence de plusieurs prédateurs autour de proies peut également produire des interactions intra- et inter-spécifiques (comme la compétition et la prédation) parmi les prédateurs eux-mêmes. Ces interactions peuvent entraîner une augmentation ou une réduction du taux de prédation attendu (Soluk 1993). Ce processus constitue la base du concept sur l'effet des prédateurs multiples tel que décrit par Sih et al. (1998).

1.2. Le cas du pétoncle géant

Les bivalves marins sont particulièrement vulnérables à la prédation aux stades larvaires et juvéniles (Jensen & Jensen 1985; Juanes 1992; Minchin 1992; Gosselin & Qian 1997).

Ainsi, la compréhension des processus qui gouvernent cette prédation est importante, en particulier pour la gestion des bivalves à intérêt commercial pour les pêcheries et l'aquaculture. Le pétoncle géant (*Placopecten magellanicus*) est une espèce intéressante pour l'étude des divers aspects entourant la prédation des bivalves marins. Tout d'abord, cette espèce, qui s'étend de la Caroline du Nord (EU) jusqu'à la côte de Terre-Neuve (Canada) (Posgay 1957; Bourne 1964), soutient l'une des pêcheries de mollusques les plus lucratives de la côte est de l'Amérique du Nord. Même si le pétoncle géant fait l'objet d'une pêcherie côtière limitée, il fait également l'objet d'une pêcherie hauturière très lucrative au large de la côte est des États-Unis et du Canada, en particulier sur le Banc à Georges avec des débarquements (en muscle) dépassant 12 000 t en 2005 (Hart 2006a).

Le pétoncle géant suscite également, depuis le début des années 1990, un grand intérêt pour son potentiel aquacole dans l'est du Canada (Cliche & Giguère 1998; Davidson & Mullen 2005). La pectiniculture a alors été vue comme une façon de rétablir et stabiliser les stocks côtiers de pétoncles avec des ensemencements de juvéniles. L'approche, inspirée de celle utilisée pour le pétoncle japonais *Pecten yessoensis* au nord du Japon (Ventilla 1982; Kosaka & Ito 2006; Uki 2006), visait à récupérer en milieu naturel des larves de pétoncle au moyen de collecteurs adaptés pour ensuite les faire grossir et les ensemencer en milieu naturel jusqu'à l'atteinte de la taille commerciale (Parsons & Robinson 2006). Toutefois, malgré les efforts, les taux de retour des pétoncles ensemencés lors de la pêche commerciale sont toujours demeurés en deçà (<16%) de ceux escomptés, soit des taux de retour de 20 à 30% (Cliche & Giguère 1998). Ces résultats mitigés ont souvent été associés au problème de prédation (Cliche et al. 1994; Barbeau et al. 1996; Wong et al. 2001; Nadeau & Tita 2005).

Dans son habitat naturel, le pétoncle géant doit cohabiter avec une variété de prédateurs. Les plus courants sont les étoiles de mer, les crustacés décapodes et les poissons plats (Thouzeau et al. 1991; Stokesbury & Himmelman 1995; Giguère et al. 2004; Hart 2006b; Marino et al. 2007, 2009). Les étoiles de mer sont des prédateurs lents et non visuels. Elles utilisent leurs récepteurs chimiques et tactiles localisés sur le bout de leur bras pour localiser leurs proies (Castilla & Crisp 1970; Zafiriou 1972; Zafiriou et al. 1972; Heeb

1973). Elles ingèrent ensuite leur proie de façon extra- ou intra-orale selon les espèces et, dans le cas des bivalves, abandonnent les coquilles vides et intactes après la consommation (Feder & Christensen 1966). Les crustacés décapodes, comme les crabes et les homards, sont des prédateurs plus rapides. Ils peuvent utiliser leur vision pour localiser leur proie mais utilisent surtout des structures sensorielles localisées sur les antennes et les pattes marcheuses (Hirtle & Mann 1978; Rebach et al. 1990; Rittschof 1992; Rebach 1996). À la suite de la rencontre d'un pétoncle, le crabe et le homard broient la coquille et consomment la chair, ne laissant que des fragments (Elner & Jamieson 1979; Jamieson et al. 1982). La prédation par les poissons est moins bien connue. Les quelques données proviennent d'observations en plongée ou d'analyses de contenus stomacaux (Medcof & Bourne 1964; Stokesbury & Himmelman 1995; Strohmeier et al. 2006). Naidu et Meron (1986) ont noté la présence de pétoncles juvéniles dans l'estomac de plies *Hippoglossoides platessoides* et de limandes à queue jaune *Limanda ferruginea*, la taille des proies étant limitée par la capacité d'extension de la mâchoire du poisson.

Le pétoncle géant mesurant entre 12 et 70 mm (largeur de coquille) nage par propulsion en utilisant le mouvement de ces valves (Dadswell & Weihs 1990; Manuel & Dadswell 1993), ce qui lui confère un refuge contre la prédation. En effet, cette aptitude lui permet de fuir certains prédateurs lors d'une rencontre (Hartnoll 1967; Stephens & Boyle 1978; Ordzie & Garofalo 1980; Winter & Hamilton 1985; Barbeau & Scheibling 1994a). La détection des prédateurs se fait grâce à la présence de tentacules en périphérie du manteau, dotés de capteurs chimiques et mécaniques et grâce aux multiples yeux aptes à détecter les mouvements (Wilkens 2006). Cette caractéristique particulière du pétoncle pose donc un défi supplémentaire pour l'étude des interactions entre le pétoncle géant et ces principaux prédateurs.

1.3. Dynamique de la prédation du pétoncle géant

Étant donné l'intérêt suscité par les ensemencements au début des années 1990, la plupart des études récentes sur la dynamique de la prédation des pétoncles ont été effectuées dans ce contexte (Tableau 1.1). Les travaux réalisés en laboratoire (par ex.

Barbeau & Scheibling 1994a; Nadeau & Cliche 1998; Wong & Barbeau 2006; Wong et al. 2006a) ont démontré que les étoiles de mer, dont *Asterias vulgaris,* passaient une proportion élevée de leur temps à la recherche de proies. Toutefois, le taux de rencontre avec les pétoncles était plutôt faible, de même que la probabilité de capture, puisque le pétoncle juvénile peut fuir par la nage. Après la capture, le taux de consommation était élevé (peu de rejets) et le processus de manipulation était plutôt lent. Pour leur part, les crabes, comme *Cancer irroratus,* passaient peu de temps à la recherche de proies. Toutefois, les taux de rencontre d'un pétoncle ont été élevés de même que la probabilité de capture après rencontre (peu de fuite). La probabilité de consommation après capture était élevée (peu de rejets) et le processus de manipulation après capture, rapide.

En milieu naturel, il existe quelques données sur la distribution des pétoncles géants et de leurs prédateurs, dans des conditions sans ensemencement (Thouzeau et al. 1991; Stokesbury & Himmelman 1995; Stokesbury & Harris 2006). La prédation y est tout de même considérée comme un processus important. En effet, Hart (2006b) a associé les secteurs de faible recrutement de pétoncles à l'abondance de certaines espèces d'étoiles de mer. De plus, une étude récente a permis de constater que les agrégations d'étoiles de mer *A. vulgaris* pouvaient se déplacer au fil des ans en fonction des secteurs à hautes densités de pétoncles (Marino et al. 2007, 2009).

La plupart des données sur la prédation des pétoncles juvéniles en milieu naturel ont été récoltées dans un contexte aquacole (par ex. Cliche et al. 1994; Barbeau et al. 1996; Hatcher et al. 1996; Wong et al. 2005). Ces études ont toutes fait ressortir la dynamique particulièrement rapide de la prédation et de la dispersion des pétoncles, après un ensemencement. Afin de faciliter les observations de prédation, Barbeau et al. (1994) ont mis au point une méthode pour retenir les pétoncles dans le site d'étude en limitant leur fuite avec une laisse. La prédation par les étoiles de mer et des crabes, estimée par l'état des coquilles, s'est alors avérée tout aussi importante qu'en laboratoire.

Les travaux en milieu naturel ont également permis de récolter des premières données sur les réponses comportementales des prédateurs en fonction de la densité des pétoncles d'élevage. Toutefois, jusqu'à présent, les informations concernant une réponse d'agrégation des prédateurs à la suite d'un ensemencement sont contradictoires. Barbeau et al. (1996), de même que Hatcher et al. (1996) et Cliche et al. (1994), n'ont pas observé, lors d'ensemencements expérimentaux, de corrélation entre l'arrivée des pétoncles sur le fond et l'abondance des prédateurs. Pourtant, Volkov et al. (1985) ont noté, avec le pétoncle *Pecten yessoensis* dans la mer du Japon, une dispersion des pétoncles ensemencés associée, entre autres, à l'arrivée des étoiles de mer, attirées par l'ensemencement. De plus, Veale et al. (2000), ont observé une attraction des prédateurs après la libération de pétoncles (*Aequipecten opercularis*) sur le fond. Ces prédateurs auraient été attirés par le panache d'odeur produit par les pétoncles endommagés ou par les densités de proies élevées. Ainsi, une réponse d'agrégation reste toujours probable d'autant plus que plusieurs études rapportent des déplacements importants de la part des étoiles de mer et des crabes à la recherche de proies préférentielles (Boulding & Hay 1984; Himmelman & Dutil 1991; Gaymer et al. 2001).

L'absence d'une réponse d'agrégation notable de la part des prédateurs à la suite d'un ensemencement et une prédation importante des pétoncles ensemencés peut suggérer une réponse fonctionnelle des prédateurs. Cette réponse fonctionnelle peut alors être de trois types (Taylor 1984). La réponse de type I survient lorsque le taux de prédation augmente de façon linéaire avec la densité de proies (Figure 1.1). La réponse de type II représente une augmentation de la prédation avec la densité de proies mais à un taux décéléré jusqu'à l'atteinte d'un plateau. Ce plateau peut être associé à l'atteinte de la satiété. Finalement, la réponse de type III présente une courbe sigmoïdale : la prédation augmente de façon rapide à faible densité de proie puis de façon ralentie à densité de proie élevée (similaire à la réponse de type II). Les travaux effectués jusqu'à présent suggèrent une réponse de type I de la part de l'étoile de mer *A. vulgaris* envers les pétoncles juvéniles (Barbeau et al. 1994; Barbeau et al. 1998) dans des conditions naturelles. Le crabe *C. irroratus* présenterait plutôt une réponse fonctionnelle de type III (Barbeau et al. 1994; Barbeau et al. 1998; Wong et al. 2005). Cette réponse refléterait un comportement de commutation (« switching ») se produisant lorsque le prédateur a accès à des proies de substitution. Par exemple, Wong et Barbeau (2005) ont noté que le crabe sélectionnait les moules lorsque la densité des pétoncles était faible, ne présentait aucune préférence entre les deux proies en densité de pétoncle intermédiaire, puis choisissait le pétoncle lorsqu'il était présent en densité élevée.

En milieu naturel, on peut également s'attendre à des interactions parmi les multiples prédateurs. Par exemple, l'étoile de mer *Leptasterias polaris* est occasionnellement kleptoparasitée et même consommée par *A. vulgaris* (Dutil 1988; Himmelman 1991; Morissette & Himmelman 2000a, b). L'étoile de mer *Crossaster papposus* peut être dominante sur *A. vulgaris*. Cette dernière répond par la fuite à la suite d'un contact ou à un signal olfactif de *C. papposus* (Sloan 1980). De plus, les cas de prédation de *C. papposus* sur *A. vulgaris* ne sont pas rares (Hancock 1974). Pour leur part, les crabes *C. irroratus* et *Hyas araneus* peuvent kleptoparasiter l'étoile de mer *L. polaris* (Morissette & Himmelman 2000b). De plus, quelques essais sur le crabe *H. araneus* démontrent que ce prédateur réagit en présence d'un conspécifique en adoptant une position de menace pour accroître l'apparence de sa taille et dévoiler ses défenses (Markowska et al. 2008). Ces divers exemples d'interactions peuvent faire en sorte que l'impact d'un prédateur à l'intérieur d'un assemblage ait un effet supérieur ou inférieur à celui d'un prédateur seul (Soluk 1993).

Peu d'études ont été effectuées sur les interactions entre les prédateurs en présence de pétoncles. La seule étude connue a été faite en laboratoire avec l'étoile de mer *A. vulgaris* et le crabe *C. irroratus* en présence de pétoncles juvéniles et n'a pas révélé d'interactions aux niveaux inter- et intra-spécifiques (d'Entremont 2005). Des suivis réalisés dans la Mer du Japon (Silina 2008) après des ensemencements de pétoncles japonais (*P. yessoensis*), ont révélé une modification de la communauté des étoiles de mer, apparemment causée par l'augmentation en abondance d'une espèce dominante (*Asterias amurensis*) attirée par les ensemencements et causant par la compétition une diminution d'autres espèces (*Asterina pectinifera* et *Distolasterias nipon*).

Ces travaux démontrent donc qu'il existe encore bien des questionnements sur la dynamique de la prédation des pétoncles juvéniles, en particulier dans des conditions naturelles et en présence de prédateurs multiples. Ainsi, l'approche des ensemencements, dans un contexte de gestion des pêcheries ou d'approche aquacole, et la dynamique prédateur-proie que peut engendrer l'arrivée de nouvelles proies en abondance suscitent un intérêt autant du point de vue écologique qu'économique.

Tableau 1.1. Bilan des récentes études sur la prédation des pétoncles géants juvéniles.

Condition expérimentale	Description	Références
En laboratoire	Effet de la fixation des pétoncles sur la prédation par *A. vulgaris* et *C. irroratus.*	(Barbeau & Scheibling 1994b)
	Effet de la température sur la prédation du pétoncle par *A. vulgaris* et *C. irroratus.*	(Barbeau & Scheibling 1994c)
	Effet du substrat sur la prédation du pétoncle par *A. vulgaris* et *C. irroratus.*	(Wong & Barbeau 2003)
	Effet de prédateurs multiples (*A. vulgaris* et *C. irroratus*) sur la prédation des pétoncles.	(d'Entremont 2005)
	Comportement de prédation des pétoncles par les étoiles de mer (*A. vulgaris*, *L. polaris* et *C. papposus*) et des crabes (*C. irroratus* et *Hyas* sp.).	(Nadeau & Cliche 1998)
	Réponse fonctionnelle et sélection de proie par *A. vulgaris* et *C. irroratus* en présence de pétoncles et de moules.	(Wong & Barbeau 2005)
	Réponse fonctionnelle de *C. irroratus* envers le pétoncle.	(Wong & Barbeau 2006)
	Réponse fonctionnelle d'*A. vulgaris* envers le pétoncle.	(Wong et al. 2006a)
En milieu naturel	Effet de la densité et de la taille des pétoncles, du site et de la saison sur la prédation de pétoncles fixés.	(Barbeau et al. 1994)
	Effet de la densité des pétoncles sur la réponse comportementale des crabes et des étoiles de mer.	(Barbeau et al. 1998)
	Effet de la densité des pétoncles et d'une proie alternative (*Mytilus edulis*) sur la prédation d'*A. vulgaris* et des crabes *C. irroratus* et *Carcinus maenas.*	(Wong et al. 2005)
	Dynamique des pétoncles juvéniles et de leurs prédateurs lors d'ensemencements expérimentaux.	(Cliche et al. 1994; Barbeau et al. 1996; Hatcher et al. 1996; Wong et al. 2001; Nadeau & Cliche 2004)

Tableau 1.1. (suite)

Condition expérimentale	Description	Références
Modélisation	Modèle matriciel pour la dynamique à court terme de populations de pétoncles ensemencées. Modélisation de la dynamique des ensemencements au Québec.	(Barbeau & McDowell 1998; Barbeau & Caswell 1999) (Gangnery et al. 2004)

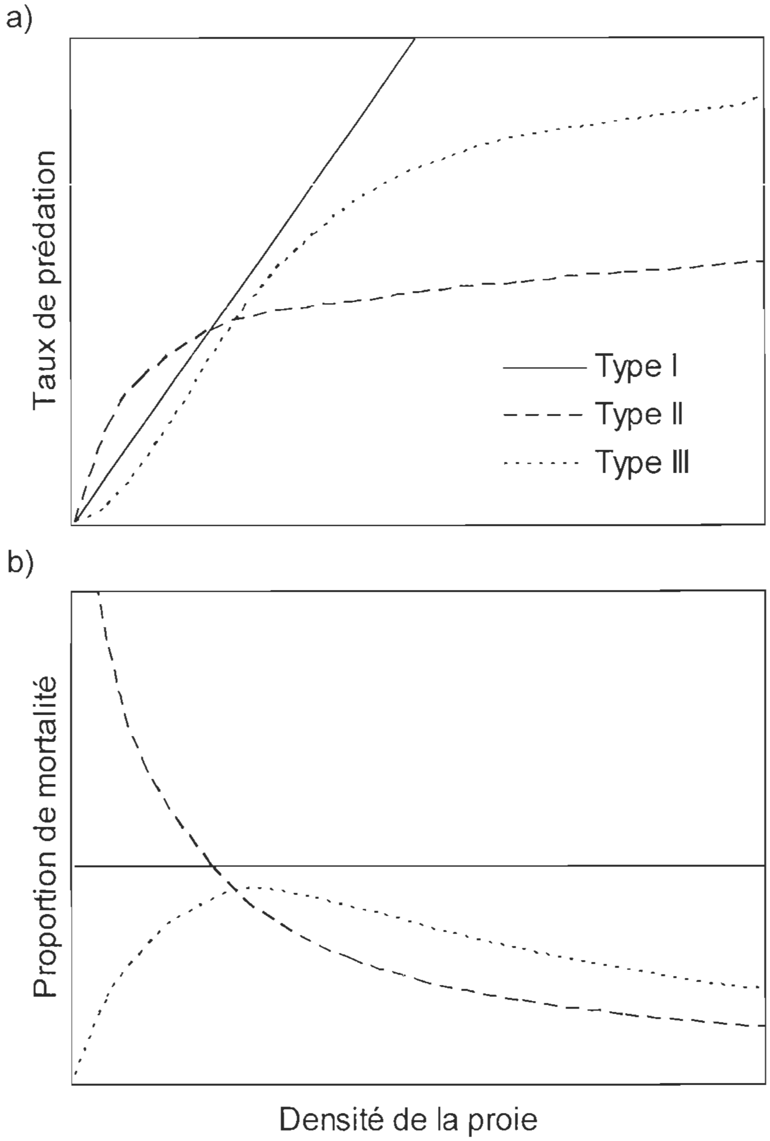

Figure 1.1. Schéma des trois types de réponses fonctionnelles représentés par a) le taux de prédation et b) la proportion de mortalité.

1.4. Objectifs de recherche

Des ensemencements de pétoncles géants juvéniles ont été réalisés au large des îles de la Madeleine, Québec, jusqu'à 2004. Au début des années 2000, les premières pêcheries sur les sites ensemencés ont démontré des taux de retour en deçà des attentes (<20%; Cliche & Giguère 1998). La prédation a alors été considérée comme un élément déterminant expliquant la perte de pétoncles.

L'objectif général de cette thèse est donc de caractériser la dynamique de la prédation des pétoncles juvéniles consécutive à un ensemencement à grande échelle. Ce type de données est rare, puisque la plupart des travaux portant sur la dynamique de la prédation des pétoncles ensemencés ont été effectués dans des conditions contrôlées en laboratoire ou lors d'ensemencements réalisés à petite échelle spatiale. L'accès à un gisement naturel de pétoncles géants fermé à la pêche commerciale s'est également présenté comme une occasion pour étudier la dynamique de la prédation des pétoncles juvéniles dans un contexte sans ensemencement sur une échelle saisonnière.

Les objectifs spécifiques de cette thèse ont donc été de:

a) Étudier le comportement et le taux de consommation des principaux prédateurs benthiques de pétoncles géants juvéniles présents sur les gisements naturels au large des îles de la Madeleine;

b) Déterminer l'abondance et le potentiel de prédation des principaux prédateurs benthiques sur les gisements naturels de pétoncles géants, en fonction des variations saisonnières (sans ensemencement);

c) Déterminer l'abondance et le potentiel de prédation des principaux prédateurs benthiques, avant, pendant et après un ensemencement de pétoncles géants juvéniles à grande échelle spatiale;

d) Étudier la dynamique de prédation et de dispersion des pétoncles géants juvéniles à court terme après un ensemencement à grande échelle spatiale.

1.5. Hypothèses de recherche

Les pétoncles géants présents sur les gisements naturels au large des îles de la Madeleine, Québec, cohabitent avec une variété de prédateurs benthiques. L'assemblage de ces prédateurs peut présenter des variations saisonnières causées par le recrutement, la mortalité et la migration. Il est possible que la dynamique de prédation connaisse également des fluctuations saisonnières en raison des variations de l'assemblage des prédateurs, mais aussi de leur comportement spécifique. Lors d'un ensemencement de pétoncles géants juvéniles à grande échelle, l'assemblage « naturel » des prédateurs peut être modifié à court terme par l'attraction que risque de susciter cette nouvelle proie en abondance. Dans cette situation, une modification du comportement spécifique de prédation est également probable (par exemple dans le cas d'une réponse fonctionnelle) contribuant alors à accroître le potentiel de prédation des pétoncles juvéniles. Finalement, le système étudié est composé de prédateurs multiples et suppose la présence d'interactions intra- et inter- spécifiques qui peuvent modifier le comportement individuel de prédation.

Les hypothèses de recherche retenues pour les travaux effectués au large des îles de la Madeleine ont donc été:

H1) La composition de l'assemblage des prédateurs présent sur un gisement naturel de pétoncles géants varie sur une échelle saisonnière;

H2) Le potentiel de prédation des pétoncles juvéniles présent sur un gisement naturel de pétoncles géants varie sur une échelle saisonnière;

H3) À la suite d'un ensemencement, la composition de l'assemblage des prédateurs est modifiée par une réponse d'agrégation;

H4) À la suite d'un ensemencement, les prédateurs augmentent leur potentiel de prédation en fonction de la densité des proies disponible (réponse fonctionnelle);

H5) Dans un assemblage de prédateurs multiples, les individus de même espèce et d'espèces différentes interagissent en présence d'une proie et ces interactions sont accentuées lors d'un ensemencement de pétoncles juvéniles.

1.6. Approches méthodologiques

L'étude de la dynamique de la prédation des pétoncles juvéniles dans un contexte avec ou sans ensemencement s'est déroulée en laboratoire et en milieu naturel. Les travaux en laboratoire, présentés au Chapitre 2, ont permis d'analyser le comportement et le taux de prédation des principaux prédateurs benthiques qui cohabitent avec le pétoncle géant au large des îles de la Madeleine. Il s'agit des étoiles de mer (*A. vulgaris* et *L. polaris*) et des crabes (*C. irroratus* et *H. araneus*). Ces travaux ont également permis de déterminer le comportement de ces prédateurs en présence de pétoncles fixés et d'estimer les biais de cette technique sur le taux de prédation pour une utilisation ultérieure en milieu naturel.

Le Chapitre 3 présente les résultats d'une étude de trois ans effectuée en milieu naturel pour étudier les variations spatio-temporelles d'un assemblage de prédateurs et de son impact sur la prédation de pétoncles géants juvéniles. Cette étude, réalisée sans ensemencement, permet d'évaluer la prédation des pétoncles en présence de prédateurs multiples. L'impact de la prédation lors d'ensemencements à grande échelle est présenté au Chapitre 4. Des suivis ont été faits pour analyser l'effet des ensemencements commerciaux de 2003 et 2004 sur l'assemblage des prédateurs et leur impact sur la prédation des pétoncles juvéniles. Finalement, afin de valider les observations précédentes, le travail de thèse se termine par la présentation, au Chapitre 5, de résultats récoltés en 2007 lors d'une plus vaste étude sur la prédation des pétoncles géants juvéniles en milieu naturel et en conditions expérimentales.

Plusieurs outils de mesure et différentes approches ont été utilisés pour les travaux en milieu naturel. Une caméra vidéo montée sur un traîneau mobile (Holme & Barrett 1977) ou sur pyramide (Stokesbury et al. 2004) a permis de caractériser les populations de prédateurs et de pétoncles à différentes périodes et sites. Le potentiel de prédation (c. à d. le taux auquel la proie d'intérêt serait consommée si elle était accessible aux prédateurs; Aronson 1989) des divers assemblages de prédateurs, a été évalué à l'aide d'une méthode d'attachement des pétoncles adaptée de Barbeau et al. (1994) et Bourgeois (2004) pour être utilisée en eaux profondes (>30 m) et sans l'usage de plongeur. Pour ensuite aider à comprendre la dynamique de la prédation en milieu naturel, les valeurs de prédation observées sur le terrain ont été comparées avec des valeurs de prédation estimées à l'aide du modèle mathématique de prédation de Barbeau et Caswell (1999) simulant l'impact de la prédation dans une situation où les prédateurs agissent de façon indépendante. Finalement, un protocole de type « beyond BACI » a été utilisé pour le suivi de l'ensemencement de 2004, tel que proposé par Underwood (1994) dans le cas d'études d'impact environnemental.

CHAPITRE 2

Mécanismes des comportements de prédation des étoiles de mer (*Asterias vulgaris* Verrill and *Leptasterias polaris* Müller) et des crabes (*Cancer irroratus* Say et *Hyas araneus* Linnaeus) envers les pétoncles géants (*Placopecten magellanicus* (Gmelin)) juvéniles et effet de la procédure d'attachement des pétoncles

Behavioural mechanisms of sea stars (*Asterias vulgaris* Verrill and *Leptasterias polaris* Müller) and crabs (*Cancer irroratus* Say and *Hyas araneus* Linnaeus) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)), and procedural effects of scallop tethering

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RÉSUMÉ

Les étoiles de mer (*Asterias vulgaris* et *Leptasterias polaris*) et crabes (*Cancer irroratus* et *Hyas araneus*) cohabitent avec les pétoncles sur le fond marin du Golfe du St-Laurent, Canada, et affectent leur survie. Les comportements de prédation de ces espèces envers les pétoncles géants juveniles (*Placopecten magellanicus*, hauteur de coquille de 25-35 mm) ont donc été étudiés en milieu contrôlé. L'effet d'un procédé consistant à attacher les pétoncles pour étudier le potentiel de prédation en milieu naturel a également été examiné. En général, les comportements de prédation d'*A. vulgaris* et de *C. irroratus* se sont avérés comparables à ceux estimés lors des études antérieures. Le crabe *C. irroratus* s'est avéré le plus efficace avec une consommation de 3,1 pétoncles · prédateur^{-1} · j^{-1}, même si seulement 0,9% de son temps a été consacré à la recherche de proie. L'étoile de mer *A. vulgaris* a consommé 0,9 pétoncle · prédateur^{-1} · j^{-1} et a passé 7,6% de son temps à la recherche. Pour sa part, l'étoile de mer *L. polaris* a démontré un plus faible taux de prédation (0,02 pétoncle · prédateur^{-1} · j^{-1}) qu'*A. vulgaris*. Son comportement d'évitement de la proie et sa faible habileté à capturer les pétoncles supportent la notion que cette proie n'est pas un aliment important à sa diète. Finalement, pour les crabes *H. araneus*, des taux de prédation de 1,3 pétoncles · prédateur^{-1} · j^{-1} ont été estimés et des comportements assez similaires à *C. irroratus* ont été observés. Toutefois, la probabilité de consommation de *H. araneus* a été affectée par un grand nombre de rejets et de fuite des proies après capture. Tel qu'attendu, la procédure d'attachement des pétoncles a augmenté le taux de prédation des étoiles de mer *L. polaris* (d'environ 19 fois), sans modifier significativement celui d'*A. vulgaris*. En particulier pour *A. vulgaris*, la probabilité de capturer des pétoncles attachés a été plus grande que ceux libres, et le temps de recherche a été plus faible (peut-être à cause de l'atteinte du niveau de satiété). Les taux de prédation et les comportements des deux crabes n'ont pas été affectés par le procédé, puisqu'en présence de pétoncles attachés c'est encore le taux de rencontre qui a été le facteur déterminant. Finalement, la quantification des divers comportements qui sous-tendent les processus de prédation ont permis de modéliser de façon mathématique la mortalité causée par les quatre espèces prédatrices étudiées.

ABSTRACT

We compared predation rates and behaviours of sea stars (*Asterias vulgaris* and *Leptasterias polaris*) and crabs (*Cancer irroratus* and *Hyas araneus*) preying on juvenile sea scallops (*Placopecten magellanicus*, 25-35 mm shell height) in the laboratory. These predatory species co-occur with sea scallops on the sea bed of the Gulf of St. Lawrence, Canada, and limit scallop survival in seeding operations. We also examined, under controlled conditions, the effect of tethering scallops on predator-prey interactions. Predation rates, time budgets and encounter behaviours observed for *A. vulgaris* and *C. irroratus* preying on free (untethered) scallops were comparable to previous studies. *C. irroratus* were more effective predators as they consumed 3.1 scallops · predator^{-1} · d^{-1}, although they spent only 0.9% of their time searching for prey. *A. vulgaris* consumed 0.9 scallops · predator^{-1} · d^{-1} and spent 7.6% of their time searching. Sea stars *L. polaris* had a lower predation rate (0.02 scallop · predator^{-1} · d^{-1}) than *A. vulgaris*. The frequent avoidance behaviour of *L. polaris* and its low ability to capture scallops support the notion that scallops are not a main component of this sea star's diet. Crabs *H. araneus* had similar predation rates (1.3 scallops · predator^{-1} · d^{-1}) and behaviours to *C. irroratus*, although the probability of consumption upon capture was affected by relatively high numbers of rejections and post-capture escapes of scallops. As expected, the tethering procedure increased predation rate of *L. polaris* (about 19 times higher), but surprisingly did not significantly affect that of *A. vulgaris*. Examination of behaviours indicated that *A. vulgaris* offered tethered scallops tended to have a higher probability of capture, but spent less time searching for prey (possibly because satiation was reached) than *A. vulgaris* offered free scallops. Predation rates and behaviours of both crab species were not affected by tethering, since encounter rate was the primary determinant of crab-scallop interactions. Identification and quantification of behaviours underlying the predation process allowed us to mathematically model predator-related mortality for the four predator species.

2.1 Introduction

Over the last two decades, there has been a strong and continuous interest in Atlantic Canada in seeding (releasing) juvenile sea scallops (*Placopecten magellanicus*) on the sea bed to enhance natural scallop populations (Robinson 1993; Cliche & Giguère 1998; Davidson & Mullen 2005). However, predation by sea stars and crabs has been a major constraint in this endeavour (Cliche et al. 1994; Barbeau et al. 1996). The importance of the common sea star *Asterias vulgaris* and the rock crab *Cancer irroratus* as predators of juvenile scallops has been confirmed in laboratory and field experiments (Barbeau & Scheibling 1994a; Barbeau et al. 1998; Nadeau & Cliche 1998; Wong & Barbeau 2006; Wong et al. 2006a). The role of the northern sea star *Leptasterias polaris* and the spider crab *Hyas araneus* has only been briefly studied (Nadeau & Cliche 1998). The present contribution investigates details of the interactions between the predators found off the coast of the Îles de la Madeleine and juvenile scallops, and the possible effects of a tool (tethering) used to study these interactions in this relatively deep-water environment (>30 m).

Sea stars and crabs are very different types of predators, and their study leads to interesting comparisons of determining behaviours underlying predation patterns. Sea stars are slow and non-visual predators. They use chemosensory receptors located on the tip of their arms to detect prey (Castilla & Crisp 1970; Zafiriou 1972; Zafiriou et al. 1972; Heeb 1973). They digest prey items extraorally or intraorally and, if the prey is a bivalve, leave a clapper (empty, intact shell) after consumption (Feder & Christensen 1966). Crabs are able to detect mobile prey visually (Rebach 1996), but they mainly react to chemical stimuli (Rebach et al. 1990; Rebach 1996; Zhou & Rebach 1999). When encountering bivalve prey, they crush the shell and consume the flesh, leaving characteristically-shaped shell fragments after consumption (Elner & Jamieson 1979).

A useful way to study predation to understand underlying mechanisms is through a series of sequential behaviours, termed the predation cycle. In this cycle, predation can be divided into three major components: encounter rate between predator and prey, probability of capture upon encounter, and probability of consumption upon capture (Holling 1966;

Osenberg & Mittelbach 1989). These components and other behaviours (e.g. time spent searching for prey and prey handling time) are different for sea stars and crabs preying on juvenile sea scallops (Barbeau & Scheibling 1994a; d'Entremont 2005; Wong & Barbeau 2006; Wong et al. 2006b). Sea stars, such as *A. vulgaris*, generally spend a high proportion of time searching for prey, and have a moderate encounter rate when searching and slow prey handling process. The probability of capture upon encounter is generally low because juvenile scallops can effectively escape by jet propulsion swimming, but the probability of consumption upon capture is high. Crabs, such as *C. irroratus,* spend a relatively low proportion of time searching for prey, and have a fairly high prey encounter rate when searching and rapid prey handling process. Both, the probability of capture upon encounter and probability of consumption upon capture for crabs are high.

The first objective of our study was to examine in detail the behaviours of sea stars (*A. vulgaris*, *L. polaris*) and crabs (*C. irroratus*, *H. araneus*) preying on juvenile sea scallops (*P. magellanicus*) in controlled conditions. We focused on the less known predator species found off the Îles de la Madeleine (*L. polaris* and *H. araneus*). *A. vulgaris* and *C. irroratus* were also chosen to compare and validate our experimental procedures against similar studies conducted elsewhere (Barbeau & Scheibling 1994a; d'Entremont 2005; Wong & Barbeau 2006; Wong et al. 2006b). The second objective was to develop a predation model for each predator species using the behavioural information. The third objective was to evaluate the effects of tethering scallops on predator rates and underlying behaviours. Tethering has previously been used with scallops in natural conditions to control their densities or movement and to identify causes of mortality from shell remains (Barbeau et al. 1994; Stokesbury & Himmelman 1995; Arsenault & Himmelman 1996a, b; Fleury et al. 1996; Bologna & Heck Jr. 1999; Kamenos et al. 2004). However, biases resulting from limited escape of tethered prey need to be assessed for an accurate estimation of predation risk. Such biases have been studied (Barbeau & Scheibling 1994b), but not with the scallop sizes used in seeding operations or the predator composition off the coast of the Îles de la Madeleine. To meet our objectives, a large laboratory experiment was conducted in which individuals of the four predator species were held separately with one of two scallop types (free or tethered).

2.2 Materials and methods

2.2.1 Experimental materials and procedures

The experiment, conducted in 3 temporal blocks between June and October 2005, used 18 tanks (42 cm wide x 66 cm long x 21 cm high; 58 L) mounted with independent running seawater (10 l/min) at ambient temperature (10 to 15 °C) and sand-filtered at 1 mm. The water temperature range recorded during the experiment often occurs in the field in one day due to current, tidal and/or wind conditions. The photoperiod was set to 16 h light: 8 h dark, to have similar conditions amongst temporal blocks. Holding tanks were maintained in the same conditions as experimental tanks.

Experimental animals were obtained locally. Juvenile scallops, within the size range of 25 to 35 mm shell height, were purchased from a scallop production company in the Îles de la Madeleine (Pétoncles 2000, Inc, now Culti-Mer). They were held in a separate tank ~2 wk prior to their use and no additional food was added to the natural seston that remained in the sea water after sand filtration. Crabs were collected using crab or lobster traps, and sea stars by SCUBA divers. Predator sizes were selected from the main size range occurring on natural scallop grounds (Nadeau, unpublished data): 70-90 mm radius (arm length) for *A. vulgaris*; 90-110 mm radius for *L. polaris*; 90-110 mm cephalothorax width for *C. irroratus* and 60-80 mm cephalothorax length for *H. araneus*. Only male crabs were used to avoid possible sex biases (Barbeau & Scheibling 1994a; Mahar 2005). Predators were maintained in separate holding tanks for 2 wk prior to their experimental use, and were fed twice a week with blue mussels (*Mytilus edulis* L.). Juvenile scallops were offered to predators at the last pre-experimental feeding to ensure that each predator was accustomed with this prey type. Predators were starved for 5 d prior to the experiment. Each individual predator was used only once.

During the experiment, individual predators were offered either free or tethered scallops. Tethering was done by gluing (cyanoacrylate glue, Bostik 7434) one end of a 18-cm nylon line (kite line, 0.5 mm diameter) onto the upper shell of a scallop. Before the glue dried, a small piece (6 mm wide, 12 mm long) of blotting paper was placed over this end of the thread to strengthen the binding to the shell. The other end of the thread was attached to a lead ring (120 g, 3 cm radius). A tethered scallop could move within an area 12 cm in radius.

Single predators were placed in experimental tanks 24 h prior to starting an experimental block. Black plastic was put over tanks with crab treatments to shade 20% of the bottom, thus providing shelter. At the start of a block, 8 scallops were placed equidistant (2 rows of 4 scallops) within a tank. This represented a density of 28 scallops · m^{-2}, which is in the high end of the range (0.1 to 30 m^{-2}) of scallop density after a seeding operation off the Îles de la Madeleine (Chapter 4).

2.2.2 Experimental design

There were 8 treatment combinations: 4 predator species (*A. vulgaris*, *L. polaris*, *C. irroratus* and *H. araneus*) and 2 scallop types (free or tethered). The experimental design was a randomised block design with replication. Three temporal blocks of 20 d were done (block 1: 1 to 21 June, block 2: 26 June 26 to 9 July and block 3: 5 to 25 October 2005). Each predator-scallop treatment combination, randomly allocated into 16 tanks, was replicated twice in each block. Thus, there were a total of 6 replicates for each treatment combination, if one pools over block. Two additional tanks per block were used as controls to monitor scallop mortality without a predator: one tank with free scallops and the other with tethered scallops. Since scallop mortality is typically very low in the absence of a predator (Barbeau & Scheibling 1994a; Wong & Barbeau 2003; Bourgeois et al. 2006), the controls were not replicated within a temporal block.

2.2.3 Collection of data on predation rates

Each tank was surveyed twice a day to count dead scallops. Shell remains were retrieved, and new live scallops were added to maintain prey density. Predation rate for a replicate unit (tank within a block) was calculated as the number of scallops eaten per day per predator by dividing the total number of scallops eaten during a temporal block by the duration in days of the block. Mortality due to causes other than predation was negligible in the control tanks (no free scallop and only one tethered scallop died in the controls during the whole experiment).

2.2.4 Collection of behavioural data

Behavioural information was collected using 2 methods: by personal observation and by video camera. For the former method, an observer monitored each tank twice a day (in the morning and in the late afternoon/evening) for a randomly chosen 30-min period during each observation period; therefore, over the duration of a temporal block, a tank was observed for a total of 20 h. Blinds were placed in front of each tank with a crab, so as to not affect crab behaviour during observation. This first method of observation was used to quantify predator time budgets, encounter rates between predators and scallops, and probabilities of various outcomes after encounter (see below). For the second method of observation, a video camera (SVS, S-500/21) was fixed over a randomly chosen tank for 24 h; therefore, each tank was monitored once over the duration of a temporal block. During this 24 h, the video camera recorded behaviours in 6 periods of 30 min (starting at 3:00, 7:00, 11:00, 14:00, 19:00 and 23:00). A red light bulb (60 W), to which invertebrates are insensitive (Cronin 1988), provided light during night hours. This second method of observation was used to quantify predator time budgets in the day and night, and movement velocity of predators while searching for prey (see below).

Predator time budgets consisted of non-foraging activity, and searching for and handling prey (for more details, see Barbeau & Scheibling 1994a; Wong & Barbeau 2003). In our study, the term "handling" included the manipulating (usually short in time) and consuming behaviours after capture (but did not include the very short time between encounter and capture). Consumption ended when sea stars moved away from empty shells (clappers) or crabs walked away from shell fragments. We quantified the proportion of time predators spent searching for and handling prey as (searching time)/(total observation time) and (handling time)/(total observation time).

An encounter between a predator and a scallop lead to different reactions such as avoidance by the predator, escape by the prey or capture of the prey. An avoidance occurred when a sea star curled its arm upon lightly touching the mantle edge or a tentacle of an encountered scallop, and then moved away (i.e., the scallop was not attacked upon encounter). Avoidances by crabs were not observed. Prey escape after encounter (and attack) was called "passive" when a scallop closed its valves (and was not captured) and "active" when a scallop jumped (one clap) or swam (successive claps) away from an encountered predator. Upon capture, a prey may escape, be rejected or be consumed. We quantified encounter rate from the number of prey encountered during searching time (number of encounters $\cdot$ h^{-1}). For sea stars, the probability of capture upon encounter was divided into two conditional probabilities based on their particular avoidance behaviour: probability of attack upon encounter, Pr[attack|encounter], and the probability of capture upon attack, Pr[capture|attack]. To do this, the number of attacks was counted using the number of encounters minus the number of avoidances. For crabs, as mentioned earlier, we could not define an avoidance behaviour; therefore, we calculated the probability of capture upon encounter, Pr[capture|encounter]. Finally, for both sea stars and crabs, the probability consumption upon capture, Pr[consumption|capture], was estimated.

With regards to escape behaviours of scallops, the proportion of active or passive escapes upon attack by sea stars or upon encounter by crabs was calculated as the number of a particular escape (jumping, swimming or passive) divided by the total number of escapes before capture. In addition for crabs, we calculated the proportion of scallop escapes after capture as (number of active escapes after capture)/(number of captures), and the proportion of rejections after capture as (number of rejections)/(number of captures).

2.2.5 Ethograms

Sequences in the behaviours of predators were examined using ethograms (Lehner, 1996), specifically between the (1) stationary, (2) moving and not foraging, (3) searching and (4) prey handling states. Relative frequencies of transition were calculated using the number of transitions between two behaviours divided by the total number of transitions.

This analysis and associated kinematic graphs were done for each predator-scallop combination. The Block factor was pooled for this analysis to have enough data.

2.2.6 Statistical analysis

All statistical analyses were done using SAS software (SAS Institute Inc., version 8.02). For all analyses, we used a critical alpha level of 0.1, because we judged that having a type II error was worse than having a type I error.

Predation rates, foraging behaviours, encounter rates and probabilities obtained from personal observation were analysed using a mixed-model analysis of variance (ANOVA) with Combination (8 levels representing the predator species-scallop type combinations: *A. vulgaris*, *L. polaris*, *C. irroratus* and *H. araneus* with either free or tethered scallops) as a fixed factor and Block as a random factor (3 levels). We used "Combination" to maximise power of the statistical test and to conduct planned comparisons. The denominator of F-ratios was calculated as in Underwood (1997). We interpreted a significant fixed factor even in the presence of an interaction between the fixed factor and random factor, as recommended by Quinn and Keough (2002, p. 240). Normality of residuals was verified visually and homogeneity of variance using Cochran's test (Winer et al. 1991). Log_{10}-transformation of data was performed when necessary to obtain homogeneity of variance. When Combination*Block and Block were highly non-significant ($p>0.20$) (Winer et al. 1991, pp. 377-382), data were pooled over these sources of variation to increase power without increasing errors in interpretation. Planned comparisons (Sokal & Rohlf 1995; Underwood 1997) were done to compare certain logical combinations and to have orthogonal comparisons; these included (1) the sea star *A. vulgaris* and the crab *C. irroratus* preying on free scallops, (2) the two sea star species with free scallops, (3) the two crab species with free scallop and (4-7) each predator species with free or tethered scallops. Power analysis was conducted when patterns were observed on graphs but not detected in the statistical analysis (Zar 1984).

Predator time budgets for day and night periods obtained from the video monitoring were compared using a one-way ANOVA with Period (6 levels: 3:00, 7:00, 11:00, 14:00, 19:00 and 23:00) as a fixed factor. The data were pooled over Block to have enough data for analysis. Statistical analyses were not performed on movement velocities of searching predators, avoidances by sea stars and probability of consumption upon capture because of a low amount of data.

Probabilities of transition in the ethograms for each predator-scallop combination were compared using the independance test (G-test) (Sokal & Rohlf 1995). Specific comparisons were performed based on the orthogonal comparisons previously described.

2.2.7 Modelling predation rates from behavioural information

Calculation of expected predation rate for sea stars offered free scallops was based on a model that links predation rate to the behaviours of the predator and prey (Wong et al. 2006a):

$$N_e = E \cdot T_s \cdot \mathrm{Pr[attack|encounter]} \cdot \mathrm{Pr[capture|attack]} \cdot \mathrm{Pr[consumption|capture]} \qquad \text{Equation 2.1}$$

where N_e is the number of prey eaten per predator per unit of time, E is the number of prey encountered per predator per time spent searching, T_s is the proportion of time a predator spent searching and Pr[A|B] is the probability of behaviour A conditional on behaviour B. The model was simplified for crabs by condensing Pr[attack|encounter] and Pr[capture|attack] into Pr[capture|encounter].

A model for encounter rate was also used to calculate E (Barbeau & Scheibling 1994a; Wong 2004), which is based on Holling's (1966) equation for number of prey encountered by a predator over a searching time, and which assumes random movements of predator and prey in a two dimensional environment:

$$E = [2V_R \cdot t \cdot (r_{predator} + r_{prey}) + \pi(r_{predator} + r_{prey})^2] \cdot N_t \qquad \text{Equation 2.2}$$

where V_R is the combined predator and prey velocity, t is a determined searching time (60 minutes in this study), $r_{predator}$ is predator radius, r_{prey} is prey radius, and N_t is prey density.

We used a scallop velocity of 0 cm/h since scallops generally do not move until physical contact with a predator (Barbeau & Scheibling 1994a; Wong et al. 2006b). As indicated above, predator velocities while searching were estimated from video recordings. Crab radius was calculated from the radius of their walking legs (0.05 cm) in contact with the tank bottom (8 legs x 0.05 cm= 0.4 cm), representing the predator area than can contact scallops (Barbeau & Scheibling, 1994a).

A mean (± standard error) expected encounter rate (Eq. 2.2) and predation rate (Eq. 2.1) for a particular predator species offered free scallops was generated using the Monte Carlo method (Barbeau & Caswell 1999). For each parameter in the two models (Eq. 2.1 and 2.2), we used the observed mean and standard error (from our experiment and observations) to define the parameter's sampling distribution (Evans et al. 1993). Parameters that represent proportions or probabilities (T_s, Pr[attack|encounter], etc.) were described by a beta distribution, which is bound between 0 and 1; parameters restricted to non-negative values were described by a gamma distribution (e.g. V_R, $r_{predator}$, r_{prey}), which has a lower bound at 0. We ran 200 simulations for each model (using MATLAB, MathWorks, Inc); at the beginning of each simulation, we randomly selected a value for each parameter from its sampling distribution. We then calculated a mean and standard error from the distribution of outputs for the predicted encounter rate and predation rate. (Note: Given that the standard errors of parameters were used to generate the various sampling distributions, the standard deviation of a distribution of outputs is essentially a standard error.) Finally, expected encounter and predation rates were compared to observed encounter and predation rates.

2.3 Results

2.3.1 Predation rate and behaviours with free scallops

On average, predation rate of sea stars *A. vulgaris* was 0.9 free scallops · predator^{-1} · d^{-1} (Fig. 2.1a). These sea stars spent 7.6% of their activity budget searching for prey (Fig. 2.2a). Encounter rate with prey was 13.3 scallops per searching hour (Fig. 2.2b). The probability of attack upon encounter was close to 1, but the probability of capture upon attack was only 0.02 (Fig. 2.2c). Finally, all scallops captured were consumed. Prey escape upon attack was mainly by swimming (Fig. 2.2d). Sea stars *L. polaris* had a lower predation rate (0.02 free scallops · predator^{-1} · d^{-1}) than *A. vulgaris* (Table 2.2, Fig. 2.1a). They spent 4.9% of their time budget searching for prey (Fig. 2.2a) and encountered 7.5 scallops per searching hour (Fig. 2.2b); these behaviours were not significantly different from *A. vulgaris* (Table 2.1). Compared to *A. vulgaris*, *L. polaris* had a significantly lower probability of attack upon encounter (Fig. 2.2c); about half of encountered scallops were avoided. When attacked, scallops mostly swam away (Fig. 2.2d). Although a few predation events did occur during the experiment, we did not observe any captures upon attack by *L. polaris* during the behavioural monitoring, and could not estimate a probability of consumption upon capture (Fig. 2.1a and 2.2c).

The behavioural transitions for both sea star species were concentrated between stationary state, non-foraging displacement and searching (Fig. 2.4a, c). The handling behaviour was only observed in the *A. vulgaris* treatment and always occurred after searching. Thus, sea star predation behaviour was linear and rarely by-passed the main sequential pattern. The relative frequency of transitions was not significantly different between sea star species (Table 2.2).

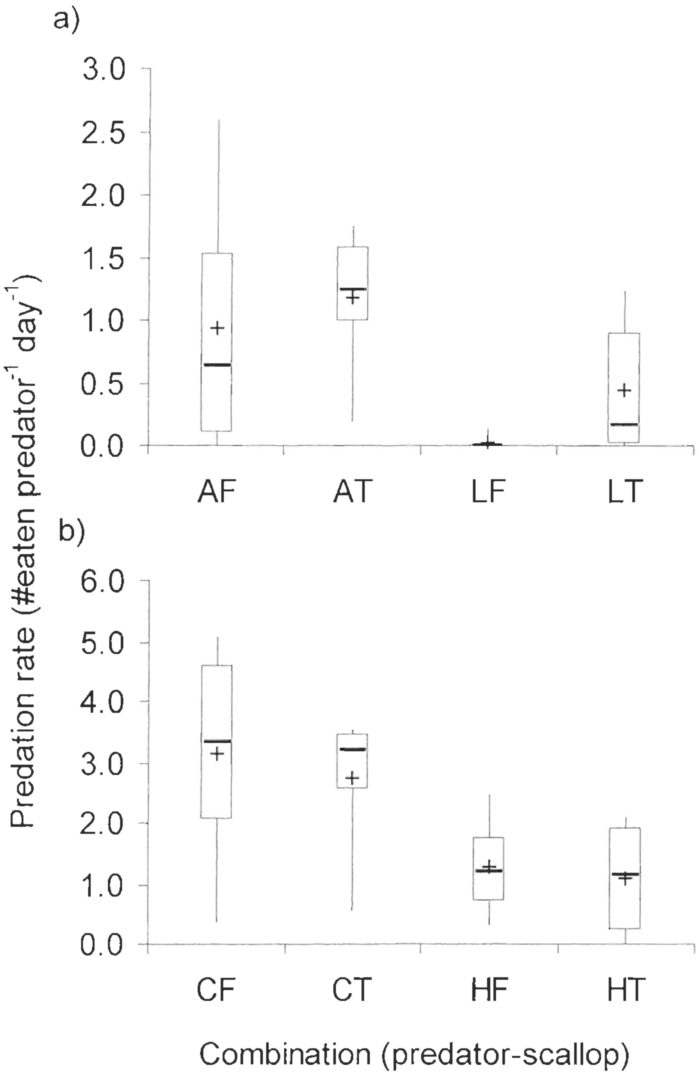

Figure 2.1. Predation rates of sea stars *A. vulgaris* (A) and *L. polaris* (L), and crabs *C. irroratus* (C) and *H. araneus* (H) offered free (F) and tethered (T) juvenile scallops (*P. magellanicus*) (+: mean; horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values).

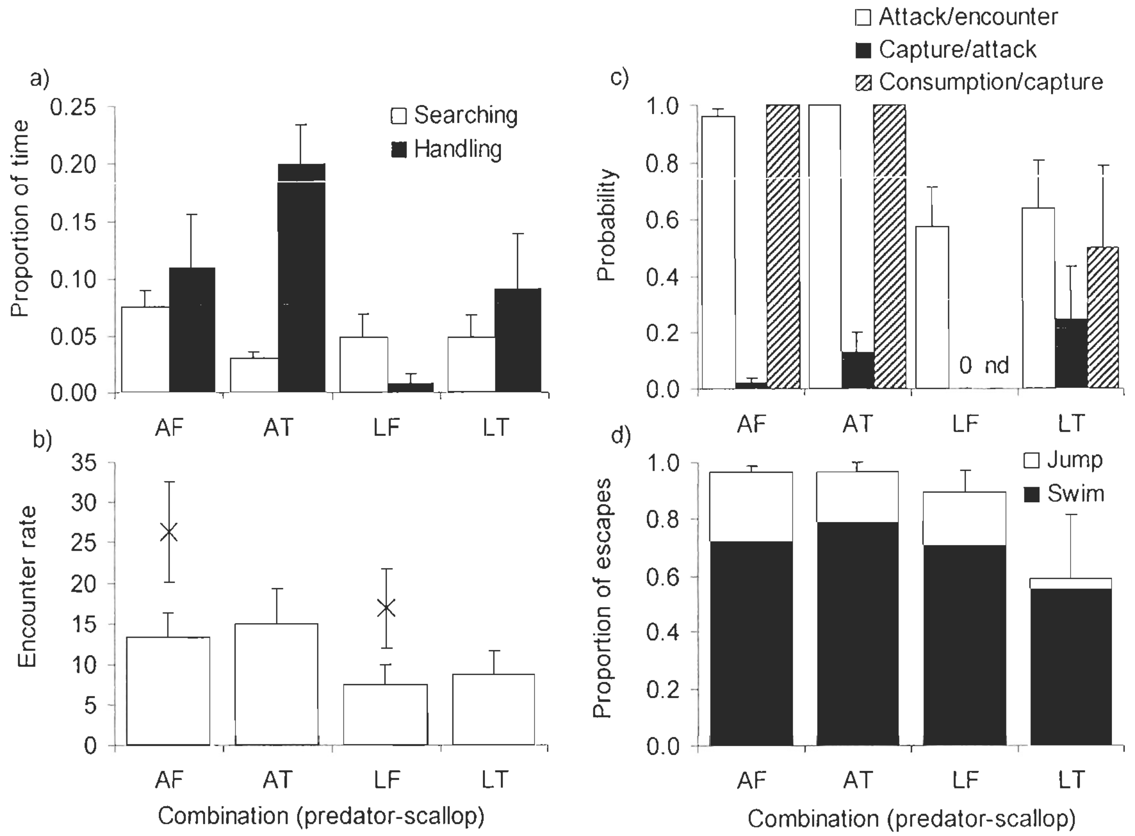

Figure 2.2. Mean (± SE) predator and prey behaviours of sea stars *A. vulgaris* (A) and *L. polaris* (L) preying on free (F) and tethered (T) juvenile scallops (*P. magellanicus*). a) Proportion of time spent foraging on (searching for and handling) scallops; n = 6. The remaining time was spent immobile or in non-foraging activities. b) Encounter rate per searching hour, as observed (histogram bars, n = 4-6) and as predicted (x). c) Probabilities upon encounter; n = 3-6. "nd" indicates no data. d) Proportion of active escapes; n = 4-6. The remaining proportion represents passive escapes.

Table 2.1. Results of mixed-model ANOVAs and planned comparisons for predation rate, foraging behaviours and encounter probabilities of 2 species of sea stars and 2 species of crabs preying on juvenile sea scallops (*P. magellanicus*). Block and Combination*Block were pooled when they were not significant (*p*>0.20). Predation rate, proportion of time spent handling prey and probability of capture upon attack were $\log_{10}$-transformed for homogeneity of variance. Significant differences (*p*>0.10) are indicated in bold characters.

Dependent variable	Source of variation	df	MS	F	*p*
Predation rate	Combination	7	6.397	3.93	**0.014**
	AF vs CF	*1*	*5.386*	*3.31*	***0.090***
	AF vs LF	*1*	*8.451*	*5.19*	***0.039***
	CF vs HF	*1*	*0.382*	*0.23*	*0.635*
	AF vs AT	*1*	*2.687*	*1.65*	*0.219*
	LF vs LT	*1*	*5.522*	*3.394*	***0.087***
	CF vs CT	*1*	*0.00004*	*0.00001*	*0.995*
	HF vs HT	*1*	*2.409*	*1.48*	*0.244*
	Block	2	0.969	1.27	0.298
	Combination*Block	14	1.627	2.14	**0.049**
	Error	24	0.761		
Proportion of time spent searching	Combination	7	0.004	3.39	**0.006**
	AF vs CF	*1*	*0.014*	*11.74*	***0.001***
	AF vs LF	*1*	*0.002*	*1.86*	*0.181*
	CF vs HF	*1*	*0.00002*	*0.02*	*0.893*
	AF vs AT	*1*	*0.006*	*5.48*	***0.024***
	LF vs LT	*1*	*0.0000002*	*0.002*	*0.967*
	CF vs CT	*1*	*0.0001*	*0.09*	*0.761*
	HF vs HT	*1*	*0.002*	*1.42*	*0.240*
	Error	40	0.001		
Proportion of time spent handling	Combination	7	2.109	2.47	**0.071**
	AF vs CF	*1*	*0.364*	*0.43*	*0.524*
	AF vs LF	*1*	*4.031*	*4.72*	***0.047***
	CF vs HF	*1*	*0.942*	*1.10*	*0.311*
	AF vs AT	*1*	*1.942*	*2.27*	*0.154*
	LF vs LT	*1*	*1.999*	*2.34*	*0.148*
	CF vs CT	*1*	*0.020*	*0.02*	*0.880*
	HF vs HT	*1*	*0.422*	*0.49*	*0.494*
	Block	2	0.397	0.78	0.470
	Combination*Block	14	0.853	1.67	0.130
	Error	24	0.510		

Table 2.1 (continued)

Dependent variable	Source of variation	df	MS	F	*p*
Encounter rate	Combination	7	34182.203	3.88	**0.003**
	AF vs CF	*1*	*44745.066*	*5.42*	***0.026***
	AF vs LF	*1*	*78.287*	*0.01*	*0.925*
	CF vs HF	*1*	*5885.424*	*0.67*	*0.418*
	AF vs AT	*1*	*9.325*	*0.001*	*0.974*
	LF vs LT	*1*	*2.889*	*0.0003*	*0.985*
	CF vs CT	*1*	*24603.4599*	*2.79*	*0.102*
	HF vs HT	*1*	*435.998*	*0.05*	*0.825*
	Error	35	8804.703		
Pr[capture|encounter]	Combination	4	0.482	2.74	0.105
	AF vs CF	*1*	*0.726*	*4.12*	
	CF vs HF	*1*	*0.015*	*0.09*	
	CF vs CT	*1*	*0.223*	*1.26*	
	HF vs HT	*1*	*0.095*	*0.54*	
	Block	2	0.309	4.45	**0.036**
	Combination*Block	8	0.176	2.54	**0.071**
	Error	12	0.069		
Pr[attack|encounter]	Combination	3	0.186	6.34	**0.006**
	AF vs LF	*1*	*0.360*	*12.29*	***0.004***
	AF vs AT	*1*	*0.005*	*0.15*	*0.702*
	LF vs LT	*1*	*0.010*	*0.36*	*0.560*
	Block	2	0.090	3.07	**0.078**
	Error	14	0.029		
Pr[capture|attack]	Combination	3	2.320	2.13	0.137
	Error	16	1.092		
Active escapes	Combination	7	0.654	9.95	**<0.001**
	AF vs CF	*1*	*1.221*	*18.59*	***<0.001***
	AF vs LF	*1*	*0.014*	*0.21*	*0.653*
	CF vs HF	*1*	*0.009*	*0.13*	*0.720*
	AF vs AT	*1*	*0.00001*	*0.0001*	*0.991*
	LF vs LT	*1*	*0.179*	*2.73*	*0.122*
	CF vs CT	*1*	*0.080*	*1.22*	*0.289*
	HF vs HT	*1*	*0.142*	*2.16*	*0.165*
	Block	2	0.109	2.81	**0.097**
	Combination*Block	13	0.066	1.69	0.178
	Error	13	0.039		

Table 2.1 (continued)

Dependent variable	Source of variation	df	MS	F	*p*
Swims	Combination	3	0.029	1.29	0.318
	Block	2	0.057	2.50	0.120
	Error	13	0.023		
Rejections	Combination	3	0.107	0.71	0.562
	Error	13	0.151		

A: *A. vulgaris*, *L*: *L. polaris*, *C*: *C. irroratus*, *H*: *H. araneus*, *F*: free scallops, *T*: tethered scallops.

Table 2.2. Independence test (G-test) using the frequency of transition between two behaviours among four predator activities (stationary, moving, searching and handling) for 2 species of sea stars and 2 species of crabs preying on juvenile sea scallops (*P. magellanicus*). Significant differences (p>0.10) are indicated in bold characters.

Combination	df	Value	p
AF vs CF	6	161.891	**<0.001**
AF vs LF	6	6.871	0.333
CF vs HF	6	22.316	**0.001**
AF vs AT	6	10.989	**0.089**
LF vs LT	6	12.785	**0.047**
CF vs CT	6	12.581	**0.050**
HF vs HT	6	6.260	0.395

A: *A. vulgaris*, L: *L. polaris*, C: *C. irroratus*, H: *H. araneus*, F: free scallops, T: tethered scallops.

On average, crabs *C. irroratus* consumed 3.1 free scallops · predator^{-1} · d^{-1}, which was significantly more than for sea stars *A. vulgaris* (Fig. 2.1b, Table 2.1). They spent only 0.9% of their time searching, which was significantly less than for sea stars (Fig. 2.3a, Table 2.1). However, they encountered more scallops (139.4 scallops) per searching hour (Fig. 2.3b, Table 2.1). Encountered scallops were captured about half of the time (Fig. 2.3c) and prey escapes upon encounter were mostly passive (Fig. 2.3d). Prey rejections upon capture decreased the probability of consumption to about 50% (Fig. 2.3c, e). Although not estimated precisely in our study, handling time per prey was much faster for *C. irroratus* (few minutes) than for *A. vulgaris* (few hours). Crab and sea star behavioural sequences were very different (Fig. 2.4a, 2.5a, Table 2.3), in that crabs showed irregular sequential behaviours compared to the linear pattern in sea stars. *C. irroratus* transition behaviours were concentrated between stationary state and non-foraging displacement (Fig. 2.5a).

Predation rate and behaviours of *H. araneus* were not significantly different from *C. irroratus* (Table 2.2). Predation rate of *H. araneus* was 1.3 scallops · predator^{-1} · d^{-1} (Fig. 2.1b). These crabs spent 0.6% of their time searching for prey, and had an encounter rate of 95.1 scallops per searching hour (Fig. 2.3a, b). They captured half of the prey encountered (Fig. 2.3c), and again scallops mostly passively escaped upon encounter (Fig. 2.3d). Consumption upon capture was surprisingly low (Fig. 2.3c) and the result of a high proportion of prey rejections and escape after capture (Fig. 2.3e). The main transitions in the ethogram for *H. araneus* were between stationary state and non-foraging displacement (Fig. 2.5c). The difference between sequential frequencies of both crab species was significant (Table 2.2): searching events tended to be more frequent for *C. irroratus* and lead to handling events more often than for *H. araneus*.

The day and night time budgets were not significantly different for *A. vulgaris* and both crab species (F = 0.13-1.14, df = 5, 24-30, $p>0.30$). However, *H. araneus* tended to stay in a stationary state longer during the 14:00 recordings than in the 23:00 ones (F = 2.57, df = 5, 29, $p = 0.048$). No statistical analysis was performed for *L. polaris* behaviours as these sea stars were mostly stationary during the video recordings with a few non-foraging displacements.

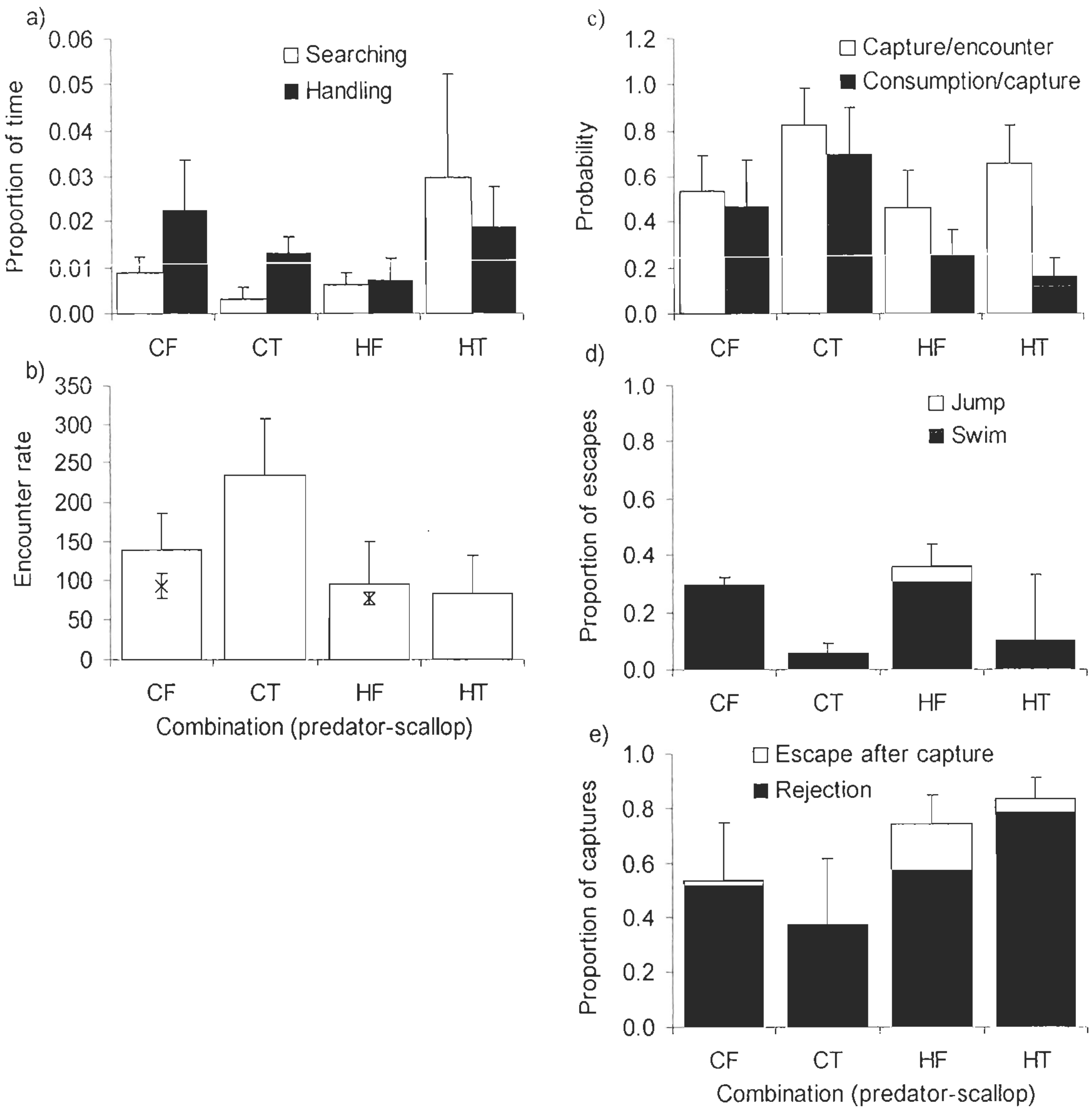

Figure 2.3. Mean (± SE) predator and prey behaviours of crabs *C. irroratus* (C) and *H. araneus* (H) preying on free (F) and tethered (T) juvenile scallops (*P. magellanicus*). a) Proportion of time spent foraging on (searching for and handling) scallops; n = 6. The remaining time was spent immobile or in non-foraging activities. b) Encounter rate per searching hour, as observed (histogram bars, n = 4-6) and as predicted (x). c) Probabilities upon encounter; n = 4-6. d) Proportion of active escapes (for escapes that occurred before capture); n = 2-5. The remaining proportion represents passive escapes. e) Proportion of captures that are escapes and rejections of prey; n=4-6. The remaining proportion represents consumptions.

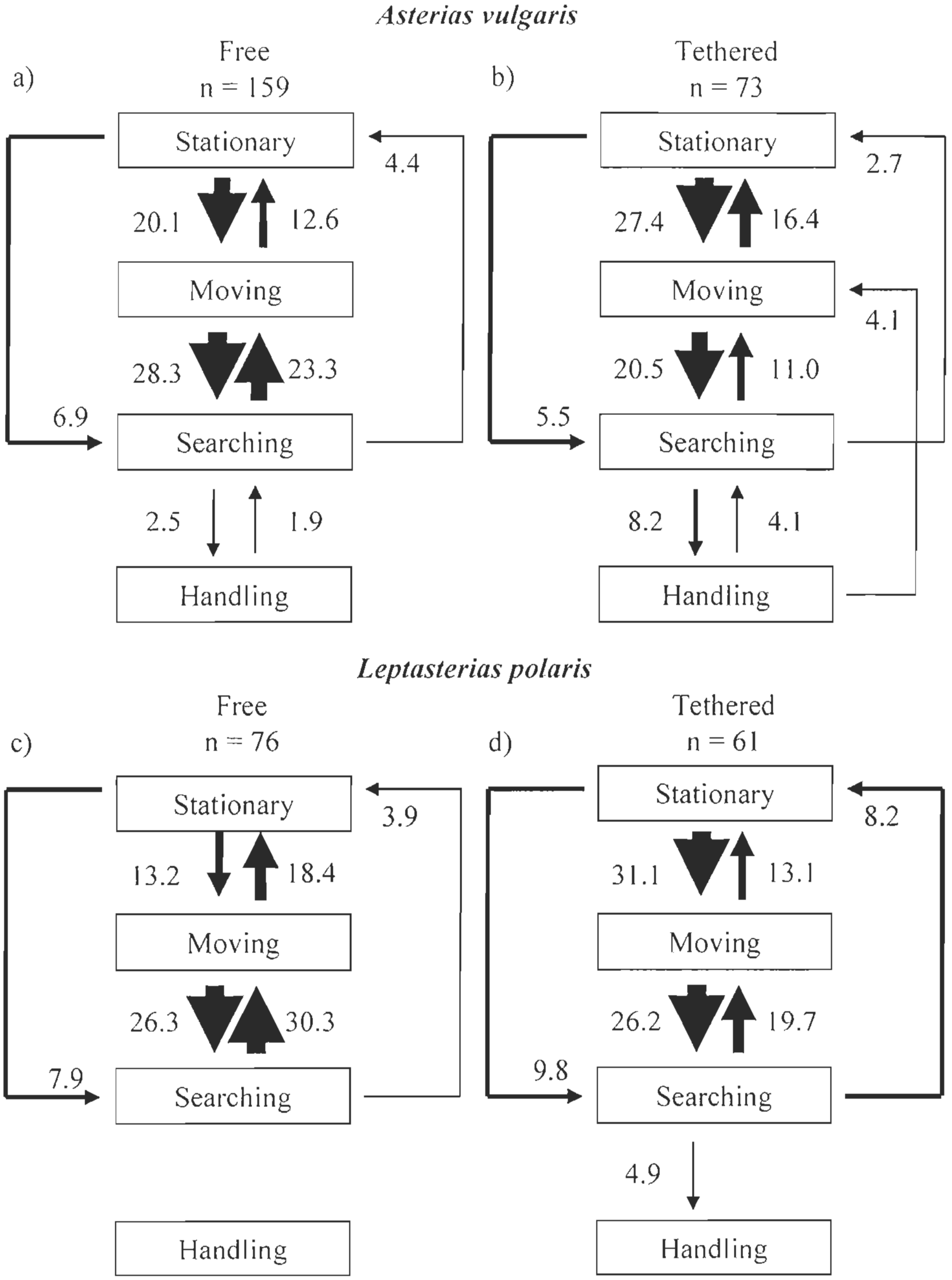

Figure 2.4. Kinematic graphs of the behavioural sequences of sea stars offered free or tethered scallops (*P. magellanicus*). The thickness of arrows and the value beside indicates the relative frequency between two behaviours; n represents total number of transitions.

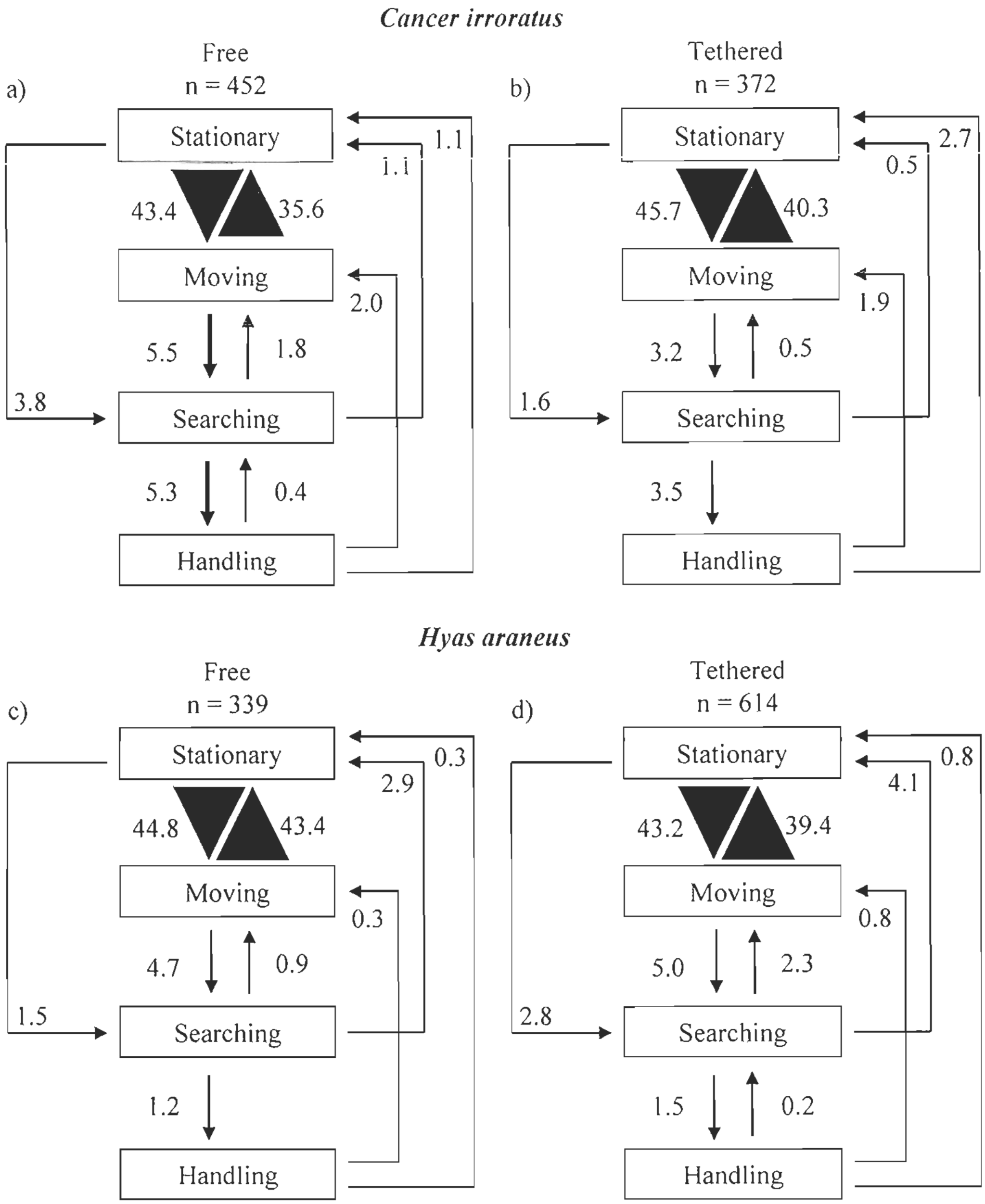

Figure 2.5. Kinematic graphs of the behavioural sequences of crabs offered free or tethered scallops (*P. magellanicus*). The thickness of arrows and the value beside indicates the relative frequency between two behaviours; n represents total number of transitions.

2.3.2 Effects of the tethering procedure

Predation rates of *A. vulgaris* on tethered scallops (1.17 scallops · predator^{-1} · d^{-1}) and free scallops were not significantly different (Table 2.2, Fig. 2.1a). The time spent searching was lower with tethered scallops than with free scallops, but encounter rates and the probability of attack upon encounter were similar (Table 2.1, Fig. 2.2a, b, c). The probability of capture upon attack for tethered scallops (0.13) tended to be higher than for free scallops (Fig. 2.2c); however this trend was not significant because of high variation and so low power (Table 2.1). This high variation occurred because in only 3 out of 6 replicate tanks were *A. vulgaris* observed to capture tethered scallops during the monitoring periods (the mean ± SE probability was 0.26 ± 0.08 for those 3 tanks). The power to detect a 10% difference in probability of capture upon attack by *A. vulgaris* was 0.30. When escaping, tethered scallops generally actively swam away from the predator as observed with free scallops. All captured tethered scallops were consumed. The ethograms for *A. vulgaris* preying on free or tethered scallops were significantly different (Table 2.2): searching lead more often to handling with tethered scallops than with free scallops (Fig. 4a, b), which supports the above-mentioned trend of a higher probability of capturing tethered scallops than free scallops.

Predation rates of *L. polaris* were significantly higher on tethered scallops (0.44 scallops · predator^{-1} · d^{-1}) than on free scallops (Table 2.1, Fig. 2.1a). Time spent searching and encounter rate were similar for both scallop treatments (Fig. 2.2a, b). Similar to when offered free scallops, *L. polaris* often avoided encountered tethered scallops, and only about the half of encountered tethered scallops were attacked (Fig. 2.2c). As with *A. vulgaris*, the probability of capture upon attack by *L. polaris* tended to be higher for tethered than free scallops but was highly variable and so not significant (Table 2.1). Again, captures of tethered scallops by *L. polaris* were observed in only 3 of the 6 replicate tanks (this probability was 0.33 ± 0.23 for those 3 tanks). The power to detect a 20% difference in probability of capture upon attack by *L. polaris* was 0.30. More passive escapes were noted with tethered than free scallops (Fig. 2.2d), but this trend was not significant (Table 2.1). In contrast to *A. vulgaris*, only half of the captured tethered scallops by *L. polaris* were consumed; the other half were rejected (Fig. 2.2c). The behavioural transitions of *L. polaris* with tethered scallops were significantly different than with free scallops (Table 2.2). Transitions from stationary state to non-foraging displacement were more frequent and transitions from searching to handling were observed with *L. polaris* offered tethered scallops (Fig. 2.4c, d), the latter supports the trend of a higher probability of capturing tethered scallops than free scallops.

Tethering did not generally significantly modify predation rates or behaviours for both *C. irroratus* and *H. araneus*. Predation rates, time budgets, encounter rates and probabilities of the various outcomes of encounter were similar in both scallop treatments (Table 2.1, Fig. 2.1b, 2.3). Tethering may have induced a bias on scallop escape behaviour as tethered scallops showed a higher (but not significant) proportion of passive escapes than free scallops for both crab species (Fig. 2.3d, Table 2.1). Rejection rates upon capture were similar in both scallop treatments. Ethograms showed a similar pattern in free and tethered scallops for both crab species (Fig. 2.5). However, the frequency of transition analysis revealed a significant difference between free and tethered prey for *C. irroratus* (Table 2.2). This difference may be related to higher transitions coming in and out of the searching behaviour (e.g. stationary to searching, moving to searching or searching to handling) when rock crabs were offered free scallops compared to those offered tethered scallops.

2.3.3 Modelling predation rates on free scallops

While searching, sea stars *A. vulgaris* and *L. polaris* moved at a velocity of 7.78 ± 1.86 and 3.87 ± 1.10 cm $\cdot$ min^{-1} (mean ± SE, n = 3), respectively. Crabs *C. irroratus* moved at a velocity of 142.45 ± 25.05 cm $\cdot$ min^{-1} (n = 6), and *H. araneus,* 114.43 ± 11.90 cm $\cdot$ min^{-1} (n = 9). Encounter rates predicted with these data and random movements (Eq. 2.2) tended to be higher than observed encounter rates for both sea star species (Fig. 2.2b), but were in the same range for both crab species (Fig. 2.3b). Predicted predation rates of sea stars and crabs were all very close to observed predation rates (Fig. 2.6), whether the predation model (Eq. 2.1) used the observed or predicted encounter rates.

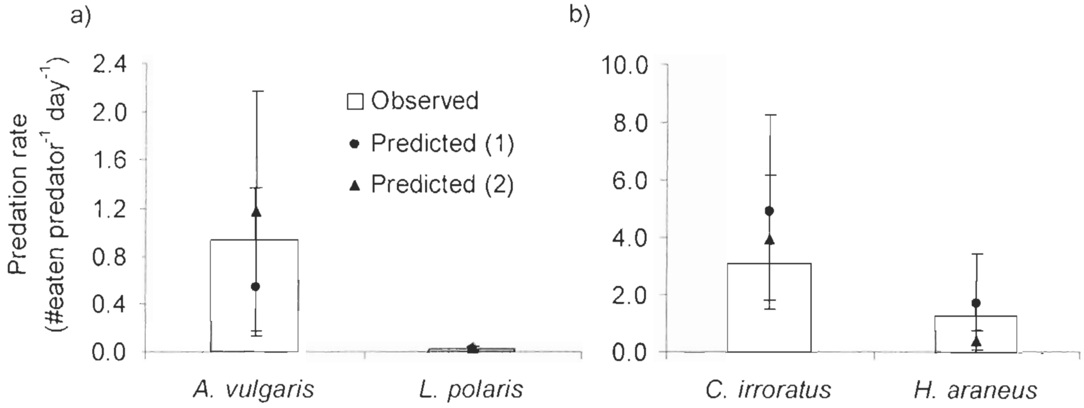

Figure 2.6. Mean (± SE) predation rates of sea stars (*A. vulgaris* and *L. polaris*) and crabs (*C. irroratus* and *H. araneus*) preying on free scallops (*P. magellanicus*), as observed (histogram bars, n=4-6) and predicted using Equation 2.1 (dark circle and triangle, n=200). Predicted predation rate (1) is calculated using observed encounter rate, whereas predicted predation rate (2) is calculated using predicted encounter rate (Eq. 2.2).

2.4 Discussion

The study presented here directly compared predation rates and behaviours of two species of sea stars (*A. vulgaris* and *L. polaris*) and two species of crabs (*C. irroratus* and *H. araneus*) preying on juvenile sea scallops (*P. magellanicus*) within a single, large laboratory experiment. The behavioural analysis provided a mechanistic understanding of predation patterns and so was helpful to mathematically model predation rates. Since predator-related mortality of scallops are being investigated in the field (see next chapters), the procedural effects of tethering, a tool commonly used in field predation experiments (Barbeau et al. 1994; Fleury et al. 1996; Bologna & Heck Jr. 1999), were also examined.

2.4.1 Predation rates and behaviours on free scallops

Predation rates, behaviours and probabilities observed for *A. vulgaris* and *C. irroratus* were comparable to those observed in previous laboratory experiments (Barbeau & Scheibling 1994a; Nadeau & Cliche 1998; Wong & Barbeau 2003; d'Entremont 2005) and to predation rates quantified in the field (Barbeau et al. 1994; Wong et al. 2005). Therefore, the present experimental procedures were appropriate and behavioural data obtained for less known predator species as *L. polaris* and *H. araneus* were reliable. Furthermore, since day- and night-time budgets observed by video camera and numbers of scallops consumed counted in the morning and evening were similar, the information collected only during daytime (encounter rates and probabilities) should also be reliable. This similarity between daytime and night-time activity of sea stars and crabs has also been reported in previous studies (Wong & Barbeau 2003; Novak 2004; d'Entremont 2005). Finally, a sequential analysis of the behavioural data using ethograms complemented and supported the other analyses. This behavioural approach has rarely been used with marine animals (but see Miron et al. 1992; Himmelman et al. 2005). In the present study, ethograms provided a synoptic overview of the major behaviour transitions that occurred within a predator-prey system.

Crabs were 3 times more effective predators of juvenile scallops than sea stars. Despite spending < 1% of their time searching, crabs moved fast ($> 100 \text{ cm} \cdot \text{min}^{-1}$) and had high prey encounter rates which led to relatively high predation rates. Sea stars spent ~10% of their time searching, but moved slowly (<10 cm · min^{-1}) and so had low prey encounter rates. The probability of capturing free scallops upon encounter tended to be higher for crabs (*C. irroratus*: 0.54 ± 0.16) than sea stars (*A. vulgaris*: 0.02 ± 0.02), although this trend was not significant due to high variation. In addition, sea stars and crabs both showed distinct patterns of transition in the ethograms. Sea stars exhibited a large variety of transitions between stationary state, non foraging displacement and searching. Crab behaviours were mainly concentrated between stationary state and non-foraging displacement with only a few transitions to other behaviours. Finally, scallops responded differently after encountering a sea star or a crab predator, as observed in previous studies (Barbeau & Scheibling 1994a; Nadeau & Cliche 1998). With sea stars, scallops actively escaped by swimming or jumping away, whereas with crabs, scallops often responded passively by closing their valves.

Based on behavioural analyses, the predation impact of *L. polaris* was 45 times lower than that of *A. vulgaris*, even if time spent searching and prey encounter rates while searching were similar for both species. The avoidance behaviour by *L. polaris* upon encountering scallops, as well as its low ability to capture an attacked scallop, support the notion that scallops are not a main component of *L. polaris*' diet. Field studies indicate that *L. polaris* specializes in digging sediment, and that its diet consists mainly of infaunal bivalves, the gastropod *Buccinum undatum* and polychaetes (Dutil 1988; Gaymer et al. 2001; Himmelman et al. 2005). In addition, the scallops' response whereby they often did not actively evade *L. polaris*, but rather simply responded by extending tentacles without closing valves, support the above notion. It is known that tentacles are implicated in reception of chemical and tactile stimuli. Chemical cues (e.g. pheromones) emitted from predators provide information about their location and intentions, which prey may use to minimize their energy expenditure by deciding to not actively escape (Chivers & Smith 1998; Kats & Dill 1998). Nevertheless, *L. polaris* may have a notable predation impact on sea scallops (Nadeau & Cliche 1998) and Iceland scallops (*Chlamys islandica*; Arsenault & Himmelman 1996b), and are still hazardous to scallops.

Even if *L. polaris* was less efficient than *A. vulgaris* at capturing scallops, they showed similar sequential activities, concentrated between stationary state, non-foraging displacement and searching. This sequential pattern was also observed with *L. polaris* during a field study conducted in the northern Gulf of St. Lawrence (Himmelman et al. 2005), in which the most frequent transitions were between moving (including searching) and being stationary on the bottom but not feeding. The other behavioural states were capturing prey (including digging and manipulating) and digesting prey. Based on this field study (conducted during summer at 2-8°C), *A. vulgaris* and *L. polaris* appeared to be more active in their natural habitat as they spent 42-46% of their time budget moving (without digging or handling prey) on the bottom compared to 15-40% (searching + moving but not foraging) in the present experiment. The lower level of displacement activity in our experiment may be associated with holding stress or confinement conditions such as low current speed. In this regard, Rochette et al. (1994) observed in their laboratory experiment that *L. polaris* increased its displacement with increasing current velocity. In the field, *L. polaris* was also observed to spend time digging (~15%; Himmelman et al. 2005), an activity not observed or considered in the present study as it focused on predation of scallops, an epifaunal prey.

Predation rates and behaviours of the crab *H. araneus* were similar to *C. irroratus*. Encounter rate was a determining component underlying predation rate of these animals (see also Barbeau & Scheibling 1994a), as half of the scallops encountered were captured. The probability of consumption upon capture was also important for *H. araneus*, and was affected by rejections and post-capture escapes. Rejection of scallops occurred in ~50% of captures. Scallop rejections have been reported in previous behavioural studies with *C. irroratus* (Barbeau & Scheibling 1994c; Barbeau et al. 1994; Wong & Barbeau 2003; Wong & Barbeau 2005, 2006), but usually to a much lower extent (<25%). Jubb et al. (1983) proposed two explanations for such rejections based on crab-mussel interactions. The first explanation involves a pre-evaluation period where crabs gauge the bivalve for a brief moment after capture; the bivalve is then accepted or rejected on the basis of shell strength or resistance to crushing. This explanation should not be applicable here as scallops of 25-35 mm shell height can easily be crushed by large crabs (Elner & Jamieson 1979, who used rock crabs 90-110 mm in carapace width). In the second explanation, retention of prey after capture depends on the strength of the sensory stimuli received by the claws relative to the walking legs; these stimuli increase with prey size and with number of prey contacted simultaneously on the bottom. In our study, tank confinement could concentrate chemical stimuli and this may have produced a strong stimulus relative to the scallop held in a claw, and caused fairly high rejection rates. What was also particular with *H. araneus* was the number of active escapes by scallops following capture. This post-capture escape behaviour by scallops has rarely been observed in other crab studies (Wong & Barbeau 2005, 2006). With *H. araneus*, this type of escape was not negligible, as it occurred in ~20% of captures. This suggests that *H. araneus* may not be a dominant predator of scallops. On scallop beds off the Îles de la Madeleine, these crabs tend to be concentrated in deeper areas (>32 m) than rock crabs. The natural abundance of scallops in these areas is not well known, but some data suggest that it may be reduced (Giguère et al. 2004). Hence, *H. araneus* may not be in contact with scallop aggregations as commonly as *C. irroratus*, except at scallop seeding sites.

2.4.2 Effects of the tethering procedure

Tethering increased predation rate of *L. polaris* as tethered scallops tended to be easier to capture than free scallops. Surprisingly, tethering did not modify predation rate by *A. vulgaris*, and this may have been related to the larger juvenile scallops used in our study (25-35 mm shell height) compared to those used in Barbeau and Scheibling's study (1994b; 8-13 mm shell height). Although the probability of capture upon attack of *A. vulgaris* tended to be higher when offered tethered scallops then free scallops, the time sea stars spent searching was reduced when offered tethered scallops. An explanation of these compensatory behaviours is that *A. vulgaris* offered tethered scallops may have reached satiation, and so searched less. According to Barbeau and Scheibling (1994a), energy per scallop increases rapidly with increasing scallop size: specifically, profitability (energy per prey per minute of handling time by a sea star predator) of scallops sized 20-25 mm was as much as 5 times higher than that of scallops sized 10-15 mm. Thus, it is possible that *A. vulgaris* (70-90 mm radius) reached satiation, resulting in non-significant differences in predation rate between tethered and free scallops. Sea stars *L. polaris* did not reduce their time spent searching when offered tethered scallops: they may have needed more energy before becoming satiated since they were larger (90-110 mm radius).

As expected, predation rate of both crab species, *C. irroratus* and *H. araneus*, was not modified by tethering scallops. Tethering generally did not affect any of the component behaviours. In particular, upon encountering a crab, scallops typically respond with a passive escape; tethering would not change the efficacy of this escape behaviour, and so should not change the probability of capture upon encounter. Encounter rate, a primary determinant of predation rate by crabs, was also not affected by tethering. Of note though, tethered scallops had a lower proportion of active escapes than free scallops with both crab species. The rings to which the tethers were attached may have been used as a shelter by scallops, which then increased the passive escape strategy.

As described above, the main bias of tethering was observed with *L. polaris*, and predation rate on tethered scallops in the field was estimated (Eq. 2.1 and 2.2) to be ~19 times higher than on free scallops. The low efficiency of *L. polaris* in capturing scallops appears overcome by tethering the prey, resulting in an overestimate of its predation potential. A bias was also estimated for *A. vulgaris*; using the predation equation (Eq. 2.1 and 2.2) and the proportion of time spent searching free scallops (to remove the possible effect of satiation), predation rate on tethered scallops in the field was estimated to be ~6 times higher than on free scallops. These correction coefficients must be used for a more accurate assessment of predation potential at field sites.

2.4.3 Mathematical modelling

Mathematical models are useful tools to integrate a variety of biological data and simulate trajectories in a particular biological system in response to environmental conditions (Conway 1977). The increasing interest in scallop seeding in the past years along the northwestern Atlantic coast led to the development of models of scallop population dynamics to assess and optimize management practices (such as selecting an appropriate seeding area based on predator composition, choosing an initial scallop density or size at seeding, or applying a predator control strategy) (Barbeau & Caswell 1999; Gangnery et al. 2005). These models incorporated the details of the predation process in the form of a predation submodel, since field and laboratory studies used to develop them identified predation as a process of primary importance. Specifically, the predation submodel is composed of component behaviours, namely movement velocities of predators and scallops, time spent searching by predators, probability of capture upon encounter (which with sea stars can be further decomposed to probability of attack upon encounter and probability of capture upon attack) and probability of consumption upon capture (Eq. 2.1). Note that since encounter rate is itself dependent on various underlying processes (movement velocities and patterns, and densities of the animals), it is not incorporated in the predation equation as a number, but rather as a submodel (Eq. 2.2). In sum, these models are mechanistic, and allow one to model trajectories in a variety of initial conditions, such as different sites or seeding practices. In Barbeau and Caswell (1999), predicted scallop survival in simulated seeding trials was in good agreement with that observed in experimental seeding trials (these observed data were collected independently of the data used to construct the model). More recently, a refinement of the predation model which consists of a mechanistic functional response (Wong et al. 2006a) produced estimated predation rate curves that fit well with observed data over a variety of prey densities. In the present study, we also found that the predation model performed well with four predator species.

The additional data collected on the predatory behaviours of *L. polaris* and *H. araneus* in the present study will be useful to adapt Barbeau and Caswell (1999)'s model to scallop ground conditions of the Îles de la Madeleine. In their model, Barbeau and Caswell did not differentiate between different sea star species or between different crab species (they had no need since *L. polaris* and *H. araneus* do not occur at their geographically different and shallower sites). The present detailed laboratory study should be useful to estimate more accurately scallop survival off the Îles de la Madeleine, especially with respect to the impact of sea stars (since *L. polaris* has a lower predatory efficiency than *A. vulgaris*). In addition, recent work investigating component behaviours of the functional response (Wong & Barbeau 2005, 2006; Wong et al. 2006a), effects of substrate type on dispersal and predator-related mortality (Wong & Barbeau 2003; Bourgeois et al. 2006), and effects of competing predators (d'Entremont 2005) will be considered in an updated model. Sensitivity analysis (Barbeau & McDowell 1998; Barbeau & Caswell 1999) of the updated model will then guide managers on the most important variables to manipulate prior to seeding trials (e.g. scallop density, substrate type, predators assemblage, etc) to improve scallop survival.

CHAPITRE 3

Variation saisonnière de l'assemblage des étoiles de mer et des crabes présents sur un gisement naturel de pétoncles géants (*Placopecten magellanicus*) au large des îles de la Madeleine, Québec, et estimation de leur potentiel de prédation sur les pétoncles juvéniles

Seasonal variation of sea star and crab assemblages on a natural sea scallops (*Placopecten magellanicus*) ground off the Îles de la Madeleine, Québec, and investigation of their predation potential on juvenile scallops

RÉSUMÉ

Les études portant sur les interactions entre les prédateurs multiples à l'intérieur des communautés sont importantes pour améliorer la gestion des populations de proies. Afin de contribuer dans ce domaine, la présente étude visait à documenter les variations saisonnières des assemblages de prédateurs benthiques durant une période de trois ans sur un gisement naturel de pétoncle géant (*Placopecten magellanicus*) au large des îles de la Madeleine, Québec, et leurs impacts sur la prédation des pétoncles juvéniles. Les données sur les prédateurs ont ensuite été utilisées dans un modèle de prédation simulant une action indépendante des prédateurs multiples envers les pétoncles juvéniles. Les potentiels de prédation estimés ont été comparés aux valeurs observées sur le terrain pour détecter la présence d'interactions (ou d'effets non-indépendants) à l'intérieur des assemblages de prédateurs. Pour réaliser cette étude, l'assemblage des prédateurs benthiques a été caractérisé de façon saisonnière sur trois sites avec une camera montée sur un traîneau mobile. Ensuite, le potentiel de prédation de ces assemblages a été évalué à l'aide de pétoncles juvéniles fixés sur des cadres. Les résultats ont démontré que l'assemblage des prédateurs était relativement constant sur une échelle saisonnière et dominé par trois espèces d'étoiles de mer (*Asterias vulgaris*, *Leptasterias polaris* et *Crossaster papposus*) et deux espèces de crabes (*Cancer irroratus* et *Hyas araneus*). Certains patrons de distribution spatiale ont tout de même été notés à l'intérieur de ces assemblages, dont une corrélation négative entre les densités des étoiles de mer et des crabes de même qu'une corrélation négative entre les densités des différentes espèces d'étoiles de mer. L'étude de la prédation a démontré une faible variation saisonnière du potentiel de prédation. Toutefois, le potentiel de prédation a varié significativement sur une échelle spatiale, surtout à l'intérieur des sites étudiés et en lien avec les étoiles de mer. Selon les débris de coquilles, l'impact de la prédation des étoiles de mer a corrélé positivement à la fois avec leur taille et leur densité, tandis qu'aucune corrélation n'a été notée avec les crabes. Finalement, le modèle de prédation a prédit des valeurs de prédation relativement rapprochées de celles observées sur le terrain et donc ne supporte pas la présence d'interaction ou d'action non-indépendante de

la part des prédateurs. Cette conclusion est plausible pour notre site d'étude composé d'une faible densité de prédateurs limitant les interactions entre les prédateurs.

ABSTRACT

Studies of multiple predator interactions in natural communities are important to enhance management of prey populations. To contribute to this domain, the goal of the present study was to investigate, on a seasonal basis over a 3-y period, benthic predator assemblages on a natural sea scallop (*Placopecten magellanicus*) ground off the coast of Îles de la Madeleine, Québec, and their impact on juvenile scallop predation. Specifically, field data on predators were collected and used to parameterize a predation model that assumes that different predator species act independently of one another. Predicted predation potentials were then compared to observed field values to assess the possibility of interaction amongst predators (or non-independent multiple predator effect) inside predator assemblages. First, the benthic predator assemblage was characterized seasonally using a video camera mounted on a mobile sleigh. Following each video survey, predation potential of the predator assemblages on juvenile scallops was quantified using a tethering approach. Field results indicated that the benthic predator assemblage varied little on a seasonal scale and was mainly composed of three sea star species (*Asterias vulgaris*, *Leptasterias polaris* and *Crossaster papposus*) and two crab species (*Cancer irroratus* and *Hyas araneus*). Various patterns were detected inside these assemblages, including a seasonal negative correlation between sea star and crab densities and a spatial negative correlation amongst densities of different sea star species. The predation assays indicated limited seasonal variation in predation potential. However, predation potential varied significantly spatially, especially within site and in association with sea stars predation. Furthermore, based on scallop shell remains, characteristics (density and size) of sea stars were positively correlated with their predation, while characteristics of crabs were not. Finally, the predation model performed moderately well in predicting predation potential in the field, and thus did not provide support for predator species interacting and acting non-independently. This conclusion makes sense for our study sites which had low predator densities (and so predator interactions should be uncommon).

3.1 Introduction

In natural communities, preys are exposed to multiple predator species. This is a complex situation, and total predation impacts may not be predicted by simply summing the effects of the different predators (Sih et al. 1998). Observed predation impacts may be more or less than that anticipated from predators separately, a situation termed non-independent, as opposed to independent, multiple predator effects (Soluk 1993). Understanding how predator species interact with each other and with their prey is crucial for modelling predator-prey dynamics.

Populations of sea scallops (*Placopecten magellanicus*) in Atlantic Canada are exposed to an assemblage of predators. Scallop loss to predation is an important issue, particularly in enhancement efforts conducted along the coast of the northern Atlantic to sustain scallop fisheries (Cliche et al. 1994; Barbeau et al. 1996). Field and laboratory experiments confirmed the importance of predation by sea stars (*Asterias vulgaris*, *Leptasterias polaris* and *Crossaster papposus*) and crabs (*Cancer irroratus* and *Hyas araneus*) on seeded juvenile scallops (Barbeau & Scheibling 1994a; Barbeau et al. 1998; Nadeau & Cliche 1998; Wong & Barbeau 2006; Wong et al. 2006b; Chapter 2). Although interactions between these predators when foraging is generally expected, only a few studies have addressed this concern. For instance, in a multiple predator assemblage, *C. papposus* may repulse *A. vulgaris* (Sloan 1980). A kleptoparasitism relationship between *A. vulgaris* and *L. polaris* may also occur (Morissette & Himmelman 2000b), whereby *A. vulgaris* steals prey from *L. polaris*. The predator *A. vulgaris* and *C. irroratus* do interact behaviourally, but the multiple predator effect was assumed independent when preying on juvenile scallops (d'Entremont 2005).

Furthermore, the functional response of a multiple predator assemblage can be modulated by various factors such as temperature (Weissberger 1999), predator density (Griffen & Williamson 2008), prey density (Soluk 1993; Bélair & Miron 2009), prey size (Wong et al. 2010), habitat complexity and availability of alternative prey (Siddon & Witman 2004). It is thus clear that more investigations are needed to improve the understanding of predator-scallop dynamics in a multiple predator system.

The main objective of this study was to investigate in the field the effect of multiple predator assemblages on juvenile sea scallops. It was hypothesized that scallop predation would vary seasonally, because of fluctuations in predator assemblage (species, density and size) and abiotic factors. It was also hypothesized that the multiple predator assemblage would exhibit a non-independent predation impact, as a result of various predator-predator interactions observed to occur in small-scale studies (e.g. Sloan 1980; Morissette & Himmelman 2000b). To test these two hypotheses, the benthic predator assemblages off the Îles de la Madeleine, Québec, Canada, was first characterized seasonally during a 3-y period. The benthic community was assessed using a video camera system mounted on a sleigh. Second, we quantified the predation potential of the predator assemblages on juvenile scallops during the same period. Predation potential, which is defined as the rate at which the prey of interest would be consumed were they readily available to predators (Aronson 1989), was estimated using the tethering approach. Tethering has been previously used in natural conditions to identify causes of scallop mortality from shell remains and estimate relative predation rates (Barbeau et al. 1994; Stokesbury & Himmelman 1995; Arsenault & Himmelman 1996a, b; Bologna & Heck Jr. 1999; Kamenos et al. 2004). Its bias has previously been assessed (Barbeau & Scheibling 1994b; Chapter 2), and a methodology has been developed for deployment in deep water (>30 m) (Bourgeois 2004). Finally, our field data were used in a predation model that estimates multiple predator effects on tethered scallops with independent predation impact (Barbeau & Caswell 1999). The estimated data were compared with observed predation potential to assess the non-independent predation impact hypothesis.

3.2 Materials and Methods

3.2.1 Study sites

The study was conducted over a 3-y period (2003 to 2005) on a natural scallop ground located 10 km off the Îles de la Madeleine, Gulf of St. Lawrence in eastern Canada and >30 m deep (Fig. 3.1). This region was closed to fishing and solely used for commercial scallop seeding. Selection of study sites within this region was based on: (i) being non-seeded areas, (ii) being suitable for juvenile scallops with heterogeneous substrate (sand and gravel; Anonymous 2007), and (iii) being known for their diversity and abundance of predators (Giguère et al. 2004). Three sites of 0.097 km^2 (0.18 km x 0.54 km) were selected for 2003, and another set of three sites of 0.360 km^2 (0.60 km x 0.60 km) were selected for 2004 and 2005 (Table 3.1). Temperature sensors (Sealog-T v1.04, Vemco Ltd.) were placed 2 m above the sea bottom to monitor water temperature on hourly basis during the 3-y period (Fig. 3.2). However, the 2004 temperature recordings were questionable and so discarded.

3.2.2 Video surveys of predators

Predator densities and sizes were quantified using video transects in four periods per year nominally called "season": spring, summer, fall and winter (Table 3.1). The video camera (Subsea Video System, model S500/21) was mounted on a metal sleigh (1.89 m length, 1.84 m width and 0.73 m height) to view the sea bed at an angle of 45 degrees, and connected to a video recorder (Video Hi8 Sony, GV-A500, in 2003 and DVD Panasonic, DMR-E50, in 2004 and 2005) on the research boat with a 115-m cable (Fig. 3.3).

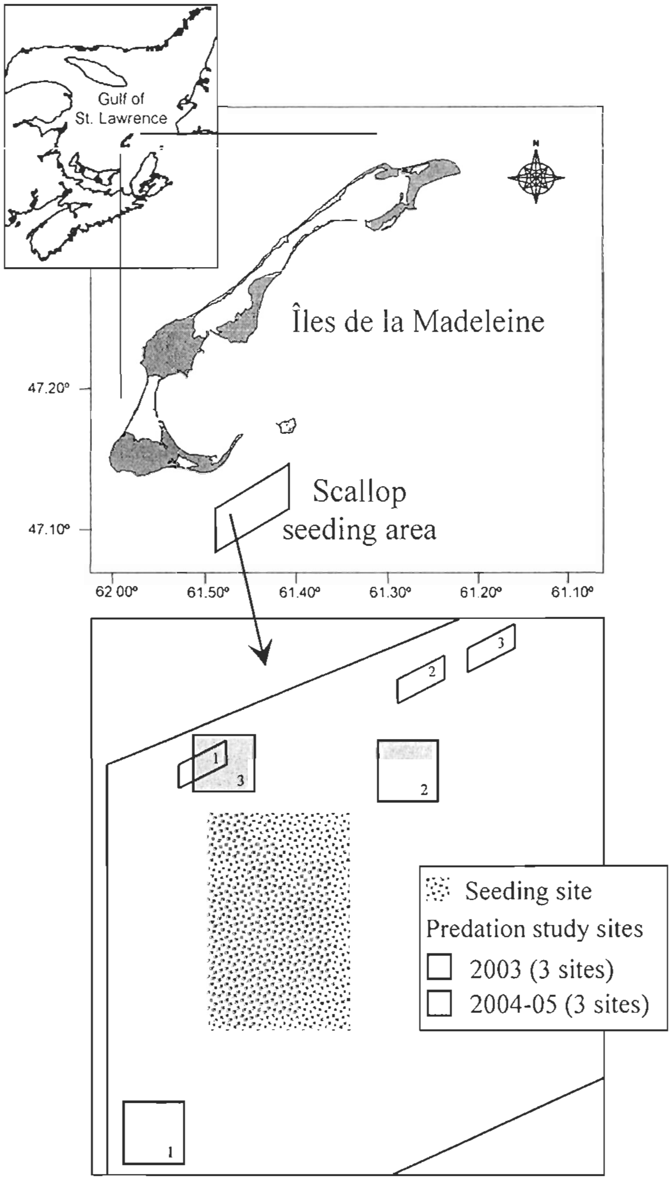

Figure 3.1. Maps of the study sites off the coast of the Îles de la Madeleine, Québec, Canada.

Table 3.1. Summary of predator surveys and predation assays conducted during the 3-y study.

Year	Season	Number of sites (area/site)	Predator densities and sizes			Predation potential		
			Date	Sampling approach	Number of replicates/ site	Date	Sampling approach and number of replicates	Immersion time (h)
2003	Spring	3 (0.1 km^2)	May 27	4 parallel video transects/site; these were then cut into multiple 100-m sequences	10 randomly chosen video sequences (100 m each)	June 7	6 tethering assays deployed randomly per site	48
	Summer		July 21			July 24		24
	"Fall"		Sept. 12			Sept. 17		24
	"Winter"		Nov. 5			Nov. 13		48
2004	Spring	3 (0.4 km^2)	June[1]	Grid of sampling stations overlaid on each site; 8 stations/site, randomly chosen on the grid	8 video sequences (180 m each, 1 sequence per station)	June 14	4 stations/site (previously sampled by video), each with 2 nested tethering assays	24
	Summer		Aug. 6			Aug. 17		24
	Fall		Sept. 24			Sept. 28		48
	"Winter"		Dec.13			Dec.[1]		48
2005	Spring		May 20			June 2		48
	Summer		July 19			July 28		48
	"Fall"		Sept. 19			Oct. 5		48
	"Winter"		Nov. 19			Nov. 24		72

[1] Data not collected because of technical problem (June) and inclement weather (December).

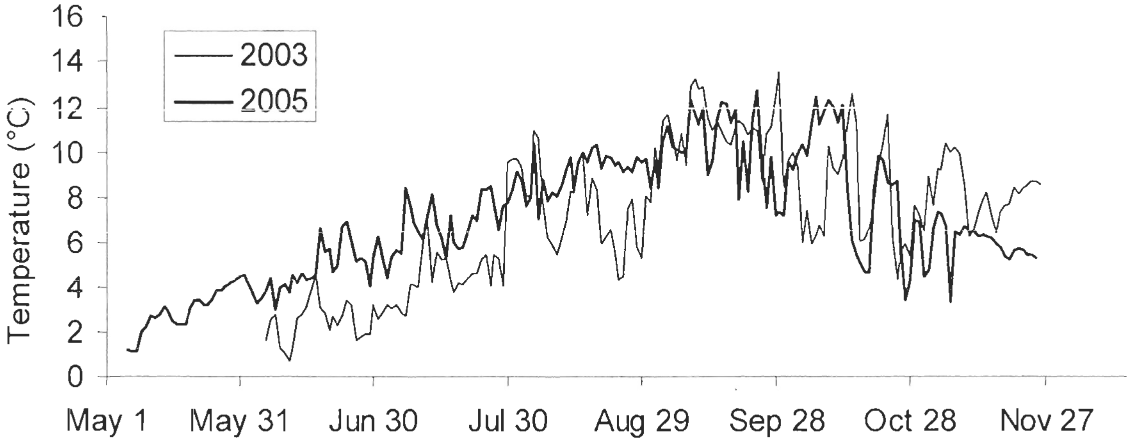

Figure 3.2. Mean daily water temperature recorded 2 m off the sea bed in the study area in 2003 and 2005.

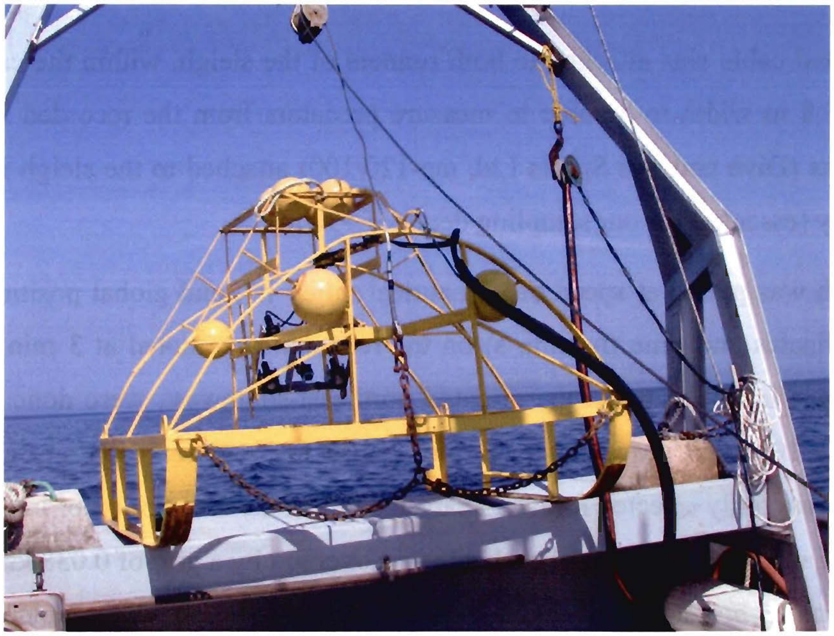

Figure 3.3. Mobile sleigh used during the camera surveys conducted in 2003, 2004 and 2005.

A graduated cable was attached to both runners of the sleigh, within the camera's field of view of 0.8 m width to be able to measure predators from the recorded images. Four halogen lights (Dive and Sea Sports Ltd, mc-120/100) attached to the sleigh increased the image quality (essential for our sampling depth of >30 m).

The sleigh was pulled at speed of ~1 nautical mile · h^{-1}, and global positioning system (GPS) coordinates and time (h, min, s) on the recorder were noted at 3 min intervals. In 2003, four parallel video transects, oriented northeast-southwest, were done in each site; subsequently, 10 video sequences of 3 min (~100 m long) for each site and sampling season were randomly selected for data analysis to meet the assumption of independence of data. In 2004 and 2005, the map of each site was overlaid by a grid of 0.038 km x 0.075 km rectangles, and eight unique rectangles (termed sampling stations) were randomly selected for each sampling season (stations were not re-sampled). One video transect oriented east-west of ~180 m long was then recorded in the middle of each sampling station for a given season.

As video surveys were conducted in daytime, small field experiments were conducted in 2003 and 2006 to assess the possibility of a difference in predator composition between daytime and night-time (Appendix 1). Predator densities and composition were not significantly different between the two periods (MANOVA, $p>0.05$). Therefore, the video surveys were considered reliable to estimate the predator assemblage independent of time of day. Image analysis software (Image-PRO Plus V4.1 software) was used to count and size sea star (*A. vulgaris*, *L. polaris* and *C. papposus*) and crab species (*C. irroratus* and *H. araneus*) from video sequences. The sea star *Solaster endeca* was not considered in our study as it feeds mostly on echinoderm species (Sloan 1980; Gaymer et al. 2004). Predator densities were calculated as number of individuals divided by surface area covered in each video sequence (number · m^{-2}); length (m) of each video sequence was estimated with Nobeltec navigation software V7. To correct for image distortion by the camera, a correction coefficients was estimated depending on the position of the object within the field of view. Specifically, a measurement grid of 10 cm x 10 cm squares was videotaped on the sea bed, and then used to estimate a correction coefficient for each square and applied it to the predator measurement within that square. Sea star size was measured as radius, which is the distance from the tip of an average-length arm to the center of the body. Crab size was measured as carapace width, which is the largest width of the cephalothorax.

3.2.3 Predation assays using tethered scallops

Assays to estimate predation potential at each site were conducted shortly following each video survey (Table 3.1). The assay consisted of a metal frame (1.2 m x 1.2 m) with three parallel lead cables (60 mm diameter) equidistantly and tightly affixed within the frame (Fig. 3.4). Four scallops, 25-35 mm shell height (from the shell ventral edge to the hinge), were tethered on each cable. A scallop was tethered by gluing one end of a 18-cm long fishing line (0.02 mm diameter, 2003 assays) or nylon line (Kite line, 0.5 mm diameter, 2004-05 assays) onto the upper shell of the scallop with cyanoacrylate glue (Bostik 7434). A small piece of blotting paper (6 mm x 12 mm) was put over that end of the tether as the glue dried to strengthen the binding to the shell (Chapter 2). The other end of the tether was attached (equidistantly) on the lead cable. Once tethered, a scallop could move in an area of 15 cm radius.

Prior to deployment in the field, lead cables with tethered scallops were held in a laboratory tank with continuous flow-through sea water for usually 1 night or occasionally up to 3 nights depending on weather conditions. During boat transportation to sites, tethered scallops were regularly sprayed with sea water. Immediately before deployment, lead cables were attached to the frames. The predation assays, each consisting of a frame with 12 tethered scallops, a cement block and surface float (Fig. 3.4), were then deployed from the boat, and usually retrieved after 24 h (2003 and 2004 trials) or 48 h (2005 trials). Occasionally, predation assays were retrieved later than planned because of inclement weather.

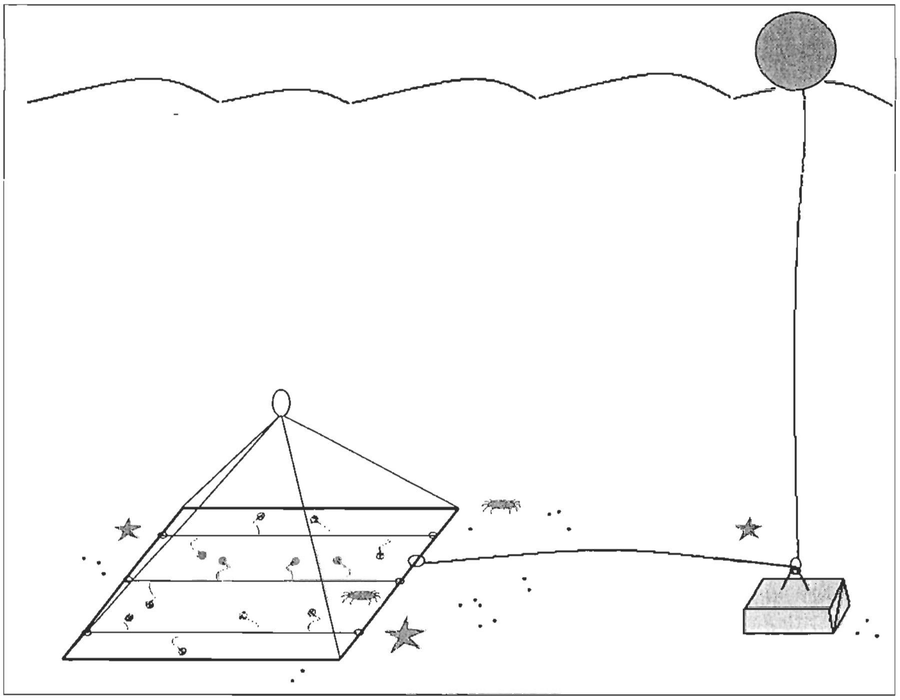

Figure 3.4. Schematic of a frame with tethered scallops deployed in deep water (>30 meters). The metal square frame lies on the sea bed with a small float held by four lines above the frame to facilitate its handling and maintain the frame horizontally upon immersion. Tethered scallops are attached to 3 parallel cables within the frame. A cement block and attached float on the water surface allow easy deployment and retrieval.

In 2003, six predation assays were deployed at each site and sampling season. In 2004-05, the experimental design was revised to increase statistical power and detect a difference over 15% between seasons (power of 0.30 in 2003 increased to 0.60 in 2005-05): predation assays were deployed in pairs, in four stations previously sampled by the video camera at each of the three sites. The average of the two frames per station was calculated for a total of four predation values per site per sampling season. Upon retrieval, the number of each type of shell remains (dead scallops) was counted. Shell remains were categorized as cluckers (intact upper and lower shells still attached at the hinge) and intact upper shells, both associated with sea star predation, and shell fragments, associated with crab predation (Barbeau et al. 1994). Scallop losses (tether line without a scallop or shell remains) were observed upon each retrieval in 2003 (0.31 ± 0.03 scallops; mean ± SE, n=69) and in 2004-05 (0.17 ± 0.02; n=168). Losses were reduced in 2004 and 2005 when using the nylon line. Based on laboratory observations (Chapter 2) and on a small field experiment (Appendix 2), these losses appeared to be scallops that became unglued as the predation assay was sunk to the sea bed, and not due to predation events. Thus, the proportion of dead scallops (by sea stars or crabs) was estimated using the total number of scallops (dead or alive) that remained on cables at retrieval, i.e., number of dead scallops divided by total number of scallops retrieved.

To adjust predation data to a common time of immersion for later analysis, the proportion of surviving scallops and the proportions of scallops not dying from a particular cause of mortality (1-Proportion died from sea stars or from crabs) were modelled by an exponential decay equation passing through the origin. This model was previously validated during a small field experiment that showed that the overlap between observed and predicted data was good (Appendix 2). Although 48 h period was used to observe predation events, the exponential decay equation was used to standardize predation potential data collected in 2003-2005 to 24 h from 48 or 72 h for data analysis.

3.2.4 Statistical analysis

Statistical analyses were performed using SAS software (v8.02). For ANOVAs, each dependent variable was assessed graphically for normality of residuals and using Cochran's test (Winer et al. 1991) for homogeneity of variance. When necessary, data were transformed using $\log_{10}$ or arsin-square root to obtain homogeneity of variance. For MANOVAs, assumptions of ANOVA of each dependent variable as well as equal covariances among groups were assessed (Scheiner 2001).

Densities of the main predator species and proportions of tethered scallops dying from different causes of mortality (standardized to 24 h) were analysed using MANOVAs with Season as a fixed factor and Site as a random factor. When a significant Pillai's trace (converted to an F-value) was detected, the standardized canonical coefficients were calculated (1) to evaluate contribution of different predator species or causes of mortality to the overall difference and (2) to identify correlations between densities of different predator species or proportions of different causes of mortality (Scheiner 2001). As well, planned comparisons were done when Season was significant to compare certain logical combinations in respect to orthogonal comparisons (Sokal & Rohlf 1995; Underwood 1997; Quinn & Keough 2002). Specifically, for 2003, the selected comparisons focused on spring and fall, two periods usually aimed for scallop seeding. For 2004-05, comparisons were conducted between years as well as focused on spring and fall. Variance components were also estimated when the random factor Site was significant to see which spatial level (i.e., site, unit) contributed most to the variation (Searle et al. 1992).

Size of each predator species and proportion of tethered scallops surviving (standardized to 24 h) were analysed using ANOVAs with Season as a fixed factor. Site was a random factor for the proportion of tethered scallops surviving and for *A. vulgaris* size in 2003 (because there were enough sea stars measured that year). Planned comparisons were done when Season was significant and variance components were estimated when Site was significant as described above. In both types of analysis (ANOVA and MANOVA), we interpreted a significant fixed factor even in the presence of an interaction between the fixed factor and random factor, as recommended by Quinn and Keough (2002, p. 240).

A correlation analysis was conducted to examine the strength of association between densities of sea stars and crabs, sizes of *A. vulgaris* and *C. irroratus*, and the mortality of tethered scallops associated with sea star and crab predation and so, for all years.

3.2.5 Predation model

The predation model developed by Barbeau and Caswell (1999) was used to predict predation potential for the different sites and dates. The model assumes that multiple predator effects are independent (i.e., that predator species act independently of one another) and that predator individual move randomly on the sea bottom (see Appendix 3 for further details). Predicted predation potential values were compared to observed ones to test the non-independent predation impact hypothesis.

The model parameters were quantified using predator densities and sea star sizes observed in the field. Crab size was estimated from the radius of their walking legs (0.05 cm) in contact with the bottom (8 legs x 0.05 cm = 0.4 cm; Barbeau & Scheibling 1994a; Chapter 2). Scallop size was the average shell height of tethered scallops (3 cm). Scallop densities were very low, and so were quantified using the number of juvenile scallops tethered per frame (n=12) and the number of frame immersed per site divided by the area of each studied sites (Table 3.1). Thus, even if tethered scallops were clustered in frames, they were considered, in the model, randomly distributed over site.

Behaviours and probabilities underlying predator-prey interactions were those observed in various studies for each predator species (Table 3.2). Probabilities were estimated from the trials using tethered scallops conducted in tanks (Chapter 2). Values for sea stars, $P[\text{die}|\text{enc}]_s$, were entered directly into the model. For crabs, values of $P[\text{die}|\text{enc}]_c$ that vary with prey density as a type III functional response (Barbeau et al. 1994, 1998, Appendix 3) were used. Foraging time (searching + handling time) and velocities while searching for *A. vulgaris* and *C. irroratus*, which are likely not affected by tethering (Chapter 2), were estimated as the average of multiple studies (Barbeau & Scheibling 1994a, b and c) for foraging time and from the study of Barbeau et al. (1994) for field measurements for velocity. Prey handling time was estimate from Barbeau and Caswell (1999)'s equation which was determined from observed handling time in laboratory (Barbeau & Scheibling 1994a; handling times per prey for each predator type were unfortunately not recorded in the tank experiments described in Chapter 2). Behaviours influenced by water temperature (velocity, foraging and handling time) were adjusted using a Q_{10} of 2, except for sea star velocity which have a Q_{10} of 3.8 (Barbeau & Scheibling 1994b), and field temperatures collected in 2003 and 2005 (Fig. 3.2; for 2004, we averaged the 2003 and 2005 daily temperatures).

We deemed it necessary to develop a second model to try to take into account the spatial structure that we introduced by deploying tethered scallops in clusters (i.e. groups of 12 scallops attached to a frame). We developed the simplest possible model to gain insight into two possible scenarios (note there may be other possible scenarios). (i) It may be that predators moved randomly until they encountered a cluster of tethered scallops, and then limited their search area to the area of the cluster, thus exhibiting higher predation rates then if tethered scallops had been deployed singly (for the same overall density of tethered scallops per site). Or (ii) it may be that predators were attracted to clusters of tethered scallops, and for this reason had higher predation rates then if predators moved randomly and tethered scallops were deployed singly. For this second model, we simply assumed that each scallop was surrounded by a detection zone (that is wider than their shell height) for predators. The concept of a detection zone is discussed in Holling (1966) as the area of reaction of a predator for a prey item. Scallops in the second model were assumed to be randomly distributed in each study site as in the first model (hereafter called the "basic model"), but have a size (radius) that included a detection zone corresponding to the area of a cluster (a.k.a. the area of a frame = 1.44 m^2, radius = 0.677 m^2).

Mean expected density of tethered scallops alive or dying from sea star or crab predation after 24 h were calculated for each predator assemblage (over sites, seasons and years) and each model. For each parameter, the observed mean and standard error (Table 3.2) were used to define the parameter's sampling distribution (Evans et al. 1993). Parameters that represent proportions or probabilities (T, P[attack|enc], etc.) were described by a beta distribution, which is bound between 0 and 1; parameters restricted to non-negative values ($V_{predator}$, $r_{predator}$, r_{prey}, h, etc.) were described by a gamma distribution, which has a lower bound at 0. At the beginning of each simulation, a value was randomly selected for each parameter from its sampling distribution. A total of 200 simulations of each predator assemblage were run using MATLAB, MathWorks, Inc. The standard deviation (which is a standard error since inputted information were means ± SE) was then calculated from the distribution of outputs and converted to 95% confidence interval (Zar 1984, p. 103). The means and 95% confidence intervals of the predicted data and observed values were then compared.

Finally, to help tease apart whether predators were attracted or not to the clusters (frames) of tethered scallops, we calculated the probability of predators not encountering a frame when they were moving in a random fashion, and compared this to the fraction of frames with no mortality. This allowed us to assess if scallop clusters had modified the random searching movement of predators to a directed movement (attraction effect). If the calculated probability is equal to or less than the observed fraction (indicating a number of attacks equal to or less than expected), then predators were not attracted to clusters (and likely moved in a random fashion). If the calculated probability is greater than the observed fraction (indicating higher attacks than expected), then predators may have been attracted to clusters.

The equation to estimate the encounter rate of each predator species with a frame (E_{fm}) was slightly modified from the predator-scallop encounter equation shown in Chapter 2 (Eq. 2.2):

$$E_{fm} = \left[2 \cdot \left(V_{predator\_m}\right) \cdot S_m \cdot \left(r_{predator\_m} + r_{frame}\right) + \pi \cdot \left(r_{predator\_m} + r_{frame}\right)^2\right] \cdot M_m \,,$$

Equation 3.1

where $V_{predator}$ is searching velocity of predator species m, $r_{predator}$ is radius of predator species m, r_{frame} is radius of frame ($\sqrt{1.44\text{cm}^2 / \pi}$), and M is density of predator species m.

Then, the probability that a frame was not encountered by a predator was based on the Poisson distribution and estimated as below:

$$\mathrm{P}[\text{no enc frame}] = \exp\left(-\left(E_{fAv} + E_{fLp} + E_{fCp} + E_{fCi} + E_{fHa}\right)\right), \qquad \text{Equation 3.2}$$

where *Av*, *Lp*, *Cp*, *Ci* and *Ha* are the different predator species.

Table 3.2. Parameter estimates (mean ± SE) used in the predation model.

Parameter	*A. vulgaris*	*L. polaris*	*C. papposus*	*C. irroratus*	*H. araneus*
Velocity (cm/min)	1.10 ± 0.10 [1]	3.87 ± 1.10 [2]	3.83 ± 0.12 [3]	66.60 ± 19.10 [1]	114.43 ± 11.90 [2]
Foraging time (d)	0.30 ± 0.04 [1]	0.14 ± 0.05 [2]	0.26 ± 0.09 [3]	0.08 ± 0.02 [1]	0.05± 0.03 [2]
Prey handling time (min)	132.45 ± 16.79 [1]	132.45 ± 16.79 [1]	132.45 ± 16.79 [1]	9.30 ± 1.87 [1]	9.30 ± 1.87 [1]
P[attack|encounter]	1.0 [2]	0.64 ± 0.17 [2]	1.0 [3]	N/A	N/A
P[capture|attack]	0.13 ± 0.07 [2]	0.25 ± 0.19 [2]	0.5 [3]	N/A	N/A
P[capture|encounter]	N/A	N/A	N/A	0.82 ± 0.18 [2]	0.66 ± 0.18 [2]
P[consumption|capture]	1.0 [2]	0.50 ± 0.29 [2]	1.0 [3]	0.70 ± 0.20 [2]	0.17 ± 0.08 [2]

1- Barbeau and Caswell 1999; 2- Chapter 2; 3- Nadeau (unpublished data). Movement velocity, foraging time and prey handling time are dependent on temperature; water temperature was 10.7°C in Barbeau's laboratory and 12.5 °C in Nadeau's laboratory. For the probabilities, *P*[A|B] is the probability of behaviour A conditional on behaviour B.

3.3 Results

3.3.1 The 2003 study

3.3.1.1 Predator assemblage

In 2003, sea stars *A. vulgaris* were the most abundant predators on studied sites with an overall mean (± SE) density of 0.15 ± 0.02 ind. · m^{-2} (Fig. 3.5). The other two sea stars *L. polaris* and *C. papposus* and the crab *C. irroratus* showed lower overall densities (<0.01 ind. · m^{-2} each). The crab *H. araneus* had very low densities (0.0007 ± 0.0002 ind. · m^{-2}), so it was not included in the statistical analysis. The predator assemblage revealed a seasonal variation, as spring was significantly different from other nominal seasons (Table 3.3). This variation was mainly due to *A. vulgaris* and *C. irroratus* densities (based on the absolute values of the canonical coefficients) and these two species were seasonally negatively correlated to each other (based on the different signs of the canonical coefficients): *A. vulgaris* density decreased with season, whereas *C. irroratus* increased (Fig. 3.5). A significant site effect on predator assemblage was also detected, and *A. vulgaris* density was mainly associated to this spatial variation (Fig. 3.5, Table 3.3). Furthermore, the four predator species were spatially positively correlated. According to the variance components analysis, spatial variability at the scale of sites accounted for 25 to 37% of the random variation for all four predator species (Table 3.4); spatial variation was most important at the scale of sampling sequences (error term, 62 to 75%).

Sea stars *A. vulgaris* displayed an overall mean size of 5.5 ± 0.1 cm radius. Significant seasonal variation was detected in size measurements as *A. vulgaris* were larger in fall (6.3 ± 0.4 cm) than in winter (5.2 ± 0.8 cm) and in spring (5.4 ± 0.9 cm) (Fig. 3.6, Table 3.5). Spatial variation was also significant and the site effect accounted for 30% of the random variation (Table 3.5). Variation at smaller scale, among sampling sequences, was however more important (67%), indicating that different cohorts of *A. vulgaris* can co-occur at this scale.

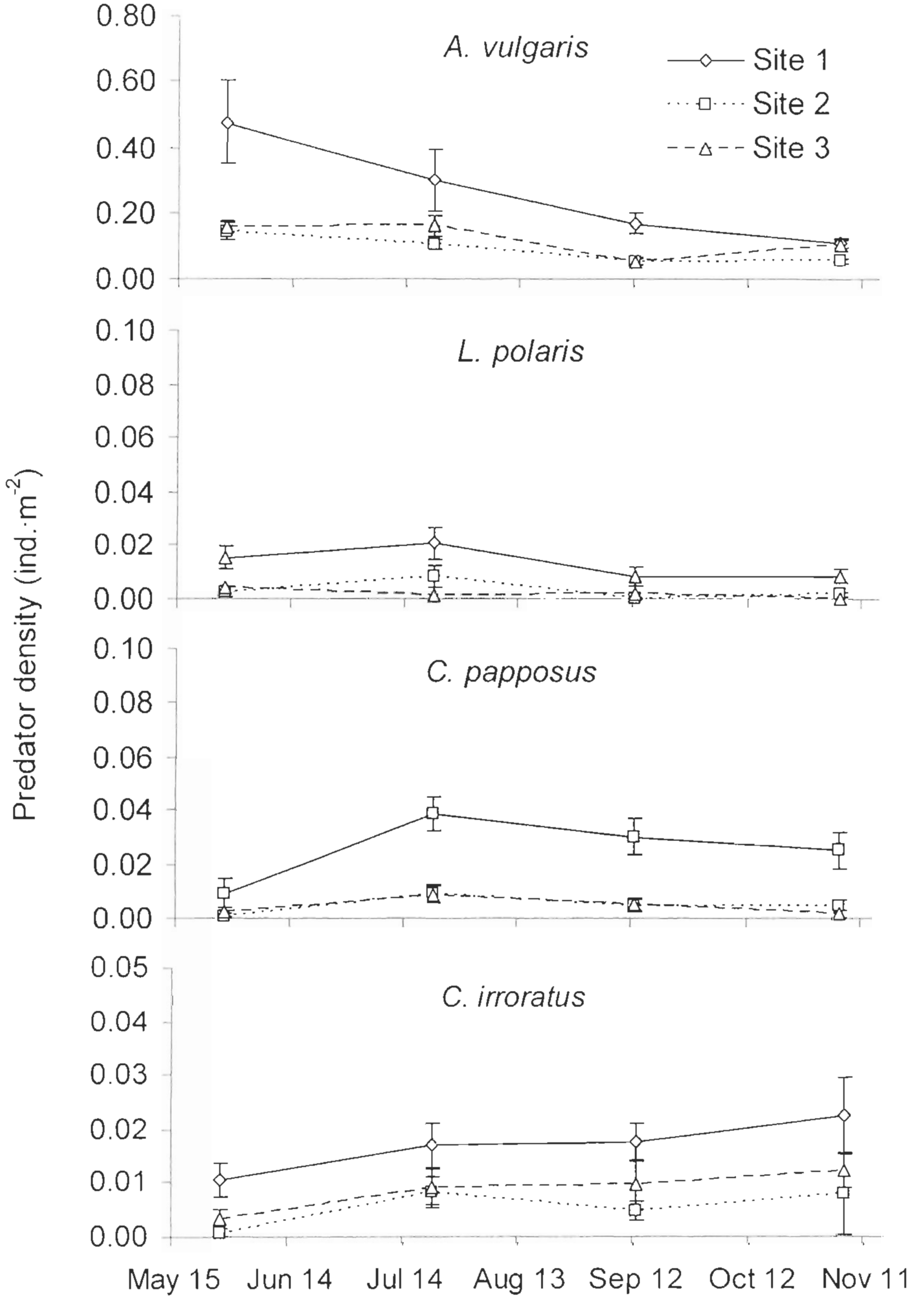

Figure 3.5. Mean densities (± SE, n = 10) of four predator species at 4 times and 3 sites in 2003.

Table 3.3. Results of mixed-model MANOVAs on densities (ind.· m^{-2}) of predators in 2003 and in 2004-05. Data were transformed using $\log_{10}$(datum+0.01). Orthogonal planned comparisons between nominal seasons were performed when Season (fixed factor) was significant. Significant differences ($p<0.05$) are indicated in bold. Standardized canonical coefficients were calculated for significant sources of variation and important canonical coefficients are also indicated in bold.

Year	Source of variation	df1, df2	F	*p*	Canonical coefficients			
					Av	*Lp*	*Cp*	*Ci*
2003	Season	12, 15	4.68	**0.003**	**4.74**	1.94	1.30	**-6.50**
	Spring vs. Summer	*4, 3*	*43.93*	***0.005***				
	Fall vs. Winter	*4, 3*	*2.66*	*0.224*				
	Spring vs. Fall	*4, 3*	*195.49*	***<0.001***				
	Site	8, 212	10.57	**<0.001**	**0.77**	0.41	0.49	0.45
	Season*Site	24, 432	1.07	0.371				
2004-05	Season	24, 48	1.31	0.207				
	Site	8, 276	31.33	**<0.001**	**1.74**	-0.28	-0.41	0.005
	Season*Site	48, 560	1.59	**0.009**	**1.69**	0.26	-0.19	-0.24

Av: A. vulgaris; Lp: L. polaris; Cp: C. papposus; Ci: C. irroratus

Table 3.4. Variance components when at least one random source of variation was significant in the mixed-model ANOVAs on densities (ind.· m^{-2}) of predators in 2003 and in 2004-05. Data were transformed using $\log_{10}$(datum+0.01). No values are presented for *C. irroratus* in 2004-05 as the random sources of variation were not significant.

Dependant variable	Source of variation		2003		2004-05	
			Estimate	%	Estimate	%
A. vulgaris density	Site	σ^2_S	0.039	35.3	0.512	65.4
	Season*Site	σ^2_{SS}	0.002	1.6	0.063	8.0
	Error	σ^2_e	0.069	63.1	0.208	26.6
L. polaris density	Site	σ^2_S	0.139	37.1	0.116	28.7
	Season*Site	σ^2_{SS}	0.003	0.7	0.000	0.0
	Error	σ^2_e	0.233	62.2	0.289	71.3
C. papposus density	Site	σ^2_S	0.162	33.2	0.061	16.3
	Season*Site	σ^2_{SS}	0.007	1.4	0.008	2.3
	Error	σ^2_e	0.319	65.4	0.303	81.4
C. irroratus density	Site	σ^2_S	0.094	25.2		
	Season*Site	σ^2_{SS}	0.000	0.0		
	Error	σ^2_e	0.279	74.8		

Both *L. polaris* and *C. papposus* were the largest sea stars, and were 9.5 ± 0.3 cm and 7.1 ± 0.1 cm in overall mean radius, respectively. Contrary to *L. polaris*, *C. papposus* showed significant seasonal variation as they were larger in spring (7.6 ± 0.3 cm) than in summer (5.7 ± 0.3 cm) and larger in fall (7.8 ± 0.2 cm) than in winter (6.9 ± 0.2 cm) (Fig. 3.7, Table 3.5). Crabs *C. irroratus* had an overall mean size of 9.5 ± 0.2 cm carapace width, and their size was significantly larger in fall (11.0 ± 0.4 cm) than in winter (9.2 ± 0.3 cm). The few crabs *H. araneus* observed had an overall mean size of 8.1 ± 0.8 cm carapace length.

3.3.1.2 Predation potential

In 2003, 87.0 ± 3.2 % of tethered scallops were still alive after an immersion of 24 h (Fig. 3.8), and most of the dead scallops (87%) were attributed to sea star predation. No seasonal pattern was detected for the proportion of tethered scallops surviving or for the proportion of scallops dying from sea star or crab predation (Tables 3.6 and 3.7). However, spatial variation in the form of a significant site effect and interaction between season and site was detected, and sea star predation contributed most to these effects (Table 3.7). Furthermore, sea star and crab predation were spatially negatively correlated. Variance component analysis indicated that most of the random variation in survival was attributed to variation between frames (error term, 65%), and to a lesser extent to the interaction between season and site (28%).

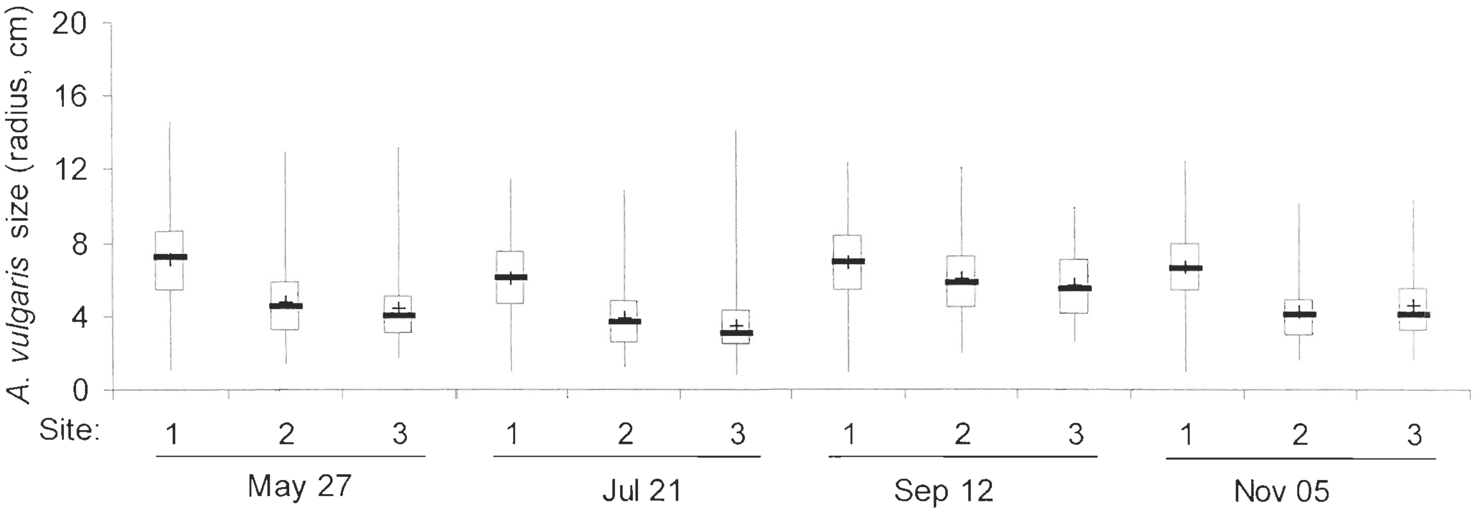

Figure 3.6. Box plots of sea stars *A. vulgaris* sizes at 4 times and 3 sites in 2003 (+: mean; horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values).

Table 3.5. Results of mixed-model ANOVAs on predator sizes (cm) in 2003. Abundances of *A. vulgaris* at different sites were high enough to enable us to conduct a full analysis with Season as a fixed factor and Site as a random factor. Orthogonal planned comparisons between nominal seasons were performed when Season was significant. Significant differences (*p*<0.05) are indicated in bold. Variance components are provided when random sources of variation are significant.

Dependant Variable	**Source of variation**	df	MS	F	*p*	Variance components		
							Estimate	%
A. vulgaris size	**Season**	3	261.545	6.98	**0.022**			
	Spring vs. Summer	*1*	*168.301*	*4.49*	*0.078*			
	Fall vs. Winter	*1*	*276.865*	*7.39*	***0.035***			
	Spring vs. Fall	*1*	*384.904*	*10.27*	***0.019***			
	Site	2	1044.945	181.15	**<0.001**	σ^2_S	2.59	29.8
	Season*Site	6	37.469	6.50	**<0.001**	σ^2_{SS}	0.32	3.6
	Error	3309	5.768			σ^2_e	5.77	66.5
L. polaris size	**Season**	3	15.274	1.85	0.144			
	Error	96	8.278					
C. papposus size	**Season**	3	50.464	10.55	**<0.001**			
	Spring vs. Summer	*1*	*112.942*	*23.62*	***<0.001***			
	Fall vs. Winter	*1*	*24.848*	*5.20*	***0.023***			
	Spring vs. Fall	*1*	*1.988*	*0.42*	*0.520*			
	Error	256	4.781					
C. irroratus size	**Season**	3	36.018	7.69	**<0.001**			
	Spring vs. Summer	*1*	*7.489*	*1.60*	*0.208*			
	Fall vs. Winter	*1*	*77.139*	*16.48*	***<0.001***			
	Spring vs. Fall	*1*	*7.684*	*1.64*	*0.202*			
	Error	146	4.681					

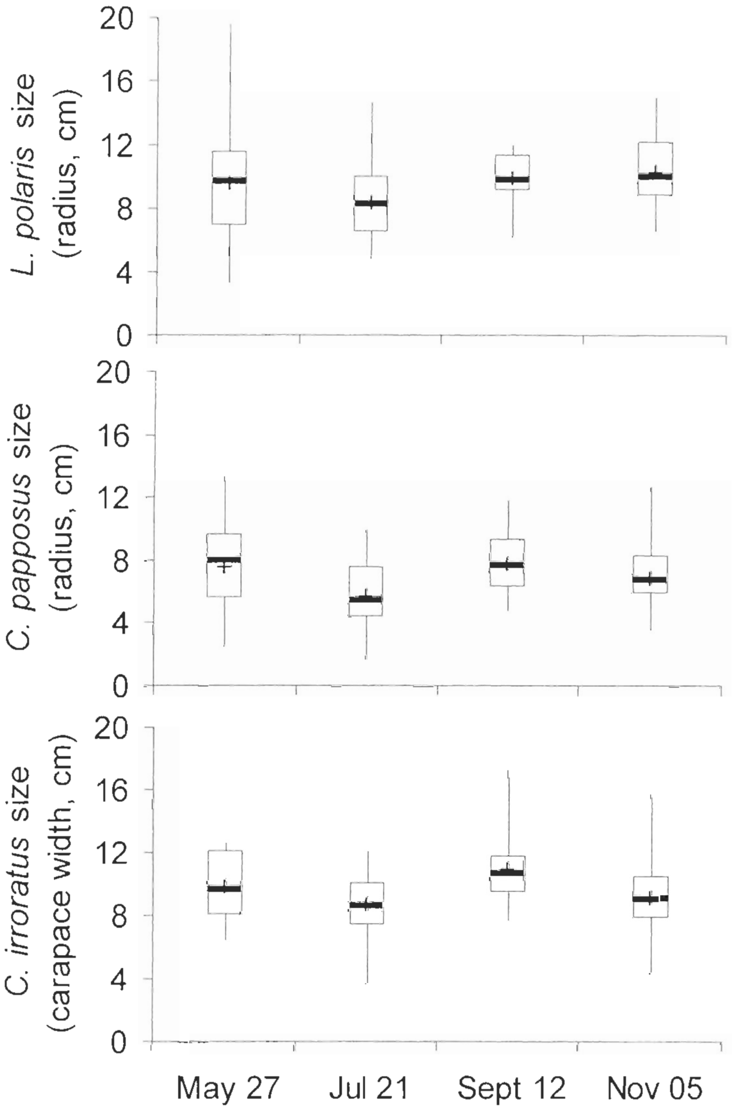

Figure 3.7. Box plots of sea stars *L. polaris*, *C. papposus* and crabs *C. irroratus* sizes at 4 times in 2003 (+: mean; horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values). Data are pooled over sites.

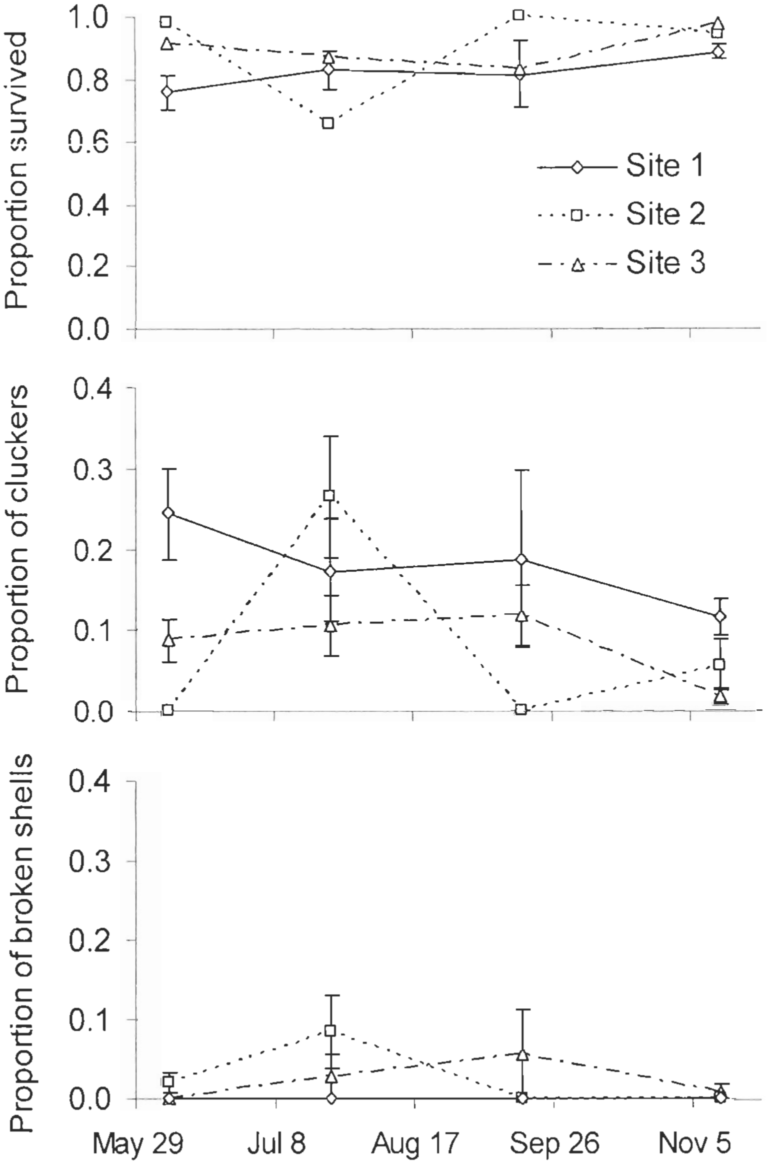

Figure 3.8. Proportion (mean ± SE, n = 6) of deployed tethered scallops that survived after 24 h or died from predation by sea stars (cluckers) and crabs (broken shells), at 4 times and 3 sites in 2003.

Table 3.6. Results of mixed-model ANOVAs on proportion of tethered scallops surviving in 2003 and in 2004-05. Data from 2003 were transformed using arcsin-square root. Planned comparisons between nominal seasons were performed when Season (fixed factor) was significant. Significant differences (*p*<0.05) are indicated in bold. Variance components are provided when at least one random source of variation is significant.

Year	Source of variation	df	MS	F	*p*	Variance components		
							Estimate	%
2003	Season	3	0.159	0.86	0.512			
	Site	2	0.184	3.60	**0.034**	σ^2_S	0.006	7.0
	Season*Site	6	0.185	3.63	**0.004**	σ^2_{SS}	0.022	28.3
	Error	57	0.051			σ^2_e	0.051	64.7
2004-05	Season	6	0.024	6.31	**0.003**			
	Springs	*1*	*0.0002*	*0.05*	*0.824*			
	Summers	*1*	*0.002*	*0.47*	*0.497*			
	Falls	*1*	*0.00004*	*0.01*	*0.929*			
	Springs vs. Falls	*1*	*0.008*	*1.67*	*0.201*			
	Summers vs. Falls	*1*	*0.010*	*2.15*	*0.148*			
	Summer vs. Winter 05	*1*	*0.025*	*5.57*	***0.021***			
	Site	2	0.018	4.03	**0.023**	σ^2_S	0.001	9.8
	Season*Site	12	0.004	0.83	0.616	σ^2_{SS}	0	0
	Error	63	0.005			σ^2_e	0.005	90.2

Table 3.7. Results of MANOVAs on the proportion of tethered scallops that died due to sea star (cluckers) and crab (broken shells) predation in 2003 and in 2004-05. Data from 2003 and 2004-05 were transformed using $\log_{10}(\text{datum}+0.01)$. Significant differences ($p<0.05$) are indicated in bold. Standardized canonical coefficients were calculated for significant sources of variation and important canonical coefficients are also indicated in bold.

Year	Source of variation	df1, df2	F	*p*	Canonical coefficients	
					Cluckers	Broken shells
2003	Season	6, 12	0.56	0.756		
	Site	4, 114	4.93	**0.001**	**1.11**	-0.57
	Season*Site	12, 114	2.56	**0.005**	**1.28**	-0.15
2004-05	Season	12, 24	2.06	0.064		
	Site	4, 126	2.86	**0.026**	**1.00**	0.72
	Season*Site	24, 126	1.04	0.418		

3.3.2 The 2004-05 study

3.3.2.1 Predator assemblage

In 2004-05, sea stars *A. vulgaris* remained the most abundant predator (0.11 ± 0.01 ind. · m^{-2}; Fig. 3.9). Overall mean densities of sea stars *L. polaris* and *C. papposus*, and crabs *C. irroratus* were between 0.01 and 0.03 ind. · m^{-2}. Again, only few crabs *H. araneus* were counted (0.002 ± 0.001 ind. · m^{-2}) and so not included in further statistical analysis. The predator assemblage did not show a significant temporal variation, even if peaks of densities tended to occur in fall for both years (Fig. 3.9, Table 3.3). However, the assemblage was significantly affected by site and interaction between season and site. The canonical coefficients showed that this was mostly attributed to *A. vulgaris* densities. Also, *A. vulgaris* was often spatially negatively correlated to other predators, indicating that some sites had relatively high densities of *A. vulgaris* and low densities of the other three species, and vice versa. In the variance components analysis, variation in *A. vulgaris* density at the scale of sites accounted for most of the random variation (65%). This is different than in 2003 and than for the two sea stars *L. polaris* and *C. papposus* in all years, where variation at the scale of sampling sequences was most important (Table 3.4).

Sea stars *A. vulgaris* showed an overall mean size of 3.5 ± 0.1 cm radius and, as in 2003, *L. polaris* and *C. papposus* were the largest sea stars (9.5 ± 0.1 and 7.1 ± 0.1 cm, respectively, Fig. 3.10). Crabs *C. irroratus* and *H. araneus* measured 8.8 ± 0.2 cm (carapace width) and 5.1 ± 0.4 cm (carapace length), respectively. Temporally, sea star sizes (but not crab sizes) showed significant variation (Table 3.8). Among years, *L. polaris* were clearly smaller in 2004 than in 2005. However *A. vulgaris* were larger in 2004 during summer and fall but smaller in winter. *C. papposus* were also smaller in winter 2004, otherwise they showed similar sizes. Among seasons, *A. vulgaris* were larger in summer than in fall and *L. polaris* were larger in summer than in winter. No temporal variation was detected for *C. irroratus* size measurements.

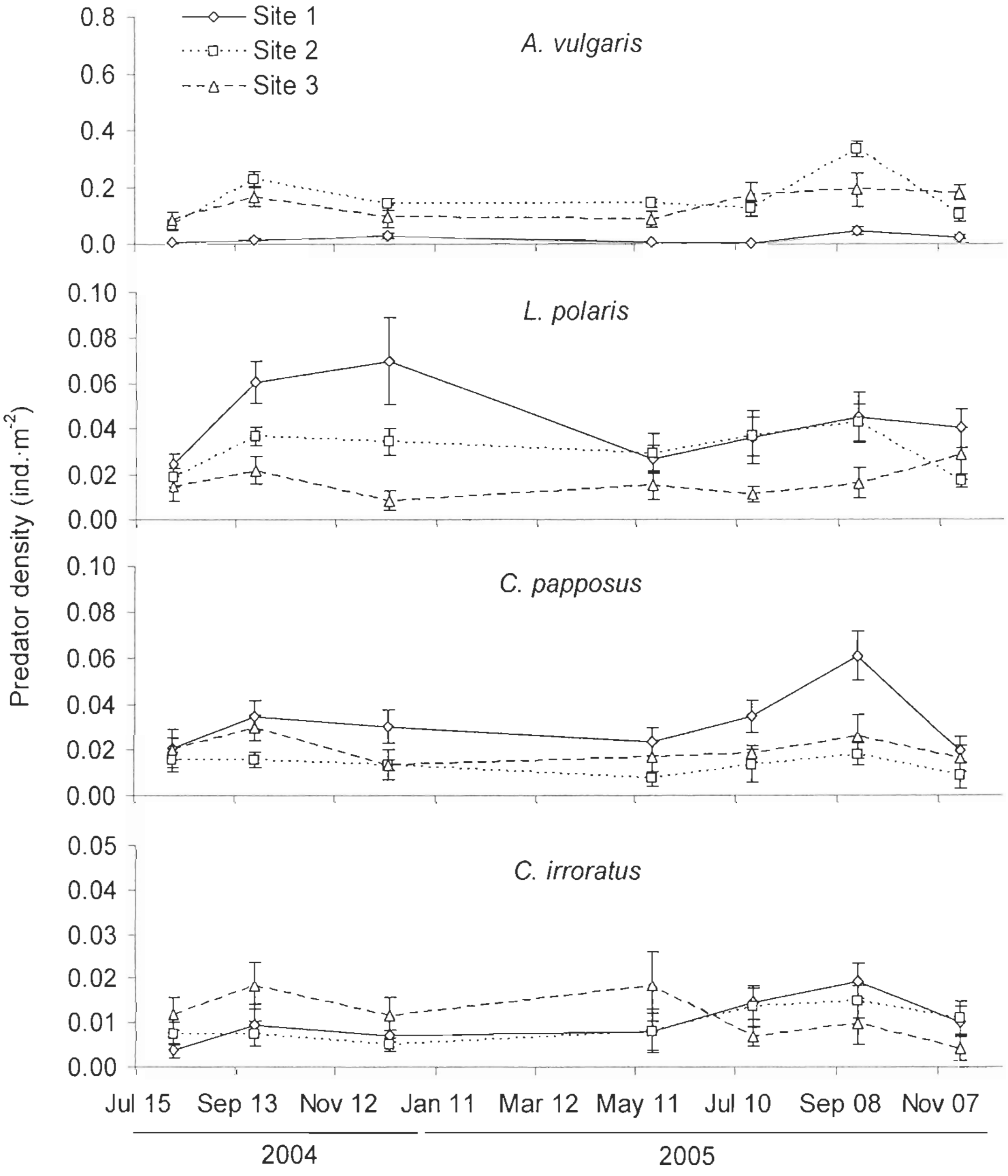

Figure 3.9. Mean densities (± SE, n = 8) of four predator species at 7 times and 3 sites in 2004-05.

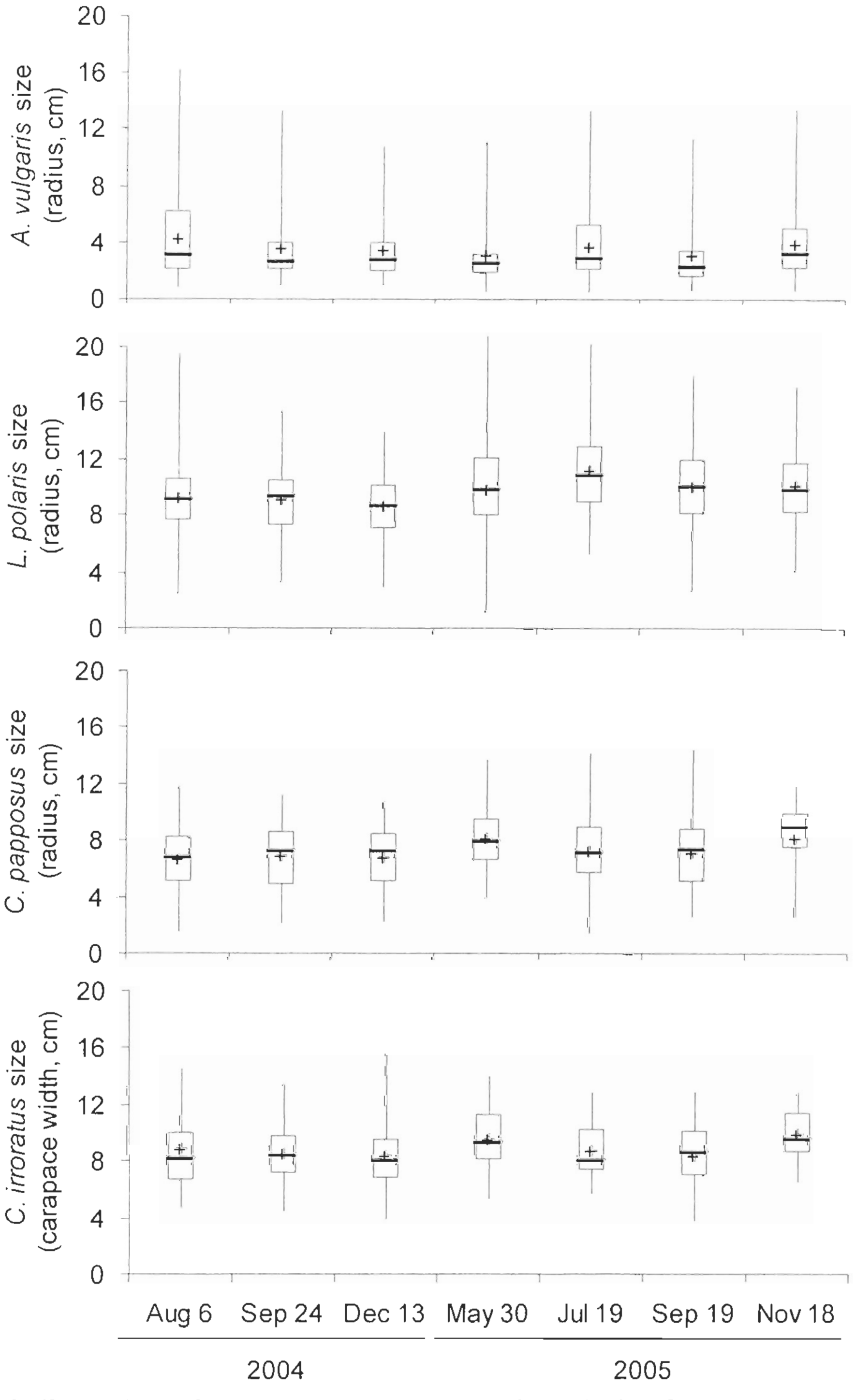

Figure 3.10. Box plot of sea stars *A. vulgaris*, *L. polaris*, *C. papposus* and crabs *C. irroratus* sizes at 7 times in 2004 and 2005 (+: mean; horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values). Data are pooled over sites.

Table 3.8. Results of ANOVAs on predator sizes (cm) estimated in 2004 and 2005. Planned comparisons between nominal seasons were performed when Season (fixed factor) was significant. Significant differences ($p<0.05$) are indicated in bold.

Dependant variable	Source of variation	df	MS	F	*p*
A. vulgaris size	Season	6	40.088	7.35	**<0.001**
	Summers	*1*	*28.485*	*5.22*	***0.022***
	Falls	*1*	*39.914*	*7.32*	***0.007***
	Winters	*1*	*31.037*	*5.69*	***0.017***
	Spring vs. Fall 05	*1*	*0.010*	*0.00*	*0.965*
	Summers vs. Falls	*1*	*111.511*	*20.45*	***<0.001***
	Summers vs. Winters	*1*	*13.660*	*2.51*	*0.433*
	Error	1710	5.453		
L. polaris size	Season	6	47.376	5.99	**<0.001**
	Summers	*1*	*110.207*	*13.93*	***0.002***
	Falls	*1*	*42.314*	*5.35*	***0.021***
	Winters	*1*	*76.9426*	*0.72*	***0.002***
	Spring vs. Fall 05	*1*	*1.513*	*0.19*	*0.662*
	Summers vs. Falls	*1*	*30.058*	*3.80*	*0.052*
	Summers vs. Winters	*1*	*47.641*	*6.02*	***0.015***
	Error	499	7.912		
C. papposus size	Season	6	15.309	2.47	**0.024**
	Summers	*1*	*12.488*	*2.01*	*0.157*
	Falls	*1*	*2.020*	*0.33*	*0.569*
	Winters	*1*	*33.693*	*5.43*	***0.020***
	Spring vs. Fall 05	*1*	*20.552*	*3.31*	*0.070*
	Summers vs. Falls	*1*	*0.0744*	*0.01*	*0.913*
	Summers vs. Winters	*1*	*13.387*	*2.16*	*0.143*
	Error	355	6.21		
C. irroratus size	Season	6	6.207	1.24	0.291
	Error	160	5.026		

3.3.2.2 Predation potential

In 2004-05, 93.7 ± 4.4% of tethered scallops were alive after 24 hours (Fig. 3.11) and most of the predation was associated to sea stars (75%). The only significant temporal difference occurred in 2005 when survival was higher in summer than in winter (Tables 3.6 and 3.7). A significant spatial variation was detected. As in 2003, sea star predation contributed most to this effect (Table 3.7) but, in contrast to 2003, sea star and crab predation were spatially positively correlated. Variance components analysis indicated that most (90%) of the random variation was attributed to the experimental units (the stations; Table 3.6), and only 10% was attributed to sites.

3.3.3 Relationship between multiple predator assemblages and scallop predation

Sea star density and *A. vulgaris* size were significantly and positively correlated to the proportion of cluckers (Table 3.9). However, no association was detected between crab density or *C. irroratus* size and the proportion of broken shells. As well there was no association between multiple predator assemblages and predation potential, as sea star characteristics did not correlate with proportion of broken shells, nor did crab characteristics with proportion of cluckers. Surprisingly, temperature was negatively correlated with proportion of cluckers. Other significant associations included negative correlations between sea star density and crab size, and between crab density and sea star size.

The two models (without and with a detection zone around scallops) used to simulate the scallop predation showed moderate agreement with observed values (Fig. 3.12 and 3.13). For 2003, there was a relatively low concordance at Site 1, where the observed values of sea star predation were regularly higher than those predicted by both models (Fig. 3.12). Overall for 2003, means and confidence intervals for sea star predation expected from the basic model and the model with the detection zone were respectively 75 and 92% superimposed. For sea stars, the use of a detection zone appeared to better estimate observed predation. For crabs, expected crab predation using the basic model was more in the range of observed predation (100% of concordance based on CI) than that using the model with a detection zone (50% concordance).

For 2004 and 2005, model predictions of scallop predation were closer to observed predation than for 2003. Expected predation by sea stars and crabs, estimated from the basic model, were 100% inside the 95% CI of observed predation (Fig. 3.13). The model with a detection zone predicted 55 and 75% of the observed sea star and crab predation, respectively; the expected values that were not within the CI of observed predation were always higher.

Finally, the calculated probability that frames were not encountered by predators was 29% in 2003 and 21% in 2004-05 which was lower or equal to the observed fraction of frames with no scallop mortality in both studied years (35% in 2003 and 24% in 2004-05). Thus, these results suggest that predators displayed a random searching displacement before encountering frames.

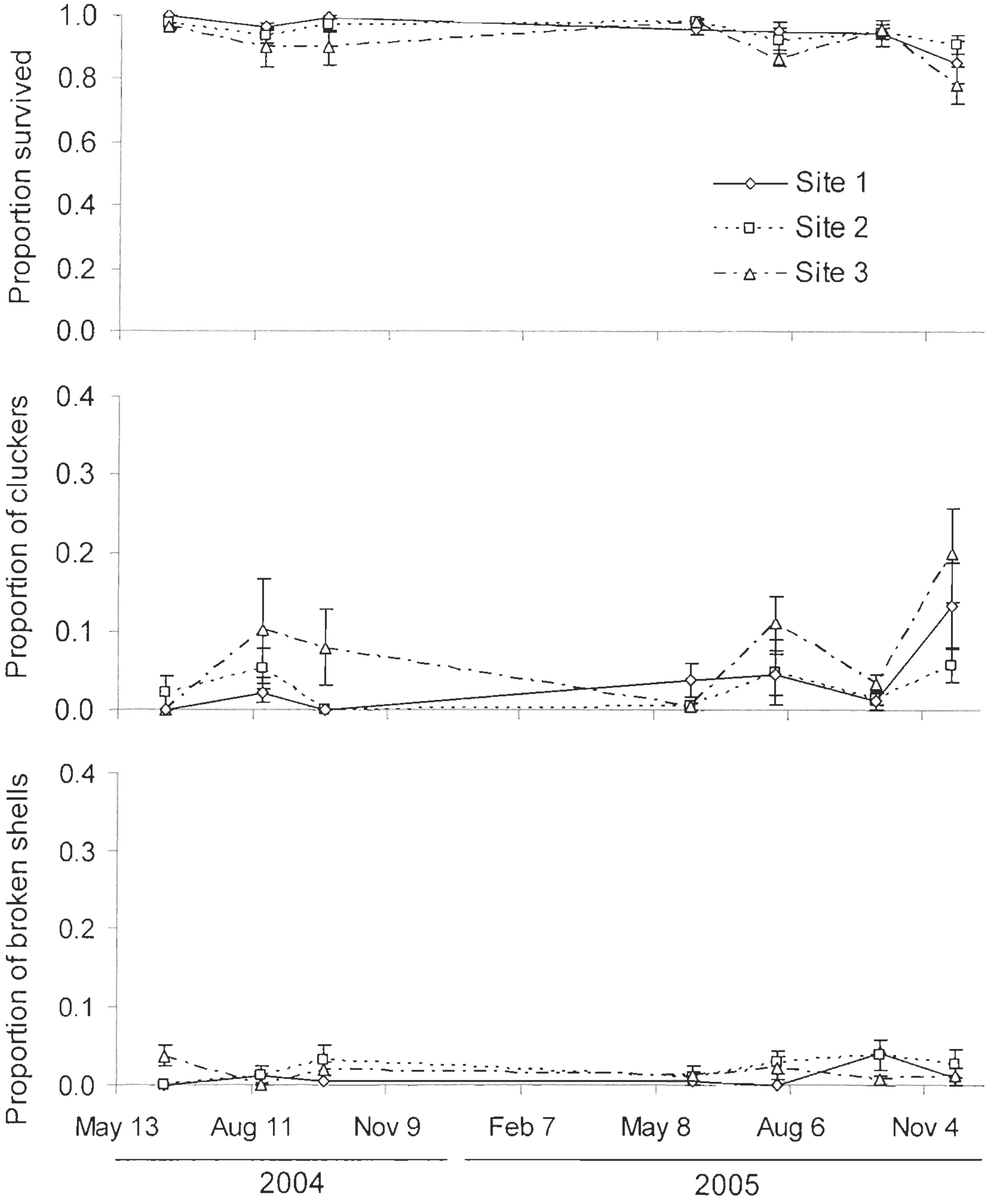

Figure 3.11. Mean proportions (± SE, n = 4) of deployed tethered scallops that survived after 24 h or died from predation by sea stars (cluckers) and crabs (broken shells), at 7 times and 3 sites in 2004 and 2005.

Table 3.9. Correlation among variables that can influence predation on scallops by sea stars (cluckers) and crabs (broken shells). Data from 2003, 2004 and 2005 were pooled for each analysis (n=31-35). Pearson's coefficient and p-value (in italics) are provided. Significant differences ($p<0.05$) are indicated in bold.

	Sea star[1] density	Crab[1] density	Sea star[2] size	Crab[2] size	Survived[3]	Cluckers[3]	Broken shells[3]
Crab[1] density	-0.10						
	0.580						
Sea star[2] size	0.09	-0.40					
	0.610	***0.023***					
Crab[2] size	-0.51	-0.13	0.38				
	<0.001	*0.466*	***0.033***				
Survived[3]	-0.37	0.17	-0.39	-0.01			
	0.035	*0.354*	***0.038***	*0.977*			
Cluckers[3]	0.41	-0.20	0.51	0.01	-0.97		
	0.020	*0.269*	***0.005***	*0.964*	***<0.001***		
Broken shells[3]	-0.03	0.07	-0.35	-0.01	-0.37	0.14	
	0.878	*0.681*	*0.066*	*0.977*	***0.037***	*0.442*	
Temperature[4]	-0.20	-0.05	-0.05	-0.05	0.34	-0.37	0.06
	0.253	*0.771*	*0.781*	*0.777*	*0.060*	***0.036***	*0.756*

1- Density pooled over species; 2- Sizes are for *A. vulgaris* or *C. irroratus* only; 3- for tethered scallops; 4-Water temperature near the sea bed

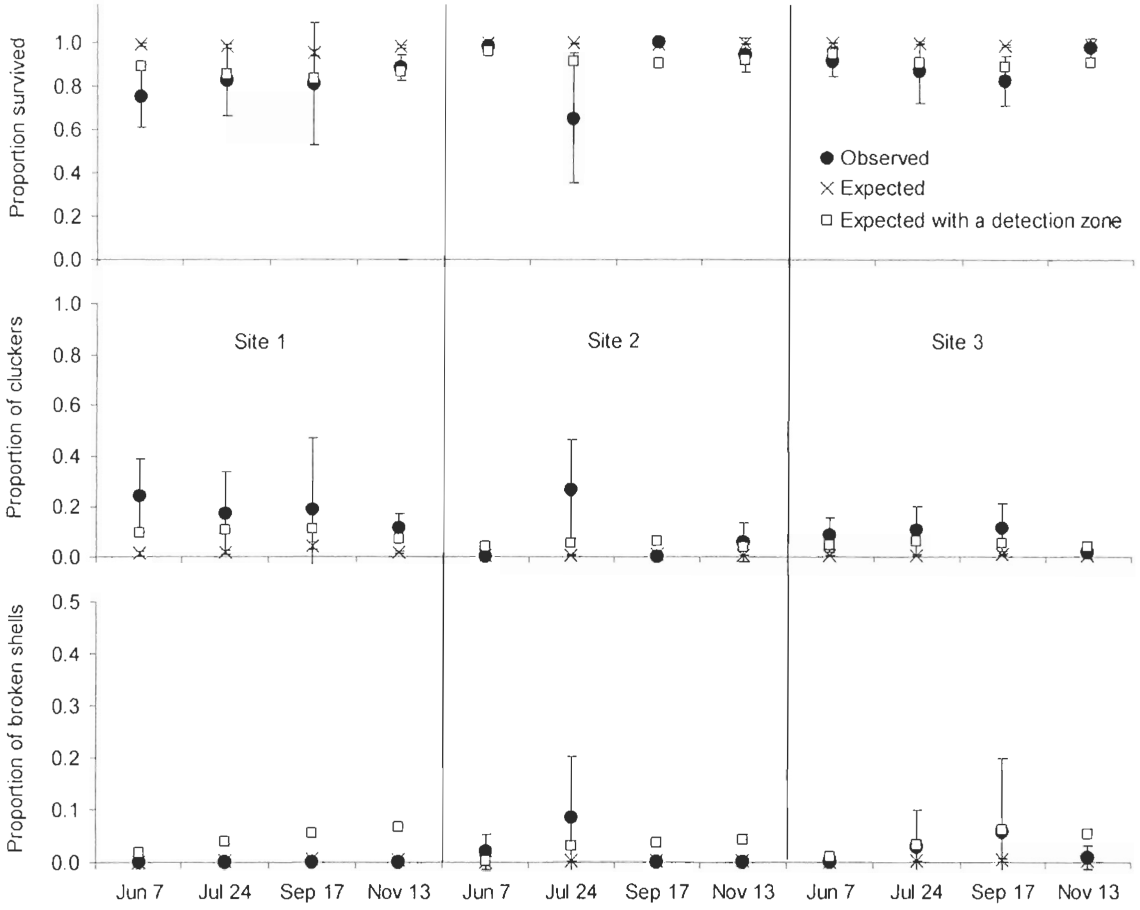

Figure 3.12. Comparison of observed proportion of tethered scallops (mean ± 95% CI) that survived and died from predation by sea stars (cluckers) and crabs (broken shells) after 24 h in 2003, and expected predation (mean ± 95% CI, confidence intervals are small so are not visible) from the basic model and the model with a detection zone around scallops.

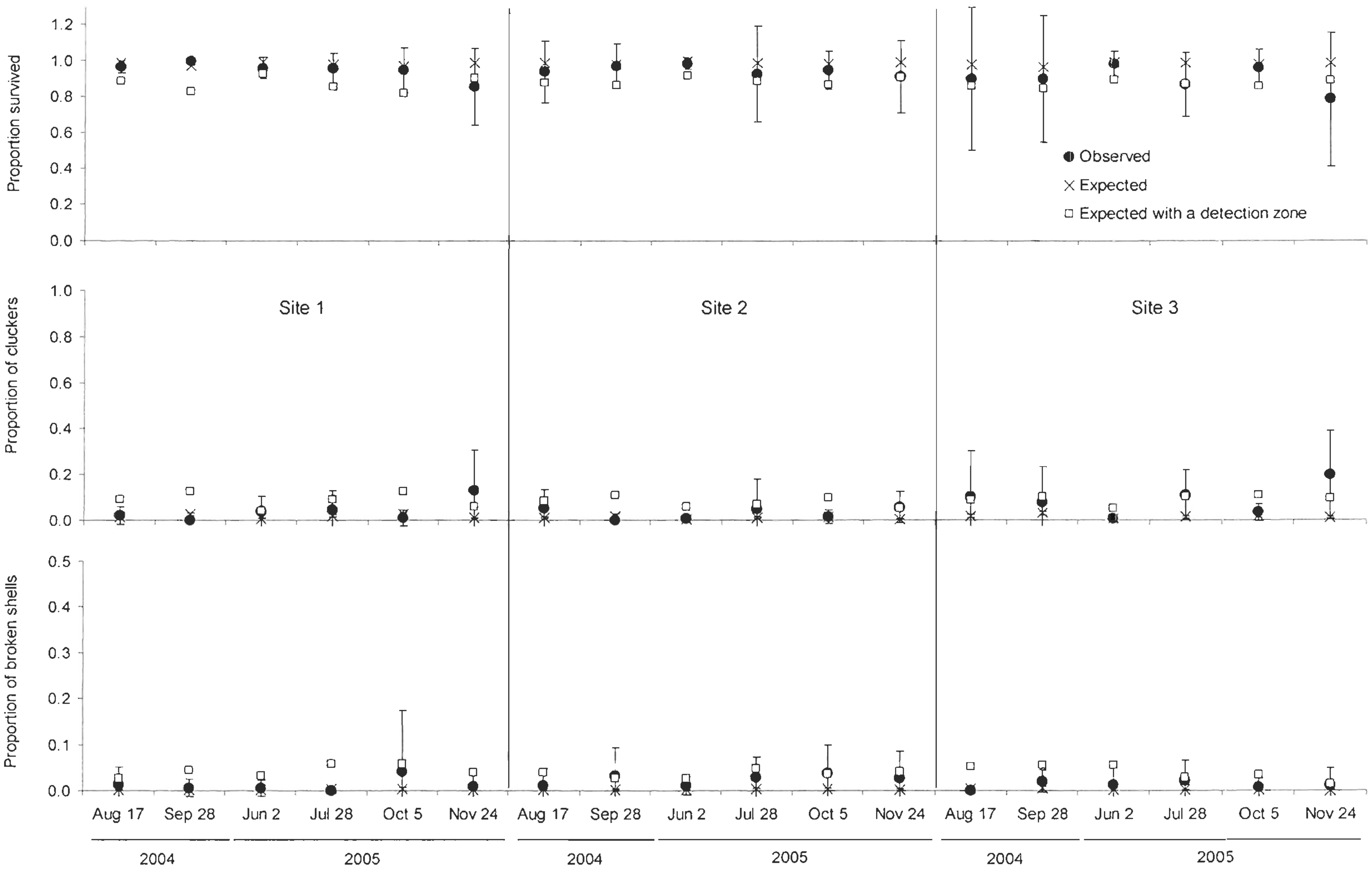

Figure 3.13. Observed proportion of tethered scallops (mean ± 95% CI) that survived and died from predation by sea stars (cluckers) and crabs (broken shells) after 24 h in 2004-05 compared to expected predation (mean ± 95% CI, confidence intervals are small so are not visible) from the basic model and the model with a detection zone around scallops.

3.4 Discussion

Our study used an alternative way to investigate predation in a multiple predator context, in natural conditions and on a seasonal basis. Predation studies of multiple predator effects are generally performed in laboratory or using enclosures in the field (Sih et al. 1998). Such set-ups enable clear comparison and collection of useful behavioural data on predators alone or in combination with conspecifics or other predator species. However, these experiments are restricted to small scales and to only a few factors studied concurrently. Our large-scale field study did not have these restrictions. In addition, the decision to use multivariate analysis (MANOVA) allowed us to characterize the whole predator assemblage instead of one predator species at a time. It also improved assessment of the contribution of each predator species to the system and of possible interspecific interactions (Quinn & Keough 2002; Tabachnick & Fidell 2007).

3.4.1 Predator assemblages

Although our study detected some temporal variation, it did not detect any large and consistent seasonal fluctuations in predator assemblage off the Îles de la Madeleine. The benthic predator assemblage was mainly composed of three sea star species (*A. vulgaris*, *L. polaris* and *C. papposus*) and two crab species (*C. irroratus* and *H. araneus*). This is similar to the faunal assemblage that co-occurs with sea scallops on Georges Bank off the coast of Nova Scotia, Canada, and northeastern USA (Thouzeau et al. 1991), an area well known for its scallop fishery. Furthermore, as in our sites, Thouzeau et al. (1991) and Marino et al. (2009) identified a close association between sea scallops and its main predator, *A. vulgaris*, on Georges Bank.

Specifically in 2003, the predator assemblage showed a seasonal negative correlation between *A. vulgaris* and *C. irroratus* densities, which may be explained by seasonal displacements. In the western Atlantic from Nova Scotia to Cape Hatteras, *C. irroratus* migrates from depths as low as 500 m to shallow inshore areas (<40 m) in October to April (Stehlik et al. 1991), and returns on deeper areas in spring when the water warms up.

Apparently, crab migration is mainly related to temperature and substrate type (Krouse 1976; Stehlik et al. 1991; Gendron & Cyr 1994). According to our results, such gradual crab migration offshore of the Îles de la Madeleine until mid-November can be suspected. However, the gradual decrease of *A. vulgaris* densities over the seasons is unexplained. In the northern Gulf of St-Lawrence, strong waves and ice abrasion in winter may cause sea stars to move to deeper water (Gaymer et al. 2001), and this may explain the highest density observed in spring. Other factors such as food attraction (Sloan 1980; Himmelman & Dutil 1991) or food depletion (Gaymer et al. 2001; Marino et al. 2009) may have influenced the change in distribution of *A. vulgaris* observed in our study.

The seasonal fluctuations in predator density and size observed in 2003 may also be related to recruitment events. For instance, according to Gemmil (1920) and Strathman (1987), *C. papposus* spawns during March and April, producing non-feeding lecithotrophic larvae. The development time to a 1 cm juvenile is about 47 days (Strathman 1987). This is consistent with our data where specimens as small as 1.5 cm were observed in mid-July to early August. For the crab *C. irroratus*, breeding occurs in fall in the southern Gulf of St Lawrence when females molt (Scarratt & Lowe 1972), and crab larvae appear from June to September. Off the coast of Maine, USA, *C. irroratus* hatch from their eggs in late spring and early summer (Krouse 1976), and young-of-the-year are observed in September through December. This timing is consistent with our observations, where peaks in density and smaller sizes of *C. irroratus* were recorded in late summer and fall.

In 2004-05, the predator assemblage did not have significant temporal fluctuations in density; rather a negative spatial correlation was denoted between the abundance of *A. vulgaris* and the abundance of *L. polaris* and *C. papposus*. The coexistence of these three sea star species (>15 cm in diameter) has been studied in the subtidal zone (8-11 m deep) of the northern Gulf of St Lawrence (Mingan Islands) (Gaymer et al. 2004), where *A. vulgaris* was documented to prey on *L. polaris*. *C. papposus* was also observed preying on *L. polaris*, *A. vulgaris* and conspecifics (see also Hancock 1958, 1974; Dutil 1988). Sloan (1980) observed in Puget Sound (USA) a discrete distribution of *A. rubens* (= *A. vulgaris*; Brunel et al. 1998) and *C. papposus*, mainly related to different recruitment strategies and heavy predation by *C. papposus* on newly settled *A. rubens*. Such interspecific interactions and recruitment strategies may partly explain the spatial segregation observed in our study (i.e., the spatial negative correlation between *C. papposus* and *A. vulgaris* densities or between *A. vulgaris* and *L. polaris* densities). The spatial distribution of these three sea stars species may also be related to their food preference. *A. vulgaris* mainly feeds on bivalves on or near the benthic surface, especially on rocky bottom, while *L. polaris* digs up and feeds on endobenthic bivalves (Gaymer et al. 2004). *C. papposus* is known as an aggressive and solitary species that is frequently observed preying on echinoderms (Mayo & Mackie 1976; Sloan 1980).

As observed in 2003, it is also plausible that small seasonal fluctuations in predator density and size in 2004-05 be related to recruitment. For *A. vulgaris*, no clear recruitment pattern was detected and small individuals occurred throughout surveys. These sea stars have a planktotrophic larval stage and, based on previous studies, water temperatures $\geq$ 15 °C are required to induce spawning (Galtsoff & Loosanoff 1939; Hancock 1958; Loosanoff 1964). Since the experimental sites never reached these temperatures (Fig. 3.3), it can be suspected that recruitment to local populations is from larvae produced in other regions. The other major sea star, *L. polaris*, is reported to brood its embryos from February through May in the northern Gulf of St. Lawrence (Himmelman et al. 1982). The reproductive period is likely that same off the Îles de la Madeleine, since we observed very few brooding individuals during our May to November camera surveys and the smallest *L. polaris* individuals were reported in spring.

3.4.2 Relationship between multiple predator assemblages and scallop predation

Assays using tethered scallops indicated that predation may have a significant impact on scallop survival: as much as 13% of scallops were estimated consumed after 24 hours in our 2003 study. Estimated predation potential was lower (7.3%) in 2004-05. In both our studies and based on shell remains, most of this predation was attributed to sea stars. However, no strong seasonal variation in predation potential was detected and so, it appears that the seasonal variation in predator assemblage observed in 2003 was not not closely linked to predation potential. Spatial variation, however, appears more important to explain patterns in predator assemblage and predation potential than temporal variation. For instance, our Site 1 in 2003 had relatively high sea stars density and was associated with the highest proportion of cluckers. Our Site 1 in 2004-05 had the lowest abundances of *A. vulgaris* and *C. irroratus*, as well as the lowest predation potential.

Thus, our hypothesis that predation potential would fluctuated seasonally was not supported by both our 2003 and 2004-05 studies, since the predation assays did not show clear seasonal variation in predator-related mortality. The relatively low water temperatures (<14 °C) at our study sites may provide an explanation. Temperature is an important factor affecting predator activity. In a review by Sloan (1980), asteroids do not feed at temperatures <5 °C, and have a peak in feeding activity at 15-20 °C. According to Barbeau and Scheibling (1994b), predation rates of *A. vulgaris* and *C. irroratus* on juvenile scallops were significantly higher at 15 °C, but not significantly different between 4 and 8 °C. We thus postulated that the relatively low temperature on the sea bed off the Îles de la Madeleine lead to small temporal variation in predation potential.

Although correlation analyses detected an association between sea star characteristics (density and size) and their predation potential (estimated from cluckers), we did not detect such an association between crab characteristics and proportion of broken shells. Other factors than density and size of crabs must be influencing their predation potential. Crabs are suspected of having a type III (sigmoid) functional response on juvenile scallop beds in the field (Barbeau et al. 1994, 1996, 1998), whereby crab predation rate is low at low scallop density (before seeding trials) and important at high scallop density (e.g. immediately upon seeding), even though crab density does not change significantly. Since our study was conducted at low density of natural scallop (0.3 ind. $\cdot$ m^{-2}; Giguère et al. 2004) and of tethered juvenile scallops ($<1x10^{-4}$ ind. $\cdot$ m^{-2}), we may have been dealing with the part of the crabs' functional response where they do not feed much on scallops, explaining the lack of association between crab characteristics and crab predation. Also, crabs usually show much more individual behavioural variation than sea stars, which is often a source of difficulty in laboratory experiments (Wong & Barbeau 2003). In addition, consumption rate of crabs may have been affected by other factors such as the presence of other predator species, conspecifics (Mansour & Lipcius 1991), alternative prey (Wong & Barbeau 2005), or by substrate type (Lipcius & Hines 1986).

The predation model developed by Barbeau and Caswell (1999) did not predict all the predation potential values observed in the field, and so did not provide support for the non-independent effect hypothesis of the multiple predator assemblage. Furthermore, the assumption of independent predation effects is reinforced by the fact that the predator abundances on our study sites were low, and so interaction among predators would be uncommon. Still, correspondence between observed and expected values was not as high as we would have liked. In Chapter 2, the predation model was more accurate in predicting the predation in experimental tanks. Likely, various other factors came into play in our field study.

First, the use of frames with tethered scallops to estimate predation, instead of a random scallop distribution over the study area, as assumed by the model, may have modified the predation process. These scallop clusters may have released a chemical attractant and then induced a directed predator displacement towards them. To assess this possible behaviour, the probability of frames not being encountered by predators was compared to the fraction of frames with no mortality. Most often (for our site-sampling date combinations), the expected probability was lower than or similar to the observed fraction, suggesting that predators did not directly target the scallop clusters, but rather moved randomly prior to encountering a cluster. To try and capture in a simple way the scenario that once a cluster is encountered, a predator has an increased predation success, we assumed that the probability of a predator-scallop encounter was 1 after the cluster was encountered. So, we assumed that each scallop was surrounded by a detection zone greater than its own physical size and equal to the cluster size. It appears that this second model (with a detection zone) performed better to predict sea star predation in areas where *A. vulgaris* was abundant (e.g. 2003, Sites 1 and 3). However, the addition of a detection zone was not as useful in predicting crab predation, which was observed to be generally low in all predation assays.

The model developed by Barbeau and Caswell (1999) incorporates predator-prey processes in a simple way to simulate predation on scallop in the field and assumes random distribution of the animals, random movements of predators in 2-dimensional space, multiple predator types acting independently, and simple conditional probabilities for events following predator-prey encounters. Its use to simulate the predation potential on tethered scallops deployed on frames (i.e. in clusters) still needs some refining. The incorporation of a detection zone around the prey is a good first step to explore the complexity in distribution (i.e., the aggregated distribution of the prey). Another avenue for further research is the concept of a two-step encounter model, whereby encounter with scallop clusters is first modelled, and then encounters with scallops inside clusters or changes in predator behaviour once inside cluster is then modelled.

3.4.3 Implications for aquaculture

Temporal variation of predator assemblages off the Îles de la Madeleine does not appear to be a major concern for scallop seeding management, given that temporal variation in predation potential was low. Barbeau and Caswell (1999)'s modelling exercise for seeded scallops off the coast of Nova Scotia also concluded that season was not a primary factor affecting scallop survival to commercial size (~4 y). On a short term (days and weeks) following seeding, temperature was important as juvenile scallop survival was higher in periods of cold water than in periods of warm water (Barbeau & Caswell 1999), but this temperature effect disappeared after a few seasons. As discussed above for our study, given the depth (>30 m) and the relatively low water temperature near the sea bed, seasonal variation in predator feeding activity should be relatively low.

With regards to spatial considerations, appropriate site selection has always been regarded as critical importance for successful aquaculture ventures (Parsons & Robinson 2006). Barbeau and Caswell (1999)'s modelling exercise, which included three sites, also found a strong site effect on survival of scallops to commercial size (~4 y). In our study, which focused on sites already identified as being potentially good for scallop seeding, there was no strong site effect. Although predator assemblages and predation potential did show significant differences at the spatial scale of sites (km's), most of the variation was at a smaller scale, that of video sequences (~100's m) for predator densities and of frames (meters) and stations (100's m) for predation assays. The present analysis suggests using a grid to precisely characterize a site prior to seeding and then to adjust the seeding strategy, such as seed density or size, in response to the within-site characterization. A management strategy similar to this is being attempted in New Zealand scallop enhancement projects (Drummond 2004), and it takes into account natural scallops and substrate characteristics. This strategy could be extended to include differences in predator composition within the site. The next step would be to determine the best size of the grid units for such a within-site characterization.

Other possible management strategies deal with predator densities and seeding density (Nadeau & Cliche 1998; Barbeau & Caswell 1999; Bergh & Strand 2001; Uki 2006). However, this study provides additional insights and ideas. Rock crabs have a type III functional response, which leads to a low proportional mortality of scallops at low scallop density and at high scallop density (Barbeau et al. 1998). Therefore, an intermediate density, such as the typical seed density of 5 scallops · m^{-2} aimed for in our system (Nadeau & Cliche 2007), may cause crabs to switch on to this now relatively abundant prey. It may also be that the intermediate seed density by itself is not high enough to cause crabs to switch to scallop prey, but, when an extensive area (e.g. 12 km^2) is seeded at that density, crabs do start to recognize scallops as prey. Based on these scenarios, possible management strategies include avoiding crab predators, for example, by better characterizing crab migration patterns and removing from consideration possible seeding sites where crabs become seasonally abundant. Another strategy is to seed pockets of areas within a site to avoid having an extensive area seeded, which brings us back to our suggestion above of characterizing within-site features and seeding accordingly. Another approach is to seed scallops at low density or at very high density to minimize crab predation (Wong & Barbeau 2006; Barbeau & Caswell 1999). In our study, conducted in a low natural scallop density, interactions among multiple predators were minimal. If a multiple predator assemblage was exposed to high densities of scallops, non-independent interactions may become important; this situation would need to be further investigated.

CHAPITRE 4

Dynamique de la prédation à court terme après un ensemencement à grande échelle de pétoncles géants (*Placopecten magellanicus*) juveniles au large des îles de la Madeleine, Québec

Short-term predation dynamics of juvenile sea scallops (*Placopecten magellanicus*) following a large-scale seeding trial off the Îles de la Madeleine, Québec

RÉSUMÉ

La prédation est considérée comme un obstacle majeur aux efforts visant à accroître les stocks de pétoncles géants (*Placopecten magellanicus*) avec des ensemencements de pétoncles juvéniles. Cependant, il existe peu d'informations sur la manière dont les prédateurs multiples interagissent pour éventuellement modifier à la hausse ou à la baisse leur impact sur la mortalité des pétoncles. La présente étude visait donc à étudier l'impact de prédateurs multiples sur la dynamique des pétoncles juvéniles ensemencés à grande échelle (>5 millions de pétoncles sur des sites de 1,2-1,7 km^2) au large des îles de la Madeleine, Québec, en 2003 et 2004. Tout d'abord, l'assemblage des prédateurs benthiques (et des pétoncles en 2004) a été caractérisé, avec une caméra, avant et après les ensemencements sur les sites ensemencés et contrôles. Durant les deux années d'étude, la densité des prédateurs a été relativement faible (~10 étoiles de mer et 1 crabe par 100 m^2) avec un assemblage dominé par les étoiles de mer *Leptasterias polaris* et *Crossaster papposus*. Quelques variations spatiales et temporelles ont été notées mais les patrons n'ont pu être uniquement associés aux ensemencements à cause de l'absence de réplication des sites contrôles, en 2003, et de données complètes sur les prédateurs, avant l'ensemencement de 2004. Malgré cela, les données récoltées n'ont pas démontré clairement de comportement d'agrégation des prédateurs en réponse à l'augmentation de la densité des pétoncles. Ensuite, après chaque inventaire de prédateurs, le potentiel de prédation des pétoncles juvéniles a été estimé à l'aide d'une technique d'attachement développée pour le travail en eau profonde. Cette technique a permis d'estimer une survie >90% des pétoncles après 24 h, pour les deux années d'étude, et aucune variation dans la survie n'a pu être associée aux ensemencements. Cependant, sur la base de l'absence d'une réponse d'agrégation des prédateurs et de potentiels de prédation indépendants à la densité de proies, les prédateurs ont semblé avoir une réponse fonctionnelle à l'augmentation de la densité des pétoncles. Pour terminer, un modèle mathématique a été utilisé pour simuler l'impact de prédateurs multiples, de façon indépendante, envers les pétoncles juvéniles fixés, et a estimé des valeurs de potentiel de prédation assez proches des valeurs observées. Cette conclusion est plausible pour notre site d'étude composé d'une faible densité de

prédateurs limitant les interactions entre les prédateurs. Ainsi, notre étude a permis de récolter de rares informations sur la dynamique des pétoncles après un ensemencement à grande échelle. La dispersion des pétoncles et l'effet de leur distribution groupée lors de l'ensemencement peuvent être des facteurs importants affectant le succès des ensemencements et devraient être davantage explorés dans les études futures.

ABSTRACT

Predation is a major constraint in efforts conducted to enhance the sea scallop (*Placopecten magellanicus*) stocks with juvenile scallop seeding trials. However, little is known on how multiple predator species interact to possibly increase or decrease predator-related mortality of scallops. The goal of the present study was to investigate the impact of multiple predators on juvenile scallop dynamics during large scale seeding trials (>5 million scallops seeded on 1.2-1.7 km^2 sites) conducted off the Îles de la Madeleine, Québec, in 2003 and 2004. First, the benthic predator assemblage (and the scallop population in 2004) was characterized before and after seeding on seeded and control sites using a camera. During the two study years, predator densities were relatively low (~10 sea stars and 1 crab per 100 m^2) with an assemblage dominated by sea stars *Leptasterias polaris* and *Crossaster papposus*. A few spatial and temporal variations were observed, but patterns could not be related solely to seeding because we did not have replicate, true control sites in 2003, and the data collected on predators prior to seeding in 2004 were not fully adequate. Nevertheless, the data collected on predators did not clearly show an aggregative response of predators to increase scallop density. Second, predation potential was estimated on juvenile scallops using a tethering approach adapted for a deep water environment, immediately after each predator survey. These predation assays estimated >90% scallop survival after 24 h in both years, and no variation could be attributed to seeding. Therefore, based on the lack of an aggregative response of predators and on proportional prey mortality independent of prey density, predators appeared to have a functional response to increased scallop density. Finally, a mathematical model was used to simulate a multiple predator effects on tethered scallops, assuming that predator species act independently of each other, and it predicted predation potential values that correspond adequately to observed values. This conclusion makes sense for our study sites which had low predator densities (and so, predator interactions should be uncommon). Overall, our study presents rarely-collected data on large scale scallop seeding trials. It identified dispersal of scallops and effects of their clumped distribution following seeding as possible

important factors influencing seeding success, that should be investigated in further in future studies.

4.1 Introduction

Over two decades, there has been a continued interest in seeding (releasing) juvenile sea scallops (*Placopecten magellanicus*) to enhance natural scallop populations in Atlantic Canada (Robinson 1993; Cliche & Giguère 1998; Davidson & Mullen 2005). However, predation by sea stars and crabs has been a major constraint in this endeavour (Cliche et al. 1994; Barbeau et al. 1996). Field and laboratory experiments confirmed the importance of predation by sea stars (*Asterias vulgaris*, *Leptasterias polaris* and *Crossaster papposus*) and crabs (*Cancer irroratus* and *Hyas araneus*) on juvenile scallops (Barbeau & Scheibling 1994a; Barbeau et al. 1998; Nadeau & Cliche 1998; Wong & Barbeau 2006; Wong et al. 2006b; Chapter 2). Although interactions among these predators when foraging is generally expected, only a few studies have examined these possible interactions (Sloan 1980; Morissette & Himmelman 2000; d'Entremont 2005). Thus, the present contribution investigates in the field the impact of multiple predators on juvenile scallop dynamics during large scale commercial seeding trials conducted off the Îles de la Madeleine, Québec.

Upon and shortly after seeding, juvenile scallops are particularly vulnerable to predation. The situation is multifaceted because the impact of predation is influenced by biological and physical factors related to both the state of the seeded scallops and the community of predators. It is common upon seeding that scallops reach the sea floor upside down, exposing the white lower shell to visual predators. Scallops must regain the normal position with their righting reflex to escape potential predators. Furthermore, their vitality may be reduced as they were previously subjected to various stressful conditions during handling and transport that may affect their righting reflex as well as their escape responses (Fleury et al. 1996; Maguire et al. 1999; Minchin et al. 2000; Lafrance et al. 2002; Guderley et al. 2008).

With regard to the predator assemblage on the seeded sites, predators may have two types of short-term predation responses to the relatively high scallop density, newly introduced on the sea floor (~5 scallops · m^{-2}): an aggregative response (sometimes less precisely called a numerical response), where predators aggregated in areas of high prey density, and a functional response, where individual predators change their consumption rate in response to prey density (Taylor 1984). Evidence for predators aggregating following seeding, presumably induced by chemical and/or visual cues from seeded scallops, is not consistent. To date, predators were not observed to aggregate significantly during scallop seeding trials in Atlantic Canada (Cliche et al. 1994; Barbeau et al. 1996; Hatcher et al. 1996; Wong et al. 2005), but were observed to aggregate in trials with other species of scallops (Volkov et al. 1985; Veale et al. 2000). With regard to the functional response, predators typically have one of three possible types: a type I response, where predation rate increases linearly with prey density (density independent); a type II response, where predation rate increases at a decelerating rate as prey density increases to a plateau at high prey density (hyperbolic shape, inversely density dependant) and a type III response where predation rate increases at an accelerating rate at low prey density and then at a decelerating rate to a plateau at high prey density (sigmoid shape, first positively and then inversely density dependant). In predation studies conducted with juvenile scallops, crabs (*C. irroratus*) tended to have a type III and sea stars (*A. vulgaris*) a type I functional response (Barbeau et al. 1994; Barbeau et al. 1998; Wong & Barbeau, 2005).

Upon reaching the sea floor, juvenile scallops are exposed to multiple predator species. In such a situation, the overall predation impact may not necessarily be predicted by simply summing the effects of the different predator species (Sih et al. 1998). Some predator-predator interactions may enhance or diminish the overall predation impact. Thus, the observed predation may be more or less than that anticipated from predator species separately, a situation termed non-additive (or non-independent), as opposed to additive (or independent), multiple predator effects (Soluk 1993). In addition, as indicated above, scallop seeding operations may modify the predator species assemblage if attraction occurs, as well as a predator's functional response. It is clear that more investigations are needed to improve our understanding of predator-scallop dynamics during large scale seeding trials in a multiple predator species system.

The main objective of the present study was to investigate in the field the response of predator assemblages to seeding, as well as the effect of these assemblages on juvenile scallop survival, shortly after a large scale seeding trial. It was hypothesized that seeded scallops will be subjected to high predation pressure shortly after seeding because of the aggregative and functional responses of predators. It was also hypothesized that the multiple predator assemblage will exhibit a non-additive predation impact, as a result of various predator-predator interactions observed to occur in smaller-scale studies (e.g. Sloan 1980; Morissette & Himmelman 2000b). To meet the objective, the benthic predator assemblage that occurs off Îles de la Madeleine was first characterized during two commercial seeding trials conducted in 2003 and 2004, to determine if significant variations occur before and after seeding at seeded and reference sites. Density of predators and scallops was quantified using a video camera mounted on a sleigh or a pyramid. Second, the predation potential of the predator assemblage was estimated on juvenile scallops during the same study period and at the same sites, to again determine if significant variations were related to seeding. Predation potential, which is defined as the rate at which prey of interest would be consumed were they readily available to predators (Aronson 1989), was estimated using the tethering approach. Tethering bias has previously been estimated (Barbeau &Scheibling 1994c; Chapter 2), and a methodology has been developed for deployment in deep water (>30 m) habitats (Bourgeois 2004). Finally, the field data were used in a predation model that estimates multiple predator effects on tethered scallops with independent predation impact (Barbeau & Caswell 1999). The predicted predation potential values were compared to observed ones to evaluate the non-independent predation impact hypothesis.

4.2 Material and Methods

4.2.1 Study sites

The study was conducted between 2003 and 2004 on a natural scallop ground located 10 km off the Îles de la Madeleine, Gulf of St. Lawrence in eastern Canada, and >30 m deep (Fig. 4.1). This region was closed to fishing and solely used for commercial scallop seeding. The selection of study areas was based on being commercially seeded in 2003 and 2004. On 16 June to 2 July 2003, 5.9 million juvenile scallops (23.6 ± 0.05 mm shell height) were released by a local scallop grower company over an area of 1.2 km^2 (0.8 km x 1.5 km; 5 scallops $\cdot$ m^{-2}). On 12 to 26 June 2004, 8.5 million juvenile scallops (28.4 ± 0.05 mm shell height) were released over another area (1.7 km^2, 1.1 km x 1.5 km). For the 2003 seeding trial, four study sites of 0.10 km^2 (0.38 km x 0.26 km), spaced out by 120 m from each other, were selected: three sites were inside the 2003 commercial seeding area and one site was outside. For the 2004 seeding trial, three study sites were selected in an asymmetrical design: one site of 0.96 km^2 (0.64 km x 1.50 km) in the commercial seeding area and two control sites of 0.36 km^2 (0.60 km x 0.60 km) outside.

Temperature sensors (Sealog-T v1.04) were immersed yearly 2 m above the sea bottom to monitor water temperature on hourly basis. However, the temperature recordings for 2004 were questionable and so discarded (Fig. 3.2, Chapter 3). A current meter (S4, InterOcean system inc.) was also deployed in 2004, from 16 June to 8 November, 2 m above the sea bottom. The water currents were predominantly in a southwest-northeast orientation, with an average (±SD) in velocity of 10.4 ± 0.1cm $\cdot$ s^{-1} and peaks in velocity up to 74.6 cm $\cdot$ s^{-1} (Fig. 4.2).

4.2.2 Video surveys of scallops and predators

In 2003, predator densities and sizes were quantified before and after scallop seeding using a video camera (field of view: 0.80 m^2) mounted on a metal sleigh as described in Chapter 3 (Fig. 3.3). Four video transects, oriented east-west, were sampled in each site and at each sampling date in 2003; subsequently, 8 video sequences of 3 min (~100 m long) for each site and sampling date were randomly selected for data analysis to meet the assumption of independence of data.

In 2004, the predator assemblage as well as the scallop population were characterized with a video camera mounted on a pyramid (in May and June) and on a sleigh (in July to November) (explained below). The pyramid set-up was initially used in the 2004 study because we presumed that juvenile scallops would be easier to detect with a camera close to the sea bottom and on a fixed image. This set-up consisted of a video camera and four lights mounted on a metal pyramid (1.20 m x 1.20 m x 0.90 m, Fig. 4.3). Two graduated lead cables, attached to the pyramid and forming a cross near the sea bed in the camera's field of view (0.5 m^2), were used to measure predator and scallop sizes from the recorded images. During sampling, the boat slowed down (~0.5 nautical mile · h^{-1}) over each station and the pyramid was lowered onto the bottom for ~4 s to record the first image. Then the pyramid was lifted up for another 4 s and lowered down again for another image. In this way, 6 images were recorded per sampling station.

For the later sampling dates in 2004, we switched back to the video camera on a sleigh, because the imaging technique with the pyramid covered too small an area during a field day (80 m^2 vs 3000 m^2 with the sleigh). To improve detection of juvenile scallops with the sleigh technique as described in Chapter 3, the camera was lowered closer to the sea bed (the field of view was reduced to a 0.6 m width) and the angle of view of the sea bed was set to 60° (instead of 45°). One video transect oriented east-west, ~180 m long, was then recorded at each sampling station. For both survey techniques, we randomly selected sampling stations for each combination of site and sampling date, using a grid of 0.038 km x 0.075 km rectangles. Specifically, ten unique sampling stations (or grid rectangles) in the seeded site and 4-5 in control sites were sampled per date (stations were sampled only once). Note that in August 2004, scallop density and sizes could not be estimated on the control sites because of poor visibility on the video sequences.

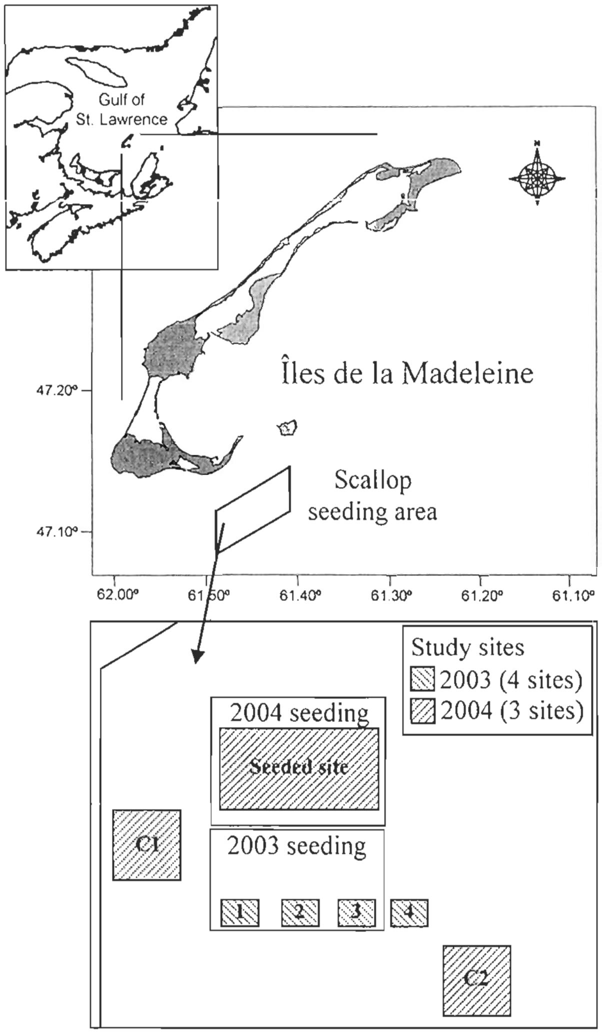

Figure 4.1. Maps of the study sites off the coast of the Îles de la Madeleine, Québec, Canada.

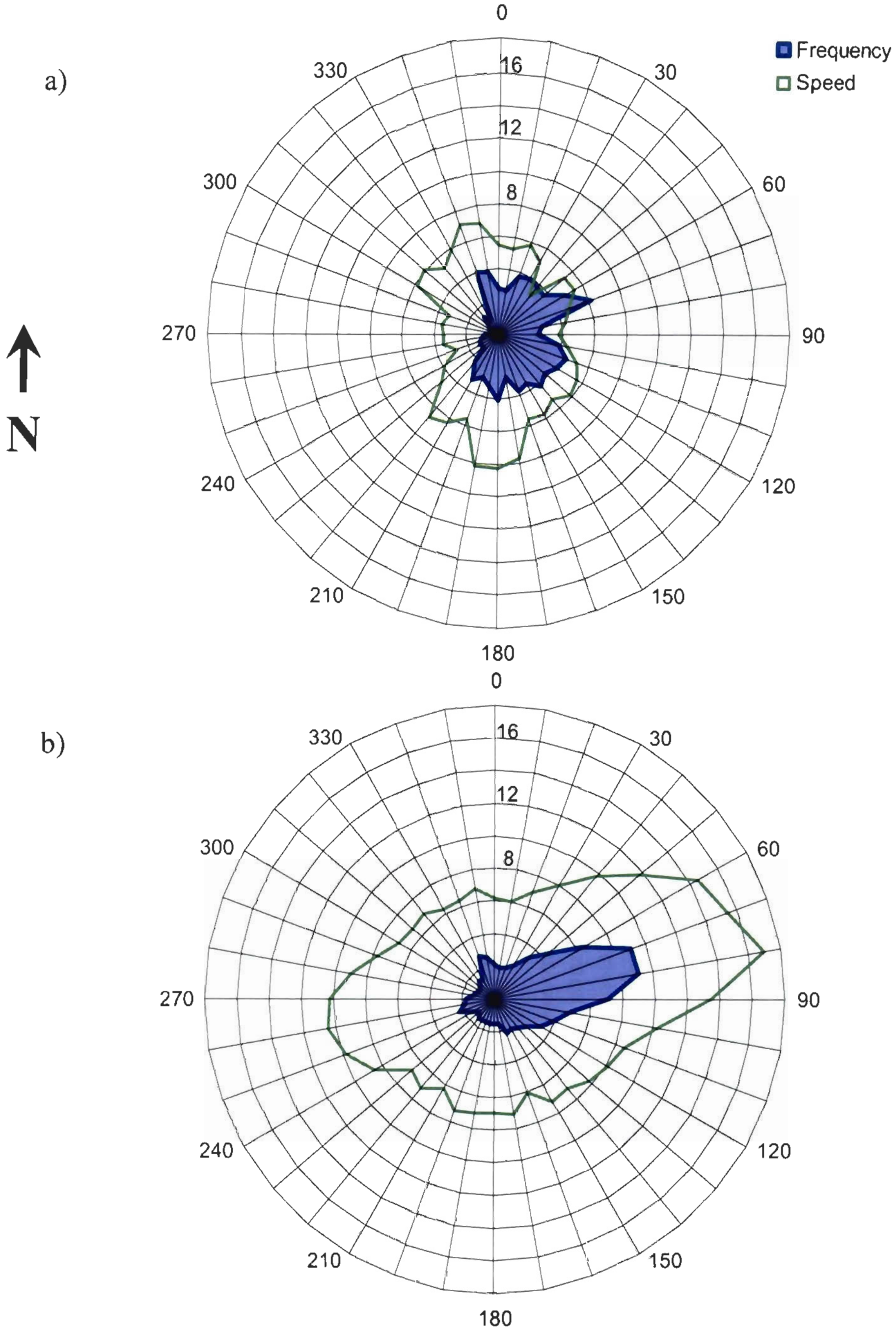

Figure 4.2. Frequency (%) and mean speed ($cm \cdot s^{-1}$) of water current in relation to the directional degrees, 2 m off the sea bed on the seeded area; a) during the seeding period from 16 to 26 June and b) during the survey period from 16 June to 8 November 2004. The scale of Y axis is the same for both dependent variables.

Table 4.1. Summary of predator surveys and predation assays conducted during the 2-y study.

Year	Number of sites (area/site)	Time	Predator densities and sizes			Predation potential		
			Date	Sampling approach	Number of replicates/site	Date	Sampling approach and number of replicates	Immersion time (h)
2003	4 ($0.10\ km^2$)	Before	June 10	4 parallel video transects/site; these were then cut into multiple video sequences ($80 \cdot m^{-2}$ ea)	8 randomly chosen video sequences	June 14	6 tethering assays, deployed randomly in each of three sites (sites 2, 3, 4)	24
		During	June 25			June 28[1]		24
		After 2 wk	July 11			July 15		24
		After 2 mo	Aug. 20			Aug. 22		24
		After 5 mo	Nov. 25			Nov. 26[2]		24
			Predator and scallop densities and sizes					
2004	1 seeded ($0.96\ km^2$) and 2 control ($0.36\ km^2$)	Before	May 26	Grid of sampling stations overlaid on each site; 4-5 stations/control site and 10 stations/seeded site, randomly selected. May-June: images ($0.5 \cdot m^{-2}$ ea) with camera on pyramid. July-Nov: transects ($100 \cdot m^{-2}$ ea) with camera on sleigh.	May-June: 6 images /station July-Nov.: 1 transect /station. Randomly selected inside each station.	May 27	3 stations/control site and 6 stations/seeded site (previously sampled by the camera), each with 2 tethering assays	24
		During	June 26			June 29		24
		After 2 wk	July 12			July 24		24
		After 2 mo	Aug. 27[3]			Sept.12		72
		After 5 mo	Nov. 12			Nov.[4]		nd

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[1] Natural mortality before transportation; [2] Assays are missing in one site; [3] No scallop data because of low visibility; [4] No data because of inclement weather.

Three small-scale field experiments or trials were conducted to validate the accuracy of the video method to estimate predator and scallop densities. (i) A field experiment was conducted to assess differences in predator assemblage between day time and night-time (Appendix 1). The results indicated that there was no significant difference between periods. Thus, the daytime estimates were considered a good representation of predators in the field. (ii) A trial was conducted to estimate the bias caused by the juvenile scallop escaping in front of the sleigh (Appendix 4). An additional camera located on the top of the sleigh (at an angle ~25° from the sea bed) and connected to a video recorder indicated that the sleigh induced very few juvenile scallop escapes, so this bias was not considered important. (iii) A field trial was conducted with SCUBA divers to determine the accuracy of scallop densities estimated from video surveys (Appendix 4). This indicated that juvenile scallop density estimated from the video was statistically similar to density estimated from divers in the same sampling quadrats. Thus, the scallop counts collected with the video camera were considered reliable.

For both the 2003 and 2004 seeding trials, the software Image-PRO Plus (V4.1 software) was used to count and size scallops, sea stars (*A. vulgaris*, *L. polaris* and *C. papposus*) and crabs (*C. irroratus* and *H. araneus*) from fixed images and video sequences. The sea star *Solaster endeca* was not considered in our study as it feeds mostly on echinoderm species (Sloan 1980; Gaymer et al. 2004). Scallop and predator densities were estimated as number of individuals divided by surface area covered in each image or video sequence (number · m^{-2}). Length (m) of each video sequence recorded in the first study was estimated with Nobeltec navigation software V7. Sea star size was measured as radius, which is the distance from the tip of an average-length arm to the center of the body. Crab *C. irroratus* size was measured as carapace width, which is the largest width of the cephalothorax. *H. araneus* was measured as carapace length, from the extreme rear of the eye socket to the opposite end of the cephalothorax. Scallops were measured as shell height, which is the distance from the shell ventral edge to the hinge. All size measurements were corrected for distortion due to the position of the animal in the camera's field of view (as explained in Chapter 3).

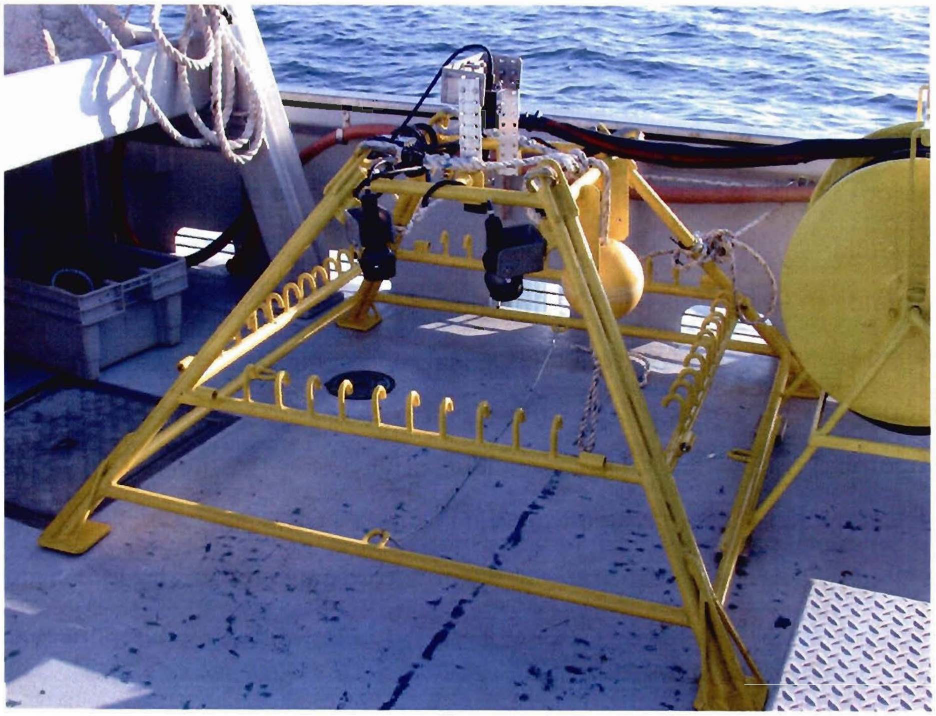

Figure 4.3. Pyramid used during the camera surveys conducted in May and June 2004.

4.2.3 Predation assays using tethered scallops

Assays to estimate predation potential at each site were conducted shortly after each video survey at each date using tethered scallops (Table 4.1). The methodology developed for deployment in deep water is described in Chapter 3. The predation assays, each consisting of a frame with 12 tethered scallops, a cement block and a surface float, were deployed from a boat, and retrieved after 24 h. In September 2004, predation assays were retrieved later (72 h), because of inclement weather. In 2003, six predation assays were deployed randomly in each site and sampling date. In 2004, the experimental design was revised from 2003 to increase the statistical power of the predation assays. Predation assays were deployed in pairs, at three stations per control site and six stations in the seeded site. All stations were previously sampled by the video camera, for a total of 24 predation assays per sampling date.

Upon retrieval, the number of live and dead scallops was counted for each frame. Shell remains of dead scallops were categorized as cluckers (intact upper and lower shells still attached at the hinge) and intact upper shells, both associated with sea star predation, and shell fragments, associated with crab predation (Barbeau et al. 1994). Scallop losses (tether line without a scallop or shell remains) were observed upon retrieval in 2003 (0.16 ± 0.02 scallops per frame, mean ± SE, n=82) and in 2004 (0.06 ± 0.01 scallops per frame, n=96). Losses were apparently reduced in 2004 when using the nylon line instead of fishing line. Based on laboratory observations (Chapter 2) and on a small field experiment (Appendix 2), it was assumed that these losses were mostly scallops that became unglued as a predation assay was lowered onto the sea bed, and not due to a predation events followed by loss of shell remains. Thus, the proportion of dead scallops (due to sea star or crab predation) was estimated using the total number of scallops (dead or alive) that remained on cables upon retrieval. Finally, we adjusted the predation data (proportion of scallops surviving and proportion of scallops not dying from a particular cause of mortality) observed after 72 h of immersion (in September 2004) to 24 h of immersion, using the exponential decay equation (an approached tested using data collected during the small field experiment; Appendix 2).

Note that predation potential estimated in late June 2003 was not used: scallop mortality was observed in tanks prior to deployment of assays in the field, and so could not have been reliably attributed to predation. Data collected in November 2003 are shown graphically but were not included in statistical analyses because a group of frames (n=6) was damaged in Site 3.

4.2.4 Statistical analysis

Statistical analyses were performed using SAS software (v8.02). For all analyses, each dependent variable was assessed graphically for normality of residuals and using Cochran's test (Winer et al. 1991) for homogeneity of variance. When necessary, data were transformed using $\log_{10}$ or arcsin-square root to obtain homogeneity of variance.

Densities of the main predator species and proportions of tethered scallops dying from different causes of mortality (standardized to 24 h) were analysed with MANOVAs (Quinn & Keough 2002; Tabachnick & Fidell 2007), with Time and Site as fixed factors. When a significant Pillai's trace (converted to a F-value) was detected for a source of variation, we calculated standardized canonical coefficients (1) to evaluate contribution of different predator species or causes of mortality to the overall difference and (2) to identify correlations between densities of different predator species or proportions of different causes of mortality (Scheiner 2001). Scallop density, size of each predator species and proportion of tethered scallops surviving (standardized to 24 h) were analysed using ANOVAs with Time and Site as fixed factors. Power analyses were performed in few situations when non-significant trends were observed (Zar, 1984; p. 173).

Planned comparisons were done when main effects and the interaction were significant to compare logical combinations and to have orthogonal comparisons (Sokal & Rohlf 1995; Underwood 1997; Quinn & Keough 2000). Specifically, temporal comparisons conducted on the 2003 data focused on before vs after seeding to evaluate if there was a press change following seeding, and during seeding vs the average of before seeding + after seeding to evaluate if there was a pulse change during the seeding period. Spatial comparisons for the 2003 data were conducted on sites inside the seeded region vs the site outside, and on sites on the border of the seeded region vs the site located in the middle of it. When the interaction was significant for the 2003 data, temporal comparisons were performed on sites inside the seeded region (pooled together) before and after seeding and on the site outside the seeded region before and after seeding. Spatial comparisons were conducted before seeding on sites inside vs outside the seeded region and after seeding on sites inside vs outside seeding. For 2004, density data prior to the seeding trial were not used in statistical analyses (because on the low surface area covered with the pyramid sampling technique) and so temporal comparisons focussed on differences that occurred shortly after seeding vs a few months after seeding. Spatial comparisons for the 2004 data were performed on the seeded site vs control sites and between control sites. Significant interactions in the 2004 data led to a temporal comparison between July and November inside the seeded site and then inside control sites. Spatially, comparisons were performed at the last survey period, in November, between seeded and control sites.

A correlation analysis was conducted to examine the strength of association between densities of sea stars and crabs and the mortality of tethered scallops associated with sea star and crab predation. As mentioned previously for the 2004 data, predator densities estimated prior to seeding were not included in the analysis. Another correlation analysis was performed between proportion scallops alive from the tethering assays and scallop density in the area at the time to assess the possibility of a functional response.

4.2.5 Predation model

The predation model developed by Barbeau and Caswell (1999) was used to predict predation potential for the different sites and dates. The model assumes that multiple predator effects are independent (i.e. that predator species act independently of one another) and that predator individual move randomly on the sea bottom (see Appendix 3 for further details). Predicted predation potential values were compared to observed ones to evaluate the non-independent predation impact hypothesis.

The model parameters were quantified as follows. Predator densities and sea star sizes were those observed in the field. Crab size was estimated from the radius of their walking legs (0.05 cm) in contact with the bottom (8 legs x 0.05 cm = 0.4 cm; Barbeau and Scheibling 1994a; Chapter 3). Scallop size was the average shell height of tethered scallops (3 cm). Juvenile scallop density on non-seeded sites (Site 4 in 2003 and control Sites 1 and 2 in 2004) was very low (<0.1 scallop $\cdot$ m^{-2}), and so that density was quantified using the number of juvenile scallops tethered per frame (n=12) and the number of frames immersed per site divided by the area of each study site (refer to Table 4.1). Juvenile scallop density on the seeded sites was estimated using the data from the 2004 seeding trial, since scallops were not sampled in 2003. Model simulations were conducted for each site x date combination, except for May and June 2004 because of the low accuracy in our estimates of predator parameters (density and size) during these surveys.

Behaviours and probabilities underlying predator-prey interactions were those observed in previous studies for each predator species (Table 3.2, Chapter 3). Probabilities were estimated from the trials using tethered scallops conducted in tanks (Chapter 2). For crabs, values of P[die|enc] varied with prey density as a type III functional response (Barbeau et al. 1994, 1998, Appendix 3). We suspected that during the seeding period, crab would exhibit an accelerate rate of predation. Foraging time (searching + handling time) and velocities while searching for *A. vulgaris* and *C. irroratus*, which are likely not affected by tethering (Chapter 2), were estimated as the average of multiple studies (Barbeau & Scheibling 1994a, b, c) for foraging time and from the study of Barbeau et al. (1994) for field measurements of movement velocity. Prey handling time was estimate from Barbeau and Caswell (1999)'s equation which was determined from observed handling time in the laboratory (Barbeau and Scheibling 1994a; handling times per prey for the different predator species were unfortunately not recorded in the study presented in Chapter 2). Behaviours influenced by water temperature (velocity, foraging and handling time) were adjusted using a Q_{10} of 2, except for sea star velocity which had a Q_{10} of 3.8 (Barbeau and Scheibling 1994b), and field temperatures collected in 2003 and 2005 (Fig. 3.2, Chapter 3; for 2004, we averaged the 2003 and 2005, Chapter 3, daily temperatures).

A second simple model to take into account the spatial structure that we introduced by deploying tethered scallops in clusters (i.e. groups of 12 scallops attached to a frame) was used (see Chapter 3 for further details). For this second model, we simply assumed that each scallop was surrounded by a detection zone (that is wider than their shell height) for predators, as discussed in Holling (1966). Scallops were assumed to be randomly distributed in each study site as in the first model (hereafter called the "basic model"), but have a size (radius) that included a detection zone corresponding to the area of a cluster (i.e., the area of a frame = 1.44 m^2, radius = 0.677 m^2).

To quantify variation in the model output (i.e., the predicted probability of tethered scallops surviving, or dying from sea star or crab predation after 24 h), 200 Monte Carlo simulations as in Chapters 2 and 3 (also Barbeau & Caswell 1999) were run for each set of initial conditions (i.e., each predation assay conducted at 3 sites over 2 years) using MATLAB, MathWorks, Inc. The standard deviation (which is a standard error since inputted information were means ± SE) was then calculated from the distribution of outputs and converted to 95% confidence interval (Zar 1984, p. 103). The means and 95% confidence intervals of the predicted data and observed values were then compared.

Finally, to help tease apart whether predators were attracted or not to the clusters (frames) of tethered scallops, we estimated the probability of each predator species to not encounter a frame, and compared this to the fraction of frames with no mortality (refer to Chapter 3). This allowed us to assess if scallop clusters had modified the random searching movement of predators to a directed movement (attraction effect). Equations to estimate the probability that a frame was not encountered by predators are presented in Chapter 3 (Eq. 3.1 and 3.2).

4.3 Results

4.3.1 Scallop seeding trial of 2003

4.3.1.1 Predator assemblage

Sea stars *L. polaris* and *C. papposus* were the most abundant predators on the seeded area with an overall mean (± SE) density of 0.029 ± 0.005 and 0.018 ± 0.004 ind. · m^{-2}, respectively (Fig. 4.4). Densities of *A. vulgaris* and of both crab species *C. irroratus* and *H. araneus* were much lower (~0.005 ± 0.001 ind. · m^{-2}). The dominant sea star *L. polaris* was also the largest predator (9.9 ± 0.2 cm radius; Fig. 4.5). The mean sizes of the two other sea stars were 5.1 ± 0.3 cm (42 ind.) for *A. vulgaris* and 6.8 ± 0.2 cm for *C. papposus*. Crab sizes were 7.8 ± 0.3 cm (carapace width, 50 ind.) for *C. irroratus* and 6.7 ± 0.2 cm (carapace length, 53 ind.) for *H. araneus*.

The densities of predators varied significantly over time and space (Table 4.2, Fig. 4.4), whereas the sizes of the predators did not vary in relation to the seeding event (Table 4.3, Fig. 4.5). Both crab species were the predators mostly associated with the significant temporal variation of predator densities (based on the absolute values of the canonical coefficients) and the two crab species were negatively correlated (based on the different signs of their canonical coefficients) (Table 4.2). The detected variation in predator density before and after seeding was driven by the response of the crab *H. araneus*: this crab was more abundant before than after seeding (Fig. 4.4). The detected variation in predator density during versus before and after seeding (to assess for a pulse pattern) was mostly driven by *C. irroratus*, and it was less abundant during than before and after seeding.

Spatially, it was the two sea star species *L. polaris* and *C. papposus* that were the most associated with the change in predator assemblage (Table 4.2, Fig. 4.4). Both sea star species were more abundant in the outer site (Site 4) than in the seeded sites (Sites 1, 2 and 3). Moreover amongst the seeded sites, the middle site (Site 2) showed lower sea star densities (especially *C. papposus*) than the two border sites.

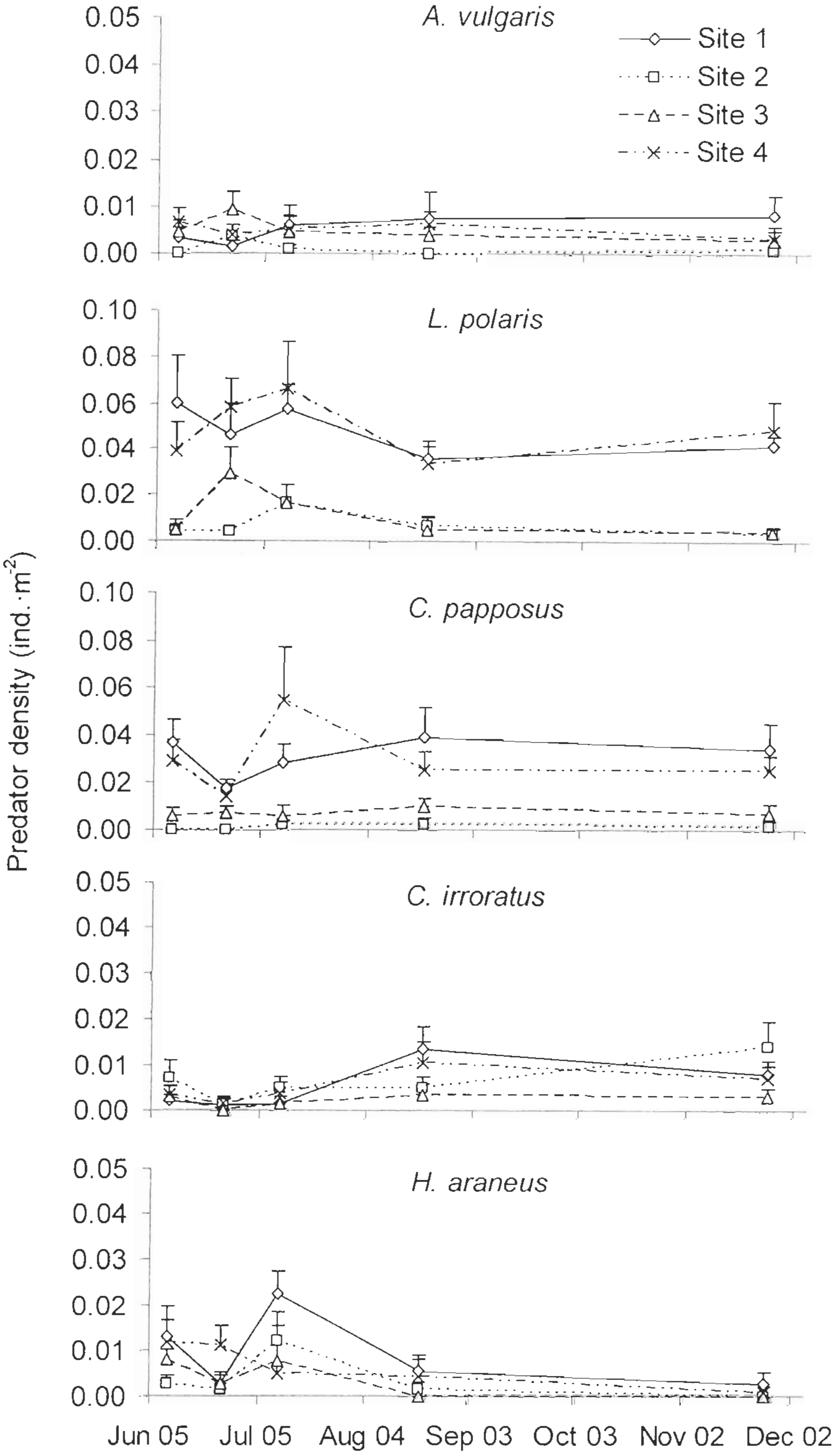

Figure 4.4. Mean densities (± SE, n=8) of five predator species before and after the 2003 scallop seeding trial. The vertical shading represent the seeding period that lasted ~2 wk.

Table 4.2. Results of a MANOVA on densities (ind.· m^{-2}) of predators in 2003. Data were transformed using $\log_{10}$(datum+0.01). Orthogonal planned comparisons were performed when fixed factors (Time and Site) were significant; significant differences ($p<0.05$) are indicated in bold. Standardized canonical coefficients were calculated for significant sources of variation, and important canonical coefficients (with relatively high absolute values for a given effect) are also indicated in bold.

Source of variation	df1, df2	F	*p*	Canonical coefficients				
				Av	*Lp*	*Cp*	*Ci*	*Ha*
Time	20, 556	2.87	**<0.001**	*0.07*	*0.16*	*-0.27*	***-0.69***	***0.86***
B vs A	*5, 136*	*3.18*	***0.009***	*0.18*	*-0.56*	*-0.13*	*-0.44*	***1.07***
D vs B, A	*5, 136*	*3.05*	***0.012***	*-0.15*	*-0.65*	*0.48*	***0.83***	*0.11*
Site	15, 414	7.95	**<0.001**	*-0.08*	***0.89***	***0.79***	*-0.10*	*-0.02*
1, 2, 3 vs 4	*5, 136*	*7.73*	***<0.001***	*0.03*	***0.94***	***0.71***	*-0.10*	*-0.04*
1, 3 vs 2	*5, 136*	*12.83*	***<0.001***	*0.15*	*0.57*	***0.95***	*-0.34*	*-0.01*
Time*Site	60, 700	0.90	0.690					

B: before seeding; A: after seeding; D: during seeding; Av: A. vulgaris; Lp: L. polaris; Cp: C. papposus; Ci: C. irroratus; Ha: H. araneus

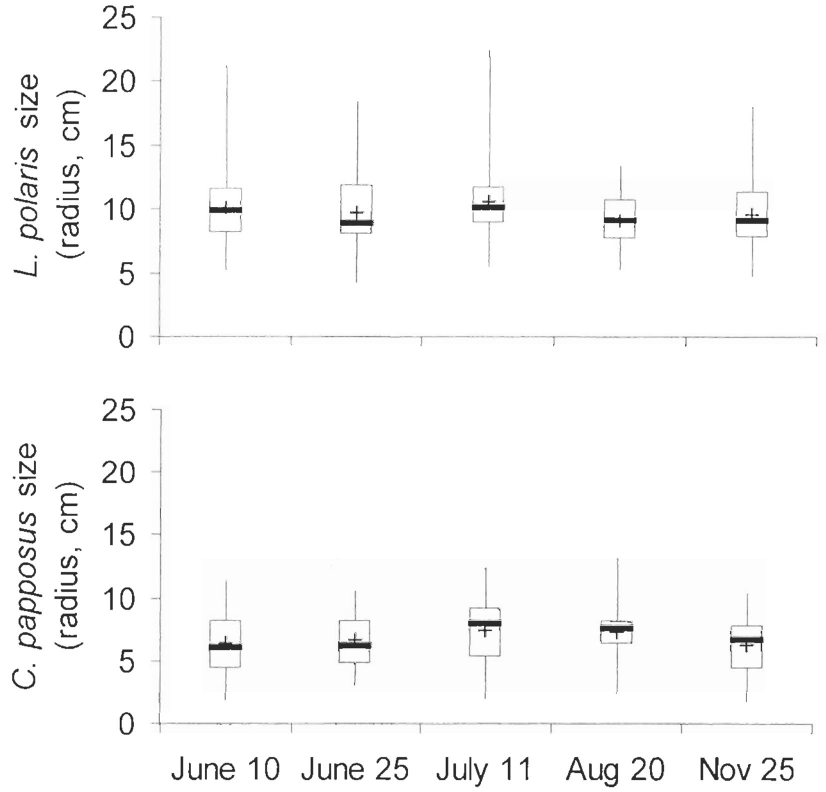

Figure 4.5. Box plots of sea star size for *L. polaris* and *C. papposus* sizes in 2003 (+: mean; horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values). Data are pooled over sites. The vertical grey shading represents the seeding period that lasted ~2 wk.

Table 4.3. Results of ANOVAs on predator sizes (cm) in 2003. Orthogonal planned comparisons were performed when Time was significant; significant differences (*p*<0.05) are indicated in bold.

Dependant variable	Source of variation	df	MS	F	*p*
L. polaris size	Time	4	9.886	1.24	0.224
	Error	582	7.991		
C. papposus size	Time	4	34.377	6.43	**<0.001**
	B vs A	*1*	*7.676*	*1.44*	*0.232*
	D vs B, A	*1*	*3.161*	*0.59*	*0.443*
	Error	404	5.348		

B: before seeding; A: after seeding; D: during seeding

4.3.1.2 Predation potential

Predation assays indicated that after an immersion of 24 h, a mean ± SE (n=82) of 84 ± 2 % of tethered scallops were still alive (Fig. 4.6). Based on the proportion of shell remains, dead scallops were attributed equally to sea star and crab predation (51 and 49%, respectively). A significant interaction between Time and Site was detected (Table 4.4). Planned comparisons showed no significant temporal difference (before vs after seeding) in scallop survival, neither inside or outside the seeded site. Moreover, no significant spatial difference amongst the sites was detected either before or after the seeding trial.

Canonical coefficients for shell remains showed that the significant interaction was mainly attributed to crab predation (Table 4.5). An ANOVA performed on crab predation (based on shell fragments) indicated that this interaction was not significantly related to the seeding event.

4.3.2 Scallop seeding trial of 2004

4.3.2.1 Seeded scallop surveys

In May, before seeding, only 8 scallops were observed on images sampled on the future seeded site and consisted of 5 juveniles (<4.5cm, shell height) and 3 adults (>10 cm) (Fig. 4.7 and 4.8). Only one adult scallop was observed on the control sites. At seeding, in late June, the scallop density on the seeded site increased abruptly from 0.29 to 2.37 scallops $\cdot$ m^{-2}. Based on size measurements, 98% of scallops seen on the seeded site were juveniles, whereas the few scallops observed on control sites were adults (>6 cm). Although scallop density was observed to increase on the seeded site, the ANOVA did not detect any temporal variation between May and June surveys (Table 4.6). Most likely, the heterogeneous distribution of juvenile scallops at seeding that fluctuated from 0 to clusters as dense as 9.3 scallops $\cdot$ m^{-2} increased the variance and so, the power to detect a temporal variation of 2 scallops $\cdot$ m^{-2} on the seeded site was estimated only 50%. However, scallop density showed a spatial difference between seeded and control sites (Table 4.6, Fig 4.7).

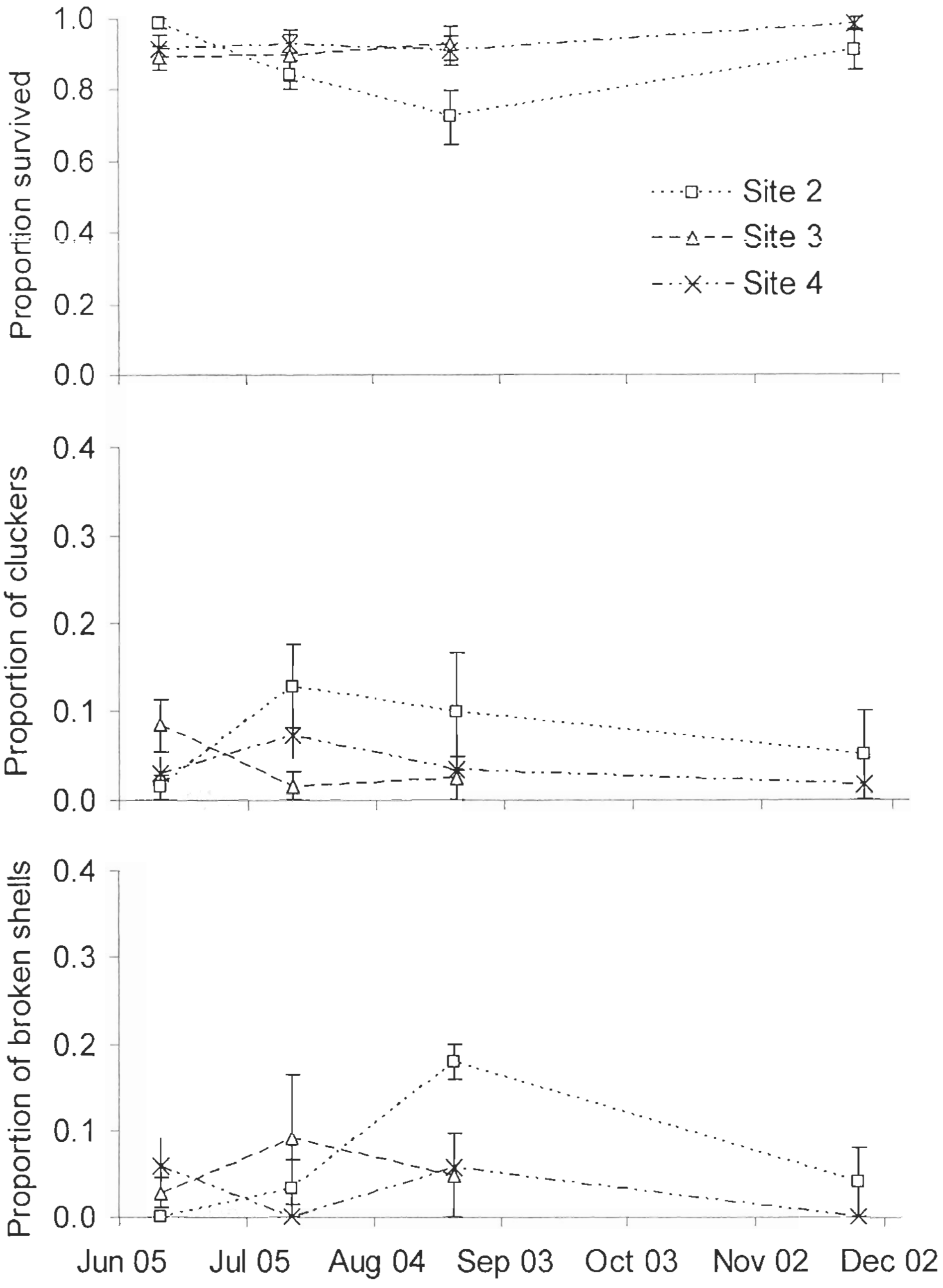

Figure 4.6. Mean proportions (± SE, n = 6) of deployed tethered scallops that survived after 24 h or died from predation by sea stars (cluckers) and crabs (broken shells), at 4 times and 3 sites in 2003. Predation data collected in June 29 were discarded because of the mortality before the frame immersion. The vertical grey shading represents the seeding period that lasted ~2 wk.

Table 4.4. Results of an ANOVA on proportion of tethered scallops surviving in 2003. June 28 and November 26 were not included because of mortality before the assay (June) and the lost frames at Site 3 (Nov). Planned comparisons were performed when the interaction was significant. Significant differences (*p*<0.05) are indicated in bold.

Source of variation	df	MS	F	*p*
Time	2	0.026	1.91	0.161
Site	2	0.023	1.73	0.189
Time*Site	4	0.041	3.07	**0.026**
2, 3 (B vs A)	*1*	*0.066*	*3.370*	*0.075*
4 (B vs A)	*1*	*0.0002*	*0.03*	*0.865*
B (2, 3 vs 4)	*1*	*0.003*	*0.43*	*0.520*
A (2, 3 vs 4)	*1*	*0.043*	*2.52*	*0.122*
Error	45	0.014		

2, 3 and 4: Sites 2, 3, and 4; B: before seeding; A: after seeding

Table 4.5. Results of a MANOVA on the proportion of tethered scallops that died due to sea star (cluckers) and crab (broken shells) predation in 2003. Data were transformed using $\log_{10}(\text{datum}+0.01)$. June 28 and November were not included in the analysis because of mortality before the assay (June) and lost frames at Site 3 (Nov). Standardized canonical coefficients were calculated for significant sources of variation, and important canonical coefficients (with relatively high absolute values for a given effect) are also indicated in bold and are discussed further in the text. An ANOVA was done on crab predation because of its large canonical coefficient in the MANOVA. Planned comparisons were performed when the interaction was significant in the ANOVA. Significant differences (*p*<0.05) are indicated in bold.

Source of Variation	df1, df2	F	*p*	Canonical coefficients Cluckers	 Broken shells
Time	4, 90	2.50	0.048		
Site	4, 90	0.33	0.860		
Time*Site	8, 90	3.29	**0.002**	0.16	**1.16**

ANOVA on proportion of broken shells

Source of Variation	df	MS	F	*p*
Time	2	3.568	4.66	0.015
Site	2	0.345	0.45	0.640
Time*Site	4	3.671	4.79	**0.003**
2, 3 (B vs A)	*1*	*3.158*	*3.11*	*0.087*
4 (B vs A)	*1*	*1.046*	*1.23*	*0.284*
B (2, 3 vs 4)	*1*	*1.517*	*1.35*	*0.253*
A (2, 3 vs 4)	*1*	*1.984*	*2.63*	*0.126*
Error	45	0.766		

2, 3 and 4: Sites 2, 3, and 4; B: before seeding; A: after seeding

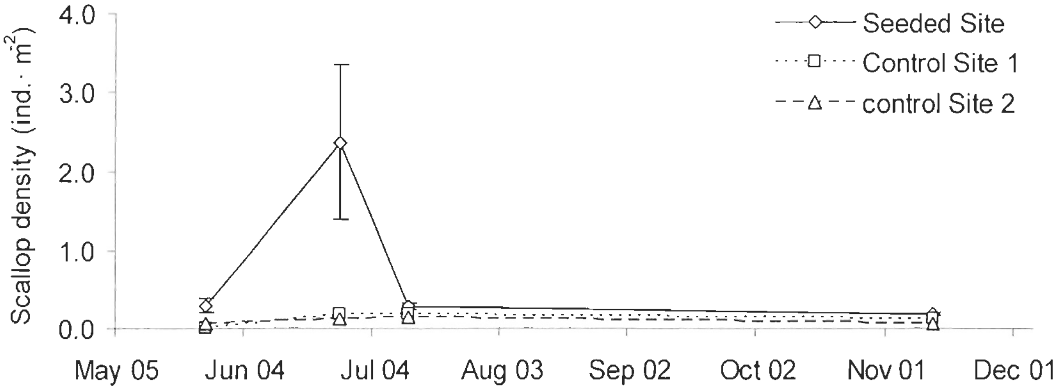

Figure 4.7. Mean densities (± SE) of juvenile scallops before, during and after the 2004 scallops seeding trial at seeded sites (n=10) and control sites (n=4-5). The vertical grey shading represents the seeding period that lasted ~2 wk. Note that May-June surveys were done using the pyramid technique and July-Nov surveys were done using the sleigh technique.

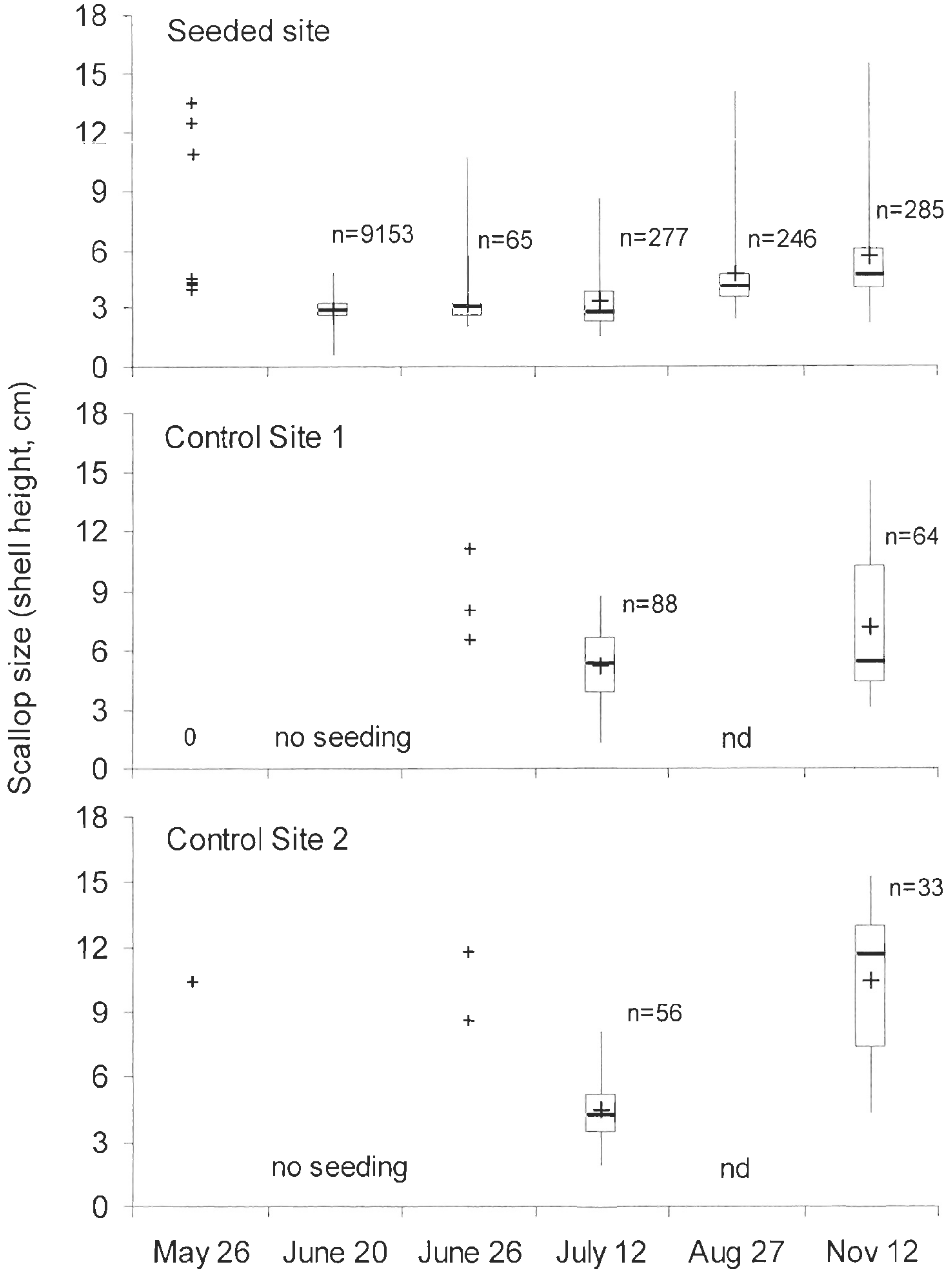

Figure 4.8. Box plots of scallop sizes in 2004 (+: mean or simple value (when <10 ind.); horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values). Note that May-June surveys were done using the pyramid technique and July-Nov surveys were done using the sleigh technique.

Table 4.6. Results of ANOVAs on scallop density (ind.· m^{-2}) in 2004 estimated with the pyramid technique in May and June and with the sleigh technique in July and November. Separate analyses for the different types of survey techniques were done. Data were $\log_{10}$(datum+0.01) transformed. Orthogonal planned comparisons were performed when Site was significant. Significant differences (p<0.05) are indicated in bold.

Month	Source of Variation	df	MS	F	*p*
May, June	Time	1	5.140	2.79	0.104
	Site	2	7.698	4.18	**0.024**
	Seeded vs Controls	1	*15.366*	*8.35*	***0.007***
	Between Controls	1	*0.000*	*0.00*	*0.999*
	Time*Site	2	1.072	0.58	0.564
	Error	35	1.839		
July, Nov	Time	1	0.449	8.20	**0.007**
	Site	2	0.729	13.31	**<0.001**
	Seeded vs Controls	1	*0.932*	*17.00*	***<0.001***
	Between Controls	1	*0.465*	*8.48*	***0.006***
	Time*Site	2	0.028	0.50	0.608
	Error	39	0.055		

In July, scallop density estimated on the seeded site with video sequences dropped to 0.28 scallop · m^{-2} and the population was 80% composed of juveniles (<4.5 cm) (Fig. 4.7 and 4.8). In both control sites, scallop density stayed low (0.16 scallop · m^{-2}). Surprisingly, 39 and 61% of scallops on control Sites 1 and 2, respectively, were now juveniles. In August, the scallop size on the seeded site showed that 77% were juveniles (Fig. 4.8), but these data could not be analysed (and compared to the control sites) because of poor visibility in the video sequences for control sites.

Between July and November, scallop density on the seeded site decreased significantly by 50 % (Table 4.6, Fig. 4.7). Taking into account growth (~1 cm since seeding; Miousse et al. 2006), 74% of scallops (<6 cm) on the seeded site can be associated to the seeding trial in November (Fig. 4.8). In control sites, scallop density also decreased significantly by 50 %. Based on growth estimates, 45% and 80% of scallops (<6 cm) on control Site 1 and 2, respectively, could be associated to seeding. Spatially, scallop density remained higher on the seeded site than the control sites (Table 4.6, Fig 4.7).

4.3.2.2 Predator assemblage

Similar to 2003, sea stars were the most abundant predators on seeded and control sites with mean densities that varied from of 0.015 to 0.065 ind. · m^{-2} for each sea star species (Fig. 4.9). Densities of crabs *C. irroratus* and *H. araneus* were much lower (0.013 ± 0.007 ind. · m^{-2} and <0.005 ind. · m^{-2}, respectively); and so crab densities were not considered in further analysis, except for modelling. The sea star *A. vulgaris* mean size was smaller than during the 2003 study (3.3 ± 0.13 cm in radius, as opposed to 5.1 cm in 2003). *L. polaris* and *C. papposus* were again the two largest sea stars (9.5 ± 0.2 cm and 8.5 ± 0.3 cm, respectively; Fig. 4.10). Crabs *C. irroratus* were 8.5 ± 0.3 cm (carapace width) and the few specimens of *H. araneus* were 4.7 ± 0.6 cm (carapace length, 10 ind.).

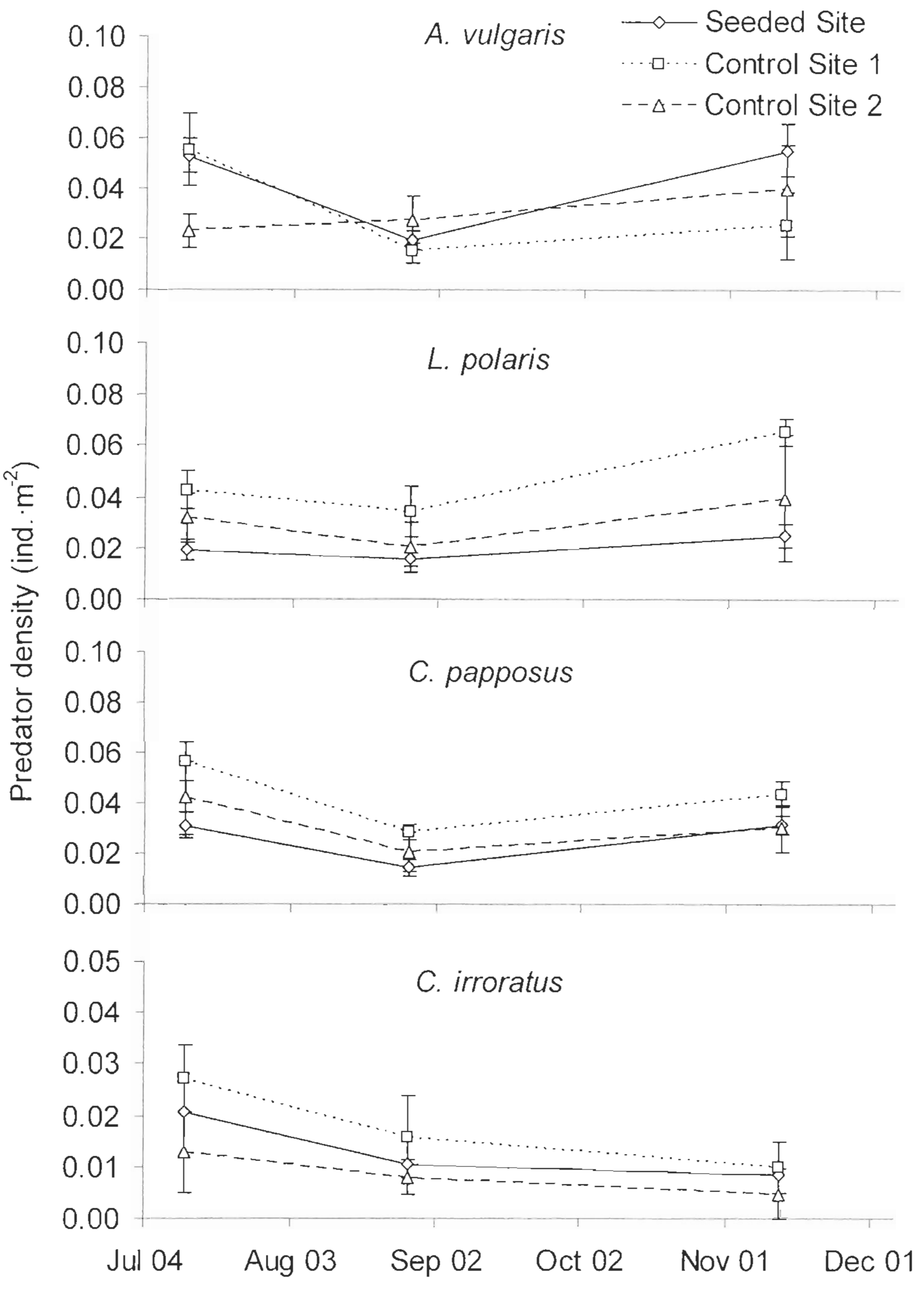

Figure 4.9. Mean densities (± SE) of four predator species after the 2004 seeding trial at the seeded site (n=10) and control sites (n=4-5). Note that July-Nov surveys were done using the sleigh technique.

Predator densities showed temporal and spatial variations (Table 4.7). However, the predator densities estimated after seeding did not differ temporally (based on our planned comparisons) one month (July) or a few months (November) after seeding. Spatially, sea stars were the main predators associated with the difference between seeded and control sites. Specifically, *A. vulgaris* density was negatively correlated to the other two sea star species, as it was more dominant on the seeded site than on control sites, and the opposite was observed for the other species (Fig. 4.9, Table 4.7).

Predator sizes showed various temporal and spatial patterns. *A. vulgaris* sizes showed a significant interaction between Time and Site (Table 4.8, Fig. 4.10). Planned comparisons confirmed that *A. vulgaris* was significantly larger in November than in July, in both the seeded site and the control sites. Also, in November, *A. vulgaris* was larger in control sites than in the seeded area. The other two sea stars species also showed temporal and spatial variations (Table 4.7). Temporally, these sea stars were also larger in November than in July. Spatially, they were smaller on seeded site than on control ones. Finally, the crab *C. irroratus* only had a temporal effect, and it was smaller in July than in November.

4.3.2.3 Predation potential

Overall, tethered scallops in predation assays had a survival mean ± SE (n=48) of 96 ± 1% after 24 hours (Fig. 4.11). This proportion of scallops varied temporally (Table 4.9), as it was significantly higher before than after seeding. The proportion of scallops dying from predation also fluctuated in time, with predation potential higher after than before seeding. Based on canonical coefficients, the significant temporal pattern before and after seeding was associated to both sea stars and crabs (Table 4.10). The proportion of scallops surviving or dying from predation did not vary spatially.

4.3.3 Relationship between multiple predator assemblages and scallop predation

In both years, the correlation analysis indicated that the proportion of cluckers was unrelated significantly to density of sea stars (n=17, r=-0.266, *p*=0.302), and that proportion of broken shells was unrelated to density of crabs (r=-0.023, *p*= 0.931). In 2004, proportion of tethered scallops surviving from predation did not correlated (n=23, r=-0.310, *p*=0.149) with the scallops density at the time of the assay suggesting a type I functional response of the predator assemblage (refer to Fig. 1.1b).

In 2003, expected predation from the basic predation model was low and relatively constant. There was a good agreement (>73%) between the expected proportions (for tethered scallop that survived and those that died from a predator type) and predation potential observed in the field (Fig. 4.12). All of the predation values expected from sea stars and 90% of the predation values expected from crabs were included in the 95% confidence interval of observations. The use of the second model with a detection zone around tethered scallops did not increase the correspondence between expected values and observed ones. However, inclusion of a detection zone led to higher expected predation from sea stars in the outer site (in Site 4) compare to the seeded sites (Site 2 and 3).

In 2004, there was very good agreement between expected (from the basic predation model) and observed predation values (100%; Fig. 4.12). The use of a detection zone tended to overestimate the predation impact of both types of predator. Overall, the fluctuations in predation potential observed in the field during both study years were not fully simulated by the models; the modelling exercise predicted a more constant predation impact than what we observed in the field.

The calculated probability that frames with tethered scallops were not encountered by predators was 59% for the seeded area in 2003, which was higher than the observed fraction of frames with no scallop mortality (39%), indicating that there were more attacks than expected. In contrast, outside the seeded area, the calculated probability of no predators encountering frames was lower (34%) to the observed fraction of frames with no mortality (49%). The same trend was observed in 2004. Inside the seeded site, the probability of a frame not encountering predators (14%) was higher to the observed fraction of frames with no mortality (0%), whereas in control sites, the calculated probability was 11% and the observed fraction was 17%. Thus, these results over 2 y suggest that predators displayed a random searching displacement outside the seeded area before encountering frames. Inside the seeded area, it appears that predators may have had a more directed displacement pattern, since we observed more frames with scallop mortality than the number of frames encountered by predators expected from the model (based on random searching displacement).

Table 4.7. Results of a MANOVA on densities (ind.· m^{-2}) of predators estimated during three sampling times (with the sleigh survey technique) after seeding: July, August and November 2004. Data were $\log_{10}$(datum+0.01) transformed. Orthogonal planned comparisons were performed when Time and Site were significant; significant differences (*p*<0.05) are indicated in bold. Standardized canonical coefficients were calculated for significant sources of variation, and important canonical coefficients (with relatively high absolute values for a given effect) are also indicated in bold.

Source of Variation	df1, df2	F	*p*	Canonical coefficients			
				Av	*Lp*	*Cp*	*Ci*
Time	8, 108	3.07	**0.004**	0.72	0.02	0.74	0.02
July vs Nov.	*4,53*	*2.39*	*0.062*				
Site	8, 108	2.77	**0.008**	-0.77	0.65	0.52	0.15
Seeded vs Controls	*4, 53*	*3.45*	***0.014***	***-0.85***	***0.53***	***0.53***	*-0.19*
Between Controls	*4, 53*	*2.36*	*0.065*				
Time*Site	16, 224	0.84	0.647				

Av: A. vulgaris; Lp: L. polaris; Cp: C. papposus; Ci: C. irroratus

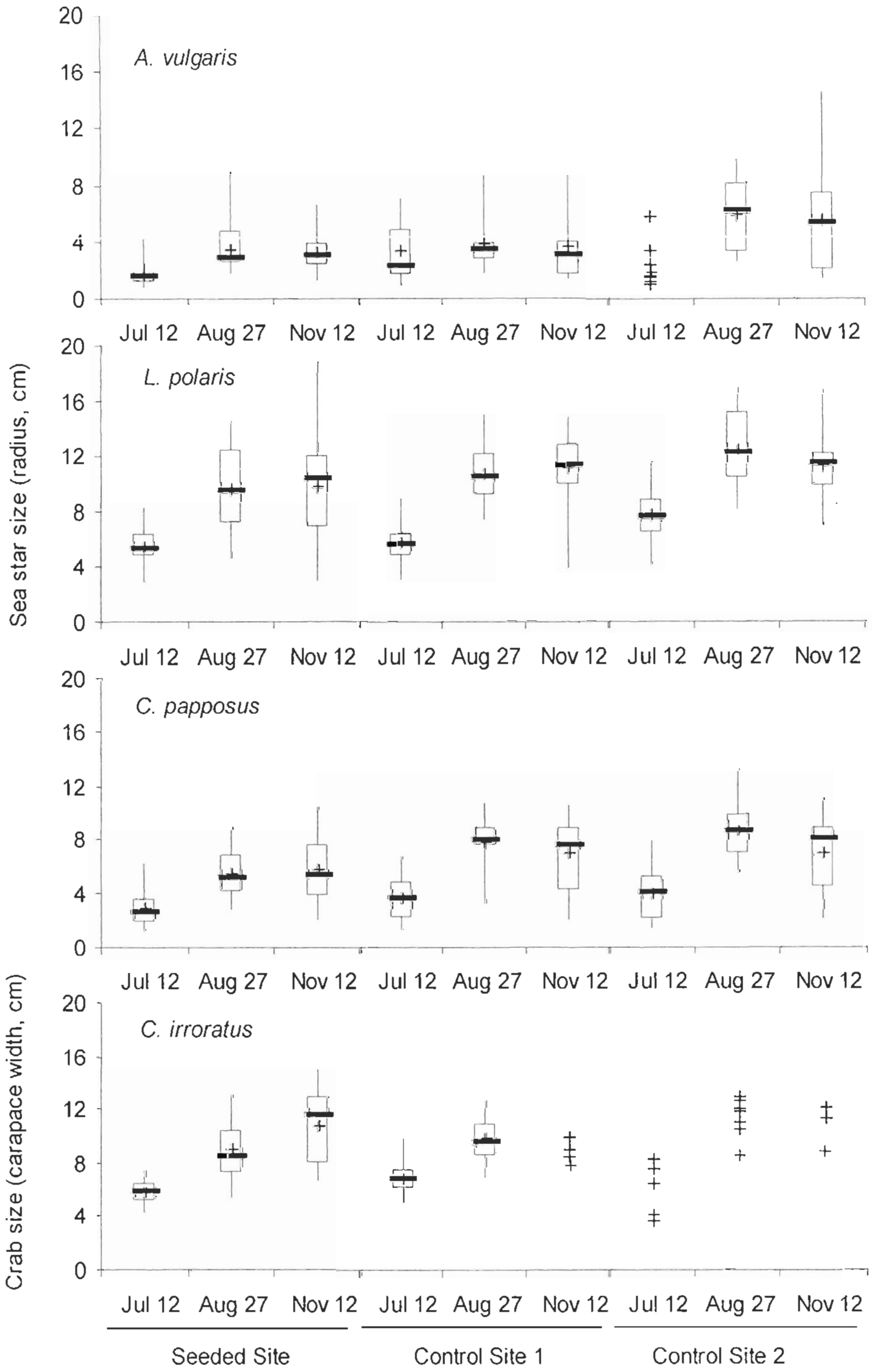

Figure 4.10. Box plots of sea star and crab sizes in 2004 (+: mean or simple value (when <10 ind.); horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values). May-June data (from the pyramid survey technique) were not included because of low number of predators (n<10 ind.).

Table 4.8. Results of ANOVAs on predator sizes (cm) in 2004 observed during three sampling times (with the sleigh survey technique) after seeding: July, August and November 2004. Station data were pooled over Site to increase the amount of data. Orthogonal planned comparisons were performed when Site and the interaction was significant. Significant differences (*p*<0.05) that are interpretable are indicated in bold.

Dependant Variable	Source of Variation	df	MS	F	*p*
A. vulgaris size	Time	2	49.383	15.63	<0.001
	Site	2	51.804	16.39	<0.001
	Time*Site	4	8.348	2.64	**0.034**
	Seeded (July vs Nov.)	*1*	*80.248*	*56.62*	***<0.001***
	Controls (July vs Nov.)	*1*	*45.317*	*6.82*	***0.010***
	Nov. (Seeded vs Controls)	*1*	*36.687*	*9.56*	***0.003***
	Nov. (Between Controls)	*1*	*27.490*	*7.17*	***0.009***
	Error	262	3.160		
L. polaris size	Time	2	357.99	51.74	**<0.001**
	July vs Nov.	*1*	*590.106*	*85.28*	***<0.001***
	Aug. vs Nov.	*1*	*0.787*	*0.11*	*0.736*
	Site	2	66.995	9.68	**<0.001**
	Seeded vs Controls	*1*	*101.491*	*14.67*	***<0.001***
	Between Controls	*1*	*41.445*	*5.99*	***0.015***
	Time*Site	4	7.054	1.02	0.398
	Error	193	6.919		
C. papposus size	Time	2	231.707	52.99	**<0.001**
	July vs Nov.	*1*	*286.557*	*65.54*	***<0.001***
	Aug. vs Nov.	*1*	*17.279*	*3.95*	***0.048***
	Site	2	55.180	12.62	**<0.001**
	Seeded vs Controls	*1*	*110.087*	*25.18*	***<0.001***
	Between Controls	*1*	*2.943*	*0.67*	*0.413*
	Time*Site	4	8.311	1.90	0.112
	Error	205	4.373		
C. irroratus size	Time	2	122.861	35.55	**<0.001**
	July vs Nov.		*136.795*	*39.65*	***<0.001***
	Aug. vs Nov.	*1*	*0.077*	*0.02*	*0.882*
	Site	2	4.638	1.34	0.267
	Time*Site	4	8.063	2.33	0.063
	Error	82	3.456		

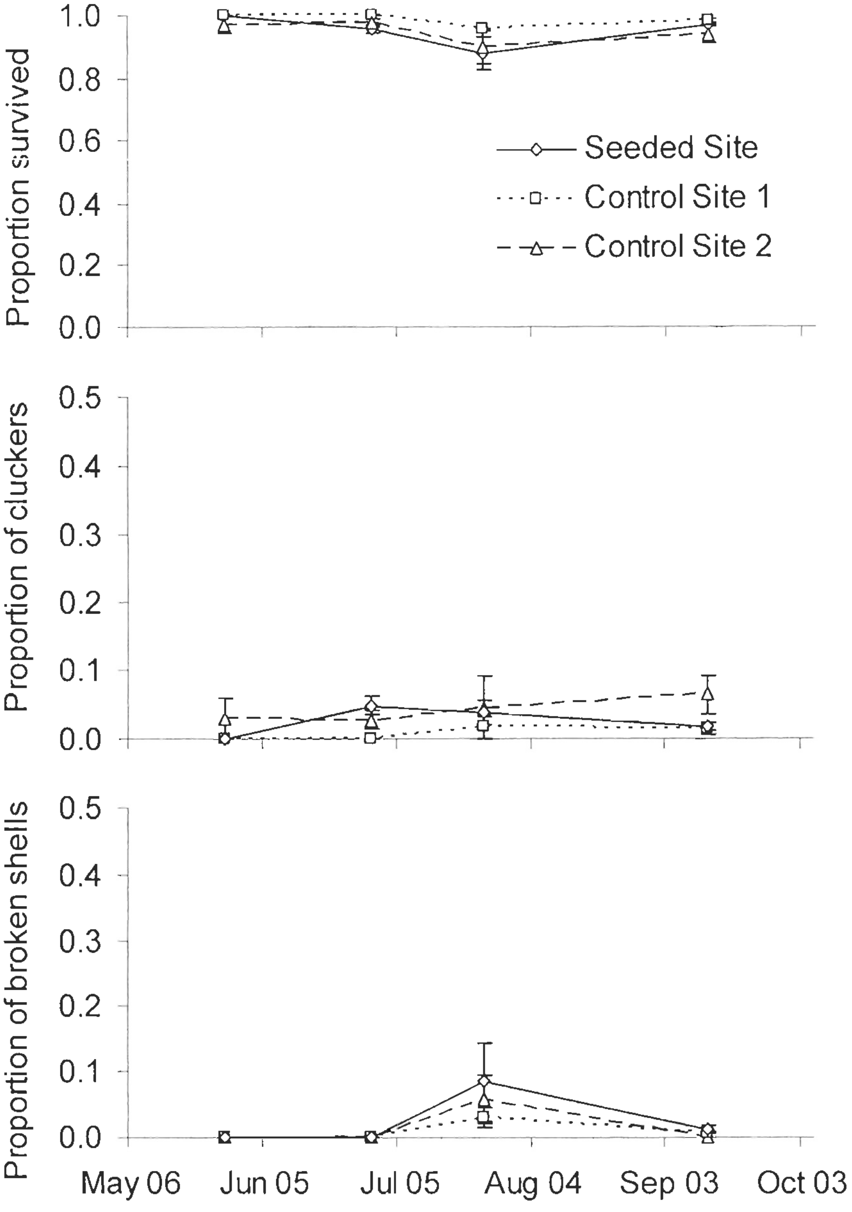

Figure 4.11. Mean proportions (± SE) of deployed tethered scallops that survived after 24 h or died from predation by sea stars (cluckers) and crabs (broken shells), before, during and after the 2004 seeding trial at the seeded site (n=6) and control sites (n=3) in 2004. The vertical grey shading represent the seeding period that lasted ~ 2 wk. Note that the 29 June assays was included in the seeding period for analysis.

Table 4.9. Results of an ANOVA on proportion of tethered scallops surviving in 2004. Planned comparisons were performed when Time was significant. Significant differences (*p*<0.05) are indicated in bold. Data were arcsin square root transformed.

Source of variation	df	MS	F	*p*
Time	3	0.286	5.90	**0.001**
B vs A	*1*	*0.711*	*14.67*	***<0.001***
D vs B, A	*1*	*0.052*	*1.07*	*0.304*
Site	2	0.141	2.91	0.060
Time*Site	6	0.029	0.60	0.731
Error	84	0.048		

B: before seeding; A: after seeding; D: during seeding

Table 4.10. Results of a MANOVA on the proportion of tethered scallops that died due to sea star (cluckers) and crab (broken shells) predation in 2004. Data were $\log_{10}$(datum+0.01) transformed. Planned comparisons were performed when Time was significant; significant differences ($p<0.05$) are indicated in bold. Standardized canonical coefficients were calculated for significant sources of variation, and important canonical coefficients (with relatively high absolute values for a given effect) are also indicated in bold.

Source of variation	df1, df2	F	*p*	Canonical coefficients	
				Cluckers	Broken shells
Time	6, 168	5.09	**<0.001**	0.46	1.07
B vs A	*2, 83*	*9.17*	***<0.001***	***0.77***	***0.91***
D vs B, A	*2, 83*	*2.28*	*0.109*		
Site	4, 168	1.65	0.165		
Time*Site	12, 168	0.70	0.747		

B: before seeding; A: after seeding; D: during seeding

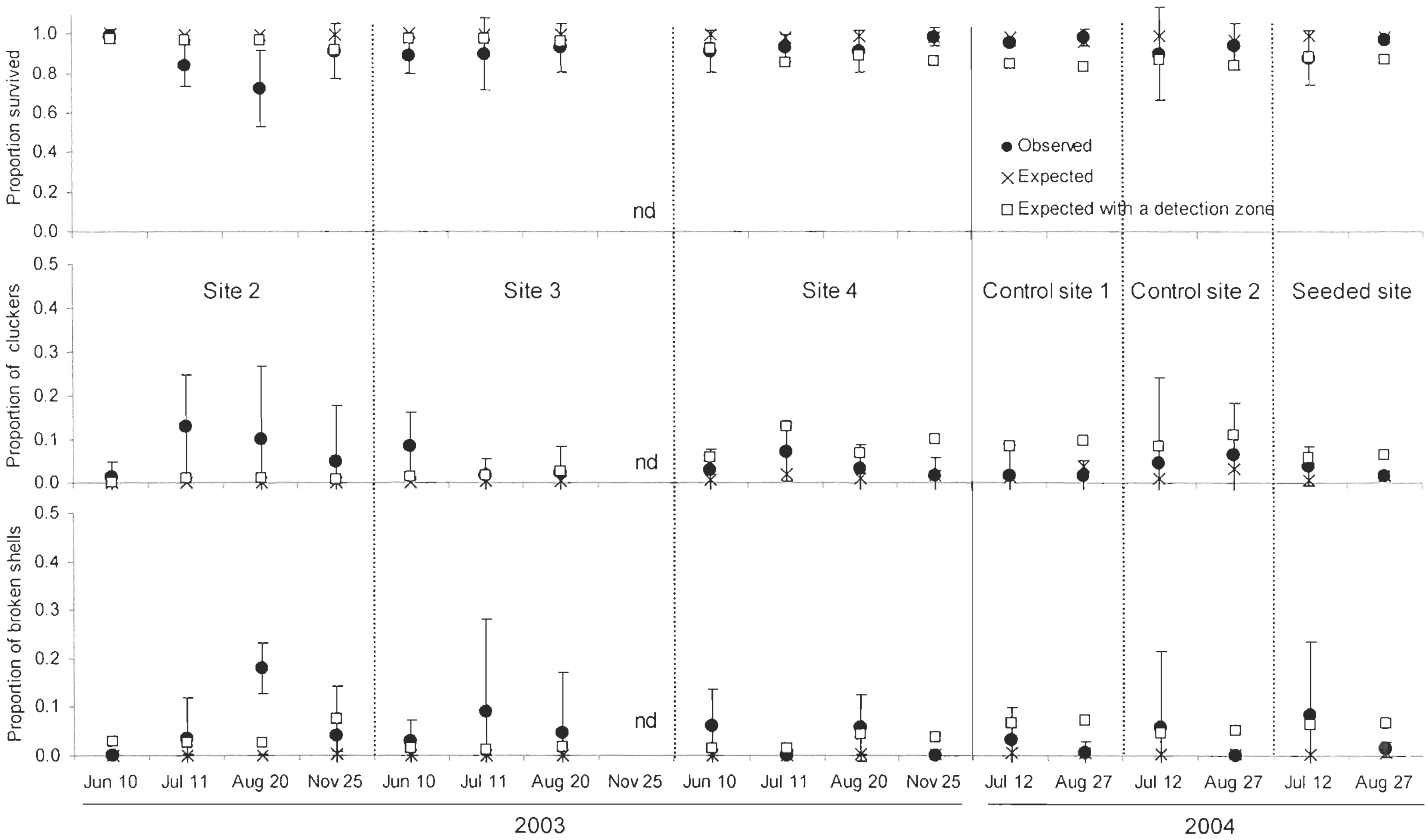

Figure 4.12. Comparison of observed proportion of tethered scallops (mean± 95% CI) that survived and died from predation by sea stars (cluckers) and crabs (broken shells) after 24 h in 2003 and 2004 and expected proportion (mean± 95% CI, confidence intervals are small so are not visible) from the basic model and the model with a detection zone around scallops. No simulation was performed in May and June 2004 because of the low accuracy of the predator surveys.

4.4 Discussion

In this study, two experimental designs were used to evaluate the predation impact after a large-scale scallop seeding trial. In 2003, the design focussed on temporal variations, without replicated, independent controls. This first design imposed limitations. For instance, temporal variations were observed but could not be related solely to seeding, since variations might be attributed to other processes such as seasonal displacement or recruitment of animals. Thus, independent, replicate control sites were required to confirm that observed variations in response variables (e.g. predator densities) were actually related to a seeding event. On this basis, the 2004 design was improved to an asymmetrical spatial design with one seeded (impacted) site and two control sites, temporally surveyed before and after seeding, following the "beyond BACI" design (Underwood 1993, 1994). Such a design is recommended in environmental impact studies, when only one putatively impacted site is available; multiple control sites are used to quantify natural variation, and then the temporal pattern in the putatively impacted site can be compared to the natural patterns. For our second experiment, however, the strength of this design was lowered because our sampling technique was different before and after seeding and because of loss of some replicate predation assays. Nevertheless, the framework of the "beyond BACI" design guided the analysis of the 2004 seeding trial.

4.4.1 Dynamics of seeded scallops

Dynamics of juvenile scallops after their release to the sea bottom are multifaceted, because of interactive effects of scallop vitality and behaviour in response to disturbance, environmental conditions (including temperature, sediment type, predators, conspecifics) and predator behaviour. In our study, we monitored, to some extent, juvenile scallops over the short term (a week to a few months) after the 2004 seeding. First, we observed that the distribution of scallops on the seabed following seeding was clumped, presumably because of the method of seeding itself. At seeding, juvenile scallops are thrown by batches (which were previously placed in baskets for transport) along predetermined transects. Videofilming by SCUBA divers during seeding (see Chapter 5) showed that scallops sank essentially straight down with a swinging motion to the sea bottom, and once there they were in clusters (Appendix 5). Second, upon reaching the sea bottom, dispersal and mortality can be important. Hatcher et al. (1996) observed that scallops move rapidly by jumps and brief swims of a few centimetres shortly after seeding. As well during this first phase after seeding, the general state (vitality state) of the scallop affects their mortality. Hatcher et al. (1996) estimated a 2% loss of scallops due to handling stress prior to and during release. Indeed, focused studies indicated that handling stress and air exposure reduces the contractile performance and energy level of muscles of cultured juvenile scallops prior to seeding (Fleury et al. 1996; Guderley et al. 2008). These physiological measures are good indicators of the scallops' escape abilities from predators and of their general state.

For the 2004 seeding trial, the initial scallop density (2.4 scallops · m^{-2}) decreased 10 times after 2 weeks. Such a rapid decline has also been observed in small-scale scallop seeding trials (Volkov et al. 1985; Cliche et al. 1994; Barbeau et al. 1996; Hatcher et al. 1996), and was attributed mostly to predator-related mortality and to dispersal of seeded scallops. These two processes are hard to discern from one another, and predation can not be responsible for all scallop losses. For our 2004 seeding trial, a daily loss of 5% from predation (estimated from the 2004 tethered scallop assays) would lead to a density of 1.3 scallops · m^{-2} after two weeks, which is about 5 times higher than the actually density observed in the field at that time.

Scallop dispersal induces greater scallop losses than expected. In support of this statement, we noticed seeded scallops on the control sites (>0.5 km away) shortly after seeding. Juvenile sea scallops are good swimmers (Caddy 1968; Dadswell & Weihs 1990; Manuel & Dadswell 1991) and several factors can trigger their swimming response and subsequent displacement. This includes predator encounters (Barbeau & Scheibling 1994a), unsatisfactory substrate (Stokesbury & Himmelman 1996; Wong & Barbeau 2003; Bourgeois et al. 2006; Wong et al. 2006b) or physical changes such as salinity and temperature (Thomas & Gruffydd 1971; Winter & Hamilton 1985; Dadswell & Weihs 1990; Orensanz et al. 1991). Scallops may also disperse to reduce competition for a limiting resource (most likely food) and to increase reproduction success (Dadswell & Weihs 1990; Orensenz et al. 1991); since our study was with juvenile scallops, this latter is not applicable to our situation. In our study, we carefully selected our seeded site to have optimal physical conditions, including appropriate substrate and good water temperature and so, predator encounters and the heterogeneous distribution of seeded scallop are most likely suspected to have induced dispersal.

Scallops may move randomly or show directional displacement (Volkov et al. 1985; Carsen et al. 1995); the latter may reflect the hydrodynamic regime (Moore & Marshall 1967; Posgay 1981; Caddy 1989; Cliche et al. 1994). For our 2004 seeding trial, water currents near the bottom were predominantly in a southwest-northeast orientation. This orientation is consistent with the presence of seeded scallops on control Site 1 located ~1 km southwest from the seeding area. However, other factors must have driven the dispersal of scallops onto control Site 2 (>1.5 km away), which was not located within the predominant current orientations at seeding and during the survey period. Previous seeding studies also denoted that the dispersal of seeded scallops did not always coincide with the primary current vectors (Cliche et al. 1994; Carsen et al. 1995; Hatcher et al. 1996), even in strong currents situations (see Hatcher et al. 1996 , with average of 16-21 cm $\cdot$ s^{-1} and peak speeds reaching 60 m $\cdot$ s^{-1}). The timing of scallops swimming relative to the current regime may better explain the direction and distance of the seeded scallop dispersal (Carsen et al. 1995; Barbeau et al. 1996). Therefore, according Carsen et al. (1995) and Brand (2006), the interaction between scallop behaviour and various physical (e.g. substrate and current regime) and biological (e.g. predator species and abundance) factors determine the patterns of scallop movement on a local scale.

The distance between seeded and control sites may appear quite large for juvenile scallops to disperse over. Juvenile sea scallops (15-30 cm, shell height) were estimated in tank to move as far as 50 cm at each swimming excursion (Gangnery et al. 2004). If scallop performs one swimming excursion per day, this will only lead to a displacement of 7 m, which is a lot lower to the observed displacement. Obviously the hydrodynamic regime did facilitate greatly the scallop displacement. In comparison, tagged scallops (larger than 60 mm) on Georges Bank were estimated to move as much as 10 km in a year (Posgay 1981). Recorded dispersal distances of juvenile sea scallops during small-scale trials and experiments were lower: e.g. less than 16 m after 3 months (Parsons et al. 1992) to more than 60 m after 44 days (Cliche et al. 1994). Hatcher et al. (1996) estimated an average net displacement of juveniles scallops over 13 months at 35 m and the furthest displacement was 93 m.

In summary, predation may be related to 50% of the scallop losses (based on the 2004 tethered assays) and so, dispersion would be related to the other half. The heterogeneous distribution of seeded scallops and the predator assemblage may have contributed in this dispersal. The main hydrodynamic condition is apparently not related with the directional pattern of scallop displacement but may still have favoured rapid scallop loss.

4.4.2 Predator assemblages

The abundance of predators was relatively low on our study areas (approx. 6 sea stars and 1 crab · 100 m^{-2}), and the predator assemblage was mainly composed of sea stars *L. polaris* and *C. papposus*. The predation effect of *L. polaris* on juvenile sea scallops, observed in the laboratory in Chapter 2, is expected to be low in the field. This sea star species specializes in digging sediment and its diet consists mainly of infaunal bivalves (Dutil 1988; Gaymer et al. 2001; Himmelman et al. 2005). The predation effect of *C. papposus* on scallops has not been fully documented. Some observations were collected in tanks (Nadeau & Cliche 1998), which suggested that it may be able to prey efficiently on juvenile scallops. The probability of scallop dying upon encountering *C. papposus* was recently estimated at 0.5 (Nadeau, unpublished data). Himmelman et al. (2005) also mentioned that *C. papposus* can be rapid at capturing epifaunal prey in the field. The diet of this sea star species typically includes mollusc, but also echinoderms, such as other sea stars, urchins and sand dollars (Sloan 1980; Gaymer et al. 2004; Himmelman et al. 2005). This diversified diet suggests that this sea star species may be a generalist, and so it may have a significant impact on the relatively abundant seeded scallops.

Unfortunately in our study, any variation in the predator assemblage observed before and after seeding cannot be fully attributed to the scallop seeding events, because we did not have enough control sites in 2003 and because of change in the camera surveying technique mid-way through the trial in 2004. In the end, we only detected one temporal change if predator density associated with the seeding event (the one in 2003): we observed a short-term increase in *H. araneus* abundance after seeding. Despite these experimental limitations, useful information was collected. In particular, a spatial segregation among sea star species was noticed in 2004 where *A. vulgaris* density was negatively correlated with the two other two sea stars *L. polaris* and *C. papposus.* A similar pattern was also observed during a seasonal survey conducted on scallop grounds off the Îles de la Madeleine (Chapter 3). This negative correlation among sea star species might be related to interspecific interactions, food preference or recruitment strategy, as discussed previously.

Despite our study limitations, the trend of our results are in agreement with small-scale scallop seeding studies conducted in Atlantic Canada, which did not find any evidence of variations in the predator assemblage at seeding (Cliche et al. 1994; Barbeau et al. 1996; Hatcher et al.1996). However, variations were observed in a large-scale seeding trial of another scallop species, the Japanese scallop (*Pecten yeossensis*) (Volkov et al. 1985). Sea star density increased following seeding of 100 000 scallops (1000 ind. · m^{-2}) in the Sea of Japan). In addition, variation in the sea star assemblage was observed by Silina (2008) after scallop seeding trials (*P. yeossensis*, ~750 000 ind.; 5-20 ind. · m^{-2}). In the latter study, large and mobile sea star species increased in abundance, and appeared to compete with other sea star species, reducing their abundances.

As mentioned previously, predator densities in our study did not show an aggregative response following the seeding event, but variation in predator size may reflect a seeding impact over a few months. In July 2004, all predator species were at their smallest mean sizes. Although we suggest the following with caution, this size pattern may be related to a general recruitment event by predator species induced by the 2003 seeding trial (conducted in the general area of the 2004 seeding trial, Fig. 4.1), which may have provided relatively high food availability and favoured predator fecundity. The pattern is consistent with the so-called "bottom up effect" where lower trophic-level species simulate changes in consumer population at higher level, by increasing their abundance, reproduction and/or growth rates (McQueen et al. 1989). Another example is the large pulse of mussel recruitment in Gulf of Maine, which was followed by an important sea star recruitment, suggesting a feedback between food supply and consumer recruitment (Witman et al. 2003).

In summary, no clear variation in the predator assemblage could have been attributed to seeding in both studied years. The only change that may be associated to seeding event was the rapid increase of *H. araneus*, after seeding in 2004.

4.4.3 Relationship between multiple predator assemblages and scallop predation

Because of the low predator densities and the lack of an aggregative response, we strongly suspect that multiple predator interactions would be uncommon. In fact, predation potential estimated using tethered scallops was relatively low (>90% of scallop surviving in 24 h) and constant over both years of the study. The few variations in predation potential observed were not clearly related to seeding events, and were not correlated with the predator characteristics.

It is actually meaningful that the proportion of tethered scallops dying did not change spatially and temporally on the seeded sites. It reflects a functional response by predators to high scallop density. Recall that for a type I response, predation rate increases linearly with prey density, and so proportional mortality of prey is independent of prey density (i.e. a straight horizontal line on a graph of proportional mortality vs. prey density; Taylor 1984). If predators did not increase their individual consumption rate as prey density increases, then proportional mortality of prey would decrease with increasing prey density. Hence, our tethering data suggest that predators had at least a type I functional response. A type II or III functional response is also possible if the predation events occur before predators become satiated at high prey density. Identification of the type of functional response can actually be quite difficult (Lipcius & Hines 1986; Wong & Barbeau 2006;

Wong et al. 2006a). Based on past studies with sea stars and crabs preying on juvenile sea scallops, a type I functional response is expected for the sea star *A. vulgaris* (Barbeau et al. 1994, 1998), and a type III response for the crab *C. irroratus* (Barbeau et al. 1994; Barbeau et al. 1998; Wong et al. 2005).

Our tethered scallop assays are clusters of scallops, which may have actually represented well the seeding situation, since seeded scallops were contagiously distributed immediately after seeding. Comparison of the observed fraction of frames with no dead tethered scallops to a calculated probability of frames not encountering a predator suggested that the scallop clusters may have attracted predators in the seeded sites. In other words, there may have been an aggregative response at a scale smaller than the one we surveyed. In contrast in the non-seeded sites, comparison of the observed fraction of frames with no scallop mortality to the calculated probability of frames not encountering predators suggested random movements of predators. Overall, the hypothesis of predators exhibiting directed movement towards prey inside the seeded area cannot be rejected. Such an interaction between prey distribution patterns and predator behaviour is reported by Hines et al. (2009) in a predation study on blue crabs and clams. Their study on predator-prey dynamics at various patch scales and inter-patch distances showed that crab aggregation was induced by chemosensory cues which facilitated predation at one scale, but if aggregations were too tight (predators to close to one another), crabs became agonistic and their feeding efficiency was reduced at a smaller scale.

The predation potential predicted from the basic model was in relatively good agreement with field observations and the use of a detection zone around each scallop did not increase the correspondence with observations. The predation model estimates predation potential using a type I response for sea stars and a type III for crabs. This information supports the functional response hypothesis described above. Furthermore based on the general agreement between predicted and observed predation potential, the hypothesis of a non-additive impact of predators is not supported, or, if it occurred, it did not greatly modify overall predation. Still, predator aggregations at a patch scale, as suggested above, may have modified predation dynamics inside the seeded area. A closer examination of our 2003 tethering results indicates that scallop survival inside the seeded area (Sites 2 and 3) was always lower than that expected from both models (the basic model and the model with the detection zone, Fig. 4.12), whereas scallop survival in outer site were similar or lower than expected. However, no such situation was detected in 2004. So, the first seeding trial seems to show that the predation model did not fully capture the predator dynamics, and it may be that predator aggregative behaviours at a small-scale contributed in this non-correspondence.

4.4.4 Evaluation of experimental tools

During this study, two techniques of video survey were used: a pyramid that provided stable images and a mobile sleigh that provided video sequences. The latter had the advantage of covering a greater surface (3000 m^2) than the pyramid (80 m^2) during a field day. This is important particularly when surveyed populations are contagiously distributed, such as scallops and sea stars, and when the budget is limited. A disadvantage of this mobile system, similar to a fishing dredge, is that it may trigger scallop swimming prior video capture and so, may introduce biases (Caddy 1968; Caddy 1989; Orensanz et al. 1991). However, preliminary trials observed minimal swimming escapes by scallops to our sleigh and so, this method was considered reliable (Appendix 4, see also Franklin et al. 1980). The pyramid is still a good approach for small-scale seeding surveys (Chapter 5) or when a high degree of accuracy and precision is needed. Such a pyramid method is described in Stokesbury (2002), and it is currently used to survey the natural sea scallop population on Georges Bank.

The tethering approach is useful to estimate predation potential as a comparative measure of predation (Aronson et al. 2001). Various biases caused by tethering have been documented in laboratory studies (Barbeau & Scheibling 1994b; Chapter 2), but have not been previously and specifically examined in the field (partly by Talman et al. 2004). First, the use of frames on the sea bottom may act as refuges for predators, because it increases substrate heterogeneity. However, Talman et al. (2004) tested the effect of a similar structure (a length of chain) alone (without tethered scallops) on predator attraction, and found no significant effect. Second, the tethering operation itself (handling, air exposure) may have affected scallop vitality. To reduce this bias, the state of tethered scallops was carefully inspected and mortality (<1%) was estimated prior to deployment of frames and removed from the predation estimation. However, assessment of vitality of tethered scallops is difficult to do, and so it was assumed to be equivalent to the vitality of seeded scallops (which were submitted to similar stress conditions). Finally, as discussed above, the relatively high scallop density deployed in clusters (i.e., the frames) may have attracted predators on a small scale. On the seeded site, this artificial spatial structure may have simulated better the seeding condition (since seeded scallops were also distributed in patches). However on control sites and later on seeding sites (when scallop density decreased), it may have contributed to increased predation potential and therefore reduced our ability to detect spatial and temporal variation in predation potential. Nevertheless, we devised a way to mathematically assess if frames of tethered scallop attracted predators by comparing observed fractions of frames with no mortality with the calculated probabilities of each predator species to not encounter a frame. We found no suggestion of predator attraction on the non-seeded sites, but attraction may have occurred in some cases later on the seeding sites.

Barbeau and Caswell (1999)'s predation model was chosen to evaluate the hypothesis for independent multiple predator impact. This model was developed to simulate survival of seeded scallops to commercial size (~4 y), and assumed a random scallop distribution. Therefore, this tool may not be fully adequate to simulate predation of scallops over a very short time (24 h) as in our situation. Furthermore, our situation involved frames with tethered scallops (i.e., clusters) which may have modified predator behaviour. For instance, the random searching behaviour assume into the model, as described in Holling (1966, p: 51-52), may have been changed to a more directed movement behaviour by presence of clusters. Thus, the model may need some refinements or extensions to take into account directional displacement of predators and cluster geometry. As well, the addition of fish predation may also contribute to the refinement of the model. All in all, though, the model was built to reflect predator-prey interactions at their simplest, using random distributions of animals, random movements of animals (based on the size and movement velocity of the types of animals involved; Holling 1966), observed probabilities of prey being consumed upon predator encounter, and predators interacting independently of one another. The only complexity built into the model was a type III functional response for crab predators. This model is thus useful to provide a null or basic scenario.

4.4.5 Implications for aquaculture

Despite unintended complexities, our study provided insights that should contribute to improve the success of large-scale scallop seeding trials. It is obvious that the dynamics of scallop clusters and of predators after seeding should be more documented to further assess the suitability of scallop seeding to the aquaculture industry.

Based on our study, the contagious distribution of seeded scallops in clusters of high densities may have contributed to the rapid predation and scallop dispersal after seeding. Recently, the effect of scallop density at seeding on predator behaviour was studied by Wong et al. (2005). They found that plots seeded at 6 scallops $\cdot$ m^{-2} decreased at a slower rate than scallop seeded at high density (69 scallops $\cdot$ m^{-2}) and so, scallops seeded at a lower density may have some short-term protection from predation. Density is thus an important factor that may influence the survival of scallops. Therefore, the method of seeding should be modified to better distribute the juvenile scallops over the seeding area.

Dispersal by scallops appeared to be a major cause of loss, even though we initially expected that the emigration out of a large scale seeding would be limited (Barbeau & Caswell 1999). As mentioned previously, various factors may explain this dispersal, but there is a need for more investigations. For instance, the effect of high scallop density on scallop dispersal is not clearly demonstrated and should be further studied (Orensanz et al. 1992; Wong et al. 2005). In addition, as mentioned in Chapter 3, the use of a grid to characterize at small scale the biophysical condition on a site prior to seeding may be worthwhile to avoid sand substrate or high density predator patches, and so, adjust the strategy to minimize dispersal potential.

In past studies, various alternatives have been proposed to reduce scallop losses at seeding and these can be relevant for the conditions at the Îles de la Madeleine. Wong et al. (2005) proposed the use of alternative prey, such as mussels, to distract predators from scallops during the vulnerable short time window after seeding. Modifying the natural sand substrate by adding scallop shells was also proposed by Bourgeois et al. (2006) to improve the seeding success, because it reduces scallop dispersal and predation. The perturbation analysis conducted in the Barbeau and Caswell (1999)'s modelling exercise for seeded scallop populations indicated that increasing the initial size of scallops at seeding increases their survival. However, as juveniles of 30-100 mm are in their most motile phase, seeding smaller sedentary juveniles (1-30 mm) may limit their short-term dispersal (Dadswell & Weihs 1990). Finally, predator control measures such as fences surrounding the seeded area were developed in Norway (Bergh & Strand 2001), but may be difficult to implement in deep water environments, and to provide the regularly needed maintenance (Boudreau et al. 2005). Some predator control strategies, such as removal of predators with dredges (Galtsoff & Loosanoff 1939; Masuda & Tsukamoto 1998; Uki 2006) can be used prior to seeding. However, such an approach did not clearly lead to better recapture rates in Îles de la Madeleine (Hébert et al. 2005). We conclude that various precautions must be taken into account to succeed with the scallop bottom seeding strategy.

CHAPITRE 5

Dynamique de la prédation des pétoncles géants (*Placopecten magellanicus*) juvéniles et de leurs prédateurs à court terme après des ensemencements à petite échelle au large des îles de la Madeleine, Québec

Short-term dynamics of juvenile sea scallops (*Placopecten magellanicus*) and their predators following a small-scale seeding trial off the Îles de la Madeleine, Québec

RÉSUMÉ

Les ensemencements de pétoncles géants (*Placopecten magellanicus*) juvéniles sur le fond marin ont été proposés aux pêcheurs des Îles-de-la-Madeleine comme un moyen pour maintenir la stabilité des récoltes sur les gisements de pétoncles. Toutefois, la sélection d'une taille appropriée des pétoncles à l'ensemencement est un facteur qui influence grandement la faisabilité économique des opérations d'ensemencement. C'est pourquoi, une étude sur le terrain a été menée pour comparer la survie des pétoncles de différentes tailles à l'ensemencement. Cette étude a aussi été une occasion pour récolter des données sur la dynamique des pétoncles et de leurs prédateurs après un ensemencement à petite échelle (0,01 km^2). Pour le besoin de cette thèse, des efforts ont été consacrés à récolter des données sur le traitement expérimental avec les pétoncles de la classe de taille de 25-35 mm de hauteur de coquille. Immédiatement après l'ensemencement, la distribution des pétoncles se présentait sous forme d'agrégations de taille et de densité variées. Ensuite, la dynamique des pétoncles a été rapide. Un mois après l'ensemencement, la plupart des pertes (63%) dans les agrégations ont été associés à la prédation par les étoiles de mer mais surtout par les crustacés décapodes. Deux mois plus tard, des pertes de 80% des pétoncles ensemencés ont été notées. L'assemblage des prédateurs a été dominé par l'étoile de mer *Asterias vulgaris* et le crabe *Cancer irroratus*, plus abondants (10 à 100 fois) que lors des études précédentes au large des îles de la Madeleine. Les étoiles de mer *A. vulgaris* ont aussi été plus petites (2 cm de rayon), limitant leur impact de prédation mais pas leur capacité d'induire la fuite des pétoncles. Aucune agrégation des prédateurs n'a été notée à la suite des ensemencements. La dispersion des pétoncles semble également avoir contribué à la perte des pétoncles ensemencés puisque des pétoncles juvéniles ont été notés sur des sites contrôles (~100 m plus loin). Les fuites associées aux prédateurs et les grandes densités des pétoncles dans les agrégations à l'ensemencement peuvent avoir contribuées à ces déplacements. Finalement, les ensemencements réalisés à petite échelle spatiale n'ont pas apporté de conclusions très différentes des ensemencements à grande échelle. Dans les deux cas, la dynamique de la prédation a semblé se dérouler à l'échelle des agrégations et donc, les études futures devraient cibler les processus à cette échelle.

ABSTRACT

Seeding juvenile sea scallops (*Placopecten magellanicus*) onto the seabed has been proposed to local scallop fishermen of the Îles de la Madeleine as a way to maintain stability of scallop bed harvests. However, selection of scallop size upon seeding is a factor that greatly influences the economical feasibility of seeding operations. For this reason, a field study was conducted to compare the survival of various scallop sizes upon seeding. It was also a good opportunity to collect additional data on dynamics of scallops and their predators after small-scale scallop seeding (0.01 km^2). For the purposes of this thesis, efforts were dedicated to collect data from the experimental treatment with seeded scallops in the 25-35 mm shell height size class. Immediately upon seeding, the seeded scallop distribution was clustered in patches of various sizes and densities. Thereafter, seeded scallop dynamics were rapid. One month after seeding, predation accounted for most of the scallop losses (63%) in patches. Sea stars and mainly decapod crustaceans caused this predation. Two months after seeding, 80% of seeded scallops were missing. The predator assemblage was dominated by the sea star *Asterias vulgaris* and crab *Cancer irroratus*, which were much more abundant (10 to 100 times) than previously studied off the Îles de la Madeleine. Sea stars *A. vulgaris* were also smaller (2 cm of radius), limiting their predation impact, but not their effect on triggering scallop swimming. No significant predator aggregation related to scallop seeding trials was detected. Sallops dispersal also contributed to scallop losses from seeded sites, based on the occurrence of small scallops one month after seeding on a few control sites (~100 m away). Escapes from predator and the high scallop density patches at seeding may have contributed to these displacements. Finally, this small scale seeding study lead to similar conclusions to those of previous large scale studies. In both cases, predation dynamics are likely occurring at the scale of patches and future studies should focus on processes on this scale.

5.1 Introduction

In 1994, a research program was started in Îles de la Madeleine (Québec) to assess the commercial feasibility of seeding juvenile scallops (*Placopecten magellanicus*) to enhance natural scallop populations (Cliche & Giguère 1998). This program was conducted with the close collaboration of local scallop fishermen and governmental research teams. However, the program was terminated in 2006, because of unsatisfactory recapture rates of scallops upon harvesting time, 4 to 5 years after seeding. At that moment, the scallop fishing plan was revised, and it was proposed that scallop seeding activity be pursued to add stability to the harvest of scallop beds off the coast of the Îles de la Madeleine. It thus became necessary to identify a seeding approach that could be managed by fishermen. To support this venture, a study was conducted between 2006 and 2008 to compare scallop survival and the economical feasibility of various seeding strategies, including the one used previously in large-scale seeding trials (which is to seed scallops of 20-40 mm shell height (SH) in June; Cliche & Giguère 1998), in a small-scale seeding experiment.

For the purpose of this thesis project, additional efforts were dedicated to collecting data on the dynamics of scallops and predators in the experimental treatment with the seeding strategy previously used in the large-scale seeding trials. These particular results will be useful to confirm (or not) the interpretation described in previous chapters, and to compensate for missing data due to the abrupt end of large-scale scallop seeding trials in 2005 and for experimental and implementation complexities that were unplanned in Chapter 4. We hypothesized that, in the small-scale seeding experiment, predators would aggregate inside the seeded sites in response to the sudden local increase in prey density, and that seeded scallops would consequently quickly disperse outside the seeded sites. The benthic predator assemblages as well as scallops were characterized before and after seeding in seeded and control sites, based on a symmetrical experimental design. Predator and scallop densities were estimated using a video camera system, and additional information on scallop survival was obtained using SCUBA diver surveys.

5.2 Material and methods

The experiment was conducted on a natural scallop ground located 8 km off the Îles de la Madeleine (Fig. 5.1). The study area is located at a depth of ~27 m, on a scallop fishing ground, closed since the mid-1990s to provide a refuge for scallop genitors. Selection of sites inside this area was based on presence of heterogeneous substrate (sand and gravel), suitable for juvenile scallops (Giguère et al. 2004). From the suitable sites, 7 sites of 0.01 km^2 (0.1 km x 0.1 km) were randomly selected for our focused study, and were separated by at least 0.1 km (Fig. 5.1). On 20 June 2007, 150 000 juvenile scallops (20-40 mm, 30.3 ± 0.2) were sown from a boat to reach a density of 5 scallops/m^2 (50 000 per site) over 3 sites chosen randomly among our sites; the 4 others were used as non-seeded control sites. Upon seeding, SCUBA divers confirmed that scallops were indeed falling onto the seeded sites.

A current meter (S4, InterOcean System Inc.) was submerged 2 m off the sea bottom prior to seeding in June 2007 to monitor water current strengths and directions until December 2007 (Fig. 5.1 and 5.2). Measurements were taken at each 10 min interval.

5.2.1 Sampling approach

Scallop and predator densities and sizes were quantified using a video camera (Multi-SeaCam, DSP&L, model S/N 2199-T) mounted on a sleigh as described in Chapters 3 and 4 for the first two surveys and thereafter mounted on a pyramid (Table 5.1, Fig. 5.3; based on Stokesbury (2002)). The pyramid was 1.4 m length, 1.4 m width and 1.1 m height and the camera was mounted vertically at a height of 0.72 m. A graduated cable was attached to the pyramid base, in a cross fashion within the camera's field of view, provided a usable field of view of 0.5 m^2 and allowed to measure animals on the recorded images. For both camera structures (the sleigh and the pyramid), four spot lights (Multi-SeaLite, DSP&L, model ML-2027) were attached around the camera to assure good image quality. The video recorder (DVD Panasonic, DMR-E50) was connected to the camera with a shielded multi-cable (McQuest Marine).

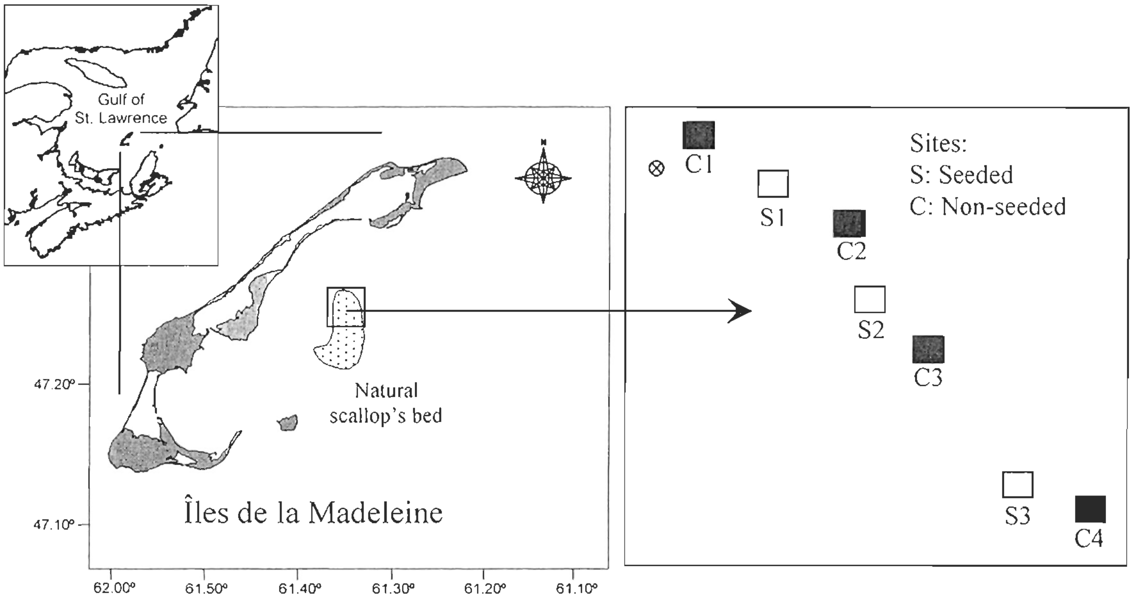

Figure 5.1. Maps of the study area off the coast of the Îles de la Madeleine, Québec. The dot indicates the approximate location of the current meter.

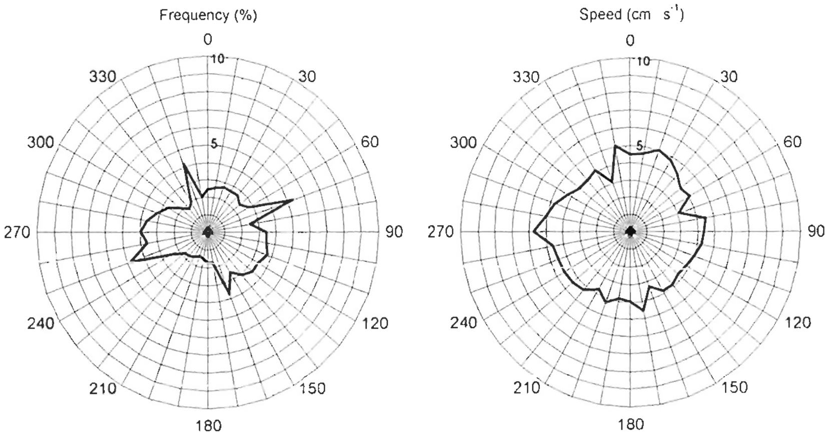

Figure 5.2. Frequency (%) and mean speed (cm · s^{-1}) of water current in relation to the directional degrees, 2 m off the sea bed on the study area from 11 July to 2 December 2007.

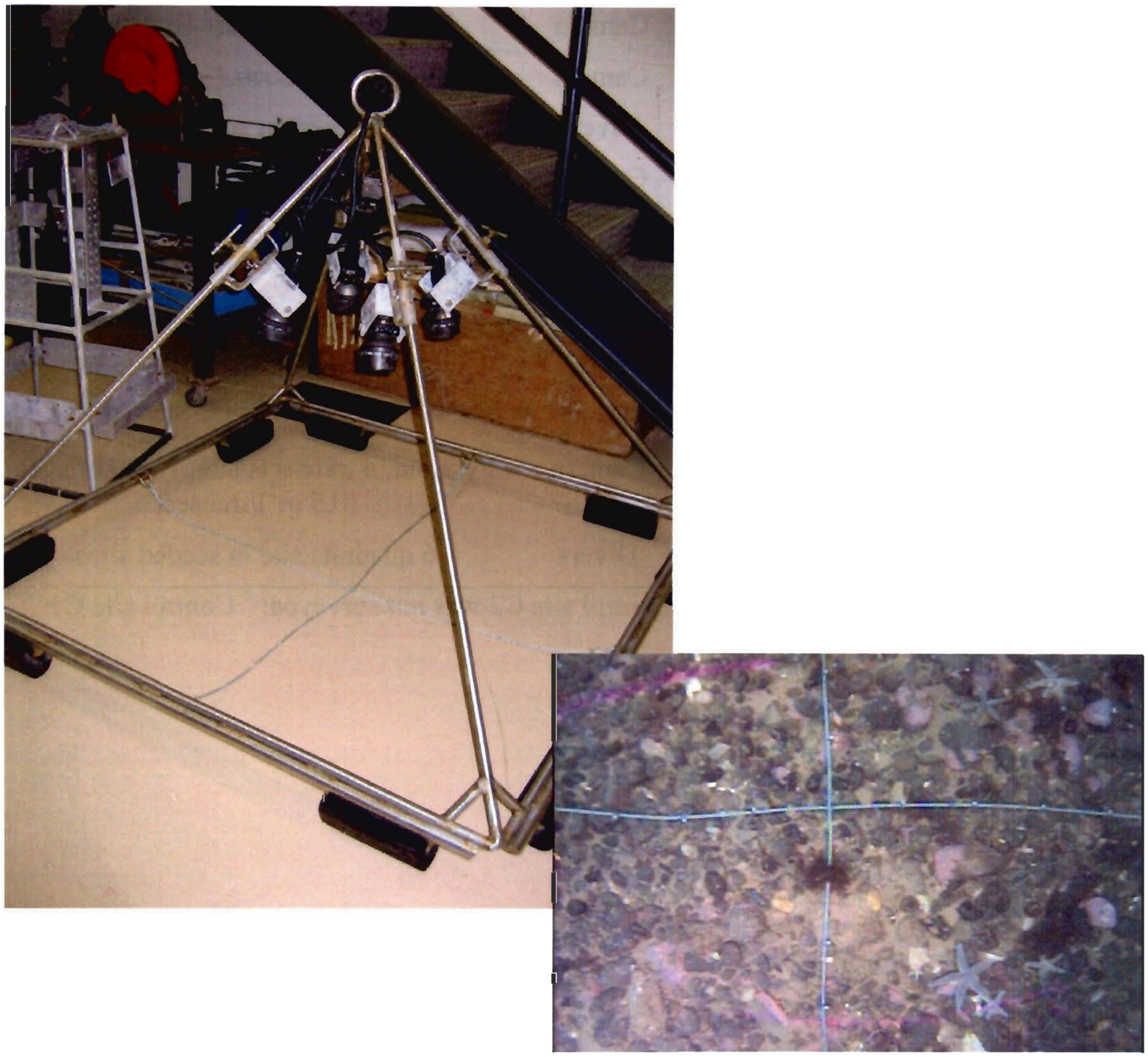

Figure 5.3. Pyramid used during the camera surveys conducted in June 26 to October 18 2004. The camera provided a usable field of view of 0.5 m^2.

Table 5.1. Summary of scallop and predator surveys conducted in 2007.

Time	Date	Approach	Sampling method
Before 3wk	May 30[1]	Camera	Sleigh, 3 transects (~10 m^2)/site
Before 1wk	June 13[2]	Camera	Sleigh, 3 transects (~10 m^2)/site
Seeding	June 20	Divers	Video camera at scallop seeding
After 1 wk	June 26[3]	Camera	Pyramid, 3 transects/site, 15-25 images (0.5 m^2)/transect
After 1 wk	June 29	Divers	6 quadrats /site in seeded sites
After 1 mo	July 23	Divers	6 quadrats /site in seeded sites
After 2 mo	Aug. 15-31 called later Aug. 23	Camera	Pyramid, 4 transects/site, 15-25 images (0.5 m^2)/transect
After 4 mo	Oct. 18	Camera	Pyramid, 4 transects/site, 10-20 images (0.5 m^2)/transect
After 4.5 mo	Nov. 9	Divers	6 quadrats/site in seeded sites

[1] Control site C4 was not surveyed; [2] Control site C2 was not surveyed; [3] Control site C1 was not surveyed.

At each survey, 3-4 replicate, random video transects were sampled per site (Table 5.1). Along each transect, the sleigh was pulled by the boat on a continuous video sequence or the pyramid was lowered to the sea floor and retrieved after a short video sequence of 5 s (10-25 short video sequences (also termed images) per transect) (Table 5.1). The GPS coordinates of each video sequence (from the sleigh and the pyramid) were noted. All video surveys were done during daytime, since no difference in predator composition and densities was detected between day and night (Appendix 1).

We used the software Image-PRO Plus (V4.1) to count and size scallops, and sea star and crab species from video sequences. Scallop and predator densities were estimated as number of individuals divided by surface area covered in each transect (number $\cdot$ m^{-2}). For the size measurement, the image distortion was rectified with a correction coefficients estimated depending on the position of each individual within the field of view (as explained in Chapter 3). Sea star size (*Asterias vulgaris*) was measured as radius, which is the distance from the tip of an average-length arm to the center of the body. Crab *Cancer irroratus* size was measured as carapace width, which is the largest width of the cephalothorax. Lobster *Homarus americanus* size was measured as carapace length, from the extreme rear of the eye socket to the opposite end of the cephalothorax. Scallops were measured as shell height, which is the diameter from the shell ventral edge to the hinge.

Periodic sampling was also performed by SCUBA divers (Table 5.1). The first dive was conducted at seeding with a video camera to confirm that released scallops from the boat were falling inside the seeded sites. Subsequent dives were conducted to estimate scallop mortality in juvenile scallop patches (>10 scallops $\cdot$ m^{-2}, sized 20-40 mm shell height) in the three seeded sites. This sampling was done with six 0.25-m^2 circular sampling units per seeded site (one unit per patch), and live and dead scallops were both counted by divers. Dead scallops were also collected to estimate in the laboratory the proportion that were associated to sea star predation (intact upper and lower shells still attached at the hinge (termed cluckers) or intact upper shells) and decapod crustacean predation (broken scallop shells) (Jamieson et al. 1982; Barbeau et al. 1994).

5.2.2 Statistical analysis

Statistical analyses were performed using SAS software (v8.02). For all analyses, each dependent variable was assessed graphically for normality of residuals and using Cochran's test (Winer et al. 1991) for homogeneity of variance. When necessary, data were transformed using $\log_{10}$(datum+0.01) to obtain homogeneity of variance.

Densities of scallops and predators were analysed using ANOVAs, with Time and Site as fixed factors. Data collected from the sleigh and the pyramid were analysed together as the area covered from both techniques was comparable. To deal with missing cells in the analysis (Table 5.2), we analysed 3 subsets of data with observations in all cells as proposed in Quinn and Keough (2002, p: 244-247). The first two ANOVAs analysed respectively the data collected 3 wk (control Site 2) or 1 wk (control Site 4) before seeding and the data collected during all samplings after seeding. These analyses were selected to evaluate if there was a press change shortly after seeding. The third ANOVA analysed the data collected from 3 control sites (Sites 1, 3 and 4) and from 3 seeded sites (Sites 1, 2 and 3) before (1 wk) and after seeding (2 and 4 mo). This analysis focussed on difference that occurred before and few months after seeding. The critical alpha was consequently adjusted using Bonferroni's method to 0.05/3= 0.017 (Quinn & Keough 2002, p. 49-50). A significant interaction between the fixed factors was further explored using relevant contrasts to assess the effect of seeding. An interaction between control and seeded sites before vs after seeding trials was used as indicative of a seeding impact (Underwood 1993). Other contrasts were also conducted to estimate the variation on control sites before (May-13 June) vs after (26 June to October) the seeding trial and on the seeded sites before and after seeding trial to evaluate if there was a press change following seeding in control and seeded sites following seeding.

An ANOVA was also performed on the size of sea stars (*A. vulgaris*) with Site and Time as fixed factors. The sea star measurements were pooled over transects, since there were occasionally not enough sea star individuals within a transect. Missing data were dealt with and planned comparisons were conducted as described above. No analysis was done on scallop, crab and lobster sizes because of the low number of individuals.

Table 5.2. Two-way structure of the field experiment, showing the missing cells (see also Table 5.1).

			Site						
			1	2	3	4	5	6	7
Time		Date	C1	C2	C3	C4	S1	S2	S3
1	Before 3 wk	May 30	μ_{11}	μ_{21}	μ_{31}	...	μ_{51}	μ_{61}	μ_{71}
2	Before 1 wk	June 13	μ_{12}	...	μ_{32}	μ_{42}	μ_{52}	μ_{62}	μ_{72}
3	After 1 wk	June 26	...	μ_{23}	μ_{33}	μ_{43}	μ_{53}	μ_{63}	μ_{73}
4	After 2 mo	Aug. 23	μ_{14}	μ_{24}	μ_{34}	μ_{44}	μ_{54}	μ_{64}	μ_{74}
5	After 4 mo	Oct. 18	μ_{15}	μ_{25}	μ_{35}	μ_{45}	μ_{55}	μ_{65}	μ_{75}

S: seeded site, C: control site, and before/after is relative to the seeding event; μ: the mean of a response variable for a given combination of Site and Time

5.3 Results

Before seeding, scallops density on seeded and control sites were estimated to be lower than 0.14 scallops · m^{-2}. A week after seeding, scallops reached a mean density of 1.1 ± 0.1 scallop · m^{-2} in seeded sites (Fig. 5.4), which is 5 times lower than the density aimed for upon seeding. This density was not maintained and dropped quickly over the next two months to reach 0.20 ± 0.06 scallop · m^{-2}. On the control sites, the overall density remained at 0.020 scallop ± 0.003 m^{-2}. An interaction was detected in all subsets analyses, before and after seeding, which is indicative of a seeding impact (Fig. 5.4; Table 5.3).

The scallop size distribution was also affected by the arrival of new juvenile scallops on the seeded sites a few days after seeding (June 26; Fig. 5). Two months after seeding, the scallop size distribution in control sites also appeared to be affected by seeding or a recruitment event, as scallop size was lower than previously (mean of 4.6 ± 0.7 cm shell height in August). Surprisingly, the mean scallop size on seeded sites was greater than that on control sites at that time. In the fall, scallop mean size in control sites was re-established, similar to before the seeding event, and the scallop size distribution in the seeded sites was still dominated by seeded scallops. The water current speed on the study area was estimated at 4.2 cm · s^{-1}, and did not show up any regular directional pattern that could be related to a northwest-southeast scallop dispersal (Fig. 5.2).

Based on SCUBA diver observations in the seeded sites, the overall average of the total (alive + dead) density of juveniles scallops in patches (± SE, n=3 sites) a few days after seeding was 31.1 ± 16.1 scallops · m^{-2}, and scallop survival in these patches was 87% (calculated as mean density of live scallops divided by mean total (alive and dead) density of scallops) (Fig. 5.6). About 75% of the shell remains were broken shells. A month later, total density of scallops (alive + dead) within patches was almost similar (37.3 ± 12.5 scallops· m^{-2}), but scallop survival dropped to 37% and shell remains were composed 50/50 of cluckers and broken shells. In the fall, the last survey detected total density in the patches had declined to 12.7 ± 12.4 scallops (alive + dead) · m^{-2} and only 14% of scallops were still alive (i.e. 1.8 ± 1.0 live scallops · m^{-2}). Broken shells mainly represented the shell remains (94%) at that time.

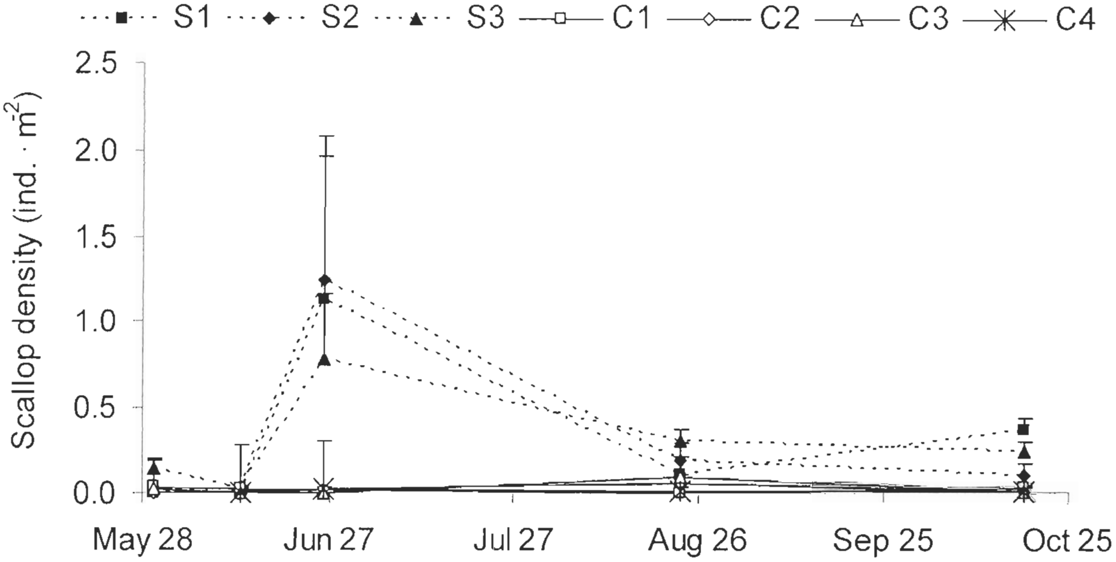

Figure 5.4. Mean densities (+ SE, n=3 or 4 transects) of scallops (all sizes) at 5 times and 6 to 7 sites (3 seeded and 3 to 4 non-seeded) in 2007. Juvenile scallops were seeded on June 20. Note: C4 is missing in May, C2 is missing on June 13 and C1 is missing on June 26.

Table 5.3. Results of ANOVAs on densities (ind.· m^{-2}) of juvenile scallops and predators in 2007. Data were transformed using $\log_{10}$(datum+0.01). Planned comparisons were conducted when the interaction term was significant. Significant and interpretable effects (p<0.017 for Bonferoni adjustment) are indicated in bold (*S: seeded and C: control sites; B: before and A: after seeding*).

Dependant variable	Source of variation	Time T2, T3, T4 and T5 Site C3, C4, S1, S2 and S3				Time T1, T3, T4 and T5 Site C2, C3, S1, S2 and S3				Time T2, T4 and T5 Site C1, C3, C4, S1, S2 and S3			
		df	MS	F	*p*	df	MS	F	*p*	df	MS	F	*p*
Scallop density	Time	3	2.960	15.16	<0.001	3	2.314	11.44	<0.001	2	2.390	11.81	<0.001
	Site	4	3.911	20.04	<0.001	4	3.711	18.34	<0.001	5	1.719	8.50	<0.001
	Time*Site	12	0.790	4.05	**<0.001**	12	0.956	4.72	**<0.001**	10	0.679	3.35	**0.001**
	S vs C (B vs A)	*1*	*2.032*	*10.41*	***<0.001***	*1*	*2.060*	*10.18*	***0.016***	*1*	*1.594*	*7.88*	***0.005***
	S (B vs A)	*2*	*0.129*	*0.66*	*0.522*	*2*	*0.915*	*4.52*	***0.016***	*2*	*0.217*	*1.17*	*0.319*
	C (B vs A)	*1*	*0.017*	*0.09*	*0.768*	*1*	*0.111*	*0.55*	*0.463*	*2*	*0.231*	*1.14*	*0.296*
	Error	50	0.195			50	0.202			48	0.185		
A. vulgaris density	Time	3	0.831	25.24	<0.001	3	0.963	27.67	<0.001	2	0.932	22.73	<0.001
	Site	4	2.818	85.62	<0.001	4	2.905	83.48	<0.001	5	2.571	62.71	<0.001
	Time*Site	12	0.230	6.98	**<0.001**	12	0.301	8.66	**<0.001**	10	0.204	4.96	**<0.001**
	S vs C (B vs A)	*1*	*0.212*	*6.43*	***0.014***	*1*	*0.609*	*17.50*	***<0.001***	*1*	*0.043*	*1.05*	*0.310*
	S (B vs A)	*2*	*0.347*	*10.54*	***<0.001***	*2*	*0.357*	*10.26*	***<0.001***	*2*	*0.676*	*16.50*	***<0.001***
	C (B vs A)	*1*	*0.208*	*6.32*	***0.015***	*1*	*0.150*	*4.32*	*0.043*	*2*	*0.171*	*4.17*	*0.021*
	Error	50	0.033			50	0.035			48	0.041		
C. irroratus density	Time	3	0.794	4.58	0.007	3	1.077	4.90	0.005	2	0.388	2.35	0.107
	Site	4	2.024	11.67	<0.001	4	1.214	5.53	<0.001	5	1.157	7.00	<0.001
	Time*Site	12	0.503	2.90	**0.004**	12	0.458	2.08	0.036	10	0.419	2.54	**0.015**
	S vs C (B vs A)	*1*	*0.311*	*1.79*	*0.186*	*1*	*0.432*	*1.96*	*0.167*	*1*	*0.158*	*0.96*	*0.333*
	S (B vs A)	*2*	*0.514*	*2.97*	*0.061*	*2*	*0.558*	*2.54*	*0.089*	*2*	*0.808*	*4.89*	***0.012***
	C (B vs A)	*1*	*0.535*	*3.09*	*0.085*	*1*	*0.005*	*0.02*	*0.880*	*2*	*0.964*	*5.83*	***0.005***
	Error	50	0.173			50	0.220			48	0.165		

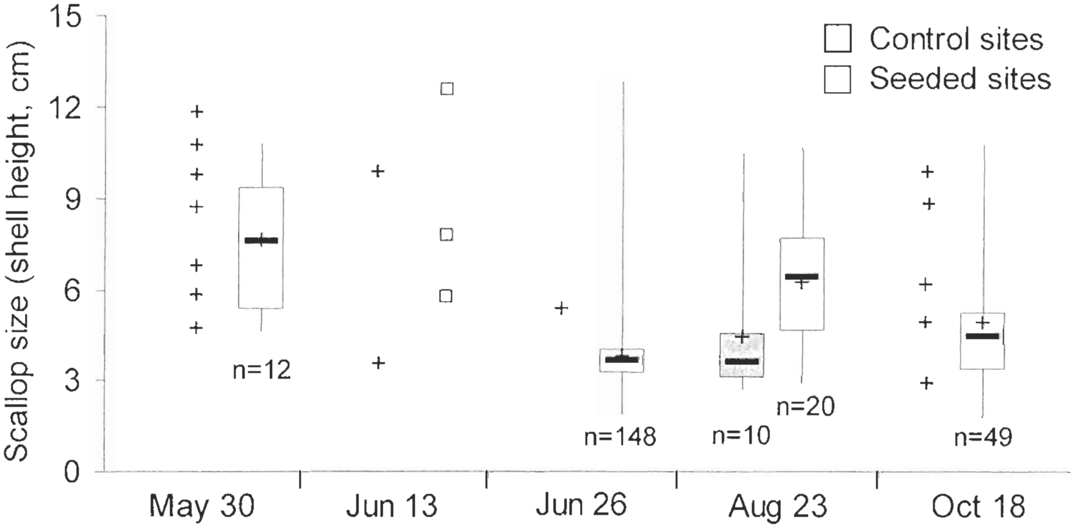

Figure 5.5. Box plots of scallop sizes (+ for control sites or □ for seeded sites: mean or simple value (when <10 ind.); horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values) at 5 times and at seeded and control sites in 2007. Data are pooled over transects and sites within each site type.

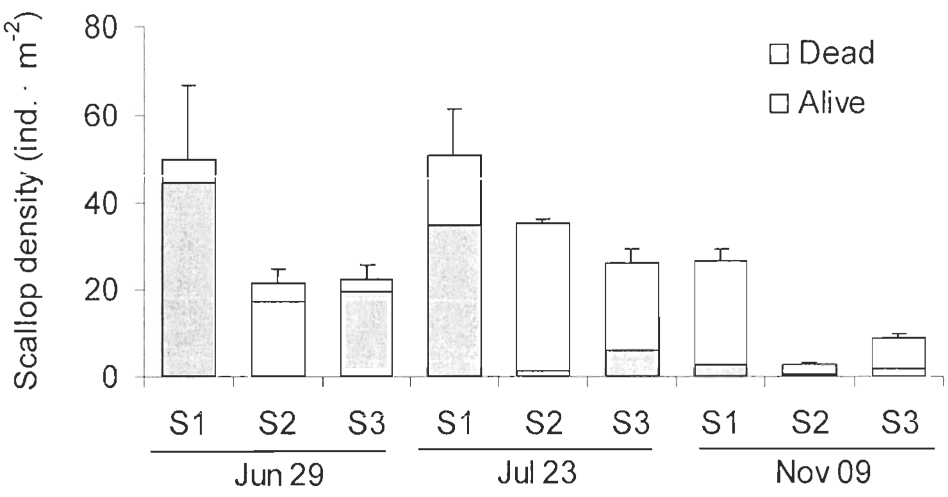

Figure 5.6. Mean densities (± SE, n= 6 quadrats) of juvenile scallops (20-40 mm, SH) alive and dead (based on shell remains, namely cluckers and broken shells), estimated by SCUBA divers inside scallop patches within each seeded site. The error bar is for the total (alive + dead) density of scallops.

The sea star *A. vulgaris* was the most abundant predator on the experimental area, peaking at 14.2 ± 3.0 ind. · m^{-2} on control site 3, prior to seeding (Fig. 5.7). No other sea star species were observed. The crab *C. irroratus* was the most abundant decapod, and its density was also particularly high on control site 3, where it reached a density of 0.30 ± 0.17 ind. · m^{-2}. A few lobsters *H. americanus* were observed on the experimental sites (0.01 ± 0.01 ind. · m^{-2}), but were not included in the statistical analysis.

Sea star density had a number of patterns among sites and time which were detected as significant interactions among control and seeded sites before vs after seeding (Table 5.3). However, based on planned comparison, these interactions cannot all be clearly attributed to seeding. For crabs, interaction mainly occurred on control sites before and after seeding and so were not be related to seeding.

Sea stars *A. vulgaris* were small in size (Fig. 5.8; overall mean of 2.4 ± 0.1 cm radius) all for all surveys, when compared to our previous studies (Chapters 3 and 4). Sea star size in seeded sites and in control sites changed over time (Table 5.4). However, it did not show significant pattern before vs after seeding trial that is different for the seeded sites and control sites, and so the observed patterns were not associated with seeding (Table 5.4). The overall mean size of crabs and lobsters was 8.8 ± 0.1 cm carapace width and 8.7 ± 0.3 cm carapace length, respectively.

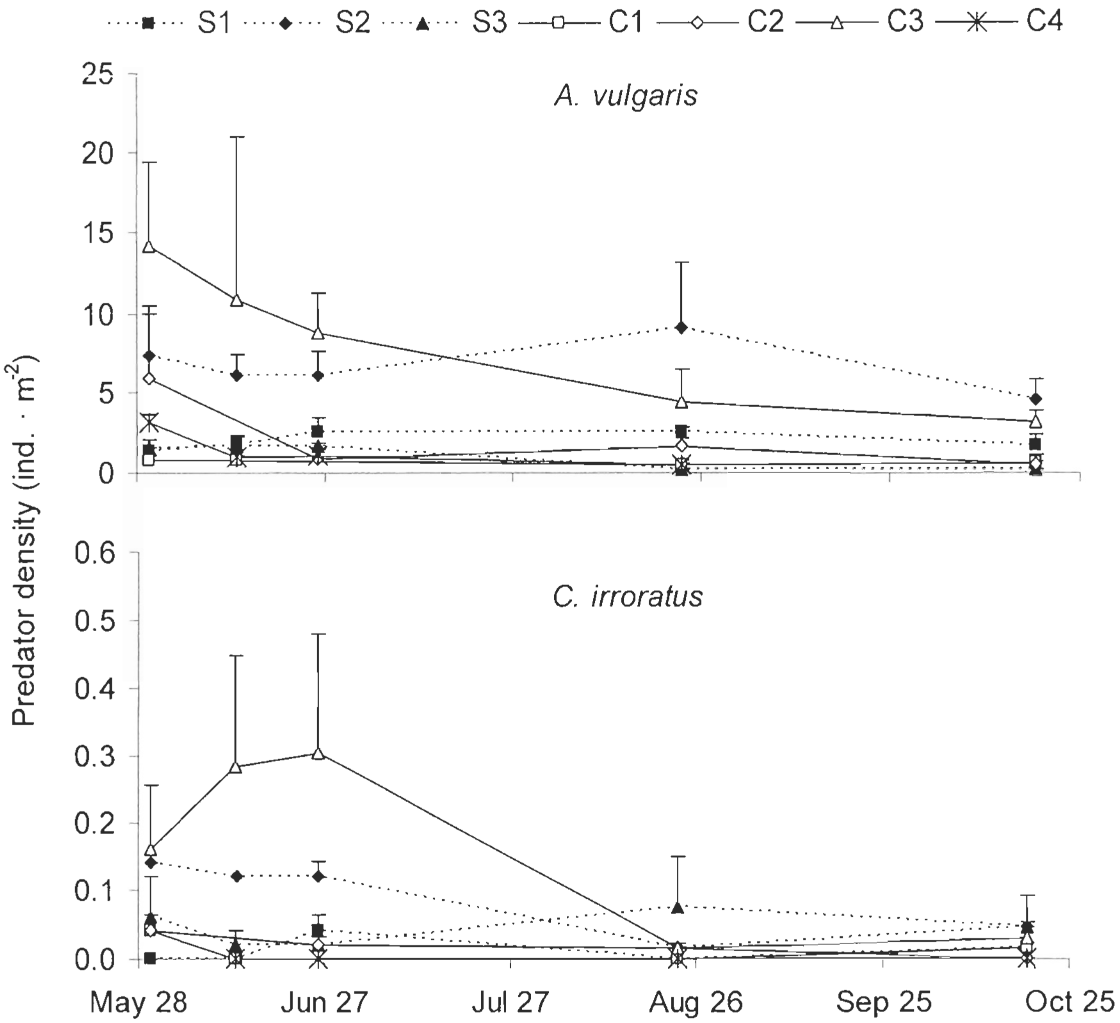

Figure 5.7. Mean densities (± SE, n=3 or 4 transects) of the two main predator species, *A. vulgaris* and *C. irroratus*, at 5 times and 6 to 7 sites (3 seeded and 3 to 4 non-seeded) in 2007. Juvenile scallops were seeded on June 20. Note: C4 is missing in May, C2 is missing on June 13 and C1 is missing on June 26.

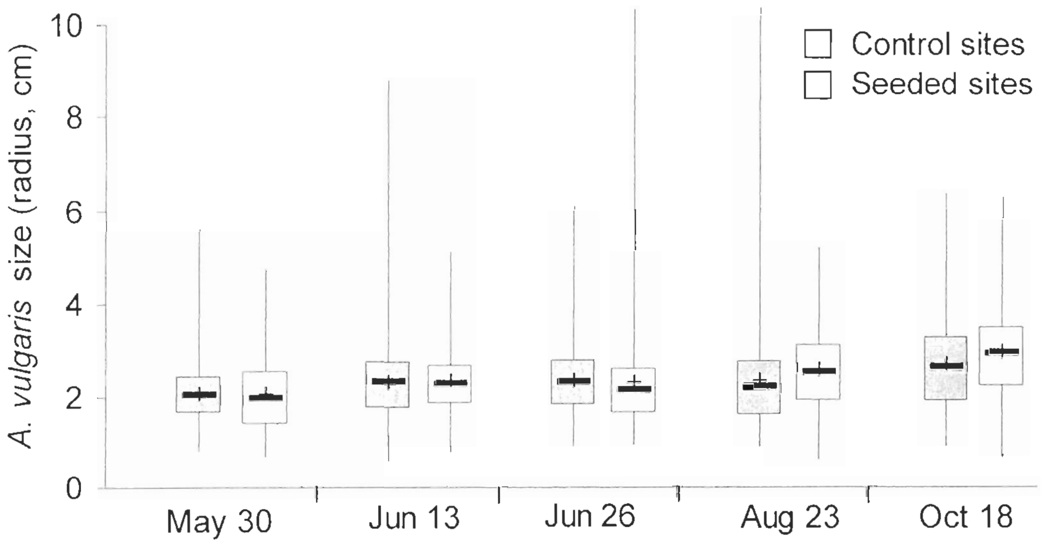

Figure 5.8. Box plots of the sea star *A. vulgaris* sizes in 2007 (+: mean or simple value (when <10 ind.); horizontal line: median; box: quartile q1 and q3; vertical lines: maximum and minimum values). Data are pooled over transects and sites within each site type.

Table 5.4. Results of ANOVAs for sea star *A. vulgaris* size (radius, cm) in 2007. Data were pooled over transects within each site. Planned comparisons were conducted when the interaction term was significant. Significant and interpretable effects (*p*<0.017 for Bonferoni adjustment) are indicated in bold.

	Time T2, T3, T4 and T5 Site C3, C4, S1, S2 and S3				Time T1, T3, T4 and T5 Site C2, C3, S1, S2 and S3				Time T2, T4 and T5 Site C1, C3, C4, S1, S2 and S3			
Source of variation	df	MS	F	*p*	df	MS	F	*p*	df	MS	F	*p*
Time	3	17.071	24.87	<0.001	3	33.221	59.90	<0.001	2	10.837	14.51	<0.001
Site	4	76.870	111.97	<0.001	4	50.943	91.86	<0.001	5	66.515	89.08	<0.001
Time*Site	12	4.490	6.54	**<0.001**	12	4.336	7.82	**<0.001**	10	5.721	7.66	**<0.001**
S vs C (B vs A)	*1*	*0.0002*	*0.0002*	*0.988*	*1*	*1.193*	*2.15*	*0.143*	*1*	*3.626*	*4.86*	*0.028*
S (B vs A)	*2*	*4.776*	*6.96*	***0.001***	*2*	*2.374*	*4.28*	***0.014***	*2*	*9.209*	*12.33*	***<0.001***
C (B vs A)	*1*	*4.031*	*5.87*	***0.015***	*1*	*7.309*	*13.18*	***<0.001***	*2*	*7.041*	*9.43*	***<0.001***
Error	3926	0.687			5407	0.555			3062	0.747		

S: seeded sites; C: control sites; B: before seeding; A: after seeding

5.4 Discussion

Our 2007 experiment provided a symmetrically-designed study on the temporal and spatial dynamics of juvenile scallops and predators upon seeding trial. The experiment also enabled us to assess if dynamics in small-scale seeding trials are similar or different to those observed in large-scale seeding operations (Chapter 4). We expected that dispersal of seeded scallops away from small seeded sites would be more important than from large seeded sites. We also expected a rapid predator aggregation into small seeded sites (in response to high local prey densities) that would affect the juvenile scallop survival and would also elicit their dispersal.

Immediately after seeding in this small-scale seeding experiment, scallop distribution was contagious within sites, as observed in the large-scale seeding trials (Chapter 4). This is presumably because of the seeding method used, which involved releasing scallops from the surface of the water (from a boat). SCUBA divers noted that upon release scallops sank almost straight to the sea bottom, where they were clustered in patches of various sizes (Appendix 5), indicating that the patches of higher scallop density were a result of the release method and not some other reason such as scallops actively aggregating upon arrival on the sea bed.

Dynamics (mortality and dispersal) of seeded scallops soon after small-scale seeding were rapid. One week after seeding, average scallop density on the seeded sites was estimated 5 times lower than the density aimed for upon seeding. The clumped distribution of seeded scallops may have contributed to lower the estimate of densities than actual densities, since many images showed no scallops and only a few images had 1 to 40 scallops. Another reason for this low density could be that some scallops were released outside the experimental sites as we did not determine scallop density on the sea bed immediately following seeding (on the same day or 1 day after). In a number of previous small scale seeding trials, SCUBA divers hand released scallops onto the seeded area to avoid this cause of initial loss (e.g. Barbeau et al 1994, 1998; Nadeau & Cliche 2004).

Nevertheless, even with this careful method of release, scallop density had decreased substantially a few days after seeding in these previous studies.

Dispersal of seeded scallops away from small seeded sites was not more important from large-scale seeded sites. Two months after our seeding, 80% of scallops were already missing from the initial seeding estimate. Dispersal distance was also suspected to be important, because small scallops were observed a month after seeding on a few control sites located about 100 m away. Recorded dispersal distances of juvenile sea scallops during small-scale trials and experiments were lower: e.g. less than 4 m after 4 months (Parson et al. 1992) to more than 60 m after 44 days (Cliche et al. 1994). Hatcher et al. (1996) estimated an average net displacement of juveniles scallops over 13 months of 35 m and the furthest displacement was 93 m.

Dispersal of scallops is always expected upon seeding, but the goal of managers is to select a site that will have the best physical and biological conditions that would limit these movements. Not considering predator abundances, our study area was obviously favourable for seeding. First, the hydrodynamic regime suspected to influence scallop movement (Posgay 1981; Caddy 1989; Cliche et al. 1994) showed no particular pattern, and was relatively low (~5 cm · s^{-1}). The substrate was also estimated adequate, being characterized as a hard heterogeneous substrate (Giguère et al. 2004) that would minimize scallop dispersal and provide refuge to juveniles (Bourgeois et al. 2006; Wong et al. 2006). Finally, among the other physical factors, water temperature and salinity were considered optimal (Carsen et al. 1995).

Scallop dispersal may have been triggered by predators. Upon crab encounter, scallop often respond by a passive escape in which they close their valves without moving, and so these encounters should not be a main trigger for movement of scallops. Upon sea star encounter, scallops often actively escape by swimming or jumping and so may disperse outside the seeding area (Barbeau & Scheibling 1994). Although sea stars on our sites were small and so likely not effective predators, they may still be effective triggers of scallop swimming. In addition, the high conspecific density (e.g. within the scallop patches) may contribute to movement of scallops (Orensanz et al. 1991), although this has not been studied for sea scallops.

Based on diver surveys, predation also contributed substantially on scallop losses. Surveys conducted one month after seeding and focusing on scallop patches, indicated that predation already affected more than half (63%; Fig. 5.6) of juvenile scallops found on the seeded sites Among all shell remains collected from divers, broken shells were more often observed suggesting that decapods would be the most efficient predators. Based on the scallop seeding modelling exercise by Barbeau and Caswell (1999), crab variables have a greater impact on juvenile scallop survival to commercial size than sea star variables. In a few studies, lobsters were also recognised as significant predators of scallops (Elner & Jamieson 1979; Jamieson et al. 1982; Stokesbury & Himmelman 1995). However, lobster predation behaviours and rates on juvenile scallops are not well studied. Predation from sea stars was probably low. Sea stars *A. vulgaris* were much smaller (2 cm of radius) than in previous studies (e.g. 5 cm radius), and actually not much larger than the seeded scallops themselves. Previous research showed that such small-sized sea stars are not efficient predators of scallops with the size we used for seeding (20-40 mm shell height). Feder and Christensen (1966) and Barbeau and Scheibling (1994) recorded no predation for sea stars of 35-45 mm radius offered scallops 20-25 mm shell height. Therefore, cluckers on our seeded sites may be related to predation from less abundant but larger sea stars or to handling mortality. Hatcher et al. (1996) estimated a 2% loss of scallops due to handling stress prior to and during release. If our handling mortality is similarly small, then most of the cluckers we observed should be due to predation.

Contrary to expectation, predators did not aggregate significantly at a small scale (0.01 km^2) during this experiment. In previous small-scale seeding trials in Atlantic Canada, strong aggregations of predators on seeded scallop patches were not detected, although some mild aggregations have been observed (Cliche et al. 1994; Barbeau et al. 1996; Hatcher et al. 1996, Wong et al. 2005). Even if predators did not aggregate at the scale of the sites (100 m), predator attraction may have nonetheless occurred at the scale of juvenile scallop patches described above (of 1 m or so). These high density patches may have attracted predators at a smaller scale that the one we surveyed. During large scale scallop seeding conducted off the coast of Îles de la Madeleine in 2003 and 2004 (Chapter 4), high density patches of tethered scallops were also suspected to attract predators at small scale.

5.4.1 Guidelines for future work

The formation of scallop patches upon seeding may increase predation on and dispersal of seeded scallops. A better understanding of predator attraction at that scale and of short-term scallop dispersal away from patches would be useful to improve the seeding strategy.

During this study, two techniques of video survey were used: a pyramid that provided stable images and a mobile sleigh that provided video sequences. The latter had the advantage of covering a greater surface (3000 m^2) than the pyramid (80 m^2) during a field day. This is important particularly when surveyed populations are contagiously distributed, such as scallops and sea stars, and when the budget is limited. A disadvantage of this mobile system, similar to a fishing dredge, is that it may trigger scallop swimming prior video capture and so, may introduce biases (Caddy 1968; Caddy 1989; Orensanz et al. 1991). However, complementary trials observed minimal swimming escapes by scallops to our sleigh and so, this method was considered reliable (Appendix 4; see also Franklin et al. 1980). The pyramid is still a good approach for small-scale seeding surveys or when high a degree of accuracy and precision is needed. Such pyramid is described in Stokesbury (2002), and it is currently used to survey the natural sea scallop population on Georges Bank.

A recurrent complaint about video sampling is differentiating between dead scallops and live scallops, and estimating mortality rates from shell remains. Cluckers may be confounded as survivors, and broken shells are hard to detect among substrate particles and other shells. This is why, in this study, we coupled video sampling with observations from SCUBA divers observations, and afterwards it became clear that their input was very valuable. Otherwise, in deep water environment where diving is limited, the use of tethered scallops on frames can be considered (see Chapters 3 and 4), but the tethering technique is still time-consuming (involving set-up in the laboratory, and deployment and retrieval from boats) and only provides short-term information about predation potential.

Contrary to our expectation, the dynamics of juvenile scallops and predators observed in a small-scale experiment were not clearly different from those observed in large-scale seeding trials. Scallop dispersal was not more important than in large seeded sites, and predators did not aggregate significantly into small seeded sites (in response to high local prey densities). Therefore, small-scale researches, less expensive and time-consuming than large-scale trials, do provide useful information for managers.

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DISCUSSION GÉNÉRALE

Cette étude visait à caractériser la dynamique à court terme de la prédation des pétoncles juvéniles dans un contexte d'ensemencement à grande échelle. Les ensemencements commerciaux de millions de pétoncles sur des superficies >1 km^2 réalisés en 2003 et 2004 ont été utilisés à cette fin. L'originalité de l'étude résidait principalement dans le fait que jusqu'à présent, la plupart des travaux portant sur la dynamique de la prédation des pétoncles juvéniles ensemencés ont été effectués en laboratoire ou lors d'ensemencements expérimentaux. L'accès à un gisement naturel de pétoncles géants fermé à la pêche et réservé aux ensemencements a également permis d'étudier la dynamique des prédateurs multiples présents sur les gisements naturels de pétoncles géants et leur impact sur les pétoncles juvéniles sur une échelle saisonnière. Ces données sont essentielles au développement d'une démarche d'ensemencement pouvant conduire à un taux de retour à la pêche satisfaisant.

Les résultats de cette étude sont donc particulièrement importants pour le développement de la pectiniculture et pour les ensemencements de fonds marins. Les données récoltées peuvent également contribuer à améliorer la gestion de la pêcherie de cette espèce par une connaissance accrue de la dynamique de la prédation sur les pétoncles juvéniles. Finalement, divers outils de mesures et de démarches expérimentales ont été utilisés lors des travaux en laboratoire et sur le terrain et peuvent servir à la structuration d'études connexes.

Les quatre volets expérimentaux de cette thèse constituent une suite logique. Tout d'abord, l'étude en laboratoire (Chapitre 2) a permis de récolter des données sur le comportement de prédation sur les pétoncles juvéniles des principaux prédateurs benthiques, retrouvés sur les gisements naturels de pétoncles géants au large des îles de la Madeleine. Ces données ont été utilisées par la suite pour modéliser l'impact de l'assemblage des prédateurs en milieu naturel. Les travaux sur le terrain ont permis de caractériser durant trois ans, sur une échelle saisonnière, l'assemblage des prédateurs benthiques présents sur un gisement naturel de pétoncles et leur potentiel de prédation des pétoncles géants juvéniles (Chapitre 3). Lors de cette étude, une technique novatrice permettant de mesurer le potentiel de prédation des pétoncles, sans l'utilisation de plongeurs, a été mise au point. Ensuite, des travaux sur la dynamique à court terme des pétoncles juvéniles et des prédateurs consécutifs à des ensemencements réalisés à grande échelle spatiale en 2003 et 2004 sont décrits dans le Chapitre 4. Certaines informations sur la dynamique des pétoncles ont finalement été validées et complétées grâce à des ensemencements expérimentaux réalisés en 2007 (Chapitre 5).

6.1 Synthèse des résultats

Cette section intègre les principaux résultats obtenus autour des deux grands volets de recherche de ce doctorat soit, i) l'étude de la variation de l'assemblage des prédateurs et de leur potentiel de prédation sur les pétoncles juvéniles sur une échelle saisonnière et ii) l'étude de la dynamique à court terme de l'assemblage des prédateurs et de leur potentiel de prédation sur les pétoncles juvéniles lors d'ensemencements à grande échelle.

Variation de l'assemblage des prédateurs et de leur potentiel de prédation sur les pétoncles juvéniles sur une échelle saisonnière

Durant les trois années d'étude, de 2003 à 2005, l'assemblage des prédateurs benthiques qui cohabitaient sur les gisements naturels de pétoncles géants au large des îles de la Madeleine s'est avéré relativement constant sur une échelle saisonnière et essentiellement composé de trois espèces d'étoiles de mer (*Asterias vulgaris*, *Leptasterias polaris* et *Crossaster papposus*) à des densités de 15 étoiles · 100 m^2 et de deux espèces de crabes (*Cancer irroratus* et *Hyas araneus*) à des densités de 1 crabe · 100 m^2. Ainsi, le peu de variations temporelles de l'assemblage des prédateurs a réfuté l'hypothèse initiale (Introduction, H1) d'une variation saisonnière sur les gisements naturels.

Malgré leur faible abondance, les prédateurs ont pu avoir un impact non négligeable envers les pétoncles juvéniles (hauteur de coquille de 25-35 mm). Durant les travaux en milieu contrôlé présentés au Chapitre 2, les étoiles de mer ont démontré des taux de prédation de 1 pétoncle · prédateur^{-1} · j^{-1} pour *A. vulgaris* et de 0,02 pétoncle · prédateur^{-1} · j^{-1} pour *L. polaris*. L'efficacité de capture de ce groupe de prédateurs a été particulièrement affectée par leur faible vitesse de déplacement durant leur temps de recherche et, ensuite, le taux élevé de fuite de pétoncles après une rencontre prédateur-proie. Les crabes *C.*

irroratus se sont avérés des prédateurs efficaces avec une consommation moyenne de 3 pétoncles · prédateur^{-1} · j^{-1} suivi du crabe *H. araneus,* avec un taux de prédation 3 fois moindre. L'efficacité de prédation des crabes a semblé principalement due à leur vitesse de déplacement rapide (et donc des taux de rencontre avec la proie élevés) avec peu de fuites des pétoncles après rencontre.

Le potentiel de prédation de l'assemblage des prédateurs a démontré une faible variation saisonnière rejetant également l'hypothèse d'une fluctuation saisonnière de la prédation (Introduction, H2). Jusqu'à 13% de pétoncles ont été consommés par jour, dont la plupart (~80%) semblent avoir été consommés par les étoiles de mer. Étant donné l'abondance de la population d'étoiles de mer sur les sites étudiés, les travaux en bassins sur l'effet du procédé d'attachement des pétoncles pour étudier le potentiel de prédation en milieu naturel ont pris toute leur importance. En effet, lors des travaux en bassins (Chapitre 2), les étoiles *A. vulgaris* et *L. polaris* ont consommé 6 et 19 fois (soit en moyenne ~12,5 fois) plus de pétoncles fixés que de pétoncles libres. Ainsi, en appliquant ce biais aux valeurs de prédation observées sur le terrain nous estimons approximativement des pertes totales de pétoncles juvéniles libres par prédation de 3,4% par jour.

Lors de ces travaux, la composition de l'assemblage des prédateurs et leur potentiel de prédation ont démontré des variations spatiales. Par exemple, une corrélation négative entre les densités des étoiles de mer et des crabes a été détectée de même qu'une corrélation négative entre les densités des différentes espèces d'étoiles de mer. Il semble bien que cette répartition spatiale ait eu également un effet sur la variation spatiale du potentiel de prédation. En effet, une corrélation a pu être établie entre la densité des étoiles de mer et la proportion de « claquettes » (coquilles vides) parmi les pétoncles fixés morts. Cependant, aucune corrélation n'a été notée entre la densité des crabes et la proportion de pétoncles cassés. Dans le cas du crabe, l'étude postule une réponse fonctionnelle de type III (sigmoïdale) en présence de pétoncles juvéniles (tel que décrit dans Barbeau et al. 1994, 1996, 1998). Ce type de réponse décrit un très faible taux de prédation du crabe dans des situations où la densité naturelle des pétoncles est également faible, comme dans le cas de notre site d'étude.

Finalement, lors de cette étude nous nous sommes également intéressés aux interactions qui pouvaient survenir entre les prédateurs multiples et ainsi moduler leur impact sur les pétoncles juvéniles (tel que décrit dans Sih et al. 1998). Pour estimer l'impact des prédateurs multiples, nous avons utilisé un modèle mathématique permettant de prédire la prédation du pétoncle juvénile (à partir de données récoltées en laboratoire et sur le terrain) en utilisant une action indépendante de chaque prédateur envers des pétoncles fixés. Les valeurs estimées comparées aux valeurs observées sur le terrain ont démontré une proximité qui a supposé un effet indépendant des prédateurs multiples.

Dynamique à court terme de l'assemblage des prédateurs et de leur potentiel de prédation sur les pétoncles juvéniles lors d'ensemencements à grande échelle

Les sites ensemencés en 2003 et 2004 ont été sélectionnés pour leur substrat hétérogène et la faible abondance des prédateurs. Ainsi, il n'est pas surprenant que l'abondance des prédateurs sur ces sites ait été moindre que lors de l'étude précédente, en particulier pour les étoiles de mer (<10 étoiles de mer · 100 m^{-2}), avec un assemblage dominé par *C. papposus* et *L. polaris*. Rappelons que les travaux en bassins (Chapitre 2) ont démontré le faible taux de prédation de *L. polaris* envers le pétoncle juvénile. Pour ce qui est de l'étoile de mer *C. papposus*, le peu de données récoltées (à cause de problèmes de survie en bassins) a révélé un comportement de prédation équivalent à celui de *A. vulgaris* mais avec une probabilité de capture après attaque élevée (0,5). Ces quelques informations ont d'ailleurs été utilisées pour le modèle mathématique (voir Chapitre 3, Tableau 3.2).

Les premiers inventaires suivant les ensemencements ont démontré une distribution contagieuse des pétoncles. Cette distribution, également observée lors des ensemencements expérimentaux décrits au Chapitre 5, s'est avérée associée à la méthode d'ensemencement qu'à un comportement subséquent d'agrégation. La dynamique des pétoncles ensemencés a ensuite été rapide. Par exemple, en 2004, la densité initiale de 2,4 pétoncles · m^{-2} a rapidement diminué de 10 fois après 2 semaines. Du côté des prédateurs, l'analyse de l'assemblage avant et après les ensemencements a démontré certaines variations, mais qui n'ont pu être associées avec certitude à l'effet des ensemencements. Des limites d'interprétation ont été imposées par le nombre insuffisant de sites contrôles en 2003 et par la modification de la technique d'inventaire durant les suivis de 2004. Les résultats du suivi des ensemencements expérimentaux de 2007 (Chapitre 5) vont également dans le même sens. Ces informations réfutent donc l'hypothèse d'une réponse d'agrégation des prédateurs, à la suite d'un ensemencement, tel que suggéré initialement (Introduction, H3).

Le potentiel de prédation des pétoncles n'a pas non plus révélé de variations associées aux ensemencements et est demeuré relativement faible (~10%). Les étoiles de mer et les crabes ont semblé être associés à parts égales à cette prédation et, en corrigeant le biais associé à la fixation des pétoncles (Chapitre 2), on estime le taux de mortalité journalier à 5,4%. L'absence de la variation du potentiel de prédation après un ensemencement peut toutefois refléter une réponse fonctionnelle de type I de la part de prédateurs. Une réponse de ce type semble probable puisque, malgré l'augmentation de la densité des proies dans le milieu, la proportion de mortalité dans les cadres est demeurée constante. Des réponses de type II et III sont tout de même possibles si le processus de prédation observé s'est déroulé avant que les prédateurs aient atteint la satiété à des densités très élevées de proie. Ces résultats tendent donc à appuyer l'hypothèse initiale (Introduction, H4) à l'effet que les pétoncles juvéniles auraient eu à faire face à une prédation plus importante à la suite de l'ensemencement à cause d'une réponse fonctionnelle des prédateurs. De plus, le modèle mathématique simulant l'activité indépendante des prédateurs multiples, en présence de pétoncles juvéniles fixés et dans un contexte d'ensemencement, a estimé des valeurs de prédation assez similaires à celles observées. Ceci réfute donc l'hypothèse d'une action non indépendante des multiples prédateurs sur les pétoncles juvéniles dans un contexte d'ensemencement (Introduction, H5).

La prédation des pétoncles juvéniles n'explique pas entièrement les pertes observées. Il semble donc que la dispersion ait également joué un rôle tout aussi déterminant. En effet, autant pour les ensemencements à grande échelle qu'expérimentaux (Chapitres 4 et 5), des pétoncles juvéniles ont été notés dans des sites contrôles situés à plus de 1,5 km des sites ensemencés. Nous suggérons que la distribution contagieuse des pétoncles à l'ensemencement et les rencontres avec les prédateurs seraient des facteurs initiateurs de dispersion. Les conditions locales de courant ont pu contribuer par la suite à accroître leur distance de déplacement.

6.2 Choix des outils et approches

Les travaux sur le terrain ont exigé l'adaptation et la validation de diverses méthodes et approches. Cet aspect a donc occupé une place importance dans le projet. Il nous apparaît donc essentiel d'expliquer nos choix méthodologiques et notre évaluation générale *a posteriori*.

Le choix du design expérimental

Le design expérimental utilisé pour les travaux sur le terrain a évolué en fonction des années. En effet, le design utilisé lors de la première récolte de données sur les ensemencements en 2003 comportait certaines lacunes qui ont été corrigées par la suite. La principale lacune résidait dans l'absence de réels sites contrôles dans le contexte des ensemencements (Chapitre 3). Les variations observées n'ont donc pu être associées uniquement à l'ensemencement. Cette situation a été corrigée en 2004 par la sélection de deux sites contrôles et un site ensemencé estimés indépendants, selon un design asymétrique (Chapitre 4). Ces sites ont ensuite été suivis sur une base temporelle avant et après l'ensemencement, sur la base du design « beyond BACI » décrit par Underwood (1993, 1994) et proposé lors d'études d'impacts environnementaux lorsque seul un site impacté est disponible. À l'interprétation des analyses, c'est l'interaction entre les Sites et le Temps qui laisse supposer un certain impact (Underwood 1993, Table 6). Une analyse de contrastes a permis par la suite d'analyser les interactions sous-jacentes (consultation statistique ULaval, D. Talbot 2010).

Le projet visait l'étude de la dynamique de la prédation à une échelle spatiale de centaines de mètres afin de se rapprocher des conditions d'ensemencement à grande échelle. Nous savons *a posteriori* que les prédateurs et pétoncles ont une distribution hétérogène et que selon l'échelle spatiale étudiée les résultats peuvent varier. Par exemple, lors des ensemencements, des comportements d'agrégation des prédateurs n'ont pas été détectés à grande échelle, mais sont soupçonnés à l'échelle des groupes de pétoncles (Chapitre 4). Il importe donc de bien définir les objectifs et de bien cibler l'échelle d'étude.

Finalement, cette étude a de nouveau démontré que, dès l'ensemencement, la dynamique des pétoncles était très rapide. Ainsi, après un ensemencement, un suivi à l'échelle des jours et non à l'échelle des semaines pourrait permettre de récolter des données importantes sur les questions qui nous préoccupent dont la prédation et dispersion des pétoncles ainsi l'interaction et attraction des prédateurs.

L'étude fait donc ressortir l'importance de bien définir le design expérimental avant de débuter des travaux d'envergure, en se basant sur des expériences passées, et de s'en tenir le plus possible lors de l'exécution des travaux. Évidemment les contraintes de terrain, la disponibilité du bateau et de son équipage, les bris et pertes, les conditions météorologiques difficiles et autres imprévus peuvent mettre à rude épreuve les intentions nobles du départ.

Le choix de la méthode d'inventaire

L'utilisation d'une caméra sous-marine sur traîneau et trépied pour l'inventaire des prédateurs et des pétoncles a comporté son lot de défis, et la plupart résidaient au niveau du suivi de l'abondance des pétoncles juvéniles. C'est pourquoi, pour éviter les biais possibles que pouvait induire la caméra sur traîneau, dont ceux de la fuite des pétoncles juvéniles et de la détection difficile des pétoncles de petite taille, nous avions choisi d'utiliser une caméra sur trépied pour le suivi de l'ensemencement de 2004 (Chapitre 4). Toutefois, les premiers inventaires ont démontré que l'utilisation du trépied ne permettait de couvrir que 80 m^2 de surface par jour de terrain comparativement à 3000 m^2 pour la caméra sur traîneau. Nous avons donc repris l'utilisation du traîneau et les biais anticipés ont été estimés (Annexe 4). Ainsi, les fuites possibles des pétoncles à l'arrivée du traîneau se sont avérées négligeables lors des essais. De plus, les estimations de densités des pétoncles juvéniles sur de courts transects se sont avérées comparables aux estimations réalisées en plongée sous-marine.

Ainsi, pour les suivis à grande échelle, l'utilisation du traîneau s'est nettement avérée plus avantageuse que le trépied puisqu'il permet de couvrir de plus grandes surfaces par jour de terrain. Toutefois, la qualité des images peut être affectée par des déplacements parfois trop rapides du traîneau et cette perte de qualité nuit particulièrement la détection des pétoncles juvéniles. L'utilisation de la pyramide permet la récolte d'images fixes souvent plus nettes qui facilite l'analyse ultérieure. Ainsi, pour sa clarté d'image, l'utilisation de la pyramide doit être favorisée lorsque possible, par exemple dans des sites à échelle spatiale réduite (voir Chapitre 5).

L'utilisation de la caméra comporte également des faiblesses au niveau de la détection des pétoncles vivants et des pétoncles morts. La présence de coquille blanche n'est pas toujours signe de mortalité, car certains pétoncles ensemencés ont naturellement une coquille supérieure blanche. De plus, la technique permet difficilement de détecter les fragments de coquilles produits par la prédation des crabes. Ainsi, des études sur la prédation à court terme après ensemencement ont avantage à prévoir des échantillonnages en plongée pour récupérer des données sur la survie et l'état des coquilles vides (voir Chapitre 5).

La mesure du potentiel de prédation

Le pétoncle géant est une espèce particulièrement mobile au stade juvénile ce qui complique l'étude de leur prédation en milieu naturel. Ainsi, la fixation des pétoncles est une approche qui s'avère fort utile pour estimer leur potentiel de prédation, en tant que mesure comparative. Évidemment, cette technique implique des biais qui doivent être documentés au préalable. Les travaux effectués en bassins ont permis d'estimer les biais de la fixation sur les comportements de prédation (Barbeau and Scheibling 1994c; Chapitre 2).

Pour les travaux sur le terrain, nous avons choisi d'utiliser des cadres sur lesquels des pétoncles étaient fixés, à cause de la capacité de les manipuler du bateau, sans l'usage de plongeurs. Ces cadres ont été adaptés de ceux développés par Bourgeois (2004). L'utilisation de ces cadres a nécessité des réflexions au niveau du choix de la durée d'immersion et des ajustements quant aux pertes en pétoncles associés aux manipulations de mise à l'eau (Chapitre 3, Annexe 2). Malgré tous ces efforts, nous soupçonnons que d'autres biais ont pu survenir. Ces biais possibles se situeraient au niveau de l'attraction des prédateurs à la structure en tant que telle (par ex. pour la recherche d'abris) et au niveau de l'attraction des prédateurs pour les pétoncles fixés à densité élevée (réponse d'agrégation). Cette abondance de proie peut également modifier le taux de consommation des prédateurs (réponse fonctionnelle) en comparaison avec une proie présente à faible densité.

Les résultats des travaux de Talman et al. (2004) utilisant des pétoncles fixés sur une chaîne nous permettent de croire que l'effet du cadre serait négligeable sur l'attraction des prédateurs. De plus, on peut supposer que les concentrations de pétoncles dans les cadres représentent bien les conditions qui prévalent sur les sites récemment ensemencés puisque les pétoncles y sont également distribués en agrégats. Cependant, ces concentrations de pétoncles peuvent modifier la réponse des prédateurs (réponse d'agrégation et réponse fonctionnelle) dans des conditions sans ensemencement et avoir pour effet de surestimer le potentiel de prédation. À cet effet, nous avons utilisé le modèle mathématique sur la prédation pour estimer la probabilité que les cadres ne soient pas rencontrés par les prédateurs et avons comparé cette valeur à la fraction de cadre sans mortalité (Chapitres 3 et 4). Les résultats ne suggèrent pas réponse d'attraction ou de déplacement dirigé des prédateurs vers les cadres dans les secteurs sans ensemencement, mais suppose une attraction dans les sites ensemencés.

Ainsi, la fixation de pétoncles sur les cadres a permis de récolter des données sur la prédation en milieu naturel, données difficilement accessibles à cause de la motilité de ces pétoncles. Nous reconnaissons toutefois que la technique a des limites, elle doit être davantage validée et utilisée avec précaution.

La modélisation de la prédation

Les modèles mathématiques sont des outils très utiles pour intégrer une variété de données biologiques et simuler des réponses en fonction des conditions environnementales. Le modèle de prédation du pétoncle utilisé pour notre étude est composé de données comportementales des prédateurs et de la proie en lien avec les données biophysiques du site étudié (Barbeau & Caswell 1999). Le modèle suppose une distribution aléatoire des pétoncles de même qu'un comportement de recherche aléatoire des prédateurs. La prédation des étoiles de mer est estimée en postulant une réponse fonctionnelle de type I tandis que la prédation des crabes est estimée de type III (Introduction, Annexe 3). Les données de survie du pétoncle estimées par ce modèle correspondent jusqu'à présent assez bien aux données observées (données récoltées de façon indépendante aux données utilisées pour le modèle) (Barbeau & Caswell, 1999; Gangnery et al. 2004; Wong et al. 2006). Le modèle s'est également avéré approprié pour estimer les taux de rencontre et la survie des pétoncles en bassins (Chapitre 2).

Le modèle de prédation a donc été utilisé pour estimer le potentiel de prédation des pétoncles fixés en milieu naturel et en fonction des dates et sites étudiés. Comme le modèle suppose que l'effet des prédateurs est indépendant (c.-à-d. qu'ils agissent de façon indépendante les uns des autres), nous l'avons également utilisé pour évaluer l'hypothèse d'un effet non-indépendant des prédateurs en milieu naturel. De plus, puisque l'utilisation des cadres de pétoncles fixés pouvait comporter des biais au niveau de la réponse des prédateurs, nous avons adapté le modèle pour tenir compte de l'effet d'attraction de cette structure spatiale. Dans un souci de simplicité, le modèle de base a été modifié par l'ajout d'une zone de détection (Holling 1966) autour de chaque pétoncle correspondant à la taille des cadres.

Certaines variations entre les valeurs observées et estimées ont été notées, et ce, malgré l'utilisation d'une zone de détection autour des pétoncles. Ces variations tendent donc à démontrer que la dynamique des prédateurs n'est pas complètement simulée par le modèle. La distribution grégaire des pétoncles et des prédateurs peut être associée à ces différences. De plus, le modèle utilise des données comportementales récoltées en milieu contrôlé. Ces valeurs (vitesse de déplacement, temps consacré à la recherche de proie, etc.) peuvent différer de celles du milieu naturel et biaiser à la base les prédictions du modèle. Le modèle ne tient pas non plus compte de la présence potentielle d'autres proies qui peuvent également distraire les prédateurs de la proie principale ou des prédateurs pélagiques qui peuvent interférer dans le système.

Finalement, l'utilisation des cadres avec pétoncles fixés a pu modifier le comportement de prédation qui peut être différent de celui simulé dans le modèle. Par exemple, le comportement de recherche aléatoire des prédateurs peut avoir été modifié pour un mouvement dirigé (plutôt qu'aléatoire) en présence d'un groupe de pétoncles. D'ailleurs, tel que mentionné ci-dessus, il semble possible que le mouvement des prédateurs sur les sites ensemencés ait effectivement été dirigé vers les pétoncles fixés. Ainsi, le modèle nécessite certains raffinements ou extensions pour tenir compte entre autres du mouvement dirigé et de la géométrie des concentrations de pétoncles et de prédateurs.

6.3 Perspectives de recherche

Cette étude a permis de récolter diverses informations sur la dynamique des pétoncles et de leurs prédateurs benthiques à la suite d'un ensemencement. Il apparaît toutefois évident que d'autres travaux sont nécessaires pour préciser certaines informations afin de conseiller adéquatement l'industrie pectinicole sur cette stratégie de production.

Tout d'abord, les suivis menés en milieu naturel ont révélé que les principales variations au niveau des prédateurs et de leur potentiel de prédation se situaient non pas sur une échelle temporelle, mais plutôt sur une échelle spatiale. Une analyse de la composition de la variance de la variable spatiale a révélé que les différences se situaient essentiellement au dernier niveau d'échantillonnage de la grille d'échantillonnage, soit au niveau des séquences ou transects vidéo pour l'assemblage des prédateurs et au niveau des cadres pour l'estimation du potentiel de prédation (Chapitre 3). Ces résultats tendent donc à démontrer qu'une augmentation du nombre de stations échantillonnées dans la grille pourrait permettre d'accroître la précision des valeurs estimées. De plus, la récolte de données plus précises sur la distribution spatiale des prédateurs et des pétoncles ensemencés en lien avec la dynamique de la prédation et de la dispersion pourrait permettre de mieux conseiller l'industrie dans le choix des sites et des approches d'ensemencement les plus productifs.

Notre étude n'a pas révélé d'interaction entre les prédateurs multiples ni d'agrégation des prédateurs lors d'un ensemencement. Il est possible que le niveau spatial de nos travaux (à l'échelle de centaine de mètres) ait été trop élevé pour déceler des phénomènes qui en fait se déroulent à une échelle plus fine (échelle des mètres) (voir Wiens 1989). De telles études sur les comportements d'attraction et d'interaction menées en milieu naturel, et couplées par des observations en laboratoire devraient permettre de mieux comprendre la dynamique prédateur-proie à l'intérieur d'un site ensemencé et l'importance de ces comportements sur le succès ultime (au niveau survie et dispersion des pétoncles) d'un ensemencement.

La distribution hétérogène (par agrégat) des pétoncles à l'ensemencement (Chapitres 4 et 5) suscite des questionnements sur le succès ultime d'un ensemencement. L'effet de la densité des pétoncles sur la réponse fonctionnelle des prédateurs, et donc sur la survie des pétoncles, a été démontré par diverses études. Il est suggéré que le taux de prédation des étoiles de mer et des crabes augmente en fonction de la densité des proies (voir Introduction). Toutefois, chez le crabe, cette réponse serait plutôt sigmoïdale (i.e. une réponse de type III, faible proportion de mortalité à faible et haute densité de proie). Ainsi, selon ces informations, il y aurait avantage à uniformiser la densité des pétoncles à 5 pétoncles · m^{-2} (ou moins) afin de limiter la réponse prédatrice des étoiles de mer et éviter de « stimuler » une réponse prédatrice accélérée des crabes (voir les travaux de Wong et al. 2005). Cette recommandation devrait être validée sur le terrain entre autres par l'utilisation des cadres avec pétoncles fixés à des densités variables. Toutefois, cette technique de mesure de la prédation du pétoncle en milieu naturel devrait auparavant faire l'objet de validation supplémentaire.

Bien que nos travaux ne visaient pas une étude exhaustive sur la dispersion des pétoncles juvéniles, les données récoltées tendent à démontrer que la dispersion des pétoncles serait principalement associée à leur distribution hétérogène à l'ensemencement. En fait, il existe dans la littérature peu de données sur l'effet de la densité sur la dispersion des pétoncles géants juvéniles. Le facteur dispersion devrait donc être davantage documenté étant donné son importance dans la dynamique des pétoncles après un ensemencement. Les méthodes d'étude de la dispersion en milieu naturel sont toutefois laborieuses, surtout quand cette dispersion peut s'étendre sur plus d'une centaine de mètres rapidement. Des opérations de marquage individuel ont été menées lors d'ensemencements semi-commerciaux au large des îles de la Madeleine et les pétoncles marqués récupérés au moment de la pêche, 4 ans plus tard, ont démontré une certaine dispersion hors des sites ensemencés, mais limitée à l'échelle des gisements naturels (Hébert et al. 2003). L'étude de la dispersion à court et moyen terme après un ensemencement, et les facteurs déterminant ces déplacements, exigent des outils plus raffinés. De plus, le développement d'un modèle de dispersion couplé avec le modèle de prédation pourrait s'avérer fort utile comme outil de gestion des ensemencements.

Le modèle mathématique développé par Barbeau et Caswell (1999) est un outil permettant de simuler, sans trop de complexité, l'impact de la prédation d'un assemblage de prédateurs selon les conditions du milieu naturel. Depuis sa conception, diverses informations, dont celles provenant de nos travaux, ont été recueillies sur les réponses fonctionnelles des prédateurs (par ex. Wong & Barbeau 2005, 2006; Wong et al. 2006a), l'effet du type de substrat sur la dispersion et sur la prédation (Wong & Barbeau 2003; Bourgeois et al. 2006), l'effet des interactions entre les prédateurs (d'Entremont 2005) et devraient donc être considérées pour une mise à jour et un raffinement du modèle. Gangnery et al. (2004) proposent également certaines voies pour raffiner le modèle en tenant compte de la croissance et de la dispersion des pétoncles juvéniles. La récolte de données sur la prédation des poissons, sur la dispersion et sur l'effet des courants dans la dynamique des pétoncles serait également bénéfique au modèle. Une analyse de sensibilité (Barbeau & McDowell 1998; Barbeau & Caswell 1999) devrait par la suite guider les gestionnaires sur les variables les plus importantes à considérer pour améliorer la survie des pétoncles ensemencés et pour limiter la dispersion afin de réussir un ensemencement.

L'utilisation du modèle pour simuler le potentiel de prédation de pétoncles fixés sur des cadres doit également être raffinée. Rappelons que les pétoncles à l'ensemencement sont également distribués par agrégat (et non de façon aléatoire comme simulé par le modèle) et qu'un ajustement du modèle à ce type de distribution serait des plus avantageux. La présence de ces agrégats fait intervenir une structure spatiale dans le modèle qui peut modifier le comportement de recherche des prédateurs (le comportement de recherche est simulé par le modèle de façon aléatoire) par l'attraction qu'elle peut induire (voir Chapitre

4 pour plus de détails). L'utilisation d'une zone de détection autour des pétoncles telle que présentée au Chapitre 4 est une première tentative d'ajustement de cette structure. Un modèle à deux étapes (c.-à-d. un modèle avant la rencontre des cadres (ou d'une concentration) de pétoncles et un autre après la rencontre d'un cadre) peut être également une alternative à explorer.

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Appendix 1. Comparison of multiple predator assemblages estimated in daytime and at night-time.

To assess the possibility of a difference in predator composition between daytime and night-time, two video surveys were conducted on each of 25 November 2003 and 15 September 2006: one in daytime (8:00-10:00) and one in the ensuing night (20:00-22:00). Predator densities were estimated from 10 video sequences (each ~100 m long) randomly chosen (to have independent data) from within three long parallel video transects in a 0.35 km² site (1.4 km x 0.25 km) in 2003 and from within seven long video transects distributed to cover a 0.9 km² site (1.5 km x 0.6 km) in 2006 (Fig. A1.1). The same transects were run during day and night for a given sampling year but video sequences were separately randomly selected for each of the surveys.

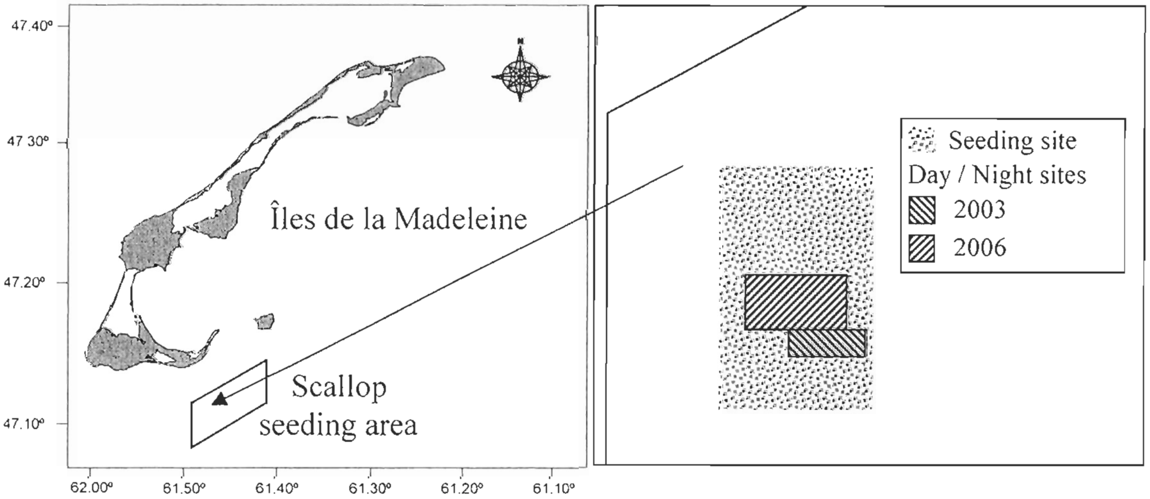

Figure A1.1. Maps of the study sites off the coast of Îles de la Madeleine selected for the day and night comparison.

The possible diel variation in predator assemblages and densities that could cause a bias in our study (since we sampled in daytime) was assessed using MANOVAs with Period (daytime, night-time) as a fixed factor.

Predator densities and composition were not significantly different between daytime and night-time in 2003 and in 2006 (Table A1.1, Fig. A1.2). Therefore, the video surveys conducted in daytime for the rest of our study were considered reliable to estimate the predator assemblage on a 24 hour basis.

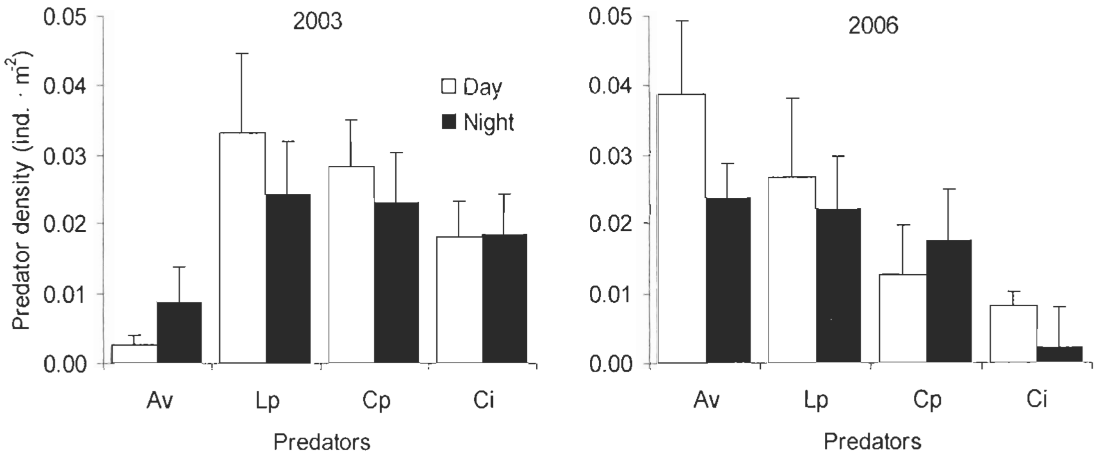

Figure A1.2. Mean densities (± SE, n = 10 video transects) of four predator species estimated in daytime and night-time in 2003 and 2006 (Av: *A. vulgaris*; Lp: *L. polaris*; Cp: *C. papposus*; Ci: *C. irroratus*).

Table A1.1. Results of MANOVAs on predator densities in the predator assemblage (see Fig. 2) during 2 periods (day and night) in 2003 and 2006.

Year	Source of Variation	df1, df2	F	*p*
2003	Period	4, 15	0.58	0.6791
2006	Period	4, 15	0.62	0.6527

Appendix 2. Estimation of biases in the predation assays using tethered scallops.

A small field experiment was conducted in summer 2005 to assess possible biases in our predator assay data set. Specifically, we wanted (i) to know whether lost scallops were mainly due to loss upon deployment (as field observations seem to indicate) and (ii) to model the number of scallops surviving over time to adjust our data to a common time of immersion for later analysis. We deployed 27 predation assays on 5 July 2005 for different immersion times: 0, 24, 48 and 72 h. We had three replicates for time 0 and eight replicates for each of the other times. The 0 time of immersion consisted of deployment to the sea bed followed by immediate retrieval. Upon retrieval, live, dead and lost scallops were identified and counted.

Effect of immersion time on the number of tethered scallops lost.

When predation assays (the frames) with tethered scallops are retrieved in the field, a number of scallops are lost (tether line without a scallop or shell remains). These lost scallops may be due to (i) a predation event where the predator pulled the scallop off of its tether while on the sea bed, (ii) live scallops being lost upon lowering (deploying) the frames onto the sea bed (>30 m deep), or (iii) live or dead scallops being lost upon raising (retrieving) the frames onto the boat.

The number of lost scallops estimated at retrieval reached 6% after 24 hours and 19% after 48 hours. However after 72 hours, no scallops were lost, indicating that scallop losses were not related to immersion time (Fig. A2.1). The proportion lost did not show a pattern over time, but did differ significantly between immersion times (Table A2.1). We used post hoc Dunnett's test to compare treatment levels to a control; specifically, for our experiment, we compared 24, 48 and 78 h to the control 0 h (Day & Quinn 1989). The post hoc test did not detect a difference between time 0 and times 24, 48 or 72 h ($q_{\mathrm{calc}} < q'_{23,\,4}$), supporting our previous observations that scallop loss occurred mainly upon deployment.

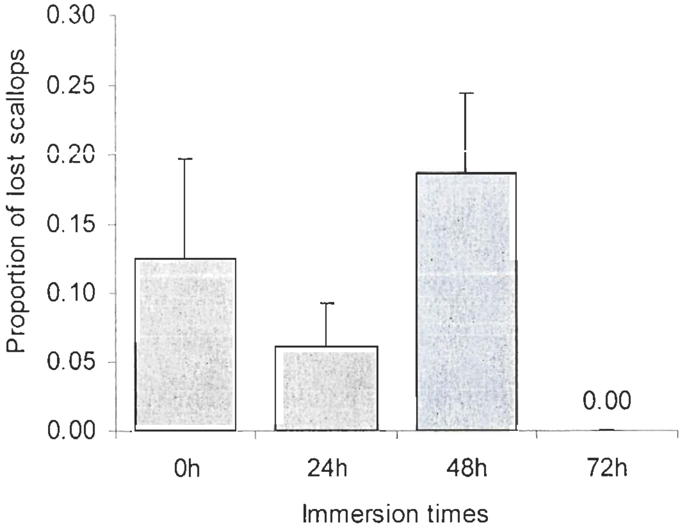

Figure A2.1. Mean proportions (+ SE, n=3-8) of tethered scallops that were lost after 0, 24, 48 and 72 h of immersion onto the sea bed, in a field experiment conducted in July 2005.

Table A2.1. Results of the ANOVA on proportion tethered scallops that were lost at different immersion times (0, 24, 48 and 72 h). Post-hoc Dunnett's Test was performed, since immersion time was significant. Significant differences (p > 0.05) are indicated in bold.

Source of variation	df	MS	F	*p*	Post hoc Dunnett's Test *q*	 $q'_{0.05(2),23,4}$	
Immersion time	3	0.050	4.43	**0.013**			
0-24h					1.7351	2.51	H_0 not rejected
0-48h					0.8675	2.51	H_0 not rejected
0-72h					0.8675	2.51	H_0 not rejected
Error	23	0.011					

Based on this result, we decided to calculate the proportion of tethered scallops that died (due to sea star predation or crab predation) in all of our other predation trials using the total number of recovered scallops (dead + alive) on the frames upon retrieval. In other words, we calculated the proportion of dead (or live) scallops as the number of dead (or live) scallops divided by the total number of scallops recovered.

Model to adjust the predation data to a common time of 24 hours

In 2003, our aim was to retrieve deployed predation assays after 24 hours. In 2004-05, our aim was to retrieve deployed assays after 48 hours, because we determined that 48 hours was an appropriate duration of time in the field for enough predation events to occur (to see differences between sites and times) and not too long for the frames to start becoming depleted of live tethered scallops. However, our actual retrieval times varied between 24 and 72 hours; the latter one because of inclement weather at our off-shore sites. This small field experiment was thus used to assess a model (the exponential decay equation) to emulate the decrease in number of deployed scallops surviving over time. If appropriate, this model would enable us to adjust our data to a common time of immersion for later analysis.

Figure A2.2 shows that the proportion of tethered scallops surviving had an exponential decay trend over time. Thus, the proportion of scallops surviving and the proportions of scallops not dying from a particular cause of mortality (1 - proportion of scallops that died from sea star predation or from crab predation) can be modelled by an exponential decay equation passing through the origin (Equation A2.1):

$$N_T = N_0 e^{-\lambda T}, \qquad \text{(Equation A2.1)}$$

where N_T is the number of scallops (alive or not dead from a particular cause of mortality) at immersion time T, N_0 is the initial number of scallops, and $-\lambda$ is the rate of decay or decrease. The probability of surviving (P) or proportion surviving at a given time is thus:

$$P_T = \frac{N_T}{N_0} = e^{-\lambda T}, \qquad \text{(Equation A2.2)}$$

We transform this equation using the natural logarithm (ln) to obtain a negative linear regression equation between P_T and immersion time T:

$$\ln P_T = \ln e^{-\lambda T}; \quad \ln P_T = (-\lambda T) * \ln e^1 \quad \text{or} \quad \ln P_T = -\lambda T. \qquad \text{(Equation A2.3)}$$

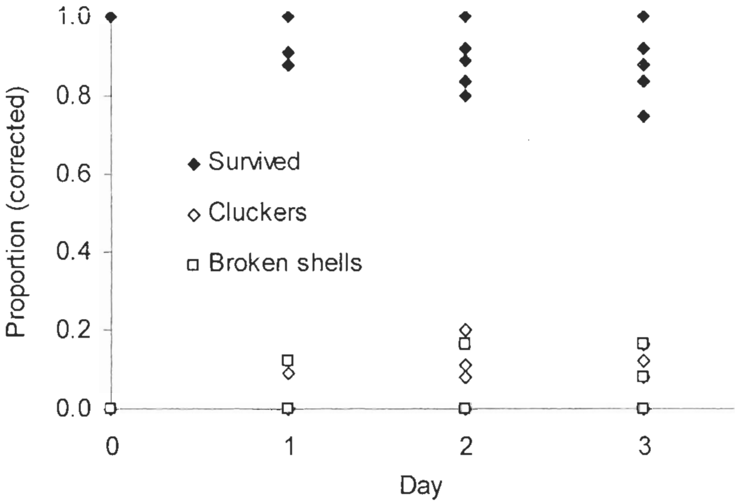

Figure A2.2. Proportion of tethered scallops that survived and died from sea star and crab predation after an immersion of 0 (n=3), 24 (n=8), 48 (n=8) and 72 h (n=8) during a field experiment conducted the 5 July 2005. At time 0, there were no dead scallops, only live and lost scallops. The proportions presented here were corrected to remove lost scallops (as described above); i.e. they were calculated using the total number of recovered scallops (live + dead).

Each regression equation (Table A2.2, Fig. A2.3), with the intercept set at the origin and immersion time (*T*) in days, was assessed. Homogeneity of variance was met by using weighed least squares regression (Quinn & Keough 2002). Each observation was weighted by the reciprocal of an estimate of its variance ($w_i = \frac{1}{s_i^2}$).

The ln-transformed predation data and the regression line are shown in Figure A2.3 and the overlap between observed and predicted is good. All three equations were significant ($p<0.009$) and explained 24-54% of the total variation (Table A2.2). Therefore, we deemed that the exponential decay equation was an appropriate model to standardize to 24 h (Time = 1 day) the predation data collected in our field studies in 2003-2005. To be clear, we did not use the actual regression equations in Table A2.2, but rather simply used the equation $\ln P_T = -\lambda T$, set at the origin. Our July 2005 experiment and modelling exercise above allowed us to evaluate if the exponential decay equation was suitable.

Table A2.2. Weighed least square regression equations for proportion of tethered scallops surviving over time, and proportion of tethered scallops not dying from sea star or crab predation over time. *T* is immersion time in days.

Dependent variable	Equation	df1, df2	r^2	p
ln(Proportion surviving)	$-0.04415 \cdot T$	1, 26	0.54	<0.001
ln(1-Proportion died from sea stars)	$-0.02286 \cdot T$	1, 26	0.37	<0.001
ln(1-Proportion died from crabs)	$-0.01664 \cdot T$	1, 26	0.24	0.009

So, to standardize the predation data from our studies in 2003-2005 to a 1 day (24 hour) immersion time, we used the simple linear equation (with the intercept set at 0):

$$y = mx. \qquad \text{(Equation A2.4a)}$$

To solve for the slope (*m*), we used the general formula for a straight line:

$$m = \frac{y_2 - y_1}{x_2 - x_1}. \qquad \text{(Equation A2.4b)}$$

The variable y_2 is the observed ln(proportion alive) at day x_2 (day 2 or 3), and y_1 and x_1 are equal to the intercept 0. Thus, we estimate ln(proportion) of tethered scallops in a frame that survived or that did not die from sea star or crab predation) at day 1 (t) as follows:

$$\ln(proportion) = \frac{y_2}{x_2} \cdot t, \qquad \text{(Equation A2.4c)}$$

where y_2/x_2 is really m (or also $-\lambda$, the rate of decay).

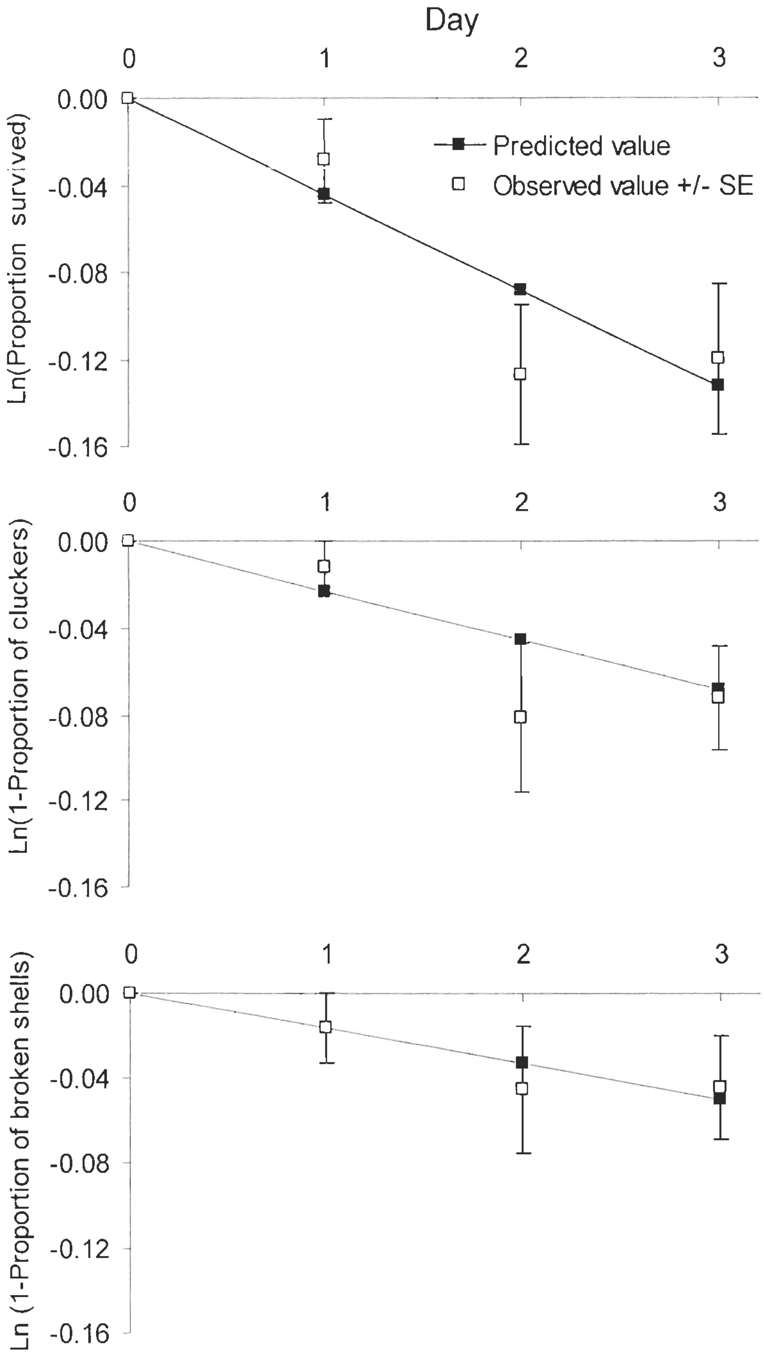

Figure A2.3. Mean (±SE) observed proportion (ln-transformed) and predicted value from the regression equation (see Table A2.2) of tethered scallops that survived and died from sea star predation or from and crab predation over immersion time in days.

Appendix 3. Formulation of the mathematical model for predation.

Basically, we used in the present study the predation model developed by Barbeau and Caswell (1999). In this model, the number of encounters (E_m) between predators of species m (i.e., *A. vulgaris*, *L. polaris*, *C. papposus*, *C. irroratus* or *H. araneus*) and scallops while predators are spending time searching for prey (S_m) are estimated based on Holling's (1966) equation, assuming random movements of predators and prey in a two dimensional environment:

$$E_m = \left[2 \cdot \left(V_{predator\_m}\right) \cdot S_m \cdot \left(r_{predator\_m} + r_{prey}\right) + \pi \cdot \left(r_{predator\_m} + r_{prey}\right)^2\right] \cdot M_m \cdot N \,,$$

(Equation A3.1)

where $V_{predator}$ is searching velocity of predator species m, $r_{predator}$ is radius of predator species m, r_{prey} is radius of prey, M is density of predator species m, and N is density of prey. Prey velocity is not in the equation because scallops generally do not move until physical contact with a predator (*i.e.*, 0 cm/h; Barbeau & Scheibling 1994a; Wong et al. 2006).

Upon encountering and capturing a scallop, predators take a certain amount of time to handle (manipulate and consume) the scallop and they typically do not search for other prey during that time. Thus, the amount of time spent searching (S_m) is equal to the amount of time available for foraging (T_m) minus the time spent handling prey – this is the concept that lead to the establishment of the functional response of predators (Holling 1966). The time spent handling prey is a function of the handling time per prey (h_m), number of prey encountered per predator (E_m/M_m) and the probability of scallops dying upon a predator encounter ($P[\text{die}|\text{end}]_m$). Thus:

$$S_m = T_m - \frac{h_m \cdot E_m \cdot P[\text{die}|\text{enc}]_m}{M_m} \,. \qquad \text{(Equation A3.2)}$$

The Equation A3.2 is incorporated into Equation A3.1 to include a type II functional response into the calculation of numbers of predator-prey encounters during a time interval, and solved for numbers of encounters from the scallop's point of view (i.e., the number of encounters with predator species m per scallop in a time interval; R_m):

$$R_m = \frac{E_m}{N} = \frac{\left[2 \cdot V_{predator\_m} \cdot \left(r_{predator\_m} + r_{prey}\right) \cdot T_m + \pi \cdot \left(r_{predator\_m} + r_{prey}\right)^2\right] \cdot M_m}{1 + 2 \cdot V_{predator\_m} \cdot \left(r_{predator\_m} + r_{prey}\right) \cdot h_m \cdot P\left[\text{die}|\text{enc}\right]_m \cdot N}.$$

(Equation A3.3)

Scallops encounter different species of predators in a time interval; therefore, the competing risks theory (David & Moeschberger 1978) is used to model the probability of a scallop encountering predators (P[enc]), and daily encounter rates with different predator species (R_m) as hazards:

$$P[\text{enc}] = 1 - \exp\left(-\sum_m R_m\right).$$

(Equation A3.4)

This equation assumes that different predator species (or hazards) act independently, which is supported by detailed experiments examining the effect of competing sea star and crab predators on scallop mortality (d'Entremont 2005). The probability of a scallop encountering a certain predator species, say *A. vulgaris* ($P[\text{enc}]_{Av}$), is then modelled as:

$$P[\text{enc}]_{Av} = \frac{R_{Av}}{R_{Av} + R_{Lp} + R_{Cp} + R_{Ci} + R_{Ha}} \cdot P[\text{enc}],$$

(Equation A3.5)

where Av, Lp, Cp, Ci and Ha are the different predator species.

For sea stars, the probability of a scallop dying upon encountering a sea star species s was calculated as:

$$P[\text{die}|\text{enc}]_s = P[\text{attack}|\text{enc}]_s \cdot P[\text{capture}|\text{attack}]_s \cdot P[\text{consumption}|\text{capture}]_s,$$

(Equation A3.6a)

where P[A|B] is the probability of behaviour A conditional on behaviour B estimated on tethered scallops. For crabs, P[attack|enc] and P[capture|attack] are condensed to P[capture|enc] (Wong et Barbeau 2005; Chapter 2). As well for crabs, we used an estimate of P[die|enc] that varies with prey density and take into account their type III functional response (in a sigmoid fashion) (Barbeau et al. 1994, 1998), whereby crab predation rate is low at low scallop density, increases at an accelerating rate as prey density increases (presumably as crabs recognize scallops as prey), and then increases at a decelerating rate (like a type II response) before levelling off at high prey density (Taylor, 1984). So, the probability of a scallop dying upon encountering a crab species *c* was calculated as:

$$P[\text{die}|\text{enc}]_c = \frac{K_c}{1 + \frac{K_c - k}{k}\exp(-\rho N_{total})}, \qquad \text{(Equation A3.6b)}$$

where K is the probability of a scallop dying upon encountering a crab at high scallop density (essentially a maximum observed P[die|enc]). The probability of a scallop dying upon encountering a crab at low scallop density (k) was estimated as $K/5$ (Barbeau and Caswell 1999), ρ is a coefficient related to strength of the density dependence (estimated value=3; Barbeau and Caswell 1999) and N_{total} is the density of all scallops observed at the study sites (natural and tethered scallops).

Finally, the density of juvenile scallops surviving (N) from time t to time t+1 is calculated as:

$$N_{t+1} = \left(1 - \sum_m P[\text{enc}]_m P[\text{die}|\text{enc}]_m\right) \cdot N_t . \qquad \text{(Equation A3.7a)}$$

Note, then, that the density of dead scallops (D) at time t+1, after encountering an assemblage of crab species (c) or and assemblage of sea star species (s) was estimated as:

$$D_{t+1,c} = \left(\sum_c P[\text{enc}]_c P[\text{die}|\text{enc}]_c\right) \cdot N_t \quad \text{or}$$

$$D_{t+1,s} = \left(\sum_s P[\text{enc}]_s P[\text{die}|\text{enc}]_s\right) \cdot N_t . \qquad \text{(Equation A3.7b)}$$

Appendix 4. Biases of the camera on a mobile sleigh as a tool to estimate the density of seeded juvenile scallop.

A small-scale seeding trial of 32 000 juvenile scallops (2.2 scallops /m^2) sized 25-30 mm shell height, was performed on 20 June 2005 over a site of 0.01 km^2 (0.06 km x 0.12 km) located southeast the commercial seeding area. The seeding was done by inverting, from the boat, buckets of scallops at 2 m over the sea bottom at various positions inside the study area. This small seeding trial was used to estimate i) the frequency of scallop escaping in front of the sleigh and ii) the accuracy of the camera this estimation compared to a SCUBA diver's estimation. It was also an opportunity to collect additional data on seeded scallops and predator dynamics following a small-scale seeding trial.

Estimation of amount of scallop escapes induced by the sleigh

We estimated in the field the number of scallops that escaped beyond the sleigh during video surveys. We hypothesised that the sleigh would induce scallop escapes, similar to what has previously been observed with scallop dredges (Caddy 1968), possibly due to vibrations near or on the sea bed (cause by the moving sleigh) and due to the fact that juvenile scallops are particularly mobile.

The number of scallop escapes was quantified with an additional video camera (SVS, model S512HV/29/F) connected to a video tape recorder (JVC, HR-J693U) and mounted on the top of the sleigh with an angle that allowed a field of view of about 2 m beyond the sleigh (Fig. A4.1). Surveys were conducted in 3 periods. On 18 July, four transects of 3 min (~100 m long) oriented north-south and equidistant by 15-20 m were done. Ten transects were done during the two other surveys, on 16 August and 13 October, over a larger area of 0.04 km^2 (0.20 km x 0.20 km) as juvenile scallops had dispersed after seeding.

In all surveys, only one juvenile scallop was observed lifting up and escaping in front of the moving sleigh. We thus estimated that this bias was negligible. The reason for how little our sleigh induced scallop swimming may be that it is small and light with relatively little contact with the sea bottom compared to a commercial scallop dredge.

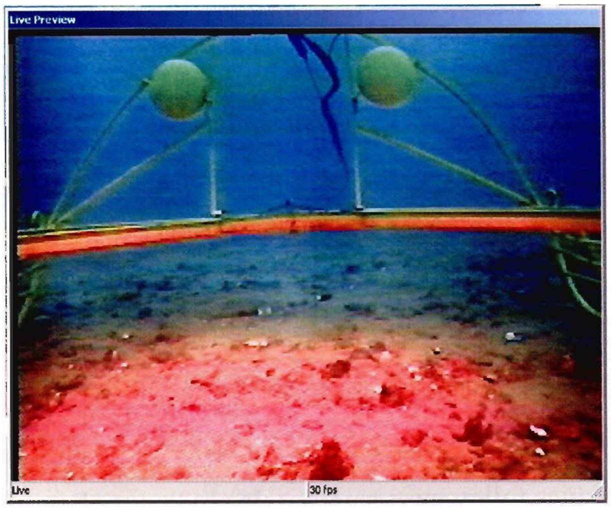

Figure A4.1. Example of the video image used to estimate the number of scallop escapes.

Comparison of the scallop density estimated from the video analysis and SCUBA divers

The density of juvenile scallops estimated from the video camera mounted on the sleigh was validated three times. We hypothesised that our estimation may be biased, and lower than reality, because of the small sizes of scallops we were working with, the scallop's ability to hide in refuge (Arsenault & Himmelman 1996a) or that scallops may be covered by a thin layer of sediment (personal observation). To estimate this possible bias and eventually use a correction factor, our video estimation of scallop density was compared with the estimation of SCUBA divers i) a short time after seeding on 27 June, ii) after about two months, on 19 August and iii) after four months, on 30 October. Although it is unlikely that divers provided a perfect measure of juvenile scallop density, it was assumed that they would provide a more accurate measure on the bottom than the video camera.

The video camera and lights were mounted in the same way as than for the 2004 seeding surveys, as described in Chapter 4. For the present small-scale trial, we also placed a roller with a 20-m graduated lead cable (marked at each 2 m) in the front-middle of the sleigh (see Fig. A4.2). At each survey period, camera and diver estimations were compared on four transect of 20 m long. Before each transect, the sleigh was immersed onto the sea bottom, followed by the diver team. Rapidly, divers attached one end of the lead cable (on the roller) to a cement weight. After a starting signal, the video recorder onboard was started and the sleigh was pulled by the boat at a speed of ~1 nautical mile · h^{-1} until the lead cable end, so that the image of each 20 m transect was videotaped. Therefore, the lead cable was visible in the middle of each video transect. Thereafter, divers counted juvenile scallops alive, on the sea bottom, within a width of 0.25 m on each side of the lead cable and for each 2-m section of the cable. Finally, the sleigh and the lead cable were brought back onboard and reinstalled for another transect. Image analysis was performed as usual and juvenile scallops alive were counted for each section of 2 m x 0.5 m (i.e., 0.25 m on each side of the lead cable). Scallops were considered dead when they were cluckers, broken shell or showing the white lower shell.

Two transects had to be discarded from the August survey because of technical problems. In addition, to ensure the independence of data, 15 quadrats (2 m x 0.5 m) were randomly selected from each survey period. At first, we wanted to perform a correlation analysis on these 15 pairs of data to know how closely both estimates were related on a fine scale. However, because of the high frequency of 0 scallop · m^{-2} (82% of quadrats) and the general low density of scallops (<2 ind. · m^{-2}) estimated by divers, we had to modify the initial plan.

The video analysis detected 90% of the 0 density quadrats. However the video detect only 30% of the 1 scallop · m^{-2} quadrats estimated by divers and did not detect the one quadrat with 2 scallops · m^{-2}. It was thus assumed that the video analysis was not fully accurate at a small spatial scale. To further examine the difference between the two estimation methods (video camera vs divers) at a larger spatial scale, we conducted a split plot analysis with Method (2 levels: video and divers) and Time (3 surveys) as fixed factors. Each pair of estimates on the same quadrat was treated as block (n=15). No significant difference was detected between the methods (Fig. A4.3, Table A4.1). So, juvenile scallop density estimated from video and divers at a larger spatial scale was considered similar. In addition, no significant difference was detected between times. Based on these results and the fact the studies presented in Chapters 3, 4 and 5 are also conducted at a larger scale, no correction factor was applied to scallops densities estimated from video surveys.

Figure A4.2. Pictures of the set-up used to compare the scallop density estimated by SCUBA divers and with the video analysis.

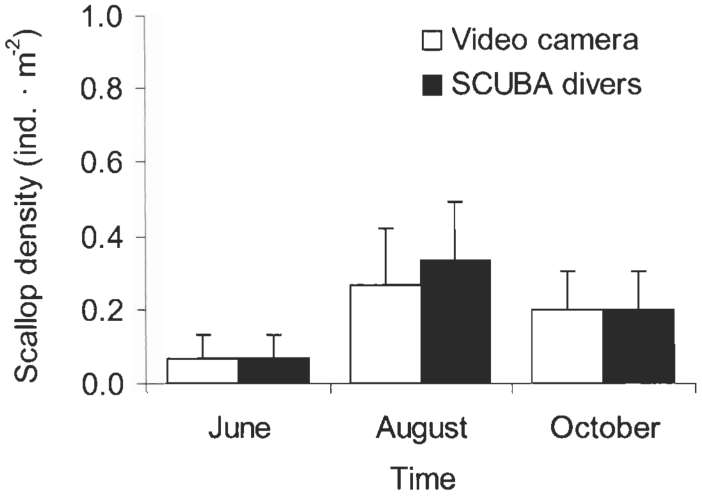

Figure A4.3. Scallop density (mean ± SE, n=15) estimated by SCUBA divers and video camera at three survey periods in 2005.

Table A4.1.Results of a split plot analysis on scallop density estimated by divers and video camera (Method), during three time periods and in 15 blocks. Data were transformed using $\log_{10}$(datum+0.001).

Source of variation	df	MS	F	*p*
Between subjects				
Time	2	2.225	1.34	0.273
Error [i.e.Block(Time)]	42	1.661		
Within subjects				
Method	1	0.100	0.10	0.751
Method*Time	2	0.100	0.10	0.903
Error [Method*Block(Time)]	42	0.981		

Appendix 5. Pictures of scallops during the 2007 seeding trial.

a) Scallops sinking to the sea bottom after being released from the surface (from a boat).

b) Close-up within a patch of seeded scallops on the sea bottom.

c) A SCUBA diver with a circular sampling unit (0.25 m^2).