

# Benthic–pelagic coupling and bottom-up forcing in rocky intertidal communities along the Atlantic Canadian coast

RICARDO A. SCROSATI † AND JULIUS A. ELLRICH

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

**Citation:** Scrosati, R. A., and J. A. Ellrich. 2018. Benthic–pelagic coupling and bottom-up forcing in rocky intertidal communities along the Atlantic Canadian coast. *Ecosphere* 9(5):e02229. 10.1002/ecs2.2229

**Abstract.** Benthic species from rocky intertidal systems are irregularly distributed along marine coastlines. Nearshore pelagic conditions often help to explain such variation, but most such studies have been done on eastern ocean boundary coasts. We investigated possible benthic–pelagic coupling along the Atlantic coast of Nova Scotia, a western ocean boundary coast. In 2014, we surveyed high-intertidal habitats from nine wave-exposed bedrock locations spanning 415 km of coastline. At each location in the spring, we measured the recruitment of barnacles and mussels, the two main filter-feeders. Recruitment varied irregularly along the coast. Satellite data on coastal phytoplankton and particulate organic carbon (food for intertidal filter-feeders and their pelagic larvae) and in-situ data on sea surface temperature explained, to varying degrees, the geographic structure of recruitment. In turn, the summer abundance of barnacles and mussels was positively related to their spring recruitment. Ultimately, intertidal predator (dogwhelk) abundance was positively related to the recruitment and/or abundance of barnacles and mussels (the main prey of dogwhelks). Sea ice may also have influenced this predator–prey interaction. Drift ice leaving the Gulf of St. Lawrence in late winter strongly disturbed the northern surveyed locations, making barnacles (through high spring recruitment) the only food source for dogwhelks (which survived ice scour in crevices) in such places. Overall, this study supports the occurrence of benthic–pelagic coupling and bottom-up forcing on this coast. Investigating the oceanographic drivers of pelagic food supply and seawater temperature should help to further understand how this large metacommunity is organized.

**Key words:** benthic–pelagic coupling; bottom-up forcing; intertidal; *Mytilus*; *Nucella*; pelagic food supply; recruitment; *Semibalanus*; wave exposure.

**Received** 25 December 2017; revised 26 March 2018; accepted 18 April 2018. Corresponding Editor: Sean P. Powers.

**Copyright:** © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** rscrosat@stfx.ca

## INTRODUCTION

A central goal of ecology is to understand spatial variation in ecological systems. Rocky intertidal systems have often been studied in this regard and have helped to advance, for example, concepts such as benthic–pelagic coupling and bottom-up forcing. Benthic–pelagic coupling refers to the influence of nearshore pelagic conditions on benthic coastal processes (Navarrete et al. 2005, Griffiths et al. 2017), while bottom-up forcing refers to the effects of food or nutrient

supply on basal trophic levels that propagate through consumption to higher trophic levels (Menge 1992).

Pelagic conditions that affect intertidal communities vary at several spatial scales. At local scales, wave exposure varies due to topography and affects food supply rates (Steffania and Branch 2003, McQuaid and Lindsay 2007), larval dispersal (Bertness et al. 1992), and benthic survival (McQuaid and Lindsay 2000, Larsson and Jonsson 2006, D'Amours and Scheibling 2007), in that way influencing intertidal species

distribution (Heaven and Scrosati 2008). At regional scales, seawater temperature and planktonic food supply vary due to oceanography and generate regional patterns in intertidal species distribution (Menge et al. 2003, Blanchette et al. 2008, Shanks et al. 2017a). This paper is mainly concerned with advancing knowledge at regional scales.

Benthic–pelagic coupling and bottom-up forcing have often been studied using wave-exposed intertidal habitats, as such places face the open ocean and thus facilitate the identification of pelagic influences. Those studies were mainly done on temperate shores in the northern (Menge et al. 2009) and southern (Navarrete et al. 2005) hemispheres. However, they were overwhelmingly conducted on eastern ocean boundary coasts (Menge and Menge 2013). Such coasts frequently experience upwelling and are biologically productive, supporting important fisheries (Food and Agriculture Organization 2016). Those studies concluded that spatial changes in phytoplankton abundance and particulate organic carbon (POC; food for intertidal filter-feeders) and seawater temperature influence intertidal community structure (Menge et al. 1997a, 2009, Wieters 2005, Shanks et al. 2017a). Influences can be direct (e.g., phytoplankton increasing intertidal filter-feeder abundance; Menge et al. 1997b) or indirect (e.g., phytoplankton increasing intertidal predator abundance through effects on filter-feeding prey; Leonard et al. 1998). Whether similar relationships are common on western ocean boundary coasts is less clear, which needs to be addressed to produce a more general predictive framework.

Studies on benthic–pelagic coupling and bottom-up forcing have used large-scale mensurative surveys, local-scale experiments, or combinations of both (Menge and Menge 2013). For unstudied coasts, mensurative approaches are particularly useful to identify regional patterns, a necessary precondition for more detailed studies (Underwood et al. 2000, Hughes et al. 2002, Sagarin and Pauchard 2010). This paper provides large-scale mensurative evidence supporting the occurrence of benthic–pelagic coupling and bottom-up forcing on the Atlantic coast of Nova Scotia, Canada. There is a rich history of rocky intertidal research for this coast (McCook and Chapman 1997, Hunt and Scheibling 1998,

Scrosati and Heaven 2007, and references therein), but studies have largely been restricted to a few locations near research institutions. For instance, there is no comprehensive account of latitudinal changes in intertidal invertebrate recruitment and abundance and the relationships with important pelagic characteristics (e.g., seawater temperature and food supply) and intertidal predator abundance.

As on other temperate shores (Bustamante and Branch 1996, Navarrete and Castilla 2003, Nakaoka et al. 2006, Blanchette and Gaines 2007, Hawkins et al. 2009, Lathlean et al. 2010, Arribas et al. 2013, Menge and Menge 2013), barnacles and mussels are often dominant organisms in wave-exposed rocky intertidal habitats in Nova Scotia (Hunt and Scheibling 1998, Scrosati and Heaven 2007). Because of their ecological relevance, their recruitment is commonly measured to investigate benthic–pelagic links (Menge and Menge 2013, Mazzuco et al. 2015, Shanks and Morgan 2018). Therefore, the first objective of our study was to investigate the latitudinal variation in intertidal barnacle and mussel recruitment along the Atlantic coast of Nova Scotia. To seek evidence of benthic–pelagic coupling, we examined how barnacle and mussel recruitment was related to coastal seawater temperature, phytoplankton abundance, and POC. We then evaluated how barnacle and mussel recruitment was related to the abundance of these organisms later in the year. Finally, to evaluate the possibility of bottom-up forcing, we investigated whether the recruitment and abundance of barnacles and mussels were related to the abundance of their main predators (dogwhelks) along the coast.

## METHODS

### Locations

In 2014, we studied nine intertidal bedrock locations spanning the full Atlantic coast of mainland Nova Scotia, nearly 415 km between Glasgow Head and Baccaro Point (Fig. 1). For ease of interpretation, these locations are referred to in this paper as L1–L9, from north to south (their names and coordinates are given in Table 1). These locations are wave-exposed, as they directly face the open waters of the Atlantic Ocean (Fig. 2). Values of daily maximum

water velocity (an indication of wave exposure) measured with dynamometers (see design in Bell and Denny 1994) in such habitats range between 6 and 12 m/s (Hunt and Scheibling 2001, Scrosati and Heaven 2007, Ellrich and Scrosati 2017).

We made the intertidal measurements described below (temperature and invertebrate recruitment and abundance) at the high-intertidal zone. We selected this zone because, due to the limited tidal amplitude of our coast, surveying lower elevations would have prevented us

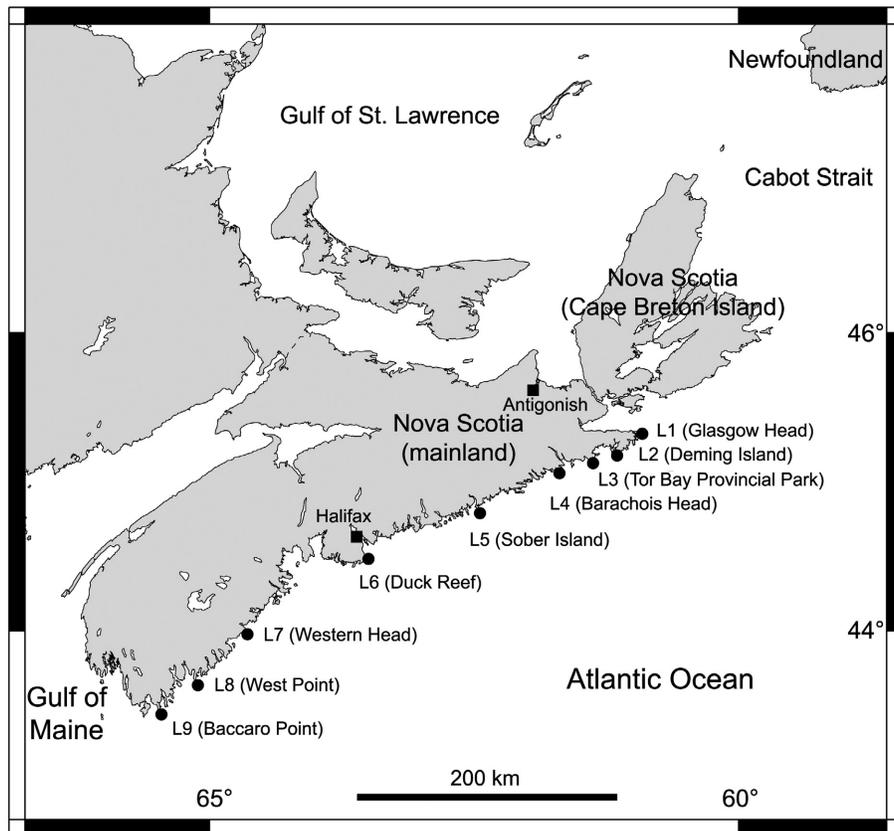


Fig. 1. Map indicating the nine wave-exposed locations surveyed along the Atlantic coast of mainland Nova Scotia, Canada.

Table 1. Basic information about the nine wave-exposed locations surveyed for this study.

Location code	Location name (geographic coordinates)	Closest location with tide data (geographic coordinates)
L1	Glasgow Head (45.3203, -60.9592)	Canso (45.3500, -61.0000)
L2	Deming Island (45.2121, -61.1738)	Whitehead (45.2333, -61.1833)
L3	Tor Bay Provincial Park (45.1823, -61.3553)	Larry's River (45.2167, -61.3833)
L4	Barachois Head (45.0890, -61.6933)	Port Bickerton (45.1000, -61.7333)
L5	Sober Island (44.8223, -62.4573)	Port Bickerton (45.1000, -61.7333)
L6	Duck Reef (44.4913, -63.5270)	Sambro (44.4833, -63.6000)
L7	Western Head (43.9896, -64.6607)	Liverpool (44.0500, -64.7167)
L8	West Point (43.6533, -65.1309)	Lockport (43.7000, -65.1167)
L9	Baccaro Point (43.4496, -65.4697)	Ingomar (43.5667, -65.3333)



Fig. 2. Typical view of wave-exposed intertidal habitats facing the open Atlantic Ocean in Nova Scotia. Photograph taken at Tor Bay Provincial Park by R. A. Scrosati.

from sampling all nine locations within a few days of difference during periods of high wave action, which are common for these locations. For each location, we considered the intertidal range as the vertical distance between chart datum (0 m in elevation) and the highest elevation where perennial sessile organisms (the barnacle *Semibalanus balanoides*) occurred on the substrate outside of crevices (Scrosati and Heaven 2007). For each location, we divided the vertical intertidal range by three and collected the data described in the following paragraphs just above the bottom boundary of the upper third of the intertidal range. Since tidal amplitude increases from 1.8 m in L1 to 2.4 m in L9 (Tide-Forecast 2018), this method allowed us to take intertidal data along the coast at comparable elevations in terms of exposure to aerial conditions during low tides.

#### Barnacle recruitment

For barnacles, recruitment is the appearance of new organisms in a benthic habitat after the metamorphosis of settled pelagic larvae. On the Atlantic coast of Nova Scotia, *S. balanoides* is the only intertidal barnacle species. It is a cross-fertilizing hermaphrodite that, in Atlantic Canada, mates in autumn, broods in winter, and releases pelagic larvae in spring (Bousfield 1954, Crisp 1968, Bouchard and Aiken 2012). In May and June on the studied coast, larvae settle in

intertidal habitats and quickly metamorphose into benthic recruits, so the barnacle recruitment season spans May–June (Ellrich et al. 2015a, 2016a). Thus, we measured recruitment at our nine locations in late June (Table 2). We used two methods that provided bare substrate shortly before the recruitment season (in late April). One method consisted in attaching to the substrate PVC tiles (8.9 × 4.6 × 0.4 cm) covered by gray Safety-Walk tape (3M, St. Paul, Minnesota, USA; pictured in Menge et al. 2010). This rubberized

Table 2. Dates when barnacle recruitment, mussel recruitment, and the abundance of barnacles, mussels, and dogwhelks were measured at the nine studied locations.

Location	Barnacle recruitment	Mussel recruitment	Species abundance
L1	27 June (0, 8)	–	9 August (30)
L2	24 June (24, 8)	27 May (20)	9 August (30)
L3	24 June (24, 8)	27 May (13)	10 August (30)
L4	23 June (21, 8)	30 May (18)	13 August (30)
L5	23 June (23, 8)	29 May (19)	13 August (30)
L6	22 June (19, 8)	29 May (16)	12 August (30)
L7	21 June (22, 8)	28 May (10)	12 August (30)
L8	21 June (9, 2)	28 May (9)	11 August (30)
L9	21 June (7, 6)	28 May (6)	11 August (10)

Note: Sample sizes are given in parentheses (for barnacle recruitment, the first number is the number of Safety-Walk tiles and the second number is the number of substrate clearings).

vinyl tape has a rugose texture and has been used to measure barnacle recruitment on other shores (Menge 2000, Lagos et al. 2008, Mazzuco et al. 2015). The other method consisted in clearing the natural rocky substrate (10 × 10 cm) by removing all pre-existing organisms with a chisel and a metallic mesh scourer. The number of tiles and clearings established at each location is stated in Table 2 (some tiles were lost likely because of waves). We measured recruit density (hereafter, recruitment) on the tiles and clearings by analyzing pictures taken during low tides in late June (Table 2).

### *Mussel recruitment*

Two mussel congeners occur in rocky intertidal habitats on the Atlantic coast of Nova Scotia, *Mytilus edulis* and *Mytilus trossulus* (Tam and Scrosati 2011, 2014). These species show only subtle morphological differences (Innes and Bates 1999) and can form hybrids (Riginos and Cunningham 2005), so their visual identification is difficult, especially at the recruit stage. Thus, we counted mussel recruits as *Mytilus* spp., as done in other field studies with these species (Cusson and Bourget 2005, Le Corre et al. 2013, Ehlers et al. 2018) and other mussel species (Wieters et al. 2008). To measure recruitment, we installed plastic mesh scourers (Our Compliments Poly Pot Scrubbers, Mississauga, Ontario, Canada) at each location in late April and collected them at the end of May (Table 2) to measure recruit density in the laboratory. Mesh scourers have often been used to measure intertidal mussel recruitment (Menge and Menge 2013, Mazzuco et al. 2015, South 2016), as the scourers resemble habitats where pelagic mussel larvae preferentially settle (filamentous algae or byssal threads of established mussels; Menge 1992, Le Corre et al. 2013). For *M. edulis* and *M. trossulus*, pediveliger larvae of at least 0.25 mm in length settle in those habitats and metamorphose, becoming benthic recruits (Bayne 1965, Menge et al. 2009, Martel et al. 2014). After growing to a shell length of about 0.5 mm (Hunt and Scheibling 1996, Le Corre et al. 2013), such recruits may enter a second pelagic dispersal phase (Bayne 1964). For instance, recruits of *M. edulis* up to 2.5 mm long can drift in the water aided by a byssus thread (Sigurdsson et al. 1976). Microscope observations

indicated that 70–80% of the recruits found in our scourers belonged to the first phase. Accurate estimates were not possible because the precise size threshold between both phases is unknown (Le Corre et al. 2013). Nonetheless, since all of those organisms contribute to recruitment, we counted the recruits of both phases together to determine recruit density for each scourer, as often done in field studies (Menge and Menge 2013).

### *Chlorophyll-a concentration (Chl-a) and POC*

We used MODIS-Aqua satellite data on Chl-*a* and POC for the 4 × 4 km cells that include our nine locations (National Aeronautics and Space Administration 2017). Chl-*a* data are a proxy for phytoplankton abundance (Menge and Menge 2013). Coastal Chl-*a* data from satellites are often used in intertidal ecology (Navarrete et al. 2005, Burrows et al. 2010, Arribas et al. 2014, Mazzuco et al. 2015, Lara et al. 2016). Small differences between satellite and in-situ data may exist. However, satellite data were the only available descriptors of Chl-*a* and POC for our locations. These data should be adequate for at least two reasons. One is that there were clear differences in Chl-*a* and POC among locations (see *Results*), suggesting that the signal was stronger than potential noise. The other reason is that our data analyses identified Chl-*a* and POC as relevant for barnacle and mussel recruitment and, on wave-exposed shores, pelagic larvae respond to Chl-*a* and POC conditions across areas that are covered by the satellite cells. Overall, satellite data are practical when studying large extents of coastline (Legaard and Thomas 2006).

To evaluate possible Chl-*a* and POC forcing on barnacle recruitment, we used the April and May means of Chl-*a* and POC and the June mean of Chl-*a* and POC calculated for the period between the beginning of that month and the dates when barnacle recruitment was measured (Table 2). We used May means of Chl-*a* and POC because barnacle recruits start to appear in early May (Ellrich et al. 2015a) and April means because the nauplius larvae of *S. balanoides* feed over 5–6 weeks in coastal waters before reaching the settling cyprid stage (Bousfield 1954, Drouin et al. 2002). A study done in 2013 at a nearby location revealed that most of the barnacle recruits appeared during May. As dead recruits

(indicated by empty shells) were rare in June, that study concluded that most of the larvae that generated the June values of recruit density were likely in the water column in April (Scrosati and Ellrich 2016). To evaluate possible Chl-*a* and POC forcing on mussel recruitment, we used the April and May means of Chl-*a* and POC.

#### *Sea surface temperature*

We measured intertidal temperature every 30 min using four HOBO Pendant loggers (Onset Computer, Bourne, Massachusetts, USA) that were secured to the substrate at each location (except at L1, where no loggers were deployed) in late April. We collected the loggers when we measured barnacle recruitment (Table 2). As temperature was highly correlated between loggers within locations ( $r = 0.84\text{--}0.99$ ), we generated a single time series for each location by averaging the corresponding half-hourly values from the replicate loggers. From those time series, we extracted for each location the values of daily sea surface temperature (SST) for the study period, which we considered to be the temperature recorded at the time of the highest tide of each day. We determined the time of such tides using online information available for the closest places to our locations (Table 1, Tide and Current Predictor 2017).

#### *Barnacle, mussel, and dogwhelk abundance*

We measured the abundance of barnacles, mussels, and dogwhelks in natural communities in August (Table 2). We sampled 30 random quadrats (20 × 20 cm) at each location, except at L9, where we only sampled 10 quadrats. As often done in intertidal studies (Navarrete and Manzur 2008, Bryson et al. 2014), we measured during low tides the percent cover of barnacles and mussels (using a metallic frame divided into 100 squares with monofilament line) and the density of dogwhelks (number of organisms per quadrat divided by quadrat area).

#### *Data analyses*

We evaluated whether barnacle recruitment depended on substrate type (fixed factor with two levels: cleared rocky substrate vs. Safety-Walk tape) through a two-way analysis of variance considering locations as a random factor (Sokal and Rohlf 2012). As Safety-Walk tape was generally a poorer surface (see *Results*), only data from the

rock clearings were used for subsequent analyses on barnacle recruitment. We evaluated whether barnacle and mussel recruitment and the abundance of barnacles, mussels, and dogwhelks differed among locations through separate one-way analyses of variance (Sokal and Rohlf 2012). Parametric assumptions were tested and accepted under the notion that the analysis of variance is a robust test (Sokal and Rohlf 2012). We searched for evidence of benthic–pelagic coupling following a model selection approach using the location averages of intertidal recruitment and pelagic characteristics. Specifically, we considered either barnacle recruitment or mussel recruitment as the dependent variable and the monthly means of Chl-*a*, POC, or SST as independent variables. Separately for these three pelagic characteristics, we compared all possible linear models (representing all possible combinations of months) using their values of the corrected Akaike’s information criterion (AIC<sub>c</sub>). For each set of models, we considered the most plausible model as that with the lowest AIC<sub>c</sub> score. Any other model within the set exhibiting a difference in AIC<sub>c</sub> ( $\Delta\text{AIC}_c$ ) of <2 relative to the most plausible model was also considered to have substantial support (Burnham and Anderson 2004). We then calculated the relative likelihood of each model within the different sets (Anderson 2008). We looked for evidence of bottom-up forcing by separately evaluating the linear relationships between dogwhelk abundance and the recruitment and abundance of barnacles and mussels (Sokal and Rohlf 2012). We conducted these data analyses with JMP 9.0 (SAS, Cary, North Carolina, USA) for MacOS.

## RESULTS

#### *Barnacle recruitment*

Combining all locations, barnacle recruitment was marginally lower on tiles covered by Safety-Walk tape than on clearings of the natural rocky substrate ( $F_{1,7} = 2.97$ ,  $P = 0.086$ ). Combining both substrate types, barnacle recruitment differed among locations ( $F_{7, 189} = 21.38$ ,  $P < 0.001$ ). Since the interaction between locations and substrate type was significant ( $F_{7, 189} = 8.35$ ,  $P < 0.001$ ), pairwise tests were done and revealed that barnacle recruitment was higher ( $P < 0.05$ ) on rock clearings than on Safety-Walk tape at L2, L5, L6, L7, and L8 and similar

( $P > 0.05$ ) between both surfaces at L3, L4, and L9 (Fig. 3; no Safety-Walk tiles were established at L1). Therefore, we used the data from the rock clearings to do the recruitment analyses reported hereafter. Based on those data, barnacle recruitment varied along the Nova Scotia coast ( $F_{8, 55} = 8.74$ ,  $P < 0.001$ ), peaking at one northern location (L2) and two southern locations (L7 and L8; Fig. 3).

Chl-*a* and POC also varied along the coast (Fig. 4). The best model relating Chl-*a* with barnacle recruitment was the one including only April Chl-*a*, a positive relationship that explained 46% (adjusted  $R^2 = 0.46$ ) of the observed variation in recruitment (Table 3, Fig. 5). A similar result was obtained for POC, as the model that included only April POC was the best one, a positive relationship that explained 48% of the variation in recruitment (Table 3, Fig. 5). The AIC<sub>c</sub> scores of the models with April Chl-*a* and with April POC were similar (Table 3). April Chl-*a* and April POC were positively related, although not significantly ( $r_7 = 0.54$ ,  $P = 0.132$ ).

Sea surface temperature also varied along the coast (Fig. 4). No model with SST was found suitable to explain barnacle recruitment (Table 4). However, because of the apparently overwhelming influence of Chl-*a* on recruitment in L2 (Figs. 3, 4), we explored excluding L2 from the SST analyses and applied a  $\log_{10}$  transformation to the recruitment data. Then, model

selection separately identified June SST and April SST as suitable explanatory variables through positive relationships (Fig. 5), although the intercept-only model was similarly likely (Table 4).

#### Mussel recruitment

Mussel recruitment varied along the coast ( $F_{7, 103} = 30.55$ ,  $P < 0.001$ ), peaking at a southern location where barnacle recruitment also peaked (L8; Fig. 3). No model considering Chl-*a* was suitable to explain mussel recruitment (Table 5). However, the model including May POC was plausible, a positive relationship that explained 70% of the observed variation in recruitment (Table 5, Fig. 6). None of the models with SST was adequate (Table 5), and no data transformations such as those applied to barnacle recruitment modified this outcome.

#### Barnacle and mussel abundance

Barnacle abundance in natural communities varied along the coast in August ( $F_{8, 241} = 38.58$ ,  $P < 0.001$ ; Fig. 7). The August abundance of barnacles was positively related to their June recruitment (adjusted  $R^2 = 0.82$ ,  $P < 0.001$ ; Fig. 7). Mussel abundance in natural communities also varied along the coast in August ( $F_{8, 241} = 55.51$ ,  $P < 0.001$ ; Fig. 7). The August abundance of mussels was positively related to their May recruitment (adjusted  $R^2 = 0.87$ ,  $P < 0.001$ ; Fig. 7).

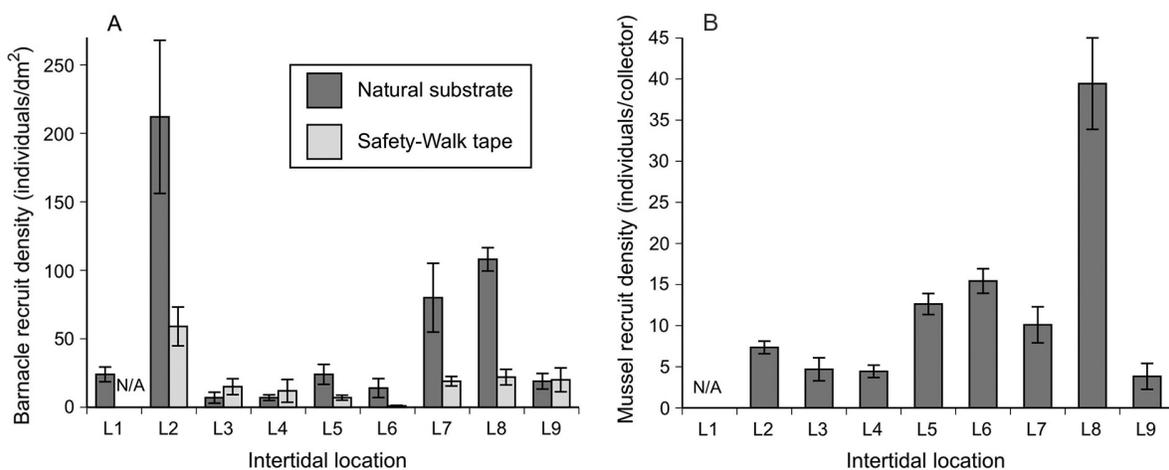


Fig. 3. (A) Barnacle recruitment and (B) mussel recruitment (mean  $\pm$  standard error; see Table 2 for sample sizes) along the Atlantic coast of Nova Scotia. N/A means that data were not available.

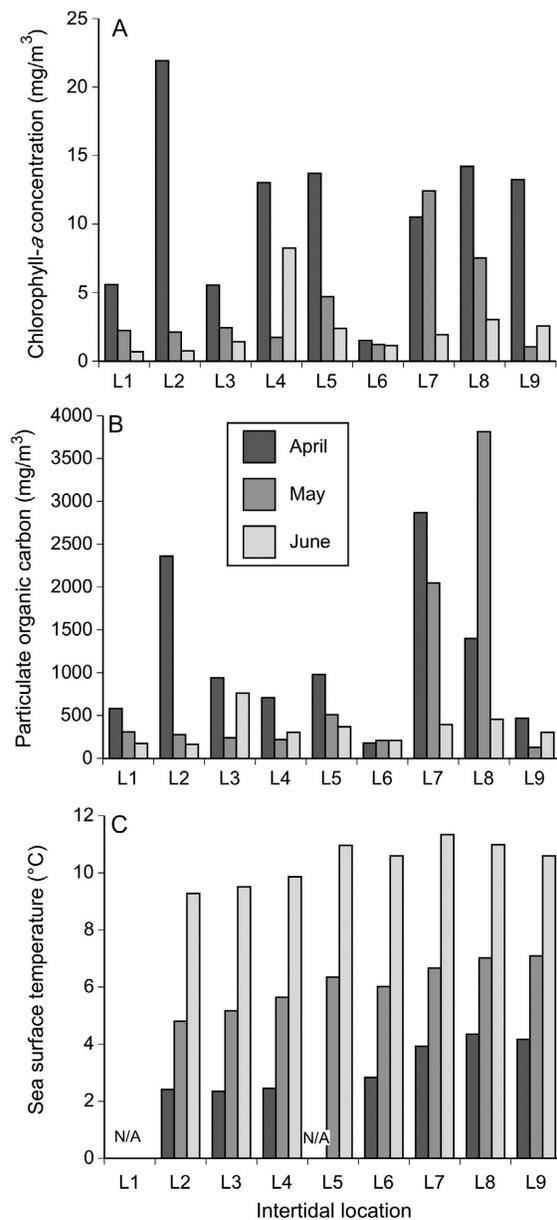


Fig. 4. (A) Chlorophyll-*a* concentration, (B) particulate organic carbon, and (C) sea surface temperature along the Atlantic coast of Nova Scotia. N/A means that data were not available.

#### Dogwhelk abundance

Dogwhelk abundance in natural communities varied along the coast in August ( $F_{8, 241} = 6.48$ ,  $P < 0.001$ ; Fig. 8). Dogwhelk abundance was positively related to barnacle recruitment (adjusted  $R^2 = 0.70$ ,  $P = 0.003$ ) and barnacle abundance

(adjusted  $R^2 = 0.45$ ,  $P = 0.029$ ; Fig. 8), but unrelated to mussel recruitment (adjusted  $R^2 = 0.20$ ,  $P = 0.150$ ) or mussel abundance (adjusted  $R^2 = 0.09$ ,  $P = 0.222$ ). However, because of intense ice scour at the four northernmost locations (L1–L4) in early April (Petzold et al. 2014), the substrate at those locations lacked organisms capable of attracting mussel recruits (filamentous algae or mature mussels) during the evaluation of mussel recruitment with mesh collectors. Thus, for those four locations, our values of mussel recruitment indicate potential recruitment. After excluding the recruitment results for those locations, dogwhelk abundance and mussel recruitment became significantly correlated (adjusted  $R^2 = 0.93$ ,  $P = 0.005$ ; Fig. 8), a remarkable outcome given that it was based on only the five remaining locations (L5–L9).

## DISCUSSION

#### Benthic–pelagic coupling

Recruitment of intertidal barnacles and mussels varied markedly along the Atlantic coast of Nova Scotia in 2014. Such differences were not related to latitude, however, as recruitment peaked in southern and northern locations. Our data analyses suggest that pelagic food supply was influential for intertidal recruitment, as it would be expected given that the larvae and recruits of barnacles and mussels are filter-feeders (Sprung 1984, Jarrett 2003).

Model selection identified phytoplankton abundance (Chl-*a*) and POC as important for barnacle recruitment. It is not possible to tell, however, if both variables were biologically relevant or simply collinear. Phytoplankton is the main food source for nauplius larvae (Walker et al. 1987, Turner et al. 2001), so the relationship with Chl-*a* probably reflects a true biological effect through influences on larval nutrition. Another study done in Nova Scotia concluded that most of the barnacle larvae that make up recruit counts in June are in the water column in April (Scrosati and Ellrich 2016). This could explain why the best model based on Chl-*a* only included April Chl-*a*. Interestingly, Barnes (1956) found that the development of *Semibalanus balanoides* larvae on a British shore improved with planktonic diatom abundance. Regarding mussel recruitment, model selection identified only May POC as relevant,

Table 3. Summary information for the models relating barnacle recruitment and the April, May, and June means of Chl-*a* and POC.

Variable	Intercept	April	May	June	Adjusted $R^2$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Relative likelihood
Chl- <i>a</i>	–35.707	8.220	–	–	0.46	104.549	0	1
	55	–	–	–	0	106.576	2.027	0.363
	–13.969	9.279	–	–13.566	0.65	106.650	2.101	0.350
	76.195	–	–	–8.600	0.05	110.577	6.028	0.049
	34.433	–	4.720	–	0.07	110.743	6.194	0.045
	–45.623	7.982	3.183	–	0.42	111.143	6.594	0.037
	57.745	–	4.420	–8.175	0.14	117.173	12.624	0.002
	–22.314	9.066	2.497	–13.212	0.61	117.997	13.448	0.001
POC	–10.542	0.056	–	–	0.48	104.265	0	1
	55	–	–	–	0	106.576	2.311	0.314
	29.384	0.058	–	–0.119	0.53	109.158	4.893	0.087
	38.947	–	0.019	–	0.01	110.255	5.990	0.050
	90.873	–	–	–0.103	0.06	110.659	6.394	0.041
	–10.715	0.056	0.001	–	0.60	111.458	7.193	0.027
	84.438	–	0.024	–0.144	0.01	115.906	11.641	0.003
	31.728	0.054	0.006	–0.129	0.46	120.885	16.620	<0.001

Notes: The numbers shown in the third, fourth, and fifth columns are the regression coefficients for April, May, and June, respectively. AIC<sub>c</sub>, corrected Akaike's information criterion; POC, particulate organic carbon.

suggesting that POC might influence late-stage mussel larvae and perhaps early recruits. Support for this notion exists for freshwater mussels (Nalepa et al. 1995).

Given those results, an emerging question is why pelagic food supply varied along the coast. The intermittent upwelling hypothesis (IUH; Menge and Menge 2013) posits that nearshore phytoplankton abundance is influenced by wind-driven coastal upwelling. Frequent, intense upwelling would drive upwelled inorganic nutrients offshore, preventing the occurrence of near-shore phytoplankton blooms. Intermittent upwelling would allow for upwelled nutrients to stay near the coast for longer periods, increasing phytoplankton abundance (Menge and Menge 2013). Wind-driven upwelling has been reported for the Nova Scotia coast (Petrie et al. 1987, Shan et al. 2016), making this line of research worth pursuing. The IUH also predicts that intermittent upwelling increases intertidal filter-feeder recruitment also by enhancing the coastal retention of pelagic larvae (Menge and Menge 2013). The IUH has been supported by field data from Oregon, California, and New Zealand (Menge and Menge 2013). Recently, however, alternative analytical approaches failed to support the IUH and suggested that surf zone width and tidally generated internal waves are more important for

coastal phytoplankton abundance and intertidal recruitment (Shanks et al. 2017a, b, Shanks and Morgan 2018). Local winds might also influence larval transport to the shore (Bertness et al. 1996). In combination, those studies suggest potentially useful approaches to investigate the oceanographic basis of the observed benthic–pelagic coupling on the Nova Scotia coast.

Sea surface temperature also varied along the Nova Scotia coast, but its relevance to intertidal recruitment was less clear. High seawater temperatures limit *S. balanoides* recruitment, as seen on European shores (Abernot-Le Gac et al. 2013, Rognstad et al. 2014). However, on the Gulf of St. Lawrence coast (with low temperatures in spring, as the sea surface freezes in winter), a 12-yr study showed that seawater temperature was in fact positively related to *S. balanoides* recruitment, presumably through the enhancement of larval performance (Scrosati and Ellrich 2016). Thus, it was not surprising to find positive relationships between *S. balanoides* recruitment and SST in our study. However, our analyses also indicated that no recruitment–SST relationship was similarly likely. Overall, these results suggest that, on our coast, pelagic food supply has a larger influence on barnacle recruitment than seawater temperature. This notion is further supported by the larger variation (coefficient of

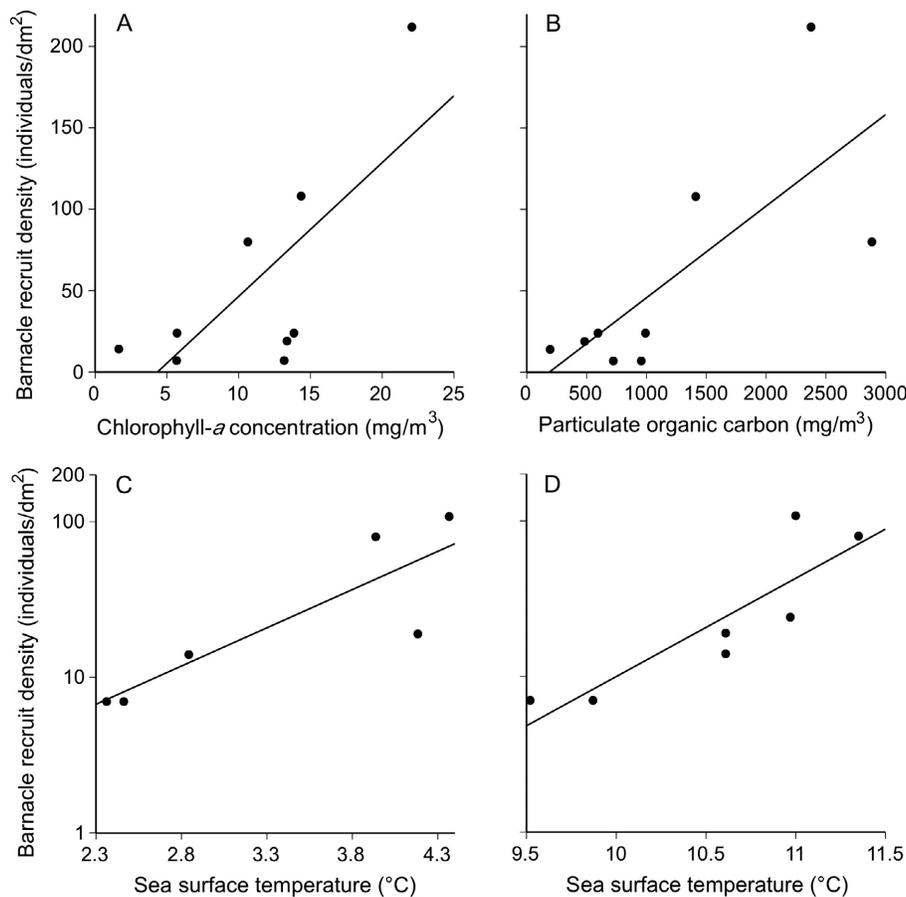


Fig. 5. Relationships between barnacle recruitment and (A) April Chl-*a*, (B) April particulate organic carbon, (C) April sea surface temperature (SST), and (D) June SST, identified as relevant by corrected Akaike's information criterion-based model selection.

variation based on location means) exhibited among locations by April Chl-*a* and POC (55% and 77%, respectively) than by April, May, or June SST (28%, 14%, and 7%, respectively). For mussels, our analyses did not detect any recruitment–SST relationship, leaving POC as the only studied pelagic variable with a possible influence, further supporting the relevant role of pelagic food supply for filter-feeder recruitment on this coast.

On the NE Atlantic coast, *S. balanoides* recruitment can be similar or higher (Hawkins and Hartnoll 1982, Kendall et al. 1985, Jenkins et al. 2000, 2008, Kent et al. 2003, Rognstad et al. 2014) than for the Nova Scotia coast. The fact that, in combination, those studies surveyed a wider range of wave exposure, intertidal elevation, and

food supply than ours may explain the higher recruitment range that they found. On the NE Pacific coast, intertidal barnacle recruitment is often high. In Oregon and California, recruits of *Balanus glandula* and *Chthamalus dalli* appear throughout most of the year and can reach, when combined, mean densities of 1800 recruits/dm<sup>2</sup> in one month (Navarrete et al. 2008). On that coast, either intermittent upwelling or surf zone characteristics would allow for barnacle larvae to remain near the coast and would favor high coastal Chl-*a* (above 23 mg/m<sup>3</sup>), enhancing intertidal barnacle recruitment (Menge and Menge 2013, Shanks and Morgan 2018). The low SST found on the Nova Scotia coast in April might further limit recruit density relative to the NE Pacific coast. The higher recruitment reported for

Table 4. Summary information for the models relating barnacle recruitment and the April, May, and June means of SST and (excluding L2)  $\log_{10}$  SST.

Variable	Intercept	April	May	June	Adjusted $R^2$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Relative likelihood
SST	63.857	–	–	–	0	86.509	0	1
	192.324	–	–21.204	–	0.13	93.054	6.545	0.038
	55.917	2.470	–	–	0.20	93.503	6.994	0.030
	242.667	–	–	–17.341	0.16	93.290	6.781	0.034
	765.093	229.960	–237.772	–	0.68	96.801	10.292	0.006
	613.914	53.666	–	–70.077	0.29	106.432	19.923	<0.001
	51.613	–	–40.251	24.837	0.39	106.961	20.452	<0.001
$\log_{10}$ SST	598.801	230.897	–261.480	29.764	0.60	138.200	51.691	<0.001
	–5.758	–	–	0.677	0.77	15.944	0	1
	1.342	–	–	–	0	15.984	0.040	0.980
	–0.304	0.492	–	–	0.68	17.824	1.880	0.391
	–1.931	–	0.522	–	0.54	20.044	4.100	0.129
	–1.677	0.946	–0.952	0.555	0.88	39.894	23.950	<0.001
	–4.058	0.21	–	0.448	0.76	44.404	28.460	<0.001
	–5.451	–	0.082	0.599	0.70	45.797	29.853	<0.001
	1.919	1.037	–0.646	–	0.65	46.606	30.662	<0.001

Notes: The numbers shown in the third, fourth, and fifth columns are the regression coefficients for April, May, and June, respectively. AIC<sub>c</sub>, corrected Akaike's information criterion; SST, sea surface temperature.

the NE Atlantic (Jenkins et al. 2000) and NE Pacific (Navarrete et al. 2008) coasts might also result from the elevation where data were taken. We surveyed the bottom of the upper third of the intertidal range (see *Methods* for rationale), but those studies surveyed middle (Jenkins et al. 2000) and middle-to-low (Navarrete et al. 2008) elevations. On the Gulf of St. Lawrence coast of Nova Scotia, barnacle recruitment in 2006 was higher at middle and low elevations than at high elevations (MacPherson and Scrosati 2008). Thus,

recruitment differences between these coasts could be smaller if data were available for the same relative elevations.

Regarding the methodology to measure barnacle recruitment, the tiles covered by Safety-Walk tape often yielded lower values than clearings of the rocky substrate. A poor performance of Safety-Walk tape has also been reported for the Pacific coast (Shanks 2009). Nonetheless, such tiles have been used extensively on the Pacific coast of North and South America (Lagos et al.

Table 5. Summary information for the models relating mussel recruitment and the April and May means of Chl-*a*, POC, and SST.

Variable	Intercept	April	May	Adjusted $R^2$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Relative likelihood
Chl- <i>a</i>	12.239	–	–	0	67.463	0	1
	7.281	–	1.195	0.03	71.624	4.161	0.125
	11.687	0.582	–	<0.01	73.058	5.595	0.061
	7.347	–0.006	1.196	0.17	80.957	13.494	0.001
POC	5.12	–	0.008	0.70	62.083	0	1
	9.525	–0.005	0.009	0.80	66.945	4.862	0.088
	12.239	–	–	0	67.463	5.380	0.068
SST	11.284	0.001	–	0.16	73.033	10.950	0.004
	12.183	–	–	0	61.364	0	1
	–12.153	7.569	–	0.14	66.001	4.637	0.098
	–27.498	–	6.550	0.06	66.643	5.279	0.071
	5.298	13.167	–5.85	0.05	79.830	18.466	<0.001

Notes: The numbers shown in the third and fourth columns are the regression coefficients for April and May, respectively. AIC<sub>c</sub>, corrected Akaike's information criterion; POC, particulate organic carbon; SST, sea surface temperature.

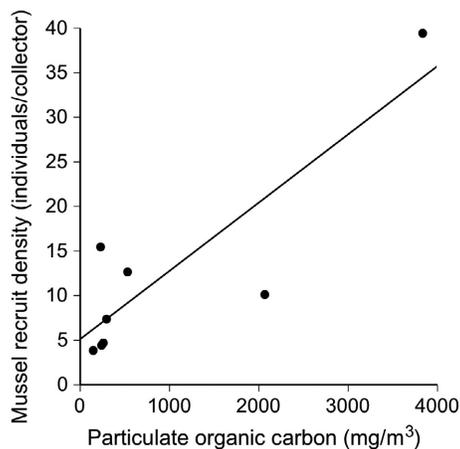


Fig. 6. Relationship between mussel recruitment and May particulate organic carbon, identified as relevant by corrected Akaike's information criterion-based model selection.

2008, Menge et al. 2010). On high-recruitment Pacific shores, such tiles are quickly covered by barnacle recruits (R. A. Scrosati, pers. obs.), so substrate type (tape vs. rock) might be relatively unimportant for larval settlement choices. On the Atlantic coast of Nova Scotia, however, where recruitment is often lower, Safety-Walk tape seems to be generally less appropriate. We note that we left the Safety-Walk tiles attached to the substrate for more years, but visual surveys in 2017 revealed that, even after 3 yr of in situ acclimation, the tiles had not only generally very few barnacles but almost no algae as well. We also point out that recent field experiments that measured barnacle recruitment in Nova Scotia (Ellrich et al. 2015a, b, 2016a, b, Ellrich and Scrosati 2016) also used tiles covered by a rugose tape, but that tape (Permastik self-adhesive anti-skid safety tread, RCR International, Boucherville, Quebec, Canada) has a sandpaper texture and yielded similar recruitment values as the adjacent rock.

#### Bottom-up forcing

On the Atlantic coast of Nova Scotia, dogwhelks are the main predators of intertidal barnacles and mussels (Hunt and Scheibling 1998, Ellrich et al. 2015a, Sherker et al. 2017). This seems to be especially true in high-intertidal, wave-exposed habitats. Sea stars (Keppel et al. 2015) and crabs (Boudreau et al. 2017) also prey

on mussels in Atlantic Canada, but we never found them in the surveyed habitats. At low intertidal elevations, where emersion-related abiotic stress is lower (Eckersley and Scrosati 2012), sea stars and crabs were sometimes present, but in very low abundances. It is only in wave-sheltered intertidal habitats where crabs are more common in Nova Scotia (Boudreau et al. 2017), although sea stars are still rare in such places (Scrosati and Heaven 2007), unlike on other shores of the world (Hayne and Palmer 2013). For these reasons, it was reasonable to find that dogwhelk abundance was related to barnacle recruitment and abundance and to mussel recruitment. Remarkably, these relationships were based on a limited number of locations, indicating the strength of these patterns.

Although our data are mensurative, it is worth speculating on possible underlying processes to orient future research. Our results suggest that barnacle recruitment is relevant for dogwhelks. This is especially apparent at northern locations. In early April (before we initiated field work), sea ice drifted off the Gulf of St. Lawrence and reached our four northernmost locations (L1–L4), causing extensive intertidal disturbance (Petzold et al. 2014). After ice melt (before late April), the main organisms that recolonized such locations were barnacles. This was most clear at L2, the location where barnacle recruits were most abundant and, by far, the main organisms during early post-ice succession. Only the seaweed *Fucus vesiculosus* recolonized that location more or less abundantly, but only later in the summer. Dogwhelks were not affected by ice scour, because they stay in deep crevices during the cold season (Crothers 1985, Gosselin and Bourget 1989, R. A. Scrosati, *personal observation*) and start foraging only in the spring (Hughes 1972, Hunt and Scheibling 1998). Although many barnacle recruits reached adult sizes by the fall, many recruits were eaten by dogwhelks. Dogwhelk density in August was not determined exclusively by the barnacles recruited in the previous spring, as most dogwhelks were older (based on their size). However, barnacle recruits were the only food source for dogwhelks in the northern locations because of the previous ice scour. Also, observations made just before ice scour indicated that mussels were then present, but rare, at such locations (Petzold et al. 2014). In addition, field

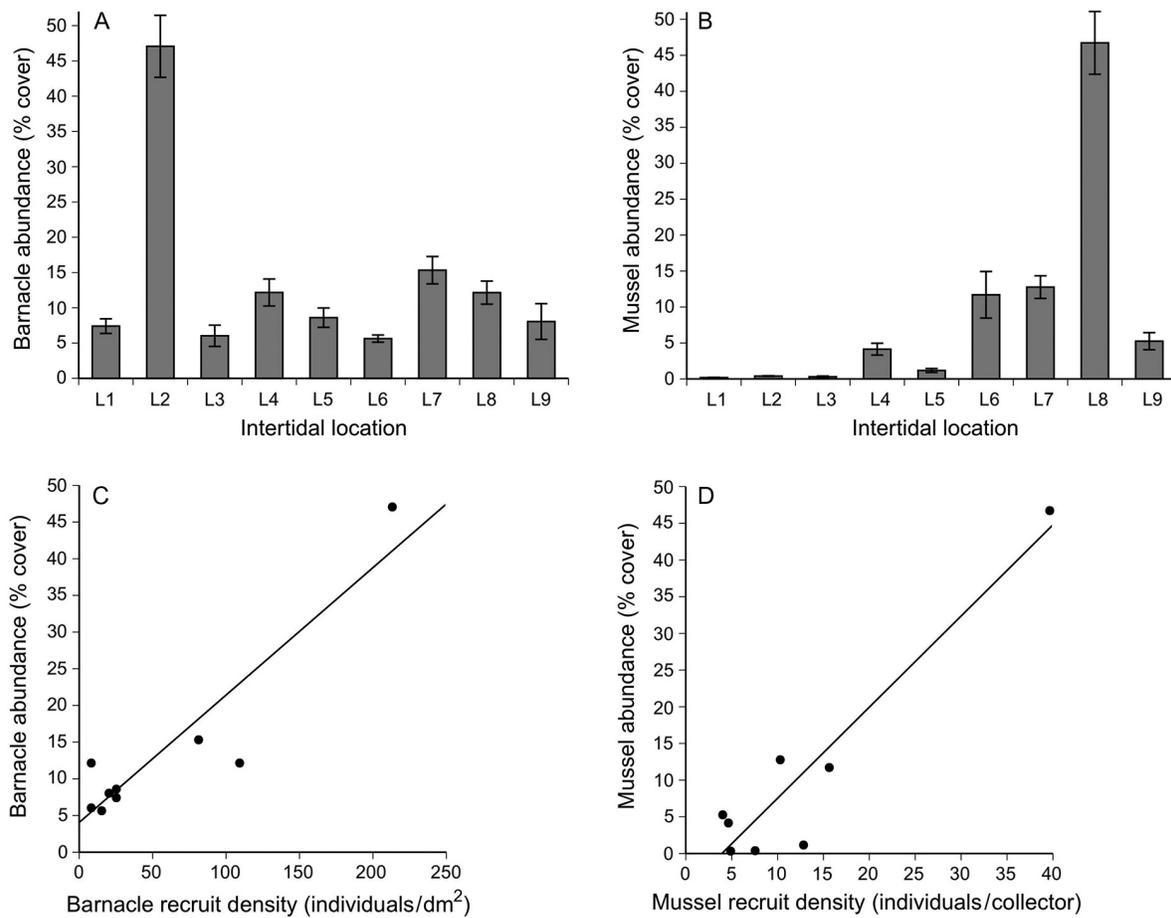


Fig. 7. Summer abundance of (A) barnacles and (B) mussels (mean  $\pm$  standard error; see Table 2 for sample sizes) along the Atlantic coast of Nova Scotia and relationships with the spring recruitment of (C) barnacles and (D) mussels.

observations in previous years indicated that barnacle recruitment was always higher at L2 than at the other northern locations, as seen in 2014. These combined lines of evidence suggest that barnacle recruitment plays an important role for dogwhelk abundance.

The correlation between spring recruitment and summer abundance for barnacles suggests that the pelagic signal persists for some time. A positive recruit–adult relationship has also been observed for barnacles on the Pacific coast (Blanchette et al. 2006). On the other hand, the positive barnacle–dogwhelk relationship in August also highlights the trophic relevance of barnacles for dogwhelks, although this result must be seen with caution because abundance was measured at the same time for both species.

Our data also suggest that mussel recruitment may also be relevant for dogwhelks, although primarily at central and southern locations. At northern locations, the biological landscape while we measured mussel recruitment was simple (mostly only barnacle recruits) because of the previous ice scour, so our mussel recruitment data indicate only potential recruitment. Considering only central and southern locations, mussel recruitment and dogwhelk abundance were strongly correlated, suggesting a relevant trophic link. As mussel abundance was not correlated to dogwhelk abundance in summer, it could be inferred that mussels did not influence dogwhelks. However, since barnacles were seemingly the only food source for dogwhelks at northern locations, excluding L1–L4 from analyses yielded a significant correlation

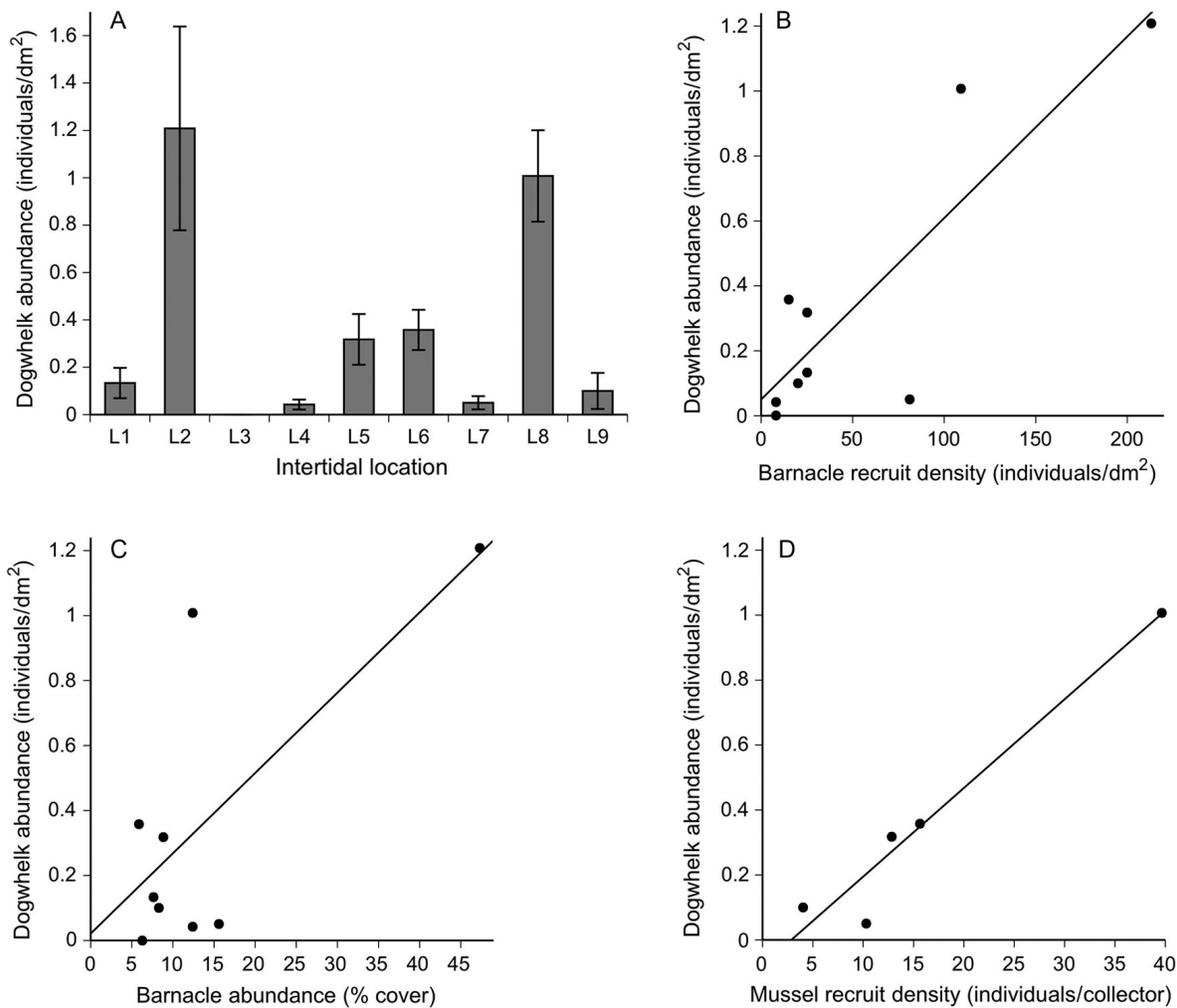


Fig. 8. (A) Dogwhelk summer abundance (mean  $\pm$  standard error; see Table 2 for sample sizes) along the Atlantic coast of Nova Scotia and relationships with (B) barnacle recruitment, (C) barnacle abundance, and (D) mussel recruitment (see the *Results* section for details on sample size).

between mussel and dogwhelk abundance (adjusted  $R^2 = 0.70$ ,  $P = 0.049$ ), suggesting a role for mussels at central and southern locations. A larger study spanning 1800 km between Newfoundland and Long Island (with a poorer coverage of Nova Scotia than this study) also found a positive correlation between mussel and dogwhelk abundance (Tam and Scrosati 2011).

The relationship between mussel recruitment and abundance is also worth discussing. Although summer abundance did not result only from the growth of the spring recruits (because many mussels were older in summer, indicated by shell growth rings), the positive correlation

indicates that, as noted for barnacles, the pelagic signal persists for some time. On other coasts, mussel recruitment and abundance may (Blanchette et al. 2006, Arribas et al. 2014) or may not (Menge et al. 2004, Wieters et al. 2008) be correlated across locations.

The importance of barnacle and mussel recruitment for dogwhelks is also supported by *Nucella lapillus* being a direct developer, without pelagic stages (Crothers 1985). This trait is expected to make dogwhelk abundance more dependent on local food sources than if pelagic dispersal were possible (Navarrete and Manzur 2008). In fact, dogwhelk abundance is also related to barnacle

and mussel recruitment on the Pacific coast (Wieters et al. 2008) and to mussel recruitment in New England (Menge 1976). Although sea stars have pelagic larvae and thus higher dispersal than dogwhelks, bottom-up effects of mussel recruitment on sea star recruitment have been reported for subtidal habitats in Maine (Witman et al. 2003). Recent studies in the Gulf of Maine have further concluded that oceanographically driven variation in intertidal recruitment likely explains the observed changes in community organization along the coast (Bryson et al. 2014).

Overall, this study has revealed a geographic structure in filter-feeder recruitment and suggests that benthic–pelagic coupling and bottom-up forcing influence intertidal communities along the Atlantic coast of Nova Scotia. This contribution thus adds to the few equivalent studies done on western ocean boundary coasts (Menge and Menge 2013, Arribas et al. 2014, Mazzucco et al. 2015). Future research could explore the oceanographic basis of the spatial differences in pelagic food supply and seawater temperature and experimentally investigate the interspecific interactions that are seemingly influenced by those pelagic features.

## ACKNOWLEDGMENTS

We appreciate the constructive comments from two anonymous reviewers and the field and laboratory assistance provided by Willy Petzold and Melanie Spieker. Funding for this project came from grants awarded to R. A. Scrosati by the Canada Research Chairs program (CRC grant #210283), the Natural Sciences and Engineering Research Council (NSERC Discovery Grant #311624), and the Canada Foundation for Innovation (CFI Leaders Opportunity Grant #202034) and by a postdoctoral scholarship awarded to J. A. Ellrich by the German Academic Exchange Service (DAAD, #91617093).

## LITERATURE CITED

- Abernot-Le Gac, C., E. Antajan, D. Devreker, L. Drévès, J. Martin, P. Monbet, M. Schapira, and I. Schlaich. 2013. Surveillance écologique et halieutique du site de Flamanville, année 2012. Ifremer Report RST LER/BO/13.004, France.
- Anderson, D. R. 2008. Model-based inference in the life sciences: a primer on evidence. Springer, New York, New York, USA.
- Arribas, L. P., M. Bagur, J. L. Gutiérrez, and M. G. Palomo. 2014. Matching spatial scales of variation in mussel recruitment and adult densities across southwestern Atlantic rocky shores. *Journal of Sea Research* 95:16–21.
- Arribas, L. P., M. Bagur, E. Klein, P. Penchaszadeh, and M. G. Palomo. 2013. Geographic distribution of mussel species and associated assemblages along the northern Argentinean coast. *Aquatic Biology* 18:91–103.
- Barnes, H. 1956. *Balanus balanoides* (L.) in the Firth of Clyde: the development and annual variation of the larval population, and the causative factors. *Journal of Animal Ecology* 25:72–84.
- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513–523.
- Bayne, B. L. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). *Ophelia* 2:1–47.
- Bell, E. C., and M. W. Denny. 1994. Quantifying “wave exposure”: a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181:9–29.
- Bertness, M. D., S. D. Gaines, E. G. Stephens, and P. O. Yund. 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 156:199–215.
- Bertness, M. D., S. D. Gaines, and R. A. Wahle. 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* 137:103–110.
- Blanchette, C. A., B. R. Broitman, and S. D. Gaines. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. *Marine Biology* 149:689–701.
- Blanchette, C. A., and S. D. Gaines. 2007. Distribution, abundance, size, and recruitment of the mussel, *Mytilus californianus*, across a major oceanographic boundary at Point Conception, California, USA. *Journal of Experimental Marine Biology and Ecology* 340:268–279.
- Blanchette, C. A., C. M. Miner, P. T. Raimondi, D. Lohse, K. E. K. Heady, and B. R. Broitman. 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography* 35:1593–1607.
- Bouchard, G. M., and R. B. Aiken. 2012. Latitudinal variation in the reproductive cycle and size of the northern rock barnacle *Semibalanus balanoides* (L.) (Cirripedia, Archaeobalanidae) in the Bay of Fundy. *Crustaceana* 85:779–787.

- Boudreau, M. L., R. A. Scrosati, and M. C. Wong. 2017. Limitation of dogwhelk consumption of mussels by crab cues depends on dogwhelk density and cue type. *bioRxiv* article 123653. <https://doi.org/10.1101/123653>
- Bousfield, E. L. 1954. The distribution and spawning seasons of barnacles on the Atlantic coast of Canada. *Bulletin of the National Museum of Canada* 132:112–154.
- Bryson, E. S., G. C. Trussell, and P. J. Ewanchuk. 2014. Broad-scale geographic variation in the organization of rocky intertidal communities in the Gulf of Maine. *Ecological Monographs* 84:579–597.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference. *Understanding AIC and BIC in model selection. Sociological Methods & Research* 33:261–304.
- Burrows, M. T., S. R. Jenkins, L. Robb, and R. Harvey. 2010. Spatial variation in size and density of adult and post-settlement *Semibalanus balanoides*: effects of oceanographic and local conditions. *Marine Ecology Progress Series* 398:207–219.
- Bustamante, R. H., and G. M. Branch. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *Journal of Experimental Marine Biology and Ecology* 196:1–28.
- Crisp, D. J. 1968. Differences between North American and European populations of *Balanus balanoides* revealed by transplantation. *Journal of the Fisheries Research Board of Canada* 25:2633–2641.
- Crothers, J. H. 1985. Dog-whelks: an introduction to the biology of *Nucella lapillus* (L.). *Field Studies* 6:291–360.
- Cusson, M., and E. Bourget. 2005. Small-scale variations in mussel (*Mytilus* spp.) dynamics and local production. *Journal of Sea Research* 53:255–268.
- D'Amours, O., and R. E. Scheibling. 2007. Effect of wave exposure on morphology, attachment strength, and survival of the invasive green alga *Codium fragile* ssp. *tomentosoides*. *Journal of Experimental Marine Biology and Ecology* 351:129–142.
- Drouin, C. A., E. Bourget, and R. Tremblay. 2002. Larval transport processes of barnacle larvae in the vicinity of the interface between two genetically different populations of *Semibalanus balanoides*. *Marine Ecology Progress Series* 229:165–172.
- Eckersley, L. K., and R. A. Scrosati. 2012. Temperature, desiccation, and species performance trends along an intertidal elevation gradient. *Current Development in Oceanography* 5:59–73.
- Ehlers, S. M., R. A. Scrosati, and J. A. Ellrich. 2018. Nonconsumptive predator effects on prey demography: Dogwhelk cues decrease benthic mussel recruitment. *Journal of Zoology, in press*. <https://doi.org/10.1111/jzo.12555>
- Ellrich, J. A., and R. A. Scrosati. 2016. Water motion modulates predator nonconsumptive limitation of prey recruitment. *Ecosphere* 7:e01402.
- Ellrich, J. A., and R. A. Scrosati. 2017. Maximum water velocities in wave-exposed rocky intertidal habitats from Deming Island, Atlantic coast of Nova Scotia, Canada. *Pangaea*. <https://doi.org/10.1594/pangaea.880722>
- Ellrich, J. A., R. A. Scrosati, C. Bertolini, and M. Molis. 2016a. A predator has nonconsumptive effects on different life-history stages of a prey. *Marine Biology* 163:5.
- Ellrich, J. A., R. A. Scrosati, K. Romoth, and M. Molis. 2016b. Adult prey neutralizes predator nonconsumptive limitation of prey recruitment. *PLoS ONE* 11:e0154572.
- Ellrich, J. A., R. A. Scrosati, and M. Molis. 2015a. Predator nonconsumptive effects on prey recruitment weaken with recruit density. *Ecology* 96:611–616.
- Ellrich, J. A., R. A. Scrosati, and W. Petzold. 2015b. Predator density affects nonconsumptive predator limitation of prey recruitment: field experimental evidence. *Journal of Experimental Marine Biology and Ecology* 472:72–76.
- Food and Agriculture Organization. 2016. The state of world fisheries and aquaculture 2016. Food and Agriculture Organization, Rome, Italy.
- Gosselin, L. A., and E. Bourget. 1989. The performance of an intertidal predator, *Thais lapillus*, in relation to structural heterogeneity. *Journal of Animal Ecology* 58:287–303.
- Griffiths, J. R., et al. 2017. The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology* 23:2179–2196.
- Hawkins, S. J., and R. G. Hartnoll. 1982. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *Journal of Experimental Marine Biology and Ecology* 62:271–283.
- Hawkins, S. J., et al. 2009. Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series* 396:245–259.
- Hayne, K. J. R., and A. R. Palmer. 2013. Intertidal sea stars (*Pisaster ochraceus*) alter body shape in response to wave action. *Journal of Experimental Biology* 216:1717–1725.
- Heaven, C. S., and R. A. Scrosati. 2008. Benthic community composition across gradients of intertidal elevation, wave exposure, and ice scour in Atlantic Canada. *Marine Ecology Progress Series* 369:13–23.

- Hughes, R. N. 1972. Annual production of two Nova Scotian populations of *Nucella lapillus* (L.). *Oecologia* 8:356–370.
- Hughes, T. P., A. H. Baird, E. A. Dinsdale, V. J. Harriott, N. A. Moltschanivskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2002. Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. *Ecology* 83:436–451.
- Hunt, H. L., and R. E. Scheibling. 1996. Physical and biological factors influencing mussel (*Mytilus trossulus*, *M. edulis*) settlement on a wave-exposed rocky shore. *Marine Ecology Progress Series* 142:135–145.
- Hunt, H. L., and R. E. Scheibling. 1998. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trossulus* (Gould), *M. edulis* (L.)) assemblages in tidepools and on emergent rock on a wave-exposed rocky shore in Nova Scotia, Canada. *Journal of Experimental Marine Biology and Ecology* 226:87–113.
- Hunt, H. L., and R. E. Scheibling. 2001. Patch dynamics of mussels on rocky shores: integrating process to understand pattern. *Ecology* 82:3213–3231.
- Innes, D. J., and J. A. Bates. 1999. Morphological variation of *Mytilus edulis* and *Mytilus trossulus* in eastern Newfoundland. *Marine Biology* 133:691–699.
- Jarrett, J. N. 2003. Seasonal variation in larval condition and postsettlement performance of the barnacle *Semibalanus balanoides*. *Ecology* 84:384–390.
- Jenkins, S. R., J. Murua, and M. T. Burrows. 2008. Temporal changes in the strength of density-dependent mortality and growth in intertidal barnacles. *Journal of Animal Ecology* 77:573–584.
- Jenkins, S. R., et al. 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology* 243:209–225.
- Kendall, M. A., R. S. Bowman, P. Williamson, and J. R. Lewis. 1985. Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast 1969–1981. *Journal of the Marine Biological Association of the United Kingdom* 65:1009–1030.
- Kent, A., S. J. Hawkins, and P. Doncaster. 2003. Population consequences of mutual attraction between settling and adult barnacles. *Journal of Animal Ecology* 72:941–952.
- Keppel, E. A., R. A. Scrosati, and S. C. Courtenay. 2015. Interactive effects of ocean acidification and warming on subtidal mussels and sea stars from Atlantic Canada. *Marine Biology Research* 11:337–348.
- Lagos, N. A., J. C. Castilla, and B. R. Broitman. 2008. Spatial environmental correlates of intertidal recruitment: a test using barnacles in northern Chile. *Ecological Monographs* 78:245–261.
- Lara, C., G. S. Saldías, F. J. Tapia, J. L. Iriarte, and B. R. Broitman. 2016. Interannual variability in temporal patterns of chlorophyll-*a* and their potential influence on the supply of mussel larvae to inner waters in northern Patagonia (41–44° S). *Journal of Marine Systems* 155:11–18.
- Larsson, A. I., and P. R. Jonsson. 2006. Barnacle larvae actively select flow environments supporting post-settlement growth and survival. *Ecology* 87:1960–1966.
- Lathlean, J. A., D. J. Ayre, and T. E. Minchinton. 2010. Supply-side biogeography: geographic patterns of settlement and early mortality for a barnacle approaching its range limit. *Marine Ecology Progress Series* 412:141–150.
- Le Corre, N., A. L. Martel, F. Guichard, and L. E. Johnson. 2013. Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels *Mytilus* spp. *Marine Ecology Progress Series* 481:133–146.
- Leggaard, K. R., and A. C. Thomas. 2006. Spatial patterns in seasonal and interannual variability of chlorophyll and sea surface temperature in the California Current. *Journal of Geophysical Research* 111:C06032.
- Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79:1395–1411.
- MacPherson, E. A., and R. Scrosati. 2008. Population structure of the barnacle *Semibalanus balanoides* (Cirripedia) across intertidal environmental stress gradients in northern Nova Scotia, Canada. *Crustaceana* 81:725–736.
- Martel, A. L., R. Tremblay, N. Toupoint, F. Olivier, and B. Myrand. 2014. Veliger size at metamorphosis and temporal variability in prodissococonch II morphology in the blue mussel (*Mytilus edulis*): potential impact on recruitment. *Journal of Shellfish Research* 33:443–455.
- Mazzuco, A. C. A., R. A. Christofolletti, J. Pineda, V. R. Starczak, and A. M. Ciotti. 2015. Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-*a* concentration, and sea surface temperature. *Marine Biology* 162:1705–1725.
- McCook, L. J., and A. R. O. Chapman. 1997. Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology and Ecology* 214:121–147.
- McQuaid, C. D., and T. L. Lindsay. 2000. Effect of wave exposure on growth and mortality rates of the

- mussel *Perna perna*: bottom-up regulation of intertidal populations. *Marine Ecology Progress Series* 206:147–154.
- McQuaid, C. D., and T. L. Lindsay. 2007. Wave exposure effects on population structure and recruitment in the mussel *Perna perna* suggest regulation primarily through availability of recruits and food, not space. *Marine Biology* 151:2123–2131.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46:355–393.
- Menge, B. A. 1992. Community regulation: Under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755–765.
- Menge, B. A. 2000. Recruitment vs. post-recruitment processes as determinants of barnacle population abundance. *Ecological Monographs* 70:265–288.
- Menge, B. A., C. A. Blanchette, P. Raimondi, T. L. Freidenburg, S. D. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684.
- Menge, B. A., F. Chan, K. J. Nielsen, E. Di Lorenzo, and J. Lubchenco. 2009. Climatic variation alters supply-side ecology: impact of climate patterns on phytoplankton and mussel recruitment. *Ecological Monographs* 79:379–395.
- Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997a. Benthic-pelagic links and rocky intertidal communities: bottom-up effects or top-down control? *Proceedings of the National Academy of Sciences of the United States of America* 94:14530–14535.
- Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997b. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnology and Oceanography* 42:57–66.
- Menge, B. A., M. M. Foley, J. Pamplin, G. Murphy, and C. Pennington. 2010. Supply-side ecology, barnacle recruitment, and rocky intertidal community dynamics: Do settlement surface and limper disturbance matter? *Journal of Experimental Marine Biology and Ecology* 392:160–175.
- Menge, B. A., and D. N. L. Menge. 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs* 83:283–310.
- Menge, B. A., et al. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences of the United States of America* 100:12229–12234.
- Nakaoka, M., N. Ito, T. Yamamoto, T. Okuda, and T. Noda. 2006. Similarity of rocky intertidal assemblages along the Pacific coast of Japan: effects of spatial scales and geographic distance. *Ecological Research* 21:425–435.
- Nalepa, T. F., J. A. Wojcik, D. L. Fanslow, and G. A. Lang. 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density, and size structure. *Journal of Great Lakes Research* 21:417–434.
- National Aeronautics and Space Administration. 2017. Database: ocean color radiometry online visualization and analysis. <http://seadas.gsfc.nasa.gov>
- Navarrete, S. A., B. R. Broitman, and B. A. Menge. 2008. Interhemispheric comparison of recruitment to intertidal communities: pattern persistence and scales of variation. *Ecology* 89:1308–1322.
- Navarrete, S. A., and J. C. Castilla. 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. *Oikos* 100:251–262.
- Navarrete, S. A., and T. Manzur. 2008. Individual- and population-level responses of a keystone predator to geographic variation in prey. *Ecology* 89:2005–2018.
- Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. *Proceedings of the National Academy of Sciences of the United States of America* 102:18046–18051.
- Petrie, B., B. J. Topliss, and D. G. Wright. 1987. Coastal upwelling and eddy development off Nova Scotia. *Journal of Geophysical Research* 29:12979–12991.
- Petzold, W., M. T. Willers, and R. A. Scrosati. 2014. Visual record of intertidal disturbance caused by sea ice in the spring on the Atlantic coast of Nova Scotia. *F1000Research* 3:112.
- Riginos, C., and C. W. Cunningham. 2005. Local adaptation and species segregation in two mussel (*Mytilus edulis* × *Mytilus trossulus*) hybrid zones. *Molecular Ecology* 14:381–400.
- Rognstad, R. L., D. S. Wetthey, and T. J. Hilbish. 2014. Connectivity and population repatriation: limitations of climate and input into the larval pool. *Marine Ecology Progress Series* 495:175–183.
- Sagarin, R., and R. Pauchard. 2010. Observational approaches in ecology open new ground in a changing world. *Frontiers in Ecology and the Environment* 8:379–386.
- Scrosati, R. A., and J. A. Ellrich. 2016. A 12-year record of intertidal barnacle recruitment in Atlantic Canada (2005–2016): relationships with sea surface

- temperature and phytoplankton abundance. PeerJ 4:e2623.
- Scrosati, R., and C. Heaven. 2007. Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Marine Ecology Progress Series* 342:1–14.
- Shan, S., J. Sheng, K. Ohashi, and M. Dever. 2016. Assessing the performance of a multi-nested ocean circulation model using satellite remote sensing and in-situ observations. *Satellite Oceanography and Meteorology* 1:39–59.
- Shanks, A. L. 2009. Barnacle settlement versus recruitment as indicators of larval delivery. I. Effects of post-settlement mortality and recruit density. *Marine Ecology Progress Series* 385:205–216.
- Shanks, A. L., and S. G. Morgan. 2018. Testing the intermittent upwelling hypothesis: upwelling, downwelling, and subsidies to the intertidal zone. *Ecological Monographs* 88:22–35.
- Shanks, A. L., P. Sheesley, and L. Johnson. 2017a. Phytoplankton subsidies to the intertidal zone are strongly affected by surf zone hydrodynamics. *Marine Ecology* 38:e12441.
- Shanks, A. L., S. G. Morgan, J. MacMahan, and A. J. H. M. Reniers. 2017b. Alongshore variation in barnacle populations is determined by surf zone hydrodynamics. *Ecological Monographs* 87:508–532.
- Sherker, Z. T., J. A. Ellrich, and R. A. Scrosati. 2017. Predator-induced shell plasticity in mussels hinders predation by drilling snails. *Marine Ecology Progress Series* 573:167–175.
- Sigurdsson, J. B., C. W. Titman, and P. A. Davies. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature* 262:386–387.
- Sokal, R. R., and F. J. Rohlf. 2012. *Biometry. The principles and practice of statistics in biological research.* W. H. Freeman, New York, New York, USA.
- South, P. M. 2016. An experimental assessment of measures of mussel settlement: effects of temporal, procedural, and spatial variations. *Journal of Experimental Marine Biology and Ecology* 482: 64–74.
- Sprung, M. 1984. Physiological energetics of mussel larvae (*Mytilus edulis*). II. Food uptake. *Marine Ecology Progress Series* 17:295–305.
- Steffania, C. N., and G. M. Branch. 2003. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: response to wave exposure. *Marine Ecology Progress Series* 246:197–209.
- Tam, J. C., and R. A. Scrosati. 2011. Mussel and dogwhelk distribution along the northwest Atlantic coast: testing predictions derived from the abundant-centre model. *Journal of Biogeography* 38:1536–1545.
- Tam, J. C., and R. A. Scrosati. 2014. Distribution of cryptic mussel species (*Mytilus edulis* and *M. trossulus*) along wave exposure gradients on northwest Atlantic rocky shores. *Marine Biology Research* 10:51–60.
- Tide and Current Predictor. 2017. Tidal height and current site selection. <http://tbone.biol.sc.edu/tide/index.html>
- Tide-Forecast. 2018. Tide times and tide charts worldwide. <http://www.tide-forecast.com>
- Turner, J. T., H. Levinsen, T. G. Nielsen, and B. W. Hansen. 2001. Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepods and barnacle nauplii in Disko Bay, West Greenland. *Marine Ecology Progress Series* 221:209–219.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: You can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250:97–115.
- Walker, G., A. B. Yule, and J. A. Nott. 1987. Structure and function in balanomorph larvae. Pages 307–328 in A. J. Southward, editor. *Barnacle biology.* A. A. Balkema, Rotterdam, The Netherlands.
- Wieters, E. A. 2005. Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Marine Ecology Progress Series* 301:43–54.
- Wieters, E. A., S. D. Gaines, S. A. Navarrete, C. A. Blanchette, and B. A. Menge. 2008. Scales of dispersal and the biogeography of marine predator–prey interactions. *American Naturalist* 171:405–417.
- Witman, J. D., S. J. Genovese, J. F. Bruno, J. F. McLaughlin, and B. Pavlin. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. *Ecological Monographs* 73:441–462.