Periwinkle surveys 2020-21

Beth Harvey

NORTHUMBERLAND INSHORE FISHERIES AND CONSERVATION AUTHORITY
8 Ennerdale Road, Blyth, NE24 4RT
www.nifca.gov.uk

Contents

Summary

Gathering of periwinkles (*Littorina littorea*) occurs on rocky shores throughout the Northumberland IFCA (NIFCA) district both commercially and recreationally, with concerns raised by the public about levels of collection in certain areas. From June 2020 until April 2021 NIFCA surveyed five known collection sites (Berwick-Upon-Tweed, Boulmer Haven, Cresswell, Holy Island and St Mary's Island), ranking them in terms of collection intensity from NIFCA patrol sightings of intertidal activity. Surveys were carried out every two months where possible, measuring periwinkle densities and sizes in addition to faunal and algal assemblages and substrate cover.

There was no correlation between collection intensity and periwinkle densities or sizes at different locations. Periwinkle size was instead negatively related to density, probably due to competition for available food causing lower growth rates where high densities of periwinkles occur. Neither faunal nor algal abundance/percentage cover, species richness or diversity were correlated with collection pressure. However, Berwick, which had the highest levels of collection, had the lowest periwinkle densities in addition to the highest macroalgal abundance and diversity which could be due to lower grazing pressure from periwinkles compared to other sites.

Periwinkle density overall was negatively related to abundance of algae and slightly positively related to cover of gravel substrate. The highest densities of periwinkle were found on boulder- and cobble-covered areas of shore which has been found in previous studies. Overall, environmental variables such as substrate type and other factors not measured in this study such as organic content and elevation are likely to cause the observed differences in periwinkle densities. Periwinkles are generally resilient to localised impacts due to their ability to recolonise from larvae which disperse widely in the sea, therefore harvested populations could be maintained from uncollected populations elsewhere.

Rocky shore communities remained consistent over the year, though periwinkle densities were higher in summer surveys which should be considered in future survey work. Periwinkle gathering and populations will continue to be monitored by NIFCA, particularly at Berwick, to ensure sustainable levels of collection and populations are maintained in the future.

Introduction

The periwinkle (*Littorina littorea*), known as the common or edible periwinkle, is commonly found around the coast of the United Kingdom (Moore, 1937; Smith & Newell, 1955). *L. littorea* is found in a variety of intertidal habitats including rocks, mud and sand however is most abundantly found on rocky shores (Smith & Newell, 1955; Storey et al., 2013). They prefer more complex rugose shore offering increased protection against predation and pressures of exposure at low tide (Carlson, 2006) and are often found in clusters in crevices or rockpools (Newell, 1958).

Periwinkle gathering occurs both recreationally and commercially on rocky intertidal areas up and down the Northumberland Coast. It is difficult to accurately assess the size of periwinkle fisheries as they are unregulated, under reported, and often black market in nature (Cummins et al., 2002; Crossthwaite et al., 2012). There is a peak in price and demand at Christmas with more intense harvesting, however periwinkles are harvested year-round with summer demand from restaurants in France (Crossthwaite et al., 2012).

A PhD study was conducted by Tinlin-Mackenzie (2018) on intertidal collection within the Berwickshire and North Northumberland Coast (BNNC) EMS which covers a significant proportion of the NIFCA district from Alnmouth to north of the Scottish border. Overall, Tinlin-Mackenzie estimated that over 3 million periwinkles are removed from the BNNC EMS every year and the estimated economic value of the fishery is £133,982.

Potential impacts of periwinkle gathering on rocky shores are reductions in their abundance, altered size structures of the population as a result of targeting the largest individuals, as well as altering community structure. Removal of *L. littorea* has the potential to reduce grazing pressure, increase algal cover, enhance sedimentation, and control the recruitment of sessile organisms (e.g. Petraitis, 1989; Crossthwaite, 2012). Physical disturbance of the habitat and organisms can also have negative effects, from trampling and stoneturning (Fowler, 1999; Berthelon et al., 2004; Tyler-Walters and Arnold, 2008; JNCC and Natural England, 2011).

For more information on periwinkle biology and size at maturity, as well as the Northumberland periwinkle fishery, please refer to other NIFCA reports[1,2].

NIFCA surveyed five known periwinkle collection hotspots within the district every two months (when possible, due to Covid-19 restrictions) from June 2020 until April 2021 to understand more about differences in periwinkle density between shores and in relation to collection pressure over

---

[1] NIFCA report: *Description of the Northumberland IFCA Periwinkle Fishery*. Aitken & Harvey, 2021

[2] NIFCA report: *Periwinkle Ecology and Size of Maturity Study*. Harvey, 2021

time, any impacts of periwinkle gathering on rocky shore communities, and periwinkle size at maturity.

Methods

Site selection

Study methodology broadly followed Tinlin-Mackenzie (2018) in comparing communities impacted by different levels of periwinkle collection. Five sites (Berwick-Upon-Tweed, Boulmer Haven, Cresswell, Holy Island and St Mary's Island) were selected within the NIFCA district to survey periwinkles, based on known hotspots of periwinkle collection from NIFCA patrols. Sites were ranked in terms of collection pressure based on data from NIFCA patrols from 2016-2020 (Table 1).

Table 1. Collection pressure classifications of each site, from NIFCA intertidal patrols between 2016-2020. Showing total number of patrols, the proportion of patrols periwinkle harvesting was sighted on, the average number of collectors per sighting of periwinkle harvesting, the average number of collectors per patrol (proportion of patrols x average number per sighting), the maximum number of collectors sighted on a single patrol, and the ranking of collection intensity based on average number of collectors per NIFCA patrol (1= high, 5=low).

Location	Number of patrols	Proportion of patrols activity sighted	Average no. of collectors per sighting	Average no. of collectors per patrol	Max. no. collectors	Collection intensity ranking
Berwick	23	0.70	3.00	**2.09**	7	1
Boulmer	10	0.40	2.75	**1.10**	4	2
Cresswell	12	0.50	1.67	**0.83**	3	4
Holy Island	11	0.27	4.00	**1.09**	7	3
St Mary's Island	15	0.27	2.00	**0.53**	2	5

Survey methods

Sampling was carried out in June, August, October, December 2020 and March and April 2021, though due to logistical constraints all survey sites were only able to be surveyed in June, August and April. At each shore, 15 0.25m^2 quadrats were placed on the intertidal rocky shore randomly along set transects perpendicular to the shore, with five each in the lower, middle and upper shore zones. Within each quadrat, all periwinkles were counted and shell height measured using Vernier callipers. Abundance of all macroalgae (seaweed) and other faunal (animal) taxa was recorded to species level where possible. Count data were recorded for most faunal taxa, while percentage cover was used for sessile invertebrates (e.g. barnacles), macroalgae and encrusting algae or lichen. Within the same quadrats, percentage cover of substrates was recorded (exposed bedrock, boulders, cobbles, pebbles, gravel and sand).

In addition to quadrat surveys for periwinkle densities, timed searches were also carried out where officers manually searched for periwinkles for set time periods (normally 10 minutes) to include areas unsuitable for quadrat surveys such as within rockpools, in crevices and under boulders. Density in terms of numbers found per minute was calculated.

Analysis

Since periwinkle density was found to vary between sites and also within sites over time, when comparing between locations only surveys from June, August and April were used where all sites were surveyed. All months and survey sites were used to analyse changing periwinkle density over time. Median densities of periwinkles were calculated per quadrat for quadrat surveys, and per minute for timed searches, and compared between locations using the Kruskal-Wallis and pairwise post-hoc Dunn tests.

Total abundance of faunal counts and summed percentage cover of algae, faunal (count and percentage) and algal species richness (number of species), and faunal and algal Shannon Weiner diversity (H) index were calculated for each quadrat and the median values compared between sites using the Kruskal-Wallis and pairwise post-hoc Dunn tests. Community structure was analysed using Bray-Curtis Similarity index on log(x+1)-transformed averaged data to down-weigh dominant species abundances and bring out the signals of less common species. Average percentage cover of sediment types was compared between shores and Bray-Curtis index on averaged data used to analyse similarity between sites in terms of sediment composition.

Correlations between periwinkle density and substrate types in addition to community measures of abundance/cover, species richness and Shannon diversity in each quadrat were analysed using a negative binomial GLM to take account of the over-dispersion in the count data.

Results

Periwinkle density compared between sites

There were significant differences between median periwinkle densities at different locations for both quadrat surveys (Kruskal-Wallis test: $H(4)= 63.196$, $p < 0.0001$) and timed searches (Kruskal-Wallis: Kruskal-Wallis test: $H(4)= 15.34$, $p < 0.01$). Quadrat and timed search densities correlated well, though at Holy Island comparatively more were found during quadrat surveys than in timed searches, while more were found in timed searches compared to quadrat surveys at Cresswell and Boulmer.

A pairwise post-hoc Dunn test showed that Berwick and Boulmer had the smallest median densities (0 and 1 per quadrat respectively) which were significantly smaller than at St Mary's and Cresswell, while Holy Island had the highest densities with an average of 14 per quadrat as well as the highest variability between different quadrats. The pairwise post-hoc Dunn test showed similar results for timed searches with Berwick having the smallest median density, St Mary's and Boulmer had higher densities but not significantly so, and both Cresswell and Holy Island having the highest densities.

There was no correlation found between median periwinkle density (either quadrat or timed searches) and collection intensity (Figure 1). However, Berwick, which had the highest collection intensity, also had the lowest periwinkle densities of any location for both survey methods. Boulmer, which had the next highest levels of collection, also had low density in quadrat surveys however comparatively higher densities were found in timed searches, which also occurred at Cresswell. This could indicate periwinkles in those sites are located in areas unsuitable for quadrat surveys for example within crevices or rockpools.

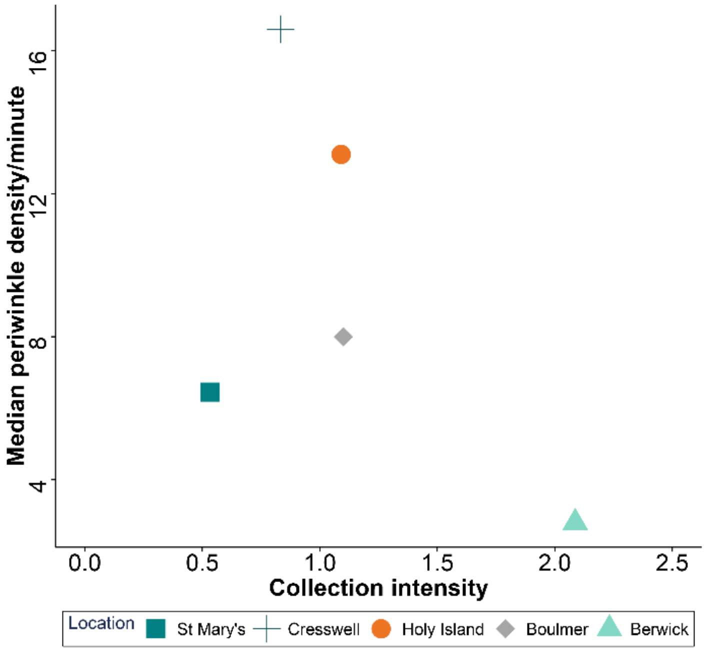

Figure 1. Median periwinkle density a) per quadrat and b) per minute from timed searches, correlated with collection intensity, measured as the average number of collectors seen on patrol at each location.

Periwinkle size compared between sites

Periwinkle size varied between locations, with the largest average sizes at Berwick and Boulmer, and the lowest at Cresswell (Figure 2). Size did not appear to be related to collection intensity however was negatively related to periwinkle density: shores with higher densities had lower average sizes.

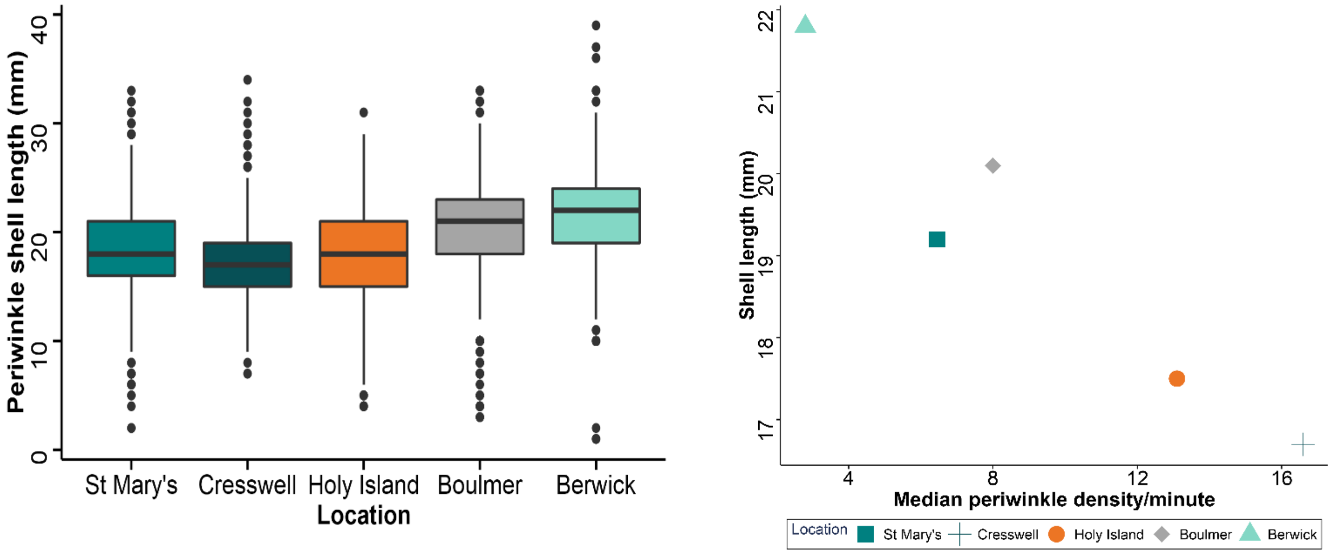

Figure 2. Median periwinkle shell length (mm) from quadrat and timed searches compared between locations at increasing collection intensities and b) compared to median periwinkle density per minute from timed searches. Survey data from June, August and April only.

Rocky shore community

The occurrence and abundances of all taxa recorded at each site for all quadrats combined from June, August and April surveys can be seen in the Appendix (Table A1). Average species abundance, species richness and Shannon diversity for animals and algae varied significantly at different locations (Table 2). Holy Island is the most distinct location with much lower percentage cover and diversity of algae than other sites, though similar levels of faunal abundance and diversity. Berwick has the highest algae percentage cover and diversity, though has relatively low faunal abundance and diversity. St Marys has the highest faunal abundance and diversity compared to other sites, while Cresswell and Boulmer are less distinct. Overall, neither animal nor algal abundance, species richness or diversity is related to periwinkle collection intensity.

Bray Curtis similarity, calculated for all animal and algae species, shows differences in the community structure at different sites (Figure 3). Berwick and Boulmer are the most similar (63%), while Cresswell and St Mary's are also similar (61%). Berwick/Boulmer and Cresswell/St Mary's share about 50% similarity while Holy Island is distinct, less than 50% similar to St Mary's and Cresswell and only 24% similar to Berwick. Bray-Curtis analysis of different times of year showed that communities at different locations remain similar throughout the year.

Table 2. Median (± 95% confidence intervals) faunal abundance (count species only, not including periwinkles), algal abundance (sum of % cover), faunal (all organisms) and algal species richness and Shannon's diversity per quadrat for each site. Sites are in order of increasing collection pressure (arrow). Significant differences between values are shown by different letters for each parameter (abundance/richness/diversity) with darker colours showing locations with higher values of these parameters compared to other sites. Samples taken in June, August 2020 and April 2021 (n=45). Results of Kruskal-Wallis tests for each parameter show p-value significance (p<0.01 =*, p<0.001 =**, p<0.0001 =***, p<0.00001 =****) and chi-squared values.

Location	Animals			Algae		
	Abundance	Richness	Diversity	% cover	Richness	Diversity
St Mary's	22^{a} (19-25)	6^{a} (6-7)	0.98^{a} (0.87-1.03)	67^{c} (28-86)	6^{b} (5-7)	1.21^{b} (1.07-1.34)
Cresswell	16^{b} (14-20)	5^{b} (5-6)	0.84^{ab} (0.73-1.04)	112^{b} (103-125)	6^{b} (5-7)	1.07^{bc} (0.90-1.19)
Holy Island	10^{b} (8-13)	6^{a} (6-7)	0.94^{ab} (0.83-1.04)	18^{d} (11-31)	3^{d} (2-4)	0.63^{d} (0.00-0.805)
Boulmer	11^{b} (7-22)	5^{b} (4-5)	0.69^{b} (0.60-0.87)	130^{b} (104-144)	5^{c} (4-5)	0.97^{c} (0.87-1.03)
Berwick	11^{b} (8-15)	5^{b} (4-6)	0.86^{ab} (0.69-1.03)	159^{a} (145-180)	8^{a} (7-9)	1.39^{a} (1.28-1.52)
Kruskal-Wallis test	*** 63.196	**** 30.88	* 12.455	**** 102.49	**** 92.728	**** 74.644

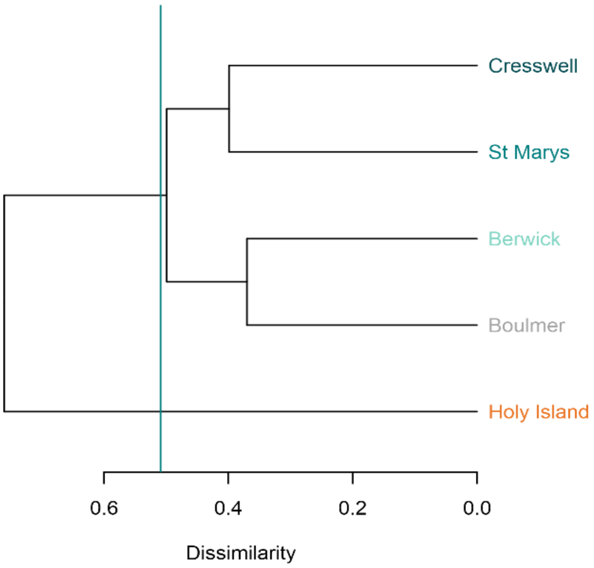

Figure 3. Plot of Bray-Curtis dissimilarity index for different sites, based on rocky shore communities. Line shows the mean dissimilarity score for all sites.

Sediment characteristics

Sites differed greatly in terms of their sediment characteristics (Figure 4). Boulmer and Cresswell were the most similar shores (93% similarity) with high proportions of exposed bedrock and the remainder mostly sand, with very little intermediate sized mixed sediment. Berwick also shared 83% similarity with Boulmer and Cresswell but had less exposed bedrock and slightly more mixed sediments. Holy Island and St Mary's both had much more mixed sediment types of different sizes, though only shared 30% similarity with each other. St Mary's had very little sand while Holy Island was almost 50% sand cover and had the lowest proportion of exposed bedrock.

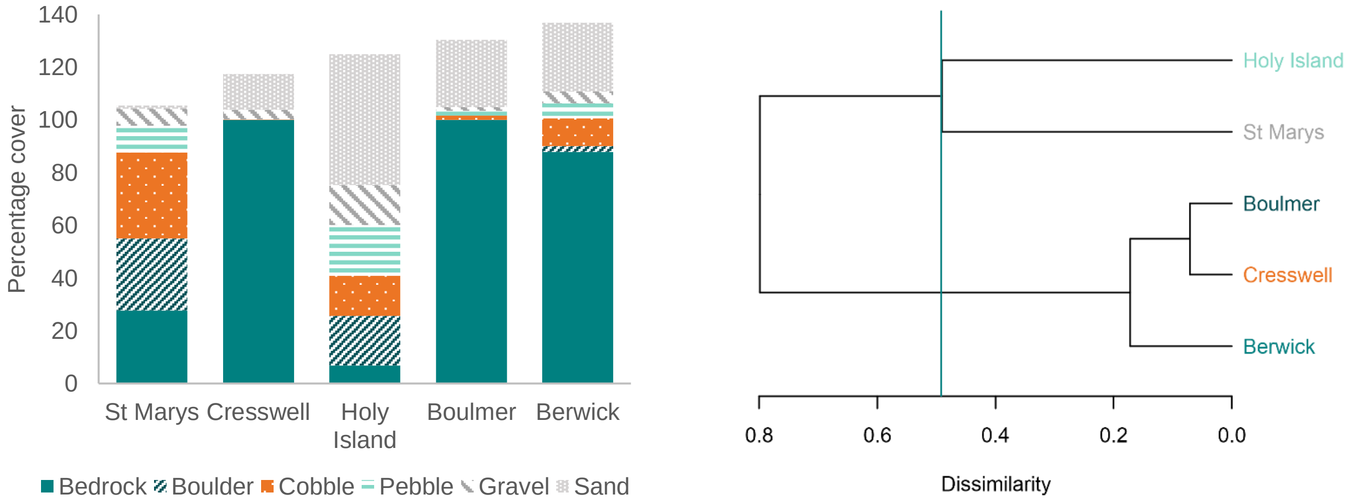

Figure 4. Substrate types found in quadrat surveys. a) Average percentage cover of quadrats at different sites and b) plot of Bray-Curtis dissimilarity index for different sites when comparing average sediment compositions. Overall percentages are greater than 100% due to overlapping sediment coverage. Line shows the mean dissimilarity score for all sites.

Periwinkle density, rocky shore communities and substrate type

Though overall faunal abundance is not correlated with the percentage of algae cover, periwinkle abundance is significantly negatively correlated with algae cover ($p<0.001$). Cover of algae was strongly related to algae species richness ($p<0.01$) and diversity ($p<0.05$) therefore generally, sites with higher numbers of periwinkles have both lower percentage cover of algae and algae species richness/diversity (Figure 5). Holy Island quadrats have high densities of periwinkles but low percentage cover of algae, while Berwick has high algae cover and species richness, with the lowest densities of periwinkles.

Higher cover of algae was related to increased amounts of exposed bedrock and boulders ($p<0.001$), although periwinkle density was only correlated with cover of gravel ($p<0.001$; Figure 5c). Periwinkle density was not significantly related to cover of other substrate types within quadrats.

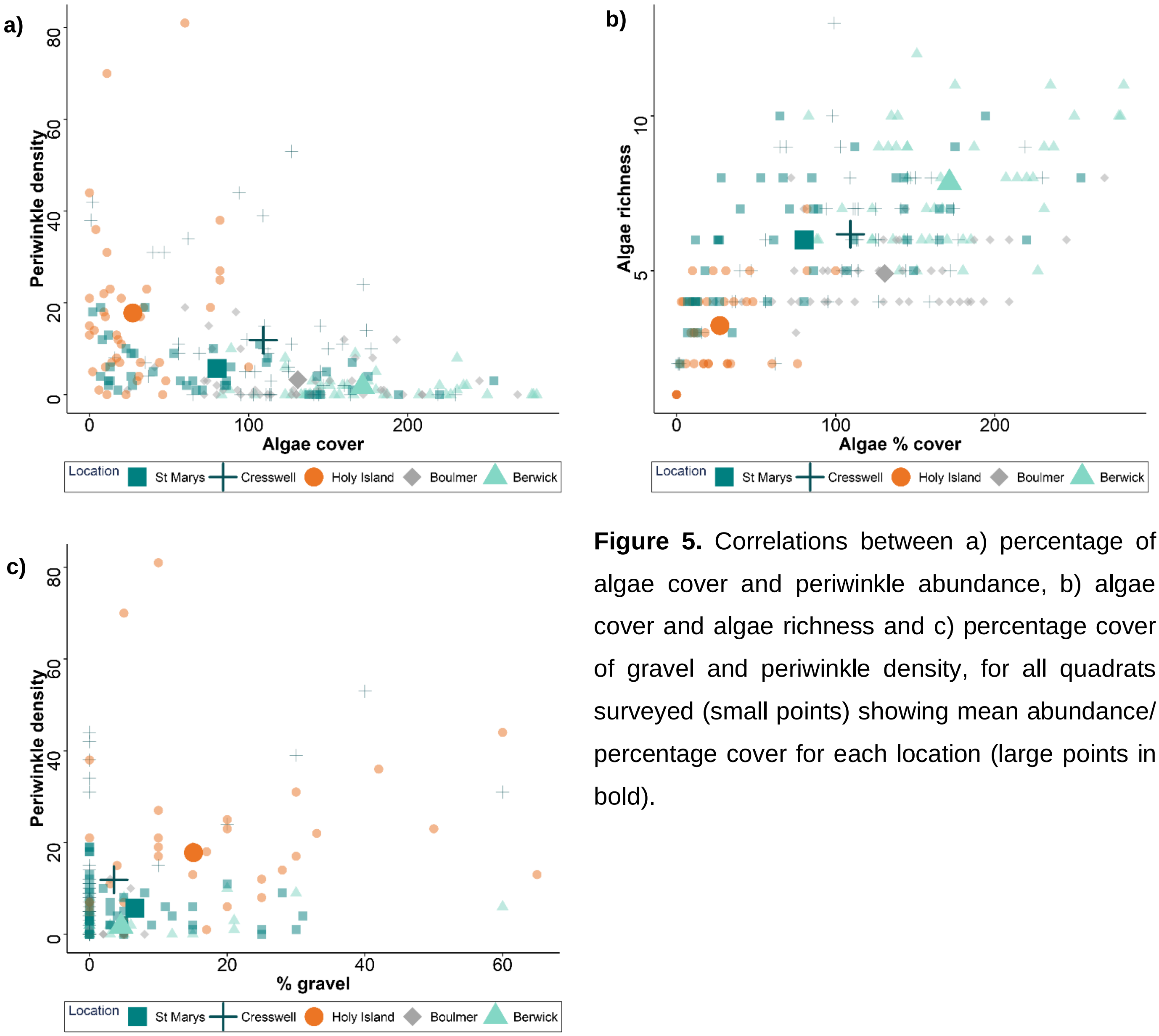

Figure 5. Correlations between a) percentage of algae cover and periwinkle abundance, b) algae cover and algae richness and c) percentage cover of gravel and periwinkle density, for all quadrats surveyed (small points) showing mean abundance/ percentage cover for each location (large points in bold).

Periwinkle density over time

Periwinkle density varied over time, with higher densities found in June 2020 surveys than in other months consistently surveyed (Figure 6). Results overall were similar for both quadrat and timed search surveys. There was a high degree of variation between sites. The site sampled for the most months, Cresswell, had the same pattern of highest densities in June and lower densities thereafter. St Mary’s, Boulmer and Berwick also had the highest densities in June in timed searches though in quadrat surveys Berwick had the highest densities in August.

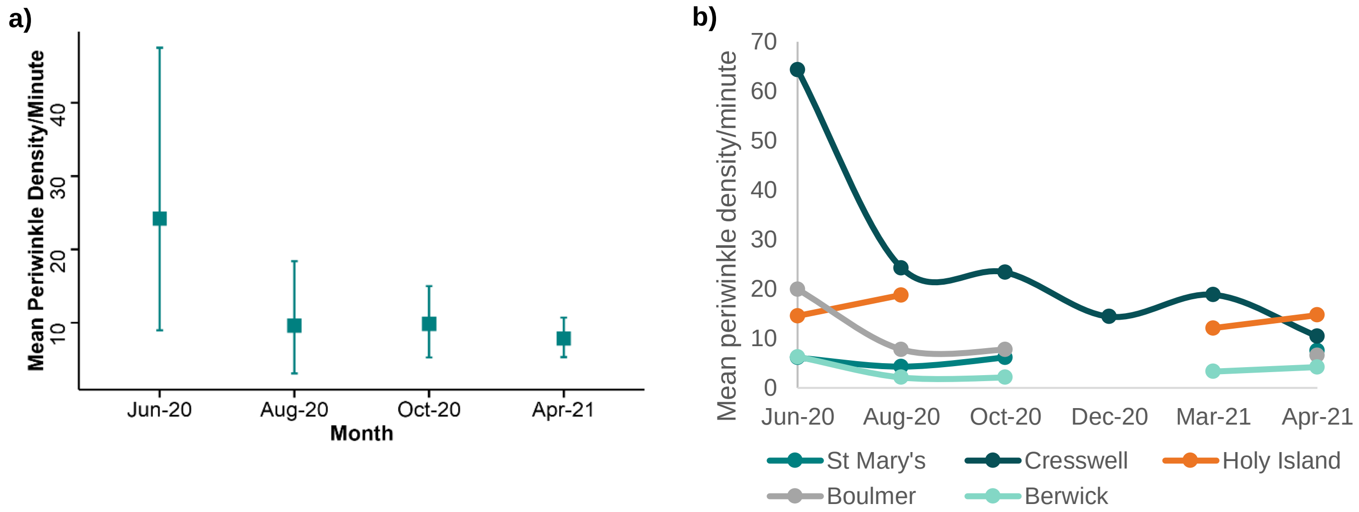

Figure 6. Mean periwinkle density per minute, over time at different locations a) for sites surveyed in June, August, October 2020 and March 2021 (all except Holy Island) and b) for all individual sites and every surveyed month.

Discussion

Periwinkle density

While periwinkle density varied significantly between sites, there was no clear relationship to collection intensity. Berwick, the location with the highest levels of collection, did have the lowest density of periwinkles for both quadrat and timed search surveys, however other sites had varying densities of periwinkles not dependent on collection intensity.

Periwinkle density was related to environmental factors: cover and diversity of macroalgae, and percentage cover of gravel. A previous study (Eddy & Roman 2016) found that environmental variables collectively explained 67% of the variation in species assemblages on rocky shores, including sediment type (up to 33% of the variation explained) as well as organic and water content and elevation, which were not measured in this study but are likely to contribute to differences in communities and periwinkle density.

Up to 23% of the variation in epifaunal assemblages was explained by algae cover, as algae stabilise the substrate, protect from desiccation stress and provide protection (Eddy & Roman 2016). We also found a positive relationship between algae cover and faunal species richness and diversity, though there was no relationship to faunal abundance, and there was a negative relationship of algae cover with periwinkle densities. A previous study also found that algae cover generally decreased with increasing periwinkle densities (Carlson et al., 2006), as periwinkles graze on the algae. The removal of littorinid snails such as periwinkles on rocky shores results in an increase in the abundance of algae (Norton et al., 1990).

Our finding that periwinkles were found at higher densities on more gravel-covered sites was consistent with a previous study in Ireland (Cummins et al., 2002), which also found no significant effect of other substrate types. However, another study (Carlson et al., 2002) found increased densities of periwinkle with higher percentages of bare rock, which we did not find here. They also found increased densities of periwinkle with higher substrate rugosity, or more complex substrates. Littorinid snails are particularly abundant on broken shores or where there are many crevices (Norton et al., 1990), and have been previously found to congregate near boulders and larger cobbles when on mixed substrates (Tillin & Hill, 2016). In general, habitat complexity is linked with higher diversity and abundance of organisms in intertidal and other habitats (e.g. Meager et al.,2011).

Locations varied significantly in terms of their substrate composition and rocky shore communities, which in addition to other environmental factors likely explains the differences in periwinkle densities. Holy Island, the most distinct site, had particularly high densities of periwinkle especially in the upper shore more dominated by boulders and cobbles. Though Cresswell had high percentages of exposed bedrock in surveys, areas of shore unsuitable to place quadrats such as over very uneven ground may have been missed. The high shore at Cresswell has high boulder coverage like at Holy Island, and this is where the highest densities of periwinkle occur. This could help explain the high densities of periwinkles at Cresswell compared to Boulmer and Berwick where the substrate is mainly exposed bedrock, with very few boulders at any shore height.

Berwick and Boulmer had the most similar rocky shore communities of any sites as well as similar substrate compositions, however Berwick had lower periwinkle densities as well as higher algae cover, richness and diversity. The bedrock at Boulmer is very flat while Berwick has higher rugosity, so might be expected to have higher densities of periwinkle than Boulmer. The fact that it does not could be an indication that the higher levels of periwinkle gathering at Berwick are impacting the population, and potentially influencing the algal communities, although there could be other unexplained sources of environmental variation not accounted for.

Results from these surveys are similar to the PhD by Tinlin-Mackenzie in 2018, which included Holy Island, Boulmer and Marshall Meadows (an uncollected site). A key difference is the addition of the highly collected site, Berwick, which has around two times the average number of collectors seen on a patrol than any other site within the NIFCA district.

In the PhD Holy Island had the highest periwinkle densities and smallest shell height, while Boulmer had lower densities but larger shells which is consistent with our results. Neither study found a correlation between periwinkle size or density, and harvesting pressures. Tinlin-Mackenzie concluded that communities likely vary from natural variation rather than impacts of periwinkle harvesting, which this study supports.

Neither study found evidence of indirect impacts of periwinkle gathering at these sites, for example changes in community structure through trampling. Differences in rocky shore communities are more likely due to environmental variation, although it is unlikely this study could differentiate any impacts of gathering from environmental factors or from other rocky shore activities such as rockpooling.

Density over time

Periwinkles typically migrate down shore in the winter to reduce exposure to sub-zero temperatures, even into subtidal areas, and back up shore in spring (Tillin & Hill, 2016). Therefore, periwinkles in the intertidal are less common in the winter.

We found a higher density of periwinkles in June overall than in other months. This was mainly driven by the significantly higher densities at Cresswell although most other locations had higher densities as well. However, densities in August were similar to those in October, March and April when temperatures would be lower which is unexplained. Cresswell, the only location surveyed across all months, did have the lowest densities in the colder months of December, March and April. The spring and early summer of 2020 were hotter than average which could have influenced the higher densities of periwinkles found in June, or it could have been another factor such as increased abundance of algae in intertidal areas.

Periwinkle size

Periwinkle size varied between sites and was not related to collection intensity but rather to periwinkle density: the higher the density of periwinkles, the smaller the average size. This may be due to increased competition for food at higher densities, which has been shown experimentally to reduce growth rates in periwinkles (Petraitis, 2002). Tinlin-Mackenzie (2018) suggested that smaller periwinkles at Holy Island were due to slow growth because of low availability of algae.

Periwinkle gathering can alter the size structure of populations with collection causing an average reduction in size by 10-20% in most studies (Tinlin-Mackenzie, 2018), however we found the opposite: Berwick and Boulmer, the most collected sites, had the largest periwinkles. This indicates environmental variation and differences in periwinkle density have a larger impact on periwinkle size structure than collection and could show that populations are resilient to the current levels of harvesting.

Previous maximum shell heights measured at Boulmer (28mm, 30mm and 30mm) are consistent with the maximum shell height found here, 33m, which was the same as in Tinlin-Mackenzie (2018). This suggests maximum shell height has not decreased over time despite intermediate levels of periwinkle harvesting.

Conclusions

Periwinkle harvesting at current levels in collection hotspots within the NIFCA district does not appear to be negatively impacting periwinkle populations or other rocky shore communities. Environmental variation in terms of substrate cover and other factors likely have a greater impact on periwinkle densities than collection pressures, however it should be noted that Berwick does have particularly low densities of periwinkle and should be monitored over time for changes in both collection pressure and periwinkle density. Periwinkles are generally resilient to localised impacts due to their ability to recolonise from larvae which disperse widely in the sea, therefore harvested populations could be maintained from uncollected populations elsewhere.

Indirect impacts of periwinkle harvesting were also not detected in this study and would be indistinguishable from other users of the rocky shore. However, study sites now have baseline data on their communities and could be monitored over time to ensure communities do not substantially change in the future.

NIFCA will continue to survey periwinkle populations and rocky shore communities, annually at sites of lower concern and more frequently at Berwick and Boulmer. Periwinkle gathering will also be monitored to detect any future changes in effort which could have a greater impact on periwinkles and rocky shores than current levels of harvesting.

References

Berthelon, S., Paramor, O.A.L. and Frid, C.L.J. (2004) *Effects of bait collection on intertidal ecosystems and Littorina littorea populations*. Report. Newcastle University.

Carlson, R.L., Shulman, M.J. And Ellis, J.C. (2006) Factors contributing to spatial heterogeneity in the abundance of the common periwinkle *Littorina littorea* (L.). *Journal of Molluscan Studies*, 72(2), pp.149-156.

Crossthwaite S.J., Reid N., Sigwart, J.D. (2012) Assessing the impact of shore-based shellfish collection on under-boulder communities in Strangford Lough. Report prepared by the Natural Heritage Research Partnership (NHRP) between Quercus, Queen's University Belfast and the Northern Ireland Environment Agency (NIEA) for the Research and Development Series No. 13/03, 2012.

Cummins V., Coughlan S., McClean O., Connolly N., Mercer J., Burnell G. (2002) An assessment of the potential for the sustainable development of the edible periwinkle, *Littorina littorea*, industry in Ireland. Marine Resource Series, Marine Institute, 2002. [cited 20-09-2020]. Available at https://oar.marine.ie/handle/10793/218

Eddy, E.N. and Roman, C.T., 2016. Relationship between epibenthic invertebrate species assemblages and environmental variables in Boston Harbor's intertidal habitat. *Northeastern Naturalist*, *23*(1), pp.45-66.

Fowler, S.L. (1999) *Natura 2000: Guidelines for managing the collection of bait and other shoreline animals within UK European marine sites*. English Nature UK Marine SACs Project.

JNCC and Natural England (2011) *Advice from the Joint Nature Conservation Committee and Natural England with regard to fisheries impacts on Marine Conservation Zone habitat features.*

Meager, J.J., Schlacher, T.A. and Green, M., 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Marine Ecology Progress Series*, *428*, pp.1-12.

Moore H.B. (1937) The biology of *Littorina littorea*. Part 1: growth of the shell and tissues, spawning, length of life and mortality. *J Mar Biol Assoc UK* 24: 721–742.

Newell, G.E. (1958) 'The behaviour of *Littorina littorea* (L.) under natural conditions and its relation to position on the shore', *Journal of the Marine Biological Association of the United Kingdom*, 37(01), pp. 229-239.

Norton, T.A., Hawkins, S.J., Manley, N.L., Williams, G.A. and Watson, D.C., 1990. Scraping a living: a review of littorinid grazing. *Progress in Littorinid and Muricid Biology*, pp.117-138.

Petraitis, P.S., 2002. Effects of intraspecific competition and scavenging on growth of the periwinkle Littorina littorea. *Marine Ecology Progress Series*, *236*, pp.179-187.

Petraitis, P.S. (1989) 'Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmea testudinalis* (Muller)', *Journal of Experimental Marine Biology and Ecology*, 125(2), pp. 99-115.

Smith J.E., Newell G.E. (1955) The dynamics of the zonation of the common periwinkle (*Littorina littorea* (L.)) on a stony beach. *J Anim Ecol* 24: 35–56.

Storey, K.B., Lant, B., Anozie, O.O. and Storey, J.M. (2013) 'Metabolic mechanisms for anoxia tolerance and freezing survival in the intertidal gastropod, *Littorina littorea*', *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, 165(4), pp. 448-459.

Tillin, H.M. & Hill, J.M., 2016. Barnacles and [Littorina] spp. on unstable eulittoral mixed substrata. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 23-07-2021]. Available from: https://www.marlin.ac.uk/habitat/detail/340

Tinlin-Mackenzie A.R. (2018) Intertidal collection within the Berwickshire and North Northumberland Coast European Marine Site: investigating the scale, locale, and ecological impacts of harvesting *Arenicola marina, Arenicola defodiens*, and *Littorina littorea*, PhD thesis, University of Newcastle, 2018.

Tyler-Walters, H. (2008) Arenicola marina. Blow lug. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]. Available from: http://www.marlin.ac.uk/speciesfullreview.php?speciesID=2592 (Accessed: 13th August 2019).

Appendix

Table A1. Presence and abundance of faunal and algal species

Total abundance of count data for faunal taxa and presence (+) and absence (left blank) of taxa recorded as percentage cover, within quadrats (50x50cm) collected from five shores in the NIFCA district. Samples were collected in June and August 2020 and April 2021 on low water spring tides. Unidentified algae were not included.

Species/taxa	St Mary's	Cresswell	Holy Island	Boulmer	Berwick
ALGAE					
Verrucaria mucosa					+
Cladophora spp.	+	+	+	+	+
Ulva/Monostroma spp.	+	+			+
Chaetomorpha spp.	+				
Filamentous green algae	+	+			+
Ascophyllum nodosum			+	+	+
Cladostephus spongiosus		+			+
Fucus serratus	+	+	+	+	+
Fucus spiralis	+		+	+	
Fucus vesiculosus	+	+	+	+	+
Himanthalia elongata			+		
Laminaria digitata	+				+
Colpomenia peregrina	+	+			
Filamentous brown algae					+
Ahnfeltia plicata		+			
Ceramium spp.		+			
Chondrus crispus	+	+	+	+	+
Corallina spp.	+	+	+	+	+
Delesseria sanguinea				+	
Dumontia contorta		+			
Lomentaria articulata	+	+			+
Mastocarpus stellatus	+	+	+	+	+
Membranoptera alata					+
Osmundea pinnatifida	+	+	+		+
Palmaria palmata					+
Phycodris rubens					+
Plocamium spp.	+	+	+		+
Plumaria plumosa		+			
Polysiphonia spp.	+	+		+	+
Porphyra / Pyropia spp.			+		
Rhodothamniella floridula		+	+		+
Elachista fucicola		+			
Osmundea osmunda	+				
Rhodomela confervoides					+
Gelidium spp.	+				
Ptilota gunneri	+				
Encrusting red algae	+			+	+
Encrusting pink algae	+	+	+	+	+
TOTAL ALGAE SPECIES	***21***	***21***	***14***	***12***	***24***
PORIFERA					
Halichondria panicea	+				+
CNIDARIA					
Actinia equina				+	+
Dynamena pumila		+			+
Obelia geniculata			+		
ANNELIDA					
Polydora/Boccardiella					+
Spirobranchus spp.	+	+	+	+	+
Spirorbis spp.	+			+	+
Unidentified worm					+

BRYOZOA					
Electra pilosa		+	+		+
Flustrellidra hispida					+
Membranipora membranacea	+				
Unidentified bryozoan				+	
CRUSTACEA					
Semibalanus balanoides	+	+	+	+	+
Cancer pagurus	1				
Carcinus maenas	5	2	12	7	8
Paguridae indet.	12	2	13	5	32
Porcellana platycheles					3
Pisidia longicornis				1	
TOTAL CRUSTACEA	*18*	*4*	*25*	*13*	*43*
MOLLUSCA					
Littorina littorea	182	421	522	126	57
Littorina obtusata/fabalis	56	87	114	581	208
Littorina saxatilis	191	152	146	6	23
Melarhaphe neritoides	16				
Mytilus edulis	+		+		
Nucella lapillus	2	46	7	10	10
Patella pellucida	3				
Patella spp.	363	245	20	76	153
Steromphala cineraria	60	9	18	6	27
Polyplacophora spp.		2		3	2
Aplysia punctata				6	
*TOTAL MOLLUSCS**	*691*	*541*	*305*	*688*	*423*
TOTAL ANIMAL SPECIES	***17***	***13***	***13***	***16***	***20***

**discounting L. littorea*