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PEDUNCULATE CIRRIPEDES OF THE GENUS *POLLICIPES*: 25 YEARS AFTER MARGARET BARNES' REVIEW

TERESA CRUZ[1,2], DAVID JACINTO[1], JOANA N. FERNANDES[1],
MARIA INÊS SEABRA[1], ROBERT J. VAN SYOC[3], ANNE MARIE POWER[4],
GONZALO MACHO[5], ALINA SOUSA[1], JOÃO J. CASTRO[1,2], & STEPHEN J. HAWKINS[6,7,8]

[1]*MARE - Marine and Environmental Sciences Centre & ARNET - Aquatic Research Network, Laboratório de Ciências do Mar, Universidade de Évora, Sines, Portugal*
[2]*Departamento de Biologia, Escola de Ciências e Tecnologia, Universidade de Évora, Portugal*
[3]*Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, CA, USA*
[4]*Ryan Institute, School of Natural Sciences, National University of Ireland Galway, Galway, Ireland*
[5]*Fisheries Consultant, Fisherman's Cove, Mahé, Seychelles*
[6]*School of Ocean and Earth Science, National Oceanography Centre Southampton, Waterfront Campus, University of Southampton, Southampton SO14 3ZH UK*
[7]*Marine Biological Association of the UK, The Laboratory, Citadel Hill, Plymouth, PL 1 2PB UK*
[8]*School of Biological and Marine Sciences, University of Plymouth, Drakes Circus, Plymouth, PL4 8AA UK*

Abstract Twenty-five years ago, Margaret Barnes reviewed the genus *Pollicipes* published in *Oceanography and Marine Biology: An Annual Review*. Our review complements and updates Barnes (1996). An endemic species of *Pollicipes*, *P. caboverdensis*, from Cape Verde Islands, has since been described, joining the three previously known extant species (*P. polymerus*, north-eastern Pacific Ocean*, P. elegans,* tropical eastern Pacific Ocean, and *P. pollicipes,* north-eastern Atlantic Ocean). Most research has been on *Pollicipes polymerus* and *P. pollicipes*. We provide a georeferenced map of the worldwide distribution of *Pollicipes*. All *Pollicipes* species are harvested throughout their geographic distributions with varying intensity and levels of management. Phylogeography and population genetics are new areas developed since Barnes (1996). We update systematics and morphological studies (adult descriptions, cirral form and function, and adhesion). Various aspects of the life history of *Pollicipes* (reproduction, larval phase, settlement, recruitment and growth), the biological assemblages associated with *Pollicipes* and post-settlement population processes are reviewed. Pollution and geochemical studies are outlined before a detailed appraisal of Atlantic and Pacific fisheries. Considerable progress has been made in emerging areas, particularly phylogeography, adhesion and cement, fisheries management and aquaculture. Research gaps are highlighted, despite the much progress in the last quarter-century.

Keywords: Stalked barnacles, *Pollicipes,* Systematics, Phylogenetics, Ecology, Fisheries

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Introduction

Twenty-five years ago, Margaret Barnes made an extensive and thoughtful review of the genus *Pollicipes,* published in *Oceanography and Marine Biology: An Annual Review* (Barnes 1996). In the penultimate paragraph, she stated that "The commercial exploitation of *Pollicipes,* particularly in Europe, has encouraged a renewed interest in these pedunculate cirripedes and hopefully it will also increase some fundamental research on their biology and ecology". She ended the review with a general description of the challenges of living in the wave-swept intertidal zone.

The species of *Pollicipes* have many common names (e.g. percebe in Spanish and Portuguese), but the one that best illustrates the way of life of these species is the name given by the First Nations in Canada. They call it '*caʔinwa*', which means 'playing with the waves'. Twenty-five years after Barnes (1996), what have we learned about those who play with the waves? What have been the scientific advances and what are the research gaps and challenges? Answering these questions is the main objective of the present review.

We use the structure of the sections of Barnes' (1996) review wherever deemed appropriate. Thus, some sections have been retained with the same titles, such as 'Geographical distribution' or 'Description of adults'. We have chosen to coalesce other topics that were scattered in several sections of Barnes (1996) into unifying sections, such as 'Settlement and recruitment' or 'Post-settlement processes of distribution and abundance'. Moreover, there are completely new sections on emerging topics, such as phylogenetics and population genetics, which have led to the recent recognition of a new species, *Pollicipes caboverdensis*, or aquaculture because of the recent progress in addressing the challenges it poses. In contrast, some sections of Barnes (1996) are not included in this review, such as various aspects of functional morphology or physiology, as they have not developed much in the last 25 years. On these topics, Barnes (1996) should be consulted. Thus, the order roughly follows Barnes (1996). In turn, we consider the following: systematics and taxonomy, evolution and population genetics, geographic distributions, habitat along with local distribution patterns and associated biota, description of adults, cirral morphology and feeding, and adhesion and cement. We then review various aspects of life history: reproduction, larval biology, settlement and recruitment, growth, post-settlement processes determining population processes and community structuring. Pollution and geochemical studies are then outlined, before giving a detailed consideration of fisheries and then aquaculture. The cultural importance of *Pollicipes* is highlighted. We conclude by outlining research gaps and making some final remarks.

In each section, we begin with briefly recapping Barnes (1996) and then describe new knowledge, before ending with research gaps and challenges. In a few sections, we have integrated studies prior to Barnes (1996) and cited in Barnes (1996), to better contextualize the section (e.g. 'Ecological habitat, and patterns of distribution and abundance'). Barnes (1996) predicted that the commercial interest in the European species, *Pollicipes pollicipes*, would drive more studies of its biology and ecology. It has, but it has also brought about considerable development of the knowledge and the management of these fisheries. All species of the genus *Pollicipes* (*Pollicipes polymerus*, *P. elegans*, *P. pollicipes* and *P. caboverdensis*) are harvested. In fact, the 'Fisheries, management and conservation' section of this review is the longest.

All sections of this review 'play with the waves'. The very exposed shores where the species of *Pollicipes* occur can be considered as some of the most extreme habitats on our planet, as well as being some of the most difficult to make a living as a fisher or study as an ecologist. These habitats modulate the biology of these species and their interactions with other species. They also challenge those exploiting *Pollicipes* species and constrain scientific research. Our review aims to complement and update Barnes (1996). It is also a tribute to Margaret, a leading light who guided and edited OMBAR for many years, as well as being an expert barnacle biologist, despite never having a paid position at the research institutes in which she worked.

Systematics and taxonomy

Barnes (1996) used the classification proposed by Anderson (1994). Here, we endorse the revised classification proposed by Chan et al. (2021), currently recognized in the World Register of Marine Species (WoRMS; Table 1). A major change in this classification is the new order Pollicipedomorpha (Chan et al. 2021). Both classification systems and the extant and fossil species, including invalid species names and generic reassignments, are listed in Table 1. We also include in the list the extant species and the two fossil species of the genus *Capitulum*, formerly placed in the genus *Mitella*, along with species now in the genus *Pollicipes*. Since the Barnes' (1996) review, a new living species (Fernandes et al. 2010) and two new fossil species of *Pollicipes* have been described (Gale & Sørensen 2015).

Table 1 Taxonomical classification used in Barnes (1996) and in the present review, with a list of extant and fossil species of the genus *Capitulum* and the genus *Pollicipes*, including invalid species names and generic reassignments

Classification proposed by Anderson (1994) and used by Barnes (1996)	Classification proposed by Chan et al. (2021), used in WoRMS (2021) and in the present review
Class Thecostraca	Class Thecostraca Gruvel, 1905
Subclass Cirripedia	Subclass Cirripedia Burmeister, 1834
Superorder Thoracica	Infraclass Thoracica Darwin, 1854
Order Pedunculata	Superorder Thoracicalcarea Gale, 2015
Superfamily Scalpelloidea	Order Pollicipedomorpha Ord. nov. Chan, Dreyer, Gale, Glenner, Ewers-Saucedo, Pérez-Losada, Kolbasov, Crandall, & Høeg, 2021
Family Scalpellidae	
Subfamily Pollicipedinae	Family Pollicipedidae Leach, 1817
Pollicipes	*Anelasma* Darwin, 1852
Capitulum	*Capitulum* Gray, 1825
	(formerly placed in the genus *Mitella* with current *Pollicipes* species)
	One living species:
	Capitulum mitella (Linnaeus, 1758)
	Two fossil species:
	Capitulum sklenari Veselská, Kočí, Collins & Gale, 2015
	Capitulum caelatum (Withers, 1935)

(*Continued*)

Table 1 (*Continued*) Taxonomical classification used in Barnes (1996) and in the present review, with a list of extant and fossil species of the genus *Capitulum* and the genus *Pollicipes*, including invalid species names and generic reassignments

Classification proposed by Anderson (1994) and used by Barnes (1996)	Classification proposed by Chan et al. (2021), used in WoRMS (2021) and in the present review
	Pollicipes Leach, 1817
	Four living species:
	Pollicipes caboverdensis Fernandes, Cruz, & Van Syoc, 2010
	Pollicipes elegans (Lesson, 1831)
	Pollicipes pollicipes (Gmelin, 1791 [in Gmelin, 1788–1792])
	Pollicipes polymerus Sowerby, 1833
	Seven fossil species:
	Pollicipes davisi (Withers, 1953)
	Pollicipes italica (Withers, 1953)
	Pollicipes (?) lailae (Withers, 1953)
	Pollicipes toombsi (Withers, 1953)
	Pollicipes (?) striatum Gale & Sørensen, 2015
	Pollicipes vansyoci Gale & Sørensen, 2015
	Pollicipes venablesi (Withers, 1953)
	Invalid species names and generic reassignments:
	Pollicipes aboriginalis Buckeridge, 1983, accepted as *Pachyscalpellum glauerti* (Withers, 1935) (listed as synonym by Gale & Sørensen, 2015)
	Pollicipes cornucopia Leach, 1824, accepted as *Pollicipes pollicipes* (Gmelin, 1791 [in Gmelin, 1788–1792]) (listed as synonym by Zevina, 1981)
	Pollicipes darwini Hutton, 1879 accepted as *Smilium spinosa* (Quoy & Gaimard, 1834) (listed as synonym by Foster, 1978)
	Pollicipes darwini Quinteiro, Rodríguez-Castro, López, López-Jurado, González-Henríquez & Rey-Méndez, 2011, junior synonym of *Pollicipes caboverdensis* Fernandes, Cruz, & Van Syoc, 2010
	Pollicipes mitella (Linnaeus, 1758), accepted as *Capitulum mitella* (Linnaeus, 1758) (generic reassignment)
	Pollicipes mortoni Conrad, 1837 accepted as *Pollicipes polymerus* Sowerby, 1833 (listed as synonym by Young, 2007)
	Pollicipes rigidus Sowerby, 1839 accepted as *Pollicipes elegans* (Lesson, 1831) (listed as synonym by Young, 2007)
	Pollicipes ruber Sowerby, 1833 accepted as *Pollicipes elegans* (Lesson, 1831) (listed as synonym by Young, 2007)
	Pollicipes sertus Darwin, 1851 accepted as *Calantica spinosa* (Quoy & Gaimard, 1834) accepted as *Smilium spinosa* (Quoy & Gaimard, 1834) (generic reassignment)
	Pollicipes sinensis Chenu, 1843 accepted as *Capitulum mitella* (Linnaeus, 1758) (listed as synonym by Young, 2007)
	Pollicipes smythii Leach, 1818, accepted as *Pollicipes pollicipes* (Gmelin, 1791 [in Gmelin, 1788–1792]) (listed as synonym by Young, 2007)
	Pollicipes spinosus (Quoy & Gaimard, 1834), accepted as *Smilium spinosa* (Quoy & Gaimard, 1834) (generic reassignment)
	Pollicipes villosus Leach, 1824 accepted as *Calantica villosa* (Leach, 1824)

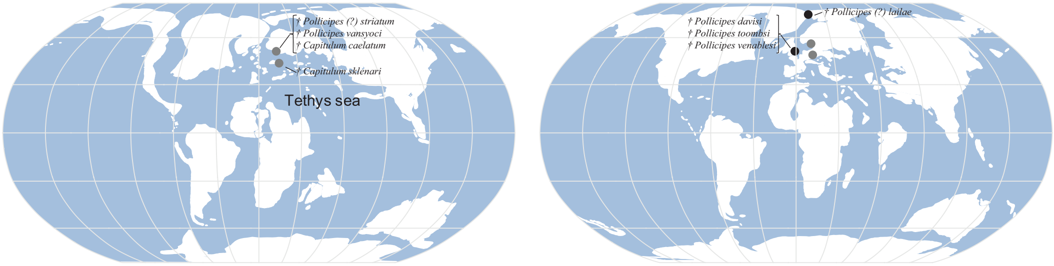
References to taxonomical authorities are only stated in the list of references for the descriptions of new taxa. See Chan et al. (2021) and WoRMS (2021) for the missing references concerning taxonomic authorities

Phylogeny, evolution and population genetics

Fossil record and biogeography

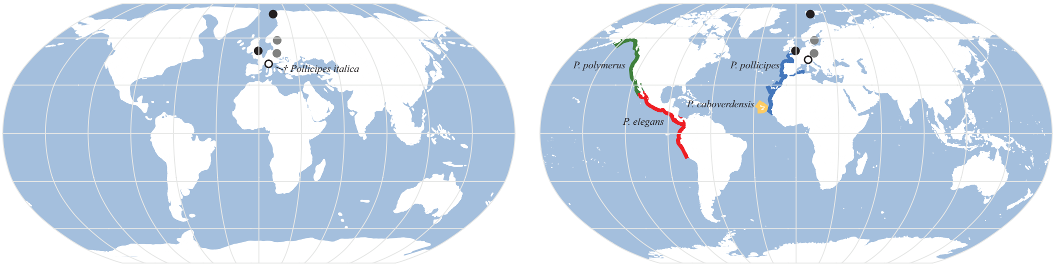
The distribution of the four living species in the genus *Pollicipes* is best explained as the relicts of Pollicipedidae that evolved along the margins of what was once the Tethys Sea (Figure 1). The closest living relative to *Pollicipes*, *Capitulum mitella*, inhabits the western Pacific Ocean, on what was the eastern margin of the ancient Tethys Sea (Newman 1992, Van Syoc 1995). The known fossil record of these two genera has expanded somewhat since Barnes (1996). At that time, the only known fossils of *Pollicipes* were *Pollicipes aboriginalis* from Western Australia in deposits aged at 85 Ma (Buckeridge 1983), the four species Withers (1953) described from England and Norway (55–60 Ma) and one species from younger deposits in Italy (Withers 1953; 15–20 Ma) (see Figure 1 for map).

Since then, Gale & Sørensen (2015) considered *Pollicipes aboriginalis* to be a junior synonym of *Pachyscalpellum glauerti* (Withers 1935) and unrelated to *Pollicipes*, and fossils of two *Pollicipes* species have been described from the Late Cretaceous (80 Ma) in rocky shoreline deposits of Sweden (*Pollicipes vansyoci*; *Pollicipes (?) striatum;* Gale & Sørensen 2015). In addition, one



(A) 90 Ma. Late Cretaceous – Late Tethys

(B) 53 Ma. Eocene – Fragmented Tethys with widening of Atlantic



(C) 22 Ma. Miocene – Further fragmented Tethys, maturing Atlantic and Caribbean

(D) 0 Ma. Holocene

Figure 1 Maps of land masses and oceans showing the evolution of the Tethyan relict distribution for the Pollicipedidae (*Pollicipes* and *Capitulum*). Continental reconstructions were based on Matthews et al. (2016). (A) The Tethys Sea with the Atlantic Ocean forming, 90 Ma, with Pollicipedidae fossil records in areas that will become Sweden and Czech Republic. *Pollicipes* in Sweden (*Pollicipes vansyoci* Gale & Sørensen 2015 and *Pollicipes (?) striatum* Gale & Sørensen 2015; 80 Ma). *Capitulum sklenari* Veselská, Kočí, Collins & Gale, 2015 in the present-day Czech Republic (94 Ma). *Capitulum caelatum* (Withers 1935) Gale & Sørensen 2015 in the present-day Sweden (80 Ma). (B) Fragmented Tethys with a widening Atlantic, 53 Ma. Four additional records of species of *Pollicipes* from England and Norway. (C) Evolving Atlantic, 22 Ma. Emergent Cape Verde Islands, hypothesized date of divergence of *Pollicipes caboverdensis*, 25 Ma. One additional record of species of *Pollicipes* in Italy (*Pollicipes italica* (Withers 1953), 15–20 Ma). (D) Present time, showing the four living *Pollicipes* species distributions after the Eocene/Oligocene boundary radiation of the current species.

fossil species of the closely related genus *Capitulum* is known from Sweden (*Capitulum caelatum*; 80 Ma; Gale & Sørensen 2015) and a second species from similar, but slightly older (94 Ma), deposits in the Czech Republic (*Capitulum sklenari*; Veselská et al. 2015) (Figure 1).

Based on morphological similarities of the three species of *Pollicipes* known prior to the description of *Pollicipes caboverdensis* in 2010, it has been hypothesized that *Pollicipes pollicipes* and *Pollicipes elegans* are more closely related than either is to *Pollicipes polymerus*, with all of the living *Pollicipes* species representing relict elements of this Tethys Sea fauna that became restricted to the eastern boundary conditions of the Atlantic and Pacific Oceans (Newman & Killingley 1985, Newman & Foster 1987, Newman 1992).

The present biogeography of the living species, in conjunction with the fossil records for *Pollicipes* and *Capitulum* coupled with molecular phylogenetics of the four living species of *Pollicipes* (Van Syoc et al. 2010), supports a hypothesis of a radiation of pollicipedine species during the Tethys Sea era (see maps, Figure 1).

Molecular phylogenetics: relationship among living species of Pollicipes

Barnes (1996) did not include any molecular-level analyses in her review of *Pollicipes*. Polymerase chain reaction (PCR) and DNA sequencing were first applied to *Pollicipes* in the early 1990s (Van Syoc & Newman 1992, Van Syoc 1993, 1994a, b, 1995) shortly before Barnes published her review. These early papers on molecular relationships among barnacles relied on comparative analyses of the nucleotide sequences of fragments of the mitochondrial DNA cytochrome oxidase subunit 1 gene (CO1). Since that time, sequences from additional mitochondrial DNA genes (e.g. ribosomal subunits 12S and 16S) and nuclear DNA genes (e.g. H3 and 5.8s rDNA) have been analysed in various barnacle taxa, including *Pollicipes* (e.g. Van Syoc et al. 2010, Quinteiro et al. 2011, Seoane-Miraz 2015). More recently, entire mitochondrial genome sequences have added to our knowledge of barnacle molecular phylogenetic relationships (e.g. Lim & Hwang 2007, Tsang et al. 2017, Tian et al. 2020).

Several recent molecular-based studies (Tsang et al. 2017, Kim et al. 2018, 2019b, Tian et al. 2020) have generally confirmed the suggestion, from earlier morphologically based taxonomic and paleontological studies, that the extant genera of pollicipedines, *Pollicipes* and *Capitulum,* may have diverged from each other 100 or more Ma (e.g. Newman 1987, Withers 1953).

The first study of the genus *Pollicipes* to use DNA sequence data (Van Syoc 1995) analysed nucleotide sequence data from CO1, along with a suite of traditional and new morphological characters, that supported the suggested morphology-based relationship among the then three known species of *Pollicipes* identified from prior studies (see section 'Description of adults'). The tree generated from the DNA sequence data placed *Pollicipes pollicipes* and *P. elegans* together in a branch, with *P. polymerus* occupying another branch.

Subsequently, additional molecular-level studies of the relationships of species within the genus *Pollicipes* (using DNA sequences from more individuals and more gene fragments) have also confirmed this general relationship among the extant species, also leading to the discovery of a new species, *P. caboverdensis*, endemic to the Cape Verde Islands (Fernandes et al. 2010, Van Syoc et al. 2010, Quinteiro et al. 2011). This new species was previously considered a genetically differentiated population of *Pollicipes pollicipes* (Quinteiro et al. 2007). Using mtDNA (CO1 and 16S) and nDNA (H3) genes, Van Syoc et al. (2010) supported the hypothesis that the two eastern Atlantic species, *Pollicipes pollicipes* and the Cape Verde Islands *Pollicipes* species (described as *P. caboverdensis* in a subsequent paper by Fernandes et al. 2010), are most closely related to *P. elegans*, the tropical eastern Pacific species. They found the northern Pacific species, *Pollicipes polymerus*, to be the outlying species within the genus. Quinteiro et al. (2011), using the sequence data from mtDNA (CO1) and nDNA (5.8s rDNA and two flanking interspacer regions), produced a similar tree topology. However, the relationships among the four species were not strongly supported by their data using neighbour-joining distance or parsimony-calculated bootstrap values. The topology of a phylogenetic tree for the extant *Pollicipes* species will continue to be elusive until additional molecular-level data can be obtained.

A broad-stroke phylogenetic tree for the Cirripedia generated by Pérez-Losada et al. (2008, Figure 3), using morphological and multi-gene molecular data in the context of the fossil record, aged the ancestral node of *Pollicipes polymerus* and *P. pollicipes* at about 65 Ma. This correlates somewhat with Van Syoc's (1995) estimate of about 55 Ma for the same node in his early CO1 tree.

Using similar estimates of lineage divergence times, Van Syoc et al. (2010) concluded that *Pollicipes caboverdensis*, *P. pollicipes* and *P. elegans* are the most recently diverged species in the genus, some time after the Eocene/Oligocene boundary radiation of *Pollicipes*, about 25–34 Ma. *Pollicipes polymerus* emerged much earlier at around 55–65 Ma, on the north-western margin of the Tethys, in what is now the north-eastern Pacific. Sal Island, the first of the Cape Verde Islands to emerge, dates to about 25 Ma (Ramalho 2011). Therefore, that would be the earliest time of divergence for *Pollicipes caboverdensis*.

Producing a well-supported molecular phylogenetic tree will continue to be challenging, due to the apparently short time of divergence among the extant species of *Pollicipes* and the relatively long time since those times of divergence. Future research using additional genes, complete mitochondrial genomes or chromosome-level assembled genome analyses may yield data more suitable to resolving the various branch patterns.

Phylogeography and population genetics

The four species of the genus *Pollicipes* have received different levels of attention regarding phylogeographic and population genetic studies, with a stronger effort and more publications regarding *Pollicipes pollicipes*. In contrast, there are no published studies on the genetic structure of populations of *Pollicipes caboverdensis*.

With the advancement of molecular techniques, different DNA markers have been used to analyse the genetic structure of *Pollicipes* species (see Table 2 with summary of studies and methods). A few older studies have used allozymes (Van Syoc 1994a, Miner 2002), but the majority have used fragments of the mitochondrial DNA gene cytochrome oxidase c subunit 1 (CO1) (e.g. Van Syoc 1994a – *Pollicipes polymerus*, Van Syoc 1994b – *P. elegans*, Campo et al. 2010 – *P. pollicipes*), the mitochondrial hypervariable non-coding control region (Quinteiro et al. 2007, Barazandeh 2014) or

Table 2 Summary of phylogeographic/population genetic studies and respective methods (molecular markers and sampling design) of *Pollicipes* species

Molecular marker	Number of loci/ fragment length	Sampling regions	Number of sites	Sample size	Reference
Pollicipes polymerus					
Allozymes	3	California (the USA)	2	43–62	Van Syoc (1994a)
CO1	403 bp	Vancouver Island (Canada)	1	8	
		San Diego (California, the USA)	1		
Allozymes	8	South California (the USA)	5	27–40	Miner (2002)
CO1	550 bp	North-eastern Pacific (57.05°N–135.33°W–34.43°N –119.71°W)	6	12–26	Kelly & Palumbi (2010)
CO1	658 bp	North-eastern Pacific (45.75°N–123.97°W–30.47°N –116.05°W)	32	14–15	Dawson et al. (2014)

(*Continued*)

Table 2 (*Continued*) Summary of phylogeographic/population genetic studies and respective methods (molecular markers and sampling design) of *Pollicipes* species

Molecular marker	Number of loci/ fragment length	Sampling regions	Number of sites	Sample size	Reference
CO1/mtDNA control region	773 bp/601 bp	Vancouver Island (Canada)	8	24	Barazandeh (2014)
SNPs	16	Vancouver Island (Canada)	2	48–50	
Pollicipes elegans					
CO1	312 bp	Mexico	1	7	Van Syoc (1994b)
		Peru	1		
CO1/6 nuclear genes	590 bp/109–803 bp	Mexico	3	Unknown	Marchant (2014)
		El Salvador	3		
		Peru	2		
Microsatellites	11	Mexico	1	47–48	Plough & Marko (2014)
		Peru	1		
CO1	590 bp	Mexico	3	15–31	Marchant et al. (2015)
		El Salvador	3		
		Peru	2		
Pollicipes pollicipes					
mtDNA control region	505 bp	Brittany (France)	1	9–56	Quinteiro et al. (2007)
		Asturias (Spain)	1		
		Galicia (Spain)	9		
		Portugal	1		
		Morocco	1		
		Canary Islands	1		
		Cape Verde Islands[a]	1		
CO1	444 bp	Brittany (France)	2	31–128	Campo et al. (2010)
		Basque Country (Spain)	2		
		Asturias (Spain)	2		
		Galicia (Spain)	1		
		Portugal	2		
		Morocco	1		
		Mauritania	1		
Microsatellites/ CO1	11 loci/609 bp	Brittany (France)	1	13–54/13–32	Fernandes et al. (in prep.)
		Galicia (Spain)	1		
		Portugal	6		
		Morocco	3		
		Western Sahara	1		
		Mauritania	1		
		Senegal	3		
Microsatellites	20	Asturias	5	42–50 (juveniles)/ 44–50 (adults)	Parrondo et al. (2022)
		Galicia	5		
		Portugal	5		

[a] In this study, individuals from Cape Verde Islands were still considered as a population of *Pollicipes pollicipes*, although they were later described as *Pollicipes caboverdensis* (Fernandes et al. 2010).

nuclear genes (Marchant 2014). More recently, nuclear microsatellite markers have been developed and used with success for *Pollicipes elegans* (Plough & Marko 2014) and *P. pollicipes* (Parrondo et al. 2022, Fernandes et al. in prep.). In addition, single nucleotide polymorphisms (SNPs; 16 loci) have been developed for *Pollicipes polymerus* (Barazandeh & Davis 2012).

Regarding *Pollicipes polymerus*, most studies have found high gene flow and genetic homogeneity across the geographic range of this species (Van Syoc 1994a, Miner 2002, Kelly & Palumbi 2010, Dawson et al. 2014). Van Syoc (1994a), using both allozymes and a fragment of CO1 gene, found genetic homogeneity among two populations of the north-eastern Pacific coast. A similar result was obtained by Miner (2002) when using allozymes to analyse five populations from the southern California coast (the USA). More recently, several populations of *Pollicipes polymerus* were sampled across its entire geographic range in multi-species comparative genetic studies using CO1 data (Kelly & Palumbi 2010, Dawson et al. 2014). In these studies, gene flow and genetic diversity were high and population genetic structure was very low, although Kelly & Palumbi (2010) did find a mild differentiation of a population from Monterey (California) from the other sampled populations.

Small-scale spatial genetic structure in *Pollicipes polymerus* was also analysed using the CO1 gene, the mitochondrial control region and 16 SNPs, when testing the effects of wave action and tidal height in genetic patterns of this species, but again, genetic homogeneity was found (Barazandeh 2014).

Contrary to *Pollicipes polymerus*, genetic studies of *P. elegans* found strong genetic structure among populations of this species. Early work by Van Syoc (1994b) using CO1 data showed significant genetic divergence between populations in Mexico and Peru, suggesting limited gene flow across the two localities. This is probably due to higher seawater temperatures in the tropical zone north of the equator (Van Syoc 1994b) where the distribution of this species is fragmented (see section ‘Geographical distribution’). In this study, genetic diversity was higher in Peru than in Mexican populations and the time of divergence of these two populations was estimated to have occurred between 2.36 Ma and 590 Ka. This estimated time window coincides with: (1) a general warming of the tropical eastern Pacific during the Pliocene that could have caused an initial vicariant event of a once continuous trans-tropical population; (2) periods of cooling and warming during the Pleistocene that could have allowed a series of expansions and contractions and intermittent genetic exchange of *Pollicipes elegans* populations (Van Syoc 1994b). However, *Pollicipes elegans* populations from the middle of the species range (El Salvador and Costa Rica) were not sampled in this early study. More recently, Marchant et al. (2015) analysed *Pollicipes elegans* populations using the CO1 gene and, in addition to several Mexican and Peruvian populations, three populations from El Salvador. The populations from El Salvador had higher genetic diversity and older estimated population ages than those from Mexico and Peru. Consequently, these authors proposed that tropical populations from El Salvador could be relicts of a once continuous ancestral distribution, supporting the theory that *Pollicipes elegans* had a tropical origin. The decline and extinction of tropical populations and the current disjunct distribution of *Pollicipes elegans* (see section ‘Geographical distribution’) might be explained by Pleistocene glacial cycles and present-day sea surface temperature and habitat availability (Marchant et al. 2015). Moreover, similar to the results obtained by Van Syoc (1994b), two highly differentiated genetic clusters were found, one consisting of Mexican populations and the other including all the southern populations of El Salvador and Peru. Considering this clear phylogeographic break, Marchant (2014) analysed CO1 data plus additional data from six nuclear genes, proposing an ongoing cryptic speciation process within *Pollicipes elegans* between the Mexican and the southern populations. The time since the divergence of these populations was estimated around 150–350 Ka, with negligible gene flow since separation. Supporting these findings, a significant genetic differentiation between Peruvian and Mexican populations of *Pollicipes elegans* was also revealed in preliminary analyses using microsatellite loci, as well as a markedly reduced genetic diversity in Peru (Plough et al. 2014).

Population genetic studies of *Pollicipes pollicipes* have revealed high gene flow, but some genetic differentiation of populations across the Atlantic distribution range of the species, although the patterns of genetic structure have not always been concordant among studies (Quinteiro et al. 2007, Campo et al. 2010, Parrondo et al. 2022, Fernandes et al. in prep.).

Quinteiro et al. (2007), using the mitochondrial control region, found the following differentiated populations/groups of populations of *Pollicipes pollicipes*: (1) Brittany, (2) Asturias, (3) Galicia, Portugal and Morocco, (4) Canary Islands and (5) Cape Verde Islands. However, populations from Cape Verde were later described as a new species (*Pollicipes caboverdensis*; Fernandes et al. 2010). In the study by Campo et al. (2010) using CO1 data, only populations from Brittany were genetically differentiated from the southern populations of Iberia/north-western Africa (Basque Country, Asturias, Galicia, Portugal, Morocco and Mauritania), but the Canary Islands were not sampled. Contrastingly, Fernandes et al. (in prep.), when analysing CO1 data, found genetic homogeneity among populations from Brittany as far south as Mauritania (again the Canary Islands were not included in that study), and a differentiated genetic group of populations from Senegal, the southern range of the species, which were not sampled in the previous studies. However, the lack of separation between Brittany and Iberia found by these authors might be explained by the low sample size used with the CO1 marker (Fernandes et al. in prep.). Moreover, in this study, more discriminatory analyses of microsatellite data (11 loci) confirmed the divergent group of populations from Senegal and revealed two other genetic clusters, corresponding to Brittany/Iberian populations and north-western African populations (Morocco, Western Sahara and Mauritania), although considerable admixture occurred among these latter two clusters. Parrondo et al. (2022), using microsatellites (20 loci) and sampling fifteen populations of adult individuals from three regions in Iberia (Asturias, Galicia and Portugal), also observed the same pattern of genetic homogeneity along the Iberian coast.

Several different explanations were given for the genetic patterns of *Pollicipes pollicipes* observed in the above studies, related to both historical and contemporary processes (Quinteiro et al. 2007, Campo et al. 2010, Fernandes et al. in prep.). According to Quinteiro et al. (2007), the differentiated populations found by these authors are exclusively related to the main oceanographic features (e.g. the gyres and eddies in the Bay of Biscay and in the Cantabrian shelf) in the region that may constitute barriers to larval dispersal.

In contrast, the two genetic clusters (Brittany versus all southern populations) observed by Campo et al. (2010) were suggested to be the result of a past fragmentation of *Pollicipes pollicipes* populations into three refugial areas (Brittany; north-western Iberia; and North Africa) during Pleistocene glaciations, with a subsequent demographic expansion and rapid homogenization of populations from North Africa and Iberia. This process could have been slower between Iberia and Brittany, explaining the genetic differentiation between these populations detected using CO1 data, since the lack of suitable rocky habitat between these regions may constitute a partial barrier to larval dispersal (Campo et al. 2010) (see section 'Geographical distribution').

Based on these previous studies and on the combined results obtained with CO1 and microsatellites, Fernandes et al. (in prep.) suggested the following overall patterns and processes of genetic structure for *Pollicipes pollicipes*. Genetic homogeneity between Brittany and Iberian populations occurs due to contemporary larval dispersal and high gene flow between these regions (Fernandes et al. in prep.), although a signal of a past fragmentation during Pleistocene glaciations can still be detected with mitochondrial data (Quinteiro et al. 2007, Campo et al. 2010). The differentiation of north-western African populations from those in Iberia is caused by a contemporary oceanographic barrier to larval dispersal and gene flow located at the Gulf of Cadiz/Strait of Gibraltar (Fernandes et al. in prep.). The differentiation of the Canary Islands is the result of contemporary oceanographic processes (Quinteiro et al. 2007). The differentiation of Senegal populations result from the lack of suitable habitat along the 750 km sandy coast from Mauritania to Dakar (Senegal), which, together with the main currents in the region, may constitute an old and established barrier to larval dispersal (Fernandes et al. in prep.).

In the study by Parrondo et al. (2022) using microsatellites, besides analysing the populations of adults across the Iberian coast, juveniles of the same size were also analysed, which revealed less diversity and higher relatedness than adults, showing a significant spatial genetic differentiation. Several populations of juveniles from Galicia were genetically differentiated from those of Asturias and Portugal, with a mild differentiation also occurring between juveniles of these last two regions. The spatial patterns of genetic homogeneity in adults *versus* complex patterns of genetic heterogeneity in juveniles (chaotic genetic patchiness) could be caused by the aggregation of related dispersing larvae, by sweepstakes reproductive success or by self-recruitment events (Parrondo et al. 2022).

There are no published population genetic studies for *Pollicipes caboverdensis*. This is a major research gap that should be addressed in the future, especially given the extent and scattered nature of the Cape Verde archipelago and that these are exploited populations.

Overall, in future studies, efforts should be directed to sampling potential phylogeographic discontinuity regions and to developing new molecular markers in *Pollicipes* species. For example, it would be important to sample *Pollicipes pollicipes* from the Mediterranean coast, as the Strait of Gibraltar and the Almeria/Oran front are well-known phylogeographic barriers for other marine invertebrate species including barnacles (e.g. Pannacciulli et al. 1997, 2017). More intensive sampling of *Pollicipes elegans* along the Pacific north and central coast of Mexico between Mazatlán, Sinaloa (23°10′N) and the state of Oaxaca (~15°N) (see section 'Geographical distribution') would also allow more exact location of the strong phylogeographic break found by Marchant et al. (2015) in this species. More genetic data on multiple loci are needed, especially for *Pollicipes polymerus*, as most of the inferences for this species were based on a single mitochondrial DNA gene or allozymes. Cross-amplification of microsatellite markers already developed for *Pollicipes pollicipes* and *P. elegans* in congeneric species should be investigated, together with the development of new microsatellites for *P. polymerus* and *P. caboverdensis*. Moreover, the development of SNP loci for all of the *Pollicipes* species should be addressed in the future. The recent availability of the complete genome of *Pollicipes pollicipes* (RefSeq GCA_011947565.3) opens new possibilities for research. Genome-wide markers can detect subtle genetic differentiation that may exist among populations, thereby helping to identify adequate fishery management units in commercially exploited *Pollicipes* species.

Geographical distribution

The four extant species of *Pollicipes* have an East Pacific/East Atlantic longitudinal disjunct distribution that is considered to be a Tethyan relict pattern (see section 'Phylogeny, evolution and population genetics', Figures 1 and 2). *Pollicipes polymerus* lives in the north-eastern Pacific Ocean. *Pollicipes elegans* inhabits the tropical eastern Pacific Ocean. *Pollicipes pollicipes* occurs in the north-eastern Atlantic Ocean. *Pollicipes caboverdensis* occurs in the Cape Verde Islands only (tropical eastern Atlantic Ocean) (Figure 2). *Pollicipes elegans* and *P. caboverdensis* are warm-water species, with *P. pollicipes* being mostly a warm temperate species and *P. polymerus* being a warm and cold temperate species (Southward 2008, and Figure 6 of Briggs & Bowen 2012).

In the Barnes' (1996) review, the geographical distributions of *Pollicipes polymerus*, *P. elegans* and *P. pollicipes* were thoroughly reviewed, mostly based on published articles. Herein, we have built a georeferenced map of the worldwide distribution of *Pollicipes* species (Figure 2 and georeferenced database in supplementary material). Using *Pollicipes* records in Barnes (1996), we mapped their occurrence data ('Barnes points', Figure 2). In addition, we mapped the sites where the presence of these species and *Pollicipes caboverdensis* has been detected, based on an extensive review of the literature published after Barnes (1996), locations where these species have been recorded based on our personal observations and those of colleagues, personal communications and websites with geographic information (Figure 2 and Table 3). We used only the presence data for *Pollicipes* species taken from websites in regions corresponding to range limits and gaps in the distribution, as was the case in Alaska (the USA) and Baja California (Mexico) for *P. polymerus*; Mexico, Costa Rica and northern Ecuador for *P. elegans*; and the British Isles, southern coast of

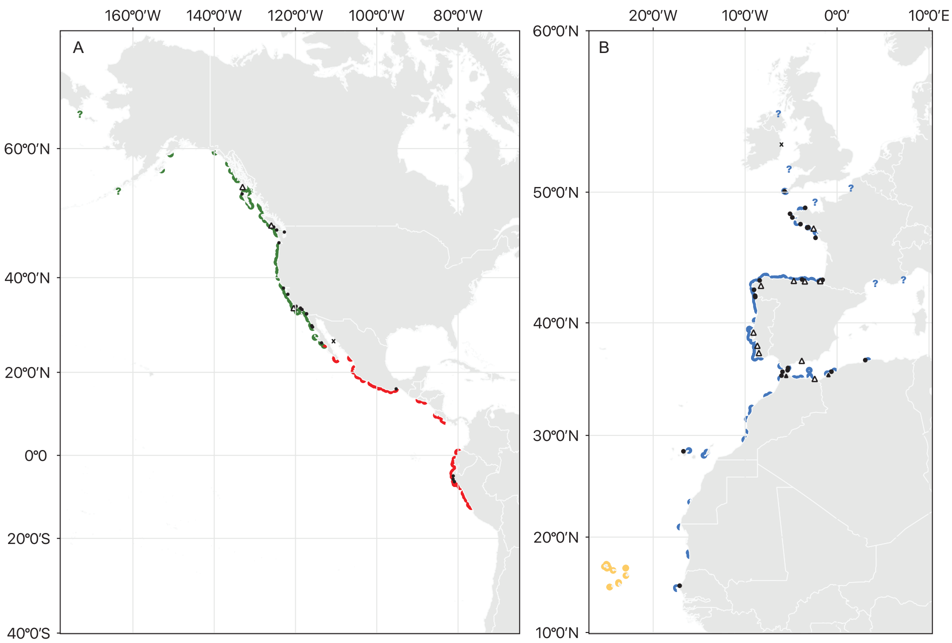


Figure 2 Global distribution of *Pollicipes*. Maps with georeferenced sites ($n = 664$) where *Pollicipes* species were sampled or detected, based on published information after Barnes (1996) or not referred to in Barnes (1996), in personal observations and communications and on websites with geographical information (see Table 3 and georeferenced database in supplementary material). Symbols (colour scheme according to each species): ● *P. polymerus*; ● *P. elegans*; ● *P. pollicipes*; ● *P. caboverdensis*; ● sites mentioned in Barnes (1996); × sites mentioned in Barnes (1996) that were considered an error; "?" dubious records of *Pollicipes*; ▲ Pre-historic shell middens where *Pollicipes* were found and cited by Barnes (1996); Δ Pre-historic shell middens where *Pollicipes* were found after Barnes (1996). Projected coordinate system used: WGS 84/Pseudo-Mercator (EPSG: 3857).

Table 3 Published and unpublished data on the presence of *Pollicipes* species by country after Barnes (1996) that were used for building the georeferenced map of Figure 2

Species/Range	Country	References
P. polymerus NE Pacific 59°N–26°N	Alaska, the USA	Kelly & Palumbi (2010), Alaskafisheries.noaa.gov (2021), MARINe (2021), Inaturalist.org (2021).
	Canada	Van Syoc (1994a), Jamieson et al. (2001), Lessard et al. (2003), Marchinko & Palmer (2003), Marchinko et al. (2004), Quinteiro et al. (2011), Barazandeh et al. (2013), Barazandeh (2014), Schiller (2015), Gagne et al. (2016), Inaturalist.org (2021), MARINe (2021).
	The USA	Carrington-Bell & Denny (1994), Pineda (1994), Wootton (1994), Van Syoc (1994a), Wootton (1997), Harris et al. (2000), Miner (2002), Helms (2004), Marchinko et al. (2004), Pérez-Losada et al. (2004), Phillips (2005), Tapia (2005), Phillips (2006), Dudas et al. (2009), Shanks & Shearman (2009), Tallis (2009), Kelly & Palumbi (2010), Morgan & Fisher (2010), Tapia et al. (2010), Van Syoc et al. (2010), Wootton (2010), Menge et al. (2011), Perina et al. (2011), Dawson et al. (2014), Seoane-Miraz (2015), Seoane-Miraz et al. (2015), Bingham (2016), Morgan et al. (2017), Perina (2018), Romersa (2018), Hagerty et al. (2019).

(*Continued*)

Table 3 (*Continued*) Published and unpublished data on the presence of *Pollicipes* species by country after Barnes (1996) that were used for building the georeferenced map of Figure 3

Species/Range	Country	References
	Mexico	Ladah et al. (2005), Van Syoc et al. (2010), Dawson et al. (2014), Hagerty et al. (2019), Rani Gaddam (pers. comm.); MARINe (2021), Benthic Invertebrate Collection of Scripps Institution of Oceanography (C6703).
P. elegans Tropical E Pacific 26°N–8°N	Mexico	Van Syoc (1994a), Van Syoc et al. (2010), Walther et al. (2013), Plough & Marko (2014), Plough et al. (2014), Crickenberger et al. (2015), Marchant et al. (2015), Gutiérrez & Cabrera (2019), Pedro Flores (pers. comm. 2014) in Marchant et al. (2015), Inaturalist.org (2021).
0°–6°/12°S	El Salvador	Van Syoc (1994a), Walther et al. (2013), Marchant et al. (2015), Inaturalist.org (2021).
	Costa Rica	Mora-Barboza & Sibaja-Cordero (2018), Inaturalist.org (2021).
	Ecuador	Ladines (2018), Cárdenas-Calle et al. (2020), youtube.com/watch?v=9zkNYlOucLQ, Inaturalist.org (2021).
	Peru	Tarazona et al. (1985), Arntz et al. (1987), Kameya & Zeballos (1988), Van Syoc (1994a), de la Cruz et al. (2001), Samamé & Quevedo (2001), Stucchi & Figueroa (2006), Van Syoc et al. (2010), Zapata et al. (2010), Perina et al. (2011), Quinteiro et al. (2011), Walther et al. (2013), Plough & Marko (2014), Crickenberger et al. (2015), de la Cruz et al. (2015), Marchant et al. (2015), Ramírez & de la Cruz (2015), Seoane-Miraz (2015); Seoane-Miraz et al. (2015), Alemán et al. (2016), Alegre (2017), Ramírez et al. (2017), Ibanez-Erquiaga et al. (2018); Perina (2018); Valqui et al. (2021), Leonardo Romero (pers. comm.).
P. pollicipes	The UK	Southward (2008), Stephen J. Hawkins, Keith Hiscock and Nova Mieszkowska (pers. comm.), marlin.ac.uk 2021.
NE Atlantic 50°N–14°N	France	Quinteiro et al. (2007), Southward (2008), Campo et al. (2010), Van Syoc et al. (2010), Seoane-Miraz et al. (2015), Aguión et al. (2022b), Fernandes et al (in prep), Eric Thiebaut (pers. comm.).
	Spain	de la Hoz & Garcia (1993), Mas et al. (1996), Pérez-Losada et al. (2004), Candeias (2005), Macho et al. (2005), Borja et al. (2006a, b), Macho (2006), Quinteiro et al. (2007), Campo et al. (2009), Álvarez-Fernández et al. (2010), Macho et al. (2010), Perina et al. (2011), Sestelo & Roca-Pardiñas (2011), Parada et al. (2012), Álvarez-Fernández et al. (2013), Parada et al. (2013), Gofas et al. (2014), Perina et al. (2014), Rivera et al. (2014), Bidegain et al. (2015), Seoane-Miraz (2015), Seoane-Miraz et al. (2015), Höfer et al. (2016), Bidegain et al. (2017), Perina (2018), Aguión et al. (2022a, 2022b), Román et al. (2022), Parrondo et al. (2022), Inaturalist.org (2021), Fernandes et al (in prep).

(*Continued*)

Table 3 (*Continued*) Published and unpublished data on the presence of *Pollicipes* species by country after Barnes (1996) that were used for building the georeferenced map of Figure 3

Species/Range	Country	References
	Portugal	Van Syoc (1994a), Cardoso & Yule (1995), Kugele & Yule (1996), Norton (1996), Cardoso (1998), Cruz & Hawkins (1998), Cruz & Araújo (1999), Cruz (2000), Kugele & Yule (2000), Jesus (2004), Candeias (2005), dos Santos et al. (2007), Quinteiro et al. (2007), Cruz et al. (2008), Valente (2008), Campo et al. (2010), Cruz et al. (2010), Fernandes et al. (2010), Jacinto et al. (2010), Van Syoc et al. (2010), Jacinto et al. (2011), Costa (2012), Reis et al. (2012), Rodharth (2013), Sousa et al. (2013), Albuquerque (2014), Franco (2014), Ramos et al. (2014), Almeida et al. (2015), Figueira (2015), Jacinto et al. (2015), Rocha (2015), Seoane-Miraz (2015), Albuquerque et al. (2016), Jacinto (2016), Jacinto & Cruz (2016), Darras (2017), Lobo-da-Cunha et al. (2017), Mateus (2017), Pedro (2017), Belela (2018), Fernandes (2018), Torres (2018), Machado et al. (2019), Tilbury et al. (2019), Domínguez-Perez et al. (2020), Aguión et al. (2022b), Fernandes et al. (2021), Parrondo et al. (2022); Inaturalist.org (2021), Fernandes et al. (in prep).
	Gibraltar	Inaturalist.org (2021).
	Algeria	Kallouche et al. (2014), Bachetarzi et al. (2016).
	Morocco	Quinteiro et al. (2007), Bazairi (2010), Campo et al. (2010), Perina et al. (2011), Boukaici et al. (2012, 2015), Seoane-Miraz (2015), Seoane-Miraz et al. (2015), Perina (2018), Bourassi et al. (2019), Fernandes et al (in prep), Laura Palacín-Fernández (pers. comm.).
	Canary Islands, Spain	Marín & Luengo (1998), Quinteiro et al. (2007), González et al. (2012).
	Western Sahara	Fernández de Larrinoa & Cedenilla (2003), Van Syoc et al. (2010), Inaturalist.org (2021), Fernandes et al. (in prep).
	Mauritania	Campo et al. (2010), Fernandes et al. (in prep).
	Senegal	Fernandes et al. (2010). Fernandes et al. (in prep).
P. caboverdensis Tropical E Atlantic 17°N–14°N	Cape Verde	Quinteiro et al. (2007), Fernandes et al. (2010), Van Syoc et al. (2010), Quinteiro et al. (2011), Baessa (2015), Seoane-Miraz (2015), Seoane-Miraz et al. (2015), Soares (2018).
P. polymerus middens	Canada	Moss & Erlandson (2010), Efford (2019).
	The USA	Erlandson et al. (2004).
P. pollicipes middens	Spain	Álvarez-Fernández et al. (2010), Aristu et al. (2011), Gutiérrez-Zugasti (2011), Gibaja et al. (2012), Álvarez-Fernández et al. (2013), Fernández-Rodríguez et al. (2014), García-Escárzaga et al. (2017).
	Portugal	Valente (2008), Bicho (2009), Dean (2010), Bicho et al. (2013), Valente (2014), Callapez & Pimentel (2018).

Georeferenced database in supplementary material.

Portugal and Spain, Gibraltar and the Western Sahara for *P. pollicipes*. Occasionally, publications before, but not included in, Barnes (1996) were considered (e.g. Tarazona et al. 1985, Kameya & Zeballos 1988, Laguna 1990 and Van Syoc 1994a for *P. elegans*), particularly where it was important to define the limits of each species. We have considered species limits records as dubious when there was contradictory information, or when references were old and not possible to confirm with recent observations ('?' in Figure 2). As *Pollicipes* species have been exploited since prehistoric times, we also mapped the locations of the presence of these species in shell middens (Figure 2, and see section ‘Fisheries, management and conservation’). In total, we mapped 664 points of presence (61 points were taken from websites) of *Pollicipes* species recorded after Barnes (1996), including points of shell middens and overlapping points (Figure 2).

When compared with Barnes (1996), the main differences found in the geographical distribution of *Pollicipes* species were as follows: changes in the northern limit of *P. polymerus*; the detailed description of the geographical distribution of *P. elegans*, including the southward extension of its southern limit and relationship with El Niño Southern Oscillation events; and the description of the geographical distribution of the newly described *P. caboverdensis* (see sections ‘Systematics and taxonomy’ and ‘Description of adults’, Figure 2).

Pollicipes polymerus

According to several references in Barnes (1996), the latitudinal range of *Pollicipes polymerus* was considered to be from 64°N to ~27°N. This northern limit was defined at Plover Bay, Bering Strait, but its presence was associated with other barnacles on a humpback whale (Pilsbry 1907). There is also a reference in Barnes (1996) to the presence of *Pollicipes polymerus* on wave-exposed rocky shores at Sakhalin Island (Tarasov & Zevina 1957 cited in Bernard 1988). However, in the original publication (Tarasov & Zevina 1957), the specimens were described as included in a museum collection and associated with an unknown substrate, probably the bottom of a vessel. Since neither reference is on rocky coasts, these records are difficult to verify and thus we consider them to be doubtful. The northernmost rocky coast regions described in Barnes (1996) are the Aleutian Archipelago (the USA) (Bernard 1988) and further south in British Columbia (Canada) (see several references in Barnes 1996). There are no recent references to the presence of *Pollicipes polymerus* in the Aleutian Archipelago, and one of us (Robert J. Van Syoc) has not found this species at these islands; therefore, we also consider the presence of this species in these islands doubtful. However, since Barnes (1996), there are records of this species at several locations on the rocky coasts of Alaska (the USA) (Figure 2). Hence, we consider the northern limit of this species to be Kenai Peninsula (59° 18′N) and the north-western limit to be Kodiak Island (57° 15′N 152°56′W) (Alaskafisheries.noaa.gov 2021).

In addition, there are several recent records of this species on the coasts of British Columbia (Canada), Washington, Oregon and California (the USA), as far south as Baja California (Mexico) (Figure 2).

Regarding the southern limit of *Pollicipes polymerus*, Barnes (1996) mentioned that the most southern records are Punta Abreojos (26° 42′N) (Newman & Abbott 1980, Newman & Killingley 1985) and Punta Santa Domingo (26° 31′N; Bernard 1988), both in Baja California, Mexico. Bernard (1988) also noted that this species is found sporadically south of Cedros Island (~28°N), in areas cooled by upwelling currents as far south as Punta Santa Domingo, but did not present any data regarding its presence in these locations. However, we found a record of specimens of *Pollicipes polymerus* at Punta Santa Domingo in the Benthic Invertebrate Collection of Scripps Institution of Oceanography (catalogue number C6703, collected in 1979 by R. Cimberg). After the 1980s, there is apparently no further record of the presence of *Pollicipes polymerus* at this location. Based on the information from the Multi-Agency Rocky Intertidal Network (MARINe 2021), the southern record of *Pollicipes polymerus* is from Punta Abreojos, but no sites south of this location were sampled (Rani Gaddam pers. comm.). In conclusion, we consider the historical record in Punta Santa Domingo to be the southern limit of *Pollicipes polymerus*, but further sampling in this location is needed.

In a 1953 record that was subsequently found to be incorrect, *Pollicipes polymerus* specimens attached to floating wood near Madras, India, were described as a new subspecies, *Pollicipes polymerus madrasensis* (Daniel 1953). However, Newman & Killingley (1985) used ^{18}O fractionation in calcite from the capitular plates of the putative subspecies to discover that these specimens had grown in seas much cooler than the Indian Ocean. Therefore, the specimens Daniel (1953) described are *Pollicipes polymerus*, but are not a distinct subspecies and did not live and grow in the Indian Ocean (Trivedi et al. 2021). It is unclear how they arrived there.

Pollicipes elegans

Citing several authors (Darwin 1852, Gruvel 1905, Pilsbry 1909), Barnes (1996) considered that the northern limit of the distribution of *Pollicipes elegans* was Lobos Island located in the Gulf of California, Mexico. We consider that this record is probably a misidentification of Lobos Island, as the reference of Lobos Island in Darwin (1852) and in Pilsbry (1909) is in Peru, not in Mexico, and the location is not clear in Gruvel (1905). There are several recent references to the presence of *Pollicipes elegans* in Lobos Islands, Peru (~6°S–7°S, Islas Lobos de Tierra, e.g. de la Cruz et al. 2015b; Islas Lobos de Afuera, e.g. Ramírez & de la Cruz 2015), so we consider the northern limit of Lobos Island, Mexico, suggested in Barnes (1996) as incorrect. Based on this misidentification of Lobos Island, Barnes (1996) noted that the southern record of *Pollicipes polymerus* (Punta Abreojos and Punta Santa Domingo, Newman & Killingley 1985, Bernard 1988) were at approximately the same latitude as Lobos Island (26°N–27°N).

Although the northern boundary of Lobos Island for *Pollicipes elegans* is incorrect, Newman & Killingley (1985) (based on a personal communication with R. Brusca and R. Cimberg) and Laguna (1990) indicated a region of sympatry between *P. polymerus* and *P. elegans* at 26°N. In addition, Van Syoc (1994a) mentioned specimens of *Pollicipes elegans* collected at Punta Santa Domingo (26° 31′N) based on the database of records in the Benthic Invertebrate Collection of Scripps Institution of Oceanography. *Pollicipes elegans* has, however, never been observed at Punta Abreojos (26° 42′N) (Rani Gaddam pers. comm., based on Multi-Agency Rocky Intertidal Network, MARINe 2021). In more recent studies, samples of *Pollicipes elegans* have been taken from sites located south of Punta Abreojos and Punta Santa Domingo – Cape San Lucas, 22° 53′N (Van Syoc 1994a), and Punta Gasparino, 23° 10′N (Walther et al. 2013, Plough & Marko 2014, Plough et al. 2014, Crickenberger et al. 2015, Marchant et al. 2015). In conclusion, we consider that the northern limit of *Pollicipes elegans* is Punta Santa Domingo, based on Van Syoc (1994a), with a possible region of sympatry between *P. elegans* and *P. polymerus* at Punta Santa Domingo.

In addition to Lobos Island, Mexico, Barnes (1996) reported the presence of *Pollicipes elegans* from the west coast of Mexico to Peru, indicating its presence in Tehuantepec, Mexico (~16°N), citing Darwin (1852), and in Paita, Peru (several references in Barnes, 1996, ~6°S), which she considered to be the southern limit of its distribution (Figure 2).

Barnes (1996) did not mention the fragmented nature of the distribution of this species with several gaps, which is characteristic of *Pollicipes elegans* and different from the more continuous distributions of the other *Pollicipes* species. Marchant et al. (2015) have described the fragmented distribution of *Pollicipes elegans* as including extra-tropical populations in north and central Mexico and northern Peru and populations within the Intertropical Convergence Zone (El Salvador and Costa Rica), the warmest waters of the eastern Pacific (see Figure 2). According to Manuel Ixquiac-Cabrera (pers. comm. in Marchant et al. 2015), *Pollicipes elegans* was not detected on the coast of Guatemala. Apparently, the coast of Nicaragua has never been sampled for the presence of *Pollicipes elegans*. The southern limit of *Pollicipes elegans* in the northern hemisphere is Punta Burica (~8°N) on the southern Pacific coast of Costa Rica (Mora-Barboza & Sibaja-Cordero 2018), close to the border of Panama, since the presence of *P. elegans* in Panama (Marchant et al. 2015) and in Colombia (Lozano-Cortés & Londoño-Cruz 2013) has not been detected. This species appears again near the equator, its most northern record being at Punta Tortuga, Ecuador (0° 46′N, Inaturalist.org 2021). In the southern hemisphere, *Pollicipes elegans* has also been found in Manabi and Santa Elena provinces of Ecuador (e.g. Isla Salango, ~1° 35′S, Inaturalist.org 2021; Chocolatera, 2° 11′S, Cárdenas-Calle et al. 2020), which are far north of the previous locations mentioned for South America that were in Peru (Figure 2). *Pollicipes elegans* is not present in the Galápagos Islands (Ecuador). The disjunct distribution of *Pollicipes elegans* was considered by Marchant et al. (2015) as paramphitropical, as Newman & Foster (1987) had already suggested, a trans-tropical distribution in which a species is more abundant towards the periphery than at the centre of its latitudinal range.

Regarding the southern limit of *Pollicipes elegans*, Tarazona et al. (1985) and Kameya & Zeballos (1988) detected the presence of this species at several sites in Peru south of the southern limit considered by Barnes (1996) (Figure 2). The southernmost site sampled by Kameya & Zeballos (1988) was Playa Yaya, Chilca (Lima) (12° 29′S). This can be considered the southern limit of the distribution of this species, as we are unaware of any studies further south in Peru where it has been found, and the species is not distributed along the coast of Chile (Juan Carlos Castilla pers. comm.).

The distribution and abundance of *Pollicipes elegans* in Ancon (~11° 46′S) by Tarazona et al. (1985), and between Yasila (Paita, ~5°S) and Chilca (~12°S), recorded in Kameya & Zeballos (1988), was associated with the warm episode of El Niño of 1982/1983 (Paredes et al. 2004, Arntz et al. 2006). Kameya & Zeballos (1988) considered that there was an unusual increase in *Pollicipes elegans* in response to this warm episode. We are not aware of any study with the same territorial coverage, but several have been made in Islas Lobos de Tierra and Islas Lobos de Afuera (~6° 26′S –6° 57′S), where the presence of *Pollicipes elegans* was recorded (e.g. Samamé & Quevedo 2001, de la Cruz et al. 2002, Ramírez et al. 2008, de la Cruz et al. 2015a, b, Ramírez & de la Cruz 2015), with some observations further south: Ancon (~11° 46′S) (in 1997/1998 and 2001, Leonardo Romero pers. comm.), and Isla San Lorenzo, Callao, Lima (~12° 09′S) in 1997/1998 (Alegre 2017). This last record was also associated with an El Niño episode (1997/1998). In conclusion, the southern distribution of this species is Punta Aguja, Piura (5° 47′S) and the Lobos de Tierra (~6° 26′S) and Lobos de Afuera (~6° 57′S) islands in Peru, but during El Niño or warm conditions, it may extend as far south as Chilca (12° 29′S), as had been reported by Kameya & Zeballos (1988) (Carmen Yamashiro pers. comm.), persisting for a few years after a warm episode. The dynamic nature of the southern limit of *Pollicipes elegans* merits investigation in the future in the context of global change, as does the extent of the zone of overlap with *P. polymerus* in the north.

Pollicipes pollicipes

The northern and southern limits of the geographic distribution of *Pollicipes pollicipes* are similar to those considered in Barnes (1996) (Figure 2). Some earlier records in Ireland and Scotland mentioned in Barnes (1996) are considered to be erroneous or doubtful, including the British records of *Pollicipes* quoted by Darwin (1852) that were considered misidentifications by other authors according to Southward (2008). However, there is a vague mention of *Pollicipes pollicipes* in Ireland by Fischer-Piette (1936) cited by Barnes (1996) and there are two recent observations in Ireland and Northern Ireland (Darrynane Bay, Kerry 51°45′ in 2016, and White Park Bay, 55°13′ in 2015, in records.nbnatlas.org). Nevertheless, we were able to confirm that the reference from Kerry in Ireland was wrong, so it cannot be considered and has already been removed from this website. Regarding the reference to Northern Ireland, as well as another reference recorded on this website with respect to the presence of *Pollicipes pollicipes* in Wales, the UK (the Dakotian, Dale, 51°42′N in 2016, in records.nbnatlas.org), we were unable to confirm that these are indeed locations where this species occurs, so the presence of this species in Wales and Northern Ireland was considered doubtful (Figure 2). In south-western England, on the other hand, there are observations of occasional individuals found around the Land's End peninsula, from Lamorna to Sennen Cove, dating back to the late nineteenth century (specimens in the Natural History Museum, London). On this peninsula, there is a solitary record from the 1980s, which is mentioned in Barnes (1996), with several recent observations of scattered individuals since 2005 (e.g. Porthcurno, Tator Du Lighthouse) with animals found in most years just west of Sennen Cove, with a maximum of eight individuals being found in a suitable 20×20 m area in 2021 (Southward 2008, Stephen J. Hawkins, Keith Hiscock and Nova Mieszkowska pers. obs.; Barnes 2021). In the Channel Islands, there are nineteenth century observations of *Pollicipes pollicipes* at Guernsey and Sark (Ansted & Latham 1865 in le Mao et al. 2020), but no recent observations. Therefore, we have considered that the northern limit of the distribution of this species in Europe is Sennen Cove, Land's End peninsula, the UK (50°4′N) (Figure 2), and that the distribution of *Pollicipes pollicipes* in Ireland, Northern Ireland and Wales (the UK) should be further investigated.

On the European and African Atlantic continental coast, this species is found from north Brittany (France) southwards down the coasts of France, Spain, Portugal, Morocco, Western Sahara, Mauritania and Senegal (Figure 2). In mainland Europe, the northern limit of distribution of *Pollicipes pollicipes* is plateau de la Méloine (48°43′N –03°47′W; Eric Thiébaut pers. comm.) in the north-east of the Bay of Morlaix, although there is a nineteenth century record from Berck-sur-Mer (50°24′N, Musée des Confluences, in gbif.org) that was considered doubtful, as it is a very sandy coast (Figure 2). The most southern location where this species has been observed is Cape Manuel, Dakar (14°38′N, Fernandes et al. 2010), which can be considered the southern limit of this species. Stubbings (1967) had already mentioned that there was no doubt in considering Dakar as the southern limit of *P. pollicipes*.

In Macaronesia, *P. pollicipes* only occurs in the Canary Islands, at Tenerife (Marín & Luengo 1998) and Fuerteventura (González et al. 2012), and there are no records of its presence in the Azores (Southward 2008), as Barnes (1996) had already mentioned, or in Madeira (Wirtz et al. 2006).

Regarding the distribution of this species in the Mediterranean, there is no doubt about its presence on the North African coast, with recent records along this coast (e.g. Kallouche et al. 2014) as far east as Aguelli Island, Algiers, Algeria (36°47′N –3°21′E) (Bachetarzi et al. 2016). Barnes (1996) had also noted the presence of *Pollicipes pollicipes* in Algiers. In addition, there is a record of this species on Isla de Alborán in the Alboran Sea, part of the western Mediterranean Sea (Mas et al. 1996). However, there is more doubt regarding its presence on the northern Mediterranean coast of Spain and France. Barnes (1996) mentioned its presence in Catalan Bay, Gibraltar, and considered that this species extended along the southern Spanish and French coast to the "Mer de Nice" (Caziot 1921). There is also a nineteenth century record of *Pollicipes pollicipes* near Montpellier (Sète) (Museum of Comparative Zoology, Harvard University in gbif.org). As there are no recent observations of the presence of *Pollicipes pollicipes* on the southern Spanish and French coasts, we consider these records from the environs of Nice and near Montpellier (Sète) as doubtful and are in need of a sampling effort directed at this species and the type of habitat where it occurs (wave-exposed shores).

Pollicipes caboverdensis

The description of *Pollicipes caboverdensis* came after the review of Barnes (1996) (Fernandes et al. 2010). According to personal observations and studies (Fernandes et al. 2010, Quinteiro et al. 2007, 2011, Baessa 2015, Soares 2018), and information provided by local fishermen and local restaurant employees, *Pollicipes caboverdensis* is present on all the islands of Cape Verde (Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal, Boavista, Santiago, Fogo and Brava), with the exception of Maio where it was not possible to confirm its presence (Figure 2).

Considering all *Pollicipes* species and their respective geographical limits, observations should be made on the exposed rocky coastline of some regions, where there are doubts, or need of more recent observations, about the presence of these species: the Aleutian Archipelago and the Pacific coast of Baja California for *P. polymerus*; the Pacific coast of Baja California, the coast of Nicaragua and the central and southern coasts of Peru for *P. elegans*; and the coast of Ireland and of Northern Ireland and South West Wales (the UK), the south Mediterranean coast of Spain and the north Mediterranean coast of Africa from Algiers eastwards for *P. pollicipes*. The most intriguing question is the extent of overlap in the distributions of *Pollicipes polymerus* and *P. elegans* in Baja California at Punta Santa Domingo.

Ecological habitat, and patterns of distribution and abundance

Barnes (1996) described the ecological habitat of *Pollicipes* species by reviewing the knowledge of its physical features and noting a few abundant species or taxa that co-occurred with *Pollicipes polymerus* and *Pollicipes pollicipes*, as well as other barnacles that were more abundant close to the upper and lower limits of these species. We have reviewed the literature concerning the abiotic and biotic environment of the habitats inhabited by each *Pollicipes* species, as well as their patterns of distribution and abundance.

Physical habitat and distribution

The physical habitat features that we identified from subsequent, more recent publications are similar to those described by Barnes (1996). We have also updated information regarding *Pollicipes elegans* and *Pollicipes caboverdensis*.

All species occur on wave-exposed coasts (*Pollicipes polymerus* Gagne et al. 2016; *P. pollicipes* Sousa et al. 2013; *P. elegans* Oliva 1995 in Monsalve 2016; *P. caboverdensis* Fernandes et al. 2010), usually on vertical or steep-sided rocks where wave action is strong (*P. polymerus* Barnes & Reese 1960, Bingham 2016; *P. pollicipes* Macho 2006, Boukaici et al. 2015; *P. elegans* Samamé & Quevedo 2001, Barraza et al. 2014, Ramírez et al. 2017). They also occur in localized areas protected from the direct force of waves, but that are characterized by constant water turbulence, or by strong currents, such as surge gullies and channels (*Pollicipes polymerus* Barnes & Reese 1960 and *P. pollicipes* Barnes 1996). Passages with fast tidal currents (*Pollicipes polymerus* Lamb & Hanby 2005) are also colonized, as well as crevices, rock fissures and caves (*P. pollicipes* Cruz 2000, Fernandes et al. 2010; *P. elegans* Kameya & Zeballos 1988, Monsalve 2016, Ladines 2018). *Pollicipes polymerus* is perhaps the most opportunistic species, being found on rocky substrata of different geologies, or attached to mussels and acorn barnacles (Austin 1987 in Lauzier 1999b), colonizing surfaces cleared by storm disturbance such as gaps in mussel beds (Paine & Levin 1981, Meese 1993), overhangs and boulders (Barnes 1996), as well as diverse artificial structures (Barnes & Reese 1960), including buoys (Austin 1987 in Lauzier 1999b), seawater intakes (Newman & Abbott 1980) and the supports connected to offshore oil platforms (Page 1986). In contrast, there are very few records of the other *Pollicipes* species on substrata other than rock – a population of *P. pollicipes* on a ship stranded on a beach in Nouakchott, Mauritania (Fernandes et al. in prep.), and the presence of *P. elegans* on buoys (Ladines 2018).

All *Pollicipes* species seem to be mostly intertidal, although there are references to their occurrence in the shallow subtidal zone (*P. polymerus* McDaniel 1985 in Lauzier 1999b, Austin 1987 in Lauzier 1999b; *P. pollicipes* Cruz 2000, Borja et al. 2006a, b; *P. elegans* Alegre 2017). Barnes (1996) described the presence of *Pollicipes pollicipes* in channels that may be 100 m deep, and Lamb & Hanby (2005) outlined the lower limit of the vertical distribution of *P. polymerus* as 30 m water depth. The interest of recreational divers about the large aggregations of *Pollicipes polymerus* at Nakwakto Rapids, Slingsby Channel, British Columbia (Lamb & Hanby 2005) has provided consistent depth records of 12–15 m for this subtidal population (north-east Pacific diving websites, e.g. Rogers 2016). Besides these observations, the actual measurements of the maximum depth of occurrence of *Pollicipes* species are rare. Exceptionally, Borja et al. (2006a) stated maximal depths of 1.5 or 2 m below the Lowest Astronomical Tide for *Pollicipes pollicipes* within the Gaztelugatxe Marine Reserve (north-west Spain). In the intertidal zone, all *Pollicipes* species commonly occur in the mid-shore (*P. polymerus* Paine 1974, Jamieson et al. 2001; *P. pollicipes* Cruz 2000, Macho 2006, Fernandes et al. 2010; *P. elegans* Kameya & Zeballos 1988, Ramírez et al. 2017; and *P. caboverdensis* Fernandes et al. 2010). Their intertidal distributions have been also described to include the low-shore level for *Pollicipes pollicipes* (e.g.

Cruz 2000, Macho 2006, Sousa et al. 2013, Jacinto et al. 2015), *P. polymerus* (Menge et al. 2011, Bingham 2016, Gagne et al. 2016) and *P. elegans* in Ecuador (Ladines 2018). The upper limit of their vertical distribution has been described to reach 4.1 m above chart datum for *Pollicipes polymerus* in British Columbia (Jamieson et al. 1999) and 4–5 m above chart datum for *P. pollicipes* in SW Portugal (Cruz 2000).

Abundance

We have reviewed the literature regarding quantitative population assessments of abundance for species of the genus *Pollicipes*. To our knowledge, there are no studies on the abundance of *Pollicipes caboverdensis*. Generally, abundances of the other three species have been locally assessed, either by measuring their percentage cover or by quantifying their number and/or weight of individuals per unit area. While percentage cover has widely been used as a proxy of abundance of *Pollicipes polymerus* (Dawson et al. 2014 "Appendix B", Menge et al. 2011) and *P. pollicipes* (Spain – Borja et al. 2006a, Parada et al. 2012, Bidegain et al. 2017; Portugal – Sousa et al. 2013, Jacinto & Cruz 2016, Neves 2021), this variable has never been used in the case of *P. elegans*. On the other hand, density and/or biomass quantifications are currently widespread in the literature for *Pollicipes polymerus* (e.g. Austin 1992 in Jamieson et al. 1999, Dawson et al. 2014 "Appendix B", Gagne et al. 2016), *P. pollicipes* (Spain – Borja et al 2006a, b, Bidegain et al. 2017; Portugal – e.g. Sousa et al. 2013, Cruz et al. 2015c, Neves 2021; Morocco – Boukaici et al. 2012, Bourassi et al. 2019) and *P. elegans* (Costa Rica – Mora-Barboza & Sibaja-Cordero 2018; Ecuador – Ladines 2018; Peru mainland – e.g. Pinilla 1996, Ordinola et al. 2010, Alemán et al. 2016; Lobos de Tierra Island and Lobos de Afuera Islands – e.g. Samamé & Quevedo 2001, Ramírez & de la Cruz 2015). The following examples refer to estimates of biomasses per area of three species: *Pollicipes polymerus* ranged from 0 to 39 kg/m^2 across the total estimated area of intertidal distribution of this species within 19 rocks off the west coast of Vancouver Island (Gagne et al. 2016); *P. pollicipes* ranged from 1.3 to 7.7 kg/m^2 on mid-shore and from 0.5 to 2.4 kg/m^2 on low-shore populations within three regions in Portugal (Sousa et al. 2013); and *P. elegans* averaged 21.1 kg/m^2 across the total estimated area of intertidal distribution of this species within ten sites in Lobos de Afuera Islands (Ramírez & de la Cruz 2015).

This wealth of research was, however, undertaken with a diversity of objectives and methodologies, hindering the combined analysis of data from multiple studies and precluding interspecific comparisons. Several studies were part of stock assessment surveys and protocols for monitoring local *Pollicipes* species fisheries (e.g. Ramírez & de la Cruz 2015, Bingham 2016, Bidegain et al. 2017), aiming to provide baseline data on temporal or spatial comparisons of abundance (e.g. de la Cruz et al. 2001, Borja et al. 2006a, Menge et al 2011), which can support the evaluation of the resource status (e.g. Cruz et al. 2015c, de la Cruz et al. 2015b) and the effects of management strategies (e.g. Borja et al. 2006b, Cruz et al 2008). Due to the role of *Pollicipes* as habitat-forming species, qualitative or quantitative information on abundance has also been important for the conservation of priority areas (Rubidge et al. 2020, Neves 2021).

The more standardized methodologies (*Pollicipes polymerus* – Lauzier 1999a; *P. pollicipes* – Sousa et al. 2013; *P. elegans* – Kameya & Zeballos 1988, Samamé & Quevedo 2001) were based on the relative density/biomass per size class, taken from a series of destructive samples, and then corrected by the total area of *Pollicipes* species spatial coverage, allowing calculation of the overall size of a population, or the proportion of its harvestable fraction. As an alternative approach, the integration of local ecological knowledge (LEK) on scientifically based assessments and management plans has been proposed for the First Nations' fishing territories of *Pollicipes polymerus* in British Columbia, namely through the inclusion of estimates of harvestable biomass provided by experienced harvesters (Lessard et al. 2003, Gagne et al. 2016). In fact, experienced harvesters of *Pollicipes* species possess much relevant empirical knowledge and wisdom about traditional issues related to harvesting locations, conditions and techniques. They often develop visual skills to estimate the availability of the resource and detect its population changes within localities where they usually operate; thus, their involvement in management decisions and compliance should be encouraged (Gagne et al. 2016 and references therein). Therefore, by adapting knowledge transfer procedures in the context of other *Pollicipes* species fisheries, LEK can be acquired as quantifiable information to supplement scientific data. LEK could be a potentially useful tool for assessing abundance in fragmented three-dimensional habitats (such as crevices/caves) and for overcoming the challenges of surveying subtidal areas or remote and risky intertidal areas.

Recently, other promising approaches have been developed to estimate the extent of intertidal areas occupied by *Pollicipes* species using advanced technological tools, namely GPS mapping handheld devices (Gagne et al. 2016) or unmanned aerial vehicles (drones) (Neves 2021). The feasibility of using drones equipped with high-resolution digital cameras to quantify the abundance of *Pollicipes pollicipes* has been tested on several shores in central and SW Portugal (see Neves 2021 for the Berlengas Nature Reserve). Drone imagery has proven successful in covering large spatial extents in a timely manner, with sufficient resolution to assess *Pollicipes pollicipes* populations in extreme environments, such as wave-swept rocky shores located in islets of difficult and dangerous access (TC and DJ pers. obs.). Stalked barnacle percentage cover was estimated from images collected through a low-altitude (<5 m) drone (DJI phantom 4+) and compared with estimates derived from photo-quadrats (25 × 25 cm and 50 × 50 cm). These two methods described similar spatial patterns of abundance of *Pollicipes pollicipes*, demonstrating the suitability of drone imagery as an alternative method to study the intertidal distribution of this species (Neves 2021). In other regions and for the other *Pollicipes* species, this new technology-based approach should be tested, ground-truthed with *in situ* sampling, and, where appropriate, validated with LEK-based approaches, to obtain multiple abundance estimates at relevant scales, which could hopefully inform stock assessment and management, as well as allow adequate intra- and interspecific comparisons.

Associated taxa

We have reviewed the biological assemblages associated with each of the *Pollicipes* species, considering taxa (nomenclature following WoRMS Editorial Board (2021)) that have been described as co-occurring with *Pollicipes* species in the same habitat (i.e. every taxon whose presence was observed in overlapping distribution ranges, or forming an ecological interaction with a *Pollicipes* species – see Table 4 and associated taxa table in supplementary material which presents bibliographic references and geographic region of records for each taxon). The following co-occurring categories were defined: (1) “Accompanying” – taxa interspersed with specific *Pollicipes* species at the same vertical intertidal level(s) and/or microhabitat(s), with the symbol (+) applied to those accompanying taxa registered in greatest abundance and/or referred to as “dominant” in the source texts; (2) “Near limits – Upper and Lower intertidal limit or Adjacent microhabitats” – taxa, respectively, present at or near the vertical or horizontal limits of *Pollicipes* species and interspersed among *Pollicipes* species at those limits; (3) “Endozoic and Epizoic” – taxa, respectively, found to be resident on the interior or the exterior of a *Pollicipes* species; (4) “Predators” – taxa found to prey upon a *Pollicipes* species (Table 4).

The inclusion of taxa in Table 4 required information, either qualitative or quantitative, concerning the association of those taxa with *Pollicipes* species. Consequently, studies presenting just lists of taxa for a given shore/region, with inclusion of a *Pollicipes* species but lacking any other information on co-occurrence, were not included. We have included the references from the “Ecological Habitat” section of Barnes’ (1996) review, studies made since Barnes (1996) and some relevant references prior to Barnes (1996) (some of these also considered in other sections of Barnes 1996). The references presented in Table 4 were all based on non-destructive sampling procedures. The presence of every taxon was visually recorded within the same sampling areas where a *Pollicipes* species was found, but information on abundance was not provided among the whole set of taxa references.

Table 4 Co-occurring category, taxonomic group and taxa associated with *Pollicipes* species (scientific names following WoRMS Editorial Board 2021), considering non-destructive surveys of biological assemblages

Accompanying	Near distribution limits	Endozoic/epizoic and predators
Pollicipes polymerus		
Rhodophyta (Red algae): *Callithamnion pikeanum, Corallina vancouveriensis* (+), *Endocladia muricata,* genus *Lithophyllum,* genus *Polysiphonia,* genus *Porphyra, Halosaccion glandiforme, Mastocarpus papillatus, Neorhodomela larix, Plocamium violaceum, Pyropia pseudolanceolata* Ochrophyta (Brown algae): genus *Alaria/Alaria marginata, Hedophyllum sessile, Postelsia palmaeformis* Chlorophyta (Green algae): genus *Ulva* Porifera (Sponges): genus *Haliclona, Halichondria (Halichondria) panicea* Cnidaria, Anthozoa (Anemones): *Anthopleura elegantissima, Anthopleura xanthogrammica* Bryozoa: Phylum *Bryozoa* Mollusca, Polyplacophora (Chitons): *Dendrochiton flectens, Katharina tunicata, Tonicella lineata* Mollusca, Gastropoda (Limpets): *Lottia austrodigitalis, Lottia digitalis, Lottia pelta, Lottia strigatella* Mollusca, Bivalvia (Mussels and other bivalves): *Mytilus californianus* (+), *Mytilus trossulus, Penitella penita* Echinodermata, Echinoidea (Urchins): *Strongylocentrotus purpuratus* Echinodermata, Asteroidea (Seastars): *Leptasterias hexactis* Arthropoda, Cirripedia (Barnacles): *Balanus glandula* (+), *Balanus nubilus, Chthamalus dalli, Chthamalus fissus, Megabalanus californicus, Tetraclita rubescens, Semibalanus cariosus* (+)	Rhodophyta (Red algae): *Endocladia muricata* (*A*) Ochrophyta (Brown algae): genus *Fucus* (*U*), genus *Pelvetiopsis* (*U*), *Postelsia palmaeformis* (*U*) *Egregia menziesii* (*A*), genus *Alaria/Alaria marginata* (*A*), *Nereocystis luetkeana* (*A*), *Postelsia palmaeformis* (*A*) Tracheophyta (Seagrasses): *Phyllospadix scouleri* (*A*) Cnidaria, Anthozoa (Anemones): *Anthopleura xanthogrammica* (*A*) Mollusca, Bivalvia (Mussels and other bivalves): *Mytilus trossulus* (*L*) Echinodermata, Echinoidea (Urchins): *Strongylocentrotus purpuratus* (*A*) Echinodermata, Asteroidea (Seastars): *Pisaster ochraceus* (*L, A*) Arthropoda, Cirripedia (Barnacles): *Balanus glandula* (*U*), *Chthamalus dalli* (*U*), *Chthamalus fissus* (*U*) *Semibalanus cariosus* (*L*), *Tetraclita rubescens* (*L*)	*Endozoic* Ascomycota, Dothideomycetes (Fungi): *Pharcidia balani* *Epizoic* Chlorophyta (Green algae): Unidentified filamentous green alga(e) Mollusca, Gastropoda (Limpets): *Lottia austrodigitalis, Lottia digitalis, Lottia pelta, Lottia strigatella, genus Notoacmaea* Arthropoda, Cirripedia (Barnacles): *Chthamalus fissus* *Predators* Mollusca, Gastropoda, Dogwhelks: *Nucella canaliculata, Nucella emarginata, Nucella lamellosa* Nemertea, Hoplonemertea (Ribbon worms): *Emplectonema gracile* Echinodermata, Asteroidea (Seastars): *Leptasterias hexactis, Pisaster ochraceus* Chordata, Aves (Birds): *Aphriza virgata, Corvus brachyrhynchos*/genus *Corvus, Haematopus bachmani, Larus glaucescens, Larus occidentalis*

References: Feder (1959) *in* Paine (1980), Giesel (1968), Jobe (1968), Giesel (1969, 1970), Dayton (1971), Paine (1974), Murphy (1978), Brym (1980), Paine (1980), Hartwick (1981), Paine & Levin (1981), Vermeer (1982), Hoffman (1984), Palmer (1984), Mercurio et al. (1985), Marsh (1986), Page (1986), West (1986), Austin (1987) in Lauzier (1999b), Bernard (1988), Byers (1989), Hoffman (1989), Lindberg & Pearse (1990), Wootton (1992), Meese (1993), Wootton (1994), References *in* Barnes (1996), Wootton (1997), Sanford (1999), Jamieson et al. (2001) (Appendix A – Site descriptions), Kay (2002), Crummett & Eernisse (2007), Wootton (2010), Menge et al. (2011), Murphy (2014), Bingham (2016).

(+): accompanying taxa registered in greatest abundance.

(*U, L, A*): taxa, respectively, present at or near the upper/lower limits of *Pollicipes* species or in adjacent microhabitats.

(*Continued*)

Table 4 (*Continued*) Co-occurring category, taxonomic group and taxa associated with *Pollicipes* species (scientific names following WoRMS Editorial Board 2021), considering non-destructive surveys of biological assemblages

Accompanying	Near distribution limits	Endozoic/epizoic and predators
Pollicipes pollicipes		
Rhodophyta (Red algae): *Asparagopsis armata, Callithamnion granulatum, Chondrus crispus, Corallina officinalis* (+), *Ellisolandia elongata, Gelidium corneum,* genus *Ceramium,* genus *Polysiphonia,* "*Lithothamnia*" *sensu Hawkins & Jones 1992/Lithophyllum incrustans* (+), *Lomentaria articulata, Mastocarpus stellatus, Nemalion elminthoides, Osmundea pinnatifida, Plocamium cartilagineum, Pterocladiella capillacea, Tenarea tortuosa* Ochrophyta (Brown algae): *Caulacanthus ustulatus/genus Caulacanthus, Ralfsia verrucosa* Chlorophyta (Green algae): genus *Ulva* Porifera (Sponges): genus *Hymeniacidon* Cnidaria, Hydrozoa: class Hydrozoa Cnidaria, Anthozoa (Anemones): *Actinia equina* Mollusca, Gastropoda (Periwinkles, Dogwhelks, Limpets): *Melarhaphe neritoides, Nucella lapillus,* genus *Patella, Patella depressa, Patella ulyssiponensis* (+), *Siphonaria pectinata* Mollusca, Bivalvia (Mussels): *Mytilus galloprovincialis* (+), *Perna perna* Echinodermata, Echinoidea (Urchins): *Paracentrotus lividus* Echinodermata, Asteroidea (Seastars): *Marthasterias glacialis* Arthropoda, Cirripedia (Barnacles): *Chthamalus montagui, Chthamalus stellatus, Megabalanus tintinnabulum, Perforatus perforatus*	Rhodophyta (Red algae): *Corallina officinalis* (*U, L*), "*Lithothamnia*" *sensu* Hawkins & Jones 1992/ *Lithophyllum incrustans* (*U, L*), genus *Ceramium* (*U, L*) *Nemalion elminthoides* (*U*), genus *Polysiphonia* (*U*) *Asparagopsis armata* (*L*), *Plocamium cartilagineum* (*L*), *Tenarea tortuosa* (*U*) Ochrophyta (Brown algae): *Caulacanthus ustulatus* (*U*), *Ralfsia verrucosa* (*U*) genus *Cystoseira* (*L*), genus *Fucus* (*L*), genus *Laminaria* (*L*), *Saccorhiza polyschides* (*L*) Chlorophyta (Green algae): *Codium tomentosum* (*L*) Cnidaria, Anthozoa (Anemones): *Anemonia viridis* (*A*) Mollusca, Gastropoda (Limpets and Periwinkles): *Patella ulyssiponensis* (*U, L*) *Melarhaphe neritoides* (*U*), *Patella depressa* (*U*), *Siphonaria pectinata* (*U*) Mollusca, Bivalvia (Mussels): *Mytilus edulis* (*U*), *Mytilus galloprovincialis* (*U*) Echinodermata, Echinoidea (Urchins): *Paracentrotus lividus* (*L, A*) Arthropoda, Cirripedia (Barnacles): *Chthamalus montagui* (*U*), *Chthamalus stellatus* (*U*) *Megabalanus tintinnabulum* (*L*)	*Endozoic* Rhodophyta (Red algae): Unidentified endolithic alga, *Porphyra* sp. (*Conchocelis* phase) *Epizoic* Rhodophyta (Red algae): *Corallina officinalis,* "*Lithothamnia*" *sensu* Hawkins & Jones 1992, *Tenarea tortuosa* Ochrophyta (Brown algae): *Caulacanthus ustulatus, Ralfsia verrucosa* Chlorophyta (Green algae): genus *Ulva* Bryozoa: Phylum *Bryozoa* Mollusca, Bivalvia (Mussels): *Mytilus galloprovincialis* Arthropoda, Cirripedia (Barnacles): *Chthamalus dentatus, Chthamalus montagui, Perforatus perforatus* Mollusca, Gastropoda (Limpets): *Patella ulyssiponensis* *Predators* Mollusca, Gastropoda (Dogwhelks): *Nucella lapillus* Annelida, Polychaeta (Worms): *Eulalia viridis* Echinodermata, Asteroidea (Seastars): *Marthasterias glacialis* Chordata, Aves (Birds): *Larus michahellis* Chordata, Pisces (Fishes): genus *Diplodus/Diplodus sargus* *Balistes capriscus*

References: Broch (1927), References in Barnes (1996), Cruz (2000), Macho (2006), Fernandes et al. (2010), Moreno et al. (2010), Boukaici et al. (2012, 2015), Pedro (2017), Neves (2021), Personal observations.

(+): accompanying taxa registered in greatest abundance.

(*U, L, A*): taxa, respectively, present at or near the upper/lower limits of Pollicipes species or in adjacent microhabitats.

(*Continued*)

Table 4 (*Continued*) Co-occurring category, taxonomic group and taxa associated with *Pollicipe*s species (scientific names following WoRMS Editorial Board 2021), considering non-destructive surveys of biological assemblages

Accompanying	Near distribution limits	Endozoic/epizoic and predators
Pollicipes elegans		
Chlorophyta (Green algae): genus *Chaetom*orpha (+) Mollusca, Polyplacophora (Chitons): *Acanthopleura echinata, Chiton (Chiton) granosus, Enoplochiton niger* Mollusca, Gastropoda (Limpets and Trochids): genus *Fissurella* *Tegula atra* Mollusca, Bivalvia (Mussels): *Modiolus capax* (+)*, Perumytilus purpuratus* (+)*, Semimytilus algosus* (+) Annelida, Polyc`haeta (Worms): *Nereis grubei* Arthropoda, Decapoda (Crabs): *Acanthocyclus gayi* Echinodermata, Holothuroidea (Sea cucumbers): *Pattalus mollis*	Rhodophyta (Red algae): *Gymnogongrus durvillei* (*U*) Mollusca, Gastropoda (Periwinkles): *Echinolittorina peruviana* (*U*) Arthropoda, Cirripedia (Barnacles): *Austromegabalanus psittacus* (*L*) Arthropoda, Decapoda (Crabs): *Acanthocyclus gayi* (U) Echinodermata, Asteroidea (Seastars): *Heliaster helianthus* (*L*)*, Stichaster striatus* (*L*)	*Epizoic* Chlorophyta (Green algae): genus *Chaetom*orpha *Predators* n/a
References: Kameya & Zeballos (1988) (Figure 3, adapted from Paredes 1974), Barraza et al. (2014).		
Pollicipes caboverdensis		
Chlorophyta (Green algae): genus *Chaetom*orpha (+)	n/a	*Epizoic* Chlorophyta (Green algae): genus *Chaetom*orpha *Predators* n/a

References: Fernandes et al. (2010).
(+): accompanying taxa registered in greatest abundance.
(*U, L, A*): taxa, respectively, present at or near the upper/lower limits of *Pollicipes* species or in adjacent microhabitats.
n/a: information not available.
Information organized by taxon (with bibliographic references and geographic region of records) is presented in supplementary material (associated taxa table).

From the total of 126 taxa mentioned in Table 4, the great majority were associated with *Pollicipes polymerus* (45%) and *P. pollicipes* (40%), with only 13% recorded with *P. elegans* and 1% with *P. caboverdensis*. This reflects the higher number of ecological studies on the two former species and their associated assemblages, compared with much less research effort expended on the other two species. The overall biological composition of *Pollicipes* species assemblages comprised the following categories: 1% fungi, 40% macrophytes, 2% Porifera, 4% Cnidaria, 2% Bryozoa, 1% Nemertea, 2% Annelida, 25% Mollusca, 12% Crustacea, 6% Echinodermata and 6% Chordata.

Apart from *Pollicipes caboverdensis* habitat, mussels were invariably described as the dominant species, and accompanying mussel clusters are a characteristic element of these communities (Table 4, Figure 3). Acorn barnacles were also consistently present as major co-occurring filter-feeders in the habitats of *Pollicipes* species (Table 4, Figure 3). Calcareous turfs and crusts were both abundant in association with *Pollicipes polymerus* and *P. pollicipes*, and a diverse assemblage

Figure 3 *Pollicipes* species in natural habitats. (A) *Pollicipes polymerus* (courtesy of Jesús Pineda); (B) panoramic view of *Pollicipes pollicipes* in Berlenga (Portugal); (C) *Pollicipes elegans* (Jicalapa, La Libertad, El Salvador, www.inaturalist.org/observations/69057855); (D) *Pollicipes caboverdensis* (Santiago Island, Cape Verde). Approximate scale presented when appropriate.

of foliose red and brown algae is also present in the habitats of both species (Table 4). Thus, not surprisingly, the assemblages described are typical of wave-exposed and very wave-exposed steep rocky shores in the regions where *Pollicipes* species occur. Remarkably, the green alga, *Chaetomorpha*, was recorded as a very conspicuous element of the habitat of both *Pollicipes elegans* in El Salvador and *P. caboverdensis* in Sal and Santiago islands (Table 4). Several sessile taxa, usually abundant in these assemblages, have been frequently observed as epizoics of large specimens of *Pollicipes* (Table 4). Brym (1980) recorded several biofilm and algal items when scrutinizing the surfaces of *Pollicipes polymerus* capitula, while Hoffman (1989) recorded "epiphytic algae" attached to their peduncles; both studies were carried out in California. In *Pollicipes pollicipes* from Morocco, Broch (1927) noted external colonization by "algae, bryozoans and lamellibranchs" on the peduncle, and by *Perforatus perforatus* on the capitulum.

North-eastern Pacific limpets, mostly belonging to the genus *Lottia*, have frequently been recorded living on the capitular plates (usually, the scutum is the limpet's home scar) of *Pollicipes polymerus* and on nearby rock surfaces (Table 4). The association of *Pollicipes polymerus* with the fingered limpet, *Lottia digitalis,* and its sibling species, the southern finger limpet, *L. austrodigitalis,* has been widely documented along the west coast of North America (associated taxa table in supplementary material). The patterns of shell colour and shape of these two limpet species, when living epizoically on *Pollicipes polymerus,* were described as identical to those of the barnacle's plates (see Section 'Post-settlement processes of distribution and abundance'). North-eastern Atlantic limpets, mostly belonging to the genus *Patella*, have also been described as common inhabitants on rocky intertidal habitats where *Pollicipes pollicipes* occurs (Table 4) and can be seen moving on *P. pollicipes* capitula (Cruz 2000, Figure 12). Limpet populations, surveyed within areas comprising *Pollicipes pollicipes* clumps in the Cape of Sines (SW Portugal), were mostly found on rock surfaces, located underneath or adjacent to *P. pollicipes* peduncles, and were mainly composed of *Patella ulyssiponensis* (95% of 383 individuals), with approximately half of the total number of limpets (52%) being juveniles (maximum shell length lower than or equal to 10 mm) (Cruz et al. unpublished data).

Predation of *Pollicipes polymerus* and *P. pollicipes* by birds (mostly gulls) and dogwhelks (muricid snails of the genus *Nucella*) has been clearly documented (Table 4). Starfish were found to prey upon *Pollicipes polymerus* (*Pisaster ochraceus*: references *in* Lauzier 1999b and Jamieson et al. 2001; *Leptasterias hexactis*: Wootton 1994) and *Pollicipes pollicipes* in SW Portugal (*Marthasterias glacialis*, TC pers. obs., see Figure 11), and to occur close to the lower vertical limit of *Pollicipes elegans* in Peru (*Stichaster striatus* and *Heliaster helianthus*, Table 4).

The infection of *Pollicipes polymerus* by the ascomycete *Pharcidia balani* (Table 4), also known as *Didymella conchae*, might be dubious, as it was reported by Giesel (1968) apparently based only on the texture of capitular plates and on previous references to parasitized limpets in California (Test 1945), but the genus *Pollicipes* was indeed described as one of many hosts of this endozoic fungus (Kohlmeyer & Kohlmeyer 2013). Endolithic algae have been also reported to infect peduncular scales and capitular plates of *Pollicipes pollicipe*s (Table 4, Drew & Richards 1953).

The faunal diversity associated with *Pollicipes* species is not fully considered in Table 4. In fact, the infauna, as well as part of the epifaunal community, living within *Pollicipes* species and their accompanying mussel clusters is characterized by many invertebrates, particularly inconspicuous species of small size and/or cryptic behaviour. Barnes & Reese (1960) stated that dense aggregates formed by *Pollicipes polymerus* and *Mytilus californianus* provide shelter for a great number of animals, in particular crustaceans, flat worms and annelids. A similar richness of invertebrate groups (crabs, amphipods and polyclad flatworms, as well as opisthobranch molluscs and nemerteans) residing within *Pollicipes polymerus* clumps was found by Hoffman (1989), who emphasized their possible role as predators of young barnacles. When disturbed, numerous specimens of an unidentified isopod, possibly belonging to the genus *Dynamenella*, emerged from their hiding places within the Nakwakto *Pollicipes polymerus* clusters (Lamb & Hanby 2005). Likewise, huge numbers of amphipods are also commonly encountered while collecting *Pollicipes pollicipes* clumps in SW Portugal (TC pers. obs.). Extensive faunal lists have been presented in two studies, where destructive samples were collected from *Pollicipes polymerus* (Vancouver Island, Canada – Jamieson et al. 2001 "Appendix B") and *P. elegans* (Yasila to Chilca, Peru – Kameya & Zeballos

1988 "Tabla 2") assemblages. Both studies recorded many polychaete taxa (Kameya & Zeballos 1988, Jamieson et al. 2001), previously described as potentially active predators on newly settled *Pollicipes polymerus* (Bernard 1988). The following taxa were recorded by Jamieson et al. (2001) as "species predominating numerically" (>1000 individuals/species collected, 85% of all individuals found) within the *Pollicipes polymerus-Mytilus californianus* matrix: the small holothurid *Cucumaria pseudocurata*; the snail *Lacuna vincta*, the eelgrass limpet *Lottia alveus* and other small-sized gastropods of the genera *Amphissa* and *Margarites*; the isopod *Cirolana harfordi*, the amphipod genera *Corophium* and *Hyale*, and porcelain crabs such as *Petrolisthes cinctipes* and the genus *Pachycheles*. Small crabs were also observed by Bernard (1988), who suggested them as potential predators of *Pollicipes polymerus*. Additional taxa associated with *Pollicipes elegans* were the predatory gastropod *Concholepas concholepas*, the anemone *Phymactis clematis* and the brittle star *Ophiactis kroeyeri* (Kameya & Zeballos 1988).

It should be noted that observations on the accompanying fauna of *Pollicipes elegans* in Peru by Kameya & Zeballos (1988) were made in 1985, following an El Niño event (1982–1983), and included locations where this species was previously absent (the more southern surveyed sites). A remarkable population increase in *Pollicipes elegans* and a major change in marine community composition were documented along this coast during the El Niño of 1982–1983 (e.g. Tarazona et al. 1985, references in Arntz et al. 2006), possibly affecting local occurrence patterns and hence ecological relationships. Finally, all taxon references that are presented in Table 4 regarding Jamieson et al. (2001) and Kameya & Zeballos (1988) were, respectively, retrieved from "Appendix A – Site descriptions" and "Figure 3, adapted from Paredes 1974", or from the text of methods or discussion sections, and not based on results derived from destructive sampling procedures.

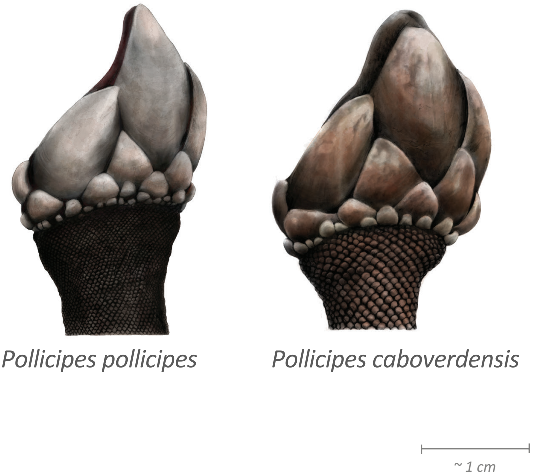
Further information on the co-occurring species of *Pollicipes pollicipes* is expected in the near future, as relevant data (e.g. destructive samples of aggregates and time-series photographs of habitat area) were recently collected from intertidal shores in SW Portugal, Galicia, Asturias and Brittany, under the scope of the European project PERCEBES promoted by BiodivERsA research network (Acuña et al. 2020).

Description of adults

At the time of the Barnes (1996) review, the genus *Pollicipes* included three species (*P. polymerus*, *P. elegans* and *P. pollicipes*) (Foster 1979, Newman & Killingley 1985, Newman 1987). These three species were those that, according to Darwin (1852), "form one thoroughly natural genus" from his list of six originally described species (see section 'Systematics and taxonomy'). Surprisingly, it was only in 2010 that a fourth species of *Pollicipes* was described as an addition to Darwin's original list – *Pollicipes caboverdensis,* endemic to the Cape Verde Islands (Fernandes et al. 2010). This surprise was even greater given that *Pollicipes caboverdensis* is an exploited species with commercial value (Fernandes et al. 2010, Cruz et al. 2015a). Moreover, Darwin visited Cape Verde in 1832 (Darwin 1839), at the beginning of the voyage of the Beagle. Darwin spent 23 days on the island of Santiago in Cape Verde and walked along its coastline (Darwin 1839, Vala 2009), but apparently only near the port of Praia In the coastal zone of the city of Praia, *Pollicipes caboverdensis* does not seem to occur today (TC and JNF pers. obs.). This species is mainly abundant in the northern part of Santiago Island (Baessa 2015). Moreover, Darwin's great interest in barnacles only began later, after he collected an empty 'loco' shell (*Concholepas concholepas*), covered with hundreds of millimetre perforations, on a beach in Chile in 1835 (Stott 2003, Castilla 2009). The small organisms living inside those orifices were shell burrowing barnacles (*Cryptophialus minutus*, 'Mr. Arthrobalanus'), considered to mark Darwin's taxonomical interest in Cirripedia (Stott 2003, Castilla 2009). After returning to England, specimens of barnacles from around the world were posted to Darwin by an army of collectors, friends, missionaries, naturalists, mineralogists and shell collectors (Stott 2003), but probably, no *Pollicipes* were sent to him from the Cape Verde Islands. Given Darwin's extraordinary observation skills, we can speculate that, if he had seen specimens of *Pollicipes caboverdensis*, he would have realized it was a different species.

We have illustrated the four species of the genus *Pollicipes* together for the first time (Figure 4). Externally, as in all pedunculate cirripedes, the capitulum can be distinguished from the peduncle, which has an uncalcified basis. The capitulum is formed by a series of plates composed of calcite: the paired plates – scutum and tergum; the unpaired plates – carina and rostrum; and several other plates of different sizes which may be paired (e.g. lateral or median latus, rostrolatus, carinolatus) or unpaired (subcarina, subrostrum) (nomenclature of plates according to Newman 1987 and Fernandes et al. 2010, see Figure 5). We follow the definition of axes and sides of Anderson (1994): the long axis of the animal is baso-apical; the axis perpendicular to this is rostrocarinal; capitular valves can be identified as right and left relative to carina (dorsally) and the peduncle (anteriorly). The peduncle is narrower and generally longer than the capitulum, consisting of small calcareous scales or spicules arranged in an elastic organic matrix (Chaffee & Lewis 1988). The size of these calcareous scales varies along the peduncle, due to the addition of new scales occurring from the apical end of the peduncle (Chaffee & Lewis 1988).

Pollicipes polymerus *Pollicipes elegans*



Pollicipes pollicipes *Pollicipes caboverdensis*

Figure 4 Colour drawing of the four species of *Pollicipes* by Cristina Espírito Santo. Specimens preserved in alcohol of *Pollicipes elegans* (Ñuro, Peru) and of *Pollicipes caboverdensis* (Tarrafal, Santiago, Cape Verde), frozen specimen of *Pollicipes pollicipes* (Berlengas, Portugal) and a photo of a fresh specimen of *Pollicipes polymerus* (California, the USA) were used for the drawings.

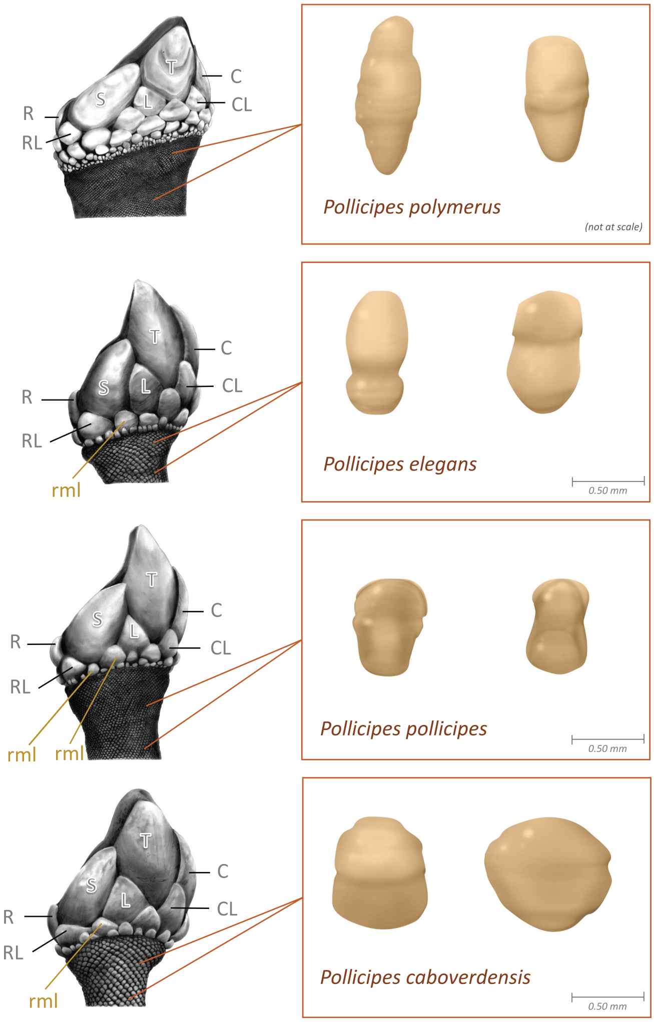


Figure 5 Illustration of the scales of the peduncle of the four species of *Pollicipes* by João Tiago Tavares (based in photos), and of capitular plates of the four species of *Pollicipes* (drawing by Cristina Espírito Santo). Plates: R – rostrum; C – carina; L – median latus; S – scutum; RL – rostrolatus; CL – carinolatus; RML – rostral median latus. Nomenclature of Newman 1987 and Fernandes et al. 2010.

Based on Darwin (1852) and other studies carried out mainly in the first half of the twentieth century (e.g. Gruvel 1905, Pilsbry 1909), Barnes (1996) described in detail the external and internal morphological characteristics of the three *Pollicipes* species known at that time. Herein, we review the diagnostic characteristics of the new order Pollicipedomorpha and the family Pollicipedidae according to Chan et al. (2021); the diagnostic characteristics of the genera *Capitulum* and *Pollicipes* based on Van Syoc (1995) (not cited by Barnes 1996), and the diagnostic characteristics of the four *Pollicipes* species taken from Van Syoc (1995), Fernandes et al. (2010) and Quinteiro et al. (2011) (Table 5, Figures 4 and 5). These diagnostic characteristics are mostly related to external morphology. Regarding internal morphology, besides Barnes' (1996) review of *Pollicipes polymerus*, *P. elegans* and *P. pollicipes*, Fernandes et al. (2010) and Quinteiro et al. (2011) described some aspects of the internal morphology of *P. caboverdensis*. However, no comparative analysis of the internal morphology of the four species has been made.

Table 5 Morphological diagnosis of the four *Pollicipes* species within the new order Pollicipedomorpha (Chan et al. 2021)

Taxa	Diagnosis	Reference
Order Pollicipedomorpha	Capitulum includes a large number (20– 40+) of imbricating, secondary lateral plates, which decrease in size towards the basal margin.	Chan et al. (2021)
Family Pollicipedidae	Small accessory lateral plates present on basal lateral surfaces of capitulum.	Chan et al. (2021)
Genus *Pollicipes*	Filamentary processes.	Van Syoc (1995)
	Lower latera of different sizes.	Van Syoc (1995)
	Tuft of spines at the end of caudal appendages.	Van Syoc (1995)
	Scutum is not triangular.	Van Syoc (1995)
	Carina with sub-equal diamond shape.	Van Syoc (1995)
Pollicipes polymerus (Figure 5)	More than a single row/whorl of capitulum plates below sublatera/subrostrum.	Van Syoc (1995) & TC pers. observations
	Uni-articulate caudal appendages.	Van Syoc (1995) & Barnes (1996)
	Peduncle scales pointed outwards rather than up towards capitulum.	Van Syoc (1995)
	Peduncle scales spine-like or spindle shaped.	Van Syoc (1995) & Barnes (1996)
Pollicipes pollicipes, *Pollicipes elegans* & *Pollicipes caboverdensis* (Figures 5 and 6)	A single row/whorl of capitulum plates below sublatera/subrostrum.	Van Syoc (1995) & Fernandes et al. (2010)
	Multi-articulate caudal appendages.	Van Syoc (1995), Barnes (1996) & Fernandes et al. (2010)
	Peduncle scales pointed up towards capitulum.	Van Syoc (1995) & Fernandes et al. (2010)
	Peduncle scales not spine-like or spindle shaped.	Van Syoc (1995) & Fernandes et al. (2010)
Pollicipes pollicipes (Figures 5 and 6)	Rostrolatus and carinolatus are more separated from median latus than in *P. elegans* and *P. caboverdensis*.	Newman (1987) & TC pers. observations
	Two plates between each median latus and each rostrolatus named as rostral median latus by Fernandes et al. (2010) (named “r” plates by Newman 1987, imbricating plates added between rostrum and median latus).	Fernandes et al. (2010)
	Colour of capitular plates more whitish-grey than in *P. elegans* and *P. caboverdensis*.	Fernandes et al. (2010)
	Peduncle scales narrower than in *P. caboverdensis,* sub-equal oval shaped, with a smaller width than height.	Fernandes et al. (2010)
Pollicipes elegans (Figures 5 and 6)	Rostrolatus and carinolatus are less separated from median latus than in *P. pollicipes*.	Newman (1987)
	A single pair of rostral median latus.	Fernandes et al. (2010)
	Colour of capitular plates more reddish-orange than in *P. pollicipes.*	Fernandes et al. (2010)
	Peduncle scales narrower than in *P. caboverdensis,* sub-equal oval shaped, with a smaller width than height.	Fernandes et al. (2010)

(Continued)

Table 5 (*Continued*) Morphological diagnosis of the four *Pollicipes* species within the new order Pollicipedomorpha (Chan et al. 2021)

Taxa	Diagnosis	Reference
Pollicipes caboverdensis (Figures 5 and 6)	Rostrolatus and carinolatus are less separated from median latus than in *P. pollicipes.*	TC and JNF pers. observations
	A single pair of rostral median latus.	Fernandes et al. (2010)
	Colour of capitular plates more reddish-orange than in *P. pollicipes.*	Fernandes et al. (2010)
	Peduncular scales about the same width as height or peduncle scales wider than long.	Fernandes et al. (2010) Quinteiro et al. (2011)

The following basic description of the internal morphology of *Pollicipes* is based on Anderson (1994), Molares (1994) and Barnes (1996). The capitulum is formed by a bivalved carapace that encloses the body and limbs (cirri) of the barnacle. The opening of the capitular valves along one margin is the aperture of the capitulum. The cavity enclosed by the capitular valves and housing the body and cirri is the mantle cavity. The inner lining of the capitular valves is a respiratory surface (the mantle). The body consists of the prosoma, the thorax and a vestigial abdomen. The prosoma is an extension of the thorax and contains the stomach and the mouth parts (labrum, mandibular palps, mandibles, maxillule and maxillae). The thoracic limbs are biramous (see discussion on section 'Cirral morphology and feeding behaviour' regarding the identification of the maxillipeds), with the first pair modified into a maxilliped, the function of which is to transfer food from the cirri to the mouth. Associated with these structures are several groups of salivary glands. The prosoma is confluent with the capitular plates at the level of the inner face of the scutum, through an adductor muscle. Behind the prosoma, the remaining five pairs of biramous thoracic limbs, cirri II–VI, form the captorial feeding apparatus (see section 'Cirral morphology and feeding behaviour'). The digestive tract extends from the mouth to the anus, the latter situated between the bases of cirri VI. Parallel and posterior to the digestive tract paired seminal vesicles extend, to which numerous testicles are attached. The testicles are scattered in the connective tissue of the prosoma and thorax, and in the filamentary appendages. The filamentary appendages are projections of the prosoma and thorax. The seminal vesicles join at their dorsal ends to form the penis. On each side of the anus, just above the penis, are two small projections, the caudal appendages, which may be uni- (*Pollicipes polymerus*) or multi-articulate (*P. elegans*, *P. pollicipes* and *P. caboverdensis*) (Table 5). The caudal appendages, anus and penis form the vestigial abdomen. The interior of the peduncle consists externally of layers of circular and longitudinal muscles. The adhesive gland (see section 'Adhesion and cement') and the ovary are located central to these muscles. A pair of oviducts pass apically along the rostral side of the peduncle and mantle cavity, before entering the prosoma and opening at the bases of the first pair of cirri.

Considerable intraspecific morphological variation can be observed in *Pollicipes*, such as in the colour and form of the capitular plates, the colour of the capitular aperture, the colour and shape of the peduncle, and the morphology of the cirri (see section 'Cirral morphology and feeding behaviour'). Regarding intraspecific colour variation of the capitulum, in *Pollicipes caboverdensis*, the reddish-orange colour of the capitular plates, which easily separates *P. caboverdensis* from *P. pollicipes* and *P. polymerus* (Figure 4, Table 5), is not always evident in small individuals (Fernandes et al. 2010). Additionally, in *Pollicipes caboverdensis* and *P. elegans*, some plates such as the tergum (see illustration of *P. elegans* in Figure 4) may, in some specimens, have a brighter orange colour than the other plates (TC pers. obs.). Finally, alterations in the morphology of juvenile *Pollicipes pollicipes* maintained in laboratory conditions and mostly fed with *Artemia* sp. nauplii, compared with wild individuals, were observed (e.g. pink capitular plates, plate decalcification and plate deformation) (Franco 2014). These changes may have been caused by diet (Franco 2014).

The capitular aperture may also show considerable intraspecific colour variation. Darwin (1852) noted that the edges of the capitular aperture (mantle edges) in *Pollicipes pollicipes* “are widely bordered by membrane, coloured fine crimson red”. The red-coloured mantle edge of *Pollicipes pollicipes* is common in individuals from the low shore and subtidal zone, whereas barnacles from the upper shore have mantle edges with a brownish colour (Cardoso 1998, TC pers. obs.). The red mantle edge was also noted in *Pollicipes polymerus* by Darwin (1852) and in subtidal specimens of *P. polymerus* found in Nakwakto Rapids (British Columbia, Canada) (Nakwakto gooseneck barnacles), where their large and dense clumps form “spectacular formations” that display a “glorious red colour” (Lamb & Hanby 2005). This “Nakwakto variety” of *Pollicipes polymerus* has been reported in two other subtidal areas in British Columbia, namely a sea cave on Calvert Island (Brietzke et al. 2013) and Race Rocks (Fletcher 2011), with the red colour seemingly caused by the lack of black pigments that are present in sun-exposed barnacles (Lamb & Hanby 2005). Barnes & Reese (1960) noted that the development of the deep purple colour of the peduncle of *Pollicipes polymerus* seems to be, in part, dependent upon exposure to light, as the more basal parts of crowded peduncles are coloured light orange, turning black within a few days after removal of surrounding animals. According to these authors, whether the pigment is formed under the influence of light, or whether migration to the epidermis of pre-formed pigment or its precursor (the peduncular fluid is strongly pigmented) is involved, is not yet known. More research is needed to unravel the processes behind these phenotypical variations in colour.

The most obvious phenotypic variability in *Pollicipes* is probably the variation in peduncle length and water content, and the corresponding variation in condition and food quality of the barnacles. In wave-exposed situations, the peduncles of *Pollicipes polymerus* are strong, relatively short and attached over a considerable basal area, while in less wave-exposed situations, as well as among the more sheltered mussel beds, the peduncles are often greatly elongated and attached to a relatively smaller basal area (Barnes & Reese 1960). Chaffee & Lewis (1988) described a morphological variation in *Pollicipes polymerus* between stouter barnacles and slender animals. Stouter barnacles on the periphery of clusters showed marked thickening of the exoskeleton at the base of the stalk, while slender animals in the centre of clusters showed no thickening at all (Chaffee & Lewis 1988). Thicker stalks have been associated with a higher product quality in the fishery of *Pollicipes polymerus* on the west coast of Vancouver Island, Canada (Lessard et al. 2003).

Phenotypic variation of peduncular shape was also detected in *Pollicipes pollicipes* from the Iberian Peninsula, with two extreme forms recognized: large and short barnacles (Portugal, Cruz et al. 2016b), barnacles with a standard form with a smooth peduncle (Galicia, Spain, Parada et al. 2012), barnacles with a greater amount of muscle in the peduncle (Asturias, Spain, Rivera et al. 2014); versus an elongated form of thin and long barnacles (Portugal, Cruz et al. 2016b), with a wrinkled peduncle (Galicia, Spain, Parada et al. 2012). In Portugal, thin and long barnacles are called ‘*percebe mijão*’ (‘pissing’ barnacles), due to their high water content and the fact that they can squirt water when caught or eaten. The elongated form is considered to be of a low quality by the fishers and the market, having a lower commercial value (Parada et al. 2012, Sousa et al. 2021). The knowledge of the fishers to be able to classify different stretches of coast based on the quality of the barnacles has been used in a few studies (Galicia, Parada et al. 2012; Asturias, Rivera et al. 2014), as well as being used in the co-management system of *Pollicipes pollicipes* in West Asturias (Rivera et al. 2014). The commercial quality of stalked barnacles depends on the relationship between the length, width and weight of the barnacle (Molares et al. 1987) and has been measured by the ratio of the capitular base diameter to total height (Parada et al. 2012) or by the ratio between maximal rostral-carinal length and total height (Cruz et al. 2016b, Sousa et al. 2021) (lower values in low-quality barnacles). The biochemical composition of low- and high-quality *Pollicipes pollicipes* collected along the Portuguese coast was significantly different, with low-quality barnacles showing higher values of water content and lower values of fat, total protein content and energetic value (Cruz et al. 2016b). No genetic or epigenetic differences have been found to date between these two morphotypes (Sousa et al. 2021).

Thin and long barnacles tended to be at higher densities, although density may have been confounded with other factors such as hydrodynamics or predation (Cruz 2000). More research is needed to understand and disentangle the factors responsible for the phenotypic variation associated with the elongation of the peduncle and the quality of *Pollicipes pollicipes*.

Cirral morphology and feeding behaviour

Morphology and function

As in other Cirripedia Thoracica, *Pollicipes* are suspension-feeders employing six pairs of biramous thoracic appendages (cirri I–VI) to capture food items from the water (Anderson 1994). In the Thoracica, up to three of the anterior pairs of cirri can be modified to generally shorter maxillipeds that are specialized for transferring food to the mouth, with the long and slender posterior cirri forming a fan (captorial cirri), for capturing food from the water column (Chan et al. 2008). Feeding relies on the action of the captorial cirri, maxillipeds, mouth parts and the oral cone. Barnes (1996) provided a brief description of the cirri of the three species of *Pollicipes* known at that time, based on Darwin (1852) (Table 2 in Barnes 1996). She did not, however, include the detailed cirral morphology of *Pollicipes polymerus* presented by Barnes & Reese (1959). Subsequent to Barnes (1996), Norton (1996) described the morphology of the cirri of adults and juveniles of *Pollicipes pollicipes* and Pérez-Losada et al. (2004) classified the degree of similarity of cirrus III of *Pollicipes* (*P. polymerus* and *P. pollicipes*) to cirrus II and to cirrus IV. Chan et al. (2008) examined the cirral setation and setal morphology of *Pollicipes polymerus*, describing cirri I and II. To our knowledge, there has been no further description of the morphology of the cirri of *Pollicipes elegans* other than that by Darwin (1852). There is no description of the morphology of the cirri of *Pollicipes caboverdensis*.

Each cirrus has two rami that are multi-articulated and supported by a two-segmented protopod (or pedicel), the anterior ramus being designated as the exopod and the posterior as the endopod (Anderson 1994). The anterior side of a cirrus corresponds to the side of its greater curvature, while the posterior to the side of lesser curvature (Chan et al. 2008). Cirri carry setae that may be diverse and of various types (Chan et al. 2008). Based on the descriptions of Barnes & Reese (1959) (*Pollicipes polymerus*) and Norton (1996) (*P. pollicipes*), cirri IV–VI are described as similar, although the length of the cirri increases from IV to VI, each cirrus consisting of 16–21 (*P. polymerus*) or 13–19 (*P. pollicipes*) laterally flattered segments, protuberant on their anterior faces, with the two rami of each cirrus equal in length. Distribution of the setae (called spines by Barnes & Reese 1959) on the segments of both rami of cirri IV–VI is similar in both species, but the number of pairs of setae per segment seems to differ (five in *Pollicipes pollicipes*, usually six in *P. polymerus*). Moreover, the degree of setal overlap in *Pollicipes pollicipes* has been considered lower than in *P. polymerus*, which may indicate a higher degree of carnivory in *P. pollicipes*, associated with a larger setal mesh size (Norton 1996). In both species, the endopods of cirri III and of cirri II have fewer segments (cirrus III, 12–15, cirrus II, 10–14, in *Pollicipes pollicipes;* not specified for *P. polymerus*), but otherwise are similar to cirri IV–VI. In both species, the distal segments of the exopods of cirri II and III are also similar to the segments of the endopods and, consequently, to cirri IV–VI. In contrast, the proximal segments of the exopods of cirrus III (three proximal segments) and of cirrus II (four proximal segments) are highly modified in both species in terms of the number, types and distribution of setae. Furthermore, Norton (1996) described that in *Pollicipes pollicipes,* the rami of cirrus III are approximately equal in length, while the exopod is longer than the endopod in cirrus II. In a study on the evolution of Cirripedia Thoracica using molecular and morphological evidence, cirrus III of *Pollicipes* (*P. polymerus* and *P. pollicipes*) was considered as resembling cirrus IV more than cirrus II (Pérez-Losada et al. 2004, appendix 1 and 2). Cirrus I in both *Pollicipes polymerus* (Barnes & Reese 1960) and *P. pollicipes* (Norton 1996) is described as arising from the side of the mouth and being much modified in all segments of both rami, with dense setation. In both species, it was observed that the rami of cirrus I arise from the pedicel at a sharper angle than taken by those of the other cirri. Regarding *Pollicipes pollicipes*, Norton (1996) described the exopod of cirrus I as being longer than the endopod.

The definition of which cirri in *Pollicipes* species serve as maxillipeds is not completely clear. Anderson & Southward (1987) considered that cirri I of *Pollicipes polymerus* are the maxillipeds, while Norton (1996) considered that cirri I–III in *P. pollicipes* are the maxillipeds. According to Chan et al. (2008), in *Pollicipes polymerus*, cirrus I and the exopod of cirrus II serve as maxillipeds to transfer the food to the mouth. In this study, it was found that cirrus I of *Pollicipes polymerus* carries serrulate setae only, while cirri II–VI carry serrulate, pappose and multicuspidate setae (terminology of Garm 2004a, b in Chan et al. 2008). The functions of these types of setae, assuming similar functions as those of the various types of setae that have been defined for decapods (Garm 2004b in Chan et al. 2008), are the following: serrulate setae are used for gentle prey handling; pappose setae are for water current generation and filter-feeding purposes; and multicuspidate setae are for rough prey handling. In comparison with species from the orders Iblomorpha, Lepadomorpha and Balanomorpha, Chan et al. (2008) considered that *Pollicipes polymerus* as well as *Capitulum mitella* (both now included in the new order Pollicipedomorpha, Chan et al. 2021) had a more diverse diet than the species of Iblomorpha and Lepadomorpha (by having more types of setae than in these orders). However, they were more limited regarding food manipulation behaviour compared with balanomorphan species, by having only the first pair of cirri and one of the rami of the second cirri serving as maxillipeds. Balanomorphan species have two or three pairs of maxillipeds and a highly complex setation. Considering that the number, types and distribution of setae on the cirri reflect adaptations to the various feeding modes that have emerged throughout barnacle evolution (Chan et al. 2008), it would be very interesting to compare in detail the cirral morphology within the genus *Pollicipes*, and also to clarify the function of cirri II–III.

Cirral activity and feeding

Barnes (1996) described in detail the captorial feeding mode in adults of *Pollicipes polymerus*, based on Barnes & Reese (1959, 1960), showing that the extension of the cirri and their reaction to stimuli depended on water flow above a certain critical level. Anderson & Southward (1987) revised the various types of cirral behaviour in several species of Cirripedia and considered that adults of *Pollicipes polymerus* exhibit captorial extension of the cirri outside the capitulum in a prolonged manner (Barnes & Reese 1959, 1960). They also considered that juveniles of this species (Lewis 1981) and of *Pollicipes pollicipes* (Hui 1983) displayed a pumping beat (curled cirri protruded and retracted in a rhythmic manner). However, as Barnes (1996) had already pointed out for juvenile *Pollicipes polymerus*, this pumping beat appeared to be more associated with still water conditions, as in higher flow laboratory conditions, the juveniles of *P. pollicipes* also exhibited prolonged cirral extension (Norton 1996). In *Pollicipes pollicipes*, a critical velocity, when beating ceases and extension takes over, is apparent at flow rates between 8 and 14 cm/s under laboratory conditions (Norton 1996). Cirral extension was still exhibited at the higher flow rate examined (~48 cm/s). As well as these extension and pumping beat behaviours, Norton (1996) also described two more types of cirral activity in addition to those identified by Anderson & Southward (1987) in *Pollicipes pollicipes*. These were testing (the capitular aperture open, but the cirri not extended) and very slow normal beat (cirri unrolled and spread out as a fan, then curled up and withdrawn into the mantle cavity). All the rhythmic behaviours were at much lower rates and hence not equivalent to the cirral beating of balanomorph species, with rhythmic activity occurring only in laboratory conditions of very low flow or no flow (Norton 1996). Rhythmic cirral activity was considered to have a respiratory function that might be more important in low flow conditions. As such hydrodynamic conditions would be rarely experienced by adult *Pollicipes pollicipes* in the wild, Norton (1996) considered that cirral extension should predominate in natural conditions. In laboratory conditions, the most common activity for *Pollicipes pollicipes* of various sizes in conditions of moderate to high flow was cirral extension of various types, with the in-curling of at least one cirrus to the mouth to transport and ingest captured food (Norton 1996). The observations made by Norton (1996) do not support the hypothesis of Lewis (1981) for *Pollicipes polymerus*, and Hui (1983) for *P. pollicipes*, for a juvenile to adult switch in feeding strategies from cirral beating to cirral extension in *Pollicipes*.

Barnes (1996) reviewed the available studies on the diet of *Pollicipes* species (Barnes 1959, Howard & Scott 1959, Lewis 1981), which all concerned *P. polymerus*. With the exception of Norton (1996) (*Pollicipes pollicipes*), there have been no further studies on this subject. Based on Lewis (1981), the following patterns have been identified for *Pollicipes polymerus*: (1) little inorganic material (< 12% of total volume), namely a few grains of sand, which seems to be associated with a capacity to reject this kind of material (Barnes & Reese 1959); (2) higher relative percentage of organic particulate food items (< 10 μm diameter) in small barnacles (1–6 mm rostrocarinal length, RC) (e.g. detritus and diatoms) than in larger barnacles (15–28 mm RC); (3) higher percentage of large organic material (e.g. copepods, barnacle moults, polychaetes) in larger barnacles than in smaller ones. Howard & Scott (1959) also detected the usual presence of cyprids, amphipods, small clams and hydroids in the gut of *Pollicipes polymerus*. In *Pollicipes pollicipes*, Norton (1996) found a similar pattern of the relative importance of the different types of food items (inorganic, organic particulate and large organic material) in relation to size. In this study, the most common food types identified were diatoms, other unicellular phytoplankton, large algae, crustaceans and their remains, cirripede larvae (nauplii and cyprids) and moults. According to Norton (1996), *Pollicipes pollicipes* from the high shore had more homogeneous gut contents, with less identifiable material, than the lower shore animals, and smaller barnacles appeared to have more thoroughly digested gut contents than larger animals.

Phenotypic variation of the cirri and behaviour

In the last 20 years, several studies on the phenotypic variation of the cirri of several cirripede species, including *Pollicipes polymerus,* have been carried out: *Pollicipes polymerus* (Marchinko & Palmer 2003, Marchinko et al. 2004), *Chthamalus dalli* (Marchinko & Palmer 2003, Marchinko et al. 2004), *Chthamalus fissus* (Miller 2007), *Tetraclita japonica* (Chan & Hung 2005), *Balanus glandula* (Arsenault et al. 2001, Marchinko 2003, Marchinko & Palmer 2003, Li & Denny 2004, Marchinko et al. 2004, Marchinko 2007, Kaji & Palmer 2017) and *Semibalanus cariosus* (Marchinko & Palmer 2003). The most commonly used response variables in these studies were the ramus length and the ramus diameter of cirri IV–VI, namely of cirri VI, corrected for body size, as cirral dimensions increase with increased body size (Marchinko & Palmer 2003). The most common environmental predictor related to phenotypic variation of the cirri is the degree of wave exposure. In general, barnacles growing on less exposed shores have longer, thinner cirri than conspecifics growing on wave-exposed sites, and these cirral traits can be altered between moults in response to changing flow patterns (Marchinko 2003). However, there may be a threshold water velocity above which barnacles cease responding plastically to flow (Li & Denny 2004, Miller 2007). It was predicted that variation in feeding behaviour compensates or substitutes for further morphological variation (Marchinko & Palmer 2003, Li & Denny 2004), a hypothesis supported by field observations of the feeding behaviour of *Chthamalus fissus* (Miller 2007). *Chthamalus fissus* has the ability to withdraw and avoid individual breaking waves that generate high flow speeds (Miller 2007). However, the high peak flows of breaking waves are extremely transient (often lasting <1 s), and the turbulent bore that continues up the shore and eventually washes back down moves much more slowly than the peak flows. *Chthamalus fissus* reacted quickly to the decelerating flows and began feeding again shortly after withdrawing to avoid the initial breaking wave (Miller 2007). Although there are no field observations of the cirral behaviour of *Pollicipes* species in response to hydrodynamic conditions (e.g. wave impact, wave velocity), field observations on the orientation of the capitular aperture of *P. polymerus* suggest that it feeds after the initial wave impact (Barnes & Reese 1960). As Barnes (1996) described in detail, it appears that *Pollicipes polymerus* faces the backwash and not the incoming wave. In contrast, Norton (1996), from field observations on the orientation of the capitular aperture in *Pollicipes pollicipes*, did not find such a clear pattern, recording much small-scale variability, probably related to microtopographic variation.

The only known studies of phenotypic variability of the cirri of species of *Pollicipes* are related to *P. polymerus* (Marchinko & Palmer 2003, Marchinko et al. 2004). The lengths of the rami of cirrus VI of *Pollicipes polymerus* specimens were significantly longer in semi-exposed sites (2.66 m/s) in comparison with high wave exposure sites (4.41 m/s) (Marchinko & Palmer 2003). Compared with other barnacle species, the proportional difference in cirral length between exposed and semi-exposed sites was 75%–80% in *Balanus glandula*, 47%–68% in *Chthamalus dalli*, 29%–37% in *Semibalanus cariosus*, 7%–12% in *Pollicipes polymerus* (all data from Marchinko & Palmer 2003) and ~4% in *Tetraclita japonica* (Chan & Hung 2005). The lower relative plastic variation exhibited by *Pollicipes polymerus* was associated with a narrower range of hydrodynamic conditions where this species naturally occurs (Marchinko & Palmer 2003). Chan & Hung (2005) suggested that *Tetraclita japonica* and *Pollicipes polymerus* do not have much longer cirri in semi-exposed sites, as their feeding mode is prolonged extension of the cirral net. Consequently, shorter cirri might reduce the chance of being damaged and of being preyed upon.

Adhesion and cement

Despite excellent progress in understanding barnacle adhesion, advances since Barnes (1996) have mainly been restricted to acorn barnacles. Description of adhesion in stalked barnacle species is much less common and, of these, only *Lepas anatifera* and *Pollicipes pollicipes* have received much attention, with no progress on the remaining species within the genus *Pollicipes*. Nevertheless, it is possible to draw some parallels from the better-described groups, which is the approach adopted in the following sections.

The adhesive gland

Three types of adhesion are generally recognized in barnacles: larval temporary adhesion, larval permanent adhesion and adult permanent adhesion, with a metamorphosis step between larval and adult adhesion events (Liang et al. 2019). Each life-history event, or phase, has a corresponding adhesive. In keeping with the structure of Barnes (1996), we mainly consider adult adhesives (but see Liang et al. 2019, for a recent review on larval adhesives). The understanding of adhesion specific to *Pollicipes* has forged ahead, in several ways, since the review of Margaret Barnes (1996). At the time of her review, most of what was known regarding the biochemistry of the *Pollicipes* adhesive was extrapolated from balanomorph barnacles (e.g. Yule & Walker 1987), or from preliminary analyses in stalked barnacles, such as *Lepas anatifera* (Walker & Youngson 1975) and *Dosima (=Lepas) fascicularis* (Barnes & Blackstock 1974, 1976). But structural studies of the adhesive interface in *Pollicipes* (*polymerus*) go back to Darwin (1852) who showed a drawing of canals or 'ducts' terminating in pores at the base of the peduncle, for the delivery of adhesive to the substratum (Figure 6). Notwithstanding this very early knowledge, the *Pollicipes* adhesive gland was still unstudied at the time of Barnes (1996), so the description of the gland given at that time was extrapolated from observations made in *Lepas* (Lacombe & Ligouri 1969, Lacombe 1970; the latter have since been updated by Jonker et al. 2012 and Power et al. 2010).

The adhesive gland in *Pollicipes pollicipes* was finally described by McEvilly (2011) and Lobo-da-Cunha et al. (Figure 1 therein, 2017). Its structure follows the same scheme as in other stalked barnacle species, with some minor variations. Gland tissue is located in the peduncle, immediately beneath the capitulum and somewhat interspersed with the ovarian tissue (not in the 'basal' portion of the peduncle, as suggested in Koehler 1888, cited in Barnes 1996). Unicellular in structure, the gland comprises a series of 'giant' cells, which are identical and responsible for synthesising all of the adhesive components. This differs markedly from other adhesive-producing organisms such as

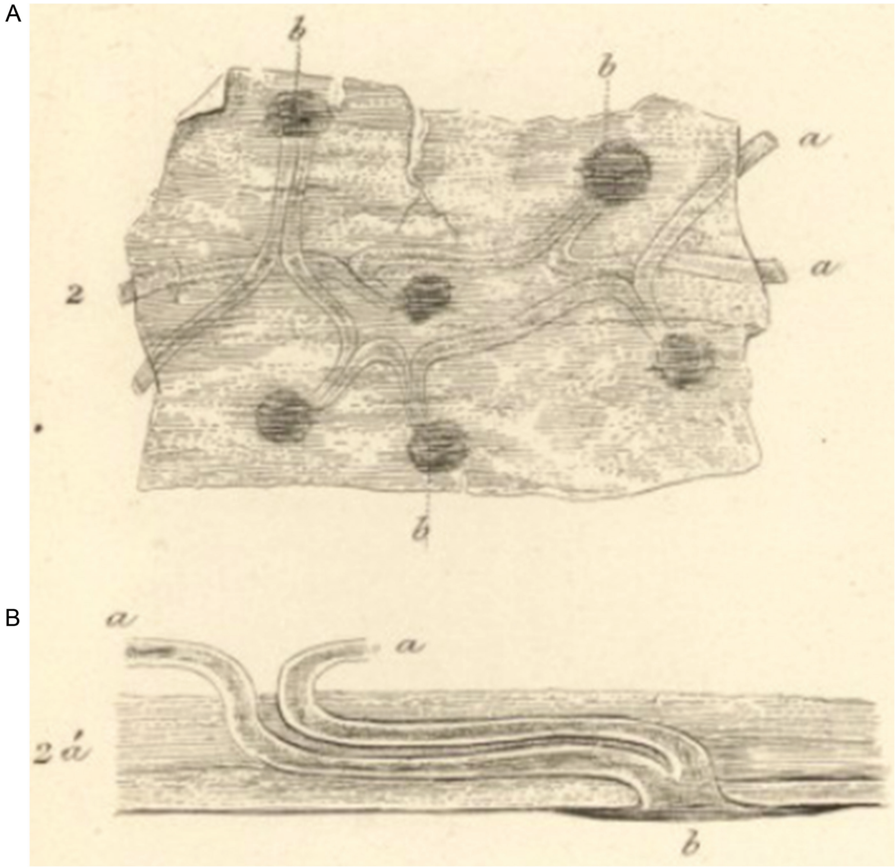


Figure 6 (A) “A portion (about 1/10th of an inch square) of the surface of the peduncle of *Pollicipes polymerus*, seen from the outside, greatly magnified, showing the small circular (bb) patches of cement, poured out from the cement ducts (aa) which lie within the peduncle”. (B) “A secretion, still more magnified, through the basal membrane of the peduncle, through one of the loops of the cement ducts (aa), and through one of the circular patches (b) of cement.” Both drawings are reproduced from Darwin (1852).

mytilids (mussels) (Wiegemann 2005), sabellariid worms (sandcastle worms or honeycomb worms) (Wang et al. 2010) and echinoderms such as *Asterias rubens* (Flammang et al. 1998). These organisms have several different gland cell types, each producing unique components that are clearly separated prior to secretion, which is a possible strategy to prevent premature polymerization of the adhesive. The lack of any such strategy, in the adhesion system of barnacles, is probably due to a much slower ‘curing’ (hardening) process in adult barnacle adhesives, compared with other systems. In marked contrast, larval barnacle adhesives possess a subdivided glandular system and a much faster-acting adhesive (Walker 1971). Indeed, this is one of several differences setting barnacles apart from other adhesion systems – unlike the adhesives of mussel byssus and reef-building sabellariid adhesives, barnacle cements do not contain L-dopa (L-3,4-dihydroxyphenylalanine) and, therefore, must contain molecular novelties compared to those systems (Wiegemann 2005, Jonker et al. 2012). Within the giant gland cells of barnacles, adhesive components are packaged into vesicles, which congregate in intracellular canals. They leave the gland cell in extracellular canals, which are drained by larger secondary canals, before being delivered to the substratum by two principal canals that run down the remaining length of the peduncle (Figure 7). McEvilly (2011) noted that intracellular canals may or may not be present in *Pollicipes pollicipes*. According

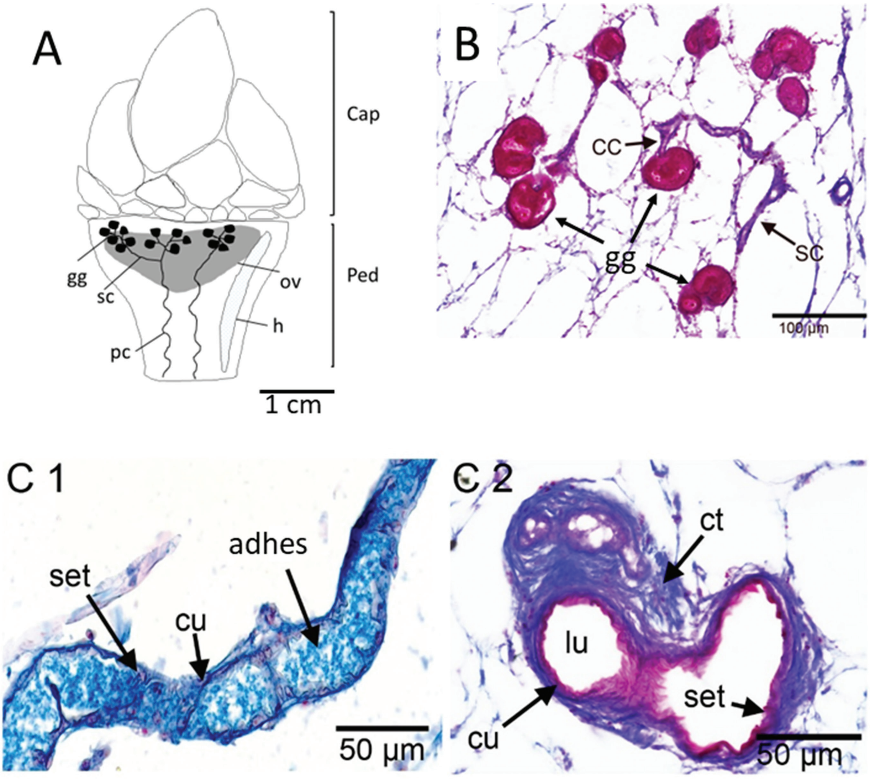


Figure 7 (A) Schematic of *Pollicipes pollicipes* showing the position of the giant adhesive gland cells that are drained by a series of canals in the peduncle. (B) *Pollicipes pollicipes* rosette of gland cells. (C1) *Dosima fascicularis* principal canal containing adhesive. (C2) *Pollicipes pollicipes* principal canal with cuticle lining. Cap, capitulum; Ped, peduncle; gg, glue gland; h, haemolymph; ov, ovary; pc, principal canal; cc, collecting canal; sc, secondary canal; set, squamous epithelial tissue; cu, cuticle; lu, lumen; adhes, adhesive; and ct, connective tissue. Adhesive secretion can be seen inside the lumen in C1. All sections were stained using AZAN. Scale bars are indicated in each image. Images are adapted from McEvilly (2011).

to McEvilly (2011), the gland cells in *Pollicipes pollicipes* were 40–70 µm in diameter (described by Lobo-da-Cunha et al. (2017) as up to 100 µm long) and were arranged in distinct circular arrangements, ‘rosettes’, of 5–10 gland cells, rather than singly or in groups as seen in other barnacle species. The giant cells possess a large-lobed nucleus, numerous nucleoli and a high concentration of heterochromatin, along with large amounts of rough endoplasmic reticulum, indicating exceptionally high protein synthesis levels within these cells. Fine details of the gland cells and secretory canals are given in McEvilly (2011) and Lobo-da-Cunha et al. (2017), including the evidence that adhesive proteins in *Pollicipes pollicipes* may be secreted through the endoplasmic reticulum secretory pathway (Lobo-da-Cunha et al. 2017).

According to Barnes (1996), the adhesive glands are ‘always active’ to maintain adhesion, but the inner tegumental glands (i.e. the thin lining of the mantle cavity) are only active during moulting, while the outer tegumental glands (i.e. the ones supplying the calcareous ‘scales’ of the peduncle) may also be active at all times, to repair damage and produce new scales. However, regarding the adhesive glands, this is far from clear. Early studies suggested secretion of glue into the canal system coincided with moulting of the exoskeleton, at least in some species (Fyhn & Costlow 1976). A link between adhesive production and moulting was further supported by molecular studies, which showed the expression level of adhesive protein mRNA increases towards moulting and is at its highest immediately after moulting (Kamino 2006). However, Wang et al. (2015) found no major differences in adhesion gene expression (i.e. adhesion transcriptome) in pre- and post-moult tissues. They did, however, find upregulated genes in the pre-moult sub-mantle tissues functioning in cuticular development, bio-mineralization and proteolytic activity.

Movement on the substratum

Despite being known for their 'permanent' adhesive, adult barnacles move slightly (Davey et al. 2021), particularly species with membraneous bases, and this is taken to extremes in *Pollicipes*. Adult *Pollicipes* can voluntarily detach and relocate along the substrate at a mean rate of 50 µm per day (Kugele & Yule 2000). Also noteworthy is the high degree of movement in *Pollicipes* juveniles along the substratum as they grow (i.e. along the peduncle of an adult, due to settling as larvae on conspecific adults). Barnes (1996) described cement 'tracks' in *Pollicipes pollicipes* adults, which got wider in the direction of movement. This suggested that movement could be brought about during growth, via a series of directed extensions of the peduncle base (Kugele & Yule 1993). The question remained open as to the degree of muscular involvement in this process, for instance *via* hydrostatic pressure, created through a combination of haemolymph pressure and the three muscle layers within the peduncle. However, Kugele & Yule (2000) have since ruled out involvement of muscular activity in the movement of *Pollicipes pollicipes*, deeming that this was unnecessary. They also provided evidence that the initial larval fixation points (i.e. the larval antennules that become embedded in the adhesive plaque and are usually visible even in adults) are lost in *Pollicipes*, due to sloughing off of the trailing edge of the basis following movement. However, these initial antennule attachment points can still be seen in species that move much less, such as *Lepas anatifera* (Kugele & Yule 2000). Although Barnes (1996) described the *Lepas* adhesive as being delivered through a canal (duct) system, leading to an opening through each antennule in the base of the peduncle (citing Lacombe & Ligouri 1969, Lacombe 1970), this is not quite correct. The adhesive is delivered via new pores, which are created off the principal canal, and the antennules are only used for the initial attachment (Jonker et al. 2012). Returning to *Pollicipes*, it was observed that directed movement in response to gravity, or a unidirectional water flow, was absent in adults and was only observed in juveniles, which always moved down the peduncle of their adult host, towards the substratum (Kugele & Yule 2000).

Biochemistry of barnacle adhesives

According to Barnes (1996) citing Naldrett (1993), the only clue to the *Pollicipes* adhesive mechanism was that saltwater had a part in curing its adhesive. This was based on observations that the addition of Tris buffer without salt inhibited the adhesive changing from liquid to opaque ('cured' form). Beyond this limited information, all knowledge of the adhesive biochemistry came from other barnacle species. Early studies ignored *Pollicipes pollicipes*, although Barnes & Blackstock (1974, 1976) outlined how stalked barnacle (*Dosima fascicularis*) adhesive mostly comprised protein (along with <2% carbohydrate, ~8% lipid and some 'ash'). These two studies also described the proportion of amino acids in the bulk cement. That the adult barnacle adhesive is primarily protein-based is important, from an experimental point of view, as this means that the adhesive is accessible to proteomic and gene expression profiling (Davey et al. 2021). A year after Barnes (1996), Naldrett & Kaplan (1997) solubilized the bulk cement in acorn barnacles (*Balanus* species), separating this complex into individual proteins, a process which itself offered clues as to the adhesive characteristics. This was also the first study to describe partial amino acid sequence information for individual adhesive proteins, underlining how the adhesive mechanism in barnacles differed from other adhesive animals, without polyphenolic chemistries involving L-dopa, as seen in mussels and tubeworms. Since it was only possible to render the bulk barnacle cement soluble using denaturants with heating and the addition of a strong reductant, the authors concluded that hydrophobic interactions (and possibly sulfur cross-links) were important in conferring insolubility, and hence strength, in the hardened barnacle adhesive (Naldrett & Kaplan 1997). Meanwhile, the rubbery nature of the barnacle adhesive, which confers flexibility and prevents cracking, was suggested to be associated with abundant small amino acids (alanine, serine and glycine) (Naldrett & Kaplan 1997). The absence of L-dopa was later confirmed histochemically (Arnow's assay) in other species – *Lepas anatifera* (Jonker et al. 2012) and *Dosima fascicularis* (Zheden et al. 2014) – and, although this has not been confirmed in *Pollicipes pollicipes*, L-dopa is almost certain to be absent in the latter case as well. The only post-translation modification (i.e. changes which take place in a protein after it is translated in the ribosome) identified on a barnacle protein was O-glycosylation (Naldrett & Kaplan 1997). This was later found on the N-terminal of a 52 kilodalton (kD) barnacle adhesion protein (Kamino 2013; see below). No other evidence of the post-translation modifications, common to other marine bioadhesives, such as hydroxylation of tyrosine residues to form L-dopa (see above) or phosphorylation of serines (Jonker et al. 2012) has been documented to date.

Individual adhesive proteins in barnacles

Next, it is important to look in detail at individual adhesive proteins in barnacles, what is known about these and how adhesion in *Pollicipes* fits inside that framework. Beginning with Naldrett & Kaplan (1997), a number of studies on individual adhesive proteins in various barnacle species have been made in the last 25 years. Most prominent is a series of pioneering studies by Kamino and colleagues, working on acorn barnacles. They identified five main proteins that were characterized by their apparent molecular weight (i.e. 19, 20, 52, 68 and 100 kD) and by particular amino acid biases, which resulted in a protein being either hydrophobic (52 and 100 kD) or hydrophilic (19 and 68 kD) (Kamino et al. 2000, Kamino 2013). Markers, developed against the relevant mRNA sequences in these proteins, showed that their expression was localized at or near the location of the adhesive gland. Each had different empirical functionality; for example, the 20 kD protein from *Megabalanus rosa* was recombinantly expressed in *E. coli* and bound to calcite, something which might be relevant for binding a calcium carbonate baseplate to the surface (Mori et al. 2007). Meanwhile, the 19 and 68 kD proteins were rather similar, with strong biases towards the amino acids serine, threonine, glycine, alanine, lysine and valine. The recombinantly expressed 19 kD protein adsorbed to more varied material surfaces (Urushida et al. 2007). No enzymes were identified in the adhesive with reactivity against these proteins. Thus, the mechanism underpinning adhesion and strength (i.e. 'cohesion') within the protein complex remained a matter of speculation.

Kamino et al. (2000, 2012) described the 52 kD protein, which, with the 100 kD protein, is together responsible for the insoluble nature of barnacle cement, being hydrophobic. Another important avenue of research was protein folding into amyloids, which are particular secondary structures made of cross-β-sheets that take a fibrillar form in certain proteins. Nakano & Kamino (2015) identified certain 'amyloidogenic motifs' in the 52 kD protein using a ThT assay on various peptides, showing that environmental factors (pH and ionic/salt conditions) could induce self-assembly of synthetic peptides derived from these motifs into a β-sheet structure (i.e. a precursor of amyloid fibre formation). These authors suggested that proteins are transformed to the cross-β-sheet conformation by environmental conditions and are fibrillated simultaneously or subsequently (Nakano & Kamino 2015). Hence, the two smaller proteins in acorn barnacles (19 and 20 kD) were proposed to have surface coupling functions, while the larger proteins (52 and 100 kD) were suggested to be involved in more bulk cohesion functions within the cement (Kamino 2013). Repeated peptide sequences were evident in some of the proteins (e.g. the 20 and 52 kD cases), but strong molecular 'motifs', as seen in mussel byssus, were absent. No means of intermolecular cross-linking of proteins were found; rather, the characteristics of the proteins suggested non-covalent mechanisms of curing the adhesive into cement. These included molecular conformation (folding) with intensive hydrogen bonding and hydrophobic interactions. These processes would contribute to self-assembly of protein into sheets and, in some cases, ultimately into fibrils. Thus, the adhesive, which takes hours to harden into a cement (Cheung et al. 1977), has an action that involves protein folding triggered by changes in pH and ionic environment.

Biochemistry of Pollicipes *adhesive*

Although many gaps remain, much progress has been made in understanding the mode of adhesion in *Pollicipes*. Despite low sequence similarities, homology was evident, on the basis of histochemical staining, between the 52 and 68 kD adhesive proteins from acorn and stalked barnacles, with homologues for the 19 and 100 kD proteins from acorn barnacles being identified bioinformatically in *Pollicipes pollicipes* (Jonker et al. 2014).

The full sequences of three adhesive proteins for *Pollicipes pollicipes* are now verified and available – 19, 52 and 100 kD (Rocha et al. 2019). A principal component analysis (i.e. statistical similarity exploration) of 23 adhesive proteins (various barnacle species including *Pollicipes pollicipes*) showed no significant differences, between acorn and stalked barnacles, in residue composition of homologous adhesive proteins (Rocha et al. 2019). The gene sequence encoding the 19 kD adhesive protein in *Pollicipes pollicipes* was identified from an expressed sequence tag (EST) database of arthropods published by Meusemann et al. (2010), later being verified by RACE-PCR sequencing and proteomic analysis using LC-MS/MS (Rocha 2015, Rocha et al. 2019). This protein was expressed in an *E. coli* recombinant expression system and purified, and its nanomechanical properties were characterized using surface plasmon resonance (Tilbury et al. 2019). The results of nanomechanical tests, on surface types that included hydrophobic, hydrophilic, charged and neutral surfaces, showed that the adsorption of the *Pollicipes pollicipes* 19 kD protein (i.e. 'Ppolcp19k') was not elevated, compared with the controls, in conditions designed to mimic either the barnacle cement gland or seawater (Tilbury et al. 2019). Hence, this small protein did not demonstrate enhanced binding to diverse surface types described for the homologous protein in *Megabalanus rosa* (Urushida et al. 2007). Tilbury et al. (2019) noted that, while the same amino acid bias in the 19 kD protein was seen in all barnacle species, including *Pollicipes pollicipes* (where serine, threonine, glycine, alanine, lysine and valine made up 70.5% of all amino acids), the isoelectric point (pI) in *Megabalanus rosa* was lower (pI = 5.8) than in *Pollicipes pollicipes* and several other barnacle species (pI = 9.26–9.80).

Unpublished results (AMP pers. obs.) show that the *Pollicipes pollicipes* 19 kD adhesive protein self-assembles into fibrils, which stain positively for amyloid at given pH and salt concentrations, behaving in a similar fashion to the 52 kD acorn barnacle protein outlined above. This agrees with the analysis of Rocha et al. (2019), who predicted the secondary structure of three *Pollicipes pollicipes* adhesive proteins, based on sequence information. Of these, the 19 kD protein in *Pollicipes pollicipes* was the protein with the highest predicted percentage of β-sheets encompassing 26.4% of its amino acid residues (Rocha et al. 2019). The predicted secondary structure of the 52 and 100 kD proteins from *Pollicipes pollicipes* were, respectively, classified as mixed (52 kD) and α-helix (100 kD). Not all β-sheets form amyloid; however, Barlow et al. (2010), working on the cements of *Amphibalanus amphitrite*, showed that these are highly hydrated (20%–50%) and comprised nanofibrillar matrices. Using various spectroscopic techniques, these authors showed that the nanofibrils are consistent with amyloid (as opposed to non-amyloid β-sheets) and that amyloid made up a large proportion (perhaps 30%) of the cement, with globular protein components also present (Barlow et al. 2010). Amyloid may form in some proteins due to conserved β-motifs, which act as nuclei in amyloid formation, or due to the alternating polar and non-polar residues in the 100 kD *Megabalanus rosa* protein (e.g. Davey et al. 2021). Overall, research in *Pollicipes pollicipes* showed no major differences from acorn barnacle proteins, apart from minor features, such as a shorter than usual form of the 52 kD protein, which at 356 residues is 209–274 residues smaller than the homologous protein in *Megabalanus rosa* or *Amphibalanus amphitrite* (Rocha et al. 2019). *Pollicipes pollicipes* joins only a handful of barnacle species for which recombinant expression of an adhesive protein has been attempted and surface dynamics tested (see also Liang et al. 2015 and Liu et al. 2017 working on *Balanus albicostatus* and Mori et al. 2007 and Urushida et al. 2007 working on *Megabalanus rosa*).

Current and future research in bioadhesion

The most recent research on barnacle bioadhesion has suggested additional proteins may be involved. A proteomic analysis found ~ 50 new proteins active at the barnacle adhesive interface, including new 114 kD (Wang et al. 2015) and 43 kD proteins (So et al. 2016; note that this may be homologous to the 68 kD protein from *Megabalanus rosa* – see Lin et al. (2021), and also that the molecular weight from SDS-PAGE gel migration and the predicted molecular weight from the protein sequence do not agree for 'AaCP43', as is common with adhesion proteins). Of most interest among these were enzymes that could have activity upon previously described adhesion proteins, including lysyl oxidases, peroxidases, peroxinectins and proteases. The former could mediate cross-linking in proteins with prominent abundances of lysine amino acids (So et al. 2016, 2017, Davey et al. 2021). Further work is required in this area since Cheung et al. (1977) claimed that inhibitors of enzymes, such as lysyl oxidase, did not prevent polymerization. While all these new proteins were being added into the mix, one may potentially be removed. The 20 kD protein has since been suggested to be a shell protein rather than an adhesive protein (Fears et al. 2019, Davey et al. 2021). That this protein had never been described from membraneous-based barnacles, including *Pollicipes pollicipes*, was consistent with that view (Lin et al. 2014, Jonker et al. 2015). However, new research described 20 kD protein homologues from three membraneous-based species, *Capitulum mitella*, *Conchoderma hunteri* (of which both are stalked barnacle species, as well as being pollicipedid, in the case of *C. mitella*) and *Chthamalus malayensis* (Lin et al. 2021). Fresh perspectives from all of this new information include a new way of categorising barnacle adhesive proteins into those that are rich in glycine/serine/alanine/threonine and those that are rich in leucine/valine/isoleucine (So et al. 2016, Rocha et al. 2019). This would place the 19 kD protein and a new 57 kD protein into the first group, with polar and hydrophilic side chains and a tendency to display domains otherwise seen in silk-producing arthropods. Meanwhile, the 52 and 100 kD proteins fall into the second group, which is hydrophobic with aliphatic groups (So et al. 2016). The glycine-serine-rich category above is a key component in the nanofibrillar structures observed in barnacle cement (So et al. 2016).

The future of bioadhesion research, including in *Pollicipes*, seems assured, given an explosion in the quantity and quality of data available in the era of 'omics' (Davey et al. 2021). Machado et al. (2019) presented the first assembled transcriptome for adhesive glands of *Pollicipes pollicipes* and *Lepas anatifera* (150 bp paired-end reads on the Illumina HiSeq 4000 platform) and deposited raw RNA-Seq data, transcriptome shotgun assemblies and final *de novo* assembly contigs on publicly available databases. In addition, Perina et al. (2014) added to the existing EST database of Meusemann et al. (2010), with genes specific to the body and foot tissues of adult individuals of *Pollicipes pollicipes*, discovering two 100 and 52 kD cement protein transcripts in the process. Finally, Domínguez-Pérez et al. (2020) provided a high-throughput proteome of the *Pollicipes pollicipes* adhesive gland and cement. This showed that, although the 52 kD protein was abundant in the cement, known adhesive proteins only made up a minor portion of the proteome. The remainder comprised several undescribed 19 kD-like proteins, along with 12 unannotated proteins, enzymes, chemical cues and protease inhibitors within the cement proteome (Domínguez-Pérez et al. 2020). All in all, these resources should greatly add to a fuller understanding of barnacle adhesion, including that of *Pollicipes pollicipes* in the decade to come. Finally, and remarkably, there has until recently been no good-quality barnacle genome available, despite this being a prerequisite for functional studies and for properly assembling and annotating a burgeoning number of transcriptomes (Rosenblad et al. 2021). Recently, two acorn barnacle genomes (with N50 > 100kbp) have been made available (*Balanus* (*Amphibalanus*) *improvisus*, Rosenblad et al. 2021, and *Balanus* (*Amphibalanus*) *amphitrite*, Kim et al. 2019a), along with one stalked barnacle genome (*Lepas anserifera*, Ip et al. 2021). Unpublished genome assemblies are also available for *Pollicipes pollicipes* (see Rosenblad et al. 2021 and Schultzhaus et al. 2021 for details).

Reproduction

The section on reproduction in Barnes (1996) is the longest of the whole review. The probable reasons for its length were not only the considerable knowledge that was available at that time, but also the interest and effort that Margaret Barnes devoted to this field of research, including two reviews on reproduction in Cirripedia published in *Oceanography and Marine Biology: An Annual Review* (Barnes 1989, 1992). Barnes' (1996) review of reproduction in the genus *Pollicipes* encompassed the following topics: size at maturity, number of broods and number of eggs, breeding season, spermatogenesis and spermatozoa, oogenesis, fertilization, ultrastructural investigations of fertilization and embryo development and chemical composition of ovary and egg lamellae. The only known studies on the reproduction in *Pollicipes* at that time were on *P. polymerus* and *P. pollicipes*.

Twenty-five years after Barnes' review, studies on the reproduction in *Pollicipes* are still primarily on these two species, especially *P. pollicipes*, but we also have some information on *P. elegans* and *P. caboverdensis*. All species are hermaphrodites. However, one of the most surprising advances in the study of reproduction in *Pollicipes* species, and one that challenges our knowledge of barnacle reproductive biology, came from the studies of Barazandeh et al. (2013) and Barazandeh & Palmer (2015) on the modes of fertilization in *P. polymerus*. Additionally, the first study to demonstrate high levels of multiple paternity in barnacles was in a *Pollicipes* species, *P. elegans*, by Plough et al. (2014).

Fertilization and mating

At the time of Barnes' (1996) review, it was assumed that there was no self-fertilization in *Pollicipes polymerus* based on the studies of Hilgard (1960) and Lewis & Chia (1981), although cases of self-fertilization had been identified in several species of Thoracica (see Barnes 1989). At that time, evidence of self-fertilization came from the presence of isolated barnacles carrying egg masses. On the other hand, Margaret Barnes stated that in many thousands of *Pollicipes polymerus* examined by her over the years,

> …the penis has never been found to vary in length (it is about half the length of the cirral net) or in the position it occupies in the mantle cavity. It is heavily pigmented, always very rigid and always lies over the body of the animal with its tip near the base of the first cirri, that is the atrium of the oviduct
>
> *Barnes (1992).*

In addition, she stated that "Animals have often been found with blobs of spermatozoa over the ends of the oviduct…", but "Copulation has, however, never been seen" (Barnes 1992) "…even after hundreds of hours of observing animals in aquaria" (C.A. Lewis pers. comm.in Barnes 1992). Margaret Barnes made the same kind of observations and considerations regarding *Pollicipes pollicipes* (Barnes 1992), but in this case, she questioned whether this species was capable of self-fertilization, as there were no studies that refuted self-fertilization in that species at that time. She also cited the question posed by Gruvel (1893): "How does this species fertilize?" and noted the hypothesis that Gruvel (1893) had suggested, in which spermatozoa might be passed into seawater and be transported by the cirri of adjacent functional females into their mantle cavities (Barnes 1992). However, this hypothesis was considered unlikely by Gruvel (1893) and by Barnes (1989, 1992), and self-fertilization was suggested as a possible mode of fertilization as "*P. pollicipes* has never been seen to cross-fertilize" (Barnes 1992). In parallel to these observations and considerations, Barnes (1996) noted that species of *Pollicipes* can manoeuvre themselves by means of the peduncle (Barnes & Reese 1960) and an extendable penis may not be so vital to copulation as it is in acorn barnacles. Therefore, at the time of Barnes' (1996) review, it was thought that species of *Pollicipes* could (i.e. *P. pollicipes*) or most likely could not (i.e. *P. polymerus*) self-inseminate and probably would be able to copulate as most thoracican barnacles do, although copulation in *Pollicipes* had never been observed.

In contrast, it is common to observe copulation, also called pseudo-copulation (release of sperm into a functional female mantle cavity), in balanomorphan species (see Anderson 1994 for a review). Mating in hermaphrodite thoracicans was described by Anderson (1994) as the extension of the penis of a 'functional male' by turgor pressure, followed by searching movements of the penis to detect a 'functional female' leading to penetration and ejaculation. For pseudo-copulation to take place, a barnacle must be within the penis range of at least one neighbour. According to Anderson (1994), several functional males may copulate with a functional female simultaneously, but copulation is never reciprocal.

Over the last 25 years, observations of pseudo-copulation in *Pollicipes polymerus* (observations in the field by Barazandeh & Palmer 2015; see online videos in supplementary material) and in *P. pollicipes* (observations in aquaria from Aquarium Finisterrae, Spain, https://youtu.be/Wuqz4fC9gLk, plus field observations in Portugal, TC and DJ pers. obs., https://youtu.be/EEN-Rq9klXc) have been made. Based on the film from Aquarium Finisterrae, we have made an illustration of the pseudo-copulation in *Pollicipes pollicipes* (Figure 8), in which mating between a functional female and two functional males is represented. Conversely, evidence has also been obtained that self-fertilization in *Pollicipes pollicipes* does not appear to occur, since barnacles with a carina-to-carina distance of >5 cm (after pushing them towards each other), hence regarded as isolated, did not contain egg lamellae (60% of non-isolated barnacles sampled at the same site and sampling date had eggs) (Cruz & Hawkins 1998).

Therefore, there is no longer any doubt that both *Pollicipes pollicipes* and *P. polymerus* copulate, and probably, self-fertilization does not seem to occur in *P. pollicipes*, as in *P. polymerus*. Surprisingly, however, a third mode of fertilization has been described in *Pollicipes polymerus* that

Figure 8 Illustration of pseudo-copulation in *Pollicipes pollicipes* by João Tiago Tavares, based on a film from Aquarium Finisterrae, Spain (https://youtu.be/Wuqz4fC9gLk).

had never been observed in barnacles: sperm-cast mating – where sperm released into the water by males fertilize eggs retained in the body of a female (Barazandeh et al. 2013). This discovery began with the field observation of occasional *Pollicipes polymerus* individuals leaking a foamy white liquid (confirmed to be sperm in a subsequent study by Barazandeh & Palmer 2015) between capitular plates, namely at the junction between the scutal and tergal plates, during low tide (see Figure 1b in Barazandeh et al. 2013 and Figure 1 in Barazandeh & Palmer 2015), and of isolated (outside penis range) yet fertilized individuals (Barazandeh et al. 2013). In comparison with other thoracican barnacles, species of *Pollicipes* have short penises, shorter than the cirri (Barnes 1992). Barnacles are sessile and most have a long penis that can extend multiple body lengths to reach neighbours and cross-fertilize (Neufeld & Palmer 2008), but *Pollicipes polymerus* has a relatively short penis (~twice body length after full extension) in comparison with acorn barnacles such as *Chthamalus dalli* and *Balanus glandula* (~seven times body length after full extension) (Barazandeh et al. 2013, 2014, Barazandeh & Palmer 2015). By using 16 single nucleotide polymorphism (SNP) markers, Barazandeh et al. (2013) found that sperm capture (presence of non-parent SNP alleles) occurred in 100% of the eggs from isolated individuals/mothers and, remarkably, even in 24% of the eggs from individuals/mothers that had just one adjacent partner. Therefore, these authors suggested that sperm capture might be a common supplement to pseudo-copulation in *Pollicipes polymerus*. At the time of their study (Barazandeh et al. 2013), observations of the pseudo-copulation in *Pollicipes polymerus* were not available. However, several observations of pseudo-copulation in this species were made in a later study by Barazandeh & Palmer (2015), by recording the behaviour of this species during flood and ebb conditions on short videos. Furthermore, in this study, the mantle cavity of individuals leaking sperm was inspected. Among the 13 leaker individuals examined, eight individuals had no eggs or sperm in the mantle cavity, four had newly released egg sacks or sperm blobs in the mantle cavity, and one had fully mature egg lamellae (Barazandeh & Palmer 2015). According to these authors, the observations might indicate that sperm leakage is an active process. Rates of copulation in the field were about four times those of sperm leakage, which was classified as an infrequent event, suggesting that it might be a secondary mode of fertilization in *Pollicipes polymerus* (Barazandeh & Palmer 2015). In this study, aerial copulation of *Pollicipes polymerus* was observed, a unique mode of mating among barnacles, as pseudo-copulation occurred mainly when barnacles were partially emersed, shortly after contact with breaking waves on an incoming tide. In Portugal, field observations of pseudo-copulation in *Pollicipes pollicipes* were also made in these conditions (TC and DJ pers. obs.). An extraordinary observation made by Barazandeh & Palmer (2015) was the occasional reciprocal copulation in *Pollicipes polymerus* (11% of 106 individuals), which had never been recorded for barnacles in general (Anderson 1994).

In parallel to these studies, multiple paternity in a natural population of *Pollicipes elegans* (416 nauplius II larvae cultivated in the laboratory from 14 broods and their respective mothers) was investigated using microsatellite markers (Plough et al. 2014). Multiple paternity was considered common (over 70% of broods and up to five fathers), and the number of fathers contributing to a brood was positively related to the field density of conspecifics in a cluster. In the three observed cases of single paternity, offspring inherited at least one allele that was not present in the mother's genotype, showing that self-fertilization is improbable (Plough et al. 2014). The upper limit to multiple paternity (five fathers) might be apparent, due to the lack of power of this study, but it might also be real and set by the number of neighbours within reach, or by the discarding of sperm, or the rejection of copulation by females (Plough et al. 2014). In this study, no evidence of long-distance sperm-casting was found. In fact, most broods had microsatellite alleles that matched those found in adults sampled from their mother's cluster, showing that fertilization occurs primarily by physically proximal males (Plough et al. 2014). Consequently, these authors suggested that if sperm-casting occurs in *Pollicipes elegans*, it is only effective over short distances, or within clusters. Nevertheless, some caution is needed when comparing the genetic studies of Barazandeh et al. (2013) and Plough et al. (2014). In addition to the different methods used (SNPs and microsatellites markers, respectively), the sampling units were also different: mothers (barnacles with eggs) and portions of egg lamellae in different stages of development and holding an undetermined number of individuals (Barazandeh et al. 2013); mothers and individual nauplius II larvae that were cultivated in laboratory conditions after taking the egg lamellae from the mothers (Plough et al. 2014). In addition, in *Pollicipes elegans* (Plough et al. 2014), determining the genetic structure of eggs from isolated individuals and mothers was not possible, because no isolated barnacles with eggs were found.

In summary, now we know that *Pollicipes polymerus* exhibits sperm-cast mating (Barazandeh et al. 2013) and pseudo-copulation (Barazandeh & Palmer 2015) and that there are still doubts regarding the possibility of partial self-fertilization (Barazandeh et al. 2013). Sperm capture in this species occurred in isolated individuals and in individuals that had only one adjacent partner (Barazandeh et al. 2013). Sperm-cast mating in *Pollicipes polymerus* might be an active process (Barazandeh & Palmer 2015), but this needs further research, namely by investigating the genetic structure of leaking sperm and leaking individuals. Field observations of sperm leaking during low tide and of copulation activity during flood and ebb suggested that pseudo-copulation is the major mode of sperm transfer in *Pollicipes polymerus* when potential mates are nearby, but observations under water are lacking (Barazandeh & Palmer 2015). The aerial copulation and reciprocal copulation that have been described for *Pollicipes polymerus* correspond to the first descriptions of these processes in barnacles (Barazandeh & Palmer 2015). Although there are no observations of pseudo-copulation in *Pollicipes elegans*, multiple paternity in this species was common (up to five fathers), fertilization occurred primarily by physically proximal males, but there is no evidence of long-distance sperm-cast mating and self-fertilization seems unlikely.

Gametogenic cycles

Gametogenic cycles of *Pollicipes* species have been described based on macroscopical observations of the female gonad and seminal vesicles of *P. polymerus* by Hilgard (1960) in California (the USA) and of *P. pollicipes* by Cardoso & Yule (1995) in SW Portugal. Histological observations of both male and female gonads and of seminal vesicles of *Pollicipes pollicipes* have been made by Molares et al. (1994b) in Galicia (Spain), Cruz & Hawkins (1998) in SW Portugal, Pavón (2003) in Asturias (Spain) and Boukaici et al. (2015) in SW Morocco.

The following description is based on the study of gametogenic cycles in *Pollicipes pollicipes* in SW Portugal by Cruz & Hawkins (1998). From October to January, most female gonads were resting and egg lamellae were absent. From March to August, the joint observation of the stage of the female gonad and the stage of development of the eggs (when egg lamellae were present) permitted the identification of the following reproductive conditions: (1) beginning of gonad maturation (a few mature oocytes and absence of egg lamellae); (2) pre-fertilization (gonad dominated by mature oocytes and frequent presence of egg lamellae, 22%, $n=64$); (3) fertilization (disintegrated ovarioles with no mature oocytes and presence of egg lamellae in all individuals); (4) post-fertilization (ovarioles dominated by residual material, atretic oocytes and immature oocytes and a few mature oocytes, and common presence of egg lamellae, 71%, $n=45$); and (5) recovery (ovarioles dominated by mature oocytes, some presence of residual material and atretic oocytes, and common presence of egg lamellae, 82%, $n=33$). In September, most gonads were in a fertilization or post-fertilization condition, while in October, most of the gonads were resting (a few empty and/or degenerated ovarioles, or sometimes with a few oogonia inside). The joint observations of the female gonad and stage of egg development suggested that, at the beginning and in the middle of the reproductive season (March to August), the ovary became disrupted after fertilization and recovered at the same time as, or before, the complete development of the eggs. However, most female gonads in pre-fertilization condition did not have egg lamellae, suggesting a delay before fertilization of the new batch. At the end of the season (September and October), the recovery of the ovary was slower than egg development and, by the time of larval hatching, the ovary had still not recovered in most of the cases. It was suggested that the pre-fertilization condition of the ovary that was common in September might change to the resting condition without fertilization occurring, as most of the female gonads were resting in October and just a few barnacles with eggs were observed (41% of barnacles with eggs in September versus 8% in October).

A similar pattern, of synchrony between female gonad and egg development during most of the reproductive period and of delayed ovary recovery relative to embryonic development at the end of this period, was observed in *Pollicipes polymerus* (Hilgard 1960). This pattern of female gonad functioning should allow *Pollicipes pollicipes* and *P. polymerus* to produce several sequential broods during the reproductive season. Hilgard (1960) suggested the existence of a time lag between broods in *Pollicipes polymerus*, as she had never observed the entire population sexually active (at most, 60% of animals with eggs). In Cruz & Hawkins (1998), similar observations were made. Most animals whose ovaries were full of mature oocytes did not contain eggs and seemed to be awaiting fertilization. These observations suggest that in *Pollicipes pollicipes*, egg production also does not seem to be continuous.

Cruz & Hawkins (1998) identified three reproductive conditions of the male gonad gametogenic cycle of *Pollicipes pollicipes* in SW Portugal: (1) the resting period (absence of testes or presence of a few small testes without sperm); (2) the beginning or end of the reproductive period (small testes present, some with a mass of sperm); and (3) the main reproductive period (numerous big testes filled with sperm). Additionally, the storage of sperm was assessed by the examination of the size of seminal vesicles using the method of Molares et al. (1994b). Throughout the year, spermatozoa were stored in the seminal vesicles, although testes were mostly absent or without sperm (resting condition) from October to December, while in the rest of the year, testes were numerous and filled with masses of sperm.

In Galicia, Spain, Molares et al. (1994b) also observed this male reproductive pattern and suggested that the duration of the reproductive period in *Pollicipes pollicipes* is primarily dependent on the development of the female gonad. The same pattern was observed in Asturias (Pavón 2003). Although no observations were made of the seminal vesicles, the results presented by Boukaici et al. (2015), regarding the development of the male gonad of *Pollicipes pollicipes* in SW Morocco, show a less pronounced seasonality between the resting period and the main reproductive period than that observed on the Iberian Peninsula by Molares et al. (1994b), Cruz & Hawkins (1998) and Pavón (2003). In other studies on male reproductive activity in *Pollicipes* (*P. polymerus* – Hilgard 1960, Lewis & Chia 1981; *P. pollicipes* – Cardoso & Yule 1995), only macroscopic observations were made on the relative size of the seminal vesicles and, as in the above Iberian studies, no seasonal pattern of variation was detected.

Regarding the female gonad, histological studies of *Pollicipes pollicipes* in Asturias (Pavón 2003), Galicia (Molares et al. 1994b), SW Portugal (Cruz & Hawkins 1998) and SW Morocco (Boukaici et al. 2015) seem to indicate an increase in the length of the reproductive period from north to south, controlled by the development of the female gonad. The ovary is dominated by mature oocytes between April and September in Asturias (Pavón 2003) and between March and September in Galicia (Molares et al. 1994b) and SW Portugal (Cruz & Hawkins 1998). In these regions, a resting period of the female gonad was identified between October and February (March in Asturias). On the contrary, in SW Morocco, ovaries with mature oocytes were observed throughout the year, although the relative abundance of individuals with mature oocytes was higher between March and October (Boukaici et al. 2015). No histological studies have been made on the development of the female gonad on the other species of *Pollicipes*.

Cruz & Hawkins (1998) did not find differences in gametogenic patterns of *Pollicipes pollicipes* at two intertidal levels (mid- and low shore), but found differences in gonad development of isolated individuals and individuals in groups, both sampled on the upper-shore. At the peak of the reproductive period, the ovaries of the isolated animals showed signs of advanced degeneration that was not a consequence of recent fertilization (as they had no eggs in the mantle cavity), while in the grouped animals, the ovaries were dominated by mature oocytes (pre-fertilization condition) or, in post-fertilization and recovery conditions, with egg lamellae in the mantle cavity. No sperm were observed in the testes of most of the isolated animals, although sperm storage was observed in their seminal vesicles, while all grouped barnacles had numerous big testes filled with sperm. These observations suggest that, in *Pollicipes pollicipes*, the presence or absence of adjacent mature animals of the same species is an important factor, through triggering or interrupting gametogenesis, respectively.

Breeding patterns

The breeding cycles of *Pollicipes* species have been studied by describing the spatial and temporal variation in the percentage of barnacles with eggs (see Table 6). The paired egg lamellae inside the mantle cavity are conspicuous and easily collected for further observations, such as grading the stage of egg development (e.g. Cruz & Araújo 1999, Macho 2006, Román et al. 2022), measuring individual egg size (e.g. Hilgard 1960, Lewis 1975a, Barnes 1989) and counting eggs (e.g. Hilgard 1960, Lewis & Chia 1981, Barnes 1989, Cruz & Araújo 1999). All studies of breeding patterns in *Pollicipes polymerus* preceded Barnes' (1996) review and were cited therein. By contrast, most studies concerning *Pollicipes pollicipes* have been made in the last 25 years (Table 6). We are not aware of any published studies on the breeding cycle of *Pollicipes elegans*, and for *P. caboverdensis*, there is a single study (Cruz et al. in prep). In most of these studies, values of the monthly variation of seawater temperature were presented (see Table 6 for range values during the main breeding season). There are several examples of cyclic breeding activities in marine invertebrates associated with seawater temperature (Orton 1920), temperature being a major environmental factor influencing physiology and ecology of marine species (Kinne 1970). Table 6 summarizes studies on the breeding patterns of the three species, including those presented in Barnes (1996). Although some caution is needed when comparing these studies, as they relate to observations in different years, different habitats and different sizes of individuals sampled and sampling size, we can identify some patterns. Moreover, reproductive phenology can alter with climate change, as shown in other intertidal species such as *Patella* (e.g. Moore et al. 2011).

One pattern is the apparent greater variation between intertidal levels that were detected at several locations for *Pollicipes polymerus* (higher values of percentage of barnacles with eggs at lower intertidal levels), whereas this variation was considered negligible in most studies of *P. pollicipes*. In the only study on the breeding pattern conducted other than under natural conditions (sea-water system of the Marine Laboratory, UC Santa Barbara, SWS, Page 1984), it was observed that most animals had egg lamellae throughout the year. Barnacles were fully submerged in the seawater system, leading Page (1984) to investigate in the laboratory whether the period of submergence had an influence on breeding activity. The percentage of *Pollicipes polymerus* with eggs was significantly greater in the continuously submerged treatment than in the exposed treatment after 6 weeks, but not after 3 weeks (Page 1984). In contrast, observations over 1 year on *Pollicipes pollicipes* in a subtidal environment (Cape of Sines, SW Portugal) revealed no variation between the breeding patterns found in intertidal and subtidal conditions (Cruz & Araújo 1999). A general pattern common to both *Pollicipes polymerus* and *P. pollicipes* is a positive relationship between barnacle size and the percentage of barnacles with eggs (Page 1986, Cruz & Araújo 1999). In *Pollicipes pollicipes*, brooding activity in small adults (12.5–15.0 mm rostrocarinal length, RC) was significantly less than in large animals (RC > 15 mm) (average of two times less in the peak of the breeding season) (Cruz & Araújo 1999).

Breeding patterns of *Pollicipes polymerus* have been studied at several locations along the American western coast, between San Juan Island, Washington (~47°N) (Lewis & Chia 1981), and Santa Catalina Island, California (~33°N) (Cimberg 1981), building on earlier observations made in the 1950s (Hilgard 1960) and 1970s (Cimberg 1981, Lewis & Chia 1981, Page 1984). Twelve degrees of latitude separate San Juan Island (Lewis & Chia 1981) from Monterey, the USA (Hilgard 1960). There was greater seasonal variation between the main breeding season (>50% of animals with eggs) and the period of lower breeding activity (<5% of animals with eggs) at the northernmost site compared with the less seasonal southernmost site, with a shorter main breeding season at San Juan Island (Hilgard 1960, Lewis & Chia 1981) (Table 6). In both studies, the main breeding

Table 6 *Pollicipes* species. Breeding patterns (% of barnacles with eggs) according to species, location and habitat (when available and when there are differences), period of observation, seawater temperature in the main breeding season, size of barnacles and sampling size

Species/latitude/location/habitat		% Of barnacles with eggs/month												Period of observation	Seawater temperature (main breeding season)	Size of barnacles and sampling size	References
Pollicipes polymerus		J	F	M	A	M	J	J	A	S	O	N	D				
48°N	San Juan Island, Washington, the USA (mean 2 sites, 2 tidal levels)	░	░	░	░	▓	■	■	■	▓	░	░	░	1971–1973	9°C–10°C	>14 mm (RC), *n* = ?	Lewis & Chia (1981)[a]
36°N	Mussel Point, Monterey Bay, California, the USA (mid-shore)	░	░	░	■	■	■	■	■	■	▓	▓	■	1956–1957	14°C–17°C	>27.5 mm (RC), *n* = 10–25	Hilgard (1960)[a]
35°N	Pismo Beach, California, the USA (low shore)	▓	░	□	▓	▓	■	▓	■	■	■	■	■	1972–1974	14°C–17°C	*n* = 10–80	Cimberg (1981)[a]
34°N	Goleta Point, California, the USA (low shore)	■	■	■	■	■	▓	▓	▓	▓	▓	▓	■	1978–1979	12°C–14°C	>15 mm (CH), *n* = 45–80	Page (1984)[a]
34°N	Latigo Point, California, the USA (low shore)	■	░	░	░	▓	▓	▓	▓	▓	■	▓	▓	1976–1977	15°C Jan; 18°C Oct	*n* = 10–80	Cimberg (1981)[a]
33°N	Santa Catalina Island, California, the USA (low shore)	■	■	■	■	▓	▓	▓	▓	▓	▓	■	■	1973	12°C–16°C	*n* = 10–80	Cimberg (1981)[a]
33°N	Santa Catalina Island, California, the USA (low shore)	■	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	■	1976	13°C–17°C	*n* = 10–80	Cimberg (1981)[a]
34°N	Sea-water system, Marine Laboratory UC Santa Barbara, the USA	■	■	■	■	■	■	■	■	■	■	■	■	1978–1979	12°C–17°C	>15 mm (CH), *n* = 20–35	Page (1984)[a]
35°N	Pismo Beach, California, the USA (upper shore)	░	░	□	▓	░	▓	▓	▓	▓	▓	▓	▓	1972–1974		*n* = 10–80	Cimberg (1981)[a]
34°N	Goleta Point, California, the USA (upper shore)	▓	▓	▓	▓	▓	▓	▓	░	░	▓	▓	▓	1978–1979		>15 mm (CH), *n* = 20–25	Page (1984)[a]
34°N	Latigo Point, California, the USA (upper shore)	░	░	░	░	░	▓	░	░	▓	▓	░	░	1976–1977		*n* = 10–80	Cimberg (1981)[a]
33°N	Santa Catalina Island, California, the USA (upper shore)	▓	▓	■	■	░	░	░	░	░	░	▓	▓	1973	13°C	*n* = 10–80	Cimberg (1981)[a]
33°N	Santa Catalina Island, California, the USA (upper shore)	▓	▓	▓	░	░	░	░	▓	▓	░	▓	▓	1976		*n* = 10–80	Cimberg (1981)[a]

(*Continued*)

Table 6 (*Continued*) *Pollicipes* species. Breeding patterns (% of barnacles with eggs) according to species, location and habitat (when available and when there are differences), period of observation, seawater temperature in the main breeding season, size of barnacles and sampling size

Species/latitude/location/habitat		% Of barnacles with eggs/month												Period of observation	Seawater temperature (main breeding season)	Size of barnacles and sampling size	References
Pollicipes pollicipes																	
47°N	Brittany, *Belle-Ile*					▒	█	█	▒					1982	ND	>15 mm (RC), $n>70$	Girard (1982)
47°N	Brittany, *Saint-Guénolé* (mid-shore)					░	▒	█	▒	█	▒			2005	ND	>15 mm (RC), $n>170$	Joncourt (2005)
47°N-48°N	Brittany, France (mid-shore, 1 or average of up to 3 sites)		░	░	░	░	█	█	█	▒	░	░		2018	16.5°C–20.1°C	>15 mm (RC), $n=40$ per site	Aguión et al. (2022a)
43°N	Biarritz, France (sublitorally)	░	░	░	▒	█	█	█	█	█	▒	░	░	<1992	ND	ND	Barnes (1992)
43°N	Asturias (1–2 sites, mostly different among dates)	░		▒	▒	█	█	█	█	█				1990–1991	ND	>15 mm (AC), $n=35–150$ per site	de la Hoz & Garcia (1993)
43°N	*Punta la Cruz*, Asturias, Spain (low shore)	░		░	▒	█	█	▒	█	█	▒	░	░	1999	14.5°C–19.5°C	>12.14 mm (LRT), $n=50$	Pavón (2003)
43°N	Asturias, Spain (mid-shore, 1 or average of up to 6 sites)	░	░	░	▒	█	█	█	█	█	▒	░	▒	2018	14.8°C–21°C	>15 mm (RC), $n=40$ per site	Aguión et al. (2022a)
42°N	*Cabo Home*, Galicia, Spain	░	░	░	▒	█	█	█	█	█	▒	░	░	1998–2001	15.1°C–17.2°C	>10 mm (LBC), $n=70$	Macho (2006)
42°N-43°N	Galicia, Spain (mid-shore, 1 or average of up to 6 sites)	▒	▒	▒	▒	▒	█	█	█	█	▒	▒	▒	2018	14.5°C–17°C	>15 mm (RC), $n=40$ per site	Aguión et al. (2022a)
37°N	SW Portugal (average low and mid-shore, 2 sites)	░	░	░	▒	█	█	█	█	▒	▒	░	░	1990–1992	15°C–20°C	>15 mm (RC), $n>80$ per site	Cruz & Araújo (1999)
37°N	Castelejo, Algarve, Portugal	░	░	░	▒	▒	▒	█	▒	▒	░	░	░	1992–1993	17°C	> 8 mm (CH), $n=?$	Cardoso & Yule (1995)[a]
37°N	SW Portugal (mid-shore, 1 or average of up to 5 sites)	░	▒	▒	█	█	█	█	█	▒	▒	░	░	2018	15.5°C–16.8°C	>15 mm (RC), $n=40$ per site	Aguión et al. (2022a)
Pollicipes caboverdensis																	
15°N	Tarrafal, Santiago Island, Cape Verde	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	2014–2016	22°C–28°C (all year)	>15 mm (RC), $n=40$	Cruz et al. (in prep.)

Light grey stands for the non-breeding season (<5%), middle grey for 5%–49%, and black for the main breeding season (>50%). Data for blank cells are missing.
CH, capitulum height; LBC, length of capitulum base; ND, no data; RC, rostrocarinal length.

[a] Studies cited in Barnes 1996.

season occurred when seawater temperatures were highest (summer, 9°C–10°C in San Juan Island; spring and summer, 14°C–17°C in Monterey). The results of studies conducted south of Monterey (33°N–35°N) by Cimberg (1981) and Page (1984) are more intriguing and have even led Cimberg (1981) to propose that there are two physiological races of *Pollicipes polymerus*: a northern race with maximum brooding activity at cold water temperatures (14°C or less, Pismo Beach and Santa Catalina Island) and a southern one which broods in warmer temperatures (20°C, Latigo Point). According to Cimberg (1981), these races correspond, respectively, to the cold and warm temperate zones located north and south of Point Conception (34°N 27′N). However, Santa Catalina Island is located south of Point Conception, and Cimberg (1981) proposed that animals at Santa Catalina Island were derived from populations north of Point Conception. We are not aware of any subsequent genetic studies that have supported the existence of these two physiological races.

Revisiting the studies of breeding patterns in *Pollicipes polymerus* in California (see Table 6), and considering only the animals sampled at low shore in the studies of Cimberg (1981) (Pismo Beach, Latigo Point and Santa Catalina Island) and Page (1984) (Goleta Point), we can identify the following patterns (Table 6): (1) 'summer breeders', sites north of Point Conception (Monterey and Pismo Beach), with low breeding activity in winter at both sites and higher breeding activity in spring and summer (Monterey) and in summer and autumn (Pismo Beach) (in both sites, the higher breeding activity is observed when seawater temperature is relatively high, ranging from 14°C to 17°C), and (2) 'winter breeders', sites south of Point Conception (Goleta Point and Santa Catalina Island), with less pronounced seasonality (>5% of animals with eggs all year), relatively lower breeding activity in summer and higher breeding activity from late autumn, through winter, until early spring (higher breeding activity when seawater temperature is relatively lower, from 12°C to 14°C at Goleta Point, and from 12°C to 16°C at Santa Catalina Island). The location that departs from this pattern is Latigo Point, located south of Point Conception, with lowest breeding activity in late winter and early spring when seawater temperatures range between 12°C and 15°C (data from Cimberg 1981). At this site, the highest breeding values (~50%) were observed in January and October, when seawater temperatures were ~14.5°C and 18.5°C, respectively, but with much small-scale variation of the percentage of animals with eggs (error bars in Figure 2B in Cimberg 1981). More studies are needed on the reproductive patterns of the southernmost populations of *Pollicipes polymerus*, including California (the USA) and Baja California (Mexico) (no published studies) where this species reaches its southern limit of distribution (see section 'Geographical distribution'). The existing studies are more than 40 years old, and there are patterns that require further concurrent investigation in order to infer the processes that may cause them and to inform the management of the exploited populations of Baja California (see section 'Fisheries, management and conservation').

The only reference found concerning the breeding pattern of *Pollicipes elegans* is from Peru (Yacila, Paita), where the percentage of animals with eggs was higher in November (Villena 1995 in Pinilla 1996). It was suggested that the percentage of eggs varied depending on the density of the groups of this species.

Several studies have been made since Barnes (1996) of the breeding patterns of *Pollicipes pollicipes*, namely in Brittany (France), Asturias and Galicia (Spain) and SW Portugal (Table 6). The latitudinal patterns of biological processes are sometimes difficult to compare because the same methodology has not been used throughout the geographical distribution of a species. In a recent study, populations located near the northern limit of distribution of *Pollicipes pollicipes* (Brittany, France) were compared with Iberian populations (Asturias, Galicia and SW Portugal) using a standardized protocol (Aguión et al. 2022a). Brittany populations had a significantly lower reproductive effort characterized by a shorter main brooding season (3 months, July to September) than Iberian populations (5 months, May to September in Spain, and April to August in SW Portugal) (Aguión et al. 2022a). With the exception of SW Portugal, the main breeding period corresponded to the period when the sea temperature was at its highest (16.5°C–21°C in Brittany, 14.8°C–21°C in Asturias and 14.5°C–17°C in Galicia) (Aguión et al. 2022a). The average values during this period were 2°C–4°C higher than in autumn (Aguión et al. 2022a). On the contrary, the average seawater temperature between April and August in Portugal was 16.3°C, slightly lower than that recorded between September and December (17.2°C) (based on data from Aguión et al. 2022a). As suggested in a previous study in SW Portugal (Cardoso & Yule 1995), breeding patterns of *Pollicipes pollicipes* in this region seem to be positively associated with air temperature that is lower during autumn. Breeding patterns identified in this recent study (Aguión et al. 2022a) match previous observations made in France, Spain and Portugal, although a 1-month earlier start to the main breeding season was recorded in SW Portugal (Table 6). In studies made in the early 1990s, the majority of the population in SW Portugal were only observed to have ≥ 50% of barnacles with eggs from May onwards (e.g. Cruz & Araújo 1999), while in 2018, it was from April onwards (Table 6). The breeding patterns of populations to the south of Portugal are not known. However, based on the study of gametogenic cycles of *Pollicipes pollicipes* in SW Portugal and SW Morocco (see subsection above, Cruz & Hawkins 1998, Boukaici et al. 2015), we can predict a similar pattern in SW Morocco to that observed in Portugal, with a likely decline in seasonality and a potential reduction in the length of the non-breeding period. In a study rearing adults of *Pollicipes pollicipes* in the laboratory, it was observed that adults, reared for 28 days when the temperature was gradually increased from 16°C to 24°C, had a percentage of eggs (~27%) about twice as high as that observed for adults kept at 16°C (~12%) (the percentage of animals with eggs at the beginning of the experiment was ~5%) (Franco et al. 2015).

The breeding pattern of *Pollicipes caboverdensis* appears to be very different from that of its Atlantic congener, *P. pollicipes*. In the sole study conducted on the breeding of *Pollicipes caboverdensis,* monthly observations of the percentage of barnacles with eggs over 3 years (2014–2016) in Tarrafal, Santiago Island, Cape Verde, revealed that a value above 50% was recorded only in March 2016 (Cruz et al. in prep.). Although no pronounced seasonality was observed and there was variation among sampling years, the lowest values were recorded in May and June and the highest values in February and March (Cruz et al. in prep.). Seawater temperature in Santiago Island is in general lower in winter (~22°C–24°C) and higher from August to November (~26°C–28°C) (Cruz et al. in prep.). Consequently, it seems that there is a tendency in *Pollicipes caboverdensis* to breed at the coldest time of the year, while its congener, *P. pollicipes*, breeds more in warmer waters.

Size at maturity, number of broods and fecundity

The minimum size of female sexual maturity in *Pollicipes* corresponds to the minimum size at which an individual contains egg lamellae in the mantle cavity. Most studies use the rostral-carinal length (RC) as the variable to measure this size, with the following values being found: *Pollicipes polymerus* – 11 mm (Barkley Sound, British Columbia, Canada, Barazandeh et al. 2013); 14 mm (San Juan Island, Washington, the USA, Lewis & Chia 1981); 17 mm (Monterey, California, the USA, Hilgard 1960); *P. elegans* – 17 mm (Yacila, Peru, Villena 1995 in Pinilla 1996); *P. pollicipes* – 12.5 mm (SW Portugal, Cruz & Araújo 1999), ~12 mm (Galicia, Spain, from Figure 7 in Sestelo & Roca-Pardiñas 2007); *P. caboverdensis* – 13.9 mm (Tarrafal, Santiago Island, Cape Verde, Baessa 2015). Other studies have used capitular height (*Pollicipes polymerus* – 12 mm, Goleta Point, California, the USA, Page 1986; *P. pollicipes* – 8 mm, SW Portugal, Cardoso & Yule 1995) or the diameter of the base of the capitulum (13.4 mm, Parada et al. 2013). Estimates of the minimum age of *Pollicipes polymerus* for reaching female maturity, varied between: 175 days at Goleta Point, California, the USA, Page (1986); 1 year at San Juan Island, Washington, the USA, Lewis & Chia (1981); 13 months at Santa Catalina Island, the USA, Cimberg (1981); to 2 years at Vancouver Island, Canada, Bernard (1988). Most individuals of *Pollicipes pollicipes* in Galicia and SW Portugal reach female maturity within 1 year (Cruz & Hawkins 1998, Cruz & Araújo 1999, Parada et al. 2012, Parada et al. 2013).

The minimum size of male sexual maturation is not as easy to estimate as the minimum size of female maturity. Based on histological observations, Cruz & Hawkins (1998) observed that individuals of *Pollicipes pollicipes* smaller than 10 mm (RC) did not contain sperm, and thus, 10 mm (RC) was defined as the minimum size of male sexual maturation in Cape of Sines, SW Portugal. As the minimum size of female maturity was 12.5 mm (RC) at the same site, this species can be considered a simultaneous hermaphrodite with a slight protandric tendency (Cruz & Hawkins 1998).

For both *Pollicipes polymerus* and *P. pollicipes*, the number of broods per individual per year is likely to be greater than one. The number of broods has been estimated according to methods proposed or adapted from Hilgard (1960), Page (1984), Burrows et al. (1992), Aguión et al. (2022a) or Román et al. (2022). In all cases, it is necessary to assume a value of the time for complete development of embryos, from oviposition to release. Larval hatching in *Pollicipes polymerus* reared in vitro occurred on average 25.4 days (13°C–15°C, Lewis 1975b) and 30 days (13°C, Hilgard 1960) after fertilization. Molares et al. (1994a), taking egg lamellae from the mantle cavity of *Pollicipes pollicipes* and culturing them in vitro at 20°C, observed that their incubation period varied from 1 to 25 days, depending on their initial developmental stage. Larval hatching does not appear to be simultaneous for all eggs present on a single lamella. Hatching began in the peripheral eggs and ended 2 or 3 days later in the central eggs (Molares et al. (1994a). Based on a study in which adults of *Pollicipes pollicipes* were reared in the laboratory, Franco et al. (2015) observed that a low number of nauplii were released daily and that embryos at the periphery of the egg lamellae were often several developmental stages ahead of the central embryos, hatching between 2 and 10 days earlier. These authors also suggested that, in nature, the hatching process may be extended over several days, rather than occurring in a single event. Traditionally, to calculate the number of broods, a fixed embryo time of 25 days (Lewis & Chia 1981, Cardoso & Yule 1995, Cruz & Araújo 1999, Macho 2006) or 1 month (Girard 1982, Hilgard 1960) is assumed. However, a novel approach was used recently, which considered embryo development time as a function of seawater temperature (Aguión et al. 2022a, Román et al. 2022), based on Patel & Crisp (1960). Table 7 summarizes the various estimates of the number of broods per individual per year that were calculated for *Pollicipes polymerus* and *P. pollicipes*. As these estimates also use in their calculation the values of the percentage of animals with eggs, the number of broods will also be positively associated with the size of the individuals. In SW Portugal, while the estimated number of broods for animals with RC between 14 and 16 mm ranged between one and two broods, for animals with RC between 18.5 and 21 mm, it was four (Cruz & Araújo 1999). Broods of *Pollicipes pollicipes* in SW Portugal are apparently produced asynchronously, as several stages of embryonic development were always observed in individuals collected on a same sampling date (fortnightly samples taken during the breeding season) (Cruz & Araújo 1999).

The few studies that estimate the number of eggs per brood (partial fecundity) in *Pollicipes* are as follows: *Pollicipes polymerus* – 144,000–288,000 eggs (San Juan Island, Lewis & Chia 1981), 104,000–240,000 eggs (barnacles with RC between 27.5 and 32.5 mm, Monterey, Hilgard 1960); *P. pollicipes* – 16,229 eggs (average per adult with RC between 14 and 16 mm), 34,172 eggs (average per adult with RC between 18.5 and 21 mm) and a maximum of 130,000 eggs for a barnacle with RC of 25 mm (all estimates from SW Portugal, Cruz & Araújo 1999); and *P. caboverdensis* – 29,000 eggs (average per adult with RC between 18.5 and 21 mm) (Cruz et al. in prep.). Attention must be paid to the size of individuals when comparing fecundities estimated in different studies and species. Individual size (RC) was considered to positively affect the fecundity of *Pollicipes pollicipes* in SW Portugal (see estimates above), but other factors (e.g. age and density) might also be important (Cruz & Araújo 1999). For example, it was estimated that animals with RC 23–25 mm produced from 30,000 to 130,000 eggs (Cruz & Araújo 1999). Total fecundity is calculated as the product of partial fecundity and the number of broods. As an example, using the data from the study by Cruz & Araújo (1999), it can be estimated that an adult *Pollicipes pollicipes* with RC between 23 and 25 mm can produce a total of 120,000–520,000 eggs/year, while one with RC of ~15 mm will produce ~32,500 at most.

More studies are needed to estimate embryo development time (from oviposition to release). This is a key value to use in the calculation of number of broods and to describe the patterns of

Table 7 *Pollicipes* species. Estimates of number of broods per individual per year with notes on period of observation, methods used, embryo development time and study locations

Species/location	Methods	Period of observation	Number of broods and size (RC)	Embryo development time	References
Pollicipes polymerus					
San Juan Island, the USA	Adapted from Hilgard (1960)	1971–1973	2–4 (mostly < 27.5 mm)	25 days	[a]Lewis & Chia (1981)
Monterey, the USA	Hilgard (1960)	1956–1957	4–7 (27.7–32.5 mm)	30 days	[a]Hilgard (1960)
Santa Barbara, the USA	Adapted from Hilgard (1960)	1956–1957	1 (upper shore) 6.6 (low shore) 11 (seawater system)	25 days	[a]Page (1984)
Pollicipes pollicipes					
Brittany, France	Hilgard (1960)	1982	2–3	25 days	Girard (1982)
Brittany, France	Hilgard (1960)	2018	2.6 (mean 3 sites) (RC > 15 mm)	25 days	Aguión et al. (2022a)
Brittany, France	Aguión et al. (2022a)	2018	2.3 (mean 3 sites) (RC > 15 mm)	Function of seawater temperature	Aguión et al. (2022a)
Asturias, Spain	Page (1984) and Burrows et al. (1992)	2001	2.1–2.4	25 days	Pavón (2003)
Asturias, Spain	Hilgard (1960)	2018	4.5 (mean 6 sites) (RC > 15 mm)	25 days	Aguión et al. (2022a)
Asturias, Spain	Aguión et al. (2022a)	2018	3.7 (mean 6 sites) (RC > 15 mm)	Function of seawater temperature	Aguión et al. (2022a)
Galicia, Spain	Hilgard (1960)	1998–2001	3.4–4.9	25 days	Macho (2006)
Galicia, Spain	Page (1984) and Burrows et al. (1992)	2006–2007	1.73	25 days	Sestelo & Roca-Pardiñas (2007)
Galicia, Spain	Hilgard (1960)	2018	5.5 (mean 6 sites) (RC > 15 mm)	25 days	Aguión et al. (2022a)
Galicia, Spain	Aguión et al. (2022a)	2018	3.7 (mean 6 sites) (RC > 15 mm)	Function of seawater temperature	Aguión et al. (2022a)
Galicia, Spain	Román et al. (2022)	2017–2019	3.6 to 9.6 (RC > 15 mm)	25 days	Román et al. (2022)
Galicia, Spain	Román et al. (2022)	2017–2019	2.7 to 6.6 (RC > 15 mm)	Function of seawater temperature	Román et al. (2022)
SW Portugal	Hilgard (1960)	1992–1993	1–3	25 days	Cardoso & Yule 1995
SW Portugal	Page (1984) and Burrows et al. (1992)	1990–1992	1–2 (14–16 mm, RC) 4 (18.5–21 mm, RC)	25 days	Cruz & Araújo 1999
SW Portugal	Hilgard (1960)	2018	4.9 (mean 5 sites) (RC > 15 mm)	25 days	Aguión et al. (2022a)
SW Portugal	Aguión et al. (2022a)	2018	3.7 (mean 5 sites) (RC > 15 mm)	Function of seawater temperature	Aguión et al. (2022a)

[a] Studies cited in Barnes (1996).

variation in fecundity in *Pollicipes* and understand the processes causing this variation. Given that these species are exploited, estimating reproductive output and describing its variation is important, particularly for use in population dynamic models, such as that of Bald et al. (2006).

Larval phase and metamorphosis

The review by Barnes (1996) considered only three studies of larval development in *Pollicipes*, based on laboratory-reared larvae of *Pollicipes polymerus* (Lewis 1975a, b) and *Pollicipes pollicipes* (Molares et al. 1994a). Four other studies had been published prior to Barnes (1996): the descriptions of laboratory-reared larval stages of *Pollicipes pollicipes* (Coelho 1990) and its cyprid carapace shape and lattice organs, based on scanning electron microscopy (SEM) images (Jensen et al. 1994), and the descriptions and comparisons of several barnacle larvae of the Oregon and California coasts (the USA), including those of *P. polymerus* (Standing 1981, Miller & Roughgarden 1994).

Since that time, several laboratory studies of larval development, settlement and metamorphosis, and the optimization of culture conditions of larvae of *Pollicipes pollicipes* have been published (Kugele & Yule 1996, Candeias 2005, Rocha 2015, Franco 2014, Franco et al. 2016, 2017). In contrast, there have been no studies on larval rearing of *Pollicipes polymerus* since Lewis (1975a, b). Moreover, only two studies concerning the physiological temperature tolerance of nauplius II larvae of *Pollicipes elegans* have been published (Walther et al. 2013, Crickenberger et al. 2015).

The emphasis on supply-side ecology has led to several field studies that analysed the spatial and temporal patterns of larval occurrence in the wild, for both *Pollicipes polymerus* (Pineda 1999, Dudas et al. 2009, Shanks & Shearman 2009, Morgan & Fisher 2010, Tapia et al. 2010, Morgan et al. 2017, Hagerty et al. 2019) and *P. pollicipes* (Macho et al. 2005, dos Santos et al. 2007, Macho et al. 2010, Figueira 2015, Höfer et al. 2017, Mateus 2017, Fernandes in submission). Moreover, the development of physical oceanographic models enabled the estimation of larval dispersal distances and predictions of connectivity patterns in *Pollicipes pollicipes* (Rivera et al. 2013, Nolasco et al. 2022).

To our knowledge, there is no published laboratory or field research on larval phases of *Pollicipes caboverdensis*.

Description and identification of the nauplii

Laboratory-reared naupliar stages of *Pollicipes pollicipes* were first described in a preliminary study by Coelho (1990), followed by Molares et al. (1994a) and Kugele & Yule (1996). Kugele & Yule (1996) gave a detailed description of naupliar larvae, with illustrations of morphological characteristics of the naupliar stages I–VI (shape of the carapace, caudal thoracic spine and thoracic process, antennules, antennae and mandibles), including setation formulae. In *Pollicipes pollicipes*, size measurements (total length and carapace width; Table 8) are considered good predictors to distinguish naupliar stages, except for stages II and III, for which morphological characteristics are also needed, as differentiation based on size alone is not possible (Kugele & Yule 1996, Candeias 2005). Based on Molares et al. (1994a) and Kugele & Yule (1996), Candeias (2005) developed a dichotomous key for the identification of naupliar stages of *Pollicipes pollicipes*, including recognizable features in fast-moving larvae. Moreover, Macho (2006) presented a key with diagnostic characters for quick and easy identification of naupliar stages, and another to distinguish larvae of *Pollicipes pollicipes* from other intertidal barnacle larvae found in plankton samples from the NW Spanish coast.

Based on Lewis (1975a) and Miller & Roughgarden (1994), Shanks (2001) published an identification guide to the invertebrate larvae of the Pacific Northwest, including larvae of *Pollicipes polymerus*.

Effects of different culture conditions on naupliar development

Several studies have tested the effects of different environmental factors, such as temperature (Coelho 1990, Rocha 2015, Franco et al. 2017), salinity and photoperiod (Franco et al. 2017) or rearing diets (Coelho 1990, Candeias 2005, Franco et al. 2017), on the development time, survival and size of *Pollicipes pollicipes* naupliar larvae.

Table 8 Mean sizes (μm) of naupliar stages of *Pollicipes pollicipes*

	Coelho (1990)		Molares et al. (1994a)		Kugele & Yule (1996)			Candeias (2005)		
Stage	TL	W	TL	W	TL	W	CL	TL	W	CL
N I	235	149	245 (225–295)	151 (125–180)	212 (163–265)	118 (97–163)			218 (143–255)	
N II	238	235	370 (325–395)	218 (200–225)	349 (311–383)	205 (189–219)		379 (285–459)	255 (194–296)	
N III	292	296	406 (395–415)	245 (235–250)	372 (326–408)	224 (194–255)		424 (364–459)	289 (235–337)	
N IV	351	351	437 (405–490)	284 (265–300)	429 (347–469)	302 (286–337)	295 (255–367)	442 (408–479)	338 (255–398)	289 (235–326)
N V	411	403	485 (450–505)	321 (320–325)	490 (434–531)	354 (316–388)	344 (286–393)	472 (347–530)	386 (347–469)	330 (275–398)
N VI	414	407	558 (550–580)	367 (360–380)	561 (490–612)	403 (352–454)	392 (337–449)	542 (490–612)	218 (143–255)	390 (326–439)

Size ranges are given in parentheses, when available in the literature.
N I, nauplii stage I; N II, nauplii stage II; N III, nauplii stage III; N IV, nauplii stage IV; N V, nauplii stage V; N VI, nauplii stage VI; CL, carapace length; TL, total length; W, width.

Table 9 Larval development time in culture for *Pollicipes pollicipes,* according to temperature, and corresponding development stages reached in each study

Larval development time	Development stages	Reference
20 days at 15°C	NI to NVI	Coelho (1990)
9 days at 22°C		
23–28 days at 20°C	NI to C	Molares et al. (1994a)
11–24 days at 15°C–24°C	NI/II to C	Kugele & Yule (1996)
9–14 days at 17.5°C	NI to NVI	Candeias (2005)
24 days at 16°C	NI to NVI	Rocha (2015)
21 days at 22°C	NI to C	
17 days at 24°C	NI to NVI	
25 days at 11°C	NI to C	Franco et al. (2017)
18 days at 15°C		
15–16 days at 20°C		
13 days at 22°C		
10 days at 24°C		

C, cyprid; NI, nauplii stage I; NII, nauplii stage II; NVI, nauplii stage VI.

Temperature has a significant effect on the development time of *Pollicipes pollicipes* from naupliar stages I–VI to the cyprid stage (Table 9), with cultures having shorter development times with higher temperatures (Coelho 1990, Rocha 2015, Franco et al. 2017). Optimum growth and survival rates were accomplished at 15°C–20°C (Franco et al. 2017). Salinity (20–40 psu) did not affect growth rates or survival. A full-day photoperiod (24:0 L:D) provided the highest growth and shortest development time through the naupliar stages (Franco et al. 2017). Although the nutritional requirements of *Pollicipes pollicipes* nauplii appear to change during naupliar development (Candeias 2005), several tested algal monodiets provided successful development of naupliar larvae to the cypris stage, such as the flagellates *Rhinomonas reticulata* (Candeias 2005), *Isochrysis galbana* (Coelho 1990) and *Tetraselmis suecica* (Coelho 1990, Franco et al. 2017), or the diatom *Skeletonema marinoi* (Franco et al. 2017). However, higher survival rates and high-quality larvae occurred when using mixed diets of *Tetraselmis suecica/Skeletonema marinoi* or *Isochrysis galbana/Skeletonema marinoi* (Franco et al. 2017).

Two recent studies of *Pollicipes elegans* have tested population-specific, physiological temperature tolerance of stage II naupliar larvae in the laboratory (Walther et al. 2013, Crickenberger et al. 2015). Both studies found that larvae from three different populations of *Pollicipes elegans* (Mexico, El Salvador and Peru) had distinct thermal tolerance windows, with larvae from El Salvador being the most thermally tolerant of the three populations (Walther et al. 2013). Moreover, larvae from Mexico had higher thermal tolerances when collected in the northern hemisphere summer compared with the winter, an indication of seasonal acclimatization that was not seen in larvae from Peru (Crickenberger et al. 2015).

Occurrence of nauplii in the plankton

A few studies have analysed nauplii of *Pollicipes pollicipes* in plankton samples (Macho et al. 2005, Macho 2006, Macho et al. 2010, Höfer et al. 2017). In these studies, most sampled larvae were early-stage nauplii (I–III) in low numbers compared with total cirripede larvae (nauplii and cyprids): 0.1% (Macho et al. 2010), 1.5% (Macho 2006) and 4.3% (Macho et al. 2005). Macho et al. (2005) sampled early-stage nauplii (I and II) of *Pollicipes pollicipes* in NW Spain, finding that larval release of *P. pollicipes* occurred mainly during waxing and full moon and at morning high tide. In a long-term study over 3 years in estuaries (‘*rias*’) of NW Spain (Macho 2006), abundance of *Pollicipes pollicipes* nauplii was always < 30 individuals/m^3 and was higher during summer and autumn, with no larvae present from December to March. By contrast, at another location (30 km to the south) closer to adult populations, larvae reached a maximum of 145 individuals/m^3 and were present from the middle of spring through summer, with very few larvae detected in autumn (Macho 2006). In the southern Bay of Biscay (Spain), Höfer et al. (2017) found consistently high densities (maximum of 300 individuals/m^3) of *Pollicipes pollicipes* nauplii inside a river plume. In this study, naupliar abundance was strongly correlated with chlorophyll concentration. These authors suggested that river plumes may act as nurseries for *Pollicipes pollicipes* naupliar larvae, due to local enhanced food supply and convergent currents that promote the aggregation of larvae.

Regarding *Pollicipes polymerus* naupliar larvae, while assessing the vertical and horizontal distribution of nauplii (II–VI) collected on the Oregon coast (the USA), Shanks & Shearman (2009) found that all larval stages remained close to the shore (within 5 km) and that upwelling/downwelling events had no influence on their distribution. In this study, larvae were rare in surface waters, in contrast to the study of Tapia et al. (2010), in which nauplii of *Pollicipes polymerus* were mainly found near the surface in a fixed nearshore station in Southern California (the USA). Tapia et al. (2010) also tested day/night patterns of larval vertical distribution, but no differences were found. In their study, nauplii of *Pollicipes polymerus* represented 15% of the total barnacle larvae.

Description and identification of the cyprids

Cypris larvae of *Pollicipes pollicipes* reared in the laboratory were first described by Coelho (1990) and Molares et al. (1994a). However, in the latter study, cyprids were probably in a poor nutritional condition and the authors incorrectly used the absence of oil droplets as a diagnostic characteristic of *Pollicipes pollicipes* larvae (Kugele & Yule 1996, Cruz 2000). Kugele & Yule (1996) presented detailed descriptions and illustrations of the thoracic and caudal appendages of *Pollicipes pollicipes* cyprids. Furthermore, studies based on SEM images of *Pollicipes pollicipes* cyprids have provided detailed descriptions of their carapace shape and lattice organs (Jensen et al. 1994) and the morphology of their attachment organs (Al-Yahya et al. 2016).

Table 10 Mean sizes of cyprid larvae of *Pollicipes pollicipes* and *P. polymerus*, either reared in laboratory conditions (L) or collected in the field (F)

Species	Length (µm)	Height (µm)	Width (µm)	Lab/field	Field location	Reference
Pollicipes pollicipes	299	153		L		Coelho (1990)
	402 (390–420)	231 (210–250)		L		Molares et al. (1994a)
	433 (403–455)	215 (170–248)		L		Kugele & Yule (1996)
	487	252	164	F[a]	Cape of Sines, SW Portugal	Cruz (2000)
		200 to 212		L		Franco et al. (2017)
	503 (487–525)	250 (237–262)	158 (147–175)	F	Cape of Sines, SW Portugal	Fernandes (in submission.)
Pollicipes polymerus	425	232		L		Lewis (1975a)
	622	320		F	Monterey Bay, CA, the USA	Miller & Roughgarden (1994)
	494 (420–520)	256 (220–260)	177 (160–200)	F	Bodega Harbour, CA, the USA	Standing (1981)

Size ranges are given in parentheses, when available in the literature.

[a] Settled cyprids collected from the peduncle of conspecifics, not from plankton.

A combination of size measurements (carapace length, height and width; Table 10) and morphological characteristics can be used to distinguish cyprids of *Pollicipes pollicipes* from those of other cirripede larvae found in Atlantic Iberian waters (Cruz 2000, O'Riordan et al. 2001, Fernandes in submission). Carapace length alone can separate cyprids of *Pollicipes pollicipes* and of *Chthamalus montagui* from the other cirripedes. Although both the length and the height of the cyprid carapace of *Pollicipes pollicipes* and *Chthamalus montagui* overlap, the width in dorsal view can be used to distinguish cyprids of these two species (Cruz 2000, Fernandes in submission). Moreover, several morphological characteristics can be used to clearly and easily distinguish *Pollicipes pollicipes* cyprids collected in the plankton: (1) the carapace shape, with a broadly rounded anterior end visible in side view and a very narrow profile detected in dorsal view, (2) the carapace ornamentation, with rounded or polygonal contiguous depressions, and (3) the size of the compound eyes, which are bigger than in *Chthamalus montagui* cyprids (Fernandes in submission; Figure 9).

Cyprids of *Pollicipes polymerus* have been described in detail by Standing (1981) and Miller & Roughgarden (1994), based on plankton samples collected along the California coast (the USA). Lamont & Emlet (2018) also described the morphology of plumose setae and their relationship with swimming motions in cyprids of *Pollicipes polymerus* and detected that setules are permanently fused, as in other cirripede groups. Cyprids of *Pollicipes polymerus* are morphologically similar to those of *P. pollicipes* (Kugele & Yule 1996) and are also similar in size (Table 10) to cyprids of *Chthamalus* species from the Oregonian province (Standing 1981).

The main characteristics distinguishing cyprids of *Pollicipes polymerus* from those of other cirripedes found in the plankton of the NE Pacific coast are as follows: the broadly rounded anterior end in side view, the narrow carapace profile in dorsal view, a carapace sculptured with small papillae, a break in the posterodorsal margin and the greater depth of the carapace located at the level of the compound eyes (Standing 1981, Miller & Roughgarden 1994). This last characteristic is not present in *Pollicipes pollicipes* cyprids (Fernandes in submission), and the break in the posterodorsal margin is also not as clear (Cruz 2000, Fernandes in submission).

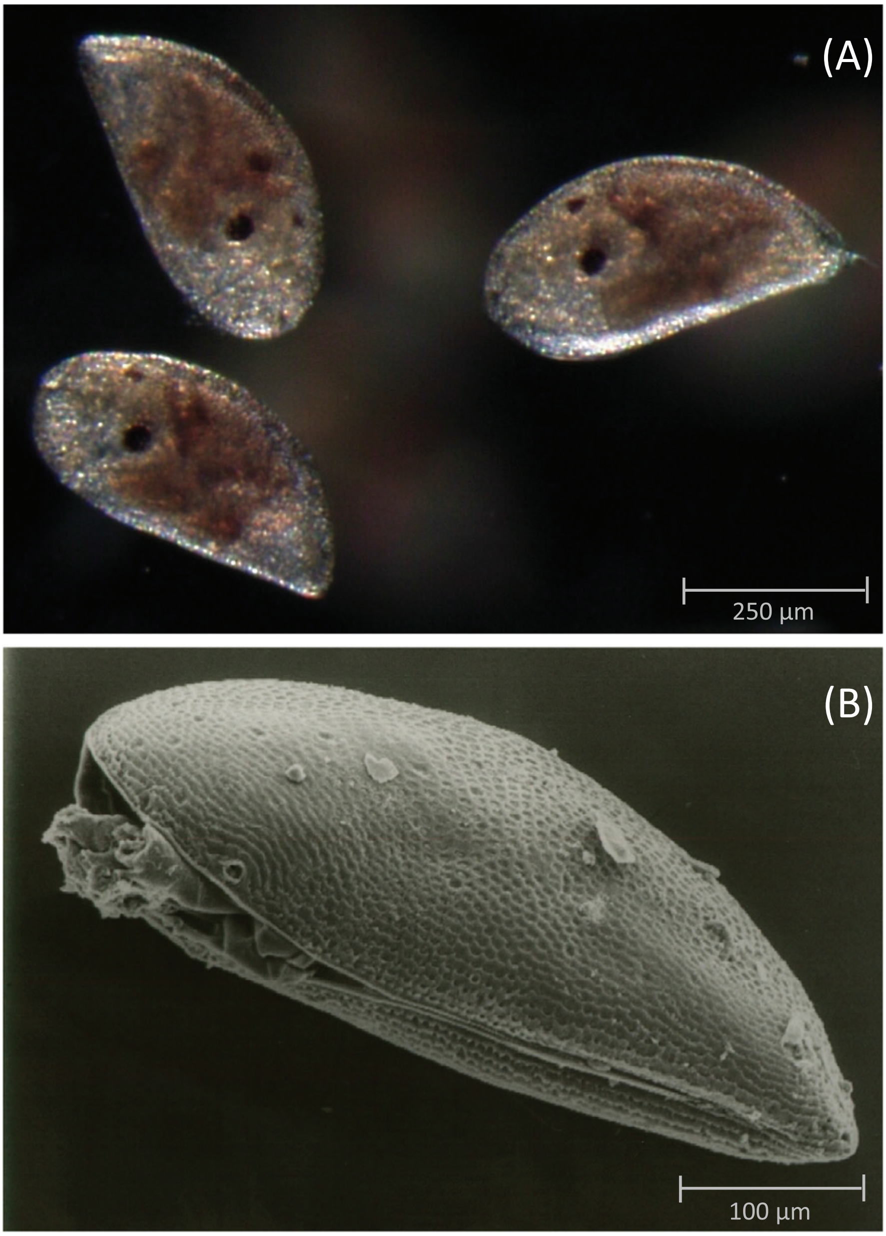


Figure 9 Cyprids of *Pollicipes pollicipes* collected (A) in plankton samples from SW Portugal and (B) from the peduncle of an adult *Pollicipes pollicipes* individual, where the cyprid was starting to metamorphose (SEM image).

Settlement and metamorphosis in culture

The conditions necessary to promote settlement and metamorphosis of cyprids of *Pollicipes* species in culture are still poorly understood, with very few studies to date (Lewis 1975a, Kugele & Yule 1996, Franco 2014, Franco et al. 2016). The work by Lewis (1975a) regarding *Pollicipes polymerus* settlement in culture was reviewed by Barnes (1996). Overall results from these studies suggest high cyprid selectivity in these species.

Settlement experiments with *Pollicipes pollicipes* cyprids in laboratory conditions compared several different natural and artificial substrata, with the majority of total settled cyprids (93%, Kugele & Yule 1996; 82%–97%, Franco 2014) consistently being found on live adults. Nevertheless, settlement rates of cypris larvae on conspecifics were low in these studies and varied between less than 1% (Kugele & Yule 1996) and 30%–40% (Franco 2014, Franco et al. 2016). Kugele & Yule (1996) found that only cyprids aged less than 10 days settled and metamorphosed and 78% of these were aged 4 days or less. Nevertheless, cyprids older than 17 days (Kugele & Yule 1996) or 20 days (Franco et al. 2016) were still alive in cultures. Franco et al. (2016) showed that preferential environmental conditions needed to maximize settlement and metamorphosis rates include natural salinities (30–40 psu), a temperature of 20°C, illumination, water circulation and cyprid age not exceeding 3 days.

Cyprid metamorphosis is a complex process that involves a series of morphological, physiological and biochemical events. To our knowledge, there are no published studies of this process in *Pollicipes* species. However, a description of cyprid metamorphosis of the closely related species, *Capitulum mitella* (Family Pollicipedidae), was published recently (Lin & Rao 2016), where a timeline and a detailed description of the morphological events are given, based on light microscopy and SEM analyses.

Occurrence of cyprids in the plankton

Several field studies have investigated the spatial and temporal patterns of the natural distribution and abundance of larvae of *Pollicipes* species, namely *P. pollicipes* and *P. polymerus*. These studies used neustonic and water-column plankton trawls (dos Santos et al. 2007, Shanks & Shearman 2009, Macho et al. 2010, Morgan & Fisher 2010, Höfer et al. 2017, Morgan et al. 2017, Fernandes in submission), pump sampling (Pineda 1999, Macho et al. 2005, Tapia et al. 2010, Hagerty et al. 2019), cyprid traps (Dudas et al. 2009, Figueira 2015, Mateus 2017) or a combination of several of these methods.

Studies where cypris larvae of *Pollicipes pollicipes* were collected in the plankton are scarce. In a study of spatial distribution of cypris larvae in the central Portuguese coast, dos Santos et al. (2007) only considered the cypris carapace length as a criterion for species distinction. Consequently, these authors were unable to distinguish cyprids of *Pollicipes pollicipes* from those of *Chthamalus montagui*. These authors found that cyprids of these species (*Chthamalus montagui* and *Pollicipes pollicipes*) were close to the coast and mainly in the neuston during the day. However, some doubts remain as to whether these data can be attributed to *Pollicipes pollicipes* larvae. Indeed, a very small proportion of *Pollicipes pollicipes* larvae (1%–3%) was reported out of the combined total of *Chthamalus montagui* and *Pollicipes pollicipes* larvae in a study on the temporal and spatial distribution of cyprid larvae in SW Portugal (Fernandes in submission). In this study, cyprids of *Pollicipes pollicipes* reached a maximum of 126 larvae/m^3 at the neuston layer and 33 larvae/m^3 in the water column. Also, in the same region (SW Portugal), but inside the Port of Sines where adults of *Pollicipes pollicipes* are absent or rare, Figueira (2015) and Mateus (2017) found cypris larvae of this species using neustonic trawls (maximum densities 36 cyprids/m^3 during summer and autumn). Moreover, in a study over 3 years in NW Spain, cyprids of *Pollicipes pollicipes* were found in very low numbers (maximum of 5 cyprids/m^3) during summer (Macho 2006).

Besides using plankton trawls, Figueira (2015) and Mateus (2017) also used cyprid traps (adapted from those used in Dudas et al. 2009) to study the spatial patterns of *Pollicipes pollicipes* cyprid distribution. However, cyprids were not efficiently retained in the traps (Mateus 2017). The number of cyprids found in the cyprid traps deployed during either a 4-day or a 12-hour period was consistently much lower than the number of cyprids collected during 1-minute plankton trawls for the same location and dates (Mateus 2017).

Several studies in the NE Pacific coast have analysed patterns of abundance of invertebrate larvae in the plankton, including the cyprids of *Pollicipes polymerus*, relating those patterns to physical transport processes to the shore. In the nearshore of southern California (the USA), Pineda (1999) showed that *Pollicipes polymerus* cypris larvae accumulated in internal tidal bore warm fronts. Accumulation of these larvae was also found in the offshore warmer side of these features, but not in the onshore colder side of the fronts (Pineda 1999). It was suggested that, if these fronts propagate all the way to the shore, larvae will be transported onshore. In this study, the first to analyse the vertical distribution of *Pollicipes polymerus* cyprids, larvae were not strictly neustonic, but their abundance peaked at the sea surface (~56% of total cyprids). In contrast, a study by Tapia et al. (2010), in the same location, found cyprids of *Pollicipes polymerus* (6.8% of total barnacle larvae) located mainly within the mid-depth and bottom layers, suggesting that changes in their mean depth of distribution may be correlated with the pycnocline depth. Moreover, the distribution of cyprids of *Pollicipes polymerus* on the Oregon coast (the USA) and its relationship with upwelling/downwelling events was investigated by Shanks & Shearman (2009). This study found that cypris larvae always remained close to the shore (less than 2 km) during both sets of oceanographic conditions. Conversely, on the same coast, Dudas et al. (2009) did not find any differences in the abundance of *Pollicipes polymerus* cyprids along shore, across shore or at different depths. The importance of surf-zone hydrodynamics to onshore larval transport was studied by Morgan et al. (2017), but total barnacle cyprids were analysed as a group, with few details about the distribution and abundance of *Pollicipes polymerus* cyprids. On reflective beaches, and contrary to most zooplankters, barnacle cyprids were mainly located inside the surf zone, and in those situations, *Pollicipes polymerus* represented 12.1% of total barnacle cyprids (Morgan et al. 2017). Finally, barnacle cyprid distribution in the nearshore of southern California was analysed before, during and after the 2015–2016 El Niño event (Hagerty et al. 2019). In summer 2016, after the El Niño event, Hagerty et al. (2019) documented a large peak in the density of *Pollicipes polymerus* cyprids, which were found to be closer to shore during fall-winter than during spring-summer sampling periods.

Larval dispersal and connectivity

Biophysical models of larval dispersal have long been the dominant approach for estimating contemporary marine larval dispersal (see the review of Swearer et al. 2019). According to this review, there is a need for greater emphasis on the validation of model assumptions, as well as testing of dispersal predictions with empirically derived data. For the first time, Nolasco et al. (2022) have described and validated a biophysical model of larval dispersal with *Pollicipes pollicipes*. Furthermore, in the latter study, predictions of supply (from the model) have been compared against observations of recruitment on conspecifics at monthly intervals (see next section) in three regions: Asturias and Galicia (Spain) and SW Portugal. The main results were the following: estimates of average realized dispersal were –73 to +63 km in the S/W and N/E directions and of larval retention were 2.0 to 2.4%; extensive larval exchange occurred within regions; Galicia and Asturias regularly exchanged larvae; and SW Portugal does not seem to be directly connected to Galicia and Asturias through larval dispersal (Nolasco et al. 2022).

A more simplistic biophysical model of *Pollicipes pollicipes* larval dispersal, based on current profiles of a single nearshore location on the Cantabrian coast, was also developed by Rivera et al. (2013). These authors predicted high recruitment success, with a peak at 56 km west of the emission point, in a year of high upwelling activity. In contrast, in a year of low upwelling, theoretical recruitment success was low and peaked 13 km east of the emission point (Rivera et al. 2013). Furthermore, estimates of population migration rates, obtained in a reanalysis of genetic data for five populations of the Cantabrian coast, pointed to a net long-term, westward larval transport along this coast (Rivera et al. 2013).

Lewis (1975a) made a theoretical estimation of *Pollicipes polymerus* larval dispersal from Bodega Bay (California, the USA) of 187–933 km, based on current speeds in that area and on a larval development time of 42 days.

The main shortcomings in knowledge of the larval biology of *Pollicipes* species are the absence of studies concerning larval phases, and metamorphosis of *P. caboverdensis* and *P. elegans*, either in the field or in laboratory conditions. The clear identification of the various larval stages of these two species, estimates of larval development time in culture, and the study of their distribution and abundance in the plankton are essential for a better understanding of the mechanisms of larval release, dispersal and transport back to the coast.

Biophysical models of larval dispersal, such as that developed for *Pollicipes pollicipes* in the study by Nolasco et al. (2022), should be pursued for the other three *Pollicipes* species. These are powerful models and, when coupled with empirical data such as larval distribution in the plankton, or settlement data, can give us important new insights into ecological questions or management strategies of *Pollicipes* species.

Settlement and recruitment

Barnes (1996) had no specific section on settlement and recruitment within the genus *Pollicipes*. The knowledge available at that time regarding these processes was reviewed and integrated into the sections 'Orientation and movement of peduncle' and 'Moulting and growth'. This knowledge was mainly related to the spatial variation of these processes in *Pollicipes polymerus*, namely the distribution and abundance of cyprids and juveniles on peduncles of conspecifics and on other habitats (Barnes & Reese 1960, Lewis 1975b, Hoffman 1984, 1988, Bernard 1988, Hoffman 1989, Satchell & Farrell 1993), and on the ability of juveniles to move along the peduncle (Kugele & Yule 1993).

The concepts of settlement and recruitment that Barnes (1996) used ("the settlement period begins when an animal first lands on a substratum, that is when a cyprid has cemented itself to the surface" and "recruitment is a measure of recently-settled juveniles that have survived for a period of time after settlement") are the same as those previously defined by Connell (1985), which are particularly suitable for both acorn and stalked barnacles after metamorphosis. Other definitions of recruitment are also widely used: in many studies of population biology, recruitment is defined as entry to the adult population (see Pineda et al. 2006); in fisheries research, recruitment is generally considered to be to the exploited population, which is usually also the adult breeding population. As juvenile barnacles occur on or among the peduncles of adults which are harvested, they can certainly be considered to have entered the exploited population, albeit as by-catch and although not yet adult.

As Connell (1985) noted, however, the measurement of settlement of planktonic propagules of marine benthic organisms is very complex (with a need for observations at very frequent intervals to avoid missing any larvae that attach and then become detached within a short period), since most larvae or algal propagules either are very small when they attach, or attach in cryptic habitats (e.g. crevices, among algae). There is some consensus that daily sampling of settlement is a good compromise between logistical difficulty and accuracy of estimating settlement (Connell 1985, Pineda et al. 2010). In the case of *Pollicipes*, the measurement of settlement rate is even more complex due to the very hydrodynamic locations where these species live, hindering observations, especially those with high temporal resolution, such as on a daily basis. To our knowledge, Pineda (1991, 1994) made the only field studies of *Pollicipes* in which daily settlement rates were measured. Pineda (1991, 1994) used white polyvinyl chloride semi-pipes, with grooves in their inner face, to measure daily settlement of *Pollicipes polymerus* (Dike Rock, La Jolla, California, the USA). These studies were not cited in Barnes (1996). Thus, we can consider that all other field studies regarding settlement and recruitment of *Pollicipes* species have effectively measured recruitment as defined by Connell (1985) (e.g. Hoffman 1989, Satchell & Farrell 1993, Cruz et al. 2010a, Fernandes et al. 2021).

Do cyprids of Pollicipes *prefer to settle on conspecifics?*

A major paradigm that exists in relation to the settlement of *Pollicipes polymerus*, and that has also been stated for *P. pollicipes*, is that cyprids settle preferentially on adult peduncles. The references commonly cited to support this paradigm are Barnes & Reese (1960), Lewis (1975b) and Hoffman (1989). Barnes (1996) did not specifically refer to the term 'preference', although she mentioned that "cyprids and young spat are almost always found on peduncles of older *Pollicipes* (*P. polymerus*) as this provides an ideal substratum for settlement". However, none of the studies cited above tested specific hypotheses regarding preference behaviour of cyprids for the peduncles.

Barnes & Reese (1960) observed that in the field, solitary individuals of *Pollicipes polymerus* were rare, stating that "…neither cyprids nor young spat (which are more easily detected) are found in numbers on the rocks. By contrast, the peduncles of adults, both small and large, are covered with cyprids and young spat" and that "it is curious that this restriction to the adult as a settling surface is virtually limited to the peduncle; very rarely are cyprids found on the capitulum". In the study by Lewis (1975b), laboratory observations were made, from fertilization through to settlement of *Pollicipes polymerus*. Very few cyprids were successful in settling: two cyprids settled on mudstone rock adjacent to the base of an adult *Pollicipes polymerus*; one cyprid settled on the base of the peduncle of a healthy adult *P. polymerus* (Lewis 1975b). Based on this study, no cyprids were observed to settle on the epidermis of the peduncle of *Pollicipes polymerus*, on slides dipped in *P. polymerus* extract and/or on slides with primary films. In parallel with this laboratory study, based on field observations, Lewis (1975b) noted that settled juveniles were never found far from established adult clusters and stated that "From 37 adult clusters, an average of 81% of the associated juveniles preferred the adult peduncle to any other available substrate", but no detail on these observations was given. The conclusion of Lewis' (1975b) study was that "it appears that both chemosensory and tactile responses are necessary for the specific settling behaviour of *Pollicipes polymerus* cyprids". Hoffman (1989) assumed preferential attachment of cyprids of *Pollicipes polymerus* on conspecifics, having observed very high recruitment on conspecifics (recently settled spat reaching very high densities on the peduncular surface, >300 cm^2). He also considered that there was little evidence that *Pollicipes polymerus* had established new aggregates on open hard substrates, although he did observe recruitment on primary substrata (the under surface of a rock that had been cut by a storm, and on a denuded rock).

On the other hand, there are several observations of recruitment of *Pollicipes polymerus* onto substrates other than conspecific adults. Artificial substrates on which settlement occurred were terra-cotta tiles (intake seawater system, La Jolla, California, the USA, Hoffman 1988), grooved polyvinyl chloride plates (intertidal, La Jolla, California, the USA, Pineda 1991, 1994), fibre glass plates covered by safety walk tape (intertidal, Monterey, California, the USA, Satchell & Farrell 1993) and Plexiglas plates covered by safety walk tape (intertidal, four sites along the central coast of Oregon, the USA, Dudas et al. 2009). Natural substrates included cleared rock, laminarian fronds, coralline algae in tide pools, any solid substrate (Amphitrite Point, British Columbia, Canada, Bernard 1988); primary substrate (intertidal, La Jolla, California, the USA, Hoffman 1989, Pineda 1994); and mussels and acorn barnacles (Clayoquot Sound, western Canada, Gagne et al. 2016).

Field recruitment of *Pollicipes pollicipes* on artificial substrates is apparently more difficult to observe, as there are descriptions of several failed attempts of observation on various substrates: Tufnol, plastic net, rubber and sisal ropes with or without extracts of crushed *P. pollicipes* (Coelho 1991); grooved marble stone, grooved rectangular PVC plates, PVC threaded cylinders similar in size to an adult *P. pollicipes* (Cruz 2000); epoxy biomimetics, calcium silicate, Tufnol, glass epoxy, carbon epoxy, glass vinyl ester, nylon and slate (Franco 2014). However, recently, recruitment *of Pollicipes pollicipes* has been observed on artificial substrates: marine epoxy (Cape Sardão, SW Portugal, Franco 2014); PVC half-pipes covered by safety walk tape with the concavity facing the rock surface (Cape of Sines, SW Portugal, Jacinto 2016); and a specifically designed settlement substratum, the 'barticle'(Cape of Sines, SW Portugal, Fernandes 2018, European Patent nr. EP3372073B1, see Figure 15). Recruitment of Pollicipes pollicipes on natural substrates other than conspecifics (rock, calcareous algae and acorn barnacles, Coelho 1991, Cruz 2000, Franco 2014; mussels GM, DJ and AS pers.obs.) has also been observed.

In conclusion, we are not aware that the theory of preferential settlement of cyprids of *Pollicipes* species on adult peduncles has ever been tested directly and clearly by addressing specific hypotheses. Differences in settlement and post-settlement mortality of *Pollicipes* on conspecifics versus other natural substrates have never been tested in the field. What we do know today is what Margaret Barnes stated in 1996: "There is little doubt that settlement is heavy among adults of the same species". Challenging questions to answer in the future are the following: 'Is there preferential settlement of cyprids of *Pollicipes* species on adult peduncles?' and 'Is heavy recruitment on conspecifics the result of post-settlement processes (e.g. more benign physical habitat and/or lower predation on conspecifics)?'.

Settlement and recruitment on artificial substrates: small-scale spatial patterns

Satchell & Farrell (1993) observed that *Pollicipes polymerus* consistently settled in a strongly aggregated pattern, since typically three to eight cyprids settled in contact with each other (settlement on plates collected every 8 days, Monterey, California, the USA). These authors also observed a positive association between densities of barnacle settlers and the degree of aggregation among cyprids. Contrasting spatial patterns among sites and vertical levels (intertidal, La Jolla, California, the USA) of daily settlement of *Pollicipes polymerus* and *Chthamalus* species on artificial plates prompted Pineda (1994) to suggest that settlement is intensified by behaviour in *Pollicipes polymerus*, but much less so in *Chthamalus* species. In relation to *Pollicipes pollicipes*, a higher intensity of recruitment was detected on artificial substrates placed at sites where this species naturally occurs than at sites located relatively close (from metres to 100s metres), but where the abundance of this species is much lower or absent (sites relatively less exposed) (Jacinto 2016, Mateus 2017, Cruz et al. unpublished observations).

Recruitment indices

As recruitment of *Pollicipes polymerus* and *P. pollicipes* is high on conspecifics, Barnes (1996) considered that the recruitment rate could be determined with relative ease. Different types of indices of recruitment on conspecifics have been used: the number of cyprids and/or juveniles of different sizes attached to adults (Hoffman 1989, de la Hoz and Garcia 1993, Cruz 2000, Pavón 2003, Cruz et al. 2010a, Fernandes et al. 2021, Aguión et al. 2022a), and percentage of adults with attached barnacles (Molares 1994) or juveniles (Macho 2006). Artificial substrates have also been used to describe the temporal and spatial variation of settlement and recruitment in *Pollicipes polymerus* (Pineda 1991, 1994, Dudas et al. 2009), but were not compared with indices of recruitment on conspecifics. Unlike indices of recruitment on conspecifics, which measure recruitment to a certain size of juveniles (typically juveniles with maximum distance between the rostrum and the carina, RC of <0.6 mm or RC < 1 mm), indices that use artificial substrates can measure recruitment over an exact period corresponding to time of field deployment of the substrates. Recently, a new recruitment index for *Pollicipes pollicipes* has been developed for monitoring purposes in ecological or fisheries studies, in which the recruitment rate of *P. pollicipes* on an artificial substratum ('barticles', European Patent nr. EP3372073B1, see Figure 15) was measured over a given period (Mateus 2017). A comparison was made among the index of recruitment on 'barticles' and indices of recruitment of *Pollicipes pollicipes* on conspecifics (see above) based on observations in SW Portugal (Mateus 2017). The conclusion from this study was that the mean number of cyprids and juveniles (RC < 0.6 mm) attached to conspecific adults ($n = 15$–20 adults) represents the best estimate of recruitment on conspecifics that occurred 15 days or 1 month before sampling. The use of artificial substrates ('barticles' or others) can enable comparisons of recruitment rates of *Pollicipes* among different locations, periods or experimental situations, making them less confounded, and avoiding destructive sampling (Mateus 2017).

Recruitment on conspecifics: small-scale spatial patterns

Small-scale spatial patterns of settlement and recruitment of *Pollicipes polymerus* and *P. pollicipes* on conspecifics (adults) have been described in relation to: position along the adult (both species, Hoffman 1984, Cruz et al. 2010a, Helms 2004), position around the peduncle (*P. polymerus*, Helms 2004), location within the cluster of conspecifics (edge, middle and centre) and cluster size (small – 4.7 cm diameter, large – 8–14 cm diameter) (*P. polymerus*, Helms 2004), intertidal levels (both species, Hoffman 1989, Pavón 2003, Cruz et al. 2010a), subtidal versus intertidal level (*P. pollicipes*, Cruz 2000), and horizontally among places (*P. pollicipes*, Cruz 2000).

The distribution of juveniles along the adult (capitulum and peduncle) is not random, with *Pollicipes polymerus* and *P. pollicipes* showing opposite patterns of distribution along the peduncle. In both studies conducted with *Pollicipes polymerus* (La Jolla, California, the USA, Hoffman 1984; Cape Arago, Oregon, the USA, Helms 2004), a gradient was observed, from the smallest and most abundant juveniles on the peduncle near the junction with the capitulum ('growth zone', see section 'Growth and size') to the largest and fewest near the base of the peduncle. In *Pollicipes pollicipes*, most small juveniles (RC < 0.6 mm) were located on the basal half of the peduncle and only a few (<5%) were located on the 'growth zone' (SW Portugal, Cruz et al. 2010a). These patterns might be explained by differential settlement and post-settlement processes between species and along the peduncle. As already noted in Barnes (1996), we know that individuals of the species *Pollicipes polymerus* and *P. pollicipes* are able to move along the peduncle towards the base. This mobility was first suggested by Hoffman (1984. in *Pollicipes polymerus*) and later confirmed by Kugele & Yule (1993, 2000 in *P. pollicipes*). The active relocation of juveniles along the peduncle might explain the pattern of larger juveniles being more abundant near the base. The higher abundance of small juveniles of *Pollicipes polymerus* on the growth zone might be not only due to a potential greater attractiveness of this zone (new cuticle) for cyprid settlement (Hoffman 1984), but also due to the suppression of juvenile growth in this zone, as a result of intraspecific competition for food with adult conspecifics ('shading effect') (Cimberg unpublished observations in Hoffman 1984). The discrepancy in the patterns observed in the two species may also result from possible differences in the density of *Pollicipes* clumps and, consequently, in the availability of settlement substrate (Cruz et al. 2010a). If there are differences in adult density between California/Oregon and SW Portugal (no data available), namely more dense and packed clumps in California/Oregon since *Pollicipes pollicipes* is heavily exploited in Portugal (see section 'Fisheries, management and conservation'), the basal area of the peduncles might be less accessible for settlement in California/Oregon (Cruz et al. 2010a). Recruitment on the capitulum of the adults was considered to occur rarely (*Pollicipes polymerus*, Hoffman 1984, 1989) or at a significantly lower rate than on the peduncle (*P. pollicipes*, <5% on the capitulum, Cruz et al. 2010a). Another explanation for the lower recruitment on the capitulum might be due to higher mortality of cyprids and settlers due to grazing/bulldozing of limpets that can be abundant on the capitular plates (Hoffman 1984, unpublished observations, see section 'Post-settlement processes of distribution and abundance' and Figure 12), or by higher selectivity of cyprids for the scales of the peduncle than the capitulum (Barnes & Reese 1960, Chaffee & Lewis 1988).

Juveniles of *Pollicipes polymerus* on adults, in clusters, were observed to aggregate more frequently below the rostrum and carina of the adult conspecific than at other locations around the peduncle (Cape Arago, Oregon, the USA, Helms 2004). Previously, this pattern had been described by Hoffman (1989). Helms (2004) suggested that individuals in a cluster might act as a filter, creating dead spaces around their peduncles below the rostrum and carina, or that abrasion (and consequent mortality) by adjacent adults is less intense below the rostrum and carina.

The distribution of juveniles of *Pollicipes polymerus* on adults within clusters is not random (Cape Arago, Oregon, the USA, Helms 2004), and, according to this study, there was a significantly higher abundance of juveniles on adults at the edges of the clusters that in the centre of the clusters. Helms (2004) suggested that settlers on adults at the edges of clusters might have higher survival if cluster edges have higher food availability, reduced crowding by adults, or reduced predation, namely from within-cluster predators (e.g. flatworms and crabs). The cluster size of *Pollicipes polymerus* was not as important in determining the abundance of recruits as location within the cluster (Helms 2004).

Regarding variation in recruitment of species in *Pollicipes*, at different tidal levels, no consistent patterns have been found. Higher recruitment of *Pollicipes pollicipes* occurs on the low shore of SW Portugal than higher on the shore (two sites in SW Portugal, Cruz et al. 2010a). In contrast, no consistent patterns were observed between tidal levels regarding the recruitment of *P. pollicipes* in Figueras, Asturias, Spain (Pavón 2003) or of *P. polymerus* in La Jolla, California, the USA (Hoffman 1989). In a unique study of *Pollicipes* in which recruitment on adults of *P. pollicipes* collected in the intertidal and subtidal was compared, no consistent patterns were found between the two habitats (Cruz 2000).

Concerning horizontal patterns in recruitment, several observations were made of *Pollicipes pollicipes* in SW Portugal. This species is abundant on very exposed shores, but even on these shores, abundance can drop dramatically between seaward rock walls directly facing the swell compared with the landward walls of those same rocks (Cruz 2000). No differences in the recruitment on conspecifics were observed in adults collected in the centre of their horizontal distribution or in adults located at the edge of that same horizontal distribution, in slightly less exposed locations (Cruz 2000). However, when transplanting adults of *Pollicipes pollicipes* in cages to areas where barnacles were much less abundant, or absent (rock walls not directly facing the swell on very wave-exposed shores, less-exposed shores), less recruitment on transplanted adults was observed than on adults collected from naturally occurring areas (Cruz et al. unpublished observations).

Settlement and recruitment: large-scale spatial patterns and temporal patterns

The only study mentioned by Barnes (1996) on the temporal variation of recruitment of species of *Pollicipes* was the study by Hoffman (1989) (La Jolla, California, the USA), of the monthly recruitment on conspecifics by *P. polymerus* over 1 year (Table 11). At the time of Barnes' (1996) review, two studies of the daily variation in the settlement of *P. polymerus* were also published (artificial substrates, April to July 1989, La Jolla, California, the USA, Pineda 1991, 1994), but were not cited by Barnes (1996).

Twenty-five years after Barnes (1996), there have been various studies investigating the temporal variation of recruitment of *Pollicipes polymerus* during periods of 3–14 days (artificial plates, July to September 1998 and 1999, four sites along the central coast of Oregon, Dudas et al. 2009), of the monthly recruitment of *P. pollicipes* on conspecifics at various sites in Europe and over various years (Pavón 2003, Macho 2006, Cruz et al. 2010a, Fernandes et al. 2021, Aguión et al. 2022a) and of the monthly recruitment of *P. caboverdensis* on conspecifics (Tarrafal, Santiago, Cape Verde, 2014–2016, Cruz et al. in prep.) (see Table 11). At the time of Barnes' (1996) review, there is no published information on spatial or temporal variation in the recruitment of *Pollicipes elegans*.

The description and comparison of large-scale spatial patterns and temporal patterns of recruitment in *Pollicipes* is hampered when not using the same methods, namely the same recruitment index. However, since many of these studies did use the same recruitment index (average number of cyprids

Table 11 Recruitment in *Pollicipes* species

Species/latitude/location/habitat		Recruitment on conspecifics/month												Period of observation	Index of recruitment (size of juveniles)	Size of adults and sampling size	References
Pollicipes polymerus		J	F	M	A	M	J	J	A	S	O	N	D				
32°N	Dike Rock, La Jolla, California, the USA (low/mid-shore)	■	■	■	■	■	■	■	■	■	■	■	■	1983–1985	RC < 1 mm	> 9 mm (RC), $n=30–120$	Hoffman (1989)[a]
Pollicipes pollicipes																	
47°N–48°N	Brittany, France (mid-shore, 1 or average of up to 3 sites)		░	░	░	░	░	▓	░	░	▓	░		2018	Cyprids + RC < 0.6 mm	>15 mm (RC), $n=20$ per site	Aguión et al. (2022a)
43°N	*Punta la Cruz*, Asturias, Spain (low shore)		░	░	░	░	░	░	▓	▓	▓	▓	▓	2000	Cyprids + RC < 1 mm	>12.14 mm (LRT), $n=50$	Pavón (2003)
43°N	*Punta la Cruz*, Asturias, Spain (low shore)	░	░	░	░	░	░	░	■	■	■	▓	■	2001	Cyprids + RC < 1 mm	>12.14 mm (LRT), $n=50$	Pavón (2003)
43°N	Asturias, Spain (mid-shore, 1 or average of up to 6 sites)	▓	░	░	░	░	░	■	■	■	■	▓	▓	2018	Cyprids + RC < 0.6 mm	>15 mm (RC), $n=20$ per site	Aguión et al. (2022a)
42°N–43°N	Galicia, Spain (mid-shore, 1 or average of up to 6 sites)	░	░	░	░	░	░	░	■	▓	▓	░	░	2018	Cyprids + RC < 0.6 mm	>15 mm (RC), $n=20$ per site	Aguión et al. (2022a)
37°N	Cape of Sines, SW Portugal (mid-shore)										■	▓	░	1990	Cyprids + RC < 0.6/1 mm	>15 mm (RC), $n=50$	Cruz et al. (2010a)
37°N	Cape of Sines, SW Portugal (mid-shore)	░	░	░	░	░	░	■	■	■	■	■	■	1991	Cyprids + RC < 0.6/1 mm	>15 mm (RC), $n=50$	Cruz et al. (2010a)
37°N	Cape of Sines, SW Portugal (mid-shore)	■	▓	░	░	░	░	░	░	■	■			1992	Cyprids + RC < 0.6/1 mm	>15 mm (RC), $n=50$	Cruz et al. (2010a)
37°N	Cape of Sines, SW Portugal (mid-shore)							░	▓	■	■	■		2007	Cyprids + RC< 1 mm	>15 mm (RC), $n=20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	▓					░	▓	▓	■	■			2008	Cyprids + RC < 1 mm	>15 mm (RC), $n=20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)					░	░	▓	■	■	■	■		2009	Cyprids + RC < 1 mm	>15 mm (RC), $n=20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	■		▓	░	░	░	▓	■	■	■	■		2010	Cyprids + RC < 1 mm	>15 mm (RC), $n=20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	▓		▓		░	░	■	■	■	■	■	■	2011	Cyprids + RC < 1 mm	>15 mm (RC), $n=20–50$	Fernandes et al. (2021)

(*Continued*)

Table 11 (*Continued*) Recruitment in *Pollicipes* species

Species/latitude/location/habitat		Recruitment on conspecifics/month	Period of observation	Index of recruitment (size of juveniles)	Size of adults and sampling size	References
37°N	Cape of Sines, SW Portugal (mid-shore)	■■▓░░■■■■■■■	2012	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	■■▓▓░▓■■■■■■	2013	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	□□▓░░░■■■■■■	2014	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	▓▓▓▓░░■■■■■■	2015	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	■■▓▓░▓■■■■■■	2016	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Fernandes et al. (2021)
37°N	Cape of Sines, SW Portugal (mid-shore)	■■▓▓░■■■■■■■	2017	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Fernandes et al. (2021), Aguión et al. (2022a)
37°N	Cape of Sines, SW Portugal (mid-shore)	▓□□□░░░■■■■■	2018	Cyprids + RC < 1 mm	>15 mm (RC), $n = 20–50$	Aguión et al. (2022a)
37°N	SW Portugal (mid-shore, 1 or average of up to 5 sites)	▓░░░░░▓■■■■■	2018	Cyprids + RC < 0.6 mm	>15 mm (RC), $n = 20$ per site	Aguión et al. (2022a)
Pollicipes caboverdensis						
15°N	Tarrafal, Santiago Island, Cape Verde	□□░▓░▓░▓▓▓▓▓	2014	Cyprids + RC < 1 mm	>15 mm (RC), $n = 40$	Cruz et al. (in prep.).
15°N	Tarrafal, Santiago Island, Cape Verde	░░▓■▓■□░░▓░□	2015	Cyprids + RC < 1 mm	>15 mm (RC), $n = 40$	Cruz et al. (in prep.).
15°N	Tarrafal, Santiago Island, Cape Verde	▓░░▓▓▓░□░░□░	2016	Cyprids + RC < 1 mm	>15 mm (RC), $n = 40$	Cruz et al. (in prep.).

Seasonal patterns of recruitment on conspecifics (average number of cyprids and juveniles (RC < 0.6 mm or RC < 1 mm) per adult) according to species, location and habitat (when available and when there are differences), period of observation, index of recruitment and size of juveniles, size of adult conspecifics and sampling size. Light grey stands for the non-recruitment season (<1 recruit per barnacle), middle grey for 1–3 recruits per adult, and black for the main recruitment season (>3 recruits per adult). Data for blank cells are missing.

LRT, length between rostrum and tergum; RC, rostrocarinal length.

[a] Study cited in Barnes (1996). For a few dates in Fernandes et al. (2021) (Nov 2012, Jan 2013, Nov 2014 and Dec 2015), we did not have data, but as these months were in the main recruitment season, we considered them as part of the main recruitment season.

and juveniles with RC < 0.6 mm or RC < 1 mm per adult), we have compiled Table 11, summarizing the information on the timing and intensity of recruitment in species of *Pollicipes.* The main recruitment season was defined when this index was greater than 3. This threshold has been used in previous studies on *Pollicipes pollicipes* (Cruz et al. 2010a, Fernandes et al. 2021, Aguión et al. 2022a), but it is arbitrary and only serves to compare the patterns exhibited by the various species at the various sites and years of observation. The non-recruitment season was defined when this index was lower than one.

Although there is only one study on recruitment in *Pollicipes polymerus* based on observations made approximately 35 years ago (La Jolla, California, the USA, Hoffman 1989), it appears that the intensity of recruitment is much higher than that observed in the two Atlantic *Pollicipes* species (Table 11). Hoffman (1989) described the recruitment of *Pollicipes polymerus* as occurring year-round, with peak recruitment in early spring (March–April, 74–190 recruits per adult). From September to February, recruitment values were lower (8–22 recruits per adult) (Hoffman 1989). This continuous recruitment pattern observed in La Jolla may be directly related to the reproductive pattern that has been observed at some sites in Southern California, identified as 'winter breeders' (see reproductive pattern in Goleta Point and Santa Catalina Island, Table 6 and section 'Reproduction').

At the other extreme of recruitment intensity is *Pollicipes caboverdensis*, which showed very low recruitment values throughout the year, with only 2 months in 3 years of observations with recruitment values above three (April and June) (Cruz et al. in prep. a). Again, this recruitment pattern appears to be directly related to the reproductive pattern of this species (see Table 6). Reproduction of *Pollicipes caboverdensis* did not show pronounced seasonality, and the highest values were observed in late winter and early spring (Cruz et al. in prep.).

Regarding *Pollicipes pollicipes*, there are several studies, in several European locations, and in several years (see Table 11). In a recent study, populations located near the northern limit of distribution of *P. pollicipes* (Brittany, France) were compared with Iberian populations (Asturias, Galicia and SW Portugal) by using a standardized protocol (Aguión et al. 2022a). Using the criterion of three recruits per adult for the definition of the lower limit of the main recruitment season, there is no main recruitment season in Brittany comparable to that occurring with other locations (Table 11). The highest values of recruitment (1–3 recruits per adult) in Brittany were observed in July and October (based on 2018 data, Aguión et al. 2022a). The low recruitment rates of *Pollicipes pollicipes* observed in Brittany in comparison with most locations in Iberia might be explained by: lower reproductive effort (see Table 6), and potential lower larval supply due to Brittany's more 'insular' situation (absence of *P. pollicipes* north of Brittany and on most of the French coast south of Brittany) (Aguión et al. 2022a).

Considering the studies conducted to date on large-scale spatial patterns and temporal patterns of recruitment on conspecifics of *Pollicipes pollicipes* in Iberia, using the same index (see Table 11), we can define the following main patterns:

1. interannual variation of recruitment patterns, but months with the highest recruitment intensity occurred in summer and autumn;
2. the sole month that was classified as belonging to the non-recruitment season (<1 recruit per adult), in all locations and years, was May;
3. although there is interannual variation, the main recruitment season in SW Portugal is longer than in Asturias and Galicia, and the non-recruitment season in SW Portugal is shorter than in Asturias and Galicia;
4. in 12 consecutive years of recruitment observations in SW Portugal (2007–2018), there were some years in which the duration of the main recruitment season was longer than in others (i.e. 9 months in 2012 and 2017 compared with < 5 months in 2007 and 2010).

A positive relationship between recruitment and seawater temperature was suggested in the study of recruitment of *Pollicipes pollicipes* in Europe (Brittany, Asturias, Galicia and SW Portugal, Aguión et al. 2022a). This had been previously detected and found to be significant in a 10-year study monitoring the recruitment of *P. pollicipes* at Cape of Sines (SW Portugal) (Fernandes et al. 2021). In this study, a clear association between recruitment and both relaxation of upwelling and seawater warming was detected.

However, this association has not been detected in other studies with *Pollicipes pollicipes* or *P. polymerus*. In a previous study at Cape Home, Galicia (Spain), Macho (2006), using a different recruitment index (percentage of adults with one or more recruits), observed a decline in the recruitment rate of *Pollicipes pollicipes* during a 5-month period of strong downwelling. In relation to *Pollicipes polymerus*, Dudas et al. (2009) did not find any significant correlation between recruitment (3–14 days recruitment on artificial plates, Oregon) and several physical variables (across-shore and alongshore currents, seawater temperature and wind intensity). Pineda (1991) found a significant negative correlation between daily settlement of *Pollicipes polymerus* and surface water temperature (La Jolla, California). In that study, internal tidal bores were suggested as the mechanism that was driving decreases in water temperature and larval transport onshore. These contradictions may be related to the different scales at which recruitment was measured, to the different indices of recruitment used, or to different processes acting at different locations, and also differences between species, which, in turn, could reflect local coastal oceanographic context. Recruitment, measured on the scale of 1 month at a particular site, may not be related to the settlement that has occurred at that site. On the other hand, the settlement rate can underestimate or overestimate larval supply (e.g. due to predation, behaviour). Thus, as noted by Pineda et al. (2010), "knowledge of physical transport processes derived from settlement time series may be flawed". Further studies are needed to describe and understand the patterns and processes of settlement and recruitment of species of *Pollicipes*, namely *P. polymerus* and *P. elegans*. Further studies are also needed to understand the relative importance of settlement and post-settlement processes in the recruitment to the reproductive (and exploitable) populations.

Growth and size

Growth in *Pollicipes* is continuous throughout the life of the individual. Upon settlement onto an appropriate substrate and subsequent metamorphosis into the juvenile form, stalked barnacles grow by increasing the length of peduncle and by calcareous accretion of the plates in the capitulum (thoroughly described in Anderson 1994). Unlike most crustaceans, complete moulting of the exoskeleton does not occur in stalked barnacles. The outer integument (i.e. the outer covering of the peduncle and capitulum) is not shed at a moult, as is the inner integument (i.e. covering of the mantle cavity and the soft parts of the body) (Anderson 1994).

Barnes (1996) described the post-settlement development and growth of *Pollicipes* species based on the work by Darwin (1852), Broch (1922), Mahmoud (1959b, 1960), Koehler (1889, Chaffee & Lewis (1988) and Anderson (1994). This included a description of the appearance of the primordial valves of the capitular and peduncular scales and of the development of secondary capitular plate development, addition of new scales in the 'growth zone' (i.e. the transition zone between the capitulum and the peduncle), the growth of the stalk exoskeleton and embedded spicules, and some species-specific differences within the genus *Pollicipes*, namely of *P. polymerus* and *P. pollicipes*. In 1996, studies reporting estimates of the growth rates of *Pollicipes* were relatively scarce and most concerned *P. polymerus* (8 out of 9 references in Table 15 in Barnes 1996; see also Table 12), with only one concerning *P. pollicipes* (see Table 12). Most estimates were based on field measurements of marked individuals (*in situ* or transplanted), or barnacles that had recruited on cleared surfaces on ambient intertidal rocky shores (Barnes & Reese 1960, Paine 1974, Newman & Abbot 1980, Lewis & Chia 1981, Page 1986, Bernard 1988, Cruz 1993). There were also references to growth rate estimates observed in ambient subtidal conditions (Hoffman 1989) and artificial conditions (an intertidally located offshore oil platform and on a submerged intake seawater system) (Page 1986, Hoffman 1988). These studies suggested that the growth rates of *Pollicipes* species were variable at different multiple spatial and temporal scales. Barnes (1996) addressed such variation, discussing how it might be affected by abiotic and biotic interacting factors, such as water temperature, light, water flow, food availability and consumption, season, intra- and interspecific competition, and ecological context.

Herein, we compile and summarize the main findings of work concerning *Pollicipes* growth rates subsequent to Barnes' review. In Table 12, we compile ranges of estimates of average growth rate (mm/month; min-max) observed in ambient intertidal conditions, irrespective of intertidal height, season and methods used in different studies cited in Barnes (1996) as well as those published thereafter. Two size classes were considered: small (RC < 15 mm) and large (RC > 15 mm). Data are listed per species and country, with notes on methods used, study location and data source. Some progress has been made during the last 25 years, mainly regarding *Pollicipes pollicipes* (e.g. Cardoso 1998, Cruz 2000, Cruz et al. 2010a, Boukaici et al. 2012, Jacinto et al. 2015, Neves 2021) and, to a lesser extent, *P. polymerus* (Helms 2004, Phillips 2005) and *P. elegans* (e.g. Pinilla 1996, Samamé & Quevedo 2001). To date, no studies have been carried out on the growth of *Pollicipes caboverdensis*, despite being an endemic species with increasing economic importance. In general, growth in the various *Pollicipes* species is highly variable at multiple temporal and spatial scales. Mean growth rates are higher and more variable in juveniles, gradually decreasing with age and/or size (Table 12).

Table 12 Growth rates of *Pollicipes* spp.

Species	Methods and location	Growth rate (mm RC/month)		References
		Small	Large	
Pollicipes polymerus				
Canada	Size increments of marked individuals (physical tags). Size structure analysis of recruits on cleared surfaces British Columbia	0.80–1.25	0.54	Bernard (1988)[a]
The USA	Size increments of marked individuals (physical and calcein tags) on natural or transplanted clumps. Size structure analysis of recruits on cleared surfaces. Washington State, Oregon and California.	0.03–4.07 0.20–0.60	0.04–0.67	Barnes & Reese (1960)[a], Lewis & Chia (1981)[a], Paine (1974)[a], Page (1984)[a] Helms (2004), Phillips (2005)
Pollicipes elegans				
Peru	Size structure analysis of natural population; size increments of marked individuals (physical tags) on natural clumps. Piura.	3.00	2.34 (CH)	Pinilla Garcia (1996), Samamé & Quevedo (2001)
Pollicipes pollicipes				
Spain	Size structure analysis of natural population. Galicia.	-	0.34	Sestelo & Roca-Pardiñas (2007, 2011)
Portugal	Size increments of marked individuals (physical and calcein tags) on natural or transplanted clumps and artificial substrata; size structure analysis of recruits on cleared surfaces and artificial substrata. SW Portugal; RNB Portugal	0.17–0.66 0.18–5.20	0.08–0.48 0.11–0.47	Cruz (1993)[a] Cruz (2000), Cruz et al. (2010a), Figueira (2015), Jacinto et al. (2015), Mateus (2015), Cruz et al. (2016a,b), Darras (2017), Mateus (2017), Belela (2018), Fernandes (2018), Santos (2019), Cruz et al. (2020), Neves (2021)
Morocco	Size structure analysis of natural population; SW Morocco	1.03	0.20–0.45	Boukaici et al. (2012)

Range of estimates on average growth rate observed in ambient intertidal conditions (mm RC/month; min - max) per size class (small: RC < 15 mm; large: RC > 15 mm; RC: rostrocarinal length) with notes on methods used and study locations.

[a] Studies cited in Barnes (1996).

Field studies on the growth of Pollicipes *species*

Field studies on the growth of *Pollicipes* species have been based on population size structure analyses (Cardoso 1998, Cruz 2000, Samamé & Quevedo 2001, Sestelo & Roca-Pardiñas 2007, Cruz et al. 2010a, Sestelo & Roca-Pardiñas 2011, Boukaici et al. 2012), monitoring size increments of barnacles that have recruited on cleared natural surfaces or artificial substrata (Cruz 2000, Cruz et al. 2010a, Mateus 2015, Cruz et al. 2016a, b, Mateus 2017, Belela 2018, Santos 2019, Cruz et al. 2020) and estimates of growth rates of marked individuals (Pinilla 1996, Helms 2004, Phillips 2005, Cruz et al. 2016a, b, Figueira 2015, Jacinto et al. 2015, Neves 2021).

The most widely used biometric variable for growth and size structure studies in *Pollicipes* species (e.g. Phillips 2005, Cruz et al. 2010a, Boukaici et al. 2012) and the one that best represents linear growth (Cruz 1993) is the maximum rostrocarinal length (RC). However, other variables such as total length (Hoffman 1984, Boukaici et al. 2012), capitular height (Page 1986, Cardoso & Yule 1995, Pinilla 1996) and capitular base diameter (Parada et al. 2012) have also been used.

Growth estimates in all studied *Pollicipes* species suggest a rapid increase in size (up to 11–17 mm RC) during the first year, with most individuals reaching maturity within 1 year (Lewis & Chia 1981, Hoffman 1989, Bernard 1988, Pinilla 1996, Samamé & Quevedo 2001, Cruz 2000, Cruz et al. 2010a, Boukaici et al. 2012, Parada et al. 2012, 2013, see section 'Reproduction'), followed by a decline in growth rates in subsequent years. For example, Boukaici et al. (2012) estimated growth rates of *Pollicipes pollicipes* on the intertidal rocky shores of SW Morocco as approximately 1.0 mm RC/month during the first year, decreasing to 0.5 RC/month in the second year and 0.2 RC/month in the fifth year.

Age determination

A major limitation in stalked barnacle growth studies is that age determination is difficult to obtain through methods such as length frequency, or shell band analyses. Studies that have tried to establish size:age relationships, based on growth curve analyses, have estimated maximum ages of 7 or more years (*Pollicipes pollicipes*, 26 mm RC; Boukaici et al. 2012), 12 years (*P. polymerus*, 31 mm RC; Bernard 1988) and 15–20 years (*P. polymerus* Barnes & Reese 1960). Several studies considered that length frequency data should not be used to determine age and growth parameters in *Pollicipes pollicipes*, due to the constant settlement of larvae throughout the summer months and the difficulties of successfully following cohorts through time, namely for more than 1 year after settlement (Cardoso 1998, Cruz 2000, Cruz et al. 2010a, Sestelo & Roca-Pardiñas 2011, Parada et al. 2012). Likewise, the use of shell bands in age determination in *Pollicipes pollicipes* is prone to error (Mahmoud 1959a, Broch 1922 in Barnes 1996, Cardoso 1998). Despite the successful identification of shell bands and several environmental influences on banding periodicity (e.g. tidal periodicity), Cardoso (1998) questioned the applicability of such technique in barnacle age determination, since band widths were very similar throughout the shell length, with no regular 'check' marks that could provide age estimation. Also, fracturing of the capitular plates is quite common in *Pollicipes* (Cornwall 1925 in Barnes 1996, Wootton 1993, Cruz 2000) and sections through capitular plates show that the number of laminae is variable, even in the same plate, as well as in different plates of the same animal (Mahmoud 1959a in Barnes 1996). Analysing the banding on polished and etched cross sections of the carina of *Pollicipes polymerus*, Bernard (1998) observed a reasonable correlation with capitular width and estimated age in years, but considered that age estimation by such a method was not reliable, except during the active growth phase. Growth and age determination of field populations of *Pollicipes pollicipes* seems attainable only by mark and recapture experiments.

Individual marking techniques

Individual marking techniques in *Pollicipes* studies include mapping individuals in relation to marks made in adjacent substrata, or using marks, such as insect tags glued to the capitular plates of suitably sized individuals (e.g. Phillips 2005, Cruz et al. 2010a). Despite the valuable data obtained, such individual physical marking techniques are very difficult to implement in the field, often resulting in low numbers of marked individuals and size constraints in marking efficiency. A major advance in this field was the successful use of chemical marking with calcein in *Pollicipes polymerus*, pioneered by Helms (2004), and later applied in *P. pollicipes* by Jacinto et al. (2015) and several others thereafter (Figueira 2015, Mateus 2015, Cruz et al. 2016a, b, Mateus 2017, Belela 2018, Santos 2019, Cruz et al. 2020, Neves 2021). Such techniques have a great potential in stalked barnacle growth studies, mainly because they allow mass marking of individual barnacles of different size cohorts within a short period (e.g. less than 1 day of manipulation) and involve less fieldwork time (Jacinto et al. 2015), which is a major advantage since this species lives on extremely exposed rocky shores. Immersion of *Pollicipes* individuals in a calcein solution leaves a fluorescent mark in calcified structures. Calcein is incorporated into the growing calcium carbonate of the capitular plates of the barnacles. Because these plates grow in thickness and in area, through laminar accretion or basal marginal accretion (Anderson 1994), the entire original plate is stained. When marked animals are returned to the field, new and unmarked plate material is added during growth. Calcein marks are visible under epifluorescent light and may be used to identify marked individuals and to estimate growth rates in *Pollicipes* species, mostly by estimation of the marginal growth of the capitular plates (Figure 10). Consequently, calcein marking has been applied with great success in several studies, both in field and laboratory conditions, to address spatial and temporal variability in stalked barnacle growth, namely of *Pollicipes pollicipes* (Figueira 2015, Jacinto et al. 2015, Mateus 2015, Cruz et al. 2016a, b, Mateus 2017, Belela 2018, Santos 2019, Cruz et al. 2020, Neves 2021).

Spatial and temporal variability in growth

Variability in patterns of growth in *Pollicipes* has been addressed at multiple spatial and temporal scales. At minute spatial scales, the effect of location within the cluster and cluster size, on the growth rates of juvenile *Pollicipes polymerus*, was studied *in situ* over a 2-month period at Cape Arago, Oregon, the USA (Helms 2004). Findings suggest a negative effect of density on juvenile stalked barnacle growth, namely that the location of juvenile barnacles within the cluster significantly influenced their growth rates. The average growth rates of juveniles located at the edges of the clusters were 1.4 higher than those of juveniles located on the inside of the clusters. Such an effect of location within the cluster on juvenile growth rates was discussed in the context of intraspecific competition for space and food between juveniles and adults. Helms (2004) also noted that cluster size was less important in explaining differences in the growth of juvenile barnacles than was location within the cluster, because the growth rates of juveniles in small and large clusters were similar. However, the growth rates of juveniles on solitary adults were almost twice as fast as those of juveniles in clusters. These results indicate that there may be important differences in growth between clusters and solitary adults, which may help explain how clusters are formed and maintained, and how *Pollicipes polymerus* may compete with other intertidal organisms (e.g. the mussel, *Mytilus californianus*) (Helms 2004). Increased knowledge of hydrodynamics and water flow at the cluster scale, along with experiments testing the effects of the location of the cluster and cluster size on food capture by adults and larger juveniles, would enable questions regarding competition among adults or between juveniles and adults to be tackled.

Variation in growth rate with intertidal height has been hypothesized as a driver of size structure differences found between low-shore and high-shore barnacles in SW Portugal (Cruz 2000,

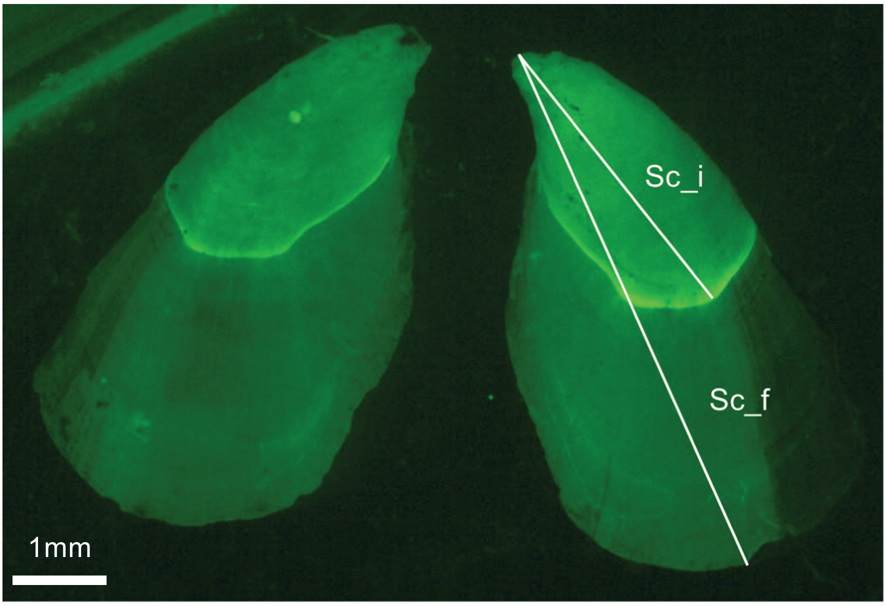


Figure 10 *Pollicipes pollicipes. Scuta* with visible fluorescent calcein mark (Sc_i and Sc_f are initial and final maximal lengths, respectively).

Cruz et al. 2010a). Barnacles at low tide levels reach a higher maximum size, possibly indicating that growth at this level is higher than at the high shore (Cruz 2000, Cruz et al. 2010a). This hypothesis has been supported by studies carried out at the Cape of Sines and at the Berlengas Nature Reserve (Portugal), where growth rates of juvenile *Pollicipes pollicipes* in the low intertidal were about twice those at the mid-intertidal (Figueira 2015, Neves 2021). Other studies, however, did not find an effect of intertidal height on *Pollicipes pollicipes* growth rates (Pavón 2003, Jacinto et al. 2015). Growth rate variability with intertidal height may be the result of less intraspecific competition, due to lower barnacle density and/or increased feeding time on the low shore. Further support, for the positive effect of increased feeding time on growth rates, comes from observations of *Pollicipes pollicipes* growth in permanently submerged conditions. Recently settled *Pollicipes pollicipes* individuals (RC < 5 mm) on artificial substrata were reallocated to permanently submerged conditions on an experimental aquaculture raft, located inside the Port of Sines (SW Portugal), and then compared with growth rates on the nearby natural intertidal shores of the Cape of Sines (SW Portugal) on several occasions (Mateus 2015, Cruz et al. 2016a, Darras 2017, Belela 2018, Santos 2019, Cruz et al. 2020). In general, juvenile growth rates were 1.5–3.0 times higher in permanently submerged conditions compared with ambient intertidal conditions. Caution should be exercised when interpreting these results, however, as the ecological context in which these permanently submerged barnacles were growing may have been quite different from the shallow subtidal, rocky shores where *Pollicipes pollicipes* naturally occurs.

Seasonal variation in stalked barnacle growth rates has also been observed in natural intertidal habitats, but patterns are inconsistent. Growth rates in recently settled *Pollicipes pollicipes* juveniles on artificial substrata were ca. 1.5 times larger during summer than during winter (Cruz et al. 2016a), ca. two times larger during winter, spring and summer than during autumn (Belela 2018) and ca. 3.4 times larger during autumn compared with spring/summer (Cruz et al. 2020). No effect of season (summer vs winter) was found in the growth rates of juveniles in transplanted barnacle clumps (Cruz et al. 2016a). Likewise, field measurements of the maximum size of barnacles recruiting onto cleared surfaces do not reveal any seasonal variation in juvenile growth, but in adult barnacles, growth rates were ca. 4.3 times larger in winter and spring than in summer (Cruz 2000). Pavón (2003) also did not find significant differences in growth rates of *Pollicipes pollicipes* between sampling seasons, but did observe a positive relationship between growth rates and wave period, wind velocity and direction. It is still not clear weather *Pollicipes pollicipes* growth rates vary with season, or wether these observations mainly reflect the immense variability between individual growth rates, and other site-specific factors.

Phillips (2005) also observed inconsistent seasonal variation (spring vs summer) in growth rates of *Pollicipes polymerus* individuals (6.6–15.4 mm RC), marked with insect tags and planted out on intertidal rocky shores of California (the USA). He described contrasting patterns strongly affected by regional oceanographic effects (e.g. upwelling intensity). During spring, growth was similar at all studied sites, while during summer, growth rates were higher at southern sites (relative to Point Conception, California), but lower at northern sites. Other previous observations carried out by Bernard (1988) on Vancouver Island (BC, Canada), based on individuals with capitular length 15 mm in the active growth phase, suggested that maximum growth occurs between May and July. Given these observations, it seems that growth in *Pollicipes* might be affected by seasonal changes, but patterns of variation are site dependent and probably related to specific nearshore oceanographic processes that affect the local barnacle population.

The growth rate variability in *Pollicipes* has been linked to the oceanographic and ecological contexts of its populations. A striking geographic pattern of growth has been observed by Phillips (2005), who examined growth rates of intertidal benthic filter-feeders, *Pollicipes polymerus* included, over a geographic region that contains sites where upwelling is typically weak (south of Point Conception, California, the USA) and sites where upwelling is often strong and frequent (at and to the north of Point Conception). Growth rates of *Pollicipes polymerus* at southern sites were relatively high and declined moving around Point Conception and to northern sites. Although the author was not able to isolate the underlying cause, there was clear evidence for a geographic gradient in growth rates (higher at southern sites where upwelling is weaker) for other species of common and abundant benthic filter-feeders (e.g. *Mytilus californianus* and *Balanus glandula*). Spatial variation in food availability and quality, and tidal height, did not seem to explain these patterns of growth. On the other hand, water temperature varied in a pattern consistent with growth rates (i.e. mean temperatures were warmer in the south). This study suggests that temperature may be an important driver of large-scale differences in benthic filter-feeder growth rates.

In conclusion, there has been a significant increase in knowledge on *Pollicipes* growth since Barnes' review, except for the lack of studies on *Pollicipes caboverdensis*. However, the different approaches to growth studies that have been applied worldwide make it difficult to meta-analyse the available results. It is important to establish a standard methodology in *Pollicipes* growth studies. The use of calcein marking techniques to estimate growth rates, and the RC length as a standard biometric variable to report growth estimates are good contenders and should be adopted in future work regarding all *Pollicipes* species. Such approaches could be used to estimate von Bertalanffy growth parameters, by measuring growth increments in differently sized individuals, as recently utilized for intertidal limpets (e.g. Oróstica et al. 2021).

The ecological and economical importance of *Pollicipes* species makes it extremely important to have good estimates of growth rates which may be incorporated into ecological and fisheries management models. All evidence gathered to date regarding growth rates in *Pollicipes* species suggests that these are highly variable at multiple temporal and spatial scales. It is, however, difficult to untangle the relative importance of different abiotic and biotic factors that influence growth in natural populations of *Pollicipes*, especially when they seem to covary and interact at multiple scales affecting growth. Observations suggest a rapid increase in size during the first year, with most individuals reaching maturity within the first year after settlement, followed by a gradual decrease with barnacle age and/or size. More observations are needed at suitable spatial and temporal scales and must include ecologically relevant covariates, in order to explain the high intraspecific variability in growth rates observed in *Pollicipes* species. Additionally, while RC may be the best indicator of linear growth in *Pollicipes*, other biometric variables, such as peduncular length, which have been linked to stalked barnacle quality (see section 'Description of adults'), are highly variable at different spatial scales and should be addressed in future work. Age estimation in *Pollicipes* is still unattainable, and longevity estimates are scarce and prone to error.

Post-settlement processes of distribution and abundance

The main ecological processes determining the patterns of distribution and abundance of *Pollicipes* species after settlement were not placed in a single section in the review by Barnes (1996), but were considered as separate sections ("Effect of temperature change and desiccation" and "Predation"). Furthermore, other abiotic or biotic factors (wave action, or intraspecific and interspecific competition), as well as their relationship to behavioural, functional, demographic and life-history traits of *Pollicipes* species, were treated in various other places in Barnes (1996).

We have reviewed the relevant literature on the post-settlement processes affecting the occurrence of *Pollicipes* recruits, juveniles and adults. This was mostly based on observational and experimental evidence acquired after Barnes (1996), but work carried out prior to Barnes (1996) was also integrated. Although an outline on the sole effects of physical factors is included, herein we have mostly focused on the role of biological factors on *Pollicipes* assemblages, particularly on species interactions. This section mainly reports on *Pollicipes polymerus* and *P. pollicipes*, due to the scarcity of ecological studies on the other two species, for which information has been included when available and appropriate.

Physical factors

Barnes (1996) reviewed the work on the eco-physiology of *Pollicipes polymerus,* namely on its tolerance to body temperature changes, desiccation and osmotic stress (Fyhn et al. 1972), on the temperature sensitivity of heart activity and high pressure of pulsating haemolymph (Fyhn et al. 1973) and on the dynamics of aquatic and aerial respiration (Petersen et al. 1974). Barnes (1996) considered *Pollicipes polymerus* as a eurythermal species and "more permeable to water than many balanids", enabling cooling by evaporation from the peduncle, leading to high rates of water and body weight losses during low tide, and compensating rehydration rates during the next submersion at high tide. Physiological regulation is a likely adaptive trait for the survival of *Pollicipes polymerus* in the intertidal zone, driving the metabolism and allocation of energy of barnacles, and allowing them to adjust to periods of submersion and emersion, fluctuating air and water temperatures and gaseous exchange under changing environmental conditions (Barnes 1996 and references therein).

Despite the recognisable tolerance of *Pollicipes* species to adverse intertidal conditions, desiccation has been suggested as physiologically challenging during low-tide periods for *Pollicipes* recruits and adults living at higher tidal levels, possibly setting their upper limit of vertical distribution (Barnes 1996). Moreover, the vertical and local-scale distribution of intertidal invertebrates has often been found to be strongly influenced by lethal and sub-lethal stress associated with heat and/or water loss while exposed to air (e.g. Somero 2002, Miller et al. 2009). To our knowledge, the potential role of thermal and/or desiccation stress during low tide on the intertidal patterns of distribution and abundance of *Pollicipes* species has yet to be investigated. Since *Pollicipes* live in wave-exposed conditions on oceanic, swell-dominated coastlines, considerable swash and spray will ameliorate stresses when the tide is out, except during calm conditions.

A positive relationship with seawater temperature has recently been demonstrated across most of the life cycle of *Pollicipes pollicipes*, including larval survival and growth (Franco et al. 2017), cyprid metamorphosis into juveniles (Franco et al. 2016), recruitment of cyprids and juveniles onto conspecific adults (Fernandes et al. 2021), adult feeding behaviour (Franco 2014) and reproduction (Cruz & Hawkins 1998, Cruz & Araújo 1999, Cruz et al. 2010a). In turn, these processes are known to strongly affect the occurrence of benthic life stages of *Pollicipes* species on the shore. Therefore, seawater temperature might have indirect effects on the patterns of distribution and abundance of *Pollicipes pollicipes* after settlement, with consequences for density-independent population processes. During the El Niño 1982–1983, Tarazona et al. (1985) and Kameya & Zeballos (1988) reported major increases in the abundance of *Pollicipes elegans* on the mid-shore of several locations in Peru associated with conditions of seawater warming, abrupt changes in salinity and increased dissolved oxygen. Conversely, in the same region after the end of the El Niño 1982–1983, a decrease in the abundance of *Pollicipes elegans*, in parallel with increases in dominant native species, such as mytilids (‘choritos’ *Semimytilus algosus* and *Perumytilus purpuratus*) and large acorn barnacles (‘picos de loro’ *Austromegabalanus psittacus*), were both described and suggested to follow changes in abiotic conditions (Kameya & Zeballos 1988).

As described in the section ‘Ecological habitat, and patterns of distribution and abundance’, *Pollicipes* species are associated with habitats with strong wave action throughout their geographical ranges. The restriction of *Pollicipes polymerus* to shores exposed to heavy surf and strong water flows has long been related to a suggested need for a certain hydrodynamic stimulation, to initiate activity of the cirri and to maintain an effective macro-feeding behaviour (Barnes & Reese 1959). Additionally, turbulent flow and water mixing after wave breaking were also suggested to facilitate settlement of *Pollicipes polymerus* (Lauzier 1999b). Likewise, greater water movement in the laboratory was found to stimulate *Pollicipes pollicipes* cyprid attachment (Franco et al. 2016), as well as feeding behaviour of adults (Franco 2014) and their survival and growth (Cribeiro 2007).

Two studies have shown a clear, positive relationship between wave exposure and abundance of *Pollicipes pollicipes*: Borja et al. (2006a) in the Gaztelugatxe Marine Reserve (Basque Country, Spain) and Jacinto & Cruz (2016) in a stretch of coast in SW Portugal. Both studies provided numerical models, based on locally derived wave exposure indices, with strong predictive power of barnacle distribution patterns across the studied regions. These can be used as simple and cost-effective tools to resource assessment and management in different areas, with direct application in the fishery and conservation of this species. *Pollicipes pollicipes* mostly occurs at wave-exposed coastal features, such as capes and headlands (Barnes 1996), and within these coastal features, its abundance varies at small spatial scales (metres apart), depending on the orientation of the site to the prevailing wave direction (Borja et al. 2006a, Jacinto 2016, Jacinto & Cruz 2016). Additionally, another model based on landscape metrics (distance to the coast, convexity at a 25 km scale and wave exposure at 1 km scale) predicted that higher quality (shorter and more robust morphology) *Pollicipes pollicipes* in Asturias would be present in areas that are relatively more distant to the coast, more convex and highly exposed (Rivera 2015).

Among other effects of physical disturbance, abrasion by drift logs has been documented to knock sea mussel clumps free (Dayton 1971), as well as clusters of *Pollicipes polymerus* (Jamieson et al. 1999). Despite these destructive effects on intertidal organisms, the battering by these logs, as well as storm damage, is crucial for the provision of space in exposed intertidal areas and, consequently, for the structure and dynamics of rocky-shore communities (Dayton 1971). These physical factors create patchiness in north-eastern Pacific and Atlantic *Pollicipes* assemblages, often resulting from an initial clearing in *Mytilus* beds, which is then enlarged by wave shock ripping newly vulnerable mussels from the surrounding substratum. These scattered patches and mussel gaps can be subsequently colonized by *Pollicipes* individuals (Dayton 1971).

Competition

Competition between individuals of the same or different species occurs when resources are limited, leading to a change in fitness (survival and reproductive success), which can result in competitive exclusion (elimination of weaker competitors by superior competitors) and set the population carrying capacity of a given area over time (e.g. Hardin 1960, Sommer & Worm 2002). In stable conditions with limiting resources, coexistence between species will only occur if they differ in niche characteristics (e.g. Paine 1984, Sommer & Worm 2002 and references therein). Fluctuating environmental conditions influencing relative competitive ascendency of co-occurring species, and variable recruitment due to supply-side processes and disturbance can all promote coexistence on rocky shores (Worm & Karez 2002 and references therein).

Competitive interactions involving *Pollicipes* species include a variety of forms and mechanisms, as they occur between members of the same species (intraspecific, i.e. among conspecific individuals of a *Pollicipes* species, e.g. Page 1986, Hoffman 1989, Barnes 1996) and of different species (interspecific, i.e. between a *Pollicipes* species and mussels or acorn barnacles or coralline algae, e.g. Wootton 1994, 2010). The ultimate limiting resource is space to settle, grow and have access to food, similar to most intertidal species (Connell 1961, Dayton 1971, Connell 1972, Paine 1980, Worm & Karez 2002). For several intertidal species, intraspecific competition can be more intense than interspecific competition (e.g. Creese & Underwood 1982, Boaventura et al. 2002), although this has been largely tested in grazing molluscs using factorial designs that segregate effects of intra- versus interspecific competition (e.g. Underwood 1978, 1984). Less experimental work has been done on the relative importance of intraspecific competition in sessile species, but self-thinning (i.e. competitively induced mortality within a cohort of organisms growing on shared substratum) has long been recognized in mussels and acorn barnacles (Hughes & Griffiths 1988). In acorn barnacles, density-dependent effects of intraspecific competition and facilitation have been both assessed, particularly concerning their configuration of packing and structural morphological modifications of individuals within hummocks (e.g. Bertness 1989, Bertness et al. 1998, López et al. 2007). In the case of *Pollicipes* species, manipulative studies on the effects of conspecific density have rarely been published (but see Page 1986 and Helms 2004 on individual growth rate response). Given that *Pollicipes* recruitment is high on conspecifics (see section ‘Settlement and recruitment’), intraspecific competition for both space and food might be important and should be investigated in the future. Thus, as the role of intraspecific competition on the distribution and abundance of *Pollicipes* species is still to be determined, the account below focuses on interspecific interactions in the context of community structure.

Competition can occur through a direct type of struggle to attain resources (i.e. interference, when one individual stops the access of another individual to mutually desired resources). The following examples of interference competition involving *Pollicipes* species have been documented: (1) interactions by which canopy algae may overgrow *Pollicipes* individuals and possibly kill them, as observed in the case of the annual macroalga, *Postelsia palmaeformis* (sea palm), relative to *Pollicipes polymerus* (Carefoot 1977 in Jamieson et al. 1999); (2) large-sized individuals of *Pollicipes polymerus* and the mussel *Mytilus californianus* are frequently seen overgrowing *Semibalanus cariosus* acorn barnacles (Wootton 1994); (3) *Pollicipes polymerus* individuals can directly decrease recruitment of *Mytilus californianus*, by filtering out mussel larvae before the latter can settle (Wootton 1993); and (4) *Mytilus californianus* can directly subdue *Pollicipes polymerus*, through the growth of its rigid shell, by crushing *P. polymerus* individuals between mussel shells, or by abrasion of the barnacle body wall by the mussel shell edge (Wootton 1993).

An alternative mechanism of competition is through dominance, in which organisms consume common resources without direct confrontation (i.e. exploitation, when the use of a resource by one individual will decrease the amount available for others). The most emblematic example of exploitation competition concerning *Pollicipes* species is the strongly hierarchical dominance of *Mytilus californianus* in the rocky intertidal community of the north-eastern Pacific, which is mainly achieved by monopolizing space, rendering it unavailable for all other animals and algae (e.g. Paine 1966, 1974, Connolly & Roughgarden 1999) and hence outcompeting and displacing *Pollicipes polymerus*, especially on horizontal mid-intertidal surfaces (e.g. Dayton 1971, Paine 1974, Paine & Levin 1981, Wootton 1993, 1994, 2010). In contrast, on very exposed steep vertical cliffs or overhangs, *Pollicipes polymerus* dominates and outcompetes *Mytilus californianus* by holding space, possibly due to the stronger adherence of the goose barnacles to the substratum (Paine 1974, Barnes 1996). Additionally, Wootton (1993) demonstrated that *Pollicipes polymerus* dominates vertical walls, mainly because loose *Mytilus californianus* adults are not able to recruit onto these habitats where the time of contact with the substratum is insufficient for their reattachment, hindering *M. californianus* invasion.

Additionally, apparent competition can occur when two individuals affect each other indirectly by being prey for the same predator. This was detected by Wootton (1994) in the interaction between *Pollicipes polymerus* and *Nucella* sp. Regarding this interaction, reciprocal negative effects (increased density of one species when the density of the other is reduced), as well as depletion by avian predation, were experimentally demonstrated (Wootton 1994).

Space on which to live is likely critical in *Pollicipes*-associated assemblages composed of a matrix of sessile organisms, specifically among dense turfs of coralline/foliose algae or beds of dominant filter-feeders (Table 4). In these assemblages, competition for space can be intense (e.g. Dayton 1971, Paine 1974, Worm & Karez 2002) and the availability of primary substratum (such as bare-rock or algal crusts) might be scarce and dependent on localized events of disturbance (e.g. Paine 1974, Paine & Levin 1981, Sousa 1984). Disturbance has been experimentally demonstrated to modulate competitive interactions in ecosystems characterized by high diversity, such as exposed rocky intertidal shores, where physical (drift logs and winter storm damage, e.g. Dayton 1971) or biological (predation, e.g. Paine 1974) factors often renew space, by adding patches of cleared substratum and gaps in aggregations of dominant competitors. Heavy catastrophic, physical damage to mussel beds of *Mytilus californianus* creates unique opportunities for colonization by competitively inferior species, such as *Pollicipes polymerus* and *Semibalanus cariosus* (Paine & Levin 1981). Similarly, keystone predation by the seastar (starfish), *Pisaster ochraceus*, on competitively dominant species (*Mytilus californianus* or *M. trossulus*) strongly influences the community structure on shores in California and the Pacific Northwest, potentially shaping the distribution and abundance patterns of a variety of coexisting species, including *Pollicipes polymerus* (e.g. Paine 1974, Menge et al. 1994, Sanford 1999). Rates and patterns of succession in areas subject to disturbance and subsequent recovery result in a heterogeneous progression of species invasion and occupancy, enhancing interspecific facilitation and coexistence while preventing monopolization of substrata and competitive exclusion (Menge et al. 2011).

Competition for food in interactions between *Pollicipes* species and co-occurring filter-feeders could also be possible, due to potentially similar planktonic diets. Common detrital food sources (kelp, intertidal macroalgae, seagrasses and particulate organic matter) assimilated by four common, sympatric, rocky intertidal filter-feeders (*Mytilus californianus*, *Balanus glandula*, *Semibalanus cariosus* and *Pollicipes polymerus*), living near river mouths in the Pacific Northwest, were identified by Tallis (2009) using a dual stable isotope approach, showing that all species shared a common resource base. However, these species occupied distinct trophic positions, with estimated trophic level increasing with barnacle size, being lowest in *Mytilus californianus* and highest in *Pollicipes polymerus* (Tallis 2009). Therefore, interspecific competitive interactions for food including *Pollicipes* species seem improbable given trophic partitioning among abundant filter-feeding species, as well as the flexible peduncle adjustments during feeding and the longer cirri of *Pollicipes polymerus* relative to the two other barnacle species (Barnes 1996, Tallis 2009 and references therein).

The coexistence of *Pollicipes* and *Mytilus* species is found on the Pacific coasts of North, Central and South America, in Europe and the west coast of Africa (Kameya & Zeballos 1988, Barnes 1996, Barraza et al. 2014). *Pollicipes polymerus* is often abundantly interspersed with the mussel complex *Mytilus californianus* and *M. trossulus* to form the North American distinctive *Pollicipes*-*Mytilus* community (Barnes & Reese 1960, Hoffman 1989). Numerous studies have been carried out on the influence of competition and disturbance on biological succession in this community (Dayton 1971, Paine 1974, 1980, Paine & Levin 1981, Wootton 1992, 1993, 1994, 2010, Menge et al. 2011). Despite among-region variability in natural rates of change on rock patches available for colonization, the basic successional sequence is generally an early establishment of *Pollicipes polymerus* with a subsequent increase in the abundance of the dominant species, *Mytilus californianus* (Paine & Levin 1981, Paine 1974, Menge et al. 2011). Wootton (1993, 1994, 2010) clearly demonstrated that while experimentally induced changes of the competitive hierarchy of the *Pollicipes polymerus*-*Mytilus californianus* interaction can affect the ecological dynamics of intertidal succession, they do not affect its end point (a mussel-dominated community). Much of this work has consisted of species removal experiments, where the ecological role of a species is inferred by comparing controls versus manipulative treatments with reduced abundance. One lesson that can be learnt from these experiments is that the role of each species on communities, and the strength of interactions, varies locally, depending on the timing, habitat and geographical location.

Image analysis of time-series photographs of intertidal habitat areas of *Pollicipes pollicipes*, taken of fixed plots for up to 2 years in the scope of the European project PERCEBES promoted by BiodivERsA (Acuña et al. 2020), will provide information with unprecedented latitudinal coverage on the temporal variation of *P. pollicipes* assemblages. In particular, the abundance patterns of *P. pollicipes* and other accompanying sessile species potentially competing with stalked barnacles will give further insight into the biological processes governing the observed patterns.

Predation

Predation requires that predators kill and eat prey, and predator-prey interactions can be complex due to adaptations of both organisms. Barnes (1996) stated that predation was “sometimes not considered as seriously as it should be” as a process driving distribution and abundance of intertidal organisms, and thoroughly reviewed the studies of predation upon *Pollicipes* carried up to the early 1990s.

These pioneering studies were entirely concerned with the predation of *Pollicipes polymerus*, except for one reference to predation of *P. pollicipes* by crabs (Hui 1983). Initial evidence of *Pollicipes polymerus* as prey included: (1) observations of its predation by many invertebrates – *Pisaster ochraceus* with *P. polymerus* individuals in their hollow oral region (Feder 1959, Paine 1980, Bernard 1988); *Nucella* species drilling between *P. polymerus* capitular plates (Palmer 1984, West 1986, Bernard 1988); small pagurid crabs and polychaetes feeding on newly settled *P. polymerus* (Bernard 1988); *Emplectonema gracile* nemerteans wrapped around small *P. polymerus* juveniles (Hoffman 1989); (2) signs of its predation by gulls i.e. presence in faecal pellets and regurgitations (Vermeer 1982, Marsh 1986); and (3) the first experimental study addressing the effects of predation by seabirds – western gull *Larus occidentalis*, glaucous-winged gull *L. glaucescens* and surfbirds *Aphriza virgata* (Meese 1993). Meese (1993) reported on a bird-exclusion caging experiment within the Bodega Marine Reserve in North California, finding that predation by birds was both spatially and temporally patchy, with a relatively large impact in reducing the local percentage cover of *Pollicipes polymerus* during the wintertime.

Further work was carried out on avian predation of *Pollicipes polymerus* (Wootton 1993, 1994, 1997) and of *P. pollicipes* (Moreno et al. 2010). These studies highlighted: (1) the generalist nature of gulls' diets, whose temporal and spatial shifts in *per capita* interaction strength and species impacts were associated with changes in community composition, and (2) the relative importance of *Pollicipes* species, being dependent on their abundance and/or on the availability of other prey. Moreno et al. (2010) considered *Pollicipes pollicipes* as "occasional prey" of the yellow-legged gull (*Larus michahellis*) in north-west Spain. Conversely, Wootton (1997) found that *Pollicipes polymerus* accounted for 88% of the intertidal organisms taken by *Larus glaucescens* on wave-exposed shores of Washington. However, the importance of *Pollicipes polymerus* in the diet of gulls was much lower in nearby wave-sheltered shores (Wootton 1997). A similar spatial pattern was found previously by Vermeer (1982), who reported that the percentage of regurgitated pellets of *Larus glaucescens* containing *Pollicipes polymerus* was much higher on the west than on the east coast of Vancouver Island. *Pollicipes polymerus* was also preyed upon by other actively foraging intertidal birds, the American black oystercatcher (*Haematopus bachmani*) and north-western crows (*Corvus caurinus*) (Wootton 1994, 1997), but was only a minor component of their diets (Wootton 1997).

In the intertidal community of Tatoosh Island (Washington), both direct and indirect effects of *Pollicipes polymerus* consumption by birds were assessed by examining populations of *P. polymerus* and of other invertebrate species (Wootton 1992, 1993, 1994). When birds were experimentally excluded by cages, the percentage cover of *Pollicipes polymerus* increased by more than 5.5 times (Wootton 1994). By feeding on *Pollicipes polymerus*, gulls were found to indirectly enhance the cover of *Mytilus californianus* by releasing it from space competition (Wootton 1992), promoting recovery of mussel beds in gaps created by physical disturbance (Wootton 1993). Using a combined experimental and path analysis approach, Wootton (1994) demonstrated that the decrease in abundance of *Pollicipes polymerus*, due to avian predators, was followed by an increase in the abundance of its major spatial competitors (*Semibalanus cariosus* and *Mytilus californianus*), with a consequent rise in the density of *Nucella* predatory snails, due to the increased abundance of *Semibalanus cariosus*, its major food resource. However, in contrast to avian predation, *Nucella* predation on *Pollicipes polymerus* was considered a weak direct interaction, occurring at relatively low rates and causing no indirect effects on the rest of the community (Wootton 1994).

Predation upon *Pollicipes polymerus* by seastars has been systematically observed when examining the wide variety of the diet of *Pisaster ochraceus* (Feder 1959, Paine 1980, Sanford 1999), the principal predator on rocky intertidal communities of central California and the Pacific Northwest (Paine 1966, 1974, Menge et al. 1994, Connolly & Roughgarden 1999 and references therein). Spatial variation has been recognized in the overall trophic patterns of *Pisaster ochraceus* (Feder 1959, Paine 1980), with the importance of *Pollicipes polymerus* as a food species for this large starfish also apparently varying with local ecological conditions. An exceptionally high importance was found within Neptune State Park in Oregon, where 41.8% of actively feeding *Pisaster ochraceus* individuals were recorded preying on *Pollicipes polymerus*, which was the second most common prey item (Sanford 1999). According to Paine (1980), the percentage of *Pollicipes polymerus* consumption by *Pisaster ochraceus* decreased with increasing latitudes, when comparing three geographic regions with similar species composition of intertidal communities (Punta Baja in Mexico, Monterey Bay in California and Outer coast in Washington: 10%, 4% and 3%, respectively). In the Monterey Bay area, Feder (1959) found that, while both mussels and acorn barnacles were preyed upon by *Pisaster ochraceus* in proportion to their relative abundance, the relative frequency with which *Pollicipes polymerus* was eaten by *Pisaster ochraceus* was lower than expected when considering its local availability in sampled habitats. Lauzier (1999b) and Jamieson et al. (1999) stated that the incidence of *Pollicipes polymerus* predation by *Pisaster ochraceus* was "fairly low" and occurred "in the lower midtidal", since only the upper distribution of the starfish coincides with the lower distribution of the barnacle. Similarly, the middle intertidal assemblage, where *Pollicipes* *polymerus* occurs on Tatoosh Island in Washington, was described to be located "above the effective feeding range of *Pisaster ochraceus*" (Wootton 1994).

Observational evidence of predation of *Pollicipes pollicipes* has been frequently recorded on the Portuguese coast (Figure 11): partially ingested *P. pollicipes* individuals observed in the oral region of the spiny starfish, *Marthasterias glacialis*, while preying upon clumps of stalked barnacles (Figure 11A, TC pers. obs.); large specimens (> 0.5 kg) of sea bream, *Diplodus vulgaris*, captured

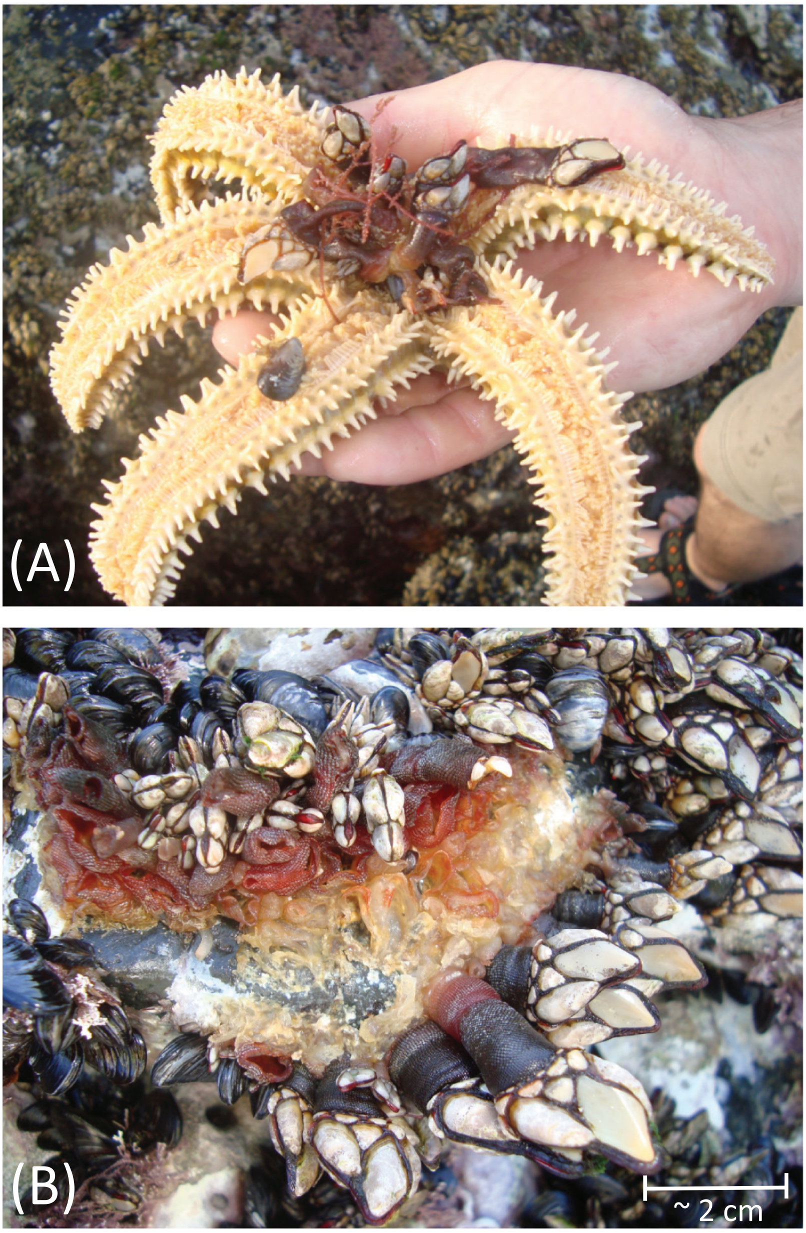


Figure 11 Predation of *Pollicipes pollicipes* in the Portuguese coast. (A) A seastar (*Marthasterias glacialis*) observed while eating several *Pollicipes pollicipes* individuals. (B) Predation signs on a *P. pollicipes* clump. Approximate scale presented when appropriate.

with the stomach holding high quantities of *P. pollicipes* individuals (Cruz 2000, JJC pers. obs.); trigger fish, *Balistes capriscus*, observed biting and probably ingesting *P. pollicipes* (TC and JJC pers. obs.); and cleared areas within *P. pollicipes* clumps denoting signs of recent losses of stalked barnacles from the rock and partially eaten peduncles (Figure 11B). Furthermore, the restricted occurrence of *Pollicipes pollicipes* to very wave-exposed rocky shores, as well as the variation of its distribution and abundance at small scales, suggested that predation on these barnacles might vary along hydrodynamic exposure gradients, being less intense at exposed sites (Sousa 2007, Jacinto 2016). The hypothesis of higher predation in sheltered sites was supported in a series of manipulative experiments, undertaken in different years and locations of Central and SW Portugal (Sousa 2007, Jacinto 2016, Cruz et al. unpublished observations). When kept in cages, transplanted stalked barnacles were able to survive in places where they normally do not occur (e.g. inside the Port of Sines) (Cruz et al. unpublished observations). These results have provided experimental evidence of predation as a cause of post-settlement mortality of *Pollicipes pollicipes*, and as a highly variable process in space that might play a major role shaping the abundance patterns of *P. pollicipes* and limiting this species' distribution (Sousa 2007, Jacinto 2016, Cruz et al. unpublished observations).

Associations between Pollicipes *species and limpets*

As described in the section 'Ecological habitat, and patterns of distribution an abundance' (see Table 4), limpets are one of the taxonomic groups commonly associated with *Pollicipes* species assemblages (e.g. *Pollicipes polymerus* – genus *Lottia, Pollicipes pollicipes* – genus *Patella,* and *Pollicipes elegans* – genus *Fissurella*).

A considerable amount of literature has been published on *Pollicipes*-limpet interactions, despite predominantly being restricted to the species pair formed by *Pollicipes polymerus* and the fingered limpet *Lottia digitalis* (associated taxa table in supplementary material). Barnes (1996) referred to the classical work of Giesel (1969, 1970) by mentioning the influence of the *Pollicipes polymerus-Lottia digitalis* interaction on the growth form and shell pattern of limpets involved in the interaction, in comparison with conspecific limpets inhabiting intertidal rock. Overall, Giesel (1968, 1969, 1970) and subsequent studies on *Pollicipes*-limpet interactions have been mostly focused on issues concerning the biology of limpet populations, specifically their morphology and/or behaviour (e.g. Brym 1980, Byers 1989, Lindberg & Pearse 1990), or their genetics and evolution (Murphy 1978, Crummett & Eernisse 2007, Murphy 2014). In contrast, there is much less information on the effects of interactions with limpets on *Pollicipes* themselves. Nevertheless, some ecological evidence reveals that the association of *Pollicipes* species with limpets may provide mutual benefits for both interacting organisms.

Limpets can act as surface cleaners of *Pollicipes* species while feeding on algal spores, algal propagules and biofilms present on the capitula. Limpets of the genus *Lottia* (*L. digitalis, L. pelta* and *L. strigatella*) have been observed scraping *Pollicipes polymerus* plates in Monterey Bay (California), both in the field and in the laboratory (Brym 1980). Similarly, patellogastropods of the genus *Patella* and the false limpet, *Siphonaria pectinata*, have often been sighted on the plates of *Pollicipes pollicipes*, mostly foraging when awash by waves in the south-west Portuguese coast (Figure 12, MIS pers. obs.). Moreover, the major food types ('*Hildenbrandia*, *Ectocarpus*, blue green algae, fungi, *Ulva* and diatoms'), identified in the stomach contents of limpets (*Lottia* species) that occurred within *Pollicipes polymerus* clusters, were found to grow on barnacle capitula, being only conspicuous in the grooves between the plates (Brym 1980). This constrained distribution of epizoic algae on *Pollicipes polymerus*, mostly visible in-between capitular plates, has also been observed in the other *Pollicipes* species in nature (*P. caboverdensis*: Figure 5 in Fernandes et al. 2010; *P. elegans*: photograph on p.71, Barraza et al. 2014; *P. pollicipes*: Figure 12, MIS pers. obs.). The same spatial pattern has been also found for acorn barnacles that are natural epizoans on *Pollicipes* species (e.g. *Chthamalus fissus* on *Pollicipes polymerus*: Figure 15 in Barnes 1996). In

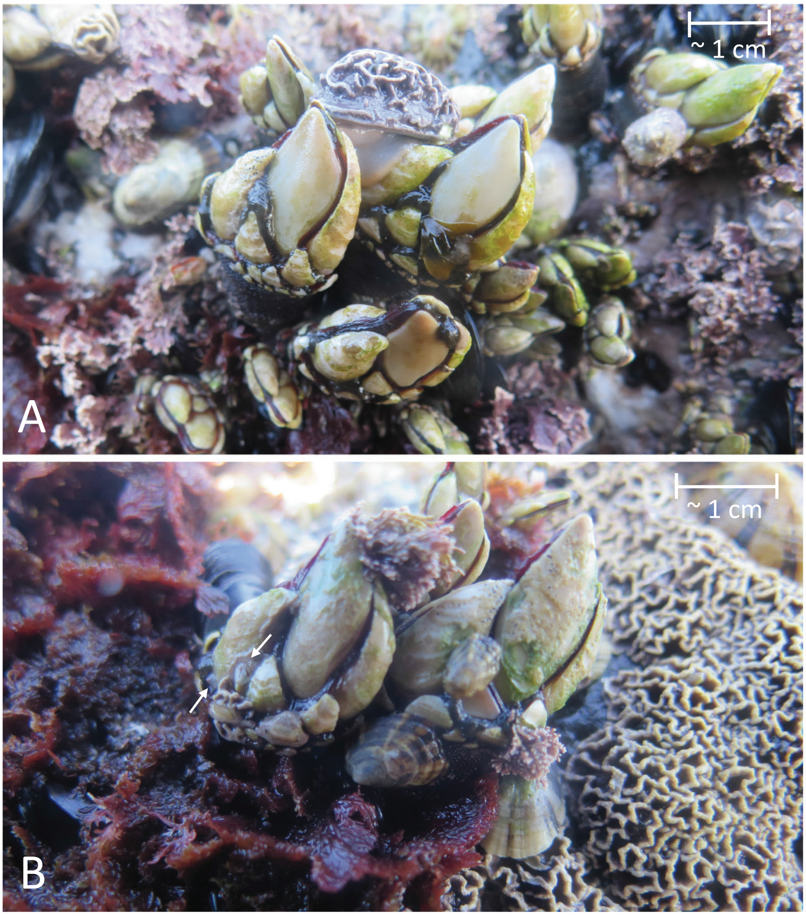


Figure 12 Limpets observed on *Pollicipes pollicipes* capitula in SW Portugal, during low-tide periods while awash by waves. (A) An actively foraging *Patella ulyssiponensis*. (B) Arrows indicate two juveniles of *P. ulyssiponensis* attached to a *Pollicipes pollicipes* individual. Approximate scales presented.

fact, the overgrowth of large areas of the capitulum by sessile organisms (macroalgae, acorn barnacles and mussels) was shown to be lethal for *Pollicipes pollicipes* growing on artificial substrata deployed in an extensive system of production, where grazers were nearly absent (Fernandes 2018). Therefore, the anti-fouling effect potentially produced by the grazing activity of limpets on the capitula of *Pollicipes* species can play a vital role in the maintenance of their feeding and respiratory capacities and hence on their survival and growth.

In turn, *Pollicipes* species offer a hard substratum for settling limpet larvae (Kay 2002) or for the fixation of juvenile and adult limpets (e.g. Giesel 1968, Jobe 1968, Hartwick 1981, Hoffman 1984). Giesel (1969, 1970) showed that specimens of *Lottia digitalis*, naturally occurring within *Pollicipes polymerus* clusters, are behaviourally confined to a single cluster, being resident on the capitulum and commonly fixed to an individual home scutum. In SW Portugal, *Pollicipes pollicipes* clusters have been observed to be used by limpets, primarily during low-shore wave-splash periods, as possible feeding grounds, being climbed on by many actively foraging *Patella* individuals (moving foot across the capitulum, Figure 12) that have their home scars on neighbouring substrata (patches of rock and algal crusts) (MIS pers. obs.). Less frequently, small juveniles of *Patella ulyssiponensis* can be found firmly attached to the barnacle's capitulum (Figure 12), even in non-splash conditions at low tide, suggesting a possible use of *Pollicipes pollicipes* as a microhabitat for recruitment and early-shore residency of this limpet species (MIS pers. obs.). Furthermore, *Pollicipes* species can act as a protective living host by providing limpets: (1) ameliorated physical conditions compared with other microhabitats, mainly by absorbing the force of waves and by offering moisture and shade for limpets (Giesel 1969, Brym 1980, Crummett & Eernisse 2007), and/or (2) a hiding place from visual predators, mainly for avoiding avian predation through cryptic mimesis (Giesel 1970, Frank 1982, Byers 1989, Mercurio et al. 1985, Wootton 1992). Given all of these benefits for limpets, the association between *Pollicipes polymerus* and the limpet taxonomic complex formed by *Lottia digitalis* and *L. austrodigitalis* has become a classic case study on the adaptive value of polymorphism and crypsis (e.g. Giesel 1970, Murphy 1978), phenotypical plasticity (Lindberg & Pearce 1990), habitat partitioning and the role of ecotypes in speciation (Crummett & Eernisse 2007, Murphy 2014). Thus, there is some evidence of the symbiotic nature of these associations.

Despite these mutual gains, some disadvantages of *Pollicipes*-limpet interactions have also been discussed. While grazing by limpets is likely to have a positive effect on keeping *Pollicipes* species free from encrusting organisms, a negative effect can also arise since limpets can account for the dislodgment, ingestion or bulldozing of *Pollicipes* cyprids and juveniles from the capitula of their conspecific adults. The putative influence of limpets on the distribution of *Pollicipes* recruits on conspecifics, particularly on the higher abundance of recruits onto the peduncle than onto the capitulum, has been suggested for *Pollicipes polymerus* (Hoffman 1984) and *P. pollicipes* (Cruz 2000). Moreover, a reduction in barnacle recruitment by limpets has been confirmed for other limpet-barnacle interactions (Dayton 1971, Denley & Underwood 1979, Hawkins 1983). Manipulative experiments in which limpet density would be effectively controlled would be important to understand the effects of limpets on *Pollicipes* species, especially on their fouling and recruitment patterns.

Pollution, contamination and geochemical structure

Barnes (1996) addressed the sparse literature on the effects of pollution on *Pollicipes* by recounting the effects on *Pollicipes polymerus* of an oil spill in 1969 that occurred in Santa Barbara (California, the USA), and on the effects of radiation by tritiated seawater on larval development. Intertidal stalked barnacle populations in oil-polluted areas suffered higher mortality (due to smothering from thickened oil covering capitular plates), reduced breeding and reduced space for settlement (Straughan 1969a, b, 1971, Foster et al. 1971 in Barnes 1996). Negative effects on larval development, namely a reduced moulting index, were observed with increasing tritiated seawater concentration (Abbott & Mix 1979 in Barnes 1996).

In the years that followed Barnes' review, *Pollicipes pollicipes* was used to assess the accumulation of petroleum hydrocarbons in commercial shellfish from the Galician coast (NW Spain) affected by the *Prestige* oil spill (Viñas et al. 2009) and more chronic coastal contamination in NW Portugal (Reis et al. 2012, 2013, Ramos et al. 2014, 2016, Reis et al. 2017, 2019) (see Table 13). Biotoxin uptake of putative phytoplankton and bacterial origin (associated with toxic algal blooms) was reported in *Pollicipes pollicipes* from NW Morocco (Silva et al. 2015, 2018, 2020) (see Table 13) and in *Pollicipes polymerus* from California (Sharpe 1981, cited by Austin 1987 in Lauzier 1999b). Geochemical trace element signatures have also been used as tools to discriminate harvesting origin (Albuquerque et al. 2016).

On November 13, 2002, a major oil spill occurred off Cape Finisterre (NW Spain), when the oil tanker *Prestige* suffered hull damage, due to a heavy sea and high winds, and eventually sank. After the accident, a monitoring programme was established (January 2003–October 2004) to assess the spatial distribution and temporal persistence of petrogenic hydrocarbons in the affected area for regulatory purposes regarding public health (see Viñas et al. 2009). This involved water and sediment sampling, plus monthly sampling of bivalves and other species with high commercial value,

Table 13 Contaminant markers assessed (chemical and biological, biotoxins) and ranges of values observed in *Pollicipes pollicipes* from the Iberian Peninsula and NW Morocco

Contaminant marker	Ranges of observed values	
Chemical markers	*NW Portugal (July 2010)*	*NW Portugal (2011)*
Metals (mg/kg)	Reis et al. (2012)	Reis et al. (2013, 2017)
Cd: Cadmium	0.70–2.22	0.35–3.75
Cr: Chromium	0.49–1.40	0.25–1.79
Cu: Copper	2.4–3.3	0.76–6.09
Fe: Iron	134–578	55–614
Mn: Manganese	5–59	2.89–48.33
Ni: Nickel	1.37–2.07	-
Zn: Zinc	728–1854	413–976
	NW Spain (2003–2004)	*NW Portugal (2011)*
PAH (μg/kg)	Viñas et al. (2009)	Reis et al. (2019)
A: Anthracene	0–1	0.24–15.47
Ace: Acenaphthylene	-	0.07–2.03
AcP: Acenaphthene	-	0.78–5.63
BaA: Benz[a]anthracene	0.1–5	-
BaPy: Benzo[a]pyrene	0.2–9	-
BbFl: Benzo[b]fluoranthene	0.9–39	-
BePy: Benzo[e]pyrene	0-6–35	-
BkFl: Benzo[k]fluoranthene	0.2–12.5	-
BPer: Benzo[ghi]perylene	0.1–8	-
C: Chrysene	0.5–38	-
DBA: Dibenz[ah]anthracene	0–7.5	
F: Fluorene	-	0.08–3.34
Fl: Fluoranthene	5–20	0.26–26.42
IPy: Indeno[1,2,3-cd]pyrene	0.5–7	-
N: Naphthalene	-	0.10–1.79
P: Phenanthrene	6–18	0.24–16.03
Py: Pyrene	1.2–18	0.28–10.56
Biological markers	*NW Portugal (2010–2011)*	*NW Portugal (2013–2014)*
Indicative of oxidative stress	Ramos et al. (2014)	Ramos et al. (2016)
GSTs – isoenzymes glutathione-S-transferases (mmol thioether produced/min/mg protein)	20–1600	50–1000
Indicative of neurotoxicity		
Che – inhibition of cholinesterase activity AChE activity (nmol/min/mg protein)	1.5–4.5	10–125
Indicative of oxidative damage		
TBARS – lipid peroxidation (nM/MDA equivalents mg protein)	$5\ (\times 10^{-8})$ to $1.2\ (\times 10^{-6})$	0.025–0.22
Indicative of stress		
Glycogen levels (μg/mg protein)	-	1–6
Haemocyte counts ($\times 10^{3}$ mL/haemolymph)	-	3–4.5
Biotoxins	*NW Morocco (July 2013)*	
Paralytic shellfish toxins (μg/kg)	Silva et al. (2015, 2018, 2020)	
Saxitoxin and its analogues	17.4–17.6	
Diarrhetic shellfish toxins (μg/kg)		
Okadaic acid	Not detected	
Lipophilic toxins (μg/kg)		
Azaspiracids (AZA-2)	0.83	

such as *Pollicipes pollicipes*. Polyaromatic hydrocarbons (PAHs) obtained from petroleum oil are considered as environmental pollutants and carcinogens, and their concentrations in *Pollicipes pollicipes* tissues were high after the spill (430 µg/kg dry weight of the sum of 13 PAHs: phenanthrene, anthracene, fluoranthene, pyrene, benz[a]anthracene, chrysene, benzo[b]fluoranthene, benzo[k]fluoranthene, benzo[e]pyrene, benzo[a]pyrene, benzo[ghi]perylene, dibenz[a,h]anthracene and indeno[1,2,3-cd]pyrene; Viñas et al. 2009). However, ~6 months after the accident, these PAH concentrations were already below the threshold level proposed by the Spanish Agency for Food Safety and Nutrition for commercial exploitation of these organisms (200 µg/kg dry weight of the sum of 6 PAHs: benzo[a]anthracene, benzo[b] and benzo[k]fluoranthene, benzo[a]pyrene, dibenz[a,h]anthracene and indeno[1,2,3-cd]pyrene). One year after the accident, the median values in PAH concentrations were 26 µg/kg for *Pollicipes pollicipes* and 74 µg/kg for mussels (Viñas et al. 2009). Physiological factors, including the rates of uptake and elimination (metabolism, diffusion and excretion), also determine PAH accumulation in tissues of different marine organisms. Therefore, species occupying the same habitat, such as *Pollicipes pollicipes* and mussels, may be accumulating different hydrocarbons at different rates during normal feeding and other biological activities (Viñas et al. 2009). Despite being sampled on the same heavily impacted shores, the PAH accumulation in soft tissues of *Pollicipes pollicipes* was generally lower than that found in mussels (Viñas et al. 2009). Nevertheless, this study demonstrated that *Pollicipes pollicipes* can also be a suitable species for monitoring the biological effects of oil spills in wave-exposed areas (Viñas et al. 2009) where such spills often occur (see Hawkins et al. 2017 for a review).

Reis et al. (2019) also showed that *Pollicipes pollicipes* might be an adequate species to assess spatial and seasonal variations of PAHs, since there were always significant positive correlations between PAH concentrations in seawater and in *P. pollicipes* on the NW coast of Portugal. Maximum concentrations of PAHs were found in locations in the proximity of an oil refinery plant and an industrial wastewater treatment plant. *Pollicipes pollicipes* accumulation rates varied for different PAHs dissolved in the seawater, which might reflect the physico-chemical properties of these compounds, the feeding strategy and the physiological inability to regulate and/or eliminate them (Reis et al. 2019). Based on the total PAH concentrations accumulated by *Pollicipes pollicipes*, and following the OSPAR guidelines for PAHs in shellfish (mussels and oysters – OSPAR 461/2009) as a reference, Reis et al. (2019) suggested that the NW coast of Portugal did not have significant contamination of PAHs during the four seasons of 2011. Since the bioaccumulation of PAHs differs between stalked barnacles and mussels (e.g. Viñas et al. 2009), Reis et al. (2019) noted that future adaptations to the OSPAR guidelines for PAHs in shellfish might be required to accommodate reference values for other important benthic marine resources, such as stalked barnacles.

Different pedunculate and acorn barnacle species have also been shown to bioaccumulate different amounts of metals in their soft tissues, reflecting both short- and long-term metal level environmental variations (reviewed by Reis et al. 2011). Subsequently, Reis et al. (2012, 2013, 2017) used the stalked barnacle, *Pollicipes pollicipes,* to monitor metal contamination on the NW coast of Portugal. The metals that *Pollicipes pollicipes* bioaccumulated more efficiently were Fe, Cd and Zn, reflecting the species' high sensitivity to these elements (Reis et al. 2012, 2013, 2017). Spatial variability observed in metal contamination levels in the soft tissues of *Pollicipes pollicipes* in NW Portugal revealed potential metal anthropogenic contamination, with the most metal-contaminated locations near to, and the least contaminated locations away from, the Oporto metropolitan area (Reis et al. 2012, 2013, 2017). Reis et al. (2013) suggested that, due to the high Cd concentrations bioaccumulated in *Pollicipes pollicipes* from the most contaminated locations (above the 2.50 mg/kg dry wt maximum concentration of Cd allowed in soft tissues of crustacean species by the European Community Commission Regulation No. 629/2008 for food consumption safety), the collection of barnacles for human consumption in these locations should be banned, or individuals collected should be depurated. The results of these studies showed that soft tissues of *Pollicipes pollicipes* can be used for monitoring metal contamination in coastal seawater.

Ramos et al. (2014, 2016) used a biomarker-based approach to assess the spatial and seasonal variation in the physiological responses of *Pollicipes pollicipes*, prompted by anthropogenic compounds (e.g. metals, hydrocarbons, pesticides and several other contaminants) that contaminate coastal waters in NW Portugal. Sources of contamination in coastal waters may include agriculture, industrial and urban run-off, released directly in the coastal area or into the adjacent environment. In these studies, several biochemical parameters (e.g. oxidative stress, peroxidative damage, neurotoxicity and general fitness) were quantified in different tissues (such as cirri and peduncle, but also haemolymph as a non-lethal source tissue for the determination of biomarkers). Fluctuations in these biomarkers were strongly related to seasonality, but also influenced by patterns of chemical contamination, confirming the use of *Pollicipes pollicipes* in biomonitoring coastal pollution.

Stalked barnacles of the genus *Pollicipes* have been found also to accumulate biotoxins (e.g. as a result of exposure to harmful algal blooms). Tests for paralytic shellfish poisoning (PSP) in *Pollicipes polymerus* and California mussels (*Mytilus californianus*) carried out in California (the USA) showed an accumulation of 85 µg toxin/100 g tissue in stalked barnacles, compared with 6400 µg toxin/100 g tissue in mussels (Sharpe 1981, cited by Austin 1987 in Lauzier 1999b). Biotoxin uptake by *Pollicipes pollicipes* was also observed in NW Morocco (Silva et al. 2018, 2020) at concentrations well below limits that represent serious threat to public health. Samples of *Pollicipes pollicipes* collected in July 2013 in NW Morocco tested positive for the presence of PSP toxins (saxitoxin and its analogues; 17.6 µg/kg; Silva et al. 2018), lipophilic toxins (azaspiracid, AZA-2; 0.83 µg/kg; Silva et al. 2020), but not of diarrhetic shellfish poisoning toxins such as okadaic acid and its analogues (Silva et al. 2015). Despite the low levels of biotoxins detected in *Pollicipes* species in these studies, the authors stress the importance of these types of studies in different invertebrates, especially in edible species such as *Pollicipes* species, and the need for revision and update of legislative policies.

Pollicipes pollicipes barnacles are, thus, sufficiently sensitive to several chemical and biological markers commonly used to evaluate contamination caused by human activities (Table 13). However, the species is not commonly used as a bioindicator (compared to mussels) due to its restricted occurrence on highly hydrodynamic shores, which are often less polluted, which present difficulties for routine sampling and which usually do not enable comparisons between sites in different ecological contexts, or along contamination gradients. *Pollicipes pollicipes*, however, is a widely consumed, high-value, coastal marine resource (see section ‘Fisheries, management and conservation’). For this reason, it should be monitored for contaminants at different spatial and temporal scales, especially widely dispersed contaminants such as persistent organic pollutants.

The geochemical structure of *Pollicipes pollicipes* capitular plates was studied by Albuquerque et al. (2016) as a potential tool to discriminate their origin along the Portuguese coast, based on trace elemental signatures (Ba, B, Cd, Cr, Li, Mg, Mn, P, Pb, S and Zn). In stalked barnacles, capitular plates are not shed during the moult, but are maintained, increasing in size through peripheral accretion over time (see section ‘Growth and size’), putatively preserving imprinted trace elemental signatures over their lifespan. Significant differences were recorded between locations for all elements (Albuquerque et al. 2016), demonstrating that the geochemical structure of the capitular plates of *Pollicipes pollicipes* can be used to assign individuals to their harvesting site at different geographic scales along the Portuguese coastline. This approach has potential implications for the management of stalked barnacle fisheries, enforcement of conservation *policies* and labelling, such as Marine Stewardship Council accreditation.

Fisheries, management and conservation

Worldwide fisheries of marine crustaceans mainly focus on the order Decapoda, with barnacle fisheries generally considered as marginal and only exploited at smaller scales by artisan fishers and shore harvesters (López 2020). Only a few barnacle species are commercially exploited for human consumption: the stalked barnacles *Capitulum mitella* or 'kamemoto' in southern Japan (López 2020) and China (Lin & Rao 2016), plus the four species of *Pollicipes*, along with eight species of acorn barnacles, three of which support the most relevant fisheries (*Austromegabalanus psittacus* or '*picoroco*' in Peru, Chile and Argentina; *Balanus rostratus* or '*mine fujit subo*' in Russia and northern Japan; and *Megabalanus azoricus* or '*craca*' in the Azores, Portugal) (López et al. 2010, López 2020).

In Barnes' (1996) review, commercial exploitation of *Pollicipes* was described mainly for *Pollicipes polymerus* and *Pollicipes pollicipes*, since only a small localized fishery of *Pollicipes elegans* in Costa Rica was mentioned. Regarding *Pollicipes polymerus*, Barnes (1996) noted the traditional use by native people living in the coastal areas of North America of this species as food, also describing the interest of the Iberian market for this species in the late 1980s and the consequent export from British Columbia to Iberia. In relation to *Pollicipes pollicipes*, Barnes (1996) mentioned the probable use of this species as food since the Neolithic period in North Africa, the great and growing commercial interest in this resource in Spain and Portugal in the late 1980s and early 1990s, the depletion of stocks in Spain in the early 1990s and the importation of this species from France and Morocco to Spain.

Twenty-five years after Barnes' review, we know that all *Pollicipes* species (including *Pollicipes. caboverdensis*, first described in 2010) are exploited throughout their geographic distributions (see section 'Geographical distribution' and Figure 2). The common names differ depending on the region, language and history: '*caʔinwa*' in Canada; 'gooseneck barnacle' or 'goose barnacle' in Canada and the USA; '*pouce-pied*' or '*pied de biche*' in France, Morocco and Senegal; '*percebe*' in Portugal, Spain, Mexico, Costa Rica and Cape Verde Islands; '*percebe*' or '*manitas*' in El Salvador; and '*percebe*' or '*uña de cabra*' in Ecuador and Peru. All *Pollicipes* species are exploited, although with different intensities. Despite the lack of local or national data for some of these fisheries, the available data and our overall perception show that the most intensively exploited species is *Pollicipes pollicipes* in Portugal and Spain.

Pollicipes harvesting is a risky activity since the species inhabit very wave-exposed rocky shores (see Figure 13), with reports of serious accidents and deaths of fishers. Most of this harvesting is carried out at low tide (Figure 13, either by hand (only evidence *for P. caboverdensis*, Baessa 2015, Soares 2018; and *P. elegans*, YouTube video on this fishery in Salango Island is available online) or using a scraper or similar equipment (all fisheries)). There is also tradition as well as permission to harvest *Pollicipes pollicipes* in Portugal (Jacinto et al. 2011) and *P. caboverdensis* in Cape Verde (Soares 2018) by free diving/snorkelling (see Figure 14).

Based on a literature review, personal communications, online information, personal observations and our own expertise, we have identified that *Pollicipes* species are harvested in the following regions/countries: *P. polymerus* in Vancouver Island (Canada), Washington and Oregon (the USA) and Baja California (Mexico); *P. elegans* in Guerrero (Mexico), Costa Rica, Ecuador and Peru; *P. pollicipes* in Brittany (France), Basque Country, Cantabria, Asturias and Galicia (Spain), in three marine protected areas in Portugal ('*Parque Natural do Litoral Norte*', '*Reserva Natural das Berlengas*' – RNB and '*Parque Natural do Sudoeste Alentejano e Costa Vicentina*' – PNSACV) and in the rest of mainland Portugal, Morocco, Western Sahara and Mauritania and Senegal; and *P. caboverdensis* in Cape Verde Islands (see Table 15). Table 15 presents a summary of the general characteristics of each fishery, including the following aspects (when information was available): type of harvesting (recreational and professional), main management measures, management level, access type (according to Hilborn et al. 2005, see Aguión et al. 2022b), number of fishers, official annual landings and respective references. We have considered the following five management levels: co-management (when some sort of consultation with the fishers exists) divided into three levels, (1) co-management high level – consultative-cooperative regime and interactive or functional participation of users (see Aguión et al. 2022b), (2) co-management mid-level – consultative or instructive-consultative regime and functional or consultation participation of users (see Aguión

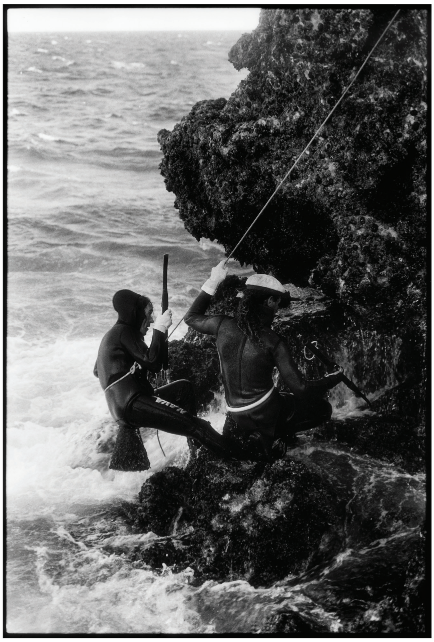


Figure 13 Exploitation of *Pollicipes pollicipes* in SW Portugal during low tide. Photos by João Mariano from the book “Warriors of the sea” © João Mariano.

et al. 2022b, scale modified from Sen & Nielsen 1996) and (3) incipient co-management – when there is a mechanism for the administration to consult users, but all decisions are taken by the administration; (4) top-down – absence of mechanisms for dialogue with users, imposed by the administration, and when we have found or received information specific to this fishery (e.g. licences, landings, stock status and fishery measures); and (5) mainly unregulated and unreported (hereinafter referred to as unregulated) – when we did not find or receive any specific information regarding this fishery (e.g. licences, landings, stock assessments and fishery measures). To provide context, below we start by reviewing archaeological evidence for their use in prehistoric times and their record in shell middens. We then consider each species in turn.

Figure 14 Exploitation of *Pollicipes pollicipes* by free diving in the Berlengas Nature Reserve, Portugal.

Prehistoric harvesting

Calcareous plates of *Pollicipes* capitula were found in several archaeological sites, mostly of prehistoric periods and in Iberian or Northern African regions (Table 14; Figure 2). The identification of these plates was made according to where they were found, with the northern American specimens being assigned to *Pollicipes polymerus* and the European and Northern African ones to *P. pollicipes*. One plate was found with features indicating a possible human use as an adornment, shown in Table 14 as one of the oldest findings (Upper Palaeolithic). Lateral notches, abrasion and polishing of a large *Pollicipes pollicipes* carina plate indicate its use as a suspended object (Aristu et al. 2011). All of the other *Pollicipes* plates from excavations listed in Table 14 were found in deposits as middens, together with molluscan shells or other skeletal remains of fish or shellfish, indicating that these stalked barnacles were intentionally collected, transported to the (archaeological) site and eaten by humans, raw or after burning (e.g. Álvarez-Fernández et al. 2010).

Most of those findings were from archaeological sites, used during Mesolithic and/or Neolithic times in the Iberian Peninsula and Northern Africa, and were assigned to *Pollicipes pollicipes*

Table 14 Archaeological findings (calcareous plates) of *Pollicipes* used by humans in prehistory and history

Prehistoric/historic	Date (years)	Archaeological site	Pollicipes relative abundance (%)	References
Pollicipes polymerus				
?	9400–8000 BP	Busted Balls Cove, San Miguel Is., CA, the USA	0.8–0.9 (MNI); <0.1–0.1 (WMSR)	Erlandson et al. (2004)
?	5600–2500 cal. BP	Kit'n'Kaboodle Cave, Dall Is., AK, the USA	0.014 (WMSR)	Moss & Erlandson (2010)
?	2900–1700 cal. BP	Kit'n'Kaboodle Cave, Dall Is., AK, the USA	0.005 (WMSR)	Moss & Erlandson (2010)
Neolithic-XIXth cent.	5300–150 BP	Several sites, Vancouver Is., BC, Canada	72 ('ubiquity'); 0.094 (WMSR)	Efford (2019)
?	1130-1080 BP	Obsidian Cove, Suemez Island, AK, the USA	0.2 (WMSR)	Moss & Erlandson (2001)
Pollicipes pollicipes				
Upper Palaeolithic (Gravettian)	30211-26288 cal. BP	*Vale Boi*, Algarve, Portugal	0.3–1.3 (MNI of marine shellfish)	Bicho et al. (2013)
	30180-28550 cal. BP	Nerja Cave, Malaga, Spain		Aristu et al. (2011)
Epipaleolithic (Azilian)	13400-10800 cal. BP	*La Fragua*, Cantabria, Spain	0.01 (MNI of shellfish)	Gutiérrez-Zugasti (2011)
Epipaleolithic	11000-7632 cal. BP	*Ifri Oudadane*, NE Morocco	0.59 (MNI of marine shellfish)	Hutterer et al. (2021)
Mesolithic	10800-6800 cal. BP	Several caves, Cantabria, Spain	0.01–3.1 (MNI of shellfish)	Gutiérrez-Zugasti (2011)
	9200-7800 BP	*Toledo*, Lourinhã, Portugal	1.23 (MNI of marine shellfish)	Dupont (2011)
	9020-8360 BP	*B. das Quebradas*, Algarve, Portugal	0.028–1.1 (MNI); 0.007–1 (WMSR)	Bicho (2009); Valente (2008)
	8900-7600 cal. BP	*El Mazo*, Asturias, Spain		Gutiérrez-Zugasti et al. (2016)
	9009-8724 cal. BP		0.05 (MNI of marine shellfish)	García-Escárzaga et al. (2017)

(*Continued*)

Table 14 (*Continued*) Archaeological findings (calcareous plates) of *Pollicipes* used by humans in prehistory and history

Prehistoric/historic	Date (years)	Archaeological site	Pollicipes relative abundance (%)	References
	7839-7607 cal. BP	*El Toral III*, Asturias, Spain	0.5 (MNI of marine shellfish)	Bello-Alonso et al. (2015)
	?	Several caves, Cantabria, Spain		Álvarez-Fernández et al. (2010); Álvarez-Fernández (2011)
	?	*Kobeaga*, Basque Country, Spain		López (1998-2000) in Álvarez-Fernández et al. (2010)
	7520 BP	*Samouqueira I*, Alentejo, Portugal	1.54 (WMSR)	Silva & Soares (1997)
	7450 BP	*Castelejo*, Algarve, Portugal		Silva & Soares (1997)
Mesolithic/ Neolithic	10000-5600 BP	Several sites, Algarve, Portugal		Bicho (2009), Dean (2010), Valente (2014)
	8965-6820 BP (Mesolithic)	*Rocha das Gaivotas*, Algarve, Portugal	Mesolithic – 17.2 (MNI of shellfish)	Dean (2010), Valente (2008)
	6801 BP (Neolithic)		Neolithic – 40 (MNI of shellfish)	
	?	*Jaizkibel*, Basque Country, Spain	0.31–3.95 (NR of marine fauna)	Álvarez-Fernández et al. (2013)
Early Neolithic	7610-6700 cal. BP	*Ifri Oudadane*, NE Morocco	0.48–0.55 (MNI of marine shellfish)	Hutterer et al. (2021)
	6820 BP	*Medo Tojeiro*, Alentejo, Portugal		Silva & Soares (1997)
	6800-5700 cal. BP	Several caves, Cantabria, Spain	0.1–7.5 (MNI of shellfish)	Gutiérrez-Zugasti (2011)
	5600-5280 BP	*El Zafrín*, Chafarinas Is., Spain		Gibaja et al. (2012)
	?	*Padrão I*, Algarve, Portugal	1.47 (MNI of marine shellfish)	Callapez & Pimentel (2018)
Neolithic	6900-4800 BP	*Cueva de los Gitanos*, Cantabria, Spain		Álvarez-Fernández et al. (2010)
	?	Near Oran, Algeria		Doumergue (1921) in Barnes (1996)
	?	Cape Spartel, Morocco		Doumergue (1921) in Barnes (1996)
	?	*Vale Santo I*, Algarve, Portugal	30.2 (NR)	Carvalho & Valente (2005) in Dean (2010)

(*Continued*)

Table 14 (*Continued*) Archaeological findings (calcareous plates) of *Pollicipes* used by humans in prehistory and history

Prehistoric/historic	Date (years)	Archaeological site	Pollicipes relative abundance (%)	References
Chalcolithic	4550 BP	*Montes de Baixo*, Alentejo, Portugal	2.57 (WMSR)	Silva & Soares (1997)
	4500 BP	ETAR, V. N. Milfontes, Portugal	5.3 (WMSR)	Silva & Soares (1997)
	?	*Cueva de los Gitanos*, Cantabria, Spain		Álvarez-Fernández (2011)
Early Bronze Age	?	*Catalão*, Algarve, Portugal	'Dominant in the assemblage'	Carvalho (2007) and Carvalho & Valente (2005) in Dean (2010)
Middle Bronze Age	3460 BP	*P. da Oliveirinha*, Alentejo, Portugal	0.24 (WMSR)	Silva & Soares (1997)
Bronze Age	4200-2800 BP	Several sites, Channel-Atlantic, France		Mougne & Dupont (2020)
Iron Age	?	*Port Blanc*, Höedic Is., Morbihand, France		Dupont et al. (2008)
	2400-2100 BP	*Queiruga*, Galiza, Spain	2.7 (MNI of marine shellfish)	Fernández-Rodríguez et al. (2014)
	2200-1900 BP	*Facho de Donón*, Galiza, Spain	26.1 (MNI of marine shellfish)	Fernández-Rodríguez et al. (2014)
Roman Age	2000-1700 BP	*Punta Atalaia*, Galiza, Spain	12.8 (MNI of marine shellfish)	Fernández-Rodríguez et al. (2014)
	2000-1600 BP	*Santa Trega*, Galiza, Spain	11.1 (MNI of marine shellfish)	Fernández-Rodríguez et al. (2014)

BP, before present; cal., calibrated; MNI, minimum number of individuals; NR, number of remains; WMSR, weight of marine shellfish remains; pers. comm., personal communication; ?, information not provided by cited authors.

(Table 14; Figure 2). Some of these sites are located on the Mediterranean coast, but most are Atlantic, probably due to the occurrence of this species on very exposed shores. According to Álvarez-Fernández et al. (2010), Álvarez-Fernández (2011) and Gutiérrez-Zugasti (2011), the absence of remains of these crustaceans at archaeological sites in the Upper Palaeolithic in southwest Europe could be explained: (1) by the flooding of the archaeological deposits nearer the prehistoric coastline (which potentially may have contained the remains of this resource) owing to the Flandrian transgression, (2) by the absence of this species in a cold climate (the most likely explanation) and/or (3) because human groups did not gather them (the least likely hypothesis). The following Holocene climatic conditions enabled an increase in the diversity and abundance of several marine species, and intensification in the gathering strategies of human groups resulted in enlarged gathering areas during the Mesolithic, especially in the Neolithic, favouring an increase in the diversity of taxa exploited and introducing the use of resources such as stalked barnacles (Gutiérrez-Zugasti 2011). In the western coast of the Algarve, Portugal, *Pollicipes* collection in the early Neolithic replaced Mesolithic economies focused on larger shellfish such as limpets (*Patella*) and mussels (*Mytilus*) (Dean 2010, Valente 2008, 2014). According to Dean (2010), this change indicated a reduction in foraging efficiency, through resource overexploitation, which may have preceded the introduction of agriculture into the region, and may have been a reason for the adoption of new economic adaptations, as happened in other European coastal regions (Schulting et al. 2004, Bonsall et al. 2009, Dupont et al. 2009, Gutiérrez-Zugasti 2011).

The relative abundance of *Pollicipes* plates is low in the remains found in most sites referred to in Table 14, due to the dominance of molluscan shells, mostly of marine or estuarine species of gastropods and bivalves. In sites close to Atlantic and Mediterranean shores, the main molluscan genera found in such shell middens are *Patella* (limpets), *Littorina* (periwinkles), *Phorcus* and *Steromphala* (topshells), *Stramonita* (whelk), and *Mytilus* and *Perna* (mussels), possibly collected on marine rocky shores, although bivalves such as oysters (*Ostrea*), clams (*Ruditapes* and *Scrobicularia*), cockles (*Cerastoderma*) and razor clams (*Solen*) were also found in sites close to estuaries or coastal lagoons (Silva & Soares 1997, Valente 2008, Bicho 2009, Álvarez-Fernández et al. 2010, Álvarez-Fernández 2011, Gutiérrez-Zugasti 2011, Valente 2014, Bello-Alonso et al. 2015, Callapez & Pimentel 2018, Hutterer et al. 2021). Skeletal remains of marine fishes, birds, reptiles and mammals also occur in some of these deposits (Silva & Soares 1997, Valente 2008, Álvarez-Fernández 2011, Gibaja et al. 2012). The same pattern of relative abundance regarding *Pollicipes polymerus* remains was observed in the prehistoric north-eastern Pacific sites listed in Table 14 (Erlandson et al. 2004, Moss & Erlandson 2010, Efford 2019). While the occurrence in middens of several barnacle species indicated reduced use over time, Efford (2019) considered that *Pollicipes polymerus* has remained a significant resource, despite its low proportional weight, across several sites studied on the west coast of Vancouver Island, Canada. Ubiquity-based analyses from this study showed that *Pollicipes polymerus* is far more abundant in shell midden remains than previously appreciated.

As stated by several authors (Silva & Soares 1997, Álvarez-Fernández et al. 2010, Álvarez-Fernández 2011, Álvarez-Fernández et al. 2013, Gutiérrez-Zugasti 2011, Valente 2014, Gutiérrez-Zugasti et al. 2016), it appears that molluscan resources formed an important part of the diet of Mesolithic/Neolithic human groups of hunter-fisher-gatherers, contrasting with the relativily limited importance of other marine shellfish resources collected on oceanic shores, such as *Pollicipes*, sea urchins and crabs. Although the continuity in their exploitation pattern observed at several sites suggests that they were a regular food source, at most sites, their collection was probably opportunistic and sporadic, possibly due to the difficulties of exploitation in the habitats where they occur (low intertidal or shallow subtidal levels, and/or very wave-exposed rocky shores) and their low food value (Álvarez-Fernández et al. 2010, Álvarez-Fernández 2011, Álvarez-Fernández et al. 2013, Gutiérrez-Zugasti 2011, Gutiérrez-Zugasti et al. 2016). Supporting these observations of relatively small fishing intensity, results of biometric analyses indicate that these barnacles were not overexploited by human groups in a northern Spain Mesolithic/Neolithic site (Álvarez-Fernández et al. 2013), although the opposite trend has been suggested by Valente (2008, 2014) in a study of southern Portugal sites of the same periods. However, given the pattern of continuous exploitation of these species in northern Iberia and other areas of Atlantic Europe, Gutiérrez-Zugasti et al. (2016) suggested that they can be interpreted, from a qualitative perspective, as stable resources with a significant social value, and proposed that they could have been sought after as delicacies involved in the celebration of social activities (at group and/or inter-group level), which would increase their social significance and general importance.

Pollicipes polymerus

The only regulated professional fisheries of *Pollicipes polymerus* are along the west coast of Vancouver Island (British Columbia, Canada), Oregon (the USA) and in Baja California (Mexico). The former is also a unique example of a co-managed *Pollicipes* fishery on the Pacific Ocean. In 2015, the *Pollicipes polymerus* fishery in Vancouver Island was considered to be sustainable by the Monterey Bay Aquarium Seafood Watch (Schiller 2015).

Vancouver Island, British Columbia, Canada

In this region, *Pollicipes polymerus* or '*caʔinwa*' (First Nations name, which means 'playing with the waves or in the waves') is a traditional food source for the Nuu-chah-nulth First Nations, who have harvested these barnacles along the north-west coast of North America for millennia (Gagne et al. 2016). A modern commercial fishery started in 1978 (Gagne et al. 2016), and six phases can be identified. The first (1978–1985) and second phases (1985–1999) of this fishery are similar (unlimited entry, open year-round, no size limits), but have one fundamental difference, which was the reporting of landings since 1985. During the second phase, this fishery peaked in 1988 (467 licences and 49 t landed) (Lauzier 1999b). From 1995 to 1997, landings decreased to 8-12 t per year and were associated with a high economic value for fishers (> Can$9 per kg, ~€6.1) (Lauzier 1999b). At that time, barnacles were harvested by both commercial and First Nation harvesters (Jamieson et al. 2001). The third phase corresponded to the closure of this fishery in 1999 due to various reasons, including a lack of information for performing stock assessments (Lauzier 1999a, b). The fourth phase (2000–2002) was characterized by two experimental fisheries with low catches (1.3–1.8 t/year) and the collection of information to develop a management plan (DFO 2005 in Gagne, 2016). In the fifth phase (2003–2005), an experimental multi-stakeholder (including administration, First Nations, fishers, buyers, NGOs) co-management fishery was implemented, which included the assessment and management of the fishery based on the local ecological knowledge (Schiller 2015). However, this first co-management attempt failed, due to management costs and the increasing market competitiveness of cheaper South American stalked barnacles in the European market (Gagne et al. 2016).

The current (sixth) phase (from 2009) of this fishery followed the implementation of *T'aaq-wiihak* (harvesting with permission of the *Ha'wiih* (hereditary chiefs)), after the recognition in 2009 by the British Columbia Supreme Court of the rights of five Nuu-chah-nult Nations to catch and sell species traditionally harvested within their territories, including *Pollicipes polymerus* (T'aaq-wiihakfisheries.ca 2021). This second experimental co-management attempt between the Nuu-chah-nult Nations and the Department of Fisheries and Oceans Canada (DFO) was initiated in 2013 and is exclusively a First Nations' fishery (Gagne et al. 2016). The general rules adopted are described in Table 15 and also include submission of harvest log data and stock assessment (Schiller 2015, Gagne et al. 2016, Fisheries and Oceans Canada 2021). The monitoring assessment techniques have been

Table 15 *Pollicipes* species. Fisheries identified by country, main management measures (for recreational and professional harvesting), management level, access type, number of fishers and official annual landings

Species/country/ fishery	Recreational harvesting? Main management measures	Professional harvesting? Main management measures	Management level	Access type	Number of fishers	Official annual landings (tonnes)	References
Pollicipes polymerus							
Canada							
Vancouver Island	Yes IQ-day (2 kg) Type of gear – handpicking	Yes IQ-month (453 kg, but never achieved), rotation (rock-by-rock basis), TAC (5,4 t)	Co-management High level	TURF	2–6 (On average from 2013 to 2016)	1,1 (On average from 2013 to 2016)	British Columbia Sport Fishing Regulations (1996), Lauzier (1999a, b), Edwards (2020), Jamieson & Levings (2001), Jamieson et al. (2001), Lessard et al. (2003), Schiller (2015), Bingham (2016), Gagne et al. (2016), T'aaq-wiihak (2016), T'aaqwiihakfisheries.ca (2021)
The USA							
Washington	*Yes?* TC in open coast (Apr–Oct), NTZs (Olympic National Park & several MPAs in Puget Sound), IQ-day (4,5 kg)	*No* NA	Top-down	NA	NA	NA	Washington Department of Fish and Wildlife (2021)
Oregon	*Yes* NTZs (large MPAs network), IQ-day (ten individuals)	*Yes* IQ-day (50 individuals – any size), on man-made structures such as rock jetties	Top-down	ND	ND	0,2 (On average from 2015 to 2019)	ZAGAT (2014), Bingham (2016), Eater (2020), Oregon Department of Fish and Wildlife (2021), Julia Bingham & Alan Shanks (pers. comm.)
Mexico							
Baja California	*No* NA	*Yes* ND	Top-down	ND	Three companies	28[a] (On average from 2014 to 2018)	Rogelio Cano (pers. comm.), Mario J. Escobedo (pers. comm.)

(*Continued*)

Table 15 (*Continued*) *Pollicipes* species. Fisheries identified by country, main management measures (for recreational and professional harvesting), management level, access type, number of fishers and official annual landings

Species/country/ fishery	Recreational harvesting? Main management measures	Professional harvesting? Main management measures	Management level	Access type	Number of fishers	Official annual landings (tonnes)	References
Pollicipes elegans							
Mexico							
Guerrero	*?* ND	*Yes* Mainly unregulated	Mainly unregulated and unreported	ND	ND	ND	Gutiérrez & Cabrera (2012, 2019)
Costa Rica	*?* ND	*?* ND	Mainly unregulated and unreported	ND	ND	ND	Mora-Barboza & Sibaja-Cordero (2018), Restaurante Costa del Sol Puntarenas (2018)
Ecuador	*?* ND	*Yes* Mainly unregulated	Mainly unregulated and unreported	ND	ND	ND	Cadena et al. (2008), Guilelrmo9111 (2015), Ladines (2018), López (2018), Cárdenas-Calle et al. (2020), Restaurant '*Delfim Mágico*', Restaurant '*Sabor Españo*l', Maritza Cárdenas-Calle (pers. comm.)
Perú							
Tumbes	*?* ND	*?* ND	Top-down	ND	ND	ND	Ordinola et al. (2010), Alemán et al. (2016)
Piura	*No* NA	*Yes* IQ-month (3–100 kg) 100 kg in 2017 and 3 kg in 2019	Top-down	Individual quotas	ND	ND	Kameya & Zeballos (1988), Pinilla (1996), '*Resolución Directoral Regional Nº 166-2019-GORE Piura*', '*Resolución Directoral Regional Nº 026.2017-GORE Piura*', '*Resolucion Ministerial 319-2007 PRODUCE*', '*Resolucion Ministerial 031-2002 PRODUCE*', '*Resolucion Ministerial 197-2002 PRODUCE*', Villena (1995), Oliva (1995)

(*Continued*)

Table 15 (*Continued*) *Pollicipes* species. Fisheries identified by country, main management measures (for recreational and professional harvesting), management level, access type, number of fishers and official annual landings

Species/country/ fishery	Recreational harvesting? Main management measures	Professional harvesting? Main management measures	Management level	Access type	Number of fishers	Official annual landings (tonnes)	References
Islas Lobos	*No* NA	*Yes* But closed since 2007	Top-down	ND	ND	6,6 (On average from 1997 to 2006)	Kameya & Zeballos (1988), de la Cruz et al. (2001), Samamé & Quevedo (2001), Ramírez et al. (2008), de la Cruz et al. (2015a,b), Ramírez & de la Cruz (2015), de la Cruz et al. (2016), Ramírez et al. (2017), Ladines (2018), Ramírez et al. (2019)
Pollicipes pollicipes							
France							
Finistère	*Yes* NTZs (areas with total and partial protections: Cap Sizun Special Protection Area), IQ-day (3 kg)	*Yes* TC (Jul-Aug), NTZs (areas with total and partial protections: Cap Sizun Special Protection Area), IQ-day (90 kg)	Co-management Mid-level	Limited entry	18 (In 2020)	5,6[a] (Annual average estimated)	Aguión et al. (2022b), '*Comite Regional des Peches Maritimes et des Elevages Marins de Bretagne* (161-2020)', Dominique Davoult pers. comm.
Morbihan	*Yes* NTZs (areas with total and partial protections), IQ-day (3 kg)	*Yes* TC (Jul-Aug), NTZs (2 no-take areas in Groix Island), IQ-day (120 kg)	Co-management Mid-level	Limited entry	30 (On average from 2013 to 2016)	50[a] (On average from 2013 to 2016)	Aguión et al. (2022b), '*Comite Regional des Peches Maritimes et des Elevages Marins de Bretagne (181-2020)*'
Spain							
Orio and Bakio	*No* NA	*Yes* MLS (TL > 40 mm = RC > 17 mm), TAC (4 t)	Co-management Mid-level	Limited entry	<10 (On average from 2013 to 2016)	0,1 (On average from 2013 to 2016)	Aguión et al. (2022b)

(*Continued*)

Table 15 (*Continued*) *Pollicipes* species. Fisheries identified by country, main management measures (for recreational and professional harvesting), management level, access type, number of fishers and official annual landings

Species/country/ fishery	Recreational harvesting? Main management measures	Professional harvesting? Main management measures	Management level	Access type	Number of fishers	Official annual landings (tonnes)	References
Basque Country General	*Yes* MLS (40 mm TL = 17 mm RC), TC (closed May-September), NTZs (Gaztelugatxe Marine Reserve), IQ-day (0,5 kg)	*Yes* MLS (TL > 40 mm = RC > 17 mm), NTZs (Gaztelugatxe Marine Reserve)	Top-down	Open access	ND	ND	Bald et al. (2006), Borja et al. (2006a, b), Aguión et al. (2022b)
Cantabria	*No* NA	*Yes* MLS (RC > 18 mm), TC (May–Sep), NTZs (three types of protection regimes; permanently open, seasonally closed and permanently closed – Sonabia)	Top-down	Limited entry	ND	4,6 (On average from 2019 to 2020 – before 2019, landings were very low due to misreporting)	Gutiérrez-Cobo & Bidegain. (2012), Bidegain et al. (2015, 2017), '*Orden MED/15/2020, de 20 de julio*'
Asturias East	*No* NA	*Yes* MLS (RC > 18 mm), TC (Oct–Apr), IQ-day (5–8 kg)	Top-down	Limited entry	234 (On average from 2013 to 2016)	11 (On average from 2013 to 2016)	Rivera et al. (2013, 2014), Rivera (2015), Rivera et al. (2016a, b, c, 2017, 2019), Aguión et al. (2022b)
Asturias West	*No* NA	*Yes* MLS (RC > 18 mm C), TC (May–Sep), Rotation, IQ-day (5–8 kg), SE	Co-management High level	TURF	204 (On average from 2013 to 2016)	44 (On average from 2013 to 2016)	Aguión et al. (2022b)

(*Continued*)

Table 15 (*Continued*) *Pollicipes* species. Fisheries identified by country, main management measures (for recreational and professional harvesting), management level, access type, number of fishers and official annual landings

Species/country/ fishery	Recreational harvesting? Main management measures	Professional harvesting? Main management measures	Management level	Access type	Number of fishers	Official annual landings (tonnes)	References
Galicia	*No* NA	*Yes* MLS (DBC $>$ 15 mm $=$ RC $>$ 18.3 mm), rotation, IQ-day (3–10 kg), SE	Co-management High level	TURF	1308 (On average from 2013 to 2016)	333 (On average from 2015 to 2019)	Freire & Garcia-Allut (2000), Molares & Freire (2003), Molares et al. (2008), Navarrete (2009), García-Negro et al. (2009), Parada et al. (2012, 2013), Macho et al. (2013), Vázquez-Rowe et al. (2013), Pita et al. (2019), Aguión et al. (2022b)
Canary Islands	*No* NA	*Yes* But closed since 2011	Top-down	ND	ND	ND	Marín & Luengo (1998), '*Orden 2 de mayo de 2011*'
Portugal							
RNB	*No* NA	*Yes* MLS (RC $\geq$ 23 mm – at least in 50% of the volume), TC (Jan-Mar & Aug-Sep), NTZs, IQ-day (20 kg)	Co-management Mid-level	Limited entry	40 (Maximum allowed)	16 (On average from 2015 to 2019)	Jacinto et al. (2010, 2011), Sousa et al. (2013), Albuquerque (2014), Cruz et al. (2015c), Albuquerque et al. (2016), Sousa et al. (2020), Aguión et al. (2022b), Neves (2021)
PNSACV	*Yes* MLS (R C $\geq$ 20 mm – at least in 75% of the volume), TC (15 Sep–15 Dec), NTZs, IQ-day (2 kg)	*Yes* MLS (RC $\geq$ 20 mm – at least in 75% of the volume), TC (15 Sep–15 Dec), NTZs, IQ-day (10–15 kg)	Incipient co-management	Limited entry	80 (Maximum allowed)		Cruz (2000), Castro & Cruz (2002), Castro (2004), Jesus (2004), Penteado (2011), Costa (2012), Sousa et al. (2013), Stewart et al. (2014), Cruz et al. (2015c), Jacinto (2016), Jacinto & Cruz (2016), Carvalho et al. (2017), Diogo et al. (2020), Aguión et al. (2022b)

(*Continued*)

Table 15 (*Continued*) *Pollicipes* species. Fisheries identified by country, main management measures (for recreational and professional harvesting), management level, access type, number of fishers and official annual landings

Species/country/fishery	Recreational harvesting? Main management measures	Professional harvesting? Main management measures	Management level	Access type	Number of fishers	Official annual landings (tonnes)	References
Portugal General	*Yes* MLS (RC≥20 mm – at least in 75% of the volume), TC (15 Sep–15 Oct), IQ-day (2 kg), NTZs (Marine Park – Parque Marinho Luíz Saldanha)	*Yes* MLS (RC≥20 mm – at least in 75% of the volume), TC (15 Sep–15 Oct), IQ-day (20 kg), NTZs (Marine Park – Parque Marinho Luíz Saldanha)	Top-down	Limited entry	456	136 (On average from 2015 to 2019 – including RNB & PNSACV)	Sousa et al. (2013), Cruz et al. (2015c), Aguión et al. (2022b)
Morocco	*?* ND	*Yes* MLS (RC > 25mm), TC (Jun–Oct)	Top-down	Limited entry	ND	ND	Boukaici et al. (2012, 2015), Boukaici (2015), Bourrassi et al. (2019), Hakima Zidane (pers. comm.)
Western Sahara & Mauritania	*?* NA	*Yes* Mainly unregulated	Mainly unregulated and unreported	ND	ND	ND	Fernández de Larrinoa & Cedenilla (2003), Pablo Fernández de Larrinoa (pers. comm.)
Senegal	*?* NA	*Yes* Mainly unregulated	Mainly unregulated and unreported	ND	ND	ND	‘*Direction des pêches maritimes – Rapport statistique 2002 – La mer: richesse et avenir du Sénégal*’; online information of selling barnacles
Pollicipes caboverdensis							
Cape Verde	*?* NA	*Yes* Mainly unregulated	Mainly unregulated and unreported	ND	ND	ND	Fernandes et al. (2010), Baessa (2015), Cruz et al. (2015a), Soares (2018)

References in this table include references used for building this table and other references found related to each fishery.

DBC, diameter of the *capitulum* base; IQ-day, individual quota per day; IQ-month, individual quota per month; MLS, minimum legal size; MPAs, marine protected areas; NA, not applicable; ND, no data; PNSACV, ‘*Parque Natural do Sudoeste Alentejano e Costa Vicentina*’; RC, maximum distance between the *carina* and *rostrum* plates; Rotation, rotation of the harvesting areas; RNB, ‘*Reserva Natural das Berlengas*’; SE, self-enforcement; TAC, total allowable catch per year; TC, temporal closure; TL, total length; TURF, Territorial User Rights for Fishing; ? – We have doubts on the existence of a type of harvesting, or we have a recent reference (personal communication, online information) that the species is exploited or sold, but no further data were obtained.

[a] Based on personal communications.

updated from Lauzier (1999a) and now include new techniques, such as the use of GPS technology, and the inclusion of local ecological knowledge (Gagne et al. 2016). The amount of barnacles sold ranged from 659 lb (299 kg) in 2013 to 6279 lb (2848 kg) in 2015 (T'aa q-wiihak 2016). These values are lower than the DFO *caʔinwa* harvest allocation of 12,000 lb per year (5443 kg), due to a limited market and a limited number of harvesters (T'aa q-wiihak 2016). According to Edwards (2020), the small available quota makes it difficult to attract buyers.

A profound change in the commercial market has taken place from the 1970s and 1980s to the present day. By the time of Barnes' (1996) review, the main market of the British Columbia barnacles was Spain (Jamieson et al. 2001). Barnes (1996) described in detail the difficulties and logistical problems associated with the export of live animals to Europe, as it would be unlikely that the European market would pay the prices for a frozen product. Currently, approximately 75% of the barnacles harvested at Vancouver Island are sent to the USA, while the remainder is sold domestically (Schiller 2015). The annual amount earned ranged between Can$4400 (~€2987) in 2013 and Can$51,000 (~€34,630) in 2015 (T'aa q-wiihak 2016), fetching about US$9–12 per kg (~€7.6–10.1), with a maximum price of US$22 per kg (~€18.5) (Schiller 2015).

In British Columbia, *Pollicipes polymerus* can also be harvested recreationally, although participation is assumed to be negligible (Gagne et al. 2016). A recreational management plan allows the collection by hand of 2 kg by fishers who must have a recreational licence (British Columbia Sport Fishing Regulations 1996).

Washington and Oregon, the USA

Despite having extensive populations in the three Pacific states of the USA and the historic use of this species as food (Bingham 2016), no professional harvesting of *Pollicipes polymerus* is allowed in Washington and California (Washington Department of Fish and Wildlife 2021, California Department of Fish and Wildlife 2021). In Oregon, in the last decade, several attempts have been made to develop a professional fishery on man-made structures (jetties) (Bingham 2016). Despite some general regulations being in place, there is only an incipient commercial fishery (Oregon Department of Fish and Wildlife 2021, Alan Shanks pers. comm., see Table 15). In California, *Pollicipes polymerus* is not allowed to be harvested recreationally (California Department of Fish and Wildlife 2021); in the states of Oregon and Washington, licensed recreational harvesting is allowed, although under minimal regulations, and focused on a daily quota and a strong network of MPAs where shellfish harvesting is banned (Oregon Department of Fish and Wildlife 2021, Washington Department of Fish and Wildlife 2021).

Baja California, Mexico

In this region, *Pollicipes polymerus* recreational harvesting is not allowed, but a small and fluctuating professional fishery has been developed (Rogelio Cano, pers. comm., Mario J. Escobedo, pers. comm.). Most of the harvesting takes place around the coast of Ensenada (Baja California). These barnacles are mainly sold to local tourist restaurants, but can also be sent to Mexico City, where the product can be found in the main markets (e.g. *'Mercado de San Juan'*) and restaurants, or even exported to the USA.The *Pollicipes* fishery in Baja California is managed through a special prospective fisheries permit ('*pesca de fomento*'), granted to three companies by the Federal Government through CONAPESCA ('*Comisión Nacional de Acuacultura y Pesca*'). Since 2009, professional harvesting has only taken place in some years (2009, 2011, 2014-16 and 2018, while in 2019 and 2020 no professional harvesting took place). Annual landings were very variable, ranging from 0.02 t in 2011 to 88 t in 2016 (average of 28 t, 2014-2018).

Pollicipes elegans

Pollicipes elegans is harvested in Mexico, Costa Rica, Ecuador and Peru. Regarding its geographical distribution area (see section 'Geographical distribution', Figure 2), only in El Salvador could no information be found on this species being fished. With the exception of Peru, all of these *P. elegans* fisheries can be considered as unregulated small-scale fisheries.

Guerrero, Mexico

In Mexico, the only accessible information on the fishing of *Pollicipes elegans* is the reference to its exploitation on the coast of the state of Guerrero (Gutiérrez & Cabrera 2012, 2019). Here, this species has been classified as having local and regional economic importance, being commercially important for consumption in tourist areas (Gutiérrez & Cabrera 2019). This fishery is seasonal, namely in December (Gutiérrez & Cabrera 2012) and in the months before the rainy season, reaching first sale values between Mex$85.00 and 100.00 per kg (~3.5€–4.0€/kg) and restaurant sale values between Mex$180.00 and Mex$260.00 per kg (~7.4€–10.7€/kg) (Gutiérrez & Cabrera 2019).

Costa Rica

The small-scale fishery of *Pollicipes elegans* in Costa Rica was identified by Bernard (1988) and cited in Barnes (1996) and appears to remain small-scale. Mora-Barboza & Sibaja-Cordero (2018) reported that *Pollicipes elegans* is not a very common species on the Pacific coast of Costa Rica and is not a traditional source of food as in Peru. However, it was found as an appetizer in a restaurant menu in the province of Puntarenas (price in 2021 of ₡12,000, ~€16 per portion, restaurant "Costa del Sol", online information).

Ecuador

In Ecuador, *Pollicipes elegans* has limited commercial interest (Cárdenas-Calle et al. 2020), is exploited in an unregulated manner and is not in great demand, being harvested mainly in the province of Manabi (Maritza Cárdenas-Calle, pers. comm.). In Manabi, this species seems to be of special interest in Puerto López canton (Cadena et al. 2008, López 2018), namely in Salango, in front of Salango Island where it is harvested (a YouTube video on this fishery in Salango Island is available online). In Salango, *Pollicipes elegans* is consumed as an appetizer in restaurants and can reach a considerable price, ranging from US $10 (~€8, 2021 price in restaurant "Sabor Español" per ~0.5 kg, online information) to US $25 (~€21, 2021 price in restaurant "Delfin Mágico" per portion, online information). In a survey of people of both sexes in Guayaquil (Guayas province) aged between 18 and 50 ($n = 164$), the vast majority (85%) did not consume this species, indicating a lack of knowledge of these barnacles (López 2018), but in Puerto Engabao (Guayas), *Pollicipes elegans* is harvested locally (Ladines 2018).

Peru

Historically, the main commercial fishery of *Pollicipes elegans* in Peru took place in Isla Lobos de Tierra and Islas Lobos de Afuera (Lambayeque), in the north of Peru. In the 1990s and early 2000s, these islands supported a fluctuating fishery, focused on exporting fresh and frozen stalked barnacles to Spain and Portugal (IMARPE 2005), taking advantage of the overfishing in many Spanish fisheries, such as Galicia (Molares & Freire 2003). The fishery in these islands had two main harvesting periods, the first during 1992–1995, with annual landings between 14 and 34 t, and the second in 2001–2002, with landings between 19 and 28 t, while in the other years, the fishery was below 4 t (IMARPE 2005, and Jaime de la Cruz, IMARPE – *Instituto del Mar del Perú*, pers. comm.). The lack of regulations and enforcement resulted in massive overexploitation of the resource and collapse of the stock of both Islas Lobos by the mid-2000s (Jaime de la Cruz – IMARPE, pers. comm.). The IMARPE monitoring reported an abundance of 39.5 million individuals at the Islas Lobos in 1995, dropping to 2.5 in 2002 and 0.4 in 2010 and 2015 (the biomass in 2015 was only 3 t) (Ramírez & de la Cruz 2015, Ladines 2018). Consequently, the fishery in Islas Lobos was closed in 2007 ('*Resolución Ministerial n° 319-2007-PRODUCE*'), with no recovery observed to date (Ladines 2018, and Jaime de la Cruz – IMARPE, pers. comm.). Currently, some small, subsistence harvesting is done by local fishers (Jaime de la Cruz – IMARPE, pers. comm.). Some commercial fishing still takes place along the continental coast of Piura. It seems that *Pollicipes elegans* populations in this region are also overexploited based on the individual quotas allowed to be harvested and their recent drop from 100 kg/month per fisher in 2017 to only 3 kg in 2019, based on the administrative decisions of the regional government of Piura ('*Resolución Directoral Regional Nº 026, 2017*' and '*Resolución Directoral Regional Nº 166-2019*'). At Tumbes, IMARPE monitors *Pollicipes elegans* populations on the shore. A slight decrease in size was found compared with Ordinola et al. (2010) by Alemán et al. (2016), but it is not clear if these populations are currently supporting any fishery. *Pollicipes elegans* exports to the Iberian Peninsula no longer take place, following the closure of the Islas Lobos fishery (Jaime de la Cruz – IMARPE, pers. comm.).

Pollicipes pollicipes

Pollicipes pollicipes is the only *Pollicipes* species that is heavily harvested throughout its range, wherever significant populations are present (i.e. France, Spain, Portugal and Morocco). The species has long been considered a seafood delicacy in Spain and Portugal, where it is the most important fishery in the rocky intertidal (Cruz et al. 2010a, Aguión et al. 2022b). The main fishery is located in Galicia (Spain) (average of 333 t and 8.9 million € per year between 2015 and 2019), which is larger in terms of volume harvested and market value than all of the other *Pollicipes pollicipes* fisheries combined (Aguión et al. 2022b). In Brittany (France) and Morocco, this species is also extensively harvested, but, since it is rarely sold locally, most catches are exported to the Iberian countries, where it costs much less than the locally fished species. In Western Sahara, Mauritania and Senegal, harvesting appears to be residual.

Brittany, France

The *Pollicipes pollicipes* fishery in Brittany is the third largest in the world, after Galicia and Portugal, in terms of landed weight (around 55 t in recent years, but with peaks over 100 t in the early 2000s), although its socio-economic relevance is much smaller than in the Spanish and Portuguese fisheries (Aguión et al. 2022b). Around 90% of the landings in Brittany come from the department of Morbihan, with the rest from Finistère (Dominique Davoult, pers. comm.). In Morbihan, a co-management system has been implemented with around 50 harvesters involved. Fishers can harvest large amounts of barnacles per day (120 kg), the highest in any *Pollicipes* fishery, that nevertheless fetch a very low market value (5–8 €/kg) (Table 15) due to the lack of a local market, with almost everything being exported to Spain and Portugal. A similar system in terms of governance and management measures is found in Finistère, although at a much smaller scale (Table 15 and Dominique Davoult, pers. comm.). Despite the strong tradition in French cuisine for seafood (e.g. bivalves, gastropods and decapods), *Pollicipes pollicipes* has never been locally appreciated, which has prevented the development of a more locally significant fishery. In the 1970s, Spanish middlemen went to France, attracted by the amount of unharvested stock and the low prices, and today, the fishery is driven by Spanish demand. Consequently, this strong link with Spanish markets has created a trans-national poaching system, from France to Spain, due to the large respective differences in governance, control and surveillance, in the social structure of the fishery, and in the demand and market prices (Geiger et al. 2022).

Spain

In Spain, only commercial harvesting of *Pollicipes pollicipes* is allowed, while recreational fishing is forbidden, with the exception of a residual recreational fishery in the Basque Country. The species is mainly harvested in Galicia, but also in Asturias, Cantabria and residually in the Basque Country, while in the Canary Islands, its small fishery has been closed by the regional government since 2011, due to overfishing (‘*Order 2 Mayo, 2011, Gobierno de Canarias*’). *Pollicipes pollicipes* is a highly appreciated seafood in Spain, with an average first-sale price of 17–32 €/kg, which is much higher in premium areas (e.g. 65 €/kg in Cangas, Galicia), with record prices at Christmas up to 250–350 €/kg (Pescadegalicia.gal 2021).

Historically, this species has been commercially harvested in the NW of Spain since at least the 1930s (Dirección General de la Marina Civil y Pesca, 1935), without much regulation until its collapse in the 1970s and 1980s (Molares & Freire 2003), despite initial measures being introduced, such as a summer reproductive closure in Galicia (Goldberg 1984). Since the 1970s, and while the local stocks were becoming depleted, the large Spanish market demand was partly met through importation from France, Portugal, Morocco, and even Canada and Peru (Molares & Freire 2003). Imports to Spain from Canada and Peru continued until the 2000s, when they stopped for a combination of reasons: the difficulty of importing fresh product from so far away, the collapse of the Peruvian stocks and the recovery of the Spanish stocks. Nevertheless, importation from France, Portugal and Morocco was consolidated during the last two decades and continues until the present.

Barnes’ (1996) review concluded with the depletion of the Spanish populations of *Pollicipes*, and she noted the recent implementation of “strict conservation measures”. A profound change has occurred since that time, not merely through the implementation of new management measures, but mainly due to a totally new governance approach. This required the strengthening and empowerment of the fisher’s associations, who were granted exclusive access to the fishing beds under a co-management approach (Molares & Freire 2003, Macho et al. 2013, Rivera et al. 2014, 2016a, Aguión et al. 2022b). The most prominent examples are Galicia and Asturias, with steps in this direction also taking place in other regions (Cantabria and Basque Country).

In Spain, several professional *Pollicipes pollicipes* fisheries currently operate in place in Galicia, Asturias, Cantabria and the Basque Country. The main management measures for each fishery are summarized in Table 15 and include a maximum number of harvesting licences (limiting access to the fishery), minimum sizes, temporal and spatial closures (including no-take zones), and even individual daily quotas, fishing bed rotation and self-enforcement in the most developed fisheries in Galicia and Asturias, based on exclusive access to fishing grounds (*i.e.* Territorial User Rights for Fishing – TURF), which are granted to the fishers’ organizations locally known as *cofradías* (Aguión et al. 2022b).

Galicia supports the main and oldest regulated *Pollicipes pollicipes* Spanish fishery. Historically, despite the secular tradition of the *cofradías* since the Middle Ages, shellfishing was mostly a *de facto* open access system until the 1990s (Macho et al. 2013). In 1992, the first co-management system in Spanish fisheries started in Galicia using TURF, where the responsibility for the exploitation was shared between the cofradías (fishers’ guilds supervised by the regional government) and the fishery authorities (Molares & Freire 2003). This change opened new opportunities for innovation and improvement in the management system, following an adaptive process necessary to design and implement fishery management plans that have become mandatory since 1992 (Molares & Freire 2003). The management plans specify annually (triennially for the future 2022–2024 period) the different components of the management system: authorized fishers, fishing grounds, general objectives, state of the fishery and stock assessment analyses, harvesting and trade plans, actions for stock enhancement, and a financial plan (Macho et al. 2013). The *cofradías* have to design the management plan and seek approval from the regional fishery administration, who evaluates them. The introduction of management plans was a key step in the management of this fishery, and their numbers quickly grew, from 12 plans in 1992, to 29 in 2001 and to 37 in 2021 (Molares & Freire 2003, Aguión et al. 2022b), now covering all the fishing beds. The performance of the fisheries managed by the *cofradías* using the plans was generally positive, and the production (both in biomass and in economic value) showed an increasing trend, despite some isolated cases of overexploitation (Molares & Freire 2003). One key aspect when developing these plans, and in general for the management of the fishery, is the role of the biologist, directly working for the *cofradías* with government funding. This role matches the 'barefoot ecologist' concept (Prince 2003, 2010), who gives management advice and facilitates communication between stakeholders. Formally known as technical assistants, these biologists enable the provision of good-quality and organized fisheries data, to facilitate and support decision-making processes. They also build robust social capital, by acting as knowledge collectors and translators between fishers, managers and scientists (Macho et al. 2013). In 2018, there were 41 technical assistants in Galician cofradías, overseeing almost all *Pollicipes pollicipes* fishery management plans (our unpublished data). Another key aspect is that most of the *cofradías* have their own surveillance service, co-paid by the fishers. This effectively enforces the management measures internally, and externally promotes collaboration with the government fishery inspection service to avoid poaching by illegal fishers (Molares & Freire 2003). Stalked barnacle harvesters also participate in the enforcement activities personally, in coordination with the surveillance service (Aguión et al. 2022b). Furthermore, the *cofradías* also have the capacity to commercialize the catch as they generally manage the first-sale markets (Molares & Freire 2003), giving them strong economic status.

The stalked barnacle fishery is one of the most important artisanal fisheries in Galicia, from a socio-economic point of view (~1300 harvesters, 333 t and ~9 millions of € per year), although still far from the clam fishery, the largest artisanal fishery in Spain (~7100 fishers, ~7.900 t and ~74 millions of € per year) (Domínguez et al. 2021). Around 80% of the harvesters access the intertidal fishing grounds by boat, and the rest by land (*i.e.* by car, on foot). The latter specialize in harvesting stalked barnacles, but the boat fishers also use other gear during the year, mainly octopus traps, depending on the market. Harvesters actively participate in all aspects of the management and share responsibilities with the administration in decision-making. The key decisions deal with the rotation scheme between fishing beds and the daily individual quotas allowed for each harvester, although the system is very flexible and adaptive to accommodate changes regarding new and unforeseen circumstances. The Galician stalked barnacle fishery has a very strong governance framework, focused on promoting participation by harvesters, which has rendered a very high number of sustainability attributes in a recent European stalked barnacle fisheries review (Aguión et al. 2022b).

In Asturias, there are two very different stalked barnacle fisheries, a co-management system in the west and a top-down system in the east. The former, as in Galicia, is a highly participatory system, based on adaptive management plans and exclusive access rights to the fishing beds (TURF) granted to the *cofradías*, who share responsibilities with the administration in the decision-making (Rivera et al. 2014). In Asturias-West, the eight management plans are subdivided into 250 zones, according to resource quality, and catch monitoring is done at this micro-/patch scale (from single rocks 3 m long up to 3.3 km extents of coastline) (Rivera et al. 2014). Such a detailed spatial scale is only possible due to the close collaboration between harvesters and managers (Rivera et al. 2014). Another key attribute of this fishery is the strong monitoring and control system (MCS) at various scales: (1) the official control and surveillance system from the regional government, (2) the presence of one enforcement officer on each of the cofradías with TURF, who are mainly focused on this fishery and (3) the direct involvement of the stalked barnacle harvesters in the surveillance and control activities (Rivera et al. 2014). Before the early 1990s, stalked barnacles in Asturias were only harvested sporadically, but in 1994, and led by the fisheries administration, a pilot TURF programme started in the *cofradía* of Ortiguera, which was expanded to seven *cofradías* by 2001 (Rivera et al. 2014). The system has received public approval, where 73% of the stakeholders indicated that the only way to maintain a sustainable stalked barnacle fishery in Asturias is through the current management regime (Rivera et al. 2016a). Recently, the TURF system in Asturias has also been found to achieve high sustainability scores (Aguión et al. 2022b), where social factors (e.g. conflict resolution mechanisms and strong leadership) are the key drivers for the sustainability of this bottom-up management system (Rivera et al. 2019).

The other *Pollicipes pollicipes* fishery of Asturias, on the east coast, is a top-down limited-entry system. It has similar management measures (size limit and daily individual quotas), except that the open harvesting period is set from May to September, but with much less involvement of the harvesters in the decision-making, a much broader spatial scale of management and a much weaker MCS (Aguión et al. 2022b). This fishery has much less socio-economic significance (Table 15).

In Cantabria, a small top-down limited-entry system is in place in the stalked barnacle fishery. It is not clear how many fishers are involved, since it is not mandatory for the harvesters to be associated with any *cofradía*, but a regional census was established in 2018 ('*Orden MED/25/2018, Gobierno de Cantabria*'). Since 2016, a daily reporting system requires all catches to go through official landing points so that catch statistics are available (annual landings of 4.6 t and average price of 22 €/kg) (Gorka Bidegain, pers. comm.). The fishery is managed based on three measures: a minimum size, a temporal closure and a spatial harvesting system with areas permanently open, seasonally closed and permanently closed (Bidegain et al. 2015, '*Orden MED/7/2021, Gobierno de Cantabria*'). In 2017, the regional government of Cantabria promoted a pilot co-management plan with some harvesters, but the lack of a united harvesters' association led to failure (Gorka Bidegain, pers. comm.).

Finally, in the Basque Country, a residual stalked barnacle fishery takes place. There are two management plans in Orio and Bakio under a co-management approach, with fewer than 10 harvesters involved and annual catches of only 0.1 t (Aguión et al. 2022b). In the rest of the region, a top-down open access system is in place for the small fishing beds available. The Basque Country is also the only region in Spain where recreational harvesting of stalked barnacles is allowed, although not in the areas of Bakio, Orio and the MPA Biotopo Protegido de San Juan de Gaztelugatxe (Borja et al. 2006b).

Portugal

In Portugal, there is a long tradition of exploiting *Pollicipes pollicipes* by professional and recreational fishers. The fishery is regulated differentially along the Portuguese mainland coast. The first Portuguese legislation relating specifically to this fishery was in 1989, when the '*Reserva Natural da Berlenga*' (called '*Reserva Natural das Berlengas*' after 1998, RNB, an archipelago in the central coast of Portugal) was created. At that time, the *Pollicipes pollicipes* fishery was totally banned in the RNB area. In 2000, the first specific regulation for this fishery in a marine protected area (RNB) was published, together with the first Portuguese general fisheries legislation with specific reference to *Pollicipes pollicipes* (Sousa et al. 2013). After 2000, several changes were made to these professional fishing regulations (RNB, modified in 2011; general legislation modified in 2006 and 2011). Specific regulation for this professional fishery was also created in another marine protected area, the '*Parque Natural do Sudoeste Alentejano e Costa Vicentina*' (PNSACV) in 2006, and modified in 2008 and 2011 (Sousa et al. 2013). Additionally, recreational harvesting with specific reference to *Pollicipes pollicipes* has been regulated since 2006 and changed in 2009, 2011 and 2014 (Cruz et al. 2015c). Consequently, three main *Pollicipes pollicipes* fisheries can be identified in Portugal: RNB and PNSACV, corresponding to two marine protected areas, and the rest of the mainland coast outside the marine protected areas (referred to as Portugal General, Aguión et al. 2022b). A large marine protected area where *Pollicipes pollicipes* harvesting is prohibited is the '*Parque Marinho Professor Luiz Saldanha*', a 38 km area of coast near to Cape Espichel, central Portugal (Sousa et al. 2013). The current management measures for each fishery are summarized in Table 15. They include temporal and spatial closures, individual quotas, minimum size (maximum distance between the carinal and rostral plates in relation to a given catch volume), a ceiling of harvesting licences (in all fisheries) and catch reporting in logbooks (in RNB and PNSACV) (Sousa et al. 2013, Aguión et al. 2022b). In Portugal, and in contrast to Spain, *Pollicipes pollicipes* is harvested both professionally and recreationally, with the exception of RNB and a few small areas in PNSACV, where recreational harvesting is prohibited (Table 15).

Official statistical data from the exploitation of *Pollicipes pollicipes* in Portugal are centralized and managed by the '*Direção Geral de Recursos Naturais, Segurança e Serviços Marítimos*' (DGRM). Most of the catches of this species are sold directly to intermediaries or final consumers, and not in official auctions. Until 2006, the official data did not include catches sold outside of auctions, which meant that the official statistics could not be considered representative of the amounts caught. Since 2006, professional fishers have also been required to report what they sell outside of auctions. Thus, the most recent official estimates are more representative of the professional fishing effort. However, it is known that there are many unreported catches, and there are also no records of the recreational fishing effort. The most recent statistical data available on this fishery in Portugal (2015–2019, unpublished data from DGRM) report an average of 456 licensed professional fishers and 136 t of annual catches (maximum of 146 t in 2016). This corresponds to a mean annual value of €1,622,131 and reveals a slight positive trend in the price of €10.1 kg^{-1} in 2015 to €11.3 kg^{-1} in 2019. Nevertheless, the average first-sale prices charged by fishers, based on surveys conducted in 2013 (and 2018 only for RNB), was higher than these official data, being higher in the RNB than in other fisheries. The variation reported is as follows: RNB, €23.3 kg^{-1} (2013), €28.8 kg^{-1} (2018) (maximum of €173 kg^{-1} in 2013 and €100 kg^{-1} in 2018) ($n=32$ in 2013, $n=39$ in 2018); central coast, €14.4 kg^{-1} (maximum of €70 kg^{-1}) ($n=26$); PNSACV, €13.1 kg^{-1} (maximum of €168 kg^{-1}) ($n=49$) (Cruz et al. 2016b; unpublished observations).

In a study of European *Pollicipes pollicipes* fisheries, of the three main Portuguese fisheries identified (RNB, PNSACV and Portugal General), the RNB fishery showed the highest levels of governance and sustainability attributes (based on Gutiérrez et al. 2011) (Aguión et al. 2022b). RNB was considered a bottom-up harvester-governed fishery at an intermediate sustainability level, while PNSACV and Portugal General scored low in sustainability, despite PNSACV being subjected to bottom-up governance. The rest of Portugal (Portugal General) has governance that was considered to be top-down. The classification of bottom-up versus top-down governance was based on a governance score obtained by summing the levels of four governance elements: spatial scale of management, co-management, access structure and participation of fishers (Aguión et al. 2022b). Several factors contribute to RNB having the highest sustainability classification among Portuguese fisheries: no recreational harvesting, being a marine reserve and being the first area in Portugal with a managed *Pollicipes pollicipes* fishery (Sousa et al. 2013), low accessibility (i.e. it is a group of islands), long-term professional licences granted in this fishery and a constant number of licences through time (Jacinto et al. 2011). Furthermore, several scientific projects and studies, which monitor the state of the resource and the state of management, have the participation of fishers (e.g. Sousa et al. 2013, Cruz et al. 2015c, Sousa et al. 2020, Neves 2021). In the RNB, a higher biomass of stalked barnacles (mid-shore, 7.7 kg/m^2) and a higher proportion of adults with commercial value were observed when compared to other Portuguese fisheries (PNSACV and the central coast, data from 2011, Sousa et al. 2013). Recently, Portuguese commercial fisheries legislation has changed and now includes the possibility of implementing co-management ('*Decreto-Lei n.º 73/2020*'). Consequently, a formal co-management system for the *Pollicipes pollicipes* fishery in RNB was implemented in 2021 ('*Portaria n.º 309/2021*'). This is the first case of co-management of a fishery in Portugal. Consequently, we have classified the management level of this fishery in Table 15 as 'co-management mid-level', but consider that it will probably progress to 'co-management high level' in the very near future.

An assessment of the state of the fishery and the management of *Pollicipes pollicipes* in RNB, PNSACV and the coastal area from Cape Carvoeiro to Cape Raso (in the central coast of Portugal, regulated by Portugal General legislation) was made in 2013 using different approaches (independent observations, enquiries to the fishers and logbook information) (Cruz et al. 2015c). This assessment has not been repeated in the PNSACV or the central coast, but there have been recent monitoring studies in RNB (Sousa et al. 2020, Neves 2021). An overall decline in the state of the fishery and conservation of this resource was observed in all regions in 2013, with the exception of a stable tendency detected in the PNSACV when using the enquiries approach. The worst situation was observed in the central coastal area. Reasons for this include the following: not being part of a marine protected area; less management measures in practice; no specific licences for exploiting barnacles in this area (Cruz et al. 2015c); and the fact that the maximum number of licences available for this coast has not yet been reached ('*Direção Geral de Recursos Naturais, Segurança e Serviços Marítimos – DGRM*' information, 2021). This diagnosis was also identified by Aguión et al. (2022b), where the Portugal General fishery, which includes the central Portuguese coast, was classified as low in sustainability. In the PNSACV, although also scoring low on sustainability (Aguión et al. 2022b), the *Pollicipes pollicipes* fishery is more regulated and prospects are more promising, as there is bottom-up involvement through consultative participation of the fishers in the management of the fishery (Aguión et al. 2022b). Consequently, the management level of the PNSACV was considered as 'incipient co-management' (Table 15). Furthermore, there are several characteristics of this fishery that might favour improvement in the current management and promote the sustainability of this activity, such as the existence of specific professional licences, a constant number of licences over time, and several associations that represent the fishers of this area. Studies conducted in the PNSACV recommend greater involvement of fishers and the local community in the management of *Pollicipes pollicipes* (Castro & Cruz 2009, Stewart et al. 2014, Cruz et al. 2015c, Carvalho et al. 2017). Based on public debates, surveys and information from professional fishers, the main problems of the RNB fishery are poaching and poor surveillance (Sousa et al. 2020, Geiger et al. 2022), while in the PNSACV (Stewart et al. 2014, Cruz et al. 2015c, b, Carvalho et al. 2017) and the central coast (Cruz et al. 2015c, 2016b), there is excessive exploitation, poaching, unorganized harvesting, lack of association and union among fishers, and insufficient surveillance.

Morocco

Of the fisheries that exist in Africa, a regulated fishery of *Pollicipes pollicipes* exists only in Morocco. According to Hakima Zidane from the laboratory '*Prospections des Ressources Littorales*', *Institut National de Recherche Halieutique* (INRH), Morocco (June 2021), the exploitation of this species is not a traditional activity in this country and local consumption of these barnacles is very limited. Boukaici (2015) described this fishery in the Mirleft region, southern Morocco. Hakima Zidane (pers. comm.) added that *Pollicipes pollicipes* is harvested all along the Atlantic coast, namely in Mansouria, Sidi Abed and Souiria Kdima, and that there are no fisheries on the Mediterranean coast. This fishery is regulated by several ministerial decrees (Bourassi et al. 2019), which include the establishment of the following management measures: seasonal closure (exploitation is allowed from 1st November to 31st May and prohibited from 1st June to 31st October), size limit (RC of 2.5 cm, since 2015) and licences for professional fishmongers (Hakima Zidane pers. comm.). Hakima Zidane (pers. comm.) stated that these professionals mainly sell barnacles for export to Spain and Portugal and to a few five-star hotels in the Casablanca region. These professionals hire the services of an intermediary, who in turn sub-contracts the services of several fishers who collect the barnacles (Hakima Zidane pers. comm.). According to Hakima Zidane (pers. comm.), this fishery has increased in the last 10 years. The price charged by fishers at first sale is around €3 to €7 kg^{-1}, depending on the quality and the size of the barnacles, while the price charged by professional fishmongers is, on average, 60–80 DH/kg (~€6–€8 kg^{-1}) and can reach 120 DH per kg (~€12 kg^{-1}). Boukaici (2015) presented photographs of large quantities of barnacles stored in burlap sacks in the intertidal zone of the Bay of Agadir, illustrating the intermediate step of the sales circuit which precedes their export, carried out by professional fishmongers. According to Boukaici (2015) and Hakima Zidane (pers. comm.), poaching is the biggest threat to the fishery of *Pollicipes pollicipes* in Morocco.

Western Sahara and Mauritania

In the Western Sahara and Mauritania, there is indication of disturbance by *Pollicipes pollicipes* fishers at the Cape Blanco Monk Seal Colony (Fernández de Larrinoa & Cedenilla 2003). These fishers descend from the clifftops to harvest the barnacles in the intertidal zone, and although they do not interact negatively with the seals, they do cause disturbance in the locations occupied by these animals. Fernández de Larrinoa & Cedenilla (2003) determined through interviews with these fishers that this activity originated at a time when the territory was still a Spanish colony. At present, Pablo Fernández de Larrinoa (pers. comm.) considers that this unregulated fishery is not important in the Cape Blanco peninsula and that these barnacles are not consumed locally, being sold abroad. According to this researcher, it is currently forbidden to harvest *Pollicipes pollicipes* in the seal reserve.

Senegal

Although Senegal corresponds to the southern limit of distribution of *Pollicipes pollicipes* (see section ‘Geographical distribution’), this species is considered to be an exploited species in this country (‘*Direction des pêches maritimes*’, Senegal, 2002). Although this fishery is not regulated, there are records of the sale of these barnacles in Senegal to foreigners (informal online information in 2021 of the sale at 3000 West African CFA franc per kg (~4.6 euros)).

Pollicipes caboverdensis

In 2010, populations of *Pollicipes* from the Cape Verde Islands were described as a new species, *Pollicipes caboverdensis* (Fernandes et al. 2010). This species, endemic to Cape Verde, is exploited in an unregulated manner, and no statistical data regarding this small-scale artisanal fishery exist (Cruz et al. 2015a, b). Based on personal observations, enquiries to fishers (Baessa 2015, Soares 2018) and contacts with restaurants, we found that this fishery occurs on all Cape Verde Islands, with the exception of the island of Maio, where this activity does not seem to exist.

Two studies have been carried out on the fishery of *Pollicipes caboverdensis* in Cape Verde: on the island of Santiago in the Sotavento Islands (leeward) (Baessa 2015, Cruz et al. 2015a) and on the Barlavento Islands (windward) of Santo Antão, São Vicente and São Nicolau (Soares 2018). According to these studies, this fishery appeared to be more important in São Nicolau, where most of the fishers interviewed considered it to be their main activity and very important for their family income. On the other islands, all, or the vast majority of the fishers interviewed, had other main activities, although they considered the fishery of *Pollicipes caboverdensis* important for their family income. The fishing effort on Santiago was found to be very variable: 4–10 kg of barnacles per day and per fisher; from 3 to 4 days of harvesting per week to 2 days every 3 months (Baessa 2015, Cruz et al. 2015a). On the islands of Santo Antão, São Vicente and São Nicolau, the fishing effort appeared to be higher than that reported for Santiago, although harvesting is apparently restricted between May and October (Soares 2018). In these islands, the amounts harvested per day varied between a maximum of 50 kg when fishers were alone or with a partner, to a maximum of 300 kg when fishers were in a group of 3–4 (Soares 2018). Most of the fishers interviewed sell the barnacles to the general population and tourists, intermediaries (fishmongers) and owners of bars, restaurants and hotels. The selling price varied between 200 CVE/kg (~€2) in Santo Antão (in 2017, Soares 2018) to 1000 CVE/kg (~€9) in Santiago (in 2015, Cruz et al. 2015a) and São Nicolau (in 2017, Soares 2018). Regarding the abundance of *Pollicipes caboverdensis*, the fishers perceived a decline at Santiago (Baessa 2015, Cruz et al. 2015a) and Santo Antão (Soares 2018), most considering that the amount and size of the barnacles had decreased over time ($n = 12$ enquiries performed in 2014 in Santiago and $n = 7$ enquiries performed in 2017 in Santo Antão). On the contrary, the vast majority of fishers from São Vicente and São Nicolau had a positive perception regarding the state of the resource, considering that the quantity of *P. caboverdensis* has increased or remained similar and that their size has not decreased ($n = 9$ enquiries performed in São Vicente and n = 4 enquiries performed in São Nicolau, both in 2017) (Soares 2018). Considering that *Pollicipes caboverdensis* is an endemic species of Cape Verde, and that there is little knowledge of its fishery, biology and ecology, this species should be considered for special status with regard to its conservation, with further studies recommended.

Integrative summary and critical view

When comparing *Pollicipes*' fisheries worldwide, a clear contrast shows up among countries. In Spain, Portugal, France and Canada, co-management systems (with different degrees of fisher participation) are in place or in development, mostly under limited-entry systems, as well as under TURF systems (Galicia and Asturias in Spain), although some top-down systems still exist (e.g. in Portugal). In the USA, there is a top-down system, but apparently there is not much interest in harvesting *Pollicipes*. In Morocco, Baja California-Mexico and Peru, top-down approaches are the norm. Fisheries are still mostly unregulated in many countries (Western Sahara & Mauritania, Senegal, Cape Verde, Guerrero-Mexico, Costa Rica and Ecuador). In Canadian and in some European fisheries, the focus has been on the social component of the fishery promoting the bottom-up participation of the harvesters in decision-making, by empowering the fishers' associations. By contrast, in Latin American countries (Peru and Mexico) and Morocco, the focus has been more top-down, with scientific institutions (IMARPE in Perú, INAPESCA in Mexico and INRH in Morocco) conducting stock assessments on which to base the management of the fishery. In this stock assessment-driven approach, fisheries management depends on monitoring the stock status, through periodic direct assessment, which has been found to be unsuitable for most small-scale fisheries in developing countries (see Berkes et al. 2001 for a review). Moreover, the tendency for managers of fisheries of small stocks in developing countries to believe that stock assessment is essential for successful fishery management often leads to disproportionate allocation of resources to stock assessment, rather than other critical components of management (Mahon 1997). More focus should be placed on top-down and incipient co-management fisheries on the social component, mainly by strengthening and empowering the associations of fishers, and promoting their participation in the MCSs and the decision-making. The case of Islas Lobos in Peru should be carefully analysed. It has been closed since 2007, but the stalked barnacle populations are still depleted. MCSs have to be strengthened, incorporating the role of the fishers as stewards of their marine resources. The analysis of the European *Pollicipes pollicipes* fisheries clearly shows that strong governance frameworks, in the form of exclusive property rights, nested spatial scales of management, fishers' participation and co-management, all promote sustainability. By reinforcing the social dimension, the system achieves both socio-economic and ecological sustainability (Aguión et al. 2022b). However, independent observations about the state of these resources, as well as on the ecological impacts of harvesting on biodiversity, are needed. The development of local markets for stalked barnacles, and a new wave cuisine that exalts the local products (e.g. Peru, Mexico and the USA) could help foster new co-management systems around this fishery in Latin America. In Peru, where there was an important export-driven stalked barnacle fishery in the past, a new law, approved in July 2021 for benthic marine invertebrates (‘*Decreto Supremo 018-2021-PRODUCE*’), sets a new framework and opportunity to develop co-managed plans with the active participation of the local fishing communities. In NW Africa, in both the endemic *Pollicipes caboverdensis* fishery and the *P. pollicipes* fishery, more steps have to be taken in order to start with a simple regulation of the fishery and the empowerment of the fishers associations, which we hope to see in a future review of the genus *Pollicipes*.

Aquaculture

In Barnes’ (1996) review, there was no section devoted to the aquaculture of *Pollicipes* species. However, in the subsection “*Pollicipes pollicipes*” under “Commercial exploitation”, Barnes (1996) stated that there was “…a great desire in Spain, and in Portugal particularly, to encourage the cultivation of *P. pollicipes*…”. López et al. (2010, 2012) presented a list of barnacles with commercial value, including *Pollicipes* species, and discussed the potential for and challenges of their cultivation. *Pollicipes* species have several features that give them high interest and potential for aquaculture. They are harvested species that can fetch a high price (see section ‘Fisheries, management and conservation’). They occur on very wave-exposed shores, where exploitation activity is dangerous and can lead to damage to the rest of the community on rocky shores, prompting conservation concerns. They are low trophic level species with low energy requirements. They can potentially be cultured in extensive systems in an environmentally sustainable way.

In the 25 years since Barnes (1996), there are no known cases of successful commercial aquaculture of *Pollicipes* species. However, several research projects and development trials have attempted cultivation, particularly of *Pollicipes pollicipes* (e.g. Goldberg 1984, Norton 1996, Franco 2014, Franco et al. 2015, 2016, 2017, Bingham et al., 2017, Darras 2017, Belela 2018, Fernandes 2018, Romersa 2018, Torres 2018, Santos 2019) (see Table 16). The aim of this section is to summarize the current state of these efforts.

The following types of potential production of *Pollicipes* species can be identified: (1) production based on collection of wild cyprids/juveniles and subsequent transfer to extensive systems of grow-out of juveniles and adults; (2) production based on collection of wild cyprids/juveniles and subsequent transfer to semi-intensive or intensive systems of grow-out of juveniles and adults; (3) production based on collection of egg lamellae from wild adults, followed by production phases in an intensive system (larval rearing, settlement and early juvenile rearing) and subsequent transfer to systems of grow-out of juveniles and adults; and (4) production based on reproduction by adults in captivity – with initial production phases in an intensive system (broodstock conditioning, larval release, larval rearing, settlement and early juvenile rearing) followed by transfer to systems for grow-out of juveniles and adults. The main results achieved to date and the main problems and challenges for each type of production and production phase are summarized in Table 16.

The first attempt to cultivate *Pollicipes* species was in Santander (Spain) in the 1980s with *P. pollicipes* (Goldberg 1984). This was based on the collection of wild juveniles (pieces of rock with barnacles) and subsequent transfer to an extensive system of grow-out of juveniles and adults, suspended on a floating platform. Besides the impact of destruction of the natural habitat, this trial was neither successful (75% of the structures were lost), nor had any follow-up. The current only known case of aquaculture of a barnacle species (giant barnacle, ‘*picoroco*’, *Austromegabalanus psittacus,* Chile) uses the same production method (López et al. 2010, 2012). Artificial substrata in the wild are used for larval settlement and metamorphosis of *Austromegabalanus psittacus*, followed by a grow-out system of juveniles in suspension (long lines) (López et al. 2010, 2012). According to these authors, the productivity of such farming systems is very high in relation to the productivity from the artisanal fishery of this resource, but there is spatial and temporal variability and, consequently,

Table 16 Aquaculture of *Pollicipes* species

Species/location or laboratory conditions/ production type and production phase		Methods and main achievements	Problems and challenges	References
Pollicipes polymerus				
Laboratory conditions, the USA	(2) Production based on wild cyprids/juveniles and transfer to semi-intensive systems *Collection of wild barnacles* *Rearing of juveniles in a semi-intensive system*	Collection of wild barnacles off the University of Oregon Institute of Marine Biology boathouse breakwater. Development of a novel aquaculture system with vertical tubes, low flow and air supply. Low cost. Use of unfiltered seawater. *P. polymerus* glued to plates. Effect of type of diet (no additional food, microalgae, *Artemia*) on growth. High survival in general. Highest growth in *Artemia* treatment. Settlement and recruitment during the experiment. Success of cultivation despite the low water velocity used. Barnacles can be stimulated to feed using aeration.	Need for research on dietary enhancement and for increasing the barnacle capacity of the system.	Bingham et al. (2017)
Laboratory conditions, the USA	(2) Production based on wild cyprids/juveniles and transfer to semi-intensive systems *Collection of wild barnacles* *Rearing of juveniles in a semi-intensive system*	Collection of wild barnacles at Drakes Point, South Cove, Oregon, the USA. Development of a novel infrastructure to cultivate *Pollicipes*: vertical aquaculture tanks and flow system based on ABS (acrylonitrile butadiene styrene) tubes (ABS tanks, adapted from Bingham et al. 2017). Low cost of ABS tanks. Effect of type of diet (cultured rotifers and seafood industrial by-product and waste material) on growth. No consistent effect of diet on growth. Settlement and recruitment on cultivated barnacles. Low cost of ABS tanks and of feeding. Use of upcycled fish is promising to enable sustainable aquaculture.	Development of more efficient infrastructure to increase feeding time.	Romersa (2018)
Oregon, the USA	(1) Production based on wild cyprids/juveniles and transfer to extensive systems *Collection of wild barnacles* *Extensive system of grow-out of juveniles*	Collection of wild barnacles at Drakes Point, South Cove, Oregon, the USA. Use of ABS tanks adapted to be moored to docks in Charleston Boat Basin, Oregon. 29% survival after 2.5 months. No increment of size/no growth.	Lack of water movement. Feeding limitation. Potential predation. Fouling problems, namely of air flow supplementary system. Need for scaling up air flow. ABS tanks are a unique system specific to *P. polymerus*, not ideal for a more complex farming system. Need to investigate the polyculture (e.g. abalone, mussels) potential of *P. polymerus* in a well-aerated system.	Romersa (2018)

(*Continued*)

Table 16 (*Continued*) Aquaculture of *Pollicipes* species

Species/location or laboratory conditions/ production type and production phase		Methods and main achievements	Problems and challenges	References
Pollicipes pollicipes				
Santander, Spain	(1) Production based on wild cyprids/juveniles and transfer to extensive systems *Collection of wild barnacles and extensive system of grow-out of juveniles and adults*	Pieces of rock with barnacles transplanted to an extensive system of grow-out of juveniles and adults (floating platform with ropes, *Baía de Santander).* Higher growth rates in the floating system than in the intertidal zone.	Destruction of the natural habitat. Loss of 3 of the 4 cultivation structures due to vandalism, accident or rough sea.	Goldberg (1984)
Sines, SW Portugal	(1) Production based on wild cyprids/juveniles and transfer to extensive systems *Collection of wild juveniles*	Development of a device (‘barticle’) and process for fixation of larvae and growth of juveniles. European Patent. Choice of mid-shore as the most suitable intertidal level for the deployment of ‘barticles’. Optimization of the method of deployment. Collection of wild juveniles attached to ‘barticles’ (Cape of Sines, SW Portugal).		Patent nr. EP3372073B1, Fernandes (2018)
	Extensive system of grow-out of juveniles	Development of an extensive system of grow-out of juveniles: use of a floating platform in a less exposed area (Port of Sines). Plates within individual cages chosen as the best option for suspension in the floating platform. Optimization of the transfer method. High rates of survival and growth after transfer of ‘barticles’/barnacles to floating platform during first months (winter).	Fouling problems. Total mortality of barnacles after one year.	Fernandes (2018)
		Test of several anti-fouling methods (e.g. manual cleaning, water jet). Survival after one year after the transfer of ‘barticles’/ barnacles to floating platform. Biological viability with the application of anti-fouling methods.	Do not reach commercial size after one year. Quality of barnacles not measured. Not economically viable (e.g. human resources costs). Need for alternative anti-fouling methods.	Darras (2017), Belela (2018), unpublished data

(*Continued*)

Table 16 (*Continued*) Aquaculture of *Pollicipes* species

Species/location or laboratory conditions/ production type and production phase		Methods and main achievements	Problems and challenges	References
Laboratory conditions, the UK	(2) Production based on wild cyprids/juveniles and transfer to intensive systems *Collection of wild juveniles* *Rearing of juveniles in an intensive system*	Collection of wild animals in SW Portugal. Individuals were glued to Velcro that was stuck to the inside walls of a plastic container. Effect of type of diet (several species of microalgae, *Artemia*, rotifers) on ingestion rate, growth and biochemical variables. Highest growth rates, faecal production, food capture efficiency and energy and digestion efficiency when barnacles are fed with *Artemia*. Protein digestion is high.	Possibility to culture *P. pollicipes* with several artificial diets. Need for research into lipid and carbohydrate digestion to aid diet formulation. Fouling problems and fungal infection indicate that culturing in tanks is not ideal. Bottleneck of settlement to sustainable farming.	Norton (1996)
Laboratory conditions, Spain	(2) Production based on wild cyprids/juveniles and transfer to intensive systems *Collection of wild juveniles* *Rearing of juveniles in an intensive system*	Collection of wild animals in Galicia, Spain. Preliminary experiments on rearing juveniles and adults and on effects of diet on feeding behaviour and growth. Acceptability of prey higher for live foods (*Artemia*). Inert diets not consumed. Turbulent conditions essential to stimulate feeding.	Need for control of culture conditions.	Cribeiro (2007)
Laboratory conditions, the UK	(2) Production based on wild cyprids/juveniles and transfer to intensive systems *Collection of wild juveniles* *Rearing of juveniles in an intensive system*	Collection of wild juveniles attached to pieces of rock from Cape Sardão, SW Portugal. Experiments in aquaria. Effects of different conditions of feeding, temperature, tidal cycle and photoperiod on growth, survival and external morphology. High survival rates. Food quantity variation and photoperiod did not affect growth. Higher growth was observed in individuals kept without a tidal cycle. Higher growth at 15°C than at 10°C or 20°C.	Changes in *P. pollicipes* juvenile morphology during growth in intensive system (plate colouration, deformation and decalcification).	Franco (2014)
	Finishing in an extensive system of grow-out of juveniles	Transfer of juveniles cultured in the intensive system (see above) to the wild (pieces of rock with the cultivated juveniles glued to rock, intertidal of Cape Sardão, SW Portugal). Control barnacles. Monitoring after 6 months. Low survival of transferred juveniles. Reversal of morphological changes.	High mortality of transferred juveniles. Need for the development of extensive systems of grow-out of juveniles (onshore or suspended culture systems).	Franco (2014)

(*Continued*)

Table 16 (*Continued*) Aquaculture of *Pollicipes* species

Species/location or laboratory conditions/ production type and production phase		Methods and main achievements	Problems and challenges	References
Laboratory conditions, Portugal	(2) Production based on wild cyprids/juveniles and transfer to intensive systems *Collection of wild juveniles* *Rearing of juveniles in an intensive system*	Collection of wild juveniles attached to ‘barticles’ deployed at Cape of Sines, SW Portugal. Experiments in aquaria. Effect of hydrodynamic conditions, food type, food density and frequency of feeding on survival, size and growth. High rates of survival. No effect of factors on survival. Growth rate is higher in more hydrodynamic conditions. Highest growth rates when barnacles are daily fed with *Artemia*.	Production costs (e.g. feeding) are potentially high. Quality of barnacles not measured.	Torres (2018), Santos (2019), unpublished data
Laboratory conditions, the UK	(3) Production based on wild egg lamellae *Collection of wild egg lamellae from adults* *Larval rearing*	Mature egg lamellae taken from adults collected at SW Portugal. Experiments in aquaria. Preliminary experiments of the effect of diet on larval development, survival and ingestion rate. Indication of preferred diets.	Poor knowledge on the effects of environmental conditions in larval development. No cultivation to cyprid stage.	Candeias (2005)
Laboratory conditions, the UK	(3) Production based on wild egg lamellae *Collection of wild egg lamellae from adults* *Larval rearing*	Mature egg lamellae taken from adults collected at Cape Sardão, SW Portugal. Experiments in aquaria. Effects of temperature (11°C–24°C), diet, photoperiod and salinity on larval development and survival. No salinity effect. Best growth and survival using rearing temperatures of 15°C–20°C, daily feeding with *Tetraselmis suecica*/*Skeletonema marinoi* or *Isochrysis galbana*/*S. marinoi* and a photoperiod of 24:0L:D. High-quality cyprids were obtained.	No cultivation to settlement. Need to investigate the implications of larval culture conditions (e.g. density) towards larval quality, competence to settle and ability to complete metamorphosis. Use of recirculating systems should be examined.	Franco (2014), Franco et al. (2017)

(*Continued*)

Table 16 (*Continued*) Aquaculture of *Pollicipes* species

Species/location or laboratory conditions/ production type and production phase		Methods and main achievements	Problems and challenges	References
Laboratory conditions, the UK	(3) Production based on wild egg lamellae *Collection of wild egg lamellae from adults* *Larval rearing and settlement*	Mature egg lamellae taken from adults collected at Cape Sardão, SW Portugal. Cultivation of larvae until cyprid stage. Design and use of a new device to study the settlement of cyprids in the presence of an individual conspecific adult. Effects of hydrodynamics, temperature, light, salinity, larval age and batch on % of attached cyprids, % of metamorphosed cyprids and survival of cyprids. Maximum attachment on adults of 30%–35%, with a one-week metamorphosis rate of 70%–80%. Cyprid attachment stimulated by light conditions and circulating water. Temperature did not affect attachment rate. Metamorphosis rate decreased at 14°C (compared with 17°C or 20°C). Higher settlement rates than in previous studies. Cyprids survived (in the absence of settlement substrata) for prolonged periods (20 days; 40% survival). First laboratory investigation about factors affecting settlement of *P. pollicipes*.	Need of further research on the importance of substrata-related biotic and abiotic factors on settlement, namely the relative importance of settlement-inducing protein complex (SIPC). Need for further observations on the maximum survival duration of cyprids in the absence of settlement substrata. Settlement phase remains the largest limitation to culture.	Franco (2014), Franco et al. (2016)
Laboratory conditions (the UK)	(4) Production based on reproduction by adults in captivity *Collection of wild adults* *Broodstock conditioning*	Barnacles collected at Cape Sardão, SW Portugal. Experiments in aquaria. Effects of rearing temperature (16°C–24°C) on reproductive condition (% of barnacles with eggs, egg lamellae development, larval release, nauplius size and survival over 24 h). Increasing temperature treatment led to greater maturation of egg lamellae and higher % of barnacles with eggs. Low nauplius release daily, but production of continuous supply of nauplius during most of the experiment. First working protocol for *P. pollicipes* reproduction and larval collection in laboratory conditions.	Need for further optimization of cultivation protocol and study of the effects of food quality (including alternative diets) and photoperiod. Need for development of larval release induction protocols.	Franco (2014), Franco et al. (2015)

Summary of main achievements, problems and challenges in the context of aquaculture of four production types: (1) production based on collection of wild cyprids/juveniles and subsequent transfer to extensive systems of grow-out of juveniles and adults; (2) production based on collection of wild cyprids/juveniles and subsequent transfer to semi-intensive or intensive systems of grow-out of juveniles and adults; (3) production based on collection of egg lamellae from wild adults followed by production phases in an intensive system (larval rearing, settlement and early juvenile rearing) and subsequent transfer to systems of grow-out of juveniles and adults; (4) production based on reproduction by adults in captivity – with initial production phases in an intensive system (broodstock conditioning, larval release, larval rearing, settlement and early juvenile rearing) followed by transfer to systems for grow-out of juveniles and adults. Information on larval rearing is only provided in an aquaculture context (more information in section 'Larval phase and metamorphosis').

a certain degree of unpredictability of production. In the Azores, experimental studies on the settlement of *Megabalanus azoricus* (‘*craca*’) on artificial substrata were successful, and the species has been considered as having high potential for aquaculture (Pham et al. 2011).

Regarding the aquaculture of *Pollicipes* species (Table 16), the studies and progress can be divided into three lines of research: (1) projects with *P. polymerus* mostly devoted to the development of cultivation infrastructure that address the challenge of cultivating a species described as having high water flow requirements (high energy, high costs) (Bingham et al. 2017, Romersa 2018); (2) projects with *P. pollicipes* in intensive systems, motivated by the limited knowledge of the cultivation of *Pollicipes*, to optimize production in captivity, and to investigate fundamental production phases such as larval cultivation and settlement (e.g. Norton 1996, Franco 2014, Franco et al. 2015, 2016, 2017); projects with *P. pollicipes* initiated with the discovery of a device (‘barticle’) and process for settlement of larvae and growth of juveniles (European Patent nr. EP3372073B) (Figure 15), which resolved the major bottleneck of finding an artificial substrate where cyprids

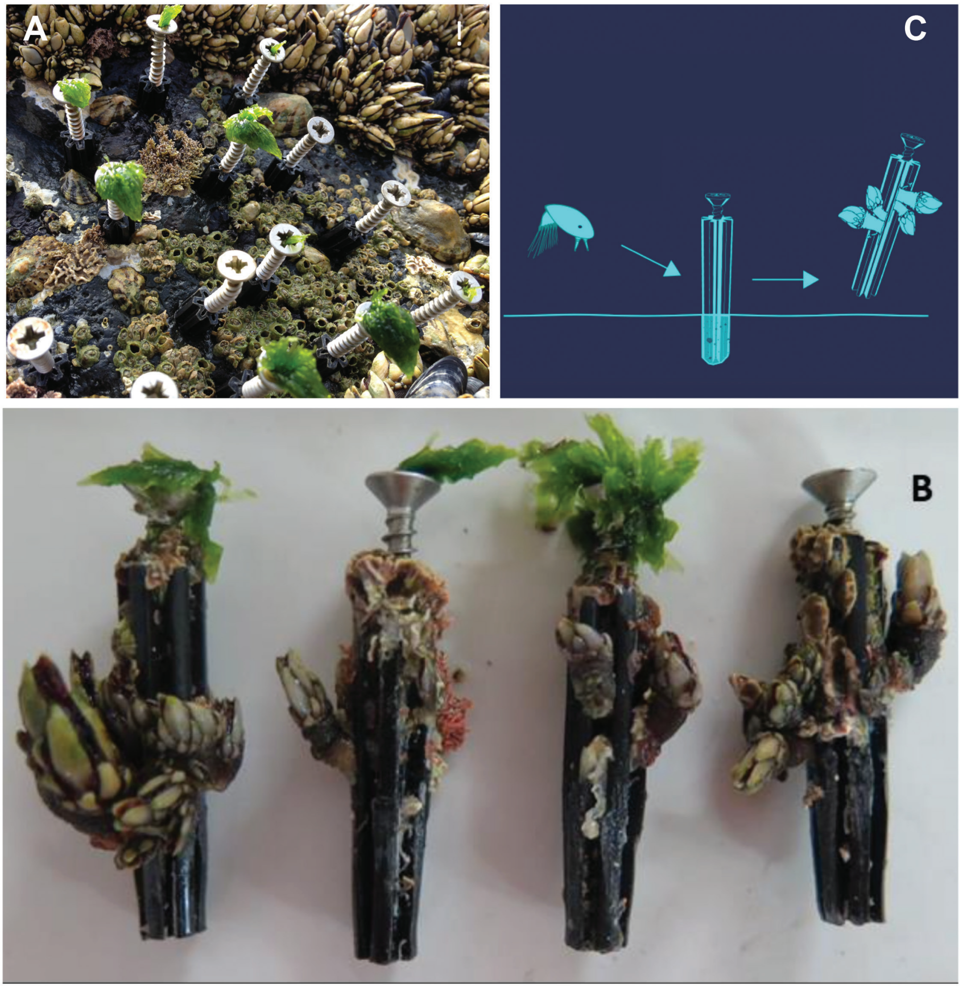


Figure 15 Artificial substrate designated as ‘barticle’ used to collect cyprids and juveniles *of Pollicipes pollicipes* in SW Portugal. (A) ‘Barticles’ deployed in the intertidal where *P. pollicipes* naturally occurs. (B) ‘Barticles’ taken from the field with juveniles attached. (C) Illustration of the process of settlement on ‘barticles’ and collection of juveniles.

in the wild would settle, and which was easy to deploy and remove (Darras 2017, Belela 2018, Fernandes 2018, Torres 2018, Santos 2019).

From the summary in Table 16, and as Barnes (1996) predicted, considerable progress has been made during the last 25 years in the development of aquaculture of *Pollicipes* species. However, there are still several problems and challenges, such as fouling problems in extensive systems of grow-out of juveniles and adults. These problems, the new bottleneck of this type of production, will have to be solved by alternative anti-fouling methods that are environmentally friendly and low cost. The biological viability of the system tested in SW Portugal was partially achieved, but economic viability was not, due to the high personnel costs associated with the anti-fouling methods applied (Cruz et al. 2020). In theory, an extensive farming system is expected to have the lowest costs. However, the extensive experimental system tested was found to be non-viable. Another important challenge is to resolve the bottleneck of the larval settlement and metamorphosis phases in intensive cultivation systems. Progress has been made, but this phase still needs to be investigated and optimized (Franco et al. 2016). Diversifying aquaculture and ensuring that aquaculture is environmentally sustainable are global challenges. The next 25 years will show whether we can overcome the old and new barriers to the cultivation of *Pollicipes* species.

Pollicipes in local cultures

In addition to the socio-economic importance that *Pollicipes* species have worldwide, due to their exploitation and consumption (provisioning services), these barnacles also have been extensively used culturally. They provide iconic inspiration for cultural heritage in various ways: gastronomy, painting, sculpture, photography, graphic and fashion design, handicrafts, and local festivals dedicated to *Pollicipes pollicipes* (e.g. in Aguiño and Corme, both in Galicia, Spain; in Vila do Bispo and Aljezur, both in Algarve, Portugal).

In Figure 16, we show some examples of these uses and representations: a traditional alcoholic beverage from Cape Verde ('*grogue*'), made with *Pollicipes caboverdensis* that is locally considered to have aphrodisiac properties (Figure 16A); in jewellery, such as the silver earrings shown in Figure 16B; a painting used on a stamp from Senegal (Figure 16C, note that the taxonomy is not that currently used); diverse forms of handicrafts, such as a *P. pollicipes* princess created by a Portuguese artisan (Figure 16D); and public sculptures in several localities in SW Portugal (Rogil and Carrapateira, both in Algarve) and Spain (Aguiño, Galicia, Figure 16E). These demonstrate the important cultural services provided by *Pollicipes* around the world.

Research gaps and challenges

In each section, we identified the main research gaps and challenges regarding the genus *Pollicipes*. Herein, we summarize and integrate this information.

Considering the imbalance of the current knowledge of the four known *Pollicipes* species, it is important to study the basic aspects of the biology and ecology of the less studied species: *Pollicipes elegans* and *P. caboverdensis*. Information is also needed on the fishing effort associated with these resources. In the case of *Pollicipes caboverdensis*, there is no official information on this fishery, and this is also lacking for *P. elegans* in various regions and countries (e.g. Guerrero (Mexico), Costa Rica, Ecuador). Considering that *Pollicipes caboverdensis* is an endemic species of Cape Verde, this species should be considered for designation of special conservation status.

Despite the various molecular-level studies of the relationships of the species within *Pollicipes* that have been developed over the last 25 years, the topology of a phylogenetic tree for living *Pollicipes* will continue to elude us until additional molecular-level data can be obtained. Future research, using additional genes, may yield data more suitable to resolving the various different branch patterns that have been detected.

Figure 16 Examples of uses and representations of *Pollicipes* in local cultures: (Top left) traditional alcoholic beverage from Cape Verde ('grogue') with *Pollicipes caboverdensis*. Photo by Correia PM; Public Domain; (Top right) silver earrings by Tânia Gil (© Tânia Gil Jewelry, Portugal); (Middle left) stamp from Senegal. Photo by Wim Decock; (Middle right) handmade doll by Paula Estorninho (Portugal); (Bottom) public sculptures in Aguiño (Spain). Photo by Carmela Queijeiro, La Voz de Galicia.

Based on the new map of *Pollicipes* species worldwide produced in this review, observations should be made on the exposed rocky coastlines of regions where there are doubts, or where more recent observations are needed regarding the presence of these species e.g. Aleutian Archipelago and Pacific coast of Baja California for *P. polymerus*; Pacific coast of Baja California, coast of Nicaragua and central and southern coast of Peru for *P. elegans*; and British Isles, south Mediterranean coast of Spain and France and north Mediterranean coast of Africa, from Algiers eastwards, for *P. pollicipes*. The most intriguing question is whether there is overlap in the distributions of *Pollicipes polymerus* and *P. elegans* in Baja California. Furthermore, the dynamic nature of the southern limit of *Pollicipes elegans* merits future investigation in the context of global change.

Regarding population genetics, an effort should be directed to sampling potential phylogeographic discontinuity regions (e.g. Mexican Pacific coast for *Pollicipes polymerus*, Mediterranean coast for *P. pollicipes*) and to the development of new molecular markers in *Pollicipes* species. Cross-amplification of microsatellite markers, already developed for *Pollicipes pollicipes* and *P. elegans* in congeneric species, should be investigated, together with the development of new microsatellites for *P. polymerus* and *P. caboverdensis*. Moreover, the development of SNP loci for all *Pollicipes* species should be addressed in the future. Finally, there is a need to clarify the patterns of genetic structure of *Pollicipes pollicipes* across the north-east Atlantic.

Pollicipes species appear to be mostly intertidal, although there are references to their occurrence in the shallow subtidal zone. However, actual measurements on the maximum depth of occurrence of *Pollicipes* species are rare, due to difficulties associated with sampling the shallow subtidal zone of extremely exposed shores by snorkelling or diving. Quantitative population assessments of abundance for species of *Pollicipes* are available, but have been undertaken with a diversity of objectives and methodologies, hindering the combined analysis of data from multiple studies and precluding interspecific comparisons. Classical approaches, using a standardized protocol, or using new technology-based methods (e.g. drones), are needed to obtain multiple abundance estimates at relevant scales, important for stock assessment, management and conservation, as well as for allowing adequate intra- and interspecific comparisons.

The four species of *Pollicipes* can be identified on the basis of diagnostic features of the capitular plates and peduncular scales. However, the species also show considerable phenotypic variation in colour and peduncular length. Variations in peduncular length, and of water content, are associated with variations regarding the condition and food quality of the barnacles, (e.g. in *Pollicipes pollicipes*, longer peduncles, higher water content, lower quality). More research is needed to understand and disentangle the factors responsible for this phenotypic variation.

In the last 25 years, less importance has been given to the study of functional morphology and physiology of *Pollicipes* species than in the past. We still do not know the basic aspects of the physiology of these species, given the extreme habitats and very exposed shores on which they live. Regarding functional morphology, exceptions have been studies on cirral morphology and feeding of both *Pollicipes polymerus* and *P. pollicipes*, and on adhesion and the cement of *P. pollicipes*. Considering that cirral morphology reflects adaptations to the various feeding modes that have emerged throughout barnacle evolution, it would be very interesting to compare, in detail, the cirral morphology within *Pollicipes*. Moreover, the hypothesis that there is a juvenile-to-adult shift in feeding strategies, from cirral beating to cirral extension, in *Pollicipes* (originally suggested for *P. polymerus*) needs further investigation, namely whether it also applies *to P. pollicipes*, as there are contradictory observations. Additional adhesive proteins remain to be discovered in *Pollicipes pollicipes*, and the detection of a range of enzymes that are active at the adhesive interface in acorn barnacle species also makes this an important direction for future research. The recent publication of the genomes of acorn barnacle species and of *Pollicipes pollicipes* will make the task of adhesive protein discovery and characterization easier in future.

The major research gaps to determine and investigate life-history traits of *Pollicipes* species are listed as follows: (1) investigate whether the newly described mode of fertilization in *P. polymerus*, sperm-cast mating, is an active process; (2) investigate the occurrence of sperm-cast mating in other *Pollicipes* species; (3) investigate whether self-fertilization or partial self-fertilization occurs in *Pollicipes* species; (4) update information on the breeding patterns of *P. polymerus* in southern California and Baja California, taking into account that observations were made more than 40 years ago and that reproductive phenology might alter with climate change; (5) describe the breeding patterns of *P. pollicipes* populations to the south of Portugal; (6) estimate embryo development time (from oviposition to release); (7) describe the patterns of variation in fecundity in *Pollicipes;* (8) investigate the contrasting patterns of vertical distribution of cyprids of *P. polymerus* observed in California (more on the surface or nearer to the bottom); (9) describe the temporal and spatial patterns of distribution of cyprids of *P. pollicipes*; (10) develop and apply biophysical models of larval dispersal to estimate larval dispersal; (11) test specific hypotheses about preferential settlement of cyprids of *Pollicipes* species on adult peduncles; (12) describe and investigate the patterns and processes of spatial and temporal variation of recruitment of *Pollicipes* species at different scales; (13) understand the relative importance of settlement and post-settlement processes (especially intraspecific competition and predation) in the recruitment to adult (and exploitable) populations; and (14) unravel the processes causing the high intraspecific variability in growth rate observed in *Pollicipes* species.

All *Pollicipes* species are exploited throughout their geographic distributions. However, knowledge about these fisheries is uneven and more information is needed from several fisheries (e.g. Mexico, Ecuador, Morocco and Cape Verde). Additionally, there are fisheries that remain largely unregulated and unreported (e.g. Ecuador and Cape Verde), contrasting strongly to those managed through high-level, co-management systems (British Columbia, Canada, and Galicia and Asturias, Spain). More focus should be placed on the social component of top-down and incipient co-management fisheries, mainly by strengthening and empowering the associations of fishers, and promoting their participation in MCSs and decision-making. Moreover, independent observations regarding the state of these resources are needed, as well as on the ecological impacts of harvesting on biodiversity. These could benefit from studies within marine protected areas. Finally, further studies are needed on the use of geochemical structure as a potential tool to discriminate harvesting sites and *Pollicipes* populations. This approach has potential implications for the management of *Pollicipes* fisheries, enforcement of conservation policies, and labelling.

Despite the considerable progress made in developing the cultivation of *Pollicipes* species, there are two main challenges: to develop alternative anti-fouling methods, which are environmentally friendly and low cost, in extensive systems of production of *Pollicipes*; and to resolve the bottleneck of the larval settlement and metamorphosis phase in intensive cultivation systems.

While much has been done since Barnes (1996), more still needs to be done.

Concluding remarks

After the review of *Pollicipes* by Barnes (1996), a new species, *Pollicipes caboverdensis*, was described, joining the three previously extant species (*Pollicipes polymerus*, *Pollicipes elegans* and *Pollicipes pollicipes*). Knowledge about *Pollicipes caboverdensis*, endemic to the Cape Verde Islands, is scarce. This is also the case for *Pollicipes elegans*, which inhabits the tropical eastern Pacific Ocean. Most of the research conducted on *Pollicipes* is based on *P. polymerus* (north-eastern Pacific Ocean) and *P. pollicipes* (north-eastern Atlantic Ocean). We have built a new georeferenced map of the worldwide distribution of *Pollicipes* species. Twenty-five years after Barnes' (1996) review, we know that all *Pollicipes* species are harvested throughout their geographic distributions, with varying levels of intensity. There is archaeological evidence for their use in prehistoric times and their record in shell middens. The oldest record, assigned to *Pollicipes pollicipes,* is from the Upper Palaeolithic, but most findings are from archaeological sites used during the Mesolithic and/or Neolithic, in the Iberian Peninsula and Northern Africa. At the present time, the most intensively exploited species is *Pollicipes pollicipes* in Portugal and Spain. Some fisheries are mainly unregulated and unreported (e.g. Mexico, Costa Rica, Ecuador, Cape Verde), while others are subject to high levels of co-management (e.g. Galicia and Asturias in Spain). Although we have more information on these fisheries, we still lack information on the real fishing effort applied to these resources. Poaching is a common problem across several fisheries. Strengthening and empowering the associations of fishers, to promote their participation in monitoring, in control systems and in decision-making, is highly recommended.

All living *Pollicipes* species are considered to represent relict elements of a Tethys Sea fauna, which became restricted to the eastern boundary conditions of the Atlantic and Pacific Oceans. The present biogeography of the living species, in conjunction with fossil records and coupled with molecular phylogenetics, supports a hypothesis of radiation of pollicipedine species during the Tethys Sea era. Currently, all *Pollicipes* species are placed in a new order, the Pollicipedomorpha Chan et al. 2021. Population genetics is a new area of knowledge in development since Barnes' (1996) review, and considerable progress has been made, with genetic studies leading to the discovery of the new species *Pollicipes caboverdensis*.

Since the extensive review by Barnes (1996) of the functional morphology of *Pollicipes* species, there has been little further development in the last 25 years. However, structural studies of the adhesive interface in *Pollicipes* are an important exception, highlighted in the present review. Although many gaps remain, much progress (e.g. description of adhesive proteins) has been made in understanding the mode of adhesion, namely of *Pollicipes pollicipes*.

Pollicipes species are mostly intertidal and inhabit very exposed shores. *Pollicipes polymerus* is perhaps the most opportunistic species, being found on the greater diversity of substrata. We have made an extensive review of the biological assemblages associated with each *Pollicipes* species. In the last 25 years, our knowledge of life history has increased considerably, particularly for *Pollicipes pollicipes*. All species are hermaphroditic. There is now evidences of pseudo-copulation in *Pollicipes,* which was not available at the time of Barnes' (1996) review. The most surprising advances relate to the study of reproduction in *Pollicipes polymerus*, as two main aspects challenge the accepted wisdom of barnacle reproductive biology: (1) evidence of a novel mode of fertilization, sperm-cast mating, where sperm, released into the water by males, fertilize eggs retained in the body of a female, and (2) the observation of occasional reciprocal copulation, previously never observed in barnacles. Breeding and recruitment patterns were extensively reviewed. The description of recruitment and reproductive phenology are particularly important in the context of climate change. Our knowledge of patterns and processes of growth in *Pollicipes* has progressed considerably due to the use of calcein marking techniques. Although much remains to be studied, there is growing evidence of the importance that post-settlement processes might play in the distribution and abundance of *Pollicipes* species (e.g. the role of species interactions) and in the recruitment (e.g. the role of intraspecific competition and predation) to adult (and exploitable) populations.

In the 25 years since Barnes (1996), there are no known cases of commercially successful aquaculture with *Pollicipes* species. However, several research projects and development trials have attempted to cultivate *Pollicipes* species. The most relevant advance was the discovery of a device ('barticle') and process for the settlement of larvae and the growth of juveniles of *Pollicipes pollicipes* (European Patent nr. EP3372073B1). This solved the major bottleneck of the quest for an artificial substrate, where cyprids could settle in the wild, and which could be easily deployed and removed. This discovery opens the possibility of developing extensive and sustainable cultivation systems and complementary experiments of optimal conditions in the laboratory.

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Nearly 30 years ago, William (Bill) Newman advised Margaret Barnes that Teresa Cruz was studying *Pollicipes* in Portugal. At that time, Margaret was gathering material for her 1996 review.

She wrote to Teresa Cruz asking for information – “I was talking to Dr Newman (Scripps) recently and he mentioned your possible work on the cirripeds of the Portuguese coast…”, “…I think there are so few people in Europe working on cirripedes that it is good to know one who is interested. I also think *Pollicipes* is an intriguing genus and I often wish I had access to living material on a regular basis…” (letters from Margaret, 1992). This was a time when information for a review article came by letter and with a different speed – “…My *Pollicipes* notes go very slowly; there has been so much editing to do recently…” (letter to Teresa Cruz from Margaret, 1994).

In addition to the collective gratitude we have for the role Margaret played in the study of cirripedes, we also want to emphasize the support and care Margaret gave to younger researchers. I (Teresa Cruz) felt this support in those early days studying these amazing living creatures. Later, in 2008, we had the opportunity to organize the “*Pollicipes* international conference”, the first and only conference dedicated to the genus *Pollicipes*, which was dedicated to Margaret Barnes (Cruz et al. 2010b) and several papers included in “The Biology of Barnacles” (*Journal of Experimental Marine Biology and Ecology*, 392). Like that conference, our review, 25 years after Barnes (1996), is a tribute to Margaret Barnes.

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References

Abbott, D.T. & Mix, M.C. 1979. Radiation effects of tritiated seawater on development of the goose barnacle, *Pollicipes polymerus*. *Health Physics* **36** (3), 283–287.

Acuña, J.L., Cruz, T., Dubert, J., Nicole, A., Thiébaut, E. & Vázquez, E. 2020. PERCEBES - tools for the transition to spatial management of coastal resources: The Stalked Barnacle fishery in SW Europe. Final report of PERCEBES project, funded by BiodivERsA. Oviedo, Spain: University of Oviedo.

Aguión, A., Cruz, T., Acuña, J.L., Broudin, C., Castro, J.J., Davoult, D., Dubert, J., Fernandes, J.N., Geiger, K.J., Jacinto, D., Mateus, D., Muñiz, C., Nolasco, R., Perrier, L., Queiroga, H., Román, S., Silva, T., Thiébaut, E., Vázquez, E. & Macho, G. 2022a. A large-scale comparison of reproduction and recruitment of the stalked barnacle *Pollicipes pollicipes* across Europe. *Marine Biology*, **169** (63), doi.org/10.1007/s00227-022-04050-x

Aguión, A., Ojea, E., García-Flórez, L., Cruz, T., Garmendia, J.M., Davoult, D., Queiroga, H., Rivera, A., Acuña-Fernández, J.L. & Macho, G. 2022b. Establishing a governance threshold in small-scale fisheries to achieve sustainability. *Ambio*, **51**, 652-665, doi:10.1007/s13280-021-01606-x

Al-Yahya, H., Chen, H.N., Chan, B.K.K., Kado, R. & Høeg, J.T. 2016. Morphology of cyprid attachment organs compared across disparate barnacle taxa: Does it relate to habitat? *Biological Bulletin* **231** (2), 120–129, doi:10.1086/690092

Alaskafisheries.noaa.gov. 2021. *Pollicipes*. Online. https://alaskafisheries.noaa.gov/mapping/sz_js/index.html?tab=sz&layout=h2# (Accessed 1 June 2021).

Albuquerque, R. 2014. Elemental microchemistry, fatty acid profile and geometric morphometrics signatures of Goose Barnacles (*Pollicipes Pollicipes*) reveal their place of origin. Masters Thesis, Polytechnic of Leiria, Portugal.

Albuquerque, R., Queiroga, H., Swearer, S.E., Calado, R. & Leandro, S.M. 2016. Harvest locations of goose barnacles can be successfully discriminated using trace elemental signatures. *Scientific Reports* **6** (1), 27787, doi:10.1038/srep27787

Alegre, A.R. 2017. Cambios en la estructura del megabentos asociado al submareal rocoso en las islas San Lorenzo y Palomino (Callao, Perú) durante el evento El Niño 1997–98. Honor Thesis, Universidad del Perú, Perú.

Alemán, S., Montero, P., Vera, M., Luque, C. & Ordinola, E. 2016. Natural banks of commercial benthic invertebrates and artisanal fishing areas. Tumbes, Peru. Autumn 2014. *Instituto de Mar del Perú* **43** (3), 275–297.

Almeida, J.R., Freitas, M., Cruz, S., Leão, P.N., Vasconcelos, V. & Cunha, I. 2015. Acetylcholinesterase in biofouling species: Characterization and mode of action of cyanobacteria-derived antifouling agents. *Toxins* **7** (8), 2739–2756, doi:10.3390/toxins7082739

Álvarez-Fernández, E. 2011. Humans and marine resource interaction reappraised: Archaeofauna remains during the late Pleistocene and Holocene in Cantabrian Spain. *Journal of Anthropological Archaeology* **30** (3), 327–343, doi:10.1016/j.jaa.2011.05.005

Álvarez-Fernández, E., Barrera, I., Borja, A., Fernández, M.J., Iriarte, M.J. & Arrizabalaga, A. 2013. Biometric analysis of the stalked barnacle *Pollicipes pollicipes*, at a holocene archaeological site in Jaizkibel (Basque Country, northern Spain). *journals.sagepub.com*, doi: 10.1177/0959683613489584

Álvarez-Fernández, E., Ontañón-Peredo, R. & Molares, J. 2010. Archaeological data on the exploitation of the goose barnacle *Pollicipes pollicipes* (Gmelin, 1790) in Europe. *Journal of Archaeological Science* **37** (2), 402–408, doi:10.1016/J.JAS.2009.10.003

Anderson, D.T. 1994. *Barnacles: Structure, Function, Development and Evolution*. London: Chapman and Hall.

Anderson, D.T. & Southward, A.J. 1987. Cirral activity of barnacles. In *Crustacean Issues*, *5. Barnacle Biology*, A.J. Southward (ed.). Rotterdam: A. A. Balkema, 135–174.

Ansted, D. T. & Latham, R. G. (1865). *The Channel Islands*. London: Hallen & Co.

Aristu, B.A., Álvarez-Fernández, E., Pardo, J.J. & Tortosa, E.A. 2011. The barnacles: A new species used to make a Gravettian suspended object from Nerja Cave (Málaga, Spain). In *Written in Bones,* J. Baron & B. Kufel-diakowska (eds). Wrocław: Instytut Archeologii, Uniwersytet Wrocławski, 53–62.

Arntz, W.E., Brey, T., Tarazona, J. & Robles, A. 1987. Changes in the structure of a shallow sandy-beach community in Peru during an El Niño event. *South African Journal of Marine Science* **5** (1), 645–658, doi:10.2989/025776187784522504.

Arntz, W.E., Gallardo, V.A., Guti, D., Ci, I. De, Csic, M. & Mar, P. 2006. El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela current upwelling ecosystems. *Advances In Geosciences* **1983** (1984), 243–265.

Arsenault, D.J., Marchinko, K.B. & Palmer, A.R. 2001. Precise tuning of barnacle leg length to coastal wave action. *Proceedings of the Royal Society B: Biological Sciences* **268** (1481), 2149–2154, doi:10.1098/rspb.2001.1776

Austin, W.C. 1987. A feasibility study for the commercial harvesting of the goose barnacle *Pollicipes polymerus*. Final report to Department of Fisheries and Oceans. Canada: Khoyatan Marine Laboratory, 171.

Austin, W.C. 1992. Goose barnacle survey. Report PPS1-073 prepared to Department of Fisheries and Oceans, Canada: Khoyatan Marine Laboratory, 24.

Bachetarzi, R., Zahaf, C.R. & Benabdi, M. 2016. Biodiversity marine assessment of “Agueli Island” (Wilaya of Algiers), Algeria. *Rapports et Proces-Verbaux des Reunions Commission Internationale Pour l’Exploration Scientifique de la Mer Mediterranee* **41**, 446.

Baessa, E. 2015. Ecologia e pesca de percebe, *Pollicipes caboverdensis*, na ilha de Santiago (Cabo Verde). Honors thesis, Universidade de Cabo Verde, Cabo Verde.

Bald, J., Borja, A. & Muxika, I. 2006. A system dynamics model for the management of the gooseneck barnacle (*Pollicipes pollicipes*) in the marine reserve of Gaztelugatxe (Northern Spain). *Ecological Modelling* **194** (1–3), 306–315, doi:10.1016/J.ECOLMODEL.2005.10.024

Barazandeh, M. 2014. New insights about barnacle reproduction: Spermcast mating, aerial copulation and population genetic consequences. PhD Thesis, University of Alberta, Canada.

Barazandeh, M. & Davis, C.S. 2012. Identification and characterization of 16 single nucleotide polymorphisms (SNPs) in the northeast intertidal gooseneck barnacle, *Pollicipes polymerus. Conservation Genetics Resources* **4** (2), 217–219, doi:10.1007/s12686-011-9510-8.

Barazandeh, M., Davis, C.S., Neufeld, C.J., Coltman, D.W. & Palmer, A.R. 2013. Something Darwin didn’t know about barnacles: Spermcast mating in a common stalked species. *Proceedings of the Royal Society B: Biological Sciences* **280** (1754), 20122919, doi:10.1098/rspb.2012.2919

Barazandeh, M., Davis, C.S. & Palmer, A.R. 2014. Where even a long penis can’t help: Evidence of long-distance spermcast mating in two acorn barnacles. *Journal of Experimental Marine Biology and Ecology* **454**, 49–54, doi:10.1016/j.jembe.2014.02.003

Barazandeh, M. & Palmer, A.R. 2015. Novel mating modes on wave-swept shores: Aerial copulation and sperm release in an intertidal stalked barnacle. *Marine Biology* **162** (4), 881–888, doi:10.1007/s00227-015-2631-y

Barlow, D.E., Dickinson, G.H., Orihuela, B., Kulp, J.L., Rittschof, D. & Wahl, K.J. 2010. Characterization of the adhesive plaque of the barnacle Balanus amphitrite: Amyloid-like nanofibrils are a major component. *Langmuir* **26** (9), 6549–6556, doi:10.1021/la9041309

Barnes, H. 1959. Stomach contents and microfeeding of some common cirripedes. *Canadian Journal of Zoology* **37** (3), 231–236, doi:10.1139/z59-027

Barnes, H. & Blackstock, J. 1974. The biochemical composition of the cement of a pedunculate cirripede. *Journal of Experimental Marine Biology and Ecology* **16** (1), 87–91, doi:10.1016/0022-0981(74)90073-2

Barnes, H. & Blackstock, J. 1976. Further observations on the biochemical composition of the cement of *Lepas fascicularis* Ellis & Solander; electrophoretic examination of the protein moieties under various conditions. *Journal of Experimental Marine Biology and Ecology* **25** (3), 263–271, doi:10.1016/0022-0981(76)90128-3

Barnes, H. & Reese, E.S. 1959. Feeding in the pedunculate cirripede *Pollicipes polymerus* In *Proceedings of the Zoological Society of London*, J.B. Sowerby (ed.). **132** (4), 569–585, doi:10.1111/j.1469-7998.1959.tb05537.x

Barnes, H. & Reese, E.S. 1960. The behaviour of the stalked intertidal barnacle *Pollicipes polymerus* J. B. Sowerby, with special reference to its ecology and distribution. *The Journal of Animal Ecology* **29** (1), 169, doi:10.2307/2276

Barnes, M. 1989. Egg production in cirripedes. *Oceanography and Marine Biology: An Annual Review* **27** 91–166.

Barnes, M. 1992. The reproductive periods and condition of the penis in several species of common cirripedes. *Oceanography and marine biology: An annual review* **30**, 483–525.

Barnes, M. 1996. Pedunculate cirripedes of the genus *Pollicipes*. *Oceanography and Marine Biology: An Annual Review* **34**, 303–394.

Barnes, M.K.S. 2021. Rocky shore goose barnacle (*Pollicipes pollicipes*). Online. https://www.marlin.ac.uk/species/detail/43 (Accessed 1 June 2021).

Barraza, J.E., Mariona, G.I. & Rivera, C.G. 2014. *Invertebrados marinos de El Salvador*. San Salvador: Ministerio de Medio Ambiente y Recursos Naturales (MARN).

Bazairi, H. 2010. *Rapport national pour l'identification des propriétés majeures des écosystèmes et l'évaluation de l'état écologique et des pressions sur la biodiversité marine et côtière en Méditerranée marocaine*. Contrat CAR/ASP n°59/RAC/SPA_2009. 59.

Belela, N. 2018. Estudo do crescimento, sobrevivência e estratégias de controlo das incrustações, num sistema extensivo de cultivo de *Pollicipes pollicipes* (Gmelin, 1790). Masters Thesis, University of Algarve, Portugal.

Bello-Alonso, P., Ozkorta-Escribano, L. & Gutiérrez-Zugasti, I. 2015. Un acercamiento al aprovechamiento de los recursos litorales durante el Mesolítico: los invertebrados marinos del abrigo de El Toral III (Llanes, Asturias), In *La Investigación Arqueomalacológica en la Península Ibérica: Nuevas Aportaciones*, I. Gutiérrez-Zugasti et al., (eds). Santander: Nadir Ediciones, 91–99.

Berkes, F., Mahon, R., McConney, P., Pollnac, R. & Pomeroy, R. 2001. *Managing Small-Scale Fisheries: Alternative Directions and Methods*. Ottawa: IDRC.

Bernard, F.R. 1988. Potential fishery for the gooseneck barnacle *Pollicipes polymerus* (Sowerby, 1833) in British Columbia. *Fisheries Research* **6** (3), 287–298, doi:10.1016/0165-7836(88)90020-3

Bertness, M.D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* **70** (1), 257–268, doi:10.2307/1938431

Bertness, M.D., Gaines, S.D. & Yeh, S.M. 1998. Making mountains out of barnacles: The dynamics of acorn barnacle hummocking. *Ecology* **79** (4), 1382–1394, doi:10.1890/0012-9658(1998)079[1382:MMOOBT]2.0.CO;2

Bicho, N.F. 2009. On the edge: Early holocene adaptations in Southwestern Iberia. *Journal of Anthropological Research* **65** (2), 185–206, doi:10.3998/jar.0521004.0065.202

Bicho, N.F., Manne, T., Marreiros, J., Cascalheira, J., Pereira, T., Tátá, F., Évora, M., Gonçalves, C. & Infantini, L. 2013. The ecodynamics of the first modern humans in Southwestern Iberia: The case of Vale Boi, Portugal. *Quaternary International* **318**, 102–116, doi:10.1016/j.quaint.2013.06.029

Bidegain, G., Guinda, X., Puente, A. & Juanes, J.A. 2017. Distribution patterns of the gooseneck barnacle (*Pollicipes pollicipes* [Gmelin, 1789]) in the Cantabria Region (N Spain): Exploring different population assessment methods. *Journal of Shellfish Research* **36** (3), 787–797, doi:10.2983/035.036.0328

Bidegain, G., Guinda, X., Sestelo, M., Roca-Pardiñas, J., Puente, A. & Juanes, J.A. 2015. Assessing the suitability of the minimum capture size and protection regimes in the gooseneck barnacle shellfishery. *Ocean and Coastal Management* **104**, 150–158, doi:10.1016/j.ocecoaman.2014.12.015

Bingham, J. 2016. Sensitive barnacles: A case study for collaborative sustainable fishery development. Honors Thesis, Oregon State University, Canada.

Bingham, J., Thomas, M. & Shanks, A. 2017. Development of a sustainable gooseneck barnacle fishery; initial investigations. *Oregon Sea Grant Report* **41**, 1–41.

Boaventura, D., da Fonseca, L. & Hawkins, S. 2002. Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. on the northern coast of Portugal. *Journal of Experimental Marine Biology and Ecology* **271**, 171–188, doi:10.1016/S0022-0981(02)00044-8

Bonsall, C., Cook, G.T., Pickard, C., McSweeney, K. & Bartosiewicz, L. 2009. Edinburgh research explorer dietary trends at the Mesolithic – Neolithic transition in North-west Europe. In *Chronology and Evolution within the Mesolithic of North-West Europe*, P. Crombé et al. (eds). Newcastle upon Tyne: Cambridge Scholars Publishing.

Borja, A., Liria, P., Muxika, I. & Bald, J. 2006a. Relationships between wave exposure and biomass of the goose barnacle (*Pollicipes pollicipes*, Gmelin, 1790) in the Gaztelugatxe Marine Reserve (Basque Country, northern Spain). *ICES Journal of Marine Science* **63** (4), 626–636, doi:10.1016/j.icesjms.2005.12.008

Borja, A., Muxika, I. & Bald, J. 2006b. Protection of the goose barnacle *Pollicipes pollicipes*, Gmelin, 1790 population: The Gaztelugatxe Marine Reserve (Basque Country, northern Spain). *Scientia Marina* **70** (2), 235–242, doi:10.3989/scimar.2006.70n2235

Boukaici, M. 2015. Contribution à l'étude de la dynamique des populations et la biologie de reproduction du crustacé *Pollicipes pollicipes* (Gmelin, 1789) dans la région de Mirleft (Province de Sidi Ifni - Sud Ouest Marocain). PhD Thesis, Centre Des Etudes Doctorales Ibn Zohr, Agadir, Marroco.

Boukaici, M., Bergayou, H., Kaaya, A. & Elkhou, A. 2012. *Pollicipes pollicipes* (Gmelin, 1789) (Cirripedia, Lepadomorpha): Its growth and population dynamics in the region of Mirleft (southwest Morocco). *Crustaceana* **85** (PART9), 1073–1097, doi:10.1163/156854012X651259

Boukaici, M., Bergayou, H., Kaaya, A. & Elkhou, A. 2015. *Pollicipes pollicipes* (Gmelin, 1789) (cirripedia, lepadomorpha): Its cycle of reproduction in the region of Mirleft (Southwest Morocco). *Journal of Materials and Environmental Science* **6** (10), 2673–2680.

Bourassi, H., Zidane, H., Haddi, I., Charouki, N. & Yahyaoui, A. 2019. Growth and population dynamic of crustacean cirriped *Pollicipes pollicipes*, in the Moroccan Atlantic Coast. *Frontiers in Marine Science*, doi:10.3389/conf.fmars.2018.06.00070

Brietzke, C., Fretwell, K. & Starzomski, B. 2013. *Goose Neck Barnacle, Goose-Necked Barnacle, Goose Barnacle, Leaf Barnacle. Pollicipes polymerus.* Online. https://www.centralcoastbiodiversity.org/goose-neck-barnacle-bull-pollicipes-polymerus.html (Accessed 1 July 2021).

Briggs, J.C. & Bowen, B.W. 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography* **39** (1), 12–30, doi:10.1111/j.1365-2699.2011.02613.x

British Columbia Sport Fishing Regulations. 1996. *British Columbia Sport Fishing Regulations, Schedule V.* Online. https://laws-lois.justice.gc.ca/eng/regulations/SOR-96-137/index.html (Accessed 1 July 2021).

Broch, H. 1922. Papers from Dr. Th. Mortensen's Pacific expedition 1914–1916. X. Studies on Pacific cirripedes. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn* **73**, 215–358.

Broch, H. 1927. Studies on Moroccan cirripeds (Atlantic coast). *Bulletin de la Société des Sciences Naturelles du Maroc* **7** (1–3), 11–38.

Brym, P.R. 1980. The morphology and behavior of intertidal limpets on *Pollicipes* in Monterey Bay. Biology 175H, Stanford University, Student Paper. https://purl.stanford.edu/nj453dh1459.

Buckeridge, J.S. 1983. Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. *New Zealand Department of Scientific and Industrial Research, Geological Survey, Paleontological Bulletin No* **50**, 1–151.

Burrows, M.T., Hawkins, S.J. & Southward, A.J. 1992. A comparison of reproduction in co-occurring chthamalid barnacles, *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward. *Journal of Experimental Marine Biology and Ecology* **160** (2), 229–249, doi:10.1016/0022-0981(92)90240-B

Byers, B. 1989. Habitat-choice polymorphism associated with cryptic shell-color polymorphism in the limpet *Lottia digitalis*. *The Veliger* 32 (4), 394–402.

Cadena, A., Carrera Nicola, R. & Villavicencio, I. 2008. Elaboración del inventario de recursos gastronómicos con potencial turístico del cantón Puerto López. Honor Thesis. Escuela Superior Politécnica Del Litoral Facultad De Ingeniería Marítima Y Ciencias Del Mar, Guayaquil.

California Department of Fish and Wildlife. 2021. *Fishing and Hunting Regulations*. Online. https://wildlife.ca.gov/Regulations (Accessed 1 July 2021).

Callapez, P.M. & Pimentel, R. 2018. Moluscos e crustáceos do sítio de ocupação do menir de Padrão 1 (Vila do Bispo, Algarve, Portugal): aspetos da dieta alimentar e da ecologia litoral num contexto costeiro do Neolítico antigo. *Boletín de la Real Sociedad Española de Historia Natural* **1**, 53–72, doi:10.29077/bol/112/ce06_callapez

Campo, D., Molares, J., Garcia, L., Fernandez-Rueda, P., Garcia-Gonzalez, C. & Garcia-Vazquez, E. 2010. Phylogeography of the European stalked barnacle (*Pollicipes pollicipes*): Identification of glacial refugia. *Marine Biology* **157**, 147–156, doi:10.1007/s00227-009-1305-z

Candeias, A. 2005. Aspects of feeding in barnacle larvae (Cirripedia: Thoracica). PhD Thesis, University of Wales, United Kingdom.

Cárdenas-Calle, M., Mora, E., Torres, G., Pérez-Correa, J., Bigatti, G., Signorelli, J. & Coronel, J. 2020. Marine invertebrate and seaweed biodiversity of continental coastal Ecuador. *Biodiversity Data Journal* **8** (July), doi:10.3897/BDJ.8.e53818

Cardoso, A.C. 1998. The population biology of the gooseneck barnacle *Pollicipes pollicipes* (Gmelin, 1790) in the Algarve, Southwest Portugal. PhD Thesis, University of Wales, United Kingdom.

Cardoso, A.C. & Yule, A.B. 1995. Aspects of the reproductive biology of *Pollicipes pollicipes* (Cirripedia; Lepadomorpha) from the southwest coast of Portugal. *Netherlands Journal of Aquatic Ecology* **29** (3–4), 391–396, doi:10.1007/BF02084238

Carrington-Bell, E. & Denny, M. 1994. Quantifying wave exposure - a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* **181**, 9–29.

Carvalho, A.F. 2007. Ossos, pedras e isótopos. Contribuições para o estudo de dois temas da Pré-História do Sul de Portugal. *III Encontro de Arqueologia do Sudoeste Peninsular*. Silves: Câmara Municipal de Silves.

Carvalho, A.F. & Valente, M.J. 2005. Novos contextos conquíferos pré-históricos na Costa Vicentina. *Encontro de Arqueologia do Algarve 2*. Silves: Câmara Municipal de Silves.

Carvalho, A.N., Vasconcelos, P., Piló, D., Pereira, F. & Gaspar, M.B. 2017. Socio-economic, operational and technical characterisation of the harvesting of gooseneck barnacle (*Pollicipes pollicipes*) in SW Portugal: Insights towards fishery co-management. *Marine Policy* **78**, 34–44, doi:10.1016/j.marpol.2017.01.008

Castilla, J.C. 2009. Darwin taxonomist: Barnacles and shell burrowing barnacles. *Revista Chilena de Historia Natural* **82** (4), 477–483, doi:10.4067/S0716-078X2009000400002

Castro, J.J. 2004. Predação humana no litoral rochoso alentejano: caracterização, impacte ecológico e conservação. PhD Thesis, University of Évora, Portugal.

Castro, J.J. & Cruz, T. 2009. Marine conservation in a Southwest portuguese natural park. *Journal of Coastal Research* **I** (56), 385–389.

Caziot, L.C. 1921. Les cirripèdes de la Mer de Nice. *Bulletin de la Société Zoologique de France* **46**, 51–54.

Chaffee, J. & Lewis, C.A. 1988. Pedunculate barnacle stalk growth. *Journal of Experimental Marine Biology and Ecology* **124** (3), 145–162, doi:10.1016/0022-0981(88)90169-4

Chan, B.K.K., Dreyer, N., Gale, A.S., Glenner, H., Ewers-Saucedo, C., Pérez-Losada, M., Kolbasov, G.A., Crandall, K.A. & Høeg, J.T. 2021. The evolutionary diversity of barnacles, with an updated classification of fossil and living forms. *Zoological Journal of the Linnean Society* **XX**, 1–58, doi:10.1093/zoolinnean/zlaa160

Chan, B.K.K., Garm, A. & Høeg, J.T. 2008. Setal morphology and cirral setation of thoracican barnacle cirri: Adaptations and implications for thoracican evolution. *Journal of Zoology* **275** (3), 294–306, doi:10.1111/j.1469-7998.2008.00441.x

Chan, B.K.K. & Hung, O.S. 2005. Cirral length of the acorn barnacle *Tetraclita japonica* (Cirripedia: Balanomorpha) in Hong Kong: Effect of wave exposure and tidal height. *Journal of Crustacean Biology* **25** (3), 329–332, doi:10.1651/C-2535

Cheung, P.J., Ruggieri, G.D. & Nigrelli, R.F. 1977. A new method for obtaining barnacle cement in the liquid state for polymerization studies. *Marine Biology* **43** (2), 157–163, doi:10.1007/BF00391263

Cimberg, R.L. 1981. Variability in brooding activity in the stalked barnacle *Pollicipes polymerus*. *The Biological Bulletin* **160** (1), 31–42, doi:10.2307/1540898

Coelho, M.R. 1990. Descrição dos estados larvares do perceve (*Pollicipes cornucopia*). Honor Thesis, Universidade do Algarve, Portugal.

Coelho, M.R. 1991. A field study on *Pollicipes pollicipes* settlement. Master Thesis, University College of North Wales, United Kingdom.

Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42** (4), 710–723, doi:10.2307/1933500

Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* **3** (1), 169–192.

Connell, J.H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93** (1–2), 11–45, doi:10.1016/0022-0981(85)90146-7

Connolly, S.R. & Roughgarden, J. 1999. Theory of marine communities: Competition, predation, and recruitment-dependent interaction strength. *Ecological Monographs* **69**, 277–296, doi:10.1890/0012-9615(1999)069[0277:TOMCCP]2.0.CO;2

Cornwall, I.E. 1925. A review of the cirripedia of the coast of British Columbia, with glossary, and key to genera and species. *Contributions to Canadian Biology and Fisheries, New Series* **2**, 469–502, doi:10.1139/f24-018

Costa, A.B. 2012. Fishing on Alentejo rocky shores - Intensity, yield and protection effects. Master Thesis, University of Évora, Portugal.

Creese, R.G. & Underwood, A.J. 1982. Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* **53** (3), 337–346, doi:10.1007/BF00389010

Cribeiro, A.P. 2007. Explotacion del percebe, *Pollicipes pollicipes* (Gmelin, 1789), na costa do Ortegal. influencia dos factores abioticos, estudo en condicions experimentais da estrutura poboacional. Honor thesis, Universidade de Santiago de Compostela, Spain.

Crickenberger, S., Walther, K., Marchant, S., Marko, P.B. & Moran, A.L. 2015. Population-dependent acclimatization capacity of thermal tolerance in larvae of the rocky-shore barnacle *Pollicipes elegans*. *Invertebrate Biology* **134** (4), 291–302, doi:10.1111/ivb.12104

Crummett, L.T. & Eernisse, D.J. 2007. Genetic evidence for the cryptic species pair, *Lottia digitalis* and *Lottia austrodigitalis* and microhabitat partitioning in sympatry. *Marine Biology* **152** (1), 1–13, doi:10.1007/s00227-007-0621-4

Cruz, T. 1993. Growth of *Pollicipes pollicipes* (Gmelin, 1790) (Cirripedia, Lepadomorpha) on the SW coast of Portugal. *Crustaceana* **65** (2), 151–158, doi:10.1163/156854093X00522

Cruz, T. 2000. Biologia e ecologia do percebe *Pollicipes pollicipes (*Gmelin, 1790), no litoral sudoeste portugês. PhD Thesis, University of Évora, Portugal.

Cruz, T. & Araújo, J. 1999. Reproductive patterns of *Pollicipes pollicipes* (Cirripedia: Scalpellomorpha) on the southwestern coast of Portugal. *Journal of Crustacean Biology* **19** (2), 260–267, doi:10.2307/1549232

Cruz, T., Baessa, E., Almada, C.H. & Fernandes, J.N. 2015a. O percebes e Cabo Verde (*Pollicipes caboverdensis*): Desafios para a sua gestão e conservação. *VIII Congresso sobre Planeamento e Gestão das Zonas Costeiras dos Países de Expressão Portuguesa*, 1–10.

Cruz, T., Baessa, E., Soares, V., Almada, C.H. & Fernandes, J.N. Reproduction and recruitment of the endemic stalked barnacle from Cabo Verde Islands, *Pollicipes caboverdensis*. In prep.

Cruz, T., Castro, J.J. & Hawkins, S.J. 2010a. Recruitment, growth and population size structure of *Pollicipes pollicipes* in SW Portugal. *Journal of Experimental Marine Biology and Ecology* **392** (1–2), 200–209, doi:10.1016/j.jembe.2010.04.020

Cruz, T., Fernandes, J.N., Jacinto, D., Seabra, M.I., Silva., T. & Castro, J.J. 2016a. AQUAPOLLIS: Viabilidade biológica e económica da aquacultura de percebe (*Pollicipes pollicipes*) em Portugal (Relatório final do projeto piloto 31-03-05-FEP-46). Parte I: Estudo da viabilidade biológica. Évora, Portugal: Universidade de Évora.

Cruz, T., Fernandes, J.N., M.I., S., Jacinto, D., Nobre, D., Silva, T., Castro, J.J., Fragoso, R. & Ruivo, J. 2020. AQUAPOLLIS+: Aquacultura do percebe (*Pollicipes pollicipes*) (Relatório final do projeto ALT20-03-0145-FEDER-000003). Évora, Portugal: Universidade de Évora.

Cruz, T., Fernandes, J.N., Van Syoc, R.J. & Newman, W.A. 2015b. Classe thecostraca subclasse cirripedia superordem thoracica. *Revista IDE@-SEA* **99A**, 13.

Cruz, T. & Hawkins, S.J. 1998. Reproductive cycle of *Pollicipes pollicipes* at cabo de Sines, south-west coast of Portugal. *Journal of the Marine Biological Association of the United Kingdom* **78** (02), 483–496, doi:10.1017/S0025315400041576

Cruz, T., Hawkins, S.J., Macho, G., Pineda, J. & Van Syoc, B. 2010b. Introduction. *Journal of Experimental Marine Biology and Ecology* **392** (1–2), 1, doi:10.1016/j.jembe.2010.07.009

Cruz, T., Jacinto, D., Silva, T., Castro, J.J., Marcelino, A., Maranhão, P. & Teixeira, A. 2008. Exploração e gestão do percebe (*Pollicipes pollicipes*) na Reserva Natural das Berlengas: padrões e impactes. Relatório final de execução científica (POCI/ BIA-BDE/58206/2004). Universidade de Évora, Portugal.

Cruz, T., Jacinto, D., Sousa, A., Penteado, N., Pereira, D., Fernandes, J.N., Silva, T. & Castro, J.J. 2015c. The state of the fishery, conservation and management of the stalked barnacle *Pollicipes pollicipes* in Portugal. *Marine Environmental Research* **112**, 73–80, doi:10.1016/J.MARENVRES.2015.10.005

Cruz, T., Jacinto, D., Sousa, A., Penteado, N., Silva, T., Fernandes, J.N. & Castro, J.J. 2016b. PERCEBES - Gestão, Ecologia e Conservação do Percebe em Portugal. Relatório final do projeto piloto 31-03-05-FEP-11. Évora, Portugal: Universidade de Évora.

Daniel, A. 1953. XXV.- On a new barnacle, *Pollicipes polymerus madrasensis*, subsp. nov., in Madras. *Annals and Magazine of Natural History* **6** (64), 286–287, doi:10.1080/00222935308654423

Darras, J. 2017. Aquaculture of the stalked barnacle *Pollicipes pollicipes*: Improving farming techniques in an extensive system located in Sines (Portugal). Master Thesis, University of Algarve, Portugal.

Darwin, C. 1839. *The Voyage of the Beagle*. London: Penguin Books Ltd.

Darwin, C. 1852. *A monograph of the Subclass Cirripedia, with Figures of All the Species. The Lepadidæ or pedunculated cirripedes*. London: The Ray society.

Davey, P.A., Power, A.M., Santos, R., Bertemes, P., Ladurner, P., Palmowski, P., Clarke, J., Flammang, P., Lengerer, B., Hennebert, E., Rothbächer, U., Pjeta, R., Wunderer, J., Zurovec, M. & Aldred, N. 2021. Omics-based molecular analyses of adhesion by aquatic invertebrates. *Biological Reviews* **96** (3), 1051–1075, doi:10.1111/brv.12691

Dawson, M.N., Hays, C.G., Grosberg, R.K. & Raimondi, P.T. 2014. Dispersal potential and population genetic structure in the marine intertidal of the eastern North Pacific. *Ecological Monographs* **84** (3), 435–456, doi:10.1890/13-0871.1

Dayton, P.K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41** (4), 351–389, doi:10.2307/1948498

Dean, R. 2010. Delicacy or desperation? Eating peduncular barnacles in Neolithic Portugal. *Journal of Ethnobiology* **30** (1), 80–91, doi:10.2993/0278-0771-30.1.80

de la Cruz, J., Castro, J., Carbajal, W. & Ramírez, P. 2001. Evaluación de la población del percebes *Pollicipes elegans* en las islas Lobos de Afuera (18–20 julio 2001). *Informe Progressivo Instituto del Mar del Perú* **146**, 11–19.

de la Cruz, J., Castro, J., Carbajal, W. & Ramírez, P. 2002. Evaluación de la población del "percebe" *Pollicipes elegans* en las islas Lobos de Afuera (8–10 de mayo del 2002). *Informe progressivo Instituto del Mar del Perú*, 1–17.

de la Cruz, J., Ramirez, P. & Llanos, J. 2015a. Islas Lobos de Afuera: Evaluación de pulpo *Octopus mimus* Gould, 1852 y percebes *Pollicipes elegans* (Lesson, 1831), Lambayeque, 2010. *Informe Instituto del Mar del Perú* **42** (3), 273–281.

de la Cruz, J., Ramírez, P. & Llanos, J. 2015b. *Isla Lobos de Tierra: Evaluación de invertebrados en bancos naturales, 2010. Instituto del Mar del Perú* **42** (3), 293–306.

de la Cruz, J., Ramírez, P. & Llanos, J. 2016. Evaluación de bancos naturales de concha de abanico (*Argopecten purpuratus*) y de pulpo (*Octopus mimus*). Isla Lobos de Tierra (Noviembre 2009). *Informe Instituto del Mar del Perú* **43** (1), 10.

de La Hoz, J.J. & Garcia, L. 1993. Datos para el estudio de la distribución y reproducción del percebe, *Pollicipes cornucopia* (Leach), en Asturias. *Publicaciones Especiales Instituto Español de Oceanografia* **11**, 65–71.

Denley, E.J. & Underwood, A.J. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology* **36** (3), 269–293.

DFO. 2005. *West Coast Vancouver Island Goose Barnacle Experimental Fishery Guidelines & Harvest Plan*. Vancouver, Canada: Fisheries and Oceans Canada and West Coast Vancouver Island Aquatic Management Board.

Diogo, H., Veiga, P., Pita, C., Sousa, A., Lima, D., Pereira, G., Gonçalves, J.M.S., Erzini, K. & Rangel, M. 2020. Marine recreational fishing in Portugal: Current knowledge, challenges, and future perspectives. *Reviews in Fisheries Science & Aquaculture*, doi:10.1080/23308249.2020.1777083

Domínguez-Pérez, D., Almeida, D., Wissing, J., Machado, A.M., Jänsch, L., Castro, L.F., Antunes, A., Vasconcelos, V., Campos, A. & Cunha, I. 2020. The quantitative proteome of the cement and adhesive gland of the pedunculate barnacle, *Pollicipes pollicipes. International Journal of Molecular Sciences* **21** (7), 20, doi:10.3390/ijms21072524

Domínguez, R., Olabarria, C., Woodin, S.A., Wethey, D.S., Peteiro, L.G., Macho, G. & Vázquez, E. 2021. Contrasting responsiveness of four ecologically and economically important bivalves to simulated heat waves. *Marine Environmental Research* **164**, 105229, doi: 10.1016/j.marenvres.2020.105229

dos Santos, A., Santos, A. & Conway, D.V.P. 2007. Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast. *Marine Ecology Progress Series* **329**, 145–155, doi:10.3354/meps329145

Doumergue, F. 1921. Le cimetière des Escargots. Valves de pouce-pied. *Bulletin de la Société de Géographie (et d'Archéologie) de la Province d'Oran*, 1921: 52–54.

Drew, K.M. & Richards, K.S. 1953. Studies in the Bangioideae. 2. The Conchocelis-phase of Porphyra sp. in *Pollicipes cornucopia* Leach at Roscoff. *Botanical Journal of the Linnean Society of London, Botany* **55** (356), 84–87, doi:10.1111/j.1095-8339.1953.tb00005.x

Dudas, S.E., Rilov, G., Tyburczy, J. & Menge, B.A. 2009. Linking larval abundance, onshore supply and settlement using instantaneous versus integrated methods. *Marine Ecology Progress Series* **387**, 81–95, doi:10.3354/meps08095

Dupont, C. 2011. Les invertébrés marins du “concheiro” de Toledo (Lourinhã, Portugal), In *O Concheiro de Toledo no Contexto do Mesolítico inicial do Litoral da Estremadura*. Trabalhos de Arqueologia, **51**, 185–227.

Dupont, C., Álvarez-Fernandez, E. & Gruet, Y. 2008. Un nouveau crustacé identifié sur le site gaulois de Port Blanc (île d’Hoedic, Morbihan): le pouce-pied *Pollicipes pollicipes*. *Bulletin de l’A.M.A.R.A.I.* **21**, 17–23.

Dupont, C., Tresset, A., Desse-Berset, N., Gruet, Y., Marchand, G. & Schulting, R. 2009. Harvesting the seashores in the late mesolithic of Northwestern Europe: A view from Brittany. *Journal of World Prehistory* **22** (2), 93–111, doi:10.1007/s10963-009-9017-3

Eater. 2020. *How to Harvest and Cook Gooseneck Barnacles — Deep Dive*. Online. https://www.youtube.com/watch?v=f7gWQNQF8mE (Accessed on 1 July 2021).

Edwards, J.C. 2020. Post-harvest recovery of a co-managed First Nations’ gooseneck barnacle fishery. Master Thesis, University of Victoria. Canadá.

Efford, M. 2019. Ts’a7inwa (gooseneck barnacles) as a proxy for archaeological efforts to understand shellfish. Master Thesis, University of Victoria, Canada.

Erlandson, J.M., Batterson, M.R. & Rick, T.C. 2004. Busted balls shell midden (CA-SMI-606): An early coastal site on San Miguel island, California. *North American Archaeologist* **25** (3), 251–272, doi:10.2190/1YQB-Q2BR-UK2L-AADJ

European patent nr. EP3372073A1 from 17-06-2020. *Device and Process for Fixation of Larvae and Growth of Juveniles of the Stalked Barnacle* Pollicipes pollicipes. University of Évora. Inventors: Cruz, T., Jacinto, D., Fernandes, J., Seabra, M., Silva, T., Castro, J.

Fears, K.P., Barnikel, A., Wassick, A., Ryou, H., Schultzhaus, J.N., Orihuela, B., Scancella, J.M., So, C.R., Hunsucker, K.Z., Leary, D.H., Swain, G., Rittschof, D., Spillmann, C.M. & Wahl, K.J. 2019. Adhesion of acorn barnacles on surface-active borate glasses. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374** (1784), doi:10.1098/rstb.2019.0203

Feder, H.M. 1959. The food of the starfish, *Pisaster ochraceus* along the California coast. *Ecology* **40** (4), 721–724, doi:10.2307/1929828

Fernandes, J.N. Genetic structure, recruitment and larval abundance of the intertidal barnacle *Pollicipes pollicipes*. PhD Thesis, University of Évora, Portugal. In submission.

Fernandes, J.N. 2018. Recruitment of the stalked barnacle *Pollicipes pollicipes* on an artificial substratum (“barticle”) and transfer to an extensive system of production: Success techniques and pitfalls. Master Thesis, University of Évora, Portugal.

Fernandes, J.N., Cruz, T., Ginja, C. & Grosberg, R.K. Genetic differentiation in the European and African edible stalked barnacle *Pollicipes pollicipes*. In prep.

Fernandes, J.N., Cruz, T. & Van Syoc, R.J. 2010. *Pollicipes caboverdensis* sp. nov. (Crustacea: Cirripedia: Scalpelliformes), an intertidal barnacle from the Cape Verde islands. *Zootaxa* **2557**, 29–38.

Fernandes, J.N., Jacinto, D., Penteado, N., Sousa, A., Mateus, D., Seabra, M.I., Silva, T., Castellanos, P., Castro, J.J. & Cruz, T. 2021. Ten years of monitoring recruitment of the edible stalked barnacle *Pollicipes pollicipes*: Linking to oceanographic variability. *Limnology and Oceanography* **66** (6), 2309–2318, doi:10.1002/lno.11755

Fernández de Larrinoa, P. & Cedenilla, M.Á. 2003. Human disturbance at the Cabo Blanco monk seal colony. *The Monachus Guardian* 6 (1), 2.

Fernández-Rodríguez, C., Bejega-García, V. & González-Gómez-de-Agüera., E. 2014. 12- Shellfish gathering during the iron age and roman times in the northwest of the Iberian Península. *Archaeomalacology: Shells in the Archaeological Record*, 2666: 135–145.

Figueira, M. 2015. Disponibilidade larvar, recrutamento, estrutura dimensional e crescimento de percebes (*Pollicipes pollicipes*) no Cabo de Sines. Master Thesis, University of Évora, Portugal.

Fischer-Piette, E. 1936. Études sur la biogéographie intercotidale des deux rives de la Manche. *Journal of the Linnean Society of London, Zoology* **40** (270), 181–272, doi:10.1111/j.1096-3642.1936.tb01683z.x

Fisheries and Oceans Canada. 2021. *Pacific Region Five Nations Multi-Species Fishery Management Plan*. Vancouver, Canada: Fisheries and Oceans Canada.

Flammang, P., Michel, A., van Cauwenberge, A., Alexandre, H. & Jangoux, M. 1998. A study of the temporary adhesion of the podia in the sea star *Asterias rubens* (Echinodermata, Asteroidea) through their footprints. *Journal of Experimental Biology* **201** (16), 2383–2395, doi:10.1242/jeb.201.16.2383

Fletcher, G. 2011. *Pollicipes Polymerus – Nakwakto Variety of Goose-Neck Barnacle-The Race Rocks Taxonomy*. Online. https://racerocks.ca/pollicipes-polymerus-nakwakto-variety-of-goose-neck-barnacle-the-race-rocks-taxonomy/ (Acessed 1 July 2021).

Foster, B.A. 1979. The marine fauna of New Zealand: Barnacles (Cirripedia: Thoracica). *New Zealand Oceanographic Institute* **69**, 1–160.

Foster, M., Neushul, M. & Zingmark, R. 1971. The Santa Barbara oil spill part 2: Initial effects on intertidal and kelp bed organisms. *Environmental Pollution* **2**, 115–134.

Franco, S.C. 2014. Aquaculture of stalked barnacles (*Pollicipes pollicipes*). PhD Thesis, University of Newcastle, United Kingdom.

Franco, S.C., Aldred, N., Cruz, T. & Clare, A. 2016. Modulation of gregarious settlement of the stalked barnacle, *Pollicipes pollicipes*: A laboratory study. *Scientia Marina* **80** (2), 217–228, doi:10.3989/scimar.04342.01A

Franco, S.C., Aldred, N., Cruz, T. & Clare, A. 2017. Effects of culture conditions on larval growth and survival of stalked barnacles (*Pollicipes pollicipes*). *Aquaculture Research* **48** (6), 2920–2933, doi:10.1111/are.13125

Franco, S.C., Aldred, N., Sykes, A.V., Cruz, T. & Clare, A.S. 2015. The effects of rearing temperature on reproductive conditioning of stalked barnacles (*Pollicipes pollicipes*). *Aquaculture* **448**, 410–417, doi:10.1016/J.AQUACULTURE.2015.06.015

Frank, P.W. 1982. Effects of winter feeding on limpets by black oystercatchers, *Haematopus bachmani*. *Ecology* **63** (5), 1352–1362.

Freire, J. & García-Allut, A. 2000. Socioeconomic and biological causes of management failures in European artisanal fisheries: The case of Galicia (NW Spain). *Marine Policy* **24** (5), 375–384, doi:10.1016/S0308-597X(00)00013-0

Fyhn, H.J., Petersen, J.A. & Johansen, K. 1972. Eco-physiological studies of an intertidal crustacean, *Pollicipes polymerus* (Cirripedia, Lepadomorpha) I. Tolerance to body temperature change, desiccation and osmotic stress. *The Journal of Experimental Biology* **57**, 83–102.

Fyhn, H.J., Petersen, J.A. & Johansen, K. 1973. Heart activity and high-pressure circulation in cirripedia. *Science* **180** (4085), 513–515, doi:10.1126/science.180.4085.513

Fyhn, U.E.H. & Costlow, J.D. 1976. A histochemical study of cement secretion during the intermolt cycle in barnacles. *The Biological Bulletin* **150** (1), 47–56.

Gagne, A., Picco, C., Rutherford, D. & Rogers, J. 2016. Update to the assessment framework for goose barnacles (Ca?inwa; *Pollicipes polymerus*) incorporating local ecological knowledge and advancements in technology in Clayoquot Sound off the west coast of Canada. Vancouver, Canada: Fisheries and Oceans Canada.

Gale, A.S. & Sørensen, A.M. 2015. Taxonomy and palaeoecology of thoracican cirripedes (Crustacea) from a Campanian rocky shoreline at Ivö Klack, southern Sweden. *Cretaceous Research* **54**, 212–242, doi:10.1016/j.cretres.2014.09.004

García-Escárzaga, A., Gutiérrez-Zugasti, I., González-Morales, M.R. & Cobo-García, A. 2017. Shells and humans: Molluscs and other coastal resources from the earliest human occupations at the mesolithic shell midden of El Mazo (Asturias, northern Spain). *Papers from the Institute of Archaeology* **27** (1), doi:10.5334/pia-481

García-Negro, M.C., Villasante, S., Carballo Penela, A. & Rodríguez Rodríguez, G. 2009. Estimating the economic impact of the Prestige oil spill on the Death coast (NW Spain) fisheries. *Marine Policy* **33** (1), 8–23, doi:10.1016/j.marpol.2008.03.011

Garm, A. 2004a. Mechanical functions of setae from the mouth apparatus of seven species of decapod crustaceans. *Journal of Morphology* **260**, 85–100.

Garm, A. 2004b. Revising the definition of the crustacean seta and setal classification system based on examinations of the mouthpart setae of seven species of decapods. *Zoological Journal of the Linnean Society* **142**, 233–252.

Geiger, K.J., Rivera, A., Cruz, T., Davoult, D., Dubert, J., Feis, M., Fernandes, J.N., Fernández, C., García-Flórez, L., Jacinto, D., Jollivet, D., Macho, G., Mateo, E., Mateus, D., Morán, P., Muñiz, C., Nicolle, A., Nolasco, R., Parrondo, M., Queiroga, H., Rico, J., Sousa, A., Román, S., Silva, T., Thiébaut, E., Vázquez, E. & Acuña J.L. 2022. Coping with poachers in European stalked barnacle fisheries: Insights from a stakeholder workshop. *Marine Policy* **135**, 104826, doi:10.1016/j.marpol.2021.104826

Gibaja, J.F., Carvalho, A.F., Rojo, M., Garrido, R. & García, I. 2012. Production and subsistence strategies at El Zafrín (Chafarinas Islands, Spain): New data for the early Neolithic of North-West Africa. *Journal of Archaeological Science* **39** (10), 3095–3104, doi:10.1016/j.jas.2012.04.042

Giesel, J.T. 1968. An analysis of the maintenance and control of a polymorphism in the limpet *Acnaea digitalis* eschscholtz. PhD Thesis, University of Oregon. Oregon.

Giesel, J.T. 1969. Factors influencing the growth and relative growth of *Acmaea digitalis*, a limpet. *Ecology* **50** (6), 1084–1087, doi:10.2307/1936900

Giesel, J.T. 1970. On the maintenance of a shell pattern and behavior polymorphism in *Acmaea digitalis*, a limpet. *Evolution* **24** (1), 98, doi:10.2307/2406717

Girard, S. 1982. Etude du stock de pouces pieds de Belle-Ile et de son exploitation. *Mémoire de fin d'études. ENSAR*. "Unpublished report", 79.

Gofas, S., Goutayer, J., Luque, A.A., Salas, C. & Templado, J. 2014. Espacio marino de Alborán. Proyecto LIFE+ INDEMARES. Fundación Biodiversidad del Ministerio de Agricultura, Alimentación y Medio Ambiente. Gobierno de España, Spain.

Goldberg, H. 1984. Posibilidades de cultivo de percebe, *Pollicipes cornucopia* Leach, en sistemas flotantes. *Instituto Español de Oceanografia* **19**, 4–13.

González, J.A., Martín, L., Herrera, R., González-Lorenzo, G., Espino, F., Barquín-Diez, J. & Southward, A.J. 2012. Cirripedia of the Canary islands: Distribution and ecological notes. *Journal of the Marine Biological Association of the United Kingdom* **92** (1), 129–141, doi:10.1017/S002531541100066X

Gruvel, A. 1893. Contribution à l'étude des cirrhipèdes. *Archives de Zoologie Expérimentale et Générale, Serie* **3** (1), 401–610.

Gruvel, A. 1905. *Monographie des Cirrhipèdes ou Thécostracés*. Paris: Masson.

Guilelrmo9111. 2015. *Percebes en Salango, islote los Ahorcado, Manabí, Ecuador*. Online. https://www.youtube.com/watch?v=9zkNYlOucLQ&t=35s (Accessed 1 June 2021).

Gutiérrez-Cobo, M.B., Bidegain, G. & Juanes, J.A. 2012. Reclutamiento, crecimiento y estructura de tallas de *Pollicipes pollicipes* en la costa de Cantabria: Consideraciones para la gestión de la pesca. In *Oral Presentation*.

Gutiérrez-Zugasti, F.I.G. 2011. The use of echinoids and crustaceans as food during the pleistocene-holocene transition in northern Spain: Methodological contribution and dietary assessment. *Journal of Island and Coastal Archaeology* **6** (1), 115–133, doi:10.1080/15564894.2010.487421.

Gutiérrez-Zugasti, I., Tong, E., García-Escárzaga, A., Cuenca-Solana, D., Bailey, G.N. & González-Morales, M.R. 2016. Collection and consumption of echinoderms and crustaceans at the mesolithic shell midden site of El Mazo (northern Iberia): Opportunistic behaviour or social strategy? *Quaternary International* **407**, 118–130, doi:10.1016/j.quaint.2015.11.149

Gutiérrez, N.L., Hilborn, R. & Defeo, O. 2011. Leadership, social capital and incentives promote successful fisheries. *Nature* **470** (7334), 386–389, doi:10.1038/nature09689

Gutiérrez, R.M. & Cabrera, E. 2012. *La pesca ribereña de Guerrero*. Santa Cruz Atoyac, México: Instituto Nacional de Pesca, 86.

Gutiérrez, R.M. & Cabrera, E. 2019. *Especies marinas de valor comercial en el Estado de Guerrero – II*. Instituto Nacional de Pesca. México.

Hagerty, M.L., Reyns, N., Pineda, J. & Govindarajan, A.F. 2019. Diversity and distribution of nearshore barnacle cyprids in southern California through the 2015–16 El Niño. *PeerJournal* **2019** (7), 1–21, doi:10.7717/peerj.7186

Hardin, G. 1960. The competitive exclusion principle. *Science* **131** (3409), 1292–1297.

Harris, D.J., Maxson, L.S., Braithwaite, L.. & Crandall, K.A. 2000. Phylogeny of the *Thoracican barnacles* based on 18S rDNA sequences. *Journal of Crustacean Biology* **20** (2), 393–398.

Hartwick, B. 1981. Size gradients and shell polymorphism in limpets with consideration of the role of predation. *The Veliger* **23** (3), 254–264, doi:10.18941/venusjjma.21.1_118_2

Hawkins, S.J. 1983. Interactions of Patella and Macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Biology and Ecology* **71**, 55–72, doi:10.1126/science.192.4237.364-a

Hawkins, S.J., Evans, A.J., Mieszkowska, N., Adams, L.C., Bray, S., Burrows, M.T., Firth, L.B., Genner, M.J., Leung, K.M.Y., Moore, P.J., Pack, K., Schuster, H., Sims, D.W., Whittington, M. & Southward, E.C. 2017. Distinguishing globally-driven changes from regional- and local-scale impacts: The case for long-term and broad-scale studies of recovery from pollution. *Marine Pollution Bulletin* **124** (2), 573–586, doi:https://doi.org/10.1016/j.marpolbul.2017.01.068

Helms, A. 2004. Living on the edge: Juvenile recruitment and growth of the gooseneck barnacle. Masters Thesis, University of Oregon, Charleston.

Hilborn, R., Orensanz, J.M. & Parma, A.M. 2005. Institutions, incentives and the future of fisheries. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360** (1453), 47–57, doi:10.1098/rstb.2004.1569

Hilgard, G.H. 1960. A study of reproduction in the intertidal barnacle, *Mitella polymerus*, in Monterey bay, California. *The Biological Bulletin* **119** (2), 169–188, doi:10.2307/1538919

Höfer, J., Muñiz, C., Weidberg, N., García-Flórez, L. & Acuña, J.L. 2017. High densities of stalked barnacle larvae (*Pollicipes pollicipes*) inside a river plume. *Journal of Plankton Research* **39** (2), 316–329, doi:10.1093/plankt/fbw093

Hoffman, D.L. 1984. Size-frequency distribution patterns of the juvenile stages of the pendunculate barnacle, *Pollicipes polymerus* Sowerby, 1833 (Cirripedia, Lepadomorpha). *Crustaceana* **46** (3), 295–299.

Hoffman, D.L. 1988. Settlement and growth of the pedunculate barnacle *Pollicipes polymerus* Sowerby in an intake seawater system at the scripps Institution of Oceanography, La Jolla, California! *Pacific Science* **42**, 3–4.

Hoffman, D.L. 1989. Settlement and recruitment patterns of a pedunculate barnacle, *Pollicipes polymerus* Sowerby, off La Jolla, California. *Journal of Experimental Marine Biology and Ecology* **125** (2), 83–98, doi:10.1016/0022-0981(89)90036-1

Howard, G.K. & Scott, H.C. 1959. Predaceous feeding in two common gooseneck barnacles. *Science* **129** (3350), 717–718, doi:10.1126/science.129.3350.717

Hughes, R.N. & Griffiths, C.L. 1988. Self-thinning in barnacles and mussels: The geometry of packing. *The American Naturalist* **132** (4), 484–491.

Hui, E. 1983. Observations on cirral activity in juvenile pollicipoid barnacles (Cirripedia, Lepadomorpha). *Crustaceana* **45** (3), 317–318, doi:10.1163/156854083x00406

Hutterer, R., Schröder, O. & Linstädter, J. 2021. Food and ornament: Use of shellfish at Ifri Oudadane, a holocene settlement in NE Morocco. *African Archaeological Review* **38** (1), 73–94, doi:10.1007/s10437-020-09409-3

Ibanez-Erquiaga, B., Pacheco, A.S., Rivadeneira, M.M. & Tejada, C.L. 2018. Biogeographical zonation of rocky intertidal communities along the coast of Peru (3.5–13.5 S Southeast Pacific). *PLoS One* **13** (11), 1–19, doi:10.1371/journal.pone.0208244

IMARPE. 2005. *Catálogo de recursos marinos exportables de la región Lambayaque - "Percebe"* Pollicipes elegans. Online. https://docplayer.es/38407224-Dosidicus-gigas-calamar-gigante-pota.html (Accessed on 1 July 2021).

Inaturalist.org. 2021. *Pollicipes*. Oline. https://www.inaturalist.org/observations?place_id=any&taxon_id=48788 (Accessed 1 June 2021)

Ip, J.C.H., Qiu, J.W. & Chan, B.K.K. 2021. Genomic insights into the sessile life and biofouling of barnacles (Crustacea: Cirripedia). *Heliyon* **7** (6), e07291, doi:10.1016/j.heliyon.2021.e07291

Jacinto, D. 2016. Living on the intertidal/subtidal edge: Ecology of the stalked barnacle *Pollicipes pollicipes* and of the sea urchin *Paracentrotus lividus*. PhD Thesis, University of Évora, Portugal.

Jacinto, D. & Cruz, T. 2016. Predicting *Pollicipes pollicipes* (Crustacea: Cirripedia) abundance on intertidal rocky shores of SW Portugal: A multi-scale approach based on a simple fetch-based wave exposure index. *Scientia Marina* **80** (2), 229–236, doi:10.3989/scimar.04330.27A

Jacinto, D., Cruz, T., Silva, T. & Castro, J.J. 2010. Stalked barnacle (*Pollicipes pollicipes*) harvesting in the Berlengas Nature Reserve, Portugal: Temporal variation and validation of logbook data. *ICES Journal of Marine Science* **67** (1), 19–25, doi:10.1093/icesjms/fsp226

Jacinto, D., Cruz, T., Silva, T. & Castro, J.J. 2011. Management of the stalked barnacle (*Pollicipes pollicipes*) fishery in the Berlengas Nature Reserve (Portugal): Evaluation of bag and size limit regulation measures. *Scientia Marina* **75** (3), 439–445.

Jacinto, D., Penteado, N., Pereira, D., Sousa, A. & Cruz, T. 2015. Growth rate variation of the stalked barnacle *Pollicipes pollicipes* (Crustacea: Cirripedia) using calcein as a chemical marker. *Scientia Marina* **79** (1), 117–123, doi:10.3989/scimar.04135.08B

Jamieson, G.S., Dixon, S. & Lauzier, R. 2001. Initial evaluation of community structure in goose barnacle (P*ollicipes polymerus*) and sea mussel (*Mytilus californianus*) beds off the west coast of Vancouver island, British Columbia. Vancouver, Canada: *Canadian Science Advisory Secretariat. Research Document 2001/124*, 1–59.

Jamieson, G.S., Lauzier, R. & Gillespie, G. 1999. Phase 1 Framework for undertaking an ecological assessment of the outer coast rocky intertidal zone. Vancouver, Canada: *Canadian Stock Assessment Secretariat. Research Document 99/209*, 1–33.

Jamieson, G.S. & Levings, C.O. 2001. Marine protected areas in Canada - Implications for both conservation and fisheries management. Canada: *Canadian Journal of Fisheries and Aquatic Sciences* **58** (1), 138–156, doi:10.1139/cjfas-58-1-138

Jensen, P.G., Moyse, J., Høeg, J. & Al-Yahya, H. 1994. Comparative SEM studies of lattice organs: Putative sensory structures on the carapace of larvae from Ascothoracida and Cirripedia (Crustacea Maxillopoda Thecostraca). *Acta Zoologica* **75** (2), 125–142, doi:10.1111/j.1463-6395.1994.tb01117.x

Jesus, D. 2004. Gestão do percebe (*Pollicipes pollicipes*) no Parque Natural do Sudoeste Alentejano e Costa Vicentina. Master Thesis, University of Algarve, Portugal.

Jobe, A. 1968. A study of morphological variation in the limpet *Acmaea pelta*. *Veliger* **11** (Suppl.), 69–72.

Joncourt, Y. 2005. Étude socio-biologique appliquée à la gestion d'une pêcherie de loisir: cas des pouces-pieds (*Mitella pollicipes*) de Saint-Guénolé. Master Thesis, Université de Caen, France.

Jonker, J.L., Abram, F., Pires, E., Coelho, A.V., Grunwald, I. & Power, A.M. 2014. Adhesive proteins of stalked and acorn barnacles display homology with low sequence similarities. *PLoS One* **9** (10), doi:10.1371/journal.pone.0108902

Jonker, J.L., Morrison, L., Lynch, E.P., Grunwald, I., von Byern, J. & Power, A.M. 2015. The chemistry of stalked barnacle adhesive (*Lepas anatifera*). *Interface Focus* **5** (1), 1–13, doi:10.1098/rsfs.2014.0062

Jonker, J.L., von Byern, J., Flammang, P., Klepal, W. & Power, A.M. 2012. Unusual adhesive production system in the barnacle *Lepas anatifera*: An ultrastructural and histochemical investigation. *Journal of Morphology* **273** (12), 1377–1391, doi:10.1002/jmor.20067

Kaji, T. & Palmer, A.R. 2017. How reversible is development? Contrast between developmentally plastic gain and loss of segments in barnacle feeding legs. *Evolution* **71** (3), 756–765, doi:10.1111/EVO.13152

Kallouche, M., Bouras, D. & B, K.H. 2014. Faunal composition, distribution and richness of the Oran's intertidal coastal zone (Mediterranean Sea, Algeria). *Journal of Biodiversity and Environmental Sciences* **5** (4), 122–132.

Kameya, A. & Zeballos, J. 1988. Distribución y densidad de percebes *Pollicipes elegans* (Crustacea: Cirripedia) en el mediolitoral peruano (Yasila, Paita; Chilca, Lima). *Boletín Instituto del Mar del Perú* **12** (1), 22.

Kamino, K. 2006. Barnacle underwater attachment. In *Biological Adhesives*. A.M. Smith & J.A. Callow (eds). Berlin: Springer-Verlag, 145–166.

Kamino, K. 2013. Mini-review: Barnacle adhesives and adhesion. *Biofouling* **29** (6), 735–749, doi:10.1080/08927014.2013.800863

Kamino, K., Inoue, K., Maruyama, T., Takamatsu, N., Harayama, S. & Shizuri, Y. 2000. Barnacle cement proteins. *Journal of Biological Chemistry* **275** (35), 27360–27365, doi:10.1016/s0021-9258(19)61519-x

Kamino, K., Nakano, M. & Kanai, S. 2012. Significance of the conformation of building blocks in curing of barnacle underwater adhesive. *FEBS Journal* **279** (10), 1750–1760, doi:10.1111/j.1742–4658.2012.08552.x

Kay, M.C. 2002. Recruitment in the intertidal limpet *Lottia digitalis* (Patellogastropoda: Lottiidae) may be driven by settlement cues associated with adult habitat. *Marine Biology* **141** (3), 467–477, doi:10.1007/s00227-002-0846-1

Kelly, R.P. & Palumbi, S.R. 2010. Genetic structure among 50 species of the northeastern pacific rocky intertidal community. *PLoS ONE* **5** (1), doi:10.1371/journal.pone.0008594

Kim, J.-H., Kim, H., Kim, H., Chan, B.K.K., Kang, S. & Kim, W. 2019a. Draft genome assembly of a fouling barnacle, *Amphibalanus amphitrite* (Darwin, 1854): The first reference genome for thecostraca. *Frontiers in Ecology and Evolution* **7**, 465, doi:10.3389/FEVO.2019.00465

Kim, R.-O., Chan, B.K.K., Hou, B.K., Ju, S.J. & Kim, S.J. 2019b. Complete mitochondrial genome of the deep-water epibiotic stalked barnacle, *Glyptelasma annandalei* (Cirripedia, Lepadiformes, Poecilasmatidae). *Mitochondrial DNA Part B: Resources* **4** (1), 99–100, doi:10.1080/23802359.2018.1536487

Kim, S.J., Kang, H.M., Corbari, L. & Chan, B.K.K. 2018. First report on the complete mitochondrial genome of the deep-water scalpellid barnacle *Arcoscalpellum epeeum* (Cirripedia, Thoracica, Scalpellidae). *Mitochondrial DNA Part B: Resources* **3** (2), 1288–1289, doi:10.1080/23802359.2018.1532844

Kinne, O. 1970. *Marine Ecology, v. 1. Environmental Factors, Part 1. A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters*. New York: Wiley-Interscience.

Koehler, R. 1888. Recherches sur la structure du pedoncule des cirrhipedes. *Revue Biologique du Nord de la France Année* **1888** (2), 41–55.

Koehler, R. 1889. Recherches sur l'organisation des cirrhipédes (Lepadide et Balane). *Archives de Biologie* **9**, 311–402.

Kohlmeyer, J. & Kohlmeyer, E. 2013. *Marine Mycology: The Higher Fungi*. New York: Academic Press.

Kugele, M. & Yule, A.B. 1993. Mobility in lepadomorph barnacles. *Journal of the Marine Biological Association of the United Kingdom* **73** (3), 719–722, doi:10.1017/S0025315400033245

Kugele, M. & Yule, A.B. 1996. The larval morphology of *Pollicipes pollicipes* (Gmelin, 1790) (Cirripedia: Lepadomorpha) with notes on cypris settlement. *Scientia Marina* **60** (4), 469–480.

Kugele, M. & Yule, A.B. 2000. Active relocation in lepadomorph barnacles. *Journal of the Marine Biological Association of the United Kingdom* **80**, 103–111.

Lacombe, D. 1970. A comparative study of the cement glands in some balanid barnacles (Cirripedia, Balanidae). *The Biological Bulletin* **139** (1), 164–179, doi:10.2307/1540134

Lacombe, D. & Liguori, V.R. 1969. Comparative histological studies of the cement apparatus of *Lepas anatifera* and *Balanus tintinnabulum*. *The Biological Bulletin* **137** (1), 170–180, doi:10.2307/1539940

Ladah, L.B., Tapia, F.J., Pineda, J. & López, M. 2005. Spatially heterogeneous, synchronous settlement of *Chthamalus* species larvae in northern Baja California. *Marine Ecology Progress Series* **302**, 177–185, doi:10.3354/meps302177

Ladines, D.M. 2018. Evaluación poblacional de *Pollicipes elegans* en la zona rocosa de Puerto Engabao, Cantón Playas, Provincia del Guayas. Honors Thesis, Universidad estatal Peninsula Santa de Elena, Ecuador.

Laguna, J.E. 1990. Shore barnacles (Cirripedia, Thoracica) and a revision of their provincialism and transition zones in the tropical eastern Pacific. *Bulletin of Marine Science* **46** (2), 406–424.

Lamb, A. & Hanby, B.P. 2005. *Marine Life of the Pacific Northwest*. Madeira Park, British Columbia: Harbour Publishing.

Lamont, E.I. & Emlet, R.B. 2018. Permanently fused setules create unusual folding fans used for swimming in cyprid larvae of barnacles. *The Biological Bulletin* **235** (3), 185–194, doi:10.1086/700084

Lauzier, R.B. 1999a. *Framework for Goose Barnacle (*Pollicipes polymerus *Sowerby, 1833) Fishery in Waters Off the West Coast of Canada*. Vancouver, Canada: R.B. Canadian Stock Assessment Secretariat.

Lauzier, R.B. 1999b. *A Review of the Biology and Fisheries of the Goose Barnacle* (Pollicipes polymerus *Sowerby, 1833)*. Vancouver, Canada: R.B. Canadian Stock Assessment Secretariat.

le Mao, P., Godet, L., Fournier, J., Desroy, N., Gentil, F. & Tiebout, H. 2020. *Atlas de la Faune Marine Invertébrée du Golfe Normano-Breton - Volume 4 – Arthropodes*. Éditions de la Station biologique de Roscoff. Roscoff: Station biologique de Roscoff.

Lessard, J., Osborne, J., Lauzier, R., Jamieson, G. & Harbo, R. 2003. Applying local and scientific knowledge to the establishment of a sustainable fishery: The west coast Vancouver island goose barnacle fishery experience. *Putting Fishers' Knowledge to Work* **11** (1), 36–43.

Lewis, C.A. 1975a. Development of the gooseneck barnacle *Pollicipes polymerus* (Cirripedia: Lepadomorpha): Fertilization through settlement. *Marine Biology* **32** (2), 141–153, doi:10.1007/BF00388507

Lewis, C.A. 1975b. Some observations of factors affecting embryonic and larval growth of *Pollicipes polymerus* (Cirripedia: Lepadomorpha) *in vitro*. *Marine Biology* **32** (2), 127–139, doi:10.1007/BF00388506

Lewis, C.A. 1981. Juvenile to adult shift in feeding strategies in the pedunculate barnacle *Pollicipes polymerus* (Sowerby)(Cirripedia, Lepadomorpha). *Crustaceana* **41**, 14–20.

Lewis, C.A. & Chia, F. 1981. Growth, fecundity, and reproductive biology in the pedunculate cirripede *Pollicipes polymerus* at San Juan Island, Washington. *Canadian Journal of Zoology* **59** (6), 893–901, doi:10.1139/z81-128

Li, N.K. & Denny, M.W. 2004. Limits to phenotypic plasticity: Flow effects on barnacle feeding appendages. *Biological Bulletin* **206** (3), 121–124, doi:10.2307/1543635

Liang, C., Li, Y., Liu, Z., Wu, W. & Hu, B. 2015. Protein aggregation formed by recombinant cp19k homologue of *Balanus albicostatus* combined with an 18 kDa N-terminus encoded by pET-32a(+) plasmid having adhesion strength comparable to several commercial glues. *PLoS One* **10** (8), 1–18, doi:10.1371/journal.pone.0136493

Liang, C., Strickland, J., Ye, Z., Wu, W., Hu, B. & Rittschof, D. 2019. Biochemistry of barnacle adhesion: An updated review. *Frontiers in Marine Science* **6** (September), 1–20, doi:10.3389/fmars.2019.00565

Lim, J.T. & Hwang, U.W. 2007. The complete mitochondrial genome of *Pollicipes mitella* (Crustacea, Maxillopoda, Cirripedia): Non-monophylies of maxillopoda and crustacea arthropod phylogeny and centipede genomics View project. *Molecules and Cells* **22** (3), 314–322.

Lin, G. & Rao, X. 2016. Metamorphosis of the pedunculate barnacle *Capitulum mitella* Linnaeus, 1758 (Cirripedia: Scalpelliformes). *Journal of the Marine Biological Association of the United Kingdom* **97** (8), 1643–1650.

Lin, H.C., Wong, Y.H., Sung, C.H. & Chan, B.K.K. 2021. Histology and transcriptomic analyses of barnacles with different base materials and habitats shed lights on the duplication and chemical diversification of barnacle cement proteins. *BMC Genomics* **22**, 783.

Lin, H.C., Wong, Y.H., Tsang, L.M., Chu, K.H., Qian, P.Y. & Chan, B.K.K. 2014. First study on gene expression of cement proteins and potential adhesion-related genes of a membranous-based barnacle as revealed from next-generation sequencing technology. *Biofouling* **30** (2), 169–181, doi:10.1080/08927014.2013.853051

Lindberg, D.R. & Pearse, J.S. 1990. Experimental manipulation of shell color and morphology of the limpets *Lottia asmi* (Middendorff) and *Lottia digitalis* (Rathke) (Mollusca: Patellogastropoda). *Journal of Experimental Marine Biology and Ecology* **140** (3), 173–185, doi:10.1016/0022-0981(90)90125-V

Liu, X., Liang, C., Zhang, X., Li, J., Huang, J., Zeng, L., Ye, Z., Hu, B. & Wu, W. 2017. Amyloid fibril aggregation: An insight into the underwater adhesion of barnacle cement. *Biochemical and Biophysical Research Communications* **493** (1), 654–659, doi:10.1016/J.BBRC.2017.08.136

Lobo-da-Cunha, A., Alves, Â., Oliveira, E. & Cunha, I. 2017. The cement apparatus of the stalked barnacle *Pollicipes pollicipes*. *Marine Biology* **164** (1), 1–8, doi:10.1007/s00227-016-3047-z

López, B.A. 2020. Marginal marine crustacean fisheries. In *Fisheries and Aquaculture*, G. Lovrich & M. Thiel (eds). Oxford: Oxford University Press.

López, D.A., López, B.A., Burgos, I.C., Arriagada, S.E. & González, M.L. 2007. Consequences of base modification in hummocks of the barnacle *Austromegabalanus psittacus*. *New Zealand Journal of Marine and Freshwater Research* **41** (3), 291–298, doi:10.1080/00288330709509916

López, D.A., López, B.A., Christopher, K.P. & Isidro, E.J. 2012. Potency of barnacle in aquaculture industry. *Aquaculture*, doi:10.5772/30396

López, D.A., López, B.A., Pham, C.K., Isidro, E.J. & de Girolamo, M. 2010. Barnacle culture: Background, potential and challenges. *Aquaculture Research* **41** (10), 1–9, doi:10.1111/j.1365–2109.2010.02508.x

López, J.C. 1998–2000. El yacimiento prehistórico de la cueva de Kobeaga II (Ispaster, Bizkaia): cazadores-recolectores en el País Vasco atlántico durante el VIII y VII milenio b. p. *Illunzar* **4**, 83–162.

López, M. 2018. Elaboración de propuestas gastronómicas a partir del percebe (*Pollicipes Pollicipes*). Honor Thesis, Universidad de Guayaquil, Ecuador.

Lozano-Cortés, D.F. & Londoño-Cruz, E. 2013. Checklist of barnacles (Crustacea; Cirripedia: Thoracica) from the Colombian Pacific. *Marine Biodiversity* **43** (4), 463–471, doi:10.1007/s12526-013-0175-2

Machado, A.M., Sarropoulou, E., Castro, L.F.C., Vasconcelos, V. & Cunha, I. 2019. An important resource for understanding bio-adhesion mechanisms: Cement gland transcriptomes of two goose barnacles, *Pollicipes pollicipes* and *Lepas anatifera* (Cirripedia, Thoracica). *Marine Genomics* **45**, 16–20, doi:10.1016/J.MARGEN.2018.11.001

Macho, G. 2006. Ecología reproductiva y larvaria del percebe y otros cirrípedos en Galicia - Reproductive and larval ecology of barnacles in Galicia (NW Spain). PhD Thesis, University of Vigo, Spain.

Macho, G., Molares, J. & Vázquez, E. 2005. Timing of larval release by three barnacles from the NW Iberian Peninsula. *Marine Ecology Progress Series* **298** (February 2014), 251–260, doi:10.3354/meps298251

Macho, G., Naya, I., Freire, J., Villasante, S. & Molares, J. 2013. The key role of the barefoot fisheries advisors in the co-managed TURF system of galicia (NW Spain). *Ambio* **42** (8), 1057–1069, doi:10.1007/s13280-013-0460-0

Macho, G., Vázquez, E., Giráldez, R. & Molares, J. 2010. Spatial and temporal distribution of barnacle larvae in the partially mixed estuary of the Ría de Arousa (Spain). *Journal of Experimental Marine Biology and Ecology* **392** (1–2), 129–139, doi:10.1016/j.jembe.2010.04.017

Mahmoud, M.F. 1959a. The structure of the outer integument of some pedunculate cirripedes (barnacles). *Proceedings of the Egyptian Academy of Sciences* **14**, 61–69.

Mahmoud, M.F. 1959b. The development of new scales in *Pollicipes* and *Scalpellum*. *Proceedings of the Egyptian Academy of Sciences* **14**, 70–73.

Mahmoud, M.F. 1960. The moulting and the increase in length of the outer integument of pedunculate cirripedes. *Proceedings of the Egyptian Academy of Sciences* **15**, 1–10.

Mahon, R. 1997. Does fisheries science serve the needs of managers of small stocks in developing countries. *Canadian Journal of Fisheries and Aquatic Sciences* **54** (9), 2207–2213, doi:10.1139/f97-112

Marchant, S. 2014. Phylogenomics and historical biogeography of the gooseneck barnacle *Pollicipes elegans*. PhD Thesis, Clemson University, United States of America.

Marchant, S., Moran, A.L. & Marko, P.B. 2015. Out-of-the tropics or trans-tropical dispersal? The origins of the disjunct distribution of the gooseneck barnacle *Pollicipes elegans*. *Frontiers in Zoology* **12** (1), 1–16, doi:10.1186/s12983-015-0131-z

Marchinko, K.B. 2003. Dramatic phenotypic plasticity in barnacle legs (*Balanus glandula* Darwin): Magnitude, age dependence, and speed of response. *Evolution* **57** (6), 1281–1290, doi:10.1111/j.0014-3820.2003.tb00336.x

Marchinko, K.B. 2007. Feeding behavior reveals the adaptive nature of plasticity in barnacle feeding limbs. *Biological Bulletin* **213** (1), 12–15, doi:10.2307/25066613

Marchinko, K.B., Nishizaki, M.T. & Burns, K.C. 2004. Community-wide character displacement in barnacles: A new perspective for past observations. *Ecology Letters* **7**, 114–120, doi:10.1046/j.1461-0248.2003.00557.x

Marchinko, K.B. & Palmer, A.R. 2003. Feeding in flow extremes: Dependence of cirrus form on wave-exposure in four barnacle species. *Zoology* **106** (2), 127–141, doi:10.1078/0944-2006-00107

Marín, C. & Luengo, A. 1998. *Tenerife y el Mar*, I. Santa Cruz: Cabildo de Tenerife, UNESCO [ed.].

MARINe. 2021. *Pollicipes*. Online. http://rockyintertidal.cisr.ucsc.edu (Accessed 1 June 2021).

Marsh, C.P. 1986. Impact of avian predators on high intertidal limpet populations. *Journal of Experimental Marine Biology and Ecology* **104** (1–3), 185–201, doi:10.1016/0022-0981(86)90104-8

Mas, J., Ballesteros, E., Ballesteros, M. & Flores, A. 1996. Cartografiado y evaluación de las comunidades bentónicas de la isla de Alborán. *IX Simposio Ibérico de Estudios del Bentos Marino*, 226–227.

Mateus, D. 2015. Crescimento de juvenis de percebe (*Pollicipes pollicipes*) em diferentes condições ambientais. Honor Thesis, University of Évora, Portugal.

Mateus, D. 2017. Variabilidade espacial e temporal do recrutamento de *Pollicipes pollicipes* na região de Sines. Master Thesis, University of Aveiro, Portugal.

Matthews, K.J., Maloney, K.T., Zahirovic, S., Williams, S.E., Seton, M. & Mueller, R.D. 2016. Global plate boundary evolution and kinematics since the late Paleozoic. *Global and Planetary Change* **146**, 226–250, doi:10.1016/j.gloplacha.2016.10.002

McDaniel, N.G. 1985. Goose barnacles. *Diver Magazine* **11** (1), 45–46.

McEvilly, P. 2011. A look at some components of the adhesive of the pedunculate barnacles *Dosima fascicularis*, *Lepas anatifera*, *Conchoderma auritum*, *Lepas pectinata* and *Pollicipes pollicipes*. Master Thesis, National University of Ireland, Galway.

Meese, R.J. 1993. Effects of predation by birds on gooseneck barnacle *Pollicipes polymerus* Sowerby distribution and abundance. *Journal of Experimental Marine Biology and Ecology* **166** (1), 47–64, doi:10.1016/0022-0981(93)90078-3

Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A. & Yamada, S.B. 1994. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* **64** (3), 249–286, doi:10.2307/2937163

Menge, B.A., Hacker, S.D., Freidenburg, T., Lubchenco, J., Craig, R., Rilov, G., Noble, M. & Richmond, E. 2011. Potential impact of climate-related changes is buffered by differential responses to recruitment and interactions. *Ecological Monographs* **81** (3), 493–509, doi:10.1890/10-1508.1

Mercurio, K.S., Palmer, A.R. & Lowell, R.B. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic intertidal limpets. *Ecology* **66** (5), 1417–1425, doi:10.2307/1938004

Meusemann, K., von Reumont, B.M., Simon, S., Roeding, F., Strauss, S., Kück, P., Ebersberger, I., Walzl, M., Pass, G., Breuers, S., Achter, V., von Haeseler, A., Burmester, T., Hadrys, H., Wägele, J.W. & Misof, B. 2010. A phylogenomic approach to resolve the arthropod tree of life. *Molecular Biology and Evolution* **27** (11), 2451–2464, doi:10.1093/molbev/msq130

Miller, L.P. 2007. Feeding in extreme flows: Behavior compensates for mechanical constraints in barnacle cirri. *Marine Ecology Progress Series* **349**, 227–234, doi:10.3354/meps07099

Miller, L.P., Harley, C.D.G. & Denny, M.W. 2009. The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. *Functional Ecology* **23** (4), 756–767, doi:10.1111/j.1365-2435.2009.01567.x

Miller, K.M. & Roughgarden, J. 1994. Descriptions of the larvae of *Tetraclita rubescens* and *Megabalanus californicus* with a comparison of the common barnacle larvae of the central California coast. *Journal of Crustacean Biology* **14** (3), 579–600, doi:10.1163/193724094X00146

Miner, B.G. 2002. Are the two physiological races of *Pollicipes polymerus* (Cirripedia) genetically divided along the California coast? *Invertebrate Biology* **121** (2), 158–162.

Molares, J. 1994. Estudio del ciclo biologico del percebe (*Pollicipes cornucopia* Leach) de las costas de Galicia. PhD Thesis, Xunta de Galicia, España.

Molares, J. & Freire, J. 2003. Development and perspectives for community-based management of the goose barnacle (*Pollicipes pollicipes*) fisheries in Galicia (NW Spain). *Fisheries Research* **65** (1–3), 485–492.

Molares, J., Parada, J.M., Navarro-Pérez, E. & Fernández, A. 2008. Variabilidad interanual de las ventas de los principales recursos marisqueros de Galicia y su relación con las condiciones ambientales. *Revista Galega de Recursos Marinos* **2** (1), 1–42.

Molares, J., Tilves, F. & Pascual, C. 1994a. Larval development of pedunculate barnacle *Pollicipes cornucopia* (Cirripedia: Scalpellomorpha) reared in the laboratory. *Marine Biology* **120**, 261–264.

Molares, J., Tilves, F., Pascual, C. & Quintana, R. 1987. Método de determinación del tamaño y calidad del percebe (*Pollicipes corunucopia*, Leach). *II Congreso Nacional de Acuicultura* **12**, 331–336.

Molares, J., Tilves, F., Quintana, R., Rodríguez, S. & Pascual, C. 1994b. Gametogenesis of *Pollicipes cornucopia* (Cirripedia: Scalpellomorpha) in north-west Spain. *Marine Biology* **120** (4), 553–560, doi:10.1007/BF00350075

Monsalve, E. 2016. Categorización de especies marinas de mayor importancia comercial de la pesqueria artesanal en la región Lambayeque según los criterios de la lista roja regional de la UICN. Honor Thesis. Universidad Nacional "Pedro Ruiz Gallo", Perú.

Moore, P.J., Thompson, R.C. & Hawkins, S.J. 2011. Phenological changes in intertidal conspecific gastropods in response to climate warming. *Global Change Biology* **17** (2), 709–719, doi:10.1111/j.1365-2486.2010.02270.x

Mora-Barboza, C. & Sibaja-Cordero, J.A. 2018. Occurrence, demography, and habitat features of *Pollicipes elegans* (Pollicipedidae: Scalpelliformes), an amphitropical species at a rocky intertidal shore, Costa Rica. *Pacific Science* **72** (4), 449–461, doi:10.2984/72.4.5

Moreno, R., Jover, L., Munilla, I., Velando, A. & Sanpera, C. 2010. A three-isotope approach to disentangling the diet of a generalist consumer: The yellow-legged gull in northwest Spain. *Marine Biology* **157** (3), 545–553, doi:10.1007/s00227-009-1340-9

Morgan, S.G. & Fisher, J.L. 2010. Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Marine Ecology Progress Series* **404**, 109–126, doi:10.3354/meps08476

Morgan, S.G., Shanks, A.L., MacMahan, J., Reniers, A.J.H.M., Griesemer, C.D., Jarvis, M. & Fujimura, A.G. 2017. Surf zones regulate larval supply and zooplankton subsidies to nearshore communities. *Limnology and Oceanography* **62** (6), 2811–2828, doi:10.1002/lno.10609

Mori, Y., Urushida, Y., Nakano, M., Uchiyama, S. & Kamino, K. 2007. Calcite-specific coupling protein in barnacle underwater cement. *FEBS Journal* **274** (24), 6436–6446, doi:10.1111/j.1742-4658.2007.06161.x

Moss, M.L. & Erlandson, J.M. 2001. The archaeology of obsidian cove, Suemez Island, southeast Alaska. *Artic Anthropology* **38** (1), 27–47.

Moss, M.L. & Erlandson, J.M. 2010. Diversity in north Pacific shellfish assemblages: The barnacles of Kit'n'Kaboodle cave, Alaska. *Journal of Archaeological Science* **37** (12), 3359–3369, doi:10.1016/J.JAS.2010.08.004

Mougne, C. & Dupont, C. 2020. Exploitation et utilisation des invertébrés marins durant l'âge du Bronze sur la façade Manche-Atlantique française. *Entre terres et eaux Les sites littoraux de l'âge du Bronze : spécificités et relations avec l'arrière-pays Actes de la séance de la Société préhistorique française d'Agde (20-21 octobre 2017)* **14**, 355–376.

Murphy, P. 2014. *Lottia austrodigitalis* revisited: Are acomorphs incipient species? *The veliger* **51** (4), 208–215, doi:10.18941/venusjjma.21.1_118_2

Murphy, P.C. 1978. *Collisella austrodigitalis* sp. nov.: A sibling species of limpet (Acmaeidae) discovered by electrophoresis. *The Biological Bulletin* **155** (1), 193–206, doi:10.2307/1540875

Nakano, M. & Kamino, K. 2015. Amyloid-like conformation and interaction for the self-assembly in barnacle underwater cement. *Biochemistry* **54** (3), 826–835, doi:10.1021/bi500965f

Naldrett, M.J. 1993. The importance of sulfur cross-links and hydrophobic interactions in the polymerization of barnacle cement. *Journal of the Marine Biological Association of the United Kingdom* **73** (3), 689–702, doi:10.1017/S0025315400033221

Naldrett, M.J. & Kaplan, D.L. 1997. Characterization of barnacle (*Balanus eburneus* and *B. cenatus*) adhesive proteins. *Marine Biology* **127** (4), 629–635, doi:10.1007/S002270050053

Navarrete, C. 2009. Análisis de las estrategias y gestión de la pesqueria del percebe (*Pollicipes pollicipes*) en Galicia. PhD Thesis, Mendel University in Brno, Czechia.

Neufeld, C.J. & Palmer, A.R. 2008. Precisely proportioned: Intertidal barnacles alter penis form to suit coastal wave action. *Proceedings of the Royal Society B: Biological Sciences* **275** (1638), 1081–1087, doi:10.1098/rspb.2007.1760

Neves, F. 2021. Biologia e conservação do percebe (*Pollicipes pollicipes*) na Reserva Natural das Berlengas. Master Thesis, University of Évora, Portugal.

Newman, W.A. 1987. Evolution of cirripedes and their major groups. In *Crustacean Issues, 5. Barnacle biology*. A.J. Southward (ed.). Rotterdam: A.A. Balkema, 3–42.

Newman, W.A. 1992. Biotic cognates of eastern boundary conditions in the Pacific and Atlantic: Relicts of tethys and climate change. *Proceedings of the San Diego Society of Natural History* **16** (1), 1–7.

Newman, W.A. & Abbott, D.P. 1980. *Cirripedia: The Barnacles. Intertidal Invertebrates of California*. Stanford, California: Stanford University Press, 504–535.

Newman, W.A. & Foster, B.A. 1987. Southern hemisphere endemism among the barnacles: Explained in part by extinction of northern members of amphitropical taxa? *Bulletin of Marine Science* **41** (2), 361–377.

Newman, W.A. & Killingley, J.S. 1985. The north-east Pacific intertidal barnacle *Pollicipes polymerus* in India? A biogeographical enigma elucidated by 18O fractionation in barnacle calcite. *Journal of Natural History* **19** (6), 1191–1196, doi:10.1080/00222938500770741

Nolasco, R., Dubert, J., Acuña, J.L., Aguión, A., Cruz, T., Fernandes, J.N., Geiger, K., Jacinto, D., Macho, G., Mateus, D., Rivera, A., Román, S., Thiébaut, E., Vazquez, E. & Queiroga, H. 2022. Biophysical modelling of larval dispersal and population connectivity of a stalked barnacle: A validation exercise with field data in three regions across Europe. *Marine Ecology Progress Series*, **694**, 105–123. doi.org/10.3354/meps14097

Norton, R. 1996. Feeding and energetic relationships of *Pollicipes pollicipes* (Gmelin, 1790) (Cirripedia; Lepadomorpha). PhD Thesis, University College of North Wales, United Kingdom.

O'Riordan, R.M., Delany, J., McGrath, D., Myers, A.A., Marie Power, A., Ramsay, N.F., Alvarez, D., Cruz, T., Pannacciulli, F.G., Range, P. & Relini, G. 2001. Variation in the sizes of Chthamalid Barnacle post-settlement cyprids on European shores. *Marine Ecology* **22** (4), 307–322, doi: 10.1046/j.1439-0485.2001.01760.x

Oliva, J. 1995. Ecología y dinámica poblacional del "percebe" *Pollicipes elegans*, Bahía de Yacila-Paita (Perú). Master's Thesis, Universidad Nacional, Perú.

Ordinola, E., López, E., Gonzales, I., Montero, P., Agurto, K., Torres, E., Vera, M. & Inga, C. 2010. Invertebrados bentónicos comerciales y areas de pesca artesanal en el litoral de Tumbes. *Instituto del Mar del Perú*, 79.

Oregon Department of Fish and Wildlife. 2021. *Oregon Shellfish Regulations*. Online. https://myodfw.com/articles/oregon-shellfish-regulations (Accessed 1 July 2021).

Oróstica, M.H., Richardson, C.A., Estrella-Martínez, J., Jenkins, S.R. & Hawkins, S.J. 2021. Shell growth and age determined from annual lines in the southern warm-water limpet *Patella depressa* at its poleward geographic boundaries. *Journal of the Marine Biological Association of the United Kingdom*, 1–10, doi:10.1017/S0025315421000539

Orton, H. 1920. Sea-temperature, breeding and distribution in marine animals. *Journal of the Marine Biological Association UK* **12** (2), 339–366.

Page, H.M. 1984. Local variation in reproductive patterns of two species of intertidal barnacles, *Pollicipes polymerus* Sowerby and *Chthamalus fissus* Darwin. *Journal of Experimental Marine Biology and Ecology* **74** (3), 259–272, doi:10.1016/0022-0981(84)90129-1

Page, H.M. 1986. Differences in population structure and growth rate of the stalked barnacle *Pollicipes polymerus* between a rocky headland and an offshore oil platform. *Marine Ecology Progress Series* **29**, 157–164, doi:10.3354/meps029157

Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist* **100** (910), 65–75.

Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator published by: Springer in cooperation with International Association for Ecology. *Oecologia* **15** (2), 93–120.

Paine, R.T. 1980. Food webs: Linkage, interaction strength and community infrastructure. *The Journal of Animal Ecology* **49** (3), 666–685.

Paine, R.T. 1984. Ecological determinism in the competition for space. *Ecology* **65** (5), 1339–1348.

Paine, R.T. & Levin, S.A. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecological Monographs* **51** (2), 145–178.

Palmer, A.R. 1984. Prey selection by thaidid gastropods: Some observational and experimental field tests of foraging models. *Oecologia* **62** (2), 162–172, doi:10.1007/BF00379009

Pannacciulli, F.G., Bishop, J.D.D. & Hawkins, S.J. 1997. Genetic structure of populations of two species of *Chthamalus* (Crustacea: Cirripedia) in the north-east Atlantic and Mediterranean. *Marine Biology* **128**, 73–82.

Pannacciulli, F.G., Maltagliati, F., de Guttry, C. & Achituv, Y. 2017. Phylogeography on the rocks: The contribution of current and historical factors in shaping the genetic structure of *Chthamalus montagui* (Crustacea, Cirripedia). *PLoS One* **12** (6), 1–17, doi:10.1371/journal.pone.0178287

Parada, J.M., Iglesias, E., Outeiral, R. & Molares, J. 2013. Diameter of the base of the capitulum as a biometric variable of the goose barnacle *Pollicipes pollicipes* (gmelin, 1789) (Cirripedia, Lepadomorpha). *Crustaceana* **86** (13–14), 1527–1538, doi:10.1163/15685403–00003251

Parada, J.M., Outeiral, R., Iglesias, E. & Molares, J. 2012. Assessment of goose barnacle (*Pollicipes pollicipes* Gmelin, 1789) stocks in management plans: Design of a sampling program based on the harvesters' experience. *ICES Journal of Marine Science* **69** (10), 1840–1849, doi:10.1093/icesjms/fss157

Paredes, C. 1974. El modelo de zonacion en la orilla rocosa del departamento de Lima. *Revista Peruana de Biologia* **1** (2), 168–191.

Paredes, C., Cardoso, F. & Tarazona, J. 2004. Distribución temporal de moluscos y crustáceos tropicales en la provincia Peruana y su relación con los eventos El Niño. *Revista Peruana de Biologia* **11** (2), 213–218.

Parrondo, M., Morán, P., Macho, G., Ballenghien, M.,Acuña, J.L., Aguión, A., Arrontes, J., Chiss, J., Cruz, T., Fernandes, J.N., García-Flórez, L., García-Vázquez, E., Geiger, K.J., Macho, G., Thiébaut, E., Weidberg, N., Jollivet, D.,& Borrell, Y.J.. 2022. Chaotic genetic patchiness in the high valued Atlantic stalked barnacle *Pollicipes pollicipes* from the Iberian Peninsula: Implications for fisheries management. *Frontiers in Marine Science* **9**, 801780, doi.org/10.3389/fmars.2022.801780

Patel, B. & Crisp, D.J. 1960. Rates of development of the embryos of several species of barnacles. *Physiological Zoology* **33** (2), 104–119, doi:10.1086/physzool.33.2.30152298

Pavón, I. 2003. Biología y variables poblacionales del percebe, *Pollicipes pollicipes* (gmelin, 1790) en Asturias. PhD Thesis, Universidade de Oviedo, Spain.

Pedro, H.C. 2017. Caracterização da zona entre-marés da Reserva Mundial de Surf da Ericeira – padrões gerais e pressões humanas. Master Thesis, University of Lisbon, Portugal.

Penteado, N. 2011. Co-gestão da pesca marinha no Parque Natural do Sudoeste Alentejano e Costa Vicentina: Estudo da sua implementação no concelho de Odemira. Master Thesis, University of Évora, Portugal.

Pérez-Losada, M., Harp, M., Høeg, J.T., Achituv, Y., Jones, D., Watanabe, H. & Crandall, K.A. 2008. The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution* **46** (1), 328–346, doi:10.1016/j.ympev.2007.10.004

Pérez-Losada, M., Høeg, J.T. & Crandall, K.A. 2004. Unraveling the evolutionary radiation of the thoracican barnacles using molecular and morphological evidence: A comparison of several divergence time estimation approaches. *Systematic Biology* **53** (2), 244–264, doi:10.1080/10635150490423458

Perina, A. 2018. Analyses of molecular markers and gene expression in crustacean species. PhD Thesis, Universidade da Coruña, Spain.

Perina, A., von Reumont, B.M., Martínez- Lage, A. & González-Tizón, A.M. 2014. Accessing transcriptomic data for ecologically important genes in the goose barnacle (*Pollicipes pollicipes*), with particular focus on cement proteins. *Marine Genomics* **15**, 9–11, doi:10.1016/j.margen.2014.02.003

Perina, A., Seoane, D., González-Tizán, A.M., Rodríguez-Farĩa, F. & Martínez-Lage, A. 2011. Molecular organization and phylogenetic analysis of 5S rDNA in crustaceans of the genus *Pollicipes* reveal birth-and-death evolution and strong purifying selection. *BMC Evolutionary Biology* **11** (1), 304, doi:10.1186/1471-2148-11-304

Pescadegalicia.gal. 2021. *Estatísticas*. Online. www.pescadegalicia.gal (Accessed on 1 July 2021).

Petersen, J.A., Fyhn, H.J. & Johansen, K. 1974. Eco-physiological studies of an intertidal crustacean, *Pollicipes polymerus* (Cirripedia, Lepadomorpha): Aquatic and aerial respiration. *The Journal of Experimental Biology* **61** (2), 309–320.

Pham, C., De Girolamo, M. & Isidro, E. 2011. Recruitment and growth of *Megabalanus azoricus* (Pilsbry, 1916) on artificial substrates: First steps towards commercial culture in the Azores. *ARQUIPÉLAGO. Life and Marine Sciences* **28**, 47–56.

Phillips, N.E. 2005. Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. *Marine Ecology Progress Series* **295**, 79–89, doi:10.3354/meps295079

Phillips, N.E. 2006. Natural variability in size and condition at settlement of 3 species of marine invertebrates. *Integrative and Comparative Biology* **46** (5), 598–604, doi:10.1093/icb/icl008

Pilsbry, H.A. 1907. *The Barnacles (Cirripedia): Contained in the Collections of the US National Museum*, United States National Museum Bulletin No.60. Washington, D.C., USA: US Government Printing Office, No. 60, 1–222

Pilsbry, H.A. 1909. Report on barnacles of Peru, collected by Dr. R. E. Coker and others. *Proceedings of the United Stares National Museum* **37**, 63–74.

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* **253** (5019), 548–551, doi:10.1126/science.253.5019.548

Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* **107**, 125–138.

Pineda, J. 1999. Circulation and larval distribution in internal tidal bore warm fronts. *Limnology and Oceanography* **44** (6), 1400–1414.

Pineda, J., Porri, F., Starczak, V. & Blythe, J. 2010. Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. *Journal of Experimental Marine Biology and Ecology* **392** (1–2), 9–21, doi:10.1016/j.jembe.2010.04.008

Pineda, J., Starczak, V. & Stueckle, T.A. 2006. Timing of successful settlement: Demonstration of a recruitment window in the barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* **320**, 233–237, doi:10.3354/meps320233

Pinilla, F. 1996. Variación temporal de la densidade y biomasa de la población del percebe *Pollicipes elegans* de la zona de Lobitos, Piura, Perú. Honor Thesis. Universidad Nacional Agraria La Molina. Lima, Perú.

Pita, P., Fernández-Márquez, D., Antelo, M., Macho, G. & Villasante, S. 2019. Socioecological changes in data-poor S-fisheries: A hidden shellfisheries crisis in Galicia (NW Spain). *Marine Policy* **101**, 208–224, doi:10.1016/j.marpol.2018.09.018

Plough, L.V. & Marko, P.B. 2014. Characterization of microsatellite loci and repeat density in the gooseneck barnacle, *Pollicipes elegans*, using next generation sequencing. *Journal of Heredity* **105** (1), 136–142, doi:10.1093/jhered/est064

Plough, L.V., Moran, A. & Marko, P. 2014. Density drives polyandry and relatedness influences paternal success in the Pacific gooseneck barnacle, *Pollicipes elegans*. *BMC Evolutionary Biology* **14** (1), 1–10, doi:10.1186/1471–2148–14–81

Power, A.M., Klepal, W., Zheden, V., Jonker, J., McEvilly, P. & von Byern, J. 2010. Mechanisms of adhesion in adult barnacles. In *Biological Adhesive Systems*, I. Grunwald & J. von Byern (eds). Vienna: Springer-Verlag, 153–168.

Prince, J. 2010. Rescaling fisheries assessment and management: A generic approach, access rights, change agents, and toolboxes. *Bulletin of Marine Science* **86** (2), 197–219.

Prince, J.D. 2003. The barefoot ecologist goes fishing. *Fish and Fisheries* **4** (4), 359–371, doi: 10.1046/j.1467-2979.2003.00134.x

Quinteiro, J., Rodríguez-Castro, J., López, P., López-Jurado, L.F., González-Henriquez, N. & Rey-Méndez, M. 2011. Morphological and molecular characterization of a new species of Atlantic stalked barnacle (Scalpelliformes: Pollicipedidae) from the Cape Verde Islands. *Journal of the Marine Biological Association of the United Kingdom* **91** (7), 1537–1545, doi:10.1017/S0025315411000166

Quinteiro, J., Rodríguez-Castro, J. & Rey-Méndez, M. 2007. Population genetic structure of the stalked barnacle *Pollicipes pollicipes* (Gmelin, 1789) in the northeastern Atlantic: Influence of coastal currents and mesoscale hydrographic structures. *Marine Biology* **153** (1), 47–60, doi:10.1007/s00227-007-0783-0

Ramalho, R.A.S. 2011. *Building the Cape Verde Islands*, Berlin, Heidelberg: Springer Science.

Ramírez, P. & de la Cruz, J. 2015. Lobos de Afuera islands: Evaluation of octopus *Octopus mimus* Gould, 1852 and barnacles *Pollicipes elegans* (Lesson, 1831), Lambayeque 2010. *Instituto del Mar del Perú* **42** (3), 273–281.

Ramírez, P., de la Cruz, J., Castañeda, J. & Galán, J. 2008. Prospeccion de los bancos naturales de pulpo *Octopus mimus* y la evaluacion de percebes *Pollicipes elegans* en las Islas Lobos de Afuera, Lambayeque (11 – 16 Julio 2008). *Informe técnico, Instituto del Mar del Perú*, 20.

Ramírez, P., de la Cruz, J. & Castro, J. 2019. Prospección del pulpo *Octopus mimus* en Las Islas Lobos de Afuera, 2014. *Informe, Instituto del Mar del Perú* **46** (3), 312–322.

Ramírez, P., de la Cruz, J., Galán, J. & Castro, J. 2017. Characterización de bancos naturales de invertebrados marinos comerciales y áreas de pesca artesanal. Región Lambayeque, Perú. Junio 2014. *Instituto del Mar del Perú* **44** (1), 63–82.

Ramos, A.S., Antunes, S.C., Gonçalves, F. & Nunes, B. 2014. The gooseneck barnacle (*Pollicipes pollicipes*) as a candidate sentinel species for coastal contamination. *Archives of Environmental Contamination and Toxicology* **66** (3), 317–326, doi:10.1007/s00244-013-9978-1

Ramos, A.S., Antunes, S.C. & Nunes, B. 2016. Biomonitoring of environmental stress in *Pollicipes pollicipes* from the northern coast of Portugal: A non-destructive approach using haemolymph. *Ecotoxicology and Environmental Safety* **126**, 1–13, doi:10.1016/j.ecoenv.2015.12.008

Reis, P.A., Salgado, M.A. & Vasconcelos, V. 2011. Barnacles as biomonitors of metal contamination in coastal waters. *Estuarine, Coastal and Shelf Science* **93** (4), 269–278, doi:10.1016/j.ecss.2010.12.022

Reis, P.A., Salgado, M.A. & Vasconcelos, V. 2012. Goose barnacle *Pollicipes pollicipes* as biomonitor of metal contamination in the northwest coast of Portugal. *Environmental Monitoring and Assessment* **184** (11), 6987–7000, doi:10.1007/s10661-011-2474-z

Reis, P.A., Salgado, M.A. & Vasconcelos, V. 2013. Seasonal variation of metal contamination in the barnacles *Pollicipes pollicipes* in northwest coast of Portugal show clear correlation with levels in the surrounding water. *Marine Pollution Bulletin* **70** (1–2), 155–161, doi:10.1016/j.marpolbul.2013.02.027

Reis, P.A., Salgado, M.A. & Vasconcelos, V. 2017. Barnacle species as biomonitors of metal contamination in the northwest coast of Portugal: Ecological quality classification approach. *Human and Ecological Risk Assessment* **23** (5), 1219–1233, doi:10.1080/10807039.2017.1312277

Reis, P.A., Salgado, M.A. & Vasconcelos, V. 2019. *Pollicipes pollicipes* as a biomonitor of PAHs contamination in seawaters of the northwest coast of Portugal. *Polycyclic Aromatic Compounds* **39** (2), 172–189, doi:10.1080/10406638.2017.1296873

Rivera, A. 2015. Sustainability of the gooseneck barnacle fishery in Asturias: Trends, drivers and lessons. PhD Thesis, Universidad de Oviedo, Spain.

Rivera, A., Gelcich, S., García-flórez, L. & Acuña, J.L. 2016a. Trends, drivers, and lessons from a long-term data series of the Asturian (northern Spain) gooseneck barnacle territorial use rights system. *Bulletin of Marine Science* **92** (3), 1–18, doi:10.5343/bms.2015.1080

Rivera, A., Gelcich, S., García-Flórez, L. & Acuña, J.L. 2016b. Incorporating landscape metrics into invertebrate fisheries management: Case study of the gooseneck barnacle in Asturias (N. Spain). *ICES Journal of Marine Science* **73** (6), 1570–1578, doi:10.1093/icesjms/fsw029 Original

Rivera, A., Gelcich, S., García-Flórez, L. & Acuña, J.L. 2016c. Assessing the sustainability and adaptive capacity of the gooseneck barnacle co-management system in Asturias, N. Spain. *Ambio* **45** (2), 230–240, doi:10.1007/s13280-015-0687-z

Rivera, A., Gelcich, S., García-Flórez, L. & Acuña, J.L. 2017. Heterogeneous management and conservation perceptions within the gooseneck barnacle co-management system in Asturias (N. Spain). *Marine Policy* **81**, 229–235, doi:10.1016/j.marpol.2017.03.020

Rivera, A., Gelcich, S., García-Flórez, L. & Acuña, J.L. 2019. Social attributes can drive or deter the sustainability of bottom-up management systems. *Science of the Total Environment* **690**, 760–767, doi:10.1016/j.scitotenv.2019.06.323

Rivera, A., Gelcich, S., García-Flórez, L., Alcázar, J.L. & Acuña, J.L. 2014. Co-management in Europe: Insights from the gooseneck barnacle fishery in Asturias, Spain. *Marine Policy* **50**, 300–308, doi:10.1016/J.MARPOL.2014.07.011

Rivera, A., Weidberg, N., Pardiñas, A.F., González-Gil, R., García-Flórez, L. & Acuña, J.L. 2013. Role of upwelling on larval dispersal and productivity of gooseneck barnacle populations in the Cantabrian sea: Management implications. *PLoS One* **8**, (11), 78482, doi:10.1371/journal.pone.0078482

Rocha, M., Antas, P., Castro, L.F.C., Campos, A., Vasconcelos, V., Pereira, F. & Cunha, I. 2019. Comparative analysis of the adhesive proteins of the adult stalked goose barnacle *Pollicipes pollicipes* (Cirripedia: Pedunculata). *Marine Biotechnology* **21** (1), 38–51, doi:10.1007/S10126-018-9856-Y

Rocha, M.S. 2015. Molecular targets involved in the goose barnacle *Pollicipes pollicipes* (Cirripedia) larvae metamorphosis and settlement. Master Thesis, University of Porto, Portugal.

Rodharth, E. 2013. A comparative study of the adhesive in different species of Cirripedia Thoracica (Crustacea). Honor Thesis, University of Wien, Austria.

Rogers, R. 2016. *The Nakwakto Rapids- Dive Into the Guinness Book of World Records*. Online. https://divertrek.com/the-nakwakto-rapids-dive-into-the-guinness-book-of-world-records/ (accessed 19 July 2021).

Román, S., Weidberg, N., Muñiz, C., Aguion, A., Vázquez, E., Santiago, J., Seoane, P., Barreiro, B., Outeiral, R., Villegas-Ríos, D., Fandiño, S., & Macho, G. 2022. Mesoscale patterns in barnacle reproduction are mediated by upwelling-driven thermal variability. *Marine Ecology Progress Series* **685,** 153–170, doi:10.3354/meps13992

Romersa, A. 2018. Growing goosenecks: A study on the growth and bioenergetics of *Pollicipes polymerus* in aquaculture. Master's Thesis, University of Oregon, Eugene.

Rosenblad, M.A., Abramova, A., Lind, U., Ólason, P., Giacomello, S., Nystedt, B. & Blomberg, A. 2021. Genomic characterization of the barnacle *Balanus improvisus* reveals extreme nucleotide diversity in coding regions. *Marine Biotechnology* 402–416, doi:10.1007/s10126-021-10033-8

Rubidge, E., Jeffery, S., Gregr, E.J., Gale, K.S.P. & Frid, A. 2020. Assessment of nearshore features in the Northern shelf bioregion against criteria for determining ecologically and biologically significant areas (EBSAs). *Fisheries and Oceans Canada. Canadian Science Advisory Secretariat. Research Document* **023**, 63.

Samamé, M. & Quevedo, M. 2001. Población y biomasa del percebes *Pollicipes elegans* Lesson, 1830 en las islas Lobos de Tierra y Lobos de Afuera, Perú. 1995–1997. *Informe Progressivo Instituto del Mar del Perú* **137**, 23.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* **283** (5410), 2095–2097, doi:10.1126/science.283.5410.2095

Santos, M. 2019. Sobrevivência e crescimento de percebes (*Pollicipes pollicipes*) em sistemas alternativos de cultivo. Master Thesis. Politécnico de Leiria. Portugal.

Satchell, E.R. & Farrell, T.M. 1993. Effects of settlement density on spatial arrangement in four intertidal barnacles. *Marine Biology* **245**, 241–245.

Schiller, L. 2015. Leaf barnacle (gooseneck barnacle) about seafood watch®. Monterey Bay Aquarium's Seafood Watch®, British Columbia. Monterey Bay Aquarium's Seafood Watch®, British Columbia.

Schulting, R., Tresset, A. & Dupont, C. 2004. From harvesting the sea to stock rearing along the atlantic façade of north-west Europe. *Environmental Archaeology* **9** (2), 131–142, doi:10.1179/146141004790734478

Schultzhaus, J.N., Hervey, W.J., Taitt, C.R., So, C.R., Leary, D.H., Wahl, K.J. & Spillmann, C.M. 2021. Comparative analysis of stalked and acorn barnacle adhesive proteomes. *Open Biology* **11**, 1–16, doi:doi.org/10.1098/rsob.210142

Sen, S. & Nielsen, J.R. 1996. Fisheries co-management: A comparative analysis. *Marine Policy* **20** (5), 405–418, doi:10.1016/0308-597X(96)00028-0

Seoane-Miraz, D. 2015. Genetic analyses in the gooseneck barnacles (Genus "*Pollicipes*"). PhD Thesis, Universidade de Coruña, España.

Seoane-Miraz, D., Martínez-Lage, A. & González-Tizón, A.M. 2015. Characterization of 15 polymorphic microsatellite loci in gooseneck barnacle *Pollicipes pollicipes* (Gmelin, 1789), and cross-amplification in other *Pollicipes* species. *Conservation Genetics Resources* **7** (2), 591–593, doi:10.1007/s12686-015-0436-4

Sestelo, M. & Roca-pardiñas, J. 2007. Length-weight relationship of *Pollicipes pollicipes* (Gmelin, 1789) on the Atlantic coast of Galicia (NW Spain). Some aspects of its biology and management. Report 10/02. Discussion Papers in Statistics and Operation Research. Departamento de Estatística e Investigación Operativa. Universidade de Vigo, Vigo

Sestelo, M. & Roca-Pardiñas, J. 2011. A new approach to estimation of the length—Weight relationship of *Pollicipes pollicipes* (Gmelin, 1789) on the Atlantic coast of Galicia (northwest Spain): Some aspects of its biology and management. *Journal of Shellfish Research* **30** (3), 939–948, doi:10.2983/035.030.0336

Shanks, A. 2001. *An Identification Guide to the Larval Marine Invertebrates of the Pacific Northwest*. Corvallis, Oregon: Oregon State University Press.

Shanks, A.L. & Shearman, R.K. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. *Marine Ecology Progress Series* **385** (1988), 189–204, doi:10.3354/meps08043

Silva, C.T. & Soares, J. 1997. Economias costeiras na pré-história do sudoeste Português o concheiro de Montes de Baixo. *Setúbal Arqueológica* **11–12**, 69–108.

Silva, M., Rey, V., Barreiro, A., Kaufmann, M., Neto, A.I., Hassouani, M., Sabour, B., Botana, A., Botana, L.M. & Vasconcelos, V. 2018. Paralytic shellfish toxins occurrence in non-traditional invertebrate vectors from north Atlantic waters (Azores, Madeira, and Morocco). *Toxins* **10** (9), doi:10.3390/toxins10090362

Silva, M., Rodriguez, I., Barreiro, A., Kaufmann, M., Neto, A.I., Hassouani, M., Sabour, B., Alfonso, A., Botana, L.M. & Vasconcelos, V. 2015. New invertebrate vectors of okadaic acid from the North Atlantic waters—Portugal (Azores and Madeira) and Morocco. *Toxins* **7** (12), 5337–5347, doi:10.3390/toxins7124885

Silva, M., Rodríguez, I., Barreiro, A., Kaufmann, M., Neto, A.I., Hassouani, M., Sabour, B., Alfonso, A., Botana, L.M. & Vasconcelos, V. 2020. Lipophilic toxins occurrence in non-traditional invertebrate vectors from north Atlantic waters (Azores, Madeira, and Morocco): Update on geographical tendencies and new challenges for monitoring routines. *Marine Pollution Bulletin* **161** (September), 111725, doi:10.1016/j.marpolbul.2020.111725

So, C.R., Fears, K.P., Leary, D.H., Scancella, J.M., Wang, Z., Liu, J.L., Orihuela, B., Rittschof, D., Spillmann, C.M. & Wahl, K.J. 2016. Sequence basis of barnacle cement nanostructure is defined by proteins with silk homology. *Scientific Reports* **6**, 1–14, doi:10.1038/srep36219

So, C.R., Scancella, J.M., Fears, K.P., Essock-Burns, T., Haynes, S.E., Leary, D.H., Diana, Z., Wang, C., North, S., Oh, C.S., Wang, Z., Orihuela, B., Rittschof, D., Spillmann, C.M. & Wahl, K.J. 2017. Oxidase activity of the barnacle adhesive interface involves peroxide-dependent catechol oxidase and lysyl oxidase enzymes. *ACS Applied Materials and Interfaces* **9** (13), 11493–11505, doi:10.1021/acsami.7b01185

Soares, V. 2018. Pesca de percebes, *Pollicipes caboverdensis*, nas ilhas de Santo Antão, São Vicente e São Nicolau (Cabo Verde) e contribuição para o estudo da sua ecologia e conservação. Honor Thesis, Universidade de Cabo Verde, Cabo Verde.

Somero, G.N. 2002. Thermal physiology and vertical zonation of intertidal animals: Optima, limits, and costs of living. *Integrative and Comparative Biology* **42** (4), 780–789, doi:10.1093/icb/42.4.780

Sommer, U. & Worm, B. 2002. *Competition and Coexistence.* Berlin, Germany: Springer Science & Business Media.

Sousa, A. 2007. Distribuição e abundância do percebe, *Pollicipes pollicipes* (Gmelin, 1790) na Reserva Natural das Berlengas: Relação com o hidrodinamismo e efeitos da predação. Honor Thesis, University of Évora, Portugal.

Sousa, A., Jacinto, D., Penteado, N., Martins, P., Fernandes, J.N., Silva, T., Castro, J.J. & Cruz, T. 2013. Patterns of distribution and abundance of the stalked barnacle (*Pollicipes pollicipes*) in the central and southwest coast of continental Portugal. *Journal of Sea Research* **83**, 187–194, doi:10.1016/J.SEARES.2013.04.005

Sousa, A., Jacinto, D., Penteado, N., Pereira, D., Silva, T., Castro, J.J., Leandro, S.M. & Cruz, T. 2020. Temporal variation of the fishers' perception about the stalked barnacle (*Pollicipes pollicipes*) fishery at the Berlengas Nature Reserve (Portugal). *Regional Studies in Marine Science* **38**, 101378, doi:10.1016/j.rsma.2020.101378

Sousa, A., Vázquez, E., Macho, G., Acuña, J. L., Cruz, T. & Morán, P. 2021. The stalked barnacle *Pollicipes pollicipes* elongated morphology: no evidence for epigenetic variation. In *Proceedings of the XVII International Symposium on Oceanography of the Bay of Biscay* (ISOBAY 17), A. Arias et al. (eds). Oviedo,Spain: University of Oviedo, 92 pp.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**, 353–391, doi:10.1146/annurev.ecolsys.15.1.353

Southward, A.J. 2008. *Barnacles*, Shrewsbury: Field Studies Council (FSC).

Standing, J.D. 1981. Common inshore barnacle cyprids of the Oregonian faunal province (Crustacea: Cirripedia). *Proceedings of the Biological Society of Washington* **93**, 1184–1203.

Stewart, A., Fragoso, B.D.D., Clímaco, R. & Icely, J.D. 2014. Evaluation of stakeholder perspectives on the management of the stalked barnacles (*Pollicipes pollicipes*) resource in the Parque Natural do Sudoeste Alentejano e Costa Vicentina, Portugal. *Marine Policy* **43**, 71–79, doi:10.1016/j.marpol.2013.03.016

Stott, R. 2003. *Darwin and the Barnacle*. London: Faber & Faber.

Straughan, D. 1969a. Santa Barbara oil pollution project: 8-month progress report. 2. Breeding activity in intertidal species. *Marine Pollution Bulletin* **18**, 1–2.

Straughan, D. 1969b. Breeding activity of intertidal species. *Marine Pollution Bulletin* **13**, 5 only.

Straughan, D. 1971. Breeding and larval settlement of certain intertidal invertebrates in the Santa Barbara channel following pollution by oil. In *Biological and Oceanographical Survey of the Santa Barbara Channel Oil Spill 1969–1970. Vol. I. Biology and Bacteriology*, D. Straughan (ed.). Santa Maria, California: Allan Hancock Foudation, University of California, 223–244.

Stubbings, H.G. 1967. The cirriped fauna of tropical west Africa. *Bulletin British Museum (Natural History), Zoology* **15** (6), 229–319.

Stucchi, M. & Figueroa, J. 2006. *La avifauna isla Lobos de Afuera y algunos alcances sobre su biodiversidad. Reporte de investigación Nº 2*. Lima, Perú: Asociación Ucumari.

Swearer, S.E., Treml, E.A. & Shima, J.S. 2019. A review of biophysical models of marine larval dispersal. *Oceanography and Marine Biology: An Annual Review* **57**, 325–356.

T'aa q-wiihak. 2016. *T'aaq-wiihak Fishery Indicators - Information About How the t'aaq-wiihak Fisheries Are Reflecting nuu-chah-nulth Vision, Values, and Priorities*. Vancouver, Canada: T'aaq-wiihak.

T'aaq-wiihakfisheries.ca. 2021. *Implementing Nuu-Chah-Nulth fishing rights*. Online. https://taaqwiihakfisheries.ca/ (Accessed 1 July 2021).

Tallis, H. 2009. Kelp and rivers subsidize rocky intertidal communities in the pacific northwest (USA). *Marine Ecology Progress Series* **389** (Kingsford 1992), 85–96, doi:10.3354/meps08138

Tapia, F.J. 2005. Adult demography and larval processes in coastal benthic populations intertidal barnacles in Southern California and Baja California. PhD Thesis, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution, Chile.

Tapia, F.J., DiBacco, C., Jarrett, J. & Pineda, J. 2010. Vertical distribution of barnacle larvae at a fixed nearshore station in southern California: Stage-specific and diel patterns. *Estuarine, Coastal and Shelf Science* **86** (2), 265–270, doi:10.1016/j.ecss.2009.11.003

Tarasov, N.I. & Zevina, G.B. 1957. Barnacles (Cirripedia, Thoracica) of the seas of the USSR. In *Fauna of the USSR. Vol. 6: Crustaceans*. Tom Rakoobraznye (ed.)., Moscow: Fauna Russian Natural Science, 267.

Tarazona, J., Paredes, C., Romero, L., Blaskovic', V., Guzmán, S. & Sánchez, S. 1985. Características de la vida planctónica y colonización de los organismos betónicos epilíticos durante el fenómeno El Niño. *Instituto del Mar del Perú. Boletín Extraordinario*, 41–50.

Test, A.R. 1945. Ecology of california *Acmaea*. *Ecology* **26** (4), 395–405, doi:10.2307/1931661

Tian, M., Chen, P., Song, J., He, F. & Shen, X. 2020. The first mitochondrial genome of *Capitulum mitella* (Crustacea: Cirripedia) from China: Revealed the phylogenetic relationship within Thoracica. *Mitochondrial DNA Part B: Resources* **5** (3), 2573–2575, doi:10.1080/23802359.2020.1781564

Tilbury, M.A., McCarthy, S., Domagalska, M., Ederth, T., Power, A.M. & Wall, J.G. 2019. The expression and characterization of recombinant cp19k barnacle cement protein from *Pollicipes pollicipes*. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374** (1784), doi:10.1098/rstb.2019.0205

Torres, A. 2018. Crescimento e sobrevivência do percebe *Pollicipes pollicipes* (Gmelin, 1790) em condições laboratoriais. Master Thesis, Politechnic of Leiria, Portugal.

Trivedi, J., Patel, K., Chan, B.K.K., Doshi, M. & Padate, V. 2021. Diversity of indian barnacles in marine provinces and ecoregions of the indian ocean. *Frontiers in Marine Science* **8**, doi:10.3389/fmars.2021.657651

Tsang, L.M., Shen, X., Cheang, C.C., Chu, K.H. & Chan, B.K.K. 2017. Gene rearrangement and sequence analysis of mitogenomes suggest polyphyly of *Archaeobalanid* and *Balanid* barnacles (Cirripedia: Balanomorpha). *Zoologica Scripta* **46** (6), 729–739, doi:10.1111/zsc.12246

Underwood, A.J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* **33** (2), 185–202, doi:10.1007/BF00344847

Underwood, A.J. 1984. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* **64** (2), 211–222, doi:10.1007/BF00376873

Urushida, Y., Nakano, M., Matsuda, S., Inoue, N., Kanai, S., Kitamura, N., Nishino, T. & Kamino, K. 2007. Identification and functional characterization of a novel barnacle cement protein. *FEBS Journal* **274** (16), 4336–4346, doi:10.1111/j.1742-4658.2007.05965.x

Vala, F. 2009. *Darwin em Cabo Verde*, Lisboa: Fundação Calouste Gulbenkian.

Valente, M.J. 2008. As últimas sociedades de caçadores-recolectores no Centro e Sul de Portugal (10.000 - 6.000 anos BP): Aproveitamento dos recursos animais. PhD Thesis, University of Algarve, Portugal.

Valente, M.J. 2014. Mesolithic and neolithic shell middens in Western Algarve: Issues in ecology, taphonomy and economy. In *Proceedings of the First Zooarchaeology Conference in Portugal*, University of Lisbon.

Valqui, J., Ibañez-Erquiaga, B., Pacheco, A.S., Wilbur, L., Ochoa, D., Cardich, J., Pérez-Huaranga, M., Salas-Gismondi, R., Pérez, A., Indacochea, A., Avila-Peltroche, J., Ch, M.R. & Carré, M. 2021. Changes in rocky intertidal communities after the 2015 and 2017 El Niño events along the Peruvian coast. *Estuarine, Coastal and Shelf Science* **250** (March 2020), doi:10.1016/j.ecss.2020.107142

Van Syoc, B. 1993. PCR primers for the COT gene in barnacle mtDNA. *Newsletter Crustacean Molecular Techniques* **4**, 1–2.

Van Syoc, R.J. 1994a. Molecular phylogenetics and population structure derived from mitochondrial DNA sequence variation in the edible goose barnacle genus *Pollicipes* (Cirripedia, Crustacea). PhD Thesis, University of California, United States of America.

Van Syoc, R.J. 1994b. Genetic divergence between subpopulations of the eastern Pacific goose barnacle *Pollicipes elegans*: Mitochondrial cytochrome c subunit 1 nucleotide sequences. *Molecular Marine Biology and Biotechnology* **3** (6), 338–346.

Van Syoc, R.J. 1995. Barnacle mitochondrial DNA: Determining genetic relationships among species of *Pollicipes*. In *New frontiers in Barnacle evolution. Crustacean Issues, 10*, J.H. Schram (ed.). Rotterdam: A. A. Balkema, 269–296.

Van Syoc, R.J., Fernandes, J.N., Carrison, D.A. & Grosberg, R.K. 2010. Molecular phylogenetics and biogeography of *Pollicipes* (Crustacea: Cirripedia), a Tethyan relict. *Journal of Experimental Marine Biology and Ecology* **392** (1–2), 193–199, doi:10.1016/J.JEMBE.2010.04.024

Van Syoc, R.J. & Newman, W.A. 1992. Genetic divergence between reproductive types. In *California Sea Grant Biennial Report of Completed Projects 1988–1990*. La Jolla: University of California, 210.

Vázquez-Rowe, I., Moreira, M.T. & Feijoo, G. 2013. Carbon footprint analysis of goose barnacle (*Pollicipes pollicipes*) collection on the Galician coast (NW Spain). *Fisheries Research* **143**, 191–200, doi:10.1016/J.FISHRES.2013.02.009

Vermeer, K. 1982. Comparison of the diet of the Glaucous-Winged gull on the East and West coasts of Vancouver island. *The Murrelet* **63** (3), 80, doi:10.2307/3534286

Veselská, M. k., Kočí, T., Collins, J.S.H. & Gale, A.S. 2015. A new species of scalpelliform cirripede (Crustacea, Cirripedia) from the upper cenomanian-lower turonian shallow-water facies at Velim (Bohemian Cretaceous Basin) and its palaeoecological implications. *Neues Jahrbuch fur Geologie und Palaontologie - Abhandlungen* **278** (2), 201–211, doi:10.1127/njgpa/2015/0525

Villena, G. 1995. Aspectos reproductivos del percebes *Pollicipes elegans* de la zona de Yacila, Paita- Perú. Honor Thesis, Universidad Nacional Agraria La Molina, Perú.

Viñas, L., Franco, M.A., Soriano, J.A., González, J.J., Ortiz, L., Bayona, J.M. & Albaigés, J. 2009. Accumulation trends of petroleum hydrocarbons in commercial shellfish from the Galician coast (NW Spain) affected by the Prestige oil spill. *Chemosphere* **75** (4), 534–541, doi:10.1016/j.chemosphere.2008.12.003

Walker, G. 1971. A study of the cement apparatus of the cypris larva of the barnacle *Balanus balanoides*. *Marine Biology* **9**, 205–212.

Walker, G. & Youngson, A. 1975. The biochemical composition of *Lepas anatifera* (L.) cement (crustacea: Cirripedia). *Journal of the Marine Biological Association of the United Kingdom* **55** (3), 703–707, doi:10.1017/S0025315400017367

Walther, K., Crickenberger, S.E., Marchant, S., Marko, P.B. & Moran, A.L. 2013. Thermal tolerance of larvae of *Pollicipes elegans*, a marine species with an antitropical distribution. *Marine Biology* **160**, (10), 2723–2732, doi:10.1007/s00227-013-2265-x

Wang, C.S., Svendsen, K.K. & Stewart, R.J. 2010. Morphology of the adhesive system in the sandcastle worm, *Phragmatopoma californica*. In *Biological Adhesive Systems*, I. Grunwald & J. Von Byern (eds). Vienna: Springer-Verlag, 169–179.

Wang, Z., Leary, D.H., Liu, J., Settlage, R.E., Fears, K.P., North, S.H., Mostaghim, A., Essock-Burns, T., Haynes, S.E., Wahl, K.J. & Spillmann, C.M. 2015. Molt-dependent transcriptomic analysis of cement proteins in the barnacle *Amphibalanus amphitrite*. *BMC Genomics* **16** (1), 1–14, doi:10.1186/s12864-015-2076-1

Washington Department of Fish and Wildlife. 2021. *Washington Fishing Regulations Now Online for 2020-2021 Season*. Online. https://wdfw.wa.gov/news/washington-fishing-regulations-now-online-2020-2021-season (Accessed 1 July 2021).

West, L. 1986. Interindividual variation in prey selection by the snail *Nucella (= Thais)* e*marginata*. *Ecology* **67** (3), 798–809, doi:10.2307/1937702

Wiegemann, M. 2005. Adhesion in blue mussels (*Mytilus edulis*) and barnacles (genus *Balanus*): Mechanisms and technical applications. *Aquatic Sciences* **67** (2), 166–176, doi:10.1007/s00027-005-0758-5

Wirtz, P., Araújo, R. & Southward, A.J. 2006. Cirripedia of Madeira. *Helgoland Marine Research* **60** (3), 207–212, doi:10.1007/s10152-006-0036-5

Withers, T.H. 1935. *Catalogue of Fossil Cirripedia in the Department of Geology. Vol. II. Cretaceous*. London: The British Museum (Natural History).

Withers, T.H. 1953. *Catalogue of Fossil Ciripedia in the Department of Geology. III. Tertiary*. London: London: British Museum (Natural History).

Wootton, J.T. 1992. Indirect effects, prey susceptibility, and habitat selection: Impacts of birds on limpets and algae. *Ecology* **73** (3), 981–991.

Wootton, J.T. 1993. Size-dependent competition: Effects on the dynamics vs. the end point of mussel bed succession. *Ecology* **74** (1), 195–206, doi:10.2307/1939514

Wootton, J.T. 1994. Predicting direct and indirect path analysis. *Ecology* **75** (1), 151–165.

Wootton, J.T. 1997. Estimates and tests of per capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* **67** (1), 45–64.

Wootton, J.T. 2010. Experimental species removal alters ecological dynamics in a natural ecosystem. *Ecology* **91** (1), 42–48, doi:10.1890/08-1868.1

Worm, B. & Karez, R. 2002. Competition, coexistence and diversity on rocky shores. In *Competition and Coexistence,* Sommer, U. & Worm, B. (eds). Berlin, Heidelberg: Springer, 133–163.

WoRMS. 2021. Pollicipes *Leach, 1817.* Online. http://www.marinespecies.org/aphia.php?p=taxdetails&id=106101 (accessed on 20 July 2021).

WoRMS Editorial Board. 2021. *World Register of Marine Species*. Online. https://www.marinespecies.org (Accessed on 1 July 2021).

Young, P.S. 2007. The Scalpellomorpha (Crustacea, Cirripedia), with a list of extant species (except the Calanticidae). *GALATHEAReport* **21**, 7–73.

Yule, A.B. & Walker, G. 1987. Adhesion in barnacles. In *Crustacean Issues, 5. Barnacle Biology,* A.J. Southward (ed.). Rotterdam: A. A. Balkema, 389–402.

ZAGAT. 2014. *Percebes: Hunting for Oregon's Secret Ingredient - Zagat Documentaries, Episode 9*. Online. https://www.youtube.com/watch?v=qHVvaXuJpE8 (Accessed on 1 July 2021).

Zevina, G.B. 1981. Barnacles of the suborder Lepadomorpha (Cirripedia, Thoracica) of the world ocean. Part 1: Family Scalpellidae. In *Guides to the Fauna of the USSR*. Leningrad: Zoological Institute of the Academy of Sciences of the USSR, **127**, 406.

Zheden, V., Klepal, W., von Byern, J., Bogner, F.R., Thiel, K., Kowalik, T. & Grunwald, I. 2014. Biochemical analyses of the cement float of the goose barnacle *Dosima fascicularis* – a preliminary study. *Biofouling* **30** (8), 949–963, doi:10.1080/08927014.2014.954557

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