# What have limpets ever done for us? On the past and present provisioning and cultural services of limpets

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## Abstract

Limpets are one of the most abundant and familiar rocky shore organisms globally. They are perhaps most famous for their ability to cling onto rocks, but they are also well known for their grazing activity, which has an important structuring function. In contrast to other molluscs, such as oysters and mussels, which are celebrated for their gastronomic and cultural importance, little is known about the provisioning and cultural services of the humble limpet, and they are often referred to as 'famine food'. Using an interdisciplinary approach, this paper describes the importance of limpets in the diets and cultures of humans globally. Not only were limpets often the dominant shellfish eaten by early modern humans, but also they sustained the poor during times of famine and destitution. Today, they are considered a delicacy in many cultures. They are popular as bait and their shells have been used for a wide variety of uses, including tools, currency, offerings, traditional medicine, jewellery and artworks. They have important spiritual and religious relevance, featuring in myriad traditions, superstitions and folklore. Whilst limpets are not exploited on a global scale, there are many regions where populations are vulnerable to over-exploitation and possible extinction. Appropriate management is required if we are to protect these underappreciated animals. This comprehensive review rectifies the limpet's reputation as 'famine food' and attests to the important role that limpets played in past and present coastal cultural heritage and food culture.

Keywords: ecosystem services, environmental history, culture, shellfish, midden, folklore, limpet

## Background and scope

My research career started with studying the ecology of limpets (Figure 1). On telling people about my project, many reminisced about kicking them off the rocks as children and laughed about having to get them first time or they would clamp down. Some did not even realise that they were animals. One person even expressed wonder about why on Earth I would spend three years working on such 'boring

animals'. In comparison to other molluscs (e.g. oysters, mussels and cowries), which are renowned for their gastronomic, economic or aesthetic value,[1] the 'drab' limpet does not win any prizes, and in many regions is commonly considered 'poor food'[2] and even 'famine food'.[3] I felt that it was high time that someone 'flew the flag' for limpets! Through integrating the fields of ecology, anthropology, history and social science, in this review, I endeavour to celebrate the past and present importance of limpet for humans globally.

This review is framed in an ecosystem services context. Ecosystem services are considered the 'benefits that people derive from ecosystems' and are generally classed into four major categories that are underpinned by the species within ecosystems.[4] Provisioning services provide food, medicinal resources and raw materials. Regulating services are the services that ecosystems provide by acting as regulators such as carbon sequestration, erosion and pest control. Cultural services are usually defined as the intangible and non-material benefits ecosystems provide and include aesthetics and inspiration, cultural heritage, spiritual and religious values, knowledge and education, and recreation and tourism. Supporting services includes biodiversity and processes such as soil formation, primary production and habitat provision. Limpets are often the most abundant and familiar organisms in coastal habitats (Figure 1). They are a group of aquatic gastropods that exhibit a conical shell shape (patelliform) and a strong, muscular foot that sucks onto the substratum. The three main families (Fissurellidae, Patellidae, and Acmaeidae) all have a low, more or less symmetrically conical shell and a legendary ability to cling to rocks (see Box 1). Other families include the air-breathing false limpets (Siphonariidae) and slipper limpets (Calyptraeidae). They are primarily distributed along coastlines but are also found in the deep sea (Lepetodrilidae) and freshwater lakes and rivers (Ancylidae). This review focuses on coastal groups and typically features true limpets (Patellidae) and keyhole limpets (Fissurellidae), but other

1 Marion Johnson, 'The cowrie currencies of West Africa. Part I', *Journal of African History* (1970): 17–49; Loren D. Coen et al., 'Ecosystem services related to oyster restoration', Marine Ecology Progress Series 341 (2007): 303–7, doi.org/10.3354/meps341303; Stefanie Broszeit, Caroline Hattam and Nicola Beaumont, 'Bioremediation of waste under ocean acidification: Reviewing the role of *Mytilus edulis*', *Marine Pollution Bulletin* 103, no. 1–2 (2016): 5–14, doi.org/10.1016/j.marpolbul.2015.12.040; Anaëlle J. Lemasson et al., 'Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: A review', *Journal of Experimental Marine Biology and Ecology* 492 (2017): 49–62. doi.org/10.1016/j.jembe.2017.01.019; Caryn C. Vaughn, 'Ecosystem services provided by freshwater mussels', *Hydrobiologia,* 810 (2018): 15–27.

2 Walter F. Campbell, *Life in Normandy* (Edinburgh: Edmonston & Douglas, 1863).

3 Andrew B. Smith, 'Excavations at Plettenberg Bay, South Africa of the camp-site of the survivors of the wreck of the São Gonçalo, 1630', *International Journal of Nautical Archaeology* 15, no. 1 (1986): 53–9, doi.org/10.1111/j.1095–9270.1986.tb00544.x; Carolynn M. Harris et al., 'Analysis of the size, shape, and modeled age of common limpets (*Patella vulgata*) from Late Norse middens at Sandwick, Unst, Shetland Islands, UK: Evidence for anthropogenic and climatic impacts', *Journal of Island and Coastal Archaeology* 13, no. 3 (2018): 341–70, doi.org/10.1080/15564894.2017.1368743; Nyree Finlay et al., 'Calling time on Oronsay: Revising settlement models around the Mesolithic–Neolithic transition in Western Scotland, new evidence from Port Lobh, Colonsay', *Proceedings of the Prehistoric Society* 85 (2019): 83–114, doi.org/10.1017/ppr.2019.2.

4 Millennium Ecosystem Assessment, 2005, www.millenniumassessment.org/en/index.html, accessed 14 August 2020.

groups occasionally feature. Whilst the scope of this review is the global coastline, many of the case studies and examples are drawn from temperate systems or in developed countries, reflecting the distribution of published research. In this review, I focus on the provisioning and cultural services only, because they are more directly related to human uses than regulating and supporting services. I also briefly describe the ecosystem disservices associated with limpets before finishing on conservation efforts that will help to protect these often-underappreciated animals into the future.

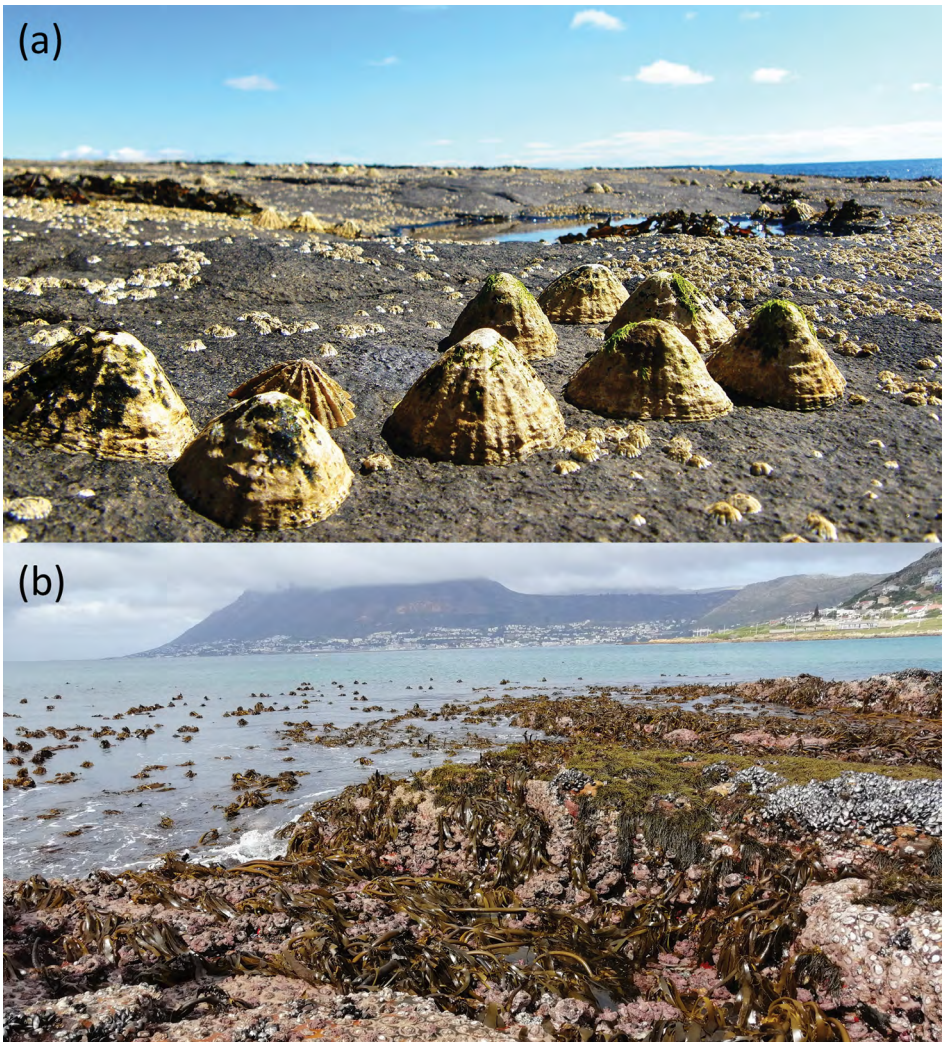


**Figure 1: Limpets on the rocky shore: (a) The common limpet, *Patella vulgata* L. 1758, at Port St. Mary Ledges, Isle of Man; (b) Very high densities of pear limpets, *Scutellastra cochlear*, Born 1778 (foreground) at Glencairn, Cape Town, South Africa.**

Source: Louise Firth.

# Provisioning services

As limpets are abundant and easy to collect when the tide is out, they have long been subjected to human exploitation for a wide range of provisioning services. Archaeological research on coastal middens revealed that stone tools, 'limpet hammers', were used to knock limpets from the rocks. They were extracted from their shells by stone 'limpet scoops' and either eaten as food or used as bait for fishing (see the 'cultural heritage' section below). Whilst there is some evidence to suggest that limpets were used as mineral resources for construction materials[5] and animal fodder,[6] they were much more important as food and, to a lesser degree, medicine, tools and implements, which is reflected in the focus of the sections below.

## Food

> The hoosh-pot with our precious limpets and seaweed was kicked over in the rush. There, just rounding the island … we saw a little ship flying the Chilean flag.
>
> Sir Ernest Shackleton, *South* (1919)[7]

### Past and present harvesting

Limpets were exploited for food by early hominids, including Neanderthals, from the Palaeolithic period.[8] It is generally considered that a switch to a seafood diet led to the evolution of the large, complex, metabolically expensive brain characterised by modern *Homo sapiens* (L.).[9] The earliest known evidence of limpet consumption by modern *Homo sapiens* dates back 164,000 years to a cave in South Africa.[10] When modern humans first started to migrate, it is thought that they followed

5 M. S. Lovell, *The Edible Mollusks of Great Britain and Ireland: With Recipes for Cooking Them* (London: Reeve & Company, 1867); Dang Hanh Nguyen et al., 'Valorization of seashell by-products in pervious concrete pavers', *Construction and Building Materials* 49 (2013): 151–60, doi.org/10.1016/j.conbuildmat.2013.08.017.

6 Edward Forbes and Sylvanus Charles Thorp Hanley, *A History of British Mollusca, and Their Shells*, vol. 1. (London: J. van Voorst, 1853); Lovell, *The Edible Mollusks of Great Britain and Ireland.*

7 Ernest Henry Shackleton, *South: The Endurance Expedition* (London: William Heinemann, 1919).

8 Gertrude Caton-Thompson, 'The Aterian industry: Its place and significance in the Palaeolithic world', *Journal of the Anthropological Institute of Great Britain and Ireland* (1946): 87–130, doi.org/10.2307/2844512; Henry de Lumley, 'A Paleolithic camp at Nice', *Scientific American* 220, no. 5 (1969): 42–51; João Zilhão et al., 'Last Interglacial Iberian Neandertals as fisher-hunter-gatherers', *Science* 367, no. 6485 (2020), doi.org/10.1126/science.aaz7943.

9 Catherine Leigh Broadhurst et al., 'Brain-specific lipids from marine, lacustrine, or terrestrial food resources: Potential impact on early African *Homo sapiens*', *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 131, no. 4 (2002): 653–73, doi.org/10.1016/S1096-4959(02)00002-7.

10 Curtis W. Marean et al., 'Early human use of marine resources and pigment in South Africa during the Middle Pleistocene', *Nature* 449, no. 7164 (2007): 905–8, doi.org/10.1038/nature06204.

coastal routes, due to the year-round accessibility of food, including limpets.[11] They were known to have been eaten by civilisations including the ancient Greeks[12] and Romans[13] and the early medieval Vikings.[14] Archaeological work from prehistoric middens has revealed that not only were limpets eaten all over the world but also that they were often the dominant shellfish in people's diets.[15] This potentially reflects their greater accessibility compared to other shellfish such as mussels and oysters, which tend to be found lower on the shore.[16] More recently, limpets featured in the diets of Caribbean slaves[17] and indigenous populations in Chile[18] and British Columbia.[19] Whilst in modern times, they are widely considered to be 'famine food',[20] they are still subsistence-harvested in California,[21] Chile,[22] New Zealand[23] and South Africa.[24] In some places, subsistence harvesting has been replaced by highly profitable commercial exploitation; much of which has since collapsed

11 Chris Stringer, 'Coasting out of Africa', *Nature* 405, no. 6782 (2000): 25–7, doi.org/10.1038/35011166; Jon M. Erlandson, 'Food for thought: The role of coastlines and aquatic resources in human evolution', in *Human Brain Evolution: The Influence of Freshwater and Marine Food Resources*, ed. Stephen C. Cunnane and Kathlyn Moore Stewart (Hoboken, NJ: Wiley-Blackwell, 2010), 125–36; Jon M. Erlandson et al., 'Ecology of the kelp highway: Did marine resources facilitate human dispersal from Northeast Asia to the Americas?', *Journal of Island and Coastal Archaeology* 10, no. 3 (2015): 392–411, doi.org/10.1080/15564894.2014.1001923.

12 Michael Lovano, *The World of Ancient Greece: A Daily Life Encyclopedia*, 2 vols (Santa Barbara, CA: ABC-CLIO, 2019.

13 Roy W. Davies, 'The Roman military diet', *Britannia* 2 (1971): 122–42.

14 Nicky Milner et al., 'Marine resource intensification in Viking Age Europe: The molluscan evidence from Quoygrew, Orkney', *Journal of Archaeological Science* 34, no. 9 (2007): 1461–72, doi.org/10.1016/j.jas.2006.11.004.

15 John Parkington, 'Middens and moderns: Shellfishing and the middle stone age of the Western Cape, South Africa', *South African Journal of Science* 99, no. 5–6 (2003): 243–7; Milner, 'Marine resource intensification in Viking Age Europe'; Esteban Alvarez-Fernández et al., 'Entre lapas: Primera valoración de los restos de origen marino del yacimiento holoceno de J3 (Hondarribia, País Vasco)', *Munibe (Antropologia–Arkeologia)* 65 (2014): 67–78.

16 Katherine Szabó et al., 'Shell artefact production at 32,000–28,000 BP in Island Southeast Asia: Thinking across media?', *Current Anthropology* 48, no. 5 (2007): 701–23, doi.org/10.1086/520131.

17 John M. Chenoweth, 'Marine shell and small-island slavery in the Caribbean', *Historical Archaeology* 52, no. 2 (2018): 467–88, doi.org/10.1007/s41636-018-0101-3.

18 John Byron, *The Narrative of the Honourable John Byron … Containing an Account of the Great Distresses Suffered by Himself and His Companions on the Coasts of Patagonia, etc*. (Wigan: W. Bancks, 1784).

19 Chris Moss, *Patagonia: A Cultural History* (New York: Oxford University Press, 2008).

20 For example, Campbell, *Life in Normandy*; R. Nicholson, J. Robinson, M. Robinson and E. Rowan, 'From the waters to the plate to the latrine: Fish and seafood from the Cardo V Sewer, Herculaneum', *Journal of Maritime Archaeology* 13, no. 3 (2018): 263–84. doi.org/10.1007/s11457-018-9218-y.

21 Oscar Alberto Pombo and Anamaria Escofet, 'Effect of exploitation on the limpet *Lottia gigantea*: A field study in Baja California (Mexico) and California (USA)', *Pacific Science* 50, no. 4 (1996): 393–403.

22 Doris Oliva and Juan Carlos Castilla, 'The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile', *Marine Ecology* 7, no. 3 (1986): 201–217, doi.org/10.1111/j.1439-0485.1986.tb00158.x.

23 Priscilla Wehi et al., 'Marine resources in Māori oral tradition: He kai moana, he kai mā te hinengaro', *Journal of Marine and Island Cultures* 2, no. 2 (2013): 59–68, doi.org/10.1016/j.imic.2013.11.006.

24 W. R. Siegfried et al., 'The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa—an overview', in *Rocky Shores: Exploitation in Chile and South Africa* (Berlin and Heidelberg: Springer, 1994), 1–15; Charles L. Griffiths and George M. Branch, 'The exploitation of coastal invertebrates and seaweeds in South Africa: Historical trends, ecological impacts and implications for management', *Transactions of the Royal Society of South Africa* 52, no. 1 (1997): 121–48, doi.org/10.1080/00359199709520619.

(e.g. Hawai'i,[25] California,[26] Mexico,[27] Chile[28] and the Azores[29]). In Asia, limpets are canned and marketed as 'poor man's abalone'. Today, they feature in many regional traditional recipes, some featuring in recipe books of celebrity chefs.[30] They are expensive delicacies in some gastronomical cultures with dishes such as limpet escabèche and grilled limpets (*lapas grelhadas*) featuring on gourmet websites.[31]

## Limpets associated with starvation, destitution and survival

Limpets have long been associated with starvation and destitution, and are often referred to as 'famine food'[32] or 'poor food'.[33] This is perhaps best captured through narratives from the Irish potato famines (See Box 2) and Highland Clearances of Scotland (1750–1860) when tenants were evicted from their homes and driven to hunger and destitution. In Scotland, many people relied on harvesting from the shore for survival, and limpets were both an important source of food[34] and bait (see the 'cultural heritage' section below). Gathered after a bad harvest, limpets became the focus of rioting in Orkney, Scotland, in 1762 when it was perceived that overharvesting the kelp impacted the limpets by denying them shade, thus depriving the poor of food—the so-called Kelp Riot of 1762.[35]

25 For a comprehensive review of feasibility options, see Anthony Mau and Rajesh Jha, 'Aquaculture of two commercially important molluscs (abalone and limpet): Existing knowledge and future prospects', *Reviews in Aquaculture* 10, no. 3 (2018): 611–25, doi.org/10.1111/raq.12190.

26 Jon M. Erlandson et al., '10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California', *Journal of Archaeological Science* 38, no. 5 (2011): 1127–34, doi.org/10.1016/j.jas.2010.12.009.

27 José Luis Carballo et al., 'Decimation of a population of the endangered species *Scutellastra mexicana* (Broderip and Sowerby, 1829) (Mollusca, Gastropoda) in the Marías Island (Eastern Ocean Pacific) Biosphere Reserve', *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, no. 1 (2020): 20–30, doi.org/10.1002/aqc.3239.

28 Juan Carlos Castilla, 'Chilean resources of benthic invertebrates: Fishery, collapses, stock rebuilding and the role of coastal management areas and national parks', in *Developing and Sustaining World Fisheries Resources: The State of Science and Management. Second World Fisheries Congress*, ed. Donald A. Hancock (Collingwood, Vic.: CSIRO Publishing, 1996), 130–5.

29 Gustavo M. Martins et al., 'Illegal harvesting affects the success of fishing closure areas', *Journal of the Marine Biological Association of the United Kingdom* 91, no. 4 (2011): 929–37, doi.org/10.1017/S0025315410001189.

30 Hugh Fearnley-Whittingstall and Nick Fisher, *The River Cottage Fish Book* (London: Bloomsbury, 2007); Darina Allen, *Irish Traditional Cooking* ([London]: Kyle Books, 2012).

31 Pieter A. Folkens, 'Symbolic and cultural uses', in *Encyclopedia of Tidepools and Rocky Shores*, ed. Steven Dean Gaines and Mark W. Denny (Berkeley, CA: University of California Press, 2007).

32 Andrew B. Smith, 'Excavations at Plettenberg Bay, South Africa of the camp-site of the survivors of the wreck of the São Gonçalo, 1630', *International Journal of Nautical Archaeology* 15, no. 1 (1986): 53–9, doi.org/10.1111/j.1095-9270.1986.tb00544.x; Harris et al., 'Analysis of the size, shape, and modeled age of common limpets'; Nyree Finlay et al., 'Calling time on Oronsay: Revising settlement models around the Mesolithic–Neolithic transition in Western Scotland, new evidence from Port Lobh, Colonsay', *Proceedings of the Prehistoric Society* 85 (2019): 83–114, doi.org/10.1017/ppr.2019.2.

33 Campbell, *Life in Normandy*.

34 Robert A. Dodgshon, 'Coping with risk: Subsistence crises in the Scottish Highlands and Islands, 1600–1800', *Rural History* 15, no. 1 (2004): 15.

35 Folkens, 'Symbolic and cultural uses'.

In his book *South*, the Irish explorer Sir Ernest Shackleton[36] recounts the fate of his 22 men left behind on Elephant Island after their ship the *Endurance* became trapped in ice during the Imperial Trans-Antarctic Expedition of 1914–17. Near the end of their four-month stay on the island, as their stocks of seal and penguin meat dwindled, they derived a major portion of their sustenance from harvesting limpets from the shores of the Southern Ocean. Similarly, during the German occupation of Jersey in the Second World War, food was scarce and limpet stew flavoured with curry powder became a staple dish.[37]

**Figure 2: A plate of *lapas grelhadas* (grilled limpets) on the Macaronesian Island of Tenerife.**

Source: Craig Wilding.

In a cultural turnaround, harvesting and foraging for wild food is now considered a middle-class leisure pursuit with numerous books and companies promoting the practice as part of sustainable living and team-building activities. Many children are taught survival skills in school and through outdoor pursuits clubs, with foraging limpets commonly featuring as a survival technique. For instance, limpets feature in British television personality Ray Mears' *Outdoor Survival Handbook*.[38] Some species of limpet are highly prized and considered delicacies (Figure 2).[39] In Hawai'i,

36 Shackleton, *South*.

37 Chris Addy, *Limpet Stew and Potato Jelly: Lillian Aubin Morris' Occupation Recipes* ([Jersey]: Jersey Heritage Trust, 2014).

38 Raymond Mears, *The Outdoor Survival Handbook: A Guide to the Resources & Material Available in the Wild & How to Use Them for Food, Shelter, Warmth, & Navigation* (New York: St Martin's Press, 2001).

39 Michael Harold Depledge et al., 'The Azores exploitation and pollution of the coastal ecosystem', *Marine Pollution Bulletin* 24, no. 9 (1992): 433–5, doi.org/10.1016/0025-326X(92)90341-3; Hugo Diogo et al., 'Catch me if you can: Non-compliance of limpet protection in the Azores', *Marine Policy* 63 (2016): 92–9, doi.org/10.1016/j.marpol.2015.10.007; Mau and Jha, 'Aquaculture of two commercially important molluscs'.

the limpet (*opihi*) is called 'the fish of death' because many people lose their lives annually harvesting them from wave-exposed locations.[40] Similarly, in the Azores, people have also been known to die collecting limpets, *lapas*.[41]

## Cultural recognition

The importance of limpets as food is documented through a range of different cultural formats. For instance, on the Macaronesian Islands, there is an annual limpet festival (*Festa da lapa*) held on Madeira, and there is an exhibit on limpet harvesting in the Jandía Lighthouse Museum on Fuerteventura. The harvesting of limpets from the shore has been captured in paintings including those of James Clarke Hook (1819–1907) and Kate E. Booth (1850–1898). Limpets are symbolic of the almost complete degradation of the Scottish Highlands after the Clearances.[42] This symbolism is epitomised by author Neil Gunn who makes myriad references to eating limpets in his books (e.g. *The Silver Darlings* and *Off in a boat*).[43] Similarly, many other authors refer to collecting limpets in their books, including Victor Hugo,[44] Robert Louis Stevenson[45] and William Golding.[46] Limpets as a survival food is even captured in a modern computer game—'Don't Starve: Shipwrecked'. Finally, in his play *Assemblywomen* (*Ecclesiazousae*) written in 391 BC, the ancient Greek comedic playwright Aristophanes created one of the longest words ever (182 Latin characters), which describes a dish (that includes limpets) by stringing together its ingredients: 'Lopadotemachoselachogaleokranioleipsanodrimhypotrimmatosilphioparaomelitokatakechymenokichlepikossyphophattoperisteralektryonoptekephalliokigklopeleiolagoiosiraiobaphetraganopterygon'. It is a transliteration of the Ancient Greek word 'λοπαδοτεμαχοσελαχογαλεοκρανιολειψανοδριμυποτριμματοσιλφιοκαραβομελιτοκατακεχυμενοκιχλεπικοσσυφοφαττοπεριστεραλεκτρυονοπτοκεφαλλιοκιγκλοπελειολαγῳοσιραιοβαφητραγανοπτερύγων'. The original word was translated by the Revd Rowland Smith:[47]

> Limpets, oysters, salt fish,
> And a skate too a dish,
> Lampreys, with the remains
> Of sharp sauce and birds' brains,

40 E. Alison Kay and Olive Schoenberg-Dole, *Shells of Hawai'i* (Honolulu, HI: University of Hawaii Press, 1991).
41 Alison Laurie Neilson et al., 'Speaking of the sea in the Azores islands: We sometimes went for lapas', in *Heritages and Memories from the Sea: Conference Proceedings*, ed. Filipe Themudo Barata and João Magalhães Rocha (Évora: University of Évora, 2015), 118–31.
42 Donald S. Murray, *Herring Tales: How the Silver Darlings Shaped Human Taste and History* (London: Bloomsbury, 2015).
43 Neil M. Gunn, *The Silver Darlings* (London: Faber & Faber, 1941); Neil M. Gunn, *Off in a Boat* (London: Faber & Faber, 1938).
44 Victor Hugo, *The Toilers of the Sea* (Brussels: A. Lacroix, Verboeckhoven et Cie., 1866).
45 Robert Louis Stevenson, *Kidnapped* (London: Cassell, 1886).
46 William Golding, *Pincher Martin* (London: Faber & Faber, 1956).
47 Roland Smith, *The Ecclesiazusae, or Female Parliament* (Oxford, J. H. Parker, 1833).

With honey so luscious,
Plump blackbirds and thrushes,
Cocks' combs and ring doves,
Which each epicure loves,
Also wood-pigeons blue,
With juicy snipes too,
And to close all, O rare!
The wings of jugged hare!

## Medicinal resources

> [A]nd yet there was not a child in Jura, or any of the adjacent isles, wholesomer than this poor infant.
>
> Martin Martin, *A Description of the Western Islands of Scotland* (1703)[48]

In general, limpets are not very well known for their medicinal properties. Keyhole limpet haemocyanin (KLH) is by far the most well known and studied example.[49] KLH is a large, multi-subunit, oxygen-carrying metalloprotein that is found in the haemolymph of the Californian giant keyhole limpet (*Megathura crenulata*, Sowerby 1825), which is used extensively as a carrier protein in the production of antibodies for research, biotechnology and therapeutic applications. KLH is a highly immunogenic T-cell dependent antigen that is used increasingly in immunotoxicological studies, including the treatment of bladder cancer,[50] atopy and asthma[51] and autoimmune diseases such as Lupus.[52]

Historical examples of traditional medicine exist but no scientific research has been conducted to verify these treatments. For instance, in ancient Greece, the rayed Mediterranean limpet (*Patella caerulea* L. 1758) was consumed in a broth as a laxative.[53] In Somerset, England, raw limpets (*Patella* spp.) and snails were recommended for bronchitis.[54] In the Scottish Western Isles, limpets were parboiled

48 Martin Martin, *A Description of the Western Islands of Scotland* (London, 1703).

49 J. Robin Harris and Jürgen Markl, 'Keyhole limpet hemocyanin (KLH): A biomedical review', *Micron* 30, no. 6 (1999): 597–623, doi.org/10.1016/S0968-4328(99)00036-0.

50 C. D. Jurincic-Winkler et al., 'Keyhole limpet hemocyanin for carcinoma in situ of the bladder: A long-term follow-up study', *European Urology* 37, suppl. 3 (2000): 45–9, doi.org/10.1159/000052392.

51 D. Spazierer et al., 'T helper 2 biased *de novo* immune response to Keyhole Limpet Hemocyanin in humans', *Clinical & Experimental Allergy* 39, no. 7 (2009): 999–1008, doi.org/10.1111/j.1365-2222.2008.03177.x.

52 John Ferbas et al., 'A novel assay to measure B cell responses to keyhole limpet haemocyanin vaccination in healthy volunteers and subjects with systemic lupus erythematosus', *British Journal of Clinical Pharmacology* 76, no. 2 (2013): 188–202, doi.org/10.1111/bcp.12172.

53 Hippocrates, cited in Eleni Voultsiadou, 'Therapeutic properties and uses of marine invertebrates in the ancient Greek world and early Byzantium', *Journal of Ethnopharmacology* 130, no. 2 (2010): 237–47, doi.org/10.1016/j.jep.2010.04.041.

54 Ruth L. Tongue, *Somerset Folklore*, vol. 8 (London: Folk-lore Society, 1965).

in water and consumed by poorly nourished nursing mothers to increase milk supply.[55] Martin Martin[56] describes a personal account of a woman from the Isle of Jura who:

> was almost reduced to a starving condition; so that she lost her milk quite, by which her Infant had nothing proper for its sustenance, upon this she boil'd some of the tender fat limpets, and gave it to her infant, to whom it became so agreeable, that it had no other food for several months together; and yet there was not a child in Jura, or any of the adjacent isles, wholesomer than this poor infant, which was expos'd to so great a strait.

## Tools and implements

> Here they first wash their feet in one of the rock pools before approaching the spring, in front of which they kneel and pray, afterwards drinking a little from a limpet shell.
>
> J. H. Hutton, 'Pilgrimages to the Holy Well and Ruined Church of St. Conal on the Island Inishkeel, Gweebarra Bay, Co. Donegal' (1920)[57]

Given their wide variety of shapes and forms, shells are commonly used as implements and tools for a wide range of purposes. Shell deposits dated between 26 and 17 thousand years ago from a cave at Altamira, Spain, indicate that limpets were used for scraping ochre (a natural clay earth pigment) that was used to paint the graphic representations in the cave.[58] In Hawai'i, the shells were used for scraping the skin off taro plants and sweet potatoes and for grating coconut meat,[59] and particular species were used as drinking vessels and for dispensing different volumes of traditional medicine.[60] In Tasmania, the Aboriginal Christian community at Leprena drink the sacramental wine from limpet shells.[61] The shells are used to collect and drink water from holy wells to relieve illness in Wales[62] and Ireland. I have even heard of very recent instances where large shells (>6 cm depth) from the Falkland Islands were brought back from a research cruise and used as 'shot glasses' by PhD students in the United Kingdom.

55 Alexander Robert Forbes, *Gaelic Names of Beasts (Mammalia), Birds, Fishes, Insects, Reptiles, Etc: In Two Parts. I. Gaelic-English; II. English-Gaelic* (Edinburgh: Oliver and Boyd, 1905).

56 Martin, *A Description of the Western Islands of Scotland*.

57 J. H. Hutton, 'Pilgrimages to the Holy Well and Ruined Church of St. Conal on the Island Inishkeel, Gweebarra Bay, Co. Donegal', *Folklore* 31, no. 3 (1920): 231–3, doi.org/10.1080/0015587X.1920.9719154.

58 David Cuenca-Solana et al., 'Painting Altamira Cave? Shell tools for ochre-processing in the Upper Palaeolithic in northern Iberia', *Journal of Archaeological Science* 74 (2016): 135–51, doi.org/10.1016/j.jas.2016.07.018.

59 Edward Smith Handy et al., *Native Planters in Old Hawaii: Their Life, Lore, and Environment*, vol. 233 (Honolulu, HI: Bernice P. Bishop Museum Press, 1991).

60 Beatrice H. Krauss, *Plants in Hawaiian Medicine* (Honolulu, HI: Bess Press, 2001).

61 Mark Brett and Jione Havea, eds, *Colonial Contexts and Postcolonial Theologies: Storyweaving in the Asia-Pacific* (Basingstoke: Palgrave Macmillan, 2014).

62 Folkens, 'Symbolic and cultural uses'.

In the Scottish Western Isles, Martin describes how limpet shells (*Patella* spp.) were traditionally used to apply treatments to cure sciatica.[63] The spirewort plant (*Flamula jovis*) was cut up and stuffed into an empty limpet shell that was held against the thigh, causing a blister to rise. Following the emptying of the blister three times, the sea plant Linarich (samphire, *Crithmum maritimum*) was applied to the place to cure and dry the wound. This traditional practice is reflected in Neil Gunn's novel *The Butcher's Broom*,[64] which is set during the Scottish Highland Clearances.

Limpet shells are used by nursing mothers as nipple shields to collect leaking milk and to soothe and protect sore and cracked nipples. This practice is thought to date back to the Vikings and was traditionally practised in Norway, Denmark, Sweden, France, Ireland, Wales and Scotland. In Breconshire, Wales, it was customary for women to collect limpets during seaside holidays and bring them home to be applied to the breasts of those having feeding troubles after childbirth; the local name for the limpet was '*cragen y fron*' (breast shell).[65] Today, Norwegian and French companies sell pairs of 'breast shells' for €11–31. The shells are provided to breast-feeding mothers suffering from nipple soreness by many Norwegian maternity hospitals and are recommended by Norwegian midwives.

# Cultural services

Cultural services comprise myriad categories, depending on one's perspective. The categories below were established by the Millennium Ecosystem Assessment[66] and are used here due to their suitability in the context of limpets. Cultural services are deeply interconnected with each other and often link to provisioning and regulating services. For instance, the use of limpets as bait falls under cultural heritage below but it could equally fall under recreation and tourism. Many of the examples given below could feature under other subheadings, and should thus be considered in a broader cultural sense.

## Aesthetic and inspiration

> With what truly romantic ideas must it inspire one, to sit in a room furnished with riches of the most distant shores and oceans!
>
> Griffith Hughes, *The Natural History of Barbados* (1750)[67]

63 Martin, *A Description of the Western Islands of Scotland*.
64 Neil M. Gunn, *Butcher's Broom* (Edinburgh: Porpoise, 1934).
65 Anne E. Jones, 'Folk medicine in living memory in Wales', *Folk Life* 18, no. 1 (1980): 58–68, doi.org/10.1179/043087780798254729.
66 Millennium Ecosystem Assessment, 2005.
67 Griffith Hughes, *The Natural History of Barbados: In Ten Books* (London: The author, 1750).

The human obsession with seashells is age-old. Shells have long been collected as ornaments and crafts. They regularly feature in art and have also inspired many architectural and engineering designs and their tenacity (i.e. their ability to suck onto rocks) is widely appreciated and has inspired myriad cultural references (see Box 1).

With the advent of the seaside holiday, the Victorians became avid admirers and collectors of plants and animals,[68] which they displayed in curiosity cabinets alongside other natural history phenomena. The most famous and best-documented cabinets formed collections that were precursors to museums.[69] So great was the obsession with shells ('conchylomania', derived from the colonial trade and exploration of the Dutch East India Company),[70] that John Foster[71] recounts the Northern Irish town of Bangor being gripped by 'limpet fever' in the 1820s when one of the first natural history societies was established. Shells, including limpets, were collected and traded between countries (often in exchange for slaves),[72] with rare specimens fetching high prices. Today, limpets are still traded through collectors' clubs and are available to buy in shell shops.[73]

Limpet shells regularly featured in decorative pictures and crafts that were composed entirely of shells. For instance, the author Agatha Christie was famously a keen collector, and visitors to her home in Devon, England, can enjoy her beautiful shell pictures dating from c.1800. Originating in Barbados in the 1830s, the 'sailor's valentine' is a form of shell craft, a type of souvenir, or sentimental gift made from large numbers of small seashells, with limpets being a prominent feature (Figure 3). They were designed to be brought home from a sailor's voyage and given to a loved one.[74] Today, antique sailors' valentines are collectibles, but renewed collector interest has sparked the sale of DIY shell kits and patterns at craft shops.[75] Similarly, dolls made from shells were popular in the 1800s. The salt marsh workers of Brittany ('paludiers') made souvenirs depicting their way of life.[76] Dolls in paludier costumes made from seashells are now collectors' items. At the time of writing, a pair featuring limpet shells were being sold online for €1,500.

68 Phillip Henry Gosse, *Tenby: A Sea-Side Holiday* (London: John van Vorst, 1856); Charles Kingsley, *Glaucus; or, The Wonders of the Shore*, 3rd ed. (Cambridge: Macmillan, 1856).

69 Sharon Macdonald, ed., *A Companion to Museum Studies*, vol. 39 (Malden, MA, and Oxford: John Wiley & Sons, 2011).

70 Om Prakash, *The Dutch East India Company and the Economy of Bengal, 1630–1720* (Princeton, NJ: Princeton University Press, 2014).

71 John Wilson Foster, 'Natural history, science and Irish culture', *The Irish Review* 9 (1990): 61–9, doi.org/10.2307/29735546.

72 Jan Hogendorn and Marion Johnson, *The Shell Money of the Slave Trade*, vol. 49 (Cambridge: Cambridge University Press, 2003).

73 José Luis Carballo et al., 'Decimation of a population of the endangered species *Scutellastra mexicana*'.

74 John Fondas, *Sailors' Valentines: Their Journey through Time* (New York: Rizzoli, 2002).

75 Grace L. Madeira et al., *Sailors' Valentines: Their Journey through Time* (Atglen, PA: Schiffer, 2006).

76 Mark Kurlansky, *Salt: A World History* (New York: Random House, 2011).

**Figure 3: Shell craft—a sailor's valentine featuring many small limpet shells.**
Source: Neochichiri11, commons.wikimedia.org/w/index.php?curid=37606754, accessed 22 August 2020.

Limpets occasionally feature as the main subject of artworks and paintings. One example is the Human–Limpet Project (Figure 4), which is exploring, from an archaeological perspective, the entangled relationship between limpets and humans over time. They feature very commonly in plates of illustrations that were included in historical books on morphological and taxonomic descriptions. Many of these old plates are collectors' items today and some even feature in some of the most famous art galleries in the world (e.g. Edward Donovan's (1768–1837) 'Limpets' at the New York Metropolitan Museum of Art). Limpets typically feature in artwork for cultural or symbolic purposes. For instance, J. M. W. Turner's (1775–1851) 'War. The Exile and the Rock Limpet' was interpreted by Winston Ponder et al.[77] as comparing the exile of Napoleon to the island of St. Helena with the solitary existence of the limpet. Limpets featuring in art as symbols of tenacity or as cultural references to famine food are dealt with in Boxes 1 and 2, respectively.

77 Winston Frank Ponder et al., *Biology and Evolution of the Mollusca*, vol. 2 (Boca Raton, PL: CRC Press, 2020).

**Figure 4: The Human Limpet Project. The artist invited people to sit or stand inside to experience being a limpet. Image of a human-sized felt limpet that the artist made. Image taken at Lybster, Caithness, Scotland.**

Source: Helen Garbett.

The internal nacreous layer of some limpets is highly valued. A 1694 report published by the Royal Society in London described how the inside of limpet and abalone shells were sold in shops as true mother of pearl.[78] The nacreous layer of the large Azorean limpet (*Patella aspera* Röding, 1798) is often painted upon and sold as art (Figure 5). Possibly linked to their aesthetic value, there is evidence to suggest that shells of the giant keyhole limpet (*M. crenulata*) were used as currency and for trade by native Californian populations.[79]

78 Nehemiah Grew, *Musæum Regalis Societatis: A catalogue & Description of the Natural and Artificial Rarities Belonging to the Royal Society and Preserved at Gresham Colledge* (London: Hugh Newman, 1694).

79 Walker A. Tompkins, *Santa Barbara's Royal Rancho: The Fabulous History of Los Dos Pueblos* (Chicago: Papamoa, 2019; Robert Fleming Heizer, ed., *Aboriginal California: Three Studies in Culture History*, vol. 54 (Berkeley, CA: University of California Press, 1963); José Luis Carballo et al., 'Decimation of a population of the endangered species *Scutellastra mexicana*'.

**Figure 5: Montage of limpet appreciation in various forms of cultural media: (a) Limpet necklace; (b) the Mediterranean ribbed limpet (*Patella ferruginea*) featured on a stamp from the Comoros Islands; (c) a painted limpet from the Azores.**

Sources: (a, c) Louise Firth; (b) VLIZ Collection, www.marinespecies.org/photogallery.php?album=702&pic=48106, accessed 22 August 2020.

Research on limpets has implications for technology development. The 'teeth' of limpets are known to be composed of goethite—the strongest material known in nature.[80] As limpet teeth are resistant to abrasion (from the rasping of the radula over rock surfaces), corresponding structural design features are expected to be significant for novel biomaterials with extreme strength and hardness, such as next-generation dental restorations. Similarly, recent research assessed the optical properties of the blue colouration on the rays of blue-rayed limpets (*Patella pellucida* L. 1758).

80 Asa H. Barber et al., 'Extreme strength observed in limpet teeth', *Journal of The Royal Society Interface* 12, no. 105 (2015), doi.org/10.1098/rsif.2014.1326.

The authors of this research, Ling Li et al., suggest that this discovery may be of interest to materials scientists and engineers to engineer advanced transparent optical displays.[81]

Limpets also feature on a range of items that may be interpreted as appreciation for their aesthetic appeal. For instance, the shell form features regularly in modern jewellery (Figure 5) and has been replicated in glassware and tableware. Images of limpets have featured on collectible cigarette pack cards and postage stamps from a range of different countries including Namibia, Madeira, Jersey, the Falkland Islands, the Pitcairn Islands, St. Vincent and the Grenadines, and the Comoros Islands (Figure 5). Finally, many place names reference limpets, particularly in Scotland (e.g. Clach Bharnach Bhraodag on North Uist: limpet stone of Freya) and Ireland (e.g. Cnocán na mBairneach in Cork: little hill of the limpets), but also in Hawai'i (e.g. opihikao on the Island of Hawai'i: opihi = limpet), Singapore (e.g. Kampong Tumbok Opih: kampung = village, tumbok = to pound, opih = a type of limpet) and Antarctica (e.g. Limpet Island) to name but a few.

## Cultural heritage

> Tormad had taken a fancy to the limpets.
>
> Neil Gunn, *The Silver Darlings* (1941)

Limpets appear to have cultural importance as bait in Britain, especially in Scotland,[82] but also to a lesser degree in other parts of the world, including Mexico and the United States,[83] Australia,[84] Ireland[85] and the Mediterranean.[86] In California, owl limpets (*Lottia gigantea* Sowerby, 1834) are collected for fishing bait and used alongside California giant keyhole limpets (*Megathura crenulata*) in spiny lobster traps.[87] Ethnographic evidence from the Channel Island of Guernsey demonstrates that limpets had holes knocked through them and were strung up in willow pots to

81 Ling Li et al., 'A highly conspicuous mineralized composite photonic architecture in the translucent shell of the blue-rayed limpet', *Nature Communications* 6, no. 1 (2015): 1–11, doi.org/10.1038/ncomms7322.

82 Martin, *A Description of the Western Islands of Scotland*.

83 Pombo and Escofet, 'Effect of exploitation on the limpet *Lottia gigantea*'.

84 Christine Porter and Geoff Wescott, 'Recreational use of a marine protected area: Point Lonsdale, Victoria', *Australasian Journal of Environmental Management* 11, no. 3 (2004): 204, doi.org/10.1080/14486563.2004.10648614.

85 House of Commons, *Reports from Commissioners*, 18 vols. *Irish Fisheries; Herring Fishery*, vol. 22 (London, 1837).

86 F. Laborel-Deguen and J. Laborel, 'Statut de *Patella ferruginea* Gmelin en Méditerranée', *Les Espèces marines à protéger en Méditerranée* (1991): 91–103, cited in Free Espinosa et al., 'Effect of human pressure on population size structures of the endangered ferruginean limpet: Toward future management measures', *Journal of Coastal Research* 25, no. 4 (254) (2009): 857–63, doi.org/10.2112/08-1005.1.

87 Pombo and Escofet, 'Effect of exploitation on the limpet *Lottia gigantea*'.

catch crayfish.[88] The large Mediterranean ribbed limpet (*Patella ferruginea* Gmelin, 1791) was used as fishing bait in the past,[89] and despite now being subject to strict legal protection,[90] it continues to be collected.[91]

Whilst three large patellid species occur in Britain, only the common limpet, *Patella vulgata* L. 1758, is considered good for bait. In the early 1800s, *P. vulgata* was commonly collected for bait by fishwives in Cullercoats, north-east England.[92] The lower-shore China limpet (*P. ulyssiponensis* Gmelin, 1791) was described as 'almost worthless as baits' and the black-footed limpet (*Patella depressa* Pennant, 1777) that occurs on the south coast of England was considered to be too tough.[93] Edward Forbes and Sylvanus Hanley report that Dr Johnson estimated that there was an annual consumption of no fewer than 11,880,000 limpets for this purpose in Berwick-upon-Tweed and due to 'constant warfare' the numbers had, by 1853, greatly decreased, such that 'there is now not one out of ten that were twenty years ago, and the collecting of them has become tedious enough'.[94]

In Scotland, it could be argued that an entire culture and language[95] has developed around the use of limpets for bait. The use of *P. vulgata* for bait in Scotland is known from archaeological research carried out on shell middens dating back more than 4,000 years in the Western Isles.[96] Biot Edmondston and Jessie Saxby describe how limpets were removed from the rocks at low tide using a limpet pick or knife called a 'sprud'.[97] They were taken home and 'leepit' (parboiled), which made them easier to remove from the shell, before being carried off in a 'limpet cuddy' (basket made with dock leaves) to go fishing. This routine is reflected in the opening scene of Neil Gunn's *The Silver Darlings*, which depicts the brutality of life in a fishing community after the Highland Clearances.

88 Karen Hardy, 'Shell as a raw material for tools and jewellery in Mesolithic Scotland', *Munibe Suplemento-Gehigarria* 31 (2010): 128–37.

89 Laborel-Deguen and Laborel, 'Statut de *Patella ferruginea* Gmelin en Méditerranée'.

90 Free Espinosa and Georgina Alexandra Rivera-Ingraham, 'Biological conservation of giant limpets: the implications of large size', *Advances in Marine Biology*, 76 (2017): 105–55, doi.org/10.1016/bs.amb.2016.10.002.

91 Georgina Alexandra Rivera-Ingraham et al., 'Conservation status and updated census of *Patella ferruginea* (Gastropoda, Patellidae) in Ceuta: Distribution patterns and new evidence of the effects of environmental parameters on population structure', *Animal Biodiversity and Conservation* (2011): 83–99, www.raco.cat/index.php/ABC/article/view/243396.

92 William Beattie et al., *The Ports, Harbours, Watering-Places and Coast Scenery of Great Britain* (London: George Virtue, 1842).

93 Forbes and Hanley, *A History of British Mollusca, and Their Shells*, vol. 1.

94 Ibid.

95 Donald Macintosh, *A Collection of Gaelic Proverbs and Familiar Phrases* (Edinburgh: Maclachlan and Stewart, 1882); George T. Flom, 'Noa words in North Sea regions; A chapter in folklore and linguistics', *Journal of American Folklore* 38, no. 149 (1925): 400–18.

96 House of Commons, *Reports from Commissioners*, 18 vols. *Irish Fisheries; Herring Fishery*, vol. 22 (London, 1837); Nyree Finlay et al., 'Calling time on Oronsay: Revising settlement models around the Mesolithic–Neolithic transition in Western Scotland, new evidence from Port Lobh, Colonsay', *Proceedings of the Prehistoric Society* 85 (2019): 83–114, doi.org/10.1017/ppr.2019.2.

97 Biot Edmondston and Jessie Margaret Edmondston Saxby, *The Home of a Naturalist* (London: James Nisbet, 1888).

In the northern Scottish isles, limpets have long been synonymous with 'craig-fishing' or fishing from the rocks.[98] This involved mashing limpets for ground bait in cup-shaped hollows in the rocks near the favoured spots using a stone and pounder. The jelly of the smashed limpets was scattered on the surface of the water to attract coalfish. The fisherperson would then take several limpets in their mouth and chew them to the correct degree of softness for putting on the hook. It is said that an expert could bait the hook by slipping the chewed limpet between their clenched teeth onto it.[99] An advantage of spreading the crushed limpets as ground bait was that the oiliness from the gut of the limpet helped to smooth the surface and provide a further attraction for the coalfish. Crushed or chewed limpet bait was called 'soe' (Shetland,) 'furto', 'raa-saithe' or 'saithe' (Orkney) and 'soll' (Gaelic). The ancient art of limpet chewing and spreading on the water is celebrated in the 1981 song 'Rubh nan Cudaigean'[100] by the Isle of Skye band Runrig; part of the Gaelic lyrics translates as 'we will chew the limpets, the limpets the limpets, and we will scatter them on the sea at the headland'.

Since the arrival of the non-native slipper limpet (*Crepidula fornicata* L. 1758) in 1893,[101] this species has also been used for bait, particularly on the south coasts of England and Wales, where it is particularly prevalent.[102] Outside its native range, *C. fornicata* has myriad negative environmental impacts including the alteration of sedimentary and water flow dynamics through the production of pseudofaeces,[103] competition for food with other species,[104] and modifications in the trophic and community structure of benthic communities.[105] Consequently, the UK government have banned their use as bait or disposal at sea.[106]

98 Alexander Fenton, *The Northern Isles: Orkney and Shetland* (East Linton: Tuckwell, 1997).

99 T. Christopher Smout, ed., *Scotland and the Sea* (Laham, MD: Rowman & Littlefield, 1992.

100 Runrig, Rubh nan cudaigean, www.songlyrics.com/runrig/rubh-nan-cudaigean-lyrics, accessed 14 August 2020.

101 Walter Crouch, 'On the occurrence of *Crepidula fornicata* in Essex', *Journal of Molluscan Studies* 1, no. 1 (1893): 19, doi.org/10.1093/oxfordjournals.mollus.a064069.

102 Hilmar Hinz et al., 'Temporal differences across a bio-geographical boundary reveal slow response of sub-littoral benthos to climate change', *Marine Ecology Progress Series* 423 (2011): 69–82, doi.org/10.3354/meps08963; Katrin Bohn et al., 'The distribution of the invasive non-native gastropod *Crepidula fornicata* in the Milford Haven Waterway, its northernmost population along the west coast of Britain', *Helgoland Marine Research* 69, no. 4 (2015): 313–25, doi.org/10.1007/s10152-015-0439-2.

103 Axel Ehrhold et al., 'Conséquences de la prolifération de la crépidule (*Crepidula fornicata*) sur l'évolution sédimentaire de la baie du Mont-Saint-Michel (Manche, France)', *Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science* 327, no. 9 (1998): 583–88, doi.org/10.1016/S1251-8050(99)80111-6.

104 Michel Blanchard, 'Spread of the slipper limpet *Crepidula fornicata* (L. 1758) in Europe. Current state and consequences', *Scientia Marina* 61, suppl. 2 (1997): 109–18, archimer.ifremer.fr/doc/00423/53398/; David W. Thieltges, 'Impact of an invader: Epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels', *Marine Ecology Progress Series* 286 (2005): 13–19, doi.org/10.3354/meps286013.

105 Laurent Chauvaud et al., 'Long-term variation of the Bay of Brest ecosystem: Benthic-pelagic coupling revisited', *Marine Ecology Progress Series* 200 (2000): 35–48, doi.org/10.3354/meps200035; Thibault Androuin et al., 'The dark side of soft tissues: Unexpected inorganic carbonate in the invasive slipper limpet *Crepidula fornicata* and its implications for stable isotope interpretations', *Rapid Communications in Mass Spectrometry* 33, no. 1 (2019): 107–15, doi.org/10.1002/rcm.8322.

106 Marine Management Organisation, 'Slipper limpets not permitted to be used as bait or disposed at sea' (2015), www.gov.uk/government/news/slipper-limpets-not-permitted-to-be-used-as-bait-or-disposed-at-sea, accessed 15 May 2020.

## Spiritual and religious values

> But then there come erudite limpets, limpets who write histories of philosophy and give lectures on comparative religion, and who have never had any vision of their own.
>
> C. S. Lewis, *Miracles* (1947)[107]

There is evidence that limpet shells were and are used as offerings in a range of different cultures. For instance, *S. mexicana* shells were found in the Pyramid of the Feathered Serpent in the Xochicalco deposit (600–900 CE) located in Mexico's interior.[108] *P. ulyssiponensis* shells were found in the sanctuary of Apollo at Delphi, Greece, and Alexandra Livarda et al. speculate that, due to the large size and good condition of the shells, they may represent votive offerings dedicated to the divinity, perhaps to ask favours or avert anger.[109] In Hawai'i, opihi shells were placed on 'ahu' (shrines), and certain families revere the opihi as their ancestral spirits or 'aumakua'.[110]

In Scotland, limpet shells have been found kilometres from the sea on mountain tops near locations that were known to be pagan temples or high places of idolatry.[111] It is thought that limpets were part of the ritual of pagan human sacrifice in eastern Scotland.[112] In his book, *The Road to the Isles*, Kenneth McLeod tells of boys crushing limpet shells and throwing them into the sea to attract fish, which, representing the boys' ancestors, would come out of the sea onto land as a 'libation unto Lear, the Sea-God'.[113]

Limpets are commonly found in burial sites. In the Channel Islands and Brittany, limpet shells (*Patella* sp.) have been found in huge abundance in cromlechs (subterranean burial chambers), where they covered skeletons to depths of one metre.[114] The significance of the shells is unknown, but Nick and Philippe Aubin

107 Clive Staples Lewis, *Miracles* (London: Geoffrey Bles, 1947).

108 Luis Gómez-Gastélum, 'Los colores de las conchas marinas en el antiguo occidente de México. El caso del Posclásico', *Revista Mexicana de Biodiversidad* 78 (2007): 41–59.

109 Alexandra Livarda and Richard Madgwick, 'Ritual and religion: Bioarchaeological perspectives', in *The Bioarchaeology of Ritual and Religion* (Oxford: Oxbow, 2017), 1–13.

110 J. S. Emerson, *The Lesser Hawaiian Gods. Haw*, Papers of the Hawaiian Historical Society, 2 ([Honolulu, HI: The society], 1892); Martha Warren Beckwith, 'Hawaiian shark aumakua', *American Anthropologist* 19, no. 4 (1917): 503–17; Shauna Kehaunani Tom, 'An investigation of the cultural use and population characteristics of 'opihi (Mollusca: *Cellana* spp.) at Kalaupapa National Historical Park' (M.Sc. diss., University of Hawai'i at Hilo, 2011).

111 Royal Society, *Philosophical Transactions, Giving Some Account of the Present Undertakings, Studies and Labours of the Ingenious in Many Considerable Parts of the World*, vol. 21 (London: The society, 1699).

112 George Sligo, 'Notes on an Ancient Cave, &c., discovered at Aldham, now called Seacliff, in East Lothian, in 1831', *Archaeologia Scotica* 4 (1857): 353–61; Nina Frances Layard, 'Evidence of Human Sacrifice in Seacliff Cave, Scotland', *Proceedings of the Prehistoric Society of East Anglia* 7, no. 3 (1934): 399–401, doi.org/10.1017/s0958841800026934.

113 Kenneth MacLeod, *The Road to the Isles: Poetry, Lore, and Tradition of the Hebrides* (Edinburgh: Grant, 1927).

114 Frederick C. Lukis, 'Cromlech du Tus, Guernsey', *Journal of the British Archaeological Association* 1, no. 1 (1845): 25–9, doi.org/10.1080/00681288.1845.11886757, cited in Lovell, *The Edible Mollusks of Great Britain and Ireland.*

propose that the quantities of limpet shells suggest a ritual element and that the seeming preference for limpet shells might be linked to how these animals adhere to rocks with exceptional strength[115] (see Box 1).

Limpet shells have also been found as jewellery, ornaments or ceremonial objects in the Philippines,[116] Mexico,[117] California[118] and Ireland,[119] and in Phoenician burial chambers in Carthage, Tunisia.[120] Free Espinosa and Georgina Rivera-Ingraham describe how archaeological evidence from the Postclassic period (1100–1350 CE) in Pacific Mexico shows that *Scutellastra mexicana* Broderip & Sowerby, 1829, was used for bracelets and earrings.[121] In pre-Columbian central Mexican cultures, *S. mexicana* was cut to leave a hole in the middle and worn as a pendant called 'oyohualli', which is thought to have connotations with the female genitalia.[122] Carved figurines wearing pectoral oyohualli have been found in burial sites in Guatemala.[123]

In the Macaronesian Islands and Brazil, 'lapinhas' are miniature nativity scenes made from shells (including limpets), clay, wood, dried flowers and moss that can be assembled on wooden supports and protected by glass cases (Figure 6). In many of these displays, the infant Jesus is lying in a limpet shell. This tradition began in convents in the twelfth century but many people now make their own lapinhas, which are displayed in family homes during Christmas.[124] Incidentally, whilst the word lapinha could be interpreted as the diminutive of 'lapa' meaning limpet, in this instance, it refers to a small grotto or rock shelter.

115 Nick Aubin and Philippe Aubin, 'The Neolithic passage graves of the Channel Islands: Stone selection and the sun' (2019), www.researchgate.net/publication/337874586_The_Neolithic_Passage_Graves_of_the_Channel_Islands_Stone_Selection_and_the_Sun, accessed 23 August 2020.

116 Grace Barretto-Tesoro, 'Burial goods in the Philippines: An attempt to quantify prestige values', *Japanese Journal of Southeast Asian Studies* 41, no. 3 (2003): 299–315, doi.org/10.20495/tak.41.3_299.

117 John M. Goggin, 'An archaeological survey of the Rio Tepalcatepec Basin, Michoacán, Mexico', *American Antiquity* (1943): 44–58, doi.org/10.2307/275451.

118 Waldo Rudolph Wedel, *Archeological Investigations at Buena Vista Lake, Kern County, California* (Washington, DC: US Government Printing Office, 1941); Edward Winslow Gifford, *California Shell Artifacts* (Berkeley, CA: University of California Press, 1947).

119 Finbar McCormick, 'Faunal remains from prehistoric Irish burials', *Journal of Irish Archaeology* (1985): 37–48.

120 Marianne E. Bergeron, 'Death, gender, and sea shells in Carthage', *Pallas. Revue d'études antiques* 86 (2011): 169–89, doi.org/10.4000/pallas.2143.

121 Espinosa and Rivera-Ingraham, 'Biological conservation of giant limpets'.

122 Michael D. Coe, *The Maya Scribe and His World* (New York: Grolier Club, 1973).

123 Vera Tiesler et al., *Before Kukulkán: Bioarchaeology of Maya Life, Death, and Identity at Classic Period Yaxuná* (Tucson, AZ: University of Arizona Press, 2017); Colin Renfrew et al., eds, *Ritual, Play and Belief, in Evolution and Early Human Societies* (Cambridge: Cambridge University Press, 2017).

124 Ribeira Grande, 'Local Products: Lapinhas' (2020), www.ribeiragrande.pt/en/produtoslocais, accessed 6 August 2020.

**Figure 6: Example of a lapinha—a miniature nativity scene made from shells (note shells on the back and side walls and the infant Jesus in a limpet shell), clay, wood, dried flowers and moss. This example is wall-mounted but many are assembled on wooden supports and protected by glass domes or cases.**

Source: Centro Regional de Apoio ao Artesanato, Azores.

Limpets are associated with many superstitions. In the English coastal town of Shoreham, limpets and other seashells feature in the archway decoration of St Nicholas' Church. Limpets are considered a symbol of fortitude and are thought to represent a tribute to Shoreham's former maritime importance. In the Channel Islands, a kind of limpet 'is the eye of someone who has been drowned, which, at the end of the world, will grow wings, and fly away to take its place in the head to which it belongs'.[125] In his memoirs in which he recounts making one of the first European contacts with indigenous people in Chilean Patagonia, John Byron

125 A.F. Chamberlain, 'The origins of art by Yrjö Hirn', *The Journal of American Folklore* 14, no. 53 (1901): 143–6. doi.org/10.2307/532872.

reports having been thrashed by the natives for throwing empty limpet shells over the side of a canoe—something he attributed to being a bad luck superstition.[126] In some villages around Galway Bay, Ireland, there was a tradition of placing live limpets or periwinkles in each corner of the house to bring good luck with the fishing in the coming year and to ensure a good harvest from the shore.[127]

Limpets also feature in mythology and folklore. In Canadian Haida culture, Raven is a central character. It is believed that he created the first two women from clam shells. As the women felt that they should not have both been created as women, to make them happy, Raven threw limpet shells at one and turned her into a man, creating the Haida Gwaii people.[128] In New Zealand Māori culture, it is believed that the spirit, Hinemoana (the ocean) gave birth to shellfish in general and it seems Hinemoana's descendant Hunga-terewai produced various whelks and limpets.[129] In Cornish legend, Jan Tregeagle's punishment for making a pact with the Devil was the hopeless task of emptying the bottomless Dozmary Pool on Bodmin Moor with a leaking limpet shell.[130] Dozmary Pool is one site of many that is claimed to be the home of the Lady of the Lake, from whom the legendary King Arthur received the sword Excalibur. In Scottish Hebridean folklore, lamenting the lack of wisdom among women, the maiden queen of wisdom invited women to drink from the 'copan Moire' (Cup of Mary)—a blue-rayed limpet shell (*Patella pellucida*).[131]

Limpets have been connected to folk stories about changelings and witches. A changeling is a fairy child that has been left in place of a human child stolen by the fairies. In one story from Guernsey, a local limpet dish forced a changeling to reveal itself to its mother.[132] In the Scottish Hebrides, it is said that witches could sail in egg or limpet shells and turn into hares or crows. On the Hebridean Island of Harris, there is a sea stack called 'An t-ord-bairneach' (the limpet hammer). It is said that a witch, who was going to the shore for food or bait, threw it at some person, with or at whom she was enraged.[133] In another story from the Isle of Skye, Mary MacCulloch[134] writes of the widower of a witch and his daughter who also possessed the 'wicked arts'. On discovering that his daughter could sink ships by turning a live limpet upside down in a tub, he stabbed her and let her bleed to death in accordance with an old law about witches.

126 Byron, *The Narrative of the Honourable John Byron*.
127 Brian Wright, *Brigid: Goddess, Druidess and Saint* (New York: History Press, 2011).
128 Ella Elizabeth Clark, *Indian Legends of Canada* (New York: McClelland & Stewart, 2011).
129 Michael Shirres, 'Maori religion and mythology, being an account of the cosmogony, anthropogeny, religious beliefs and rites, magic and folk lore of the Maori folk of New Zealand. Part 2', *Journal of the Polynesian Society* 92, no. 1 (1983): 125–7.
130 Lovell, *The Edible Mollusks of Great Britain and Ireland.*
131 Alexander Carmichael, *Carmina Gadelica: Hymns and Incantations* (Edinburgh: The author, 1900).
132 Edgar MacCulloch, *Guernsey Folk Lore* (London: Elliot Stock, 1903).
133 Forbes, *Gaelic Names of Beasts*.
134 Mary Julia MacCulloch, 'Folk-Lore of the Isle of Skye', *Folklore* 33, no. 2 (1922): 201–14, doi.org/10.1080/0015587X.1922.9719240.

In modern times, limpets still feature in local traditions. For Christians, there is a strong tradition for eating limpets on Good Friday particularly around the United Kingdom, Ireland and the Azores.[135] In Ireland, collecting food from the shore rather than going to sea was linked to the belief that the sea craved dead bodies on Good Friday. People believed that everything they gathered from the shore on Good Friday would result in good health; there are historical accounts of droves of children and adults picking the shores clean at low tide. On the Isle of Man, 'flitters' (limpets) were harvested from the shore and cooked directly on the fire for breakfast. As no iron could be used (out of respect for the nails that were used to nail Jesus to the cross), rather than using a pot, the flitters were cooked in their shells in the embers of the fire.[136] A traditional dance associated with the custom appears to have experienced a revival in recent years. In Cornwall, England, pies made of limpets, raisins and sweet herbs are eaten during the Feast of St Constantine.[137]

## Knowledge and education

> So, how does the limpet do it? (return to its homescar)
> And why, says the anthropocentric Philistine at my elbow, should
> anybody care?
> Because.
>
> Martin Wells, *Civilization and the Limpet* (1998)[138]

Given their familiarity and abundance on the shore, limpets are a common feature of educational field trips and often feature in touch tanks in aquariums, and experiences with them can have lasting effects on education and literacy.[139] Aquariums are often the only experience that people from land-locked regions have with marine life and can provide an essential window to the marine world.[140] Rocky shores represent 'living laboratories' and are excellent, accessible locations for children and adults to experience marine life face to face.[141] Limpets can be the focus of many targeted field-based teaching exercises due to their responses to a range of factors affecting their distribution on the shore.[142]

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135 Margaret A. Courtney, 'Cornish feasts and "feasten" customs', *The Folk-Lore Journal* 4, no. 1 (1886): 221–49, doi.org/10.1080/17442524.1886.10602817; Mona Douglas, 'Manx Folk Dances: Their notation and revival', *Journal of the English Folk Dance and Song Society* 3, no. 2 (1937): 110–16; Allen, *Irish traditional cooking*; Neilson et al., 'Speaking of the sea in the Azores islands'.

136 Arthur William Moore, 'Customs and Superstitions Connected with the Seasons', in *The Folk-Lore of the Isle of Man: Being an Account of its Myths, Legends, Superstitions, Customs, & Proverbs* (Douglas, Man: Brown, 1891).

137 Courtney, 'Cornish feasts and "feasten" customs'.

138 Martin John Wells, *Civilization and the Limpet* (Reading, MA, and Oxford: Perseus, 1998).

139 Graham W. Scott and Margaret Boyd, 'A potential value of familiarity and experience: Can informal fieldwork have a lasting impact upon literacy?', *Education 3-13* 42, no. 5 (2014): 517–27, doi.org/10.1080/03004279.2012.731418.

140 Leighton R. Taylor, *Aquariums: Windows to Nature* (New York: Macmillan General Reference, 1993).

141 Allison Whitmer, 'Education and outreach', in *Encyclopedia of Tidepools and Rocky Shores*, ed. Gaines and Denny.

142 Stephen J. Hawkins and Hugh D. Jones, *Marine Field Course Guide*, vol. 1: *Rocky Shores*.

There are increasing numbers of co-ordinated educational and citizen science programs emerging. For instance, on the west coast of the United States, the LimPETS project[143] is an environmental monitoring and education program for students, educators and volunteer groups throughout California. Similarly, in Europe, the Shore Thing,[144] Capturing our Coast[145] and Coastwatch Europe[146] projects have all trained and engaged thousands of members of the public to gather data on rocky shore species (including limpets) in the United Kingdom and Ireland.

Limpets have long been the focus of scientific research and the findings of this research have been the subject of many subject-specific reviews. I do not cover this here, but, briefly, some major reviews entail the general biology of limpets,[147] evolution and adaptation,[148] phylogeny, systematics, evolution,[149] phylogeography,[150] biomedical review of KLH,[151] limpets as bioindicators of environmental quality,[152] and conservation.[153] Research describing how DNA metabarcoding of macroalgal seed banks on the shell surface of the limpet *Niveotectura pallida,* Gould 1859, in Japan has potential implications for the restoration of macroalgal beds in areas where they have become depleted due to overgrazing by exploding urchin populations.[154]

143 The Limpets Project. Long-term Monitoring Program and Experiential Training for Students, limpets.org, accessed 14 August 2020.

144 The Shore Thing Project, www.mba.ac.uk/shore_thing, accessed 14 August 2020.

145 The Capturing our Coast Project, www.capturingourcoast.co.uk, 14 August 2020.

146 The Coast Watch Europe Project, coastwatch.org/europe, accessed 14 August 2020.

147 George M. Branch, 'The biology of limpets: Physical factors, energy flow, and ecological interactions', *Oceanography and Marine Biology: An Annual Review* 19 (1981): 235–379; Alan N. Hodgson, 'The biology of siphonariid limpets (Gastropoda: Pulmonata)', *Oceanography and Marine Biology: An Annual Review* 37 (2002): 253–322.

148 George M. Branch, 'Limpets: evolution and adaptation', in *The Mollusca*, ed. E. R. Trueman and M. R. Clark (Orlando, FL: Academic Press, 1985).

149 S. A. Ridgway et al., 'A cladistic phylogeny of the family Patellidae (Mollusca: Gastropoda)', *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 353, no. 1375 (1998): 1645–71, doi.org/10.1098/rstb.1998.0316; Stephanie W. Aktipis et al., 'Another step towards understanding the slit-limpets (Fissurellidae, Fissurelloidea, Vetigastropoda, Gastropoda): A combined five-gene molecular phylogeny', *Zoologica Scripta* 40, no. 3 (2011): 238–59, doi.org/10.1111/j.1463-6409.2010.00468.x; Tomoyuki Nakano and Takenori Sasaki, 'Recent advances in molecular phylogeny, systematics and evolution of patellogastropod limpets', *Journal of Molluscan Studies* 77, no. 3 (2011): 203–17, doi.org/10.1093/mollus/eyr016.

150 Tomoyuki Nakano and Tomowo Ozawa, 'Worldwide phylogeography of limpets of the order Patellogastropoda: Molecular, morphological and palaeontological evidence', *Journal of Molluscan Studies* 73, no. 1 (2007): 79–99, doi.org/10.1093/mollus/eym001.

151 J. Robin Harris and Jürgen Markl, 'Keyhole limpet hemocyanin (KLH): A biomedical review' *Micron* 30, no. 6 (1999): 597–623, doi.org/10.1016/S0968-4328(99)00036-0.

152 Pablo Reguera et al., 'A review of the empirical literature on the use of limpets *Patella* spp. (Mollusca: Gastropoda) as bioindicators of environmental quality', *Ecotoxicology and Environmental Safety* 148 (2018): 593–600, doi.org/10.1016/j.ecoenv.2017.11.004.

153 Espinosa and Rivera-Ingraham, 'Biological conservation of giant limpets'; Paulo Henriques et al., 'Patellid limpets: An overview of the biology and conservation of keystone species of the rocky shores', in *Organismal and Molecular Malacology*, ed. Sajal Ray (Rijeka, Croatia: InTech, 2017): 71–95.

154 Shingo Akita et al., 'DNA metabarcoding analysis of macroalgal seed banks on shell surface of the limpet *Niveotectura pallida*', *European Journal of Phycology* (2020): 1–11, doi.org/10.1080/09670262.2020.1750056.

## Recreation and tourism

> Buain nam bairnich, nam bairnich, nam bairnich
> (Harvest of the limpets, of the limpets, of the limpets)
>
> Runrig, *Rubh nan cudaigean*[155]

**Figure 7: Limpet shell exhibit at the Princess Maha Chakri Sirindhorn Natural History Museum, Prince Songkla University, Hat Yai, Thailand. All shells in this collection were collected in Thailand by a shell trader and donated to the university.**

Source: Louise Firth.

For many children, their first experiences of the marine environment and inspiration to study conservation or biology is through rockpooling. Rockpooling, snorkelling, baiting and shelling are important recreational activities, some locations attracting tourists and, occasionally, illegal harvesters.[156] Shell collecting is such an important pastime in Florida that the popular shelling islands of Sanibel and Captiva have shelling behaviours associated with them—the 'Sanibel stoop' and the 'Captiva crouch'. Private limpet collections can develop into educational resources through their inclusion in education centres, schools, university collections and formal display cabinets (Figure 7). Some locations, such as South Africa, attract limpet enthusiasts for tourism (including myself) due to the exceptionally high diversity, large sizes and interesting behaviours exhibited by species there.[157]

## Ecosystem disservices

> [N]ibbling away at the soft rocks round our shores year by year, undermining Britain's chalk cliffs and sea defences and whittling away the coastline.
>
> Paul Brown, 'Limpets threaten coast' (2000)[158]

155 Runrig, *Rubh nan cudaigean*: www.songlyrics.com/runrig/rubh-nan-cudaigean-lyrics/, accessed 15 November 2021.

156 Ricardo S. Santos et al., 'Background document for Azorean limpet *Patella aspera*', *OSPAR Commission-Biodiversity Series* (London, 2010), www.ospar.org/documents?d=7230, accessed 23 August 2020.

157 For review, see George M. Branch, 'The biology of limpets: Physical factors, energy flow, and ecological interactions', *Oceanography and Marine Biology: An Annual Review* 19 (1981): 235–379.

158 Paul Brown, 'Limpets threaten coast', *The Guardian*, 8 January 2000, www.theguardian.com/uk/2000/jan/08/paulbrown, accessed 9 June 2020.

I have dealt with the various provisioning and cultural services that limpets provide to humans in depth in the above sections. We are becoming increasingly aware of ecosystem disservices, which are classed as the functions or properties of species that cause effects that are perceived as harmful, unpleasant or unwanted. Here, I highlight some of the documented ecosystem disservices that are associated with limpets.

Limpets are the champion grazers of the rocky intertidal zone. They are known to graze on bacteria,[159] diatoms (single-celled algae) and algal spores in biofilms that coat rocky substrata,[160] in addition to both attached[161] and drifting macroalgae.[162] Their grazing activity has been widely shown to have an important structuring function on rocky shores.[163] In locations that are characterised by soft rock, the physical scraping of the ribbon-like radula (feeding structure) during feeding can erode the underlying rock.[164] Homing individuals that develop 'homescars' can form depressions in the rock (up to 10 mm)[165] through a combination of physical (from the grinding of their shells against the rock) and chemical erosion (through the mucus they produce) whilst stationary (Figure 8).[166] Claire Andrews and Rendel Williams[167] experimentally investigated the erosion of chalk platforms in south-east England and estimated that, on average, limpets were responsible for approximately 12 per cent of the erosion, and in areas of maximum densities, up to 35 per cent

159 Paolo Della Santina et al., 'Food availability and diet composition of three coexisting Mediterranean limpets (*Patella* spp.)', *Marine Biology* 116, no. 1 (1993): 87–95, doi.org/10.1007/BF00350735.

160 Stephen J. Hawkins et al., 'A comparison of feeding mechanisms in microphagous, herbivorous, intertidal, prosobranchs in relation to resource partitioning', *Journal of Molluscan Studies* 55, no. 2 (1989): 151–65, doi.org/10.1093/mollus/55.2.151; Richard C. Thompson et al., 'Physical stress and biological control regulate the producer–consumer balance in intertidal biofilms', *Ecology* 85, no. 5 (2004): 1372–82, doi.org/10.1890/03-0279.

161 Robert G. Creese and Antony J. Underwood, 'Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding', *Oecologia* 53, no. 3 (1982): 337–46, doi.org/10.1007/BF00389010; Gillian M. Notman et al., 'Macroalgae contribute to the diet of *Patella vulgata* from contrasting conditions of latitude and wave exposure in the UK', *Marine Ecology Progress Series* 549 (2016): 113–23, doi.org/10.3354/meps11691.

162 Rodrigo H. Bustamante et al., 'Maintenance of an exceptional intertidal grazer biomass in South Africa: Subsidy by subtidal kelps', *Ecology* 76, no. 7 (1995): 2314–29, doi.org/10.2307/1941704.

163 Robert S. Steneck and L. Watling, 'Feeding capabilities and limitation of herbivorous molluscs: A functional group approach', *Marine Biology* 68, no. 3 (1982): 299–319, doi.org/10.1007/BF00409596; Stephen J. Hawkins and Richard G. Hartnoll, 'Grazing of intertidal algae by marine invertebrates', *Oceanography and Marine Biology: An Annual Review* 21 (1983): 195–282; Nessa E. O'Connor and Tasman P. Crowe, 'Biodiversity loss and ecosystem functioning: Distinguishing between number and identity of species', *Ecology* 86, no. 7 (2005): 1783–96, doi.org/10.1890/04-1172.

164 T. Spencer, 'Limestone coastal morphology: The biological contribution', *Progress in Physical Geography* 12, no. 1 (1988): 66–101, doi.org/10.1177/030913338801200103; Stephen Trudgill, 'Integrated geomorphological and ecological studies on rocky shores in southern Britain', *Field Studies* 7, no. 1 (1988): 239–79.

165 Claire Andrews and Rendel B. G. Williams, 'Limpet erosion of chalk shore platforms in southeast England', *Earth Surface Processes and Landforms: the Journal of the British Geomorphological Research Group* 25, no. 12 (2000): 1371–81.

166 J. Clarke Hawkshaw, 'On the action of limpets (*Patella*) in sinking pits in and abrading the surface of the chalk at Dover', *Zoological Journal of the Linnean Society* 14, no. 76 (1878): 406–11, doi.org/10.1111/j.1096-3642.1878.tb01543.x; David R. Lindberg and K. R. Dwyer, 'The topography, formation and role of the home depression of *Collisella scabra* (Gould)', *The Veliger* 25 (1983): 229–34.

167 Andrews and Williams, 'Limpet erosion of chalk shore platforms in southeast England'.

of the erosion. Whilst this is a completely natural process, this could be perceived as an ecosystem disservice, which is captured by the media quote at the beginning of this section.

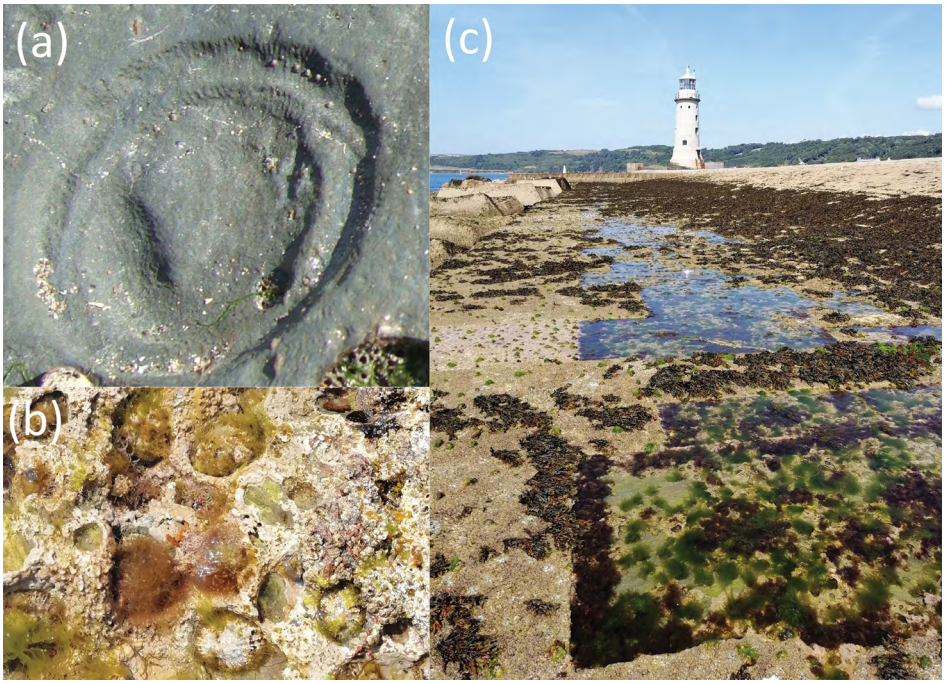


**Figure 8: Limpet homescars and coastal erosion.**

(a) Close up of deep-eroded home-scar on soft rock at Garretstown, Co. Cork, Ireland. Note the obvious radula (teeth) marks around the edges. (b) Live *Patella ulyssiponensis* on their homescars excavated into depressions on soft limestone blocks on Plymouth Breakwater, UK. (c) Wider perspective of Plymouth Breakwater. Constructed of both limestone and harder granite blocks, the limestone rocks are being eroded quicker (the rock pools) through a combination of physical erosion by waves and tides, but also through physical and chemical erosion caused by limpets. Each of the green tufts of algae in the pool in the foreground is attached to a limpet shell. There are no excavations of homescars evident on the granite rock.

Source: Louise Firth.

Whilst limpets are commonly eaten in many parts of the world, there may also be hazards with this practice. For instance, Martin mentions the risk of jaundice from eating too many limpets in June.[168] Despite there being no references to this since 1703, it has been stated by others that limpets may be unsuitable for people with delicate stomachs[169] and that the radula should be removed before consumption.[170]

168 Martin, *A Description of the Western Islands of Scotland*.

169 Jonathan Pereira, *A Treatise on Food and Diet* (London: Longman, Brown, Green and Longmans, 1843), 297, cited in Anne Hardy, 'Exorcizing Molly Malone: Typhoid and shellfish consumption in urban Britain 1860–1960', *History Workshop Journal* 55, no. 1 (2003): 72–90, doi.org/10.1093/hwj/55.1.72.

170 A. Solem, 'Snails and human welfare', *Health* 10 (1965): 31–7, cited in Karen Hardy, 'Shell as a raw material for tools and jewellery in Mesolithic Scotland', *Munibe Suplemento-Gehigarria* 31 (2010): 128–37.

Limpets can ingest harmful phycotoxins,[171] but to date, there is little evidence that the consumption of limpets causes Paralytic Shellfish Poisoning (PSP) in humans. In comparison to filter-feeding bivalves, which are well known for accumulating phycotoxins,[172] grazing limpets are less likely to consume them.

**Figure 9: Invasive slipper limpet (*Crepidula fornicata*) death assemblage on a Normandy beach, France.**

Source: Louise Firth.

The slipper limpet (*Crepidula fornicata*) is native to North America and Mexico but has successfully invaded many parts of Europe and the Mediterranean, where it is considered an invasive species due to its negative ecological impacts on sediment dynamics and competition with other species,[173] including commercial species.[174] The slipper limpet has negative socio-economic consequences on scallop

171 Hermann Sommer and K. F. Meyer, 'Paralytic shell-fish poisoning', *A.M.A. Archives of Pathology* 24 (1937): 560–98; Jonathan R. Deeds et al., 'Non-traditional vectors for paralytic shellfish poisoning', *Marine Drugs* 6, no. 2 (2008): 308–48, doi.org/10.3390/md6020308.

172 Sandra E. Shumway, 'Phycotoxin-related shellfish poisoning: Bivalve molluscs are not the only vectors', *Reviews in Fisheries Science* 3, no. 1 (1995): 1–31, doi.org/10.1080/10641269509388565

173 J. Grall and Jason M. Hall-Spencer, 'Problems facing maerl conservation in Brittany', *Aquatic Conservation—Marine and Freshwater Ecosystems* 13 (2003); Olivier le Pape et al., 'Effect of an invasive mollusc, American slipper limpet *Crepidula fornicata*, on habitat suitability for juvenile common sole *Solea solea* in the Bay of Biscay', *Marine Ecology Progress Series* 277 (2004): 107–15, doi.org/10.3354/meps277107.

174 Thieltges, 'Impact of an invader'.

and oyster farming[175] and areas with very high numbers have been deemed unfit for commercial fisheries.[176] Furthermore, high infestations by *C. fornicata* on infrastructure associated with the culture of molluscs make expensive cleaning operations necessary,[177] and their shells can dominate beaches, potentially making them less desirable to walk or lie on (Figure 9).

## Conservation

> The limpet … does not seem to have much to fear from active enemies … while man is, in some districts, a serious enemy.
>
> James Davis and Herbert Fleure, *Patella* (1903)[178]

In the above sections, I have shown how limpets have faced myriad anthropogenic threats that differ both spatially and temporally. In some regions they are seriously threatened. An historical perspective is essential for guiding future conservation goals. Shifting baseline syndrome[179] refers to changing human perceptions of biological systems due to lack of knowledge or loss of experience about past conditions. It is a key issue for the conservation of all habitats and species, including limpets. Without knowledge of past limpet population states and trends or an appreciation of their importance in providing provisioning and cultural services, shifting baseline syndrome could influence the validity of local ecological knowledge, monitoring, conservation and education.[180]

175 Michel Blanchard, 'Spread of the slipper limpet *Crepidula fornicata*'.

176 Gérard Thouzeau et al., 'Rôle des interactions biotiques sur le devenir du pré-recrutement et la croissance de *Pecten maximus* (L.) en Rade de Brest', *Comptes Rendus de l'Académie des Sciences-Series III—Sciences de la Vie* 323, no. 9 (2000): 815–25, doi.org/10.1016/S0764-4469(00)01232-4; Gérard Thouzeau et al., 'Impact des polluants d'origine anthropique sur les organismes benthiques marins: Notions d'indicateurs biologiques de perturbation et de réseaux de surveillance', in *Zones côtières et questions d'environnement: Réflexions méthodologiques* (Paris: Institut de France, Académie des Sciences, 2003), 177–214; Marjolaine Frésard and Jean Boncoeur, 'Costs and benefits of stock enhancement and biological invasion control: The case of the Bay of Brest scallop fishery', *Aquatic Living Resources* 19, no. 3 (2006): 299–305, doi.org/10.1051/alr:2006031.

177 Blanchard, Michel, 'Spread of the slipper limpet *Crepidula fornicata*'.

178 James Richard Ainsworth Davis and Herbert John Fleure, *Patella: The Common Limpet* (London: Williams & Norgate, 1903).

179 Daniel Pauly, 'Anecdotes and the shifting baseline syndrome of fisheries', *Trends in Ecology & Evolution* 10, no. 10 (1995): 430, doi.org/10.1016/S0169-5347(00)89171-5; Jeremy B. C. Jackson et al., 'Historical overfishing and the recent collapse of coastal ecosystems', *Science* 293, no. 5530 (2001): 629–37, doi.org/10.1126/science.1059199.

180 Sarah K. Papworth et al., 'Evidence for shifting baseline syndrome in conservation', *Conservation Letters* 2, no. 2 (2009): 93–100, doi.org/10.1111/j.1755-263X.2009.00049.x.

Due to the availability of historical data,[181] at least two species of limpet are officially listed as extinct on the International Union for Conservation of Nature (IUCN) Red List:[182] one due to habitat loss (*Lottia alveus* Conrad 1831),[183] the other to coastal development (*Lottia edmitchelli* Lipps 1963).[184] Two other species with very narrow niches (*Siphonaria compressa* Allanson 1958, which lives on seagrass in South African lagoons, and *Ancylastrum cumingianus* Bourguignat 1853, which lives in Tasmanian freshwater lakes) are currently listed as critically endangered. Whilst neither *Patella ferruginea* nor *Scutellastra mexicana* (rocky shore species that occur in the Mediterranean and the eastern Pacific, respectively) are listed, it is argued by some that they are on the brink of extinction, primarily due to over-exploitation.[185]

Many other species that have been subjected to long-term sustained harvesting and exploitation have undergone population depletions and size shifts towards smaller individuals. Population depletion is particularly evident in larger species.[186] As the largest individuals tend to be harvested first, there is both historical and modern evidence for size reductions over time.[187] Occasionally, there are sufficient data available to provide evidence of recovery following periods of reduced harvesting.[188]

181 Timothy A. Conrad, 'Description of fifteen new species of recent, and three of fossil shells, chiefly from the coast of the United States', *Journal of the Academy of Natural Sciences of Philadelphia* 6, no. 2 (1831): 256–68; David R. Lindberg, 'A recent specimen of *Collisella edmitchelli* from San Pedro, California (Mollusca: Acmaeidae)', *Bulletin of the Southern California Academy of Sciences* 83, no. 3 (1984): 148–51.

182 P. Bouchet, *Lottia alveus*. The IUCN Red List of Threatened Species 1996: e.T12382A3339013, doi.org/10.2305/IUCN.UK.1996.RLTS.T12382A3339013.en; P. Bouchet, *Collisella edmitchelli*. The IUCN Red List of Threatened Species 1996: e.T5119A11116006, doi.org/10.2305/IUCN.UK.1996.RLTS.T5119A11116006.en.

183 James T. Carlton et al., 'The first historical extinction of a marine invertebrate in an ocean basin: The demise of the eelgrass limpet *Lottia alveus*', *The Biological Bulletin* 180, no. 1 (1991): 72–80, doi.org/10.2307/1542430.

184 Callum M. Roberts and Julie P. Hawkins, 'Extinction risk in the sea', *Trends in Ecology & Evolution* 14, no. 6 (1999): 241–6, doi.org/10.1016/S0169-5347(98)01584-5.

185 Free Espinosa et al., 'Updated global distribution of the threatened marine limpet *Patella ferruginea* (Gastropoda: Patellidae): An example of biodiversity loss in the Mediterranean', *Oryx* 48, no. 2 (2014): 266–75, doi.org/10.1017/S0030605312000580; José Luis Carballo et al., 'Decimation of a population of the endangered species *Scutellastra mexicana*'.

186 Espinosa and Rivera-Ingraham, 'Biological conservation of giant limpets'.

187 George M. Branch, 'Notes on the ecology of *Patella concolor* and *Cellana capensis*, and the effects of human consumption on limpet populations', *African Zoology* 10, no. 1 (1975): 75–85; Pombo and Escofet, 'Effect of exploitation on the limpet *Lottia gigantea*'; Jerardino, Antonieta, 'Large shell middens in Lamberts Bay, South Africa: A case of hunter–gatherer resource intensification', *Journal of Archaeological Science* 37, no. 9 (2010): 2291–302, doi.org/10.1016/j.jas.2010.04.002; Jon M. Erlandson et al., '10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California', *Journal of Archaeological Science* 38, no. 5 (2011): 1127–34, doi.org/10.1016/j.jas.2010.12.009; Carolynn M. Harris et al., 'Analysis of the size, shape, and modeled age of common limpets'.

188 Judith C. Sealy et al., 'Isotope assessment and the seasonal-mobility hypothesis in the Southwestern Cape of South Africa' [and comments and replies], *Current Anthropology* 27, no. 2 (1986): 135–50, doi.org/10.1086/203404; Mark D. McCoy, 'Hawaiian limpet harvesting in historical perspective: A review of modern and archaeological data on *Cellana* spp. from the Kalaupapa Peninsula, Moloka'i Island', *Pacific Science* 62, no. 1 (2008): 21–38, doi.org/10.2984/1534-6188(2008)62[21:HLHIHP]2.0.CO;2.

The loss of larger and older individuals has cascading effects on populations, including changes in life-history parameters, demographics, reproductive success and ecological interactions.[189] For instance, in protandrous hermaphrodite species that begin as male and switch to female, the exploitation of larger individuals can lead to earlier sex change[190] and altered sex ratios, which can contribute to reduced reproductive success[191] and even the eventual collapse of the exploited populations.[192] Furthermore, the removal of grazing limpets facilitates algal growth,[193] leading to further cascading ecosystem effects.[194]

Regional comparisons between the South African east and west coasts provide a useful recent example of the cascading effects of human over-exploitation, which is linked to urbanisation and national policy on the movement of people. W. R. Siegfried et al.[195] describe how a modified form of the hunter-gatherer lifestyle

189 Phillip B. Fenberg and Kaustuv Roy, 'Ecological and evolutionary consequences of size-selective harvesting: How much do we know?', *Molecular Ecology* 17, no. 1 (2008): 209–20, doi.org/10.1111/j.1365-294X.2007.03522.x; reviewed in Henriques et al., 'Patellid limpets'.

190 Carla D. G. Borges et al., 'The influence of simulated exploitation on *Patella vulgata* populations: Protandric sex change is size-dependent', *Ecology and Evolution* 6, no. 2 (2016): 514–31, doi.org/10.1002/ece3.1872; Gustavo M. Martins et al., 'Exploitation promotes earlier sex change in a protandrous patellid limpet, *Patella aspera* Röding, 1798', *Ecology and Evolution* 7, no. 10 (2017): 3616–22, doi.org/10.1002/ece3.2925.

191 Free Espinosa et al., 'Aspects of reproduction and their implications for the conservation of the endangered limpet, *Patella ferruginea*', *Invertebrate Reproduction & Development* 49, no. 1–2 (2006): 85–92, doi.org/10.1080/07924259.2006.9652197; Gustavo M. Martins et al., 'Rocky intertidal community structure in oceanic islands: Scales of spatial variability', *Marine Ecology Progress Series* 356 (2008): 15–24, doi.org/10.3354/meps07247.

192 J. Núnez et al., 'Present distribution of the populations of *Patella candei* D'Orbigny, 1840 (Mollusca: Gastropoda) in the Canary Islands. A species in danger of extinction', *Boletin-Instituto Español de Oceanografia* 19, no. 1/4 (2003): 371; Jose M. Guerra-García et al., 'Assessing habitat use of the endangered marine mollusc *Patella ferruginea* (Gastropoda, Patellidae) in northern Africa: Preliminary results and implications for conservation', *Biological Conservation* 116, no. 3 (2004): 319–26, doi.org/10.1016/S0006-3207(03)00201-5; Free Espinosa et al., 'Effect of human pressure on population size structures of the endangered ferruginean limpet: Toward future management measures', *Journal of Coastal Research* 25, no. 4 (254) (2009): 857–63, doi.org/10.2112/08-1005.1.

193 Sheila M. Lodge, 'Algal growth in the absence *of Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man', *Proceedings and Transactions of the Liverpool Biological Society* 56 (1948): 78–83; A. H. Dye, 'The effects of excluding limpets from the lower balanoid zone of rocky shores in Transkei, South Africa', *South African Journal of Marine Science* 15, no. 1 (1995): 9–15, doi.org/10.2989/025776195784156313; Diana Boaventura et al., 'The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain', *Journal of Experimental Marine Biology and Ecology* 267, no. 2 (2002): 185–206, doi.org/10.1016/S0022-0981(01)00372-0; Andrew J. Davies et al., 'Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales', *Marine Ecology Progress Series* 339 (2007): 131–41, doi.org/10.3354/meps339131; Pippa Moore et al., 'Effects of grazer identity on the probability of escapes by a canopy-forming macroalga', *Journal of Experimental Marine Biology and Ecology* 344, no. 2 (2007): 170–80, doi.org/10.1016/j.jembe.2006.12.012; Ana Chaverra et al., 'Removal of intertidal grazers by human harvesting leads to alteration of species interactions, community structure and resilience to climate change', *Marine Environmental Research*, 146 (2019): 57-65, doi.org/10.1016/j.marenvres.2019.03.003.

194 David R. Lindberg et al., 'Human influences on trophic cascades along rocky shores', *Ecological Applications* 8, no. 3 (1998): 880–90, doi.org/10.1890/1051-0761(1998)008[0880:HIOTCA]2.0.CO;2; Stuart R. Jenkins et al., 'Regional scale differences in the determinism of grazing effects in the rocky intertidal', *Marine Ecology Progress Series* 287 (2005): 77–86, doi.org/10.3354/meps287077; Ross A. Coleman et al., 'A continental scale evaluation of the role of limpet grazing on rocky shores', *Oecologia* 147, no. 3 (2006): 556–64.

195 George Branch and Rodrigo Bustamante (unpublished), cited in W. R. Siegfried et al., 'The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa—an overview', in *Rocky Shores*, 1–15.

persisted on the east coast but not on the west coast. The abolition of apartheid laws led to the relocation of people from the 'homelands' to cities, resulting in dramatic increases in urban populations (e.g. Cape Town grew from 900,000 in 1980 to 2.5 million in 1992). This led to an intensification of subsistence exploitation of the shore in the Western Cape and shores that were previously grazer-dominated became algal-dominated due to the exploitation of limpets.

The over-exploitation of limpets has prompted the implementation of management strategies to protect exploited populations and mitigate human impacts in many regions.[196] The establishment of species-specific total allowable catches, minimum capture sizes, closed seasons and closed areas have been the most common measures that are currently in place, with varying levels of success. Gustavo Martins et al.[197] concluded that the establishment of Limpet Protection Zones (LPZs), seasonal closures and minimum catch sizes in the Azores are insufficient for the effective management of *Patella candei* d'Orbigny, 1840, and *P. aspera*. Hugo Diogo et al.[198] confirmed high levels of non-compliance with LPZs and that seasonal closures were largely ignored, highlighting the fact that new regulations will need a strong enforcement policy. For instance, *Patella ferruginea* is protected under Spanish law (Natural Heritage and Biodiversity 42/2007), and, in 2008, it was the first marine animal to have a species-specific conservation strategy. The illegal harvesting of *P. ferruginea* in Spain induces a harvesting ban and brings up to two years in prison. For those species heavily harvested as food resources, future research on rearing limpets in low trophic aquaculture systems would be a way to provide the needed biomass by diverting pressure from the intertidal zone. A lot could be learned from abalone aquaculture with regard to the needed adaptations.[199] Alternatively, another approach would be to give local communities some responsibilities for the study and management of limpet stocks.[200]

In the United Kingdom and Ireland, harvesting is not generally considered to be a major threat to limpets today. As mentioned in the opening of this review, kicking limpets off the rocks is a popular activity. The establishment of LPZs, combined with volunteer patrols and a public education campaign to prevent this activity,

196 For reviews, see Espinosa and Rivera-Ingraham, 'Biological conservation of giant limpets'; Henriques et al., 'Patellid limpets'.

197 Gustavo M. Martins et al., 'Illegal harvesting affects the success of fishing closure areas', *Journal of the Marine Biological Association of the United Kingdom* 91, no. 4 (2011): 929–37, doi.org/10.1017/S0025315410001189.

198 Diogo et al., 'Catch me if you can'.

199 For a comprehensive review of feasibility options, see Mau and Jha, 'Aquaculture of two commercially important molluscs'.

200 Patricio A. Bernal et al., 'New regulations in Chilean fisheries and aquaculture: ITQ's and territorial users rights', *Ocean & Coastal Management* 42, no. 2–4 (1999): 119–42, doi.org/10.1016/S0964-5691(98)00049-0; J. Carlos Castilla and S. Gelcich, 'Management of the loco (*Concholepas concholepas*) as a driver for self-governance of small-scale benthic fisheries in Chile', *FAO Fisheries Technical Paper* 504 (2008): 441; Elinor Ostrom, 'The challenge of common-pool resources', *Environment: Science and Policy for Sustainable Development* 50, no. 4 (2008): 8–21, doi.org/10.3200/ENVT.50.4.8-21, reviewed in Carla Debora Borges, 'The influence of environment and exploitation on sex change limpets' (PhD diss., University of Southampton, 2013), 186–8.

alongside bait collecting, was found to be successful at Kimmeridge Bay on the south coast of England.[201] Given that pressures vary regionally, specific policies and actions need to be developed at a regional level, but where funding allows, the employment of new technologies in auxiliary surveillance methods, such as drones and monitoring cameras, could improve the applicability of management measures for resource protection and sustainability.[202]

With urbanisation and artificialisation of the global coastline, artificial substrata such as sea walls and coastal defence structures are proliferating.[203] In some regions, these artificial substrata can be used for the conservation of over-exploited limpets. For instance, both *P. ferruginea* and the saffian limpet (*Cymbula safiana* Lamarck 1819) settle in high densities on artificial substrata,[204] which has led to the concept of artificial environments being designated 'artificial marine microreserves'.[205] As some harbours are smaller and easier to police, they could potentially serve as important refuges from illegal harvesting and function as networks.[206] Furthermore, artificial substrata can be manipulated to promote certain species.[207] In the Azores, pits drilled into vertical sea walls resulted in enhanced recruitment and survival of the over-exploited *Patella candei* over both short (four-month) and long (seven-year) timescales.[208]

201 Eunice H. Pinn and Michelle Rodgers, 'The influence of visitors on intertidal biodiversity', *Journal of the Marine Biological Association of the United Kingdom* 85, no. 2 (2005): 263–8, doi.org/10.1017/S0025315405011148h.

202 Diogo et al., 'Catch me if you can'.

203 Louise B. Firth et al., 'Ocean sprawl: Challenges and opportunities for biodiversity management in a changing world', *Oceanography and Marine Biology: an Annual Review*, 54 (2016): 189–262; Su Yin Chee et al., 'Land reclamation and artificial islands: Walking the tightrope between development and conservation', *Global Ecology and Conservation*, 12 (2017): 80-95, doi.org/10.1016/j.gecco.2017.08.005; Louise B. Firth et al., 'Greening of grey infrastructure should not be used as a Trojan horse to facilitate coastal development', *Journal of Applied Ecology* (2020), doi.org/10.1111/1365-2664.13683.

204 Rivera-Ingraham et al., 'Conservation status and updated census of *Patella ferruginea*; Georgina Alexandra Rivera-Ingraham et al., 'Present status of the endangered limpet *Cymbula nigra* (Gastropoda, Patellidae) in Ceuta: How do substrate heterogeneity and area accessibility affect population structure?', *Animal Biodiversity and Conservation* 34, no. 2 (2011): 319–30, www.raco.cat/index.php/ABC/article/view/248924.

205 José C. García-Gómez et al., 'Marine artificial micro-reserves: A possibility for the conservation of endangered species living on artificial substrata', *Marine Ecology* 32, no. 1 (2011): 6–14, doi.org/10.1111/j.1439-0485.2010.00409.x.

206 José C. García-Gómez et al., 'Artificial Marine Micro-Reserves Networks (AMMRNs): An innovative approach to conserve marine littoral biodiversity and protect endangered species', *Marine Ecology* 36, no. 3 (2015): 259–77, doi.org/10.1111/maec.12167.

207 For a comprehensive review, see Kathryn A. O'Shaughnessy et al., 'Design catalogue for eco-engineering of coastal artificial structures: A multifunctional approach for stakeholders and end-users', *Urban Ecosystems* 23, no. 2 (2020): 431–43, doi.org/10.1007/s11252-019-00924-z.

208 Gustavo M. Martins et al., 'Enhancing stocks of the exploited limpet *Patella candei* d'Orbigny via modifications in coastal engineering', *Biological Conservation* 143, no. 1 (2010): 203–11, doi.org/10.1016/j.biocon.2009.10.004; Gustavo M. Martins et al., 'Long-term modifications of coastal defences enhance marine biodiversity', *Environmental Conservation* 43 (2016), 109–16.

Limpets are vulnerable to a wide range of other anthropogenic threats. I only briefly cover these here as it is beyond the scope of this review. Many species are sensitive to water pollution,[209] which is known to have negative effects on heart rate,[210] reproduction,[211] pedal mucus production,[212] tenacity[213] and survival,[214] but positive impacts on growth.[215] Whilst limpets have been shown to ingest fewer microplastics compared to other species,[216] microplastics are known to have negative effects on their growth and development.[217] Climate change in its various forms (e.g. rising temperatures, extreme weather, increased storminess) has myriad individual and synergistic impacts on limpets,[218] ranging from proximate impacts on physiology,[219]

209 Free Espinosa, José M. Guerra-García, and José C. García-Gómez, 'Sewage pollution and extinction risk: An endangered limpet as a bioindicator?', *Biodiversity and Conservation* 16, no. 2 (2007): 377–97, doi.org/10.1007/s10531-005-3014-3.

210 Guido Chelazzi et al., 'Different cardiac response to copper in limpets from metal polluted and clean shores of Hong Kong', *Marine Environmental Research* 58, no. 1 (2004): 83–93, doi.org/10.1016/j.marenvres.2004.01.001.

211 J. H. Liu and B. Morton, 'The impacts of pollution on the growth, reproduction and population structure of Hong Kong limpets', *Marine Pollution Bulletin* 36, no. 2 (1998): 152–58 doi.org/10.1016/S0025-326X(97)00175-6.

212 Mark S. Davies, 'Heavy metals in seawater: Effects on limpet pedal mucus production', *Water Research* 26, no. 12 (1992): 1691–3, doi.org/10.1016/0043-1354(92)90169-5.

213 Stephen R. Cartwright et al., 'Ecologically relevant effects of pulse application of copper on the limpet *Patella vulgata*', *Marine Ecology Progress Series* 326 (2006): 187–94, doi.org/10.3354/meps326187; Mark Anthony Browne et al., 'Organophosphorous biocides reduce tenacity and cellular viability but not esterase activities in a non-target prosobranch (limpet)', *Environmental Pollution* 203 (2015): 208–13, doi.org/10.1016/j.envpol.2015.04.001.

214 Stephen J. Hawkins et al., 'From the *Torrey Canyon* to today: A 50-year retrospective of recovery from the oil spill and interaction with climate-driven fluctuations on Cornish rocky shores', *International Oil Spill Conference Proceedings*, 1 (2017): 74–103, doi.org/10.7901/2169-3358-2017.1.74.

215 Liu and Morton, 'The impacts of pollution on the growth, reproduction and population structure of Hong Kong limpets'; Alejandro Tablado et al., 'Growth of the pulmonate limpet *Siphonaria lessoni* (Blainville) in a rocky intertidal area affected by sewage pollution', *Journal of Experimental Marine Biology and Ecology* 175, no. 2 (1994): 211–26, doi.org/10.1016/0022-0981(94)90027-2.

216 Lars Gutow et al., 'Gastropod pedal mucus retains microplastics and promotes the uptake of particles by marine periwinkles', *Environmental Pollution* 246 (2019): 688–96, doi.org/10.1016/j.envpol.2018.12.097.

217 Hau Kwan Abby Lo and Kit Yu Karen Chan, 'Negative effects of microplastic exposure on growth and development of *Crepidula onyx*', *Environmental Pollution* 233 (2018): 588–95, doi.org/10.1016/j.envpol.2017.10.095.

218 For reviews, see Brian Helmuth et al., 'Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change', *Annual Review of Ecology, Evolution, and Systematics* 37 (2006): 373–404, doi.org/10.1146/annurev.ecolsys.37.091305.110149; S. J. Hawkins et al., 'Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores', *Marine Ecology Progress Series* 396 (2009): 245–59, doi.org/10.3354/meps08378.

219 Gray A. Williams et al., 'Come rain or shine: the combined effects of physical stresses on physiological and protein-level responses of an intertidal limpet in the monsoonal tropics', *Functional Ecology* 25, no. 1 (2011): 101–10, doi.org/10.1111/j.1365-2435.2010.01760.x; Ivana Prusina et al., 'Variations in physiological responses to thermal stress in congeneric limpets in the Mediterranean Sea', *Journal of Experimental Marine Biology and Ecology* 456 (2014): 34–40, doi.org/10.1016/j.jembe.2014.03.011.

morphology,[220] and phenology,[221] which affects behaviour,[222] biotic interactions[223] and survival,[224] to emergent impacts on vertical[225] and geographic distributions.[226]

Many species of limpet have been seriously impacted by over-exploitation, habitat alteration and other anthropogenic threats. It is imperative that management efforts are established and enforced, but coupled with this, promoting education and positive experiences will encourage better understanding and appreciation, not only of limpets but of the wider natural environment.[227] For instance, Susan Gubbay describes how children are encouraged to imagine what it is like to be an organism on the shore. She argues that children will be considerably less likely to kick limpets off rocks if they are asked to 'consider what it is like being a limpet'.[228] If bait collectors and illegal harvesters knew how important limpets were for the ecosystem, or indeed that some species can live for up to 35 years,[229] arguably, they may be less likely to illegally collect them from the shore. Where limpets are being collected for subsistence and bait, this requires a different approach and wider coordinated government support.[230]

220 Christopher D. G. Harley et al., 'Thermal stress and morphological adaptations in limpets', *Functional Ecology* (2009): 292–301.

221 Pippa J. Moore et al., 'Phenological changes in intertidal con-specific gastropods in response to climate warming', *Global Change Biology* 17, no. 2 (2011): 709–19, doi.org/10.1111/j.1365-2486.2010.02270.x.

222 Simon A. Morley et al., 'Limpet feeding rate and the consistency of physiological response to temperature', *Journal of Comparative Physiology B* 184, no. 5 (2014): 563–70, doi.org/10.1007/s00360-014-0814-3.

223 Pippa Moore et al., 'Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change', *Marine Ecology Progress Series* 334 (2007b): 11–19, doi.org/10.3354/meps334011; Louise B. Firth et al., 'Predicting impacts of climate-induced range expansion: an experimental framework and a test involving key grazers on temperate rocky shores', *Global Change Biology* 15, no. 6 (2009): 1413–22, doi.org/10.1111/j.1365-2486.2009.01863.x.

224 Louise B. Firth and Gray A. Williams, 'The influence of multiple environmental stressors on the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong', *Journal of Experimental Marine Biology and Ecology* 375, no. 1–2 (2009): 70–5, doi.org/10.1016/j.jembe.2009.05.011.

225 Yunwei Dong and George N. Somero, 'Temperature adaptation of cytosolic malate dehydrogenases of limpets (genus *Lottia*): Differences in stability and function due to minor changes in sequence correlate with biogeographic and vertical distributions', *Journal of Experimental Biology* 212, no. 2 (2009): 169–77, doi.org/10.1242/jeb.024505.

226 Lara L. Sousa et al., 'Fate of a climate-driven colonisation: Demography of newly established populations of the limpet *Patella rustica* Linnaeus, 1758, in northern Portugal', *Journal of Experimental Marine Biology and Ecology* 438 (2012): 68–75, doi.org/10.1016/j.jembe.2012.09.005; Michael T. Burrows et al., 'Global-scale species distributions predict temperature-related changes in species composition of rocky shore communities in Britain', *Global Change Biology* 26, no. 4 (2020): 2093–105, doi.org/10.1111/gcb.14968.

227 Masashi Soga and Kevin J. Gaston, 'Extinction of experience: the loss of human–nature interactions', *Frontiers in Ecology and the Environment* 14, no. 2 (2016): 94–101, doi.org/10.1002/fee.1225.

228 Susan Gubbay, 'Marine protected areas—past, present and future', in *Marine Protected Areas: Principles and Techniques for Management* (Dordrecht: Springer, 1995), 1–14.

229 Free Espinosa et al., 'Responses of the endangered limpet *Patella ferruginea* to reintroduction under different environmental conditions: survival, growth rates and life-history', *Italian Journal of Zoology* 75, no. 4 (2008): 371–84, doi.org/10.1080/11250000801887740.

230 Robert S. Pomeroy and Fikret Berkes, 'Two to tango: The role of government in fisheries co-management', *Marine Policy* 21, no. 5 (1997): 465–80, doi.org/10.1016/S0308-597X(97)00017-1; Juan C. Castilla and Miriam Fernandez, 'Small-scale benthic fisheries in Chile: On co-management and sustainable use of benthic invertebrates', *Ecological Applications* 8 (1998): S124-32, doi.org/10.1890/1051-0761(1998)8[S124:SBFICO]2.0.CO;2; Antony J. Underwood, 'Exploitation of species on the rocky coast of New South Wales (Australia) and options for its management', *Ocean & Coastal Management* 20, no. 1 (1993): 41–62, doi.org/10.1016/0964-5691(93)90012-N; Jean Harris et al., 'The Sokhulu subsistence mussel-harvesting project: Co-management in action', *Waves of change: Coastal and fisheries co-management in South Africa* (Lansdowne: University of Cape Town Press, 2003), 61–98.

# Concluding remarks

This comprehensive review rectifies the limpet's reputation as 'famine food' and attests to the important role that limpets played in past and present coastal cultural heritage and food culture globally. Limpets featured in the diets of early hominids and Neanderthals and undoubtedly contributed to the evolution of the large, complex, metabolically expensive brain characterised by modern *Homo sapiens.* They were often the dominant shellfish in the diet of early modern humans and played an important role in sustaining the poor during times of famine and destitution. In a cultural turnaround, they are considered a delicacy in many cultures and feature in middle-class foraging and survival activities. Limpets appear to have a special importance as bait in several parts of the world, with an entire culture and language having developed around the use of limpets for bait in Scotland. The shells have been exploited for a wide variety of uses, including as tools, currency, offerings, traditional medicine, jewellery and artworks. They have important spiritual and religious relevance, featuring in myriad traditions, superstitions and folklore. This review primarily focused on information that was available in online resources and through information provided through online communications with the global community. Future work would benefit from specifically targeting information from oral histories and discourses with a particular consideration of indigenous populations and languages other than English.

**Box 1: The tenacity of limpets.**

> Better not stick here all night like a limpet. This weather makes you dull.
>
> James Joyce, *Ulysses* (1922)[231]

Limpets are celebrated for their tenacity. Their ability to cling to rocks and other hard surfaces has made them synonymous with persistence and determination. This trait was recognised by Aristotle (350 BCE) who noted 'even the limpet releases its hold in order to search for food'.[232] Historically, this trait was attributed to God,[233] and whilst this trait is now known to have evolved, Charles Darwin observed that it is an instinct, not learned behaviour.[234] The word 'limpet' is thought to have origins relating to tenacity. The Old English term lempedu ('lamprey'), links to Late Latin lampetra ('lamprey'), whose further origin is unknown, but is traditionally thought to derive from lambō ('I lick') + petra ('rock'). In the northern Scottish isle of Stronsay, sailors whose boats never left port were ridiculed, suggesting that they 'stick to the pier like limpets'. In Scottish Gaelic, the idiom 'cho ceangailte is a tha bàirneach ris an lic', translates as 'stick like a limpet', is a figurative way of saying the more well-known phrase 'sticks like shit [apologies!] to a blanket'.

231 James Joyce, *Ulysses.* ed. Hans Walter Gabler (New York: Vintage, 1986).

232 Aristotle, *The History of Animals* (350 BC).

233 John Wesley, *A Survey of the Wisdom of God in the Creation: Or, A Compendium of Natural Philosophy*, vol. 1 (London: William Pine, 1770).

234 Charles R. Darwin, *Journal of Researches into the Natural History and Geology of the Various Countries Visited by H.M.S. Beagle etc.* (New York: Appleton, 1878).

Developed during the Second World War, the naval 'Limpet mine' was designed to be attached to the hulls of warships by divers ('frogmen'). The prototype was an English invention reportedly based on materials bought from the department store Woolworths (a large tin bowl, a condom, and a packet of aniseed balls), which dissolve in acid at just the right rate to set off a timed detonation.[235] 'Limpet ports' refer to the British colonial settlements of Australia—'clinging to the hull of the continent' like limpets to a rock.[236] Limpet tenacity is also acknowledged in the 'Cape Town Limpet'—a device that was designed to use suction to treat a crushed human chest;[237] 'The Limpet'—a remotely operated multi-sensing platform that can be attached to offshore platforms;[238] and adhesive products such as the 'Limpet vaccination dressing', 'Limpet clamps' and 'Limpet labels'.

The clamping behaviour of limpets can be harmful to other organisms, particularly other invertebrate predators such as starfish[239] and crabs.[240] There are several reports of limpets being responsible for causing the death of rats,[241] cats[242] and foxes[243] through trapping their tongues. Nathaniel Colgan tells of 'wild bornyacks' (limpets, *Patella ulyssiponensis*) trapping rats on Clare Island off the west coast of Ireland—as explained to him by an old islander:

> Of a soft evening them bornyacks do rise up and go travelling a bit over the rocks, and the rat'll come up and slip in her tongue to lick the meat, and the bornyack'll clap down its shell and catch her by the tongue. And I tell you the power of man couldn't loose the hold of the bornyack, and the rat is caught there till the tide comes up and drowns her. I seen them myself hanging there by the tongue and they dead.

Arthur Stelfox reported that 'according to Mr. [P.] Condron the dead cat was still held by the tongue when the tide again retreated'.[244] It has also been known for limpets to cause the death of birds[245] through clamping their shells down on their claws or feet.

235 Peter Marren and Richard Mabey, *Bugs Britannica* (London: Chatto & Windus, 2010).
236 Jim Allen, 'Port Essington—a successful limpet port?', *Australian Historical Studies* 15, no. 59 (1972): 341–60, doi.org/10.1080/10314617208595477; Geoffrey Blainey, *The Tyranny of Distance: How Distance Shaped Australia's History*, revised ed. (Sydney: Pan Macmillan, 2001).
237 T. Schrire, 'Control of the crushed chest: The use of the "Cape Town Limpet"', *Diseases of the Chest* 44, no. 2 (1963): 141–5, doi.org/10.1378/chest.44.2.141.
238 Mohammed E. Sayed et al., 'The limpet: A ROS-enabled multi-sensing platform for the ORCA hub', *Sensors* 18, no. 10 (2018): 3487, doi.org/10.3390/s18103487.
239 G. M. Branch, 'The responses of South African patellid limpets to invertebrate predators', *African Zoology* 13, no. 2 (1978): 221–32.
240 M. A. Aguilera et al., 'Similarity in predator-specific anti-predator behavior in ecologically distinct limpet species, *Scurria viridula* (Lottiidae) and Fissurella latimarginata (Fissurellidae)', *Marine Biology* 166, no. 4 (2019): 41.
241 Forbes, *Gaelic Names of Beasts*; Nathaniel Colgan, 'Part 4. Gaelic plant and animal names, and associated folk-lore', *Proceedings of the Royal Irish Academy. Section A: Mathematical and Physical Sciences* 31 (1911): 4.1–30.
242 A. W. Stelfox, 'The limpet as a cat-catcher', *The Irish Naturalists' Journal* (1935): 229–30.
243 C. McGinley, National Folklore Collection UCD Digitization Project. The Schools' Collection, vol. 1048 (1937), 54, www.duchas.ie/en/cbes/4428331/4396413/4481530, accessed 23 August 2020.
244 Stelfox, 'The limpet as a cat-catcher'.
245 Lovell, *The Edible Mollusks of Great Britain and Ireland*; Carmichael, *Carmina Gadelica*.

Limpet tenacity features in art and film and abounds in literature with myriad references in both poetry and prose. The illustration 'Blasting Limpets on the Barbary Coast' by William Heath Robinson (1906) is interpreted as a tribute to the tenacity of Mediterranean limpets.[246] The film *The Incredible Mr Limpet*, adapted from the book *Mr Limpet* by Theodore Pratt,[247] tells the story of Henry Limpet's determination to help the US Navy during the Second World War. Children's books such as *Sally and the Limpet*[248] and *Iki, the Littlest Opihi*[249] tell stories about limpets clinging to the rocks as a way of communicating the importance of determination and resolve. Authors such as Charles Dickens, James Joyce, Hans Christian Anderson and Robert Louis Stevenson,[250] amongst many others (too many to be named here), make specific references to limpets in their books. Below is a poem by William Wordsworth:

> At distance viewed, it seems to lie
> On its rough bed so carelessly,
> That 'twould an infant's hand obey,
> Stretched forth to seize it in his play,
> But let that infant's hand draw near,
> It shrinks with quick instinctive fear,
> And clings as close as though the stone,
> It rests upon, and it, were one;
> And should the strongest arm endeavour
> The Limpet from its rock to sever,
> 'Tis seen its loved support to clasp,
> With such tenacity of grasp,
> We wondered that such strength should dwell
> In such a small and simple shell.

246 Winston Frank Ponder et al., *Biology and Evolution of the Mollusca*, vol. 2 (Boca Raton, PL: CRC Press, 2020).
247 Theodore Pratt, *Mr Limpet* (New York: Alfred A. Knopf, 1942).
248 Simon James, *Sally and the Limpet* (New York: M. K. McElderry Books, 1991).
249 Tammy Yee, *Iki, The Littlest Opihi* (Waipahu, HI: Island Heritage, 1998).
250 Charles Dickens, *The Letters of Charles Dickens: 1857–1870*, vol. 2 (London: Macmillan, 1880); Michael Redgrave, *Fairy Tales of Hans Christian Andersen* (New York: Caedmon, 1958); Joyce, 'Ulysses. 1922'; Robert Louis Stevenson, *Kidnapped*.

## Box 2: Limpets and the Irish famines.

Seachain an teach an tábhairne no báirnigh is beatha duit
(Beware of the public house or limpets will be your life)

Bia rí isea dúilicíní ach bia tuathaigh isea báirnigh
(Mussels are the food of kings, limpets are the food of peasants)

Two old Irish proverbs

In the 1800s, Ireland was hit by a series of famines with drastic consequences for the population. Due to the failure of the potato crop, 'An Gorta Mór', or the Great Hunger (1845–49), was a period of mass starvation, disease and emigration when the population decreased from approximately 8.6 million to about 6.6 million.[251] In coastal areas, many people survived through harvesting shellfish and seaweed from the shore. Margaret Crawford reports that not only were 'beaches stripped of the tidal crop', but also 'so intense was the harvesting of limpets that rocks were picked clean'.[252] During this time, 'paupers' were the poor who were recipients of relief under the provisions of the Irish Poor Laws.[253] When the paupers were working in the Atlantic Hotel auxiliary workhouse at Spanish Point, County Clare, 'there was not a periwinkle or a limpet left in the strand but they picked'.[254] There are some reports that people living in coastal areas survived better than those inland due to access to coastal resources.[255] Whilst few data are available from this time, many oral histories captured what life was like and how people survived. For instance, Christine Kinealy describes a personal account of Condy Molloy, his wife and daughter having 'existed on 'barnaghs' (limpets) for the last fortnight, and are now scarcely able to move from consequent exhaustion'.[256] Another account describes how limpets were boiled, a little salt added, were put in bowls or mugs, and drunk and eaten with potatoes.[257] Prior to the nineteenth century, it was mainly the poor that gathered shellfish from the shore. Such fare was referred to as 'cnuasach mara' (sea pickings). This association was compounded by the famines of the 1800s. Accordingly, many people in Ireland today, associate limpets with destitution and starvation, often referring to them as 'bia bocht' (poor food) and 'famine food'.[258]

251 Cormac Ó Gráda and Kevin H. O'Rourke, 'Migration as disaster relief: Lessons from the Great Irish Famine', *European Review of Economic History* 1, no. 1 (1997): 3–25, doi.org/10.1017/S1361491697000026.
252 E. Margaret Crawford, 'Food and famine', in *The Great Irish Famine*, ed. Cathal Póirtéir (Dublin: Mercier, 1995), 60–73; Máirtín Mac Con Iomaire, 'The History of Seafood in Irish Cuisine and Culture', *History Studies* 5 (2004): 61–76, arrow.tudublin.ie/cgi/viewcontent.cgi?article=1002&context=tfschafart, accessed 3 September 2021.
253 Hugh Chisholm, 'Pauperism', *Encyclopædia Britannica*, 11th ed., vol. 20 (Cambridge: Cambridge University Press, 1911), 967.
254 M. Morrissey, National Folklore Collection UCD Digitization Project. The Schools' Collection, vol. 622 (1938): 290, www.duchas.ie/en/cbes/4922387/4876582, accessed 23 August 2020.
255 Tom Jones-Hughes, 'East Leinster in the mid-19th century', *Irish Geography* 3 (1965): 227–41.
256 Christine Kinealy et al., eds, *The History of the Irish Famine* (London: Routledge, 2018).
257 Cathal Póirtéir, *Famine Echoes–Folk Memories of the Great Irish Famine: An Oral History of Ireland's Greatest Tragedy* (Dublin: Gill & Macmillan, 1995).
258 Máirtín Mac Con Iomaire, 'The History of Seafood in Irish Cuisine and Culture'.

**Figure 10: 'Distress in the west of Ireland: Families collecting seaweed and limpets for food on Inisbofin Island', *The Illustrated London News* (1886).[259]**
Source: Alamy.

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259 'Distress in the west of Ireland: Families collecting seaweed and limpets for food on Inishboffin Island', *The Illustrated London News* (1886), www.iln.org.uk/iln_years/year/1886.htm, accessed 23 August 2020.

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