Spatial distribution of adult and juvenile softshell clams (*Mya arenaria*) in two tidally contrasted regimes in New Brunswick

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ABSTRACT

LeBlanc, S. and G. Miron. 2005. Spatial distribution of adult and juvenile softshell clams (*Mya arenaria*) in two tidally contrasted regimes in New Brunswick. Can. Tech. Rep. Fish. Aquat. Sci. Xxxx: vii + 21 p.

This study describes the distribution of the softshell clam (*Mya arenaria*) in two regions of New Brunswick that display strongly contrasted tidal regimes: the Bay of Fundy (strong tides) and the Northumberland Strait (weak tides). Clam beds were sampled at three different sites within each tidal region, using ten stations distributed along the intertidal axis. Within site hydrodynamics were indirectly studied using a plaster dissolution technique. Granulometry and organic matter analyses were also carried out. All sites, except Herring Cove and Red Head (Bay of Fundy), had a mean sand content of 93 % or more (all sampling stations confounded). Mean gravel contents at the latter sites were about 25 %. Organic matter contents were similar at all intertidal levels in the Northumberland Strait ranging between 1.2 and 2.4 %. Organic matter contents varied from 1.4 to 3.8 % in the Bay of Fundy, but were generally less important at mid intertidal level. All sites had greater plaster dissolution rates seaward, except for the Bouctouche and Cocagne sites (Northumberland Strait) which showed little differences between intertidal levels. Overall, our results showed that there was no difference in the distribution of softshell clams in relation to the studied tidal regimes. Distibution patterns varied between sites regardless of the tidal region. The Kouchibouguac site (Northumberland Strait) had more individuals at low intertidal level compared to the high intertidal level, the Bouctouche site displayed no difference between intertidal levels while the Cocagne site had more individuals at mid intertidal level. The St. Andrews site (Bay of Fundy) had more individuals in the high intertidal level compared to the lower intertidal level while the Red Head site showed no clear distribution pattern. These results suggest that local factors (e.g. small-scale hydrodynamics) are more important in regulating the population dynamics of softshell clams than the dominant regional tidal regime.

RÉSUMÉ

LeBlanc, S. and G. Miron. 2005. Spatial distribution of adult and juvenile softshell clams (*Mya arenaria*) in two tidally contrasted regimes in New Brunswick. Can. Tech. Rep. Fish. Aquat. Sci. Xxxx: vii + 21 p.

Cette étude décrit la distribution de la mye commune (*Mya arenaria*) dans deux régions du Nouveau-Brunswick ayant des régimes tidaux fortement contrastés: la baie de Fundy (fortes marées) et le détroit de Northumberland (faibles marées). Des bancs de myes furent échantillonnés à trois sites dans chacune des régions tidales en utilisant dix stations distribuées le long de l'axe intertidal. L'hydrodynamique de chaque site fut étudiée indirectement en utilisant une technique de dissolution de plâtre. Des analyses granulométriques et de matière organique ont également été effectuées. Tous les sites, à l'exception des sites de Herring Cove et de Red Head (baie de Fundy), avaient un contenu moyen de sable de plus de 93 % (toutes stations confondues). Ces derniers avaient un contenu en gravier d'environ 25 %. Le contenu en matière organique était semblable à tous les niveaux intertidaux dans le détroit de Northumberland, variant entre 1,2 et 2,4 %. Le contenu en matière organique dans la baie de Fundy oscillait entre 1,4 et 3,8 %, les stations aux niveaux intertidaux intermédiaires ayant les contenus les plus faibles. Tous les sites ont montré une dissolution de plâtre plus importante en bas de plage, sauf pour les sites de Bouctouche et de Cocagne (détroit de Northumberland) où peu de différences furent observées entre les stations. Dans l'ensemble, nos résultats ont montré qu'il n'y avait pas de différence dans la distribution des myes en relation avec les grands régimes tidaux étudiés. Les patrons de distribution variaient entre les sites peu importe la région tidale. Le site de Kouchibougac (détroit de Northumberland) avait plus d'individus en bas de plage qu'en haut de plage. Le site de Bouctouche n'a pas montré de différences significatives entre les niveaux tandis que le site de Cocagne avait plus d'individus en milieu de plage. Le site de St. Andrews (baie de Fundy) avait plus d'individus en haut de plage qu'en bas de plage alors que le site de Red Head ne montrait pas de patron spécifique de distribution. Ces résultats suggèrent que des facteurs locaux (e.g. l'hydrodynamique à petite échelle) sont plus importants dans la régulation de la dynamique des populations de la mye commune que le régime tidal dominant d'une région donnée.

INTRODUCTION

Many factors can affect the distribution and abundance of benthic species in intertidal communities (see reviews by Menge and Sutherland 1987, Underwood and Fairweather 1989, Underwood 2000). Predation, competition and recruitment processes represent the most common biotic parameters while nutrient availability, habitat structure, light, salinity and physical stress constitute the main abiotic ones (see review by Menge and Branch 2001). Because most invertebrates living in intertidal communities display a complex life history including a phase of larval dispersal in the water column (e.g. Thorson 1950, Scheltema 1986), hydrodynamic processes, which can occur at various scales, can be very important in shaping these communities.

Soft-bottom shores are three-dimensional habitats where sediments are more or less unstable compared to rocky shores. On the one hand, these types of habitat allow organisms to burrow into the sediments. On the other hand, sediments may be eroded by currents, turbulences and waves. Endobenthic organisms may then be vulnerable to such physical stress, be resuspended in the water column and subsequently transported to other sites. Post-settlement dispersal, for instance, has been observed in many bivalve species (Baggerman 1953, Butman 1987, Beukema and de Vlas 1989, Armonies 1992, 1994a, b, Günther 1992a, 1992b, Cummings et al. 1995, Commito et al. 1995a, 1995b, Roegner et al. 1995, Jaklin and Günther 1996, Hewitt et al. 1997). This transport can be passive through bedload transport (Emerson and Grant 1991, Commito et al. 1995b, Turner et al. 1997), or active through byssus-drifting (Sigurdsson et al. 1976, Beukema and de Vlas 1989, Armonies 1992, Cummings et al. 1993).

The softshell clam *Mya arenaria* is an important species found in intertidal soft-bottom communities on the eastern coast of Canada. In addition to having an ecological importance, softshell clams are also economically important (Department of Fisheries and Oceans 2001). Studies from various locations within its geographical range have shown that their distribution is often patchy (Evans and Tallmark 1977, Brousseau 1978, Robert 1981, Goshima 1982, Witherspoon 1982, 1984, Möller and Rosenberg 1983, Emerson et al. 1988, Roseberry et al. 1991, Strasser et al. 1999). This has been related in part to pre-settlement processes such as substrate choice by settling larvae (Smidt 1951, Kühl 1981, Reise 1987, Brousseau and Baglivo 1988, Beal 1989, Günther 1992b). Aggregation of individuals can also be the result of spat concentration induced by hydrodynamic forces (Newell and Hidu 1986). Post-settlement processes are also known to explain patchiness. For instance, modification of distribution patterns by bedload transport in recent settlers and/or juveniles of softshell clams has been demonstrated by Emerson and Grant (1991), Roegner et al. (1995), Roegner (1996), Dunn et al. (1999), Hunt (2004a, 2004b) and St-Onge and Miron (unpublished data).

Currents generated by tidal regimes may act as a driving force in shaping the distribution pattern of benthic species in the intertidal zone. As this force differs from one place to another, it could thus influence the selection of habitat, larval recruitment and ultimately population dynamics. The present study describes the intertidal distribution of the softshell clam in various study sites within two tidally contrasted regions, the Bay of Fundy (strong tides) and the Northumberland Strait (weak tides). Results will help to cast the general framework of a larger study that will investigate the influence of tidal currents on larval recruitment and underline, or not, if similarity exists between larval and adult distributions of softshell clams in the intertidal zone.

MATERIALS AND METHODS

Study sites

The study was carried out off the New Brunswick coasts of the Bay of Fundy and Northumberland Strait in the summer of 2002. The Bay of Fundy is characterized by lunar semi-diurnal tides with a period of 12.4 hours. Mean tidal height is 7.0 m, reaching 16.0 m in the Minas Basin. Because of a large tidal amplitude that creates intense mixing of water, very little ice is formed in the Bay of Fundy, except on coasts, small bays and in estuaries (Trites and Garrett 1983). The Northumberland Strait has a complicated tidal regime, with diurnal tides at its western extremity and semi-diurnal tides at its eastern extremity. The amplitude varies between 1.2 to 1.8 m (Environment Canada 2001). The Northumberland Strait is also much shallower than the Bay of Fundy. Therefore, it becomes much warmer in summertime, and freezes over in wintertime.

Sampling was conducted on 8 July in Northumberland Strait and on 15 July in the Bay of Fundy. Each sampling day was carried out during a spring tide. Three sites were chosen in each tidal region in order to estimate the variability of the softshell clam's population structure (Fig. 1). Sites were chosen based on the occurrence of a fair population and accessibility, while trying to minimize physical differences (e.g. type of sediments). In the Bay of Fundy, the sampling sites were Blockhouse beach (near St Andrews), Red Head (near St John) and Herring Cove (in Fundy National Park). Blockhouse beach is a sheltered site at the mouth of the St. Croix River estuary that opens on to the Passamaquody Bay. This site had the largest intertidal zone of all our sites, with a distance of 500 m between the first and last sampling stations. The slope of the beach was about 0.90 %. This site was characterized mostly by coarse sand. The Red Head site is in a small cove on the South side of St John Harbour. It is a very heterogeneous beach, with mud patches alternating with rocky segments covered with *Ascophyllum* sp. and *Fucus* spp. The slope was about 1.50 % with an intertidal distance of 200 meters. The Herring Cove site is a beach directly open to the Bay of Fundy. The slope was 2.50 %, with an intertidal zone of 200 meters. The sediment was much coarser on this site compared to the others.

In the Northumberland Strait, the sites were Ryans beach (in Kouchibouguac National Park), Bouctouche and Côte d'Or (near Cocagne). Ryans beach is a site with a narrow intertidal zone of 45 meters. It is located at the mouth of the Kouchibouguac river, where the current is quite strong (personal observation). The slope of this site was less than 0.30 %. Bouctouche is a sheltered site located behind a 12 km sand dune. The intertidal zone is 100 meters wide, with a slope of 0.24 % between our highest and lowest sampling stations. This site has a strong fishing pressure (personal observation). Côte d'Or is located in the Bay of Cocagne, next to a small brook. The intertidal zone of this site was 125 meters wide, with a slope of 0.40 % between the high and low intertidal levels. All three sites in the Northumberland Strait had high sand contents. Of all the sites, only Red Head and Bouctouche sites were officially open to clam fishing, with Bouctouche being the only site with active digging.

Experimental design

Each site had ten sampling levels within the intertidal zone (1: high intertidal, 10: low intertidal). The intertidal levels for the Bay of Fundy were set as follow (height above the low water line at low tide): station 1: 4.00 m, station 2: 3.60 m, station 3: 3.15 m, station 4: 2.70 m, station 5: 2.25 m, station 6: 1.80 m, station 7: 1.35 m, station 8: 0.90 m, station 9: 0.45 m, station 10: 0.00 m The levels used for the Northumberland Strait were: station 1: 0.30 m, station 2: 0.27 m, station 3: 0.23 m, station 4: 0.20 m, station 5: 0.17 m, station 6: 0.13 m, station 7: 0.10 m, station 8: 0.07 m, station 9: 0.03 m, station 10: 0.00 m.

There were three replicates at each level, with a total of 180 samples: 10 intertidal levels X 3 replicates X 3 sites X 2 regions. At each station, a sample of 40 X 40 cm (20 cm deep) was collected with a trowel. The samples were sieved through a 1 mm mesh screen and sorted in the laboratory. Only softshell clams were collected. Shell length was measured and individuals grouped within three size-classes. The juvenile size-class of <35.0 mm was the same as that used by Witherspoon (1982, 1984) in Nova Scotia. Adults were divided in two size-classes: 35.0-49.9 mm and ≥50.0 mm, the latter being the minimum legal size for harvesting clams in New Brunswick (Department of Fisheries and Oceans 2001).

A single sample of sediment (10 cm deep) was collected with a trowel at each sampling level to determine organic matter, mud (<63 µm), sand (63 µm-2 mm) and gravel (>2 mm) contents. Samples (n=60) were deep-frozen to ensure preservation of organic matter and later analyzed using Rivière's (1977) technique. A hydrodynamic profile of each site was determined using cylinders made from plaster of Paris. These cylinders measured 3 cm in diameter and 10 cm in length. Cylinders were placed at each sampling station for a period of 24 hours. Flow was thus estimated indirectly by measuring weight loss of the plaster (Cusson and Bourget 1997). The cylinders were dried at a temperature of 40ºC during 48 hours and weighed (±0.01 g), both before and after their use in the field. The difference in weight allowed us to estimate the relative speed of current at each station.

Data analysis

Nested ANOVAs were used on plaster dissolution rates. The factor Region had two levels (Northumberland Strait, Bay of Fundy) and was a fixed factor. Three random sites were nested within each level of the factor Region. The factor Intertidal level was fixed and had ten levels. Nested ANOVAs were also used for each size-class of individuals to examine the effects of region and intertidal level on juvenile and adult densities. The significance level was fixed at 0.05. A Ln(X+1) transformation was used on dependant variables except on the plaster dissolution rates. Though transformations were carried out, homoscedasticity requirements were not always met. However, according to Underwood (1997), balanced experiments with a large sample size in each treatment, such as in the present study should not cause any problems for the interpretation of an analysis with heterogeneous variances.

RESULTS

Sediment characteristics

In the Northumberland Strait, all sites were dominated by a high percentage of sands at all intertidal levels (Fig. 2). The Bouctouche and Ryans beach sites had sand contents of 98.0 % or more. In the Côte d'Or site, there was also some gravel, mostly at stations 1 and 2 (less than 10.0 %). In the Bay of Fundy, the Blockhouse beach site was different from the ones in Red Head and Herring Cove. All intertidal levels consisted mostly of sand, with small amounts of gravel in stations 1, 2 and 3 (less than 5.0 %). There was more gravel in the Red Head and Herring Cove sites (means of about 25.0 % in each site, all sampling stations confounded) than in the Blockhouse beach site (mean of 1.5 %, all sampling stations confounded). The Red Head site was the most heterogeneous of the three sites, with varying amounts of sand and gravel at each intertidal level. This was also the site with the highest amounts of mud, found mostly in the high intertidal level (stations 1, 2, 4 and 5). The Herring Cove site showed less variation between the intertidal levels.

In the Northumberland Strait, all intertidal levels showed similar percentages of organic matter, ranging from 1.2 to 2.4 % (Fig. 3). There were no important differences between sites. In the Bay of Fundy, both the Blockhouse beach and Red Head sites generally had more organic matter than the Herring Cove site. At the Red Head site, the mid intertidal levels (stations 4 to 7) had lower percentages of organic matter than the high and low intertidal levels. For instance, stations 1 and 10 had organic contents of 3.4 %, compared to mid intertidal stations which were all under 2.8 % (stations 4 to 6). Such a trend was not so apparent at the other sites, where the organic content was higher in the high intertidal level. The Blockhouse beach site had the highest percentages of organic matter at stations 1 and 2. The Herring Cove site had low percentages of organic matter overall (mean of 2.1 % all stations confounded), with the highest percentage at station 1 (3.4 %).

Plaster dissolution

The nested ANOVA carried out on plaster dissolution rates failed to show any effect from the regional tidal regime (Table 1). It, however, showed a significant effect from the Region X Level interaction. In general, there was more dissolution seaward in the Bay of Fundy, while the Northumberland Strait did not show a lot of variation between intertidal levels for both Bouctouche and Côte d'Or sites (Fig.4). The Ryans beach site showed higher rates of dissolution at mid and low levels. This site also had higher dissolution rates in general compared to other sites. Important currents caused by the nearby Kouchibouguac river were possibly responsible for the latter.

Adults and juveniles

Results from the nested ANOVA for the distribution of softshell clams showed a significant effect from the Level X Site (Region) interaction for all size-classes (Table 2). There was also an effect of Region X Level for the size-class <35.0 mm. Except for the Herring Cove site, where softshell clams were absent, the <35.0 mm size-class was the most abundant (Figs. 5 and 6). In the Ryans beach site (Fig. 5), this size-class was located at mid and low levels. The two adult size-classes were also more important seaward. This contrasted with the Blockhouse beach site (Bay of Fundy), which had members of the <35.0 mm size-class located mostly in the high and mid-intertidal zones between stations 2 to 5 (Fig. 6). The 35.0-49.9 mm and ≥50.0 mm individuals were present only in the high intertidal levels (stations 1, 2 and 3) in very low densities. The Red Head site had no clear pattern for the softshell clam distribution, maybe reflecting the patchiness of adequate substrates at this beach (Fig. 6). The Côte d'Or site had <35.0 mm individuals at all levels, but concentrated in the mid intertidal zone (Fig. 5). The distribution of the 35.0-49.9 mm individuals did not show any differences between intertidal levels while the ≥50.0 mm individuals were practically absent. The Bouctouche site showed no important differences between the intertidal levels. The two adult size-classes were almost absent from this site.

DISCUSSION

The objective of this study was to underline that contrasting tidal regimes could have a generally marked effect on the distribution of juvenile and adult *Mya arenaria*. Overall, our results showed that there was no significant effect of the regional tidal regime on the distribution of softshell clams along the intertidal axis. All sites within each tidal region displayed different distribution patterns, suggesting that local factors may be important in regulating population dynamics than the dominant tidal regime. The different patterns of distribution could be in part explained by the physical differences observed in our sites including small-scale hydrodynamics.

Softshell clam populations of the Bay of Fundy

All sites within the Bay of Fundy were quite different from each other. The Herring Cove site was apparently an unsuitable site for clam beds although some adult individuals were found during preliminary surveys (personal preliminary observations, park warden). Being directly open onto the Bay of Fundy, this site probably had the highest wave energy of all the studied sites. This is outlined by the fact that this site had the highest gravel percentage and slope of all the studied sites. According to Pfitzenmeyer and Drobeck (1967), softshell clams will have difficulty burrowing in sediments larger than 0.5 mm.

The Red Head site showed the patchiest distribution of softshell clams. This could be related to the heterogeneity of the beach in terms of granulometry. Suitable substrates were not available throughout the site because many areas were covered with gravel, cobbles and boulders. Lavoie (1967) noted that gravel and pebbles are not favourable grounds to support important softshell clam populations.

The Blockhouse beach site was different from the other two sites. The site is fairly protected, surrounded by land to one side and a natural jetty to the other side, which is submerged during high tide. Wave energy is also not very strong in Passamaquody Bay (Steele 1983). This would explain the lower dissolution rate of plaster cylinders observed on this site, compared to the Herring Cove and Red Head sites. Chandler et al. (2001) found, for the same beach, that settlement took place in the low intertidal zone, and that early juveniles may moved up the beach. Hydrodynamic forces can cause the passive transport of juveniles through bedload transport (Emerson and Grant 1991, Roegner et al. 1995, Roegner 1996, Dunn et al. 1999, Hunt 2004a, 2004b). St-Onge and Miron (unpublished data) showed in the laboratory that juveniles softshell clams < 5 mm were highly vulnerable to resuspension, beginning at a speed of 16 cm s^{-1} with almost total resuspension at speeds of 29 and 35 cm s^{-1}. Highest resuspension rates were associated with the sandy sediments while the lowest rates were associated with muddy sediments. Hunt (unpublished data) observed a tight relationship between the volume of sediment and the proportion of softshell clams eroded. The Blockhouse site has a maximum tidal range of 8.3 m (Trites and Garrett 1983), and according to personal observations by Robinson (in Chandler et al. 2001), the wind can create 1 m high waves during a flood tide. Such hydrodynamic forces could thus cause some juvenile transport. This could explain why most of the juveniles observed in this study were found at the high intertidal level. Predator–prey relationships can also affect resuspension of individuals. According to Hunt (2004a), predators such as the shrimp *Crangon septemspinosa* can increase the rate of transport of juvenile softshell clams by disturbing the sediment. This was also demonstrated with the non-predatory snail *Ilyanassa obsoleta* (Mullineaux et al. 1999). The common periwinkle (*Littorina littorea*) found on this beach might also have an effect on softshell clam resuspension as well.

Softshell clams are not completely subject to passive erosion through sediment transport, but can also display active behaviour such as burrowing which allow them to find a refuge from water flow (Hunt 2004b). Certain studies have also demonstrated that bivalves may disperse actively using their byssal threads (Sigurdsson et al. 1976, Cummings et al. 1993). Armonies (1994b), for instance, showed that softshell clams were found regularly, at low abundance, in nets designed for byssal drifting. However, Hunt (2004b) observed that softshell clams may have a greater propensity to anchor themselves with byssal threads.

The concentration of juveniles at high intertidal level could also be due to a lower predation pressure. Juveniles are vulnerable to predation from green crabs (Glude 1955, Elner 1981, Miron et al. 2002, Floyd and Williams, 2004) and fish such as winter flounder (Medcof and MacPhail 1955) and mummichog (Kelso 1979). Softshell clams are more at risk to predation from crabs at low intertidal level (Zaklan and Ydenberg 1997). Also because of longer submersion times at low intertidal level, predation from fish might be more important in this area (Bertness 1999). Green crabs were routinely seen at the Blockhouse beach site.

The Blockhouse beach site displayed important mats of *Enteromorpha* sp. in the lower parts of the high intertidal level down to the mid intertidal level. High quantities of juveniles, as small as 2 mm, were observed in these mats (personal observation). Vadas and Beal (1987) also reported such findings in Maine. This could explain the important number of juveniles found at stations 2, 3, 4 and 5. The patchiness of the algal cover could also explain the important variability observed at these intertidal levels. However, it is not known if juveniles found in these mats survive.

Softshell clam populations of the Northumberland Strait

In the Northumberland Strait, the physical differences between the sites were not as marked as in the Bay of Fundy. The Ryans beach site was located at the mouth of the Kouchibouguac river. Water currents were strong and parallel to the shore. Such a current could inhibit the recruitment of softshell clams since juveniles living close to the sediment surface can be eroded and transported downshore (Emerson and Grant 1991, Hunt and Mullineaux 2002). Yet clam beds were quite dense in the lower parts of the beach. This could be explained by the presence of seagrass beds (*Zostera* sp.) in the low intertidal level, which can reduce current velocities and enhance larval recruitment (Eckman 1979, 1983).

Because of reduced currents, seagrass beds can also enhance the stability of surface sediments. This would allow juvenile individuals to burrow in order to avoid currents (Roegner et al. 1995). Zühlke et al. (1998) also suggest that juveniles may have the capacity to attach to objects on the seabed with their byssus. Yet the presence of patchy seagrass cannot fully explain the distribution of softshell clams on this site because it was only located at stations 9 and 10. More precise data on the water flow would be required in order to determine if postlarval and juvenile transport is important at this site.

The Bouctouche site has very strong fishing pressure as it is easily accessed by locals and tourists. Our results showed that there were practically no adults ≥50 mm at this site. We also observed the presence of the milky ribbon worm (*Cerebratulus lacteus*), a very efficient predator of softshell clams (Rowell and Woo 1990, Bourque et al. 2001, 2002). The fact that juveniles were equally distributed between all the sampled stations could be explained partially by the relatively low currents on this site, being protected by the Dune of Bouctouche. Hydrodynamic forces may not be important enough for juvenile transport.

For the Côte d'Or site, it is unclear if the discharge of a small brook next to the site had any effect on the softshell clam distribution, although it is probably not likely because of its fairly weak currents. Even though this site has been closed to harvesting since 1965 (Sirois, personal communication), there were very few adults. This may indicate that recruitment is very poor at this site.

CONCLUSION

The present study did not show any consistent patterns in the distribution of juvenile and adult of the softshell clam *Mya arenaria* in relation to both tidal regions. In soft-bottom environments, there is more and more evidence of post-larval and juvenile movement in bivalve species (see Introduction section). This movement can be site specific. For example, Beal and Fegley (1996) have done an extensive study on the recruitment of softshell clams in Maine. They found site-specific differences in migration of one-year olds, indicating that the nature of juvenile migration differs among habitats and locations. Günther (1992b) also found similar results in settlement studies carried out on the same species in the Wadden Sea. She suggested that settlement is a process strongly determined by local hydrodynamics and topographic conditions, and that the importance in dispersal of postlarval stages varies with species and the habitat.

Few studies have taken into account all three components of the recruitment process simultaneously in soft-bottom communities: supply of larvae from the water column, initial larval settlement and juvenile abundance. It is important to further study the tight relationship between these events and investigate if the intertidal distribution of earlier life stages, including veliger larvae, pediveliger larvae and juveniles, are similar within a given site and if they vary in relation to large scale tidal regimes.

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REFERENCES

Armonies, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Mar. Ecol. Prog. Ser. 83: 197-206.

Armonies, W. 1994a. Turnover of postlarval bivalves in sediments of tidal flats in Königshafen (German Wadden Sea). Helgol. Meeresunters. 48: 291-297.

Armonies, W. 1994b. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgol. Meeresunters. 48: 299-320.

Baggerman, B. 1953. Spatfall and transport of *Cardium edule.* L. Arch. Néerl. Zool. 10: 315-342.

Beal, B. F. 1989. Biotic and abiotic factors influencing the recruitment of soft-shell clams, *Mya arenaria* L. to soft-bottom intertidal areas in Downeast Maine, USA. J. Shellfish Res. 9: 455.

Beal, B. F. and S. R. Fegley. 1996. Biotic and abiotic factors influencing recruitment and subsequent mortality of soft-shell clams in Eastern Maine and Southwestern Maine. Final Report NA46FD0328, National Marine Fisheries Service, Gloucester, MA.

Bertness, M. D. 1999. The Ecology of Atlantic Shorelines. Sinauer Associates, Sunderland, MA.

Beukema, J. J. and J. de Vlas. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. Mar. Ecol. Prog. Ser. 52: 293-300.

Bourque, D., G. Miron and T. Landry. 2001. Predation on soft-shell clams (*Mya arenaria*) by the nemertan *Cerebratulus lacteus* in Atlantic Canada: implications for control measures. Hydrobiologia 456: 33-44.

Bourque, D., G. Miron and T. Landry. 2002. Predator-prey relationship between the nemertean *Cerebratulus lacteus* and the soft-shell clam *Mya arenaria*: surface exploration activities and qualitative observations on feeding behaviour. Can. J. Zool. 80: 1204-1211.

Brousseau, D. J. 1978. Spawning cycle, fecundity and recruitment in a population of soft-shell clam, *Mya arenaria* from Cape Ann, Massachusetts. Fish. Bull. 76: 155-166.

Brousseau, D. J. and J. A. Baglivo. 1988. Life tables for two field populations of soft-shell clam, *Mya arenaria*, (Mollusca: Pelecypoda) from Long Island Sound. Fish. Bull. 86: 567-579.

Butman, C. A. 1987. Larval settlement and soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr. Mar. Biol. Annu. Rev. 25: 113-165.

Canadian Ice Service. 2001. Sea ice climatic atlas, East Coast of Canada, 1971-2000. Minister of Public Works and Government Services of Canada.

Chandler, R. A., S. M. C. Robinson and J. D. Marin. 2001. Collection of soft-shell clam (*Mya arenaria* L.) spat with artificial substrates. Can. Tech. Rep. Fish. Aquat. Sci. 2390.

Commito, J. A., C. A. Currier, L. R. Kane, K. A. Reinsel and I. M. Ulm. 1995a. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. Ecol. Monogr. 65: 1-20.

Commito, J. A., S. F. Thrush, R. D. Pridmore, J. E. Hewitt and V. J. Cummings. 1995b. Dispersal dynamics in a wind-driven benthic system. Limnol. Oceanogr. 40: 1513-1518.

Cummings, V. J., R. D. Pridmore, S. F. Thrush and J. E. Hewitt. 1993. Emergence and floating behaviours of post-settlement juveniles of *Macoma liliana* (Bivalvia: Tellinacea). Mar. Behav. Physiol. 24: 25-32.

Cummings, V. J., R. D. Pridmore, S. F. Thrush and J. E. Hewitt. 1995. Post-settlement movement by intertidal benthic macroinvertebrates: do common New Zealand species drift in the water column ? NZ. J. Mar. Freshw. Res. 29: 59-67.

Cusson, M. and E. Bourget. 1997. The influence of topographic heterogeneity and spatial scales on the structure of the neighboring intertidal endobenthic macrofaunal community. Mar. Ecol. Prog. Ser. 150: 181-193.

Department of Fisheries and Oceans. 2001. Integrated management plan clam fishery: Eastern New Brunswick Area Gulf Region 2001-2006. Tracadie-Sheila, NB.

Dunn, R., L. S. Mullineaux and S. W. Mills. 1999. Resuspension of postlarval soft-soft shell clam *Mya arenaria* through disturbance by the mud snail *Ilyanassa obsoleta*. Mar. Ecol. Prog. Ser. 180: 223-232.

Eckman, J. E. 1979. Small-scale patterns and processes in a soft-substratum intertidal community. J. Mar. Res. 37: 437-457.

Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 18: 241-257.

Elner, R. W. 1981. Diet of green crab *Carcinus maenas* (L.) flora Port Hebert, southwestern Nova Scotia. J. Shellfish. Res. 1: 89-94.

Emerson, C. W., T. E. Minchinton and J. Grant. 1988. Population structure, biomass, and respiration of *Mya arenaria* L. on temperate sandflat. J. Exp. Mar. Biol. Ecol. 115: 99-111.

Emerson, C. W. and J. Grant. 1991. The control of soft-shell clam (*Mya arenaria*) recruitment on intertidal sanflats bedload sediment transport. Limnol. Oceanogr. 36: 1288-1300.

Evans, S. and B. Tallmark. 1977. Growth and biomass of bivalve molluscs on a shallow, sandy bottom in Gullmar Fjord (Sweden). Zoon. 5: 33-38.

Floyd, T. and J. Williams. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the southern Gulf of St. Lawrence. J Shellfish. Res. 23: 457-462.

Glude, J. B. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans. Am. Fish. Soc. 14: 13-26.

Goshima, S. 1982. Population dynamics of the soft clam, *Mya arenaria* L., with special reference to its life history pattern. Publ. Amakusa Mar. Biol. Lab. Kyushu Univ. 6: 119-165.

Günther, C. P. 1992. Settlement and recruitment of *Mya arenaria* L. in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 159: 203-215.

Hewitt, J. E., R.D. Pridmore, S. F. Thrush and V. J. Cummings. 1997. Assessing the short-term stability of spatial patterns of macrobenthos in a dynamic estuarine system. Limnol. Oceanogr. 42: 282-288.

Hunt, H. L. 2004a. Effects of epibenthic predators in flow: transport and mortality of juvenile soft shell clams (*Mya arenaria*). Mar. Ecol. Prog. Ser. 279: 151-160.

Hunt, H. L. 2004b. Transport of juvenile clam: effects of species and sediment grain size. J. Exp. Mar. Biol. Ecol. 312: 271-284.

Hunt, H. L. and L. S. Mullineaux. 2002. The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). Limnol. Oceanogr. 47: 151-164.

Jaklin, S. and C. P. Günther. 1996. Macrobenthic driftfauna of the Gröninger Plate. Senckenb. Marit. 26: 127-134.

Kelso, W. E. 1979. Predation of soft-shell clams, *Mya arenaria*, by the common mummichog, *Fundulus heteroclitus*. Estuaries 4: 249-59.

Kühl, H. 1981. The sand gaper *Mya arenaria*. *In* Invertebrates of the Wadden Sea. Final report of the section 'Marine Zoology' of the Wadden Sea Working Group. Edited by N. Dankers, H. Kühl and W. J. Wolff. pp. 118-119.

Lavoie, R. 1967. Inventaire des myes communes (*Mya arenaria* L.) dans l'estuaire du St. Laurent. St. Biol. Mar. Grande-Rivière. Rapp. Ann. 1966.

Medcof, J. C. and J. S. MacPhail. 1955. Survey of bar clam resources of the Maritime Provinces. Fish. Res Board Can. Bull. 169: 1-192.

Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130: 730-757.

Menge, B. A. and G. M. Branch. 2001. Rocky Intertidal Communities. *In* Marine Community Ecology. Edited by M. D. Bertness, S. D. Gaines and M. E. Hay. Sinauer Associates, Sunderland, MA. pp. 221-251.

Miron, G., T. Landry and N. MacNair. 2002. Predation potential by various epibenthic organisms on commercial bivalves species in Prince Edward Island: preliminary results. Can. Tech. Rep. Fish. Aquat. Sci. 2392.

Möller, P. and K. Rosenberg. 1983. Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine waters, Western Sweden. Ophelia 22: 33-35.

Mullineaux, L. S., R. Dunn, S. W. Mills, H. L. Hunt and L. K. Gulmann. 1999. Biological influences on transport of postlarval soft-shell clams (*Mya arenaria*). *In* Coastal Ocean Processes Symposium: a Tribute to William D. Grant. Woods Hole Oceanog. Inst. Tech. Rept. WHOI-99-04, pp. 155-162.

Newell, C. R. and H. Hidu. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): soft-shell clam. Biological Report 82. Fish and Wildlife Service.

Pfitzenmeyer, H. T. and K. G. Drobeck. 1967. Some factors influencing reburrowing activity of soft-shell clam, *Mya arenaria*. Chesapeake Sc. 8: 193-199.

Reise, K. 1987. Distribution and abundance of small and juvenile macrofauna on the tidal flats in the Frisian Wadden Sea. *In* Proceedings of the 5th international Wadden Sea Symposium. Edited by S. Tougard and S. asbirk. National Forest Nature Agency and Museum and Fishery and Shipping, Esbjerg. pp. 7-25.

Rivière, A. 1977. Méthodes granulométriques: Techniques et interprétations. Masson, Paris.

Robert, G. 1981. Stock assessment of soft-shell clam in open shellfish growing areas of Prince Edward Island. DFO, Halifax.

Roegner, G. C. 1996. Hydrodynamic factors affecting the recruitment of bivalve molluscs in a tidally dominated estuary. Thesis (Ph. D.) Dalhousie University, Halifax.

Roegner, G. C., C. Andre, M. Lindegarth, J. E. Eckman and J. Grant. 1995. Transport of recently settled soft-shell clams (*Mya arenaria* L.) in laboratory flume flow. J. Exp. Mar. Biol. Ecol. 187: 12-26.

Roseberry, L., B. Vincent and C. Lemaire. 1991. Croissance et reproduction de *Mya arenaria* dans la zone intertidale de l'estuaire du Saint-Laurent. Can. J. Zool. 69: 724-732.

Rowell, T. W. and P. Woo. 1990. Predation by the nemertan worm, *Cerebratulus lacteus* Verrill, on the soft-shell clam, *Mya arenaria* Linneaus, 1758, and its apparent role in the destruction of a clam flat. J. Shellfish Res. 9: 291-297.

Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull. Mar. Sci. 39: 290-322.

Smidt, E. L. B. 1951. Animal production in the Danish Wadden Sea. Medd. Dan. Fisk. Havunders. (Ser Fiskeri) 11: 1-51.

Sigurdsson, J. B., C. W. Titman and P. A. Davies. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. Nature 262:386-387.

Steele, D. 1983. Coarse sedimentary shores. *In* Marine and Coastal Systems of the Quoddy Region, New Brunswick. Edited by M. L. H. Thomas. Can. Spec. Publ. Fish. Aquat. Sci. 64. pp. 75-88.

Strasser, M., M. Walensky and K. Reise. 1999. Juvenile-adult distribution of the bivalve *Mya arenaria* in the Wadden Sea: why are there so few year classes ? Helgol. Mar. Res. 53: 45-55.

Thorson, G. 1950. Reproduction and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1-45.

Trites, R. W. and C. J. R. Garrett. 1983. Physical oceanography. *In* Marine and Coastal Systems of the Quoddy Region, New Brunswick. Edited by M. L. H. Thomas. Can. Spec. Publ. Fish. Aquat. Sci. 64. pp. 9-35.

Turner, S. J., J. Grant, R. D. Pridmore, J. E. Hewitt, M. R. Wilkinson, T. M. Hume and D. J. Morrisey. 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: does infaunal density matter? J. Exp. Mar. Biol. Ecol. 216: 51-75.

Underwood, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press.

Underwood, A. J. 2000. Experimental ecology of rocky intertidal habitats: what are we learning ? J. Exp. Mar. Biol. Ecol. 250: 51-76.

Underwood, A. J. and P. G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. Trends Ecol. Evol. 4: 16-20.

Vadas, R. L. and B. Beal. 1987. Green algal ropes: A novel estuarine phenomenon in the Gulf of Maine. Estuaries 10: 171-176.

Witherspoon, N. B. 1982. Population surveys of the soft-shell clam (*Mya arenaria*) in selected estuaries on the eastern shore of Nova Scotia, 1981. Estuarine and Inland Fisheries. Nova Scotia Department of Fisheries.

Witherspoon, N. B. 1984. Commercial soft-shell clam (*Mya arenaria*) resource on the North shore of the Minas Bassin, 1982. Estuarine and Inland Fisheries. Nova Scotia Department of Fisheries.

Zaklan, S. D. and R. Ydengerg. 1997. The body size-burial relationship in the infaunal clam *Mya arenaira.* J. Exp. Mar. Biol. Ecol. 215: 1-17.

Zühlke, R., D. Blome, H. Bernem and S. Dittman. 1998. Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. Senckenb. Marit. 29: 131-138.

Table 1. Nested ANOVA analysis examining the effect of region, site and intertidal level on plaster dissolution rates.

Source of variation	SS	df	MS	F	p
Region	12.73	1	12.73	0.03	0.875
Site (Region)	1800.43	4	450.11	22.9	<0.001
Level	1254.81	9	139.42	7.1	<0.001
Region X Level	431.94	9	47.99	2.4	0.028
Level X Site (Region)	707.01	36	19.64	1.3	0.135
Error	1784.42	120	14.87		
Total	5991.34	179			

Table 2. Nested ANOVA analyses examining the effect of region, site and intertidal level on the density of three size classes of softshell clams. A Ln(X+1) transformation was applied to all data. The Herring Cove site was omitted because of the absence of clams.

Size classes	Source of variation	SS	df	MS	F	p
<35.0 mm	Region	112.5	1	112.5	5.76	0.074
	Site (Region)	78.05	4	19.51	16.26	0.000
	Level	18.29	9	2.03	1.69	0.127
	Region X Level	28.85	9	3.21	2.67	0.017
	Level X Site (Region)	43.20	36	1.2	1.71	0.017
	Error	84.20	120	0.7		
	Total	365.09	179			
35.0-49.9 mm	Region	2.18	1	2.18	0.15	0.714
	Site (Region)	56.55	4	14.14	15.89	0.000
	Level	3.89	9	0.43	0.49	0.875
	Region X Level	12.91	9	1.43	1.61	0.149
	Level X Site (Region)	32.03	36	0.890	2.04	0.002
	Error	52.29	120	0.436		
	Total	159.85	179			
≥ 50.0 mm	Region	0.04	1	0.04	0.02	0.909
	Site (Region)	10.04	4	2.50	5.33	0.002
	Level	1.80	9	0.20	0.43	0.913
	Region X Level	2.78	9	0.31	0.66	0.741
	Level X Site (Region)	16.96	36	0.47	2.07	0.002
	Error	27.38	120	0.23		
	Total	59.00	179			

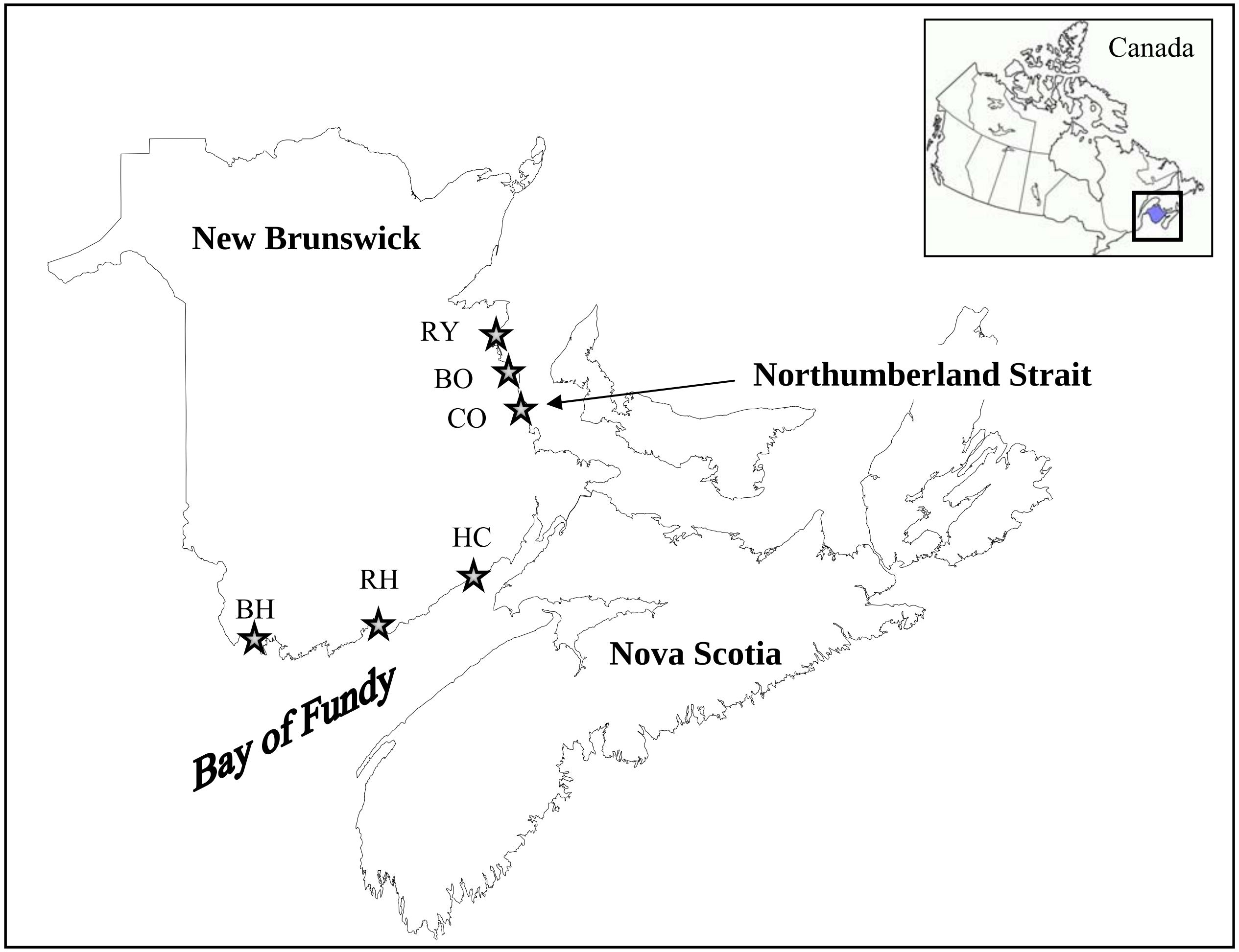

Figure 1. Location of sampling sites in the Northumberland Strait (RY=Ryans beach, BO=Bouctouche, CO=Côte d'Or) and the Bay of Fundy (BH=Blockhouse beach, RH=Red Head, HC=Herring Cove).

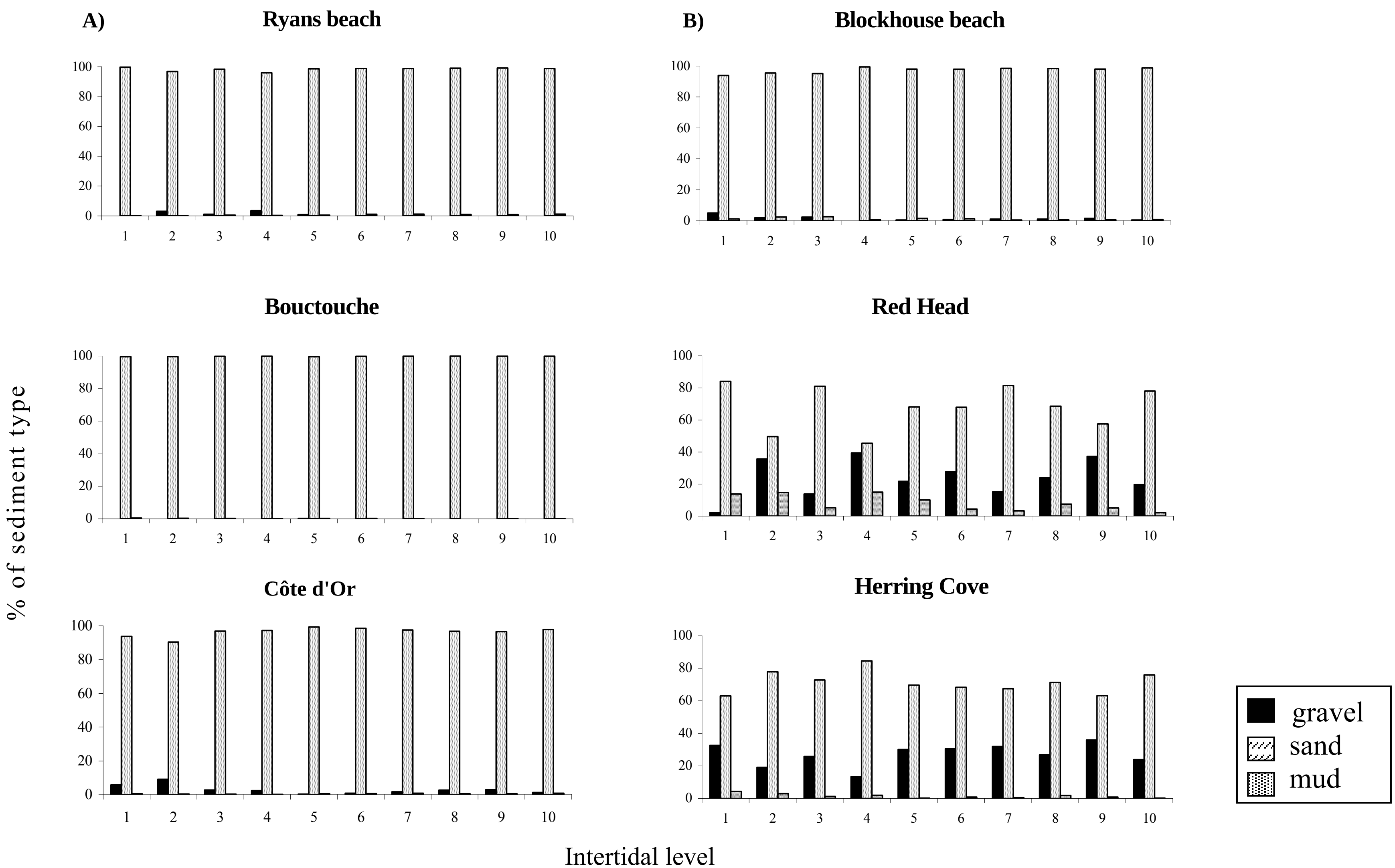

Figure 2. . Proportion (%) of gravel (> 2 mm), sand (63 µm-2mm) and mud (<63µm) along the intertidal axis (1=high intertidal, 10=low intertidal) for sites within the A) Northumberland Strait and B) Bay of Fundy.

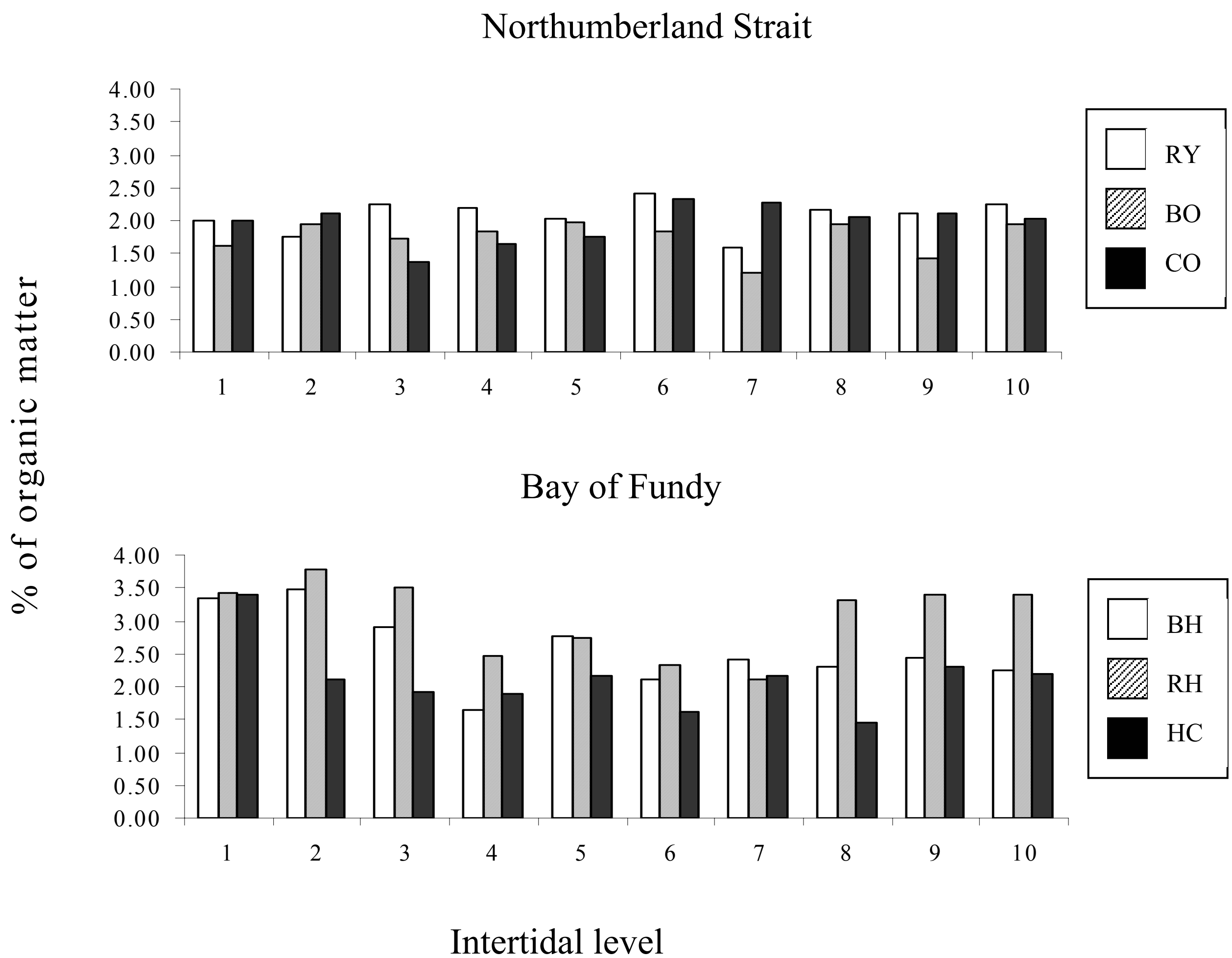

Figure 3. Proportion (%) of organic matter along the intertidal axis (1=high intertidal, 10=low intertidal) for sites within the Northumberland Strait (RY=Ryans beach, BO=Bouctouche, CO=Côte d'Or) and the Bay of Fundy (BH=Blockhouse beach, RH=Red Head, HC=Herring Cove).

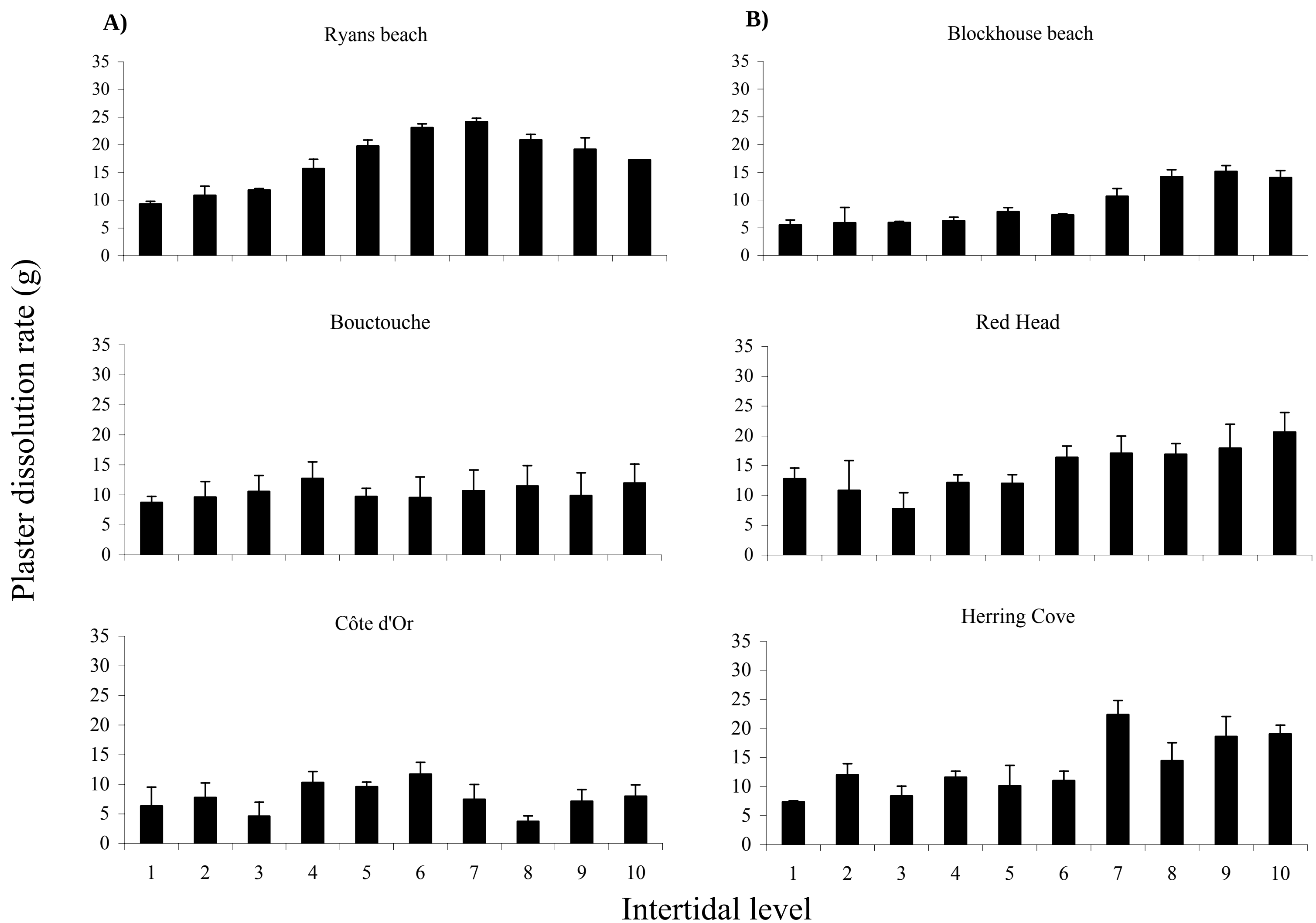

Figure 4. Plaster dissolution (mean ± SE, n=3) in g per 24 hours of tidal exposure along the intertidal axis (1=high intertidal, 10=low intertidal) for the A) Northumberland Strait (8th of July 2002) and B) Bay of Fundy (15th of July 2002).

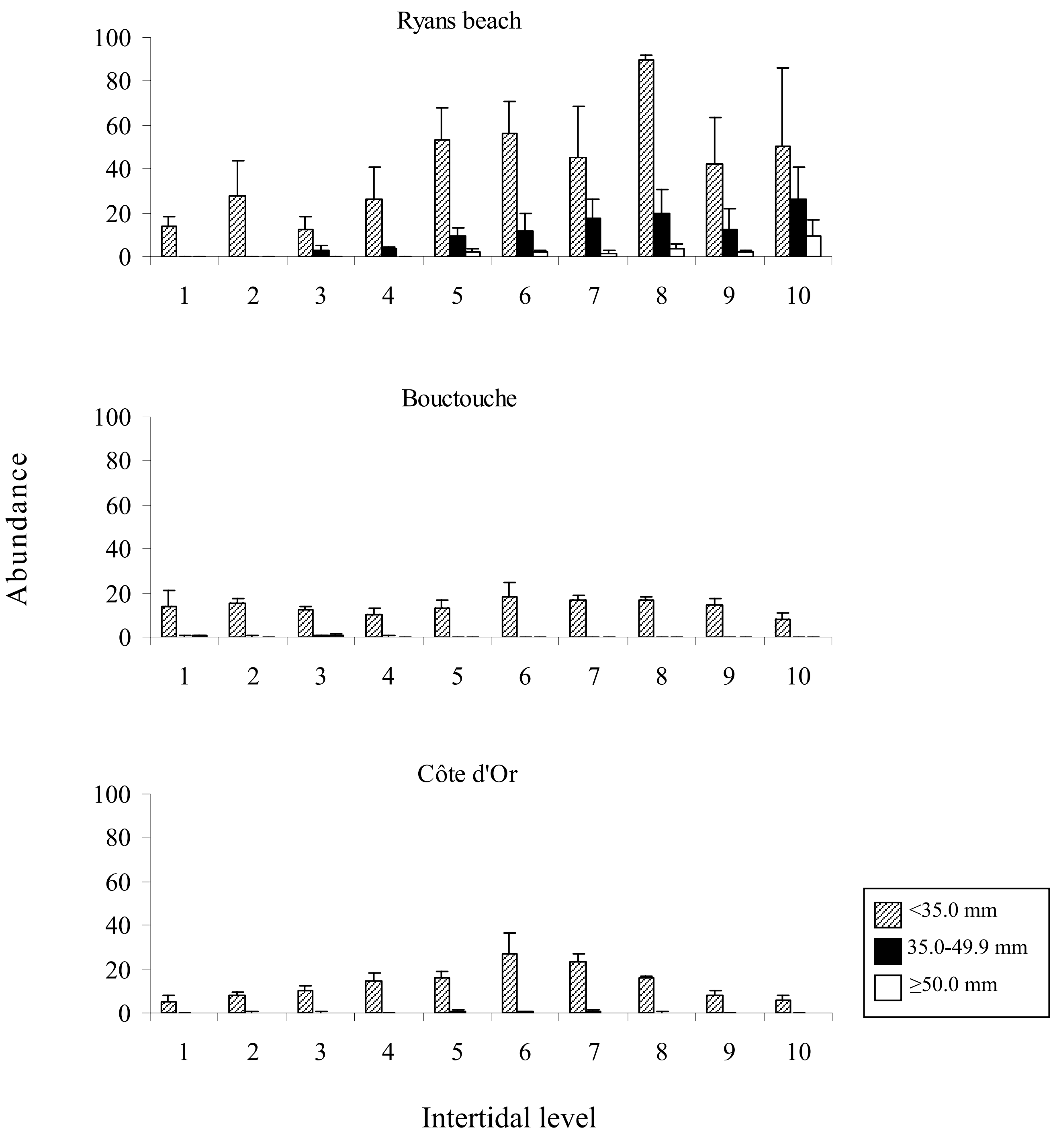

Figure 5. Abundance (mean number of individual per 1600 cm^2 ± SE, n=3) of softshell clams along the intertidal axis (1=high intertidal, 10=low intertidal) for three size-classes for sites within the Northumberland Strait.

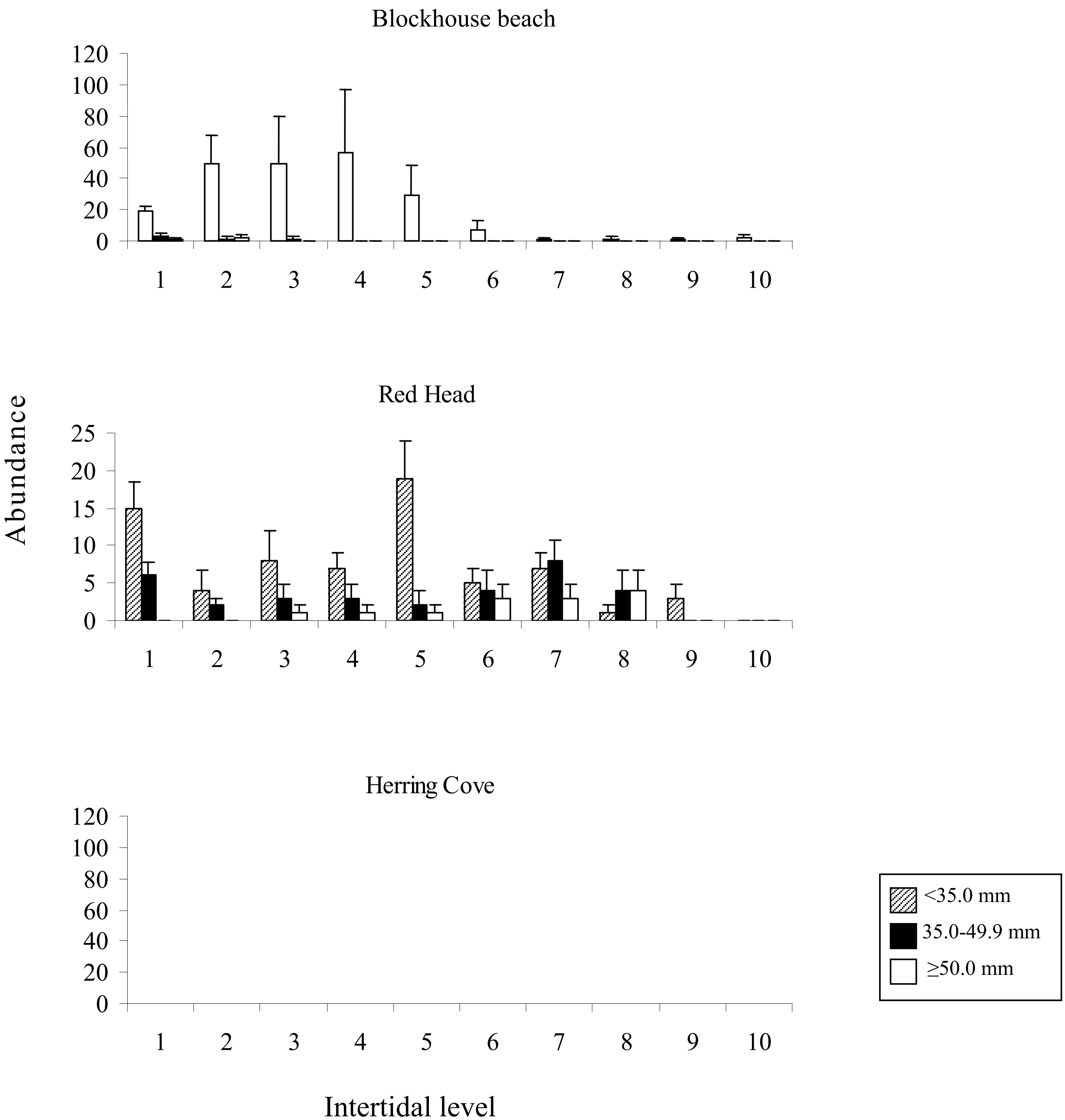

Figure 6. Abundance (mean number of individuals per 1600 $cm^2 \pm$ SE, n=3) of softshell clams along the intertidal axis (1=high intertidal, 10=low intertidal) for three size-classes for sites within the Bay of Fundy.