2005

Changes In the biogeographic distribution of the trochid gastropods Osilinus lineatus (da Costa) and Gibbula umbilicalis (da Costa) in response to global climate change: range dynamics and physiological mechanisms

MIESZKOWSKA, NOVA

http://hdl.handle.net/10026.1/1072

http://dx.doi.org/10.24382/3465
University of Plymouth

CHANGES IN THE BIOGEOGRAPHIC DISTRIBUTION OF THE TROCHID GASTROPODS OSILINUS LINEATUS (da COSTA) AND GIBBULA UMBILICALIS (da COSTA) IN RESPONSE TO GLOBAL CLIMATE CHANGE: RANGE DYNAMICS AND PHYSIOLOGICAL MECHANISMS

N. MIESZKOWSKA

PhD 2005

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Nova Mieszkowska

September 2005

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by

NOVA MIESZKOWSKA

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences
Faculty of Sciences

September 2005

ABSTRACT

NOVA MIESZKOWSKA

Changes in the biogeographic distribution of the trochid gastropods *Osilinus lineatus* (da Costa) and *Gibbula umbilicalis* (da Costa) in response to global climate change: range dynamics and physiological mechanisms

There is an urgent need to understand the effects of climatic variability on species' distributions. This thesis uses an integrative approach to identify and explain the changes in geographical distribution of two rocky intertidal, warm water species of trochid gastropod, *Osilinus lineatus* (da Costa) and *Gibbula umbilicalis* (da Costa) that have occurred since the onset of rapid climate warming in the mid-1980s. The potential physiological mechanisms causing the range shifts are examined, and the effects on population dynamics quantified.

I resurveyed sites in Britain and northern France previously surveyed by Southward & Crisp (1950s), Hawthorne (1960s) and Kendall, Williamson & Lewis (1970s and 1980s) to record the current north and east distributional limits of *Osilinus lineatus* and *Gibbula umbilicalis* between 2002-2004. The range of *O. lineatus* had extended north by 100km and east by 55km since 1986, and *G. umbilicalis* had extended its northern limits by 85km since 1985. Concordant increases in abundance had occurred in both species across all quantitative survey sites between 1985/6 and 2002-2004. Studies of the effects of increased sea temperatures on gonad development and spawning were run concurrently in the field and the laboratory. The reproductive cycle occurred 2 months earlier in all field populations studied over a distance of 4° latitude during the warmer years of 2003 and 2004, compared to studies made in the cooler 1960s and 1980s. No gonad re-maturation was observed in field or laboratory populations. Analyses of *O. lineatus* and *G. umbilicalis* population data from the 1970s, 1980s and 2000s showed that recruitment success had increased as winter sea temperatures had warmed. Field and laboratory studies of survival and growth of newly settled recruits was positively related to sea temperature, with greater survival at increased winter temperatures. Plasticity in the timing of the reproductive cycle and increased recruitment success in response to increased sea temperatures are suggested as the physiological mechanisms driving range extensions in *O. lineatus* and *G. umbilicalis* during the current period of rapid climate warming

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Acknowledgements

I would like to thank my supervisors Steve Hawkins and Richard Thompson for their input and advice throughout my thesis, and Mike Kendall for initiating my obsession with trochids.

I am privileged to have shared many pleasant hours of discussions with Alan and Eve Southward, whose original data have been invaluable to me both in this thesis and in the parallel work I have conducted for the MarClim project.

I am grateful to Phil Williamson and Jack Lewis who were involved with the original data collection, and to Michelle Colley from the United Kingdom Climate Impacts Programme for information and discussions regarding future climate scenarios for the UK. Global Ice coverage and SST (1856-2004) data was provided by kind permission of the British Atmospheric Data Centre (BADC).

Thanks to Anthony Richardson, Mike Burrows and Stuart Jenkins for discussions regarding my results, John Rundle and Pete Rendle for their help with aquarium facilities and Rebecca Leaper for the many field trips we shared. I am also grateful to Kirsten, Olivia and Shell for always being there for me.

Finally I would like to thank Wil for his unfailing support and encouragement, for tolerating me during my worst moments and for being a constant source of happiness in my life.

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

This study was supported by the Marine Biological Association of the U.K. and the University of Plymouth.

Relevant scientific seminars and conferences were regularly attended at which work was often presented; external institutions were visited for consultation purposes and several papers prepared and submitted for publication.

Publications:

Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R. Williamson, P., Hardman-Mountford, N.J. & Southward, A.J., 2005. Changes in the range of some common rocky shore species in Britain - a response to climate change? Hydrobiologia in press.

Hardman-Mountford, N.J., Allen, J.I., Frost, M., Hawkins, S.J., Kendall, M.A., Mieszkowska, N., Richardson, K., & Somerfield, P., 2005. Diagnostic monitoring of a changing environment: An alternative UK perspective. Marine Pollution Bulletin in press.

Mieszkowska, N., Kendall, M.A., Lewis, J.R., Richardson. A.J., Williamson, P. & Hawkins, S.J., 2005. Range expansion of the southern trochid gastropod *Gibbula umbilicalis* during recent climate warming. Journal of Biogeography. In review.

Presentations and Conferences Attended:

Countryside Council for Wales Marine Monitoring Workshop, Aberystwyth (30th October – 2nd November 2004). *Invited Speaker:* Accounting for climate change in monitoring intertidal communities in Wales.

National Academy for Gifted Talented Youth outreach programme. September 28th 2004. *Invited Speaker:* Seashore animals and what they can tell us about our changing climate.

Countryside Council for Wales Baseline Monitoring Workshop, Bangor (September 22nd-23rd 2004). *Invited Speaker:* MarClim – monitoring in the intertidal.

National Science Foundation (USA) network to co-ordinate research on the North Atlantic (CORONA). Plymouth July 28-30th 2004. *Paper presentation:* MarClim Marine Biodiversity and Climate Change research in Britain.

Climate change and aquatic systems conference. Past, present and future. Plymouth (July 21st-23rd 2004). *Paper presentation*: Is climate change driving increased reproductive success in British trochid gastropods?

UKCIP United Kingdom Climate Impacts Programme workshop for marine decision-makers – climate change impacts – what do we need to know? London (April 29th 2004) *Invited speaker:* Application of the Marine Biodiversity and Climate Change Project research to marine policy making.

National Science Week, Plymouth (9th March 2004). *Invited speaker*: What can intertidal invertebrates tell us about our climate?

UKCIP User Forum, Newcastle (24-25th February 2004). *Invited speaker*: Marine biodiversity and climate change.

Countryside Council for Wales Marine Monitoring Workshop, Bangor (22-23rd November 2003). *Invited speaker:* Tracking climate change in the Welsh marine environment using rocky intertidal species.

Looking Back for the Future: the use of long-term data for predicting ecological change. Linnean Society of London (23-24th October 2003). *Paper presentation*: Detecting the effects of climate change on intertidal diversity using long-term datasets.

Global Climate Change and Biodiversity International Conference. University of East Anglia, Norwich (8-10th April 2003). *Poster presentation:* The advance of southern species in Britain: a response to rapid climate change?

11th Annual Post-graduate Research in the Marine and Earth Sciences Conference, Southampton Oceanography Centre (31st March – 1st April 2003). *Paper presentation*: Intertidal indicators of climate change. Conference Prize for best presentation.

External Contacts:

MONARCH Modelling Natural Resource Responses to Climate Change: Steering Group member 2003-2005.

Informal working group on nature conservation policy in a changing climate. LURA Science Unit, Defra: Member 2004-2005.

Word count of main body of thesis: 35,899

Signed ..N. Mieszkowska..........

Date.......19 September 2005..........

Global climate change and the effects on natural systems: a review

Part of this Chapter has been submitted to Hydrobiologia and is currently in press: see Appendix 1

1.1 Introduction

The global average surface temperature has been increasing since records began in 1861, with an acceleration in the rate of warming since the mid-1980s (Levitus et al. 2000, Houghton et al. 2001, Hulme et al. 2002). Proxy data for the Northern Hemisphere indicate that the increase in temperature observed during the twentieth century is the largest in the last 1000 years (Hulme et al., 2002), with the 1990s the warmest decade and 1998 the warmest year on record (Houghton et al., 2001). The ocean heat content has also increased since modern measurements began in the 1950s (Hulme et al. 2002). Global Climate Models (GCMs) predict that this warming trend will continue and potentially accelerate throughout the 21st century under current and future emissions scenarios (Hulme et al., 2002), with further increases in the global mean climate of between 1.4-5.8°C (Houghton et al. 2001). These are probably the most rapid changes experienced since the end of the last ice age (Severinghaus et al. 1998, Severinghaus & Brook 1999, Rahmsdorf 2002).

Global warming has been attributed (Houghton et al. 1995, Easterling et al. 2000, Houghton et al. 2001, Hughes et al. 2002) and is now widely accepted (http://scrippsnews.ucsd.edu/article_detail.cfm?article_num=666) to be of anthropogenic origin, and results from emissions of greenhouse gases into the atmosphere as the by-product of industrial activities. Concentrations of carbon dioxide in the environment have increased by 50% since the mid-twentieth century (Houghton et al. 2001). The current levels of ~ 367ppm are greater than at any time over the last 420,000 years (Petit et al. 1999) and are predicted to increase further (Houghton et al. 2001, Hughes et al. 2002) due to a combination of inertia of the climate system (Caldeira et al. 2003) and continuation of socio-economic growth (Hughes et al. 2002)).

Many of the effects of anthropogenic emissions are also being felt in the oceans (Barnett et al. 2000). Climate change is a complex phenomenon, and additional changes in the global climate include ocean acidification (Turley et al. 2004, Schiermeir 2004), rising sea levels (Houghton et al.2001), decreasing polar ice cap thickness (Thomson et al. 2003), sea ice thinning (Laxton et al. 2003), an increase in the frequency and magnitude of extreme events including storms, flooding, droughts and heat-waves (Easterling et al. 2000, Meehl et al. 2000, Houghton et al 2001). The global heat content has significantly increased since the mid-1900s (Levitus et al. 2000). Changes in phase and frequency of large-scale climate oscillation events including the North Atlantic Oscillation (Southward 1991, Weaver et al. 2001, Edwards et al. 2002) and El Nino Southern Oscillation (Timmermann et al. 1999, Walther et al. 2002) have also occurred.

Regional variations in oceanic heating have also been detected, due to the shallow mixed layer depth at tropical latitudes and deep mixed layer in polar regions (Schneider & Thompson 1981). Significant changes in regional oceanic temperature can be detected within 10 years in the tropics, but can take an order of magnitude longer to be observed at the poles (Schneider & Thompson 1981, Washington & Meehl 1989). The temperate seas of north-west Europe have experienced phases of warming (e.g. 1920s to 1950s) and cooling (early 1960s to mid 1980s) throughout the 20th century (Southward & Butler, 1972; Southward, 1980). The North Atlantic has shown some of the largest increases in sea surface temperatures globally; coastal seas of northern Europe have warmed by between 0.5 and 1°C over the last 20 years (Hawkins et al., 2003; Schär et al., 2004; Southward et al., 2005; Woehrling et al., 2005) which is twice the rate of any previous warming event on record (Mann et al., 1998, 1999). In the western English Channel off Plymouth a 1°C increase in mean sea surface temperature has occurred since 1990. This increase exceeds any other change recorded over the past 100 years (Hawkins et al., 2003) and is most apparent in winter months (Figure 1). The rate of warming cannot be predicted with certainty but models based on medium-high CO_2 emissions scenarios indicate that sea surface temperatures around Britain will increase by between 0.5 and 5°C by 2080 (Hulme et al., 2002).

1.2 Effects of climate change

Climate is a pervasive influence at all levels of organisation in biotic systems because of temperature-dependent processes from enzyme reactions through to ecosystems (Cain 1944, Atkinson et al. 1987, Saether 1997, Stenseth et al. 2002, Parmesan & Yohe 2003). Concerns regarding the responses of natural systems to climate change in recent decades have prompted a vast research effort to assess and understand the type and extent of responses that have already occurred, and develop the ability to predict future changes as global warming continues. Extensive disruptions of most terrestrial (Peters 1992, Walther et al. 2002, Parmesan & Yohe 2003) and marine (Peters & Lovejoy 1992, Ray et al. 1992, Fields et al. 1993, Schneider 1993, Vitousek 1994, Vitousek et al. 1996, Holbrook et al. 1997, Graus & MacIntyre 1998, Hoegh-Guldberg 1999, Precht & Aronson 2004) ecological assemblages are expected during the 21st century as species are forced to move, adapt or suffer extirpation (Holt 1990) in response to the unprecedented levels of global climate change predicted by GCMs (Houghton et al. 1995, Houghton et al. 2001). Climate change may affect species via long-term, low-amplitude directional shifts in temperature (Southward 1963, Russell 1973, Southward et al. 1991), or by acute, short-term events including changes in temperature, droughts and flooding which have spatially-extensive impacts that last for decades (Huntsman 1946, Bailey 1955, Crisp 1964, Mattson & Haack 1987, Hawkins & Holyoak 1998).

The environmental factors controlling abundance and distribution of species have long been of interest to theoretical ecologists. Nevertheless, better understanding is required of the biological mechanisms enabling species to survive and the environmental drivers of these processes in light of the current period of global warming (Mooney 1991, Lodge 1993b, Lubchenco et al. 1993, Mooney et al. 1993, Holbrook et al 1997). Climate effects may occur at the local (<10km), regional (100-1000km) or global scale, and over temporal scales ranging from daily through seasonal, annual, and decadal to the geological.

The primary prediction is that biogeographic ranges of species will shift polewards in response to the polewards movement of seasonal isotherms as the global climate warms (Lodge 1993b, Lubchenco et al. 1993). Suitable habitat exists beyond the distributional limits of many species of plants (Grace 1987, Woodward 1987), mammals (Andrewartha & Birch 1954, Graham & Grimm 1990), birds (Root 1988) and marine invertebrates (Lewis 1964, Kendall & Lewis 1986) but the unsuitability of environmental conditions currently prevents their colonisation and therefore the ranges are assumed to be limited by climate. Alternatively, the range edge may lie some distance inside the 'envelope' of suitable climate space due to local factors such as a lack of suitable habitat, poor dispersal and connectivity of suitable habitat space (Kendall 1987) or if biological interactions are important in setting distributional limits. Species extinctions are also predicted at local, regional and global scales (Dukes & Mooney 1999, McLaughlin et al. 2002, Walther et al. 20023, Thomas et al. 2004).

Range shifts have already been documented globally for species covering a diverse range of terrestrial taxa including plants (Grabherr et al. 1994, Parmesan & Yohe 2003, Root et al. 2003), insects (Dennis 1993, Parmesan 1996, Parmesan et al. 1999, Roy et al. 2001), amphibians (Parmesan & Yohe 2003), birds (Hill et al. 1999, Parmesan et al. 1999, Thomas & Lennon 1999, Rehfisch et al. 2005) and mammals (Payette 1987, Hersteinsson & MacDonald 1992, Root et al. 2003). There have been similar observations for marine biota including macroalgae (Navarette et al. 1993, Lubchenco et al. 1993), zooplankton (Beaugrand et al. 2002, Beaugrand 2003, Beaugrand & Ibanez 2004), intertidal invertebrates (Bianchi & Morri 1994, Francour et al. 1995, Chevaldonne & Lejeusne 2003, Root et al. 2003, Zacherl et al. 2003), reef-forming corals (Hoegh-Guldberg 1999, Fenner 2001, Precht & Aronson 2004) and fish (McFarlane et al. 2000, Stebbing et al. 2002, Parmesan et al. 2003, Perry et al. 2005). Global 'fingerprints' of climate change show coherent patterns of range shifts (Root et al. 2003) at an average rate for 1700 species of

6.1km per decade (Parmesan & Yohe 2003), illustrating that the impacts of global warming are already apparent. Global species extinctions (Logde 1993a, Grabherr et al. 1994, Pounds et al. 1999, Thomas & Lennon 1999) and invasions (Lodge et al. 1993a,b, Carlton 2000, Sakai et al. 2000) are also predicted as climate warming renders current habitats unsuitable for survival and makes new habitats available for colonisation.

Temporal changes in species abundances within populations have also been recorded for birds (Veit et al. 1996, Veit et al. 1997, Lusk et al. 2001, Thompson & Ollason 2001), mammals (Stenseth et al. 1999, MacDonald & Brown 2002), zooplankton (Roemmich & MacGowan 1995), intertidal invertebrates (Barry et al. 1995, Southward et al. 1995, Sagarin et al. 1999, Murray et al. 2001) fish (McFarlane et al. 2000, Beaugrand 2003, Genner et al. 2004) and corals (Sheppard 2003). Increasing numbers of species from warm climatic regions are expected to replace those with colder climate affinities, leading to alterations in the composition of local assemblages (Southward et al. 1995, Barry et al. 1995, McGowan et al. 1996, Holbrook et al. 1997, Sagarin et al. 1999). These local scale changes will also facilitate the pole-ward spread of species by altering the ratio of extinction to colonisation events within range edge populations (Parmesan et al. 1999). There is a general pattern evident across a wide range of marine and terrestrial taxa of highest population densities occurring at the centre of distribution of a species, with abundances decreasing towards the range edges (Brown 1984). A positive relationship between abundance and geographic distribution has been identified for many coastal marine species, however, the spatial and temporal coverage of past data has often made it difficult to resolve whether increases or decreases in species abundance represent actual changes in biogeography, or merely fluctuating population dynamics within a species range (Barry et al. 1995, Sagarin et al. 1995, Veit et al. 1997, Murray et al. 2001, Lohnhart & Tupen 2001, Parmesan et al 2005).

The possibility of differential rates and extents of climate warming between local and regional scales may also result in variations in the biological responses (Schneider & Thompson 1981, Washington & Meehl 1989). In order to accurately predict the rate and extent of future biogeographic shifts in species distributions, the biological mechanisms driving these changes need to be better understood. Physical, ecological, evolutionary and physiological factors acting on the processes of reproduction, birth, dispersal, recruitment and mortality are all involved in shaping species' ranges (Carter & Prince 1981, Lodge 1993b, Brown et al. 1996, Lennon et al. 1997) and must also be considered when studying the effects of a changing environment. These processes operate predominantly at the local scale, and the effects of environmental change will be most apparent at the population and meta-population level (McCarty 2001). Close to the northern limits of distribution of a southern species, populations will be exposed to environmental temperatures (i.e. cold) which approach their thermal tolerance limits more often than at locations in the centre of the range (Wethey 1982, Fields et al. 1993, Bertness et al. 1999). Physiological tolerances of individuals to adverse conditions will determine individual survival and maintenance of the local population, and may shape the range limits as a direct result (Newell 1979, Lewis et al 1982, Lewis 1986, Bauer 1992).

The role of climate signals in the timing of phenological events in terrestrial plant and animal species are already well understood (Walther et al. 2002). The annual growing season has advanced by up to 8 days in northern latitude plants (Keeling et al. 1996, Myeni et al. 1997) with records of earlier flowering (Oglesby & Smith 1995, Bradley et al. 1999). Migration events in temperate species of birds have begun earlier during the spring (Oglesby & Smith 1995, Crick pers comm.) and later during the autumn (Gatter 1992, Bezzel & Jetz 1995), along with earlier egg laying (Crick et al. 1997, Winkel & Hudde 1997, McCleary & Perins 1998, Brown et al. 1999) and increases in clutch size (Jaervinen 1996, Winkel & Hudde 1997). Similar changes have been observed in marine systems, with peak abundance of phytoplankton, zooplankton in the north sea (Edwards & Richardson 2004), pre-spawning migration events in squid (Sims et al. 2001) and spawning in fish (Sims et al., 2004) occurring earlier each year in the 2000s than in the 1980s. Nearly all phenophases show strong correlations with spring temperature with a 1-month time lag, indicating that these shifts are being driven by climate warming (Walther et al. 2002). The variation in the timing of reproductive events suggest that many responses may be species specific, and may lead to changes in timing of lifestages in relation to the availability of food sources and alterations in competitive, predatory and mutualistic interactions between species (Davis et al. 1998, Bertness et al. 1999).

Global climate shifts are not a new phenomenon. Paleoecological data on the abundance and distributions of organisms during previous warm and cold climatic periods highlights strong correlations between environmental change and variations in species ranges, and can help predict the responses of species to the current period of warming. Global range shifts in response to increases in temperatures during the Pleistocene have occurred in taxa as diverse as insects (Coope 1995), mammals (Graham 1986), gastropods (Hellberg et al. 2001) ostracods (Cronin 1985) and corals (Potts & Garthwaite 1991, Pandolfi & Jackson 1997a,b). Paleoecological methods allow the biotic responses to climatic shifts of similar magnitude to be evaluated, but is limited due to the lack of information on the relative importance of gradual climatic trends in comparison to extreme weather events in shaping ecological patterns (Roy et al. 2001). Historical weather reconstructions rely on environmental processes that differ from those driven by the radiative effects of greenhouse gases (Crowley 1993, Schneider 1993, Means et al. 1999), introducing an element of uncertainty into predictions of species responses to future climate change.

1.3 Gaps in Current Research

The role of climate in regulating marine populations and communities is still not well understood (Viner et al. 1995, McGowan et al. 1998) due to problems within both the physical and ecological disciplines and the lack of connectivity between them. Most of the studies that have identified range shifts (outlined above) have examined the relationship between climate change and the biogeography of species by overlaying the species' distribution with the distribution of environmental factors and identifying those that coincide with species' borders (see Parmesan et al. 2005 for review). This is not a new concept; biogeographical studies were first introduced by Tournefort in the 1700s, and work undertaken in the early 1900s (Grinnell 1917, Orton 1920a, Setchell 1920, Cain 1944, Hutchins 1947, Wulff 1950, Andrewartha & Birch 1954) is used as the basis for ecological principles today. The relationship between species' distributions and climate, however, is not simple, and biogeographic studies can often be complicated by covarying environmental parameters, preventing cause-and-effect relationships from being understood.

The research focus of many climate programmes is directed towards climatic means, and problems with the quantification of short-term fluctuations and maximum/minimum patterns on a daily, monthly and seasonal basis on local and regional scales have resulted in the paucity of such data (Parmesan & Yohe 2003, Schiel et al. 2004, Parmesan et al. 2005). Biological studies are often temporally discontinuous and short-term (but see Parmesan 1996, Southward et al. 2005), spatially fragmented (Roemmich & McGowan 1995) and ecologically narrow, leading to inherent uncertainties in the detection and determination of the effects of climatic variation.

There is an urgent need to disentangle the ecological consequences of climatic variation over short and long temporal periods (McCarty 2001, Stenseth et al. 2002) and understand the processes and mechanisms that influence species' responses so that we may predict the nature and amplitude of future responses of natural systems to environmental change with confidence (McGowan et al. 1998, Townsend Peterson et al. 2001, Harley & Helmuth 2003). Studies that track changes in species' distributions through time are critical to understanding the underlying causative factors of range limits (Guo et al. 2005, Parmesan et al. 2005) as they provide information on the rate, extent and direction of change to allow comparisons with environmental variables. Long-term, spatially extensive datasets also allow separation of anthropogenic effects from natural perturbations and can be used to detect the relative extent of inter-annual fluctuations versus decadal-scale changes (Southward & Boalch 1986, Southward et al. 1995, Maurer & Taper 2002, Beaugrand 2003, Hawkins et al. 2003, Genner et al. 2005, Hardman-Mountford et al. 2005, Southward et al. 2005).

Population-level effects of past and present environmental perturbations can reveal the nature, rate and magnitude of a species' response, and provide insight into the biological mechanisms regulating the geographic distribution (Hutchins 1947, Lewis 1986), but such analyses require long-term datasets (Maurer & Taper 2002) of which few exist. Research into the effects that climate exerts on the physiology of marine organisms is also essential to understanding the factors setting range limits (Oullet 1997). As far back as 1920, Orton proposed that the range and abundance of species were directly determined by a physiological response to temperature, via the mechanism of reproduction. Although there has been controversy in the literature regarding the validity of this generalisation (Davies et al. 1998, Hodkinson 1999) the general consensus is that range limits may be set by infrequent recruitment due to either low adult fecundity, irregular larval supply and/or low juvenile survival (Lewis et al 1982, Kendall 1987, Lewis 1996, Hughes et al. 2002 Zacherl et al. 2003). Identification of the physiological mechanisms setting distributional limits is an important step in the development of better predictive models (Stachowicz et al. 2002).

Interactive, multi-scale studies coupling large-scale ecological investigations with population studies and detailed research into physiological mechanisms are required if cause and effect relationships are to be identified. This is not a new concept; the disciplines of biogeography and population biology were combined by MacArthur and co-workers in the 1960s (MacArthur 1965, 1972) to investigate the dynamics of species distributions. Subsequent research trends, however, have not expanded this idea to incorporate a wider range of geographical, biological and ecological facets into single studies, and climate related studies have been limited to correlational relationships between organisms and environmental change as a result. Only recently have ecologists begun to combine some of these disciplines to map the fingerprint of global change on natural systems (Caughley et al. 1988, Precht & Aronson 2000, Parmesan & Yohe 2003, Ricklefs 2004).

1.4 Study area and test system

Britain and Ireland straddle a biogeographic boundary between cold boreal 'northern' waters and warmer lusitanean 'southern' waters (Forbes, 1853, Lewis, 1964) and many intertidal species including *Osilinus lineatus* and *Gibbula umbilicalis* reach their northern or southern limits of distribution in or close to the British Isles. Thus it is an ideal location for studying the effects of climate change on these species. The increase in temperature of the marine climate in north-east Europe is greater than the global average (Houghton et al. 2001, Hawkins et al. 2003, Mieszkowska et al. 2005) and responses of marine species to global warming may be more easily detectable at this biogeographic transition zone.

Intertidal rocky shore communities have been used as model systems for the development of ecological theory since the middle of the twentieth century, and have therefore been extensively studied (Connell 1961, Paine 1966, 1974, Paine & Levine 1981, Lewis 1964, Dayton 1971, Menge 1976, Southward 1955, 1957). Intertidal animals often have complex life histories, with pelagic larvae and sedentary or sessile juvenile and adult stages that are physiologically and ecologically distinct, and spatially separated. Specific environmental conditions are crucial to the successful completion of the lifecycle due to the direct effects (Orton 1920, Barnes 1953, 1956, 1962, Crisp & Clegg 1960, Newell 1970, Bayne & Newell 1983) and the timing relative to food supply (Barnes 1956, 1962, Cushing 1990, Brockington & Clarke 2001). The wealth of information on these lifestages is invaluable in the detection and classification of climate-induced effects in the marine environment.

Intertidal invertebrate species are ectotherms and therefore track environmental temperature very closely. They experience extremes of temperature and desiccation due to emersion and immersion during the diurnal tidal cycle, and are often living close to their thermal tolerance limits as a result (Stillman & Somero 1996, Helmuth et al. 2002, Stillman 2002). Marine species respond faster than terrestrial species to environmental change due to the typically short lifespans (Carr et al. 2003) and the sessile nature of the adult stage, preventing escape from changing environmental regimes. Few intertidal species are commercially exploited, especially in Britain, and changes in distribution and abundance are therefore likely to be driven by the direct response of organisms to changes in the environment. Most intertidal invertebrates are from lower trophic levels, and thus would be expected to respond quicker to alterations in local conditions than species at higher trophic levels; they often show the first response in a cascade of effects up the food chain to tertiary and apex predators including fish (Smith 1985), birds (Jenouvrier et al. 2003) and seals (Barlow et al. 1998), which all may display a time lag in their response.

Variation in the abundance of keystone species can also alter the composition and dynamics of rocky shore communities (Connell 1961, Lewis 1976, Hawkins & Hartnoll 1982) and thus small changes in temperature can lead to major alterations in community structure and functioning (Barry et al 1995, Bertness et al. 1999, Sagarin et al. 1999). Intertidal species are therefore likely to be one of the natural systems most sensitive to global warming, with changes at the level of species' distribution and systematic changes within communities to species with greater affinities for warmer temperature (Barry et al. 1995, Sagarin et al. 1999).

1.4 Study species

Osilinus lineatus is a lusitanian 'southern' species of prosobranch trochid gastropod occurring in the rocky intertidal zone of moderately exposed shores (Ballantine 1961) in the north-east Atlantic. This species reaches its northern limits of distribution in Wales and Ireland, and its north-eastern limits in southern England (Fisher Macmillan 1944, Southward & Crisp 1954a, Crisp & Southward 1958, Lewis 1964). Distribution is continuous along the Portuguese, Spanish and French coastlines, and the southern limits of distribution are reached in Morocco, (Gaudencio & Guerra 1986, Lewis 1986). *O. lineatus* is a grazing species, feeding predominantly off the biofilm on rock surfaces (Desai

1966, Hawkins et al. 1989). The adult stage is sedentary and is found predominantly in the midshore region, although some vertical movement within a shore can occurr in response to daily and seasonal cycles of tides and environmental regimes (Little et al. 1986, Crothers 2001). *O. lineatus* is an annual broadcast spawner (Garwood & Kendall 1985, Bode et al. 1986, Gaudencio & Guerra 1986, Kendall 1987), with a lecithotrophic larval stage lasting only a few days (Desai 1966). New recruits settle within the same habitat on the shore as adults, but microhabitat segregation may exist as recruits tend to favour more cryptic habitats (Crothers 2001). Juveniles become sexually mature at approximately two years of age as they enter the adult population (Desai 1966, Garwood & Kendall 1985, Crothers 2001). Adult *O. lineatus* can live in excess of 10 years (Kendall 1987) although lifespans are thought to be shorter at lower latitudes (Bode et al. 1986).

Gibbula umbilicalis is another lusitanian 'southern' species of trochid gastropod found in the rocky intertidal zone of moderate to exposed shores in the north-east Atlantic. The geographic distribution of *G. umbilicalis* extends from the north-west coast of Scotland southwards along the Atlantic coastline of Europe to Cap Blanc, West Africa, where the southern limits have been recorded (Lewis, 1964; Lewis et al., 1982). It too grazes predominantly on biofilms and occupies the same habitat as *O. lineatus* on the shore. There is some vertical overlap in occurrence of the two species, with *G. umbilicalis* occupying the mid- to lowshore area. *G. umbilicalis* is also a broadcast spawner with lecithotrophic larvae, and new recruits are also considered to begin sexual maturity around two years old (Kendall pers comm., Bode et al. 1986, Guerra & Gaudencio 1986). *G. umbilicalis* is thought to survive for ten years or less, but accurate ageing has not yet been achieved.

1.6 Specific Aims

This thesis adopts an integrative approach using both population level and mechanistic individual level approaches to investigate the responses of two 'southern', warm water species of trochid gastropod to the current period of rapid climate change across a range of temporal and spatial scales. *Osilinus lineatus* and *Gibbula umbilicalis* belong to the same tribe (Gibbulini). They have similar geographic distributions and occupy similar niches in the rocky intertidal and therefore are used as 'replicates' to see whether responses to climate are similar within taxa. Studies of the distribution, population dynamics, reproductive cycles and recruitment are investigated to determine which mechanisms acting at the local scale may have given rise to the large scale associations between geographic ranges and marine climate. This combined research strategy adds rigour and consistency to the findings of each component of the study, and provides an integrated insight into the temporal and spatial scales over which climate-induced responses are occurring. Baseline data on the distribution of both species in the 1950s and 1960s, and population data collected from 1977 to 1986 is used in conjunction with resurveys between 2002 and 2004 to examine the temporal and spatial extent of the effects of rapid climate warming.

In Chapters 2 and 3 I have investigated long-term changes in the geographical distribution of *Osilinus lineatus* and *Gibbula umbilicalis.* The dynamics of the northern and eastern range boundaries in Britain are tracked prior to the start of accelerated climate warming during the 1970s and 1980s and after two decades of climate change in the 2000s using archived datasets and resurvey data.

Chapters 2 and 3 also use these datasets to analyse the dynamics of populations along a latidudinal gradient from the range edges to locations further into the geographic range. Population studies are often demographic (birth, mortality, dispersal), temporal (abundance and distribution changes over time) or experimental (manipulation of factors and individuals). This thesis uses a combined approach, incorporating meta-analyses to look at changes in demographic parameters over time, the degree of concordance across regions and years and the extent of decadal-scale trends in population dynamics.

The underlying mechanisms causing population-level changes are considered in Chapters 4 & 5. Chapter 4 examines the functional relationship between environmental temperature and reproduction to determine the role that reproduction plays in setting northern limits. The reproductive cycle of *Osilinus lineatus* was tracked over a two-year period at locations over a latitudinal gradient of 4° from the northern range edge in Wales to northern France. The timing and duration of phases of the cycle were mapped onto sea surface temperature records and compared to research carried out in previous decades to compare cycles during varying climatic regimes. These studies were complemented by laboratory studies of the effects of sea temperature on the duration of spawning and the potential for redevelopment of gonads in warmer conditions.

Chapter 5 investigates the relationship between recruitment success and environmental temperature via juvenile survival, growth and abundance to determine the role that reproduction plays in setting northern limits. The recruitment dynamics of *Osilinus lineatus* and *Gibbula umbilicalis* were studied over a two year period on a shore in south west England to ascertain the effects of seasonal environmental temperature regimes and extremes on the success of the year class. Laboratory studies, run in parallel with the field studies, isolated the effects of temperature to gain further insight into the extent that winter temperatures control the survival of newly-settled recruits.

Chapter 6 summarises the findings of this thesis and demonstrates the value of integrated research from physiological studies to large-scale ecological analyses in understanding the patterns and processes of species responses to rapid climate change. Shortcomings of current approaches are discussed, including limitations of biological studies. A quantitative, mechanistic model is proposed for the role of reproduction and recruitment in responses of populations to climate change, and the importance of incorporating biological information into a new generation of mathematical climate modelling is emphasised. Finally, I identify the main priorities for further research, and discuss the prognosis for natural systems in a rapidly warming world.

Chapter 2. Long-term changes in the geographic distribution, size, age and longevity of some near-limit populations of the trochid gastropod *Osilinus lineatus*.

2.1 Introduction

Correlational studies have already demonstrated that shifts in the geographic distribution of species have occurred during the current period of global warming (see Chapter 1 for review), and further shifts are expected in most terrestrial and marine ecosystems as the climate continues to warm (Lubchenco et al. 1993, Southward et al. 1995, Lewis et al. 1996). This type of broadscale approach has its limitations, however. While correlational biogeographic studies can be used to obtain probabilistic maps of species occurrence and generate testable hypotheses, they cannot provide information on cause and effect (Parmesan & Yohe 2003, Fortin et al. 2005, Parmesan et al. 2005). In order to detect and quantify the extent of changes in species distributions, quantitative characterization of the biogeography of the species is required, in particular detailed information on the location of boundaries and the structure and abundance of populations at range borders (Maurer 1994, Maurer & Nott 1998, Maurer 1999, Gaston 2003, Fortin et al. 2005). It is also necessary to separate short-term and small-scale natural spatial and temporal variability from the changes driven by global climate change. This requires data to be collected over a time period of the same magnitude as the rate of change in forcing factor, but with sufficient resolution to segregate small-scale temporal variation. For climate change studies, annual data collection with multi-decadal coverage is required. But there are few such data sets in existence (but see the work using the Continuous Plankton Recorder; Beaugrand et al. 2002, Beaugrand & Ibanez 2004). The ability to detect and characterise species' distributions and range borders is therefore limited by the type and quality of data, which seldom have the temporal resolution required.

2.1.1 The effects of recent climate change in Britain and Ireland

Britain and Ireland straddle a biogeographic boundary between cold, boreal waters to the north and warm, lusitanian waters to the south (Forbes 1857) and many mairne species reach their northern or southern limits of distribution close to this border (Eckman 1953, Lewis 1964, Briggs 1974a,b, 1995). It is therefore an ideal location for studying the effects of climate warming on marine species. As the current warming trend continues, lusitanian 'southern' species are expected to extend their distributions and increase in abundance, whilst boreal 'northern' species are likely to show range contractions and decreases in abundance around the British coastline (Southward et al. 1995). The effects of changes in environmental conditions on individuals are likely to be most severe close to the limits of distribution where stressful environmental conditions are experienced more often and individuals are operating close to their physiological tolerance limits (Hutchins 1947, MacArthur 1972, Lewis 1986, Brown et al. 1996, Hoffman & Parsons 1997). Effects on physiological processes, phenology and adaptive responses of species have been predicted (Lodge 1993a,b, Lubchenco et al. 1993) and have already been observed (e.g. intertidal invertebrates - Bianchi & Morri 1994, Francour et al. 1995, Chevaldonne & Lejeusne 2003, Root et al. 2003, Zacherl et al. 2003), which will in turn affect interactions between species, changes in diversity and ultimately responses at the ecosystem level (Hughes 2000).

Extensive surveys of the distribution of rocky intertidal species were made around the coastlines of Britain, Ireland and the northern European mainland from the 1930s to the 1950s (Southward & Crisp 1954, Crisp & Southward 1958a, Fischer-Piette 1936, Fischer-Piette 1955, Crisp & Fischer-Piette 1959). The northern range limit and structures of near limit populations of intertidal trochid and limpet species were studied in the 1960s, 1970s and 1980s (Hawthorne 1965, Kendall & Lewis 1986, Kendall 1987, Bowman & Lewis 1986). Much of the raw data are still in existence, and represents some of the longest time-series data available. In this chapter I demonstrate the value and applications of long-term observations in determining the dynamics of biogeographic ranges using the trochid gastropod *Osilinus lineatus* as a case-study.

The distribution of *O. lineatus* was extensively mapped in Britain and Ireland during a warm period in the 1950s (Crisp & Southward 1958a). Range contractions were recorded after the cold winter of 1962/63 (Crisp 1964, Hawthorne 1965). Some re-surveys were made in the in the 1980s, immediately prior to the onset of rapid warming (Hawkins, unpublished). A quantitative baseline of the distribution and population dynamics of *O. lineatus* at sites close to the northern and north-eastern range limits in Britain was also collected at the start of the current period of rapid warming in 1986 by the NERC Rocky Shore Surveillance Group (Kendall 1987).

This chapter combines archived records recent data collected during resurveys of populations at sites previously surveyed by Kendall, Southward, Crisp, Hawthorne & Hawkins between 2002 and 2004. The data are used to investigate the structure and dynamics of populations of the northern and north-eastern range limits of *O. lineatus* and quantify the spatial and temporal variation in abundance within the range that have occurred since accelerated warming began by testing the following hypotheses:

1. The range limits of *O. lineatus* in Britain have re-extended during the current period of rapid warming in Wales, Northern Ireland and Southern England, and exceeded the previously recorded range limits from the last warm period prior to the cold winter of 1962/1963.
2. Abundance has increased in populations from the northern range edge in Britain and northern France as environmental conditions have become more favourable for survival and reproduction.
3. Size and age of animals has decreased in response to increased abundances in surveyed populations, due to greater intraspecific competition first suggested by Kendall (1987).

2.2 Methods

2.2.1 Temperature data

Mean monthly sea surface temperature (SST) data from 1980 -2004 were obtained from the Hadley Centre's HadISST Version 1.1 dataset with a spatial resolution of 1° latitude by 1° longitude for the western English Channel. From this the annual mean SST and mean winter SST were extracted.

2.2.2 Field Surveys

Searches were carried out in suitable habitat on shores immediately beyond the recorded geographic limits in England and Wales (Crisp & Knight-Jones 1954, Crisp & Southward 1958, Crisp 1964, Hawthorn 1965, Kendall 1987). Each shore was searched by two operators for a 30-minute period. Any animals encountered were measured, aged and released. If more than a few individuals were found, five replicate searches of three minutes duration were carried out as described below. Sites around the coast of Northern Ireland where semi-quantitative baseline surveys had been made in 1952/3 were also re-surveyed (Southward & Crisp 1954).

The 16 sites from Kendall's 1986 quantitative survey of English, Welsh and French coasts were resurveyed during 2002 (Figure 2.1) using the original methodology of replicated timed collections to estimate abundance. These were made by the same operator as in 1986 (Kendall) and/or a cross-calibrated operator (Mieszkowska). At each shore collections were always made in the optimal habitat for O. *lineatus.* Collection involved intensive searching of small areas between MTL and MHWN, particularly medium sized rocks over gravel, or rock fragments in which '0' cohort individuals (animals less than 1 year old) occur. At each site five replicate three minute long collections of snails were made. Repeat surveys were also made in 2003 and 2004 at a subset of 10 sites in south west Wales and England to provide data on inter-annual fluctuations in abundance.

The basal diameter of all animals collected was measured to the nearest millimetre. Individuals were then aged by counting the annual growth checks on the shell to determine their year of settlement (Williamson & Kendall 1981). Occasionally, winter growth checks were indistinct, but the number of individuals that could not be aged was less than 5% of any sample.

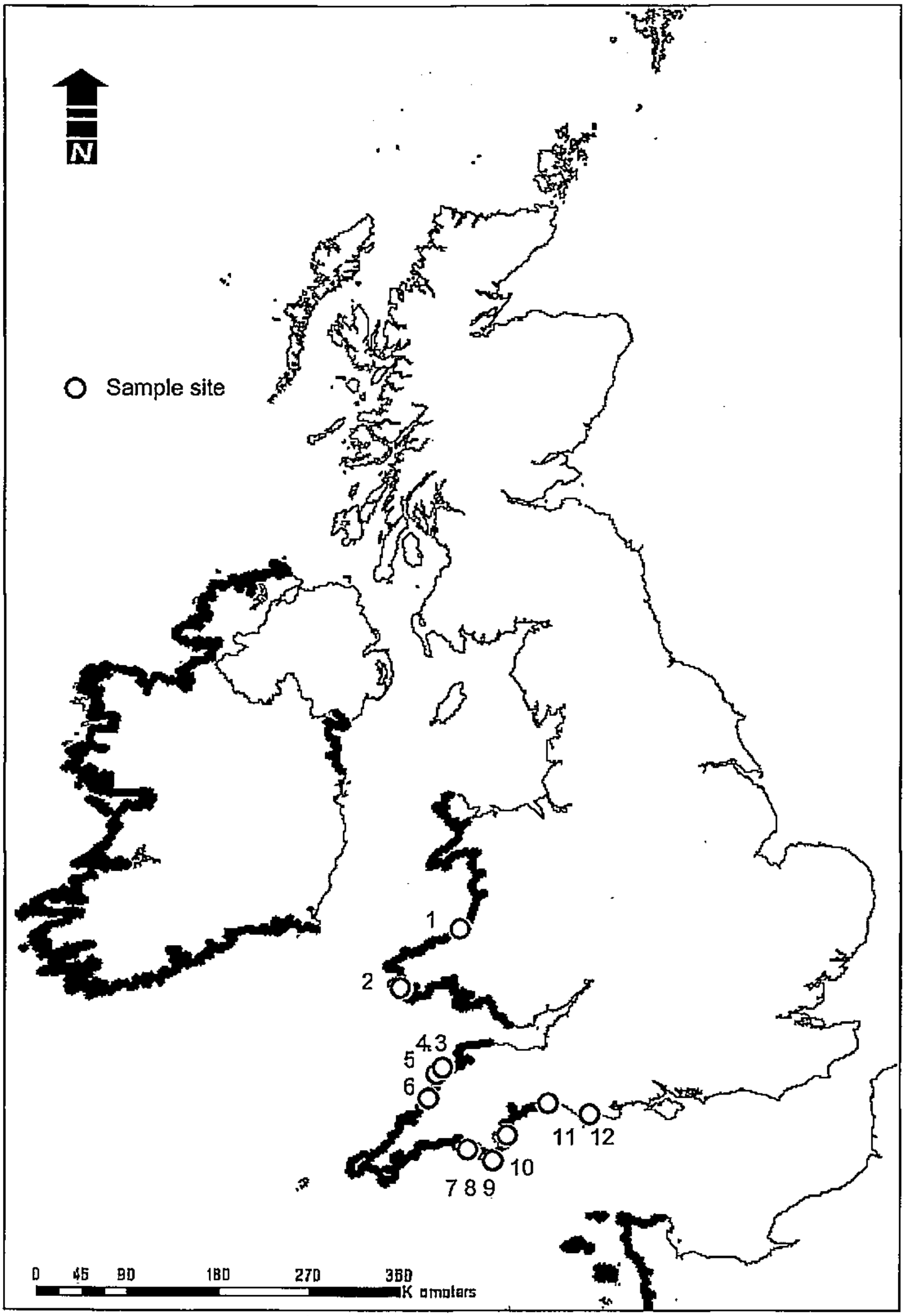


Figure 2.1. Previous recorded north and eastern limits of distribution of O. *lineatus* (black line) and quantitative sample sites in Britain (circles): 1. Aberaeron, 2. West Angle Bay, 3. Hartland Quay, 4. Wellcombe, 5. Widemouth, 6. Crackington Haven, 7. Wembury, 8. Noss Mayo, 9. Prawle, 10. Churstone, 11. Lyme Regis, 12. Osmington Mills (from Southward & Crisp 1954,Crisp & Southward 1958, Lewis 1964).

2.2.3 Data analysis

Abundance was compared at all 16 sites in 1986 and 2002 using a matched-pairs t-test. The variation in abundance between the years 1986, 2002, 2003 and 2004 was compared at a subset of 10 sites where repeat data had been collected, using a 2-way ANOVA, with site and year as the main effects. A planned comparison test was then made between 1986 and 2002-2004 to partition the variance associated with the 'years' effect computed by the ANOVA and determine whether the inter-annual variation in abundance across the sites was less than the between-decade variation. The degree of synchrony of changes in abundance across 9 sites for which data exists in 1986, 2002, 2003 and 2004 was calculated using Kendall's test for concordance, followed by a Friedman ANOVA to determine significance.

The changes in maximum size (D_{max}) and size at the 90th percentile (D90) of cumulative age frequencies between 1986 and 2002 were tested using matched pairs t-tests (on $\log_{10}$ transformed data for D90) from 15 and 16 sites respectively where mean data exists from 1986. D90 was obtained by calculating the diameter at the point on the size frequency curve where 90% of the sample population were included. Regression analysis was carried out on the 1986 and 2002 data to examine the relationship between size (shell diameter) and abundance across all 16 sites close to range edges in both years. The variation in the slopes of the resulting regression lines was compared using an analysis of covariance to determine whether the relationship between abundance and size had altered between the 1980s and 2000s.

The differences in maximum age (A_{max}) and age at the 90th percentile of cumulative frequency plots (A90) between 1986 and 2002 were tested using matched pairs t-tests to compare the mean values across all 16 sites. The mean size of each individual year cohort was then calculated for 12 sites for which data were available and matched pairs t-tests run on selected year cohorts using these data. The mean size of new recruits (year 1 cohort), animals reaching sexual maturity (year 2 cohort) and adult animals (year 4 cohort) were compared in 1986 and 2002 to determine if the growth suppression that was indicated by the results of the tests on age and size could be identified within a particular life-stage.

2.2.4 Limitations of data

Unfortunately the raw data from 1986 is no longer in existence, and the only data available is in the format published by Kendall (1987). This limits comparisons to mean and standard deviation for abundance, mean values only for diameter and age at the 90th percentile, and percentage values for age frequency from published graphs. The majority of the analyses performed on this dataset are matched pairs t-tests on means, due to this being the most powerful parametric test that can be applied to the limited data available from 1986. This is a very conservative test and therefore any differences detected have strong inferential power.

2.3 Results

2.3.1 Changes in Temperature

Britain's climate has warmed in the twentieth century that exceed the global average, with air temperatures increasing by ~1°C and SST by 0.6 – 1°C since the start of the 1900s (Hulme et al. 2002). Strong warming of surface waters has occurred in the North Atlantic (~35 – 65°N) since the mid-1980s causing greater increases than the global average rise of 0.15 ±0.05 °C (Houghton et al. 2001).

The temporal and spatial extent of warming has varied around the British coastline. Mean surface temperatures of the western English Channel have increased by ~1°C between 1950 and 2004 (Figure 2.2) (Hawkins et al. 2003, Mieszkowska et al. 2005), whereas sea surface temperatures in the Irish Sea have increased by ~ 0.5°C (Hulme et al. 2002). Seasonal SST ranges have also decreased in Britain over the last two decades as winter temperatures have increased at a faster rate than summer temperatures (Figure 2.3) (Mieszkowska et al. 2005).

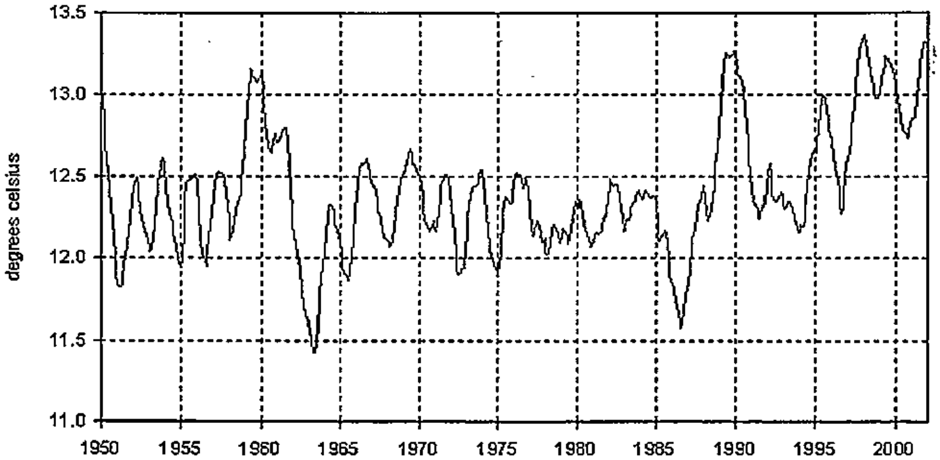


Figure 2.2. Annual mean sea surface temperature (SST) in the Western English Channel (50-51° N, 4-5 ° W). Met Office - GISST/MOHMATN4/MOHSST6 - Global Ice coverage and SST (1856-Feb 2003) data provided to the MarClim project by kind permission of the British Atmospheric Data Centre (BADC). (reprinted from Mieszkowska et al. 2005)

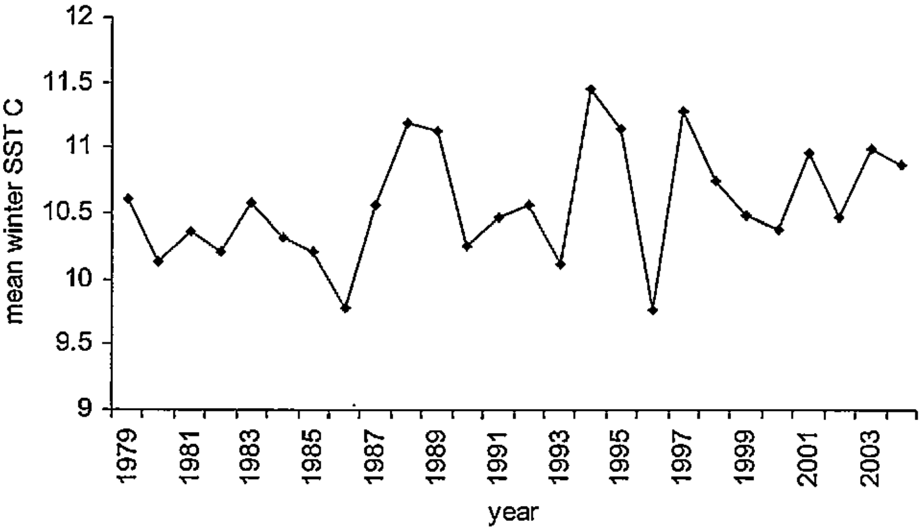


Figure 2.3. Mean winter (Jan-Mar) SST for the Western English Channel (50-51° N, 4-5 ° W). Met Office - GISST/MOHMATN4/MOHSST6 - Global Ice coverage and SST (1856-Feb 2003) data provided to the MarClim project by kind permission of the British Atmospheric Data Centre (BADC).

2.3.2 Geographic Distribution

Previous confirmed records of distribution of *O. lineatus* in the British Isles extend as far north as Point Lynas in Anglesey, with an additional unconfirmed record of an individual at the Great Orme, North Wales pre-1946 (Crisp & Knight-Jones 1954, Lewis 1964). Northern limits in Ireland (last breeding population) were recorded at Malin Head in the north-west and Killough in the north-east, with no animals occurring along the northern Irish coastline between these locations (Crisp & Southward 1954). In addition, isolated individuals had been recorded in the eastern basin of the English Channel as far as St Aldhelm's Head (Hawthorn 1965) although the most eastern multi-age population in the English Channel was recorded at Lyme Regis (Southward & Crisp 1958, Hawthorne 1965, Kendall 1987). In the southern Bristol Channel *O. lineatus* had been found as far east as Swill Point, although this population had missing year classes indicating successful recruitment was sporadic (Crothers 1998). Range extensions recorded in the 2002 survey are detailed further below.

In North Wales, populations of *O. lineatus* were eradicated or cut back in the cold winter of 1962-63 (Crisp 1964) to the south of the Lleyn Peninsula (Figures 2.4, 2.5), with the last multi-age breeding population being found at Porth Neigwl. Animals were slow to re-colonise all sites up to Point Lynas, the previous northern limit (Crisp & Knight-Jones 1954). Single specimens were recorded by Hawkins and co-workers in the mid 1980s on the south west coast of Anglesey at Rhosneigr (Figure 2.6). In 2002 small numbers of individuals were recorded on the north east coast of Anglesey for the first time since 1963, with the most easterly location of animals occurring at Cemlyn Bay. A breeding population was found at Porth Swtan in 2002 and was still present in 2004 (Figure 2.7).

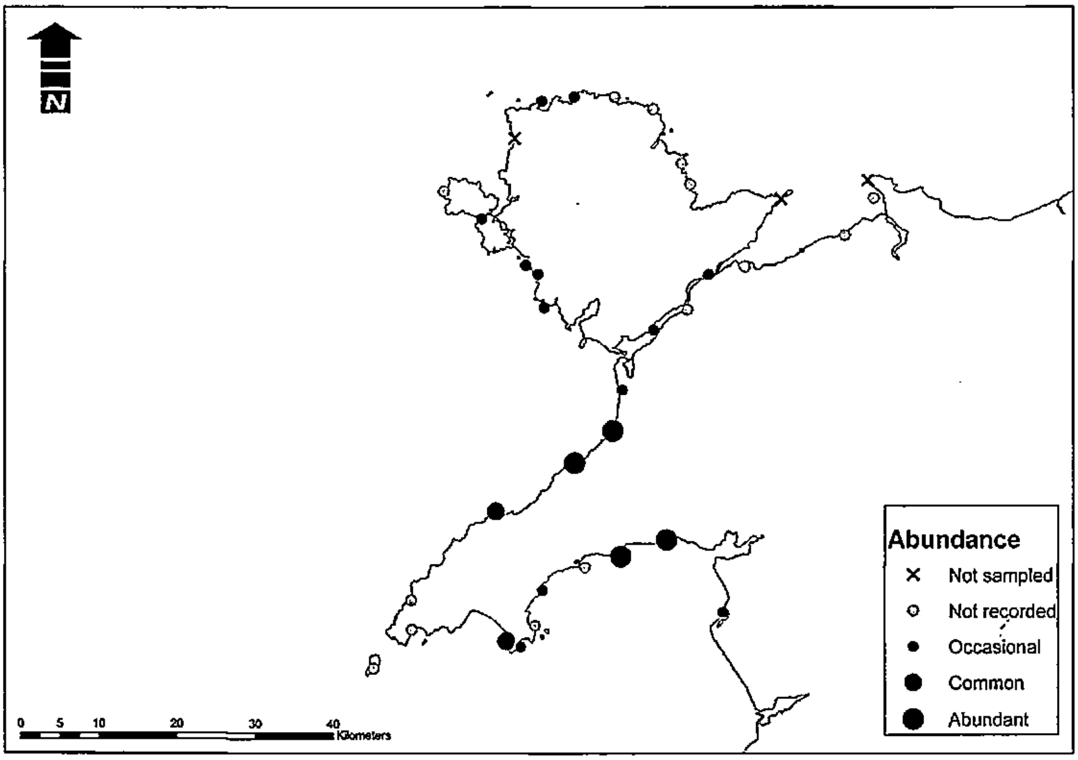


Figure 2.4. Abundance of *O. lineatus* at sites close to the northern range edge, north Wales in the 1950s.

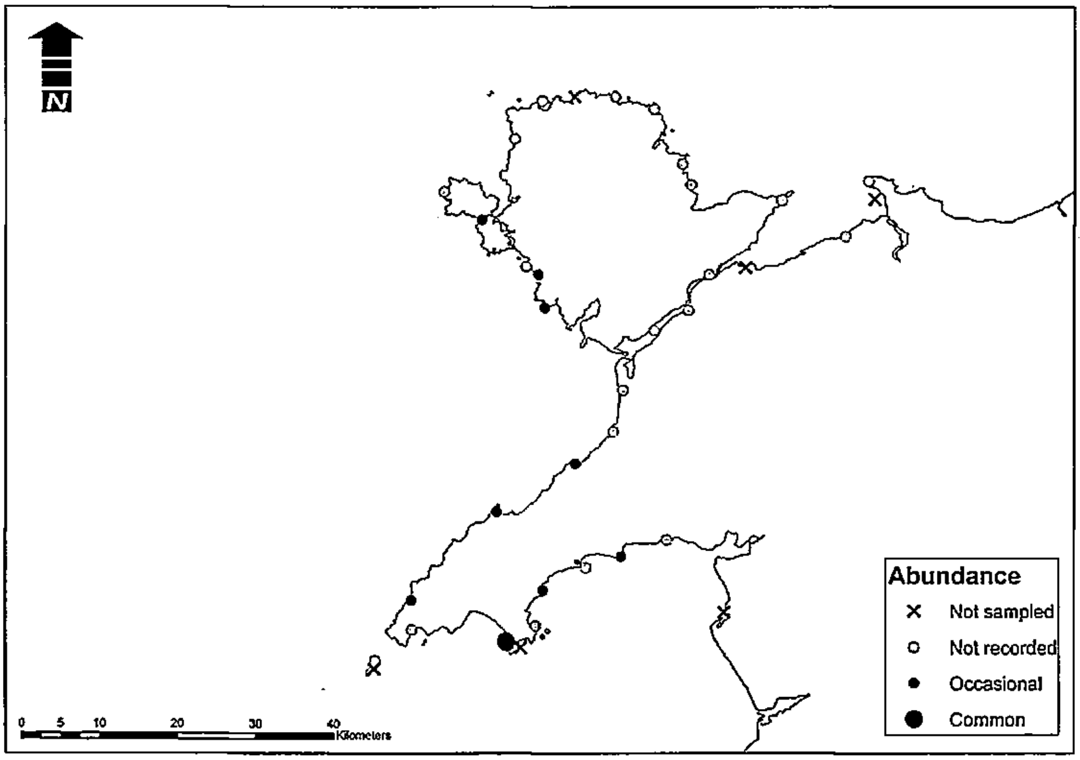


Figure 2.5. Abundance of *O. lineatus* at sites close to the northern range edge, north Wales in 1964 after the cold winter 1962/63.

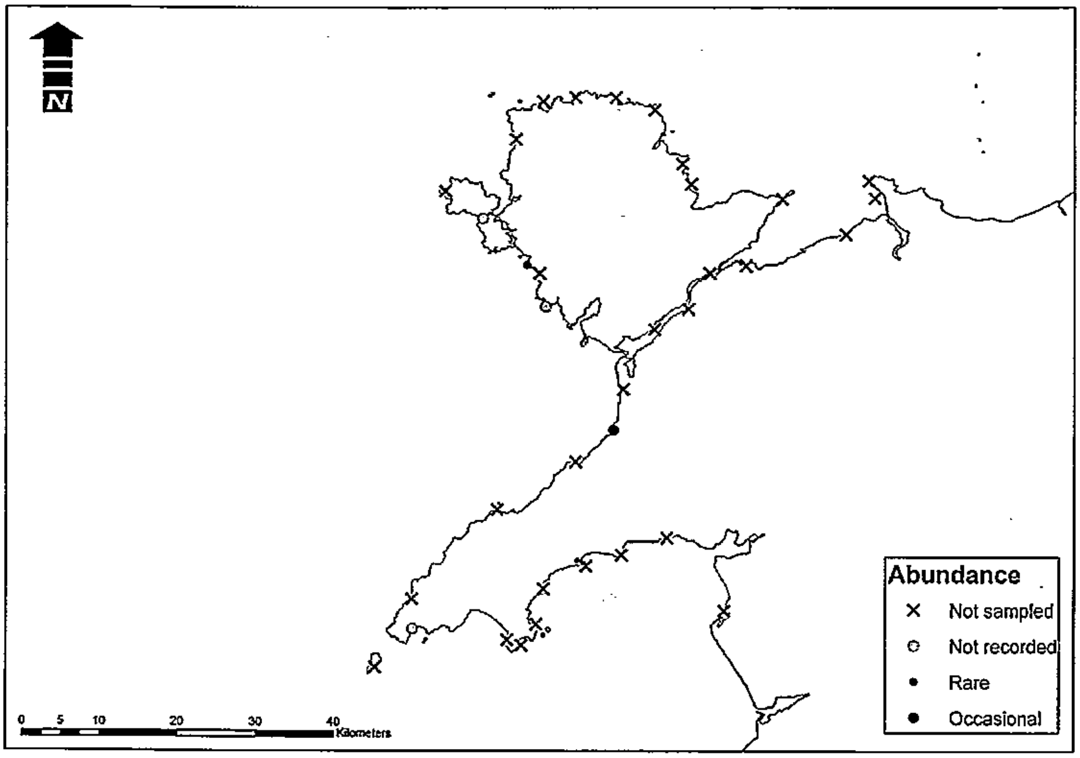


Figure 2.6. Abundance of *O. lineatus* at sites close to the northern range edge, north Wales in the 1980s.

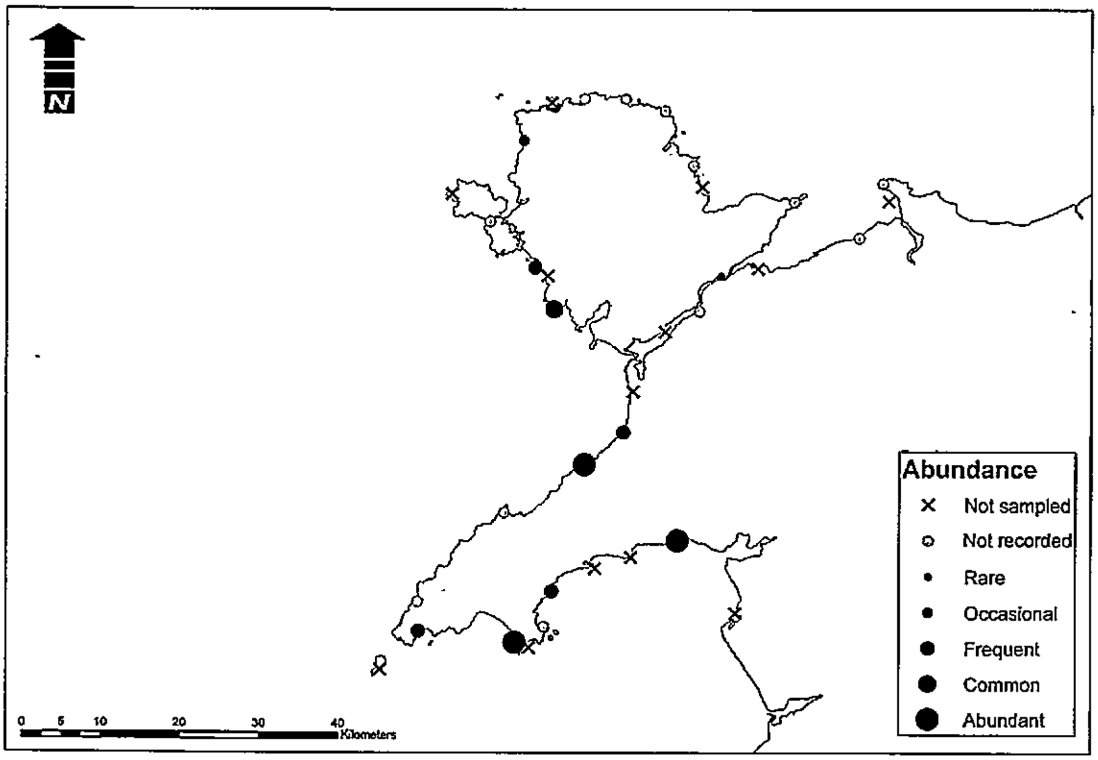


Figure 2.7. Abundance of *O. lineatus* at sites close to the northern range edge, north Wales in the 2000s.

In the English Channel a small population containing a range of sizes was found in 2002 close to Weymouth at Osmington Mills, a site at which earlier visits in the 1960s and 1980s had only revealed occasional large animals (Figures 2.8, 2.9) (Hawthorn 1965, Kendall 1987). This mixed age and size population east of the Portland Bill headland was approximately 55 km further east than the previous range edge population at Lyme Regis. Repeat surveys in 2003 and 2004 confirmed that this population was still present. A mixed size population was also recorded at Clay Ope Cove on the western side of the Isle of Portland in 2002 (Mieszkowska & Herbert, pers obs.). Occasional individuals were found on Portland Bill in 2003 as observed in the 1960s (Hawthorne 1965) and the 1980s (Kendall 1987). Records of an isolated individual have also been made from Freshwater Bay on the Isle of Wight in 2004 (Hawkins pers comm.) and 2005 (Herbert pers comm.).

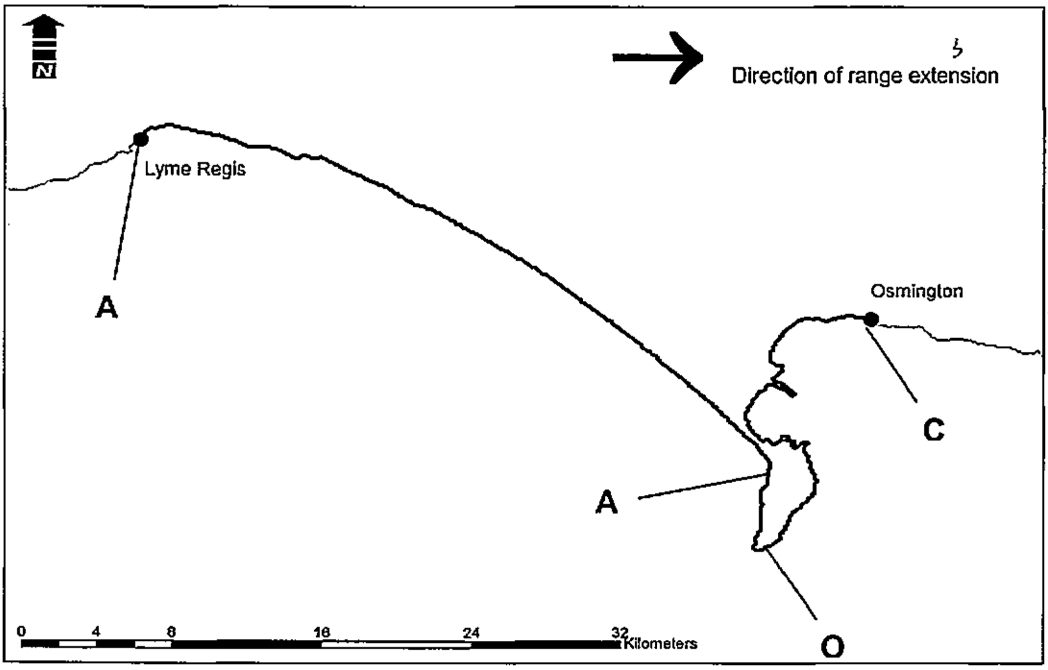


Figure 2.8. Eastern range extension (black line) of *O. lineatus* along the English Channel, 1986-2002 (Crisp & Southward 1958, Kendall 1987), A = abundant, C = common, O = occasional (ACFOR scale from Southward & Crisp 1954).

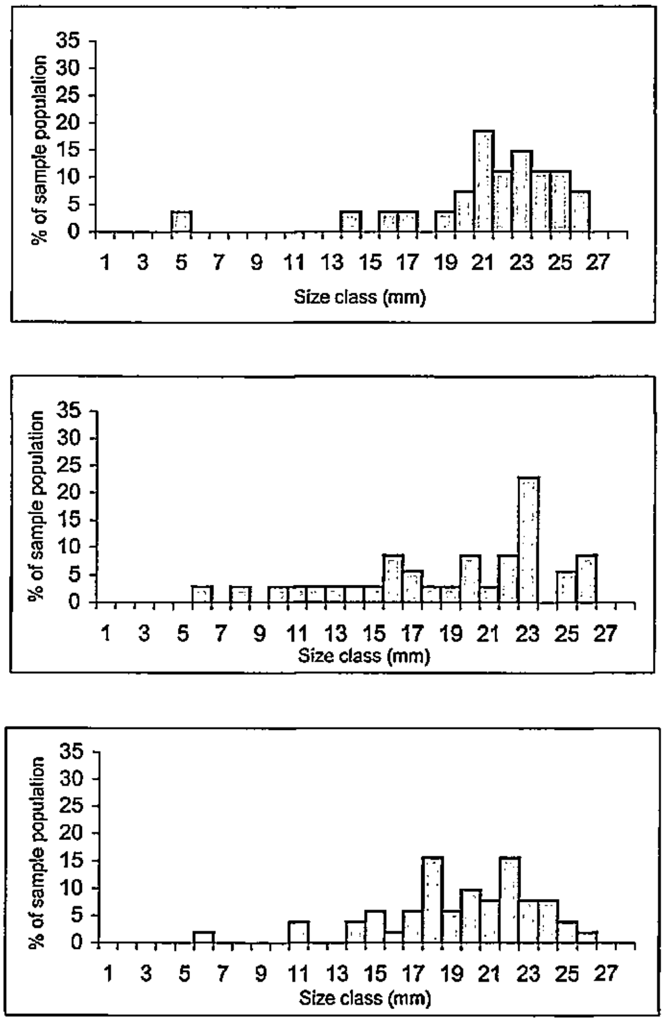


Figure 2.9. Size frequency histogram of *O. lineatus* found at Osmington, a) 2002, b) 2003, c) 2004

In Northern Ireland the north-eastern limit was previously recorded at Killough on the east coast (Southward & Crisp 1954). In 2003 breeding popuations had extended north by 10km to Ardglass on the north west coast, with individuals being found 20km further north at Ballyquintan Point (Figure 2.10), so closing the gap between the north-western limit populations at Malin Head.

Figure 2.10. Sites sampled in N. Ireland 2004: *O. lineatus* not found (white circles), present (black circles), previous range limit (grey line) (Southward & Crisp 1954), range extension 2003 (black line).

2.3.3 Abundance

The abundance of *Osilinus lineatus* was greater (matched pairs t-test (t=6.87, df = 15, P<0.001)) at all 16 sites (UK and France) revisited in 2002 (Figure 2.11). The greatest changes occurred at Noss Mayo and Prawle, where abundance was five times higher. The lowest increases were seen at Aberaeron, West Angle Bay, Widemouth and Wembury, where abundances increased by less than 100%, whereas the remaining 10 sites all showed increases in abundance of between two and three times in 1986.

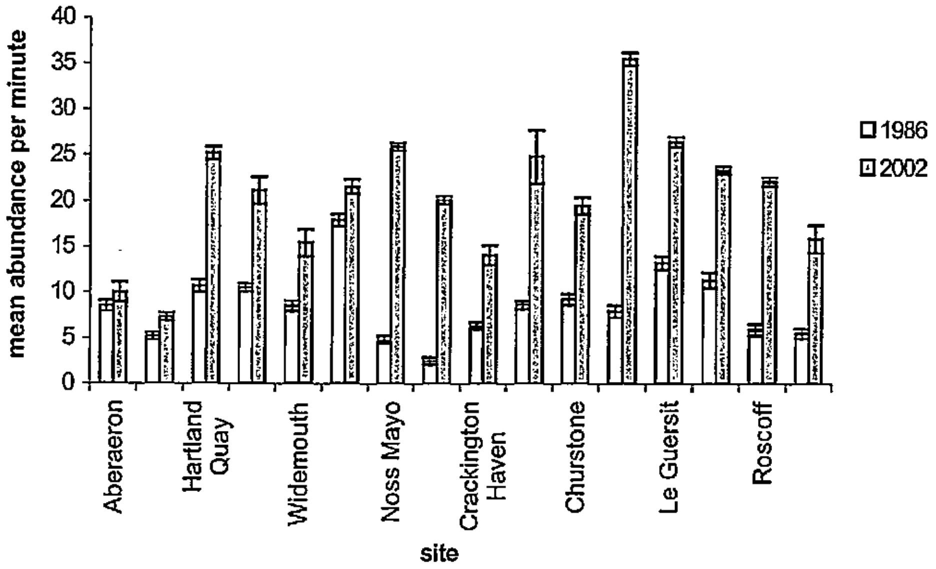


Figure 2.11. Mean abundance (number per minute searched) at 16 sites in 1986 and 2002 (± 1SE of the mean).

The results of the two-way ANOVA showed that the variation in abundance between years, and between sites were both significant (Table 2.1). The variance associated with the 'years' effect was partitioned such that the contrast sum of squares accounted for most (90%) of the total variance among years (402.15), with the variance between the 2002, 2003 and 2004 years accounting for the remaining 10%. The variance between 1986 and the 2000s was much greater (P<0.0001) than the variance within years in the 2000s, demonstrating major decadal-scale changes.

Table 2.1. ANOVA table for variance in abundance between 1986, 2002, 2003 and 2004 across 9 study sites.

Source	df	Sum of Squares	Mean Square	F	P
Site	8	397.6829	49.7104	5.77	0.0004
Year	3	442.0030	147.3343	17.10	<0.0001
Error	24	206.81900	8.6175		
Corrected Total	35	1046.5050			

The increase in abundances between 1986, 2002, 2003 and 2004 across 9 sites situated close to northern and north-eastern limits and further into the range showed a significantly high level of concordance (coefficient of concordance 0.6947, Friedman ANOVA: Chi squared n=4, df=8, χ^2=22.2297, p<0.0045).

2.3.4 Size structures

A significant decrease in the maximum size, and size of animals at the 90th percentile of a size frequency histogram between 1986 and 2002 had occurred across the sites for which data exist (D_{max}: t=2.3769, P=0.0322, n=15, df=14, D90: t=4.94, P=0.0002, n=16, df=15). The regression analyses showed a significant relationship between mean abundance and mean size at the 90th percentile in 1986, accounting for 36% of the variance (F= 7.8258, R^2 = 0.3586, P=0.0140, df=1, n=16, y=-0.4351x + 25.525). In contrast there was a non-significant relationship in 2002 (F= 3.8480, R^2 = 0.2156, P=0.0700, df=1, n=16, y=-0.175x + 23.078). Increases in abundance had a stronger negative effect on size at lower densities such as encountered in 1986, but not at the higher densities found at all sites in 2002.

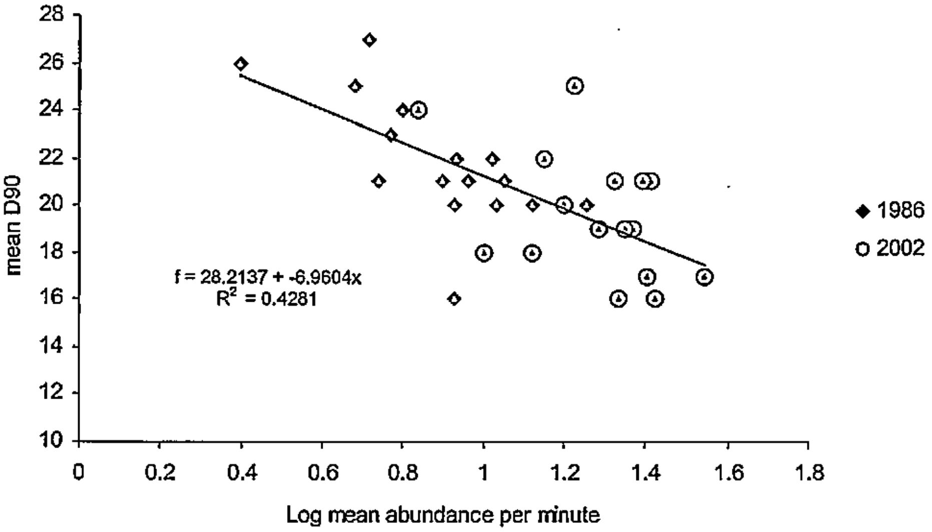


Figure 2.12. Linear regression of mean shell diameter at the 90th percentile against log mean abundance for all sites in 1986 and 2002 and for both years combined.

An ANCOVA showed that the difference between the two regression lines was not significant and so a combined relationship was calculated (Figure 2.12). A linear regression model fitted to the combined data showed a significant relationship between log abundance and D90 (F = 22.4595, R^2 = 0.42813075, P<0.001, df = 31).

2.3.5 Population structures

Across 14 sites for which comparable data were available, the age of snails at the 90th percentile of an age frequency histogram (A_{90}) had declined significantly (t=2.88, p=0.0029, df=13) between 1986 and 2002. Age frequency structures were dominated by animals between 1-2 years old in 1986, with much smaller percentages of 3+ animals in the populations. In 2002, the 1-4 year cohorts dominated the population, with evidence of strong recruitment of the '0' cohort at 7 out of 14 sites. There was no significant change in mean size of animals in the 1,2 or 4 year cohorts between 1986 and 2002 across the 11-12 sites analysed (1 cohort: t=-1.865, p=0.889, df=11, 2 cohort: t=0.773, p=0.4544, df=12, 4 cohort: t=2.367, p=0.1341, df=11). This indicates that there had not been a reduction in the size of new recruits, nor animals reaching sexual maturity, nor adults across the suite of sites close to the northern limit of *Osilinus lineatus.*

Plots of the numbers of year cohorts in 1986 and 2002 show mixed changes between the 14 shores for which data exists (Figure 2.13). The number of age cohorts had decreased at 3 sites: Aberaeron, Crackington Haven and Widemouth, where the oldest, largest animals found in 2002 were 1, 2 and 3 years respectively younger than in 1986. At 2 sites: Hartland Quay and Ile Callot, the same number of age classes was present in 1986 and 2002, indicating no change in the composition of these populations. An increase in the number of age classes in 2002 was recorded at 7 sites: Wellcombe, Prawle, Roscoff, Le Guersit, Brignogan, Le Guersit and Lyme Regis, where the maximum age cohorts have increased by between 1 and 5 years. The largest of these changes have occurred at Lyme Regis and Brignogan. At Lyme Regis, only young animals up to the age of 3 years were found during the 1986 survey, whereas the population now comprises of both juvenile and adult animals up to 8 years old. The Brignogan population was composed of 1,2,3 and 5-year old animals in 1986, but by 2002 this population contained individuals in every age cohort up to 10 years. At the northern limits of distribution in north Wales, population size frequencies show that recruitment is still infrequent, with evidence of missing year classes (Figure 2.14). Populations are dominated by old, large individuals with the exception of Aberffraw and Criccieth, where the population structures show evidence of recent recruitment and abundances are an order of magnitude higher than other adjacent locations. Both of these sites are located in bays, and larval dispersal may be more limited than on adjacent open coast sites, resulting in increased numbers of recruits settling on these shores.

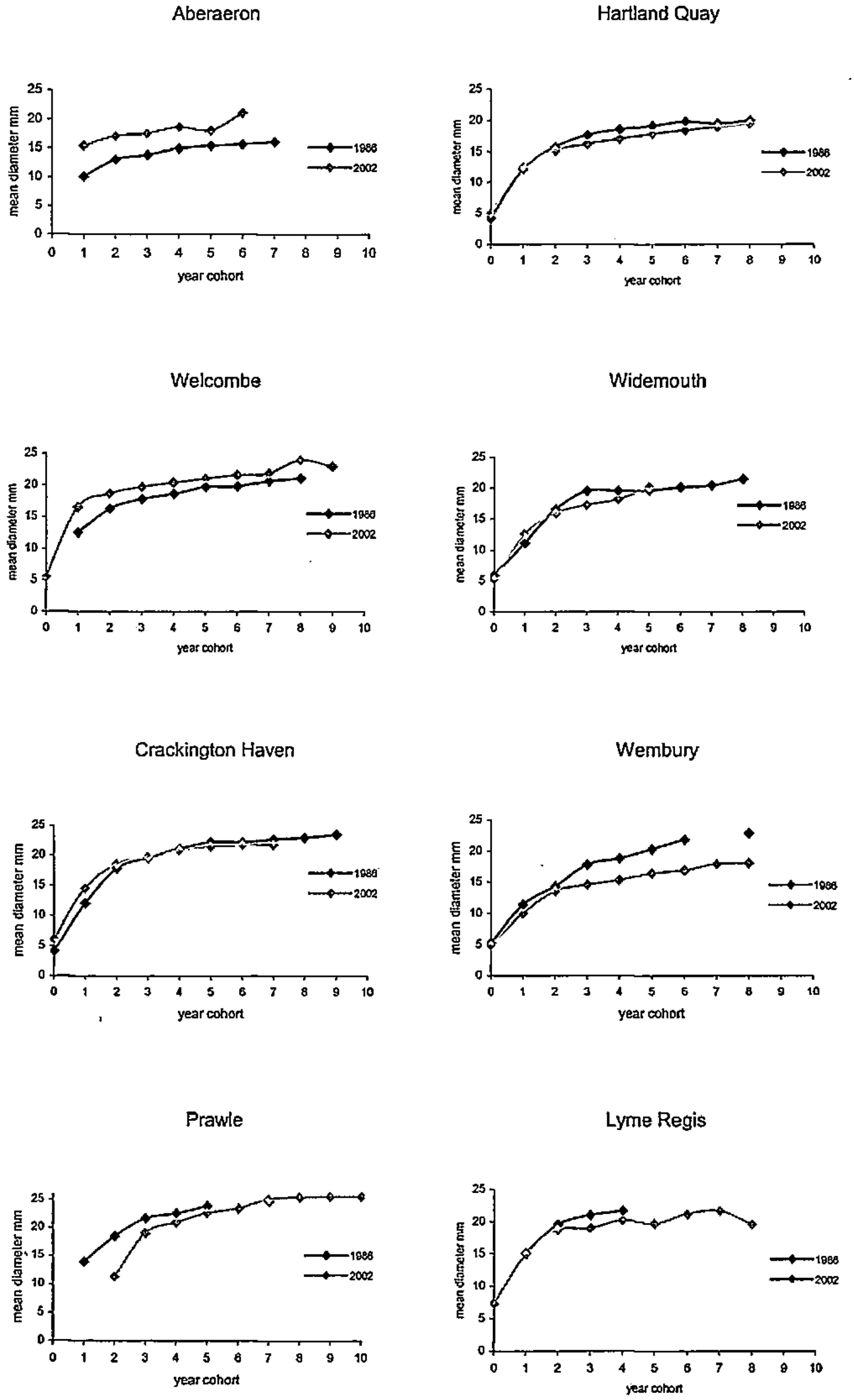


Figure 2.13. Mean body diameter of each year cohort in 1986 and 2002, Britain.

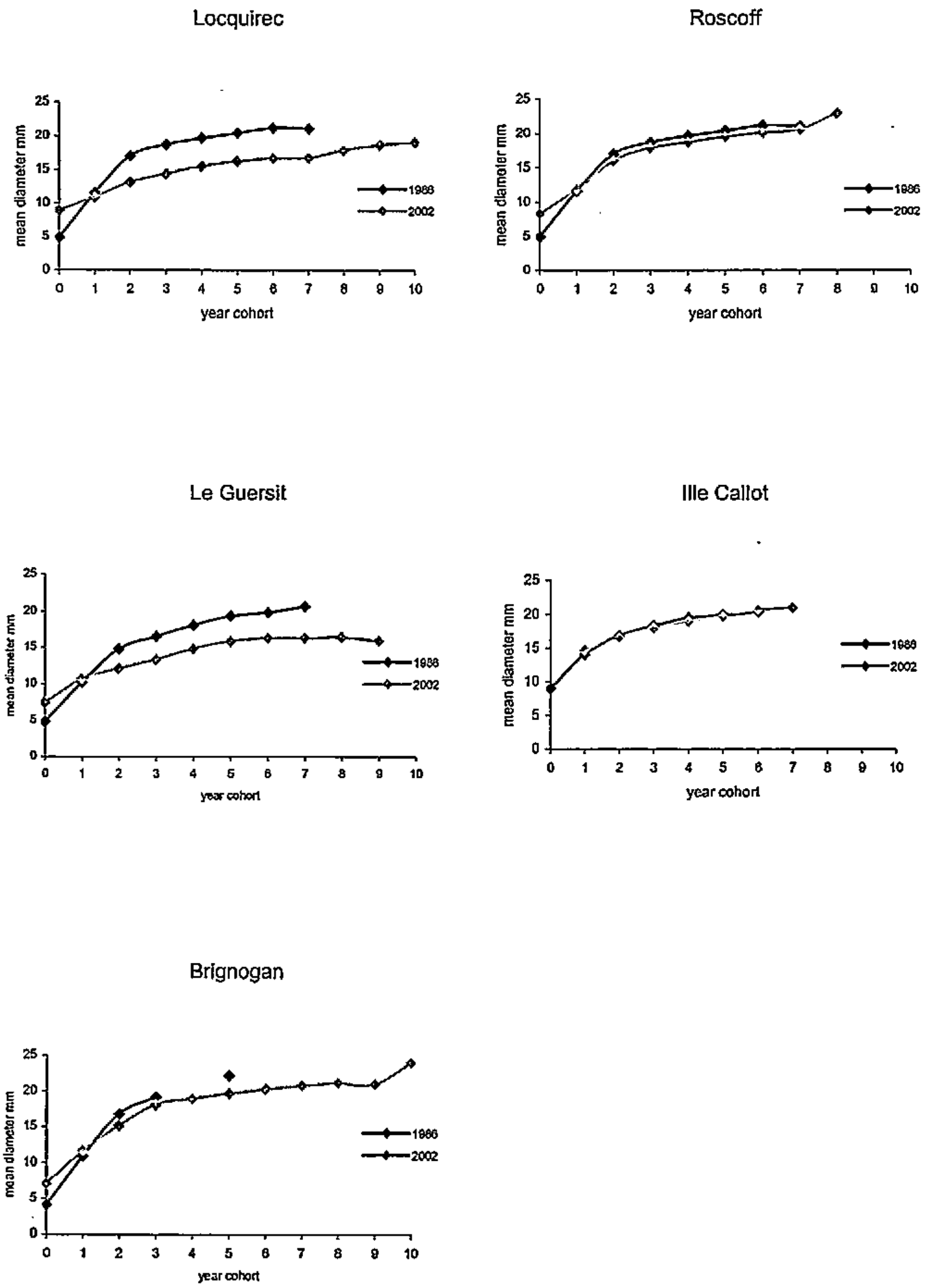


Figure 2.13b. Mean body diameter of each year cohort in 1986 and 2002, northern France.

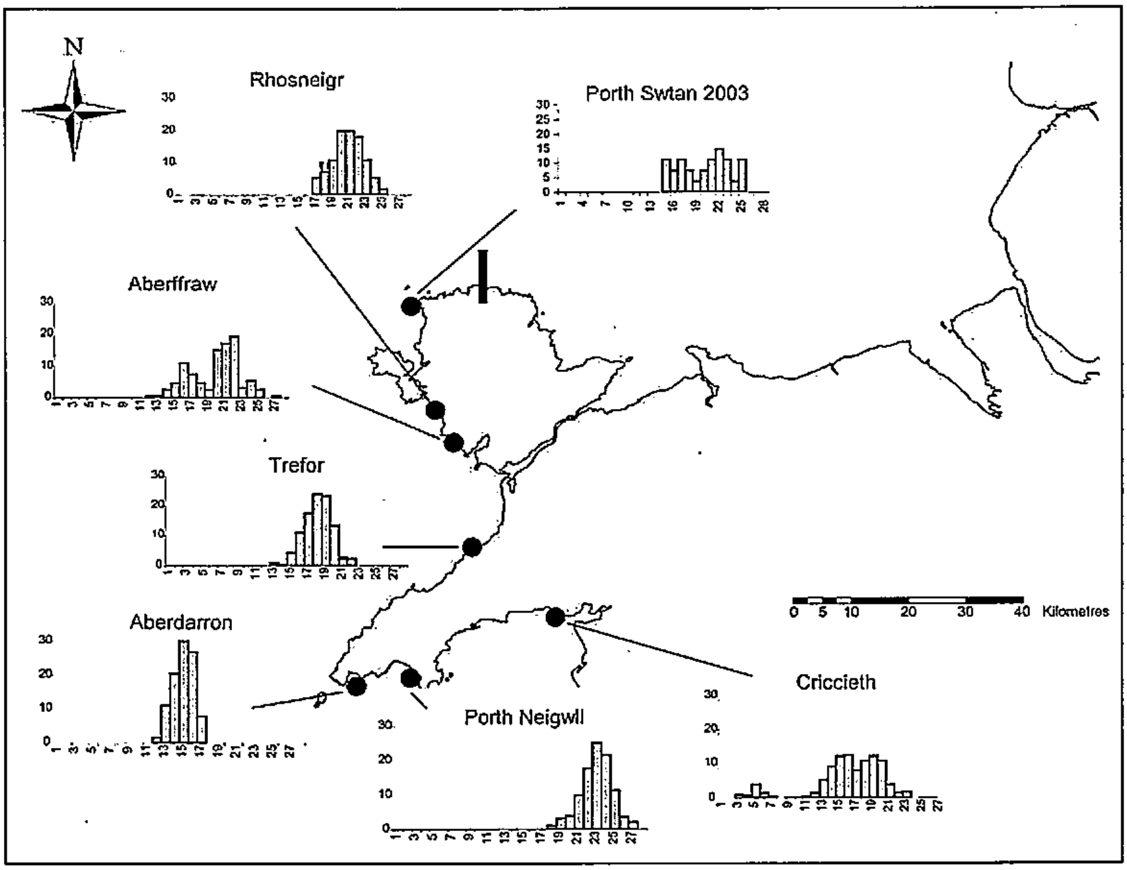


Figure 2.14. Population structure of *O. lineatus* at sites close to the current northern limits of distribution at Porth Swtan in north Wales. Black vertical line indicates location of most northerly individuals found.

2.4 Discussion

2.4.1 Climate change over the study period and recent rapid responses

The British marine climate has undergone oscillations between warmer periods (1930s – 1960s) and cooler periods (1970s – mid 1980s) in the twentieth century before entering the current period of rapid climate warming (Southward & Butler 1972, Southward 1980, Hulme et al. 2002). Air and sea surface temperatures in Britain are now 0.5 – 1°C greater than in the mid 1980s, and the seasonal and diurnal temperature range has decreased. The resulting thermal regime is now similar to that experienced further south towards the centre of the range of *O. lineatus* in Europe (Bode et al. 1987). Populations within a few hundred kilometres of northern limits (Figure 2.1) now more closely resemble those in southern Spain, with bi- or trimodal size frequencies, regular recruitment, no evidence of missing year classes and high abundances. Climate warming is therefore strongly implicated in these changes, but the inference is limited by the existence of only one year of quantitative data prior to the warming event.

The northern (N. Wales) and eastern (English Channel) distributional limits of *Osilinus lineatus* in Britain were cut back by ~120km and 70km respectively during the extreme cold winter of 1962/3 (Crisp 1964). Subsequent surveys conducted in the 1980s showed that re-colonization of sites close to these range edges was very limited, with few populations becoming re-established even after two decades. Between the mid-1980s and the present, however, *O. lineatus* has rapidly re-extended its northern limits of distribution to the north-east coast of Anglesey, and populations have become re-established at all locations previously surveyed in north Wales. New populations have been found at locations within the range where no animals had been recorded prior to the 2000s. A range extension of 55km beyond all previous records has also occurred in the English Channel, with the most eastern breeding population now present at Osmington Mills and isolated individuals found as far east as Freshwater Bay on the Isle of Wight (Hawkins & Herbert, pers comm., Hawthorne & Wiffen in review). This is the first time breeding populations have been recorded beyond Portland Bill. Thus the range of the 1950s has been re-colonised and the range edge has expanded beyond that of the last warm period, as predicted in hypothesis 1.

Abundances have also shown large increases of up to 800% since 1985 at sites originally surveyed by Kendall (1987) and are concordant across all 16 locations for which quantitative data exists. These increases in densities of near-edge populations, coupled with recolonization and extension of range limits support hypothesis 2 and show that *O. lineatus* is surviving and recruiting more successfully since the climate began to rapidly warm in the mid-1980s.

2.4.2 Mechanisms setting range edges

2.4.2.1 *Abiotic factors*

Strong currents around Point Lynas on Anglesey, and the tip of the Lleyn Peninsula, and off Portland Bill in the English Channel were proposed as the factors setting the north and north-eastern limits by posing a hydrographic barrier to further spread of the range (Crisp & Southward 1958, Kendall 1987). Settlement and subsequent survival of animals was thought to be prevented at shores beyond these locations due to the small numbers of larvae being produced from the range edge populations being unable to breach the offshore current flows.

The slow rates of re-colonisation on the north shore of the Lleyn Peninsula and on Anglesey seen after the cold winter of 1962/63 suggest that the offshore currents in these areas were preventing the low numbers of larvae from small northern populations from being dispersed to shores beyond these locations. As these populations have rapidly increased in abundance in recent years due to increased suitability of local climate, the density of larvae in the water column may be sufficient that some larvae manage to breach the current barriers and settle on shores further north.

The emergence and persistence of populations of *O. lineatus* at shores beyond the eastern barrier at Portland in the 2000s illustrate that this hydrographic barrier has been breached in recent years. Kendall (1987) suggested that the offshore current was a permanent barrier to larval transport from the east to west side of Portland headland.

Numerical simulation of the Portland tidal eddies shows that although the tidal streams do indeed flow in a westerly direction around Portland Bill during the 5 hours prior to high water, they reverse their direction 1 hour before high water and for 4 hours the flow of surface water is to the west (Maddock & Pingree 1977). Although the main directional flow of water occurs seawards on either side of Portland for 9 hours of the tidal cycle (either east or west), an anticlockwise eddy develops to the east of Portland in Weymouth Bay during the ebb phase, retaining water that has flown from the western side of the peninsula. Therefore, as fertilisation of gametes and larval formation occur in the water column during high water, they will be dispersed from shores to the west of Portland around to shores in the eastern side.

The tidal regime of Portland has not altered since the studies on O. *lineatus* were undertaken in the 1960s and 1980s. The oceanographic data suggests that the current was a porous barrier to larval transport. Low numbers of larvae reaching Portland after dispersal from the range edge population at Lyme Regis, some 50km west in earlier decades were further reduced in number by the offshore current, probably resulting in densities of larvae settling in Weymouth Bay being too small to establish new populations. In recent years, the warming of the western basin of the English Channel has facilitated an increase in the population density at Lyme Regis and the establishment of a population at Clay Ope Cove on the western side of Portland Bill. The increased numbers of larvae dispersed in the region of the Portland current system are likely to have been sufficient that some larvae have breached the hydrographic barrier. These larvae have subsequently settled in sufficient numbers to allow establishment of new populations. As recruitment was seen to be successful at Lyme Regis every year between 2002 and 2004, these new populations will have received regular input of new recruits, helping to sustain the population at Osmington until adult densities were sufficient to allow self-recruitment. The potential for further expansion is demonstrated by the single individual found on the Isle of Wight in 2004 (Hawkins, unpublished), where previous searches of shores on the island throughout the 1990s failed to find any animals (Herbert, unpublished).

The physical processes setting range boundaries may influence local variation in abundance at sites within the range, and changes in abundance can in turn provide information on the spatial extent of such processes (Legendre & Fortin 1989, Villard & Maurer 1996, Maurer 1999). The large difference between decadal and inter-annual variance in changes in abundance, in conjunction with the concordant increases in abundance between sites across Britain and northern France suggest that the range extensions of *O. lineatus* between 1986 and 2004 were caused by a large-scale driver such as climate acting over a decadal-scale time period. Few processes operate over such a large spatio-temporal scale other than climate or hydrography. It is unlikely that increased nutrient or pollutant levels have caused the observed responses as neither acute nor diffuse releases into coastal waters would result in alterations in oceanic concentrations over such a large scale, or concordantly in two different coastal seas.

All populations of *O. lineatus* away from immediate range edges that were surveyed during Kendall's 1986 survey had low densities and were dominated by older individuals. Size frequencies show that most of these populations had missing year classes, indicating that recruitment was not successful in all years (Kendall 1987) and the relationship between abundance and size was strongly influenced by the few large, old animals that had survived. The population structures in 2002, 2003 and 2004 show no evidence of recruitment failure in the previous 9 years, greater proportions of juveniles in all populations and an increase in the numbers of age classes present in the English Channel populations. Large, old animals are still present, and populations now exhibit bi- or trimodal population size frequency structures. So, whilst abundance has increased, and recruitment has successfully occurred more frequently in recent years, the size of animals at the 90th percentile of the population has not significantly decreased, and the relationship between these two factors observed in 1986 has broken down.

The populations that have re-colonised sites at the northern range edge on Anglesey do not exhibit this structure, but are characterised by large, older individuals and have missing age classes. Range edge populations exhibiting irregular size structures and a bias towards older animals, such as in the near-limit populations of *O. lineatus* indicate that recruitment is the biological mechanism setting the geographical limits of the species. The data presented here show that new populations within a hundred kilometres of the current northern range edge (Figure 2.14) have been able to persist and increase in abundance from the low numbers of individuals observed in the 1980s. The greater proportions of juveniles in these populations indicate that this is due to recruitment occurring in recent years. Conditions at these locations are still not suitable to facilitate successful recruitment in every year, but abundances are increasing.

Survival rates will be lower in fringe populations where environmental conditions were least suitable, and frequent local extinctions may occur. Populations of *O. lineatus* were indeed cut back after the cold winter of 1962/63 due to mass mortality of adult and juvenile individuals, but this was an isolated event where animals experienced extreme environmental temperatures. No evidence of adult mortality setting limits has been observed since this time (Kendall 1987, Lewis et al. 1982), even in the winter of 1979, which was the second coldest winter recorded in Britain in the twentieth century (Rayner 2003).

2.4.2.2 *Size – evidence for density dependence?*

As the climate has warmed between the 1980s and the 2000s, populations of *O. lineatus* close to northern range limits have been exposed to increased temperatures. The thermal regime has become more similar to that previously experienced towards the centre of its distribution and the maximum size of animals within the populations has decreased. The age of animals in populations close to the northern range edges has also decreased, as individuals occurring towards the centre of the range in thermal regimes have much shorter lifespans (Bode et al. 1987).

Previous work indicated a negative relationship between maximum size and density. Therefore intraspecific competition (Kendall 1987) was inferred to be less in range edge populations with low recruitment. As the climate has warmed I expected density dependent effects to be increased as has been observed in many taxa (Lawton 1989, McArdle et al. 1990, Gaston & Blackburn 1996, Blackburn et al. 1999b), and therefore the relationship between maximum size and density was re-examined.

As abundances of O. *lineatus* have increased, the maximum and 90th percentile size and age of the populations have declined. The comparisons of mean size for individual year classes, however, show that mean size of animals has not changed between 1986 and 2002 in the juvenile, maturing and adult stages of British and northern French populations as temperature has increased. The regression analyses also show that the relationship between abundance and size has become non-significant between 1986 and 2002.

Increased recruitment success in recent years compared to the 1980s is the most likely cause of the reduction in maximum and 90th percentile values in the survey populations. This highlights the problem of the relevance of maximum and 90th percentile values, and demonstrates the value of archiving raw data, which has allowed the change in size of individual year classes to be determined in this chapter. This type of selective analysis on year classes filters out the effects of massive increases in recruitment, which will tend to skew age and size data analysed at the whole or 90th percentile level of the population and can lead to erroneous conclusions being drawn.

The greater numbers of juveniles will result in reduced values despite there being no change in the mean size of animals within each year cohort and an increase in the number of age cohorts in many of the populations during the 2002 resurvey. Additionally, the relationship between size and number of animals is seen to break down at the higher densities recorded in the 2000s, indicating that body size is no longer density-dependent.

Although there is evidence of metabolic compensatory adjustments (acclimation) in several species of intertidal molluscs that reduce the magnitude of the responses predicted above (Thorson 1936), the relationship between temperature and growth is apparent across a wide range of marine invertebrates (Orton 1920a, Newcombe 1936, Swan 1952). Growth rate may also be affected by other abiotic factors such as nutrient availability, salinity, dessication, oxygen levels, tidal exposure, and by biotic factors, particularly competition for food (Underwood 1979, MacDonald & Thompson 1985, Niewiarowski 1995, Brockington & Clarke 2001, Boaventura et al. 2002). These factors act predominantly on a local scale, and are unlikely to have caused the synchronous increases in abundance or reduction in the 90th percentile values for size and age observed throughout Britain and northern France in this case. Countergradient variation may explain the observed pattern, if *O. lineatus* is compensating for seasonal limitations at higher latitudes by the evolution of faster growth and larger body sizes compared to lower latitude conspecifics (Conover & Present 1990, Blanckenhorn & Demont, 2004), although research on the phylogenetics of *O. lineatus* along the geographic range do not support this theory given the connectivity between populations (Preston, unpublished). More data on the physiology and phylogenetics of *O. lineatus* along a latitudinal gradient is required before these hypotheses can be fully tested.

2.4.3 Future requirements

Previous data on the distributional limits of *O. lineatus* has enabled the dynamics of the north and north-eastern range limits to be identified and related to climatic changes over the second half of the twentieth century. This has in turn allowed the changes in distribution observed between 1986 and the 2000s to be put into a wider temporal context and increased the confidence in the conclusions drawn from this study. The availability of population structure and abundance data has also allowed the physical factors driving the observed changes to be investigated, and provided information on the biological mechanisms acting in response.

Chapter 3. Range expansion of the southern trochid gastropod *Gibbula umbilicalis* during recent climate warming..

This Chapter has been submitted to the Journal of Biogeography for publication

3.1 Abstract

The northern range limit of the lusitanian, warm-water trochid *Gibbula umbilicalis* has extended since the mid 1980s. Synchronous increases in abundance have also occurred at sites stretching from the range edge to 7° latitude further south between 1986 and 2002. These changes in populations close to the northern range edge have been driven by increased recruitment resulting from warmer sea surface temperatures in recent years. My analyses show that the increases in size of existing populations and establishment of new populations beyond previous limits has been caused, at least in part, by enhanced survival of the '0' class over the first winter after settlement in response to warmer winter sea temperatures.

3.2 Introduction

The North Atlantic has shown some of the largest increases in sea surface temperatures globally; coastal seas of northern Europe have warmed by between 0.5 and 1°C over the last 20 years (Hawkins et al. 2003, Schär et al. 2004, Southward et al. 2005, Woehrling et al. 2005) which is twice the rate of any previous warming event on record (Mann et al. 1998, 1999). Distributions of species are likely to move polewards in response to this warming (Graham & Grimm 1990, Fields et al. 1993, Southward et al. 1995, Jeffree & Jeffree 1994, 1996, Parmesan 1996, Sagarin et al. 1999). The poleward movement of seasonal or annual isotherms is also expected to alter the relative abundances of 'southern' warm-water and 'northern' cold-water species at fixed locations, as well as the geographic limits themselves (Lubchenco et al. 1993, Southward et al. 1995, Lewis et al. 1996).

It can be difficult to resolve whether increases or decreases in species abundance represent actual changes in biogeography, or merely fluctuating population dynamics within a species range (Barry et al. 1995, Sagarin et al. 1999, Veit et al. 1997, Murray et al. 2001, Lohnhart & Tupen 2001, Parmesan et al. 2005) because of limitations in the spatial and temporal coverage of datasets. Where multiple sites within the geographic range of a species have been studied, few time-series have temporal coverage extending over more than two decades (but see Southward 1991, Southward et al. 1995). Moreover, many studies are based on only two discrete points in time, making quantitative assessments of temporal variation and the interpretation of any observed changes difficult (Underwood 1991, Barry et al. 1995, Hughes 2000).

Fortunately, extensive datasets for intertidal species including barnacles, limpets, trochids and macroalgae are available for north-west Europe (Fisher-Piette 1936, Southward & Crisp 1954, Crisp & Southward 1958, Crisp & Fisher-Piette 1959, Crisp 1964, Kendall & Lewis 1986, Kendall 1987, Kendall et al. 1987). These include extensive surveys during a cold phase just prior to the period of accelerated warming in the late 1980s (Southward et al. 1995) to estimate the abundance, recruitment and population structure of selected species, which were undertaken by the Natural Environment Research Council (NERC) Rocky Shore Surveillance Group at Robin Hood's Bay between 1977 and 1985. These observations formed part of a research programme to gain an understanding of the natural variability of coastal ecosystems, prompted by the perceived need to interpret pollution impacts (Lewis et al. 1982, Bowman & Lewis 1986, Kendall & Lewis 1986).

Here we examine the changes in distribution, abundance and recruitment success of a southern species of rocky intertidal gastropod *Gibbula umbilicalis* at its northern limits of distribution in Britain, at a suite of sites over three decades in response to climate warming. The geographic distribution of *G. umbilicalis* extends from Cap Blanc, West Africa to the British Isles, reaching its northern limit of distribution in north-west Scotland (Lewis 1964, Lewis et al. 1982). Patterns of poor recruitment and the dominance of northern populations by large, older animals observed in the late 1970s and early 1980s suggested that climatic or hydrographic factors were setting the northern range boundary of this species (Kendall & Lewis 1986).

We have examined whether the northern range limit of *G. umbilicalis* in Britain has extended in response to recent warming. Our work focuses on Scotland, but makes comparisons with data collected further south in Wales and England. The dataset from 1977 to 1985 and resurveys in 2002 to 2004 not only allowed us to place more recent data in a longer-term perspective and separate inter-annual from decadal scale changes, but the large geographic coverage of ~8 ° of latitude also enabled us to distinguish local from broad-scale influences. The availability of population structure data has enabled investigations of the relationship between recruitment success and temperature within populations close to the northern limits of distribution. This has allowed us to ascertain whether temperature-dependent recruitment success was driving increases in population, abundance and range extensions in *G. umbilicalis.*

3.3 Methods

3.3.1 *Gibbula umbilicalis* – the test species

Gibbula umbilicalis is a lusitanian species of trochid occurring between mean high water neaps and mean low water springs on rocky shores in the north east Atlantic (Figure 1). Its southern boundary has been recorded near Cap Blanc, West Africa (Fischer-Piette 1955, Fischer-Piette & Gaillard 1959) with a continuous distribution along the Atlantic coasts of Iberia, France, Ireland and the British Isles (Bode et al. 1986, Gaudencio & Guerra 1986, Lewis 1986) reaching its northern limits of distribution in Scotland (Lewis 1964, Kendall & Lewis 1986). It has been recorded in the English Channel east to Calais on the French coast, and the Isle of Wight on the English coast (Crisp & Southward 1958). Surveys in the 1950s did not find it along the English coast in the eastern basin of the English Channel, nor in the North Sea or large sections of the east coast of Ireland (Southward & Crisp 1954, Crisp & Southward 1958, Lewis 1964). It occurs along the western Scottish coastline, with the northern range limit recorded at Skerray on the north coast of Scotland (Lewis 1964, Lewis et al. 1982).

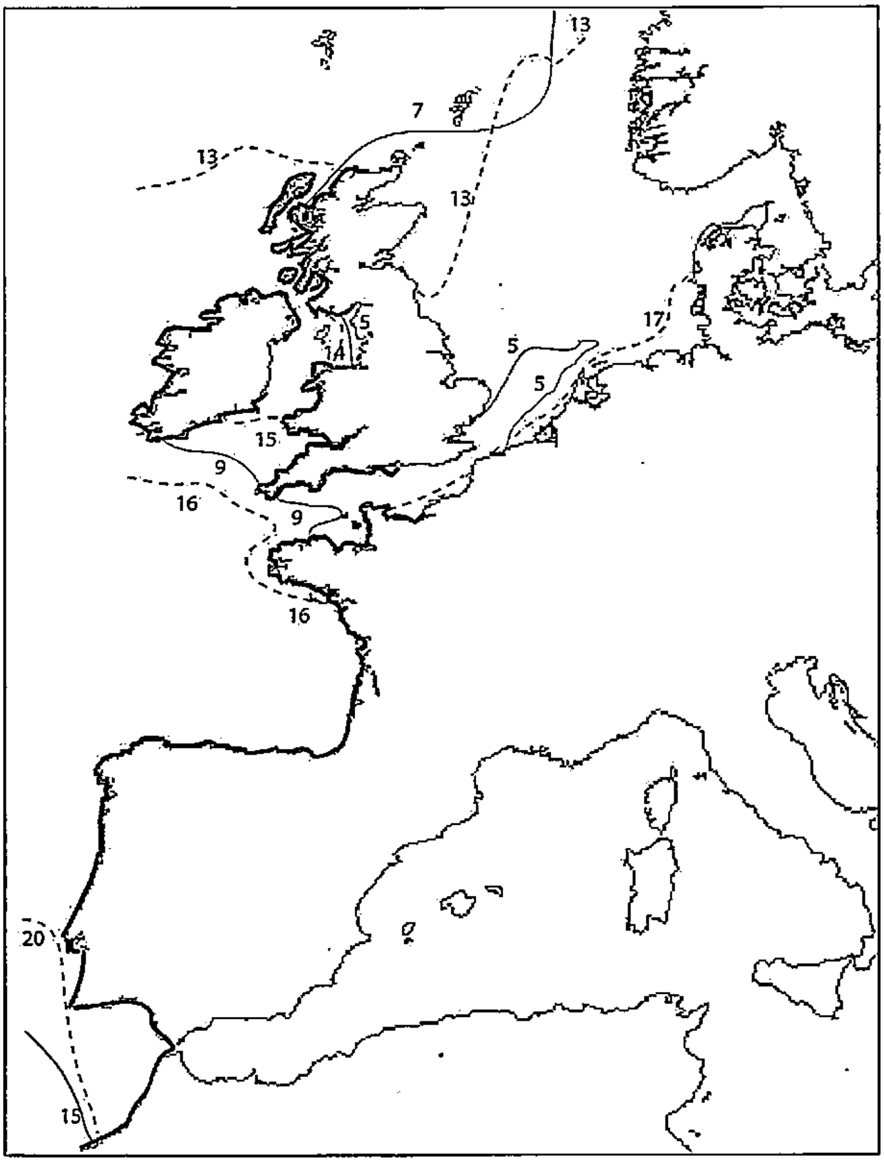


Figure 3.1. The biogeographic distribution of *Gibbula umbilicalis* from historical data records (thick grey line show distribution of *G. umbilicalis*, dashed lines represent annual summer SST isotherm ^{0}C (1960-1991 mean), filled lines represent annual winter sea surface isotherm ^{0}C (1960-1991 mean))

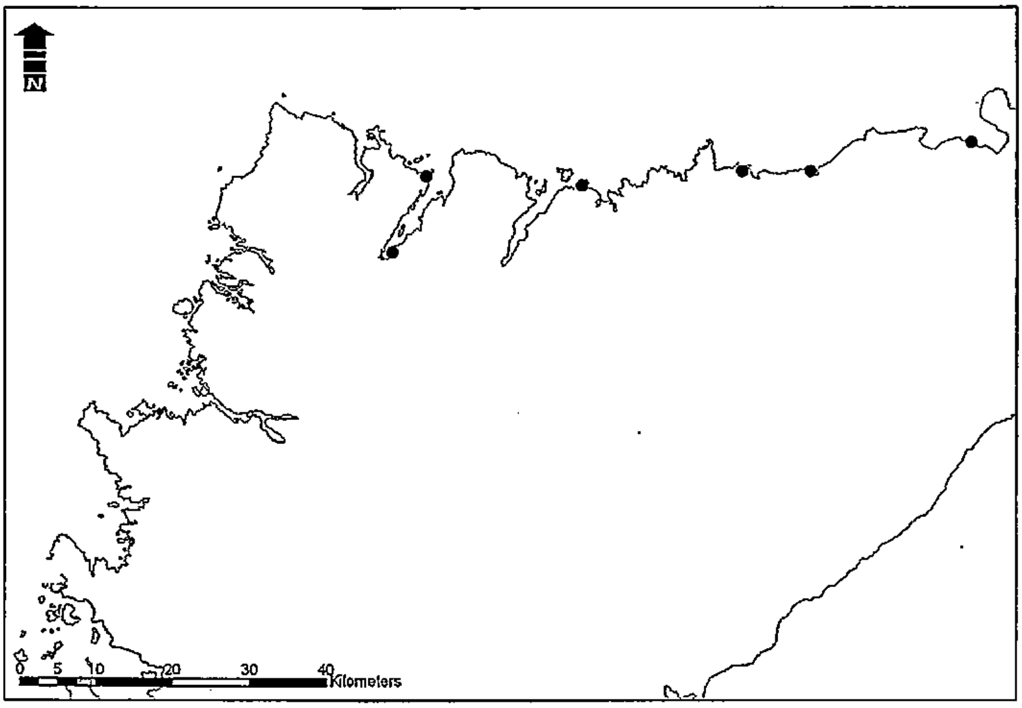


Figure 3.2. Survey sites visited between 1977 & 1985, and resurveyed between 2002 & 2004. Black circles indicate sites searched to determine range limits.

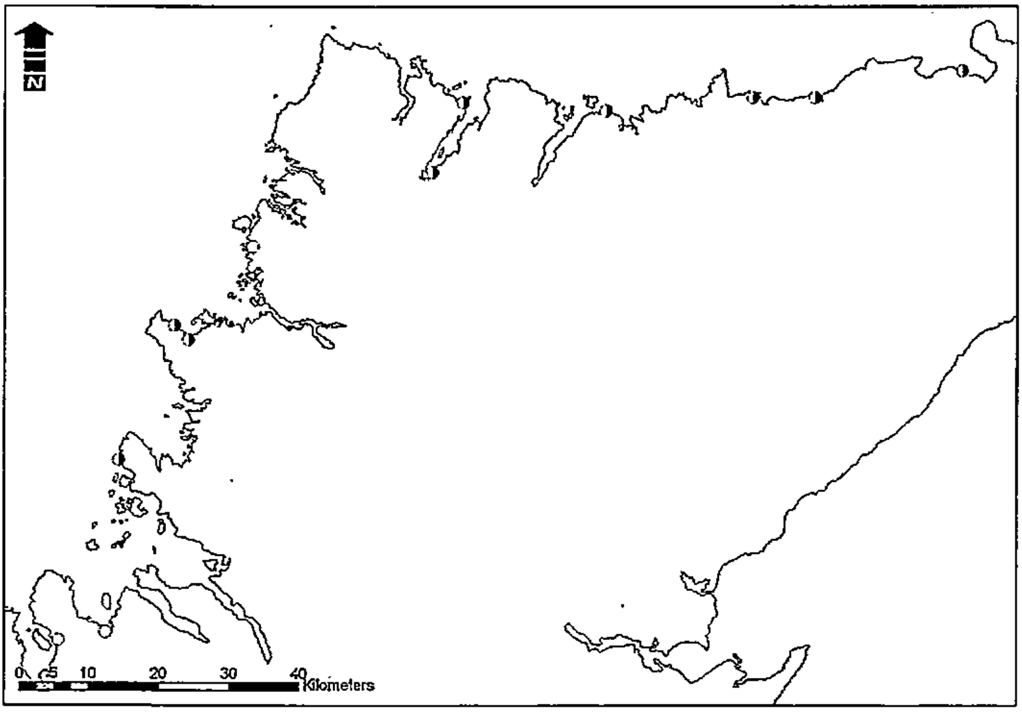


Figure 3.3. Sites in north-west Scotland where population structure data was collected between 1997 & 1985 and between 2002 & 2004 on the north coast. Black and white circles indicate sites where quantitative data were collected.

3.3.2 Temperature

Sea surface temperature (SST) has been used as an available environmental proxy for changes in climate. The physiology and survival of many rocky shore organisms are known to be highly sensitive to temperature, especially during the juvenile stage (Southward & Crisp 1954, Kendall et al. 1985, Kendall 1987, Kendall & Bedford 1987, Burrows et al. 1992). Monthly SST data on a 1° by 1° grid for the period 1860-2004 were obtained from the Hadley Centre, UK Met Office (HadISST, Version 1.1). This dataset is a gridded product combining in situ sea surface observations and satellite-derived estimates (Rayner 2003). Winter SST (Dec-Feb) each year was then calculated for the nearest pixel to each of our study sites.

3.3.3 Field surveys

Surveys to estimate population structures and delimit the northern distributional limits of *Gibbula umbilicalis* were made between 1977 and 1985 at shores with suitable habitat along the north coast of Scotland (Figure 3.2). Repeat surveys were made at these sites in 2002, 2003 and 2004 to quantify possible extensions of the range. Data on population size-frequency distributions of *G. umbilicalis* were collected between 1977 and 1984 at 9 sites around northern Scotland (Figure 3.3, Table 3.1) (Kendall & Lewis 1986).

Sites were selected to include populations at and close to the northern limits of distribution in Scotland. Nine of these sites were visited between 1-3 times per year, although none of the sites was visited in every year of the survey programme. Approximately 200 individuals (where available) were collected from the area of each shore where the abundance of *G. umbilicalis* appeared to be greatest, with additional individuals collected if time permitted. Areas searched included boulders overlying gravel and bedrock with cracks and fissures to ensure both juvenile and adult habitats were sampled. In 1985, seven sites in Scotland were resurveyed using ten replicated searches of 5 minutes duration, again targeted in the region of greatest abundance on the shore.

Table 3.1. Locations where timed searches for *Gibbula umbilicalis* were undertaken.

Site	**Location (WGS84 latitude longitude)**	**Years sampled**
Murkle Bay	58.6056, -3.4232	1977-1981, 1985, 2002, 2004
Fresgoe	58.5670, -3.7913	1977-1981, 1985, 2002-2004
Portskerra	58.5674, -3.9444	1977-1981, 1985, 2003, 2004
Skerray	58.5444, -4.3040	1977-1985, 2002-2004
Loch Eriboll	58.4570, -4.7269	1977-1984, 2002, 2004
Rispond	58.5483, -4.6583	1979, 1984,1985, 2003, 2004
Culkein	58.2467, -5.3380	1979-1985, 2002, 2004
Clashnessie	58.2296, -5.3023	1981-1985, 2002, 2004
Reiff	58.0709, -5.4555	1981, 1984, 1985, 2002-2004

Re-surveys of six of the original sites, including five locations where replicated timed counts were made in 1985, were undertaken annually in the spring/early summer of 2002-2004 (Figure 3.3). This season was chosen as it has the best data coverage across sites between 1977 and 1985. Re-surveys were designed to determine the current abundance and population structures of *G. umbilicalis* at sites close to their northern and eastern limits of distribution. Five replicated timed searches of 3 minutes duration were undertaken at each site between 2002 and 2004 by the same operator as in 1977-1985 or a fully-trained and calibrated substitute using the same search criteria employed during the original surveys (Kendall & Lewis 1986). All *G. umbilicalis* individuals found were collected, their basal diameters measured to the nearest millimetre, and individuals returned to the shore. To ensure comparability of search methodology between operators and the original and resurvey methods, inter-calibrations were undertaken at a subset of these shores. Similar data was collected at a site in Wales and three sites close to the north-eastern range edge in south England between 1977 and 1985, and during resurveys between 2002 and 2004.

3.3.4 Data analysis

To compare mean abundance between the 1985 data and 2002-2004 data across all Scottish sites, paired t-tests were used. The success of annual recruitment within each population was investigated using a measure of recruitment strength. The recruitment strength at each site was selected to represent '0' class individuals surviving the first post-settlement winter. It was not possible to calculate absolute recruitment strength because the original data were not collected per unit time or area, so a standardised index was calculated as the proportion of the total of each sample population represented by the '0' cohort of juveniles. The Rmix programme (http://icarus.math.mcmaster.ca/peter/mix/mix.html) was used to calculate the recruitment strength for each population from both the original surveys and the resurveys. This software produces a constrained estimate of a finite mixture distribution with grouped data using the maximum likelihood method. This method was more suitable than traditional maximum likelihood techniques (MacDonald & Pitcher 1979) for data such as ours where cohort size distributions overlapped, and the actual number of age classes in the population was unknown.

Data from the original surveys in Scotland showed that recruitment in most years was virtually zero, with only small numbers of the cohort apparent as '1' class juveniles at Clashnessie and Culkein between 1982 and 1985. For the current study it is assumed that recruitment was so low in those years that searches did not find any '0' class individuals. The '1' year cohort was not analysed instead, as this year class often merged with the adult mode of the population and could not be consistently separated from it, even using the Rmix analysis. A comparative approach has been used to test whether the impact of climate change on the recruitment of *G. umbilicalis* on the edge of the range is similar in north Scotland and south England. This was achieved by conducting a meta-analysis (Worm & Myers 2003) to combine individual correlation coefficients between *G. umbilicalis* recruitment and SST for Scotland. As the variances among sites in Scotland were not significantly different, a fixed effects meta-analysis was used. This approach synthesises results across the four sites by subsuming the local variation that can often obscure a climate signal, providing greater statistical power and increasing the confidence (degrees of freedom) in the correlation. Local variation is often problematic in individual studies undertaken at a small number of sites within a species range.

3.4.5 Potential biases

The change in collection protocols from the original methodology, which lacked standardization, to replicated timed counts in the resurveys is a cause for concern when using the combined data in the meta-correlation analysis of recruitment. However, the samples were collected by the same operator for the resurveys as the original surveys, or by a trained and cross-calibrated substitute, and the same search techniques were employed, increasing our confidence in the quality and comparability of the data. Additionally, by comparing recruitment strength against the whole population in the form of proportional data, the problem of non-comparability of numbers of individuals between the original and new surveys has been overcome.

3.4 Results

3.4.1 Sea Surface Temperature

A temperature gradient was evident across the 3° latitude by longitude range of the Scottish sites surveyed over the three decades between the start of the original surveys in 1977 and the last re-survey in 2004 (Figure 3.4). Coolest mean winter SSTs consistently occurred in the 59°N, 4°W grid square, beyond the previous range edge. Winter SSTs showed greater variation in the years between the two survey periods, with the coldest and warmest mean temperatures in 1993 and 1997 respectively. SST has been more stable since 2000, but at levels up to 1°C warmer than experienced during the original survey period of 1977-1985.

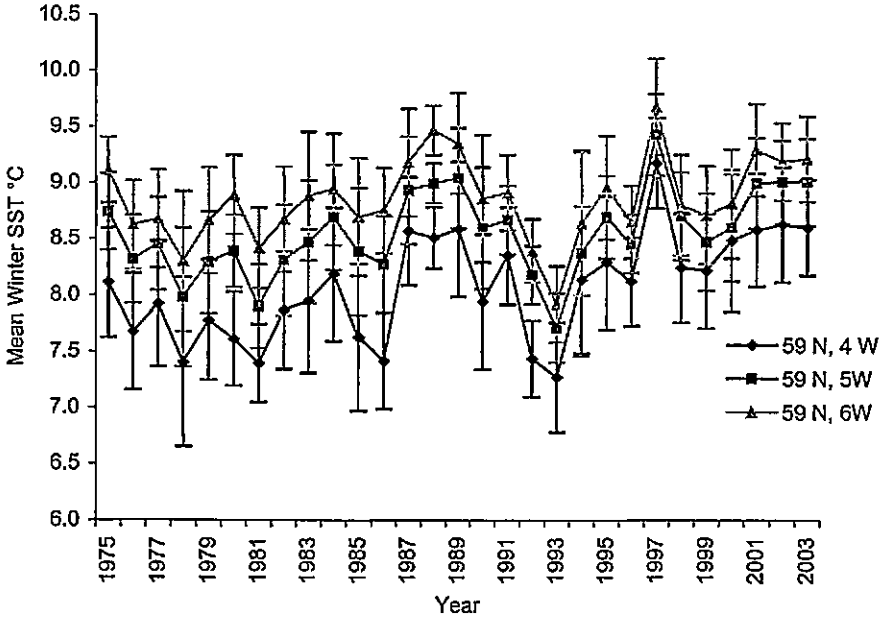


Figure 3.4. Mean Winter SST (December – February) at grid squares in northern Scotland where sites with long-term population data are located.

3.4.2 Changes in geographic range

No animals were found during previous searches at Fresgoe in the 1970s and 1980s. In 2002 a mixed-age breeding population of *Gibbula umbilicalis* was found at Fresgoe, northern Scotland (Figure 3.5). This population was still present in 2003 and 2004 with increasing abundances, constituting an extension of the northern limits of 55 km beyond the previous range edge population at Skerray in 1985. At Murkle Bay, 80 km east of Skerray, two individuals were found in 2002 and three individuals in 2004. Isolated individuals had occasionally been found at Murkle Bay during previous searches in the 1980s.

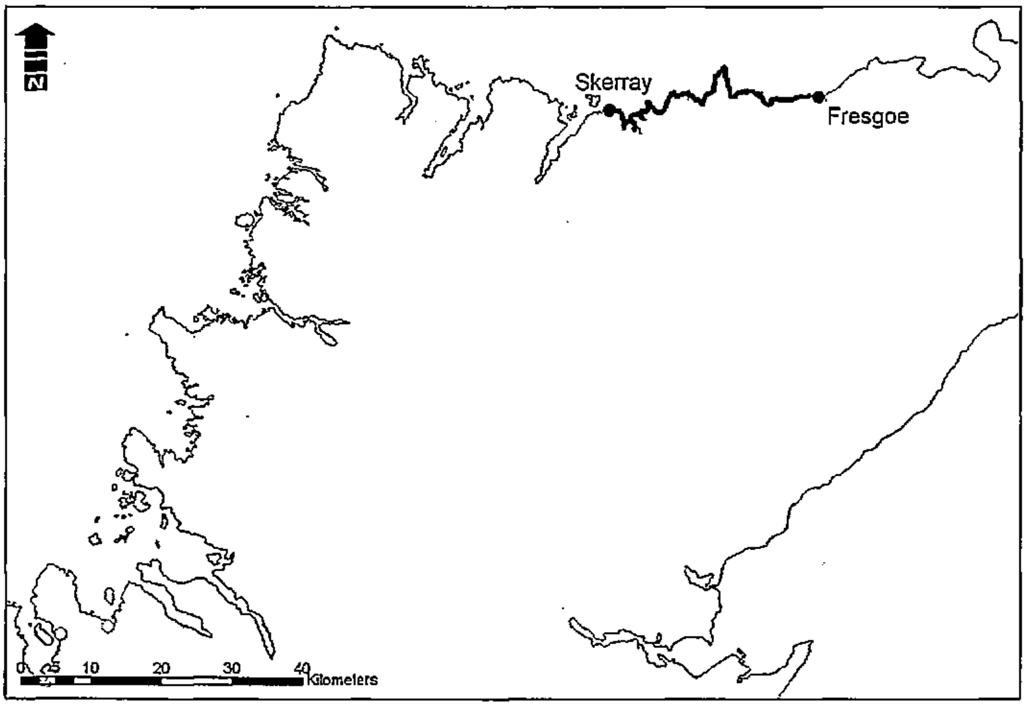


Figure 3.5. Extension of the northern range limit of *Gibbula umbilicalis* in northern Scotland between 1985 and 2002.

3.4.3 Changes in population abundance and structure

In 2002, abundances were significantly greater at the two sites resurveyed, Clashnessie and Culkein, than in 1985 (paired t-test, t=74.47, n=2, df=1, p<0.01). In 2003, abundances had significantly increased at Fresgoe, Skerray and Rispond, the three sites resurveyed (paired t-test, t=4.36, n=3, df=2, p<0.01). Abundance had significantly increased in 2004 compared to the 1985 baseline when all 6 sites in Scotland were resurveyed (paired t-test, t=9.95, n=6, df=5, p<0.01) (Figure 3.6). The largest increase was at Fresgoe, where no individuals had been recorded during previous surveys, but a multi-cohort population was evident in 2002, 2003 and 2004. At sites where populations had been found in 1986, increases in abundance in 2004 ranged from 1.6 times at Loch Eriboll to 12 times at Skerray, where the most northerly population was found in 1986.

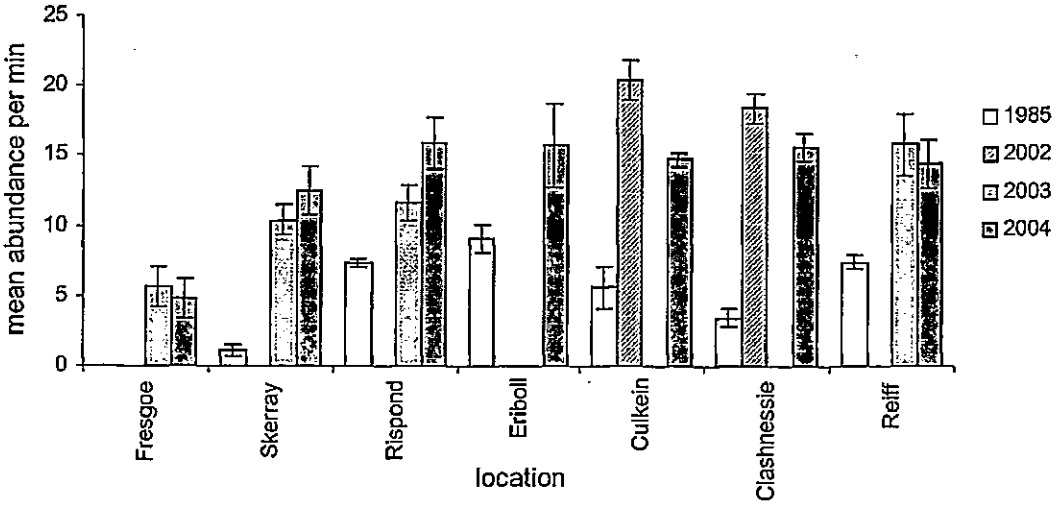


Figure 3.6. Increases in abundance at Scottish sites between 1985 and 2002, 2003 and 2004 for six sites resurveyed and the new population at Fresgoe.

Population size-frequency plots show that '0' cohort individuals were either not found or were present in very low numbers at the range edge site Skerray, in northern Scotland throughout the late 1970s and early 1980s (Figure 3.7). Population structures at all Scottish sites were predominantly unimodal, reflecting consistently poor recruitment and the dominance of large, old individuals. In the 2000s there was a change towards bimodal distributions, as greater numbers of '0' cohort juveniles were present at all locations close to the northern range edge. The new range edge population at Fresgoe shows a dominance of older age classes in 2002 and 2003, but in 2004 recruits from the 2003 cohort were evident and the population structure was bimodal. In contrast, successful recruitment was evident in most years of the original study period and throughout the resurvey period of 2002-2004 at Osmington, near the eastern range edge in south England (Figure 3.7). The population structures were predominantly bimodal, with little evidence of missing year classes.

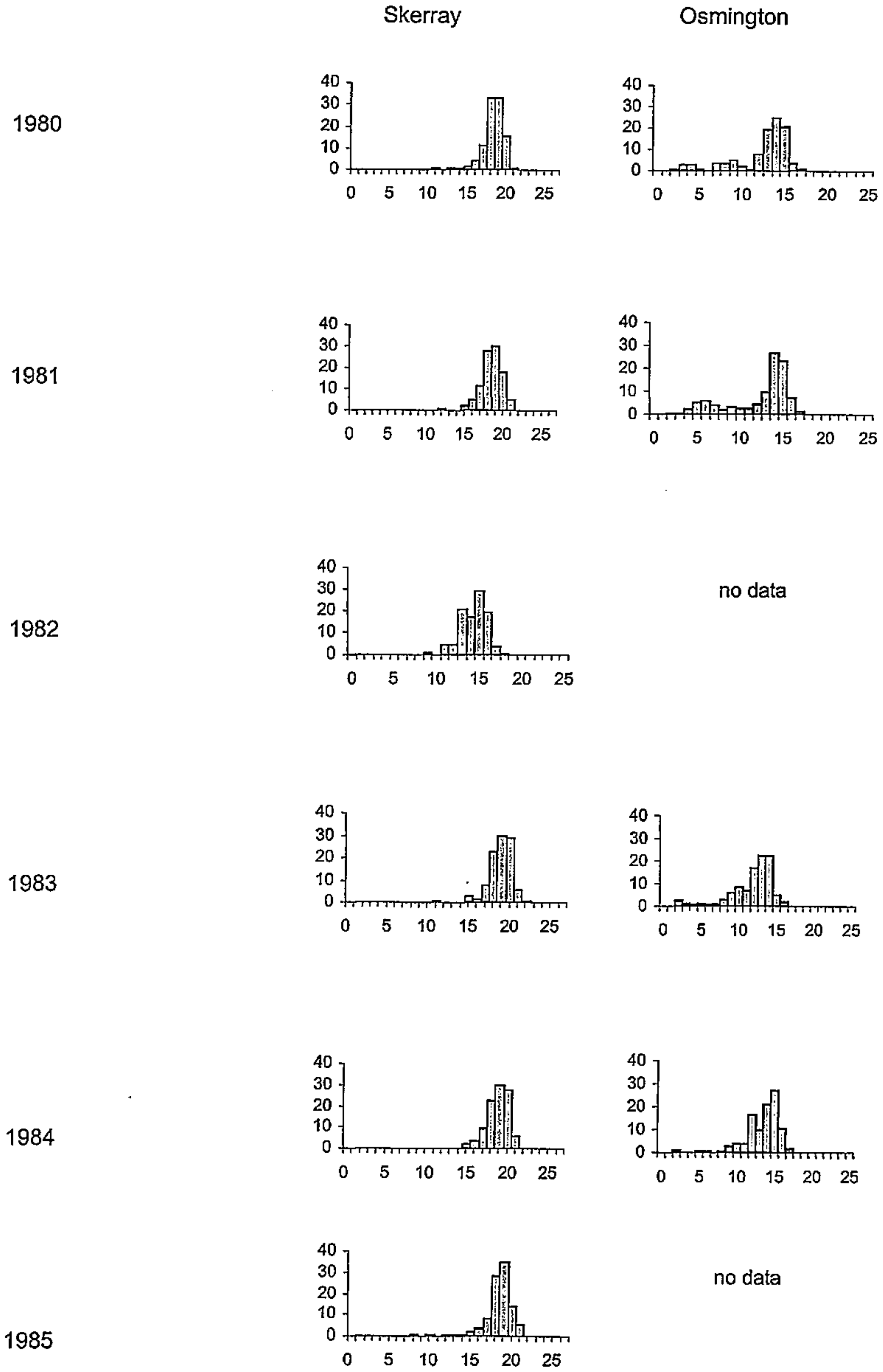


Figure 3.7. Size frequency distributions for *Gibbula umbilicalis* in the 1980s and 2000s. X axes: Basal diameter (mm), Y axes: percentage of sample population.

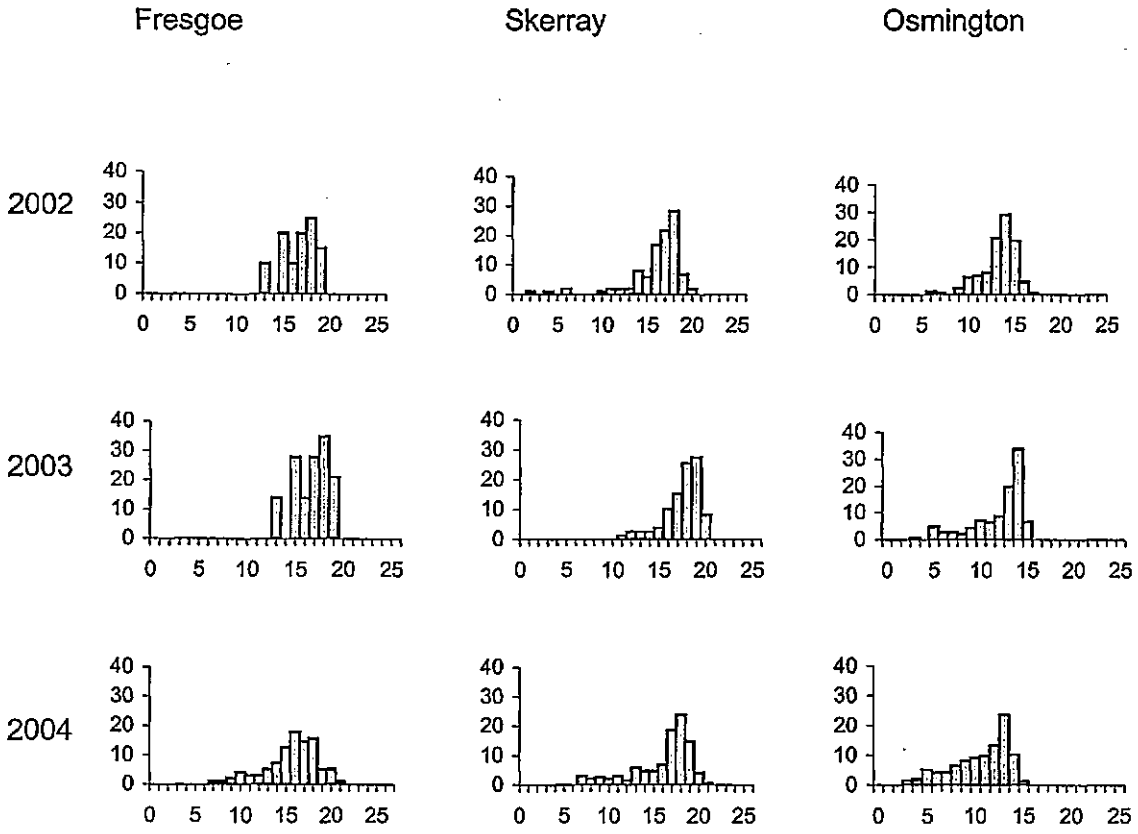


Figure 3.7b. Size frequency distributions for *Gibbula umbilicalis* in the 1980s and 2000s. X axes: Basal diameter (mm), Y axes: percentage of sample population.

In Scotland, all correlations between recruitment and winter SST were positive (Figure 3.8), although most correlations were not significant individually (the 95% confidence intervals overlap zero for Eriboll and Culkein). Nevertheless, the meta-analysis indicates that the overall relationship between *G. umbilicalis* recruitment and SST in Scotland was positive and highly significant, ($\bar{r}$=0.61, df = 3, Z=4.10, p<0.0001) demonstrating that recruitment success is greater when milder temperatures occur during the first winter after settlement on the shore. The correlation between winter temperatures and recruitment was not significant in south England.

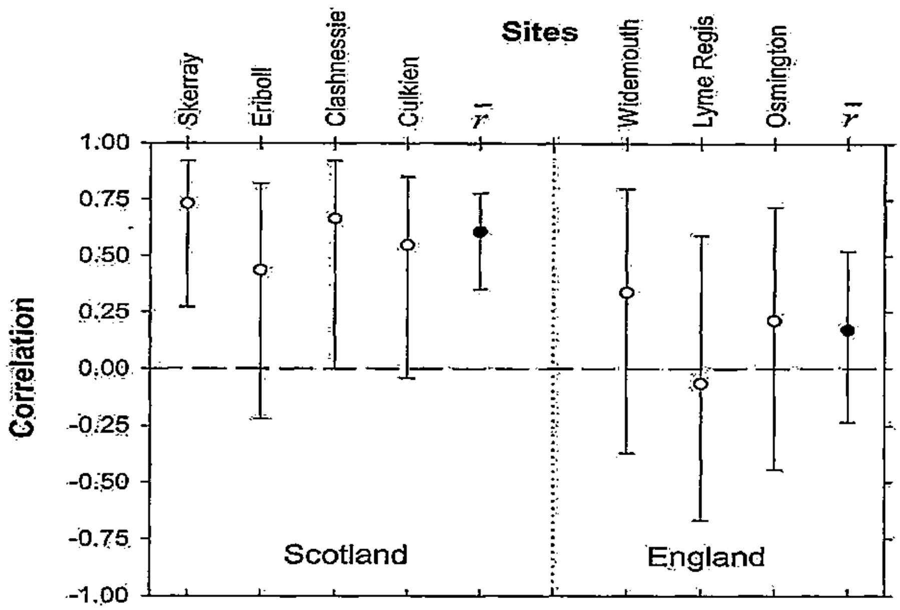


Fig. 3.8. Meta-analysis of the relationship between top-shell recruitment strength and winter SST for sites in Scotland and England. Weighted mean correlations (circles) are shown with 95% confidence limits (bars) calculated with a fixed-effects model. Bars not overlapping zero are significant.

3.5 Discussion

In the 17 years between the last survey completed by the NERC Rocky Surveillance Unit in 1985, and the first re-survey in 2002, the European marine climate has warmed markedly (Hulme et al. 2002). Sea surface temperatures close to the existing northern limits of *G. umbilicalis* have increased. More critically, seasonal differences in the magnitude of the response have been evident: mean summer SST around the coastline of north Scotland has warmed by up to 0.5°C; whereas mean winter SST has warmed by up to 1°C. These changes are in agreement with the rest of Britain, where annual coastal SSTs have warmed predominantly as a result of increased winter temperatures (Hawkins et al. 2003, Mieszkowska et al. 2005). During this period of milder winters the range edge of *G. umbilicalis* has extended north-east by 55 km, with multiple breeding populations becoming established beyond previous limits. This rate of change, equivalent to 32.6km per decade is greater than the overall observed global 'fingerprints' of changes in species distributions, which average a poleward shift of 6.1km per decade (Parmesan & Yohe

2003) and exceeds most terrestrial range shifts (Root 1993, Parmesan et al. 1999, Thomas & Lennon 1999). In addition, abundances of populations close to the northern range edge have significantly increased since 1985 due to an increase in frequency of recruitment success. Recruitment at each of the Scottish sites (over a distance of ~220 km) is positively correlated with SST at all sites in Scotland between the years 1985, 2002, 2003 and 2004, suggesting that a large-scale physical driver is responsible.

3.5.1 Changes in northern populations

The northwest European climate was in a relatively cool phase during the late 1970s and early 1980s (Southward & Butler 1972, Southward 1980). Kendall & Lewis (1986) suggested that the primary physical factor setting the northern range edge of *G. umbilicalis* at this time was an insufficiency of summer warmth, limiting or delaying gamete production compared to further south in the range in Spain and Portugal (Bode et al. 1986, Gaudencio & Guerra 1986, Kendall & Lewis 1986). In consequence, juveniles would settle late on the shore in the autumn and be exposed to cold winter temperatures. The northern range limit of breeding populations of *G. umbilicalis* remained at Skerray, north Scotland throughout the duration of the original surveys from 1977-1985. Occasional individuals were found at sites past this location, but no new populations became established during this time.

The change from a static range boundary of G. *umbilicalis* in the 1970s and early 1980s to a rapidly extending range edge concurs with range extensions of another southern intertidal trochid gastropod *Osilinus lineatus* (Mieszkowska et al. 2005) and by the southern barnacles *Balanus perforatus* (Herbert et al. 2002) and *Solidobalanus fallax* (Southward et al. 2004). These mirror the changes in the coastal shelf zooplankton and fish distributions observed in the North East Atlantic and North Sea (Perry et al. 2005). During the 1960s and 1970s southern shelf-edge planktonic species were restricted to waters south of Britain and south west of Ireland, whereas the 1980s marked the beginning of a large-scale northward movement of warm water species to the north of Scotland and into the northern North Sea, which is still occurring at the present time (Beaugrand et al. 2002, Beaugrand & Ibanez 2004). This pole-ward range extension and increase in abundance of southern species have been accompanied by the contraction of cold-temperate and sub-arctic species, indicating that large-scale alterations in biodiversity of the north east Atlantic have occurred in response to rapid warming of the shelf seas in this area.

3.5.2 Biological mechanisms driving observed range extensions

Recruitment success appears to be one of the main biotic factors driving the observed changes in population size, structure and ultimately extensions in range in *G. umbilicalis*. In the original surveys, all five Scottish populations were dominated by 1-2 year old animals in 1977 and 1978, which proceeded mild winters and summers in 1976 and 1977. Between 1979 and 1982, recruitment was poor at all sites, with little or no evidence of new recruits on the shores, and populations were composed of animals that had settled prior to this period. Recruitment patterns observed during these years agree with the predictions of Hutchins (1947) and Lewis et al. (1982) that recruitment failure would occur most frequently at the limits of distribution of a species, although Kendall & Lewis (1986) were unable to demonstrate a link between recruitment and climate. The addition of three years of data obtained during a warmer period has allowed the relationship between climate and recruitment success to be tested. We report a strong positive correlation between winter SST and recruitment strength across all sites in Scotland, demonstrating that more juveniles are entering the population each year now that the mean winter sea temperatures do not drop to the low levels experienced in the mid 1980s. The observed increase in recruitment success may be due to a combination of increased gametic output by adults, earlier release of gametes and increased survival of newly- settled juveniles on the shore. Adults may reproduce earlier and/or for a prolonged period in warmer summers (Bode et al. 1986, Gaudencio & Guerra 1986, Kendall & Lewis 1986), resulting in greater numbers of juveniles settling on the shore, and providing many recruits with a longer period to accumulate metabolic reserves prior to the onset of winter. Although a significant relationship between summer SST and recruitment success was not evident at 5 of the 7 sites in north Scotland, reasonably high correlation values of r were obtained, and the relationship between temperature and adult reproductive success merits further study. The significant relationship between winter SST and recruitment does, however, point strongly to the effect of cold temperatures on the survival of new recruits and suggests that winter mortality is reduced in near-limit populations during warmer winters.

In contrast, established populations surveyed in England over 1000 km south of the northern range limits showed evidence of recruitment failure throughout the 1970s and 1980s. The relationship between recruitment and summer SST is weaker, but also follows the same general pattern of warmer summers coinciding with higher recruitment success, suggesting the possibility that there is autocorrelation between warmer winters and warmer summers within years. Examination of SST time series shows that mean winter and summer SST are ~2.0 and ~3.0°C respectively warmer for the south of England than in northern Scotland throughout the decades investigated here. There was no significant relationship between winter SST and recruitment success within the sites studied in south England, indicating that the eastern limits of distribution are not primarily set by temperature. It is more likely that lack of suitable rocky habitat further east in the English Channel set the previous limits (see Crisp & Southward 1958).

The overall pattern observed from our results shows that as the climate has warmed in Britain, populations close to the northern distributional limits have experienced increased frequency and magnitude of recruitment success, which has in turn led to sustained increases in abundance. More recruits entering the adult population has led to population increases due to self-recruitment within each location and provided greater numbers of larvae for dispersal beyond the range edge. New populations have become established at shores beyond the previous northern limit as temperatures are now sufficiently and consistently warm at these locations for the survival of juveniles and consolidation of populations.

Gaylord & Gaines (2000) suggested that species ranges are determined solely by the effect of flow on larval transport, and that species with a longer planktonic phase should be more affected by changes in ocean flows. However, results from our surveys of additional species show that the greatest range extensions have occurred in the southern trochid species *G. umbilicalis* and *Osilinus lineatus* (Mieszkowska et al. submitted) which both have limited larval dispersal. In contrast, the southern barnacle species *Chthamalus montagui* and *Chthamalus stellatus*, which have long planktonic life stages and are also sensitive to climatic fluctuations (Southward et al. 1995), have not shown the same range extensions of breeding populations in Scotland over the same time period (Leaper, Burrows & Mieszkowska, unpublished). This apparent contradiction to Gaylord & Gaines (2000) may be explained by the absence of directly competing species of northern geographical distribution for *G. umbilicalis* on shores in Britain, whereas the northern barnacle *Semibalanus balanoides* has been shown to compete with the southern chthamalid species on shores where they co-exist (Connell 1961, Wethey 1984, Tomanek & Helmuth 2002). Furthermore, as suitable climate space becomes available, *G. umbilicalis* may be able to increase its range at a faster rate than species with longer planktonic phases due to limited dispersal of large numbers of larvae to neighbouring shores where they can establish populations in the absence of competing species. Further extensions occur as regular recruitment consolidates these new populations and produces larvae that can be dispersed in high densities to the next suitable, available habitat with appropriate temperature conditions.

There is the potential for further expansion of the northern range edge of *G. umbilicalis* as warming continues, due to the availability of suitable habitat beyond the current limits on the north Scottish coast. Work underway has shown that further extensions of the eastern limits in the English Channel are also occurring as individuals are perhaps using artificial sea defences along the predominantly soft sediment coastline of the eastern English Channel as stepping-stones (Hawkins et al. unpublished data). Based on the rates of range extension documented here, it is recommended that future surveys be carried out at and beyond the current limits of distribution every five years to quantify the rate and extent of any future changes as the climate continues to warm. Annual surveys are also required, however, to tease out inter and intra decadal changes in abundance.

It is apparent that even datasets with good temporal and spatial coverage have limitations when attempting to attribute a cause-and-effect relationship between range extensions and global warming. There is a growing realisation that the physiological mechanisms underlying climate-related changes in species distribution and abundance need to be identified, and their roles in promoting these changes understood (see Helmuth et al. 2005 for review). To tease out the effects of climate on the various life stages of a species, and to increase confidence in conclusions drawn from correlative analyses, long-term studies of the distribution and abundance of species need to be combined with field and laboratory experiments to determine the individual-level responses to global warming. Despite these shortcomings, the role of recruitment success in driving population abundances and range extensions has been clearly shown.

Chapter 4. Does a latitudinal gradient exist in reproductive cycle of *Osilinus lineatus*, and is this related to temperature?

4.1 Introduction

Geographical limits of distribution have been shown to broadly coincide with summer or winter isotherms for marine and terrestrial species across a diverse range of taxonomic groups (Hutchins 1947) – (marine algae -Setchell 1920, Michanek 1979, Lühning 1990, Voskoboinikov et al 1996, Molenaar & Breenan 1997, Orfanidis et al 1999, phytoplankton - Dodge & Marshall 1994, zooplankton - Beaugrand & Reid 2003, Beaugrand 2004, molluscs - Franz & Merrill 1980, terrestrial plants - Iversen 1944, Lassiter et al. 2000, insects - Gressit 1974, birds - Root 1988, mammals - Andrewartha & Birch 1954).

Sea temperature has been assumed to ultimately set range edges of marine species, with southern lethal limits associated with August sea surface isotherms and northern lethal limits linked to February isotherms (Hutchins 1947, Southward 1950, Southward & Crisp 1954, Vermeij 1982, Lühning 1990). There is little direct evidence for a causal relationship between temperature and distribution, except mortality associated with extreme events such as hot summers (Crothers 1998, Williams et al. 1996, Chevaldonné & Lejeusne 2003) or cold winters (Crisp 1964, Coles & Fadlallah 1991 Strand & Brynjeldsen 2003). In many cases of summer mortalities, the associated presence of increased numbers of pathogens cannot be ruled out as the ultimate cause of deaths (Cerrano et al. 2000, Garrabou et al. 2001). Isotherms only define the distribution of a few individuals at the fringe of the biogeographic range of a species, however, and therefore no single isotherm can define the boundary for more than a limited time (Jeffree & Jeffree 1994).

The 'climate envelope' approach to modelling the biogeographic range of species, where the suitable climate space that a species can inhabit is mapped to define its global distribution, has been used to predict future shifts in range with climate warming (Jeffree & Jeffree 1996, Berry et al. 2002, Pearson et al. 2002, Pearson & Dawson 2003, Pearson et al. 2004, Thomas et al. 2004). This method has, however, been shown to over-simplify the response of species to changes in environmental temperature as it ignores factors such as habitat availability and connectivity (Travis 2003, Pearson et al. 2004), dispersal capabilities (Higgins & Richardson 1999, Clark et al. 2001, Hampe 2004) and species interactions (Davies et al. 1998, Samways et al. 1999, Schmitz et al. 2003a,b), all of which are known to influence the geographic distribution of both marine and terrestrial species.

In order to identify and interpret the relationship between the geographic distribution of species and climate it is therefore imperative that the physiological processes driving observed changes are identified and understood (Hodkinson 1999, Kearney & Porter 2002). Such understanding will enable better quantitative forecasts of the future distributional patterns of species as they respond to rapid change. Environmental conditions can influence the physiological performance of organisms via phenotypic plasticity, physiological adaptation and genetic selection, depending on the temporal and spatial scale of the event (Helmuth et al. 2005). The current challenge is to identify and better understand the plasticity of phenotypic responses of organisms to climate change (Helmuth et al. 2005), the implications of such responses for population dynamics (Schmitz et al. 2003a), particularly through reproductive output and hence recruitment success (Kingsolver & Moffat 1982). Species distributions will ultimately be set by the integration of individual physiological responses through to population processes and biological interactions within communities.

4.1.1 The role of temperature in setting biogeographic distributions of marine species

Variations in sea and air temperatures have long been known to influence the distribution, physiological performance and reproductive success of marine species (Orton 1920a, Loosanoff 1945, Hutchins 1947, Loosanoff et al. 1951, Southward 1957, Boolootian 1966, Cocanour & Allen 1967, Stephens 1972, Frank 1975, Snell 1986, Bauer 1992, Olive 1995, Sagarin et al. 1999, Helmuth & Hofmann 2001). Many summer spawning species have cycles broadly in phase with seasonal rises in temperature (Orton 1920b, Kjesbu 1994, Olive 1995). Although temperature is only one of many physical factors likely to influence the reproductive cycle, the consensus from research carried out to date suggests that the timing and duration of reproduction of trochid gastropods is broadly related to higher coastal water temperatures (e.g. Gersch 1936, Ducros 1957, Williams 1965, Underwood 1972a Bode et al. 1986, Gaudencio & Guerra 1986, Garwood & Kendall 1987). Increases in temperature have been seen to coincide with the onset of gametogenesis and spawning of trochid gastropods in the field, although there is little experimental evidence to support this (Clare 1986, 1990).

Reproductive processes occur over a narrower thermal range than most other physiological functions (Vernon 1899, Stauber 1950, Loosanoff et al. 1951, Vernberg & Vernberg 1972). Therefore they are more likely to be affected by changes in thermal regime, especially at the geographic range limits where adverse environmental conditions are encountered more frequently than at locations further into the range. Reproduction incurs a high metabolic cost and selection must favour the reproductive strategy that results in the greatest number of viable offspring per unit of energy (Vance 1973). In species with broad geographical ranges this can lead to the breeding season varying at different latitudes.

Temperature is directly linked to latitude, with a temperature gradient extending from the tropics to the poles, although local modifications can occur for example due to upwelling and continental influences etc. (Hutchins 1947, Eckman 1967). There is a general trend of species and populations at high latitudes exhibiting short period of synchronised intensification of gametogenesis followed by a synchronous spawning event (Thorson 1950, Barnes 1957, Giese 1959, Kinne 1970, Sastry 1983, Bauer 1992, Swiney & Shirley 2001, Tyler et al. 2003). Close to northern limits of distribution environmental conditions are less favourable (ie colder), and reproductive periods require precise timing in order to coincide with optimal environmental conditions, thus ensuring that this energetically demanding phase of the life-cycle is completed successfully by the individual. Timing of larval release is also synchronised with the occurrence of maximum food availability for planktivorous species and in northern species which have a single, short, intense period of annual reproduction (Barnes 1962, Cushing & Dixon 1976, Hawkins & Hartnoll 1982, Kautsky 1982, Clarke 1988, Garrido & Barber 2001, Niehoff et al. 2002, Niehoff 2003, Tyler et al. 2003).

At lower latitudes breeding periods are extended and gonad development begins earlier in the year (Boolootian 1966, Cocanour & Allen 1967, Cochran & Englemann 1975, Bowman & Lewis 1977, Garwood & Kendall 1985, Bauer 2002, Defeo & Cardoso 2002). Spawning is less synchronous, and in some tropical species continuous reproduction throughout the year has been documented reflecting the seasonal stability of temperature regimes (Orton 1920a, Millar 1974, Giese & Pearce 1974, Pouvreau et al. 2000, Rocha-Barreira 2002, Carvalho & Ventura 2002). Assuming that the breeding season of each species occurs at the same temperature throughout its range (Orton 1920a), warmer or longer summers experienced in temperate/tropical latitudes are likely to increase the period available for gonad development and successful establishment of post-larval recruits in southern, warm water species of prosobranch gastropods (Lebour 1945, Kuznetsov 1963, Lewis et al. 1982, Kendall & Lewis 1986, Kendall et al. 1987).

Latitudinal gradients in the timing of reproduction are common in lusitanian species including gastropods (Bowman & Lewis 1977), bivalves (Garcia-Dominguez et al. 1998), crustaceans (Defeo & Cardoso 2002) and echinoderms (Garrido & Barber 2001). As latitude increases the length of the reproductive cycle decreases, fecundity increases and gonad size may increase due to an increase in oocyte volume (Lasiak 1987). These physiological processes have all been shown to have a direct relationship with temperature (Lozada & Bustos 1984, Manzi et al. 1985, Malachowski 1988, Hesselman et al. 1989, Garcia-Dominguez et al. 1998). Although these are general patterns that are evident across several invertebrate taxa, some species are able to acclimate to or compensate for variations in local environmental temperature (see Newell & Bayne 1973 for review, Newell 1979), which can result in deviations from the general pattern of a latitudinal gradient in the reproductive season (Newell & Kofoed 1977, Egan et al. 1989, Tomanek & Somero 1999).

Various studies have documented the timing and duration of the reproductive cycle at locations along the biogeographic range of *O. lineatus* (Williams 1965, Desai 1966, Underwood 1972a, Garwood & Kendall, 1985, Bode et al, 1986) and from comparisons of these datasets, variation in maturation rates and spawning frequencies were identified between sites at different latitudes (Garwood & Kendall, 1985, Bode et al, 1986). These studies pointed to the existence of a latitudinal gradient in reproduction in both *O. lineatus* and *G. umbilicalis*, with a short midsummer period of gonad maturation characterised by a single spawning event close to the northern distributional limits (Desai 1965, Williams 1966, Garwood & Kendall 1985), when temperatures were hypothesised to reach high enough levels for spawning to occur. In contrast, populations at the centre of the range where temperatures remained higher for an extended period during summer and autumn exhibited protracted periods of gonad ripeness, with multiple spawning events (Bode et al. 1986). The suggestion of a general latitudinal cline in the length of the reproductive cycle and spawning periodicity in *O. lineatus* therefore indicated a correlation with environmental temperature, which decreases with increasing latitude.

4.1.2 Investigating the relationship between latitude, temperature and the reproductive cycle

The northern extensions of range and synchronous increases in abundance within near-limit populations that have been quantified in *Osilinus lineatus* and *Gibbula umbilicalis* in Britain since the late 1980s have been shown to be driven by an increase in the frequency of annual recruitment success, leading to greater numbers of juveniles entering the populations as sea surface temperatures around the British coastline have increased (Chapters 2 & 3). Previous observations of extended periods of reproductive activity of trochid species at lower latitudes have been linked to increased sea temperatures (Lasiak 1982, Frank 1975, Bode et al. 1986). Therefore as sea temperatures increase at northern range edges due to climate warming, it is predicted that the reproductive cycle of range edge populations will alter to become more like that observed in the centre of the range, resulting in increased reproductive success of near-limit populations.

This chapter focuses on the reproductive mechanisms hypothesised to be driving the observed extension of northern range limits of British trochid gastropods in response to increasing environmental temperatures, using a combined field and laboratory approach. *Osilinus lineatus* was used as a test organism due to the presence of a simple reproductive system and simple reproductive pattern that is characteristic of trochid species (Fretter & Graham 1977, 1994, Hickman 1992), the recorded distributional responses to climate warming (as shown in Chapter 2) and the availability of previous data on reproductive cycles (Williams 1965, Desai 1966, Underwood 1972a, Garwood & Kendall, 1985, Bode et al, 1986). The mechanisms likely to be driving these changes are: earlier onset of spawning at increased sea surface temperatures, leading to an increased period of gonad maturation, and more spawning events per annual reproductive cycle. The effect of latitude on the timing and duration of the reproductive life-stages has been investigated by examining the reproductive cycle in populations at northern limits and further south into the range in mainland Europe along a latitudinal gradient of environmental temperatures to test the hypotheses below. Laboratory manipulations of thermal regime have also been made to gain an insight into how temperature influences reproduction.

Thus the specific hypotheses tested by field observations (1-4) and laboratory experiments (5-6) were:

A latitudinal gradient in the timing (1) and duration (2) of gametogenesis exists in *O. lineatus,* with earlier onset (1) and longer periods of activity (2), resulting in increased frequencies of spawning events at lower latitudes (3). This latitudinal gradient in reproductive activity (1-3) is linked to the latitudinal gradient in sea temperatures (4).

The gonads of *O. lineatus* will remain in a mature state for longer periods at increased water temperatures (5), resulting in a greater number of spawning events at increased sea temperatures (6).

The laboratory experiments have been placed in the context of *in situ* measurements of gonad condition and temperature at field sites from which reproductive cycles have been described and individuals collected for experiments. The results of my work in North Wales and South England are also compared to past studies at the same and adjacent locations (Williams 1965, Desai 1966, Underwood 1972a, Garwood & Kendall, 1985) to determine if the timing of key reproductive events has changed. The results of this chapter inform the next chapter which considers the role of increased survival of newly-settled juveniles over the first winter with increased winter sea temperatures as a mechanism for the extensions in range edges considered in Chapters 2 & 3.

4.2 Methods

4.2.1 Temperature

Ibutton® temperature loggers were deployed in the midshore region of Mothecombe (Figure 4.1) between November 2003 and October 2004 to record air and sea temperatures every 20 minutes. These *in situ* loggers had an accuracy of ±0.5°C.

Monthly mean sea surface temperature (SST) data from the HadISST (Version 1.1) dataset were obtained for the degree latitude by longitude grid square for each location. Satellite temperature data has been examined to determine whether there is a relationship between annual cycles of SST and annual reproductive cycles, and whether the relationships are in phase or a time lag exists between the potential thermal cue and biological response. Data from both sources were examined to see if any thermal cues for the onset of the stages of the reproductive cycle were evident.

4.2.2 Variation in the gametogenic cycle with latitude

Three sample sites were selected, covering a geographical extent of ~4.2^0 latitude (Table 1, Figure x.1) from the northern range edges in Britain to northern France. Criccieth (52.91 N, -4.23 E) was chosen due to its location close to the northern limits of distribution of *O. lineatus* in Britain in the Irish Sea. Mothecombe (50.30 N, -3.95 E) and Roscoff (48.71 N, -3.98 E) were selected to provide coverage on the north and south coasts of the English Channel. Some samples were also opportunistically collected in Porto (41.09N, -8.37 E), increasing the latitudinal extent of the survey to the middle of the geographic range of *O. lineatus* on the north Atlantic coast of northern Portugal. All sites were moderately exposed boulder or cobble shores (Figs 4.2, 4.3, 4.4) where the population densities were sufficiently large to withstand the monthly removal of 30 adult individuals without exerting a detrimental effect on population size.

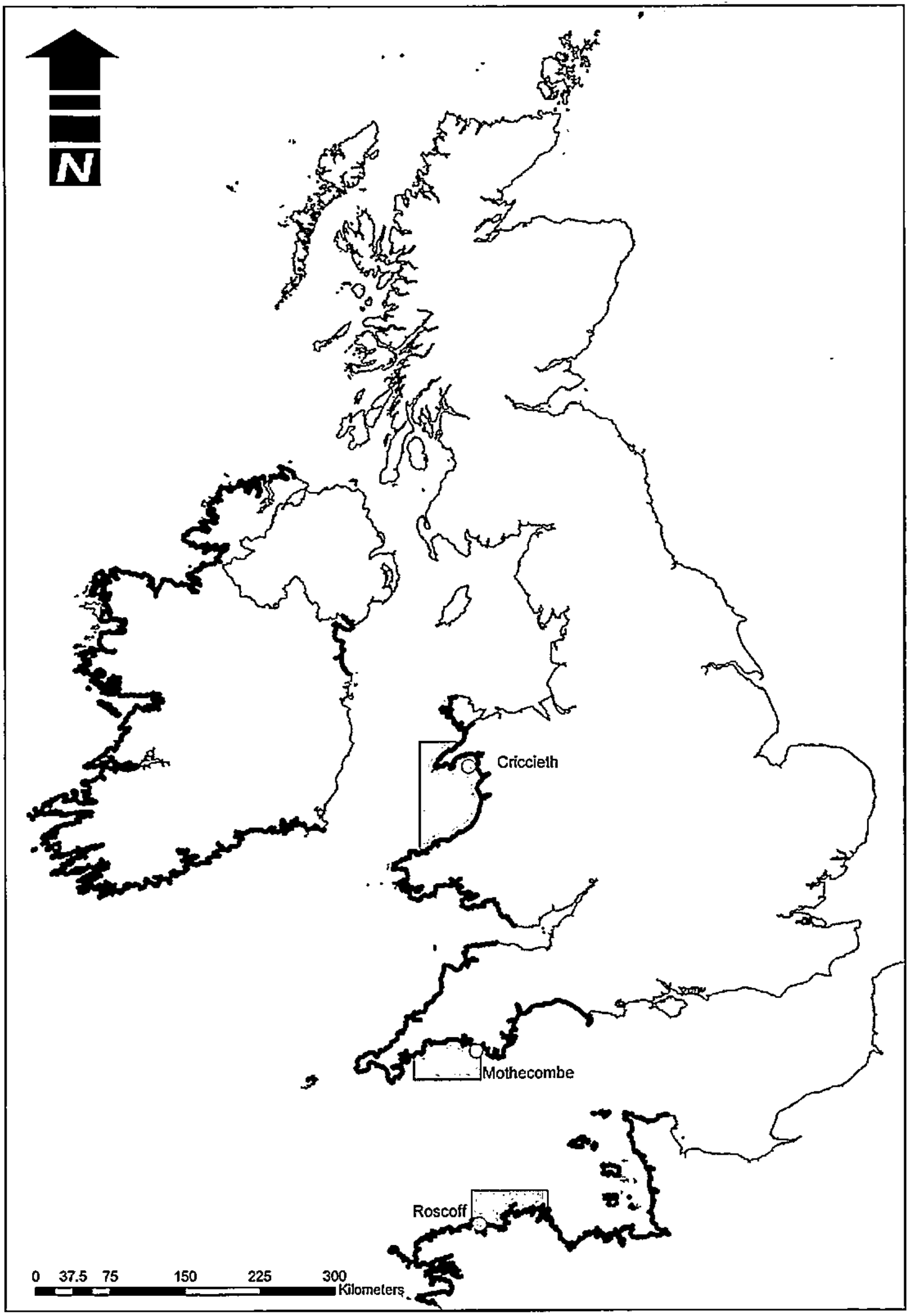


Figure 4.1. Range of *Osilinus lineatus* in Britain, Ireland and France (black line) and gonad sample locations (circles). Sea surface temperatures for the sample locations are obtained from the 1° latitude x longitude grid squares marked (grey box).

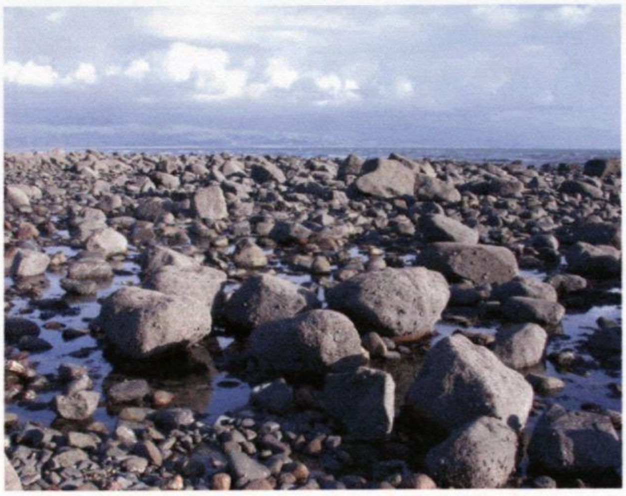


Figure 4.2. Criccieth

Figure 4.3. Mothecombe

Figure 4.4. Roscoff

Thirty individuals were collected once a month from each sample location to enable comparison with past work (Desai 1965, Williams 1966, Underwood 1972a, Bode et al. 1986, Garwood & Kendall 1986). The sampling frequency was increased to once a fortnight at Mothecombe in July 2003 to allow increased resolution of the reproductive cycle over the predicted spawning period (Underwood 1972a, Garwood & Kendall 1986). Sampling of *O. lineatus* at Criccieth and Mothecombe were continued on a monthly basis throughout 2004. Opportunistic sampling was also undertaken at Porto, northern Portugal between March and May 2004. All individuals selected were over 2 years of age, confirmed by analysis of annual growth checks on the shells of *O. lineatus* (Garwood & Kendall 1985), as sexual maturity does not occur until the second year in either species (Desai 1964). *O. lineatus* is dioecious, but the sex of the animal cannot be determined from external examination. The sex ratio has been shown not to deviate significantly from 1:1 (Desai 1964, Bode et al. 1986) and the samples were expected to contain roughly equal numbers of males and females.

The animals were narcotised in a 7.7% solution of $MgCl_2$ for 12 hours. Individuals were then fixed in 4% buffered formalin after cracking the shells to allow formalin to penetrate the gonads. Due to the shells being cracked the shell width could not be used to obtain a size-independent measure of gonad maturity unlike previous work (Bode et al. 1986), but gonads of animals stored in formalin without prior cracking of the shell did not have well-fixed gonads and deterioration of the gonad tissue was sufficient to prevent accurate analysis. Operculum diameter was therefore recorded to allow variation in individual body sizes to be taken into account, as it grows in direct proportion to the whole animal ($R^2 = 0.8744$, $P = 0.05$).

The soft body parts of each animal were extracted from the shell prior to analysis. A 1 mm thick transverse section of the gonad was removed immediately posterior to the digestive gland and the diameter of the gonad in each section was measured under a binocular microscope with a graticule eyepiece (Figure 4.5). Each individual was then sexed under the microscope using the same gonad section. Gonad diameter was used to determine the extent of gonad maturation for each of the sample populations. This method has been shown to accurately quantify the extent of sexual maturity (Garwood & Kendall 1985) and had the additional benefit of allowing the reproductive cycles of both females and males to be determined, facilitating the analysis of a greater number of samples than histological methods due to faster assessment of the reproductive condition of an individual animal. Each gonad diameter measurement was divided by the operculum of each individual to standardise measurements against variation in individual body size, and multiplied by the magnification at which the section was measured to obtain a measurement of diameter in mm. Male and female data were treated independently, allowing synchronisation of male and female cycles to be studied at each location.

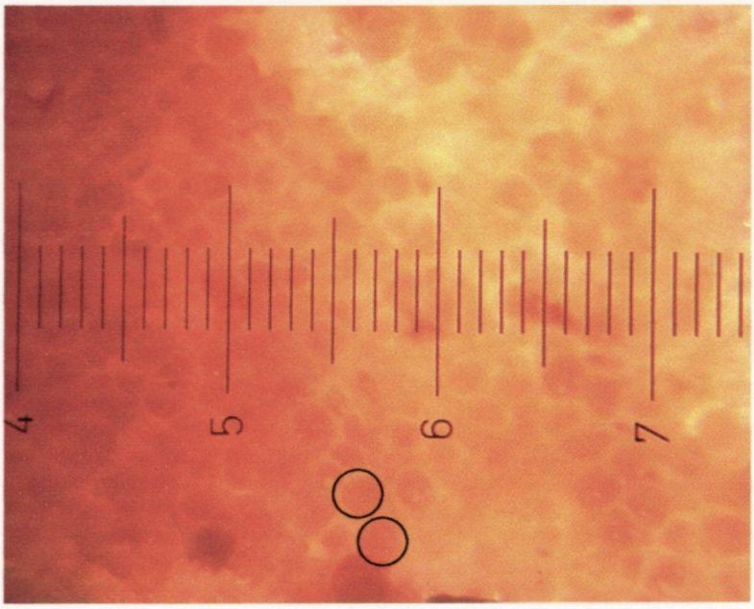


Figure 4.5. Cross section of female gonad under microscope (examples of mature oocytes circled).

This method of gonad measurement and data collection was selected instead of the developmental staging method described by Williams (1965) based on staging of the limpet *Patella vulgata* (Orton et al. 1956) and used by Bode et al. (1986) in the analysis of *O. lineatus* gonads. Some of these stages were defined by the size of individual gametes and the appearance of cellular structures that can only be determined using histological techniques. This was too time consuming for a sampling strategy containing such large

numbers of individuals as this study. The staging technique was also based on the analysis of fresh samples. Due to the large numbers of animals collected each month in 2003 from a variety of locations, the samples were preserved in formalin and gonad colour did not match the tabulated colouration. Misidentification of the stage due to different preservation methods and discrepancies between observers could have resulted in an incorrect interpretation of the reproductive cycle at a vital period when more southerly populations may have exhibited partial re-maturation of the gonads, in contrast to northern populations.

4.2.3 Laboratory manipulations of sea temperature

A laboratory experiment tested the role of temperature on gametogenesis in *O. lineatus* during 2003. The experiment was designed for analysis using a 2-way ANOVA, using temperature and replicate tanks as the independent variables.

Three treatment temperature regimes were selected:

1. Ambient: field: 17^{0}C (mean summer sea surface temperature experienced during June and July 2002 off Plymouth).
2. Field + 2^{0}C: 19^{0}C (to represent the predicted temperature of British coastal waters in 2050 under the medium-high UKCIP climate scenario (Hulme et al. 2002))
3. Field + 5^{0}C: 22^{0}C (to represent temperatures currently experienced by populations of both species towards the southern end of their ranges in Portugal and British SST predicted under the 2080 high UKCIP scenario).

Four replicate 50 litre tanks were set up for each treatment. Six hundred individuals of each species were collected from Challaborough, a rocky shore on the South Devon coast on 17/06/03. Four replicate random collections of 10 individuals of were made and the animals narcotised in $MgCl_2$ prior to fixing in formalin using the methods detailed above to determine the initial gonad condition of the population in the field. Fifty individuals were held in each replicate tank and fed on microalgae brought in on rocks from the shore. Animals were held for 24 hours at ambient temperatures to allow them to acclimate to the tank environment before the experiment was started. Ten individuals of *O. lineatus* were sampled from each replicate tank on 0, 14, 21, 29 and 43 days after the start of the experiment. Marked individuals were added to each tank to replace individuals removed on each sample date to ensure that the density of animals in each tank remained constant throughout the experiment, and therefore would not affect the results. Individuals were narcotised and preserved using the methods outlined above, and retained for gonad analysis. The experiment was run from 18/06/2003 to 30/07/2003.

4.2.4 Data analysis

4.2.4.1 *Field data*

The timing of the seasonal peak of gonad size (and therefore maturation) was estimated throughout the whole year using the month co-ordinate of the centre of gravity (centroid) of the area below graphs of monthly mean gonad diameter (for both sexes combined) at each site. This index has been shown to be sensitive to changes in the timing of seasonal cycles (Colebrook 1979, Colebrook and Robinson 1965, Edwards & Richardson 2004) and was used to examine differences in timing between, and inter-annual variation within sample sites.

The interdependence between the reproductive state of male and female gonads throughout the annual cycle was examined using a correlative approach, incorporating a time lag of plus and minus 1 month to determine whether changes in gonad size were synchronous for both sexes. Differences in mean gonad size between males and females, and between sites were tested during the peak maturation and resting phases of gonad development using a two-way analysis of variance, with sex and site as fixed factors. Ten individuals of each sex were randomly selected from each site in each month to balance the dataset, as the proportion of males and females in each sample was not always equal.

4.2.4.2 *Experimental data*

Variation in mean gonad diameter between the three temperature treatments and the source field population was analysed at the start of the experiment using a 2-way ANOVA with treatment as a fixed factor and tank as a random factor. The significant tank effect in replicate 4 of the ambient treatment prevented this replicate from being included in the remaining experiment. One replicate tank from each additional treatment was randomly removed to balance the design and the experiment was continued.

A 3-way ANOVA with treatment, time and tank fixed factors was run on the dataset to determine whether gonads remained in the active stage for protracted periods at increased temperature conditions compared to ambient temperatures. The field data were also included to see whether the ambient treatment was acting as a control for the field. If this was the case, predictions of the response of the reproductive cycle to future warming events in the field could then be made with a high degree of confidence. Post-hoc SNK tests were run to identify which treatments differed significantly, and whether there were any tank effects within replicates for each treatment. Samples were removed from the same replicate tanks at each time step (Figure 4.6). This design was not thought to compromise the analysis of the data as the individuals were destructively sampled and therefore every individual removed from the tank throughout the experiment was independent.

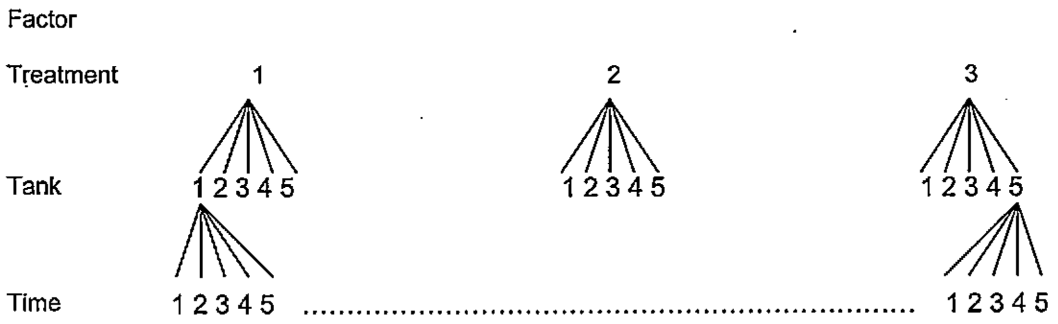


Figure 4.6. Design of laboratory experiment to determine whether duration of gonad activity is increased at increased seawater temperatures.

4.3 Results

4.3.1 Latitudinal Gonad Cycles

4.3.1.1 *2003*

The onset of gametogenesis commenced between March and April at Criccieth, Mothecombe and Roscoff (Figure 4.7) and was characterised at all locations by the gonads of both sexes becoming distended and oocytes being visible in all females examined. The peak period of gonad maturation was reached in May at all 3 sites, when maximum gonad size was significantly greater at Criccieth than at Roscoff for males. Maximum gonad size was significantly greater at Criccieth than at Mothecombe and Roscoff for females (Tables 4.1-4.4).

Gonad diameter decreased between May and mid-August at Mothecombe and Roscoff, indicating that spawning had occurred. During this period, oocytes became less densely packed within the ovaries. Gonad diameter also decreased between May and June at Criccieth as spawning occurred but increased again between June and July, indicating that either some individuals had spawned prior to others, or that individuals of both sexes had undergone re-maturation of the gonads (Figure 4.7). A second spawning event was indicated by a rapid decrease in gonad diameter in both sexes between July and August, before gonad diameter levelled off between 2-3mm. The total length of spawning period for individuals sampled from all 3 locations was 4 months, extending from May to August.

By September, the gonads of males and females at all 3 sites were loose, empty sacs, indicating that gonads in all populations were in the spent, resting phase. A few females still contained large oocytes during the resting period, suggesting that these individuals had not fully spawned out. Gonads remained in the resting phase until March 2004 at Criccieth and Mothecombe. The Roscoff population were still in the resting phase when sampling finished in December 2003. The reproductive cycle extended over 6-7 months in all three populations.

Tables 4.1-4. ANOVA at peak and resting periods of the gonad cycle in 2003 and 2004 with site and sex as fixed factors. Cochran's test: May 2003 (C=0.24, NS), November 2003 (C = 0.41 significant at $P < 0.05$), May 2004 (C=0.39, NS), November 2004 (C=0.37, NS).

Table 4.1. ANOVA results for maximum gonad size, May 2003.

Source	SS	df	MS	F	P	F versus
Site (si)	31.66	2	15.83	16.52	0.0001	residual
Sex (se)	4.91	1	4.91	5.13	0.0276	residual
si x se	9.87	2	4.94	5.15	0.0090	residual
residual	51.74	54	0.96			
total	98.19	59				

Student-Newman-Keuls test	se(si)
site x sex interaction si(se)	Criccieth: male < female
sex 1 (male): Criccieth > Roscoff = Mothecombe	Mothecombe: male = female
sex 2 (female): Cricceith > Mothecombe = Roscoff	Roscoff: male < female

Table 4.2. ANOVA results for gonads in the resting phase, November 2003.

Source	SS	df	MS	F	P	F versus
Site (si)	8.11	2	4.05	9.61	0.0003	residual
Sex (se)	0.49	1	0.49	1.17	0.2845	residual
i x se	12.34	2	6.17	14.62	0.0001	residual
residual	22.79	54	0.42			
total	43.74	59				
SNK				se(si)		
site x sex interaction si(se)				Criccieth: male > female		
sex 1 (male): Criccieth > Mothecombe > Roscoff				Mothecombe: male = female		
sex 2 (female): Cricceith = Mothecombe = Roscoff				Roscoff: male > female		

Table 4.3. ANOVA results for maximum gonad size, May 2004.

Source	SS	df	MS	F	P	F versus
Site (si)	0.26	1	0.26	0.35	0.5552	residual
Sex (se)	0.07	1	0.07	0.1	0.7595	residual
i x se	0.67	1	0.67	0.93	0.3420	residual
residual	26.14	36	0.73			
total	27.14	39				

Table 4.4. ANOVA results for gonads in the resting phase, November 2004.

Source	SS	df	MS	F	P	F versus
Site (si)	1.66	1	1.66	5.56	0.0240	residual
Sex (se)	0.19	1	0.19	0.63	0.4338	residual
si x se	0.17	1	0.17	0.58	0.4507	residual
residual	10.79	36	0.30			
total	12.81	39				
Site effect: Criccieth < Mothecombe						

4.3.1.2 *2004*

Gametogenesis began in March for both sexes at Mothecombe and in females at Criccieth. The gonad size of males did not increase at Criccieth until April, although peak gonad diameter was reached in both sexes in May at both locations with no significant difference between mean size between sexes, indicating that the males had ripened quicker than females at Criccieth. A single spawning period was observed in both populations, commencing in June at Criccieth and in May at Mothecombe. Opportunistic samples from Porto showed that the spawning period began in April. It is not known whether this was the only spawning event of the cycle as no samples were available after May. Gonads entered the resting phase between August and September at Criccieth and Mothecombe, with animals from both locations still in this stage when sampling ceased in November.

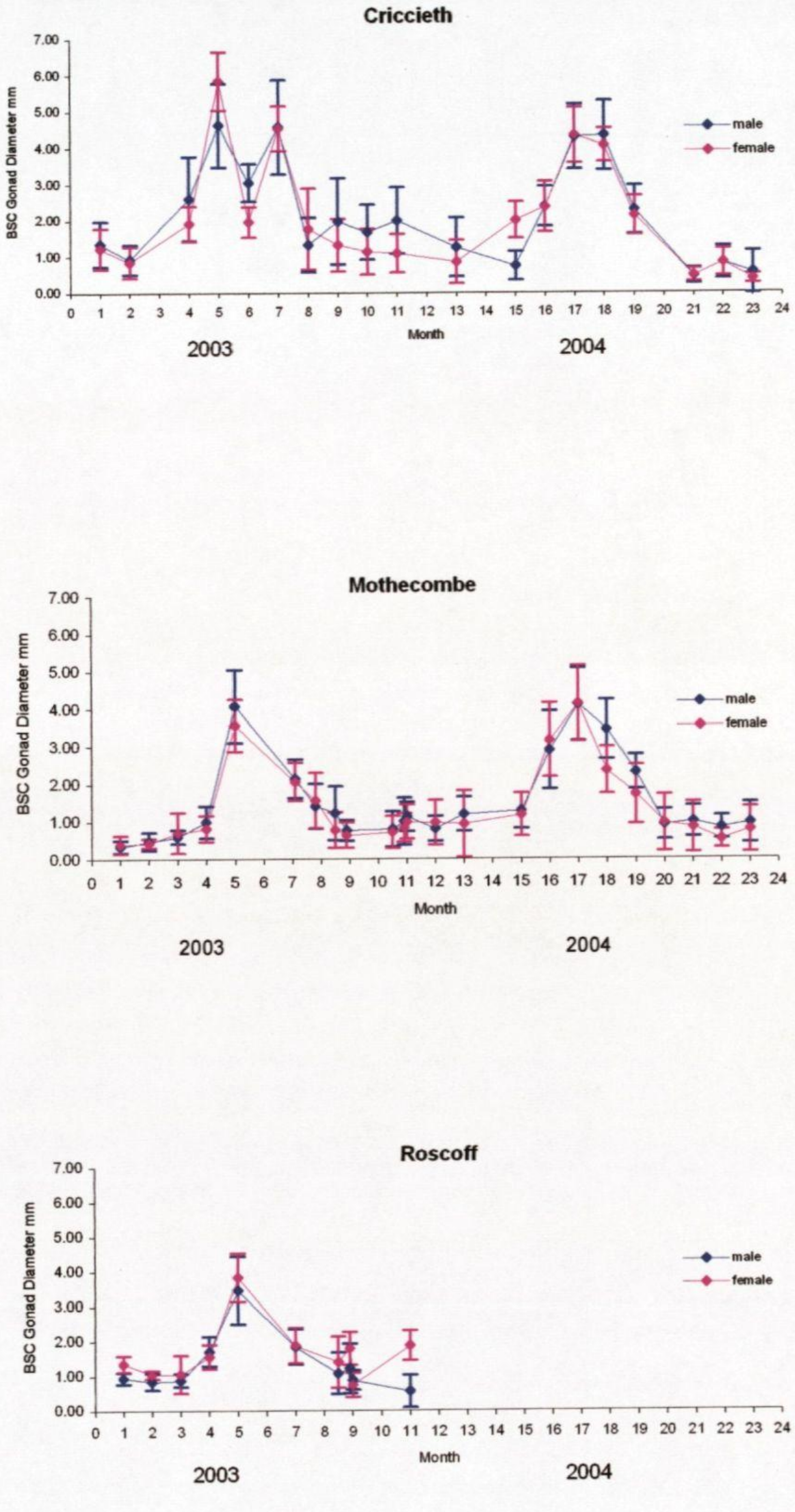


Figure 4.7. Gonad cycles of *O. lineatus* at locations covering 4° latitude during 2003 and 2004. Y axis denotes body-size-compensated gonad diameter (gonad diameter divided by operculum diameter).

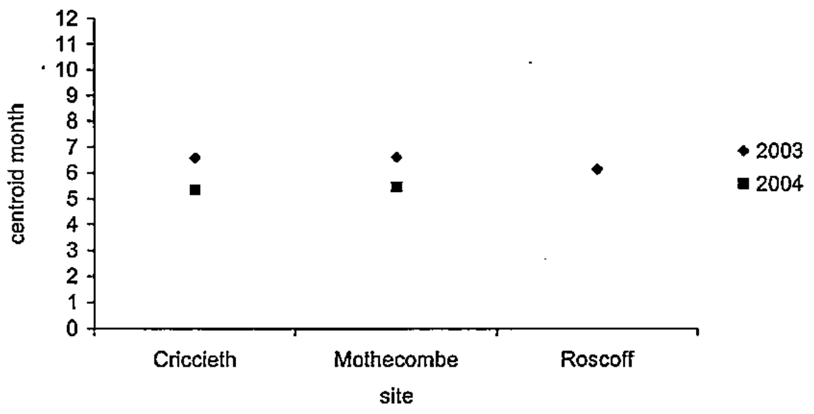


Figure 4.8. Timing of the seasonal peak of reproduction using the central tendency index.

The centroid indicator provides a more precise measurement of the timing of the seasonal reproductive peak of *O. lineatus* than visual inspection of graphs of gonad diameter. The centroid of reproduction was 6.60, 6.63 and 6.14 months for Criccieth, Mothecombe and Roscoff respectively in 2003, and 5.30 and 5.54 months for Criccieth and Mothecombe in 2004 (Figure 4.8). Although the number of reproductive cycles observed is insufficient to allow further use of data derived from the central tendency method, it does permit comparisons of the timing of peak maturation at the 3 sites. In 2004, the peak occurred 1.26 months earlier at Criccieth (SST ~ 1 C higher in May 2004 than May 2003) and 1.09 months at Mothecombe (SST ~ 0.15 C higher in May 2004 than May 2003).

4.3.2 Temperature data

4.3.2.1 *HadISST data*

Monthly SST data on a 1° latitude by 1° longitude grid for the grid squares corresponding to the locations of the three sample sites from 2002 to 2005 was obtained from the Hadley Centre, UK Met Office (HadISST, Version 1.1). This dataset is a gridded product combining *in situ* sea surface observations and satellite-derived estimates (Rayner 2003). SST showed a latitudinal gradient in 2003 and 2004, with consistently colder temperatures further north (Figure 4.9). The annual pattern was the same, however, with increases, decreases, maxima and minima occurring during the same months at all 3 sample locations.

Gonad development was seen to commence as monthly SST started to increase between March and April at all sites in 2003 and 2004 (Figure 4.10). Peak gonad size was reached and spawning commenced prior to the warmest month in both 2003 and 2004 at each location, and the resting phase was entered as temperatures began to decrease in September of each year. Correlations between mean monthly sea surface temperature (HadISST version 1.1) showed the best relationship with a +2 month offset in temperature, followed by a –2 month lag (Table 4.5). Gonad development was proposed to be temperature dependent, and therefore increases in gonad size were expected to occur with either a zero or minus 1-2 month time-lag.

Table 4.5. Correlations of mean gonad diameter with mean monthly SST 2003-2004.

Site	Sex	Month lag	r	p
Criccieth	Male	-2	-0.5886	0.10
		+2	0.7357	0.01
	Female	-2	-0.6514	0.003
		+2	0.6870	0.02
Mothecombe	Male	-2	-0.5839	0.005
		+2	0.5280	0.014
	Female	-2	-0.5719	0.07
		+2	0.4367	0.048
Roscoff	Male	-2	-0.5996	0.088
		+2	0.7873	0.012
	Female	-2	-0.3899	0.03
		+2	0.5888	0.095

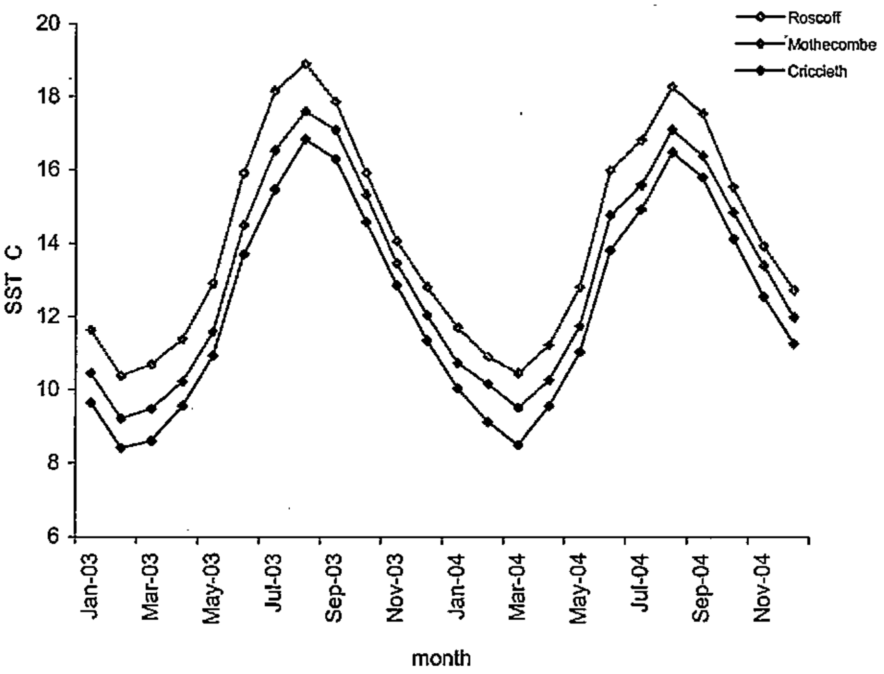
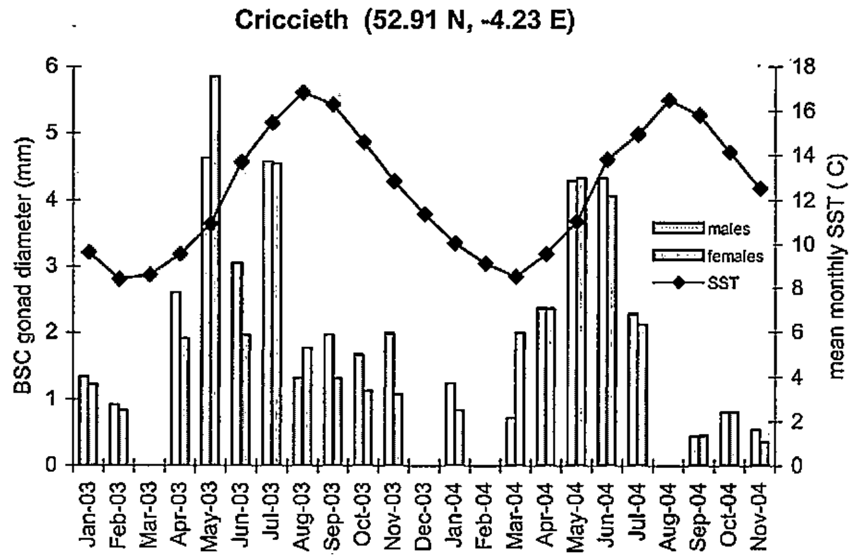
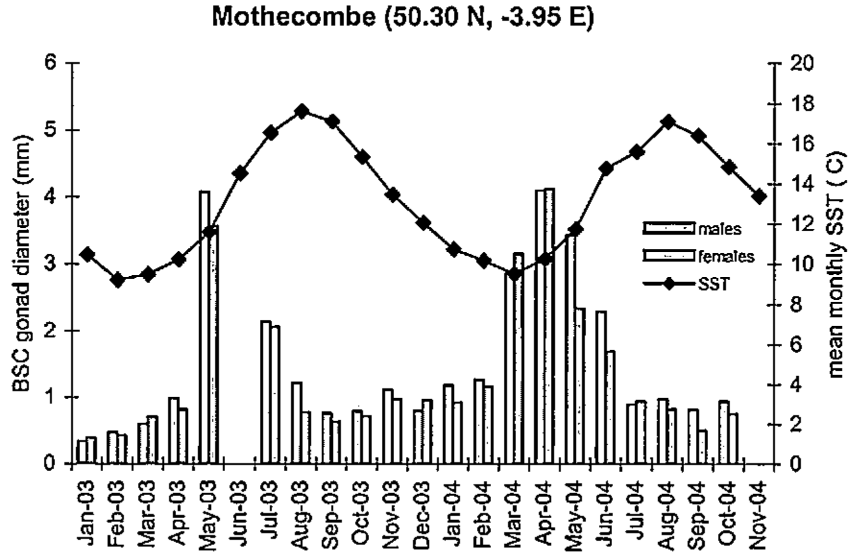


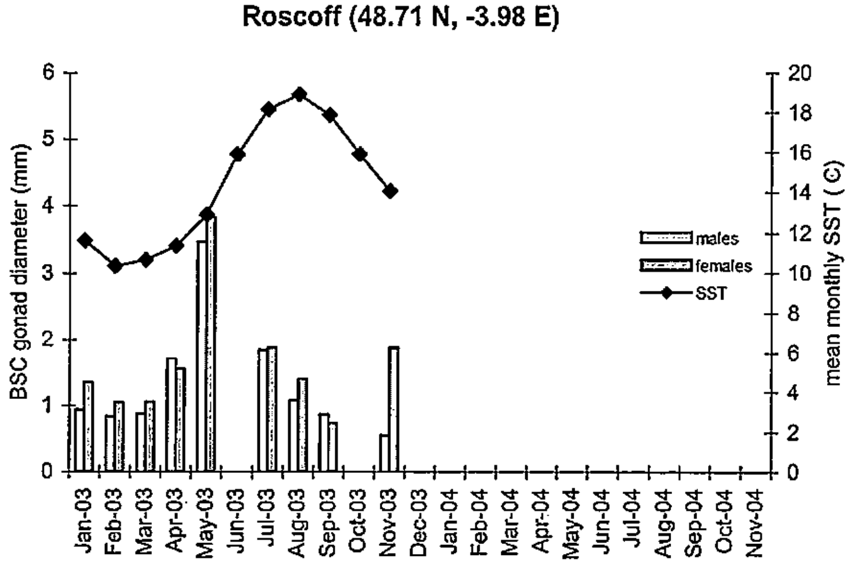
Figure 4.9. Mean monthly SST (HadISST Version 1.1) for the grid square in which each sample site was located.



Criccieth (52.91 N, -4.23 E)



Mothecombe (50.30 N, -3.95 E)



Roscoff (48.71 N, -3.98 E)

Figure 4.10. Mean monthly gonad diameter and mean monthly SST, 2003-2004 Y axis denotes body-size-compensated gonad diameter (gonad diameter divided by operculum diameter).

4.3.2.2 *In situ logger data*

The onset of gonad development detected between March-April 2004 was immediately preceded by a sudden increase in air temperature between 08 and 09 March from the monthly mean of 9.64°C to 16.92°C. No corresponding increase was seen in the sea surface temperature data collected by the *in situ* loggers (20 min sampling frequency) or in the monthly mean values from the satellite data. This is the first record of acute changes in air temperature corresponding to changes in gonad activity.

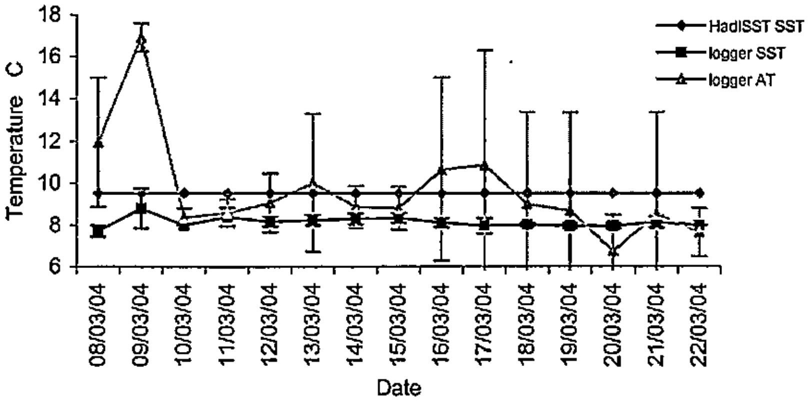


Figure 4.11. *In situ* logger sea surface and air temperature data and satellite sea surface temperature data for Mothecombe, March 2004.

4.3.2.3 *Differences between sexes*

Correlations between mean male and female gonad diameter over the duration of the sample period indicate a tight synchrony between the reproductive cycles of males and females within each site (Criccieth: r=0.92, P<0.001, Mothecombe: r=0.9668, P<0.001, Roscoff: r=0.8811, P=0.002), over a latitudinal distance of ~4 degrees from the northern range edge towards the centre of the range.

In 2003, a sex x site interaction was evident for both periods analysed using a 2 way ANOVA (Table 4.6). Gonads were larger in females than in males at the peak of the reproductive cycle at Criccieth and Roscoff, but smaller during the resting phase. There was no significant difference between sexes in either month at Mothecombe, and no overall trend was evident between the sexes.

A latitudinal gradient in maximum male gonad diameter was found in 2003. Gonad size significantly increased with latitude from Roscoff to Mothecombe and Criccieth during both the peak maturation and resting phases. Females also showed the same latitudinal trend in peak gonad size, but there was no significant difference in resting gonad size between locations. Cochran's test showed significant differences among the variances for gonads in November 2003 ($C=0.4149$, $p< 0.05$) even when the data were transformed. The analysis of variance computation is relatively robust against data displaying moderate heterogeneity of variance so long as the comparison involves more than one degree of freedom, but the results of this analysis must be treated with caution. In contrast, no latitudinal gradient in size of either sex was observed in 2004.

4.3.2.4 *Laboratory manipulations of temperature*

The timing of the experiment was designed to follow individuals from the period of peak maturation through to the resting stage, and was therefore based on previous data on the spawning period of *O. lineatus* (Underwood 1972a, Garwood & Kendall 1987) in Britain. In 2003, however, the field population began to spawn two months earlier than in previous study years and the experiment was not started until approximately 4 weeks after the spawning period had begun. Therefore the data collected was analysed to test hypothesis 5 proposed in this chapter, but was only partially able to address hypothesis 6, as the initial spawning event had occurred prior to the beginning of the experiment.

Mean gonad diameter was analysed for samples taken at the start of the experiment on day 0 using a 2-way ANOVA with treatment and tank as fixed factors. The results of a post-hoc SNK test showed that there was no significant difference between replicate tanks in each treatment except for tank 4 in treatment 1 (ambient), which was significantly different from the other 3 replicates (Table 4.6). Therefore this tank was removed from the experiment. In order to maintain a balanced design, one replicate tank was randomly removed from each of the other 2 treatments so that all treatments contained 3 replicates, and 3 replicate samples of 10 individuals were collected from the shore on each future sample date. The +2°C was excluded from further analyses as parasitism in all replicate tanks caused mass mortalities after day 197 of the experiment.

Table 4.6. 18/06/03 ANOVA including all 4 replicate tanks for 3 treatments and 4 replicate field samples.

Source	SS	df	MS	F	P	F versus
Treatment (tr)	5.61	2	2.81	4.02	0.0200	residual
Tank (ta)	9.88	3	3.29	4.7	0.0100	residual
trxta	14.39	6	2.40	3.44	0.0100	residual
residual	75.38	108	0.70			
total	105.26	119				

SNK

Treatment x Tank interaction tr(ta)

tank 1: ambient = +2°C = +5°C

tank 2: ambient = +2°C = +5°C

tank 3: ambient = +2°C = +5°C

tank 4: ambient < +2°C = +5°C

ta(tr)

treatment ambient: 1 = 2 = 3 > 4

treatment +2°C: 1 = 2 = 3 = 4

treatment +5°C: 1 = 2 = 3 = 4

A treatment x time x tank interaction was evident in the 3 way ANOVA run on the experimental data. The mean squares values show that some of the variance was accounted for by time (6.61) and replicate tanks (2.80), but the majority of the variance (20.98) was between treatments (Table 4.7). In 12 out of 15 tests, mean gonad diameter was smaller in the animals sampled from the field than from animals in the ambient and +5°C treatments, significantly so in 6 cases (Table 4.8). This pattern became more consistent in the experiment as time progressed, with gonad size being smaller in field samples than for either treatment from day 21 to day 42. No significant difference between the ambient and +5°C treatments was found except in tank 3 on day 14 and day 28 of the experiment.

Table 4.7. ANOVA results: treatment, time and tank as fixed effects (Cochran's test C = 0.0052, NS).

Source	SS	df	MS	F	P	F versus
treatment	41.95	2	20.98	27.11	0.0001	residual
time	26.44	4	6.61	8.54	0.0001	residual
tank	5.59	2	2.80	3.61	0.0278	residual
treatment x time trxti	10.52	8	1.32	1.70	0.0966	residual
treatment x tank trxta	12.35	4	3.09	3.99	0.0035	residual
time x tank tixta	8.05	8	1.01	1.30	0.2419	residual
treatment x time x tank trxtixta	22.75	16	1.42	1.84	0.0248	residual
residual	313.41	405	0.77			
total	441.07	449				

Table 4.8. Post-hoc SNK tests on treatment x time x tank interaction (*> significantly greater P+0.05, → ,← NS change in the direction of the arrow).

Time	Replicate	Treatment				
		Ambient		+2°C		Field
1	1	3.06	→	3.24	←	3.18
1	2	3.82	←	3.20	←	3.09
1	3	3.51	←	3.36	*>	2.49
2	1	4.13	*>	2.26	→	2.41
2	2	3.76	←	3.20	*>	2.37
2	3	2.90	→	3.36	←	2.48
3	1	3.03	←	2.81	←	2.16
3	2	3.08	→	3.73	*>	2.60
3	3	2.67	→	2.99	←	2.39
4	1	3.86	*>	2.37	←	2.16
4	2	2.67	→	2.74	←	2.10
4	3	2.75	←	2.53	←	2.32
5	1	3.21	←	2.93	←	2.27
5	2	3.07	←	2.63	←	2.33
5	3	1.89	→	2.60	←	2.11

The mean gonad diameter for each replicate tank was plotted for all 3 treatments at each sample time. The area under the curve was compared for each treatment and the field population using a one-way ANOVA with treatment as the fixed factor, to determine if there was evidence of a protracted breeding period in animals exposed to increased temperatures. There was no significant difference between the area under the gonad maturation curve for the ambient, +5°C treatments and field samples (Table 4.9, Figure 4.12). Cochran's test showed that there was the variances were significantly different despite various transformations of the data. However, the results of the analysis showed that there was no significant difference between the area under the gonad size curve for the ambient, +5°C and field animals and therefore the results of this analysis were still used as ANOVA techniques are relatively robust to non-homogeneity of variances.

Table 4.9. One-way ANOVA for area under gonad maturation curves (Cochran's test C = 0.94, $P<0.05$).

Source	SS	df	MS	F	P	F versus
Treatment (tr)	1887.70	2	943.85	2.95	0.13	residual
residual	1922.46	6	320.41			
total	3810.16	8				

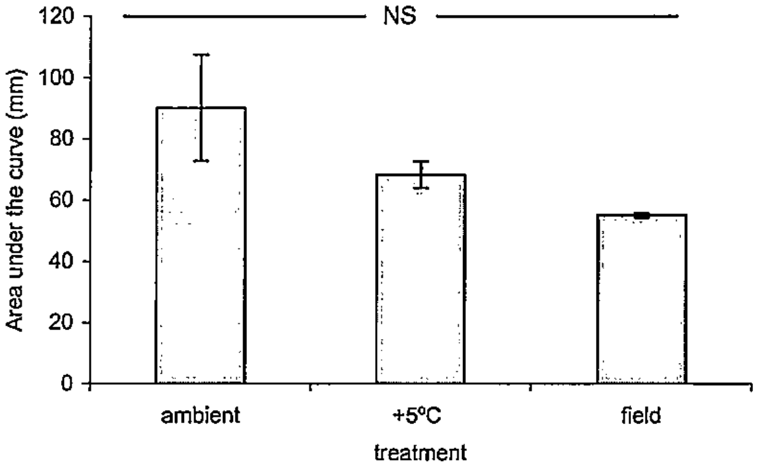


Figure 4.12. Total gonad activity, presented as the area under the maturation curve (± 1 SE), of sample populations in the ambient, +5°C treatments and field source population.

The results of both the 3 way ANOVA and the one way ANOVA show that the period of gonad maturation was not significantly extended in the +5°C increased temperature treatment or the ambient treatment in comparison to the field population. No gonad re-maturation or multiple spawning events were detected in any animal from any of the three treatments, or the field population.

4.4 Discussion

4.4.1 Limitations of study

The SST data is obtained from satellite imagery that is calculated with 1° latitude by 1° longitude spatial resolution. This covers a large area of the sea, and may not be of sufficient resolution to detect the changes occurring in inshore waters, which are known to be more variable than SST further offshore (Lee & Ramster 1981). Therefore the thermal regimes at the three sample sites may actually be more similar than the general SST pattern, thus overriding the broad-scale latitudinal gradient in temperature. Alternatively, the latitudinal extent of the study may not be sufficient to detect changes in the breeding period, as the only recorded observations of protracted maturation and spawning events are from a Spanish population located 5° further south at 43.6° N (Bode et al. 1987). This chapter only looks at sea surface temperature data, but air temperature and the temperature of the rock on which the animals are situated may also affect the time of spawning.

It is unlikely that the temporal resolution of field sampling was too coarse to detect slight extensions in breeding periods at lower latitudes as this sampling interval has been shown to be sufficient to show variation in maturation, spawning and resting phases between Wales and Spain in previous work on *O. lineatus* (Garwood & Kendall 19865, Bode et al.

1986) and is the standard for many studies on reproductive cycles (Grant & Tyler 1983 a,b, Lasiak 1987, Garcia-Dominguez et al. 1998, Carvalho & Ventura 2002, Defeo & Cardoso 2002, Rocha-Barreira 2002, Tyler et al. 2003). Laboratory studies were started after spawning had started, due to the early onset of maturation and spawning in 2003 compared to previous field studies. This limited the applications of the data, but did provide an insight into the effects of increased sea temperatures on the length of time that gonads remained active and the inability of animals to re-ripen at artificially increased temperatures.

4.4.2 Latitudinal trends

Populations of *Osilinus lineatus* studied in Britain and northern France in 2003 and 2004 all show an annual cycle of reproduction, with visible gametogenesis beginning over one to two months in early spring. The onset of a single spawning period follows a month later and continues for three to four months until late summer, when most individuals have completely shed all gametes and enter a resting phase. Gonads remain in this empty state throughout winter, with gametogenesis beginning again the following spring. Gonad cycles show tight synchrony between males and females at all sites, which is expected as broadcast spawners require simultaneous release of male and female gametes into the water column in order to maximise fertilization success (Giese 1959, Kinne 1963, Babcock et al. 1986, Olive 1992, Levitan 1995).

When the environment changes along the biogeographic range of a species, it is unlikely that a single phenotype will display the greatest fitness in all situations (Via et al. 1995), and so variations in the reproductive features are likely to occur as the result of phenotypic plasticity (Via & Lande 1985) and/or local genetic variation (Endler 1986) determined by the environment (Lardies & Castilla 2001). No such variation has been observed between sites spread over a distance of 4° latitude for *O. lineatus*, and the predicted latitudinal gradients in the timing and duration of the reproductive cycle and spawning frequency have not been observed in adults of either sex from these populations during 2003 and 2004. These observations are counter to the predicted trend, as reproductive processes are temperature- dependent (Orton 1920a, Newell 1971, 1973) and the timing of reproductive events is therefore expected to be delayed at higher latitudes where spring and summer temperatures are reduced and lag behind those experienced at lower latitudes. Earlier spawning was observed at Porto in 2004, where late winter and early spring mean SST prior to spawning in 2004 showed largest difference of ~4.4 – 5.8°C higher temperatures than Criccieth, and 2.6 – 3.8°C higher than Roscoff. Temperatures at Roscoff were greater than 14°C throughout the year, in contrast to the most northerly site, Criccieth, where monthly mean temperatures only exceeded 14°C between July and September. This may explain why gonads were observed to be active earlier in 2004 than in the 1960s and 1980s, and the contrast of short reproductive periods in British populations compared to the prolonged gonad activity throughout most of the year in lower latitude sites studied in Europe during these decades (Lombas et al. 1984, Bode et al. 1986). The results of the laboratory experiments also show no extension of the breeding period or multiple spawning events after the first major spawning period at elevated sea temperatures, although due to the significant differences between gonad activity in the control, treatment and field animals, these results cannot be assumed to be conclusive.

SST shows a latitudinal gradient in 2003 and 2004, with consistently colder temperatures further north (Figure 4.9). The annual pattern is the same, however, at all locations, with increases, decreases, maxima and minima occurring during the same months at all 3 sample locations. In summer the Irish Sea becomes strongly stratified, resulting in warmer SST in Cardigan Bay than in other coastal areas at the same latitude around Britain (Lee & Ramster 1981). In contrast, the waters of the Western English Channel remain mixed and SST is cooler than in nearby coastal waters of the North east Atlantic. SST are therefore more similar between Criccieth and Roscoff than would be expected from their locations along the latitudinal temperature gradient from tropical to polar latitudes along the western seaboard of Europe, and this may account for the similarities in timing of the stages of the reproductive cycle.

A latitudinal gradient in gonad size was evident across the three sites studied in 2003 and 2004. Gonad size during the spring maturation peak and the autumn/winter resting period was significantly greater at the most northerly population, Criccieth, than at Mothecombe and Roscoff in 2003. Resting gonad size was again found to be greater at the most northerly site of Criccieth than at Mothecombe in 2004, but no such difference was apparent between Criccieth and Mothecombe during the period of peak maturation in 2004.

There are many potential physiological explanations for the increase in gonad size at higher latitudes. The environmental trigger for spawning may be delayed or absent from habitats close to northern range edges. Gonads of *Osilinus lineatus* individuals that were transplanted 250km north of their northern range edge in 1978 still developed gonads and produced gametes despite winter air temperatures being 4-5°C colder than experienced (Williamson, Kendall & Lewis in press). Gonad weight was 2.7 times greater and spawning was delayed by 3 months in transplanted animals compared to the source population. No conclusions were drawn from this experiment, but summer temperatures may not have reached sufficient levels to trigger spawning in the transplanted population until later in the year than at the source population located further south, resulting in the retention of gametes as production continued and larger gonad sizes as a result.

Alternatively, summer temperatures at locations close to the northern limits may only be suitable for successful reproduction and spawning to occur for a short period during each year. The duration of gonad maturation and spawning was the same at all 3 locations in this study covering over 4 degrees latitude and a temperature gradient of 1.2-2.7°C, however, suggesting that the increase in gonad size observed with increasing latitude was not the result of a change in reproductive strategy between these populations. There is a general inverse relationship between metabolic rate and latitude (Clarke 1993, Gillooly et al. 2001, Allen et al. 2002, Clarke 2004, Clarke & Fraser 2004), leading to lower maturation and growth rates at lower temperatures (Kinne 1970, Newell 1979, Ikeda et al. 2001). This hypothesis may account for the increase in gonad size found in transplanted populations by Williamson et al. (in press) but is counter to the greater growth of reproductive tissue in animals from higher latitudes observed in this study. *O. lineatus* has been shown to exhibit acclimatory responses to temperature (Newell et al. 1971) and therefore this observed trend merits further investigation.

4.4.3 Decadal change

In the late 1950s and early 1960s, populations close to the northern limits of distribution in Wales show a five month period of rapid gonad development (stage DII+ in early literature by Desai 1965, Williams 1966) followed by a three month spawning period from May to August. This pattern is also observed in my study in 2003 and 2004. Gonads were empty until October, when some limited activity was observed. The gonads remain in a resting phase for 5-6 months over the autumn and winter. In contrast, during the cooler early 1980s, gonad development is delayed until May, with ripe gonads being attained in August, 3 months later than in warmer decades. Spawning occurs for only one month before the population enters a resting phase for seven months from September. In south-west England, gonad development and spawning occurs two months later in the cool year of 1969 (Underwood 1972a) than in the warmer years of 2003 and 2004. Data are only available for the cooler period of the early 1980s in Spain, but a protracted period of gonad activity is observed compared to populations in Wales studied in the same years. There is a general trend of earlier onset of gonad development and earlier spawning during warmer climatic periods or at locations with warmer climatic regimes in comparison to cooler years and cooler locations. The temporal trend is evident over a distance of 4° latitude, and the spatial trend between populations over 9° latitude. The timing of spawning has been shown to have a significant impact on recruitment patterns at the local and regional scale (10-1000km) for corals (Hughes et al. 2002), with increased recruitment success during warmer years. The earlier onset of spawning in *O. lineatus* observed in the warmer 2000s in this study compared to the cooler 1970s and 1980s may explain the greater success of near-limit populations during this period.

4.4.4 Physiological mechanisms

The observed plasticity in the annual timing of the gonad cycle within and between locations suggests that *O. lineatus* is able to respond to environmental cues irrespective of when they occur during the year. Food supply or temperature are the most likely factors that individuals are responding to, as few other abiotic or biotic factors have the same seasonal periodicity as the reproductive cycle. The timing of the reproductive cycle is related to the phytoplankton bloom for phytotrophic veligers, but the larvae of *O. lineatus* are lecithotrophic and feed on their yolk sac until they have undergone torsion and settled on the shore. Diatom biomass is greatest on the rocky shores in Britain in autumn/winter (Thompson et al. 2005), so if food supply is critical, and temporal pattern in diatom availability on the shore is the limiting factor, the spawning peak would be expected to occur in late summer/early autumn, not in spring. Irradiance levels have been shown to influence the timing of breeding in the boreo-arctic barnacle *Semibalanus balanoides* over a latitudinal gradient (Davenport et al. 2005), but for species with lusitanean distributions such as *O. lineatus,* daylength at the northern limits is not limited to the short periods experienced by species whose northern limits approach the Arctic circle.

Adaptation to the local environmental temperatures may cause the patterns observed in *O. lineatus.* Individuals at each site may have adapted their thermal cues for reproductive activity to match the local seasonal temperature regime. Maturation and spawning will still occur at the same period of the year in response to temperatures reaching a critical level in the thermal cycle, but the critical temperature will vary with location, and spawning will occur at lower temperatures in populations towards the northern end of the biogeographic range. (Orton 1920a, Kessel 1964, Rasmussen 1973, Fretter 1984). This mechanism may account for the maturation phase occurring in the same months in populations with different temperature regimes, and the timing of spawning occurring three months before the maximum monthly temperature at all locations.

The fundamental period of gonad activity may be extended within northern populations now that the climate is more similar to that previously experienced at the range centre, but the effective period may be smaller due to the absence of the environmental cue for gonad redevelopment after the first spawning event. This would account for the earlier onset of development in northern populations in warmer years, mirroring populations towards the middle of the range, and explain the short active period and long resting period despite warmer autumn and winter temperatures in the 2000s compared to the 1970s and 1980s. The internal control and external cues of the reproductive cycle of prosobranchs are relatively unknown (Fretter 1984, Clare 1990) and thus inferences drawn in this chapter remain speculative.

Chapter 5. Investigations of the role of climate on recruitment and juvenile survival in *Osilinus lineatus* and *Gibbula umbilicalis*.

5.1 Introduction

Recruitment is likely to play a dominant role in determining patterns of population densities and community structures from local (Connell 1961, Lewis 1976, Connell & Slayter 1977, Denley & Underwood 1979, Caley et al. 1996, Strathmann et al. 2002) to regional scales (Lewis et al. 1982, Gaines & Roughgarden 1985, Hughes et al. 2002, O'Riordan et al. 2004) over a range of temporal periods (Van der Meer 2001). Survival rates during the first year of life have been shown to determine the year class strength in marine invertebrates (Kinne 1963, Denley & Underwood 1979, Caffey 1985, Bowman & Lewis 1986, Menge 2000) and vertebrates (Hjort 1919, Limburg et al. 1999) and have also been seen to affect the fecundity of the cohort upon maturity as a consquence (Lindstroem & Kotto 2002). Marine intertidal species show a general trend of infrequent post-recruitment success at the edge of their geographical distributions (Hutchins 1947, Kendall et al., 1982; Lewis et al., 1982; Kendall 1987). At the range edge the conditions necessary for growth, successful reproduction and hence consistent recruitment are likely to occur less frequently and over shorter durations than at locations further into the range (Crisp 1950, Barnes 1953, 1956, 1958, 1962, Lewis 1982).

Chapters 2 and 3 demonstrated that populations of *Osilinus lineatus* and *Gibbula umbilicalis* had more frequent recruitment success in recent warmer years than during the 1978-1986 study period. Recruitment failures observed at and close to the northern limits of intertidal species during the cooler decades of the 1970s and early 1980s (Lewis & Kendall 1986, Kendall 1987) were not thought to result from failure or inadequate production of gonads in mature adults (Lewis 1964, Bowman & Lewis 1986, Williamson et al. in press). Differences in the length of time gonads remain reproductively active has not been observed in trochid species over small latitudinal distances in the British Isles and northern France (Chapter 4), but longer breeding periods in the centre of the range were observed (Bode et al. 1986) in contrast to northern populations during consecutive years in the 1980s (Garwood & Kendall 1985).

It has been generally assumed that the recruitment failure of British trochids observed at northern limits is influenced by the inability of larvae or newly settled juveniles to survive in adverse environmental conditions (Lewis et al. 1982, Garwood & Kendall 1985, Kendall 1987). Specifically, winter temperatures encountered by newly settled recruits near northern limits occur earlier in the year, are lower and persist for longer durations than at locations closer to the centre of the range, and lower numbers of recruits are thought to survive as a result. This mechanism may explain the range extensions recently observed (see Chapters 2 & 3).

To test the role of temperature in recruitment success I focussed on the recruitment dynamics of newly settled juveniles of both *Osilinus lineatus* and *Gibbula umbilicalis* over a two-year period from 2002 to 2004 in Devon, well within the range of the species. Larvae were not studied because of the logistical problems and the difficulty of identifying early trochophores or veligers in the plankton (Lebour 1937, Desai 1966). In the field, detailed information on the time of settlement, growth, and abundance was analysed in conjunction with sea surface and air temperature data to investigate the role that environmental temperature plays in the survival of newly settled juvenile individuals. The effect of sea temperature on the survival of '0' cohort juveniles during their first winter on the shore was also experimentally tested in isolation using laboratory studies. Treatments simulated sea temperatures experienced in the coastal waters off Plymouth in the cold winter of 1983 (during the period of original data collection by Kendall), winter temperatures recorded in 2003 off Plymouth, and warm winter temperatures experienced in the middle of the distribution of *O. lineatus* in Portugal during 2003. The following specific hypotheses were tested:

In the field:

1. Winter growth cessation of the newly settled juvenile cohort is related to decreases in environmental temperature
2. Spring continuation of growth of juvenile cohorts is related to increases in environmental temperature
3. Cohort growth rate is greater when spring and summer temperatures are higher
4. Survival is reduced at lower temperatures

In the laboratory, focussing on *Osilinus lineatus*:

5. Juvenile '0' cohort overwinter survival is higher at higher sea temperatures
6. The magnitude of the increase in survival at higher sea temperatures is greatest in the smallest, late settling size class of the '0' cohort.
7. Feeding activity is greater at warmer sea temperatures

5.2 Methods

5.2.1 Study Site

The recruitment dynamics of *O. lineatus* and *G. umbilicalis* were studied between October 2002 and October 2004 at Mothecombe, southern England (50.30° N, 3.95° W). Both *O. lineatus* and *G. umbilicalis* were abundant on this boulder shore.

5.2.2 Temperature

The Hadley Centre HadISST mean monthly sea surface temperatures for the grid square covering Mothecombe (50-51° N, 3-4° W) were extracted for the years 2001 - 2004. Sea and air temperatures were also recorded at 20 minute intervals on the shore during 2003 and 2004 using *in situ* temperature loggers (Ibutton®) to an accuracy of ±0.5°C. The loggers equilibrated rapidly (10 minutes) to surrounding temperatures, giving a reliable estimate of environmental temperature. Loggers were placed on the underside of boulders in the midshore region where juvenile *Osilinus lineatus* and *Gibbula umbilicalis* were most abundant. Both data sets were used to examine relationships with growth and recruitment, particularly whether there was evidence of thresholds for cessation and initiation of growth in juvenile (0+, 1+) trochids. Seasonal changes in abundance due to recruitment or mortality were also compared to seasonal temperature trends. Broadscale offshore sea surface temperatures were compared to temperatures experienced by the population under study, which were measured using *in situ* loggers.

5.2.3 Field surveys of recruitment dynamics

Fortnightly collections of '0', '1' and '2' class juveniles were made between MTL and MLWN. Five replicated counts of three minutes duration were made for both species, during which all individuals less than 16mm in diameter (determined from a size frequency distribution of the population) were collected. These collections involved intensive searches of boulders, cracks, crevices and gravel underlying boulders, where the density of juveniles was greatest. The use of timed counts removed the potentially confounding effects of spatial variation in recruitment due to the heterogeneous nature of the habitat (Gotelli 1987, Kendall 1987, Blanchard & Bourget 1999) and localised settlement during the planktonic larval phase (Keough & Downes 1982, Bryant & Hartnoll 1995). Quadrat based methods were impossible for such cryptic habitats. The basal diameter of every individual was measured to the nearest 0.1mm and all animals were returned to the shore.

5.2.4 Data analysis

Mean abundance, standard error, the modal size and size range of the '0' class were calculated. The data were plotted as size frequency histograms with 0.5mm size categories to allow analysis of the size, abundance and distribution of the newly recruited '0' class cohort for each sample date. The modal basal diameter of the '0' cohort was selected as a measure of cohort growth as this reflected the size class that contained the most observations from the '0' cohort distribution, and was used to track the growth of each year class throughout the study period. Size ranges of the '0', '1' and '2' year old cohorts were easily distinguishable in *O. lineatus* due to their separation on size frequency plots, and by counting the annual growth rings laid down each winter on the shell (Williamson & Kendall 1981). Accurate quantification of the '2' year cohort of *G. umbilicalis* was more difficult due to this class merging with the adult section of the size distribution, and therefore this cohort was excluded from the studies at the end of 2003 when it could no longer be separated from the adult size classes.

Mean abundance was calculated for each sample date. The abundance of '0' cohort juveniles was compared immediately prior to and after their first winter on the shore in 2002/3 and 2003/4 using a one-way ANOVA to investigate survival rates of recruits on the shore. For both *O. lineatus* and *G. umbilicalis,* summer growth rates (changes in size over time) of the 2002-2004 year cohorts were compared for using analysis of covariance to detect any inter-annual variation. The growth rates of the '0', '1' and '2' year classes were compared in 2003. Changes in mean monthly SST (using HadISST data) were correlated with the size of the '0' cohort in 2002 and 2003 incorporating a +2 to –2 month phase difference to see how juvenile growth covaried with environmental temperature.

5.2.5 Laboratory studies of winter juvenile survival

The effects of artificially controlled sea temperature on the survival of new recruits were experimentally determined for O. *lineatus* in the laboratory. A population size frequency distribution was determined for '0' cohort juveniles at Challaborough, S.W. England 5km from Mothecombe (50.29° N, 3.90° W) in January 2004 during the period of winter growth cessation (Figure 5.1). From this field collection the minimum (1.5-1.9mm), modal (3.5-3.9mm) and maximum (5.0-5.5mm) size classes were determined. Ten individuals from these three size classes were removed from the Challaborough population and placed in each of five replicate 10 litre tanks for each of three temperature treatments:

1. 4^0C (consistent with sea temperatures experienced during the winter of 1983, an extremely cold winter that occurred during the historical time-series of Kendall & Lewis (1986))
2. 9 ^{0}C (sea temperatures during the winter of 2003/2004 on the shore in S.W. England)
3. 13^0C (winter sea temperatures currently experienced by populations of O. *lineatus* close to its southern range edge in Portugal)

Tanks were maintained on a closed circulation system in a controlled-temperature room. Treatments were then held at the respective temperatures using AquaEl 100W aquarium heaters, and water temperatures monitored on an hourly basis within all tanks using Ibutton® temperature loggers. The irradiance regime was set to the winter cycle of 10 hours daylight for southern England. Food was supplied on flat rocks approximately 10 x 10 x 1cm that were changed for similar rocks freshly removed from the shore on a weekly basis. This ensured equal amounts were placed in each tank. The mortality of individuals in the three size classes was recorded in each tank at the start of the experiment on

28/01/04 and at the end on 14/04/05. Dead individuals were replaced by marked individuals that had been held at the treatment temperature in a separate tank to maintain constant density within the experimental tanks. The difference in juvenile survival between the three temperature treatments, and the variation in survival between the minimum, modal and maximum size classes at the end of the experiment was analysed using a 2-way ANOVA with replication, with temperature and size as fixed factors.

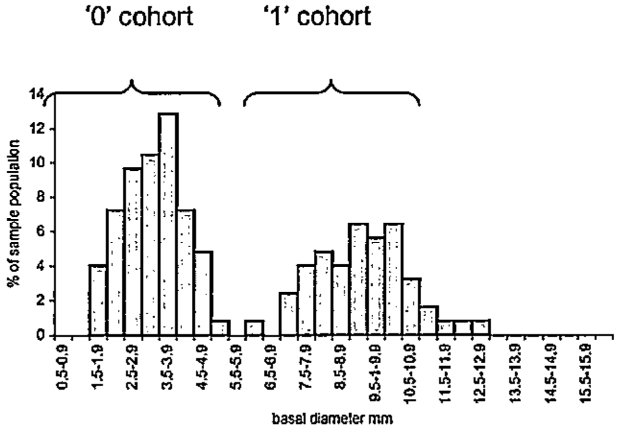


Figure 5.1. Juvenile size/frequency of '0' and '1' year cohorts of *O. lineatus* at Challaborough, 28/01/04.

The numbers of recruits actively grazing in each tank was recorded at the start of the experiment once animals had acclimated for 24 hours, again after 9 weeks and at the end of the experiment after 21 weeks.

5.3 Results

5.3.1 Temperature

Annual SST cycles from the Hadley Centre HadISST dataset for the grid square covering Mothecombe were similar between 2001 to 2004, but with some seasonal differences (Figure 5.2). Mild winter temperatures >10°C were recorded between January and March 2002 and January and February 2004, although SST decreased to ~9.5°C in March 2004. Colder, longer winters occurred in 2001 and 2003, when SST remained <10°C between January and April. The greatest seasonal variation was seen in 2003, with the warmest summer and coldest winter recorded over the four year period.

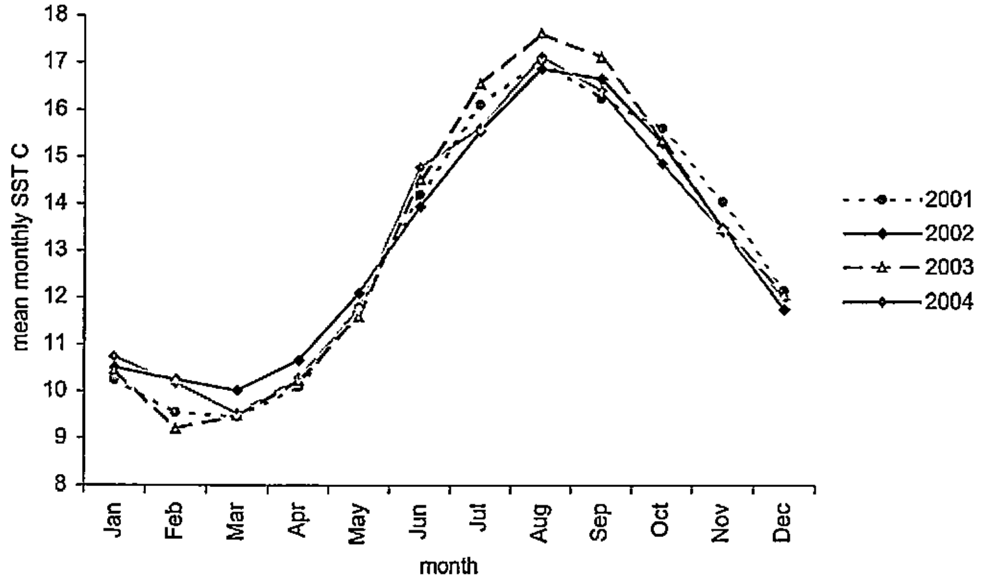


Figure 5.2. Monthly mean SST for the grid square 50-51°N, 3-4°W between 2001 and 2004.

Mean daily data for inshore sea and air temperatures obtained from Ibutton ® temperature loggers deployed in the intertidal zone at Mothecombe were plotted against the HadISST data for periods during 2003 and 2004 when changes in growth and abundance were recorded (Figures 5.3, 5.4, 5.5). SST values were consistently higher than inshore sea temperatures recorded by the loggers for every recorded month except October 2004, when inshore sea temperature was between 1.5 and 2°C warmer than the monthly SST record.

Analysis of the HadISST SST data showed that growth ceased for the winter when SST dropped below ~13°C in November 2002 & 2003. HadISST records were ~1°C higher than daily means and 1.5°C greater than the monthly mean in November 2003 (Figure 5.3). A rapid decrease in air temperature from~12 to ~8°C occurred around this time, and may have prompted juveniles to enter the winter dormant phase. Mean inshore SST remained around 12°C until the start of February 2003, when temperatures dropped to ~11°C.

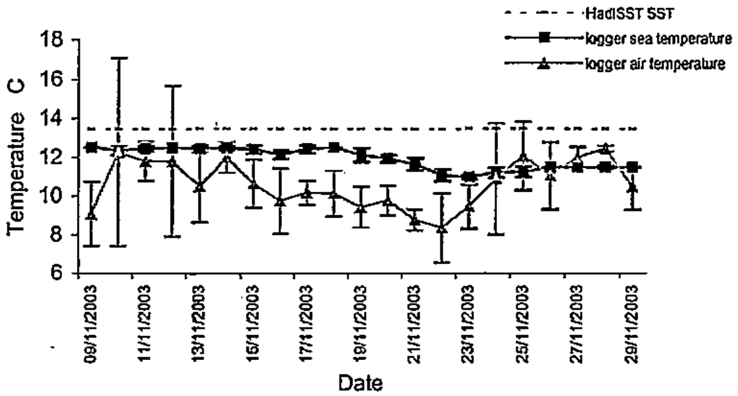


Figure 5.3. Environmental temperatures recorded by satellite and *in situ* loggers November 2003.

Recommencement of growth was observed during May 2004. Mean inshore SST had increased from 8.5 to 10.85°C in the 3 months prior to this, with satellite data following the same trend but approximately 1°C higher. A sharp increase in air temperature from 12-16°C was recorded on 09/03/04, before temperatures decreased to similar levels to inshore SST (Figure 5.4).

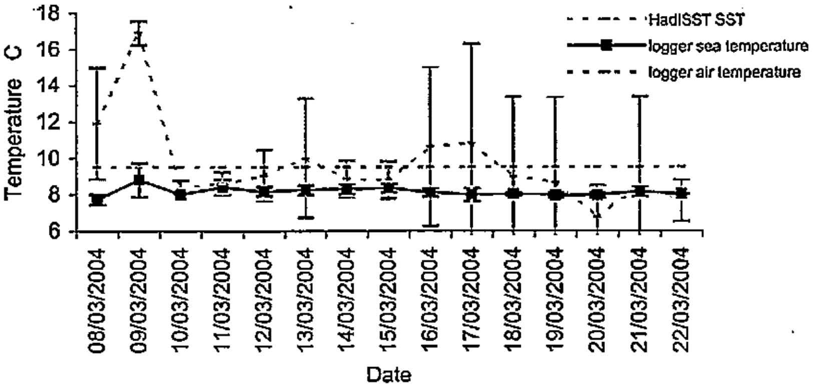


Figure 5.4. Environmental temperatures recorded by satellite and *in situ* loggers March 2004.

Sea temperatures recorded on the shore during the period of rapid growth of juveniles in August ranged between 14-15°C. The largest discrepancies between logger and satellite data were seen during this month, with inshore temperatures being ~3.4°C less than near-shore temperatures. Air temperatures remained between 2-4 °C higher than inshore SST throughout this month. In October 2004 when juveniles stopped growing for winter, logger temperatures were between 1-2°C greater than HadISST data (Figure 5.5). Inshore air and sea temperature was very similar during this month.

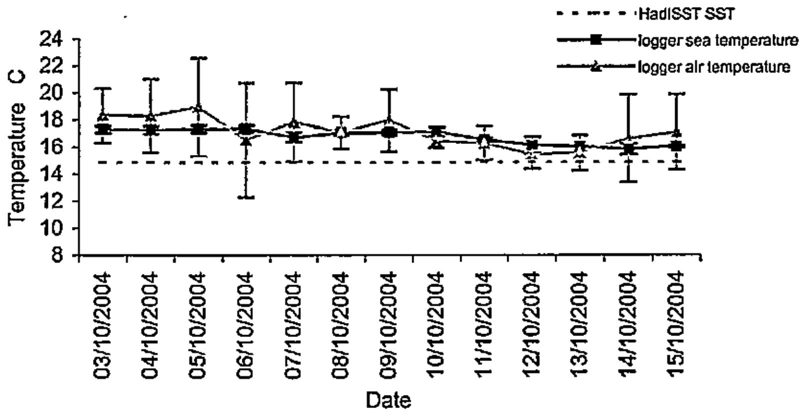


Figure 5.5. Environmental temperatures recorded by satellite and *in situ* loggers October 2004.

5.3.2 Abundance

A single annual recruitment event was observed between 2002 and 2004 in both *Osilinus lineatus* and *Gibbula umbilicalis*. New recruits of both species were first recorded on the shore between August and September, 3-4 months after spawning had occurred at the same and adjacent shores. Abundance increased through autumn as the modal size of the cohort increased to between 3.5mm for *O. lineatus* (Figure 5.6) and 4.0 mm for *G. umbilicalis* (Figure 5.7) due to a combination of later settling individuals from the 3 month spawning period and individuals being easier to detect as they increased in size. Growth ceased in the '0', '1' and '2' year old animals in November 2002 and 2003 for both species, coinciding with a decrease in mean monthly SST below 13°C. No further growth was recorded throughout the 2002/03 and 2003/04 winters.

5.3.2.1 *Osilinus lineatus*

In 2002 and 2003, densities of new recruited '0' cohorts were similar prior to the onset of winter (7-8 per minute searched) (Figure 5.6). The result of a one-way ANOVA on the 2002 cohort showed that abundance significantly decreased by almost 50% over the 2002/03 winter (Table 5.1). Abundances began to increase again in April 2003 and peaked at three times the abundances recorded at the end of winter. In contrast, densities of the 2003 cohort were only reduced by a quarter in over the 2003/04 winter, and this difference was not significant (Table 5.2). The spring increase in '0' cohort abundance began a month earlier in 2004, and continued until September, when the abundance (12 individuals per minute) had increased to double the amount recorded at the end of the 2003/04 winter (again not significant, Table 5.1). Densities of animals of 1+ years decreased throughout the year in 2003 and 2004.

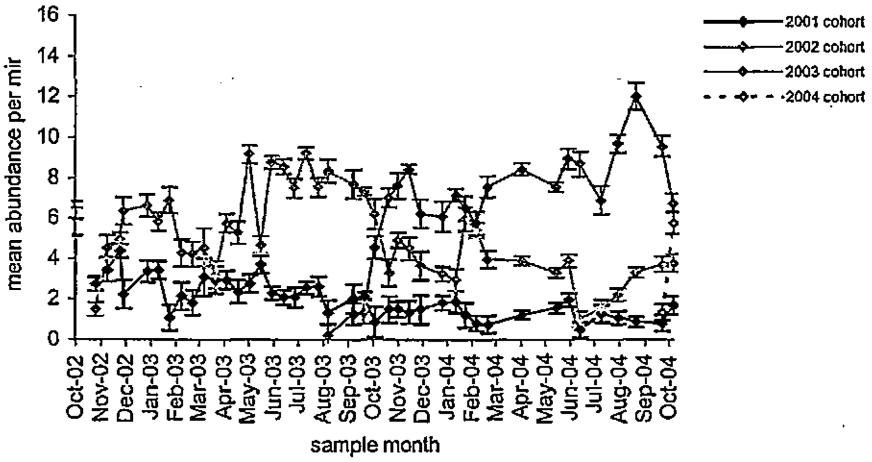


Figure 5.6. Abundance of 2002, 2003 and 2004 year cohorts of *O. lineatus*.

Table 5.1. one way ANOVA of '0' cohort *O. lineatus* abundances before and after winter 2003.

Effect	SS	df	MS	F	P
Date	220.9000	1	220.9000	8.2600	0.0207
Residual	214.0000	8	26.7500		
Total	434.0000	9			
SNK Pre winter 2002/03 > post winter 2002/03					

Table 5.2. one way ANOVA of '0' cohort *O. lineatus* abundances before and after winter 2004.

Effect	SS	df	MS	F	P
Date	78.40000	1	78.4000	1.15	0.3157
Residual	547.6000	8	68.4500		
Total	626.0000	9			
SNK Pre winter 2002/03 NS > post winter 2002/03					

5.3.2.2 *Gibbula umbilicalis*

The '0', '1' and '2' cohorts showed similar levels of abundance during their first year on the shore, and an increase to abundances of similar magnitude during the second year (Figure 5.7). The 2001 cohort suffered ~60% decrease in abundance during the winter of 2002/03, before abundances increased again by over 270% in the spring of 2003. Numbers decreased from 12 to 6 individuals found per minute between the end of April until the cohort size became too large to be included in the search methodology in October 2003. Low mean abundances of 2.5 individuals per minute were recorded for the 2002 cohort between October 2002 and February 2003, with no significant winter mortality recorded in either year (Table 5.2). A sudden increase in numbers to a mean abundance of 9 individuals per minute was recorded during the summer, before abundances dropped to a winter mean of 7 individuals per minute. Juveniles increased in abundance during the summer 2004 to levels similar to those recorded in summer 2003. The 2003 cohort increased in abundance from less than one individual per minute when was first recorded on the shore in August to four per minute in December. No significant winter mortality event was recorded in this cohort (Figure 5.7) and abundances continued to increase throughout 2004, reaching a peak of 15 animals per minute in August. Abundances were still at a similar level when sampling ceased in October 2004.

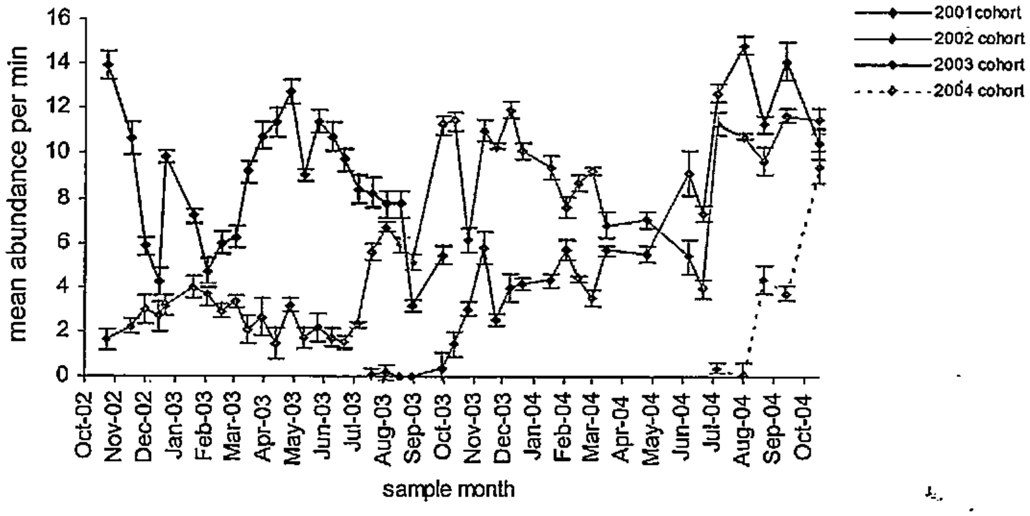


Figure 5.7. Abundance of 2002, 2003 and 2004 year cohorts of *G. umbilicalis*.

Table 5.3. one way ANOVA of G. *umbilicalis* '0' cohort abundances before and after winter 2003.

Effect	SS	df	MS	F	P
Date	16.9000	1	16.9000	0.4700	0.5126
Residual	288.0000	8	36.0000		
Total	304.9000	9			
SNK Pre winter 2002/03 ← post winter 2002/03 (← = NS direction of increase)					

Table 5.4. one way ANOVA of G. *umbilicalis* '0' cohort abundances before and after winter 2004.

Effect	SS	df	MS	F	P
Date	32.4000	1	32.4000	0.7000	0.4269
Residual	370.0000	8	46.2500		
Total	402.4000	9			
SNK Pre winter 2002/03 ← post winter 2002/03 (← = NS direction of increase)					

5.3.3 Growth

Newly settled '0' cohort juveniles of O. *lineatus* and G. *umbilicalis* were first visible on the shore at diameters of 0.5-3.0 mm during August 2003 and September 2004, three to four months after spawning began in adults from Challaborough and at the neighbouring shore of Mothecombe (see Chapter 4). Growth of the '0' cohorts was initially rapid after settlement, with a modal increase of 0.5mm (O. *lineatus*) and 1.5mm (G. *umbilicalis*) in 2003 and >1.0mm (O. *lineatus*) and > 3.0mm (G. *umbilicalis*) in 2004 before the onset of winter (Figures 5.8, 5.9). Growth ceased in all populations in November each year, when SST dropped below 13°C. By this time *Osilinus lineatus* had reached a modal size of 3.5mm (2002) and 3.5-4.0mm (2003) and G. *umbilicalis* were 3.5-4.0mm (2002) and 4.0-4.5mm (2003).

Juveniles did not increase in size again until the onset of spring, with rapid growth beginning in both species between March and May 2003 when SST exceeded 13°C (Figure 5.10). The period of winter growth cessation was shorter in 2003/04, with growth recommencing in February. The 2001 cohort of *O. lineatus* and *G. umbilicalis* were already 1 year old when the survey began in October 2002. Growth ceased over the 2002/03 winter and resumed in April 2003 in both populations, but was significantly less than that observed in the 2002 and 2003 cohorts in both their first and second spring after settlement (Table 5.5, 5.6).

An analysis of covariance carried out on the sizes of the '0', '1' and '2' cohorts of *O. lineatus* during the summer growth period of 2003 showed that all three slopes were significantly different from each other (Table 5.5, Figure 5.11), with the '0' year old cohort having the fastest growth rate, followed by the '2' class and then the '1' class, which was the slowest growing cohort. The same analysis of '0' and '1' cohorts of *G. umbilicalis* showed that there was no significant difference in growth rates (Table 5.6, Figure 5.12).

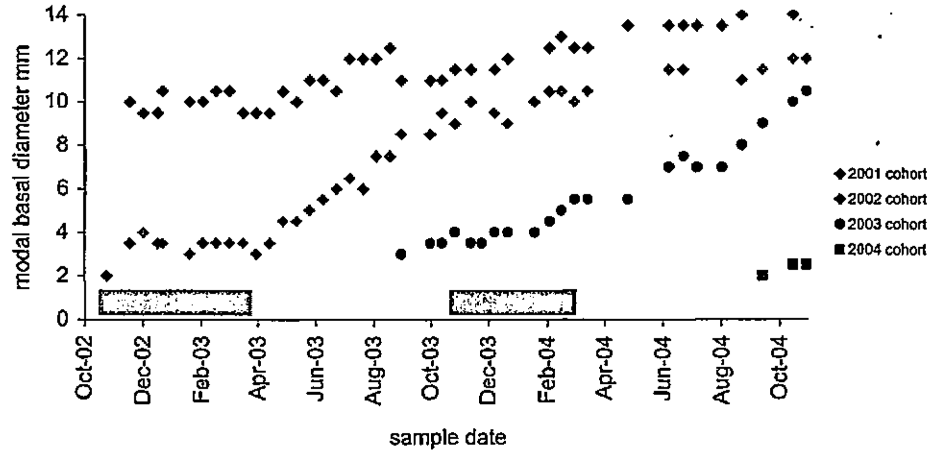


Figure 5.8. Growth of juvenile cohorts of *O. lineatus* between 2002 and 2004 periods where mean monthly SST (HadISST) dropped below 12°C (grey bars).

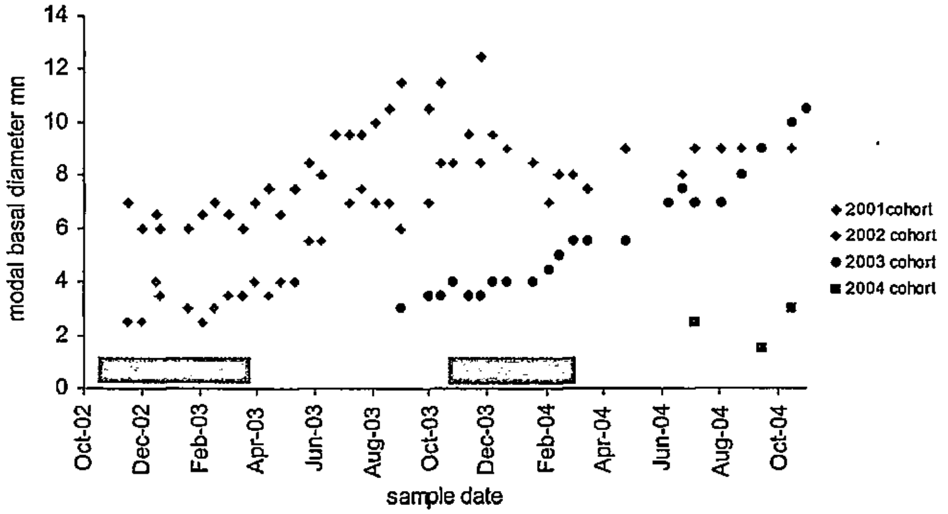


Figure 5.9. Growth of juvenile cohorts of *G. umbilicalis* between 2002 and 2004, periods where mean monthly SST (HadISST) dropped below 12°C bounded by grey lines.

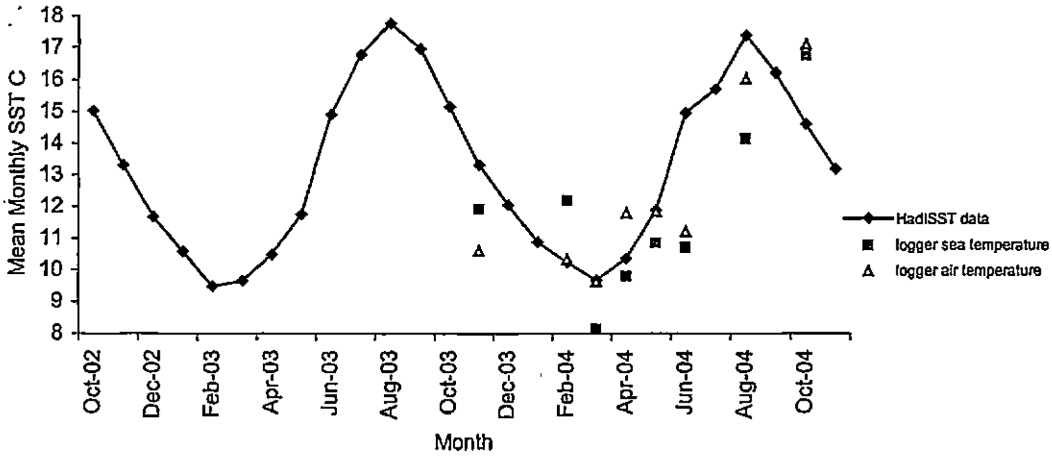


Figure 5.10. Mean monthly SST (HadISST) over the period of juvenile surveys 2002 – 2004.

Table 5.5. ANCOVA of *O. lineatus* juvenile cohort growth rates in 2003.

Effect	SS	df	MS	F	P
Intercept	9.4701	1	9.4701	24.8256	<0.0001
Cohort	6.2310	2	3.1155	8.1672	0.0036
Month	16.1389	1	16.1389	42.3077	<0.0001
Cohort* Month	5.2021	2	2.6011	6.8186	0.0072
Error	6.1034	16	0.3815		
SNK '0' cohort > '1' cohort > '2' cohort					

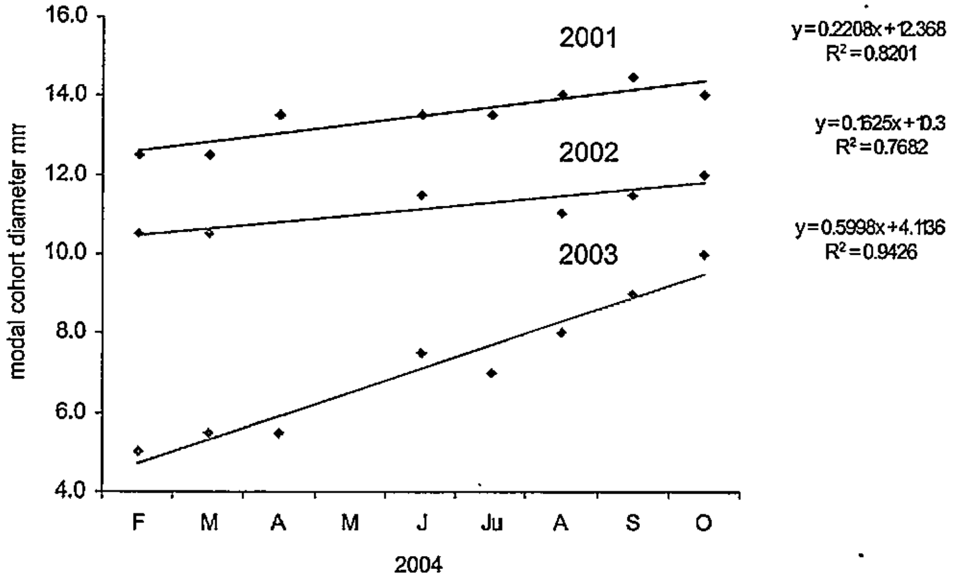


Figure 5.11. Modal growth rate of the '0', '1' and '2' cohort juvenile populations of *O. lineatus* in 2004

Table 5.6. ANCOVA of *G. umbilicalis* juvenile cohort growth rates in 2003.

Effect	SS	df	MS	F	P
Intercept	56.6168	1	54.6168	270.0267	<0.0001
Cohort	4.2219	1	4.2119	20.8239	0.0010
Month	1.5146	1	1.5146	7.4880	0.0210
Cohort * Month	0.0342	1	0.0342	0.1692	0.689
Error	2.0226	10	0.2023		

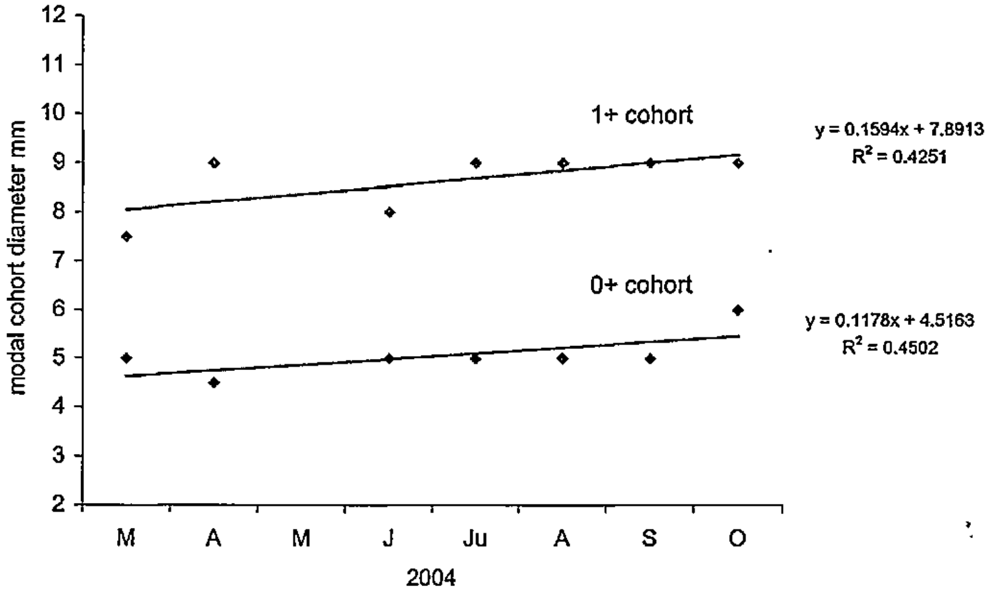


Figure 5.12. Modal growth rate of the '0' and '1' cohort juvenile populations of *G. umbilicalis* in 2003.

An ANCOVA carried out for the '0' cohorts showed that newly settled juveniles had significantly greater growth rates in 2002 compared to 2003 in both *O. lineatus* and *G. umbilicalis* (Tables 5.7, 5.8, Figures 5.13, 5.14).

Table 5.7. ANCOVA of *O. lineatus* juvenile '0' cohort growth rate.

Effect	SS	df	MS	F	P
Intercept	14.1958	1	14.1958	115.5087	<0.0001
Year	2.1077	1	2.1077	17.1497	0.0012
Month	59.1524	1	59.1524	481.3133	<0.0001
Year * Month	0.5751	1	0.5751	4.6797	0.0497
Error	1.5977	13	0.1229		

Table 5.8. ANCOVA of *G. umbilicalis* juvenile '0' cohort growth rates.

Effect	SS	df	MS	F	P
Intercept	15.6016	1	15.6016	94.1670	<0.0001
Year	3.0051	1	3.0051	18.1384	0.0011
Month	13.3601	1	13.3601	80.6407	<0.0001
Year * Month	6.0268	1	6.0268	36.3773	<0.0001
Error	1.9881	12	0.1657		

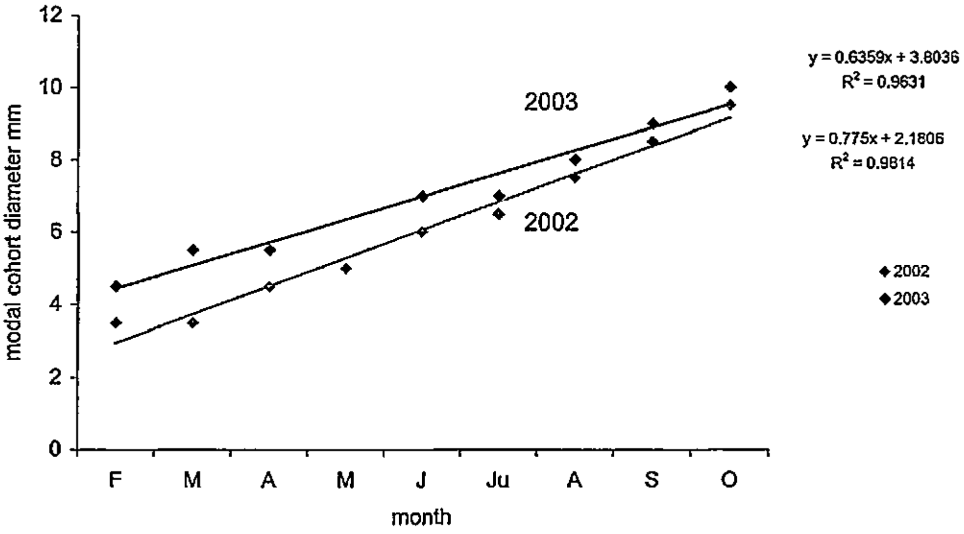


Figure 5.13. Comparisons of the modal growth rate of the '0' cohort juvenile populations of *O. lineatus* in 2002 and 2003.

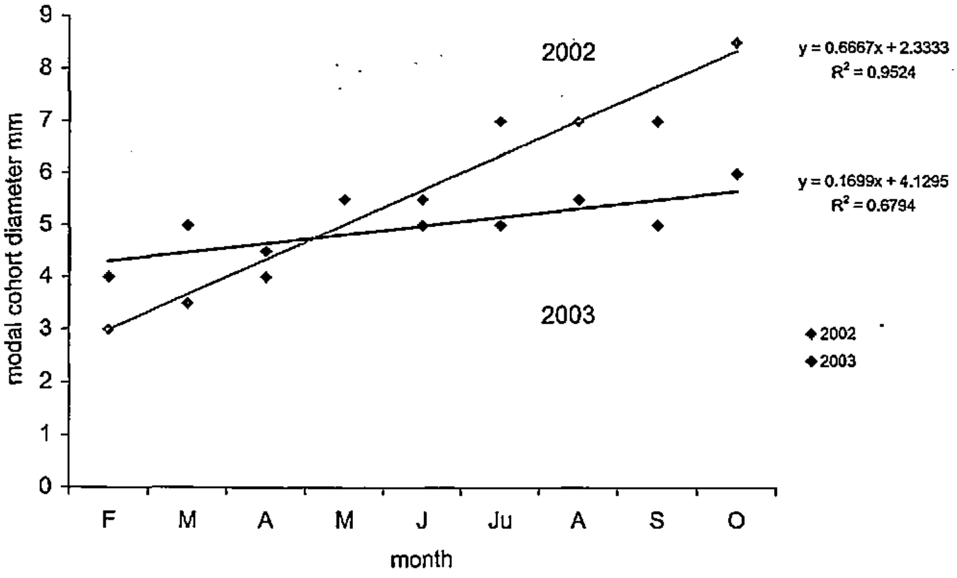


Figure 5.14. Comparisons of the modal growth rate of the '0' cohort juvenile populations of *G. umbilicalis* in 2002 and 2003.

Comparisons of monthly modal '0' cohort size with mean monthly SST derived from HadISST satellite data showed that growth covaried with sea temperature, with the highest correlation occurring with no time lag for both *O. lineatus* (2001 cohort; r= 0.45, p=0.003, 2002 cohort; r= 0.37, p=0.024) and *G. umbilicalis* (2001 cohort; r= 0.79, p<0.0001, 2002 cohort; r= 0.48, p=0.002).

5.3.4 Laboratory temperature experiments

Survival of juveniles was lowest in the 4°C treatment, with only 18 of the original 150 individuals still alive at the end of the experiment. Survival was significantly greater (P=0.001) in the ambient 9°C treatment, with 113 animals still alive on 14/04/05 (Table 5.9). The highest number of survivors occurred in the warmest 13°C treatment, with 134 individuals remaining alive at the end of the experiment (Figure 5.15). Survival in the 13°C treatment was significantly greater than both the ambient 9°C and 4°C treatments (Table 5.9).

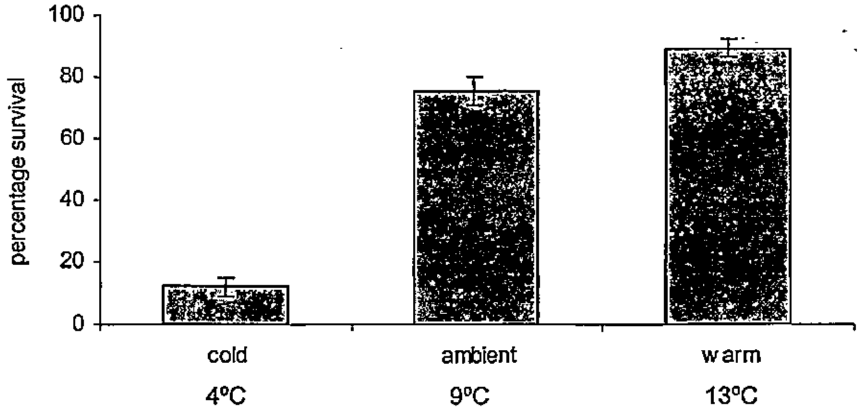


Figure 5.15. Survival of '0' cohort juveniles exposed to winter sea temperatures.

Table 5.9. ANOVA of '0' cohort juvenile overwinter survival, Cochran's test (C=0.5506, NS).

Source	SS	DF	MS	F	P	F versus
Temperature treatment	509.3778	2	254.6889	128.78	0.0001	Residual
Residual	83.0667	42	1.9778			
Total	592.4444	44				
SNK 13°C > 9°C > 4°C						

The difference in survival between minimum, modal and maximum size classes was not significant across the treatments (ANOVA F = 2.98, p = 0.0637, df = 44, n = 45), or within the cold treatment (ANOVA F = 0.95, p = 0.4124, df = 14, n = 15) but fewer small size class juveniles and larger class juveniles survived in comparison to modal sized individuals.

Grazing activity was recorded at week zero, week 9 and at the end of the experiment in week 12. In the cold 4°C treatment, all individuals remained static throughout the first 8 weeks. In week 9, 30% of surviving individuals were actively feeding on the rocks, and by the end of the experiment 100% of animals were feeding. Feeding activity was observed in animals in both the ambient 9°C and hot 13°C treatments throughout the experiment. Numbers of individuals feeding increased with time in the ambient 9°C treatment from

30% at the start to 65% at the end, whereas animals feeding in the hot 13°C tank started and finished at 40%, rising to 54% at week 9.

5.4 Discussion

Understanding the effect of short-term variations in environmental conditions is a new approach to developing better predictive models regarding the ecological effects to future climate change (Stachowicz et al. 2002). This chapter examined the role of winter temperatures in recruitment success, to inform the current climate change debate on the relationship between temperature and the success of populations and allow increased confidence in future predictions of the responses of species to future warming events.

Abundance of the '0' and '1' cohort juveniles decreased during the winter period each year. The most likely cause was mortality at low temperatures, but may also have been due in part to animals moving to more cryptic habitats to ameliorate the winter environmental regime and therefore they were not found during the collections. The change in habitat preference over winter, with spring re-emergence may have masked some of the effects of winter mortality by spring migration back into the areas where they were visible. The low winter mortality may explain the increases in abundance observed in *O. lineatus* and *G. umbilicalis* during the 2000s compared to the historical data collected in the 1970s and 1980s, when winter sea temperatures were ~0.5°C colder at northern range edges and further into the range in south west England. The results of the laboratory experiments supported this hypothesis, with much higher mortalities of up to 88% of the captive population of *O. lineatus* occurring at lower sea temperatures. Mortality of the '0' cohort was not instantaneous with the onset of winter conditions in either the field and the laboratory, but declined throughout the winter period of low sea and air temperatures between November 2002 and February 2003 and December 2003 and March 2004 in the field, and over 10 weeks in the laboratory, indicating that animals were not dying due to thermal shock as an acute response to the drop in temperature.

Animals were seen to cease feeding during the winter in the field in both species, as recorded in previous studies (Williams 1965, Desai 1966, Crothers 2001, Kendall pers comm.). In the laboratory *O. lineatus* was inactive at low winter temperature treatment of 4°C, in contrast to animals held at 9°C, where ~50% of individuals were active. The highest numbers of active animals were recorded in tanks held at 13°C. Individuals in the cold 4°C treatment therefore had to survive on metabolic reserves accumulated prior to the onset of winter. After 6 weeks exposed to 4°C in the laboratory, surviving animals were seen to start actively feeding in all replicate tanks. These combined observations in conjunction with data from echinoderms (Chen & Chen 1993, Roller & Stickle 1993), fish (Duellet 1997, Myers 1998, Planque & Fredou 1999) and seabirds (Thompson & Ollason 2001) lend support to the hypothesis that sea temperatures influence the survival of new recruits during the first winter due to complete utilisation of metabolic reserves leading to starvation and ultimately death. The feeding activity observed throughout the winter in the 13°C laboratory tanks may be the result of sea temperatures not decreasing below the apparent threshold at which feeding and growth stopped on the shore at Mothecombe. Growth cessation also occurred in all cohorts during this winter period, which supports the idea of recruits metabolising most of their energy reserves to ensure survival, at the expense of less essential processes (i.e. growth). A period of winter cessation was also recorded in juvenile and adult *O. lineatus* on British shores by Williams (1965), Desai (1966), Garwood & Kendall (1985) and Crothers (2001).

Abundances increased once SST increased above 12°C and recruits began to grow again in spring. Numbers of '0' cohort juveniles rose throughout the summer before decreasing again during the following winter. This pattern of increase after the winter suggests that not all juveniles within the population had been accounted for in pre-winter searches. Mortalities of '0' cohort individuals will have increased the number of empty areas of suitable habitat for new recruits on the shore, and the surviving recruits are likely to have emerged from their cryptic winter habitats and spread into nearby vacant areas to reduce local intraspecific competition for food resources.

Modal size of recruits showed significantly high correlations with SST in 2002 and 2003, but the growth rates were cohort-specific, with fastest growth occurring in the '0' cohort. As animals do not reach maturity until 2 years of age, all available energy in the youngest animals is channelled into somatic growth rather than a proportion being diverted for reproduction (Crothers 2001). The 2002 cohort may have overwintered with a smaller modal body size than the 2003 cohort due to slower warming of sea temperatures in spring and colder summer temperatures causing later spawning and therefore settlement, combined with colder temperatures during the winter of 2002/03. The warmer early summer temperature in 2003 may explain the faster growth rate of the surviving 2002 cohort compared to 2004, when the 2003 cohort experienced summer temperatures ~1°C cooler.

Cohort differences are most commonly caused by climatic variation during early development (Post et al. 1997, Lindstrom 1999). Although no difference in the annual SST regime of the satellite data was detected, large scale data can obscure short-scale temperature deviations of importance (Bhaud et al 1995) as seen in the logger data, and this may have been the case here. The faster growth rates of juveniles exposed to higher SST was likely to have contributed to increased overwinter survival due to greater accumulation of metabolic reserves before the onset of winter (thus reducing the starvation risk) and reduction of predation risk by small crabs due to individuals reaching a greater basal diameter. It is interesting that recruits of both *O. lineatus* and *G. umbilicalis* ceased growing and abundances began to decline during the same sample period in November prior to the winters of 2002/03 and 2003/04, and increases in body size and abundance were first detected during the same spring sample occasion.

Temperature may also exert indirect effects on population dynamics via changes in water stratification, nutrient cycling, light intensity and primary production (Chelton et al. 1982, McGowan et al. 1998, Rothschild 1994). Food availability has been shown to be a primary factor determining the timing of recruitment in some marine taxa (Hawkins & Hartnoll 1982, Brockington & Clarke 2001, Barradas-Ortiz et al. 2003) but temperature effects can also exist independently of food-related control on recruitment (Bowman 1985, Planque & Fredou 1999). Food availablilty was not manipulated in these field studies but was controlled for in the laboratory experiments, therefore increasing the confidence with which observed survival rates can be related to the direct effects of sea temperature.

5.4.1 The relationship between climate change, recruitment and geographic distribution

The ability to demonstrate the relationship between environmental temperature and recruitment success suggests that the effects of large-scale climate anomalies may be predictable. Since the mid 1980s, British coastal seas have increased in temperature by 0.6 – 1°C (Hulme et al. 2002), due predominantly to the increase in winter temperatures (Mieszkowska et al. 2005). Earlier spawning has been demonstrated in populations of *O. lineatus* close to northern range edges in the warmer 2000s (Chapter 4), leading to earlier settlement of new recruits on the shore and faster initial growth of new recruits prior to winter. In addition, warmer summer temperatures and shorter, milder winters combine to increase recruitment survival to levels similar to those recorded in populations closer to the centre of the range. As the climate continues to warm, population dynamics of northern populations are thus predicted to increasingly resemble more southern populations, and further extensions of the northern distributional limits are likely to occur. The results of this chapter indicate that such range shifts are likely to be driven by the regulation of species distributions from the individual and population levels. Northern range limits of southern, warm water species are therefore likely to continue to extend as the climate warms. Greater numbers of individuals dispersed to shores with suitable habitat, combined with an increase in the numbers successfully surviving to maturity will facilitate the establishment and maintenance of populations beyond existing limits.

Local and regional scale variation in recruitment by marine organisms can reflect large-scale environmental forcing of early juvenile mortality (Hughes et al. 2002). Temperature sensitivity of new recruits has been suggested as a mechanism for the latitudinal gradient in recruitment success and the inability to recruit successfully at northern limits (Lewis 1964, Lewis et al. 1982, Bowman 1985, Kendall 1987,). Juvenile recruits at the northern edge of the range of *Osilinus lineatus* and *Gibbula umbilicalis* are exposed to lower environmental temperatures for longer periods than recruits in populations further south and the results of this Chapter and Chapters 2 & 3 suggest that high juvenile mortality at lower temperatures is the most likely mechanism setting the northern limits of distribution in these species. Survival of recruits increases away from limits due to a combination of faster growth before winter, reducing the risk of mortality from starvation and predation and individuals being exposed to less severe winter temperatures over a shorter period. This probably leads to higher abundances of '2' class animals that become sexually mature and enter the adult breeding population. My work demonstrates that environmental temperature is strongly linked to the observed increase in success of populations near to northern limits.

Chapter 6. Overview and General Discussion

Part of this chapter has been submitted to Marine Pollution Bulletin as a contribution to a manuscript by Hardman-Mountford et al.: see Appendix 3.

6.1 Scope

This final chapter discusses the limitations of long-term studies based on historical data including my own resurveys. The main findings of the thesis are then summarised and the implications of these findings for future climate change research discussed. This concluding I emphasise the use of multidisciplinary studies in determining the links between climate and the biogeographic distribution of species, and the importance of investigating the effects of climate at the local and regional scale to in order to predict the global changes in response to future warming.

6.2 Problems of undertaking long-term studies

The temporal coverage of the quantitative data available extends from 1977 to 1986 (Kendall & Lewis 1986, Kendall 1987). The data collected formed a significant part of the original research programme of the NERC Coastal Surveillance Unit at Robin Hood's Bay, Leeds University (Bowman & Lewis 1977, Garwood & Olive 1982, Kendall et al. 1982, Lewis et al. 1982, Olive & Garwood 1983, Garwood & Kendall 1985, Kendall 1985, Lewis et al. 1986) which was unfortunately terminated in the mid-1980s, just as the physical effects of rapid climate change began to manifest themselves (Houghton et al. 2001, Hughes et al. 2002). There are also semi-quantitative mapping studies made by Crisp & Southward around Britain, predominantly in the 1950s (Crisp & Southward 1958), and detailed mapping of the distribution of *Osilinus lineatus* in Dorset by Hawthorne in the 1960s (Hawthorne 1965). Although it is now recognised that long-term, continuous data series are of paramount importance in climatic research, datasets such as these and many other series around Britain were not considered to be the most effective use of scientific resources and were discontinued in the 1980s.

The spatial coverage of the quantitative data encompassing Britain and northern France was sufficient for the original aim of the surveys to quantify spatial and temporal variation in the context of pollution-related monitoring of British rocky coasts (Lewis 1976, Lewis et al. 1982), and was placed in a broader context through the COST 647 Project (Keegan, 1986; Lewis, 1997). My study was therefore limited to the northern third of the range of both *Osilinus lineatus* and *Gibbula umbilicalis*, and did not allow the dynamics of the southern range edges to be compared. Few studies have examined the southern limits of species, and those that have are limited to a few years of data with occasional 'baseline' data for comparison (Fischer-Piette 1935, Fischer-Piette & Gaillard 1959, Fischer-Piette & Prenant 1965, Rivadeneira & Fernandez 2005).

The original surveys were not designed to take climate change into account, and the methodologies are therefore not ideal for the detection of broadscale, decadal change. In the 1970s, statistical data analysis was not as inherent in experimental design as it is today, and the methodologies were not as rigorously designed as a result. The historical datasets used in this thesis are often based on collections of individuals with no standardisation of area searched, duration of searches or number of individuals collected. Replication of searches was not introduced until the final two years of study in 1985 and 1986. Visits were not always made in the same season each year, and sites were frequently missed out during annual survey trips due to time constraints (Kendall pers comm.). As a result, the data needed to be standardised prior to statistical analysis using parametric techniques. Some of the data could not be analysed using analysis of variance methods, due to the collection techniques or the loss of the raw data when the Robin Hood's Bay laboratory was closed down. Alternative tests for significance had to be used to compare subsets of the original data, reducing their analytical power.

It must be recognised, however, that long-term ecological data sets are rare and those with good spatial coverage rarer still, and we must accept and utilise as best we can such incomplete datasets in our attempt to understand the effects that climate change is exerting on marine ecosystems. They are extremely valuable as they allow the direction, magnitude, periodicity and concordance of the effects of climate change to be quantified, and facilitate the separation of small-scale fluctuations (noise) from the bigger effect (signal). The Robin Hood's Bay Laboratory datasets were collected in a cool period immediately prior to the onset of the current warming event, and thus provide an idea of the northern range boundaries and population structures before the British climate began to rapidly increase in temperature. The existence of multiple years of abundance data for the 1970s, 1980s and 2000s also allows the comparison of inter-annual versus decadal variation. It is fortunate that the researchers responsible for the collection of the population data (M.A. Kendall, P. Williamson) and the distributional data (A.J. Southward, S.J. Hawkins) are still actively engaged in research and were available to train and cross-calibrate me in the original methodologies and discuss the findings of my thesis.

6.3 Approaches used in this thesis

The methodologies applied to the resurveys were constrained by the original protocols to allow comparisons between decades. Rreplicated, timed searches were employed for all surveys conducted in this thesis. This has allowed improved statistical analysis to be carried out on the current data, and will facilitate both univariate and multivariate comparisons with any future surveys. Re-surveys were constrained to the same seasons as the original surveys to prevent seasonal variation from influencing the results. Sample sites located across 4 degrees of latitude south from the northern range edge of *O. lineatus* were considered to be sufficient to detect latitudinal variation in the timing and duration of the reproductive cycle. No such changes were observed, and although this may have been due to the absence of a latitudinal gradient in reproduction, a recommendation for a greater latitudinal coverage is made here, and has been incorporated into ongoing studies for *G. umbilicalis.*

Early larval stages evidently play an important role in the population dynamics of many marine invertebrates, as seen in the increasing body of new research from 'supply side' ecologists (Underwood & Fairweather 1989, Minchinton & Scheibling 1991, Hughes et al. 2000, Jenkins et al. 2000, Svennson et al. 2004). The tracking of trochid larvae after external fertilisation of the gametes was not attempted in this thesis due to the labour-intensive nature of such a study and the problems anticipated from previous total failures of any researcher to sample and identify trochid larvae in the coastal waters of Britain (Lebour 1937, Underwood 1972b, Crothers 2001, Kendall & Williamson pers comm.).

The confidence with which the observed changes in recruitment success are due to changes in environmental temperature seen in Chapter 5 and other recruitment studies (Paine 1986, Ebert et al. 1994, Davies 1998) are limited by the short temporal and spatial extent of these studies due to the labour-intensive nature of such research. As a result, the spatial heterogeneity at the local or regional scale may mask the effects of larger scale processes such as climate change. Ideally, testing the effects of environmental factors on key processes of the life cycle requires intensive sampling on multiple shores within a region, replicated over multiple geographical regions, but this was beyond the scope of this thesis. I decided that an intensive study of the population dynamics at a single shore, incorporating high temporal resolution was preferable to a broad-brush approach on a seasonal basis across a wider section of the geographical ranges of *O. lineatus* and *G. umbilicalis*. This work has begun to address the requirement for increased understanding of the effects of variation in temperature on rates of supply, settlement and survival of juveniles in intertidal populations (Connell 1985, Menge 1991, Petraitis 1991, Swearer et al. 2002). Now that links between temperature, recruitment, population abundance and range extensions have been indicated both in the field and in the laboratory, future work combining more intensive field studies over a latitudinal gradient with laboratory studies are justified. Such work is necessary in order for accurate predictions of future changes in the geographic distribution of species in response to climate change to be made.

6.4 Main findings

6.4.1 Patterns

Range limits are ultimately set by environmental temperature for the lusitanian trochid gastropod species *Osilinus lineatus* and *Gibbula umbilicalis.* In the British Isles, the northern and eastern boundaries of both *O. lineatus* and *G. umbilicalis* remained static throughout the late 1970s and early 1980s (Kendall & Lewis 1986, Kendall 1987, Williamson, Kendall & Lewis unpublished data). Between the last surveys in 1985/86 and 2002 the ranges of both species have extended northwards and eastwards along the British coastlines in response to environmental warming of ~ 0.5 to 1°C.

The northern range edge of *O. lineatus* in north Wales did not show much recovery from the retraction caused by the extreme cold winter of 1962/63 (Crisp 1964) until the 1980s (Hawkins, unpublished data). In the intervening two decades the range has re-extended by ~100km around the coastline and multi-age, breeding populations have become established within 15km of the previous limits. The eastern range edge in Britain extended by 55km between 1986 and 2002, and breeding populations are now present east of Portland Bill for the first time on record (Hawthorne 1965, Kendall 1987, Hawthorne & Wiffen in review). The realised geographical distribution can lie inside the potential distribution where additional physical factors prevent further expansion of the range. Hydrographic barriers appear to have previously restricted the northern range edge of *O. lineatus* in north Wales and the eastern edge to the western English Channel. Low numbers of larvae from small populations close to these boundaries were insufficient to breach these barriers created by offshore currents. Since the climate has warmed, populations have increased in abundance and therefore total fecundity. Increased numbers of larvae have apparently breached these porous barriers to settle in sufficient numbers to establish populations beyond previous limits. The north east and north west range edges in N. Ireland have both extended by 10km (Chapter 2, Simkanin, pers comm.) since the original broadscale surveys were conducted in the 1950s (Southward & Crisp 1954). The rate of change cannot be determined as no surveys were conducted in the second half of the 1900s, but this is much slower than the range changes observed on mainland Britain, despite similar changes in the rate and extent of environmental warming (Hughes et al. 2002).

The northern range limits of G. *umbilialis* on the north coast of Scotland extended by 85km from Skerray to Fresgoe between 1985 and 2002. The eastern range limit had not been found to extend past the Isle of Wight between 1985 and 2002, although subsequent searches further east along the channel have shown that G. *umbilicalis* has used artificial structures to colonise new areas where it had not been previously recorded due to lack of rocky habitat (Herbert pers comm., Hawkins & Moschella, pers comm.). These artificial stepping stones have also allowed animals to populate isolated areas of suitable natural rocky habitat in the eastern basin of the English Channel (Hawkins & Moschella, pers comm.). Abundances have synchronously increased in all populations studied in the North East Atlantic, Irish Sea and English Channel since 1985, indicating that a large-scale driver has been responsible for these changes.

Suitable natural habitat exists along the entire coastline of north Scotland and for a short distance (<50km) beyond the current eastern limits of both species in the English Channel. Artificial coastal defences have also been constructed in the eastern basin of the English Channel. The Northern Ireland coastline is predominantly rocky shore and populations of G. *umbilicalis* are already established in this area. Future range expansions with continued climate warming are therefore likely to occur in Northern Ireland and south England as areas of suitable habitat (natural or artificial) become climatically suitable for successful recruitment and subsequent establishment of new populations.

The rates of change of these northern and eastern boundary shifts (potentially up to 50km and 35km per decade for O. *lineatus* and 50km per decade for G. *umbilicalis*) are greater than the average polewards shift of global species distributions of 6.1km per decade (Root et al. 2003, Parmesan & Yohe 2003). These conclusions, in combination with the findings of the Continuous Plankton Recorder surveys (Beaugrand et al. 2002, Beaugrand & Reid 2003, Beaugrand & Ibanez 2004) indicate that range shifts are occurring faster in the marine environment than for terrestrial species. This likely to be due to a combination of factors including; greater connectivity within the marine system (Thorson 1950, Menge 2000), less habitat fragmentation and fewer land-use changes (Pearson & Dawson 2003), coupled with the shorter life-span of many marine species, the predominance in many benthic species of sessile adults that are unable to move away from unsuitable conditions (Newell 1979), and pelagic larval stages with high dispersal potential (Roughgarden et al. 1985, Gaines & Bertness 1992) .

There is a general pattern evident across a wide range of marine and terrestrial taxa of highest population densities occurring at the centre of distribution of a species, with abundances decreasing towards the range edges (Brown 1984). A positive relationship between abundance and geographic distribution has been identified for many coastal marine species, however, the spatial and temporal coverage of past data has often made it difficult to resolve whether increases or decreases in species abundance represent actual changes in biogeography, or merely fluctuating population dynamics within a species range (Barry et al. 1995, Sagarin et al. 1999, Veit et al. 1997, Murray et al. 2001, Lohnhart & Tupen 2001, Parmesan et al 2005). This thesis has demonstrated that positive relationships do exist between abundance and distance from the northern range edge for both *O. lineatus* and *G. umbilicalis,* (Figures 6.1, 6.2), and increases in abundance within the range are indicative of changes in the biogeographic ranges.

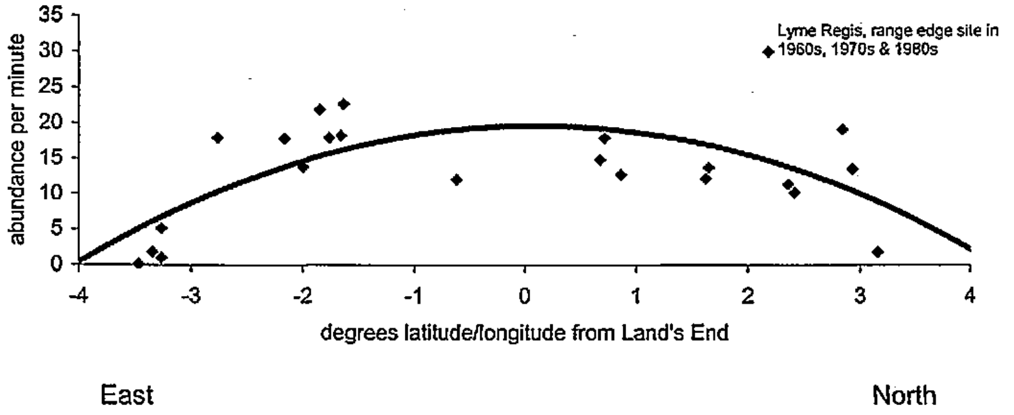


Figure 6.1. Abundance of *Osilinus lineatus* per minute search plotted against distance from Land's End. Site coverage extends from the northern range edge in north Wales to the eastern range edge in south England.

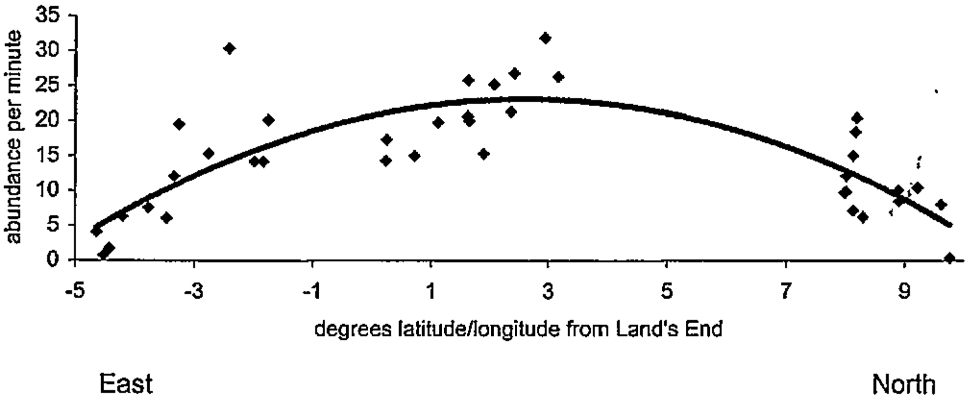


Figure 6.2. Abundance of *Gibbula umbilicalis* per minute search plotted against distance from Land's End. Site coverage extends from the northern range edge in north Scotland to the eastern range edge in south England.

Increases in abundance were concordant across all 16 quantitative survey sites for *O. lineatus* and *G. umbilicalis* in Britain during the years for which data exist, showing that a large-scale driver was responsible, acting through recruitment. Higher densities of individuals were found at every location during the resurveys compared to the original surveys, with increases of as much as 600% at some sites by 2002. Interannual fluctuations in abundance were very small compared to the change between the 1980s and 2000s, increasing the confidence that observations of the decadal-scale change were real and not the result of anomalous years in 1985 and 1986. New populations of *O. lineatus* and *G. umbilicalis* that had become established since the previous surveys in Scotland, Wales and England also showed evidence of recruitment in recent years and increasing abundances between 2002 and 2004. These characteristics indicate that the populations were reasonably stable and had regular input of juveniles either from nearby populations or from self-recruitment.

Mean cohort body size did not change in any year class of *O. lineatus* between 1986 and 2002. Upon inspection of the data it was clear that density-dependent effects of intraspecific competition may have been acting on body size at low densities recorded in 1986, but population densities had exceeded the point at which abundance exerted a significant effect on body size by 2002 and the relationship broke down. This was not detected by analysis using the 90th percentile and maximum values for size in the sampled populations, which showed an apparent decrease in size as the result of significantly higher numbers of new recruits in the 2000s compared to the mid 1980s.

Bergmann's rule states that body size is a function of temperature, with animals at higher, colder latitudes displaying slower growth rates and attaining larger maximum sizes compared to individuals at lower latitudes (Bergmann 1847, Mayr 1970, McNab 1971, Gaston & Loder 1999, Ashton et al. 2000, Ashton 2001, Chown & Klok 2003, Meri & Dayan 2003). This general ecological principle of adaptation to ambient temperature applies to both endotherms and some ectotherms (Connell 1961, Kondoh 1977, Cushman et al. 1993, Chown & Klok 2003) (but see Van Voorhies 1996, Mousseau 1997, Blackburn et al 1999a). Bergmann's rule has already been demonstrated in the response of species to global warming, with declines in body mass and size occurring in passerine birds (Yom-Tov 2001, Yom-Tov et al. 2002). However, it did not appear to apply to *O. lineatus* or *G. umbilicalis*. Local factors including food supply, predation and competitive interactions may have been imposing constraints on the size of animals within a population, masking the effects of low temperature on growth (Vermeij 1978). Changes in temperature may also have induced individuals to allocate increased amounts of energy into the production of reproductive tissue at the expense of somatic growth, altering the relationship between temperature and body size.

Increased population abundances were predicted to result in a decrease in age of the population due to a greater influx of new recruits. Analysis of the maximum and 90th percentile age of the populations showed a decrease in both values, but inspection of the population structures showed that at seven out of the 12 sites for which data exists, the number of age classes had in fact increased, with animals surviving to older ages in the 2000s (Chapter 2). Recruitment strength had increased as predicted, but the effects of repeated strong year classes over the past decade have resulted in more animals surviving into adulthood. The use of the maximum and 90th percentile measurements were thus deemed unsuitable for detecting changes in age structures, as incorrect conclusions on the effects of density on ages within populations may be drawn.

6.4.2 Processes

The effects of temperature acting on physiological mechanisms can be seen on a local scale at the population level, and such changes have been shown contribute to regional-scale variation in species distributions and range limits. The main processes by which population success at locations close to the northern and eastern range edges has increased are the reproductive output of adults and greater and more frequent recruitment of juveniles.

6.4.2.1 *Reproductive Output*

Warmer spring temperatures in recent years have resulted in earlier onset of gametogenesis, and spawning events are now occurring 2 months earlier in spring in comparison with the summer spawning event observed in cooler years of the late 1960s and early 1980s (Underwood 1972b, Garwood & Kendall 1985). This early release of gametes results in veligers settling on the shore earlier in the summer (Garwood & Kendall 1985, Kendall pers comm., Chapter 4). Microbial film levels are not at their peak on the shore until late autumn (Thompson et al. 2005), so the spawning strategy does not appear to be one of match/mismatch to food resources in either warm or cool decades. It is more likely that early arrival on the shore allows new recruits to feed for longer, thus accumulating more metabolic reserves and increasing their body size prior to exposure to extreme cold temperatures once the temperature drops below a threshold (12°C in south England) in the winter and feeding stops.

No gradient in timing or duration of the reproductive cycle was evident in the study conducted in 2003 and 2004 with *Osilinus lineatus* from populations spanning 4° latitude in Britain and northern France. This was in contrast to the short, midsummer period of gonad development in a northern population and protracted period of gonad development in a southern population recorded in the early 1980s and may have been due to the latitudinal extent of the study being insufficient to detect the presence of a latitudinal cline. The samples from Porto, northern Portugal showed spawning beginning a month earlier than in France and Britain, but no firm conclusions can be drawn due to the sample period covering only 3 months of 2004. Alternatively, there may not be a gradient in the periodicity of reproduction for *O. lineatus*, or the cue for re-maturation of the gonads may not have been present in northern populations.

6.4.2.2 *Juvenile survival and recruitment*

The juvenile stage of the lifecycle of invertebrates is often the most sensitive to environmental stress including extreme temperatures (Newell 1979, Lewis et al 1982, Lewis 1986, Bauer 1992). From 1977 - 1985 and 2002 – 2004, *G. umbilicalis* showed a significant positive correlation between recruitment strength and winter sea surface temperatures at sites from the northern limits across the entire coastline of northern Scotland. Greater numbers of '0' class recruits have survived each year since warmer temperatures have occurred further east and seasonal sea surface isotherms have shifted north-east along the northern Scottish coastline. This has resulted in the exposure of populations to mean winter sea temperature regimes up to 1°C higher in the 2000s than during the 1970s and 1980s. Sharp latitudinal variation in recruitment was evident in *Osilinus lineatus* and *Gibbula umbilicalis* during the 1970s and 1980s. Recruitment failure of *G. umbilicalis* occurred in most years at sites close to northern limits in Scotland, but occurred less frequently at sites further south in the range in England. Missing year classes were also evident in populations of *O. lineatus* surveyed close to northern and eastern limits in the early 1980s, in contrast to populations away from the range edges in northern France.

The frequency of annual recruitment success has also increased in both species, with no observed failures during the 2000s at any survey site. The increase in recruitment success observed during warmer winters of the 2000s from the northern range edges across almost a third of the range of both species suggests that the effects of large scale warming of the climate are essentially predictable. Future increases in temperature are likely to cause further extension of the northern and eastern limits of *O. lineatus* and *G. umbilicalis* via increases in the frequency of annual recruitment success and increases in the numbers of individual recruits surviving each year. Should the thermohaline circulation slow down or stop, as is predicted by some GCMs (Wood et al 1999, Cubasch et al. 2001, Vellinga & Wood 200, Clark et al. 2002), the resultant cooling in sea temperatures would probably result in cut-backs to the northern and eastern limits, and cause synchronous reductions in abundances from the range edges to sites further south into the range in Britain and northern France.

The greatest change in environmental temperature that has been recorded in British coastal waters since the mid-1980s is the rise in mean winter SST (Sheppard 2004). The seasonal increase has been significantly greater than summer warming, and has resulted in winters becoming milder and low temperatures occurring for a shorter period of time in recent years (Mieszkowska et al. 2005). There is a degree of inherent autocorrelation between winter and summer seasonal thermal regimes in adjacent years, and weaker relationships between mean summer temperatures and population-level responses were also evident in my data. The conclusions from the field and laboratory data support the idea that the extensions of range and increases in population abundances seen from northern and eastern range limits of both *O. lineatus* and *G. umbilicalis* are driven by seasonal warming of environmental temperatures acting independently on the reproductive and recruitment life stages. The processes are summarised in the conceptual model below (Figure 6.3).

Increased spring temperatures promote earlier onset of gametogenesis, and ripe gametes are spawned earlier in the year as a result. New recruits settle on the shore at the start of summer in warm years, resulting in recruits being able to feed and grow for longer periods before the onset of winter. The reduction in the severity and duration of winter also assists the survival of new recruits on the shore, compounding the effects of earlier settlement and greater time for energy accumulation induced by the effect of warmer spring temperatures on the reproductive cycle of the adults. New recruits ceased growth with the onset of winter. Recruits in the modal size class of the '0' cohort show increased survival at cold winter temperatures compared to the smallest recruits, although this difference was not significant (Chapter 5) and therefore does not present strong support for the theory that the amount of metabolic reserves accumulated during the first summer after settlement determines winter survival.

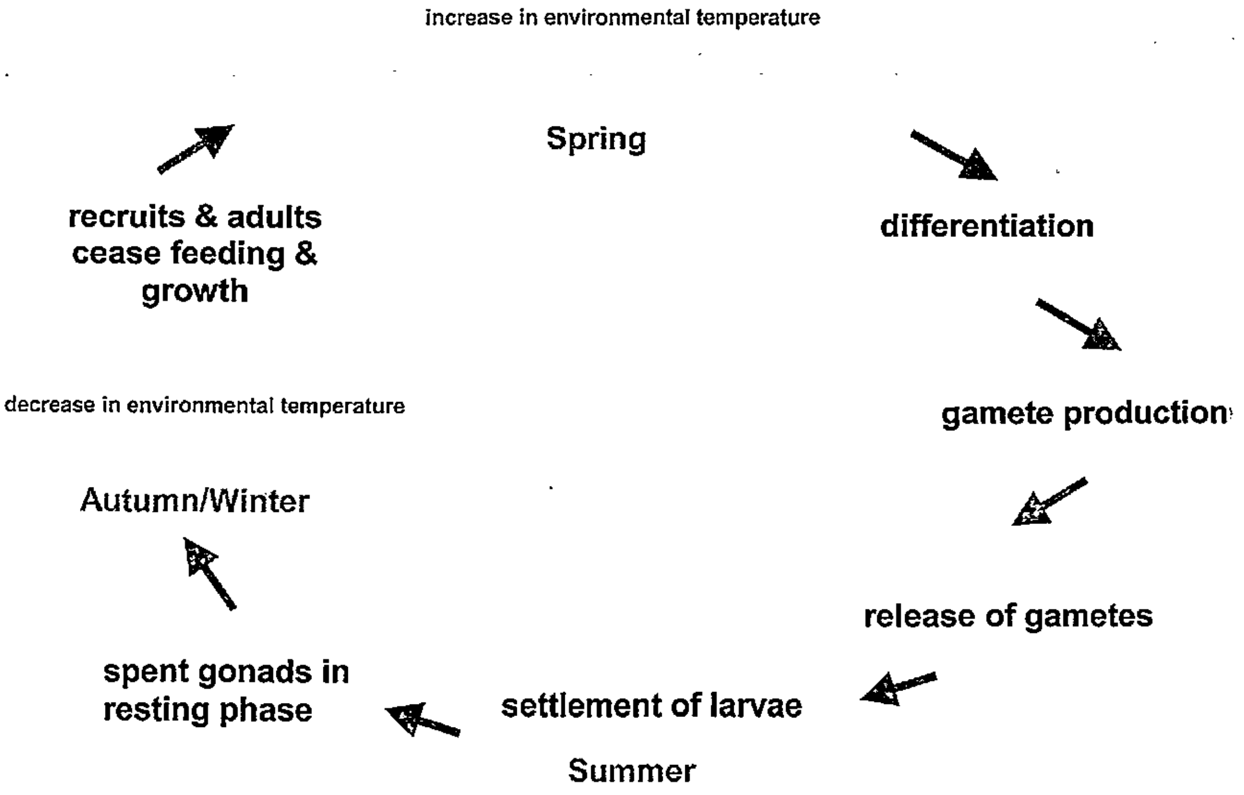


Figure 6.3. Conceptual model of the key stages of the lifecycle of *Osilinus lineatus* and their timing in relation to seasonal changes in the environmental temperature regime.

Populations with multiple age classes now exist beyond previous limits, and established populations close to the range edges have shown concordant increases in abundance as the result of synchronous increases in recruitment success across all survey populations during the study years. The results of the regional meta-analysis of field data and laboratory manipulations of temperature suggest that the greatest effects of climate change on these two species is due to seasonal and potentially daily maximum and minimum temperatures, rather than annual means. Population changes at the local scale driven by changes in temperature show trends relating to climate warming at the regional scale, demonstrating the interconnectivity of effects of climate and importance of studying effects at both of these scales.

Phenotypic consequences of global climate change have remained largely unresearched, especially in the marine environment. Terrestrial research has shown that for insects (Parmesan 1996) and birds (Root 1993), extreme weather events appear to drive local population dynamics. The cold winter of 1962/63 did have a severe effect on populations of O. *lineatus* close to northern limits by preventing the survival of adult individuals, but the effect was not as extreme for *G. umbilicalis*, and the dynamics of the northern and eastern range edges of both species have not been controlled by subsequent extreme events. For both O. *lineatus* and *G. umbilicalis* the biological mechanisms driving survival and range dynamics appear to be driving reproductive output and juvenile survival, both of which are influencing recruitment success, acting in response to increases in environmental temperature.

Both species are trochid gastropods with a lusitanean origin and similar current biogeographic distributions. They are both grazing species that occupy similar habitat within the intertidal zone of moderate to exposed rocky shores. Both species have an annual reproductive cycle of similar timing and duration (Garwood & Kendall 1985, Bode et al. 1986, Gaudencio & Guerra 1986, Kendall 1987, Chapter 4), and produce lecithotrophic larvae, which remain in the plankton for up to 4 days before settling on the shore (Desai 1966). Newly settled juveniles of both species occupy the same cryptic habitats under boulders, and co-occur in the midshore area. The results of this thesis are very similar for both species, which are similar in terms of their biogeographic origins, current distributions, habitat preference, reproductive mode, timing and duration of reproductive cycles and recruitment processes. This suggests that the findings are not artefacts of the data, and that climate exerts a similar effect on these two species.

6.5 Implications of the research

Intertidal animals and plants have the potential to be used as indicator species for climate change in the marine environment, due to their fast response to warming temperatures (Southward & Crisp 1956, Crapp 1970, Southward 1991, Chapters 2, 3) and the evidence of a cause-and-effect relationship between the sea temperatures and recruitment success for *O. lineatus* and *G. umbilicalis* demonstrated in this thesis (Chapters 4,5). The larvae and young juveniles of many intertidal animals are pelagic, and the impacts of changing environmental temperatures on these life stages may therefore provide an indication of changes occurring in offshore marine species such as plankton and fish. Although my work has shown that the responses of closely related species is similar, the differences in rate and extent of range shifts in intertidal barnacles, limpets and algae (Mieszkowska et al. unpublished) suggests that individual species responses may not accurately predict changes at the community or ecosystem level. This limits their application in British and European marine monitoring schemes at present, as they are currently focussed on the quantification of changes in biodiversity at the ecosystem level (OSPAR 2003, UNEP 2004, Rogers & Greenaway 2005).

The use of single-species studies such as this thesis have been criticised (Parmesan et al. 2005) for ignoring the effects of species interactions, which are typical of rocky shore systems (Connell 1961, Dayton 1971, Menge 1976). The results presented here, along with other results from the Marine Biodiversity and Climate Change project (MarClim) highlight important differences in response of intertidal plants and animals to climate warming (Hiscock et al. 2004, Poloczanska et al. in submission, Mieszkowska et al. 2005). Ecosystem-level responses are difficult to categorize and quantify in marine systems due to the lack of long-term, multi-species data and the differential rates of range shifts observed between species.

The southern range boundaries of northern cold-water species including the barnacle *Semibalanus balanoides* and limpet *Patella vulgata* are not retreating as quickly as their southern counterparts *Chthamalus stellatus, C. montagui* and *Patella depressa* are increasing in abundance and expanding their northern range limits in Britain (Mieszkowska. al. unpublished data). Research on the southern distributional limits of marine intertidal species also shows large variation in the rate, extent and direction of southern range boundaries of warm water species (Rivadeneira & Fernandez 2005). The rapid spread of invasive species such as the barnacle *Elminius modestus* (Bishop 1947, Beard 1957, Crisp 1958, Crisp & Southward 1959) and macroalga *Sargassum muticum* (Rueness, 1989, Viejo 1997), which have wide tolerances to environmental fluctuations (Norton 1976, Critchley et al. 1990) are displacing native species in many locations in southern Britain. The spread of such species is likely to be compounding the effects of climate change on native species with northern distributions. These changes are likely to lead to short-term increase in biodiversity on British shores, before northern species are completely replaced by their southern equivalents. Unexpected results including the faster rate of range expansion by southern trochid species with short pelagic larval stages in comparison to southern barnacle species with long pelagic stages (Chapter 3) also highlight the need for detailed research into the responses of the different life stages of species to climate. This may be due to the lack of competitors of northern biogeographic origins for *O. lineatus* and *G. umbilicalis*, making colonisation of new shores easier than for barnacle and limpet species. As a result, community and ecosystem-level changes are likely, and will be difficult to predict without further studies focussing on both individual species and interactions between species.

Models of the responses of species and natural systems to global change are at present mostly limited to correlational studies of climate warming and concurrent biogeographic shifts. The development of ecological forecast models based on large-scale, multispecies datasets is essential for realistic ecological impact assessments (Root et al. 2003, Helmuth pers comm.). In order for these models to be an accurate representation of future biotic responses, individual level physiological studies are required to determine the causal mechanisms underpinning the responses to large-scale climate drivers.

The population data collected from this thesis and the rest of the MarClim project has been incorporated into a coastal model for the prediction of future distributions of intertidal species in Britain (Burrows et al. in prep.). The model uses the association between observed current distributions, SST and a wave fetch index to build future distributions of species based on United Kingdom Climate Impacts Partnership future regional climate change scenarios for Britain as predicted by the HadCM3 global circulation model. This species response model is based on the climate envelope approach criticised by some researchers (see Chapter 3 for review) but incorporates local source and sink data for populations and the location and dynamics of range boundaries, thus addressing some of the problems raised with existing 'envelope' models.

The new generation of biotic response models will increase our ability to manage and conserve coastal marine biodiversity, via the accurate prediction of the rate and direction of change within ecosystems. Prior knowledge of the likely responses of biological systems can assist policy makers in the mitigation of potential impacts, and inform the design of future protected areas to help ameliorate the effects of warming on native species. There is also an urgent need to incorporate climate change into monitoring strategies, despite some misgivings (Rogers & Greenaway 2005). The ability to measure biological change from a fluctuating baseline that incorporates climate-driven change will allow the extent of perturbations to a system from additional anthropogenic factors such as acute pollution events to be identified (Hardman-Mountford et al. 2005).

6.6 Future research requirements

The lack of time-series data for many natural systems, especially with temporal coverage before to the start of accelerated climate warming in the mid-1980s necessitates the development of alternative methods for determining biological responses to global

environmental change. A combination of field and laboratory investigations into the physiological mechanisms causing changes in the geographic distribution of species with commercial value, community keystone species and those already under threat of extinction must be a research priority. The bias in climate research to date towards the responses of warm water species also needs to be addressed. Greater emphasis must be placed on the identification of the responses of cold-water species, which are likely to suffer constrictions in their biogeographic distributions and potential extinctions. My thesis has shown the importance of individual species studies, but these must be combined with research into the effects of environmental warming on species interactions in order to determine how communities and ecosystems will respond in the future.

6.7 Concluding remarks

Climate change is implicated as the primary factor driving the expansion of northern range limits in the southern trochid gastropod species *Osilinus lineatus* and *Gibbula umbilicalis* since the mid 1980s. Range limits are determined by a complex interplay between physical, physiological and ecological processes interacting with the organism at the individual physiological and population level. Responses can be similar within closely related species, but vary in rate, direction and extent across taxa, highlighting the need for research into individual species responses and the subsequent effects at the community and ecosystem levels.

Combined investigations of the ecological patterns and biological mechanisms of species currently responding to global warming show clear links between climate and the geographic distribution of marine species, and bring us a step closer towards the main goal of establishing a cause and effect. In addition, such studies provide information that is fundamental to the development of accurate predictive models, which will be essential in the assessment of future responses of natural systems.

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