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Recruitment and Post-recruitment Dynamics of the Barnacle *Semibalanus balanoides* on a Wave-Exposed Headland in Atlantic Canada

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INTRODUCTION

The intertidal barnacle *Semibalanus balanoides* (Crustacea, Cirripedia) is a common organism on North Atlantic rocky shores (Hutchins, 1947; Bousfield, 1954; Crisp, 1964; Jenkins et al., 2000; Flight et al., 2012; Crickenberger and Wethey, 2018). Adults are sessile and reproduce through pelagic larvae. Due to its wide niche breadth, its various ecological roles (filter-feeder, competitor, facilitator, and prey), and its utility as an ecological indicator, it has often been used as a model species to advance ecological theory (Connell, 1961; Menge and Sutherland, 1976; Bertness et al., 1999; Belt et al., 2009; Burrows et al., 2010; Crickenberger and Wethey, 2018; Scrosati and Freeman, 2019; Scrosati, 2021). Recruitment is an aspect of its life cycle that has particularly been investigated, given its relevance for population replenishment and persistence. For barnacles, recruitment refers to the appearance of new organisms on the substrate as a result of the metamorphosis of settled larvae. Settlement refers to the permanent attachment that the pelagic larvae establish on a substrate (Jenkins et al., 2000; Blythe and Pineda, 2009).

The magnitude of annual recruitment is often estimated as recruit density measured at a point in time selected by the researcher. When the timing of the recruitment season (the period during which recruits appear on the shore) can be anticipated with some confidence, recruit density is typically measured as close as possible to the end of this period to quantify annual recruitment. This approach, however, may miss early recruits that may die and be removed from the substrate by natural causes before recruit density is measured. The resulting underestimation of annual recruitment may thus limit our understanding of recruit ecology (Minchinton and Scheibling, 1993; Shanks et al., 2014). On the other hand, unpredictable natural variation may add additional recruits after recruit density is measured if the recruitment season is longer than anticipated. Thus, recruitment dynamics are best studied through frequent field surveys spanning the recruitment season and dates beyond its suspected end. Conducting frequent surveys during the recruitment season also matters because the drivers of recruit performance (e.g., pelagic food supply, environmental stressors, and benthic predators) often vary in intensity during that period (Menge, 2000).

On the open Atlantic coast of Nova Scotia (Canada), the recruitment of *Semibalanus balanoides* typically takes place in May and June (Ellrich et al., 2016a). This article discusses the recruitment and post-recruitment dynamics of *S. balanoides* from this coast using data on recruit appearance, mortality, density, and size collected frequently between May and October 2019. We discuss the salient temporal patterns in a context related mainly to *S. balanoides* recruitment.

MATERIALS AND METHODS

We did this study at Western Head, a prominent rocky headland located on the Atlantic coast of Nova Scotia (43.9896° N, 64.6607° W; **Figure 1A**). We took all measurements in intertidal bedrock areas that directly face the open ocean, so these are wave-exposed habitats (**Figure 1B**). Maximum water velocity measured in nearby wave-exposed intertidal habitats can reach 12 m s^{-1} (Hunt and Scheibling, 2001). To establish our sampling units, we first determined the elevation (in m above chart datum, or lowest normal tide) of the upper distribution boundary of the sessile perennial species that occurred highest on the shore (coincidentally, *Semibalanus balanoides*) on rocky surfaces excluding tide pools and crevices. This vertical distance was 2.2 m, which is similar to the maximum tidal amplitude for this location (2.3 m, Tide and Current Predictor, 2021). We then divided this vertical distance in three and measured all recruit variables (named below) just above the lower boundary of the upper third of this vertical range. Therefore, our barnacle data were measured at an elevation of 1.5 m. This high-to-middle elevation was selected because barnacles are abundant there and also to make our data comparable with recent barnacle surveys done at that elevation at other wave-exposed locations along the Atlantic coast of Nova Scotia (Scrosati and Ellrich, 2018, 2019).

To measure barnacle recruitment unaffected by other sessile species, in late April 2019 (shortly before the recruitment season) we cleared eight patches of rocky substrate spaced at random along the coastline at the targeted elevation. From each patch, we removed all sessile organisms with a chisel and a metallic scrubber. At the center of each patch, we delimited a square area (10 cm × 10 cm) permanently by marking two vertices on the substrate to ensure accurate relocation of such clearings across sampling dates. On the Nova Scotia coast, natural rock clearings provide more realistic measures of barnacle recruitment than plates covered with 3M Safety-Walk tape, which are used on other coasts (Scrosati and Ellrich, 2018). We took photographs of the square clearings during low tides (framing the clearings with a 100-cm^2 quadrat) on 2 May, 9 May, 10 May, 17 May, 23 May, 28 May, 1 June, 9 June, 13 June, 24 June, 3 July, 22 July, 20 August, 2 September, and 26 October. The surveys were more frequent during May and June to discern the dynamics of recruitment, although surveys could not then be done more often because of tide dynamics and wave action.

We analyzed the photographs with ImageJ to determine the appearance, size, and survival of each recruit throughout time. These measurements were possible because barnacles remain permanently attached to the substrate after larval settlement and metamorphosis (Blythe and Pineda, 2009). The appearance of a recruit was recorded for a given sampling date when that recruit was absent in the previous sampling date. The size of a recruit was measured as the basal diameter of its shell (Bertness et al., 1991). The mortality of a recruit was recorded for a given sampling date when only the shell plates of a previously live individual were observed on that date ("empty" shell).

Because of natural topographic heterogeneity (Helmuth et al., 2006; Harley, 2008; Mislan et al., 2011; Sejr et al., 2021), differences among the clearings relevant to this study became apparent during the surveys. Some clearings seemed to receive more wave splash than others. Thus, for most dates in May (when wave action was often intense), a visually reflective film of water remained over four of the eight clearings during the low tide; this water layer could not be removed to take pictures due to wave action. In addition, ephemeral green algae appeared on those four clearings during May, likely favored by those conditions. These unexpected developments prevented us from accurately identifying the barnacle recruits from those four clearings for most of May. Therefore, we are reporting results for the four clearings that were possible to monitor in detail throughout the entire study period. These clearings are representative of Western Head because they spanned the studied coastline along the targeted elevation.

In this article, the barnacles that appeared in May and June and were monitored until October are always referred to as recruits even though many of them reached adult size in October. This approach facilitates the description of temporal patterns by making clear that only the organisms recruited in May and June 2019 were monitored. The data collected for this article are freely available from the figshare online repository (Scrosati and Holt, 2021).

RESULTS

Barnacle Recruitment

The first recruits appeared at some point between 2 and 9 May (no recruits were seen on 2 May) and the last recruits appeared between 13 and 24 June (no new recruits were seen after 24 June). During this period, the daily rate of barnacle recruitment varied significantly over time (repeated-measures ANOVA, $F = 3.43$, $P = 0.017$; **Figure 2A**). By 17 May, 74% of the recruits identified in this study had already appeared on the substrate, while 90% of all identified recruits were on the substrate by 28 May. Therefore, recruitment in June was low. The highest value of recruitment rate obtained for a single quadrat (11 recruits dm^{-2} day^{-1}) was recorded on 10 May. A visual example of the temporal changes in recruitment is offered in **Figure 1C**.

Recruit Mortality

No recruit deaths were recorded during the recruitment season (May and June) or in early July. Dead recruits were only found between 22 July and the end of the study on 26 October. During this period, the daily mortality rate of recruits did not vary significantly (repeated-measures ANOVA, $F = 0.95$, $P = 0.456$; **Figure 2B**). Overall, mortality was considerably lower than the recruitment seen during May. Relative to the values of recruit density recorded on 24 June (peak recruit density before any mortality had occurred), the average percent mortality rate on 26 October was 10.5% (N = 4 quadrats).

Recruit Density

During the studied period, the density of live recruits varied significantly over time (repeated-measures ANOVA, $F = 7.70$, $P < 0.001$; **Figure 2C**). One of the four clearings could not be surveyed on 10 and 17 May because of intense wave

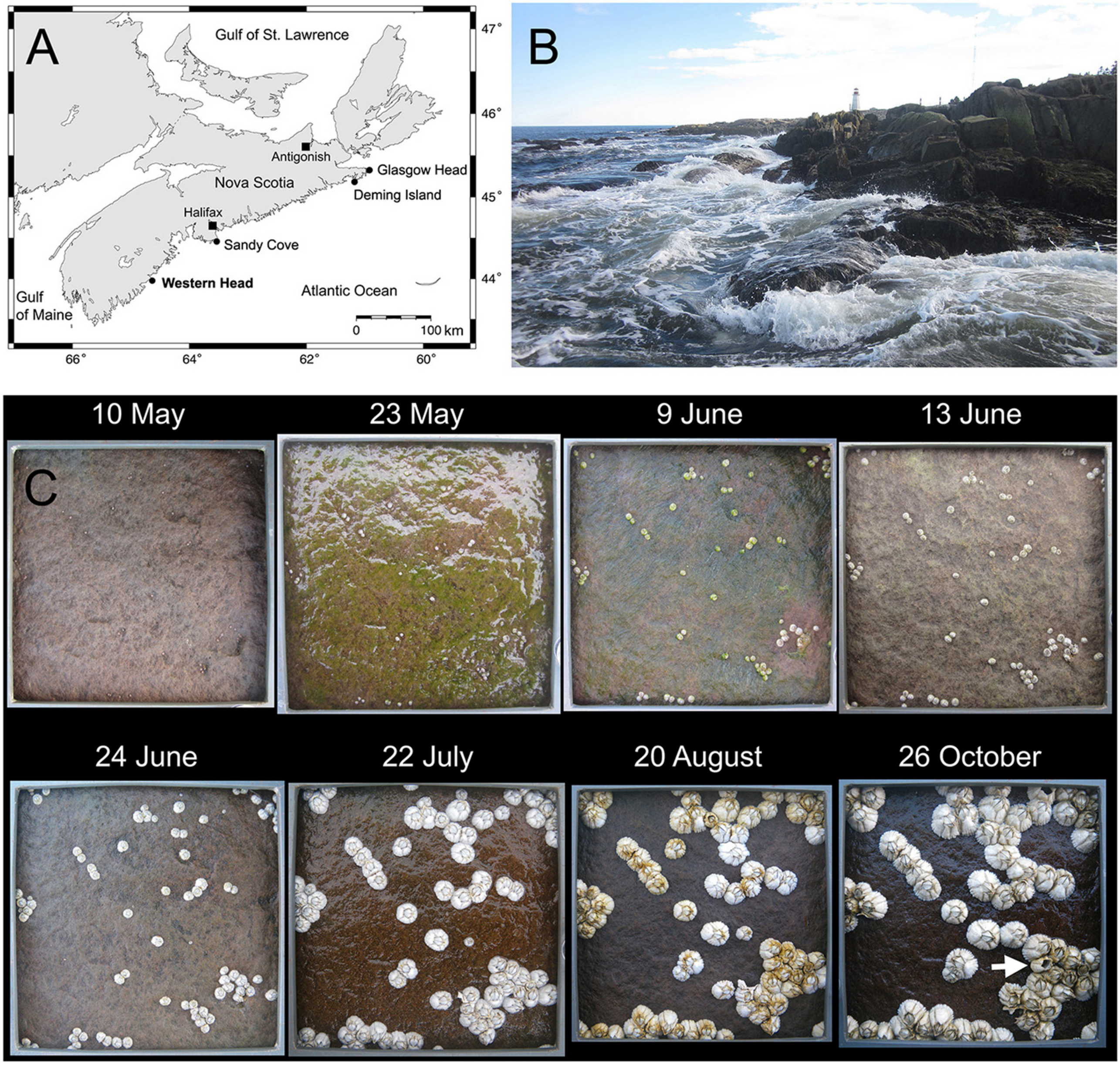

FIGURE 1 | (A) Map showing the position of Western Head and other intertidal locations from the Nova Scotia coast mentioned in the text. **(B)** View of the coast of Western Head during a low tide. **(C)** Photographs of one of the clearings taken at low tide on eight representative sampling dates (see section Materials and Methods for the full list of sampling dates). Each photograph shows the inner frame (10 cm × 10 cm) of the PVC quadrat that was used as a size reference to measure the body size of each barnacle recruit. The arrow in the photograph for the last sampling date points to a dead barnacle (empty shell). These photographs were taken by R. A. Scrosati.

action. As that clearing had a lower recruit density than the others, the mean recruit density reported for those two dates is higher than the means expected from the dotted line shown in **Figure 2C** joining the means for 9 and 23 May, which were calculated (like for all other dates) using density data for all four clearings. Overall, recruit density increased strongly during May and weakly during June and decreased weakly due to mortality between late July and October. On average for the four surveyed clearings, peak recruit density (recorded on 24 June at the end of the recruitment season) was 58.5 recruits dm^{-2}.

Recruit Size

The temporal change in recruit size is shown in **Figure 2D**. This figure summarizes the data for the recruits found on 9 May because those are the earliest (and most numerous) group of recruits that appeared on the shore. This approach allows us to evaluate growth during the entire study period

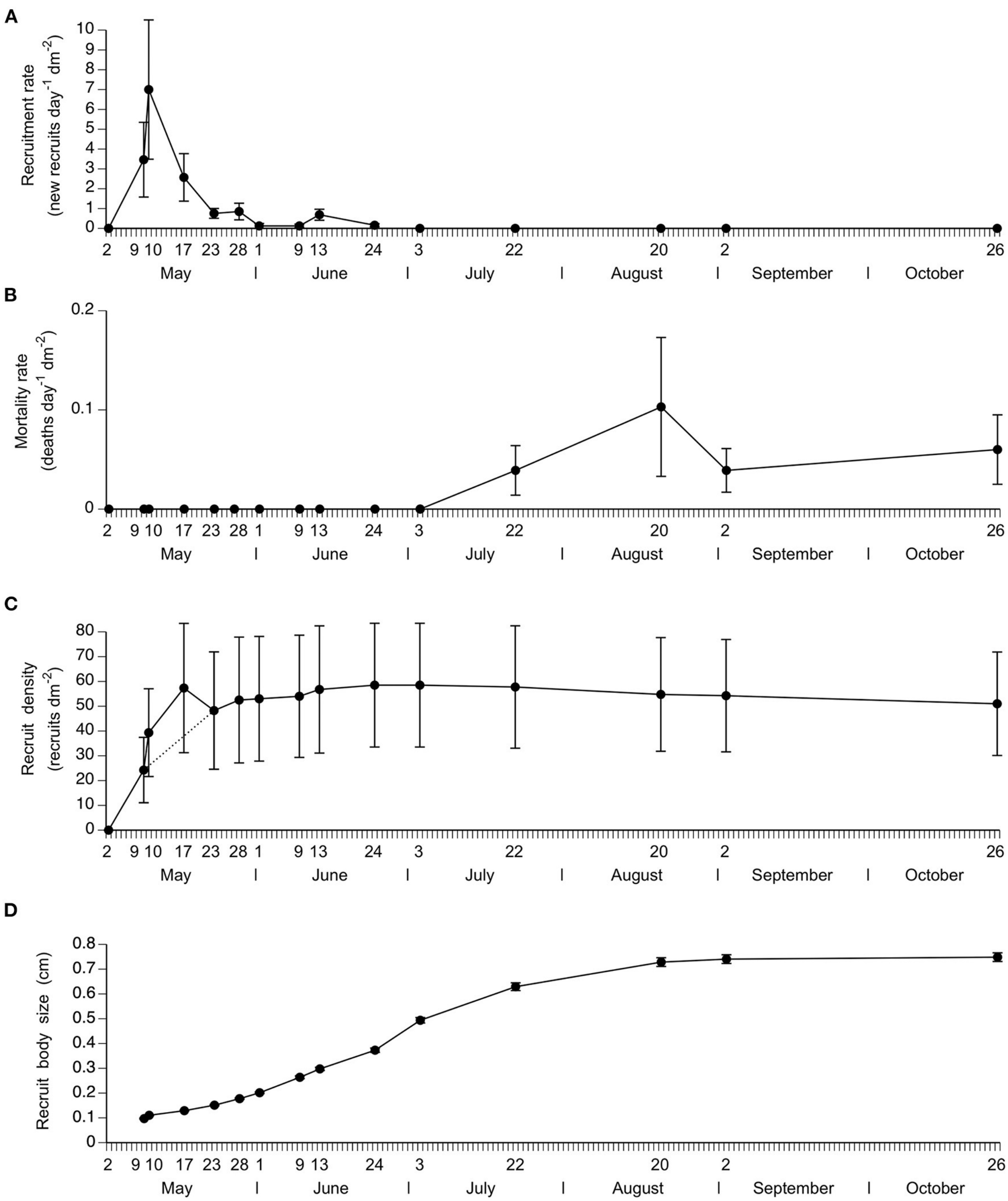

FIGURE 2 | Temporal change (mean ± SE) in **(A)** barnacle recruitment rate (number of recruits appeared on the substrate since the previous sampling date expressed per day and per unit area), **(B)** mortality rate of recruits (number of dead recruits appeared on the substrate since the previous sampling date expressed per day and per unit area), **(C)** recruit density (number of live recruits per unit area), and **(D)** barnacle body size (basal shell diameter of live recruits).

using the same organisms. During the studied period, recruit size varied significantly over time (repeated-measures ANOVA, $F = 1{,}028.95$, $P < 0.001$). For size calculations, we did not measure the size of the empty barnacle shells found between 22 July and 26 October because they indicated dead barnacles. Overall, recruit size followed a sigmoidal pattern throughout the study period, growth increasing from May to July and decreasing from July to October. The largest barnacle recorded at the end of the study period on 26 October was 1.1 cm in basal shell diameter. A visual example of the temporal changes in recruit size is offered in **Figure 1C**.

DISCUSSION OF THE SALIENT PATTERNS

The short recruitment season of *Semibalanus balanoides* compared with other barnacle species whose recruitment spans several months (e.g., on the NE Pacific coast; Navarrete et al., 2008) suggests that monthly variation in the drivers of recruitment may be particularly critical for *S. balanoides*. For example, unusually extreme events (e.g., food shortages, heat waves) in May might result in recruitment failures or diminished recruitment affecting population persistence. Such monthly events would not equally affect barnacle species for which strong recruitment in other months could have a compensatory influence. On the other hand, the appearance of most *S. balanoides* recruits in the first few weeks of the recruitment season at Western Head parallels the general trend found for *S. balanoides* in Europe, even though differences among sites naturally occur (Jenkins et al., 2000).

The timing of recruitment of *Semibalanus balanoides* changes latitudinally along the Atlantic coast of North America. Past studies in Nova Scotia yielded similar results. For example, a study done in 1988 at Sandy Cove (103 km northeast of Western Head) found that settlement started on 22 April and that the main settlement period ended on 15 June at middle and low elevations (Minchinton and Scheibling, 1993). A study done in 2011 at Glasgow Head (328 km northeast of Western Head) in semi-exposed habitats found that recruitment started after 2 May and that no settlement occurred after 15 June at the high intertidal zone (Ellrich et al., 2016a). Studies done at Deming Island (308 km northeast of Western Head) in semi-exposed habitats found that recruitment started on 30 April in 2012 and on 9 May in 2013 on areas located predominantly at the mid-intertidal zone (Ellrich et al., 2016b). It is thus possible that, in Nova Scotia, recruitment may start a few days earlier at middle elevations than at high elevations. Field observations done by R. Scrosati at various wave-exposed locations spanning 415 km of the Atlantic coast of Nova Scotia between 2014 and 2021 never found any settled cyprids or recruits before early May at high-to-middle elevations (the zone surveyed for this study). Therefore, the recruitment season in these environments spans May and June. Toward lower latitudes along the Atlantic coast of North America, recruitment occurs increasingly earlier in the year. For example, in southern New Brunswick (situated between Nova Scotia and New England, USA), settlement begins in April and ends in May (Bousfield, 1954; Le Tourneux and Bourget, 1988). In New England itself, recruitment takes place between January or February and April or May (Hutchins, 1947; Bertness et al., 1992; Jarrett and Pechenik, 1997; Pineda et al., 2002, 2006; Blythe and Pineda, 2009) and settlement ceases in late May in Maine, to the north, but in late March in Rhode Island, to the south (Bertness and Gaines, 1993). A similar latitudinal gradient in the timing of *S. balanoides* recruitment occurs in Europe, as recruitment occurs in summer on the Barents Sea coast in northern Russia (Hutchins, 1947) but in mid- to late winter in the United Kingdom and NW Spain, near its southern distribution limit (Hutchins, 1947; Lewis, 1986).

The mortality of recruits observed between July and September at Western Head was likely caused by heat and desiccation stress during low tides (Bertness and Gaines, 1993; Menge, 2000). For instance, temperature measured at low tide on the rocky substrate near the surveyed clearings at Western Head exceeded 30°C on 8 days in July-August 2019 (with a maximum value of 35°C), while sea surface temperature (SST) measured at high tide barely surpassed 17°C during that period. In June, temperature at low tide only surpassed 28°C in 2 days and was lower than 25°C in 22 days (Scrosati et al., 2020). At the surveyed high-to-middle elevations in these wave-exposed habitats, barnacle predators (dogwhelks, *Nucella lapillus*) were rare during the studied period. Dogwhelks are more common at lower elevations on more sheltered habitats (Minchinton and Scheibling, 1993; Menge, 2000).

The ultimate drivers of recruit density at the end of the recruitment season at Western Head remain to be determined, although larval and food supply (Menge and Menge, 2019; Shanks and Morgan, 2019) together with benign conditions before the summer and scarcity of predators must play a predominant role. At lower elevations in wave-exposed habitats at Western Head, recruitment is higher, likely because of increased larval supply due to the longer submergence periods (Scrosati, 2020); a similar pattern was found in Rhode Island (Bertness et al., 1992). At other wave-exposed locations surveyed at high-to-middle elevations on the Nova Scotia coast, recruit density can be higher (up to a locationwise average of 212 recruits dm^{-2}) and positively related to planktonic food supply and SST (Scrosati and Ellrich, 2018). On other shores, *Semibalanus balanoides* can exhibit even higher recruitment. For example, recruit density in wave-exposed locations can range between 800–1,100 recruits dm^{-2} in Maine (Menge, 1978) and 1,600–2,000 recruits dm^{-2} in Ireland (Jenkins et al., 2000). Thus, wave-exposed intertidal environments on the open Atlantic coast of Nova Scotia show relatively moderate values.

The recruits of *Semibalanus balanoides* showed a classic sigmoidal growth pattern (Sköld et al., 2001; Tjørve and Tjørve, 2017) until reaching adult sizes in the fall. Organisms of a similar age collected in 2011 at Glasgow Head, north of Western Head on the Nova Scotia coast, had reached reproductive maturity because they had eggs (Ellrich et al., 2016a). Thus, the grown recruits seen in October at Western Head may have been reproductive as well. This assumption is further supported by the notion that *S. balanoides* individuals with basal widths <4 mm are typically non-reproductive (Pineda et al., 2002; Bouchard and Aiken, 2012). We also note that, at Western Head, *S. balanoides* recruits generally grow larger than at other wave-exposed sites surveyed at the same elevation zone along the Atlantic coast of Nova Scotia. This growth is positively related to nearshore phytoplankton abundance (Scrosati and Ellrich, 2019), which could be driven in part by coastal upwelling, a phenomenon that is prevalent in summer at Western Head (Scrosati and Ellrich, 2020a,b). Body size and coastal phytoplankton abundance are also related in *S. balanoides* from Europe (Burrows et al., 2010).

Finally, the relative importance of recruitment vs. post-recruitment processes for population maintenance has received considerable attention in intertidal ecology, with results that often depend on the environmental context (Scrosati, 1998; Menge, 2000; Svensson et al., 2004). The data hereby described for Western Head and the positive recruit–adult relationship found for similar habitats along the Nova Scotia coast (Scrosati and Ellrich, 2018) suggest that recruitment plays an important role in structuring barnacle populations in mid-to-high intertidal, wave-exposed environments on this coast.

MAIN CONCLUSIONS

- Recruitment of *Semibalanus balanoides* in wave-exposed rocky intertidal habitats at Western Head occurred in May and June, which is thus confirmed to be the recruitment season.
- Nearly 3/4 of the recruits appeared during the first half of May, while 9 in 10 recruits were on the substrate by the end of May, so recruitment during June was low, with no recruits appearing near the end of that month.
- No recruit mortality occurred during the recruitment season or in early July.
- Recruit mortality only occurred between late July and the end of the study (late October), although with rates considerably lower than May recruitment rates.
- Recruits grew in size following a sigmoidal pattern until reaching adult sizes in the fall.
- Overall, these findings indicate that recruit density measured between late June and early July would accurately represent the rate of annual recruitment for *S. balanoides*.

DATA AVAILABILITY STATEMENT

The full data set described in this Data Report is freely available from the figshare online repository: https://doi.org/10.6084/m9.figshare.16847206.v1.

AUTHOR CONTRIBUTIONS

RS designed the study, conducted the field surveys, and wrote the manuscript. JH and RS analyzed the photographs. Both authors approved the final manuscript version.

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