



# Regional decoupling between NW Atlantic barnacle recruit and adult density is related to changes in pelagic food supply and benthic disturbance

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## ABSTRACT

We investigated the regional variation in barnacle (*Semibalanus balanoides*) recruit and adult abundance on the NW Atlantic coast. At the end of the recruitment season (June–July), we sampled wave-exposed rocky intertidal sites in two regions on the open Atlantic coast (Maine, AM, and Nova Scotia, AN) and in two regions on the Gulf of St. Lawrence coast (Northumberland Strait, GN, and Cape Breton Island, GC). Recruit density was highest in the southernmost region (AM), followed by GN and, then, by AN and GC. Regional values of nearshore primary productivity (satellite data of chlorophyll-*a* concentration, a surrogate for phytoplankton abundance) were highest for AM and GN, suggesting that food supply (barnacles are filter feeders) is an important factor determining regional recruitment patterns. Adult barnacle density was regionally decoupled from recruit density. Adults occurred in very low abundances on the Gulf of St. Lawrence coast (GN and GC) and were relatively abundant on the Atlantic coast (AM and AN), although always in much lower abundances than recruits. The low adult densities on the Gulf of St. Lawrence coast seem to result mainly from intense ice scour, as this coast freezes extensively every winter, as opposed to the ice-free Atlantic coast. Ice scour thus appears to override regional recruitment differences in determining adult density. Therefore, our data suggest that both pelagic food supply and benthic disturbance contribute to setting regional patterns in barnacle population structure on the NW Atlantic coast.

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## 1. Introduction

For intertidal sessile invertebrates with planktonic larvae, recruitment refers to the appearance of new individuals that have developed after larval settlement and have reached an arbitrary size that allows them to be counted. The transition from settler to recruit takes a few days or weeks, depending on species and conditions (Pineda et al., 2009). For such species, population persistence is often affected by recruitment rates (Menge, 2000a; Jonsson et al., 2004; Broitman et al., 2008). However, most research on recruit ecology has been done at small spatial scales, for which substrate and interspecific interactions are important regulating factors (Underwood and Keough, 2001).

At large spatial scales, regional differences in the recruitment of rocky intertidal invertebrates may occur as a result of large-scale oceanographic changes (Lagos et al., 2008; Menge et al., 2009). A well-studied system is the NE Pacific coast, where coastal upwelling, when intense, generates offshore transport of larvae of intertidal filter feeders (barnacles and mussels) that limits benthic recruitment (Connolly et al., 2001). Also on that coast, nearshore primary productivity (as determined by

the concentration of chlorophyll *a* in seawater, a surrogate for phytoplankton abundance) is positively related to barnacle and mussel recruitment, seemingly through positive effects on reproductive adults, larvae, and settlers, which feed on phytoplankton (Menge et al., 1997, 2009; Leslie et al., 2005). Regional differences in benthic invertebrate recruitment have also been found on the NW (Noda, 2004), SW (Menge et al., 1999; Menge, 2000b), and SE Pacific coasts (Palma et al., 2006; Lagos et al., 2008; Navarrete et al., 2008) and on the NE Atlantic coast (Jenkins et al., 2000; O'Riordan et al., 2004; Burrows et al., 2010) and are also generally related to coastal oceanographic variation.

On the NW Atlantic coast, barnacle recruitment differs at local and mesoscales in New England (USA) because of variation in algal cover and water circulation and flow (Bertness et al., 1992, 1996; Leonard et al., 1998). However, regional-scale patterns for any intertidal invertebrate remain poorly documented. Barnacle recruitment rates are often assumed to decrease with latitude from New England towards the Canadian Maritimes, possibly because of the more oligotrophic nature of Canadian waters, which could result in a lower nearshore primary productivity there (Adey and Hayek, 2005; Bertness, 2007). Recruitment data for Canadian shores exist for the central Atlantic coast of Nova Scotia, but those sites had experienced an unusual disturbance before data collection (Minchinton and Scheibling, 1991). Recruit data also exist for the Gulf of St. Lawrence coast of Nova Scotia, but for a single

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location (MacPherson et al., 2008). To fill this information gap, we determined regional differences in barnacle recruit density on the NW Atlantic coast through a mensurative experiment, placing emphasis on Nova Scotia shores but also collecting data for Maine (USA) for comparison. We selected regions that differ in nearshore primary productivity. This approach led us to our first hypothesis, which stated that barnacle recruit density would be positively related to nearshore primary productivity at the regional scale.

We also compared barnacle recruit and adult density at the regional scale, as spatially heterogeneous post-recruitment processes may decouple both variables (Bertness, 1989; Hughes et al., 2000; Menge, 2000a; Svensson et al., 2004). We identified regions in Nova Scotia that differ in winter ice load, as this is a powerful agent of intertidal disturbance that may determine adult density more than recruitment rates (Barnes, 1999; Gutt, 2001). In Atlantic Canada, intertidal barnacle recruitment occurs in the spring (Bousfield, 1954; Minchinton and Scheibling, 1991; MacPherson et al., 2008), but the occurrence of winter ice scour markedly reduces the survival of recruits during their transition to adults (Belt et al., 2009). Thus, our second hypothesis was that recruit density would not necessarily be coupled with adult density across regions, adult density being inversely related to the occurrence of winter sea ice.

## 2. Materials and methods

In June–July 2007, we measured the density of barnacle (*Semibalanus balanoides*) recruits and adults in two regions on the open Atlantic coast (Maine, AM, and Nova Scotia, AN) and in two regions on the Gulf of St. Lawrence coast (Northumberland Strait, GN, and Cape Breton Island, GC; Fig. 1). Each region represents a different combination of levels of nearshore primary productivity and winter ice load.

We determined nearshore primary productivity using data of chlorophyll-*a* concentration in coastal waters as determined by MODIS (Moderate Resolution Imaging Spectroradiometer) satellite passes. For *Semibalanus balanoides* from the NW Atlantic coast, fertilization occurs in the autumn, while spawning and recruitment occur between winter and spring (Bousfield, 1954; Minchinton and Scheibling, 1991; Bertness et al., 1992; Pineda et al., 2006; MacPherson et al., 2008). Since phytoplankton abundance, as indicated by chlorophyll-*a* concentration, may enhance the reproductive condition of adults and the growth and survival of larvae and recruits (Leslie et al., 2005; Pineda et al., 2005; Vargas et al., 2006), we analyzed chlorophyll-*a*

data between June 2006 and July 2007. We obtained such data from Fisheries and Oceans Canada's (2010) website, which provides bi-monthly composite images for the NW Atlantic coast between 39° N and 62.5° N, indicating chlorophyll-*a* concentration through a color scale. Each composite image results from the combination of the available data for each half month. We produced monthly values by averaging the two values given for each month (or from the only value provided for some months because of cloud or ice cover). These data revealed clear regional differences: AM and GN have relatively productive coastal waters, while AN and GC exhibit low productivity levels (Table 1).

Regional differences in winter ice load are also evident. Every winter, sea ice develops extensively on the Gulf of St. Lawrence coast (Saucier et al., 2003; Scrosati and Eckersley, 2007), which causes intense disturbance on rocky intertidal habitats through scouring (Bergeron and Bourget, 1986; Scrosati and Heaven, 2006). On the contrary, sea ice does not form on the sea surface on the Atlantic coast at the latitudes we surveyed. Rarely, floating sea ice from the Gulf of St. Lawrence may reach the Atlantic coast of mainland Nova Scotia and cause intertidal disturbance there (McCook and Chapman, 1997; Minchinton et al., 1997). However, the last time such an event occurred was 23 years ago (as of 2010) and it had previously occurred 26 years before 1987 (Minchinton and Scheibling, 1991). Therefore, in broad terms, GN and GC sustain high levels of intertidal disturbance every winter, while AM and AN do not.

We employed a nested design, sampling 3 sites along 10 km of coastline in AM, 6 sites along 34 km in AN, 6 sites along 20 km in GN, and 6 sites along 15 km in GC. We only sampled sites that faced open waters directly, so all sites were subjected to a similar (high) degree of wave exposure. At each site, we determined recruit and adult density in 20 quadrats (10 cm × 10 cm) randomly placed at the mid-to-high intertidal zone (approximately at 2/3 of the full intertidal range above the low-water mark). Recruits were distinguished from adults (the organisms that overwintered at least once, thus holding reproductive capacity; Pineda et al., 2006) by the large size differences between them (Fig. 2). We only counted living individuals, which showed firmly closed valves at low tide. We placed the quadrats on stable bedrock, avoiding boulder fields and tide pools. We calculated adult density by dividing the number of adult barnacles in a quadrat by quadrat area (100 cm<sup>2</sup>). At the sampled elevations, barnacles are often the only macroscopic species. Since the number of recruits in a quadrat depends on the area that is available for settlement, we calculated a standardized form of recruit density. For each quadrat, we calculated the proportion of the total area

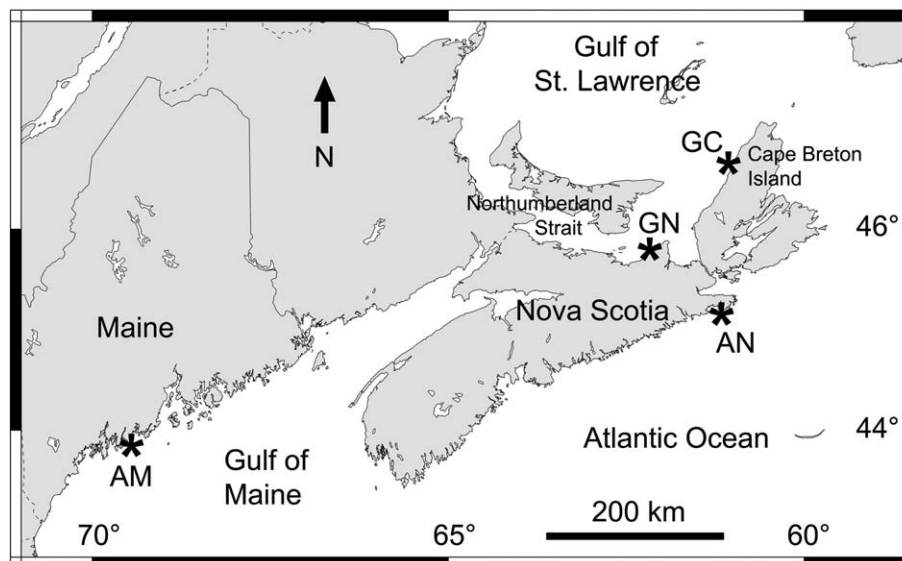


Fig. 1. Map of the NW Atlantic coast showing the 4 studied regions: southern Maine (AM), Atlantic coast of Nova Scotia (AN), Northumberland Strait coast of Nova Scotia (GN), and western Cape Breton Island coast of Nova Scotia (GC).

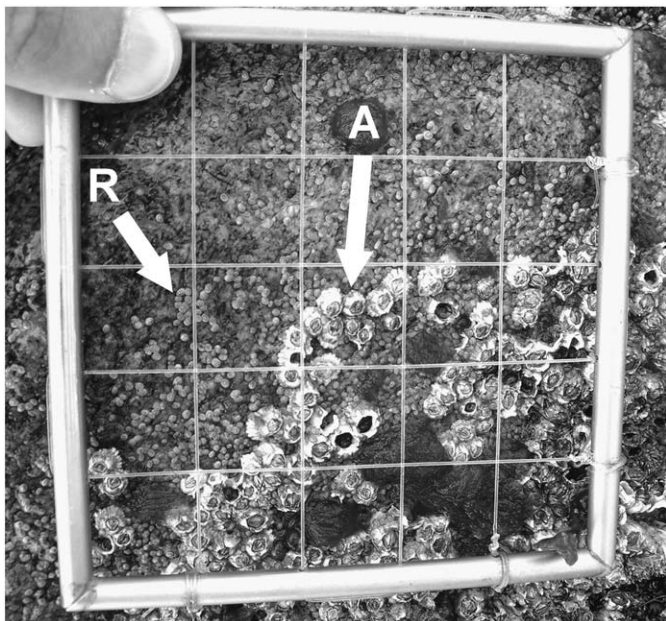
**Table 1**

Summary of coastal chlorophyll-*a* concentration in seawater ( $\text{mg m}^{-3}$ ) in the 4 studied regions between June 2006 and July 2007. Means were calculated from 12 monthly values (January and February 2007 were excluded because data were not available then for all regions). The regions were southern Maine (AM), Atlantic coast of Nova Scotia (AN), Northumberland Strait coast of Nova Scotia (GN), and western Cape Breton Island coast of Nova Scotia (GC).

Region	Mean ( $\text{mg m}^{-3}$ )	95% confidence interval ( $\text{mg m}^{-3}$ )
AM	9.6	7.3–11.9
AN	3.3	1.7–5.0
GN	9.7	8.3–11.0
GC	3.9	1.5–6.3

that was covered by adult barnacles. To calculate standardized recruit density (hereafter simply referred to as recruit density), we divided the number of recruits counted in a quadrat by the available area for settlement, which we calculated as: “quadrat area  $\times$  (1 – proportion of quadrat covered by adults)”. By sampling in June–July, we ensured that counting was done at the end of the recruitment season. Virtually no new recruits appeared later, as indicated by site inspections. Since we collected our data on natural intertidal surfaces instead of on artificial settlement plates (e.g., Menge, 2000a), our recruit density values are realistic measures of the annual recruitment rate, unaffected by any sampling artifacts (see Bertness et al., 1992, for a criticism of using cleared surfaces to measure recruitment).

We separately compared recruit and adult density among regions using a linear mixed model with restricted maximum likelihood estimation (Pinheiro and Bates, 2009). We considered “region” as a fixed factor because its 4 levels were selected a priori (sites were nested within the regions). We used *F* tests to evaluate significance. We tested the normality and homoscedasticity assumptions using normal probability plots and residuals-versus-fits plots, respectively. The assumptions were not met and data transformations did not correct the violations. Therefore, we used the raw data for the analyses but considering a conservative significance level that was 10 times lower (0.005) than the conventional level of 0.05 (Underwood, 1997). After *F* tests revealed significant regional differences, we compared regional means with Student–Newman–Keuls (SNK) tests. We did the analyses using *R* software (*R* Development Core Team, 2010).



**Fig. 2.** View of barnacle recruits (R) and adults (A) at the intertidal zone. The inner border of the quadrat's frame is 10 cm  $\times$  10 cm. Photo by R. A. Scrosati.

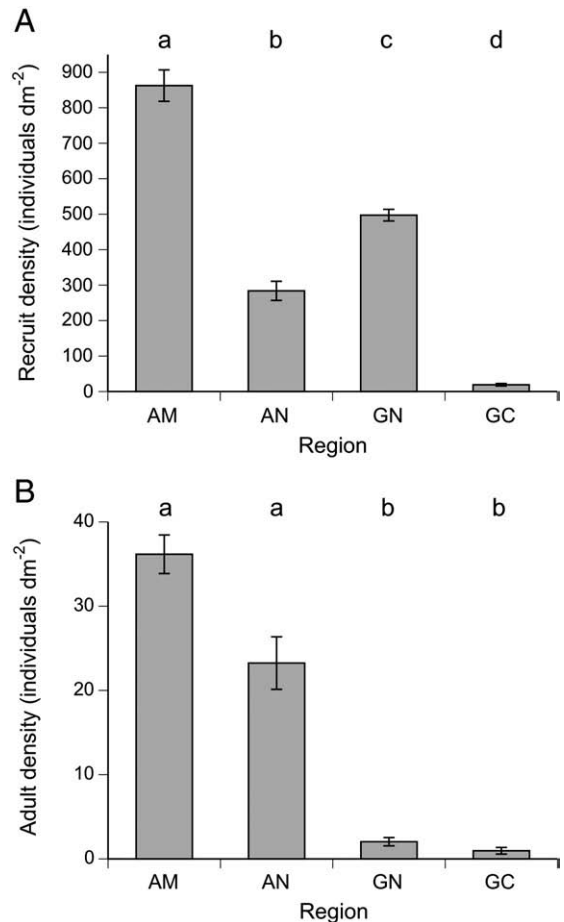
### 3. Results

Barnacle recruit density differed among the 4 studied regions ( $F_{3, 17} = 19.22$ ,  $p < 0.0001$ ). SNK tests indicated that recruit density was significantly highest in AM, followed by GN, then by AN and finally by GC (Fig. 3A). With a value of 863 recruits  $\text{dm}^{-2}$  (referred to the available area for settlement), mean recruit density for AM was 1.7 times higher than for GN (497 recruits  $\text{dm}^{-2}$ ), 3.0 times higher than for AN (284 recruits  $\text{dm}^{-2}$ ), and 45.2 times higher than for GC, which showed a mean density of only 19 recruits  $\text{dm}^{-2}$ .

Adult barnacle density also differed among regions ( $F_{3, 17} = 7.57$ ,  $p = 0.002$ ). SNK tests indicated that adult barnacle density was statistically similar in AM and AN. These two regions on the Atlantic coast showed, in turn, significantly higher adult densities than the two regions on the Gulf of St. Lawrence coast, GN and GC, which did not differ statistically from one another (Fig. 3B). The mean density of adult barnacles for AM–AN combined was 20.5 times higher than for GN–GC combined. Mean adult density was 23.8, 11.0, 243.7, and 19.7 times lower (paired *t*-tests,  $p < 0.001$ ) than mean recruit density for AM, AN, GN, and GC, respectively.

### 4. Discussion

Our results support the traditional assumption that barnacle recruitment is lower in Nova Scotia than in New England. Since our data were collected for the same season and year, temporal environmental variation is excluded as an explanation for the observed regional



**Fig. 3.** Density of (A) barnacle recruits and (B) barnacle adults (means  $\pm$  SE) in the 4 studied regions: southern Maine (AM), Atlantic coast of Nova Scotia (AN), Northumberland Strait coast of Nova Scotia (GN), and western Cape Breton Island coast of Nova Scotia (GC). See “Materials and methods” for the calculation of (standardized) recruit density. Significant differences between regions ( $p < 0.005$ ) are indicated with different letters above the bars.

differences. As *Semibalanus balanoides* was by far the main macroscopic species in our quadrats (Fig. 2), interspecific competition and facilitation (by mussels or seaweeds; Menge, 1976; Peterson, 1979; Leonard, 2000) should not have determined the regional differences in recruitment. Predation (by whelks) should not have determined such differences either, because we sampled the mid-to-high intertidal zone of wave-exposed habitats, where predator activity is minimal (Menge, 1978; Gosselin and Bourget, 1989; Minchinton and Scheibling, 1991, 1993; Scrosati and Heaven, 2007). Nearshore primary productivity, however, was related to barnacle recruit density. Coastal chlorophyll-*a* concentration was relatively high in AM and GN, suggesting that barnacle recruitment may be highest there because of an increased food supply for reproductive adults, larvae, and developing settlers (Leslie et al., 2005; Pineda et al., 2005; Vargas et al., 2006). In turn, the relatively low productivity of AN and GC coastal waters support the notion that recruitment may be lowest there because of food limitation. Nearshore primary productivity did not explain all recruitment patterns, however, as differences in recruit density existed between AM and GN and between AN and GC. It is noteworthy, though, that, in each pair of regions with a similar coastal productivity (AM-GN and AN-GC), recruitment was always higher on the Atlantic coast. This suggests that adult barnacle density (considerably lower on the Gulf of St. Lawrence coast) may also influence recruit density in a region.

Our data also revealed a regional decoupling between recruit and adult density. Before attempting to explain this pattern, we note that the surveyed adult barnacles resulted from recruitment in previous years, so the analysis offered below assumes that patterns are similar at least for a few years. This notion is supported by a study on the Gulf of St. Lawrence coast that showed that relative patterns in barnacle recruit and adult density were similar in two consecutive spring seasons in 2005 and 2006 (MacPherson et al., 2008). Also, trends in chlorophyll-*a* concentration are similar throughout years in our regions (Devred et al., 2007). In general, regional-scale patterns in rocky intertidal populations are consistent throughout years (Menge, 2000b; Navarrete et al., 2008). In our regions, adult barnacle density was markedly lower than recruit density. Summer exposure to desiccation and high temperatures during low tides (Chan et al., 2006) and self-thinning due to competition for space as recruits develop (López and González, 2003; Jenkins et al., 2008) may locally explain such a decrease. However, regional differences in adult density were clearly related to differences in winter ice load. Despite their high difference in recruitment, the two regions on the Gulf of St. Lawrence coast (GN and GC) showed a very low abundance of adult barnacles, which is consistent with the intense intertidal disturbance that ice scour generates on that coast every winter (Bergeron and Bourget, 1986; MacPherson et al., 2008; Belt et al., 2009). On the contrary, the two regions surveyed on the Atlantic coast (AM and AN) showed higher densities of adult barnacles, which is consistent with the lack of ice scour on that coast. Thus, the degree of predictable physical stress on a shore (winter ice scour) is inversely related to the abundance of adult barnacles and seems to override recruitment effects on adult density.

Despite the lack of significant differences in adult barnacle density between AM and AN, differences in total biomass might exist. We commonly observed dense stands of hummocking barnacles in AM, as reported for New England shores before (Grant, 1977; Bertness et al., 1998). However, hummocks virtually never occurred in our Nova Scotia sites, as adult barnacles merely showed the typical truncated-cone shape and did not grow in height (dog-tooth form) when space was limiting. Thus, quantifying adult barnacle abundance in terms of total biomass might reveal a relationship with nearshore primary productivity at the regional scale along the open Atlantic coast.

In summary, we have identified regional differences in barnacle recruit and adult density on the NW Atlantic coast. Our data suggest that primarily bottom-up forcing (pelagic food supply) and secondarily adult density are important factors driving regional recruitment patterns, while benthic disturbance (winter ice scour) is an important factor influencing adult density.

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## References

- Adey, W.H., Hayek, L.C., 2005. The biogeographic structure of the western North Atlantic rocky intertidal. *Cryptogamie: Algol.* 26, 35–66.
- Barnes, D.K.A., 1999. The influence of ice on polar nearshore benthos. *J. Mar. Biol. Assoc. UK* 79, 401–407.
- Belt, K.M., Cole, S.W.B., Scrosati, R.A., 2009. Intertidal barnacles as indicators of the intensity of scour by sea ice. *Mar. Ecol. Prog. Ser.* 381, 183–187.
- Bergeron, P., Bourget, E., 1986. Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice-disturbed environment. *Mar. Ecol. Prog. Ser.* 28, 129–145.
- Bertness, M.D., 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* 70, 257–268.
- Bertness, M.D., 2007. *Atlantic shorelines. Natural history and ecology.* Princeton University Press, Princeton.
- Bertness, M.D., Gaines, S.D., Stephens, E.G., Yund, P.O., 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 156, 199–215.
- Bertness, M.D., Gaines, S.D., Wahle, R.A., 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.* 137, 103–110.
- Bertness, M.D., Gaines, S.D., Yeh, S.M., 1998. Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology* 79, 1382–1394.
- Bousfield, E.L., 1954. The distribution and spawning seasons of barnacles on the Atlantic coast of Canada. *Bull. Nat. Mus. Canada* 132, 112–154.
- Broitman, B.R., Blanchette, C.A., Menge, B.A., Lubchenco, J., Krenz, C., Foley, M., Raimondi, P.T., Lohse, D., Gaines, S.D., 2008. Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. *Ecol. Monogr.* 78, 403–421.
- Burrows, M.T., Jenkins, S.R., Robb, L., Harvey, R., 2010. Spatial variation in size and density of adult and post-settlement *Semibalanus balanoides*: effects of oceanographic and local conditions. *Mar. Ecol. Prog. Ser.* 398, 207–219.
- Chan, B.K.K., Morrill, D., De Pirro, M., Leung, K.M.Y., Williams, G.A., 2006. Summer mortality: effects on the distribution and abundance of the acorn barnacle *Tetraclita japonica* on tropical shores. *Mar. Ecol. Prog. Ser.* 328, 195–204.
- Connolly, S.R., Menge, B.A., Roughgarden, J., 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82, 1799–1813.
- R Development Core Team, 2010. R: a language and environment for statistical computing. Last accessed on 14 June. <http://www.r-project.org>.
- Devred, E., Sathyendranath, S., Platt, T., 2007. Delineation of ecological provinces using ocean colour radiometry. *Mar. Ecol. Prog. Ser.* 346, 1–13.
- Fisheries and Oceans Canada, 2010. Operational remote sensing. Last accessed on 14 June. [http://www.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs\\_3.html](http://www.mar.dfo-mpo.gc.ca/science/ocean/ias/seawifs/seawifs_3.html).
- Gosselin, L.A., Bourget, E., 1989. The performance of an intertidal predator, *Thais lapillus*, in relation to structural heterogeneity. *J. Anim. Ecol.* 58, 287–303.
- Grant, W.S., 1977. High-intertidal community organization on a rocky headland in Maine, USA. *Mar. Biol.* 44, 15–25.
- Gutt, J., 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biol.* 24, 553–564.
- Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschanivsky, N.A., Pratchett, M.S., Tanner, J.E., Willis, B.L., 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81, 2241–2249.
- Jenkins, S.R., Åberg, P., Cervin, G., Coleman, R.A., Delany, J., Della Santina, P., Hawkins, S.J., LaCroix, E., Myers, A.A., Lindgarth, M., Power, A.M., Roberts, M.F., Hartnoll, R.G., 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *J. Exp. Mar. Biol. Ecol.* 243, 209–225.
- Jenkins, S.R., Murua, J., Burrows, M.T., 2008. Temporal changes in the strength of density-dependent mortality and growth in intertidal barnacles. *J. Anim. Ecol.* 77, 573–584.
- Jonsson, P.R., Bertness, M.D., Larsson, A.I., 2004. Linking larval supply to recruitment: flow-mediated control of initial adhesion of barnacle larvae. *Ecology* 85, 2850–2859.
- Lagos, N.A., Castilla, J.C., Broitman, B.R., 2008. Spatial environmental correlates of intertidal recruitment: a test using barnacles in northern Chile. *Ecol. Monogr.* 78, 245–261.
- Leonard, G.H., 2000. Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81, 1015–1030.
- Leonard, G.H., Levine, J.M., Schmidt, P.R., Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79, 1395–1411.

- Leslie, H.M., Breck, E.N., Chan, F., Lubchenco, J., Menge, B.A., 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proc. Natl Acad. Sci. USA* 102, 10534–10539.
- López, D.A., González, M.L., 2003. Density-dependent effects in *Jehlius cirratus* (Darwin, 1854) (Cirripedia: Chthamalidae) under different growth conditions. *Mar. Ecol. Prog. Ser.* 249, 289–302.
- MacPherson, E.A., Scrosati, R., Chareka, P., 2008. Barnacle recruitment on ice-scoured shores in eastern Canada. *J. Mar. Biol. Assoc. UK* 88, 289–291.
- McCook, L.J., Chapman, A.R.O., 1997. Patterns and variations in natural succession following massive ice scour of a rocky intertidal seashore. *J. Exp. Mar. Biol. Ecol.* 214, 121–147.
- Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46, 355–393.
- Menge, B.A., 1978. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action, and desiccation on predator feeding rates. *Oecologia* 34, 17–35.
- Menge, B.A., 2000a. Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecol. Monogr.* 70, 265–288.
- Menge, B.A., 2000b. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.* 250, 257–289.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proc. Natl Acad. Sci. USA* 94, 14530–14535.
- Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G., Burnaford, J.L., 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecol. Monogr.* 69, 297–330.
- Menge, B.A., Chan, F., Nielsen, K.J., Di Lorenzo, E., Lubchenco, J., 2009. Climatic variation alters supply-side ecology: impact of climate patterns on phytoplankton and mussel recruitment. *Ecol. Monogr.* 79, 379–395.
- Minchinton, T.E., Scheibling, R.E., 1991. The influence of larval supply and settlement on the population structure of barnacles. *Ecology* 72, 1867–1869.
- Minchinton, T.E., Scheibling, R.E., 1993. Free-space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Mar. Ecol. Prog. Ser.* 95, 233–244.
- Minchinton, T.E., Scheibling, R.E., Hunt, H.L., 1997. Recovery of an intertidal assemblage following a rare occurrence of scouring by sea ice in Nova Scotia. *Canada. Bot. Mar.* 40, 139–148.
- Navarrete, S.A., Broitman, B.R., Menge, B.A., 2008. Interhemispheric comparison of recruitment to intertidal communities: Pattern persistence and scales of variation. *Ecology* 89, 1308–1322.
- Noda, T., 2004. Large-scale variability in recruitment of the barnacle *Semibalanus cariosus*: its cause and effects on the population density and predator. *Mar. Ecol. Prog. Ser.* 278, 241–252.
- O’Riordan, R.M., Arenas, F., Arrontes, J., Castro, J.J., Cruz, T., Delany, J., Martínez, B., Fernández, C., Hawkins, S.J., McGrath, D., Myers, A.A., Oliveros, J., Pannacciulli, F.G., Power, A.M., Relini, G., Rico, J.M., Silva, T., 2004. Spatial variation in the recruitment of the intertidal barnacles *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli) (Crustacea: Cirripedia) over an European scale. *J. Exp. Mar. Biol. Ecol.* 304, 243–264.
- Palma, A.T., Pardo, L.M., Veas, R., Cartes, C., Silva, M., Manríquez, K., Díaz, A., Muñoz, C., Ojeda, F.P., 2006. Coastal brachyuran decapods: settlement and recruitment under contrasting coastal geometry conditions. *Mar. Ecol. Prog. Ser.* 316, 139–153.
- Peterson, C.H., 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* 39, 1–24.
- Pineda, J., DiBacco, C., Starczak, V., 2005. Barnacle larvae in ice: survival, reproduction, and time to postsettlement metamorphosis. *Limnol. Oceanogr.* 50, 1520–1528.
- Pineda, J., Starczak, V., Stueckle, T.A., 2006. Timing of successful settlement: demonstration of a recruitment window in the barnacle *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.* 320, 233–237.
- Pineda, J., Reyns, N.B., Starczak, V.R., 2009. Complexity and simplification in understanding recruitment in benthic populations. *Popul. Ecol.* 51, 17–32.
- Pinheiro, J.C., Bates, D.M., 2009. Mixed-effects models in S and S-plus. Springer, Berlin.
- Saucier, F.J., Roy, F., Gilbert, D., Pellerin, P., Ritchie, R., 2003. Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada. *J. Geophys. Res.* 108 (C8), 326910.1029/2000JC000686.
- Scrosati, R., Eckersley, L.K., 2007. Thermal insulation of the intertidal zone by the ice foot. *J. Sea Res.* 58, 331–334.
- Scrosati, R., Heaven, C., 2006. Field technique to quantify intensity of scouring by sea ice in rocky intertidal habitats. *Mar. Ecol. Prog. Ser.* 320, 293–295.
- Scrosati, R., Heaven, C., 2007. Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Mar. Ecol. Prog. Ser.* 342, 1–14.
- Svensson, C.J., Jenkins, S.R., Hawkins, S.J., Myers, A.A., Range, P., Paula, J., O’Riordan, R.M., Åberg, P., 2004. Models of open populations with space-limited recruitment in stochastic environments: relative importance of recruitment and survival in populations of *Semibalanus balanoides*. *Mar. Ecol. Prog. Ser.* 275, 185–197.
- Underwood, A.J., 1997. Experiments in ecology. Cambridge University Press, Cambridge.
- Underwood, A.J., Keough, M.J., 2001. Supply-side ecology. The nature and consequences of variations in recruitment of intertidal organisms. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer, Sunderland, pp. 183–200.
- Vargas, C.A., Manríquez, P.H., Navarrete, S.A., 2006. Feeding by larvae of intertidal invertebrates: assessing their position in pelagic food webs. *Ecology* 87, 444–457.