

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

DOMINIC A. EDWARD¹, JENNIFER E. BLYTH², RODERICK MCKEE¹ and ANDRÉ SIMON GILBURN¹ ¹School of Biological and Environmental Sciences, University of Stirling, Stirling, Scotland, U.K. and ²Environmental and Marine Biology, Åbo Akademi University, Turku, Finland

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).

Correspondence: Andre Gilburn, School of Biological and Environmental Sciences, University of Stirling, Stirling, Scotland FK9 4LA, U.K. E-mail: andre.gilburn@stir.ac.uk

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 (Egglisshaw, 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 (Egglisshaw, 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.

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

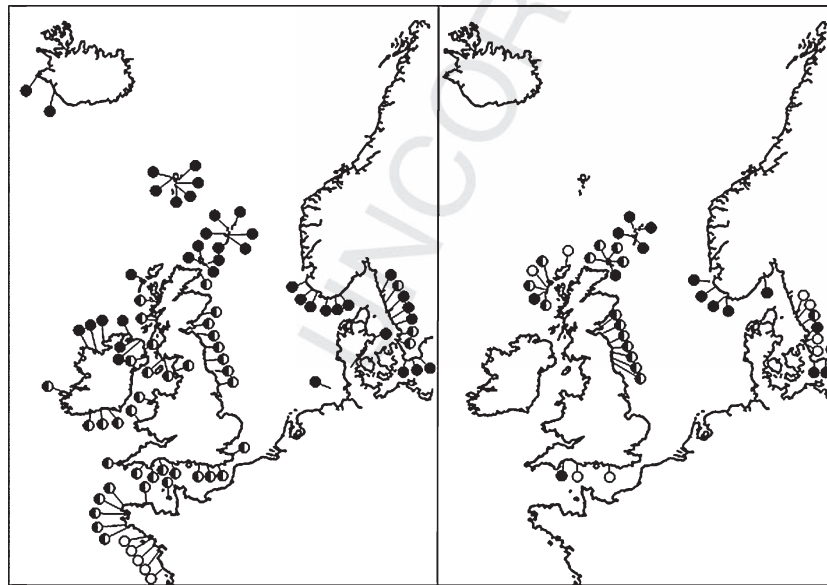


Fig. 1. Distribution maps of *C. frigida* and *C. pilipes*, past and present. The map on the left shows the historical distribution, adapted from Phillips *et al.* (1995b), while on the right data from the current study are shown. Filled circles represent populations of *C. frigida* (*C. pilipes* rare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

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 \pm 6%). This had increased to 55% (SE \pm 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 \pm 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 ($F_{1,66} = 0.06$, $P = \text{NS}$).

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

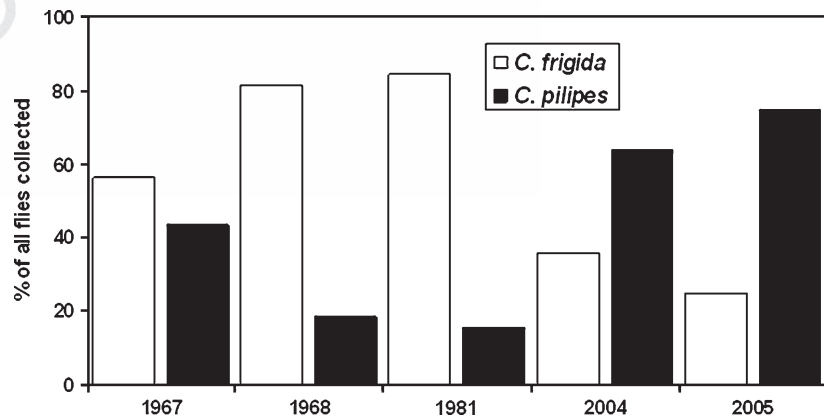


Fig. 2. The proportion of individuals of the two common British coelopid species collected across mainland British populations in 1967, 1968, 1981, 2004, and 2005.

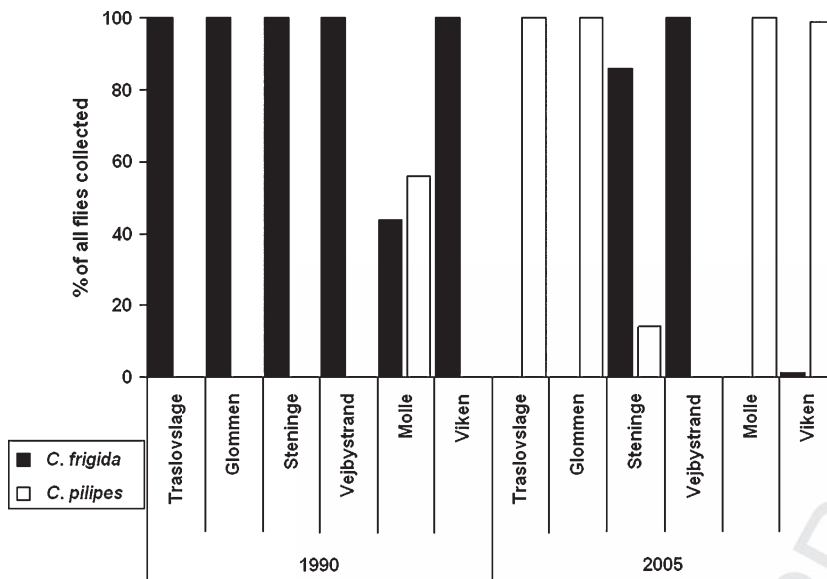


Fig. 3. The proportion of individuals of the two common coelipid species collected from wrack beds along the west coast of Sweden in 1990 and 2005. Sites are listed from left to right in order of decreasing latitude.

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 coelipid 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 coelipid 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 coelipid 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 coelipid 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; Egglisshaw, 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 coelipid 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

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 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; 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 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.

Acknowledgements

This work was supported by a studentship (to D.A.E.) from the Natural Environment Research Council. We are also extremely grateful to the Carnegie Trust who provided funding for collections in the Western and Northern Isles.

References

- Barry, J.P., Baxter, C.H., Sagarin, R.D. & Gilman, S.E. (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science*, **267**, 672–675.
- Beukema, J.J., Dekker, R., Essink, K. & Michaelis, H. (2001) Synchronised reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Marine Ecology Progress Series*, **211**, 143–155.
- Blyth, J.E. & Gilburn, A.S. (2005) The effect of time interval between matings on post-copulatory sexual selection in the seaweed fly, *Coelopa frigida*. *Heredity*, **95**, 174–178.
- Breeman, A.M. (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phylogenetic evidence. *Helgolander Meeresuntersuchungen*, **42**, 199–241.
- Breeman, A.M. (1990) Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. *Expected effects of Climate Change on Marine Coastal Ecosystems* (ed. by J. J. Beukema *et al.*), pp. 69–76.
- Butlin R.K. (1983) *The maintenance of an inversion polymorphism in Coelopa frigida (Diptera: Coelopidae)*. PhD thesis, University of Nottingham, Nottingham, U.K.
- Cullen, S.J., Young, A.M. & Day, T.H. (1987) Dietary requirements of seaweed flies (*Coelopa frigida*). *Estuarine, Coastal and Shelf Science*, **24**, 701–710.
- Dobson, T. (1974) Mechanisms controlling species composition in natural populations of the seaweed fly, *Coelopa (frigida)*. *Journal of Natural History*, **8**, 653–673.
- Dugan, J.E., Hubbard, D.M., McCrary, M.D. & Pierson, M.O. (2003) The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal and Shelf Science*, **58S**, 25–40.
- Dunn, D.W., Crean, C.S. & Gilburn, A.S. (2002) The effects of exposure to seaweed on willingness to mate, oviposition and longevity in seaweed flies (Diptera: Coelopidae). *Ecological Entomology*, **27**, 554–564.

- Egglisshaw, H.J. (1960) Studies on the family Coelopidae (Diptera). *Transactions of the Royal Entomological Society of London*, **112**, 109–140.
- Egglisshaw, H.J. (1961) Mass migrational flights of *Coelopa frigida* (Fabricius) and *C. pilipes* (Haliday). (Diptera, Coelopidae.) *The Entomologist*, January, 11–18.
- 6 Feare, C.J. & Summers, R.W. (1985) Birds as predators on rocky shores. *The Ecology of Rocky Coasts* (ed. by P. G. Moore and R. Seed), pp. 249–264. Hodder and Stoughton, London.
- Gilburn, A.S. (1992) *Sexual selection by female mate choice in the seaweed fly, Coelopa frigida*. PhD thesis, University of Nottingham, Nottingham, U.K.
- Gilburn, A.S., Foster, S.P. & Day, T.H. (1993) Genetic correlation between a female mating preference and the male preferred character in seaweed flies (*Coelopa frigida*). *Evolution*, **47**, 1788–1795.
- Harrison, P.G. (1977) Decomposition of macrophyte detritus in seawater: effects of grazing by amphipods. *Oikos*, **28**, 165–170.
- Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hiscock, K., Southward, A., Tittley, I. & Hawkins, S. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **14**, 333–362.
- Hodge, S. & Arthur, W. (1997) Asymmetric interactions between species of seaweed fly. *Journal of Animal Ecology*, **66**, 743–754.
- van den Hoek, C., Breeman, A.M. & Stam, W.T. (1990) The geographic distribution of seaweed species in relation to temperature: present and past. *Expected effects of Climate Change on Marine Coastal Ecosystems* (ed. by J. J. Beukema *et al.*), pp. 55–67.
- 7 Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchell, T.D., Jones, R.G. *et al.* (2002) *Climate Change Scenarios for the United Kingdom*. The UKCIP02 Scientific Report. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich, U.K.
- IPCC (2001) *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, U.K.
- 8 Jiang, L. & Morin, P.J. (2004) Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *Journal of Animal Ecology*, **73**, 569–576.
- Jones, P.D., New, M., Parker, D., Martin, S. & Rigor, I.G. (1999) Surface air temperatures and its changes over the past 150 years. *Reviews of Geophysics*, **37**, 173–199.
- Kendall, M.A., Burrows, M.T., Southward, A.J. & Hawkins, S.J. (2004) Predicting the effects of marine climate change on the invertebrate prey of birds of rocky shores. *Ibis*, **146**, S40–S47.
- Koop, K. & Griffiths, C.L. (1982) The relative significance of bacteria, meio- and macrofauna on an exposed sandy beach. *Marine Biology*, **66**, 295–300.
- Lawrence, A.J. & Soame, J.N. (2004) The effects of climate change on the reproduction of coastal invertebrates. *Ibis*, **146**, S29–S39.
- Leggett, M.C., Wilcockson, R.W., Day, T.H., Phillips, D.S. & Arthur, W. (1996) The genetic effects of competition in seaweed flies. *Biological Journal of the Linnean Society*, **57**, 1–11.
- Levitus, S., Antonov, J.I., Boyer, T.P. & Stephens, C. (2000) Warming of the world ocean. *Science*, **287**, 2225–2229.
- Llewellyn, P.J. & Shackley, S.E. (1997) The effects of mechanical beach-cleaning on invertebrate populations. *British Wildlife*, **7**, 147–155.
- Luning, K. (1990) *Seaweeds: Their Environment, Biogeography & Ecophysiology*. Wiley, New York.
- 9 Mann, K.H. (1973) Seaweeds: their productivity and strategy for growth. *Science*, **182**, 975–981.
- Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P., Hardman-Mountford, N.J. *et al.* (2006) Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia*, **555**, 241–251.
- Oldroyd, H. (1954) The seaweed fly nuisance. *Discovery*, **15**, 198–202.
- Paine, R.T. (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature*, **355**, 73–75.
- Parmesan, C. (1996) Climate and species' range. *Nature*, **382**, 765–766.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Phillips, D.S., Arthur, W., Leggett, M. & Day, T.H. (1995a) Differential use of seaweed species by British seaweed flies, *Coelopa* spp. (Diptera: Coelopidae) with a description of the egg morphology of the two species. *The Entomologist*, **114**, 158–165.
- Phillips, D.S., Leggett, M., Wilcockson, R., Day, T.H. & Arthur, W. (1995b) Coexistence of competing species of seaweed flies: the role of temperature. *Ecological Entomology*, **20**, 65–74.
- Pienkowski, M.W. (1982) Diet and energy intake of grey and ringed plovers (*Pluvialis squatarola* and *Charadrius hiaticula*) in the non-breeding season. *Journal of Zoology*, **197**, 511–549.
- R Development Core Team (2005) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Remmert, H. (1965) Distribution and the ecological factors controlling distribution of the European wrack fauna. *Proceedings of the Fifth Marine Biological Symposium*, Gothenburg.
- 12 Robertson, A.I. & Mann, K. (1980) The role of isopods and amphipods in the initial fragmentation of eelgrass detritus in Nova Scotia, Canada. *Marine Biology*, **59**, 63–69.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–59.
- Sanford, E. (1999) Regulation of keystone predation by small changes in ocean temperature. *Science*, **283**, 2095–2097.
- 13 Schiel, D.R., Steinbeck, J.R. & Foster, M.S. (2004) Ten years of-induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*, **85**, 1833–1839.
- Shuker, D.M. & Day, T.H. (2001) The repeatability of sexual conflict over mating. *Animal Behaviour*, **61**, 755–762.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Walther, G.R., Berger, S. & Sykes, M.T. (2005) An ecological 'footprint' of climate change. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 1427–1432.
- Watkinson, A.R., Gill, J.A. & Hulme, M. (2004) Flying in the face of climate change: a review of climate change, past, present and future. *Ibis*, **146**, S1–S10.
- Wootton, J.T. (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *American Naturalist*, **141**, 71–89.
- 14
15

Accepted XX XXXXXX 2007

Author Query Form

Journal: Ecological Entomology

Article: een_919

Dear Author,

During the copy-editing of your paper, the following queries arose. Please respond to these by marking up your proofs with the necessary changes/additions. Please write your answers on the query sheet if there is insufficient space on the page proofs. Please write clearly and follow the conventions shown on the attached corrections sheet. If returning the proof by fax do not write too close to the paper's edge. Please remember that illegible mark-ups may delay publication. Many thanks for your assistance.

Query No.	Query	Remark
1	Au: Please clarify whether the in-text citation 'Phillips et al. (1995)' in the 'Phillips et al. (1995) ...' refers to Phillips et al. (1995a) or Phillips et al. (1995b).	
2	Au: Please note that the reference 'Edward & Gilburn (in press)' is not listed. Please add it to the list or delete the citation.	
3	Au: Please note that the reference 'Gilburn & Day (1997)' is not listed. Please add it to the list or delete the citation.	
4	Au: Edward & Gilburn, in press = Still in press—any more details yet?	
5	Au: Please provide all the editors' names and also publisher name and location in the reference Breeman (1990).	
6	Au: Egglshaw, H.J. (1961) Mass migrational flights of <i>Coelopa frigida</i> (Fabricius) and <i>C. pilipes</i> (Haliday). (Diptera, Coelopidae.) <i>The Entomologist</i> , January, 11–18. = please add vol. no rather than month.	
7	Au: Please provide all the editors' names and also publisher name and location in the reference van den Hoek et al. (1990).	
8	Au: Please note that the reference 'Jiang & Morin (2004)' is not cited in the text. Please cite it in text or delete from the list.	
9	Au: Please note that the reference 'Luning (1990)' is not cited in the text. Please cite it in text or delete from the list.	
10	Au: Please note that the reference 'Mann (1973)' is not cited in the text. Please cite it in text or delete from the list.	

-
- 11 Au: Please note that the reference 'Paine (1992)' is not cited in the text. Please cite it in text or delete from the list.
-
- 12 Au: Please provide the editor names (if any), publisher name and location and page range in the reference Remmert (1965).
-
- 13 Au: Please note that the reference 'Sanford (1999)' is not cited in the text. Please cite it in text or delete from the list.
-
- 14 Au: Please note that the reference 'Wootton (1993)' is not cited in the text. Please cite it in text or delete from the list.
-
- 15 Ed: Accepted XX XXXXXX 2007—please provide the accepted date.
-
- 16 All figures are in poor quality. Please re-supply the figure to ensure good reproduction. For more information about supplying electronic artwork, please see the journal webpage or our electronic artwork guidelines at <http://www.blackwellpublishing.com/authors/digill.asp>

MARKED PROOF

Please correct and return this set

Please use the proof correction marks shown below for all alterations and corrections. If you wish to return your proof by fax you should ensure that all amendments are written clearly in dark ink and are made well within the page margins.

<i>Instruction to printer</i>	<i>Textual mark</i>	<i>Marginal mark</i>
Leave unchanged	... under matter to remain	Ⓟ
Insert in text the matter indicated in the margin	∧	New matter followed by ∧ or ∧ [Ⓢ]
Delete	/ through single character, rule or underline or ┌───┐ through all characters to be deleted	Ⓞ or Ⓞ [Ⓢ]
Substitute character or substitute part of one or more word(s)	/ through letter or ┌───┐ through characters	new character / or new characters /
Change to italics	— under matter to be changed	↙
Change to capitals	≡ under matter to be changed	≡
Change to small capitals	≡ under matter to be changed	≡
Change to bold type	~ under matter to be changed	~
Change to bold italic	≈ under matter to be changed	≈
Change to lower case	Encircle matter to be changed	≠
Change italic to upright type	(As above)	⊕
Change bold to non-bold type	(As above)	⊖
Insert 'superior' character	/ through character or ∧ where required	Υ or Υ under character e.g. Υ or Υ
Insert 'inferior' character	(As above)	∧ over character e.g. ∧
Insert full stop	(As above)	⊙
Insert comma	(As above)	,
Insert single quotation marks	(As above)	ʹ or ʸ and/or ʹ or ʸ
Insert double quotation marks	(As above)	“ or ” and/or ” or ”
Insert hyphen	(As above)	⊥
Start new paragraph	┌	┌
No new paragraph	┐	┐
Transpose	└┘	└┘
Close up	linking ○ characters	○
Insert or substitute space between characters or words	/ through character or ∧ where required	Υ
Reduce space between characters or words		↑