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Change in the distribution of a member of the strand line community: the seaweed fly (Diptera: Coelopidae)

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Abstract. 1. Coastal organisms are predicted to be particularly susceptible to the impact of global warming. In this study the distribution and relative abundance of two coastal invertebrates, *Coelopa frigida* (Fabricius) and *C. pilipes* are investigated.

2. *Coelopa pilipes* has a more southerly distribution than *C. frigida*, and prefers a warmer climate. *Coelopa pilipes* is less resistant to sub-zero temperatures than *C. frigida* and its northerly distribution is probably limited by cold winter days.

3. The most recent distribution map of *C. frigida* and *C. pilipes* in northern Europe was published a decade ago and showed the northerly extent of the distribution of *C. pilipes* reaching the north coast of mainland Scotland but its complete absence from the Western and Northern Isles.

4. *C. pilipes* has now spread throughout the Western Isles and the Orkney Islands but is still absent from Shetland. There has also been an increase in the relative frequency of *C. pilipes* at sites harbouring coelopids on the British mainland. A similar pattern of distribution change along the west coast of Sweden is reported.

5. It is proposed that these changes have occurred primarily as a result of global warming and in particular due to the recent increase in winter temperatures. A number of other indirect effects may have also contributed to these changes, including a probable change in macroalgae distribution. The implications of these changes for the wrack bed ecosystem and at higher trophic levels are considered.

Key words. Climate change, Coelopidae, competition, distribution change, global warming, seaweed fly.

Introduction

Global temperatures have increased by approximately 0.6 °C over the past century (Jones *et al.*, 1999; IPCC, 2001). In Central England, the 1990s were approximately 0.5 °C warmer than the 1961–1990 average; with the greatest increase in temperature being experienced during the winter months (Hulme *et al.*, 2002; Watkinson *et al.*, 2004). It is now increasingly apparent that climatic change will not only contribute to ecological changes in the future, but that change is occurring in the present (Hughes, 2000; Root *et al.*, 2003). One widely predicted outcome is that the ranges of many species will shift either poleward or to higher altitudes (Barry *et al.*, 1995; Parmesan, 1996; Hughes, 2000). Poleward range shifts have since attracted empirical support on a global scale (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Hickling *et al.*, 2005, 2006; Mieszkowska *et al.*, 2006) and models show that these changes can be associated with a changing climate (Walther *et al.*, 2005).

Coastal organisms may be particularly susceptible to the impacts of global warming resulting from increases in both sea temperature and rising sea levels (Lawrence & Soame, 2004; Watkinson *et al.*, 2004). Correspondingly, a number of intertidal organisms found on rocky shores around Britain have undergone poleward range shifts associated with climate change (Mieszkowska *et al.*, 2006). Among the organisms most likely to be affected are the coastal invertebrates (Beukema *et al.*, 2001; Lawrence & Soame, 2004; Kendall *et al.*, 2004). Changes to coastal invertebrate communities may be expected to have a subsequent effect upon other species, particularly avifauna, that depend upon them as a food source (Kendall *et al.*, 2004; Lawrence & Soame, 2004).

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One particularly understudied coastal ecosystem is the strand line community (Kendall *et al.*, 2004), which is founded primarily upon marine macroalgae deposited on beaches by storms and tides. Seaweed flies (Diptera: Coelopidae) inhabit deep algal deposits, known as wrack beds, deposited on the strand line close to rocky shores (Dobson, 1974). Coelopid larvae are entirely dependent upon algae for their development and adults mate and feed within deposits, using them as places of shelter. Both the larval and adult life stages play an important functional role; accelerating decomposition and recycling of nutrients (Harrison, 1977; Robertson & Mann, 1980; Koop & Griffiths, 1982; Cullen *et al.*, 1987) and providing a food source for coastal bird species (Feare & Summers, 1985).

The relative distribution and abundance of two northern European coelopids, *Coelopa frigida* (Fabricius) and *Coelopa pilipes* (Halliday), has been studied on a number of previous occasions (Egglishaw, 1960; Dobson, 1974; Butlin, 1983; Phillips *et al.*, 1995b; see Fig. 1). *Coelopa frigida* occupies higher latitudes ranging from the north coast of France as far north as Iceland and Spitzbergen. In contrast, the range of *C. pilipes* extends farther south down the Atlantic coastline of France yet north only so far as the northern coast of the Scottish mainland. *C. pilipes* is notably absent from the Western and Northern Isles of Scotland. While both species occur sympatrically throughout much of their range, within British wrack beds *C. frigida* has been described as the most abundant of the large Diptera (Egglishaw, 1960). On mainland Europe *C. pilipes* has been recorded as far north as the west coast of Sweden though only very rarely at greater abundances than *C. frigida*.

While various factors may play a part in determining the relative abundances of *C. frigida* and *C. pilipes* the most important is almost certainly temperature (Phillips *et al.*, 1995b). This is reflected in a greater abundance of *C. pilipes* during the summer months (Remmert, 1965; Phillips *et al.*, 1995b) and a greater susceptibility of this species to the effects of freezing temperatures. In addition, the larvae of *C. frigida* are found to prefer cooler microhabitats within wrack beds (Phillips *et al.*, 1995b). Data on the relative abundance of northern European populations of Coelopids going back nearly 40 years provide an excellent opportunity to consider the impacts of climate change upon the strand line community. The aim of this study is therefore to assess the relative responses of *C. frigida* and *C. pilipes* to climate change.

Materials and methods

Experimental procedure

Historical data were collated from previous collections made between February 1967 and October 1990 (Butlin, 1983; Gilburn, 1992; Phillips et al., 1995; Day & Gilburn, unpubl. data). The same areas as for the historical collections were re-sampled between August 2004 and December 2005, returning to the same beach and at the same time of year where possible. If no wrack bed could be found at a site then we located and sampled from the nearest wrack bed to the original site. In some regions no information was available on the exact location of past collections, for example Norway and the Scottish Islands. In these cases, a number of sampling sites were identified to give a comprehensive description of coelopid populations. 1

The same two collection techniques were adopted as used to collect the historical data. If sufficient adult flies were present at a site then they were collected by mouth pooter and transported back to Stirling, where the relative abundance of the two species was calculated. At sites lacking large numbers of adults, collections of larvae were made from various locations and depths within the wrack bed and placed in large plastic tanks. Larvae were transported back to Stirling and allowed to develop within the seaweed in which they were collected. Any

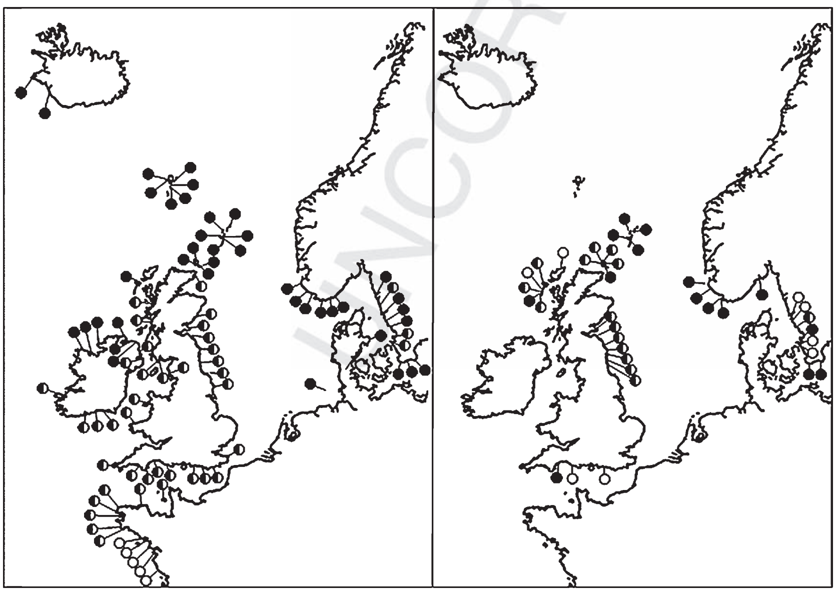

Fig. 1. Distribution maps of *C. frigida* and *C. pilipes*, past and present. The map on the left shows the historical distribution, adapted from Phillips *et al.* (1995b), while on the right data from the current study are shown. Filled circles represent populations of *C. frigida* (*C. pilipes* rare if present), empty circles populations of *C. pilipes* (*C. frigida* rare if present) and half filled circles mixed populations. 16

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collections at high larval density were given additional seaweed to reduce the effects of larval competition. The relative number of *C. frigida* and *C. pilipes* adults eclosing from these cages was then determined.

Statistical analysis

All analyses were carried out using R 2.0.1 (R Development Core Team, 2005). A quasibinomial model of the proportion of *C. pilipes* flies at each location, using year and latitude as the independent variables, was used as the data set was overdispersed.

Results

Change in relative frequency of C. frigida *and* C. pilipes *in mainland Britain*

Some limited historical data were available for the south coast of Britain. During the summer of 1981 all of the populations sampled at each site (Rustington, Portland, and Beer) were comprised of at least 90% *C. frigida* (Butlin, 1983). In August 2005 only one site, Beer, still contained *C. frigida*. The populations at Rustington and Osmington (a site close to Portland) were comprised entirely of *C. pilipes*. A considerable amount of historical data exists for the east coast of England. In samples made between 1967 and 1981 the average proportion of *C. pilipes* found on east coast sites was 34% (SE ± 6%). This had increased to 55% (SE ± 10%) in 2005. Precise historical data for *C. pilipes* populations in Scotland are not available, although limited records suggest that *C. pilipes* was relatively rare compared with *C. frigida*. Samples taken from around the Forth Estuary during 2004 and 2005 revealed that the mean proportion of *C. pilipes* was 81.7% (SE ± 7.71%) with all sites containing a majority of *C. pilipes.*

A quasibinomial model showed that the proportion of *C. pilipes* within British mainland populations has increased over the last four decades ($F_{1,66} = 15.2$, $P < 0.001$, parameter estimate = +0.0641, SE = 0.0153). In both 2004 and 2005 more *C. pilipes* were collected than *C. frigida* (Fig. 2). Latitude was not found to affect the proportion of *C. pilipes* within British mainland populations ($F_{1,66} = 0.06$, $P =$ NS).

Scottish Island populations of Coelopids

Phillips *et al.* (1995b) reported the absence of *C. pilipes* from the Western and the Northern Isles of Scotland. We collected coelopids from populations on seven islands within the Western Isles in August 2004, and five islands in the Orkney Isles in June 2005 and nine sites in Mainland Shetland in August 2005.

C. pilipes was found on all seven islands (Vatersay, Barra, South Uist, Benbecula, North Uist, Harris, and Lewis) within the Western Isles that hosted wrack bed communities. *C. frigida* was only found on six (absent from the one wrack bed investigated on Benbecula). *C. pilipes* was found on all five islands on which we sampled wrack beds within the Orkneys (Mainland, Burray, South Ronaldsay, Westray, and Sanday). Of the 15 wrack beds sampled in Orkney, five contained only *C. frigida* and three contained only *C. pilipes*. Nine wrack beds were found to contain *C. frigida* on the Shetland mainland. All of the sites lacked *C. pilipes*.

West and south coasts of Sweden

Collections of coelopids were carried out on an annual basis on the west and south coasts of Sweden from 1986 to 1995 (Phillips *et al.*, 1995b; Day & Gilburn, unpubl. results). *C. pilipes* was usually found to be the commonest coelopid at Mølle, but was usually absent from other sites (Fig. 3). It was occasionally found at Torekov, Bua, and Steninge, also on the west coast, but never as the more common coelopid at these sites. *C. pilipes* was never found at any of the six sites on the south coast that were regularly found to harbour populations of *C. frigida*.

We found *C. pilipes* to be absent from the two wrack beds harbouring *C. frigida* populations on the south coast in September 2005. We found six wrack beds harbouring coelopid populations on the west coast of Sweden in September 2005. Of these, one consisted only of *C. frigida*, three consisted only of *C. pilipes* and two were mixed populations, one of which was

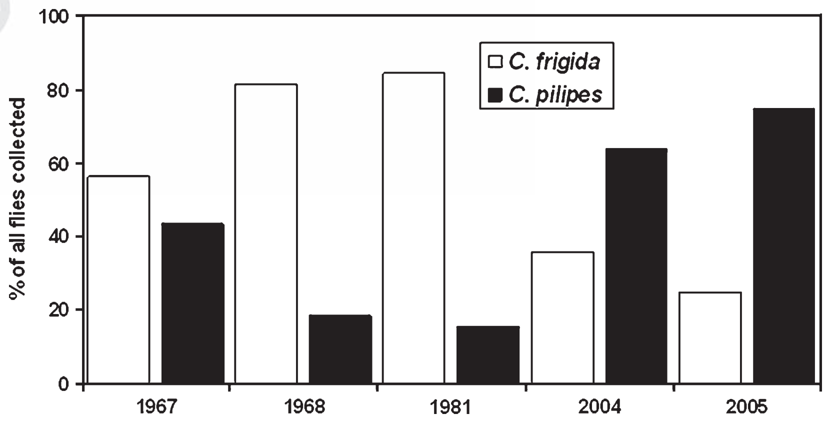

Fig. 2. The proportion of individuals of the two common British coelopid species collected across mainland British populations in 1967, 1968, 1981, 2004, and 2005.

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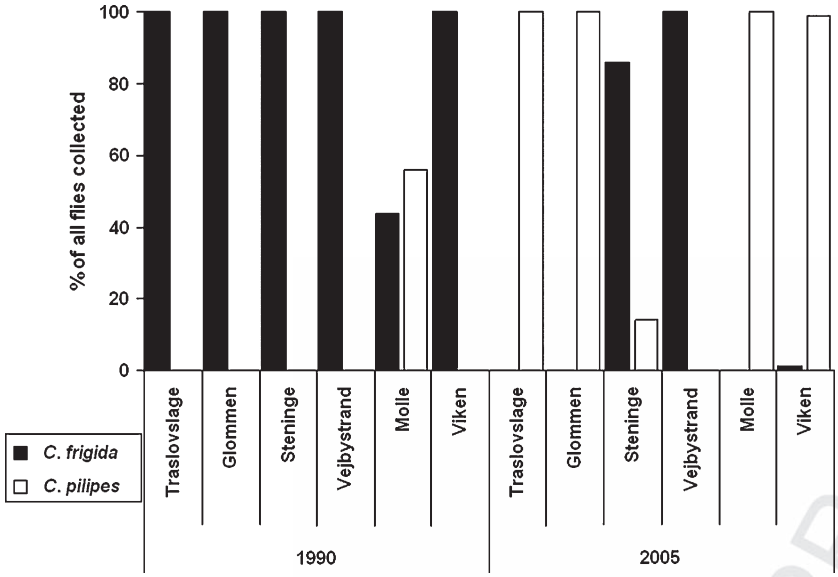

Fig. 3. The proportion of individuals of the two common coelopid species collected from wrack beds along the west coast of Sweden in 1990 and 2005. Sites are listed from left to right in order of decreasing latitude.

99% *C. pilipes* (Fig. 3). Two of the three wrack beds lacking *C. frigida* were sites not previously known to host *C. pilipes*, including the wrack bed at Träslövsläge, which has previously always hosted a huge and well studied population of *C. frigida* (Gilburn *et al.*, 1993). The wrack bed at Viken with 99% *C. pilipes* also has previously lacked *C. pilipes*. Thus, there has been a substantial shift towards *C. pilipes* as the predominant coelopid on the west coast of Sweden.

Norway

Much of the Norwegian coastline from Bergen in the west to Holmestrand in the east consists of rocky slabs descending directly into the sea, making it difficult for large amounts of debris to accumulate. Five locations were sampled along this coastline in December 2005 and July 2006. *C. frigida* was found exclusively at the four westernmost sites; however at the easternmost site, Stavern, a solitary male *C. pilipes* was recorded. This is the first record of *C. pilipes* occurring in Norway.

Discussion

The results of this study suggest a shift in the distribution of coelopid species in northern Europe commensurate with predictions of poleward range expansions resulting from climate change. Wrack beds are a highly stochastic resource, dependent upon weather and tidal patterns. Persistence of a wrack bed may vary from just a few days to a month or more. Their transient nature is known to influence the density of coelopid populations that may vary substantially from week to week (Dobson, 1974; Hodge & Arthur, 1997). This incurs difficulties when visiting sites in finding suitable strand line deposits comparable with those of previous years. Though care was taken to visit sites at a similar time of year and to collect flies in a consistent manner, few conclusions can be drawn about changes occurring at specific locations. Nevertheless, due to the numerous and wide distribution of sites studied, and considering in particular the apparent invasion of *C. pilipes* at previously unrecorded locations, these results clearly demonstrate a change in coelopid distribution.

While Norway and the Orkney Isles now appear to be the new northern limit of *C. pilipes* range, this may be determined as much by physical as ecological constraints. *C. frigida* and *C. pilipes* have been reported to migrate in large numbers and over long distances; however, it is predicted that the direction of migrations should follow coastlines in the direction of fresh wrack beds (Oldroyd, 1954; Egglishaw, 1961). The Western Isles of Scotland and the Orkney Isles can be reached by traversing far shorter stretches of open water than would be required to reach the Shetland Isles. While not an absolute barrier to colonisation such distances would certainly be expected to slow the rate of range expansion. The southern coastline of Norway was found to be lacking in wrack beds suitable for the maintenance of coelopid populations due to topography. A reduced frequency of suitable habitat along this portion of coast may be limiting the rate of *C. pilipes* range expansion. Consequently the potential effect of climate change upon *C. pilipes* range may be easily underestimated. The continuing absence of *C. pilipes* from the South coast of Sweden is likely to be due to the low percentage of brown algae within wrack beds along this coastline. The predominant component of wrack beds along this coast is eel grass, *Zostera marina*, which may limit the decomposition of brown algae so that these wrack beds remain relatively cold, thus favouring *C. frigida*.

Phillips *et al.* (1995b) proposal that temperature is the most important factor determining the relative abundance and distribution of *C. frigida* and *C. pilipes* predicts that any changes in climate affecting temperature are likely to alter the relative abundance and distribution of these species in northern Europe. The rise in temperatures observed in Britain over the past

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30 years have been much more pronounced in winter, increasing by 1.1 °C, compared with only a 0.2 °C rise in summer temperatures (Watkinson *et al.*, 2004). Furthermore, there has been a substantial reduction in the number of winter days below 0 °C (Watkinson *et al.*, 2004). The seasonal pattern of *C. pilipes* prevalence may easily have extended during recent mild winters. It has also been shown that at increased temperatures *C. pilipes* are better able to develop when in competition with *C. frigida* (Phillips *et al.*, 1995b). Thus a small change in temperature could exhibit a greater ecological effect as the balance of competition falls in favour of *C. pilipes*.

Accompanying the increase in air temperature has also been a global increase in sea water temperatures (Levitus *et al.*, 2000; Hulme *et al.*, 2002). Around the British Isles an increase of about 0.5 °C has been experienced over the last 70–100 years, with the greatest increase being during the past 20 years (Hulme *et al.*, 2002). A number of warm water benthic species are now beginning to appear around the coast of Britain while cold water species are in decline (Hiscock *et al.*, 2004). The distribution of the primary constituent of wrack beds harbouring coelopids, brown algae, is also determined by sea temperatures (Breeman, 1988; van den Hoek *et al.*, 1990). It has been suggested that brown algae genera such as *Laminaria* may currently be in decline (Breeman, 1990; Barry *et al.*, 1995; Schiel *et al.*, 2004) and that *Fucus* is predicted to decline in the future (Kendall *et al.*, 2004) around the British Isles. It is suggested that *C. frigida* and *C. pilipes* have preferences for different species of seaweed (Dobson, 1974; Phillips *et al.*, 1995a; Edward & Gilburn, in
2 press) and that the level of competitive interaction between coelopids can be dependent on the rate of wrack bed decomposition (Leggett *et al.*, 1996; Hodge & Arthur, 1997). A change in macroalgae distribution associated with climate change represents an additional indirect mechanism by which climate change may have influenced coelopid distribution.

It has already become much harder to find *C. frigida* on beaches of mainland Britain, something that has been of concern as this species has been established as an important model organism for the study of sexual conflict and sexual selection (Gilburn & Day, 1997; Shuker & Day, 2001; Dunn *et al.*, 2002;
3 Blyth & Gilburn, 2005). Perhaps more importantly, a change in coelopid distribution may be indicative of wider ecological impacts of climate change on our beaches. The importance of the strand line ecosystem has recently been demonstrated where beaches are mechanically cleared for aesthetic purposes; resulting in a loss of biodiversity and negative effects on bird populations (Llewellyn & Shackley, 1997; Dugan *et al.*, 2003). Decomposed wrack material can support the establishment of terrestrial plants that act as the precursors for sand dunes and a wide variety of coastal bird species feed upon wrack macrofauna and nematodes in the organically rich subsurface (Pienkowski, 1982; Feare & Summers, 1985; Llewellyn & Shackley, 1997; Dugan *et al.*, 2003). It is not clear what direct effect the changes in relative abundance of *C. frigida* and *C. pilipes* will have on strand line communities. The loss of *C. frigida* may be particularly important as this is usually the first large dipteran to lay eggs in freshly deposited algae. *C. pilipes* has been observed to colonise wrack beds up to 3 days after deposition, considerably later than *C. frigida*, and mating behaviour is also known to be delayed (Edward & Gilburn, in press). As wrack beds are commonly a 4
short-lived resource this represents a substantial delay to the decomposition process that could have subsequent effects on other members of the wrack bed community as well as the recycling of nutrients.

This study demonstrates that the relative abundance of coelopids in northern Europe has changed in recent decades. The likely cause of these observations is the recent change in climate that may have affected coelopids species directly, the interaction between coelopid species or composition of their habitat. We suggest that further work need not necessarily be focused upon coelopids, but should consider the wider implications of climate change on the strand line ecosystem.

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