Unimodal relationship between small-scale barnacle recruitment and the density of pre-existing barnacle adults (#17214)

First revision

Please read the **Important notes** below, the **Review guidance** on page 2 and our **Standout reviewing tips** on page 3. When ready **submit online**. The manuscript starts on page 4.

Important notes

Editor
Donald Kramer

Files	1 Tracked changes manuscript(s) 1 Rebuttal letter(s) 2 Figure file(s) 1 Table file(s) 1 Raw data file(s) Please visit the overview page to **download and review** the files not included in this review PDF.
Declarations	No notable declarations are present

For assistance email **peer.review@peerj.com**

Review guidelines

Please read in full before you begin

How to review

When ready **submit your review online**. The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

📄 You can also annotate this PDF and upload it as part of your review

To finish, enter your editorial recommendation (accept, revise or reject) and submit.

BASIC REPORTING

✔ Clear, unambiguous, professional English language used throughout.

✔ Intro & background to show context. Literature well referenced & relevant.

✔ Structure conforms to **PeerJ standards**, discipline norm, or improved for clarity.

✔ Figures are relevant, high quality, well labelled & described.

✔ Raw data supplied (see **PeerJ policy**).

EXPERIMENTAL DESIGN

✔ Original primary research within **Scope of the journal**.

✔ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.

✔ Rigorous investigation performed to a high technical & ethical standard.

✔ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

ℹ Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.

✔ Data is robust, statistically sound, & controlled.

✔ Conclusions are well stated, linked to original research question & limited to supporting results.

✔ Speculation is welcome, but should be identified as such.

The above is the editorial criteria summary. To view in full visit **https://peerj.com/about/editorial-criteria/**

7 Standout
reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that your international audience can clearly understand your text. I suggest that you have a native English speaking colleague review your manuscript. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. ...* *4. The least important points*
Give specific suggestions on how to improve the manuscript	*Line 56: Note that experimental data on sprawling animals needs to be updated. Line 66: Please consider exchanging "modern" with "cursorial".*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Unimodal relationship between small-scale barnacle recruitment and the density of pre-existing barnacle adults

Ricardo A Scrosati [Corresp., 1] , Julius A Ellrich [1]

[1] Department of Biology, St. Francis Xavier University, Antigonish, Nova Scotia, Canada

Corresponding Author: Ricardo A Scrosati
Email address: rscrosat@stfx.ca

Recruitment is a key demographic process for population persistence. This paper focuses on barnacle (*Semibalanus balanoides*) recruitment. In rocky intertidal habitats from the Gulf of St. Lawrence coast of Nova Scotia (Canada), ice scour is common during the winter. At the onset of intertidal barnacle recruitment in early May (after sea ice has fully melted), mostly only adult barnacles and bare substrate are visible at high elevations in wave-exposed habitats. We conducted a multiannual study to investigate if small-scale barnacle recruitment could be predicted from the density of pre-existing adult barnacles. In a year that exhibited a wide adult density range (ca. 0–130 individuals dm^{-2}), the relationship between adult density and recruit density (scaled to the available area for recruitment, which excluded adult barnacles) was unimodal. In years that exhibited a lower adult density range (ca. 0–40/50 individuals dm^{-2}), the relationship between adult and recruit density was positive and resembled the lower half of the unimodal relationship. Overall, adult barnacle density was able to explain 26–40% of the observed variation in recruit density. The unimodal adult–recruit relationship is consistent with previously documented intraspecific interactions. Between low and intermediate adult densities, the positive nature of the relationship relates to the previously documented fact that adult barnacles attract settlement-seeking larvae, which likely enhances local population persistence where it is most needed. Between intermediate and high adult densities, where population persistence may be less compromised and the abundant adults may limit recruit growth and survival, the negative nature of the relationship suggests that adult barnacles at increasingly high densities stimulate larvae to settle elsewhere. The unimodal pattern may be especially common on shores with moderate rates of larval supply to the shore, because high rates of larval supply may swamp the coast with settlers, decoupling recruit density from local adult abundance.

1 **Unimodal relationship between small-scale barnacle recruitment and the**

2 **density of pre-existing barnacle adults**

3 Ricardo A. Scrosati *, Julius A. Ellrich

4 St. Francis Xavier University, Department of Biology, Antigonish, Nova Scotia B2G 2W5,

5 Canada

6 * Corresponding author. Email: rscrosat@stfx.ca. Phone: 1-902-867-5289

7   **Abstract**

8   Recruitment is a key demographic process for population persistence. This paper focuses on

9   barnacle (*Semibalanus balanoides*) recruitment. In rocky intertidal habitats from the Gulf of St.

10   Lawrence coast of Nova Scotia (Canada), ice scour is common during the winter. At the onset of

11   intertidal barnacle recruitment in early May (after sea ice has fully melted), mostly only adult

12   barnacles and bare substrate are visible at high elevations in wave-exposed habitats. We

13   conducted a multiannual study to investigate if small-scale barnacle recruitment could be

14   predicted from the density of pre-existing adult barnacles. In a year that exhibited a wide adult

15   density range (ca. 0–130 individuals dm^{-2}), the relationship between adult density and recruit

16   density (scaled to the available area for recruitment, which excluded adult barnacles) was

17   unimodal. In years that exhibited a lower adult density range (ca. 0–40/50 individuals dm^{-2}), the

18   relationship between adult and recruit density was positive and resembled the lower half of the

19   unimodal relationship. Overall, adult barnacle density was able to explain 26–40% of the

20   observed variation in recruit density. The unimodal adult–recruit relationship is consistent with

21   previously documented intraspecific interactions. Between low and intermediate adult densities,

22   the positive nature of the relationship relates to the previously documented fact that adult

23   barnacles attract settlement-seeking larvae, which likely enhances local population persistence

24   where it is most needed. Between intermediate and high adult densities, where population

25   persistence may be less compromised and the abundant adults may limit recruit growth and

26   survival, the negative nature of the relationship suggests that adult barnacles at increasingly high

27   densities stimulate larvae to settle elsewhere. The unimodal pattern may be especially common

28   on shores with moderate rates of larval supply to the shore, because high rates of larval supply

29   may swamp the coast with settlers, decoupling recruit density from local adult abundance.

30   **Introduction**

31   Recruitment is a key demographic process that affects the persistence of populations. Thus,

32   ecological research has often aimed at understanding its drivers (*Caley et al., 1996; Beck et al.,*

33   *2001; Palumbi & Pinsky, 2014*). As barnacles are abundant organisms on seashores worldwide,

34   they have often been used as model systems to study recruitment (*Jenkins et al., 2000; Navarrete*

35   *et al., 2008; Lathlean et al., 2013; Menge et al., 2015; Barbosa et al., 2016*). For barnacles,

36   settlement refers to the permanent contact with the substrate established by pelagic larvae

37   (*Jenkins et al., 2000*), while recruitment is the appearance of new organisms in a benthic habitat

38   that have resulted from the metamorphosis of settled larvae (*Ellrich et al., 2016a*). At regional

39   spatial scales, common drivers of barnacle recruitment are seawater temperature and pelagic

40   food (phytoplankton) supply, as both factors influence the growth and survival of the pelagic

41   larvae (*Menge & Menge, 2013; Rognstad et al., 2014; Scrosati & Ellrich, 2016*). At small spatial

42   scales, factors such as substrate rugosity (*Coombes et al. 2015*), water motion (*Bertness et al.,*

43   *1992; Ellrich & Scrosati, 2016*), macroalgal canopies (*Beermann et al., 2013*), and predator

44   chemical cues (*Johnson & Strathmann, 1989; Ellrich et al., 2015*) influence barnacle recruitment

45   in a variety of ways.

46   The presence of benthic conspecifics also influences barnacle recruitment at small scales.

47   For instance, experiments conducted under laboratory (*Crisp & Meadows, 1962; Matsumura et*

48   *al., 2000; Matsumura & Qian, 2014*) and field (*Chabot & Bourget, 1988; Raimondi, 1988;*

49   *Jarrett, 1997*) conditions have shown that chemical and visual cues from adult barnacles attract

50   pelagic conspecific larvae that are seeking settlement. Such an attraction is believed to aid larvae

51   to locate adequate areas for growth and reproduction (*Clare, 2011*). In agreement with those

52   findings, field experiments found that the presence of adult barnacles in moderate densities

53   enhance barnacle recruitment at small spatial scales (*Bertness et al., 1992; Kent et al., 2003;*

54   *Beermann et al., 2013; Ellrich et al., 2016a*).

55   The above studies suggest that small-scale recruitment in barnacle populations could be

56   predicted from the density of pre-existing adult barnacles. Between low and intermediate adult

57   densities, larval attraction by conspecific adults should result in a positive relationship between

58   adult and recruit density. However, between intermediate and high adult densities, the abundant

59   conspecific cues might indicate to pelagic larvae the potential for detrimental intraspecific

60   interactions, as the resulting recruits might be crushed by growing adults or experience a reduced

61   food supply outcompeted by the abundant adults (*Bertness et al., 1998; Hooper & Eichhorn,*

62   *2016*). In such conditions, recruit density (scaled to the substrate area available for settlement)

63   could decrease with adult density because of larval repulsion. Therefore, for a wide range of

64   adult density spanning low to high values, the adult–recruit relationship might be unimodal. This

65   paper tests this hypothesis using field data from rocky intertidal habitats from Atlantic Canada.

66   **Materials and methods**

67   We measured barnacle adult and recruit density at Sea Spray (45° 46.4' N, 62° 8.7' W), on

68   the southern coast of the Gulf of St. Lawrence, Nova Scotia. This is a long-term reference

69   location where we have monitored barnacles for several years (*Scrosati & Ellrich, 2016*). We

70   surveyed habitats that face open waters, which makes these habitats wave-exposed, with daily

71   values of maximum water velocity ranging between 4–8 m s^{-1} (*Scrosati & Heaven, 2007*). The

72   substrate is volcanic bedrock with a homogeneous rugosity and slope. On this coast,

73   *Semibalanus balanoides* is the only species of intertidal barnacle (*Scrosati & Heaven, 2007*). In

74   Atlantic Canada, this species mates in autumn, broods in winter, and releases larvae to the water

75   column in spring (*Bousfield, 1954; Crisp, 1968; Bouchard & Aiken, 2012*). On the studied coast,

76   recruits of *S. balanoides* appear in May and June (*Ellrich et al., 2015*) along the full vertical

77   intertidal range (*MacPherson & Scrosati, 2008; MacPherson et al., 2008*). The recruited

78   organisms reach reproductive maturity and adult size in the following fall (*Ellrich et al., 2016b*).

79   In winter, the sea surface of the Gulf of St. Lawrence freezes extensively (*Galbraith et al., 2015*)

80   and the ice causes physical disturbance in intertidal habitats as it moves with tides, winds,

81   currents, and waves (*Scrosati & Heaven, 2006; Musetta-Lambert et al., 2015*). The ice melts

82   before barnacle recruitment begins. As a result of ice scour, the macroscopic organisms

83   occurring in high-intertidal habitats facing open waters (habitats where winter ice scour is

84   intense) just before barnacle recruitment are almost exclusively adult barnacles scattered across

85   otherwise bare rocky substrate. Benthic macroalgae and mobile consumers (*e.g.*, snails) remain

86   virtually absent in such places during the barnacle recruitment season. Those organisms begin to

87   appear at such elevations mostly after barnacle recruits have ceased to appear (*Scrosati &*

88   *Heaven, 2007*). Thus, no interspecific interactions seemingly influence barnacle recruitment in

89   those habitats, leaving adult barnacle density as an important potential predictor of barnacle

90   recruitment.

91   We measured barnacle adult and recruit density at the lower part of the high intertidal zone,

92   at an elevation of approximately 1.2 m above chart datum (lowest normal tide). During the

93   second or third week of June between 2007 and 2016, we took digital pictures of 29–33

94   (depending on the year) 10 cm x 10 cm quadrats randomly positioned at that elevation spanning

95   20 m of coastline. With this approach, we were able to remove the influence of large-scale

96   oceanographic factors on larval and recruit ecology (*Menge & Menge, 2013*) and, thus, to focus

97   on small-scale influences at the patch (quadrat) level. We used the pictures of the quadrats to

98   measure adult and recruit density on a computer. In June, barnacle recruits are easily

99   distinguished from adults, because recruits are only 1–2 mm in basal diameter (Fig. 1). Barnacle

100   recruits were always abundant in the studied years (*Scrosati & Ellrich, 2016*), but adult barnacles

101   were often absent in the quadrats between 2010 and 2016, preventing us from considering those

102   years to meaningfully test our hypothesis. Therefore, we evaluated the hypothesis of this study

103   using the datasets for 2007, 2008, and 2009.

104   For each quadrat, we calculated barnacle adult density by dividing the number of adult

105   barnacles found therein by quadrat area (1 dm^2). To calculate recruit density, we divided the

106   number of recruits found in a quadrat by the area that was available for larvae to settle (and, thus,

107   for recruits to occur), which was quadrat area minus the area covered by adult barnacles because

108   larvae did not settle on the shells of adult barnacles. Under this analytical approach, if barnacle

109   adults had no ecological effect on larval settlement and subsequent recruitment, there would be

110   no relationship between adult density and recruit density (standardized as indicated above). A

111   positive relationship would indicate attraction of larvae by adults, while a negative relationship

112   would indicate repulsion of larvae by adults.

113   We tested our hypothesis by analyzing the 2007, 2008, and 2009 datasets separately. For

114   each year, we fitted the data to a linear model, a power model, and a quadratic model,

115   considering adult barnacle density as the independent variable and recruit density as the

116   dependent variable. Then, we compared the three models using an information-theoretic

117   approach. We considered linear and power models to evaluate potentially positive adult–recruit

118   relationships. While a linear model would describe a constant rate of change of recruit density

119   along the observed gradient of adult density, a power model would allow that rate to vary along

120   that gradient, potentially making the model more realistic. We considered a quadratic model to

121   evaluate the potential unimodal nature of the adult–recruit relationship. All models included an

122   intercept to acknowledge the possibility that recruit density could have non-zero values in the

123   absence of adult barnacles. The models were: $N_R = a\,N_A + b$ (linear), $N_R = a\,N_A{}^b + c$ (power), and

124    $N_R = a\,N_A{}^2 + b\,N_A + c$ (quadratic), where N_R is recruit density and N_A is adult density.

125   For each year, we compared the models based on their values of the corrected Akaike's

126   information criterion (AICc). With such values, we calculated the weight of evidence for each

127   model, which we used to identify the best model (the one with the highest weight of evidence)

128   for each year. Then, for each year, we evaluated the plausibility of the best model relative to the

129   two least favoured ones by calculating the corresponding evidence ratios between the weight of

130   evidence for the best model and the weight of evidence for the two least supported models

131   (*Anderson, 2008*). We calculated the adjusted squared correlation coefficient (R^2) for all models

132   to determine the amount of variation in recruit density that was statistically explained by adult

133   density (*Sokal & Rohlf, 2012*). We conducted these analyses with PRISM 6.0c for MacOS.

134   **Results**

135   In 2007 and 2009, adult barnacle density at the quadrat scale was never higher than 46

136   individuals dm^{-2}, while barnacle recruits occurred abundantly in all quadrats (Fig. 2). For both

137   years, the best model describing the adult–recruit relationship was the power model (Table 1).

138   For 2007, the power model was 1.8 times more plausible than the linear model and 4.3 times

139   more plausible than the quadratic model while, for 2009, it was 1.9 times more plausible than the

140   linear model and 3.5 times more plausible than the quadratic model (Table 1). The power model

141   also explained a higher percentage of the observed variation in recruit density (31% in 2007 and

142   26% in 2009) than the other two models (Table 1).

143   In 2008, adult barnacle density exhibited a wider range than in 2007 and 2009. The highest

144   value found in 2008 (129 individuals dm^{-2}) was almost three times higher than the highest value

145   found for the other two years. In 2008, barnacle recruits were also abundant on the shore (Fig. 2).

146   The best model describing the adult–recruit relationship in 2008 was the quadratic one, which

147   was 4.1 times more plausible than the power model and 14.2 times more plausible than the linear

148   one (Table 1). For 2008, the quadratic model explained a higher percentage of the observed

149   variation in recruit density (40%) than the other two models (Table 1).

150   **Discussion**

151   By monitoring a natural barnacle population spanning a wide range of adult density (in

152   2008), the predicted unimodal adult–recruit relationship was supported. When the available

153   range of adult density covered only low to intermediate values (in 2007 and 2009), a positive

154   relationship resembling the lower half of the unimodal relationship was found. This is a valuable

155   outcome for two reasons. The first one is that this study provides an example of how the shape of

156   a natural trend can be predicted from experiments that evaluated intraspecific interactions under

157   different densities of adult barnacles separately, either under moderate densities (*Raimondi,*

158   *1988; Kent et al., 2003; Beermann et al., 2013; Ellrich et al., 2016a*) or high densities (*Bertness*

159   *et al., 1998; Hooper & Eichhorn, 2016*). The second reason is that local-scale recruitment, a key

160   driver of population persistence for sessile invertebrates (*Minchinton & Scheibling, 1993;*

161   *Lathlean et al., 2013*), is hereby shown to be linked to the abundance of adult conspecifics. At

162   small spatial scales, adult barnacles generally do not contribute to local population persistence

163   through the larvae they spawn, because pelagic larvae are taken elsewhere by water motion

164   (*Caley et al., 1996*). However, the fact that adult barnacles attract settlement-seeking larvae

165   (regardless of where larvae come from) determines a positive adult–recruit relationship for

166   moderate adult densities, which likely enhances local population persistence where it is most

167   needed. Habitat areas with higher adult densities, where population persistence may be less

168 compromised and the abundant adults may hinder recruit growth and survival, seem to stimulate

169 larvae to settle elsewhere.

170 Using observed patterns of recruit density to infer patterns of larval settlement requires the

171 assumption that post-settlement mortality until recruit counts are done is unimportant. This was

172 seemingly the case for our system, because empty recruit shells (indicative of recruit mortality)

173 were very rare at the time of our surveys (see, for example, Fig. 1). Mortality becomes important

174 only later in the year, especially as the growing organisms experience thermal and desiccation

175 stress during the summer low tides.

176 It is worth noting that an observational study done on the coast of New Brunswick, also in

177 Atlantic Canada, reported a unimodal relationship for *Semibalanus balanoides* between recruit

178 density and the percent cover of pre-existing adults (*Chabot & Bourget, 1988*). However, that

179 study scaled recruit density to quadrat area. Given that larvae were noted (as in our study) to

180 avoid settling on adults, that study suggested that recruit density decreased from intermediate to

181 high values of adult cover because of the decreasing area available for larval settlement (*Chabot*

182 *& Bourget, 1988*). As we scaled recruit density to the available area for settlement (which

183 excludes adult barnacles), the present study in fact reveals that repulsion of settling larvae by

184 adults operates from intermediate to high values of adult abundance.

185 Immigration also represents the arrival of new organisms to a place, although it differs from

186 recruitment because immigrants are normally actively moving juveniles and adults, not recruits.

187 Thus, it is worth noting that a recent study using damselfish has experimentally demonstrated a

188 unimodal relationship between local fish density and the density of conspecific immigrants

189 (*Turgeon & Kramer, 2016*). The reasons for such a pattern seem also related to conspecific

190   attraction at moderate densities and the potential for competitive interactions at high densities

191   (*Turgeon & Kramer, 2016*).

192   The unimodal adult–recruit relationship for barnacles would likely hold mainly on shores

193   where the supply of pelagic larvae to intertidal habitats is moderate. On shores subjected to a

194   very high larval supply (e.g., because of mild water temperatures or high planktonic food

195   supply), larvae quickly colonize preferred substrate and new larvae arriving to the shore

196   eventually colonize less preferred areas also abundantly (*Bertness et al., 1992*). This suggests

197   that, under very high larval supply rates, barnacle recruit density could be unrelated to the

198   density of pre-existing adults. Seemingly in support of this notion, a study on Scottish shores

199   subjected to an unusually high supply of *S. balanoides* larvae reported no linear relationship

200   between the density of recruits and that of pre-existing adults (*Hansson et al., 2003*). However,

201   the possible occurrence of nonlinear relationships was not evaluated in that study. In addition,

202   the data examined in that study included density values from several intertidal elevations, which

203   likely increased data variability because larval settlement rates increase towards lower elevations

204   because of the longer immersion times (*Bertness et al., 1992*). It would thus appear useful to

205   apply the methodology of the present study to evaluate on a suitable shore the notion that

206   barnacle recruit density is unrelated to the density of pre-existing adults under very high rates of

207   larval supply.

208   Finally, despite the variety of factors that influence barnacle recruitment at small scales

209   (*Johnson & Strathmann, 1989*; *Bertness et al., 1992*; *Beermann et al., 2013*; *Coombes et al.*

210   *2015*; *Ellrich et al., 2015*; *Ellrich & Scrosati, 2016*), it is remarkable that a single factor (adult

211   barnacle density) was able to explain 26–40% of the variation in recruit density observed on our

212   shore. This may have been the case because the surveyed habitats exhibit a similar degree of

213 wave exposure and substrate rugosity, composition, and slope. This was, in fact, the main reason

214 to select this coast to address the objective of this study. In any case, a multifactorial field

215 experiment could evaluate the relative explanatory ability of several small-scale factors acting

216 simultaneously. This would be a profitable exercise, as the majority of studies have generally

217 evaluated the influence of only one or two factors at a time (*Johnson & Strathmann, 1989;*

218 *Beermann et al., 2013; Coombes et al., 2015; Ellrich et al., 2015; Ellrich & Scrosati, 2016*).

219 **Acknowledgements** We thank Donald Kramer, Augusto Flores, and an anonymous

220 reviewer for constructive comments on an earlier version of this paper.

221 **References**

222 **Anderson DR. 2008.** *Model-based inference in the life sciences: a primer on evidence.* New

223 York: Springer.

224 **Barbosa ACC, Gomes CC, Pereira GC, Bueno M, Flores AAV. 2016.** Local biological

225 drivers, not remote forcing, predict settlement rate to a subtropical barnacle population. *Marine*

226 *Ecology Progress Series* **543**:201–208.

227 **Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B,**

228 **Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP. 2001.** The

229 identification, conservation, and management of estuarine and marine nurseries for fish and

230 invertebrates. *BioScience* **51**:633–641.

231 **Beermann AJ, Ellrich JA, Molis M, Scrosati RA. 2013.** Effects of seaweed canopies and adult

232 barnacles on barnacle recruitment: the interplay of positive and negative influences. *Journal of*

233 *Experimental Marine Biology and Ecology* **448**:162–170.

234   **Bertness MD, Gaines SD, Stephens EG, Yund PO. 1992.** Components of recruitment in

235   populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental*

236   *Marine Biology and Ecology* **156**:199–215.

237   **Bertness MD, Gaines SD, Yeh SM. 1998.** Making mountains out of barnacles: the dynamics of

238   acorn barnacle hummocking. *Ecology* **79**:1382–1394.

239   **Bouchard GM, Aiken RB. 2012.** Latitudinal variation in the reproductive cycle and size of the

240   northern rock barnacle *Semibalanus balanoides* (L.) (Cirripedia, Archaeobalanidae) in the Bay

241   of Fundy. *Crustaceana* **85**:779–787.

242   **Bousfield EL. 1954.** The distribution and spawning seasons of barnacles on the Atlantic coast of

243   Canada. *Bulletin of the National Museum of Canada* **132**:112–154.

244   **Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA. 1996.** Recruitment and

245   the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*

246   **27**:477–500.

247   **Chabot R, Bourget E. 1988.** Influence of substratum heterogeneity and settled barnacle density

248   on the settlement of cypris larvae. *Marine Biology* **97**:45–56.

249   **Clare AS. 2011.** Toward a charaterization of the chemical cue to barnacle gregariousness. In:

250   Breithaupt T, Thiel M, eds. *Chemical communication in crustaceans.* New York: Springer,

251   431–450.

252   **Coombes MA, La Marca EC, Naylor LA, Thompson RC. 2015.** Getting into the groove:

253   Opportunities to enhance the ecological value of hard coastal infrastructure using fine-scale

254   surface textures. *Ecological Engineering* **77**:314–323.

255   **Crisp DJ. 1968.** Differences between North American and European populations of *Balanus*

256   *balanoides* revealed by transplantation. *Fisheries Research Board of Canada* **25**:2633–2641.

257   **Crisp DJ, Meadows PS. 1962.** The chemical basis of gregariousness in cirripedes. *Proceedings*

258   *of the Royal Society of London B* **156**:500–520.

259   **Ellrich JA, Scrosati RA. 2016.** Water motion modulates predator nonconsumptive limitation of

260   prey recruitment. *Ecosphere* **7**:e01402.

261   **Ellrich JA, Scrosati RA, Molis M. 2015.** Predator nonconsumptive effects on prey recruitment

262   weaken with recruit density. *Ecology* **96**:611–616.

263   **Ellrich JA, Scrosati RA, Romoth K, Molis M. 2016a.** Adult prey neutralizes predator

264   nonconsumptive limitation of prey recruitment. *PLoS ONE* **11**:e0154572.

265   **Ellrich JA, Scrosati RA, Bertolini C, Molis M. 2016b.** A predator has nonconsumptive effects

266   on different life-history stages of a prey. *Marine Biology* **163**:5.

267   **Galbraith PS, Larouche P, Chassé J, Petrie P. 2012.** Sea-surface temperature in relation to air

268   temperature in the Gulf of St.Lawrence: interdecadal variability and long-term trends. *Deep-*

269   *Sea Research II* **77–80**:10–20.

270   **Hansson LJ, Hudson IR, Seddon RJ, Shaw O, Thomason JC. 2003.** Massive recruitment of

271   the barnacle *Semibalanus balanoides* in the Clyde Sea (Scotland, UK) in the spring of 2000.

272   *Journal of the Marine Biological Association of the United Kingdom* **83**:923–924.

273   **Hooper RC, Eichhorn MP. 2016.** Too close for comfort: spatial patterns in acorn barnacle

274   populations. *Population Ecology* **58**:231–239.

275   **Jarrett JN. 1997.** Temporal variation in subtratum specificity of *Semibalanus balanoides*

276   (Linnaeus) cyprids. *Journal of Experimental Marine Biology and Ecology* **211**:103–114.

277 **Jenkins SR, Åberg P, Cervin G, Coleman RA, Delany J, Della Santina P, Hawkins SJ,**

278 **LaCroix E, Myers AA, Lindegarth M, Power AM, Roberts MF, Hartnoll RG. 2000.**

279 Spatial and temporal variation in settlement and recruitment of the intertidal barnacle

280 *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of*

281 *Experimental Marine Biology and Ecology* **243**:209–225.

282 **Johnson LE, Strathmann RR. 1989.** Settling barnacle larvae avoid substrata previously

283 occupied by a mobile predator. *Journal of Experimental Marine Biology and Ecology* **128**:87–

284 103.

285 **Kent A, Hawkins SJ, Doncaster CP. 2003.** Population consequences of mutual attraction

286 between settling and adult barnacles. *Journal of Animal Ecology* **72**:941–952.

287 **Lathlean JA, Ayre DJ, Minchinton TE. 2013.** Temperature variability at the larval scale

288 affects early survival and growth of an intertidal barnacle. *Marine Ecology Progress Series*

289 **475**:155–166.

290 **MacPherson EA, Scrosati R. 2008.** Population structure of the barnacle *Semibalanus*

291 *balanoides* (Cirripedia) across intertidal environmental stress gradients in northern Nova

292 Scotia, Canada. *Crustaceana* **81**:725–736.

293 **MacPherson EA, Scrosati R, Chareka P. 2008.** Barnacle recruitment on ice-scoured shores in

294 eastern Canada. *Journal of the Marine Biological Association of the United Kingdom* **88**:289–

295 291.

296 **Matsumura K, Hills JM, Thomason PO, Thomason JC, Clare AS. 2000.** Discrimination at

297 settlement in barnacles: laboratory and field experiments on settlement behaviour in response to

298 settlement-inducing protein complexes. *Biofouling* **16**:181–190.

299   **Matsumura K, Qian P-Y. 2014.** Larval vision contributes to gregarious settlement in barnacles:

300   adult red fluorescence as a possible visual signal. *Journal of Experimental Biology* **217**:743–

301   750.

302   **Menge BA, Menge DNL. 2013.** Dynamics of coastal meta-ecosystems: the intermittent

303   upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs* **83**:283–

304   310.

305   **Menge BA, Gouhier TC, Hacker SD, Chan F, Nielsen KJ. 2015.** Are meta-ecosystems

306   organized hierarchically? A model and test in rocky intertidal habitats. *Ecological Monographs*

307   **85**:213–233.

308   **Minchinton TE, Scheibling RE. 1993.** Free space availability and larval substratum selection as

309   determinants of barnacle population structure in a developing rocky intertidal community.

310   *Marine Ecology Progress Series* **95**:233–244.

311   **Musetta-Lambert JL, Scrosati RA, Keppel EA, Barbeau MA, Skinner MA, Courtenay SC.**

312   **2015.** Intertidal communities differ between breakwaters and natural rocky areas on ice-scoured

313   Northwest Atlantic coasts. *Marine Ecology Progress Series* **539**:19–31.

314   **Navarrete SA, Broitman BR, Menge BA. 2008.** Interhemispheric comparion of recruitment to

315   intertidal communities: pattern persistence and scales of variation. *Ecology* **89**:1308–1322.

316   **Palumbi SR, Pinsky ML. 2014.** Marine dispersal, ecology, and conservation. In: Bertness MD,

317   Bruno JF, Silliman BR, Stachowicz JJ, eds. *Marine community ecology and conservation.*

318   Sunderland: Sinauer, 57–83.

319   **Raimondi PT. 1988.** Settlement cues and determination of the vertical limit of an intertidal
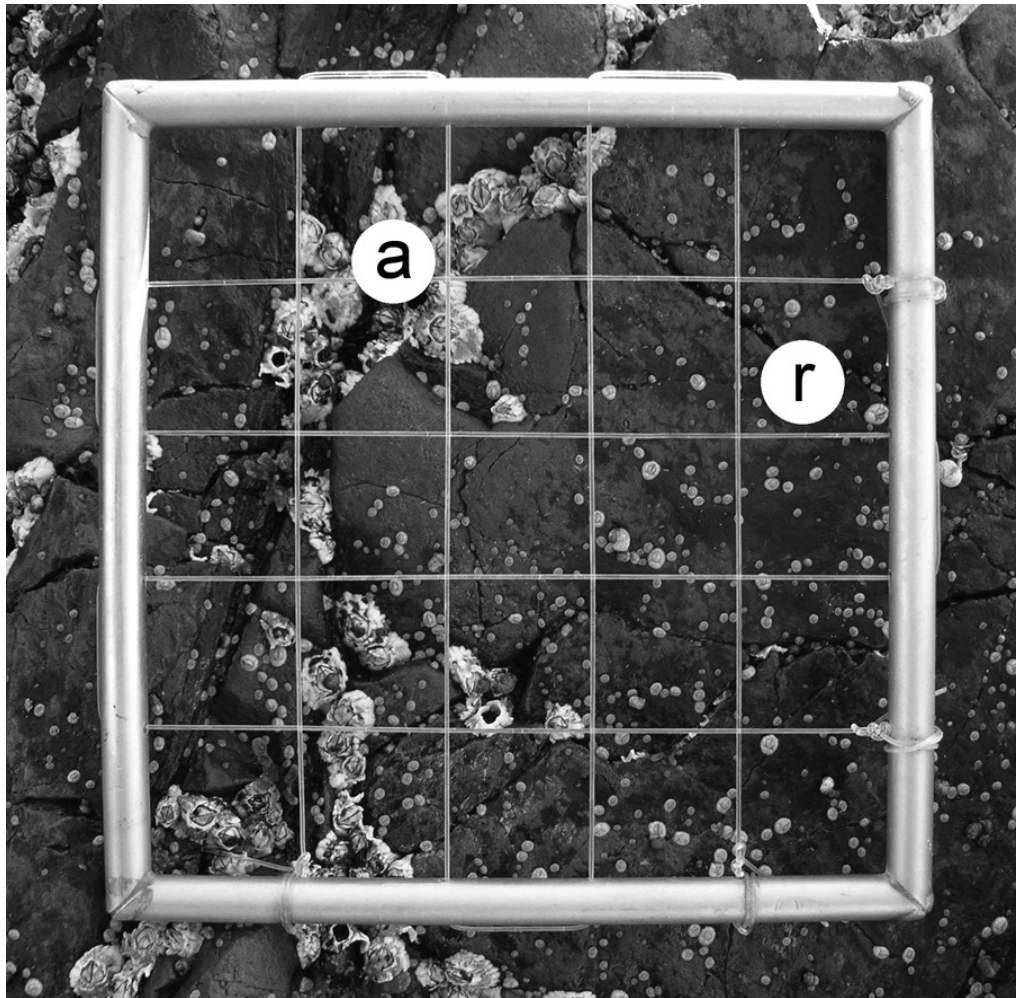
320   barnacle. *Ecology* **69**:400-407.

321   **Rognstad RL, Wethey DS, Hilbish TJ. 2014.** Connectivity and population repatriation:

322   limitations of climate and input into the larval pool. *Marine Ecology Progress Series* **495**:175–

323   183.

324   **Scrosati R, Heaven C. 2006.** Field technique to quantify intensity of scouring by sea ice in

325   rocky intertidal habitats. *Marine Ecology Progress Series* **320**:293–295.

326   **Scrosati R, Heaven C. 2007.** Spatial trends in community richness, diversity, and evenness

327   across rocky intertidal environmental stress gradients in eastern Canada. *Marine Ecology*

328   *Progress Series* **342**:1–14.

329   **Scrosati RA, Ellrich JA. 2016.** A 12-year record of intertidal barnacle recruitment in Atlantic

330   Canada (2005-2016): relationships with sea surface temperature and phytoplankton abundance.

331   *PeerJ* **4**:e2623.

332   **Sokal RR, Rohlf FJ. 2012.** *Biometry. The principles and practice of statistics in biological*

333   *research.* New York: W. H. Freeman.

334   **Turgeon K, Kramer DL. 2016.** Immigration rates during population density reduction in a coral

335   reef fish. *PLoS ONE* **11**:e0156417.

336   **Table 1.** Summary information for the models describing the adult–recruit relationship in

337   2007, 2008, and 2009: a, b, and c are the parameters of the equations described in Methods, *w*

338   is the weight of evidence for each model, and n is the number of surveyed quadrats.

339

Model	a	b	c	Adjusted R^2	AICc	*w*	Evidence ratio
2007 (n = 30)							
Linear	12.82	912.80	-	0.22	328.9	0.3077	1.8
Power	138.20	0.34	815.80	0.31	326.8	0.5607	1
Quadratic	-0.34	25.44	877.90	0.25	329.7	0.1315	4.3
2008 (n = 29)							
Linear	2.02	329.90	-	0.24	288.5	0.0536	14.2
Power	61.65	0.35	218.00	0.35	286.0	0.1872	4.1
Quadratic	-0.04	7.65	228.80	0.40	283.2	0.7592	1
2009 (n = 32)							
Linear	15.86	779.40	-	0.20	352.8	0.2887	1.9
Power	175.70	0.33	617.30	0.26	351.5	0.5529	1
Quadratic	-0.49	31.49	736.10	0.20	354.0	0.1584	3.5

340

341   **Fig. 1.** Typical view of a wave-exposed, high-intertidal habitat on the Gulf of St. Lawrence

342   coast of Nova Scotia in June, showing barnacle adults (a) and recruits (r). The sampling quadrat

343   is 10 cm x 10 cm. Photograph by R. A. Scrosati.

344   **Fig. 2.** Relationships between standardized barnacle recruit density (scaled to the available area

345   for recruitment in each quadrat) and the density of pre-existing adult barnacles (always scaled to

346   quadrat area) in June 2007 (A), 2008 (B), and 2009 (C) for wave-exposed, high-intertidal

347   habitats on the Gulf of St. Lawrence coast of Nova Scotia. Each graph shows the model that best

348   describes the adult–recruit relationship (see Table 1 for model parameters).
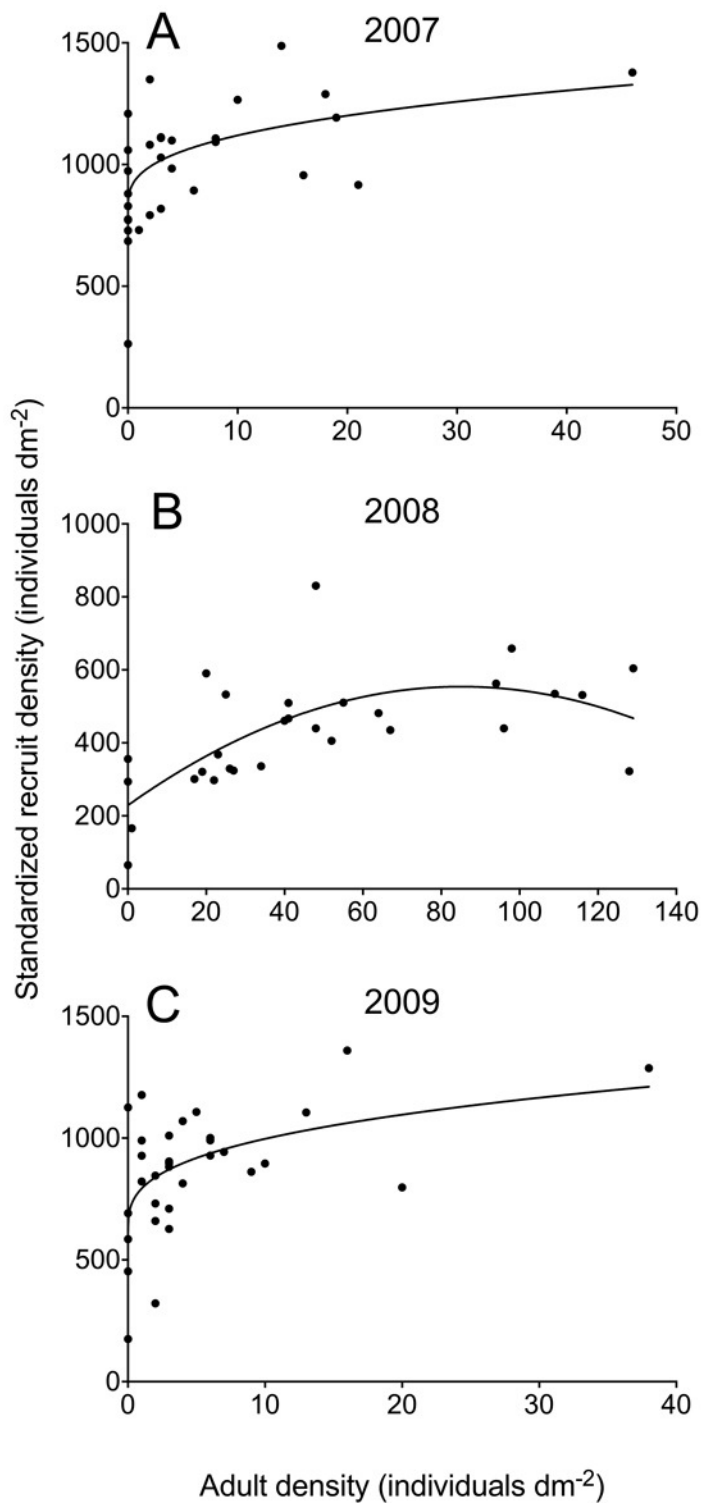
349

350   Figure 1

351

352   Figure 2