Differential recolonization of Atlantic intertidal habitats after disturbance reveals potential bottom-up community regulation [version 1; peer review: 2 approved]

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Abstract

In the spring of 2014, abundant sea ice that drifted out of the Gulf of St. Lawrence caused extensive disturbance in rocky intertidal habitats on the northern Atlantic coast of mainland Nova Scotia, Canada. To monitor recovery of intertidal communities, we surveyed two wave-exposed locations in the early summer of 2014. Barnacle recruitment and the abundance of predatory dogwhelks were low at one location (Tor Bay Provincial Park) but more than 20 times higher at the other location (Whitehead). Satellite data indicated that the abundance of coastal phytoplankton (the main food source for barnacle larvae) was consistently higher at Whitehead just before the barnacle recruitment season, when barnacle larvae were in the water column. These observations suggest bottom-up forcing of intertidal communities. The underlying mechanisms and their intensity along the NW Atlantic coast could be investigated through studies done at local and regional scales.
**Observation**

The NW Atlantic coast displays cold-temperate intertidal environments. In Nova Scotia (Canada) in winter, ice does not form on the sea surface on the open Atlantic coast. However, sea ice readily forms in relatively enclosed water bodies such as gulfs, causing physical disturbance on intertidal communities as the ice moves with tides, currents, waves, and wind. In particular, abundant sea ice forms every winter on the large Gulf of St. Lawrence (Canadian Ice Service). Between late winter and early spring, fragments of sea ice drift out of the gulf through the Cabot Strait (between Nova Scotia and Newfoundland) towards the open ocean. Such drift ice then travels south following the open Atlantic coast of Nova Scotia (Figure 1), reaching different distances every year depending on the ice load (Canadian Ice Service).

The open Atlantic coast of mainland Nova Scotia (Figure 1) is reached by drift ice only in some years, more often in northern sections of this coast because of their closer proximity to the Cabot Strait (Canadian Ice Service). In the early spring of 2014, large amounts of sea ice drifted out of the Gulf of St. Lawrence, blocking northern sections of this coast for several days (Canadian Ice Service). In some sections of the northern coast, drift ice was still present in early April, although it had rapidly retreated to the Cabot Strait by the third week of April (Canadian Ice Service). In the first half of April, drift ice was present in some areas of the southern coast of Nova Scotia, but ice was still very much present at Cape Breton Island, which is the southernmost point of Nova Scotia. In early April, large amounts of drift ice were present at the Cabot Strait and Cape Breton Island, blocking the open Atlantic Ocean directly. On 23 June 2014, at each location we measured the density of barnacle recruits (*Semibalanus balanoides*) in 8 quadrats (10 cm × 10 cm) that we had randomly established along 30-m transect lines at the mid-to-high intertidal zone in late April. Because of the intense ice scour in early April, macroscopic organisms were absent at this zone in mid-April, so the substrate was then fully available for barnacle recruitment (barnacles are often the first sessile invertebrates to recolonize disturbed intertidal habitats).

*Semibalanus balanoides* is the only species of intertidal barnacle on this coast. Every year, recruits of *S. balanoides* accumulate in intertidal habitats on this coast during May and June. Our measurements (Dataset 1) on 23 June (after which no new recruits appeared) indicated that barnacle recruit density was significantly higher than at Tor Bay Provincial Park (7.3 ± 4.2 recruits dm⁻²; Figure 3). This statistical
test was performed in Excel 2004 for Mac. No other sessile macroscopic species occurred at that time in the quadrats.

**Dataset 1. Abundance of barnacle recruits at the end of the 2014 recruitment season**

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Number of barnacle recruits (*Semibalanus balanoides*) occurring on 23 June 2014 in 8 quadrats (10 cm × 10 cm) that had been randomly established along 30-m transect lines at the mid-to-high intertidal zone in late April (just before the beginning of barnacle settlement) at a wave-exposed site in Whitehead and in Tor Bay Provincial Park.

The greater density of barnacle recruits at Whitehead than at Tor Bay Provincial Park was related to a higher nearshore chlorophyll-*a* concentration during late March and April at Whitehead, according to MODIS satellite data (Table 1; National Aeronautics and Space Administration). Nearshore chlorophyll-*a* concentration indicates coastal phytoplankton abundance, and phytoplankton is the main food source for barnacle nauplius larvae. For *S. balanoides* from the Atlantic coast of Nova Scotia, nauplius larvae occur in coastal waters for 5–6 weeks before metamorphosis to cyprids and then intertidal settlement, which starts in early May on our studied coast. Thus, it is possible that the higher food supply for larvae at Whitehead than at Tor Bay Provincial Park may have ultimately contributed to determining the higher barnacle recruitment at Whitehead. A positive relationship between nearshore phytoplankton abundance and intertidal barnacle recruitment was previously documented for NW Atlantic intertidal systems at a regional scale.

To see whether barnacle recruitment could influence higher trophic levels, we measured the abundance of dogwhelks (*Nucella lapillus*; Figure 4) shortly after the end of the barnacle recruitment season. *Nucella lapillus* is the main predator of barnacles on the studied coast, so presumably a higher barnacle recruitment could locally increase dogwhelk abundance. On 15 July 2014, at each of the

**Table 1. Nearshore chlorophyll-*a* concentration (mg m⁻³) on dates shortly before the 2014 barnacle recruitment season (May–June) measured for the coast of Whitehead and Tor Bay Provincial Park by MODIS-Aqua satellite technology with a 9 km × 9 km spatial resolution.**

| Date      | Whitehead | Tor Bay Provincial Park |
|-----------|-----------|-------------------------|
| 14 March  | 3.27      | 2.11                    |
| 22 March  | 3.67      | 2.38                    |
| 30 March  | no data   | 1.48                    |
| 7 April   | 14.28     | 4.29                    |
| 15 April  | 18.08     | 10.56                   |
| 23 April  | no data   | 3.53                    |
| 1 May     | 2.00      | 1.81                    |

**Figure 4. Dogwhelks on a barnacle bed.** Picture taken at low tide on 15 July 2014 at the mid-to-high intertidal zone at a wave-exposed habitat in Whitehead, showing dogwhelks foraging on the bed of barnacle recruits. A few barnacle shells appear empty likely as a result of recent dogwhelk predation.
two studied locations we measured during low tide the density of *N. lapillus* in 30 quadrats (50 cm × 50 cm) randomly established at the mid-to-high intertidal zone (Dataset 2). Dogwhelk density was significantly higher (Student’s *t* = 2.64, *P* = 0.013) at Whitehead (39.6 ± 14.2 individuals m⁻², mean ± SE, *n* = 30 quadrats) than at Tor Bay Provincial Park (1.9 ± 0.8 individuals m⁻²). Barnacle recruitment in June 2014 may not fully explain dogwhelk density in July 2014, as dogwhelks had not undergone their 2014 recruitment season as yet (mainly in late summer). However, visits to both studied locations in 2012 and 2013 revealed a similar difference in barnacle recruitment between both locations (R.A.S., pers. obs.), supporting the notion that dogwhelk abundance may be driven by barnacles on this coast. Interestingly, in 2014, barnacle recruits and dogwhelks were more abundant at Whitehead than at Tor Bay Provincial Park by a similar ratio (27.6 times higher for barnacles and 7.8 times higher for dogwhelks), further suggesting a possible dependency of dogwhelk abundance on barnacle recruitment.

Relationships between coastal chlorophyll-*a* concentration, intertidal barnacle recruitment, and intertidal predator impacts have been identified on Pacific rocky shores. The positive influence of prey food supply on predators mediated by prey recruitment is referred to as bottom-up regulation of community structure. Coastal configuration and water column movements influence nearshore phytoplankton abundance. What caused the phytoplankton difference between our two studied locations remains to be determined. However, the observed link between phytoplankton abundance, barnacle recruitment, and dogwhelk density does suggest that bottom-up forcing may also structure NW Atlantic intertidal communities. Understanding the underlying mechanisms and their intensity along the coast could be achieved with a larger spatial monitoring and field experimentation.

Data availability
F1000Research: Dataset 1. Abundance of barnacle recruits at the end of the 2014 recruitment season, 10.5256/f1000research.5545.d37093

F1000Research: Dataset 2. Abundance of dogwhelks shortly after the 2014 barnacle recruitment season, 10.5256/f1000research.5545.d37094

Author contributions
WP and RAS did the field surveys. RAS wrote the manuscript and WP provided critical comments to produce the final version.

Competing interests
No competing interests were disclosed.

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In this article, Petzold and Scrosati provide observational evidence suggesting that food supply drives the re-colonisation of benthic organisms in wave-exposed intertidal communities after being disturbed by drifting ices. The title and abstract of the article are appropriate for the content of the work and represent a suitable summary of it. Although the authors report the results of only one site for each “condition” (i.e. one site with high and one site with low Chlorophyll-a concentration), the differences in food supply between these sites are strong enough to propose further studies analysing the role of bottom-up forcing in this system. Accordingly, the conclusions of the study are sensible and justified on the basis of the results. As a follow-up approach, the authors may consider first, to expand the study to a larger set of sites in order to confirm the pattern, and second, to construct competing hypotheses (in addition to the “bottom-up hypothesis”) that would be tested by means of manipulative experiments replicated at those sites. This article is a necessary benchmark from which further hypothesis-driven research should be conducted.

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

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This study is an interesting first approach to understanding the factors that affect the ability to recruit sessile benthic organisms after disturbances in an intertidal community. Petzold and Scrosati address the issue concerning the role of larval supply and its relation to phytoplankton abundance, which leads directly to considering that a bottom up mechanism may be acting in these communities. Furthermore, the idea that began the work is clearly stated and the theoretical context is appropriate, as well as the statistical treatment of the data. Although a more deep and permanent approach to the problem requires the carrying out of further studies, perhaps with the incorporation of field experiments, this initial statement is correct and I recommend its indexing.

**Competing Interests:** No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.