1   **Longterm variation of trochid populations in an Irish sea lough**

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14   Running Head: Longterm population dynamics of Irish trochids

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ABSTRACT

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22   Snapshot assessments of species, which live for a number of years, are often misleading if
23   they are conducted at an inappropriately short temporal scale. Densities of the trochid
24   gastropods *Steromphala umbilicalis* (da Costa, 1778) and *S. cineraria* (Linnaeus, 1758)
25   fluctuated widely between 1996 and 2014 at 10 rocky-shore sites within Lough Hyne,
26   southwest Ireland. Between 2014 and 2019, the abundance of *S. cineraria* decreased to levels
27   not seen in the previous two decades. This significant reduction was possibly in response to
28   extreme dissolved oxygen fluctuations related to eutrophication of the semi-enclosed lough.
29   *Steromphala umbilicalis* showed low density in 2018 and 2019, but this was within the limits
30   of interannual fluctuations. The Lusitanian trochid *Phorcus lineatus* (da Costa, 1778) was first
31   recorded by us in the lough in the early 2000s, just as it was establishing a flourishing
32   population with densities of *c.* 6 snails/0.25 m^2. Although this native trochid survived the cold
33   winters of 2009–2012, the population suffered high adult mortality and little recruitment.
34   Between 2013 and 2019, the population increased and the population density stabilized. The
35   increase in *P. lineatus* reflects its position high on the shore, where air temperatures have
36   risen over the last two decades. It may therefore be a sentinel species to detect the effects of
37   climate change. By contrast, the decrease in *S. cineraria* was related to its shallow subtidal
38   habitat where hypoxia and superoxia have recently become marked in the lough. This trochid,
39   therefore, offers potential as an indicator of eutrophication-associated stress. These temporal
40   variations in trochid species emphasize the need for longer-term assessments when estimating
41   the importance of any one species to the ecosystem.
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INTRODUCTION
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47   Trochid gastropods (*sensu* Williams & Ozawa, 2006; Williams *et al.*, 2010) are prominent
48   members of the guilds of microphagous grazers or detritivores on rocky shores, and play
49   important roles in intertidal food webs (Hickman & McLean, 1990; Herbert, 1992). Although
50   the genera *Tegula*, *Chlorostoma*, and *Calliostoma* no longer belong to the Trochidae
51   (Williams *et al.*, 2010 and references therein), the remaining members of this family have
52   radiated to occupy shores worldwide, including the *Austrocochlea constricta* species complex
53   in Australia (Colgan & Schreiter, 2011), the genus *Diloma*, which occupies a wide range of
54   tidal heights in New Zealand (Mitchell, 1980), the genus *Oxystele* in South Africa (McQuaid
55   1982, 1983; Lasiak 1987) and *Monodonta labio*, a common species on boulder shores in
56   Hong Kong (Chin, 2003; Hutchinson *et al.*, 2007), China and Japan (Takada, 1995, 1996;
57   Iijima, 2001). In Europe, *Steromphala* spp. (formerly *Gibbula*) and *Phorcus lineatus*
58   (formerly *Osilinus lineatus* and *Monodonta lineata*) are common on sheltered shores,
59   particularly in southern regions (Fretter & Graham, 1977; Graham, 1988).
60   Although some species of *Steromphala* do graze on epiphytic microalgae from seagrass
61   leaves (Mazzella & Russo, 1989), the grazing of trochids appears to be mainly restricted to
62   sweeping particles into the mouth with a radula composed of numerous delicate teeth (see e.g.
63   Little *et al.*, 2009). Using detritus and benthic microalgae as food sources (Zeldis & Boyden,
64   1979), trochid snails can be some of the most numerous molluscan grazers on rocky shores
65   (Crothers, 2001), and can be important in controlling epifaunal assemblages (Turner & Todd,
66   1991; Hily *et al.*, 2004). In addition to being ecologically important, some intertidal trochids
67   have a long history of use as a human food source. In the Mediterranean, for example,
68   *Phorcus turbinatus* is abundant in Palaeolithic and Mesolithic shell middens (Colonese *et al.*,
69   2011), together with other species of *Steromphala*, and *P. turbinatus* is still widely consumed
70   in Italy (Davidson, 1981). Studies on oxygen isotopes in the shell of this species from
71   archaeological sites (Mannino *et al.*, 2003, 2008; Yanes *et al.*, 2018) have allowed estimation
72   of past temperatures, and even of the seasons at which *P. turbinatus* was collected for food.
73   In the Caribbean, *Cittarium pica* is commercially harvested (Diaz-Ferguson *et al.*, 2010),
74   while in the Pacific, *Trochus* spp. are widely harvested for food and for their shells (e.g. Foale,
75   1998; Dumas *et al.*, 2013). Despite their artisanal and ecological importance, longterm
76   records of trochid populations are sparse, although studies of the changes in community
77   composition at several sites have allowed some interpretation of possible latitudinal range
78   shifts of species. In Europe, for example, monitoring studies have shown that between the
79   1980s and early 2000s species' range margins, including those of *S. umbilicalis*, shifted
80   polewards by as much as 50 km (Helmuth *et al.*, 2006; Mieszkowska *et al.*, 2006). The recent
81   study by Noke (2016) has shown that between 2000 and 2015 *S. umbilicalis* has extended its
82   range eastwards by 140 km along the south coast of Britain. A broader-scale investigation of
83   the changing distribution of species assemblages on European shores, which compared
84   differences between the 1950s and 2001–3, showed that some species had north and north-
85   eastern range extensions, suggesting a potential relationship with changing climate
86   (Mieszkowska *et al.*, 2006). One particular trochid, *Phorcus lineatus*, showed significant
87   movement east along the southern coast of Britain (Mieszkowska *et al.*, 2007). This species
88   has recently expanded its distribution into Lough Hyne, in southwest Ireland (Nunn, 2005;
89   Little *et al.*, 2012), although it has not apparently increased its general abundance around the
90   Irish coast (Simkanin *et al.*, 2005).
91   Historically, the three common trochid species in Lough Hyne are *Steromphala*
92   *umbilicalis*, *S. cineraria* and *Phorcus lineatus*. Generally found on the midshore (between
93   limits of mean low water spring (MLWS) and mean high water neap (MHWN), *S. umbilicalis*
94   has a relatively warm-temperate distribution, being absent from the east coast of Britain, but
95   present on the west, where it occurs as far north as Orkney and throughout Ireland (Graham,
96   1988). It breeds in summer or early autumn, when the eggs are laid singly and fertilized
97   externally (Underwood, 1972a; Garwood & Kendall, 1985); and the eggs hatch into free-
98   swimming trochophore larvae that settle low on the shore, with juveniles later migrating

99 upshore (Graham, 1988). In contrast, *S. cineraria* is generally found on the lowshore and
100 subtidally (at or below mean low water neaps (MLWN)). It is a more boreal species, ranging
101 from Iceland in the north to Gibraltar in the south, and breeds in spring (Underwood, 1972b),
102 the eggs being planktonic and hatching into trochophore larvae that settle randomly on the
103 shore (Graham, 1988). Finally, *P. lineatus* is a warm-temperate Lusitanian species, found
104 relatively high on the shore (between MLWN and MHWN). It occurs only in the south and
105 west of Britain, and on the south and west coasts of Ireland. Spawning occurs in summer or
106 early autumn (Underwood, 1972a; Garwood & Kendall, 1985), eggs being laid on the shore.
107 After hatching, a veliger larva swims for 4–5 days and then settles low on the shore; juveniles
108 migrate up the shore with age (Graham, 1988).
109   While much of the research devoted to trochids has been relatively short-term involving,
110 for example, experimental approaches to grazing, population biology, behaviour and
111 physiological tolerance (e.g. Thain, 1971; McQuaid, 1982; 1983; Thain *et al.*, 1985;
112 McMahon, 1990; Takada, 1995, 1996; Hutchinson *et al.*, 2007). extensive surveys have
113 suggested their possible use as biomonitors (Atalah & Crowe, 2012). While these short-term
114 studies have elucidated much about trochid biology, longterm monitoring studies have a
115 different focus. Bishop (2003) revealed gradual population increases in *S. umbilicalis* at one
116 site on Sherkin Island, Ireland, but erratic fluctuations at another, with the latter population
117 apparently disappearing in some years during the 20-year survey. Kendall (1987) followed the
118 population structure of *P. lineatus* for 9 years at a number of sites and concluded that this
119 species recruited regularly, even at the edge of its range. Kendall *et al.* (1987) followed the
120 population structure and recruitment of *S. umbilicalis* and *P. lineatus* in mid Wales for 9 years
121 and showed that the cold winter of 1978/9 reduced numbers of *P. lineatus* by 42%, with little
122 recovery of the population in subsequent years The same authors concluded, however, that
123 there must have been substantial adult mortality, as well as a lack of recruitment, to account
124 for the population decline. Using abundance data gathered from many sites in Britain and
125 northwest France between 2002 and 2010, and making year-to-year comparisons,
126 Mieszkowska *et al.* (2013) produced predictive models for the distributions of *S. umbilicalis*
127 and *P. lineatus*. These models showed that although populations of *P. lineatus* were rare in
128 areas with low winter sea-surface temperatures and high wave fetch, they were expected to
129 persist for longer there than *S. umbilicalis* because of longer lifespans. Whilst the status of
130 current populations is often assessed by comparing present-day snapshots with past records,
131 the purpose of the present paper was to establish the extremes of natural variation over a long
132 period so that the validity of using such snapshots could be assessed. We therefore
133 documented changes in trochid abundance over two decades (1994–2014) in Lough Hyne,
134 southwest Ireland, which allowed us to assess the validity of making comparisons with
135 records from 1955 (by Ebling *et al.*, 1960), as well as those from 2018 and 2019 (this study).
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138   **MATERIAL AND METHODS**
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140 *Study area*
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142 Lough Hyne is a semi-enclosed sea-lough in southwest Ireland (Fig. 1A), which is
143 approximately 1 km^2 and is connected to the sea by narrow 'Rapids' (Bassindale *et al.*, 1948).
144 Consequent upon the small fetch, all its shores are relatively sheltered and, because of the
145 restricted inflow at the Rapids, the tidal cycle is asymmetrical, with a *c.* 1m range, so the
146 intertidal zone is compressed (Rees, 1931, 1935; Little, 1991). Much of the intertidal zone is
147 either bedrock or shingle, and varies from nearly vertical to shallow slopes (Williams *et al.*,
148 1999). There are several areas where small freshwater flows enter the lough and locally
149 dilute the surface water (Rees, 1935). However, there is almost no dilution of the main water
150 column below a salinity of *c.* 34 (Kitching, 1987). At times of exceptionally high rainfall, a
151 localized thin freshwater lens may form at the surface (C. Little, personal observation).

152   The shoreline consists of several different habitat types that were delineated as sectors by
153   Renouf (1931) (Fig. 1B). Two areas inside the lough (above the Rapids) were investigated.
154   Renouf sectors E1/E2 consisted of shallow sloping gravel with ridges of hard rock running
155   down to low water. Sector E10 was a shallow sloping beach consisting of angular shingle
156   varying from 2–35 cm in length, resting on finer gravel and sand. This facilitated analysis of
157   trochid population density using quadrats—a method not usually possible in the boulder
158   habitats more typical for *Phorcus lineatus*. There were occasional larger boulders, and
159   occasional patches of the fucoid alga *Fucus vesiculosus* Linnaeus. The sites in Southern's Bay
160   (Fig. 1B) were below the Rapids, so were subject to symmetrical, open-coast, semi-diurnal
161   tides with a much larger range than inside the lough, but with very similar (low) wave
162   exposure. *Phorcus lineatus* was monitored on smooth bare rock ridges running downshore
163   from high water to low water. At Schull in Roaringwater Bay (Fig. 1A), *P. lineatus* was
164   monitored on a rocky outcrop that had deep crevices running down towards low water.
165
166
167   *Survey sites and monitoring*
168   Ten monitoring sites within Lough Hyne were selected (Fig. 1B), out of the 20 initially
169   surveyed by Ebling *et al*. (1960) above the Tidal Rapids, to cover as wide a range of the
170   lough's rocky shores as possible within a logistical time constraint of 2 weeks. Each site
171   consisted of a 10-m length of rocky shore that was marked at each end with a stainless-steel
172   plate to enable exact recognition at future times. For the monitoring surveys, each site was
173   subdivided into five, 2 m-long sections, giving a total of 50 sections monitored from 1994 to
174   2014. In 2018, all 20 monitoring sites were surveyed to allow direct comparison with the
175   results of Ebling *et al*. (1960), and in 2019 the ten annual sites were monitored in the same
176   way.
177   Surveys were carried out in the last week of August and first week of September every
178   year to ensure temporal consistency. Two observers examined the shore at low tide, from the
179   top of the high-shore fucoid *Pelvetia canaliculata* zone to the bottom of the *Fucus serratus*
180   zone and down to a depth of *c.* 0.5m below low water level, while two assistants recorded
181   results.
182
183   *Sampling and analysis of trochid abundance*
184   The relative abundances of *Steromphala umbilicalis* and *S. cineraria* were assessed using
185   abundance scales. Although quantitative abundances would have been preferable to relative
186   ones, the longterm project with the same core team of researchers necessitated this semi-
187   quantitative approach. In 1994, 1995, 2018 and 2019, to coincide with the recordings of
188   Ebling *et al*. (1960), we used a four-point abundance scale: 0, <1, <10 and >10 snails/m^2. For
189   plotting and analysis, these points were converted to numbers approximately in the mid-point
190   of each level on the scale, represented as 0, 0.75, 7.5, and 30. In the intervening years, from
191   1996 to 2014, to give finer detail, we used a five-point scale: 0, <5, <10, <50 and >50
192   snails/m^2. For plotting and analysis, these points were converted to numbers approximately in
193   the mid-point of each level on the scale, represented as 0, 2.5, 7.5, 30 and 50 snails/m^2. Data
194   were expressed as the average of the five 2-m sectors at each site. Kruskal–Wallis tests were
195   also conducted to determine the extent of spatial and temporal variation in trochid abundance
196   as the data did not meet the normality and homogeneity assumptions of parametric statistics.
197   The percent cover of the fucoids, *Fucus vesiculosus* and *F. serratus*, was also estimated
198   visually (Little *et al.*, 2017). Non-parametric Spearman rank correlations were determined to
199   evaluate if snail abundance (from 1996 to 2014) was associated with fucoid cover.
200   The numbers of the top shell *P. lineatus* were recorded when the species appeared at the
201   monitoring sites (Little *et al*., 2012), and were also monitored on the east shore in Renouf
202   sector E10. Here we recorded density by counting snails in 50 quadrats (50 cm x 50 cm)
203   randomly positioned within the area inhabited by *P. lineatus*: a 40-m line was stretched along
204   the top of the area and, at randomly determined distances along this transect, quadrats were
205   positioned at randomly determined distances down the beach; random locations were selected,
206   using the random number generator in Microsoft Excel. To estimate population structure, the

207 shell height of 200 individuals from a section of beach at the north end of E10 was measured
208 using calipers (± 0.1mm). Similar measurements of population structure were made in Renouf
209 sector E1/E2, just below the Rapids in Southern's Bay, and at Schull on the coast of
210 Roaringwater Bay (Fig. 1A) (Little *et al*., 2012). Juveniles were defined as having a shell
211 height of < 15mm, following Crothers (2001) and Little *et al*. (2012), who found this was the
212 maximum size of snails in their second year of growth.
213   In order to investigate possible interactive effects of the coexisting snail *Littorina littorea*
214 and *P. lineatus*, the density of *L. littorea* was also recorded in the same 50 quadrats on the
215 east shore in 2015. Parametric Pearson correlations were determined for the two gastropod
216 species; data were normally distributed and were discrete values (not rank values as with
217 monitoring-site data).
218
219
220   **RESULTS**
221 *Abundance of* Steromphala *species*
222 *Steromphala umbilicalis* was most commonly attached to rocky intertidal substrata, often
223 underneath seaweed cover, predominantly within the midshore fucoid zones. *Steromphala*
224 *cineraria* was, by contrast, recorded in the low intertidal zone, often on the brown alga *Fucus*
225 *serratus*, and in the shallow subtidal zone on the underside of boulders and smaller mobile
226 rocks. Surveys in 1994 and 1995 showed that both *S. umbilicalis* and *S. cineraria* were
227 widespread and abundant at most sites, at densities of 2–10 or >10 snails/m^2 (Fig. 2 for 1994
228 results; 1995 patterns were similar). By contrast, the survey of 2018 revealed a significant
229 decline in both species (Fig. 3; Kruskal–Wallis test for *S. umbilicalis*: $H = 18.4$, 2 df, $P <$
230 0.001; Kruskal–Wallis test for *S. cineraria*: $H = 15.7$, 2 df, $P < 0.001$). There were then only
231 30% of sites where *S. umbilicalis* showed an abundance greater than 1 snails/m^2, including
232 absence from two sites, while for *S. cineraria*, only 13 individuals were found in total. Similar
233 results (not presented here) were found in 2019.
234   The year-to-year surveys of 1996–2014 (Figs 4, 5) showed irregular fluctuations for both
235 species. The finer resolution of the five-point scales also demonstrated that abundances of the
236 lowshore *S. cineraria* were rarely above 10 snails/m^2, the exception being Codium Bay (Fig.
237 5); whereas in contrast, abundances of the midshore *S. umbilicalis* were often 20 snails/m^2
238 and sometimes, as at Graveyard, up to 40 snails/m^2 (Fig. 4).
239   There was no indication that abundance of *S. umbilicalis* was related to cover of the
240 brown alga *Fucus vesiculosus* (Spearman rank correlation: $r_s = 0.060$, $n = 950$, $P > 0.050$)
241 across all ten sites and two decades. There was, however, a highly significant between-site
242 variation in snail abundance (Kruskal–Wallis test: $H = 291.4$, 9 df, $P < 0.001$) and between-
243 year variation ($H = 87.0$, 18 df, $P < 0.001$). Given the necessary use of non-parametric
244 statistics, the spatio-temporal interaction effect could not be evaluated; inspection of the main
245 effects indicated that spatial variation was greater than temporal variation for this species. In
246 contrast, *S. cineraria* abundance was significantly larger in areas with greater *F. serratus*
247 cover (Spearman rank correlation: $r_s = 0.396$, $n = 950$, $P < 0.001$), and also varied
248 significantly with site and year (Kruskal–Wallis test: $H = 339.7$, $P < 0.001$ and $H = 44.0$, $P <$
249 0.001, respectively).
250
251 *Abundance of* Phorcus lineatus
252 Apart from one isolated individual recorded in 1996, *Phorcus lineatus* was first recorded by
253 our research group in 2003, and then rapidly spread to other sites (Fig. 6). Densities at Renouf
254 sector E10 (Fig. 7) on the east shore plateaued from 2008 to 2012, but then fell in 2013. A
255 one-way ANOVA on logarithm-transformed density data indicated that there was significant
256 interannual variation ($F_{12,637} = 16.1$, $n = 650$, $P < 0.001$); Tukey HSD comparisons indicated
257 that 2013 densities were significantly lower than 2012 ones ($P = 0.046$) and that 2014
258 densities were significantly greater than 2013 ($P = 0.011$). Size-frequency distributions of this
259 population showed that there was almost no recruitment in 2011, 2012 or 2013 (Fig. 8).
260 Recruitment did occur in 2014 (Fig. 8), when the population abundance returned to former
261 levels and increased to peak in 2016/7 (Fig. 7).

262   The recruitment at Renouf sector E10 in 2017 was paralleled by recruitment in sector
263   E1/2 (Fig. 9). In E10, three cohorts were visible with most snails in the 14–21mm size range,
264   and a small proportion of recruits. Cohorts were less discernible below the Rapids and in
265   Roaringwater Bay, although populations were very similar in composition to those inside the
266   lough. Kolmogorov–Smirnov tests showed no significant differences between any of the
267   populations monitored in 2017. In Southern's Bay and at Schull, the population also showed
268   recruitment. Both these sites, subject to 'normal' tides, had larger snails (25–29mm) that were
269   notably absent inside the lough (Fig. 9).
270   The coexisting littorinid, *Littorina littorea*, was abundant on the east shore of the lough.
271   Density in 2015 at sector E10 varied from 0 to 96 snails/$0.25m^2$. There was no significant
272   correlation between the abundance of this species and the trochid *P. lineatus* (Pearson
273   correlation: $r = -0.191$, $n = 50$ quadrats, $P = 0.185$).
274
275
276   **DISCUSSION**
277
278   The three species of trochid monitored in this survey showed very different fluctuations in
279   their populations over a period of 25 years. Both the lowshore *Steromphala cineraria* and the
280   midshore *S. umbilicalis* exhibited wide variations in population density, while the upper-shore
281   *Phorcus lineatus* increased from zero to very dense and widespread populations. The causes
282   of these varied fluctuations are discussed below. The high degree of year-to-year variation
283   emphasizes the need for regular monitoring when assessing the health of populations.
284
285   Steromphala umbilicalis
286   *Steromphala umbilicalis* was present at almost all sites throughout 1996–2014, and this
287   distribution was similar to that in 1955 (Ebling *et al*., 1960) and in 1990/91 (Little *et al*.,
288   1992), suggesting that there had been little change in the populations over a period of almost
289   60 years.
290   In contrast, the survey of 2018 (63 years after the initial 1955 survey) showed a
291   significant decline from 1994. This decline, however, must be seen in the context of the
292   fluctuations seen in the year-to-year records from 1996 to 2014, which varied by a factor of
293   ten, but showed no spatial or temporal trend. In some years, such as 1998, the mean density
294   approached 5 snails/m^2—very similar to the density recorded in 2018, suggesting that the
295   decline in 2018 may be part of a natural cycle. This variability emphasizes the importance of
296   carrying out longterm surveys in order to provide a baseline with which recordings for
297   individual years can be compared (Hawkins *et al*., 2013). However, in the surveys of Atalah
298   & Crowe (2012), *S. umbilicalis* was less abundant at sites contaminated with high levels of
299   nutrients (nitrate, nitrite, phosphate and ammonia) than at control (= uncontaminated) sites, so
300   it is possible that some part of the population reduction seen in 2018 in Lough Hyne could be
301   related to environmental deterioration (Trowbridge *et al.*, 2011, 2013, 2017, 2019; Little *et al*.,
302   2018).
303   One source of variability in populations could be related to the temporal effects of
304   dinoflagellate blooms, which are known to kill trochids (Cross & Southgate, 1980; Southgate
305   *et al*., 1984). The ecological role of red tides within Lough Hyne has not been well studied,
306   although they are regularly seen in summer and early autumn (C. Little & C.D. Trowbridge,
307   personal observation). Furthermore, the predatory starfish *Marthasterias glacialis* has
308   significantly increased in abundance in recent years (Trowbridge *et al.*, 2018, 2019). This
309   may have contributed to the decline of trochid snails, since *M. glacialis* is an established
310   predator of trochids (Ebling *et al*., 1966; Frid, 1992).
311
312   Steromphala cineraria
313   *Steromphala cineraria* was present at almost all sites in both 1955 (Ebling *et al*., 1960) and
314   1994–2014, suggesting that there was no major change in the populations over the 60-year
315   period (1955 to 2014). From 1996 to 2014, relative abundances fluctuated greatly, as seen for
316   *S. umbilicalis*, but with no obvious trend. Three other studies (Muntz *et al.*, 1965; Ebling *et*

317   *al*., 1966; Thain, 1971; V. M. Thain, personal communication) reported high numbers of *S.*
318   *cineraria*: > 60 snails/m^2 on the north shore stone wall and > 100 snails/m^2 on the north shore
319   of Castle Island in the 1960s–70s.
320   Our survey of 2018, however, showed an even greater decline for *S. cineraria* than for *S.*
321   *umbilicalis*. Out of 20 monitoring sites, *S. cineraria* was not recorded from 11 sites, and had
322   an overall mean density of only *c*. 0.2 snails/m^2. In contrast, the species exhibited relatively
323   high abundance at all 20 sites in 1955, at all 10 sites surveyed in 1994, and a minimum mean
324   density between 1996 and 2014 of *c*. 2 snails/m^2. It seems likely that such a large decrease in
325   abundance is not part of a natural cycle. This hypothesis was further supported by the marked
326   contrast between abundances within the lough, and at the one site surveyed directly below the
327   tidal Rapids (North Nita, at Southern's Bay in Barloge Creek), where *S. cineraria* remained
328   abundant (Fig. 2). The reduction in snail density has, thus, been limited to the lough, implying
329   a response to a change of conditions there.
330   Conditions in the shallow sublittoral zone in the lough have deteriorated in recent years
331   (Trowbridge *et al*., 2011, 2017, 2019; Little *et al*., 2018; Plowman *et al.*, unpublished data),
332   with increased areas of anoxia and superoxia (i.e. extreme dissolved oxygen fluctuations), and
333   these spatio-temporally variable changes in physical conditions could have significantly
334   affected the larval survival, metamorphosis and settlement of trochids. *Steromphala cineraria*,
335   in particular, lives at a lower tidal level than *S. umbilicalis*, and so is subject to the conditions
336   found in the shallow subtidal zone. The sensitivity of *S. cineraria* to environmental change
337   has been demonstrated on the west coast of Ireland, where reduction in its populations has
338   occurred at sites with nutrient enrichment associated with outfalls of untreated or partly
339   treated waste (Atalah & Crowe, 2012). Overall, the recent decrease in *S. cineraria* in the
340   lough is thus most likely attributable to locally decreased oxygen levels resulting from rising
341   nutrient levels and subsequent growth of filamentous algae.
342   There are, however, other factors that may have contributed to the snail's decline. At the
343   north end of the lough, there has been increasing human activity, resulting in destruction of
344   much of the shallow sublittoral biota (C. Little & C.D. Trowbridge, personal observation).
345   Between the daily swimmers, summer tourists and groups of kayakers, the north shore is the
346   primary access to the lough and is severely impacted by recreational activities and,
347   accordingly, contains few remaining mobile animals. Declines in abundance of *S. cineraria*
348   here, at the North Island site, have been progressive from 1955 to 1994 and then to 2014,
349   suggesting the influence of a longterm factor. Anthropogenic disturbance has been noted to
350   cause the decline of other trochids, such as the critically endangered species *Steromphala*
351   (*Gibbula*) *nivosa* in Malta (Evans *et al*., 2011). However, changes in abundance could be due
352   to many other influences, including predation and variation in food type which have been
353   implicated in the changing patterns of morphology of *S. cineraria* (Frid & Fordham, 1994).
354   Although *S. cineraria* declined generally around the coast of Ireland between 1958 and 2003
355   (Simkanin *et al*., 2005), it is regarded as a species with wide distribution in relation to climate
356   (Simkanin *et al*., 2005), so its decline is unlikely to be related to temperature.
357   As with *S. umbilicalis*, the year-to-year variation (shown in Fig. 5) demonstrates the
358   problems associated with occasional snapshot measurements of population density. In the first
359   and last years of our two-decade study, only one site had *S. cineraria* densities above 10
360   snails/m^2, but in the intervening years, five sites (but particularly Codium Bay) had densities
361   of ≥ 10 snails/m^2. Furthermore, the years of abundance did not coincide at the different sites.
362   Since *Fucus serratus* is often a host for *S. cineraria*, and there is a significant relationship
363   between percent cover of the alga and abundance of the trochid (see Results), it is possible
364   that fluctuations in the abundance of this alga led to changes in the abundance of *S. cineraria*.
365
366   Phorcus lineatus
367   At the start of the survey, *P. lineatus* was not present in the monitoring sites and had not been
368   recorded in the detailed surveys of Ebling *et al*. (1960) in 1955. However, by 2014 it had
369   colonized six sites. Although it was first recorded by our research group in 1996 and had been
370   occasionally observed in the lough by D. Minchin from 1976 to 1984 (Nunn *et al*., 2006), it
371   did not appear regularly at the monitoring sites until 2003 (Little *et al*., 2012). This top shell

372 is usually referred to as a 'warm-water' or 'southern' species, with a distribution extending
373 northwards to the south and west coasts of Ireland, western Wales and the southwestern
374 coasts of England (Crothers, 2001; Mieszkowska *et al*., 2007). Its distribution has also moved
375 west, with the species recently colonizing the Azores (Ávila *et al*., 2015). In the last decade it
376 has spread further east along the south coast of Britain, probably in response to increasing
377 average temperatures in the North Atlantic (Mieszkowska, 2016; Mieszkowska *et al*., 2005,
378 2006, 2007). The incursion and proliferation of *P. lineatus* in Lough Hyne up to 2010 has
379 been described by Little *et al*. (2012). No evidence was found to support the hypothesis that
380 this spread was due to rising seawater temperatures, but the authors suggested that changing
381 climate might have acted in other ways. In the present longterm study, there has again been
382 no observed increase in water temperature of the lough or surrounding areas (Bishop, 2003;
383 Trowbridge *et al.*, 2019), but the species has continued to spread around the lough and its
384 population density has continued to rise. One possible explanation for this expansion is that *P.*
385 *lineatus* has benefited more from rising air temperatures and solar heating than from rising
386 water temperature (see e.g. Marshall *et al*., 2010). As the tidal regime of the lough is
387 asymmetrical, parts of the upper shore are emersed for periods of time > 8 hours in each tidal
388 cycle. The trochid *P. lineatus* is thus subjected to more warming—or cooling—from aerial
389 conditions than on 'normal' shores (i.e. influenced by symmetrical tides). During the last four
390 decades, maximum air temperature each month at the nearby Sherkin Island (Fig. 1) has
391 significantly increased (Supplementary Material Fig. S1).
392   The rapid colonization and population growth of *P. lineatus* may, therefore, be related to
393 increasing summer air temperatures, which may mitigate the effect of the lower minimum air
394 temperatures sometimes experienced in winter. Increased summer temperatures might allow
395 both more rapid development of oocytes and an extended spawning period as seen in more
396 southerly populations (Crothers, 2001). In addition, enhanced larval retention within the
397 lough might also be a factor: larvae live for only 4–5 days and therefore have little
398 opportunity to leave the lough, which has limited water exchange with the external sea
399 (Johnson *et al*., 1995; Jessopp & McAllen, 2007). Larval retention has been suggested for
400 the sacoglossan *Elysia viridis*, which shows high levels of recruitment in the lough
401 (Trowbridge *et al*., 2008).
402   The sudden decrease in populations of *P. lineatus* during 2013 was due to a lack of
403 recruitment over 3 successive years (2011, 2012 and 2013), associated with three unusually
404 cold winters in 2009/2010, 2010/2011, and 2011/2012 (Supplementary Material Fig. S1).
405 Each cold winter was followed by a very small number of young juveniles a year later. This
406 apparent delayed effect of the cold winters was probably because recruitment occurs in
407 summer, but young snails overwinter as very small individuals (shell height 6—7mm)
408 (Crothers, 2001) and are seldom observed. As a result, these juveniles are first observed as
409 recruits only in the following year, when shell height is approximately > 10 mm (Little *et al*.,
410 2012). The effect of the cold winters demonstrates that two of the factors limiting the spread
411 of this species are the inability of the first-year cohort to survive cold conditions over the
412 winter and the increased mortality of older adults under the same cold conditions. Similar
413 effects were found by Kendall *et al*. (1987) for a mid-Wales population, where the very cold
414 winter of 1978 resulted in a diminished population size in 1979. Kendall *et al*. (1987) also
415 assumed that this was a result of mortality of adults as well as recruitment failure. However,
416 many of the larger adults did survive the cold winters in Lough Hyne, as can be seen from
417 Figure 8. The median shell height did not change significantly over the period of observation,
418 but as older cohorts with tall shells died off in 2015 and 2016, younger cohorts came to
419 dominate the population in 2018 and 2019. Since this was a period of increased density, there
420 may have been some density-dependent effect, but further monitoring would be necessary to
421 confirm this.
422   Wethey *et al*. (2011) have drawn attention to the fact that longterm climate change is
423 punctuated by extreme episodes and that these, as well as the overall change, must be taken
424 into account when considering temporal changes in species' distributions. Helmuth *et al*.
425 (2014) extended this argument, by pointing out that species respond more directly to changing
426 weather rather than to changes in the average climate. This occurs in particular because,

427 depending on their phenologies, species may need many years to recover from severe
428 challenges. After the cold winter of 1963, for example, *P. lineatus* died back from its northern
429 limits and did not regain its former position until decades later (Mieszkowska *et al*., 2007).
430 However, the present situation in Lough Hyne does not seem to represent recovery to a
431 former abundance as only very few individuals were recorded in 1976–1984 (Nunn *et al*.,
432 2006), and the species was not recorded in the surveys of common animals in 1955 (Ebling *et
433 al*., 1960), or by Renouf (1931). The incursion into the lough thus appears to represent a
434 genuine range extension, comparable to the appearance of the snail on Clare Island (western
435 Ireland) (McGrath & Nunn, 2002) and Strangford Lough (Northern Ireland) (Nunn, 2004).
436   Among the factors determining the distribution and abundance of *P. lineatus*, competition
437 with other grazing snails may be important. Hawkins *et al*. (1989) found that there were
438 differences in diet between *P. lineatus* and the littorinid *Littorina littorea*, and suggested that
439 there was little evidence for competition between such generalist grazers. The lack of
440 correlation in the lough between densities of *P. lineatus* and *L. littorea*, the other common
441 grazer at the same sites, suggests that on the shore investigated, food was unlikely to be a
442 limiting resource in late summer.
443   Another variable may also restrict the distribution of *P. lineatus*. Qualitative observations
444 revealed that areas covered by fucoids such as *Fucus vesiculosus* and *Ascophyllum nodosum*
445 supported sparse populations of the trochid snail (C. Little, personal observation). In some
446 years, on the east shore, a belt of *F. vesiculosus* developed on the midshore, and this was
447 apparently avoided by *P. lineatus*. There may thus be an interaction between algal cover and
448 trochid density, although this remains to be quantitatively evaluated.
449   The longterm (two-decade) monitoring of Lough Hyne has allowed us to differentiate
450 short-term ('natural') fluctuations from longterm trends in response to environmental
451 changes. The time series data have made possible a clearer interpretation of the notable
452 changes identified in 2018. The high degree of year-to-year variation identified in this study
453 clearly emphasizes the need for regular monitoring when assessing the health of populations
454 and urges caution when evaluating results from studies over short temporal scales.
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723 YANES, Y., HUTTERER, R. & LINSTÄDTER, J. 2018. On the transition from hunting-
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729
730

FIGURE CAPTIONS
732

733   **Figure 1.** Map of study area. **A.** Southwest Ireland. **B.** Lough Hyne, showing Renouf sectors
734   on each shore and ten long-term monitoring sites surveyed annually (1994 to 2014) and ten
735   historical sites (above the Tidal Rapids) surveyed in 1955, 1990/1991 and 2018. Site names in
736   the lough abbreviated as follows: BB, Boundary Bay; BH, Bohane Harbour; CB, Codium
737   Bay; EC, East Castle; EG, East Goleen; GQ, Glannafeen Quay; GY, Graveyard; NC, North
738   Castle; NI, North Island; NL, North Labhra; NWC, Northwest Castle; RN, Rookery Nook;
739   SC, South Castle; SEL, Southeast Labhra; SL, South Labhra; WC, West Concrete; WL, West
740   Labhra; WP, Whirlpool Point; WWN, Westwood North; and WWS, Westwood South. Two
741   historical monitoring sites below the Rapids: NN, North Nita (surveyed in 1955, 1990/1991
742   and 2018); SB, Southern's Bay (surveyed in 2017). Renouf sectors (short lines perpendicular
743   to the shore) are designated by shore (W, west; S, south; E, east, N, north; I, island) and sector
744   number (Renouf, 1931). Arrows indicate the following regions of the lough: Goleen, Tidal
745   Rapids and Barloge Creek. The latter two regions connect the lough to the Atlantic Ocean.
746

747   **Figure 2.** Maps showing intertidal distributions and population densities (snails/m^2) within
748   Lough Hyne of *Steromphala umbilicalis* and *S. cineraria* in 1955 (from Ebling *et al.*, 1960),
749   1994 and 2018 (this study).
750

751   **Figure 3.** Estimated abundances (snails/m^2) of *Steromphala umbilicalis* and *S. cineraria* in
752   1994, 1995 and 2018 (mean values from ten monitoring sites; error bars indicate +1 SE). Data
753   were based on four abundance-scale categories, following the methods of Ebling *et al.* (1960).
754

755   **Figure 4.** *Steromphala umbilicalis* densities from 1996 to 2014 for the ten monitoring sites in
756   Lough Hyne together with the average densities (bottom panel). Error bars indicate ±1 SE.
757   Data were based on five abundance-scale categories and, thus, differ from those in Figure 3.
758

759   **Figure 5.** *Steromphala cineraria* densities from 1996 to 2014 for the ten monitoring sites in
760   Lough Hyne as well as the average densities (bottom panel). Error bars indicate ±1 SE.
761

762   **Figure 6.** Proportion of 10 sites or 50 shoreline divisions (sections) occupied by *Phorcus*
763   *lineatus* from 1994 to 2018 in Lough Hyne.
764

765   **Figure 7.** Densities of *Phorcus lineatus* from 2005 to 2018 at Renouf sector E10, a shingle
766   shore on the east side of Lough Hyne (*n* = 50 quadrats; error bars denote +1 SE).
767

768   **Figure 8.** Size-frequency distributions of 200 specimens of *Phorcus lineatus* measured
769   annually from 2005 to 2018 (note that the population was not sampled in 2009) at Renouf
770   sector E10, a shingle shore on the east side of Lough Hyne. Colour of bars indicate following
771   stages: black, juveniles or young-of-the-year specimens; white, large, old individuals; grey,
772   intermediate sizes.
773

774   **Figure 9.** Size-frequency distributions of 200 specimens of *Phorcus lineatus* measured at
775   each of four sites in 2017: Renouf sectors E1 and E10, above the Rapids inside Lough Hyne;
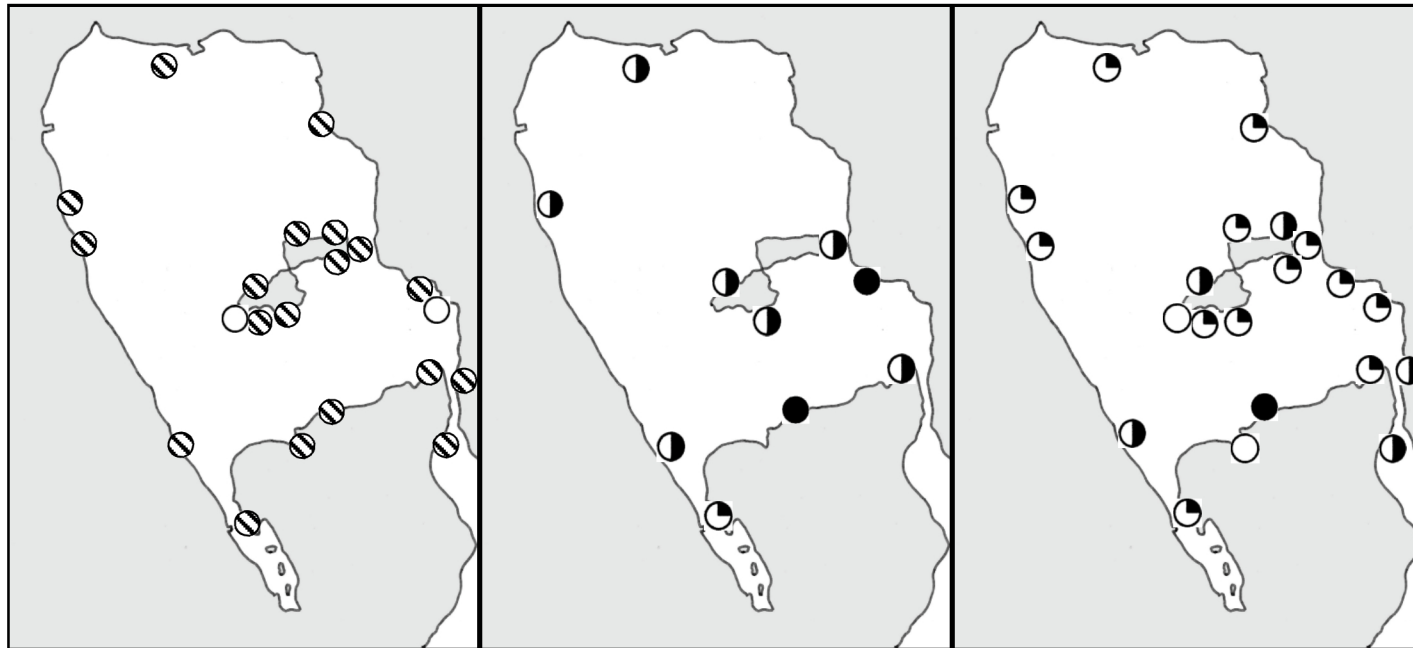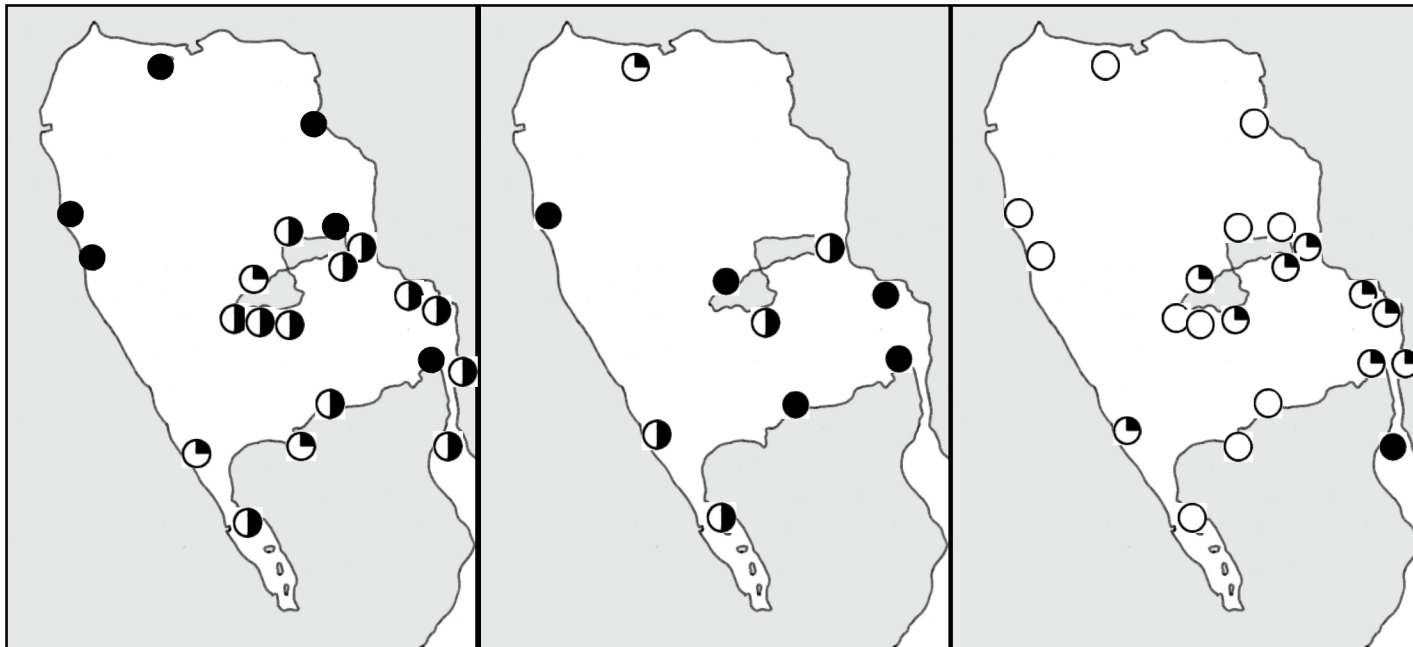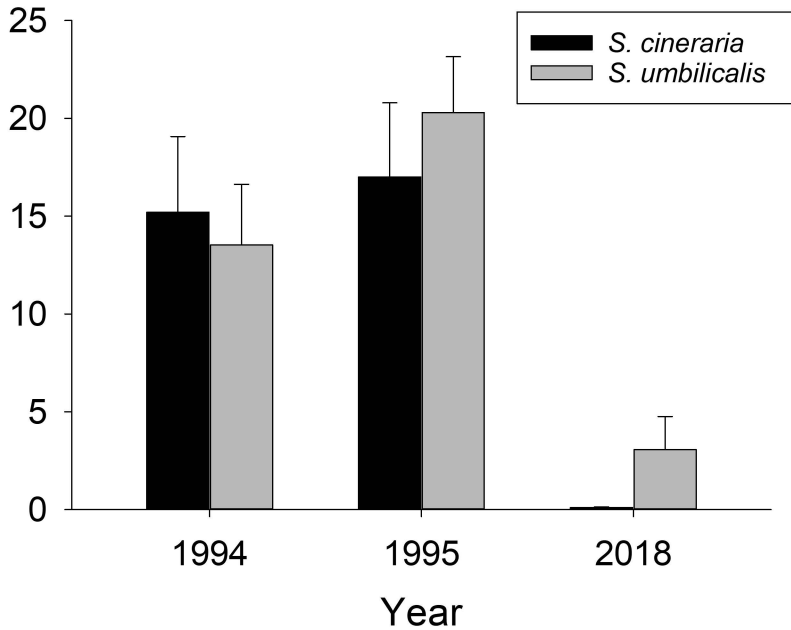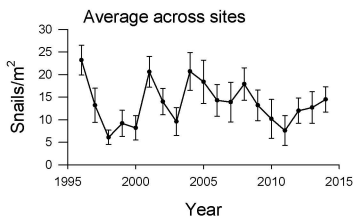776   Southern's Bay (SB) below the Rapids; and Schull (Sch) outside the marine reserve.
777
778

A

Dunmanus Bay

Schull

Roaringwater Bay

Toe Head

Lough Hyne

Sherkin Island

Clear Island

10 km

B

● Annual sites
○ Historical sites

N1

W 1

2

6 7 8 9 N10 N12

3 4

NI

11

N5

E1

2

W5 W6

E3 4 E5

7

RN

6

8

NORTH BASIN

9

8

WWN

E10

W10

NWC

NC

11

WC

I 5 6 7 8 9

EC

12

4

13 14 E15

13

3

11

BB

16

14

2

13 12 SC

WP

18

NL

14

E17

19

W15

I 1

E20

16

I 21

17

18

WL SL 16 SEL

CB S16

I 20

1817 I 15

BH

SOUTH BASIN

14

S10

11

12 13 S17

19

W20

WWS

S5 6 7 8 9

21

GY

NN

22

GQ

23

4

Tidal
Rapids

SB

24

S1

2 3

W38

37

W35

W25

EG

32

34 31

26

33 W30

29

Goleen

27

28

Barloge
Creek

0 100 200 300

m

Western Trough

	1955	1994	2018

S. umbilicalis

S. cineraria

○ Absent
⊘ Present
◔ <1
◑ 2-10
● >10

Steromphala umbilicalis
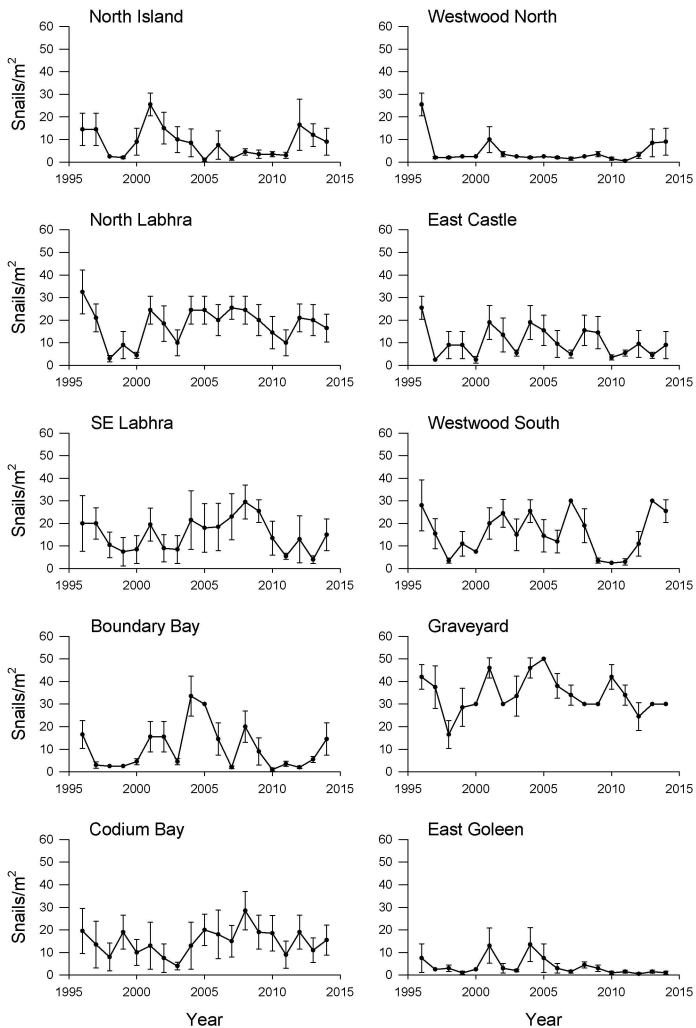
Steromphala cineraria
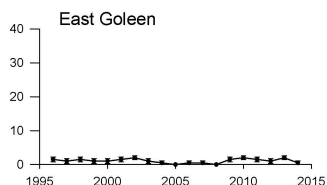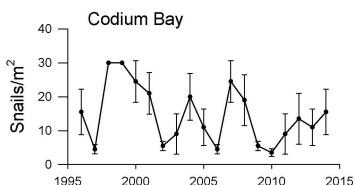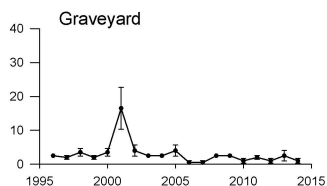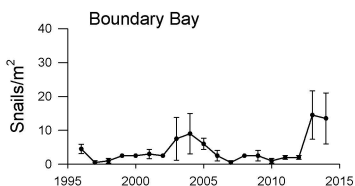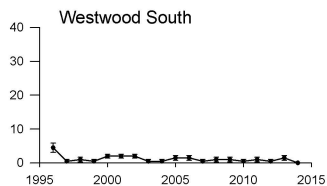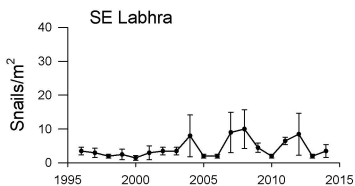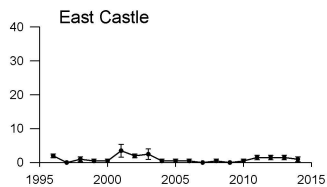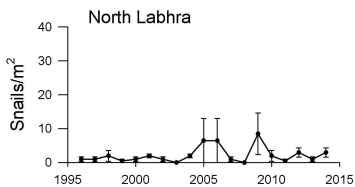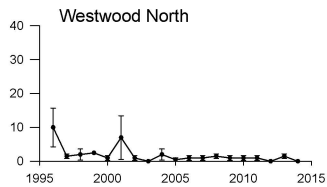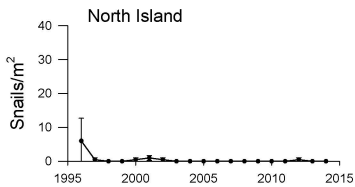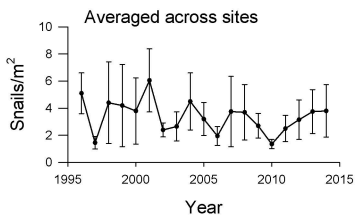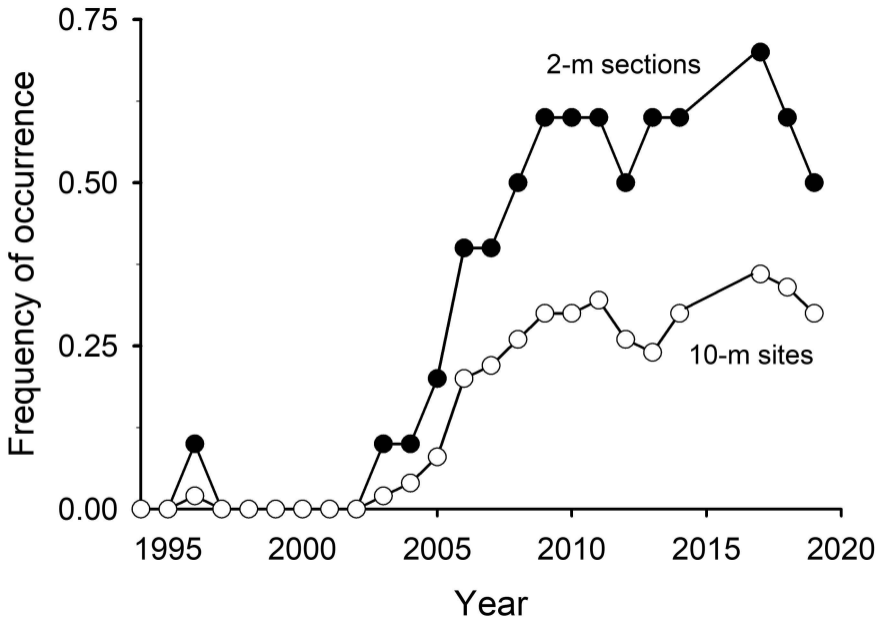
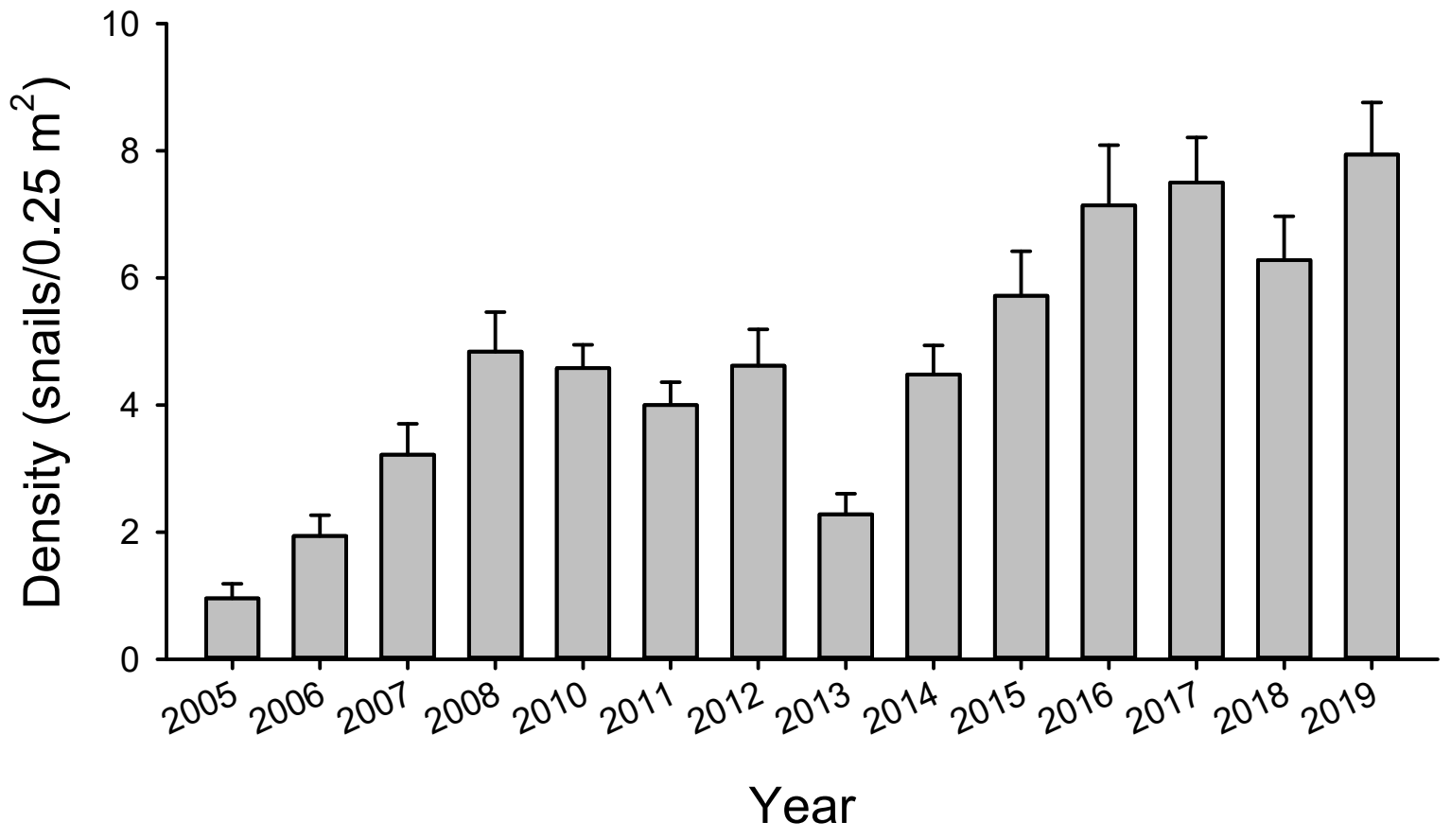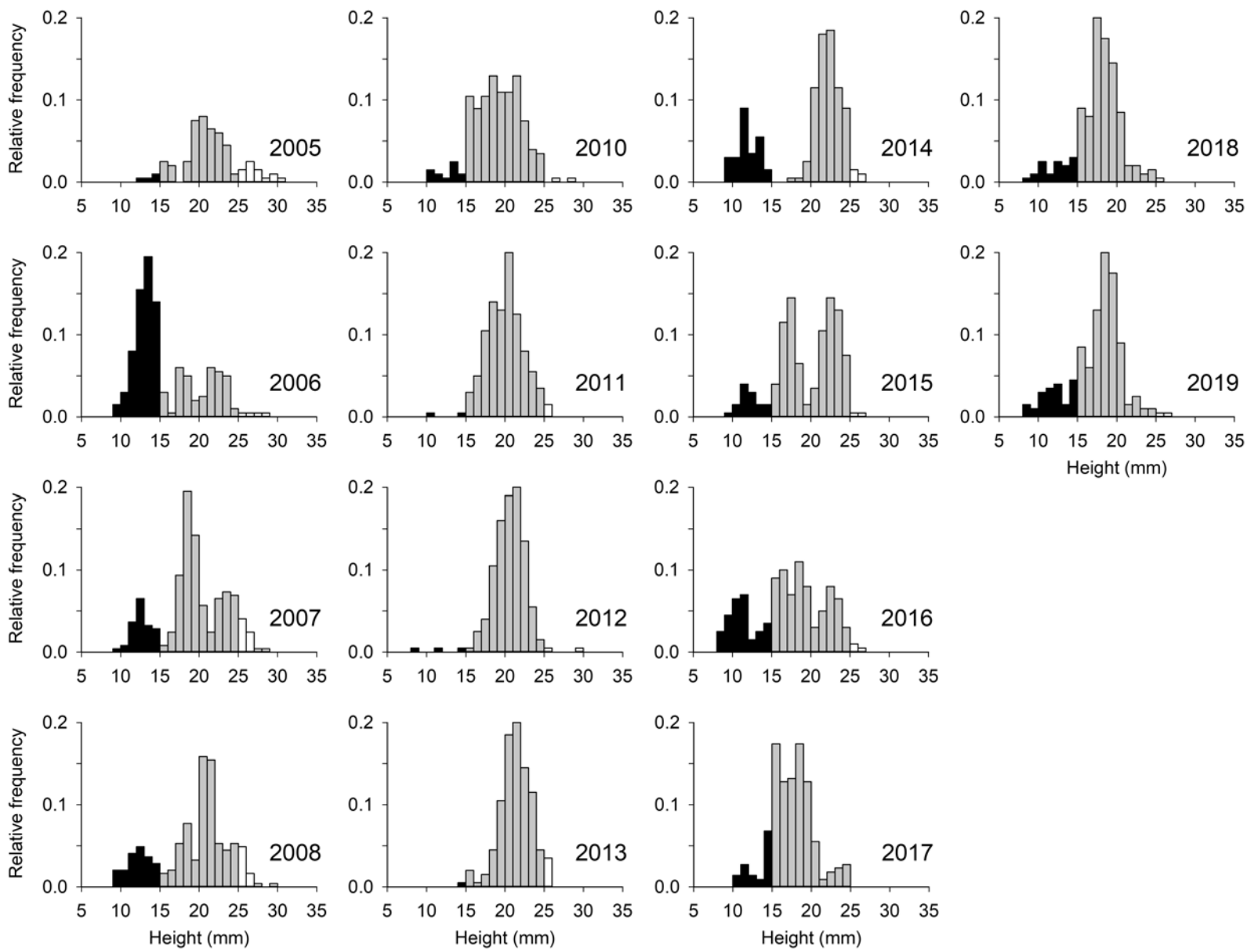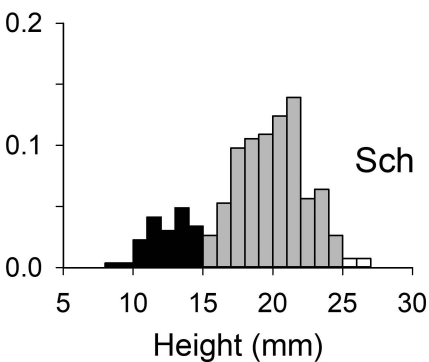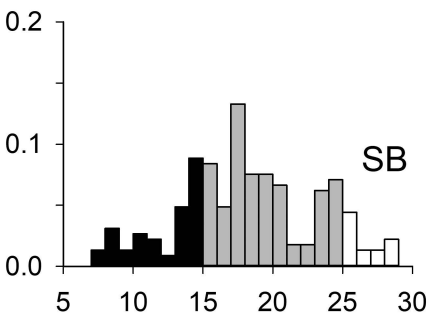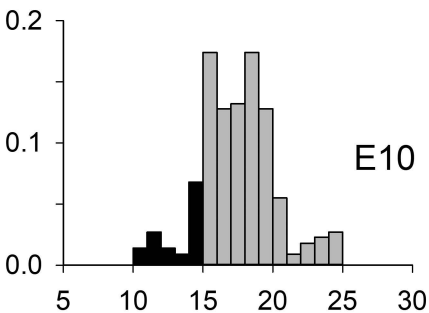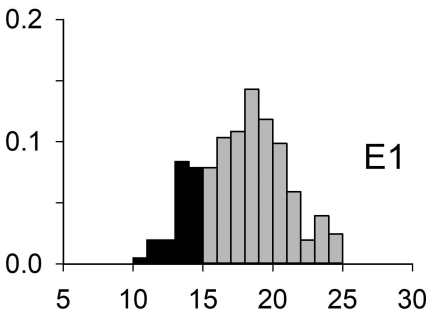**Supplemental Material Figure 1.** Regressions of maximum and minimum daily air temperatures at the Sherkin Island weather station from 1974 to 2018. Data obtained from the Met Éireann.

A

$y = 0.0802 (x) - 146.0221$
$R^2 = 0.02873$
$n = 528$
$P < 0.0001$

B

$y = - 0.0635 (x) + 134.3801$
$R^2 = 0.0504$
$n = 526$
$P < 0.0001$