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ORIGINAL ARTICLE

Mussel and dogwhelk distribution along the north-west Atlantic coast: testing predictions derived from the abundant-centre model

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ABSTRACT

Aim We performed the first test of predictions from the abundant-centre model using north-west Atlantic coastal organisms. We tested the hypotheses that the density of intertidal mussels (*Mytilus edulis* and *M. trossulus*) and dogwhelks (*Nucella lapillus*) and mussel age and size would peak at an intermediate location along their distribution range. We also assessed the latitudinal variation in critical aerial exposure time.

Location North-west Atlantic coast between Newfoundland (Canada) and New York (USA), covering 1800 km of shoreline.

Methods Using a nested design, we measured mussel density, age and size and dogwhelk density in 60 wave-exposed rocky intertidal sites spread evenly in six regions. Critical aerial exposure times were determined using online data.

Results *Mytilus edulis* peaked in abundance in Maine and was much less abundant in the other regions. *Mytilus trossulus* peaked in abundance in southern Nova Scotia and Maine, was less abundant in the other regions to the north, and was absent in the southernmost region (New York). Both mussel species were least abundant in a northern region (Cape Breton), although not in the northernmost region (Newfoundland). Critical aerial exposure times were negatively correlated with overall mussel density. Mussel age and size were similar among regions. Dogwhelks peaked in abundance in Maine and were much less abundant in the other regions, being positively correlated with overall mussel density across regions.

Main conclusions Density data for *M. edulis* and *N. lapillus* provide limited support for an abundant-centre pattern, while *M. trossulus* shows a clear ramped-south distribution. Critical aerial exposure times suggest that physiological stress during summer and winter low tides may be lowest in Maine and southern Nova Scotia, which might partially explain mussel predominance in those regions. Winter ice scour in Cape Breton may explain the abundance trough observed there. Mussel size and age may be more limited by wave exposure at our sites (as they all face open waters) than by regional differences in environmental stress. Dogwhelks, which prey on mussels, seem to respond positively to prey density at the regional scale. Our study supports the notion that, while the abundant-centre model is a useful starting point for research, it often represents an oversimplification of reality.

Keywords

Abundant-centre model, dogwhelk, intertidal, macroecology, mussel, *Mytilus edulis, Mytilus trossulus,* north-west Atlantic, *Nucella lapillus,* predator–prey interactions.

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INTRODUCTION

The abundant-centre hypothesis (ACH) is frequently used to predict species distributions (Sagarin & Gaines, 2002a,b; Samis & Eckert, 2007; Tuya *et al.*, 2008; Rivadeneira *et al.*, 2010); it states that the abundance of any species is greatest at the centre of its range and declines towards the edges. The ACH derives from what may be termed the abundant-centre model (ACM), which proposes the reasons behind such a pattern. Abundance is predicted to peak at the distribution centre because the most favourable environmental conditions are expected to occur there, whereas reproduction and survivorship (and hence abundance) should decrease away from this point (Brown, 1984).

The ACM has been used as the basis for several hypotheses on evolutionary and ecological processes. For instance, predictions on how species evolve within their ranges and how genes flow across populations have been made using the ACM. Many believe that, for any given species, genetic diversity is greatest at the centre of its distribution range and lowest at the edges (Brussard, 1984; Safriel *et al.*, 1994). Thus, edge populations have a greater chance of speciation, as they are more inclined to become genetically distinct (Brown, 1984; Smith & Theberge, 1986; Lesica & Allendorf, 1995). The lowered genetic diversity towards the range edges also implies a greater chance of population extinctions (Channell & Lomolino, 2000). In ecological terms, the ACM has been used to address issues related to conservation and climate change. For endangered species, reintroduction into the range centres is thought to increase the success rate through increased ecological performance (Lawton *et al.*, 1994). When establishing reserves, the preservation of central populations is an important consideration (Brown *et al.*, 1995). However, edge populations are also thought to be more resistant to climate change because they have a more variable thermal tolerance (Stillman, 2003).

The generalized use of the ACM to develop such hypotheses, however, is potentially misleading because the few studies that have been carried out on it have yielded varying results. For example, some studies have tested ACH-predicted patterns using intertidal organisms. Intertidal species are useful for studying abundance distributions because they are spread across a nearly unidimensional range along a coastline that can span hundreds of kilometres, with narrow widths of < 0.1 km. This property helps to avoid the logistical problems inherent in sampling populations with clearly two- or three-dimensional ranges. Thus, defining the centre and range edges of an intertidal species is relatively easy for regional scales, which frequently involve latitudinal gradients. Furthermore, because intertidal species are often slow-moving or sessile (Menge & Branch, 2001), they are easy to sample accurately. Despite this simplicity, however, coastal studies have revealed a variety of species distributions. Sagarin & Gaines (2002a) and Rivadeneira *et al.* (2010) found that some rocky intertidal invertebrates along the north-east and south-east Pacific coasts do show an abundant-centre distribution, but several species do not. Samis & Eckert (2007) did a range-wide survey of two Pacific coast dune plants that revealed that their density did not fit the ACH. Other studies have reported similar conflicting results, with some species following ACH predictions and others failing to do so (Sagarin & Gaines, 2002b; Parmesan *et al.*, 2005; Gilman, 2006; Tuya *et al.*, 2008). Overall, these results undermine the ubiquity of the ACH, although the lack of biogeographical data from other coasts makes cross-system comparisons impossible.

To investigate potential generalizations, we studied the north-west Atlantic coast, which has not been sampled in the context of the ACH. A cold-temperate intertidal biota occurs on this coast (Adey & Hayek, 2005), and excellent model organisms with which to test the ACH are blue mussels, as they have a wide latitudinal range (Hunt & Scheibling, 2001; Bertness, 2007). Two species of blue mussel often coexist on this coast: *Mytilus edulis* Linnaeus, 1758 and *M. trossulus* Gould, 1850 (McDonald *et al.*, 1991; Comesaña *et al.*, 1999; Innes & Bates, 1999; Riginos & Cunningham, 2005; Rawson & Harper, 2009). They have well-documented life histories, predators and physiological limits and can have a longer life span than other sessile intertidal species, making them good indicators of long-term environmental trends (Seed, 1969b; Richardson *et al.*, 1981; Hunt & Scheibling, 1995; Petraitis, 1995; Richardson, 2001; Norkko *et al.*, 2006). Although not explicitly testing the ACH, some studies on blue mussels suggest that these species might follow the ACH along the north-west Atlantic coast. High mussel abundances have been recorded in southern Nova Scotia and Maine (Hunt & Scheibling, 1995, 1996; Bertness *et al.*, 2004), but at higher latitudes populations are sparse (Adey & Hayek, 2005; Scrosati & Heaven, 2007). These observations led to the first hypothesis of our study, namely that intertidal mussel abundance would peak at intermediate latitudes between our northernmost (Newfoundland) and southernmost (New York) sampled regions along the north-west Atlantic coast.

An additional gap in the understanding of species distributions at regional scales arises from the scarcity of age and size data. Age and size are normally important traits for examining growth rates, reproductive success and survivorship (Seed, 1969b; Richardson *et al.*, 1981; Hunt & Scheibling, 1995; Richardson, 2001; Cole *et al.*, 2011). The mean age and size of species may also peak at the centre of their geographical range, as conditions there may be least stressful according to the ACM, resulting in a larger size and greater longevity than at the extremes (Samis & Eckert, 2007). Organisms from edge populations are also predicted to remain small because they lack the adaptations to grow optimally under the habitat conditions found at range margins (Samis & Eckert, 2007). Thus, our next two hypotheses were that the average age and size of mussels would be higher at their distribution centre than at their range edges.

A basic component of the ACM is that environmental conditions are expected to be best for a species at the centre of its distribution (Brown, 1984). This assumption would ideally be tested by transplanting a mixture of specimens from a diversity of habitats (to avoid the confounding effects of local adaptations; Feder, 2007) to several sites across the distribution range, excluding interspecific interactions by experimental means. Then, the performance of the transplanted organisms could be measured to produce a spatial profile of stress changes for that particular species (Menge & Sutherland, 1987). However, that method is highly impractical for regional scales spanning hundreds of kilometres. For intertidal organisms, exposure to aerial conditions during low tides greatly affects their performance because of stresses such as those caused by air temperature extremes, especially in winter and summer (Raffaelli & Hawkins, 1996). Such stresses depend on the daily timing of low tides, which may change in a nonlinear manner with latitude (Helmuth *et al.*, 2002, 2006a,b; Harley & Helmuth, 2003). In that context, critical exposure times are the periods during which organisms at low tide are likely to experience the coldest (early morning in winter) or warmest (around noon in summer) air temperatures (Helmuth *et al.*, 2002). Therefore, using online databases, we calculated the changes in critical aerial exposure time along our studied coastal range as an indication of differences in physiological stress along the coast. According to the ACM, we hypothesized that critical aerial exposure times would be lowest at the centre of mussel distribution.

We also quantified the variation in the density of dogwhelks, *Nucella lapillus* (Linnaeus, 1758), along the north-west Atlantic coast. These snails are common predators of intertidal mussels (Hunt & Scheibling, 2001). Thus, dogwhelk data might indicate whether predation could influence the regional changes in mussel population traits along the coast. We also used the dogwhelk data to test for an abundant-centre pattern as predicted by the ACH.

MATERIALS AND METHODS

Study sites

To determine the geographical changes in blue mussel and dogwhelk population traits, we sampled six regions along the north-west Atlantic coast between Newfoundland (Canada) and New York (United States), covering *c.* 1800 km of coastline (Fig. 1). The sampled areas were around St John's, Newfoundland (47°37.121′ N, 52°39.005′ W to 47°01.266′ N, 52°41.087′ W); Ingonish, Cape Breton Island, Nova Scotia (46°48.127′ N, 60°19.319′ W to 46°36.289′ N, 60°40.334′ W); Tor Bay, Nova Scotia (45°06.119′ N, 60°57.425′ W to 45°10.158′ N, 61°27.117′ W); Shelburne County, Nova Scotia (43°27.007′ N, 65°29.651′ W to 43°32.249′ N, 65°22.349′ W); Damariscotta Region, Maine (43°56.119′ N, 69°28.215′ W to 43°47.218′ N, 69°37.833′ W); and Montauk, Long Island, New York (41°05.209′ N, 71°25.091′ W to 41°03.076′ N, 71°51.001′ W). This selection of regions resulted from considering idealized properties of a sampling design and practical limitations when surveying large ranges. For example, many sections along the north-west Atlantic coast lack adequate access from land (no roads) or safe access from the sea. In addition, all data had to be gathered for the same sampling season, but detailed intertidal samplings could only be carried out during low tides with relatively calm seas, which occurred during limited periods every month, restricting the available time for field work. Thus, we selected regions that covered our targeted geographical range well. On the north-west Atlantic coast, intertidal blue mussels and dogwhelks occur commonly between Newfoundland, Canada, and New England, United States (Adey & Hayek, 2005). South of New England, the combination of the lack of suitable substrate (stable bedrock) and high-temperature stress means that stable populations are largely absent (Bertness, 2007; Jones *et al.*, 2010). In each of our selected regions, we sampled 10 rocky intertidal sites made up of stable substrate (bedrock) facing open waters, yielding a total of 60 wave-exposed sites. Each site consisted of a 10-m-long transect line parallel to the coastline. On north-west Atlantic shores, intertidal mussels occur most abundantly in the mid-to-low intertidal zone (Bertness, 2007). Thus, at each site, we divided the intertidal range into three zones of equal vertical extent (high, middle and low zones) and sampled in the lower third of the middle zone and upper third of the low zone.

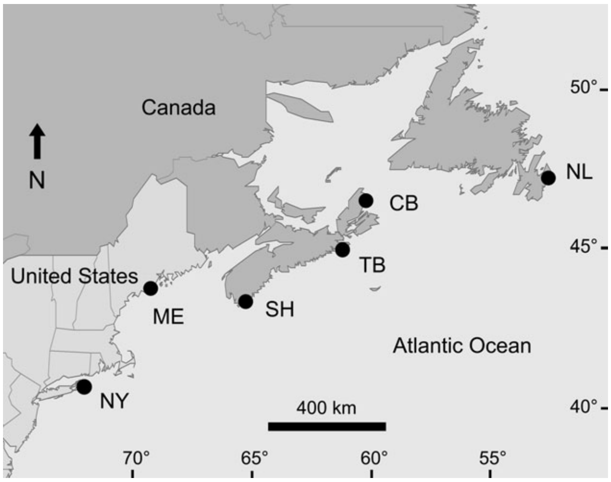

Figure 1 Map of the north-west Atlantic coast, showing the six regions surveyed for blue mussels (*Mytilus edulis*, *M. trossulus*) and dogwhelks (*Nucella lapillus*): Newfoundland (NL), Cape Breton Island (CB), Tor Bay (TB), Shelburne County (SH), Maine (ME) and New York (NY).

Mussel population traits

We took field measurements during low tides between late spring and early summer in 2007. At each site, we measured mussel abundance by counting all *Mytilus* spp. individuals present in each of 15 quadrats (50 cm × 50 cm) randomly placed along the transect line (using a random number table). The minimum length (length being the distance between the umbo and the most distant point of the shell) that we were able to determine consistently was 2 mm. Some mussel species from other shores around the world may form layers of organisms on the substrate (Suchanek, 1986; Guiñez & Castilla, 1999). However, at our wave-exposed sites, mussels were generally small (see Results) and layering was minimal. Thus, our counts of mussels yielded accurate values of natural densities. From each site, we randomly collected 40 mussels to determine their size and age in the laboratory. We determined size (shell length) with a calliper, and age by counting the number of annual growth rings on shells. A noticeable growth ring develops annually on the shell owing to the winter cessation of growth, so such rings have been used previously to age mussels (Seed, 1969a; Hunt & Scheibling, 1995). To test the effectiveness of such rings to age north-west Atlantic mussels, we performed a preliminary study in Nova Scotia. In November 2006, at the mid-intertidal zone, we tagged 20 mussels *in situ* by affixing bee tags (Bee Works, Orillia, Ontario, Canada) to the edge of the ventral shell margin. We also painted a band of red nail enamel along the ventral shell margin of each individual as an additional way of monitoring growth. We surveyed the mussels again after the winter, in July 2007, when we looked for the occurrence of an evident ring on the newly grown area of the shell.

Species identification

The two mussel species on the north-west Atlantic coast (*M. edulis* and *M. trossulus*) are morphologically very similar and, thus, virtually impossible to identify under field conditions; in addition, hybrid specimens may occur (Comesaña *et al.*, 1999; Innes & Bates, 1999). Because the ACH applies to individual species, we performed genetic analyses of field samples to obtain species-specific values of abundance for each region. For this purpose, we randomly collected 20 mussels from each of the six regions (two individuals from each of the 10 sites per region) and determined the species ratio (*M. edulis*: *M. trossulus*: hybrids) using the polymerase chain reaction (PCR)-based internal transcribed spacer (ITS)-I and ITS-II markers as specified in Heath *et al.* (1995). The region-specific species ratios were applied to the corresponding *Mytilus* spp. density values to generate density data for each species. Because we could not assume that *M. edulis*, *M. trossulus* and their hybrids grow at the same rate, we did not apply the species ratios to age and size data.

Critical aerial exposure times

We calculated the length of time during which the lower boundary of the sampled elevation range in each region was theoretically exposed to aerial conditions (low tide) during winter and summer critical hours. For winter, we considered critical hours to be the period between 01:00 and 03:00 h, when freezing stress is most likely to occur. For summer, we considered the period between 11:00 and 13:00 h as critical hours, as irradiance and heat stresses are then most likely to occur at low tide (Helmuth *et al.*, 2002). Aerial exposure times were calculated by considering whether online tidal height estimates (Tide and Current Predictor, 2011) were higher or lower than the lower boundary of the sampled elevation range in each region for the hours stated above on each day between June and August 2006 (summer) and between December 2006 and February 2007 (winter). We considered those intervals because the aerial exposure times of the previous year are thought to be an important influence on mussel abundance (Helmuth *et al.*, 2002). Although we used online tidal data appropriate for each sampled region, small differences may have existed between the stations for which the online data were generated and our exact study sites.

Dogwhelk density

At each of the sites where we determined mussel abundance, we also measured the density of dogwhelks (*N. lapillus*) by counting all of the individuals present in 15 quadrats (50 cm × 50 cm) that were randomly established along the transect line.

Statistical analyses

Before analysing the data for patterns, we tested the normality assumption using normal probability plots, and the homoscedasticity assumption using residuals versus predicted plots. To meet these assumptions, density and size data were $\log(x + 1)$-transformed (Quinn & Keough, 2002), while age data met both assumptions. To examine the differences in density of *M. edulis*, *M. trossulus*, *Mytilus* hybrids and *N. lapillus*, and in the age and size of *Mytilus* spp. among regions, we used nested analyses of variance (ANOVA), accounting for the variability in both site and region. As we selected the regions based on placement along the coast, 'region' was considered a fixed factor, while 'site' was considered a random factor nested within region. Whenever an ANOVA yielded a significant result, we assessed pairwise differences between regions using Tukey's honestly significant difference (HSD) tests (Quinn & Keough, 2002). We performed the analyses with JMP 5.1 for Macintosh, considering 0.05 as the significance level.

RESULTS

Mussel age determination and species identification

All of the tagged mussels showed a distinct depression as a new ring between the shell edge as seen in the autumn (indicated by the tags) and the shell edge as seen in the following summer. Our field observations during this study indicated that growth rings were evident in all of the studied regions in a similar manner. The genetic analyses revealed that *M. edulis* prevailed over *M. trossulus* and hybrids on southern shores (Maine and New York), peaking in relative abundance in the southernmost sampled region, where it was the only *Mytilus* entity (Table 1). By contrast, *M. trossulus* prevailed on northern shores (Newfoundland and Nova Scotia), peaking in relative abundance in the northernmost sampled region. Hybrids were

Table 1 Proportions of *Mytilus edulis*, *M. trossulus* and hybrid mussels in the six regions surveyed along the north-west Atlantic coast: Newfoundland (NL), Cape Breton Island (CB), Tor Bay (TB), Shelburne County (SH), Maine (ME) and New York (NY).

Region	*Mytilus edulis*	*Mytilus trossulus*	*Mytilus* hybrids
NL	0.05	0.90	0.05
CB	0.05	0.65	0.30
TB	0.10	0.80	0.10
SH	0.05	0.85	0.01
ME	0.73	0.27	0
NY	1.00	0	0

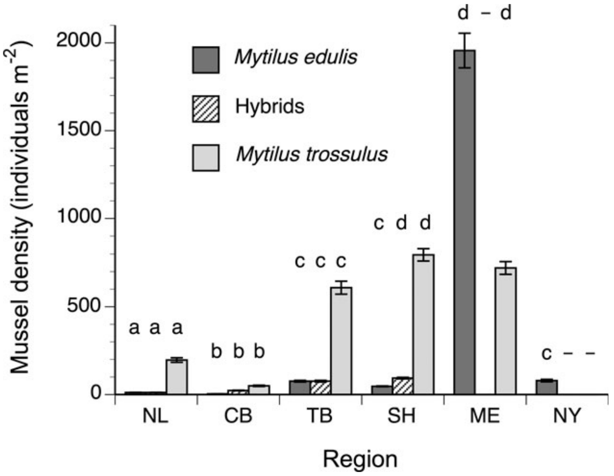

Figure 2 Density of *Mytilus edulis*, *M. trossulus* and hybrid mussels (mean ± SE) in the six regions surveyed along the north-west Atlantic coast (ordered in the figure as per their location along the coastline): Newfoundland (NL), Cape Breton Island (CB), Tor Bay (TB), Shelburne County (SH), Maine (ME) and New York (NY). For each species, different letters indicate significant differences between regional means.

present only in Newfoundland and Nova Scotia, peaking in relative abundance in Cape Breton.

Mussel population traits

The density of *M. edulis* differed significantly among regions ($F_{5,54} = 976.29$, $P < 0.0001$), showing a significant peak in Maine and decreasing dramatically (by a factor of at least 25) on northern and southern shores (Fig. 2). Differences among the other regions were much smaller, with a significantly lowest value occurring in Cape Breton (Fig. 2). Hybrid mussels were absent in southern regions (Maine and New York), but occurred in the northern regions, differing significantly in density among them ($F_{3,36} = 372.13$, $P < 0.0001$). Within their distribution range, hybrids were significantly more abundant in Tor Bay and Shelburne than in Cape Breton and Newfoundland (Fig. 2). *Mytilus trossulus* was absent in the southernmost region (New York) but present in all others, differing significantly in density among them ($F_{4,45} = 469.12$, $P < 0.0001$). Within its distribution range, *M. trossulus* was highest in density between Tor Bay and Maine, peaking significantly in Shelburne and Maine (Fig. 2). As with *M. edulis*, density was lowest in Cape Breton for *M. trossulus* (Fig. 2). In Maine, where overall mussel density was highest, individuals covered up to 80% of the rocky substrate, while populations were sparser in the other regions, being consistently lower than 50% cover within quadrats.

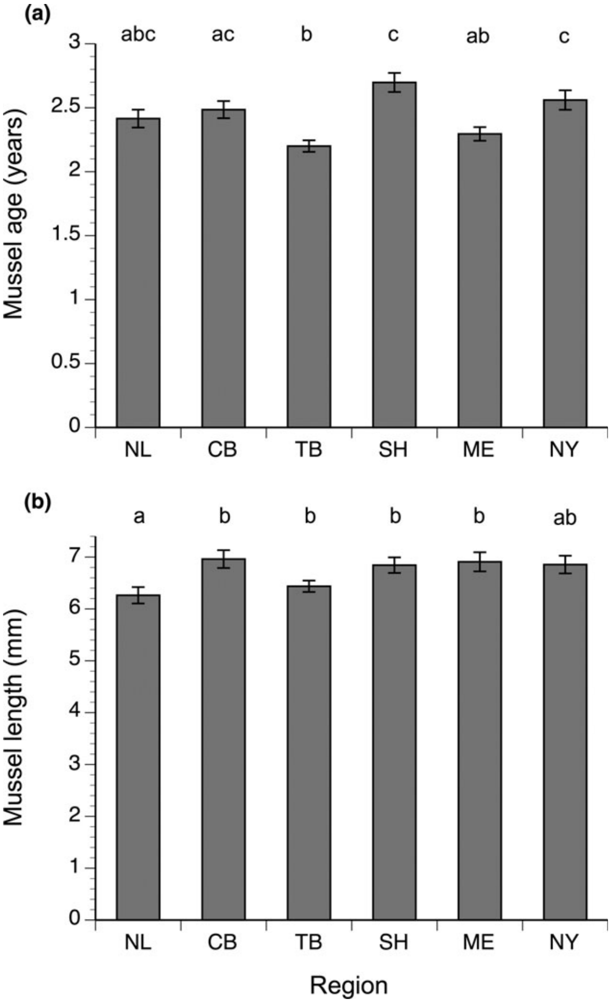

Figure 3 Age (a) and size (b) of *Mytilus* spp. (mean ± SE) in the six regions surveyed along the north-west Atlantic coast (ordered in the figure as per their location along the coastline): Newfoundland (NL), Cape Breton Island (CB), Tor Bay (TB), Shelburne County (SH), Maine (ME) and New York (NY). Different letters indicate significant differences between regional means.

The age of *Mytilus* spp. differed significantly among regions ($F_{5,54} = 7.97$, $P < 0.0001$), although there was no clear trend across latitude, and differences between regions were small (Fig. 3a). The size of *Mytilus* spp. ranged between 2 and 54 mm, although most organisms were small: 6.7 ± 0.1 mm (mean ± SE, $n = 2400$). Mussel size differed significantly among regions ($F_{5,54} = 4.12$, $P = 0.0010$), although size differences between the regions were also small. There was a mild trend of decreasing size towards the northernmost sampled region (Fig. 3b).

Critical aerial exposure times

During winter months (December–February), the aerial exposure time during early morning hours was considerably lower in Shelburne and Maine than that recorded in northern and southern regions (Fig. 4). The region-wise average exposure time for Newfoundland, Cape Breton, Tor Bay and New York was 55 h higher than that for Shelburne and Maine, more than a two-fold difference. During summer months (June–August), the critical exposure time in each region was lower than the corresponding winter values. However, the summer pattern was similar to the winter one, with the lowest duration of aerial exposure during critical hours occurring in Shelburne and Maine, closely followed by values for Tor Bay (Fig. 4). In summer, the region-wise average exposure time for Newfoundland, Cape Breton and New York was 38 h higher than that for Tor Bay, Shelburne and Maine, almost a two-fold difference. Critical exposure times for both winter and summer were negatively related to overall mussel density across regions ($r = -0.84$, $P = 0.037$ in winter; $r = -0.85$, $P = 0.034$ in summer; $n = 6$ regions).

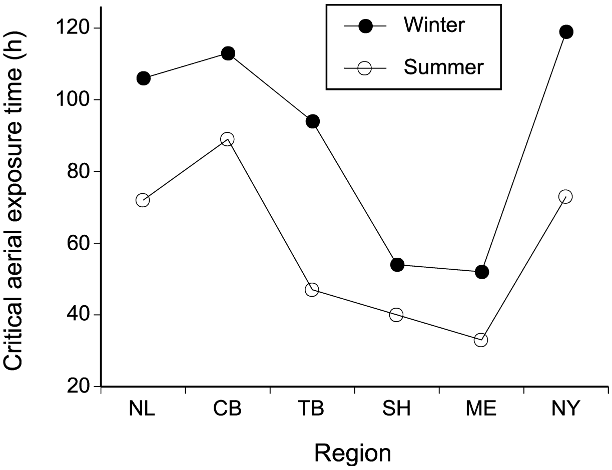

Figure 4 Summer and winter critical aerial exposure times for the six regions surveyed along the north-west Atlantic coast (ordered in the figure as per their location along the coastline): Newfoundland (NL), Cape Breton Island (CB), Tor Bay (TB), Shelburne County (SH), Maine (ME) and New York (NY).

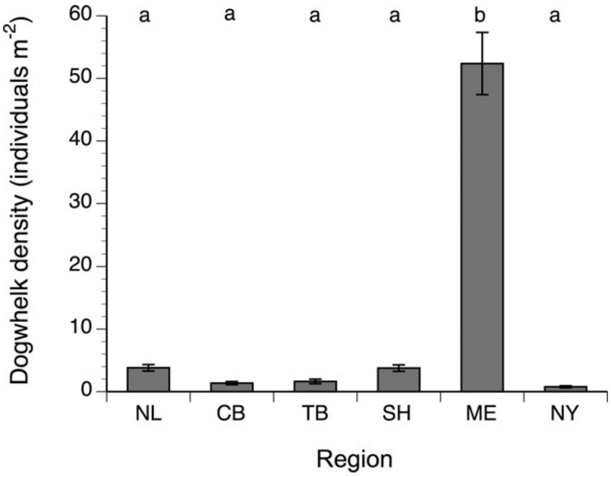

Figure 5 Density of *Nucella lapillus* (mean ± SE) in the six regions surveyed along the north-west Atlantic coast (ordered in the figure as per their location along the coastline): Newfoundland (NL), Cape Breton Island (CB), Tor Bay (TB), Shelburne County (SH), Maine (ME) and New York (NY). Different letters indicate significant differences between regional means.

Dogwhelk density

The density of *N. lapillus* differed significantly among regions ($F_{5,54} = 38.28$, $P < 0.0001$), being much higher in Maine than in any other region (Fig. 5). Dogwhelk density was positively related to overall mussel density across regions ($r = 0.94$, $P = 0.006$, $n = 6$).

DISCUSSION

Overall, the distribution of the two species of intertidal mussel on the north-west Atlantic coast provides very little support for the ACH. While *M. edulis* exhibited a clear peak in abundance between the two most extreme regions, it did so at a relatively southern location (Maine). On the other hand, *M. trossulus* showed a ramped-south distribution, peaking in abundance in southern Nova Scotia (Shelburne) and Maine and being absent in the southernmost region. A departure from an abundant-centre distribution was further indicated by the lowest density of both species occurring in Cape Breton, between two other sampled regions.

Ramped and bimodal distributions are often attributed to abrupt changes in habitat properties or environmental conditions (Brown, 1984; Samis & Eckert, 2007), which could apply to north-west Atlantic intertidal mussels. For instance, sandy shores replace rocky shores south of New England, resulting in a lack of suitable substrate for intertidal blue mussels (Bertness, 2007). In addition, extreme heat stress is thought to limit mussel development on the few places (man-made structures) where organisms could potentially settle at those southern latitudes (Jones *et al.*, 2010). Regarding the lowest mussel abundance occurring in Cape Breton, a possible explanation relates to the effects of sea ice. Every winter, sea ice develops extensively on the Gulf of St Lawrence (Saucier *et al.*, 2003), and, towards the end of the winter, ice floes are carried out of the gulf by winds and currents. Thus, many fragments of pack ice reach the north-east coast of Cape Breton Island (Canadian Ice Service, 2010), including our sampled sites. The scouring action of ice on intertidal habitats causes a great deal of disturbance (Scrosati & Heaven, 2006), resulting in sessile organisms surviving mostly in protected places such as cracks and crevices (Bergeron & Bourget, 1986; Belt *et al.*, 2009). In contrast, sea ice does not form on any of the other shores that we sampled. On rare occasions, pack ice from the Gulf of St Lawrence may reach the north-east coast of mainland Nova Scotia, including Tor Bay. However, the last time sea ice reached the Tor Bay area before our samplings was apparently for a few days in 2004 (Canadian Ice Service, 2010) and it had previously occurred, in a more extensive manner along the north-east coast of mainland Nova Scotia, in 1987 and 1961 (Minchinton & Scheibling, 1991). Our surveys also revealed that the regional average in the abundance of *Fucus* spp. (common north-west Atlantic intertidal macroalgae) was markedly lower in Cape Breton (mean cover < 1%) than in the other sampled regions (mean cover > 20%). Thus, the annual occurrence of ice scour in north-east Cape Breton Island might explain the pronounced drop in mussel density that we observed there.

We stress, again, that we sampled only wave-exposed sites along the coast. It would be interesting to analyse latitudinal patterns using samples from wave-sheltered habitats, where blue mussels also occur.

Although an abundant-centre distribution was not found for either mussel species, the negative relationship between environmental stress and species abundance, a basic component of the ACM, did receive some support. Aerial exposure times during critical hours in winter and summer were lower in southern Nova Scotia and Maine than in northern and southern regions, coinciding with the highest overall mussel density occurring in those two regions. This inverse relationship suggests that blue mussel populations may be affected by the number of hours they are exposed to acute temperature, irradiance, desiccation, and hypoxic stress (Altieri, 2006; Helmuth *et al.*, 2006a). Helmuth *et al.* (2002, 2006a) examined the effects of critical summer aerial exposure times on the north-east Pacific mussel *Mytilus californianus* Conrad, 1837 and concluded that prolonged exposure to acute heat and desiccation were detrimental regardless of latitude. For north-west Atlantic mussels, summer stresses might therefore be particularly strong in our southernmost sampled region. With a similar rationale, our northern sampled regions might experience prolonged chronic exposure to cold temperatures in winter. Although blue mussels are known to tolerate freezing down to a thermal limit of −6 °C, they still experience high mortality when exposed for long periods to sub-lethal temperatures (Aunaas, 1982; Ansart & Vernon, 2003). In the northern regions of our sampled range, air temperature can reach −20 °C, which can cause mortality in intertidal mussels that are not thermally protected by the presence of a stable ice foot (Scrosati & Eckersley, 2007).

The high correlation observed between the density of dogwhelks and overall mussel density across regions suggests that these predatory snails may not be controlling mussel abundance at the regional scale. Instead, dogwhelk abundance seems to respond closely to variation in prey abundance across regions. This could be a case of bottom-up regulation of predator density, similar to that found for a mussel–seastar system on the north-east Pacific coast (Menge, 1992, 2000; Menge *et al.*, 1997, 1999). This issue warrants further attention, including studies on possible changes in interaction strength (Wootton & Emmerson, 2005) for the mussel–dogwhelk system along the north-west Atlantic coast. In any case, the observed pattern in dogwhelk density along the coast constitutes yet another example providing little support for the ACH.

The poor fit of mussel and dogwhelk distributions to an abundant-centre pattern thus adds Atlantic examples to those recorded for Pacific species. Sagarin & Gaines (2002a) and Samis & Eckert (2007) found that north-east Pacific intertidal invertebrates and coastal dune plants rarely adhered to the ACH, as only 2 of 12 benthic invertebrate species and no dune plants fitted an abundant-centre distribution. On the south-east Pacific coast, only two of the five tested intertidal species of porcelain crab showed an abundant-centre distribution along the shore (Rivadeneira *et al.*, 2010).

Because of the nature of age and size data for our cryptic mussel species, neither variable could be determined separately for each species. However, the fact that both age and size varied relatively little within regions and among regions suggests that the patterns may be similar for both species (and also that our age determinations were reliable). Thus, it is useful to analyse such data in the context of the ACM. We found that the observed variation in mussel age and size along the north-west Atlantic coast did not support the hypotheses derived from the ACM, as both variables showed little change across regions. The region-wide mean age of mussels ranged only between 2 and 3 years, while mean size ranged only between 6 and 7 mm. Since intertidal mussels are, on average, larger and older in wave-sheltered habitats (J.C. Tam & R.A. Scrosati, pers. obs.), our results suggest that most mussels live for a few years in intertidal habitats facing open waters, which is consistent with the notion that wave action is an important factor limiting growth on exposed shores (Carrington *et al.*, 2009; Denny *et al.*, 2009). Thus, any potential influence of critical aerial exposure times on mussel age and size across latitude might be overridden by the action of waves on exposed sites. This suggests that physiological stress could be decoupled from physical stress (disturbance resulting from wave action) in determining population traits of intertidal mussels at the regional scale. The observed pattern in mussel age along the north-west Atlantic coast contrasts with patterns found for dune plants along the Pacific coast, for which size did peak at the distribution centre, although seed production did not (Samis & Eckert, 2007). Thus, although the ACM assumes that there is a positive link between size, progeny production, and abundance, the connection between size and abundance may be more complex than traditionally thought (see also Rivadeneira *et al.*, 2010).

In summary, our study has revealed a low-to-absent support of mussel and dogwhelk data to an abundant-centre distribution. Physical factors such as the lack of suitable substrate and the occurrence of high heat stress on southern shores and ice scour on some northern shores might explain in part the departure from the idealized pattern predicted by the ACH. On the other hand, the data on critical aerial exposure times suggest that environmental conditions might be less stressful for intertidal mussels in southern Nova Scotia and especially Maine, which may in turn favour dogwhelks through bottom-up effects. At the sampled sites, which face open waters, mussel age and size may be limited more by wave action than by regional differences in physiological stress. When logistically feasible, manipulative experiments should test these possible mechanisms. Overall, while the ACH may be an oversimplifying concept, it has certainly stimulated ecologists to study species patterns at regional scales, which should ultimately help us to understand what drives species distribution at large scales as further field data are generated.

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