The predation of zooplankton by the blue mussel (*Mytilus edulis*) and the clubbed tunicate (*Styela clava*).

A. R. LeBlanc, D. Bourque, T. Landry, J. Davidson and N.G. MacNair

Department of Fisheries and Oceans Gulf Fisheries Centre, Science Branch P. O. Box 5030 Moncton, New Brunswick E1C 9B6

2007

Canadian Technical Report of Fisheries and Aquatic Sciences 2684

Canadian Technical Report of Fisheries and Aquatic Sciences 2684

2007

The predation of zooplankton by the blue mussel (*Mytilus edulis*) and the clubbed tunicate (*Styela clava*)

by

A. R. LeBlanc¹, D. Bourque¹, T. Landry¹, J. Davidson² and N.G. MacNair³

¹Department of Fisheries and Oceans Gulf Fisheries Centre, Oceans & Science Branch P. O. Box 5030 Moncton, New Brunswick E1C 9B6

²Atlantic Veterinary College ³Department of Agriculture, Fisheries, Aquaculture and Forestry

© Her Majesty the Queen in Right of Canada 2007 Cat. No. Fs 97-6/2684E ISSN 0706-6457

This is report MG-01-06-029 for the Aquaculture Collaborative Research and Development Program

Correct citation for this publication is:

LeBlanc, A. R., D. Bourque, T. Landry, J. Davidson and N.G. MacNair. 2007. The predation of zooplankton by the blue mussel (*Mytilus edulis*) and the clubbed tunicate (*Styela clava*). Can. Tech. Rep. Fish. Aquat. Sci. 2684 :vii + 18 p.

Table of contents

| List of Tables | iv |
|-----------------|-----|
| List of Figures | v |
| Abstract | vi |
| Résumé | vii |
| Introduction | 1 |
| Methodology | 2 |
| Results | 4 |
| Discussion | 5 |
| References | |

List of Tables

Table 1. Abundance of zooplankton (mean number \pm SE) found in experimental treatments at the end of each experiment carried out in June 2003......7

List of figures

| Figure 1. Clearance rates of bivalve larvae by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.051) and stars represent differences between dates (P = 0.005)10 |
|--|
| Figure 2. Ingestion rates of bivalve larvae by the two experimental groups on a) June 13^{th} 2003 (P = 0.435), b) June 17^{th} 2003 (P = 0.226) and c) June 27^{th} 2003 (P = 0.104). Error bars represent ± SE |
| Figure 3. Clearance rates of copepods by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.220) or between dates (P = 0.457) |
| Figure 4. Ingestion rates of copepods by the two experimental groups on a) June 13^{th} 2003 (P = 0.977), b) June 17^{th} 2003 (P = 0.207) and c) June 27^{th} 2003 (P = 0.035).Error bars represent ± SE. Letters represent significant differences between groups |
| Figure 5. Clearance rates of gastropod larvae by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.144) and stars represent differences between dates (P = 0.009) |
| Figure 6. Ingestion rates of gastropod larvae by the two experimental groups on a) June $13^{\text{th}} 2003 \text{ (P} = 0.457) \text{ and b)}$ June $27^{\text{th}} 2003 \text{ (P} = 0.106)$. Error bars represent \pm SE. |
| Figure 7. Clearance rates of polychaete larvae by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.226) or between dates (P = 0.250) |
| Figure 8. Ingestion rates of polychaete larvae by the two experimental groups on a) June $13^{\text{th}} 2003 \text{ (P} = 0.726) \text{ and b)}$ June $17^{\text{th}} 2003 \text{ (P} = 0.407)$. Error bars represent \pm SE. |
| Figure 9. Clearance rates of different zooplankton taxa by <i>Mytilus edulis</i> (P=0.431) and <i>Styela clava</i> (P=0.290) in experiments carried out in June 2003. Error bars represent ± SE |

ABSTRACT

LeBlanc, A. R., D. Bourque, T. Landry, J. Davidson and N.G. MacNair. 2007. The predation of zooplankton by the blue mussel (*Mytilus edulis*) and the clubbed tunicate (*Styela clava*). Can. Tech. Rep. Fish. Aquat. Sci. 2684 :vii + 18 p.

Consumption of planktonic larvae of bivalves, copepods, gastropods and polychaetes by *Mytilus edulis* and *Styela clava* was evaluated in the laboratory. Two experimental groups of filter feeders were compared: 1 *M. edulis* and 1 *S. clava*. Clearance rates of all prey taxa were similar for *M. edulis* and *S. clava*. Ingestion rates (IR) were not different between the two predators except for one occasion when *M. edulis* had higher IR of copepods. Clearance rates of the different prey taxa were not different for either predator species. Mussels and tunicates both consume larvae. However, the abundance of tunicates in certain areas of PEI may increase the predation pressure on larvae which may decrease mussel larvae collection. Also, tunicates may reduce the food available to mussels which might, in turn reduce their reproductive potential.

RÉSUMÉ

LeBlanc, A. R., D. Bourque, T. Landry, J. Davidson and N.G. MacNair. 2007. The predation of zooplankton by the blue mussel (*Mytilus edulis*) and the clubbed tunicate (*Styela clava*). Can. Tech. Rep. Fish. Aquat. Sci. 2684 :vii + 18 p.

La consommation de larve planktonique de bivalves, de copépodes, de gastéropodes et de polychètes par *Mytilus edulis* et *Styela clava* a été comparée dans un laboratoire à système fermé. Deux groupes expérimentaux de filtreurs ont été comparés : 1 *M. edulis* et 1 *S. clava*. Les taux de filtration de tous les groupes de proie étaient semblables pour *M. edulis* et *S. clava*. Les taux d'ingestion n'étaient pas différents entre les deux espèces de prédateurs sauf en une occasion où le taux d'ingestion de copépodes par les moules était plus élevé. Les taux de filtration des différents groupes de proies n'étaient pas différents pour aucun des prédateurs. Les résultats indiquent que les moules et les tuniciers consomment des larves. L'abondance de tuniciers à certains endroits à l'IPE peut donc augmenter le taux de prédation de larve de moules ce qui peut réduire l'abondance de naissains de moules. En plus, les tuniciers peuvent réduire la quantité de nourriture disponible aux moules et ainsi, réduire leur potentiel de reproduction.

Introduction

In the last few years, mussel spat collection has diminished in some areas of Prince Edward Island, specifically Murray River. This area sustains an important blue mussel (*Mytilus edulis*) aquaculture industry. Collecting mussel spat is an integral part of mussel aquaculture (Mallet and Myrand, 1995). A reliable seed source is necessary for the sustainability of mussel farms. The arrival of the clubbed tunicate, *Styela clava*, which was first identified in the area in 1998, has raised concerns regarding the potential predation of mussel spat. *S. clava* has since reached very high abundances and other species of ascidians, namely *Ciona intestinalis*, have invaded this area.

S. clava is a sessile filter feeder that settles on hard substrates. There are very few hard substrates on PEI, therefore aquaculture equipment provides an excellent substrate for settlement. Two possible ways *S. clava* can affect mussel larvae recruitment are by reducing the productivity of adult mussels or by filtering the larvae. Tunicates exploit the same food source (phytoplankton) and the same size particles as mussels (Bourque *et al.* in prep.) so they could potentially reduce the amount of food available to mussels and in turn affect mussel growth and reproductive effort. Since *S. clava* is a filter-feeder, it could reduce the number of mussel larvae by filtering them. Many species of filter feeders, including *M. edulis* and *S. clava*, have been shown to filter their own larvae and larvae of other species such as gastropods, barnacles, polychaetes and echinoderms (Mileikovsky 1974, Cowden *et al.* 1984, Bingham and Walters 1989, Osman *et al.* 1989, André and Rosenberg 1991, Osman and Whitlatch 1995, Davenport *et al.* 2000, Lehane and Davenport 2002, 2004) and other zooplankton (Davenport *et al.* 2000, Lehane and Davenport 2002, Green *et al.* 2003, Wong *et al* 2003). There is however, disagreement in the literature as to the effect of larval predation on recruitment and settlement of larvae.

It has been suggested that larvae filtered by adult mussels could still be viable after being excreted as pseudofaeces. However, pseudofaeces are composed of mucus and particles, therefore larvae have little chance of freeing themselves (Mileikovsky 1974, Lehane and Davenport 2004). On the other hand, larvae may survive filtration by ascidians. Ascidians have the ability to filter particles entering the branchial sac. When the branchial tentacles come in contact with unsuitable particles, ascidians close the

1

exhalant siphon and contract the body thus ejecting the particles without them ever entering the digestive tract. In this case, larvae would be ejected unharmed and viable (Bingham and Walters 1989, Cowden et al. 1984). In spite of this ability, larvae have been found in the gut of several species of solitary ascidians (Bingham and Walters, 1989)

This study was undertaken in response to industry concerns that tunicates may filter mussel larvae resulting in low recruitment of spat. The objective was to determine if *S. clava* as well as adult mussels significantly reduce the number of mussel larvae by filter feeding. Other zooplankton taxa were also examined to better understand the filtering capabilities of the two species and their potential to affect recruitment of nearshore marine communities.

Methodology

The experiments were carried out on 3 different occasions: June 13th, June 17th and June 27th 2003. Blue mussels (42-68 mm) and clubbed tunicates (32-69 mm) were collected from Murray River, PEI the week before the experiments and kept in an artificial seawater recirculation system (temperature 12°C, salinity 27 ppt) for acclimatization at the Atlantic Veterinary College, Charlottetown, PEI. They were not fed during this periond.

Zooplankton samples were collected from Winter Bay, PEI on the day of the experiments. Water was pumped with a Rule 2000 Bilge pump for 5 minutes (June 13^{th}) or for 3 minutes (June 17^{th} and 27^{th}). The water was filtered through a 63 µm mesh and the filtrate was rinsed into bottles. On June 13^{th} , 5 samples were taken while on June 17^{th} and 27^{th} , 3 samples were taken. At the lab, artificial seawater was added to the samples to get 700 ml on June 13^{th} and 450 ml on the other 2 dates, because there were fewer replicates. Twenty ml of water from these samples were then added to 1L beakers filled with 500 ml of artificial seawater. Each beaker was randomly assigned to one of three experimental treatments. The experimental treatment consisted of adding a predator species to the beaker. The four treatments were: 1) one mussel, 2) one tunicate, and 3) no animals (control). For the June 13^{th} experiment, there were 9 replicates of each treatment

with a predator and 5 control replicates with no animals. For the other two dates, there were 5 replicates for each experimental and control treatment. The experiments ran for 95 - 200 minutes. When the experiments were done, the water was filtered through a 63 μ m mesh and rinsed with artificial seawater into 20 ml vials. A few drops of formaldehyde were added to the vials. Zooplankton was identified to the lowest taxonomic group possible and counted with a Ward Counting Wheel under a stereomicroscope.

Zooplankton consumption was calculated with the following equation:

$$CR = (V/nt)\ln(C_o/C_t)$$

where CR is clearance rate in L indiv⁻¹ h⁻¹, V is the volume of water (L), n is the number of predator, t is the time, C_0 and C_t are the number of zooplankton taxa at time 0 (control) and at the end of the experiment (Riisgård 2001). The mean abundances of zooplankton in the control beakers were used for C_0 . Ingestion rate was calculated with the equation:

$$IR = CR * C_a$$

where IR is ingestion rate (prey indiv⁻¹ h^{-1}), CR is clearance rate (L indiv⁻¹ h^{-1}) and C_o is the number of zooplankton in the control beakers(MacIsaac *et al.* 1991).

Data were analysed with SYSTAT for Windows 11.0. Negative clearance rates were removed from the analysis. To obtain an equal number of replicates for all experiments, 5 replicates were randomly chosen from the June 13th experiment and included in the statistical analysis. Comparisons of clearance rates were done with 2-way ANOVAs with treatment and experiment (date) as factors. Ingestion rates were different for each date due to the differences in number of zooplankton present in the water. Therefore, each experiment was analysed separately with t-tests. One way ANOVAs were used to compare clearance rates of prey by each predator. Data were log-transformed to get equality of variance when necessary. Probability levels were set at 0.05.

Results

The most common zooplankton found in Winter Bay during the experimental period was mussel larvae, copepods, polychaetes and gastropods. Table 1 shows the abundances of these taxa in the control and experimental treatments when the experiments were stopped. Mussel larvae were most abundant on June 13th while gastropod larvae were most abundant on June 27th. Copepod numbers did not vary much between dates of collection. Larvae of Cnidaria, and Spirorbidae were found in low numbers on all dates. On June 27th, Rotifera, Cladocera and unidentified eggs were also found.

Results show that CR of mussel larvae varied between dates (Fig. 1). The CRs on June 13^{th} , when mussel larvae were the most abundant, were higher than for the other two dates (F = 7.464, p = 0.005). Clearance rates were not significantly different between the experimental treatments (F = 18.186, p = 0.051, Fig. 1). There was no significant difference in ingestion rates of bivalve larvae between the treatments (Fig. 2). The number of larvae in the water was different between the experiments, therefore the IRs were different on each date and were not statistically compared. However, it is clear that the IRs were higher when mussel larvae were most abundant, on June 13^{th} (Fig. 2).

There was no significant difference in the CR of copepods between treatments (F = 3.109, p = 0.220) or between dates (F = 0.812, p = 0.457, Fig 3). The IRs between the treatments were significantly different on one occasion only (Fig.4). On June 27^{th} , *M. edulis* had higher IRs than *S. clava*.

The analysis for gastropod larvae was done without the June 17^{th} data because there were very few gastropod larvae. CRs were higher on June 13^{th} than on June 27^{th} (F = 10.544, p= 0.009, Fig 5), while the number of gastropod larvae present in the water was higher on June 13^{th} (Table 1). CRs of the different treatments were similar (F = 18.782, p = 0.144, Fig. 5). IRs were not different between the treatments (Fig. 6).

The data on polychaete larvae for June 27^{th} were not included in the analysis because of low numbers. CRs of polychaete larvae did not differ between treatment (F = 8.661, p = 0.209) or dates (F = 1.438, p = 0.250, Fig. 7). IRs were not different between the groups (Fig 8).

There were no differences in clearance rates of the different prey taxa by either *M*. *edulis* (F=0.936, P=0.431) or *S. clava* (F=1.299, P=0.290).

Discussion

The results from this study show that *Mytilus edulis* and *Styela clava* are zooplankton predators. All zooplankton taxa found during the experiments were ingested by both predators. There were no differences in clearance rates or ingestion rates between mussels and tunicates. Cowden et al (1984) found that larvae generally had higher survival rates in the presence of the tunicate, *Styela gibbsii*, than in the presence of *M*. *edulis*. Another study showed that *Ciona intestinalis* and *S. clava* ingested oyster larvae at different rates (Osman et al. 1989). *S. clava* was able to clear 96% of larvae while *Ciona* cleared 29%.

This study also shows that neither *M. edulis* nor *S. clava* discriminated between prey taxa. Clearance rates and ingestion rates were similar for all taxa for both species of predators. This corroborates with other studies that indicate that *M. edulis* does not select between species of zooplankton (Cowden *et al.* 1984, Lehane and Davenport 2002) but selects for size. *M.edulis* frequently ingests zooplankton between 450-600 µm and larger mussels can ingest particles as large as 3 mm (Lehane and Davenport 2002, 2004).

Clearance and ingestion rates from this study are probably overestimates of what happens in situ. The experiments in the present study were carried out in a closed system therefore the volume of water was probably filtered a few times. Encounters between predator and larvae were most likely more frequent thus the probability of being consumed was higher. The use of artificial seawater may also increase predation rates. It is difficult to estimate the predation effect in the field from lab experiments. Predators and larvae may behave differently in their natural environment than in confined areas (Cowden *et al* 1984, Young, 1989, 1990, Lehane and Davenport 2004).

Many studies show that filter feeders have the ability to reduce zooplankton, including bivalve larvae, by predation thereby potentially reducing settlement and recruitment (Cowden *et al.* 1984, Lehane and Davenport 2002, 2004). However other studies show that the presence of adult filter feeders does in fact inhibit recruitment while others show they have a positive effect or no effect on recruitment (Bingham and Walters 1989, Osman *et al.* 1989, Young 1990). Osman *et al* (1989) demonstrated that recruitment was higher on panels adjacent to filter feeders than on clean panels. The predation effect by adult filter feeders seems to be localized because their influence is only felt on small scales. For example, *Styela plicata* can only ingest particles passing within 3 mm of its inhalant siphon (Young 1990) and the clam, *Cerastoderma edule,* reduced settlement of epifauna within 1-1.5 cm of its siphon (André et al. 1993). This indicates that only a small portion of zooplankton present in the water column would be exploitable by filter feeders and that recruitment on a large scale would not be affected.

Even though this study probably overestimates the consumption of larvae by mussels and tunicates, it shows that tunicates have similar larvae filtration as mussels. The high volume of *S. clava* in Murray River more than likely increases predation pressure, thereby causing a significant reduction in mussel larvae, at least in the vicinity of mussel longlines. During the winter of 2002, there was a high mortality rate among adult tunicates and mussel spat collection in the summer of 2003 was higher than the previous year (MacNair, pers. comm.). Increased predation could be a factor but it is probably not the only one. Competition for food may affect adult mussels' energy reserves and utilisation. Mussels might invest more energy in somatic growth at the expense of reproduction therefore fewer larvae would be produced. More studies are needed on the use of energy by adult mussels in the presence of a stressor such as competition from *S. clava*.

References

- André, C. and R. Rosenberg. 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. Mar. Ecol. Prog. Ser. 71:227-234.
- André, C., P. R. Jonsson and M. Lindegarth. 1993. Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. Mar. Ecol. Prog. Ser. 97:183-192.
- Bingham B. L. and L. J. Walters. 1989. Solitary ascidians as predators of invertebrate larvae: evidence from gut analyses and plankton samples. J. Exp. Mar. Biol. Ecol. 13:147-159.

6

- Bourque, D., A. LeBlanc, N. MacNair, T. Landry, G. Miron, J. Davidson. (in prep.). Inter-specific competition between an invasive filter-feeding tunicate (*Styela clava* Herdman) and cultivated mussels (*Mytilus edulis* Linneaus). Journal of Shellfish Research.
- Cowden, C., C. M. Young and F. S. Chia. 1984. Differential predation on marine invertebrate larvae by two benthic predators. Mar. Ecol. Prog. Ser. 14:145-149.
- Davenport, J., R. J. J. W. Smith and M. Packer. 2000. Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Mar. Ecol. Prog. Ser. 198:131-137.
- Green, S., A. W. Visser, J. Titelman and T. Kiorboe. 2003. Escape responses of copepod nauplii in the flow field of the blue mussel, Mytilus edulis. Mar. Biol. 142: 727-733.
- Lehane C. and J. Davenport. 2002. Ingestion of mesozooplankton by three species of bivalve; *Mytilus edulis*, *Cerastoderma edule* and *Aequipecten opercularis*. J. Mar. Bio. Ass. U.K. 82:615-619.
- Lehane, C. and J. Davenport. 2004. Ingestion of bivalve larvae by *Mytilus edulis*: experimental and field demonstrations of larviphagy in farmed blue mussels. Mar. Biol. 145:101-107.
- MacIsaac, H. J., W. G. Sprules and J. H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics? Can. J. Fish. Aquat. Sci. 48:2051-2060.
- Mallet, A. and B. Myrand. 1995. The culture of the blue mussel in Atlantic Canada. In A. Boghen (ed.): Cold-water aquaculture in Atlantic Canada. 2nd ed.
- Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar. Biol. 26:303-311.
- Osman, R. W., R. B. Whitlatch and R. N. Zajac. 1989. Effects of resident species on recruitment into a community: larval settlement versus post-settlement mortality in the oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 54:61-73.
- Osman, R. W. and R. B. Whitlatch. 1995. The influence of adults on larval settlement: experiments with four species of ascidians. J. Exp. Mar. Biol. Ecol. 190:199-220.
- Riisgård, H. U. 2001 On measurement of filtration rates in bivalves-the stony road to reliable data: review and interpretation. Mar. Ecol. Prog. Ser. 211:275-291.

- Wong, W. H., J. S. Levinton, B. S. Twining, N. S. Fisher, B. P. Kelaher and A. K. Alt. 2003. Assimilation of carbon from a rotifer by the mussels *Mytilus edulis* and *Perna viridis*: a potential food-web link. Mar. Ecol. Prog. Ser. 253:175-182.
- Young, C. M. 1989. Larval depletion by ascidians has little effect on settlement of epifauna. Mar. Biol. 102:481-489.
- Young, C. M. 1990. Larval predation by epifauna on temperate reefs: scale, power and the scarcity of measurable effects. Austr. J. Ecol. 15:413-426.

| | June 13 | | | June 17 | | | June 27 | | |
|-------------|-------------|----------------|--------------|------------|----------------|--------------|-------------|----------------|--------------|
| Taxa | Control | Mytilus edulis | Styela clava | Control | Mytilus edulis | Styela clava | Control | Mytilus edulis | Styela clava |
| Cnidaria | 2.6 | 2.2 | 2.2 | 0 | 0 | 0.4 | 0.2 | 0 | 0.4 |
| | ± 0.8 | ± 0.6 | ± 0.4 | | | ± 0.4 | ± 0.2 | | ± 0.2 |
| Nematoda | 2.0 | 26.6 | 23.7 | 3.0 | 4.4 | 7.4 | 1.4 | 4.4 | 23 |
| | ± 0.5 | ± 5.6 | ± 5.9 | ± 0.7 | ± 1.7 | ± 1.5 | ± 0.9 | ± 2.2 | ± 7.4 |
| Rotifera | 0 | 0 | 0 | 0 | 0 | 0 | 460.2 | 207.2 | 466.6 |
| | | | | | | | ± 100.2 | ± 104.4 | ± 34.2 |
| Bivalvia | 3603.2 | 1248.7 | 2344.8 | 11.6 | 10.0 | 12.2 | 72.4 | 36.0 | 76.4 |
| | ± 151.2 | ± 163.5 | ± 501.1 | ± 2.2 | ± 3.2 | ± 1.5 | ± 12.5 | ± 6.4 | ± 4.5 |
| Gastropoda | 16.8 | 5.2 | 9.9 | 2.6 | 2.7 | 2.0 | 572.0 | 398.2 | 568.0 |
| | ± 1.6 | ± 0.9 | ± 2.8 | ± 0.7 | ± 0.2 | ± 0.8 | ± 44.1 | ± 27.7 | ± 28.4 |
| Copepoda | 252.6 | 196.6 | 237.2 | 109.8 | 50.4 | 68.6 | 299.6 | 132.4 | 250.6 |
| | ± 13.9 | ± 14.8 | ± 27.4 | ± 15.4 | ± 7.3 | ± 10.4 | ± 22.5 | ± 31.8 | ± 18.5 |
| Cladocera | 0 | 0 | 0 | 0 | 0 | 0 | 10.6 | 15.4 | 20.0 |
| | | | | | | | ± 3.9 | ± 2.6 | ± 1.2 |
| Polychaeta | 319.2 | 175.5 | 239.9 | 19.2 | 11.2 | 15.2 | 0.8 | 0.2 | 0.8 |
| | ± 49.0 | ± 17.6 | ± 28.9 | ± 2.6 | ± 3.8 | ± 2.8 | ± 0.6 | ± 0.2 | ± 0.4 |
| Spirorbidae | 0.4 | 9.1 | 2.8 | 0 | 1.5 | 1.0 | 0 | 1.3 | 1.5 |
| | ± 0.2 | ± 2.7 | ± 0.8 | | ± 0.3 | ± 0 | | ± 0.6 | ± 0.6 |
| Total | 4196.8 | 1643.3 | 2860.4 | 145.6 | 78.4 | 105.8 | 1418.2 | 801 | 1412.4 |
| | ± 154.8 | ± 180.5 | ± 544.2 | ± 15.4 | ± 14.5 | ± 12.7 | ± 113.4 | ± 148.8 | ± 36.5 |

Table 1. Abundance of zooplankton (mean number \pm SE) found in the experimental treatments at the end of each experiment carried out in June 2003.

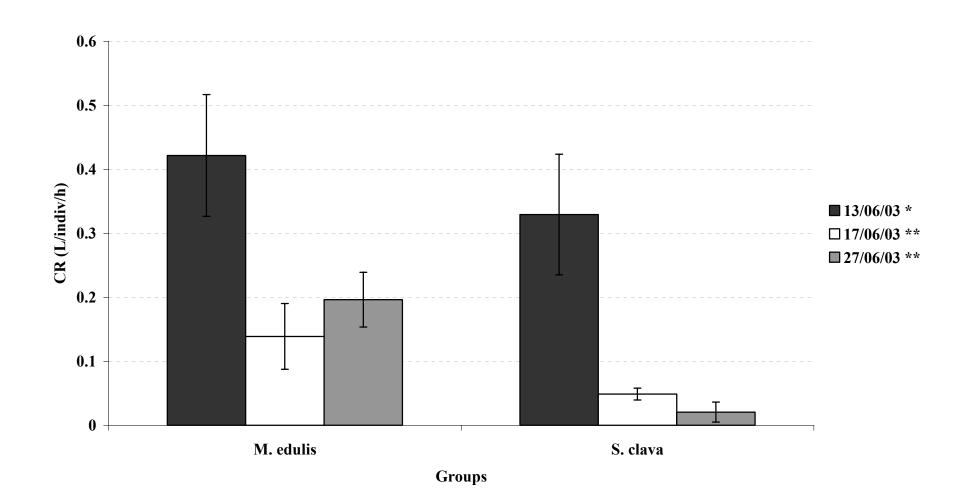


Figure 1. Clearance rates of bivalve larvae by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.051) and stars represent differences between dates (P = 0.005).

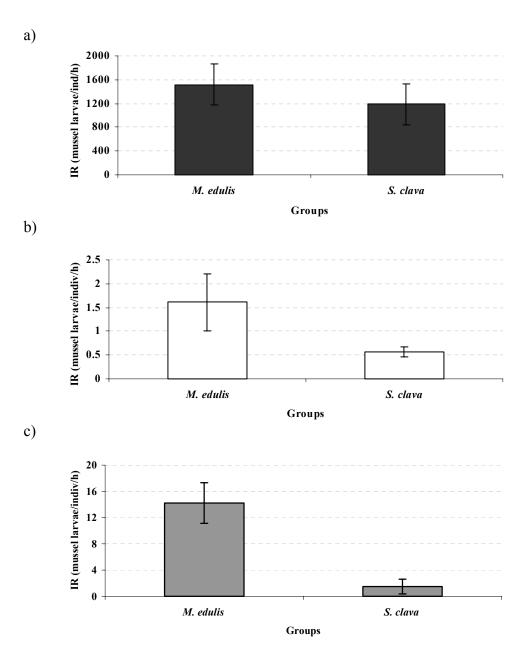


Figure 2. Ingestion rates of bivalve larvae by the two experimental groups on a) June 13th 2003 (P = 0.435), b) June 17th 2003 (P = 0.226) and c) June 27th 2003 (P = 0.104). Error bars represent \pm SE.

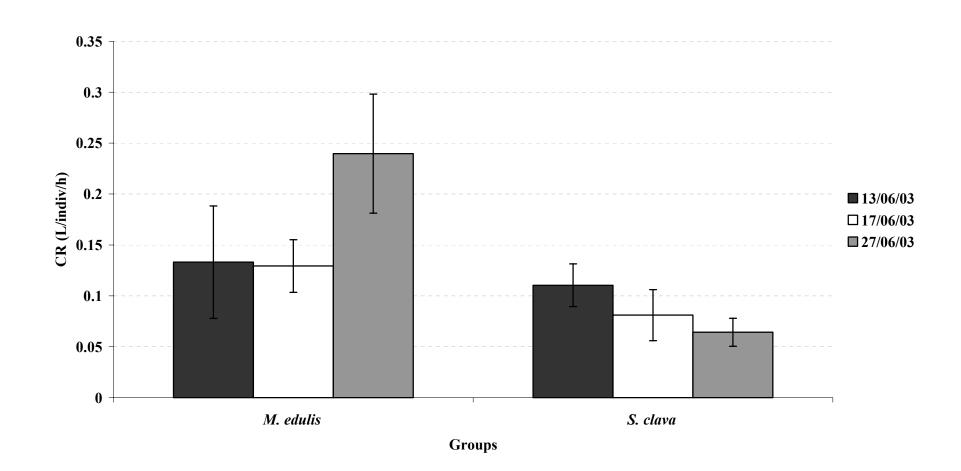


Figure 3. Clearance rates of copepods by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.220) or between dates (P = 0.457).

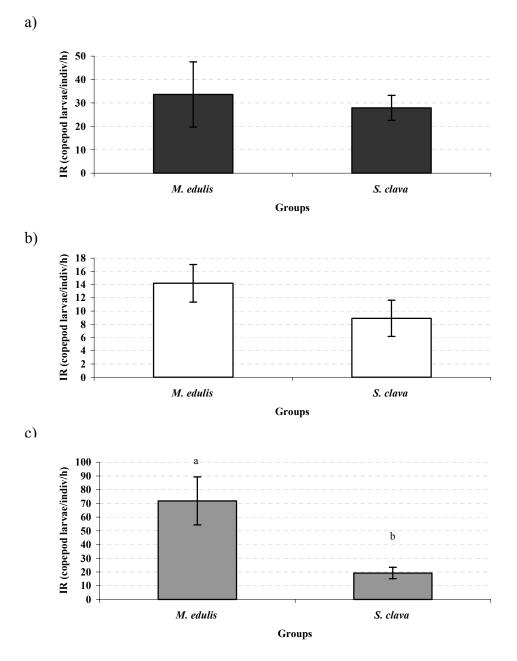


Figure 4. Ingestion rates of copepods by the two experimental groups on a) June 13^{th} 2003 (P = 0.977), b) June 17^{th} 2003 (P = 0.207) and c) June 27^{th} 2003 (P = 0.035).Error bars represent ± SE. Letters represent significant differences between groups.

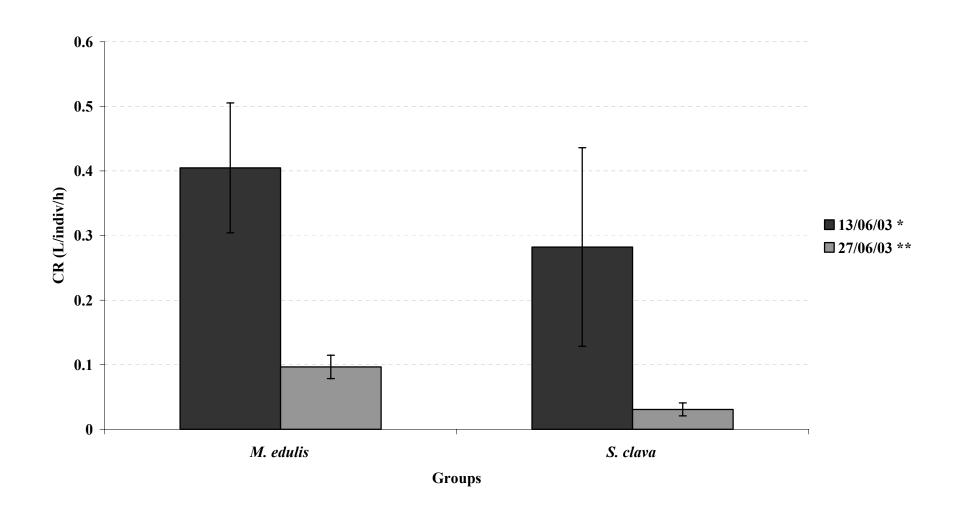
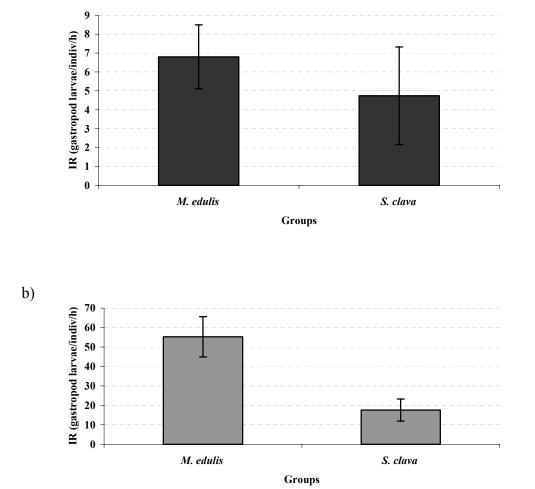


Figure 5. Clearance rates of gastropod larvae by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.144) and stars represent differences between dates (P = 0.009).



a)

Figure 6. Ingestion rates of gastropod larvae by the two experimental groups on a) June $13^{\text{th}} 2003 \text{ (P} = 0.457) \text{ and b)}$ June $27^{\text{th}} 2003 \text{ (P} = 0.106)$. Error bars represent \pm SE.

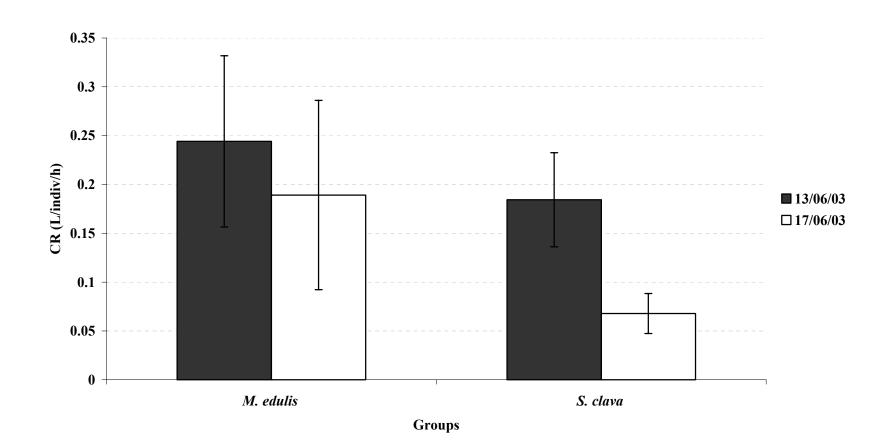


Figure 7. Clearance rates of polychaete larvae by the two experimental groups. Error bars represent \pm SE. There were no differences in clearance rates between groups (P = 0.226) or between dates (P = 0.250).

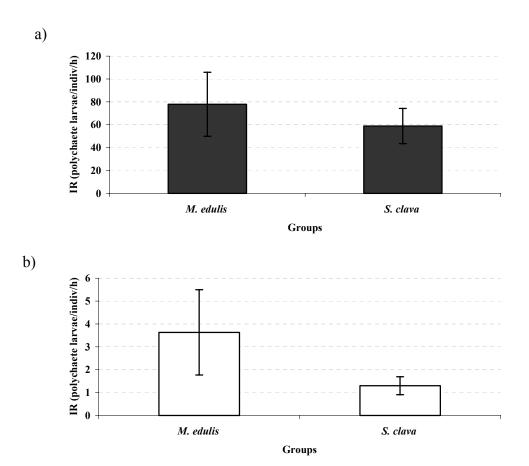


Figure 8. Ingestion rates of polychaete larvae by the two experimental groups on a) June $13^{\text{th}} 2003 \text{ (P} = 0.726)$ and b) June $17^{\text{th}} 2003 \text{ (P} = 0.407)$. Error bars represent ± SE.

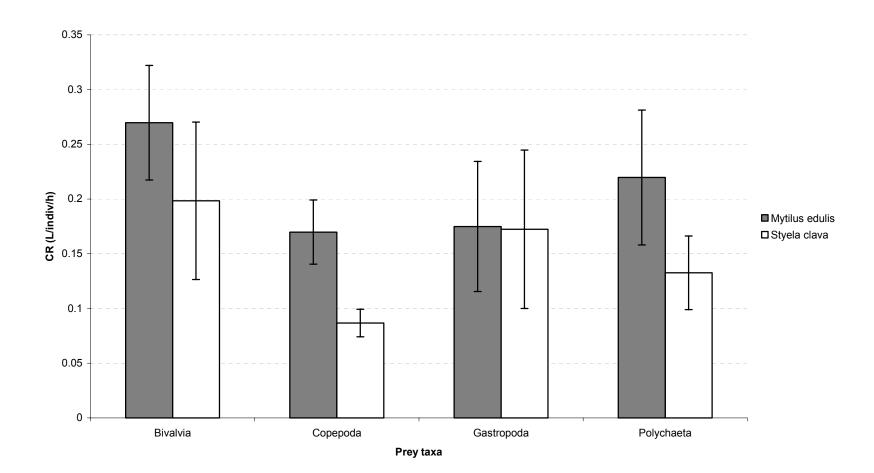


Figure 9. Clearance rates of different zooplankton taxa by *Mytilus edulis* (P=0.431) and *Styela clava* (P=0.290) in experiments carried out in June 2003. Error bars represent ± SE.