A 5-year study (2014-2018) of the relationship between coastal phytoplankton abundance and intertidal barnacle size along the Atlantic Canadian coast

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Benthic–pelagic coupling refers to the ecological relationships between benthic and pelagic environments. Studying such links is particularly useful to understand biological variation in intertidal organisms along marine coasts. Filter-feeding invertebrates are ecologically important on marine rocky shores, so they have often been used to investigate benthic–pelagic coupling. Most studies, however, have been conducted on eastern ocean boundaries. To evaluate benthic–pelagic coupling on a western ocean boundary, we conducted a 5-year study spanning 415 km of the Atlantic coast of Nova Scotia (Canada). We hypothesized that the summer size of intertidal barnacles (*Semibalanus balanoides*) recruited in the preceding spring would be positively related to the nearshore abundance (biomass) of phytoplankton, as phytoplankton constitutes food for the nauplius larvae and benthic stages of barnacles. Every year between 2014 and 2018, we measured summer barnacle size in clearings created before spring recruitment on the rocky substrate at eight wave-exposed locations along this coast. We then examined the annual relationships between barnacle size and chlorophyll-*a* concentration (Chl-*a*), a proxy for phytoplankton biomass. For every year and location, we used satellite data to calculate Chl-*a* averages for a period ranging from the early spring (when most barnacle larvae were in the water) to the summer (when barnacle size was measured after weeks of growth following spring benthic recruitment). The relationships were always positive, Chl-*a* explaining nearly half, or more, of the variation in barnacle size in four of the five studied years. These are remarkable results because they were based on a relatively limited number of locations (which often curtails statistical power) and point to the relevance of pelagic food supply to explain variation in intertidal barnacle size along this western ocean boundary coast.

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8   ABSTRACT

9   Benthic–pelagic coupling refers to the ecological relationships between benthic and pelagic

10   environments. Studying such links is particularly useful to understand biological variation in

11   intertidal organisms along marine coasts. Filter-feeding invertebrates are ecologically important

12   on marine rocky shores, so they have often been used to investigate benthic–pelagic coupling.

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14   pelagic coupling on a western ocean boundary, we conducted a 5-year study spanning 415 km of

15   the Atlantic coast of Nova Scotia (Canada). We hypothesized that the summer size of intertidal

16   barnacles (*Semibalanus balanoides*) recruited in the preceding spring would be positively related

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18   the nauplius larvae and benthic stages of barnacles. Every year between 2014 and 2018, we

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20   substrate at eight wave-exposed locations along this coast. We then examined the annual

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22   phytoplankton biomass. For every year and location, we used satellite data to calculate Chl-*a*

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24   water) to the summer (when barnacle size was measured after weeks of growth following spring

25   benthic recruitment). The relationships were always positive, Chl-*a* explaining nearly half, or

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29   intertidal barnacle size along this western ocean boundary coast.

31   INTRODUCTION

32   Benthic–pelagic coupling refers to the ecological relationships that exist between benthic

33   and pelagic environments (*Griffiths et al., 2017*). Recognition of such links has particularly

34   facilitated progress in the field of intertidal ecology. For example, understanding how pelagic

35   food supply and oceanographic features vary along coastlines frequently helps to predict, directly

36   or indirectly, alongshore properties of intertidal species. Such studies, however, have

37   overwhelmingly been conducted on eastern ocean boundaries (*Navarrete et al., 2005; Blanchette*

38   *et al., 2008; Menge & Menge, 2013; Salant & Shanks, 2018*).

39   For western ocean boundaries, a question needing more research remains to what extent

40   alongshore variation in intertidal species traits can be inferred from nearshore pelagic variables.

41   On the SW Atlantic coast, for example, the recruitment of intertidal filter-feeders (barnacles and

42   mussels) was recently found related to the abundance of phytoplankton (their main food source),

43   wave exposure, and seawater temperature (*Arribas et al., 2014; Mazzuco et al., 2015*). On the

44   NW Atlantic coast, surveys in the Gulf of Maine suggested that intertidal filter-feeder

45   recruitment might be influenced by currents affecting larval supply (*Bryson, Trussell &*

46   *Ewanchuk, 2014*). Larger-scale NW Atlantic surveys including sites on Canadian and American

47   shores have found links between coastal phytoplankton abundance and intertidal barnacle

48   recruitment (*Cole et al., 2011*) and between thermal stress during low tides and intertidal mussel

49   abundance (*Tam & Scrosati, 2011*).

50   The Atlantic Canadian coast in Nova Scotia is well suited to study benthic–pelagic coupling,

51   as it runs for some hundreds of km facing the open ocean. A study in 2014 revealed that the

52   recruitment of intertidal barnacles and mussels in wave-exposed locations along this coast was

53   positively related to pelagic food supply and, to a lesser degree, seawater temperature. In turn,

54   recruitment of these filter-feeders was related to their abundance later in the year and, ultimately,

55   to the abundance of their main predators (dogwhelks), suggesting bottom-up community

56   regulation (*Scrosati & Ellrich, 2018*). While filter-feeder recruitment may predict predator

57   abundance and even facilitation on other organisms (*Menge, 1976*), filter-feeder size is another

58   important aspect of bottom-up regulation, as larger sizes represent more food for higher trophic

59   levels (*Dunkin & Hughes, 1984; Carroll & Wethey, 1990*). Therefore, in this paper, we focus on

60   barnacle size. Using field data for five consecutive years (2014–2018), we test the hypothesis

61   that phytoplankton abundance (biomass) is positively related to intertidal barnacle size along this

62   coast.

63   MATERIALS AND METHODS

64   From 2014 to 2018, we collected data at eight intertidal locations spanning 415 km of the

65   Atlantic coast of Nova Scotia (Fig. 1). For ease of interpretation, these locations are referred to

66   as L1 to L8, from north to south (their names and coordinates are given in Table 1). They all

67   have stable bedrock as substrate and are wave-exposed, as they face the open ocean directly.

68   Daily maximum water velocity (an indication of wave exposure) measured in exposed intertidal

69   habitats along this coast ranges between 6-12 m s^{-1} (*Hunt & Scheibling, 2001; Scrosati &*

70   *Heaven, 2007; Ellrich & Scrosati, 2017*). Using wave-exposed intertidal habitats to study

71   benthic–pelagic coupling is particularly fitting because such places face the open ocean, which

72   facilitates the identification of pelagic influences.

73   We measured the size of *Semibalanus balanoides*, which is the only intertidal barnacle

74   species on this coast. For each location, we considered the intertidal range to be the vertical

75   distance between chart datum (0 m in elevation, or lowest normal tide in Canada) and the highest

76   elevation where sessile perennial organisms (coincidentally, *S. balanoides*) occurred on the

77 substrate outside of crevices (*Scrosati & Heaven, 2007*). We divided the intertidal range by three

78 and measured barnacle size just above the bottom boundary of the upper third of the intertidal

79 range. As tidal amplitude increases from 1.8 m in L1 to 2.4 m in L8 (*Tide-Forecast, 2019*), this

80 method allowed us to measure barnacle size along the coast at comparable elevations in terms of

81 exposure to aerial conditions during low tides.

82   In Atlantic Canada, *Semibalanus balanoides* mates in autumn, broods in winter, and releases

83 pelagic larvae in spring (*Bousfield, 1954; Crisp, 1968; Bouchard & Aiken, 2012*). Larvae settle

84 in intertidal habitats and metamorphose into benthic recruits during May and June, which is thus

85 considered to be the recruitment season (*Ellrich, Scrosati & Molis, 2015*). To measure barnacle

86 size unaffected by other sessile species (*Beermann et al., 2013*), we made clearings (100-cm^2

87 quadrats) of the substrate in late April of each year along the same intertidal elevation (see

88 above) at each location. Table 2 gives the number of quadrats with barnacle size data for each

89 location and year. Different quadrats were cleared each year by removing all pre-existing

90 organisms from the substrate using a chisel and a metallic mesh scourer. We measured the size

91 of the barnacles recruited therein as they looked in summer after growth (Table 2, Fig. 2). We

92 determined barnacle size as the basal shell diameter measured along a straight line passing

93 through the middle of the rostrum and the carina (*Chan et al., 2006*). To avoid influences of

94 intraspecific crowding (*Bertness, 1989*) on our size data, we only measured barnacles that were

95 not in contact with any neighbouring barnacles. Such organisms were common because, in

96 summer, barnacles constituted almost the only macroscopic species in the quadrats and their

97 density was not particularly high (Fig. 2). We measured size for a maximum of 10 such barnacles

98 per quadrat (all barnacles if there were 10 or less in a quadrat and a random selection of 10 if

99 there were more than 10 in a quadrat). For data analyses, we first calculated mean barnacle size

100   for each quadrat and, then, averaged the corresponding quadrat means to generate a value of

101   mean barnacle size per location and year.

102   To describe phytoplankton abundance, we used MODIS-Aqua satellite data on the

103   concentration of chlorophyll-*a* in seawater (Chl-*a*, hereafter) for the 4-km-x-4-km cells that

104   include our eight locations (*NASA, 2019a*). The coordinates of each cell are stated in Table 1.

105   Satellite Chl-*a* data are often used in intertidal ecology (*Navarrete et al., 2005; Burrows et al.,*

106   *2010; Arribas et al., 2014; Mazzuco et al., 2015; Lara et al., 2016*) and are especially useful

107   when studying hundreds of km of coastline for which in-situ phytoplankton data are lacking

108   (*Legaard & Thomas, 2006*). For this study, satellite data should be appropriate because

109   neighbouring locations are considerably more distant from one another than the data cell size

110   (Fig. 1). To retrieve the Chl-*a* data, we first obtained mapped Chl-*a* data from the OceanColor

111   database (*NASA, 2019a*). From these mapped data, we extracted the Chl-*a* values for our

112   locations using the pixel extraction function of SeaDAS (*NASA, 2019b*) and the coordinates of

113   our locations (Table 1). For each location and year, we calculated the mean of all of the daily

114   Chl-*a* values that were available from the beginning of April to the date when we measured

115   barnacle size in summer (Table 2). Although barnacle recruitment occurs in May and June, we

116   considered April Chl-*a* because of its possible effects on larval condition ultimately influencing

117   benthic growth (*Barnes, 1956; Emlet & Sadro, 2006*). Specifically, the nauplius larvae of *S.*

118   *balanoides* feed for 5–6 weeks in coastal waters before reaching the settling cyprid stage

119   (*Bousfield, 1954; Drouin, Bourget & Tremblay, 2002*), and a recent study in our region

120   concluded that most of the larvae that result in recruits are likely in the water in April (*Scrosati*

121   *& Ellrich, 2016*). The Chl-*a* values between May and the summer dates when we measured

122   barnacle size were used to represent pelagic food supply for the growing recruits.

123   For each year, we investigated the relationship between phytoplankton abundance and

124   barnacle size by evaluating Pearson's correlation between the location means of Chl-*a* and size.

125   As our hypothesis was directional (a positive association between both variables), we performed

126   one-tailed tests of significance (*Quinn & Keough, 2002*). We also calculated the coefficient of

127   determination for each year to evaluate the amount of variation in barnacle size that was

128   statistically explained by Chl-*a*. We did the analyses with R version 3.5.1 (*R Core Team, 2018*).

129   The data used for this study are available in figshare (doi: 10.6084/m9.figshare.7212446).

130   RESULTS

131   The observed relationships between Chl-*a* and barnacle size were always positive. The

132   correlation coefficient was significant for 2014, 2016, and 2018 under a significance level of

133   0.05 and for 2015 under a less conservative significance level of 0.10 (Fig. 3). For 2017, the

134   correlation was not significant, but still associated to a low P value ($P = 0.119$), suggesting a

135   weak relationship that was hard to detect. As more data (more locations) for 2017 were

136   unavailable, we excluded the southernmost location (L8) from that year's dataset because L8 then

137   exhibited the lowest mean barnacle size (< 0.3 cm) for the entire dataset used for this study. This

138   modification yielded a significant correlation coefficient (Fig. 3), indicating that a positive size–

139   Chl-*a* relationship also existed for 2017, although for a more limited geographic extent that

140   excluded the southern end of the studied coast. Chl-*a* explained 49 % of the variation in barnacle

141   size in 2014, 32 % in 2015, 62 % in 2016, 47 % in 2017 (excluding L8), and 47 % in 2018. Each

142   year, barnacle size was highest at the same two neighbouring southern locations (L6 and L7).

143   Both such locations also exhibited a higher average Chl-*a* than the average for the other six

144   locations each year (Fig. 3).

145   DISCUSSION

146   This 5-year study along the Nova Scotia coast has revealed that the summer size of intertidal

147   barnacles recruited in the spring was positively related to the mean phytoplankton abundance for

148   the preceding months. This outcome is remarkable because the five examined correlations were

149   based on data for just eight locations (seven in 2017), a limited number that, by curbing

150   statistical power, often prevents field studies from detecting patterns in ecology. Surveying more

151   wave-exposed locations was not feasible because of safety concerns (dangerous site access or

152   lack of roads) and the need to sample all locations within a few days of difference every year.

153   Thus, the observed correlations highlight the relevance of Chl-*a* to statistically explain the

154   alongshore variation in barnacle size. Interestingly, in four of the five studied years (2014, 2016,

155   2017 –excluding L8–, and 2018), Chl-*a* explained nearly half, or more, of such variation.

156   These results are likely explained by the fact that phytoplankton is the main food source for

157   barnacle nauplius larvae and benthic stages (*Anderson, 1994; Jarrett, 2003; Gyory, Pineda &*

158   *Solow, 2013*). This consideration bears special relevance in light of the alongshore variation of

159   Chl-*a* (Fig. 3), since, for the 5 years of this study, the mean annual coefficient of variation for

160   Chl-*a* for our locations was 61 %. Given the temporal intra-annual resolution of the Chl-*a* data,

161   however, it is not possible to ascertain if the purported role of phytoplankton may have differed

162   depending on the developmental stage of barnacles (from pelagic larvae to the successive benthic

163   stages until size was measured). Thus, this study should be best viewed as broad evidence

164   revealing benthic–pelagic coupling on the NW Atlantic coast using variables not previously

165   examined together for this system (*Bryson, Trussell & Ewanchuk, 2014; Scrosati & Ellrich,*

166   *2018*). Ultimately, this study suggests that a spatial association between phytoplankton

167   abundance and filter-feeder growth can occur on a western ocean boundary, adding to similar

168   findings reported for eastern ocean boundaries (*Menge et al., 1997, 2003*).

169   A consideration about satellite Chl-*a* data is worth making at this point. In recent years,

170   several studies on intertidal ecology that needed information on coastal phytoplankton used

171   satellite Chl-*a* data as a proxy (*Navarrete et al., 2005; Burrows et al., 2010; Arribas et al., 2014;*

172   *Mazzuco et al., 2015; Lara et al., 2016*). Although such data are useful for coasts for which in-

173   situ phytoplankton data are unavailable (*Legaard & Thomas, 2006*), the fact remains that a proxy

174   is being used. For our study, that was the only option. Because our goal was to evaluate

175   statistical relationships between summer barnacle size and average phytoplankton abundance

176   from spring to summer, having in-situ phytoplankton data would have required frequent seawater

177   samplings during those months at each of our eight locations for the five years of the study.

178   However, that was not possible for logistical reasons. Oceanographic research is continuously

179   improving the algorithms to accurately infer coastal phytoplankton abundance from satellite data

180   (*Bellacicco et al., 2016; Yang et al., 2018*). Thus, future studies could re-examine our hypothesis

181   as further improvements are made on that line. If the logistics to generate in-situ phytoplankton

182   data for the required spatial and temporal scales can be solved, our hypothesis could also be

183   examined using direct phytoplankton data. In any case, given the consistently positive

184   relationships between barnacle size and Chl-*a* found for our coast, that our wave-exposed

185   locations fully face open oceanic waters, that no major rivers occur along the studied coast, that

186   human population density is very low along this coast, and that pelagic food supply enhances

187   benthic filter-feeder growth (*Menge et al., 1997, 2003*), it seems reasonable to expect positive

188   relationships under those improved approaches as well.

189   From the results of the present study, an emerging question of interest is what may cause

190   variation in phytoplankton abundance along the Nova Scotia coast. The intermittent upwelling

191   hypothesis (IUH; *Menge & Menge, 2013*) refers to possible mechanisms. The IUH considers that

192 frequent wind-driven upwelling would limit coastal phytoplankton abundance because upwelled

193 nutrients (necessary for phytoplankton development) would be taken offshore before nearshore

194 blooms can occur. Frequent downwelling would also limit coastal phytoplankton abundance by

195 driving nutrient-poor surface waters to the coast. Intermittent upwelling, however, would allow

196 upwelled nutrients to remain near the coast long enough for phytoplankton to bloom, thus

197 favouring the growth of intertidal filter-feeders (*Menge & Menge 2013*). Wind-driven upwelling

198 has been reported for the Atlantic coast of Nova Scotia (*Petrie, Topliss & Wright, 1987; Shan et*

199 *al., 2016*), making the IUH worth testing for this coast. In particular, a study in 1984 reported

200 coastal cooling between June and July near L6 and L7, while seawater temperature increased for

201 the same period of time near our northern locations (*Petrie, Topliss & Wright, 1987*). The

202 localized upwelling on the Atlantic coast of Nova Scotia is probably intermittent, less frequent

203 and intense than on heavy-upwelling coasts like that of California. Therefore, the fact that mean

204 Chl-*a* for L6 and L7 was higher than for the other locations every year suggests that the IUH

205 might help to understand alongshore variation in phytoplankton abundance and, ultimately,

206 intertidal barnacle growth on our coast. Alternative analytic approaches, however, have found no

207 support for the mechanisms underlying the IUH, suggesting that surf zone width and tidally

208 generated internal waves better explain changes in coastal phytoplankton abundance (*Salant &*

209 *Shanks, 2018; Shanks & Morgan, 2018*). At present, this topic is undergoing an active debate

210 (*Menge & Menge, 2019; Shanks & Morgan, 2019*). Whatever the causes of Chl-*a* variation along

211 the Nova Scotia coast, it is likely that some combination of oceanographic properties is involved.

212 These properties (upwelling, surf zone width, internal waves, etc.) could change differently every

213 year along the coast, thus generating complex scenarios worth investigating from an

214 oceanographic standpoint.

215   CONCLUSIONS

216   Based on data collected over five years (2014–2018) for locations spanning 415 km of the

217   Atlantic Canadian coast, this study reveals a persistent relationship between the summer size of

218   intertidal barnacles recruited in the preceding spring and the nearshore abundance of

219   phytoplankton (food for nauplius larvae and benthic stages of barnacles). Phytoplankton

220   abundance, measured through satellite Chl-*a* data, explained nearly half, or more, of the

221   alongshore variation in barnacle size in four of the five studied years. These are remarkable

222   results because they were based on a relatively limited number of locations and point to the

223   relevance of pelagic food supply to explain variation in intertidal barnacle size along this western

224   ocean boundary coast.

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359   Figure legends

360   **Fig. 1.** Map indicating the eight wave-exposed locations studied along the Atlantic coast of Nova

361   Scotia, Canada.

362   **Fig. 2.** Example of barnacle size differences between locations: (A) L1 and (B) L6. The frame

363   bordering each photo belongs to the sampling quadrat. One full side of the quadrat (10 cm) is

364   shown at the top of both pictures. The photos were taken by R. A. Scrosati in August 2018.

365   **Fig. 3.** Relationships between coastal phytoplankton abundance (chlorophyll-*a* concentration)

366   and intertidal barnacle size in (A) 2014, (B) 2015, (C) 2016, (D) 2017, and (E) 2018. The

367   correlation and functional relationship shown for 2017 were calculated without including L8

368   (see Results for rationale); the data point for L8 is nonetheless shown in this figure simply for

369   visual reference.

370

Information on locations

Names and coordinates of the eight wave-exposed intertidal locations examined for this study and coordinates of the centre of the 4-km-x-4-km cells from which Chl-*a* data were extracted.

1   **Table 1.** Names and coordinates of the eight wave-exposed intertidal locations examined for this

2   study and coordinates of the centre of the 4-km-x-4-km cells from which Chl-*a* data were

3   extracted.

Location code	Location name	Location coordinates	Cell centre coordinates
L1	Glasgow Head	45.3203, -60.9592	45.3125, -60.9791
L2	Deming Island	45.2121, -61.1738	45.2292, -61.1875
L3	Tor Bay Provincial Park	45.1823, -61.3553	45.1875, -61.3542
L4	Sober Island	44.8223, -62.4573	44.8125, -62.4375
L5	Duck Reef	44.4913, -63.5270	44.4797, -63.5208
L6	Western Head	43.9896, -64.6607	43.9797, -64.6458
L7	West Point	43.6533, -65.1309	43.6458, -65.1458
L8	Baccaro Point	43.4496, -65.4697	43.4375, -65.4792

Survey dates and sample sizes

Dates on which the quadrats were photographed. The number of available quadrats with barnacle size data is provided in parenthesis.

1   **Table 2.** Dates on which the quadrats were photographed. The number of available quadrats with

2   barnacle size data is provided in parenthesis.

Location	2014	2015	2016	2017	2018
L1	17 August (8)	4 September (17)	22 August (8)	16 August (12)	13 August (8)
L2	9 August (8)	28 August (7)	22 August (8)	25 August (8)	13 August (8)
L3	10 August (4)	28 August (11)	25 August (3)	28 August (8)	13 August (7)
L4	13 August (7)	2 September (16)	27 August (4)	19 August (8)	14 August (8)
L5	12 August (7)	1 September (21)	21 August (7)	22 August (8)	11 August (8)
L6	12 August (8)	31 August (20)	20 August (8)	21 August (8)	10 August (8)
L7	11 August (2)	30 August (14)	19 August (7)	18 August (7)	10 August (7)
L8	11 August (6)	29 August (8)	19 August (3)	18 August (5)	10 August (7)

Figure 1

Map of the studied locations.

Map indicating the eight wave-exposed locations studied along the Atlantic coast of Nova Scotia, Canada.
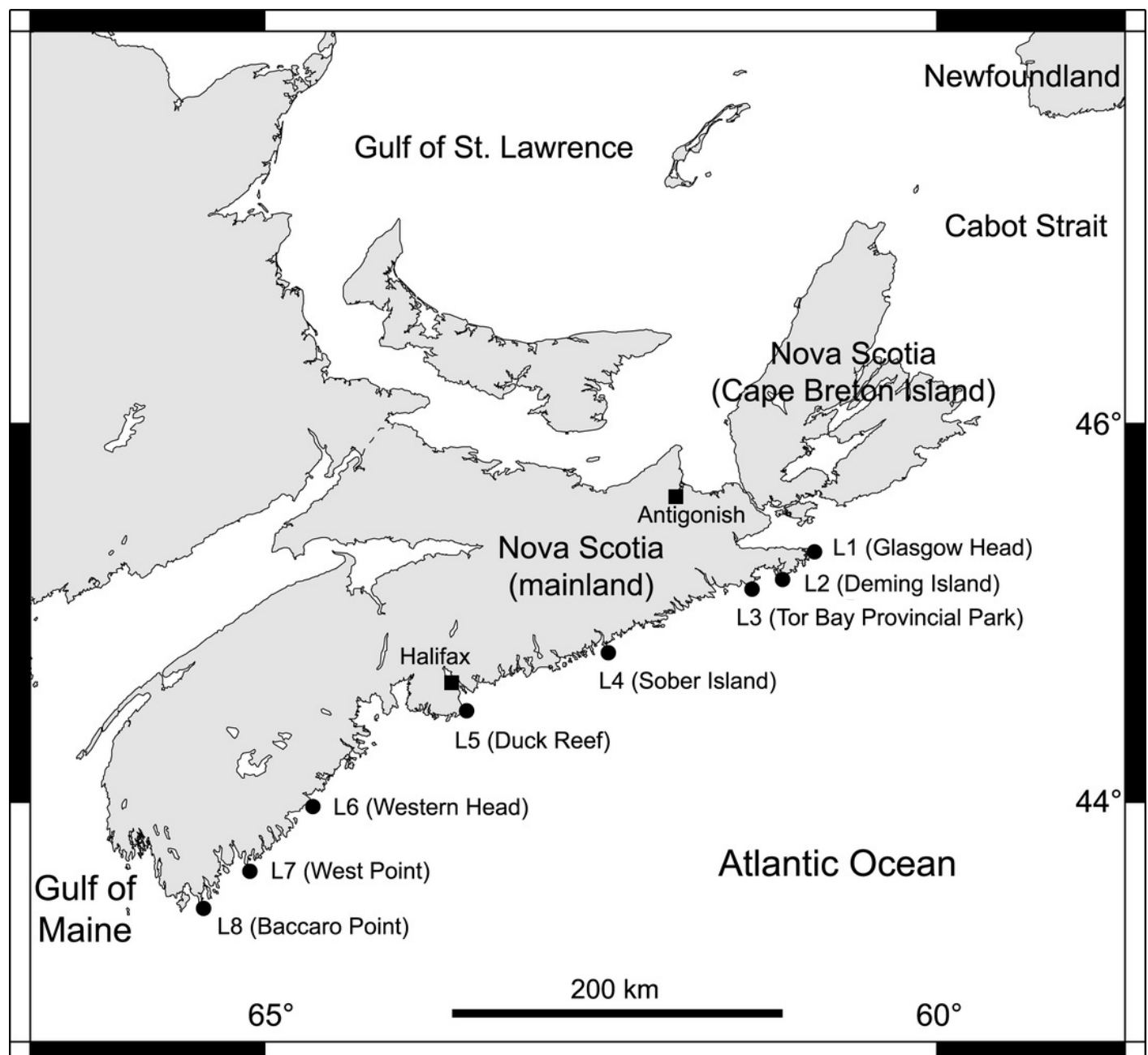
Figure 2

Barnacle size.

Example of barnacle size differences between locations: (A) L1 and (B) L6. The frame bordering each photo belongs to the sampling quadrat. One full side of the quadrat (10 cm) is shown at the top of both pictures. The photos were taken by Ricardo A. Scrosati in August 2018.
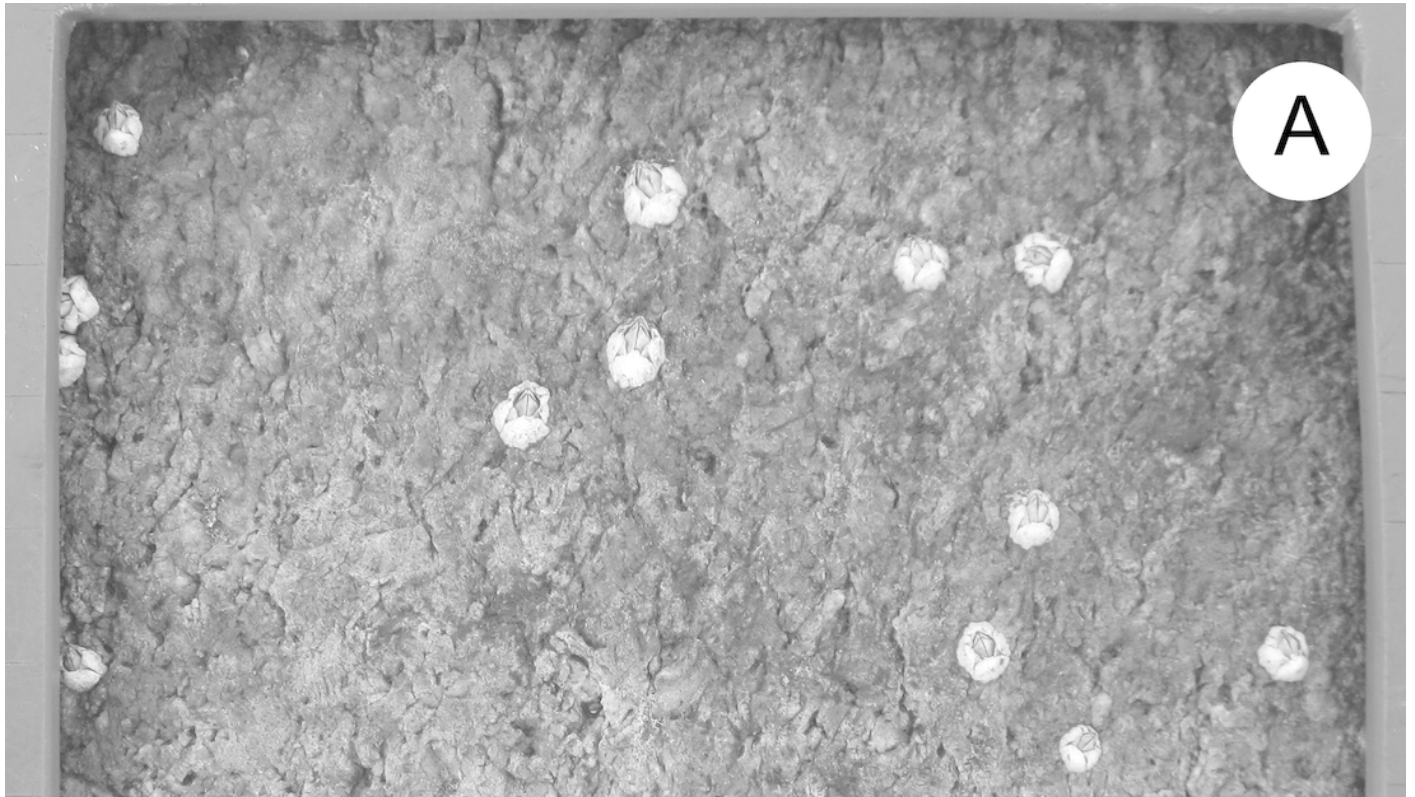
Figure 3

Relationships between coastal phytoplankton abundance (chlorophyll-*a* concentration) and intertidal barnacle size.

Relationships between coastal phytoplankton abundance (chlorophyll-*a* concentration) and intertidal barnacle size in (A) 2014, (B) 2015, (C) 2016, (D) 2017, and (E) 2018. The correlation and functional relationship shown for 2017 were calculated without including L8 (see Results for rationale); the data point for L8 is nonetheless shown in this figure simply for visual reference.

A
Barnacle size (cm)
2014
$r = 0.70$ ($P = 0.027$)

B
2015
$r = 0.57$ ($P = 0.072$)

C
Barnacle size (cm)
2016
$r = 0.79$ ($P = 0.010$)

D
2017
$r = 0.68$ ($P = 0.046$)
Chlorophyll-a concentration (mg m^{-3})

E
Barnacle size (cm)
2018
$r = 0.68$ ($P = 0.031$)
Chlorophyll-a concentration (mg m^{-3})

L1
L2
L3
L4
L5
L6
L7
L8