

2017-02-15

# Factors affecting the prevalence of the trematode parasite *Echinostephilla patellae* (Lebour, 1911) in the limpet *Patella vulgata* (L.)

Firth, Louise

<http://hdl.handle.net/10026.1/9112>

---

10.1016/j.jembe.2017.01.026

Journal of Experimental Marine Biology and Ecology

Elsevier BV

---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*

**Disclaimer:** This version is a pre-proof version of the paper. Please see final version of the paper: Firth, L.B., Grant, L.M., Crowe, T.P., Ellis, J.S., Wiler, C., Convery, C. and O'Connor, N.E., 2017. Factors affecting the prevalence of the trematode parasite *Echinostephilla patellae* (Lebour, 1911) in the limpet *Patella vulgata* (L.). *Journal of Experimental Marine Biology and Ecology*. <http://doi.org/10.1016/j.jembe.2017.01.026>

**TITLE:**

Factors affecting the prevalence of the trematode parasite *Echinostephilla patellae* (Lebour, 1911) in the limpet *Patella vulgata* (L.)

**AUTHOR NAMES & AFFILIATIONS:**

Louise B. Firth<sup>1,2</sup>, Lisa M. Grant<sup>2</sup>, Tasman P. Crowe<sup>3</sup>, Jonathan S. Ellis<sup>2</sup>, Christena Wiler<sup>3</sup>, Christopher Convery<sup>4</sup>, Nessa E. O'Connor<sup>4</sup>

1 Ryan Institute and Zoology, National University of Ireland Galway, Ireland

2 Sustainable Earth Institute and School of Geography, Earth & Environmental Science, Plymouth University, UK

3 Earth Institute and School of Biology & Environmental Science, University College Dublin, Ireland

4 Institute of Global Food Security and School of Biological Sciences, Queen's University Belfast, Northern Ireland

**CORRESPONDING AUTHOR:**

Louise Firth: Email - [louise.firth@plymouth.ac.uk](mailto:louise.firth@plymouth.ac.uk), Tel - +44 (0)1752 584977

**PRESENT ADDRESS**

School of Geography, Earth & Environmental Science, Plymouth University,  
UK

### **Abstract**

Parasites are ubiquitous throughout nature and can have dramatic effects on their hosts. Although much is known about the pathology of parasites, the environmental factors influencing the distribution and abundance of parasites are poorly understood. Investigations into these factors could help predict the effect of parasites on the functioning of ecosystems. The limpet *Patella vulgata* is a key grazer on European rocky shores and is the first intermediate host for the trematode parasite, *Echinostephilla patellae*. This study investigated the spatial distribution of *E. patellae* in relation to *P. vulgata* at fourteen rocky shores around Ireland. Despite *P. vulgata* recruiting into rock pools, adults are more abundant on emergent rock and experience greater mortality in pools compared to emergent rock. It has been purported that greater parasite prevalence in pools may be a factor driving this disjunct distribution pattern. Prevalence of infection was compared among rock and pool habitats. Size and sex of the host were also investigated in order to determine whether host phenotype influenced levels of infection prevalence. Results varied considerably among study sites, probably due to the heterogeneity of environmental conditions. No clear pattern emerged in relation to infection prevalence between habitats but this may be owing to the low numbers of limpets collected from pools. There was a significant positive relationship between infection prevalence and increasing host size. Individuals for which sex was indeterminate were more likely to be infected

than distinct males or females, suggesting that infection may be causing castration and subsequent removal of these individuals from the breeding population. We discuss the importance of considering host-parasite dynamics in a period of rapid environmental change.

### **Highlights (3-5 bullets)**

- Environmental factors determining the distribution and abundance of parasites are poorly understood
- There was no difference in infection prevalence between rock pools and emergent rock
- There was a positive relationship between infection prevalence and limpet (host) size
- Individuals for which sex was indeterminable were more likely to be infected than males or females, suggesting castration of infected individuals

### **Keywords**

Castration, host-parasite dynamics, Ireland, parasite ecology, reproduction, rocky intertidal, spatial epidemiology

## 1 Introduction

Parasites are pervasive and important components of natural systems globally. Rohde (1982) estimated that 40% of all known species were parasitic with recent estimates suggesting that vertebrates are parasitised by 75,000-300,000 helminth species alone (Dobson et al. 2008). By definition parasites impose a direct negative effect on their individual host with impacts ranging from minor metabolic changes and behavioural changes to severe tissue damage and mortality (Huxham et al. 1993; Chapuis, 2009). A growing body of research is revealing that parasites also have significant indirect effects on community structure and functioning, forming an estimated 75% of key links in food webs (Lafferty et al. 2006; but see Byers, 2009), altering outcomes of biotic interactions (Raffel et al. 2008; Dick et al. 2010; O'Shaughnessy et al. 2014), and influencing energy flow and biomass production (Kuris et al. 2008).

For parasites with multiple hosts, natural variation in the proximity to and abundance of hosts is often a key determinant of larval transmission (Hechinger and Lafferty 2005; Byers et al. 2008). Environmental gradients and habitat features can also affect the distribution and abundance of parasites if they attract host populations (Thieltges, 2007; Byers et al. 2015) or alter processes of interaction and transmission (Caceres et al. 2006).

Parasites may be highly sensitive to environmental factors such as temperature, salinity and light (Pechenik and Fried 1995; Thieltges and Rick 2006; Studer and Poulin 2012), in addition to anthropogenic drivers such as pollutants (Carroll et al. 1990; Khan and Fallon, 2013), fishing activity (Copeland et al. 1987) and road density (Altman and Byers, 2014). Thus,

natural variability in the biotic and abiotic environment can influence parasites through direct and indirect pathways. The abundance of parasites, like most free-living organisms, varies substantially, often at multiple spatial and temporal scales (Fredensborg et al. 2006; Blakeslee et al. 2012).

Characterising this variability and the factors that influence it is imperative to determining larger ecological and evolutionary consequences of parasites.

Intertidal rocky shores are exposed to a range of different environmental gradients, which are major drivers of diversity patterns (Menge and Sutherland, 1976; Raffaelli and Hawkins, 1996; Firth et al. 2014a). On rocky shores in northwest Europe the common limpet *Patella vulgata* (L.) is abundant throughout the intertidal and is considered a key grazer (Hawkins and Hartnoll 1983; O'Connor and Crowe, 2005; Moore et al. 2007). It is a protandrous hermaphrodite, becoming sexually mature around 9 months transitioning from male to female at around 2-3 years (Orton et al. 1956; LeQuesne and Hawkins, 2006). *P. vulgata* is preyed upon by a range of predators including crabs, fish (Silva et al. 2004, 2008, 2010) and birds, including oystercatchers, *Haematopus ostralegus* del Hoyo and Collar, 2014 (Feare, 1971; Coleman et al. 1999, 2004). Although juveniles are known to recruit into rock pools (Bowman and Lewis, 1977), as adults they are typically more abundant on emergent rock (i.e. rock not covered by water) than in pools (Firth and Crowe, 2008). Experiments have shown that adult *P. vulgata* transplanted into rock pools experienced greater mortality than they did on emergent rock (Firth and Crowe, 2010) and compete with the congeneric species *P. ulyssiponensis* (Gmelin, 1791; Firth and Crowe, 2010) and *P.*

*depressa* (Pennant, 1777; Firth et al. 2009). Little is known about the factors driving mortality in pools but it has been purported that greater rates of parasitism in pools may be one of many potential factors causing this mortality, thus driving this disjunct distribution pattern (Firth and Crowe, 2008).

The trematode *Echinostephilla patellae* (Lebour, 1911) can infect up to three hosts throughout its life cycle (Kollien, 1996; Prinz et al. 2010a). Sporocysts and redial stages infect limpets (the primary intermediate host). Cercarial stages emerge from limpets, undergo a free-living stage before infecting either limpets or mussels (the secondary intermediate hosts) where they encyst to become metacercariae. If infected limpets are consumed by oystercatchers (the definitive host), the life cycle is completed as metacercariae develop into adult flukes. Adults produce miracidia which are egested with faeces and consumed by grazing limpets – thus beginning the life cycle again.

Previous studies have reported higher infection rates in rock pools than on emergent rock (Crewe, 1951; Thomas, 1965; Copeland et al. 1987), whilst others have found the opposite pattern (Kollien, 1996). All of the above studies (except Crewe, 1951) were conducted at either a single site or a small number of sites quite close together. As parasite infection rates are known to increase with increasing temperatures (Prinz et al. 2010b, 2011), it is timely to revisit some of these older studies following a period of rapid environmental change, including continued ocean warming and coastal development (Firth and Hawkins, 2011; Hawkins et al. 2013, 2016; Mieszkowska et al. 2014).

We aimed to characterise the patterns of parasite prevalence in relation to host sex (indeterminate and male/female), size and habitat (emergent rock and pool). Specific hypotheses were: (1) prevalence of infection would be greater in pools than on emergent rock; (2) “indeterminate” individuals would exhibit greater infection prevalence than male/female individuals; and (3) there would be a significant positive relationship between infection prevalence and increasing host size.

## **2 Material and Methods**

### **2.1. Study sites**

A total of fourteen rocky shore sites were surveyed around Ireland (Figure 1). Kilkee, Spiddal, Muighinis and Dog’s Bay were sampled in September-October 2012; Millisle, Portavogie, Kearney Point, Ardglass, Clanmagy and Kilkeel were sampled in September-November 2013; and Rush, Portmarnock, Sandycove and Bray were sampled in October-November 2014. Sampling was done in these months because the timing is before the spawning period for *P. vulgata* and therefore gonads were easily identifiable; in summer they are harder to distinguish (Orton et al. 1956). At each location, a minimum of 50 individuals was collected from emergent rock; a further minimum of 50 individuals was also collected from pools at a subset of the locations (Table 1, Rush, Portmarnock, Sandycove, Bray, Kilkee, Spiddal, Muighinis, Dog’s Bay). Due to time constraints only 42 individuals in total were collected from Spiddal.



## 2.2. Sample processing

In the laboratory, the foot of each limpet was dissected away while the sample was still semi-frozen as it proved to be the most efficient and least destructive method. After removal of the foot, the gonads were clearly visible. Using the methods described by Orton et al. (1956), sex was determined as male, female (grouped together as “male/female”) or “indeterminate”. Following McCarthy et al. (2008) we defined “indeterminate” individuals as those that had no discernible gonad, a gonad no longer identifiable as male or female, or a shrunken gonad with an appearance matching neither male nor female.

Maximum shell length was measured using vernier callipers. In some individuals, infection by *E. patellae* was immediately visible following removal of the foot. In these cases, cercariae could often be seen burrowing through the gonad, which in severe cases distorted the colouring of the gonad causing it to appear white or grey. If there was no presence of cercariae in the gonad, the limpet was released from its shell by dissecting along the muscular shell attachment. Following this, the tunica propria was gently dissected away the using a scalpel and forceps to reveal the visceral mass. Cercariae or metacercarial cysts were often found within the visceral mass, however, if none were initially detected, a gastric smear was used to fully discount the possibility of parasitism in specimens that were not visibly infected. This was done by emptying the contents of the digestive gland into a petri dish, diluting with water using a pipette and investigating under a microscope.

## 2.3. Statistical analyses

Differences in infection prevalence among sex and habitat categories were tested using chi-squared test of association. In order to test for differences in infection prevalence and limpet size, limpets were grouped into 1 mm size categories; % parasitism for each size category was calculated and tested using regression analysis.

### 3 Results

Of the total of 1580 limpets that were destructively sampled during this study 440 (28%) were infected (Table 1). Infection prevalence varied considerably among sites with the highest infections observed in Rush (83%) and Portmarnock (59%) and lowest observed in Kearney Point (4%), Dog's Bay (4%) and Bray (3%). Any sites where fewer than 10 individuals were infected were omitted from statistical analyses (Figure 1).

Table 1. Summary of the (a) total numbers of individuals that were collected at each site; (b) total number of infected individuals at each site; and (c) % of infected individuals in each sex category at each site.

Site no.	Site name	(a) Total number of individuals			(b) Number of infected individuals			(c) % infected		
		Male/Female	Indeterminate	Total	Male/Female	Indeterminate	Total	Male/Female	Indeterminate	Total
1	Millisle	47	3	50	1	3	4	25	75	8
2	Portavogie	45	5	50	3	5	8	38	63	16
3	Kearney Point	48	2	50	0	2	2	0	100	4
4	Ardglass	39	11	50	2	11	13	15	85	26
5	Clanmagy	48	2	50	1	2	3	33	67	6
6	Kilkeel	44	6	50	0	6	6	0	100	12
7	Rush	150	50	200	116	50	166	70	30	83
8	Portmarnock	147	53	200	64	53	117	55	45	59
9	Sandycove	196	4	200	28	4	32	87	13	16
10	Bray	173	5	178	2	3	5	40	60	3
11	Kilkee	125	38	163	7	37	44	16	84	27
12	Spiddal	36	6	42	1	2	3	33	67	7
13	Muighinis	154	18	172	16	16	32	50	50	19
14	Dog's Bay	112	13	125	0	5	5	0	100	4
	All sites	1364	216	1580	241	199	440	55	45	28

### 3.1. Sex comparison

Of the 1580 individuals that were destructively sampled during this study, the sex was determinable (male/female) in 1364 individuals (86%) and the sex was indeterminable in 216 individuals (14%). Of the 440 that were infected 241 were male/female (55%) and 199 were indeterminate (45%). Of the 216 that were indeterminate 199 were infected (92%) and 17 were uninfected (8%). Abundances varied considerably among sites, but there was a general trend for greater infection prevalence in “indeterminate” individuals compared to male/female individuals at all sites and this was statistically significant for five of the six sites for which a statistical comparison was made (Figure 1, Table 2).

Figure 1. (a) Map of Ireland showing the distribution of the 14 study sites. Pie charts illustrate the relative proportions of infected individuals for which sex was distinguishable as either male or female – classed as “male/female” (grey) or sex was indistinguishable – classed as “indeterminate” (black). The relative size of the pie charts depicts the proportion of the overall population that was infected. (b) Bar chart illustrating the total number of parasitised individuals (red line) and the percentage of “indeterminate” and male/female individuals (black and grey bars respectively) that were infected at each site.

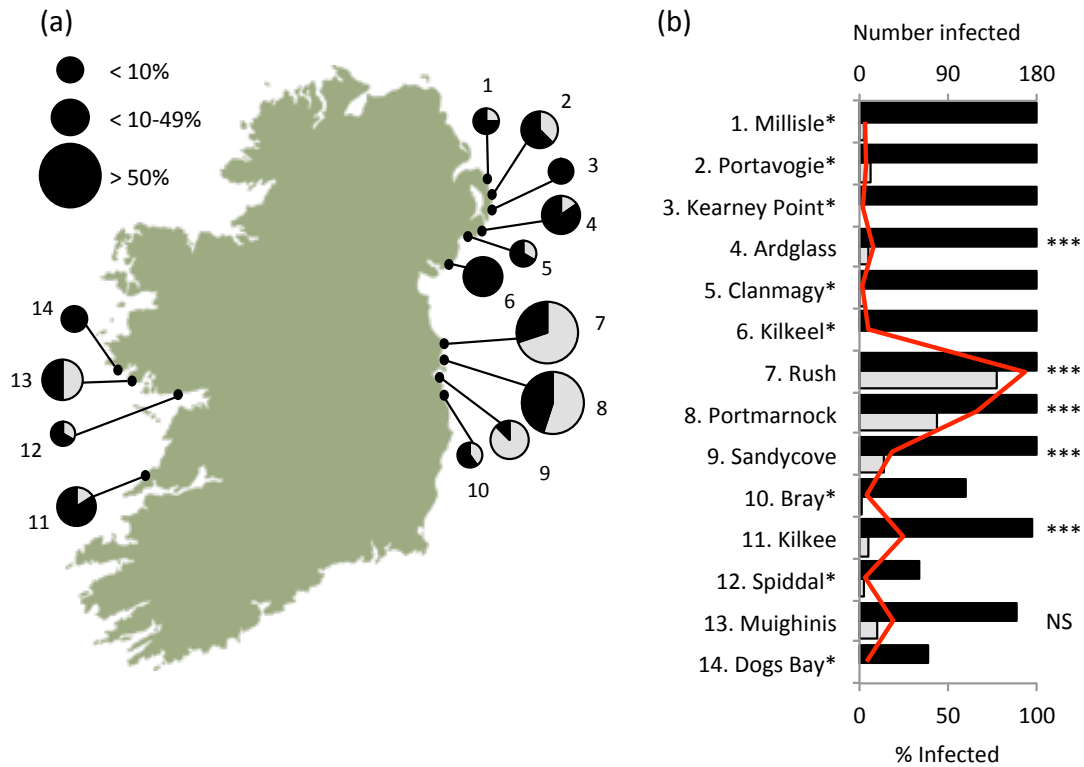


Table 2. Summary of results of  $\chi^2$  analyses (1 df) for sex and habitat comparisons. Sites with fewer than 10 infected individuals were omitted from the analyses. Note that no habitat comparison was performed for Ardglass. I = "Indeterminate"; M/F = Male/Female; R = Rock; P = Pool; \*  $P < 0.05$ ;  $P < 0.001$ .

Site no.	Site name	Sex: Indeterminate vs Male/Female			Habitat: Pool vs Rock		
		$\chi^2$	<i>P</i>	Outcome	$\chi^2$	<i>P</i>	Outcome
4	Ardglass	26.7	0.0001	I>M/F***	-	-	-
7	Rush	12.1	0.0005	I>M/F***	5.989	0.0144	P>R*
8	Portmarnock	48.9	0.0001	I>M/F***	1.318	0.2509	P=R
9	Sandycove	15.5	0.0001	I>M/F***	1.823	0.177	P=R
11	Kilkee	45.4	0.0001	I>M/F***	2.651	0.1035	P=R
13	Muighinis	0.0	1.0000	I=M/F	15.427	0.0001	R>P***
	All sites	353.4	0.0001	I>M/F***	10.713	0.0011	P>R*

### 3.2. Size comparison

Due to low numbers of infected individuals at many sites (Table 1), data for all sites were combined and only size classes for which there were > 10 individuals were included in the analysis (30-51 mm inclusive). There was a

strong significant positive relationship between infection prevalence and increasing shell length (Figure 2,  $R^2 = 0.64$ ,  $P < 0.0001$ ).

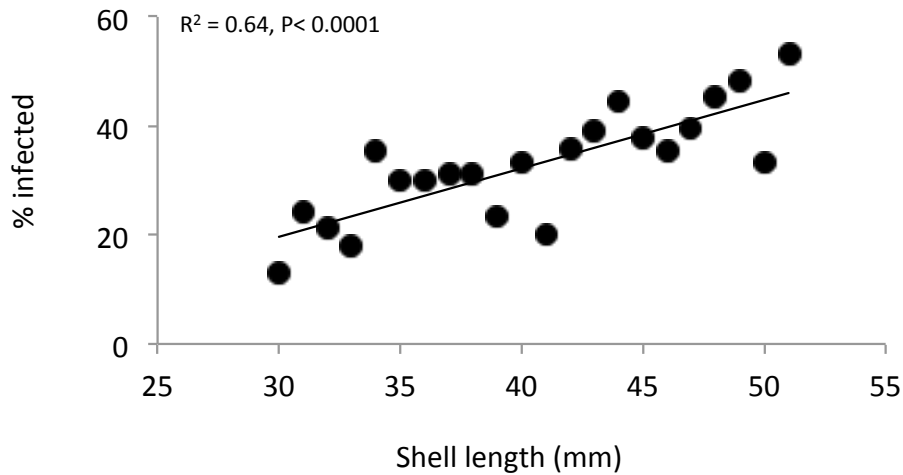


Figure 2. Relationship between shell length (mm) and infection prevalence (%) in *Patella vulgata*. Each dot represents the % of infected individuals for that size class. Data pooled across sites and only size classes with > 10 individuals are included here (30-51 mm inclusive).

### 3.3. Habitat comparison

Of the eight sites which were specifically sampled for the habitat comparison only five had sufficient numbers of infected individuals (> 10) to perform statistical analyses (Table 2). Results were variable with the majority of sites showing no significant difference in infection prevalence among habitats (Table 2). Only two sites exhibited significant results and these showed opposing patterns with pools having significantly greater infection prevalence than rock at Rush (on the east coast of Ireland) and rock having significantly greater infection prevalence than pools at Muighnis (on the west coast; Figure 1, Table 2).

#### 4 Discussion

Using data from 14 sites spanning the east and west coasts of Ireland we provide an account of the broad-scale distribution of *E. patellae* infection of the limpet *P. vulgata* in relation to host sex and size and habitat features that may be important for transmission. Results were highly variable among sites with infection prevalence ranging from 3% at Bray to 83% at Rush (Figure 1, Table 1). Low infection rates (< 15%) have been reported in the majority of previous studies (e.g. Rees, 1934; Crewe, 1951; Thomas, 1965; James, 1968; Prinz et al. 2010b), but studies in Northern Ireland (Copeland et al. 1987) and Scotland (Kollien, 1996) reported up to 90% of *P. vulgata* to be infected. Kollien (1996) reported high prevalence (10-90%) from high shore samples suggesting that prevalence of infection is greatest in areas where birds feed (Crewe, 1951). Copeland et al. (1987) found that prevalence of infection was substantially greater closer to the busy fishing port of Portavogie, where it was reasoned that high densities of birds attracted by the fish offal possibly led to higher infection prevalence. In the present study only 16% of individuals were infected at Portavogie, considerably lower than what was observed by Copeland et al. (1987); this could be linked to the decline of the fishing industry along the Ards Peninsula (Kelly, 2002). High infection rates at Rush and Portmarnock in the current study may in part be explained by proximity to sewage and groundwater outflows (O'Connor, 2013) in addition to observed high densities of mussels (the secondary intermediate host).

As hypothesised, the prevalence of infection was significantly greater in “indeterminate” individuals than male/females at five of the six sites for which formal statistical comparisons were possible (Crewe, 1951; Thomas, 1965; James, 1968). Nine of the fourteen sites exhibited 100% infection prevalence in “indeterminate” individuals (Figure 2b). The pattern is striking, irrespective of low numbers of either indeterminate or infected individuals at six of nine sites (Table 1). Infection by parasites commonly reduces the reproductive output of the host and has been reported to lead to castration in a range of molluscan groups (see Mouritsen and Poulin, 2002 for review). *P. vulgata* is a boreal species and is sensitive to increasing temperatures. In a study comparing the breeding phenology of *P. vulgata* between the colder 1940s and the warmer 2000s Moore et al. (2011) found that during warmer periods, fewer *P. vulgata* reach reproductive maturity and the breeding season is shortened; the opposite was found for the Lusitanian species *P. depressa*. Increasing temperatures have been shown to have a positive effect on parasite infection rates (Poulin, 2006; Rohr and Raffel, 2010; Paull and Johnson, 2011) and the interactive effects of parasite loads and impacts on breeding phenology (Moore et al. 2011) may have implications for population dynamics of *P. vulgata* and wider community and ecosystem structure and functioning.

As hypothesised there was a significant positive relationship with infection prevalence and increasing limpet size (Rees, 1935; Crewe, 1951; Kollien, 1996; Copeland et al. 1987). Although some authors have described accelerated growth rates (“gigantism”) in response to parasitism (e.g.

Minchella et al. 1985; Mouritsen and Jensen, 1994), it is assumed that this is not the case here. As *P. vulgata* is a protandrous hermaphrodite (LeQuesne and Hawkins, 2006) changing from male to female, typically the larger individuals are female. Oystercatchers, the definitive host of *E. patellae* (Kollien, 1996) preferentially feed on larger, solitary individuals which are easier to dislodge (Feare, 1971; Coleman et al. 1999). This preference for larger individuals perpetuates the life cycle of *E. patellae* by increasing the chances that infected individuals will be consumed by the definitive host, thus completing the life cycle. A recent study by Borges et al. (2016) found that simulated exploitation of the largest individuals of *P. vulgata* led to an earlier induced sex change at smaller sizes. The removal of larger individuals may have dramatic consequences for population and community dynamics.

The results from this study failed to support the hypothesis that prevalence of infection would be greater in rock pools than on emergent rock. Despite attempts to acquire equal numbers of limpets from both habitats, this was only achieved at three (Rush, Portmarnock, Sandycove) of the eight sites. At the remainder of the sites (except Spiddal) numbers of *P. vulgata* collected from pools ranged from 29 (Dog's Bay) to 72 (Muighinis). As prevalence of infection is generally low, it is very possible that these numbers were too low for any meaningful comparisons to be made. Future attempts to test infection prevalence among habitats should ensure that sufficient numbers (i.e. > 100 individuals) are collected from each habitat. This may prove difficult for some sites as *P. vulgata* are known to be more common on emergent rock (Firth and Crowe, 2008), therefore, care should be taken when selecting sites to



ensure that sufficient numbers can be achieved. Furthermore it should be noted that all sites were only sampled in a single year, and in different years. Repeated monitoring over consecutive years would yield valuable information about temporal variability. Future studies should also quantify temperature variation among habitats, oystercatcher abundances at selected sites and employ histopathology to unequivocally assign a causal effect of parasitism on the health of the gonad.

The importance of microhabitat for infection transmission is of particular interest under current sustainable coastal development practice. An emerging body of research is advocating the incorporation of “desirable habitat features” such as pits, crevices and rock pools into constructed coastal infrastructure (seawalls, rock revetments; Moschella et al. 2005; Dafforn et al. 2015; Dyson & Yocom, 2015; Bishop et al. 2016; Firth et al. in review). Much of this research to date has focused on the enhancement of native benthic biodiversity (Martins et al. 2010; Firth et al. 2013a,b, 2014; Loke et al. 2015; Evans et al. 2016) and the potential role of these habitat features in host-parasite dynamics has been overlooked to date.

## **5 Conclusions**

Parasites are ubiquitous throughout nature and can have dramatic effects on their hosts. Although much is known about the pathology of parasites, the factors that influence the distribution and abundance of parasites within an environment are relatively understudied. The majority of studies investigating the effect of environmental factors on *E. patellae* have been conducted either

on small spatial scales or a long time ago. The present study found that infection prevalence was greater in larger individuals and in individuals for which sex was indeterminable; indicating that infection was causing castration and removal from the breeding population. *P. vulgata* is a key grazer on European rocky shores and is sensitive to environmental change. Continued warming may affect host-parasite dynamics with indirect consequences for community dynamics and ecosystem functioning.

### **Acknowledgements**

The authors wish to thank Eoin MacLoughlin and Josephine Carlin for assistance with sample collection and processing.

### **Figure titles**

Figure 1. (a) Map of Ireland showing the distribution of the 14 study sites. Pie charts illustrate the relative proportions of infected individuals for which sex was distinguishable as either male or female – classed as “male/female” (grey) or sex was indistinguishable – classed as “indeterminate” (black). The relative size of the pie charts depicts the proportion of the overall population that was infected. (b) Bar chart illustrating the total number of parasitised individuals (red line) and the percentage of “indeterminate” and male/female individuals (black and grey bars respectively) that were infected at each site.

Figure 2. Relationship between shell length (mm) and infection prevalence (%) in *Patella vulgata*. Each dot represents the % of infected individuals for

that size class. Data pooled across sites and only size classes with > 10 individuals are included here (30-51 mm inclusive).

### Table titles

Table 1. Summary of the (a) total numbers of individuals that were collected at each site; (b) total number of infected individuals at each site; and (c) % of infected individuals in each sex category at each site.

Table 2. Summary of results of  $\chi^2$  analyses (1 df) for sex and habitat comparisons. Sites with fewer than 10 infected individuals were omitted from the analyses. Note that no habitat comparison was performed for Ardglass. I = "Indeterminate"; M/F = Male/Female; R = Rock; P = Pool; \*  $P < 0.05$ ;  $P < 0.001$ .

### Literature cited

Altman, I., Byers, J.E. 2014. Large-scale spatial variation in parasite communities influenced by anthropogenic factors. *Ecology*, 95(7), 1876-1887.

Bishop, M.J., Mayer Pinto, M., Morris, R.L., Loke, L.H.L., Firth, L.B., Hawkins, S.J., Naylor, L.A., Chee, S.-Y., Airoidi, L., Dafforn, K.A. 2016. Effects of ocean sprawl on connectivity: impacts and solutions. *J. Exp. Mar. Biol. Ecol.* **THIS ISSUE**

Blakeslee, A.M., Altman, I., Miller, A.W., Byers, J.E., Hamer, C.E., Ruiz, G.M. 2012. Parasites and invasions: a biogeographic examination of parasites and hosts in native and introduced ranges. *J. Biogeogr.* 39(3), 609-622.

Borges, C.D.G., Hawkins, S.J., Crowe, T.P., Doncaster, C.P. 2016. The influence of simulated exploitation on *Patella vulgata* populations: protandric sex change is size-dependent. *Ecol. Evol.* doi:10.1002/ece3.1872

Bowman, R.S., Lewis, J.R. 1977. Annual fluctuations in the recruitment of *Patella vulgata* L. *J. Mar. Biol. Assoc. UK* 57, 793–815.

Byers, J.E., Blakeslee, A.M., Linder, E., Cooper, A.B., Maguire, T.J. 2008. Controls of spatial variation in the prevalence of trematode parasites infecting a marine snail. *Ecology*, 89(2), 439-451.

Byers, J.E. 2009. Including parasites in food webs. *Trends in Parasitology*, 25(2), 55-57.

Byers, J.E., Malek, A.J., Quevillon, L.E., Altman, I., Keogh, C.L. 2015. Opposing selective pressures decouple pattern and process of parasitic infection over small spatial scale. *Oikos*, 124(11), 1511-1519.

Cáceres, C.E., Hall, S.R., Duffy, M.A., Tessier, A.J., Helmle, C., MacIntyre, S. 2006. Physical structure of lakes constrains epidemics in *Daphnia* populations. *Ecology*, 87(6), 1438-1444.

Carrol, H., Montgomery, W.I., Hanna, R.E.B. 1990. Dispersion and abundance of *Maritrema arenaria* in *Semibalanus balanoides* in north-east Ireland. *J. Helminth.* 64(02), 151-160.

Chapuis, E. 2009. Correlation between parasite prevalence and adult size in a trematode-mollusc system: evidence for evolutionary gigantism in the freshwater snail *Galba truncatula*? *J. Moll. Stud.* 75(4), 391-396.

Coleman, R.A., Goss-Custard, J.D., dit Durell, S.E.L.V., Hawkins, S.J. 1999. Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. *Mar. Ecol. Prog. Ser.* 183, 253-261.

Coleman, R.A., Browne, M., Theobalds, T. 2004. Aggregation as a defense: limpet tenacity changes in response to simulated predator attack. *Ecology*, 85(4), 1153-1159.

Crewe, W. 1951. The occurrence of *Cercaria patellae* Lebour (Trematoda) and its effects on the host; with notes on some other helminth parasites of British limpets. *Parasitology*, 41(1-2), 15-22.

Dafforn, K.A., Glasby, T.M., Airoidi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L. 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. *Front. Ecol. Env.* 13(2), 82-90.

Dick, J.T., Armstrong, M., Clarke, H.C., Farnsworth, K.D., Hatcher, M.J., Ennis, M., Kelly, A., Dunn, A.M. 2010. Parasitism may enhance rather than reduce the predatory impact of an invader. *Biol. Lett.* rsbl20100171.

Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F., Jetz, W. 2008. Homage to Linnaeus: How many parasites? How many hosts?. *Proc. Nat. Acad. Sci.* 105(Supplement 1), 11482-11489.

Dyson, K., Yocom, K. 2015. Ecological design for urban waterfronts. *Urban Ecosyst.* 18(1), 189-208.

- Evans, A.J., Firth, L.B., Hawkins, S.J., Morris, E.S., Goudge, H., Moore, P.J. 2016. Drill-cored rock pools: an effective method of ecological enhancement on artificial structures. *Mar. FW Res.*, 67(1), 123-130.
- Feare, C.J. 1971. Predation of limpets and dogwhelks by oystercatchers. *Bird Study*, 18(3), 121-129.
- Firth, L. B., Crowe, T. P. (2008). Large-scale coexistence and small-scale segregation of key species on rocky shores. *Hydrobiologia*, 614(1), 233-241.
- Firth, L. B., Crowe, T. P., Moore, P., Thompson, R. C., Hawkins, S. J. (2009). Predicting impacts of climate - induced range expansion: an experimental framework and a test involving key grazers on temperate rocky shores. *Glob. Change Biol.* 15(6), 1413-1422.
- Firth, L.B., Crowe, T.P. 2010. Competition and habitat suitability: small-scale segregation underpins large-scale coexistence of key species on temperate rocky shores. *Oecologia*, 162(1), 163-174.
- Firth, L.B., Hawkins, S.J. 2011. Introductory comments-Global change in marine ecosystems: Patterns, processes and interactions with regional and local scale impacts. *J. Exp. Mar. Biol. Ecol.*, 400(1), 1-6.
- Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P., Jackson, J., Knights, A.M., Hawkins, S.J. 2013a. The importance of water - retaining features for biodiversity on artificial intertidal coastal defence structures. *Divers. Distrib.* 19(10), 1275-1283.
- Firth, L.B., Mieszkowska, N., Thompson, R.C., Hawkins, S.J. 2013b. Climate change and adaptational impacts in coastal systems: the case of sea defences. *Env. Sci. Proc. Impact.* 15(9), 1665-1670.
- Firth, L.B., Schofield, M., White, F.J., Skov, M.W., Hawkins, S.J. 2014a. Biodiversity in intertidal rock pools: informing engineering criteria for artificial habitat enhancement in the built environment. *Mar. Env. Res.*, 102,122-130.
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoidi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J., Hawkins, S.J. 2014b. Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. *Coast. Engineer.* 87, 122-135.
- Firth, L.B., Knights, A.M., Thompson, R.C., Mieszkowska, N., Bridger, D., Evans, A., Moore, P.J., O'Connor, N.E., Sheehan, E.V., Hawkins, S.J. 2016. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanogr. Mar. Biol. Ann. Rev.* 54, 189-262.

- Fredensborg, B.L., Mouritsen, K.N., Poulin, R. 2006. Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail—from small to large scale. *Mar. Biol.* 149(2), 275-283.
- Hawkins, S.J., Hartnoll, R.G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.* 21, 195-282.
- Hawkins, S.J., Firth, L.B., McHugh, M., Poloczanska, E.S., Herbert, R.J.H., Burrows, M.T., Kendall, M.A., Moore, P., Thompson, R.C., Jenkins, S.R., Sims, D.W. 2013. Data rescue and re-use: recycling old information to address new policy concerns. *Mar. Pol.* 42, 91-98.
- Hawkins, S.J., Mieszkowska, N., Firth, L.B., Bohn, K., Burrows, M.T., MacLean, M.A., Thompson, R.C., Chan, B.K.K., Little, C., Williams, G.A. 2016. Looking backwards to look forwards: the role of natural history in temperate reef ecology. *Mar. FW Res.* 67(1), 1-13.
- Hechinger, R.F., Lafferty, K.D. 2005. Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proc. R. Soc. Lond. B: Biol. Sci.* 272(1567), 1059-1066.
- Huxham, M., Raffaelli, D., Pike, A. 1993. The influence of *Cryptocotyle lingua* (Digenea: Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia); an ecological approach. *J. Exp. Mar. Biol. Ecol.* 168(2), 223-238.
- James, B.L. 1968. The occurrence of larval Digenea in ten species of intertidal prosobranch molluscs in Cardigan Bay. *J. Nat. Hist.* 2(3), 329-343.
- Khan, A.R., Fallon, P.G. 2013. Helminth therapies: translating the unknown unknowns to known knowns. *Int. J. Parasit.* 43(3), 293-299.
- Kollien, A.H. 1996. *Cercaria patellae* Lebour, 1911 developing in *Patella vulgata* is the cercaria of *Echinostephilla patellae* (Lebour, 1911) n. comb.(Digenea, Philophthalmidae). *Syst. Parasitol.* 34(1), 11-25.
- Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J. 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature*, 454(7203), 515-518.
- Lafferty, K.D., Dobson, A.P., Kuris, A.M. 2006. Parasites dominate food web links. *Proc. Nat. Acad. Sci.* 103(30), 11211-11216.
- Lebour, M.V. 1911. A review of the British marine cercariae. *Parasitology* 4(04), 416-456.
- Le Quesne, W.J.F., Hawkins, S.J. 2006. Direct observations of protandrous sex change in the patellid limpet *Patella vulgata*. *J. Mar. Biol. Assoc. UK* 86(01), 161-162.

- Loke, L.H., Todd, P.A. 2015. Structural complexity and component type increase intertidal biodiversity independently of area. *Ecology*. In press. DOI <http://dx.doi.org/10.1890/15-0257.1>.
- Martins, G.M., Thompson, R.C., Neto, A.I., Hawkins, S.J., Jenkins, S.R. 2010. Enhancing stocks of the exploited limpet *Patella candei* d'Orbigny via modifications in coastal engineering. *Biol. Conserv.* 143(1), 203-211.
- McCarthy, M., Woosnam, P., Culloty, S.C. 2008. Histological investigation of the reproductive cycles of the limpets *Patella vulgata* and *Patella ulysiponensis*. *Mar. Biol.* 153(5), 871-877.
- Menge, B.A., Sutherland, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.*, 110, 351-369.
- Mieszkowska, N., Sugden, H., Firth, L.B., Hawkins, S.J. 2014. The role of sustained observations in tracking impacts of environmental change on marine biodiversity and ecosystems. *Phil. Trans. R. Soc. Lond. A*: 372(2025), 20130339.
- Minchella, D.J. 1985. Host life-history variation in response to parasitism. *Parasitology*, 90(01), 205-216.
- Moore, P., Thompson, R.C., Hawkins, S.J. 2007. Effects of grazer identity on the probability of escapes by a canopy-forming macroalga. *J. Exp. Mar. Biol. Ecol.* 344(2), 170-180.
- Moore, P.J., Thompson, R.C., Hawkins, S.J. 2011. Phenological changes in intertidal conspecific gastropods in response to climate warming. *Glob. Change Biol.* 17(2), 709-719.
- Moschella, P. S., Abbiati, M., Åberg, P., Airoidi, L., Anderson, J. M., Bacchiocchi, F., ... & Granhag, L. (2005). Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. *Coast. Engineer.* 52(10), 1053-1071.
- Mouritsen, K.N., Jensen, K.T. 1994. The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant)(Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* 181(1), 53-66.
- Mouritsen, K.N., Poulin, R. 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology*, 124(07), 101-117.
- O'Connor, N.E., & Crowe, T.P. 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology*, 86(7), 1783-1796.

O'Connor, N.E. 2013. Impacts of sewage outfalls on rocky shores: Incorporating scale, biotic assemblage structure and variability into monitoring tools. *Ecol. Indic.* 29, 501-509.

Orton, J.H., Southward, A.J., Dodd, J.M. 1956. Studies on the biology of limpets: II. The breeding of *Patella vulgata* L. in Britain. *J. Mar. Biol. Assoc. UK*, 35(01), 149-176.

O'Shaughnessy, K.A., Harding, J.M., Burge, E.J. 2014. Ecological effects of the invasive parasite *Loxothylacus panopaei* on the flatback mud crab *Eurypanopeus depressus* with implications for estuarine communities. *Bull. Mar. Sci.* 90(2), 611-621.

Paull, S.H., Johnson, P.T. 2011. High temperature enhances host pathology in a snail-trematode system: possible consequences of climate change for the emergence of disease. *Fresh. Biol.* 56(4), 767-778.

Pechenik, J.A., Fried, B. 1995. Effect of temperature on survival and infectivity of *Echinostoma trivolvis* cercariae: a test of the energy limitation hypothesis. *Parasitology* 111, 373-373.

Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology*, 132(01), 143-151.

Poulin, R. 2010. Parasite manipulation of host behavior: an update and frequently asked questions. *Adv. Study Behav.* 41, 151-186.

Prinz, K., Kelly, T.C., O'Riordan, R.M., Culloty, S.C. 2010a. Occurrence of macroparasites in four common intertidal molluscs on the south coast of Ireland. *Mar. Biodiv. Record.* 3, e89.

Prinz, K., Kelly, T.C., O'Riordan, R.M., Culloty, S.C. 2010b. Temporal variation in prevalence and cercarial development of *Echinostephilla patellae* (Digenea, Philophthalmidae) in the intertidal gastropod *Patella vulgata*. *Acta Parasitologica*, 55(1), 39-44.

Prinz, K., Kelly, T.C., O'Riordan, R.M., Culloty, S.C. 2011. Factors influencing cercarial emergence and settlement in the digenean trematode *Parorchis acanthus* (Philophthalmidae). *J. Mar. Biol. Assoc. UK.*, 91(08), 1673-1679.

Raffaelli, D. Hawkins, S.J. 1996. Intertidal ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Raffel, T.R., Martin, L.B., Rohr, J.R. 2008. Parasites as predators: unifying natural enemy ecology. *Trend. Ecol. Evol.* 23(11), 610-618.

Rees, P.G. 1934. *Cercaria patellae* Lebour, 1911, and its effect on the digestive gland and gonads of *Patella vulgata*. *Proc. Zool. Soc. Lond.* 104, 45-53



Rohde, K. 1982. Ecology of Marine Parasites. In: H. Heatwole, ed. Australian Ecology Series. St Lucia, QLD, Australia: University of Queensland Press, p. 245.

Silva, A., Boaventura, D., Flores, A., Re, P., Hawkins, S.J. 2004. Rare predation by the intertidal crab *Pachygrapsus marmoratus* on the limpet *Patella depressa*. J. Mar. Biol. Assoc. UK, 84(02), 367-370.

Silva, A.C.F., Hawkins, S.J., Boaventura, D.M. and Thompson, R.C. 2008. Predation by small mobile aquatic predators regulates populations of the intertidal limpet *Patella vulgata* (L.). J. Exp. Mar. Biol. Ecol., 367(2), 259-265.

Silva, A.C., Hawkins, S.J., Clarke, K.R., Boaventura, D.M. Thompson, R.C. 2010. Preferential feeding by the crab *Necora puber* on differing sizes of the intertidal limpet *Patella vulgata*. Mar. Ecol. Prog. Ser., 416, 179-188.

Studer, A., Poulin, R. 2012. Effects of salinity on an intertidal host–parasite system: Is the parasite more sensitive than its host?. J. Exp. Mar. Biol. Ecol. 412, 110-116.

Rohr, J.R., Raffel, T.R. 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. Proc. Nat. Acad. Sci., 107(18), 8269-8274.

Thieltges, D.W., Rick, J. 2006. Effect of temperature on emergence, survival and infectivity of cercariae of the marine trematode *Renicola roscovita* (Digenea: Rencolidae). Disease. Aquat. Org. 73(1), 63.

Thieltges, D.W. 2007. Habitat and transmission–effect of tidal level and upstream host density on metacercarial load in an intertidal bivalve. Parasitology, 134(04), 599-605.