

Periwinkle Ecology and Size of Maturity Study

Beth Harvey

Contents

Summary	3
Description	3
Distribution	3
Habitat.....	3
Ecology	3
Reproductive Life History.....	4
A note on measurements of periwinkle shell size:.....	5
Size of maturity.....	6
Northumberland IFCA Size of Maturity Study	9
Implications of periwinkle SOM for management	10
That.....	Error! Bookmark not defined.
Conclusions.....	12
References	13

Common/edible periwinkle (*Littorina littorea*)

Summary

Size	Max. 52mm shell length but usually <35mm
Lifespan	5-10 years
Size of maturity	11-17 mm
Fecundity	Up to 100,000 eggs per year
Reproductive frequency	Annual episodic spawning
Capture methods	Hand gathering
Fishing season	Year round



Description

The marine gastropod *Littorina littorea* (common or edible periwinkle) is commonly found around the coast of the United Kingdom (Moore, 1937; Smith & Newell, 1955). It is the largest British periwinkle species reaching a maximum height of 52mm (Reid, 1996) though normally does not exceed a height of approximately 35mm (Cummins et al., 2002).

Distribution

L. littorea is found on North Atlantic coasts of Western Europe and Northeast America (Fretter & Graham, 1962; Jackson, 2008). In the UK it is distributed on all coasts however is rarely found in the Channel Islands and Isles of Scilly (Cummins et al., 2002; Jackson, 2008). *L. littorea* can reach densities of hundreds of individuals per square metre; in the UK densities are normally <200 per square metre (Norton et al., 1990).

Habitat

L. littorea is typically found in rocky intertidal area, with a vertical range extending from the high-water neap tide level to the extreme low water spring tide level (Moore, 1937). It can be found sublittorally to depths of approximately 60m (Fretter & Graham, 1962). *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).

Ecology

L. littorea is an omnivorous grazer and is highly selective in favour of the foliose ephemeral green algae *Ulva lactuca* and *Enteromorpha intestinalis* (Cummins et al., 2002). Their grazing activity can significantly modify intertidal habitats by altering the distribution and abundance of algae on rocky shores and converting soft-sediment habitats to hard substrates through the removal of sediments bound by algal cover (Bertness, 1984). Due to their role as bioengineers, harvesting of periwinkles can have negative impacts on the intertidal environment as well as reduce the prey availability for birds and fish (Tinlin-Mackenzie, 2018, Crossthwaite et al., 2012).

Reproductive Life History

L. littorea normally have a life span of 5-10 years, though one individual reached over 20 years in an aquarium (Woodward, 1913 as cited in Cummins et al., 2002). Periwinkles reach maturity at around 2-3 years depending on environmental conditions (Jackson, 2008). *L. littorea* are annual episodic spawners however are capable of breeding all year round (Williams, 1964; Jackson, 2008). The majority of spawning occurs in March and April (Grahame, 1975) however in the UK can occur from January to June (Cummins et al., 2002), with significant variation in spawning time in different geographic locations depending on food availability and exposure (Fish, 1972).

Reproduction involves internal fertilisation after which the female releases planktonic egg capsules which contain up to nine eggs, though normally two to three (Linke, 1933). After hatching the larvae remain in the plankton for 6-7 weeks and have an average dispersal distance of 22.9km before settling (Kinlan & Gaines, 2003). If conditions are unfavourable larvae can delay metamorphosis which results in variation in settlement times, with larvae settling over several months of the year (Cummins et al., 2002).

L. littorea settles at sizes of 0.25-0.5mm (Smith & Newell 1955). Growth is rapid immediately following settlement at rates of 1-2mm per month (Williams, 1964), and decreases with age (Fretter & Graham, 1962). Up to shell heights of around 12mm growth is fairly rapid after which it is reduced, and growth in individuals over 19mm is slow (Williams, 1964). Growth rate varies between populations, but on average periwinkles grow to about 10mm by the end of their first year, 16mm in their second, and 20mm in their third before growth slows significantly (see Table 1). The largest recorded individual came from Scotland and was 52.8mm long (Reid, 1996).

Growth rate depends on food availability, habitat quality and competition and therefore varies between individuals (Griffin, 2000). Growth rate also varies with age, slowing considerably in the winter due to reduced feeding activity and with longer periods of slow growth due to sexual activity (Williams, 1964). This prolonged pause first occurs when shell lengths of around 12mm are reached.

Table 1. Size of *L. littorea* at the end of one year, 18 months, two, three and four years (shell measurements in mm). Where size was measured at different times of year, age in months is shown in brackets.

Study location	Shell measurement	Age (years)					Reference
		1	1.5	2	3	4	
Whitstable, Kent	Length	2 – 12	–	13 – 16	>17	–	Smith & Newell, 1955
Scalby Rocks, Yorkshire	Length	12 – 15	–	18 – 20	–	–	Robson & Williams, 1971
La Roque-Mignon, France	Length	9 – 10	–	15 – 16	–	–	Guyomarc'h-Cousin, 1975
County Cork, Ireland	Length	7 (8 mo.)	10 (15 mo.)	–	14 (27 mo.)	20 (39 mo.)	Cummins et al., 2002

Strangford Lough, N. Ireland	Length	8.1	–	15.6	24.8	–	Johnson & McDermott, 2018
Plymouth, Devon	Height*	14 (7 mo.)	17.4 (19 mo.)	–	22.4 (31 mo.)	25.4 (43 mo.)	Moore, 1937
Aberystwyth, Wales	Height*	8 – 9	11.5 – 12	13 – 14	15.5 – 16.5	>17.5	Williams, 1964
Aberystwyth, Wales	Height*	>10	11 – 12	16	–	–	Fish, 1972 (estimated from Fig. 4)
Anglesey, Wales	Height*	–	–	–	16 (29 mo.)	–	Hughes and Answer, 1982

* denotes studies where the shell measurement was not defined in the methods (see note)

A note on measurements of periwinkle shell size:

The use of the terms shell 'height' and 'length' is inconsistent in the literature which makes reviewing size of maturity (SOM) challenging. Older studies tend to refer solely to shell height, often without defining it (e.g. Williams, 1964), some refer to both height and length interchangeably (e.g. Cummins et al., 2002), while Johnson & McDermott (2018) define length as from the apex of the shell to the anterior margin of the aperture and height as from the dorsal point of the body whorl to the base of the snail (see Figure 1).

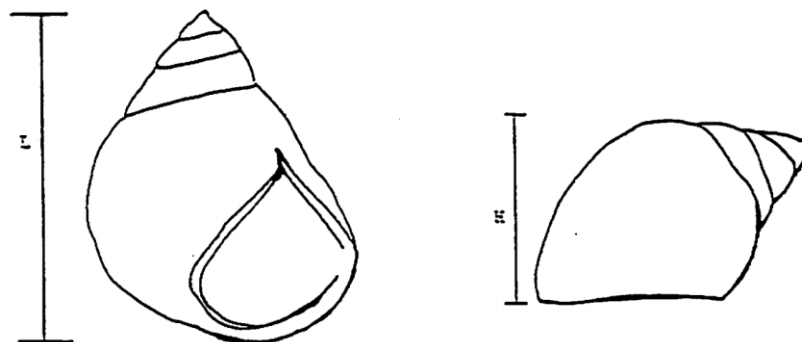


Figure 1. Shell length (L) and height (H) periwinkle shell measurements used in Johnson & McDermott (2018) and taken from Cashmore & Burton (1998).

Johnson & McDermott (2018) determined an equation to calculate length from height measurements ($\text{length} = \text{height} \times 1.66 - 0.04$) derived from individual periwinkles measured at Silverstrand in Galway, Ireland. For consistency, NIFCA will define length and height as in Fig. 1 and use this equation to convert between the two where appropriate. Studies which used the term 'height' but did not define the method used to measure shells are shown in Tables 1 and 2 and discussed in relation to size of maturity.

Size of maturity

Size of maturity (SOM) is often used to help establish an appropriate minimum size to ensure individuals can reproduce at least once before capture. Maturity in periwinkles is determined by dissection. Williams (1964) distinguished five development stages for each sex: immature virgin, maturing individuals/recovering spents, fully mature and spawning, partially spent, and spent.

Maturity is thought to occur around 12 – 18 months after settlement (see Table 2). *L. littorea* first breed in the winter of their second year (Williams, 1964; Robson & Williams, 1971), though some individuals which do not breed in that year first breed in the winter of their third year (Fish, 1972). Female fecundity is related to size, and therefore age; as periwinkles grow their breeding output increases (Hughes & Answer, 1982) and a large female (27mm shell height) can produce 100,000 eggs per year (Grahame, 1973).

Although 11 – 12mm shell height is a generally accepted size of first maturity for periwinkles (Wolf et al., 2001; Jackson, 2008; Doyle et al., 2020), this is based on limited studies (Williams, 1964; Fish, 1972) and authors do not define height (see note on shell measurements). Discounting studies where the authors did not define the shell measurements used, size at maturity ranges from shell lengths of 10 – 17mm (Table 2). However, the smaller measurement of 10mm length is from one study in Sweden (Erlandsson & Johannesson, 1994) with a limited sample size (n=30), measuring only male size at maturity and assuming males and females mature at the same size. Males are believed to mature earlier than females and at a smaller size (Williams, 1964; Cummins et al., 2002) therefore this is probably not representative of the population and average size of maturity is likely to be larger than 10mm.

Of the four studies measuring shell 'height' without defining the measurement, estimates of periwinkle SOM ranged from 11 – 17mm, similar to those which measured shell length (Table 2). If the authors measured height as defined in Figure 1, these estimates would range from shell lengths of 18.2 – 28.2mm (using the equation in Johnson & McDermott (2018) to determine length) which is a higher estimate than the other studies. 28mm shell length would represent an individual which would be over four years of age (Table 1), therefore is highly unlikely to be the size at maturity.

Additional studies measured growth rates of *L. littorea* over their first 2-4 years of growth (Table 1). Most individuals reach maturity in the winter of their second year and have matured by end of their second year in the spring therefore SOM can be corroborated from these studies. Including only those studies which define shell measurements, periwinkles reached 10mm long at 15 months in one study (Cummins et al., 2002), ranging from 13 – 20mm at the end of year two (Table 1). This matches with a periwinkle SOM at 18 months of 11 – 17mm not 18.2 – 28.2mm therefore in the studies which only mentioned shell 'height' but did not define it, it is likely that the authors measured shell length as defined in Figure 1.

Table 2. Estimates of *Littorina littorea* size and age at maturity, with information on each study conducted.

Study location	Total No. of individuals surveyed	Shell measurement	Size surveyed (mm)		Smallest mature individual	Size of maturity (mm)	Age at first maturity (months)	Reference
			Minimum	Maximum				
Scalby Rocks, Yorkshire	5 250	Length	<10.1	>30	15	16	–	Robson & Williams, 1971
North west Sweden	30	Length	7	15	–	10 (males only)	–	Erlandsson & Johannesson, 1994
County Cork, Ireland	6 056	Length	5	34.1	17 (females)	15 (males)	–	Reported in Cummins, 2002
Plymouth, Devon	–	Height*	<1	36	–	17	18	Moore, 1937
Aberystwyth, Wales	29 498	Height*	0.65	28	11	11.5 – 12	17 – 18	Williams, 1964
Aberystwyth, Wales	>4 200	Height*	–	–	–	11 – 12	11 – 18	Fish, 1972
Anglesey, Wales	<3 000	Height*	8	30	–	11 – 16	–	Hughes and Answer, 1982

* denotes studies where the shell measurement was not defined in the methods (see note on shell measurements)

In conclusion, discounting the study in Sweden which only measured male individuals and including all other studies which likely measured shell length, periwinkle SOM is between 11 – 17mm and varies geographically (Figure 2). Periwinkle populations in Welsh studies mature from 11mm, while studies in County Cork, Devon and Yorkshire recorded larger sizes. Periwinkle growth rates and SOM are likely to vary with latitude and sea temperature (M Johnson, pers. comm., 10/09/20), though the geographic variation in studies in the UK does not seem consistent in terms of latitude or east vs west coasts. A study in Massachusetts, USA found *L. littorea* individuals exhibited high physiological plasticity, with higher growth rates in colder waters possibly due to higher food availability (Yamada, 1987). This suggests that periwinkles can adapt to spatially or temporally variable conditions, for example exploit better conditions one year, and could explain the variation in studies of periwinkle growth and SOM.

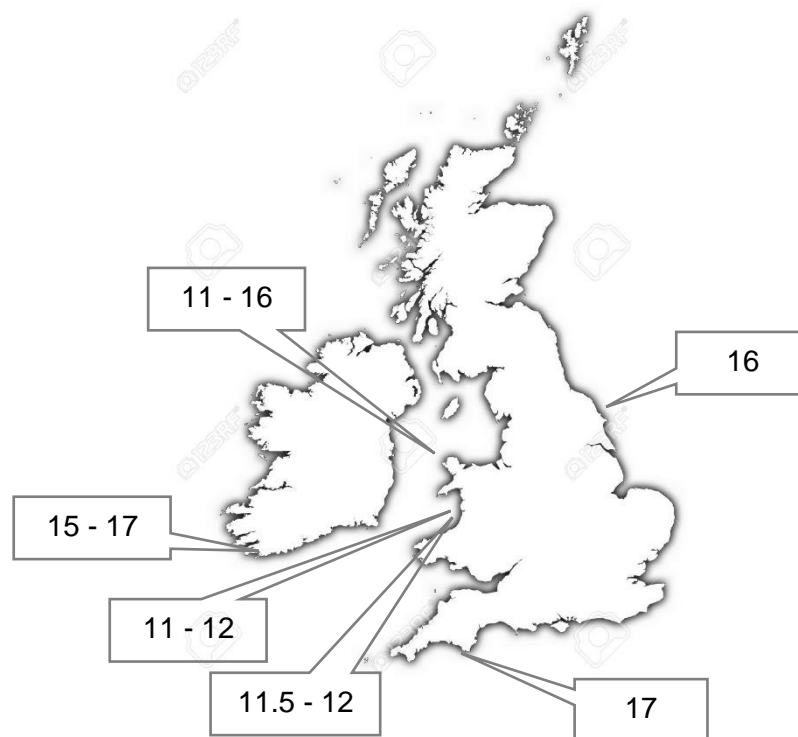


Figure 2. Geographical variation in periwinkle size at maturity (shell length in mm) in the UK and Ireland. Studies referenced in Table 2.

No studies have been conducted into *L. littorea* growth and maturity in Northumberland therefore size of maturity may differ to previous research. The nearest location is at Scalby Rocks in Yorkshire by Robson & Williams (1971) who found most *L. littorea* maturing for the first time were 16mm long, reaching 18 – 20mm at the end of their second year. There were very few mature periwinkles less than 15mm long recorded. These measurements are higher than many other studies (see Tables 1 and 2) perhaps indicating a faster growth rate in the North Sea than other study locations in Kent, Wales and Ireland; though measurements are similar to one study in Devon (Moore, 1937). In the absence of localised data on *L. littorea* SOM, the study by Robson & Williams (1971) study indicates it is likely periwinkles in Northumberland mature at >15mm shell length.

Northumberland IFCA Size of Maturity Study

Five study sites in the NIFCA district were selected based on known hotspots of periwinkle collection from NIFCA patrols. Periwinkle sizes were measured in quadrat surveys and timed searches (for a full description of methods see previous report¹). Periwinkle size frequency distributions were analysed to determine if size classes could be detected, and from this size of maturity calculated. Changes to size frequency distributions over time were also investigated.

In total, the shell lengths of 13,265 individual periwinkles were measured, ranging from 1-39mm. Distributions were unable to be resolved into separate size classes for population modelling as in Johnson & McDermott (2018) because they do not have separate peaks for different size classes (Figure 3). Distributions are near-normal though tend to be skewed slightly towards smaller sizes. Very few individuals under 10mm were found in surveys. The mean shell length overall was 18mm and did not vary much over time, with the highest in August 2020 (19.8mm) and the lowest in April 2021 (17.4mm), with higher proportions of periwinkles under 15mm in April than other months.

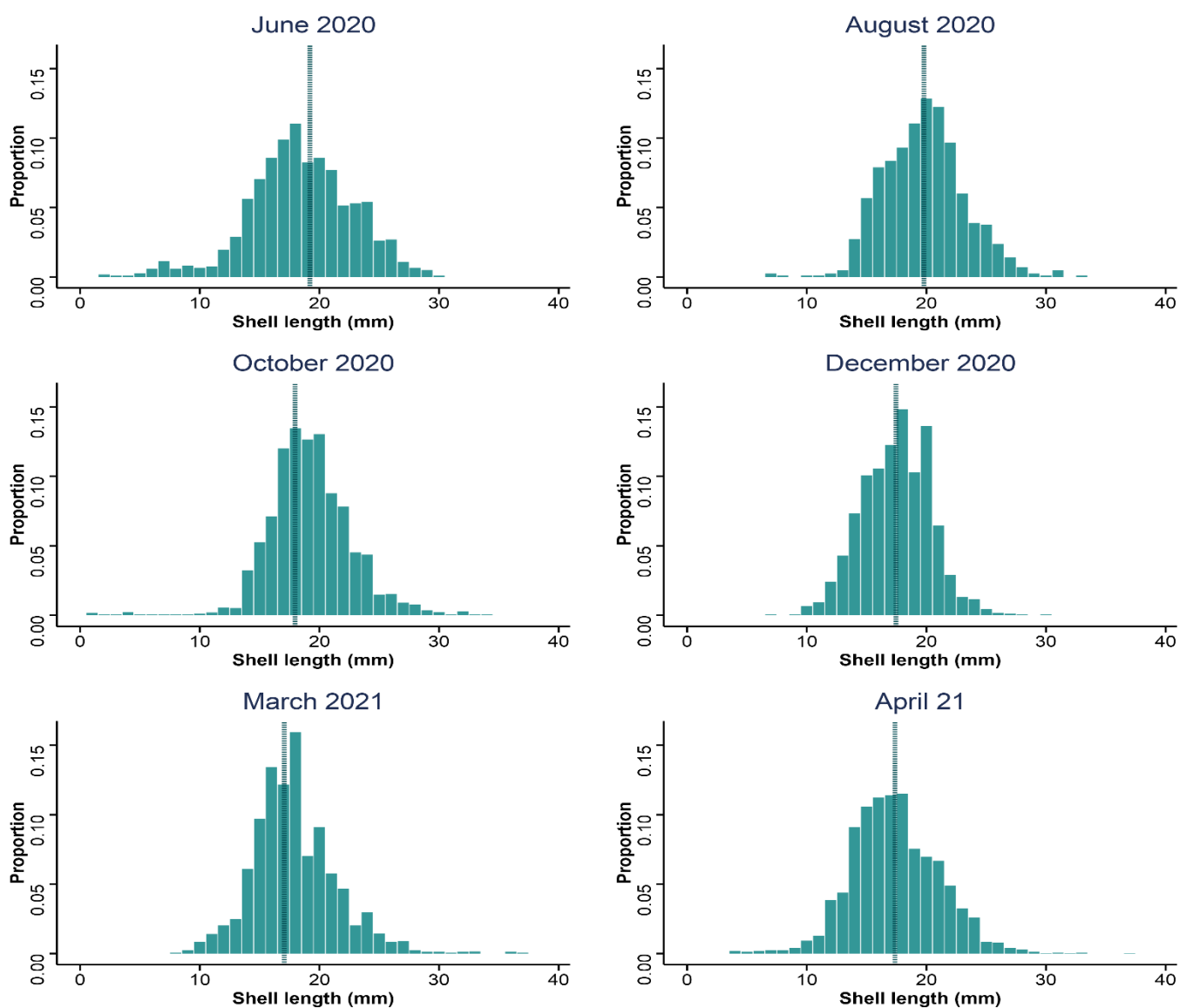


Figure 3. Distribution of periwinkle shell lengths sampled from all survey sites in different months, shown as proportion of each size of total number of periwinkles each month.

¹ NIFCA report: *Periwinkle surveys 2020-21*. Harvey, 2021

Unfortunately, unlike in previous studies (e.g. Williams, 1964; Johnson & McDermott, 2018) where periwinkle populations have been resolved into separate size classes, and size at maturity calculated, periwinkles surveyed here did not follow the same shell length distribution with distinct size classes. There were low numbers of periwinkles under 10mm found in this study, which could either be a result of them not being present, or lower detectability leading to them being missed. This approach did not specifically aim to measure size at maturity, but rather infer it from the sizes of each age class and previous literature on the timing of onset of sexual maturity. An alternative approach would be to dissect samples of individuals at regular intervals to identify minimum sizes with ripe gonads, which would specifically measure size of maturity. However this would be resource intensive and perhaps only worthwhile if periwinkle populations were threatened by harvesting.

Implications of periwinkle SOM for management

One management tool is the use of minimum harvest sizes, which would protect periwinkles before breeding and allow intermediate sizes to thrive and is 16mm in other IFCA districts. However, it also has the potential to perpetuate the problem with increased targeting of the very largest individuals leading to a smaller average size (Tinlin-Mackenzie, 2018).

Minimum harvest sizes should be based on evidence of accurate localised age/size of maturity data, which we were unable to obtain for the NIFCA district although the SOM is likely >15mm shell length, based on the study in Yorkshire (Robson & Williams, 1971).

Currently, wholesalers in Northumberland use riddles with gaps of the following sizes: Small (10mm), Medium (12mm) and Large (14mm), which sort winkles into size classes discarding those too small to be retained. Periwinkles are roughly sorted by the riddles and may be sorted by either their length or height (many are sorted at the same time and are not individually turned). Using the equation in Johnson & McDermott (2018) to convert from height to length, shell dimensions retained in lengths are therefore larger than:

- Small: 10 – 16.6mm
- Medium: 12 – 19.9mm
- Large: 14 – 23.2mm

This suggests some periwinkles at sizes 10 – 15mm, likely not to have reached SOM, are being retained and sold in Northumberland. However, the proportion of periwinkles sorted by length vs height is unknown. If the majority are sorted by height, most periwinkles under 16.6mm length would be discarded and should be returned to intertidal areas by collectors. NIFCA have anecdotal evidence from wholesalers that they are either taken back to the shore by selected gatherers or taken by a potting boat and thrown back at sea, though the location of this and whether it actually occurs in practice is unknown. There are no regulations for discards. Measurements of retained periwinkles could be investigated at wholesalers to determine shell lengths of those retained for sale in practice.

Another consideration is whether to only protect periwinkles below the first size of maturity, i.e. when they first mature, or also protect some fully mature breeding individuals. Though Williams (1964) estimated the size of maturity at 11 – 12mm (18 months), he concluded that ‘the maintenance of the population in the intertidal zone is largely due to the spawning of animals with a shell height of 13.5 mm or more’ (those at the end of their second year and above) because a significant proportion of *L. littorea* do not spawn until their third winter (Williams, 1964; Fish, 1972). Therefore, in terms of conserving stock, it may not be enough to protect periwinkles when they reach first size at maturity at 18 months, but some of those in their third year as well. This would enable those which did not breed in their second year to breed before being harvested. A conservative approach could be to set a threshold to protect all of the second-year size periwinkles (M Johnson, pers. comm., 10/09/20), and perhaps some of the third year sizes.

Periwinkle sizes range from 13 – 20mm at the end of year two (18 – 20mm in Yorkshire) and 15.5 – 24.8mm at the end of year three (Table 1). Protecting periwinkles 20mm shell length and under would protect those in their second year as well as some of those in their third, and has been suggested elsewhere (Crossthwaite et al., 2012; Johnson & McDermott, 2018) as a simple harvest rule.

However, the use of a minimum harvest size should be used on shores where there is evidence that periwinkle harvesting is having an impact on periwinkle populations. There is no evidence for this on collected shores in the NIFCA district (Tinlin-Mackenzie 2018; NIFCA report¹) therefore the use of a minimum size is not deemed necessary at this time, but could be considered in the future should management become necessary.

Knowledge gaps and possible future work

NIFCA’s work on periwinkles has answered some of the knowledge gaps on this species and the fishery, however there remains unanswered questions that could form future work:

- ? Localised, accurate SOM data for *L. littorea* in the NIFCA district could be identified by dissecting samples of individuals at regular intervals to identify minimum sizes with ripe gonads, however this would be resource intensive.
- ? The sizes and proportions of periwinkles sorted through riddles at wholesalers, to determine whether periwinkles are predominantly sorted by their shell length or height, the minimum size of those retained and sold, and the numbers discarded.
- ? Whether the NIFCA Code of Conduct is well-known and adhered to.
- ? Whether the Code of Conduct is being followed in terms of minimum recommended sizes (12mm) taken to wholesalers.
- ? Harvest rates – how many periwinkles are taken per month (from each area or location). NIFCA are liaising with collectors and wholesalers to try and determine this although it remains challenging since many collectors harvest from outside of the NIFCA district (Scotland) and do not want to give this information.

¹ NIFCA report: *Periwinkle surveys 2020-21*. Harvey, 2021

Conclusions

The 'generally accepted' periwinkle size of maturity (11 – 12mm) is not evidenced by the available literature, which instead shows that SOM ranges from 11 – 17mm and varies geographically. In the NIFCA district this is likely to be >15mm however this is based on a single study from Yorkshire (Robson & Williams, 1971), as our own study did not provide results on SOM. A conservative management approach could be to protect all periwinkles in their second year and some in their third, allowing harvesting of individuals >20mm as suggested elsewhere.

Tinlin-Mackenzie (2018) concludes that in the BNNC EMS in Northumberland, 'periwinkle stocks appear to be relatively resilient to harvesting. The biggest and most worrying potential impacts appear to be those for non-target rocky shore dwelling plants and animals which experience physical disturbance. Management could be done using education and codes of conduct'. The NIFCA Code of Conduct aims to minimise disturbance and ensure periwinkles <12mm are not harvested, so the efficacy of this management measure needs to be evaluated before considering any regulations or byelaws. Before introducing minimum harvest sizes, other potential management measures (see Tinlin-Mackenzie, 2018) such as the use of permits, bag or weight limits to control the intensity of commercial harvests, should be explored. No additional management measures are deemed necessary at this time.

References

- Cashmore D, Burton CA. Seafish Report No. 483: Feasibility study into the ongrowing potential of the periwinkle (*Littorina littorea* L.). Report prepared by Seafish Aquaculture, Marine Farming Unit, Ardtoe 02/1998
- Crossthwaite SJ, Reid N, Sigwart, JD. Assessing the impact of shorebased 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. 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>
- Bertness, M.D., 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology*, 65(2), pp.370-381.
- De Wolf, H., De Coen, W., Backeljau, T. and Blust, R., 2001. Intersex and sterility in the periwinkle *Littorina littorea* (Mollusca: Gastropoda) along the Western Scheldt estuary, the Netherlands. *Marine Environmental Research*, 52(3), pp.249-255.
- Doyle, D., Frias, J., Nash, R. and Gammell, M., 2020. Current environmental microplastic levels do not alter emergence behaviour in the intertidal gastropod *Littorina littorea*. *Marine Pollution Bulletin*, 151, p.110859.
- Erlandsson, J. and Johannesson, K., 1994. Sexual selection on female size in a marine snail, *Littorina littorea* (L.). *Journal of Experimental Marine Biology and Ecology*, 181(2), pp.145-157.
- Fish, J. D. 1972. The breeding cycle and growth of open coast and estuarine populations of *Littorina littorea*. *Journal of the Marine Biological Association, UK*. 52: 1011-1019.
- Fretter, R. and Graham, A. 1962. *British Prosobranch Molluscs: Their Functional Anatomy and Ecology*. London Ray Society.
- Grahame, J., 1973. Breeding energetics of *Littorina littorea* (L.) (Gastropoda: Prosobranchiata). *The Journal of Animal Ecology*, pp.391-403.
- Grahame, J. 1975. Spawning in *L. littorea* (L). (Gastropoda: Prosobranchiata). *Journal of Experimental Marine Biology and Ecology*, 18:185-196
- Griffin, T. 2000. Natural growth rates of the gastropod *Littorina littorea*. Submitted in part candidature to the National University of Ireland for the degree of M.S.c in Fisheries Management Development and Conservation. Department of Zoology and Animal Ecology, University College Cork
- Guyomarch-Cousin, C., 1975. Etude de la croissance d'un gastéropode prosobranchie gonochorique: *Littorina littorea*. *L. Cah. Biol. Mar*, 16, pp.483-494.
- Hughes, R. N. and Answer, P. 1982. Growth, spawning and trematode infection of *Littorina littorea* (L.) from an exposed shore in North Wales. *Journal of Molluscan Studies*. 48: 321-330.
- Jackson, A. 2008. *Littorina littorea* Common periwinkle. 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 03-09-2020]. Available from: <https://www.marlin.ac.uk/species/detail/1328>
- Johnson, M.P. and McDermott, T., 2018. Picking a way forward: valuing and managing traditional shellfish gathering for *Littorina littorea*. *Aquatic Living Resources*, 31, p.35.
- Kinlan BP, Gaines SD. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84: 2007–2020
- Leiva, G.E. and Castilla, J.C. (2001) 'A review of the world marine gastropod fishery: evolution of catches, management and the Chilean experience', *Reviews in Fish Biology and Fisheries*, 11(4), pp. 283-300
- Linke, O. 1933. Morphologie und physiologie des genitalapparates der Nordsee littorinen. *Wis Meeresuntersuch Abt. Helgoland*, Bd. XIXAbh Nr 5, 1-60.

- Moore HB. 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
- Norton, T.A., Hawkins, S.J., Manley, N.L., Williams, G.A.& Watson D.C., 1990. Scraping a living: a review of littorinid grazing. *Hydrobiologia* 193:117-138
- Reid, D. G. 1996. Systematics and Evolution of *Littorina*. The Ray Society. 164. 463pp
- Robson, E.M. and Williams, I.C., 1971. Relationships of some species of digenea with the marine prosobranch *Littorina littorea* (L.) II. The effect of larval digenea on the reproductive biology of *L. littorea*. *Journal of Helminthology*, 45(2-3), pp.145-159.
- Smith JE, Newell GE. 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.
- Tinlin-Mackenzie AR. 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.
- Williams EE. 1964. The growth and distribution of *Littorina littorea* (L.) on a rocky shore in Wales. *J Anim Ecol* 33: 413–432.
- Wilson A. Shellfish Industry Development Strategy: A 'Best-Practice' Guide of Sea Fisheries Committee Shellfish Byelaws. Seafish Report, 05/2009
- Yamada, S.B., 1987. Geographic variation in the growth rates of *Littorina littorea* and *L. saxatilis*. *Marine Biology*, 96(4), pp.529-534.