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Predation potential by various epibenthic organisms on commercial bivalve species in Prince Edward Island: preliminary results

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Abstract

The culture of bivalve species in their natural habitat is a common practice in Prince Edward Island (PEI). Depending on the type of culture methods being used the cultured bivalves may be vulnerable to a variety of predators. The predation behaviour of three marine epibenthic invertebrates was examined in a laboratory setting at the Ellerslie Shellfish Hatchery (PEI) in December 2000. Experiments conducted addressed prey species and prey size selection by predators. Predator species used were green crab (*Carcinus maenas*), common starfish (*Asterias vulgaris*) and moon shell (*Lunatia heros*). Predation was monitored by determining the mortality rates of four bivalve species in 4 d trials where predators were present or absent (control). Single- and multiple-choice experiments were carried out in relation to the prey species being challenged by the predator. Bivalve prey species used were quahaug (*Mercenaria mercenaria*), eastern oyster (*Crassostrea virginica*), blue mussel (*Mytilus edulis*l) and soft-shell clam (*Mya arenaria*). Results from the single-choice experiment showed that the crabs and starfish were the most active predators. Moon shells displayed a much lower predation activity. Blue mussels were the preferred prey species of crabs and starfish. Crabs preyed upon all prey species including quahaugs from all size-classes. The multiple-choice experiment showed different results in that predation rates were lower than in cases where predators were facing one prey species at a time. Crabs and starfish both displayed a generalist feeding behaviour. A complementary experiment examined the effect of water temperature and sediment type on the predator-prey relationship between the green crab and the soft-shell clam. Mortality rates of clams decreased with decreasing water temperature. Sediment type did not modify the predation behaviour of the green crab.

Résumé

La culture des bivalves en milieu naturel est couramment pratiquée dans la province de l'Île-du-Prince-Édouard (IPE). Les bivalves cultivés sont vulnérables, selon la méthode de culture, aux prédateurs. Le comportement de prédation de trois espèces d'invertébrés épibenthiques a été étudié à l'écloserie de Ellerslie (IPE), en décembre 2000. Les expériences réalisées cherchaient à décrire la sélectivité des prédateurs tant au niveau spécifique qu'au niveau de la taille des proies. Les prédateurs étudiés furent le crabe vert (*Carcinus maenas*), l'astérie boréale commune (*Asterias vulgaris*) et la lunatie de l'Atlantique (*Lunatia heros*). La prédation fût suivie en mesurant le taux de mortalité de quatre espèces de bivalves suite à l'introduction ou non (témoin) d'un prédateur au bout d'une période de quatre jours. Les expériences ont été réalisées en présentant au prédateur 1) une des quatre espèces de bivalves ou 2) toutes les espèces à la fois. Les proies utilisées furent le quahaug (*Mercenaria mercenaria*), l'huître américaine (*Crassostrea virginica*), la moule bleue (*Mytilus edulis*) et la mye commune (*Mya arenaria*). Les résultats des expériences utilisant une espèce de proie montrent que les crabes et les astéries sont les prédateurs les plus efficaces. La lunatie a démontré beaucoup moins d'activités de prédation. La moule bleue est la proie favorite des crabes et des astéries. Les crabes se sont alimentés sur toutes les espèces présentées y compris le quahaug, peu importe la taille. Les résultats de l'expérience utilisant les quatre espèces de proie à la fois ont montré des résultats différents. De manière générale, le taux de mortalité des proies fût inférieur à celui observé dans l'expérience utilisant qu'une seule espèce de proie à la fois. Les crabes et les astéries montrent un comportement alimentaire de type généraliste. Une étude complémentaire fût effectuée afin d'étudier l'effet de la température de l'eau et du type de sédiment sur la relation prédateur-proie entre le crabe vert et la mye commune. Les taux de mortalité des myes ont significativement diminué avec la baisse de température. Le type de sédiments n'a pas modifié le comportement de prédation du crabe vert.

Introduction

The culture of bivalve species represents one of the most important aquaculture industries in Atlantic Canada. A large proportion of the total bivalve aquaculture production originates from Prince Edward Island (PEI). The most important species cultivated in PEI are blue mussel (*Mytilus edulis* L.) and eastern oyster (*Crassostrea virginica* Gmelin) (Boghen 1995). The PEI shellfish industry has also shown, over the last decade, an increasing interest in diversifying cultured bivalve species (Brown *et al.* 1995). Two new native species, the quahaug (*Mercenaria mercenaria* L.) and the soft-shell clam (*Mya arenaria* L.), are presently undergoing trials by the aquaculture industry.

Predators play an important role in structuring marine benthic communities (see reviews by Connell 1983; Commito and Ambrose 1985; Menge and Sutherland 1987; Ambrose 1991; Ebenhöh *et al.* 1995). Many investigations identified various endo- and epibenthic predators in soft- and hard-bottom communities including invertebrates (e.g., polychaetes, nemerteans, crabs, gastropods, echinoderms) and vertebrates (e.g., fish, birds, mammals). Since most bivalve aquaculture operations occur directly in the marine environment, cultured animals are vulnerable to predators. Predation at culture sites is a major concern of bivalve farmers (Flimlin 1993; Rosenthal *et al.* 1995). For instance, commercial bivalve aquaculture ventures in the US spend a fair proportion of their budget every year in anti-predation material and techniques to control quahaug mortality due to predators (Menzel 1989).

Many potential predators were identified by PEI shellfish farmers and various stakeholders to be threats to their operations. These predators include the common starfish (*Asterias vulgaris* Verril), the moon shell (*Lunatia heros* Say), as well as various crab species including the green crab (*Carcinus maenas* L.), which was accidentally introduced to North America in the 19th century. The green crab was noted for the first time off southeastern shores of PEI in 1997 (Gillis *et al.* 2000). It has since progressed toward the northwest of the island on both shores (MacNair, personal observation).

Without adequate knowledge of the biology and the impact of these predators on cultured bivalve populations, little can be done to suggest anti-predation techniques. The objective of this study was to evaluate and document the predation behaviour of various species in order to understand and establish the priority of implementing predator control measures and further research & development projects. This study was carried out by determining mortality rates of four PEI commercial bivalve species in the presence and absence of green crab, common starfish and moon shell. It was expected that mortality rates of the prey species would increase in the presence of predators, that mortality rates of prey would vary according to the predator species and that mortality rates per predator species would decrease with increasing prey size. A complementary experiment was also undertaken to see if water temperature and sediment type affected the predator-prey relationship between green crab and soft-shell clam. The green crab's optimal habitats are estuarian shallow mud flats in temperate waters (e.g., Williams 1984; Squires 1990). It was expected that low temperatures and coarse sediments would decrease the predation activities of the green crab.

Material and methods

Study site and experimental organisms

The study was carried out at the Ellerslie Shellfish Hatchery, PEI, in December 2000 and January 2001. Trials were held in thirty 38-cm wide X 54-cm long X 16-cm high plastic containers that were placed in larger tanks supplied with salt water. Each container was divided into two equal sections (38-cm wide X 27-cm long) with a PVC separator for a total of 60 experimental enclosures. The water was pumped from Bideford Estuary (0^{o} C, 20‰) through a sand filter. Small-size mesh nets (1 cm) were clipped on containers to prevent predators from escaping. Photoperiod was maintained at 8 hours of light and 16 hours of darkness in all experiments. The predator and prey species were obtained from various PEI locations: green crabs and moon shells from St. Mary's Bay; common starfish and blue mussels from Tracadie Bay; eastern oysters from Malpèque Bay; soft-shell clams from North River; and quahaugs from the Ellerslie hatchery. Quahaugs were of the *notata* variety.

Predation trials

1) Prey and prey size selections

Experimental enclosures were filled with a 10-cm-deep layer of homogeneous sandy sediments and placed in larger experimental tanks. Water was heated to 12^{o} C (12.40 ± 0.15^{o} C) in holding tanks and then supplied to the experimental tanks by gravity. Sediments were sieved through a 1-mm mesh prior to use (removal of macro-invertebrates) but were not sterilized. Experimental enclosures were left for 1 wk to allow the sediments to stabilize. Bivalves were placed in the enclosures 24 h before predators were introduced (1 individual per aquarium except in control treatments). This allowed the endobenthic species (quahaugs and soft-shell clams) an opportunity to burrow into the sediments. Three size-classes were used to determine the preferred size-classes of predators: 0-15 mm; 15-25 mm; and > 25 mm. Ten individuals per size-class were used for a total of 30 individuals per single experimental enclosure. Trials were organized to have one of the three predator species combined with one of the four prey species at a time (single-choice experiment). Another set of trials were designed to combine one of the predator species (1 individual) with all the prey species within the enclosure (multiple-choice experiment). A total of 5 different prey treatments were used. Four different predator treatments, including controls (no predator), were also used. All trials were performed in triplicate for a total of 60 experimental enclosures (4 predator treatments X 5 prey treatments X 3 replicates). Three individuals per size-class were used in enclosures bearing all the prey species for a total of 36 individuals. Predator-prey combinations were randomly assigned to enclosures and tanks. Individuals, within each predator group, had a similar weight: green crab: 59.47 ± 9.14 g; common starfish: 8.93 ± 3.69 g; moon shell: 15.13 ± 2.26 g (mean ± SD). All enclosures were emptied 4 d after the introduction of predators and the mortality rate of bivalves was determined. The number of damaged bivalves was also determined (chipped, cracked, or bored shells).

2) Effect of water temperature and sediment type on the predation behaviour of the green crab

A second set of trials was carried out to study the effect of sediment type and water temperature on the predation behaviour of the green crab. Only soft-shell clams were used as a prey species in these trials. A total of 18 containers (as described previously) divided into two equal sections were used (36 experimental enclosures). All enclosures were filled with a 10-cm-deep layer of sediments. Sediment types used were sand (see sediment procedure above) and pea gravel (particle mean size: 10 mm). The mortality rates of clams was determined in presence and absence (control) of the crab. Six containers (12 experimental enclosures) were placed in larger tanks, each tank being supplied with salt water with a specific temperature. Experimental enclosures (sediment type X predator treatment) were randomly assigned in each temperature-fixed tank. Water temperature used were 0^{o} C ($1.30 \pm 0.57\,^{o}$ C), 10^{o} C ($11.05 \pm 0.21\,^{o}$ C) and 20^{o} C ($19.10 \pm 0.82\,^{o}$ C) (mean temperature ± SD). All treatments were performed in triplicate for a total of 36 experimental enclosures (2 predator treatments X 2 sediment type treatments X 3 temperature treatments X 3 replicates). A total of 25 clams were used per enclosure. Clam sizes ranged between 15 and 25 mm long. The prey were introduced into containers 24 h before the crabs (1 crab per aquarium except in control treatments). Crabs used had a mean blotted wet weight of 65.43 ± 14.04 g (mean ± SD). All containers were emptied 4 d after the introduction of crabs and the mortality rate of clams was determined.

Data analysis

The data were analyzed with SPSS 10.00© for Windows©. All analyses were calculated at a confidence level of $P < 0.05$. Mortality rates for each prey species were arcsin transformed to meet normality requirements and analyzed with a two-way ANOVA for each predator species. The factors were prey species and size-class. Percentages of damaged clams were arcsin transformed and similarly analyzed. The factors were predator species and size-class. A three-way ANOVA was used for the temperature/sediment experiment. Factors included in the model were water temperature, sediment type, presence/absence of the predator and the interaction terms. Tukey multiple comparisons were applied when significant differences were found on factors.

Results

1) Prey and prey size selections

A) <u>Single-choice experiment</u>

The green crab was an active predator during the 4 d trials (Fig.1). Crabs preyed upon all prey species. Blue mussels and soft-shell clams were the first and second preferred prey species, respectively. The ANOVA analysis (Table 1) showed a significant prey species X size-class interaction effect on mortality rates in the green crab treatments suggesting that the preferred size-class varied between prey species. For instance, our results showed that the eastern oysters were preyed more heavily at 0 - 15 mm and blue mussels at 15 - 25 mm. Mortality rates for quahaugs and soft-shell clams did not vary significantly between size-classes.

The common starfish was also very active during the trials (Fig. 1). Blue mussel, as observed in green crab treatments, was the preferred prey species. The eastern oyster, however, represented the second preferred prey species. The starfish did not prey upon other prey species. No prey species X size-class interaction effect was observed on mortality rates in the starfish trials (Table 2). The ANOVA analysis showed a significant variation in mortality rates in relation to prey species and none from the size-class.

The moon shell was the least active predator (Fig. 1). No predation was observed on quahaugs and oysters. Mean mortality rates for blue mussel and soft-shell clam were less than 10 %. The ANOVA analysis (Table 3) did not show any interaction effect on mortality rates nor from the prey size. A statistically significant effect of prey species was observed. The multiple comparisons test, however, did not discriminate mortality rates in relation to prey species.

Mortality rates in control treatments were 0 % regardless of the size-class for all prey species except for soft-shell clams (Fig. 1). Clams suffered low mortality in all size-classes (*ca* 5 %). This means there could be a slight overestimation of mortality rates for clams. The ANOVA analysis (Table 4) did not show any significant variation on mortality rates from prey species, size-class, and their interaction.

Though mortality rates in soft-shell clams were small overall (except for the > 25 mm size class in the green crab treatments), all predators were observed manipulating clams during the 4 d trials. The percentage of clams that were damaged (cracked, chipped, or bored shells) was relatively important on small- and mid size-classes (0 - 25 mm) (Fig. 2). The ANOVA analysis (Table 5) showed that percentages of damaged individuals varied significantly in relation to the predator species. The common starfish was the species that damaged clams the least (< 20%) while moon shells damaged them the most (30 to 40 %). Percentages in the green crab treatments were intermediate (20 to 30 %). No prey size-class nor predator species X prey size class interaction effects were observed.

B) Multiple-choice experiment

Trials where all prey species were challenged with a single predator showed different results from what was observed in single-choice experiments (Fig. 3). Overall, predation was lower than in cases where a single prey species was challenged with a single predator. Our results, however, showed that predation was extremely variable. The ANOVAs failed to show any significant effect from prey species, size-class, and prey species X size-class interaction regardless of the predator species or the control (Tables 6 to 9).

The green crab preyed upon all prey species except for quahaugs while the common starfish preyed upon all prey species including small-size quahaugs. The moon shells was again the least active predator. Large-size quahaugs were, however, preyed upon in the moon shell trials. Low mortality rates were observed in small-size oysters and mussels and mid-size clams (< 5 %).

2) Effect of water temperature and sediment type on the predation behaviour of the green crab

Mortality rates by green crabs differed between water-temperature treatments (Fig. 4, Table 10). However, clam mortalities were observed in control treatments which showed that predation was overestimated. Correcting for this natural mortality, there was still a significant decline in prey consumption with regard to temperature in green crab treatments. The ANOVA analysis did not show any significant variation in relation to sediment type. In the latter case, a trend could be seen at 20° C where mortality rates were higher in sand treatments compared to gravel ones. Variability was, however, high. No double or triple interactions were observed.

Discussion

1) Prey and prey size selections

The present laboratory experiments suggested that the green crab and the common starfish are important predators in bivalve aquaculture sites off PEI shores. Single-choice experiments showed that blue mussels were selected more often by these predators compared to moon shells. This was particularly true for small-size individuals (< 25 mm). O'Neill *et al.* (1983) and ap Rheinalt (1986) documented similar results with seastars and crabs (including green crabs), respectively, versus cultivated blue mussels. This suggests that large mussels probably attained a partial prey refuge in size (at about 25 mm) from predators. Several authors came to the same conclusions while studying the relationship between various species of crabs and bivalve species, including the one between the green crab and the blue mussel (e.g., Elner 1980; Townsend and Hughes 1981; Navarrete and Castilla 1988; Eggleston 1990; Juanes 1992; MacNair, personal observation). Large-size prey may be more difficult to handle by crabs (manipulation with the chela) as well as being more difficult to open by seastars (large prey have stronger adductor muscles).

This response may, however, vary in relation to the size of the predator. Eggleston (1990), for instance, observed that large-size crabs may feed on large eastern oysters (> 45 mm) as larger individuals display an increased crushing strength. Furthermore, male crabs will exhibit a larger crusher chela height, and in turn, more strength, than a female of the same year class (Hines *et al.* 1990).

Soft-shell clams and quahaugs are both endobenthic organisms. The fact that both species bury themselves in the sediments may provide them a spatial refuge from some predators. However, our results suggests that crabs were able to detect and handle soft-shell clams without any difficulty. The summed % of individuals eaten and/or damaged was important regardless of prey size. In large clams (> 25 mm), over 55 % were preyed upon. The shape and hardness of quahaugs may offer some protection from predators compared to soft-shell clams which has a weaker shell (Blundon and Kennedy 1982a, Boulding 1984) as well as exposed siphon and pedal gapes (Bloudon 1984). Burial depth, for soft-shell clams, is apparently the only refuge from epibenthic predators (Blundon and Kennedy 1982b). Because the green crab may dig pits up to 15 cm deep (Williams 1984), the predation level observed during this study may be higher than in nature where burial depth is not limited. Maximum burial depth was only 10 cm in our experimental enclosures.

The multiple-choice experiment suggests that the predation behaviour of green crab and common starfish may be more general when several prey species are challenged at the same time. Results showed that prey species were more homogeneously selected compared to single-choice trials. This was particularly true for starfish, which also preyed on small-size quahaugs. Various feeding studies showed that green crabs may feed on various taxonomic groups including polychaetes, gastropods and barnacles (e.g., Le Calvez 1984; Williams 1984). Field trials conducted in 2000 by the Department of Fisheries, Aquaculture and Environment of PEI (DFAE) showed, however, that in multiple-choice experiments with green crabs, mussels were the preferred food over soft-shell clams and oysters (MacNair, personal communication).

Single-choice and multiple-choice experiments suggests that moon shells were the least active predator. Observed predation rates were generally low for all prey species. This was a surprising result since soft-shell clams and blue mussels are reported to be heavily preyed upon by this gastropod (Vencile 1997). The percentage of live clams demonstrating moon shell drill holes, however, was relatively high in the present study. This was also the case in the DFAE field study carried in 2000 (MacNair, personal communication). A longer experimental period probably would give a higher mortality rate than that observed in laboratory.

2) Effect of water temperature and sediment type on the predation behaviour of the green crab

The water temperature and sediment type experiment demonstrated interesting results. Mortality rates of clams in the presence of crabs, after a 4 d trial, were maximum at 20° C (*ca* 20 %) while they were low at 10° C (*ca* 5 %). No predation was observed at 0° C. Elner (1980) presented similar results while studying the foraging strategy of european green crabs. In his study, feeding rates, in terms of number of mussels eaten per day was higher at 17° C than at 10° C. Energy intake (KJ) per day, however, was not significantly different between both temperatures. No effect on size selectivity was observed. Our results agree with results from a physiology study carried out by Wallace (1973) and field observations gathered by Naylor (1962) and MacNair (personal communication) on the green crab's activity level. Another similar predator-prey relationship was recently shown to be affected by water temperature. Burleigh (unpublished data) showed that the mud crab *Panopeus herbstii* gradually ate less quahaugs with decreasing temperature. In his study, quahaug mortality rates after 67 hours were 48, 43, 28 and 6% under water temperature of 25, 20, 10 and 7.5° C, respectively.

Cold water temperature could impede the progression of the green crab as well as its general behaviour (including the feeding activities) in the Gulf of St. Lawrence, unless climatic changes occur. Northumberland Strait's water temperatures are already relatively warm near the shore during the summer period compared to the rest of the Gulf. Damage caused by green crabs in PEI aquaculture operations would then be seasonal (late spring to early fall). Higher temperatures during a longer period (spring and fall) would probably increase the feeding activities of the crab to a broader temporal window during the year.

The sediment type experiment did not show any significant effect on the mortality rate of clams. This is in agreement with the habitat preferences and tolerance of the green crab (Williams 1984). However, our results displayed an apparent trend in relation to sediment type. Mortality rates of clams were higher in sand than in gravel at 20° C. Gravel environments may impede the predation behaviour of crabs. Gravel environments could offer a better refuge to endobenthic prey from crabs that are able to dig pits. Gravel environments are, however, not the best substratum to grow clams and quahaugs.

Preliminary results from a distribution study showed that green crabs trapped off the southeastern coast of PEI (St. Mary's Bay) were only found in soft-bottom environments in shallow brackish water (Audet, personal communication).

Conclusion

The present laboratory study has provided information on the potential effect of three common predators found off PEI shores on the mortality rates of four cultured bivalve species. Overall, results confirm that the common starfish is a potential threat for small-size blue mussels and eastern oysters (< 25 mm). Our multiple-choice experiment also suggests that the common starfish may prey upon small quahaugs (< 15 mm) and large soft-shell clams (> 15 mm). The moon shell did not appear to be an important predator except for large-size quahaugs (> 25 mm) and mid-size clams. The introduced green crab appears to be a threat to all the studied species, particularly blue mussel and soft-shell clam. Small-size oysters (< 15 mm) were also heavily preyed upon in the multiple-choice experiment.

Low water temperature may impede the green crab's predation behaviour. This was not the case with sediment type, though crabs had a tendency to eat more prey in the sandy experimental enclosures (at 20^{o} C).

The potential for the green crab to cause heavy damage to commercial bivalve species appears to be a reality. The status of the green crab around the coasts of PEI should continue to be monitored yearly. Further projects should be aimed toward population dynamics and more precise predation behaviour studies. The effect of the green crab's sex and size on its predation behaviour, as well as prey densities on its feeding habits, appears relevant to investigate. The relationship between the green crab and potential indigenous competitors [e.g. the rock crab (*Cancer irroratus*)] should also be investigated (e.g., space and food competition). Anti-predation measures at sites where these predators are found in great numbers may be considered to help decrease economic losses. Laboratory and field experiments should be designed to test and suggest adequate anti-predation techniques to be adapted to PEI aquaculture operations.

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Table 1. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in single-choice experiments using the green crab (*C. maenas*) as predator. The interaction effect was examined using a Tukey multiple comparisons test. Prey size-classes are presented in increasing order of mortality rates. Non-significant differences among prey size-classes are underlined.

Source of variation	SS	Df	MS	F	p
Prey species	2832.168	3	944.056	3.001	0.050
Prey size-class	2179.520	2	1089.760	3.464	0.048
Prey species X prey size-class	12943.742	6	2157.290	6.857	< 0.001
Error	7550.969	24	314.624		
Corrected total	25506.399	35			

Interaction

Prey species	Prey size-class (mm)		
Quahaugs	15-25	>25	0-15
Eastern oysters	15-25	>25	0-15
Blue mussels	0-15	>25	15-25
Soft-shell clams	0-15	15-25	>25

Table 2. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in single-choice experiments using the common starfish (*A. vulgaris*) as predator. Multiple comparisons were carried out with a Tukey test . Prey species are presented in increasing order of mortality rates. Non-significant differences among prey species are underlined.

Source of variation	SS	df	MS	F	p
Prey species	6694.987	3	2231.662	4.548	0.012
Prey size-class	2129.310	2	1064.655	2.170	0.136
Prey species X prey size-class	2784.330	6	464.055	0.946	0.481
Error	11776.097	24	490.671		
Corrected total	23384.723	35			

Multiple comparisons

<u>Quahaugs Soft-shell clams</u> <u>Eastern oysters</u> <u>Blue mussels</u>

Table 3. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in single-choice experiments using the moon shell (*L. heros*) as predator. Multiple comparisons were carried out with a Tukey test . Prey species are presented in increasing order of mortality rates. Non-significant differences among prey species are underlined.

Source of variation	SS	df	MS	F	p
Prey species	195.242	3	65.081	3.083	0.048
Prey size-class	16.477	2	8.239	0.387	0.684
Prey species X prey size-class	175.246	6	29.208	1.370	0.266
Error	511.541	24	21.314		
Corrected total	898.506	35			

Multiple comparisons

<u>Quahaugs Eastern oysters Blue mussels Soft-shell clams</u>

Table 4. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in single-choice experiments in the absence of predators.

Source of variation	SS	df	MS	F	p
Prey species	157.398	3	52.466	2.959	0.053
Prey size-class	0.729	2	0.365	0.021	0.980
Prey species X prey size-class	2.188	6	0.365	0.021	0.999
Error	425.562	24	17.732		
Corrected total	585.877	35			

Table 5. Two-way ANOVA analysis examining the effect of predator species and prey size-class on percentage of damaged soft-shell clams (*M. arenaria*). Multiple comparisons were carried out with a Tukey test . Predator species are presented in increasing order of percentage of damaged individuals. Non-significant differences among predator species are underlined.

Source of variation	SS	df	MS	F	p
Predator species	1818.459	2	909.229	3.852	0.040
Prey size-class	1100.307	2	550.153	2.331	0.126
Predator species X prey size-class	1086.170	4	271.542	1.151	0.365
Error	4248.236	18	236.013		
Corrected total	8253.172	27			

Multiple comparisons

<u>Common starfish</u>   <u>Green crab</u>   <u>Moon shell</u>

Table 6. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in multiple-choice experiments using the green crab (*C. maenas*) as predator.

Source of variation	SS	df	MS	F	p
Prey species	648.130	3	216.043	0.483	0.697
Prey size-class	108.022	2	54.011	0.121	0.887
Prey species X prey size-class	3101.843	6	516.974	1.155	0.362
Error	10740.593	24	447.525		
Corrected total	14598.586	35			

Table 7. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in multiple-choice experiments using the common starfish (*A. vulgaris*) as predator.

Source of variation	SS	df	MS	F	p
Prey species	1111.074	3	370.358	0.387	0.763
Prey size-class	432.105	2	216.052	0.226	0.800
Prey species X prey size-class	3888.981	6	648.164	0.677	0.669
Error	22963.259	24	956.802		
Corrected total	28395.420	35			

Table 8. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in multiple-choice experiments using the moon shell (*L. heros*) as predator.

Source of variation	SS	df	MS	F	p
Prey species	190.972	3	63.657	0.733	0.542
Prey size-class	104.167	2	52.083	0.600	0.557
Prey species X prey size-class	590.278	6	98.380	1.133	0.373
Error	2083.333	24	86.806		
Corrected total	2968.750	35			

Table 9. Two-way ANOVA analysis examining the effect of prey species and prey size-class on mortality rates in multiple-choice experiments in the absence of predators.

Source of variation	SS	df	MS	F	p
Prey species	587.052	3	195.684	0.577	0.635
Prey size-class	798.167	2	399.083	1.178	0.325
Prey species X prey size-class	1912.920	6	318.820	0.941	0.485
Error	8133.259	24	338.886		
Corrected total	11431.398	35			

Table 10. Three-way ANOVA analysis examining the effect of water temperature, sediment type and predator treatment [presence/absence of green crabs (*C. maenas*)] on the mortality rate of soft-shell clams (*M. arenaria*). Multiple comparisons were carried out with a Tukey test. Water temperatures are presented in increasing order of mortality rates. Non-significant differences water temperatures are underlined.

Source of variation	SS	df	MS	F	p
Water temperature	595.214	2	297.607	7.893	0.003
Sediment type	24.569	1	24.569	0.652	0.433
Predator treatment	164.436	1	164.436	4.361	0.048
Water temperature X sediment type	97.110	2	48.555	1.288	0.302
Water temperature X predator treatment	135.247	2	67.623	1.793	0.195
Sediment type X predator treatment	38.275	1	38.275	1.015	0.329
Water temperature X sediment type X predator treatment	78.484	2	38.275	1.015	0.377
Error	904.927	24	37.705		
Corrected total	2038.259	35			

Multiple comparisons

0° C 10° C 20°C

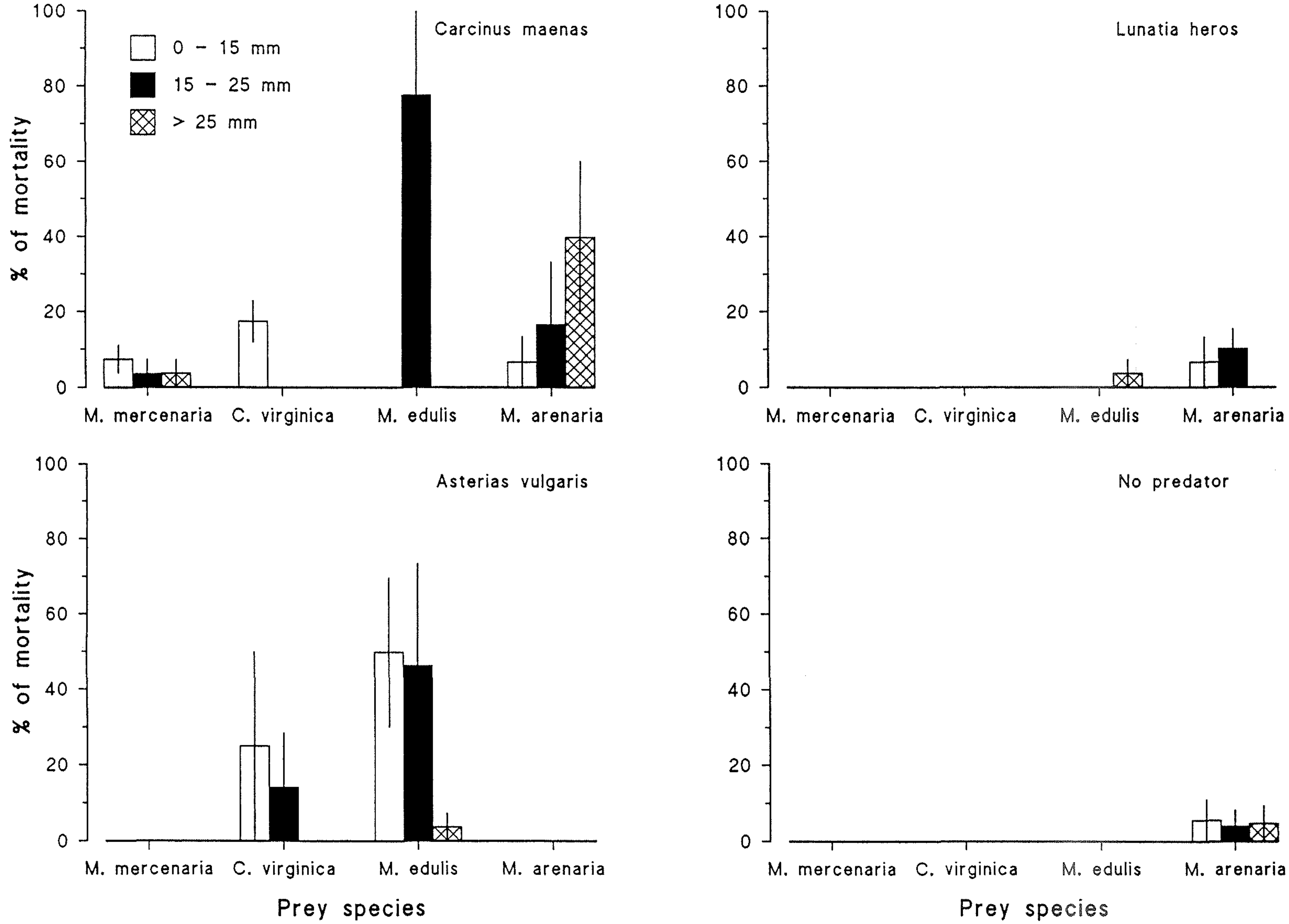

Figure 1: Percentage (mean ± SE, n = 3) of mortality per size-class of four bivalve species (single-choice experiment) in the presence of various predator species.

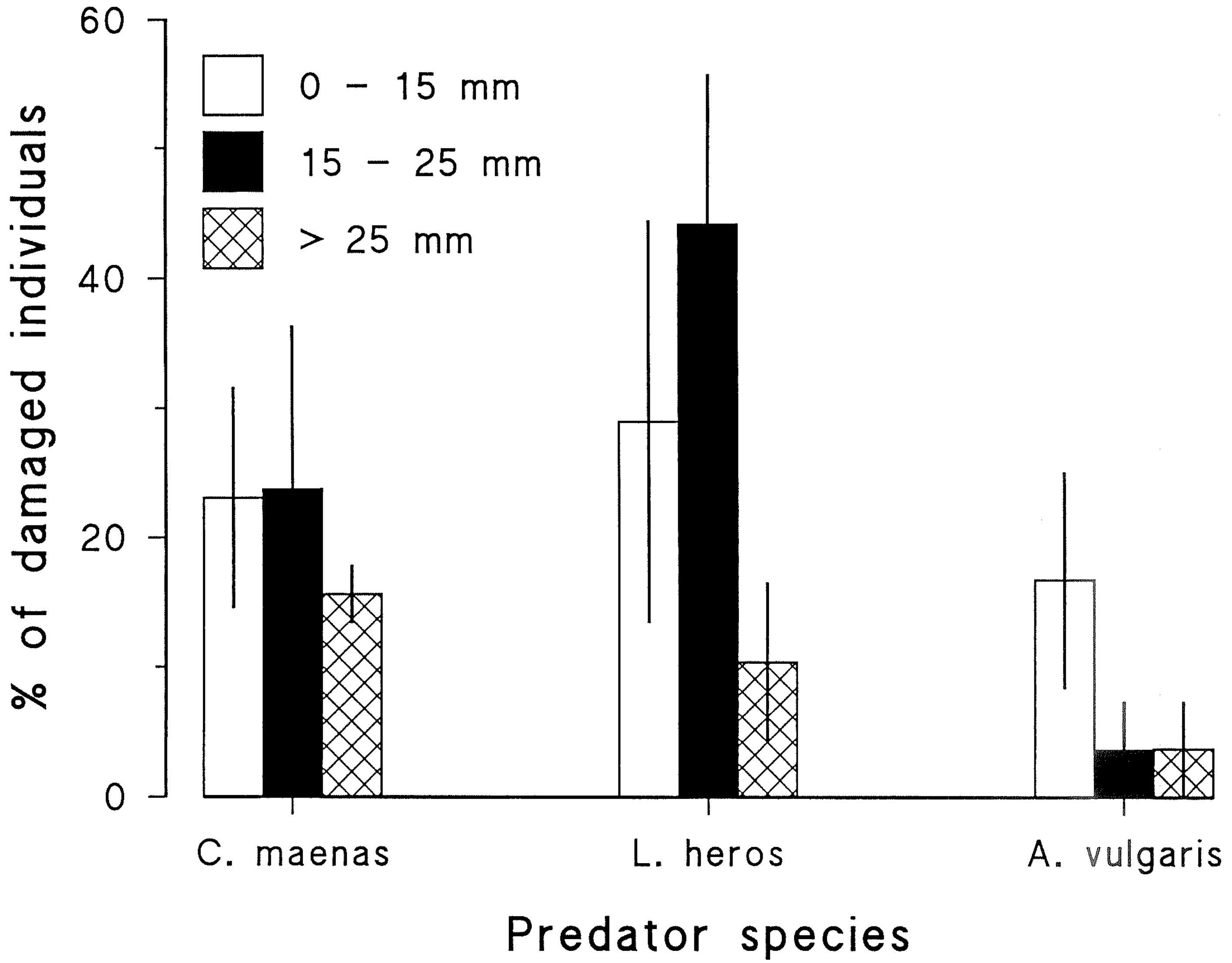

Figure 2: Percentage (mean ± SE, n = 3) of damaged individuals per size-class of soft-shell clams (*Mya arenaria*) in the presence of various predator species.

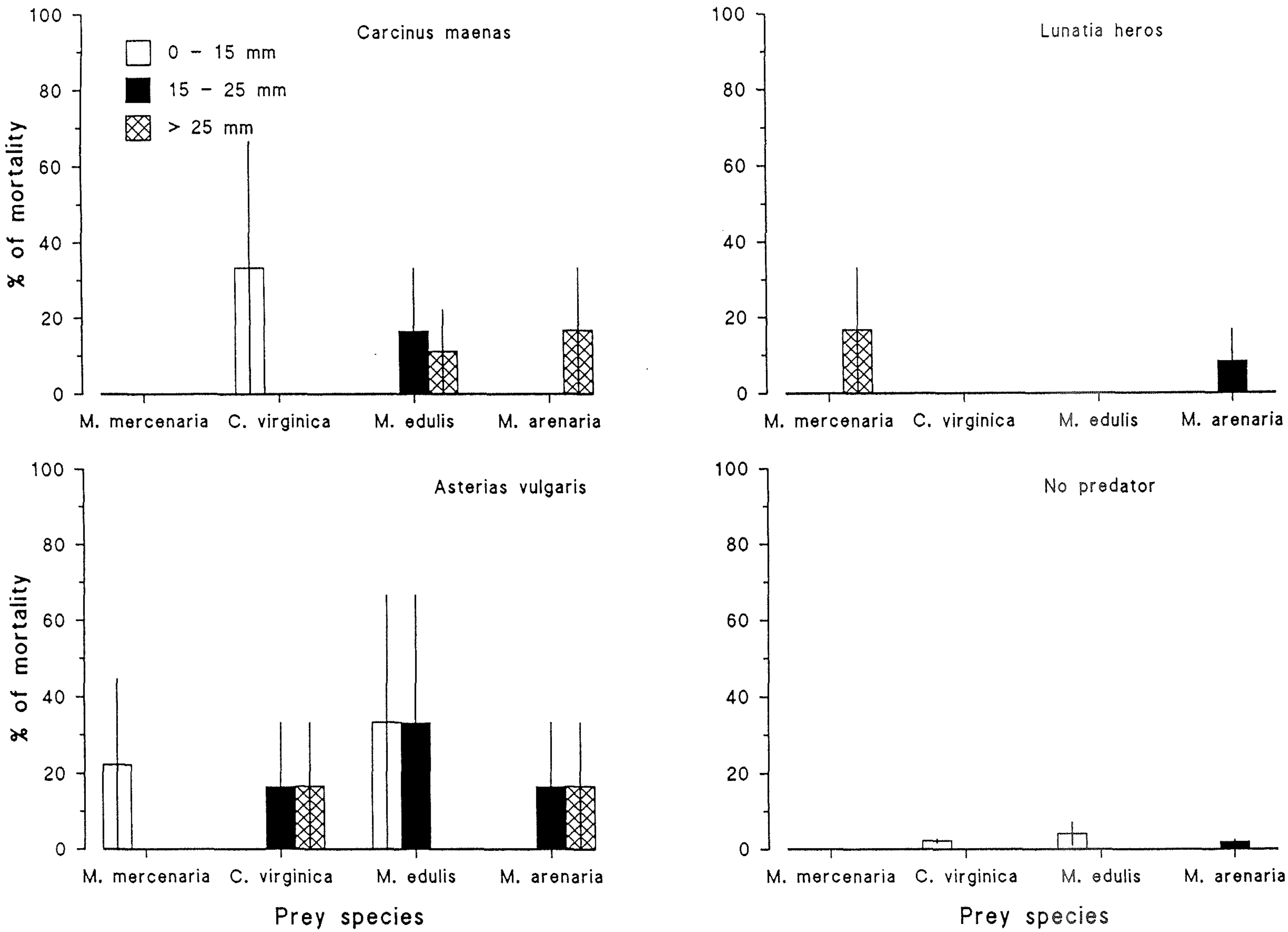

Figure 3: Percentage (mean ± SE, n = 3) of mortality per size-class of four bivalve species (multiple-choice experiment) in the presence of various predator species.

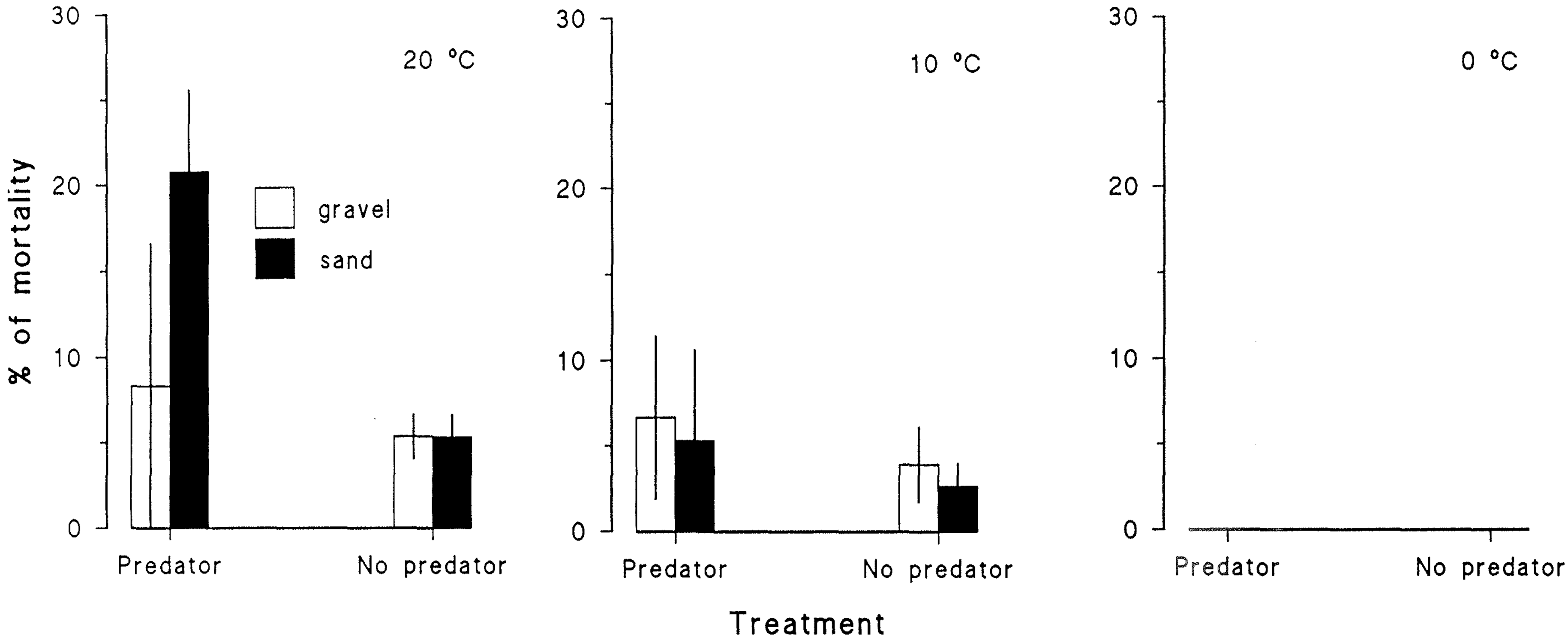

Figure 4: Percentage (mean ± SE, n = 3) of soft-shell clam (*Mya arenaria*) mortality in relation to temperature, sediment type, and the presence or absence of green crabs (*Carcinus maenas*).