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**Écologie de population du bivalve *Pinna carnea***

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## Résumé

Mon étude, effectuée en République dominicaine, indique que *Pinna carnea* est un mollusque que l'on trouve dans les prés sous-marins et non pas dans les replats sableux adjacents. Les densités de population étaient basses ( $1-7/100\text{ m}^2$ ) et les structures de taille étaient biaisées envers les gros individus. Des expériences indiquent, que les larves n'ont pas de préférence de substrat lors de la fixation, qu'il y a moins de prédation chez les gros individus, et qu'il y a une mortalité réduite dans les prés sous-marins. *P. carnea* semble être limité aux prés sous-marins car cet habitat fournit une protection contre les prédateurs et les perturbations physiques. La croissance juvénile rapide peut être une stratégie évolutive pour réduire sa vulnérabilité aux prédateurs. La prédominance de gros individus peut représenter une accumulation d'événements de recrutement causée par le ralentissement de croissance lorsqu'ils ont atteint  $>150\text{ mm}$  de longueur.

## Abstract

Surveys in the Dominican Republic showed that the penshell *Pinna carnea* is consistently found in seagrass beds, but is absent in adjacent sandflats. Population densities were low ( $1-7/100\text{ m}^2$ ) and the size structure was skewed towards large individuals. Experiments indicated that penshell larvae do not select a particular substratum to settle on, that post-settlement mortality decreases with increasing size, and that mortality is less in seagrass than sandflat habitats. *P. carnea* is likely restricted to seagrass beds because this habitat provides some protection from predators. Also, the consolidated sediments in seagrass beds provide protection from physical disturbances. Growth measurements showed that juveniles grow very rapidly. This has likely evolved as a strategy for reducing the period of high vulnerability to predators. The dominant mode of large individuals in populations likely represents the accumulation of successive recruitment events caused by the slowing of growth when individuals attain  $>150\text{ mm}$  in length.

## **Avant-propos**

Je voudrais sincèrement remercier toutes les personnes et les organisations qui ont permis à ce projet de se réaliser. Je suis, avant tout, redevable à mon directeur, le Professeur John Himmelman, pour m'avoir accordé sa confiance dans l'élaboration d'un projet sortant du cadre traditionnel de son laboratoire, et de m'avoir permis d'entreprendre de nombreux projets au cours des années (à l'extérieur de mon programme), qui m'ont épanouis autant sur un niveaux professionnel que personnel. Pour sa patience, je suis spécialement reconnaissant. Je remercie aussi les membres de mon comité d'évaluation, Ladd Johnson et Karen Harper, les personnes qui m'ont assisté dans mes travaux de terrain, José 'Chapo' Ledesma, Åsa Kestrup, Clément Dumont, Alex Tewfik qui a fourni des données utiles, ainsi qu'à tous les étudiant(e)s, technicien(ne)s, et chercheur(euse)s du département de biologie qui n'ont jamais hésité de m'aider. Enfin, et surtout, je voudrais remercier mes parents, Paul et Marielle Aucoin, qui m'ont donné le goût de l'aventure et de la découverte.

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Avec les conseils judicieux de mon directeur, j'ai développé les dispositifs expérimentaux, entrepris les travaux, et analysé les données pour accomplir cette maîtrise. Le contenu de mon mémoire correspond à un article qui sera soumis sous peu pour publication. Cet article est signé par moi-même, Serge Aucoin, et mon directeur John Himmelman.

“The true biologist deals with life, with teeming boisterous life, and learns something from it, learns that the first rule of life is living.” – John Steinbeck

à Aurélien Aumjaud

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## **Introduction générale**

En écologie des populations, les généralisations sont souvent difficiles à établir car les populations peuvent varier dans l'espace et le temps en passant par une gamme de patterns dynamiques (Butler, 1994; Begon, 1996). Les variables d'une population, comme l'abondance, la structure d'âge, et la distribution d'individus, peuvent être stables ou elles peuvent changer continuellement. En plus, plusieurs variables peuvent rester semblables entre les populations, tandis que d'autres seront différentes. Par exemple, deux populations ayant une densité semblable, peuvent toutefois avoir une structure de taille ou un arrangement spatial d'individus distinct l'un de l'autre. Ce faisant, pour arriver à comprendre les causes sous-jacentes, ou de parvenir à une compréhension de tous les facteurs ou processus interagissant, responsables de tels patterns, nous devons considérer diverses étapes du développement de l'organisme et plusieurs facteurs écologiques, incluant tout type d'interactions physiques et biologiques (passant par plusieurs niveaux trophiques). Ces facteurs causals et interactifs peuvent se révéler complexes, même dans une population simple.

Les patterns que l'on observe dans beaucoup de populations d'organismes marins sont déterminés par divers facteurs physiques et biologiques agissant sur le stade larvaire et benthique (i.e., avant et après la fixation). À chaque stade, l'impact relatif exercé sur la population (e.g., l'influence sur l'abondance, la distribution, et la structure de taille des individus de la population) est souvent d'intérêt et de sujet de débats courants dans beaucoup d'études concernant les communautés marines. Le premier déterminant d'une population est fréquemment l'abondance de larves prêtes à s'établir (Gaines et Roughgarden, 1985; Minchington et Scheibling, 1991) sous l'influence de facteurs comme la dispersion et la mortalité larvaire (Eckman, 1983; Gaines et Bertness, 1992; Levin, 2006). Les patterns d'une population sont aussi affectés par le comportement des larves et les réponses larvaires aux différents substrats (Butman, 1987; Pawlik, 1992; Li et al., 2006). Après la fixation, la mortalité, particulièrement celle qui est causée par les prédateurs, peut exercer une importante influence sur la population (voir les revues par Gosselin et Qian, 1997; Hunt et Scheibling, 1997).

Les effets de la prédation sur les bivalves, comme sur la plupart des invertébrés benthiques, peuvent varier selon l'espèce, l'habitat, l'endroit et le temps, ainsi qu'avec la dimension du prédateur et celle de la proie (Barbeau et Scheibling, 1994; Barbeau et al., 1994). La dimension des proies choisies par les prédateurs va souvent déterminer la structure de taille des individus de la population de l'espèce servant de proie (Moran, 1985; Kvitek et al., 1992; Arsenault et Himmelman, 1996). La mortalité causée par d'autres facteurs, comme les perturbations physiques et le manque de ressources alimentaires, peut aussi affecter les populations (Constable, 1999; Lenihan et Micheli, 2001; Olafsson et al., 1994). En raison de la complexité de tous ces facteurs de mortalité, la majorité des études ont tendance de se concentrer sur un seul facteur; toutefois, l'étude de la dynamique d'une population nécessite l'examen de divers facteurs et composantes ensemble (Gaines et Roughgarden, 1985; Bertness et al., 1992; Eggleston et Durham, 1995).

Mon étude a examiné la Pinna ambrée, *Pinna carnea* Gmelin 1791, dans le parc national de Jaragua (qui fait partie des réserves de la biosphère de l'UNESCO, Jaragua-Barahuco-Enriquillo) et ses environs, dans la région du sud-ouest de la République dominicaine (Fig. 1). *P. carnea* est un bivalve sessile de la famille Pinnidae, une petite famille de bivalves très spécialisés de l'ordre Anisomyaria (des bivalves avec un gros muscle adducteur postérieur et un adducteur antérieur réduit ou absent) (Turner et Rosewater, 1958). Sa distribution géographique est répandue à partir du sud de la Floride jusqu'au Brésil (Turner et Rosewater, 1958; Narváez et al., 2000) dans les habitats de prés sous-marins (Young, 1953; Tewfik et al., 2005).

Comme première étape d'étude, j'ai fait des recensements benthiques à plusieurs endroits en République dominicaine pour documenter les patterns présents dans les populations de *P. carnea*. En 2002, j'ai examiné six sites près de Barahona et le long de la côte du parc national de Jaragua, près de Pedernales. En 2005, j'ai examiné deux nouveaux sites dans cette région, Trudillé et Cabo Rojo. Mes recensements benthiques ont indiqué que *P. carnea* était répandu, quoique présent à une faible densité, dans les prés sous-marins de cette région, mais absent dans les habitats voisins comme les replats sableux. Dans tous les recensements benthiques, très peu de petits individus ont été trouvés - la majorité des individus présents étaient gros.

Deuxièmement, j'ai examiné plusieurs facteurs et processus écologiques qui pourraient exercer une influence sur l'abondance, la distribution, et la structure de taille de la population. Mes objectifs généraux étaient de découvrir ce qui peut causer les patterns observés, notamment pourquoi *P. carneae* est si peu abondant et limité aux prés sous-marins, et d'apporter quelques connaissances à l'étude de la dynamique de population. D'abord, pour identifier les facteurs biologiques, et certains composants d'habitat, qui pourraient exercer une influence importante sur *P. carneae*, j'ai comparé la diversité de macro-invertébrés benthiques, et quelques caractéristiques souterraines et en surface des prés sous-marins, aux deux sites, Trudillé et Cabo Rojo. Lors de mes recensements, puisque j'ai seulement observé des Pinna ambrées dans les prés sous-marins, j'ai alors posé des collecteurs pour évaluer divers substrats, que l'on retrouve dans cet habitat, pour déterminer lesquelles substrats du pré sous-marin vont influencer la fixation de larves. En plus, j'ai déployé des collecteurs dans d'autres habitats pour examiner la distribution larvaire, et pour ensuite comparer les taux de fixation, au-delà de celle qui a lieu dans les prés sous-marins.

Troisièmement, puisque l'abondance de bivalves colonisateurs peut, dans un premier temps, influencer les patterns d'une population, j'ai examiné le recrutement, et la mortalité, le plus rapidement possible après la fixation. J'ai comparé de nouvelles recrues de *P. carneae* fixées sur des collecteurs (en cages et sans cages) que j'ai posés dans des prés sous-marins et des replats sableux, aux deux sites. La mortalité qui a lieu dans les stades de développement plus avancés peut aussi être un déterminant important de la structure de la population (Gosselin et Qian, 1997; Hunt et Scheibling, 1997). Alors j'ai aussi examiné la survie d'individus de plus grandes tailles. J'ai transplanté des individus de tailles croissantes dans un pré sous-marin et dans un replat sableux, avec cages et sans cages, pour évaluer le taux de prédation selon les différentes tailles et le type d'habitat. Plusieurs expériences du genre ont été répétées dans le temps, et l'une d'elles a subi une perturbation majeure, le passage d'un ouragan. J'ai également évalué la survie des Pinna ambrées, de différentes tailles, avec le prédateur potentiel *Meoma ventricosa*, un oursin qui se trouvait à Cabo Rojo et pas à Trudillé.

Plusieurs expériences ont déjà démontré que les types de ressources alimentaires et la sédimentation pourraient jouer un rôle dans la structuration des populations et des communautés benthiques (voir la revue d'Olafsson et al., 1994). Ainsi, j'ai évalué les

sources alimentaires disponibles et les quantités de sédiments vaseux dans des prés sous-marins et des replats sableux, et la croissance de *P. carneae* de différentes tailles dans ces deux différents habitats, comme facteurs pouvant affecter la population.

## **Chapitre I**

### **Factors determining the abundance, distribution and size- structure of populations of the penshell *Pinna carnea* (Bivalvia: Pinnidae)**



## Résumé

Mon étude, effectuée dans le sud-ouest de la République dominicaine, indique que *Pinna carnea* est un mollusque que l'on trouve dans les habitats de prés sous-marins et non pas dans les replats sableux adjacents. Les densités de population étaient réduites (1-7/100 m<sup>2</sup>) et la structure de taille des populations était composée principalement de gros individus. Des expériences avec 5 types de substrats, incluant des brins d'herbes marines et des racines, indiquent que les larves n'ont pas de préférence de substrats lors de la fixation. Notre comparaison de juvéniles qui se sont fixés sur des collecteurs (suspendus avec cages et sans cages) indique des pertes semblables (84 %) dans chaque habitat. D'autres expériences se servant de plus grands bivalves (10-30, 50-70, 90-110 mm de longueur le long de la charnière), transplantés dans les deux habitats indiquent qu'il y a moins de prédation chez les gros individus, et qu'il y a une mortalité réduite dans l'habitat de prés sous-marins. Dans une expérience de 10 jours, la survie d'individus, incluant les trois classes de tailles, était 27 fois plus grande dans le pré sous-marin que dans le replat sableux. À la fin d'une expérience de 100 jours, durant laquelle l'ouragan Dennis a eu lieu, seulement 30 % des individus de la plus grande taille ont survécu dans un pré sous-marin, et aucun individu n'a pu survivre dans un replat sableux. Durant mon expérimentation de 3 jours effectués dans le replat sableux, le taux de survie des bivalves transplantés a passé de 6 % pour les individus 50-100 mm à 93 % pour les individus de 150-170 mm de longueur. Diverses mesures de croissance prises pour évaluer le taux de croissance indiquent que *P. carnea* croît rapidement (jusqu'à 2.2 mm/jour). La croissance rapide durant le stade juvénile peut être une stratégie pour réduire cette période de forte vulnérabilité face aux prédateurs. *P. carnea* est forcément limité aux habitats de prés sous-marins surtout parce que l'habitat offre une certaine protection contre les prédateurs. En plus, la consolidation du sédiment (dû aux racines et rhizoïdes) fournit une protection contre les perturbations physiques. La prédominance de gros individus peut représenter une accumulation d'événements de recrutement causée par le ralentissement de croissance lorsqu'ils ont atteint >150 mm de longueur. Bien que les habitats de prés sous-marins soient avantageux pour ces bivalves, ils possèdent tout de même un désavantage, c'est-à-dire un facteur de mortalité (possiblement la quantité de vases qui est ~3 fois plus élevé dans cet habitat) qui est absent dans les replats sableux.

## **Abstract**

Surveys conducted in southwestern Dominican Republic showed that the penshell *Pinna carnea* is a consistent component of seagrass beds and is absent in adjacent habitats such as sandflats. Population densities were low (1-7/100 m<sup>2</sup>) and the size-structure skewed towards large individuals. Trials with five types of substrata in spat collectors, including seagrass blades and roots, indicated no settlement preference for a particular substratum. Comparison of suspended caged and uncaged spat collectors indicated similar predation losses (84 %) for recently settled penshells in seagrass beds and adjacent sandflats. Experiments with older penshells (10-30, 50-70, 90-110 mm in hinge length) transplanted to plots in both habitats showed that predation losses decreased with increasing size and were less in the seagrass bed. In 10-d trials, the survival of these size-groups was 27-fold greater in a seagrass bed than in an adjacent sandflat. At the end of 100-d trials, during which our study area was subjected to Hurricane Dennis, only 30 % of the largest individuals survived in the seagrass bed, and no individuals survived in the sandflat. Penshell survival increased from 6 % for 50-100 mm individuals to 93% for 150-170 mm individuals during 3-d trials in the sandflat. Growth measurements showed that small penshells grow rapidly (up to 2.2 mm/d), but the growth rate drops markedly at ~150 mm. Rapid juvenile growth may be a strategy for reducing the period of high vulnerability to predators. *P. carnea* is likely restricted to seagrass beds mainly because this habitat provides some protection from predators. The consolidation of sediments in seagrass beds by roots and algal rhizoids also provides protection from physical disturbances. The predominance of large individuals in the populations likely represents the accumulation of successive recruitments as growth slows. The advantages provided by the seagrass habitat come at a minor cost as we observed a mortality factor in the seagrass bed (possibly related to the ~3-fold higher silt load) that was absent on the sandflat.

## Introduction

Population patterns of benthic invertebrates (e.g., abundance, distribution, size-structure) are determined by a variety of biological and physical factors acting on both larval and benthic phases (Thorson, 1966). The first determinant of population patterns is often the abundance of larvae ready to settle (Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989; Minchington and Scheibling, 1991), which is influenced by such factors as larval dispersal and mortality (Eckman, 1983; Roughgarden et al., 1988; Rumrill, 1990; Gaines and Bertness, 1992; Morgan et al., 1996; Levin, 2006). Population patterns are also affected by larval behavior and responses to settlement cues (Butman, 1987; Pawlik, 1992; Harvey et al., 1995; Kingsford et al., 2002; Li et al., 2006). One can infer larval responses to substrata by studying the abundance and distribution of early settlers before patterns are masked by post-settlement mortality (Keough and Jones, 1982; Connell, 1985). Populations are further affected by post-settlement mortality, particularly from predation (see reviews by Gosselin and Qian, 1997; Hunt and Scheibling, 1997). Gosselin and Qian (1997) indicate benthic invertebrates commonly have high mortality rates after settlement, for example, juvenile mortality was >90 % in 20 of the 30 studies they examined (and ~98.6 % for the studies on bivalves).

The effect of predation on bivalves, as on most benthic invertebrates, likely varies with habitat, site, time, and the size and type of predators and prey (Barbeau and Scheibling, 1994; Barbeau, et al., 1994). Size selection of prey by predators often plays a role in determining the size-structure of prey populations (Moran, 1985; Kvitek et al., 1992; Arsenault and Himmelman, 1996). Physical disturbances and inadequate food resources can also cause mortality of benthic invertebrates (see reviews by Constable, 1999; Lenihan and Micheli, 2001; Olafsson et al., 1994). Most studies focus on single factors causing mortality. A more comprehensive understanding of population dynamics requires the examination of various factors together (Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989; Bertness et al., 1992; Eggleston and Durham, 1995).

The present study considers the pen shell *Pinna carnea* Gmelin, 1791, a sessile bivalve that is distributed from southern Florida to Brazil (Turner and Rosewater, 1958; Narváez et al., 2000). It is reported to occur in medium to coarse sandy substrata or mixed substrata (sand-rocks-corals) in Columbia (Urban, 2001), whereas it is found in eelgrass

(*Zostera* sp.) beds in the Bahamas (Yonge, 1953) and in turtle grass (*Thalassia testudinum*) and manatee grass (*Syringodium filiforme*) beds in the Dominican Republic (Tewfik et al., 2005). The anterior portion of the penshell (umbo) is buried and attached by byssal threads to subsurface materials (sand, pebbles and seagrass roots), whereas the posterior portion (beyond the posterior adductor muscle) protrudes vertically above the substratum. Although this position allows penshells to filter water from above silty bottoms, it could also increase exposure to predators. Penshells often show breaks or scars on the posterior shell margin that likely result from predatory attacks (Yonge, 1953; Turner and Rosewater, 1958; Dietl and Alexander, 2005). Only a few studies report aspects of the biology of *P. carneae*. Yonge (1953) describes the morphology of this penshell, whereas others discuss aspects of its reproduction and aquaculture potential (Castellanos et al., 1997; Garcia-Valencia et al., 1997; Narváez et al., 2000; Urban, 2001; Núñez et al., 2006).

Our study evaluates factors determining the abundance, distribution, and size structure of the penshell *P. carneae*. We first document population patterns at a number of locations in southwestern Dominican Republic, and then describe experiments performed to examine: (1) substratum and habitat choice for settlement, (2) early post-settlement mortality (in the first 1-2 months), (3) subsequent mortality relative to size, habitat (seagrass beds and adjacent sandflats) and disturbance (from urchins and a hurricane), and (4) the growth rate relative to size and habitat. As *P. carneae* and other members of the family Pinnidae have a unique waste canal that facilitates living in silty habitats (see Winckworth, 1929; Yonge, 1953; Turner and Rosewater, 1958; Rosewater, 1961), we also examine the importance of sedimentation and food availability.

## Methods

### Habitat description and population patterns

Our first observations of *P. carnea* populations were made near Pedernales and Barahona (Fig. 1) during surveys on macro-invertebrates in seagrass beds made from February to June 2002 (in the context of the benthic foodweb study of Tewfik et al., 2005). In 2005, we examined populations at two new locations (4-8 m depth), near Trudillé and Cabo Rojo (Fig.1). We first examined 6 transects at Trudillé and 4 at Cabo Rojo during May, and followed with 5 transects at each location during late-August and early-September. These locations were exposed to Hurricane Dennis on 7-8 July. All survey locations supported similar sheltered seagrass habitats, although Trudillé had markedly more calcareous green algae (family Halimedacea). In each survey, two SCUBA divers searched through 3 x ~60 m transect corridors across the seagrass bed, recording the density of macro-invertebrates and hinge length (umbo to posterior dorsal tip) of each penshell encountered.

To provide information on factors that could affect penshell populations at Cabo Rojo and Trudillé, we first examined the diversity of the benthic macro-invertebrates encountered along all transects made at both sites (11 at Trudillé and 9 at Cabo Rojo). This was done by applying the Shannon-Weiner index ( $H$ ) to consumer functional groups as defined for benthic communities in seagrass beds in the Dominican Republic (Tewfik et al. 2005). We also evaluated different features of habitat structure by quantifying the above- and belowground portions of the seagrass beds at both locations. Aboveground canopy cover was quantified by sampling 10 x 10 cm quadrats that were haphazardly placed, but at least 15 m apart. We took 15 samples at Trudillé and 16 at Cabo Rojo. The belowground portion of seagrass habitats was also quantified from 196 cm<sup>3</sup> sediment cores (5 cm diameter, 10 cm depth) taken in the middle of each of the above quadrats. Contents from each sediment core were wet sieved (3.5-mm pore size) and then separated into (1) consolidated sediment with roots and algal rhizoids, and (2) large loose sediment (>3.5 mm diameter). All seagrasses and macrophytes sampled, and the sediment in the cores, were oven-dried at 80 °C for 24 h and then weighed.

### **Substratum preference for larval settlement**

Since penshells were found only in seagrass beds, we evaluated the suitability of various potential settlement substrata from the seagrass habitat. The substrata tested were: (1) seagrass blades and roots (the root portion in sand), (2) blades only (the bottom portions of the blades implanted into sand), (3) roots only (largely buried in sand), and (4) only sand. We also added a treatment consisting of 2-cm-wide strips of plastic scouring pads (total surface of 0.15 m<sup>2</sup>). This treatment allowed us to compare the settlement in this experiment with that in subsequent experiments where scouring pads were the only settlement substratum used.

We deployed 25 collectors, 5 replicates for each treatment, at both Trudillé and Cabo Rojo. Each collector consisted of a large PVC cap (9 cm depth, 13 cm diameter), which held the substratum (Fig. 2). Each collector was protected in a cylindrical cage (30 cm height, 13 cm diameter, ~1 cm<sup>2</sup> mesh). The collector was attached to floats and suspended at ~1 m above the seagrass bed. In this and the following experiments, the experimental units (collectors with different substrata in this case) were haphazardly placed but at least 5 m from one another. All treatments were mixed and interspersed within a hectare. We counted penshells and other bivalves on the collectors once they were retrieved after ~75 d at Trudillé (21-23 March to 1-4 June 2005) and after ~130 d at Cabo Rojo (11-12 April to 16-20 August 2005). In this and several other experiments, the delayed retrieval of data at Cabo Rojo was due to unforeseen circumstances (an injury).

### **Settlement intensity and early post-settlement mortality**

As numbers of settlers and their subsequent survival can be major determinants of population patterns, we evaluated larval settlement and early post-settlement mortality of *P. carnea* by deploying collectors at both Trudillé and Cabo Rojo. The collectors were either caged or uncaged and were deployed on the seafloor and at ~1 m above the bottom, both in seagrass beds and adjacent sandflats. There were 10 caged and 10 uncaged replicates for each position in each habitat at both locations (80 experimental units per location). All collectors were made with two rectangular scouring pads (each 10 x 15 cm; similar to ‘scotch-bright’ pads) wrapped around a plastic soda bottle and held in place by a crinoline (onion-sac material) sleeve (Fig. 2). In the caged collectors (30 cm height, 19 cm

diameter,  $\sim 5 \text{ mm}^2$  mesh) the scouring pad substratum was separated from the cage walls by  $\sim 6 \text{ cm}$ . Collectors were retrieved after  $\sim 75 \text{ d}$  at Trudillé (21-23 March to 1-4 June 2005) and after  $\sim 130 \text{ d}$  at Cabo Rojo (11-12 April to 16-20 August 2005), and penshells and other bivalves were counted.

To provide further information on the settlement of *P. carnea* larvae in other habitats, on 12-13 April 2005, we also suspended 5 caged collectors  $\sim 1 \text{ m}$  above the bottom in each of two additional habitats at Cabo Rojo: a rocky-coral-sponge habitat ( $\sim 6 \text{ m}$  depth) and a seagrass bed off a headland, where the brown algae *Lobophora variegata* was abundant ( $\sim 12 \text{ m}$  depth). These collectors were also retrieved  $\sim 130 \text{ d}$  later.

### **Penshell mortality in seagrass beds and sand barrens**

To determine the impact of predators on older penshells, we quantified the survival of three size-groups of penshells, 10-30, 50-70, 90-110 mm, in a seagrass bed and an adjacent sandflat at Cabo Rojo. Each replicate consisted of a  $50 \times 50 \text{ cm}$  plot into which we transplanted 4 penshells (evenly dispersed) of a given size-group. We deployed 5 replicates with predator exclusion cages ( $50 \text{ cm}$  height,  $\sim 1 \text{ cm}^2$  mesh) and 5 replicates without cages for each of the three size-groups in both habitats (60 plots). The above experiment was repeated three times in 2005. In the first trial, survival was measured after a period of 1 d (12-13 May), in the second after 10 d (14-23 May), and in the third after 100 d (24 May to 31 August). Hurricane Dennis passed through the region during the 100-d trial (7-8 July). The penshells used in these experiments were collected from fishing moorings located  $\sim 3 \text{ km}$  offshore south of Barahona (Fig. 1). They were transported to Cabo Rojo in buckets and then maintained in cages for at least 2 wk prior to the trials to allow them to acclimatize to conditions at Cabo Rojo.

To evaluate survival rates of still larger penshells, we compared 50-100 mm and 150-170 mm individuals transplanted to the sandflat at Cabo Rojo. We ran 5 consecutive 3-d trials (23 August to 8 September 2005) and each trial was set up with three large penshells and three small penshells. Finally, we transplanted 17 penshells (111 to 244 mm) to within 2 m of the edge of the seagrass bed and recorded their survival 100 d later (21 May 2005 to 29 August 2005). These individuals were also subjected to Hurricane Dennis.

### **Impact of specific predators**

Observations during our transect surveys suggested that the red-heart urchin *Meoma ventricosa* and the balloonfish *Diodon holocanthus* could be potential predators of penshells. The red-heart urchin disturbs the sediment while foraging and balloonfish are capable of cracking the shells of crustaceans and molluscs. In late June 2005, we evaluated the effect of these animals by measuring the numbers of penshells they ate or unearthed during 3-d trials in 1 m<sup>3</sup> caged plots. For each predator, we set up 3 caged plots at the same time, each cage holding one predator and 4 penshells for each of four size-groups (25-30, 40-45, 65-80, 180-200 mm). The different-sized penshells were mixed and placed at about equal distances from one another in each cage 5 d prior to each trial to allow them to reattach with their byssal threads.

### **Sedimentation in seagrass beds and sand flats**

The amount and types of material falling to the seafloor from the water column and from resuspended sediment are often critical to bivalves and other suspension feeders. In 2005, we quantified numbers of settling bivalves, particulate organic matter (POM), and silt mass using sediment traps that were deployed in seagrass beds and adjacent sandflats at both Trudillé and Cabo Rojo (8 traps/habitat/location; the experimental units were separated by at least 20 m). Traps were made of PVC pipes (30 cm length, 2.5 cm diameter) that were driven into the sediment. Only the upper 2 cm of the pipes extended above the seafloor. These traps collect both particles sinking from the water column and resuspended particles carried by eddies formed at the trap mouth (e.g., sediment, detritus, larvae; Butman 1989). To preserve collected materials, the bottom half of each trap was filled with a tinted 10 % formalin-seawater solution and topped off with filtered seawater. The higher density of the bottom formalin layer may reduce resuspension of settled materials and the added color provides an indication of loss of material from the traps (Yund et al. 1991, McNaught and Steneck, 1998). The traps were retrieved after ~75 d at Trudillé (16 March to 29-30 May) and after ~145 d at Cabo Rojo (8 April to 30 August).

The contents from each trap were first wet sieved using a 0.45-µm filter (using a manual vacuum pump) to remove water and formalin residue. Invertebrates were then separated using a stereomicroscope, and the remaining material was dried at 80 °C for 24 h.

To determine silt content, we first weighed the dried material that passed through a 2.8-mm<sup>2</sup> sieve (to remove large pebbles and detritus). We then stirred in a solution of sodium polyphosphate dissolved in water for 15 min to aid in the dispersion of clay particles (silt). This was done a second time after 24 h and then the material was placed on a 63-µm sieve and washed with running water until no further silt could be removed. The material remaining on the sieve was dried at 100 °C for 24 h and then weighed. The silt content was calculated as the percentage weight loss from the washing process (Bale and Kenny, 2005). We further measured the weight of POM by ashing (at ~350 °C) the materials collected on both the 2.8-mm and 63-µm sieves (thus including pebbles and detritus, but not silt). Removing the silt before ashing reduces bias due to structural water within clay interstices (Craft et al., 1991). The muffle furnace was not set at a higher temperature to avoid decomposition of carbonate in shells (Welikey et al., 1983).

To evaluate potential pico- to micro-plankton food sources in the water, we analyzed 3.8-L water samples collected just above the seafloor in seagrass beds and adjacent sandflats. Samples were taken at Trudillé on 26-27 May 2005 (3 samples from the seagrass bed and 2 from the sandflat) and at Cabo Rojo between 22 April to 1 September 2005 (7 samples from the seagrass bed and 7 from the sandflat). Each water sample was first pre-filtered through a 263-µm sieve and then filtered through a 0.45-µm combusted and pre-weighed Whatman GF/F glass filter. The material collected on the filter was weighed after being dried at 80 °C for 24 h. The percentage organic content of the materials (0.45-263 µm) on the filters was then determined by gas chromatography carried out at the Centre GEOTOP-UQAM-McGill in Montreal, Canada.

## Growth

To obtain an approximate growth curve for *P. carneae*, we measured increases in shell hinge length of 62 individuals, ranging from 10.5 to 220 mm in hinge length, that were transplanted to seagrass beds at Cabo Rojo. The measurements were made over various time periods between March through June 2002, and also between May through August 2005. For the small penshells, measurements were taken after a few days to a week, whereas for larger individuals, measurements were taken after a few weeks to a month. The smallest penshells were maintained in cages to protect them from predators.

During 23 August to 9 September 2005, we also compared the increase in hinge length of penshells transplanted to the seagrass bed and an adjacent sandflat at Cabo Rojo. We ran three 9-d trials, each with an array of similar-sized penshells (11 to 60 mm). In each trial, 5 penshells per habitat were individually maintained in cages (30 cm height, 19 cm diameter) to exclude predators.

## Results

### *P. carnea* population patterns and habitat descriptions

Low numbers of penshells were found in the seagrass beds surveyed at the 6 locations in 2002, and the population size-structure was skewed towards large individuals (Fig. 3). An ANOVA applied to penshell density at the 6 locations (4-8 transects per location) indicated that density did not vary with location ( $F_{5,25}=1.06$   $p=0.41$ , Levene's test  $p=0.06$ ). The mean density across the locations surveyed was 0.016 penshells/m<sup>2</sup> (SD=0.010).

Student's *t*-tests comparing the numbers of penshells encountered in transects surveyed before and after Hurricane Dennis in 2005 showed no change in either penshell density or mean size due to the passage of the hurricane at either Trudillé (*density*:  $t_{0.05(2)9}=0.70$   $p=0.50$ , Levene's test  $p=0.95$ ; *size*: unequal variance *t*-test  $t_{0.05(2)93.9}=-0.92$   $p=0.36$ ) or Cabo Rojo (*density*:  $t_{0.05(2)7}=0.71$   $p=0.50$ , Levene's test  $p=0.14$ ; *size*:  $t_{0.05(2)13}=0.67$   $p=0.52$ , Levene's test  $p=0.74$ ). The mean density of penshells at Cabo Rojo (before and after hurricane pooled) was similar to the values observed at the 6 locations studied in 2002, but the density at Trudillé (for all transects pooled) was 7-fold greater (0.070 penshells/m<sup>2</sup>, SD=0.032) than at Cabo Rojo (0.010/m<sup>2</sup>, SD=0.015) (unequal variance *t*-test  $t_{0.05(2)14.7}=-5.6$   $p<0.001$ ). At both Trudillé and Cabo Rojo, the size range was similar and larger individuals predominated (Fig. 3); however, mean size was smaller at Trudillé (134 mm, SD=39) than at Cabo Rojo (171 mm, SD=55) (*t*-test  $t_{0.05(2)152}=3.3$   $p=0.001$ , Levene's test  $p=0.09$ ).

### Comparisons of consumer functional groups and seagrass habitats

Shannon-Weiner indices (*H*) indicated that the diversity of different consumer functional groups did not vary between Trudillé and Cabo Rojo ( $H_{\text{Trudillé}}=1.23$ , SD=0.26;  $H_{\text{CaboRojo}}=1.25$ , SD=0.27) ( $t_{0.05(2)18}=-0.14$   $p=0.89$ , Levene's test  $p=0.78$ ). In our survey the main species in the different functional groups were as follows: (1) the bivalves *P. carnea* and *Atrina* sp. as suspension feeders, (2) conchs *Strombus gigas*, *S. costatus* and *S. raninus* as epibiont/detritus specialists, (3) urchins *Lytechinus variegatus*, *Tripneustes ventricosus*, *Diadema antillarum* and *Eucidaris tribuloides* as generalists, (4) sea stars *Oreaster reticulates*, *Luidia alternata* and sea cucumbers as surface deposit feeders, (5) the urchin

*Meoma ventricosa* and sand dollars as sub-surface deposit feeders, and (6) gastropods *Murex* sp., *Charonia* sp., and *Cassis* sp., and decapod crabs, lobsters and mantis shrimp in the predator/scavenger group.

To compare the structure of seagrass beds at Trudillé and Cabo Rojo, one MANOVA was applied to data on the seagrass and algal dry mass (from quadrats) and a second on the dry mass of belowground large loose sediment particles and the consolidated sediment with roots and rhizoids (from sediment cores taken within the quadrats) (Fig. 4). Seagrass dry mass was similar at Trudillé and Cabo Rojo ( $F_{1,29}=4.1$   $p=0.05$ ,  $\alpha$ -level=0.025; Levene's test  $p=0.51$ ), but algal dry mass was ~50 times greater at Trudillé than at Cabo Rojo ( $F_{1,29}=42.1$   $p<0.001$ ). The comparisons of the belowground portion of the habitat indicated that there was more large loose sediment (>3.5 mm), as well as more consolidated sediment (with roots and rhizoids), at Trudillé than at Cabo Rojo. The dry mass of >3.5 mm sediment was >3 times greater at Trudillé than at Cabo Rojo ( $F_{1,29}=31.1$   $p<0.001$ ), and the dry mass of belowground consolidated matter was >5 times greater at Trudillé than at Cabo Rojo ( $F_{1,29}=55.1$   $p<0.001$ ). As  $p$  values are the same for MANOVAs and ANOVAs in the SPSS statistical package, version 11.04, we set the  $\alpha$ -level at 0.025 (0.05 divided by the number of univariate tests conducted) to control for Type I error (Green and Salkind, 2003). The data in this analysis, except for that on seagrass biomass, did not meet the assumption of equal variances, but the validity of these tests and the probabilities associated with the  $F$ -ratio distribution were probably not greatly affected because the sample size was relatively large and the numbers of samples per location or treatment was almost the same (i.e., balanced sampling) (Weerahandi, 1995; Underwood, 1997).

### **Substratum choice for larval settlement**

Our settlement collectors at Trudillé only contained 2 penshells, which compared with 150 other bivalves, whereas at Cabo Rojo there were 50 penshells (2.1/collector, SD=1.6) and 170 other bivalves. The posterior ends of the penshell recruits were buried in the same way as individuals encountered in the field surveys. An ANOVA applied to the data at Cabo Rojo indicated that a similar number of penshells settled on the five substrata tested (Fig. 5) ( $F_{4,20}=0.48$   $p=0.75$ , Levene's test  $p=0.22$ ). The common egg cockle *Laevicardium laevigatum* was a conspicuous bivalve in the collectors at both locations. An

ANOVA applied to data from Trudillé indicated a significant variation in numbers of cockles on different substrata ( $F_{4,19}=4.77$   $p=0.01$ ). The analyses did not meet the assumption of equal variances because there were many zero values. Nevertheless, we continued with post hoc pair-wise comparisons using the conservative Holm's sequential Bonferroni approach (to control for Type I error). This indicated that more cockles settled on treatments with no roots than on the treatments with roots and the treatment with scouring pads. An ANOVA applied to data from Cabo Rojo indicated the number of cockles on different substrata tended to vary ( $F_{4,20}=4.77$   $p=0.06$ ). The recruitment pattern of cockles at Cabo Rojo was similar to that at Trudillé, there being more recruits in the treatments 'only sand' and 'only blades' than in the other treatments (Fig. 5).

### **Settlement and early post-settlement mortality**

In the experiment examining recruitment on scouring pads (caged, uncaged) in two different habitats (seagrass bed, adjacent sandflat) and at two positions (seafloor, ~1 m above the bottom), 69 bivalves, but no penshells, were collected after the ~75-d deployment at Trudillé. In the parallel experiment at Cabo Rojo, but with a ~140-d deployment period, 26 penshells and 115 other bivalves were collected. The data did not support the use of factorial analysis because there were no penshells on many collectors and all of the caged collectors on the seafloor had disappeared (likely because of Hurricane Dennis). Thus, for both penshells and other bivalves we applied one unequal variance *t*-test to compare recruitment on caged and uncaged collectors suspended at ~1 m above the bottom, and another to compare uncaged collectors on the bottom and at ~1 m above the bottom. We found a difference between caged and uncaged suspended collectors for both the number of penshells ( $t_{0.05(2)21.04}=2.20$   $p=0.04$ ) and number of other bivalves ( $t_{0.05(2)24.34}=5.09$   $p<0.001$ ). This difference, which reflects post-settlement mortality due to predation, was 84 % for penshells and 63 % for the other bivalves. The number of penshells in uncaged collectors did not vary between the bottom and ~1 m above ( $t_{0.05(2)25.17}=1.14$   $p=0.27$ ) but the number of other bivalves was greater above the bottom ( $t_{0.05(2)22.79}=2.87$   $p=0.009$ ).

The caged collectors retrieved in the two additional habitats, the rocky-coral-sponge habitat and the seagrass bed with *Lobophora variegata*, showed that penshell larvae are present outside coastal sandflats and seagrass beds. An ANOVA comparing numbers of

recruits in the four different habitats sampled demonstrated variation in recruitment with habitat ( $F_{3,24}=0.40$   $p=0.02$ , Levene's test  $p=0.17$ ). Post hoc Least Significant Difference (LSD) tests indicated that there were more penshell recruits at the site with *L. variegata* than at the other sites, which each had similar numbers of recruits (Fig. 6).

### Penshell survival in seagrass beds and sandflats

#### *Predation after 1 day*

In our experiments on penshell survival, we considered there had been predation when penshell remains were observed or when individuals were missing. Missing penshells were likely either completely consumed or could have been carried away by predators. Individuals could not have been transported away by water motion, since underwater conditions were calm except during Hurricane Denis (7-8 June). The high survival of penshells in caged control plots indicated that mortality from sources other than predators was negligible (97 % in the seagrass bed and 100 % in the sandflat). Thus, to increase the power of analysis, we applied an ANOVA only to the data on penshell survival in the uncaged plots. The predation trials, in which we evaluated survival of different size-groups in two different habitats after 1 d, suggested predation mortality varied with both penshell size ( $F_{2,24}=18.82$   $p=0.05$ ) and habitat ( $F_{1,24}=49.39$   $p<0.001$ ). However, there was an interaction between these factors ( $F_{2,24}=18.95$   $p<0.001$ ) indicating any effect due to penshell size also depends on the type of habitat. Least Significant Difference (LSD) tests indicated that predation on medium and large penshells was greater in the sandflat and that predation decreased with penshell size in the seagrass habitat (Fig. 7). Although the data did not meet the assumption of equal variances, the number of treatments was relatively large and there were equal numbers of samples per treatment. Thus, the validity of the test and probabilities associated with the *F*-ratio distribution were probably not greatly affected by the unequal variance (Weerahandi, 1995; Underwood, 1997).

#### *Predation after 10 days*

As survival was still high in the caged control plots after 10 d (89 % in the seagrass bed and 100 % in the sandflat), we again examined the relation between predation mortality and size by applying an ANOVA to the data from the uncaged plots. Predation mortality

once more varied with both penshell size ( $F_{2,24}=15.97$   $p<0.001$ ) and habitat ( $F_{1,24}=47.53$   $p<0.001$ ) and again there was an interaction between these factors ( $F_{2,24}=21.09$   $p<0.001$ ). There was almost no survival of small penshells in either habitat but there was an increase in survival with size in the seagrass bed. The analysis did not meet the assumption of equal variances (Levene's test  $p=0.01$ ) because many replicates had zero survival values. Least Significant Difference (LSD) comparisons indicated a similar predation pattern as in the preceding experiment, although with a greater mortality from predation (Fig. 7).

During the 10-d trial, 16 individuals died of unknown causes (and were replaced during daily inspections of the plots). They were standing vertically and were not unearthed or broken. All of these 'dead-standing' individuals were in the seagrass bed (8 in caged plots, 8 in uncaged plots). This indicated there was a mortality factor in the seagrass habitat that was absent on the sandflat.

#### *Survival after 100 days (Hurricane Dennis)*

At the end of the 100-d predation trial, during which our study sites were subjected to Hurricane Dennis, all plots (caged and uncaged) in the sandflat had disappeared, as well as all of the plots with small individuals in the seagrass. However, 7 of the 10 plots with medium-sized penshells and all of the 10 plots with large individuals remained in the seagrass bed. The only living penshells found were large individuals (from the 90-110 mm group). A *t*-test indicated that survival of these large individuals did not vary between the caged (30 %, SD=37) and uncaged (30 %, SD=33) plots ( $t_{0.05(2)8}=-15.8$   $p=0.88$ , Levene's test  $p=0.26$ ). In the caged plots all of the mortalities were 'dead-standing' individuals, whereas in the uncaged plots about one third of the mortalities were dead-standing and two thirds were missing. For medium-sized penshells (50-70 mm), we found only 2 of the caged plots but all of 5 uncaged plots. In the caged plots 62 % of the individuals were dead-standing and 38 % missing, whereas the proportions were 25% and 75 %, respectively, in the uncaged plots.

In the other experiment, in which large penshells (111-244 mm,  $n=17$ ) were transplanted near the edge of the seagrass bed for ~100 d (also subjected to the hurricane), the survival rate was similar (24 %).

### *Predation on larger penshells*

A binary regression applied to the data on the survival of 50-100 mm and 150-170 mm penshells (five 3-d trials) in the sandflat (where our 10-d predation trials indicated survival was much less than in the seagrass bed) indicated a difference in survival between these two size-groups (Wald=11.53, df=1,  $p=0.001$ ) and a constant rate of loss in the different 3-d periods (Wald=0.42, df=1,  $p=0.52$ ). Because of the low number of replicates, we did not include the interaction in our regression model. There was 6 % survival ( $SD=26$ ) for 50-100 mm penshells, which compared with 93 % ( $SD=26$ ) for 150-170 mm individuals.

### **Impact of specific predators**

The red-heart urchin *Meoma ventricosa*, which feeds on materials in the sediment, was only found at Cabo Rojo during our transect surveys in 2005 ( $0.093\text{ urchins/m}^2$ ,  $SD=0.26$ ). Although the urchin did not feed on penshells in the experiment evaluating predation on four size-groups, 25-30, 40-45, 65-80, 180-200 mm, it did unearth several of the penshells in the 3 smaller size-groups. A binary regression applied to the data on penshells unearthed, and those that had likely been unearthed but could not be found, indicated that resistance to *M. ventricosa* varied with size (Wald=10.24, df=3,  $p=0.02$ ), and no differences were detected among the three simultaneous trials (Wald=2.01, df=2,  $p=0.37$ ). Again, because of the low number of replicates, we did not include the interaction in the regression model. Post hoc tests using Wald's  $\chi^2$  indicated no differences among the three smaller size-groups (8-42 %) but a higher resistance (83 %) of the largest penshells (180-200 mm). In the experiment with the balloonfish *Diodon holocanthus* (which occurred at a density of  $0.016/\text{m}^2$  at Trudillé and  $0.058/\text{m}^2$  at Cabo Rojo), no penshells were killed or disturbed, but the cages were probably a confounding factor as the balloonfish were visibly stressed and showed minor injuries from contact with the cage mesh.

### **Sedimentation in seagrass beds and sand flats**

Most materials collected in the sediment traps deployed at Trudillé were likely retained, as the tinted formalin that had been placed in the traps was readily visible. At Trudillé, we found 2 penshells in one trap in the seagrass bed, which represented <2 % of

the bivalves collected by all the traps. Although the mean number of all bivalves collected in traps was greater in the seagrass bed (9.6 bivalves/trap, SD=5.3) than the sandflat (5.6 bivalves/trap, SD=4.4), the difference was not significant (*t*-test  $t_{0.05(2)14}=-1.63$   $p=0.13$ , Levene's test  $p=0.60$ ). The percentage of silt in the traps was ~3-fold greater in the seagrass bed than in the sandflat (*t*-test  $t_{0.05(2)14}=-7.25$   $p<0.001$ , Levene's test  $p=0.18$ , after arcsin-root transformation). The tint was not visible in any of the traps at Cabo Rojo (subjected to Hurricane Dennis) and collected materials that filled most of the traps were decaying. The traps at Cabo Rojo provided a comparison of bottom stability between the sandflat and seagrass bed at this location. Traps in the sandflat had been unearthed on average by 38 % of their initial burial depth. In contrast, in the seagrass bed, two of the traps were undisturbed and one was buried under <2 cm of sediment. We suspect the remaining 5, which were not found, were also buried.

Our various measurements of food availability did not indicate a difference between seagrass beds and adjacent sandflats. The materials collected in the sediment traps at Trudillé provided an index of potential food materials for penshells in the two habitats. Although the dry mass of organic matter per trap varied from 0.38 g (SD=0.23) for the sandflat to 0.18 g (SD=0.14) for the seagrass bed, the difference was not significant (unequal variance *t*-test  $t_{0.05(2)11.7}=2.1$   $p=0.06$ ). Analysis of the 3.7-L water samples taken just above seagrass beds and sandflats at Trudillé and Cabo Rojo showed no differences in the dry mass of plankton-sized materials (i.e., particulate matter measuring 0.45–263  $\mu\text{m}$ ) with either habitat or location (Table 1). The mean values were  $8.54 \cdot 10^{-3}$  g/L for seagrass beds (SD= $4.11 \cdot 10^{-4}$ ) and  $9.70 \cdot 10^{-3}$  g/L for sandflats (SD= $3.27 \cdot 10^{-3}$ ). Out of 19 water samples collected, we obtained only one measure of percentage organic content for each habitat at each location because of a laboratory mishap. Analysis of the two values for each habitat suggested that percent organic carbon content was similar for the two habitats (unequal variance *t*-test  $t_{0.05(2)1.1}=0.63$   $p=0.61$ ).

## Growth

The penshell growth data was best described by an exponential growth curve (Fig. 8;  $r^2=0.63$ ). Small penshells grew rapidly (up to 2.2 mm/d), but the growth rate dropped markedly at ~150 mm in hinge length (the beginning of the asymptote in growth).

An ANCOVA applied to growth data for the small penshells that had been maintained for three 9-d trials in a seagrass bed and an adjacent sandflat at Cabo Rojo indicated no difference in growth rate with habitat or over time (Table 2). The mean growth rate was 1.2 mm per day ( $SD=0.66$ ). The rate varied with initial length ( $F_{1,12}=7.83\ p=0.02$ ), being greater for smaller individuals.

## Discussion

### *Settlement and reproduction*

Our settlement experiment indicated penshells are not restricted to seagrass beds because of substratum preferences at the time of larval settlement. Our trials with 5 types of substrata in cages (Fig. 2), including blades, seagrass roots and only sand, showed similar numbers of recruits on all substrata (Fig. 5). This suggests that competent larvae do not actively select a specific substratum, but settle wherever they can attach byssal threads. Penshell larvae can even settle in habitats far away from seagrass beds, for example on offshore fishing moorings. In contrast, these same trials showed a strong substratum preference for larvae of the common cockle *Laevicardium laevigatum*, there being a much higher number of recruits on collectors that contained sand but no roots (i.e., the treatments 'only sand' and 'blades implanted in sand'). The markedly reduced numbers in the treatments with roots suggest that *L. laevigatum* larvae avoid roots (Fig. 5). They also settled less in the treatment with scouring pads where sand was absent. The cockle's preference for sand without roots could be adaptive as this bivalve species buries itself in loose sand. It would likely have difficulty burying itself in sand that was held together with roots. Interestingly, most studies focus on cues that trigger settlement (i.e., positive cues) (see review by Rodriguez et al., 1993). Woodin (1991) hypothesized that inhibitors or negative cues should be as important as positive ones. Our data on *L. laevigatum* provide an example of larvae choosing to avoid a specific substratum, thus supporting Woodin's hypothesis.

Our comparisons of numbers of penshells settling on a common substratum (scouring pads in cages; Fig. 2) suspended ~1 m above four contrasting habitats indicated no difference in settlement intensity between a seagrass bed and an adjacent sandflat, nor in a rocky-coral-sponge habitat (all at ~6 m in depth), but markedly greater settlement above a seagrass bed in which the brown drift alga *Lobophora variegata* was abundant (Fig. 6). However, the seagrass bed with *L. variegata*, also differed from the other habitats because it was deeper, more exposed (being off a headland) and subjected to stronger tidal currents. The heavy settlement of penshells that we observed on mooring lines was also in a deeper open area with stronger currents. Thus, the greater settlement in this habitat may have been more related to depth and current than to the presence of *L. variegata*.

For a number of bivalves, settlement has been shown to increase with habitat complexity (Eckman, 1983; Peterson, 1986; Harvey et al., 1995 Bologna and Heck, 2000). It is hypothesized that if larvae or small bivalves drifting in the water column behave as suspended sedimentary particles, they will collect more under a seagrass canopy because seagrasses act as a hydrodynamic baffle (Eckman, 1983; Hannan, 1984; Snelgrove, 1994; Wildish and Kristmanson, 1997). Our observations do not support this hypothesis, as our sediment traps collected a similar number of post-larval bivalves (<3 mm) in the sandflat and seagrass bed.

Although we did not make a systematic study on reproduction, our observations appear to corroborate previous reports from Columbia indicating that *P. carneae* has two major peaks in recruitment, May to July and September to December (Garcia-Valencia and Urban, 1996; Urban, 2001; but see Narváez et al., 2000). We recorded little recruitment on our caged collectors (substratum preference experiments) deployed from 21 March to 4 June at Trudillé (0.08 recruits per collector). However, a recruitment pulse was recorded by our collectors deployed from 11 April to 16 August at Cajo Rojo (2.1 recruits per collector) and periodic inspection of these collectors until 25 May showed that the recruitment occurred sometime after this date. During our benthic surveys in 2005, we observed that individuals had large ripe gonads in late-August through early-September, suggesting a recruitment event would follow. This would correspond to the second peak reported in Columbia.

#### *Mortality from predation*

Predation on early post-settlement stages would not appear to explain why penshells are restricted to seagrass beds. Our trials with caged and uncaged collectors (scouring pads) placed above seagrass and sandflat habitats for ~140 d indicated that predation on recently settled penshells was high (84 %), but similar in both habitats. On the other hand, predation at older stages appeared to have a strong impact. Our predation trials with older individuals transplanted to plots in the field indicated that losses differed between seagrass and sandflat habitats. For penshell transplants measuring 10 to 110 mm, the loss was >4-fold greater in the sandflat than the seagrass bed in our 1-d trials and 27-fold greater in our 10-d trials. Predation losses decreased as penshells increased in size, as seen in the trials in the seagrass

bed (Fig. 7). In both the 1-d and 10-d trials, most penshells of all sizes disappeared in the sandflat in the first 24 h. These experiments demonstrate that predation is a major factor regulating the abundance and distribution of penshells. Indeed the loss of new recruits likely acts as a recruitment bottleneck for the population, as described for a number of benthic invertebrates (Underwood and Denley, 1984; Gaines and Roughgarden, 1987; Smith and Herrnkind, 1991).

Interestingly, the few penshells that survived in the sandflat in our trials were small individuals (10-30 mm). It is likely that the impact of predators varies between seagrass beds and sandflats because of the differing numbers, types and activities of the predators found in each habitat. Possibly, the small penshells that survived on the sandflats were less visible to the large predators found in this habitat. Small penshells are translucent in contrast to larger penshells that are brownish in color. Alternatively, predators of small penshells may be less abundant in sandflats than in seagrass beds because they themselves are vulnerable to higher-order predators. We occasionally observed small lizardfish and crustaceans inside penshell cages in the seagrass bed, but never inside cages in the sandflat. In our 10-d predation trials, 11 % of the small penshells in cages were found as shell remains or missing in the seagrass bed whereas all small penshells in cages were found alive in the sandflat. This suggested that small predators of small penshells are less abundant in sandflats than seagrass beds.

Faunal abundance and diversity are greater in seagrass beds than in unvegetated areas (Heck and Wetstone, 1977; Orth, 1977; Peterson, 1979; Heck and Orth, 1980; Stoner, 1980). Many benthic predators stay inside seagrass beds during daylight hours but move to sandflats during the night (Summerson and Peterson, 1984; Wielderholm, 1987). We observed several goatfish and wrasse species foraging in seagrass beds during the day and in sandflats at night. Although such predators may prey on penshells in both habitats, penshells appear to be less vulnerable in seagrass beds. This is likely because seagrass provides camouflage against visually-oriented predators. In reviewing the literature on early post-settlement mortality of benthic invertebrates, Hunt and Sheibling (1997) emphasize that predation intensity is generally reduced in vegetation and other structurally complex habitats. This review mainly covers sedentary and infaunal species. In contrast, Orth et al. (1984) and Worthington et al. (1992) report that there is no clear relationship

between predation intensity and seagrass cover for mobile epibenthic species. This was also the case for *P. carnea*, which is partly buried. A linear regression analysis applied to the 2002 survey data (quadrats taken along 3-4 transects at five locations) indicated no correlation between penshell abundance and estimates of seagrass dry biomass ( $F_{1,20}=0.01$   $p=0.86$ ) (A. Tewfik, unpubl. data; seagrass biomass values ranged from 52 to 206 g/m<sup>2</sup>). However, Nelson (1979) hypothesized predation intensity may only drop once a threshold seagrass density is attained.

#### *Habitat stability and sedimentation*

Why *P. carnea* penshells are found in seagrass beds and not in sandflats may also be related to the greater long-term stability of the seafloor, given that seagrass roots and associated algal rhizoids consolidate sediment particles. Our observations before and after Hurricane Dennis showed that seagrass beds were less affected by disturbance than sandflats. All penshells that had been transplanted to the sandflat were unearthed by the hurricane, whereas 30 % of individuals measuring 90-110 mm transplanted to the seagrass bed remained.

The differences between penshell populations at Trudillé and Cabo Rojo, specifically the higher density and greater proportion of small individuals at Trudillé, may also be related to the nature of the seafloor, particularly to the degree of consolidation of the sediments. Whereas many factors were similar at the two locations (the types of consumer functional groups, including some potential predators, and seagrass biomass that provided an index of cover), our sampling showed several parameters that indicated greater bottom stability at Trudillé than at Cabo Rojo. These included the total mass of roots, algal rhizoids and consolidated sediment that was >3-fold greater, the mass of loose large sediment particles (>3.5-mm) that was also 5-fold greater and the above ground algal biomass that was ~50-fold greater. Calcareous algae, *Halimeda* spp., accounted for 96 % of algal biomass, but only slightly to above-ground cover. Decaying calcareous algae likely formed most of the coarse carbonate sands at Trudillé (see Scullion Littler et al., 1989). The more consolidated sediment and coarser grain size at Trudillé appeared to better anchor penshells. This was seen when we collected the penshells, as it was more difficult to unearth penshells at Trudillé than at Cabo Rojo.

Coarse sands and seagrass roots have been shown to provide a barrier against certain predators (Reise, 1976; Orth, 1977; Peterson, 1982). The more consolidated sediment at Trudillé may also provide protection from predators. Possibly the absence of the urchin *M. ventricosa* at Trudillé was because the roots, algal rhizoids, and consolidated sediment prevent it from plowing through the sediments to feed. When *M. ventricosa* was maintained in caged plots with penshells on the less consolidated sediments at Cabo Rojo, we found that the urchin readily unearthed small penshells.

Particulate organic matter (POM) from resuspended sediment can be a valuable food source for some suspension feeders (Grant and Griswold, 1990; Navarro et al., 1992), but elevated levels of resuspended sediment can be deleterious and limit where animals can live, as reported for the penshell *Atrina zelandica* (Norkko et al., 2001; Ellis et al., 2002). Increasing concentrations of fine sediment such as silt or clay can have detrimental effects on an array of filter-feeding invertebrates, including bivalves (Peddicord, 1977; Robinson et al., 1984; Rogers, 1990; Shumway et al., 2003). Our sediment traps showed that silt levels were ~3-fold greater in the seagrass bed than in the adjacent sandflat. Thus, silt was possibly the cause of penshells that were found standing vertically but dead and without signs of predatory attacks. These 'dead-standing' penshells were only found in seagrass beds. They made up 13 % of mortalities in the 10-d predation trials and ~27 % of mortalities in the growth experiments in the seagrass beds. We also found dead-standing penshells among the individuals transplanted to the seagrass bed during our 100-d predation trial that was subjected to Hurricane Dennis. Food conditions (POM, potential plankton and carbon content) were similar in seagrass beds and adjacent sandflats, and thus could not have accounted for the dead-standing individuals in seagrass beds.

#### *Growth and refuge in size*

Growth rates of young *P. carnea* are among the highest known for molluscs (Castellanos et al., 1997; Garcia-Valencia et al., 1997; Narváez et al., 2000). Our measurements of penshells transplanted to a seagrass bed and adjacent sandflat indicated no difference in growth rates between these habitats. The approximate growth curve we calculated for *P. carnea* (Fig. 8) showed a rapid decrease in growth rate when a shell hinge

length of ~150 mm was attained. A reduction in growth at a similar size (155 mm) was also reported for *P. carneae* in suspended culture in Venezuela (Narváez et al., 2000).

As small benthic organisms are generally vulnerable to a larger suite of predators than large individuals, survival often increases with increasing size (Paine, 1976; Peterson and Wroblewski, 1984; Seed, 1993; Gosselin and Qian, 1997). This is the case for *P. carneae*, as the probability of survival increased with size. We hypothesize that the extremely rapid growth of small penshells represents an evolutionary adaptation for attaining a size that is less vulnerable to predators as soon as possible (a response to the intense predation on small individuals). We observed that large penshells attain a refuge in size, as reported for other bivalves (Seed and Brown, 1978; Commito, 1982; Arsenault and Himmelman, 1996). In the sandflat where mortality was highest, the survival rate of transplanted penshells increased from 6 % for 50-100 mm individuals to 93 % for 150-170 mm individuals. We also observed that only large penshells survived Hurricane Dennis. Thus, the extremely rapid growth rate of small penshells could also reflect a strategy for limiting vulnerability to physical perturbations.

The increased numbers of large individuals in the size distributions of *P. carneae* in the Dominican Republic (Fig. 3) likely represents the merging of successive recruitment events caused by the decrease in growth rate at ~150 mm. Butler (1987) suggests a similar scenario for *Pinna bicolor* in Australia. The population size-structure for *P. carneae* provides little information about the age-structure of the population. We suggest using measurements of shell thickness as well as hinge length in future studies, as thickness may be a better indicator of age. Measurements of shell thickness (at the center of the posterior adductor muscle scar) indicated that growth in thickness increased coincident with the decrease in growth in length at ~150 mm (S. Aucoin, unpubl. data). Our growth measurements (Fig. 8) suggest that recently settled penshells, measuring 107 mm (SD=36) in hinge length (the mean size observed on collectors after 2-3 months), would take at least 3 to 4 years to attain 270 mm, the maximum size observed in our field surveys. Other species of penshells in the Mediterranean and tropical regions have been estimated to live between 8 and 17 years (Butler, 1987; Wu and Shin, 1998; Richardson et al., 1999; Rodriguez-Jaramillo et al., 2001; Garcia-March et al., 2002).

### *Summary and further research*

Our studies on various stages in the benthic life of penshells indicate that the distribution and population structure of penshells is explained as follows. Settlement does not appear to be associated with a specific substratum, and occurs in similar levels in seagrass beds and adjacent sandflats. Also, our trials with suspended collectors suggest early post-settlement mortality is high and similar in seagrass and sandflat habitats. Predation also has a strong impact on individuals that recruit onto the bottom, although slightly less in seagrass beds. The survival of some individuals in seagrass beds (but not on sandflats) accounts for the low density of penshells associated with this habitat. This survival is likely because seagrasses provide camouflage from visual predators, and possibly also because the suite of predators in seagrass beds is different than on sandflats. The long-term survival of penshells in seagrass beds is also favored by the stability of this habitat, caused by consolidation of the sediments by seagrass roots and associated algal rhizoids. Sediments are not consolidated on sandflats and if penshells were to escape predators in this habitat they would later be removed by the perturbations caused by hurricanes. Whereas the risk of mortality is high for small penshells, even in seagrass beds, the risk decreases as individuals increase in size. Juveniles grow extremely rapidly, which may be a strategy for decreasing the period of high vulnerability to predators. The predominance of large individuals in penshell populations likely represents an accumulation of successive recruitment pulses caused by a marked slowing of growth at about 150 mm.

To provide further understanding of the population dynamics of the penshell *P. carneae*, future studies should focus on quantifying recruitment and in determining causes of mortality. Further studies are needed to quantify variations in recruitment in different habitats and locations as well as to document variations in different seasons. Preferably, collectors should be deployed for the same periods at different locations (this was not possible during our study). We demonstrate that mortality is extremely high in both sandflats and seagrass beds at Cabo Rojo (even within 24 h), and that small penshells are most vulnerable. However, it is critical that similar trials be run at other locations to ensure that this pattern is not specific to Cabo Rojo. To elucidate the causes of mortality, the most productive approach would likely be videofilming of penshells transplanted to different

habitats and locations. This would likely allow identification of the predators causing mortality, along with their specific activity rhythms and size selection of penshells.

**Table 1.** Results of a nested ANOVA applied to data on the mass of plankton-sized materials (i.e., particulate matter measuring 0.45-263 µm) in 3.7-L water samples taken just above seagrass beds and sandflats (habitat) at both Trudillé and Cajo Rojo (location) from 26 May to 1 September 2005.

Dependent variable: Dry mass of plankton-sized materials

Source	SS	df	MS	F	P value
Model <sup>a</sup>	2.17x10 <sup>-2</sup>	4	5.42x10 <sup>-3</sup>	71.3	<0.001*
Habitat	2.38x10 <sup>-5</sup>	1	2.38x10 <sup>-5</sup>	0.31	0.584
Location	3.22x10 <sup>-5</sup>	1	3.22x10 <sup>-5</sup>	0.42	0.525
Habitat(Location)	3.14x10 <sup>-5</sup>	1	3.14x10 <sup>-5</sup>	0.41	0.530
Error	1.14x10 <sup>-3</sup>	15	7.60x10 <sup>-5</sup>		
Total	2.28x10 <sup>-2</sup>	19			

<sup>a</sup>  $r^2 = 0.95$  (Adjusted  $r^2 = 0.94$ )

\* significant difference  
(Levene's test,  $p=0.13$ )

**Table 2.** Results of an ANCOVA applied to data on the growth of the penshell *Pinna carnea* in a seagrass bed and adjacent sandflat (habitat), with 3 trials conducted between 23 August and 9 September 2005 at Cabo Rojo.

Dependent variable: Growth rate

Source	SS	df	MS	F	P value
Model <sup>a</sup>	40.8	12	3.40	11.7	<0.001*
Habitat	0.26	1	0.26	0.89	0.364
Trial	1.83	2	0.92	3.15	0.080
Initial length <sup>b</sup>	2.28	1	2.28	7.83	0.016*
Habitat x trial	0.82	2	0.41	1.41	0.281
Trial x initial length	2.96	2	1.48	5.08	0.025*
Habitat x initial length	0.28	1	0.28	0.97	0.344
Habitat x trial x initial length	0.88	2	0.44	1.52	0.258
Error	3.49	12	0.29		
Total	44.3	24			

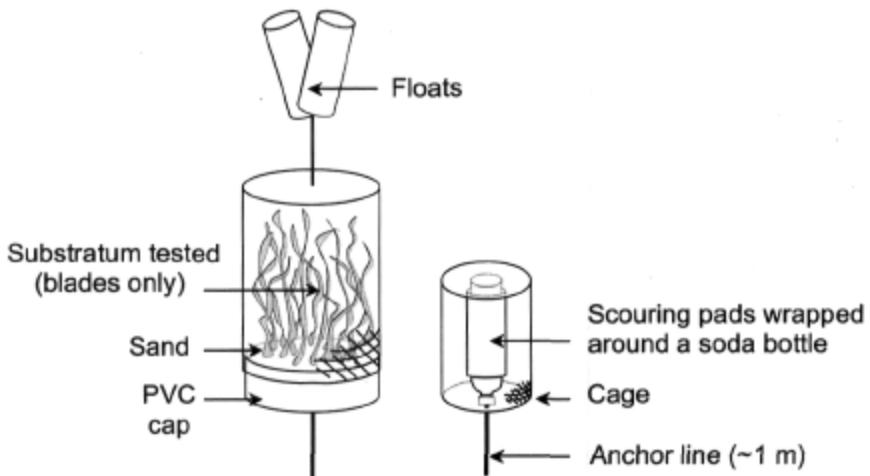
<sup>a</sup>  $r^2 = 0.92$  (Adjusted  $r^2 = 0.84$ )

<sup>b</sup> covariate

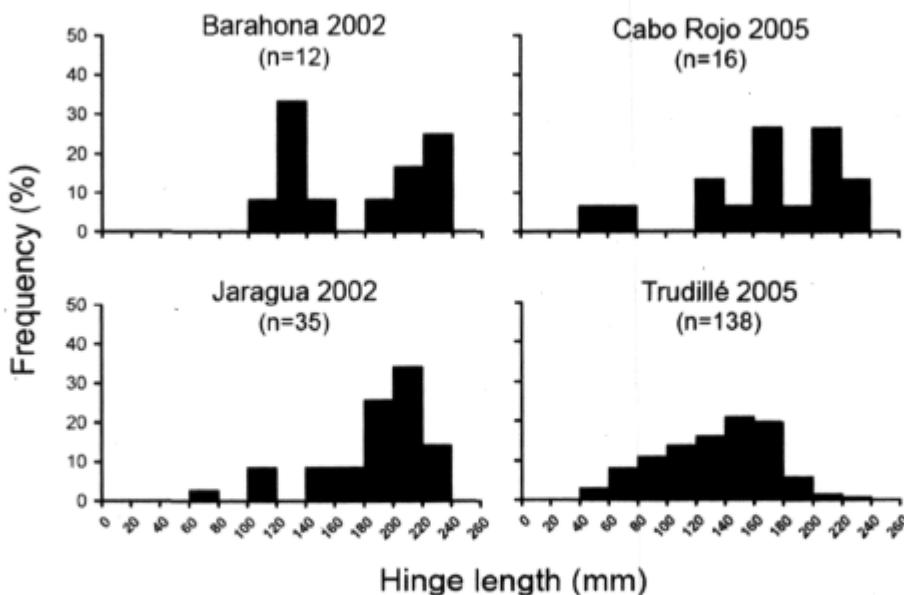
\* significant difference  
(Levene's test,  $p=0.43$ )



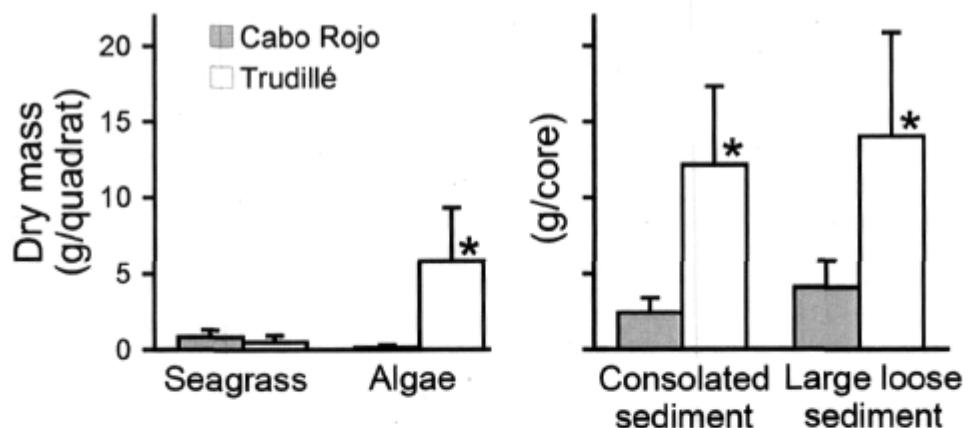
**Figure 1.** Locations where the penshell *Pinna carnea* was studied in southwestern Dominican Republic. Black dots (●) are locations where surveys were made in 2002 and open dots (○) are Cabo Rojo and Trudillé, where surveys and experiments were conducted in 2005.



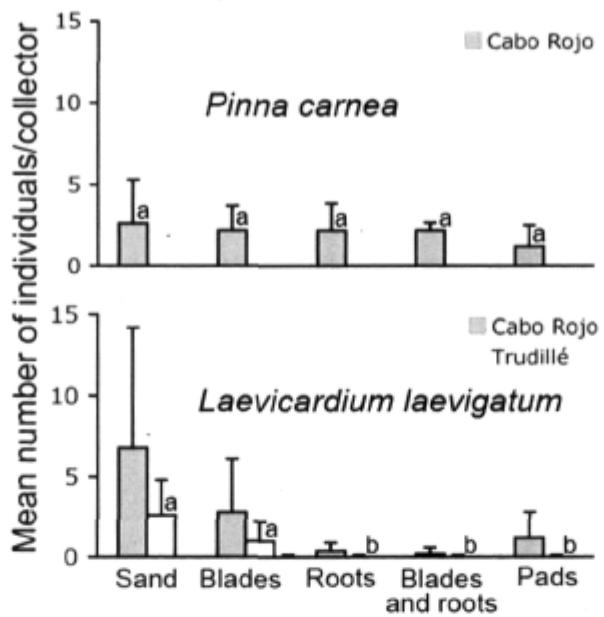
**Figure 2.** Two types of collectors used to investigate larval settlement of the penshell *Pinna carnea*, (1) on the left is the caged collector used to evaluate substratum preference for settlement, and (2) on the right the collector (which was either caged or uncaged) used to evaluate variations in numbers of larvae settling, and early post-settlement survival, in different habitats.



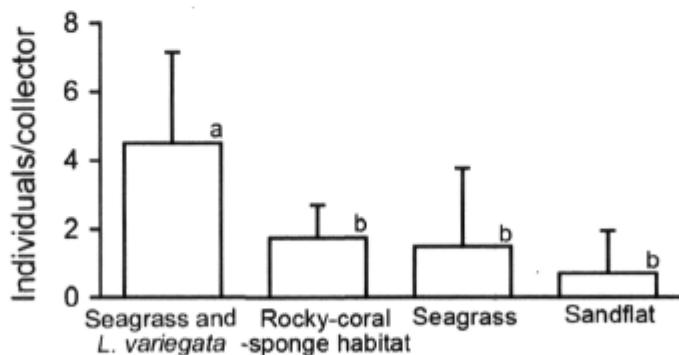
**Figure 3.** Population size-frequency distributions for the penshell *Pinna carnea* encountered in transect surveys near Barahona (4 transects) and at the 5 locations in Jaragua National Park (4-8 transects per location) in 2002, and at Cabo Rojo (9 transects) and at Trudillé (11 transects) surveyed in 2005.



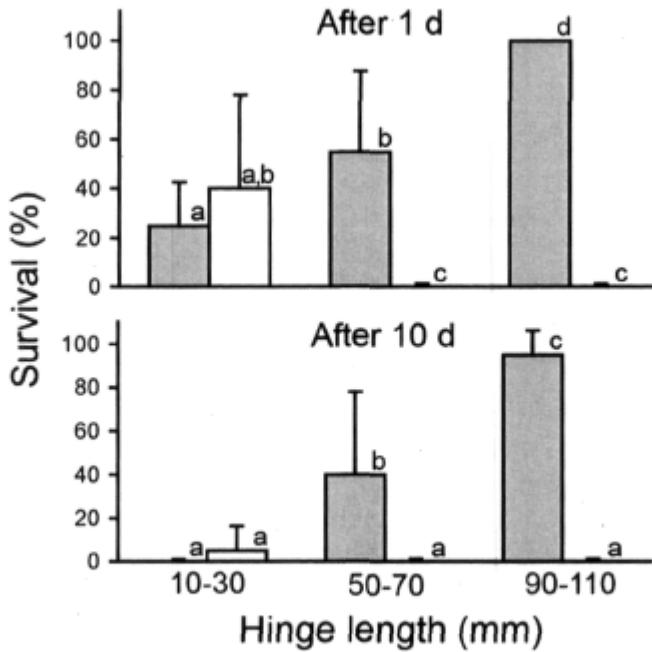
**Figure 4.** Comparison of seagrass beds at Trudillé (□) and Cabo Rojo (■) in respect to the dry mass of seagrass, algae, consolidated sediment with roots and rhizoids, and large loose sediment (>3.5 mm diameter). Vertical lines represent standard deviations and \* indicates a significant difference in mass between the two locations (MANOVA).



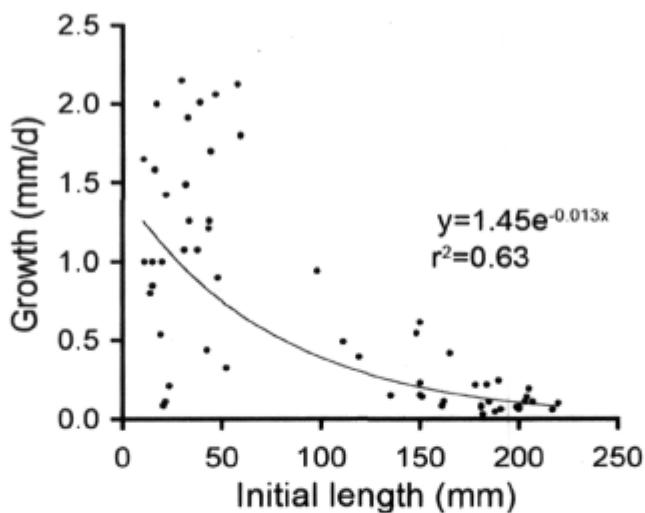
**Figure 5.** Mean number of penshell *Pinna carnea* spat setting on collectors with five different substrata after a deployment period of ~130 d at Cabo Rojo, and mean number of cockle spat settling on collectors with the same five substrata after a deployment period of ~75 d at Trudillé and after a ~130 d deployment period at Cabo Rojo. Vertical lines represent standard deviations. Bars not sharing the same letter (in each graph) are significantly different (ANOVA followed by the post hoc Bonferroni test).



**Figure 6.** Mean number of penshell *Pinna carnea* spat observed on the same type of caged collector (with scouring pads) deployed for ~130 d at ~1 m above four different habitats at Cabo Rojo, (1) a seagrass bed where the brown algae *Lobophora variegata* was abundant, (2) a rocky-coral-sponge habitat, (3) a sandflat, and (4) a seagrass bed. Vertical lines represent standard deviations. Bars not sharing the same letter are significantly different (ANOVA followed by the post hoc Least Significant Difference tests).



**Figure 7.** Mean survival after 1 d and after 10 d of three size classes of penshell *Pinna carnea* transplanted to a seagrass bed (■) and an adjacent sandflat (□) at Cabo Rojo. Vertical lines represent standard deviations. Bars not sharing the same letter are significantly different (ANOVA followed by the post hoc Least Significant Difference tests).



**Figure 8.** Relation of daily increase in hinge length to initial hinge length as recorded for the penshell *Pinna carnea* during various periods between March and June 2002, and between May and August 2005, in southwestern Dominican Republic. An exponential curve best fits the data points.

## Conclusion générale

Mes recherches fournissent quelques arguments qui nous permettent de répondre à trois questions fondamentales venant de mes observations initiales sur les populations de *Pinna carnea* en République dominicaine, c'est-à-dire, (1) pourquoi est-ce que la distribution de *P. carnea* est-elle limitée aux prés sous-marins, (2) pourquoi est-ce que ces bivalves se trouvent seulement à faibles densités dans cet habitat, et (3) pourquoi est-ce que la plupart des individus sont gros. Les informations disponibles sur l'écologie de *P. carnea* étaient très limitées, et mon étude est une première tentative d'élucider l'écologie de la population de ce bivalve.

Mon expérimentation sur la fixation a indiqué que les larves semblaient se fixer partout, même sur les petites particules de sable non-consolidé, pourvu que les bivalves pussent s'attacher avec leurs byssus. Dans les expériences où j'ai utilisé des collecteurs artificiels, suspendus juste au-dessus des habitats de prés sous-marins et de replats sableux, la fixation (ou la survie dans un premier temps) était semblable dans les deux habitats. Les facteurs majeurs qui déterminent la distribution et la structure de taille des populations de *P. carnea* semblent être la prédation intense, et une plus grande probabilité de survie pour les gros individus. Plusieurs expériences ont indiqué que la mortalité était élevée dans les deux habitats. Toutefois, les individus auraient une meilleure chance de survivre dans les prés sous-marins plutôt que dans les replats sableux. Ceci expliquerait pourquoi *P. carnea* se trouve seulement dans les habitats de prés sous-marins, à faible densité, et avec une structure qui tend vers les grandes tailles.

Les juvéniles de petites tailles ont des taux de croissance extrêmement rapide, par contre, cette croissance est ralentie, d'une façon marquée, une fois que le bivalve a atteint ~150 mm de longueur. Cette longueur correspond à une taille qui est beaucoup moins vulnérable aux prédateurs. La croissance juvénile rapide peut être une stratégie évolutive pour réduire sa vulnérabilité aux prédateurs. La prédominance de gros individus peut représenter une accumulation d'événements de recrutement causée par le ralentissement de croissance lorsqu'ils ont atteint >150 mm de longueur.

Bien que les mesures de croissance aient fourni une courbe de développement, celle-ci est approximative car les mesures ont été prises de façon irrégulière, au cours de

différentes années et à des endroits différents. Il serait utile d'obtenir des données de croissance d'une façon plus systématique, c'est-à-dire, sur les mêmes individus, avec des observations régulières, et pendant une plus grande période de temps. Puisque, dans une population de *P. carnea*, plusieurs cohortes de différents âges peuvent s'entasser dans un groupe de même taille (i.e., mode), il est difficile de différencier l'âge des individus uniquement par la longueur. Des mesures d'épaisseur de *P. carnea*, ainsi que des mesures de longueur, pourraient aider dans l'identification de différentes cohortes d'âges dans la population.

Mes expériences sur la prédation ont indiqué que les prédateurs jouent un rôle très important dans la structuration des populations de *P. carnea*. Néanmoins, ces observations ont été faites à un seul endroit, Cabo Rojo. De plus, en raison de la rareté d'individus de *P. carnea*, en particulier des petits individus, les expérimentations ont été limitées dans le nombre de réplicats possibles. D'autres expérimentations à plusieurs endroits seront nécessaires pour mieux évaluer la prédation. Mes observations sur la survie d'individus de *P. carnea*, transplantés dans les deux habitats, et ayant des tailles différentes, ont démontré que ces bivalves courraient un risque très élevé de mourir. Les études à venir sur *P. carnea* devraient se concentrer sur l'identification des différents prédateurs, leurs périodes d'activités, leurs taux de consommation, et leurs choix par rapport aux dimensions des bivalves (qui également changeront par rapport aux dimensions des prédateurs). Ces objectifs pourraient être facilement atteints en commençant par filmer en vidéo des individus de *P. carnea* transplantés dans différents habitats, et certainement dans les habitats de prés sous-marins et dans les replats sableux.

Bien que mes expériences aient démontré que les larves de *P. carnea* n'avaient pas de préférence de substrats pour se fixer, cet examen n'a pas été fait de façon exhaustive. Étant donné que l'expérimentation examinant la variation dans le recrutement de *P. carnea*, sur des mêmes collecteurs, dans d'autres endroits et dans différents habitats, ait indiqué qu'il y avait un plus grand nombre de recrues qui s'étaient posées au-dessus d'un habitat de pré sous-marin, dans lequel l'algue brune, *Lobophora variegata* était abondante, il serait nécessaire de continuer l'expérimentation avec cette algue. J'inclurais alors, cette algue, *L. variegata*, et également les algues calcaires *Halimeda* spp., comme traitements supplémentaires aux expériences déjà réalisées.

En 2002, j'ai trouvé l'algue *L. variegata* attaché sur 20 % des *P. carnea* dans mes recensements benthiques. La souillure d'invertébrés marins, par exemple, la colonisation d'éponges et d'algues sur la surface d'un autre, peut leurs permettre de se camoufler de certains prédateurs (Marin & Lopez Belluga, 2005; Thangh et al., 2003). S'il y a un avantage d'être souillé par *L. variegata*, les larves de *P. carnea* pourraient sélectionner de s'établir où l'algue est présente. En plus, les coquilles de *P. carnea* ont des épines qui pourraient aussi faciliter la capture de spores d'algues ou d'attraper des agglomérats de *L. variegata* flottant à la dérive. Marin et Lopez Belluga (2005) ont démontré que les coquilles de *Arca noae*, avec épines, tendaient à faciliter le recrutement d'éponge sur ce bivalve.

Mon étude a été limitée à une courte période de temps, et s'est concentrée sur les processus post-larvaires. D'autres recherches sur *P. carnea* devraient examiner les changements annuels en reproduction, et la disponibilité de larves. J'ai observé une activité de reproduction qui a coïncidé avec une augmentation de températures de la mer pendant la saison d'été (mai à novembre) en République dominicaine. Il y a corrélation entre l'augmentation de températures de la mer et les activités reproductrices de *P. carnea* en Colombie (Urbain 2001) et de *Pinna rugosa* dans le nord-ouest du Golfe de Mexique (Ceballos-Vazquez et al., 2000). Garcia-Valencia et al. (1997) et Urban (2001) ont aussi démontré que d'autres périodes de recrutement, c'est-à-dire, d'événements de recrutement plus petits, pouvaient avoir lieu à l'extérieur de la période reproductrice principale observée en été. Les amas de *P. carnea*, avec des tailles différentes (10-110 mm de longueur), que j'ai observé, au début mai 2005, sur plusieurs amarrages de pêcheurs (à environ 100 Km du parc national de Jaragua), nous suggèrent que le recrutement puisse se prolonger pendant une plus longue période.

Pour conclure, mes recherches, se concentrant sur la survie de *P. carnea* après la fixation et le recrutement, nous ont fourni divers aperçus par rapport aux facteurs pouvant expliquer les patterns observés de l'abondance d'individus, leur distribution, et la structure de la population de *P. carnea*. La force de cette étude réside dans le fait que j'ai examiné divers facteurs agissant sur la fixation, et sur plusieurs différents stades de vie (i.e., différentes tailles) après la fixation. En même temps, mes observations ont soulevé beaucoup de questions concernant l'écologie de la population de *P. carnea*, qui devront être résolus pour une meilleure compréhension de cette espèce.

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